

Cephalic Morphology of *Pythonichthys macrurus* (Heterenchelyidae: Anguilliformes): Specializations for Head-First Burrowing

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ABSTRACT The Heterenchelyidae, a family of Anguilliformes, are highly specialized fossorial eels. This study was conducted to evaluate the cranial specialization in relation to head-first burrowing behavior in the heterenchelyid, *Pythonichthys macrurus*. Thereby, detailed descriptions are provided of the cranial myology and osteology of *P. macrurus* and its differences with that of representatives of three families: the Moringuidae (*Moringua edwardsi*), a head-first burrower; the Anguillidae (*Anguilla anguilla*), a nonburrowing representative and the Ophichthidae (*Pisodonophis boro*), a head and tail-first burrower. This comparison may help to get a better understanding of the cranial specialization of head-first burrowers in heterenchelyids and moringuids. We recognize as morphological adaptations to burrowing: reduced eye size, a caudoventral orientation of the anteromedial section of the adductor mandibulae muscle complex, the posterior position of the quadrate-mandibular joint, a solid conical skull, large insertion sites of epaxial and hypaxial muscle on the neurocranium, a widened cephalic lateral line canals extending into the dermal cavities, and a ventral position of the gill opening. *J. Morphol.* 271:1053–1065, 2010. © 2010 Wiley-Liss, Inc.

KEY WORDS: Anguilliformes; Heterenchelyidae; cranial morphology; adaptation; burrowing behavior

INTRODUCTION

Anguilliform fishes, a large group of elongated, cosmopolitan teleosts (Nelson, 2006), are adapted for wedging through small openings or crevices (Gosline, 1971; Smith, 1989c). They have evolved to a range of different life styles from pelagic to burrowing, the latter from head-first (Heterenchelyidae, Moringuidae) to tail-first (Ophichthidae). The head-first burrowers have been shown to have specific cephalic features (McCosker et al., 1989; Smith 1989a,b,c; De Schepper et al., 2005, 2007), but an interesting question is whether head-first burrowing eels converge on a similar morphology or whether there are different ways to be a head-first burrower. De Schepper et al. (2005, 2007) considered some features such as eye reduction, modifications of the cranial lateral line system, jaw adductor hypertrophy, hyperossification, and taper-

ing of the skull as cephalic adaptations for head-first burrowing behavior in Ophichthidae and Moringuidae.

The mud eels or heterenchelyids, one of the 15 families of the Anguilliformes, are a highly specialized family of burrower eels. They comprise two genera (*Panturichthys* and *Pythonichthys*) with eight species and are considered well adapted to their burrowing habits (Smith, 1989a). The members of this family are found in the tropical zone of the Atlantic, Mediterranean, and eastern Pacific and virtually nothing is known about their behavior, except for their burrowing habits (Smith, 1989a). Blache (1968) described that they live on sandy or silty bottoms and feed on small worms, crustaceans, and molluscs. In contrast to tail-first burrowing taxa, such as Ophichthidae, the heterenchelyids are head-first burrowers, thereby resembling the habit of the Moringuidae (Smith and Castle, 1972; Smith, 1989a).

The aim of this study was to describe the cranial morphology and recognize possible specializations for head-first burrowing behavior in *Pythonichthys macrurus*, a member of the Heterenchelyidae. Hence, a comparison of the cephalic characteristics of this heterenchelyid species with those of another group of head-first burrowing eels, the Moringuidae, is conducted. Also, a comparison of the cranial morphology of head-first burrower eels with that of a nonburrowing, closely related anguilliform family will allow to recognize structural changes that are adaptive for a head-first burrowing lifestyle. Hence, *P. macrurus* will be compared with representatives of three families: the Moringuidae (*Moringua edwardsi*), a head-first burrower; the Anguillidae

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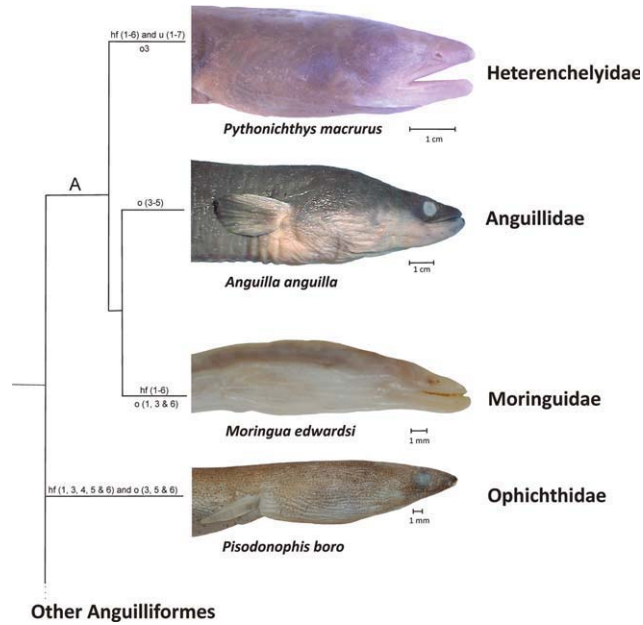


Fig. 1. Cladogram of the taxa examined in this study (modified after Böhlke (1989a). Anguillidae and Moringuidae are monophyletic following Obermiller and Pfeiler (2003). Features related to head-first burrowing: Eye reduction (hf1), Widened cephalic lateral line system that extends into the dermal cavities (hf2), Ventral positioning of gill opening (hf3), Caudoverventral orientation of the anterior section of the adductor mandibulae muscle complex (hf4), Skull with short and sharp snout (hf5), Large insertion sites of body muscles on the neurocranium (hf6); Unique characters of *Pythonichthys macrurus*: Frontal arches (u1), Preopercle with arch-like structures (u2), Tubular and arch-like circumorbital bones (u3), Arch-like supraopercular bone (u4), Two ring-like extrascapular bones (u5) and Caudal positioning of the levator arcus palatini muscle (u6), Merging left and right bundles of the sternohyoideus and protractor hyoidei muscles (u7); Others: Absence of basisphenoid (o1), Separate vomeronasal bone (o2), Premaxillo-ethmovomerine complex (o3), Connection of the palatopterygoid at its two ends (o4), Well-developed pectoral fins (o5), Absence of A1 section of the adductor mandibulae muscle complex (o6). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

(*Anguilla anguilla*), a nonburrowing representative; and the Ophichthidae (*Pisonodonphis boro*), a head- and tail-first burrower.

Böhlke (1989a) considered the Heterenchelyidae, Anguillidae, and Moringuidae to form a monophyletic clade based on morphological data (see Fig. 1). However, Smith (1989a) mentioned that the relationship of the Heterenchelyidae and Moringuidae is a matter of conjecture and resemblances between them are based on plesiomorphic characters or characters related to their fossorial habits. Smith (1989a) also pointed out that it is difficult to find synapomorphies that are not based on reduction or losses of characters in Heterenchelyidae and Moringuidae. Because earlier studies have based the relationship of Heterenchelyidae and Moringuidae on the analysis of external morphology and osteological data, we hope to add val-

uable data to the cladistic analysis by studying their cranial myology. It seems that these head-first burrowers have undergone a strong selection for protecting the head during burrowing. By analyzing character state transformations of the myological components involved, the evolution of these adaptations for head-first burrowing may become evident in an explicit phylogenetic context. In particular, the study of Belouze (2001) did not support the monophyly of Heterenchelyidae and Moringuidae. Also, the phylogenetic tree based on mitochondrial ribosomal DNA sequences did not support the monophyly of the Anguillidae and Moringuidae (Obermiller and Pfeiler, 2003). Although Anguillidae and Moringuidae are more closely related to each other than to heterenchelyids, we predict that the heterenchelyid, *P. macrurus* will exhibit more morphological features in common with *M. edwardsi*, but with different pattern being related to synapomorphies of the Moringuidae and Anguillidae. Also, the presence of the convergent features observed in strictly head-first burrowers is predicted in the non-strictly head-first burrower, *P. boro*, but to a lesser degree.

MATERIALS AND METHODS

Five alcohol-preserved specimens of *Pythonichthys macrurus*, obtained from the Musée National d'Histoire Naturel of Paris (MNHN 1965-0640), were examined. The specimens were the following sizes in Standard Length (SL): PM1: SL = 288.9 mm, PM2: SL = 229.6 mm, PM3: SL = 442.5 mm, PM4: SL = 245 mm, and PM5: SL = 189.3 mm). Five commercially obtained specimens of *Anguilla anguilla* (AA1: SL = 503 mm, AA2: SL = 484 mm, AA3: SL = 548 mm, AA4: SL = 518 mm, and AA5: SL = 491 mm) were examined. Two specimens (PM2 and PM4) of *P. macrurus* were cleared and stained with alizarin red S and alcian blue according to the protocol of Hanken and Wassersug (1981). Muscle fibers of the dissected specimens were stained according to Bock and Shear (1972). The specimens were studied using a stereoscopic microscope (Olympus SZX-7), equipped with a camera lucida. To examine the histological nature of two orobranchial tongue-like appendages of *P. macrurus*, a series of histological sections (5 μ m) was cut, stained with an improved trichrome staining protocol and mounted with DPX (based on PM1). Images of the sections were captured using a digital camera (Colorview 8, Soft Imaging System, Munster, Germany).

Muscle terminology follows Winterbottom (1974) and De Schepper et al. (2005). Terminology of cranial skeletal elements follows Böhlke (1989b) and Rojo (1991). The epiotic of teleosts is considered to be an ossification of the occipital arch that has invaded the otic region and so this bone is termed "epioccipital" (Patterson, 1975). The cranial osteology of *Moringua edwardsi*, *Pisonodonphis boro*, and *Anguilla anguilla* has been described in detail by De Schepper et al. (2005), Tilak and Kanji (1969), and Tesch (2003), respectively. The head myology of *M. edwardsi*, *P. boro*, and *A. anguilla* have already been described in detail by De Schepper et al. (2005), De Schepper et al. (2007), and De Schepper (2007), respectively.

RESULTS

Osteology of *Pythonichthys macrurus*

The neurocranium of *Pythonichthys macrurus* forms one solid unit and tapers from the otic

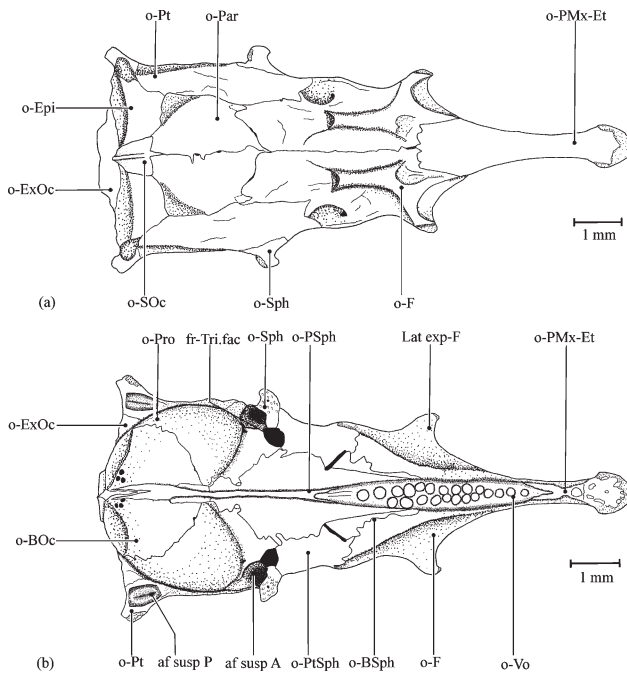


Fig. 2. Neurocranial bones of *Pythonichthys macrurus*. (a) Dorsal view and (b) Ventral view. Abbreviations: af susp A, anterior suspensorial articulation facet; af susp p, posterior suspensorial articulation facet; fr-Tri.fac, foramen trigemino-facialis; Lat exp-F, lateral expansion of frontal bone; o-BOc, basioccipital bone; o-BSph, basisphenoid; o-Epi, epioccipital bone; o-ExOc, exoccipital bone; o-F, frontal bone; o-Par, parietal bone; o-PMx-Et, premaxillo-ethmoid complex; o-Pro, prootic bone; o-PSph, parasphenoid; o-Pt, pterotic bone; o-PtSph, pterosphenoid; o-SOc, supraoccipital bone; o-Sph, sphenotic bone; o-Vo, vomeral bone.

region toward the tip of the snout (see Fig. 2). The ethmoid region is comprised of the premaxillo-ethmoid complex, vomeral bone and nasal bones. The latter are described with respect to the lateral line system (see below). The vomeral bone forms the anterior base of the skull and is situated ventral to the parasphenoid (Figs. 2b and 3a). The vomerine teeth are arranged in one to two rows with teeth of various lengths. The olfactory fossa is relatively small and lies between the pars ethmoid of the premaxillo-ethmoid complex and the anterior border of the lateral expansion of the frontal bone (Fig. 3a). A pore is present on the olfactory fossa (Fig. 3a).

Anteriorly, a small median ridge is present where the two frontal bones meet. Each frontal bone bears two arches on its dorsal surface, which support the posterior part of the supraorbital canal and the frontal commissure (Figs. 3a and 4a). These two frontal arches are in a perpendicular position to each other, with the lateral expansions of the frontal bones forming the base of these arches (Fig. 2a). The small eye of *P. macrurus* is situated under the lateral expansion of the frontal bone. Anteriorly, the frontal bones border the pre-

maxillo-ethmoid complex. The entire frontal arches and the arch-like infraorbital bones are covered with thick connective tissue. The basisphenoid forms the posterior border of a small orbit and is situated dorsal to the parasphenoid. It bears two dorsal wings that are surrounded by the frontal bones, pterosphenoids, and parasphenoids (Fig. 2b). The foramen opticum is present between the two wings of the basisphenoid that bears a tube-like structure on its anteroventral portion. The parasphenoid runs from the orbits posteriorly, with its middle ridge continuing below the prootic and basioccipital bones (Fig. 2b). The parasphenoid is bifurcated at its posterior end with a basioccipital process wedged in-between (Fig. 2b). Together with the prootic bone, the pterosphenoid borders the foramen for the trigemino-facial nerve complex (Fig. 2b). The lacrimal and infraorbital bones are described with respect to the cranial lateral line system (see below).

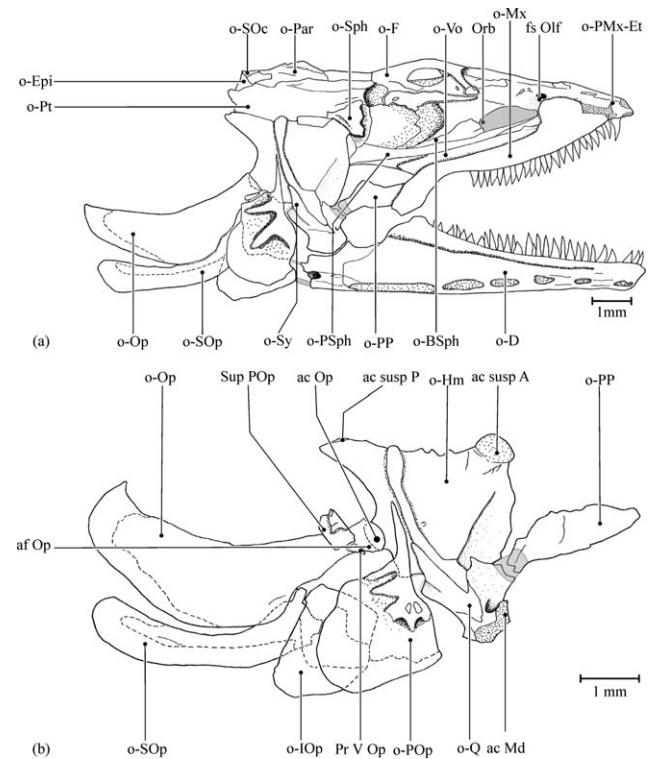


Fig. 3. Cranial skeleton in *Pythonichthys macrurus* (lateral view). (a) complete skull (right side) and (b) suspensorium (right side). Abbreviations: ac Op, opercular articular condyle; af Op, opercular articular facet; ac susp A, anterior suspensorial condyle; ac susp P, posterior suspensorial condyle; fs Olf, olfactory fossa; o-BSph, basisphenoid bone; o-D, dentary olflex; o-Epi, epioccipital bone; o-F, frontal bone; o-Hm, hyomandibular bone; o-Iop, interopercle; o-Mx, maxillary bone; o-Op, opercle; o-Par, parietal bone; o-PMx-Et, premaxillo-ethmoid complex; o-POp, preopercle; o-PP, palatopterygoid; o-PSph, parasphenoid; o-Pt, pterotic bone; o-PtSph, pterosphenoid bone; o-SOc, supraoccipital bone; o-Q, quadrate; o-SOp, subopercle; o-Sph, sphenotic bone; o-Sup Pop, suprapreopercular bone; o-Sy, symplectic bone; o-Vo, vomeral bone; Orb, orbit.

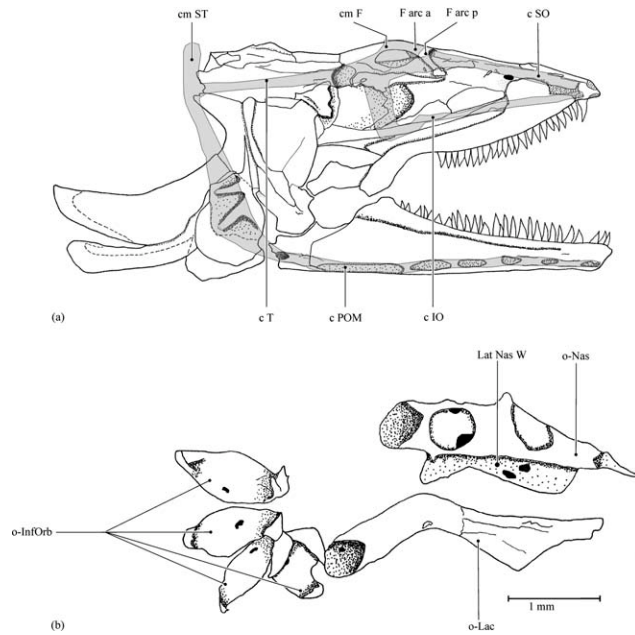


Fig. 4. The cranial lateral line system of *Pythonichthys macrurus*. (a) Lateral view of the composing canals (right side). (b) Dorsal view of the left nasal bone, lacrimal bone and infraorbital bones. Abbreviations: c IO, infraorbital canal; c POM, preopercular mandibular canal; c SO, supraorbital canal; c T, temporal canal; cm F, Frontal commissure; cm ST, supratemporal commissure; F arc a, anterior frontal arch; F arc p, posterior frontal arch; La Nas W, lateral nasal wings; o-Nas, nasal bone; o-InfoOrb, infraorbital bone; o-Lac, lacrimal bone.

The otic region comprises the sphenotic, pterotic, prootic, epioccipital, and parietal bones. The sphenotic bone bears a rostroventrally directed process and forms the anterior wall of the anterior articular facet of the hyomandibula (Fig. 2b). The process bears a small pore on its ventral face, whereas the rest of the ventral surface is pitted. The pterotic bone overlaps with the frontal, parietal, and prootic bones. The pterotic bone anteriorly bears a tubular structure in which the temporal canal enters and which opens at its posterior end. The posterior facet of the hyomandibula and the posterior portion of the anterior articular facet are enclosed by the pterotic bone. The prootic bones form the anterior portion of the large otic bullae, which are also enclosed by the exoccipital bones and basioccipital bone. The epioccipital bones form the medial margin of the posterior opening of the pterotic tubular structure. The parietal bones show a serrated suture at the midline (Fig. 2a). They bear an anterolateral processes that overlaps with the frontal bones.

The occipital region comprises the exoccipital bones, basioccipital bone, and supraoccipital bone. The supraoccipital bone is surrounded by the epioccipital and parietal bones and bears a small crest at the midline (Fig. 2a). The exoccipital bones are domed and bear pitted borders with the fora-

men magnum. Two ring-like extrascapular bones are present posterior to the occipital region. They are covered with a thick layer of the connective tissue and also support the supratemporal commissure.

The maxillary bone is ankylosed anteromedially to the neurocranium. Anteriorly, it bears a dorsal ascending process that medially possesses a maxillary condyle (Fig. 3a). The posterior end of the maxillary bone is connected to the dorsolateral face of the lower jaw via the primordial ligament. The conical maxillary teeth lie in two rows (Fig. 5a,b). The anterior tip of the lower jaw is positioned slightly anterior to the upper jaw and its teeth run up to the coronoid process (Fig. 5c). The coronomeckelian is a small element on the anteroventral side of the Meckelian fossa, enclosed by the dentary bone (Fig. 5c). The dentary bone forms the coronoid process that is connected to the angular bony complex. The mandibular teeth are arranged in two rows with a medial row and a longer lateral row (Fig. 5c). The angular bony complex consists of the fused retroarticular, angular, and articular bones. The mandibular articulation facet is dorsal to the angular bony complex (Fig. 5c). The retroarticular process is directed caudally. The preopercle-angular and interopercle-angular ligaments connect the retroarticular to the medial

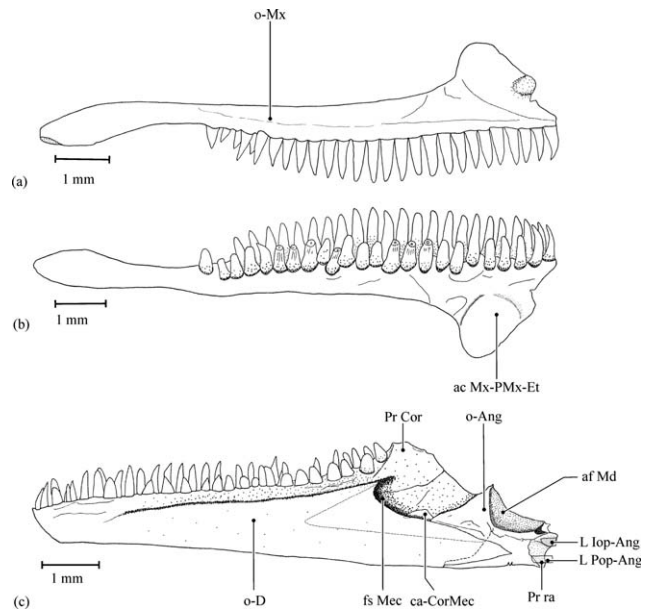


Fig. 5. Jaw of *Pythonichthys macrurus* (right side) (a,b) maxillary bone; lateral view (a), medial view (b) and (c) lower jaw (medial view). Abbreviations: af Md, mandibular articulation facet; ac Mx-Et, maxillo-ethmoidal articulation condyle; ca-CorMec, coronomeckelian cartilage; L Iop-Ang, interoperculo-angular ligament; L Pop-Ang, preoperculo-angular ligament; o-Ang, angular bony complex; o-D, dentary; o-Mx, maxillary bone; fs Mec, Meckelian fossa; Pr Cor, coronoid process; Pr ra, process of retroarticular bone.

faces of the preopercle and interopercle bones, respectively.

The suspensorium consists of four bones, i.e., the hyomandibula, quadrate, palatopterygoid, and preopercle. The preopercle is described as part of the opercular series (see below). The symplectic bone is fused to the posterior portion of the quadrate. The hyomandibula bears a distinct ridge on its lateral surface. The hyomandibula articulates dorsally with the neurocranium via two articular condyles, the anterior one situated on its anterodorsal corner (Fig. 3b). The long, posterior suspensorial articular condyle is formed by a caudally extended posterodorsal process of the hyomandibula (Fig. 3b). The opercular bone articulates with a ventrocaudally directed condyle, at the posterior edge of the hyomandibula. The hyomandibula-quadrate axis is directed vertically, thus positioning the quadrate-mandibular articulation posterior to the orbit. The palatopterygoid is a broad bone and only its posterior end is connected to the quadrate by connective tissue (Fig. 3b). The hyomandibular-palatopterygoid ligament connects the dorsal margin of the palatopterygoid to the hyomandibular ridge.

The opercular series comprises five elements (opercle, preopercle, interopercle, subopercle, and supra-preopercle). The preopercle bears a tubular, arch-like structure with an anterodorsal projection on its anterolateral face (Fig. 3b). This arch-like structure, which is covered by thick connective tissue, encloses a part of the preoperculo-mandibular canal (Figs. 3b and 4a). The posterior portion of the preopercle overlaps and is connected to the anterior half of the interopercle. The preopercle-angular ligament connects the anteromedial rim of the preopercle to the angular bony complex. The interopercle is a relatively large rectangular bone. The interopercle-angular ligament is attached to the anteromedial face of the interopercle and continues posteriorly to the posterior end of the posterior ceratohyal bone. The subopercle is situated ventral to the opercle, to which it is firmly attached. Connective tissue also attaches it to the interopercle. A small ventral process is present on the rostroventral end of the opercle and acts as the attachment point for the dilatator operculi muscle. The supra-preopercular bone, which encloses part of the preoperculo-mandibular canal, lies above the anterior portion of the opercle (Fig. 3b).

The hyoid complex consists of the unpaired median basihyal and urohyal bones and paired anterior and posterior ceratohyal bones (see Fig. 6). This expansion, comprising the urohyal articular facets, lies ventrally against the anterior end of the ceratohyal bones, and the basihyo-ceratohyal ligaments connects the lateroventral faces of the basihyal bone to the ventral face of the anterior ceratohyal bones (Fig. 7a). The urohyal bone is expanded anteriorly and is connected to the ante-

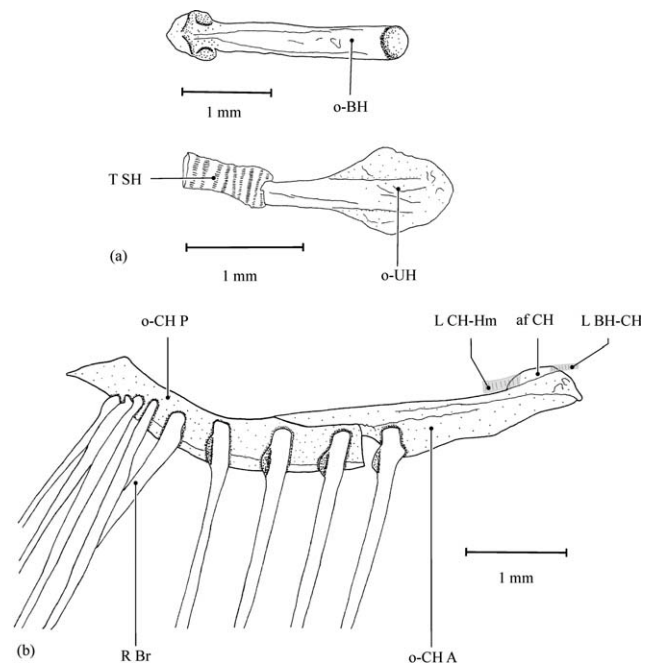


Fig. 6. Hyoid apparatus of *Pythonichthys macrurus*. (a) Dorsal view of the basihyal and urohyal bones; (b) The anterior and posterior ceratohyal bones in a medial view (right side). Abbreviations: af CH, ceratohyal articular facet; L BH-CH, basihyo-ceratohyal ligament; L CH-Hm, ceratohyo-hyomandibular ligament; o-BH, basihyal bone; o-CH A, anterior ceratohyal bone; o-CH P, posterior ceratohyal bone; R Br, branchiostegal rays; o-UH, urohyal bone.

rior end of the anterior ceratohyal bones via small urohyo-ceratohyal ligaments (Fig. 7a). The basihyal bone is a cylindrical bone, which is expanded posteriorly (Fig. 6a). No separate urohyal bone could be distinguished. The anterior ceratohyal bone is connected to the suspensorium by means of the ceratohyo-hyomandibular ligament (Fig. 7a). A total of nine branchiostegal rays are supported by the anterior and posterior ceratohyal bone (Fig. 6b). All of them articulate with the posterior ceratohyal bone, with the exception of one. The branchiostegal rays curve dorsally along the ventral border of the interopercle and reach up to the caudal border of the opercle.

The cranial lateral line system comprises the supraorbital, infraorbital, temporal and preoperculo-mandibular canals, and the frontal and supra-temporal commissures. The ethmoid and adnasal canals are absent. The cranial lateral line canals are widened due to the arched bony elements that enclose them. The nasal bone lies on the anterodorsal face of the olfactory organ and supports the anterior portion of the supraorbital canal. The main body of the nasal bone is tube-like, bearing a ventrolaterally positioned wing (Fig. 4b). The frontal-nasal ligament connects the nasal bone to the anteroventral corner of the lateral expansion of the frontal bone (Fig. 7b). The posterior part of the

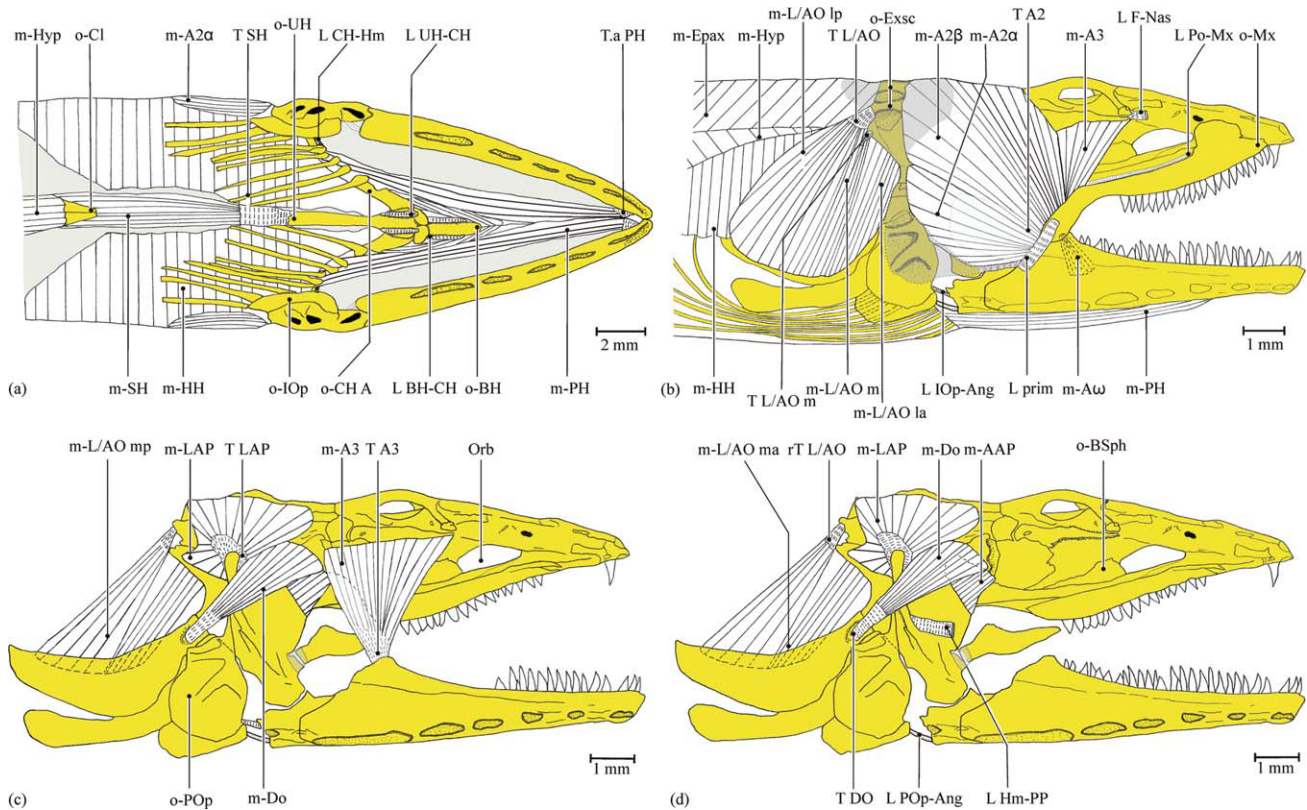


Fig. 7. The cranial muscles of *Pythonichthys macrurus*. (a) Ventral view of the cranial muscles (skin is removed); (b) skin is removed (lateral view); (c) maxillary bone, primordial ligament and sections of A2 are removed (lateral view); (d) section A3 are removed (lateral view). Abbreviations: L CH-Hm, ceratohyo-hyomandibular ligament; L F-Nas, frontal-nasal ligament; L Hm-PP, hyomandibula-palatopterygoid ligament; L Iop-Ang, interoperculo-angular ligament; L Po-Mx, preorbital-maxillary ligament; L prim, primordial ligament; L Pop-Ang, preoperculo-angular ligament; L UH-CH, urohyo-ceratohyal ligaments; m-A2 β , dorsal subsection of A2; m-A2 α , A2 section of the adductor mandibulae muscle complex; m-A3, A3 section of the adductor mandibulae muscle complex; m-AAP, adductor arcus palatini muscle; m-A ω , A ω section of adductor mandibulae muscle complex; m-DO, dilatator operculi muscle; m-Epax, epaxial muscles; m-HH, hyohyoideus muscle; m-Hyp, hypaxial muscles; m-LAP, levator arcus palatini muscle; m-L/AO la, lateroanterior bundle of levator/adductor operculi muscle; m-L/AO m, mesial bundle of levator/adductor operculi muscle; m-L/AO mp, medioposterior bundle of levator/adductor arcus palatini muscle; m-L/AO ma, medioanterior bundle of levator/adductor operculi muscle; m-PH, protractor hyoidei muscle; m-SH, sternohyoideus muscle; o-BH, basihyal bone; o-BSph, basisphenoid; o-CH A, anterior ceratohyal bone; o-Cl, cleithrum; o-ExOc, exoccipital bone; o-IOP, interopercle; o-Mx, maxillary bone; o-PMx-Et, premaxillo-ethmoid complex; o-POP, preopercle; o-UH, urohyal bone; Orb, orbit; r-T L/AO, rest of levator/adductor operculi muscle tendon; T A2, tendon of A2; T A3, tendon of A3; T DO, tendon of dilatator operculi muscle; T LAP, tendon of levator arcus palatini; T L/AO, tendon of levator/adductor operculi; T L/AO m, tendon of mesial bundle of levator/adductor operculi muscle; T.a PH, anterior tendon of protractor hyoidei; T SH, tendon of sternohyoideus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

supraorbital canal is supported by the anterior frontal arch, which is expanded laterally (Fig. 4a). The frontal commissure is enclosed by the posterior frontal arches (Fig. 4a). Four infraorbital bones seem merely to be lying in an arched position (Fig. 4b). The lacrimal and four infraorbital bones support the infraorbital canal. The anterior part of the infraorbital canal is enclosed by the lacrimal bone. The tubular lacrimal bone bears an anteriorly flattened part superimposing the maxillary dorsal process. Dorsally, this flattened part of the lacrimal bone bears a more narrow tubular structure (Fig. 4b). The primordial ligament continues anteriorly and connects to the posterior part of the lacrimal bone. The supra- and infraor-

bitar canal anastomose in the front of the pterotic opening and continue into the temporal canal. The preoperculo-mandibular canal begins in the ventroanterior tip of the dentary bone. It runs inside the mandibula, which bears six pores (Fig. 4b). The preoperculo-mandibular canal is curved caudodorsally after exiting the mandibula and is enclosed by the arch-like structure of the preopercle (Fig. 4b). A supra-preopercular bone encloses the posterior portion of the preoperculo-mandibular canal before anastomosing with the temporal canal. The supratemporal commissure is enclosed by two ring-like extrascapular bones (Fig. 7b). Despite existing pores on some bony elements that enclose the lateral line system, such as those of

the lower jaw, the cephalic lateral line system bears few tiny pores on the preoperculo-mandibular canal. These are visible under high magnification, implying reduced head pores.

Myology of *Pythonichthys macrurus*

Muscles of the cheek. The adductor mandibulae complex, the most conspicuous muscle of the cheek, is subdivided into the sections A2, A3, and A ω . The section A2 is subdivided into two subsections: A2 α and A2 β . The A2 α is the ventral element of the adductor mandibulae muscle complex and has a fleshy origin at the lateral face of the hyomandibula, quadrate, and the anterior rim of the preopercle; it has an additional origin as a tendon from the posterolateral face of the hyomandibula. This tendon is also connected to the thick connective tissue, which covers the arch-like structure of the preopercle. The A2 α inserts as a tendon on the medial face of the coronoid process and as a muscle on the posteromedial face of the angular bony complex. The lateral face of the A2-tendon connects to the posterior edge of the primordial ligament and inserts on the posteromedial face of the mandibula (Fig. 7b). The subsection A2 β is the largest and most posterodorsal element of the adductor mandibulae muscle complex. It has a muscular origin on the frontal, parietal, and supraoccipital bones and inserts as a muscle and with tendons on the dorsomedial face of the Meckelian fossa. A posterior portion of the subsection A2 β that is situated lateral to the levator arcus palatini muscle, bulges posteriorly. The A3-section of the adductor mandibulae muscle complex has a fleshy origin from the ventral face of the lateral expansion of the frontal bone, the anterolateral face of the sphenotic process and the pterosphenoid bone, and inserts as a tendon onto the Meckelian fossa. The posterior fibers of the section A3 are directed ventrally whereas its anterior fibers are directed more caudoventrally (Fig. 7c). The section A ω arises as a tendon from the anteroventral fibers of the subsection A2 β . It inserts into the Meckelian fossa along with the ventral fibers of the subsection A2 β .

The levator arcus palatini muscle originates as a tendon from the dorsal portion of the hyomandibular ridge. Its fibers are spread radially and insert on the parietal bone, the supraoccipital bone, the posterior region of the pterotic bone, and the posterodorsal process of the hyomandibular bone (Fig. 7c).

The adductor arcus palatini is a rectangular muscle with its fibers originating from the posteroventral side of the pterosphenoid and the ventrolateral face of the sphenotic bone. It inserts with fibers on both the lateral and medial face of the anterodorsal part of the hyomandibular bone. There is no insertion on the palatopterygoid. Its dorsal fibers are covered by the anterior portion of the dilatator operculi muscle (Fig. 7d).

The adductor hyomandibulae muscle connects with fibers to the basioccipital, prootic, and parasphenoid bones and runs to the dorsomedial face of the hyomandibular bone. Its anterior margin is situated at the level of the anterior margin of the hyomandibular bone.

The undifferentiated levator operculi and adductor operculi muscles, which can be considered as a single levator/adductor opercula muscle, direct caudoventrally (Fig. 7b). Based on different origins of muscle parts, the levator/adductor operculi muscle can be divided into an anterior, mesial, and posterior bundle. The anterior bundle has a fleshy origin from the ventral edge of the posterodorsal process of the hyomandibular bone. Its lateral fibers insert on the dorsolateral face of the opercle, whereas the medial fibers insert on the dorsomedial face of the opercle. The mesial bundle originates as a tendon from the posterior end of the posterodorsal process of the hyomandibular bone and inserts with fibers on the dorsolateral face of the opercle (Fig. 7b). The posterior bundle originates as a tendon from the posterior process of the pterotic bone and its lateral and medial fibers insert on the dorsolateral and dorsomedial faces of the opercle, respectively (Fig. 7d).

The dilatator operculi is triangular in shape (Fig. 7d). It originates with muscle fibers from the posterolateral face of the sphenotic bone and ventrolateral face of the pterotic bone. It inserts as a tendon on the rostroventral process of the opercle.

Ventral muscles of the head. Left and right halves of the protractor hyoidei muscle merge at the midline of their length, but remain separated at their ends. Each halves of this muscle originate as a tendon from the medial face of the dentary bone, just at the rear of the dental symphysis. They insert with muscle fibers on the ventral faces of the anterior and posterior ceratohyal bones (Fig. 7a).

Left and right bundles of the sternohyoideus muscle merge in the midline after originating with fibers from the entire anterior and the anterolateral margin of left and right cleithra. They insert on the posterior end of the urohyal bone via the sternohyoideus tendon (Fig. 7a).

The hyohyoideus muscle complex in teleosts generally includes three components (the hyohyoideus inferioris, hyohyoideus abductor, and hyohyoidei adductores). However, in *P. macrurus* they are undifferentiated, merging anteriorly as a thin sac-like muscle sheet meeting their counterparts at the ventral midline. Posteriorly, both muscle halves remain separate at the end of the orobranchial cavity. This sac-like muscle interconnects the medial faces of the branchiostegal rays, opercle, and subopercle and reaches dorsally up to the horizontal septum between the epaxial and hypaxial muscles.

Body muscles. The epaxial muscles insert directly on the epioccipital bones, dorsal rim of the exoccipital bone, and as an aponeurosis on the

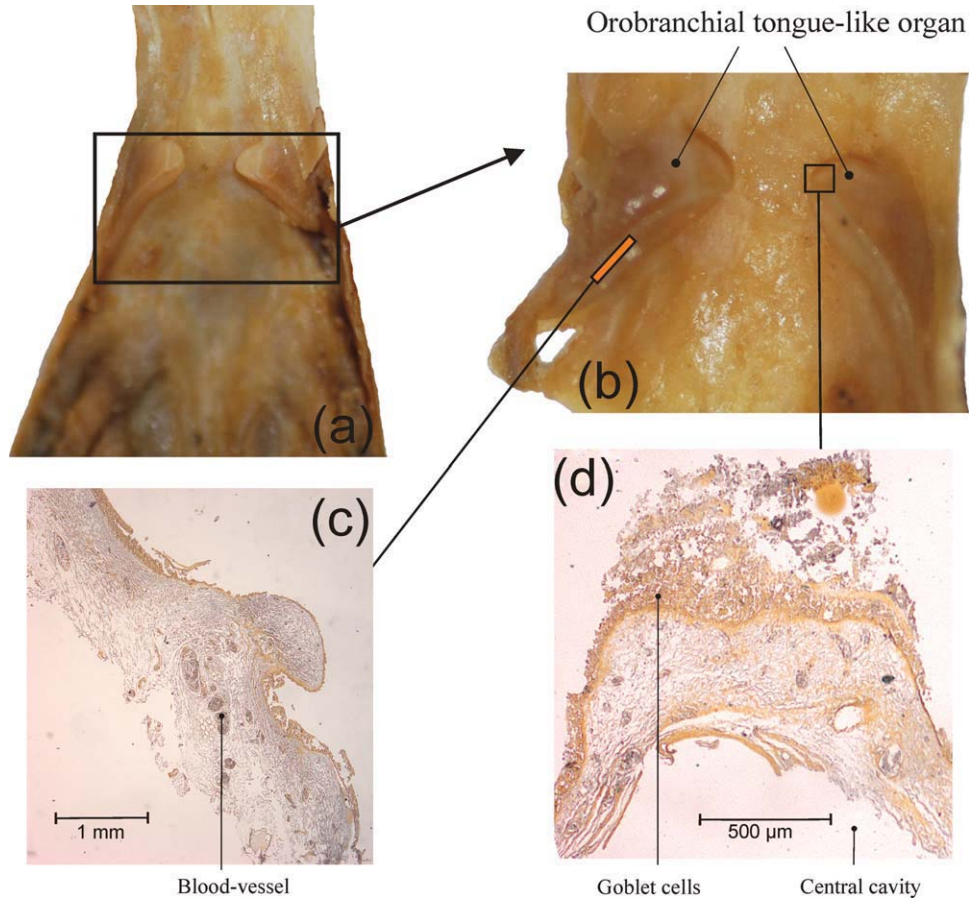


Fig. 8. The orobranchial organ of *Pythonichthys macrurus*. (a) Two tongue-like appendages of the orobranchial organ on the roof of the mouth; (b) Closer view of the two tongue-like appendages of the orobranchial organ; (c,d) sagittal section of the orobranchial organ (c) base region; (d) apex region. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

supraoccipital bone. The dorsal fibers of the epaxial muscles connect to the fascia of the adductor mandibulae muscle complex and thick connective tissue, which covers the ring-like extrascapular bones. The hypaxial muscles insert as an aponeurosis on the ventrocaudal border of the basioccipital and exoccipital bones.

Two tongue-like appendages are present in the roof of the orobranchial mucosa (see Fig. 8). Each appendage contains of a cavity with few, short muscle fibers inserting on its internal base. This may resemble a morphology similar to that of the palatal organ of cypriniform fishes, and hence a similar function in assisting the transport of food could be speculated (Sibbing et al., 1986, Hernandez et al., 2007). However, further research is required to elucidate the true nature of this organ.

DISCUSSION

Cranial Specializations Related to Head-First Burrowing

Burrowing behavior is considered useful to use the substratum for protection, crypsis, and feeding

purposes (Subramanian, 1984; Bozzano, 2003), and is observed to occur in various degrees in anguilliform fishes. *Pythonichthys macrurus* appears to remain buried in the substratum except, perhaps, for brief excursions in search of food (Smith, 1989a). *Moringua edwardsi* spends all its time burrowed in the sand when it is immature (Gordon, 1954; Gosline, 1965), whereas adults of this species limit their fossorial behavior to when they leave their burrows during the night (Smith, 1989b). *Pisodonophis boro* penetrates the substrate tail-first but it is able to burrow head-first as well (Tilak and Kanji, 1969; Subramanian, 1984; Atkinson and Taylor, 1991). It is known to burrow for shelter and to find food (Subramanian, 1984). *Anguilla anguilla* is a nonburrowing species (Tesch, 2003).

Eye reduction. *Pythonichthys macrurus* shares several cranial features with two non-heterenchelyid burrowing anguilliforms. One of these characters is eye reduction. Eye reduction in ophichthids and moringuids are considered to be adaptations to head-first burrowing (De Schepper et al., 2005, 2007). Eye reduction is observed in many other

fossorial elongated fishes such as Clariidae (Devaere et al., 2001, 2004), Mastacembelidae (Poll, 1973), and Anguilliformes (De Schepper et al., 2004, 2005, 2007; Aoyama et al., 2005). The reduced eye of the Ophichthidae and Moringuidae has been reported to be adaptations for head-first burrowing (McCosker et al., 1989; Smith 1989b,c; De Schepper et al., 2005, 2007). The smaller eye size, particularly in relation to the macrophthalmic ancestral state of Anguilliformes (Böhlk, 1989a), can have a substantial effect on the spatial design of head (Boel, 1985). Eye reduction allows a caudoventral orientation of the anteromedial section of the adductor mandibulae muscle complex in *P. boro* and *M. edwardsi* (De Schepper et al., 2005, 2007), and the reduction of the circumorbital bones to small tubular bones in *M. edwardsi*, clariids and ophichthids (Tilak and Kanji, 1969; McCosker et al., 1989; Bozzano, 2003; Devaere et al., 2004; De Schepper et al., 2007). Eye reduction also has been linked to the hypertrophy of the jaw muscle in anguilliform clariids (Devaere et al., 2001). Hence, the reduction of the eye in *P. macrurus* may be linked to the caudoventral orientation of the anteromedial section of the adductor mandibulae muscles complex (the section A3) and tubular circumorbital bones. Furthermore, the opaque skin of the eye in *P. macrurus* may also be adaptive to burrowing. This feature has been reported in *Ophichthus rufus* (Ophichthidae) as an adaptation to protect from mechanical injury when this eel routinely enters and leaves a burrow (Bozzano, 2003).

Widened cephalic lateral line canals.

Because of the associated reduced vision, other sensory systems (such as olfactory, somatosensory, lateral line, and auditory systems) may become more important to provide environmental information (Gordon, 1954; Montgomery, 1989). Chemical sensory cues may predominate in burrowing organisms that their vision is considered poorly developed (Pankurst and Lythgoe, 1983). Klages et al. (2002) has pointed out that finding prey for organisms that usually wait for food by resting on the sea floor or inside burrows is based on the detection of the noise (the residual low-level sound) produced by elastic waves at the water-sea floor interface. Unlike *M. edwardsi*, which has its cephalic lateral line canals widened into dermal cavities, *P. macrurus* has widened canals enclosed in the arched bony elements of the skull under the skin. This widened cephalic lateral line canals may function as a kind of sensory pads, which are stimulated mechanically during burrowing when in contact with prey (De Schepper et al., 2005). Most of the widened canals of the cephalic lateral line system of *P. macrurus* lack external pores, except for the tiny pores of the preoperculo-mandibular canal. *Moringua edwardsi* lacks any external pores of the cephalic lateral line system,

whereas tail-first burrower, *P. boro*, retains pores in all the canals of the cephalic lateral line system. The lack of head pores has the advantage of avoiding the entering of sediment into the canals during head-first burrowing (De Schepper et al., 2005).

Gill opening. From hyomandibula-opercle articulation, the opercle is orientated posteroventrally in *P. macrurus*, *M. edwardsi*, and *P. boro* whereas that one of *A. anguilla* is directed caudally. As a result of this configuration, the gill opening is positioned more ventrally in the burrowing species. This may prevent entering of sediment into gill cavity (Gosline, 1971; Smith, 1989c).

Different orientation of the anterior section of the adductor mandibulae muscle complex. The hyomandibulo-quadrate axis of *P. macrurus*, *M. edwardsi*, and *P. boro* is directed dorsoventrally, in contrast to the forwardly inclined one in *A. anguilla*. As a result, the quadrate-mandibular articulation is positioned posterior to the orbit. In addition to the small size of eye, the posterior position of the quadrate-mandibular joint in these species also creates space allowing a caudoventral orientation of the anterior section of the adductor mandibulae muscle complex. The anterior fibers of the section A3 in *P. macrurus* are directed caudoventrally, whereas its posterior fibers are directed vertically. An opposite orientation of the different section of the adductor mandibulae muscle complex (caudoventrally versus rostroventrally) can thereby help in preventing the dislocation of the mandibular joint, even when large forces are exerted that induce torque forces (De Schepper et al., 2007). This stabilization of the mandibular joint may especially prevent the dislocation of the lower jaw during initial head-first penetration considered as first stage of burrow construction (James et al., 1995).

Despite of a short and sharp snout, which is considered to be an adaptation to head-first burrowing (McCosker et al., 1989; Smith, 1989b,c), the posterior position of the quadrate-mandibular joint also results in a large mouth gap and a longer lower jaw. A large gape and longer lower jaw combined with large teeth on the upper and lower jaws in *P. macrurus* suggest a potential for rapid mouth closing and dealing with large prey items. Many benthic, lie-in-wait or cryptic predators have particularly large mouths that can be opened and closed rapidly to grasp prey (Helfman et al., 1997; Mehta and Wainwright, 2007; Mehta, 2009; Eagderi and Adriaens, 2010).

Skull shape and large insertion sites of body muscles on the neurocranium. The modification of the skull into a solid conical structure with sharp snout, as seen in *P. macrurus* and two other fossorial species, *M. edwardsi* and *P. boro*, may facilitate burrowing, where power is provided

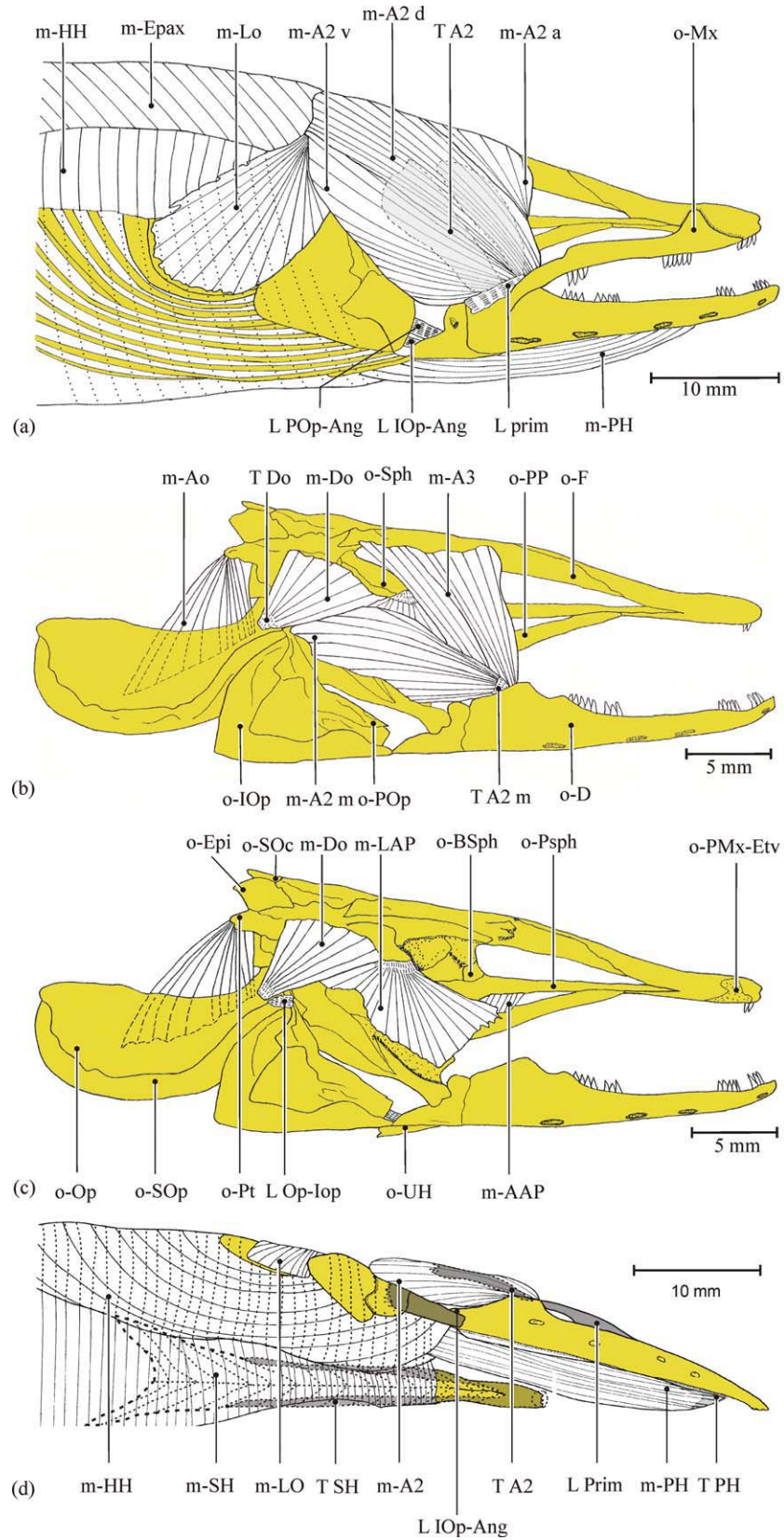


Figure 9

by the cylindrical body (Castle, 1968; Smith, 1989b). Smith (1989b) mentions rapid movements of the body, just beneath the surface, for subterranean hunting and feeding in burrowing Anguilliformes. The large insertion sites of the epaxial and hypaxial muscles on the neurocranium (comprising exoccipital, epioccipital, basioccipital, and supraoccipital bones), which are also connected to the adductor mandibulae muscle complex, in *P. macrurus* can be considered an advantage for transferring forces from the body onto the head. The physical coupling between the jaw muscles and the epaxial muscles has been observed in *M. edwardsi* and *P. boro* (De Schepper et al., 2005, 2007). Burrowing fishes appear to use two main strategies: mouth excavation or compression and displacement of sediment by body movement (Atkinson and Taylor, 1991). The head morphology of *P. macrurus* suggest that the second strategy is the burrowing method applied.

Variable Degree of Head-First Burrowing Specializations in Anguilliformes

Compared with *Anguilla anguilla*, *Moringua edwardsi*, and *Pisodonophis boro*, *Pythonichthys macrurus* exhibits several unique characters such as presence of the frontal arches, the preopercle with its arch-like structures, the tubular and arch-like circumorbital bones, the arch-like suprapreopercular bone, and two ring-like extrascapular bones, which support portions of the cephalic lateral line canals. These characters are all considered synapomorphies for heterenchelyids (Belouze, 2001).

Only *M. edwardsi* lacks a basisphenoid, and *P. macrurus* was the only anguillid in this study to exhibit a separate vomeral bone. Fusion of premaxillary, ethmoid, and vomeral bones, forming the premaxillo-ethmovomerine complex in *M. edwardsi*, *A. anguilla*, and *P. boro*, is considered synapomorphic for Anguilliformes (Eaton, 1935; Gosline, 1980; Smith, 1989c). The palatopterygoid of *A. anguilla* is connected at both ends to the

quadrate bone and the premaxillo-ethmovomerine complex, respectively, whereas the palatopterygoid of *M. edwardsi*, *P. macrurus*, and *P. boro* attaches only to the suspensorium. The pectoral fins are present in both *A. anguilla* and *P. boro* but are weakly developed in *M. edwardsi*. According to Böhlke (1989a), all heterenchelyids lack pectoral fins, whereas moringuids have weakly developed pectoral fins. Body elongation combined with limblessness allows unhindered movement below the substrate surface (Gans, 1975; Pough et al., 1998).

The adductor mandibulae muscle complex of *P. macrurus* shows similar components but a different configuration with that of the other fossorial species studied, except for the lack of the section A1 in *M. edwardsi* and *P. boro*. In basal actinopterygian fishes, the section A1 is defined by its dorsal position in the adductor mandibulae muscle complex and its insertion on the maxillary bone through a long tendon or on the maxillary bone itself (Eaton, 1935; Winterbottom, 1974). The presence of such a section A1 has been reported in *M. edwardsi* and *P. boro* (De Schepper et al., 2005, 2007). In *A. anguilla* and *P. macrurus*, a small tendinous connection was found between the ventral subsection of the section A2 and the maxillary bone via the primordial ligament. Based on the terminology of Winterbottom (1974) and regarding its main insertion on the lower jaw, this section in *A. anguilla* and *P. macrurus* was considered as a subsection of A2. Hence, the section A2 of the adductor mandibulae muscle complex of *A. anguilla* consists of four subsections (A2a, A2d, A2v, and A2m; Fig. 9a,b,d). The homology of each muscle of the adductor mandibulae complex (variously determined as a subdivision, section, or subsection) is accepted on the basis of sharing an identical insertion pattern onto the jaws, following the traditional nomenclature used for the adductor mandibulae muscles (Vetter, 1878; Winterbottom, 1974; Nakae and Sasaki, 2004). Migrations of the muscle insertions have likely occurred in evolutionary history of the elopomorphs, resulting in the lumping of nonhomologous muscles under a single name. Hence, the insertion of the ventral

Fig. 9. The cranial muscles of *Anguilla anguilla*. (a) Skin is removed (lateral view); (b) Sections A2 except the medial fibers of subsection A2m, hyohyoideus muscle, levator operculi muscle, epaxial muscles, hypaxial muscles, maxillary bone, and primordial ligament are removed (lateral view); (c) Subsection A2m and subsection A3 are removed (lateral view); (d) Ventral view of the right side of the cranial muscles (skin is removed; modified after De Schepper, 2007). Abbreviations: L Iop-Ang, interoperculo-angular ligament; L Op-Iop, preoperculo-interopercular ligament; L prim, primordial ligament; L Pop-Ang, preoperculo-angular ligament; m-A2 a, anterior subsection of A2; m-A2 d, dorsal subsection of A2; m-A2 v, ventral subsection of A2; m-A2 m, medial subsection of A2; A3 section of the adductor mandibulae muscle complex; m-AAP, adductor arcus palatini muscle; m-DO, dilatator operculi muscle; m-Epax, epaxial muscles; m-HH, hyohyoideus muscle; m-LAP, levator arcus palatini muscle; m-AO, adductor operculi muscle; m-LO m, levator operculi muscle; m-PH, protractor hyoidei muscle; m-SH, sternohyoideus muscle; o-BSph, basisphenoid; o-D, dentary complex; o-Epi, epioccipital bone; o-F, frontal bone; o-Iop, interopercle; o-Op, opercle; POp, preopercle; o-PP, palatopterygoid; o-PSph, parasphenoid; o-Pt, pterotic bone; o-Mx, maxillary bone; SOc, supraoccipital bone; o-SOp, subopercle; o-Sph, sphenotic bone; o-UH, urohyal bone; T A2, tendon of A2; T A2 m, tendon of A2 m; T DO, tendon of dilatator operculi muscle; T PH, tendon of protractor hyoidei; T SH, tendon of sternohyoideus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

subsection of the A2 in *A. anguilla* and *P. macrurus* may have migrated from the maxillary bone to the lower jaw as a non-homologous subsection of the A2.

Despite external, osteological and musculature similarities among the fossorial species studied, the configuration of their head musculature exhibits more diversity. The anterior part of the section A2 and entire section A3 is directed caudoventrally in *M. edwardsi*, whereas only the section A3 in *P. boro* and anterior fibers of the section A3 in *P. macrurus* are directed caudoventrally. The levator arcus palatini muscle is positioned caudally in *P. macrurus* compared with the one in the other species studied. Also, the levator arcus palatini muscle connects the posterior elements of the neurocranium, such as the parietal, supraoccipital, and pterotic bones to the posterodorsal face of the hyomandibular bone. In the three others, however, this muscle connects the ventrolateral face of the orbitotemporal elements of the neurocranium, such as the sphenotic and parasphenoid bones, to the lateral face of the suspensorium. Merging left and right bundles of the sternohyoideus and protractor hyoidei muscles in *P. macrurus* is another difference in the head musculature of the species studied.

The cephalic features that are considered specializations for a burrowing mode of life, such as a reduced eye, dorsoventral positioning of the hyomandibula-quadrata axis, caudoventral orientation of the anteromedial section of the adductor mandibulae muscle complex, a widened cephalic lateral line system that extends into the dermal cavities, ventral positioning of the gill opening, and large insertion sites of epaxial and hypaxial muscles on the neurocranium are absent in non-burrowing anguillids (*A. anguilla*). Characteristics that are shared exclusively by *M. edwardsi* and *A. anguilla*, such as the premaxillo-ethmoverine complex, the pectoral fin and separate protractor hyoidei muscle are considered as synapomorphies for the monophyletic group that comprised the Anguillidae and Moringuidae. The presence of features that are associated with head-first burrowing in *P. boro* suggest convergence with the studied fossorial fishes.

Different patterns of head-first burrowing features for the Heterenchelyidae and Moringuidae reveal that there is more than one way to restructure the skull for head-first burrowing. Alternatively, similar morphological characteristics, resulting from similar environmental pressures related to fossorial habit, may also explain the clustering of heterenchelyids and moringuids in the phylogenetic tree presented by Böhlke (1989a). Including data of the head musculature of the three studied fossorial eels, may provide additional information which we can use to resolve the phylogenetic relationship if anguilliform fishes (Diogo, 2004).

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LITERATURE CITED

- Aoyama J, Shinoda A, Sasai S, Miller MJ, Tsukamoto K. 2005. First observations of the burrows of *Anguilla japonica*. *J Fish Biol* 67:1534–1543.
- Atkinson RJ, Taylor AC. 1991. Burrows and burrowing behaviour of fish. In: Meadows PS, Meadows A, editors. *The Environmental Impact of Burrowing Animals and Animal Burrows*. Oxford: Clarendon Press. p 133–155.
- Boel CDN. 1985. *A Matter of Space* [Dissertation]. The Netherlands: Leiden University.
- Belouze A. 2001. *Compréhension Morphologique et Phylogénétique des Taxons Actuels et Fossils Rapports aux ANGUILLIFORMES (Poissons, Téléostéens)* [Dissertation]. Lyon: Paléoenvironnement et Paléobiosphère l'Université Claude Bernard Lyon I. 407 p.
- Blache J. 1968. Contribution a la Connaissance de Poissons Anguilliformes de la Cote Occidentale d'Afrique (Neuvieme Note/les Heterenchelyidae). *Bulletien de l' I.F.N.T.* XXX, ser, A, no 4.
- Bock WJ, Shear RC. 1972. A staining method for gross dissection of vertebrate muscles. *Anat Anz Bd* 130:222–227.
- Böhlke EB, Editor. 1989a. In *Fishes of the Western North Atlantic*. Part 9. New Haven, CT: Sears Foundation for Marine Research. 1055 p.
- Böhlke EB, Editor. 1989b. *Methods and terminology*. In *Fishes of the Western North Atlantic. Anguilliformes and Saccopharyngiformes*. New Haven, CT: Sears Foundation for Marine Research. pp 1–7.
- Bozzano A. 2003. Vision in the rufus snake eel. *Ophichthus rufus*: Adaptive mechanisms for a burrowing life-style. *Mar Biol* 143:167–174.
- Castle PHJ. 1968. A contribution to a revision of the moringuid eels. Special Publication 3. Grahamstown, South Africa: Rhodes University Department of Ichthyology. pp 1–29.
- De Schepper N. 2007. *Evolutionary Morphology of Body Elongation in Teleosts: Aspects of Convergent Evolution* [Dissertation]. Ghent: Evolutionary Morphology of Vertebrates. Ghent University. 305 p.
- De Schepper N, Adriaens D, Teugels GG, Devaere S, Verraes W. 2004. Intraspecific variation in the postcranial skeleton morphology in African clariids: A case study of extreme phenotypic plasticity. *Zool J Linn Soc Lond* 140:437–446.
- De Schepper N, Adriaens D, and B.De Kegel. 2005. *Moringua edwardsi* (Moringuidae: Anguilliformes): Cranial specialization for head-first burrowing? *J Morphol* 226:356–368.
- De Schepper N, De Kegel B, Adriaens D. 2007. *Pisodonophis boro* (Ophichthidae: Anguilliformes): Specialization for head-first and tail-first burrowing? *J Morphol* 268:112–126.
- Devaere S, Adriaens D, Verraes W, Teugels GG. 2001. Cranial morphology of the anguilliform clariid *Channallabes apus* (Günther, 1873) (Teleostei: Siluriformes): Adaptations related to powerful biting? *J Zool* 255:235–250.
- Devaere S, Teugels GG, Adriaens D, Huysentruyt F, Verraes W. 2004. Redescription of *Dolichallabes micropthalmus* (Poll, 1942) (Siluriformes. Clariidae). *Copeia* 1:108–115.
- Diogo R. 2004. Muscles versus bones: Catfishes as a case study for an analysis on the contribution of myological and osteological structures in phylogenetic reconstructions. *Anim Biol* 54:373–391.

- Eagderi S, Adriaens D. (2010). Head morphology of the Duckbill Eel, *Hoplunnis punctata* (Regan, 1915; Nettastomatidae: Anguilliformes): A case of jaw elongation. *Zool*, doi: 10.1016/j.zool.2009.09.004.
- Eaton TH Jr. 1935. Evolution of the upper jaw mechanism in teleost fishes. *J Morphol* 58:157–72.
- Gans C. 1975. Tetrapod limblessness: Evolution and functional corollaries. *Anim Zool* 15:455–467.
- Gordon SM. 1954. The eel genus *Stilbiscus*. *Copeia* 1:11–15.
- Gosline WA. 1965. Teleostean phylogeny. *Copeia* 1:186–194.
- Gosline WA. 1971. Functional morphology and classification of teleostean fishes. Honolulu, HI: University Press of Hawaii. 208 p.
- Gosline WA. 1980. The evolution of some structural systems with reference to the interrelationships of modern lower teleostean fish groups. *Jap J Ichth* 21:1–24.
- Hanken J, Wassersug R. 1981. The visible skeleton. A new double-stain technique reveals the nature of the “hard” tissues. *Funct Photogr* 16:22–26.
- Helfman, GS, Collette BB, Facey DE. 1997. *The Diversity of Fishes*. Malden, MA: Blackwell Science, Inc. 507 p.
- Hernandez LP, Bird NC, Staab KL. 2007. Using zebrafish to investigate cypriniform evolutionary novelties: Functional development and evolutionary diversification of the kinethmoid. *J Exp Zool* 308B:625–641.
- James R, Atkinson A, Roger S, Pullin V. 1995. Observations on the burrows and burrowing behavior of the red band-fish. *Sepola rubescens* L. *Mar Ecol* 17(1–3):23–40.
- Klages M, Muyakshin S, Soltwedel T, Arntz WE. 2002. Mechanoception, a possible mechanism for food fall detection in deep-sea scavengers. *Deep-SEA Res I* 49:143–155.
- McCosker JE, Böhlke EB, Böhlke JE. 1989. Family Ophichthidae. In: Böhlke EB, editor. *Fishes of the Western North Atlantic*. New Haven, CT: Sears Foundation for Marine Research. pp 254–412.
- Mehta RS. 2009. Ecomorphology of the moray bite: Relationship between dietary extremes and morphological diversity. *Physiol Biochem Zool* 82:90–103.
- Mehta RS, Wainwright PC. 2008. Functional morphology of the pharyngeal jaw apparatus in moray eels. *J Morphol* 269:604–619.
- Montgomery JC. 1989. Lateral line detection of planktonic prey. In: Coombs S, Görner P, Münz H, editors. *The Mechanosensory Lateral Line*. New York: Springer-Verlag. Chapter 28.
- Nakae M, Sasaki K. 2004. Homologies of the adductor mandibulae muscles in Tetraodontiformes as indicated by nerve branching patterns. *Ichthyol Res* 51:327–336.
- Nelson JS. 2006. *Fishes of the World*, Forth edition. Hoboken, NJ: Wiley. 601 p.
- Obermiller LE, Pfeiler E. 2003. Phylogenetic relationships of elopomorph fishes inferred from mitochondrial ribosomal DNA sequences. *Mol Phylogenet Evol* 26:202–214.
- Pankurst NW, Lythgoe JN. 1983. Changes in vision and olfaction during sexual maturation in the European eel. *J Fish Biol.* 23:229–240.
- Patterson C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philos Trans R Soc London B Biol Sci* 269:275–579.
- Poll M. 1973. Les yeux des poissons aveugles Africains et de *Caecomastacembelus brichardi* Poll en particulier. *Ann du Spéléologie* 28:221–230.
- Pough HF, Andrews RM, Cadle JE, Crump ML, Savitzky AH, Wells KD. 1998. Body support and locomotion. In: Pough HF, editor. *Herpetology*. New Jersey: Prentice Hall. Chapter 8.
- Royo AL. 1991. *Dictionary of Evolutionary of Fish Osteology*. Florida: CRC Press. 273 p.
- Sibbing FA, Osse JWM, Terlouw A. 1986. Food handling in the carp (*Cyprinus carpio*): its movement patterns, mechanisms and limitations. *J Zool Lond A* 210:161–203.
- Smith DG. 1989a. Family Heterenchelyidae. In: Böhlke EB, editor. *Fishes of the Western North Atlantic. Anguilliformes and Saccopharyngiformes*. New Haven, CT: Sears Foundation for Marine Research. pp 48–54.
- Smith DG. 1989b. Family Moringuidae. In: Böhlke EB, editor. *Fishes of the Western North Atlantic. Anguilliformes and Saccopharyngiformes*. New Haven, CT: Sears Foundation for Marine Research. pp 55–71.
- Smith DG. 1989c. Family Congridae. In: Böhlke EB, editor. *Fishes of the Western North Atlantic. Anguilliformes and Saccopharyngiformes*. New Haven, CT: Sears Foundation for Marine Research. pp 460–567.
- Smith DG, Castle PHJ. 1972. The eel genus *Neoconger* Girard: Systematics, osteology, and life history. *Bull Mar Sci* 22:196–249.
- Subramanian A. 1984. Burrowing behavior and ecology of the crab-eating Indian snake eel *Pisodonophis boro*. *Environ Biol Fish* 10:195–202.
- Tesch F-W. 2003. *The Eel*. Third edition. Oxford: Blackwell Science. 408 p.
- Tilak R, Kanji SK. 1969. Studies on the osteology of *Pisodonophis boro* (Hamilton). *Gegenbaurs Morphol Jahrb* 113:501–523.
- Vetter B. 1878. Untersuchungen zur vergleichende anatomie der kiemen und kiefermuskulatur der fische. II. *Jenaische Zeitschrift für Naturwissenschaft* 12:431–550.
- Winterbottom R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proc Acad Nat Sci Phil* 125:225–317.