Pisodonophis boro (Ophichthidae: Anguilliformes): Specialization for Head-First and Tail-First Burrowing?

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ABSTRACT The rice paddy eel, *Pisodonophis boro (P. boro)*, is of special interest because of its peculiar burrowing habits. *P. boro* penetrates the substrate tail-first, a technique common for ophichthids, but it is able to burrow head-first as well. *P. boro* exhibits three feeding modes: inertial feeding, grasping, and spinning. Rotational feeding is a highly specialized feeding mode, adopted by several elongate, aquatic vertebrates and it is likely that some morphological modifications are related to this feeding mode. The detailed morphology of the head and tail of *P. boro* is examined with the goal to apportion the anatomical specializations among head-first burrowing, tail-first burrowing, and rotational feeding. The reduced eyes, covered with thick corneas may be beneficial for protection during head-first burrowing, but at the same time decreased visual acuity may have an impact on other sensory systems (e.g. cephalic lateral line system). The elongated and pointed shape of the skull is beneficial for substrate penetration. The cranial bones and their joints, which are fortified, are advantageous for resisting high mechanical loads during head-first burrowing. The aponeurotic connection between epaxial and jaw muscles is considered beneficial for transferring these forces from the body to the head during rotational feeding. Hypertrophied jaw muscles facilitate a powerful bite, which is required to hold prey during spinning movements and variability in the fiber angles of subdivisions of jaw muscles may be beneficial for preventing the lower jaw from being dislodged or opened. Furthermore, firm upper (premaxillo–ethmovomerine complex) and lower jaws (with robust coronoid processes) and high neurocranial rigidity are advantageous for a solid grip to hold prey during rotational feeding. The pointed shape of the tail and the consolidated caudal skeleton are beneficial for their tail-first burrowing habits. It is quite likely that the reduction of the caudal musculature is related to the tail-first burrowing behavior because the subtle movements of the caudal fin rays are no longer required. J. Morphol. 268:112–126, 2007. © 2007 Wiley-Liss, Inc.

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Anguilliformes is a large group of elongated, cosmopolitan teleosts (Nelson, 1994). Eels are considered to be well adapted for wedging through small openings, which is their basic mode of life (Gosline, 1971; Smith, 1989b). In this regard, several morphological specializations may benefit the entering of such crevices (elongated body and skull), moving back and forth (scales not overlapping or absent) or preventing sediments from entering into the gill cavities (gill openings small) (Gosline, 1971; Smith, 1989b). However, several clades of Anguilliformes adopted different fossorial life styles: Heterocongrinae and Ophichthidae penetrate the substrate tail-first, whereas Heterenchelyidae and Moringuidae burrow head-first (Castle, 1968; Smith and Castle, 1972; Smith, 1989a).

Pisodonophis boro (P. boro), the species dealt with in this study, belongs to the family Ophichthidae (Tilak and Kanji, 1969). Ophichthids, or snake eels, have a worldwide distribution and inhabit a wide range of different substrates, from coral reefs to sand and mud in rivers and estuaries (McCosker et al., 1989). This diverse group of species (>250) live mainly burrowed in soft sediments (McCosker et al., 1989). *P. boro* penetrates the substrate tail-first, a technique common for ophichthids, but it is able to burrow head-first as well (Tilak and Kanji, 1969; Subramanian, 1984; Atkinson and Taylor, 1991). *P. boro* burrows for shelter and feeding and it exhibits three feeding modes: inertial feeding, grasping, and spinning (Subramanian, 1984).

Understanding possible structural specializations of the systems involved in burrowing in *P. boro*, i.e. the head and the tail, requires a comparison at two levels. First, outgroups must be phylogenetically closely related in order to eliminate possible evolutionary shared traits (thus independent of burrowing) as much as possible. Second, outgroups must use the systems involved especially for burrowing (so adaptations for it can be expected) or not at all for burrowing (so adaptations for it can be expected to be absent). This may allow to extract indications about 1) the presence of specializations that could be adaptations for a specific way of burrowing, and 2) the possible

trade-offs in the allocation of structural adaptations in the head and tail. For that reason, outgroups in this study are *Moringua edwardsi* (*M. edwardsi*) and *Heteroconger longissimus*, both Anguilliformes. *M. edwardsi* is a strict head-first burrower with a well-developed caudal fin (Castle, 1968; Smith and Castle, 1972; Smith, 1989a; De Schepper et al., 2005), whereas *H. longissimus* is a strict tail-first burrower (Rosenblatt, 1967; Castle and Randall, 1999).

M. edwardsi belongs to the Moringuidae, which appear to be phylogenetically related to Anguillidae and Heterenchelidae (Smith, 1989a; Nelson, 1994). According to Smith (1989a), Moringuidae share pronounced morphological specialization for a fossorial life style with Heterenchelidae and Ophichthidae: reduced eyes, lack of color, low vertical fins, elongated, cylindrical body, and reduced head pores. Being a head-first burrower, *M. edwardsi* has shown to possess some extreme adaptive skull modifications (De Schepper et al., 2005). Smith (1989a) also mentions rapid movements of the body, just beneath the surface for subterranean hunting and feeding, thus also relying on the head for substrate penetration.

Heteroconger longissimus is an obligate tail-first burrower belonging to the Heterocongrinae, which shows extreme modifications in its tail morphology (Smith, 1989b). According to Smith (1989b) and Nelson (1994), Heterocongrinae belong, as the Ophichtidae, to the suborder Congroidei. Garden eels, as they are called, live in a colony, where each individual lives in separate, strengthened burrows in sandy or silty-sand substrate, which are used for long periods (Casimir and Fricke, 1971; Smith, 1989b). They project the front portion of the body from the burrow, their heads turned to the plankton loaded currents to snap and pick small zooplanktonic particles (Bath, 1960; Fricke, 1969; Smith, 1989b; Vigliola et al., 1996; Castle and Randall, 1999).

MATERIALS AND METHODS

Eight specimens of *Pisodonophis boro* (*P. boro*) (Hamilton, 1822) were used, measuring between 8.4 cm and 30.6 cm. These specimens were obtained commercially (Poisson d'Or, Moeskroen, Belgium) and preserved in ethanol (70%). Four ethanol preserved specimens of *Heteroconger longissimus* were used from the United States National Museum of Natural History (USNM 316037). Their total length ranged from 22.5 cm to 26.8 cm. Standard lengths were measured with a ruler to the nearest 0.1 cm. Standard length was used instead of total length because of potential damage to the fin rays of caudal fins during collection and preservation or because of potential reductions of the caudal fin.

To study the osteology, the clearing and staining protocol of Hanken and Wasserzug (1981) was used. Examination of cleared and stained specimens was done using a stereoscopic microscope (Olympus SZX-9), equipped with a camera lucida and a Colorview 8 digital camera. For osteological descriptions of *P. boro,* we refer to Tilak and Kanji (1969). Terminology of musculature follows Winterbottom (1974).

Detailed morphology was studied using serial histological cross sections. Specimens were fixed with a formaldehyde solution (8%), decalcified with Decalc 25% (Histolab), dehydrated through an alcohol series, and embedded in a Technovit 7100 (Kulzer-Heraus). Series of thin sections (2 µm) were cut using a Leica Polycut SM 2500, stained with toluidine blue, and mounted with DPX. Images of the sections were obtained using a digital camera (Colorview 8, Soft Imaging System) mounted on a light microscope (Polyvar – Reichert) and processed with analysis Docu software (Soft Imaging System GmbH, version 3.0). Based on the serial histological sections, graphical 3D reconstructions were generated using Corel-Draw 8 (Corel) for tracing contours of the structures and Amira (TGS) and Rhinoceros 3.0 (McNeel) for making reconstructions.

RESULTS
Cranial Osteology

The osteology of *P. boro* has already been described in detail by Tilak and Kanji (1969). Figure 1 shows a 3D reconstruction of the cranial skeleton and its constituent elements. The skull is elongate, tapering form the otic region to the tip of the snout. The cranial bones are heavily ossified and strongly connected to each other, with the exception of the mobile maxillae. The frontals are fused and form one massive element. A robust and compact premaxillo–ethmovomerine complex is present. The orbits are small and separated dorsally by a wide interorbital distance. Neighboring bones form joints with oblique edges (scarf joints, according to the terminology of Hildebrand, 1995) and are interconnected by dense connective tissue (Fig. 2A,C). The bones forming the skull roof (premaxillo–ethmovomerine complex, frontals, parietals, supraoccipital, epiotics, and exoccipitals) show a high amount of overlap, formed by the extension of the oblique edges of the scarf joints (Fig. 2B). The suspensorium comprises the quadrate, hyomandibula, and palatopterygoid (separated bones not shown in Fig. 1), which are strongly interconnected by ligaments. The hyomandibula bears an anterior suspensorial articulation condyle for the articulation with the sphenotic and a posterior one for the articulation with the pterotic. Dorsocaudally, the hyomandibula bears the opercular articular condyle for the articulation with the articulatar facet of the opercle.

Cranial lateral line system. The cephalic lateral line system comprises the supra- and infra-orbital canals, ethmoidal canals, temporal canals, mandibular canals, preopercular canals, and frontal and supratemporal commissures (Fig. 3). The ethmoidal canals are ventral branches of the supraorbital canals, surrounded by the premaxillo–ethmovomerine complex. Anteriorly, each ethmoidal canal opens in an anteroventral, external pore. The supraorbital canal includes four external pores (exclusive of the ethmoid and frontal commissural pores) and is enclosed anteriorly by the main part of the wing-like nasal bone (Fig. 4A). A branch exiting the nasal runs ventrally and has no
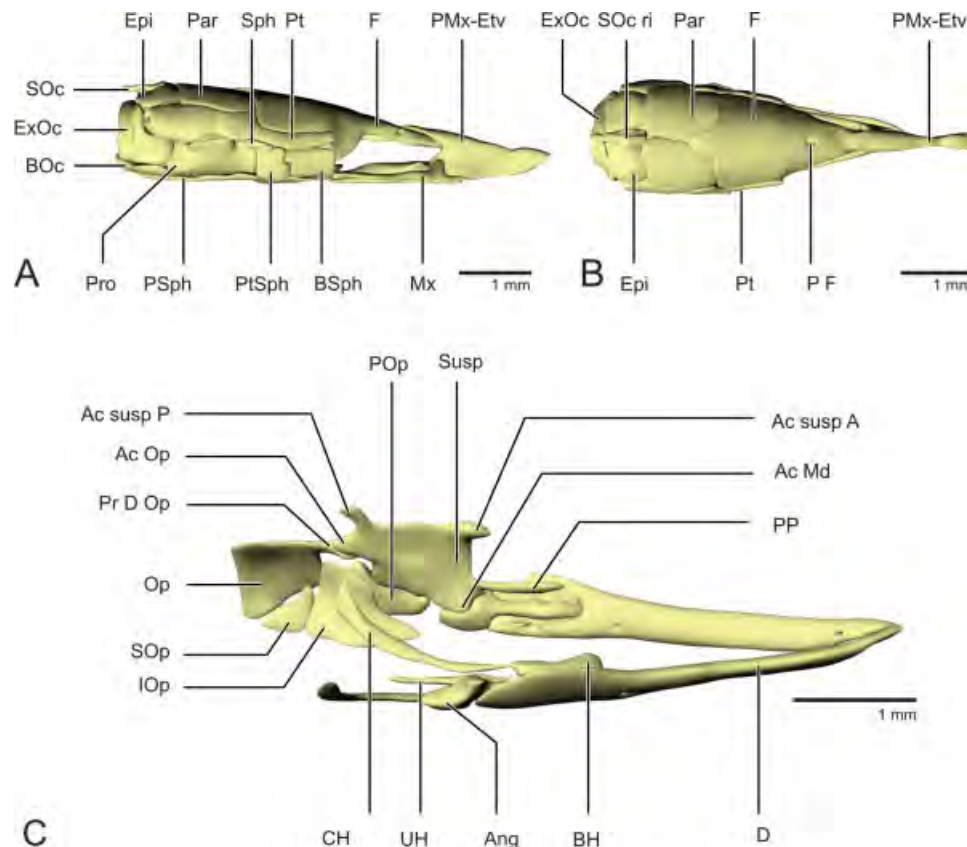
Fig. 1. 3D reconstruction of the neurocranium of *Pisodonophis boro* in (**A**) lateral view and (**B**) dorsal view. (**C**): Illustration of the lower jaw, suspensorium, hyoid, and opercular apparatus of *P. boro*. The image is slightly turned to the right, exposing the medial surfaces. Because the quadrate, hyomandibula and palatopterygoid are strongly interconnected, they are considered in this reconstruction as one unit. Abbreviations: Ac Md, mandibular articular condyle of the hyomandibula; Ac Op, opercular articular condyle of the hyomandibula; Ac Susp A, anterior suspensorial condyle of the hyomandibula; Ac susp P, posterior suspensorial condyle of the hyomandibula; Ang, angular complex; BH, basihyal; BOc, basioccipital; BSph, basisphenoid; CH, ceratohyal; D, dentary complex; Epi, epiotic; ExOc, exoccipital; F, frontal; IOp, interopercle; Mx, maxilla; Op, opercle; P F, frontal commissural pore; Par, parietal; PMx-Etv, Premaxillo-ethmovomerine complex; POp, preopercle; PP, pterygoid; Pr D Op, dorsal process of the opercle; Pro, prootic; PSph, parasphenoid; Pt, pterotic; PtSph, pterosphenoid; SOc ri, supraoccipital ridge; SOp, subopercle; Sph, sphenotic; Susp, suspensorium; UH, urohyal.

pore. The posterior part of the supraorbital canal runs in the frontal. The frontal commissure, situated above the eyes, connects the left and right parts of the supraorbital canal dorsally, and opens in a single dorsal, external pore. The infraorbital canal opens through four external pores and is surrounded anteriorly by the preorbital, whereas the posterior part is enclosed by two infraorbitals and three postorbitals. Behind the eyes, the supra- and infra-orbital canals anastomose, forming the temporal canal. The temporal canal is enclosed completely by the pterotic and the left and right halves of the canal are interconnected through the supratemporal commissure. This commissure is connected to the external environment by one external pore (Figs. 4 and 6A). The mandibular canal is enclosed in the dentary and angular complexes. Behind the articulation between the lower jaw and the suspensorium, the preopercular bone surrounds the preopercular canal. This canal bears

a nonenclosed ventrocaudal branch, ending in an external pore. The mandibulo-preopercular canal bears six external pores. The preopercular canal and temporal canal fuse, extending caudally in the lateral line system of the body, which is supported by ossicles. No dermal cavities, connected with the canals of the cranial lateral line system, are observed (cf. De Schepper et al., 2005).

The nasals are flat triangular bones, lying apposed to the dorsolateral edges of the premaxillo–ethmovomerine complex and covering the olfactory chamber. The small orbits are surrounded by a ring of six small, thin, and weak bones: the preorbital forms the anterior edge and is connected to the nasal, the two infraorbitals form the ventral edge, and the three postorbitals form the posterior edge (Fig. 3).

Some aspects of the eyes. The eye diameter of *P. boro* measures between 1.05 and 2.24 mm (53% of skull height). The cornea in *P. boro* is thick, pre-
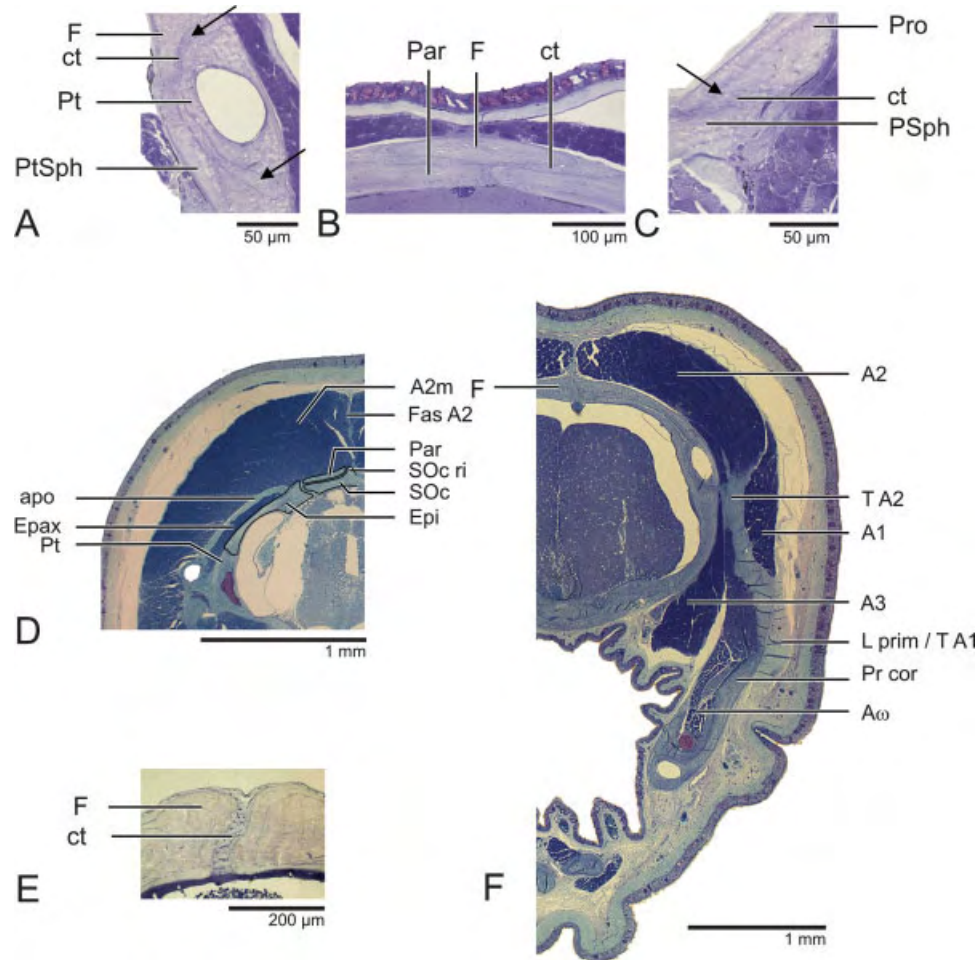
Fig. 2. Cross sections of the cranium of *Pisodonophis boro* (**A–C**) and *M. edwardsi* (**D–F**). The cranium is fortified by the presence of heavily ossified bones, which are strongly interconnected. The arrows indicate oblique edges of the joints. A: Scarf joints between frontal, pterotic and pterosphenoid in *P. boro*. B: Area of overlap between frontal and parietals formed by the extension of the oblique edges of the joints in *P. boro*. C: Scarf joints between parasphenoid and prootic in *P. boro*. D: Aponeurosis between adductor mandibulae complex and epaxials in *M. edwardsi*. E: Scarf joints between frontals in *M. edwardsi*. F: Cross section of the head of *M. edwardsi* at the level of the insertion of the adductor mandibulae complex. Abbreviations: A1, A2, A2m, A3, Aω, subdivisions of the adductor mandibulae complex; apo, aponeurosis; ct, connective tissue; Epax, epaxial; Epi, epiotic; F, frontal; L prim, primordial ligament; Par, parietal; Par, parietal; Pr cor, processus coronoideus; Pro, prootic; PSph, parasphenoid; Pt, pterotic; Pt, pterotic; PtSph, pterosphenoid; SOc ri, supraoccipital ridge; Soc, supraoccipital; T A1, T A2, tendon of subdivisions.

sumably to protect the eyes during head-first burrowing. The eyes of *M. edwardsi* are smaller compared with those of *P. boro*. The corneal epithelium and especially the corneal dermis are extremely thick (Fig. 10B). In *Heteroconger longissimus,* the eyes are extremely large and the cornea is markedly thinner (Fig. 10D), compared with that of *M. edwardsi* and *P. boro* (Fig. 5).

Cranial Myology

The adductor mandibulae complex, comprising four parts (A1, A2, A3, and Aω), is hypertrophied and expanded dorsocaudally (Fig. 4). The counterparts of the A2 contact each other medially, covering the dorsal skull roof up to the level of the supratemporal commissural pore. The jaw muscles are connected caudally to the epaxial musculature by an aponeurosis (Fig. 6A). The A1, lying superficial to the A2, forms a thin sheet of muscle fibers. Its medial fibers are connected to the frontals and more posteriorly to the lateral tendon of the A2 (Fig. 4A). The A1 inserts by a tendinous sheet (T A1: Fig. 4A) on the dorsal edge of the dentary, medial to the primordial ligament (Fig. 6B). This ligament runs from the maxilla to the dorsolateral edge of the dentary (Fig. 4A); the fibers are directed ventrocaudally.

The A2 has no subdivisions and forms the largest part of the adductor mandibulae complex, extending dorsally and caudally (Fig. 4A,B). The counterparts of the A2 are interconnected dorsally by an aponeurosis, originating from the frontal, parietal, epiotic, and supraoccipital surfaces. The
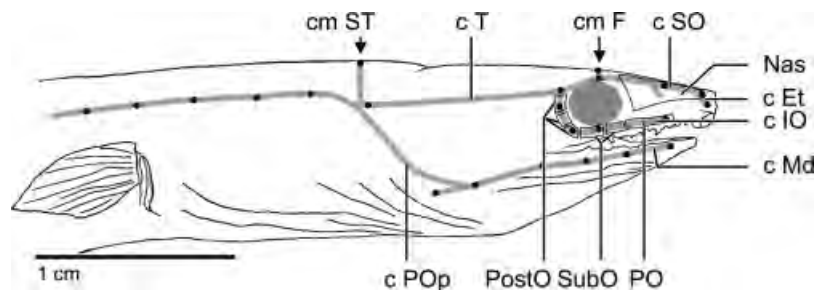
Fig. 3. The cephalic lateral line system of *Pisodonophis boro*. Black dots indicate external pores. Abbreviations: c Et, ethmoid canal; c IO, infaorbital canal; c Md, mandibular canal; c POp, preopercular canal; c SO, supraorbital canal; c T, temporal canal; cm F, frontal commissure; cm ST, supratemporal commissure; Nas, nasal; PO, preorbital; PostO, postorbital; SubO, suborbital.

muscular origin includes the frontal, pterotic, parietal, epiotic, and supraoccipital. The A2 has a tendinous insertion (T A2: Fig. 4B) on the dorsal edge of the coronoid process of the lower jaw (Fig. 6B). This tendon partially covers the lateral surface of the A2. The A2 inserts indirectly on the inner surface of dentary by the fusion of the ventral fibers of the A2 with the posterior fibers of the Aω (Fig. 6B). The anterior fibers are ventrocaudally directed, whereas the remaining fibers are directed ventrally to rostroventrally.

The muscular origin of the A3 includes the ventrolateral surface of the posterior part of the frontal, the ventrolateral surface of the anterior part of the pterotic, and the dorsolateral surface of the pterosphenoid, the hyomandibula, and palatopterygoid (Figs. 4C and 6B). The A3 inserts tendinously (T A3) on the ventromedial ridge of the angular complex, ventromedial to the fibers of Aω (Fig. 5B). The fibers are directed ventrocaudally.

The fibers of the Aω arise from the anteroventral part of the tendon T A2. More caudally fibers of the Aω fuse with ventral fibers of the A2, and this complex is connected to the palatopterygoid. The Aω inserts into the Meckelian fossa on the mediodorsal surface of the angular complex and the medial surface of the dentary (Fig. 6B).

The levator arcus palatini inserts muscularly on the lateral surface of the hyomandibula and dorsal edge of the palatopterygoid (Fig. 4C). Its fibers, directed ventrocaudally, merge onto a tendon, which originates from the lateral ridge of the sphenotic and pterosphenoid.

The adductor arcus palatini has muscular origin and insertion sites (Fig. 6A). Its fibers, inclined ventrolaterally, originate from the parasphenoid and insert on the medial surfaces of the palatopterygoid and ventromedial surface of the hyomandibula.

The adductor hyomandibulae originates muscularly from the prootic and inserts muscularly on the dorsomedial surface of the hyomandibula (Fig. 5B). The fibers are directed ventrolaterally.

The dilatator operculi lies with its apex pointing caudoventrally (Fig. 4C). The fibers are directed ventrocaudally. The muscle originates muscularly from the lateral surface of the pterotics and the posterior process-like extension of the dorsal edge of the hyomandibula (Fig. 6A). It inserts by its tendon on the dorsal process of the opercle.

The adductor operculi has both a muscular origin and insertion (Figs. 4C, 5B, and 6A). The fibers originate from the ventrolateral surface of the pterotics and exoccipitals and insert on the dorsomedial surface of the dorsal process of the opercle and on the anterior part of the dorsal edge of the opercle. The fibers are directed dorsoventrally and inclined caudally.

The levator operculi runs from the neurocranium to the opercle. Its tendon originates from the caudoventral surface of the exoccipitals and the posterodorsal edge of the hyomandibula (Fig. 6A). This muscle inserts muscularly on the dorsal opercular process and the dorsal edge and lateral surface of the opercle. The fibers of this large muscle are directed dorsoventrally and inclined caudally.

The intermandibularis is absent.

The protractor hyoidei comprises a separated left and right bundle, which are attached tendinously to the medial surfaces of the left and right dentary, respectively (Figs. 4A and 5B). Anteriorly, these tendons cover the dorsal surface of the anterior part of the muscle bundles. Posteriorly, both bundles diverge and arise separately by a posterior tendon from the laterodorsal surface of the anterior ceratohyal.

The left and right bundles of the sternohyoideus insert by means of a common, well developed tendon (Figs. 5B and 6A) on the posterodorsal region of the urohyal. This muscle comprises three myomeres separated by two myosepta, and the left and right bundles connect aponeurotically in the midline. The sites of origin include the medial side of the cleithrum dorsally, whereas the ventral fibers insert on a myoseptum, separating them from the hypaxial muscles.

The successive branchiostegal rays are interconnected by the hyohyoideus, forming a sheet of fibers (Fig. 6A). The muscle halves extend ventrally and connect to the ventral surface of the
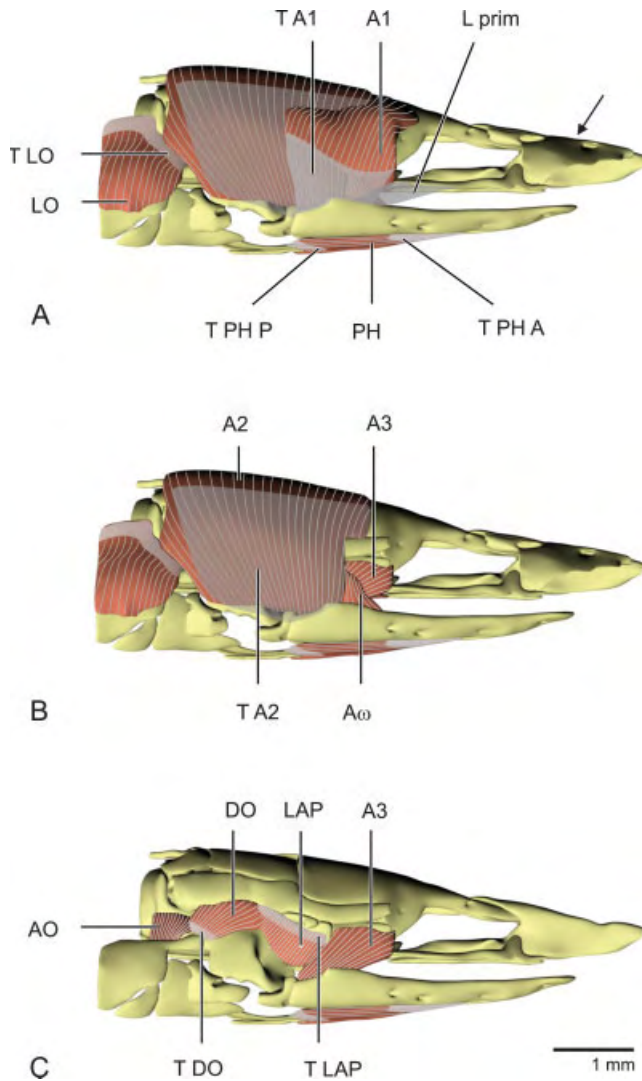
Fig. 4. 3D reconstruction of the cranial muscles of *Pisodonophis boro*. The nasal is indicated by an arrow. **A:** The skin is removed; **B:** the A1 of the adductor mandibulae complex is removed; **C:** A2 and Aω of the adductor mandibulae complex and LO are removed. Abbreviations: A1, A2, A3, Aω, subdivisions of adductor mandibulae complex; DO, dilatator operculi; L prim, primordial ligament; LAP, levator arcus palatini; LO, levator operculi; PH, protractor hyoidei; T A1, T A2, tendons of subdivisions; T DO, tendon of dilatator operculi; T LAP, tendon of levator arcus palatine; T LO, tendon of levator operculi; T PH A, anterior tendon of protractor hyoidei; T PH P, posterior tendon of protractor hyoidei.

urohyal. Dorsally, the fibers attach muscularly on the ventromedial surface of the dorsal opercular process and the medial surface of the opercle (Fig. 6A). Posteriorly, the fibers attach to the horizontal septum, which interconnects the hypaxial and epaxial muscles. Whether the hyohyoidei abductores and inferior are absent or not differentiated remains uncertain, and ontogenetic series are necessary to resolve this.

The epaxial muscles insert on the epiotics and the dorsal ridge of the supraoccipital by a fascia

(Fig. 6A). The hypaxial muscles inserts aponeurotically on the ventrocaudal border of the basioccipital and exoccipitals (Figs. 6A and 7).

Tail: Osteology

P. boro has a reduced caudal fin (Fig. 8A). The caudal skeleton comprises a dorsal and ventral hypural plate, the result of the fusion of hypurals three and four and hypurals one and two, respectively. The bifurcation point of the dorsal aorta marks the boundary between preural and ural vertebrae. The first and second ural vertebrae are fused, forming the urostyle. This integrates the uroneurals. Rostrolaterally, on each side of the ventral hypural plate, a hypurapophysis can be discerned. An epural element is absent. The first preural vertebra is situated in front of the caudal skeleton. The parhypural is the modified hemal spine of the first preural centrum and is the last hemal spine crossed by the dorsal aorta. The neural arches of the preural centra are large and robust. Their bases are as wide as the centra and
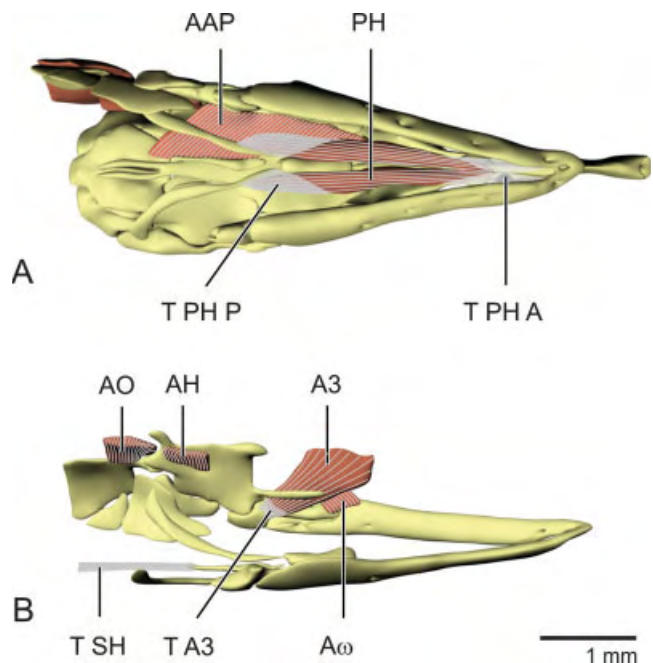

Fig. 5. 3D reconstruction of the cranial muscles of *Pisodonophis boro*. **A:** cranial muscles in ventral view; adductor mandibulae complex is removed. **B:** neurocranium is removed to show the small muscles situated between the neurocranium and suspensorium (adductor hyomandibulae) or between the neurocranium and the opercle (adductor operculi). This image is slightly laterally inclined. Branchiostegal rays and hyohyoideus are not shown. Abbreviations: A3, Aω, subdivisions of adductor mandibulae complex Aω; AAP, adductor arcus palatini; AH, adductor hyomandibulae; AO, adductor operculi; PH, protractor hyoidei; T A3, tendons of subdivisions; T PH A, anterior tendon of protractor hyoidei; T PH P, posterior tendon of protractor hyoidei; T SH, tendon of sternohyoideus.
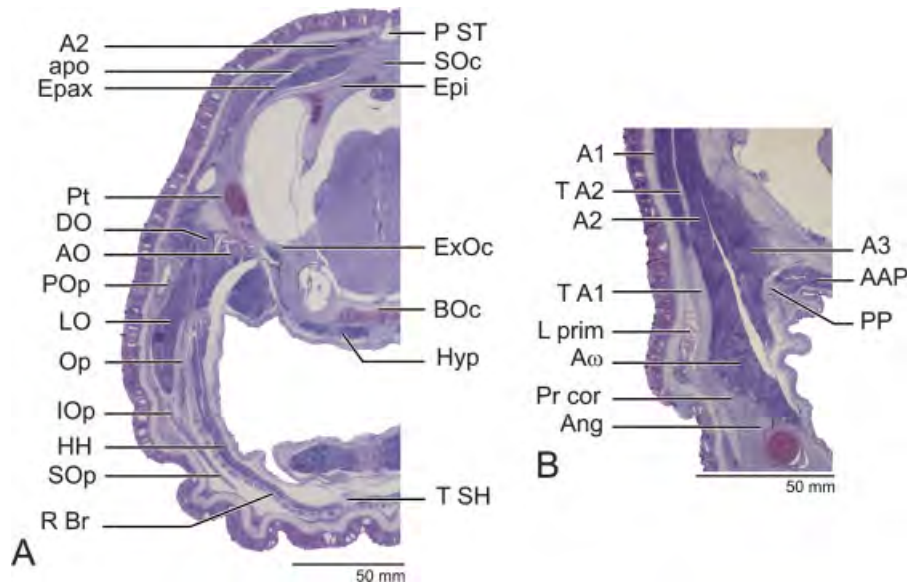
Fig. 6. **A:** Cross section of the head of *Pisodonophis boro* at the level of the supraoccipital. **B:** cross section at the level of the insertion of the A1 and A2 onto the lower jaw. Abbreviations: A1, A2, A3, Aω, subdivisions of the adductor mandibulae complex; AAP, adductor arcus palatini; Ang, angular complex; AO, adductor operculi; apo, aponeurosis; BOc, basioccipital; DO, dilatator operculi; Epax, epaxials; Epi, epiotic; ExOc, exoccipitals; HH, hyohyoideus; Hyp, hypaxials; IOp, interopercle; L prim, primordial ligament; LO, levator operculi; Op, opercle; P ST, supratemporal pore; POp, preopercle; PP, pterygoid; Pr cor, processus coronoideus; Pt, pterotics; R Br, branchiostegal rays; SOc, supraoccipital; SOp, subopercle; T A1, A2, tendons of subdivisions; T SH, tendon of the sternohyoideus.

they are fused dorsally in the midline, covering the neural canal. A neural spine is lacking. The left and right halves of the hemal arch of the preural centra are not fused in the midline. The posterior base of the hemal arch supports a large processus posthaemalis. Neural and hemal spines are absent in the proceeding caudal vertebrae. In some cases, two neural arches and two hemal arches are discerned (Fig. 8A). This may indicate the fusion of two vertebrae during development. Ontogenetic studies are needed to confirm this hypothesis.
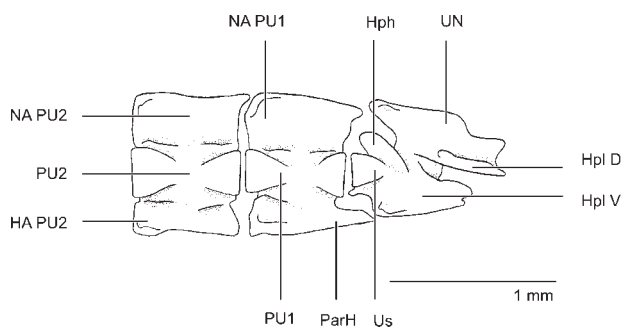

Fig. 7. Illustration of the osteological characteristics of the caudal skeleton of *Pisodonophis boro* in lateral view. Abbreviations: HA PU2, hemal arch of second preural centrum; Hph, hypurapophysis; Hpl D, dorsal hypural plate; Hpl V, ventral hypural plate; NA PU1, neural arch of first preural centrum; NA PU2, neural arch of second preural centrum ParH, parhypural; PU1, first preural centrum; PU2, second preural centrum; UN, uroneural; Us, urostyle.

Tail: Myology

Interradials are absent (Fig. 8B–D). The flexor dorsalis passes from the lateral surface of the uroneural to the three uppermost caudal fin rays, inserting via a tendinous sheet. The hypochordal longitudinalis originates from the ventrolateral surface of the ventral hypural plate and passes to the ventrolateral surface of the uroneural. The flexor ventralis originates form the lateral surface of the parhypural and inserts through a tendon on the ventral caudal fin ray. Medial to the hypochordal longitudinalis, the proximalis is present. This muscle connects the parhypural and first preural centrum to the lateral surface of the ventral and dorsal hypural plate. The trunk musculature, including both epaxial and hypaxial muscles, attaches to the bases of the caudal fin rays by broad tendinous sheets.

DISCUSSION
Morphology Related to Head-First Burrowing?

Eye protection and eye reduction. The eyes of *P. boro* (Tilak and Kanji, 1969), measuring 53% of skull height), and those of other Ophichtids (Bozzano, 2003) are reduced (Fig. 10A). Eye reduction is a feature observed in several groups of vertebrates adapted to the benthic, cryptic, or fossorial environments (Rieppel, 1996). In some mammals (e.g., Spalacidae [mole rats], Chrysochloridae
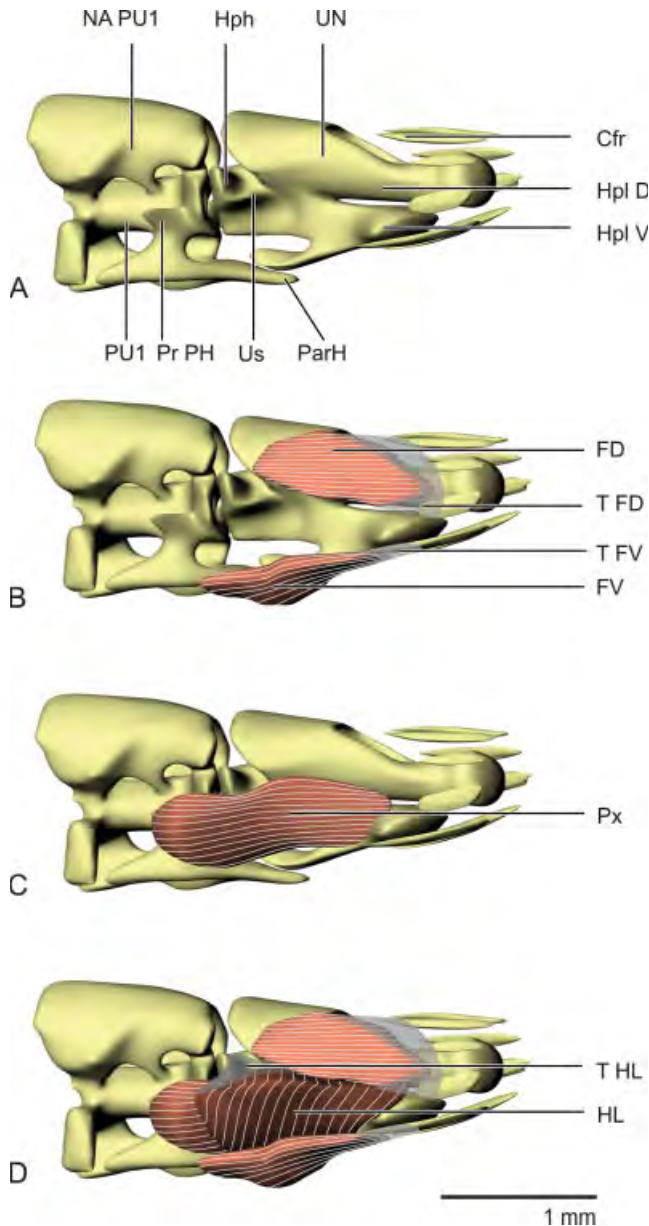
Fig. 8. 3D reconstruction of the tail of *Pisodonophis boro*. Tendons are shown in transparent gray. **A:** The caudal skeleton in lateral view. **B–D:** The intrinsic caudal musculature. Abbreviations: Cfr, caudal fin rays; FD, flexor dorsalis; FV, flexor ventralis; HL, hypochordal longitudinalis; Hph, hypurapophysis; Hpl D, dorsal hypural plate; Hpl V, ventral hypural plate; NA PU1, neural arch of first preural centrum; ParH, parhypural; PU1, first preural centrum Pr PH; Px, proximalis; T FD, tendon of the flexor dorsalis; T FV, tendon of the flexor ventralis: T HL, tendon of the hypochordal longitudinalis; UN, uroneural; Us, urostyle.

[golden moles] and Notoryctidae [marsupial moles]), the eyes are almost completely reduced and this is associated with the use of the head as a wedge while digging (Borghi et al., 2002). Reduced eyes have been documented for reptiles (amphisbeanians, some lizards and many primitive snakes (Lee, 1998; Wiens and Slingluff, 2001), as

well as for several elongate fishes (e.g. Clariidae [(Devaere et al., 2001, 2004)], Mastacembelidae [(Poll, 1973)], Anguilliformes [(Bozzano, 2003; De Schepper et al., 2004; Aoyama et al., 2005)]) in which the eye reduction is generally considered to be adaptive for a cryptic or burrowing life-style. Because of the reduction of vision, other sensory systems (olfaction, touch, lateral line system, etc.) may become more important to provide environmental information (Gordon, 1954; Montgomery, 1989; Smith, 1989a). The importance of olfaction, touch, and taste in eels in general is well known (Bantseev et al., 2004) and has been documented in detail for Muraenidae (Santos and Castro, 2003), Anguillidae (Pankhurst and Lythgoe, 1983) and Ophichthidae (Bozzano, 2003). Observations on foraging behavior of *P. boro* confirm the importance of olfaction and touch, as the fish move actively along the bottom, regularly probing into the sediment with their snout (personal observation).

The cornea comprises the corneal epithelium, dermis, and endothelium (Bozzano, 2003) (Fig. 6A). The thick cornea in *P. boro* presumably has a protective role during head-first burrowing. In *Moringua edwardsi*, which has smaller eyes compared to *P. boro*, the corneal epithelium and especially the corneal dermis are extremely thickened (Figs. 9 and 10B), in contrast to the tail-first burrowing species *H. longissimus*, in which the cornea is markedly thinner (Fig. 10D). The eyes of burrowing fish need to be protected from mechanical injuries during substrate contact. In *Ophichthus rufus*, another anguilliform head-first burrowing species, protection of the eye is offered by the presence of a corneal dermis and thick corneal epithelium covered by protective mucus (Bozzano, 2003). This supports our hypothesis of the protective role of the thick cornea in *P. boro*.

A substantial impact on the spatial design of the head due to the reduction of the eyes can be expected, especially given the macrophthalmic ancestral state in Anguilliformes (Böhlke, 1989). In other eel-like teleosts, like the elongate clariid cat-
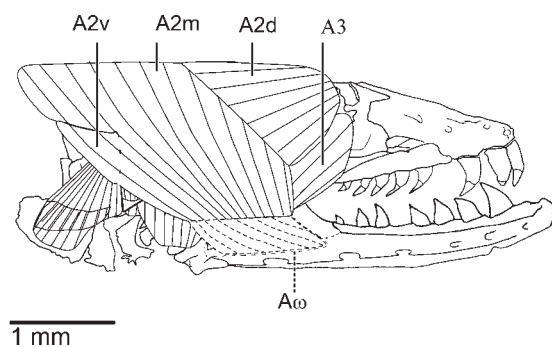

Fig. 9. The adductor mandibulae complex of *Moringua edwardsi*. Abbreviations: A1, A2d, A2m, A3, Aω, subdivisions of the adductor mandibulae complex.
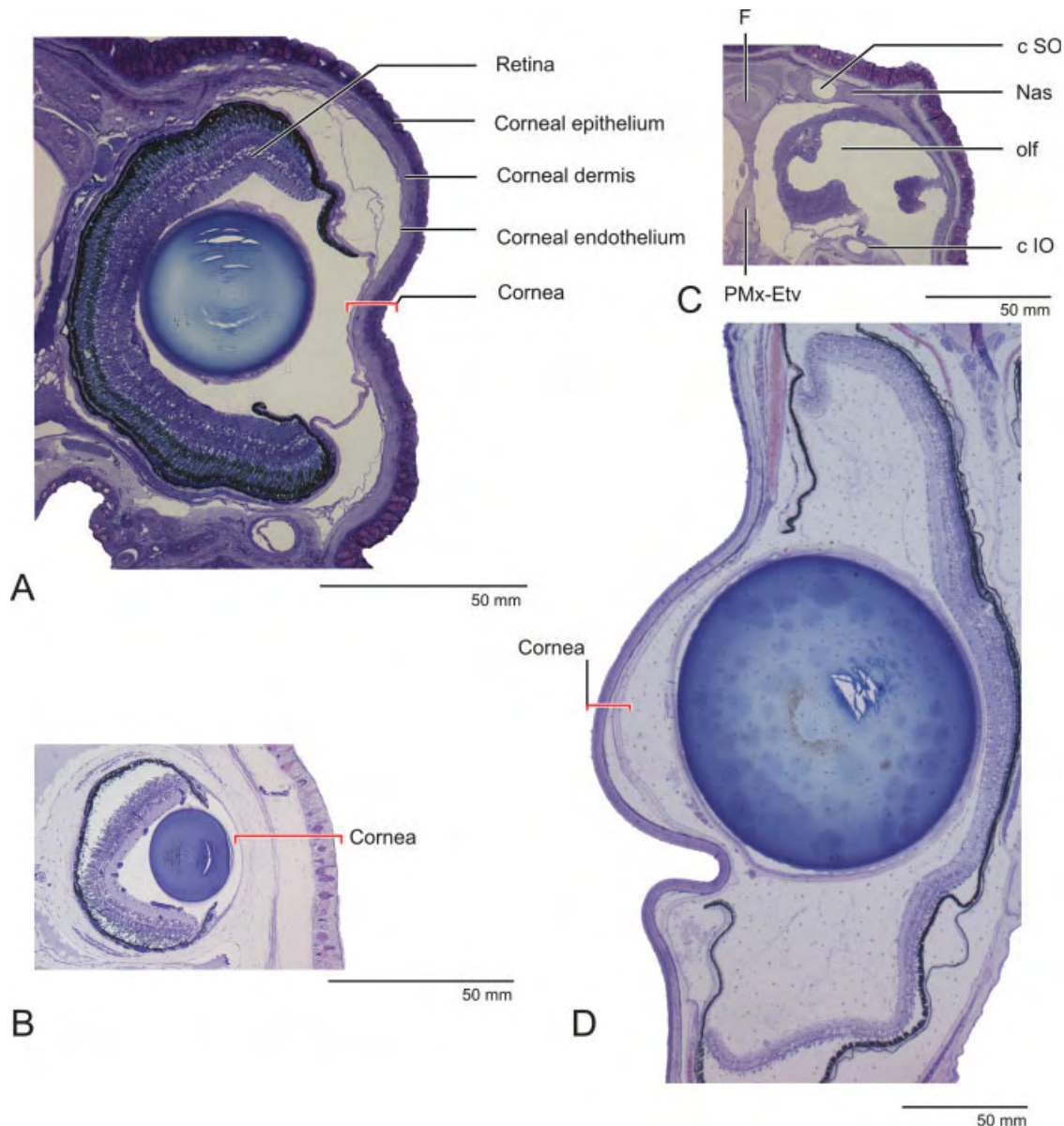
Fig. 10. Cross section at the level of the eye in (**A**) *Pisodonophis boro*, (**B**) *Moringua edwardsi,* and (**D**) *Heteroconger longissimus*. (**C**): the olfactory organ, covered by the winglike nasal in *P. boro*. Abbreviations: c IO, infraorbital canal; c SO, supraorbital canal; Nas, nasal; olf, olfactory chamber.

fish, hypertrophy of the jaw muscles has been linked to eye reduction (Devaere et al., 2001). In *P. boro* and *M. edwardsi* (De Schepper et al., 2005), the reduced eyes also create space for housing enlarged adductor mandibulae muscles and for allowing an unusual orientation of some fibers (see below). Next to the relation between hypertrophy of the jaw muscles and eye reduction in clariids (Devaere et al., 2001), eye reduction is linked to the reduction of circumorbital bones (reduced to small tubular bones) (Devaere et al., 2004). In *P. boro,* these bones are small and tubular as well. Interestingly and in accordance with the situation

in clariids (Devaere et al., 2004), the reduction in size of the circumorbital bones and the reduction in eye size co-occur in Ophichthids (Tilak and Kanji, 1969; McCosker et al., 1989; Bozzano, 2003).

Lateral line system. The cephalic lateral line system of *P. boro* is well-developed and follows the general pattern characteristic for other Anguilliformes as described by Böhlke (1989). This pattern contrasts with that of *Moringua edwardsi*, in which the cephalic lateral line system is aberrant (De Schepper et al., 2005); dermal cavities are present, presumably functioning as a kind of sen-

sory pads, which are stimulated mechanically during burrowing or when in contact with prey. External pores are absent in *M. edwardsi*, impeding the connection with the environment, but avoiding the entrance of sediment. Focusing on the head-first burrowing behavior, the question may arise why the cephalic lateral line system in *P. boro* is not modified as in *M. edwardsi*, to protect the canals from obstruction with sediment. The answer may be found in differences in the burrowing behavior between *P. boro* and *M. edwardsi*, especially related to the level of mechanical loading exerted onto the skull while burrowing. Immature specimens of *M. edwardsi* (dealt with in (De Schepper et al., 2005) spend all their time burrowed in the sand (Gordon, 1954; Gosline, 1956), hunting and feeding subterraneously (Smith, 1989a). Behavioral observations in our laboratory on *P. boro*, and on a closely related ophichthid, *Ophichthus rufus* (Bozzano, 2003), indicate that, after burrowing, this species remains stationary for a long period of time with its head protruding from the burrow entrance. Living in burrows with the head protruding is useful for protection and hiding against predators and for ambushing prey. Of course, locating predators or prey in time is crucial and may be mediated by the cephalic lateral line system. Because the eyes are reduced in *P. boro*, the cephalic lateral line system may be one of the dominant sensory systems. This has likewise been reported for blind fish (e.g. *Anoptichthys jordani*), in which the lateral line system becomes the most important sensory organ for scanning the surroundings (Hassan, 1989; Montgomery, 1989). So, the absence of external pores in *M. edwardsi* may be related to being permanently subterraneous (but the system remains functional due to its modifications), whereas in *P. boro* the presence of external pores is likely to be related to the habit of scanning the surroundings.

Hyperossification. Lee (1998) demonstrated that in amphisbaenians, dibamid lizards, and snakes, convergent evolutionary traits (miniaturization, cranial consolidation, body elongation, limb reduction) are clearly related to head-first burrowing. These characters frequently co-occur in other tetrapods (e.g. caecilians, frogs) with similar habits, showing that extreme skull modifications can be linked to resisting compressive and torque forces during burrowing (Gans, 1975; Hanken, 1983; Duellman and Trueb, 1986; Pough et al., 1998). Interestingly, *P. boro* shows similar traits that are considered to be advantageous for head-first burrowing.

The skull of *P. boro* is elongated and tapers toward the tip of the snout, facilitating penetration into the substrate. Fortification of the skull is improved by the broad, strong bones, by the fusions in the upper jaw and between the frontals, by the wide interorbital skull roof (as a result of the reduction of the eyes and orbits), by the large nasals (protecting the olfactory organ), by scarf joints and by large overlaps between successive bones of the skull roof (Figs. 1 and 10C). Duellman and Trueb (1986) reported that the distribution of different types of joints or fusions between bones may reflect the presence of high mechanical loads. Rafferty et al. (2003) and Sun et al. (2004) similarly found in pigs that fusions and enhanced bone growth appeared to be associated with increased suture strain. Some of these skull modifications in *M. edwardsi* are even more extreme compared with *P. boro*: paired dorsal skull bones are broader in cross section and show a larger surfaces of overlap at the midline (De Schepper et al., 2005).

Jaw adductor hypertrophy. The jaw muscles of *P. boro* are hypertrophied and expanded dorsocaudally, covering the complete postorbital skull roof (Figs. 2 and 5). The adductor mandibulae complex comprises four parts (A1, A2, A3, and Aω). The A2 has no subdivisions. The anterior fibers of the A2 are directed slightly ventrocaudally, whereas the remaining fibers are directed ventrally to rostroventrally. In *Moringua edwardsi,* the anterior part of the A2, in which the fibers are more oblique and directed ventrocaudally, is separated from the medial part of the A2 by the tendon T A2. An additional difference in jaw muscles of both species is found at the level of the A1. In *P. boro,* fibers of the A1 are directed ventrocaudally to ventrally and the tendon of this part is separate from the primordial ligament. In *M. edwardsi,* these fibers are directed ventrorostrally, with the A1 tendon merging with the primordial ligament.

In *P. boro*, head-first burrowing occurs via head probing and body undulations (personal observations), not through mouth excavation (e.g. *Cepola rubescens* (Cepolidae, Perciformes; (Atkinson and Taylor, 1991)). Consequently, powerful biting during excavation cannot explain the presence of the hypertrophied jaw muscles in *P. boro*. As the jaw muscles are hypertrophied in *P. boro*, it is reasonable to assume that these have a negative impact on head-first burrowing performance because of the increase in the head diameter. Logically the force required to penetrate the substrate increases exponentially with head diameter. However, hypertrophied jaw muscles may hold some benefit for head-first burrowing. As some parts of the jaw muscles show the aberrant fiber direction and as these muscles substantially enclose the posterior part of the skull, they may reinforce the lower jaw during head probing, thereby protecting it from being disarticulated (see below). The above-mentioned benefits of hypertrophied jaw muscles in head-first burrowing can count for *M. edwardsi* as well (De Schepper et al., 2005). As mentioned above, in *M. edwardsi* more fibers (A2d, A3) show the aberrant (ventrocaudal) fiber direction than is the case in *P. boro* (anterior fibers of A2 and A3

only). This may reflect the stronger need for rein-forcement of the lower jaw during head-first bur-rowing in *M. edwardsi* because this species is an obligate head-first burrower, whereas *P. boro* bur-rows tail-first as well.

Morphology Related to Feeding Habits and Prey Capture?

Rotational feeding. Three feeding modes (suc-tion, shaking and rotational feeding) to capture and handle food are observed in *P. boro*, depending on the size and consistency of the offered food items (personal observation). Helfman and Winkel-man (1991) already discerned the feeding modes in anguillids: 1) inertial suction, which draws small items into the mouth; 2) shaking, which entails grasping of large items and shaking or twisting the head and body, tearing small pieces from the prey; and 3) rotational feeding, which entails grasping large prey items and spinning around the body axis, thereby tearing small pieces from the prey. As the choice of feeding mode depends on prey size and food consistency, rotational feeding is performed when the prey item is firm and exceeds 85% of the eel's jaw width (Helfman and Clark, 1986; Helfman and Winkelman, 1991). The impor-tance of rotational feeding in *P. boro* can be de-duced from the dietary data reported by Subrama-nian (1984). Field observations showed selective feeding of *P. boro* on the crab *Uca annulipes*. The large size and high consistency of the carapace of these prey types require a spinning feeding mode to tear off consumable pieces.

Several morphological modifications in *P. boro* may be related to this specialized feeding mode. Rotational feeding starts at the anterior one-third of the body (Helfman and Clark, 1986). The com-mon aponeurosis separating the epaxial muscles and adductor mandibulae complex in *P. boro* may be considered beneficial for transferring these rota-tional forces from the body to the head (Figs. 2D and 6A). During rotational feeding, a powerful bite is required to be able to hold prey during spinning movements and to help prevent the lower jaw from being dislodged. Hypertrophied jaw muscles may exert large forces that can help resist torque forces during rotational feeding. The presence of a hyper-trophied adductor mandibulae complex, which leads to the assumption that powerful biting may occur (Devaere et al., 2001; Herrel et al., 2002; Van Wassenbergh et al., 2004), could be considered in this context. Consequently, an increase in me-chanical loads at the level of the insertion of the muscle complex onto the neurocranium and the upper and lower jaw may be expected, as well as in their articulations. Neurocranial rigidity in *P. boro* is improved by the extensive overlap between successive cranial bones, which are additionally very broad in cross section (Fig. 2A–D). The lower

jaw of *P. boro* is robust and bears a coronoid pro-cess. This process, however, is substantially shorter than in *Moringua edwardsi*. Similar struc-tural adaptations in the lower jaw and the coro-noid process have been linked previously to preda-tion and powerful biting (Böhlke, 1989; Cabuy et al., 1999; Devaere et al., 2001).

Rotational feeding also requires a solid grip on the prey, which is enhanced by the presence of numerous, pointed and recurved teeth, as observed in *Pisodonophis boro*. The absence of cutting denti-tion excludes the possibility to remove pieces of prey by nibbling, as reported by Helfman and Clark (1986) for anguillid eels. A solid grip during rotational feeding also requires a high structural rigidity of the upper and lower jaws to resist tor-que forces. In Anguilliformes, the robustness of the upper jaw results from the fusion of the premax-illa, ethmoid and vomer to form the premaxillo–ethmovomerine complex. This fusion is synapomor-phic for Anguilliformes and is assumed to be a specialization for predatory feeding (Eaton, 1935; Gosline, 1980; Smith, 1989a). Independently in Syn-branchidae, the upper jaw has become a strong, nonprotrusible element as a specialization for this particular feeding method (Liem, 1980).

Not only the jaw muscle size, but also the orien-tation of the different bundles composing this com-plex and the robust coronoid process, may contrib-ute preventing the lower jaw from being dislodged during rotational feeding (Figs. 9 and 4A). The an-terior fibers of the A1 and A2, and the fibers of the A3 are directed ventrocaudally. This is in contrast to the posterior fibers of the A1 and A2, which are directed rostroventrally. The resulting forces gener-ate both a vertical adduction component and a hori-zontal component acting on the lower jaw articula-tion (Fig. 8 in (De Schepper et al., 2005). Both hori-zontal components pointing in opposite directions and partially neutralize each other, and thus both vertical components prevent dislocation of the jaw joint (P. Aerts, personal communication).

Rotational feeding has been reported for eels (Anguilliformes (Helfman and Clark, 1986)), eel-like fish Clariidae, (Helfman and Clark, 1986); Synbranchidae, (Liem, 1980) and vertebrates with elongate bodies and small or lost appendages (sirens, caecilians, crocodilians, (Helfman and Clark, 1986). The convergence in some aspects of the morphology and behavior of these species with *P. boro* and *M. edwardsi* (De Schepper et al., 2005) is noteworthy. The following characteristics are observed in these spinning species and are assumed to be related to rotational feeding: the aponeurotic connection between epaxials and jaw muscles, hypertrophied jaw muscles (except in cae-cilians), increased neurocranial rigidity, robust lower jaws, non-cutting dentition and rigid upper jaw. These features have been linked to their spe-cialized rotational feeding feeding mode (Liem,

1980). The statement of Liem (1980) considering rotational feeding in *Monopterus,* "Once prey is captured, the highly hypertrophied adductor mandibulae complex plays a key role in conjunction with the corkscrew-like twisting motion of the body in breaking up the prey into pieces," further supports our assumptions.

Morphology Related to Tail-First Burrowing?

Osteology and caudal fin rays. The caudal skeleton is highly consolidated, lacking an externally visible caudal fin. The caudal fin rays are present but they are covered with muscles, a thick layer of connective tissue and a thick dermis and epidermis. This results in a hard, pointed tail, which appears to provide an added advantage to tail-first burrowing. The presence of long and pliable caudal fin rays would not benefit penetration of the substrate tail first. Garden eels (Heterocongrinae: *Heteroconger* and *Gorgasia*) also excavate their burrows tail-first and show a similarly modified tail morphology (shortened caudal fin rays, with stout and reduced caudal skeleton) to ensure an effective penetration into the sediment (Atkinson and Taylor, 1991; Castle and Randall, 1999).

Caudal fin myology. The intrinsic caudal musculature of the caudal fin of *P. boro* is highly reduced and presumably related to the modifications of the tail skeleton and its function. In teleosts, the caudal fin musculature generally allows a precise control of tail movements through caudal fin conformation (Lauder and Ducker, 2004). The interradials, which generally interconnect and adduct caudal fin rays (and consequently reduce the caudal fin area) in teleosts (Winterbottom, 1974), are absent completely in *P. boro*. The flexor dorsalis usually runs from the last few neural spines and centra and the upper hypurals to the dorsal caudal fin rays in teleosts (Winterbottom, 1974). In teleosts, the flexor ventralis usually connects the lateral surfaces of the hemal spines and arches of the last few vertebrae, parhypural and lower hypurals to the lateral bases of the ventral caudal fin rays (Winterbottom, 1974). The flexor dorsalis and flexor ventralis are known to move the dorsal and ventral caudal fin rays separately (Lauder and Drucker, 2004). In *P. boro,* the flexor dorsalis and flexor ventralis are reduced in size and their origins do not include the last few vertebrae. The hypochordal longitudinalis passes from the lower hypurals to three or four of the more dorsal fin rays in the dorsal half of the caudal fin in teleosts (Winterbottom, 1974). The hypochordal longitudinalis allows the dorsal fin margin to move separately from the ventral fin margin, turning them into the leading edge (Lauder and Drucker, 2004). It is surpring that in *P. boro* this muscle connects two immobile elements (ventral hypural plate to uroneural).

The actions of the intrinsic caudal fin musculature in *P. boro* are presumably no longer required with the loss of the need for subtle movements of individual fin rays. This may explain the absence of the interradials, the size reduction of the flexors and the absence of the insertion of the hypochordal longitudinalis onto the dorsal caudal fin rays in *P. boro*. Reduction and even absence of this muscle has been observed in several species with highly reduced caudal skeletons, especially those known for high-speed locomotion (e.g., tuna; (Lauder and Drucker, 2004). In these cruisers, fine movements of separate caudal fin rays are also less important. The proximalis generally connects the centra of the last few vertebrae, though its occurrence and position is highly variable in teleosts (Winterbottom, 1974). In *P. boro,* the proximalis muscle connects the parhypural and first preural centrum to the ventral and dorsal hypural plates. The presence of the proximalis muscle and the presence of broad tendinous insertions of the epaxial en hypaxial muscles onto the caudal fin rays may strengthen the tail to withstand bending forces during tail-first burrowing. Reduction or loss of these intrinsic muscles has been observed previously in species in which sophisticated movements of individual fin rays are no longer required (Winterbottom, 1974; Lauder and Drucker, 2004). The supracarinalis posterior generally runs from the last basal pterygiophore of the dorsal fin to the neural spine, epurals, uroneurals or dorsal caudal fin rays. The infracarinalis posterior runs from the last basal pterygiophore of the anal fin to the hemal spine of the last complete vertebrae, parhypural or ventral caudal fin rays. These muscles are not discerned in *P. boro,* which is likely related to the fact that the dorsal, anal and caudal fins are confluent.

The tail musculature of the obligate tail-first burrower *Heteroconger longissimus* (see Fig. 11) is even more extremely reduced compared to that of *P. boro*. The interradials in *H. longissimus* are absent as well and the flexor dorsalis has similar origin and insertion sites as in *P. boro*. The hypochordal longitudinalis is smaller in *H. longissimus*, whereas it is more rostrally expanded in *P. boro*. The flexor ventralis is highly different in both species. It originates from the ventral hypural plate and attaches to three caudal fin rays in *H. longissimus*, whereas it runs from the parhypural and attaches to only one caudal fin ray in *P. boro*. The proximalis is very small in *H. longissimus*, and the origin and insertion site is restricted to the urostyle and hypural plates, whereas in *P. boro* the origin includes the parhypural and centrum of the first preural vertebra. The reduction of the caudal fin musculature in *H. longissimus* is not surprising considering their life-style. They rarely leave their burrows and consequently they seldom swim (Rosenblatt, 1967). Complex caudal fin muscula-
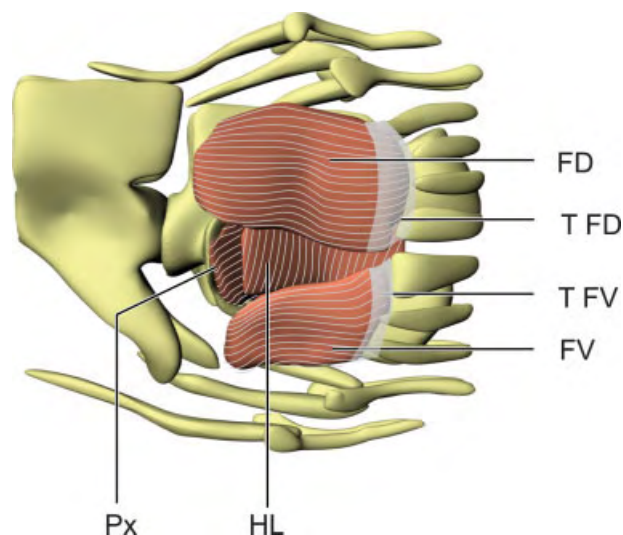
Fig. 11. 3D reconstruction of the tail of *Heteroconger longissimus*. Tendons are shown in semi-transparent gray. Abbreviations: FD, flexor dorsalis; FV, flexor ventralis; HL, hypochordal longitudinalis; ParH, parhypural; PU1, first preural centrum; Px, proximalis.

ture is therefore no longer required with the loss of the need for subtle movements of individual fin rays to generate propulsion or to maneuvre. The caudal fin muscles of *P. boro* are reduced to a lesser degree compared to those in *H. longissimus*. This difference may be related to the more active life-style of *P. boro*. The highly consolidated caudal fin skeleton in both species is strong enough to fortify the tail during tail-first burrowing so that the caudal fin musclulature can be reduced.

Functional Trade-Offs

Comparison of morphological alterations in head and tail of *Pisodonophis boro*. As in *P. boro* both terminal parts of the body need to be able to penetrate the substrate, one would expect similar kinds of external and internal modifications in the head and tail. However, as the head is not only used for burrowing but also has to accommodate the apparatus for feeding, constraints on the functional morphology of the head, associated with feeding are expected and are likely to prevent certain kinds of transformations or reductions.

Theoretically, a pointed end that has a small cross section and that is supported by a strong, consolidated skeleton would be the optimal design for burrowing. Indeed, such modifications (stout and reduced caudal skeleton) are found in the tail of *P. boro* (Fig. 8). The head on the other hand is also pointed and slender, but due to the hypertrophy of the jaw muscles, the cross section of the head is decreased to a lesser degree. Further more, several skull bones are fused and thick, thus providing extra strength. Though some degree of

kinesis (jaws, suspensorium) is still needed in the skull for feeding, consequently consolidation in the skull is limited at this level.

As protruding structures would have a negative effect or would be damaged during burrowing or substrate contact, it is expected that external structures would be reduced. This is again found in the tail with caudal fin rays being reduced. Again, similar modifications are found to a lesser degree in the head morphology. The eyes are reduced though still present and functional even though they may be damaged during substrate contact. The lateral line system is well developed, even though the canals are not specifically protected from being obstructed with sediment (which is the case in for example *M. edwardsi* (De Schepper et al., 2005).

At the level of the musculature, reductions are expected, except when they consolidate the structural components of the burrowing apparatus. The muscles in the tail are reduced when compared to the situation in generalized teleosts that need complex movements of individual fin rays. The muscles, which are present in the tail in *P. boro* are likely to strengthen the tail during burrowing. In agreement with our hypothesis, the skull shows no myological reductions, but incorporates hypertrophied jaw muscles (see below).

It is obvious the head is specialized for burrowing to some degree, though shows less far going transformations than the caudal fin. Clearly the mechanical design of the head allows animals to perform in different functions (locomotion and feeding) and shows trade-offs.

Trade-offs. A number of crucial biological functions must be fulfilled by the cranial musculo-skeletal system: capturing, processing and transporting prey, breathing water or air, providing protection for the major sense organs and brain, and serving as a streamlined bow in locomotion (Liem, 1980). Whenever two relevant functions require opposing biomechanical or physiological adaptations, the evolution towards optimal performance is assumed to be prevented (Stearns, 1992; Van Wassenbergh et al., 2004). An important goal in functional morphology is to identify how the mechanical design allows animals to perform in different functions that are essential, but require a trade-off with each other. As this study is based on morphological data, only indirect assumptions can be made of their biological function.

Feeding and head-first burrowing in *P. boro* can be two important functions that call for different requirements in the morphology of the jaw muscles. In the previous sections the hypertrophied jaw muscles of *P. boro* are associated with a strong bite needed to crush hard and large prey (cancrivory) and with their possible advantage during rotational feeding. Additionally, they may be advantageous during head-first burrowing as they may

reinforce the lower jaw during head probing, thereby protecting it from being disarticulated. However, the comment may arise that large jaw muscles would decrease head-first burrowing performance as the force required to penetrate the substrate increases exponentially with head diameter (reflecting the amount of pressure drag experienced during substrate penetration). The jaw muscles are likely to be involved in feeding and locomotion, and as *P. boro* performs head-first burrowing despite the presence of a wider head diameter, we consequently may assume trade-offs occur in these jaw muscles.

CONCLUSIONS

P. boro is able to burrow head-first but can penetrate the substrate tail-first as well. Focusing on the morphology of *P. boro,* several features may be related to either one or both burrowing habits. The reduced eyes, covered with thick protecting cornea, may be beneficial for protection during head-first, but at the same time decreased vision acuity may have an impact on other sensory systems (increase of olfaction, touch, lateral line system). Eye reduction may be related to the hypertrophy of the jaw muscles. The presence of a well-developed cephalic lateral line system is advantageous when the head is positioned at the entrance of a burrow. Hypertrophied jaw muscles may be advantageous for protecting the lower jaw from disarticulation during head-first burrowing. However, they probably are more important during feeding. The shape of the skull is beneficial for substrate penetration. The cranial bones and their joints, which are fortified, are advantageous to resist high mechanical loads during head-first burrowing. It is likely the hypertrophied mouth closing muscles yield a benefit for a predatory life-style. A specialized feeding mode is observed in *P. boro*: rotational feeding. The aponeurotic connection between epaxial and jaw muscles is considered beneficial for transferring forces from the body to the head during spinning. Hypertrophied jaw muscles enhance a powerful bite, which is required to hold prey during spinning movements. Different orientations of lower jaw muscle bundles may be beneficial to prevent the lower jaw from being dislodged. Furthermore, firm upper jaws (premaxillo–ethmovomerine complex) and lower jaws (with robust coronoid process), high neurocranial rigidity and non-cutting dentition are advantageous for a solid grip to hold prey during rotational feeding. The pointed shape of the tail and the consolidated caudal skeleton are beneficial for tail-first burrowing. It is quite likely that the reduction of the caudal musculature is related to the tail-first burrowing, because subtle movements of the caudal fin rays are no longer required. Furthermore, additional strength may be offered by the presence of broad tendinous connection of the epaxial and hypaxial muscles as well as by the presence of the proximalis.

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 RJA, Taylor AC. 1991. Burrows and burrowing behavior of fish. Symp Zool Soc Lond 63:133–155.

Bantseev V, Moran KL, Dixon DG, Trevithick JR, Sivak JG. 2004. Optical properties, mitochondria and sutures of lenses of fishes: A comparative study of nine species. Can J Zool 82:86–93.

Bath H. 1960. Uber die Korperhaut des Röhrenaals *Xarifania hassi* (Heteroncongeridae). Z Zellforschung. 51:728–734.

Böhlke EB. 1989. Methods and terminology. In: Böhlke EB, editor. Fishes of the Western North Atlantic. New Haven, CT: Sears Foundation for Marine Research. pp 1–7.

Borghi CE, Giannoni SM, Roig VG. 2002. Eye reduction in subterranean mammals and eye protective behavior in *Ctenomys*. J Neotropical Mammal 9:123–134.

Bozzano A. 2003. Vision in the rufus snake eel, *Ophichthus rufus*: Adaptive mechanisms for a burrowing life-style. Mar Biol 143:167–174.

Cabuy E, Adriaens D, Verraes W, Teugels GG. 1999. Comparative study on the cranial morphology of *Gymnallabes typus* (Siluriformes: Clariidae) and their less anguilliform relatives. *Clariallabes melas* and *Clarias gariepinus*. J Morphol 240: 169–194.

Casimir MJ, Fricke HW. 1971. Zur Funktion, Morphologie und Histochemie der Schwanzdrüse bei Röhrenaalen (Pisces, Apodes, Heterocongridae). Mar Biol. 9:339–346.

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.

Castle PHJ, Randall JE. 1999. Revision of Indo-Pacific garden eels (Congridae: Heterocongrinae), with descriptions of five new species. Indo Pac Fish 30:2–53.

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, De Kegel B, Adriaens D. 2005. *Moringua edwardsi* (Anguilliformes, Moringuidae): Cranial adaptations for head-first burrowing. J Morphol 266:356–4.

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 microphthalmus* (Poll, 1942) (Siluriformes, Clariidae). Copeia 1:108–115.

Duellman WE, Trueb L. 1986. Musculoskeletal system. In: Duellman WE, Trueb L, editors. Biology of Amphibians. New York: McGraw-Hill. Chapter 13, pp 289–364.

Eaton TH Jr. 1935. Evolution of the upper jaw mechanism in teleost fishes. J Morphol 58:157–172.

Fricke HW. 1969. Okologische und verhaltensbiologische Beobachtungen an den Röhrenallen *Gorgasia sillneri* und *Taenioconger hassi* (Pisces, Heteroncongridae). Z Tierpsychol. 27:1076–1099.

Gans C. 1975. Tetrapod limblessness: Evolution and functional corollaries. Am Zool 15:455–467.

Gordon SM. 1954. The eel genus *Stilbiscus*. Copeia 1:11–15.

Gosline WA. 1956. The Hawaiian fishes of the family Moringuidae: Another eel problem. Copeia 1:9–18.

Gosline WA. 1971. Functional Morphology and Classification of Teleostean Fishes. Honolulu, HI: University Press of Hawaii.

Gosline WA. 1980. The evolution of some structural systems with reference to the interrelationships of modern lower teleostean fish groups. Jpn J Ichthyol 21:1–24.

Hanken J. 1983. Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae). II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. J Morphol 177:255–268.

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.

Hassan ES. 1989. Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish *Anoptichthys jordani*. In: Coombs S, Görner P, Münz H, editors. The Mechanosensory Lateral Line. New York: Springer-Verlag. Chapter 10.

Helfman GS, Clark JB. 1986. Rotational feeding: Overcoming gape-limited foraging in anguillid eels. Copeia 3:679–685.

Helfman GS, Winkelman DL. 1991. Energy trade-offs and foraging mode choice in American eels. Ecology 72:310–318.

Herrel A, Adriaens D, Verraes W, Aerts P. 2002. Bite performance in clariid fishes with hypertrophied jaw adductors as deduced by bite modelling. J Morphol 253:196–205.

Hildebrand CM. 1995. Analysis of Vertebrate Structure, 4th ed. New York: Wiley.

Lauder GV, Drucker G. 2004. Morphology and experimental hydrodynamics of fish fin control surfaces. IEEE J Ocean Eng 29:556–571.

Lee MSY. 1998. Convergent evolution and character correlation in burrowing reptiles: Towards a resolution of squamate relationships. Biol J Linn Soc 65:369–453.

Liem KF. 1980. Air ventilation in advanced teleosts: Biomechanical and evolutionary aspects. In: Ali MA, editor. Environmental Physiology of Fishes. New York: Plenum. pp 57–91.

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.

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.

Nelson JN. 1994. Fishes of the World. New York: Wiley.

Pankhurst NW, Lythgoe JN. 1983. Changes in vision and olfaction during sexual maturation in the European eel *Anguilla anguilla* (L.). J Fish Biol 23:229–240.

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.

Rafferty KL, Herring SW, Marshall CD. 2003. Biomechanics of the rostrum and the role of facial sutures. J Morphol 257:33–44.

Rieppel OC. 1996. Miniaturization in tetrapods: Consequences for skull morphology. In: Miller PJ, editor. Miniature Vertebrates. Oxford: Clarendon. pp 15–45.

Rosenblatt RH. 1967. The osteology of the Congrid eel *Gorgasia punctata* and the relationships of the heterocongrinae. Pac Sci 21:91–97.

Santos FB, Castro RMC. 2003. Activity, habitat utilization, feeding behavior, and diet of the sand moray *Gymnothorax ocellatus* (Anguilliformes, Muraenidae) in the South Western Atlantic. Biota Neatropica 3:1–7.

Smith DG. 1989a. Family moringuidae. In: Böhlke EB, editor. Fishes of the Western North Atlantic. New Haven, CT: Sears Foundation for Marine Research. pp 55–71.

Smith DG. 1989b. Family congridae. In: Böhlke EB, editor. Fishes of the Western North Atlantic. 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.

Stearns SC. 1992. The Evolution of Life Histories. New York: Oxford University Press.

Subramanian A. 1984. Burrowing behavior and ecology of the crab-eating Indian snake eel *Pisoodonophis boro*. Environ Biol Fish 10:195–202.

Sun Z, Lee E, Herring SW. 2004. Cranial sutures and bones: Growth and fusion in relation to mastication strain. Anat Rec Part A 276:150–161.

Tilak R, Kanji SK. 1969. Studies on the osteology of *Pisoodonophis boro* (Hamilton). Gegenbaurs Morphol Jahrb 113:501–523.

Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2004. Effects of jaw adductor hypertrophy on buccal expansions during feeding of airbreathing catfishes (Teleostei, Clariidae). Zoomorphology 123:81–93.

Vigliola L, Galzin R, Harmelin-Vivien ML, Mazeas F, Salvat B. 1996. Les Heterocongrinae (Teleostei: Congridae) de la pente externe de Moorea (île de la Société, Polynésie Française): distribution et biologie. Cybium 20:379–393.

Wiens JJ, Slingluff JL. 2001. How lizards turn into snakes: A phylogenetic analysis of body-form evolution in anguid lizards. Evolution 55:2303–2318.

Winterbottom R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. Proc Acad Nat Sci Phila 125:225–317.