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Osteology and myology of the cephalic region and pectoral girdle of *Plotosus lineatus*, with comments on Plotosidae (Teleostei: Siluriformes) autapomorphies

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KEYWORDS: Catfish; myology; osteology; Plotosidae autapomorphies; Plotosus lineatus; Siluriformes.

ABSTRACT

From comparisons of the cephalic and pectoral girdle structures of *Plotosus lineatus* with those of other plotosid as well as non-plotosid siluriforms, plotosid catfishes can be defined by at least six autapomorphies. These are: (1) the absence of the ventral division of the muscle arrector dorsalis; (2) the double articulation between the neurocranium and the anterior part of the suspensorium; (3) the greatly enlarged utricular otolith, which profoundly inflates the ventral surfaces of both the prootic and the pterotic; (4) the attachment of the muscle extensor tentaculi on the neurocranium lies further anteriorly than its insertion on the autopalatine; (5) the coronoid process of the mandible is linked to the maxillary by means of two thick, long ligaments; (6) the enlarged base of the maxillary barbel.

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Introduction

The Siluriformes, with their 2584 species, represent about 32% of all freshwater fishes and are one of the most economically important groups of fresh- and brackish-water fishes in the world (Teugels, 1996). Among the 35 siluriform families (Ferraris & de Pinna, 1999), the family Plotosidae, with *c.* 31 species in 10 genera (Allen & Feinberg, 1998), is surely one of the least studied. In fact, despite the large number of studies on catfish anatomy (Regan, 1911; Kindred, 1919; Alexander, 1965; Gauba, 1966, 1970; Chardon, 1968; Jayaram, 1971; Gosline, 1975; Fagade, 1980; Howes, 1983*a*, *b*, 1985; Jayaram & Singh, 1984; Vandewalle *et al.*, 1985, 1986, 1993, 1995, 1997; Lundberg & McDade, 1986; Arratia, 1987, 1990, 1992; Bornbusch, 1991*a*, *b*; Mo, 1991; Adriaens & Verraes, 1994, *1997a*, *b*, *c*; de Vos, 1995; Diogo *et al.*, 1999*a*, 2000*a*; Diogo & Chardon, *2000a*, *b*, *c*), the only papers in which the morphology of plotosids is described with some detail are those of Takahasi (1925), Tilak (1963), Srinivasachar (1958) and Chardon (1968). Even these are somewhat incomplete descriptions, exclusively devoted to specimens of the genus *Plotosus*. This probably explains why, although the family Plotosidae is commonly considered as monophyletic (Regan, 1911; Chardon, 1968; Mo, 1991; de Pinna, 1993), not even a single plotosid autapomorphy has been suggested.

The aim of this work was to study the detailed anatomy (osteology, myology and arthrology) of the cephalic region (branchial apparatus excluded) and pectoral girdle of *Plotosus lineatus* (Thunberg 1787), and to compare these structures with those of some other plotosid and non-plotosid siluriforms as the basis for an analysis on the Plotosidae autapomorphies.

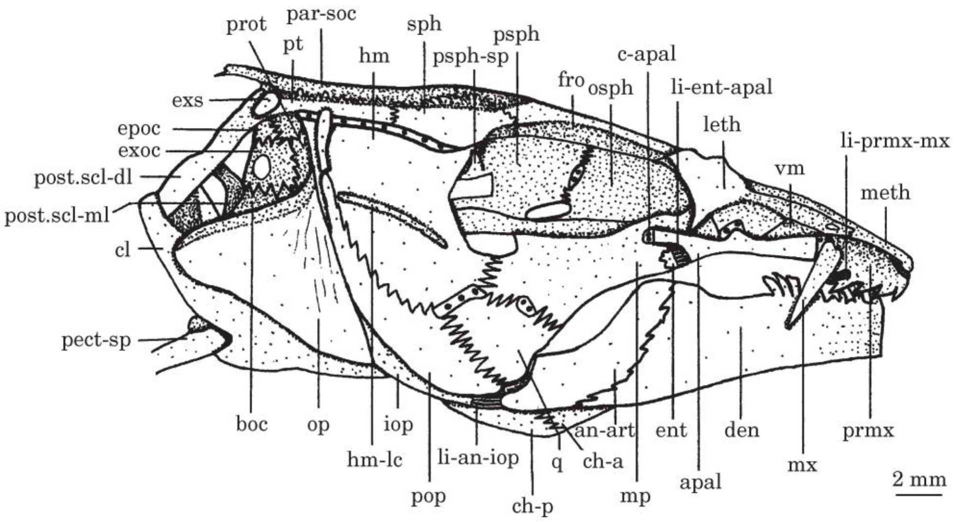
Materials and methods

The fishes studied are from the private collection of the Laboratory of Functional and Evolutionary Morphology (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 of Paris (MNHN), from the University of Gent (UG) and from the National Museum of Natural History of Washington (USNM). Anatomical descriptions are made after dissection of alcohol fixed or trypsin-cleared and alizarine-stained specimens (Taylor & Van Dyke, 1985). Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The trypsine-cleared and alizarine-stained (t&a) or alcohol fixed (alc) condition of the studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

Amphilius brevis (Amphiliidae): MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (t&a). *Amphilius jacksoni* (Amphiliidae): LFEM, 2 (alc). *Andersonia leptura* (Amphiliidae): MNHN 1961-0600, 1 (alc). *Arius hertzbergii* (Ariidae): FFEM, 1 (alc). *Arius heudelotii* (Ariidae): FFEM, 4 (alc). *Auchenoglanis biscutatus* (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Bagre marinus* (Ariidae): LFEM, 1 (alc); LFEM, 1 (t&a). *Bagrus bayad* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Bagrus docmak* (Bagridae): MRAC 86-07-P-512, 1 (alc); LFEM, 2 (alc); MRAC 86-07-P-516, 1 (t&a). *Belonoglanis tenuis* (Doumeinae): MRAC P.60494, 1 (alc); *Chrysichthys cranchii* (Claroteidae): LFEM, 1 (alc); LFEM, 1 (t&a). *Chrysichthys auratus* (Claroteidae): UNB, 2 (alc); UNB, 2 (t&a). *Chrysichthys nigrodigitatus* (Claroteidae): UNB, 2 (alc); UNB, 2 (t&a). *Clarias gariepinus* (Clariidae): MRAC 93-152-P-1356, 1 (alc); LFEM, 2 (alc). *Cnidoglanis macrocephalus* (Plotosidae): USNM 219580, 2 (alc). *Diplomystes chilensis* (Diplomystidae): LFEM, 2 (alc). *Doumea typica* (Doumeidae): MRAC 93-041-P-1335, 1 (alc); MRAC 93-052-P-152, 1 (alc). *Genidens genidens* (Ariidae): LFEM, 2 (alc). *Hemibagrus wycki* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Heterobranchus longifilis* (Clariidae): LFEM, 2 (alc). *Ictalurus punctatus* (Ictaluridae): LFEM, 5 (alc). *Mochokus niloticus* (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Bagridae): LFEM, 1 (alc). *Neosilurus rendahli* (Plotosidae): USNM 173554, 2 (alc). *Paramphilius trichomycteroides* (Amphiliidae): LFEM, 2 (alc). *Paraplotosus albilabris* (Plotosidae): USNM 173544, 2 (alc). *Phractura brevicauda* (Doumeidae): MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (t&a). *Pimelodus clarias* (Pimelodidae): LFEM, 2 (alc); LFEM, 2 (t&a). *Plotosus lineatus* (Plotosidae): USNM 200226, 2 (alc), 2 (t&a); UG, 6 (alc); UG, 3 (t&a). *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Schilbe intermedius* (Shilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* (Siluridae): LFEM, 2 (alc). *Tandanus tandanus* (Plotosidae): LFEM, 3 (alc).

In the anatomical descriptions, the nomenclature for the osteological structures of the cephalic region follows basically that of Arratia (1997). The myological nomenclature is based mainly on Winterbottom (1974). However, for the different adductor mandibulae sections, Diogo & Chardon (2000*b*) is followed since recent works have pointed out that, with respect to these sections, Winterbottom's (1974) nomenclature presents serious limitations (Gosline, 1989; Diogo & Chardon, 2000*b*). In relation to the muscles associated with the mandibular barbels, which were not studied by Winterbottom (1974), Diogo & Chardon (2000*c*) is followed. With respect to the nomenclature of the pectoral girdle muscles, Diogo *et al.* (2001) is followed.

Fig. 1. Lateral view of the skull of *Plotosus lineatus.* Infraorbital series removed. an-art, Angulo-articular; apal, autopalatine; boc, basioccipital; c-apal, cartilage of autopalatine; ch-a, anterior ceratohyal; ch-p, posterior ceratohyal; cl, cleithrum; den, dentary; ent, entopterygoid; epoc, epioccipital; exoc, exoccipital; exs, extrascapular; fro, frontal; hm, hyomandibula; hm-lc, lateral crest of hyomandibula; iop, interopercular; leth, lateral ethmoid; li-an-iop, angulo-interopercular ligament; li-ent-apal, entopterygoid-autopalatine ligament; li-prmx-mx, premaxillary-maxillary ligament; meth, mesethmoid; mp, metapterygoid; mx, maxillary; op, opercular; osph, orbitosphenoid; par.soc, parieto-supraoccipital; pect.sp, pectoral spine; pop, preopercular; post.scl-dl, dorsal limb of posttemporo-supracleithrum; post.scl-ml, median limb of posttemporo-supracleithrum; prmx, premaxillary; prot, prootic; psph-sp, spine of pleurosphenoid; pt, pterotic; q, quadrate; sph, sphenotic; vm, vomer.



Results

PLOTOSUS LINEATUS

OSTEOLOGY

Mesethmoid. Situated on the antero-dorsal surface of the neurocranium (**Figs 1, 2, 3** and **4**). Each of its antero-lateral arms is connected ligamentously to the premaxillary.

Lateral ethmoid. With a postero-laterally directed articulatory facet for the autopalatine (**Fig. 3**). In the adult specimens dissected (**Figs 1** and **3**), but not in the youngest ones (**Fig. 2**), there is a prominent dorsal projection of both the postero-dorsal surface of the lateral ethmoid and the antero-dorsal surface of the frontal.

Vomer. T-shaped (**Fig. 4**), with a ventral tooth-plate bearing large conical teeth rostrally (**Figs 2** and **4**).

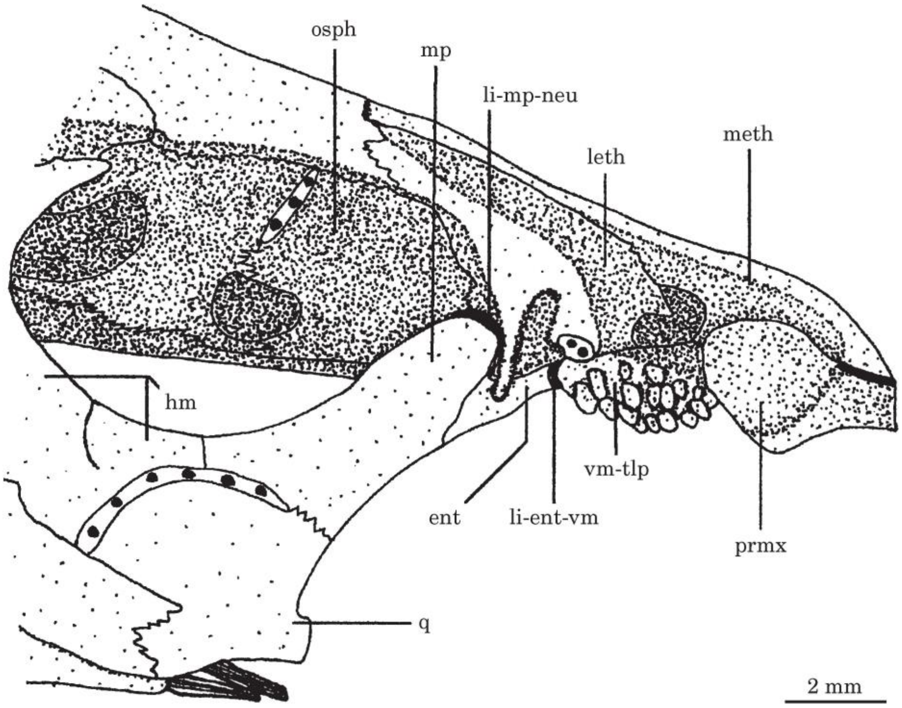
Orbitosphenoid. Posterior to the lateral ethmoid (**Figs 1, 2** and **4**). The dorsal edge of its lateral wall sutures with the ventral surface of the frontal (**Fig. 1**).

Parasphenoid. The longest bone of the cranium (**Fig. 4**). Its anterior extension overlies the vomerine shaft (**Fig. 4**). It bears a pair of ascending flanges which suture with the pterosphenoids and prootics.

Pterosphenoid. Posterior to the orbitosphenoid (**Figs 1** and **2**), covering, together with this bone, the gap between the frontals and the parasphenoid (**Fig. 1**). Its postero-lateral surface presents a prominent postero-dorso-lateral spine (**Fig. 1**; psph-sp), which contacts the well-developed antero-dorsal spine of the hyomandibula (**Fig. 1**).

Frontal. The frontals are large bones (**Figs 1** and **3**) that are largely separated by the elongated anterior fontanel, which lies in a deep oval depression of the dorsal surface of the neurocranium (**Fig. 3**). Posterior to the fontanel, each frontal bears a prominent dorsal projection (**Fig. 3**; fro-dpo), which interdigitates with its counterpart mesially, thus forming a V-shaped structure (**Fig. 3**).

Fig. 2. Lateral view of the connection between the anterior part of the suspensorium and the ethmoideal region in *Plotosus lineatus*. ent, Entopterygoid; hm, hyomandibula; leth, lateral ethmoid; li-ent-vm, entopterygoid-vomer ligament; li-mp-neu, metapterygoid-neurocranium ligament; meth, mesethmoid; mp, metapterygoid; prmx, premaxillary; osph, orbitosphenoid; q, quadrate; vm-tlp, vomerine tooth-plate.



Sphenotic. It bears, together with the pterotic, an articulatory facet for the hyomandibula (**Figs 1** and **4**).

Pterotic. The dorsal surface of this bone, together with those of the extrascapular, epioccipital, parieto-supraoccipital, sphenotic and frontal, form a deep, large concavity to receive the anterior portion of the muscle obliquus superioris (**Fig. 3**).

Prootic. It borders part of the foramen of the trigemino-facial nerve complex, which, however, lies mainly within the pterosphenoid (**Fig. 4**). The greatly enlarged utricular otolith profoundly expands ventrally the ventral surfaces of both the prootic and the pterotic (**Fig. 5**).

Epioccipital. Situated on the postero-ventral surface of the neurocranium (**Figs 1, 3, 4** and **5**).

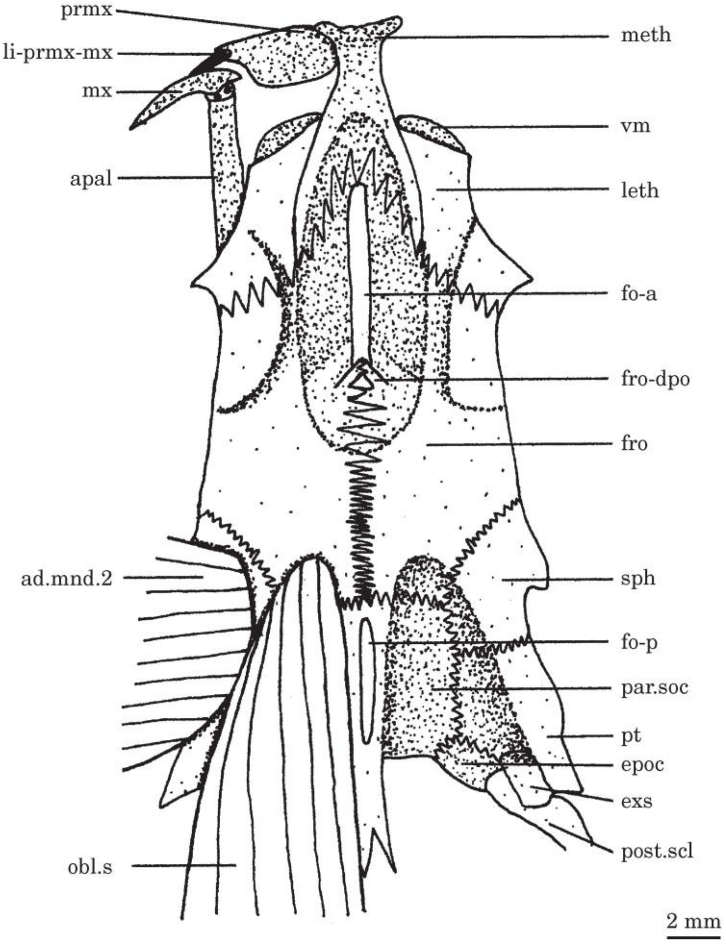
Exoccipital. Small, situated laterally to the basioccipital (**Figs 4** and **5**).

Basioccipital. Well-developed bone, forming the posterior-most part of the floor of the neurocranium (**Fig. 4**). It has two well-developed ventro-lateral processes connected by means of thick ligamentous tissue to the ventro-medial limbs of the posttemporo-supracleithrum (**Fig. 4**).

Parieto-supraoccipital. Large bone with a well-developed, posteriorly directed postero-dorsal process (**Fig. 3**). It borders the well-developed posterior fontanel (**Fig. 3**).

Extrascapular. Situated posteriorly to the pterotic (**Figs 1** and **3**).

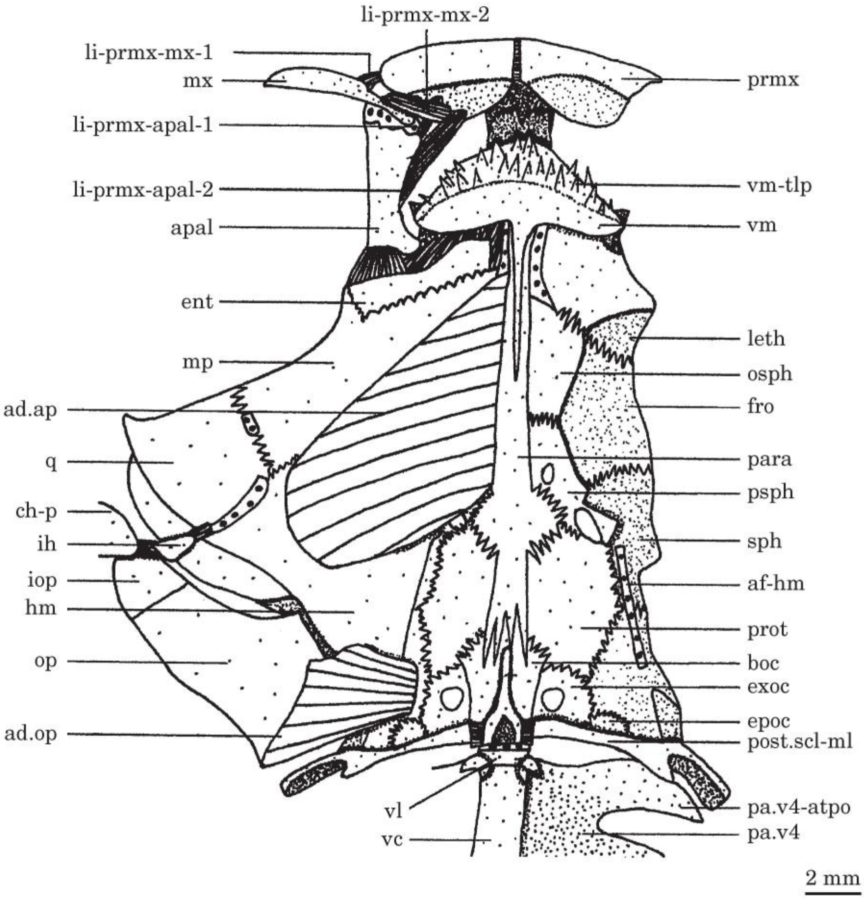
Fig. 3. Dorsal view of the neurocranium of *Plotosus lineatus*. On the left side, the palatine-maxillary system, as well as the muscles adductor mandibulae and obliquus superioris, are also represented. ad.mnd.2, Adductor mandibulae A2; apal, autopalatine; epoc, epioccipital; exs, extrascapular; fo-a, anterior fontanelle; fo-p, posterior fontanelle; fro, frontal; dorsal process of fronta; leth, lateral ethmoid; li-prmx-mx, premaxillary-maxillary ligament; meth, mesethmoid; mx, maxillary; obl.s, muscle obliquus superioris; par.soc, parieto-supraoccipital; post.scl, posttemporo-supracleithrum; prmx, premaxillary; pt, pterotique; sph, sphenotic; vm, vomer.



Angulo-articular. This bone, together with the dentary, coronomeckelian and Meckel's cartilage, constitute the mandible. Its antero-dorsal surface, together with the postero-dorsal surface of the dentary, form a prominent dorsal process (processus coronoideus), which is linked to the maxillary by means of two thick, long ligaments [**Fig. 6(a)**; li.pri-1, li.pri-2]. The posterior end of the angulo-articular has an articulatory surface for the quadrate (**Figs 1, 6** and **7**), and is linked to this bone, as well as to the interopercular and the posterior ceratohyal, by means of three strong ligaments (**Figs 6** and **8**).

Dentary. The dentaries are firmly connected, near to their symphysis, to the supporting parts of the cartilages associated with the mandibular barbels by means of a large number of short and thin fibres (**Fig. 8**).

Fig. 4. Ventral view of the neurocranium of *Plotosus lineatus*. On the left side the suspensorium and the palatine-maxillary system, as well as the ligaments and muscles associated with these complex structures, are also illustrated. apal, Autopalatine; ad.ap, adductor arcus palatini; ad.op, adductor operculi; af-hm, articulatory facet for the hyomandibular; boc, basioccipital; ch-p, posterior ceratohyal; ent, entopterygoid; epoc, epioccipital; exoc, exoccipital; fro, frontal; hm, hyomandibula; ih, interhyal; iop, interopercular; leth, lateral ethmoid; li-prmx-apal-1, premaxillary-autopalatine ligament 1; li-prmx-apal-2, premaxillary-autopalatine ligament 2; li-prmx-mx-1, premaxillary-maxillary ligament 1; li-prmx-mx-2; premaxillary-maxillary ligament 2; mp, metapterygoid; mx, maxillary; op, opercular; osph, orbitosphenoid; para, parasphenoid; pa.v4, parapophysis of vertebra 4; pa.v4-atpo, anterior transversal process of parapophysis of vertebra 4; post.scl-ml, median limb of posttemporo-supracleithrum; prot, prootic; prmx, premaxillary; q, quadrate; sph, sphenotic; vc, complex vertebra; v1, vertebra 1; vm, vomer; vm-tlp, vomerine toothplate.

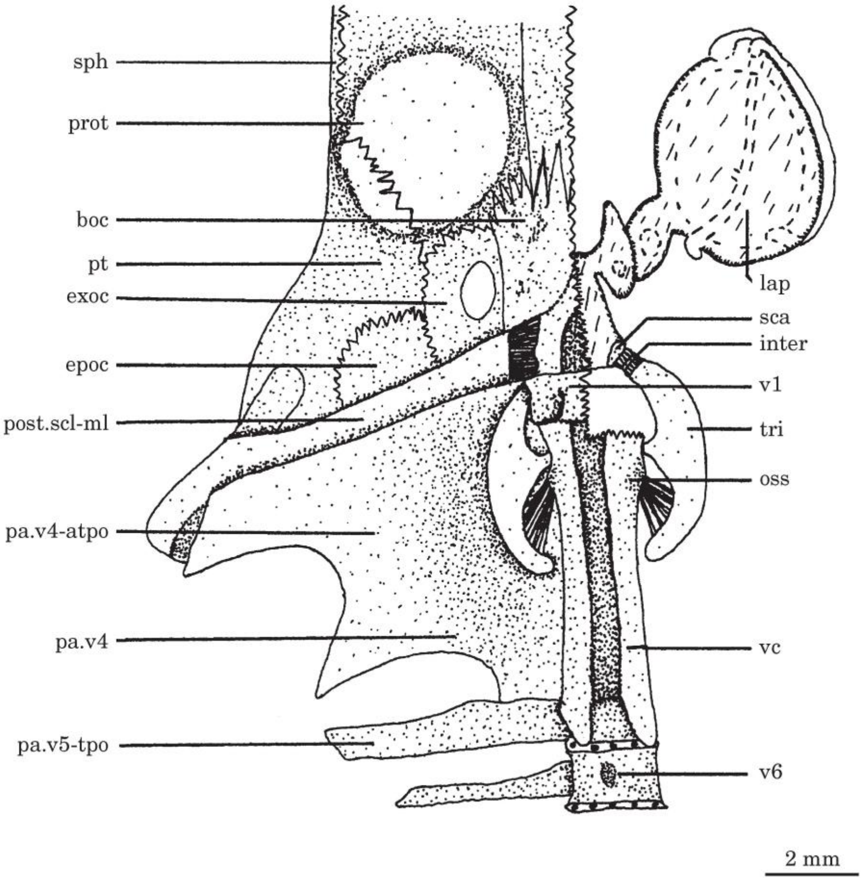


Coronomeckelian. Small bone lodged in the medial surface of the mandible. Postero-dorsally it bears a crest for attachment of the adductor mandibulae A3'-d **[Fig. 7(c)**].

Premaxillary. The broad premaxillaries are slightly mobile with respect to the mesethmoid, to which they are linked by means of ligamentous tissue (**Figs 1, 2, 3** and **4**).

Maxillary. The maxillary is connected to the premaxillary via two well-developed ligaments (**Fig. 4**). As in most catfishes, the maxillary barbels are supported by the maxillaries. However, in *P. lineatus* each of these barbels derives basally from a large, circular structure, the histological nature of which is unclear. Gross structural similarity suggests that it is composed of the same tissue as the internal core of the maxillary barbel, that is, elastin with or without cartilage (Ghiot, 1978; Ghiot & Bouchez, 1980; Benjamin, 1990). In fact, this structure, which is more highly developed in the adult specimens than in juveniles, looks clearly like an enlarged base of the maxillary barbels [**Fig. 6(c)**]. Curiously, the relation between the maxillary barbel and this structure is quite similar to that between the mandibular barbels and the structures usually named cartilages of the mandibular barbels (Diogo & Chardon, 2000*c*) [**Fig. 6(c)**, cf. **Fig. 8(a)**].

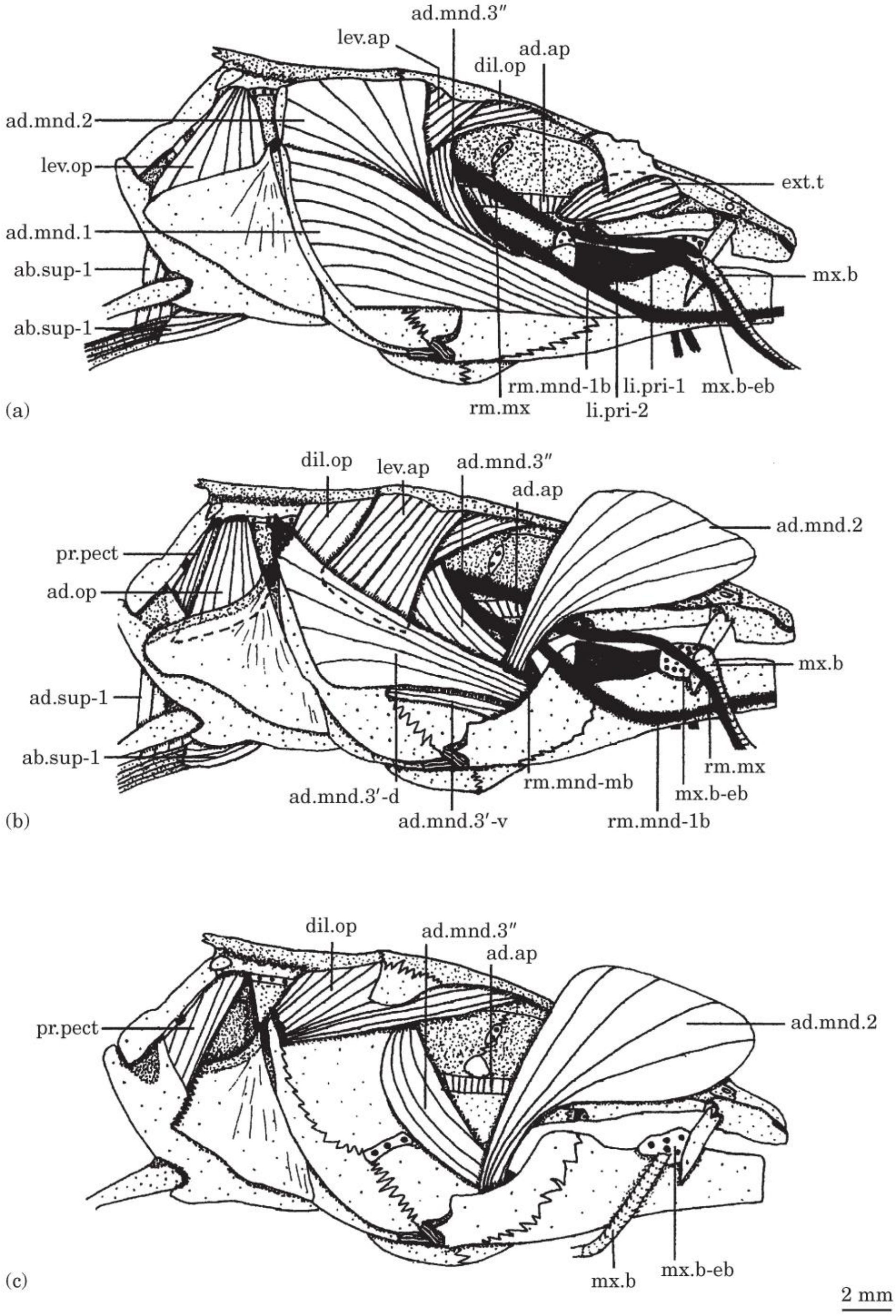
Fig. 5. Ventral view of the posterior region of the neurocranium, Weberian ossicles, and inner ear of *Plotosus lineatus*. On the right side only the inner ear and the Weberian ossicles are represented. boc, Basioccipital; cv, complex vertebra; epoc, epioccipital; exoc, exoccipital; int, intercalarium; lap, lapillus; oss, os suspensoria; pa.v4, parapophysis of vertebra 4; pa.v4-ptpo, transversal process of parapophysis of vertebra 4; pa.v5-ptpo, transversal process of parapophysis of vertebra 5; post.scl-ml, median limb of posttemporo-supracleithrum; prot, prootic; pt, pterotic; sca, scaphium; sph, sphenotic; tri, tripus; vc, complex vertebra; v1, vertebra 1; v6, vertebra 6.



Autopalatine. It articulates with the maxillary and the lateral ethmoid via, respectively, its anterior cartilage and its mesial surface (**Figs 1** and **4**). Its postero-ventral surface is attached firmly, by means of ligamentous tissue, to the entopterygoid (**Figs 1** and **4**). Antero-mesially the autopalatine is linked to the premaxillary by means of two thick ligaments (**Fig. 4**).

Fig. 6. Lateral view of the cephalic musculature of *Plotosus lineatus.* (a) All the muscles are exposed. (b) Primordial ligament 1, levator operculi and adductor mandibulae A1 were removed; adductor mandibulae A2 was folded back. (c) Adductor mandibulae A3'-d, adductor mandibulae A3'-v, levator arcus palatini; adductor operculi; adductor superficialis 1, abductor superficialis 1, pectoral fin, ramus maxillaris and

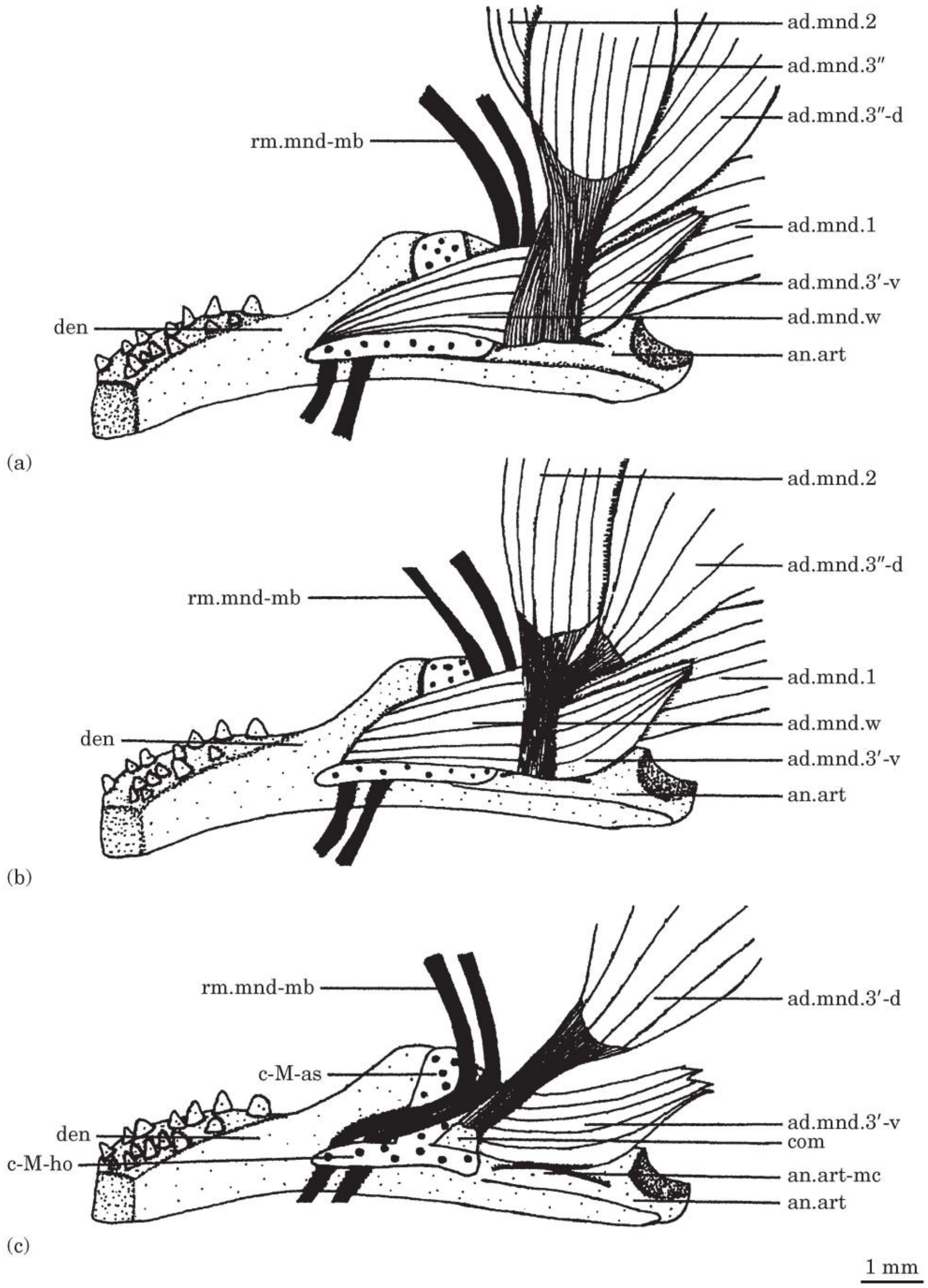
ramus mandibularis were removed; opercular cut to show the protractor pectoralis muscle. ab.sup-1, Abductor superficialis 1; ad.ap, adductor arcus palatini; ad.op, adductor operculi; ad.mnd.1, ad.mnd.2, ad.mnd.3'-d, ad.mnd.3'-v; ad,mnd.3'', different sections of the adductor mandibulae; ad.sup-1, adductor superficialis 1; dil.op, dilatator operculi; ext.t, extensor tentaculi; lev.ap, levator arcus palatini; lev.op, levator operculi; li.pri-1, primordial ligament 1; li.pri-2, primordial ligament 2; mx.b, maxillary barbel; mx.b-eb, enlarged base of maxillary barbel; pr.pec, protractor pectoralis; rm.mnd-lb, lateral branch of ramus mandibularis nerve; rm.mnd-mb, median branch of ramus mandibularis nerve; rm.mx, ramus maxillaris nerve.



Entopterygoid. The anterior margin of each entopterygoid bears a short, strong ligament that attaches to each antero-lateral arm of the vomer (**Fig. 2**). The ectopterygoids are absent.

Metapterygoid. Large, rectangular bone firmly attached, by means of short, massive ligamentous tissue, to the neurocranium (orbitosphenoid and lateral ethmoid) antero-mesially and to the entopterygoid antero-laterally (**Fig. 2**).

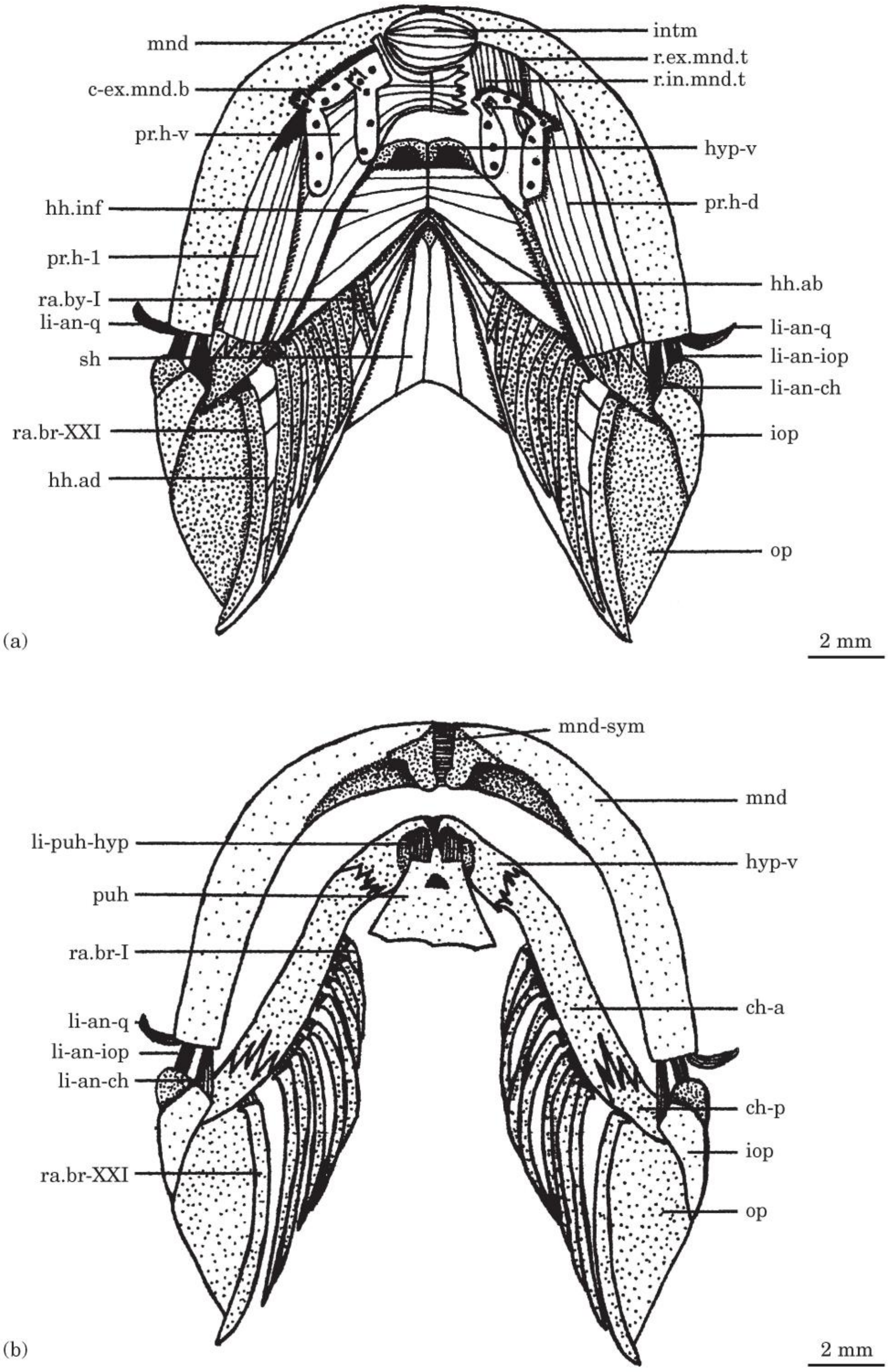
Fig. 7. Medial view of the mandible and adductor mandibulae muscle of *Plotosus lineatus*. (a) Adductor mandibulae complex exposed. (b) Adductor mandibulae A3'' was removed. (c) Adductor mandibulae A2, adductor mandibulae A1 and adductor mandibulae Aω were removed. ad.mnd.1, ad.mnd.2, ad.mnd.3'-d, ad.mnd.3'-v; ad.mnd.3'', ad.mnd.w, different sections of the adductor mandibulae; an.art, angulo-articular; c-M-as, ascending portion of Meckel cartilage; c-M-ho, horizontal portion of Meckel cartilage; den, dentary; rm.mnd-mb, median branch of ramus mandibularis nerve.



Quadrate. Its postero-dorsal surface is separated from the hyomandibula by means of a narrow cartilaginous band (**Figs 1** and **4**).

Hyomandibula. The homology, and, thus, the correct denomination, of this bone, as well as of the other suspensorium components of catfish, has been the subject of endless controversies (e.g. McMurrich, 1884; *Hoedeman, 1960a*, *b*; Gosline, 1975; Arratia & Menumarque, 1981; Howes, 1983*a*, *b*, 1985; Arratia, 1987, 1990, 1992; Howes & Teugels, 1989; Diogo & Chardon, 1998; Diogo *et al*., 2000*b*). However, for the time being, the suspensorial bones are described by their commonly used names (Arratia, 1992). The hyomandibula articulates dorsally with both the pterotic and the sphenotic (**Figs 1** and **4**).

Fig. 8. Ventral view of the cephalic musculature (a) and of the splanchnocranium (b) of *Plotosus lineatus.* c-ex.mnd.b, Cartilage associated with the external mandibular barbel; ch-a, anterior ceratohyal; ch-p, posterior ceratohyal; hh.ab, hyohyoideus abductor; hh.ad, hyohyoideus adductor; hh.inf, hyohyoideus inferioris; hyp-v, ventral hypohyal; intm, intermandibularis; iop, interopercular; li-an-ch, angulo-ceratohyal ligament; li-an-iop, angulo-interopercular ligament; li-an-q, angulo-quadrate ligament; li-puh-hyp, parurohyal-hypohyal ligament; mnd, mandible; mnd.sym, mandibular symphysis; op, opercular; pr.h-d, protractor hyoidei pars dorsalis; pr.h-l, protractor hyoideus pars lateralis; pr.h-v, protractor hyopideus pars ventralis; puh, parurohyal; ra.br-I, branchiostegal ray I; ra.br-XXI, branchiostegal ray XXI; r.ex.mnd.t, retractor externi mandibularis tentaculi; r.in.mnd.t, retractor interni mandibularis tentaculi*;* sh, sternohyoideus.



Preopercular. Long and thin bone sutured firmly to the hyomandibula and to the quadrate (**Figs 1** and **4**).

Opercular. Triangular (**Figs 1** and **4**). Antero-dorsally it articulates with the hyomandibula.

Interopercular. Its anterior and antero-medial surfaces are linked, by means of thick ligamentous tissue to the angulo-articular and to the posterior ceratohyal, respectively (**Fig. 8**).

Interhyal. The interhyal is a small bone attached, by means of ligaments, to both the posterior ceratohyal and the quadrato-hyomandibular cartilage (**Fig. 4**).

Posterior ceratohyal. Linked by ligaments to the angulo-articular (**Fig. 8**), interhyal (**Fig. 4**) and interopercular.

Anterior ceratohyal. Paired. Together with the posterior ceratohyal, it supports the branchiostegal rays [**Fig. 8(b)**].

Ventral hypohyal. Each ventral hypohyal contains a ventral concavity to receive one of the antero-lateral edges of the parurohyal [**Fig. 8(b)**].

Dorsal hypohyal. Small bone situated dorsally to the ventral hypohyal.

Parurohyal. The parurohyal (Arratia & Schultze, 1991) is a sub-triangular bone, lying medially behind the symphysis of the ventral hypohyals and connected to these bones by means of two short and thick ligaments [**Fig. 8(b)**].

Posttemporo-supracleithrum. This bone, together with the cleithrum and the scapulo-coracoid, constitute the pectoral girdle (**Figs 1, 3** and **4**). Its dorso-mesial limb is connected with the pterotic, extrascapular, epioccipital and supraoccipital by means of extensive ligamentous tissue (**Figs 1** and **3**). Its thin ventro-mesial limb is attached firmly to the basiocccipital by a strong and short ligament (**Fig. 4**). Its ventro-lateral limb is forked, forming an articulating groove for the upper edge of the cleithrum (**Fig. 1**).

Cleithrum. The cleithrum is a large, well-ossified stout structure forming the major part of the pectoral girdle and the posterior boundary of the branchial chamber [**Fig. 9(a)**]. It bears a deep crescentic, medially faced groove, with rough surfaces, which accommodates [**Fig. 9(a)**] the thick crescentic dorsal condyle of the pectoral spine [**Fig. 9(b)**]. The two cleithra are attached in the antero-mesial line by a strong ligament [**Fig. 9(a)**]. The humeral process is absent (**Fig. 1**).

Scapulo-coracoid. Elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge [**Fig. 9(a)**]. Mesially it joins its counterpart in an interdigitation of several strong serrations [**Fig. 9(a)**]. Antero-laterally, it presents an anteriorly directed process, sometimes called the coracoid bridge, which extends ventrally to the ventro-lateral surface of the cleithrum, fusing with an antero-ventral ridge of this bone [**Fig. 9(a)**]. The posterolateral end of the scapulo-coracoid bears two condyles, which articulate, respectively, with the pectoral spine and the complex radial (Mo, 1991). There is a well-developed mesocoracoid arch [**Fig. 9(a)**].

Vertebra I. Very small bone, connecting the basioccipital to the complex vertebra (**Fig. 5**).

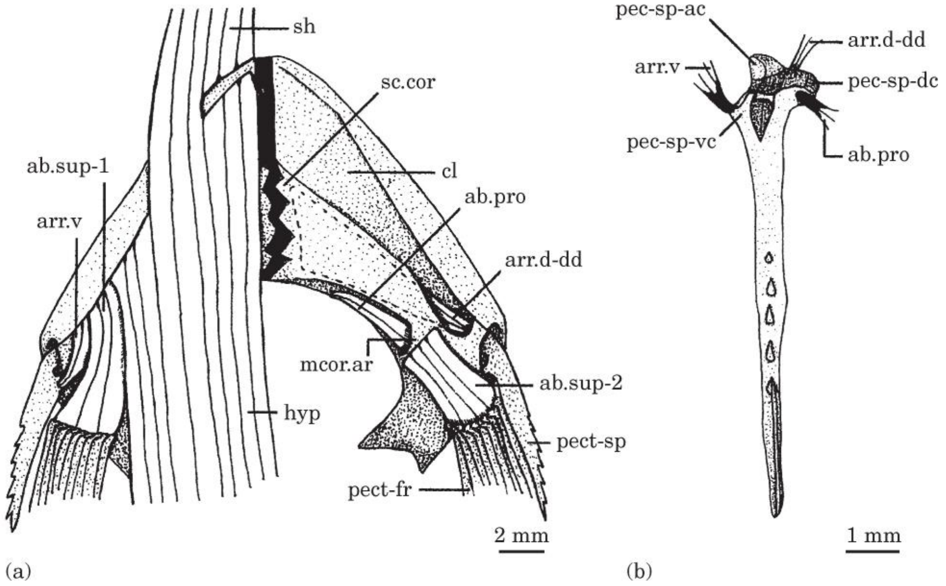
Complex vertebra. The complex vertebra is a compound formed by the fusion of the 2, 3, 4 and 5 vertebrae (**Fig. 5**).

Tripus. Boomerang-shaped bone connected, by means of ligamentous tissue, to the os suspensoria posteriorly and to the intercalarium anteriorly (**Fig. 5**).

Intercalarium. Very small bone ligamentously linked to both the tripus and the scaphium (**Fig. 5**).

Scaphium. Small bone associated mesially with the sinus impar perilymphaticus (**Fig. 5**).

Fig. 9. *Plotosus lineatus.* (a) Ventral view of the pectoral girdle. In the left side all the muscles are exposed; in the right side the hypaxialis, sternohyoideus, arrector ventralis, section 1 of the abductor superficialis were removed. (b) Medial view of the pectoral spine, showing the insertions of the muscles responsible for its movement. ab-pro, Abductor profundus; ab-sup-1, abductor superficialis 1; ab-sup-2, abductor superficialis 2; arr-d-dd, dorsal division of arrector dorsalis; arr-v, arrector ventralis; cl, cleithrum; hyp, hypaxialis; mcor-ar, mesocoracoid arch; pec-fr, pectoral fin rays; pec-sp, pectoral spine; pec-sp-ac, pec-sp-dc, pec-sp-vc, anterior, dorsal and ventral condyles of pectoral spine; sc-cor, scapulo-coracoid; sh, sternohyoideus.



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Musculus adductor mandibulae. The adductor mandibulae A1 originates on the preopercular and quadrate and inserts on the lateral surfaces of both the angulo-articular and the dentary [**Fig. 6(a)**]. The adductor mandibulae A2, which lies dorso-mesially to the A1, attaches posteriorly on the lateral surface of the preopercular and on the dorsal surfaces of both the pterotic and sphenotic [**Figs 4** and **Fig. 6(a)**]. Anteriorly, it attaches on the mesial crest of the angulo-articular [**Fig. 7(c)**]. The adductor mandibulae A3' is divided into dorsal and ventral parts. The dorsal part (A3'-d) originates on the pterotic, hyomandibula and preopercular [**Fig. 6(b)**], and inserts on the coronomeckelian bone [**Fig. 7(c)**]. The ventral part originates on the quadrate [**Fig. 6(b)**] and inserts on the mesial surface of the angulo-articular [**Fig. 7(c)**]. The deeper bundle of the adductor mandibulae, A3'', runs from the hyomandibula [**Fig. 6(c)**] to the medial crest of the angulo-articular [**Fig. 7(a)**]. Lastly, the Aω, which is lodged in the medial face of the mandible, is attached anteriorly in the postero-mesial surface of the dentary and posteriorly on the tendon of the adductor mandibulae A2 [**Fig. 7(b)**].

Musculus levator arcus palatini. It originates on the dorsal surface of the sphenotic, as well as on the lateral surface of the frontal, and inserts on the lateral face of the hyomandibula [**Fig. 6(b)**].

Musculus adductor arcus palatini. It extends from the lateral sides of the parasphenoid, pterosphenoid and orbitosphenoid to the medial sides of the hyomandibula and metapterygoid (**Figs 4** and **6**).

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Musculus dilatator operculi. Thick muscle situated medially to the levator arcus palatini [**Fig. 6(b)**]. It runs from the dorsal surfaces of both the pterotic and the sphenotic, as well as from the ventro-lateral surface of the frontal, to the antero-dorsal edge of the opercular (medial to the preopercular but lateral to the articulatory facet of the opercular for the hyomandibula) [**Fig. 6(c)**].

Musculus levator operculi. It originates on both the ventro-lateral surface of the pterotic and the postero-dorsal surface of the hyomandibula and inserts on the dorsal edge of the opercular [**Fig. 6(a)**].

Musculus adductor operculi. Situated medially to the levator operculi, it originates on the ventro-medial surface of the pterotic and inserts on the dorso-medial surface of the opercular [**Figs 4** and **6(b)**].

Musculus extensor tentaculi. It runs from the antero-lateral surface of the lateral ethmoid to the dorsal surface of the posterior limb of the autopalatine [**Fig. 6(a)**].

Musculus protractor hyoidei. This muscle has three parts. The pars ventralis, in which are lodged the moving parts of the cartilages associated with the mandibular barbels, originates on the anterior ceratohyal and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis [**Fig. 8(a)**]. The pars lateralis originates on the anterior ceratohyal, inserting, by means of a thick tendon, on the ventro-medial face of the dentary [**Fig. 8(a)**]. The pars dorsalis runs from the anterior ceratohyal to the dentary [**Fig. 8(a)**].

Musculus retractor externi mandibularis tentaculi. Small muscle running from the moving part of the cartilage associated with the outer mandibular barbel to the dentary (**Fig. 8**).

Musculus retractor interni mandibularis tentaculi. Small muscle that originates on the moving part of the cartilage associated with the internal mandibular barbel and inserts on the dentary (**Fig. 8**).

Musculus hyohyoideus inferior. Thick muscle attached laterally on the ventral surface of the ceratohyals and medially on a median aponeurosis [**Fig. 8(a)**].

Musculus hyohyoideus abductor. It runs from the first (medial) branchiostegal ray to a median aponeurosis, which is associated with two long, strong tendons, attached, respectively, to the two ventral hypohyals (**Fig. 8**).

Musculus hyohyoideus adductor. Each hyohyoideus adductor connects the branchiostegal rays of the respective side (**Fig. 8**).

Musculus sternohyoideus. It originates on the anterior region of the cleithrum [**Fig. 9(a)**] and inserts on the posterior region of the urohyal [**Fig. 8(a)**]. Some of its fibres are continuous which those of the hypoaxialis muscle [**Fig. 9(a)**].

Musculus arrector ventralis. It runs from the ventro-lateral surface of the cleithrum [**Fig. 9(a)**] to the ventral condyle of the pectoral spine [**Fig. 9(b)**].

Musculus arrector dorsalis. Only the dorsal division (Diogo *et al.*, 2001) of this muscle is present in *P. lineatus*, running from the dorso-mesial edge of the scapulo-coracoid [**Fig. 9(a)**] to the antero-lateral edge of the pectoral spine [**Fig. 9(b)**].

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Musculus abductor profundus. It originates on the postero-mesial edge of the coracoid [**Fig. 9(a)**], passes anteriorly to the mesocoracoid arch and to the adductor superficialis muscle and inserts on the mesial surface of the dorsal condyle of the pectoral spine [**Fig. 9(b)**].

Musculus adductor superficialis. It is differentiated in two sections. The larger section [**Fig. 6(a),(b)**; ad.sup-1] 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 differentiated in two sections. The larger section [**Fig. 9(a)**; ab.sup-1] attaches medially on the ventral face of both the cleithrum and the scapulo-coracoid and laterally on the antero-ventral margin of the ventral part of the pectoral fin rays. The smaller section [**Fig. 9(a)**; ab.sup-2] runs from the postero-lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of the pectoral fin rays.

Discussion

The present observations on *P. lineatus* reveal some morphological features that, by their rarity, could constitute potential autapomorphies. These are: (1) the absence of the ventral division of the muscle arrector dorsalis; (2) the absence of the humeral process of the cleithrum; (3) the double articulation between the neurocranium and the anterior part of the suspensorium; (4) the presence of a prominent dorsal projection of the frontal, just behind the anterior fontanel; (5) the greatly enlarged utricular otolith, which profoundly inflates the ventral surfaces of both the prootic and the pterotic; (6) the attachment of the muscle extensor tentaculi on the neurocranium lies further anteriorly than its insertion on the autopalatine; (7) the coronoid process of the mandible is linked to the maxillary by means of two thick, long ligaments; (8) the enlarged base of the maxillary barbel; (9) the thin medial limb of the post-temporo-supracleithrum.

In order to appraise the phylogenetic significance of these nine morphological features present in *P. lineatus*, the osteology and myology of the cephalic region and pectoral girdle of representatives of some other genera were studied. These were *Cnidoglanis macrocephalus*, *Neosilurus rendahli*, *Paraplotosus albilabris* and *Tandanus tandanus*, as well as other non-plotosid catfishes (Materials and Methods). In addition, the catfishes examined were compared with other siluriforms described in the literature. A discussion on the phylogenetic worth of each of these features follows. It should be noted that the term autapomorphy is employed here as it was originally defined by Hennig (1966), that is, as a derived character that was acquired by, and is restricted to, a phyletic line after it branched off from its sister group, and that can be used phylogenetically to separate this phyletic line from all the others.

ABSENCE OF THE VENTRAL DIVISION OF THE MUSCLE ARRECTOR DORSALIS

The plesio-morphic configuration of the muscle arrector dorsalis in catfishes seems to be that found in the diplomystids, in which, like in almost all the non-siluriform teleosts, the arrector dorsalis is a well-developed, undivided muscle (Diogo *et al.*, 2001). In almost all non-diplomystid catfishes in which the pectoral girdle muscles have been studied (Jaquet, 1898; Alexander, 1965; Saxena & Chandy, 1966; Gainer, 1967; Taverne & Aloulou-Triki, 1974; Brosseau, 1978; Bornbusch, 1991*a*; Diogo *et al.*, 2001) the arrector dorsalis is differentiated in two (dorsal and ventral) well-developed divisions. In the majority of these fishes, the ventral division, situated on the ventral surface of the pectoral girdle, inserts on the antero-lateral edge of the pectoral spine, and the dorsal division, situated on the dorsal surface of the pectoral girdle, inserts on the anterior edge of the dorsal condyle of the pectoral spine. However, in *P. lineatus* (**Fig. 9**), as well as in all the other plotosids studied in this work, there is only one division of the arrector dorsalis, which clearly corresponds to the dorsal division of other catfishes. Such a configuration of the arrector dorsalis is clearly a derived one, since, although there is only one division of this muscle, as in the diplomystids and in non-siluriform teleosts, this division does not lie in the ventral (the plesiomorphic condition: see above), but in the dorsal side of the pectoral girdle (**Fig. 9**) (see Diogo *et al.*, 2001). The presence of this derived character in all the plotosids studied, and its absence in non-plotosid catfishes, suggests that the absence of the ventral division of the muscle arrector dorsalis is a Plotosidae autapomorphy.

ABSENCE OF THE HUMERAL PROCESS OF THE CLEITHRUM

In the majority of other catfishes (Regan, 1911; Alexander, 1965; Chardon, 1968; Lundberg, 1970, 1975, 1982; Howes, 1983*a*, 1985; Arratia, 1987; Grande & Lundberg, 1988; Schaefer, 1990; Mo, 1991; de Pinna, 1993, 1998), the upper limb of the cleithrum bears a roughly triangular, pointed process directed posteriorly, the humeral process. According to most authors (Tilak, 1963; Alexander, 1965; Chardon, 1968; Mo, 1991; de Pinna, 1996), the presence of a well-developed humeral process is the primitive condition for siluriforms. In *P. lineatus* (**Fig. 1**), and also in all the other plotosids studied in this work, this process is absent. However, this character does not seem to represent a Plotosidae autapomorphy, since it is present also in the amphiliids and clariids examined, as well as in certain other siluriforms (e.g. nematogenyids, callichthyids, loricariids, trichomycterids, astroblepids, amblycipitids and some sisorids) described in the literature (Tilak, 1963; Alexander, 1965; Schaefer, 1990; Mo, 1991; de Pinna, 1996; Reis, 1998). It should be noted that the presence of this character in these families does not preclude it being a plotosid autapomorphy, since it could be ascribed to secondary loss. However, loss characters are only detectable on the basis of a consistent cladogram reflecting the phylogenetic relationships between the different catfish families. Since such a cladogram is not available at the moment (de Pinna, 1998; R. Diogo, pers. obs.), the absence of the humeral process of the cleithrum in the plotosids cannot be ascribed, with confidence, to secondary loss, and, consequently, cannot be identified as a Plotosidae autapomorphy.

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DOUBLE ARTICULATION BETWEEN THE NEUROCRANIUM AND THE ANTERIOR PART OF THE SUSPENSORIUM

In most catfishes the pterygoid series of the suspensorium is only loosely attached, by means of long, massive ligaments, to the ethmoideal region (Alexander, 1965; Gosline, 1975; Arratia, 1990, 1992; Diogo & Chardon, 1998, *2000a*, 2001; *Diogo et al., 1999b*, 2000*b*). However, in a few catfishes the pterygoid series are firmly attached to the neurocranium. This is the case, for example, of some clariids (David, 1936; Diogo & Chardon, 1998, 2001; Cabuy *et al.*, 1999; Diogo *et al.*, 2000*b*), sisorids (Gauba, 1966, 1970; de Pinna, 1996; He, 1997) and amphiliids (He, 1997; Diogo & Chardon, 1998, 2001; Diogo *et al., 2000a*, *b*). In these fishes the antero-mesial surface of the entopterygoid is firmly linked to the ethmoideal region, by means of very short, strong ligamentous tissue. In the loricariids (Arratia, 1990, 1992; Diogo & Chardon, 1998; Schaefer, 1990, 1991) there is a direct, firm articulation between the dorsal margin of the metapterygoid and the neurocranium. In *P. lineatus*, as well as in all the other plotosids examined, the pterygoid series is also attached firmly to the ethmoideal region. However, in these fishes, contrary to all the taxa mentioned above, such a firm attachment is made by two, rather than one, regions of firm contact between the pterygoid series and the neurocranium. Here the antero-mesial edge of the metapterygoid is linked firmly, by means of short, strong ligamentous tissue, with the antero-lateral and postero-lateral surfaces of, respectively, the orbitosphenoid and the lateral ethmoid. The anterior margin of the entopterygoid is attached firmly, by means of a very short, strong ligament to the postero-lateral surface of the vomer (**Fig. 2**). The uniform presence of this derived character in all the plotosids studied, and its absence in all other catfishes, indicates that it represents a Plotosidae autapomorphy.

PRESENCE OF A PROMINENT DORSAL PROJECTION OF THE FRONTAL, JUST BEHIND THE ANTERIOR FONTANEL

As described above, in *P. lineatus* each frontal presents, just behind the anterior fontanel, a prominent dorsal projection (**Fig. 3**; fro-dpo), which interdigitates with its counterpart mesially, thus forming a V-shaped unit (**Fig. 3**). Such a dorsal projection of the frontal is absent in all the non-plotosid catfishes either examined in the present study or described in the literature. However, the fact that this dorsal projection of the frontal is well-developed only in *Plotosus*, being developed poorly in *Paraplotosus* and absent in *Cnidoglanis*, *Tandanus* and *Neosilurus*, clearly indicates that the presence of such a projection does not constitute a Plotosidae autapomorphy.

THE GREATLY ENLARGED UTRICULAR OTOLITH PROFOUNDLY INFLATES THE VENTRAL SURFACES OF BOTH THE PROOTIC AND THE PTEROTIC

The plesiomorphic condition for siluriforms is that in which the utriculus is not a particularly conspicuous element, being confined within the central area of the prootic (Mo, 1991; de Pinna, 1993). According to Mo (1991) and de Pinna (1993), this situation is present in all catfishes, except in ariids and in *Horabagrus* [the taxonomic position of this genus is not clear (Mo, 1991; de Pinna, 1993)], where the utriculus is enlarged conspicuously relative to the plesiomorphic condition, occupying an area corresponding to the prootic, pterotic and exoccipital. However, as stressed by Chardon (1968), and supported by the present work, in *P. lineatus*, as well as in the other plotosids, the utricular otolith is also a greatly enlarged element, which profoundly inflates the ventral surfaces of both the pterotic and the pterotic (**Fig. 5**). Due to the apparent (the phylogenetic relationships between the different catfish families are not completely clear at the moment) phylogenetic distance between the ariids, the plotosids and *Horabagrus* (Chardon, 1968; Mo, 1991; de Pinna, 1993, 1998; C. Oliveira & M. Chardon, pers. obs.), it is very likely that the enlargement of the utriculus has appeared independently in the evolution of these three groups. The presence of a greatly enlarged utricular otolith, with a prominently convex ventral surface, which profoundly inflates the ventral surfaces of both the prootic and the pterotic, but not of the exoccipital (see above), is exclusive to the plotosids and appears to be a Plotosidae autapomorphy.

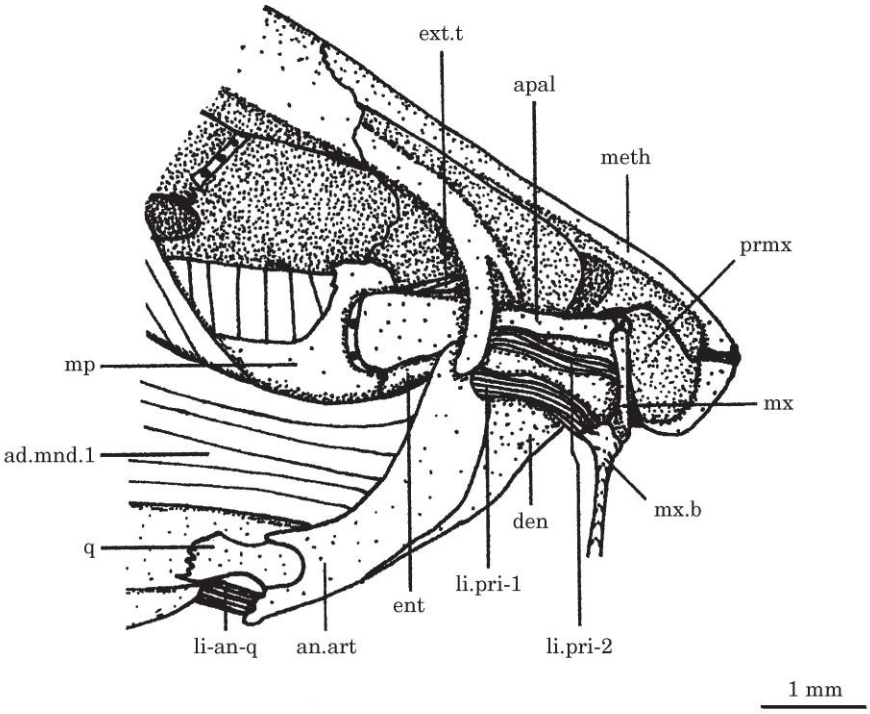
THE ATTACHMENT OF THE MUSCLE EXTENSOR TENTACULI ON THE NEUROCRANIUM LYING FURTHER ANTERIORLY THAN ITS INSERTION ON THE AUTOPALATINE

In almost all catfishes, the origin of the muscle extensor tentaculi on the neurocranium lies postero-mesially or mesially to its insertion on the autopalatine (Alexander, 1965; Gosline, 1975; *Diogo et al., 1999b*, *2000c*; Diogo & Chardon, 2001). However, as Gosline (1975) pointed out, in *P. lineatus* the attachment of the extensor tentaculi on the neurocranium lies much more anteriorly to its insertion on the autopalatine [**Fig. 6(a)**]. Although there are some differences between the configuration of the extensor tentaculi of the other plotosids examined and that of *P. lineatus*, in all these fishes the origin of this muscle lies much more anteriorly to its insertion on the autopalatine. The uniform distribution of this derived character in the plotosids studied, coupled with its absence in non-plotosid catfishes, suggests it is an autapomorphy of the family Plotosidae.

CORONOID PROCESS OF THE MANDIBLE LINKED TO THE MAXILLARY BY MEANS OF TWO THICK, LONG LIGAMENTS

The plesiomorphic condition for siluriforms, present in most of these taxa, is that in which there is a thick, long ligament (named primordial ligament) between the coronoid process of the mandible and the maxillary (Alexander, 1965; Gosline, 1975; *Diogo et al., 1999b*; *Diogo & Chardon, 2000a*, *b*, 2001). In some specialized catfishes, such as amphiliids or clariids, such a connection between the coronoid process and the maxillary is absent (Diogo *et al., 1999b*, *2000a*; *Diogo & Chardon, 2000a*, *b*, 2001). The situation present in *P. lineatus* [**Fig. 6(a)**] and the other plotosids studied (**Fig. 10**), in which there are two, rather than one, thick, long ligaments between the coronoid process and the maxillary is, however, exclusive to the plotosids and therefore represents a Plotosidae autapomorphy.

Fig. 10. Lateral view of the anterior region of the skull of *Neosilurus rendahli*. ad.mnd.1, Adductor mandibulae A1; an.art, angulo-articular; apal, autopalatine; den, dentary; ent, entopterygoid; ext.t, extensor tentaculi; mp, metapterygoid; mx, maxillary; li-an-q, angulo-quadrate ligament; li-pri-1, primordial ligament 1; li-pri-2, primordial ligament 2; meth, mesethmoid; mx.b, maxillary barbel; prmx, premaxillary; q, quadrate.



ENLARGED BASE OF THE MAXILLARY BARBEL

As described above, in *P. lineatus* each of the maxillary barbels stems from a large, circular structure, the histological nature of which seems to be similar to that of the internal core of the maxillary barbel, that is, elastin with or without cartilage (Ghiot, 1978; Ghiot & Bouchez, 1980; Benjamin, 1990). A detailed histological analysis of this structure is necessary to test this gross structural similarity. This structure clearly looks like a posterior extension of the proximal part of the maxillary barbels [**Fig. 6(c)**]. However, it should be noted that there are some differences between the different plotosid specimens examined concerning the shape of the enlarged base of the maxillary barbel, e.g. it is much more developed in the adult specimens of *P. lineatus* than in juveniles of the same species, and also more than in both the adult and young specimens of the other plotosid species analysed. Since such an enlarged base is uniformly present in all the plotosids studied and is absent in non-plotosid taxa it is assumed to represent a Plotosidae autapomorphy.

THIN MEDIAN LIMB OF THE POSTTEMPORO-SUPRACLEITHRUM

The plesiomorphic condition in siluriforms for the median limb of the posttemporo-supracleithrum (usually called ossified Baudelot's ligament; Arratia & Gayet, 1995) seems to be that of *Diplomystes* and most other catfishes, in which this limb is a thick, well-developed structure connected, by means of a short, strong ligament, to the basioccipital and or exoccipital bones (Regan, 1911; Srinivasachar, 1958; Alexander, 1965; Chardon, 1968; Mo, 1991; Diogo *et al.*, 2001). In a small number of Siluriformes, such as clariids, heteropneustids, akysids and astroblepids, this limb is absent (Srinivasachar, 1958; Alexander, 1965; Chardon, 1968; Mo, 1991). In *P. lineatus* (**Fig. 4**), as well as in all the other plotosids examined, the median limb of the posttemporo-supracleithrum is noticeably compressed anteroposteriorly. However, such an anteroposterior compression is found also in some non-plotosid catfishes, such as chacids and silurids *(Bornbusch, 1991b*; Pinna, 1993), as well as amphiliids (Diogo *et al.*, 2000*a*). The phylogenetic significance of this character is thus not clear. According to Bornbusch (1991*b*) the anteroposterior compression of the median limb of the posttemporo-supracleithrum represents an autapomorphy of the Siluridae. However, de Pinna (1993) suggested two derived character states. Character state 1 represents the moderate condition, which is only found in the Chacidae and the Plotosidae, being an autapomorphy of the taxon composed by these two sister-groups (de Pinna, 1993). Character state 2 represents the extreme condition, which is only found in the Siluridae, being an autapomorphy of this group. In any case, the thin median limb of the posttemporo-supracleithrum cannot be accepted as a Plotosidae autapomorphy.

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