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Phylogenetic relationships of the suborder Notacanthoidei (Teleostei: Albuliformes) reassessed from osteological characters, with a proposed new classification

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Abstract

The phylogenetic relationships of Notacanthoidei were reassessed on the basis of osteological characters and the classification of the suborder reconstructed on the basis of inferred relationships. The monophyly of the suborder is supported by two synapomorphies commonly recognized in all included genera. The phylogenetic analysis also revealed support for the suborder by five synapomorphies characterized by reversals or character transformations. In addition, notacanthoids share five apomorphies, present also in Anguilliformes, which may prove to be valid synapomorphies for the former. A phylogenetic analysis based on characters in 30 transformation series resulted in a single most parsimonious tree, which indicated that *Aldrovandia* branched off initially from other notacanthoids, followed by *Lipogenys*, and *Polyacanthonotus* and *Notacanthus*, which share a sister relationship with each other. Based on the reconstructed relationships, Notacanthoidei is classified into two families, Halosauridae and Notacanthidae, the latter being separated into subfamilies Lipogenyinae and Notacanthinae. Such a classification of Notacanthoidei, recognizing Lipogenyinae as a subfamily of Notacanthidae, has not been previously proposed.

Key words: Osteology, Phylogenetic relationships, Notacanthoidei, New classification

Introduction

The suborder Notacanthoidei (sensu Nelson, 2006), including six genera and 25 species, inhabits deep oceanic waters worldwide (Nelson, 2006). It is characterized by an eel-like body, the snout projecting conspicuously beyond the mouth, large connective tissue nodules inserted between the pterygoid arch and maxilla, and pelvic fin webs joined in the ventral midline (McDowell, 1973; Nelson, 2006; Wiley and Johnson, 2010).

The systematics of Notacanthoidei has been studied by many ichthyologists (e.g., McDowell, 1973; Greenwood, 1977; Forey et al., 1996; Nelson, 2006; Wiley and Johnson, 2010), three major classifications having been suggested. McDowell (1973) divided the suborder into three families, Halosauridae, Lipogenyidae and Notacanthidae, with Greenwood (1977) later recognizing Halosauridae and Notacanthidae, the latter including two subfamilies (Polyacanthonotinae including *Lipogenys* and *Polyacanthonotus*, and Notacanthinae including *Notacanthus*). This was followed by Forey et al. (1996), who evaluated the interrelation-

ships of elopomorphs, including Notacanthoidei, based on cladistic methodology utilizing both morphological and molecular data. In contrast, Nelson (2006) recognized only Halosauridae and Notacanthidae, without any subfamilial division. Accordingly, the status of Lipogenyidae, and the subfamilies of Notacanthidae have remained problematic, any subsequent classification of Notacanthidae at the subfamilial level needing to consider all three genera (*Lipogenys*, *Polyacanthonotus* and *Notacanthus*) previously included in the family. In addition, the phylogenetic position of *Lipogenys* is vital to any revision of the validity of Lipogenyidae. Although Forey et al. (1996) inferred the phylogenetic relationships of the suborder, *Lipogenys* was not included in that study. To date, no further hypotheses regarding the phylogenetic relationships of Notacanthoidei have been proposed.

The goals of this study were: (1) to describe the osteological morphology of notacanthoids, including *Lipogenys*, thereby providing a basis for a reassessment of their phylogenetic relationships; and (2) to reconstruct the classification of Notacanthoidei at the generic level on the basis of the proposed relationships.

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Materials and Methods

Specimens were dissected after staining with Alizarin Red-S and Alcian Blue, and observed under a binocular microscope with a camera lucida. Terminology follows Forey (1973), Greenwood (1977) and Rojo (1991). The measurement of gnathoproctal length (GL) follows McDowell (1973), and those of standard length (SL) and total length (TL), Hubbs and Lagler (1958). Damage to some of the specimens examined precluded detailed descriptions of some posterior body characters, including those of the caudal fin. Accordingly, caudal fin characters were excluded from the description and phylogenetic analysis. The specimens examined are deposited at the Hokkaido University Museum, Hakodate (HUMZ) and Division of Fisheries Sciences, Faculty of Agriculture, Miyazaki University (MUFS).

The cladistic approach formulated by Hennig (1966) was adopted to estimate the phylogenetic relationships of Notacanthoidei. Outgroup comparisons were used to determine character polarity (Watrous and Wheeler, 1981; Wiley, 1981). Data were analyzed by PAUP*4.0b10 (Swofford, 2002) with ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) optimizations, and the exhaustive search option. Character evolution was assumed as “ordered” with Wagner parsimony (Farris, 1970), or “unordered” with Fitch parsimony (Fitch, 1971), when the order of multistate characters could not be determined due to their complex variations. Autapomorphic characters found only in terminal taxa among ingroups and outgroups, thereby having no effect on the phylogenetic analysis, were excluded from consideration. Character evolution indicated on cladograms was estimated by MacClade ver. 4.0 (Maddison and Maddison, 2000), which was also used for the construction of a character matrix for the phylogenetic analysis.

The megalopid *Megalops* and albulid *Pterothrissus* were selected as outgroups in this study, Inoue et al. (2004) having inferred that *Megalops* represented an early branch from other elopomorphs and that *Pterothrissus* was closely related to Notacanthoidei.

Material examined. Ingroups. Halosauridae: *Aldrovandia affinis*, HUMZ 141891 (145 mm GL, TL unknwn). Lipogenyidae: *Lipogenys gillii*, HUMZ 163759 (89.9 mm GL, TL unknown). Notacanthidae: *Polyacanthonotus challengerii*, HUMZ 196369 (144 mm GL, 413 mm TL); *Polyacanthonotus rissoanus*, HUMZ 126505 (129 mm GL, 405 mm TL); *Notacanthus chemnitzii*, HUMZ 208582 (121 mm GL, 301 mm TL), HUMZ 206822 (129 mm GL, 362 mm TL, circumorbital bones and lower jaw examined); *Notacanthus spinosus*, HUMZ 169980 (88.6 mm GL, 234 mm TL).

Outgroups. Megalopidae: *Megalops cyprinoides*, MUFS 30949 (146 mm SL). Albulidae: *Pterothrissus gissu*, HUMZ 208752 (176 mm SL).

Monophyly of Notacanthoidei

The monophyly of Notacanthoidei has been evaluated in several studies (e.g., Forey et al. 1996; Inoue et al. 2004). Forey et al. (1996) suggested such monophyly to be supported by three synapomorphies: large connective tissue nodule inserted between pterygoid arch and maxilla; maxilla with posteriorly directed spine; and pelvic fin webs joined in ventral midline. Although the first and third synapomorphies were recognized in all of the notacanthoid species examined in the present study, the second (maxilla with posteriorly directed spine) was not regarded as a valid synapomorphy of the suborder (see Remarks under section Jaws). Of the two valid synapomorphies, a variation was apparent in the number of connective tissue nodules in notacanthids (two in *Aldrovandia*, one in others), and was therefore used in the phylogenetic analysis (see TS 11 under “Characters available for phylogenetic analysis”). An additional character, presence of cartilage D (defined in this study; see description under section Cranium), which has not been reported in other elopomorphs (including *Megalops* and *Pterothrissus* examined here), was commonly found in notacanthoids and recognized here as an additional synapomorphy of the suborder.

In Forey et al.’s (1996) reconstruction of the phylogenetic relationships of elopomorph fishes, the monophyly of the orders Albuliformes (Halosauridae and Notacanthidae examined) and Anguilliformes (Anguillidae, Ophichthidae and Saccopharyngidae) was supported by 20 characters. Of those, one (their character 6-1) and 11 (characters 37-0, 39-1, 40-0, 42-1, 43-1, 44-1, 45-1, 46-0, 47-0, 48-1 and 49-1) characters were associated with the epaxial musculature and caudal fin, respectively, and could not be evaluated in the present study. Of the remaining eight synapomorphies, character 26-0 (uncinate process on second epibranchial absent) was contradicted in *Lipogenys*, having two uncinate processes on the second epibranchial (present study), and characters 27-0 (uncinate process on third epibranchial absent) and 31-1 (pectoral girdle free from cranium) contradicted in *Aldrovandia* (one uncinate process on third epibranchial and pectoral girdle attached to cranium—present study). Characters 2-1 (parasphenoid with dorsal process meeting pterosphenoid), 3-0 (orbitosphenoid absent), 9-0 (intercalar absent), 30-0 (postcleithra absent) and 32-0 (mesocoracoid absent) were commonly recognized in all presently examined ingroups, although absent in the two outgroups used here. Although the latter five apomorphic characters are also found in anguilliforms, according to Forey et al. (1996), they may support the monophyly of Notacanthoidei.

In addition to the above morphological evidence, Inoue et al. (2004) recently reported the monophyly of Notacanthoidei based on molecular phylogeny. Such monophyly of Notacanthoidei is also supported by the present study.

Osteological description

Circumorbital bones (Fig. 1). The circumorbital bones comprise the infraorbitals, antorbital and rostral ossicles, having a tubular structure supporting the sensory canal, which is continuous with that posterodorsally on the cranium. The identities of some anterior elements (infraorbital or rostral ossicle) were unclear in *Lipogenys*, *Polyacanthonotus* and *Notacanthus*, each circumorbital bone, except the antorbital, being similarly shaped. They are tentatively described here as “infraorbitals”. The supraorbital and dermosphenotic are absent.

The infraorbitals include seven elements in *Aldrovandia*, 11 in *Notacanthus spinosus*, 12 in *Lipogenys*, 15 in *Polyacanthonotus challengerii*, and 13 in *P. rissoanus* and *N. chemnitzii*. In *Aldrovandia*, the first to fifth are large and ossified, being rolled laterally to form an incomplete tube; the first infraorbital has a projection on the anterior margin; the sensory canals of the sixth and seventh are separated from that formed by the anterior five elements. All infraorbitals are small and tube-like, and continuous with each other in the other three genera.

The antorbital is thin and enlarged anteriorly in *Aldrovandia*, but is elongate and trench-like in *Polyacanthonotus* and *Notacanthus*. A distinct antorbital is absent in *Lipogenys*.

The rostral ossicles include four small sickle-like elements in *Aldrovandia*.

Cranium (Figs. 2-5). The cranium is composed of the

unpaired ethmoid, dermethmoid, vomer, parasphenoid, supraoccipital, basioccipital, ethmoid cartilage and four unidentified cartilages, and paired nasal, frontal, pterosphenoid, parasphenoid, parietal, pterotic, sphenotic, prootic, epiotic and exoccipital. The posterior portion of the cranium includes a cartilaginous mass. The lateral ethmoid, orbitsphenoid, basisphenoid and intercalar are commonly absent.

The nasal, a thin fragile bone, supports the sensory canal, which is continuous with that on the infraorbital anteriorly and frontal posteriorly. The bone is large and rolled dorso-laterally to form an incomplete tubular structure in *Aldrovandia*, moderate and trench-like in *Lipogenys* and *Notacanthus*, and moderate, trench-like and enlarged posteriorly in *Polyacanthonotus*. The bone is attached posteroventrally to the olfactory rosette via connective tissue.

The ethmoid is situated on the anteriormost part of the cranium in *Aldrovandia*, but is absent in the other genera. The bone is depressed, with a spine-like anterior process and a hook-like, upwardly curved ventral process. Two tubular structures occupy the middle portion. The ethmoid is connected to the posterior process of the maxilla via a lateral ligament and to the premaxilla via a ventral ligament from the ventral process.

The dermethmoid is slightly compressed anteriorly in *Aldrovandia* and situated posterior to the ethmoid, compared with deeply compressed and situated on the anteriormost part of the cranium in the other genera. The bone has upper and lower anterolateral processes in *Aldrovandia*, and a postero-

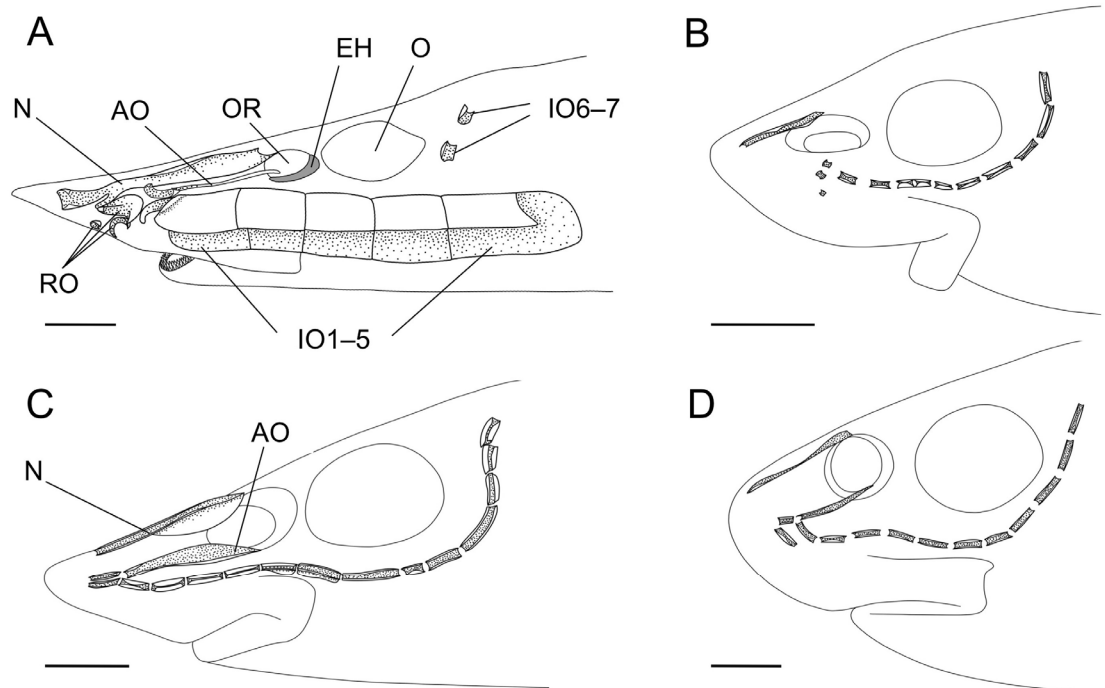


Fig. 1. Lateral aspects of the circumorbital bones and nasal in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengerii* (C) and *Notacanthus chemnitzii* (D). AO, antorbital; EH, ethmoid cartilage; IO, infraorbital; O, orbit; OR, olfactory rosette; RO, rostral ossicle; N, nasal. Scales indicate 5 mm.

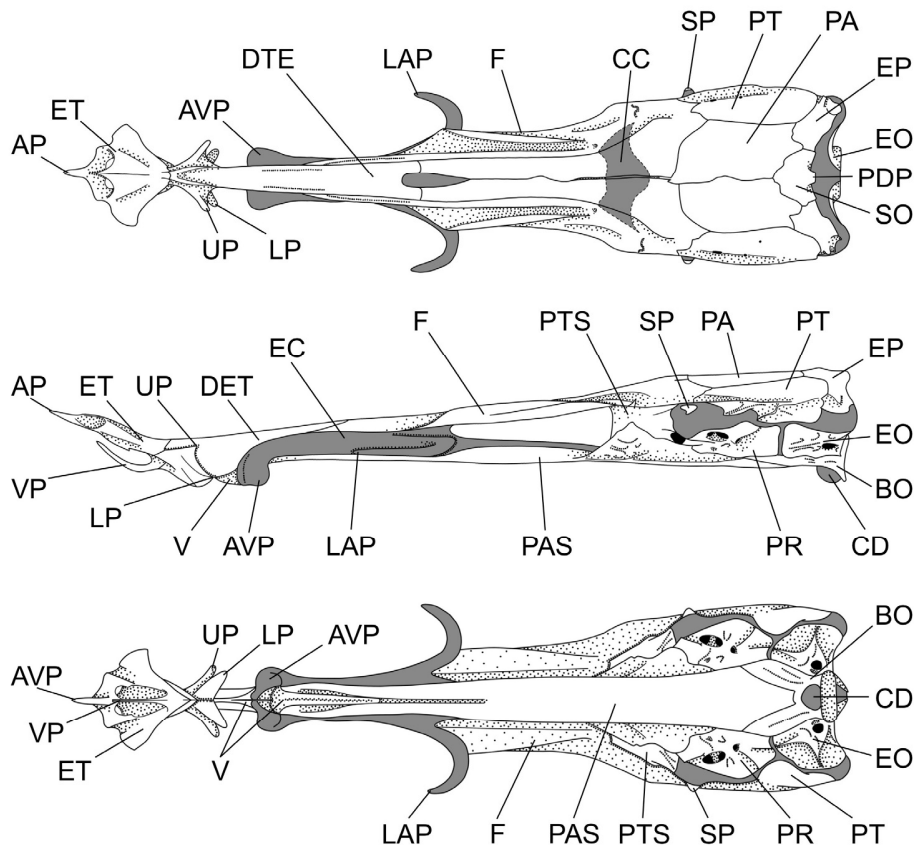


Fig. 2. Dorsal (upper), lateral (middle) and ventral (lower) aspects of the cranium in *Aldrovandia affinis*. AP, anterior process; AVP, anteroventral process; BO, basioccipital; CC, cartilage C; CD, cartilage D; DET, dermethmoid; EC, ethmoid cartilage; EO, exoccipital; EP, epiotic; ET, ethmoid; F, frontal; LAP, lateral process; LP, lower process; PA, parietal; PAS, parasphenoid; PDP, posterodorsal process; PR, prootic; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital; SP, sphenotic; UP, upper process; V, vomer; VP, ventral process. Scales indicate 5 mm.

ventral process for articulation with the ascending process of the premaxilla in *Notacanthus*. Such processes are absent in the other two genera. The anterior margin of the dermethmoid has a shallow notch in *Lipogenys* (deep in *Polyacanthonotus* and absent in the other two genera). Two foramina occur, anteriorly and posteriorly, in *Notacanthus*, being terminal openings to a canal. The bone forms a suture with the frontal and is firmly attached to the ethmoid cartilage. It is also sutured to the vomer and ethmoid in *Aldrovandia*, and to the vomer and parasphenoid, in addition to its attachment to an unidentified cartilage (defined here as “cartilage A”), in *Lipogenys*. The upper process is connected to the premaxilla and maxilla via a ligament in *Aldrovandia*, and to the latter and the connective tissue nodule via a lateral ligament in the other genera. The dermethmoid is attached laterally to an upper connective tissue nodule in *Aldrovandia* and a single connective tissue nodule in *Polyacanthonotus*, but separated from such tissue nodules in the other two genera.

The vomer is long and flat in *Aldrovandia*, long and deeply compressed in *Lipogenys*, moderately long and flat in *Polyacanthonotus*, extremely short and flat in *Notacanthus chem-*

nitzi and absent in *N. spinosus*. The bone was sutured to the parasphenoid in all of the notacanthoids examined, and also to the dermethmoid in *Aldrovandia* and *Lipogenys*. It was firmly attached to the ethmoid cartilage in *Aldrovandia* and *Polyacanthonotus* and to an unidentified cartilage (defined here as “cartilage B”) in *Notacanthus*, and was continuous with cartilage A in *Lipogenys*.

The frontal, rectangular in *Aldrovandia* and triangular in the other genera examined, has a tubular structure, continuous with those on the nasal anteriorly and pterotic posteriorly, which dorsally supports the sensory canal. It forms the anterior portion of a large unossified space in the skull roof in *Lipogenys*, *Polyacanthonotus* and *Notacanthus*. However, the skull roof is completely ossified in *Aldrovandia*. The frontal is sutured to the dermethmoid, pterosphenoid, parietal and pterotic, and is firmly attached to the ethmoid cartilage anteroventrally and an unidentified cartilage (defined here as “cartilage C”) posteroventrally.

The pterosphenoid is small in *Lipogenys* and moderately sized in the other genera. It is associated with the parasphenoid and prootic to form a large foramen posteroventrally in

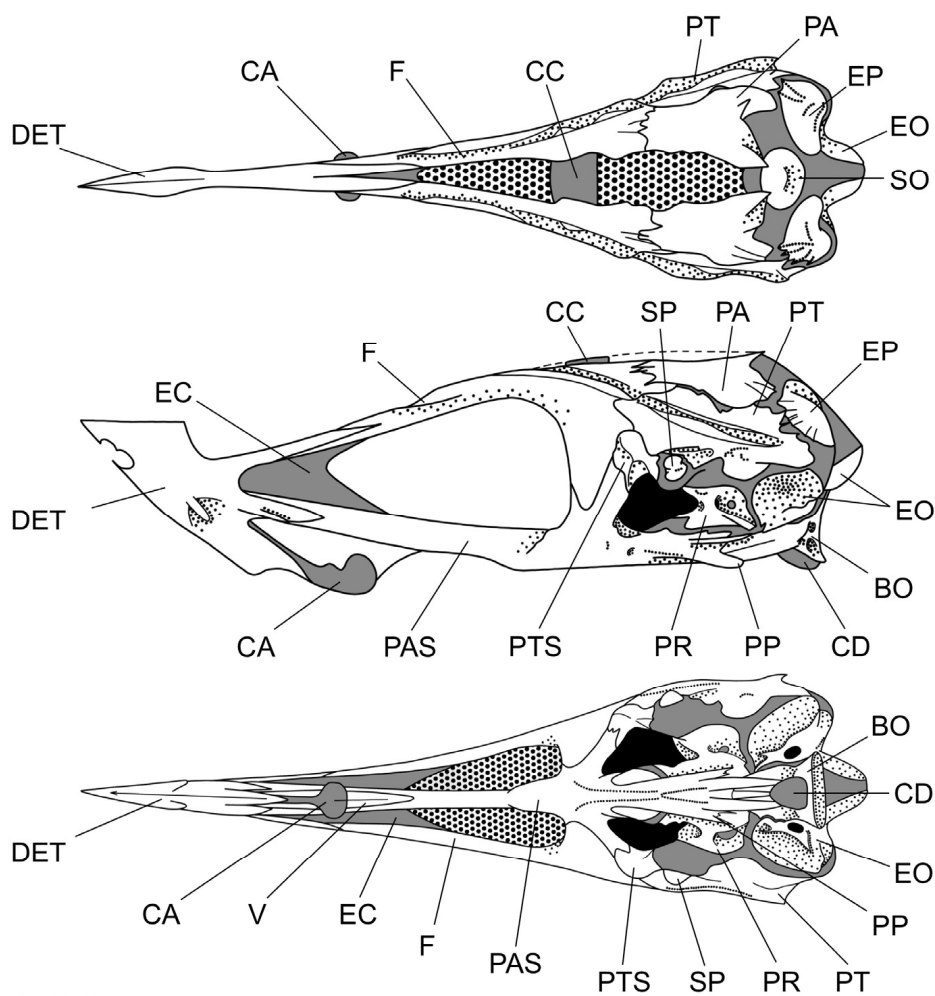


Fig. 3. Dorsal (upper), lateral (middle) and ventral (lower) aspects of the cranium in *Lipogenys gillii*. BO, basioccipital; CA, cartilage A; CC, cartilage C; CD, cartilage D; DET, dermethmoid; EC, ethmoid cartilage; EO, exoccipital; EP, epiotic; F, frontal; PA, parietal; PAS, parasphenoid; PP, posterior process; PR, prootic; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital; SP, sphenotic; V, vomer. Scales indicate 5 mm.

Aldrovandia and ventrally in *Lipogenys*, respectively, and with the parasphenoid forming a foramen ventrally in the other two genera. The bone was sutured to the frontal and parasphenoid in all genera examined, and to the pterotic in *Lipogenys*, *Polyacanthonotus* and *Notacanthus*.

The parasphenoid is an extremely long bone, with a pair of posterior processes in *Lipogenys*, *Polyacanthonotus* and *Notacanthus* (absent in *Aldrovandia*). The process is short in *Lipogenys*, long in *Polyacanthonotus* and *Notacanthus*. The parasphenoid forms a posterodorsal foramen with the pterosphenoid and prootic in *Aldrovandia*, *Lipogenys* and *Polyacanthonotus rissouanus*, and with the pterosphenoid only in *P. challengerii* and *Notacanthus*, being sutured to the vomer, pterosphenoid and basioccipital, and firmly attached to the ethmoid cartilage. It is also sutured to the dermethmoid and frontal in *Lipogenys*, and to the prootic in the other genera. It is continuous with cartilage A in *Lipogenys* and firmly attached to cartilage B in *Notacanthus*.

The parietal is sutured to the frontal, pterotic, epiotic (separated in *Lipogenys*) and supraoccipital. It is attached to its antimere in *Aldrovandia*, but separated from the latter by an intervention of the posterior portion of the large unossified space on the dorsal skull roof in the other genera.

The pterotic, which laterally has a tubular structure supporting the sensory canal, continuous with that on the frontal, forms an articular socket with the sphenotic and prootic for insertion of the dorsal head of the hyomandibula. The former is also sutured to the frontal, parietal and epiotic in all genera, with the pterosphenoid in *Lipogenys*, and with the pterosphenoid and exoccipital in *Polyacanthonotus* and *Notacanthus*.

The sphenotic is a small bone, forming an articular socket with the pterotic and prootic for insertion of the dorsal head of the hyomandibula. It is free from other bones, being attached by cartilage.

The prootic forms an articular socket with the pterotic and

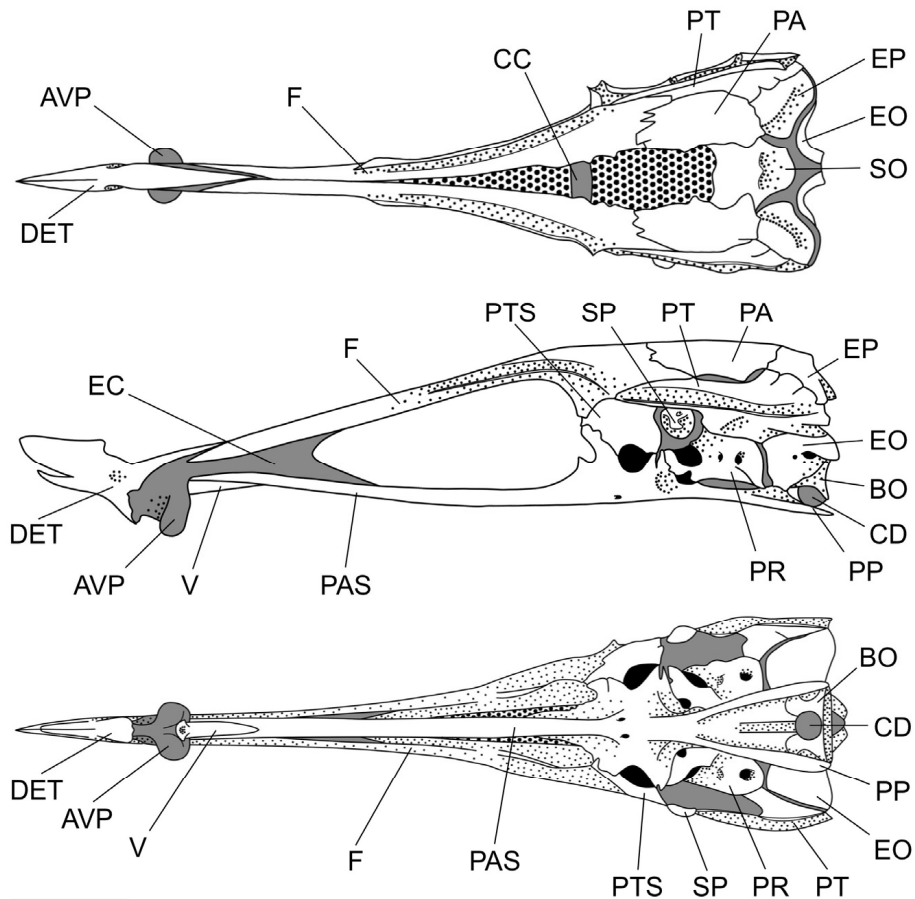


Fig. 4. Dorsal (upper), lateral (middle) and ventral (lower) aspects of the cranium in *Polyacanthonotus challengeri*. AVP, anteroventral process; BO, basioccipital; CC, cartilage C; CD, cartilage D; DET, dermethmoid; EC, ethmoid cartilage; EO, exoccipital; EP, epiotic; F, frontal; PA, parietal; PAS, parasphenoid; PP, posterior process; PR, prootic; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital; SP, sphenotic; V, vomer. Scales indicate 5 mm.

sphenotic for insertion of the dorsal head of the hyomandibula. Anteriorly, it forms a large foramen with the pterosphenoid and parasphenoid in *Aldrovandia* and *Lipogenys*, and surrounds a second large foramen in the other two genera. The prootic is sutured to the parasphenoid in *Aldrovandia*, *Polyacanthonotus* and *Notacanthus*, to the pterotic in *Polyacanthonotus*, and to the basioccipital in *Aldrovandia* and *Notacanthus*, but is separated from other bones in *Lipogenys*.

The supraoccipital has an extremely small posterodorsal process in *Aldrovandia*, but lacks such a process in the other genera. It is sutured to the parietal in all genera, but is also attached to the epiotic in *Aldrovandia*.

The epiotic is generally sutured to the pterotic and parietal, but is also sutured to the supraoccipital in *Aldrovandia*.

The exoccipital forms a large posteromedial foramen for the spinal cord and is sutured to the basioccipital.

The basioccipital has a glenoid cavity for posterior articulation with the first centrum. It is sutured to the parasphenoid and exoccipital, and also to the prootic in *Aldrovandia* and *Notacanthus*. Ventrally, it is firmly attached to an unidentified cartilage (defined here as "cartilage D").

The ethmoid cartilage has a pair of knob-like anteroventral processes, restricted to *Aldrovandia* and *Polyacanthonotus*, and a pair of lateral, hook-like, anteriorly curved processes in *Aldrovandia*. Each anteroventral process is laterally inserted into a space formed on the anterior portion of the upper jaw, autopalatine and two connective tissue nodules in *Aldrovandia*, whereas it articulates with a cup-like process on the premaxilla and is attached anteriorly to the ascending process of the latter in *Polyacanthonotus*. The lateral process supports the olfactory rosette medially, being firmly attached distally to the dermethmoid, frontal and parasphenoid. It is also attached to the vomer in *Aldrovandia* and *Polyacanthonotus*, and to the vomer and cartilage B in *Notacanthus*.

Cartilage A is situated ventral to the vomer in *Lipogenys*, being continuous with the dermethmoid and vomer, but is absent in the other genera. The cartilage has a pair of knob-like posteroventral processes for articulation anteriorly with a horizontal ridge of the premaxilla, and attachment posteriorly with the connective tissue nodule.

Cartilage B is situated anterior to the parasphenoid in *Notacanthus* and *Polyacanthonotus rissoanus*, but is absent in the

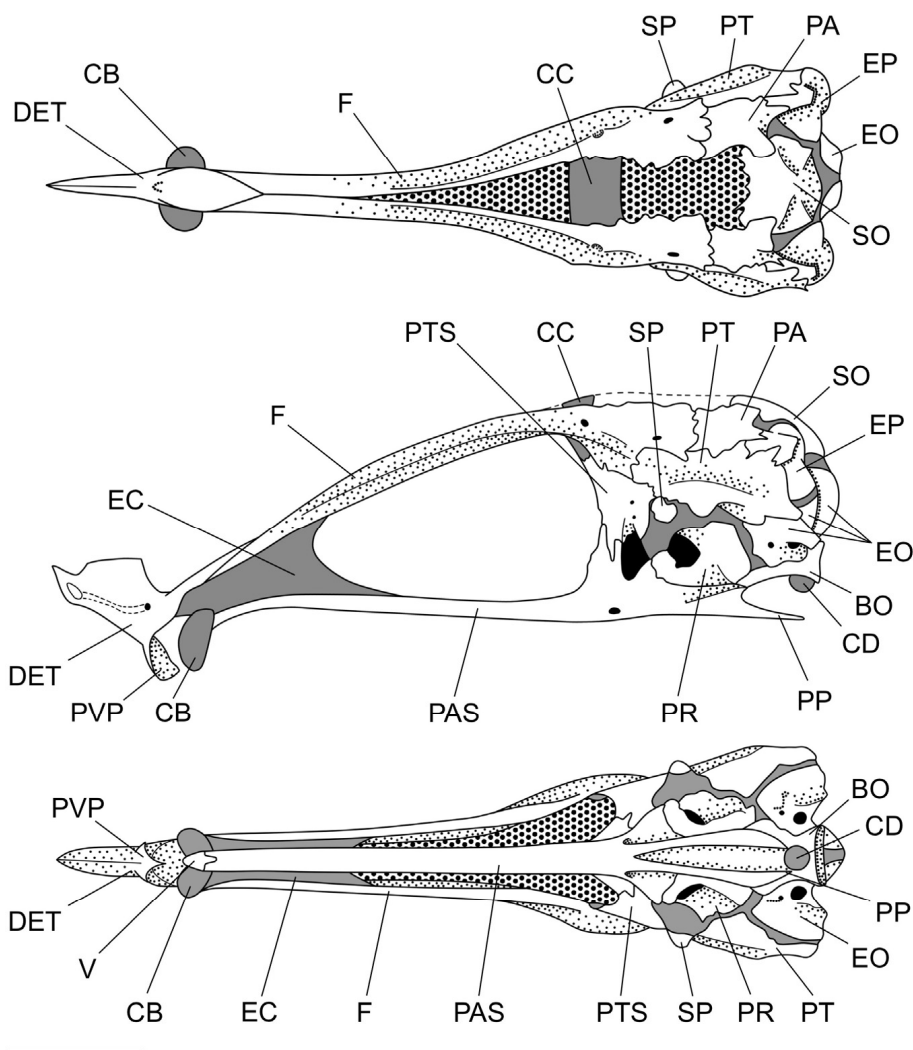


Fig. 5. Dorsal (upper), lateral (middle) and ventral (lower) aspects of the cranium in *Notacanthus chemnitzii*. BO, basioccipital; CB, cartilage B; CC, cartilage C; CD, cartilage D; DET, dermethmoid; EC, ethmoid cartilage; EO, exoccipital; EP, epiotic; F, frontal; PA, parietal; PAS, parasphenoid; PP, posterior process; PR, prootic; PT, pterotic; PTS, pterosphenoid; PVP, posteroventral process; SO, supraoccipital; SP, sphenotic; V, vomer. Scales indicate 5 mm.

other genera. An autogenous element, it is firmly attached to the vomer, parasphenoid and ethmoid cartilage, and has a pair of knob-like ventrolateral processes articulating with the ascending process of the premaxilla.

Cartilage C was flat and firmly attached posteriorly to the frontals on both sides in the notacanthoids examined, except in *Polyacanthonotus rissoanus* (absent).

Cartilage D is ball-like and firmly attached to the ventral surface of the basioccipital, in addition to the parasphenoid in *Lipogenys*, *Polyacanthonotus* and *Notacanthus*. A long ligament from this cartilage passed along the ventral surface of many centra.

Remarks. — Cartilages A and B were recognized only in *Lipogenys*, and *Notacanthus* and *Polyacanthonotus rissoanus*, respectively. Although differing, the former being continuous with the dermethmoid and vomer, and the latter autogenous, they may have both been derived from the eth-

moid cartilage, thereby being homologous, since their positions, configuration and function are similar. Because ontogenetic examination is needed to verify this hypothesis, characters associated with cartilages A and B have been excluded from the phylogenetic analysis.

Jaws (Figs. 6-7). The upper jaw comprises the premaxilla, maxilla and supramaxilla, and the lower jaw, the dentary, angular, retroarticular, coronomeckelian and Meckelian cartilage.

The premaxilla is semi-elliptical, becoming narrower posteriorly, with several small concavities laterally, in *Aldrovandia*. It is incurved and square, medially with a horizontal ridge articulating with cartilage A in *Lipogenys*. It is L-shaped and bears an ascending process in *Polyacanthonotus* and *Notacanthus*. The bone possesses two foramina anteriorly and a cup-like process articulating with the anteroventral process of the ethmoid cartilage extending medially

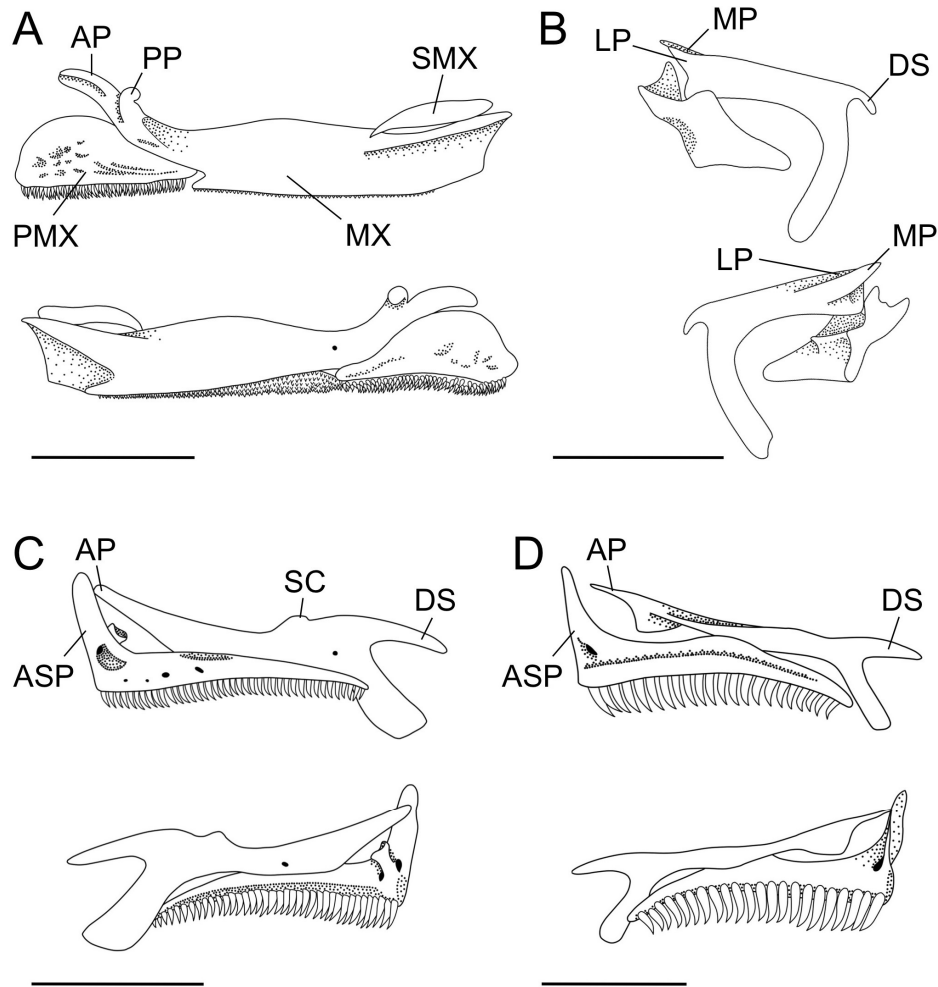


Fig. 6. Lateral (upper) and medial (lower) aspects of the upper jaw in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengeri* (C) and *Notacanthus chemnitzii* (D). AP, anterior process; ASP, ascending process; DS, dorsal spine; LP, lateral process; MP, medial process; MX, maxilla; PMX, premaxilla; PS, posterior spine; SC, small convexity; SMX, supramaxilla. Scales indicate 5 mm.

between the aforementioned foramina in *Polyacanthonotus*; the two anterior foramina are large in *P. challengeri*, small in *P. rissoanus*. Medially, the premaxilla has an ascending process which articulates with cartilage B in *Notacanthus*. Anteriorly, a large foramen is present in *Notacanthus chemnitzii*, two small foramina in *N. spinosus*. The premaxilla is connected with the dermethmoid via a ligament, a shallow concavity for such being present posterodorsally in *Polyacanthonotus*, but absent in the other genera. It is also connected with the ethmoid laterally and with the maxilla through its medial ridge posterodorsally in *Aldrovandia*, with the maxilla posterodorsally in *Lipogenys*, and with a connective tissue nodule posterodorsally in *Notacanthus* via one or two ligaments. Many small villiform teeth are present on the ventral margin of the premaxilla in *Aldrovandia*, compared with hook-like teeth in *Polyacanthonotus* and *Notacanthus*. Teeth are absent in *Lipogenys*.

The maxilla is rectangular and plate-like posteriorly, with a horizontal ridge dorsolaterally and without a dorsal process posteriorly in *Aldrovandia*. It is strongly curved, posteriorly having a single small, downwardly directed dorsal spine in *Lipogenys*. It is slightly curved, becoming narrower anteriorly, with a single backwardly directed dorsal spine posteriorly in *Polyacanthonotus* and *Notacanthus*. The anterior portion of the maxilla has two processes in *Aldrovandia* (anterior and posterior) and *Lipogenys* (lateral and medial), and one in *Polyacanthonotus* and *Notacanthus*. The anterior process is stick-like and upwardly directed, and the posterior process, connected to the angular and ectopterygoid, and situated lateral to the anteroventral process of the ethmoid cartilage, is knob-like and backwardly directed in *Aldrovandia*. The lateral and medial processes are spine-like and anteriorly directed in *Lipogenys*. The anterior process is thin and spine-like in *Polyacanthonotus* and *Notacanthus*. The max-

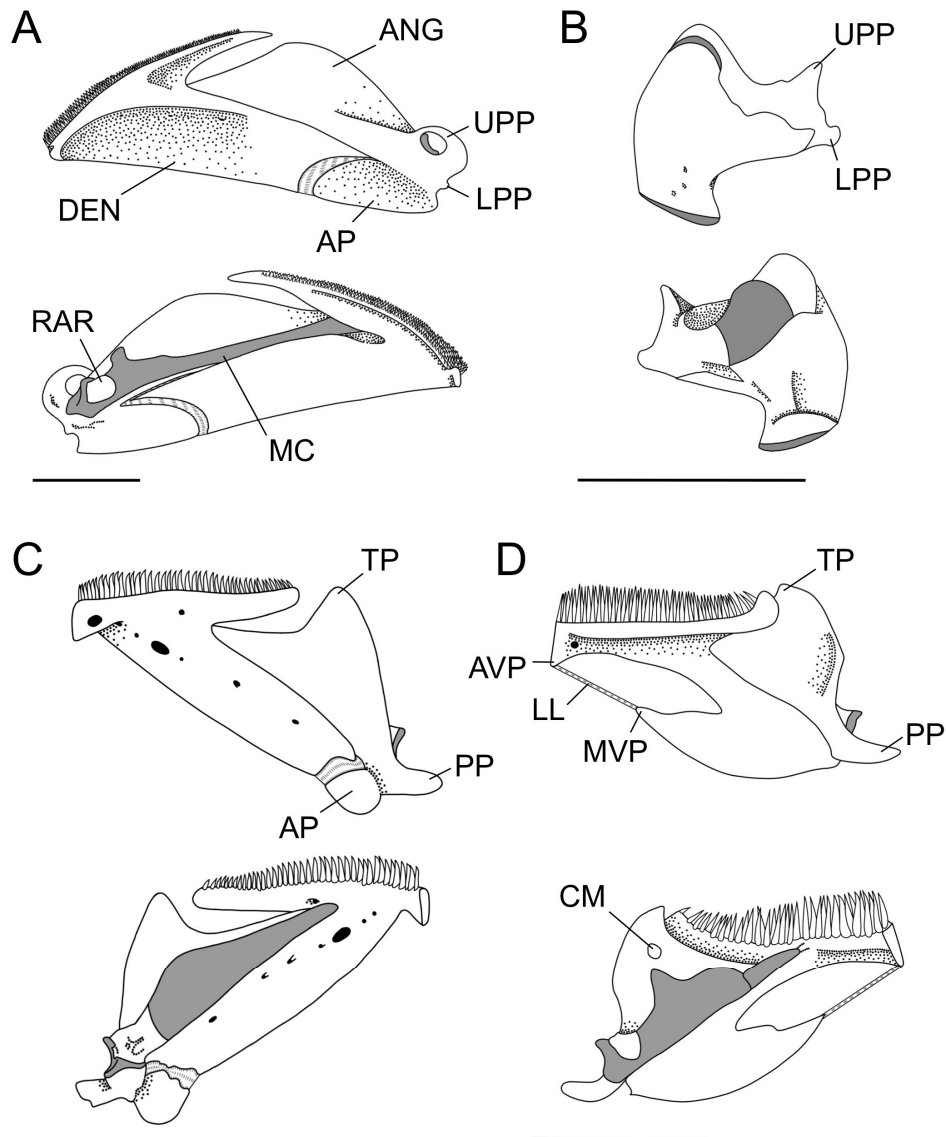


Fig. 7. Lateral (upper) and medial (lower) aspects of the lower jaw in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengerii* (C) and *Notacanthus chemnitzii* (D). AP, antorse process; ANG, angular; AVP, anteroventral process; CM, coronomeckelian; DEN, dentary; LL, long ligament; LPP, lower posterior process; MC, Meckelian cartilage; MVP, midventral process; PP, posterior process; RAR, retroarticular; TP, triangular process; UPP, upper posterior process. Scales indicate 5 mm.

illa is connected anteroventrally to the upper process of the dermethmoid in *Aldrovandia*, anteriorly to the premaxilla through its lateral and medial processes and laterally through the dermethmoid in *Lipogenys*, dorsally to the antorbital and dermethmoid through a small convexity in *Polyacanthonotus*, and dorsolaterally to the dermethmoid through a shallow concavity in *Notacanthus*. Many small villiform teeth are present on the ventral margin of the maxilla in *Aldrovandia*, teeth being absent in the other genera.

The supramaxilla is small, flat and tear drop-shaped in *Aldrovandia*, but absent in the other genera.

The dentary is short, deep and T-shaped, having a shallow notch for the angular and Meckelian cartilage medially in

Lipogenys, but is triangular with a deep notch for the angular and Meckelian cartilage posteriorly in the other genera. Posteroventrally, a concavity occurs below the notch, in addition to several foramina laterally and medially in *Aldrovandia* and *Polyacanthonotus*. A deep notch is present anteroventrally and a single foramen anterolaterally in *Notacanthus*. The anteroventral and midventral processes on the anterior margin are connected by a long ligament in *Notacanthus*. Dorsally, the dentary has many small villiform teeth forming a narrow band in *Aldrovandia*, a single row of canine teeth in *Polyacanthonotus* and a few rows of canine teeth in *Notacanthus*. Teeth are absent in *Lipogenys*.

The angular has a robust process deeply inserted into the

medial notch of the dentary in *Lipogenys*, and a sharp process shallowly inserted into the deep posterior notch in the other genera. An antrorse process, connected to the shallow concavity of the dentary via a wide ligament, occurs below the sharp process in *Aldrovandia* and *Polyacanthonotus challengeri*, but is absent in the other genera. The angular has two posterior processes in *Aldrovandia* and *Lipogenys*, one in the other genera. The upper posterior process is semicircular, possessing one large pore lateral to a glenoid cavity for articulation with the quadrate and Meckelian cartilage, the lower process being much smaller than the upper in *Aldrovandia*. The posterior process(es) are spine-like in the other three genera. The lower process in *Aldrovandia* and *Lipogenys* is connected to the epiphyal, and the upper process in *Lipogenys* and single process in *Polyacanthonotus* and *Notacanthus* to the quadrate via a ligament; the upper process in *Aldrovandia* lacks any connections to other bones. The angular has a glenoid cavity for articulation with the quadrate posterodorsally only in *Lipogenys* (absent in other genera) and a triangular process posterodorsally in *Polyacanthonotus* and *Notacanthus*.

The retroarticular is thin, small and trapezoidal in *Aldrovandia*, *Polyacanthonotus* and *Notacanthus*, an autogenous retroarticular being absent in *Lipogenys*. The bone forms a glenoid cavity with the Meckelian cartilage for articulation with the quadrate in *Polyacanthonotus*.

The coronomeckelian is small and knob-like, situated on the medial surface of the angular near the dorsal process of the Meckelian cartilage in *Notacanthus*, but is absent in the other genera.

The Meckelian cartilage is deeply inserted into the dentary ventrally in *Lipogenys*, slightly inserted into the dentary anteriorly in the other genera. It is thin and stick-like in *Aldrovandia*, oval in *Lipogenys*, and slender and triangular in the other two genera. The dorsal margin forms a glenoid cavity with the angular for articulation with the quadrate in *Lipogenys*, the posterior end possessing a cavity in the other genera. A single upwardly directed process is present posterodorsally in *Aldrovandia* and *Notacanthus chemnitzii*, and a low convexity posterodorsally in *Polyacanthonotus* and *N. spinosus*. A distinct process or convexity is absent in *Lipogenys*. The Meckelian cartilage usually comprises a single element, but was separated into two elements (anterior and posterior) in the left side of a specimen of *Notacanthus chemnitzii* (HUMZ 208582).

Remarks. — An autogenous retroarticular was apparently absent in *Lipogenys* and *Pterothrissus* (outgroup), but present in the other three genera and *Megalops* (outgroup) in this study. In contrast, the retroarticular has been reported fused with the angular in large specimens of *Megalops* and *Pterothrissus* (Forey, 1973; Wiley and Johnson, 2010). However, it was unclear if the retroarticular was indeed fused with the angular or absent in *Lipogenys*. Because the conditions

in *Lipogenys* and the outgroups cannot be considered homologous or otherwise with certainty, characters associated with the retroarticular were excluded from the phylogenetic analysis.

The Meckelian cartilage was separated into two elements on the left side of a specimen of *Notacanthus chemnitzii* (see above), but comprised a single element on the right side of that specimen and on both sides of another example of the species (HUMZ 206822), as in other ingroups. Although the former condition can be considered to be derived, a single element being present in the outgroups, it provides no help in determining relationships, being restricted to a single species.

Suspensorium and opercular bones (Figs. 8–10). The suspensorium comprises the palatine, autopalatine, dermopalatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic, hyomandibula, an unidentified bone, an unidentified cartilage and the connective tissue nodule, in addition to the preopercle, opercle, interopercle and subopercle.

The palatine is small and flat, and sutured to the autopalatine and ectopterygoid medially, being situated anteroventral (*Aldrovandia* and *Lipogenys*) or anterior (*Polyacanthonotus*) to the autopalatine. It is absent in *Notacanthus*. Medially, the bone is directly attached to the connective tissue nodule in *Polyacanthonotus* (in addition to a ligamentous connection), and to the latter via a ligament in *Aldrovandia*. The bone is attached anteriorly to cartilage A in *Lipogenys*.

The autopalatine is cartilaginous and elongate horizontally, the anterior portion being exposed in *Aldrovandia* and *Lipogenys*, and partly or completely covered by the ectopterygoid in the other two genera. The autopalatine is sutured to the palatine, ectopterygoid, endopterygoid, metapterygoid and quadrate, and is firmly attached to the dermopalatine medially in *Lipogenys*, and to the symplectic posteromedially in *Aldrovandia* and posteriorly in *Lipogenys*. The autopalatine is attached to an unidentified cartilage anteriorly in *Aldrovandia*, being also loosely attached anteriorly to the connective tissue nodule in that genus and firmly attached to the latter in *Lipogenys* and *Polyacanthonotus*.

The dermopalatine is situated anteroventral to the ectopterygoid in *Aldrovandia*, *Polyacanthonotus* and *Notacanthus*, medial to the latter in *Lipogenys*. The bone is flat and elliptical in *Aldrovandia*, flat and trapezoidal with a triangular process medially in *Lipogenys*, and triangular and incurved in the other two genera. The dermopalatines on each side are broadly connected to each other through the medial process in *Lipogenys*, but narrowly so via an anterior ligament in the other genera. Dorsally, the bone is attached to the palatine, autopalatine, ectopterygoid and an unidentified cartilage via connective tissue in *Aldrovandia*. It is firmly attached to the autopalatine and ectopterygoid laterally in *Lipogenys*, and articulates with the ectopterygoid dorsally in *Polyacanthonotus* and *Notacanthus*. A ligament connecting these bones is also present in *Polyacanthonotus*. Ventrally, the dermopala-

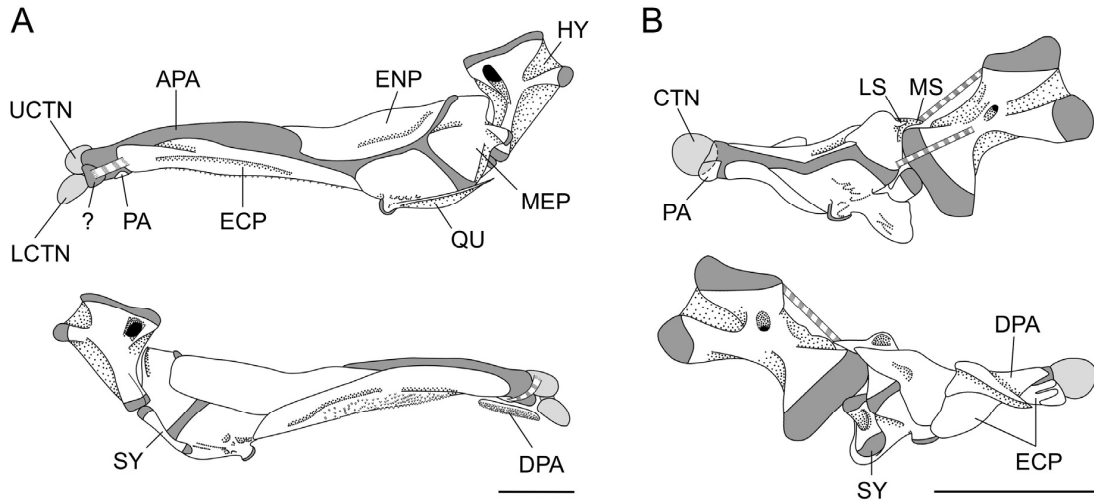


Fig. 8. Lateral (upper) and medial (lower) aspects of the suspensorium in *Aldrovandia affinis* (A) and *Lipogenys gillii* (B). APA, autopalatine; CTN, connective tissue nodule; DPA, dermopalatine; ECP, ectopterygoid; ENP, endopterygoid; HY, hyomandibula; LCTN, lower connective tissue nodule; MEP, metapterygoid; PA, palatine; QU, quadrate; SY, symplectic; UCTN, upper connective tissue nodule; ?, unidentified cartilage. Scales indicate 5 mm.

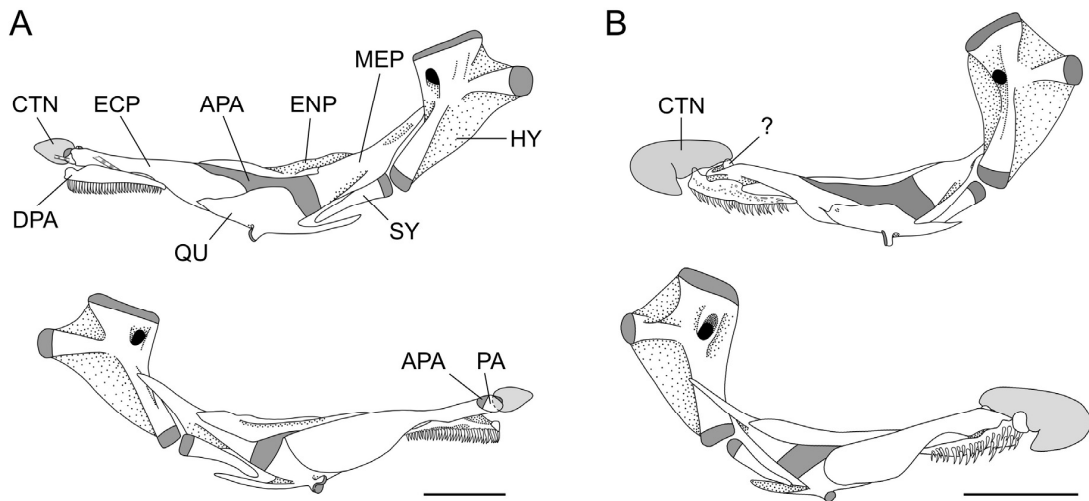


Fig. 9. Lateral (upper) and medial (lower) aspects of the suspensorium in *Polyacanthonotus challengeri* (A) and *Notacanthus chemnitzii* (B). APA, autopalatine; CTN, connective tissue nodule; DPA, dermopalatine; ECP, ectopterygoid; ENP, endopterygoid; HY, hyomandibula; MEP, metapterygoid; PA, palatine; QU, quadrate; SY, symplectic; ?, unidentified element. Scales indicate 5 mm.

tine has a band of many small villiform teeth in *Aldrovandia*, a single row of canine teeth in *Polyacanthonotus* and irregularly arranged canine teeth in *Notacanthus*. Teeth are absent in *Lipogenys*.

The ectopterygoid is triangular in *Lipogenys* and slender in the other genera. A concavity for anterodorsal attachment to an unidentified bone is present in *Notacanthus*, but otherwise absent. The bone is sutured to the palatine, autopalatine, endopterygoid and quadrate, and connected via a ligament to the posterior process of the maxilla and an unidentified cartilage in *Aldrovandia*, and to the ectopterygoid anterolaterally in *Polyacanthonotus*. It is connected to the dermopalatine via connective tissue ventrally in *Aldrovandia*, firmly attached

to it medially in *Lipogenys*, and articulates with it anteroventrally in the other two genera. The ectopterygoid is attached to the connective tissue nodule in *Notacanthus*. It has many small teeth ventromedially in *Aldrovandia*, but lacks teeth in the other genera.

The endopterygoid is wide in *Aldrovandia* and *Lipogenys*, slender in the other two genera. It lacks teeth and is sutured to the autopalatine, ectopterygoid, metapterygoid and quadrate, and connected dorsally to the parasphenoid via a ligamentous sheet.

The metapterygoid is triangular with a cartilage-capped posterior process in *Aldrovandia*. It is triangular with two spines (lateral and medial) posterodorsally, a concavity filled

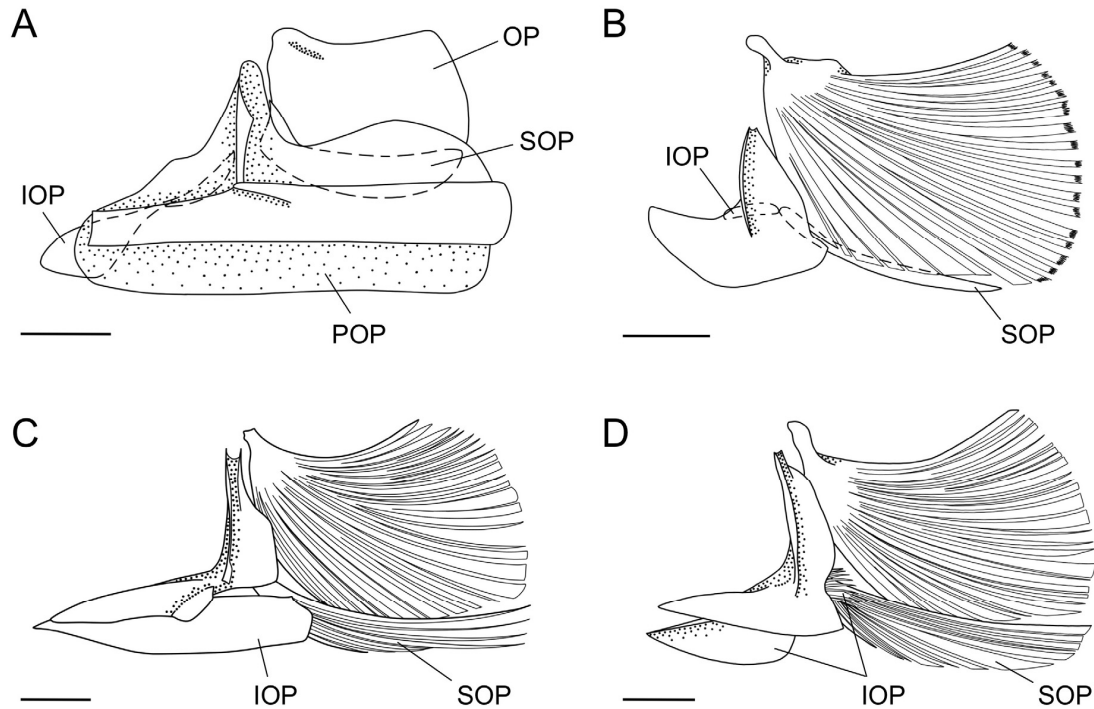


Fig. 10. Lateral aspects of the opercular bones in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengeri* (C) and *Notacanthus chemnitzii* (D). IOP, interopercle; OP, opercle; POP, preopercle; SOP, subopercle. Scales indicate 5 mm.

with connective tissue dorsomedially and a glenoid cavity for posterior articulation with the hyomandibula in *Lipogenys*. It is slender and triangular, its posterior portion produced into a long spine in *Polyacanthonotus* and *Notacanthus*. The bone is sutured to the autopalatine and endopterygoid, and connected to the parasphenoid via a ligamentous sheet. It is attached to the hyomandibula posteromedially in *Aldrovandia*, posterolaterally in *Polyacanthonotus* and *Notacanthus*. The medial spine and posteroventral corner are connected to the hyomandibula via a ligament in *Lipogenys*. The metapterygoid is firmly attached to the symplectic ventromedially in *Aldrovandia* and ventrally in *Lipogenys*, being connected to the latter via a ligamentous sheet in the other two genera. It is also connected to the interhyal via a ligament posteromedially in *Aldrovandia*, and posteroventrally in *Polyacanthonotus* and *Notacanthus*.

The triangular quadrate has a ventral condyle and posteroventral process, the latter being broad in *Lipogenys* and slender in the other genera. The quadrate is sutured to the autopalatine and ectopterygoid, and also to the endopterygoid in *Aldrovandia* and *Lipogenys*. It is firmly attached to the symplectic in *Aldrovandia* and *Lipogenys*, but separated from the latter, except for a ligamentous sheet, in the other two genera. The ventral condyle articulates with the glenoid cavity of the angular in *Lipogenys*, but with the glenoid cavity of the Meckelian cartilage in the other genera. The condyle is connected laterally via a ligament to the upper posterior process of the angular in *Lipogenys*, and to the posterior process of the angular in *Polyacanthonotus* and *Notacanthus*.

The symplectic is robust in *Lipogenys*, slender in the other genera. The anterior tip only is covered by a cartilaginous cap in *Polyacanthonotus*, both the anterior and posterior tips being so covered in the other genera. Posteriorly attached to the hyomandibula, the symplectic has a medial concavity filled with connective tissue in *Lipogenys*. The bone is firmly attached to the autopalatine, metapterygoid and quadrate laterally in *Aldrovandia* and *Lipogenys*, and via a ligamentous sheet to the autopalatine and metapterygoid dorsally and quadrate ventrally in the other two genera.

The hyomandibula, rectangular in *Lipogenys* and triangular in the other genera, has dorsal and posterior articular heads and a ventral attachment head, all with cartilaginous caps. The dorsal head is inserted into the articular socket formed by the sphenotic, pterotic and prootic, and the posterior head into a glenoid cavity on the opercle. The ventral head is attached to the symplectic anteroventrally in *Aldrovandia* and *Lipogenys*; similarly in the other two genera, although via connective tissue. The ventral head articulates ventrally with the epihyal in *Lipogenys* and is also attached ventrally to the interhyal in the other genera. The bone is attached to the metapterygoid ventrolaterally in *Aldrovandia*, ventromedially in *Polyacanthonotus* and *Notacanthus*, and articulates with it anterodorsally in *Lipogenys*.

An unidentified knob-like element, firmly attached to the anterodorsal concavity of the ectopterygoid and connected dorsally to the connective tissue nodule, is present only in *Notacanthus*. It is ossified in *N. chemnitzii* and cartilaginous in *N. spinosus*.

An unidentified pyramidal cartilage (= nubbin of cartilage *sensu* Greenwood, 1977) is present only in *Aldrovandia*, being attached anteriorly to the autopalatine and connected laterally via a ligament to the posterior process of the maxilla and ectopterygoid.

The connective tissue nodule is situated anterior to the suspensorium. Two nodules (upper and lower) are present in *Aldrovandia*, a single nodule in the other genera. The nodules are small and oval in *Aldrovandia*, compared with moderate and ball-shaped in *Lipogenys*, small and tear drop-shaped in *Polyacanthonotus*, and large and kidney-shaped in *Notacanthus*. The upper nodule is posteriorly attached to the autopalatine and medially to the palatine via a ligament, the lower nodule being connected to the upper one and attached anteriorly to the premaxilla, in *Aldrovandia*. The single nodule is firmly attached posteromedially to the palatine in *Lipogenys* (posterolaterally in *Polyacanthonotus*), being also firmly attached posteromedially to the autopalatine in *Lipogenys* and posteroventrally to an unidentified bone (see above) in *Notacanthus*. The nodule is attached medially to the anteroventral process of the ethmoid cartilage in *Aldrovandia* and *Polyacanthonotus*, cartilage A in *Lipogenys* and cartilage B in *Notacanthus*, and via a ligament to the dermethmoid in *Lipogenys*, *Polyacanthonotus* and *Notacanthus*, in addition to the premaxilla in *Notacanthus* and palatine in *Polyacanthonotus*.

The preopercle is large and very fragile in *Aldrovandia*, moderately sized and very fragile in *Lipogenys*, and slender and rather hard in the other two genera. A tubular structure supporting the sensory canal is continuous anteroventrally with that on the lower jaw. The preopercle is attached to the opercle, interopercle and subopercle medially, and firmly so via connective tissue to the quadrate and interhyal anterodorsally in *Aldrovandia*, *Polyacanthonotus* and *Notacanthus*.

The opercle is flat and rounded, with a glenoid cavity for anterodorsal articulation with the hyomandibula. The bone is relatively small, simple and very fragile in *Aldrovandia*, whereas it is large, hard and divided into many branches in the other genera. The tips of the posterior branches are subdivided in *Lipogenys*, not so in *Polyacanthonotus* and *Notacanthus*. The lateral aspect of the opercle is attached ventrally to the preopercle in *Aldrovandia*, anteroventrally in the other genera. The bone is also attached to the subopercle ventromedially in *Aldrovandia* and *Lipogenys*, and posteriorly in the other two genera.

The interopercle is moderately sized and fragile in *Aldrovandia*, small and fragile in *Lipogenys*, and moderate and rather hard in the other two genera. The posterior portion is divided into several branches in *Notacanthus*, but is simple in the other genera. The bone is connected to the angular via a ligament anteriorly. Posteriorly, it is attached directly to the subopercle in *Lipogenys*, posteromedially in *Polyacanthonotus* and *Notacanthus*, but is also attached to the

latter via a posterior ligament in *Aldrovandia*. The lateral aspect of the interopercle is broadly attached to the preopercle in *Aldrovandia* and *Lipogenys*, but narrowly attached to the latter anterodorsally in *Polyacanthonotus* and posterodorsally in *Notacanthus*.

The subopercle is fragile and feather-shaped in *Aldrovandia*, fragile and slender in *Lipogenys*, and hard and crescentic in the other two genera. It is divided posteriorly into many branches in *Polyacanthonotus* and *Notacanthus*, but is simple in the other two genera. The subopercle is connected anteroventrally to the interopercle via a ligament in *Aldrovandia*, but is attached to the latter directly in the other genera. Its lateral aspect is attached to the preopercle, ventrally in *Aldrovandia* and anterodorsally in the other genera. The bone is also attached to the opercle, dorsolaterally in *Aldrovandia* and *Lipogenys* and posterodorsally in the other two genera. The lateral aspect is also attached to the interopercle, anteriorly in *Lipogenys* and ventrally in *Polyacanthonotus* and *Notacanthus*, although these bones are separated in *Aldrovandia*.

Remarks. — An unidentified knob-like element attached to the anterodorsal concavity of the ectopterygoid is present in *Notacanthus* (ossified in *N. chemnitzii* and cartilaginous in *N. spinosus*), being absent in the other three genera and both outgroups. Greenwood (1977) considered it to have been derived from the autopalatine but provided no evidence for such homology. Because the derivation of the element was unclear, it was treated as unidentified in this study, characters associated with it being excluded from the phylogenetic analysis.

An unidentified cartilage is attached anteriorly to the autopalatine in *Aldrovandia*, being absent in the other genera and *Megalops* (outgroup). Although a cartilage is also present between the maxilla and autopalatine in *Pterothrissus* (outgroup), homology of the two cartilages is equivocal, their position, size and configuration differing in the two genera. Characters associated with the cartilage are therefore excluded from the phylogenetic analysis.

Hyoid arch (Figs. 11–14). The hyoid arch is composed of the hypohyal, ceratohyal, epihyal, interhyal, branchiostegal rays, basihyal and urohyal.

The hypohyal comprises anterior and ventral elements in *Lipogenys*, dorsal and ventral elements in the other genera. The dorsal hypohyal has a medial knob for articulation with the cartilaginous first basibranchial in *Aldrovandia*, and attachment to the latter in *Polyacanthonotus* and *Notacanthus*, whereas the anterior hypohyal lacks such a knob in *Lipogenys*, being connected to the ceratohyal via a posterodorsal cartilage in that genus (posterior cartilage from the dorsal hypohyal in the other genera). Both the dorsal and anterior hypohyals are connected to the first hypobranchial via a ligament. The ventral hypohyal was connected to the urohyal via a strong ligament in the notacanthoids examined, except

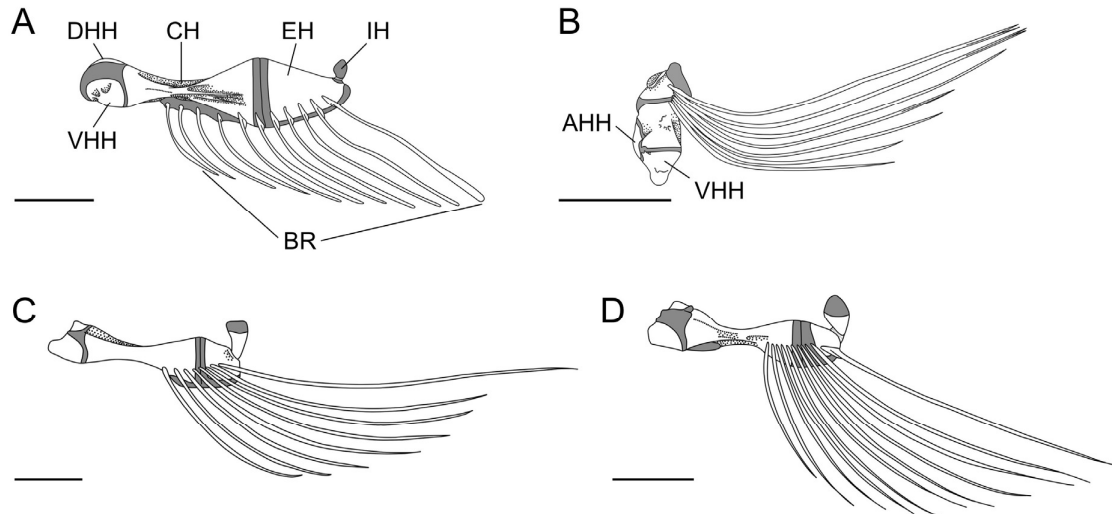


Fig. 11. Lateral aspects of the hyoid arch in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengeri* (C) and *Notacanthus chemnitzii* (D). AHH, anterior hypohyal; BR, branchiostegal rays; CH, ceratohyal; DHH, dorsal hypohyal; EH, epihyal; IH, interhyal; VHH, ventral hypohyal. Scales indicate 5 mm.

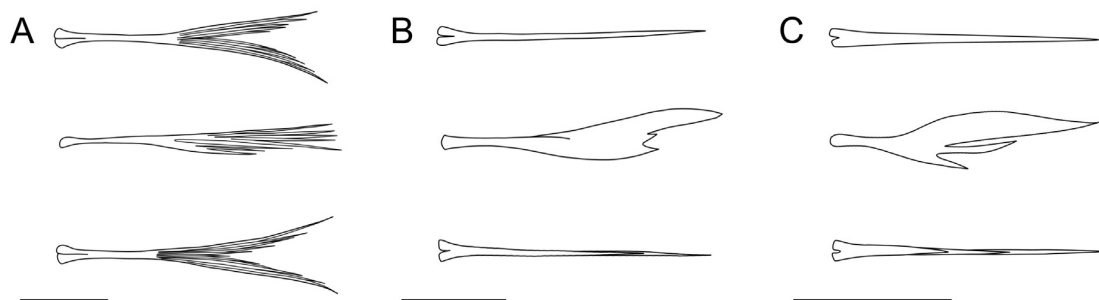


Fig. 12. Dorsal (upper), lateral (middle) and ventral (lower) aspects of the urohyal in *Aldrovandia affinis* (A), *Polyacanthonotus challengeri* (B) and *Notacanthus chemnitzii* (C). Scales indicate 5 mm.

Lipogenys which lacked the ligament.

The ceratohyal is short and robust in *Lipogenys*, long and stick-like with a narrow mid portion in the other genera. The bone has a single thin cartilage anteroventrally in *Notacanthus chemnitzii* and posteroventrally in *Aldrovandia* (supporting the anterior four branchiostegal rays), but two (anteroventral and posteroventral) cartilages in *N. spinosus*. The ceratohyal is connected via an anteroventral cartilage to the hypohyals and interdigitates dorsomedially with the epihyal in *Lipogenys*, whereas it is connected via cartilage to both the hypohyals anteriorly and epihyal posteriorly in the other genera. Laterally, it is connected to the basihyal via two ligaments in *Aldrovandia* and the ectopterygoid via one ligament in *Lipogenys*. There is no ligamentous connection with other bones in the other two genera.

The epihyal has a glenoid cavity for articulation with the hyomandibula dorsally in *Lipogenys*, and with the interhyal posterodorsally in the other genera. The bone is connected to the angular via a ligament dorsolaterally in *Lipogenys*, posterolaterally in the other genera.

The interhyal had a ventral ligamentous articulation with a glenoid cavity situated on the posterodorsal portion of the epihyal in the notacanthoids examined, except *Lipogenys*, which lacked the interhyal. The bone is oval and cartilaginous in *Aldrovandia*, and stick-like and ossified, with a cartilaginous cap dorsally, in *Polyacanthonotus* and *Notacanthus*. It is attached to the hyomandibula.

The branchiostegal rays are long and thin, attached to the ceratohyal and epihyal posterolaterally in *Lipogenys*, ventrolaterally in the other genera. They comprise 11 elements in *Aldrovandia* and *Notacanthus chemnitzii*, 13 in *N. spinosus*, seven in *Lipogenys* and eight in *Polyacanthonotus*. The tips of the fourth, sixth and seventh rays are branched only in *Lipogenys*.

The basihyal is firmly attached posteriorly to the cartilaginous first basibranchial and has a cartilaginous anterior margin. It is wide, spatular and toothless in *Aldrovandia* and *Notacanthus*, hook-like and toothless in *Lipogenys*, and shoe-horn-like with a single (*Polyacanthonotus challengeri*) or four (*P. rissoanus*) small teeth dorsally in *Polyacanthono-*

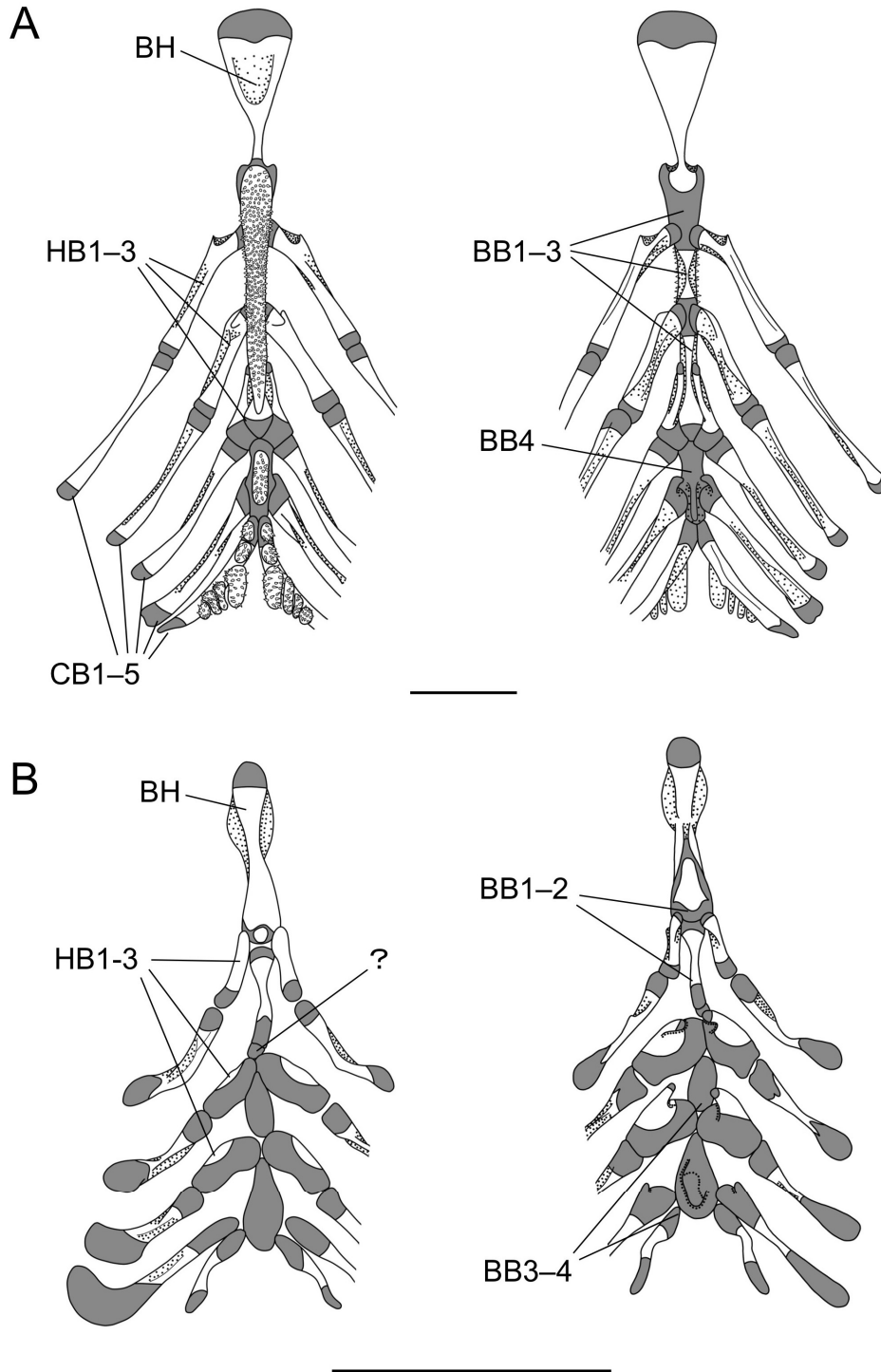


Fig. 13. Dorsal (left) and ventral (right) aspects of the ventral branchial arch in *Aldrovandia affinis* (A) and *Lipogenys gillii* (B). BB, basibranchial; BH, basihyal; CB, ceratobranchial; HB, hypobranchial; ?, unidentified cartilage. Scales indicate 5 mm.

tus. It is connected to the ceratohyal via two ligaments in *Aldrovandia* and covered anteriorly by a large connective tissue nodule in *Lipogenys*.

The urohyal is thin and stick-like, anteriorly having two processes for connection to the ventral hypohyal via a strong ligament. The bone is posteriorly divided into many branches in *Aldrovandia*, three branches in *Polyacanthonotus*

and *Notacanthus*. It is absent in *Lipogenys*.

Branchial arch (Figs. 13-15). The branchial arch comprises the basibranchial, hypobranchial, ceratobranchial, an unidentified cartilage, epibranchial, pharyngobranchial, accessory cartilages and two tooth plates. The suprpharyngobranchial is absent.

The basibranchial is unpaired, consisting of four serial ele-

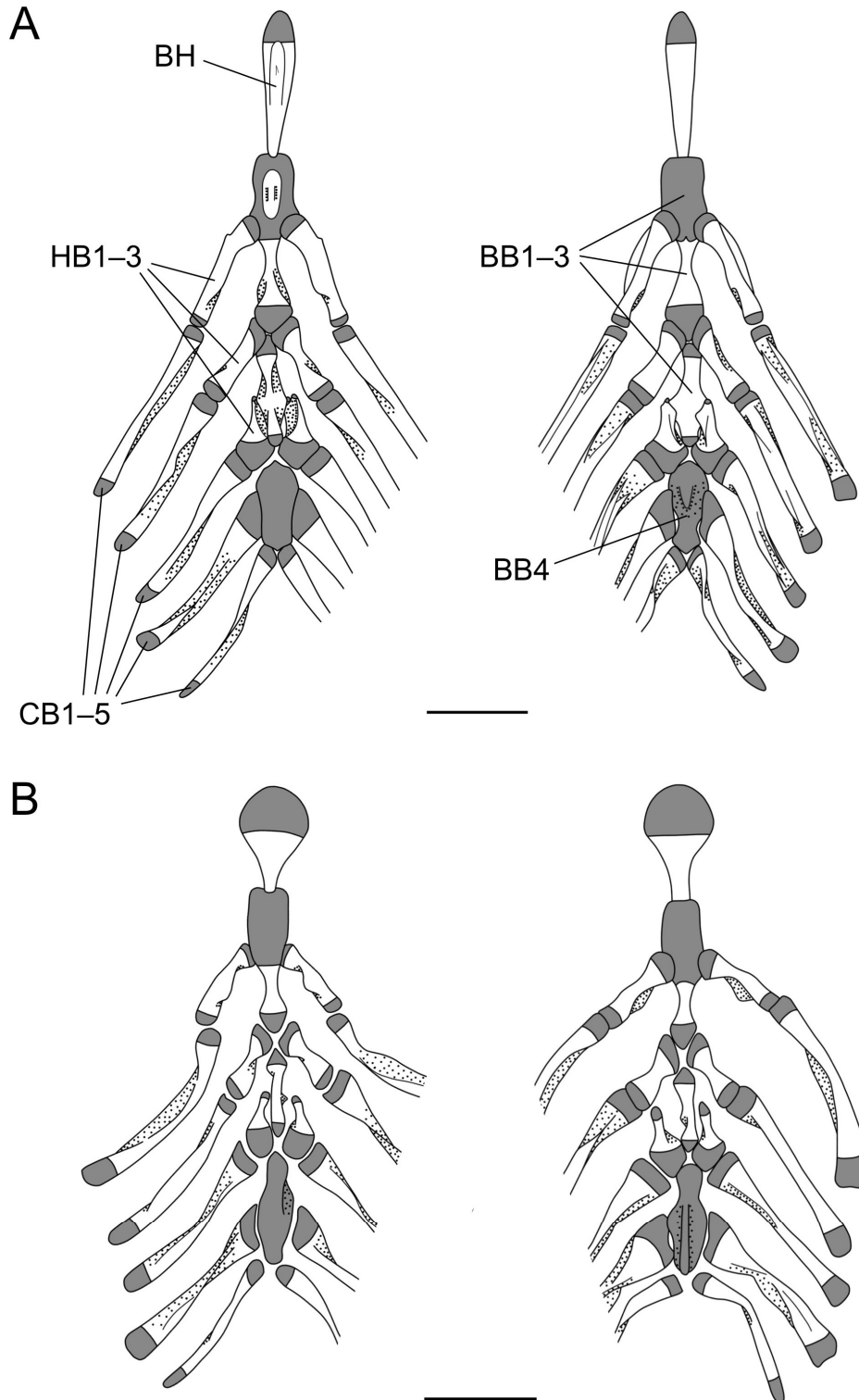


Fig. 14. Dorsal (left) and ventral (right) aspects of the ventral branchial arch in *Polyacanthonotus challengerii* (A) and *Notacanthus chemnitzii* (B). BB, basibranchial; BH, basihyal; CB, ceratobranchial; HB, hypobranchial. Scales indicate 5 mm.

ments. The first basibranchial is cartilaginous, being rectangular in *Aldrovandia* and *Notacanthus*, triangular with a triangular bony plate ventrally and circular one posterodorsally in *Lipogenys*, and rectangular with an oval bony plate dorsally in *Polyacanthonotus*. Anteriorly, the bone has a

pair of glenoid cavities for articulation with the dorsal hypohyal in *Aldrovandia*, but lacks such cavities and is directly attached anteriorly to the latter in the other genera. The basibranchial also has a pair of glenoid cavities for posterior articulation with the first hypobranchial in *Aldrovandia*,

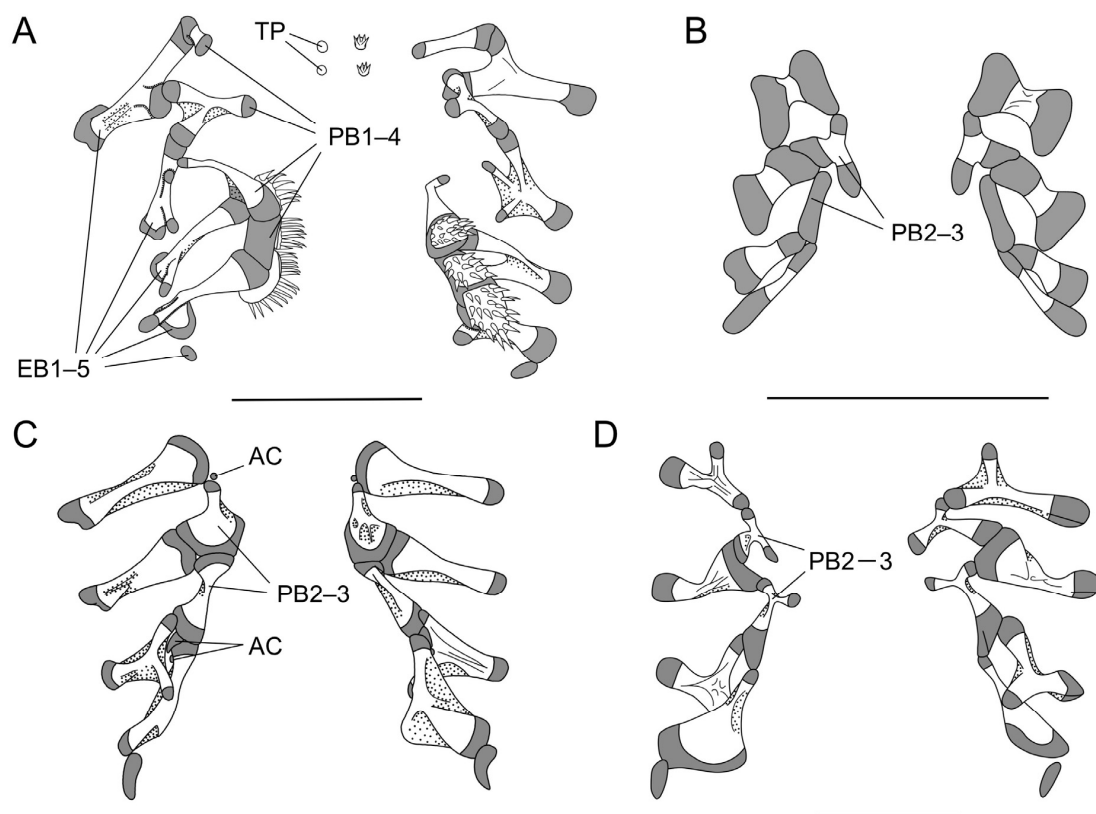


Fig. 15. Dorsal (left) and ventral (right) aspects of the dorsal branchial arch in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengerii* (C) and *Notacanthus chemnitzii* (D). AC, accessory cartilage; EB, epibranchial; PB, pharyngobranchial; TP, tooth plate. Scales indicate 5 mm.

Polyacanthonotus and *Notacanthus*, but lacks such cavities and is connected with the latter via a posterior ligament in *Lipogenys*. It is firmly attached to the basihyal anteroventrally in *Aldrovandia*, anterodorsally in the other genera, and is loosely attached to the second basibranchial via a ligament in *Lipogenys* (sutured posteriorly to the latter in the other genera). The second basibranchial is stick-like with a narrow mid portion in *Aldrovandia*, stick-like with a cartilaginous cap anteriorly and posteriorly in *Lipogenys*, and spatular-like with a cartilaginous cap posteriorly in the other two genera. It is posteriorly continuous with the third basibranchial via a cartilage in *Aldrovandia* and *Notacanthus spinosus*, but is loosely attached to the latter via a ligament in the other genera. Posteriorly, the second basibranchial is connected ligamentously to the second hypobranchial in *Polyacanthonotus* and *Notacanthus*, but separated from the latter in *Lipogenys*. In *Aldrovandia*, the cartilage connecting the second and third basibranchials has a pair of glenoid cavities for articulation with the second hypobranchials. An unidentified autogenous cartilage, attached anteriorly to the second basibranchial, is present in *Lipogenys*. The third basibranchial is stick-like with a cartilaginous cap posteriorly in *Aldrovandia*, oval and cartilaginous in *Lipogenys*, lozenge-shaped and flat with a cartilaginous cap on its four apices in *Polyacanthonotus*, and rectangular and flat with a cartilagi-

nous cap anteriorly and posteriorly in *Notacanthus*. It is connected posteriorly to the fourth basibranchial and third hypobranchial via a ligament, and anteriorly to the second hypobranchial via a ligament in *Lipogenys*, *Polyacanthonotus* and *Notacanthus*, being separated from the latter in *Aldrovandia*. A long tooth plate is firmly attached ventrally to the first three basibranchials in *Aldrovandia*, but is absent in the other genera. The fourth basibranchial, cartilaginous and oval with a ventral process but lacking a posterior process, has a pair of glenoid cavities for posterior articulation with the fourth ceratobranchial in *Aldrovandia*. Such cavities are absent, connection to the fourth ceratobranchial being via a posterolateral ligament, in the other genera. The fourth basibranchial is also connected ligamentously to the third hypobranchial anteriorly and fifth ceratobranchial posteriorly. An oval tooth plate is firmly attached ventrally in *Aldrovandia*, but is absent in the other genera.

The hypobranchial comprises three serial elements, the first being triangular with a cartilaginous cap on the anterodorsal and posterior apices in *Lipogenys*, stick-like with a cartilaginous cap anteriorly and posteriorly in the other genera. It is connected ligamentously to the first ceratobranchial posteriorly and to the glenoid cavity of the first basibranchial anteriorly in *Lipogenys*, but articulates with the latter anteriorly in the other genera. A ligament connects the first hypobran-

chial to the anterior hypohyal medially in *Lipogenys*, to the dorsal hypohyal anteriorly in the other genera. The second hypobranchial is triangular with a cartilaginous cap dorsally and ventrally in *Lipogenys*, stick-like with a cartilaginous cap anteriorly and posteriorly in the other genera. It is connected to the second ceratobranchial via a ligament posteriorly in *Aldrovandia*, *Polyacanthonotus* and *Notacanthus*, and posterodorsally in *Lipogenys*. The bone articulates anteriorly with the glenoid cavity of the cartilage connecting the second and third basibranchials in *Aldrovandia*, and is connected dorsomedially via a ligament to an unidentified cartilage and the third basibranchial in *Lipogenys*, and anteriorly via a ligament to the second and third basibranchials in the other two genera. The third hypobranchial is triangular with a cartilaginous cap dorsally and ventrally in *Lipogenys*, anteriorly and posteriorly in the other genera. In *Lipogenys*, it is connected posterodorsally to the third ceratobranchial and dorsomedially to the third and fourth basibranchials via ligaments, posterolaterally and posteromedially, respectively, to those elements in the other genera.

The ceratobranchial comprises five serial elements, having cartilaginous caps anteriorly and posteriorly. The first and second ceratobranchials are stick-like and anteriorly connected via a ligament to the first and second hypobranchials, respectively. They are posterodorsally connected via a ligament to the first and second epibranchials, respectively. The third ceratobranchial is hook-like in *Lipogenys*, stick-like in the other genera, and connected via a ligament to the third hypobranchial anteriorly and third epibranchial posterodorsally. The fourth ceratobranchial is hook-like in *Lipogenys*, but otherwise stick-like, and has an anteroventral process in all of the genera. It articulates anteriorly with the glenoid cavity of the fourth basibranchial in *Aldrovandia*, but is connected to the latter via an anterior ligament in the other genera. Posterodorsally, it is connected to the fourth and fifth epibranchials via a ligament. The fifth ceratobranchial is stick-like and connected anteriorly to the fourth basibranchial via a ligament. Six small tooth plates are firmly attached dorsally to the fifth ceratobranchial in *Aldrovandia*, but are absent in the other genera.

A small, ball-like unidentified cartilage is sutured anteriorly to the second basibranchial and connected via a posterior ligament to the second hypobranchial in *Lipogenys*. Such a cartilage is absent in the other genera.

The epibranchial comprises four serial elements in *Lipogenys*, five in the other genera. The first epibranchial is Y-shaped with three (anterodorsal, posterodorsal and ventral) cartilage-capped heads in *Aldrovandia* and *Notacanthus*, rectangular with a narrow medial portion and wide cartilaginous cap anteriorly and posteriorly in *Lipogenys*, and stick-like with a narrow cartilaginous cap anteriorly and posteriorly in *Polyacanthonotus*. Ventrally, the bone is connected to the first ceratobranchial. The posterodorsal head (= uncinat

process) is connected via a ligament to the second pharyngobranchial, dorsally in *Aldrovandia* and *Notacanthus*, posterodorsally in the other two genera. The anterodorsal head has a dorsal ligamentous connection to the first pharyngobranchial in *Aldrovandia* and to an accessory cartilage in *Polyacanthonotus*. The second epibranchial is trident-shaped with four [anterodorsal, middorsal (= anterior uncinat process), posterodorsal (= posterior uncinat process) and ventral] cartilage-capped heads in *Aldrovandia*, rectangular with a wide cartilaginous cap anteriorly and posteriorly, and lacking uncinat processes in *Lipogenys*, and stick-like with a narrow cartilaginous cap anteriorly and posteriorly, and lacking uncinat processes in the other two genera. It is connected ventrally to the second ceratobranchial. The anterodorsal head is connected via a ligament to the second pharyngobranchial, dorsally in *Aldrovandia*, *Lipogenys* and *Polyacanthonotus*, anterodorsally in *Notacanthus*. The second epibranchial is separated from the third pharyngobranchial in *Aldrovandia*, but is connected via a posterodorsal ligament to the latter in the other genera. The third epibranchial is triangular in *Lipogenys*, with cartilaginous caps dorsally and ventrally, and lacking uncinat processes, but Y-shaped with three [anterodorsal, posterodorsal (= uncinat process) and ventral] cartilage-capped heads in the other genera. The bone is connected to the third ceratobranchial via a ventral ligament and to the third pharyngobranchial via an anterodorsal ligament. The fourth epibranchial is Y-shaped with three (anterodorsal, posterodorsal and ventral) cartilage-capped heads in *Aldrovandia*, stick-like with cartilaginous caps anteriorly and posteriorly in *Lipogenys*, and triangular with cartilaginous caps anterodorsally and ventrally in *Polyacanthonotus*, anteriorly and posteriorly in *Notacanthus*. Ventrally, the fourth epibranchial is connected to the fourth ceratobranchial. It is separated from the third pharyngobranchial in *Aldrovandia*, but connected anteriorly to the latter via a ligament in the other genera. The anterodorsal head is connected anteriorly via a ligament to the fourth pharyngobranchial in *Aldrovandia*. The bone is also connected ligamentously to two anterior accessory cartilages in *Polyacanthonotus*. The fifth epibranchial is small and cartilaginous in notacathoids (absent in *Lipogenys*), being oval in *Aldrovandia* and *Notacanthus*, and tear drop-like in *Polyacanthonotus*. Ventrally, it is connected via a ligament to the fourth ceratobranchial.

The pharyngobranchial comprises four elements in *Aldrovandia*, two in the other genera. The first is stick-like with cartilaginous caps dorsally and ventrally, and connected via a ligament to the prootic dorsally and first epibranchial ventrally in *Aldrovandia*. It is small and cartilaginous in *Notacanthus spinosus*, and absent in the other genera. The second pharyngobranchial is triangular with cartilaginous caps anteriorly and posteriorly in *Polyacanthonotus*, and Y-shaped with three (anterior, posterolateral and posterome-

dial) cartilage-capped heads in the other genera. The anterior head is connected via a ligament to the first epibranchial, laterally in *Aldrovandia*, anteriorly in *Lipogenys* and *Notacanthus*, and anterolaterally in *Polyacanthonotus*. The posterolateral head is connected via a ligament to the second epibranchial, posteriorly in *Aldrovandia* and *Lipogenys*, laterally in *Notacanthus*, and posterolaterally in *Polyacanthonotus*. The second pharyngobranchial is connected to the third via a posterior ligament in *Polyacanthonotus*, but is separated from the latter in the other genera. It was connected via an anterior ligament to an accessory cartilage on the left side of a specimen of *Polyacanthonotus challengerii* (HUMZ 196369). The third pharyngobranchial is triangular with cartilaginous caps anteriorly and posteriorly in *Aldrovandia*, stick-like and cartilaginous in *Lipogenys*, rectangular with cartilaginous caps anteriorly and posteriorly in *Polyacanthonotus*, and Y-shaped with three (anterolateral, anteromedial and posterior) cartilage-capped heads in *Notacanthus*. It is connected via a posterior ligament to the third epibranchial, but separated from the second in *Aldrovandia* and *Polyacanthonotus*, although connected to the latter via an anterior ligament in *Lipogenys* and *Notacanthus*. It is also separated from the fourth epibranchial in *Aldrovandia*, but connected to the latter via a posterior ligament in the other genera. The third pharyngobranchial is connected to the second via an anterior ligament in *Polyacanthonotus*, but is otherwise separated from the latter. It is also connected posteriorly to the fourth pharyngobranchial in *Aldrovandia*, and to an accessory cartilage in *Polyacanthonotus*. It bears a dorsal tooth plate attached by connective tissue in *Aldrovandia*, such being absent in the other genera. The fourth pharyngobranchial is cartilaginous and rectangular in *Aldrovandia*, but is absent in the other genera. It is connected via a ligament to the third pharyngobranchial anteriorly and fourth epibranchial posteriorly, and has two tooth plates firmly attached to its dorsal aspect.

Three accessory cartilages were present on the left side of a specimen of *Polyacanthonotus challengerii* (HUMZ 196369), but were absent from the right side of the specimen and from both sides in other ingroup specimens. The anteriormost cartilage was small and ball-like, being connected posteriorly via a ligament to the first epibranchial and second pharyngobranchial. The middle cartilage was slightly larger and triangular, and connected dorsally via a ligament to the fourth epibranchial and third pharyngobranchial. The posteriormost cartilage was small and ball-like, and connected to the fourth epibranchial via a dorsal ligament.

Two small circular tooth plates, supported by connective tissue on the dorsal aspect of the branchial arch, are present in *Aldrovandia*, but otherwise absent.

Remarks. — The variable condition demonstrated by the three accessory cartilages in the left side upper branchial arches of a specimen of *Polyacanthonotus challengerii* (HUMZ 196369), but which were otherwise absent from

ingroup specimens examined, had no effect on the reconstruction of phylogenetic relationships. Nevertheless, because the condition may occur variably within the other species used in this study, characters associated with the cartilages were not used for the analysis.

Pectoral girdle and fin rays (Fig. 16). The pectoral fin comprises the supratemporal, posttemporal, supracleithrum, cleithrum, scapula, coracoid, actinosts, radials and an unidentified cartilage. The mesocoracoid and postcleithrum are absent.

The scapula and coracoid are included in a large cartilaginous plate, which possesses a coracoid fenestra situated dorsally to the coracoid in *Aldrovandia*, *Polyacanthonotus* and *Notacanthus*, but lacks such a feature, possessing only a single small dorsal foramen in *Lipogenys*. The cartilaginous plate has an anterior process in *Aldrovandia* and *Polyacanthonotus rissouanus*, an upwardly directed anterodorsal process in *Lipogenys*, and two anterior processes (upper and lower) in *P. challengerii* and *Notacanthus*. The anterior process is connected ligamentously to the cleithrum in *Aldrovandia*, the upper anterior process in *Notacanthus* being attached laterally to the cleithrum. The cartilaginous plate in *Polyacanthonotus* is separated from the cleithrum. The plate also possesses a posteroventral postcoracoid process in *Polyacanthonotus* and *Notacanthus*, being single and downwardly directed in the former, but comprising two component processes (anterior and posterior) directed anteriorly and posteriorly, respectively, in *Notacanthus*. The postcoracoid process is absent in *Aldrovandia* and *Lipogenys*.

The supratemporal bone was very small in *Polyacanthonotus challengerii* and absent in the other species examined.

The posttemporal is attached to the epiotic and pterotic anteriorly, and the supracleithrum ventromedially in *Aldrovandia*, and to the supracleithrum posterolaterally in *Polyacanthonotus challengerii*. It was absent in the other species examined. The bone has an upward spine-like process dorsally and a tubular structure anterodorsally supporting the sensory canal continuous with that on the cranium in *Aldrovandia*, whereas it is small, lacking spines and a tubular structure in *Polyacanthonotus*.

The supracleithrum is long and triangular with a long vertical concavity in *Aldrovandia*, somewhat shorter and thin in *Polyacanthonotus challengerii*, and long and shallowly notched in *Notacanthus*. It is absent in *Lipogenys* and *P. rissouanus*. Posteromedially, the supracleithrum is attached to the cleithrum, being also attached to the posttemporal dorso-laterally in *Aldrovandia* and anteromedially in *Polyacanthonotus*.

The cleithrum is upwardly curved and tube-shaped anteriorly, with two dorsal spines and a concavity posteriorly and two pores medially in *Aldrovandia*. It is L-shaped with a process supporting a cartilage anteromedially in *Polyacanthonotus* and *Notacanthus*, and has a concavity for insertion of

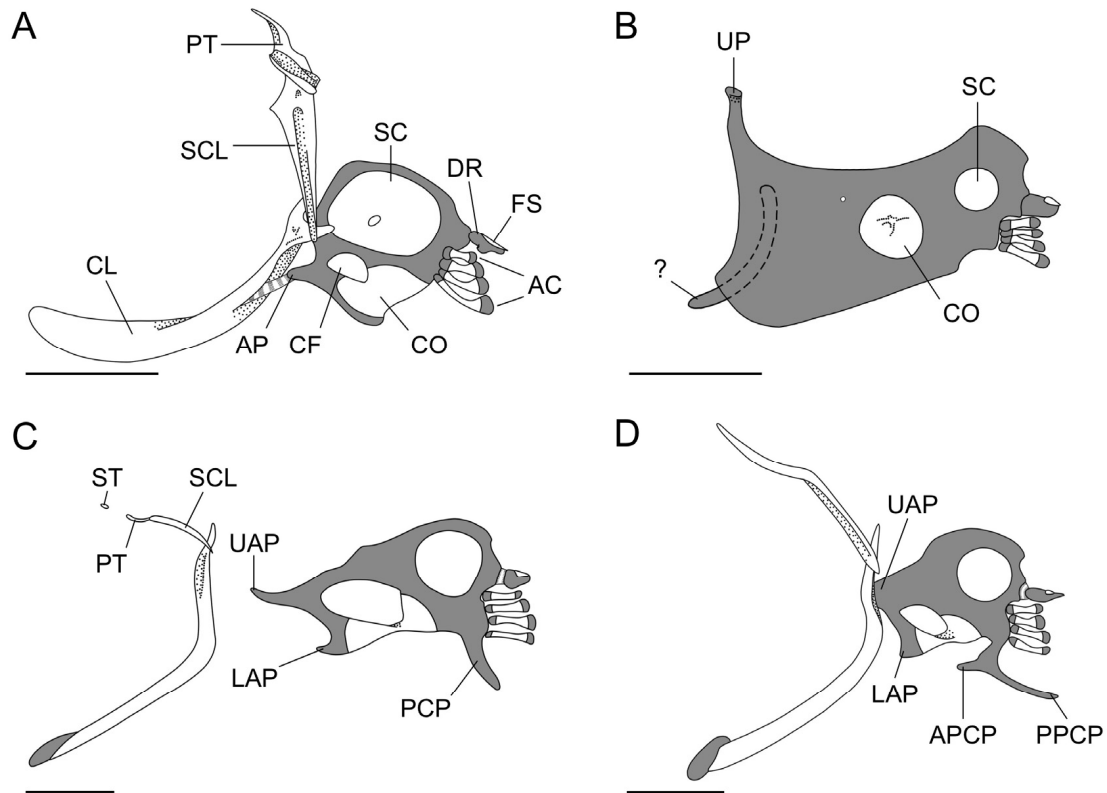


Fig. 16. Lateral aspects of the pectoral girdle in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengeri* (C) and *Notacanthus chemnitzii* (D). AC, actinosts; AP, anterior process; APCP, anterior postcoracoid process; CF, coracoid fenestra; CL, cleithrum; CO, coracoid; DR, dorsalmost radial; FS, fulcral spine; LAP, lower anterior process; PCP, posterior postcoracoid process; PPCP, posterior postcoracoid process; PT, posttemporal; SC, scapula; SCL, supracleithrum; ST, supratemporal; UAP, upper anterior process; UP, upward process; ?, unidentified cartilage. Radials embedded under connective tissue not illustrated. Scales indicate 5 mm.

the arrector ventralis and abductor superficialis posteriorly in *Notacanthus*. It is absent in *Lipogenys*. The cleithrum is attached to the supracleithrum dorsolaterally and connected via an anteromedial cartilage to its antimere. The dorsal spines are connected medially via a ligament to the cartilaginous plate including the scapula and coracoid, the posterior concavity being similarly connected to the anterior process of the cartilage plate in *Aldrovandia* and serving for insertion of the abductor superficialis.

The disk-like scapula is situated on the posterior portion of the cartilaginous plate in *Lipogenys*, and posterior to the cleithrum in the other genera. It is connected to the coracoid via the cartilaginous plate ventrally in *Aldrovandia* and anteroventrally in the other genera. The scapula is large, possessing a single central foramen in *Aldrovandia*, but small in *Lipogenys*, and moderate in *Polyacanthonotus* and *Notacanthus*.

The coracoid is disc-like in *Lipogenys*, but plate-like with a narrow mid portion in the other genera. It is connected to the scapula via the cartilaginous plate, dorsally in *Aldrovandia* and posterodorsally in the other genera.

The actinosts are stick-like, comprising four serial elements with cartilaginous caps anteriorly and posteriorly. They are

extended ventrally in *Aldrovandia* and *Lipogenys*, but are similar in length in the other two genera.

The pectoral radials are cartilaginous, supporting the pectoral fin rays. The dorsalmost radial is larger than the others, being dorsally attached to the fulcral spine and anteriorly to the cartilaginous plate via a ligament. It is stick-like with a tube-shaped process ventrally in *Aldrovandia*, oval in *Lipogenys* and *Polyacanthonotus*, and tear drop-shaped in *Notacanthus*.

An unidentified cartilage, thin and stick-like and curved anteriorly, is situated between the anterior portions of the pectoral girdles on both sides in *Lipogenys*, but is absent in the other genera.

The pectoral fin has a single fulcral spine (= pectoral splint *sensu* Forey et al., 1996) in the dorsalmost position among the fin rays, and an additional 14 soft rays in *Aldrovandia*, 12 in *Lipogenys* and *Polyacanthonotus challengeri*, 13 in *Notacanthus* and 17 in *P. rissoanus* in examined specimens. The fulcral spine is long in *Aldrovandia*, but considerably shorter in the other genera.

Pelvic girdle and fin rays (Fig. 17). The pelvic girdle, supporting the pelvic fin rays, comprises the basipterygium and radials.

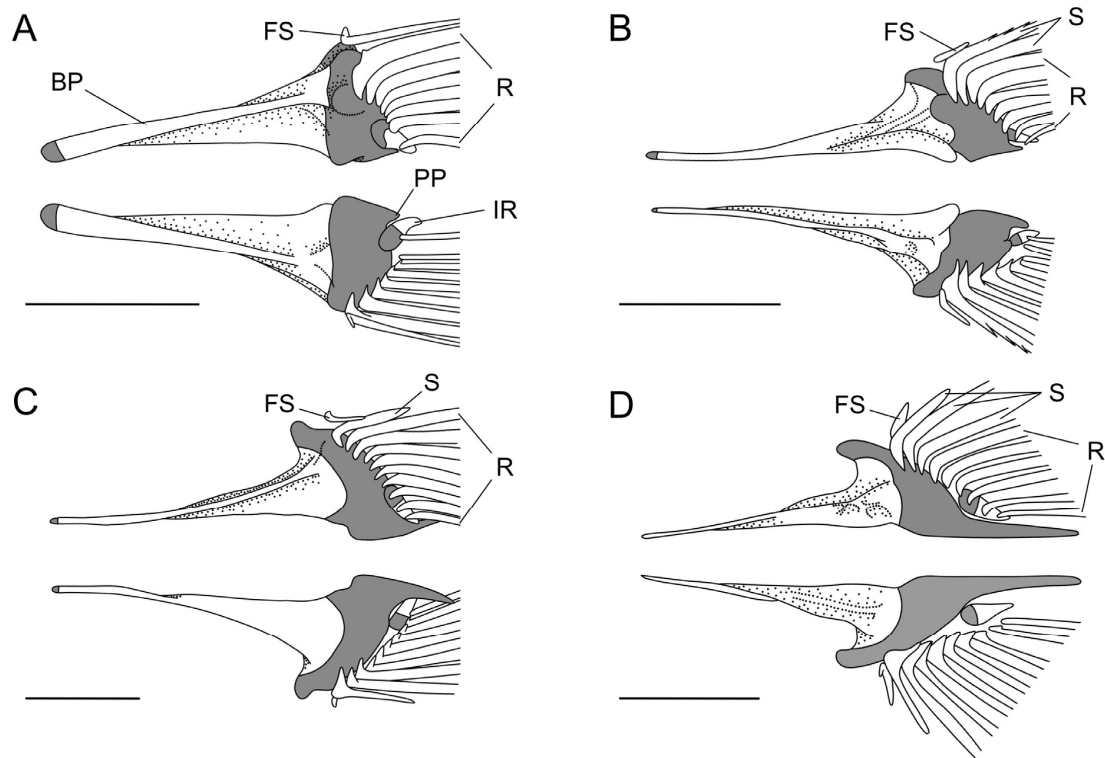


Fig. 17. Ventral (upper) and dorsal (lower) aspects of the pelvic girdle and pelvic fin in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengerii* (C) and *Notacanthus chemnitzii* (D). BP, basipterygium; FS, fulcral spine; IR, innermost radial; PP, posterior process; R, pelvic fin soft ray; S, pelvic fin spine. Cartilaginous radials embedded under connective tissue not illustrated. Scales indicate 5 mm.

The basipterygium is triangular, with a cartilaginous anterior tip and posterior portion. Anteriorly, the bone narrows slightly in *Aldrovandia*, but considerably more so in the other genera. A single posteromedial process is short in *Aldrovandia* and *Lipogenys*, and long in the other two genera.

The pelvic radials, situated posterior to the basipterygium, support the pelvic fin rays. The innermost radial is ossified posteriorly, being triangular in *Aldrovandia* and tear drop-like in the other genera. The other radials are cartilaginous and oval.

The pelvic fin has a single fulcral spine, occupying the outermost position among the fin rays, and an additional eight soft rays in *Aldrovandia*, 10 soft rays in *Polyacanthonotus rissoanus*, two spines and seven soft rays in *Lipogenys*, one spine and nine soft rays in *P. challengerii*, and three spines and six soft rays in *Notacanthus*. The fulcral spine is long in *Aldrovandia*, short in the other genera. The first and second spines and first soft ray are serrated, and the first soft ray hard in *Lipogenys*, whereas all of the pelvic fin rays lack serrations, the soft rays all being flexible, in the other genera.

Postcranial axial skeleton and median fin supports (Figs. 18–20). The postcranial axial skeleton comprises the vertebrae, epineurals and pleural ribs. The median fins include one dorsal and one anal fin, which are supported by the proximal, median and distal pterygiophores and stay. Supraneurals are absent.

The vertebrae include abdominal and caudal elements. The former numbered 64 in *Aldrovandia* and *Polyacanthonotus rissoanus*, 62 in *Lipogenys*, 57 in *P. challengerii*, 50 in *Notacanthus chemnitzii* and 45 in *N. spinosus* specimens examined in this study, each being made up of the centrum, neural spine, neural arch and a pair of parapophyses. The neural spines of the anterior abdominal vertebrae are plate-like, becoming slender posteriorly. The third to ninth parapophyses are elongate and fused to their counterparts in *Lipogenys*, but are short and separated in the other genera. The fourth to 47th parapophyses are attached to the pleural ribs in *Aldrovandia*. Each caudal vertebra typically comprises the centrum, neural spine, neural arch, hemal spine and hemal arch. The first caudal vertebra is the 65th overall vertebra in *Aldrovandia* and *Polyacanthonotus rissoanus*, 64th in *Lipogenys*, 58th in *P. challengerii*, 51st in *Notacanthus chemnitzii* and 46th in *N. spinosus*.

The epineurals, connected to the lateral surface of the anterior centra, are slender bones embedded under the body muscle.

The pleural ribs, attached to the fourth to 47th parapophyses, are slender in *Aldrovandia* and absent in the other genera.

The proximal pterygiophores, divided into dorsal and anal series, support the fin rays. The dorsal series are stick-like in *Aldrovandia*, but triangular in the other genera. The second to 10th proximal pterygiophores of the dorsal series are

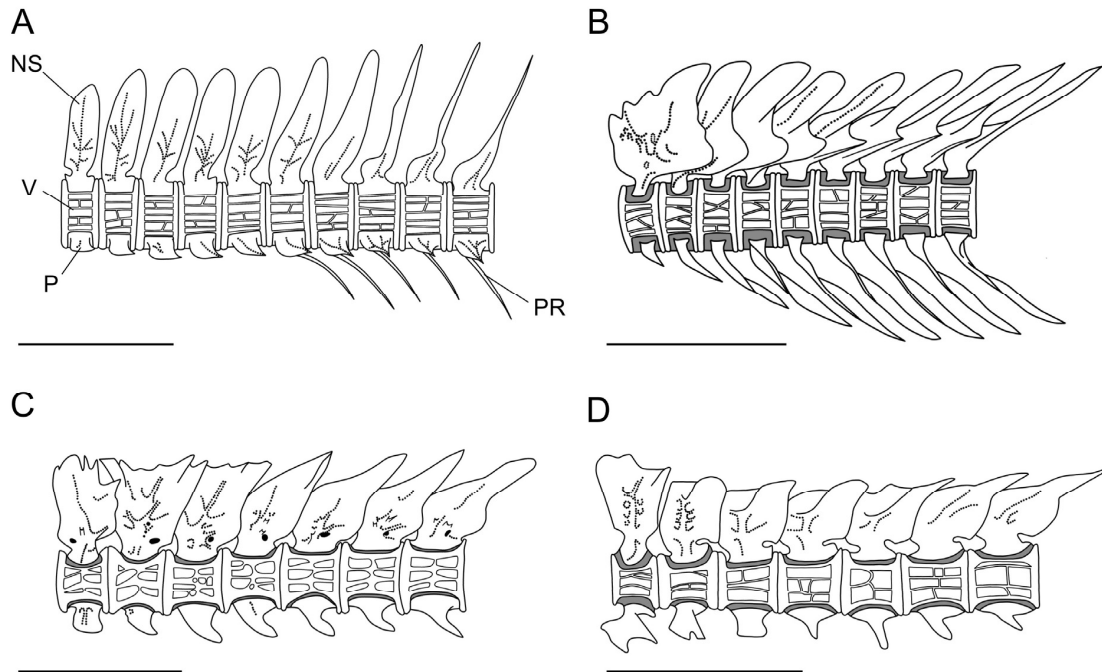


Fig. 18. Lateral aspects of anterior vertebrae in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengeri* (C) and *Notacanthus chemnitzii* (D). NS, neural spine; P, parapophysis; PR, pleural rib; V, vertebra. Epineurals embedded under muscle not illustrated. Scales indicate 5 mm.

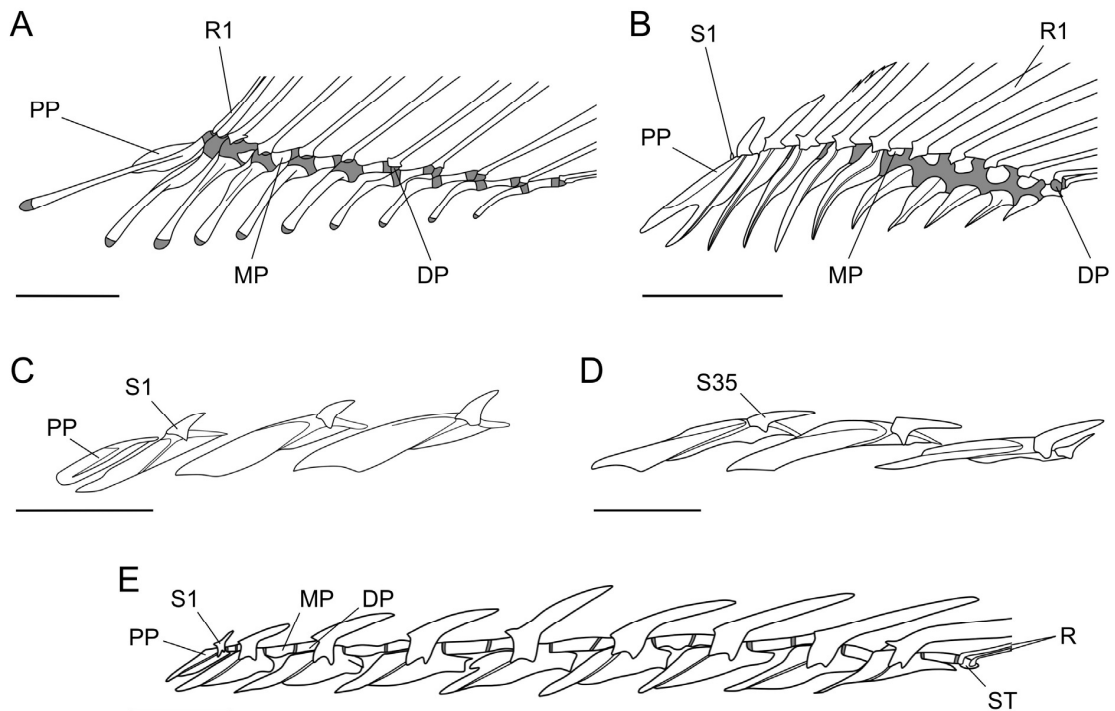


Fig. 19. Lateral aspects of the dorsal fin and its pterygiophores in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengeri* (C and D) and *Notacanthus chemnitzii* (E). DP, distal pterygiophore; MP, medial pterygiophore; PP, proximal pterygiophore; R, dorsal fin soft ray; S, dorsal fin spine. Scales indicate 5 mm.

continuous in *Lipogenys*, but are otherwise separated. The first proximal pterygiophore of the dorsal series supports one soft ray in *Aldrovandia*, two spines in *Lipogenys* and one

spine in *Notacanthus*, but supports no rays in *Polyacanthonotus*. The last proximal pterygiophore of the dorsal series supports two soft rays in *Aldrovandia* and *Lipogenys*, two

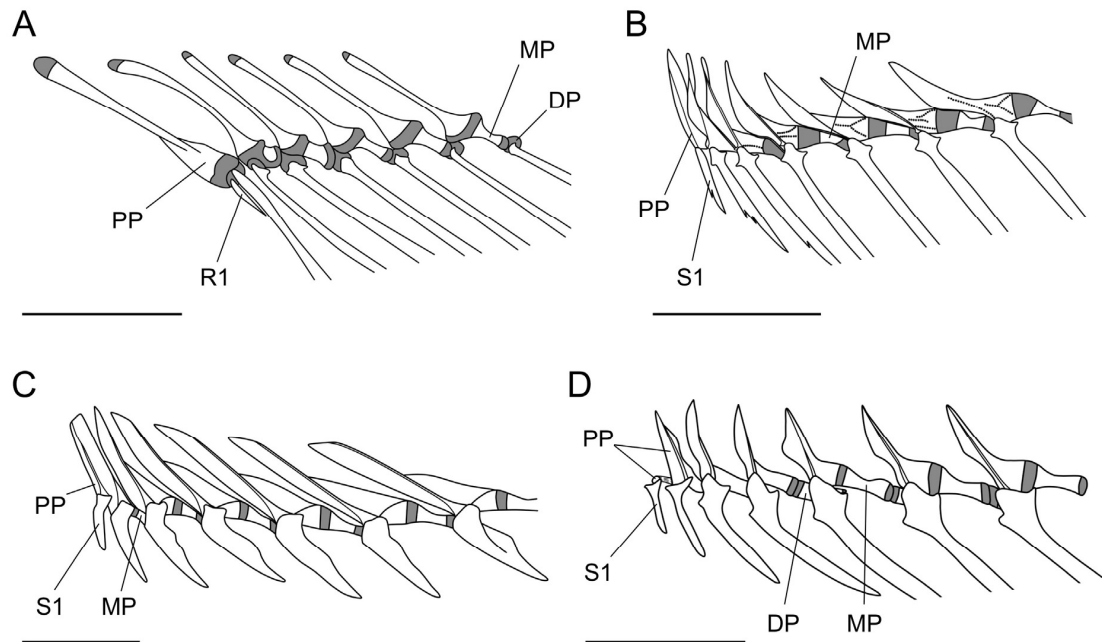


Fig. 20. Lateral aspects of the anal fin and its pterygiophores in *Aldrovandia affinis* (A), *Lipogenys gillii* (B), *Polyacanthonotus challengerii* (C) and *Notacanthus chemnitzii* (D). DP, distal pterygiophore; MP, medial pterygiophore; PP, proximal pterygiophore; R, anal fin soft ray; S, anal fin spine. Scales indicate 5 mm.

spines in *Polyacanthonotus* and one spine in *Notacanthus*. The anal series are stick-like in *Aldrovandia*, compared with triangular anteriorly and becoming stick-like posteriorly in the other genera. The first proximal pterygiophore of the anal series is extremely small in *Notacanthus*, but large and distinct in the other genera. The first proximal pterygiophore of the anal series supports two soft rays in *Aldrovandia*, one spine in *Lipogenys*, *Polyacanthonotus rissoanus* and *Notacanthus chemnitzii*, two spines in *P. challengerii*, and three spines in *N. spinosus*.

The medial pterygiophores are situated between the proximal and distal pterygiophores, being divided into dorsal and anal series. A dorsal series is absent in *Polyacanthonotus*, but present from the third pterygiophore in *Aldrovandia*, fifth pterygiophore in *Lipogenys* and first pterygiophore in *Notacanthus*. The dorsal series are triangular or stick-like in *Aldrovandia*, irregular in *Lipogenys* and stick-like in *Notacanthus*. The anal series are present from the second pterygiophore in *Aldrovandia*, fourth pterygiophore in *Lipogenys*, first pterygiophore in *Polyacanthonotus challengerii*, third pterygiophore in *P. rissoanus* and *Notacanthus spinosus*, and fifth pterygiophore in *N. chemnitzii*. The component elements are circular or stick-like in *Aldrovandia*, stick-like in the other taxa.

The distal pterygiophores are situated posterior to the proximal or medial pterygiophores, being divided into the dorsal and anal series. Those of the dorsal series are present from the first pterygiophore in *Aldrovandia* and *Notacanthus*, and from the eighth in *Lipogenys*. Individual elements are ball-like and cartilaginous in *Aldrovandia* and *Lipogenys*, com-

pared with stick-like and ossified (except for the posteriormost ball-like cartilaginous element) in *Notacanthus*. The dorsal series is absent in *Polyacanthonotus*.

A stay is situated posterior to the dorsal series pterygiophores in *Notacanthus chemnitzii*, being small and oval, and supporting two soft rays. It is absent in the other taxa. An anal series stay is absent in all genera.

Characters Available for Phylogenetic Analysis

Characters in the following 30 transformation series (TS) were considered to be available for the phylogenetic analysis, based on comparisons with two outgroups.

TS 1. Large unossified space on skull roof (0, absent; 1, present). The skull roof is completely ossified in *Aldrovandia* (character 1-0), whereas an unossified space is present in the other ingroups, as well as in both outgroups (character 1-1).

TS 2. Posterior process on parasphenoid (0, absent; 1, present). The parasphenoid has a pair of posterior processes in *Lipogenys*, *Polyacanthonotus* and *Notacanthus* (character 2-1), such being absent in *Aldrovandia* and both outgroups (character 2-0).

TS 3. Posterodorsal process on supraoccipital (0, absent; 1, present). The supraoccipital has a posterodorsal process in *Aldrovandia* and both outgroups (character 3-0), which is absent in the other ingroups (character 3-1).

TS 4. Cartilage C in cranium (0, absent; 1, present). Cartilage C is absent from the cranium in *Polyacanthonotus rissoanus*, as well as in both outgroups (character

4-0), but present in the other taxa (character 4-1).

TS 5. Teeth on maxilla (0, present; 1, absent). Teeth are present on the maxilla in *Aldrovandia* and both outgroups (character 5-0), but absent in the other three ingroup genera (character 5-1).

TS 6. Dorsal spine on maxilla (0, absent; 1, present). The maxilla has a single dorsal spine posteriorly in *Lipogenys*, *Polyacanthonotus* and *Notacanthus* (character 6-1), such being absent in *Aldrovandia* and both outgroups (character 6-0).

Remarks. — Forey et al. (1996) supported Marshall's (1962) suggestion that Halosauridae had a single spine on the posterior margin of the maxilla, as did Notacanthidae (including *Lipogenys*, *Polyacanthonotus* and *Notacanthus*). However, it was determined in the present study that a posteriorly positioned spine was absent on the maxilla in the halosaurid *Aldrovandia*, although a dorsal spine was present posteriorly on the bone in *Lipogenys*, *Polyacanthonotus* and *Notacanthus*. However, it was also found here that one or two anterior processes are present on the maxilla in *Aldrovandia* and Notacanthidae, including *Lipogenys*, *Polyacanthonotus* and *Notacanthus*. Because Marshall (1962) referred to "the spine-like process of the maxilla", it is probable that he had observed the anterior processes, instead of the dorsal spine identified here.

TS 7. Supramaxilla (0, present; 1, absent). The supramaxilla is present in *Aldrovandia* and both outgroups (character 7-0), but absent in the other ingroups (character 7-1).

TS 8. Coronomeckelian (0, present; 1, absent). The coronomeckelian is present in *Notacanthus*, as well as in both outgroups (character 8-0), but absent in the other three ingroup genera (character 8-1).

TS 9. Teeth on ectopterygoid (0, absent; 1, present). Teeth are present on the ectopterygoid in *Aldrovandia* (character 9-1), but absent in the other three ingroup genera (character 9-0). Similarly, teeth are present on the ectopterygoid in *Megalops*, but absent in *Pterothrissus*.

TS 10. Quadrate and symplectic (0, firmly attached; 1, separated). The quadrate is firmly attached to the symplectic in *Aldrovandia* and *Lipogenys*, as well as in both outgroups (character 10-0). It is separated from the symplectic in *Polyacanthonotus* and *Notacanthus* (character 10-1).

TS 11. Number of connective tissue nodules (0, absent; 1, one; 2, two) (ordered as 0-1-2). Two connective tissue nodules are present in *Aldrovandia* (character 11-2), whereas one nodule is present in the other ingroups (character 11-1). A connective tissue nodule is absent in both outgroups (character 11-0).

TS 12. Opercle (0, simple; 1, branched). The opercle is simple in *Aldrovandia* and both outgroups (character 12-0), but divided into many branches in the other ingroups (character 12-1).

TS 13. Posterior portion of subopercle (0, simple; 1,

branched). The posterior portion of the subopercle is simple in *Aldrovandia* and *Lipogenys* (character 13-0), but divided into many branches in the other ingroups (character 13-1). The posterior portion of the subopercle is simple in both outgroups.

TS 14. Teeth on basihyal (0, present; 1, absent). The basihyal has a single tooth in *Polyacanthonotus challengeri* and four in *P. rissoanus* (character 14-0), whereas teeth are absent in the other ingroups (character 14-1). Both outgroups possess a tooth plate on the basihyal.

TS 15. First and second basibranchials (0, sutured; 1, separated). The first and second basibranchials are sutured to each other in *Aldrovandia*, *Polyacanthonotus* and *Notacanthus* (character 15-0), but separated in *Lipogenys* (character 15-1). They are also separated in *Megalops*, but sutured together in *Pterothrissus*.

TS 16. Second and third basibranchials (0, continuous; 1, separated). The second and third basibranchials are continuous via cartilage in *Aldrovandia* and *Notacanthus spinosus*, as well as in both outgroups (character 16-0), whereas they are separated in the other ingroups (character 16-1).

TS 17. Long tooth plate firmly attached to first, second and third basibranchials (0, present; 1, absent). A long tooth plate is firmly attached ventrally to the first three basibranchials in *Aldrovandia* and both outgroups (character 17-0), but is absent in the other ingroups (character 17-1).

TS 18. Tooth plate on fourth basibranchial (0, present; 1, absent). A tooth plate is firmly attached ventrally to the fourth basibranchial in *Aldrovandia* and both outgroups (character 18-0), but is absent in the other ingroups (character 18-1).

TS 19. Tooth plates on fifth ceratobranchial (0, present; 1, absent). Tooth plates are firmly attached dorsally to the fifth ceratobranchial in *Aldrovandia* and both outgroups (character 19-0), but are absent in the other ingroups (character 19-1).

TS 20. Uncinate process on first epibranchial (0, present; 1, absent). An uncinat process is present on the first epibranchial in *Aldrovandia* and *Notacanthus*, as well as in both outgroups (character 20-0). It is absent in the other ingroups (character 20-1).

TS 21. Uncinate process on second epibranchial (0, absent; 1, one process present; 2, two processes present) (ordered as 0-1-2). Two uncinat processes were recognized in *Aldrovandia* (character 21-2), such processes being absent in the other ingroups (character 21-0). An uncinat process is present on the second epibranchial in both outgroups (character 21-1).

TS 22. First pharyngobranchial (0, present, ossified; 1, present, cartilaginous, 2; absent) (unordered). The first pharyngobranchial is ossified in *Aldrovandia* and both outgroups (character 22-0), and cartilaginous in *Notacanthus spinosus* (character 22-1). The bone is absent in the other ingroups

(character 22-2).

TS 23. Tooth plate on third pharyngobranchial (0, present; 1, absent). A tooth plate is present dorsally on the third pharyngobranchial in *Aldrovandia* and both outgroups (character 23-0), but absent in the other ingroups (character 23-1).

TS 24. Fourth pharyngobranchial (0, present; 1, absent). The fourth pharyngobranchial is present in *Aldrovandia* and both outgroups (character 24-0), but absent in the other three genera (character 24-1).

TS 25. Supratemporal (0, present; 1, absent). The supratemporal is present in *Polyacanthonotus challengerii* and both outgroups (character 25-0), but absent in the other ingroups (character 25-1).

TS 26. Posttemporal (0, present; 1, absent). The posttemporal is present in *Aldrovandia* and *Polyacanthonotus challengerii*, as well as in both outgroups (character 26-0), whereas it is absent in the other ingroups (character 26-1).

TS 27. Posttemporal and cranium (0, attached; 1, separated). The posttemporal is attached anteriorly to the cranium in *Aldrovandia* (character 27-0), but separated from the latter in *Polyacanthonotus challengerii* (character 27-1). The bone is absent in *Lipogenys* and *Notacanthus*, thus being coded as “?” for those two genera. Although *Polyacanthonotus rissoanus* also lacks the posttemporal and should be coded as “?”, coding of both “1” and “?” for a generic taxon in a character matrix results in an automatic coding of “1” by MacClade ver. 4.0. Accordingly, *Polyacanthonotus* is coded as “1”. The supratemporal is attached to the cranium in both outgroups.

TS 28. Posterior process on basipterygium (0, long; 1, short; 2, absent) (ordered as 0-1-2). The posterior process of the basipterygium is short in *Aldrovandia* and *Lipogenys* (character 28-1), and long in *Polyacanthonotus* and *Notacanthus* (character 28-0). It is also long in *Megalops*, but is absent in *Pterothrissus* (character 28-2).

TS 29. Innermost radial (0, triangular; 1, tear drop-like). The innermost radial is triangular in *Aldrovandia*, as well as in both outgroups (character 29-0). It is tear drop-like in the other ingroups (character 29-1).

TS 30. Pleural ribs (0, present; 1, absent). Pleural ribs are present in *Aldrovandia* and both outgroups (character 30-0), but absent in the other three genera (character 30-1).

Interrelationships of the Suborder Notacanthoidei

Characters in 30 transformation series were used for the phylogenetic analysis to reconstruct the interrelationships of the suborder Notacanthoidei. The matrix of characters used for the analysis is given in Table 1. As a result of the analysis, a single most parsimonious tree was obtained (Fig. 21), with a consistency index of 0.84, rescaled consistency index 0.74 and tree length 39. Characters supporting each clade in the tree are also shown in Figure 21. Clade A, including all of the examined notacanthoids, is supported by four synapomorphies, 4-1 (presence of cartilage C on cranium), 8-1 (absence of coronomeckelian), 14-1 (presence of teeth on basihyal) and 25-1 (absence of supratemporal), including subsequent reversals or character transformations. In addition, it was confirmed that character 11-1 (one connective tissue nodule) also supports Notacanthoidei monophyly, which, in addition to two other apomorphies commonly recognized in all examined notacanthoids, gives a total of seven synapomorphies (plus five potential synapomorphies shared with Anguilliformes) supporting the monophyly of the suborder. Detailed descriptions of other clades and characters supporting them are given below. Characters labeled “r” indicate reversals.

Clade B1. Includes *Aldrovandia*. This clade is unambiguously supported by two apomorphies, characters 11-2 and 21-2, plus a further apomorphy, character 9-1, according to ACCTRAN. In addition, *Aldrovandia* has the following three autapomorphies: (1) sensory canal of sixth and seventh infraorbitals separated from that formed by the remaining five infraorbitals; (2) presence of ethmoid; and (3) interhyal cartilaginous.

Clade B2. Includes *Lipogenys*, *Polyacanthonotus* and *Notacanthus*. This clade is unambiguously supported by 18 synapomorphies, characters 1-1, 2-1, 3-1, 5-1, 6-1, 7-1,

Table 1. Matrix of characters in 30 transformation series in four notacanthoid genera and two outgroups

| Taxon | Transformation series and characters | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|-------------------------|--------------------------------------|---|---|-----|---|---|---|---|---|----|----|----|----|----|----|-----|----|----|----|----|----|-----|----|----|-----|-----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
| Outgroup | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Megalops</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Pterothrissus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| Ingroup | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Aldrovandia</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | |
| <i>Lipogenys</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | ? | 1 | 1 | 1 |
| <i>Polyacanthonotus</i> | 1 | 1 | 1 | 0&1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0&1 | 0&1 | 1 | 0 | 1 | 1 |
| <i>Notacanthus</i> | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0&1 | 1 | 1 | 1 | 0 | 0 | 1&2 | 1 | 1 | 1 | 1 | ? | 0 | 1 | 1 |

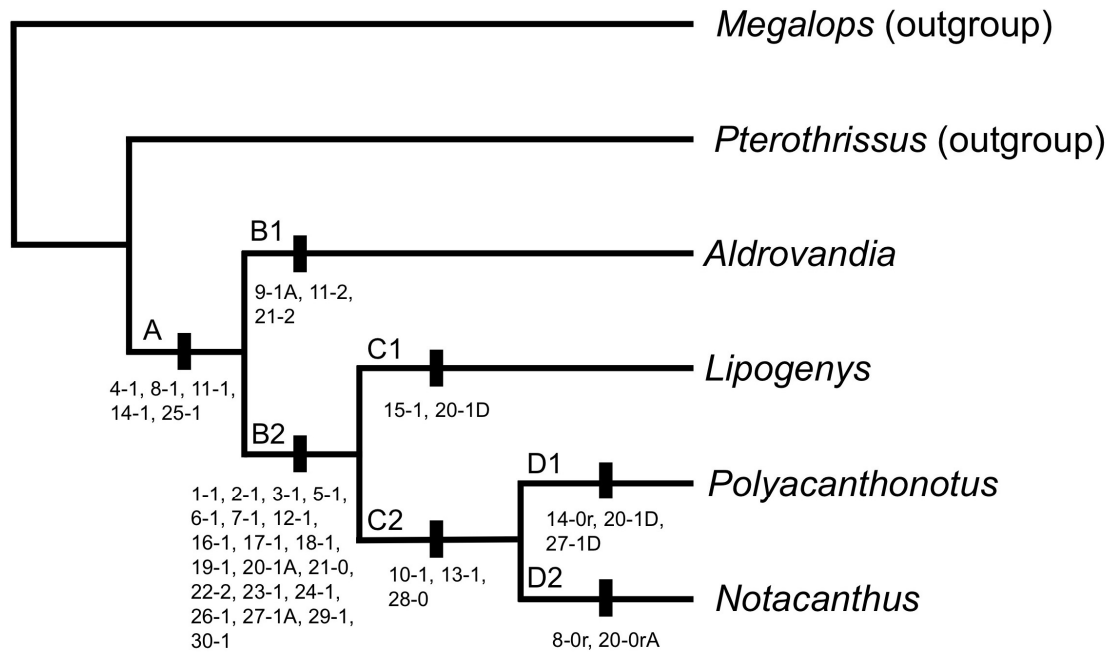


Fig. 21. Most parsimonious phylogenetic relationships of Notacanthoidei. Character numbers correspond to those in text and TABLE 1. Characters labeled “r”, and “A” and “D” indicate reversals, and apomorphies supporting each clade when ACC-TRAN and DELTRAN are employed, respectively.

12-1, 16-1, 17-1, 18-1, 19-1, 21-0, 22-2, 23-1, 24-1, 26-1, 29-1 and 30-1, plus a further two synapomorphies, characters 20-1 and 27-1, according to ACC-TRAN.

Clade C1. Includes *Lipogenys*. This clade is unambiguously supported by one apomorphy, character 15-1, plus a further apomorphy, character 20-1, according to DEL-TRAN. In addition, *Lipogenys* has the following 19 apomorphies: (1) absence of teeth on premaxilla; (2) dentary with a shallow notch receiving articular and Meckelian cartilage medially; (3) absence of teeth on dentary; (4) broad posteroventral process of quadrate; (5) absence of hypohyal knob; (6) glenoid cavity present for articulation with first basibranchial dorsally; (7) absence of interhyal; (8) absence of urohyal; (9) third basibranchial cartilaginous; (10) presence of an unidentified autogenous cartilage attached anteriorly to second basibranchial; (11) absence of uncinat process on third epibranchial; (12) absence of fifth epibranchial; (13) third pharyngobranchial cartilaginous; (14) absence of supraclithrum; (15) absence of cleithrum; (16) an unidentified cartilage present between anterior portions of pectoral girdles; (17) first and second spines, and first soft ray of pelvic fin serrated; (18) first soft ray of pelvic fin hard; and (19) third to ninth parapophyses fused with those on opposite side.

Clade C2. Includes *Polyacanthonotus* and *Notacanthus*. This clade is unambiguously supported by three synapomorphies, characters 10-1, 13-1 and 28-0.

Clade D1. Includes *Polyacanthonotus*. This clade is unambiguously supported by one apomorphy, character

14-0r, plus a further two apomorphies, characters 20-1 and 27-1, according to DELTRAN. In addition, *Polyacanthonotus* has two autapomorphies, (1) presence of an accessory cartilage on dorsal branchial arch and (2) absence of medial and distal pterygiophores in dorsal series.

Clade D2. Includes *Notacanthus*. This clade is unambiguously supported by one apomorphy, character 8-0r, plus a further apomorphy, 20-0r according to ACC-TRAN. In addition, *Notacanthus* has one autapomorphy, absence of palatine.

Classification

Monophyly of the suborder Notacanthoidei is supported by two synapomorphies, presence of cartilage D on the cranium and pelvic fin webs joined in the ventral midline, which were commonly found in all examined members of the suborder. Furthermore, following the phylogenetic analysis of Notacanthoidei, additional support was inferred for the suborder by another five synapomorphies: presence of cartilage C on the cranium, one connective tissue nodule, absence of the coronomeckelian, presence of teeth on the basihyal and absence of the supratemporal. In addition, because five synapomorphies were shared with the order Anguilliformes, the subordinal name “Notacanthoidei” should be used for the strongly-supported monophyletic group (being a valid taxonomic group) so as to distinguish it from other albuliforms, a definition consistent with that in Nelson (2006). It is cladistically reasonable to provide taxonomic names for clades B1

(including *Aldrovandia*), C1 (*Lipogenys*) and C2 (*Polyacanthonotus* and *Notacanthus*), respectively. For example, McDowell (1973) gave family names to these groups, recognizing Halosauridae, Lipogenyidae and Notacanthidae. However, clade B2, including *Lipogenys*, *Polyacanthonotus* and *Notacanthus*, forms a distinct monophyletic group, which is strongly supported by 18 unambiguous synapomorphies. Therefore, a taxon name should be provided for clade B2. Because family rank in Notacanthoidei is usually utilized for taxa representing the next lowest taxonomic category below suborder, Halosauridae and Notacanthidae are retained for clades B1 and B2, having a sister relationship with each other, respectively. Because clade C1 is a distinct group, having one unambiguous synapomorphy and 19 autapomorphies, it is appropriate to recognize subfamilial status for clades C1 and C2, such having a sister relationship with each other, viz. “Lipogenyinae” and “Notacanthinae”, respectively. Such a classification of Notacanthoidei, recognizing the subfamily Lipogenyinae in the family Notacanthidae, has not been previously proposed. The new classification is summarized below. Asterisks indicate genera not examined in this study.

Suborder Notacanthoidei

Family Halosauridae

Genus *Aldrovandia* Goode and Bean, 1896

Genus *Halosauropsis* Collett, 1896*

Genus *Halosaurus* Johnson, 1864*

Family Notacanthidae

Subfamily Lipogenyinae

Genus *Lipogenys* Goode and Bean, 1895

Subfamily Notacanthinae

Genus *Polyacanthonotus* Bleeker, 1874

Genus *Notacanthus* Bloch, 1788

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