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Morphology of the cranial system of *Platyclarias machadoi*: interdependencies of skull flattening and suspensorial structure in Clariidae

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Abstract The African catfish *Platyclarias machadoi* stands out from other clariid species by its extremely dorsoventrally flattened skull. This paper focuses on the spatial constraints and consequent functional interdependencies in this very low skull (average skull height of $27.5 \pm 3.0\%$ skull length); such as the medial position of the retroarticular process on the lower jaw, the horizontal position of the suspensorium, the lateral tilting of the pterygoid bones and the anterior part of the quadrate with regard to the suspensorial transverse long axis. These characteristics can be presumed to have major influences on the capacity of suspensorial adduction, influencing the feeding and respiratory mechanisms. A comparison with other clariid species showed that one of the apomorphies is the presence of an extra muscle (musculus adductor mandibulae A₃" pars levator tendinis) in the adductor mandibulae complex. This extra muscle lifts the tendon complex of the adductor mandibulae, resulting in a higher moment on the lower jaw. Some comments on the original species/genus descriptions are given.

Keywords Catfish · *Platyclarias machadoi* · Osteology · Myology

Introduction

The freshwater clariids are one of the 37 catfish taxa in the Siluriformes (Sabaj et al. 2004). Although they occur

in Syria, southern Turkey and large parts of Southeast Asia, their diversity is the largest in Africa (Teugels 1996). This African richness is demonstrated by the presence of 12 genera with up to 74 species (Teugels 1996). Clariid catfishes are characterized by an elongate body, the presence of four barbels, long dorsal and anal fins, and especially by the autapomorphic presence of a suprabranchial organ, formed by arborescent structures from the second and fourth gill arches (Greenwood 1961; Teugels and Adriaens 2003).

Unique for these clariids is the presence of an evolutionary range between fusiform and anguilliform representatives, with *Heterobranchus* at one end and *Dolichallabes* at the other end (Pellegrin 1927), and with *Platyclarias* as one of the intermediate morphs. Although this trend towards anguilliformity has been observed in other taxa of Teleostii, and even Amphibia and Sauropsida (Lande 1978), it is never as extreme as within the Clariidae. Together with this tendency, a whole set of morphological changes have been observed, such as decrease and loss of the adipose fin, continuous unpaired fins, reduction of paired fins, reduction of the eyes, reduction of the skull bones and hypertrophied jaw muscles (Devaere et al. 2001). Another characteristic in clariids is a dorsoventrally flattened skull. Even though all clariid representatives have a flattened head, it is quite extreme in *Platyclarias machadoi* Poll, 1977 [still not as extreme as in, for example, the Asian and non-clariid catfish species *Chaca chaca* (Hamilton, 1822) (Tilak 1971)]. Such extensive flattening of the skull imposes substantial changes in those physical parameters that are crucial for the head kinematics during feeding and respiration. Trade offs can especially be suspected at the level of the suprabranchial organ and the hypertrophied jaw muscles, which will undoubtedly have an impact on the functioning of the respiratory and feeding apparatuses.

As with all other economically less important representatives of the clariid taxa, the morphology of *Platyclarias machadoi* is poorly understood. This also accounts for the taxonomy and systematics. Poll (1977) only provides some characteristic, external

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morphological features, as well as some gross osteological characters. A detailed morphological study is thus required before any inferences can be made with respect to spatial constraints. As a result, this study focuses on morphological (gross morphology and histology) and biometrical data (metric and meristic) of the cranial bones and muscles.

These data serve the aim of this paper to identify possible spatial constraints and consequent functional implications of an extremely dorsoventrally flattened skull, which may interfere with respiration and feeding. The observations in *P. machadoi* are compared with that of representative species of non-anguilliform and anguilliform clariids, where an evaluation of species-specific traits for *P. machadoi* is subsequently done. The species used for comparison are *Clarias gariepinus* (Burchell, 1822), having a non-anguilliform shape, *Gymnallabes typus* Günther, 1867 having an anguilliform shape and *Platyallabes tihoni* (Poll, 1944) having an intermediate shape.

Materials and methods

The material examined in this study was obtained from the Royal Museum for Central Africa (MRAC) (Teruren, Belgium). These specimens include the holotype and the 21 paratypes of *Platyclarias machadoi* Poll, 1977 (MRAC 13307). The specimens were all collected in Upper Cuango, Cafunfo, Borio River, Angola. One specimen (MRAC 78-6-P-1348-364 (paratype 14), SL: 123 mm) was cleared and stained following the procedure of Taylor and Van Dyke (1985), for osteological examination. One specimen (MRAC 78-6-P-1348-364 (paratype 16), SL: 113 mm) was used to study the external morphology as well as the myology by means of dissection and muscle fibre staining (Bock and Shear 1972). Furthermore one specimen (MRAC 78-6-P-1348-364 (paratype 17), SL: 119 mm) was used for serial sectioning after embedding in Technovit 7100 (Kulzer). The obtained 5 µm thick sections were stained with Toluidin Blue (Adriaens 1998). Sections were studied using a Leitz Diaplan light microscope. This helped to better visualize the attachment areas of the muscles, the contact area of the bones and the angles between the different suspensorial bones, adductor arcus palatine and the neurocranium. Because of the assumed homology of the bones with those of *Clarias gariepinus*, for the terminology and the nomenclature we refer to Adriaens and Verraes (1997a, b, 1998), for pelvic girdle we use Arratia (2002), whereas for the cranial myology we follow Winterbottom (1974) and Adriaens and Verraes (1996, 1997c, d). Drawings of both cleared and dissected material were made using a stereoscopic microscope (Wild M5) with a camera lucida. We compared this material with that of seven other clariid species, as well as one heteropneustid species (which is presumed to be the sistergroup of clariids) (Teugels and Adriaens 2003): *Clarias gariepinus* (Teugels 1986), *Heterobranchus*

longifilis Valenciennes, 1840 (David 1935) and *Heteropneustes fossilis* (Bloch, 1794) (David 1935) as representatives of the fusiform genera; *Gymnallabes typus* (Cabuy et al. 1999), *Channallabes apus* (Günther, 1873) (Devaere et al. 2001) and *Dolichallabes micropthalmus* Poll, 1942 (Devaere et al. 2004) as anguilliform representatives and *Platyallabes tihoni* as a more intermediate representative. Between brackets are the references from which the measurements were obtained. Other data were obtained in this study.

Furthermore, 38 measurements were taken point-to-point using digital callipers to 0.1 mm (Digital ruler, Mauser), interfaced directly with a computer, on a set of 22 specimens of *Platyclarias machadoi*. Measurements terminology follows that of Devaere et al. (2004): total length (TL); standard length (SL); preanal length (PaL); anal fin length (AFL); dorsal fin length (DFL); prepelvic length (PPvL); prepectoral length (PPcL); predorsal length (PdL); distance between the occipital process and the dorsal fin (SPDFL); pelvic fin length (PvFL), pectoral fin length (PcFL); pectoral spine length (PcSL); caudal peduncle depth (CPD); body depth at anus (ABD); maxillary barbel length (MxB); external mandibular barbel length (EmnB); internal mandibular barbel length (ImnB); nasal barbel length (NB); interpelvic distance (IpdD); interpectoral distance (IpcD); skull length (SkL); preorbital length (PoL); skull width (SkW); supraoccipital process length (SpL); supraoccipital process width (SpW); interorbital distance (IoD); anterior nostril interdistance (ANID); posterior nostril interdistance (PNID); rostral skull width (RSkW); orbital skull width (OskW); skull height (SkH); eye diameter (ED); snout height (SnH); prehyoid length (PhL); internal mandibular interdistance (ImnID); external mandibular interdistance (EmnID); mouth width (MW) and skull roof width (SkR). The morphology of the vertebrae and the following meristic counts were made on each specimen using the radiographies made with a MPG 65 generator and a RSN 620 X-ray-tube (General Electric) (42 kV, 320 Ma, 10 ms, focus distance 1 m): total number of vertebrae (TV), number of ribs (RB).

Comparative material examined

Museum abbreviations are listed in Leviton et al. (1985)

Platyallabes tihoni Dem. Rep. Congo. Kingabwa, Stanley pool, MRAC 13307 (Holotype); Kinsuka, MRAC 73-68-P-143, MRAC 138698-699 ($n=2$), 125345-349 ($n=4$), MRAC 73-22-P-3127 ($n=3$); Bulu, Luozi, BMNH 1976.5.21.30-39 ($n=9$), MCZ 50239 ($n=13$); Inga, MCZ 88947, MCZ 50537 ($n=15$); Tadi, Kibunzi, MCZ 50297 ($n=5$).

Channallabes apus Angola. Ambriz, BMNH 1873.7.28.16 (Holotype); other specimens, Dem. Rep. Congo. Bokalakala, MRAC 175247-270 ($n=10$);

Kinshasa, MRAC 97-056-P-0001-0003 ($n=2$); Bumba, MRAC 88-25-P-2192-227 ($n=36$); Boma, MRAC 939; Riv. Lula, Bushimaie, MRAC 153505; Kelé, MRAC 1491; Stanleyville, MRAC 30893-30900 ($n=8$), MRAC 88-01-P-1976-1992 ($n=17$); Riv. Ruki, Eala, MRAC 14747-49 ($n=3$); Lake Tumba swamp area, MRAC 46299; Katanga, MRAC 39480; Riv. Botota, keseki, MRAC 67763-77 ($n=15$); Mwilambongo, MRAC 72886-887 ($n=2$); Dekese, Riv. Lofu, Anga, MRAC 153352; Yangambi, MRAC 68700; Riv. Oubangu, Imfondo, MNHN 1922-0029; Loango, MNHN 1924-0079, MNHN 1924-0080; Sangha, MNHN 1925-0137; Mogende, MNHN 1926-0155-59 ($n=5$); Riv. Congo, MNHN, 1937-0124-25; Stanley pool, Bamu, MNHN 1958-0111; Boloko, Riv. Likouala, MNHN 1962-0401 ($n=7$); Mossaka, Riv. Likouala, MNHN 1963-0402 ($n=2$); Riv. Loadjili, Songolo, MNHN 1967-0143 ($n=6$); Mangala, BMNH 1896.3.9.17; Riv. Lebuzi, Kaka Muno, BMNH 1912.4.1411-12 ($n=2$); Lower Congo, BMNH 1887.1.13.8-9 ($n=2$); Stanley Falls, BMNH 1889.11.20.5; New Antwerp, Upper Congo, BMNH 1899.2.20.16; Siala-Ntoto swamps, BMNH 99.11.27.92; Bangyville, Ubangi, BMNH 1907.12.26.34; Kashi, Lulua, MHNG 1248.3; Banana, NMW 47240-42; Mollunda, NMW 47245 ($n=4$), NMW 47246. Congo. Yangala Youbi, MNHN 1967-0146; Djembo, Kouilou, MNHN 1967-0147; Cayo, MNHN 1989-0527; Riv. Nanga, between Boukou-Zassi and Kouilou swamp area, MRAC 90-57-P2315; Sintou, Riv. Kibombo, Kouilou, MNHN 1967-0144; Riv. Loadjili, Songolo, Pointe Noire, MNHN 1967-0145 ($n=6$); Riv. Youbi, Noubi. Angola. Caungula, Mabete, Riv. Uamba, MRAC 162088; Riv. Camuconda, Tchimenji, MRAC 162089, MRAC 162090-094 ($n=5$), MRAC 162095-100 ($n=6$); Riv. Ganga-Ludchimo, MRAC 162083-086 ($n=4$).

Gymnallabes typus Nigeria. Old Calabar, BMNH 1866.12.4 ($n=2$) (Syntypes); other specimens, Nigeria. Umu-Eze Amambra, MRAC 84-16-P-1-2; Riv. Sombreiro, East of Erema, MRAC 91-067-P0134; Niger Delta, MRAC 97-030-P-0001-0010 ($n=10$); lake Odediginni, Agudama, Yenagoa, MRAC 92-083-P-0035-0036; Okaka, Epie Creek, between Nun and Rashi Riv., MRAC 97-085-P-0001-0004 ($n=4$); Riv. Sombreiro, Odiemerenyi, Ahoada, MRAC 91-067-P-0135-0136; New Calabar, Choba, MRAC 91-105-P-1; Rumuji swamps, MRAC 86-10-P-72; Oshika, MRAC 84-28-P-28, MRAC 84-28-P-25; Riv. Cron, Itu, MRAC 88-36-P-10; between Sapele and War, Niger Delta, MRAC 74-29-P-600; Muoha, New Calabar, MRAC 91-10-P-478; Biseni, Taylor Creek, MRAC 91-01-P278; Ossomari, BMNH 1902.11.10.119. Cameroun. Riv. Kom, Ntem, Aboulou, MRAC 73-18-P-3307-309.

Dolichallabes microphthalmus Dem. Rep. Congo. Kuningu, MRAC 44655, adult male, 229 mm SL (holotype), MRAC 44656-659 ($n=3$) (196–210 mm SL) and 62407, 188 mm SL (paratypes), MRAC 57662, 196 mm

SL, MRAC 18850, 90 mm SL; Boende swamps, MRAC 101843, 149 mm SL, MRAC 176123-124 ($n=1$), 68 mm SL; Bokuma, MRAC 79093, 134 mm SL, MRAC 93774, 66 mm SL; Bokuma-Tchuapa, MRAC 79258-260 ($n=3$) (85-126 mm SL); Ndwa (Boloko), MRAC 78808-810 ($n=3$) (99-110 mm SL); Inonge, MRAC 96672, 110 mm SL; Maylimbe, Tshela, MRAC 66721, 97 mm SL.

Clarias gariepinus Artificially cultivated specimens ($n=10$), Ghent University.

Heterobranchus longifilis Egypt. Nile, AMNH 3054 SW.

Heteropneustes fossilis Aquarium specimen, AMNH 172276 SW.

Results

External morphology

Platyclarias machadoi has a dorsoventrally flattened body. The body is elongated, ovoid behind the head and laterally compressed caudally. The preserved specimens of *Platyclarias machadoi* show an even somewhat dark-brownish colour, with a slightly lighter ventral side (Fig. 1).

Even more striking than the flattening of the body is the extremely dorso-ventrally compressed head. Although the jaw muscles are clearly visible, they are not bulging out. The triangular skull roof is the only bony part of the skull that is distinctly visible without removing the skin. On top of the skull roof there is a well-defined, lightly-coloured stain (otherwise only seen in *Gymnallabes alvarezi*, current study), although not always sharply delimited. The eyes are always clearly visible in all specimens. When removing the skin, many hidden fat particles emerge. The lower lip slightly extends beyond the upper lip.

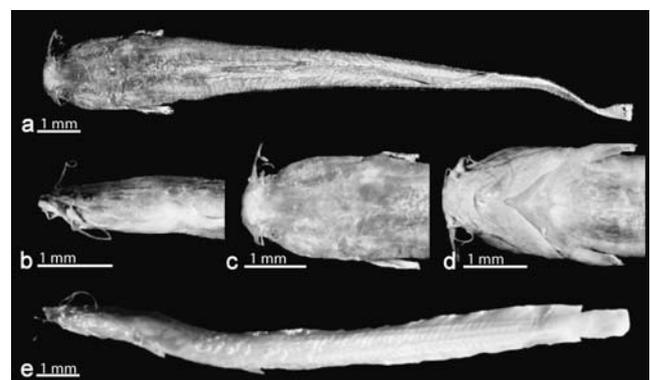


Fig. 1 *Platyclarias machadoi* (132 mm SL) (MRAC 78-6-P-1348-364, paratype 12); a dorsal overall view, b lateral side, c dorsal side and d ventral side of head, e lateral overall view. (Photographs: S. Devaere)

The unpaired fins (dorsal, anal and caudal) are not fused. The dorsal fin originates far behind the supraoccipital process of the parieto-supraoccipital bone. Also the anal fin originates far behind the head (Fig. 1e). The paired fins are always present. The large pectoral fins are preceded by a large, non-serrated pectoral spine. Also the pelvic fins are distinctly present.

Cranial skeleton

Neurocranium

In general, the skull of *Platyclarias machadoi* is reduced. The skull roof shows a limited constriction in the orbitoethmoid region. The overall skull has a wide appearance and this is mainly due to the horizontal position of the suspensorium (Fig. 2).

Ethmoid region The nasal bone bears a distinct expansion on the lateral side and a small plate on the medial side. The nasal bone covers the nasal sac and encloses the rostral end of the supraorbital canal of the lateral line system, which splits up in this bone. The nasal bone is medially enclosed by the mesethmoid. It is attached to all surrounding bones by connective tissue, allowing the nasal cavity to expand. The solid mesethmoid shows a moderate constriction behind the two firm, rostral wings. It interdigitates caudally with the

frontals and laterally makes contact with the lateroethmoid. The supraorbital canal runs between the latero- and mesethmoid and forms rostrally a clear superficial separation of these two bones. The mesethmoid forms the short anterior border of the anterior fontanel. The lateroethmoid shows a distinct, laterally pointed process. Although there is no direct contact between the lateroethmoid and the infraorbital II, this latter bone shows a limited articulation ridge and there is a strong connective tissue link between the two. Ventrolaterally, the lateroethmoid shows a clear articular facet for the articulation with the rod-shaped autopalatine. Ventrally, the premaxillaries are supported by the mesethmoid. The arrow-shaped prevomer adjoins the mesethmoid and interdigitates caudally with the parasphenoid through a variable number of pointed spines (one to three). The prevomer carries one continuous large tooth plate (Fig. 3).

Orbital region The largest bones of the neurocranium are the contralateral frontals. Rostrally, they interdigitate with the latero- and mesethmoid. On the caudal side, each frontal makes contact with the sphenotic, pterotic and the parieto-supraoccipital. The two frontals broaden somewhat caudally. Both halves are connected to each other, except on their rostral side, where they enclose the anterior fontanel. Ventrally, the frontals show two lateral flanges, expanding clearly the orbitosphenoid outlines. The anastomosis of the supraorbital and infraorbital canals of the lateral line system is situated at the boundary of the frontals and the sphenotics.

The lateral walls of the neurocranium are formed by the orbitosphenoid and the pterosphenoid, which both connect to the ventrally situated parasphenoid. This bone reaches backward and upward to the temporal region, covering a major part of the skull floor. It bears one elongated and several short processes, reaching occipital region (Fig. 3).

Lateral of the skull roof lie the circumorbital series, comprising four infraorbitals and the antorbital bone. Except for infraorbital IV and to some extent infraorbital III, all other circumorbital bones are tubular. The small antorbital bone is the most rostrally situated bone in the series, lying at the rostral tip of the autopalatine, close to the base of the nasal barbel. The tubular lacrimal lies at the level of the olfactory organ. The infraorbitals II to IV surround the eye. The fourth infraorbital is the largest and bears a supraorbital outgrowth bordering the eye posterodorsally. It is situated laterally against the frontals, from which it is rather widely separated by connective tissue.

Temporal region The sphenotic of *Platyclarias machadoi* interdigitates rostromedially with the frontals and caudally with the pterotic. The latter interdigitates rostrally over a small length with the frontal, medially to the parieto-supraoccipital and caudally to the posttemporo-supracleithrum. Both sphenotic and pterotic bones take a more or less horizontal position, with

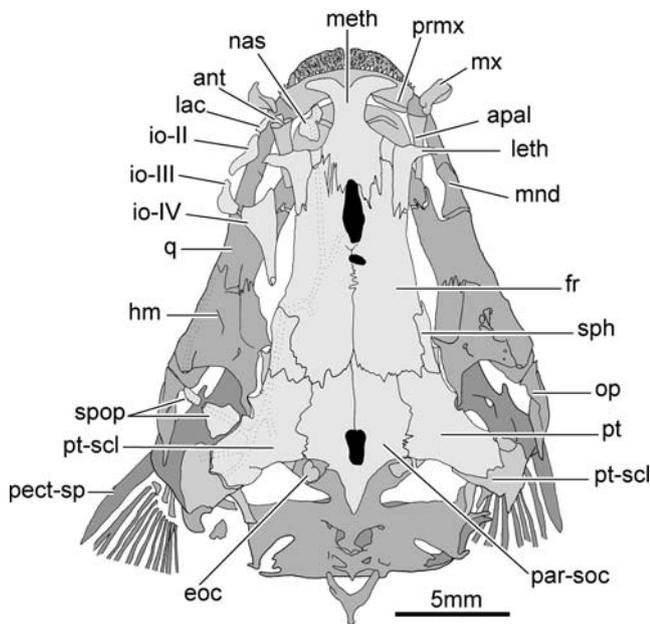


Fig. 2 Dorsal view of the skull of *Platyclarias machadoi* (123 mm SL) (MRAC 78-6-P-1348-364, paratype 14), right nasal, infraorbital series and suprapraopercular bones are removed. *ant* antorbital, *apal* autopalatine, *eoc* epioccipital, *fr* frontal, *hm* hyomandibula, *io-II-IV* infraorbital II-IV, *lac* lacrimal, *leth* lateral ethmoid, *meth* mesethmoid, *mnd* mandibula, *mx* maxilla, *nas* nasal, *op* opercle, *par-soc* parieto-supraoccipital, *pect-sp* pectoral spine, *prmx* premaxilla, *pt* pterotic, *pt-scl* posttemporo-supracleithrum, *q* quadrate, *sph* sphenotic, *spop* suprapraopercle

some downward curving, especially at the level of the sphenotic. Both bones form the only connection between the neurocranium and the suspensorium, by means of a set of processes and an articular ridge. Anterolaterally on the sphenotic and posterolaterally on the pterotic one large process can be distinguished. Between these two processes a distinct cartilaginous ridge, articulating with the hyomandibula, can be found on both bones. Ventrally, this region is covered by the paired prootic.

Occipital region The parieto-supraoccipital complex is situated in the medio-caudal part of the skull roof, rostrally enclosed by the frontals and medially by the pterotic bones. This bone is characterized by a large, somewhat pointed process on the caudal edge. The parieto-supraoccipital encloses the posterior fontanel, which lies in the caudal part of this bone. The separation between the two parietal halves is still partially visible on one specimen (MRAC 78-6-P-1348-364, paratype 14), from the medio-rostral border to the posterior fontanel. The posttemporo-supracleithrum is rostrally attached to the pterotic and connects caudoventrally to the pectoral girdle. Furthermore, *Platyclarias machadoi* shows two clear epioccipitals. Ventrally, the unpaired basioccipital and a paired exoccipital border this region.

Splanchnocranium

Maxillary bones The premaxillaries are plate-shaped bones, ventrally supporting the nasal sac. Almost the complete ventral surface of this bone is covered with

posteriorly directed teeth. There is only a limited caudal outgrowth of the plate. The maxillaries form a cup-like bone. They enclose the bases of the maxillary barbels and each bear two articular facets for the articulation with the autopalatine.

Mandibula The long lower jaw consists of two parts: the os dento-splenio-mentomeckelium and the os angulo-articulo-retroarticulare (Fig. 4). The coronoid process, which is situated at the interdigitation between the two above-mentioned mandibular bone complexes, is distinct. The tooth battery runs close up to the coronoid process. The retroarticular process is highly asymmetrical and situated completely medial from the quadrate. Caudally of the mandibular bone complex up to two small, tubular splenials can be discerned. The lower jaw complex embeds the rostral end of the preoperculo-mandibular canal of the lateral line system and shows five pores for branches of this canal. The first three pores lie in the os dento-splenio-mentomeckelium, the fourth is situated on the border of both bone complexes, while the fifth one is located on the caudal end of the lower jaw.

Palatine The rod-like autopalatine has two cartilaginous ends. Anteriorly, it articulates with the maxillary part. Furthermore, the palatine lies ventrolaterally from the lateroethmoid and articulates with it through a central, elliptic articulation facet.

Suspensorium As in most Siluriformes, the suspensorium consists of the hyomandibula, quadrate,

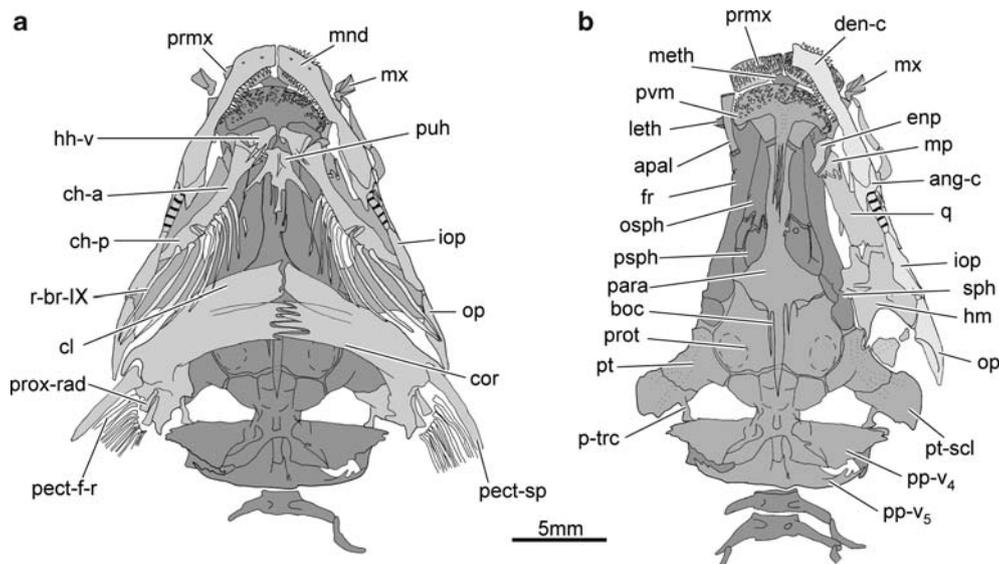


Fig. 3 a Ventral view of the skull of *Platyclarias machadoi* (123 mm SL) (MRAC 78-6-P-1348-364, paratype 14); b ventral view of the upper cranium, pectoral girdle, hyoid skeleton and lower jaw (partly removed) (dotted areas indicate cartilage). *ang-c* angulo-splenio-articulo-retroarticular complex, *apal* autopalatine, *boc* basioccipital, *ch-a* ceratohyal anterior, *ch-p* ceratohyal posterior, *cl* cleithrum, *cor* coracoid, *den-c* dento-splenio-mentomeckelium complex, *enp* entopterygoid, *fr* frontal, *hh-v* ventral hypohyal, *hm* hyomandibula, *iop* interopercle, *leth* lateral ethmoid, *meth*

mesethmoid, *mnd* mandibula, *mp* metapterygoid, *mx* maxilla, *op* opercle, *osp* orbitosphenoid, *p-trc* process transscapular, *para* parasphenoid, *pect-f-r* pectoral fin ray, *pect-sp* pectoral spine, *pp-v4* parapophysis of vertebra 4, *pp-v5* parapophysis of vertebra 5, *prm* premaxilla, *prot* prootic, *psph* pterosphenoid, *prox-rad* proximal radialia, *pt* pterotic, *pt-scl* posttemporo-supracleithrum, *pvm* prevomer, *puh* parurohyal, *q* quadrate, *r-br-IX* branchiostegal ray IX, *sph* sphenotic

entopterygoid, metapterygoid and the preopercle (Figs. 2, 4). In *Platyclarias machadoi*, the suspensorium takes a remarkable horizontal position. The hyomandibula connects the suspensorium to the neurocranium, through a set of interdigitating processes. At the level of the sphenotic, this connection occurs through one long, pointed process. Also at the level of the pterotic, only one process is present. In between these processes lies the articulation ridge, close to the border of the sphenotic and pterotic bones. At the anterior margin of the hyomandibula, no distinct bulgy outgrowth can be discerned. On both sides, the hyomandibula bears a ridge; on the medial side, for the attachment of the ligamentum hyomandibula-ceratohyale, on the lateral side for the insertion of several muscles (levator arcus palatini, A_3'' part of the adductor mandibular complex and the retractor tentaculi). The opercular process of the hyomandibula is caudoventrally orientated. The dorsal edge of the hyomandibula and the quadrate shows almost a straight line, with little indentation. Rostrally, the quadrate only makes contact with the metapterygoid and has no direct contact with the entopterygoid, as these two are separated by the metapterygoid. At the ventro-rostral side of the quadrate a broad, flat slightly rounded surfaced articular facet, for the articulation with the mandibula, is present. The metapterygoid connects caudally with the quadrate through a synchondrosis and an interdigitation zone, and is rostradorsally enclosed by the larger entopterygoid. Anteriorly, the entopterygoid is connected ligamen-

tously to the prevomer, the palatine and the lateral ethmoid, thus corresponding to a sesamoid 'entopterygoid type 4' (Arratia 1992).

Hyoid arches The hyoid arch consists of two ceratohyals (anterior and posterior) and two hypohyals (ventral and dorsal) (Fig. 3a). Ventrocaudally, the hyoid arch articulates with eight (up to nine) branchiostegal rays. The parurohyal lies in between the two hyoid arches and bears two caudo-lateral processes and one large, broad, forked, caudal process (Fig. 3a). The parurohyal is connected to the ventral hypohyal by means of two separate paruro-hypohyal ligaments (Fig. 7c).

Branchial arches The branchial morphology resembles that of *Clarias gariepinus* (Adriaens and Verraes 1998). One exception is the low number of gill rakers (up to seven).

Opercular The main opercular bone is the opercle; this triangular, long, flattened bone shows a large articular facet for the hyomandibula on its rostradorsal side (Fig. 2). The opercular muscles attach on the distinct ridge on the medial side of the posterior part. The opercle and the interopercle are ligamentously connected to each other (Fig. 3b). The interopercle, on its turn is also ligamentously attached to the lower jaw. The interopercle is a long, flat bone, situated medially of the suspensorium. As already mentioned, the preopercle is incorporated into the suspensorium. This bone surrounds a part of the preoperculo-mandibular canal. The caudal part of this canal is guided by up to two supra-preopercular bones. The most proximal supra-preopercular bone has a plate-like expansion, while the second bone, when present, is tubular (Fig. 2).

Cranial myology

Muscles of the lower jaw (Fig. 5)

M. adductor mandibulae This complex forms a large jaw-closing muscle, covering a large part of the latero-dorsal side of the head in *Platyclarias machadoi*. It consists, as in other clariids, of an external A_2A_3' -part and an internal A_3'' , which are separated by the levator arcus palatini (Adriaens and Verraes 1996).

The bipennate A_2A_3' forms the biggest part of the complex (Fig. 5a-c). This part covers the A_3'' completely, as well as the levator arcus palatini and the adductor and dilatator operculi. It can be divided into a dorsal $A_2A_3'\alpha$ -part and a ventral $A_2A_3'\beta$ -part. Both these parts attach to the lower jaw through an aponeurosis, which inserts on the angular complex, close to the coronoid process. The $A_2A_3'\alpha$ -part originates at the frontal, the sphenotic, the pterotic, the supra-preopercular series, and even the posttemporo-supracleithrum. This part is dorsorostrally covered by the fourth infra-orbital. The more ventrally situated $A_2A_3'\beta$ connects the

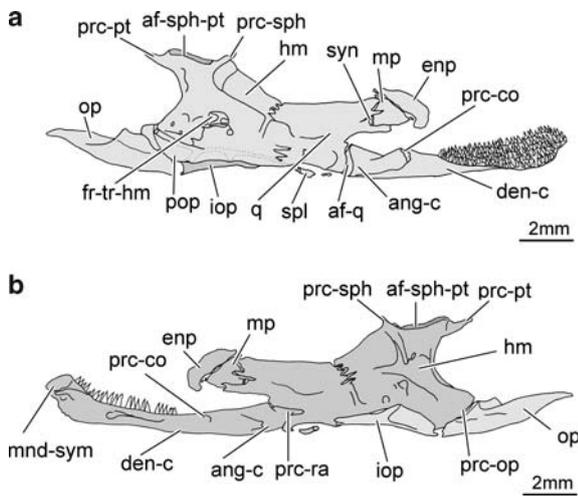


Fig. 4 Lateral (a) and medial (b) view of the splanchnocranium of *Platyclarias machadoi* (123 mm SL) (MRAC 78-6-P-1348-364, paratype 14) (dotted areas indicate cartilage). *af-q* articular facet of the angulo-splenio-articulo-retroarticular with the quadrate, *af-sph-pt* articular facet of the hyomandibula with the sphenotic and the pterotic, *ang-c* angulo-splenio-articulo-retroarticular complex, *den-c* dento-splenio-mentomeckelium complex, *enp* entopterygoid, *fr-tr-hm* foramen truncus hyomandibularis, *hm* hyomandibula, *iop* interopercle, *mnd-sym* mandibular symphysis, *mp* metapterygoid, *op* opercle, *pop* preopercle, *prc-co* coronoid process, *prc-op* processus opercle, *prc-pt* processus pterotic, *prc-ra* processus retroarticularis, *prc-sph* processus sphenotic, *q* quadrate, *spl* splenial, *syn* synchondrosis

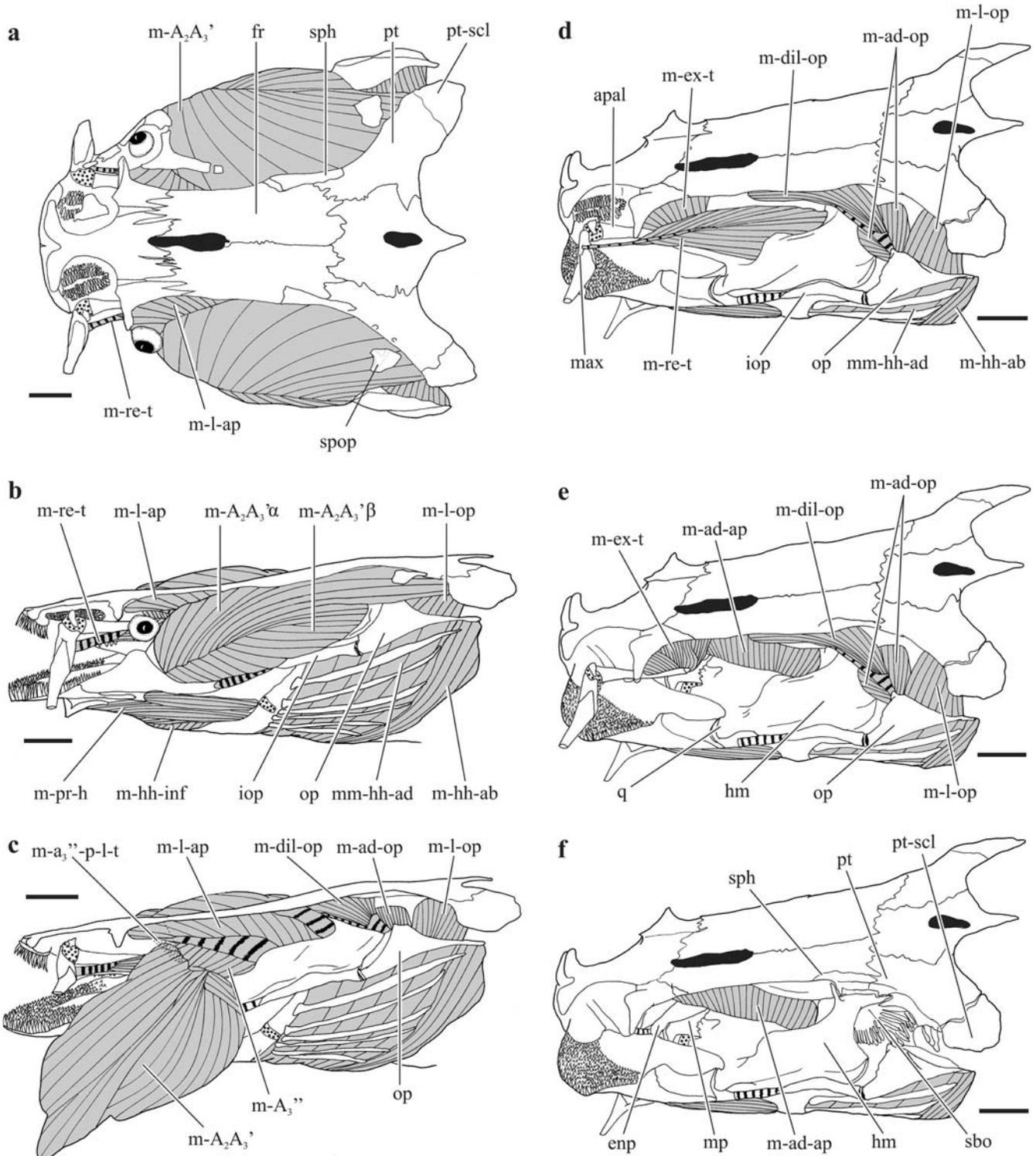


Fig. 5 Cranial musculature of *Platyclarias machadoi* (113 mm SL) (MRAC 78-6-P-1348-364, paratype 16). **a** Dorsal view, skin removed; **b** lateral view, skin removed; **c** lateral view, skin removed and A_2A_3' -part folded back; **d** laterodorsal view, jaw muscles and levator arcus palatini removed; **e** laterodorsal view, retractor tentaculi removed; **f** laterodorsal view, extensor tentaculi, dilatator operculi, adductor operculi and levator operculi (dotted areas indicate cartilage). *apal* autopalatine, *enp* entopterygoid, *fr* frontal, *hm* hyomandibula, *iop* interopercle, *mp* metapterygoid, *max* maxilla, $m-A_2A_3'\alpha$ dorsal part of the musculus adductor mandibulae, $m-A_2A_3'\beta$ ventral part of the $m-A_2A_3'$ (musculus adductor

mandibulae A_2A_3'), $m-A_3''$ musculus adductor mandibulae A_3'' , $m-A_3''-p-l-t$ musculus adductor mandibulae A_3'' pars levator tendinis, *m-ad-ap* musculus adductor arcus palatini, *m-ad-op* musculus adductor operculi, *m-dil-op* musculus dilatator operculi, *m-ex-t* musculus extensor tentaculi, *m-hh-ab* musculus hyohyoideus abductor, *m-hh-inf* musculus hyohyoideus inferior, *m-l-ap* musculus levator arcus palatini, *m-l-op* musculus levator operculi, *mm-hh-ad* musculi hyohyoidei adductores, *m-re-t* musculus retractor tentaculi, *m-pr-h* musculus protractor hyoidei, *op* opercular, *pt* pterotic, *pt-scl* posttemporo-supracleithrum, *q* quadrate, *sbo* suprabranchial organ, *sph* sphenotic, *spop* suprapreopercle

lower jaw to the suspensorium. More specifically it originates from the angular complex and inserts on the hyomandibula, the quadrate and the preopercle. The muscle fibre direction of the A_2A_3' has a range of almost 160° . Medially, a tendon originates caudally at the levator arcus palatini and has its insertion on the most anteriorly situated tendon of this muscle (Fig. 6)

The deeper part of the adductor mandibulae, the A_3'' , is connected to the neurocranium and the suspensorium as well. More specific, the horizontally situated muscles fibres originate both directly and through a tendon at the angular complex and attach to the medial side of the suspensorium, on the hyomandibula and the rostro-dorsal rim of the quadrate and furthermore to the frontal, the sphenotic and the pterosphenoid. The A_3'' lies medially from the levator arcus palatini and laterally of the retractor tentaculi (Fig. 5c). In between this A_3'' and the more laterally situated levator arcus palatini runs an extra muscle. This muscle is situated close to the anterior border of the levator arcus palatini, where it originates on the lateral ethmoid and the frontal and inserts on the large tendon complex of the jaw muscle and more posterior on a medial tendon of the A_2A_3' . Until now, such a separate muscle could not be observed in other clariids.

M. intermandibularis This compact muscle covers the mandibular symphysis, ventral on the rostral end of the mandibula (Fig. 7a). The intermandibular muscle is separated from the protractor hyoidei through the wide interconnecting tissue of the left and right mandibular barbel base.

Suspensorial muscles

M. levator arcus palatini This thin muscle sheet has a complex morphology, consisting of a muscle part and a complex of aponeuroses (Figs. 5b, c, 6). This muscle is situated between two parts of the adductor mandibulae complex and runs medially from the eye. There is a predominantly dorsoventral fibre direction, with more

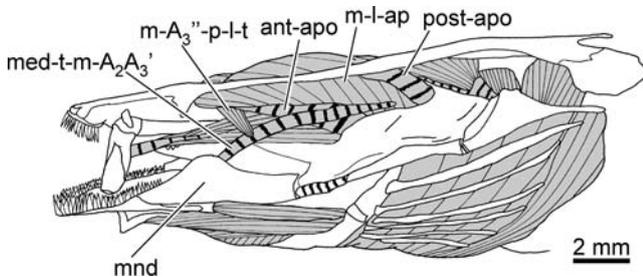


Fig. 6 Musculus adductor mandibulae A_3'' pars levator tendinis morphology of *Platyclarias machadoi* (113 mm SL) (MRAC 78-6-P-1348-364, paratype 16). *ant-apo* anterior aponeurosis of the musculus levator arcus palatini, *med-t-m-A₂A₃'* medial tendon of musculus adductor mandibulae A_2A_3' , *mnd* mandibula, *m-l-ap* musculus levator arcus palatini, *m-A₃''-p-l-t* musculus adductor mandibulae A_3'' pars levator tendinis, *post-apo* posterior aponeurosis of the musculus levator arcus palatini

horizontal fibres anteriorly. This muscle originates on the caudolateral side of the lateral ethmoid, the ventrolateral side of the frontal back to the sphenotic and inserts at the dorsal side of the corpus of the hyomandibula and the quadrate. Although this muscle originates for a large part directly on the neurocranium, the attachment at the sphenotic is through an aponeurosis.

M. adductor arcus palatini The adductor arcus palatini connects the skull floor and the mediodorsal rim of the suspensorium. This muscle takes the most medial position of all cranial muscles, lining the mouth cavity dorsolaterally. On the neurocranium, it originates mostly at the parasphenoid, but also at the orbitosphenoid and the pterosphenoid. On the suspensorium, the adductor arcus palatini inserts on the dorsal rim of the hyomandibula, the quadrate, the metapterygoid and the entopterygoid. The fibres run in a transversal plane, with the rostral fibres more obliquely orientated (Fig. 5e, f).

Opercular muscles

Of the three opercular muscles that were discerned, the dilatator operculi is the one most rostrally situated, partially covering the adductor operculi. Caudally lies the levator operculi.

M. dilatator operculi (Fig. 5c) The flattened dilatator operculi originates from halfway up the ventrolateral side of the frontal, medial to the levator arcus palatini, up to the ventrolateral part of the sphenotic (Fig. 5c). It inserts through a large tendon on the lateral side of the dorsal process of the opercle. This long tendon runs along the rostroventral side of the muscle.

M. adductor operculi (Fig. 5d, e) This shortest muscle of the three opercular muscles connects the posterior side of the suspensorium with the opercle. The adductor operculi originates at the dorso-caudal part of the hyomandibula and the most ventro-caudal part of the pterotic and inserts at the dorsal process of the opercle, medial to the insertion of the dilatator operculi, but still lateral to the processus opercularis. The caudal part abuts the posteriorly situated levator operculi. It is also attached to the connective tissue covering the dorso-lateral side of the deformed suprabranchial cavity. The fibre direction is predominantly dorso-ventral.

M. levator operculi (Fig. 5d, e) The levator operculi is the most caudally situated and robust of the three opercle muscle. It connects the most posterior part of the neurocranium with the opercle, originating at the ventro-caudal part of the pterotic and the ventrorostral side of the posttemporo-supracleithrum, the suprapreopercular bones and the connective tissue covering the suprabranchial cavity. Ventrally, the levator operculi inserts on almost the complete dorsal side of a ridge of the opercular bone.

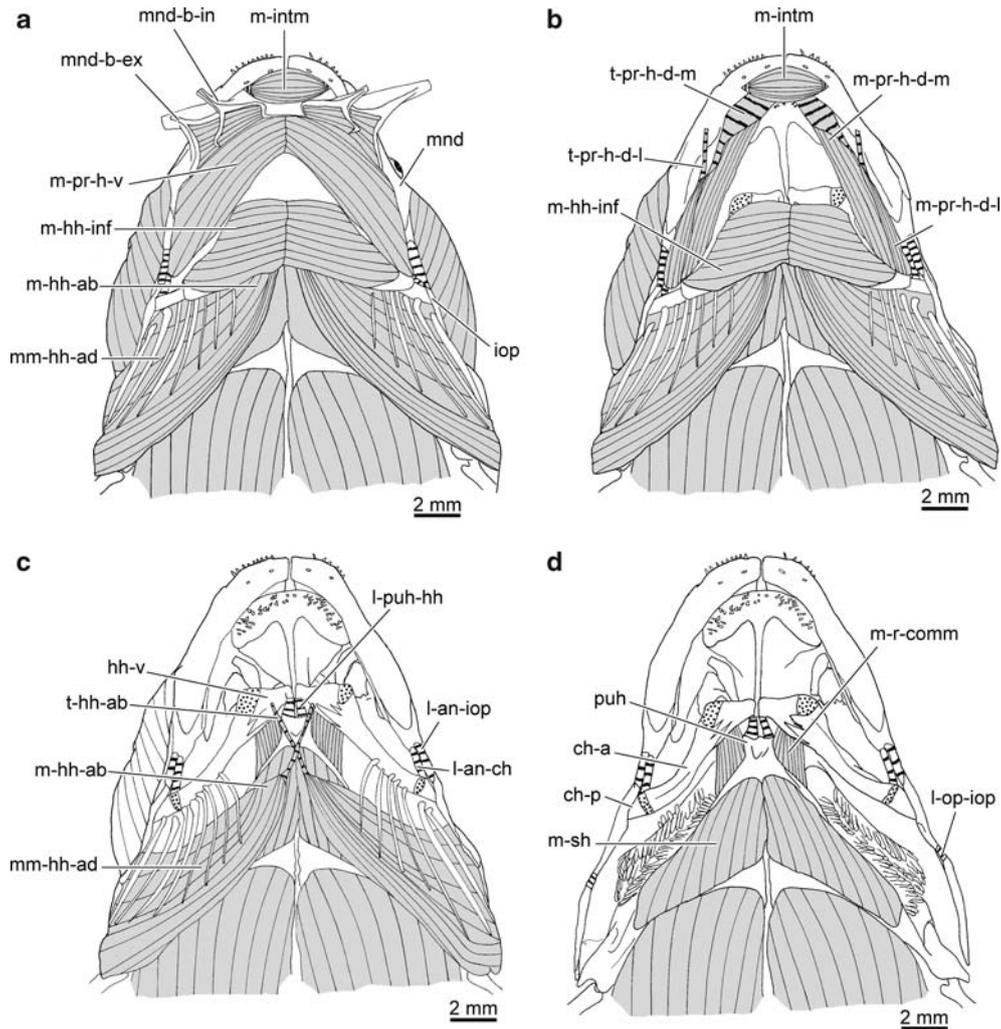


Fig. 7 Ventral view of the cranial musculature of *Platyclarias machadoi* (113 mm SL) (MRAC 78-6-P-1348-364, paratype 16). **a** Skin removed; **b** ventral part of the hyoid protractor removed; **c** dorsal part of hyoid protractor, intermandibular and hyohyoideus inferior removed; **d** hyohyoideus abductor and the hyohyoidei adductores removed (dotted areas mark cartilage). *ch-a* Ceratohyal anterior, *ch-p* ceratohyal posterior, *hh-v* ventral hypohyal, *iop* interopercle, *l-an-ch* ligamentum angulo-ceratohyale, *l-an-iop* ligamentum angulo-interopercle, *l-op-iop* ligamentum operculo-interopercle, *l-puh-hh* ligamentum parurohyalo-hypohyale, *mnd* mandibula, *mnd-b-ex* external mandibular barbel, *mnd-b-in* internal

mandibular barbel, *m-hh-ab* musculus hyohyoideus abductor, *mm-hh-ad* musculi hyohyoidei adductores, *m-hh-inf* musculus hyohyoideus inferior, *m-intm* musculus intermandibularis, *m-pr-h-d-l* musculus protractor hyoidei pars dorsalis lateralis, *m-pr-h-d-m* musculus protractor hyoidei pars dorsalis medialis, *m-pr-h-v* musculus protractor hyoidei pars ventralis, *m-r-comm* musculus rectus communis, *m-sh* musculus sternohyoideus, *puh* parurohyal, *t-hh-ab* tendon of the m. hyohyoideus abductor, *t-pr-h-d-l* tendon of the m. protractor hyoidei pars dorsalis lateralis, *t-pr-h-d-m* tendon of the m. protractor hyoidei pars dorsalis medialis

Maxillary barbel muscles

M. retractor tentaculi (Fig. 5d) The retractor is a large bundle of fibres running from the suspensorium to the maxillary bone. It originates on the rostral side of the hyomandibula and the quadrate. The fibres are all inserted on the centrally situated tendon, which runs from the postero-dorsal side of the maxillary bone up to half-way into the muscle. The fibres follow an oblique rostrocaudal direction, dorsally and ventrally of the tendon in a way that a feathered appearance results. The muscle lies medially of the A_3'' and laterally of the adductor arcus palatini and extensor tentaculi. Furthermore, the

retractor lies laterally of the autopalatine. On the cross sections two bundles are distinguished.

M. extensor tentaculi (Fig. 5e) This muscle is the antagonist of the above-mentioned muscle, abducting the maxillary barbel. The origin of the extensor tentaculi covers the ventral and ventrolateral side of the lateroethmoid, the rostroventral side of the frontal and the lateral side of the orbitosphenoid and runs to the autopalatine. Several, differently oriented, bundles of fibres attach to the upper half of the autopalatine, caudally of the articular facet. They consequently enclose the caudal end of the autopalatine.

Hyoid muscles

M. protractor hyoidei (Fig. 7a, b) The protractor hyoidei connects the lower jaw with both hyoid bars. It can be divided into a larger ventral and smaller dorsal part. They both insert on the ventral side of the anterior ceratohyal. The ventral part originates at the whole length of the ventral side of the lower jaw and at the bases of the mandibular barbels. The ventral part is rather U-shaped (Fig. 7a); left and right half are attached to each other by a fascia at the level of the mandibular symphysis. Several fields of fibres can be distinguished interconnecting different parts of the bases of the mandibular barbels. There is a large gap between the rostral part of this muscle and the posteriorly lying hyohyoideus inferior. A smaller gap is discerned between the mediorostral part of the protractor hyoidei and the intermandibularis. The dorsal part originates at the medial side of both mandibulae (Fig. 7b). This part can be further divided into two subunits, a medial and a lateral one. The lateral subunit originates tendinously at the lateroventral side of the mandibula, while the larger medial subunit originates caudomedially on the mandibula, through aponeuroses and not contacting each other but running up to the intermandibularis. Both parts insert on the ventrolateral side of the anterior ceratohyal. The protractor hyoidei pars dorsalis lies completely laterally of the hyohyoidei inferiores.

M. hyohyoideus inferior (Fig. 7b) This massive muscle covers the ventral side of the contralateral anterior ceratohyal and parts of both ventral hypohyals. The muscle inserts on the ventral side of the anterior ceratohyal, medial from the insertions of the protractor hyoidei, and at the ventral hypohyals. Caudally, it is also attached to the bases of the branchiostegal rays. The contralateral fibres originate from a fascia.

Mm. hyohyoidei adductores (Fig. 7c) The hyohyoidei adductores muscles form a series of sheets between successive branchiostegal rays, starting from the first one and ending onto the medial side of the opercular bone.

M. hyohyoideus abductor (Fig. 7c) The hyohyoideus abductor links the rostral tip of the hyoid bars with the first contralateral branchiostegal rays. The muscles originate tendinously onto the ventral hypohyal of the opposite side and insert on the medial face of this branchiostegal ray.

M. sternohyoideus (Fig. 7d) This muscle forms a broad fibre mass, connecting the pectoral girdle to the hyoid bars through the parurohyal. Posteriorly, the sternohyoideus originates at the cleithrum. On the rostral side, both muscle-heads insert into the double forked parurohyal. No myocommata could be observed.

Postcranial skeleton

The total number of vertebrae in the studied specimens of *Platyclarias machadoi* (80.5–181 mm SL) ranges from 65 up to 71 (mode: 70). The number of precaudal vertebrae varies from 19 to 22 (mode: 20) and the number of caudal vertebrae from 44 to 50 (mode: 50). *Platyclarias machadoi* has 9 up to 11 pairs of ribs.

The pectoral fins of *Platyclarias machadoi* have 11 branched fin rays that articulate with two proximal radials. The fins are preceded by non-serrated spines. The pectoral girdle shows a robust bond between the coracoid and the cleithrum bones, with one small, lateral fenestra. Furthermore, the cleithrum shows an anterior process (Fig. 2). The pelvic fins each carry six, branched fin rays, which articulate with the broad and flat basipterygium of the pelvic girdle. Rostrally, an internal and external anterior process can be distinguished (Fig. 8a). The dorsal and anal fins are clearly separated from the caudal fin. The number of dorsal and anal fin rays varies respectively around 77–87 and 69–80.

The morphology of the caudal endoskeleton of *Platyclarias machadoi* shows some intraspecific variation but always consists of the parhypural, five hypurals, an epurale and an urostyl. Different fusion patterns can be discerned; even though Poll (1977) previously stated that no fusions within the hypurals are present, and only the fifth hypural and the urostyl show a fusion. However, our observations show that hypural four and five are fused, with or without a fusion of the urostyl. Dorsally of the hypurals and the urostyl lies the broadly tipped epurale. Only the haemal spine of the second preural vertebra is unpaired, elongated and broadly tipped. The remainder (on the neural side of the second and third preural vertebra and on the haemal side of the third preural vertebra) shows slender elongate paired neural and haemal spines. No pterygiophores are observed. Figure 8 shows an additional fusion of the third and fourth preural vertebrae.

Discussion

Spatial constraints and functional implications of the low skull

Platyclarias machadoi has an extremely flattened skull (average skull height of $27.5 \pm 3.0\%$ skull length) compared to that of other clariids (*Platyallabes tihoni*: $34.6 \pm 6.9\%$, *Gymnallabes typus*: $40 \pm 5.8\%$) (Table 1). This can be expected to impose spatial constraints on the surrounding structures, in all three dimensions of the 'construction' framework (Barel 1984).

One striking similarity with *Platyallabes tihoni* is the medial position of the retroarticular process on the lower jaw, presumably the simple consequence of the topographic relation between lower jaw, the plane of mandibular movements and the fact that the suspensorium is extremely tilted, up to an almost horizontal

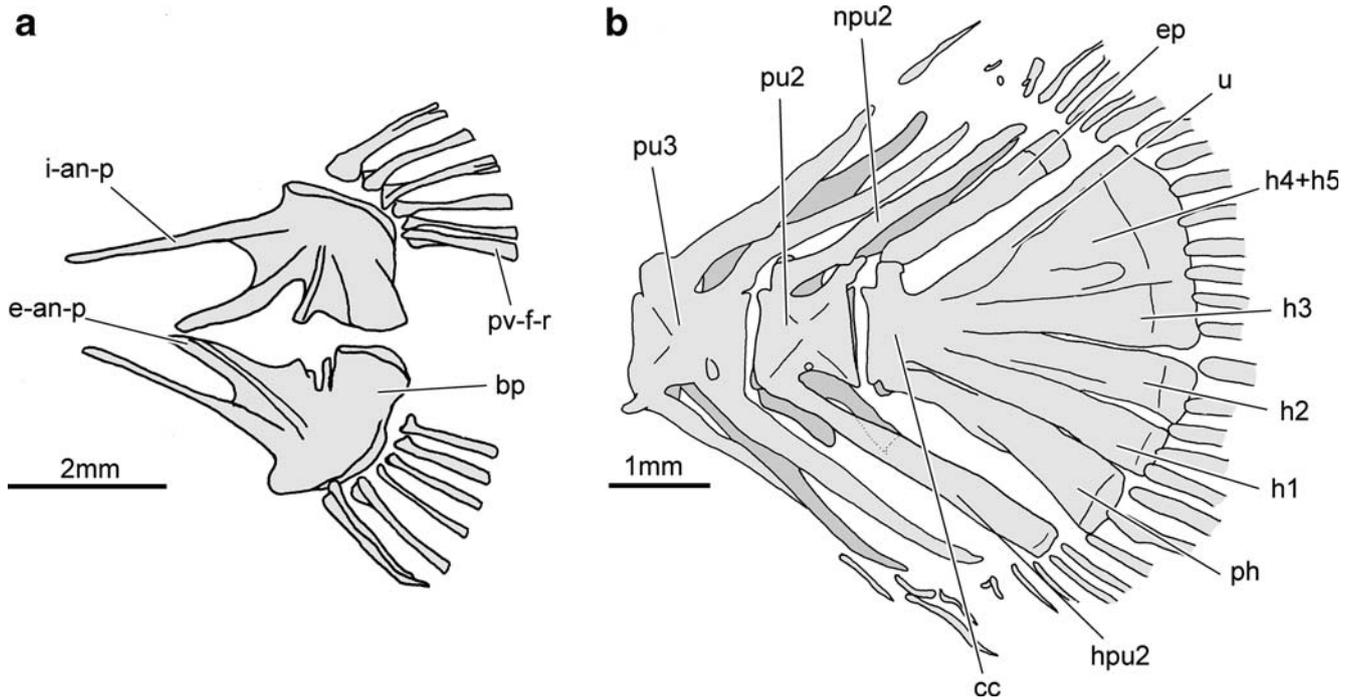


Fig. 8 **a** Pelvic girdle, **b** caudal skeleton of *Platyclarias machadoi* (123 mm SL) (MRAC 78-6-P-1348-364, paratype 14). *bp* Basipterygium, *cc* composed centre, *e-an-p* external anterior process, *ep* epural, *h1/5* hypural 1/5, *hpu2* haemal arch of preural vertebrae

2, *i-an-p* internal anterior process, *npu2* neural arch of preural vertebrae 2, *ph* parhypural, *pu2/3* preural vertebrae 2/3, *pv-f-r* pelvic fin rays, *u* urostyl

position. Another resemblance is the caudal orientation of the opercular process on the hyomandibula (instead of caudoventrally), giving the opercle a more posterior position with respect to the suspensorium. Also the dorsoventrally compressed suspensorium is a shared characteristic (Devaere et al. 2005).

The most impressive spatial reorganization of the skull elements in *Platyclarias machadoi*, however, is the almost completely horizontal position of the suspensorium. Only *Platyallabes tihoni* shows a comparable horizontal position, as can be shown when superimposing the cross sections of the neurocranium and suspensorium at the level of their articulation (Fig. 9). It could be argued that these sections only represent one phase in the dynamic system of the suspensorium, during abduction or adduction. However, as the axis through the articular facet at the neurocranium lies in line with the axis through the hyomandibula, this gives us a good indication of the position of the suspensorium at rest. Apparently, in the species studied, three levels of tilting can be observed: $\pm 30^\circ$ in *Clarias gariepinus* (angle of axis through suspensorium with respect to mediosagittal plane), $\pm 40^\circ$ – 46° in *Clariallabes longicauda* and *Gymnallabes typus*, and 69° – 76° in *Platyallabes tihoni* and *Platyclarias machadoi* [Fig. 10b (hyo-med)].

It can be expected that this horizontal tilting will also have a substantial influence on the morphology of the anterior part of the suspensorium. Variation in the morphology and especially orientation of the plate-like entopterygoid, metapterygoid and the anterior part of

the quadrate can be observed. As judged from the histological sections, it becomes clear that the entopterygoid plate has a comparable horizontal orientation in *Clarias gariepinus*, *Gymnallabes typus*, *Platyallabes tihoni* and *Platyclarias machadoi*, with respect to the mediosagittal plane (Fig. 11, entopterygoid). However, compared to the orientation of the hyomandibula (at the level of the articulation with the neurocranium), some differences become clear too (Fig. 10c). In *Clarias gariepinus* the anterior part of the suspensorium shows an altered orientation with its dorsal margin being rotated medially [negative values in Fig. 10c (ento-susp)]. In *Platyclarias machadoi* and *Platyallabes tihoni*, on the other hand, the anterior part shows a slightly comparable, lateral shift in orientation (positive values) instead. For *Gymnallabes typus*, there is a small medial change in orientation visible.

Different angles at different levels of the suspensorium (with respect to the mediosagittal plane) can be expected to have different influences on the adduction forces exerted by the adductor arcus palatini onto the suspensorium. As this muscle inserts almost onto the complete dorsal margin of the suspensorium, and as the transverse axis through the suspensorium at all levels changes (Fig. 10c), the orientation of the force exerted onto this bony rim with respect to this transverse axis will change as well. In other words, the direction of the contraction force may not always be in line with the long axis through the bony plates and torsion and shear forces may thus be generated. Since the anterior part of

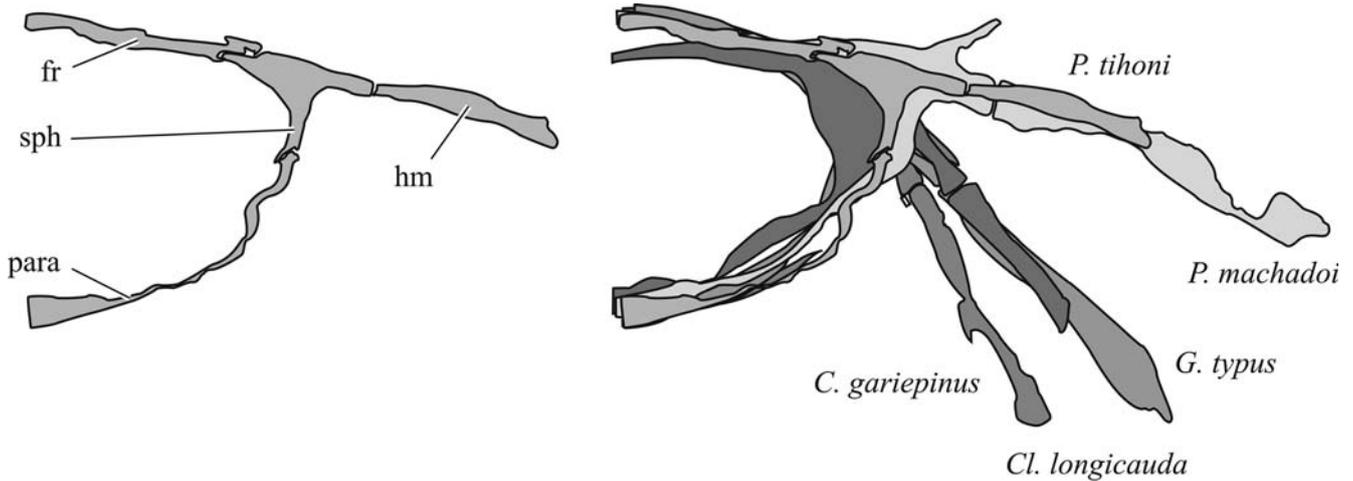


Fig. 9 Position of the hyomandibula in Clariidae: cross sections of the neurocranium and hyomandibula (at their articulation) of different clariid species superimposed and scaled to each other. *fr* frontal, *hm* hyomandibula, *para* parasphenoid, *sph* sphenotic

the suspensorium comprises plate-like, thin bones, such shear forces are a potential danger for fracturing the bones. The histological sections confirm that indeed the line of action of the adductor arcus palatini is more in line with the transverse long axis through the suspensorial bones that are thin (entopterygoid, metapterygoid, anterior part of quadrate) but less in line with that of the posterior, thick bones (posterior part of quadrate and hyomandibula) (Figs. 9, 10d). Fracturing of the suspensorium during ad- and abduction is thus avoided.

In a general situation, suspensorial adductions will generate an increase of the orobranchial cavity. However, in a dorsoventrally flattened skull with an almost horizontally situated suspensorium, the opposite may actually occur.

In a more vertically situated suspensorium, the adduction of this suspensorium results in a decrease of the branchial cavity volume. Since, a more vertical suspensorium enlarges the adduction component of the adductor arcus palatini (large angle between suspensorium and line of action of adductor arcus palatini) (Fig. 10e). This implies a less efficient adduction in both *Platyclarias machadoi* and *Platyallabes tihoni*, which could be partially overruled by a larger depression of the hyoid bars. In the dorsoventrally flattened head of *Platyclarias machadoi* and *Platyallabes tihoni* there is a relatively large cranial floor, as is the case in all platybasic benthic catfishes (Adriaens and Verraes 1997b); a depression of these bars will result in a substantial volume increase in these two species (for a certain overall skull size).

Apart from these conformities with *Platyallabes tihoni*, *Platyclarias machadoi* does show some differences. Surprisingly, these differences involve conditions, which at first sight are essential to maintain a well functioning feeding and respiration mechanism. One difference is the less hypertrophied jaw muscle in *Platyclarias machadoi*, although a hypertrophied jaw muscle complex can be expected as the suspensorium takes a more or less

horizontal position (see above). This horizontal tilting can be seen as a disadvantage to fit in the large adductor mandibulae complex, unless the large muscles would be allowed to bulge. This bulging would allow jaw muscles with a similar physiological cross section and insertion sites as in other clariid representatives, as is the case in *Platyallabes tihoni* (Devaere et al. 2005). In *Platyclarias machadoi*, however, the jaw muscles do not bulge, although the same insertion sites are present, thus resulting in a smaller muscle (Fig. 5a, b). Furthermore, the histological sections show no substantial medial increase of the muscle volume. However, even though smaller jaw muscles would suggest reduced biting forces, the spatial relationships need to be known first, before any conclusion can be drawn (Herrel et al. 2002). Herein lies a possible functional explanation for the unique extra muscle bundle, laterally from the A_3'' -part and medially from the rostral part of the levator arcus palatine. This muscle links the neurocranium to the tendon complex of the mandibular muscle complex and caudally to a medial tendon of the A_2A_3' . This would mean that during contraction a lifting of the mandibular muscle tendons would occur, thereby increasing its angle of insertion on the lower jaw. Consequently, this would result in a higher moment generated by the adductor mandibulae on the lower jaw. Within a spatially constrained, flattened 'construction' this muscular rearrangement is an advantageous solution to increase biting force, without the need to increase muscle volume. A comparable situation has been observed in gobiids (not in relation to a dorsoventrally flattened skull, though), where the A_ω is assumed to change the position of the A_3 -tendon, and thus increasing the moment during biting (Decleyre et al. 1990). Because of the plausible function of this muscle bundle, the name 'pars levator tendinis' is suggested (Fig. 6). The other dissimilarity is that both gill apparatus and suprabranchial organ are well developed in *Platyclarias machadoi*. In contrast, in *Platyallabes tihoni* there is no evidence of the

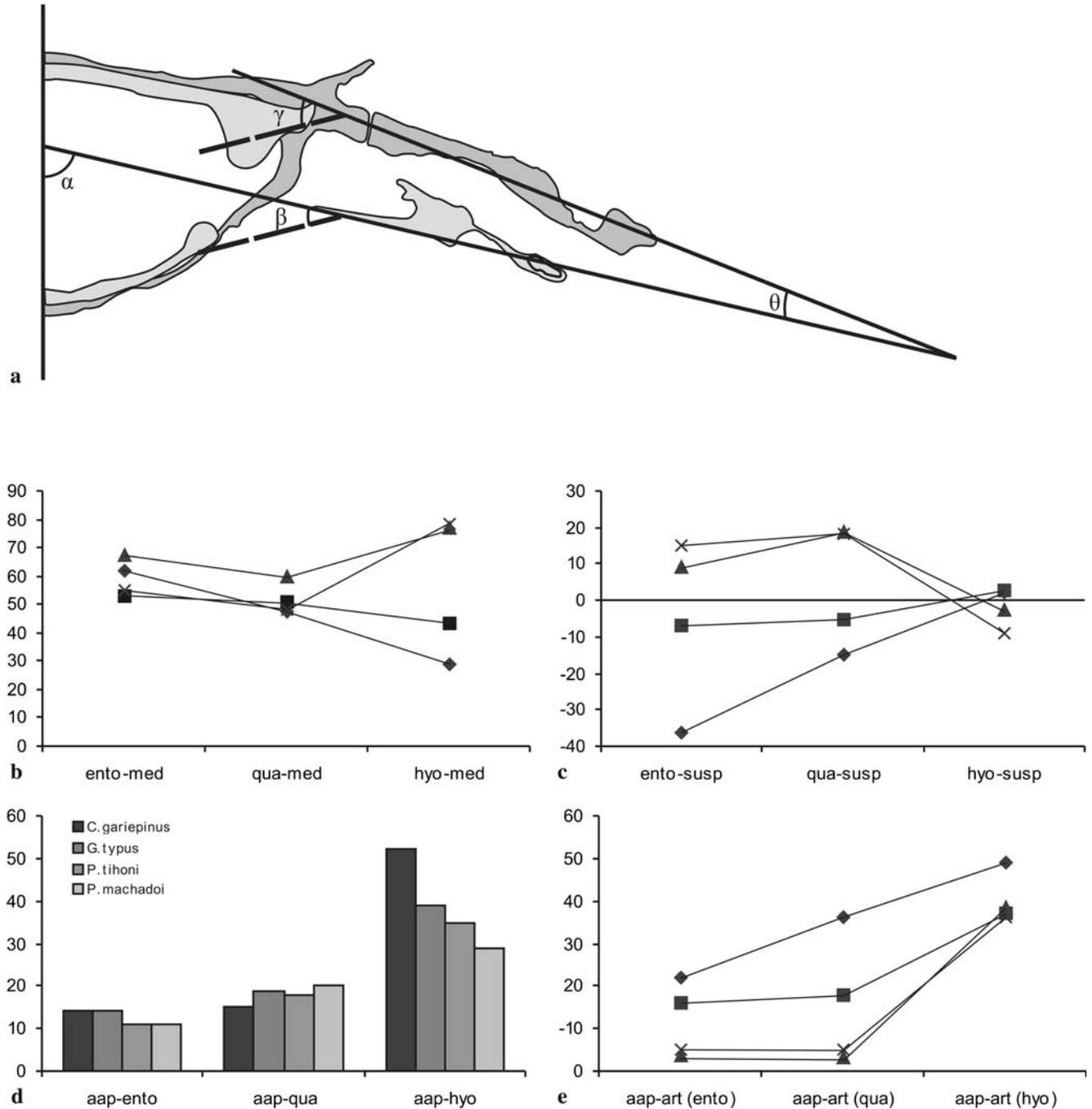


Fig. 10 Quantified overview of the suspensorial spatial traits. **a** Overview of the different angles used; **b** angles between different suspensorial bones and the mediosagittal plane (α), *ento-med* at the level of the entopterygoid, *qua-med* at the level of the quadrate, *hyo-med* at the level of the hyomandibula (anterior to its articulation with the neurocranium); **c** angles between long axis through the suspensorium at different levels, with the long axis through the hyomandibula (at the level of its articulation with the neurocranium) as a reference line (negative values medial to reference line) (θ), *ento-susp* at the level of the entopterygoid, *qua-susp* at the level of the quadrate, *hyo-susp* at the level of the hyomandibula; **d** angles between the line of action of the adductor

arcus palatini and the long axis of the different suspensorial bones (β), *aap-ento* at the level of the entopterygoid, *aap-qua* at the level of the quadrate, *aap-hyo* at the level of the hyomandibula; **e** angles between the line of action of the adductor arcus palatini at different levels of the suspensorium with respect to the long axis through the hyomandibula (at the level of its articulation with the neurocranium) (absolute values) (γ); *aap-art (ento)* at the level of the entopterygoid, *aap-art (qua)* at the level of the quadrate, *aap-art (hyo)* at the level of the hyomandibula. *x* *Platyclarias machadoi*, (filled diamond) *Clarias gariepinus*, (filled square): *Gymnallabes typus*, (filled triangle): *Platyallabes tihoni*

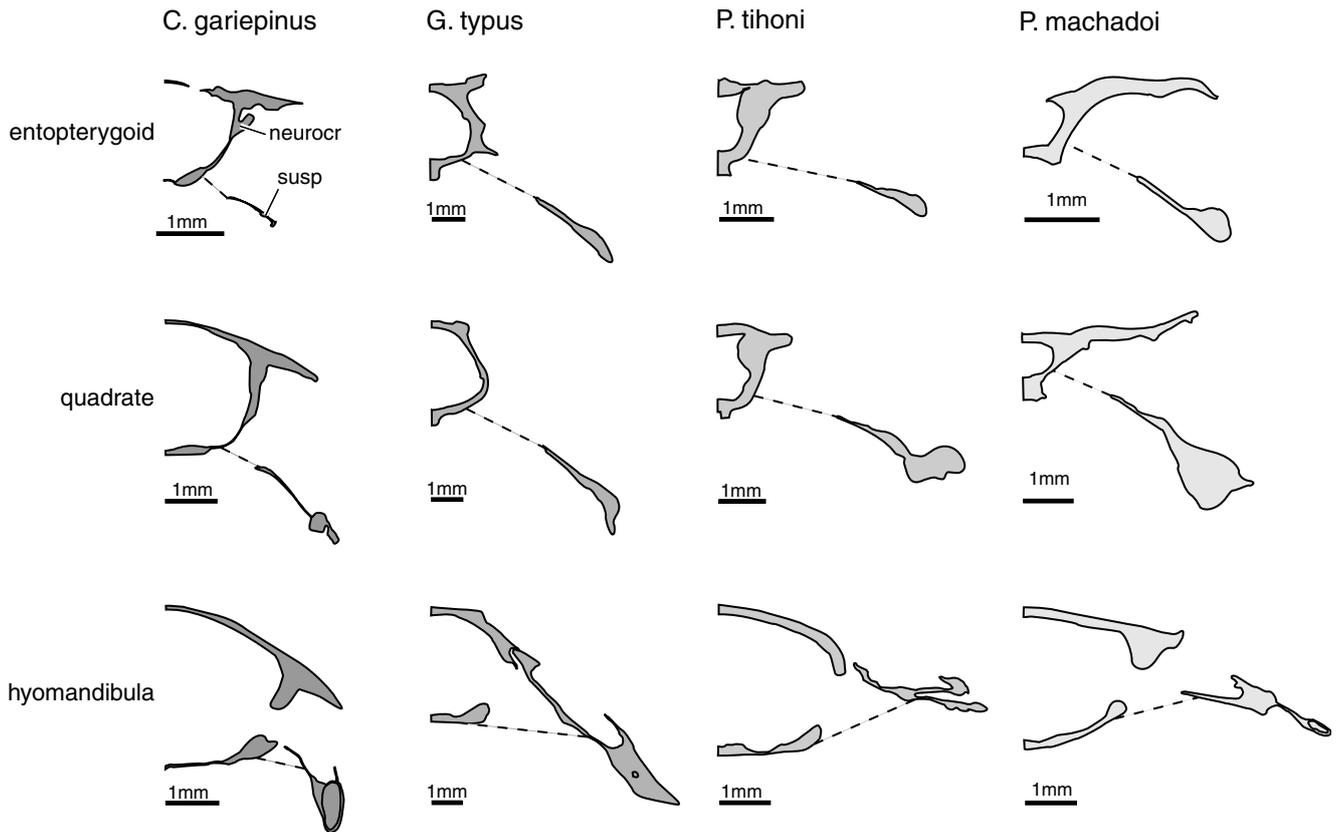


Fig. 11 Topography of the suspensorium with respect to the neurocranium at three levels: entopterygoid, quadrate and hyomandibula (close to the level of articulation with the neurocranium) in *Clarias gariepinus* (46.75 mm SL), *Gymnallabes typus* (218.4 mm SL), *Platyallabes tihoni* (139 mm SL) (MRAC 73-22-P-3127) and

Platyclarias machadoi (109 mm SL) (MRAC 78-6-P-1348-364, paratype 17). The working line of the adductor arcus palatini muscle is shown as a dotted line. neuroocr neurocranium, susp suspensorium

suprabranchial organ. The absence of this organ in *Platyallabes tihoni* could be explained by the decreased branchial cavity (Devaere et al. 2005). Apparently, different strategies with respect to spatial organization and constraints exist in *Platyclarias machadoi*.

Comparison with other Clariidae

Even though variation exists with respect to relative skull height in clariids, the extreme situation in *Platyclarias machadoi* seems to be unique (see above). Some features can be given that corroborate the distinct nature of this species, and are thus diagnostic for both the genus and the species. Evidence comes from osteological, myological and biometric (both metric and meristic) evidence of the cranial and postcranial system. For a comparison, we used representatives of the three morphotypes, with respect to the degree of body elongation, in clariids: fusiform, intermediate and anguilliform. The following species are used: *Clarias gariepinus* (fusiform morphotype), *Gymnallabes typus* and *Channallabes apus* (anguilliform morphotype) and *Platyallabes tihoni* (intermediate morphotype). The proportional measurements and counts of *Platyclarias machadoi* and some other clariid representatives are given in Table 1.

Comparison with the fusiform morphotype

Platyclarias machadoi shares a list of symplesiomorphies with *Clarias gariepinus*. They show a similar lateral plate on the frontals, the sphenotics and the pterotics. They also share a low number of processes present on the sphenotic (1 process) and pterotic (1 process) for the connection with the hyomandibula. Also on the muscular level some resemblances exist. The ventral part of the protractor hyoidei has a distinct U-shape, in contrast to the more V-shaped protractor of the anguilliform species. A postcranial similarity shared only with *Clarias gariepinus* is that no continuous fin fold is present.

Comparison with the intermediate morphotype

Platyclarias machadoi and *Platyallabes tihoni* show a reduced skull morphology, with the exception of some canal bones retaining a plate-like extension (for example, the nasal, infraorbital IV and the proximal supraopercle).

Also postcranially, the similarity with *Platyallabes tihoni* is reflected in a number of features. The most obvious is the comparable mode of the total number of

vertebrae: 70 for *Platyclarias machadoi* and 78 for *Platyallabes tihoni* ($n=33$). The number in the *Gymnallabes typus*, *Channallabes apus* and *Dolichallabes microphthalmus* is substantially higher [*Gymnallabes typus* ($n=26$): 87, *Channallabes apus* ($n=98$): 104 and *Dolichallabes microphthalmus*: 106 (Devaere et al. 2004)], while the number in the *Clarias* species is clearly lower [*Clarias gariepinus*: 56–63; *Clarias ngamensis*: 56–60; *Clarias platycephalus*: 59–63 (Teugels 1986)].

Comparison with the anguilliform morphotype

The general skull morphology of *P. machadoi* resembles that of the anguilliform species: there is a narrow skull roof, with partially reduced circumorbital and supra-preopercular bones, which are clearly separated from each other.

In general, the morphology of the cranial musculature of *Platyclarias machadoi* resembles that of *Gymnallabes typus* and *Channallabes apus* and shows the same origin and insertion sites for the different muscles. Besides this, there is also an increase in the range of muscle fibre directions of the jaw muscle, as seen in these anguilliform clariids (Devaere et al. 2005). The two contralateral parts of the pars medialis of the dorsal part of the protractor hyoidei, however, do not make contact, as is the case in *Gymnallabes typus* and *Channallabes apus* (Cabuy et al. 1999; Devaere et al. 2001).

Some comments on the genus/species description by Poll (1977)

On the basis of the morphological and biometrical data gathered in this study, the description of Poll (1977)

Table 1 Measurements and meristic data for *P. machadoi* and comparison with *P. tihoni*, *G. typus* and *C. apus* specified measurements not applicable (abbreviations are explained in text)

	Holotype	Other specimens examined					<i>P. tihoni</i>					<i>G. typus</i>					<i>C. gariepinus</i>				
		<i>n</i>	Min	Max	Mean	SD	<i>n</i>	Min	Max	Mean	SD	<i>n</i>	Min	Max	Mean	SD	<i>n</i>	Min	Max	Mean	SD
TL (mm)	195.0	21	89.5	160.0			54	63	380			32	49	44			488	33	701		
SL (mm)	181	21	80.5	146			54	58	359			32	284	259			488	27.7	600		
Measurements in % standard length																					
PaL	37.9	21	37.9	43.9	40.2	1.6	54	18.6	34.7	26.3	3.5	32	29.2	37.1	32.9	2.2	320	48.7	59.5	55.3	1.6
AFL	58.6	21	52.2	60.0	56.3	2.0	54	*	*	*	*	32	*	*	*	*	329	37.0	47.6	43.0	1.8
DFL	70.2	21	33.8	38.5	36.0	1.3	54	*	*	*	*	32	*	*	*	*	320	53.6	67.4	61.1	2.3
PPeL	16.0	21	14.7	19.3	17.1	1.2	54	8.3	17.0	12.1	2.0	32	10	19.3	13	1.9					
PPvL	33.4	21	64.2	72.0	67.6	2.0	54	18.3	30.6	23.5	3.1	32	27.2	36.2	30.5	2.3	320	42.2	51.1	47.1	1.4
PdL	28.5	21	28.2	33.5	30.8	1.6	54	12.5	23.4	16.9	2.8	32	18.1	27.8	21.6	2.4	327	21.5	27.7	24.3	1.1
SPDFL	13.0	21	10.1	17.2	13.2	2.1	54	2.2	6.6	3.7	1.0	32	5.2	11.2	8.3	1.5	329	2.7	8.6	5.2	1.0
PcFL	7.7	21	7.0	16.1	8.9	2.5	54	4.6	9.9	6.6	1.3	32	3.8	8.5	5.7	1	327	9.5	16.3	12.9	1.3
PcSL	4.1	21	3.3	5.5	4.2	0.6	54	3.3	7.0	5.0	0.8	32	1.8	3.8	2.5	0.5	315	4.4	12.1	8.3	1.5
PvFL	5.3	21	3.7	6.4	5.4	0.6	54	4.0	7.3	5.6	0.8	32	1.7	6.8	4.2	0.9	330	7.8	12.2	10.1	1.1
CPD	3.8	21	3.1	5.1	4.1	0.5	54	1.1	3.6	1.9	0.5	32	1.9	4.5	3	0.7	325	6.2	10.1	7.8	0.6
ABD	4.4	21	4.1	6.5	5.1	0.6	54	3.0	6.4	4.2	0.8	32	4.6	7.8	6.3	0.8	333	10.7	18.1	14.5	1.3
IpcD	11.5	21	11.0	12.9	12.1	0.5	54	6.9	13.0	9.3	1.5	32	5.9	11	8	1.1					
IpvD	3.8	21	2.9	5.0	4.0	0.6	54	2.9	6.2	4.2	0.8	32	1.4	4	2.5	0.6					
SkL	15.5	21	14.3	18.7	17.0	1.2	54	7.4	17.2	12.7	2.1	32	11.1	18	13.1	1.6	353	26.6	35.0	30.8	1.2
SkH	4.5	21	3.7	5.7	4.7	0.5	54	3.0	6.3	4.4	0.8	32	3.7	7.6	5.2	1.1	323	9.1	16.0	11.8	1.2
Measurements in % head length																					
Pol	71.4	21	62.9	84.7	70.6	5.0	54	61.2	119.7	74.7	9.2	32	62	74	67.7	2.4	324	17.4	26.8	31.3	1.7
SpL	14.5	21	7.1	24.6	14.5	4.3	54	6.9	20.3	13.5	3.0	32	10.2	20	15.5	2.6					
SkW	74.0	21	64.2	85.6	73.9	5.4	54	62.9	113.9	75.8	7.9	32	52.1	69.6	60.3	4.6					
SpW	12.9	21	9.5	28.8	18.6	5.3	54	10.2	22.3	16.0	3.0	32	12.1	27.3	18.8	4					
IoD	37.9	21	28.9	41.7	35.7	2.8	54	30.4	56.9	38.5	4.5	32	24.6	40.4	33	3.5	323	36.4	45.7	39.9	1.7
ANID	15.4	21	14.5	30.8	17.2	3.4	54	10.5	26.1	14.1	2.7	32	10.6	19	15	2.2					
PNID	30.2	21	15.1	35.8	29.2	4.6	54	22.6	44.8	31.2	4.5	32	23.1	34.1	27.7	2.8					
RSkW	36.6	21	29.4	43.8	36.9	3.7	54	30.3	69.0	40.0	7.4	32	28.9	53.4	42	5.5					
OSkW	40.6	21	42.9	57.8	49.2	3.5	54	43.7	92.9	54.9	6.8	32	42.5	60.8	51.4	3.4					
SkH	29.1	21	22.9	37.1	27.5	3.0	54	22.8	61.7	34.6	6.9	32	26.6	49.8	40	5.8					
ED	5.5	21	4.6	8.5	6.8	1.1	54	3.7	12.8	6.1	1.6	32	4.1	8.4	6.5	1.1	330	5.2	13.1	7.9	1.4
SnH	10.9	21	6.2	15.6	10.2	2.0	54	9.5	21.6	13.3	4.8	32	10	18.5	14.2	2					
OSkH	19.4	21	10.1	24.3	16.8	3.7	54	16.8	44.0	23.4	4.8	32	17.5	36	26	4.6					
PhL	22.3	21	16.6	29.8	23.7	3.7	54	17.2	44.5	27.6	4.1	32	18.6	31.8	24.5	3.5					
IMnID	21.2	21	15.4	26.2	21.5	3.0	54	20.3	42.0	27.5	3.7	32	18.5	37.1	24.4	3.5					
EMnID	32.9	21	18.7	41.0	32.0	4.9	54	32.1	67.8	43.2	6.0	32	31.5	44.6	39.3	3.6					
MW	30.5	21	20.3	33.6	27.1	3.5	54	19.5	76.1	32.7	8.5	32	21.5	39.3	30.8	4					
SkR	19.2	21	21.1	29.6	23.8	2.2	54	9.5	26.8	18.9	4.6	32	4	44.1	15.7	9.5					
Meristic counts																					
RB	11	20	9	11			33	4	7			22	6	12							
TV	71	20	65	71			33	59	83			22	78	92			47	56	63		

Most data for *Clarias gariepinus* were obtained from Teugels (1986)

proved to insufficiently demarcate *Platyclarias machadoi* from some other clariids species (of which a substantially larger number of specimens was studied by us). This allowed us to formulate some new diagnostic characters, which will be essential for future systematic studies on clariids. Updated ranges and morphological features are listed below.

The dorsal fin starts far behind the skull, reflected in a large distance measured between the dorsal fin origin and the occipital process on the parieto-supraoccipitale (Table 1, SPDFL). This distance is 10.1–17.2% of the standard length. The predorsal length in *Platyclarias machadoi* ranges between 28.2 and 33.5% (%SL) (30.8 ± 1.6), which is highest in all clariids studied (Table 1). Also the anal fin originates far from the snout, the preanal length ranges between 37.9 and 43.9% of the standard length. The pectoral fins are always preceded by a large, non-serrated pectoral spine (24.8–53.1% of pectoral fin length).

The total number of vertebrae ranges from 65 to 71, with 44–50 caudal vertebrae. Both ranges are the lowest compared to the anguilliform clariids (*Dolichallabes microphthalmus*, *Channallabes apus*, *Gymnallabes typus*, *Gymnallabes nops*, *Gymnallabes alvarezi*). Additionally the number appears very stable, which is not the case in some elongated clariid representatives where higher vertebral counts and a larger intraspecific variation are reported (Cabuy et al. 1999; Devaere et al. 2001, 2004, 2005).

One of the most diagnostic characters is the presence of a lightly coloured stain on the skull roof, at the level of the parieto-supraoccipital, a feature only seen in *Gymnallabes alvarezi* Roman, 1970 (this species is under taxonomic revision, current research). After removing the skin, a high amount of subcutaneous fat can be observed in *Platyclarias machadoi*, which is never observed in other clariids.

The absence of any additional outgrowth on the anterior bony plate of the hyomandibula and the dorsal edge of the hyomandibula, as well as the fact that the quadrate form almost a straight line with only a weak indentation, are autapomorphic characters. Further, the interopercle lies medial to the suspensorium, while in all clariids studied so far it lies in a lateral position (Devaere et al. 2001, 2004). The medial position of the retroarticular processes of the lower jaws, with respect to the quadrates, is shared only with *Platyallabes tihoni* (Devaere et al. 2005).

Many of the apomorphic features of *Platyclarias machadoi* involve muscular characteristics. The large jaw muscle complex shows the presence of an extra muscle bundle, laterally from the A_3'' -part and medially from the rostral part of the levator arcus palatine, the 'pars levator tendinis' (Fig. 6). Until now, such a separate muscle could not be observed in other clariids. This poses a difficult question for homology. Until this can be resolved, the most plausible explanation for now would be to consider this new muscle as a de novo splitting off of the A_3' -part fibres. In a lateral view, the dorsal $A_2A_3'\alpha$ -part of the adductor mandibulae complex runs

from the mandible up to the posttemporo-supracleithrum, which is far more caudal than the ventral part. This results in a dorsal part of the A_2A_3' clearly distinguished from the ventral $A_2A_3'\beta$.

The morphology of the hyoid musculature of *Platyclarias machadoi* is especially characterized by muscle fibre reorientations. The gap between the intermandibularis and the mediorostral part of the protractor hyoidei pars ventralis is larger than in all other clariids studied. Apparently, this is caused by the caudally subsided structure of the interconnecting bases of the internal mandibular barbels. Because of the more caudal position of the hyohyoideus inferior, as well as its rostrocaudal compression, a large gap exists between it and the protractor hyoidei. Concerning the hyohyoideus abductor, in other clariids the two contralateral parts overlap or touch each other at the level of the tendinous insertion onto the ventral hypohyal of the opposite side. In *Platyclarias machadoi*, however, a large gap remains between the two parts, causing the crossing of the tendons to occur more rostrally.

This paper shows that the constraints of a very low skull in *Platyclarias machadoi* result in some structural interdependencies. These are: the medial position of the retroarticular process on the lower jaw, the horizontal position of the suspensorium, the lateral tilting of the pterygoid bones and the anterior part of the quadrate with regard to the suspensorial transverse long axis. Besides some other unique traits, these characteristics help to refine the genus/species description.

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