

Phylogenetic relationships of the South American Doradoidea (Ostariophysi: Siluriformes)

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A phylogenetic analysis based on 311 morphological characters is presented for most species of the Doradidae, all genera of the Auchenipteridae, and representatives of 16 other catfish families. The hypothesis that was derived from the six most parsimonious trees support the monophyly of the South American Doradoidea (Doradidae plus Auchenipteridae), as well as the monophyly of the clade Doradoidea plus the African Mochokidae. In addition, the clade with Sisoroidea plus Aspredinidae was considered sister to Doradoidea plus Mochokidae. Within the Auchenipteridae, the results support the monophyly of the Centromochlinae and Auchenipterinae. The latter is composed of *Tocantinsia*, and four monophyletic units, two small with *Asterophysus* and *Liosomadoras*, and *Pseudotatia* and *Pseudauchenipterus*, respectively, and two large ones with the remaining genera. Within the Doradidae, parsimony analysis recovered *Wertheimeria* as sister to *Kalyptodoras*, composing a clade sister to all remaining doradids, which include *Franciscodoras* and two monophyletic groups: Astrodoradinae (plus *Acanthodoras* and *Agamyxis*) and Doradinae (new arrangement). Wertheimerinae, new subfamily, is described for *Kalyptodoras* and *Wertheimeria*. Doradinae is corroborated as monophyletic and composed of four groups, one including *Centrochir* and *Platyodoras*, the other with the large-size species of doradids (except *Oxyodoras*), another with *Orinocodoras*, *Rhinodoras*, and *Rhynchodoras*, and another with *Oxyodoras* plus all the fimbriate-barbel doradids. Based on the results, the species of *Opsodoras* are included in *Hemidoras*; and *Tenellus*, new genus, is described to include *Nemadoras trimaculatus*, *N. leporhinus* and *Nemadoras ternetzi*. Due to conflicting hypotheses of the phylogenetic position of *Acanthodoras*, *Agamyxis*, and *Franciscodoras*, these are considered as *incertae sedis* in Doradidae. All suprageneric taxa of the Doradoidea are diagnosed based on synapomorphic morphological characteristics.

Uma análise filogenética com base em 311 caracteres morfológicos é apresentada para a maioria das espécies de Doradidae, todos os gêneros de Auchenipteridae e representantes de outras 16 famílias de Siluriformes. A hipótese de consenso entre as seis árvores mais parcimoniosas corrobora o monofiletismo do grupo Sul-americano Doradoidea (Doradidae mais Auchenipteridae), bem como o de Doradoidea mais a família Africana Mochokidae. O clado de Sisoroidea mais Aspredinidae é considerado como grupo-irmão de Doradoidea mais Mochokidae. Dentre os Auchenipteridae, os resultados corroboraram o monofiletismo de Centromochlinae e Auchenipterinae. Esta última inclui *Tocantinsia* e outros quatro grupos monofiléticos, um com *Asterophysus* e *Liosomadoras*, um com *Pseudotatia* e *Pseudauchenipterus*, e outros dois maiores com os demais gêneros da subfamília. Dentre os Doradidae, a análise de parcimônia recuperou *Wertheimeria* como grupo-irmão de *Kalyptodoras*, formando um clado irmão de todos os demais doradídeos, que incluem *Franciscodoras* e dois grupos: Astrodoradinae (mais *Acanthodoras* e *Agamyxis*) e Doradinae (arranjo novo). Wertheimerinae, subfamília nova, é descrita para os gêneros *Kalyptodoras* e *Wertheimeria*. Doradinae é corroborada como monofilética e composta por quatro grupos de espécies, o primeiro com *Centrochir* e *Platyodoras*, o segundo com os doradídeos de grande porte (exceto *Oxyodoras*), o terceiro com *Orinocodoras*, *Rhinodoras* e *Rhynchodoras*, e o quarto com *Oxyodoras* e os doradídeos de barbilhões fimbriados. Com base nos resultados, *Opsodoras* é considerado como sinônimo júnior de *Hemidoras*; e *Tenellus*, gênero novo, é descrito para *Nemadoras trimaculatus*, *N. leporhinus* e *Nemadoras ternetzi*. Devido à existência de hipóteses conflitantes para a posição filogenética de *Acanthodoras*, *Agamyxis* e *Franciscodoras*, estes são considerados como *incertae sedis* em Doradidae. Todos os grupos supra-gênericos de Doradoidea são diagnosticados com base em caracteres morfológicos sinapomórficos.

Key words: Systematics, Taxonomy, Neotropical, Catfishes.

Introduction

Siluriformes comprises the most morphologically diverse, and geographically widespread order of Ostariophysii, with approximately 36 families, 477 genera, and 3088 valid species (Ferraris, 2007). Although most species are restricted to freshwaters, some are tolerant of brackish waters, and one family occurs almost exclusively in marine environments (Nelson, 2006).

Within the Siluriformes, the superfamily Doradoidea comprises two Neotropical families: Doradidae and Auchenipteridae. The species of Doradoidea range in length from a few centimeters (e.g., *Physopyxis*, *Gelanoglanis*) to a little more than one meter (e.g., *Oxydoras*). Most species are exclusive to freshwaters and occur in the largest river basins in South America, such as: Amazonas, La Plata, São Francisco, Parnaíba, Mearim, Orinoco, Magdalena, Maracaibo, Essequibo, and coastal rivers of Guyana, French Guiana, and Suriname. They are distinguished from other catfishes by having a wide well-developed cephalic shield that is continuous to the dorsal-fin spine, posterior cleithral process usually large, and an infranuchal ligament (= ligament between posterior nuchal plate and rib of sixth vertebra; Birindelli *et al.*, 2009; Birindelli *et al.*, 2012).

The species of Doradidae are popularly known as thorny or talking catfishes (international community); *cuiú-cuiús*, *bacus*, *botoados*, *armados*, or *rebecas* (Brazil); and *sierra* or *bagre hueso* (Argentina, Bolivia, Colombia, Ecuador, Paraguay, Peru, Uruguay, Venezuela). They are readily distinguished among catfishes by having a single row of midlateral scutes, each usually with a single posteriorly oriented thorn. Vono & Birindelli (2007) described aspects of the natural history of the monotypic *Wertheimeria*, and summarized published information on the ecology of other thorny catfishes. Quagio-Grassiotto *et al.* (2011) provided detailed descriptions and figures of sperm morphology in ten species of doradids.

The species of Auchenipteridae are popularly known as driftwood, zamora or slope-head catfishes (international community); *carataí*, *fidalgo*, *mandubé*, *palmito*, *judeu*, *ximbé*, *cangati*, or *cachorro-de-padre* (Brazil); and *manduví*, *zamora*, *docella*, or *novia* (Argentina, Bolivia, Colombia, Ecuador, Paraguay, Peru, Uruguay, Venezuela). They are readily distinguished among catfishes by exhibiting great sexual dimorphism, in which mature males have the anal fin modified for insemination. The ecology and biology of most auchenipterids are not well documented. Large-sized species of the genus *Ageneiosus* most likely undertake great reproductive migrations (Goulding, 1979, 1980). A few species of *Pseudauchenipterus* are relatively tolerant of saltwater, and have been collected on beaches near estuaries (Akama, 2004). Several species feed mainly on allochthonous items (e.g., Carvalho & Resende, 1984), especially on insects that fall into the water at night.

During the nineteenth and twentieth centuries, many genera and species of Auchenipteridae and Doradidae were

discovered and the classification of the species of both families changed many times. Nevertheless, during the last three decades, our understanding about the taxonomy and phylogenetic relationships of the species of Doradoidea has greatly improved. A review of the literature concerning the systematics of Doradoidea, and of each of its families, is presented below.

The goals of the present study are to provide evidence for the phylogenetic position of the Doradoidea within Siluriformes, to propose a hypothesis of phylogenetic relationships among genera of the Auchenipteridae and Doradidae, and to propose a new classification for Doradoidea.

Systematic history of the Doradoidea. In the tenth edition of the *Systema Naturae*, Linnaeus (1758: 304, 307) described two genera to accommodate 15 species of catfish: *Silurus*, with *S. asotus*, *S. glanis*, *S. aspredo*, *S. mystus*, *S. anguillaris*, *S. batrachus*, *S. undecimalis*, *S. militaris*, *S. catus*, *S. clarias*, *S. ascita*, *S. costatus* (= *Platydoras costatus*), *S. callichthys*, *S. cataphractus* (= *Acanthodoras cataphractus*), and the monotypic *Loricaria*, with *L. cataphracta*. In the same volume, Linnaeus (1758: 238) described another catfish, *Acipenser plecostomus* (= *Hypostomus plecostomus*, Loricariidae), among species of sturgeons (Acipenseridae). Eight years later, in the 12th edition of the *Systema Naturae*, Linnaeus (1766: 508) described *Silurus inermis* (= *Ageneiosus inermis*), *S. felis*, *S. galeatus* (= *Trachelyopterus galeatus*), *S. cous*, *S. carinatus* (= *Doras carinatus*), *S. fasciatus*, *S. bagre*, and reallocated *A. plecostomus* to *Loricaria*. Although modern zoological nomenclature dates back to Linnaeus, his classification was based on Peter Artedi's (1738) *Ichthyologiae* (Jordan, 1917). From Linnaeus to the end of the 18th century, only a few studies described species and genera of Siluriformes. The most meaningful additions to Doradoidea were: *Cataphractus* Edwards (for former *Silurus callichthys*, *S. cataphractus*, and *S. costatus*), and *Silurus nodosus* Bloch (= *Pseudauchenipterus nodosus*).

In the 19th century, Bloch & Schneider (1801) proposed a classification that grouped all species of fishes that were then known into five classes. In one of the three orders of Octopterygii, they placed the species of *Cataphractus* and *Loricaria* among non-catfishes; and in one of the three orders of Heptapterygii, they placed *Silurus* and *Platystacus*. Lacepède (1803) described several genera of catfishes, including *Doras* and *Ageneiosus*. Lacepède (1803) assigned *Silurus nodosus* and *S. galeatus* in *Pimelodus*, *S. costatus*, and *S. carinatus* in *Doras*; *Ageneiosus armatus* (junior synonym of *S. inermis*) and *S. inermis* in *Ageneiosus*; and *S. callichthys*, *Cataphractus americanus* (junior synonym of *S. cataphractus*) and *C. punctatus* in *Cataphractus*.

Rafinesque (1815) was the first to allocate all species of catfish to an exclusive group, named by him as Ophlophoria (details in de Pinna, 1998). At almost the same time, Cuvier (1816, see also Cuvier, 1829, 1836-1849), placed all known catfishes in the "Siluroides", and diagnosed it based on detailed characters, most still used nowadays (de Pinna,

1998). Cuvier (1816) considered *Ageneiosus* (including *A. inermis* and *A. militaris*), *Doras* (including *D. americanus*, *D. carinatus*, *D. cataphractus*, and *D. costatus*), as part of his “Siluroïdes”. Other auchenipterids were allocated to *Pimelodus* and *Silurus*. Contrary to Edwards (in Casteby, 1771) and Bloch (1794), who allocated both doradids and callichthyids to *Cataphractus*, Cuvier (1816) recognized for the first time an exclusive group for doradids (*Doras*) and another for callichthyids (*Callichthys*).

Spix & Agassiz (1829) studied the fishes collected by Spix in Brazil, and recognized within “Malacopterygii Abdominales”, the families Gonyodontes for loricariids and Siluroidei for the remaining catfishes including *Cetopsis*, *Doras*, *Hypophthalmus* (including *H. edentatus* and *H. nuchalis* [= *Auchenipterus nuchalis*]), *Pimelodus*, *Phractocephalus*, *Platystoma*, and *Heterobranchus*.

Cuvier & Valenciennes (1840) created a few more genera of catfishes, such as *Arius* for sea catfishes (which included the auchenipterid *Silurus nodosus*), *Auchenipterus* (which included *A. nuchalis*, *A. dentatus*, *A. furcatus*, *A. trachycorystes*, *A. maculosus*, *A. immaculatus*, and *A. punctatus* [all except the first described therein]), and *Trachelyopterus* (including *T. coriaceus*, also described as new). Cuvier & Valenciennes (1840: 231) considered *Ageneiosus* (with *A. militaris*, *A. inermis*, and *A. brevifilis*) as related to *Hypophthalmus*; they noted the resemblance of the cephalic shield in *Synodontis*, *Auchenipterus* and *Doras* (Cuvier & Valenciennes, 1840: 244); and they described several doradid species (*D. armatulus*, *D. hancockii*, *D. dorsalis* and *D. niger*), distinguishing *D. carinatus* and *D. niger* from the remaining species by having edentulous maxillae and compressed head (Cuvier & Valenciennes, 1840: 288). Müller & Troschel (in Müller, 1842a: 203) created *Euanemus* for *E. colymbetes* (= *Auchenipterus dentatus*), and reallocated *S. nodosus* to *Auchenipterus*.

Kner (1854), based on Heckel’s manuscript about sexual dimorphism of *Callichthys* and gas bladders of *Doras*, illustrated the gas bladder in *Doras polygramma* (species inquirendae in *Acanthodoras*, Sabaj & Ferraris, 2003), *D. loricatus* (= *Ossancora fimbriata*), *D. ophthalmus* (= *Anduzedoras oxyrhynchus*), *D. asterifrons*, *D. punctatus*, *D. brevis*, *D. armatulus*, *D. Hancoki* (sic), and *D. dorsalis*, the first six proposed therein as new species. Two years later, Kner (1855) provided detailed descriptions of the species he had proposed earlier, in addition to other new catfish species and genera, including *Oxydoras*, *D. fimbriatus* (replacement name for *D. loricatus*), *D. affinis*, *D. stenopeltis*, *D. humeralis*, *D. murica*, *D. dorbignyi*, and *D. heckelii*. In 1858, Kner described *Asterophysus batrachus*, *Centromochlus megalops*, *C. aulopygia*, *Auchenipterus thoracatus*, and *A. ceratophysus*.

Contemporary to Kner was Bleeker, who despite having described few Neotropical species (relative to Indo-Pacific ones), created several new genera and suprageneric taxa of catfishes. His suite of papers (1858, 1862-1863, 1863a, 1863b, 1864) was summarized in the *Systema Silurorum Revisum* (Bleeker, 1863b). In his classification, the order “Siluri” was

composed of seven subfamilies, including Trachelyopteriformes, with Trachelyopterini (composed of *Trachelyopterus*, *Trachelyopterichthys*), and Bagriformes, with Doradini (composed of *Doras*, *Rhinodoras*, *Centrochir*, *Oxydoras*, *Lithodoras*, *Pterodoras*, *Platydoras*, *Acanthodoras*, and *Amblydoras*), Pseudauchenipterini (composed of three phalanxes: Pseudauchenipteri, Centromochli, and Asterophysis), and Pangasini (composed of phalanx Pangasii, Ageneiosini [with *Ageneiosus* and *Tetranematchthys*], Auchenipterini [with *Auchenipterus*], Hypophthalmiini, Heptapterini, and Argeini. Bleeker’s classification is especially interesting within the framework of relationships of the Doradoidea for the: 1) placement of Doradini, Synodontini and Pseudauchenipterini close to each other; 2) placement of Ageneiosini and Auchenipterini close to each other and to Hypophthalmiini, Pangasini and Heptapterini. 3) treatment of auchenipterids as “polyphyletic”; and 4) consideration of doradids as “monophyletic”.

Another groundbreaking contribution to catfish classification was Günther’s (1864) Catalogue of Fishes of the British Museum. Günther (1864) recognized as part of the “Siluridae Stenobranchiae”: Doradina composed of *Ageneiosus*, *Tetranematchthys*, *Euanemus*, *Auchenipterus*, *Centromochlus*, *Trachelyopterus*, *Cetopsis*, *Asterophysus*, *Doras*, *Oxydoras*, *Rhinodoras*, and *Synodontis*; and, as such, he was the first to recognize doradids, auchenipterids and mochokids in the same group (albeit together with cetopsids).

In the last decades of the nineteenth century, several authors contributed papers more focused on species descriptions. An interesting example is *Wertheimeria maculata*, a doradid described by Steindachner (1877) and originally proposed as an auchenipterid.

Eigenmann’s early studies with his wife Rosa Smith redefined the classification of Neotropical catfishes (Eigenmann & Eigenmann, 1888, 1889, 1890, 1891); they considered doradids and auchenipterids as part of the family Siluridae composed of: Doradinae (*Physopyxis*, *Doras*, *Oxydoras*, and *Hemidoras*), Auchenipterinae (*Asterophysus*, *Trachelyopterichthys*, *Wertheimeria*, *Centromochlus*, *Trachycorystes*, *Auchenipterichthys*, *Felichthys*, *Epapterus*, *Auchenipterus*, and *Tetranematchthys*), and Ageneiosinae (*Ageneiosus*).

Bridge & Haddon (1892) and Sørensen (1894-1895) were the first to offer well-supported morphological evidence of close relationships between doradids, auchenipterids, and mochokids: the presence of the elastic spring apparatus. Noteworthy, the elastic spring apparatus was first described by Müller (1842a, 1842b, 1843) for *Auchenipterus*, *Doras*, *Synodontis*, and *Malapterurus*, and subsequently for *Pangasius* by Bridge & Haddon (1892).

Regan (1911: 556) described his views on the evolution of catfish families, and noted that Doradidae (including auchenipterids) and Ariidae may have evolved early, right after Diplomystidae, by being “generalized in form and in fin structure, but aberrant in the loss of the mesocoracoid”. On the other hand, Regan (1911) also noted morphological resemblances between Doradidae (including auchenipterids)

and mochokids, which he considered convergences, such as the restricted gill-openings, the expanded nuchal shield, and the elastic spring apparatus.

Miranda Ribeiro (1911) described *Tatia* and *Mormyrostoma* (= *Doras*, Sabaj Pérez & Birindelli, 2008), reallocated *Wertheimeria* to Doradidae, which at that time included only doradids, and classified the auchenipterids into Trachycorystidae (*Pseudauchenipterus*, *Glanidium*, *Centromochlus*, *Tatia*, *Asterophysus*, *Trachycorystes*, *Auchenipterichthys*, *Trachelyopterus*, and *Trachelyopterichthys*), Auchenipteridae (*Epapterus*, *Auchenipterus*), and Ageneiosidae (*Tetranematchthys*, *Ageneiosus*, and *Pseudogeneiosus*). Other researchers did not adopt Miranda Ribeiro's classification, and continued to follow the one previously established by Eigenmann & Eigenmann (1891) (e.g., Eigenmann, 1925; Jordan, 1929; Berg, 1940; Gosline, 1945; Van der Stigchel, 1947; Fowler, 1951).

Chardon (1968) studied the Weberian apparatus and associated structures in catfishes, classifying the Doradidae, Auchenipteridae, Ageneiosidae, and Mochokidae in the superfamily Doradoidea within the suborder Bagroidei. He diagnosed Doradoidea (*sensu* Chardon, 1968) by having: 1) the general character of Bagroidei modified by the presence of the elastic spring apparatus, 2) strong cephalic shield, except in *Ageneiosus*, 3) nuchal shield sutured to parietal-supraoccipital through an *écaille supplémentaire* (=anterior nuchal plate), except in *Ageneiosus*, 4) posttemporal-supracleithrum sutured to cranium, 5) ligament or ossified process between epiotic and posterior ramus of the parapophysis of the fourth vertebra, and 6) deep groove in cleithrum in its articulation to the cranium. Those characters were re-examined by Britski (1972), who considered characters 2 and 6 to vary among doradids and auchenipterids, character 3 to be absent in several doradids and auchenipterids, and character 5 incorrect because doradids and auchenipterids lack the posterior ramus of the parapophysis of the fourth vertebra. Britski (1972) concluded that there was no support for a close relationship between the African Mochokidae and the three Neotropical families, Ageneiosidae, Auchenipteridae, and Doradidae.

In the 1980's, with the development of the cladistic method, and the beginning of a new paradigm in Systematics, several studies focused on catfish relationships were performed. Royero (1987) studied the anatomy of the dorsal fin in catfishes, and considered Ariidae related to Ageneiosidae, Auchenipteridae, Doradidae and Mochokidae. One year later, Ferraris (1988) performed a phylogenetic analysis including most auchenipterid and a few doradid genera. His results supported a new classification for auchenipterids in which *Ageneiosus* and *Tetranematchthys* were nested within the Auchenipteridae. Ferraris (1988) divided auchenipterids into two families: Centromochlidae (with *Centromochlus*, *Gelanoglanis*, *Glanidium*, and *Tatia*), and Auchenipteridae (including *Ageneiosus* and *Tetranematchthys*).

Mo (1991), in a study focused on the Bagridae, proposed a hypothesis for the phylogenetic relationships of most catfish

families. His analysis incorporated additional characters and corroborated Royero's (1987) previous hypothesis of a close relationship among Ariidae, Auchenipteridae, Doradidae, and Mochokidae. The first comprehensive cladistic analysis including all known families of catfishes was performed by de Pinna (1993), who considered Mochokidae related to Auchenipteridae plus Doradidae, and these three not closely related to Ariidae. In that same year, Lundberg (1993) illustrated the undescribed fossil catfish "*Titanoglanis*" and discussed its relationships with Ariidae, Auchenipteridae, Doradidae, and Mochokidae.

Friel (1994) studied the Neotropical family Aspredinidae, and proposed its close relationship to Auchenipteridae, Doradidae, and Mochokidae based on a cladistic analysis of morphological data. Subsequently, de Pinna (1996) considered Aspredinidae related to Asian-endemic Amblycipitidae, Akysidae, Sisoridae, and Erethistidae, based on a comprehensive cladistic analysis of those families. De Pinna (1998) summarized what was then known on catfish relationships, establishing the suborder Doradoidei for Doradoidea plus Mochokidae (considered related to Ariidae). The Doradoidea of de Pinna (1998) includes the Doradidae plus Auchenipteridae (including Centromochlidae).

Royero (1999), focusing on auchenipterids but including in his analyses other catfishes, corroborated his previous phylogenetic hypothesis: Ariidae (Mochokidae (Doradidae, Auchenipteridae)). Britto (2002), re-evaluating all aforementioned phylogenetic hypotheses and morphological evidences for those relationships, concluded that Ariidae were not closely related to the Doradoidea plus Mochokidae. Diogo (2004), in a cladistic analysis including all catfish families, proposed the Doradoidea plus Mochokidae as sister group of Malapteruridae.

More recently, with the development of DNA sequence data as a source of characters for phylogenetic analysis, Sullivan *et al.* (2006, 2008) recovered a strong molecular support for Aspredinidae as sister to Doradidae plus Auchenipteridae, with Mochokidae more closely related to other African catfishes, and Ariidae (plus Anchariidae) in an unresolved polytomy with several other catfish families.

In conclusion, both morphological and molecular data strongly support Doradidae and Auchenipteridae as sister-group families in the superfamily Doradoidea. However, the relationships between Doradoidea and other families of catfishes are still unresolved. Historically, Doradoidea has been considered most closely related to: 1) Mochokidae and Malapteruridae (based on the presence of the elastic spring apparatus), 2) Mochokidae and Ariidae (based on features of the nuchal shield), 3) Mochokidae and Aspredinidae (based on features of the pectoral girdle), and 4) Aspredinidae (based on molecular data).

Systematic history of the Doradidae. Doradid taxonomy begins with Linnaeus (1758, 1766), who described *Silurus costatus*, *S. cataphractus*, and *S. carinatus*. The first doradid genus described was *Cataphractus* Edwards in Casteby, 1771

(type species *S. cataphractus* by tautonomy). However, it is considered a *nomen oblitum*, and as such, a junior synonym of *Acanthodoras* (Sabaj & Ferraris, 2003; Ferraris, 2007; Eschmeyer, 2014).

Lacepède (1803) created the genus *Doras*, in which most doradid species were described until the second half of the nineteenth century, when Kner (1854, 1855) described *Oxydoras*, as a subgenus, to allocate species with a compressed head. Following that classification of species (*i.e.*, *caput elevatum* vs. *caput depressum*), Bleeker (1858, 1862-1863, 1863a, 1863b, 1864) described several additional genera.

In one of his last papers, Eigenmann (1925) presented an exhaustive taxonomic revision of the Doradidae, diagnosing the family and its taxa based on detailed morphological characters. He allocated all known valid species (68 total) into 26 genera. Following previous authors, Eigenmann (1925) considered the family to be divided into species with a depressed head, wide pectoral girdle, premaxilla with several rows of teeth and simple barbels, vs. species with a compressed head and pectoral girdle, snout sometimes elongate, premaxilla reduced in size, few or no teeth, and barbels usually branched. More than 40 years later, Fernández-Yépez (1968) published a partial revision focused on Venezuelan doradids. Regionally limited, Fernández-Yépez's (1950, 1968) studies included various taxonomic mistakes and most of the taxa he described were subsequently found to be junior synonyms.

Higuchi (1992) performed the first phylogenetic analysis of doradids using the cladistic method (Fig. 1a). His results, which were based on morphology, considered doradids to be composed of *Wertheimeria*, *Franciscodoras* and three subfamilies of unresolved relationships. Subsequently, Higuchi *et al.* (2007) described Astrodoradinae for *Astrodoras*, *Amblyodoras*, *Anadoras*, *Hypodoras*, *Merodoras*, *Physopyxis*, and *Scorpiodoras*. Moyer *et al.* (2004) studied the phylogenetic relationships of doradids based on molecular data (Fig. 1b). Their results were only partially congruent with Higuchi's and were possibly misled by a lack of some relevant basal taxa in the Doradidae (*i.e.*, *Wertheimeria*, *Kalyptodoras*, and *Franciscodoras*).

More recently, Birindelli *et al.* (2009) studied the morphology of the gas bladder in 92 species of Doradidae, finding modifications associated with the presence of diverticula, additional bladders, inner septa, among other features. Sousa (2010) completed the taxonomic revision and phylogenetic analysis of 21 species included in the subfamily Astrodoradinae. Quagio-Grassiotto *et al.* (2011) studied the morphology of the sperm in 10 species of the Doradidae, finding distinct type of spermatogenesis, spermiogenesis and spermatozoa correlated with intrafamilial groups of Doradidae. Arce *et al.* (2013) performed a comprehensive phylogenetic analysis based on molecular data for 86 species of Doradidae, using both nuclear and mitochondrial gene sequences.

Sabaj (2002) and Sabaj & Ferraris (2003) compiled monographic data for all nominal doradids and resolved a number of taxonomic issues; their classification recognized 72 valid species in 30 genera. Since then, the taxonomic

knowledge of the family has greatly increased. Sousa & Rapp Py-Daniel (2005) revised *Physopyxis*, describing two new species. Sabaj (2005) revised *Leptodoras*, describing three species as new. Two years later, Birindelli *et al.* (2007) described *Rhynchodoras castilloi* from Venezuela; Higuchi *et al.* (2007) described a new genus and species, *Merodoras nheco*; and Sabaj Pérez *et al.* (2007) described †*Doras dionae*, the only named fossil species. In 2008, Sabaj *et al.* (2008) described two new species of *Rhinodoras*; Sabaj Pérez & Birindelli (2008) revised *Doras*, describing three species as new; Birindelli *et al.* (2008) described *Leptodoras oyakawai*; and Piorski *et al.* (2008) described *Platydoras brachylecis* and revalidated *P. hancockii*. Two years later, Birindelli & Sousa (2010) described *Leptodoras marki*. In 2011, Sousa & Birindelli (2011) described *Scorpiodoras liophysus*, and revalidated *S. calderonensis*; Birindelli & Sabaj-Pérez (2011) described the new genus *Ossancora* with *O. asterophysa* as a new species; and Birindelli *et al.* (2011) described *Hassar gabiru* as new species from the middle and upper rio Xingu. Last year, Sabaj-Pérez & Birindelli (2013) described *Hassar shewellkeimi* from the upper rio Tapajós. In less than eight years, those recently published papers have increased by approximately 30% the total number of species of the Doradidae, which currently comprises 93 valid species (92 extant plus one fossil), arranged in 31 genera.

Systematic history of the Auchenipteridae. The systematics of Auchenipteridae begins with Linnaeus (1766) through the description of *Silurus inermis* and *S. galeatus*. Soon thereafter, Bloch (1794) described *Silurus nodosus*. Lacepède (1803) described *Ageneiosus* for *Silurus inermis*, and allocated

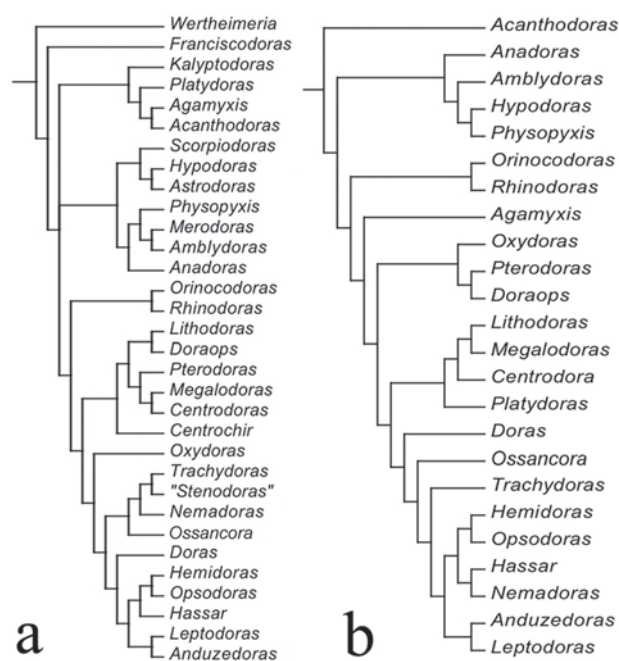


Fig. 1. Phylogenetic relationships of Doradidae, according to the hypotheses of (a) Higuchi (1992), and (b) Moyer *et al.* (2004).

Silurus galeatus and *S. nodosus* to *Pimelodus*. Spix & Agassiz (1829) described *Hypophthalmus nuchalis* (= *Auchenipterus nuchalis*). Few years later, Valenciennes in Cuvier & Valenciennes (1840) described *Auchenipterus* for *A. nuchalis*, and *Trachelyopterus* for *T. coriaceus*, while also naming six new species.

In late nineteenth and early twentieth centuries, several authors described species and/or genera that are currently classified in Auchenipteridae (e.g., Jardine, 1841; Castelnau, 1855; Kner, 1858; Bleeker, 1858, 1864; Lütken, 1874; Cope, 1878; Steindachner, 1880, 1910, 1915; Eigenmann & Eigenmann, 1888; Miranda Ribeiro, 1918). At that time, those species and genera were allocated to different groups within Siluriformes, including the Neotropical pimelodids *Hypophthalmus* and *Pimelodus*, and the Asian family Pangasiidae. Günther (1864) was the first to assemble all species of auchenipterids, and grouped them with doradids, cetopsids and mochokids. Eigenmann & Eigenmann (1888) were the first to classify auchenipterids known at that time in two exclusive families: Auchenipteridae and Ageneiosidae.

Ihering (1937) diagnosed the Auchenipteridae by the presence of a pseudopenis, distinguishing it from Ageneiosidae and Doradidae, and considered it to be composed of Auchenipterinae and Trachycorystinae. The classification of Ihering, however, was not followed by subsequent researchers (e.g., Gosline, 1945; Fowler, 1951; Chardon, 1968).

Miranda Ribeiro (1968a, 1968b, 1968c) classified auchenipterids into five families based on characters related to sexual dimorphism: Ageneiosidae (*Ageneiosus*,

Tympanopleura), Auchenipteridae (*Auchenipterus*, *Epapterus*, and *Pseudepapterus*), Trachycorystidae (*Auchenipterichthys*, *Tetranematichthys*, and *Trachycorystes*), Centromochlidae (*Centromochlus*, *Glanidium*, *Entomocorus*, *Pseudauchenipterus*, and *Tatia*), and Asterophysidae (*Asterophysus*).

Britski (1972) revised the genera of Auchenipteridae, proposed an evolutionary scheme for them (Fig. 2a), and concluded that the Ageneiosidae and Auchenipteridae are sister-families related to the Doradidae. Britski (1972) diagnosed Auchenipteridae plus Ageneiosidae by the presence of sexually dimorphic features, such as the modified anal fin in mature males. Apparently unaware of Britski's study, Mees (1974) also revised the Auchenipteridae, based mainly on specimens collected in Suriname, and also rejected the classification of Miranda Ribeiro.

Ferraris (1988) performed a comprehensive cladistic analysis of the Auchenipteridae, in which he concluded that *Ageneiosus* and *Tetranematichthys* were deeply nested within the Auchenipteridae, and that the Centromochlidae (with *Centromochlus*, *Gelanoglanis*, *Glanidium*, and *Tatia*) was a distinct family (Fig. 2b). One year later, Curran (1989) published a hypothesis of relationships for few species of auchenipterids based on limited characters that was largely incongruent with other studies (Fig. 2c).

Walsh (1990) studied the taxonomy and phylogeny of *Ageneiosus* and *Tetranematichthys* (both formerly included in the Ageneiosidae). Soares-Porto (1998) published a paper on the phylogenetic relationships of species of the Centromochlinae. One year later, Royero (1999) performed a

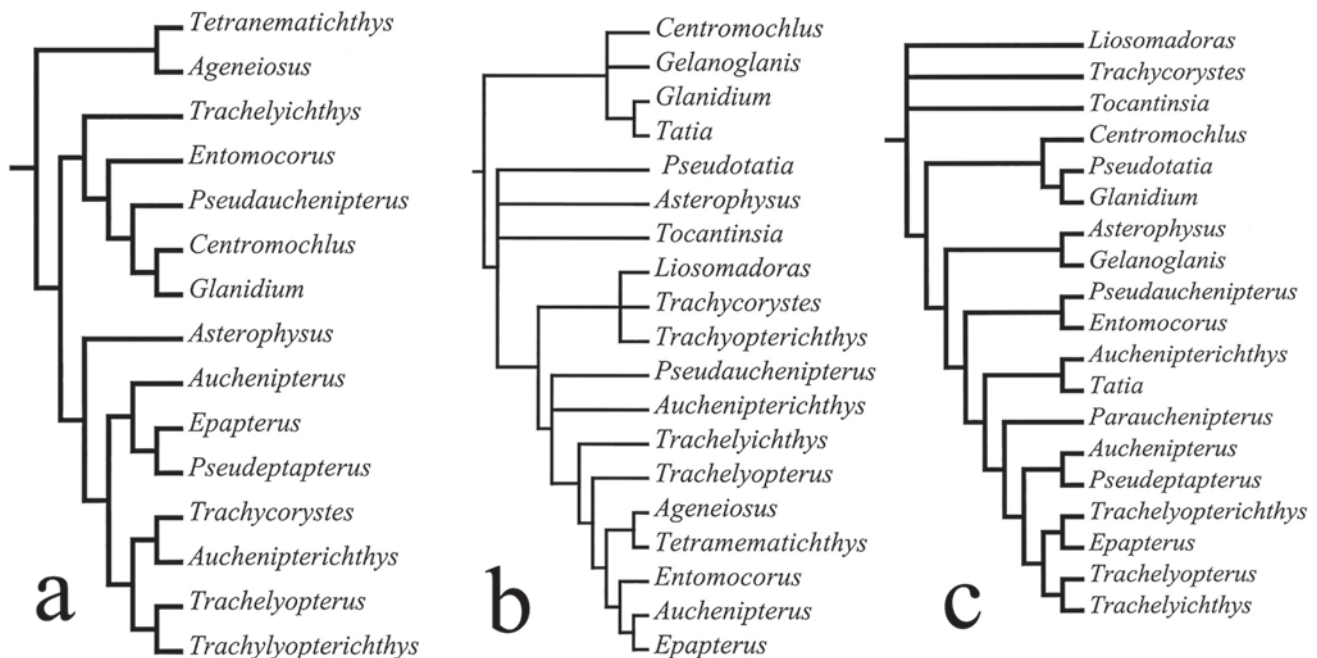


Fig. 2. Phylogenetic relationships of Auchenipteridae, according to the hypotheses of (a) Britski (1972), (b) Ferraris (1988), and (c) Curran (1989).

phylogenetic analysis of most genera of Auchenipteridae. Recently, in order to establish the phylogenetic position of *Trachelyopterus*, Akama (2004) performed another phylogenetic study including most auchenipterid genera. Sarmiento-Soares & Porto (2006) presented a study on the comparative anatomy of the cheek muscles in Centromochlinae. Ribeiro (2011) revised *Ageneiosus* and proposed a phylogenetic hypothesis for its species, including in the analysis most genera of Auchenipteridae. And finally, Birindelli *et al.* (2012) described and discussed the evolution of the morphology of the gas bladder in most species of the Auchenipteridae. There are several incongruences between results obtained in all these studies.

As for doradids, the taxonomy of auchenipterids has greatly improved in recent years. From 1998 to 2000, Vari & Ferraris (1998) revised *Epapterus*, recognizing two valid species; Ferraris & Vari (1999) revised *Auchenipterus*, describing two new species; Soares-Porto *et al.* (1999) described *Gelanoglanis nanonotocolus*; Soares-Porto (2000) described *Centromochlus macracanthus*; and Ferraris & Vari (2000) described *Pseudepapterus gracilis* as a new species from the Caura River in Venezuela. Later on, Akama & Ferraris (2003) described *Entomocorus malaphareus* as a new species from the Amazon; Sarmiento-Soares & Buckup (2005) described *Glanidium bockmanni*; and Ferraris *et al.* (2005) revised *Auchenipterichthys*, currently with three valid species. In 2006, Reis & Borges (2006) revised *Entomocorus*, describing one new species from the Pantanal; and Vari & Ferraris (2006) described *Tetranematichthys wallacei*. Two years later, Sarmiento-Soares & Martins-Pinheiro (2008) revised *Tatia*, describing three new species; and Rengifo *et al.* (2008) described *Gelanoglanis trivieso* from the Marañon River in Peru. In the following year, Pavanelli & Bifi (2009) described *Tatia jaracatia* from rio Iguaçú in Brazil. In 2010, Peixoto & Wosiacki (2010) described *Tetranematichthys barthemii*; and Ribeiro & Rapp Py-Daniel (2010) described *Ageneiosus uranophthalmus*. Britski & Akama (2011) described *Trachycorystes menezesi* from the rio Aripuanã, in Brazil; and Akama & Ferraris (2011) described *Spinipterus acsi* as a new genus and species. Birindelli & Zuanon (2012) revised *Liosomadoras*, redescribing *L. morrowi* and *L. oncinus*. Last year, Sarmiento-Soares & Martins-Pinheiro (2013) described *Glanidium botocudo*; Vari & Ferraris (2013) described two new species of *Tatia*; and Sarmiento-Soares *et al.* (2013) described *Centromochlus meridionalis*. The family Auchenipteridae now comprises 108 valid species arranged in 21 genera.

Material and Methods

Anatomical and taxonomic nomenclature. Nomenclature for muscles follows Winterbottom (1974). Nomenclature for cranial nerves follows Freihofner (1978). Osteological nomenclature according to Weitzman (1962) with the following exceptions (all detailed in the Teleostei Anatomy Ontology website at <http://bioportal.bioontology.org/ontologies/TAO>):

anguloarticular (fusion of angular, articular and retroarticular bones) replaces separate articular and angular; anterior and posterior ceratohyal replaces ceratohyal and epihyal, respectively; autopalatine replaces palatine; basiptyergium replaces pelvic bone; entopterygoid (= tendon-bone entopterygoid) replaces mesopterygoid; mesethmoid replaces ethmoid; vomer replaces prevomer; parietal-supraoccipital replaces separate parietal and supraoccipital; posttemporal-supracleithrum replaces separate posttemporal and supraacleithrum; and pharyngobranchial replaces suspensory pharyngeal. The first bone of the infraorbital series is herein referred to as infraorbital 1 (replaces lacrimal of Birindelli *et al.* 2007). It is formed from a single ossification (Birindelli, 2010), and includes the antorbital and infraorbital branches of the infraorbital canal. Some authors (*e.g.*, Arratia & Huaquín, 1995) have considered this bone homologous with the antorbital of Characiformes, which does not bear a canal (Weitzman, 1962). For the small cartilage articulating with epibranchials 1 and 2 and pharyngobranchial 3 the term pharyngobranchial accessory cartilage is used (Birindelli & Sabaj-Pérez, 2011). This structure is also referred to as accessory cartilaginous nodule (Bockmann & Miquelarena, 2008: 22), and incorrectly as pharyngobranchial 1 and/or 2 (Higuchi, 1992; Birindelli *et al.*, 2008). The term accessory element of ceratobranchial 4 is used for the small cartilage associated to ceratobranchial 4, instead of epibranchial 5 (as in Birindelli *et al.*, 2011), following Carvalho *et al.* (2013). Gas bladder terminology follows Birindelli *et al.* (2009). Abbreviations include “#” for character number, and SL for Standard Length.

Taxonomic nomenclature follows the most recent classification of the Siluriformes as summarized by Ferraris (2007), Eschmeyer (2014) and Lundberg *et al.* (2014), and includes Doradoidea (=Doradidae plus Auchenipteridae), Sisoroidea (=Amblycipitidae plus Akysidae, Erethistidae, and Sisoridae), Loricarioidei (=Loricariidae plus Astroblepidae, Callichthyidae, Nematogenyidae, Scoloplacidae, and Trichomycteridae), and Siluroidei [=Siluriformes except Loricarioidei and Diplomystoidei (=Diplomystidae)]. Doradoidei *sensu* de Pinna (1998) (=Doradidae plus Auchenipteridae and Mochokidae) is not used because the three families of this group are included in a larger suborder of Siluriformes (Siluroidei).

The new names and arrangements used throughout the text include: *Tenellus*, new genus, comprising taxa formerly treated as *Nemadoras trimaculatus* (type-species), *N. leporhinus*, and *N. ternetzi* (*sensu* Sabaj & Ferraris, 2003; Ferraris, 2007; Arce *et al.*, 2013; Eschmeyer, 2014); *Hemidoras* inclusive of *Hemidoras morrissi*, *H. stenopeltis*, *H. morei*, *H. boulengeri* and *H. stubelii*, the last three as new combinations (previously allocated to *Opsodoras* by Sabaj & Ferraris, 2003; Ferraris, 2007; Eschmeyer, 2014); Astrodoradinae inclusive of *Astroadoras*, *Anadoras*, *Amblyadoras*, *Physopyxis*, *Hypodoras*, and *Scorpiodoras* (*sensu* Higuchi *et al.*, 2007 and Arce *et al.*, 2013); Wertheimerinae, new subfamily, inclusive of *Kalyptodoras* and *Wertheimeria*; Doradinae, new

arrangement, inclusive of fimbriate-barbel doradids plus *Centrodoras*, *Centrochir*, *Doraops*, *Lithodoras*, *Megalodoras*, *Orinocodoras*, *Oxydoras*, *Platydoras*, *Pterodoras*, *Rhinodoras*, and *Rhynchodoras*; fimbriate-barbel doradids meaning *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras*. The genera *Acanthodoras*, *Agamyxis*, and *Franciscodoras* were considered as *incertae sedis* in Doradidae, due to the presence of disputing hypotheses of phylogenetic position (Higuchi, 1992; Moyer *et al.*, 2004; Higuchi *et al.*, 2007; Arce *et al.*, 2013).

Material examined and taxa selection. Observations were based on museum specimens preserved in alcohol (for myology and viscera), and prepared as clear and stained specimens (following methods of Taylor & Van Dyke, 1985), or as dry skeletons (following methods of Bemis *et al.*, 2004). Museum abbreviations are: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia; AUM, Auburn University Natural History Museum, Auburn; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; CAS-SU, CAS specimens received from Stanford University; CU, Cornell University Museum of Vertebrates, Ithaca; FMNH, Field Museum of Natural History, Chicago; INHS, Illinois Natural History Survey, Champaign; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCNG, Museo de Ciencias Naturales de UNELLEZ, Guanare; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MHNLS, Museo de Historia Natural La Salle, Fundación La Salle de Ciencias Naturales, Caracas; MNHN, Muséum National d'Histoire Naturelle, Paris; MZUEL, Museu de Zoologia da Universidade Estadual de Londrina; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NUP, Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá, Maringá; ROM, Royal Ontario Museum, Department of Natural History, Toronto; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.; ZMS, Zoologische Staatssammlung München, Munich.

A total of 100 terminal taxa were included in the phylogenetic analysis. Criteria for selecting terminals included: previous studies identifying taxon as occupying a basal position within its family (or genus), unspecialized taxa (*i.e.*, with few modifications), and taxa well represented in museum collections.

Most species of Doradidae were included (57 of 93 valid species). The taxa omitted were: *Rhinodoras armbrusteri* and *R. gallagheri*, both recently described by Sabaj *et al.* (2007) and very similar to *R. boehlkei*; *Rhynchodoras xingui*, rare in collections (Birindelli *et al.*, 2007); *Oxydoras sifontesi*, similar

to *Oxydoras niger*; †*Doras dionae*, a fossil species recently diagnosed by Sabaj-Pérez *et al.* (2007) on the basis of a partial pectoral girdle; *Doras micropoeus* and *D. zuanoni*, two of the five valid extant species of *Doras*, recently revised by Sabaj Pérez & Birindelli (2008); *Hassar shewellkeimi* and *H. wilderi*, two of the five valid species of *Hassar*, also recently revised (Birindelli *et al.*, 2011; Sabaj-Pérez & Birindelli, 2013); eight of the 12 species of *Leptodoras*, also recently revised (Sabaj, 2005; Birindelli *et al.*, 2008; Birindelli & Sousa, 2010); *Acanthodoras depressus* and *A. spinosissimus*, two of three species of the genus, in need of a taxonomic revision; *Agamyxis pectinifrons*, one of two species of *Agamyxis*, recently revised (Sousa, 2010); and all Astrodoradinae, except *Astrodoras asterifrons*, *Scorpiodoras heckelii*, and *Anadoras grypus*, a subfamily under study by Leandro Sousa (UFPA) (see Sousa, 2010 for unpublished results). On the other hand, an intriguing undescribed species of *Platydoras* was included because it possesses characters of both *Platydoras* (color pattern) and *Centrochir* (gas bladder morphology, see Birindelli *et al.*, 2009).

Twenty-three species of Auchenipteridae were included: one species of each genus, except for *Ageneiosus* and *Trachelyopterus*, diverse genera from which two species were included: *Ageneiosus atronasus*, *A. inermis*, *Trachelyopterus coriaceus*, and *T. galeatus*. The monotypic *Spinipterus acsi*, recently described and known from a single maturing male, was included based exclusively on information provided by Akama & Ferraris (2011).

To determine the position of the Doradoidea within Siluriformes, at least one representative species was included for each of the following 16 families of catfishes: Diplomystidae, Nematogenyidae, Ictaluridae, Amphiliidae, Pimelodidae, Pseudopimelodidae, Heptapteridae, Siluridae, Claroteidae, Pangasiidae, Malapteruridae, Erethistidae, Sisoridae, Aspredinidae, Ariidae, and Mochokidae. The choice of these families was based on previous phylogenetic hypotheses based on morphological and molecular characters (de Pinna, 1998; Britto, 2002; Diogo, 2004; Sullivan *et al.*, 2006, 2008). According to these studies, the selected families are possibly closely related to Doradoidea or relatively basal in other family groups of Siluriformes. Additional species of Mochokidae and Ariidae, two families previously considered to be closely related to Doradoidea by many authors (see Introduction), were included in the analyses: *Galeichthys peruvianus* and *Genidens genidens*, one taxon representative of each Galeichthyinae and Ariinae, respectively (*sensu* Marceniuk *et al.*, 2012), and *Chiloglanis disneyi*, *Mochokiella paynei*, *Mochokus niloticus*, and *Synodontis schall*, taxa representative of the major lineages of Mochokidae (*sensu* Vigliotta, 2008).

Phylogenetic analysis. Phylogenetic hypotheses were obtained using the cladistic method, originally proposed by Hennig (1950, 1966). The Diplomystidae was chosen as the rooting point because it is considered the sister-taxon of all remaining Siluriformes based on morphology, or of all non-

loricarioid catfishes (*i.e.*, the Siluroidei) based on molecular evidence. Alternative use of *Nematogenys* (a loricarioid catfish) as tree root yields the same relationships for Doradoidea and close-related families. Multistate characters were treated as ordered whenever they showed morphocline variation, inferred according to the similarities of each state or, when available, to the sequence in ontogenetic series of development. The character matrix was edited using MacClade, version 4.08 (Maddison & Maddison, 2005), and the parsimony analysis performed using TNT (Goloboff *et al.*, 2008). Heuristic search (=Tradicional search) using Tree-Bisection-Reconnection (TBR) was applied, with 10.000 replicates, saving 10 trees per replication. A strict consensus tree was calculated using all fundamental, most parsimonious, trees obtained. Characters were numbered starting from character #0, following the default of TNT and WinClada. Character state changes were optimized in the consensus tree using WinClada (Nixon, 1999-2002). Ambiguous synapomorphies in the consensus tree were optimized under ACCTRAN, whereby reversals are preferred over convergences, thus maximally preserving hypotheses of primary homology (de Pinna, 1991). Bremer support (Bremer, 1994) of each branch was calculated using the TBR algorithm in TNT. Consistency (CI) and Retention (RI) indices of fundamental cladograms and characters (on fundamental trees) were also calculated using TNT, through the scripts 'wstats' and 'stats'. Characters were coded as inapplicable if comprised a characteristic that could not be determined in the taxon even though there were specimens available for examination (*e.g.*, shape of anterior nuchal plate in taxa that lack anterior nuchal plate); or as missing data, if there were not available specimens to be examined or if the character comprised a structure that was damaged in the examined specimens (*e.g.*, dimorphic features in species from which the only known specimens are immature males and females); both cases coded as "?" in the matrix.

Results and Discussion

Character descriptions.

External morphology.

0. Coloration of head and body: 0- tan or brown background color, uniform or covered by dark or pale (faint white in life) blotches and/or stripes; 1- black background and conspicuous pale (yellow in life) blotches and/or stripes (CI 0.333, RI 0.5).

The doradids *Acanthodoras*, *Agamyxis*, *Doras zuanoni*, *Orinocodoras eigenmanni*, and *Platydoras* (except *P. costatus*) have a very distinct coloration of head and body, consisting of black background with pale conspicuous blotches and/or stripes (yellow in life) (Fig. 3). This color pattern is related to the elaborate behavior of cleaning fishes in *Platydoras armatulus* (Carvalho *et al.*, 2003), and possibly also in the others. All other examined species have pale or brown background color, uniform or covered by dark or pale (faint white in life) blotches and/or stripes.

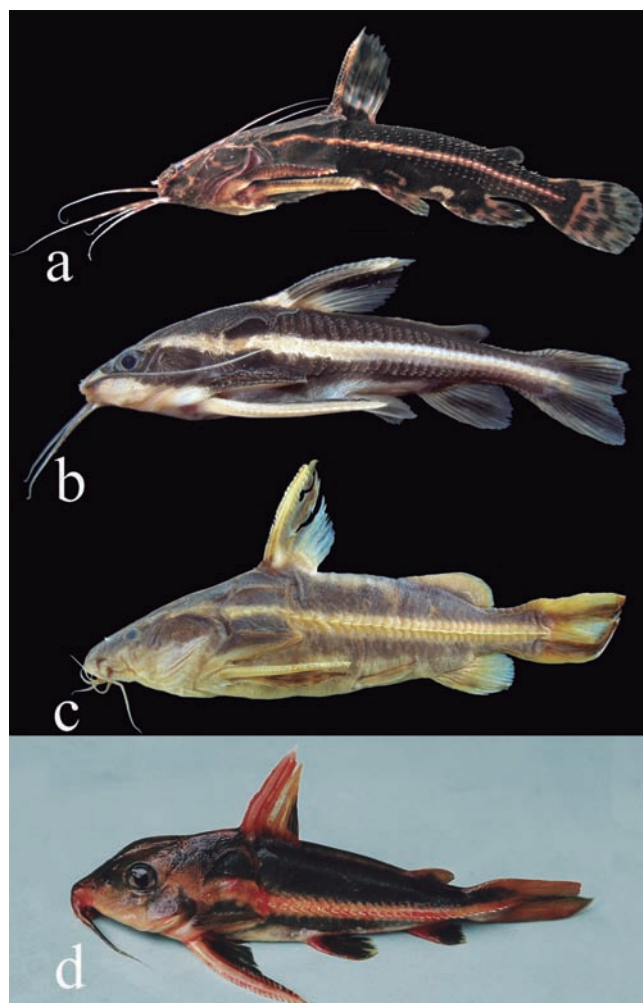


Fig. 3. (a) *Acanthodoras cataphractus*, MZUSP 103284, 76.6 mm SL, rio Jari, Monte Dourado, Pará, photographed live; (b) *Platydoras armatulus*, MZUSP 92759, approximately 55 mm SL, rio Amazonas, Santarém, Pará, photographed live by Leandro Sousa; (c) *Orinocodoras eigenmanni*, MZUSP 86807, 123 mm SL, río Apure, Arismendi, Venezuela; (d) *Doras zuanoni*, INPA uncatalogued, approximately 110 mm SL, rio Araguaia basin, photographed live by Jansen Zuanon.

1. Coloration on caudal-fin lobes: 0- uniform; 1- with a distinct dark longitudinal stripe on middle of each lobe (CI 0.167, RI 0.5).

In the doradids *Anadoras*, *Centrochir*, *Orinocodoras*, *Platydoras*, *Tenellus*, and *Leptodoras* (except *L. myersi* and *L. juruensis*), there is a conspicuous dark stripe on the middle of each caudal-fin lobe (Fig. 4b-d; Sousa, 2010: #7). The caudal-fin lobes are uniformly colored in all other examined species (Fig. 4a).

2. Adipose eyelid: 0- weakly developed, horizontal adipose eye diameter larger than horizontal diameter of eye by less than 10% (AED and ED of Sabaj, 2005, respectively); 1- well developed, horizontal adipose eye diameter larger than horizontal diameter of eye by 10% or more (CI 0.5, RI 0.889).

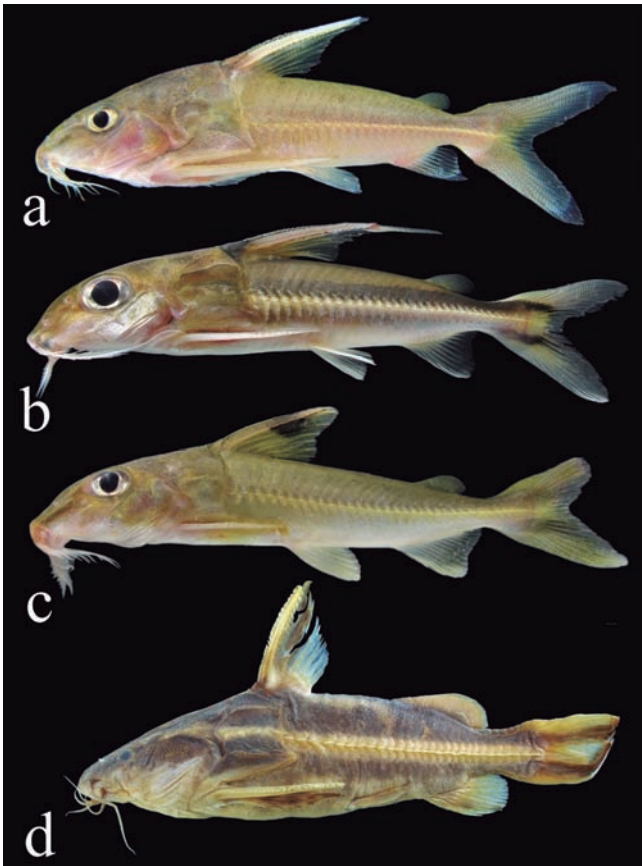


Fig. 4. (a) *Nemadoras humeralis*, INPA uncatalogued, rio Solimões, Manaus, Amazonas, photographed live by Leandro Sousa; (b) *Tenellus ternetzi*, MZUSP 103245, 84.5 mm SL, rio Jari, Monte Dourado, Pará, photographed live; (c) *Leptodoras marki*, MZUSP 103217, 80.3 mm SL, rio Fresco, São Felix do Xingu, Pará, photographed live; (d) *Orinocodoras eigenmanni*, MZUSP 86807, 123 mm SL, río Apure, Arismendi, Venezuela.

The eye is bordered by a weakly developed adipose eyelid in most catfishes, with horizontal adipose eye diameter larger than horizontal diameter of eye by less than 10% (Fig. 2a,b). However, the doradids *Anduzedoras*, *Hassar*, *Tenellus*, and most basal species of *Leptodoras*, including *L. copei*, *L. hasemani*, *L. marki*, *L. oyakawai*, and *L. praelongus*, have well-developed adipose eyelid, with horizontal adipose eye diameter larger than horizontal diameter of eye by 10% or more (Fig. 5c; Sabaj, 2002: #7).

3. Posterolateral lobe on lips: 0- absent; 1- present (CI 1.0, RI 1.0).

The lips of the doradids *Orinocodoras* and *Rhinodoras* are thick and bear posterolaterally-directed lobes at the lateral corners of the mouth (Fig. 6a), rendering those taxa with the informal name of thick-lip thorny cat (Sabaj *et al.*, 2008). All other examined species lack a posterolateral lobe on lips (Fig. 6b).

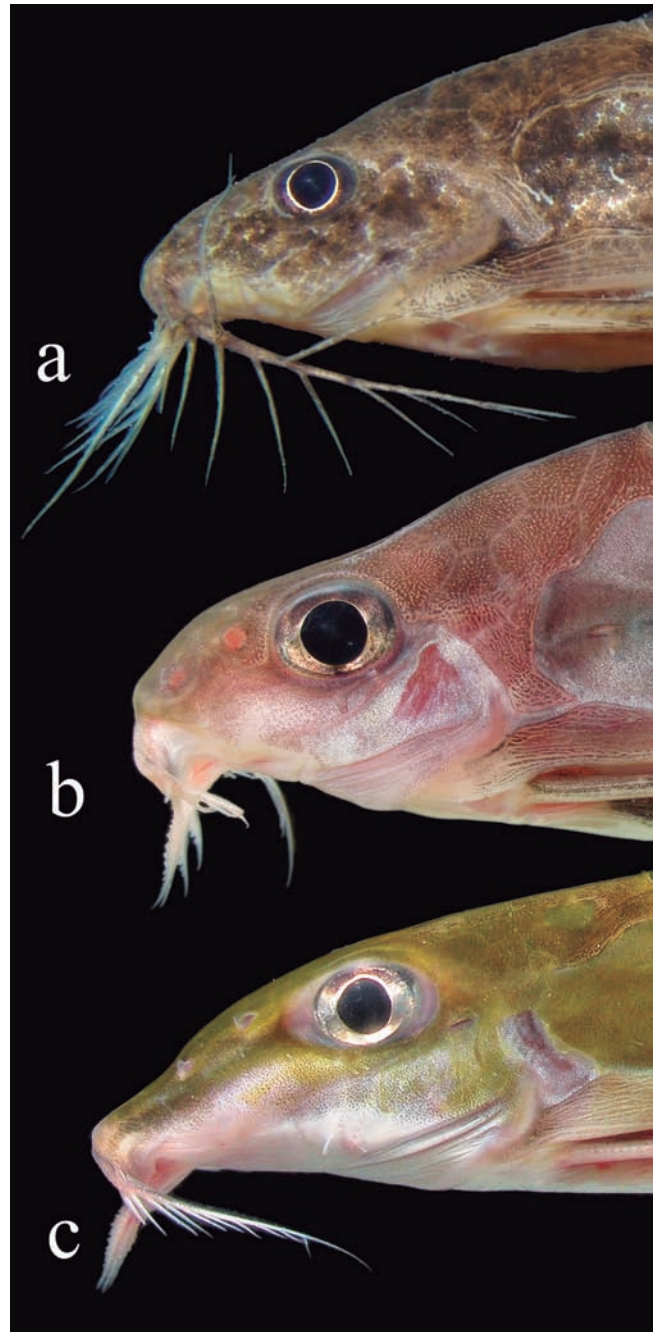


Fig. 5. Head, in lateral view, of (a) *Ossancora asterophysa*, MZUSP 92783, approximately 60 mm SL, photographed live by Leandro Sousa; (b) *Trachydoras brevis*, MZUSP 103087, approximately 70 mm SL, photographed live; (c) *Hassar orestis*, MZUSP 103327, 104 mm SL, photographed live.

4. Adipose fin: 0- present; 1- absent (CI 0.143, RI 0.0).

The adipose fin is present in most catfishes. However, it is absent in the Aspredinidae, Nematogenyidae, Siluridae, auchenipterids *Epapterus*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus coriaceus* (Ferraris, 1988: #02; Curran, 1989: #12; Royero, 1999: #143; Akama, 2004: #186), among examined species. The adipose fin is also



Fig. 6. Mouth, in ventral view, of (a) *Rhinodoras dorbignyi*, MCP 12419, 160.8 mm SL; (b) *Tenellus trimaculatus*, MZUSP 93421, 107.3 mm SL; (c) *Leptodoras hasemani*, MZUSP 37009, 133.7 mm SL; (d) *Auchenipterus nuchalis*, MZUSP 89728, 139.6 mm SL.

absent in the auchenipterid *Gelanoglanis nanonotocolus*, and some specimens of the doradids *Physopyxis ananas* and *P. lyra* (Eigenmann, 1925: 283; Sousa & Rapp Daniel, 2005), taxa not included in the present analysis.

5. Shape of adipose fin (unordered): 0- long and thick, with its base approximately as long as that of the anal fin; 1- short, thick and extended anteriorly as a low keel; 2- short, thin and teardrop-shaped (CI 0.25, RI 0.824).

In many species of catfishes the adipose fin is long and thick, with its base approximately as long as that of the anal fin (Figs. 3c, 4d), including those of the ariid *Galeichthys* (Marceniuk *et al.*, 2012: #212), Amphiliidae, Diplomystidae, Claroteidae, Erethistidae, Heptapteridae, Malapteruridae, Mochokidae, Pimelodidae, Pseudopimelodidae, and Sisoridae. However, the adipose fin is short, thick and extended anteriorly as a low keel in the doradids *Centrochir*, *Centrodoras*, *Megalodoras*, and *Platyodoras* (Fig. 3b), a characteristic noticed by Eigenmann (1925: 283), and used in his identification key. The adipose fin is short, thin, and has the contour of a teardrop (Figs. 3a,d, 4a-c) in the ariid *Genidens* (Ariidae; Marceniuk *et al.*, 2012: #212), Auchenipteridae (except *Epapterus*, *Trachelyichthys*, *Trachelyopterichthys*, and *Trachelyopterus*), Ictaluridae (Lundberg, 1970: #1), Pangasiidae, in doradids *Acanthodoras*, *Agamyxis*, *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras*, and in the species of Astrodoradinae. All other species of the Doradidae have long and thick adipose fin. This character was coded as inapplicable for all examined taxa in which the adipose fin is absent (*i.e.*, Aspredinidae, Nematogenyidae, Siluridae, and auchenipterids *Epapterus*, *Trachelyichthys*, *Trachelyopterichthys*, and *Trachelyopterus*).

6. Gill-opening membranes (unordered): 0- free from isthmus (and from each other); 1- united to isthmus at one single location; 2- united to isthmus across a large area; 3- united to each other (and free from isthmus) (CI 0.6, RI 0.818).

Members of several examined families of catfish have gill-

opening membranes free from isthmus (and from each other), including the Amphiliidae, Claroteidae, Heptapteridae, Ictaluridae, Nematogenyidae, Pangasiidae, Pimelodidae, Pseudopimelodidae, and Siluridae. The examined species of the Diplomystidae, Erethistidae and Sisoridae have gill-opening membranes united to the isthmus at a single location (Britto, 2002: #299). The species of the Aspredinidae, Auchenipteridae, Doradidae, Malapteruridae, and Mochokidae (Vigliotta, 2008: #92), on the other hand, have gill-opening membranes united to the isthmus across a large area (Fig. 6). The members of the Anchariidae and Ariidae have gill-opening membranes united to each other and free from the isthmus (Royero, 1999: #114).

7. Distance between nares: 0- relatively large, distance greater than length of opening of anterior naris; 1- relatively small, distance approximately equal or smaller than length of opening of anterior naris (CI 0.333, RI 0.5).

Most examined species of catfish have the anterior and posterior nares distinctly apart, with distance between nares greater than length of opening of anterior naris (Fig. 5). However, the species of the Ariidae, Diplomystidae, Erethistidae, and Sisoridae, have the anterior and posterior nares close to each other, with distance approximately equal or smaller than length of opening of anterior naris (Mo, 1991; Britto, 2002: #297; Marceniuk *et al.*, 2012: #221).

Barbels.

8. Oral hood: 0- absent; 1- present (CI 1.0, RI 1.0).

As previously discussed by several authors (Higuchi, 1992: #A07, #A08; Sabaj, 2002: #8, #9, #10, #11; Sabaj, 2005; Birindelli *et al.*, 2008; Birindelli & Sousa, 2010), the labial membrane in the doradids *Anduzedoras* and *Leptodoras* is expanded posteriorly and incorporates the bases of mental barbels forming the so-called oral hood (Fig. 6c; Sabaj, 2005: fig. 5). The oral hood is more developed in distal species of *Leptodoras* (Sabaj, 2005; Birindelli *et al.*, 2008), but it is also present in *Anduzedoras* and basal most species of *Leptodoras*. In all other examined catfish, the aforementioned modification is absent.

9. Dorsolateral membrane of maxillary barbel: 0- absent; 1- present (CI and RI inapplicable).

A dorsolateral membrane (= dorsolabial membrane of Sabaj, 2005: fig. 1b) is present exclusively on the maxillary barbel of distal species of the doradid *Leptodoras*, including *L. acipenserinus*, *L. cataniai*, *L. hasemani*, *L. juruensis*, *L. linnelli*, *L. myersi*, *L. nelsoni* and *L. rogersae* (Sabaj, 2002: #12; Sabaj, 2005).

10. Length of maxillary barbel: 0- maxillary barbel long, extending posteriorly beyond anterior margin of orbit; 1- maxillary barbel short, not reaching the anterior margin of orbit (CI 1.0, RI 1.0).

The maxillary barbel is relatively long in most examined species of catfish, extending posteriorly beyond the anterior margin of orbit (Figs. 5, 7). However, the auchenipterids *Ageneiosus* and *Tetranematichthys* have the maxillary barbel extremely short, not reaching the anterior margin of orbit (Ferraris, 1988: #J14; Royero, 1999: #117; Akama, 2004: #62).

11. Fimbriae on ventral face of maxillary barbel: 0- absent; 1- present (CI 1.0, RI 1.0).

Most examined species of catfish have smooth maxillary barbel, without fimbriae (Figs. 6a, 7). However, the species of *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras* have fimbriae on the ventral face of the maxillary barbel (Figs. 5, 6b,c; Higuchi, 1992: #6). *Synodontis clarias* and *S. annectes* (Mochokidae) also have fimbriae on the maxillary barbel (Poll, 1971).

12. Fimbriae on dorsal face of maxillary barbel: 0- absent; 1- present (CI 1.0, RI 1.0).

The doradids *Ossancora asterophysa*, *O. eigenmanni*, and *O. fimbriata* are the only examined species with fimbriae present on both ventral and dorsal surfaces of the maxillary barbel (Fig. 5a; Birindelli & Sabaj Pérez, 2011).

13. Maxillary barbel movement: 0- lateral; 1- vertical (CI 1.0, RI 1.0).

The maxillary barbel moves laterally in most catfishes, whereas it moves vertically in the species of the Auchenipteridae (Fig. 7; Ferraris, 1988: #J12; Akama, 2004: #60).

14. Suborbital groove: 0- absent; 1- present (CI 1.0, RI 1.0).

The species of the Auchenipteridae have a suborbital groove in which the maxillary barbel fits when adpressed to body (Fig. 7; Ferraris, 1998: #J16; Curran, 1989: #2; Royero, 1999: #116; Akama, 2004: #61). That condition is absent in all other examined species (Fig. 5).

15. Transverse striae on barbels: 0- absent; 1- present (CI 1.0, RI 1.0).

All species of the doradid *Rhinodoras* have transverse striae on the maxillary and mental barbels (Fig. 6a). This condition is absent in all other examined species (Fig. 6b-d).



Fig. 7. Head, in lateral view, of *Centromochlus heckelii*, MZUSP 104793, 100 mm SL, photographed live; arrow indicates suborbital groove.

16. Number of mental barbels at each side of head (ordered): 0- mental barbels absent; 1- one; 2- two (CI 0.333, RI 0.5).

Most catfishes have two mental barbels on each side of the head (Fig. 6). However, the Nematogenyidae, Pangasiidae, and auchenipterids *Gelanoglanis* and *Tetranematichthys* do not have the lateral mental barbel, whereas the Astroblepidae, Diplomystidae, Loricariidae, and auchenipterid *Ageneiosus* lack mental barbels entirely (Britski, 1972: 11; Arratia, 1987; Ferraris, 1988: #J19, #J22; Curran, 1989: #23; Walsh, 1990: #20, #21; Royero, 1999: #118; Akama, 2004: #63; Marceniuk *et al.*, 2012: #225, #226). In the Pangasiidae and auchenipterids *Tetranematichthys* and *Ageneiosus* the loss of mental barbels was interpreted as an adaptation to their pelagic habitat (Britski, 1972). The absence of mental barbels in the Diplomystidae is considered a primitive condition, and not a secondary loss as in the aforementioned taxa (Arratia, 1987).

17. Fimbriae on mental barbels: 0- absent; 1- present (CI 0.25, RI 0.667).

In the doradids *Ossancora* (except *O. punctata*) and *Hemidoras*, the mental barbels have long, distinct fimbriae (Fig. 5a). The same condition is also present in the mochokids *Mochokus*, *Mochokiella*, *Microsynodontis*, and *Synodontis* (Vigliotta, 2008: #88). In all other examined species, the mental barbels are either completely smooth or with delicate papillae (Figs. 5b,c). This character was coded as inapplicable for the Diplomystidae and auchenipterid *Ageneiosus*, which lack mental barbels.

18. Arrangement of fimbriae of mental barbels: 0- one row; 1- two rows (CI 0.5, RI 0.5).

The doradids *Ossancora fimbriata* and *Hemidoras*, and mochokids *Mochokus* and *Mochokiella* have only one row of fimbriae on the mental barbels, whereas doradids *Ossancora*

asterophysa and *O. eigenmanni*, and mochokids *Microsynodontis* and *Synodontis* (Vigliotta, 2008: #89) have two rows. This character was coded as inapplicable in all examined taxa that either lack fimbriae on mental barbels or lack mental barbels entirely (*i.e.*, all examined taxa except the species mentioned in this character discussion).

19. Length of mental barbels (one relative to the other): 0- lateral distinctly longer than medial; 1- lateral and medial approximately of the same length (CI 0.5, RI 0.969).

In most catfishes the lateral mental barbel is distinctly longer than the medial (Fig. 6a). However, in *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras* (Higuchi, 1992: #8), and in the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus*, the mental barbels are approximately the same length (Figs. 5, 6a,b). This character was coded as inapplicable for all species that lack at least one pair of mental barbel (*i.e.*, Diplomystidae, Nematogenyidae, Pangasiidae, and auchenipterids *Ageneiosus*, *Gelanoglanis*, and *Tetranematichthys*).

20. Length of mental barbel (relative to body length): 0- short, not reaching the posterior tip of coracoid process; 1- long, surpassing the posterior tip of coracoid process (CI 0.2, RI 0.5).

The Ariidae, Pimelodidae and auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudauchenipterus*, *Pseudepapterus*, and *Trachelyopterus coriaceus* have long mental barbels, surpassing the posterior tip of the coracoid process (Curran, 1989: #6; Akama, 2004: #64). All other examined species have mental barbels relatively short, not reaching the posterior tip of coracoid process (Fig. 6). This character was coded as inapplicable for the Diplomystidae and auchenipterid *Ageneiosus*, which lack mental barbels entirely.

21. Relative position of bases of mental barbels: 0- base of medial barbel anterior to that of lateral barbel; 1- bases on medial and lateral barbels side by side (CI 0.5, RI 0.969).

In most catfishes, the insertion of the medial mental barbel is anterior to that of the lateral (Fig. 6). However, in the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus*, and doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras*, the mental barbels have their bases close to each other (side by side) and to the lower lip (Figs. 5; 6b-d; Ferraris, 1998: #J18; Curran, 1989: #13; Walsh, 1990: #12; Ferraris & Vari, 1999; Royero, 1999: #119; Akama, 2004: #65). This character was coded as inapplicable for all species that lack at least one pair of mental barbel (*i.e.*, Diplomystidae, Nematogenyidae, Pangasiidae, and auchenipterids *Ageneiosus*, *Gelanoglanis*, and *Tetranematichthys*).

22. Nasal barbel associated with posterior naris: 0- absent; 1- present (CI 0.25, RI 0.25).

Members of the Akysidae, Amblycipitidae, Bagridae,

Chacidae, Clariidae, Claroteidae, Cranoglanidae, Erethistidae, Ictaluridae, Pangasiidae, Plotosidae, Schilbeidae, and Sisoridae have a pair of nasal barbels, associated with the posterior nares (Britto, 2002: #277). This condition is absent in all other examined species (Fig. 5).

Skin and dermal structures.

23. Unculiferous tubercles in males and females: 0- absent or weakly developed; 1- well developed (CI 0.143, RI 0.7).

Tubercles with unculi are common in species of the Siluriformes (Roberts, 1982), although absent in some families, including the Diplomystidae (Arratia & Huaquin, 1995). Among examined species, well-developed unculiferous tubercles are present in male and females of the Amphilidae, Aspredinidae, Erethistidae, Sisoridae, pseudopimelodids *Cephalosilurus fowleri* and *Lophiosilurus alexandri*, mochokid *Chiloglanis*, and doradids *Centrodoras*, *Leptodoras juruensis*, *L. myersi*, *Lithodoras*, *Megalodoras*, *Orinocodoras*, *Oxyodoras*, *Pterodoras*, *Rhinodoras*, and *Rhynchodoras* (Fig. 8; Wiley & Collette, 1970; Collette, 1977; Roberts, 1982; Arratia & Huaquin, 1995; de Pinna, 1996; Sabaj, 2005; Sousa, 2010: #101). Unculiferous tubercles are weakly developed (or completely absent) in male and females of Auchenipteridae, Ariidae, Claroteidae, Diplomystidae, Heptapteridae, Ictaluridae, Malapteruridae, Nematogenyidae, Pangasiidae, Pimelodidae, Siluridae, Mochokidae (except

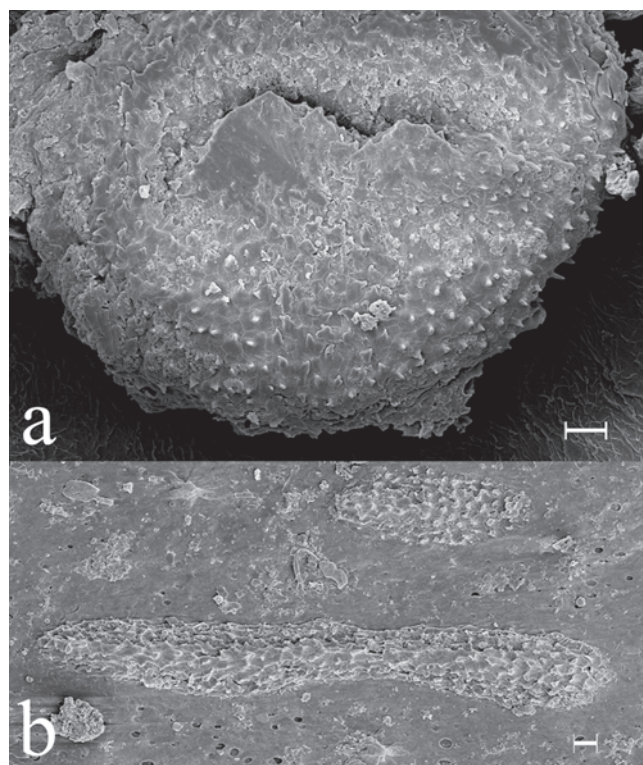


Fig. 8. SEM images of the unculiferous tubercles in (a) *Rhinodoras dorbignyi*, MZUSP 62688, 102 mm SL; and (b) *Leptodoras myersi*, MZUSP 56676, 118 mm SL. Scale bars equal 20 μ m.

Chiloglanis), and Doradidae (except taxa mentioned above). Unculiferous tubercles are present and well developed in mature males of some species of the Auchenipteridae, these are, however, nuptial and treated in distinct characters.

24. Nature of unculiferous tubercles: 0- tubercles independent, not forming plates; 1- tubercles forming plates (CI 1.0, RI 1.0).

The species of the Akysidae, Erethistidae, and Sisoridae have well-developed unculiferous tubercles forming conspicuous plates (Roberts, 1982). This character was coded as inapplicable for all examined species without well-developed unculiferous tubercles (*i.e.*, Auchenipteridae, Ariidae, Claroteidae, Diplomystidae, Heptapteridae, Ictaluridae, Malapteruridae, Nematogenyidae, Pangasiidae, Pimelodidae, Siluridae, Mochokidae, except *Chiloglanis*, and Doradidae, except mentioned in previous character).

25. Breeding tubercles on maxillary barbel: 0- absent; 1- present (CI 0.5, RI 0.75).

Some species of the Auchenipteridae have well-developed unculiferous tubercles as a sexually dimorphic feature, and in that case, these might be correctly called breeding tubercles. Mature males of the auchenipterids *Auchenipterus*, *Entomocorus*, *Pseudepapterus*, *Epapterus*, and *Tetranematichthys* have well-developed tubercles on the maxillary barbel (Ferraris & Vari, 1999; Akama, 2004: #177). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

26. Breeding tubercles on dorsal surface of head: 0- absent; 1- present (CI 1.0, RI 1.0).

Mature males of the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* have well-developed tubercles on the dorsal surface of head. These tubercles are cone-shaped and large in *Entomocorus*, dot-like in *Auchenipterus*, anastomosed in *Pseudepapterus* and dash- or dot-like in *Epapterus* (Akama, 2004: #178). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

27. Breeding tubercles on dorsal-fin spine, pectoral-fin spine, pelvic fin, abdomen and isthmus: 0- absent; 1- present (CI and RI inapplicable).

Mature males of the auchenipterid *Entomocorus* have well-developed tubercles on the dorsal-fin spine (Akama, 2004: #176), pectoral-fin spine, pelvic fin, abdomen (Akama, 2004: #179) and isthmus (Akama, 2004: #180; see also Akama & Ferraris, 2004). No other examined species have such characteristics. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

28. Breeding tubercles on tip of anteriormost anal-fin rays: 0- absent; 1- present (CI 1.0, RI 1.0).

Mature males of the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus* have well-developed

tubercles on the tip of anteriormost anal-fin rays (Akama, 2004: #182). All other examined taxa lack this feature. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

29. Papilla-like tubercles on tympanic area: 0- absent; 1- present (CI and RI inapplicable).

Species of the auchenipterid *Pseudauchenipterus* have well-developed papilla-like tubercles on the tympanic area (Akama, 1999; Royero, 1999: #148; Akama, 2004: #183). This feature is absent in all other examined species.

30. Glandular tissue on axilla: 0- absent; 1- present (CI 0.25, RI 0.864).

Glandular tissue and associated numerous pores on the axilla area, immediately ventral to the anteriormost portion of the posterior cleithral process (Fig. 9), were described for the doradid *Rhynchodoras* (Birindelli *et al.*, 2007), *Doras* (Sabaj Pérez & Birindelli, 2008: fig. 2), and are also present in *Trachydoras*, *Nemadoras*, *Tenellus*, *Hassar*, *Anduzedoras*, and the most basal species of *Leptodoras* (*L. marki*, *L. oyakawai*, *L. praelongus*, *L. copei*, *L. hasemani*; Sabaj, 2002: #30; Sabaj, 2005). As the single pore present in most catfishes, the glandular tissue and associated pores in the aforementioned taxa produce mucous (Burgess, 1989: 201).

31. Glandular tissue on surface of abdomen: 0- absent; 1- present (CI 1.0, RI 1.0).

As described by Sabaj Pérez & Birindelli (2008), the species of the doradid *Doras* have glandular tissue and associated numerous pores on the abdomen, which may be restricted to the anal opening as in *D. carinatus*, *D. micropoeus* and *D. higuchii* (Fig. 10a), or widespread on the abdomen as in *D. phlyzakion* and *D. zuanoni* (Figs. 10b,c). Like the axillary pores beneath the posterior cleithral process, the abdominal glandular tissue produces mucous. All other examined species lack this characteristic.

32. Dermal scutes between dorsal and adipose fins, and between anal opening and anal fin, in specimens of more than



Fig. 9. Posterior cleithral process in *Doras micropoeus*, ANSP 177880, 274 mm SL, photo by Mark Sabaj Pérez. Scale bar equals 10 mm.

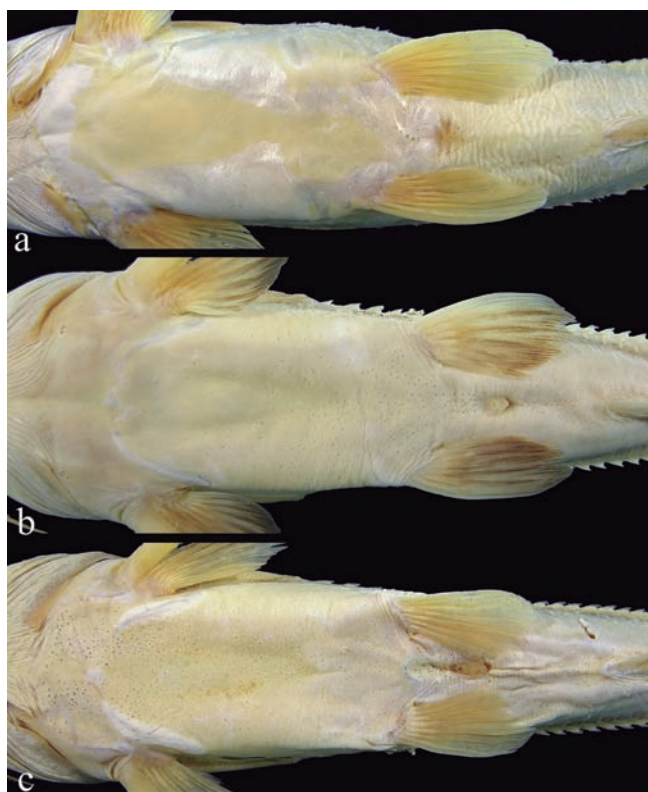


Fig. 10. Ventral body in (a) *Doras higuchii*, INPA 45052, 153 mm SL; (b) *Doras zuanoni*, INPA 5244, 124 mm SL; and (c) *Doras phlyzakion*, ANSP 181055, 169 mm SL, photos by Mark Sabaj Pérez.

50 mm SL: 0- absent; 1- present (CI 0.5, RI 0.0).

Dermal scutes between the dorsal and adipose fins, and between the anal opening and anal fin are only present in the doradids *Hemidoras morrиси* and *H. stenopeltis*. The doradid genus *Hemidoras* was erected by Eigenmann (1925) to comprise these two species on the basis of the presence of dermal scutes between the dorsal and adipose fins, and also between the anal opening and anal fin (Eigenmann, 1925: 346; Higuchi, 1992: #A85). A somewhat similar condition is present in *Lithodoras dorsalis*. The latter, however, has dermal scutes with irregular margins completely covering the ventral, lateral and dorsal surfaces of body in specimens larger than 150 mm SL (Eigenmann, 1925: 318; Higuchi, 1992: #A84). Since the condition in *Lithodoras* is distinct from that observed in *Hemidoras morrиси* and *H. stenopeltis*, the former was coded as having state 0 for this character.

Gas bladder morphology

33. Size of gas bladder: 0- large, occupying at least half of retroperitoneal cavity; 1- small, occupying less than half of retroperitoneal cavity (CI 0.333, RI 0.5).

The gas bladder occupies most of the retroperitoneal cavity in most catfishes. However, it is reduced in size, occupying less than half of the retroperitoneal cavity in the doradids *Rhynchodoras* (Birindelli *et al.*, 2007), *Leptodoras* (except *L. oyakawai* and *L. marki*) (Figs. 11d-f; Sabaj, 2005; Birindelli *et al.*, 2008; Birindelli & Sousa, 2010; Birindelli *et al.*, 2009: fig. 18), and in the auchenipterid *Ageneiosus* (except *A. atronasmus*, *A. brevis*, *A. pardalis*, and *A. piperatus*) (Figs. 11a-c; Bridge & Haddon, 1892: 156; Chardon, 1968; Britski,

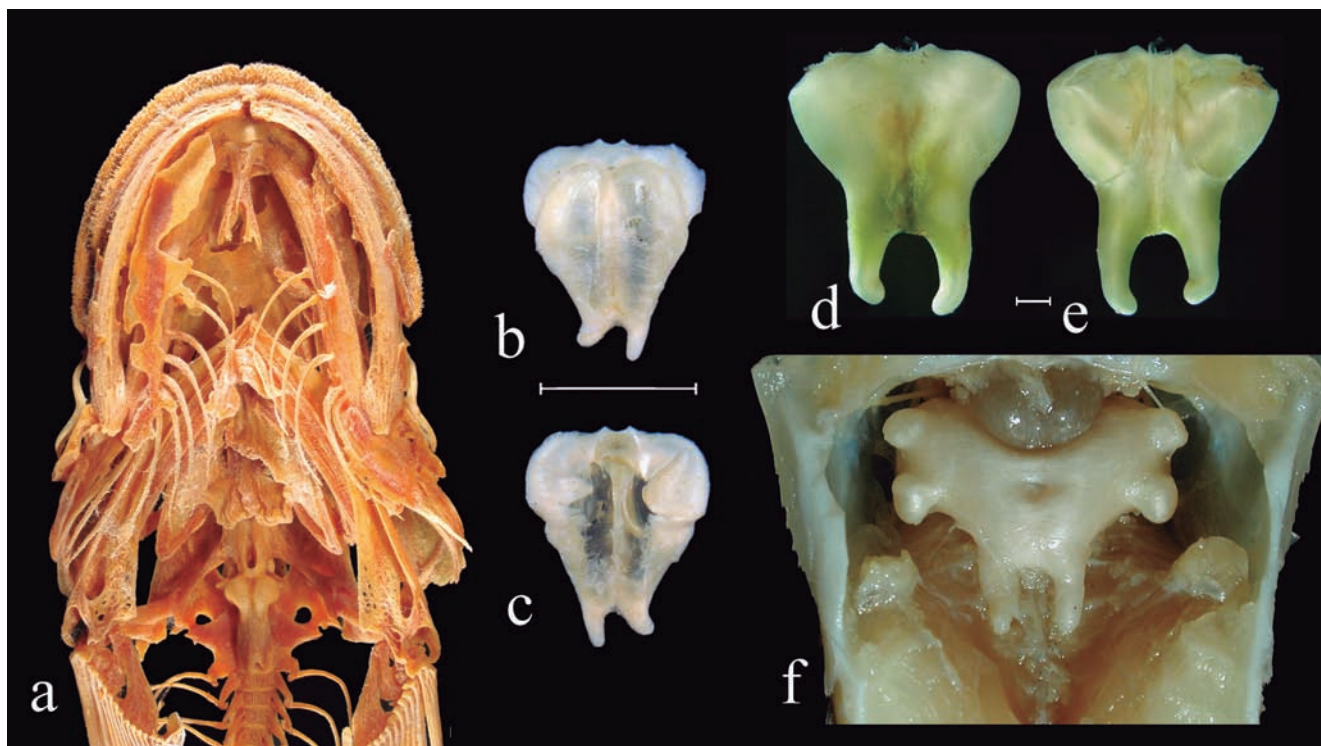


Fig. 11. Anterior portion of head and body in (a) *Ageneiosus inermis*, MZUSP 91661, 320 mm SL. Gas bladder in ventral (b,d) and dorsal (c,e) of (b,c) *Ageneiosus inermis*, MZUSP 9384, 77 mm SL; (d,e) *Rhynchodoras woodsi*, ANSP 181042, 72.5 mm SL. Ventral view of body cavity of (f) *Leptodoras cataniai*, INHS 39814, 111.1 mm SL. Scale bars equal 5 mm. Photos (d,e,f) by Mark Sabaj Pérez.

1972: 23; Ferraris, 1988: #V9; Walsh, 1990: #24; Royero, 1999: #147; Akama, 2004: #74; Birindelli *et al.*, 2012). Only a few other catfishes have a somewhat similar condition, including the bagrid *Rheoglanis dendrophorus* (see Chardon, 1968: fig. 35), and the pimelodids *Callophysus*, *Luciopimelodus*, *Aguarunichthys*, and *Pinirampus* (Chardon, 1968; Stewart, 1986). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

34. Gas-bladder wall: 0- not ossified; 1- ossified (CI and RI inapplicable).

Among examined taxa, the gas bladder is reduced and its *tunica externa* ossified only in the auchenipterids *Ageneiosus inermis*, *A. marmoratus*, *A. polystictus*, *A. vittatus*, and some specimens of *A. ucayalensis* (Figs. 11a-c; Walsh, 1990; Birindelli *et al.*, 2012). A similar condition is present in *Hypophthalmus* (Chardon, 1968). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

35. Terminal diverticula of gas bladder: 0- absent; 1- present (CI0.143, RI0.6).

The posterior chambers of the gas bladder are expanded posteriorly as terminal diverticula in the doradids *Acanthodoras*, *Agamyxis*, *Astrodoras*, *Doras zuanoni*, *Hemidoras*, *Ossancora punctata*, *Trachydoras*, and auchenipterids *Centromochlus heckelii*, *Trachelyopterus ceratophysus*, *T. fisheri*, *T. galeatus*, *T. peloichthys*, *T. porosus*, *T. teaguei*, *T. striatulus* and *Trachycorystes trachycorystes* (Fig. 12; Akama, 2004: #71; Birindelli *et al.*, 2009; Sousa, 2010: #91; Birindelli *et al.*, 2012). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

36. Tips of terminal diverticula of gas bladder: 0- medially united; 1- distally divergent (CI 0.5, RI 0.8).

The terminal diverticula of the gas bladder are medially united in the doradids *Acanthodoras*, *Agamyxis*, *Astrodoras*, *Hemidoras*, and auchenipterids *Centromochlus heckelii*, *Trachycorystes trachycorystes* and some specimens of *Trachelyopterus galeatus* (Fig. 12b). The terminal diverticula diverge distally in the doradids *Doras zuanoni*, *Ossancora punctata*, and *Trachydoras* (Fig. 12a; Birindelli *et al.*, 2009; Sousa, 2010: #93; Birindelli *et al.*, 2012), and auchenipterids

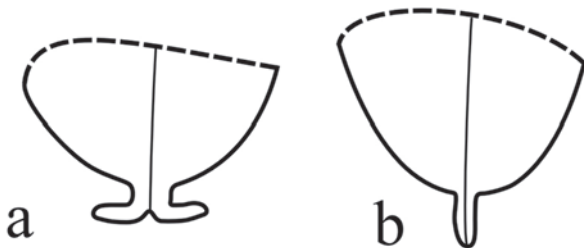


Fig. 12. Schematic drawing of the posterior portion of the gas bladder showing (a) terminal diverticula distally divergent, and (b) terminal diverticula medially united. Modified from Birindelli *et al.* (2009: fig. 2).

Trachelyopterus ceratophysus, *T. fisheri*, *T. peloichthys*, *T. porosus*, *T. striatulus*, *T. teaguei* and some specimens of *T. galeatus* (Akama, 2004: #71; Birindelli *et al.*, 2012). This character was coded as inapplicable for all taxa without terminal diverticula on the gas bladder (*i.e.*, all examined taxa except those mentioned in the previous character); as polymorphic for *Trachelyopterus galeatus*; and as missing data for *Pseudotatia* and *Spinipterus*.

37. Secondary chamber of gas bladder: 0- absent; 1- present (CI0.083, RI0.421).

The secondary chamber of the gas bladder, as defined by Birindelli *et al.* (2009), is formed by enlargement of the terminal diverticulum(a), which become(s) distinct from the main bladder by a basal constriction. The secondary chamber is present in the doradids *Centroadoras*, *Doraops*, *Doras carinatus*, *D. micropoeus*, *D. higuchii*, *Lithodoras*, *Megalodoras*, *Orinocodoras*, *Oxyodoras*, *Platyodoras* (except *Platyodoras* sp.), *Pterodoras rivasi*, *Rhinodoras thomersoni*, *R. dorbignyi* and *Scorpiodoras*, and auchenipterids *Auchenipterichthys*, and *Tetranematichthys* (Fig. 13; Britski, 1972: 33; Higuchi, 1992: #114; Akama 2004: #72; Sousa, 2010: #94; Birindelli *et al.*, 2012). The same condition is also present in members of the Malapteruridae (Bridge & Haddon, 1892: fig. 71), Pangasiidae (Bridge & Haddon, 1892: fig. 93), and in some species of the Ictaluridae (Lundberg, 1970: #91) and Pimelodidae (Lundberg & Akama, 2005). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

38. Nature of the secondary chamber of gas bladder: 0- formed by both posterior chambers, thus with an inner septum; 1- formed by a single posterior chamber, thus without an inner septum (CI 0.5, RI 0.75).

The secondary chamber of the gas bladder is formed from both posterior chambers, and thus has an medial septum in both the Malapteruridae, Pangasiidae, doradids *Centroadoras*, *Doraops*, *Megalodoras*, *Lithodoras*, *Orinocodoras*, *Pterodoras rivasi*, *Rhinodoras thomersoni*, *R. dorbignyi*, and *Scorpiodoras*, and auchenipterids *Auchenipterichthys* and *Tetranematichthys* (Fig. 13b; Britski, 1972: 33; Higuchi, 1992:

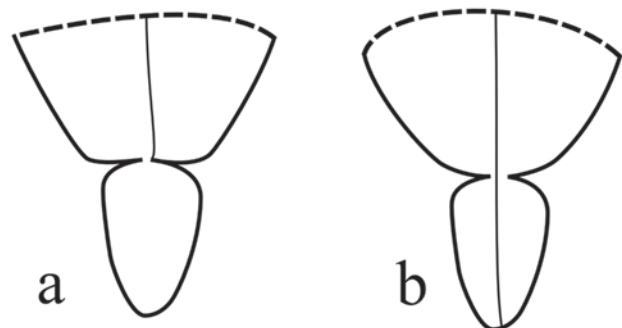


Fig. 13. Schematic drawing of the posterior portion of the gas bladder showing (a) secondary chamber formed by both posterior chambers, and (b) secondary chamber formed by a single posterior chamber. Modified from Birindelli *et al.* (2009: fig. 2).

#114; Akama 2004: #72; Sousa, 2010: #95; Birindelli *et al.*, 2012). The secondary chamber is formed by a single posterior chamber, thus without internal septum (Fig. 13a), in the doradids *Doras carinatus*, *D. higuchii*, and *D. micropoeus*, *Oxydoras* and *Platydoras* (except *Platydoras* sp. which lacks secondary chamber). This character was coded as inapplicable for all taxa that lack the secondary bladder (*i.e.*, all examined taxa, except those mentioned in the previous character); and as missing data for *Pseudotatia* and *Spinipterus*.

39. Subterminal diverticula of gas bladder (unordered): 0- absent; 1- digitiform; 2- horn-like; 3- extremely well developed and branched (CI 0.375, RI 0.375).

The doradids *Agamyxis* and *Doras phlyzakion*, and auchenipterids *Tocantinsia* and *Trachycorystes* have a pair of digitiform subterminal diverticula (Fig. 14a-d; Birindelli *et al.*, 2009; Sabaj Pérez & Birindelli, 2008; Birindelli *et al.*, 2012). The Doradids *Leptodoras* (except *L. marki* and *L. oyakawai*) and *Rhynchodoras woodsi*, and auchenipterid *Ageneiosus* (except *A. pardalis* and *A. ucayalensis*) have a pair of horn-like subterminal diverticula (Fig. 11; Walsh, 1990; Sabaj, 2002: #5; Akama, 2004: #71; Birindelli *et al.*, 2007; Birindelli *et al.*, 2009; Birindelli *et al.*, 2012). The doradid *Pterodoras granulatus* has a pair of extremely well developed and branched subterminal diverticula (Fig. 14e; Birindelli *et al.*, 2009; Sousa, 2010: #97). All other examined species have a gas bladder without subterminal diverticula. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

40. Inner trabeculae of gas bladder: 0- absent; 1- present (CI 0.167-0.2, RI 0.667-0.733).

Inner trabeculae are present in the gas bladder of most medium to large sized species of Doradidae, including *Doraops*, *Lithodoras*, *Megalodoras*, *Pterodoras*, *Orinocodoras*, *Oxydoras*, and *Rhinodoras* (Fig. 15a; Sousa, 2010: #100). The same condition is also present in the Ariidae (Bridge & Haddon, 1892: fig. 44; Marceniuk & Birindelli, 2010), Bagridae (Bridge & Haddon, 1892: fig. 18), Heptapteridae (Chardon, 1968: fig. 57), and Pimelodidae (Bridge & Haddon,

1892: fig. 34). All other examined taxa have a gas bladder without inner trabeculae. This character was coded as missing data for auchenipterids *Pseudotatia* and *Spinipterus*.

41. Lateral diverticula on gas bladder (ordered): 0- absent; 1- present only on the main bladder; 2- present on the main bladder and on the secondary chamber of the bladder (CI 0.25, RI 0.867).

All examined species of the Doradinae, except *Doras carinatus*, *D. higuchii*, *D. micropoeus*, *D. phlyzakion*, *Leptodoras oyakawai*, *Ossancora punctata*, *Rhinodoras thomersoni*, and *Rhynchodoras* have lateral diverticula on the main bladder (Fig. 15; Higuchi, 1992: #113, #115; Sabaj, 2002: #4; Sousa, 2010: #98, #99). The only other examined taxon with lateral diverticula on the main bladder is the auchenipterid *Asterophysus batrachus* (Britski, 1972; Akama, 2004; Birindelli *et al.*, 2012). Lateral diverticula are present on both the main bladder and on the secondary chamber of the gas bladder in *Centrodoras*, *Doraops*, *Lithodoras*, *Megalodoras*, and *Pterodoras* (Fig. 15a). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

42. Diverticula on ventral wall of gas bladder: 0- absent; 1- present (CI 0.5, RI 0.667).

The gas bladder in the auchenipterid *Asterophysus* and doradid *Nemadoras* is almost completely surrounded by diverticula, which are also distributed on its ventral wall (Fig. 16; Birindelli *et al.*, 2009; Birindelli *et al.*, 2012). All other examined species have a gas bladder with the ventral wall lacking diverticula. This character was coded as missing data for auchenipterids *Pseudotatia* and *Spinipterus*.

Reproductive system.

43. Mode of reproduction: 0- without insemination; 1- by insemination (CI 1.0, RI 1,0).

The Auchenipteridae is unique among catfishes in having reproduction by insemination. This characteristic was recorded for several species of auchenipterids based on observations of reproduction in captivity (Burgess & Azuma,



Fig. 14. Gas bladders in ventral view of (a) *Agamyxis pectinifrons*, MZUSP 27806, 83.3 mm SL; (b) *Doras higuchii*, ANSP 181057, 160 mm SL; (c) *Trachycorystes trachycorystes*, MZUSP 99308, 180 mm SL; (d) *Tocantinsia piresi*, MZUSP 98301, 264 mm SL; and (e) *Pterodoras granulatus*, MZUSP 91441, 202.0 mm SL. Scale bars equal 10 mm. Photo (b) by Mark Sabaj Pérez.

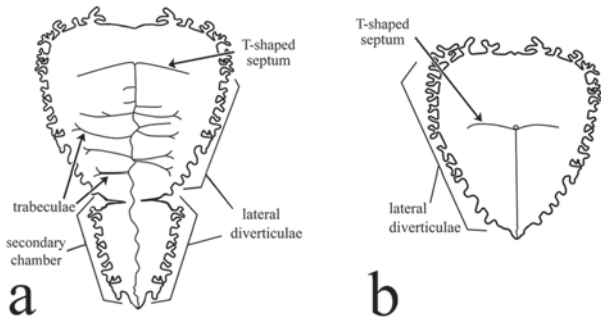


Fig. 15. Schematic drawing of gas bladders in ventral view, showing T-shaped septum, lateral diverticula, trabeculae (a), and secondary chamber (a). Modified from Birindelli *et al.* (2009: fig. 2).

1982; Franke, 1990), on studies of sperm morphology (Ihering, 1937; Burns *et al.*, 2002; Parreira *et al.*, 2009), morphology of the male reproductive tract (Mazzoldi *et al.*, 2007; Meisner *et al.*, 2009), and the presence of spermatozoa in the ovarian lumen found in some species (Parreira *et al.*, 2009). Furthermore, reproduction by insemination is herein inferred to be present in all species of Auchenipteridae due to the fact that they all have the anal fin modified in mature males for insemination.

44. Posterior testicular lobes (unordered): 0- similar to anterior ones (unmodified); 1- modified into hypertrophied storage bags; 2- rudimentary or absent (CI 0.4, RI 0.769).

Most catfishes have the posterior testicular lobes similar to the anterior ones (Figs. 17a-c; Ihering, 1937; Britski, 1972; Loir, 1989; Royero, 1999: #120; Akama, 2004: #142). However, some auchenipterids, including *Auchenipterichthys*, *Glanidium*, *Liosomadoras*, *Pseudauchenipterus*, *Pseudepapterus*, *Tetranematchthys*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, and *Trachycorystes*, have the posterior testicular lobes modified

into storage bags (Figs. 17d; Akama, 2004: #142; Mazzoldi *et al.*, 2007; Meisner *et al.*, 2009). The auchenipterids *Ageneiosus* and *Auchenipterus* lack the posterior testicular lobes (Fig. 17e). This character was coded as missing data for the auchenipterids *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Pseudotatia*, and *Spinipterus*.

45. Main testicular duct: 0- tubular (unmodified); 1- modified into a swollen storage tube (CI 0.5, RI 0.5).

The main testicular duct of most catfishes is tubular. However, the auchenipterids *Asterophysus*, *Centromochlus*, and *Tatia* have the main testicular duct modified into a swollen storage tube (Akama, 2004: #149). This character was coded as missing data for the auchenipterids *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Pseudotatia*, and *Spinipterus*.

46. Position of urogenital opening in males (ordered): 0- near anus; 1- at base of first anal-fin ray; 2- at the tip of anterior anal-fin rays (CI 1.0, RI 1.0).

Most catfishes have the urogenital opening near the anus. However, the species of Auchenipterinae possesses a long and thick urogenital tube whose opening is located at the tip of the anterior anal-fin rays (Figs. 18b-f; Ihering, 1937; Britski, 1972; Ferraris, 1988: #A3, #A4; Royero, 1999: #122; Akama, 2004: #142). The urogenital opening of species of the Centromochlinae, on the other hand, is located in the region immediately anterior to the base of the first anal-fin ray (Fig. 18a; Soares Porto, 1998; Reis & Borges, 2006). In the auchenipterid *Entomocorus* the urogenital opening in mature males is located in a small tube that runs parallel to the anterior anal-fin rays to half of their length, in a condition similar to maturing males of the auchenipterids *Asterophysus* (Fig. 18c), *Liosomadoras* and *Spinipterus* (Akama & Ferraris, 2011).

47. Urogenital opening in mature males: 0- rounded; 1- in the shape of a slit (CI 1.0, RI 1.0).

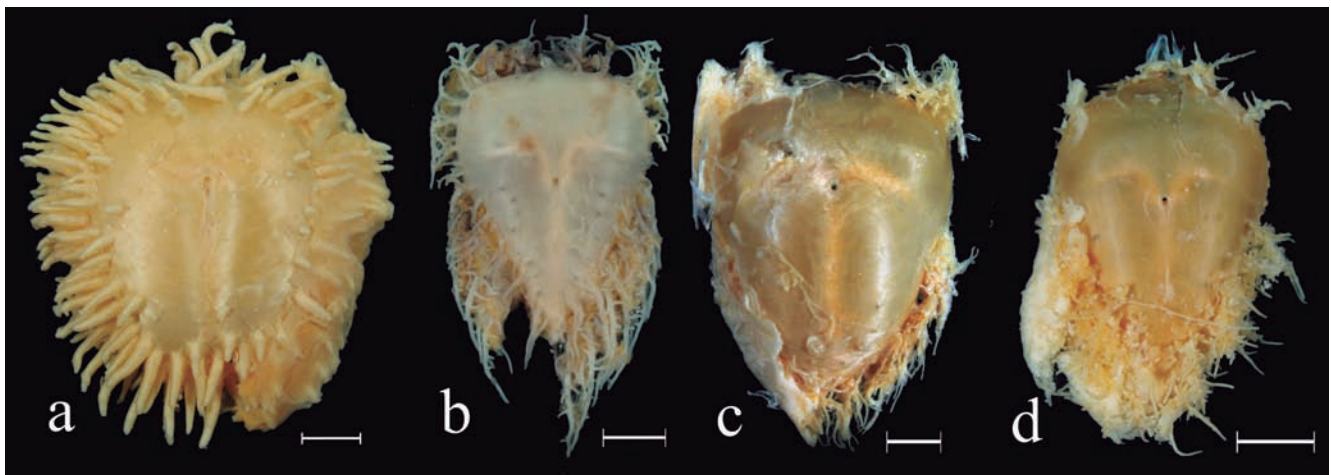


Fig. 16. Gas bladder in ventral view of (a) *Asterophysus batrachus*, MZUSP 12420, 129.7 mm SL; (b) *Nemadoras hemipeltis*, MZUSP 56688, 81.8 mm SL; (c) *Nemadoras humeralis*, MZUSP 56014, 103.8 mm SL; (d) *Nemadoras elongatus*, MZUSP 56013, 99.2 mm SL. Scale bars equal 5 mm.

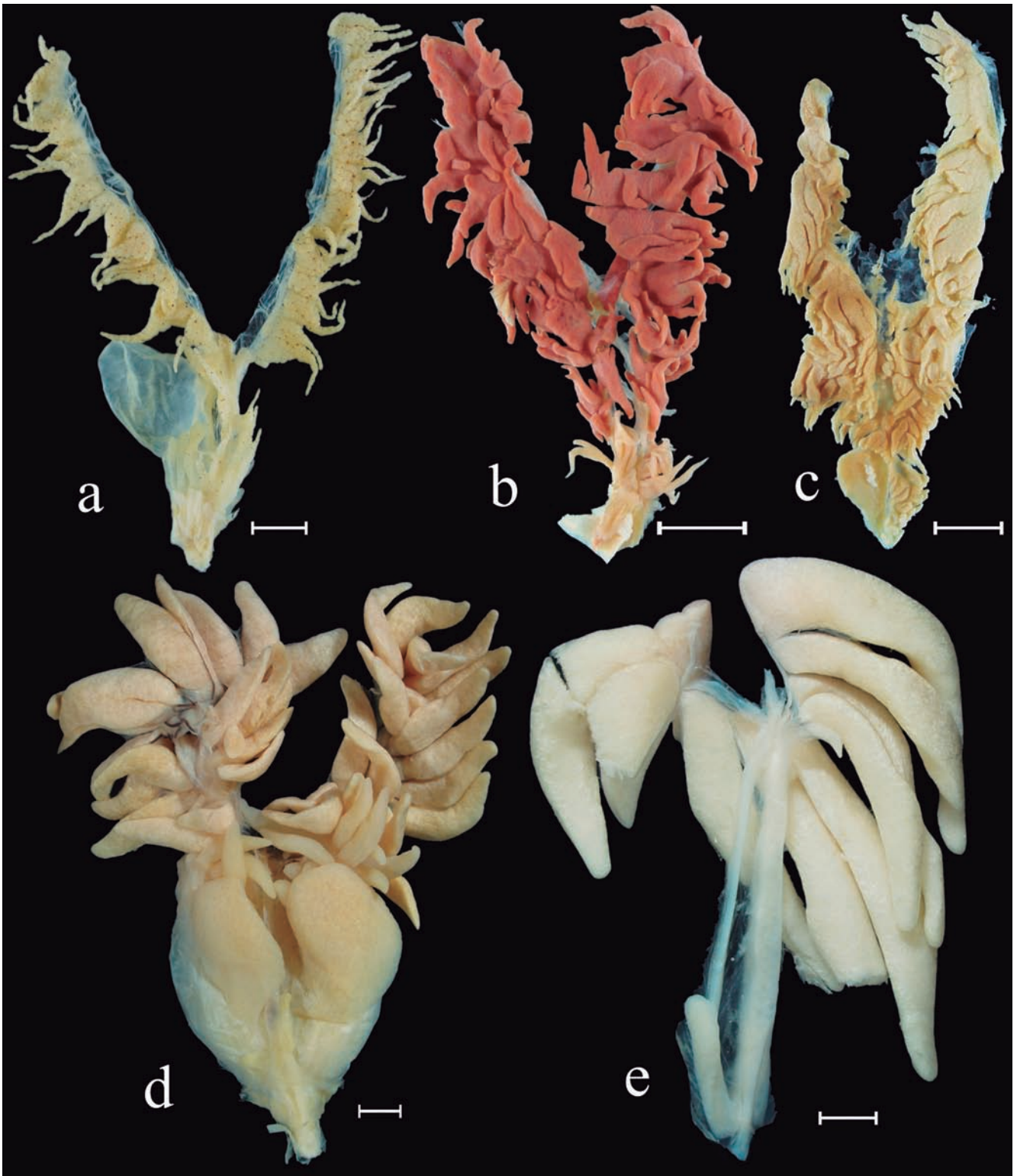


Fig. 17. Testes in ventral view of (a) *Wertheimeria maculata*, MZUSP 93658, 173 mm SL; (b) *Acanthodoras cataphractus*, MZUSP 6831, 116 mm SL; (c) *Hemidoras morei*, MZUSP 31104, 166 mm SL; (d) *Trachelyopterus galeatus*, MZUSP 90742, 154 mm SL; (e) *Ageneiosus ucayalensis*, MZUSP 98333, 165 mm SL. Scale bars equal 5 mm.

The urogenital opening is rounded in mature males of most catfishes. However, it is shaped in the form of a slit in mature males of the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus* (Akama, 2004: #149). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

48. Distal vesicle on anterior anal-fin rays of mature males: 0- absent; 1- present (CI and RI inapplicable).

Mature males of the auchenipterid *Pseudauchenipterus* have a vesicle on the distal portion of the anterior anal-fin rays (Fig. 18d; Akama, 2004: #149). This feature is not present in any other examined species. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

49. Gap between modified anterior and remaining anal-fin rays of mature males: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, only mature males of the auchenipterid *Epapterus* have a gap between the modified anterior anal-fin rays and the remaining ones (Fig. 18b). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

50. Urogenital opening in females: 0- narrow, 1- wide (modified for insemination) (CI 0.5, RI 0.941).

The urogenital opening is narrow in females of most catfishes (Fig. 19a-c). However, females of all auchenipterids, except *Centromochlus*, *Gelanoglanis*, and *Tatia*, have a wide urogenital opening, enlarged for insemination (Figs. 19d-f; Royero, 1999: #124; Akama, 2004: #144). This character was

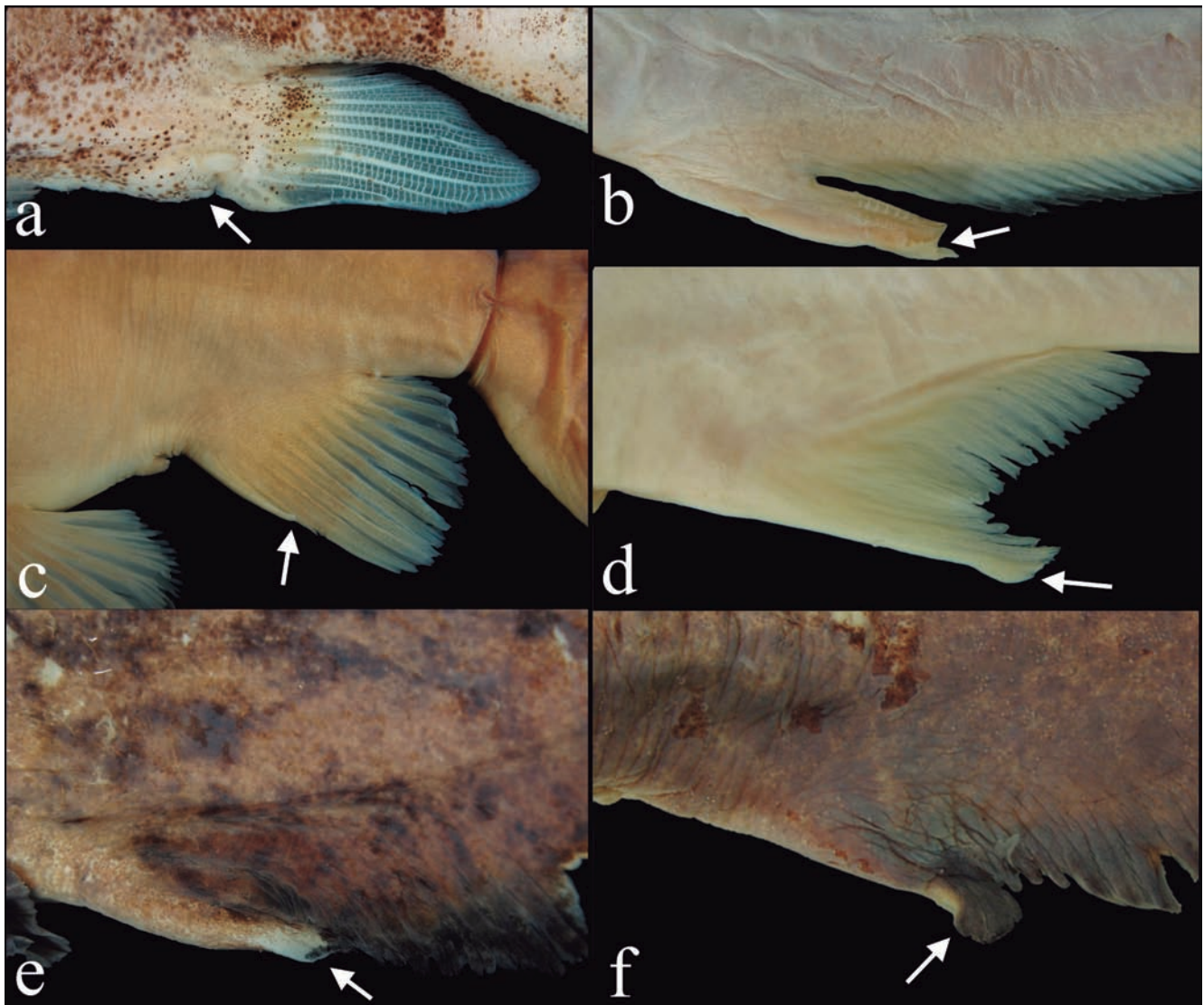


Fig. 18. Anal fin in lateral view of mature (a,b,d-f) or maturing (c) males of (a) *Glanidium melanopteron*, MZUSP 64256, 105 mm SL; (b) *Epapterus dispilurus*, MZUSP 26183, 107 mm SL; (c) *Asterophysus batrachus*, MZUSP 12420, 129.7 mm SL; (d) *Pseudauchenipterus jequitinhonhae*, MZUSP 51734, 100.9 mm SL; (e) *Trachelyopterus galeatus*, MZUSP 79345, 106.3 mm SL; (f) *Trachelyopterus* sp., MZUSP 79345, 106.3 mm SL. Arrows indicate urogenital opening.

coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

Neurocranium.

51. Origin of *adductor mandibulae* muscle: 0- on medial cephalic crest (parietal-supraoccipital); 1- on border of neurocranium (sphenotic, pterotic) (CI 0.333, RI 0.333).

In members of the Diplomystidae, Cetopsidae, Ictaluridae, Malapteruridae, and Nematogenyidae, the *adductor mandibulae* muscle has its origin on the medial cephalic crest (parietal-supraoccipital), and covers the lateral bones of the

neurocranium (sphenotic and pterotic; Fig. 20; Alexander, 1965; Lundberg, 1970; de Pinna *et al.*, 2007). However, in all other catfishes examined, the *adductor mandibulae* originates on the lateral border of the cranium (sphenotic and pterotic), leaving the dorsalmost bones exposed, especially the parietal-supraoccipital and frontals (Figs. 21-31).

52. Shape of mesethmoid (unordered): 0- in shape of an “X”; 1- wide, in shape of a square; 2- in shape of an arrow, medially dilated (CI 0.25, RI 0.895).

In most catfishes, the mesethmoid is in the shape of an

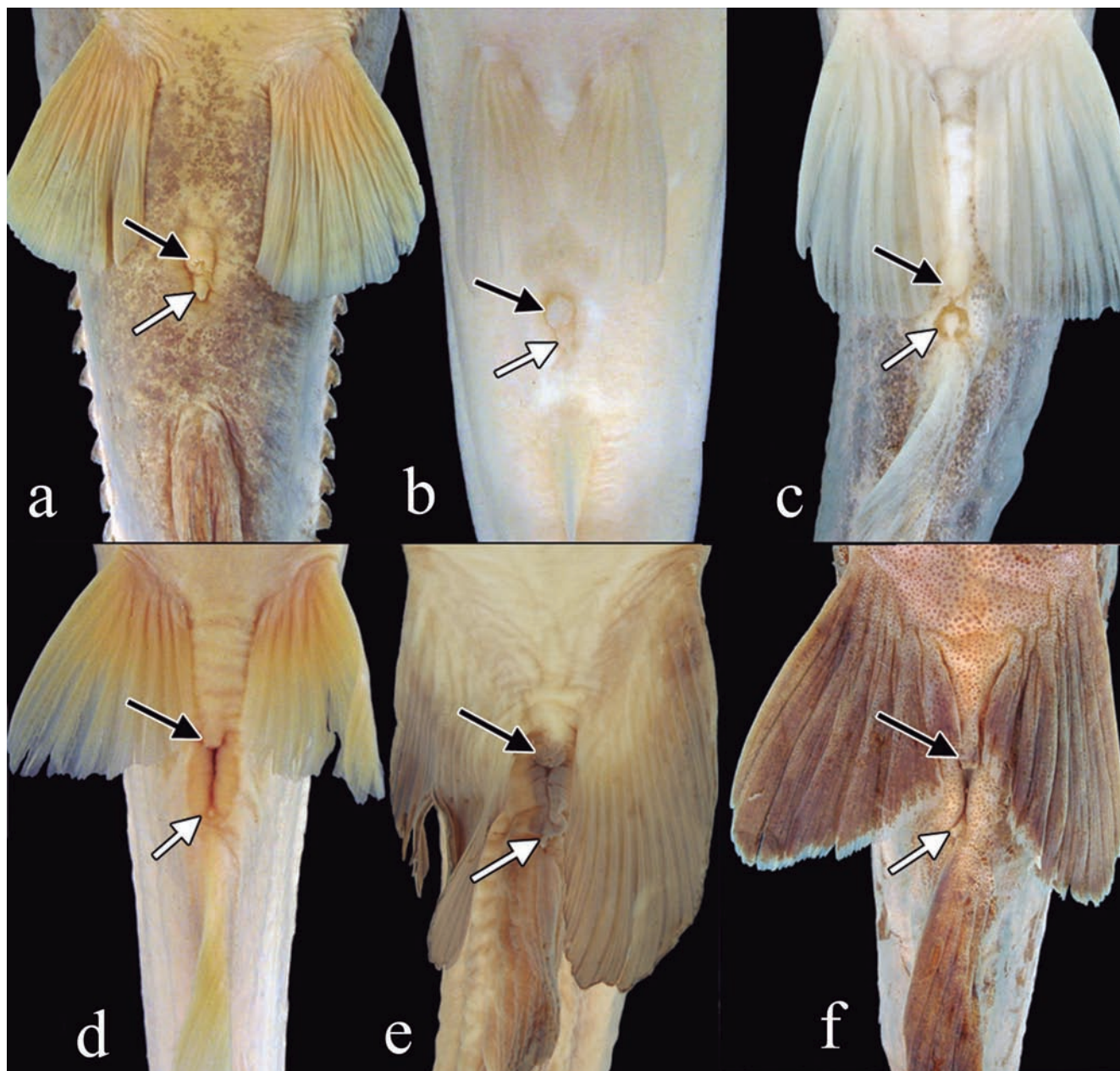


Fig. 19. Anal and urogenital opening in ventral view of females of (a) *Franciscodoras marmoratus*, MZUSP 95398, 190 mm SL; (b) *Centromochlus heckelii*, MZUSP 104793, 106 mm SL; (c) *Tatia intermedia*, MZUSP 104786, 102 mm SL; (d) *Pseudoauchenipterus affinis*, MZUSP 93092, 112 mm SL; (e) *Trachelyopterichthys taeniatus*, MZUSP 8496, 113 mm SL; (f) *Tetranematichthys wallacei*, MZUSP 85497, 191 mm SL. Black arrows indicate anal opening, white arrows indicate urogenital opening.

“X”, with paired anterior processes and a medial constriction (Fig. 20). The mesethmoid is also shaped as an “X” in the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, and *Pseudepapterus*, in Astrodoradinae and in the doradids *Acanthodoras*, *Agamyxis*, *Centrochir*, *Centrodoras*, *Franciscodoras*, *Megalodoras*, *Orinocodoras*, *Platydoras*, *Rhinodoras*, and *Rhynchodoras* (Figs. 22, 24, 30; Soares-Porto, 1998: fig. 5; Royero, 1999: #9, #10; Britto, 2002: #1; Akama, 2004: #30). However, the mesethmoid is wide and not medially constricted, resulting in a form similar to a square in the Aspredinidae, mochokids *Chiloglanis* and

Synodontis, all auchenipterids (except *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, and *Pseudepapterus*), and doradids *Doraops*, *Kalyptodoras*, *Lithodoras*, *Pterodoras*, and *Wertheimeria* (Figs. 21, 23, 28, 29, 31; Higuchi, 1992: #9; Vigliotta, 2008: #2; Sousa, 2010: #8). The mesethmoid is shaped as an arrow, medially dilated in all species of *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, *Tenellus*, and *Trachydoras* (Fig. 25-27; Higuchi, 1992: #11).

53. Length of mesethmoid: 0- relatively short, length less than

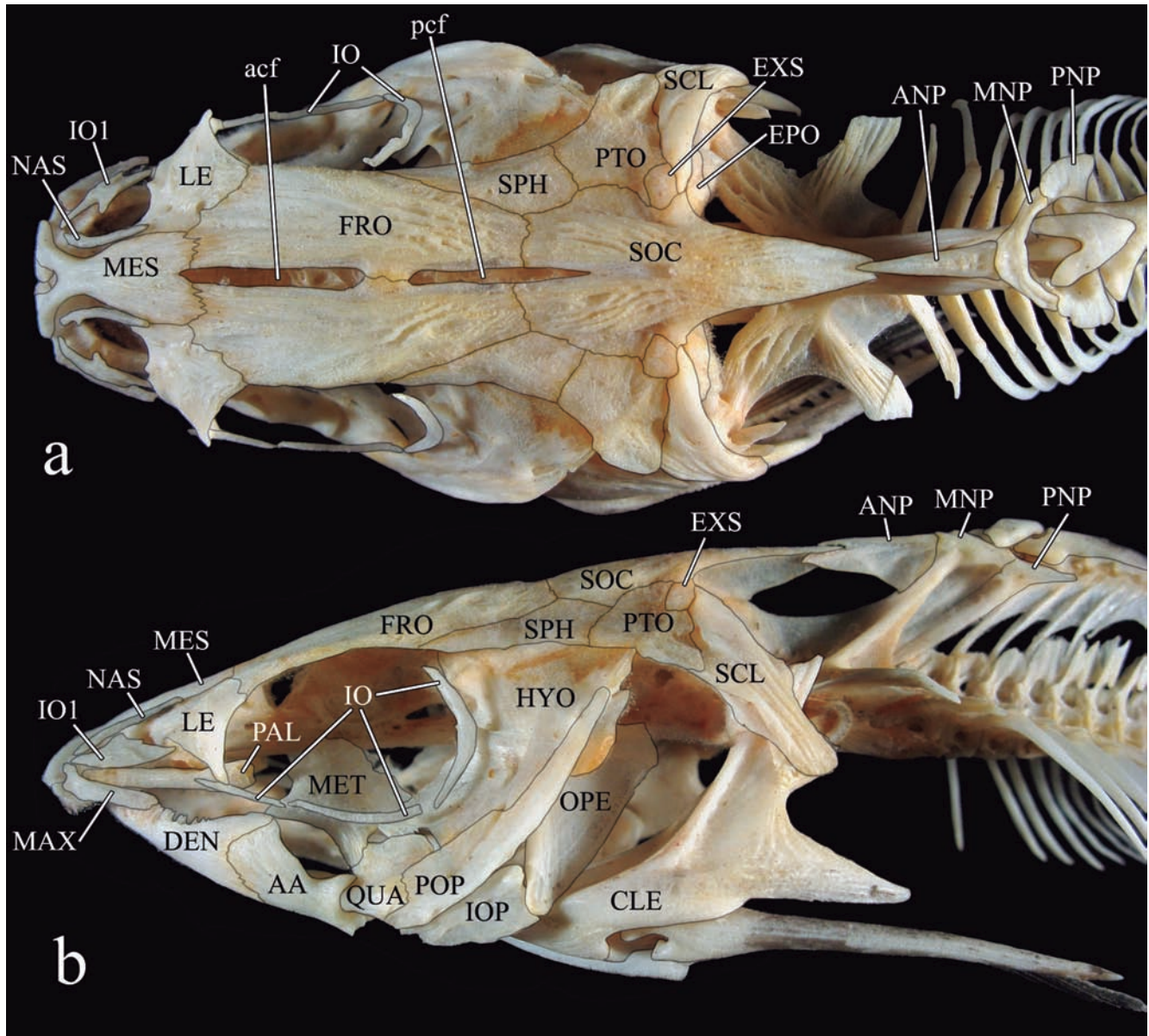


Fig. 20. Skeleton of head and anterior portion of body in *Ictalurus punctatus*, MZUSP 103256, 155 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, CLE cleithrum, DEN dentary, EPO epiotic, EXS extrascapular, FRO frontal, HYO hyomandibula, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, NAS nasal, OPE opercle, PAL autopalatine, pcf posterior cranial fontanel, PNP posterior nuchal plate, POP preopercle, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic.

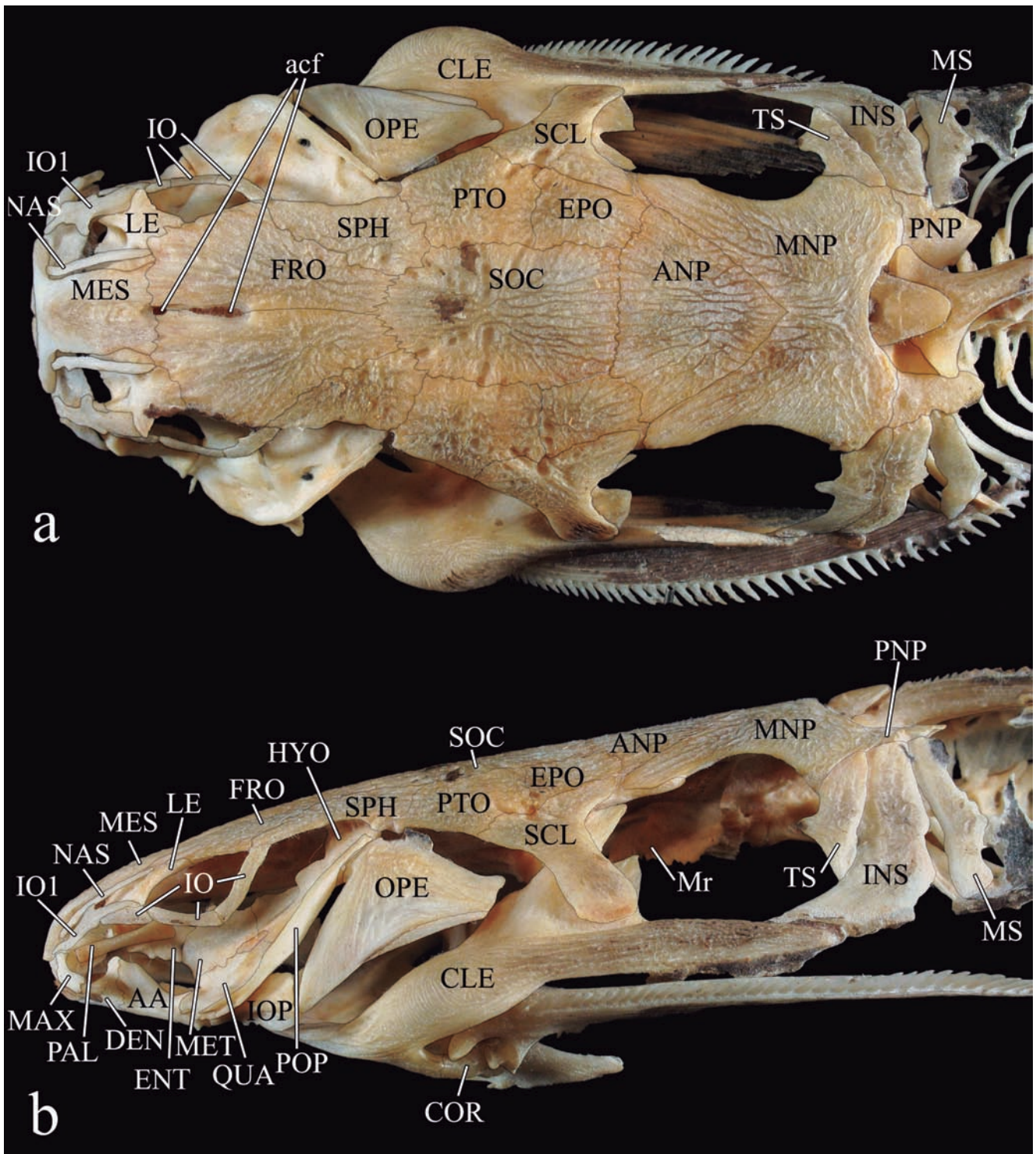


Fig. 21. Head and anterior portion of body in *Wertheimeria maculata*, MZUSP 93659, 217 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, CLE cleithrum, COR coracoid, DEN dentary, ENT entopterygoid, EPO epiotic, FRO frontal, HYO hyomandibula, INS infranuchal scute, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, Mr Müllerian ramus, MS (postinfranuchal) midlateral scutes, NAS nasal, OPE opercle, PAL autopalatine, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic, TS tympanic scutes.

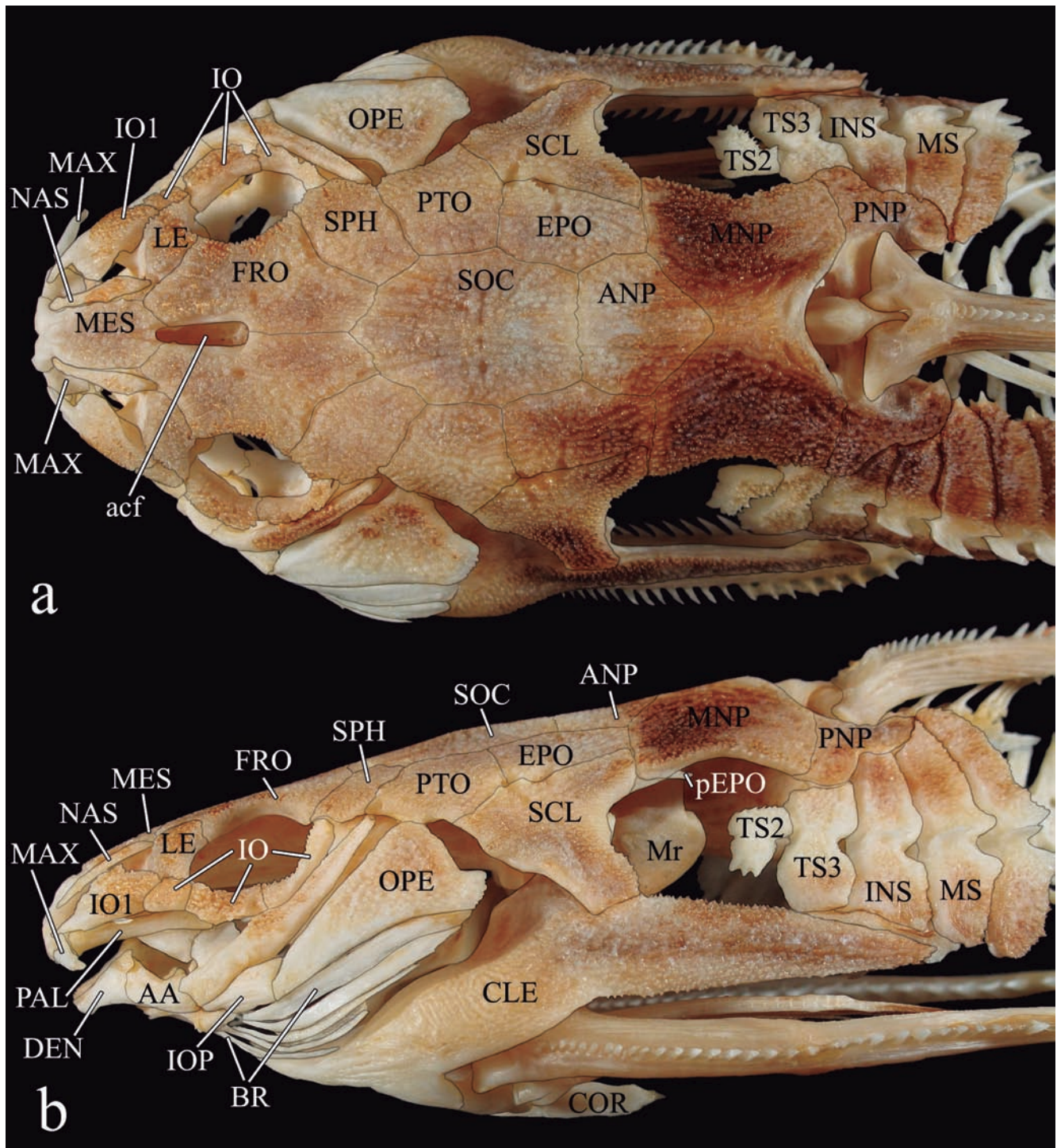


Fig. 22. Head and anterior portion of body in *Platydoros armatulus*, MZUSP 91686, 151.7 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, BR branchiostegal rays, CLE cleithrum, COR coracoid, DEN dentary, ENT entopterygoid, EPO epiotic, FRO frontal, INS infranuchal scute, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MNP middle nuchal plate, Mr Müllerian ramus, MS (postinfranuchal) midlateral scutes, NAS nasal, OPE opercle, PAL autopalatine, pEPO epiotic process, PNP posterior nuchal plate, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic, TS tympanic scutes.

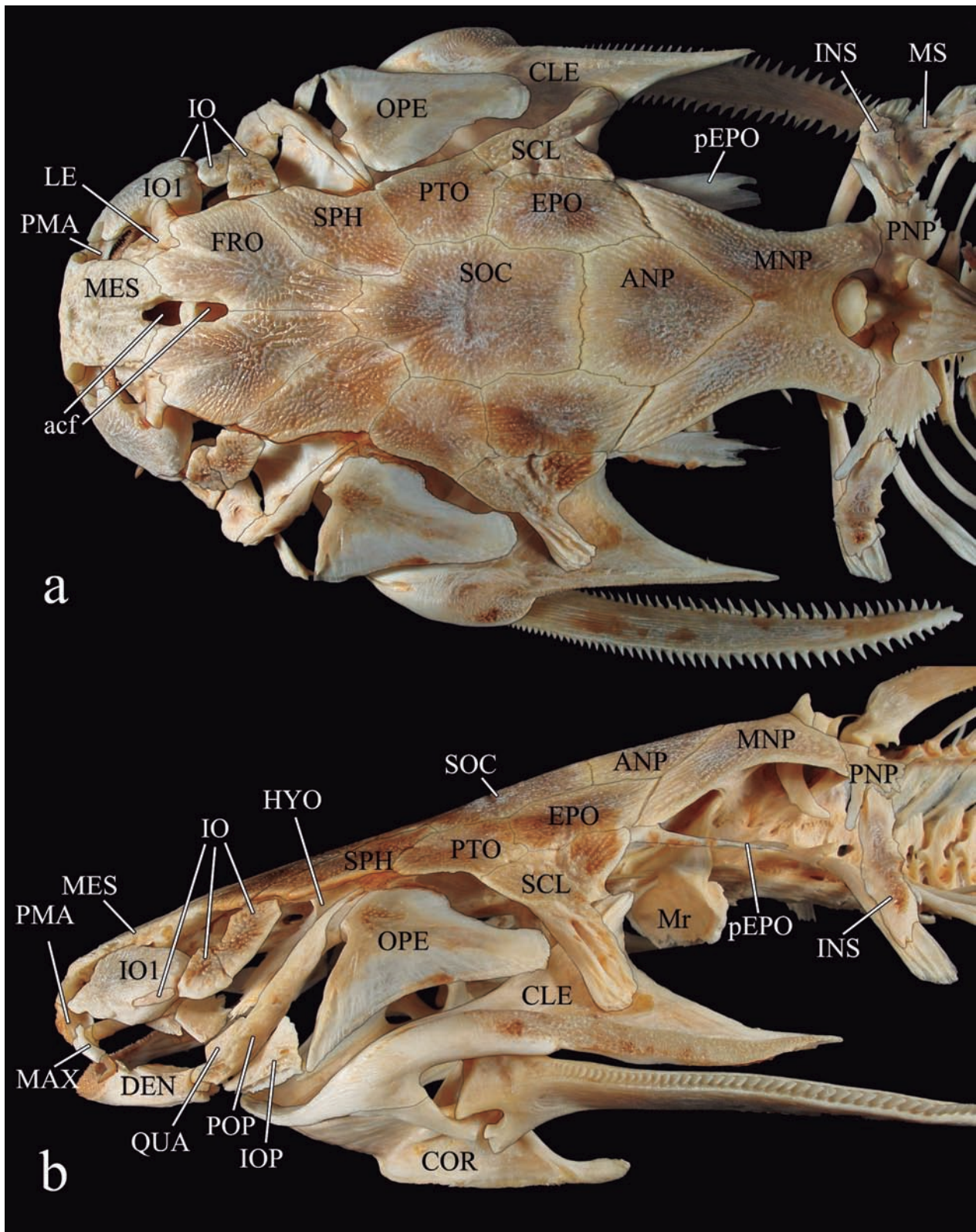


Fig. 23. Head and anterior portion of body in *Pterodoras granulosus*, MZUSP 91665, 410 mm SL, in dorsal (a) and lateral (b) views. acf anterior cranial fontanel, ANP anterior nuchal plate, CLE cleithrum, COR coracoid, DEN dentary, ENT entopterygoid, EPO epiotic, FRO frontal, HYO hyomandibula, INS infranuchal scute, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MNP middle nuchal plate, Mr Müllerian ramus, MS (postinfranuchal) midlateral scutes, OPE opercle, pEPO epiotic process, PMA premaxilla, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic.

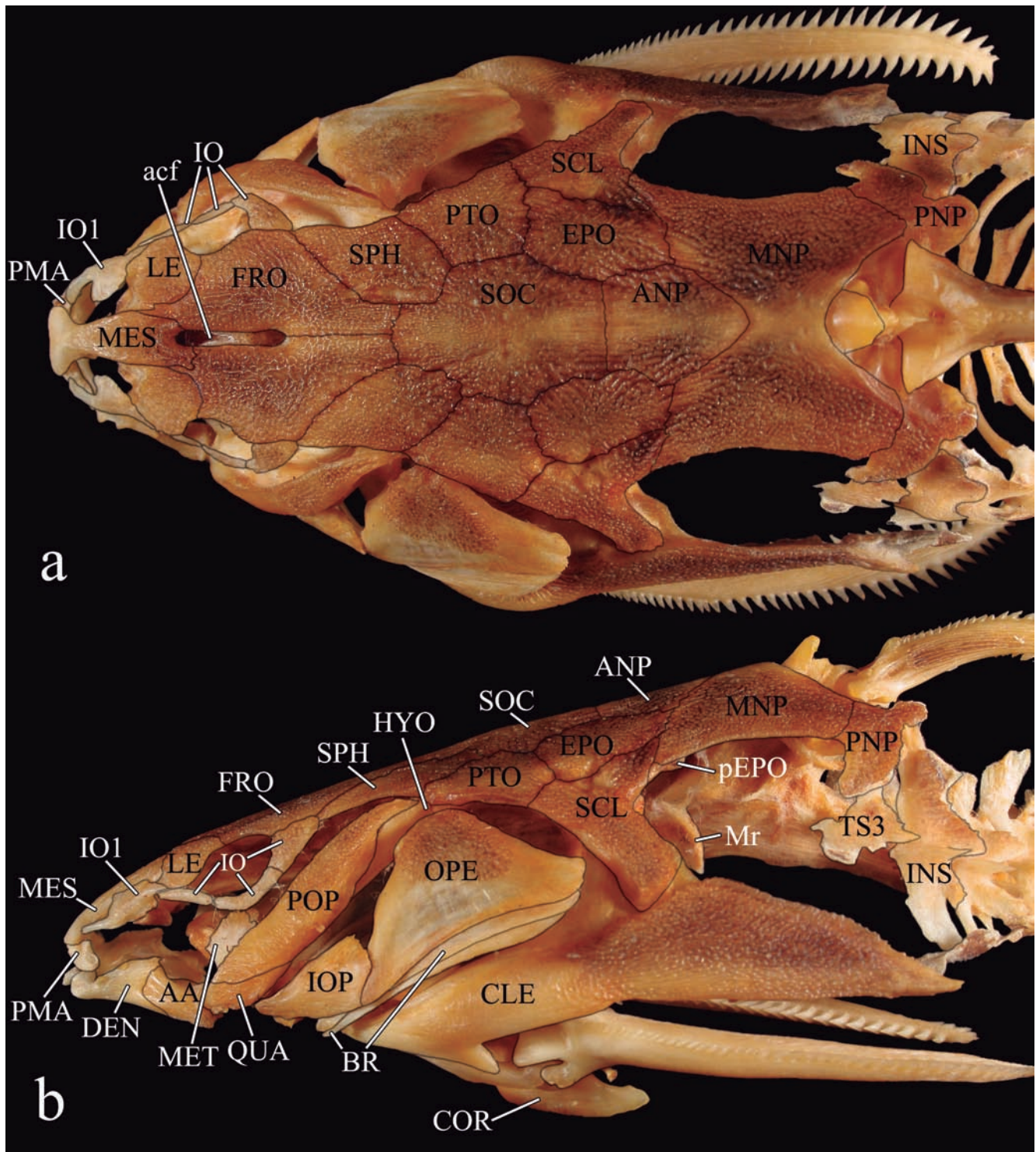


Fig. 24. Head and anterior portion of body in *Orinocodoras eigenmanni*, FMNH 105276, 193 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, BR branchiostegal rays, CLE cleithrum, COR coracoid, DEN dentary, EPO epiotic, FRO frontal, HYO hyomandibula, INS infranuchal scute, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, Mr Müllerian ramus, OPE opercle, PAL autopalatine, pEPO epiotic process, PMA premaxilla, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic, TS tympanic scutes.

three times width; 1- relatively elongate, length greater than three times width (CI 1.0, RI 1.0).

The mesethmoid is relatively elongate, with length greater than three times its width, in the doradids *Anduzedoras*, *Doras*,

Hassar, *Hemidoras*, *Leptodoras*, *Nemadoras*, and *Tenellus* (Fig. 27; Higuchi, 1992: #13). The mesethmoid is relatively short, length less than three times its width, in all other examined species (Figs. 20-26, 28-31).

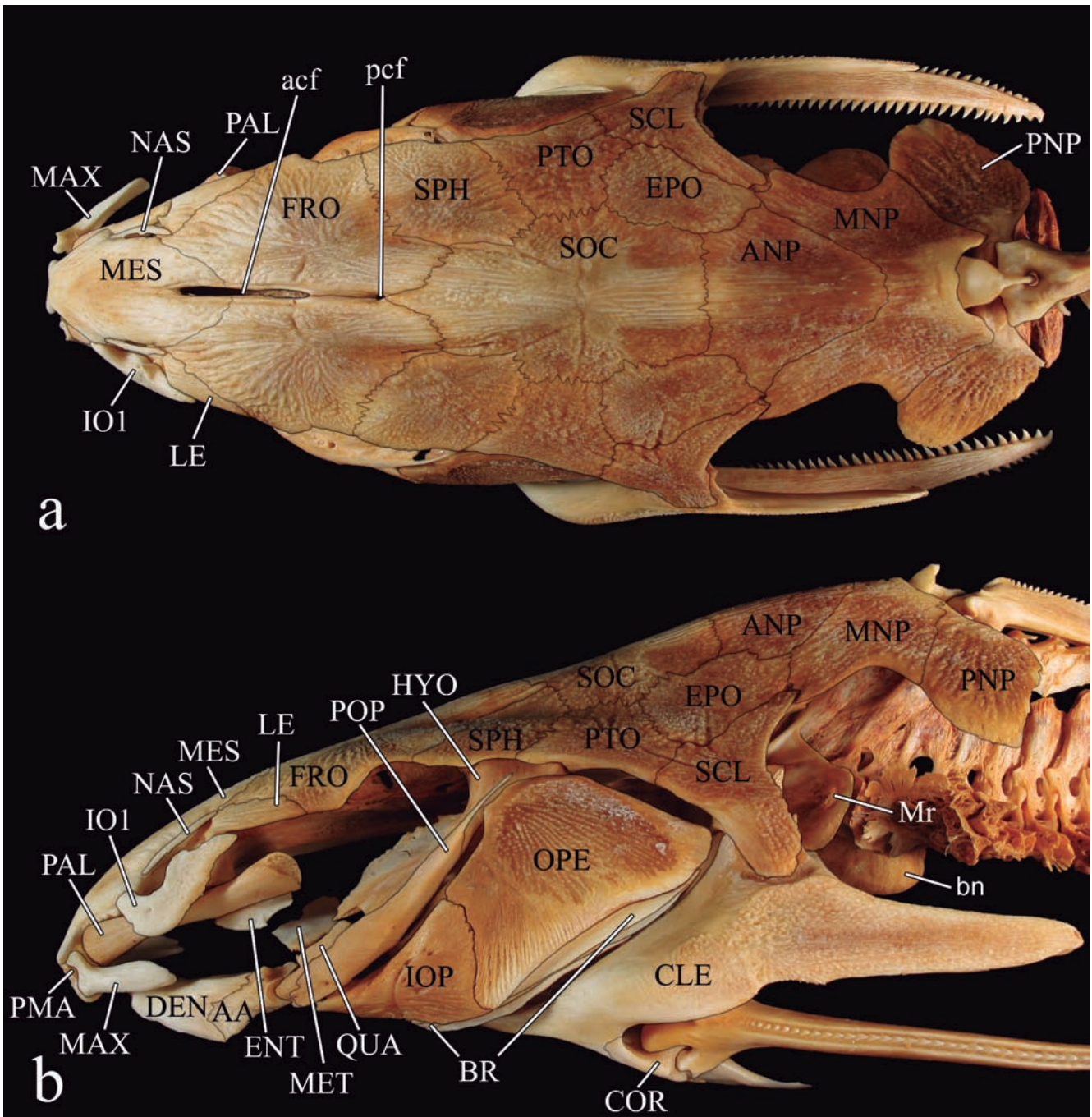


Fig. 25. Head and anterior portion of body in *Oxydoras niger*, MZUSP 91654, 555 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, BR branchiostegal rays, bn bony nodule, CLE cleithrum, COR coracoid, DEN dentary, ENT entopterygoid, EPO epiotic, FRO frontal, HYO hyomandibula, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, Mr Müllerian ramus, NAS nasal, no bony nodule, OPE opercle, PAL autopalatine, pcf posterior cranial fontanel, PMA premaxilla, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic, TS tympanic scutes.

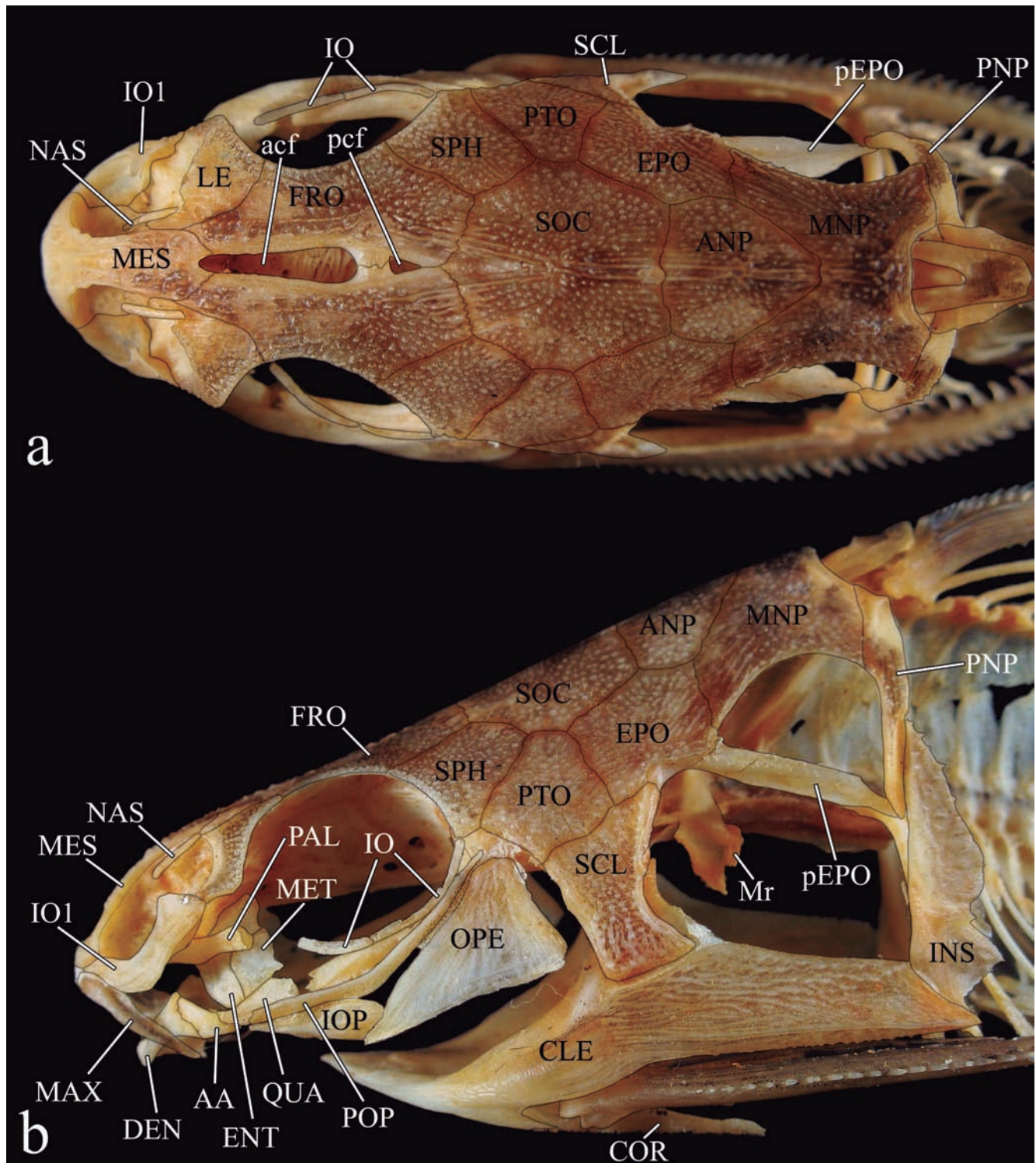


Fig. 26. Head and anterior portion of body in *Trachydoras brevis*, MZUSP 103087, 75 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, CLE cleithrum, COR coracoid, DEN dentary, ENT entopterygoid, EPO epiotic, FRO frontal, INS infranuchal scute, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, Mr Müllerian ramus, NAS nasal, OPE opercle, PAL autopalatine, pcf posterior cranial fontanel, pEPO epiotic process, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic.

54. Anterior portion of mesethmoid: 0- covered by a thin layer of skin, continuous with remaining mesethmoid; 1- covered by a thick layer of skin, distinguished from remaining mesethmoid by a distinct step (CI 0.250, RI 0.5).

In most catfishes, a thin layer of skin covers the anterior and posterior portions of the mesethmoid (Figs. 20-28, 30-31). However, in the doradids *Trachydoras steindachneri*, and auchenipterids *Liosomadoras*, *Trachelyopterus*,

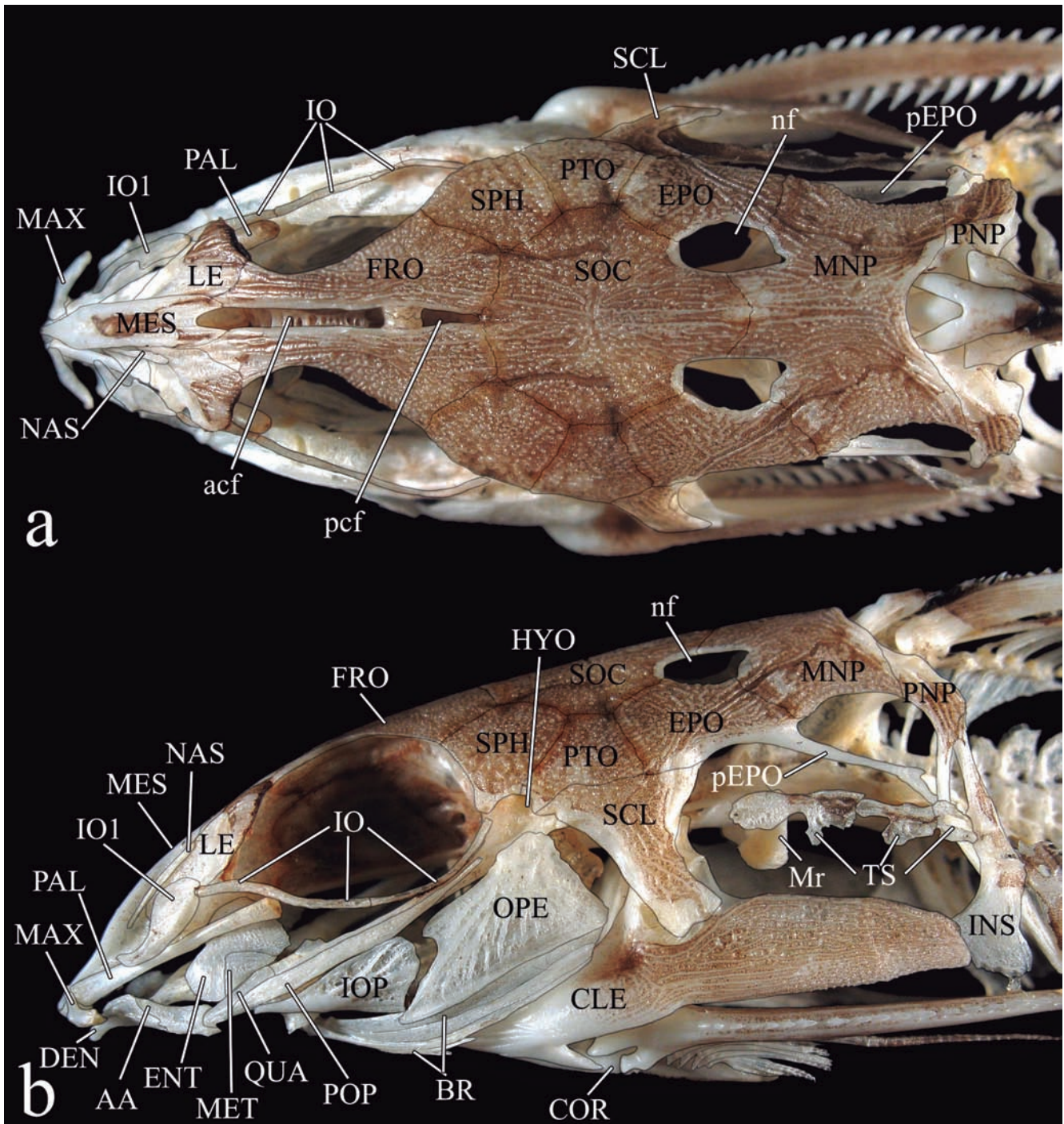


Fig. 27. Head and anterior portion of body in *Tenellus ternetzi*, MZUSP 103246, 94 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, BR branchiostegal rays, CLE cleithrum, COR coracoid, DEN dentary, ENT entopterygoid, EPO epiotic, FRO frontal, HYO hyomandibula, INS infranuchal scute, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, Mr Müllerian ramus, NAS nasal, nf nuchal foramen, OPE opercle, PAL autopalatine, pcf posterior cranial fontanel, pEPO epiotic process, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic, TS tympanic scutes.

Trachelyopterichthys, *Trachycorystes*, and *Spinipterus* (latter based on Akama & Ferraris, 2011: fig. 3), the anterior portion of the mesethmoid is covered by a thick layer of skin and distinct from the posterior region, which is covered by a thin layer of skin (Fig. 29; Higuchi, 1992: #12).

55. Anteroventral keel of mesethmoid (ordered): 0- absent; 1-

present, not distinctly developed into a ventral process; 2- present, distinctly developed into a distinct ventral process (CI 1.0, RI 1.0).

The anteroventral portion of the mesethmoid in most catfishes is ventrally flattened. However, in the species of *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, *Tenellus*, and

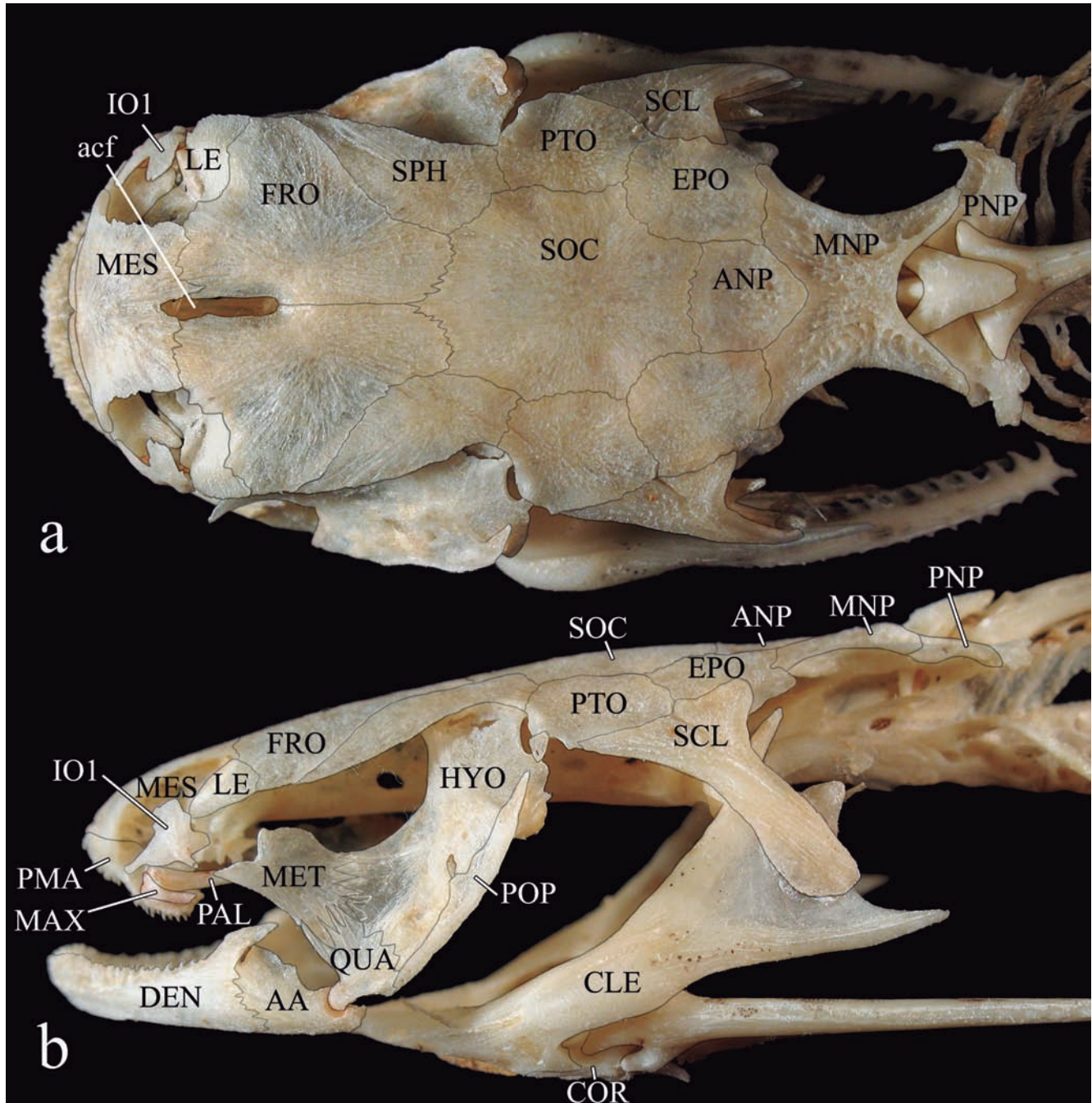


Fig. 28. Head and anterior portion of body in *Glanidium melanopterum*, MZUSP 64256, 112 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, CLE cleithrum, COR coracoid, DEN dentary, EPO epiotic, FRO frontal, HYO hyomandibula, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, PAL autopalatine, PMA premaxilla, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic.

Trachydoras there is an anteroventral keel on the mesethmoid to which are connected the reduced premaxillae (Fig. 32a). Furthermore, in the doradid *Trachydoras* this keel is developed into a distinct ventral process (Fig. 32b).

56. Shape of anterior cranial fontanel: 0- elongate; 1- rounded (CI 0.25, RI 0.0).

The anterior cranial fontanel of most catfishes is present as a large rounded opening in larvae and small juveniles, and

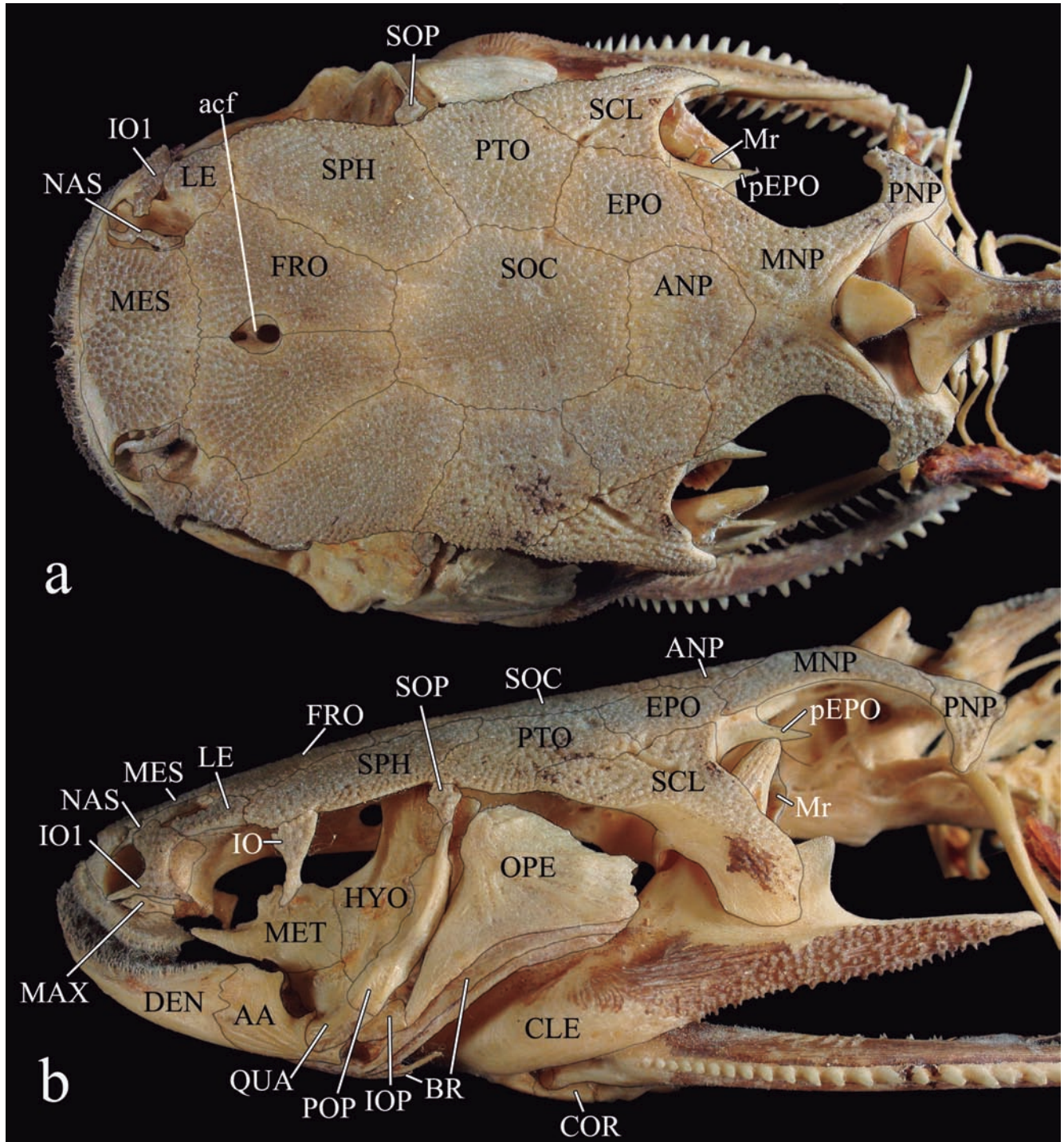


Fig. 29. Head and anterior portion of body in *Trachycorystes trachycorystes*, MZUSP 104547, 180 mm SL, in dorsal (a) and lateral (b) views. AA anguloarticular, acf anterior cranial fontanel, ANP anterior nuchal plate, BR branchiostegal rays, CLE cleithrum, COR coracoid, DEN dentary, EPO epiotic, FRO frontal, HYO hyomandibula, IO infraorbital, IOP interopercle, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, Mr Müllerian ramus, NAS nasal, OPE opercle, pEPO epiotic process, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic.

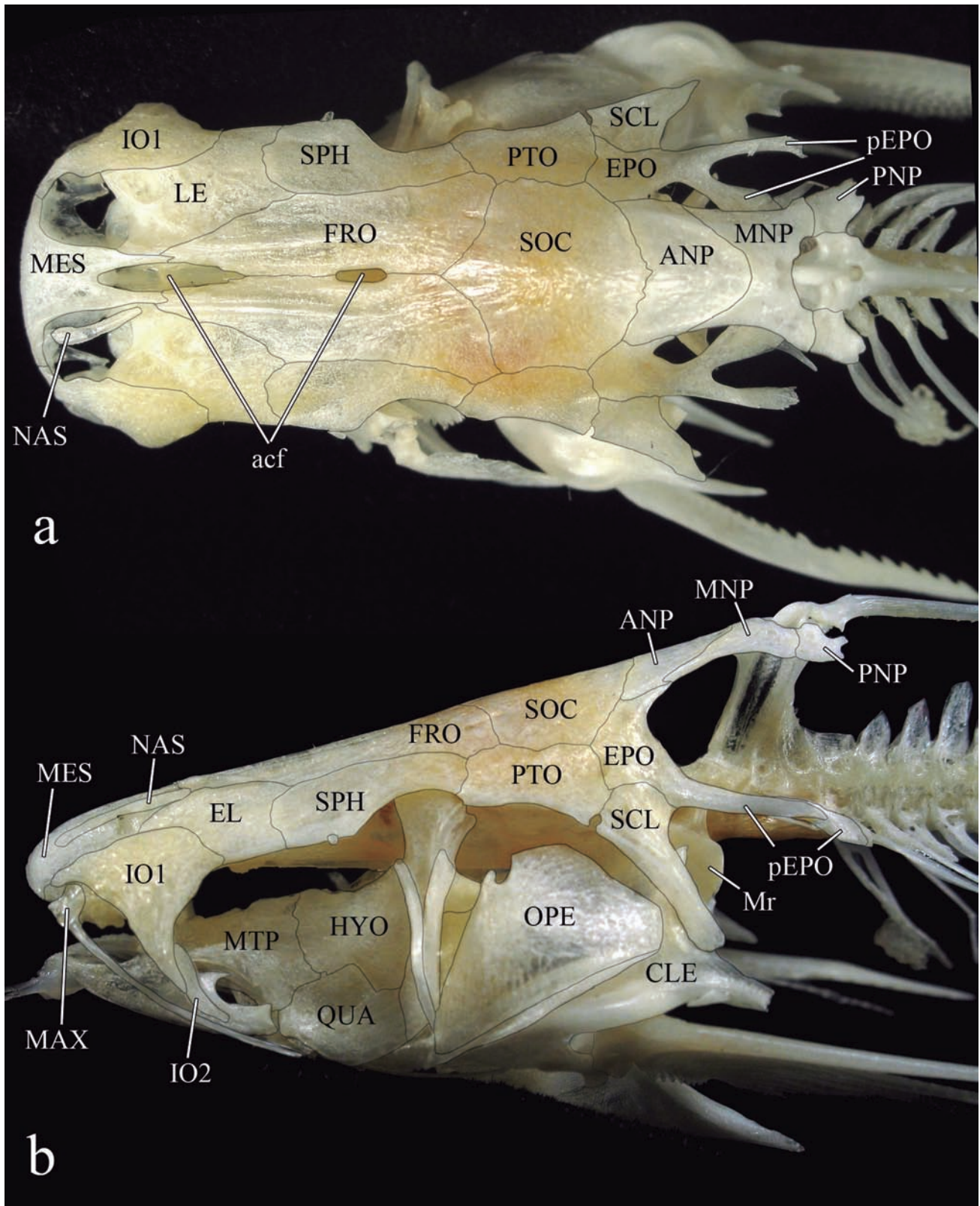


Fig. 30. Head and anterior portion of body in *Auchenipterus nuchalis*, MZUSP 97375, 120 mm SL, in dorsal (a) and lateral (b) views. acf anterior cranial fontanel, ANP anterior nuchal plate, CLE cleithrum, EPO epiotic, FRO frontal, HYO hyomandibula, IO infraorbital, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, Mr Müllerian ramus, NAS nasal, OPE opercle, pcf posterior cranial fontanel, pEPO epiotic process, PNP posterior nuchal plate, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic.

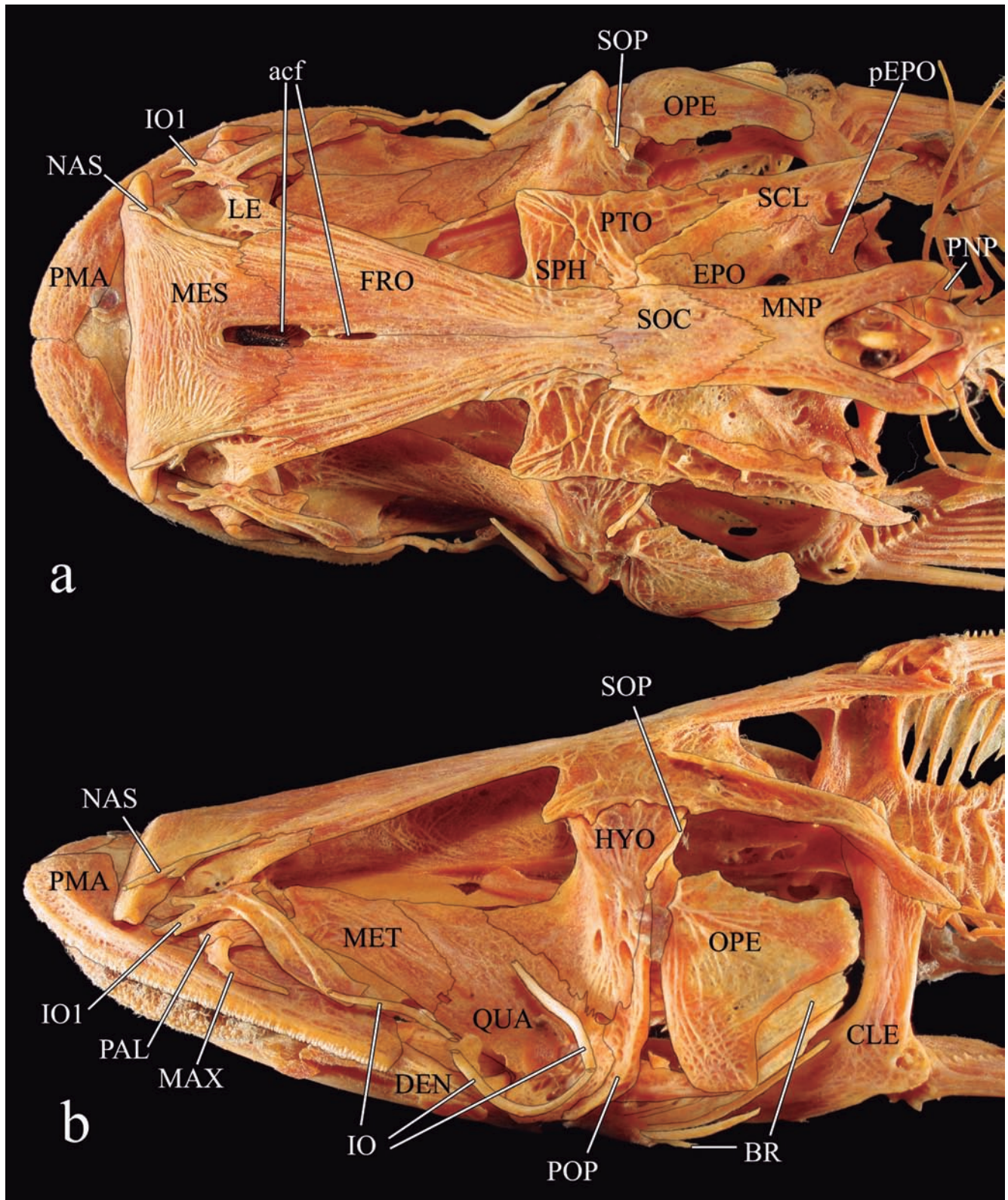


Fig. 31. Head and anterior portion of body in *Ageneiosus inermis*, MZUSP 91661, 320 mm SL, in dorsal (a) and lateral (b) views. acf anterior cranial fontanel, BR branchiostegal rays, CLE cleithrum, DEN dentary, EPO epiotic, FRO frontal, HYO hyomandibula, IO infraorbital, LE lateral ethmoid, MAX maxilla, MES mesethmoid, MET metapterygoid, MNP middle nuchal plate, NAS nasal, OPE opercle, PAL autopalatine, pEPO epiotic process, PMA premaxilla, PNP posterior nuchal plate, POP preopercle, PTO pterotic, QUA quadrate, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, SPH sphenotic.

becomes an elongate slit enclosed anteriorly by the mesethmoid and posteriorly by the frontals in large juveniles and adults (Figs. 20-31). However, in the Aspredinidae, auchenipterids *Trachelyichthys* and *Spinipterus* (Royero, 1999: #4; Akama & Ferraris, 2011), and the mochokid *Mochokus* the anterior cranial fontanel is a relatively large round opening in the adults. That feature is probably pedomorphic in those taxa. The fontanel was described as absent in *Gelanoglanis stroudi* (Ferraris, 1988: #N6; Soares-Porto, 1998; Soares-Porto *et al.*, 1999) for specimens of 23.9-24.6 mm SL. However, in the only cleared and stained specimen herein examined and tentatively identified as conspecific to *G. stroudi*, a round opening is present between the frontals.

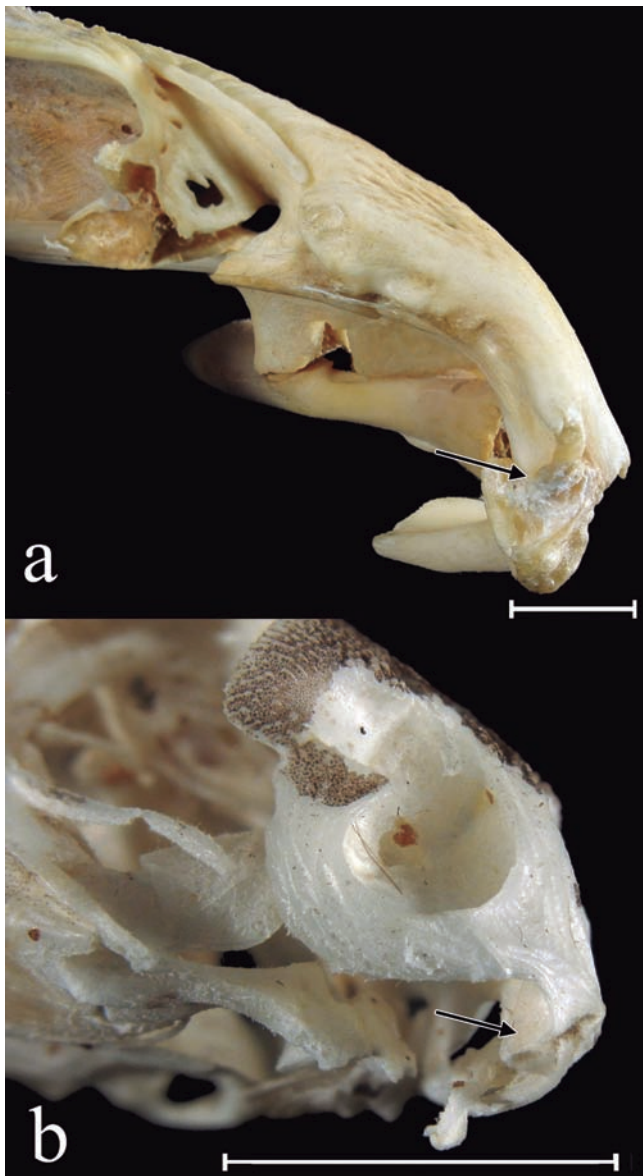


Fig. 32. Anterior portion of head in ventrolateral view of (a) *Oxydoras niger*, MZUSP 91654, 555.0 mm SL; (b) *Trachydoras brevis*, MZUSP 103087, 74 mm SL. Arrows indicate anteroventral keel of mesethmoid. Scale bars equal 10 mm.

These conflicting observations may be due to the different sizes of the specimens examined. This character is coded as missing data for *Gelanoglanis*, considering that the anterior cranial fontanel is absent in adults.

57. Anterior cranial fontanel (unordered): 0- undivided; 1- divided into two openings separated by a narrow bridge between frontals; 2- divided into two openings separated by a wide bridge between frontals (CI 0.25, RI 0.4).

In most examined taxa, the anterior cranial fontanel is a single continuous opening (Figs 20, 22, 24-28). However, in the auchenipterids *Ageneiosus inermis*, *Auchenipterichthys*, *Liosomadoras*, *Tetranematichthys*, *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus*, *Trachycorystes* and some specimens of *Centromochlus*, and *Tatia* (Figs. 29, 31; Royero, 1999: #3; Akama, 2004: #12, #13, #14), and doradids *Agamyxis*, *Anadoras*, and some specimens of *Acanthodoras*, *Kalyptodoras*, *Platydoras*, *Pterodoras granulosus*, and *Wertheimeria*, the anterior cranial fontanel is divided into two openings by a thin bridge between frontals (Figs. 21, 23; Eigenmann, 1925: 284; Higuchi, 1992: #10, #A19; Sousa, 2010: #14). In the auchenipterid *Auchenipterus*, the anterior cranial fontanel is divided into two openings by a wide bridge between frontals (Fig. 30). This character was coded as polymorphic (0,1) for the auchenipterids *Tatia* and *Centromochlus*, and doradids *Acanthodoras*, *Kalyptodoras*, *Platydoras armatulus*, *Pterodoras granulosus*, and *Wertheimeria*.

58. Posterior cranial fontanel (ordered): 0- large; 1- reduced to a small opening; 2- completely occluded (CI 0.125, RI 0.75).

Among examined species, the posterior cranial fontanel is large in the Amphiliidae, ariid *Galeichthys*, Aspredinidae, Claroteidae, Diplomystidae, Ictaluridae (Lundberg, 1970: #16), Nematogenyidae, Pangasiidae, Siluridae, and doradids *Anduzedoras*, *Hassar*, *Leptodoras*, *Nemadoras hemipeltis*, *Tenellus*, and *Trachydoras* (Higuchi, 1992: #17) (Figs. 20, 26, 27; Higuchi, 1992: #31). The ariid *Genidens* (Marceniuk *et al.*, 2012: #27), mochokid *Mochokus* (Vigliotta, 2008: 6), and doradids *Nemadoras elongatus*, *N. humeralis* and *Oxydoras* have the posterior fontanel reduced to a small opening (Fig. 25). The posterior cranial fontanel is completely occluded in the Auchenipteridae, Erethistidae, Heptapteridae, Malapteruridae, Pimelodidae, Pseudopimelodidae, Sisoridae, mochokid *Chiloglanis disneyi* (Vigliotta, 2008: #6), and remaining species of Doradidae (Figs. 21-24, 28-31).

59. Dorsal face of lateral ethmoid: 0- not participating in cephalic shield; 1- participating in cephalic shield (CI 0.143, RI 0.25).

The lateral ethmoid, a paired bone of the cranium, does not participate in the cephalic shield in most catfishes. However, in several species of the Amphiliidae, Ariidae, Aspredinidae, Claroteidae, Erethistidae, Ictaluridae, Mochokidae, Pimelodidae, Siluridae, and Sisoridae, the dorsal face of the lateral ethmoid participates in the cephalic shield

(Figs. 20-31; Alexander, 1965: 97). The same condition is present in all species of the Doradidae and of Auchenipteridae, except *Centromochlus heckelii*, *Pseudauchenipterus* and *Pseudotatia* (among examined species). Higuchi (1992: #15) considered the dorsal face of the lateral ethmoid excluded from the cephalic shield in the doradid *Wertheimeria*, an observation not corroborated herein (Fig. 21). Similarly, the specimen of the auchenipterid *Gelanoglanis stroudi* illustrated in Soares-Porto (1998) does not have the lateral ethmoid participating in the cephalic shield. However, the specimen of *Gelanoglanis* examined herein has the lateral ethmoid partially participating in the cephalic shield; this character was coded as 1 for *Gelanoglanis*.

60. Fenestra between lateral ethmoid and frontal: 0- absent; 1- present (CI 0.2, RI 0.714).

Among examined taxa, there is a fenestra between the lateral ethmoid and frontal only in the Amphiliidae, Ariidae (Marceniuk *et al.*, 2012: #3), Claroteidae, Diplomystidae, Heptapteridae, Ictaluridae, Mochokidae, Pangasiidae, Pimelodidae, Siluridae (de Pinna, 1993: #68; Britto, 2002: #6), and the auchenipterid *Pseudauchenipterus*. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

61. Spines on lateral border of lateral ethmoid: 0- absent; 1- present (CI 0.5, RI 0.0).

The lateral border of the lateral ethmoid is smooth or granulated in most catfishes. However, the doradids *Agamyxis*, *Scorpiodoras* and some specimens of *Acanthodoras* have spines on the lateral border of the lateral ethmoid (Higuchi, 1992: #14, #A15; Sousa, 2010: #16; Sousa & Birindelli, 2011). This character was coded as polymorphic for *Acanthodoras*.

62. Lateral process of sphenotic: 0- absent; 1- present (CI 0.25, RI 0.833).

Among examined species, the sphenotic has a distinct lateral process only in the Amphiliidae, Malapteruridae, auchenipterids *Ageneiosus* and *Tetranematichthys*, and doradids *Anduzedoras*, *Doras*, *Hassar*, *Leptodoras*, and *Tenellus* (Figs. 27, 31; Royero, 1999: #12; Akama, 2004: #31).

63. Lateroposterior border of sphenotic: 0- slightly concave, not exposing part of the articulation between hyomandibula and sphenotic; 1- distinctly concave, exposing part of the articulation between hyomandibula and sphenotic (CI 0.5, RI 0.857).

In the auchenipterids *Ageneiosus*, *Auchenipterus*, *Glanidium*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, and *Tetranematichthys*, the lateroposterior border of the sphenotic is distinctly concave, exposing part of the articulation between sphenotic and hyomandibula (Figs. 28, 30, 31; Royero, 1999: #20; Akama, 2004: #34), whereas it is only slightly concave in other examined species (Figs. 20-27, 29).

64. Frontal: 0- participating in orbital margin; 1- not participating in orbital margin (CI 0.333, RI 0.778).

The orbital margin is formed by the lateral ethmoid, sphenotic and infraorbitals in the auchenipterids *Asterophysus*, *Auchenipterichthys*, *Auchenipterus*, *Epapterus*, *Liosomadoras*, *Pseudepapterus*, *Trachelyopterichthys*, *Trachelyopterus*, and *Trachycorystus* (Figs. 29, 30; Britski, 1972: 13; Ferraris, 1988: #N8; Higuchi, 1992: #A21, #34; Royero, 1999: #1; Britto, 2002: #5; Akama, 2004: #17), whereas it is formed by the frontal, lateral ethmoid, infraorbitals, and sphenotic in other catfishes (Figs. 20-28, 31).

65. Lateral ethmoid: 0- participating in orbital margin; 1- not participating in orbital margin (CI 1.0, RI 1.0).

In the doradid *Oxydoras*, the orbit is displaced posteriorly, and formed by the frontals, sphenotic and infraorbitals (Fig. 25; Alexander, 1965; Higuchi, 1992: #A21, #A34). In all other examined species, the lateral ethmoid participates in the orbital taxa (Figs. 20-31).

66. Ventral process of pterotic: 0- absent; 1- present (CI 0.5, RI 0.0).

The pterotic in mochokids *Mochokiella*, *Microsynodontis*, and *Synodontis* possesses a distinct ventral process (Vigliotta, 2008: #11), which is absent in other examined taxa (Figs. 20-31).

67. Fenestra between parietal-supraoccipital, pterotic, and sphenotic: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, the auchenipterid *Pseudepapterus* is the only one with a fenestra between the parietal-supraoccipital, pterotic, and sphenotic.

68. Posterior process of parietal-supraoccipital: 0- present; 1- absent (CI 1.0, RI 1.0).

The posterior process of the parietal-supraoccipital is present in most catfishes (Fig. 20). However, it is absent in the Auchenipteridae, Doradidae, and Mochokidae (Figs. 21-31; Royero, 1999: #22). The Malapteruridae have the posterior process of the parietal-supraoccipital present but truncate. Diogo (2004: #131) considered the posterior process of parietal-supraoccipital to be absent in the Malapteruridae; and this shared absence to be a putative synapomorphy of a monophyletic clade comprising the Auchenipteridae, Doradidae, Malapteruridae, and Mochokidae.

69. Sphenotic and parietal-supraoccipital: 0- in contact; 1- not in contact (CI 0.333, RI 0.0).

In the auchenipterids *Auchenipterus* and *Epapterus* the frontal is extended posteriorly, reaching the pterotic, and leaving the sphenotic and parietal-supraoccipital separate (Fig. 30; Chardon, 1968; Britski, 1972: 13; Ferraris, 1988: #N10; Royero, 1999: #2, #18; Akama, 2004: #19, #26). The same condition is present in the Malapteruridae (Mo, 1991; Britto, 2002: #7; Diogo, 2004: #97; de Pinna *et al.*, 2007: #34). In all

other examined species, the posteromedial margin of the sphenotic contacts the parietal-supraoccipital (Figs. 20-29, 31).

70. Accessory dermal ossification between frontal, sphenotic and parietal-supraoccipital: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, only the auchenipterid *Entomocorus* has an accessory dermal ossification between the frontal, sphenotic and parietal-supraoccipital (Britski, 1972: 14; Ferraris, 1988: #N13; Akama, 2004: #22). This character was coded as missing data for the auchenipterid *Spinipterus*.

71. Accessory dermal ossification between sphenotic, pterotic, and parietal-supraoccipital: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, only the auchenipterid *Asterophysus* has an accessory dermal ossification between the sphenotic, pterotic and parietal-supraoccipital (Britski, 1972: 14; Ferraris, 1988: #N14; Akama, 2004: #21). This character was coded as missing data for the auchenipterid *Spinipterus*.

72. Vomer: 0- present; 1- absent (CI and RI inapplicable).

The vomer is present on the ventral face of the cranium in most catfishes (Fig. 33). However, in the examined specimen of the auchenipterid *Gelanoglanis* the vomer is absent, corroborating the observation of Ferraris (1988: #N11), a condition not mentioned in Soares-Porto (1998) and Soares-Porto *et al.* (1999). This character was coded as missing data for the auchenipterid *Spinipterus*.

73. Shape of vomer: 0- shaped as a “T”, with distinct anterior processes; 1- shaped as an “I”, with rudimentary anterior processes (CI 0.25, RI 0.914).

Most catfishes have a T-shaped vomer with distinct anterior processes (Fig. 33a; Lundberg, 1970). However, the vomer is shaped as an “I”, with rudimentary lateral processes anteriorly in the Diplomystidae (Arratia, 1992: #50), Malapteruridae, Nematogenyidae, species of *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras* (Higuchi, 1992: #14), and auchenipterids *Ageneiosus* and *Tetranematichthys* (Fig. 33b; Britski, 1972: 23; Ferraris, 1988: #N18; Walsh, 1990: #3; Akama, 2004: #24). Soares-Porto (1998: #11) described the vomer as I-shaped in two species of *Centromochlus* not included in the present study. This character was coded as inapplicable for the auchenipterid *Gelanoglanis*, which lacks the vomer; and as missing data for the auchenipterid *Spinipterus*.

74. Vomerian teeth: 0- absent; 1- present (CI 0.25, RI 0.4).

Some catfishes, including the Diplomystidae, Claroteidae, Pangasiidae, Pimelodidae, Siluridae, and ariid *Galeichthys*, have vomerian teeth (Lundberg, 1970; de Pinna, 1993: #60; Britto, 2002: #31; de Pinna *et al.*, 2007: #37; Marceniuk *et al.*, 2012: #53). Although specimens of Auchenipteridae and

Doradoidea herein examined lack this feature, Mees (1974: 66) mentioned their presence in *Tatia intermedia*, Royero (1999: #32) mentioned it in an undescribed species of *Tatia*, Akama (2004: #52) in *Asterophysus*, and Sarmiento-Soares & Martins-Pinheiro (2008: 519) reported it in *Tatia gyrina* and *T. intermedia*. This character was coded as inapplicable for the auchenipterid *Gelanoglanis*, which lacks the vomer; as missing data for the auchenipterid *Spinipterus*, and as polymorphic for the auchenipterid *Tatia intermedia*.

75. Accessory tooth plate on vomer: 0- absent; 1- present (CI 0.5, RI 0.667).

In the Ariidae, Claroteidae, †Hypsidoridae, Pangasiidae and Schilbeidae, there is an accessory tooth plate associated with the vomer (Ferraris, 1988: #J10; de Pinna, 1993: #72; Royero, 1999: #32; Britto, 2002: #32; Akama, 2004: #52; Marceniuk *et al.*, 2012: #56). That plate is absent in other examined taxa (Fig. 33). This character was coded as missing data for the auchenipterid *Spinipterus*.

76. Lateroventral extension of orbitosphenoid: 0- absent; 1- present (CI 0.5, RI 0.0).

In the auchenipterids *Auchenipterus* and *Pseudepapterus* there is a lateroventral extension of the orbitosphenoid (Royero, 1999: #42), which is absent in other examined taxa. This character was coded as missing data for auchenipterid *Spinipterus*.

77. Fenestra between frontal and orbitosphenoid: 0- absent; 1- present (CI 0.5, RI 0.8).

In the auchenipterids Centromochlinae, *Pseudauchenipterus* and *Pseudotatia* there is a fenestra between the frontal and orbitosphenoid (Akama, 1999; Royero, 1999: #45; Akama, 2004: #25). That fenestra is absent in other examined taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

78. Cranial ventral keel: 0- absent; 1- present (CI 0.2, RI 0.852).

Among examined species, the cranial ventral keel is well developed only in the auchenipterids *Auchenipterus* and *Centromochlus*, and doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Nemadoras*, *Scorpiodoras*, *Tenellus*, *Trachydoras*, and most basal species of *Leptodoras* (including *L. marki*, *L. oyakawai*, *L. praelongus*, excluding *L. juruensis*) (Fig. 33b; Ferraris, 1988: #N17; Akama, 2004: #23; Higuchi, 1992: #40; Sousa, 2010: #17).

79. Opening(s) for optic and trigeminofacial nerves: 0- single; 1- separate (CI 1.0, RI 1.0).

In most catfishes the optic and trigeminofacial nerves exit the cranium through separate openings. However, they exit the cranium through the same opening, which is enclosed by the orbitosphenoid, pterosphenoid, prootic and parasphenoid in the Diplomystidae and Nematogenyidae (Alexander, 1965: 95). This character was coded as missing data for the auchenipterid *Spinipterus*.

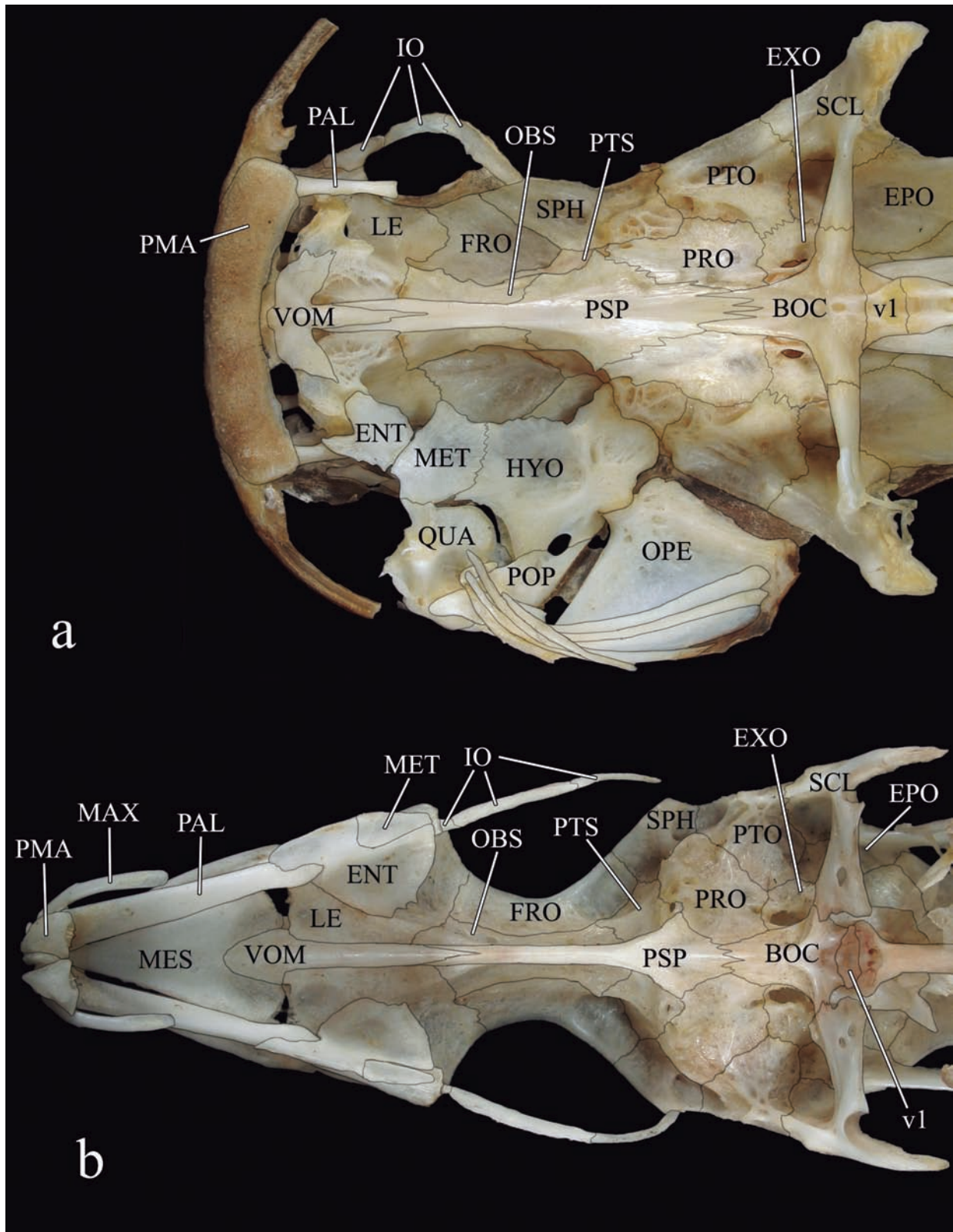


Fig. 33. Head in ventral view of (a) *Wertheimeria maculata*, MZUSP 93659, 270 mm SL; (b) *Doras higuchii*, MZUSP 101693, 172 mm SL. BOC basioccipital, ENT entopterygoid, EPO epiotic, EXO exoccipital, FRO frontal, HYO hyomandibula, IO infraorbital, LE lateral ethmoid, OBS orbitosphenoid, MET metapterygoid, OPE opercle, PAL autopalatine, PMA premaxilla, POP preopercle, PRO prootic, PSP parasphenoid, PTS pterosphenoid, QUA quadrate, SCL posttemporal-supracleithrum, SPH sphenotic, v1 vertebra 1, VOM vomer.

80. Lateral process of basioccipital: 0- absent or rudimentary; 1- present and clearly distinct (CI 0.333, RI 0.8).

Among examined species, the lateral process of the basioccipital is present and clearly distinct only in members of the Ariidae (except *Galeichthys*), Aspredinidae, Auchenipteridae, Claroteidae, Doradidae, Erethistidae, Mochokidae, and Sisoridae (Fig. 33; Royero, 1999: #46; Vigliotta, 2008: #13; Marceniuk *et al.*, 2012: #75). This feature was proposed by Lundberg (1993: 180) as support for grouping the undescribed fossil “*Titanoglanis*” with the Ariidae, Auchenipteridae, Doradidae and Mochokidae. This

character was coded as missing data for the auchenipterid *Spinipterus*.

81. Ventral extension of basioccipital (unordered): 0- absent; 1- present as a ring that ventrally surrounds the aorta; 2- present as a lamina ventrally (CI 1.0, RI 1.0).

The ventral face of the basioccipital is flat, without a ventral extension, in most catfishes (Fig. 34a-b). However, the doradid *Hassar* has the basioccipital extended as a ring that surrounds the aorta ventrally (Fig. 34c; Birindelli *et al.*, 2011), and the doradid *Trachydoras* has the basioccipital

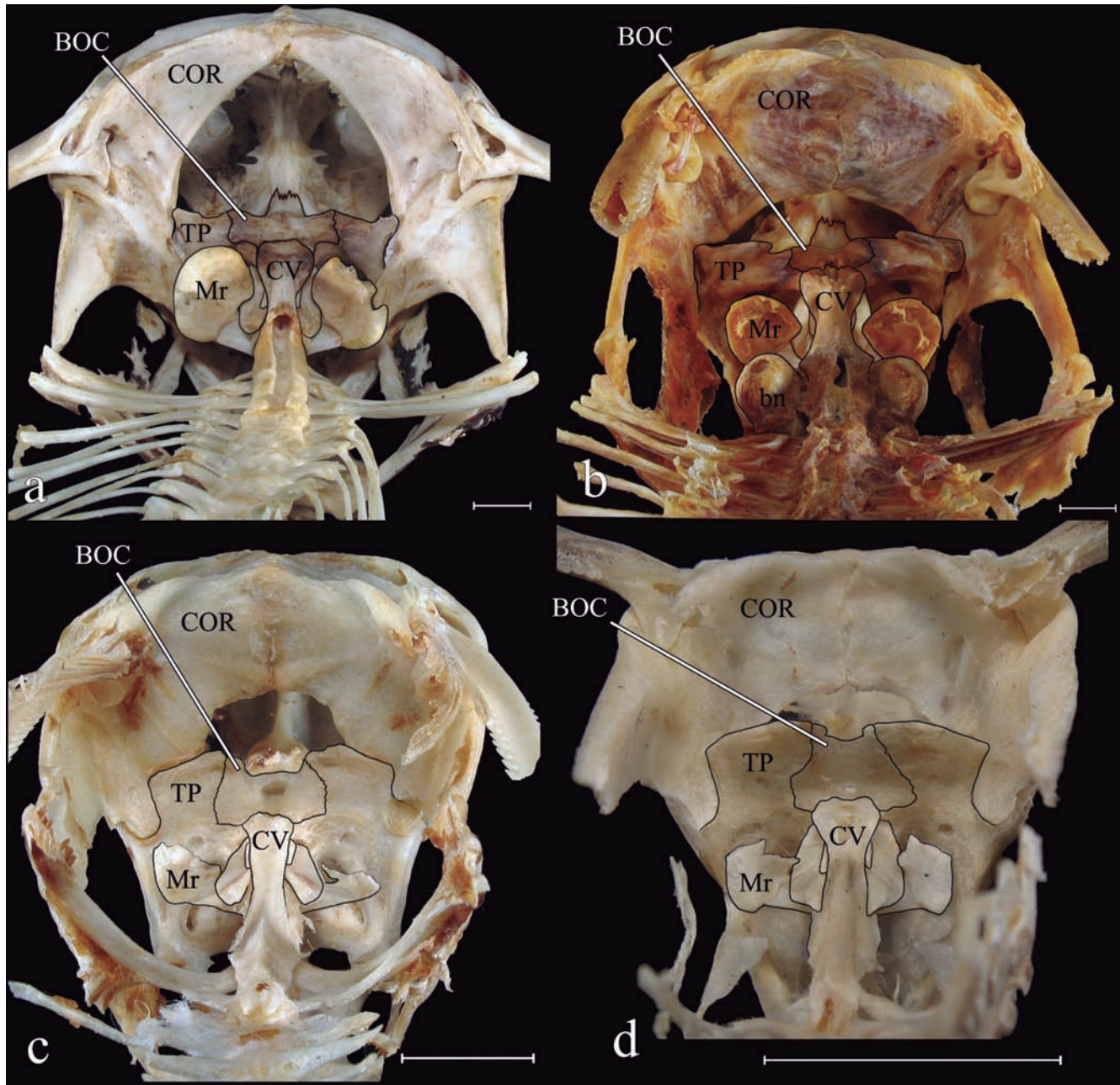


Fig. 34. Pectoral girdle, posterior portion of cranium and anterior vertebra in posteroventral view of (a) *Pterodoras rivasi*, MZUSP 105825, 350 mm SL; (b) *Oxydoras sifontesi*, MZUSP 105824, 413 mm SL; (c) *Hassar orestis*, MZUSP 32542, 220 mm SL; (d) *Trachydoras brevis*, MZUSP 103087, 74.0 mm SL. BOC basioccipital, bn bony nodule, COR coracoid, CV complex vertebra, Mr Müllerian ramus, TP transcapular process. Scale bars equal 10 mm.

ventrally extended as a lamina (Fig. 34d; Higuchi, 1992: #41). This character was coded as missing data for the auchenipterid *Spinipterus*.

82. Exoccipital and neural arch of complex vertebra: 0- connected by cartilage; 1- connected by bony suture (CI 1.0, RI 1.0).

In most catfishes, the exoccipital contacts the neural arch of the complex vertebra via cartilage (Fig. 35a; Arratia, 1987). However, in members of the Auchenipteridae and Doradidae, those two bones are sutured together (Fig. 35g; Ferraris, 1988: #V1; de Pinna, 1993: #190; Royero, 1999: #49; Akama, 2004: #45). This character was coded as missing data for the auchenipterid *Spinipterus*.

83. Dorsal surface of epiotic: 0- not participating in cephalic shield; 1- participating in cephalic shield (CI 1.0, RI 1.0).

Most catfishes have the dorsal surface of the epiotic below the dorsal surface of the neurocranium and not participating in the cephalic shield (Fig. 20). However, the dorsal face of the epiotic participates in the cephalic shield in the Auchenipteridae and Doradidae (Figs. 21-31; Regan, 1911; Ferraris, 1988: #N3; de Pinna, 1993: #77; Royero, 1999: #29; Britto, 2002: #48; Diogo, 2004: #118; Akama, 2004: #5, #38; Marceniuk *et al.*, 2012: #39). Royero (1999: 64) mentioned that the epiotic in the auchenipterid *Trachelyopterus galeatus* is a composite bone, formed by two ossifications that fuse ontogenetically, one ventral and endochondral (epiotic), and another dorsal and dermal (= parietal of Royero, 1999). The condition described by Royero (1999) was not observed among examined specimens, but if his observations are correct, it is possible that the extrascapular is not absent in the species of Auchenipteridae and Doradidae, but fused to the epiotic, forming the dorsal (dermal) face of a composite bone (see character 88 for other details). Royero (1999: #15) also mentioned that the epiotic participates in the cephalic shield in the Mochokidae, but that condition was not observed in examined specimens of that family. This character was coded as missing data for the auchenipterid *Spinipterus*.

84. Posterolateral margin of epiotic: 0- not participating in the border of cephalic shield; 1- participating in border of cephalic shield (CI 0.333, RI 0.929).

The posterolateral margin of the epiotic participates in the lateral border of the cephalic shield in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus* and *Trachydoras*, and Auchenipteridae (except *Asterophysus*, *Liosomadoras*, and

some specimens of *Trachycorystes*; Figs. 26-31). This condition is interpreted as resulting from the contact between the posttemporal-supracleithrum and middle nuchal plate, as previously observed by other authors (Higuchi, 1992: #34; Royero, 1999: #13; Akama, 2004: #33). *Trachycorystes* was coded as polymorphic for this character. This character was coded as inapplicable for all non-Doradoidea taxa, in which the epiotic does not participate in the cephalic shield (see character 83).

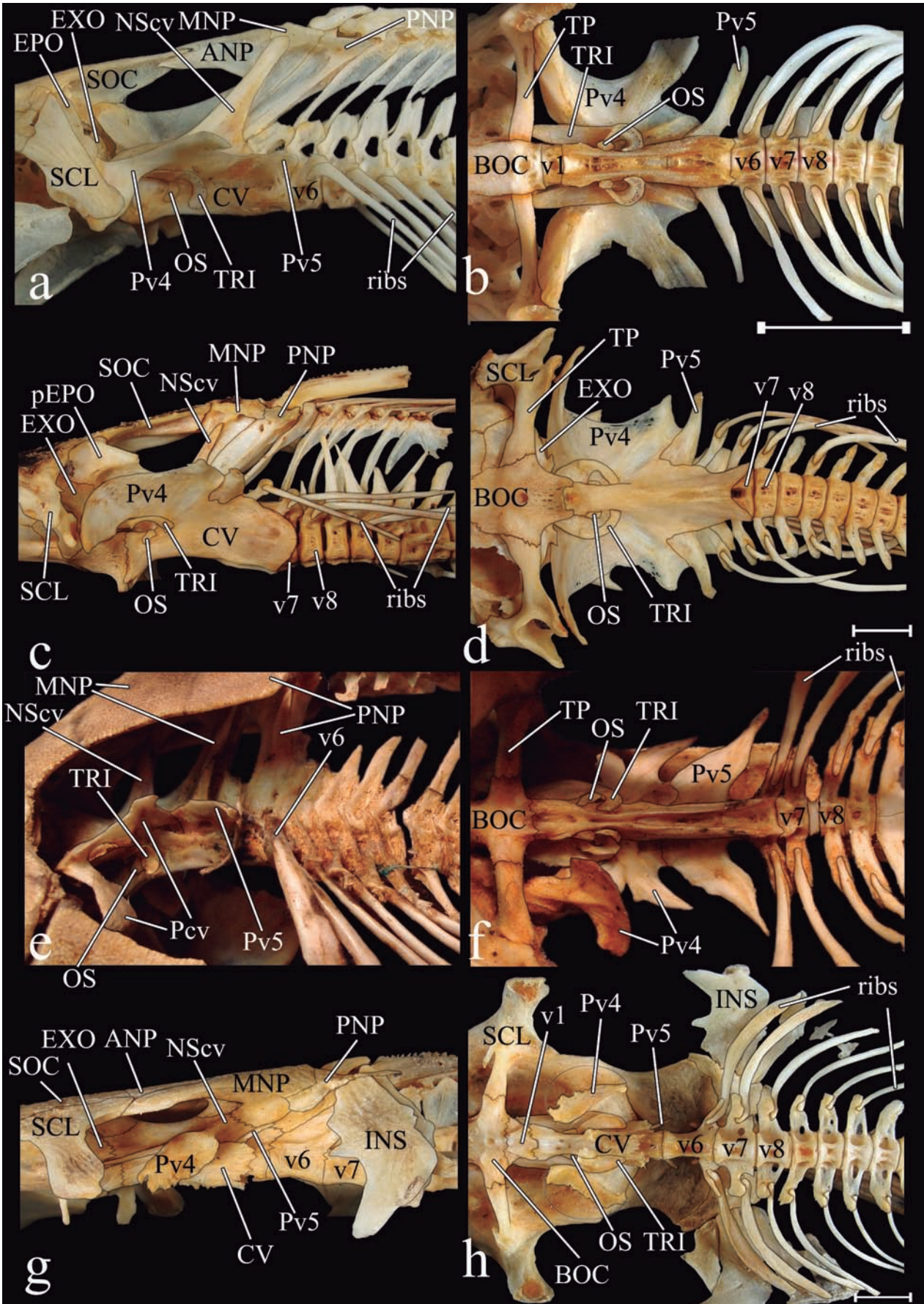
85. Posterior process of epiotic (ordered): 0- absent; 1- mainly ligamentous, formed less than half its length by bone; 2- mainly ossified, formed more than half its length by bone (CI 0.133, RI 0.759).

The epiotic has a posterior process that is ligamentous or eventually ossified in some species. The process is present and mainly ligamentous (*i.e.*, less than half its length formed by bone) in the Mochokidae, Pangasiidae, Schilbeidae, Sisoridae (de Pinna, 1993: #85; de Pinna, 1996: #29; Britto, 2002: #50), ariid *Galeichthys* (Ariidae; Mo, 1991; Acero & Betancur, 2007; Marceniuk *et al.*, 2012: #40), Centromochlinae, auchenipterids *Liosomadoras*, *Tocantinsia*, and *Trachycorystes*, and doradids *Acanthodoras*, *Agamyxis*, *Centrochir*, *Centrodoras*, *Doraops*, *Franciscodoras*, *Kalyptodoras*, *Lithodoras*, *Megalodoras*, *Orinocodoras*, *Oxydoras*, *Platydoras*, *Rhinodoras*, and *Wertheimeria* (Chardon, 1968: 229; Britski, 1972: 15; Ferraris, 1988: #N4; Lundberg, 1993; Royero, 1999: #50; Akama, 2004: #7; Sousa, 2010: #19). The epiotic process is present and mainly ossified (*i.e.*, formed more than half its length by bone) in the Amphiliidae, Ariidae (except *Galeichthys*), and in the remaining species of Auchenipteridae and Doradidae (Figs. 23, 26, 27, 29-31). This character was coded as missing data for the auchenipterid *Spinipterus*.

86. Posterior process of epiotic and posterior nuchal plate: 0- connected via ligament; 1- sutured (CI 0.5, RI 0.889).

In all Amphiliidae, Ariidae, Auchenipteridae, Mochokidae, Pangasiidae, and most members of Doradidae, the posterior process of the epiotic is connected via ligament either to the posterior nuchal plate or to the infranuchal ligament (Figs. 26-27). However, the posterior process of the epiotic is connected via bony suture to the posterior nuchal plate in the doradids *Anduzedoras*, *Doras carinatus*, *D. higuchii*, *D. micropoeus*, *Hassar* and *Leptodoras* (Higuchi, 1992: #37, #38; Birindelli *et al.*, 2011). This character was coded as inapplicable for the Aspredinidae, Claroteidae, Diplomystidae, Erethistidae, Heptapteridae, Ictaluridae, Malapteruridae,

Fig. 35 (next page). Anterior vertebrae in lateral (left) and ventral (right) views of (a,b) *Ictalurus punctatus*, MZUSP 103245, 155 mm SL; (c,d) *Genidens genidens*, MZUSP 5693, 250 mm SL; (e,f) *Synodontis schall*, ANSP 78057, unmeasured; (g,h) *Wertheimeria maculata*, MZUSP 93658, 220 mm SL. ANP anterior nuchal plate, BOC basioccipital, CV complex vertebra, EPO epiotic, EXO exoccipital, INS infranuchal scute, MNP middle nuchal plate, NScv neural spine of complex vertebra, pEPO epiotic process, PNP posterior nuchal plate, Pv4 parapophysis of fourth vertebra, Pv5 parapophysis of fifth vertebra, OS *os suspensorium*, SCL posttemporal-supracleithrum, SOC parietal-supraoccipital, TP transcapular process, TRI *tripus*, v6-8 vertebrae 6-8. Scale bars equal 10 mm.



Nematogenyidae, Pimelodidae, Pseudopimelodidae, and Siluridae, which lack an epiotic process; and as missing data for the auchenipterid *Spinipterus*.

87. Posterior process of epiotic and parapophyses of fifth and sixth vertebrae: 0- not sutured; 1- sutured (CI 0.25, RI 0.571).

In the Amphiliidae, Ariidae, Doradidae, Mochokidae, Pangasiidae, Schilbeidae Sisoridae, and most species of Auchenipteridae, the posterior process of the epiotic is not connected to the parapophyses of the fifth and sixth vertebrae (Figs. 21-29). However, it is sutured to the parapophyses of the fifth and sixth vertebrae in the auchenipterids *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Trachelyichthys*, *Trachelyopterus coriaceus*, and *Tetranematichthys* (Figs. 30, 31; Ferraris, 1988: #N5, #N7, #V10; Curran, 1989: #3; Walsh, 1990: #19; Royero, 1999: #51, #52, #53, #54; Akama, 2004: #8, #9, #10, #11). Britski (1972: 17) suggested that the development of the epiotic process is inversely proportional to the development of the nuchal shield, functioning to strengthen the connection between the cranium and the dorsal fin in catfishes with relatively less developed nuchal shields. This character was coded as inapplicable for the Aspredinidae, Claroteidae, Diplomystidae, Erethistidae, Heptapteridae, Ictaluridae, Malapteruridae, Nematogenyidae, Pangasiidae, Pimelodidae, Pseudopimelodidae, and Siluridae, which lack an epiotic process; and as missing data for the auchenipterid *Spinipterus*.

88. Extrascapular: 0- present; 1- absent (CI 0.2, RI 0.6).

The extrascapular is absent in the Aspredinidae, Auchenipteridae, Amphiliidae, Doradidae, Erethistidae, Mochokidae, Nematogenyidae, and Siluridae (Figs. 21-31; Lundberg, 1970: #24; Arratia, 1992: #43; Britto, 2002: #51; Vigliotta, 2008: #14). Royero (1999) mentioned that one dermal ossification center ontogenetically fuses to the epiotic in *Trachelyopterus galeatus*. The extrascapular of most catfishes occupies a similar position of the dermal portion of the epiotic in the Doradoidea. The similar position, the absence of a distinct extrascapular in adults, and the presence of an extra dermal ossification center ontogenetically fused to the epiotic in at least some members of the Doradoidea, suggest that the extrascapular might be present and fused to the epiotic in these taxa, and not entirely lost as in other catfishes. However, in the absence of further evidence (*e.g.*, ontogenetic series of development indicating the ontogenetic fusion between extrascapular and epiotic in some specimens), the extrascapular in the Auchenipteridae and Doradidae is herein treated as absent. This character was coded as missing data for the auchenipterid *Spinipterus*.

89. Connection between cranium and posttemporal-supracleithrum: 0- through ligaments; 1- through bony suture (CI 0.25, RI 0.727).

The posttemporal-supracleithrum is sutured to the

cranium in members of the Akysidae, Amphiliidae, Astroblepidae, Auchenipteridae, Callichthyidae, Clariidae, Doradidae, Erethistidae, Loricariidae, Mochokidae, Nematogenyidae, Scoloplacidae, and Sisoridae (Figs. 21-31; Alexander, 1965: 119; Chardon, 1968: 229; de Pinna, 1993: #26; Royero, 1999: #16; Britto, 2002: #38; Arratia, 2003a: 130; Diogo, 2004: #155; Vigliotta, 2008: #15). In other examined taxa, those structures are loosely connected by ligaments (Fig. 20).

90. Posttemporal-supracleithrum and parapophysis of fourth vertebra: 0- not connected at all; 1- connected by bony suture (CI 1.0, RI 1.0).

Among examined taxa, the posttemporal-supracleithrum is sutured to the parapophysis of the fourth vertebra only in the Aspredinidae, Erethistidae and Sisoridae (de Pinna, 1996: #27; Britto, 2002: #44). This character was coded as missing data for the auchenipterid *Spinipterus*.

91. Posttemporal fossa: 0- absent; 1- present (CI 1.0, RI 1.0).

In members of the Aspredinidae, Erethistidae and Sisoridae there is a groove between the parietal-supraoccipital, pterotic and posttemporal-supracleithrum (de Pinna, 1996: #24; Britto, 2002: #55; Diogo, 2004: #123). That groove is interpreted as the posttemporal fossa, and is absent in all other examined taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

92. Direction of transcapular process: 0- approximately transverse to body axis; 1- at an angle of approximately 45° relative to body axis (CI 0.5, RI 0.8).

The transcapular process is at an angle of approximately 45° relative to the body axis in the auchenipterids *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, and *Tetranematichthys* (Fig. 36a; Royero, 1999: #47; Akama, 2004: #44). In all other examined taxa, that process is approximately transverse to the body axis (Fig. 36b-d). This character was coded as missing data for the auchenipterid *Spinipterus*.

93. Shape of transcapular process: 0- blunt, not extended ventrally; 1- ventrally extended into bony lamina (CI 1.0, RI 1.0)

In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, *Tenellus*, and *Trachydoras*, the transcapular process is ventrally extended into a bony lamina, associated with the dorsally extended coracoid, serving as a bony diaphragm (Figs. 34b-d; Eigenmann, 1925: 287; Higuchi, 1992: #29, #30, #41). The transcapular process is blunt, not extended ventrally in all other examined species (Fig. 34a).

Laterosensory canals.

94. Shape of nasal: 0- tubular; 1- plate-like, dorsally expanded (CI 0.2, RI 0.2).

The nasal of catfishes is usually a tubular bone associated to the supraorbital canal, with a lateral branch that is variably ossified (Figs. 20-21, 25-27, 30-31). However, in the examined

species of doradids *Kalyptodoras* and *Platydoras* (except *Platydoras* sp.), and auchenipterids *Tatia*, *Trachelyopterus galeatus*, *Trachelyopterichthys*, and *Trachycorystes*, the nasal is plate-like, dorsally expanded (Figs. 22, 29; Soares-Porto, 1998: #5; Akama, 2004: #91, #93; Sousa, 2010: #20). This character is coded as missing data for *Spinipterus acsi*.

95. Contact between infraorbital 1 and lateral ethmoid: 0- weak; 1- strong (CI 0.2, RI 1.0).

In members of the Auchenipteridae and Doradidae the first infraorbital is firmly attached to the lateral ethmoid by strong ligaments or, in some species, by a bony suture (Figs.

21-31; Britski, 1972: 13; Mo, 1991: #55; de Pinna, 1993: #113; Royero, 1999: #8, #106; Britto, 2002: #65; Akama, 2004: #29). In other catfishes the first infraorbital is only weakly attached to the lateral ethmoid via ligaments (Fig. 20).

96. Length of contact between infraorbital 1 and lateral ethmoid: 0- short or absent, occupying most of medial margin of infraorbital 1; 1- long, extended over most of medial margin of infraorbital 1 (CI 1.0, RI 1.0).

In the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus*, the suture between infraorbital 1 and the lateral ethmoid is elongate, extended over most of medial margin

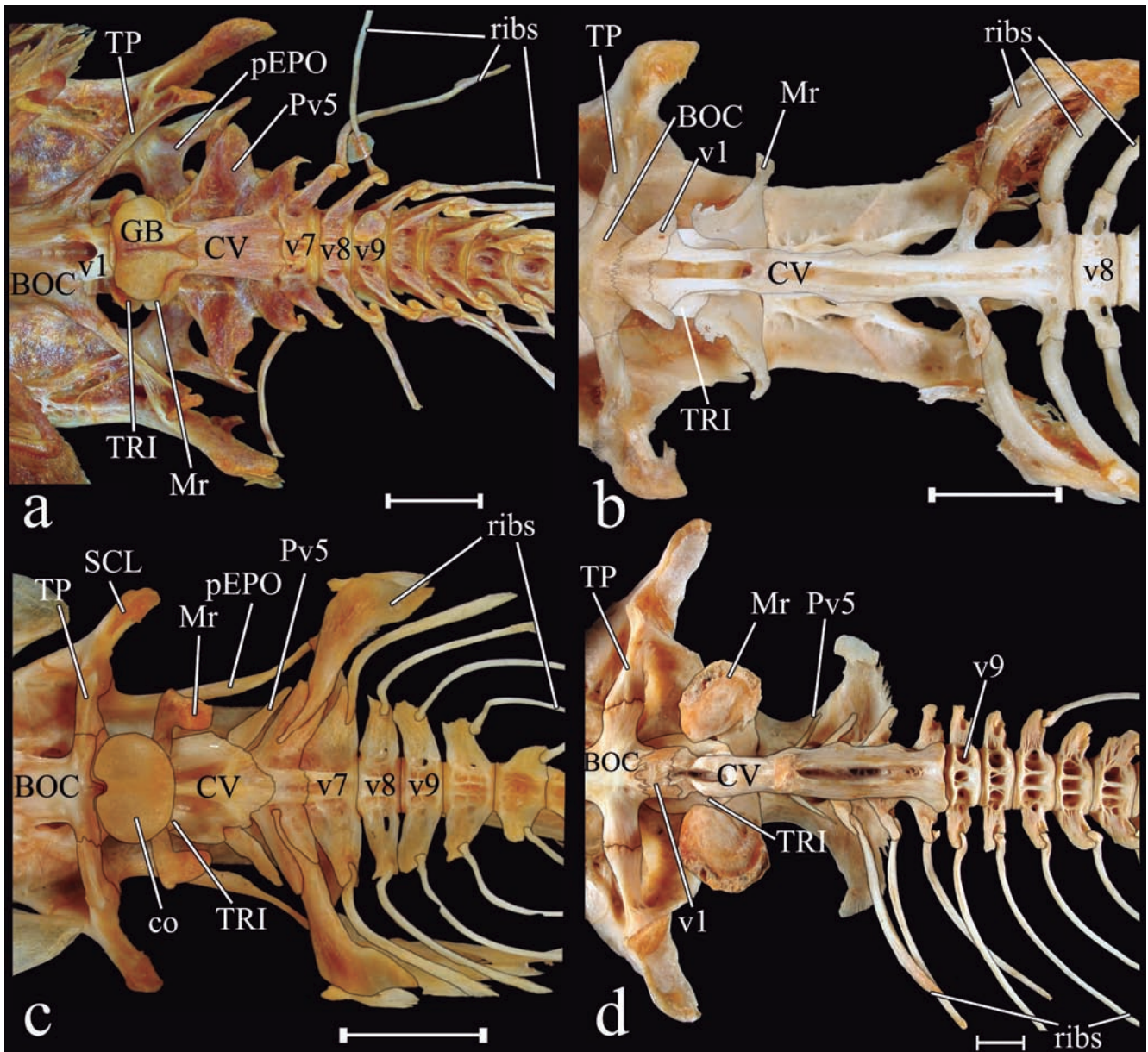


Fig. 36. Anterior vertebrae in ventral view of (a) *Ageneiosus inermis*, MZUSP 91661, 320 mm SL; (b) *Rhinodoras dorbignyi*, MZUSP 40109, 196 mm SL; (c) *Leptodoras juruensis*, MZUSP 104532, 227 mm SL; (d) *Tocantinsia piresi*, MZUSP 100031, 430 mm SL. bc bony capsule, BOC basioccipital, CV complex vertebra, GB gas bladder, Pv5 parapophysis of fifth vertebra, Mr Müllerian ramus, TP transcapular process, TRI *tripus*, v1-8 vertebrae 1-8. Scale bars equal 10 mm.

of infraorbital 1 (Fig. 30; Ferraris, 1988: #19; Royero, 1999: #8; Akama, 2004: #96); whereas in other catfishes this contact is relatively short, or eventually absent in some specimens (Figs. 20-29, 31).

97. Infraorbital 1 in orbital margin: 0- not participating; 1- participating (CI 0.333, RI 0.933).

In the Auchenipteridae, Astrodoradinae and doradids *Acanthodoras*, *Agamyxis*, *Lithodoras*, and *Pterodoras*, the infraorbital 1 participates in the orbital margin (Figs. 23, 28-30; Higuchi, 1992: #A13; Sousa, 2010: #22), whereas it is located distinctly anterior to the orbital margin in other examined taxa (Figs. 20-22, 24-27).

98. Ventral process of infraorbital 1: 0- absent; 1- present (CI 0.5, RI 0.857).

In the examined species of the auchenipterids *Ageneiosus*, *Auchenipterus*, *Centromochlus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, and *Tetranematichthys*, the infraorbital 1 has a well-developed ventral process (Figs. 30, 31; Ferraris, 1988: #12, Walsh, 1990: #13; Soares-Porto, 1998: #14; Akama, 2004: #29), which is absent in other examined taxa (Figs. 20-29). This character was coded as missing data for the auchenipterid *Spinipterus*.

99. Serrated crest on infraorbital 1: 0- absent; 1- present (CI 0.25, RI 0.667).

In the doradids *Acanthodoras*, *Agamyxis*, *Astrodoras*, *Centrochir*, *Centrodoras*, *Megalodoras*, *Platydoras*, *Scorpiodoras* and some specimens of *Anadoras* (especially small ones), infraorbital 1 has a serrated transverse crest (Eigenmann, 1925: 286; Higuchi, 1992: #20, #21; Higuchi *et al.*, 2007; Sousa, 2010: #23). *Anadoras* was coded as polymorphic for this character. All other examined species lack a serrated crest on infraorbital 1.

100. Length of anterior portion of infraorbital 1: 0- relatively small, smaller than length of posterior portion; 1- relatively large, similar in size to posterior portion (CI 0.5, RI 0.889).

In most catfishes, infraorbital 1 is shaped as a sickle with the anterior portion anteriorly acute and notably smaller than its posterior portion (Fig. 37a; Lundberg, 1970: fig. 55; Arratia, 1987: fig. 13; Sabaj Pérez & Birindelli, 2008: fig. 4A). However, in the doradids *Anduzedoras*, *Doras carinatus*, *D. higuchii*, *D. micropoeus*, *Hassar*, and *Leptodoras*, the infraorbital 1 has an expanded anterior portion, which is similar in size to the posterior portion (Fig. 37b; Sabaj Pérez & Birindelli, 2008).

101. Mesethmoid and infraorbital 1: 0- connected via ligaments, not sutured; 1- connected via bony suture (CI 1.0, RI 1.0).

The doradid *Trachydoras* has the infraorbital 1 ventrally sutured to the mesethmoid, forming a bony floor for the nasal capsule (Fig. 26; Higuchi, 1992: #A29), whereas it is connected via ligaments in other examined taxa (Figs. 20-25, 27-31). This

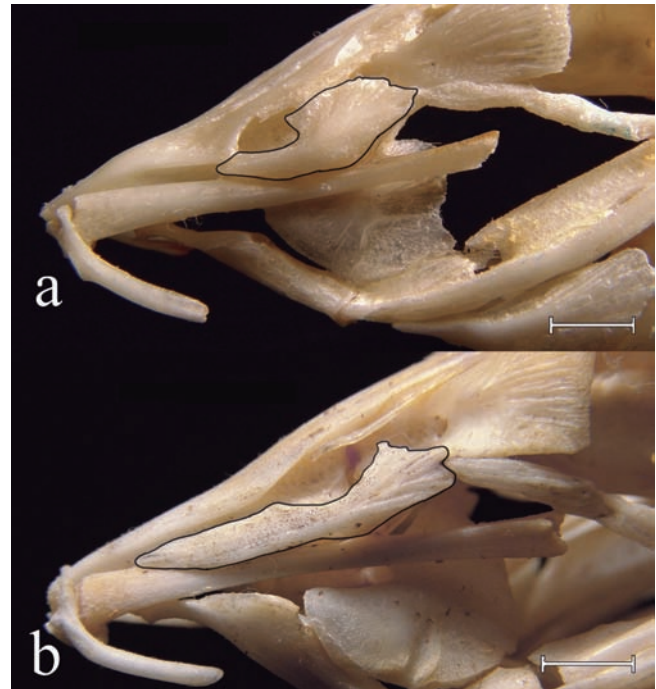


Fig. 37. Snout in lateral view of (a) *Doras phlyszakion*, MZUSP 82294, 165 mm SL; (b) *Doras higuchii*, MZUSP 96334, 185 mm SL. Infraorbitals outlined. Scale bars equal 10 mm.

character was coded as missing data for the auchenipterid *Spinipterus*.

102. Number of infraorbitals (ordered): 0- seven or more; 1- six; 2- five; 3- four (CI 0.273-0.3, RI 0.529-0.588).

Among other examined catfishes, the Diplomystidae, Ictaluridae and Nematogenyidae have seven or more infraorbitals (Lundberg, 1970: #28; Arratia, 1987; Arratia & Huaquin, 1995); Pangasiidae and Sisoridae have six; Amphiliidae, Claroteidae, Heptapteridae, Malapteruridae, and Siluridae have five; and Ariidae, Aspredinidae, Erethistidae, Pimelodidae, and Pseudopimelodidae have four (Kulongowski, 2001; Marceniuk *et al.*, 2012: #88). All mochokids have four infraorbitals, except *Synodontis zambezensis* and the Chiloglanidinae with five (Vigliotta, 2008: #23). All species of Doradidae have four infraorbitals, except *Anadoras* with five (Sousa, 2010: #21) and some specimens of *Oxydoras* (latter coded as polymorphic: 2,3) also with five. In the Auchenipteridae, most species have the tubules of the infraorbital series variably ossified, with a variable number of ossifications between two adjacent pores. Therefore, the number of ossified infraorbitals is highly variable in auchenipterids (even within a single species) (Ferraris, 1988: #11; Akama, 2004: #89). In order to establish the homology between the infraorbitals of auchenipterids and other catfishes, the number of infraorbitals for species of the former is herein considered as the number of tubules (independent of its ossification) between two pores. In this sense, all species of Auchenipteridae have four infraorbitals, except some specimens of *Glanidium* (coded as polymorphic: 2,3). This

character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

103. Shape of posteriormost infraorbital: 0- tubular; 1- plate-like (CI 0.167, RI 0.375).

The infraorbitals are numbered from anterior to posteriormost. However, their homology can also be determined by their position, relative to the cranium. Therefore, the infraorbital 4 of most auchenipterids and doradids is considered homologous to infraorbital 7 of Diplomystidae, because both are the posteriormost and in contact with the sphenoid. The posteriormost infraorbital (= infraorbital 4 in most auchenipterids and doradids) is plate-like in the doradids *Acanthodoras*, *Agamyxis*, *Kalyptodoras*, *Lithodoras*, *Orinocodoras*, *Platyodoras* (except *Platyodoras* sp.), *Pterodoras*, and auchenipterid *Trachycorystes* (Figs. 22-24, 29; Ferraris, 1988: #18; Akama, 2004: #95), whereas in other examined taxa the posteriormost infraorbital is tubular (Figs. 20-21, 26-27, 31).

104. Shape of penultimate infraorbital: 0- tubular; plate-like (CI 0.2, RI 0.5).

The second posteriormost infraorbital (= infraorbital 3 of most auchenipterids and doradids) is plate-like in doradids *Acanthodoras*, *Agamyxis*, *Kalyptodoras*, *Lithodoras*, *Megalodoras*, *Platyodoras* (except *Platyodoras* sp.), and *Pterodoras* (Figs. 22, 23; Higuchi, 1992: #26, #27), whereas in other examined taxa the structure is tubular (Figs. 20-21, 24, 26-27, 31).

105. Shape of infraorbital 2: 0- tubular; 1- plate-like (CI 0.333, RI 0.333).

The infraorbital 2 is plate-like in *Acanthodoras*, *Agamyxis*, *Kalyptodoras*, and *Platyodoras* (except *Platyodoras* sp.) (Fig. 22; Higuchi, 1992: #25), whereas it is tubular in all other examined taxa (Figs. 20-21, 23-24, 26-27, 31).

106. Spines on infraorbitals: 0- absent; 1- present (CI 0.125, RI 0.462).

The infraorbitals have small spines in the doradids *Acanthodoras*, *Agamyxis*, *Astrodoras*, *Hemidoras morei*, *H. morrisi*, *H. stenopeltis*, *Platyodoras*, *Scorpiodoras* and *Trachydoras steindachneri*, and auchenipterids *Liosomadoras*, *Trachelyopterichthys*, *Trachycorystes*, and *Spinipterus* (Figs. 22, 29; Britski, 1972: 13; Royero, 1999: #102; Akama, 2004: #100; Sousa, 2010: #25); this condition is absent in other examined taxa (Figs. 20-21, 23-24, 26-27, 31).

107. Location of exit of infraorbital canal from cranium: 0- on the anterior portion of sphenotic; 1- on the posterior portion of sphenotic (CI 0.5, RI 0.969).

In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxyodoras*, *Tenellus*, and *Trachydoras* the infraorbitals are connected to the posterior portion of the sphenotic (Figs. 25-27; Higuchi, 1992: #24). The same condition occurs in the mochokids of

the genus *Synodontis*, which also have deep head and large eye. In all other examined species, the infraorbitals are connected to the anterior portion of sphenotic (Figs. 20-24). This character was coded as missing data for the auchenipterid *Spinipterus*.

108. Temporal canal: 0- passing from pterotic to posttemporal-supracleithrum; 1- passing from pterotic, through epiotic, to posttemporal-supracleithrum (CI 1.0, RI 1.0).

In most catfishes the temporal canal passes from the pterotic, through the epiotic, to the posttemporal-supracleithrum. However, in the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* the temporal canal passes from the pterotic, through the epiotic, to the posttemporal-supracleithrum (Royero, 1999: #94; Akama, 2004: #104). This character was coded as missing data for the auchenipterid *Spinipterus*.

109. Pterotic ramus of temporal canal: 0- present; 1- absent (CI 1.0, RI 1.0).

In the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* the pterotic ramus of the temporal canal is absent (Royero, 1999: #96); in all other examined taxa, the pterotic ramus of the temporal canal is present. This character was coded as missing data for the auchenipterid *Spinipterus*.

110. Accessory pore of otic canal: 0- absent; 1- present (CI 1.0, RI 1.0).

Among examined species, there is an accessory pore on the otic canal near the lateral border of the cephalic shield only in the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* (Royero, 1999: #97; Akama, 2004: #102). This character was coded as missing data for the auchenipterid *Spinipterus*.

111. Mandibular canal: 0- present; 1- absent (CI 0.5, RI 0.667).

The mandibular canal is absent in the sisorid *Sisor*, erethistid *Conta*, Aspredinidae, and mochokids Chiloglanidinae (de Pinna, 1996: #3; Britto, 2002: #67). The mandibular canal is present in other examined taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

112. Mandibular canal: 0- passing inside lower jaw; 1- passing outside lower jaw (CI and RI inapplicable).

The mandibular canal passes outside of the anguloarticular and dentary in the auchenipterid *Gelanoglanis* (Ferraris, 1988: #110; Rengifo *et al.*, 2008). This character was coded as inapplicable for the Aspredinidae, Erethistidae and mochokid *Chiloglanis*, which lack the mandibular canal; and as missing data for the auchenipterid *Spinipterus*.

113. Number of pores on mandibular canal (ordered): 0- three or less; 1- four; 2- five or six; 3- seven or more (CI 0.176, RI 0.839).

In most catfishes, there are five or six pores along the mandibular canal (Lundberg, 1970: #42); the presence of five or six pores varying among and within the species. Most species of Auchenipteridae and Doradidae have five or six pores on the mandibular canal. However, the doradids *Acanthodoras*, *Agamyxis*, *Centrodoras*, *Megalodoras*, and *Oxydoras* have only four pores, and members of the *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras* have only three pores. On the other hand, the auchenipterids *Trachelyopterus* have seven, and *Asterophysus*, *Trachelyopterichthys*, and *Trachycorystes* have eight pores. All mochokids have two or three pores (Vigliotta, 2008: #87), whereas species of Ariidae, Claroteidae, Pimelodidae, Pseudopimelodidae, and Siluridae have eight pores, Malapteruridae have seven and Amphiliidae have three. This character was coded as missing data for auchenipterids *Tocantinsia*, *Pseudotatia*, *Spinipeterus*, and doradids *Doraops* and *Rhynchodoras*; and as inapplicable for Aspredinidae, Erethistidae, Sisoridae, and mochokid *Chiloglanis*, which lack the mandibular canal.

114. Number of pores of each exit of sensory canals: 0- one; 1- numerous (CI 0.333, RI 0.333).

Most catfishes have a single opening for each exit of the sensory canals. However, each exit of the sensory canals is branched into smaller canals with multiple pores near the skin in the Ariidae, Pangasiidae, Pimelodidae, and Plotosidae (Lundberg, 1970; Arratia, 1992: #64; de Pinna, 1993: #109; Arratia & Huaquin, 1995: #1; Royero, 1999: #98; Vigliotta, 2008: #86).

115. Lateral line shape: 0- straight; 1- sinusoidal (CI 0.333, RI 0.889).

The lateral line is sinusoidal in all species of the Auchenipteridae (Figs. 38b-d; Ferraris, 1988: #112; Akama, 2004: #97), except for the examined species of *Gelanoglanis*, *Glanidium*, *Tatia*, and *Spinipeterus* (Fig. 38a). Ferraris (1988: #112) mentioned that this feature is present in the auchenipterids *Centromochlus*, *Glanidium*, and *Tatia*, and Akama (2004: #97) in *Glanidium* and *Tatia*, but the only specimens of *Centromochlinae* examined herein with sinusoidal lateral line are those of *Centromochlus heckelii* (Fig. 38b). The lateral line is straight in other examined taxa.

116. Posterior terminus of lateral line: 0- unbranched; 1- branched into two divergent rami (CI 0.333, RI 0.778).

Most species of catfishes have the posterior terminus of the lateral line unbranched. In the auchenipterids *Ageneiosus*, *Asterophysus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*, *Trachelyopterus*, and *Trachycorystes*, the terminus of the lateral line on the caudal-fin base is posteriorly branched into two divergent rami (Britski, 1972; Ferraris, 1988: #111; Royero, 1999: #101, Akama, 2004: #88). In some of those taxa, including *Auchenipterus nuchalis* and *Trachelyopterus*, the posterior rami are parallel or weakly divergent, but in

others, such as *Auchenipterus ambyacus* and *Asterophysus*, they are widely divergent, each approximately vertical (Akama, 2004: #88). This character was coded as missing data for *Pseudotatia*, and as inapplicable for *Entomocorus*, because the lateral line terminates anterior to the caudal-fin base.

117. Vertical rows of neuromasts dorsal to lateral line: 0- absent; 1- present (CI 0.333, RI 0.846).

All auchenipterids (except *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Pseudepapterus*, *Spinipeterus* and *Tetranematichthys*) have vertical rows of neuromasts dorsal to the lateral line (Fig. 38d; Ferraris, 1988: #113); a condition absent in all other examined species.

118. Midlateral scutes (ordered): 0- absent; 1- present, but not well developed along the entire body; 2- present and well developed along the entire body (CI 0.333, RI 0.956).

The lateral-line tubules are developed as a longitudinal row of midlateral bony scutes in all species of Doradidae (Eigenmann, 1925; Ferraris, 1988: #115; Higuchi, 1992: #87; Royero, 1999: #103, #105; Akama, 2004: #99). This is the most conspicuous feature shared among doradids and was recognized by the earliest studies about these fishes (e.g., Linnaeus, 1766). In the doradids *Doras micropoetus*, *Doraops*, *Hassar*, *Kalyptodoras*, *Nemadoras hemipeltis*, *Tenellus leporhinus*, and *Wertheimeria*, however, the midlateral scutes are weakly developed (Eigenmann, 1925: 301; Higuchi, 1992: #96; Sousa, 2010: #28; Birindelli *et al.*, 2011). Midlateral scutes are absent in all other examined species. This character was ordered according to the ontogenetic series of development.

119. Retrorse thorn on midlateral scutes: 0- absent; 1- present (CI and RI inapplicable).

In most doradids, each midlateral scute has a retrorse thorn (Figs. 39b-f). In *Wertheimeria*, however, the midlateral scutes are usually smooth (without spines) and covered by thick skin (Fig. 39a). Retrorse thorns are present only in the midlateral scutes of the caudal peduncle in specimens up to 75 mm SL of *Wertheimeria*. This character was coded as inapplicable for all non-Doradidae taxa, which lack midlateral scutes.

120. Orientation of midlateral scutes: approximately perpendicular to long axis of body; 1- oblique to long axis of body (CI 1.0, RI 1.0).

In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras*, the midlateral scutes are oblique, at an approximately 60° angle relative to the longitudinal axis of the body, with the dorsal wing anterior to the ventral wing (Fig. 39f). This character was coded as inapplicable for all non-Doradidae taxa, which lack midlateral scutes.

121. Depth of midlateral scutes: 0- generally one-fifth to one-half of body depth at anal-fin origin; 1- generally more than half of body depth at anal-fin origin (CI 0.5, RI 0.667).

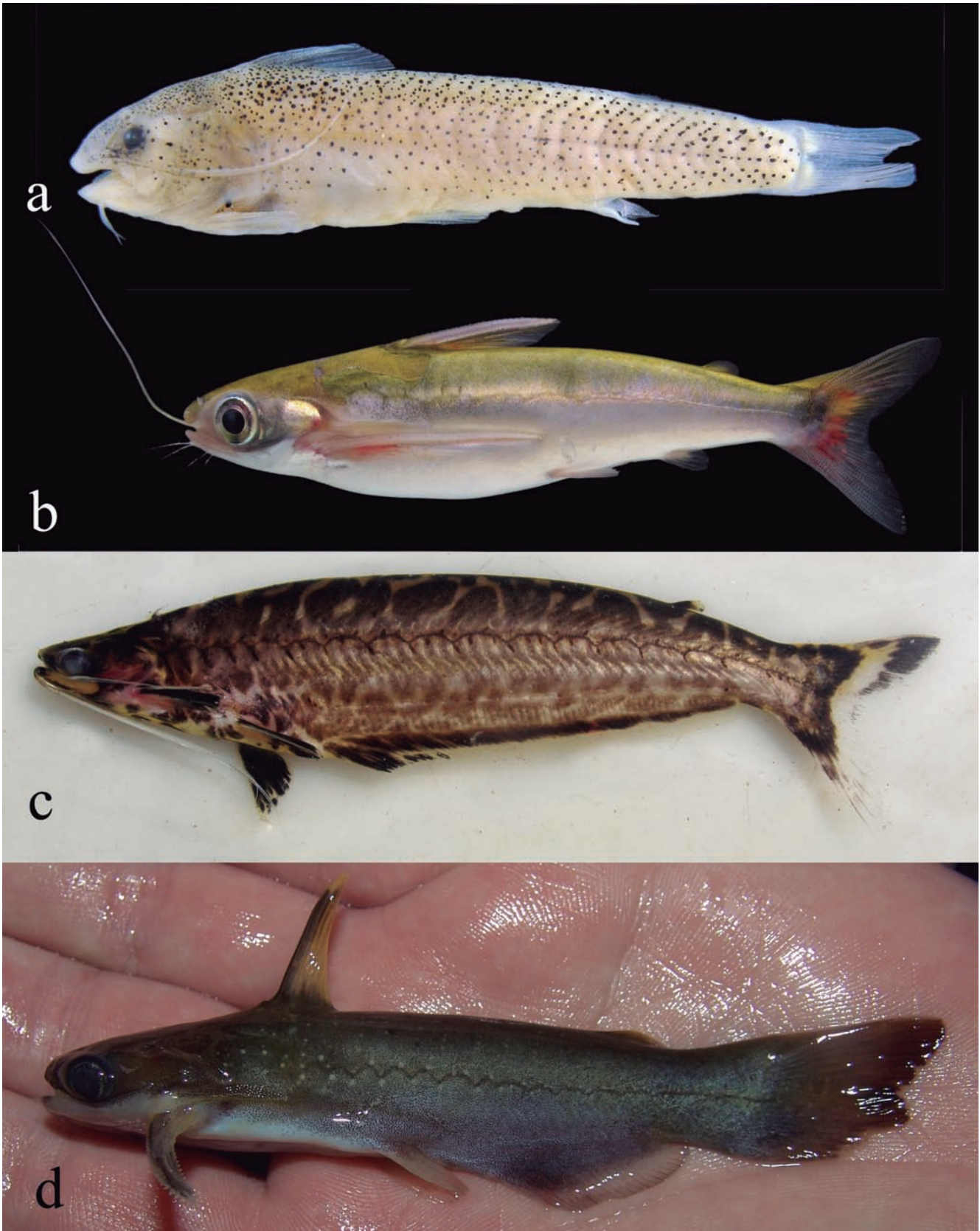


Fig. 38. *Gelanoglanis* cf. *stroudi* (a), MZUSP 96032, 26.2 mm SL, rio Teles Pires, Itaituba, Mato Grosso; (b) *Centromochlus heckelii*, MZUSP 104793, approximately 100 mm SL, rio Jari, Monte Dourado, Pará, photographed live; (c) *Pseudepapterus hasemani*, MZUSP 104772, 115.2 mm SL, rio Jari, Monte Dourado, Pará, photographed live; (d) *Auchenipterichthys longimanus*, INPA uncatalogued, approximately 80 mm SL, rio Tapajós, Itaituba, Pará, photographed live.

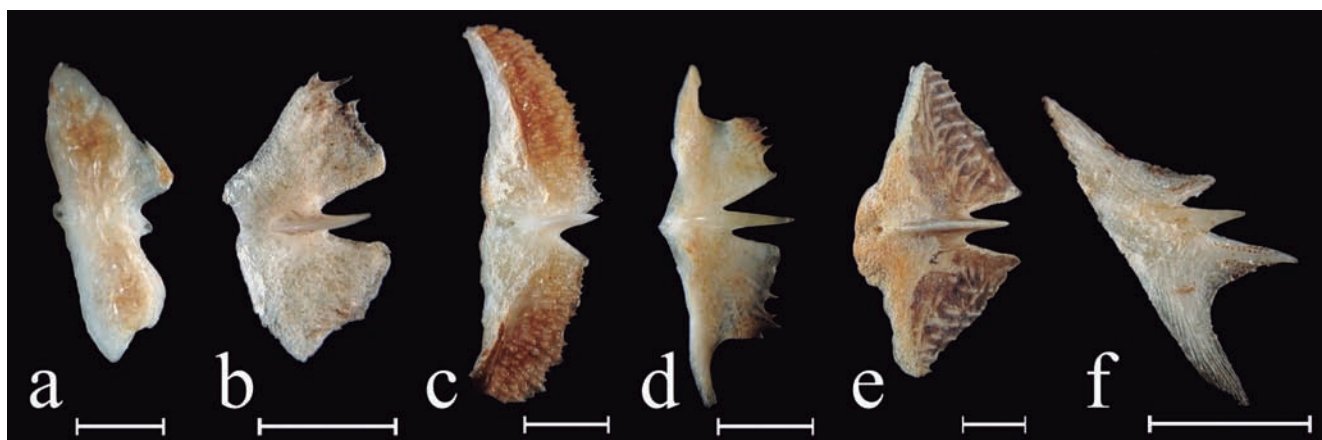


Fig. 39. Midlateral scutes of the anterior portion of body in lateral view (original orientation preserved) of (a) *Wertheimeria maculata*, MZUSP 93659, 192 mm SL; (b) *Centrochir crocodili*, MZUSP 15087, 150.8 mm SL; (c) *Platydoras armatulus*, MZUSP91686, 151.7 mm SL; (d) *Orinocodoras eigenmanni*, FMNH 105276, 193 mm SL; (e) *Oxydoras niger*, MZUSP91858, 313 mm SL; (f) *Doras phlyzaktion*, MZUSP 82294, 162 mm SL. Scale bars equals 5 mm.

In doradids *Acanthodoras*, *Agamyxis*, *Astrodoras*, *Platydoras armatulus*, *P. brachylecis*, *P. hancockii* (among examined species), the midlateral scutes are deep, with depth more than half of body depth at anal-fin origin (Fig. 39c; Higuchi, 1992: A64; Sabaj, 2002: #22; Sousa, 2010: #29). In other doradids the midlateral scutes are shallower (Fig. 39a-b,d-f). This character was coded as inapplicable for all non-doradid taxa, which lack midlateral scutes.

122. Size of third tympanal scute: 0- distinctly smaller than postinfranuchal scutes; 1- similar in size to anterior postinfranuchal scutes (CI 0.5, RI 0.95).

In the doradids *Acanthodoras*, *Agamyxis*, *Anadoras*, *Centrodoras*, *Doraops*, *Franciscodoras*, *Kalyptodoras*, *Lithodoras*, *Megalodoras*, *Platydoras*, *Pterodoras*, *Orinocodoras*, *Rhinodoras*, *Scorpiodoras*, *Wertheimeria*, and some specimens of *Centrochir*, the third tympanal scute is relatively large, similar in size to anterior postinfranuchal scutes (Figs. 21, 22, 24; Sousa, 2010: #26). The doradids *Centrochir* and *Rhinodoras dorbignyi* were coded as polymorphic for this character, for having specimens with the third infranuchal scute relatively small and others with the scute relatively large. This character was coded as inapplicable for all non-Doradidae taxa, which lack midlateral scutes.

123. Number of midlateral scutes (ordered): 0- 15 to 25; 1- 26 to 38; 2- 39 to 46 (CI 0.5, RI 0.778).

The number of midlateral scutes in doradids was conventionally established as beginning with the infranuchal scute, and is useful in species diagnosis (Sabaj, 2005; Birindelli *et al.*, 2007). The number of midlateral scutes may vary significantly among species of a single genus (*e.g.*, *Oxydoras*), but it is quite conservative within a single species. Although the variation in the number of midlateral scutes is continuous among species of Doradidae, there are two groups of species that are distinctly different from others based on the number

of scutes, the first group having 15 to 25 midlateral scutes, and the second having 39 to 46. Fifteen to 25 midlateral scutes are present in *Acanthodoras spinosissimus*, *Agamyxis pectinifrons*, *Centrodoras hasemani*, *Doraops*, *Lithodoras*, *Megalodoras*, and *Pterodoras*. On the other hand, *Anduzedoras* and distal species of *Leptodoras* (excluding *L. copei*, *L. marki*, *L. oyakawai*, *L. praelongus*, and some specimens of *L. hasemani*) have 39 midlateral scutes or more (Sabaj, 2002: #21). This character was coded as inapplicable for all non-Doradidae taxa, which lack midlateral scutes.

Jaws.

124. Shape of mandibular arch: 0- approximately straight in lateral view; 1- distinctly curved ventrally (CI 1.0, RI 1.0).

In the doradid *Rhynchodoras* both jaws have a concave

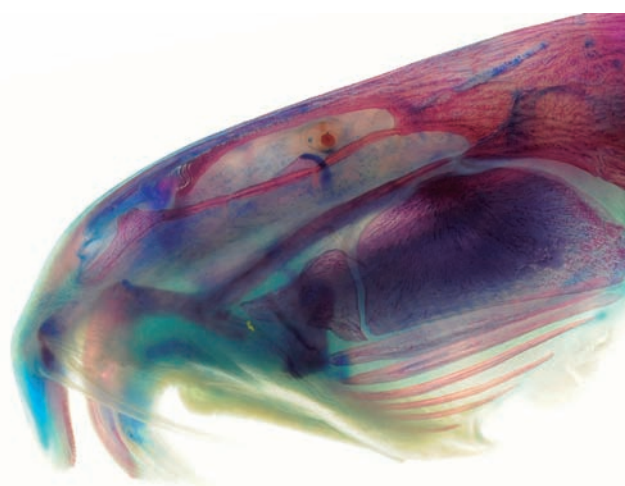


Fig. 40. Head in lateral view of a cleared and stained specimen of *Rhynchodoras woodsi*, ANSP 181042, 87 mm SL. Photo by Leandro Sousa.

ventral margin forming a forceps-like beak (Fig. 40; Birindelli *et al.*, 2007). That condition is absent in other examined taxa, in which the mandibular arch is more or less straight in lateral view.

125. Shape of premaxilla (unordered): 0- shaped like a plate, width distinctly greater than depth; 1- conical with a dorsal apex, depth distinctly greater than width; 2- shaped like a block, depth and width approximately equal (CI 1.0, RI 1.0).

The premaxilla in most catfishes is shaped as a plate, with width distinctly greater than depth (Figs. 41a,b; Lundberg, 1970). In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, *Tenellus*, and *Trachydoras*, the premaxilla is reduced in size and shaped as a cone with a dorsal apex, with depth distinctly greater than width (Figs. 41c,d; Higuchi, 1992: #42, #43). In the Mochokidae (except *Acanthocleithron*, *Mochokiella*, and *Mochokus*) the premaxilla is shaped as a block, with the depth and width approximately equal (Vigliotta, 2008: #35, figs. 12-14). The auchenipterids *Epapterus* and *Pseudepapterus* also have a reduced premaxilla, somewhat similar to that of fimbriate-barbel doradids, but shaped as a plate (state 0), whereas the auchenipterids *Ageneiosus*, *Asterophysus*, and *Tetranematichthys* have an extremely elongate premaxilla, shaped as a plate (state 0; Britski, 1972: 15; Royero, 1999: #57), and associated with an elongated dentary (Ferraris, 1988: #J9; Akama, 2004: #51). The auchenipterid *Gelanoglanis* also has premaxilla shaped as a plate (state 0), but very delicate, thin and posteriorly elongate, with teeth only on its anterior portion (Ferraris, 1988: #J20; Rengifo *et al.*, 2008).

126. Dorsolateral process of premaxilla: 0- absent; 1- present (CI 0.25, RI 0.25).

In the Claroteidae, Heptapteridae, Pimelodidae, Pseudopimelodidae, and Sisoridae, the premaxilla has a dorsolateral process articulated with the maxilla (de Pinna, 1993: #40; Britto, 2002: #135). That process is absent in other examined taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.



Fig. 41. Premaxilla in anterior (a,c) and ventral (b,d) views of (a,b) *Pterodoras granulatus*, MZUSP 91655, 410 mm SL; (c,d) *Doras higuchii*, MZUSP 101693, 172 mm SL. Scale bars equal 5mm.

127. Lateroposterior extension of premaxilla: 0- absent; 1- present (CI 0.2, RI 0.0).

In the auchenipterids *Auchenipterus* and *Epapterus*, the premaxilla has a distinct lateroposterior extension (Ferraris, 1988: #J21; Akama, 2004: #54). The same condition is present in the Heptapteridae, Pimelodidae, and Pseudopimelodidae, but is absent in other examined taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

128. Premaxillary teeth (ordered): 0- more than 30; 1- reduced in number (less than 30); 2- absent (CI 0.2, RI 0.867).

Most catfishes have numerous teeth on the premaxilla. However, the auchenipterids *Auchenipterus* and *Entomocorus* have premaxillary teeth reduced in number and arranged in only one to three rows (Ferraris, 1988: #J7; Ferraris & Vari, 1999; Akama, 2004: #49). The doradids *Doras carinatus*, *D. higuchii*, *D. micropoeus* (Sabaj Pérez & Birindelli, 2008), *Hassar*, *Hemidoras stenopeltis* and *Ossancora* also have premaxillary teeth reduced in number (Figs. 41c,d). The premaxillary teeth are absent in the adults of the auchenipterids *Epapterus* and *Pseudepapterus* (Ferraris, 1988: #J8), and doradids *Anduzedoras*, *Doras phlyzakion*, *D. zuanoni*, *Hemidoras morei*, *H. morrisi*, *H. stubelii*, *Leptodoras*, *Nemadoras*, *Oxydoras*, *Tenellus*, and *Trachydoras* (Eigenmann, 1925: 282; Higuchi, 1992: #42; Sabaj, 2002: #13). Among other examined catfishes, premaxillary teeth are also absent in the Aspredinidae (de Pinna, 1996: #7).

129. Shape of premaxillary teeth: 0- slightly curved; 1- S-shaped (CI 1.0, RI 1.0).

Most catfishes have slightly curved teeth, however, the species of Mochokidae (except *Acanthocleithron*, *Mochokiella*, and *Mochokus*) have long S-shaped premaxillary teeth (Vigliotta, 2008: #37). This character was coded as inapplicable for all taxa with an edentulous premaxilla (*i.e.*, Aspredinidae, auchenipterids *Epapterus* and *Pseudepapterus*, and doradids *Anduzedoras*, *Doras phlyzakion*, *D. zuanoni*, *Hemidoras morei*, *H. morrisi*, *H. stubelii*, *Leptodoras*, *Nemadoras*, *Oxydoras*, *Tenellus*, and *Trachydoras*).

130. Premaxillary teeth: 0- similar in size; 1- with at least two distinct sizes (CI 1.0, RI 1.0).

Most catfishes have similarly sized teeth, however, the species of Mochokidae (except *Acanthocleithron*, *Mochokiella*, and *Mochokus*) have premaxillary teeth of at least two distinct sizes separated into discrete patches (Vigliotta, 2008: #36). This character was coded as inapplicable for all taxa with an edentulous premaxilla (*i.e.*, Aspredinidae, auchenipterids *Epapterus* and *Pseudepapterus*, and doradids *Anduzedoras*, *Doras phlyzakion*, *D. zuanoni*, *Hemidoras morei*, *H. morrisi*, *H. stubelii*, *Leptodoras*, *Nemadoras*, *Oxydoras*, *Tenellus*, and *Trachydoras*).

131. Size of maxilla: 0- short; 1- elongate, rod-like (CI 0.143-0.167, RI 0.829-0.857).

Most catfishes have a short maxilla. However, members of the Siluridae, Sisoridae, and auchenipterids *Auchenipterus*, *Centromochlus heckelii*, *Gelanoglanis*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* (Ferraris, 1988: #J11) and doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Oxyodoras*, *Tenellus*, and *Trachydoras* all have an elongate, rod-like maxilla (Figs. 25, 27, 33b; Higuchi, 1992: #44; Sousa, 2010: #33).

132. Number of heads at articular end of maxilla: 0- two; 1- one (CI and RI inapplicable).

In most catfishes the maxilla has two proximal heads that form a bifurcated condyle (ventralmost head usually more developed). However, in the Cetopsidae, Diplomystidae, Scoloplacidae, and Trichomycteridae the maxilla articulates with the autopalatine via a single condyle (Arratia, 1992: #3, #4, #5; Britto, 2002: #145; de Pinna *et al.*, 2007: #2). Some authors (*e.g.*, Mo, 1991: #25; Britto, 2002: #145) have considered the dorsal head to be more developed in the Auchenipteridae, Doradidae, and mochokids *Synodontis*, compared to other catfishes, but that condition was not observed in the specimens examined. This character was coded as missing data for the auchenipterid *Spinipiterus*.

133. Maxillary teeth: 0- present; 1- absent (CI and RI inapplicable).

An edentulous maxilla is present in all catfishes except the Diplomystidae (Regan, 1911: 556; Alexander, 1965: 91; Lundberg, 1970; Arratia, 1987; Arratia, 1992: #1). This feature has long been regarded as a primitive trait of the Diplomystidae (de Pinna, 1993: 53; Grande & de Pinna, 1998; Britto, 2002: #148; Diogo, 2004: #259; de Pinna *et al.*, 2007: #3).

134. Shape of maxilla of mature males: 0- similar to those in females and immature males; 1- elongate, longer than in females and immature males (CI 0.333, RI 0.6).

Among examined species, the maxilla in mature males is elongate and proportionally longer than that in mature females and immature males only in the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys* and in some species of *Trachelyopterus*, including *T. galeatus* (Fig. 42b; Ferraris, 1988: #J13; Akama, 2004: #171). The increase in size of the maxilla in mature males is often associated with a similar enlargement of the autopalatine (Ferraris, 1988: #J5; Walsh, 1990: #15; Akama, 2004: #175). This character was coded as missing data for *Pseudotatia* and *Spinipiterus*.

135. Spines on maxilla of mature males: 0- absent; 1- present (CI 1.0, RI 1.0).

Among examined species, only in the auchenipterid *Ageneiosus* the maxilla of mature males has spines (Fig. 42a; Ferraris, 1988: #J15; Walsh, 1990: #22; Royero, 1999: #129, #130; Akama, 2004: #172), a dimorphic feature. This character was coded as missing data for *Pseudotatia* and *Spinipiterus*.

136. Coronomeckelian bone: 0- present; 1- absent (CI 0.5, RI 0.75).

Among catfishes the coronomeckelian bone is absent only in the Astroblepidae, Callichthyidae, aspredinids Hoplomyzontinae, Loricariidae, Malapteruridae, Mochokidae, and Scoloplacidae (Arratia, 1992: #47; de Pinna, 1993: #23; Diogo, 2004: #424; Vigliotta, 2008: #26). This character was coded as missing data for the auchenipterid *Spinipiterus*.

137. Contact between coronomeckelian bone and dentary: 0- absent; 1- present (CI 0.25, RI 0.927).

In most catfishes, the coronomeckelian bone is a small bony bridge surrounding the meckelian cartilage and extended immediately posterior to the mandibular ramus of the facial nerve (Fig. 43b). However, in the doradids *Anduzedoras*, *Doras*, *Franciscodoras*, *Hassar*, *Hemidoras*, *Kalyptodoras*, *Leptodoras*, *Nemadoras*, *Orinocodoras*, *Ossancora*, *Oxyodoras*, *Platyodoras* sp., *Rhinodoras*, *Rhynchodoras*, *Tenellus*, *Trachydoras*, *Wertheimeria*, and some specimens of *Pterodoras granulatus* (Fig. 43a; de Pinna, 1993: #51; Britto, 2002: #159; Sousa, 2010: #35), the coronomeckelian bone is anteriorly extended, surrounding the mandibular ramus of the



Fig. 42. Head and anterior portion of body in lateral view of mature males of (a) *Ageneiosus ucayalensis*, MZUSP104791, 171 mm SL (snout in detail, showing maxilla with spines); (b) *Auchenipterus osteomystax*, MZUSP 103352, 133 mm SL. Both collected at rio Jari, Monte Dourado, Pará, photographed live.



Fig. 43. Lower jaw in medial view of (a) *Wertheimeria maculata*, MZUSP 93659, 217 mm SL; (b) *Liosomadoras oncinus*, MZUSP 105828, 110 mm SL. Scale bars equal 10 mm. Coronomeckelian bone outlined.

facial nerve and contacting the dorsal border of the dentary. This character was coded as polymorphic for *Pterodoras granulosus*; as inapplicable for the Malapteruridae and Mochokidae; and as missing data for *Spinipterus*.

138. Ascending process of Meckel's cartilage: 0- present; 1- absent (CI 0.25, RI 0.571).

Among specimens examined, the ascending process of the Meckel's cartilage is absent only in the Amphiliidae, Malapteruridae, Mochokidae, Nematogenyidae and Siluridae (Mo, 1991: #35; de Pinna, 1993: #22; Britto, 2002: #155; Diogo, 2004: #419; Vigliotta, 2008: #24). This character was coded as missing data for the auchenipterid *Spinipterus*.

139. Coronoid process of lower jaw: 0- present; 1- absent (CI 0.5, RI 0.75).

Among examined specimens, the coronoid process of the lower jaw is absent only in the Mochokidae and auchenipterid *Asterophysus* (de Pinna, 1993: #50; Britto, 2002: #151; Diogo, 2004: #400; Vigliotta, 2008: #27). In the Siluridae, this process is extremely small, but present. This character was coded as missing data for the auchenipterid *Spinipterus*.

140. Angle between lower jaws: 0 - approximately 90°; 1- between 135° and 180° (CI 1.0, RI 1.0).

In the examined species of the Mochokidae (except *Acanthocleithron*, *Mochokiella*, *Mochokus*, and *Synodontis membranaceus*) the lower jaws meet at an angle between 135° and 180° (Vigliotta, 2008: #28). The same condition is present in the Loricariidae. In all other examined species, the lower jaws are arranged in an angle of approximately 90°.

141. Connective tissue parallel to primordial ligament: 0- absent; 1- present (CI 1.0, RI 1.0).

In members of the Anchariidae, Ariidae, Auchenoglanidae, and Claroteidae, there is a connective tissue sheath parallel

to the primordial ligament, associated with both the coronoid process of the lower jaw and the maxillary barbel (Mo, 1991: #28; de Pinna, 1993: #29; Royero, 1999: #145; Britto, 2002: #150; Marceniuk *et al.*, 2012: #112). This feature is absent in other catfishes. This character was coded as missing data for the auchenipterid *Spinipterus*.

142. Ventral process of dentary: 0- absent; 1- present (CI 0.333, RI 0.6).

In the Malapteruridae, ariid *Genidens* (Marceniuk *et al.*, 2012: #108), and the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus*, one or two ventral processes are present on the dentary. Those processes are probably associated with the mental barbels (Fig. 30; Ferraris, 1988: #J17; Akama, 2004: #53). In all other examined specimens those processes are absent. This character was coded as missing data for the auchenipterid *Spinipterus*.

143. Dentary teeth (ordered): 0- numerous (50 or more); 1- reduced in number (less than 50); 2- absent (CI 0.286, RI 0.894).

Most catfishes have numerous small teeth arranged in several rows on the dentary (Fig. 43). However, reduction in the number of teeth on the dentary occurs in some species. The doradids *Anduzedoras*, *Doras carinatus*, *D. higuchii*, *D. micropoeus*, *Hassar*, *Hemidoras stenopeltis*, *H. stubelii*, *Nemadoras*, *Ossancora*, *Tenellus* and some specimens of *Doras phlyzakion*, *Leptodoras praelongus*, and *L. juruensis* have fewer than 50 teeth on the dentary (Higuchi, 1992: #49, #A41). The auchenipterids *Auchenipterus* and *Entomocorus* have also reduced number of teeth arranged in few rows on dentary (Ferraris, 1988: #J8; Akama, 2004: #50). The auchenipterids *Epapterus* and *Pseudepapterus*, and doradids *Hemidoras morei*, *H. morrissi*, *Leptodoras marki*, *L. oyakawai*, *Oxydoras*, *Trachydoras* and some specimens of *Doras phlyzakion*, *Leptodoras juruensis* and *L. praelongus* have an edentulous dentary (Higuchi, 1992: #48; Sabaj, 2002: #14). This character was coded as polymorphic (1,2) for *Doras phlyzakion*, *Leptodoras juruensis* and *L. praelongus*.

144. Insertion of dentary teeth: 0- inserted directly on surface of dentary; 1- inserted in a depression of the dentary (CI 1.0, RI 1.0).

In most catfishes, the teeth are inserted directed on the surface of the dentary bone (Fig. 43). However, in all species of the Mochokidae (except *Mochokiella* and *Mochokus*), the dentary has a deep depression that supports the teeth (Vigliotta, 2008: #30, #32). A similar condition occurs in the Amphiliidae, Loricariidae, and Astroblepidae (de Pinna, 1993: #49; Britto, 2002: #160; Diogo, 2004: #396).

145. Ventral process on symphysis of dentary: 0- absent; 1- present (CI 0.5, RI 0.667).

Members of the Anchariidae, Ariidae, Auchenoglanidae, Callichthyidae, Claroteidae, Malapteruridae, and Schilbeidae have a ventral process on the symphysis of the dentary, onto which the *intermandibularis* muscle is attached (Britto, 2002:

#162). That process is absent in other examined taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

Suspensorium.

146. Anterior condyle of autopalatine: 0- double; 1- single (CI and RI inapplicable).

In the Diplomystidae, the autopalatine has a double condyle anteriorly for articulation with the maxilla (Lundberg, 1970; Arratia, 1987; Arratia, 1992: #9; Grande & de Pinna, 1998; Britto, 2002: #171). In all other catfishes the autopalatine has a single condyle anteriorly. This character was coded as missing data for the auchenipterid *Spinipterus*.

147. Shape of autopalatine: 0- depressed, with wide anterior end; 1- cylindrical, anterior end not distinctly enlarged (CI 1.0, RI 1.0).

In the Diplomystidae and Nematogenyidae the autopalatine is depressed and has a wide anterior end (Arratia, 1992: #7; Marceniuk *et al.*, 2012: #98). The autopalatine is more or less uniformly cylindrical in all other catfishes. This character was coded as missing data for the auchenipterid *Spinipterus*.

148. Length of autopalatine: 0- relatively short, length of autopalatine smaller than length of lower jaw; 1- relatively long, length of autopalatine greater than length of lower jaw (CI 0.5, RI 0.974).

In most catfishes, the autopalatine is relatively short, shorter than the lower jaw (Figs. 20-21, 23, 28, 33a). However, in the doradids *Anduzedoras*, *Centrodoras brachiatus*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Orinocodoras*, *Ossancora*, *Oxyodoras*, *Rhinodoras*, *Rhynchodoras*, *Tenellus*, and *Trachydoras*, it is extremely elongate and distinctly longer than the lower jaw (Figs. 25, 27, 33b; Eigenmann, 1925: 286; Higuchi, 1992: #47; Sousa, 2010: #34). This character was coded as missing data for the auchenipterid *Spinipterus*.

149. Posterior limit of autopalatine: 0- anterior orbital margin; 1- approximately at vertical through middle of orbit (CI 0.5, RI 0.833).

The posterior limit of the autopalatine is anterior to the orbital margin in most examined species, including the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxyodoras*, *Tenellus*, and *Trachydoras* that have an elongate autopalatine (Figs. 20-22, 26-28). However, the posterior limit of the autopalatine lies near the middle of the orbit in the Diplomystidae, and doradids *Orinocodoras*, *Rhinodoras* and *Rhynchodoras* (Fig. 40; Higuchi, 1992: #A40; Birindelli *et al.*, 2007). This character was coded as missing data for the auchenipterid *Spinipterus*.

150. Position of articular facet of autopalatine: 0- dorsal; 1- lateral (CI 1.0, RI 1.0).

Among catfishes, the articular facet of the autopalatine is

dorsal only in the Cetopsidae, Diplomystidae, and Loricarioidei, all of which are widely regarded as relatively basal members of the Siluriformes (Lundberg, 1970; Mo, 1991: #3; de Pinna, 1993: #59; Grande & de Pinna, 1998; Britto, 2002: #13; Diogo, 2004: #296; de Pinna *et al.*, 2007: #14). This character was coded as missing data for the auchenipterid *Spinipterus*.

151. Length of anterior cartilage of autopalatine: 0- short, length distinctly smaller than that of ossified portion of autopalatine; 1- long, length nearly equal to, or greater than, that of ossified portion of autopalatine (CI 1.0, RI 1.0).

Among examined catfishes, the anterior cartilage of the autopalatine is extremely elongate (nearly equal to or greater than of the ossified portion of the autopalatine) only in the Anchariidae, Ariidae and Claroteidae (Mo, 1991; de Pinna, 1993: #25; Britto, 2002: #172; Diogo, 2004: #277; Marceniuk *et al.*, 2012: #106). This character was coded as missing data for the auchenipterid *Spinipterus*.

152. Posterior cartilage of autopalatine: 0- present; 1- absent (CI 0.5, RI 0.0).

Among examined catfishes the posterior cartilage of the autopalatine is absent only in the Malapteruridae, mochokids Chiloglanidinae and some specimens of *Amphilius jacksoni* (Amphiliidae) (Mo, 1991; Arratia, 1992; de Pinna, 1993: #21; Diogo, 2004: #283; Vigliotta, 2008: #41). This character was coded as polymorphic for *Amphilius jacksoni*. This character was coded as missing data for the auchenipterid *Spinipterus*.

153. Medial lamina of hyomandibula: 0- present; 1- absent (CI 1.0, RI 1.0).

In most catfishes, the hyomandibula is an elongate bone with a medial lamina that supports the insertion of most of the *adductor mandibulae* muscle (Fig. 44). In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras* the hyomandibula is extremely elongate and lacks the medial lamina (Figs. 26, 27; Higuchi, 1992: #54). This character was coded as missing data for the auchenipterid *Spinipterus*.

154. Hyomandibular crest for *levator arcus palatini* muscle (ordered): 0- absent or rudimentary; 1- weakly developed; 2- well developed (CI 0.286, RI 0.839).

In several catfishes, including among examined taxa the Auchenipteridae, Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Ictaluridae, Nematogenyidae, Pangasiidae, Pseudopimelodidae, and doradid *Franciscodoras*, the hyomandibular crest, on which the *levator arcus palatini* muscle inserts, is weakly developed (Figs. 44a,b,c; Lundberg, 1970: #62; Arratia, 1992: #31). However, in the doradids *Kalyptodoras* and *Wertheimeria* the hyomandibular crest is developed as a distinct process (Fig. 44g). The hyomandibular crest is absent (Figs. 44h,i) in the Amphiliidae, Ariidae, Aspredinidae, Erethistidae, Heptapteridae, Malapteruridae, Mochokidae, Pimelodidae, Siluridae, and all species of Doradidae (except *Franciscodoras*, *Kalyptodoras*, and

Wertheimeria). This character was coded as missing data for the auchenipterid *Spinipterus*.

155. Orientation of hyomandibular crest for *levator arcus palatini* muscle: 0- horizontal; 1- vertical (CI 1.0, RI 1.0).

In the Bagridae, Cetopsidae, Claroteidae, Diplomystidae, Ictaluridae, Pangasiidae, Pseudopimelodidae, the hyomandibular crest is horizontal, parallel to the body axis. However, in the Auchenipteridae, Nematogenyidae, and doradids *Franciscodoras*, *Kalyptodoras* and *Wertheimeria* the hyomandibular crest, on which the *levator arcus palatini* muscle inserts, is vertical relative to the body axis (Figs. 44a,b,c,g; Lundberg, 1970; Arratia, 1992: 117). This character was coded as inapplicable for the Amphiliidae, Ariidae, Aspredinidae, Erethistidae, Heptapteridae, Malapteruridae,

Mochokidae, Pimelodidae, Siluridae, and all species of Doradidae (except *Franciscodoras*, *Kalyptodoras*, and *Wertheimeria*); and as missing data for the auchenipterid *Spinipterus*.

156. Hyomandibular crest for Aw section of *adductor mandibulae* muscle: 0- absent; 1- present (CI 1.0, RI 1.0).

In the doradids *Orinocodoras*, *Rhinodoras*, and *Rhynchodoras* there is a distinct crest on the hyomandibula, on which the Aw section of the *adductor mandibulae* muscle is inserted (Fig. 44h). That crest is absent in other examined taxa (Fig. 44a-c, g-h). This character was coded as missing data for the auchenipterid *Spinipterus*.

157. Hyomandibular process for *adductor mandibulae*

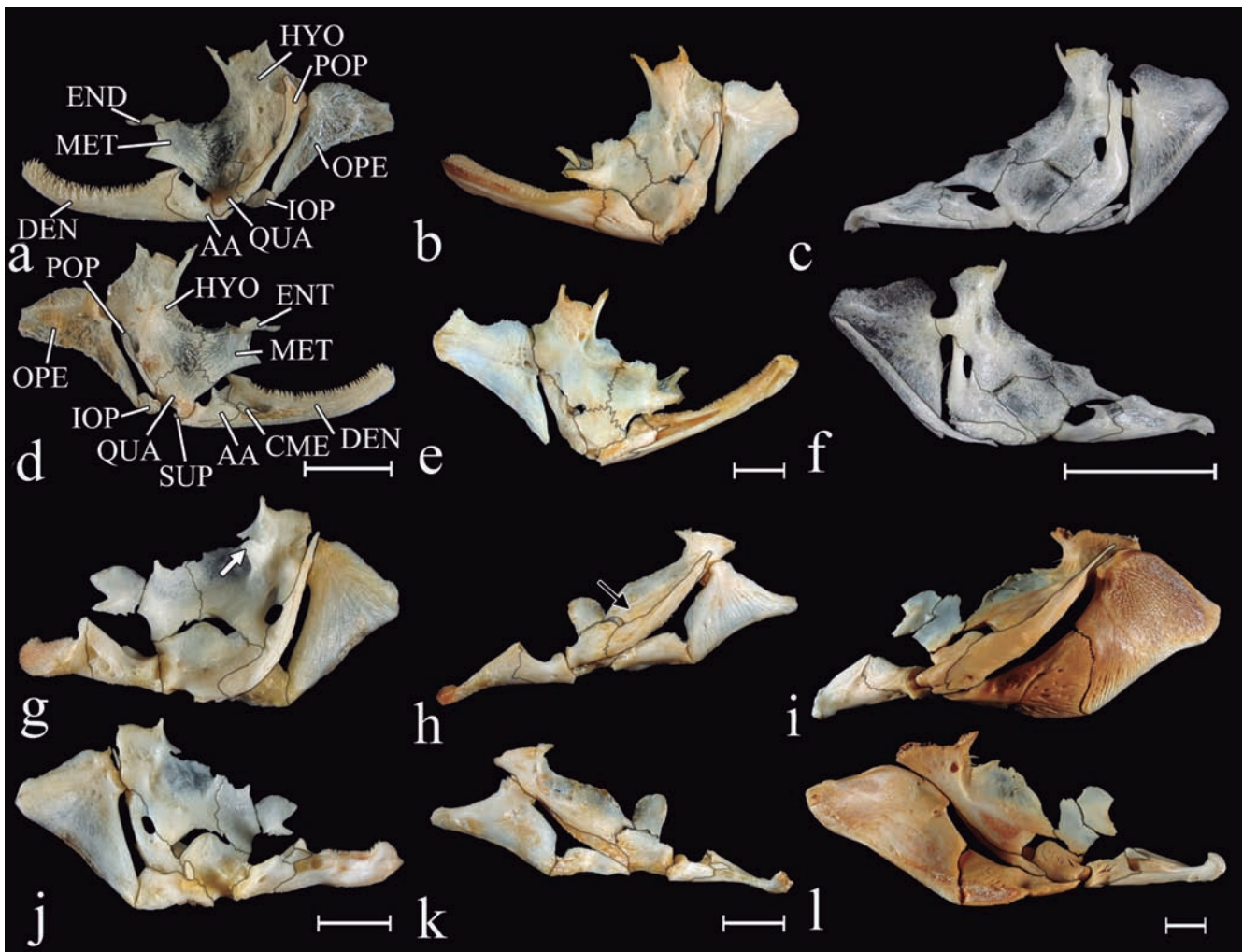


Fig. 44. Suspensorium in lateral (a-c,g-i) and medial (d-f,j-l) views of (a,d) *Glanidium melanopterum*, MZUSP 64256, 112 mm SL; (b,e) *Trachycorystes trachycorystes*, MZUSP 91659, 200 mm SL; (c,f) *Auchenipterus nuchalis*, MZUSP 97375, 117 mm SL; (g,j) *Wertheimeria maculata*, MZUSP 93659, 217 mm SL; (h,k) *Rhinodoras dorbignyi*, MZUSP 40109, 196 mm SL; (i,l) *Oxydoras niger*, MZUSP 91654, 550 mm SL. AA anguloarticular, CME coronomeckelian bone, DEN dentary, ENT entopterygoid, HYO hyomandibula, IOP interopercle, MET metapterygoid, OPE opercle, POP preopercle, QUA quadrate, SUP subpreopercle. White arrow indicates hyomandibular crest for attachment of muscle *levator arcus palatini*, black arrow indicates hyomandibular crest for section Aw of muscle *adductor mandibulae*. Scale bars equal 10 mm.

muscle: 0- absent or rudimentary; 1- well developed (CI 0.333, RI 0.6).

The hyomandibula has a distinct and well-developed process, on which the *adductor mandibulae* muscle inserts, that is positioned dorsal to the articulation between the hyomandibula and the opercle in the Ariidae, Claroteidae, Ictaluridae, Pangasiidae and Pimelodidae (Lundberg, 1970: 36; Pinna, 1993: #92; Britto, 2002: #184). This process is rudimentary (or absent) in all other examined species (Fig. 44). This character was coded as missing data for the auchenipterid *Spinipterus*.

158. Medial process of hyomandibula: 0- absent; 1- present (CI 0.5, RI 0.0).

In the mochokids *Microsynodontis*, *Mochokiella* and several species of *Synodontis* (including *S. schall*) there is a medial process on the hyomandibula (Vigliotta, 2008: #42), that is absent in other examined taxa (Fig. 44). The association between this process and muscles of the suspensorium has not been determined. This character was coded as missing data for the auchenipterid *Spinipterus*.

159. Posterodorsal process of hyomandibula: 0- absent; 1- present (CI 0.25, RI 0.8).

In all auchenipterids, except *Asterophysus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, and *Pseudepapterus*, there is a distinct posterodorsal process on the hyomandibula, posterior to the articulation between the hyomandibula and cranium (Figs. 44a,b; Royero, 1999: #61; Akama, 2004: #56). That process is absent in all other examined taxa (Fig. 44c,g-i). This character was coded as missing data for *Spinipterus*.

160. Hyomandibular condyle for opercle: 0- on a short process, which is shorter than the anterodorsal process of hyomandibula; 1- on a long process, which is longer than the anterodorsal process of hyomandibula (CI 0.5, RI 0.75).

In the Aspredinidae and auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* (de Pinna, 1996: #23), the hyomandibular condyle for the opercle is located on a distinctly elongated process, which is longer than the anterodorsal process of hyomandibula (Fig. 44c, f; Royero, 1999: #63; Akama, 2004: #58). In all other examined taxa, the hyomandibular condyle for the opercle is located on a short process (Fig. 44d-e,j-l). This character was coded as missing data for the auchenipterid *Spinipterus*.

161. Number of openings in hyomandibula for a hyomandibular branch of trigeminofacial nerve: 0- one; 1- two (CI 1.0, RI 1.0).

In most catfishes, there is a single opening in the hyomandibula for the passage of the hyomandibular branch of the trigeminofacial nerve (Fig. 44a,c). However, there are two opening in the auchenipterids *Trachelyopterus coriaceus*, *T. galeatus*, and *Trachycorystes* (Fig. 44b; Royero, 1999: #60; Akama, 2004: #55). This character was coded as

missing data for the auchenipterid *Spinipterus*.

162. Articulation between hyomandibula and cranium (ordered): 0- through sphenotic, pterotic and prootic; 1- through sphenotic and pterotic; 2- only through sphenotic (CI 0.167, RI 0.545).

In most catfishes, the articulation between the hyomandibula and cranium is through the pterotic and sphenotic (Fig. 33b; Mo, 1991: #21; Arratia, 1992: #35; Royero, 1999: #56; Britto, 2002: #181). However, in the Diplomystidae, Nematogenyidae and Mochokidae (except *Mochokus*) the articulation also occurs through the prootic (Alexander, 1965: 97; Arratia, 1992: #35; Vigliotta, 2008: #10). On the other hand, in the Amphiliidae, Ariidae, Erethistidae, auchenipterids *Asterophysus*, *Auchenipterichthys*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tatia*, *Trachelyopterichthys*, *Trachelyopterus* and *Trachycorystes*, and doradids *Acanthodoras* and *Agamyxis*, *Kalyptodoras*, and *Wertheimeria*, the hyomandibula articulates with the cranium only via the sphenotic (Fig. 33a). This character was coded as missing data for the auchenipterid *Spinipterus*.

163. Dorsomedial lamina of quadrate: 0- absent; 1- present (CI 0.5, RI 0.667).

Among examined species, the quadrate possesses a distinct dorsomedial lamina only in the auchenipterids *Ageneiosus*, *Centromochlus existimatus*, *C. heckelii* and *Tetranematichthys* (Fig. 31; Ferraris, 1988: #J2; Walsh, 1990: #1; Soares-Porto, 1998: #13; Royero, 1999: #55, #59; Akama, 2004: #47). This character was coded as missing data for the auchenipterid *Spinipterus*.

164. Hyomandibula and metapterygoid: 0- in contact; 1- separated (CI 0.143, RI 0.842).

In most catfishes, the hyomandibula articulates with the metapterygoid (Fig. 44). However, in the Amphiliidae, Aspredinidae, Claroteidae, Heptapteridae, Malapteruridae, doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus* and *Trachydoras*, and auchenipterids *Centromochlus*, *Tetranematichthys*, *Ageneiosus*, and some specimens of *Tatia aulopygia* (Britski, 1972: 23), the hyomandibula and metapterygoid are not in contact (Figs. 26, 27, 31; Arratia, 1992: #25; Britto, 2002: #189). Alexander (1965) considered this lack of contact directly associated to the enlargement of the eye. This character was coded as polymorphic for the auchenipterid *Tatia aulopygia*; and as missing data for the auchenipterid *Spinipterus*.

165. Size of entopterygoid: 0- relatively small, smaller than metapterygoid; 1- relatively large, larger than metapterygoid (CI 1.0, RI 1.0).

Although its homology remains an unsettled subject in catfish anatomy (Arratia, 1992), the entopterygoid (or 'entopterygoid' of types 3-7 of Arratia, 1992: fig. 2, formed by the ligament between metapterygoid and lateral ethmoid or

vomer) is relatively small in most catfishes (Fig. 44; Britto, 2002: #186; Arratia, 1992: #20-21; Vigliotta, 2008: #44). However, in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Tenellus*, and *Trachydoras*, the entopterygoid is relatively large, larger than the metapterygoid (Figs. 26, 27, 33b; Britski, 1972: 23; Higuchi, 1992: #50, #51; Sousa, 2010: #41). This character was coded as inapplicable for the Claroteidae and mochokids *Mochokiella* and *Mochokus* (Vigliotta, 2008: #44); and as missing data for the auchenipterid *Spinipterus*.

166. Ectopterygoid: 0- absent; 1- present (CI 0.25, RI 0.5).

Most catfishes lack an ectopterygoid. However, the Ariidae, Bagridae, Claroteidae, Pangasiidae, Pimelodidae, Pseudopimelodidae, Sisoridae (Ferraris, 1988: #J4; Arratia, 1992: #18; Britto, 2002: #188), and some specimens of *Diplomystes* (see Arratia, 1992), have an ectopterygoid. This character was coded as polymorphic for the Diplomystidae; and as missing data for the auchenipterid *Spinipterus*.

Opercular series.

167. Suprapreopercle: 0- absent; 1- present (CI 0.2, RI 0.857).

In the Amphiliidae, Auchenipteridae (except *Liosomadoras*), Bagridae, Diplomystidae, Erethistidae, Malapteruridae, Ictaluridae, Nematogenyidae, Siluridae, and Sisoridae, there are one or more tubular bones (= suprapreopercles), between the preopercle and pterotic (Figs. 28, 29, 31; Britski, 1972: 21; Lundberg, 1970: #70; Britto, 2002: #196); this condition is absent in all other examined species (Figs. 20-27). This character was coded as missing data for the auchenipterid *Spinipterus*.

168. Subpreopercle: 0- absent; 1- present (CI 0.2, RI 0.556).



Fig. 45. Urohyal in ventral (a,c) and dorsal (b,d) views of (a,b) *Ictalurus punctatus*, MZUSP 103256, 155 mm SL; (c,d) *Kalyptodoras bahiensis*, MZUSP 87841, 233 mm SL. Scale bars equal 5 mm.

Among examined species, only those of the Amphiliidae, Auchenipteridae, Bagridae, Cetopsidae, Diplomystidae, Doradidae, Erethistidae, Heptapteridae, Ictaluridae, Malapteruridae, Nematogenyidae, Pangasiidae, Pimelodidae and Sisoridae (Britto, 2002: #197) have a small ossification between the preopercle and hyomandibula, the subpreopercle (Fig. 44b). This character was coded as missing data for the auchenipterid *Spinipterus*.

Hyoid arch

169. Lateral laminar wings of urohyal: 0- present; 1- absent (CI 1.0, RI 1.0).

The urohyal possesses lateral laminar wings in all catfishes (Figs. 45a,b; Lundberg, 1970; Arratia & Schultze, 1990), except those of the Auchenipteridae, Doradidae and Mochokidae (Figs. 45c,d; Mo, 1991: #39; de Pinna, 1993: #239; Royero, 1999: #146; Britto, 2002: #81; Vigliotta, 2008: #46). Diogo (2004: #388) considered the urohyal of the mochokid *Synodontis* reduced. This character was coded as missing data for the auchenipterid *Spinipterus*.

170. Dorsal process of urohyal: 0- absent; 1- present (CI 0.5, RI 0.667).

In most catfishes, the dorsal face of the urohyal has a

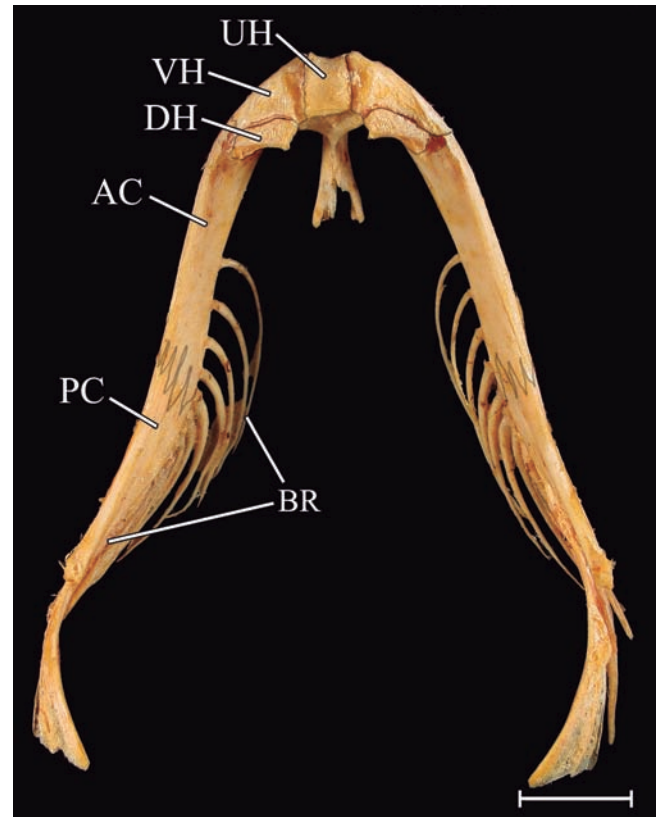


Fig. 46. Hyoid arch in dorsal view of *Ageneiosus inermis*, MZUSP 91661, 320 mm SL. AC anterior ceratobranchial, BR branchiostegal rays, DH dorsal hypophyal, PC posterior ceratohyal, UH urohyal, VH ventral hypophyal. Scale bar equals 10mm.

small crest to which the paired ventral hypohyals are dorsally attached (Fig. 45b,d). However, in the auchenipterids *Ageneiosus*, *Tetranematichthys*, and *Tocantinsia*, the urohyal has a dorsal process located between and at the same level of the paired ventral hypohyals (Fig. 46; Ferraris, 1988: #G7; Walsh, 1990: #9; Akama, 2004: #82). This process is extremely large in *Ageneiosus inermis*, and relatively small in *Ageneiosus atronatus*, *A. brevis*, *A. ucayalensis*, *Tetranematichthys*, and *Tocantinsia*. Although this feature was reported in the auchenipterids *Auchenipterus* and *Entomocorus* by Walsh (1990: #9), and in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras* by Higuchi (1992: #57), the dorsal process of the urohyal is not present in the examined specimens of those taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

171. Dorsal hypohyal: 0- present; 1- absent (CI 0.2, RI 0.0).

In the Amphiliidae, Akysidae, Aspredinidae, Astroblepidae, Loricariidae, Pseudopimelodidae, Sisoridae, Trichomycteridae,

and the mochokid *Chiloglanis*, the dorsal hypohyal is absent (Mo, 1991: #43; Britto, 2002: #75). Vigliotta (2008: #47) considered the dorsal hypohyal to be fused into the ventral hypohyal, thus present, in the mochokids *Atopodontus* and *Chiloglanis*. However, the presence of a rudimentary dorsal hypohyal in small specimens of *Chiloglanis polypogon* examined herein suggests that the dorsal hypohyal is ontogenetically reduced and lost in those taxa, rather than fused into the ventral hypohyal. Based on the present observations, *Chiloglanis* was coded as 1 for this character. The dorsal hypohyal is present in all other examined species. This character was coded as missing data for *Spinipterus*.

172. Shape of ventral hypohyal: 0- rectangular, length distinctly smaller than width; 1- quadrangular, length and width approximately equal (CI 1.0, RI 1.0).

In most catfishes, the ventral hypohyal is rectangular, with length distinctly smaller than width (Figs. 47a,b). However, it is nearly a square, with the length and width approximately equal, in the doradids *Anduzedoras*, *Doras*, *Hassar*,

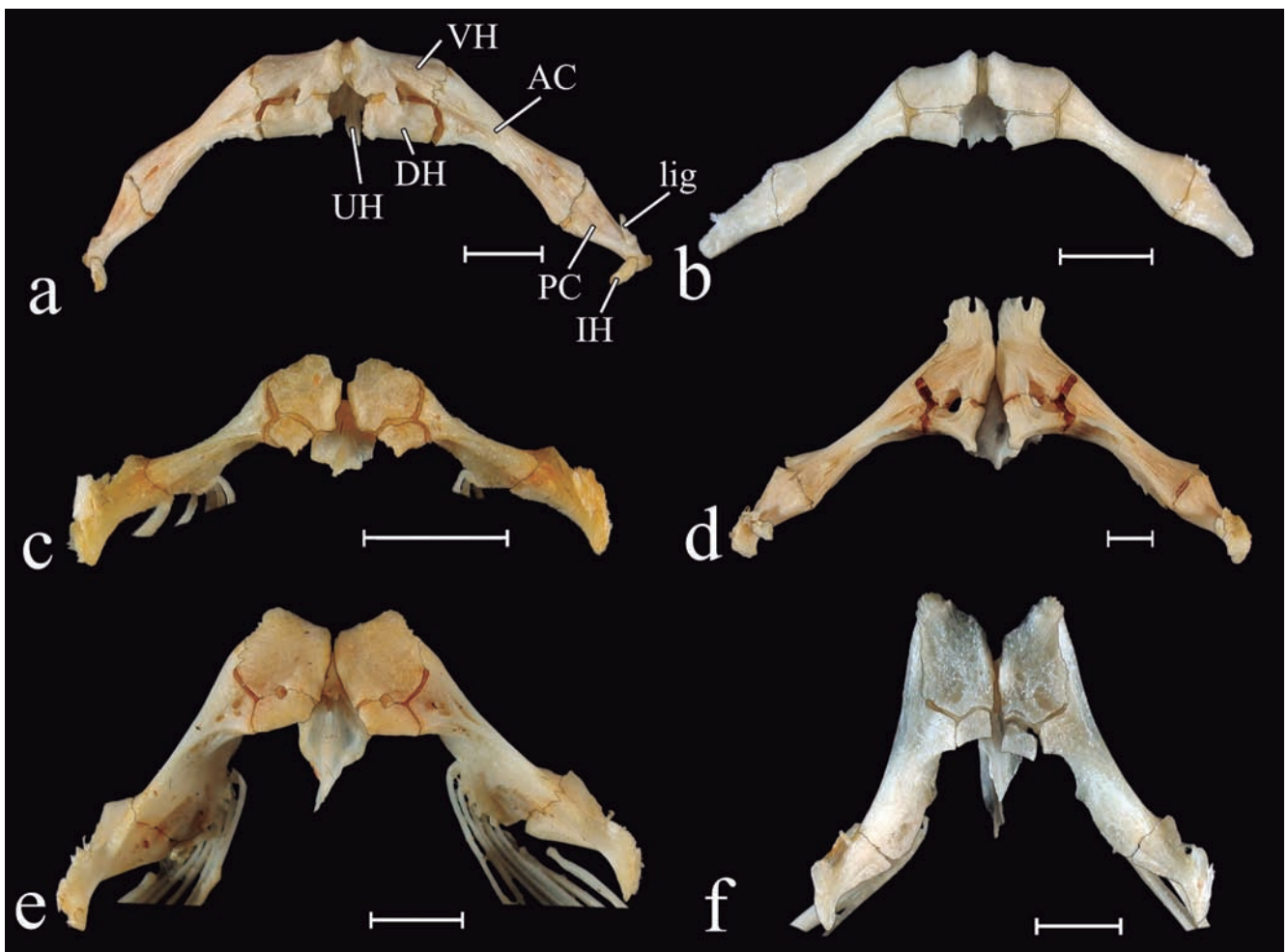


Fig. 47. Hyoid arches in dorsal view of (a) *Pterodoras granulatus*, MZUSP 91655, 410 mm SL; (b) *Kalyptodoras bahiensis*, MZUSP 87842, 152 mm SL; (c) *Trachydoras brevis*, MZUSP 103087, 74 mm SL; (d) *Oxydoras niger*, MZUSP 91658, 313 mm SL; (e) *Doras higuchii*, MZUSP 96334, 165 mm SL; (f) *Hemidoras morei*, MZUSP 32526, 153.2 mm SL. AC anterior ceratobranchial, DH dorsal hypohyal, IH interhyal, lig ligament, PC posterior ceratohyal, UH urohyal, VH ventral hypohyal. Scale bar equals 10 mm.

Hemidoras, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, *Tenellus*, and *Trachydoras* (Figs. 47c-f). This character was coded as missing data for the auchenipterid *Spinipterus*.

173. Anterior margin of ventral hypohyal: 0- smooth, without spines; 1- with spines (CI 0.5, RI 0.955).

In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Oxydoras* and *Tenellus*, the anterior margin of the ventral hypohyal has spines (Figs. 47d-f). The same condition is present in *Leptodoras oyakawai*, although not illustrated by Birindelli *et al.* (2008), due to the angle for which the bone was illustrated. In all other examined species, the anterior margin of ventral hypohyal is straight, without spines (Fig. 47a-c). This character was coded as missing data for the auchenipterid *Spinipterus*.

174. Anterior portion of anterior ceratohyal (ordered): 0- without anterior process; 1- with small anterior process sutured to ventral hypohyal (suture occupying less than half of lateral border of ventral hypohyal); 2- with long anterior process sutured to ventral hypohyal (suture occupying more than half of border of ventral hypohyal) (CI 0.5, RI 0.952).

In most catfishes, the anterior ceratohyal does not have an anterior process, being connected to the ventral hypohyal mostly via cartilage, suturing restricted to a small portion of the anterior face and present only in larger specimens (Figs. 47a,b; Lundberg, 1970). However, in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Leptodoras*, *Ossancora*, and *Trachydoras*, and there is a small anterior process of the ceratohyal sutured to the ventral hypohyal, the suture occupying less than half of the lateral border of the ventral hypohyal (Figs. 47c,d). In the doradids *Hemidoras*, *Nemadoras*, *Oxydoras*, and *Tenellus*, on the other hand, there is a long anterior process sutured to the ventral hypohyal, the suture occupying more than half of the lateral border of the ventral hypohyal (Figs. 47d,f). This character was coded as missing data for the auchenipterid *Spinipterus*.

175. Posterior portion of ventral hypohyal and anterior ceratohyal: 0- connected via cartilage; 1- connected via bony suture (CI 0.2, RI 0.5).

In the amphiliid *Amphilius jacksoni*, auchenipterids *Ageneiosus* and *Tetranematichthys*, and doradids *Lithodoras*, *Oxydoras*, and *Rhinodoras* the posterior portion of the ventral hypohyal and the anterior ceratohyal are connected via bony suture in medium and large-sized specimens (Figs. 46, 47d; Ferraris, 1898: #G8; Walsh, 1990: #10; Akama, 2004: #83; Sousa, 2010: #36). This character was coded as missing data for the doradids *Rhinodoras thomersoni* and *Megalodoras*, and the auchenipterid *Spinipterus*.

176. Interhyal: 0- present; 1- absent (CI 0.333, RI 0.667).

The interhyal is absent in the Amblycipitidae, Amphiliidae, Akysidae, Astroblepidae, Clariidae, Erethistidae, Mochokidae, Scoloplacidae, and Sisoridae (Mo, 1991: #45; Britto, 2002: #79; Vigliotta, 2008: #49), being present in members of all other

examined taxa (Fig. 47a). This character was coded as missing data for the auchenipterid *Spinipterus*.

177. Number of branchiostegal rays (ordered): 0- four to six; 1- seven to nine; 2- ten to twenty (CI 0.2, RI 0.5).

The number of branchiostegal rays varies from three to twenty in catfishes (McAllister, 1968; Lundberg, 1970; Arratia, 2003a), although eight is the most common value. In the typical condition, one or two are articulated to the interceratohyal cartilage, four or five to the anterior ceratohyal and two or three to the posterior ceratohyal. Among the examined taxa, most species have seven to nine branchiostegal rays; however members of the Ariidae, Aspredinidae, Erethistidae, Sisoridae, mochokids *Mochokiella*, *Mochokus niloticus*, and *Chiloglanis* (Vigliotta, 2008: #52), auchenipterids *Centromochlus*, *Gelanoglanis*, *Glanidium* and *Tatia*, and doradids *Acanthodoras* and some specimens of *Platyodoras armatulus* have four to six (Sousa, 2010: #39). The Bagridae, Nematogenyidae, Pangasiidae, Siluridae, and the auchenipterids *Ageneiosus* (*A. inermis*, *A. polystictus*, *A. ucayalensis*, *A. valenciennesi*, and *A. vittatus*) and *Tetranematichthys* have ten or more (Walsh, 1990: #35). This character was coded as missing data for the auchenipterid *Pseudotatia*, *Spinipterus*, and as polymorphic (0,1) for *Platyodoras armatulus*.

Brachial arches

178. Pseudobranchia: 0- present; 1- absent (CI 1.0, RI 1.0).

A pseudobranch is only present in the Diplomystidae and Nematogenyidae (Arratia, 1992: #34), among examined taxa.

179. Accessory branchial lamellae on ceratobranchial (ordered): 0- absent; 1- restricted to branchial arch; 2- distributed on branchial arch and filaments (CI 0.667, RI 0.966).

In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, and *Tenellus* there are conspicuous accessory lamellae on the medial face of the ceratobranchials (best developed on first two branchial arches; Figs. 48g,h,k,l, 49; Higuchi, 1992: #A49, #A50). In addition, these lamellae are also extended onto the branchial filaments in *Leptodoras* (Fig. 49k-l; Higuchi, 1992: #A51; Sabaj, 2002: #15; Sabaj, 2005; Birindelli *et al.*, 2008; Birindelli & Sousa, 2010). In all other examined taxa, the accessory branchial lamellae are absent from ceratobranchials (Fig. 48a-f,i-j).

180. Accessory lamellae on epibranchials (unordered): 0- absent; 1- similar to those of ceratobranchial; 2- developed as three large lamellae; 3- developed as a thick lobe (CI 0.75, RI 0.963).

In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, and *Tenellus*, there are accessory lamellae on the epibranchials, similar to those on the ceratobranchial (Figs. 48k,l, 49). The doradid *Oxydoras niger* (congeners not observed) has three large lamellae on the epibranchials, distinct from the small lamellae of the ceratobranchial (Figs. 48g,h). The doradids *Rhinodoras* and *Orinocodoras*, on the other hand, have a thick lobe on the

epibranchials (Figs. 48e,f). All other examined taxa lack accessory branchial lamellae on epibranchials (Fig. 48a-f,i-j). This character was coded as missing data for the doradid *Oxydoras kneri*.

181. Number of rows of gill rakers on first two branchial arches (ordered): 0- two; 1- one; 2- none (CI 0.2, RI 0.6).

Most examined taxa have only one row of gill-rakers on the first two branchial arches. However, the Ariidae, Cetopsidae, Diplomystidae, Siluridae (Lundberg, 1970; de Pinna, 1993: #176; Britto, 2002: #129; de Pinna *et al.*, 2007: #77), and the auchenipterids *Ageneiosus*, *Asterophysus*, *Auchenipterichthys*, *Liosomadoras*, *Pseudauchenipterus*, *Tetranematchthys*, *Trachelyichthys*, *Trachelyopterichthys*, and *Trachycorystes* (Britski, 1972: 24; Royero, 1999: #113; Akama, 2004: #85) have two rows of rakers on the first two branchial arches. On the other hand, members of the Aspredinidae, auchenipterid *Gelanoglanis*, doradids

Trachydoras, and some species of *Leptodoras*, including *L. cataniai*, *L. juruensis*, and *L. myersi* (Sabaj, 2005), have the first two branchial arches without gill rakers. This character was coded as missing data in the auchenipterids *Pseudotatia* and *Spinipterus*.

182. Number of rows of gill rakers on third and fourth branchial arches (ordered): 0- two; 1- one; 2- none (CI 0.182, RI 0.7).

Most examined taxa have only one row of gill rakers on the third and fourth branchial arches. However, the Ariidae, Cetopsidae, Diplomystidae, Siluridae (Lundberg, 1970; de Pinna, 1993: #176; Britto, 2002: #129; de Pinna *et al.*, 2007: #77), auchenipterids *Ageneiosus*, *Asterophysus*, *Auchenipterichthys*, *Liosomadoras*, *Pseudauchenipterus*, *Tetranematchthys*, *Trachelyichthys*, *Trachelyopterichthys*, and *Trachycorystes* (Britski, 1972: 24; Royero, 1999: #113; Akama, 2004: #85) have two rows of rakers on the third and fourth branchial arches. On the other hand, the Aspredinidae,

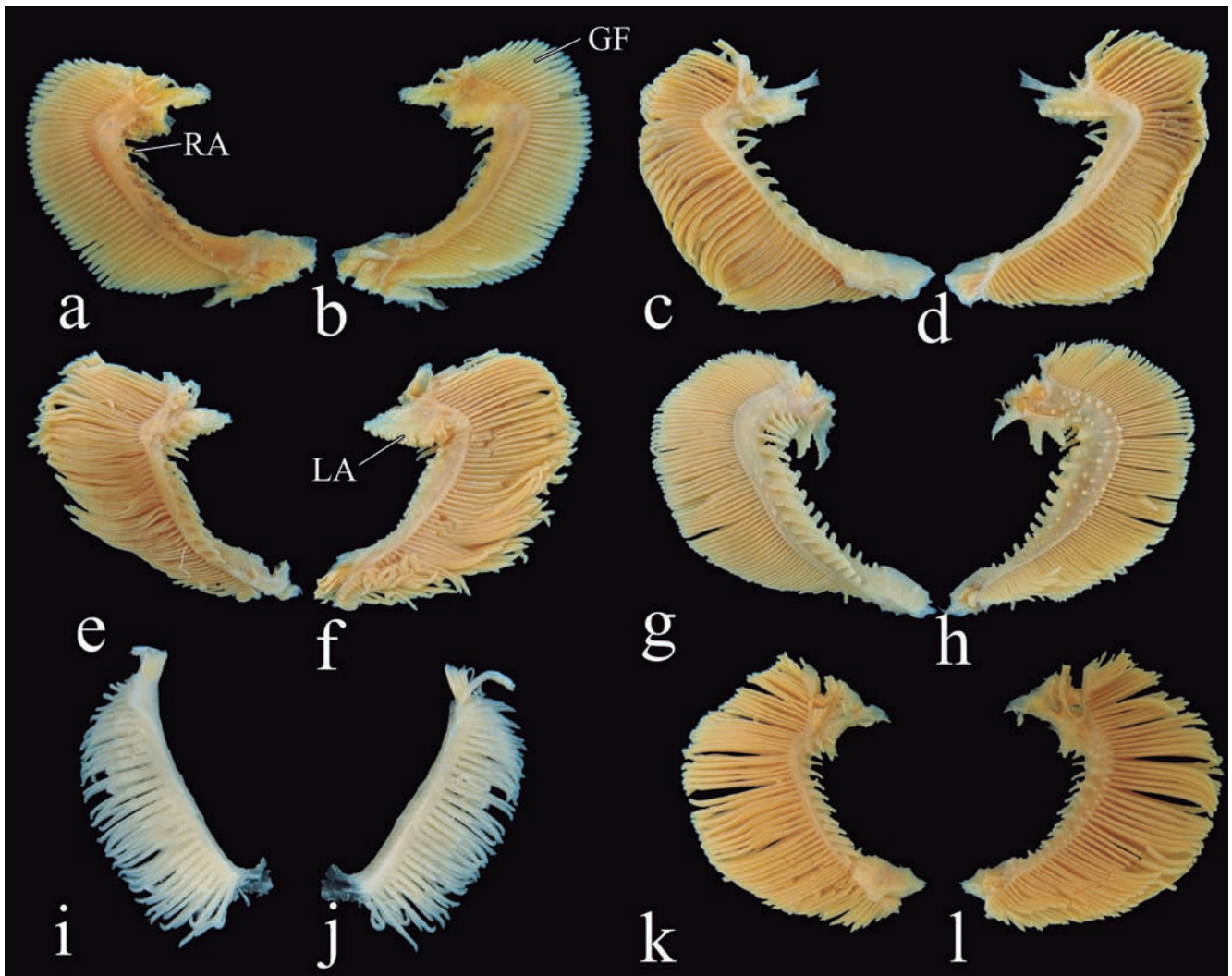


Fig. 48. First branchial arch in lateral (a,c,e,g,i,k) and medial (b,d,f,h,j,l) views of (a,b) *Platydoras armatulus*, MZUSP 94088, 135.4 mm SL; (c,d) *Centrodoras brachiatus*, MZUSP 103892, 205 mm SL; (e,f) *Rhinodoras dorbignyi*, MZUSP 36528, 141.6 mm SL; (g,h) *Oxydoras niger*, MZUSP 56162, 154.6 mm SL; (i,j) *Trachydoras steindachneri*, MZUSP 49526, 82.4 mm SL; (k,l) *Ossancora eigenmanni*, MZUSP 5646, 95.4 mm SL. GF gill filaments, LA branchial lamellae, RA gill-rakers.

auchenipterid *Gelanoglanis*, and doradids *Anduzedoras*, *Doras*, *Hassar*, *Leptodoras*, and *Trachydoras* (Sabaj & Birindelli, 2008; Birindelli *et al.*, 2009; Birindelli & Sousa, 2010), lack rakers on the third and fourth branchial arches. This character was coded as missing data in the auchenipterids *Pseudotatia* and *Spinipterus*.

183. Size of gill rakers (unordered): 0- rudimentary, length smaller

than one-tenth of that of gill filament; 1- moderately sized, length between one-tenth and half of that of gill filament; 2- elongate, longer than half of gill filament (CI 0.667, RI 0.9).

Most catfishes have moderately-sized gill-rakers, length between one-tenth and one-half that of gill filament (Figs. 48-49, 50a-b). However, the auchenipterids *Asterophysus*, *Auchenipterichthys*, *Liosomadoras*, *Pseudauchenipterus*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, and

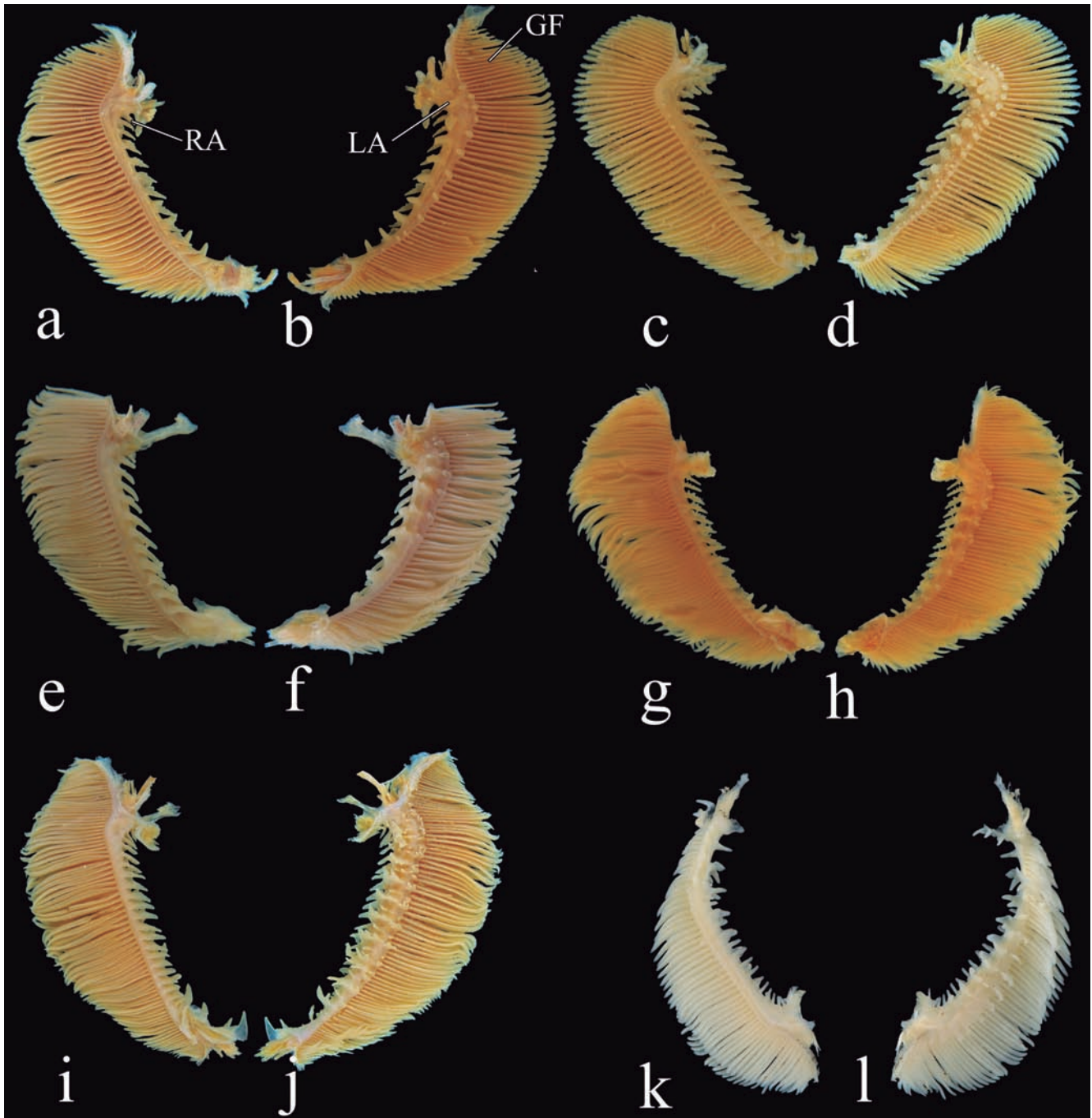


Fig. 49. First branchial arch in lateral and medial views, respectively, of (a,b) *Hemidoras morrisi*, MZUSP 23878, 161 mm SL; (c,d) *Nemadoras elongatus*, MZUSP 83211, 121.7 mm SL; (e,f) *Tenellus leporhinus*, MZUSP 95617, 136.5 mm SL; (g,h) *Hassar affinis*, 43605, 157 mm SL; (i,j) *Anduzedoras oxyrhynchus*, MZUSP 50838, 230 mm SL; (k,l) *Leptodoras marki*, MZUSP 103217, 83.2 mm SL. GF gill filaments, LA branchial lamellae, RA gill rakers.

Trachycorystes, have rudimentary gill-rakers, shorter than one-tenth of that of gill filament (Figs. 50c; Britski, 1972: 24; Ferraris, 1988: #G4; Walsh, 1990: #27; Akama, 2004: #86). Royero (1999: #111) and Akama (2004: #84) reported the gill-rakers to be lacking in *Trachelyichthys* and *Trachelyopterichthys*, but specimens observed of these taxa do indeed have short gill rakers. Elongate gill rakers, longer than half the length of a gill filament, are present in the acheniapterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus* (Fig. 50d; Britski, 1972: 24; Ferraris, 1988: #G4; Walsh, 1990: #27; Akama, 2004: #86). This character was coded as inapplicable for the Aspredinidae, acheniapterid *Gelanoglanis*, and doradids *Trachydoras*, and *Leptodoras juruensis*, which lack gill-rakers; and as missing data for the acheniapterids *Pseudotatia* and *Spinipterus*.

184. Dorsal face of gill rakers: 0- straight, without spines; 1-

with spines (CI 0.5, RI 0.0).

Among all examined species, only the acheniapterids *Tetranemataichthys* and *Tocantinsia* have gill-rakers with spines on the dorsal face (Fig. 50b; Royero, 1999: #112). Although Higuchi (1992: #A48) mentioned gill rakers with spines for the doradid *Orinocodoras eigenmanni*, and Royero (1999: #112) for the acheniapterid *Ageneiosus*; these observations were not corroborated based on the specimens examined herein. This character was coded as inapplicable for the Aspredinidae, acheniapterid *Gelanoglanis*, and doradids *Trachydoras* and *Leptodoras juruensis*, which lack gill-rakers; and as missing data for the acheniapterid *Pseudotatia* and *Spinipterus*.

185. Base of gill-rakers: 0- relatively small, not distinctly larger than diameter of gill-rakers; 1- enlarged, distinctly larger than

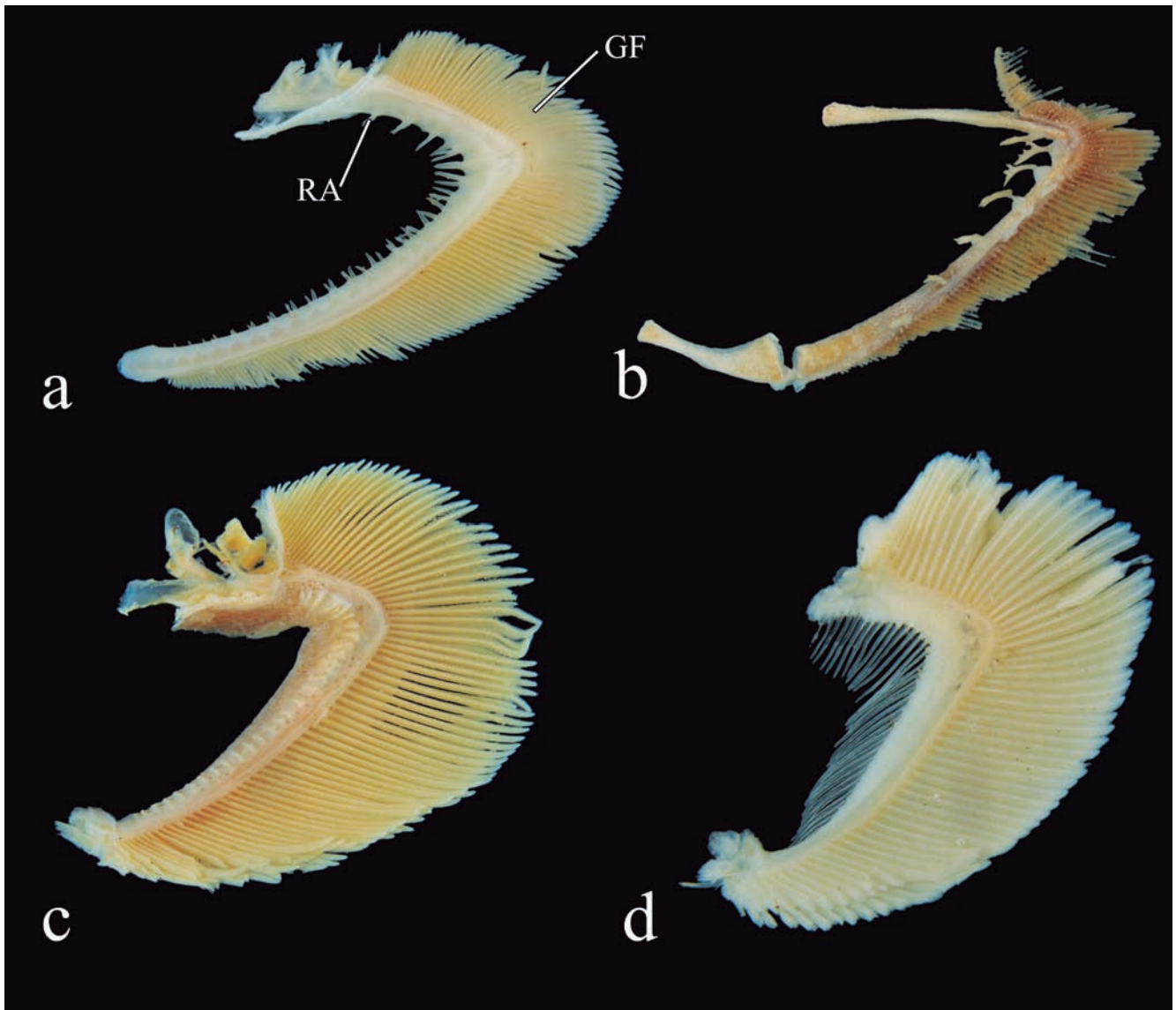


Fig. 50. First branchial arch in lateral view of (a) *Ageneiosus inermis*, MZUSP 101653, 202 mm SL; (b) *Tocantinsia piresi*, MZUSP 100031, 430 mm SL; (c) *Trachycorystes trachycorystes*, MZUSP 7381, 136.8 mm SL; (d) *Auchenipterus nuchalis*, MZUSP 101618, 152.9 mm SL. GF gill filaments, RA gill-rakers.

diameter of gill-rakers (CI 0.5, RI 0.667).

The base of the gill-rakers of the Siluridae, and auchenipterids *Ageneiosus* and *Tetranematchthys* is enlarged and firmly attached to the branchial arches (Fig. 50a). This character was coded as inapplicable for the Aspredinidae, auchenipterid *Gelanoglanis*, and doradids *Trachydoras* and *Leptodoras juruensis*, which lack gill-rakers; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

186. Number of gill-rakers on first branchial arch (unordered): 0- 15 or less; 1- 16 to 25; 2- 30 or more (CI 0.4, RI 0.571).

Although most catfishes have fewer than 15 gill-rakers on the first branchial arch, the doradids *Anadoras*, *Anduzedoras*, *Leptodoras* (Sabaj, 2005; Birindelli *et al.*, 2008; Sousa, 2010: #40; Birindelli & Sousa, 2011), and auchenipterids *Pseudepapterus cucuhyensis* and *P. hasemani* (Ferraris & Vari, 2000) have 16 to 25. On the other hand, the Siluridae, auchenipterids *Auchenipterus* (Ferraris & Vari, 1999), *Epapterus* (Vari & Ferraris, 1998) and

Pseudepapterus gracilis (Ferraris & Vari, 2000; Ferraris, 1988: #G4) have more than 30 gill-rakers on the first branchial arch. This character was coded as inapplicable for the Aspredinidae, auchenipterid *Gelanoglanis*, and doradids *Trachydoras* and *Leptodoras juruensis*, which lack gill-rakers; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

187. Second and third basibranchials: 0- moderate in size; 1- rudimentary (CI and RI inapplicable).

The auchenipterid *Asterophysus* has relatively rudimentary second and third basibranchials compared to all other catfish (Fig. 51; Ferraris, 1988: #G6; Akama, 2004: #81). This character was coded as missing data for the auchenipterid *Spinipterus*.

188. Length of ventral process of fourth basibranchial: 0- short; 1- elongate (CI 1.0, RI 1.0).

In most catfishes, the fourth basibranchial has a short ventral process that extends from the branching of the

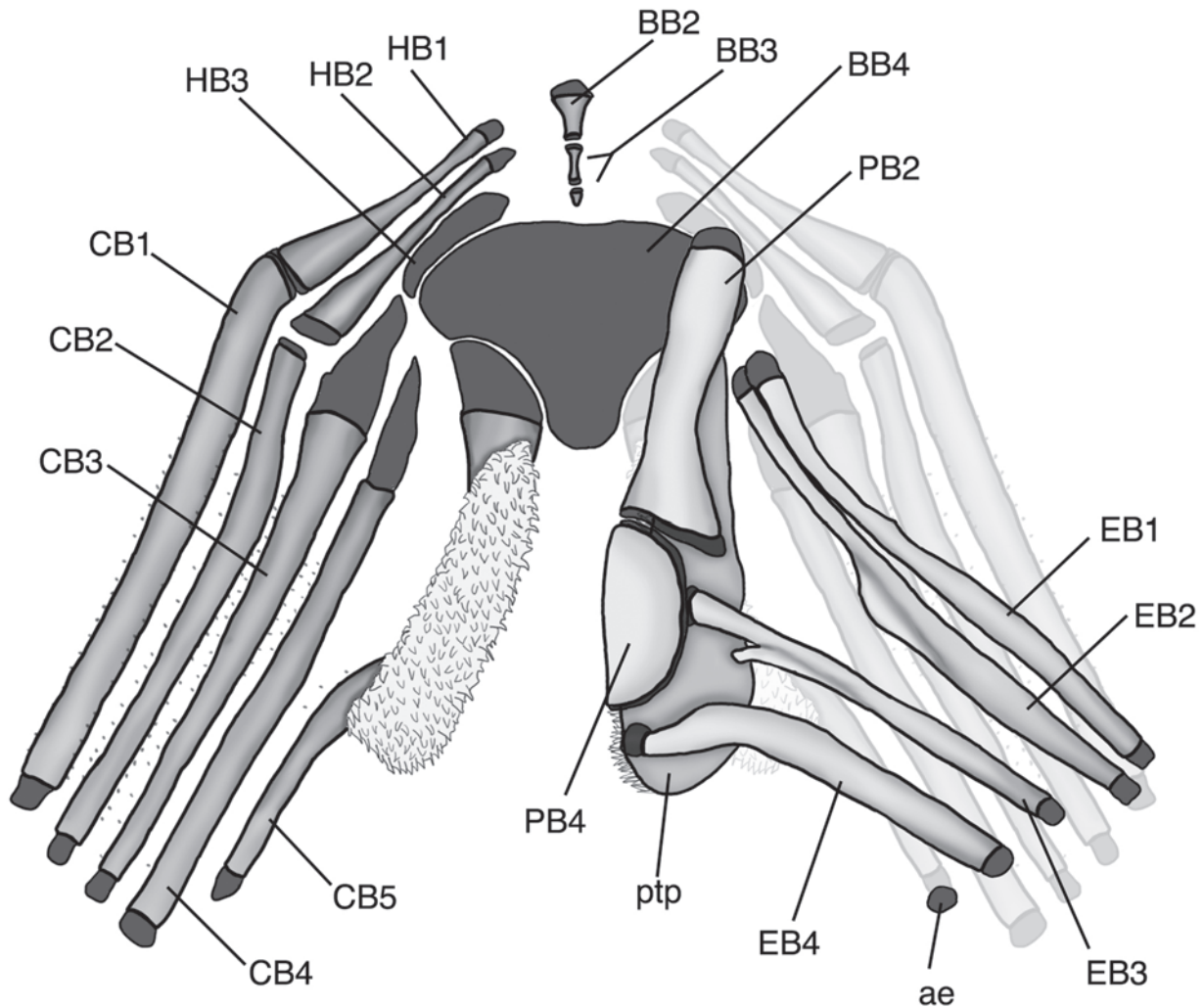


Fig. 51. Schematic drawing of the branchial arches in dorsal view of *Asterophysus batrachus*, based on INPA 24119, 127 mm SL. ae accessory element of ceratobranchial 4, BB basibranchial, CB ceratobranchial, HB hypobranchial, PB pharyngobranchial, ptp pharyngobranchial tooth plate.

branchial arteries to the anterior tip of the fifth ceratobranchial. In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxyodoras*, *Tenellus*, and *Trachydoras*, this process is elongate, extended posteriorly far beyond the anterior tip of the fifth ceratobranchial (Fig. 52). This character was coded as missing data for the auchenipterid *Spinipterus*.

189. Shape of tip of ventral process of fourth basibranchial: 0- simple; 1- trifid (CI 1.0, RI 1.0).

In the doradid *Trachydoras* the tip of the ventral process of the fourth basibranchial is trifid (Fig. 52b), whereas it is simple in all other examined taxa (Fig. 52a). This character was coded as missing data for the auchenipterid *Spinipterus*.

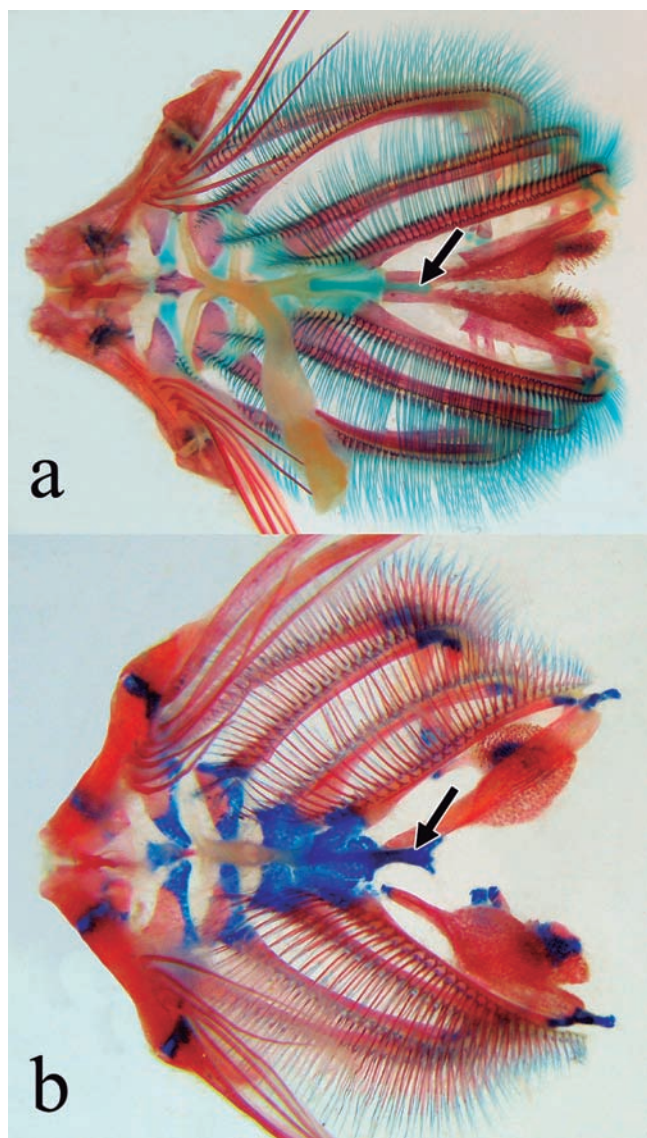


Fig. 52. Branchial arches of cleared and stained specimens in ventral view of (a) *Doras phlyzakion*, MZUSP 50836, 67.5 mm SL; (b) *Trachydoras microstomus*, MZUSP 57703, 76.6 mm SL. Arrows indicate posterior process of fourth basibranchial.

190. Accessory cartilage between third and fourth basibranchials: 0- absent; 1- present (CI 0.333, RI 0.875).

In all auchenipterids (except the Centromochlinae and *Asterophysus*) there is an accessory cartilage between the third and fourth basibranchials (Ferraris, 1988: #G2; Akama, 2004: #79). The same condition is present in the Akysidae and Sisoridae (de Pinna, 1993: #184; de Pinna, 1996: #41; Britto, 2002: #90). The accessory cartilage between the third and fourth basibranchials is absent in other examined taxa. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

191. Shape of first hypobranchial: 0- discoid; 1- cylindrical (CI 0.167, RI 0.783).

The first hypobranchial is cylindrical in the Aspredinidae, Erethistidae (de Pinna, 1996: figs. 16-20), auchenipterids *Ageneiosus*, *Asterophysus*, *Auchenipterichthys*, *Centromochlus*, *Gelanoglanis*, *Liosomadoras*, *Pseudoauchenipterus*, *Pseudotatia*, *Tatia*, *Tetranematichthys*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus* and *Trachycorystes*, and doradids *Anduzedoras*, and *Leptodoras* (Figs. 51, 53; Higuchi, 1992: #A46; Birindelli *et al.*, 2008). In some of those taxa (*e.g.*, *Asterophysus*, *Gelanoglanis*, and *Leptodoras*) the second basibranchial is also cylindrical (Fig. 51). In other catfishes, the first two hypobranchials are discoid (Fig. 54). This character was coded as missing data for the auchenipterid *Spinipterus*.

192. Second hypobranchial: 0- ossified; 1- cartilaginous (CI 0.333, RI 0.0).

The second hypobranchial is ossified in most catfishes (Figs. 51-54). However, the Aspredinidae, Erethistidae, and Nematogenyidae have a cartilaginous second hypobranchial (de Pinna, 1996: #38; Britto, 2002: #92; de Pinna *et al.*, 2007: #38). This character was coded as missing data for the auchenipterid *Spinipterus*.

193. Anterior limb of fifth ceratobranchial: 0- short, length much smaller than length of tooth patch; 1- elongate, length approximately equal to length of tooth patch (CI 1.0, RI 1.0).

In most catfishes, the anterior limb of the fifth ceratobranchial is much smaller than the associated toothplate (Fig. 55a). However, in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxyodoras*, *Tenellus*, and *Trachydoras*, the anterior limb of the fifth ceratobranchial is extremely elongate, with length approximately equal to length of tooth patch (Fig. 55b-c; Higuchi, 1992: #60). This character was coded as missing data for the auchenipterid *Spinipterus*.

194. Teeth on fifth ceratobranchial: 0- numerous, occupying most of middle portion of fifth ceratobranchial; 1- few in number and restricted to medial margin (CI 1.0, RI 1.0).

In the doradid *Leptodoras*, the teeth of the fifth ceratobranchial are few in number and restricted to a single

row on the medial margin of the bone (Fig. 55c; Birindelli *et al.*, 2008: fig. 10). All other examined taxa have numerous teeth occupying most of middle portion of fifth ceratobranchial (Fig. 5a-b). This character was coded as missing data for the auchenipterid *Spinipterus*.

195. Shape of first epibranchial: 0- roughly cylindrical, uniform; 1- with medial end enlarged, distinctly larger than lateral end (CI 1.0, RI 1.0).

In most catfishes, the first epibranchial is roughly cylindrical (Figs. 51, 53-54). However, in the auchenipterids *Ageneiosus* and *Tetranematichthys* the medial end of the first epibranchial is distinctly enlarged, distinctly larger than lateral end (Ferraris, 1988: #G3; Walsh, 1990: #8; Royero, 1999: #109; Akama, 2004: #77). This character was coded as missing data for the auchenipterid *Spinipterus*.

196. Accessory element of fourth ceratobranchial: 0- present; 1- absent (CI 0.5, RI 0.0).

The accessory element of fourth ceratobranchial is present

as a small cartilage in most catfishes. However, in the Aspredinidae and Erethistidae it is absent (de Pinna, 1993: #139; Britto, 2002: #113). This element was uncorrectly identified as the fifth epibranchial until recently (Carvalho *et al.*, 2013). This character was coded as missing data for the auchenipterid *Spinipterus*.

197. First pharyngobranchial: 0- present; 1- absent (CI 0.25, RI 0.0).

Among examined species, the first pharyngobranchial is present only in the Ariidae (except *Galeichthys*, Marceniuk *et al.*, 2012: #182), Claroteidae, Diplomystidae, and Pangasiidae (Lundberg, 1970; Mo, 1991: #47; de Pinna, 1993: #140; Britto, 2002: #116; de Pinna *et al.*, 2007: #75; Marceniuk *et al.*, 2012: #182). This character was coded as missing data for the auchenipterid *Spinipterus*.

198. Second pharyngobranchial: 0- present; 1- absent (CI 0.5, RI 0.0).

Among examined species, the second pharyngobranchial

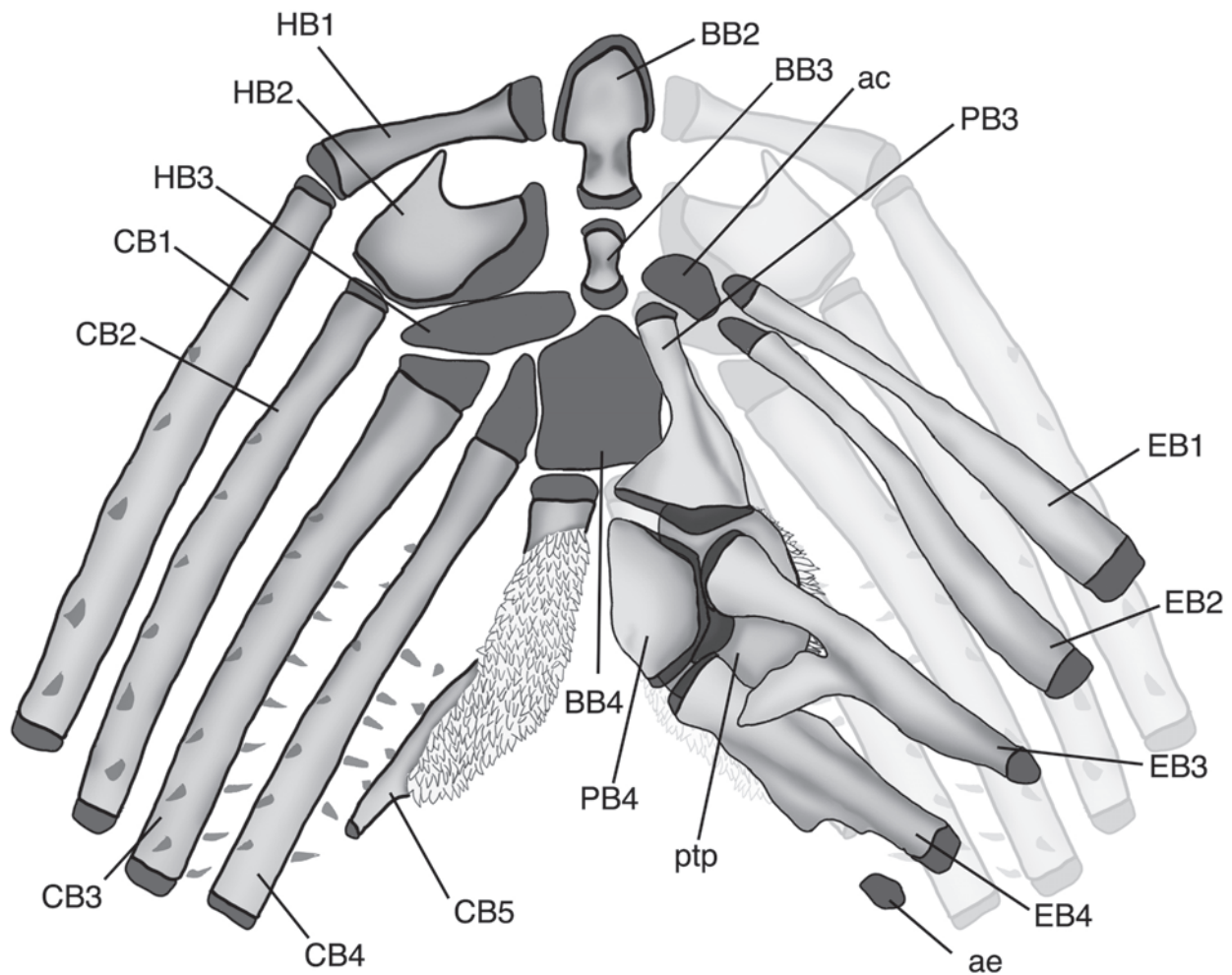


Fig. 53. Schematic drawing of the branchial arches in dorsal view of *Glanidium melanopterum*, based on MZUSP 51043, 107.9 mm SL. ac pharyngobranchial accessory cartilage, ae accessory element of ceratobranchial 4, BB basibranchial, CB ceratobranchial, HB hypobranchial, PB pharyngobranchial, ptp pharyngobranchial tooth plate.

is present only in the Diplomystidae (Arratia, 1987) and Pangasiidae (de Pinna, 1993: #185; Britto, 2002: #118; de Pinna *et al.*, 2007: #76).

199. Shape of pharyngobranchial tooth plate (ordered): 0- rounded, length slightly greater than width; 1- elongated, length approximately twice width; 2- extremely elongate, length approximately three times width (CI 0.667, RI 0.969).

The pharyngobranchial toothplate is rounded, with its length slightly greater than its width, in most catfishes (Figs. 53-54). However, in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, *Tenellus*, and *Trachydoras*, the pharyngobranchial tooth plate is elongate, with its length approximately twice its width. In the auchenipterid *Asterophysus* it is extremely elongate, with its length approximately three times its width (Fig. 51; Britski, 1972: #25; Ferraris, 1988: #G5; Akama, 2004: #80). This character was coded as missing data for the auchenipterid *Spinipterus*.

Axial skeleton

200. Lateral expansion of first vertebra: 0- absent; 1- present (CI 1.0, RI 1.0).

In the doradids *Orinocodoras* and *Rhinodoras*, the first vertebra is laterally expanded, which results in a somewhat trapezoidal shape in ventral view (Fig. 36b; Higuchi, 1992: #63). In other examined taxa, lateral expansions are absent from the first vertebra (Fig. 36a,d, 35). This character was coded as missing data for the auchenipterid *Spinipterus*.

201. Bony capsule on anterior vertebrae: 0- absent; 1- present (CI 1.0, RI 1.0).

The doradids *Anduzedoras* and *Leptodoras* have a pair of conjoined bony capsules on the ventral surface of the anterior vertebrae (Fig. 36c; Higuchi, 1992: #64; Birindelli *et al.*, 2008; Birindelli & Sousa, 2010), absent in other examined taxa (Figs. 35, 36a-b,d). This character was coded as missing data for the auchenipterid *Spinipterus*.

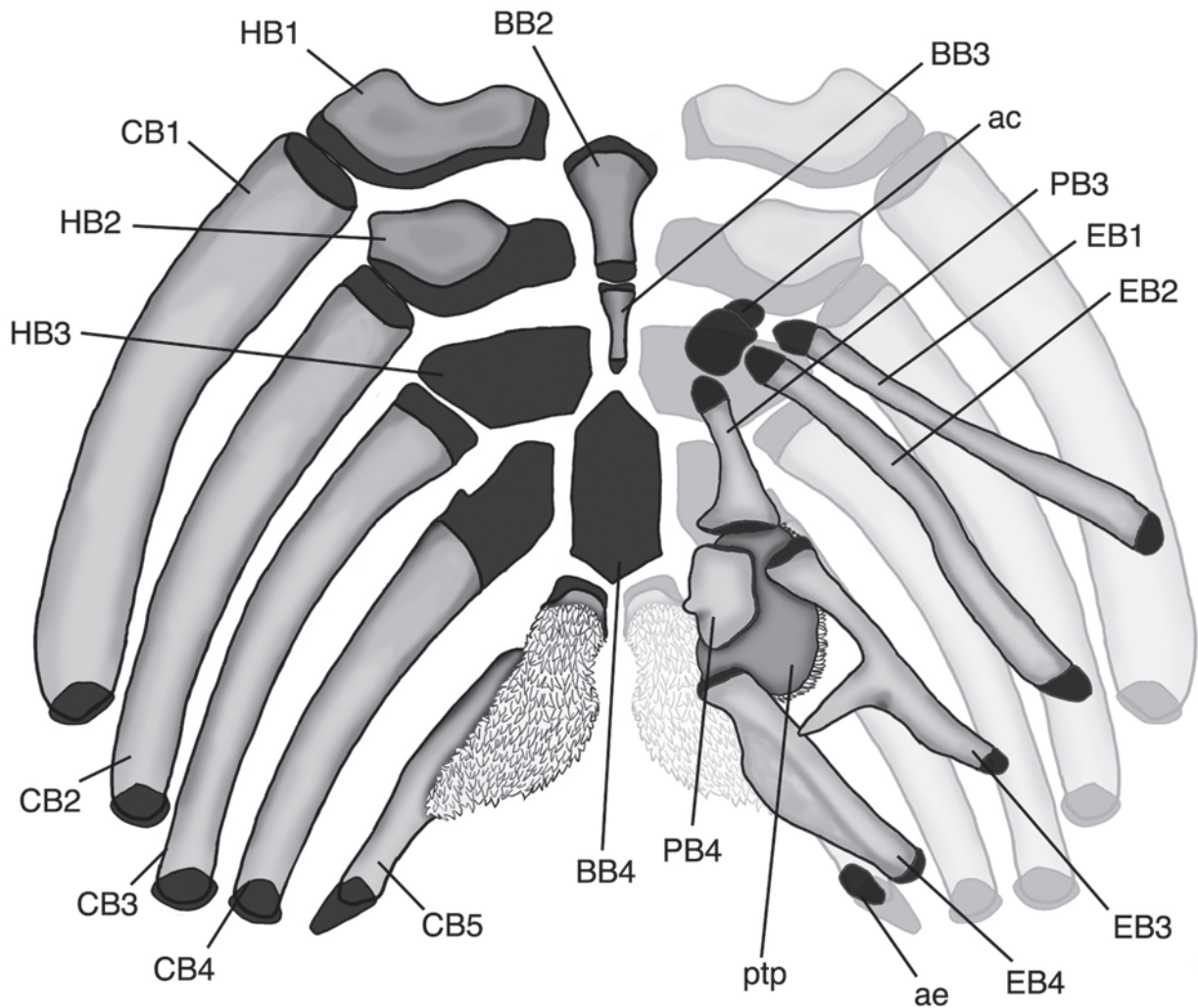


Fig. 54. Schematic drawing of the branchial arches in dorsal view of *Wertheimeria maculata*, based on MZUSP 93658, 192 mm SL. ac pharyngobranchial accessory cartilage, ae accessory element of ceratobranchial 4, BB basibranchial, CB ceratobranchial, HB hypobranchial, PB pharyngobranchial, ptp pharyngobranchial tooth plate.

202. Shape of bony capsules on anterior vertebrae (unordered): 0- small, with large posterior opening; 1- small, with small posterior opening; 2- large, with small posterior opening (CI 1.0, RI 1.0).

As discussed by Birindelli *et al.* (2008) and Birindelli & Sousa (2010), the morphology of the bony capsules varies in the species of the doradids *Anduzedoras* and *Leptodoras*, with *Anduzedoras* having small subtriangular bony capsules with small posterior opening, *Leptodoras marki* and *L. oyakawai* having small cup-like bony capsules with large posterior opening, and the other species of *Leptodoras* having large rounded bony capsules with small posterior opening. This character was coded as inapplicable for all other examined taxa.

203. Transformator process of *tripus*: 0- curved ventrally; 1- straight (CI 1.0, RI 1.0).

The transformator process of the *tripus* is curved ventrally and loosely attached to the gas bladder in most catfishes (Figs. 35b,d,f; Arratia, 1987; Lechner & Ladich, 2008). However, in the species of the Auchenipteridae and Doradidae, the transformator process of the *tripus* is straight and firmly attached to the gas bladder (Figs. 35h, 36; Bridge & Haddon, 1890: 160, 233 [referred to as crescentic process]; Britski, 1972: 19; Ferraris, 1988: #V2; Royero, 1999: #73; Akama, 2004: #69). This character was coded as missing data for the auchenipterid *Spinipterus*.

204. Size of *os suspensorium*: 0- moderate; 1- reduced (CI 1.0, RI 1.0).

The *os suspensorium* is moderate in size and firmly attached to the parapophysis of the fourth vertebra in most catfishes (Figs. 35b,d,f; Chardon *et al.*, 2003). However, in the species of the Auchenipteridae and Doradidae, the *os suspensorium* is reduced to a nodule that is loosely connected to the parapophysis of the fourth vertebra (Figs. 35h, 36; Ferraris, 1988: #V4; de Pinna, 1993: #191; Royero, 1999: #70; Britto, 2002: #213; Akama, 2004: #70).



Fig. 55. Fifth ceratobranchial in dorsal view of (a) *Kalypodoras bahiensis*, MZUSP 87841, 233 mm SL; (b) *Oxydoras niger*, MZUSP 91654, 550 mm SL; (c) *Leptodoras juruensis*, MZUSP 104532, 227 mm SL. Scale bars equal 5 mm.

205. Shape of anterior ramus of parapophysis of fourth vertebra (=Müllerian ramus) (unordered): 0- distally truncate, sutured to transcapular process; 1- distally pointed, free from transcapular process; 2- modified with long thin base and distal flexible disc, latter connected to ventral face of gas bladder; 3- modified with short thin base and distal flexible disc, latter connected to dorsal face of gas bladder (CI 0.6, RI 0.882).

In most catfishes, the anterior ramus of the parapophysis of the fourth vertebra is truncated distally and sutured to the transcapular process (Fig. 35b; Bridge & Haddon, 1892; Chardon, 1968). However, this attachment is lost, and the ramus becomes flexible (= Müllerian ramus) and associated with a modified muscle (= protractor muscle of the Müllerian ramus) in some catfishes. This modified set of structures forms the elastic spring apparatus as initially described by Müller (1842a, 1842b) for the auchenipterid *Auchenipterus*, the doradid *Doras*, the mochokid *Synodontis* and the malapterurid *Malapterurus*, later described for the pangasiid *Pangasius* by Bridge & Haddon (1892), and finally for members of the Ariidae by Tavolga (1962). The elastic spring apparatus functions to produce sounds: contraction of the modified muscle pulls the elastic spring forward, extending the gas bladder, and its relaxation allows for elastic recoil, quickly restoring the gas bladder to its normal position (Fine & Ladich, 2003). Repeated contractions of the modified muscle cause the gas bladder to vibrate, and the rapid compression and extension of the gas bladder radiates tonal sounds with fundamental frequency and harmonics (Fine & Ladich, 2003).

In the Ariidae (except *Galeichthys*), the Müllerian ramus is largely unmodified, except for its freedom from the transcapular process and distal point (Fig. 35d; Tavolga, 1962; Marceniuk & Birindelli, 2010). In the species of Mochokidae, the Müllerian ramus is modified with a long thin base and rounded distal disc, the latter attached to the ventral face of the gas bladder (Fig. 35f; Vigliotta, 2008; Ladich, 2001). In the species of Malapteruridae and Pangasiidae, the Müllerian ramus is similar to the one present in mochokids, although it is more rectangular and elongate than disc-like (state 2). In the species of Auchenipteridae and Doradidae, the Müllerian ramus is also greatly modified with a thin short base and rounded distal disc, the latter attached to the dorsal face of the gas bladder (Fig. 35h; Bridge & Haddon, 1892; Regan, 1911; Alexander, 1965: 110; Chardon, 1968; Britski, 1972: 20; Curran, 1989: #17; Royero, 1999: #67, #71; Akama, 2004: #66, #76). This character was coded as missing data for the auchenipterid *Spinipterus*.

206. Shape of disc of Müllerian ramus (unordered): 0- rounded and shallow; 1- shaped as a cone, with posterior apex; 2- compact, reduced in size (CI 0.667, RI 0.967).

In all species of Auchenipteridae (except *Ageneiosus* and *Centromochlus heckelii*), Doradidae (except *Oxydoras*, *Physopyxis* and fimbriate-barbel doradids) and Mochokidae, the disc of the Müllerian ramus is rounded and shallow. However, in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Lepodoras*, *Nemadoras*, *Ossancora*, *Tenellus*,

and *Trachydoras* (Eigenmann, 1925: 297; Higuchi, 1992: #67) and the auchenipterid *Centromochlus heckelii* (Britski, 1972: 20; Ferraris, 1988: #V8; Soares-Porto, 1996: #16; Royero, 1999: #67; Akama, 2004: #68), the disc of the Müllerian ramus is shaped as a cone, posteriorly protruded against the wall of the bladder causing it to become indented (Fig. 36c). In the doradid *Physopyxis* (Sousa, 2010: #46) and in large-sized species of the auchenipterid *Ageneiosus* (including *A. inermis*) the disc of the Müllerian ramus is compact, reduced in size (Britski, 1972: 20; Ferraris, 1988: #V3; Walsh, 1990: #23; Higuchi, 1992: #A52; Royero, 1999: #74; Akama, 2004: #67). This character was coded as inapplicable for all taxa that lack the disc of the Müllerian ramus (*i.e.*, all examined species except Auchenipteridae, Doradidae, and Mochokidae); and as missing data for the auchenipterid *Spinipterus*.

207. Protractor muscle of Müllerian ramus: 0- absent; 1- present (CI 0.25, RI 0.75).

The protractor muscle of the Müllerian ramus is present in the Ariidae, Auchenipteridae, Doradidae, Malapteruridae, Mochokidae, and Pangasiidae (Fig. 56a-d; Müller, 1842a, 1842b; Bridge & Haddon, 1892; Alexander, 1965; Chardon, 1968; Ferraris, 1988: #V6; Diogo, 2004: #256; Vigliotta, 2008: #76; Marceniuk *et al.*, 2012); it is absent in all other examined taxa (Fig. 56e-f). This character was coded as missing data for the auchenipterid *Spinipterus*.

208. Origin and insertion of protractor muscle of Müllerian ramus (unordered): 0- origin on medial portion of posterior surface of cranium, and insertion on disc of Müllerian ramus; 1- origin on posterior nuchal plate and insertion on base of Müllerian ramus; 2- origin on lateral portion of posterior cranium, and insertion on entire Müllerian ramus (CI 1.0, RI 1.0).

In the species of Auchenipteridae and Doradidae, the protractor muscle of the Müllerian ramus originates in a bony, posteriorly direct pocket formed by internal faces of parietal-supraoccipital, exoccipital, supraneurals, epiotic and anterior nuchal plate, and its insertion is restricted to the disc of the Müllerian ramus (Figs. 56a,b; Birindelli *et al.*, 2009). In the Mochokidae, the protractor muscle of the Müllerian ramus originates on the posterior nuchal plate and inserts on the base of the Müllerian ramus (Fig. 56c; Taverne & Aloulou-Triki, 1976; Ladich, 2001). In the Ariidae (except *Galeichthys*), Malapteruridae and Pangasiidae, it originates on the lateral portion of the posterior cranium (including the epiotic process in most ariids), and inserts on the entire Müllerian ramus (Fig. 56d; Tavalga, 1962; Marceniuk & Birindelli, 2010; Marceniuk *et al.*, 2012: #229).

The nerve associated with the protractor muscle present in the Doradoidea belongs to the occipital-spinal plexus. The catfish skull usually has four nerve openings posteriorly: an anterior one for nerve IX (glossopharyngeal), a large one, posterior to the first exit, and anterior to the transcapular process, for nerve X (vague) (Arratia, 1987: 21; Freihofer, 1978: fig. 26), and two smaller ones posteriorly (posterior to the

transcapular process). From the ventralmost of the two smaller exits, a nerve goes through, reaching directly the protractor muscle of the Müllerian ramus. The nerves that exit the cranium through openings located posterior to the transcapular process are the XI or XII nerve (Kesteven, 1943: 107, fig. 50), or the occipital-spinal plexus (Freihofer, 1963: 90, fig. 13). Either way, those are spinal nerves, which are also responsible for epaxial muscles (Allis, 1903: 220). These observations corroborate the hypothesis that the protractor muscles correspond to a modified part of the epaxial musculature (Tavalga, 1962). Alternatively, Royero (1999) considered the protractor muscles to be modifications of the *supracarinalis anterior* muscle, which is not present in the Auchenipteridae and Doradidae.

This character was coded as inapplicable for all taxa that lack the protractor muscle of the Müllerian ramus (*i.e.*, Amphiliidae, ariid *Galeichthys*, Aspredinidae, Claroteidae, Diplomystidae, Erethistidae, Heptapteridae, Ictaluridae, Nematogenyidae, Pimelodidae, Pseudopimelodidae, Siluridae, and Sisoridae); and as missing data for the auchenipterid *Spinipterus*.

209. Number of sections of protractor muscle of Müllerian ramus: 0- one; 1- two (CI 0.5, RI 0.0).

The protractor muscle of the Müllerian ramus of most examined species of the Auchenipteridae and Doradidae is composed of a single section. However, in the auchenipterids *Ageneiosus* (*A. atronatus* and *A. brevis*) and *Centromochlus* (*C. heckelii*), the protractor muscle is divided into two sections (Fig. 57; Diogo, 2004: #155; Parmentier & Diogo, 2006: 54). This subdivision is somewhat difficult to visualize, so it is possible that it may also be present in other taxa. This character was coded as missing data for the auchenipterids *Gelanoglanis*, *Pseudotatia*, and *Spinipterus*. This character was coded as inapplicable for all taxa that lack the protractor muscle of the Müllerian ramus.

210. Posterior ramus of parapophysis of fourth vertebra: 0- present; 1- absent (CI 1.0, RI 1.0).

Most catfishes have the parapophysis of the fourth vertebra with anterior and posterior rami (Fig. 35b,d,f). However, the posterior ramus of the parapophysis of the fourth vertebra is absent in the species of Auchenipteridae and Doradidae (Figs. 35h, 36; Regan, 1911; Vigliotta, 2008: #79). This character was coded as inapplicable for the auchenipterid *Spinipterus*.

211. Size of parapophysis of fifth vertebra (ordered): 0- reduced in size or, rarely, absent; 1- moderate in size, similar to those of subsequent vertebrae; 2- relatively large, distinctly larger than those of subsequent vertebrae (CI 0.4, RI 0.875).

Most catfishes have the parapophysis of the fifth vertebra moderate in size, similar to those of subsequent vertebrae. In the Sisoroidea, Aspredinidae, and the mochokid *Chiloglanis*, the parapophysis of the fifth vertebra is relatively large, distinctly larger than those of the subsequent vertebrae (de

Pinna, 1996: #57, #62; Britto, 2002: #231; Diogo, 2004: #138). The parapophysis of the fifth vertebra in doradids (except *Leptodoras juruensis*) and auchenipterids (except *Gelanoglanis*) is reduced in size, or occasionally [or rarely]

absent (Figs. 35g,h, 36; Bridge & Haddon, 1892: 230; Regan, 1911; Alexander, 1965: 111; Vigliotta, 2008: #80). In specimens of Auchenipteridae and Doradidae, the parapophysis may be present on one side of a specimen, but absent on the other. In

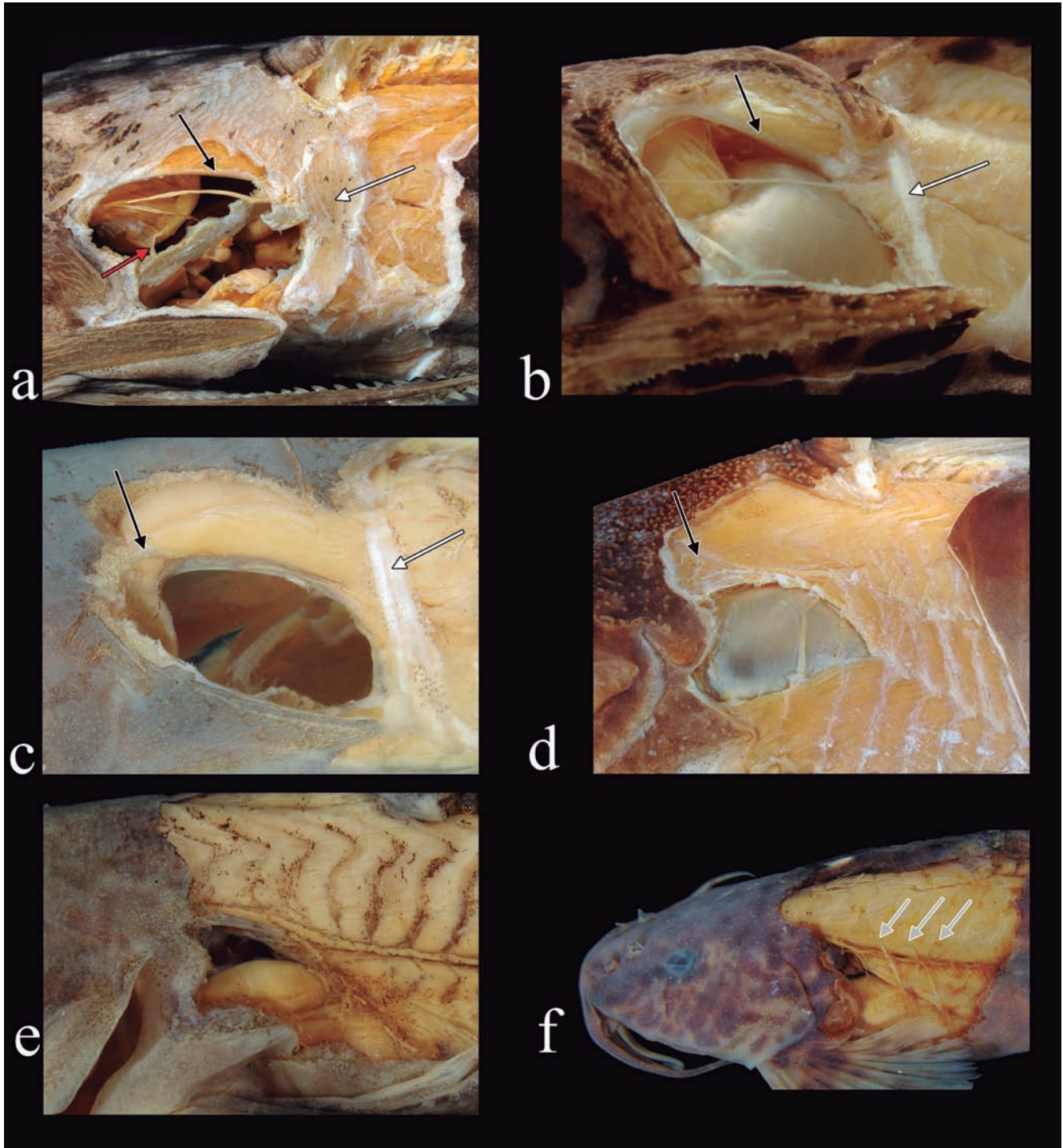


Fig. 56. Tympanic area in lateral view of (a) *Wertheimeria maculata*, MZUSP 93658, 186 mm SL; (b) *Liosomadoras oncinus*, MZUSP 93497, 74.8 mm SL; (c) *Synodontis schall*, MZUSP 84468, 76 mm SL; (d) *Sciades herzbergii*, MZUSP 48636, 72.4 mm SL; (e) *Diplomystes mesembrinus*, MZUSP 62595, 99.2 mm SL; (f) *Amphilius jacksoni*, MZUSP 48636, 72.4 mm SL. White arrows (a,b,c) indicate infranuchal ligament, black arrows (a,b,c,d) indicate epiotic-process ligament, red arrow (a) indicates the ligament between Müllerian ramus and lateral line, grey arrows (f) indicate ligament between ribs and muscle fascia.

the examined species of the auchenipterid *Gelanoglanis* and doradid *Leptodoras juruensis*, the parapophysis of the fifth vertebra is moderate in size, similar to those of subsequent vertebrae (Fig. 36c). This character was coded as missing data for the auchenipterid *Spinipterus*.

212. Ligament between Müllerian ramus and lateral line: 0- absent; 1- present (CI 1.0, RI 1.0).

A ligament between the Müllerian ramus and the lateral line is present in all species of Doradidae (Fig. 56a). This feature was reported for *Pterodoras granulosus* by Sørensen (1892: 124) and Royero (1999), and for *Platydoras* by Ladich (2001: 299). According to Sørensen (1892: 124), this ligament helps to propagate the sound produced by vibrations of the Müllerian ramus to the midlateral scute row. The Müllerian ramus is not connected to the lateral line in other examined taxa (Fig. 56b). This character was coded as missing data for the auchenipterid *Spinipterus*.

213. Infranuchal ligament (ordered): 0- absent; 1- not ossified; 2- ossified (CI 1.0, RI 1.0).

In all examined specimens of Auchenipteridae and the mochokid *Synodontis* (other mochokids not examined for this character) there is an unossified ligament that extends between the posterior nuchal plate and the first rib, the infranuchal ligament (Figs. 56b,c). In the same location in the Doradidae, there is an ossification sutured dorsally to the posterior nuchal plate and ventrally to the first rib, the infranuchal scute (Fig. 56a; Ferraris, 1988: #D6; Royero, 1999: #68, #104; Akama, 2004: #75). As discussed by Ferraris (1988), the infranuchal scute is homologous to the ligament present in auchenipterids and mochokids, and it is formed by the ossification of both the ligament between the posterior nuchal plate and first rib and the adjacent portion of the lateral line. Royero (1999: #68) and Akama (2004: #75) considered the infranuchal ligament to be absent in the auchenipterids *Ageneiosus* and *Tetranematichthys*, but members of those taxa observed herein have that ligament.

Ferraris (1988: 45) mentioned that similar (and possibly



Fig. 57. Head and tympanic area in lateral view of *Centromochlus heckelii*, MZUSP 49529, 80.5 mm SL. White arrow indicates Müllerian ramus, black arrows indicate sections of the protractor muscle of the Müllerian ramus.

homologous) ligaments are present in other catfishes (*i.e.*, species of Amphiliidae and Sisoridae). However, based on the available specimens, in the Amphiliidae there are ligaments between the anterior ribs and the fascia of the epaxial muscle (Fig. 56f), whereas in the Sisoridae, no ligament was observed, and the entire tympanic area is modified, including ribs completely covered thick muscle layers.

Bailey & Baskin (1976: 4) described a bone between the posterior nuchal plate and first rib, the lateral bone (or connecting bone of Armbruster, 2004: 32), present in the Scoloplacidae, Astroblepidae, and Loricariidae (see also Schaefer, 1990: 193, fig. 18B). In the examined specimens of Callichthyidae, there is an unossified ligament between the posterior nuchal plate and the first rib likely homologous to the lateral bone, although similar to the one observed in auchenipterids and mochokids. Nevertheless, the lateral bone of loricariids is distinct from the ossified infranuchal ligament of doradids by being covered by dermal bony plates (*vs.* exposed), and not associated to the lateral line canal (*vs.* associated). The infranuchal ligament is considered not homologous to the lateral bone (Britto, 2002: #243).

This character was coded as missing data for all species of Mochokidae (except *Synodontis*).

214. Ligament between second rib and posterior nuchal plate: 0- absent; 1- present (CI and RI inapplicable).

In the examined specimens of the mochokid *Synodontis* there is a ligament between the second rib and the posterior nuchal plate (Fig. 56c). The only other examined specimen with that ligament was a single auchenipterid specimen tentatively identified as *Tatia cf. aulopygia* (MZUSP 99309, 90 mm SL). This character was coded as absent (state 0) for *Tatia aulopygia*, because the ligament is absent in the available specimen of *Tatia aulopygia* (MZUSP 37599). This character was coded as missing data for all species of Mochokidae (except *Synodontis*), and for the auchenipterid *Spinipterus*.

215. Humerovertebral ligament: 0- absent; 1- present (CI 1.0, RI 1.0).

There is a ligament between the parapophysis of the fifth or sixth vertebra and posterior process of cleithrum, the humerovertebral ligament of de Pinna (1996), in all members of the Sisoroidea, and in the Aspredinidae (de Pinna, 1996: #64; Diogo, 2004: #164), this structure is absent in other examined taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

216. Aortic canal: 0- ventrally opened; 1- ventrally enclosed by superficial ossification (CI 0.111, RI 0.6).

The complex vertebra is covered ventrally by a superficial ossification in most catfishes (Figs. 35a,b,e,f). However, in members of the ariid *Genidens* (Alexander, 1964: 435; Arratia, 1992: #55; Marceniuk *et al.*, 2012: #69), Aspredinidae, Auchenipteridae (except *Auchenipterus*, *Epapterus*, *Pseudotatia*), Doradidae (except *Rhynchodoras*), Erethistidae,

and mochokid *Chiloglanis*, the superficial ossification also covers the aorta, forming the aortic canal (Figs. 35c,d,g,h, 36; Higuchi, 1992: #71, #72; Sousa, 2010: #49). Some specimens of the auchenipterids *Centromochlus*, *Liosomadoras* and *Tatia*, and doradid *Rhinodoras dorbignyi* present ventrally opened aortic canal whereas others have it closed; this character was coded as polymorphic for these taxa. This character was coded as missing data for the auchenipterid *Spinipterus*.

217. First free vertebra (ordered): 0- fifth; 1- sixth; 2- seventh; 3- eighth, 4- ninth (CI 0.235, RI 0.787).

The fifth vertebra is free from the complex vertebra only in the Diplomystidae and Nematogenyidae (Lundberg, 1970: #86; Arratia, 1992: #40; de Pinna, 1993: #208; de Pinna *et al.*, 2007: #87; Marceniuk *et al.*, 2012: #204). The first vertebra free from the complex vertebra is the sixth in the Amphiliidae, Aspredinidae, Claroteidae, Erethistidae, Heptapteridae, Ictaluridae, Malapteruridae, Pseudopimelodidae, Sisoridae, ariid *Galeichthys*, auchenipterid *Gelanoglanis*, and doradids Astrodoradinae, *Acanthodoras*, *Agamyxis*, *Franciscodoras*, *Kalyptodoras*, and *Wertheimeria* (Figs. 35b,h; Higuchi, 1992: #68; Sousa, 2010: #50). The first free vertebra is the seventh in the Mochokidae, Pangasiidae, Pimelodidae, Siluridae (Fig. 35f; Vigliotta, 2008: #82), and auchenipterid *Pseudepapterus*. The first free vertebra is the eighth in the ariid *Genidens*, auchenipterids *Ageneiosus*, *Asterophysus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Glanidium*, *Liosomadoras*, *Pseudauchenipterus*, *Pseudotatia*, *Tatia*, *Tetranematichthys*, *Trachelyichthys*, doradids *Anduzedoras*, *Centrochir*, *Centrodoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Orinocodoras*, *Ossancora*, *Oxydoras*, *Platydoras*, *Rhinodoras*, *Rhynchodoras*, *Tenellus* and *Trachydoras* (Figs. 35d, 36a-c). The first free vertebra is the ninth in the auchenipterids *Auchenipterichthys*, *Centromochlus heckelii*, *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus*, *Trachycorystes*, and doradids *Doraops*, *Lithodoras*, *Megalodoras*, and *Pterodoras* (Figs. 36d). This character was coded as missing data for the auchenipterid *Spinipterus*.

218. Hipertrophied bony nodule on parapophysis of sixth vertebra: 0- absent; 1- present (CI and RI inapplicable).

Among examined taxa, a hipertrophied bony nodule is present on the parapophysis of the sixth vertebra only in the doradids *Oxydoras niger* and *O. sifontesi* (Fig. 25; Higuchi, 1992: #A53). This character was coded as missing data for the auchenipterid *Spinipterus*.

219. Articulation of anterior ribs: 0- ventral; 1- dorsal (CI 1.0, RI 1.0).

In most catfishes, the anterior ribs articulate with the ventral face of the parapophysis (the posterior ribs are articulated either to the posterior or dorsal face of the parapophysis) (Figs. 35b,d,f). However, in the Auchenipteridae and Doradidae the anterior ribs articulate with the dorsal face

of the parapophysis (Figs. 35h, 36; Ferraris, 1988: #V12; Vigliotta, 2008: #84). This character was coded as missing data for the auchenipterid *Spinipterus*.

220. Shape of proximal extremity of ribs: 0- straight; 1- twisted (CI 0.333, RI 0.867).

Among examined species, the proximal extremity of the ribs is twisted only in the Amphiliidae, Aspredinidae, Auchenipteridae, Doradidae, Erethistidae, and Sisoridae (Figs. 35h, 36; Ferraris, 1988: #V12; de Pinna, 1993: #198; Britto, 2002: #239; Vigliotta, 2008: #84). This character was coded as missing data for the auchenipterid *Spinipterus*.

221. Number of ribs (ordered): 0- three to five; 1- six to 11; 2- 12 or more (CI 0.154, RI 0.577).

The number of ribs in catfishes is highly reduced when compared to other members of the Ostariophysi, and several groups show yet a greater reduction (de Pinna, 1996: #73). The Claroteidae, Mochokidae (except *Mochokus*), Pseudopimelodidae, Siluridae, Sisoridae, some Malapteruridae, and most members of Auchenipteridae and Doradidae have six to 11 ribs. The exceptions are the auchenipterids *Ageneiosus brevis*, *Epapterus*, and *Pseudepapterus* with four or five ribs (Walsh, 1990: #31); auchenipterids *Glanidium*, *Tocantinsia*, and *Asterophysus*, and doradids *Centrodoras*, *Doraops*, *Kalyptodoras*, *Lithodoras*, *Megalodoras*, *Oxydoras*, *Pterodoras*, and *Wertheimeria* with 12 or more ribs (Sousa, 2010: #52). Some specimens of the auchenipterids *Ageneiosus inermis* and *Centromochlus heckelii*, and doradids *Platydoras armatulus* and *Oxydoras niger* have 11 or less ribs while others have 12 or more; this character was coded as polymorphic (1,2) for these taxa. This character was coded as missing data for the doradid *Oxydoras kneri*, and for the auchenipterid *Spinipterus*.

222. Number of vertebrae (ordered): 0- 29 to 37; 1- 38 to 45; 2- 46 or more (CI 0.111, RI 0.698).

Most catfishes have between 38 and 45 vertebrae. However, examined specimens of the Amphiliidae, Ariidae, Heptapteridae, Ictaluridae, Pimelodidae, and Siluridae have 46 or more vertebrae, whereas those of the Aspredinidae, Erethistidae, Mochokidae (except *Synodontis schall* and *S. zambezensis*), Pseudopimelodidae, and Sisoridae on the other hand, have 29 to 37 vertebrae.

The auchenipterid *Gelanoglanis*, and doradids Astrodoradinae, *Acanthodoras*, *Agamyxis*, *Centrochir*, *Doras* (except some specimens of *D. higuchii*), *Franciscodoras*, *Hassar*, *Hemidoras* (except some specimens of *H. morrisoni* and *H. stenopeltis*), *Platydoras*, *Nemadoras*, *Orinocodoras*, *Ossancora*, *Rhinodoras*, *Tenellus*, and *Trachydoras* (Sousa, 2010: #53) have 29 to 37 vertebrae. Forty-six or more vertebrae are present in distal species of the doradids *Leptodoras* (*sensu* Birindelli *et al.*, 2008), some specimens of *Lithodoras*, and auchenipterids *Ageneiosus inermis*, *Auchenipterus*, *Pseudepapterus*, *Tetranematichthys*

(except some specimens of *T. quadrifilis*), *Trachelyopterichthys* and some specimens of *Trachelyopterus galeatus* (Walsh, 1990: #28). Britski (1972: 18) observed that a species with an elongate body tends to have more vertebrae. This character was coded as polymorphic for doradids *Doras higuchii*, *Hemidoras morrisi*, *Hemidoras stenopeltis* (0,1), *Lithodoras dorsalis*, and auchenipterids *Tetranematichthys quadrifilis* and *Trachelyopterus galeatus* (1,2); and as missing data for the doradid *Oxydoras kneri* and auchenipterid *Spinipterus*.

Dorsal fin

223. Bones of cephalic shield: 0- compact; 1- trabeculate (CI 1.0, RI 1.0).

In the auchenipterids *Ageneiosus* and *Tetranematichthys* the cephalic-shield bones are trabeculate (Fig. 31; Britski, 1972: 12; Royero, 1999: #30), whereas they are compact in all other examined taxa (Fig. 20-30).

224. Transverse dorsal margin of cephalic shield: 0- slightly convex, forming an angle greater than 90°; 1- strongly arched, forming an angle of approximately 90° (CI 0.333, RI 0.956).

In the mochokid *Synodontis* and all doradids except *Acanthodoras*, *Agamyxis*, *Kalyptodoras*, and *Wertheimeria*, the cephalic shield is strongly arched, with the transverse dorsal margin forming an angle of approximately 90° (Sousa, 2010: #55). The cephalic shield is slightly convex, with angle greater than 90° in all other examined species.

225. Lateral profile of cephalic shield in mature males: 0- approximately straight, similar to females; 1- distinctly concave, straight in females (CI 1.0, RI 1.0).

In mature males of auchenipterids *Ageneiosus*, *Tetranematichthys*, and some species of *Trachelyopterus* (including *T. striatulus* and *T. porosus*) the cephalic shield is distinctly concave in lateral view, whereas in females and immature males it is approximately straight, as in males and females of all other examined species (Ferraris, 1988: N19; Akama, 2004: #173). This character was coded as missing data for the auchenipterid *Spinipterus*.

226. Nuchal foramen (ordered): 0- absent; 1- well developed; 2- weakly developed (CI 0.5, RI 0.905).

Among examined species of catfish, there is a nuchal foramen between the parietal-supraoccipital, epiotic and anterior nuchal plate (or middle nuchal plate, when the anterior one is reduced or absent) only in doradids *Anduzedoras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora fimbriata*, and *Tenellus* (Fig. 27; Higuchi, 1992: #82, #83; Sabaj, 2002: #19). In *Anduzedoras*, *Leptodoras copei*, *L. oyakawai* and *L. praelongus*, the nuchal foramen is present and well developed in small specimens and reduced, or sometimes completely occluded in larger specimens (Birindelli *et al.*, 2008: 476). In a few species of Doradinae, there is also intra-specific variation, wherein some specimens may have the foramen occluded (Sabaj, 2002: fig. 66). This character was ordered

according to the ontogenetical development of the nuchal foramen.

227. Supraneural: 0- present; 1- absent (CI 0.333, RI 0.333).

Among catfishes, the supraneural is absent only in the Amblycipitidae, Amphiliidae, Astroblepidae, Clariidae, Loricariidae, Malapteruridae, Nematogenyidae, Trichomycteridae, and Siluridae (Britto, 2002: #280; de Pinna *et al.*, 2007: #108). This character was coded as missing data for the auchenipterid *Spinipterus*.

228. Anterior nuchal plate: 0- present; 1- absent (CI 0.125, RI 0.462).

In most catfishes, the supraneural is dorsally expanded into a bony plate, referred to as the anterior nuchal plate. This element precedes two other bony plates, the middle and posterior nuchal plates, derived from the first two pterygiophores of the dorsal fin, respectively (Fig. 20). Each of the three elements is ontogenetically formed from separate ossification centers, thus the derived pterygiophores have no trace of being formed by distinct proximal and distal radials. The only difference between the supraneural and the first two pterygiophores is that the latter support rays: the spinelet and the dorsal-fin spine, respectively. A few authors, including Arratia (2003b), interpreted the anterior nuchal plate as a homolog of the first pterygiophore, instead of the supraneural (thereby absent in catfishes). However, as discussed by Alexander (1965), this idea admits that the first dorsal-fin ray (presumably supported by the first pterygiophore) was lost in catfishes.

The anterior nuchal plate is absent in the Erethistidae, Sisoridae, doradids *Nemadoras humeralis*, *Tenellus trimaculatus*, *T. ternetzi*, *Rhynchodoras*, and auchenipterids *Ageneiosus*, *Epapterus*, *Gelanoglanis*, *Glanidium cesarpintoii*, *Pseudepapterus*, *Tetranematichthys*, some species of *Centromochlus* (Figs. 27, 31; Britski, 1972: 27; Ferraris, 1988: #D1; Walsh, 1990: #4; Soares-Porto, 1998: #9; Royero, 1999: #26; Akama, 2004: #32, #40; Sousa, 2010: #54), and mochokids *Atopodontus*, *Chiloglanis*, *Euchilichthys* and *Synodontis* (*S. nigriventris*, *S. batesii*, *S. contracta*) (Vigliotta, 2008: #19).

Although some authors concluded that, in some of those taxa, the anterior nuchal plate is fused to the middle nuchal plate (Royero, 1987: 132; Higuchi, 1992: 123; Akama, 2004: #40) or to the parietal-supraoccipital (Soares-Porto, 1996: 138), the study of an ontogenetic series of doradid *Rhynchodoras woodsi* demonstrated that the absence of the anterior nuchal plate is due to a gradual reduction and loss of this element, leaving the space to be occupied by the middle nuchal plate (Birindelli *et al.*, 2007: 680). Nevertheless, in some other catfishes (*e.g.*, Akysidae, Erethistidae, Scoloplacidae, Sisoridae, and callichthyids *Aspidoras* and *Corydoras*), the anterior nuchal plate may actually fuse into the middle nuchal plate (de Pinna, 1996: fig. 35; Britto, 2002: #280). This character was coded as inapplicable in the Amblycipitidae, Amphiliidae, Astroblepidae, Clariidae, Loricariidae, Malapteruridae,

Nematogenyidae, Trichomycteridae, and Siluridae, which lack a supraneural; and as missing data for the auchenipterid *Spinipterus*.

229. Anterior nuchal plate and parietal-supraoccipital: 0- in contact but not sutured; 1- sutured (CI 1.0, RI 1.0).

In most catfishes, the anterior nuchal plate assumes a triangular shape fitted into the posterior V-shaped border of the parietal-supraoccipital (Fig. 20; Arratia, 1987; Lundberg, 1970; Royero, 1987). However, in the Auchenipteridae, Doradidae, and Mochokidae, the anterior nuchal plate is sutured to the parietal-supraoccipital (Figs. 21-26, 28-30; Chardon, 1968: 229; Mo, 1991: #99; Royero, 1999: #25, #27; Britto, 2002: #282; Akama, 2004: #40). This character was coded as inapplicable for the Amphiliidae, Malapteruridae, Siluridae, Nematogenyidae, doradids *Nemadoras humeralis*, *Tenellus trimaculatus*, *Tenellus ternetzi*, *Rhynchodoras*, and auchenipterids *Gelanoglanis*, *Ageneiosus*, *Epapterus*, *Pseudepapterus* and *Tetranematichthys*, which lack an anterior nuchal plate; and as missing data for the auchenipterid *Spinipterus*.

230. Anterior nuchal plate and posttemporal-supracleithrum: 0- separated; 1- in contact (CI 0.5-1.0, RI 0.0-1.0).

Among examined species, there is contact between the anterior nuchal plate and the posttemporal-supracleithrum only in the mochokids *Mochokiella* and *Mochokus* (Vigliotta, 2008: #18). This character was coded as inapplicable for the Amphiliidae, Malapteruridae, Siluridae, Nematogenyidae, doradids *Nemadoras humeralis*, *Tenellus trimaculatus*, *Tenellus ternetzi*, *Rhynchodoras*, and auchenipterids *Gelanoglanis*, *Ageneiosus*, *Epapterus*, *Pseudepapterus* and *Tetranematichthys*, which lack an anterior nuchal plate; and as missing data for the auchenipterid *Spinipterus*.

231. Middle nuchal plate and parietal-supraoccipital: 0- separated; 1- in contact (CI 0.111, RI 0.68).

In most catfishes, the middle nuchal plate is separated from the parietal-supraoccipital (Figs. 20-26, 28-30). However, there is contact between the middle nuchal plate and the parietal-supraoccipital in the auchenipterids *Ageneiosus*, *Gelanoglanis*, *Glanidium cesarpintoii*, *Pseudepapterus*, *Tetranematichthys*, and some species of *Centromochlus* (Fig. 31; Britski, 1972: 27; Ferraris, 1988: #D3; Walsh, 1990: #4; Soares-Porto, 1998: #9; Royero, 1999: #23; Akama, 2004: #35, #126), doradids *Anduzedoras*, *Hassar*, *Hemidoras*, *Leptodoras praelongus*, *Ossancora asterophysa*, *O. eigenmanni*, *O. fimbriata*, *Nemadoras*, *Tenellus*, *Rhynchodoras*, some specimens of *Ossancora fimbriata* and *Oxydoras niger* (Fig. 27; Britski, 1972: 27; Higuchi, 1992: #84; Sabaj, 2002: #18), and mochokids *Atopodontus*, *Chiloglanis*, *Euchilichthys* and *Synodontis* (*S. nigriventris*, *S. batesii*, *S. contracta*) (Vigliotta, 2008: #20). This character is coded polymorphic for *Ossancora fimbriata* and *Oxydoras niger*; as inapplicable for the Malapteruridae, which lack a middle nuchal plate; and as missing data for the auchenipterid *Spinipterus*.

232. First and second pterygiophores articulated via a process: 0- absent; 1- present (CI 0.5, RI 0.667).

The first and second pterygiophore are articulated via a process in the Amphiliidae, Akysidae, Aspredinidae, Bagridae, Erethistidae, and Sisoridae (de Pinna, 1996: #90; Britto, 2002: #284). This character was coded as inapplicable for the Malapteruridae, which lack a middle nuchal plate; and as missing data for the auchenipterid *Spinipterus*.

233. Ventral portion of first dorsal-fin pterygiophore: 0- smooth and laminar; 1- rugose and thick (CI 0.5, RI 0.667).

Among examined species, only in the Akysidae, Amblycipitidae, Amphiliidae, Aspredinidae, Erethistidae, and Sisoridae, the ventral portion of the first dorsal-fin pterygiophore and corresponding neural spine is rugose and thick (de Pinna, 1996: #91; Britto, 2002: #285). This character was coded as inapplicable for the Malapteruridae, which lack a middle nuchal plate; and as missing data for the auchenipterid *Spinipterus*.

234. First two dorsal-fin pterygiophores and corresponding neural spines: 0- not sutured; 1- sutured (CI 1.0, RI 1.0).

Among catfishes, the first two dorsal-fin pterygiophores (and usually the supraneural) are sutured to their corresponding neural spines, only in the Auchenipteridae, Chacidae, Doradidae, and Mochokidae (Fig. 35e.g; 1972: 26; Royero, 1987; Royero, 1999: #75; Britto, 2002: #286; Akama, 2004: #125) whereas in other catfishes they are apart or united only by ligaments (Fig. 35a-c). This character was coded as inapplicable for the Malapteruridae, which lack a middle nuchal plate; and as missing data for the auchenipterid *Spinipterus*.

235. Dorsal-fin spinelet: 0- present; 1- absent (CI 0.25, RI 0.25).

Among catfishes, the dorsal-fin spinelet is absent exclusively in the Amphiliidae, Aspredinidae, Astroblepidae, Cetopsidae, Clariidae, Malapteruridae, Nematogenyidae, Siluridae, and Trichomycteridae (Britto, 2002: #288).



Fig. 58. Dorsal-fin spinelet in lateral view of (a) *Ictalurus punctatus*, MZUSP 103256, 155 mm SL; (b) *Platydoras brachylecis*, MZUSP no data; (c) *Rhinodoras dorbignyi*, MZUSP 61688, 102 mm SL. Scale bars equal 5 mm.

236. Ventral processes of dorsal-fin spinelet: 0- short; 1- long (CI 1.0, RI 1.0).

Among examined species, the ventral processes of the dorsal-fin spinelet are elongate, reaching ventrally the middle of the pterygiophore only in the Akysidae, Amblicipitidae, Auchenipteridae, Doradidae, Mochokidae, Erethistidae, and Sisoridae (Fig. 58b-c; Ferraris, 1988: #D7; de Pinna, 1993: #233; de Pinna, 1996: #88; Royero, 1999: #76; Britto, 2002: #289). This character was coded as inapplicable in the Amphiliidae, Aspredinidae, Malapteruridae, Nematogenyidae, and Siluridae, which lack the dorsal-fin spinelet; and as missing data for the auchenipterid *Spinipterus*.

237. Number of branched dorsal-fin rays (ordered): 0- six to eight; 1- five; 2- four; 3- three (CI 0.273, RI 0.5).

In most catfishes there are usually six or seven branched rays in the dorsal fin (Lundberg, 1970; Royero, 1987, 1999; Arratia, 2003b). Most species of Auchenipteridae and Doradidae have six branched dorsal-fin rays. However, the doradid *Acanthodoras* (Eigenmann, 1925: 283; Sousa, 2010: #59), and auchenipterids *Centromochlus heckelii*, *Entomocorus*, *Gelanoglanis*, *Glanidium*, *Pseudepapterus*, *Spinipterus*, *Trachelyopterus*, *Trachycorystes*, and *Tatia aulopygia* have five branched dorsal-fin rays (Britski, 1972: 29; Akama, 2004: #128); *Trachelyichthys* and *Trachelyopterichthys* have four (Ferraris, 1988: D13; Royero, 1999: #78), and *Epapterus* has only three (Vari & Ferraris, 1998). Although most mochokids have six or seven branched dorsal-fin rays, some species of *Chiloglanis* have only five (Vigliotta, 2008: #64). This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin.

238. Size of dorsal-fin spine (ordered): 0- greatly reduced; 1- moderate, less than one-third of SL; 2- elongate, approximately one-third of SL (CI 1.0, RI 1.0).

In the auchenipterids *Centromochlus existimatus* and *C. heckelii*, the dorsal-fin spine is elongate, approximately one-third of the SL (Soares-Porto, 1998: #23). In the auchenipterids *Epapterus* and *Pseudepapterus*, on the other hand, the dorsal-fin spine is extremely reduced in size and thickness (Fig. 38c; Britski, 1972: 27; Ferraris, 1988: #D13; Curran, 1989: #14; Ferraris, & Vari, 2000; Akama, 2004: #127). This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin.

239. Size of dorsal-fin spine in mature males: 0- same as that of females and immature males; 1- distinctly longer than that of females and immature males (CI 0.167, RI 0.444).

In the auchenipterids *Ageneiosus*, *Entomocorus*, *Epapterus*, *Liosomadoras*, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, the dorsal-fin spine is distinctly larger in mature males, relative to that of females and immature males (Royero, 1999: #126; Akama, 2004: #162). In all other examined species, the dorsal-fin spine in mature males is about the same length as in females and immature males. This character was coded as inapplicable

for the Malapteruridae, which lack a dorsal fin; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

240. Arched dorsal-fin spine in mature males: 0- absent; 1- present (CI 1.0, RI 1.0).

In mature males of the auchenipterids *Ageneiosus*, *Tetranematichthys*, *Trachelyopterus porosus* and *T. striatulus* (Akama, 2004: #165), the dorsal-fin spine is arched. In all other examined species, the dorsal-fin spine in mature males is approximately straight. This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

241. Movement of dorsal-fin spine in mature males: 0- dorsal-fin spine not extending anteriorly, forming an angle of approximately 90° relative to long body axis when fully erected; 1- dorsal-fin spine extending anteriorly forming an angle of less than 90° relative to long body axis when fully erected (CI 0.5, RI 0.857).

In mature males of the auchenipterids *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Liosomadoras*, *Pseudepapterus*, *Tetranematichthys*, *Trachelyopterus porosus*, and *T. striatulus* (Fig. 42; Ferraris, 1988: #D12; Royero, 1999: #127; Akama, 2004: #167), the dorsal-fin spine is capable of rotating anteriorly forming an angle of less than 90° angle relative to long body axis when fully erected. In all other examined species, the dorsal-fin spine in mature males does not bend forward. This character was coded as inapplicable for Malapteruridae, which lack dorsal fin; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

242. Serrations on anterior face of dorsal-fin spine: 0- absent or rudimentary; 1- present (CI 0.091-0.1, RI 0.6-0.64).

The presence of serrations on the anterior face of the dorsal-fin spine is highly variable among catfishes. Within examined taxa, serrations are present on the anterior face of dorsal-fin spine in the Ariidae, Doradidae (except *Anadoras* and some species of *Amblydoras*; Sousa, 2010: #56), Pseudopimelodidae, mochokids *Mochokus niloticus*, some species of *Synodontis* (Vigliotta, 2008: #62), auchenipterids *Ageneiosus*, *Asterophysus*, *Auchenipterichthys*, *Centromochlus*, *Liosomadoras*, *Pseudotatia*, *Spinipterus*, *Tatia*, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterichthys* and *Trachycorystes* (Royero, 1999: #80; Akama, 2004: #129). All other examined species lack serrations on anterior face of the dorsal-fin spine. This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin.

243. Serrations of anterior face of dorsal-fin spine in mature males: 0- similar to those in females and immature males; 1- distinct from those in females and immature males (CI and RI inapplicable).

In mature males of the auchenipterids *Ageneiosus inermis* and a few species of *Trachelyopterus* (including *T. insignis*),

the dorsal-fin spine is modified having serrations restricted to its basal and distal portions (Royero, 1999: #128; Akama, 2004: #166). This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

244. Number of series of serrations on anterior face of dorsal-fin spine in mature males: 0- none or one; 1- two (CI 1.0, RI 1.0).

Mature males of the auchenipterids *Ageneiosus*, *Trachelyopterus porosus* and *T. striatulus* have two series of serrations along the anterior face of the dorsal-fin spine (Fig. 42a; Akama, 2004: #164). In all other examined species, there is only one (or none) series of serrations along anterior face of dorsal-fin spine in mature males. This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

245. Serrations on posterior face of dorsal-fin spine: 0- absent; 1- present (CI 0.067, RI 0.548).

The presence of serrations on the posterior face of the dorsal-fin spine is highly variable among catfishes. Within examined taxa, posterior face of the dorsal-fin spine has serrations in the Ariidae (except *Galeichthys*), Claroteidae, Erethistidae, Pangasiidae, Pseudopimelodidae, mochokids *Mochokiella* and *Synodontis* (Vigliotta, 2008: #63), auchenipterids *Asterophysus*, *Auchenipterichthys*, *Centromochlus*, *Entomocorus*, *Liosomadoras*, *Pseudauchenipterus*, *Spinipterus*, *Tetranematchthys*, *Trachelyichthys*, *Trachelyopterichthys* and *Trachelyopterus* (Royero, 1999: #79; Akama, 2004: #130), and Doradinae (except *Leptodoras juruensis*, and some specimens of *Platydoras*; Sousa, 2010: #57). All other examined species lack serrations on posterior face of the dorsal-fin spine. This character was coded as inapplicable for Malapteruridae, which lack dorsal fin; and as polymorphic for *Platydoras armatulus* and *Platydoras* sp.

246. Size of serrations on posterior face of dorsal-fin spine in mature males: 0- moderate, similar to those of females; 1- hypertrophied, stronger than those of females (CI 0.5, RI 0.0).

In mature males of the auchenipterids *Auchenipterichthys* and *Trachelyopterichthys*, the serrations on the distal portion of the posterior face of the dorsal-fin spine are hypertrophied, stronger than those of females (Ferraris & Fernandez, 1987; Ferraris *et al.*, 2005; Akama, 2004: #163). This feature was not present in the examined specimens of *Liosomadoras*, although mentioned by Akama (2004: #163). This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin; and as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

247. Serrations on lateral face of dorsal-fin spine: 0- absent; 1- present (CI 0.5, RI 0.5).

Among examined species, only the doradids *Acanthodoras* and *Agamyxis*, and auchenipterid *Spinipterus* (Akama & Ferraris, 2011) have serrations on the lateral face of the dorsal-fin spine (Sousa, 2010: #58). This character was coded as inapplicable for the Malapteruridae, which lack a dorsal fin.

248. Number of pairs of *inclinatores dorsales* muscles of dorsal fin (ordered): 0- one; 1- two; 2- three; 3- four (CI 0.375, RI 0.444).

Most catfishes have a single pair of *inclinatores dorsales* muscles of the dorsal fin. The auchenipterids *Ageneiosus atronasmus*, *A. brevis* and *A. ucayalensis* have two pairs of *inclinatores dorsales* muscles on the dorsal fin (Fig. 59a), whereas *Ageneiosus inermis*, *A. magoi*, *Pseudepapterus* and *Trachelyopterus* have three (Fig. 59b), and *Tetranematchthys* has four (Akama, 2004: #131; Royero, 1999: table 3). This character was coded as missing data for *Epapterus*, *Gelanoglanis*, *Pseudotatia*, and *Spinipterus*; and coded as inapplicable for Malapteruridae, which lack dorsal fin.

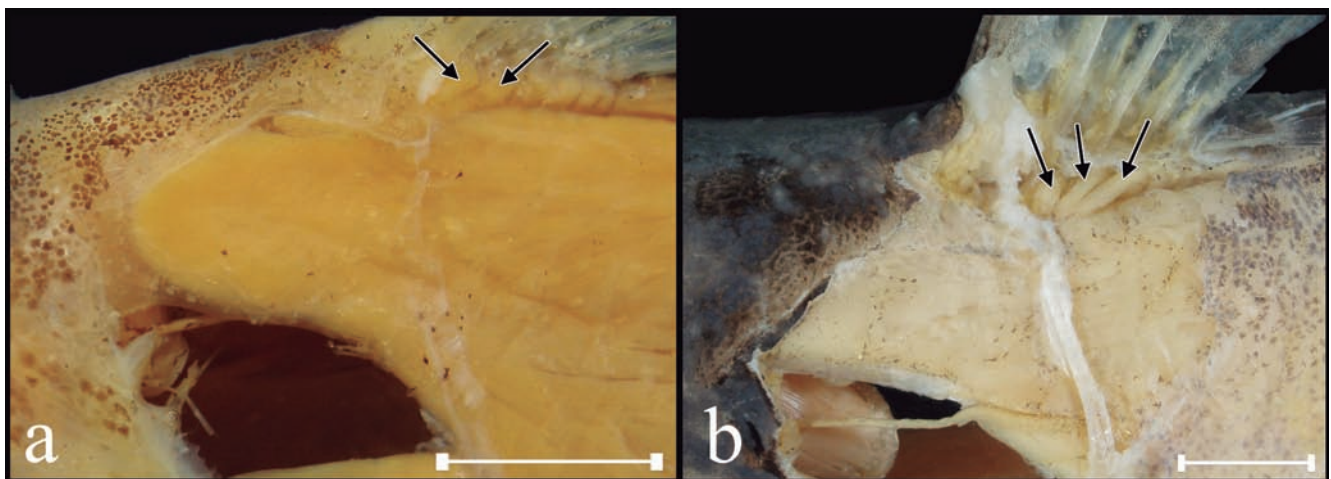


Fig. 59. Dorsal-fin base in dorsolateral view of (a) *Ageneiosus atronasmus*, MZUSP 52620, 80.1 mm SL; (b) *Trachelyopterus striatulus*, MZUSP 90742, 154 mm SL. Arrows indicate *inclinatores dorsales* muscles. Scale bars equal 5 mm.

Pectoral girdle

249. Anterior margin of pectoral girdle (ordered): 0- arched, slightly convex; 1- elongate anteriorly, with truncate tip; 2- elongate anteriorly with acute tip (CI 0.167, RI 0.783).

In most catfishes, the anterior margin of the pectoral girdle in ventral view is arched, slightly convex (Figs. 60d,g, 61). However, in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Oxydoras*, *Nemadoras*, *Tenellus* and most basal species of *Leptodoras*, the pectoral girdle is anteriorly elongate, but with a truncate tip (Figs. 60f,i). In the auchenipterids *Asterophysus*, *Centromochlus*, *Entomocorus*, *Gelanoglanis*, *Pseudauchenipterus*, *Pseudotatia*, *Tatia* (Britski, 1972; Soares-Porto, 1998: #18), and doradids *Leptodoras juruensis* and *Trachydoras* (Higuchi, 1992: #97), the pectoral girdle is anteriorly elongate with acute tip (Figs. 60e,h).

250. Mesocoracoid: 0- present; 1- absent (CI 0.333, RI 0.875).

The mesocoracoid is present as a small arch on the posterior face of the pectoral girdle in most catfishes. However, it is absent in the Anchariidae, Ariidae, Aspredinidae, Auchenipteridae, and Doradidae (Figs. 60, 61; Regan, 1911; Ferraris, 1988: #P1; Royero, 1999: #82; Britto, 2002: #247; Akama, 2004: #105; Diogo, 2004: #185; Vigliotta, 2008: #55; Marceniuk *et al.*, 2012: #219). This character was coded as missing data for the auchenipterid *Spinipterus*.

251. Cleithrum-coracoid bridge: 0- present; 1- absent (CI 0.5, RI 0.0).

There is a bony bridge between the cleithrum and coracoid, near the articular fossa of pectoral-fin spine in most catfishes (Figs. 60-61). However, in the Malapteruridae, Nematogenyidae and some species of Amphiliidae (not including *Amphilius jacksoni*, herein examined) the cleithrum-coracoid bridge is absent (Diogo, 2003: 420; Diogo, 2004: #192).

252. Length of cleithrum-coracoid bridge: 0- short, restricted to articulation fossa of pectoral-fin spine; 1- long, continuous to coracoid posterior process (CI and RI inapplicable).

In most catfishes, the bony bridge between the cleithrum and coracoid is short, restricted to articulation fossa of the pectoral-fin spine. However, the cleithrum-coracoid bridge is elongate, continuous to the coracoid posterior process, in the auchenipterid *Entomocorus*. This character was coded as inapplicable for the Malapteruridae and Nematogenyidae.

253. Pectoral-fin spine locking foramen: 0- present; 1- absent (CI 0.2, RI 0.886).

Most catfishes have a pectoral-fin spine locking foramen on the medial wall of the coracoid, which fits the tip of the medial process of the head of the pectoral-fin spine, when the spine is extended. However, that foramen is absent in the Amphiliidae, Ariidae, Doradidae, auchenipterid *Trachelyopterus* (Royero, 1999: #83), and mochokids *Atopochilus*, *Atopodontus*, *Chiloglanis* (except *C. macropterus*) and *Euchilichthys* (Vigliotta, 2008: #57). This character was coded as missing data for the auchenipterid *Spinipterus*.

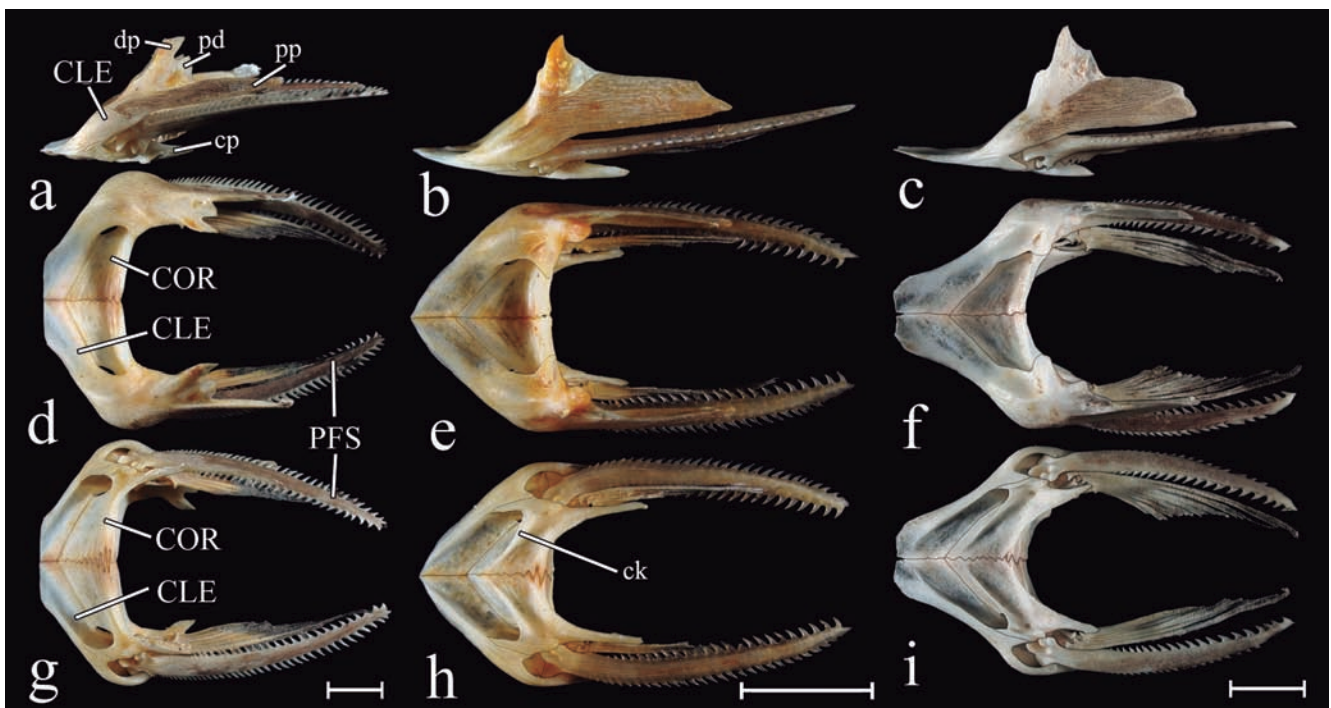


Fig. 60. Pectoral girdle in lateral (upper row), dorsal (middle row) and ventral (lower row) views of (a,d,g) *Wertheimeria maculata*, MZUSP 93658, 220.0 mm SL; (b,e,h) *Trachydoras brevis*, MZUSP 103087, 74 mm SL; (c,f,i) *Doras higuchii*, MZUSP 101693, 182 mm SL. CLE cleithrum, COR coracoid, cp coracoid process, dp dorsal cleithral process, pd posterodorsal cleithral process, PFS pectoral-fin spine, pp posterior cleithral process. Scale bars equal 10 mm.

254. Process of first proximal radial of pectoral fin (ordered): 0- absent; 1- extended ventrally; 2- extended ventral and dorsally (CI 0.333, RI 0.5).

Among examined species, there is a process that extends ventrally on the first proximal radial of the pectoral fin only in the Claroteidae, Pangasiidae, Schilbeidae (Britto, 2002: #253) and some species of Mochokidae (including *Mochokiella* and *Synodontis*; Vigliotta, 2008: #58). Furthermore, in the Ariidae and mochokid *Chiloglanis*, the process extends both ventrally and dorsally (Vigliotta, 2008: #58). This character was coded as missing data for the auchenipterid *Spinipterus*.

255. Size of second proximal radial of pectoral fin: 0- moderate, supporting fewer than three rays; 1- large, supporting more than three rays (CI 1.0, RI 1.0).

The second proximal radial of the pectoral fin is extremely enlarged distally and supports several rays in the auchenipterids *Ageneiosus* and *Tetranematichthys* (Figs. 61f,i; Ferraris, 1988: #P9; Walsh, 1990: #6; Royero, 1999: #90; Akama, 2004: #115). Although, in *Ageneiosus atronasus* this element is not as large as in congeners, it is distinctly larger than in most auchenipterids. This character was coded as inapplicable for the auchenipterid *Gelanoglanis*, which lack the second proximal radial; and as missing data for the auchenipterid *Spinipterus*.

256. Dorsal process of base of pectoral-fin spine: 0- small, non-discoid, and weakly attached to cleithrum; 1- large, discoid, firmly attached to cleithrum (CI 1.0, RI 1.0).

Among examined species, only in the auchenipterid *Ageneiosus* the base of the pectoral-fin spine has a small, non-discoid dorsal process that is weakly attached to cleithrum (Royero, 1999: #86; Akama, 2004: #117).

257. Serrations on anterior face of pectoral-fin spine: 0- absent; 1- present (CI 0.1, RI 0.438).

The presence of serrations on the anterior face of the pectoral-fin spine is highly variable among catfishes (Arratia, 1987). These serrations are present in the Ariidae, Aspredinidae (except *Xyliphius*), Auchenipteridae (exceptions listed below), Bagridae, Clariidae, Claroteidae, Doradidae, Heptapteridae, Ictaluridae (except *Pylodictis olivaris*), Pangasiidae, Pimelodidae, Pseudopimelodidae, Schilbeidae, sisorid *Sisor* and some species of Mochokidae (including *Mochokiella*, *Mochokus*, and *Synodontis*) (Britto, 2002: #255; Vigliotta, 2008: #59). The auchenipterids *Ageneiosus*, *Auchenipterus*, *Epapterus*, *Gelanoglanis*, *Pseudauchenipterus*, *Pseudepapterus*, *Tetranematichthys*, and *Trachelyopterus coriaceus* lack serrations on anterior face of the pectoral-fin spine (Ferraris, 1988: #P7; Soares-

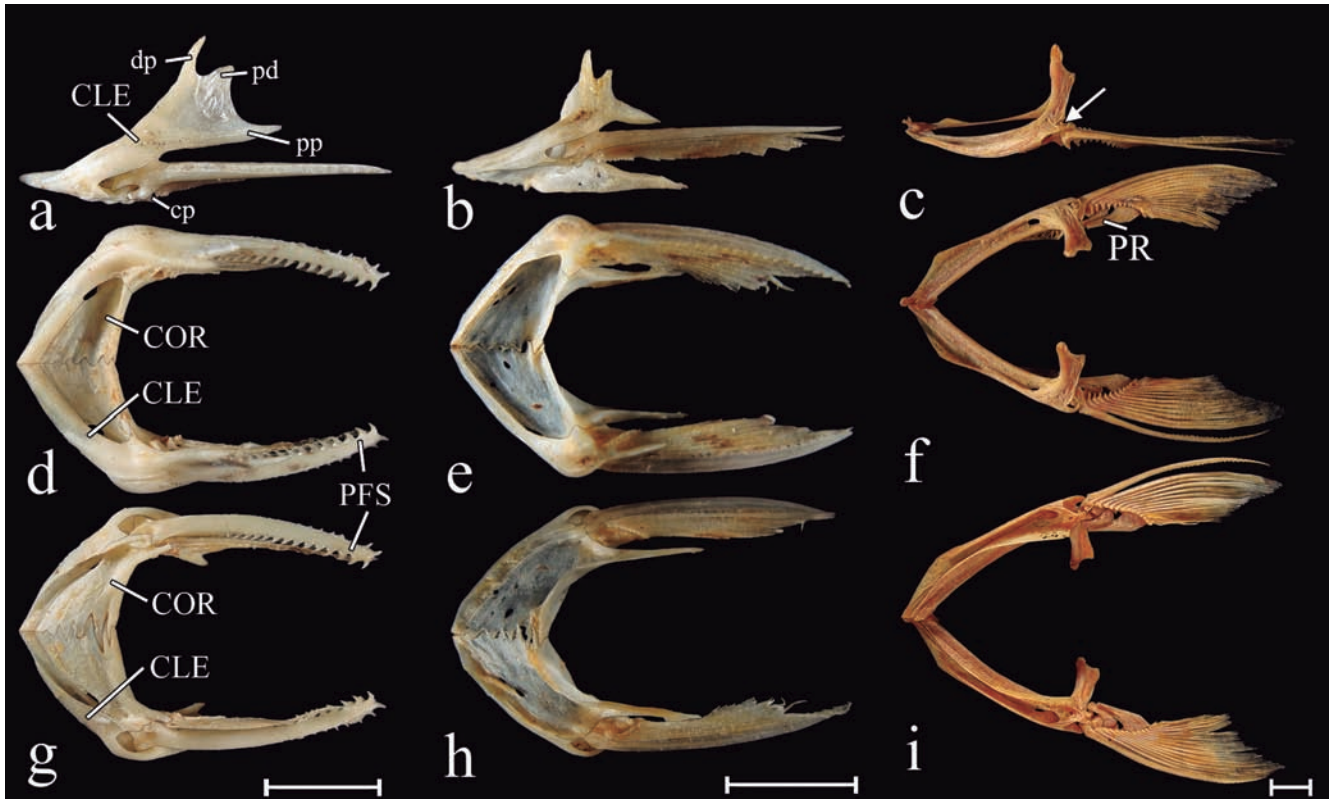


Fig. 61. Pectoral girdle in lateral (upper row), dorsal (middle row) and ventral (lower row) views of (a,d,g) *Glanidium melanopterum*, MZUSP 64256, 112 mm SL; (b,e,h) *Auchenipterus nuchalis*, MZUSP 89728, 141 mm SL; (c,f,i) *Ageneiosus inermis*, MZUSP 91661, 333 mm SL. CLE cleithrum, COR coracoid, cp coracoid process, dp dorsal cleithral process, pd posterodorsal cleithral process, PFS pectoral-fin spine, pp posterior cleithral process, PR pectoral-fin rays. Arrow indicated lateral fenestra of pectoral girdle. Scale bars equal 10 mm.

Porto, 1998: #20; Royero, 1999: #88; Walsh, 1990: #34; Akama, 2004: #107).

258. Orientation of serrations on anterior face of pectoral-fin spine: 0- antrorse; 1- retrorse (CI 0.5, RI 0.0).

In most catfishes, the serrations of the anterior face of the pectoral-fin spine are antrorse along the entire spine, or at least along the distal half. However, in the auchenipterids *Centromochlus heckelii* and *Tocantinsia*, those serrations are retrorse for the entire length of the pectoral-fin spine (Ferraris, 1988: #P5). This character was coded as inapplicable for the Amphiliidae, Diplomystidae, Erethistidae, Malapteruridae, Nematogenyidae, Siluridae, Sisoridae, mochokid *Chiloglanis*, and auchenipterids *Auchenipterus*, *Epapterus*, *Gelanoglanis*, *Pseudauchenipterus*, *Pseudepapterus*, *Tetranematichthys*, and *Trachelyopterus coriaceus*, which lack spines on the anterior face of the pectoral fin.

259. Serrations on posterior face of pectoral-fin spine: 0- present; 1- absent (CI 0.5, RI 0.5).

Most catfishes have serrations on the posterior face of the pectoral-fin spine. However, the Amphiliidae, Malapteruridae, and mochokid *Chiloglanis* (except *C. macropterus*) have the posterior face of the pectoral-fin spine without serrations (Vigliotta, 2008: #60).

260. Serrations on dorsal face of pectoral-fin spine (unordered): 0- absent; 1- present on anterior portion; 2- widespread (CI 0.667, RI 0.5).

Most catfishes have the dorsal face of the pectoral-fin spine without serrations. However, the auchenipterids *Spinipterus*, *Trachelyoptericthys taeniatus*, *Trachelyopterus porosus*, and *T. striatulus* have a row of serrations on distal portion of the dorsal face of the pectoral-fin spine (Akama, 2004: #110), and the doradids *Acanthodoras* and *Agamyxis* have serrations widespread over the dorsal face of the pectoral-fin spine (Sousa, 2010: #74).

261. Length of pectoral-fin spine: 0- moderate, less than one-third of SL; 1- elongate, longer than one-third of SL (CI and RI inapplicable).

The pectoral-fin spine in the auchenipterids *Centromochlus existimatus* and *C. heckelii* is elongate, longer than one-third of the SL (Ferraris, 1988: #P2; Royero, 1999: #91; Akama, 2004: #106). In all other examined taxa, the pectoral-fin spine is shorter than one-third of SL.

262. Number of branched pectoral-fin rays: 0- four to eight; 1- nine to 15 (CI 0.5, R 0.667).

Most catfishes have six to eight branched pectoral-fin rays (Lundberg, 1970: 51). Some species of the Auchenipteridae have more branched pectoral-fin rays (Walsh, 1990: #30; Royero, 1999: #87, #151; Akama, 2004: #118), including: *Auchenipterus* (with 10 to 14, Ferraris & Vari, 1999: table 4), *Epapterus* (*E. blohmi* with eight to 10, and *E. dispilurus* with 10 to 12, Vari &

Ferraris, 1998: 996), *Pseudepapterus* (with 10 to 14, Ferraris & Vari, 2000: table 3) and *Tetranematichthys* (with nine to 11, Vari & Ferraris, 2006: 174).

263. Lateral fenestra on cleithrum: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, there is a small fenestra on the lateral surface of the cleithrum only in the auchenipterid *Ageneiosus* (except *A. atronasus* and *A. brevis*), (Figs. 61c,f; Royero, 1999: #85; Akama, 2004: #116). A similar condition occurs in the pimelodid *Hypophthalmus* (Diogo, 2004: #160).

264. Posterodorsal process of cleithrum: 0- well developed, with acute tip; 1- weakly developed, with obtuse tip (CI 0.5, RI 0.978).

In most catfishes, the dorsal tip of the cleithrum has two well-developed processes (with acute tip): one dorsal and one posterodorsal (Figs. 60, 61a; Tilak, 1963). However, the posterodorsal process is weakly developed, with an obtuse tip in all species of Doradidae, except *Franciscodoras*, *Kalyptodoras*, *Leptodoras praelongus*, and *Wertheimeria* (Figs. 60b-c; Sousa, 2010: #61). This character was coded as missing data for the auchenipterid *Spinipterus*.

265. Posterior cleithral process (ordered): 0- absent; 1- length smaller than that of dorsal process; 2- length greater than that of dorsal process (CI 0.2, RI 0.704).

The posterior cleithral process is small in most catfishes, including the auchenipterids *Gelanoglanis*, *Glanidium*, *Tatia aulopygia*, *Tetranematichthys Trachelyopterus galeatus*, and *T. insignis* (Fig. 61a; Akama, 2004), and mochokids Chiloglanidinae (Vigliotta, 2008: #53). It is absent in several species, including the Amblycipitidae, Callichthyidae, Cetopsidae, Clariidae, Malapteruridae, Nematogenyidae, Siluridae, Trichomycteridae (Britto, 2002: #246), and the auchenipterid *Ageneiosus* (Figs. 61c; Ferraris, 1988: #P8; Walsh, 1990: #5; Royero, 1999: #84; Akama, 2004: #112). The posterior cleithral process is large, its length greater than that of the dorsal process, in the Doradidae, Auchenipteridae (except *Gelanoglanis*, *Glanidium*, *Tatia aulopygia*, *Tetranematichthys Trachelyopterus galeatus*, and *T. insignis*), and Mochokidae (except Chiloglanidinae) (Figs. 60, 61).

266. Shape of posterior cleithral process (unordered): 0- elongate, depth at base slightly greater than near tip; 1- triangular, deep at base and tapering posteriorly; 2- trapezoidal, deep at base and near tip (CI 0.667, RI 0.967).

The posterior cleithral process in catfishes is usually elongate, tapering posteriorly (fig. 60a). However, in the doradids *Orinocodoras*, *Rhinodoras*, and *Rhynchodoras*, it is triangular, deep at its base and tapering posteriorly (Fig. 24; Higuchi, 1992: #101), and in the doradids *Anduzedoras*, *Doras*, *Hassar*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras* it is trapezoidal, deep at its base and near tip (Figs. 60b,c; Sabaj, 2002: #20; Sousa, 2010: #63). This character was coded as inapplicable for the Malapteruridae,

Nematogenyidae, Siluridae, and auchenipterid *Ageneiosus*, which lack the posterior cleithral process.

267. Spines on posterior cleithral process: 0- absent; 1- present (CI 0.25, RI 0.667).

There are spines on the posterior cleithral process in the auchenipterids *Liosomadoras*, *Spinipterus*, *Trachelyopterus porosus*, *Trachelyopterus fisheri*, *T. teaguei*, and doradids Astrodoradinae, *Acanthodoras*, *Agamyxis*, *Centrochir*, and *Platydoras* (Fig. 22; Eigenmann, 1925: 287; Higuchi, 1992: #99, #A70; #A72; Sousa, 2010: #64; #66; Curran, 1989: #11; Akama, 2004: #113; Higuchi *et al.*, 2007: 33). This character was coded as 1 for *Anadoras* and *Platydoras*, although the spines may be inconspicuous in very large specimens of those species (specimens larger than 100 mm SL). On the other hand, this character was coded as 0 for doradids *Franciscodoras*, *Megalodoras*, and *Pterodoras*, even though very small specimens have spines on the posterior cleithral process (reported cases are MZUSP 97145, 30 mm SL, MZUSP 55838, 68 mm SL, MZUSP 82995, 60 mm SL, respectively). This character was coded as inapplicable for Malapteruridae, Nematogenyidae, Siluridae and auchenipterid *Ageneiosus*, which lack posterior cleithral process.

268. Arrangement of spines on posterior cleithral process (unordered): 0- scattered, widespread; 1- arranged in single row; 2- arranged in one main row accompanied by secondary rows (CI 0.667, RI 0.75).

In the auchenipterids *Liosomadoras*, *Trachelyopterus porosus* (Curran, 1989: #11; Akama, 2004: #113) and doradid *Agamyxis* (Eigenmann, 1925: 287; Higuchi, 1992: #A70; Sousa, 2010: #64), the spines are scattered and widespread on the posterior cleithral process. In the auchenipterids *Spinipterus*, *Trachelyopterus fisheri*, *T. teaguei* (Akama, 2004: #113), and doradids *Centrochir* and *Platydoras* the spines are arranged in a single row on the posterior cleithral process. In the doradid *Acanthodoras* and in the species of Astrodoradinae, the spines of the posterior cleithral process are arranged in one main row accompanied by secondary rows (Higuchi, 1992: #99, #A72; Higuchi *et al.*, 2007: 33; Sousa, 2010: #66). This character was coded as inapplicable for all taxa that lack spines on the posterior cleithral process.

269. Suture between coracoids (ordered): 0- straight; 1- interdigitating from anterior to posterior border; 2- interdigitating only near posterior border (CI 0.667, RI 0.5).

In most catfishes, the suture between the coracoids is interdigitating from anterior to posterior border (Figs. 60, 61; Britto, 2002: 249). However, in the Astroblepidae, Cetopsidae, Diplomystidae, Nematogenyidae, Siluridae, and Trichomycteridae, the suture between coracoids is straight (Mo, 1991; Grande & de Pinna, 1998; de Pinna *et al.*, 2007: #103), whereas in the auchenipterid *Pseudepapterus* the suture is interdigitating only near the posterior border of the coracoids. This character was coded as missing data for the auchenipterid *Spinipterus*.

270. Posterior coracoid process (unordered): 0- short, extending slightly posterior than base of pectoral-fin rays; 1- elongate, thick and visually exposed; 2- elongate, laminar and not visually exposed (CI 0.333, RI 0.636).

The posterior coracoid process is elongate (extending distinctly beyond base of rays), thick and visually exposed in the Aspredinidae, Erethistidae, Scoloplacidae, and Sisoridae (Alexander, 1965: 119; de Pinna, 1996: #79; Britto, 2002: #250). The same condition is present in the doradids *Astrodoras*, *Ossancora*, *Physopyxis*, and *Trachydoras paraguayensis* (Eigenmann, 1925: 287; Higuchi, 1992: #106, A75; Sousa, 2010: #71), and auchenipterids *Auchenipterichthys coracoideus* and *A. thoracatus* (Ferraris *et al.*, 2005). In the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus* the posterior coracoid process is also elongate (extending distinctly beyond base of rays), laminar and not visually exposed (Figs. 61b,e,h).

271. Dorsoposterior border of coracoid: 0- slightly elevated dorsally, length of transverse portion of coracoid much smaller than that of longitudinal portion; 1- extremely elevated dorsally, length of transverse portion of coracoid approximately equal of longer than that of longitudinal portion (CI 1.0, RI 1.0).

In most catfishes, the dorsoposterior border of the coracoid is only slightly elevated dorsally (*i.e.*, length of transversal portion of coracoid is much smaller than that of longitudinal portion). In the doradids *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Oxydoras*, *Tenellus*, and *Trachydoras*, the dorsoposterior border of the coracoid is extremely elevated dorsally, forming a bony diaphragm, and strongly associated with the ventral process of the transcapular process (Figs. 34b-d, 60e,f; Higuchi, 1992: #102; Sousa, 2010: #72). This character was coded as missing data for the auchenipterid *Spinipterus*.

272. Ventroposterior margin of coracoid: 0- laminar, developed as a shallow flap, not visually exposed in alcohol preserved specimens; 1- thick, visually exposed (CI 0.111, RI 0.6).

In most catfishes, the ventroposterior margin of the coracoid is laminar and developed as a shallow flap, not visually exposed in alcohol preserved specimens. However, in the Aspredinidae, auchenipterids *Auchenipterichthys thoracatus*, *Centromochlus*, and *Trachelyopterus coriaceus* (Soares-Porto, 1998: #35), and doradids *Acanthodoras*, *Agamyxis*, *Anadoras*, *Astrodoras*, *Hemidoras*, *Megalodoras*, *Ossancora*, *Scorpiodoras*, *Trachydoras paraguayensis*, and *T. steindachneri* (Higuchi, 1992: #105; Sousa, 2010: #67), the ventroposterior border of the coracoid is thick and visually exposed in alcohol-preserved specimens. In some species of Astrodoradinae, this feature is further developed, and the entire ventral face of the pectoral girdle is visually exposed in some cases (Sousa & Rapp Py-Daniel, 2005; Higuchi *et al.*, 2007; Sousa, 2010).

273. Bony crest of coracoid between *adductor superficialis* and *arrector ventralis* muscles: 0- absent; 1- present (CI 0.2, RI 0.778).

Among examined species, a bony crest is present on the ventral face of the coracoid between the *adductor superficialis* and *arrector ventralis* muscles in the Amphiliidae, Auchenipteridae (except *Auchenipterus*, *Epapterus*, and *Pseudepapterus*), Doradidae (except *Rhynchodoras*), Erethistidae and Mochokidae (Figs. 60g-i, 61g,i; Birindelli *et al.*, 2007: 673). This character was coded as missing data for the auchenipterid *Spinipterus*.

274. Orientation of coracoid crest between *adductor superficialis* and *arrector ventralis* muscles: 0- oblique; 1- transverse (CI 0.143, RI 0.571).

In most examined species, the bony crest of coracoid between *adductor superficialis* and *arrector ventralis* muscles is oblique, relative to long axis of body (Figs. 60g-i, 61g-i). However, in the doradids *Acanthodoras*, *Centrochir*, *Centrodoras*, *Hemidoras morrissi*, *Platydoras*, *Megalodoras*, *Orinocodoras*, *Ossancora fimbriata*, and *Rhinodoras*, and mochokid *Synodontis schall*, the coracoid crest is perpendicular to the long axis of body (Sousa, 2010: #69). This character was coded as inapplicable for the Ariidae, Aspredinidae, Claroteidae, Diplomystidae, Heptapteridae, Ictaluridae, Malapteruridae, Nematogenyidae, Pangasiidae, Pimelodidae, Pseudopimelodidae, Siluridae, Sisoridae, auchenipterids *Auchenipterus* and *Pseudepapterus*, and doradid *Rhynchodoras*; and as missing data for the auchenipterid *Spinipterus*.

Pelvic girdle

275. Position of pelvic girdle: 0- approximately halfway along SL; 1- within anterior half of SL (CI 1.0, RI 1.0).

In most catfishes, the pelvic girdle is located approximately midway along SL. However, the pelvic girdle is positioned in the anterior half of the body (SL) in *Leptodoras* (Higuchi, 1992: #108; Birindelli & Sousa, 2010).

276. Number of branched pelvic-fin rays (ordered): 0- four or five; 1- six; 2- seven; 3- eight or more (CI 0.167, RI 0.659).

According to Shelden (1937), Lundberg (1970) and Grande (1987), catfishes in general have five (or sometimes only four) branched pelvic-fin rays. However, all species of Mochokidae (Vigliotta, 2008: #65), and most species of Auchenipteridae and Doradidae have six. The exceptions include the doradids *Acanthodoras*, *Agamyxis*, *Franciscodoras*, *Kalyptodoras*, and *Wertheimeria* (Sousa, 2010: #80), and auchenipterids *Entomocorus* (Akama & Ferraris, 2004), *Trachelyopterus* (Akama, 2004), and most species of Centromochlinae (Mees, 1974) with five; auchenipterid *Pseudauchenipterus* with seven (Akama, 1999); and auchenipterids *Asterophysus*, *Auchenipterichthys* (Ferraris *et al.*, 2005), *Auchenipterus* (Vari & Ferraris, 1998), *Epapterus* (Ferraris & Vari, 2000), *Pseudepapterus* (Ferraris & Vari, 1999), *Trachelyopterichthys* (Ferraris & Fernandez, 1987), *Trachelyichthys* and *Trachycorystes*, with eight or more branched pelvic-fin rays (Ferraris, 1988: #PV3; Royero, 1999: #92; Akama, 2004: #122). In addition, the Ictaluridae has seven branched pelvic-fin rays,

and Pangasiidae and Siluridae have eight or more. This character was coded as polymorphic (0,1) for the auchenipterid *Spinipterus* (see Akama & Ferraris, 2011).

277. Pelvic splint: 0- present; 1- absent (CI 0.25, RI 0.5).

The pelvic splint, as discussed by Lundberg (1970: fig. 134) and Arratia (1987: 31), is present in the Bagridae (except *Batasio* and *Olyra*), Cetopsidae, Cranoglanidae, Diplomystidae, Ictaluridae (except *Trogloglanis*), Pangasiidae, Schilbeidae, Siluridae, Sisoridae, and was also reported to be present in the Trichomycteridae (Britto, 2002: #279), and mochokids *Chiloglanis* and *Synodontis* (Vigliotta, 2008: #66). The pelvic splint is absent in the Amphiliidae, Ariidae (Marceniuk *et al.*, 2012: #220), Aspredinidae, Auchenipteridae, Claroteidae, Doradidae, Erethistidae, Heptapteridae, Malapteruridae, Nematogenyidae, Pimelodidae, Pseudopimelodidae, and mochokids *Mochokus* and *Mochokiella*.

278. Cartilaginous radial of pelvic fin: 0- present; 1- absent (CI 0.2, RI 0.0).

Among examined taxa, the cartilaginous radial of the pelvic fin is absent only in the Aspredinidae, Auchenoglanidae, Chacidae, Diplomystidae, Malapteruridae, mochokid *Synodontis* and sisorid *Bagarius* (Lundberg, 1970; Britto, 2002: #277). This character was coded as missing data for the auchenipterid *Spinipterus*.

279. First ray of pelvic fin in mature males: 0- normal, as in females; 1- modified, distinct from that of females (CI and RI inapplicable).

In mature males of the auchenipterid *Entomocorus*, the first ray of the pelvic fin is modified, enlarged and elongate (Ferraris, 1988: #PV2, Royero, 1999: #133; Akama & Ferraris, 2003; Akama, 2004: #170). The first ray of pelvic fin is not modified in mature males of all other examined species. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

280. Spines on first two pelvic-fin rays: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, only the doradid *Agamyxis* has spines on the dorsal and ventral faces of the first two pelvic-fin rays (Sousa, 2010: #81).

281. Bases of paired pelvic fin: 0- separated; 1- united by membrane (CI 1.0, RI 1.0).

In the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus*, a membrane unites the medial portions of the paired pelvic-fin bases (Ferraris & Vari, 1999: 393; Ferraris, 1988: #PV6; Akama, 2004: #123). This membrane is absent in all other examined species.

282. Contact between cartilages of anterior rami of basipterygium: 0- absent; 1- present (CI 0.333, RI 0.333).

The cartilages of the anterior ramus of the basipterygium

contact each other in the Amphiliidae, Erethistidae, Sisoridae (except *Pseudecheneis* and *Sisor*), and mochokids *Chiloglanis*, *Atopodontus*, *Atopochilus*, and *Euchilichthys* (de Pinna, 1993: 212; Britto, 2002: #263; Vigliotta, 2008: 68). In all other examined species, the cartilages of the anterior rami of the basipterygium are separated. This character was coded as missing data for the auchenipterid *Spinipterus*.

283. Anteromedial process of basipterygium (ordered): 0- distinct, not united to basipterygium by bony lamina; 1- partially united to basipterygium by bony lamina; 2- completely united to basipterygium by bony lamina (CI 0.167, RI 0.762).

The anteromedial process of the basipterygium is distinct in most catfishes (Figs. 62a, 63a). However, they are partially incorporated in the basipterygium by a bony lamina in the doradids *Acanthodoras*, *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras stenopeltis*, *H. stubelii*, *Tenellus leporhinus*, *T. ternetzi*, and auchenipterids *Ageneiosus*, *Gelanoglanis*, and *Tetranematichthys* (Figs. 62b, 63b). On the other hand, in the doradids *Hemidoras morei*, *H. morrisi*, *Ossancora*, and *Trachydoras* (Fig. 62c; Higuchi, 1992: #109, #110; Sousa, 2010: #76), and auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus* (Fig. 63c; Shelden, 1937: fig. 20), the anteromedial processes are indistinct and incorporated in the basipterygium by bony lamina. This character was coded as inapplicable for the Aspredinidae, which lack the anterior processes of the basipterygium; and as missing data for the auchenipterid *Spinipterus*.

284. Paired anterolateral processes of basipterygium: 0- separated; 1- sutured (CI 1.0, RI 1.0).

Among examined species, a suture between the paired anterolateral processes of the basipterygium is present only in the auchenipterids *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* (Fig. 63c). This character was coded as missing data for the auchenipterid *Spinipterus*.

285. Lateral process of basipterygium: 0- short, without cartilaginous extensions; 1- with well-developed cartilaginous extension (CI 0.333, RI 0.846).

Among examined species, only the Heptapteridae, and auchenipterids *Asterophysus*, *Auchenipterus*, *Centromochlus*, *Liosomadoras*, *Pseudauchenipterus*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, and *Trachycorystes* lack a cartilaginous extension on the lateral process of the basipterygium. This character was coded as missing data for the auchenipterids *Glanidium*, *Pseudotatia*, and *Spinipterus*.

286. Shape of posterior process of basipterygium: 0- tapering posteriorly; 1- truncate (CI 1.0, RI 1.0).

The posterior process of the basipterygium is acute, tapering posteriorly, in most catfishes (Figs. 62, 63a-b). However, it is truncate in the auchenipterids *Auchenipterus*, *Entomocorus* and *Pseudepapterus* (Fig. 63c; Akama, 2004: #121). This character was coded as missing data for the auchenipterids *Epapterus* and *Spinipterus*.

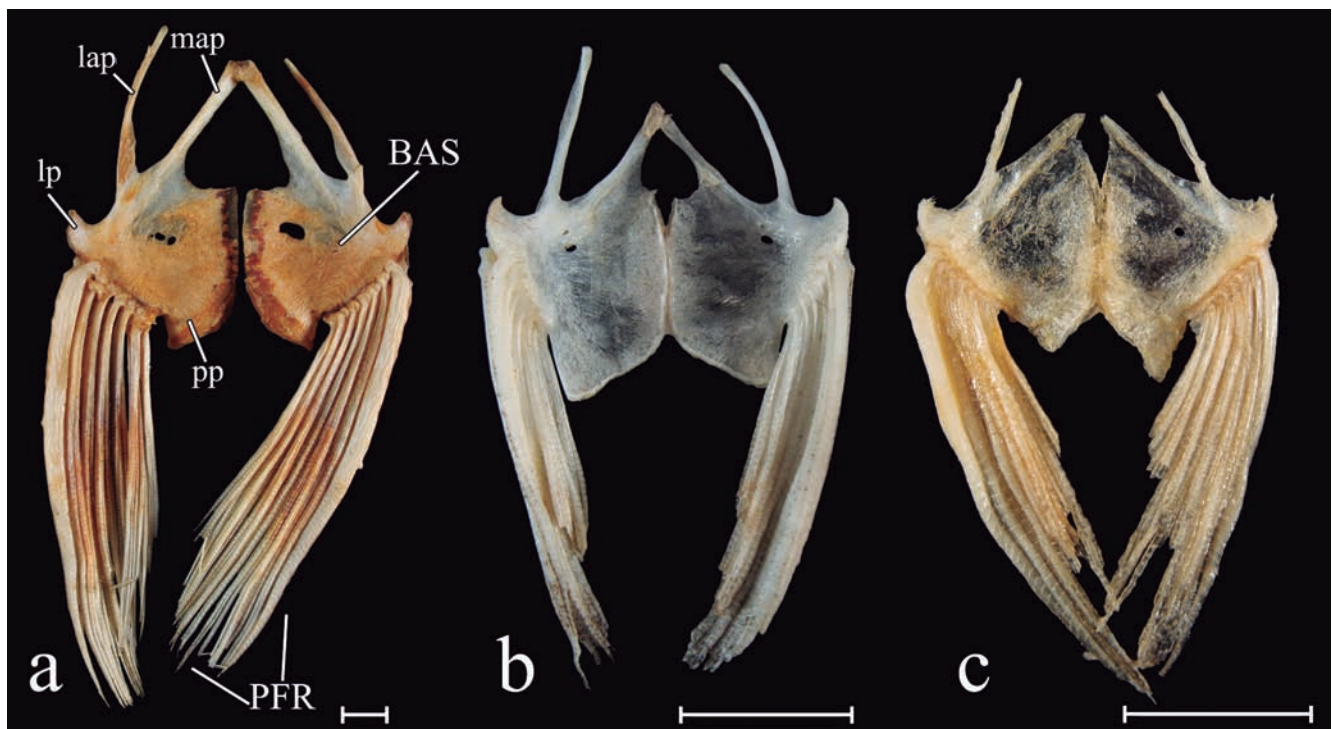


Fig. 62. Pelvic girdle in dorsal view of (a) *Lithodoras dorsalis*, MZUSP 91562, 450 mm SL; (b) *Doras higuchii*, MZUSP 101693, 172.0 mm SL; (c) *Hemidoras morei*, MZUSP 32526, 153.2 mm SL. BAS basipterygium, lap anterolateral process, lp lateral process, map anteromedial process, PFR pelvic-fin rays, pp posterior process. Scale bars equal 10 mm.

Anal fin

287. Number of branched anal-fin rays (ordered): 0- five to eight; 1- nine to 13; 2- 14 to 31; 3- 32 or more (CI 0.2, RI 0.647).

The number of branched anal-fin rays greatly varies among species of catfishes, but is usually between 9 and 13 (Lundberg, 1970: 101, #100; Arratia, 1987: 63; Friel, 1994). Among examined species, the exceptions include: Amphiliidae, Aspredinidae, Pseudopimelodidae with five, Malapteruridae with seven, Ictaluridae with 24, Pangasiidae with 32, Siluridae with about 60, and auchenipterids *Asterophysus*, *Centromochlus*, *Gelanoglanis*, *Liosomadoras*, *Tatia*, and *Tocantinsia* with five to eight, *Ageneiosus atronasus*, *A. brevis*, *A. piperatus*, *Auchenipterichthys*, *Entomocorus*, *Pseudoauchenipterus*, *Spinipterus*, *Trachelyopterus*, and *Trachycorystes* with 14 to 31, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterichthys*, and large-sized species of *Ageneiosus* with 32 to 62 branched anal-fin rays (Ferraris, 1988: #A2; Walsh, 1990: #29; Royero, 1999: #93; Akama, 2004: #132).

288. Orientation of anal fin in mature males: 0- normal, ventrally oriented; 1- oblique relative to body axis, posteriorly oriented (CI 1.0, RI 1.0).

Among examined species the anal fin is oblique relative to the body axis, and posteriorly oriented, only in mature males of the auchenipterids Centromochlinae (Figs. 18a, 38a; Royero, 1999: #132; Akama, 2004: #147).

289. Orientation of anal-fin proximal radials in mature males: 0- perpendicular to long axis of body, interdigitating with hemal spines; 1- oblique to body axis, not interdigitating with hemal spines (CI 1.0, RI 1.0).

The anal-fin proximal radials in mature males of the auchenipterids Centromochlinae are oblique relative to the body axis, and not interdigitating with the corresponding hemal spines (Fig. 64; Ferraris, 1988: #A5, #A6; Soares-Porto, 1998: #28; Akama, 2004: #133, #152). In all other examined species, the anal-fin proximal radials in mature males are transversal to long axis of body, interdigitating with the hemal spines.

290. Size of anal fin in mature males: 0- moderate, length of anterior branched rays more than 10% of SL; 1- short, length of anterior branched rays less than 10% of SL (CI 0.5-1.0, RI 0.0-1.0).

In mature males of the auchenipterids *Gelanoglanis* and *Tatia* the anal fin is relatively short, with distance from anal-fin base origin to tip of longest anal-fin ray 5 to 10% of SL (Fig. 38a; Soares-Porto, 1998: #27; Soares-Porto *et al.*, 1999). The base of the anal fin in males of *Gelanoglanis* and *Tatia* is also extremely short, 1.8 to 8.0% of SL (Soares-Porto *et al.*, 1999; Sarmento-Soares & Martins-Pinheiro, 2008: 498). Although both of those characters were treated as exclusive to *Tatia* (Sarmento-Soares & Martins-Pinheiro, 2008), they are also present in *Gelanoglanis*, as described by Soares-Porto *et al.* (1999). The length of the anterior branched anal-fin rays are more than 10% of SL in mature males of all other examined species.

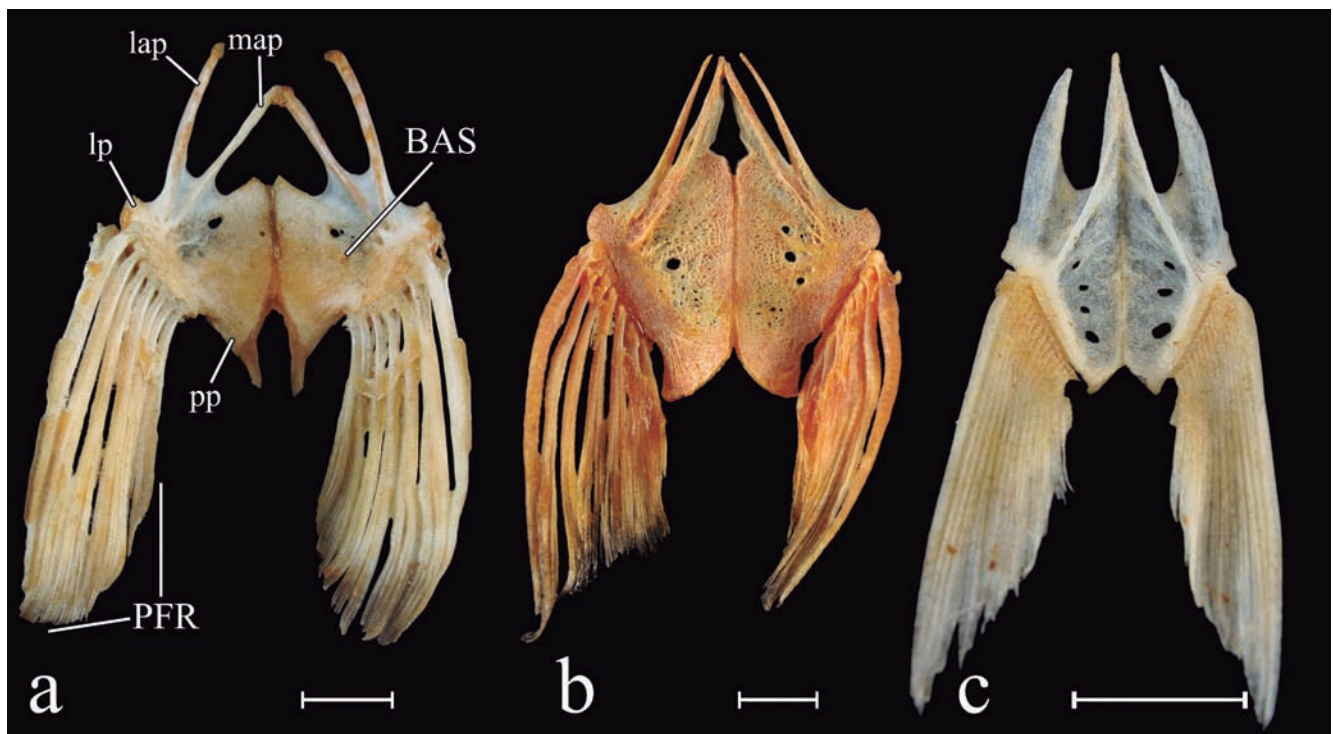


Fig. 63. Pelvic girdle in dorsal view of (a) *Tocantinsia piresi*, MZUSP 100031, 440 mm SL; (b) *Ageneiosus inermis*, MZUSP 91661, 333 mm SL; (c) *Auchenipterus nuchalis*, MZUSP 89728, 141 mm SL. BAS basipterygium, lap anterolateral process, lp lateral process, map anteromedial process, PFR pelvic-fin rays, pp posterior process. Scale bars equal 10 mm.

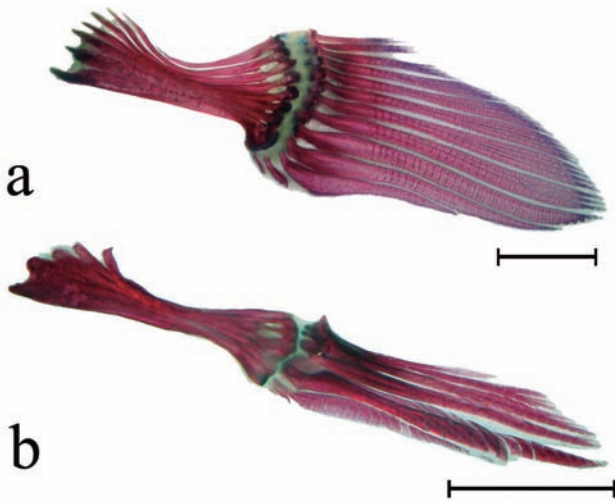


Fig. 64. Anal fin in cleared and stained specimens of mature males of (a) *Glanidium melanopterum*, MZUSP 51043, 107.9 mm SL; (b) *Centromochlus heckelii*, MZUSP 49529, 97.4 mm SL.

291. Anal-fin proximal radials in mature males (ordered): 0- separated; 1- partially fused forming a single ossification; 2- completely fused together forming a single ossification (CI 1.0, RI 1.0).

In most examined species, the proximal radials are not sutured together in mature males. However, in mature males of most species of the auchenipterid *Glanidium* (including *G. melanopterum*), the anal-fin proximal radials are partially fused to each other, *i.e.*, the anterior rays are fused and the posterior ones are not (Fig. 64a; Soares-Porto, 1998: #30; Royero, 1999: #139; Akama, 2004: #153). In mature males of the examined species of auchenipterids *Centromochlus* and *Tatia*, on the other hand, all anal-fin proximal radials are completely fused together (Fig. 64b; Ferraris, 1988: #A7; Soares-Porto, 1996: #30).

292. Shape of posteriormost four or five anal-fin proximal radials: 0- rod-like; 1- laminar (CI 1.0, RI 1.0).

Among examined species, the last four or five anal-fin proximal radials are laminar only in the auchenipterids *Auchenipterus*, *Epapterus*, and *Pseudepapterus* (Ferraris, 1988: #A8; Akama, 2004: #134). This character was coded as missing in the auchenipterid *Spinipterus*.

293. Retrorse spines on anal-fin rays in mature males: 0- absent; 1- present (CI and RI inapplicable).

In mature males of some species of the auchenipterid *Centromochlus heckelii*, there are retrorse spines on the posterolateral margin of the last unbranched and first branched anal-fin rays (Fig. 64b; Ferraris, 1988: #A9; Soares-Porto, 1998: #38; Royero, 1999: #134, #136; Akama, 2004: #157). This feature is absent in all other examined species. This character was coded as missing in the auchenipterids *Pseudotatia* and *Spinipterus*.

294. Antrorse and retrorse spines on anal-fin rays in mature males: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, there are antrorse spines on the anterior margin of the last unbranched anal-fin ray, and retrorse spines on the anterior margin of the first branched anal-fin ray only in mature males of auchenipterid *Tatia* (Ferraris, 1988: #A11; Soares-Porto, 1998: #37, #39; Royero, 1999: #134, #135, #137; Akama, 2004: #155, #156). This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

295. Posteriorly directed hook on last unbranched anal-fin ray in mature males: 0- absent; 1- present (CI and RI inapplicable).

In mature males of the auchenipterid *Auchenipterus*, there is a posteriorly directed hook on the last unbranched anal-fin ray (Akama, 2004: #158). This feature is absent in mature males of all other examined species. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

296. Spines on lateral face of anal-fin rays: 0- absent; 1- present (CI and RI inapplicable).

Among examined species, the lateral face of the anal-fin rays bears spines only in the doradid *Agamyxis*, similarly to the conditions of the pelvic and caudal-fin rays.

297. Shape of first unbranched anal-fin ray: 0- rod-like; 1- plate-like (CI and RI inapplicable).

The first unbranched anal-fin ray is modified into an ossified plate only in the doradid *Agamyxis*. All other examined species have the first unbranched anal-fin ray rod-like.

298. First unbranched anal-fin ray in mature males: 0- segmented; 1- not segmented (CI and RI inapplicable).

In the auchenipterid *Tatia* (except *T. brunnea*), the first unbranched anal-fin ray is not segmented (Soares-Porto, 1998: #33; Sarmiento-Soares & Martins-Pinheiro, 2008: 498). Even though this feature might be present in other auchenipterids, such as for example *Centromochlus meridionalis* (Sarmiento-Soares et al., 2013: fig. 5), it is absent in mature males of all other examined species.

299. Size of anterior anal-fin rays in mature males: 0- small; 1- enlarged (CI 1.0, RI 1.0).

In mature males of the auchenipterids *Ageneiosus*, *Auchenipterichthys*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, and *Trachycorystes* (Akama, 2004: #148; Royero, 1999: #131), the anterior anal-fin rays are enlarged. This feature is absent in mature males of all other examined species. This character was coded as missing data for the auchenipterids *Pseudotatia* and *Spinipterus*.

Caudal fin

300. Shape of caudal fin (unordered): 0- bifurcated; 1- truncated; 2- rounded (CI 0.286, RI 0.444).

The caudal fin is usually bifurcated in catfishes (Figs. 3b-d, 4, 38). However, in the Malapteruridae and doradid *Acanthodoras*, the caudal fin is rounded (Fig. 3a; Higuchi, 1992: #76; Sousa, 2010: #82). The caudal fin is truncate in the auchenipterids *Ageneiosus inermis*, *A. polystictus*, *Auchenipterichthys*, *Spinipterus*, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus* (Ferraris, 1988: #C1; Walsh, 1990: #26; Royero, 1999: #142; Akama, 2004: #135), and doradids *Amblyodoras*, *Astroodoras*, *Hypodoras*, and *Physopyxis* (Higuchi, 1992: #74, #75; Sousa, 2010: #82).

301. Shape of caudal-fin procurrent rays: 0- rod-like; 1- plate-like (CI 0.25, RI 0.667).

As described by Eigenmann (1925: 293, as “fulcra”), the doradids *Agamyxis*, *Franciscodoras*, *Platyodoras*, *Orinocodoras*, *Rhinodoras*, and *Rhynchodoras* have the caudal-fin procurrent rays modified into plates that frame the caudal peduncle dorsally and ventrally (Fig. 65a; Higuchi, 1992: #79; Birindelli *et al.*, 2007; Sousa, 2010: #83). As discussed by Birindelli *et al.* (2007), the first caudal-fin procurrent rays are slightly modified into plates, dorsally, and ventrally, in doradids *Anadoras*, *Astroodoras*, *Hypodoras*, *Ossancora fimbriata*, and some specimens of *Ossancora eigenmanni*. The caudal peduncle is covered by plates in *Lithodoras*; however, those are not homologous with modified procurrent rays. In all other examined species, the caudal-fin procurrent rays are rod-like (Figs. 65b-c, 66).

302. Spines on lateral face of caudal-fin rays: 0- absent; 1- present (CI 1.0, RI 1.0).

Among examined species, the lateral faces of the caudal-fin rays bear small spines only in the doradids *Acanthodoras* and *Agamyxis* (Sousa, 2010: #85).

303. Type of hypurapophysis (unordered): 0- Type A of Lundberg & Baskin (1969: fig. 3A); 1- Type B of Lundberg & Baskin (1969: fig. 3B); 2- Type C of Lundberg & Baskin (1969: fig. 3C) (CI 0.667, RI 0.667).

According to Lundberg & Baskin (1969), the primitive condition for the hypurapophysis in catfishes is Type A, which is present in the Diplomystidae, Ictaluridae, Schilbeidae, Pangasiidae, and some Bagridae. The Type B hypurapophysis is present only in the Aspredinidae, Cetopsidae, Claroteidae, and Cranoglanidae. All other taxa have hypurapophysis Type C. The present observations corroborate Walsh (1990: 129), by considering the hypurapophysis of *Ageneiosus* as Type C, contradicting some authors (Lundberg & Baskin, 1969; Ferraris, 1988: C7; Akama, 2004: #141), who considered it to be of Type B. This character was coded as inapplicable for the Nematogenyidae and Siluridae, which have other types of hypurapophysis (see Lundberg & Baskin, 1969); and as missing data for the auchenipterid *Spinipterus*.

304. Ventral process of hypurapophysis: 0- absent; 1- present (CI 1.0, RI 1.0).

Among examined species, there is a conspicuous ventral process on the hypurapophysis only in the examined species of auchenipterids *Auchenipterus*, *Centromochlus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* (Fig. 66a;

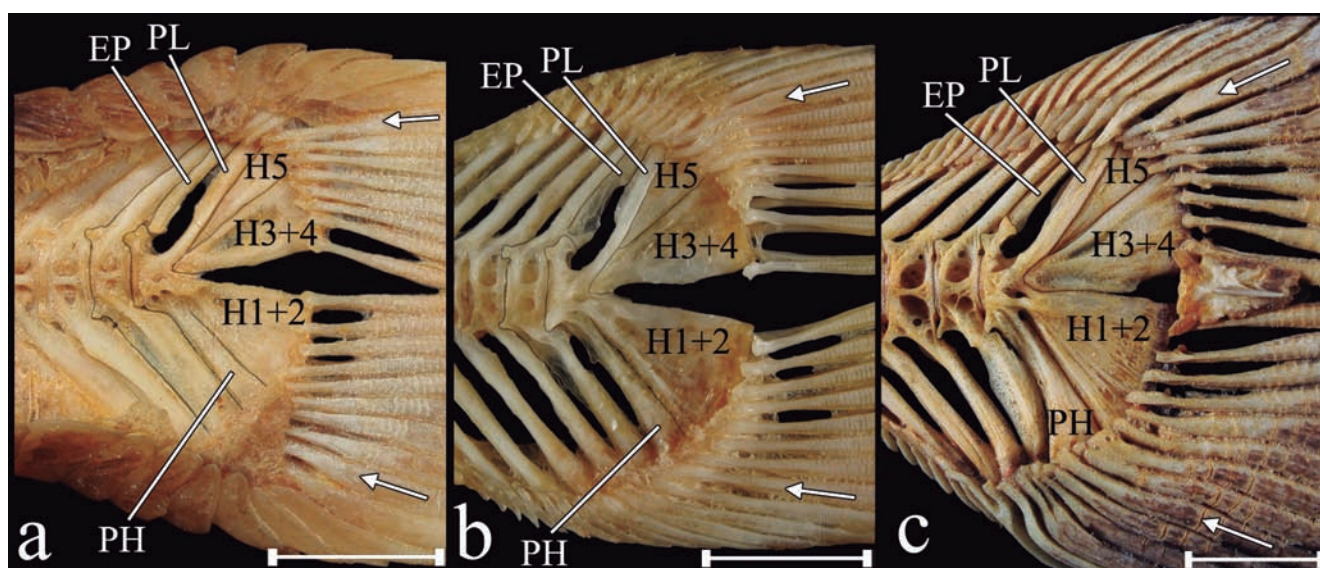


Fig. 65. Caudal fin in lateral view of (a) *Orinocodoras eigenmanni*, FMNH 105276, 193 mm SL; (b) *Wertheimeria maculata*, MZUSP 93659, 217 mm SL; (c) *Oxydoras niger*, MZUSP 91658, 113 mm SL. H1-5 hypurals 1-5, EP epural, PH parhypural, PL pleurostyle. White arrows indicate dorsal and ventralmost principal unbranched caudal-fin rays. Scale bars equal 10 mm.

Ferraris, 1988: #C5; Akama, 2004: #139). This process is extremely elongate in *Entomocorus*. This character was coded as missing data for the auchenipterid *Spinipterus*.

305. Number of branched rays in dorsal lobe of caudal fin (ordered): 0- eight; 1- seven; 2- six; 3- five (CI 0.273, RI 0.2).

Most catfishes have seven branched caudal-fin rays in the dorsal lobe (Figs. 65, 66). Exceptions include the Amphiliidae with five, ariid *Genidens*, Malapteruridae, and Pseudopimelodidae with six, Diplomystidae with eight (Lundberg & Baskin, 1969: 11, table 2; Arratia, 1992: #38; de Pinna, 1993: #237; Britto, 2002: #293). Other exceptions include the mochokids *Chiloglanis polypogon*, *Microsynodontis*, *Mochokiella*, and *Mochokus brevis* with six, *M. niloticus* and *Synodontis contracta* with five (Vigliotta, 2008: #74), and doradid *Agamyxis* with six branched caudal-fin rays in the dorsal lobe (Sousa, 2010: #86).

306. Number of branched rays in ventral lobe of caudal fin (ordered): 0- six or seven; 1- eight; 2- nine to 12 (CI 0.182, RI 0.5).

Most catfishes have eight branched caudal-fin rays in the ventral lobe (Figs. 65a,c, 66a,b). Exceptions include the Amphiliidae, Aspredinidae, Malapteruridae, Nematogenyidae, ariid *Galeichthys*, and mochokids *Mochokiella* and *Mochokus* with six or seven branched rays in ventral caudal-fin lobe (Vigliotta, 2008: #74); doradids *Acanthodoras*, *Agamyxis*, *Anadoras*, *Astrodoras*, *Franciscodoras*, *Kalyptodoras*, *Scorpiodoras*, and *Wertheimeria* with seven branched rays (Fig. 65b; Sousa, 2010: #87), and auchenipterids *Spinipterus*, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterus* and some specimens of *Trachelyopterichthys* with nine to 12 rays (Fig. 66c; Ferraris, : #C2; Walsh, 1990: #25; Akama, 2004: #136). There is intra-specific variation in some cases, such as in the auchenipterids *Trachelyopterus galeatus* (with nine or ten

and *T. coriaceus* (with ten to 12). This character was coded as polymorphic (1,2) for *Trachelyopterichthys*.

307. Articulation site of last unbranched caudal-fin ray in ventral lobe: 0- parhypural; 1- hemal spine (CI 0.333, RI 0.6).

In most catfishes, the last unbranched ray in the ventral lobe of the caudal fin is articulated with the parhypural. However, the last unbranched caudal-fin ray in the ventral lobe is articulated with the second to fifth last hemal spine in the auchenipterids *Auchenipterichthys*, *Tetranematichthys*, *Trachelyichthys*, *Trachelyopterichthys*, and *Trachelyopterus* (Figs. 66c; Ferraris, 1988: #C3; Akama, 2004: #137). This character was coded as missing data for the auchenipterid *Spinipterus*.

308. Second ural centrum: 0- reduced (Type 1 of de Pinna & Ng, 2004: 4); 1- well developed (Type 3 of de Pinna & Ng, 2004: 4) (CI 0.167, RI 0.0).

The second ural centrum is well developed (type 3 of de Pinna & Ng, 2004: 4) in the auchenipterids *Asterophysus* (de Pinna & Ng, 2004: 11) and *Entomocorus* (Ferraris, 1988: #C4; Akama, 2004: #138). The same condition is also present in the Amphiliidae, Aspredinidae, Erethistidae, Mochokidae (*Chiloglanis polypogon*), Pseudopimelodidae (*Pseudopimelodus raninus*) and Sisoridae (except *Bagarius*) (Lundberg & Baskin, 1969; Britto, 2002: #291; de Pinna & Ng, 2004). In all other examined species, the second ural centrum is reduced (Type 1 of de Pinna & Ng, 2004: 4). This character was coded as missing data for the auchenipterid *Spinipterus*.

309. Dorsal elements of caudal skeleton (ordered): 0- separated; 1- hypurals 3 and 4 fused, 5 distinct; 2- hypurals 3, 4 and 5 fused (CI 0.333, RI 0.692).

In many catfishes, hypurals 3, 4, and 5 are separate elements (Lundberg & Baskin, 1969). However, in the

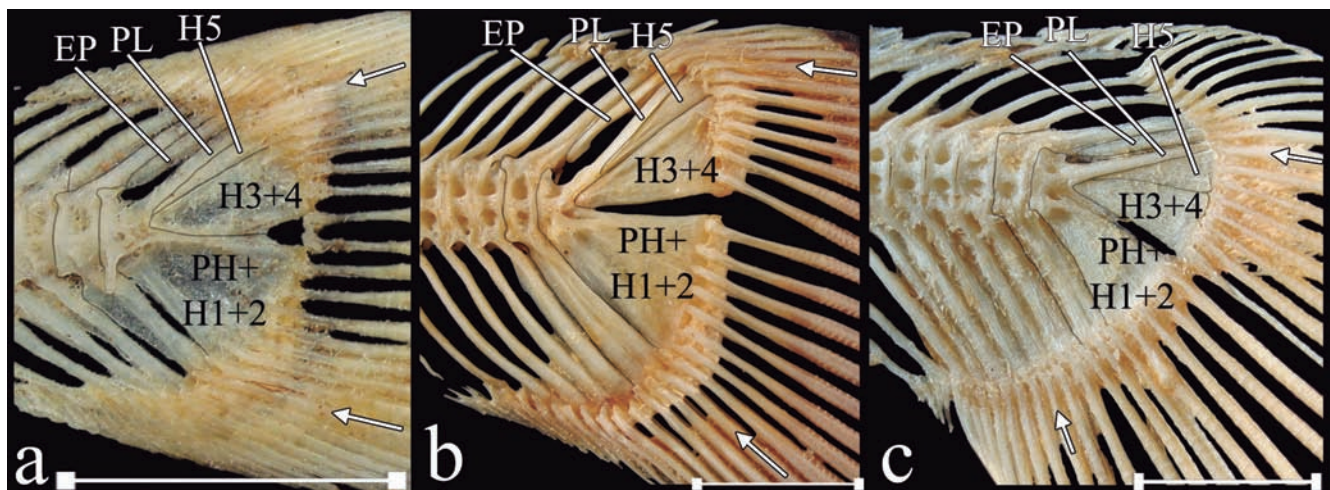


Fig. 66. Caudal fin in lateral view of (a) *Centromochlus heckelii*, MZUSP 101767, 86.8 mm SL; (b) *Trachycorystes trachycorystes*, MZUSP 91659, 200 mm SL; (c) *Trachelyopterus galeatus*, MZUSP 52088, 165 mm SL. H1-5 hypurals 1-5, EP epural, PH parhypural, PL pleurostyle. White arrows indicate dorsal and ventralmost principal unbranched caudal-fin rays, black arrow indicates ventral process of hypurapophysis. Scale bars equal 10 mm.

Amphiliidae, Ariidae, Auchenipteridae, Doradidae (except *Acanthodoras*), Heptapteridae, Malapteruridae, and Pseudopimelodidae, hypurals 3 and 4 are fused (hypural 5 is distinct) (Figs. 65, 66). In the Aspredinidae, Claroteidae, Erethistidae, Sisoridae, doradids *Acanthodoras* and most mochokids (except *Atopochilus* and *Euchilichthys*; Vigliotta, 2008: #72; Sousa, 2010: #88), hypurals 3, 4 and 5 are fused together. In some cases, as in the doradid *Franciscodoras marmoratus* (MZUSP 97145, 29.4 mm SL, MZUSP 9380, 180 mm SL), all elements are [or may be] distinct in small juveniles (*i.e.*, PH, 1, 2, 3, 4, 5) but several of them fuse together in larger specimens (PH, 1+2, 3+4, 5). This character was coded as missing data for the auchenipterid *Spinipterus*.

310. Ventral elements of caudal skeleton (ordered): 0-separated; 1-hypurals 1 and 2 fused, parhypural distinct; 2-parhypural and hypurals 1 and 2 all fused (CI 0.4, RI 0.93).

In several catfishes, the parhypural and hypurals 1 and 2 are distinct elements (Lundberg & Baskin, 1969). However, the hypurals 1 and 2 are fused (parhypural distinct) in the Ariidae, Claroteidae, Heptapteridae, Malapteruridae, Pimelodidae, and most species of Doradidae (except Astrodoradinae, *Acanthodoras*, *Agamyxis*, and *Rhinodoras thomersoni*) (Fig. 64) and the parhypural and hypurals 1 and 2 are fused together in the Amphiliidae, Aspredinidae, Auchenipteridae, Erethistidae, Mochokidae (Vigliotta, 2008: #71), Pseudopimelodidae, Sisoridae, and doradids Astrodoradinae, *Acanthodoras*, *Agamyxis*, and *Rhinodoras thomersoni* (Fig. 65; Sousa, 2010: #89). This character was coded as missing data for the doradids *Centrochir* and *Megalodoras*, and auchenipterid *Spinipterus*.

Phylogenetic Analysis

The parsimony analysis of phylogenetic relationships among species of Doradoidea, based on 311 morphological characters and 100 taxa (being 23 taxa of the Auchenipteridae, 57 taxa of the Doradidae, and 20 outgroups), resulted in six equally most parsimonious cladograms of 1079 steps, CI of 0.358 and RI of 0.820. From the six fundamental trees found, a strict consensus tree was obtained (Figs. 67-70). All character state changes (*i.e.*, synapomorphies, homoplasies and autapomorphies), resulted from ACCTRAN optimization, were listed in the Appendix.

Systematic Account. All suprageneric taxa obtained in the present study are diagnosed and discussed below. In addition, the new genus *Tenellus* is described and diagnosed.

Doradoidea Bleeker, 1858

Included taxa. Auchenipteridae and Doradidae.

Diagnosis. The Doradoidea is diagnosed by the following characters: bony suture between exoccipital and neural arch of complex vertebra (#82: 0>1, exclusive), dorsal surface of

epiotic participating in cephalic shield (#83: 0>1, exclusive), infraorbital 1 strongly connected by lateral ethmoid (#95: 0>1, exclusive), hyomandibular crest for *levator arcus palatini* muscle weakly or well developed (#154: 0>1, reversed in most doradids, and present also in some non-Doradoidea catfishes), subpreopercle present (#168: 0>1, also present in some non-Doradoidea catfishes), seven to nine branchiostegal rays (#177: 0>1, also present in some non-Doradoidea catfishes), transformator process of *tripus* straight (#203: 0>1, exclusive), *os suspensorium* reduced in size (#204: 0>1, exclusive), Müllerian ramus modified with short thin base and distal flexible disc, latter connected to dorsal face of gas bladder (#205: 2>3, exclusive), posterior ramus of parapophysis of fourth vertebra absent (#210: 0>1, exclusive), parapophysis of fifth vertebra reduced in size or eventually absent (#211: 1>0, reversed in the doradid *Leptodoras juruensis* and in the auchenipterid *Gelanoglanis*), anterior ribs articulated to the dorsal face of the parapophysis (#219: 0>1, exclusive), proximal end of ribs twisted (#220: 0>1, present also the Amphiliidae, Aspredinidae, and Sisoroidea), anterior face of dorsal-fin spine with serrations (#242: 0>1, reversed in several auchenipterids, in the doradid *Anadoras*, and present also in some non-Doradoidea catfishes), mesocoracoid absent (#250: 0>1, also present in some non-Doradoidea catfishes), hypurals 3 and 4 fused, 5 distinct (#309: 2>1, also present in some other non-Doradoidea catfishes).

Auchenipteridae Bleeker, 1862

Included taxa. Auchenipterinae and Centromochlinae.

Diagnosis. The Auchenipteridae is diagnosed by the following characters: adipose fin short, thin and teardrop-shaped (#5: 0>2, also present in some non-Auchenipteridae catfishes), maxillary barbel moving vertically (#13: 0>1, exclusive), suborbital groove present (#14: 0>1, exclusive), reproduction by insemination (#43: 0>1, exclusive), posterior testicular lobes modified into hypertrophied storage bags (#44: 0>1, reversed in *Asterophysus*, *Centromochlus*, *Glanidium*, *Tatia*, and modified in *Ageneiosus* and *Auchenipterus*), urogenital opening at base of first anal-fin rays in males (#46: 0>1, exclusive), urogenital opening wide in females (#50: 0>1, exclusive), posterolateral margin of epiotic participating in the border of cephalic shield (#84: 0>1, reversed in *Asterophysus* and *Liosomadoras*, present also in some doradids), infraorbital 1 participating in orbital margin (#97: 0>1, present also in Astrodoradinae, and in the doradids *Acanthodoras*, *Agamyxis*, *Lithodoras*, and *Pterodoras*), vertical rows of neuromasts dorsal to lateral line present (#117: 0>1, reversed in *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, *Pseudepapterus*, *Spinipterus*, and *Tetranematchthys*), posterodorsal process of hyomandibula present (#159: 0>1, reversed in *Asterophysus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Gelanoglanis*, and *Pseudepapterus*), suprapreopercle present (#167: 0>1, reversed in *Liosomadoras*, present also in some non-

Auchenipteridae catfishes), first hypobranchial cylindrical (#191: 0>1, reversed in *Auchenipterus*, *Entomocorus*, *Epapterus*, *Glanidium*, *Pseudepapterus*, present also in some doradids), first free vertebra eighth (#217: 1>3, reversed in *Gelanoglanis*, *Pseudepapterus*, modified in *Auchenipterichthys*, *Centromochlus*, *Tocantinsia*, *Trachelyopterichthys*, *Trachelyopterus*, and *Trachycorystes*, present also in some non-Auchenipteridae catfishes), lateral process of basipterygium with well-developed cartilaginous extension (#285: 0>1, reversed in *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*, present also in some non-Auchenipteridae catfishes), five to eight branched anal-fin rays (#287: 1>0, modified in most auchenipterids, present also

in some non-Auchenipteridae catfishes).

Auchenipterinae Bleeker, 1862

- Euanemini Bleeker, 1858: 39 (see also Bleeker, 1858: 49, 189) [type genus: *Euanemus* (=Auchenipterus)].
- Trachelyopterini Bleeker, 1858: 39 (see also Bleeker, 1858: 49, 250, 257) [type genus: *Trachelyopterus*].
- Pseudoauchenipterini Bleeker, 1862 (in Bleeker, 1862-1863): 6 [type genus: *Pseudoauchenipterus*].
- Astrophysi (=Asterophysis) Bleeker, 1862 (in Bleeker, 1862-1863): 7 [type genus: *Asterophysus*].
- Auchenipterini Bleeker, 1862 (in Bleeker, 1862-1863): 14 [type genus: *Auchenipterus*].

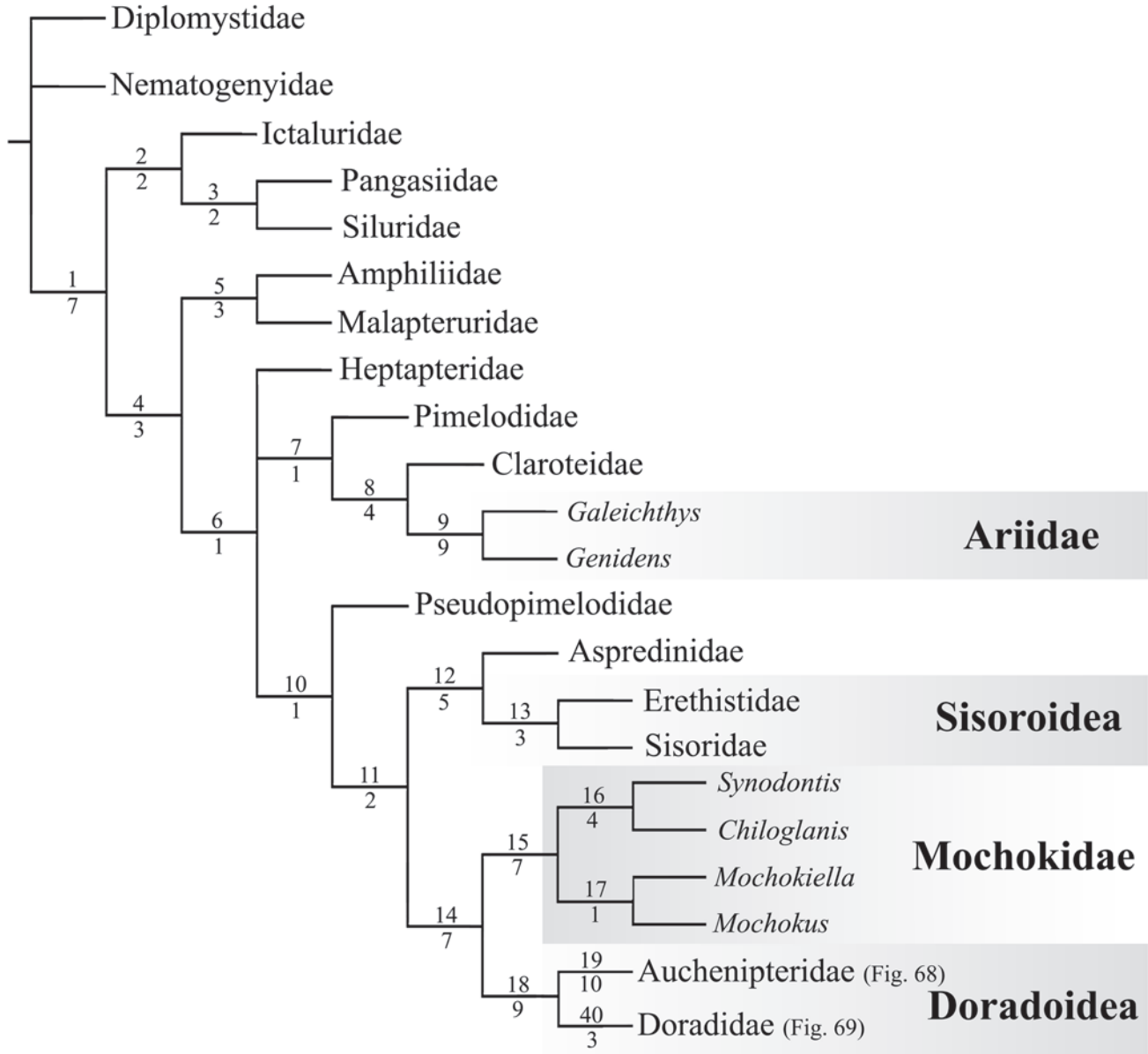


Fig. 67. Part 1: Consensus tree of phylogenetic relationships among higher-level taxa. Numbers of nodes indicated above branches and values for Bremer support indicated below branches. Character state changes (*i.e.*, synapomorphies, autapomorphies, and homoplasis) supporting for each branch listed in Appendix.

Ageneiosi Bleeker, 1862 (in Bleeker, 1862-1863): 14 [type genus: *Ageneiosus*].

Trachycorystidae Miranda Ribeiro, 1911: 352 [type genus: *Trachycorystes*].

Included taxa. *Ageneiosus*, *Asterophysus*, *Auchenipterichthys*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Liosomadoras*, *Pseudauchenipterus*, *Pseudepapterus*, *Pseudotatia*, *Spinipterus*, *Tetranematchthys*, *Tocantinsia*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus* and *Trachycorystes*.

Diagnosis. The subfamily Auchenipterinae is diagnosed by the following characters: urogenital opening at the tip of anterior anal-fin rays in males (#46: 1>2, exclusive), lateral line sinusoidal (#115: 0>1, reversed in *Spinipterus*, present also in *Centromochlus*), accessory cartilage present between third and fourth basibranchials (#190: 0>1, reversed in *Asterophysus*, present also in some non-Auchenipteridae catfishes), six branched pelvic-fin rays (#276: 0>1, reversed in *Entomocorus*, and modified in *Asterophysus*, *Auchenipterichthys*, *Auchenipterus*, *Epapterus*, *Pseudauchenipterus*, *Pseudepapterus*, *Trachelyichthys*,

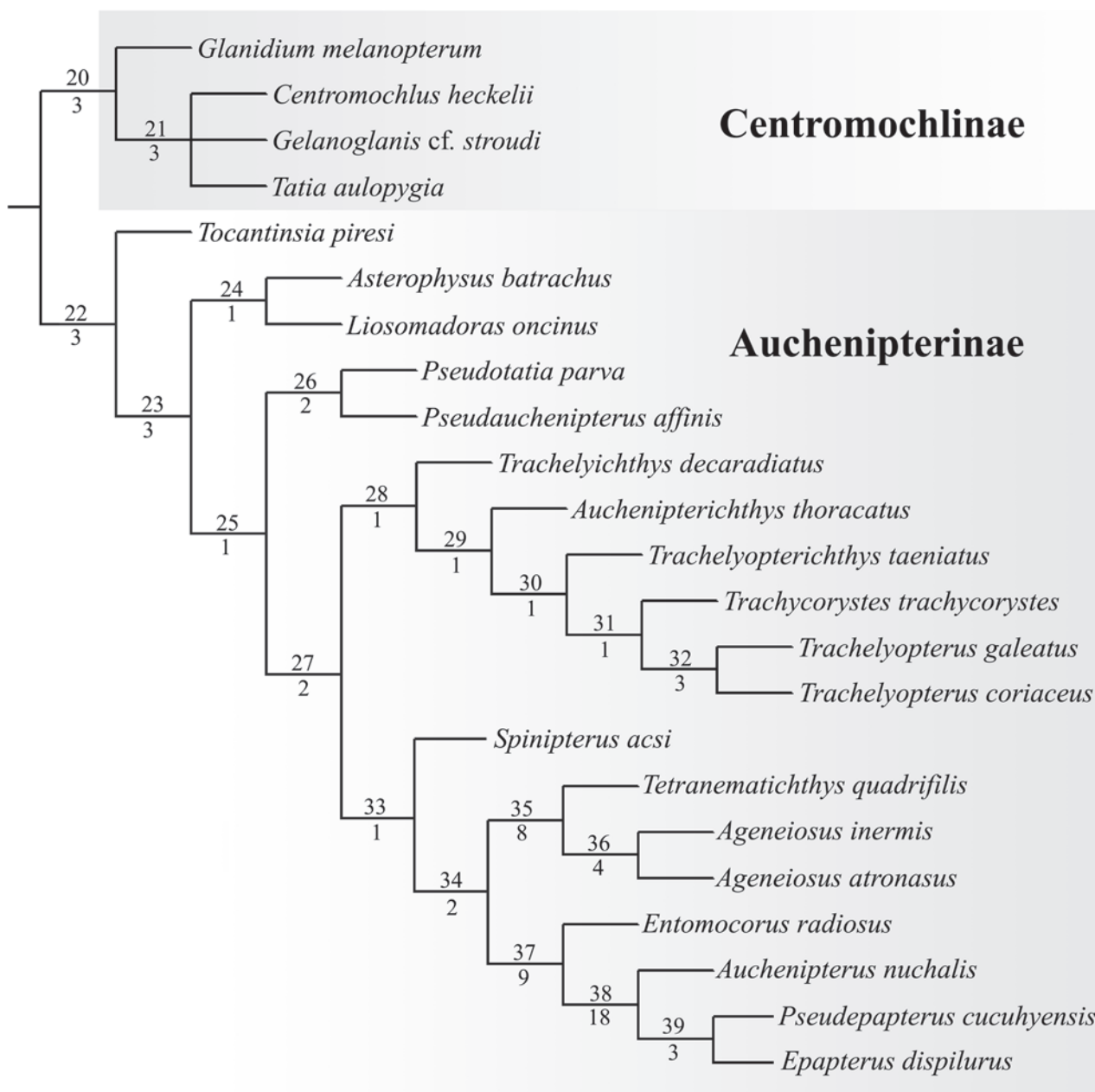


Fig. 68. Part 2: Consensus tree of phylogenetic relationships in Auchenipteridae. Numbers of nodes indicated above branches and values for Bremer support indicated below branches. Character state changes (*i.e.*, synapomorphies, autapomorphies, and homoplasy) for each branch listed in Appendix.

Trachelyopterichthys, *Trachelyopterus*, *Trachycorystes*, present also in some non-Auchenipteridae catfishes).

Remarks. The subfamily Auchenipterinae is considered to be composed of *Tocantinsia* plus four monophyletic clades (Fig. 68). Clade 1: the *Asterophysus/Liosomadoras* is supported by three characters, including the frontals not participating in the orbital margin (#64: 0>1, also present in *Auchenipterichthys*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, *Trachelyopterichthys*, *Trachelyopterus* and *Trachycorystes*), epiotic not participating in the border of the cephalic shield (#84: 1>0, present also in some specimens of *Trachycorystes*) and spines widespread on the posterior cleithral process (#268: 1>0, also present in *Trachelyopterus porosus*, coded as inapplicable for *Asterophysus*, which lack spines on the posterior cleithral process). Clade 2: the

Pseudachenipterus/Pseudotatia clade is supported by five characters, including a distal vesicle on the distal portion of the anterior anal-fin rays in mature males (#48: 0>1, exclusive, coded as missing data for *Pseudotatia*), dorsal face of the lateral ethmoid not participating in the cephalic shield (#59: 1>0, also present in *Centromochlus heckelii*), fenestra between the lateral ethmoid and frontal present (#60: 0>1, coded as missing data for *Pseudotatia*), fenestra between frontal and orbitosphenoid present (#77: 0>1, also present in Centromochlinae), and anterior margin of the pectoral girdle elongate with acute tip (#249: 0>2, also present in *Asterophysus*, *Centromochlus*, *Entomocorus*, *Gelanoglanis*, and *Tatia*). Clade 3: the *Trachelyopterus* clade, also including *Auchenipterichthys*, *Trachelyichthys*, *Trachelyopterichthys*, and *Trachycorystes*, is supported by two characters, including eight or more branched rays in the pelvic fin (#276: 1>3, also

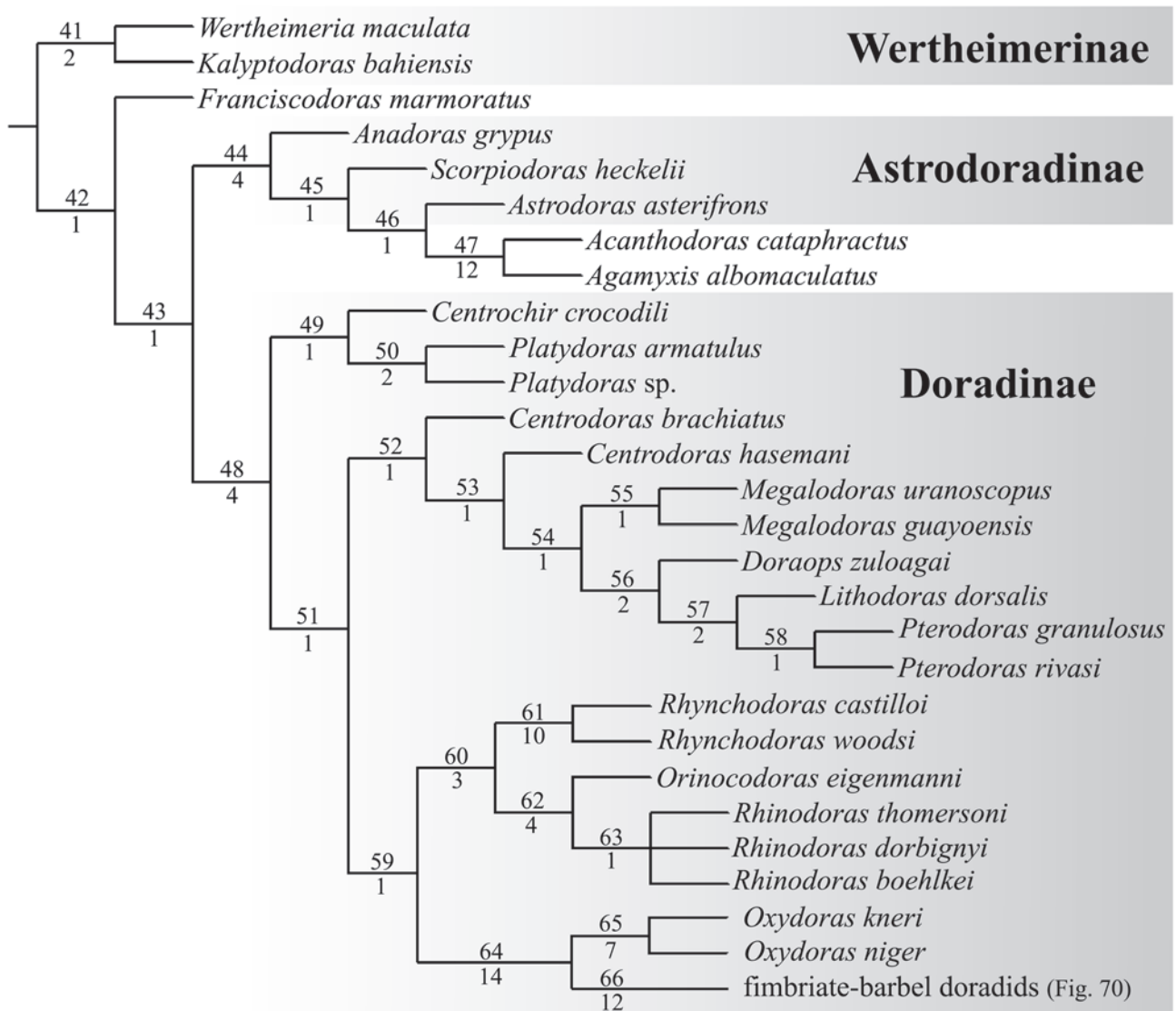


Fig. 69. Part 3: Consensus tree of phylogenetic relationships in Doradidae. Numbers of nodes indicated above branches and values for Bremer support indicated below branches. Character state changes (*i.e.*, synapomorphies, autapomorphies, and homoplasy) for each branch listed in Appendix.

present in *Asterophysus*, *Auchenipterus*, *Epapterus*, *Pseudepapterus*, and reversed [*i.e.*, rays equal to seven] in *Trachelyopterus*), and last unbranched caudal-fin ray in the ventral lobe articulated with hemal spine (#307: 0>1, also present in *Tetranematichthys*, reversed in *Trachycorystes*). Clade 4: the *Auchenipterus* clade, also including *Ageneiosus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Spinipterus*, and *Tetranematichthys*, is supported by nine characters, including the breeding tubercles on the maxillary barbels (#25: 0>1, reversed in *Ageneiosus*, character coded as missing data for *Spinipterus*), transcapular process at an angle of approximately 45° relative to body axis (#92: 0>1, reversed in *Entomocorus*, character coded as missing data for *Spinipterus*), ventral process of infraorbital 1 present (#98: 0>1, also present in *Centromochlus*, character coded as missing data for *Spinipterus*), ventral rows of neuromasts dorsal to lateral line absent (#117: 1>0, condition also present in *Gelanoglanis*), maxilla of mature males elongate (#134: 0>1, also present in some species of *Trachelyopterus*, character coded as missing data for *Spinipterus*), gill-rakers moderate in size (#183: 0>1, also present in *Glanidium*, *Centromochlus*, *Tatia*, *Tocantinsia*, reversed in *Auchenipterus*, *Epapterus*, *Pseudepapterus*, character coded as missing data for *Spinipterus*), dorsal-fin spine capable of rotating anteriorly (#241: 0>1, also present in *Liosomadoras*, and in some species of *Trachelyopterus*, character coded as missing data for *Spinipterus*), anteromedial process of basipterygium partially or completely united to basipterygium (#283: 0>1, also present *Gelanoglanis*, reversed in *Entomocorus*, character coded as missing data for *Spinipterus*), lateral process of basipterygium short (#285: 1>0, also present in *Auchenipterichthys*, *Gelanoglanis*, *Tatia*, character coded as missing data for *Spinipterus*).

Centromochlinae Bleeker, 1862

Centromochli Bleeker, 1862 (in Bleeker, 1862-1863): 7 [type genus: *Centromochlus*].

Included taxa. *Centromochlus*, *Gelanoglanis*, *Glanidium*, and *Tatia*.

Diagnosis. The Centromochlinae is diagnosed by the following characters: fenestra present between frontal and orbitosphenoid (#77: 0>1, also present in *Pseudauchenipterus* and *Pseudotatia*), four to six branchiostegal rays (#177: 1>0, present also in some non-Auchenipteridae catfishes), five branched dorsal-fin rays (#237: 0>1, also present in *Entomocorus*, *Pseudepapterus*, *Spinipterus*, *Trachelyopterus*, *Trachycorystes*, and some non-Auchenipteridae catfishes), posterior cleithral process small (#265: 2>1, also present in *Tetranematichthys*, *Trachelyopterus galeatus*, and *T. insignis*, and some non-Auchenipteridae catfishes), anal fin oblique relative to the body axis in mature males (#288: 0>1, exclusive), anal-fin proximal radials oblique relative to the body axis in mature

males and not interdigitated with hemal spines (#289: 0>1, exclusive), anal-fin proximal radials partially or completely fused together forming a single ossification in mature males (#291: 0>1, exclusive).

Doradidae Bleeker, 1858

Included taxa. *Franciscodoras*, *Acanthodoras*, *Agamyxis*, *Astrodoradinae*, *Doradinae*, and *Wertheimerinae*.

Diagnosis. The Doradidae is diagnosed by the following characters: midlateral scutes present (#118: 0>1, exclusive), coronomeckelian bone connected to dentary (#137: 0>1, reversed in *Astrodoradinae*, *Acanthodoras*, *Agamyxis*, *Centrochir*, *Centrodoras*, *Doraops*, *Lithodoras*, *Megalodoras*, *Platydoras* [except *Platydoras* sp.], and *Pterodoras*), ligament present between Müllerian ramus and lateral line (212: 0>1, exclusive), infranuchal ligament between posterior nuchal plate and the first rib ossified (#213: 1>2, exclusive), first free vertebra sixth (#217: 2>1, present also in other non-Doradidae catfishes), pectoral-fin spine locking foramen absent (#253: 0>1, foramen absent also in some non-Doradidae catfishes), six or seven branched rays in the ventral lobe of the caudal fin (#306: 1>0, reversed back to state 1 in *Doradinae*).

Wertheimerinae, new subfamily

Included taxa. *Kalyptodoras* and *Wertheimeria* [type genus].

Diagnosis. The subfamily Wertheimerinae is diagnosed by the following characters: well-developed hyomandibular crest for *levator arcus palatini* muscle (#154: 1>2, exclusive), hyomandibula articulated with cranium only via sphenotic (#162: 1>2, also present in *Acanthodoras* and *Agamyxis*), 12 or more ribs (#221: 1>2, also present in *Centrodoras*, *Doraops*, *Lithodoras*, *Megalodoras*, *Oxydoras*, and *Pterodoras*).

Remarks. According to molecular data published by Arce *et al.* (2013), *Franciscodoras* should also be included in this subfamily as sister to *Kalyptodoras*. However, the present analysis recovered *Franciscodoras* as sister to all doradids, except *Wertheimeria* and *Kalyptodoras*. Due to the existing conflict of hypotheses regarding the phylogenetic position of *Franciscodoras*, the latter is herein considered as *incertae sedis* in Doradidae.

Astrodoradinae Higuchi, Birindelli, Sousa & Britski, 2007

Astrodoradinae Higuchi, Birindelli, Sousa & Britski, 2007: 33 [type genus: *Astrodoras*].

Included taxa. *Amblydoras*, *Anadoras*, *Astrodoras*, *Hypodoras*, *Physopyxis*, and *Scorpiodoras*.

Diagnosis. The subfamily Astrodoradinae is diagnosed by the following characters: adipose fin short, thin and teardrop-shaped (#5: 1>2, also present in *Acanthodoras*, *Agamyxis*, *Anduzedoras*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras*, and in some non-Doradidae catfishes), posterior process of epiotic mainly ossified (#85: 1>2, also present in *Pterodoras*, *Rhynchodoras* and fimbriate-barbel doradids, and in some non-Doradidae catfishes), infraorbital 1 participating in orbital margin (#97: 0>1, present also in *Acanthodoras*, *Agamyxis*, *Lithodoras*, and *Pterodoras*, and in some non-Doradidae

catfishes), posterior cleithral process with spines arranged in one main row accompanied by secondary rows (#268: 1>2, also present in *Acanthodoras*), ventroposterior margin of coracoid thick, visually exposed (#272: 0>1, also present in *Acanthodoras*, *Agamyxis*, *Hemidoras*, *Megalodoras*, *Ossancora*, and *Trachydoras paraguayensis* and *T. steindachneri*, and in some non-Doradidae catfishes).

Remarks. The results of the present analysis indicate the inclusion of *Acanthodoras* and *Agamyxis* in the Astrodoradinae. However, since these findings contradicts

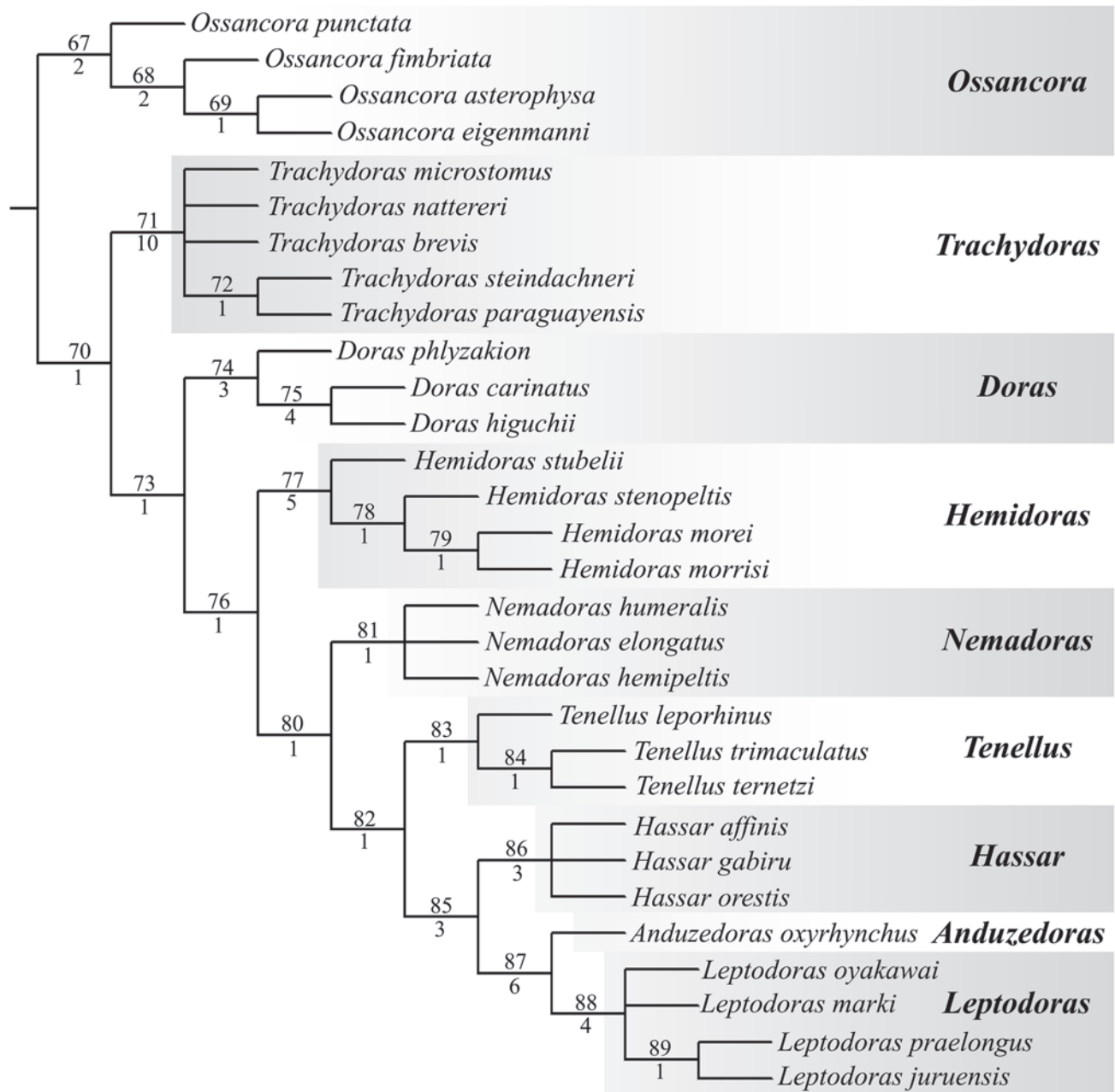


Fig. 70. Part 4: Consensus tree of phylogenetic relationships in the clade that includes the fimbriate-barbel doradids. Numbers of nodes indicated above branches and values for Bremer support indicated below branches. Character state changes (*i.e.*, synapomorphies, autapomorphies, and homoplasy) for each branch listed in Appendix.

the results obtained by Higuchi (1992), Higuchi *et al.* (2007), Moyer *et al.* (2004) and Arce *et al.*, (2013), it is yet premature to transfer these two taxa into Astrodoradinae. These two genera are herein considered as *incertae sedis* in Doradidae, until more data are available to determine their phylogenetic position. The Diagnosis presented herein for Astrodoradinae includes all characters supporting the clade that comprises all examined species of Astrodoradinae plus *Acanthodoras* and *Agamyxis*.

Doradinae Bleeker, 1858

Doradini Bleeker, 1858: 39 (see also Bleeker, 1858: 48-52) [type genus *Doras*].

Included taxa. *Anduzedoras*, *Centrochir*, *Centroadoras*, *Doraops*, *Doras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Lithodoras*, *Megalodoras*, *Nemadoras*, *Orinocodoras*, *Ossancora*, *Oxyadoras*, *Platyadoras*, *Pterodoras*, *Rhinodoras*, *Rhynchodoras*, *Tenellus*, and *Trachydoras*.

Diagnosis. The subfamily Doradinae is diagnosed by the following characters: tips of terminal diverticula of the gas bladder distally divergent (#36: 0>1, present only in *Doras zuanoni*, *Ossancora punctata*, and *Trachydoras*, coded as missing data for the remaining species of Doradinae, which lack terminal diverticula), first free vertebrae eighth or ninth (#217: 1>3, modified in *Doraops*, *Lithodoras*, *Megalodoras*, *Pterodoras*, and also present in some non-Doradidae catfishes), serrations present on the posterior face of the dorsal-fin spine (#245: 0>1, reserved in some species of *Leptodoras*, present also in some non-Doradidae catfishes), transverse coracoid crest between *adductor superficialis* and *arrector ventralis* muscles (#274: 0>1, reserved in *Doraops*, *Lithodoras*, *Oxyadoras*, *Pterodoras*, and fimbriate-barbel doradids [except *Hemidoras morrissi*, and *Ossancora fimbriata*], also present in *Acanthodoras*), eight branched rays in the ventral lobe of the caudal fin (#306: 0>1, also present in some non-Doradidae catfishes), hypurals 1 and 2 fused, parahypural distinct (#310: 2>1, reversed in *Rhinodoras thomersoni*, present also in *Franciscodoras*, *Kalyptodoras*, and *Wertheimeria*).

Remarks. The present analysis did not recover *Centroadoras* as monophyletic, however, additional study including yet undescribed species of *Centroadoras* (Sabaj Pérez, pers. comm.) is necessary to establish the status of the genus.

Two major changes in the classification of Doradidae were made based on the present hypothesis of relationships among species of Doradinae: description of *Tenellus* as a new genus, and inclusion of the species previously placed in *Opsodoras* Eigenmann, 1925 within an expanded *Hemidoras* Bleeker, 1858. *Hemidoras* was defined by Eigenmann (1925), and subsequently followed by other authors, as comprising two species, *H. stenopeltis* and *H. morrissi*, both sharing dermal scutes between dorsal and adipose fins (#34). However, other

characters analyzed herein indicate that *Hemidoras morrissi* is closely related to *Opsodoras morei* (now *Hemidoras morei*), a hypothesis corroborated by the similarity in the overall morphology of both species. Noteworthy to say, some specimens of *Hemidoras morei* (including the holotype, NMW 45433) have a single dermal plate between dorsal and adipose fins, a partial representation of the feature formerly used to distinguish *Hemidoras* from *Opsodoras*.

As discussed by Ferraris (2007: 164), the suprageneric names Centrochirinae, Hemidoradinae, and Lithodoradinae were proposed by Fowler (1951: 3) in a manner that made the names available when published, but the names were rendered unavailable in 1961 by Art. 13 of the Second Edition of the Code (ICZN, 1961). The names apparently remain unavailable, despite Art. 13.2.1 of the current version of the Code (ICZN, 1999), because they were treated as unavailable in Ferraris & de Pinna (1999: 8).

Within Doradinae, four major monophyletic groups were recovered in the present (Fig. 69). Clade 1: the *Platyadoras* clade also includes *Centrochir* and is supported by two characters: a distinct dark longitudinal stripe on the middle of each caudal-fin lobe (#1: 0>1) (#1: 0>1, also present in *Anadoras*, *Orinocodoras*, *Tenellus*, and most *Leptodoras*), and the secondary chamber of the gas bladder formed by a single posterior chamber, thus without an inner septum (#38: 0>1, also present in *Doras* and *Oxyadoras*, coded as missing data for *Centrochir* and *Platyadoras* sp., which lack the secondary chamber). Clade 2: the *Pterodoras* clade (or large-doradids clade) also includes *Centroadoras*, *Doraops*, *Lithodoras*, and *Megalodoras* and is supported by two characters: large diverticula present on the main bladder and on the secondary chamber of the gas bladder (#41: 1>2, exclusive), 12 or more ribs (#221: 1>2, also present in *Kalyptodoras*, *Oxyadoras*, and *Wertheimeria*). Clade 3: the *Rhinodoras* clade also includes *Orinocodoras* and *Rhynchodoras* and is supported by five characters: five or six pores on the mandibular canal (#113: 1>2, also present in Astrodoradinae, *Centrochir*, *Franciscodoras*, *Kalyptodoras*, *Lithodoras*, *Platyadoras*, *Pterodoras*, and *Wertheimeria*, coded as missing data for *Rhynchodoras*), posterior limit of autopalatine approximately at vertical through the middle of orbit (#149: 0>1, exclusive), hyomandibular crest for Aw section of the *adductor mandibulae* muscle present (#156: 0>1, exclusive), posterior cleithral process triangular (#266: 0>1, exclusive), procurent rays of the caudal fin plate-like (#301: 0>1, also present in *Agamyxis*, *Franciscodoras* and *Platyadoras*). Clade 4: the *Doras/Oxyadoras* clade also includes *Anduzedoras*, *Hassar*, *Hemidoras*, *Leptodoras*, *Nemadoras*, *Ossancora*, *Tenellus*, and *Trachydoras*, and is supported by 18 characters, including among others: mesethmoid medially dilated in the shape of an arrow (#52: 0>2, exclusive), anteroventral keel of mesethmoid present (#55: 0>1, exclusive), premaxilla conical with a dorsal apex, depth distinctly greater than width (#125: 0>1, exclusive), ventral hypohyal quadrangular, length and width approximately equal (#172: 0>1, exclusive), conspicuous accessory lamellae on the medial

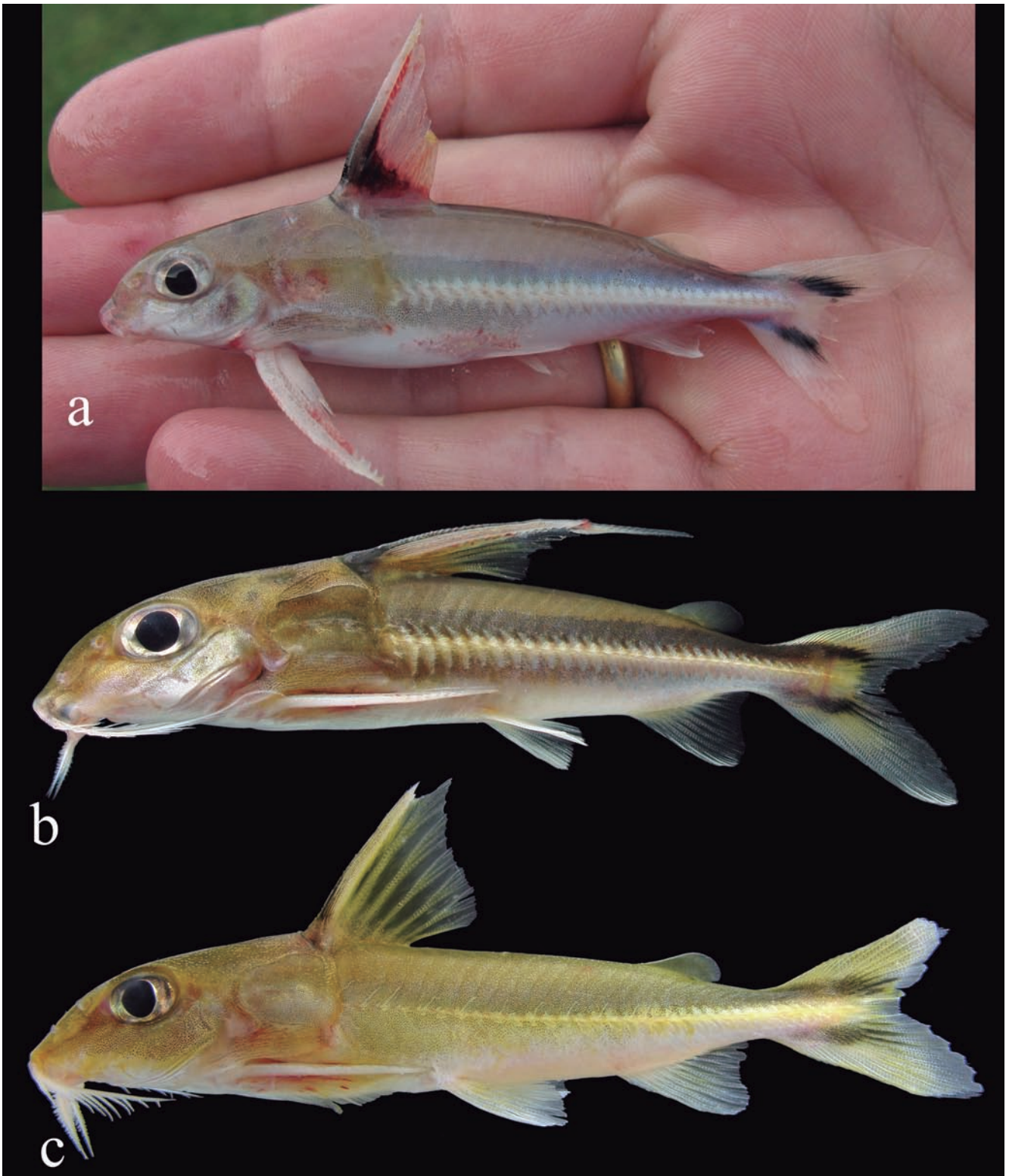


Fig. 71. *Tenellus trimaculatus* (a), AUM uncatalogued, approximately 90 mm SL, río Orinoco, Puerto Ayacucho, Venezuela; (b) *Tenellus ternetzi*, MZUSP 103245, 84.5 mm SL, río Jari, Monte Dourado, Pará State; (c) *Tenellus leporhinus*, MZUSP 96596, approximately 80 mm SL, río Teles Pires, Peixoto de Azevedo, Mato Grosso, photo by Mark Sabaj Pérez. All photographed live.

face of the ceratobranchials (#179: 0>1, reversed in *Trachydoras*), conspicuous accessory lamellae on the medial face of the epibranchials (#180: 0>1, reversed in *Trachydoras*), ventral process of fourth basibranchial elongate (#188: 0>1, exclusive), pharyngobranchial tooth plate elongate, length about twice width (#199: 0>1, exclusive), anterior margin of pectoral girdle anteriorly elongate with truncate or acute tip (#249: 0>1, reversed in *Ossancora*, *Trachydoras*, and some species of *Leptodoras*), dorsoposterior border of coracoid extremely elevated dorsally (#271: 0>1, exclusive). The *Doras/Oxydoras* clade includes the *Doras* clade, which is herein recognized as composed by the fimbriate-barbel doradids, the most well supported species group of the family with 17 characters, three of them exclusive (see Appendix).

Tenellus, new genus

Fig. 71

Type species. *Oxydoras trimaculatus* Boulenger, 1898: 422, pl. 40 (fig. 1). Rio Jurua, an affluent of the Amazon, Brazil.

Included taxa. *Tenellus trimaculatus* (Boulenger, 1898), new combination (Fig. 71a); *Tenellus ternetzi* (Eigenmann, 1925), new combination (Fig. 71b); *Tenellus leporhinus* (Eigenmann, 1912), new combination (Fig. 71c).

Diagnosis. *Tenellus* is diagnosed by a single character state change: a distinct dark longitudinal stripe on middle of each lobe of the caudal fin (#1: 0>1, also present in *Anadoras*, *Centrochir*, *Orinocodoras*, *Platydoras*, and most *Leptodoras*). In addition, *Tenellus* is distinguished from other doradids by the following combination of characters: well-developed adipose eyelid (#2: state 1, vs. weakly developed in all doradids except *Anduzedoras*, *Hassar*, and some species of *Leptodoras*), large posterior cranial fontanel (#58: state 0, vs. reduced to a small opening in *Nemadoras elongatus*, *N. humeralis*, and *Oxydoras*, or completely occluded in all other doradids, except *Anduzedoras*, *Hassar*, *Leptodoras*, *Nemadoras hemipeltis*, and *Trachydoras*), sphenotic with lateral process (#62: state 1, vs. sphenotic without lateral process in all doradids except *Anduzedoras*, *Doras*, *Hassar*, and *Leptodoras*), posterior process of epiotic connected via ligament to posterior nuchal plate (#86: state 0, vs. connected via bony suture in *Doras carinatus*, *D. micropoeus*, *D. higuchii*, *Hassar*, *Anduzedoras*, and *Leptodoras*), infraorbital 1 with relatively small anterior portion (#100: state 0, vs. anterior portion relatively large in *Doras carinatus*, *D. micropoeus*, *D. higuchii*, *Hassar*, *Anduzedoras*, and *Leptodoras*), ceratohyal with large anterior process sutured to hypohyal (#174: state 2, vs. process small or absent in most doradids, except *Hemidoras*, *Nemadoras*, and *Oxydoras*), gill-rakers present on first two gill arches (#181: state 1, vs. absent in *Trachydoras* and some species of *Leptodoras*).

Etymology. *Tenellus* comes from the Latin *tener*, meaning delicate, in the diminutive form, *tenellus*, in reference to the

delicate appearance of the species included in the new genus.

Remarks. Within *Tenellus* (Fig. 71), *T. ternetzi* and *T. trimaculatus* are considered sister taxa by sharing the loss of anterior nuchal plate (#228: 0>1). *Tenellus leporhinus* is readily distinguished from congeners by having midlateral scutes weakly developed on middle of body (#118: 2>1). *Tenellus trimaculatus* is distinguished from *T. ternetzi* by having well-developed bony lamina between internal process and basiptyrgium (#283: 1>0), and dark blotch on base of anteriormost dorsal-fin rays, including dorsal-fin spine but excluding spinelet (vs. dark blotch on spinelet but absent on dorsal-fin anteriormost rays).

Discussion

Monophyly of Doradoidea and relationships with other catfishes. The monophyly of the Doradoidea was recovered in the present analysis, corroborating previous studies based on both morphological (Ferraris, 1988; Mo, 1991; Lundberg, 1993; de Pinna, 1993; Royero, 1999; Britto, 2002; Diogo, 2004; Vigliotta, 2008) and molecular characters (Hardman, 2005; Sullivan *et al.*, 2006, 2008; Arce *et al.*, 2013). Herein, the monophyly of Doradoidea is supported by 16 characters, seven of them exclusive (see Systematic Account and Fig. 67).

The present analysis recovered Doradoidea sister to the African family Mochokidae, corroborating most previous phylogenetic studies based on morphological data (Ferraris, 1988; Mo, 1991; Lundberg, 1993; de Pinna, 1993; Royero, 1999; Britto, 2002; Diogo, 2004; Vigliotta, 2008), but contradicting recent analyses based on molecular data (Hardman, 2005; Sullivan *et al.*, 2006, 2008; Arce *et al.*, 2013). The monophyly of Doradoidea plus Mochokidae is extremely well supported by morphological data, including 13 characters, five of them exclusive (see Fig. 67 and Appendix).

Some characteristics, treated as synapomorphies for Doradoidea plus Mochokidae previously by other authors, were revealed to be complex structures that encompass distinct characters, some synapomorphic and others convergent. This is the case of the elastic spring apparatus, a complex structure that comprises the Müllerian ramus, with different shapes according to catfish families, and the protractor muscle of the Müllerian ramus, with distinct sites of origin and insertion. On the other hand, some characters that are herein considered synapomorphies for Doradoidea plus Mochokidae were previously treated as symplesiomorphies for catfishes. This is the case of the infranuchal ligament, previously considered to be present in catfishes of many other families.

The present study recovered the Doradoidea plus Mochokidae as closely related to the Sisoroidea plus Aspredinidae based on 13 characters. The Sisoroidea was herein represented by the Aspredinidae, Erethistidae, and Sisoridae, but it also includes the Akysidae, Amblicipitidae (de Pinna, 1996, 1998; Lundberg *et al.*, 2014). One of the

characters supporting the clade Sisoroidea plus Aspredinidae, Mochokidae and Doradoidea, the elongate processes of the dorsal-fin spinelet (#236: 0>1), is an exclusive feature among catfishes, present only in the Akysidae, Amblicipitidae, Auchenipteridae, Erethistidae, and Doradidae. This feature cannot be verified in the Aspredinidae and Sisoridae, because these taxa lack the dorsal-fin spinelet. The close relationship between Sisoroidea plus Aspredinidae and Doradoidea plus Mochokidae, represents a new and interesting hypothesis that should be tested in future studies. It is noteworthy to note that the molecular data support a close relationship between Aspredinidae and Doradoidea (Sullivan *et al.*, 2006, 2008), *i.e.*, part of the clade recovered herein.

Monophyly of and relationships within Auchenipteridae. The Auchenipteridae is herein recovered as monophyletic, corroborating previous studies (Britski, 1972; Ferraris, 1988; Royero, 1999; Akama, 2004). The monophyly of the family is supported by 16 characters, four of them exclusive (see Systematic Account). Almost all of these characters are related to sexually dimorphic features associated with reproduction by insemination (exclusive to auchenipterids among catfishes).

The Auchenipteridae is considered to be composed of two monophyletic clades: the Centromochlinae and Auchenipterinae. This result corroborates most previous studies (Ferraris, 1988; Soares-Porto, 1998; Akama, 2004). Nevertheless, it contradicts Britski (1972) and Walsh (1990) by considering the former Ageneiosidae as a clade nested well within the Auchenipterinae, and Royero (1999) for considering the clade composed of *Auchenipterus*, *Entomocorus*, *Epapterus*, and *Pseudepapterus* also deeply nested within the Auchenipterinae, sister to the *Ageneiosus* clade, instead of sister to all other auchenipterids.

In the present study, the most well supported clades within the Auchenipteridae were the Centromochlinae, with seven characters (three of them exclusive), and all clades inside the clade including *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, and *Tetranematichthys*, supported by up to 22 characters per ramus. It is interesting to note that *Entomocorus* is a key taxon for having many apomorphic features shared only with *Auchenipterus*, *Epapterus*, and *Pseudepapterus*, but, at the same time, having some plesiomorphic features, shared only with basal auchenipterids. This complex combination of character states may have been responsible for the whole clade associated with *Entomocorus* to assume a more basal position within auchenipterids in Royero's (1999) phylogenetic analysis.

The monophyly of the clade composed of *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, and *Tetranematichthys*, corroborates the finding of Ferraris (1988) and Akama (2004). Similarly, the monophyly of the clade composed of *Auchenipterichthys*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, and *Trachycorystes* corroborates the findings of Britski (1972) and, at least partially, the results of other authors (Ferraris, 1988; Royero,

1999; Akama, 2004).

Spinipterus acsi is hypothesized as closely related to the clade containing *Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, and *Tetranematichthys*. However, since the phylogenetic position of *Spinipterus acsi* was inferred based exclusively on the data of a single immature male provided in the description of the species (Akama & Ferraris, 2011), the present hypothesis is at best tentative. Only the study of more specimens of *Spinipterus*, including fully mature males, will confirm the result obtained herein.

Monophyly of and relationship within Doradidae. The Doradidae is recovered as monophyletic, corroborating Higuchi (1992), Moyer *et al.* (2004) and Arce *et al.* (2013). The monophyly of the family is supported by seven characters, two of them exclusive (see Systematic Account and Fig. 67). Although other authors (*e.g.*, Sørensen, 1895; Ladich, 2001) already had mentioned one of these exclusive characters, the ligament between the Müllerian ramus and the lateral line, they have never treated it as a synapomorphy for the whole family. This feature is revealed to be an exclusive character present in all examined doradids. Other synapomorphies include the ossification of the lateral-line tubules as scutes, a feature noticed in every study of the family since Linnaeus (1766); and the presence of the infranuchal scute, also previously reported (*e.g.*, Ferraris, 1988; Higuchi, 1992; Royero, 1999; Akama, 2004).

In the present analysis, *Wertheimeria*, *Kalyptodoras*, and *Franciscodoras* are considered to be at the base of the cladogram of the Doradidae. That hypothesis partially corroborates Higuchi's (1992) results by considering *Wertheimeria* and *Franciscodoras* as basal taxa, but differs by considering *Kalyptodoras* sister to *Wertheimeria*. That sister-group relationship is interesting because those two taxa are the only ones inhabiting small coastal drainages of eastern Brazil (Ribeiro, 2006), where some relatively old taxa are known (*e.g.*, Copionodontinae, Delturinae). The sister-group relationships between *Wertheimeria* and *Kalyptodoras* was already speculated by Higuchi *et al.* (1990) in their description of *Kalyptodoras bahiensis*, and Vono & Birindelli (2007) in their study of *Wertheimeria*. Higuchi's (1992) analysis failed to recognize this sister-group relationship because no specimens of *Kalyptodoras* properly prepared for osteological studies were available at the time. Higuchi's (1992) analysis coded the characters for *Kalyptodoras* based on a single alcohol-preserved specimen (paratype) with its belly cut open and gas bladder removed. As a result, important characters, such as the first free vertebra, were miscoded by Higuchi (1992). Arce *et al.* (2013) alternatively recovered *Franciscodoras* as part of the clade composed by *Wertheimeria* and *Kalyptodoras*. The conflict between the two hypotheses (Arce *et al.*'s and the present) is interesting and deserves further investigation.

The genera *Agamyxis* and *Acanthodoras* were recovered as sister taxa and deeply nested within the Astrodoradinae in the present analysis, a result that corroborates the previous

findings of Birindelli (2010) and Sousa (2010). However, this hypothesis contradicts the findings of Higuchi (1992) and the limits of the Astrodoradinae according to Higuchi *et al.* (2007), which did not include *Acanthodoras* and *Agamxis*. Based on molecular data, Moyer *et al.* (2004) and Arce *et al.* (2013) recovered *Acanthodoras* as sister to all doradids, except the Astrodoradinae. In their analyses, *Agamxis* was recovered as sister to all doradids except the Astrodoradinae and *Acanthodoras* (and the *Wertheimeria* clade in Arce *et al.*, 2013). This conflict in the hypothesis of relationships concerning *Acanthodoras* and *Agamxis* is still a matter of debate and should be focused in future studies.

Centrochir and *Platydoras* are very similar in overall body shape and external morphology, and it is no surprise that they are closely related in the present study. The present results corroborate recently analyses based on morphological and molecular data (Sousa, 2010; Arce *et al.*, 2013; respectively). Nevertheless, in Higuchi's (1992) analysis, *Platydoras* was considered to be closely related to *Kalyptodoras*, *Acanthodoras* and *Agamxis*, whereas *Centrochir* was recovered with *Centrodoras*, *Doraops*, *Lithodoras*, *Megalodoras*, and *Pterodoras*.

The present study proposed a new arrangement for the Doradinae, a group supported by six characters. This new arrangement corroborates the findings of previous studies based on morphology (Higuchi, 1992) and only partially those based on molecular data, as Moyer *et al.* (2004) included *Agamxis* in Doradinae, and Arce *et al.*, (2013) included *Platydoras* and *Centrochir* in Doradinae.

Within Doradinae, the clade composed by *Orinocodoras*, *Rhinodoras*, and *Rhynchodoras* was herein recovered as monophyletic corroborating previous studies based on morphology (Higuchi, 1992; Birindelli *et al.*, 2007) and molecular data (Moyer *et al.*, 2004; Arce *et al.*, 2013). On the other hand the monophyly of the clade composed by the large doradids (*i.e.*, *Centrodoras*, *Doraops*, *Lithodoras*, *Megalodoras*, and *Pterodoras*) recovered by morphological data (herein and in Higuchi, 1992) was not corroborated in molecular-based studies (Moyer *et al.*, 2004; Arce *et al.*, 2013).

Higuchi's (1992) hypothesis for fimbriate-barbel doradids also slightly differs from the results herein, especially in his treatment of *Nemadoras* as monophyletic and sister to *Trachydoras*, and of *Hassar* as sister to *Hemidoras* (plus former *Opsodoras*). The results herein strongly support *Nemadoras* (*sensu* Higuchi, 1992; Sabaj & Ferraris, 2003; Ferraris, 2007) as polyphyletic with neither subunits closely related to *Trachydoras*, and *Hassar* as closely related to *Anduzedoras* and *Leptodoras*. The sister-group relationship between *Anduzedoras* and *Leptodoras* was previously reported in other studies (Sabaj, 2002; Birindelli *et al.*, 2008; Birindelli & Sousa, 2010).

The synonymization of *Hemidoras* and *Opsodoras* based on the results obtained in the present analysis is corroborated by molecular data (Moyer *et al.*, 2004; Arce *et al.*, 2013). However, the monophyly of *Tenellus* and its close relationship

with *Anduzedoras*, *Hassar*, and *Leptodoras* are only partially corroborated in some of the analyses based on molecular data (Moyer *et al.*, 2004; Arce *et al.*, 2013). Similarly, despite the good support for the monophyly of *Ossancora*, and the close relationship between *Oxydoras* and fimbriate-barbel doradids, these were not recovered by the molecular data (Moyer *et al.*, 2004; Arce *et al.*, 2013).

This study represents the most comprehensive morphological data set assembled for the Auchenipteridae and Doradidae, with 311 characters presented, illustrated, discussed and coded for 23 of Auchenipteridae and 57 species of Doradidae, in addition to 20 species of 16 other catfish families included as outgroups. As a result, a new classification for the Doradoidea is proposed, as well as many new characters and interrelationship hypotheses. Furthermore, a new hypothesis for the position of the Doradoidea among catfishes is presented. The incongruences between the results obtained herein and those in the previous studies are identified, discussed, and remain to be resolved by future studies.

Comparative Material Examined. All measurements refer to standard length (SL). Specimens are listed as alcohol-preserved (alc), clear and stained (cs), and dry skeleton (sk). Taxa included in the phylogenetic matrix are indicated by asterisks. Specimens are from Brazil, unless noted otherwise. **Amphiliidae.** *Amphilius jacksoni**. UMMZ 199987 (4 cs, 30.9-100.0 mm), Zambia, Mpika, Lwitikila River. **Ariidae.** *Arius herzbergii*. MZUSP 52847 (1 alc, 192.0 mm), Alagoas, Coqueiro Seco, Lagoa Mandaú (9°37'S 35°48'W). *Galeichthys peruvianus**. MZUSP 94844 (1 alc, 105 mm, 1 sk, 208.0 mm), Perú, Lima, Callao, 12°12'35"S 77°5'15"W. *Genidens genidens**. MZUSP 51721 (1 cs, 128 mm), Bahia, Nova Viçosa, rio Peruiba, (17°54'S 39°22'W). MZUSP 51693 (1 sk, 250.0 mm), São Paulo, Juréia, Ilha do Bom Abrigo. MZUSP 49319 (1 alc, 115 mm), São Paulo, Cananéia. **Aspredinidae.** *Bunocephalus coracoideus**. MZUSP 28835 (1 cs, 68.6 mm), no data. MZUSP 30713 (1 alc, 71.0 mm), Amazonas, Tefé, rio Tefé (3°22'S 64°43'W). MZUSP 103254 (1 sk, 67.0 mm), Amapá, Lanranjal do Jari, Igarapé Arapiranga, tributary of rio Jari (0°47'41"S 52°27'10"W). *Pseudobunocephalus bifidus*. MZUSP 50107 (2 cs, 33.3-54.0 mm), Acre, Manoel Urbano, rio Purus (8°48'S 69°15'W). **Auchenipteridae.** *Ageneiosus atronanus**. MZUSP 52620 (20 alc, 80.1-89.0 mm, 2 cs, 79.8-87.0 mm), Amazonas, rio Purus at Beruri (3°55'S 61°22'W). MZUSP 63629 (1 cs, 88.0 mm), Amazonas, Purus (7°48'S 67°5'W). MZUSP 74483 (2 alc, 84.5-87.3 mm), Amazonas, Lago Janauacá, rio Solimões (3°22'S 60°11'W). *Ageneiosus brevis*. MZUSP 34417 (567 alc, 52.8-60.4 mm, 3 cs, 53.0-61.6 mm), Rondônia, rio Madeira at Calama (8°3'S 62°53'W). MZUSP 56660 (1 alc, 95.6 mm), Amazonas, rio Purus (4°3'48"S 61°33'49"W). *Ageneiosus inermis**. MZUSP 89519 (1 sk, 250 mm), Goiás, Luís Alves, rio Verde, tributary of rio Araguaia (13°9'28"S 50°30'22"W). MZUSP 91661 (2 sk, 260.0-320.0 mm), Goiás, Luís Alves, rio Verde, tributary of rio Araguaia (13°9'28"S 50°30'22"W). MZUSP 92005 (1 sk, 420 mm), Mato Grosso, Canarana, rio Culuene, tributary of rio Xingu (13°49'S 53°15'W). MZUSP 96189 (3 sk, 255-315 mm), Amazonas, Manaus, Porto Ceasa. *Ageneiosus militaris*. MZUSP 21114 (1 alc, 179 mm), Paraná, Guaíra, rio Paraná, above Cachoeira Sete Quedas (24°4'S 54°16'W). *Ageneiosus ucayalensis*. MZUSP 98333 (1 alc, 165 mm), Pará, Jacareacanga, rio Teles Pires, tributary of rio Tapajós (9°19'1"S

56°46'44"W). *Ageneiosus vittatus*. MZUSP 92185 (1 alc, 168 mm), Amazonas, Igarapé Castanha, tributary of rio Tiquié, rio Negro basin (2°4'41"N 69°41'26"W). MZUSP 101771 (1 sk, 158 mm), Pará, Monte Dourado, rio Jari (0°39'45"S 52°31'40"W). *Ageneiosus* sp. MZUSP 92639 (1 alc, 106 mm), Pará, Itaituba, rio Tapajós (4°21'34"S 56°10'3"W). *Asterophysus batrachus**. INPA 24119 (1 cs, 127.0 mm), Amazonas, Novo Airão, rio Negro, Arquipélogo de Anavilhanas (2°37'S 60°50'W). MZUSP 12420 (1 alc, 129.7 mm), Amazonas, Paricatuba, rio Negro (0°31'S 65°1'W). MZUSP 33410 (1 alc, 149.8 mm), Amazonas, São Gabriel da Cachoeira, rio Negro (0°7'S 67°5'W). *Auchenipterichthys longimanus*. MZUSP 52103 (1 sk, 167 mm), Amazonas, flood between rio Mamirauá and rio Negro (0°24'S 65°12'W). MZUSP 57109 (1 alc, 123.3 mm), Pará, Capim, rio Capim (2°2'S 47°45'W). *Auchenipterichthys punctatus*. MZUSP 43333 (1 alc, 119.7 mm), Amazonas, rio Jutai (3°11'S 67°5'W). *Auchenipterichthys coracoideus*. MZUSP 86218 (1 alc, 91.2 mm), Mato Grosso, Cocalinho, Corixo da Saudade, tributary of rio Araguaia (14°17'20"S 51°9'12"W). MZUSP 15304 (1 cs, 40.6 mm), Peru, Loreto, Iquitos, rio Nanay (3°41'S 73°13'W). *Auchenipterichthys thoracatus**. MZUSP 63034 (1 alc, 101.9 mm), Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé, tributary of rio Madeira (15°1'17"S 59°57'W). MZUSP 37518 (1 cs, 78.7 mm), Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé, tributary of rio Madeira (15°1'17"S 59°57'W). *Auchenipterus ambyacus*. MZUSP 30611 (1 cs, 103.0 mm), Amazonas, Tefé, rio Tefé (3°22'S 64°43'W). *Auchenipterus nuchalis*. MZUSP 89728 (1 alc, 130.5 mm, 1 sk, 135.2 mm), Mato Grosso, Canarana, rio Culuene, tributary of rio Xingu (13°49'S 53°15'W). MZUSP 97375 (2 sk, 117.0-120.0 mm), Pará, Novo Progresso, rio Jamanxim (7°43'51"S 55°16'36"W). *Auchenipterus osteomystax**. MZUSP 33414 (1 cs, 141.0 mm), Pará, Itaituba, rio Tapajós (4°27'S 56°15'W). *Auchenipterus brachyurus*. MZUSP 49830 (1 alc, 121 mm), Acre, rio Acre. *Centromochlus heckelii**. MZUSP 49529 (2 alc, 80.5-97.4 mm, 2 cs, 68.1-83.4 mm), Amazonas, rio Purus (8°44'S 67°24'W). MZUSP 101767 (4 sk, 82.7-84.0 mm), Pará, Monte Dourado, rio Jari (0°39'45"S 52°31'40"W). *Entomocorus radiosus**. MZUSP 59465 (1 alc, 36.8 mm, 2 cs, 37.2-41.2 mm), Mato Grosso do Sul, rio Miranda, tributary of rio Paraguay (19°37'22"S 56°57'27"W). MZUSP 59327 (1 cs, 35 mm), aquarium store. *Epapterus dispilurus**. MZUSP 26410 (1 cs, 62.0 mm), Perú, Amazonas, rio Ucayali, Pucallpa (8°23'S 74°33'W). *Gelanoglanis* cf. *stroudi**. MZUSP 96032 (5, 11.8-26.4 mm, 1 cs, 19.4 mm), rio Teles Pires (10°58'30"S 55°44'3"W). *Glanidium melanopterus**. MZUSP 51043 (1 cs, 107.9 mm), São Paulo, rio Ribeira de Iguape (24°35'S 48°36'W). MZUSP 51275 (2 cs, 74.7-79.9 mm), São Paulo, Registro, rio Ribeira de Iguape (24°35'S 47°51'W). MZUSP 64256 (1 alc, 105.0 mm, 1 cs, 108.4 mm, 2 sk, 110.0-112.0 mm), São Paulo, Iporanga, rio Ribeira de Iguape (24°35'S 48°35'W). *Liosomadoras oncinus**. MZUSP 46015 (1 alc, 55.4 mm), aquarium store. MZUSP 93497 (2 alc, 65.8-74.8 mm, 1 cs, 70.7 mm), aquarium store. MZUSP 105828 (3 sk, 110-120 mm), Venezuela, Amazonas, rio Ventuari (4°4'39"N 66°52'6"W). MNRJ 17640 (1 cs, 125 mm), no data. *Pseudauchenipterus affinis**. MZUSP 51718 (2 alc, 75.3-86.5 mm, 1 cs, 63 mm), Espírito Santo, Linhares, rio Doce (19°24'S 40°1'W). MZUSP 51720 (1 cs, 68.6 mm), Espírito Santo, São Mateus, rio São Mateus (18°44'S 39°50'W). MZUSP 60075 (1 cs, 88.7 mm), Bahia, Mucurí, rio Mucurí (18°6'S 39°32'W). *Pseudauchenipterus nodosus*. ANSP 179581 (1 sk, unmeasured), Guiana, Georgetown, fish market. *Pseudepapterus hasemani*. MZUSP 53323 (12 alc, 54.0-70.6 mm, 2 cs, 64.2-64.8 mm), Pará, Porto de Moz, rio Acaraí, tributary of rio Xingu (2°3'47"S 52°18'45"W). MZUSP 104772 (1 alc, 115.2 mm), Pará, Monte Dourado, rio Jari (0°47'55"S 52°31'50"W). *Pseudotatia parva**. FMNH 57807 (2 alc, c.35 mm, 2 cs, c.34 mm), Bahia, Juazeiro, rio São Francisco (9°26'S 40°30'W). *Tatia aulopygia**. MZUSP 37599 (2 alc, 60.8-71.1 mm, 2 cs, 48.6-58.6 mm), Mato Grosso, Aripuanã, Igarapé do Aeroporto, rio Madeira basin (9°58'S 59°19'W). *Tatia* cf. *aulopygia*: MZUSP 99309 (2 sk, 89.0-94.0 mm), no data. *Tatia intermedia*. MZUSP 89376 (2 cs, 35.2-66.0 mm), Goiás, Crixás, Córrego da Taboca, rio Araguaia basin (14°19'27"S 50°12'32"W). *Tetranematichthys quadrifilis**. MZUSP 37517 (1 cs, 114 mm), Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé, tributary of rio Madeira (15°1'17"S 59°57'90"W). *Tetranematichthys wallacei*. MZUSP 85497 (1 alc, 193 mm), Amazonas, Santa Isabel do rio Negro, rio Negro (0°24'S 65°2'W). *Tocantinsia piresi**. MZUSP 98301 (1 sk, 250.0 mm), Pará, Jacareacanga, rio Teles Pires (9°18'56"S 56°47'10"W). MZUSP 100031 (2 sk, 430.0-440.0 mm), Pará, Jacareacanga, rio Teles Pires (9°18'42'S 56°46'47"W). *Trachelyichthys decaradatus**. MZUSP 92829 (1 alc, 66.3 mm, 4 cs, 35.0-54.0 mm), Pará, Santarém, Igarapé Juá, rio Tapajós basin (2°26'0"S 54°46'51"W). MZUSP 6830 (2 cs, 53.1-55.8 mm), Amazonas, Manaus, Igarapé tributary of rio Tarumãzinho, rio Negro basin (3°10'S 60°0'W). *Trachelyopterichthys taeniatius**. MZUSP 8496 (1 alc, 107.0 mm, 2 cs, 53.8-82.4 mm), Pará, Santarém, Igarapé afluent do rio Mapiri (2°26'S 54°44'W). *Trachelyopterus ceratophysus*: MZUSP 52087 (1 cs, 165 mm), Amazonas, rio Negro (0°24'S 65°12'W). *Trachelyopterus coriaceus**. MZUSP 92767 (3 cs, 73.0-94.2 mm), Pará, Santarém, Lago Maiacá (2°27'54"S 54°39'31"W). *Trachelyopterus galeatus**. MZUSP 90831 (2 alc, 127.2-138.8 mm), Minas Gerais, Várzea da Palma, rio São Francisco (17°36'56"S 44°40'33"W). MZUSP 9304 (2 cs, 98.3-99.4 mm), Amazonas, rio Purus (3°42'S 61°28'W). MZUSP 95008 (1 alc, 143.4 mm), Mato Grosso, Barão de Melgaço, rio Miranda, tributary of rio Paraguay (16°19'30"S 55°49'59"W). *Trachelyopterus peloichthys*. MZUSP 79458 (5 alc, 109.3-135.2 mm), Venezuela, Zulia, Carrasquero, rio Limón, Lago Maracaibo basin. *Trachelyopterus porosus*. MZUSP 75365 (1 cs, 81.3 mm), Amazonas, Manaus, Lago Januári, rio Negro (3°12'S 60°1'W). MZUSP 75364 (2 cs, 65.5-77.3 mm), Amazonas, Manaus, Ilha da Marchantaria, rio Solimões. MZUSP 31889 (1 cs, 106.6 mm), Pará, Alter do Chão, rio Tapajós (2°30'S 54°57'W). *Trachelyopterus striatulus*. MZUSP uncatalogued (3 sk, 81.1-93.7 mm), no data. MZUSP 90742 (2 alc, 151-154 mm), Espírito Santo, Anchieta, rio Salinas (20°44'15"S 40°41'59"W). *Trachelyopterus teaguei*. MCP 18423 (2 cs, 115.8-123.8 mm), Santa Catarina, Concórdia, rio do Peixes at Volta Grande, rio Uruguai basin (27°21'S 51°59'W). *Trachycorystes trachycorystes**. ANSP 78079 (1 sk, unmeasured), Guiana, Essequibo. ANSP 179152 (1 sk, unmeasured), Guiana, Rupununi, Simoni River (3°43'9"N 59°15'40"W). MZUSP 7381 (1 cs, 128.8 mm), Amazonas, Maués, Igarapé Limãozinho (3°24'S 57°42'W). MZUSP 52088 (1 sk, 165 mm), Amazonas, rio Negro, Anavilhanas (2°42'S 60°45'W). MZUSP 52095 (1 alc, 310 mm), Amazonas, São Pedro, upper rio Negro. MZUSP 91659 (1 sk, 200.0 mm), no data. MZUSP 99308 (1 sk, 180.0 mm), no data. no data. **Callichthyidae**. *Corydoras aeneus*. MZUEL 8130 (1 alc, 36.0 mm), Mato Grosso, Tangará da Serra, ribeirão do Sapo (4°33'25"S 57°48'45"W). **Clariidae**. *Clarias* sp. MZUSP 91656 (1 sk, 430.0 mm), Espírito Santo, Anchieta, rio Grande (20°42'23"S 40°39'0"W). **Claroteidae**. *Chrysichthys auratus**. MZUSP 27171 (1 cs, 101.0 mm), Egito, Nilo, Nasarah. **Diplomystidae**. *Diplomystes campoensis**. MZUSP 88533 (1 sk, 172.5 mm), Chile, Los Lagos/ VIII Región, rio San Pedro, Lago Riñihue basin. *Diplomystes mesembrinus*. MZUSP 62595 (1 alc, 99.2 mm), Argentina, Chubut, Los altares, rio Chubut (43°49'S 67°54'W). **Doradidae**. *Acanthodoras cataphractus**. MZUSP 6831 (1, 119.0 mm, 1 cs, 112.0 mm), Amazonas, Manaus, tributary of rio

Tarumãzinho (3°10'S 60°0'W). MZUSP 82295 (2 alc, 156.2-185.5 mm), rio Branco, Cachoeira Bem-Querer. MZUSP 84667 (2 cs, 57.0-58.0 mm), aquarium store. *Acanthodoras spinosissimus*. ANSP 179341 (1 sk, unmeasured), Guiana, Rupununi, Simoni River (3°43'9"N 59°15'40"W). *Agamyxis albomaculatus**. ANSP 180889 (1 alc, 68.4 mm), Venezuela, río Orinoco at Isla Portuguesa. MZUSP 88607 (3, 64.3-97.7 mm, 1 cs, 72.2 mm), Venezuela, Delta Amacuro, río Orinoco (8°37'20"N 61°47'30"W). *Agamyxis pectinifrons*: INHS 43281 (1 alc, 91.7 mm), Perú, río Itaya. MZUSP 5177 (1 alc, 82.3 mm), Mato Grosso, rio Papagaio, rio Tapajós basin (13°2'S 58°17'W). MZUSP 27806 (1 alc, 83.3 mm), Bolívia, Trinidad, Laguna San José. MZUSP 57766 (1 alc, 49.4 mm), Amazonas, rio Purus (3°58'47"S 61°29'6"W). *Anadoras grypus**. ANSP 166262 (1 alc, 114.3 mm), Perú, río Marañón. ANSP 179558 (1 sk, unmeasured), Peru, Loreto, Maynas, Caño Moena (3°46'19"S 73°14'16"W). MZUSP 5934 (1 alc, 150 mm), Amazonas, rio Purus (3°42'S 61°28'W). MZUSP 5971 (1 cs, unmeasured), Amazonas, rio Purus (3°42'S 61°28'W). MZUSP 6896 (1 alc, 112.9 mm, 1 cs, 94.0 mm), Amazonas, Iranduba, Lago Janauari (3°13'S 60°4'W). MZUSP 50136 (1 alc, 115.7 mm), Amazonas, Itacoatiara, Ilha Amatari (3°18'S 58°57'W). MZUSP 50148 (1 alc, 92.5 mm), Amazonas, Lago Janauacá (3°25'S 60°17'W). MZUSP 74864 (1 alc, 140.0 mm, 1 sk, 123.2 mm), Amazonas, Lago Janauacá (3°22'S 60°11'W). *Anduzedoras oxyrhynchus**. ANSP 160628 (1 alc, 108.2 mm), Venezuela, Amazonas, río Sipapo (4°52'N 67°53'W). ANSP 178551 (1 sk, unmeasured), Amazonas, rio Negro (1°12'34"S 62°13'47"W). MZUSP 29021 (2 alc, 92.1-115.7 mm), Amazonas, rio Negro (031'S 64°50'W). MZUSP 29028 (2 alc, 34.5-56.8 mm), Amazonas, rio Negro (0°24'S 65°12'W). MZUSP 29029 (215, 31.0-92.3 mm, 2 cs, 56.0-92.3 mm), Amazonas, rio Negro (0°58'S 62°57'W). MZUSP 91454 (1 alc, 228.0 mm), Amazonas, Vista Alegre, rio Negro (0°21'S 68°27'W). *Astrodoras asterifrons**. MZUSP 8534 (3 cs, 60.0-70.0 mm), Pará, Santarém, rio Tapajós (54°44'0"W 2°25'0"S). MZUSP 50833 (1 cs, 60.0 mm), Roraima, Rorainópolis, rio Jauaperi (61°26'0"W 0°39'0"S). *Centrochir crocodili**. MZUSP 105837 (1 sk, 150.8 mm), Colombia, Tolima, río Magdalena (5°12'16"N 74°44'03"W). CU 47930 (1 cs, 130.0 mm), Colombia, río Magdalena. *Centrodoras brachiatus**. ANSP 179155 (1 sk, unmeasured), Amazonas, rio Solimões (2°44'15"S 66°56'7"W). ANSP 179164 (1 sk, unmeasured), Amazonas, Santo Antônio do Içá, rio Solimões (3°6'S 67°56'W). ANSP 181021 (1 alc, 81.5 mm), Pará, Vila Canaã, rio Amazonas. MZUSP 31306 (1 alc, 186.0 mm), no data. MZUSP 42335 (1 cs, 264.0 mm), Amazonas, Tefé, rio Solimões. MZUSP 51039 (1 alc, 230.0 mm), Pará, Juriti, (2°9'S 56°6'W). MZUSP 55776 (1 cs, 76.2 mm), Amazonas, rio Solimões (3°15'4"S 64°45'19"W). MZUSP 83313 (1 sk, 158.0 mm), Amazonas, rio Madeira, (3°38'14"S 59°2'17"W). *Centrodoras hasemani**. ANSP 17955 (1 sk, unmeasured), Amazonas, rio Negro (3°1'18"S 60°24'55"W). ANSP 177907 (1 alc, 209 mm), Amazonas, at confluence between rio Negro and rio Branco. ANSP 181031 (1 alc, 69 mm), Amazonas, rio Negro. INPA 11338 (1 alc, 147.2 mm), Amazonas, Novo Airão, rio Negro (2°37'S 60°56'W). MZUSP 56037 (1 cs, 71.9 mm), Amazonas, rio Negro (3°7'17"S 60°8'20"W). MZUSP 91675 (1 alc, 202.0 mm), Amazonas, rio Uaupés, rio Negro basin. *Doraops zuloagai**. ANSP 179558 (2 sk, unmeasured), Venezuela, Zulia, rio Catatumbo, Lago Maracaibo basin. INHS 54804 (1 alc, 273 mm), Venezuela, Lago Maracaibo basin. MCNG 33457 (1 alc, 103.8 mm), Venezuela, Zulia, río Escalante, Lago Maracaibo basin. *Doras carinatus**. ANSP 177276 (1 alc, 124.5 mm), Guiana, Essequibo River (4°42'3"N 58°42'44"W). ANSP 187399 (1 sk, 170.0 mm), Guiana, Lawa River, Maroni River basin (3°19'31"N 54°3'48"W). ANSP 180986 (1 sk, 170.0 mm), Guiana, Essequibo River (1°54'53"N 58°31'14'). AMNH 96798 (1 alc, 302 mm), Venezuela, Bolivar, rio Crapo (5°30'40"N 63°30'40"W). *Doras higuchii**. ANSP 181056 (1 cs, 60.0 mm), Mato Grosso, rio Curisevo (13°2'5"S 53°25'10"W). ANSP 181057 (1 alc, 160.0 mm), Pará, Belo Monte, rio Xingu (3°7'S 51°42'W). INPA 5568 (1 alc, 83.8 mm), Amazonas, rio Trombetas. MZUSP 96334 (1 sk, 165.0 mm), Pará, Altamira, rio Curuá (8°19'7"S 55°5'23"W). MZUSP 101693 (2 sk, 105.0-172.0 mm), Pará, Monte Dourado, rio Jari (0°33'59"S 52°34'40"W). MZUSP 110620 (1 sk, 230.0 mm), Pará, Altamira, rio Xingu (3°12'2"S 52°11'46"W). *Doras micropoeus*. ANSP 78070 (1 sk, 160 mm), no data (Hyrtl Collection). ANSP 178703 (1 alc, 222 mm), Guiana, Essequibo River (4°44'N 58°43'W). ANSP 187110 (1 alc, 174 mm, 2 sk, 205-210 mm), Suriname, Lawa River, Maroni River basin (5°31'N 57°12'W). *Doras phlyzaktion**. ANSP 181055 (1 alc, 148.0 mm), Amazonas, rio Tefé (3°38'S 64°59'W). MZUSP 82294 (2 alc, 175.0-180.0 mm, 1 sk, 162.0 mm), Amazonas, rio Tefé. MZUSP 50836 (1 cs, 67.5 mm), Amazonas, Lagoa Central, rio Negro basin. *Doras zuanoni*. MZUSP 96328 (1 alc, 96.0 mm), Tocantins, Caseara Lago Paredão, rio Araguaia basin (9°17'S 49°58'W). *Franciscodoras marmoratus**. MZUSP 2201 (1 cs, 99.0 mm), Bahia, rio São Francisco. MZUSP 9380 (1 cs, 183.0 mm), Minas Gerais, Buritis, rio Urucuia, rio São Francisco basin (15°37'S 46°25'W). MZUSP 84224 (1 cs, 103.8 mm), Minas Gerais, Três Marias, rio São Francisco. MZUSP 97145 (3 cs, 29.4-33.0 mm), Minas Gerais, Três Maria, rio São Francisco. *Hassar affinis**. MZUSP 74890 (1 cs, 85.9 mm), Parnaíba. MZUSP 43604 (1 alc, 152.0 mm), Piauí, Teresina, rio Parnaíba. MZUSP 89935 (1 cs, 108.7 mm), Piauí, Parnaíba, Lagoa de Parnaíba (10°14'41"S 44°38'50"W). MZUSP 90583 (1 alc, 54.4 mm), Piauí, Guadalupe, rio Parnaíba (6°45'44"S 43°33'53"W). *Hassar gabiru**. MZUSP 110599 (2 sk, 98.0-165.0 mm SL), Pará, Altamira, rio Xingu (3°12'2"S 52°11'46"W). *Hassar orestis**. ANSP 180294 (1 sk, unmeasured), Venezuela, Amazonas, rio Ventuari (4°45'N 66°21'W). MZUSP 6991 (1 cs, 71.0 mm), Amazonas, Nova Olinda do Norte, rio Madeira (3°53'S 59°5'W). MZUSP 15512 (1 alc, 132.0 mm), Pará, Trombetas, rio Trombetas (1°20'S 56°51'W). MZUSP 32542 (2 sk, 205.0-220.0 mm), Pará, Belo Monte, rio Xingu (3°7'S 51°42'W). MZUSP 46010 (1 cs, 76.9 mm), Amazonas, Coari, rio Solimões (3°55'S 63°20'W). MZUSP 105827 (1 sk, 138.5 mm), Venezuela, Amazonas, rio Ventuari (4°13'7"N 66°25'26"W). *Hemidoras boulengeri*. MZUSP 62641 (1 alc, 147.3 mm), Amazonas, Manaquiri, Lago Janauacá, rio Solimões (3°25'S 60°17'W). *Hemidoras morei**. MZUSP 26316 (1 alc, 102.3-115.2 mm), Perú, Pucallpa. MZUSP 27844 (1 cs, 90.6 mm), Bolívia, Beni, Trinidad, rio Ibare, rio Madeira basin. MZUSP 31104 (1 alc, 167.7 mm), Amazonas, Santa Isabel do rio Negro, rio Marauá, rio Negro basin (0°24'S 65°12'W). MZUSP 32526 (3 alc, 135.0-138.0 mm, 2 sk, 137.7-153.2 mm), Amazonas, rio Negro (0°7'S 67°5'W). MZUSP 82288 (1 alc, 154.1 mm), no data. *Hemidoras morrisi**. ANSP 180191 (1 sk, unmeasured), Perú, Loreto, Maynas, rio Nanay (3°46'45"S 73°22'6"W). MZUSP 28378 (2 alc, 157.0-164.0 mm), Rondônia, Lago Piauí, foz do rio Jamari, rio Madeira basin (8°27'S 63°30'W). MZUSP 56044 (2 alc, 58.2 mm), Amazonas, rio Jutai (2°52'36"S 66°59'20"W). MZUSP 56683 (1 cs, 93.2 mm), Amazonas, Benjamin Constant, rio Solimões (4°24'S 69°49'W). *Hemidoras stenopeltis**. ANSP 179240 (1 sk, unmeasured), Amazonas, rio Solimões (2°35'29"S 65°29'52"W). MZUSP 7541 (1 alc, 114.1 mm), Amazonas. MZUSP 7612 (2 alc, 55.3-96.0 mm, 1 cs, 74.8 mm), Amazonas, Uruará (2°37'S 57°42'). MZUSP 29052 (2 cs, 67.9-69.4 mm), Rondônia, rio Madeira at Calama (8°3'S 62°53'W). MZUSP 42772 (1 alc, 108.7 mm), Amazonas, rio Aripuanã. *Hemidoras stubelii**. MZUSP 26316 (2 alc, 102.3-114.9 mm), Perú, Pucallpa, rio Ucayali. MZUSP 56879 (1 cs, 64.5 mm), Amazonas, rio Purus (3°51'9"S 61°23'25"W). MZUSP 57620 (1 alc, 59.6 mm), Amazonas, rio Negro (3°4'4"S 60°14'58"W). *Kalyptodoras*

*bahiensis**. MZUSP 87841 (1 sk, 233.0 mm), Bahia, Itaberaba, rio Paraguassú. MZUSP 87842 (8 alc, 129.0-196.0 mm, 1 sk, 152.0 mm), Bahia, Iaçú, rio Paraguassú. *Leptodoras acipenserinus*. ANSP 178467 (1 alc, 106.7 mm), Peru, rio Nanay. *Leptodoras copei*. ANSP 162461 (1 alc, 96.5 mm), Venezuela, Amazonas, rio Orinoco. *Leptodoras hasemani*. ANSP 175888 (1 cs, 81.8 mm), Guiana, Essequibo River. ANSP 179209 (1 sk, unmeasured), Guiana, Rupununi, Rupununi river, Essequibo drainage. MZUSP 37009 (1 alc, 132.8 mm), Roraima, Boa Vista, rio Branco (2°50'N 60°40'W). MZUSP 110600 (1 sk, 118.0 mm SL), Pará, Altamira, rio Xingu (3°36'31"S 52°21'3"W). *Leptodoras juruensis**. ANSP 179168 (1 sk, unmeasured), rio Amazonas. INHS 39465 (1 alc, 117.4 mm), Peru, rio Amazonas. MZUSP 57054 (1 cs, 105.0 mm), Amazonas, rio Solimões (3°11'1'S 64°48'42"W). MZUSP 104532 (1 sk, 227.0 mm), Rondônia, Porto Velho, rio Madeira (8°32'12"S 63°34'5"W). *Leptodoras marki**. MZUSP 103217 (1 alc, 80.3 mm, 1 cs, 83.2 mm), Pará, São Felix do Xingu, Igarapé Manguari (6°35'42"S 51°48'48"W). *Leptodoras myersi*. MZUSP 55839 (1 cs, 83.8 mm), Amazonas, rio Solimões (3°11'17"S 64°48'47"W). *Leptodoras oyakawai**. ANSP 187336 (1 sk, 120 mm), Pará, Novo Progresso, rio Jamanxim, tributary of rio Tapajós (7°3'51"S 55°26'28"W). MZUSP 87028 (1 alc, 54 mm), Mato Grosso, Gaúcha do Norte, rio Curisevo, tributary of rio Xingu (13°2'5"S 53°23'19"W). MZUSP 97722 (1 cs, 73.0 mm), Mato Grosso, Paranaíta, rio Teles Pires (9°27'7"S 56°30'46"W). *Leptodoras praelongus**. ANSP 162463 (1 alc, 142 mm), Venezuela, rio Pamoni. ANSP 179156 (1 sk, unmeasured), Roraima, rio Branco, tributary of rio Negro (1°20'34"S 61°52'21"W). MZUSP 31694 (1 alc, unmeasured), Pará, Belo Monte, rio Xingu (3°7'S 51°42'W). MZUSP 56674 (1 cs, 82.7 mm), Roraima, rio Branco (1°18'49"S 61°52'3"W). *Lithodoras dorsalis**. MZUSP 9379 (1 cs, 134.0 mm), Pará, Icoaraci (1°18'S 48°29'W). MZUSP 62584 (1 alc, 163.0 mm), Pará, Vigia (0°52'S 48°8'W). MZUSP 62585 (2 alc, 115.0-118.0 mm), Pará, Icoaraci (1°18'S 48°29'W). MZUSP 58326 (1 alc, 170.0 mm), Amazonas, rio Amazonas (1°47'10"S 48°57'10"W). MZUSP 13955 (1 alc, 740.0 mm), Rondônia, rio Machado, rio Madeira basin. MZUSP 91562 (1 sk, 478.0 mm), Pará, Belém, fish market at Icoaraci. *Megalodoras guayoensis**. ANSP 177980 (143.9 mm), Venezuela, rio Orinoco. ANSP 179167 (1 sk, unmeasured), Venezuela, Delta Amacuro, rio Orinoco (8°28'24"N 61°17'12"W). *Megalodoras uranoscopus**. MZUSP 8284 (1 alc, 337.0 mm), Pará, Oriximiná, Lago Paru, rio Trombetas basin (1°52'S 55°50'W). MZUSP 5647 (1 alc, 570.0 mm), Pará, Oriximiná, Lago Paru, rio Trombetas basin (1°52'S 55°50'W). MZUSP 14026 (1 alc, 410.0 mm), Rondônia, rio Machado, rio Madeira basin. MZUSP 25308 (1 alc, 315.0 mm), Pará, Itapacura, rio Tapajós (4°37'S 56°18'W). MZUSP 46007 (1 alc, 16.02 mm), Tocantins. MZUSP 55838 (1 cs, 73.0 mm), Amazonas, Jutáí, rio Solimões (2°31'37'S 66°36'27"W). MZUSP 110601 (1 sk, 104.0 mm SL), Pará, Porto de Moz, rio Xingu (2°11'56"S 52°8'9"W). *Nemadoras elongatus**. ANSP 179239 (2 sk, unmeasured), Amazonas, rio Solimões, 2°54'34"S 67°50'1"W). MZUSP 56013 (1 alc, 99.2 mm, 1 cs, 92.0 mm, 1 sk, 101.6 mm), Amazonas, Barcelos, rio Negro (1°23'1"S 61°55'50"W). MZUSP 56021 (1 alc, 46.1 mm), Amazonas, rio Negro (3°8'24"S 60°7'20"W). *Nemadoras hemipeltis**. MZUSP 56688 (1 cs, 81.8 mm), Amazonas, Benjamin Constant, rio Içá (4°24'S 69°49'W). *Nemadoras humeralis**. ANSP 179157 (2 sk, unmeasured), Amazonas, rio Amazonas (3°21'22"S 58°38'52"W). MZUSP 6990 (1 alc, 75.6 mm), Amazonas, rio Madeira (3°53'S 59°5'W). MZUSP 19306 (1 sk, 120 mm), Amazonas, Manaus, rio Negro (3°10'S 60°0'W). MZUSP 55996 (1 cs, 58.0 mm, 1 alc, 60.1 mm), Amazonas, rio Juruá (2°37'5"S 65°47'43"W). MZUSP 56014 (1 alc, 103.8 mm), Amazonas, rio Içá (3°8'56"S 68°1'59"W). MZUSP 56606 (1 cs, 86.4 mm), Amazonas, rio Amazonas (3°19'59"S 58°35'59"W). MZUSP 104533 (1 sk, 124.1 mm), Rondônia, Porto Velho, rio Madeira (8°51'43"S 64°3'37'W). *Nemadoras* sp. (juvenile). MZUSP 74280 (2 cs, 14.8-15.7 mm), Amazonas, Anavilhanas, rio Negro (2°42'S 60°45'W). *Orinocodoras eigenmanni**. ANSP 177996 (1 sk, unmeasured), Venezuela, Delta Amacuro, rio Orinoco (8°37'20"N 61°47'30"W). AUM 5318 (1 alc, 119.6 mm), Venezuela, Portuguesa, Caño Maraca, rio Orinoco basin (8°49'N 69°20'W). INHS 40330 (1 cs, 57.8 mm), Venezuela, Caño Guaritico, rio Orinoco basin (7°33'N 69°39'W). FMNH 105276 (1 sk, 193.0 mm), Venezuela, Caño Anabata, tributary of rio Orinoco (8°37'20"N 61°47'33"W). *Ossancora asterophysa**. MZUSP 5646 (1 alc, 95.4 mm), Pará, Oriximiná, Lago Paru. MZUSP 7543 (2 alc, 50.2-73.5 mm, 1 cs, 77.3 mm), Amazonas, Urucará, rio Amazonas. MZUSP 7838 (1 sk, 65.3 mm), Pará, Faro Nhamundá, Paranã do Jacaré. MZUSP 56699 (1 alc, 85.7 mm), Pará, rio Trombetas (1°47'30"S 55°51'27"W). MZUSP 84665 (1 alc, 85.7 mm), Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé, tributary of rio Madeira (15°1'17"S 59°57'W). *Ossancora eigenmanni**. MZUSP 38176 (2 alc, 85.5-86.2 mm), Mato Grosso, Corumbá, rio Miranda, tributary of rio Paraguay (19°41'S 56°58'W). MZUSP 44423 (1 alc, 62.0 mm), Mato Grosso, Cáceres, rio Paraguay (16°4'S 57°41'W). MZUSP 95024 (2 alc, 38.3-65.3 mm, 3 cs, 35.1-65.6 mm), Mato Grosso, Barão de Melgaço, rio Mutum, rio Paraguay basin (16°19'30"S 55°49'59"W). *Ossancora fimbriata**. MZUSP 55833 (4 alc, 45.0-62.2 mm, 1 cs, 46.9 mm), Amazonas, rio Jutáí (2°54'25"S 67°0'12"W). MZUSP 56703 (1 cs, 59.0 mm), Amazonas, rio Jutáí (2°57'6"S 67°0'29"W). *Ossancora punctata**. MZUSP 7839 (1 alc, 72.6 mm, 1 cs, 61.6 mm), Pará, Faro Nhamundá, Paranã do Jacaré. MZUSP 7540 (1 cs, 61.7 mm), Amazonas, Urucará, rio Uatumã. MZUSP 26265 (1 alc, 34.2 mm), Perú, Pucallpa, rio Ucayali. MZUSP 41096 (1 alc, 59.3 mm), Mato Grosso do Sul, Corumbá, rio Miranda (20°14'S 56°22'W). MZUSP 95000 (1 alc, 65.8 mm), Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé, tributary of rio Madeira (15°1'37"S 59°49'9"W). NUP 3542 (1 alc, 65.4 mm), Mato Grosso, Santo Antônio do Leverger, rio Cuiabá, tributary of rio Paraguay (15°58'27"S 55°56'27"W). *Oxydoras niger**. ANSP 179438 (3 sk, unmeasured), Perú, Loreto, Iquitos. MZUSP 9079 (1 alc, 550.0 mm), Amazonas, Manaus. MZUSP 13366 (1 alc, 315.0 mm), Pará, rio Tapajós. MZUSP 14019 (1 alc, 420.0 mm), Rondônia, rio Machado, rio Madeira basin. MZUSP 43466 (1 alc, 109.5 mm), Pará, Baião, rio Tocantins (2°50'S 49°40'W). MZUSP 56162 (1 alc, 138 mm), Amazonas, rio Solimões (2°35'22"S 65°30'18"W). MZUSP 57320 (1 cs, 70.0 mm), Amazonas, rio Purus (3°44'30"S 61°26'48"W). MZUSP 91654 (1 sk, 550.0 mm), Goiás, Luís Alves, rio Verde, tributary of rio Araguaia (13°9'28"S 50°30'22"W). MZUSP 91658 (1 sk, 313.0 mm), Amazonas, Manaus, Porto Ceasa. *Oxydoras kneri**. MZUSP 14847 (1 alc, 393.0 mm), Mato Grosso, rio Paraguay at Ilha de Taiamã. *Oxydoras sifontesi**. MZUSP 105824 (1 sk, 413.0 mm), Venezuela, Amazonas, Puerto Ayacucho. INHS 33986 (1 alc, 187 mm), Venezuela, rio Orinoco (8°6'0"N 63°45'50"W). *Platydoras armatulus**. ANSP 149463 (1 alc, 119.9 mm), Venezuela, Delata Amacuro, rio Orinoco. ANSP 163478 (1 alc, 111.7 mm), Venezuela, Guarico, rio Portuguesa, rio Orinoco basin. ANSP 178748 (1 sk, unmeasured), Guiana, Rupununi River, tributary of Essequibo River. MZUSP 5645 (1 alc, 200.0 mm), Pará, Oriximiná, Lago Paru (1°52'S 55°50'W). Pará, rio Trombetas. MZUSP 40577 (1 cs, 87.0 mm), Goiás, Iaciara, rio Paranã, rio Tocantins basin (14°6'S 46°38'W). MZUSP 86217 (1 cs, 52.5 mm), Mato Grosso, Cocalinho, Corixo da Saudade, rio Araguaia basin (14°17'20"S 51°9'12"W). MZUSP 91686 (1 sk, 151.7 mm), Goiás, Minaçu, rio Tocantins. MZUSP 94088 (1 alc, 144.0 mm), Mato Grosso, Gaúcha do Norte, rio Culuene, tribu-

tary of rio Xingu (13°30'53"S 53°5'40"W). MZUSP 105041 (1 sk, 123.8 mm), no data. *Platydoras brachylecis*. MZUSP 5122 (1 cs, 108 mm), Piauí, rio Parnaíba. MZUSP 110621 (1 sk, 223.0 mm SL), Pará, Altamira, rio Xingu (3°49'40"S 52°41'31"W). *Platydoras* sp.* MPEG 6713 (1 cs, 107.0 mm), Pará, Altamira, rio Xingu. *Pterodoras granulatus**. ANSP 178799 (2 sk, unmeasured), Argentina, Buenos Aires, río de La Plata (34°53'S 58°9'W). ANSP 179166 (1 sk, unmeasured), Amazonas, rio Solimões. MZUSP 5681 (1 cs, 203 mm), Pará, Oriximiná, rio Trombetas (1°52'S 55°50'W). MZUSP 38177 (1 sk, 220 mm), Mato Grosso, Barão de Melgaço, rio Cuiabá (16°11'S 55°57'W). MZUSP 82343 (1 alc, 435.0 mm), no data. MZUSP 82995 (1 cs, 60.5 mm), Amazonas, rio Amazonas. MZUSP 83317 (1 alc, 143.3 mm), Amazonas, rio Amazonas (3°13'47"S 58°32'51"). MZUSP 89624 (2 sk, 208.0-262.0 mm), Mato Grosso do Sul, rio Cuiabá. MZUSP 91441 (1 alc, 330.0 mm), Amazonas, Nova Olinda do Norte, rio Madeira. MZUSP 91655 (8 sk, 260.0-410.0 mm), Goiás, Minaçu, rio Tocantins at Serra da Mesa. *Pterodoras rivasi**. ANSP 177895 (1 alc, 336.1 mm), Colombia, Lago Mozambique, rio Meta, rio Orinoco basin. MZUSP 88609 (1 alc, 82.2 mm), Venezuela, Bolivar, rio Guariquito, rio Orinoco basin (7°39'36"N 66°20'0"W). MZUSP 105825 (1 sk, 350.0 mm), Venezuela, Amazonas, Puerto Ayacucho, rio Orinoco (5°40'S 67°38'W). MZUSP 105830 (2 sk, 114.0-147.0 mm), Venezuela, Bolivar, Caicara del Orinoco, rio Orinoco (7°38'45"N 66°10'46"W). *Rhinodoras boelkhei**. MZUSP 56895 (1 cs, 31.0 mm), Amazonas, rio Solimões (3°35'S 61°5'W). MZUSP 86812 (1 alc, 95.0 mm), Amazonas, rio Solimões (3°36'16"S 61°21'12"W). MZUSP 86814 (1 alc, 41.0 mm, 1 cs, 54.0 mm), Amazonas rio Solimões (3°26'22"S 61°20'14"W). *Rhinodoras* cf. *boelkhei*. INPA 508 (1 cs, 69.0 mm), Pará, Tucuruí, rio Tocantins (3°42'S 39°42'W). INPA 22056 (1, 36.9 mm), Pará, Tucuruí, rio Tocantins (3°42'S 39°42'W). *Rhinodoras dorbignyi**. ANSP 179535 (1 alc, 194 mm), Rio Grande do Sul, São Borja, rio Uruguai (28°38'S 56°4'W). MZUSP 9381 (1 cs, 94.0 mm), São Paulo, rio Paraná (20°43'S 51°37'W). MZUSP 27724 (1 alc, 207.7 mm), Mato Grosso do Sul, Coxim, rio Taquari, tributary of rio Paraguay (18°30'S 56°20'W). MZUSP 40109 (1 sk, 196.0 mm), Rio Grande do Sul, São Borja, rio Uruguai (28°38'S 56°4'W). MZUSP 56750 (1 alc, 200.0 mm, 1 cs, 115.4 mm), Mato Grosso, Nobres, rio Cuiabazinho, rio Paraguay basin (14°44'S 56°20'W). MZUSP 61456 (2 cs, 70.4-121.9 mm), São Paulo, Pirassununga, rio Mogi Guaçu, upper rio Paraná basin (21°55'S 47°23'W). MZUSP 62683 (1 alc, 185.6 mm, 8 cs, 45.3-89.9 mm), São Paulo, Ilha Solteira, rio Paraná (20°15'S 51°7'W). MZUSP 78461 (1 alc, 168.0 mm), Rio Grande do Sul, rio Uruguai. *Rhinodoras gallagheri*. AMNH 58349 (1 cs, 52.4 mm), Venezuela, rio Apure, tributary of rio Orinoco. *Rhinodoras thomersoni**. MHNLS 0109 (1 cs, 60.9 mm), Venezuela, Lago Maracaibo. *Rhynchodoras castilloi**. ANSP 181181 (1 alc, 58.3 mm), Venezuela, Portuguesa, Barinas, Caño Bravo, rio Orinoco basin (8°0'N 67°59'W). MZUSP 88604 (2 alc, 39.1-60.6 mm, 1 cs, 45.5 mm), Venezuela, Portuguesa, Barinas, Caño Bravo, rio Orinoco basin (8°0'N 67°59'W). *Rhynchodoras woodsi**. ANSP 181042 (1 alc, 72.5 mm, 1 cs, 88.4 mm), Perú, rio Amazonas. MZUSP 56859 (1 cs, 26.0 mm), Amazonas, rio Solimões (3°35'S 61°7'W). MZUSP 56872 (3 alc, 22.5-37.3 mm, 1 cs, 23.1 mm), Amazonas, rio Amazonas (3°20'S 58°36'W). MZUSP 57316 (42.6 mm), Amazonas, rio Amazonas (3°20'28"S 58°36'25"W). MZUSP 57992 (2 alc, 35.0-45.0 mm), Amazonas, rio Amazonas (3°20'S 58°35'W). MZUSP 86815 (1 cs, 48.2 mm), Amazonas, rio Amazonas (3°20'9"S 58°36'11"W). ROM 62601 (1 alc, 44.2 mm), Guiana, Essequibo river (4°40'S 58°40'W). *Rhynchodoras xingui*. SMF 5282 (1 alc, 44.5 mm), upper rio Xingu. INPA 26540 (2 alc, 62.8-64.2 mm), Pará, Tucuruí, rio Tocantins (3°42'S 49°42'W). *Scorpiodoras heckelii**. MZUSP 84743 (2 alc, 138.0-145.0 mm), Amazonas, Santa Isabel do rio Negro, rio Negro. MZUSP 7941 (2 cs, 36.6-76.6 mm), Amazonas, Terra Santa, rio Jamarí, rio Amazonas basin. MZUSP 8493 (1 sk, 114.4 mm), Pará, Santarém, rio Mapiri (2°26'S 54°44'W). MZUSP 84203 (1 alc, 148.0 mm), Pará, Lago Jacupá, rio Amazonas basin. *Tenellus leporhinus**. MZUSP 96596 (3 cs, 42.0-43.0 mm), Mato Grosso, Peixoto de Azevedo, rio Teles Pires, tributary of rio Tapajós (10°13'14"S 54°58'2"W). MZUSP 95617 (2 alc, 89.0-138.1 mm), Mato Grosso, Paranaíta, rio Teles Pires, tributary of rio Tapajós (9°27'7"S 56°30'46"W). MZUSP 88612 (1 alc, 75.3 mm, 1 cs, 73.8 mm), Venezuela, Amazonas, rio Ventuari, tributary of rio Orinoco (4°45'0"S 66°21'13"W). MZUSP 105832 (1 sk, 97.2 mm), Venezuela, Bolivar, rio Caura, rio Orinoco basin (7°2'37"S 64°57'41"W). *Tenellus ternetzi**. ANSP 179587 (2 sk, unmeasured), Amazonas, rio Negro (1°42'4"S 61°29'1"W). MZUSP 56694 (1 sk, 76.5 mm), Pará, rio Trombetas (1°49'27"S 55°48'58"W). MZUSP 57273 (1 alc, 67.8 mm, 2 cs, 51.6-56.7 mm), Pará, Monte Dourado, rio Jari (0°43'7"S 52°29'43"W). MZUSP 76422 (2 alc, 98.4-117.2 mm, 1 cs, 111.2 mm), Pará, Santarém, rio Tapajós (2°23'S 54°46'W). MZUSP 57682 (1 alc, 110.9 mm), Pará, rio Tapajós (2°40'41"S 55°8'48"W). MZUSP 103246 (5 sk, 63.4-91.4 mm), Pará, Monte Dourado, rio Jari (0°41'28"S 52°30'44"W). MZUSP 105833 (1 sk, 87.6 mm), Venezuela, Bolivar, rio Caura, tributary of rio Orinoco (7°2'37"N 64°57'41"W). MZUSP 110598 (1 sk, 95.0 mm SL), Pará, Porto de Moz, 1°46'9"S 52°13'55"W). *Tenellus trimaculatus**. MZUSP 29030 (1 cs, 51.3-56.0 mm), Rondônia, rio Madeira (8°3'S 62°53'W). MZUSP 52314 (1 alc, 83.8-84.4 mm), Mato Grosso, Araguaiana, rio Araguaia. MZUSP 53834 (1 alc, 75.6 mm), Mato Grosso, Araguaiana, rio Araguaia. MZUSP 56706 (1 alc, 46.9 mm), Amazonas, rio Jutaf (2°56'41"S 67°0'52"W). MZUSP 57272 (1 cs, 70.1 mm), Amazonas, rio Solimões (3°52'7"S 61°39'46"W). MZUSP 62656 (1 alc, 72.8 mm), Amazonas, Fonte Boa, rio Solimões (2°31'S 66°6'W). MZUSP 92206 (1 alc, 93.9 mm), Amazonas, rio Tiquié, rio Negro basin (0°8'40"N 69°12'48"W). *Trachydoras brevis**. MZUSP 29075 (1 cs, 33.0 mm), Rondônia, rio Machado, rio Madeira basin. MZUSP 55840 (1 cs, 43.9 mm), Amazonas, rio Jutaf (2°53'26"S 66°57'55"W). MZUSP 56713 (1 alc, 66.1 mm), Amazonas, rio Jutaf (2°57'22"S 67°0'28"W). MZUSP 93094 (1 alc, 93.7 mm), Amazonas, Igarapé Castanha, rio Negro basin (0°11'N 69°35'W). MZUSP 93374 (1 alc, 46.5 mm), Amazonas, rio Tiquié, rio Negro basin (0°8'40"N 69°12'41"W). MZUSP 103087 (5 sk, 70.0-74.0 mm), Pará, Monte Dourado, rio Jari (0°41'28"S 52°30'44"W). *Trachydoras microstomus**. MZUSP 56702 (1 cs, 49.8 mm), Amazonas, rio Jutaf (2°51'6"S 66°58'7"W). MZUSP 57331 (1 cs, 57.5 mm), Pará, rio Amazonas (1°27'52"S 52°3'13"W). MZUSP 57703 (3 alc, 43.6-76.6 mm), Amazonas, Manaus, rio Negro (3°6'8"S 60°10'2"W). MZUSP 105831 (1 sk, 50.0 mm), Venezuela, Bolivar, rio Caura, tributary of rio Orinoco (7°2'37"N 64°37'41"W). *Trachydoras nattereri**. MZUSP 7837 (2 cs, 55.4-58.5 mm), Pará, Faro Nhamundá, Paraná do Jacaré, rio Amazonas basin. MZUSP 55854 (1 alc, 48.7 mm), Roraima, Caracará, rio Negro (1°18'51"S 61°55'21"W). MZUSP 31703 (1 alc, 99.3 mm), Roraima, Caracará, rio Negro (1°18'51"S 61°55'21"W). *Trachydoras paraguayensis**. ANSP 178699 (1 alc, 79.2 mm), Mato Grosso, Cácares, rio Paraguay. MZUSP 21109 (1 alc, 80.2 mm), Paraná, Bandeiras, rio Paraná (24°10'S 54°19'W). MZUSP 27801 (1 alc, 84 mm), Bolívia, Santa Cruz, Laguna San José, rio Madeira basin. MZUSP 29047 (1 alc, 115.1 mm), Rondônia, Calama, rio Madeira (8°3'S 62°53'W). MZUSP 40081 (1 alc, 101.0 mm), Mato Grosso do Sul, Aquidauana, rio Aquidauana, rio Paraguay basin (20°28'S 55°48'W). MZUSP 48315 (1 cs, 54.3 mm), Mato Grosso do Sul, Coxim, rio Paraguay (18°30'S 54°45'W). *Trachydoras*

*steindachneri**. ANSP 179171 (1 sk, unmeasured), Amazonas, rio Solimões (2°54'15"S 67°47'53"W). MZUSP 7611 (1 cs, 75.8 mm, 1 sk, 63.6 mm), Amazonas, Uruará, Paraná do Mocambo, rio Amazonas basin (2°37'S 57°43'W). MZUSP 7836 (1 cs, 70.0 mm), Pará, Faro Nhamundá, Paraná do Jacaré. MZUSP 62696 (3 alc, 38.7-77.0 mm), Amazonas, Fonte Boa, rio Solimões (2°31'S 66°6'W). MZUSP 74867 (1 alc, 75.7 mm), Amazonas, rio Solimões. *Wertheimeria maculata**. MCZ 91317 (1 cs, 65.0 mm), Minas Gerais, Itira, rio Jequitinhonha (16°46'S 42°2'W). MZUSP 40229 (10 alc, 46.7-145.0 mm, 3 cs, 25.0-112.0 mm), Minas Gerais, Itira, rio Jequitinhonha (16°47'S 42°3'W). MZUSP 88614 (1 sk, 124.0 mm), Minas Gerais, rio Jequitinhonha. MZUSP 93659 (2 sk, 195.0-217.0 mm), Minas Gerais, Araçuaí, rio Jequitinhonha. MZUSP 93658 (1 alc, 168.0 mm, 1 sk, 192.0 mm), Minas Gerais, Itira, rio Jequitinhonha (16°45'44"S 42°0'37"W). **Erethistidae**. *Conta conta**. USNM 44759 (1 cs, 52.0 mm), Myanmar, Meetan. **Heptapteridae**. *Rhamdia quelen*. MZUSP 36505 (1 alc, 170.0 mm), São Paulo, rio Ribeira de Iguape. MZUSP 79083 (1 sk, 233.0 mm), Paraná, Represa de Vossoroca, upper rio Paraná basin. MZUSP 102800 (1 sk, 160.0 mm), São Paulo, Biritiba Mirim, rio Tietê, upper rio Paraná basin (23°34'5"S 46°0'38"W). *Goeldiella eques**. MZUSP 33190 (1 cs, 103.5 mm), Amazonas, rio Negro. MZUSP 45907 (1 cs, 79.0 mm), Pará, rio Trombetas. **Ictaluridae**. *Ictalurus punctatus**. MZUSP 62602 (1 cs, unmeasured), no data. MZUSP 103256 (1 cs, 50.0 mm, 1 sk, 155.0 mm), no data. **Malapteruridae**. *Malapterurus beninensis**. MZUSP 84464 (2 alc, 64.2-69.6 mm, 2 cs, 30.6-64.2 mm), Benin, Quémé, Azowliissé, Quémé river (1°40'29"N 2°29'15"E). **Mochokidae**. *Chiloglanis disneyi**. USNM 303505 (3 cs, 50.5-53.7 mm), Camaroon, Akpa-Yafe basin, SW Korup. *Chiloglanis paratus*. MZUSP 65810 (3 alc, 60.5-61.3 mm), South Africa, Mabunga Rapids. *Chiloglanis polypogon*. USNM 304264 (4 cs, 25.3-28.9 mm), Camaroon, Munaya River. *Euchilichthys guentheri*. AMNH 6507 (2 alc, 183.5-221.0 mm), Congo, Orientale Province, Stanleyville. *Microsynodontis christyi*. ZSM 22895 (1 cs, 29.8 mm), Congo, Stanley-Pool, Leopoldville. *Microsynodontis batesii*. SU 47485 (2 alc, 51.4-53.8 mm), Camaroon, Congo river. *Mochokiella paynei**. AMNH 58398 (1 alc, 36.7 mm, 1 cs, 38.0 mm), Aquarium store. *Mochokus brevis*. CAS 211322 (1 alc, 21.7 mm), Egito. *Mochokus niloticus**. USNM 229657 (1 cs, 28.8 mm), Nigeria. *Synodontis batensoda**. AMNH 230635 (2 alc, 54.1-62.8 mm), no data. MNHN 1959-525 (1 cs, 48.4 mm), Tchad, Kousséri, Lake Tchad. *Synodontis membranaceus*. USNM 313407 (1 cs, 50.3 mm), Gana, White Volta. *Synodontis nigriventris*. MZUSP 59326 (1 cs, 39.8 mm), no data. *Synodontis schall**. ANSP 78057 (1 sk, unmeasured), Egito, Sudan, Khartoum. MZUSP 84468 (2 alc, 63.1-76.0 mm, 8 cs, 43.0-80.0 mm), Benin, Quémé, Azwliissé, Quémé river (1°40'29"S 2°29'15"E). *Synodontis sorax*. ANSP 78053 (1 sk, unmeasured), Egito, Sudan, Khartoum. *Synodontis zambezensis*. MZUSP 62621 (2 cs, 45.7-52.7 mm), South Africa, KwaZulu, Natal Phongola, Ngodo pan. **Nematogenyidae**. *Nematogenys inermis**. MZUSP 75256 (1 sk, 210 mm), Chile, Águas de La Gloria, Estero Águas de La Gloria (36°50'30"S 72°56'4"W). **Pangasiidae**. *Pangasius pangasius**. MZUSP 62587 (1 alc, 130 mm), Myanmar, Thanlyin. *Pangasius sutchi*. MZUSP 102779 (2 cs, 56.4-61.0 mm), no data. *Pangasius* sp. MZUSP 60075 (1 cs, 45.1 mm), no data. **Pimelodidae**. *Steindachneridion scriptum*. MZUSP 90279 (6 cs, 19.0-23.0 mm), Santa Catarina, rio Uruguai. *Steindachneridion parahybae**. MZUSP 100672 (1 sk, 329.0 mm, 4 cs, 74.8-93.7 mm), São Paulo, rio Paraíba do Sul. **Pseudopimelodidae**. *Pseudopimelodus bufonius**. MZUSP 94855 (1 alc, 168.0 mm, 1 cs, 68.0 mm, 2 sk, 170.0 mm), Mato Grosso Paranatinga, rio Culuene (13°49'S 53°15'W). *Lophiosilurus*

alexandri. MZUSP 73817 (1 alc, 127.8 mm), Minas Gerais, Presidente Jucelino, rio Cipó (18°41'4"S 43°59'18"W). **Siluridae**. *Wallago attu**. BMNH 1889.9.26.48-50 (1 cs, 175.0 mm), Deola, Rajputana. **Sisoridae**. *Bagarius bagarius**. USNM 186793 (1 cs, 98.5 mm), Thailand, Ubon.

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Table 1. Phylogenetic character matrix. Missing data or characters inapplicable to particular taxa are indicated by “?”; polymorphic characters indicated by A for (0,1), B for (1,2), and C for (2,3).

OUT-GROUP

Amphiliidae

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00000000000010000?10000100?100010001100010000000000000000
00020300112

Ariidae(*Galeichthys*)

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0010000000100120010000000100?10000?0011000000001000000000000
00020100011

Ariidae(*Genidens*)

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000100000000000001000?001?120010000130002200000000000000010
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00020210011

Aspredinidae

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022?00000011000111000?000?0?02000111001200000000001101?010
000000000100000010000000100?11010?00100000?000000000000000
00010300122

Claroteidae

000000000000000020?00010?0000000000?0?00000000000100000001
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011100000000000001000?000?0?01000001000110000000000000010
000001000000001001000000100?10000?0011000000001000000000000
00010110021

Diplomystidae

0000001100000000????00?0000000000?0?00000000000000000000
100000000000011000000000?0??000000000000000000000000200000?
????00000000000000000000000000001000010000000000A1100000000100
00010000000000000000?000?0?01000000002100000000000000010
0000000000000000?00000100?0000?000000000001000000000000
0000010000

Erethistidae

000000110000000020?0001110000000000?0?00000000000100000021
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0111000000011000111000?000?0?020001110012000000100011001010
00000100000000000?000000100?110010001100010000100000000000
00020110122

Heptapteridae

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011100000000000011000?000?0?01000001000220000000000000010
00000000000000001000000100?10000?0011000000101000000000000

00020110011

Ictaluridae

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00000110000

Malapteruridae

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????????001?00000?1000000??10000?001000000000000000000000
20020200011

Mochokidae(*Chiloglanis*)

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011100000000000011000?00201100201?01200010000001??100101110
000000000000012000?10000100?100010010100010000100000000000
00020110022

Mochokidae(*Mochokiella*)

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Mochokidae(*Mochokus*)

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Mochokidae(*Synodontis*)

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Nematogenyidae

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Pangasiidae

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00000110000

Pimelodidae

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Pseudopimelodidae

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Siluridae

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000?0110000

Sisoridae

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00020110022

INGROUP (Auchenipteridae)

Ageneiosus atronasus

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Ageneiosus inermis

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Asterophysus batrachus

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Auchenipterichthys thoracatus

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Auchenipterus nuchalis

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Centromochlus heckelii

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Entomocorus radiosus

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Epapterus dispilurus

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Gelanoglanis cf. stroudi

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Glanidium melanopterum

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Liosomadoras oncinus

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Pseudauchenipterus affinis

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Pseudepapterus cucuhyensi

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00021110012

Pseudotatia parva

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Spinipterus acsi

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Tatia aulopygia

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Tetranematchthys quadrifilis

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10020121012

Tocantinsia piresi

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Trachelyichthys decaradiatus

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001001000010000001000000200?1000100311000000103000000000001
10020121012

Trachelyopterichthys taeniatus

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Trachelyopterus coriaceus

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Trachelyopterus galeatus

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Trachycorystes trachycorystes

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INGROUP (Doradidae)

Acanthodoras cataphractus

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Agamyxis albomaculatus

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Anadoras grypus

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Anduzedoras oxyrhynchus

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Astrodoras asterifrons

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Centrochir crocodili

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Centrodoras brachiatus

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Centrodoras hasemani

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Doraops zuloagai

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Doras carinatus

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Doras higuchii

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Doras phylzakion

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Franciscodoras marmoratus

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Hassar affinis

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Hassar gabiru

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Hassar orestis

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Hemidoras morei

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Hemidoras morrisi

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Hemidoras stenopeltis

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Hemidoras stubelii

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Kalyptodoras bahiensis

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Leptodoras juruensis

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Leptodoras marki

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Leptodoras oyakawai

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Leptodoras praelongus

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Lithodoros dorsalis

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Megalodoras guayoensis

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Megalodoras uranoscopus

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Nemadoras elongatus

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Nemadoras hemipeltis

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Nemadoras humeralis

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Orinocodoras eigenmanni

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Ossancora asterophysa

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Ossancora eigenmanni

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Ossancora fimbriata

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Ossancora punctata

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Oxydoras kneri

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Oxydoras niger

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Platydoras armatulus

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Platydoras sp.

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Pterodoras granulosus

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Pterodoras rivasi

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Rhinodoras boehlkei

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Rhinodoras dorbignyi

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Rhinodoras thomersoni

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Rhynchodoras castilloi

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Rhynchodoras woodsi

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Scorpiodoras heckelii

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Tenellus leporhinus

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Tenellus ternetzi

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Tenellus trimaculatus

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Trachydoras brevis

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Trachydoras microstomus

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Trachydoras nattereri

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Trachydoras paraguayensis

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Trachydoras steindachneri

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Wertheimeria maculata

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Appendix. List of character state changes (*i.e.*, synapomorphies, homoplasies, autapomorphies) of the consensus cladogram. Asterisks indicate exclusive characters (*i.e.*, synapomorphies and autapomorphies). Number of nodes according to Figs. 67-70.

Outgroup terminal taxa.

- Amphiliidae: #23: 0>1, #58: 1>0, #85: 0>2, #88: 0>1, #89: 0>1, #113: 3>0, #162: 1>2, #171: 0>1, #175: 0>1, #176: 0>1, #220: 0>1, #253: 0>1, #273: 0>1, #282: 0>1, #305: 2>3, #308: 0>1, #310: 1>2.
- Ariidae (*Galeichthys*): #80: 1>0; #197: 0>1, #245: 1>0, #306: 1>0.
- Ariidae (*Genidens*): #5: 0>2, #58: 0>1, #74: 1>0, #85: 1>2, #142: 0>1, #205: 0>1, #207: 0>1, #216: 0>1, #217: 1>3, #305: 1>2.
- Aspredinidae: #4: 0>1, #56: 0>1, #58: 2>0, #89: 1>0; #128: 0>2, #160: 0>1, #164: 0>1, #181: 1>2, #182: 1>2, #235: 0>1, #250: 0>1, #272: 0>1, #287: 1>0, #303: 2>1, #305: 1>3, #306: 1>0.
- Claroteidae: #20: 1>0; #22: 0>1, #40: 1>0; #102: 3>2, #114: 1>0; #154: 0>1, #164: 0>1, #221: 2>1, #222: 2>1; #303: 2>1, #309: 1>2.
- Erethistidae: #162: 1>2, #171: 1>0, #245: 0>1, #273: 0>1, #278: 0>1.
- Heptapteridae: #59: 1>0, #102: 3>2, #164: 0>1, #285: 0>1.
- Ictaluridae: #51: 1>0, #102: 1>0.
- Malapteruridae: #6: 0>2, #37: 0>1, #51: 1>0, #58: 1>2, #60: 1>0, #69: 0>1, #73: 0>1, #113: 2>3, #136: 0>1, #142: 0>1, #145: 0>1, #205: 0>2, #207: 0>1, #222: 2>1, #251: 0>1, #265: 1>0, #278: 1>0, #300: 0>2.
- Mochokidae (*Mochokiella*): #66: 0>1, #158: 0>1, #245: 0>1.
- Mochokidae (*Mochokus*): #56: 0>1, #58: 2>1, #162: 0>1, #221: 1>0, #242: 0>1, #254: 1>0, #305: 2>3.
- Mochokidae (*Chiloglanis*): #17: 1>0, #23: 0>1, #102: 3>2, #111:

0>1, #152: 0>1, #171: 0>1, #211: 1>2, #216: 0>1, #228: 0>1, #231: 0>1, #237: 0>1, #253: 0>1, #254: 1>2, #257: 1>0, #259: 0>1, #265: 2>1, #282: 0>1.

Mochokidae (*Synodontis*): #66: 0>1, #107: 0>1, #158: 0>1, #177: 0>1, #222: 0>1, #224: 0>1, #245: 0>1, #274: 0>1, #278: 1>0.

Nematogenyidae: #4: 0>1, #60: 1>0, #88: 0>1, #89: 0>1, #138: 0>1, #177: 1>2, #192: 0>1, #227: 0>1, #235: 0>1, #251: 0>1, #265: 1>0, #305: 1>2, #306: 1>0.

Pangasiidae: #16: 2>1, #37: 0>1, #59: 1>0, #75: 0>1, #85: 0>1, #114: 0>1, #166: 0>1, #167: 1>0, #197: 1>0, #198: 1>0, #205: 0>2, #207: 0>1, #222: 2>1, #245: 0>1, #254: 0>1.

Pimelodidae: #217: 1>2, #309: 1>0.

Pseudopimelodidae: #59: 1>0, #113: 2>3, #154: 0>1, #166: 0>1, #242: 0>1, #245: 0>1, #287: 1>0, #305: 1>2.

Siluridae: #4: 0>1, #22: 1>0, #88: 0>1, #102: 1>2, #113: 2>3, #131: 0>1, #138: 0>1, #154: 1>0, #157: 1>0, #168: 1>0, #181: 1>0, #182: 1>0, #185: 0>1, #186: 0>1, #221: 2>1, #227: 0>1, #235: 0>1, #257: 1>0, #265: 1>0, #269: 1>0.

Sisoridae: #85: 0>1, #88: 1>0, #102: 3>1, #126: 0>1, #131: 0>1, #166: 0>1, #190: 0>1, #191: 1>0, #192: 1>0, #216: 1>0, #221: 2>1, #277: 1>0, #308: 1>0.

Ingroup terminal taxa (Auchenipteridae).

Ageiosus atronatus: #57: 1>0, #177: 2>1, #209: 0>1, #287: 3>2, #300: 1>0.

Ageiosus inermis: #33: 0>1, #34: 0>1*, #206: 0>2*, #222: 1>2, #243: 0>1*, #248: 1>2, #263: 0>1*.

Asterophysus batrachus: #41: 0>1, #42: 0>1, #44: 1>0, #45: 0>1, #71: 0>1*, #113: 2>3, #116: 0>1, #139: 0>1, #159: 1>0, #162: 1>2, #187: 0>1*, #190: 1>0, #199: 0>2*, #221: 1>2, #249: 0>2, #276: 1>3, #308: 0>1.

Auchenipterichthys thoracatus: #37: 0>1, #237: 1>0, #239: 1>0, #270: 0>1, #272: 0>1.

Auchenipterus nuchalis: #44: 1>2, #57: 0>2, #78: 0>1, #237: 1>0, #295: 0>1*.

Centromochlus heckelii: #35: 0>1, #59: 1>0, #78: 0>1, #98: 0>1, #115: 0>1, #163: 0>1, #164: 0>1, #206: 0>1, #209: 0>1, #217: 3>4, #238: 1>2*, #245: 0>1, #258: 0>1, #261: 0>1*, #265: 1>2, #272: 0>1, #290: 1>0, #293: 0>1*.

Entomocorus radiosus: #27: 0>1*, #70: 0>1*, #87: 1>0, #92: 1>0, #249: 0>2, #252: 0>1*, #257: 0>1, #276: 1>0, #279: 0>1*, #283: 1>0, #287: 3>2, #308: 0>1.

Epapterus dispilurus: #4: 0>1, #49: 0>1*, #76: 1>0, #237: 1>3*, #239: 0>1.

Gelanoglanis cf. stroudi: #16: 2>1, #52: 1>0, #72: 0>1*, #112: 0>1*, #117: 1>0, #159: 1>0, #181: 1>2, #182: 1>2, #211: 0>1, #217: 3>1, #222: 1>0, #228: 0>1, #231: 0>1, #242: 1>0, #257: 1>0, #283: 0>1.

Glanidium melanopterum: #63: 0>1, #191: 1>0, #221: 1>2, #242, 1>0, #287: 0>1.

Liosomadoras oncinus: #54: 0>1, #57: 0>1, #85: 2>1, #106: 0>1, #167: 1>0, #239: 0>1, #241: 0>1, #267: 0>1.

Pseudauchenipterus affinis: #20: 0>1, #29: 0>1*, #242: 1>0, #257: 1>0, #276: 1>2, #287: 1>2.

Pseudepapterus cucuhyensis: #67: 0>1*, #69: 1>0, #127: 1>0, #186: 2>1, #216: 0>1, #217: 3>2, #248: 1>2, #269: 1>2.

Pseudotatia parva: #216: 1>0, #245: 1>0.

Tatia aulopygia: #94: 0>1, #131: 1>0, #162: 1>2, #294: 0>1*, #298: 0>1*.

Tetranematchichthys quadrifilis: #37: 0>1, #184: 0>1, #248: 1>3, #262: 0>1, #306: 1>2, #307: 0>1.

Tocantinsia piresi: #39: 0>1, #57: 0>1, #170: 0>1, #184: 0>1, #217:

3>4, #221: 1>2, #242: 1>0, #258: 0>1.

Trachelyichthys decaradiatus: #4: 0>1, #56: 0>1, #237: 1>2, #287: 2>3, #306: 1>2.

Trachelyopterichthys taeniatus: #4: 0>1, #222: 1>2, #237: 1>2, #260: 0>1, #287: 2>3.

Trachelyopterus coriaceus: #4: 0>1, #20: 0>1, #35: 1>0, #87: 0>1, #94: 1>0, #257: 1>0, #272: 0>1.

Trachelyopterus galeatus: #134: 0>1, #265: 2>1.

Trachycorystes trachycorystes: #39: 0>1, #85: 2>1, #103: 0>1, #239: 1>0, #245: 1>0, #300: 1>0, #307: 1>0.

Ingroup terminal taxa (Doradidae).

Acanthodoras cataphractus: #177: 1>0, #237: 0>1, #274: 0>1, #283: 0>1, #300: 0>2, #309: 1>2.

Agamyxis albomaculatus: #39: 0>1, #268: 2>0, #280: 0>1*, #296: 0>1*, #297: 0>1*, #301: 0>1, #305: 1>2.

Anadoras grypus: #1: 0>1, #57: 0>1, #102: 3>2, #186: 0>1, #242: 1>0.

Anduzedoras oxyrhynchus: #123: 1>2, #202: 0>1*.

Astrodoras asterifrons: #61: 1>0, #99: 1>0, #270: 0>1, #300: 0>1.

Centrochir crocodili: no autapomorphies.

Centrodoras brachiatus: no autapomorphies.

Centrodoras hasemani: no autapomorphies.

Doraops zuloagai: #23: 1>0, #104: 1>0, #118: 2>1.

Doras carinatus: no autapomorphies.

Doras higuchii: no autapomorphies.

Doras phlyzakion: #39: 0>1.

Franciscodoras marmoratus: #301: 0>1.

Hassar affinis: no autapomorphies.

Hassar gabiru: no autapomorphies.

Hassar orestis: no autapomorphies.

Hemidoras morei: #32: 1>0.

Hemidoras morrisi: #274: 0>1.

Hemidoras stenopeltis: #128: 2>1.

Hemidoras stubelii: no autapomorphies.

Kalyptodoras bahiensis: #94: 0>1, #103: 0>1, #104: 0>1, #105: 0>1.

Leptodoras juruensis: #1: 1>0, #2: 1>0, #9: 0>1*, #23: 0>1, #30: 1>0, #78: 1>0, #123: 1>2, #181: 1>2, #211: 0>1, #221: 1>0, #222: 1>2, #226: 2>1, #245: 1>0, #249: 1>2.

Leptodoras marki: no autapomorphies.

Leptodoras oyakawai: #41: 1>0.

Leptodoras praelongus: #231: 0>1, #264: 1>0.

Lithodoras dorsalis: #175: 0>1.

Megalodoras guayoensis: no autapomorphies.

Megalodoras uranoscopus: no autapomorphies.

Nemadoras elongatus: no autapomorphies.

Nemadoras hemipeltis: #58: 1>0, #118: 2>1.

Nemadoras humeralis: #228: 0>1.

Orinocodoras eigenmanni: #0: 0>1, #1: 0-1, #103: 0>1.

Ossancora asterophysa: no autapomorphies.

Ossancora eigenmanni: no autapomorphies.

Ossancora fimbriata: #226: 0>1, #274: 0>1.

Ossancora punctata: #35: 0>1, #41: 1>0.

Oxydoras kneri: no autapomorphies.

Oxydoras niger: #218: 0>1*.

Platyodoras armatulus: #37: 0>1, #94: 0>1, #103: 0>1, #104: 0>1, #105: 0>1, #113: 2>0, #121: 0>1.

Platyodoras sp.: #137: 0>1.

Pterodoras granulatus: #37: 1>0, #39: 0>3.

Pterodoras rivasi: no autapomorphies.

Rhinodoras boehlkei: #37: 1>0.

Rhinodoras dorbignyi: no autapomorphies.
Rhinodoras thomersoni: #41: 1>0, #310: 1>2.
Rhynchodoras castilloi: no autapomorphies.
Rhynchodoras woodsi: no autapomorphies.
Scorpiodoras heckelii: #37: 0>1, #78: 0>1.
Tenellus leporhinus: #118: 2>1.
Tenellus ternetzi: no autapomorphies.
Tenellus trimaculatus: #283: 1>0.
Trachydoras brevis: no autapomorphies.
Trachydoras microstomus: no autapomorphies.
Trachydoras nattereri: no autapomorphies.
Trachydoras paraguayensis: #270: 0>1.
Trachydoras steindachneri: #54: 0>1, #106: 0>1.
Wertheimeria maculata: #119: 1>0*.

Nodes.

Node 1 (all taxa except Diplomystidae and Nematogenyidae):

#16: 1>2, #51: 0>1, #59: 0>1, #73: 1>0, #79: 0>1*, #102: 0>1, #147: 0>1*, #150: 0>1*, #162: 0>1, #178: 0>1*, #217: 0>1*, #222: 1>2, #257: 0>1, #269: 0>1.

Node 2 (Ictaluridae, Pangasiidae, Siluridae): #5: 0>2, #22: 0>1, #157: 0>1, #276: 0>2, #277: 1>0, #287: 1>2.

Node 3 (Pangasiidae, Siluridae): #74: 0>1, #177: 1>2, #217: 1>2, #276: 2>3, #287: 2>3.

Node 4 (all taxa except Diplomystidae, Ictaluridae, Nematogenyidae, Pangasiidae, Siluridae): #58: 0>2, #102: 1>2, #154: 1>0, #303: 0>2, #309: 0>1, #310: 0>1.

Node 5 (Amphiliidae, Malapteruridae): #62: 0>1, #138: 0>1, #152: 0>1, #164: 0>1, #227: 0>1, #232: 0>1, #233: 0>1, #235: 0>1, #257: 1>0, #259: 0>1, #287: 1>0, #305: 1>2, #306: 1>0.

Node 6 (Ariidae, Aspredinidae, Claroteidae, Doradoidea, Mochokidae, Heptapteridae, Pimelodidae, Pseudopimelodidae, Sisoroidea): #40: 0>1, #58: 1>2, #102: 2>3, #126: 0>1, #127: 0>1, #167: 1>0.

Node 7 (Ariidae, Claroteidae, Pimelodidae): #20: 0>1, #74: 0>1, #113: 2>3, #114: 0>1, #157: 0>1, #166: 0>1.

Node 8 (Claroteidae, Ariidae): #58: 2>0, #75: 0>1, #80: 0>1, #127: 1>0, #141: 0>1*, #145: 0>1, #151: 0>1*, #168: 1>0, #197: 1>0, #245: 0>1, #254: 0>1.

Node 9 (Ariidae): #6: 0>3, #7: 0>1, #85: 0>1, #126: 1>0, #162: 1>2, #177: 1>0, #181: 1>0, #182: 1>0, #242: 0>1, #250: 0>1, #253: 0>1, #254: 1>2.

Node 10 (Aspredinidae, Doradoidea, Mochokidae, Pseudopimelodidae, Sisoroidea): #40: 1>0, #60: 1>0, #168: 1>0, #171: 0>1, #208: 2>0*, #221: 2>1, #222: 2>0, #308: 0>1, #310: 1>2.

Node 11 (Aspredinidae, Doradoidea, Mochokidae, Sisoroidea): #6: 0>2, #52: 0>1, #80: 0>1, #88: 0>1, #89: 0>1, #126: 1>0, #127: 1>0, #155: 0>1*, #177: 1>0, #216: 0>1, #220: 0>1, #236: 0>1*, #309: 1>2.

Node 12 (Aspredinidae, Sisoroidea): #23: 0>1, #90: 0>1*, #91: 0>1*, #111: 0>1, #191: 0>1, #192: 0>1, #196: 0>1, #211: 1>2, #215: 0>1*, #221: 1>2, #232: 0>1, #233: 0>1, #270: 0>1, #278: 1>0.

Node 13 (Sisoridae, Erethistidae): #6: 2>1, #7: 0>1, #22: 0>1, #24: 0>1*, #52: 1>0, #167: 0>1, #168: 0>1, #176: 0>1, #228: 0>1, #257: 1>0, #282: 0>1.

Node 14 (Doradoidea, Mochokidae): #68: 0>1*, #85: 0>1, #169: 0>1*, #171: 1>0, #205: 0>2, #207: 0>1, #213: 0>1*, #217: 1>2, #229: 0>1*, #234: 0>1*, #265: 1>2, #273: 0>1, #308: 1>0.

Node 15 (Mochokidae): #17: 0>1, #60: 0>1, #113: 2>0, #138: 0>1, #139: 0>1, #162: 1>0, #176: 0>1, #208: 0>1*, #214: 0>1*, #216: 1>0, #220: 1>0, #254: 0>1, #276: 0>1.

Node 16 (mochokids *Chiloglanis*, *Synodontis*): #18: 0>1, #125: 0>2*, #129: 0>1*, #130: 0>1*, #140: 0>1*, #144: 0>1*, #277: 1>0.

Node 17 (mochokids *Mochokiella*, *Mochokus*): #52: 1>0, #230: 0>1*, #305: 1>2, #306: 1>0.

Node 18 (Doradoidea): #82: 0>1*, #83: 0>1*, #95: 0>1*, #154: 0>1, #168: 0>1, #177: 0>1, #203: 0>1*, #204: 0>1*, #205: 2>3, #210: 0>1*, #211: 1>0, #219: 0>1*, #222: 0>1, #242: 0>1, #250: 0>1, #309: 2>1.

Node 19 (Auchenipteridae): #5: 0>2, #13: 0>1*, #14: 0>1*, #43: 0>1*, #44: 0>1, #46: 0>1*, #50: 0>1*, #84: 0>1, #97: 0>1, #117: 0>1, #159: 0>1, #167: 0>1, #191: 0>1, #217: 1>3, #285: 0>1, #287: 1>0.

Node 20 (Centromochlinae): #77: 0>1, #177: 1>0, #237: 0>1, #265: 2>1, #288: 0>1*, #289: 0>1*, #291: 0>1.

Node 21 (*Centromochlus*, *Gelanoglanis*, *Tatia*): #44: 1>0, #45: 0>1, #50: 1>0, #131: 0>1, #249: 0>2, #290: 0>1, #291: 1>2*.

Node 22 (Auchenipterinae): #46: 1>2*, #115: 0>1, #190: 0>1, #276: 0>1.

Node 23 (Auchenipterinae, except *Tocantinsia*): #85: 1>2, #181: 1>0, #182: 1>0, #183: 1>0, #245: 0>1.

Node 24 (*Asterophysus*, *Liosomadoras*): #64: 0>1, #84: 1>0, #268: 1>0.

Node 25 (Auchenipterinae except *Asterophysus*, *Liosomadoras*, *Tocantinsia*): #287: 0>1, #299: 0>1*.

Node 26 (*Pseudauchenipterus*, *Pseudotatia*): #48: 0>1*, #59: 1>0, #60: 0>1, #77: 0>1, #249: 0>2.

Node 27 (Auchenipterinae except *Asterophysus*, *Liosomadoras*, *Pseudauchenipterus*, *Pseudotatia*, *Tocantinsia*): #87: 0>1, #237: 0>1, #239: 0>1, #287: 1>2, #300: 0>1.

Node 28 (*Auchenipterichthys*, *Trachelyichthys*, *Trachelyopterichthys*, *Trachelyopterus*, *Trachycorystes*): #276: 1>3, #307: 0>1.

Node 29 (*Auchenipterichthys*, *Trachelyopterichthys*, *Trachelyopterus*, *Trachycorystes*): #57: 0>1, #64: 0>1, #87: 1>0, #162: 1>2, #217: 3>4, #246: 0>1.

Node 30 (*Trachelyopterichthys*, *Trachelyopterus*, *Trachycorystes*): #54: 0>1, #94: 0>1, #106: 0>1, #113: 2>3.

Node 31 (*Trachelyopterus*, *Trachycorystes*): #35: 0>1, #116: 0>1, #161: 0>1*, #246: 1>0.

Node 32 (*Trachelyopterus*): #106: 1>0, #181: 0>1, #182: 0>1, #242: 1>0, #248: 0>2, #253: 0>1, #276: 3>0, #306: 1>2.

Node 33 (*Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Spinipterus*, *Tetranematichthys*): #25: 0>1, #92: 0>1, #98: 0>1, #117: 1>0, #134: 0>1, #183: 0>1, #241: 0>1, #283: 0>1, #285: 1>0.

Node 34 (*Ageneiosus*, *Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*, *Tetranematichthys*): #63:

- 0>1, #116: 0>1, #257: 1>0, #287: 2>3.
- Node 35 (*Ageneiosus*, *Tetranematichthys*): #10: 0>1*, #16: 2>1, #57: 0>1, #62: 0>1, #73: 0>1, #163: 0>1, #164: 0>1, #170: 0>1, #175: 0>1, #177: 1>2, #185: 0>1, #195: 0>1*, #223: 0>1*, #225: 0>1*, #228: 0>1, #231: 0>1, #237: 1>0, #240: 0>1*, #248: 0>1, #255: 0>1*, #265: 2>1.
- Node 36 (*Ageneiosus*): #16: 1>0, #25: 1>0, #39: 0>2, #44: 1>2, #134: 1>0, #135: 0>1*, #244: 0>1*, #245: 1>0, #256: 0>1*, #265: 1>0.
- Node 37 (*Auchenipterus*, *Entomocorus*, *Epapterus*, *Pseudepapterus*): #20: 0>1, #26: 0>1*, #52: 1>0, #108: 0>1*, #109: 0>1*, #110: 0>1*, #128: 0>1, #131: 0>1, #142: 0>1, #143: 0>1, #159: 1>0, #160: 0>1, #162: 1>2, #181: 0>1, #182: 0>1, #191: 1>0, #242: 1>0, #284: 0>1*, #286: 0>1*, #300: 1>0, #304: 0>1*.
- Node 38 (*Auchenipterus*, *Epapterus*, *Pseudepapterus*): #19: 0>1, #21: 0>1, #28: 0>1*, #47: 0>1*, #64: 0>1, #69: 0>1, #76: 0>1, #96: 0>1*, #127: 0>1, #183: 1>2, #186: 0>2, #216: 1>0, #222: 1>2, #239: 1>0, #245: 1>0, #262: 0>1, #270: 0>2, #273: 1>0, #276: 1>3, #281: 0>1*, #283: 1>2, #292: 0>1*.
- Node 39 (*Epapterus*, *Pseudepapterus*): #128: 1>2, #143: 1>2, #221: 1>0, #228: 0>1, #231: 0>1, #238: 1>0*, #248: 0>1.
- Node 40 (Doradidae): #118: 0>1, #137: 0>1, #212: 0>1*, #213: 1>2*, #217: 2>1, #253: 0>1, #306: 1>0.
- Node 41 (Wertheimerinae): #154: 1>2, #162: 1>2, #221: 1>2.
- Node 42 (Doradidae except Wertheimerinae): #52: 1>0, #118: 1>2, #222: 1>0, #224: 0>1.
- Node 43 (*Acanthodoras*, *Agamyxis*, *Astrodoradinae*, *Doradinae*): #5: 0>1, #99: 0>1, #137: 1>0, #154: 1>0, #264: 0>1, #267: 0>1, #276: 0>1.
- Node 44 (*Acanthodoras*, *Agamyxis*, *Astrodoradinae*): #5: 1>2, #85: 1>2, #97: 0>1, #268: 1>2, #272: 0>1.
- Node 45 (*Acanthodoras*, *Agamyxis*, *Astrodoradinae*, *Scorpidoras*): #61: 0>1, #106: 0>1.
- Node 46 (*Acanthodoras*, *Agamyxis*, *Astrodoradinae*): #35: 0>1, #121: 0>1.
- Node 47 (*Acanthodoras*, *Agamyxis*): #0: 0>1, #57: 0>1, #85: 2>1, #103: 0>1, #104: 0>1, #105: 0>1, #113: 2>1, #123: 1>0, #162: 1>2, #224: 1>0, #247: 0>1, #260: 0>2, #276: 1>0, #302: 0>1*.
- Node 48 (Doradinae): #36: 0>1, #217: 1>3, #245: 0>1, #274: 0>1, #306: 0>1, #310: 2>1.
- Node 49 (*Centrochir*, *Platydoradinae*): #1: 0>1, #38: 0>1.
- Node 50 (*Platydoradinae*): #0: 0>1, #106: 0>1, #301: 0>1.
- Node 51 (Doradinae, except *Centrochir*, *Platydoradinae*): #23: 0>1, #37: 0>1, #41: 0>1, #113: 2>1, #148: 0>1, #222: 0>1, #267: 1>0.
- Node 52 (*Centrochir*, *Doraops*, *Lithodoradinae*, *Megalodoradinae*, *Pterodoradinae*): #41: 1>2, #221: 1>2.
- Node 53 (*Centrochir*, *Doraops*, *Lithodoradinae*, *Megalodoradinae*, *Pterodoradinae*): #123: 1>0, #148: 1>0.
- Node 54 (*Doraops*, *Lithodoradinae*, *Megalodoradinae*, *Pterodoradinae*): #40: 0>1, #104: 0>1, #217: 3>4.
- Node 55 (*Megalodoradinae*): #272: 0>1.
- Node 56 (*Doraops*, *Lithodoradinae*, *Pterodoradinae*): #5: 1>0, #52: 0>1, #99: 1>0, #113: 1>2, #274: 1>0.
- Node 57 (*Lithodoradinae*, *Pterodoradinae*): #97: 0>1, #103: 0>1.
- Node 58 (*Pterodoradinae*): #85: 1>2.
- Node 59 (*Orinocodoradinae*, *Oxydoradinae*, *Rhinodoradinae*, *Rhynchodoradinae*, fimbriate-barbel doradids): #5: 1>0, #99: 1>0, #122: 1>0, #137: 0>1.
- Node 60 (*Orinocodoradinae*, *Rhinodoradinae*, *Rhynchodoradinae*): #113: 1>2, #149: 0>1, #156: 0>1*, #266: 0>1, #301: 0>1.
- Node 61 (*Rhynchodoradinae*): #30: 0>1, #33: 0>1, #37: 1>0, #39: 0>2, #41: 1>0, #85: 1>2, #124: 0>1*, #216: 1>0, #228: 0>1, #231: 0>1, #273: 1>0.
- Node 62 (*Orinocodoradinae*, *Rhinodoradinae*): #3: 0>1*, #40: 0>1, #122: 0>1, #180: 0>3, #200: 0>1*, #222: 1>0.
- Node 63 (*Rhinodoradinae*): #15: 0>1*, #175: 0>1.
- Node 64 (*Oxydoradinae*, fimbriate-barbel doradids): #38: 0>1, #52: 0>2, #55: 0>1*, #93: 0>1*, #107: 0>1, #125: 0>1*, #128: 0>1, #131: 0>1, #143: 0>1, #172: 0>1*, #174: 0>1, #179: 0>1, #180: 0>1, #188: 0>1*, #193: 0>1*, #199: 0>1, #249: 0>1, #271: 0>1*, #274: 1>0.
- Node 65 (*Oxydoradinae*): #40: 0>1, #58: 2>1, #65: 0>1*, #128: 1>2, #143: 1>2, #173: 0>1, #174: 1>2, #175: 0>1, #180: 1>2.
- Node 66 (fimbriate-barbel doradids): #5: 0>2, #11: 0>1*, #19: 0>1, #21: 0>1, #23: 1>0, #37: 1>0, #73: 0>1, #84: 0>1, #85: 1>2, #113: 1>0, #120: 0>1*, #153: 0>1*, #164: 0>1, #206: 0>1, #222: 1>0, #266: 0>2, #283: 0>1/2.
- Node 67 (*Ossancora*): #131: 1>0, #249: 1>0, #270: 0>1, #272: 0>1, #283: 1>2.
- Node 68 (*Ossancora asterophysa*, *O. eigenmanni*, *O. fimbriata*): #12: 0>1*, #17: 0>1, #231: 0>1.
- Node 69 (*Ossancora asterophysa*, *O. eigenmanni*): #18: 0>1.
- Node 70 (fimbriate-barbel doradids except *Ossancora*): #30: 0>1, #78: 0>1, #128: 1>2, #165: 0>1*, #182: 1>2.
- Node 71 (*Trachydoradinae*): #35: 0>1, #55: 1>2*, #58: 2>0, #81: 0>2*, #101: 0>1*, #143: 1>2, #179: 1>0, #180: 1>0, #181: 1>2, #189: 0>1*, #249: 1>2, #283: 1>2.
- Node 72 (*Trachydoradinae*, *T. steindachneri*): #272: 0>1.
- Node 73 (fimbriate-barbel doradids except *Ossancora*, *Trachydoradinae*): #36: 1>0, #53: 0>1*, #173: 0>1.
- Node 74 (*Doras*): #31: 0>1*, #41: 1>0, #62: 0>1.
- Node 75 (*Doras carinatus*, *D. higuchii*): #37: 0>1, #86: 0>1, #100: 0>1, #128: 2>1.
- Node 76 (*Anduzedoradinae*, *Hassar*, *Hemidoradinae*, *Leptodoradinae*, *Nemadoradinae*, *Tenellus*): #174: 1>2, #182: 2>1, #226: 0>1, #231: 0>1.
- Node 77 (*Hemidoradinae*): #17: 0>1, #30: 1>0, #35: 0>1, #266: 2>0, #272: 0>1.
- Node 78 (*Hemidoradinae*, *H. morei*, *H. morrissi*, *H. stenopeltis*): #32: 0>1, #106: 0>1.
- Node 79 (*Hemidoradinae*, *H. morrissi*): #143: 1>2, #283: 1>2.
- Node 80 (*Anduzedoradinae*, *Hassar*, *Leptodoradinae*, *Nemadoradinae*, *Tenellus*): #58: 2>1.
- Node 81 (*Nemadoradinae*): #42: 0>1, #283: 1>0.
- Node 82 (*Anduzedoradinae*, *Hassar*, *Leptodoradinae*, *Tenellus*): #2: 0>1, #58: 1>0, #62: 0>1.

Node 83 (*Tenellus*): #1: 0>1.

Node 84 (*Tenellus ternetzi*, *T. trimaculatus*): #228: 0>1.

Node 85 (*Anduzedoras*, *Hassar*, *Leptodoras*): #86: 0>1, #100:
0>1, #174: 2>1, #182: 1>2.

Node 86 (*Hassar*): #81: 0>1*, #118: 2>1, #128: 2>1.

Node 87 (*Anduzedoras*, *Leptodoras*): #8: 0>1*, #186: 0>1,
#191: 0>1, #201: 0>1*, #222: 0>1, #226: 1>2.

Node 88 (*Leptodoras*): #1: 0>1, #143: 1>2, #194: 0>1*, #231:
1>0, #275: 0>1*, #283: 1>0.

Node 89 (*Leptodoras juruensis*, *L. praelongus*): #33: 0>1, #39:
0>2, #202: 0>2*.

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