

# Morphological Specializations in Heterocongrinae (Anguilliformes: Congridae) Related to Burrowing and Feeding

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**ABSTRACT** The remarkable lifestyle of heterocongrines has drawn the attention of many authors in the past, though no or little attention has been paid to the morphology of the tail and the head of these species. In order to examine the true nature of possible morphological specializations of the head and tail and their relation to their tail-first burrowing habit and/or feeding mode, a detailed myological and osteological study of *Heteroconger hassi* and *Heteroconger longissimus* was performed. The osteological similarities of the cranial skeleton between *H. hassi* and *H. longissimus* are striking. Most of the cranial muscles show no variation in presence, insertion or origin between these two species except for the adductor mandibulae complex, the adductor hyomandibulae and the intermandibularis. The adductor mandibulae complex is small, compared to that of other anguilliform species, and is probably related to their suction-dominated feeding mode and a diet, comprising mainly small, soft prey items. Heterocongrinae have undergone several morphological specializations in the tail for their tail-first burrowing lifestyle. The skeleton and musculature of the tail of *H. hassi* and *H. longissimus* are similar. In both species the caudal skeleton is highly reduced and fortified, forming a firm, pointed burrowing tool. Intrinsic caudal musculature is reduced and some muscles (interradials, supracarinalis) are even absent. *J. Morphol.* 268:343–356, 2007. © 2007 Wiley-Liss, Inc.

**KEY WORDS:** osteology; myology; burrowing lifestyle; cranial morphology; tail

Congridae are found worldwide in tropical and subtropical latitudes and are one of the largest and most diverse families of the Anguilliformes (Smith, 1989b; Belouze, 2001). Except for the heterocongrine subfamily, Congridae are bottom dwellers that feed on a variety of fishes and invertebrates (Smith, 1989b).

Heterocongrinae are a subfamily of the Congridae (Smith, 1989b) and are the most distinct of the congrids, and among the few that show conspicuous morphological specializations related to their tail-first burrowing lifestyle. The taxonomy of Heterocongrinae has been ambiguous in the past, although recently two genera were recognized: *Heteroconger* and *Gorgasia* (Castle and Randall, 1999). *Gorgasia* is regarded as the most primitive genus of the Heterocongrinae (Tyler and Smith, 1992; Castle and Randall, 1999). Garden eels live in large colonies. Each individual lives permanent in separate,

strengthened burrows, in sandy or silty-sand substrate (Casimir and Fricke, 1971; Smith, 1989b). They project the front portion of the body from the burrow to feed on zooplankton (Casimir and Fricke, 1971; Smith, 1989b). They are able to withdraw entirely into their burrows but mostly they emerge three-fourths or more of their length from the burrow opening, while the tail remains inserted, their heads turned to the plankton-loaded currents to snap and pick small zooplanktonic particles (Bath, 1960; Smith, 1989b; Vigliola et al., 1996; Castle and Randall, 1999). Heterocongrinae feed mainly on copepods (66.3% of total stomach content volume). Tunicates form 18.6% of the stomach contents and the remaining part consists of pteropods, ostracods, shrimp larvae, unidentified eggs, and copepod larvae (Smith, 1989b).

This study is part of an ongoing project that deals with evolutionary trade-offs related to head- and tail-first burrowing. In this case-study the cranial and caudal morphology of true head-first burrowers are examined. So, morphological constraints are predominantly expected in the tail morphology as no fortification constraints on the skull are required. We hypothesize that 1) marked specializations in the musculoskeletal system of the tail are present to cope with and generate large mechanical forces, and 2) the cranial musculoskeletal system is not specialized, as suction-feeding is applied by these species.

The remarkable lifestyle of heterocongrines has drawn the attention of many authors in the past, although no attention has been paid to the musculature of the tail and the head. To examine the true nature of morphological specializations of the head and tail a detailed myological and osteological study of *Heteroconger hassi* and *H. longissimus* was performed. First, the cranial morphology is described

Contract grant sponsor: FWO; grant number: G.0388.00.

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Published online 9 March 2007 in  
Wiley InterScience (www.interscience.wiley.com)  
DOI: 10.1002/jmor.10525

for *H. hassi* into detail and subsequently a brief survey of the observed cranial morphological differences in *H. longissimus* is given. Second, the detailed morphological description of the tail of *H. hassi* is given and subsequently compared with that of *H. longissimus*. The relation between cranial morphology and feeding mode on the one hand and between morphology of the caudal fin and tail-first burrowing on the other hand are discussed to understand possible structural specializations of the systems involved.

## MATERIALS AND METHODS

For this study four specimens of *Heteroconger longissimus* (total length varies between 225 and 268 mm) and five *Heteroconger hassi* (202 and 285 mm) were used. All specimens are preserved in ethanol (70%). *Heteroconger longissimus* specimens were obtained from the National Museum of Natural History, Washington (USNM 316037). Specimens of *H. hassi* were commercially obtained (Moeskroen, Belgium) and deposited in the Zoological Museum at Ghent University (UGMD 175374). To examine osteological features specimens were cleared and the skeletal elements were stained with Alizarin red S and Alcian blue according to the protocol of Hanken and Wassersug (1981). Drawings were made using a stereoscopic microscope (Olympus SZX-9), equipped with a camera lucida and a Colorview 8 digital camera. Morphology of the head skeleton of *H. hassi* was studied by serial cross sections. Specimens were fixed with formaldehyde solution (8%), decalcified with Decalc 25% (HistoLab), dehydrated through an alcohol series, and embedded in Technovit 7100 (Kulzer-Heraeus). Series of semithin section (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 (Soft Imaging System GmbH, version 3.0). On the basis of the serial histological sections graphical 3D reconstructions were generated using Corel-Draw 8 (Corel) for tracing contours of the structures and Amira 3.0 (TGS) and Rhinoceros 3.0 (McNeel) for making reconstructions. Nomenclature of skeletal elements follows that of Smith (1989b), unless stated otherwise. The terminology of the musculature is that of Winterbottom (1974). A detailed description of the osteological features of the head morphology of *H. longissimus* was provided by Böhlke (1957) and Smith (1989b).

## RESULTS

### Head Osteology: *Heteroconger hassi*

The *ethmoid region and upper jaw* is composed of the massive premaxillo-ethmovomerine complex, formed by ankylosed premaxillaries, ethmoid, and vomer (Fig. 1). Ethmoid processes are absent. The lateral process of the pars vomeralis is well developed and elevated, bearing the vomero-pterygoid articular facet, to which the pterygoid is connected (Fig. 1C). The maxilla rests with a large pedicel on the maxillo-premaxillo-ethmovomerine articular facet, which is situated anterolaterally on the premaxillo-ethmovomerine complex (Fig. 1A,B). The posterior teeth of the maxilla are markedly enlarged and pointed forward.

The *orbital region* comprises the basisphenoid, frontals, and pterosphenoids (Fig. 1). Orbitosphenoid

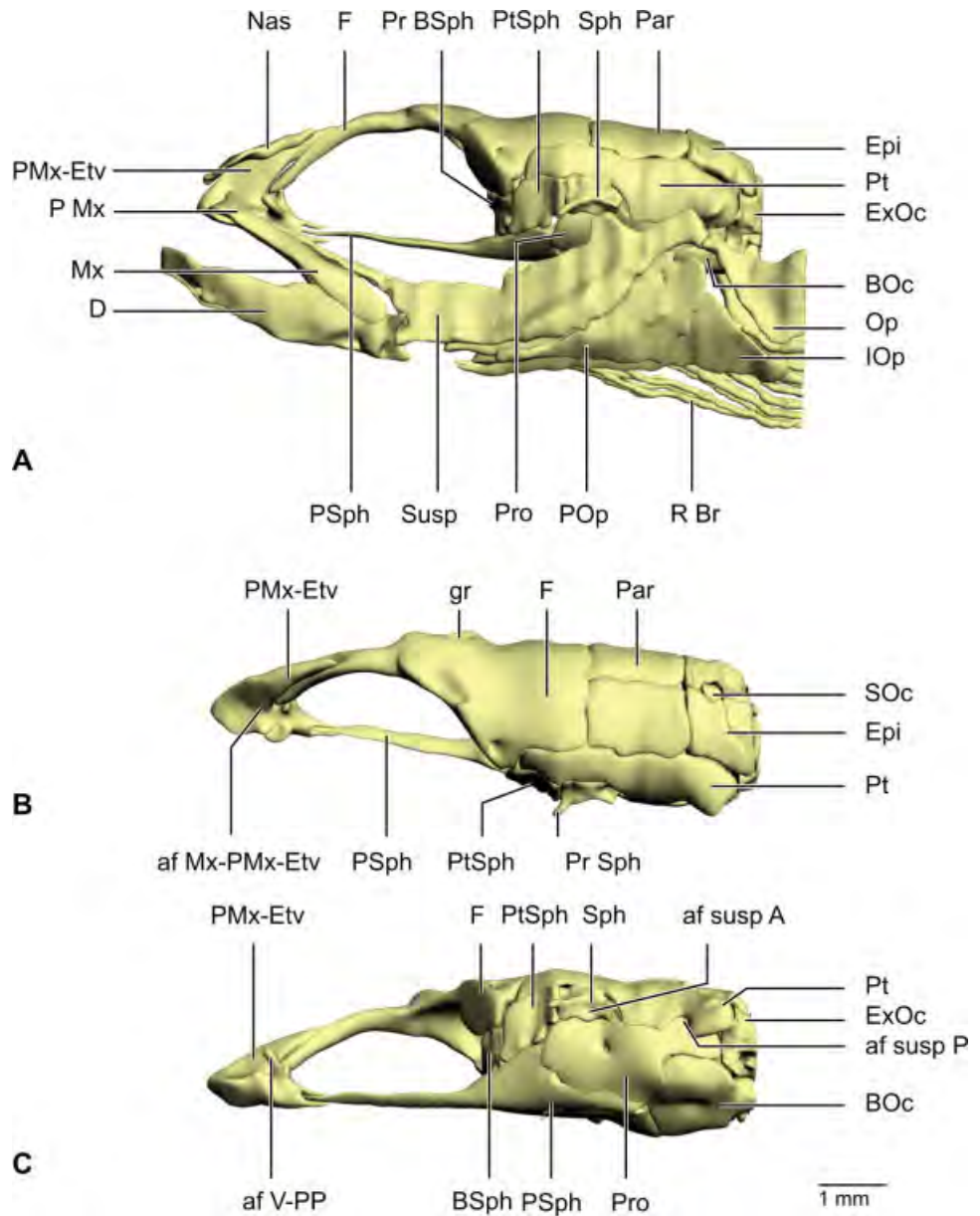
is absent. An irregularly shaped cartilage is present in front of the orbit. A relatively small, unpaired basisphenoid borders the ventroposterior edge of the orbits. A small medial basisphenoidal process, directed towards the orbits, serves for the attachment of some of the eye muscles (Fig. 1A). The frontals occupy the largest part of the skull roof and have fused. The tips of the frontals taper rostrally and are covered dorsally by the dorsocaudal projection of the pars ethmoidalis. The dorsocaudal border of the orbits is formed by the rostral part of the frontals. Above the caudal margin of the orbit, the frontals bear a groove for the entrance of the supraorbital canal (Fig. 1B). The pterosphenoids border the ventrocaudal margin of the orbits. The parasphenoid spans from the orbital region to the occipital region, forming the longest cranial element in ventral aspect. Two symmetrical, laterodorsal projections stretch towards the sphenotic, where it reaches its highest width. The anterior part of the parasphenoid borders the orbits ventrally and is in this region extremely narrow. Caudally, the parasphenoid splits into two long, narrow arms, i.e., the parasphenoidal processes.

The *otic region* comprises the sphenotics, pterotics, prootics, epiotics, and parietals (Fig. 1). The sphenotics are situated laterodorsally and bear an extensive sphenotic process or sphenotic wing (Fig. 1B). The posterior part of this sphenotic process contributes to the anterior suspensorial articulation facet (Fig. 1C). The paired pterotics, bearing a large anterior process, form a large part of the lateral skull wall and house the temporal canals (Fig. 9A). The posterior suspensorial articular facet is formed by the pterotics (Fig. 1C). The prootics, the pterotics, and sphenotics contribute to the suspensorial articular groove. The prootics are situated lateroventrally. The prootics, basioccipital, and exoccipitals are expanded to form otic bullae. The epiotics are situated at the posterodorsally. Both epiotics border the foramen magnum dorsally. The two parietals have a rectangular shape, rostrocaudally extended, and cover a large part of the skull roof. Both parietals contact in the midline.

The *occipital region* comprises the exoccipitals, basioccipital, and supraoccipital. The ventral border of the foramen magnum is formed by the unpaired basioccipital. The exoccipitals surround the foramen magnum dorsolaterally and form the ventrolateral part of the cranium in caudal view. Two exoccipital processes are present caudolaterally. The unpaired medial supraoccipital is situated dorsocaudally, in front of the caudal border of the skull, and lacks a ridge and spiny projections.

The *suspensorium* comprises three bones, the hyomandibula, quadrate, and pterygoid (Fig. 2C). The preopercle is described with respect to the opercular apparatus. The symplectic is cartilaginous and situated posterior to the quadrate (Figs. 2C and 9A). The hyomandibula and quadrate are

Fig. 1. **A:** 3D reconstruction of the skull of *Heteroconger hassi* in lateral view. **B:** 3D reconstruction of the neurocranium, with the splanchnocranium removed, in dorso-lateral view and **C:** ventro-lateral view. The suspensorium (quadrate, hyomandibula, and pterygoid), lower jaw (angular and dentary complex), and hyoid arch (anterior and posterior ceratohyal) are considered in this reconstruction as one unit. af Mx-PMx-Etv, maxillo-premaxillo-ethmovomerine articular facet; af Susp A, anterior suspensorial articular facet; af Susp P, posterior suspensorial articular facet; af V-PP, vomero-ptyergoidal articular facet; BOc, basioccipital; BSph, basisphenoid; D, dentary complex; Epi, epiotic; ExOc, exoccipitals; F, frontal; gr, frontal groove; IOp, interopercle; Mx, maxillary; Nas, nasal; Op, opercle; P Mx, pedicel of maxillary; Par, parietal; PMx-Etv, premaxillo-ethmovomerine complex; POp, preopercle; Pr BSph, Basisphenoidal process; Pro, prootic; Pr Sph, sphenotic process; PSph, parasphenoid; Pt, pterotic; PtSph, ptersphenoid; R Br, branchiostegal ray; SOc, supraoccipital; Sph, sphenotic; Susp, suspensorium.



strongly connected, forming a massive, strong trapezoidal entity, which is elongate and forwardly inclined. The lateral surfaces show slightly elevated ridges for the insertion of the adductor mandibulae complex. The anterior and posterior dorsal articular condyles fit into the anterior and posterior suspensorial articular facets of the neurocranium, respectively (Fig. 1A). The dorsal edge is attached by connective tissue to the articular groove. The hyomandibula bears the opercular articular condyl dorsocaudally for the articulation with the operculare. The posterior part of the hyomandibula is connected to the posterior ceratohyal by a strong ligament. The quadrate bears the mandibular articulation condyle. The pterygoid is a slender, elongate bone. The rostral tip of the bone is

ligamentously connected to the vomero-ptyergoidal articular facet on the pars vomeralis.

The *opercular apparatus* comprises four bones (opercle, preopercle, interopercle, and subopercle, Fig. 2D). The preopercle is situated rostrally. Its anterior edge is tightly connected to the hyomandibula and symplectic through connective tissue (Fig. 9A). The interopercle has an approximately triangular shape and is elongated in the rostrocaudal axis. Rostrally, this element is concealed by the caudal part of the preopercle. The curved subopercle follows the caudal edge of the opercle, to which it is firmly attached by connective tissue, both elements the level of the fourth vertebra. The fan-shaped opercle articulates by means of the rostro-dorsal opercular articulation facet with the dorsal opercu-

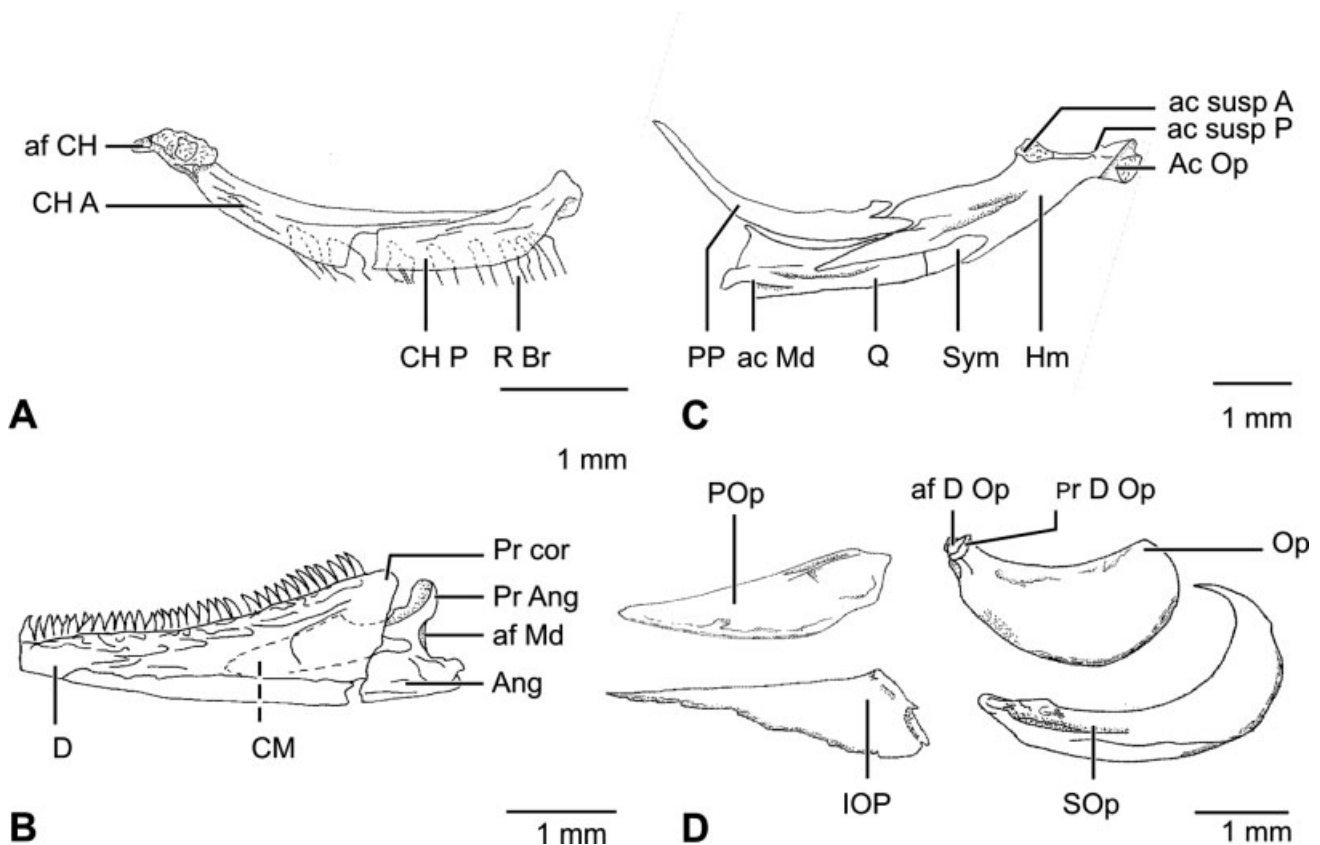


Fig. 2. Detailed morphology of *Heteroconger hassi*. **A:** The anterior and posterior ceratohyals in medial view. **B:** The lower jaw in lateral view. **C:** The quadrate, hyomandibula, and pterygoid in lateral view. **D:** The opercular apparatus in lateral view. ac Md, mandibular articular condyle of the quadrate; 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; af CH, articular facet of the anterior ceratohyal; af D Op, rostro-dorsal articular facet of the opercle; af Md, mandibular articular facet; Ang, angular complex; CH A, anterior ceratohyal; CH P, posterior ceratohyal; CM, Meckel's cartilage; D, dentary complex; Hm, hyomandibula; IOP, interopercle; Op, opercle; POp, preopercle; PP, pterygoid; Pr Ang, angular process; Pr cor, coronoid process; Pr D Op, rostro-dorsal process of the opercle; Q, quadrate; R Br, branchiostegal ray; SOP, subopercle; Sym, symplectic.

lar condyle of the hyomandibula. This facet is situated at the distal end of the rostradorsal process of the opercle (Fig. 2D).

The lower jaw is longer than the upper jaw (Figs. 1 and 2B). The anterior and largest part of the lower jaw is formed by the dento-splenio-mento-meckelian complex. This complex will be referred to as the dentary complex. The caudodorsal edge of this part bears the small coronoid process. The dentary complex encloses Meckel's cartilage anteriorly and covers its posterior part laterally. The posterior part of the lower jaw consists of the fusion of retroarticular, articular and angular bones, referred to as the angular complex. The angular complex is pointed anteriorly and partially enclosed by the dentary complex. The retroarticular process is short and directed caudally. The mandibular articulation facet, ventral to the angular process, involves the articulation between the angular complex and the quadrate.

The hyoid apparatus comprises an unpaired median basihyal and urohyal and paired anterior cera-

tohyals and posterior ceratohyals (Figs. 2A and 5). Hypohyals are absent, an observation that was confirmed using the serial histological sections. The basihyal is a long, cylindrical element. It articulates on both sides with the anterior ceratohyals and ventrally with the rostral tip of the urohyal. Caudally, the urohyal tapers and ends in a trifold process (in lateral view), which mediates the insertion of the sternohyoideal tendon. A total of 16–22 branchiostegal rays are supported by the anterior ceratohyal and posterior ceratohyal (Fig. 5A,C). The branchiostegal rays are dorsally curved and reach up to the caudal border of the opercle. The anterior ceratohyal occupies the largest part of the hyoid arch and anteriorly bears the articulation facet for the basihyal, urohyal, and contralateral hyoid arch.

#### Head Myology: *Heteroconger hassi*

**Adductor mandibulae complex:** This complex comprises three parts, their fibers only partially separated (Figs. 3 and 4). It is difficult to distin-

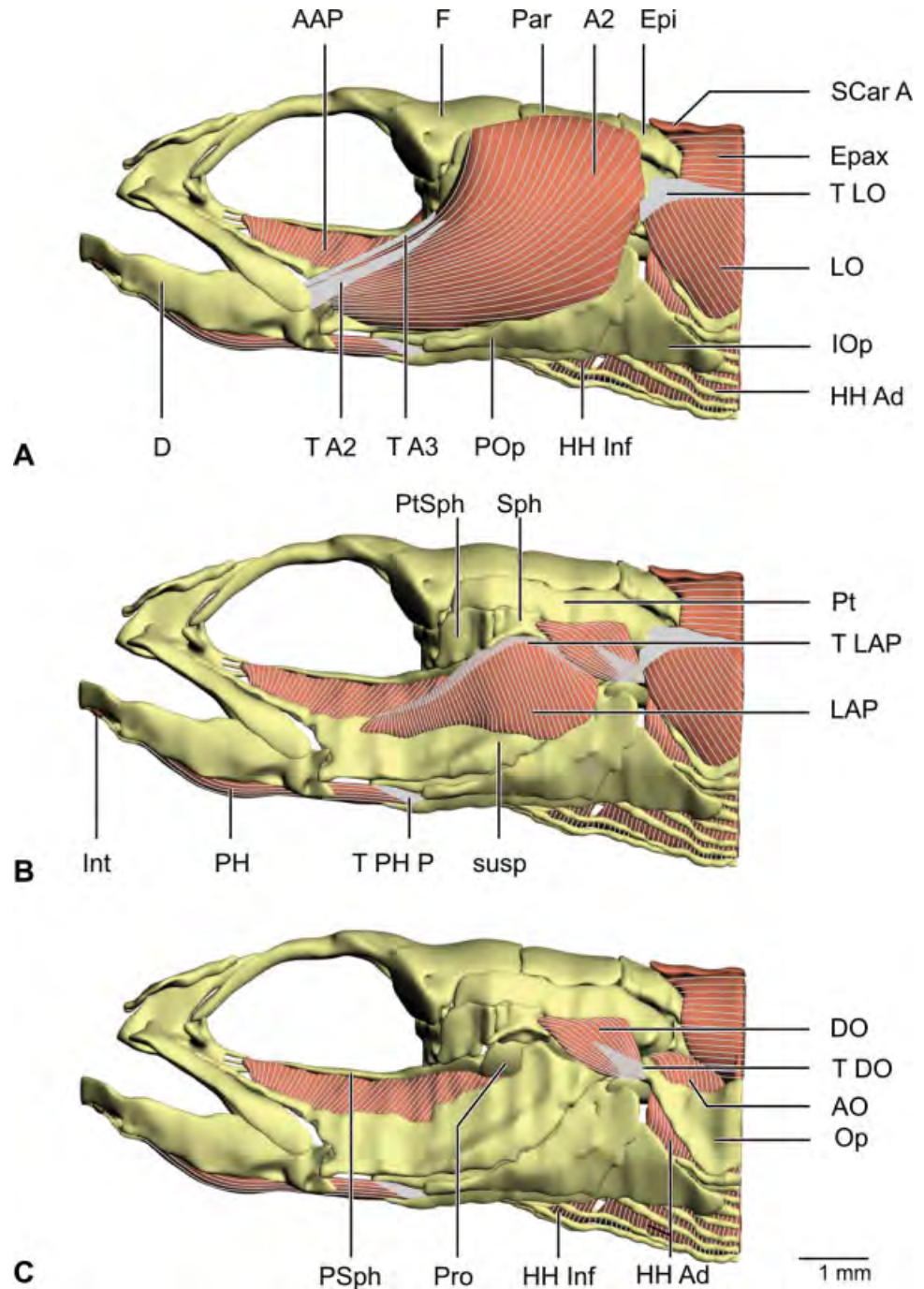


Fig. 3. 3D reconstruction of the cranial muscles of *Heteroconger hassi*. **A:** The skin is removed. **B:** The adductor mandibulae complex is removed. **C:** The levator arcus palatini and levator operculi are removed. A2, subdivision of adductor mandibulae complex; AAP, adductor arcus palatini; AO, adductor operculi; D, dentary complex; DO, dilatator operculi; Epax, epaxials; Epi, epiotic; F, frontal; HH Ad, hyohyoidei adductores; HH Inf, hyohyoideus inferior; Int, intermandibularis; IOp, interopercle; LAP, levator arcus palatini; LO, levator operculi; Op, opercle; Par, parietal; PH, protractor hyoidei; POp, preopercle; Pro, prootic; PSph, parasphenoid; Pt, pterotic; PtSph, pterosphenoid; SCar A, supracarinalis anterior; Sph, sphenotic; Susp, suspensorium; T A2, T A3, tendon of A2, A3; T DO, tendon of dilatator operculi; T LAP, tendon of levator arcus palatini; T LO, tendon of levator operculi; T PH P, posterior tendon of protractor hyoidei.

guish the different components of the complex but based on the terminology of Winterbottom (1974) the following subdivisions can be recognized: A2, A3, and A $\omega$ . The absence of a muscular or tendinous connection with the maxilla or primordial ligament suggests that the A1 is absent. The left and right halves are not connected in the midline (Fig. 9A). The A $\omega$  is present though very small. It inserts through a tendon on the medial surface of the dentary (Fig. 5A). This tendon fuses posteriorly with

the A2. The A2 is situated laterally and comprises the largest part of the complex. The A2 inserts tendinously on the dorsal edge and the lateral side of the coronoid process. It originates musculously from the lateral surface of the quadrate, frontal, pterosphenoid, sphenotic, pterotic, parietal, and epiotic (Fig. 3A). Ventrally the fibers even reach the preopercle. The fibers of A3 merge caudally with those of the A2. The A3 is the most medial part of the complex, inserting tendinously onto the medial

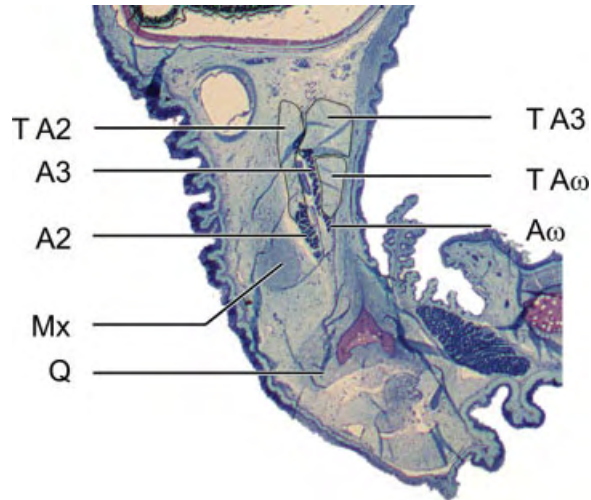


Fig. 4. Cross-section at the level of the anterior part of the adductor mandibulae complex of *Heteroconger hassi*, just behind the quadrato-mandibular articulation. The tendons of each adductor mandibulae subdivision are illustrated. A2, A3, A $\infty$ , subdivisions A2, A3, A $\infty$  of the adductor mandibulae complex; Mx maxillary; Q, quadrate; T A2, A3, A $\infty$ , tendon of subdivisions A2, A3, A $\infty$  of the adductor mandibulae complex.

surface of the dentary and originating from the lateral surface of the pterosphenoid and anterolateral surface of the sphenotic (Fig. 5A).

**Levator arcus palatine:** The apex of this muscle points dorsally and the fibers diverge ventrally (Fig. 3B). The tendinous origin includes the lateral and ventral surface of the sphenotic process. This tendon is situated internally in the (bipennate) muscle. The fibers insert muscously on the lateral surface of the pterygoid, hyomandibula, and quadrate (Fig. 5A).

**Adductor arcus palatine:** This muscle forms the floor of the orbits (Fig. 3). The fibers originate muscously from the ventral surface of prootic and ventral surface of the parasphenoid, lateral to its median ridge, which separates the left and right parts of the muscle. The muscle inserts muscously on the caudomedial surface of the pterygoid and the medial surface of the hyomandibula (Fig. 5A). The fibers are directed rostrally. The anterior margin is situated at one fourth of the length of the orbit.

**Adductor hyomandibulae:** This muscle is situated caudally to the adductor arcus palatine (Fig. 5A). The muscle tapers caudally, with its origin on the prootic. It inserts on the medial surface of the hyomandibula. Its anterior margin is situated at the level of the anterior suspensorial articulatory facet.

**Levator operculi:** The fibers of the levator operculi are directed caudoventrally (Fig. 3A). Its tendon originates from the pterotic, just behind the caudal margin of the adductor mandibulae complex. The fibers insert muscously on the lateral surface, up to its ventrolateral border, and the dorsal edge of the opercle.

**Dilatator operculi:** This muscle has a conical shape, with the apex pointing caudoventrally (Fig. 3C). The site of origin comprises the caudolateral surface of the sphenotic and the ventrolateral surface of the pterotic. Internally a tendon is present which inserts on the lateral surface of the rostradorsal process of the opercle.

**Adductor operculi:** This muscle originates muscously from the ventrolateral surface of the prootic and exoccipitals (Fig. 3C). No tendons are present. The fibers insert on the medial surface of the opercle (Fig. 5A). The insertion site varies from the surface just beneath the dorsal edge of the opercle or may extend to the middle of the opercle.

**Intermandibularis:** The intermandibularis is present (Figs. 3B and 5). This small muscle runs transversally between the medial surfaces of the left and right dentary.

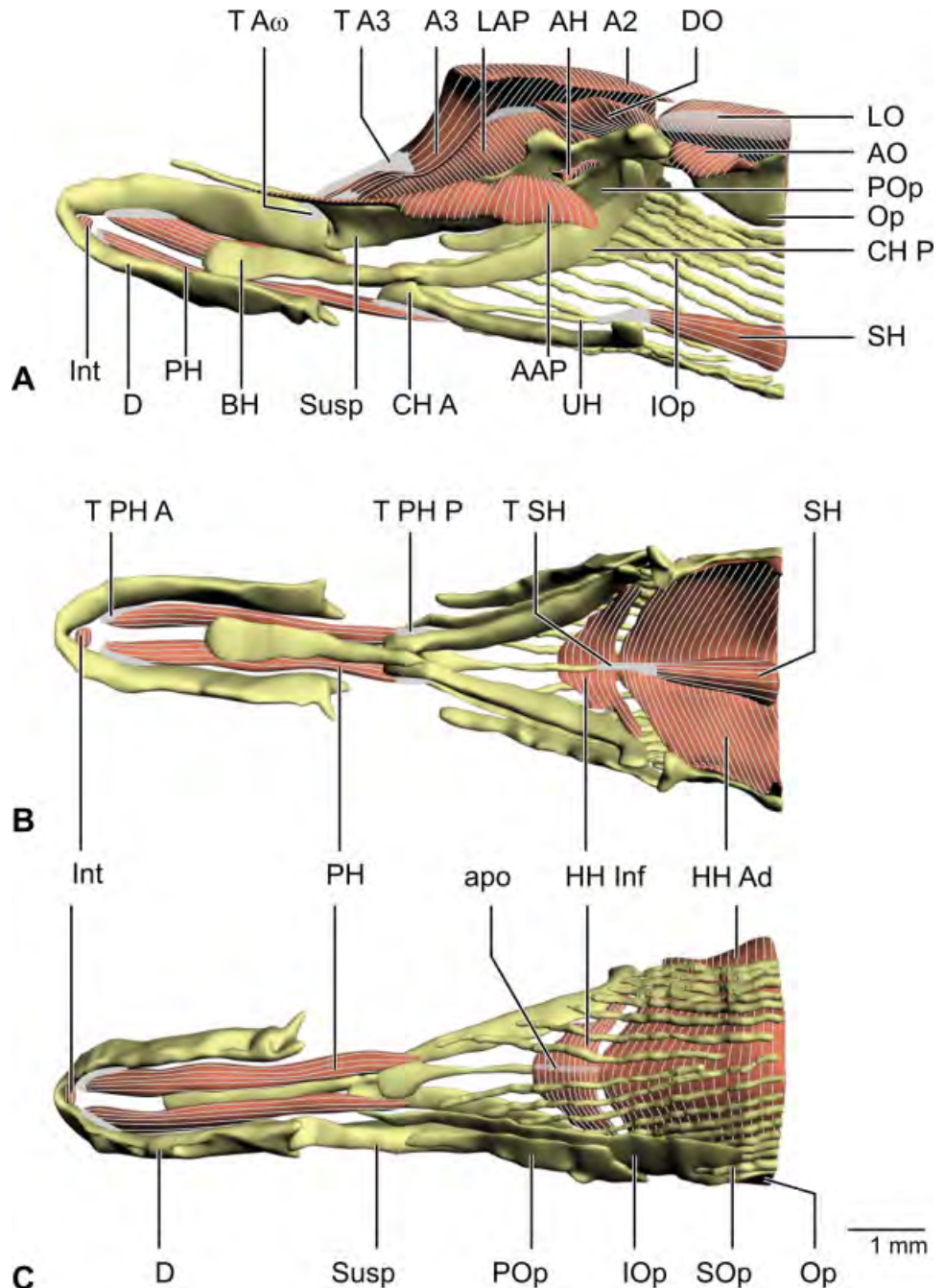
**Protractor hyoidei:** This muscle connects the lower jaw to the hyoid arch (Figs. 3 and 5). The fibers are directed rostrally. The fibers insert tendinously on the lateroventral surface of the posterior ceratohyal, and the rostroventral edge of the interopercle. The protractor hyoidei originates tendinously from the ventromedial surface of the dentary complex, just behind the dental symphysis (Fig. 5). The left and right bundles are separated over their whole length.

**Sternohyoideus:** This muscle consists of three myomeres, divided by two myocommata. The left and right, strong, well-developed tendons insert on the lateral surfaces of the caudal trifid end of the urohyal (Fig. 5A,B). The posterior fibers of the sternohyoideus are muscously attached to the lateral surface of the ventrorostral projection of the cleithrum. The fibers of the sternohyoideus merge with the hypaxial muscles ventrocaudally.

**Hyohyoideus:** This muscle complex usually comprises the hyohyoideus inferioris, hyohyoideus abductor, and hyohyoidei adductores. The hyohyoideus inferioris arises from an aponeurosis in the ventral midline (Fig. 5C). The medial fibers run to the ventral surface of the anterior ceratohyal, while the ventral fibers radiate, attaching to dorsomedial surface of branchiostegal rays. It is difficult to differentiate the hyohyoideus abductor from the hyohyoidei adductores. The hyohyoidei adductores surround the gill chamber ventrally, forming a "sac-like" muscle sheet, situated just beneath the opercular system and above the branchiostegal rays (Figs. 3 and 5B,C). This sheet attaches to the medial surface of the opercle, and more caudally, attaches to the horizontal septum (ventral to the epaxial muscles). At the level of the opercle, the sheet is interrupted by the insertion of the adductor operculi. The sheet continues ventrally, dorsal to the rays, the opposite halves meeting in the midline.

**Epaxials:** These muscles attach to the exoccipitals and supraoccipital (Fig. 3A,C). No aponeurotic

Fig. 5. 3D reconstruction of the splanchnocranium and associated muscles of *Heteroconger hassi*. **A:** The neurocranium and the suspensorium and opercular apparatus of the left side are removed to allow medial view of the muscles. Illustration of the protractor hyoideus, hyohyoideus inferioris, and hyohyoidei adductores, **B:** in dorsal view (suspensoria of both sides are removed, while the opercular apparatus of both sides are illustrated), and **C:** in ventral view (the suspensorium and opercular apparatus of the right side are removed). A2, A3, subdivisions A2, A3 of the adductor mandibulae complex; AAP, adductor arcus palatini; AH, adductor hyomandibulae; AO, adductor operculi; apo, aponeurosis; BH, basihyal; CH A, anterior ceratohyal; CH P, posterior ceratohyal; D, dentary complex; DO, dilatator operculi; HH Ad, hyohyoidei adductores; HH Inf, hyohyoideus inferior; Int, intermandibularis; IOp, interopercle; IOP, interopercle; LAP, levator arcus palatini; LO, levator operculi; Op, opercle; PH, protractor hyoidei; POp, preopercle; SH, sternohyoideus; SOp, subopercle; Susp, suspensorium; T A2, A3, A $\omega$ , tendon of subdivisions A2, A3, A $\omega$  of the adductor mandibulae complex; T PH A, anterior tendon of protractor hyoidei; T PH P, posterior tendon of protractor hyoidei; T SH, tendon of sternohyoideus; UH, urohyal.



connection between the adductor mandibulae complex and the epaxials is present.

**Hypaxials:** These muscles attach to the basioccipital and the horizontal septum.

#### Interspecific Variation in Cranial Morphology (*Heteroconger hassi* compared With *H. longissimus*)

The osteological similarities of the cranial skeleton between *Heteroconger hassi* and *H. longissimus* are striking (Fig. 6). Minor differences are found at

the level of the suspensorium. The pterygoid of *H. longissimus* is broader, compared to its slender shape in *H. hassi*. The elevated ridge on the lateral surface of the hyomandibula is present in *H. longissimus*, though it is larger in *H. hassi*.

Most of the cranial muscles show no variation in presence, insertion or origin among these two species except for the adductor mandibulae complex, the adductor hyomandibulae, and the intermandibularis (Fig. 6). The adductor mandibulae complex in both species is considerably smaller compared to several other anguilliform species (e.g., *Moringua*

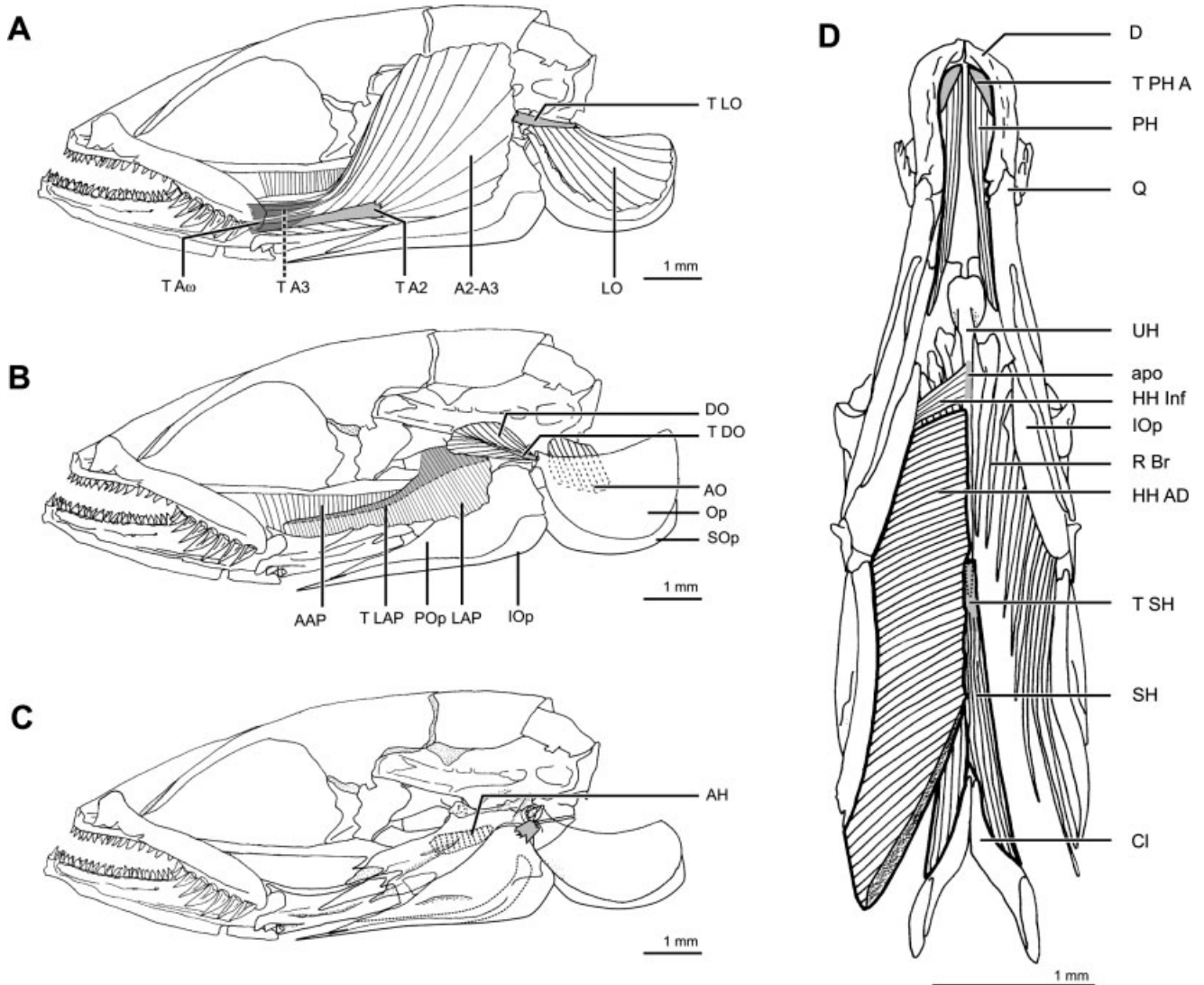


Fig. 6. **A:** Cranial muscles of *Heteroconger longissimus*. **B:** The adductor mandibulae complex and the levator operculi are removed. **C:** The levator arcus palatini, dilatator operculi, adductor operculi, and adductor arcus palatini are removed. **D:** The protractor hyoideus, hyohyoideus inferioris, and hyohyoidei adductores in ventral view. A2, A3, A $\infty$ , subdivisions A2, A3, A $\infty$  of the adductor mandibulae complex; AAP, adductor arcus palatini; AH, adductor hyomandibulae; AO, adductor operculi; Cl, cleithrum; D, dentary complex; DO, dilatator operculi; HH Ad, hyohyoidei adductores; HH Inf, hyohyoideus inferior; IOp, interopercle; LAP, levator arcus palatini; LO, levator operculi; Op, opercle; PH, protractor hyoidei; POP, preopercle; Q, quadrate; R Br, branchiostegal ray; SH, sternohyoideus; SOP, subopercle; T A2, A3, A $\infty$ , tendon of subdivisions A2, A3, A $\infty$  of the adductor mandibulae complex; T DO, tendon of dilatator operculi; T LAP, tendon of levator arcus palatini; T LO, tendon of levator operculi; T PH A, anterior tendon of protractor hyoidei; T SH, tendon of sternohyoideus; UH, urohyal.

*edwardsi*, De Schepper et al., 2005, Fig. 9C). Comparisons between both heterocongrid species reveal that the origin of the adductor mandibulae complex includes the same structure (quadrate, frontal, pterosphenoid, sphenotic, pterotic, parietal, and preopercle), though species vary in size and volume of the jaw muscles. In *H. longissimus* the origin of the jaw muscles is smaller anteriorly as well as caudally compared to that of *H. hassi*: the anterodorsal margin is restricted to a very small part of the ventrocaudal margin of the frontal; the dorsal fibers originate lower on the lateroventral surface of the

parietals; caudally no fibers reach the epiotics and a larger part of the caudal surface of the pterotic is not part of the insertion site (Figs. 3A and 6A). In cross section the jaw muscles appear as a thin sheet of fibers, so it becomes clear that the volume of the jaw muscles in *H. longissimus* are smaller (Fig. 9B). The adductor hyomandibulae shows interspecific variation as well (Fig. 9B). Its anterior margin is situated in front of the anterior suspensorial articulation condyle of the hyomandibula, while in *H. hassi* this is situated behind this articulation. The intermandibularis, which is present in *H.*



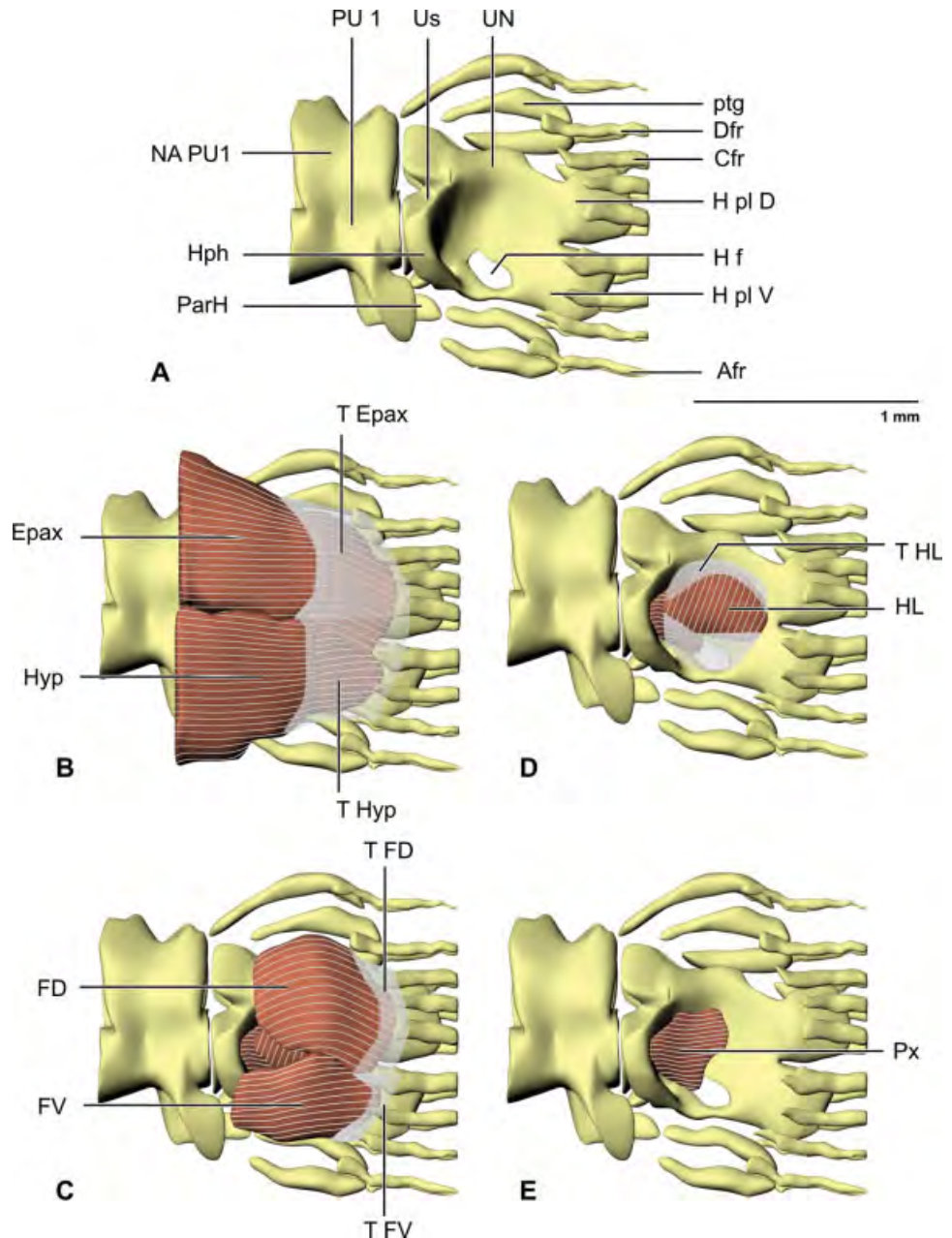


Fig. 7. 3D reconstruction of the tail of *Heteroconger hassi*. Tendons are shown in transparent gray. **A:** The caudal skeleton in lateral view. **B:** The intrinsic caudal musculature. **C:** The epaxials and hypaxials are removed. **D:** The flexor dorsalis and ventralis are removed. **E:** The hypochordal longitudinalis is removed. Cfr, caudal fin rays; D fr, dorsal caudal fin ray; Epax, epaxials; FD, flexor dorsalis; FV, flexor ventralis; H f, hypural fenestra; H pl D, dorsal hypural plate; H pl V, ventral hypural plate; HL, hypochordal longitudinalis; Hph, hypurapophysis; Hyp, hypaxials; NA PU1, neural arch of first preural centrum; ParH, parhypural; PU1, first preural centrum; Ptg, pterygiophore; Px, proximalis; T Epax, tendon of epaxials; T FD, tendon of the flexor dorsalis; T FV, tendon of the flexor ventralis; T HL, tendon of the hypochordal longitudinalis; T Hyp, tendon of hypaxials; UN, uroneural; Us, urostyle.

*hassi*, is absent in *H. longissimus*. The hyohyoideus of *H. hassi* forms a large, thick muscle mass, and occupies the ventrolateral surface of the branchial region. It comprises two parts, defined as hyohyoideus inferioris and hyohyoidei adductores. It is not clear whether the hyohyoideus abductor is fused with the hyohyoidei adductores or whether it is not yet completely differentiated, taking into account the basal phylogenetical position of the Anguilliformes. In *H. longissimus* the hyohyoideus inferioris and adductores are similar in origin and insertion sites, though the hyohyoideus inferioris is smaller in *H. longissimus* (Fig. 6D). Furthermore,

the anterior margin of the hyohyoideus inferioris is anteriorly displaced in *H. longissimus*.

#### Tail Osteology: *Heteroconger hassi*

The caudal fin is reduced (Fig. 7A). Six caudal fin rays are present, though not visible from the outside. They are covered by thick layer of soft tissue. The anal and dorsal fins are confluent with the caudal fin rays. Caudal fin rays are supported by hypurals while dorsal and anal fin rays are supported by pterygiophores. The caudal skeleton comprises a dorsal hypural plate (fused hypurals 3 and 4) and a

ventral hypural plate (fused hypurals 1 and 2). A hypural fenestra is present in the latter. The first preural vertebra is situated in front of the caudal skeleton. The boundary between preural and ural vertebrae is marked by the bifurcation point of the dorsal aorta, as could be observed in the serial sections. The parhypural, modified hemal spine of the first preural centrum, is the last hemal spine crossed by the dorsal aorta. The urostyle, formed by the fusion of the first and second ural vertebrae, bears one pair of uroneurals, as is found in all Anguilliformes (Gosline, 1971). The ventral hypural plate bears strongly developed hypurapophyses on both sides. The epural is absent. The neural canal of the first preural centrum is bordered laterally by the left and right bases of the neural arch. The neural arch is not fused in the midline. The base of the arch is as wide as the centrum. The neural spine is lacking. Neural and hemal spines are absent in the preceding caudal vertebrae. In some cases, one vertebra may bear two neural arches and two hemal arches. This may indicate the fusion of two vertebrae during development.

#### Tail Myology: *Heteroconger hassi*

Interradials are absent (Fig. 7). The flexor dorsalis originates from the lateral surface of the uroneural and inserts onto the four uppermost caudal fin rays through a tendinous sheet (Fig. 7C). The hypochordal longitudinalis originates from the lateral surface of the ventral hypural plate and passes to the lateral surface of the dorsal hypural plate (Fig. 7D). Both origin and insertion are tendinous. The flexor ventralis originates from the lateral surface of the parhypurapophysis and lateral surface of the ventral hypural plate and inserts through a tendon on the three ventral caudal fin rays (Fig. 7C). The proximalis is situated medial to the hypochordal longitudinalis (Fig. 7E). This muscle runs from the hypurapophysis to the lateral surface of the ventral and dorsal hypural plate. The body musculature, epaxials and hypaxials, is attached to the base of the caudal fin rays by broad tendinous sheets (Fig. 7B).

#### Interspecific Variation in Tail Morphology (*Heteroconger hassi* Compared With *H. longissimus*)

The skeleton and musculature of the tail of *Heteroconger hassi* and *H. longissimus* are similar. In both species the caudal skeleton is highly reduced and fortified, forming a firm pointed burrow tool. Some small differences are found in the flexor dorsalis (Fig. 8C). The anterior margin of the flexor dorsalis of *H. longissimus* is situated more anteriorly, where it reaches the anterior margin of the uroneural. The insertion site of the flexor dorsalis is restricted to the dorsal caudal fin rays in *H. longissimus* whereas in *H. hassi* its tendon additionally

inserts onto the first ventral caudal fin ray below the midline.

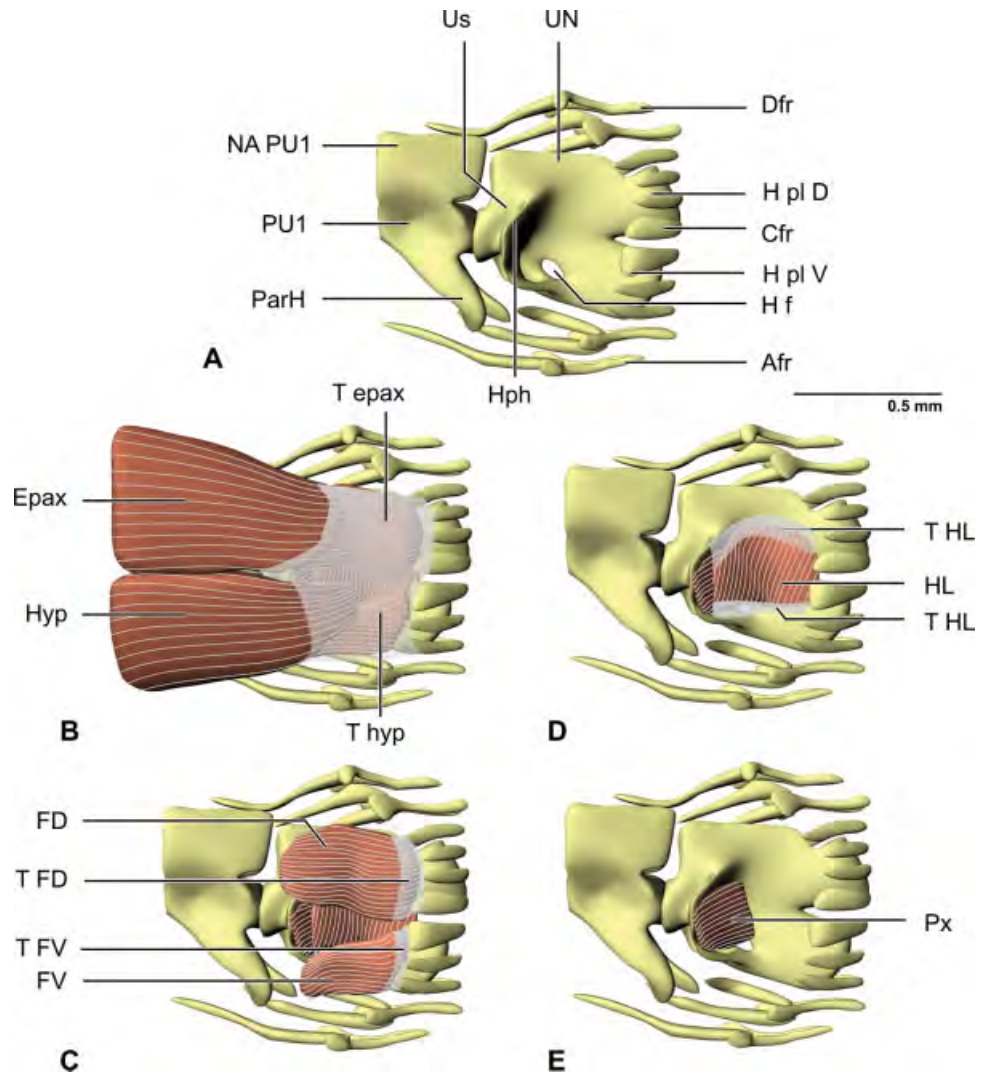
#### DISCUSSION Morphology Related to Feeding

*Heteroconger hassi* and *H. longissimus* are plankton feeders. This feeding style is reflected in the morphology of Heterocongrinae as stated by Rosenblatt (1967), Smith (1989b) and Castle and Randall (1999): one of the principal characteristics is the shortening of the snout, which brings the extremely large eyes closer to the tip, allowing close-up binocular vision. Their vision is assumed to be additionally improved by the presence of anteriorly elongated pupils (Smith, 1989b). The mouth, which is small and oblique [as in planktonic feeding serranids (e.g., *Paranthias*) and embiotocids (e.g., *Brachyistius*), is regarded as a specialization for snapping planktonic prey (Rosenblatt, 1967). The skin of the throat covering the pharyngeal cavity shows grooves and folds. Smith (1989b) stated that these folds indicate the possibility of a considerable expansion of the former, improving buccal expansions during suction feeding, necessary to catch prey from the passing current. Personal observations of feeding *H. hassi* confirm that prey capture occurs predominantly by suction as the predator's head moves slowly towards the prey item while the prey is drawn rapidly towards the mouth as the result of rapid depression of the mouth floor, thus expanding the mouth and creating suction (Liem, 1980). Prey items are ingested intact. As heterocongrines have a suction-dominated feeding mode, mainly on small, soft prey items, (Smith, 1989b), no powerful bite is required (Barel, 1983; Van Wassenbergh et al., 2005).

Consequently no hypertrophied jaw muscles are needed and no special structural reinforcements at the level of oral skeletal elements (e.g., dentary, suspensorium, and neurocranium) to resist increased mechanical loads, are required (Barel, 1983; Van Wassenbergh et al., 2005).

**Adductor mandibulae complex.** The feeding mode in *Heteroconger hassi* and *H. longissimus* is reflected in the configuration of the adductor mandibulae complex. This mouth closing muscle complex is small and the constituent subdivisions form one unit. The two halves do not meet dorsally. So, in contrast to other anguilliform species that have hypertrophied jaw muscles and which all are predators (e.g., in Anguillidae, Muraenidae, Congridae, Ophichthidae, Moringuidae, etc.), *H. hassi* and *H. longissimus* have no hypertrophied mouth-closing muscles (Böhlke et al., 1989; McCosker et al., 1989; Smith 1989a,b; De Schepper et al., 2005). Hypertrophied adductor mandibulae muscles provide a powerful bite, thus implying an increased mechanical load on skeletal elements such as dentary, suspensorium, and neurocranium (Herrel et al., 2002;

Fig. 8. 3D reconstruction of the tail of *Heteroconger longissimus*. Tendons are shown in transparent gray. **A:** The caudal skeleton in lateral view. **B:** The intrinsic caudal musculature. **C:** The epaxials and hypaxials are removed. **D:** The flexor dorsalis and ventralis are removed. **E:** The hypochordal longitudinalis is removed. Afr, anal fin ray; Cfr, caudal fin rays; Dfr, dorsal caudal fin ray; Epax, epaxials; FD, flexor dorsalis; FV, flexor ventralis; Hf, hypural fenestra; Hpl D, dorsal hypural plate; Hpl V, ventral hypural plate; HL, hypochordal longitudinalis; Hph, hypurapophysis; Hyp, hypaxials; NA PU1, neural arch of first preural centrum; ParH, parhypural; PU1, first preural centrum; Px, proximalis; T Epax, tendon of epaxials; T FD, tendon of the flexor dorsalis; T FV, tendon of the flexor ventralis; T HL, tendon of the hypochordal longitudinalis; T Hyp, tendon of hypaxials; UN, uroneural; Us, urostyle.



Van Wassenbergh et al., 2004). As aforementioned, a strong bite is not needed in *H. hassi* and *H. longissimus*. Thus, small mouth-closing muscles, without special structural reinforcements (e.g., dentary, suspensorium, and neurocranium), presumably serve their needs (Fig. 9A,B). Because 1) a predatory lifestyle represents the primitive condition of the Anguilliformes (Gosline, 1971; Smith, 1989b), 2) hypertrophied jaw muscles and thus a strong bite are advantageous for predation (Van Wassenbergh et al., 2005), and 3) hypertrophied jaw muscles are frequent in Anguilliformes (Böhlke, 1989), the question should be raised whether the presence of hypertrophied jaw muscles is the plesiomorphic condition in the Anguilliformes. This implies that the configuration of the jaw muscles of *H. hassi* and *H. longissimus* represents a derived condition. Of course such assumptions have to be tested.

**Spatial impact of large eyes.** *Heteroconger hassi* and *H. longissimus* are visual predators of small planktonic prey (Castle and Randall, 1999).

This requires the presence of well-developed, large eyes. As they burrow tail-first and retreat in burrows with a wider diameter than their body (Tyler and Smith, 1992), the eyes of *H. hassi* and *H. longissimus* need no special protection for mechanical injuries during substrate contact. This is in contrast to most head-first burrowers, which have reduced eyes (Bozzano, 2003; De Schepper et al., 2005). The size of the eyes may have a substantial impact on the spatial design of the skull (Barel, 1984). We may assume that the large eyes in *H. hassi* and *H. longissimus* are related to the smaller interorbital space of the neurocranium. Consequently, narrowing of the skull involves reduction in strength. Focusing on the sessile lifestyle of this species, a strong skull to resist external forces (e.g., during burrowing) or to resist large mechanical loads from muscle insertions (e.g., hypertrophied jaw muscles) are not required. Furthermore the large eyes limit the space for the adductor mandibulae complex and adductor arcus palatini. Ventral

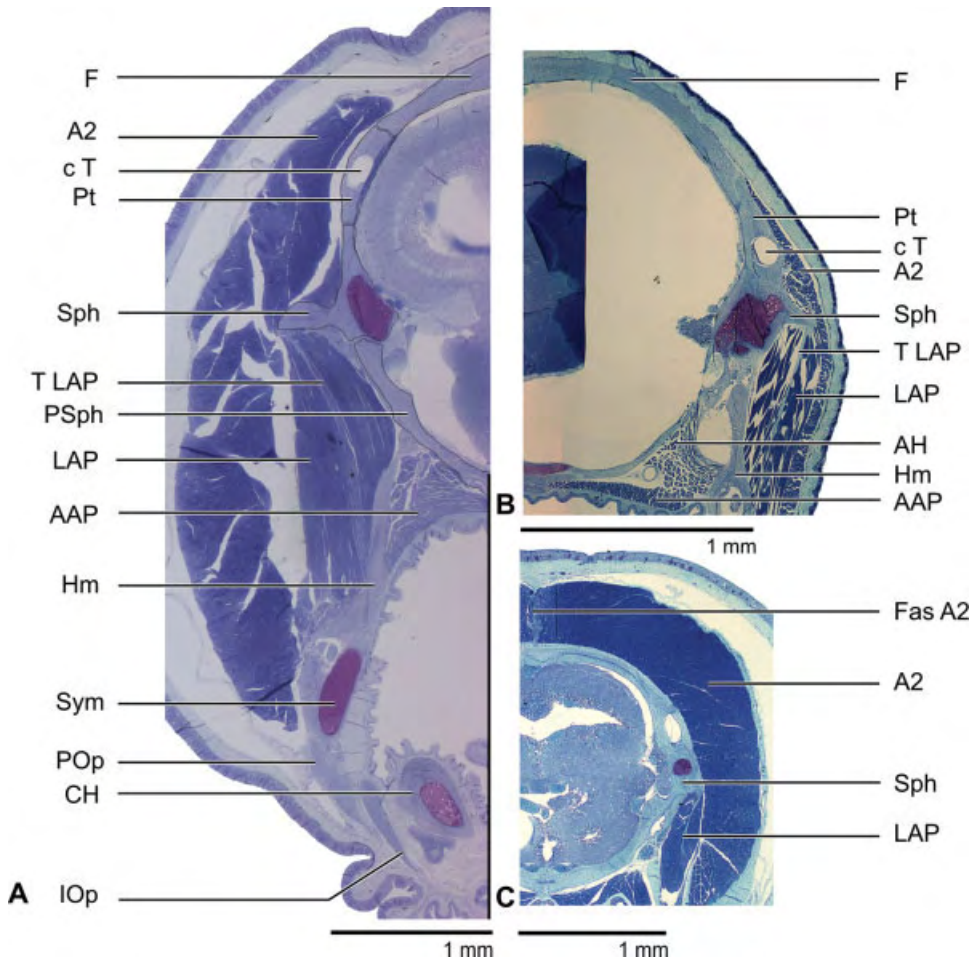


Fig. 9. Cross-section at the level of the sphenotic wing in **A:** *Heteroconger hassi*, **B:** *Heteroconger longissimus*, and **C:** *Moringua edwardsi*. Differences in hypertrophy of the adductor mandibulae complex (A2) are clearly visible. A2, subdivision of adductor mandibulae complex; AAP, adductor arcus palatini; AH, adductor hyomandibulae; C T, temporal canal; CH, ceratohyal; F, frontal; Hm, hyomandibula; I Op, interopercle; LAP, levator arcus palatini; P Op, preopercle; P Sph, parasphenoid; Pt, pterotic; Sph, sphenotic; Sym, symplectic; T LAP, tendon of levator arcus palatini.

to the eyes the adductor mandibulae appears as a compact mass that is dorsally restricted by the large eyes. Underneath the eyes the adductor arcus palatini appears as a thin muscle plate. Behind the eyes, a dorsal expansion of this muscle can be observed.

### Morphology Related to Tail-First Burrowing

Anguilliform species are primitively adapted for wedging through small openings (Gosline, 1971; Smith, 1989b). However, several anguilliform eels have evolved adaptations to a range of different lifestyles. Some are pelagic, others are adapted to burrowing lifestyles, from head-first (*Moringua*, *Neoconger*) to tail-first (Heterocongrinae, Ophichthidae). The true head-first burrowing anguilliform species (e.g., *Moringua edwardsi*) have a conical, strengthened skull (De Schepper et al., 2005). Conversely, extremely fortified skulls to resist large compressive forces during burrowing (Gans, 1975; Hanken, 1983; Duellman and Trueb, 1986; Pough et al., 1998) are unnecessary in nonburrowing or tail-first burrowing species. Since *H. hassi* and *H. longissimus* burrow tail-first, the observed reduced skull

fortification (thin, nonoverlapping bones) may be sufficient considering its sessile lifestyle.

Heterocongrinae have undergone several morphological specializations for their tail-first burrowing lifestyle: the caudal fin is reduced to a stiff fleshy point (Castle and Randall, 1999); the caudal skeleton is firm and strengthened, lacking an externally visible caudal fin; the caudal fin rays (reduced in size and number), externally invisible, are covered with muscles, connective tissue and thick skin, resulting in a pointed, burrowing tool. All this appears to provide an advantage to tail-first burrowing. Similar external tail morphology, modified to enable the excavation of burrows tail-first, is observed in ophichthid eels (Tilak and Kanji, 1969; Subramanian, 1984; Atkinson and Tayler, 1991; De Schepper et al., 2007). Considering the reduction of the caudal skeleton of *Heteroconger hassi* and *H. longissimus*, highly reduced caudal fin musculature could be expected. Furthermore, subtle movements of individual fin rays to generate propulsion or to maneuver are not needed because 1) a strong, stiff tail is needed to penetrate the substrate tail-first and 2) they rarely leave their burrows and consequently they seldom swim (Rosenblatt, 1967; Castle

and Randall, 1999). Moreover, flexible and movable fin rays might even be disadvantageous during tail-first burrowing as reduction of strength of the tail tip or damage during burrowing might occur. Thus, complex caudal fin musculature as observed in generalized teleosts (Lauder and Drucker, 2004) is no longer required.

In teleosts the caudal fin musculature generally allows a precise control of tail movements through caudal fin conformation (Lauder and Drucker, 2004). The interradians generally interconnect and adduct caudal fin rays, reducing the caudal fin area in teleosts (Winterbottom, 1974). In *Heteroconger hassi* and *H. longissimus* these muscles are completely absent. Consequently, the covered caudal fin rays are immovable, increasing strength of the tail tip. In teleosts, the flexor dorsalis usually connects the last few neural spines and centra and the upper hypurals to the dorsal caudal fin rays. The flexor ventralis usually runs from 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 in teleosts (Lauder and Drucker, 2004). In *H. hassi* and *H. longissimus* the flexor dorsalis and ventralis are reduced in size and the origin does not include the last few vertebrae, as the origin is restricted to the uroneurals and parhypurapophysis and ventral hypural plate, respectively. In teleosts, 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 (Winterbottom, 1974). It allows the dorsal fin margin to move separately from the ventral fin margin, turning them into the leading edge during swimming (Lauder and Drucker, 2004). It is surprising that in *H. hassi* and *H. longissimus* this muscle connects two immobile elements (ventral and dorsal hypural plates). Because of the absence of insertions onto caudal fin rays, contraction will not lead to the movement of rays, though it may offer strength, avoiding the tail-tip bending during burrowing. Reduction and even absence of this muscle has been observed in several species with highly reduced caudal skeletons and where fine movements of separate caudal fin rays are also less important (e.g., tuna: Lauder and Drucker, 2004). The origin and insertion of the proximalis is highly variable in teleosts though it generally connects the centra of the last few vertebrae (Winterbottom, 1974). In *H. hassi* and *H. longissimus* the proximalis muscle connects the hypurapophyse to the ventral and dorsal hypural plates. The proximalis muscle and the broad tendinous insertions of the body musculature (epaxials and hypaxials) onto the caudal fin rays may strengthen the tail to withstand bending forces during tail-first burrowing. Reduction or even loss of the proximalis and reduction of

the insertion sites of the epaxials and hypaxials has already been observed in species where sophisticated movements of individual fin rays are no longer required (Winterbottom, 1974; Lauder and Drucker, 2004). In teleosts, the supracarinalis posterior generally connects the last basal pterygiophore of the dorsal fin to the neural spine, epurals, uroneurals or dorsal caudal fin rays, while 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 *H. hassi* and *H. longissimus*, which is likely related to the fact that the dorsal, anal, and caudal fins are confluent.

The tail musculature of the tail-first burrowing ophichthid *Pisodonophis boro* (De Schepper et al., 2007), shows reductions as well, though to a lesser degree compared to *Heteroconger hassi* and *H. longissimus*. This may be related to differences in lifestyle. Ophichthids show a more active lifestyle as they spend more time in the water column, do not remain in a permanent burrow (unlike heterocongrines) and burrow head-first as well as tail-first (McCosker et al., 1989; De Schepper et al., 2007). *Heteroconger hassi* and *H. longissimus* as well as *P. boro* lack interradians. The highly consolidated caudal fin skeleton in both species is presumably strong enough to fortify the tail during tail-first burrowing so that the caudal fin musculature can be reduced.

## ACKNOWLEDGMENTS

Authors thank the National Museum of Natural History-Smithsonian Institution (Washington) for the loan of specimens.

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