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### Morphology and spatial constraints in a dorso-ventrally flattened skull, with a revised species description of *Platyallabes tihoni* (Poll, )

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## Morphology and spatial constraints in a dorso-ventrally flattened skull, with a revised species description of *Platyallabes tihoni* (Poll, 1944)

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### Abstract

This study details the morphology of *Platyallabes tihoni* (Poll, 1944) as part of a complete revision of the anguilliform clariids. The overall body form of air-breathing clariids ranges from fusiform to anguilliform genera (Boulenger 1911; Pellegrin 1927). Although *P. tihoni* has the typical external morphological features of other elongate clariids, this study shows that it occupies an intermediate position between fusiform and anguilliform taxa with regards to its cranial and postcranial morphology. The main morphological similarities of anguilliform species are a narrow skull roof with a high level of interdigitation between the bones, the reduced canal bones, a connection between the neurocranium and suspensorium via several processes, an extended tooth patch on the lower jaw, and the hypertrophied jaw muscle complex. Shared features typical for the fusiform species are a low coronoid process on the lower jaw and the posteroventral orientation of the opercular process on the hyomandibula. *Platyallabes tihoni* shows a series of unique features: an anterior fontanel situated entirely between the frontals, two tooth plates on the prevomer, a reduced height of the suspensorium, the absence of an anterior bony plate on the hyomandibula, a horizontal position of the sphenotic and pterotic, and a toothed entopterygoid. Many of these unique characters are linked to the spatial constraints associated with an extremely flattened skull in this species.

**Keywords:** *Clariidae*, *myology*, *osteology*, *Platyallabes tihoni*, *spatial constraints*

### Introduction

The Clariidae are one of the more than 30 families within the Siluriformes (de Pinna 1998; Teugels 2003), with diversity of the family largest in Africa, where 12 genera and up to 74 species are known (Teugels 1986). Clariids also occur in Syria, southern Turkey and parts of South-East Asia (Teugels 1986). Some of the generalized, fusiform species, such as *Clarias gariepinus* (Burchell, 1922), show a broad geographic distribution, whereas the

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anguilliform species occur only in Lower Guinea ichthyological province and the Congo River basin (Boulenger 1911; Poll 1957; Teugels 1986; Skelton 1993), where they occupy a more specialized, burrowing niche.

Clariids are characterized externally by long dorsal and anal fins, the presence of four pairs of barbels, a dorsoventrally flattened head, and a unique form of suprabranchial organ formed from the second and fourth gill arches (Greenwood 1961; Vandewalle and Chardon 1991; Teugels and Adriaens 2003).

The anatomy of the anguilliform clariids has barely been studied in detail to date. *Platyallabes tihoni* has been referred to in only a few papers (Poll 1944, 1957, 1977), which include descriptions of external morphology and to a limited degree a superficial cranial study. The aims of this paper are: (1) to provide a detailed description of the cranium and (2) describe the myology of the skull, (3) discuss the postcranial characteristics, (4) provide a redescription of *P. tihoni*, and (5) compare *P. tihoni* with other clariid species. For this comparison we use *Clarias gariepinus* (Burchell, 1822) as a fusiform representative and *Gymnallabes typus* (Günther, 1867), *Dolichallabes microphthalmus* (Poll, 1942), and *Channallabes apus* (Günther, 1873) as anguilliform species.

## Materials and methods

The specimens examined in this study were obtained from the American Museum of Natural History (AMNH), the Museum of Comparative Zoology, Harvard University (MCZ), the Natural History Museum, London (BMNH) and the Royal Museum for Central Africa (MRAC; Tervuren, Belgium). These specimens include the holotype of *Platyallabes tihoni* (MRAC 13307) (see list below). Two specimens (MRAC 125345–349, SL: 156 mm; 14473-68-P-144, SL: 295 mm) were cleared and stained for osteological examination following the procedure of Taylor and Van Dyke (1985). One specimen (MRAC 125345–349, SL: 136 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). One specimen (MRAC 73-22-P-3127, SL: 139) was serially sectioned after embedding in Technovit 7100 (Kulzer). The resultant 5 µm thick sections were stained with Toluidin Blue. Terminology of bones follows Adriaens and Verraes (1997a, 1997b, 1998) and Adriaens et al. (1997), except for the pelvic girdle elements for which we use Arratia (2002). Cranial myology terminology follows Winterbottom (1974) and Adriaens and Verraes (1996, 1997c, 1997d).

Measurements were taken point-to-point using digital calipers to 0.1 mm (Digital ruler, Mauser), interfaced directly with a computer, on 55 specimens of *P. tihoni*. Measurements follow Teugels (1986), with some additions. The morphology of the vertebrae and the following meristic counts were made on each specimen using the radiographs: total number of vertebrae, number of ribs, number of dorsal and anal fin rays.

A list of the species examined for comparison is given in a separate section (see below). For *Gymnallabes typus* and *Channallabes apus*, we refer to Cabuy et al. (1999) and Devaere et al. (2001), respectively, but many additional specimens have been examined for this study. The museum abbreviations are listed in Leviton et al. (1985).

The following abbreviations are used in the figures: af-q, articular facet of the angulo-splenio-articulo-retroarticular with quadrate; af-sph-pt, articular facet of hyomandibula with sphenotic and pterotic; ang-c, angulo-splenio-articulo-retroarticular complex; apal, autopalatine; boc, basioccipital; bp, basipterygium; cc, composed centre; ch-a, ceratohyal anterior; ch-p, ceratohyal posterior; cl, cleithrum; cor, coracoid; den-c, dento-splenio-mentomeckelium complex; e-an-p, external anterior process; enp, entopterygoid; eoc,

exoccipital; ep, epural; fr, frontal; fr-tr-hm, foramen truncus hyomandibularis; h1/5, hypural 1/5; hh-v, ventral hypohyal; hm, hyomandibula; hpu2, haemal arch of preural vertebrae 2; i-an-p, internal anterior process; io-I-IV, first to fourth infraorbital; 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; lac, lacrimal; leth, lateral ethmoid; m-A<sub>2</sub>A<sub>3</sub>' , adductor mandibulae A<sub>2</sub>A<sub>3</sub>' muscle; m-A<sub>3</sub>" , adductor mandibulae A<sub>3</sub>" muscle; m-ad-ap, adductor arcus palatini muscle; m-ad-op, adductor operculi muscle; m-dil-op, dilatator operculi muscle; m-ex-t, extensor tentaculi muscle; m-hh-ab, hyohyoideus abductor muscle; mm-hh-ad, hyohyoidei adductores muscles; m-hh-inf, hyohyoideus inferior muscle; m-l-ap-p-c, levator arcus palatini pars caudalis muscle; m-l-ap-p-r, levator arcus palatini pars rostralis muscle; m-l-op, levator operculi muscle; m-re-t, retractor tentaculi muscle; m-pr-h, protractor hyoidei muscle; m-pr-h-d-l, protractor hyoidei pars dorsalis lateralis muscle; m-pr-h-d-m, protractor hyoidei pars dorsalis medialis muscle; m-pr-h-v, protractor hyoidei pars ventralis muscle; m-r-comm, rectus communis muscle; m-sh, sternohyoideus muscle; mnd-b-in, internal mandibular barbel; mnd-b-ex, external mandibular barbel; m-intm, intermandibularis muscle; meth, mesethmoid; mnd-sym, mandibular symphysis; mp, metapterygoid; mx, maxilla; nas, nasal; npu2, neural arch of preural vertebrae 2; op, opercle; osp, orbitosphenoid; p-trc, process transscapular; para, parasphenoid; par-soc, parieto-supraoccipital; pect-f-r, pectoral fin ray; pect-sp, pectoral spine; ph, parhypural; pu2/3, preural vertebrae 2/3; pop, preopercle; pp-v<sub>4</sub>, parapophysis of vertebra 4; pp-v<sub>5</sub>, parapophysis of vertebra 5; prc-co, coronoid process; prc-op, processus opercle; prc-pg, processus pterigoideus; prc-pt, processus pterotic; prc-ra, processus retroarticularis; prc-sph, processus sphenotic; prmx, premaxilla; prot, prootic; prox-rad, proximal radialis; psph, pterosphenoid; pt, pterotic; pt-scl, posttemporo-supraclathrum; pty, pterygiophore; pv-f-r, pelvic fin rays; pvm, prevomer; puh, parurohyal; q, quadrate; r-br-IX, branchiostegal ray IX; sbo, suprabranchial organ; sph, sphenotic; spop, supraopercle; spl, splenial; sy, synchondrosis; t-hh-ab, tendon of hyohyoideus abductor muscle; t-pr-h-d-l, tendon of protractor hyoidei pars dorsalis lateralis muscle; t-pr-h-d-m, tendon of protractor hyoidei pars dorsalis medialis muscle; u, urotyl.

## Results

### *External morphology*

*Platyallabes tihoni* has a long, dorsoventrally flattened body, with only caudal tip laterally compressed. The specimens show an even light-brownish colour (Figure 1).

One of the most striking features is the extremely flattened head with bulging jaw muscles. The mouth is surrounded by fleshy lips, which are fused at the corners of the mouth. *Platyallabes tihoni* shows a distinct prognathism of the lower jaw (Figure 2) and the eyes are clearly visible. The dorsal fin originates very close to the tip of the supraoccipital process and forms a continuous fin-fold with the anal and caudal fins. Both pectoral and pelvic fins are typically present (pelvic fins were absent however, in one specimen; MCZ 50239). The pectoral fin has a large spine anteriorly.

### *Cranial skeleton*

*Neurocranium.* *Platyallabes tihoni* has a remarkably narrow skull roof (orbito-temporal region), though the total skull width is distinctly broad (Figure 2).

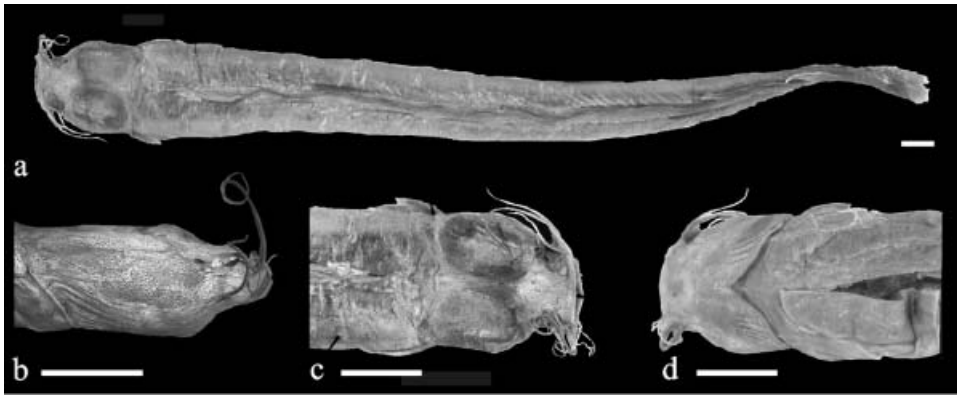


Figure 1. *Platyallabes tihoni* (197 mm SL) (MRAC 77-22-P-3127). (a) Dorsal view; (b) lateral view of the head; (c) dorsal view of the head; (d) ventral view of head. Scale bars: 1 mm. Photographs: S. Devaere.

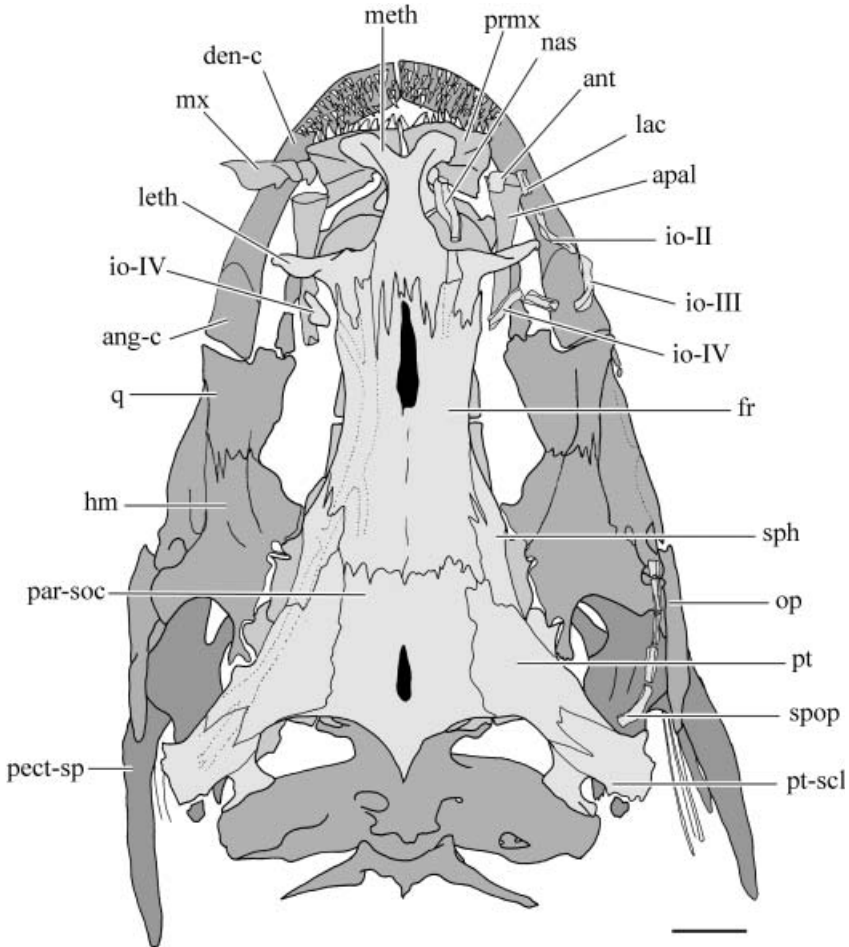


Figure 2. Dorsal view of skull of *Platyallabes tihoni* (156 mm SL) (MRAC 125345-349), left series of infraorbital and supraopercular bones removed. Scale bar: 2 mm.

*Ethmoid region*: the tubular nasal bone of *P. tihoni* is the anteriormost bone of the supraorbital portion of the laterosensory canal system. The nasal bears small, lateral plate-like extensions, as observed in some other clariids (Cabuy et al. 1999).

The large, forked mesethmoid (Figure 2) is connected to the frontals posteriorly via large interdigitations. There is a limited constriction of the mesethmoid behind the rounded, anterior wings. Further, the posterior border does not reach the anterior limit of the anterior fontanel, which as a consequence is completely surrounded by the frontals. The partially open supraorbital canal passes between the lateral ethmoid and the mesethmoid and forms a distinct boundary between the bones. The lateral ethmoid (Figure 2) bears a large, laterally pointed process but lacks any articulation with the infraorbitals and as a consequence also lacks an articular ridge. The arrow-shaped prevomer runs along the mesethmoid ventrally and interdigitates posteriorly with the parasphenoid via a pointed process. The prevomer bears contralateral tooth plates (Figure 3b).

*Orbital region* (Figure 2): the circumorbital series involves four infraorbitals and an antorbital. The antorbital is a small bone located at the base of the nasal barbel and situated dorsal to the anterior tip of the autopalatine. The tubular lacrimal (first infraorbital) lies at the level of the olfactory organ. The reduced, tubular second through fourth infraorbitals surround the eye. The fourth infraorbital lies dorsal to the adductor mandibulae complex posterolateral of the lateral ethmoid and is sometimes divided into two parts. The infraorbital canal splits within the fourth infraorbital and ends in a lateral pore ( $I_6$  in Adriaens et al. 1997).

The narrow frontals are the largest bones of the skull roof (Figure 2). The two frontals, slightly concave in the middle of their lateral margins, are strongly fused, with a barely visible median seam. These bones are anteriorly separated by the anterior fontanel, with a short anterior area of contact between these bones behind the mesethmoid. The frontal bones have two lateral plates visible on a ventral view slightly extending beyond the orbitosphenoid bone margins (Figure 3b). The anastomosis of the infraorbital and

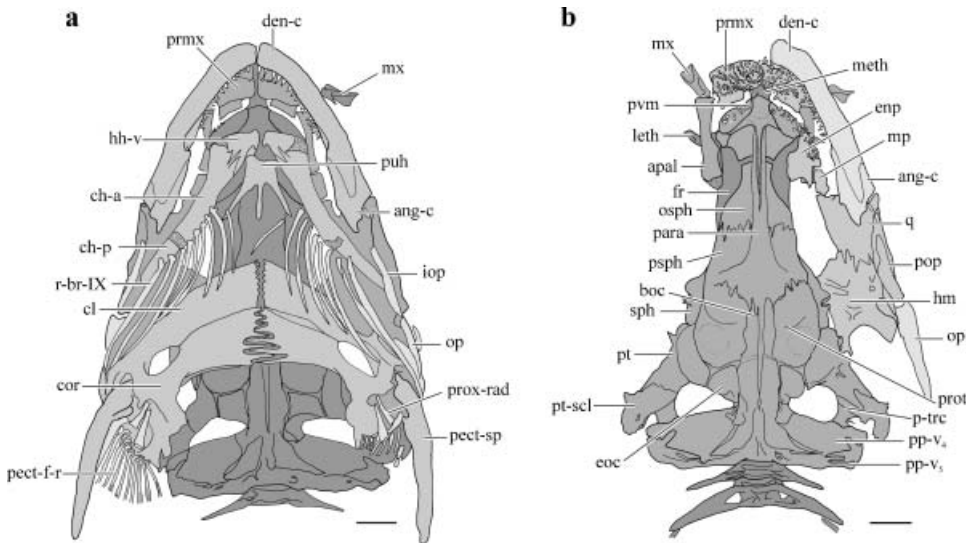


Figure 3. (a) Ventral view of skull of *Platyallabes tihoni* (156 mm SL) (MRAC 125345–349); (b) ventral view of the neurocranium. Scale bars: 2 mm. Dotted areas represent cartilage.

the supraorbital canal is situated on the anterior part of the frontal. The lateral wall of the central portion of the skull is formed by the orbitosphenoid and pterosphenoid, which connect ventrally to the dermal parasphenoid. The latter bone forms the skull floor up to the temporal region and has an elongated process extending to the occipital region (Figure 3b).

*Temporal region* (Figure 2): the sphenotic interdigitates anteromedially with the frontal and posteriorly with the pterotic. The latter interdigitates medially with the parieto-supraoccipital and the frontals and posteriorly with the posttemporo-cleithrum. The sphenotic and pterotic are horizontally aligned, with a slight ventrolateral curvature and no lateral plate. Both bones form the only firm connection between the neurocranium and the suspensorium. The sphenotic has a plate-like and a spiny process anterolaterally that extend ventrally to interdigitate with the hyomandibula. Posterolaterally, a cartilaginous facet on the pterotic and sphenotic articulates with the hyomandibula. The pterotic also has one spiny and one plate-like process. Ventrally, the brain cavity is enclosed by the paired perichondral prootics (Figure 3b).

*Occipital region* (Figure 2): the complex parieto-supraoccipital is situated on the posteromedial portion of the skull roof and is characterized by a short, pointed posteromedial process. This bone encloses the posterior fontanel in the posterior part of the bone. The dermal posttemporo-supracleithrum connects to the pectoral girdle, the parapophyses of the fourth vertebra (by means of the transscapular process) and to the pterotic anteriorly. The occipital region of the skull is ventrally bordered by the unpaired basioccipital and paired exoccipitals (Figure 3b). *Platyallabes tihoni* lacks epioccipitals.

*Upper jaw* (Figures 2, 3a, b): the premaxilla are plate-like bones supporting the nasal sac ventrally. The anterior, larger ventral portion of each premaxilla is covered with several rows of posteriorly directed teeth and the posterior half bears a small process. The maxilla forms a cup-like bone, which encloses the base of the maxillary barbel and bears two articulatory facets for articulation with the palatine.

*Splanchnocranium. Lower jaw* (Figure 4a, b): the long lower jaw consists of two components: the dento-splenio-mentomeckelium and the angulo-splenio-articulo-retroarticular complexes. The coronoid process on the lower jaw is indistinct and dorsal surface of the anterior part of the lower jaw is covered with a large tooth patch of posteriorly curved teeth that extends almost to the coronoid process. The two processes on the retroarticular process are highly asymmetrical and lie completely medial to the quadrate (Figure 4).

*Suspensorium* (Figure 4a, b): as in most siluriforms, the suspensorium consists of the hyomandibula, quadrate, preopercle, metapterygoid, and entopterygoid. The hyomandibula suspends the suspensorium from the neurocranium in the area of the sphenotic and pterotic. The hyomandibula connects to the sphenotic through one broad, anterior process and two pointed, posterior processes and to the pterotic by one pointed and one broader process. These secure the neurocranial-hyomandibula articulation. In between these two sets of processes lies a short articulatory facet. No bony process is present at the anterior margin of the hyomandibula. The opercular process of the hyomandibula is posteroventrally orientated. Medially, the hyomandibula bears a ridge for the attachment of the hyomandibula-ceratohyal ligament. The quadrate interdigitates with the metapterygoid, but no direct contact is present between the quadrate and the entopterygoid. Anteroventrally, the quadrate has a well-developed articulatory facet, articulating with the angular complex. The small metapterygoid connects with the quadrate through a synchondrosis and a bony interdigitation, and is dorsally bordered by the quadrate and the



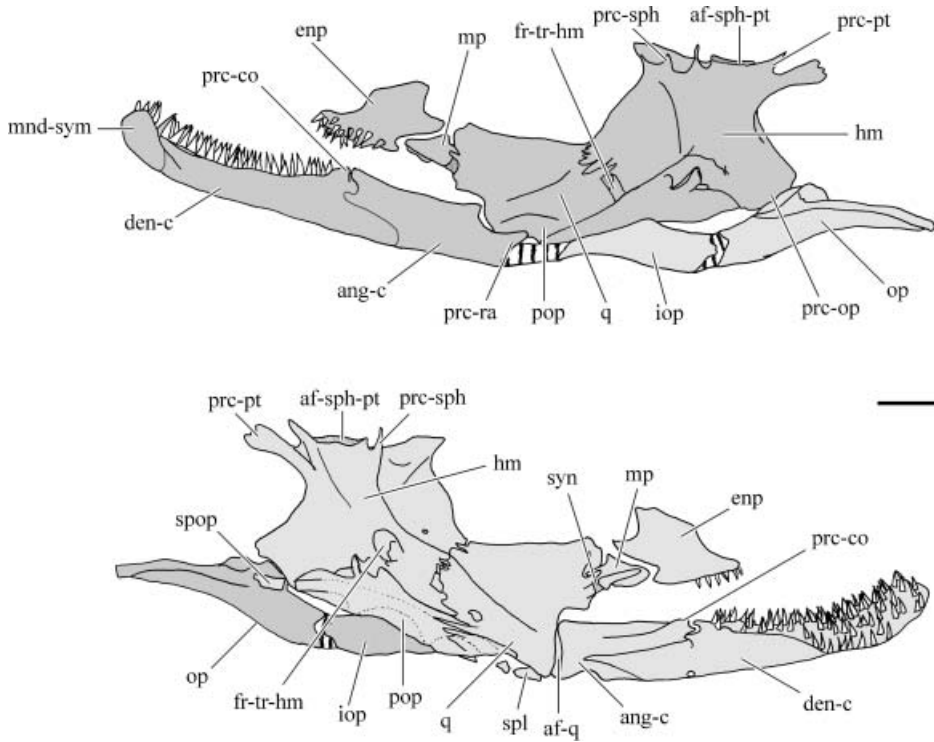


Figure 4. Lateral (below) and medial views of lower jaw, suspensorium and the opercle of *Platyallabes tihoni* (156 mm SL) (MRAC 125345–349). Scale bar: 2 mm. Dotted areas represent cartilage.

large entopterygoid. The plate-like entopterygoid lies anterodorsally to the metapterygoid. The entopterygoid bears several teeth on its ventral margin (Figure 4a). Anteriorly, the entopterygoid is connected ligamentously to the prevomer, the palatine and the lateral ethmoid, thus corresponding to a sesamoid “entopterygoid type 4” (Arratia 1992). The cylindrical autopalatine (Figure 3b) extends ventrally from the lateral ethmoid, with which it articulates through a well-developed articular facet. Both ends of the autopalatine are cartilaginous and it articulates anteriorly with the maxillary, thus being part of the palatine-maxillary mechanism.

**Hyoid arches** (Figure 3a): the hyoid arch consists of paired anterior and posterior ceratohyals and paired ventral and dorsal hypohyals. The hyoid arch articulates ventrally with nine branchiostegal rays. The parurohyal lies in between the two hyoid arches and bears two lateral processes and one medial process. The parurohyal is connected to the hypohyal by means of two separate paruro-hypohyal ligaments (Figure 6c).

**Branchial arches:** the branchial morphology resembles that of *Clarias gariepinus* (Adriaens and Verraes 1998) with the exception of the low number of gill rakers (nine or fewer).

**Opercular series** (Figure 4a, b): the opercle is a pointed, slender, somewhat triangular, dorsoventrally compressed bone, bearing a large articular facet for its articulation with the hyomandibular. The posterior part of the bone bears a horizontal ridge for the attachment of the opercular levator muscle. The opercle is ligamentously attached to the anteriorly positioned interopercle. The interopercle is a long, flat bone, ligamentously attached to the angular complex of the lower jaw. The preopercular bone is incorporated in the suspensorium and surrounds the dorsal part of the preoperculo-mandibular canal. The

posterior part of the canal extends through a series of four or five “open” tubular suprapreopercular bones (Figure 2).

### Cranial myology

*Muscles of the lower jaw (Figure 5).* *Adductor mandibulae muscle:* this complex forms an enormous, jaw-closing muscle covering most of the lateral surface of the head of *Platyallabes tihoni*. It consists, as in other clariids, of an external  $A_2A_3'$ -part and an internal  $A_3''$ , that are separated by the levator arcus palatini (Adriaens and Verraes 1996).

The bipennate  $A_2A_3'$  forms the largest part of the complex (Figure 5a–c). It is divided into a dorsal  $A_2A_3'\alpha$ -part and a ventral  $A_2A_3'\beta$ -part, both of which are attached to an aponeurosis connected to the angular complex of the lower jaw close to the coronoid process. The directions of the muscle fibres of the  $A_2A_3'$  has a range of almost  $160^\circ$ . The  $A_2A_3'\alpha$  is attached to the frontal, the sphenotic, the pterotic, the parieto-supraoccipital, and the suprapreopercular series, and is covered by the fourth infraorbital. The ventral  $A_2A_3'\beta$  is posteriorly connected to the hyomandibula, the quadrate and the preopercle. The  $A_2A_3'$  covers the levator arcus palatini, the dilatator and adductor operculi, and part of the levator operculi.

The  $A_3''$  lies between the levator arcus palatini and the medially situated retractor tentaculi (Figure 5c). The horizontally orientated muscle fibres originate on the medial side of the suspensorium, more specifically on the hyomandibula and the anterodorsal rim of the quadrate, on the frontal, on the sphenotic, and on the pterosphenoid, and insert on the angular complex of the lower jaw medial to the  $A_2A_3'$  tendons.

*Intermandibular muscle:* this muscle is a short, solid muscle with transverse fibres, lying over the mandibular symphysis connecting the contralateral lower jaws (Figure 6a, b). The intermandibularis is bordered posteriorly by the interconnecting cartilage of the left and right bases of the internal-mandibular barbels, thus separating it from the protractor hyoidei muscle.

*Suspensorial muscles. Levator arcus palatini muscle (Figure 5c):* this thin muscle sheet connects the ventrolateral side of the skull roof with the suspensorium. This muscle complex consists of two separate parts (pars rostralis and pars caudalis) and a large complex of aponeuroses. The muscle complex originates on the posterolateral surface of the lateral ethmoid, the ventrolateral side of the frontal up to the sphenotic and inserts mostly tendinously on the anterodorsal border of the interdigitation between the quadrate and the hyomandibula. The levator arcus palatini runs medially from the eye. The levator arcus palatini pars rostralis is located in the anterodorsal part of the complex. It runs from the lateral ethmoid and the frontal and attaches through a medial aponeurosis on the suspensorium. The levator arcus palatini pars caudalis lies more posteriorly and runs between the medial and lateral aponeuroses. The posterior part of the pars caudalis muscle inserts directly on the suspensorium. The predominant fibre direction in the muscle is dorsoventrally orientated, with the anterior fibres showing a more horizontal radiation anteriorly. This complex morphology appears to be two separate muscles.

*Adductor arcus palatini muscle (Figure 5f):* the adductor arcus palatini connects the skull floor and the dorsal rim of the suspensorium. This muscle has the most medial position of all cranial muscles, lining the mouth cavity dorsolaterally. On the neurocranium, it inserts primarily on the parasphenoid, but also on the orbitosphenoid and pterosphenoid. The adductor arcus palatini attaches on the suspensorium (dorsal rim of the hyomandibula, the

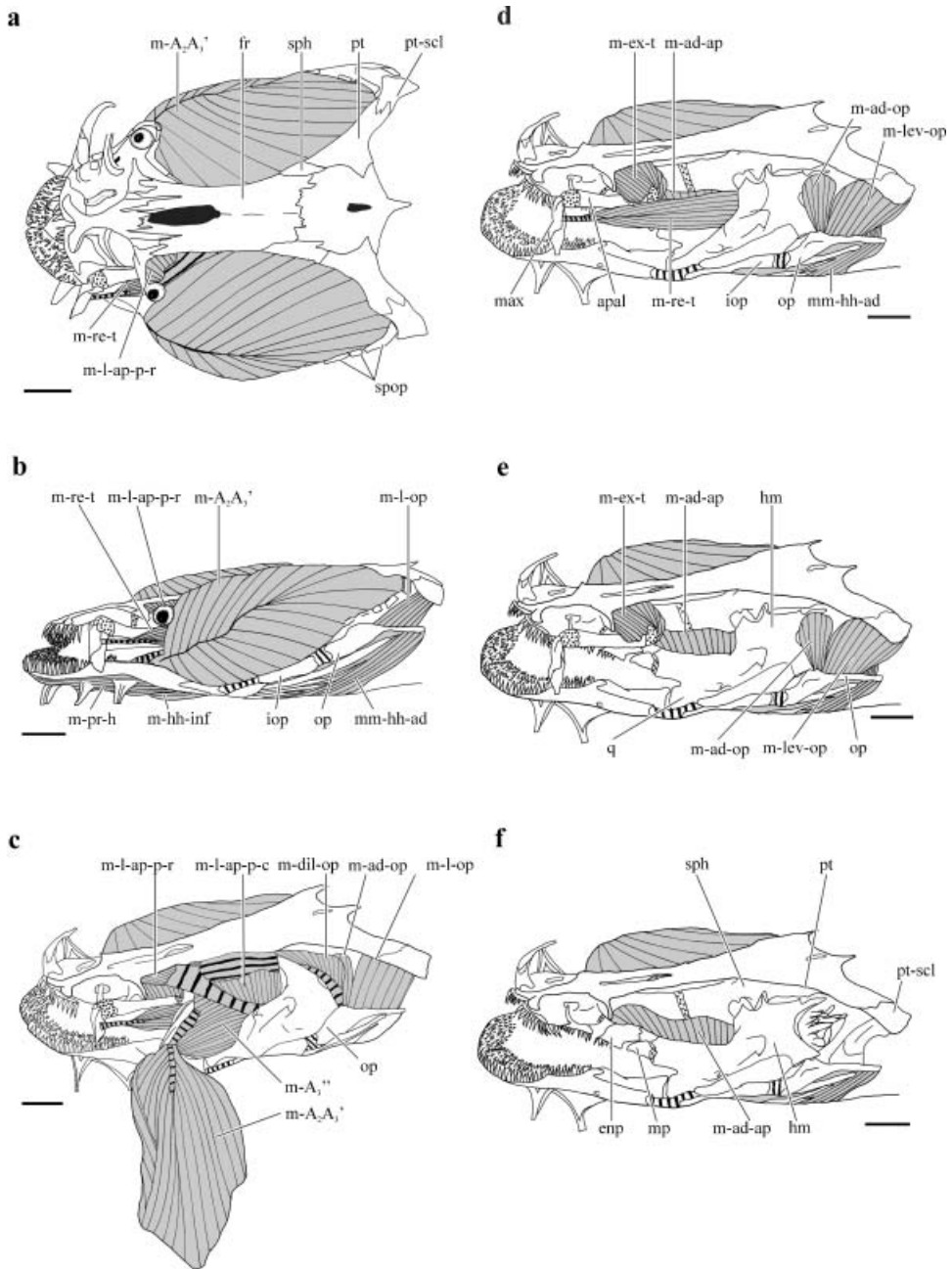


Figure 5. Head musculature of *Platyallabes tihoni* (135 mm SL) (MRAC 125345–349). (a) Dorsal view, skin, left infraorbital series removed; (b) lateral view, skin and infraorbital series removed; (c) dorsolateral view, skin, eyes and infraorbital series removed and  $A_2A_3'$ -part folded back; (d) dorsolateral view, jaw muscles, levator arcus palatini and dilatator operculi removed; (e) laterodorsal view, retractor tentaculi removed; (f) dorsolateral view, extensor tentaculi, adductor operculi and levator operculi removed. Scale bars: 2 mm. Dotted areas represent cartilage.

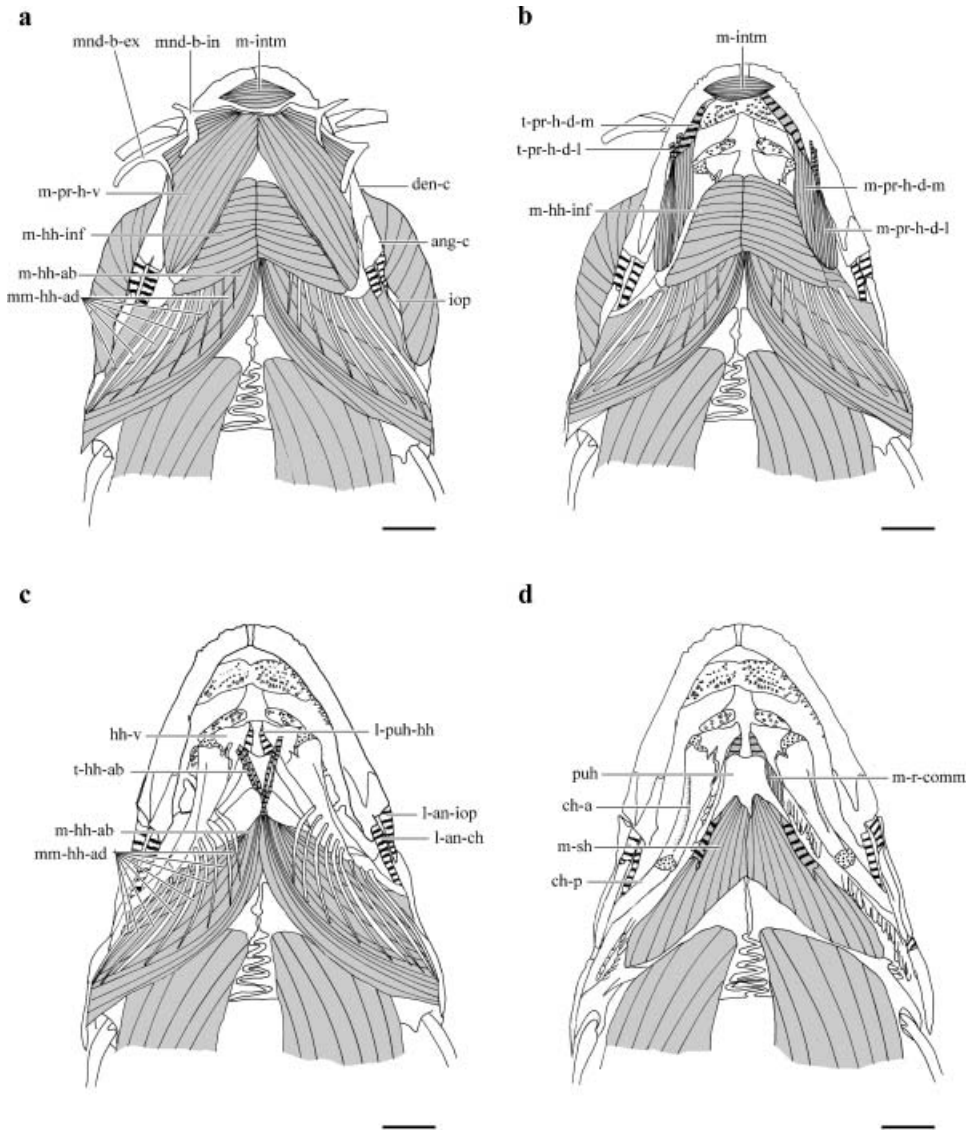


Figure 6. Ventral view of head musculature of *Platyallabes tihoni* (135 mm SL) (MRAC 125345–349). (a) Skin removed; (b) ventral part the hyoid protractor removed; (c) dorsal part of hyoid protractor, intermandibular and hyohyoideus inferior removed; (d) hyohyoideus abductor and the hyohyoidei adductores removed. Scale bar: 2 mm. Dotted areas represent cartilage.

quadrate and the entopterygoid). The fibres run in a transverse plane with the anterior fibres more obliquely orientated.

*Opercular muscles.* Three opercular muscles could be discerned. The dilatator operculi is situated most anteriorly, partially covering the adductor operculi, with the levator operculi most posteriorly.

*Dilatator operculi muscle* (Figure 5c): the flattened dilatator operculi starts from halfway up the ventrolateral surface of the frontal between the two aponeuroses of the levator arcus

palatini and the ventrolateral part of the sphenotic and the pterotic (Figure 5c). It inserts through a large tendon on the lateral surface of the dorsal process of the opercle close to the articulation with the hyomandibula. This tendon runs along the anteroventral side of the dilatator operculi.

*Adductor operculi muscle* (Figure 5d, e): this shorter and more robust muscle connects the posterior side of the suspensorium with the opercle. The adductor operculi originates on the posterodorsal part of the hyomandibula and the posteroventral part of the pterotic and inserts on the dorsal process of the opercle and thus lateral to the opercular articulation with the hyomandibula, in the region medial to the insertion of the dilatator operculi. The predominantly dorsoventrally directed fibres also attach to the connective tissue covering the dorsolateral surface of the remnant suprabranchial cavity. The posterior part lies against the posteriorly situated levator operculi.

*Levator operculi muscle* (Figure 5d, e): the levator operculi is the largest and most robust of the three opercle muscles. It connects the posteriormost part of the neurocranium with the opercle. This muscle originates on the posteroventral part of the posttemporo-supracleithrum, the suprapreopercles and the connective tissue covering the suprabranchial cavity. Ventrally, the levator operculi attaches to nearly all of the complete dorsal side on a ridge of the opercular bone.

*Maxillary barbel muscles. Retractor tentaculi muscle* (Figure 5d): the retractor is a bundle-like muscle running from the maxillary bone to the suspensorium between the  $A_3$  and the adductor arcus palatini. The fibres in general all follow the same anteroposterior direction. Anteriorly, the retractor lies medial to the eye and lateral to the autopalatine. It inserts on the anterior side of the hyomandibula and the quadrate. The muscle is divided into a dorsal and ventral part, separated by an aponeurosis, and attaches to the posterodorsal side of the maxillary through a short tendon.

*Extensor tentaculi muscle* (Figure 5e): the extensor tentaculi extends from the ventral and ventrolateral surface of the lateroethmoid, the ventral side of the frontal and the lateral side of the orbitosphenoid to the autopalatine. The fibres, organized in two separate bundles, attach to the autopalatine posterior from the articulatory facet and enclose the posterior end of the autopalatine.

*Hyoid muscles. Protractor hyoidei muscle* (Figure 6a, b): the protractor hyoidei connects the hyoid bars with the lower jaw and is divided in a ventral and dorsal part, each of which originate on the ventrolateral side of the anterior ceratohyal and inserts on both complexes of the lower jaw. The ventral part is V-shaped (Figure 6a); with the left and right halves attached medially by a fascia at the plane through the mandibular symphysis. The insertion of the muscle on the mandibula occurs over the entire antero-ventral surface of the lower jaw and on the bases of the mandibular barbels. Several fields of fibres can be distinguished interconnecting different parts of the barbel bases. The dorsal part of the protractor inserts on the medial surface of both lower jaws (Figure 6b) and is divided into a medial and a lateral part. The medial parts attach postero-medially to the dental complexes of the lower jaw through a tendon and are separate. The lateral subparts attach to the ventrolateral surface of the dental complexes through a double tendon system.

*Hyohyoidei inferior muscle* (Figure 6b): this muscle inserts on the ventral side of the anterior ceratohyal, medial to the insertions of the protractor hyoidei, and to the dorsal and ventral hypohyals. The contralateral fibres are medially connected to a fascia. Posteriorly the muscle also attaches to the bases of the branchiostegal rays.

*Hyohyoideus abductor muscle* (Figure 6c): the hyohyoideus abductor links the anterior tip of the hyoid bars with the first contralateral branchiostegal rays. The muscles originate from the anterior face of these branchiostegal rays and insert on to the ventral hypohyal of the opposite side by means of a double tendon.

*Hyohyoidei adductores muscles* (Figure 6c): the hyohyoidei adductores muscles lie between successive branchiostegal rays, starting from the first ray and attaching on to the medial surface of the opercle.

*Sternohyoideus muscle* (Figure 6d): this muscle connects the pectoral girdle to the parurohyal, which, in turn, is ligamentously connected to the ventral hypohyals of the hyoid bars. Posteriorly, the sternohyoideus inserts on the cleithrum on both its dorsal and ventral surfaces. Anteriorly, both muscle heads attach on to the double-forked parurohyal. On the anterolateral surfaces, two contralateral tendineous plates lie on top of the muscle. No myocommata were observed.

#### Postcranial skeleton

The total number of vertebrae in *Platyallabes tihoni* (58–490 mm SL) ranges from 63 to 83 (mode: 78). The numbers of precaudal vertebrae varies from 16 to 20 (mode: 17) and of caudal vertebrae from 47 to 66 (mode: 63). *Platyallabes tihoni* has from four to seven pairs of ribs. A notable feature of the vertebrae is the presence of a large foramen at the bases of the parapophyses of the precaudal vertebrae (Figure 7).

The pectoral fins of *P. tihoni* have non-serrated spines and 11 branched fin rays that articulate with two proximal radials. The pectoral girdle has a distinct fenestra between the coracoid and the cleithrum. Furthermore, the cleithrum lacks an anterior process but has a distinct anterior rim ventrally, on to which the sternohyoideus is attached. The pelvic fins each carry six, branched fin rays which articulate with the broad and flat basipterygium of the pelvic girdle. Anteriorly an internal and external anterior process can be distinguished (Figure 8a). The number of dorsal and ventral fin rays varies, respectively, from 125 to 139 and from 114 to 129.

The morphology of the caudal skeleton of *P. tihoni* shows some variation but always consists of the parhypural, five hypurals and an urostyl, but various fusion patterns can be



Figure 7. Radiography of *Platyallabes tihoni* (329 mm SL) (MRAC 138698–699). Arrows indicate large foramen at the bases of the parapophyses of the precaudal vertebrae. Scale bar: 1 cm.

discerned. Poll (1977) reported a total fusion of all hypurals and the epural; however, our observations show that hypurals 3 and 4 appear fused, as well as the urostyle and hypural 5. Dorsally of the latter complex lies the broadly tipped epural. The neural arches of the second and third preural vertebrae are spiny, not elongated and do not support fin rays. The haemal arch of the second preural vertebra is elongated, broadly tipped and supports fin rays, the haemal arch of the third preural vertebra is not elongated, spiny and does not support rays (Figure 8b). At the level of the non-supporting arches pterygiophores support the fin rays.

### Species description

The proportional measurements and counts are given in Table I. *Platyallabes tihoni* characterized by elongated, dorsoventrally flattened body; with only the caudal tip transversely flattened (Figure 1). Degree of anguilliformity as expressed by ratio of total length to body height (Poll 1942) between 15.6 and 33.9, with average of  $24.7 \pm 4.4$ , with postanal length of 65.3% up to 81.4% of SL.

Head length 7.4–17.2% of SL; and skull width 62.9–82.5% of head length. Skull roof width (exposed) 11.5–40.1% of orbital skull width. Skull roof appears very small, due to dorsomedial outgrowth of hypertrophied adductor mandibulae complex, but remains visible. Eyes clearly visible, in contrast to situation in some other anguilliform clariids (Cabuy et al. 1999; Devaere et al. 2001). Mouth width almost equals interorbital distance. Fleshy lips fused at mouth corners. Lower jaw distinctly prognathous (Figures 1, 2).

Unpaired fins form continuous fin fold. Dorsal fin origin very close to skull; with small distance between dorsal fin origin and occipital process on parieto-supraoccipital (Adriaens et al. 2002, Figure 1). Distance only 2.2–6.6% of SL.

Both pectoral fins always present. Pectoral fin length 43.3–82.0% of head length. Pelvic fins present in all except for one specimen (MCZ 50239). Pelvic fin length 31.2–71.2% of head length. Pectoral fins always preceded by non-serrated spine (59.2–95.1% of pectoral fin length). The pectoral fins have 11 fin rays; the pelvic fins carry six fin rays. Branchiostegal rays 8–10.

Teeth present on dentary, premaxilla, prevomer and on entopterygoid, with latter unique within clariids (see below). All teeth pointed and curved. Prevomer with two separate tooth plates.

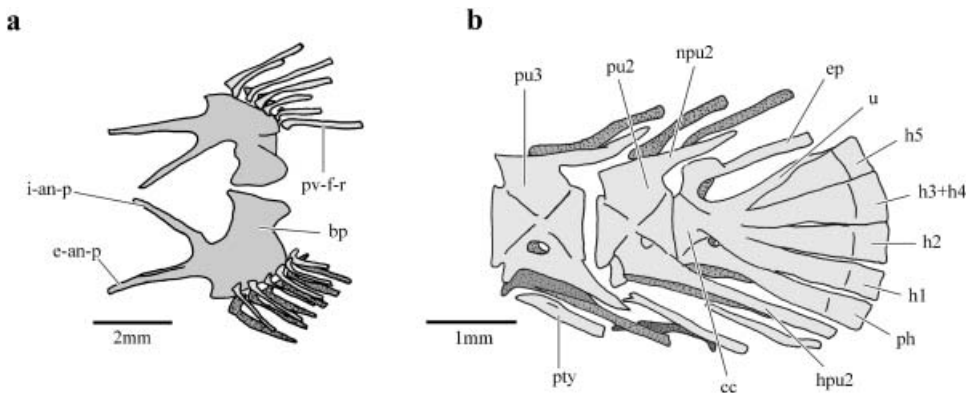


Figure 8. (a) Pelvic girdle; (b) caudal skeleton of *Platyallabes tihoni* (156 mm SL) (MRAC 125345–349).

Table I. Measurements and meristic data for *Platyallabes tihoni*.

|  | Holotype | Other specimens |         |         |      |     |
|--|----------|-----------------|---------|---------|------|-----|
|  |          | <i>n</i>        | Minimum | Maximum | Mean | SD  |
| TL (mm)  | 521      | 54              | 63      | 380     |      |     |
| SL (mm)  | 490      | 54              | 58      | 359     |      |     |
| Measurements in % SL                             |          |                 |         |         |      |     |
| Preanal length                                   | 22.8     | 54              | 18.6    | 34.7    | 26.3 | 3.5 |
| Prepectoral length                               | 10.5     | 54              | 8.3     | 17.0    | 12.1 | 2.0 |
| Prepelvic length                                 | 20.9     | 54              | 18.3    | 30.6    | 23.5 | 3.1 |
| Predorsal length                                 | 13.0     | 54              | 12.5    | 23.4    | 16.9 | 2.8 |
| Distance occipital process and dorsal fin origin | 3.0      | 54              | 2.2     | 6.6     | 3.7  | 1.0 |
| Pectoral fin length                              | 5.5      | 54              | 4.6     | 9.9     | 6.6  | 1.3 |
| Pectoral spine length                            | 3.8      | 54              | 3.3     | 7.0     | 5.0  | 0.8 |
| Pelvic fin length                                | 4.5      | 54              | 4.0     | 7.3     | 5.6  | 0.8 |
| Caudal peduncle depth                            | 1.8      | 54              | 1.1     | 3.6     | 1.9  | 0.5 |
| Body depth at anus                               | 3.9      | 54              | 3.0     | 6.4     | 4.2  | 0.8 |
| Interpectoral depth                              | 7.6      | 54              | 6.9     | 13.0    | 9.3  | 1.5 |
| Interpelvic depth                                | 3.4      | 54              | 2.9     | 6.2     | 4.2  | 0.8 |
| Head length                                      | 10.1     | 54              | 7.4     | 17.2    | 12.7 | 2.1 |
| Measurements in % head length                    |          |                 |         |         |      |     |
| Preorbital length                                | 72.4     | 54              | 61.2    | 85.5    | 74.7 | 9.2 |
| Supraoccipital process length                    | 6.7      | 54              | 6.9     | 20.3    | 13.5 | 3.0 |
| Skull width                                      | 82.6     | 54              | 62.9    | 82.5    | 75.8 | 7.9 |
| Supraoccipital process width                     | 18.9     | 54              | 10.2    | 22.3    | 16.0 | 3.0 |
| Interorbital distance                            | 44.8     | 54              | 30.4    | 56.9    | 38.5 | 4.5 |
| Anterior nostril interdistance                   | 18.3     | 54              | 10.5    | 26.1    | 14.1 | 2.7 |
| Posterior nostril interdistance                  | 35.1     | 54              | 22.6    | 44.8    | 31.2 | 4.5 |
| Rostral skull width                              | 54.8     | 54              | 30.3    | 69.0    | 40.0 | 7.4 |
| Orbital skull width                              | 85.0     | 54              | 43.7    | 92.9    | 54.9 | 6.8 |
| Skull height                                     | 40.1     | 54              | 22.8    | 61.7    | 34.6 | 6.9 |
| Eye diameter                                     | 3.9      | 54              | 3.7     | 12.8    | 6.1  | 1.6 |
| Snout height                                     | 14.6     | 54              | 9.5     | 21.6    | 13.3 | 4.8 |
| Orbital skull height                             | 30.4     | 54              | 16.8    | 44.0    | 23.4 | 4.8 |
| Prehyoid length                                  | 32.5     | 54              | 17.2    | 44.5    | 27.6 | 4.1 |
| Internal mandibular interdistance                | 32.9     | 54              | 20.3    | 42.0    | 27.5 | 3.7 |
| External mandibular interdistance                | 52.3     | 54              | 32.1    | 67.8    | 43.2 | 6.0 |
| Mouth width                                      | 44.0     | 54              | 19.5    | 76.1    | 32.7 | 8.5 |
| Skull roof width                                 | 9.8      | 54              | 9.5     | 26.8    | 18.9 | 4.6 |
| Meristic counts                                  |          |                 |         |         |      |     |
| Number of ribs                                   | 4        | 33              | 4       | 7       |      |     |
| Total number of spines                           | 76       | 33              | 63      | 83      |      |     |
| Number of dorsal fin rays                        |          | 19              | 125     | 139     |      |     |
| Number of anal fin rays                          |          | 19              | 112     | 129     |      |     |

Alcohol-preserved specimens show even, light-brownish colour over whole body, nostrils, barbels and fins.

*Platyallabes tihoni* lacks usual components of suprabranchial organ, with arborescent organs and fan-like covers completely absent. Remnant of small suprabranchial cavity apparently present.



## Discussion

The anatomy and taxonomy of the more extremely elongate clariids is poorly known. This is the case for *Platyallabes tihoni*, which has only been cited in several papers by Poll (e.g. 1944, 1957, 1977), dealing mainly with morphometric and meristic features and some gross osteological characters. These were all based solely on the holotype.

As a result, a complete description of *P. tihoni* was necessary, as is a comparison with several other representatives of the clariid family, in order to determine their affinity and the systematic position of *P. tihoni*.

### *Morphology and comparison with other clariids*

*Platyallabes tihoni* has previously been described as an anguilliform clariid (Poll 1944, 1957, 1977), with this character as one of the primary reasons for its original placement within the genus *Gymnallabes* (Poll 1944, 1957). Our own observations show that *P. tihoni* has an intermediate position with characters of both anguilliform and fusiform Bauplan.

The reduced skull and narrow skull roof is comparable to that of the anguilliform clariid species (Cabuy et al. 1999; Devaere et al. 2001, 2004). Also typical for anguilliform species is the extreme reduction of all infraorbitals and nasal bones, as they become tubular but still enclosing limited portions of the infraorbital canal of the lateral line system. A comparable reduction occurs in the suprapreopercles and the praeoperculo-mandibular canal. Although the primitive catfish family Diplomystidae has tubular infraorbitals and suprapreopercles (Arratia 1987), many clariids possess plate-like infraorbitals and suprapreopercles. Based on the widespread assumption that Heteropneustidae are the sister group of Clariidae, the presence of plate-like bones is to be considered plesiomorphic for Clariidae (Heteropneustidae have plate-like bones). However, following the phylogeny suggested by de Pinna (1993) and Diogo (2003), *Heteropneustes* is to be considered a member of the Clariidae, with *Uegitglanis* being the sister group of *Heteropneustes* and all other clariids. The blind and cave-dwelling *Uegitglanis* bears tubular infraorbitals and suprapreopercles (David 1936). This would imply that the plesiomorphic condition of Clariidae would be tubular bones, a retained plesiomorphic character of Siluriformes in general. The problematic relation of *Uegitglanis* with respect to other clariids is among other things because of the absence of the synapomorphic suprabranchial organs (Chardon 1968; Teugels and Adriaens 2003). The absence of the typical arborescent organs in Heteropneustidae also makes the phylogenetic position of this genus problematic (Diogo 2003; Teugels and Adriaens 2003). Further knowledge on the true nature of the respiratory organs, as well as morphological and molecular data, might elucidate the true relationships, and thus the status of the character of tubular bones.

The higher level of interdigitation of, among others, the skull roof bones is another correspondence with the anguilliform species and contributes to the solidity of the skull; additionally *P. tihoni* even shows a fusion of the frontals (Figure 2). Furthermore, the infraorbital-supraorbital canal anastomosis is situated in the anterior part of the frontals (Figure 2) and no longer in the sphenotic, the latter being the case in the fusiform species and in *Diplomystis chilensis* (Adriaens et al. 1997; Arratia 1987). The lateral ethmoid has no contact with the second infraorbital bone; this is also seen in *Gymnallabes typus* (Cabuy et al. 1999). The sphenotic and pterotic lack a lateral plate, as is the case in all elongated species, except for *Platyclarias machadoi* (current research). The hyomandibula has a high number of anterior and posterior processes (respectively two and three) (Figure 4),

comparable to the number in anguilliform species. The lower jaw also shows osteological similarities: the robust tooth battery that runs close up to the coronoid process (Figure 4) and the low number of gill rakers (up to nine).

Also the general muscular morphology of *P. tihoni* resembles that of the anguilliform species and shows the same insertion sites for the different muscles. A first clear example is the hypertrophied jaw muscle and more specifically the  $A_2A_3'$ -part. Compared to *C. gariepinus* additional insertion sites are found, the frontal, pterotic and posttemporo-supracleithrum. Besides this, there is also a large increase in the range of muscle fibre directions, up to almost  $160^\circ$ . This is still less than that found in most extremely elongated species (*C. gariepinus*  $105^\circ$ ; *Clariallabes* sp.  $140^\circ$ ; *G. typus*  $150^\circ$ ; *C. apus*  $180^\circ$ ). As in *C. apus* and *G. typus*, the ventral part of the protractor hyoidei is V-shaped. Consequently, the fascia, connecting the two contralateral parts of that muscle, does not overlap with the anterior side of the hyohyoideus inferior. Furthermore, the two contralateral parts of the dorsal part of the protractor hyoidei do not contact each other either through direct muscle contact or through tendons (Figure 6b), comparable to the situation in *G. typus* (Cabuy et al. 1999).

Besides these character states similar to the anguilliform clariids, *Platyallabes tihoni* shares a list of symplesiomorphies with the fusiform representatives.

#### *Special traits of Platyallabes tihoni*

The intermediate position of anguilliformity of *P. tihoni* is reflected in the number of vertebrae, as this number can give an indication of the degree of anguilliformity. The mode of the total number of vertebrae of *P. tihoni* is 78. The vertebral counts for the extremely anguilliform representatives are higher, e.g. *Dolichallabes microphthalmus* ( $n=11$ ): 106, *Channallabes apus* ( $n=98$ ): 104 and *Gymnallabes typus* ( $n=26$ ): 87, while the number of vertebrae found in a fusiform member of the family, *Clarias gariepinus* ( $n=47$ ): 56–63 (Teugels 1986), is clearly lower.

Besides the above-mentioned characters that exhibit a resemblance with the anguilliform or fusiform representatives, *P. tihoni* shows a large number of unique features. The fused frontals show a restricted concavity along their lateral sides (Figure 2), whereas the width remains the same along the whole length in anguilliform species (Cabuy et al. 1999; Devaere et al. 2001) or broadens in the middle in most fusiform representatives (Adriaens and Verraes 1998). These lateral plates slightly pass the orbitosphenoid outlines (Figure 3b); a situation otherwise only seen in *Diplomystis chilensis* (Arratia 1987) but that does not correspond with the broader plates in the fusiform clariids or the smaller extensions in the anguilliform species. The suprapreopercular bones are reduced to a set of tubular bones. This lack of any plate-like extension on the dorsal suprapreopercular is unique within the clariids, as is the higher number of bones (up to five). Both the sphenotic and pterotic, although lacking a lateral plate, exhibit a more or less horizontal position. Also, on the low suspensorium some unique features can be observed: on the anterior margin of the hyomandibula there is no bony outgrowth present, an absence only viewed elsewhere in *Heteropneustis fossilis* (sister group of the Clariidae) (Srinivasachar 1958) and *Platyclarias machadoi* (current research). The prevomer shows in all specimens two tooth plates, clearly separated from each other, a situation seen in other juvenile clariids, but never in adults (the strongly fused frontals, with a hardly visible seam, indicate that we are dealing with adult specimens of *P. tihoni*) (Cabuy et al. 1999). The feature most remarkable in *P. tihoni* is the dentigerous entopterygoid (Figure 4). This characteristic has not been

observed elsewhere in the Clariidae, except on one side in one *G. typus* specimen. This was at that point considered as an aberrant condition (Cabuy et al. 1999). Moreover, a toothed entopterygoid generally does not occur in catfishes, with the exception of some ariids (Arratia 1992). These teeth could possibly be linked to a more specialized diet. The retroarticular process on the lower jaw is extremely asymmetric, lying completely on the medial side of the angular bone. Although this process is never fully symmetrical in the other clariids, it is never asymmetrical to this degree. A last feature of *P. tihoni* is the absence of a suprabranchial organ, together with a reduced suprabranchial cavity. Such a situation can also be seen in *Uegitglanis*, *Bathyclarias* and *Xenoclarias*. In *Xenoclarias* and *Bathyclarias*, the reduction is considered to be related to living in deep waters (Chardon 1968; Poll 1977; Anseume and Teugels 1999; Agnès and Teugels 2001; Teugels and Adriaens 2003). Phylogenetically, this should consequently be considered as a secondary reduction, a hypothesis also supported by genetic evidence (Agnès and Teugels 2001).

On the muscular level, we see that there is a unique system of two tendons for the insertion of the lateral parts of the pars dorsalis of the protractor hyoidei on to the lower jaw. A similar system with two tendons is seen on the hyohyoideus abductor (Figure 6b, c). A last remarkable myological difference is the very complex morphology of the levator arcus palatini (see Results) (Figure 5c).

These unique features are not limited to cranial characteristics; post-cranially there are also some characters that are typical for *P. tihoni*. The cleithral bone has no anterior process; once more a condition only previously observed in *H. fossilis*. The same is true for the very large parapophyseal foramina present in the precaudal vertebrae (Figure 7). *Platyallabes tihoni* has a very low number of ribs (four to seven, mode: five), which is the lowest number observed among examined clariids: *C. apus* 10–17; *G. typus* 7–14; *D. microphthalmus* 6–9; *C. garipepinus* 12 (Cabuy et al. 1999).

This list of above-mentioned autapomorphies can help to indicate the validity of the species and genus, while the synapomorphies help to interpret the phylogenetic situation within the clariids and especially within the anguilliform genera.

#### *Functional implications of the extremely depressed skull*

The flattened skull can be expected to be related to spatial changes in the surrounding structures, in all three dimensions of the Bauplan framework, since the spatial constraints within an integrated design imply that trade-offs will occur (Barel 1984).

Most of these characters are situated in the splanchnocranium and the articulation with the neurocranium. As mentioned above, the sphenotic and pterotic bones are in a more or less horizontal orientation. Consequently, the interdigitation with and position of the suspensorium will also be in a more horizontal, lateral plane. This results in a dorso-ventral reduction in skull height. The orientation of these above-mentioned bones is in contrast with the tendency within the anguilliform clariids, in which the sphenotic and pterotic are in a more vertical position, which could be beneficial to accommodate the hypertrophic jaw muscles (Cabuy et al. 1999; Devaere et al. 2001). Despite this different orientation, *P. tihoni* exhibits large jaw muscles and this with similar insertion sites as within the anguilliform species (Cabuy et al. 1999; Devaere et al. 2001). The consequently more elevated position of the adductor mandibulae complex could explain the extensive bulging of these jaw muscles. More posterior on the suspensorium, the opercular process of the hyomandibular has a more posterior orientation. This means that the dorso-ventrally compressed opercle is positioned more posterior to the suspensorium instead of ventral to

it. All this leads to a decrease of the branchial cavity volume, which can have some consequences for feeding and respiratory efficiency (Adriaens and Verraes 1997d). Also the absence of the suprabranchial organ can be considered as a consequence of arising spatial constraints in the trend towards a miniaturization of the skull in the anguilliform clariids (Devaere et al. 2001). Additionally, the substantial dorso-ventral compression of the skull of *P. tihoni* will have generated a competition for space for both gill-apparatus and the suprabranchial apparatus. The combination of both constraints apparently favoured the loss of the suprabranchial organ.

The medial position of the retroarticular process in *P. tihoni*, with respect to the articulation head of the quadrate, is unique for clariids. This condition presumably is a simple consequence of the topographic relation between lower jaw and suspensorium, the plane of mandibular movements and the fact that this suspensorium has become tilted extremely, to an almost horizontal position (Figure 9a). Because the axis of rotation of the lower jaw has to run through both lower jaw articulations (in order to avoid dislocations), a horizontal tilting of the suspensorium will result in a medial shift of the articulation on the quadrate. Consequently, the post-articulation part of the lower jaw, i.e. the retroarticular process, becomes situated ventro-medially to the quadrate head (Figure 9b).

### Comparative material examined

*Platyallabes tihoni* (Poll, 1944): Democratic Republic of 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* (Günther, 1873): Angola. Ambriz, BMNH 1873.7.28.16 (holotype); Democratic Republic of Congo. Bokalakala, MRAC 175247–270 ( $n=10$ ); Kinshasa,

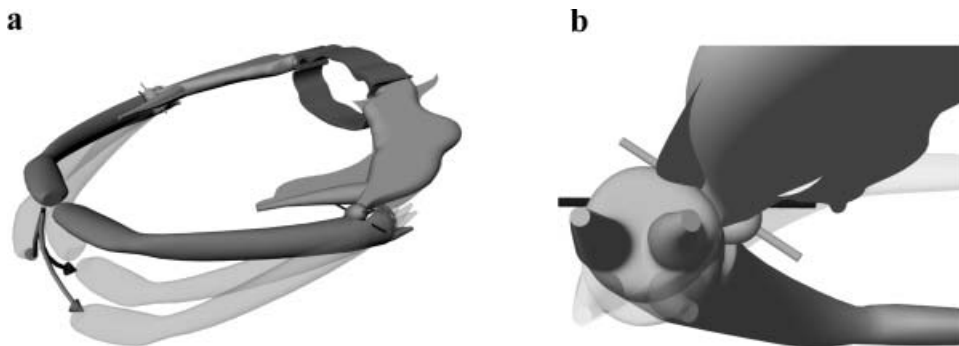


Figure 9. Schematic 3D reconstruction of the lower jaw-suspensorium articulation area. (a) Overview of the lower jaw, suspensorium and part of skull at level of articulation with suspensorium. Solid lower jaw indicates closed mouth, transparent lower jaw indicates open mouth. Black arrow shows displacement of lower jaw according to the black axis indicated at the jaw articulation. The grey arrows indicate the movements of the lower jaw halves if they were rotated along the grey axis at the articulation. (b) Detail from a postero-ventral view of the lower jaw articulation, showing the two rotation axis: black rod represents the axis which allows a proper mouth opening, grey rod represents the axis of rotation which has shifted together with the suspensorium. Rotation along the black axis results in the medial position of the retroarticular process; with respect to the suspensorium (transparent lower jaw indicates the closed mouth, solid lower jaw the open mouth).

MRAC 97-056-P-0001-0003 ( $n=2$ ); Bumba, MRAC 88-25-P-2192-227 ( $n=36$ ); Boma, MRAC 939; River Lula, Bushimaie, MRAC 153505; Kelé, MRAC 1491; Stanleyville, MRAC 30893-30900 ( $n=8$ ), MRAC 88-01-P-1976-1992 ( $n=17$ ); River Ruki, Eala, MRAC 14747-49 ( $n=3$ ); Lake Tumba swamp area, MRAC 46299; Katanga, MRAC 39480; River Botota, keseki, MRAC 67763-77 ( $n=15$ ); Mwilambongo, MRAC 72886-887 ( $n=2$ ); Dekese, River Lofu, Anga, MRAC 153352; Yangambi, MRAC 68700; River Oubangui, Imfondo, MNHN 1922-0029; Loango, MNHN 1924-0079, MNHN 1924-0080; Sangha, MNHN 1925-0137; Mogende, MNHN 1926-0155-59 ( $n=5$ ); River Congo, MNHN, 1937-0124-25; Stanley pool, Bamu, MNHN 1958-0111; Boloko, River Likouala, MNHN 1962-0401 ( $n=7$ ); Mossaka, River Likouala, MNHN 1963-0402 ( $n=2$ ); River Loadjili, Songolo, MNHN 1967-0143 ( $n=6$ ); Mangala, BMNH 1896.3.9.17; River Lebuzi, Kaka Munu, BMNH 1912.4.14.11-12 ( $n=2$ ); 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; River Nanga, between Boukou-Zassi and Kouilou swamp area, MRAC 90-57-P2315; Sintou, River Kibombo, Kouilou, MNHN 1967-0144; River Loadjili, Songolo, Pointe Noire, MNHN 1967-0145 ( $n=6$ ); River Youbi, Noumbi. Angola. Caungula, Mabete, River Uamba, MRAC 162088; River Camuconda, Tchimenji, MRAC 162089, MRAC 162090-094 ( $n=5$ ), MRAC 162095-100 ( $n=6$ ); River Ganga-Ludchimo, MRAC 162083-086 ( $n=4$ ).

*Gymnallabes typus* Günther, 1867: Nigeria. Old Calabar, BMNH 1866.12.4 ( $n=2$ ) (syntypes); other specimens, Nigeria. Umu-Eze Amambra, MRAC 84-16-P-1-2; River 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 Rivers, MRAC 97-085-P-0001-0004 ( $n=4$ ); River 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; River 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. Cameroon. River Kom, Ntem, Aboulou, MRAC 73-18-P-3307-309.

*Clarias gariepinus* (Burchell, 1822): artificially cultivated specimens ( $n=10$ ), Ghent University.

*Heteropneustes fossilis* (Bloch, 1794): aquarium specimen, AMNH 172276 SW.

*Heterobranchus longifilis* Valenciennes, 1840: Egypt. Nile, AMNH 3054 SW.

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