Osteology and myology of the cephalic region and pectoral girdle of the South African catfish *Austroglanis gilli*, with comments on the autapomorphies and phylogenetic relationships of the Austroglanididae (Teleostei: Siluriformes)

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Abstract—The cephalic and pectoral girdle structures of the South African catfish *Austroglanis gilli* are described and compared with those of other catfishes, either studied by us or described in the literature, as the foundation for a discussion on Austroglanididae autapomorphies, and also on the phylogenetic relationships between the austroglanidids and the other catfishes. Our observations, comparisons, and bibliographical overview revealed only two Austroglanidae autapomorphies, namely: 1) the peculiarly shaped, posteriorly bifurcated sesamoid bone 1 of the suspensorium; and 2) the markedly broad fourth basibranchial. Another feature, the marked lateral bifurcation of the anterodorsolateral laminar projection of the sphenotic bone, may eventually constitute an additional austroglanidid autapomorphy, but, perhaps more reasonably, be a synapomorphic feature to support a close relationship between *A. gilli* and *A. barnardi*. With respect to the phylogenetic position of the Austroglanididae within the Siluriformes, these fishes seem to be closely related to the ictalurid and the cranoglanidid, and particularly to the ariid and the claroteid catfishes.

Keywords: autapomorphies; Austroglanididae; catfish; morphology; myology; osteology; phylogeny; Siluriformes.

INTRODUCTION

The Siluriformes, or catfishes, with approximately 438 genera and over 2750 species, represent about 33% of all freshwater fishes and are one of the most

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economically important groups of fresh and brackish water fishes in the world (Teugels, 2003). Among the 35 siluriform families (Ferraris and de Pinna, 1999), the Austroglanididae, known only from the Orange and Olifants river systems in southern Africa, and including only a single genus, *Austroglanis* Skelton et al., 1984, and three species, *A. gilli* (Barnard, 1943), *A. barnardi* (Skelton, 1981) and *A. sclateri* (Boulenger, 1901), is surely one of the least studied (Teugels, 2003). In fact, among the large number of published works on catfish anatomy (Regan, 1911; Alexander, 1965; Chardon, 1968; Gosline, 1975; Lundberg 1975, 1982; Howes, 1983a, b, 1985; Mo, 1991; Bornbusch, 1995; Diogo et al., 1999, 2000a, b; Diogo and Chardon, 2000a, b, c; etc.), only two (Skelton, 1981; Skelton et al., 1984) provide detailed information on austroglanidid morphology.

   Skelton (1981) and Skelton et al. (1984) papers provide a detailed, rigorous description of the external anatomy and osteology of *Austroglanis barnardi*, with some notes on the main differences between this species and the other two austroglanidid species, *A. gilli* and *A. sclateri*. These papers provided the background for a formal exclusion of these three species from the claroteid genus *Gephyroglanis* (which at that time was included, together with the other claroteid genera, in the 'Bagridae' — see below), and, thus, the formal definition of the genus *Austroglanis* Skelton et al., 1984. A step forward was undertaken in a 1991 study by Mo, in which the 'Bagridae' was divided into the Bagridae sensu Mo (1991), the Claroteidae (see above) and the Austroglanididae, with the genus *Austroglanis* being, thus, assigned to its own family. The placement of the genus *Austroglanis* in a separate family was subsequently also supported in de Pinna's (1993) PhD thesis, which to date remains unpublished.

   As stated above, the morphological descriptions provided in the works of Skelton (1981) and Skelton et al. (1984) mainly concentrate on the external anatomy and the osteology of *Austroglanis barnardi*, with comparative notes with *A. gilli* and *A. sclateri*. Therefore, some important aspects of the morphology of members of the family Austroglanididae, such as muscle configuration or the configuration of structures associated with their mandibular barbels, remain virtually undescribed. Moreover, although these two papers, together with the Mo (1991) and de Pinna (1993) studies, support the monophyly of *Austroglanis*, and, hence, of the family Austroglanididae, no obviously unique features have yet been formally described as Austroglanididae autapomorphies in the literature. Furthermore, although all the four works mentioned above provide some discussion on the relationships between *Austroglanis* and other catfishes, the phylogenetic position of the Austroglanididae within the Siluriformes is still problematical, as explained by Diogo (2003).

   The aim of this work is, therefore, to describe the osteological and myological structures of the cephalic region (branchial apparatus excluded) and pectoral girdle of *Austroglanis gilli*, in order to provide an account of the morphology of this species and principally of previously undescribed aspects of austroglanidid anatomy such as, for example, the configuration of their musculature and of the structures associated with the mandibular barbels. In addition, the present study

includes a discussion on Austroglanididae autapomorphies, and on the phylogenetic relationships between the austroglanidids and other catfishes. It is hoped to increase knowledge of the anatomy and phylogeny of the siluriforms in general, as well as pave the way for future studies on the comparative anatomy, evolution, functional morphology, paleontology, eco-morphology and, in particular, the phylogeny of these fishes.

MATERIALS AND METHODS

The fishes studied are from the collection of our laboratory (LFEM), from the Musée Royal de l'Afrique Centrale of Tervuren (MRAC), from the Université Nationale du Bénin (UNB), from the Muséum National D'Histoire Naturelle in Paris (MNHN), from the National Museum of Natural History in Washington (USNM), and from the South African Institute for Aquatic Biodiversity (SAIAB) and the Albany Museum of Grahamstown (AMG). Anatomical descriptions are made after dissection of alcohol-fixed or trypsin-cleared and alizarine-stained (following the Taylor and Van Dyke (1985) method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The alcohol fixed (alc), trypsin-cleared and alizarine-stained (c&s), or simply alizarine-stained (s) condition of the fishes studied is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

Akysidae: *Akysis baramensis* LFEM, 2 (alc). *Akysis leucorhynchus* USNM 109636, 2 (alc). *Parakysis anomalopteryx* USNM 230307, 2 (alc); LFEM, 1 (alc).

Amblycipitidae: *Amblyceps caecutiens* LFEM, 2 (alc). *Amblyceps mangois* USNM 109634, 2 (alc). *Liobagrus reini* USNM 089370, 2 (alc).

Amphiliidae: *Amphilius brevis* MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (c&s). *Andersonia leptura* MNHN 1961-0600, 2 (alc). *Belonoglanis tenuis* MRAC P.60494, 2 (alc). *Doumea typica* MRAC 93-041-P-1335, 1 (alc). *Leptoglanis rotundiceps* MRAC P.186591-93, 3 (alc). *Paramphilius trichomycteroides* LFEM, 2 (alc). *Phractura brevicauda* MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (c&s). *Phractura intermedia* MRAC 73-016-P-5888, 1 (alc). *Trachyglanis ineac* MRAC P.125552-125553, 2 (alc). *Zaireichthys zonatus* MRAC 89-043-P-2243-2245, 3 (alc).

Ariidae: *Arius hertzbergii* LFEM, 1 (alc). *Arius heudelotii* LFEM, 4 (alc). *Bagre marinus* LFEM, 1 (alc); LFEM, 1 (c&s). *Genidens genidens* LFEM, 2 (alc).

Aspredinidae: *Aspredo aspredo* USNM 226072, 1 (alc). *Aspredo sicuephorus* LFEM, 1 (alc). *Bunocephalus knerii* USNM 177206, 2 (alc). *Xyliphius magdalenae* USNM 120224, 1 (alc).

Astroblepidae: *Astroblepus phelpis* LFEM, 1 (alc); USNM 121127, 2 (alc).

Auchenipteridae: *Ageneiosus vittatus* USNM 257562, 1 (alc). *Auchenipterus dentatus* USNM 339222, 1 (alc). *Centromochlus hechelii* USNM 261397, 1 (alc).

Austroglanididae: *Austroglanis gilli* LFEM, 3 (alc); SAIAB 58416 (c&s). *Austroglanis sclateri* AMG, 1 (c&s); SAIAB 68917 (s).

Bagridae: *Bagrichthys macropterus* USNM 230275, 1 (alc). *Bagrus bayad* LFEM, 1 (alc); LFEM, 1 (c&s). *Bagrus docmak* MRAC 86-07-P-512, 1 (alc); MRAC 86-07-P-516, 1 (c&s). *Hemibagrus nemurus* USNM 317590, 1 (alc). *Rita chrysea* USNM 114948, 1 (alc).

Callichthyidae: *Callichthys callichthys* USNM 226210, 2 (alc). *Corydoras guianensis* LFEM, 2 (alc).

Cetopsidae: *Cetopsis coecutiens* USNM 265628, 2 (alc). *Helogenes marmuratus* USNM 264030, 1 (alc). *Hemicetopsis candiru* USNM 167854, 1 (alc).

Chacidae: *Chaca bankanensis* LFEM, 3 (alc). *Chaca burmensis* LFEM, 2 (alc). *Chaca chaca* LFEM, 2 (alc).

Clariidae: *Clarias anguillaris* LFEM, 2 (alc). *Clarias batrachus* LFEM, 2 (alc). *Clarias ebriensis* LFEM, 2 (alc). *Clarias gariepinus* MRAC 93-152-P-1356, 1 (alc), LFEM, 2 (alc). *Heterobranchus bidorsalis* LFEM, 2 (alc). *Heterobranchus longifilis* LFEM, 2 (alc). *Uegitglanis zammaronoi* MRAC P-15361, 1 (alc).

Claroteidae: *Auchenoglanis biscutatus* MRAC 73-015-P-999, 2 (alc). *Auchenoglanis occidentalis* LFEM, 2 (alc). *Chrysichthys auratus* UNB, 2 (alc); UNB, 2 (c&s). *Chrysichthys nigrodigitatus* UNB, 2 (alc); UNB, 2 (c&s). *Clarotes laticeps* MRAC 73-13-P-980, 2 (alc).

Cranoglanididae: *Cranoglanis bouderius* LFEM, 2 (alc).

Diplomystidae: *Diplomystes chilensis* LFEM, 3 (alc).

Doradidae: *Acanthodoras cataphractus* USNM 034433, 2 (alc). *Anadoras weddellii* USNM 317965, 2 (alc). *Doras brevis* LFEM, 2 (alc). *Doras punctatus* USNM 284575, 2 (alc). *Franciscodoras marmoratus* USNM 196712, 2 (alc).

Erethistidae: *Erethistes pusillus* USNM 044759, 2 (alc). *Hara filamentosa* USNM 288437, 1 (alc).

Heteropneustidae: *Heteropneustes fossilis* USNM 343564, 2 (alc); USNM 274063, 1 (alc); LFEM, 2 (alc).

Ictaluridae: *Amiurus nebolosus* USNM 246143, 1 (alc); USNM 73712, 1 (alc). *Ictalurus furcatus* LFEM, 2 (alc). *Ictalurus punctatus* USNM 244950, 2 (alc).

Loricariidae: *Hypoptopoma bilobatum* LFEM, 2 (alc). *Hypoptopoma inexspectata* LFEM, 2 (alc). *Lithoxus lithoides* LFEM, 2 (alc). *Loricaria cataphracta* LFEM, 1 (alc). *Loricaria loricaria* USNM 305366, 2 (alc); USNM 314311, 1 (alc).

Malapteruridae: *Malapterurus electricus* LFEM, 5 (alc).

Mochokidae: *Mochokus niloticus* MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Synodontis clarias* USNM 229790, 1 (alc). *Synodontis schall* LFEM, 2 (alc). *Synodontis sorex* LFEM, 2 (alc).

Nematogenyidae: *Nematogenys inermis* USNM 084346, 2 (alc); LFEM, 2 (alc).

Pangasiidae: *Helicophagus leptorhynchus* USNM 355238, 1 (alc). *Pangasius larnaudii* USNM 288673, 1 (alc). *Pangasius sianensis* USNM 316837, 2 (alc).

Pimelodidae: *Batrochoglanis raninus* USNM 226136, 3 (alc). *Calophysus macropterus* USNM 306962, 1 (alc). *Goeldiella eques* USNM 066180, 1 (alc). *Hepapterus mustelinus* USNM 287058, 2 (alc). *Hypophthalmus edentatus* USNM 226140, 1 (alc). *Microglanis cottoides* USNM 285838, 2 (alc). *Pimelodus blochii* LFEM, 2 (alc). *Pimelodus clarias* LFEM, 2 (alc); USNM 076925, 1 (alc). *Pseudoplatystoma fasciatum* USNM 284814, 1 (alc). *Rhamdia guatemalensis* USNM 114494, 1 (alc).

Plotosidae: *Cnidoglanis macrocephalus* USNM 219580, 2 (alc). *Neosilurus rendahli* USNM 173554, 2 (alc). *Paraplotosus albilabris* USNM 173554, 2 (alc). *Plotosus anguillaris* LFEM, 2(alc). *Plotosus lineatus* USNM 200226), 2 (alc).

Schilbidae: *Ailia colia* USNM 165080, 1 (alc). *Laides hexanema* USNM 316734, 1 (alc). *Pseudeutropius brachypopterus* USNM 230301, 1 (alc). *Schilbe intermedius* MRAC P.58661, 1 (alc). *Schilbe mystus* LFEM, 3 (alc). *Siluranodon auritus* USNM 061302, 2 (alc).

Scoloplacidae: *Scoloplax distolothrix* LFEM, 1 (alc); USNM 232408, 1 (alc).

Siluridae: *Silurus aristotelis* LFEM, 2(alc). *Silurus glanis* LFEM, 2 (alc). *Silurus asotus* USNM 130504, 2 (alc). *Wallago attu* USNM 304884, 1 (alc).

Sisoridae: *Bagarius yarreli* USNM 348830, 2 (alc); LFEM, 1 (c&s). *Gagata cenia* USNM 109610, 2 (alc). *Glyptosternon reticulatum* USNM 165114, 1 (alc). *Glyptothorax fukiensis* USNM 087613, 2 (alc).

Trichomycteridae: *Hatcheria macraei* LFEM, 2 (alc). *Trichomycterus areolatus* LFEM, 2 (alc). *Trichomycterus banneaui* LFEM, 2 (alc). *Trichomycterus immaculatus* USNM 301015, 2 (alc).

RESULTS

In this section, the osteology and myology of the cephalic region and pectoral girdle of *Austroglanis gilli* are described. In the anatomical descriptions, the nomenclature for the osteological structures basically follows that of Arratia (1997). However, for the many reasons explained in detail in recent papers (Diogo et al., 2001a; Diogo and Chardon, 2003), Diogo et al. (2001a) are followed for the skeletal components of the suspensorium. The nomenclature of the cephalic muscles is mainly based on Winterbottom (1974), but, for the different adductor mandibulae sections, Diogo and Chardon (2000b) are followed (see Gosline 1989; Diogo and Chardon, 2000b). For the muscles associated with the mandibular barbels, Diogo and Chardon (2000c) are followed. For the nomenclature of the pectoral girdle muscles, Diogo et al. (2001b) are followed.

Osteology

Os mesethmoideum. This bone is situated on the antero-dorsal surface of the neurocranium (fig. 1). It exhibits two prominent antero-lateral arms, which are ligamentously connected to the premaxilla.

Os lateroethmoideum. The lateral ethmoid (fig. 1) exhibits a broad, dorso-lateral projection of laminar bone, which borders a significant part of the antero-dorsolateral surface of the eye. It also exhibits an antero-laterally directed articulatory facet for the autopalatine. There is a deep, dorsal concavity between the dorso-medial surface of each lateral ethmoid and the antero-dorsolateral margin of the frontals (fig. 1).

Os praevomerale. The prevomer is a T-shaped bone lacking a ventral tooth-plate.

Os orbitosphenoideum. This bone lies posterior to the lateral ethmoid, with the dorsal edge of its lateral wall being firmly sutured with the ventral surface of the frontal.
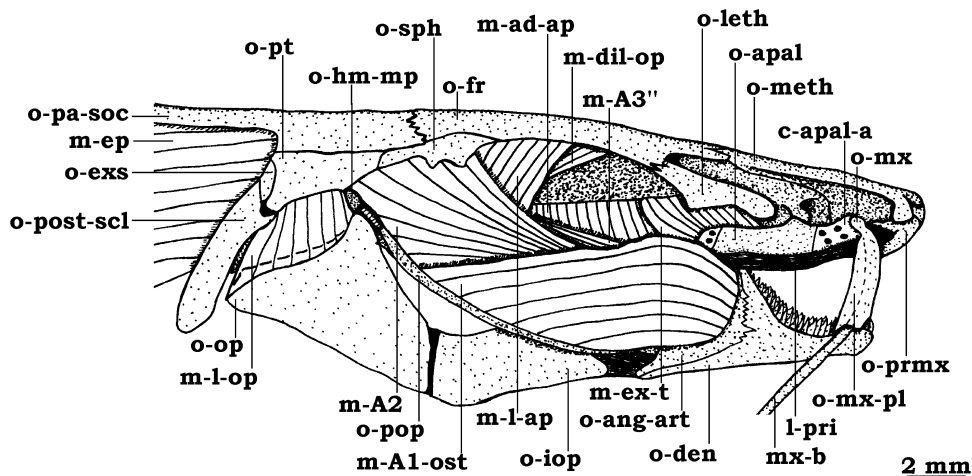
Figure 1. Right, lateral view of the cephalic musculature of *Austroglanis gilli*. All the muscles are exposed. *c-apal-a* cartilago autopalatinus anterior, *l-pri* ligamentum primordium, *m-A1-ost m-A2 m-A3″* sections of the musculus adductor mandibulae, *m-ad-ap* musculus adductor arcus palatini, *m-dil-op* musculus dilatator operculi, *m-ep* musculus epaxialis, *m-ex-t* musculus extensor tentaculi, *m-l-ap* musculus levator arcus palatini, *m-l-op* musculus levator operculi, *mx-b* maxillary barbel, *o-ang-art* os angulo-articulare, *o-apal* os autopalatinum, *o-den* os dentale, *o-exs* os extrascapulare, *o-fr* os frontale, *o-hm-mp* os hyomandibulo-metapterygoideum, *o-iop* os interoperculare, *o-leth* os latero-ethmoideum, *o-meth* os mesethmoideum, *o-mx* os maxillare, *o-mx-pl* posterior lamina of os maxillare, *o-op* os operculare, *o-pa-soc* os parieto-supraoccipitale, *o-pop*, os praeoperculare, *o-post-scl* os posttemporo-supracleithrum, *o-prmx* os praemaxillare, *o-pt* os pteroticum, *o-sph* os sphenoticum.

Os pterosphenoideum. The pterosphenoid is a large bone lying posterior to the orbitosphenoid and covering, together with this bone, the gap between the frontals and the parasphenoid.

Os parasphenoideum. This is the longest bone of the cranium. It bears a pair of prominent ascending flanges, which suture with the pterosphenoids and the prootics. Anteriorly it sutures with the elongated prevomer.

Os frontale. The frontals are large bones (fig. 1) largely separated by both the anterior and the posterior fontanels. The frontals are sutured anteriorly with the mesethmoid, antero-laterally with the lateral ethmoids, ventrally with the pterosphenoids and the orbitosphenoids, postero-laterally with the sphenotics and posteriorly with the parieto-supraoccipital.

Os *sphenoticum.* The sphenotic (fig. 1) is significantly more reduced in size than the pterotic. It bears, together with the latter bone, an elongated articulatory facet for the hyomandibulo-metapterygoid. The sphenotic exhibits a prominent antero-lateral projection of laminar bone which is markedly bifurcated laterally.

Os pteroticum. In dorsal view this bone exhibits a roughly triangular shape (fig. 1). There is a small, deep dorsal fossa between the postero-dorsolateral surface of the pterotic, the antero-dorsolateral surface of the posttemporo-supracleithrum and the dorso-lateral surface of the extrascapular (fig. 1).

Os prooticum. Together with the pterosphenoid, this bone borders the large foramen of the trigemino-facial nerve complex.

Os epioccipitale. The epioccipitals are small, roughly oval bones situated on the postero-ventral surface of the cranial roof. They are in contact with the parieto-supraoccipital, the posttemporo-supracleithra, the pterotics and the exoccipitals.

Os exoccipitale. The exoccipital is a broad bone situated laterally to the basioccipital and mesially to the epioccipital.

Os basioccipitale. This is a broad, stout, unpaired bone forming the posteriormost part of the floor of the neurocranium. Its ventro-lateral surfaces are ligamentously attached to the prominent ventro-mesial limbs of the posttemporo-supracleithra.

Os parieto-supraoccipitale. The parieto-supraoccipital is a remarkably large bone exhibiting an also remarkably elongated postero-dorsal process (fig. 1) reaching the nuchal plates posteriorly.

Os extrascapulare. This is a small, roughly oval bone situating on the postero-dorsal surface of the cranium, lying between the posttemporo-supracleithrum, the pterotic and the parieto-supraoccipital (fig. 1).

Os angulo-articulare. This bone (figs. 1, 2), together with the dentary bone, the coronomeckelian bone and Meckel's cartilage, constitute the mandible (fig. 2). Its antero-dorsal surface, together with the postero-dorsal surface of the dentary bone, forms a particularly prominent dorsal process (processus coronoideus), which is linked to the maxilla by means of a massive, long ligament (fig. 1). Postero-dorsally, the angulo-articular has an articulatory surface (fig. 1) to articulate with the quadrato-symplectic (fig. 3). Postero-ventrally, the angulo-articular is connected, by means of a strong, long ligament, to the anterior surface of the interopercle (figs. 1, 4).

Os dentale. The dentary bones (figs. 1, 2) are firmly connected ventrally to the broad cartilages (fig. 4) associated with the mandibular barbels by means of a large number of short and thin fibres. Antero-dorsally, each dentary bone bears numerous, large teeth (fig. 1).

Os coronomeckelium. The coronomeckelian bone is lodged in the mesial surface of the mandible (fig. 2). Postero-dorsolaterally and postero-dorsomesially this bone bears two crests for the attachment of the adductor mandibulae A3′-d.

Os praemaxillare. The premaxillae (fig. 1) are a pair of large triangular plates lying underneath and attaching to the mesethmoidal cornua via ligamentous tissue. Ventrally, each premaxilla bears numerous small teeth with their tips slightly turned backward.

Os maxillare. The maxillae (fig. 1) are connected to the premaxillae by a strong, short ligament. As is usual in catfishes, the maxillary barbels are supported by the maxillae (fig. 1). Each maxilla is prolonged posteriorly by a posterior laminar flange (fig. 1: o-mx-pl).

Os autopalatinum. This is a rod-like bone (fig. 1) whose anterior end is tipped by a remarkably elongated cartilage with two antero-lateral concavities that accept the
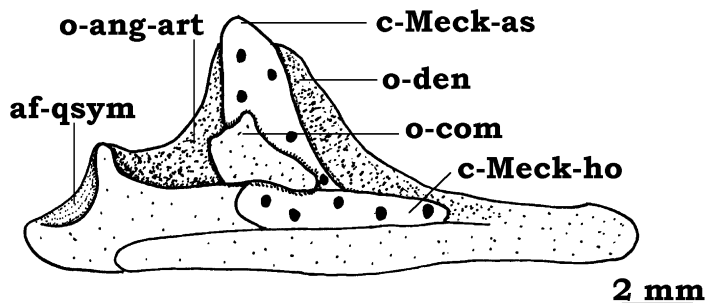
Figure 2. Medial view of the left lower jaw of *Austroglanis gilli*. *af-qsym* articulatory surface for os quadrato-symplecticum, *c-Meck-as c-Meck-ho* ascending and horizontal portions of cartilago Meckeli, *o-ang-art* os angulo-articulare, *o-com* os coronomeckelium, *o-den* os dentale.
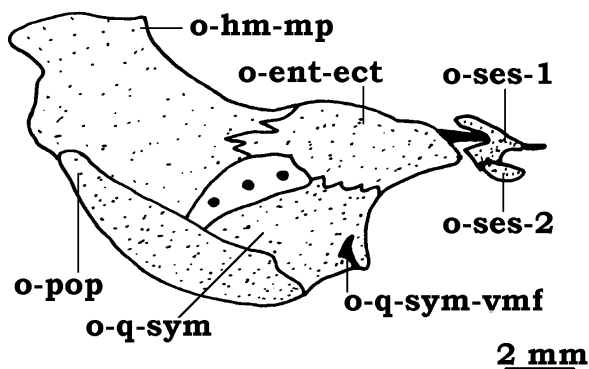

Figure 3. Mesial view of the left suspensorium of *Austroglanis gilli*. o-ent-ect os entoectopterygoideum, o-hm-mp os hyomandibulo-metapterygoideum, o-pop os praeoperculare, o-q-sym os quadrato-symplecticum, o-q-sym-vmf ventromesial fossa of os quadrato-symplecticum, o-ses-1 o-ses-2 sesamoidal bones 1 and 2 of the suspensorium.

two proximal heads of the maxilla. Its posterior tip is capped by a small cartilage. Medially, the autopalatine articulates with the lateral ethmoid (fig. 1).

Os hyomandibulo-metapterygoide. The hyomandibulo-metapterygoid (figs. 1, 3) is a large bone articulating dorsally with both the pterotic and the sphenotic and posteriorly with the opercle.

Os entopterygoide-ectopterygoideum. This bone is ventrally sutured with the quadrato-symplectic and posteriorly sutured to the hyomandibulo-metapterygoid (fig. 3). Anteriorly, the entoectopterygoid is connected, by a short but strong ligament, to the sesamoid bone 1 of the suspensorium (fig. 3).

Os quadrato-symplecticum. The quadrato-symplectic (fig. 3) presents an anterior articulatory surface to articulate with the angulo-articular. It presents a deep, somewhat triangular fossa on its ventro-mesial surface to receive the postero-ventral surface of the angulo-articular when the mandible is lowered.

Os sesamoideum 1. The sesamoid bone 1 of the suspensorium (fig. 3) is a somewhat triangular bone exhibiting a marked posterior bifurcation to receive the
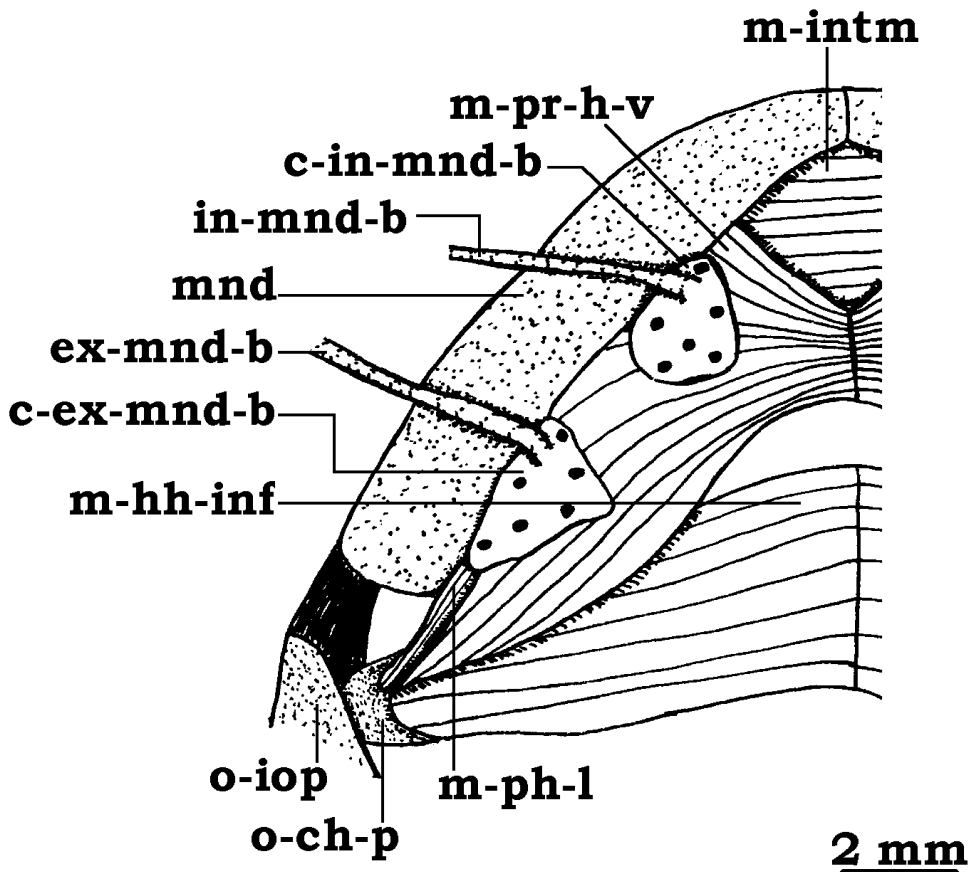
Figure 4. Ventral view of the cephalic musculature of *Austroglanis gilli*. All the muscles are exposed. *c-ex-mnd-b* cartilago externus mandibularis tentaculi, *c-in-mnd-b* cartilago internus mandibularis tentaculi, *ex-mnd-b in-mnd-b* external and internal mandibular barbels, *m-hh-inf* musculus hyohyoideus inferior, *m-intm* musculus intermandibularis, *m-pr-h-l m-pr-h-v* pars lateralis and ventralis of musculus protactor hyoideus, *o-ch-p* os ceratohyale posterior, *o-iop* os interoperculare, *mnd* mandible.

ligament connecting it to the entoectopterygoid. Anteriorly, this sesamoid bone is connected, by means of a thin and short ligament, to the prevomer.

Os sesamoideum 2. The sesamoid bone 2 of the suspensorium (fig. 3) is a small, roughly oval bone. Its mesial surface is firmly attached to the lateral surface of the sesamoid bone 1 of the suspensorium, while its lateral surface is firmly attached to the postero-ventral surface of the autopalatine.

Os praeoperculare. This is a long and large bone firmly sutured to the hyomandibulo-metapterygoid and to the quadrato-symplectic (fig. 3).

Os operculare. The opercle (fig. 1) is a broad, triangular bone, antero-dorsally articulating with the hyomandibulo-metapterygoid. It presents a dorsally-oriented antero-dorsal projection of laminar bone.
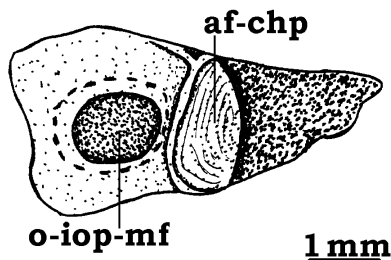
Figure 5. Mesial view of the left interopercle of *Austroglanis gilli*. *af-chp* articulatory facet for os ceratohyale posterior, *o-iop-mf* mesial formamen of os interoperculare.

Os interoperculare. The interopercle is broad and exhibits a markedly large, roughly oval, smooth surface (fig. 5: af-chp) for an articulation with the posterior ceratohyal (fig. 4). Postero-mesially the interopercle is pierced by an also markedly large, but rather circular, foramen (fig. 5: o-iop-mf).

Os interhyale. Contrary to the description of Petrick (1973), the interhyal is present in the specimens of *A. gilli* examined, being a small bone attached, by means of small ligaments, to both the posterior ceratohyal and the mesial surface of the cartilage lying between the quadrato-symplectic and the hyomandibulo-metapterygoid.

Os ceratohyale posterior. This roughly triangular, broad bone is linked by strong ligaments to the postero-ventral surface of the angulo-articular and the ventral surface of the interhyal.

Os ceratohyale anterior. The anterior ceratohyal is a somewhat tubular, stout bone that, together with the posterior ceratohyal, supports the six branchiostegal rays present in each side of the fish. The anterior head of branchiostegal ray 5 lies at the level of the cartilage situated between the anterior and the posterior ceratohyal, with the anterior head of branchiostegal ray 6 (the most posterior one) exclusively supported by the posterior ceratohyal and the remaining four branchiostegal rays exclusively supported by the anterior ceratohyal.

Os hypohyale ventrale. The ventral hypohyals are somewhat triangular bones. Each ventral hypohyal contains a deep ventral concavity to receive one of the antero-lateral edges of the parurohyal.

Os hypohyale dorsale. The dorsal hypohyals, situated, as their names indicate, dorsally to the ventral ones, are markedly smaller than the latter.

Os parurohyale. The parurohyal is a large, roughly triangular bone lying medially behind the ventro-medial surfaces of the ventral hypohyals and connected to these bones by means of two strong, thick ligaments. It is markedly truncated posteriorly, exhibiting only a single, small, short postero-mesian process.

Os posttemporo-supracleithrum. The dorso-mesial limb of this large bone (fig. 1) is strongly connected to, but not sutured with, the pterotic and the extrascapular. Its stout ventro-medial limb is ligamentously attached, as described above, to the basioccipital. Its ventro-lateral limb is deeply forked, forming an articulating groove
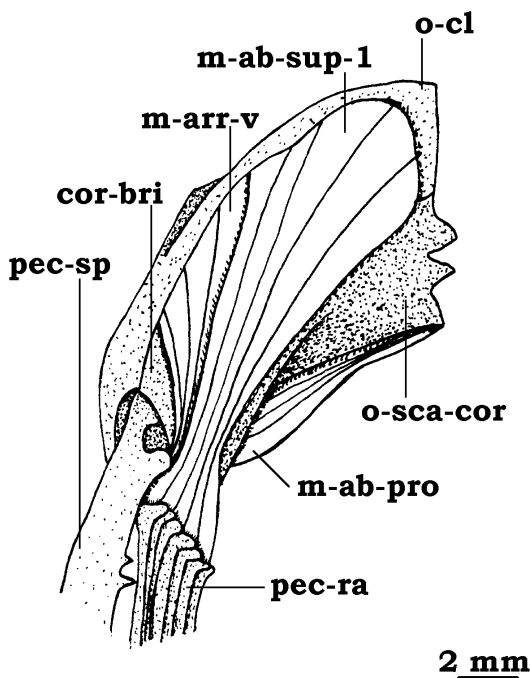
Figure 6. Ventral view of the pectoral girdle of *Austroglanis gilli*. All the muscles are exposed. *cor-bri* coracoid bridge, *m-ab-pro* musculus abductor profundus, *m-ab-sup-1* musculus abductor superficialis, *m-arr-v* musculus arrector ventralis, *o-cl* os cleithrum, *o-sca-cor* os scapulo-coracoide, *pec-ra* pectoral rays, *pec-sp* pectoral spine.

for the upper edge of the cleithrum. Its postero-ventral surface is firmly attached, by means of massive connective tissue, to the antero-ventral process of the fourth parapophysis.

Os cleithrum. The cleithrum (fig. 6) is a large, well-ossified stout structure forming a great part of the pectoral girdle and the posterior boundary of the branchial chamber. It bears a deep crescentic, medially faced groove, with rough surfaces, which accommodates the thick, crescentic dorsal condyle of the pectoral spine. The two cleithra are attached in the antero-medial line via connective tissue. The humeral process of the cleithrum is present and large.

Os scapulo-coracoideum. The scapulo-coracoid (fig. 6) is an elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge. Mesially, it joins its counterpart in an interdigitation of several strong serrations. Antero-laterally, it presents a peculiarly large anteriorly-directed process, usually called the coracoid bridge, which extends ventrally to the ventro-lateral surface of the cleithrum, fusing with an antero-ventral ridge of this bone. The postero-lateral end of the scapulo-coracoid bears two condyles, which articulate, respectively, with the pectoral spine and the complex radial (Mo, 1991). Medially to these two condyles there is a ventral groove, which accommodates the ventral condyle of the pectoral spine when this spine is erected. Posteriorly, the scapulo-coracoid presents a large foramen,

which accepts the anterior condyle of the pectoral spine when this is abducted. The mesocoracoid arch is present.

Myology

Musculus adductor mandibulae.   The adductor mandibulae A1-ost originates on the preopercle and quadrato-symplectic and inserts on the dorso-lateral and lateral surfaces of the angulo-articular (fig. 1). The A2 (fig. 2), which lies dorso-mesially to the A1-ost, attaches posteriorly to the preopercle, hyomandibulo-metapterygoid, pterotic and sphenotic. Anteriorly, it attaches tendinously to the medial crest of the angulo-articular. The adductor mandibulae A3′ is divided into a dorsal and a ventral part. The dorsal part (A3′-d), originating on the hyomandibulo-metapterygoid, is, in turn, subdivided into a lateral and a mesial bundle, attached, respectively, to the postero-dorsolateral and postero-dorsomesial surfaces of the coronomeckelian bone. The ventral part (A3′-v) originates on the quadro-symplectic and inserts on the medial surface of the angulo-articular. The deeper bundle of the adductor mandibulae, the A3″ (fig. 1), runs from the hyomandibulo-metapterygoid to the mesial surface of the angulo-articular. Last, the Aω attaches antero-ventrally on the mesial surface of both the dentary bone and the angulo-articular, and postero-dorsally on the tendon of the adductor mandibulae A2.

Musculus levator arcus palatini. This muscle (fig. 1) originates on the ventro-lateral surface of the sphenotic and the pterotic, as well as on the lateral surface of the frontal, and inserts on the lateral face of the hyomandibulo-metapterygoid.

Musculus adductor arcus palatini. This muscle (fig. 1) extends from the lateral sides of the parasphenoid, pterosphenoid and orbitosphenoid to the mesial sides of the hyomandibulo-metapterygoid and the entoectopterygoid.

Musculus adductor hyomandibularis. This is a small muscle situated laterally to the adductor operculi and mesially to the levator operculi. It originates on the ventral surface of the pterotic and inserts on the postero-dorsomesial surface of the hyomandibulo-metapterygoid.

Musculus adductor operculi. This is a thick muscle originating on the ventral surface of the pterotic and inserting on the dorso-mesial surface of the opercle.

Musculus levator operculi. The levator operculi originates on the ventro-lateral margin of the pterotic and the antero-ventrolateral surface of the posttemporo-supracleithrum, and inserts on both the dorsal and the dorso-lateral surfaces of the opercle (fig. 1).

Musculus dilatator operculi. This thick muscle is situated medially to the levator arcus palatini (fig. 1). It runs from the sphenotic, pterotic, frontal, pleurosphenoid and orbitosphenoid to the antero-dorsal edge of the opercle (mesial to the preopercle but lateral to the articulatory facet of the opercle for the hyomandibulo-metapterygoid) (fig. 1).

Musculus extensor tentaculi. The extensor tentaculi (fig. 1) runs from the ventro-mesial surface of both the lateral ethmoid and the orbitosphenoid to the postero-mesial margin of the autopalatine. The muscle retractor tentaculi is missing.

Musculus protractor hyoidei. This muscle has three parts. The pars ventralis (fig. 4: m-pr-h-v), in which are lodged the broad cartilages associated with the mandibular barbels, originates on both the anterior and the posterior ceratohyals and inserts on the dentary bone, meeting its counterpart in a broad median aponeurosis. The pars lateralis (fig. 4: m-pr-h-l) originates on the posterior ceratohyal, inserting, by means of a thick tendon, on the ventro-medial face of the dentary bone. The pars dorsalis originates on both the anterior and the posterior ceratohyals and inserts on the dentary bone, meeting its counterpart antero-medially in a medial aponeurosis.

Muscle intermandibularis. This muscle joins the two mandibles (fig. 4).

Musculus retractor externi mandibularis tentaculi. This small muscle runs from the moving part of the cartilage associated with the outer mandibular barbel to the dentary bone.

Musculus retractor interni mandibularis tentaculi. This small muscle originates on the moving part of the cartilage associated with the internal mandibular barbel and inserts on the dentary bone.

Musculus hyohyoideus inferior. The thick hyohyoideus inferior (fig. 4) attaches mesially on a median aponeurosis and laterally on the ventral surfaces of the ventral hypohyal, anterior ceratohyal and posterior ceratohyal.

Musculus hyohyoideus abductor. This muscle runs from the first (mesial) branchiostegal ray to a median aponeurosis which is associated with two long, strong tendons, attached, respectively, to the two ventral hypohyals.

Musculus hyohyoideus adductor. Each hyohyoideus adductor connects the branchiostegal rays of the respective side.

Musculus sternohyoideus. The sternohyoideus is a large muscle running from the anterior region of the cleithrum to the posterior region of the parurohyal.

Musculus arrector ventralis. This muscle (fig. 6) runs from the ventrolateral surface of the cleithrum to the ventral condyle of the pectoral spine.

Musculus arrector dorsalis. The arrector dorsalis is differentiated into two broad divisions. The ventral division, situated on the ventral surface of the pectoral girdle, originates on the ventral margin of the cleithrum and inserts on the antero-lateral edge of the pectoral spine. The dorsal division, situated on the dorsal surface of the pectoral girdle, originates on the dorso-medial edge of the scapulo-coracoid and inserts on the anterior edge of the dorsal condyle of the pectoral spine.

Musculus abductor profundus. This muscle originates on the postero-mesial edge of the coracoid (fig. 6), passes anteriorly to both the mesocoracoid arch and the adductor superficialis muscle, and inserts on the mesial surface of the dorsal condyle of the pectoral spine.

Musculus adductor superficialis. This muscle is differentiated into two sections. The larger section originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid, as well as on the dorso-lateral edge of the mesocoracoid arch, and inserts on the antero-dorsal margin of the dorsal part of the pectoral fin rays. The smaller section runs from the ventro-lateral edge of the mesocoracoid arch and the

dorsal surface of the proximal radials to the antero-ventral margin of the dorsal part of the pectoral fin rays.

Musculus abductor superficialis. This muscle is also differentiated into two sections. The larger section (fig. 6: m-ab-sup-1) runs from the ventral face of both the cleithrum and the scapulo-coracoid to the antero-ventral margin of the ventral part of the pectoral fin rays. The smaller section runs from the postero-lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of the pectoral fin rays.

Musculus protractor pectoralis. This thick muscle runs from the ventral surfaces of both the pterotic and the posttemporo-supracleithrum to the antero-dorsal surfaces of both the cleithrum and the scapulo-coracoid.

DISCUSSION

The formal exclusion of the three austroglanidid species from the claroteid genus *Gephyroglanis*, and, thus, the formal definition of the genus *Austroglanis* was, as referred above, provided in the Skelton et al. (1984) paper. However, in this paper Skelton et al. did not distinguish any unique, autapomorphic characters to diagnose the genus *Austroglanis*. In fact, the separation between *Austroglanis* and *Gephyroglanis* was, as recognised by Skelton and co-authors, influenced by other works and mainly based on three arguments. One of these arguments was related to the fact that the genus *Gephyroglanis* was firstly defined by Boulenger (1899, 1911) "on a loss trait, i.e., the absence of palatal teeth" (Skelton et al., 1984: 337-338). This had led authors such as Thys van den Audenaerde (1965), Roberts (1975), Risch and Thys van den Audenaerde (1981), Risch (1981) and Skelton (1981) to suggest that the genus *Gephyroglanis*, as recognised prior to the Skelton et al. paper, was probably polyphyletic. One second argument was the 'disjunct geographical distribution' of the three species now assigned to the genus *Austroglanis* (the Orange and Olifants rivers in South Africa) and the other *Gephyroglanis* species (mainly known from Zaire and West Africa), stressed by authors such as Barnard (1943), Roberts (1975), Thys van den Audenaerde (1965) or Skelton (1981). The third argument was the fact the two geographically disjunct groups also exhibited significant morphological differences, as emphasised by Barnard (1943) and Skelton (1981), and discussed in depth in Skelton et al. (1984). However, none of these papers formally provided a potentially unique, autapomorphic character to differentiate the austroglanidids from all the other Siluriformes (Skelton et al., 1984). Barnard (1943), Skelton (1981) and Skelton et al. (1984) did stress a peculiar main feature characterising the three species now assigned to the genus *Austroglanis*, namely the *peculiarly-shaped mesial articulatory surface of the interopercle for the posterior ceratohyal* (fig. 5: af-chp). However, as recognised by Skelton et al. (1984: 359-360), this feature is not exclusive to *Austroglanis*, and occurs "in certain other siluroid families including the Amphiliidae, the Sisoridae, and the Mochokidae".

Contrary to Skelton et al. (1984), Mo (1991: 160) formally provided a list of ten synapomorphic (but not autapomorphic) characters to diagnose the genus *Austroglanis*, and, thus, its family Austroglanididae (see above). However, Mo (1991) did not discriminate the taxonomic distribution of these characters in the Siluriformes and, therefore, did not identify which of these characters constituted autapomorphic features uniquely present in the family Austroglanididae. We provide a brief discussion of each of the ten characters.

The first of Mo's synapomorphic characters is a '*maxilla possessing a thin laminar flange along its posterior margin*'. This character (fig. 1) is indeed a peculiar feature in Siluriformes, but is also found in other catfishes, such as ariids, anchariids, pangasiids or schilbids, as clearly stated by de Pinna (1993).

The second synapomorphic feature listed by Mo (1991) is '*a strong mandible exhibiting an elevated coronoid process*'. Although the mandible of austroglanidids and its coronoid process are indeed markedly developed (figs. 1, 2), they are not significantly larger than in some diplomystids (Diogo et al., 2001a: fig. 1) or claroteids (Diogo and Chardon, 2001a: fig. 3) we examined.

However, the same cannot be said about the third synapomorphic character provided by Mo (1991), i.e. the '*distinct shape of the sesamoid bone 1 of the suspensorium (=Mo's entopterygoid)*'. In fact, a peculiar-shaped, and posteriorly, markedly bifurcated sesamoid bone 1 of the suspensorium such as that of austroglanidids (figs. 3, 7) (also see Skelton, 1981: fig. 10A) was not found in any other catfish studied by us or described in the literature. This character seems, therefore, to constitute an Austroglanididae autapomorphy.

The fourth synapomorphy listed by Mo (1991) is the configuration of the entoectopterygoid. According to Mo, in austroglanidids the '*entoectopterygoid (=Mo's metapterygoid) is split-like and situates median to the quadrato-symplectic (=Mo's quadrate)*'. However, the entoectopterygoid in the *Austroglanis gilli* examined (fig. 3), was not 'split-like', and was not median to the quadrato-symplectic, at least no more than in the other catfishes analysed. This seems be the case in the other two species of *Austroglanis* also, since those species exhibit, as stated by Skelton et al. (1984: 358), a rather "generalized" entoectopterygoid.

The fifth synapomorphic character of Mo (1991) is the '*anterior orientation of the articulatory surface of the lateral ethmoid for the autopalatine*'. According to the specimens of *Austroglanis gilli* and *Austroglanis sclateri* (see Materials and Methods), examined (fig. 1), as well as in the specimens of *Austroglanis barnardi* examined by Skelton (1981: figs. 8A, B), the articulatory surface of the lateral ethmoid for the autopalatine is indeed oriented antero-mesially, and not postero-mesially. However, this is also the case in a series of other catfishes, as clearly stated by de Pinna (1993).

'A *stout process on the dorsal limb of the posttemporo-supracleithrum contacting the ventrolateral side of the pterotic*' was the sixth synapomorphy listed by Mo to diagnose the Austroglanididae. However, neither in the austroglanidids we
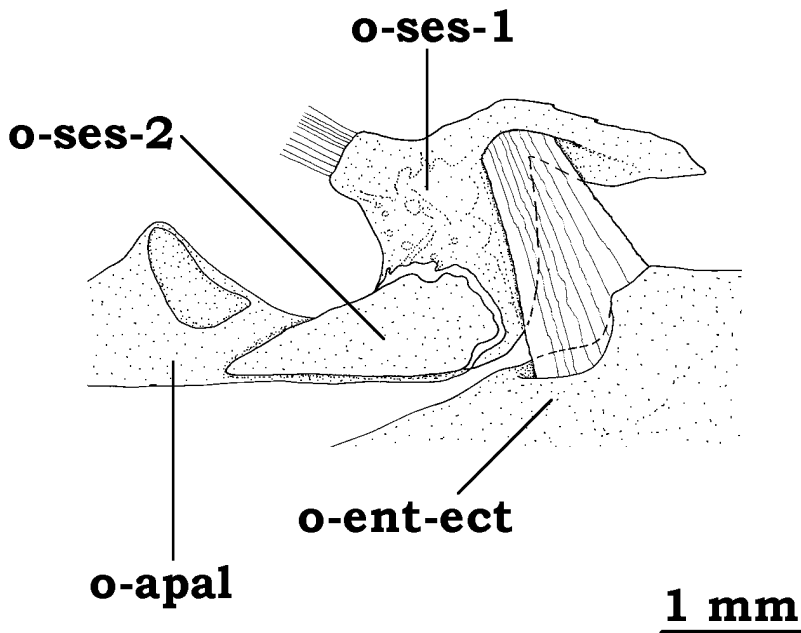
Figure 7. Ventral view of the sesamoid bone 1 of the suspensorium and its two associated ligaments in *Austroglanis sclateri* (drawing by R. Bills). *o-apal* os autopalatinum, *o-ent-ect* os entoectopterygoideum, *o-ses-1 o-ses-2* sesamoidal bones 1 and 2 of the suspensorium.

examined (fig. 1), nor in those examined by Skelton (Skelton, 1981: fig. 229: fig. 8), was it possible to discern such a stout process.

The seventh and eighth synapomorphic characters listed by Mo, the '*thick interopercle with a glenoid fact articulating with the posterior ceratohyal* and the *thick and stout posterior ceratohyal*', are related to the modification of the interopercle and the posterior ceratohyal and their peculiar articulation. As explained above, and as Skelton et al. (1984) had recognised, these latter features are not exclusive to *Austroglanis*, but occur "in certain other siluroid families including the Amphiliidae, the Sisoridae, and the Mochokidae".

The ninth synapomorphic character, '*the fifth and sixth vertebra sutured to complex vertebra*', is also present, as Mo recognised (1991: 177), in a series of other catfishes, such as cranoglanidids, pangasiids, ariids or bagrids.

The tenth, and last synapomorphic feature listed by Mo (1991) to diagnose the Austroglanididae was the '*insertion of the levator operculi muscle on the posterodorsolateral margin of the opercle*'. The insertion of this muscle on the dorso-lateral surface of the opercle, thus covering a significant pat of the dorsal surface of this bone in lateral view (fig. 1), constitutes, indeed, a particularly rare feature among siluriforms. However, such a feature is also present in fishes of the genus *Nematogenys* and *Heptapterus* (de Pinna, 1998; Diogo and Vandewalle, 2003), and, hence, could not represent an Austroglanididae autapomorphy.
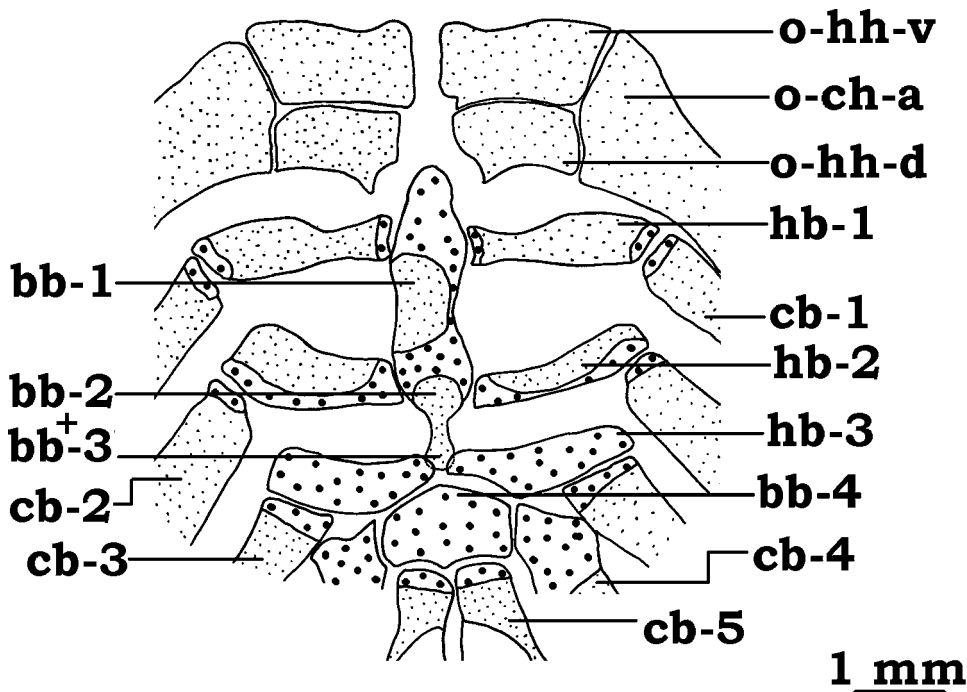
Figure 8. Dorsal view of basibranchial 4 and surrounding branchial elements in *Austroglanis gilli* (drawing by R. Bills). *bb-1 bb-2 bb-3 bb-4* basibranchials 1 2 3 and 4, *cb-1 cb-2 cb-3 cb-4 cb-5* ceratobranchials 1 2 3 4 and 5, *hb-1 hb-2 hb-3* hypobranchials 1 2 and 3, *o-ch-a* os ceratohyale anterior, *o-hh-d* os hypohyale dorsale, *o-hh-v* os hypohyale dorsale.

Therefore, the single synapomorphic character listed by Mo (1991) to define the austroglanidids, which is exclusively found in these catfishes and does seem to constitute an austroglanidid autapomorphy, is the very peculiar-shaped and, posteriorly, markedly bifurcated, sesamoid 1 of the suspensorium.

As mentioned in the Introduction, de Pinna's (1993) unpublished thesis also provides evidence to support the monophyly of the Austroglanididae. De Pinna (1993) formally listed seven synapomorphic characters to diagnose this family, namely: 1) *anterior cartilage of autopalatine enlarged*; 2) *maxilla with leaf-like morphology*; 3) *anterior portion of ethmoid cartilage extended anteriorly*; 4) *last (fourth) basibranchial much broader than long*; 5) *upper pharyngeal tooth plate far from corresponding epibranchial*; 6) *(reversion of) upper pharyngeal tooth plate articulated with 4th infrapharyngobranchial by two struts of bone*; 7) *hypobranchial 1 without posterior cartilage*. Contrary to Mo (1991), de Pinna did clearly identify that, of these seven synapomorphic features, only one, the *last (fourth) basibranchial much broader than long*, seems to be exclusively present in the austroglanidid catfishes. De Pinna's observation was corroborated by our observations in comparisons. In fact, contrary to other catfishes, in the specimens of *Austroglanis gilli* and *Austroglanis sclateri* we observed (fig. 8), as well as in those
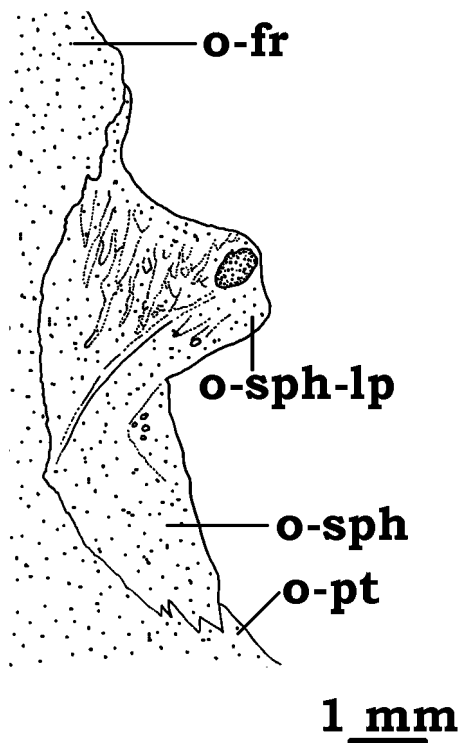
Figure 9. Dorsal view of the right sphenotic in *Austroglanis sclateri* (drawing by R. Bills). *o-fr* os frontale, *o-pt* os pteroticum, *o-sph* os sphenoticum, *o-sph-lp* anterodorsolateral laminar projection of os sphenoticum.

of *Austroglanis barnardi* described by Skelton (1981: fig. 16A) and Skelton et al. (1984: fig. 6A), the fourth basibranchial is a markedly enlarged structure.

The Austroglanididae seem, therefore, to exhibit two characters that are not found elsewhere in the order Siluriformes, i.e., the peculiar-shaped, posteriorly bifurcated sesamoid bone 1 of the suspensorium and the markedly broad fourth basibranchial. However, the present study revealed another character that is also present in some austroglanidids and in no other catfishes, namely the *lateral bifurcation of the antero-dorsolateral laminar projection of the sphenotic bone*. Most catfishes do not present a prominent antero-dorsolateral projection of the sphenotic, but this is the case in some siluriforms, such as the claroteids, plotosids or malapterurids (Diogo et al., 2001: figs. 3, 6). However, as described in the paragraph above, the sphenotic bone projection in the *Austroglanis gilli* examined exhibited a marked lateral bifurcation (fig. 1). Although in the illustrations of *Austroglanis barnardi* provided by Skelton (1981: fig. 8A) the antero-dorsolateral laminar projection is not prominent as in *A. gilli*, it seems to be somewhat bifurcated laterally. In the *A. sclateri* specimens such a bifurcation of the laminar projection of the sphenotic is practically undifferentiated (fig. 9). Attending to the phylogenetic scenario proposed by Mo (1991) suggesting that *A. sclateri* and *A. gilli* are more

closely related to each other than to *A. barnardi*, one could read the marked bifurcation of the lateral projection of the sphenotic of these former two species as an Austroglanididae autapomorphy secondarily lost in *A. sclateri*, but this feature could also be read, alternatively, as an homoplastic character independently acquired in both *A. barnardi* and *A. gilli*. Another, perhaps more reasonable, scenario would be that the marked bifurcation of the lateral projection of the sphenotic could constitute a synapomorphic feature to support a close relationship between *A. gilli* and *A. barnardi*, with *A. sclateri* being the more basal austroglanidid species, as indicated by work in progress based on genetic data by one of us (R. Bills, pers. obs). *Austroglanis sclateri* is found in large river mainstreams, which are very turbid environments for most of the time. *Austroglanis gilli* and *A. barnardi* are usually found in small, mostly very clear, mountain streams. This could make biogeographic sense, since the Orange system (which inhabits *A. sclateri*) is the largest system of the southern temperate region and has been sporadically connected with various peripheral systems (including the Olifants, which *A. gilli* and *A. barnardi* inhabit) that have allowed movements of fishes and later isolation.

With respect to the phylogenetic position of the austroglanidids within the order Siluriformes, in Skelton et al.'s (1984) formal definition of the genus *Austroglanis* (see above), these authors suggested that the members of this genus could be related to the 'remaining bagrids' (which at that time included both the Claroteidae and the Bagridae), but also to the pimelodids and/or the ictalurids. Skelton et al. (1984), however, did not formally provide a list of synapomorphic characters to support this suggestion.

The phylogenetic results of Mo (1991) were somewhat confusing: in his clado-gram I the Austroglanididae were placed in a large, unresolved polytomy, while in his cladogram II they were placed as the sister-group of the Cranoglanididae. In addition, the author did not provide any synapomorphic characters to support this latter hypothesis, with the grouping of the two families in his cladogram II (i.e., the node 49) being based on characters that are not described subsequently by the author.

A very different hypothesis was formulated by de Pinna (1993), in which the Austroglanidae were placed as the sister-group of a large clade including the genus *Horabagrus*, the schilbids, the pangasiids, the claroteins, the ancharids, the ariids, some bagrids and some pimelodids. De Pinna did provide three characters to support this phylogenetic hypothesis, namely: 1) frontal and lateral ethmoid connected by a lateral bridge of bone, mesially delimiting a space or foramen; 2) (reversion of) first pharyngobranchial absent; and 3) transverse process of the fourth vertebra with a well-defined posterior arm.

The phylogenetic analysis undertaken by Diogo, which includes 440 characters and 87 terminal taxa representing all extant catfish families (2005), partially supports and partially contradicts each of these three studies. In fact, the Austroglanididae appear as closely related to the ictalurid (Skelton et al., 1984) and the cranoglanidid (Mo, 1991), but particularly to the ariid (de Pinna, 1993) and

the claroteid (Skelton et al., 1984; de Pinna, 1993) catfishes. Two phylogenetically unambiguous characters support the grouping of these five siluriform groups, described below.

I-Lateral laminar projection of lateral ethmoid. Plesiomorphically in catfishes the lateral ethmoid does not present major broad lateral projections of laminar bone. However, in the clarotein, arid, ictalurids, austroglanidid and cranoglanidids catfishes examined, each lateral ethmoid exhibits a broad, dorso-lateral projection of laminar bone, which surrounds a significant part of the antero-dorsolateral surface of the eye (fig. 1). The absence of such a prominent lateral laminar projection of the lateral ethmoid in some auchenoglanidin claroteids (the family Claroteidae is formed by two subfamilies, the Claroteinae and the Auchenoglanidinae; Mo, 1991) seems to be related to a secondary loss (Diogo, 2005).

II-Coracoid bridge markedly enlarged. Contrarily to the plesiomorphic siluriform configuration, in which the coracoid bridge is not significantly enlarged transversally (Diogo et al., 2001b), in the clarotein, ariid, ictalurid, austroglanidid and cranoglanidid catfishes examined, but also auchenipterid, doradid, some bagrid (e.g., *Bagrichthys* and *Rita*) and some pimelodid (e.g., *Pseudopimelodus*, *Pimelodus*) specimens analysed, the coracoid bridge is markedly enlarged transversally (fig. 6). The absence of this feature in the auchenoglanidin claroteids and its presence in catfishes such as auchenipterids, doradids, bagrids and pimelodids are seemingly due to an evolutionary reversion and to an homoplastic, independent acquisition, as explained in Diogo (2005).

With respect to the characters supporting a more close relationship between the austroglanidids, the ariids and the claroteids than between the austroglanidis, the ictalurids and the cranoglanidids, these are described below.

I-Differentiation of adductor mandibulae A3'-d. Plesiomorphically in catfishes the adductor mandibulae A3′-d is constituted by a single mass of fibres (Diogo and Chardon, 2000b). However, in the auchenogladinin, ariid, and austroglanidid specimens examined, the A3′-d is differentiated into a lateral division that inserts by means of a thick tendon to the postero-dorsolateral surface of the coronomeckelian bone and a mesial division that inserts by a thin tendon to the postero-dorsomesial margin of this bone. An also derived, but different, configuration was found in analysed specimens of the genera *Bagrus* and *Hemibagrus*, in which the A3′-d is differentiated into two subdivisions, with the smallest one attached to the postero-dorsal surface of the coronomeckelian bone and the largest attached to the posterior end of this bone (see Diogo, 2005). The situation found in the auchenogladinins, ariids and austroglanidids is, thus, seen as a synapomorphic feature to unite the Austroglanididae, the Claroteidae and the Ariidae, with the absence of this derived situation in the claroteins being, thus, assigned to a secondary loss.

II-Size of anterior cartilage of autopalatine. Plesiomorphically in catfishes the anterior cartilage of the autopalatine is a small, short structure, but in all claroteids, austroglanidids and ariids examined, and also on the schilbids and cetopsids examined, the anterior cartilage of the autopalatine is markedly elongated antero-

posteriorly (fig. 1). This character thus seems to constitute a synapomorphy to support a close relationship between the Ariidae, Claroteidae and the Austroglanididae, with the situation in cetopsids and schilbids being independently acquired (Diogo, 2005).

The four derived morphological characters discussed above thus strongly indicate that the austroglanidid are closely related to the Ictaluridae and the cranoglanidid, but principally to the ariid and the claroteid siluriforms. This hypothesis is, as referred above, strongly supported by a cladistic analysis of 440 morphological characters in 87 genera representing all extant catfish families (Diogo, 2005). It should be noted that, according to that cladistic analysis, within the clade constituted by the Austroglanididae, the Ariidae and the Claroteidae, these latter two groups appear more closely related to each other than to the Austroglanididae. The two synapomorphies listed by Diogo (2005) to support the sister-group relationship between ariids and claroteids are: *the presence of a muscle depressor of the internal mandibular* (a feature independently acquired in catfishes such as, e.g., amphiliids, many clariids, *Malapterurus* and *Franciscodoras*); *the insertion of a significant part of the fibers of the extensor tentaculi on the mesial and/or dorsal surface of the sesamoid bone 1 of the suspensorium* (a feature also independently acquired in catfishes such as, e.g., *Parakysis*, *Acanthodoras*, *Cranoglanis*, or *Shilbe*) (see Diogo, 2005).

GENERAL CONCLUSIONS

As stressed by Skelton et al. (1984: 360), the austroglanidids present a rather generalised morphology. In fact, a detailed overview of the literature available, as well as an extensive phylogenetic analysis of 440 characters in 87 genera representing all extant catfish families (see above), revealed only two (the peculiarly-shaped, posteriorly bifurcated sesamoid bone 1 of the suspensorium and the markedly broad fourth basibranchial), or possibly, three Austroglanididae autapomorphies (if further studies would indicate that the marked lateral bifurcation of the anterodorsolateral laminar projection of the sphenotic would eventually constitute an austroglanidid autapomorphy). With respect to the phylogenetic relationships of the austrogladinids, these fishes are probably closely related to the also generalised ictalurid and cranoglanidid, and particularly ariid and claroteid, siluriforms. As other papers recently published by the authors (Diogo et al., 1999, 2000a, b; Diogo and Chardon, 2000b, c), the present study stresses that the analysis of certain characters that are not usually included in the study of catfish phylogeny, such as, e.g., the musculature of these fishes, could reveal useful data to infer the phylogenetic relationships between different siluriform groups.

ACKNOWLEDGEMENTS

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