

Description of *Aspidorhynchus arawaki* from the Late Jurassic of Cuba (Actinopterygii: Halecostomi)

Paulo M. BRITO

Abstract

Aspidorhynchus arawaki from the Jagua Formation, Pinar del Río Province (Oxfordian of Cuba), is described on the basis of acid prepared material. The Cuban species is distinguished from other species of the genus by the length of the premaxilla, the size of the maxillary teeth, the dimensions of the prementary, and the presence of a large median tooth in the posterior part of the prementary.

Introduction

The genus *Aspidorhynchus* is one of the earliest illustrated genera of fossil fishes, as it was figured by KNORR (1775: pls. XXIII, XXIV).

Aspidorhynchus was created by AGASSIZ (1833) to designate a Tithonian fish from the Solnhofen Limestone, Bavaria, which had been described as *Esox acutirostris* by BLAINVILLE (1818). The species of *Aspidorhynchus* from the Solnhofen Limestone have already been the subject of many studies and have been attributed to different specific names: *Aspidorhynchus longissimus* (MÜNSTER 1842), *A. speciosus* (AGASSIZ 1844), *A. mandibularis* (AGASSIZ 1844, WAGNER 1863), *A. ornatissimus* (AGASSIZ 1842, WINKLER 1871), or confounded with another species of the genus *Belonostomus*, *B. microcephalus* (WINKLER 1861).

EGERTON (1845) described *Aspidorhynchus euodus* from the Callovian of England. A few years later, two other species were discovered in England: *A. fisheri* from the Purbeckian (EGERTON 1854) and *A. crassus* from the Bathonian, this last one being the earliest known aspidorhynchid (WOODWARD 1890). SAUVAGE (1893) described *Aspidorhynchus sphenodes* from the Kimmeridgian of Ain in France. A good review of what was known up to the end of the 19th century can be found in the "Catalogue of Fossil Fishes" by WOODWARD (1895).

In the same year, ASSMANN (1906) reviewed the anatomy of *A. acutirostris* and HEINEKE (1906) indicated the presence of this taxon in the limestones of Nusplingen, Germany. A few years later, WOODWARD (1916) reviewed the *Aspidorhynchus* of the Wealdian and the Purbeckian of England. In this article, WOODWARD described a neurocranium considered an undetermined aspidorhynchid. The specimen was later studied by RAYNER (1948) and by PATTERSON (1975) who showed that it is in fact a Caturidae.

Some years later, SAINT-SEINE (1949) studied the *Aspidorhynchus* from Cerin, France, and demonstrated the similarity between this fauna and the fauna of the Solnhofen Limestone in Bavaria. SCHULTZE (1966, 1996) described the histology of the scales in aspidorhynchids and noted the absence of ganoine in *Aspidorhynchus*. RICHTER & THOMSON (1989) described two specimens of *Aspidorhynchus* from James Ross Isle, Antarctica. The first one (which is incomplete) was designed as the holotype of a new species, *A. antarcticus*, essentially based upon the shape and the histology of the scales. The second one named *Aspidorhynchus* sp., seems to be a *Vinctifer* (SCHULTZE & STÖHR 1996, BRITO 1997).

Recently, BRITO (1997) completed a revision of the family Aspidorhynchidae, giving a brief description of the Cuban species cited by GREGORY (1923) with no specific name. BRITO (1997) erected a new taxon, *Aspidorhynchus arawaki*.

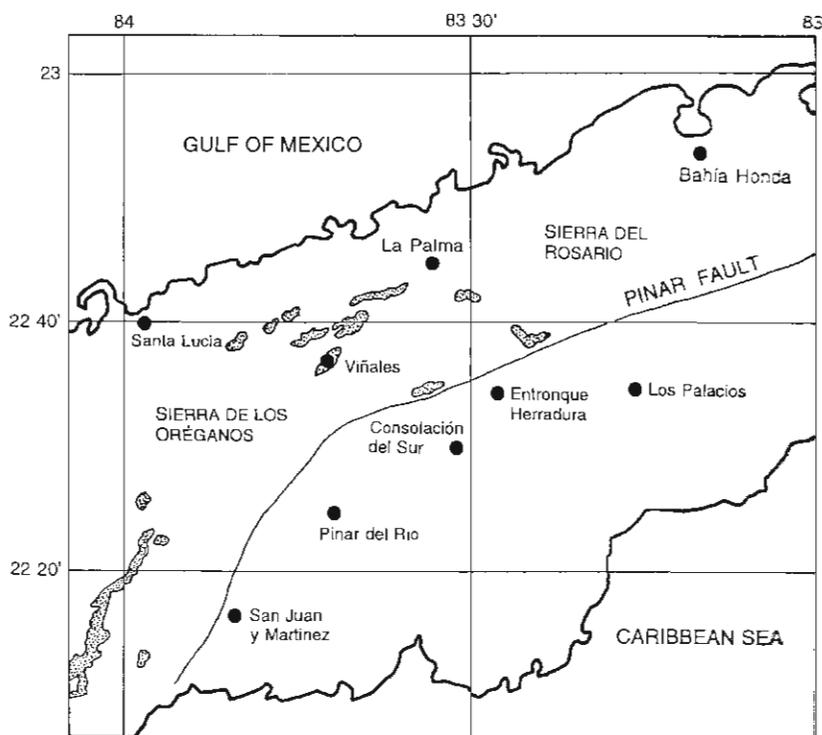
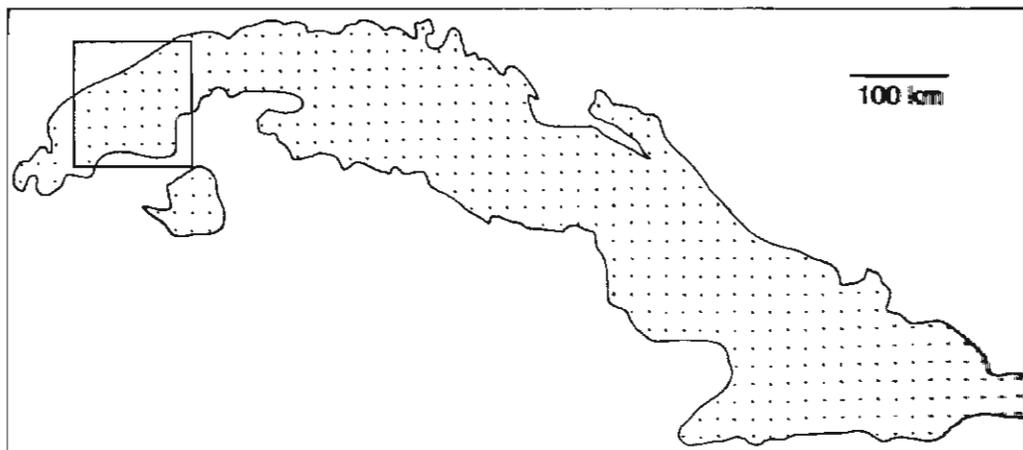


Fig. 1. Map of Cuba. The square area represents the area in where the Oxfordian localities of western Cuba are present; black stripes main outcrops. Redrawn from ITURRALDE-VINENT & NORELL (1996).

The goal of this study is to provide a more complete morphological description, as far as preservation permits, of this taxon from the calcareous concretions of the Jagua Vieja Member, Jagua Formation from Pinar del Río Province, in western Cuba (Fig. 1).

The Jagua Formation is an important Late Jurassic (Oxfordian) fossil vertebrate locality, with a diverse actinopterygian fauna known by *Gyrodus*, *Caturus*, *Sauropsis*?, *Eugnathides*, *Lepidotes*?, *Leiodontops*, and *Lepidotes* (e.g., GREGORY 1923, WHITE 1942, ARRATIA & SCHULTZE 1985, THIES 1999), as well as plesiosaurs, pterosaurs, and crocodylians (see ITURRALDE-VINENT & NORELL 1996).

Material and methods

The present study is based on four semi-complete specimens housed in the Division of Paleontology, National Museum of Natural History, Smithsonian Institution, Washinton D.C., U.S.A. (USNM 018645, USNM 018647, USNM 018648 [holotype], USNM 018653).

The specimens, lacking the posterior part of their bodies and caudal skeletons, retain some of their three dimensional characteristics and are suitable for chemical preparation. Two specimens, USNM 018648 and USNM 018653 have been acid prepared using the transfer technique of TOOMBS & RIXON (1959).

The other aspidorhynchids used for comparison were acid or mechanically prepared, using a pin vise and needles. These specimens are listed in BRITO (1997) and are housed in the following institutions: DGM-DNPM, Departamento nacional de Produção Mineral, Rio de Janeiro, Brazil; MNHN, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France; and PMB.VP, Universidade do Estado do Rio de Janeiro.

Systematic Paleontology

Division Halecostomi REGAN 1923

Family †Aspidorhynchidae NICHOLSON & LYDEKKER 1889

Genus †*Aspidorhynchus* AGASSIZ 1833

Type species: *Aspidorhynchus acutirostris* AGASSIZ 1833: 478.

†*Aspidorhynchus arawaki* BRITO 1997

For specific diagnosis see BRITO (1997).

Description

This is a medium sized aspidorhynchid. The standard length of the specimen should have been approximately 40 cm. The head of the holotype measures 14 cm from the anterior part of the rostrum until the posterior part of the operculum. By comparison of these measurements with those found in the other aspidorhynchids, one can estimate the proportions of the cranium-postcranial skeleton.

Skull roof: The skull roof is incompletely preserved, only the anterior part being accessible for study.

The premaxillae (Figs. 2A, B, 3A, B) form most of the rostrum. Each premaxilla is composed of two regions: The first one (superficial) is clearly ornamented with small longitudinal striations and forms the essential part of the rostrum. The second part (more profound and smooth) is covered by the adjacent dermal bones and forms a kind of tube (rostral tube sensu BRITO 1992) which penetrates caudally into the ethmoidal endocranial bones (e.g., lateral ethmoids).

The fine extremities of the premaxillae (right and left) are coupled along the dorsomedial line of the skull giving the impression of a single ossification (BRITO 1992, 1997). In fact, they are quite distinct throughout their length. Postero-ventrally, the premaxillae contact the unpaired and short vomer corresponding to about the posterior third of the rostrum and the parasphenoid. Caudally, they encircle the rostral and overhang the dorsal margins of the maxillae reaching the nasal region. It is at this level that the bone becomes the rostral tube, overlain by the rostral and the anterior extremities of the frontals. It is placed such that the premaxilla is fixed.

The rostral is an unpaired bone (Figs. 2A, B, 3A, B), deeply convex and twice as long as large. It inserts between the posterior right and left branches of the premaxilla in front, and overlays the anterior margin of the frontal bones at the rear. The infraorbital canal penetrates the bone at the anterior third to form the ethmoidal commissure. The latter is convex in front sending numerous canalicules (at least 10), all of which open in front of the commissure.

Only the anterior part of the frontal bones are preserved (Fig. 2A, B). They extend from the rostral bone posteriorly, having (at least on the preserved part) an equal width throughout their lengths. The supraorbital canal follows the lateral margin of the bone.

Although the parietal and the dermopterotic bones are not preserved, the pattern found in all aspidorhynchids is the fusion of the frontals with these bones (e.g., fronto-parieto-dermopterotics; BRITO 1997).

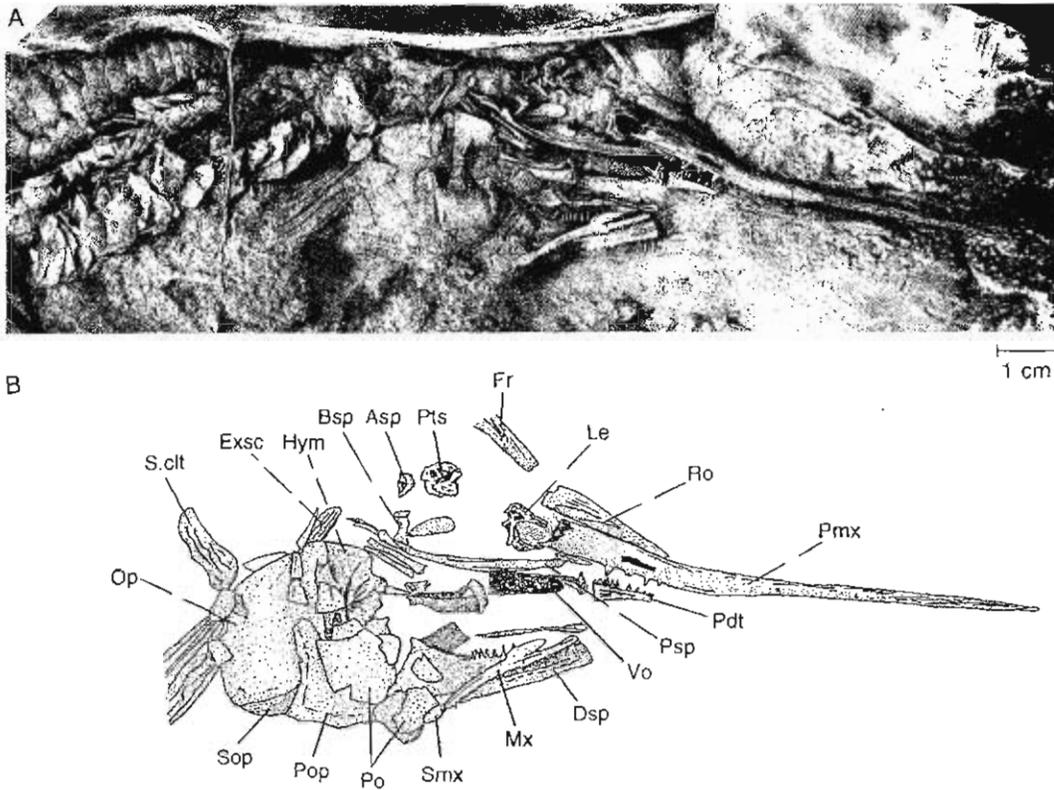


Fig. 2.
Aspidorhynchus arawaki (holotype, USNM 018648). **A**, right side of the skull and anterior part of the body; **B**, detail of the skull.

Abbreviations: **Ang**, angular; **Asp**, autosphenotic; **brc**, branchiostegal ray; **Bsp**, basisphenoid; **Cl**, cleithrum; **Dsp**, dentalosphenial; **Ecpt**, ectopterygoid; **Enpt**, endopterygoid; **Exsc**, extrascapula; **Fr**, frontal bone; **Hym**, hyomandibula; **Io**, infraorbital; **Le**, lateral ethmoid; **Mpt**, metapterygoid; **Mx**, maxilla; **Op**, operculum; **Pdt**, predentary; **Pmx**, premaxilla; **Po**, postorbital; **Pop**, preoperculum; **Psp**, parasphenoid; **Pts**, pterosphenoid; **Qu**, quadrate; **Rart**, retroarticular; **Ro**, rostral; **S.clt**, supraclithrum; **Smx**, supramaxilla; **Sop**, suboperculum; **Sy**, symplectic; **Vo**, vomer.

Therefore I presume that this is the disposition in *A. arawaki*.

Only one pair of extrascapular bones is found in *A. arawaki*, as in other aspidorhynchids (BRITO 1997). They are well-developed bones joined together along the cranial midline, slightly longer than wide, and asymmetrical. Caudally, these bones are concave in shape. Their lateral borders are linear and overlay the operculum.

Neurocranium: Although the braincase is incompletely preserved and only a few bones can be recognized in the specimen USNM 018648, the degree of fusion of the neurocranial bones found in *A. arawaki* is the same as that described for *A. acutirostris* (BRITO 1992, 1997).

The lateral ethmoids are separate bones (Figs. 2A, B, 4A, B). The anterior portion forms the innermost part of the nasal capsule. The posterior portion extends posteriorly by a horizontal process: Its dorsal surface supports the olfactory nerve, whereas the ventral border of the process forms the anterior myodome.

The pterosphenoid is a massive ossification (Fig. 2A, B) that forms the dorsal part of the trigeminofacial chamber and presents a long pedicel which determines the trajectory of the trigeminal and facial nerves (V and VII). The configuration of this chamber seems to be identical to that described and illustrated for *Vinctifer comptoni* by BRITO (1992: fig. 4).

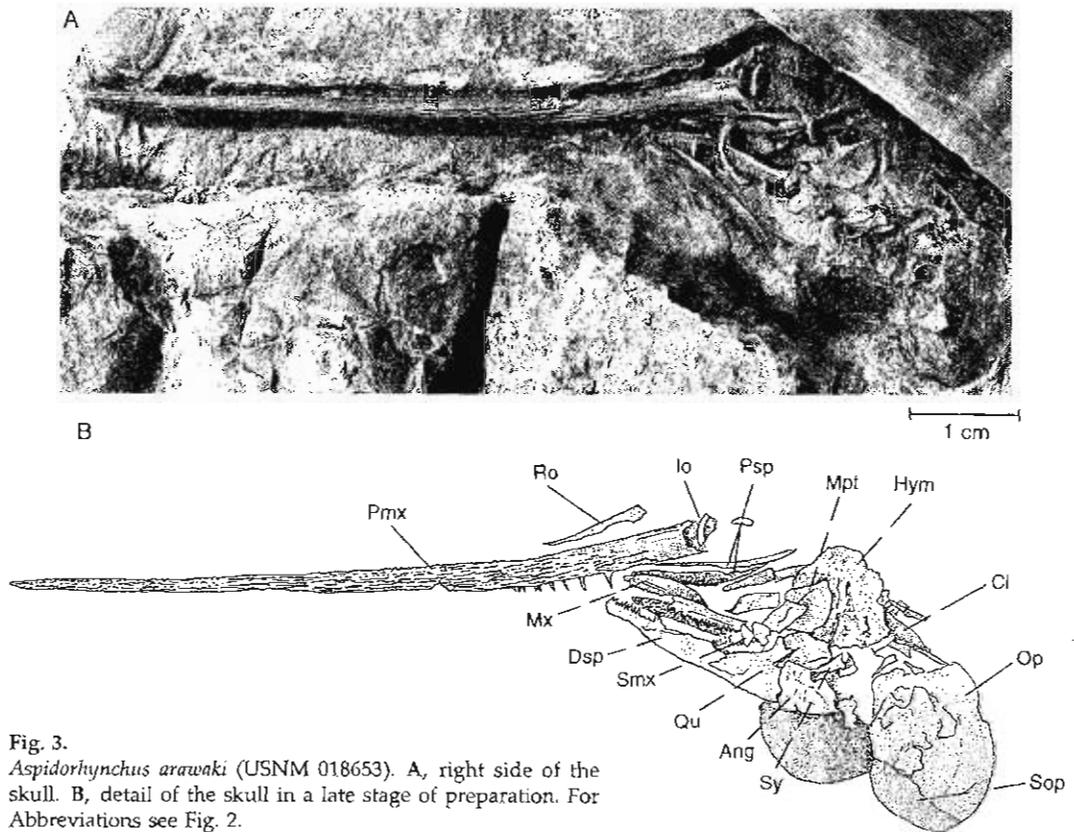


Fig. 3. *Aspidorhynchus arawaki* (USNM 018653). A, right side of the skull. B, detail of the skull in a late stage of preparation. For Abbreviations see Fig. 2.

The basisphenoid (Fig. 2A, B) has a slender ventral pedicel lying on the dorsal part of the parasphenoid, separating the right and left openings of the posterior myodome and two upper dorso-lateral arms forming the floor of the exit for the optic nerve (II). In its dorsal region, there are two small openings for the exit of the oculomotor nerve (III).

The autosphenotic (Fig. 2A, B) is a pyramidal bone which develops in the region of the post-orbital process. In aspidorhynchids with a complete preserved braincase, the anterolateral surface of the autosphenotic forms the dorso-posterior region of the orbit and reaches below the ascending process of the parasphenoid. The postero-lateral surface sutures with the prootic and presents a cavity which continues caudally forming the articular fossa for the hyomandibular bone (BRITO 1992).

The parasphenoid (Figs. 2A, B, 3A, B) is a fragile, thin bone which has a "T" cross-section along its length posterior to the ethmoidal region. Rostrally beyond the ethmoidal region, the bone is forked and compressed dorso-ventrally. As in *Vinctifer comptoni*, the bone bears only one pair of ascending processes directed upwards and backwards, and at mid-length presents a foramina for the efferent pseudo-branchial artery (BRITO 1992). Similar to the pattern found in the parasphenoid of *A. acutirostris*, the bone shows a tooth plate situated at the level of the ascending process of the parasphenoid. There is no notch for the internal carotid enclosed in the parasphenoid.

The vomer (Fig. 2A, B) is massive, three times longer than wide, and rounded in front. The ventral surface bears numerous small teeth and laterally has a depressed border corresponding to overlapping zones of the parasphenoid extremities.

Circumorbital bones: The circumorbital series is poorly preserved, thus the total number of infraorbitals is unknown. However, some of these bones were observed during the preparation of one specimen (USNM 018653). They are small rectangular elements.

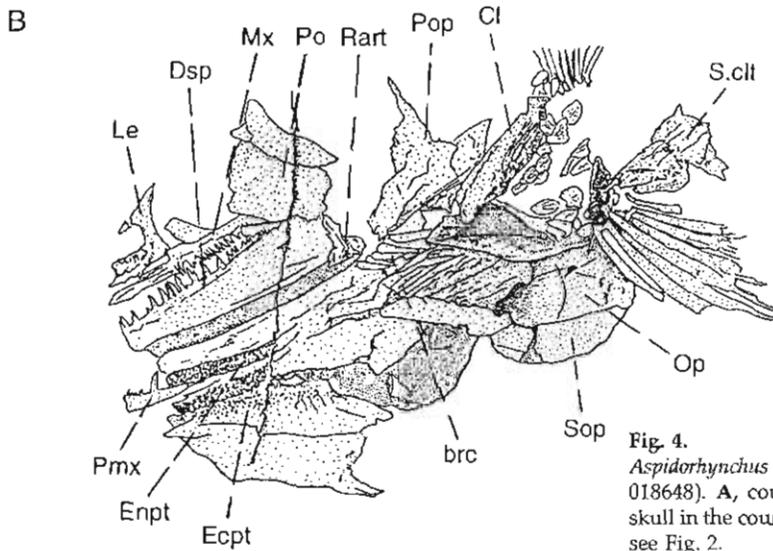
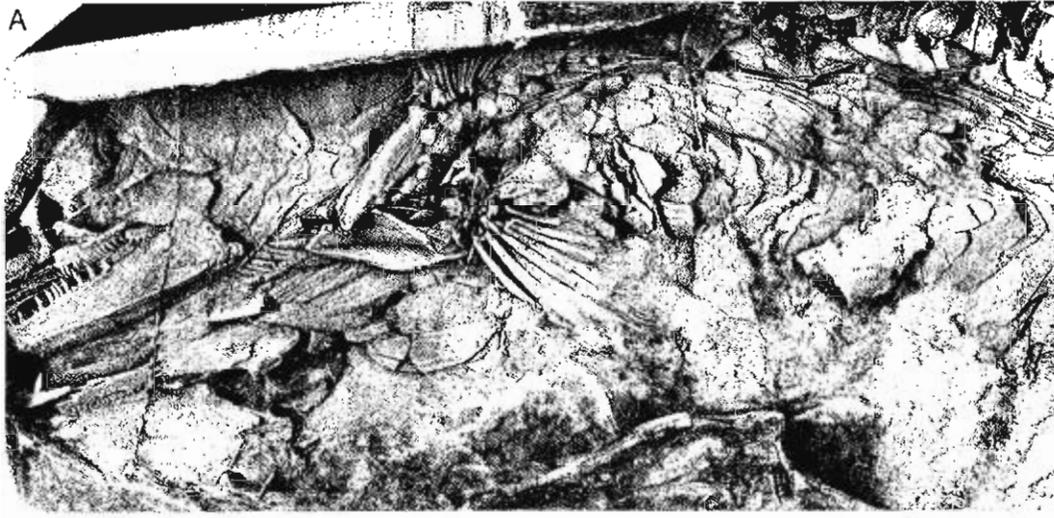


Fig. 4. *Aspidorhynchus arawaki* (holotype, USNM 018648). A, counterpart. B, detail of the skull in the counterpart. For Abbreviations see Fig. 2.

The first infraorbital bone, when duly articulated, is in ventral contact with the lamellar expansion of the maxilla that is located at mid-length of the bone and adjoins the nasal antero-dorsally. The postero-inferior part of the bone runs along the dorsal border of the entopterygoid. I could observe two others infraorbitals overlaying the anterior border of the postorbital bones as in other aspidorhynchids.

The dorsal circumorbital bones are lost. All other species of aspidorhynchids have a supraorbital and a dermosphenotic. The sclerotic ring consists of two sclerotic plates.

Cheek bones: Two large postorbital plates are present. They cover the anterior margin of the preoperculum.

The preoperculum (Fig. 2A, B) is divided into a vertical dorsal ramus and an expanded ventral part. The preopercular canal follows the posterior border of the bone and receives relatively few and undifferentiated canalicules. The posterior position of the preopercular canal is considered a familial synapomorphy (character 22 of BRITO 1997).

Opercular series: It consists of two bones: the operculum and the suboperculum (Figs. 2A, B, 3A, B, 4A, B). The interoperculum is absent.

The operculum is hypertrophied and (on its own) forms the majority of the opercular series. It is almost one and a half times deeper than long, bearing a ventral part which is more developed than the dorsal. The anterior border is straight, perpendicular to the head axis, and partially covered by the preoperculum. Its posterior border is strongly convex and overlays widely the supra-cleithrum. The dorsal linear border reaches the dermal cranial roof. The ventral border is inclined downwards at the rear, and rides over the dorsal margin of the suboperculum.

The suboperculum, reduced in size, has a triangular shape trapped in between the preopercular and opercular bones.

Twelve or thirteen branchiostegal rays are present (Fig. 4A, B). There is no gular plate.

Upper jaw: The upper jaw consists of the premaxilla, described above with the skull roof, maxilla, and one supramaxilla.

The maxilla is a long bone (Figs. 2A, B, 3A, B, 4A, B) with the same depth all along its length, with the exception of a rounded lamellar expansion jutting from the dorsal border at its midpoint. Transversely, the bone is compressed laterally in its posterior part and dorso-ventrally in its anterior third. The oral border of the maxilla bears a row of identical small teeth.

The supramaxilla (Figs. 2A, B, 3A, B) is a small oval bone whose length is about one quarter of the maxillary length. It is located above the postero-dorsal angle of the maxilla. Among aspidorhynchids, a unique supramaxilla is found in *Aspidorhynchus* and *Belonostomus* although *Vinctifer* lacks a supramaxilla due to the posterior prolongation of the maxilla (for discussion, see BRITO 1988).

Lower jaw: The lower jaw is composed by an unpaired prementary, and a pair of dentalosplenials, angulars, articulars, and retroarticulars.

The prementary (Figs. 2A, B, 5) is a short, triangular toothed bone linked to the rest of the mandible by a vertical suture. It is located above the postero-dorsal angle of the maxilla, five times as deep, and its length is equal to one quarter of that of the dentalosplenial. The oral borders of the prementary bear a row of large teeth; however, a big median tooth is at its posterior part.

The dentalosplenial constitutes the major part of the mandible, being low at its symphysis with the prementary, and increasing in height posteriorly to form the coronoid process. The bone is traversed by the mandibular sensory canal which runs along its ventral border. All teeth of the dentalosplenials are similar in size, large, though smaller than those of the prementary. The angular is reduced and I cannot distinguish a separate surangular bone, despite the fact that it was described by ASSMANN (1906) for *A. acutirostris* and by TAVERNE (1981) for *Belonostomus helgolanicus*.

The articular fossa for the quadrate is located on the dorso-posterior border of the mandible at the base of the coronoid process. The articular is a small peg-shaped bone; it forms together with the angular, the articular fossa for the quadrate. As in *V. comptoni*, there is a separate retroarticular in the ventro-posterior corner of the jaw (Fig. 4A, B) which is included in the joint facet of the quadrate.

Suspensorium and hyoid arch: The distal end of the hyomandibula presents an anterior surface pointing rostrally and downwards, upon which rests from front to back, the quadrate and the symplectic. The posterior surface of the hyomandibula contacts the posterior ceratohyal all along its length. The interhyal has not been observed. It may have been cartilaginous.

The quadrate (Fig. 3A, B) is a triangular bone, lacking the posteroventral process. The bone is characterized by a thickening of its posterior border which leans against the symplectic (Fig. 3A, B). The ventral end of the symplectic does not reach the mandible, and only the quadrate is involved in the quadrate-mandibular articulation. This pattern, which is also found in *Belonostomus*, differs from the double articulation of *Vinctifer* (BRITO 1988, 1997).

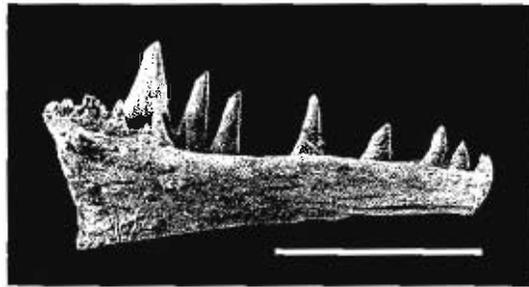


Fig. 5.
Aspidorhynchus arawaki (holotype, USNM 018648). Detail of the prementary. Scale bar = 5 mm.

I have not observed an autopalatine. The ectopterygoid has two branches: The anterior one is slightly longer than the posterior. The posterior branch overlaps the entopterygoid and is partially overlaid by the quadrate. The ectopterygoid bears teeth on its internal surface. An elongated toothed ectopterygoid with two branches is present in other aspidorhynchids.

The entopterygoid (Fig. 4A, B) presents an internal surface with small teeth similar to those of the ectopterygoid. The elongate entopterygoid doubles the dorsal length of the border of the ectopterygoid without reaching the rostral end of the latter. It goes beyond the posterior border of the ectopterygoid and abuts the internal surface of the metapterygoid, and to a lesser degree against that of the quadrate. Posteriorly, the entopterygoid reaches the hyomandibula.

The metapterygoid (Fig. 3A, B) is more or less square, barely longer than wide. It is composed of a lateral plate bearing a notch through where the trigeminal nerve passes. This notch delimits rostrally the processus basalis and externally the processus lateralis. The metapterygoid rests on the quadrate, the hyomandibula, and the ectopterygoid.

The anterior ceratohyal is a long and thin bone, approximately three times longer than deep. The dorsal border is slightly concave. The ventral one straight. The anterior border is lower than the posterior one. The bone is devoid of fenestra, canal, or groove for passage of the efferent hyoid artery.

Pectoral girdle and fin: The posttemporal bone is not preserved. The supracleithrum is a triangular bone covered anteriorly by the posterior part of the operculum. The supracleithrum covers the dorsal spinous process of the cleithrum as well as the first body scales. The bone is clearly ornamented by longitudinal striations which run parallel to its posterior border.

The vertical branch of the cleithrum (Fig. 4A, B) is short and narrow. The horizontal branch is longer, reaching the preoperculum anteriorly; it has an anterior lamella that forms the posterior wall of the branchial cavity. The exposed portion of the bone is narrow and (like the supracleithrum) ornamented by longitudinal parallel striations.

The pectoral fins are well developed and comprise eight rays preserved in the holotype (Fig. 2A, B). A similar number is preserved in specimen USNM 018653. The first ray dichotomizes in its distal region, and the following ones are segmented four times transversely. The first ray is not fused with the pterygium.

Vertebral column: The abdominal vertebrae are shorter than deep. The neural arches are not fused to the centra.

Squamation: The very thick scales are of the ganoid-type (sensu SCHULTZE 1996) and display the peg-and-socket type of articulation (BRITO & MEUNIER in progress). The flank scales are arranged in three rows of the same size. The scales may be ornamented with tubercles and/or ripples.

Dorsal to the flank scales there are three rows of small ornamented scales. The dorsalmost scale rows are ornamented by longitudinal parallel ripples separated by narrow intervals. Ventral to the flank scales, there are five or six rows of small, rectangular, smooth scales (Figs. 2A, 4A).

Comparisons between *Aspidorhynchus arawaki* and other aspidorhynchids

The identification of the Cuban species as a member of the Aspidorhynchidae was done by a comparison to other aspidorhynchid material (BRITO 1997).

Four synapomorphies of the family Aspidorhynchidae (BRITO 1997) can be recognized in *Aspidorhynchus arawaki* (e.g., presence of a long "rostrum" composed by the premaxillae; a supplementary bone in the lower jaw, the prementary; posterior position of the preopercular canal; and absence of an interoperculum).

Even though the posterior part of the body and caudal skeleton are unknown in the specimens described above, the Cuban taxon can be assigned to the genus *Aspidorhynchus* because of the presence of three rows of flank scales of the same size (BRITO 1997, SCHULTZE & STÖHR 1996) and the unfused condition of neurocranial bones. These features, plus the combination of cranial ossification patterns discussed below, confirm this taxonomic position.

A short triangular prementary is found only in the genera *Aspidorhynchus* and *Vinctifer*. In *Belonostomus*, this bone is longer, being sub-equal to the premaxilla.

The presence of a toothed premaxilla, a maxilla with a rounded lamellar expansion jutting from the dorsal borders, and a posterior supramaxilla are characters shared by the genera *Aspidorhynchus* and *Belonostomus*. In *Vinctifer*, the premaxilla is edentulous, the maxilla being divided into an anterior elongate ramus running parallel to the premaxilla, a plate-like postero-dorsal border, and there is no supramaxilla (BRITO 1988, 1997).

The parasphenoid is unknown in *Belonostomus*. It is edentulous in *Vinctifer*. A toothed parasphenoid had been described for *Aspidorhynchus acutirostris* and it is here described in the Cuban species.

The following combination of features is unique to *Aspidorhynchus arawaki* within the genus: length of the premaxilla, corresponding to 2/3 of the total length of the skull; maxillary teeth bigger than the teeth of other mandibular bones; size of the prementary three times as long as deep, and representing 1/3 of the dentalsplenic length; and the presence of a big median tooth in the posterior part of the prementary.

Conclusions

The Cuban taxon has been confirmed as a member of the Aspidorhynchidae based on four synapomorphies at least, e.g., the presence of a long "rostrum" composed by the premaxillae, presence of a prementary, the posterior position of the preopercular canal, and the absence of an interoperculum.

Aspidorhynchus arawaki shares with the other species of *Aspidorhynchus* the unfused condition of the neurocranial bones and the presence of three rows of flank scales of the same size. It differs from other species of the genus in the premaxillary length, the size of the maxillary teeth, the dimensions of the prementary, and the presence of a large median tooth in the posterior part of the prementary.

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Author's address:

Paulo M. Brito, Departamento de Biologia Animal e Vegetal, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier 524, Maracanã, Rio de Janeiro, 20559-900, Brazil. E-mail: pmbrito@uerj.br