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†*Tingitanius tenuimandibulus*, a new platyrrhinid batoid from the Turonian (Cretaceous) of Morocco and the cretaceous radiation of the Platyrrhinidae

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†*TINGITANIUS TENUIMANDIBULUS*, A NEW PLATYRHINID BATOID FROM THE TURONIAN (CRETACEOUS) OF MOROCCO AND THE CRETACEOUS RADIATION OF THE PLATYRHINIDAE

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ABSTRACT—An exceptionally well-preserved specimen of a batoid from the Turonian (Late Cretaceous) of Morocco has been named as †*Tingitanius tenuimandibulus*, sp. nov. The fossil has been identified as a member of the Platyrrhinidae and represents the oldest known example of a thornback ray. Mechanical and acid preparation of the ventral surface has revealed the general body form of the specimen and permitted teeth and three morphotypes of dermal denticles to be extracted. Computed tomographic (CT) scanning of the chondrocranium and thoracic region has allowed the detailed study of the skeletal elements concealed within the rock. The phylogenetic position of the new specimen and implications for the phylogenetic positions of the ‘rhinobatoids’ are discussed. †*Britobatos*, gen. nov., is erected to accommodate †*Raja primarmata* which is here shown to be a sister taxon to the Platyrrhinidae including †*Tingitanius*. It is likely that reassessment of isolated batoid teeth from the Cretaceous and Paleogene will confirm the former importance of the Platyrrhinidae.

INTRODUCTION

Articulated fossilized skeletal remains of batoids (skates, stingrays, electric rays, sawfish, and guitarfish) are especially rare and, if they are recovered, they are typically preserved as two-dimensional compression fossils as an artifact of their dorsoventrally flattened disc-like Bauplan. It is therefore of great scientific interest when new specimens are recovered that are not only articulated, but preserved in three dimensions and represent one of the earliest occurrences of a clade. The specimen described here was originally collected from the Cretaceous rocks near the town of Goulmima in southeast Morocco and obtained for study from a fossil dealer in the region.

The specimen is of a single individual, preserved in a concretion. Although not collected by the authors, the matrix, preservation, and fauna associated with this specimen are consistent with that of the main fossil-bearing horizon of the Goulmima region (Fig. 1; Claeson et al., 2010a). Fossils from that region are quarried and mined for commercial sale wherever the productive horizon outcrops, and a number of publications have been produced on ammonites (e.g., Kennedy et al., 2008), teleosts (e.g., Cavin et al., 2001), and reptiles (e.g., Bardet et al., 2003a, 2003b) from these excavations.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.; **NHMUK**, The Natural History Museum, London, U.K.; **SMF**, Senckenberg Museum, Frankfurt, Germany; **TNHC**, Texas Natural History Collection, Austin, U.S.A.; **UTCT**, University of Texas High-Resolution Computed Tomography Laboratory, Austin, Texas, U.S.A.; **ZMB**, Museum für Naturkunde, Berlin, Germany.

Anatomical and Miscellaneous Abbreviations—**af**, anterior fontanelle (Daniel, 1915, 1934, El-Toubi, 1949; = fontanelle antérieure, Cappetta, 1980; = median fontanelle, El-Toubi and Hamdy, 1959; = prefrontal fontanelle, Gegenbaur, 1872; = cavum praecerebrale, Allis, 1923, Holmgren and Stensiö, 1936); **af**, anterior fossa; **afu**, articular facet to the uvula; **aoc**, antorbital cartilage; **av**, abdominal vertebra; **bfl**, large basal foramina; **bfs**, small basal foramina; **br**, undifferentiated branchial elements; **cb**, ceratobranchial; **cb5**, fifth ceratobranchial; **db**, dermal buckler denticle; **eb5**, fifth epibranchial; **hb**, foramen for the hypobranchial branch of the facial nerve; **hm**, hyomandibula; **ja**, jugal arch; **mc**, Meckel’s cartilage; **mes**, mesopterygium; **met**, metapterygium; **nc**, nasal capsule; **pq**, palatoquadrate; **pr**, propterygium; **r**, rostrum; **s**, synarcual; **sc** (**s**), coracoid portion of scapulocoracoid; **sc** (**s**), scapular portion of scapulocoracoid; **sv**, first synarcual vertebral centrum; **tap**, tab-like anterior process (= horn-like anterior process, Brito and Dutheil, 2004); †, extinct.

GEOLOGIC SETTING

The general stratigraphy of the earlier Late Cretaceous of the Goulmima area of Morocco is well recorded (e.g., Lézin et al., 2012). Although microfossils (Ettachfini and Andreu, 2004; Lézin et al., 2012) and molluscs (Kennedy et al., 2008) were recorded from measured sections, the majority of the ammonite and vertebrate fossils known from the region were obtained from commercial fossil dealers, and exact provenance is lacking (Cavin et al., 2001). The majority of the excavations from which fossils were obtained are close to the top of the escarpment between 31°52′50″N, 4°50.00″W and 31°49′46″N, 4°57′22″W. Additional excavations occur along a river gorge close to the site where the measured section of Kennedy et al. (2008) was studied at 31°51′45″N, 4°56′32″W.

The geology of the area around Goulmima comprises a succession of Cretaceous rocks that unconformably overlie folded Paleozoic basement of the Anti Atlas (Fig. 1). The Cretaceous

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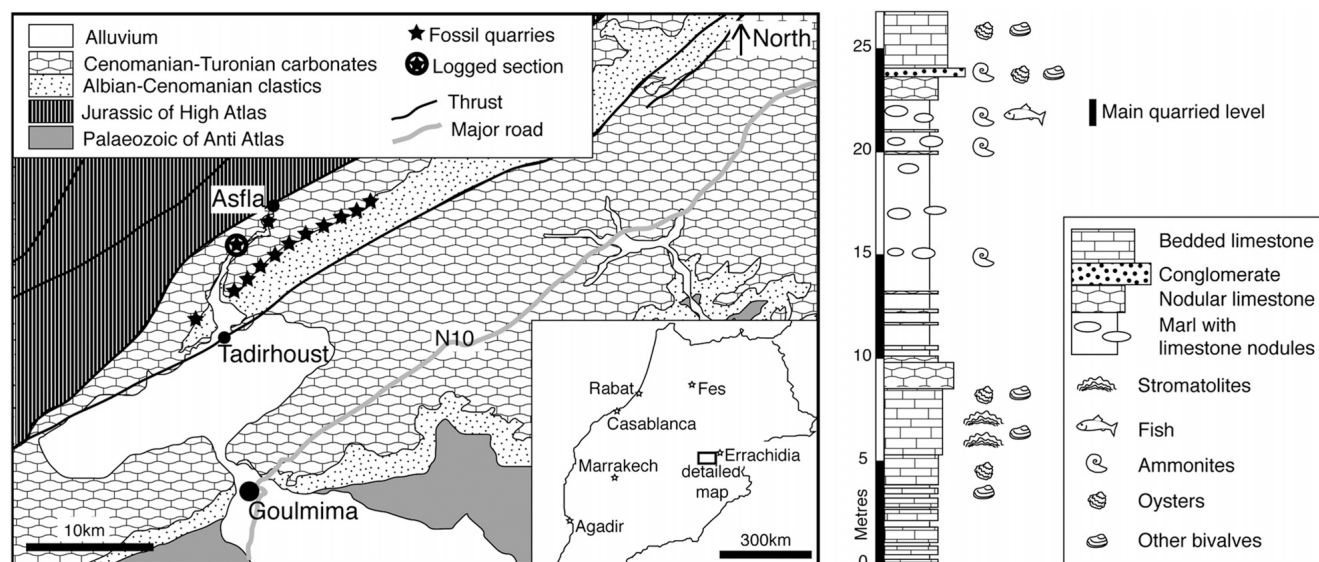


FIGURE 1. Locality map of Goulmima region.

succession forms a foreland to the folded and thrust successions of the High Atlas to the north. The Cretaceous rocks dip very gently to the northwest, and the succession is repeated by a reverse fault. The lower part of the Cretaceous succession comprises non-marine sandstones and mudstones of the Ifezouane and Aoufous formations, respectively. These formations are estimated to be Albian to middle Cenomanian in age. Above these formations are marine shelf carbonates of the Akroub Formation, which span the late Cenomanian and Turonian (Ettachfini and Andreu, 2004). Much of the Akroub Formation is composed of restricted and shallow-water limestones, with low-diversity bivalve shell beds and stromatolites at several horizons (Kennedy et al., 2008). The shallow-water carbonates pass upwards into marly limestones and marls that are themselves eroded and partly overlain by a further shallow-water succession with some deeper-water incursions (e.g., Lézin et al., 2012). The marls contain little or no benthos, but the upper part contains a rich pelagic fauna. Rounded carbonate concretions contain abundant and well-preserved ammonite and vertebrate fossils. In contrast to the other fossil groups, chondrichthyan microfossil remains are rare. An isolated tooth of the batoid *Ptychotrygon* was collected from the matrix of a fish skull collected in situ by the authors, with additional teeth of the same genus being figured by Ettachfini and Andreu (2004) and mentioned by Cavin and Dutheil (1999), Cavin et al. (2001; Cavin, pers. comm.). Furthermore, skeletal remains of chondrichthyan fossils are present but extremely rare. The authors are currently in possession of remains of three additional batoids that are currently under study: a skeleton of a small sclerorhynchid and a skull and an isolated synsacral of a large probable sclerorhynchid. There is also at least one additional sclerorhynchid specimen in a private collection.

MATERIALS AND METHODS

The specimen described here (NHMUK P66857) was obtained by the authors (D.W. and C.U.) from a fossil dealer and was evidently part of a large batch of Goulmima area material. The batoid skeleton is preserved within an oval carbonate concretion that was broken into three pieces, two of which have been reattached. The skeleton includes a nearly complete skull plus upper and lower jaw elements and supports (Fig. 2A). In addition, the axial skeleton is nearly complete and the pectoral girdle is

well preserved, although distal pectoral elements are fragmentary (Fig. 2A–C). The pelvic girdle is incomplete (Fig. 2A, E). Dorsal fins and the caudal region are missing. Teeth and denticles are present and well preserved.

Partial preparation on exposed parts of the ventral surface of the skeleton was conducted before the specimen was obtained. This preparation was rather crude, probably due to both the extremely hard matrix and lack of tools available, and some damage had occurred to parts of the skeleton. Subsequent preparation consisted of minor physical and chemical removal of the matrix. For acid removal of the matrix, exposed cartilage was hardened and the nodule placed in buffered 2% formic acid. After only a few minutes, it became obvious that the tesserae of the mineralized cartilage were often slightly disarticulated, and so acid extraction was halted to prevent damage to the specimen. The small amount of acid dissolution carried out liberated a number of teeth and denticles from the matrix, but it was not possible to record their exact provenance on the specimen (Fig. 3).

CT Scanning

The specimen was scanned at the High-Resolution Computed Tomography Laboratory at The University of Texas at Austin (UTCT) using their highest energy scanner (P250D). Slice data were further analyzed using VGStudio MAX 2.0 in the University of Texas Digital Methods Laboratory and using AVIZO in the Department of Biomedical Sciences at Ohio University. Complete CT scan details for the Goulmima specimen were previously published (Claeson et al., 2010a).

TAPHONOMY

Despite the exceptional preservation of the Goulmima fossils, there has been no systematic study of their taphonomy. In the field, the nodules containing the fossils are seen to lie parallel to bedding. When these nodules enclose fish remains, the extremities of the skeleton typically extend beyond the nodule and are either not preserved or collected.

The batoid skeleton is largely three-dimensional, with skeletal elements occupying several planes within the nodule, like the skeletons of many of the teleosts from the site (e.g., Cavin et al., 2010). This indicates that burial predated complete decay and



FIGURE 2. †*Tingitanius tenuimandibulus*, NHMUK P66857. **A**, ventral view of prepared concretion. **B**, lateral view of right scapulocoracoid, ventral is to top of page. **C**, anterior view of abdominal vertebra in cross section, dorsal is to top of page. **D**, line drawing of **C**. **E**, close up of distal clasper cartilages. (Color figure available online.)

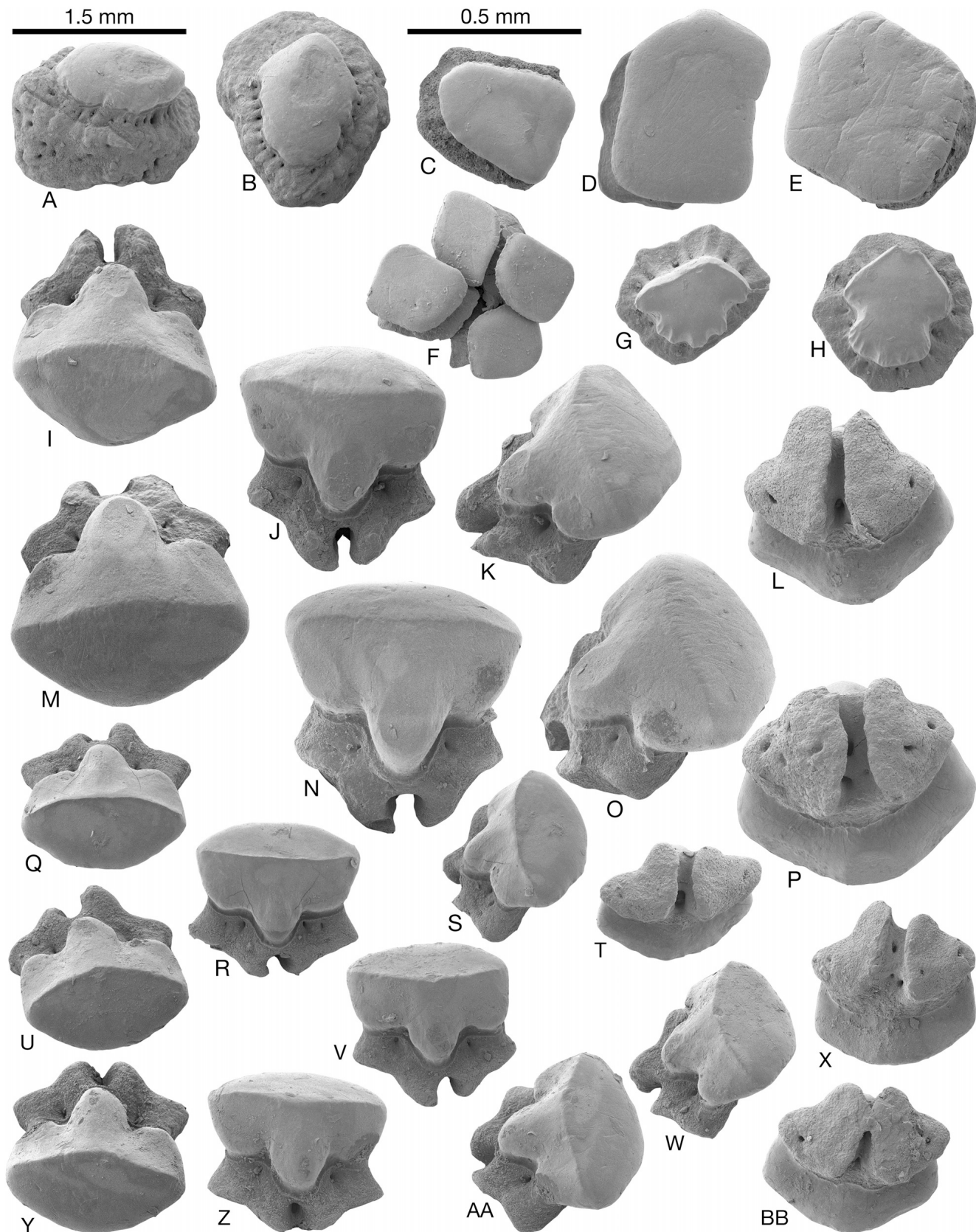


FIGURE 3. Dermal skeleton of †*Tingitanius tenuimandibulus*, NHMUK P66857. **A–E**, largest denticles; **F**, smallest denticles; **G, H**, midrange denticles with arrowhead-shaped groundmass; **I–BB**, dentition. Scale bar for **A** and **B** equals 1.5 mm Scale bar for **C–BB** equals 0.5 mm.

that there was minimal compaction prior to the lithification of the enclosing nodule. Some degree of anterodistal and dorsoventral shortening has occurred, with lateral shearing of the neurocranium, rotation of the scapulocoracoid, shattering of the supracapula, and shortening of the anterior vertebral column with breakage of several neural spines. Additionally, there was a minor amount of deformation along a plane from the left nasal capsule to the right otic capsule. As a result, the chondrocranium is shallower and elements look slightly more right-posterolaterally elongate than they would have been during life. This shear stress is repeated at different degrees in the axial skeleton. This deformation clearly predates lithification and presumably indicates initial minor compaction of a carcass resting obliquely within the soft sediment.

The batoid skeleton is associated with rare phosphatized muscle tissue (Fig. 2E). Phosphatized material is seen in the vicinity of the probable clasper and comprises fibrous material preserving original muscle fibers, but there is no apparent preservation of finer-scale details. Irregular patches of granular phosphatic material in the region of the pelvic girdle may also be somewhat degraded phosphatized soft tissue. The presence of preserved muscle tissue indicates extremely early diagenesis.

The overall taphonomic environment is similar to that of the Santana Formation of Brazil (see Martill, 1988), despite the lack of similarity of depositional environment. The fully marine setting of the Goulmima nodule bed contrasts with the marginal marine Santana Formation, which lacks fully marine invertebrates (Martill, 1988). The taphonomic conditions required for preservation of this type are therefore not restricted to any particular paleoenvironment.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880

BATOMORPHII Cappetta, 1980

RAJIFORMES Berg, 1940

PLATYRHINIDAE Jordan, 1923

TINGITANIUS, gen. nov.

Derivation of Name—After the Roman province of Tingitana, which coincides with the occurrence of this specimen in present day Kingdom of Morocco.

Type Species—†*Tingitanius tenuimandibulus*, sp. nov.

Diagnosis—Platyrrhinid batoid of moderate size. Unlike *Platyrrhina* (Müller and Henle 1838) in possessing a more medially placed anterior horn on the nasal capsule and a longer chondrocranium between the nasal capsules and the otic capsules. Unlike *Platyrrhinoidis* (Garman, 1881) in possessing a small, circular posterior dorsal roof foramen, instead of an anteroposteriorly broad and figure-eight-shaped fontanelle, and in possessing slender, laterally wide mandibular arch cartilages. Possesses short, tapered snout; plate-like antorbital cartilage; dorsal groundmass denticles are smooth and arrowhead-shaped; jaws gracile and straight; single anterior fontanelle; first complete vertebral centrum located extremely posterior along the length of the synarcual; and postpelvic processes present.

Remarks—Based on the phylogenetic analysis and apomorphy-based identification, we justify the erection of a new genus. It is most closely related to *Platyrrhinoidis*; however, unlike the extant taxon, †*Tingitanius* has straight, gracile jaws instead of stout-curved jaws, and a complete first vertebral centrum situated much farther posterior than *Platyrrhinoidis*; it also possesses a long clasper, whereas *Platyrrhinoidis* possesses a short one.

TINGITANIUS TENUIMANDIBULUS, sp. nov.

(Figs. 2–7)

Derivation of Name—From the possession of particularly slender jaws.

Holotype—Specimen NHMUK P66857 (concretion in three pieces) is housed at the Natural History Museum in London.

Diagnosis—As for genus.

Description

Comments on Preservation—The exposed skeletal elements are composed of a layer of small tesserae, prismatic cartilage (Dean and Summers, 2006), which surrounds an inner region of uncalcified cartilage (Fig. 2). This inner region is of the same X-ray attenuation as the surrounding matrix. Without petrographic thin-sections, we cannot say for certain if that is due to primary cementation or secondary replacement. Tesserae are visible around all skeletal elements, even in three-dimensional (3D) models of elements obscured by matrix (Fig. 4).

A great deal of the chondrocranium and pectoral skeleton appears weakly mineralized, especially the anterior-most portion of the rostrum and the pterygial cartilages. This is consistent with the typical pattern of cartilage density observed in volume-rendered models of extant elasmobranch taxa. A significant portion of the postcranial skeleton is also preserved, but distal appendages are absent. There is a second block to the concretion that preserves caudal vertebrae. The second block is fractured through the centrum of a caudal vertebra (Fig. 2C, D).

Denticles—The denticles extracted during the acid preparation of the specimen fall into three distinct morphological types: large, thorn-like dermal bucklers, arrowhead-shaped denticles and polygonal, smooth denticles (Fig. 3A–H). These three denticle morphologies (buckler, polygonal, and arrowhead-shaped) appear to relate to dermal covering of different parts of the body. They are all similar to the denticles of extant guitarfish such as *Aptychotrema*.

A single loose dermal buckler was recovered, but an additional segment of dermal buckler is present in situ in the specimen, where it lies on the posterior edge of the Meckel's cartilage. This is ovoid in surface view and about 1.5 mm long (Fig. 3A). The base is thick, constituting over two-thirds the height of the denticle, with a rough and irregular surface (Fig. 3B). The top surface of the base forms a narrow shelf from which a very short stem emerges. In addition to the large basal foramen, there are small foramina scattered over the surface and a row of closely spaced foramina around the base of the stem. The crown is low and smooth and smaller than the base. The crown is ovoid and on three sides hardly overhangs the stem, but it is somewhat expanded and pointed on its posterior end, with a greater degree of overhang.

The CT scan also reveals several high-density structures (HDS) of a similar size and shape to the buckler in the region just posterior to the jaws. It is likely that these represent bucklers originating from the region around or mediocaudal to the eye. Similar, but slightly larger, HDS are seen close to neural spines in the pectoral region, and appear to represent a sparse dorsal row of bucklers. A single, large HDS close to the rostrum may suggest the presence of a large rostral buckler. Small denticles are present in many places on the specimen. The polygonal denticles are widespread and common, with the arrowhead-shaped denticles being present largely in areas where the specimen is prepared to greater depth and hence further from the ventral surface.

Polygonal denticles are small, between 0.3 and 0.7 mm across, and have a rather irregular outline (Fig. 3C–E). The denticles are low, with the base and crown being of a similar size and shape and separated by a low and somewhat constricted neck. In apical view, denticles are irregularly rhombic to pentagonal, with larger denticles being more irregular, and small denticles more likely to be pentagonal. The crown is smooth with somewhat rounded

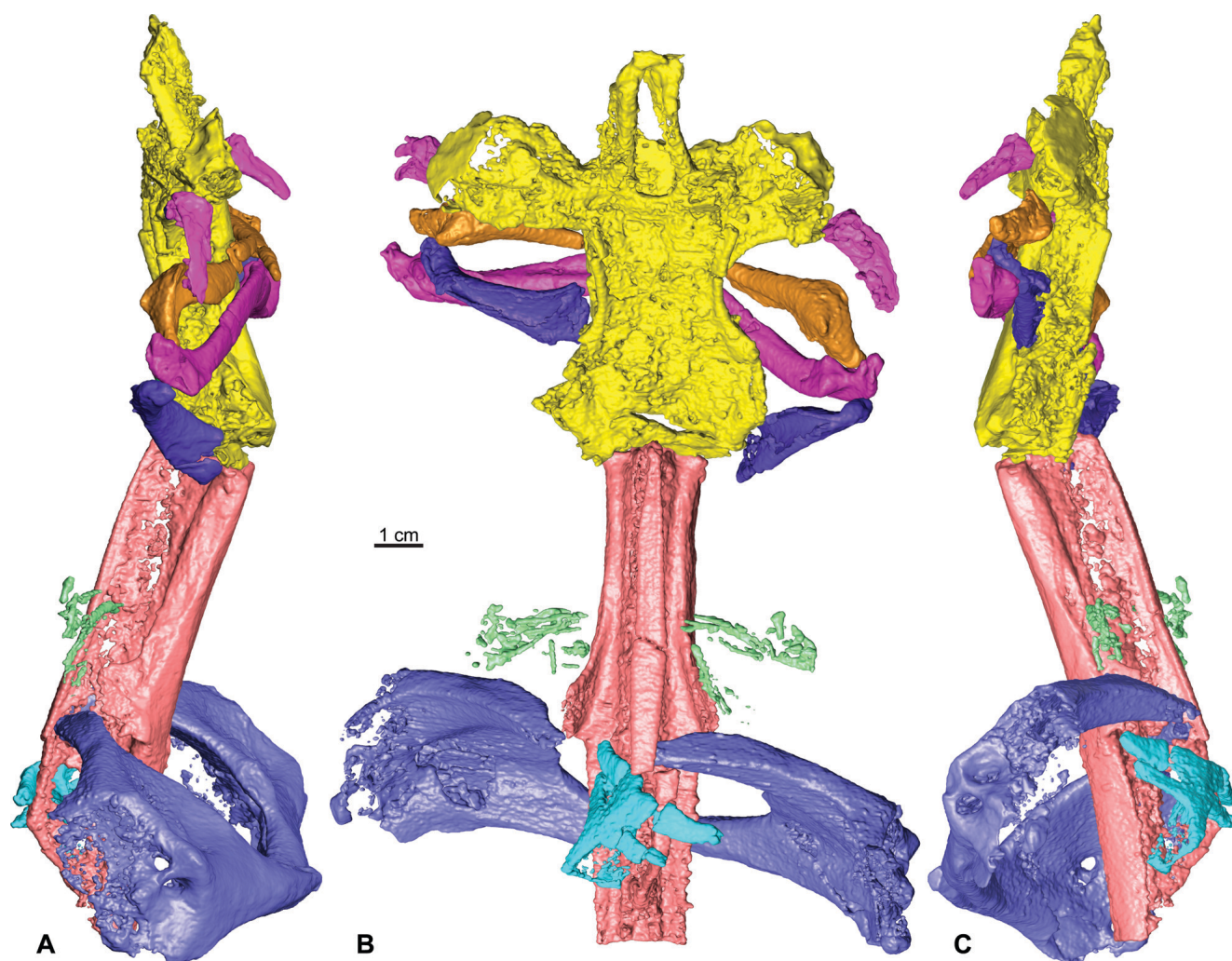


FIGURE 4. Digital surface model of anterior portion of †*Tingitanius tenuimandibulus*, NHMUK P66857, including synarcual and pectoral skeleton. **A**, right lateral view; **B**, dorsal view; **C**, left lateral view. Anterior to left of page. Gray outlines are added to help define cranial borders. Cranial images available in Figure 2 without outlines.

edges. Irregular pits and scratches are present on the surface of many denticles. A small set of articulated denticles shows them to be irregularly interlocked to form a continuous covering (Fig. 3F).

Arrowhead-shaped denticles are of a similar size to the polygonal ones, and have a more regular outline with a crown that is somewhat smaller than the base (Fig. 3G, H). The base is rounded to ovoid in surface view and slightly longer than wide. The basal face is flat and the sides of the root base taper upwards to form a low cone. Shallow grooves radiate down from the base of the denticle crown. The crown has a flat top, which varies in angle from close to parallel to the base of the denticle to an elevation of about 45 degrees. The crown is widest in the center, with a triangular apical region and a rounded posterior region. Small ridges are present on the edges of the crown but do not extend to the upper surface.

Teeth—Descriptive tooth terminology largely follows that of Cappetta (1987). Numerous teeth are visibly associated with the jaws of the specimen. Some degree of heterodonty is present within the jaw, which is largely evidenced by the size of the teeth. Upper teeth close to the symphysis are up to 0.8 mm across, whereas lateral upper and lower teeth are typically 0.4 to 0.5 mm

wide. No obvious differences can be seen between the morphologies of upper and lower lateral teeth. No unambiguous lower median teeth are visible.

The teeth are of underived ‘rhinobatoid’ form. Most teeth are close to symmetrical, but some of the smaller lateral teeth are somewhat asymmetrical (Fig. 3I–BB). The crown of each tooth is wider than deep or high. The labial face of the crown is flat to faintly convex with a smoothly oval outline. There is a sharply defined occlusal edge between the labial and lingual faces of the crown, with no central raised area or cusp, with a slightly obtuse angle between labial and lingual faces. Weak wear facets are present along the occlusal edge of some teeth (e.g., Fig. 3J). The lingual face is flat and smooth and tapers somewhat towards the base.

A short but robust uvula is present, the top of the uvula being about a third of the width of the tooth. The uvula tapers towards a rounded base and is not strongly swollen. There are no defined lateral uvulae, with the basal face of the lateral parts of the lingual crown face being gently convex. An articular facet is present on the uvulae of many teeth. (e.g., Fig. 3M). There is no ornamentation on any teeth. The tooth crown weakly overhangs the root lingually and strongly overhangs it labially.

The root is robust but lower than the crown, of a similar width, and somewhat lingually inclined. The overall shape of the root is similar in all teeth, but there is considerable variation in the form of the root basal face. The root is divided into two lobes by a well-developed nutritive groove (Fig. 3L, T, P, X), although this is partly or completely covered over by the flared base of the root lobes in some teeth (Fig. 3BB). The lingual faces of the root lobes are somewhat concave, with a poorly defined vertical groove below each pair of large foramina. The lateral and lingual faces of the root lobes are smooth and somewhat concave (Fig. 3L). The basal faces of the root lobes are flat and have a well-defined and sharp edge on all sides (Fig. 3J). The basal faces are somewhat angled away from the central groove. One or two small foramina are present towards the lateral parts of the root lobe basal faces. Where the root lobes have closed over the nutritive groove, the closure is preferentially towards the lingual side of the tooth (Fig. 3BB). The shape of the central uvula and absence of well-formed lateral uvulae are similar to that condition seen in *Platyrhinoidis*. This is different from other modern rhinobatids

and *Platyrhina*. Teeth of *Platyrhinoidis* differ in possessing a less well-defined occlusal edge and a low and bulbous cusp. Although the overall shape of the teeth is very different, the uvulae are not unlike those of *Rhynchobatus* and *Anoxypristis*.

Chondrocranium—Compared with most other extinct and extant guitarfishes and skates, this specimen possesses a stout rostral cartilage, most similar to the cartilage found in *Platyrhinoidis*. The rostrum appears to be short, although the apex is missing, and tapers a fair amount (Fig. 5A, B), though not to a distinct point as in *Platyrhina*, indicating that it probably failed to reach the tip of the snout. Present dorsally on the posterior aspect of the rostrum is a small, uncapped ovoid rim that contributes to the anterior fontanelle. Underlying the anterior fontanelle is an ovoid anterior fossa. In CT scans, it is clear that the floor of the rostrum was present, although it is only preserved at the anterior-most portion (Figs. 4A, 5B). In the ventral view of the fossil, the floor of the rostrum appears to be shaved off, exposing only a portion of the lateral walls of the rostrum and a part of the anterior-most floor (Fig. 5A). Rostral appendages were not preserved.

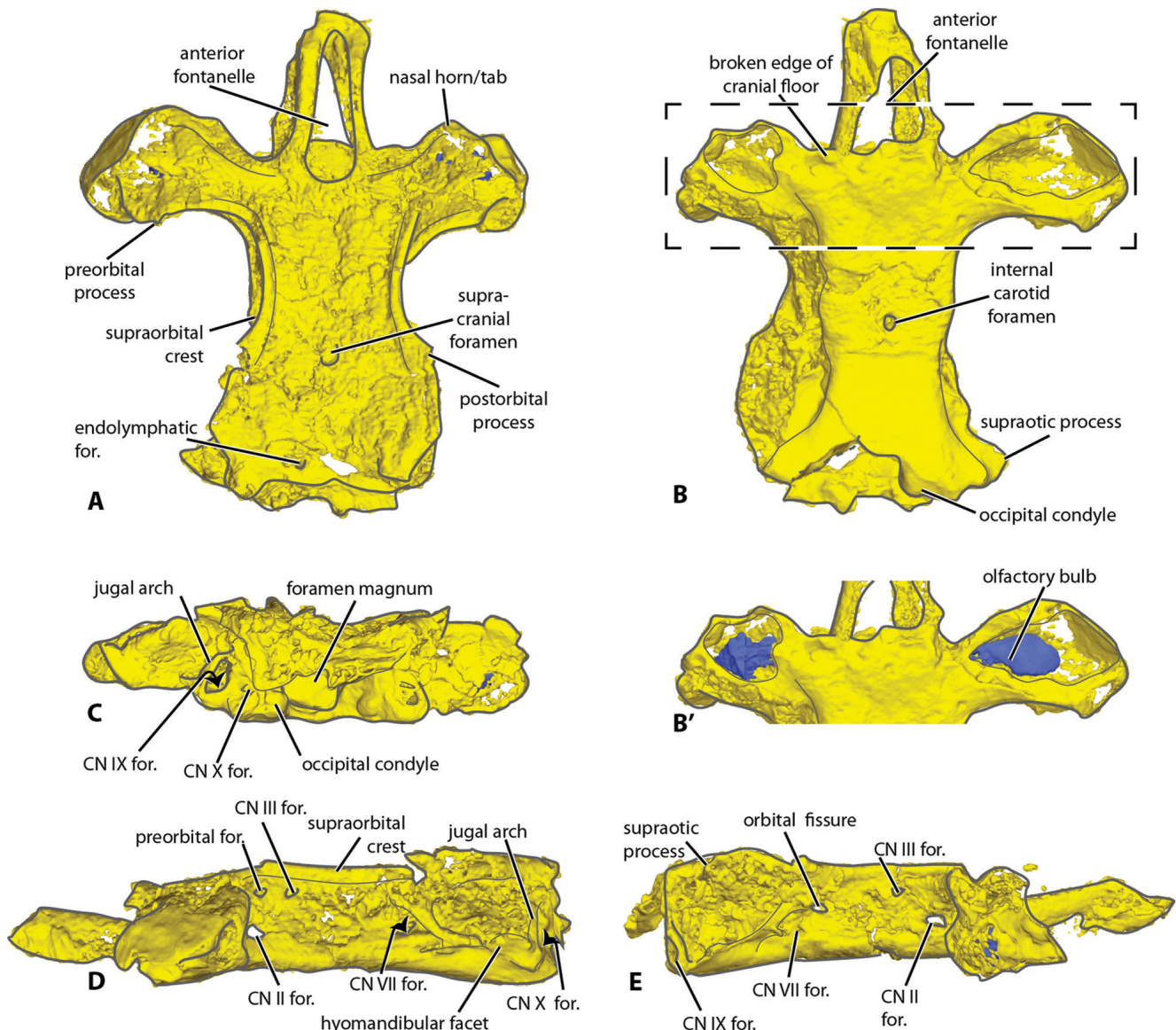


FIGURE 5. Digital surface model of chondrocranium of †*Tingitanius tenuimandibulus*, NHMUK P66857. **A**, dorsal view; **B**, ventral view; **C**, occipital view; **D**, left lateral view; **E**, right lateral view. **A**, **B**, anterior to top of page; **C**–**E**, dorsal to top of page. (Color figure available online.)

The oval nasal capsules are large, though thin-walled (Fig. 5A–C). They are anteriorly directed and laterally expanded, which is more like the condition in *Platyrhinoidis* than in *Platyrhina*, and they do not project ventrally (Fig. 5C–E). A dense mass is preserved within each nasal capsule that tapers as it approaches the olfactory foramen (Fig. 5B), which is consistent with the position and shape of cranial nerve (CN) I, olfactory bulbs (Hofmann and Northcutt, 2008). No distinct nasal cartilages were found within the nasal capsules. On the anterior margin of each nasal capsule, there is a distinct anterior tab-like process (Fig. 5A, B), considered the horn-like anterior process by Brito and Dutheil (2004). A stout plate-like antorbital cartilage articulates with the flat posterolateral surface of the nasal capsule (the ectethomoid process of Allis, 1923), and projects posterolaterally. The antorbital cartilage is narrowest distally (Figs. 2 and 4) and appears continuous with a fragment of the propterygium on the right side of the specimen. The distal end of the antorbital cartilage is incomplete so it is not clear if it was fringed like it is in *Platyrhinoidis* and *Platyrhina*. Medial to the articulation of the antorbital cartilage is a short, but well-developed preorbital process (Fig. 5A). Just posterior to the preorbital process, there is a foramen for the preorbital canal (Fig. 5D).

The chondrocranium is somewhat wide between the nasal capsules and the orbits, giving the chondrocranium a stout appearance. In this region, the braincase is wider dorsally than ventrally (Fig. 5A, B). The chondrocranium widens posterior to the orbits and the orbital rim terminates with a fairly small postorbital process. There is a small supracranial foramen on the cranial roof between the orbits and roughly one-third of the way behind the anterior fontanelle (Fig. 5A). This foramen is in the same position as, but is considerably smaller than, supracranial fontanelle, which is oval-shaped in *Platyrhina* and figure-eight-shaped in *Platyrhinoidis*.

The supraorbital crest is prominent along the dorsal-medial margin of the orbit, but it is fractured and slightly displaced on the right side of the specimen (Fig. 5A). Medial to the supraorbital crest is a narrow groove that would have contained the small foramina associated with branches of the superficial ophthalmic nerve. The otic region is approximately the same width as the width between the postorbital processes (Fig. 5). There is a fairly significant fracture through this region and thus the craniovertebral junction is incomplete and displaced (Figs. 2A, 4B, 5A, B). The left dorsal portion, however, is well preserved, and retains the endolymphatic foramen within a shallow endolymphatic fossa (Fig. 5A). The fracture appears to cross where the endolymphatic foramen would have been situated.

A jugal arch is present on the posterolateral side of the otic capsule (Fig. 5C). A facet for the hyomandibula is present just anteroventral to the jugal arch (Fig. 5C). Slightly medial to the posterior edge of the hyomandibular facet and ventral to the jugal arch is a depression containing the glossopharyngeal foramen (Fig. 5C, E). Medial to both jugal arches is the foramen for the vagus nerve (CN X foramen) and medial to CN X is the foramen magnum (Fig. 5C).

The ventral surface of the chondrocranium is smooth. It is complete between the nasal capsules until halfway between the otic capsules (Fig. 5B). Approximately central on the ventral surface is the internal carotid foramen. A portion of the unpaired notch (median facet of El-Toubi and Hamdy, 1959) that persists between the paired occipital condyles to accept the synarcual lip of the postcranial skeleton is preserved (Fig. 5B, C).

On the lateral wall of the chondrocranium, in the area of the orbit, it is possible to distinguish the preorbital foramen, the foramina for CNs II and VII, as well as the supraorbital fissure (Fig. 5D, E). Posterior to the foramen for CN II and anterior to the supraorbital fissure is a patch that probably represents the region of the optic stalk. Posterior to the foramen for CN VII is a diagonal bar, the posteroventral end of which is continuous with the hyomandibular facet (Fig. 5D, E). The hyomandibular facets on both sides of the specimen are incomplete but observable.

Visceral Skeleton—Labial cartilages are not present on this specimen. The paired Meckel's and palatoquadrate cartilages are particularly slender and approximately the same size as one another (Fig. 6). They are also straight, not sinuous as they are in some non-platyrhinid 'rhinobatoids' such as *Rhynchobatus*. The palatoquadrate is fractured on both sides of the median symphysis, but it is not significantly distorted. On the proximal (lateral) end of the Meckel's cartilage, there is a deep articular notch that accepts the tab-like process of the proximal part of the palatoquadrate (Fig. 6A, C). On the posterior surface of the proximal Meckel's cartilage is a cotylus for articulation with the narrow, knob-like distal end of the hyomandibula. The hyomandibula is narrowest behind the articulating distal knob and widest proximally (Fig. 6). The left hyomandibula is shifted at its proximal end so it rests in the orbital region. The right hyomandibula maintains its approximate articulation with the hyomandibular facet of the chondrocranium (Figs. 4 and 6).

Branchial cartilages are present but not well preserved. In the volume-rendered model, there is evidence of some gracile cartilages, perhaps ceratobranchials (Fig. 4). These appear lateral to the synarcual and therefore would have been displaced post-mortem. The basihyal and first hypobranchial cartilages are not

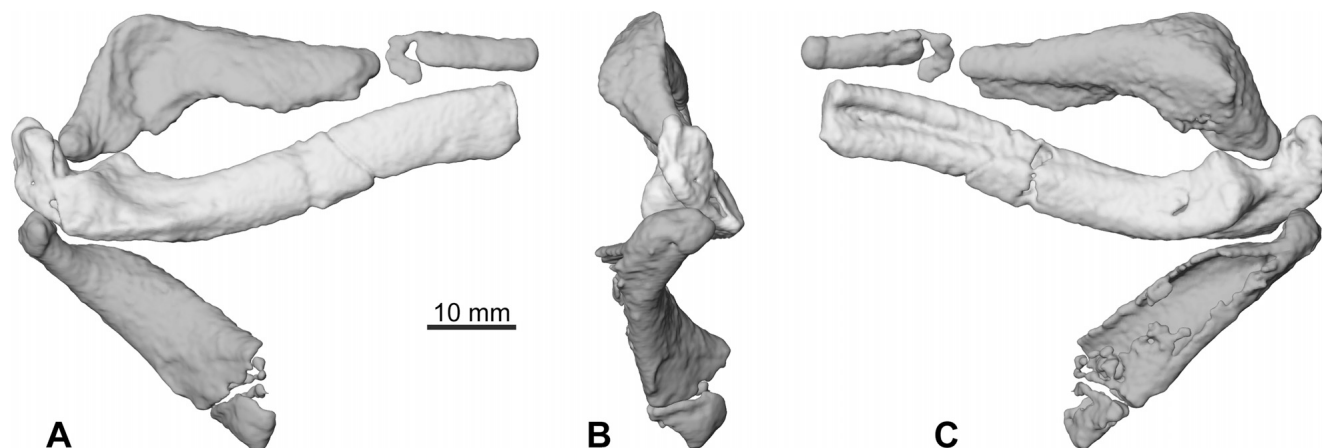


FIGURE 6. Digital surface model of right visceral skeletal elements of †*Tingitanius tenuimandibulus*, NHMUK P66857. **A**, ventral view; **B**, lateral view; **C**, dorsal view. Anterior at top of page.

present; thus, we cannot say with certainty if these cartilages were fused like they are in other rhinobatiformes (McEachran et al., 1996; McEachran and Aschliman, 2004; Aschliman et al., 2012a). Likewise, the pseudohyoid bar is not preserved, but we infer that it was present because that is the condition in all other batoids (Compagno, 1973; Maisey, 1984; Miyake and McEachran, 1991; McEachran et al., 1996; McEachran and Aschliman, 2004; Aschliman et al., 2012a). The fifth ceratobranchials are present, and their posterior-most (or distal) tip articulates with a short, pointed process on the medial inlet of the scapulocoracoid.

Postcranial Skeleton—A shallow notch beneath the foramen magnum is indicative of an articulation with a relatively short lip of the synarcual cartilage (Fig. 5B, C). However, the synarcual is slightly dislocated from that notch (Figs. 2A, 4A) and the synarcual lip is fractured (Fig. 7A–D). The synarcual is narrow in dorsal-ventral views (Fig. 7A, B). The dorsal-most median crest is wide and tapers slightly at the anterior aspect. Between the dorsal-most median crest and the neural tube, the synarcual is extremely tall and thin walled (Fig. 7C–F). In anterior and posterior views, the lateral stays are strongly curved anterolaterally (Fig. 7A, B). The first exposed vertebral centrum of the synarcual is positioned posterior to the articulation of the suprascapular cartilage with the posterior synarcual. Slightly more anterior centra, which are covered by a thin layer of tessellated cartilage, are also found posterior to the lateral stays (Fig. 7C, D). Vertebral centra are observed much farther anterior in other living platyrhinid and non-platyrhinid guitarfishes.

The pectoral girdle does not directly fuse to the synarcual, but would instead have articulated via medially fused suprascapulae. In life, suprascapulae would have articulated with the neural arches of vertebrae immediately posterior to the synarcual cartilage. In this specimen, the suprascapular cartilage is displaced so that the posterior portion is situated on the left side of the body axis (Fig. 4). The fused suprascapular cartilage is concave anteriorly, convex posteriorly, and forked laterally (Fig. 7G–L). In lateral view, the anterior-articulating edge of the suprascapula is sloped so that it is deepest posteriorly. This surface closely follows the slope of the posterior edge of the synarcual median crest, though does not form a tight joint.

The scapulocoracoid comprises a gracile, fused (but fractured), coracoid bar and a dorsoventrally rectangular scapular process that is long, slightly tapered, and inserts into those forked lateral slots of the suprascapula (Fig. 7M–P). In lateral view, the scapulocoracoid is squared and three condyles are observed in a single horizontal plane (Figs. 2B, 7O, P). The mesocondyle is slightly closer to the procondyle than it is to the metacondyles.

Robust propterygia are preserved proximally and the right propterygium is more complete than the left, which indicates that the pectoral fin was anteriorly elongate (Fig. 2A, B). The posterior section of propterygium extends behind the procondyle. The mesopterygia and metapterygia are difficult to discern on the surface of the fossil; however, CT preparation reveals a small, plate-like mesopterygium and a fractured metapterygium (Fig. 2B). It is unclear if the posterior corner of the pectoral fin was long enough to reach the pelvic fin. Thick proximal radials are present and articulating with all of the pterygia, and not directly with the scapulocoracoid (Fig. 2B). Distal radials are not preserved; thus, we cannot say for certain whether or not paired fins were apleosoid or plesiodic; however, the condition in all other living batoids is plesiodic.

Caudal vertebrae are preserved, and one is fractured in cross-section, revealing a dense notochordal center with differential folding radiating from that center (Fig. 2C, D). In addition, appositional rings of areolar cartilage are present, which is consistent with seasonal growth of elasmobranchs. The ischiopubadic bar is plate-like and straight (Fig. 2A). On the posterior margin of the ischiopubadic bar, there is a tab-like postpelvic process that resembles greatly the process found in *Platyrhinoidis*. No proximal

clasper cartilages are preserved, but there is evidence of the distal clasper glans and fibrous tissue associated with the long clasper (Fig. 2E).

BRITOBATOS PRIMARMATUS, gen. nov, comb. nov.
(Fig. 8)

Type Species—*Raja primarmata* Woodward, 1889.

Syntypes—NHMUK P4015, P4016.

Referred Specimens—MNHN 1946-18-94 A and B, 1946-18-1507.

Derivation of Name—After Paulo Brito for his work on fossil guitarfishes.

Remarks—This genus is currently known from three partial skeletons and several teeth attributed to a single species from the Santonian of Lebanon. These specimens were described under the name *Raja primarmata* Woodward, 1889, and *Rhinobatus berytensis* Signeux, 1951, later amended to *Rhinobatus primarmatus* (Woodward, 1889; Cappetta, 1980). A cladistic study of Lebanese Cretaceous batoids by Brito and Dutheil (2004) concluded that †*R. primarmatus* was closely related to extant platyrhinids, a conclusion that is confirmed here. Because *R. primarmatus* is not closely related to other species of *Rhinobatos*, it is here referred to the new genus *Britobatos*. Some other Lebanese Cretaceous nominal species of *Rhinobatos* are also clearly not congeneric with other modern species *Rhinobatos*, but a full analysis of the affinities of these is beyond the scope of this study. We do, however, discuss the issues of polyphyly in guitarfishes below.

PHYLOGENETIC ANALYSIS

Taxonomic Sample

The new fossil from Morocco, which represents a new species, is examined and compared with the skeletons of 28 other elasmobranch taxa (11 extinct and 19 extant). Eight taxa are outgroups, including the non-batoid elasmobranchs *Hexanchus* and *Pristiophorus*, and the batoids †*Sclerorhynchus*, †*Spathobatis*, *Pristis*, *Torpedo*, *Narcine*, *Myliobatis*, and *Urolophus*. The remaining 20 ingroup taxa are guitarfishes or ‘rhinobatoids’ (sensu Compagno, 1973). The ‘Rhinobatoidei’ include a number of extant genera as well as several species known from the Cretaceous fossil record. Many of the extinct taxa are represented by species from Lebanon that were referred to the extant genus *Rhinobatos* (Cappetta, 1980), although these have since been recognized as being taxonomically diverse (Brito and Dutheil, 2004). Most taxa were examined from original material (Appendix 1); however, original material could not be accessed for all characters. In those cases information was scored from the literature.

Character Sample

The character matrix of 53 morphological characters is derived from the matrices published by McEachran et al. (1996), Brito and Dutheil (2004), Kriwet (2004), McEachran and Aschliman (2004), Aschliman et al. (2012a), and new observations (Appendix 2). The matrix was compiled using Mesquite 2.74 (Maddison and Maddison, 2010). The entire data matrix is retrievable with supporting images at MorphoBank.org. Characters and states for the entire matrix are listed in Appendix 3.

Phylogenetic Methods

We treated all characters as unordered and equally weighted. Multistate characters were treated as polymorphic. The character matrix was analyzed using PAUP* 4.0b10 (Swofford, 2002) using the maximum parsimony optimality criterion. We employed heuristic searches with 1000 replicates of random stepwise

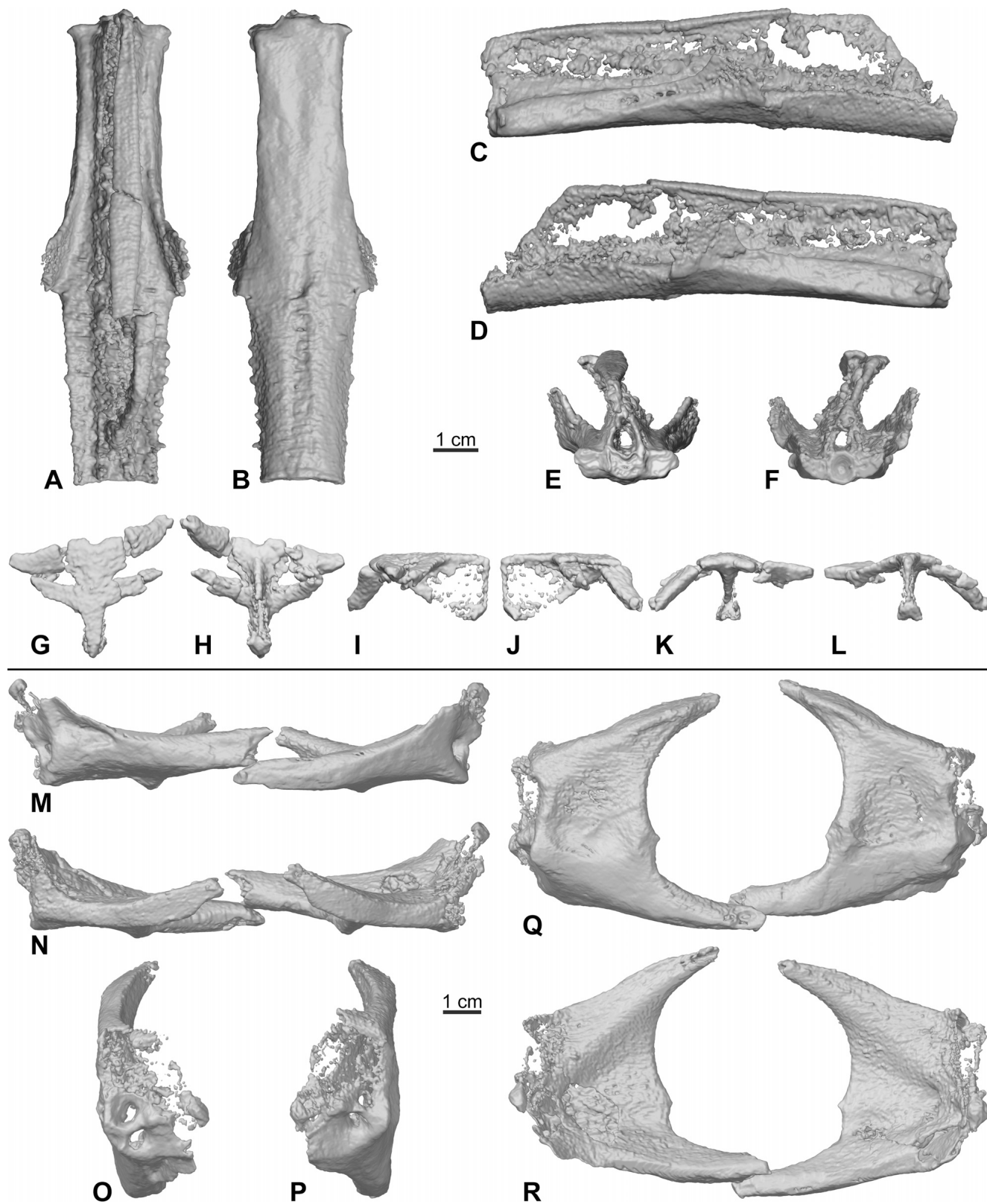


FIGURE 7. Digital surface model of postcranial skeleton of †*Tingitanius tenuimandibulus*, NHMUK P66857. **A–F**, synarcual cartilage (**A**, left lateral view; **B**, right lateral view; **C**, dorsal view; **D**, ventral view; **E**, anterior view; **F**, posterior view). **G–L**, suprascapular cartilage (**G**, dorsal view; **H**, ventral view; **I**, anterior view; **J**, posterior view; **K**, left lateral view; **L**, right lateral view). **M–R**, scapulocoracoid cartilage (**M**, anterior view; **N**, posterior view; **O**, dorsal view; **P**, ventral view; **Q**, left lateral view; **R**, right lateral view).

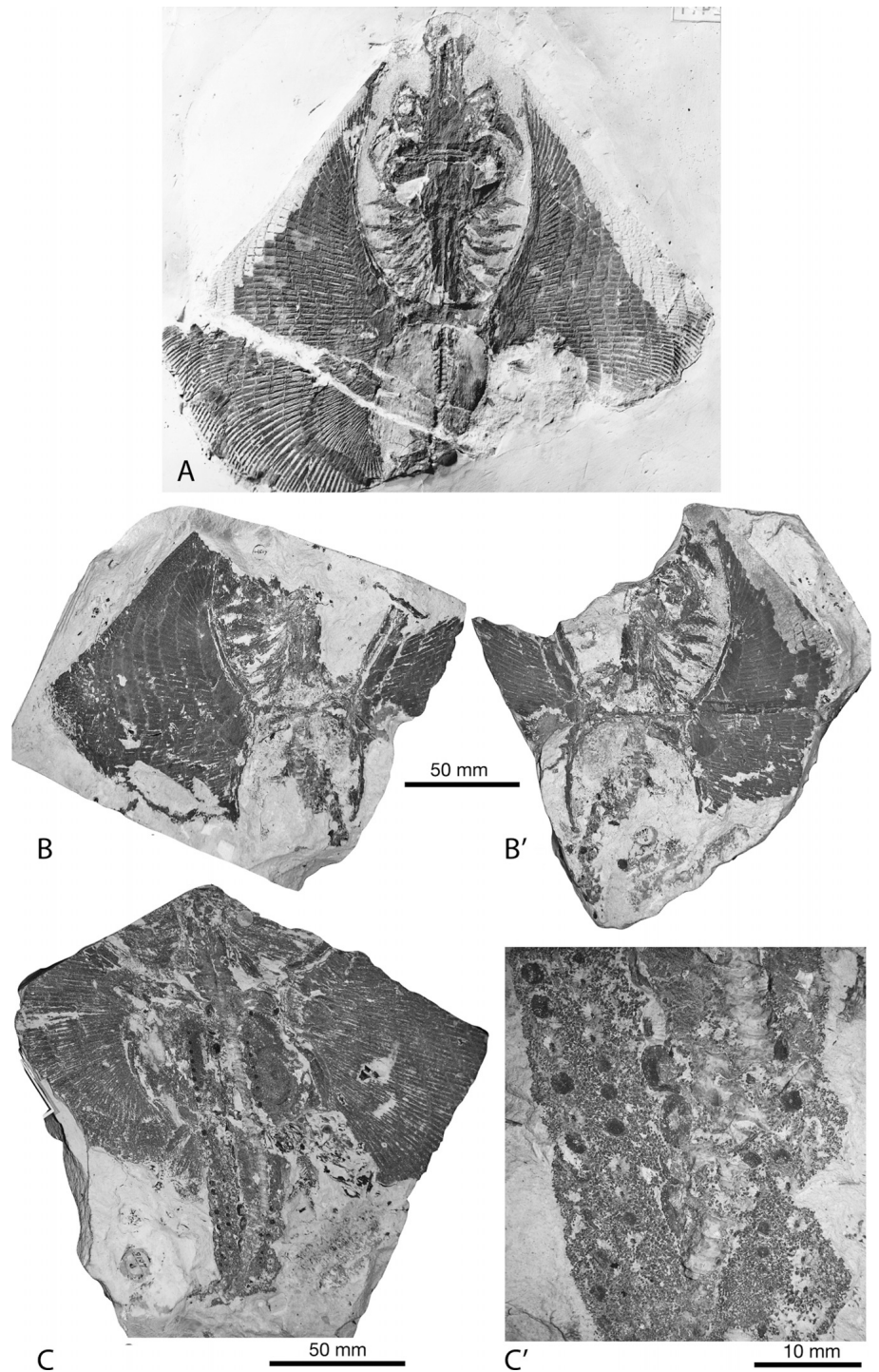


FIGURE 8. †*Britobatos primarmatus*. **A**, **B**, part and counterpart of NHMUK P4015; **C**, NHMUK P4016; **D**, close-up of NHMUK P4016.

addition (branch swapping: tree-bisection-reconnection) holding one tree at each step. Branches were collapsed to create soft polytomies if the minimum branch length was equal to zero (ambiguation); afterwards, we explored agreement subtrees (Cole and Hariharan, 1996). We calculated Bremer support (Bremer, 1994) for nodes retained in the strict consensus tree. This was done manually in PAUP* using constraint trees generated in MacClade 4.08 for OS X (Maddison and Maddison, 2005) from the Decay Index PAUP* File command. We report unambiguous optimizations for particular nodes of interest retained in the strict consensus

(optimizations were performed on individual most parsimonious trees).

Results

There were 47 of 53 parsimony informative characters and the matrix had 8.6% missing data. The heuristic search retained 52 trees with 146 steps (consistency index [CI] = 0.5274, homoplasy index [HI] = 0.4895, retention index [RI] = 0.7240, rescaled consistency index [RC] = 0.3818). The strict consensus and 50%

majority rule trees were rooted with Hexanchidae and *Pristiophorus* and are presented in Figure 9A and B. The agreement subtree removed 15 of 30 taxa (Fig. 9C).

The strict consensus tree (Fig. 9A) recovers a monophyletic Torpediniformes (clade C, Bremer = 7), which is unresolved with respect to †*Sclerorhynchus*, †*Spathobatus*, *Pristis*, and a clade comprising all remaining batoids (clade E, Bremer = 1). Within clade E, there are two well-resolved clades (clade F, Bremer = 1 and clade I, Bremer = 1). Clade F includes the extinct taxon †*Rhinobatos whitfieldi* as sister to the panrays and stingrays (*Zanobatos* + (*Myliobatos* + *Urolophus*)). Clade I includes the extinct taxa †*Rhinobatos latus* and †*Rhinobatos intermedius* as unresolved with respect to clade J, which includes the extinct taxon †*Britobatos primarmatus* + Platyrrhinidae. Within Platyrrhinidae, †*Tethybatis* is sister to *Platyrrhina* + (*Platyrrhinoidis* + †*Tingitanius*).

The 50% majority rule tree (Fig. 9B) recovers the same major clades as in the strict consensus, but with fewer polytomies, and is equivalent to the sixth of 52 retained trees in our analysis. Within Batoidea (clade B'), †*Sclerorhynchus*, †*Spathobatus*, and *Pristis* are successive sister taxa to the remaining batoids (clade E'). *Rhynchobatus*, †*Rhinobatos tenuirostris*, and †*Rhinobatos maronita* form a polytomy (clade I') that is unresolved with respect to †*Iansan* and all remaining batoids (clade J'). Within clade J', *Aptychotrema* is sister to a polytomy formed by *Zapteryx*, *Trygonorrhina*, and clade L'. Within clade L', there are two well-resolved clades, clade M' and clade Q'. Within clade M', †*Rhombopterygia* and †*Rhinobatos whitfieldi* are successive sister taxa to *Zanobatos* + stingrays. Within clade Q', *Rhinobatos rhinobatos*, †*Rhinobatos latus*, and †*Rhinobatos intermedius* are successive sister taxa to †*Britobatos* + Platyrrhinidae (clade U').

The agreement subtree (Fig. 9C) retains both rooting outgroup taxa and all taxa that are bolded in Figure 9A and B. In addition, †*Rhinobatos intermedius* is retained as the sister taxon to the clade formed by †*Britobatos* + Platyrrhinidae (clade J). Character transformations are mapped onto this tree for that clade. There are two unambiguous synapomorphies uniting Platyrrhinidae (clade K)—a rostral cartilage that fails to reach the tip of the snout and pectoral propterygia that extend far beyond the nasal capsules (although this could not be scored for †*Tingitanius tenuimandibulus*). *Platyrrhina*, *Platyrrhinoidis*, and †*Tingitanius tenuimandibulus* are united (clade L) to the exclusion of †*Tethybatis* by one unambiguous synapomorphy, the presence of a postpelvic process. *Platyrrhinoidis* and †*Tingitanius tenuimandibulus* are united as sister taxa (clade M) to the exclusion of *Platyrrhina* based on two unambiguous synapomorphies, the absence of labial cartilages (as assessed during preparation of †*Tingitanius tenuimandibulus*), and the presence of incipient lateral uvulae on teeth.

DISCUSSION

Platyrrhinid Monophyly

As noted by Carvalho (2004), Platyrrhinidae was explicitly defined by the presence of, albeit somewhat vaguely describable, postpelvic processes on the ischiopubic bar (McEachran et al., 1996; McEachran and Aschliman, 2004; Aschliman et al., 2012a). We redefined the condition of the postpelvic processes (character 33) while conducting this study; thus, we no longer consider the presence of postpelvic processes a synapomorphy for all members of Platyrrhinidae. We note the presence of these processes on †*Tingitanius tenuimandibulus* as somewhat flattened tabs, rather than truly triangular projections. These short-but-observable tabs are most like the wide tabs found on the ischiopubic bar of *Platyrrhinoidis triseriata*. This contrasts with the more pointed, though presumably incipient, projections described for *Platyrrhina* by Garman (1913:plate 66) and

also figured by Carvalho (2004:fig. 8C) for another, younger specimen of *Platyrrhina*. The presence of those postpelvic processes unites †*Tingitanius tenuimandibulus* with extant members *Platyrrhinoidis* and *Platyrrhina* to the exclusion of †*Tethybatis selachoides*.

Morphology from our study that does support Platyrrhinidae in the strict consensus tree, 50% majority rule tree, and the agreement subtree includes the presence of short, subtriangular rostral cartilages and pectoral propterygia that would extend beyond the nasal capsules. The three characters from our study that pertain to that morphology (characters 1, 2, 37) are consistent with the description of †*Tethybatis* by Carvalho (2004), though not exactly the same. The position of the propterygia in †*Tingitanius tenuimandibulus* is inferred by a fragment of cartilage presumed to be part of the propterygium found near the distal right antorbital cartilage.

An additional character related to the shape of the antorbital cartilages provides ambiguous support to Platyrrhinidae in our resulting trees. Antorbital cartilage shape was also reported to support the monophyly of the clade by Carvalho (2004) and was described in part by Brito and Duthiel (2004). Character 6 in our study combines those two descriptions and adds a state that describes antorbital cartilage shape as plate-like. However, this character could not be scored for †*Tethybatis* because antorbital cartilages were not preserved (Carvalho, 2004). However, they were observed and scored as plate-like in †*Tingitanius tenuimandibulus*, *Platyrrhinoidis*, and *Platyrrhina*.

According to the results of our study, character 25 also provides ambiguous support to a monophyletic Platyrrhinidae in the strict consensus tree, 50% majority rule tree, and the agreement subtree. Character 25 pertains to mineralized dermal denticles, which have a tendency to preserve well in the fossil record and are thus significant to cladistic study. There is a change from ribbed to smooth and oval-shaped dorsal groundmass denticles in extant members of Platyrrhinidae. Smooth, arrowhead-shaped denticles were found in †*Tingitanius tenuimandibulus*. †*Tingitanius* probably had a complete covering of denticles composed of small denticles of somewhat different morphology on the ventral and dorsal surfaces with scattered larger dermal bucklers. This style of squamation appears to be common across early batoids and is seen on specimens of the Jurassic stem batoid †*Spathobatis*. Subsequent loss of the body-covering denticles (in the Rajidae, Torpediformes, and Myliobatiformes) or dermal bucklers (in Pristidae and Torpediformes) should be regarded as the derived state. Among disparate clades and even among closely related species, there is a great variation in the degree of squamation, especially with regard to the size and number of bucklers (such as is the case in *Raja* and *Dasyatis*). Although the extant members of the Platyrrhinidae have very well-developed bucklers, in †*Tingitanius* they are apparently both smaller and fewer. If the other Cretaceous platyrrhinids are considered, †*Britobatos primarmatus* has a very well developed covering of large bucklers (Fig. 8). Character 25 could not be scored for †*Tethybatis selachoides* because the crown of each denticle was wider than its base, which obscured detailed description of said base as anything more than pedunculate (Carvalho, 2004). If a base can be described, we predict at least a smooth morphology, with the possibility of an ovoid in shape, lending further support to Platyrrhinidae.

Character 53 relates to clasper length and, when considering the agreement subtree only, it adds ambiguous support to Platyrrhinidae. An elongate and slender clasper is the condition in *Platyrrhina*, but not in *Platyrrhinoidis*, according to McEachran and Aschliman (2004). However, we observed a clasper in MCZ 99000, which is more elongate and slender than the 'elongate and slender' clasper described for †*Tethybatis* by Carvalho (2004). We, therefore, included the character but scored *Platyrrhinoidis* the same as the remaining members of Platyrrhinidae. The

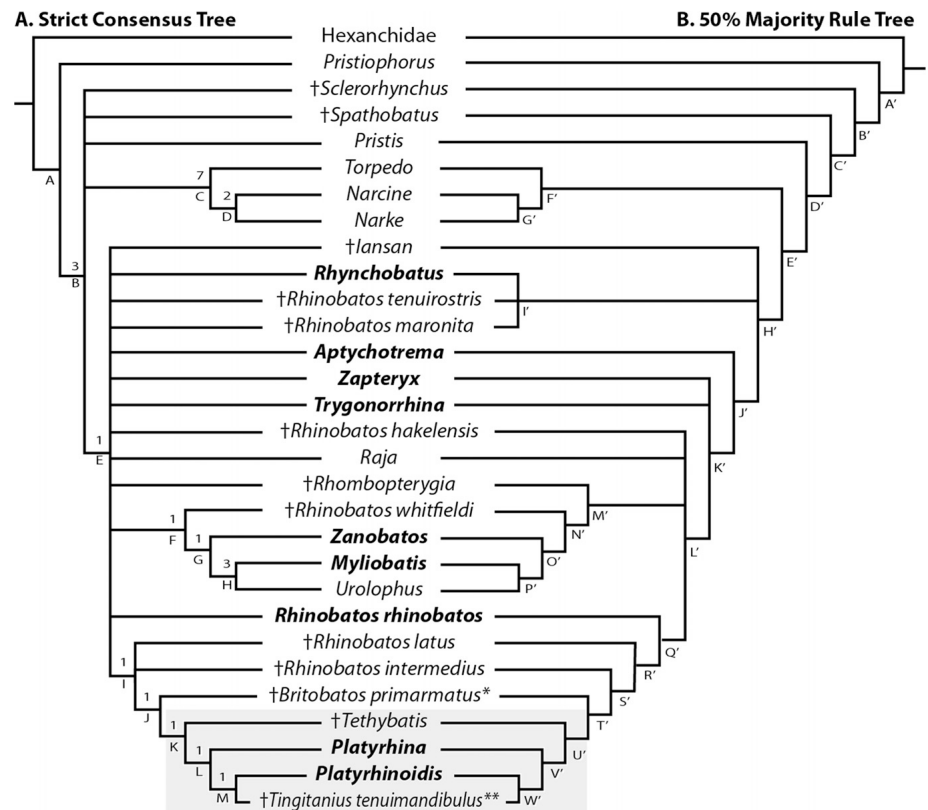
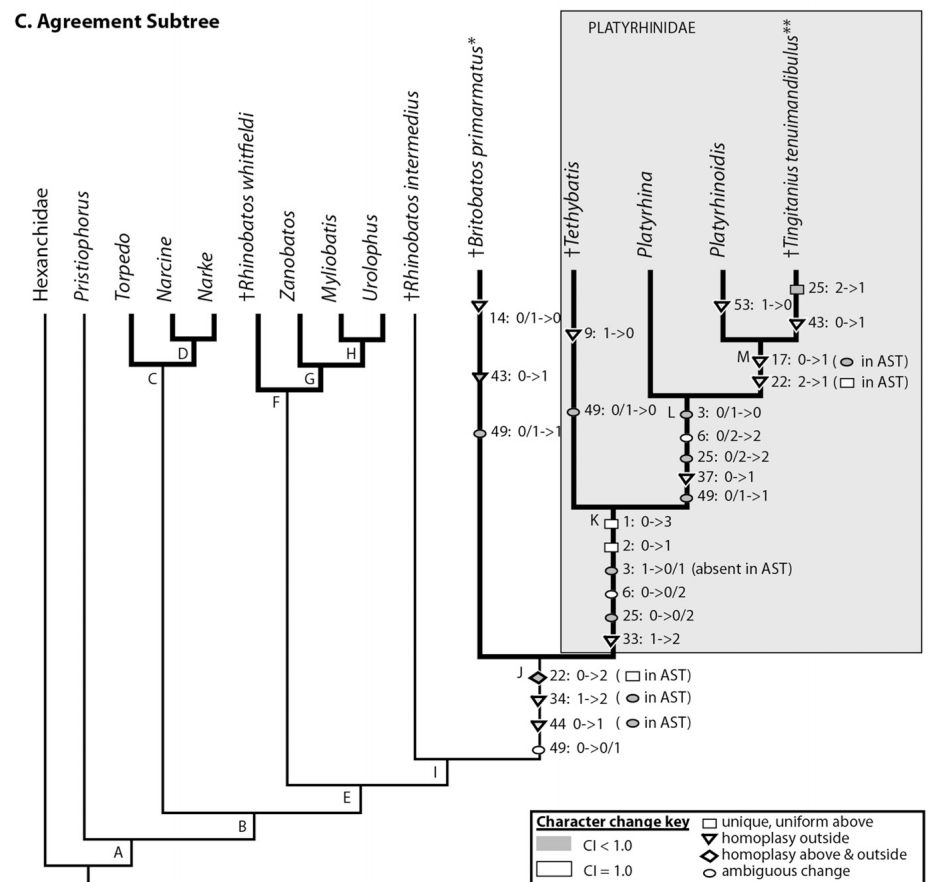


FIGURE 9. Consensus trees based on new analysis. **A**, strict consensus tree; **B**, 50% majority rule tree (= tree 6 of 52); **C**, agreement subtree (AST) with characters and state changes mapped for Platyrrhinidae and immediate outgroup, †*Britobatos primarmatus*. Numbers above internal branches are Bremer values. Letters below branches are node labels referred to in the text. Changes represented on AST occur in all three trees. Character change type differs in AST for some characters, which are indicated in parentheses. Bold names are of taxa from ‘Rhinobatoidei.’ Gray shaded regions are clades conserved in all consensus trees. Bold branches are conserved clades among all consensus trees.



presence of distal clasper tissue for †*Tingitanius* indicates that it too had a long clasper (Fig. 2E).

Guitarfish Polyphyly and the Evolution of Platyrrhinidae

To date, there have been several attempts to test hypotheses about batoid evolution (Table 1, Fig. 10) using morphology from extant taxa (McEachran et al., 1996; McEachran and Aschliman, 2004; Aschliman et al., 2012a), and even more recently the first comprehensive and robust, time-calibrated batoid phylogeny based on molecular data was published (Aschliman et al., 2012b). There have also been studies that incorporated extinct taxa, known only from fossilized specimens (e.g., Brito and Dutheil, 2004; Carvalho, 2004; Carvalho et al., 2004; Claeson et al., 2010b). Striking among the attempts that considered multiple guitarfish taxa is the discordant arrangement of taxa traditionally considered part of ‘Rhinobatoidei’ (sensu Compagno, 1973; see Table 1 and Fig. 10).

Ever since the majority of known guitarfish genera were included in phylogenetic study (9 of 10 valid taxa), the monophyly of ‘Rhinobatoidei’ has never been recovered in resulting tree topologies. However, there was a conservation of Platyrrhinidae as subclades distributed across those trees (Fig. 10). Our study also fails to recover a monophyletic ‘Rhinobatoidei’ while presenting strong support for a monophyletic Platyrrhinidae (Fig. 9).

However, the distribution of extinct ‘guitarfishes’ at the stem of several extant clades of taxa lends support to the hypothesis that guitarfishes are probably ancestral to all other batoid forms (Compagno, 1973), perhaps to the exclusion of Torpediniformes, as other morphological analyses will suggest.

Our results are the first using morphology to suggest that Platyrrhinidae and Zanobatidae (*Zanobatus*) are not successive sister taxa to Myliobatoidei (stingrays). This decoupling is consistent with molecular results that also fail to recover the relationship (Aschliman et al., 2012b). However, our results and those of the molecular study disagree on the relative position of Platyrrhinidae. According to our results, Platyrrhinidae are a group of true ‘guitarfish,’ highly nested within an expansive and paraphyletic Rajiformes (all batoids to the exclusion of Torpediniformes; paraphyletic if the Myliobatiformes are excluded). Molecular results indicate that Platyrrhinidae are the sister group to Torpediniformes to the exclusion of all remaining batoids.

Fossil Record of the Platyrrhinidae

The Platyrrhinidae constitute a very minor group within the diversity of extant batoids, comprising just four species within two genera. Despite this, platyrrhinids are represented by several different genera amongst the limited number of well-preserved skeletal remains of batoids from the Cretaceous and Paleogene.

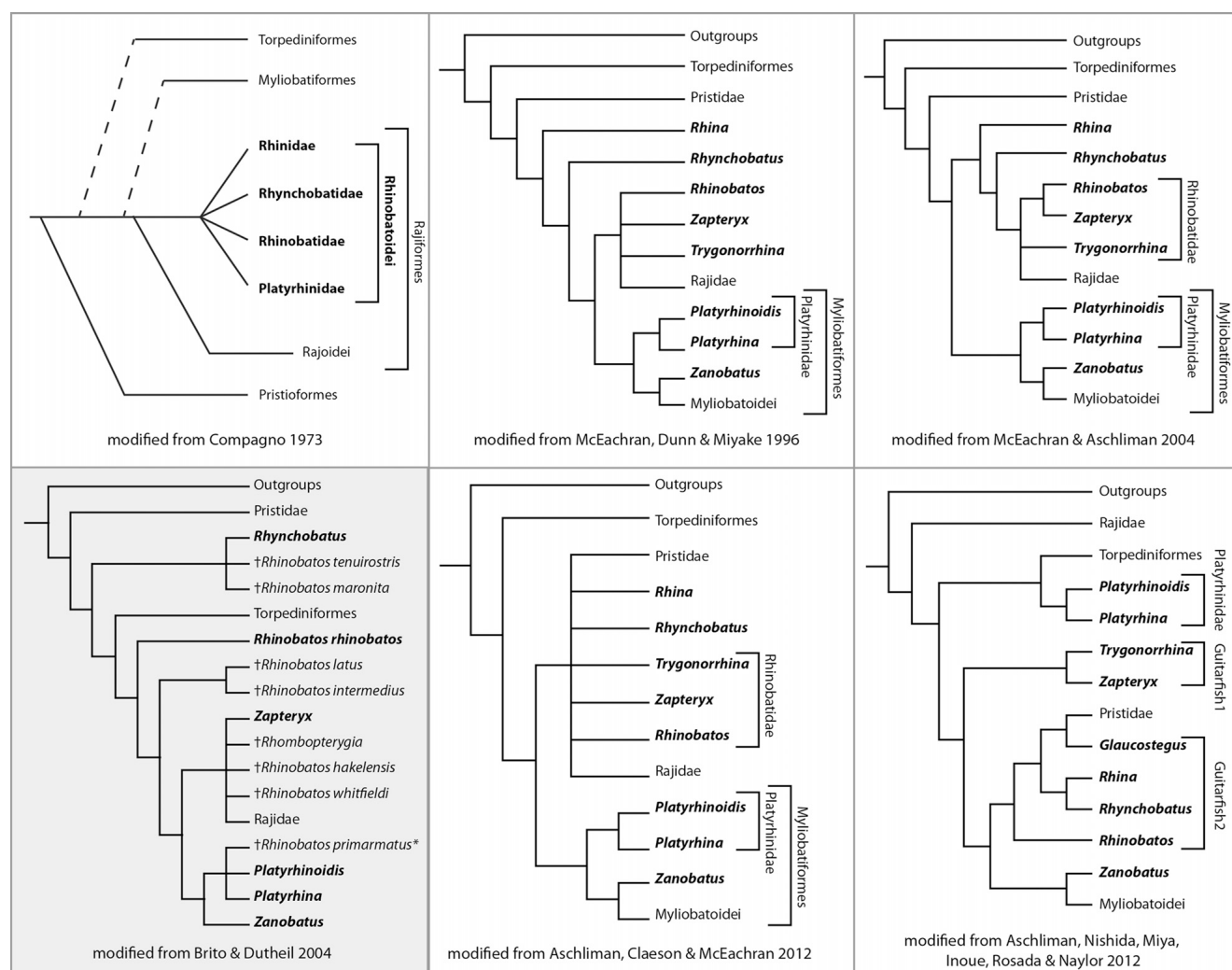


FIGURE 10. Previous hypotheses of batoid evolution, with emphasis placed on relationships of ‘Rhinobatoidei’ indicated in bold. Tree from Brito and Dutheil (2004) represents the only prior explicit attempt to resolve relationships among extinct guitarfishes.

TABLE 1. Previous classifications of living ‘guitarfishes.’

Compagno, 1973:
Order Rajiformes
Suborder Rhinobatoidei
Family Rhinidae: <i>Rhina</i>
Family Rhynchobatidae: <i>Rhynchobatus</i>
Family Rhinobatidae: <i>Aptychotrema</i> , <i>Rhinobatos</i> , <i>Trygonorrhina</i> , <i>Zapteryx</i>
Family Platyrrhinidae: <i>Platyrrhina</i> , <i>Platyrrhinoidis</i> , <i>Zanobatus</i>
McEachran et al., 1996:
Order Rhiniformes
Family Rhinidae: <i>Rhina</i>
Order Rhynchobatiformes
Family Rhynchobatidae: <i>Rhynchobatus</i> , incertae sedis: <i>Rhinobatos</i> , <i>Aptychotrema</i> , <i>Zapteryx</i> , <i>Trygonorrhina</i>
Order Myliobatiformes
Suborder Platyrrhinoidei
Family Platyrrhinidae: <i>Platyrrhina</i> , <i>Platyrrhinoidis</i>
Suborder Zanobatoidei
Family Zanobatidae: <i>Zanobatus</i>
McEachran and Aschliman, 2004:
Order Rajiformes: incertae sedis: <i>Rhina</i> , <i>Rhynchobatus</i>
Family Rhinobatidae: <i>Aptychotrema</i> , <i>Rhinobatos</i> , <i>Trygonorrhina</i> , <i>Zapteryx</i>
Order Myliobatiformes
Suborder Platyrrhinoidei
Family Platyrrhinidae: <i>Platyrrhina</i> , <i>Platyrrhinoidis</i>
Suborder Zanobatoidei
Family Zanobatidae: <i>Zanobatus</i>
Aschliman et al., 2012a:
Order Rajiformes: incertae sedis: <i>Rhina</i> , <i>Rhynchobatus</i>
Family Rhinobatidae*: <i>Aptychotrema</i> , <i>Glaucostegus</i> , <i>Rhinobatos</i> , <i>Trygonorrhina</i> , <i>Zapteryx</i> (*highly provisional)
Incertae sedis: <i>Platyrrhina</i> , <i>Platyrrhinoidis</i> (moderate support as sister group to Myliobatiformes)
Order Myliobatiformes
Suborder Zanobatoidei
Family Zanobatidae: <i>Zanobatus</i>
Aschliman et al., 2012b:
Platyrrhinoidei: <i>Platyrrhina</i> , <i>Platyrrhinoidis</i> (as sister group to Torpedinoidei)
Guitarfishes 1: <i>Zapteryx</i> , <i>Trygonorrhina</i>
Guitarfishes 2: <i>Glaucostega</i> , <i>Rhinobatos</i> , <i>Rhynchobatus</i> , <i>Rhina</i> (includes sawfish <i>Pristis</i>)
Zanobatoidei: <i>Zanobatus</i> (as sister taxon to Myliobatoidei)

In contrast, until recently, there were no published records of platyrrhinid taxa represented by isolated teeth, despite diverse batoid tooth assemblages being well known. Study of a diverse late Eocene fauna from Egypt (Underwood et al., 2011) identified isolated teeth of two taxa that agree closely with those of platyrrhinids, whereas analysis of the rare but diverse batoid teeth of the Late Cretaceous of southern England and northern France (Guinot et al., 2012) has revealed teeth of two genera that are apparently new platyrrhinid taxa. The recognition of relatively frequent occurrence of platyrrhinid teeth within tooth assemblages is consistent with their frequent occurrence within skeletal faunas. It is, therefore, likely that teeth of platyrrhinids are present within many Cretaceous and Paleogene assemblages, but they have not been recognized as such and were identified as ‘*Rhinobatos*.’

CONCLUSIONS

There is strong support for a monophyletic Platyrrhinidae and its origin and radiation is less uncertain, because two extinct members from the Cretaceous bracket the two extant genera. †*Tingitanius tenuimandibulus* is represented by a single, exceptionally well-preserved specimen in a concretion and represents both the earliest record of the Platyrrhinidae and the most derived of the three Cretaceous genera. Its recovery from southeastern Morocco extends the early biogeographic

range of Platyrrhinidae towards the Atlantic side of the Tethys Sea with a minimum age of the late Turonian (~89.3 Ma). This potentially eliminates the scenario of a westward migration of platyrrhinids during the Jurassic, because the Atlantic was incipient at that point. The discovery of the highly derived †*Tingitanius tenuimandibulus* lends additional support to the hypothesis of a Tethyan origin of that clade as per Carvalho (2004). The evolution of †*Tingitanius tenuimandibulus* may, itself, be an example of vicariance. The presence of a derived taxon so early suggests that the Platyrrhinidae originated during a relatively early phase in batoid radiation during the Early Cretaceous or possibly even Late Jurassic.

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APPENDIX 1. Materials examined.

Fossil Material

†*Asterodermus platypterus*, NHMUK P10267 (probably synonymous with †*Spathobatis bugesiacus*); †*Rhinobatos hakelensis*, NHMUK P4012, paratype; †*Rhinobatos intermedius*, NHMUK 49516, holotype; †*Rhinobatos maronita*, NHMUK P10696, NHMUK P13861, NHMUK 49511, NHMUK 49512, NHMUK 49554, SMNS 12429; †*Britobatos primarmatus*, NHMUK P4015, NHMUK P4016; †*Rhinobatos tenuirostris*, NHMUK P4770, holotype; †*Rhinobatos whitfieldi*, AMNH 3703, AMNH 3707, AMNH 3708, AMNH 3709, NHMUK P9145, NHMUK P24965, NHMUK 47519; †*Spathobatis bugesiacus*, NHMUK P2099.

Recent Material

Aptycotrema, AMNH 98512; *Myliobatis* MCZ 1343-s; *Narcine brasiliensis*, AMNH 218276, AMNH 90769, AMNH 92321.a, TNHC 18512.A-C; *Platyrrhinoidis triseriata*, MCZ 99000, MCZ S895, MCZ S750, MCZ S749; *Pristiophorus japonicus*, MCZ

APPENDIX 2. Data matrix. Genus abbreviation ‘R.’ represents *Rhinobatos*. ‘A’ = 0&1; ‘?’ = missing data; ‘-’ = not applicable. Missing and not applicable data are treated the same in PAUP*.

	10	20	30	40	50	
Hexanchidae	00000--00	000000000?	0000000000	00000000-0	0000000000	000
<i>Pristiophorus</i>	0001101000	000000100?	1010000?00	00000000-0	0000000000	000
† <i>Sclerorhynchus</i>	0001100000	000?1100?	102100?11?	110000?110	00000?0000	00?
† <i>Spathobatis</i>	000?100000	???0?1100?	20210A?010	0100000100	0000001000	011
<i>Pristis</i>	0001100000	0001011002	2121000111	0100000101	0000000000	001
<i>Torpedo</i>	0000111000	11-0111000	0022312111	1101111100	1000000000	200
<i>Narcine</i>	0000111001	11-0110000	0022302111	1101110110	1000000000	200
<i>Narke</i>	0000111001	11-0110000	0022302011	1101110110	10000?0000	200
† <i>Iansan</i>	00?0100000	000111100?	2221000111	1101100111	0020000000	01?
<i>Rhynchobatus</i>	0011100010	0001110100	2021000111	1100000111	0000010000	011
† <i>R. tenuirostris</i>	001010001?	000??1?0??	222100?111	1100?001?1	00???000?	01?
† <i>R. maronita</i>	0010100010	000??1?0??	1021?0?111	1100000101	0001000000	01?
<i>Aptychotrema</i>	0010100000	0101111001	212100?111	110110?111	00100?1000	01?
<i>Zapteryx</i>	0010100100	0001111002	2121000111	1112100111	0010001000	011
<i>Trygonorhina</i>	0010100100	000111?000	2121000111	1112100111	0010001000	011
† <i>R. hakelensis</i>	0010100100	0001?1?00?	1021?0?111	1112100111	0011001000	01?
<i>Raja</i>	1010100100	0001111010	1021300111	1112100112	0010001100	111
† <i>Rhombopterygia</i>	0010100100	000?11?00?	1021?0?111	11121001?1	0010011000	01?
† <i>R. whitfieldi</i>	0010100100	0001?1?00?	1021?0?111	1112100111	0001111000	01?
<i>Zanobatos</i>	2200100100	000111?002	1022000111	1122101111	0001112000	010
<i>Myliobatis</i>	2200100101	0030111023	0032302111	1122000102	0131122001	200
<i>Urolophus</i>	2200100101	0020111001	0022300111	1122000102	0121110001	200
<i>R. Rhionobatos</i>	0010100100	0001110102	1021000111	1101100111	0010001000	011
† <i>R. latus</i>	0010100110	000??1?0??	102100?111	1111100101	0000001000	01?
† <i>R. intermedius</i>	001010011?	000??1?0??	202100?111	11111001?1	0000000000	01?
† <i>Britobatos</i>	0010100110	0000?1000?	222100?111	111210?101	0011000010	01?
† <i>Tethybatis</i>	31???--00	?00?11?0--	-----0????	1122100101	?0?0000000	011
<i>Platyrrhina</i>	3100120110	0001110002	2122100111	11221011?1	0001000010	011
<i>Platyrrhinoides</i>	3100120110	0001111002	2121200111	1122101101	0001000010	011
† <i>Tingitanius</i>	3?00120?10	000111100?	212110--1-	-1---01101	0011000010	011

1045-s, MCZ 1283; *Pristis*, AMNH 55624, MCZ S105; *Raja inornata*, FMNH 2754; *Rhinobatos lentiginos*, MCZ 57799; *Torpedo*, ZMB 33932, ZMB 33933; *Tryphonorrhina*, CJU ?; *Urolophus*, AMNH 214469; *Zapteryx exasperata*, SMF 26135; SMF 30674.

APPENDIX 3. Characters and states. BD2004 = Brito and Dutheil (2004); Brito and Séret (1996); MA2004 = McEachran and Aschliman (2004).

- (1) Rostral cartilage shape (BD2004, char. 1; Carvalho, 2004): (0) stout; (1) filamentous; (2) absent; (3) subtriangular.
- (2) Rostral cartilage (MA2004, char. 24): (0) complete; (1) fails to reach tip of the snout; (2) absent.
- (3) Rostral appendix (MA2004, char. 25): (0) absent; (1) present.
- (4) Precerebral fossa (BD2004, char. 11): (0) present as a circular ovoid concavity; (1) extending anteriorly and roofed to form a tube.
- (5) Antorbital cartilage (BD2004, char. 2): (0) absent; (1) present.
- (6) Antorbital cartilage shape (BD2004, char. 3; Carvalho, 2004): (0) unbranched and narrow, tapering distally; (1) long and branched; (2) plate-like.
- (7) Antorbital cartilage projection direction: (0) posterolaterally; (1) anteriorly.
- (8) Antorbital-propterygium connection (BD2004, char. 4; MA2004, char. 7): (0) free; (1) directly jointing.
- (9) Nasal capsules (BD2004, char. 5): (0) with a straight and or blunt anterior margin; (1) with a horn-like anterior process.
- (10) Nasal capsule (MA2004, char. 27): (0) laterally expanded; (1) ventrolaterally expanded.
- (11) Supraorbital crest (BD2004, char. 6; MA2004, char. 30): (0) present; (1) absent.
- (12) Postorbital process (BD2004, char. 7; MA2004, char. 32): (0) present; (1) reduced.
- (13) Location of postorbital process (MA2004, char. 32): (0) narrow and in otic region; (1) absent; (2) broad and shelf-like and in otic region; (3) broad and shelf-like in orbital region.
- (14) Jugal arch (MA2004, char. 35): (0) absent; (1) present.
- (15) Basal angle of neurocranium (BS1996, char. 12; MA2004, char. 28): (0) present; (1) absent.
- (16) Relation between palatoquadrate and neurocranium (BD2004, char. 8; MA2004, char. 2): (0) articulated; (1) loss of orbital articulation.
- (17) Labial cartilages (MA2004, char. 38): (0) present; (1) absent.
- (18) Jaw shape: (0) straight; (1) with sigmoidal curvature.
- (19) Osteodentine in tooth root (MA2004, char. 17): (0) absent; (1) present in roots of large teeth only; (2) widespread occurrence in tooth roots.
- (20) Pulp cavity of tooth root (MA2004, char. 16): (0) large; (1) roots with large pulp cavities; (2) tooth roots with small pulp cavities; (3) roots that lack pulp cavities.
- (21) Lingual uvula on teeth: (0) absent; (1) incipient or poorly developed; (2) well developed.
- (22) Differentiated lateral uvulae on teeth: (0) absent; (1) incipient; (2) well developed.
- (23) Tooth root main vascularization: (0) multiple, irregular (anaulacorhizous); (1) single paired opening (hemiaulacorhizous); (2) open or secondarily roofed (holaulacorhizous); (3) fused teeth that are polyaulacorhizous.
- (24) Lingual projection of root lob median to paired lingual foramina: (0) paired foramina absent; (1) lingual projection present; (2) lingual projection absent.
- (25) Dorsal groundmass denticles (Deynat, 2005): (0) ribbed; (1) smooth, arrowhead shaped; (2) smooth, oval; (3) absent.
- (26) Medial part of hyomandibular (MA2004, char. 39): (0) narrow; (1) expanded.
- (27) Basihyal and first hypobranchial (MA2004, char. 43): (0) both present and unsegmented; (1) basihyal is segmented;

- (2) basihyal is absent; (3) basihyal and first hypobranchial cartilages are absent.
- (28) Ceratohyal (MA2004, char. 44): (0) fully developed; (1) reduced or absent.
- (29) Distal tip of last ceratobranchial (BD2004, char. 9; MA2004 char. 4): (0) independent of scapulocoracoid; (1) articulating with scapulocoracoid.
- (30) Pseudohyoid bar (BD2004, char. 10; MA2004, char. 3): (0) absent; (1) present
- (31) Paired fins (BD2004, char. 13 and char. 19; MA2004, char. 60): (0) aplesodic; (1) plesodic.
- (32) Form of pectoral fin (BD2004, char. 14) (is nearly the same as antorbital-propterygium articulation and origin of pectoral fin): (0) not elongated anteriorly; (1) anteriorly elongated.
- (33) Pectoral propterygium (BD2004, char. 15; MA2004, char. 55): (0) not reaching the nasal capsules; (1) extending as far as the nasal capsules; (2) extending far beyond the nasal capsules.
- (34) Pectoral radials (BD2004, char. 16): (0) not reaching the nasal capsules; (1) extending as far as the nasal capsules; (2) extending far beyond the nasal capsules.
- (35) Posterior corner of the pectoral fin (BD2004, char. 17): (0) not reaching the pelvic fin; (1) extending to the pelvic fin origin.
- (36) Electric ampullae on the pectoral fins (BD2004, char. 18): (0) absent; (1) present.
- (37) Postpelvic process (BD2004, char. 20; MA2004, char. 63): (0) absent; (1) present.
- (38) Synarcual (BD2004, char. 23): (0) absent; (1) present.
- (39) Extent of synarcual lip (new): (0) short; (1) long.
- (40) Suprascapulae (BD2004, chars. 24 + 25; MA2004, char. 6; new observations): (0) free of vertebral column; (1) articulated with vertebral column; (2) fused to vertebral column (new).
- (41) Scapular process (BD2004, char. 26; MA2004, char. 49): (0) long; (1) short.
- (42) Ball and socket articulation (MA2004, char. 46): (0) absent; (1) present.
- (43) Mesocondyle (MDM1996, char. 48): (0) equidistant; (1) scapulocoracoid is elongated between mesocondyle and metacondyle; (2) scapulocoracoid is elongated between procondyle and mesocondyle; (3) replaced with a ridge.
- (44) Posterior section of propterygium (MA2004, char. 56): (0) does not extend posterior to procondyle; (1) extends behind procondyle.
- (45) Mesopterygium (MA2004, char. 58): (0) present and single; (1) fragmented or absent.
- (46) Shape of puboischadic bar (MA2004, char. 62): (0) plate-like; (1) narrow and strongly arched without distinct prepelvic processes; (2) narrow, strongly arched with a triangular medial prepelvic process; (3) narrow, moderately arched with bar-like medial prepelvic process.
- (47) Pectoral radials (BD2004, char. 28; MA2004, char. 57): (0) all articulating with the propterygium, mesopterygium, and metapterygium; (1) some articulating directly with the scapulocoracoid, between the meso- and the metapterygium; (2) many articulating with the scapulocoracoid due to the lack of mesopterygium.
- (48) Alar thorns (BD2004, char. 21, MD1998): (0) absent; (1) present.
- (49) Parallel rows of enlarged thorns over the posterior part of the disc and tail (BD2004, char. 22): (0) absent; (1) present.
- (50) Serrated tail spine (MA2004, char. 13): (0) absent; (1) present.
- (51) Placoid scales (MA2004, char. 14): (0) uniformly present; (1) sparsely to densely covered with placoid scales on the dorsal surface only; (2) free of denticles.
- (52) Large placoid scales or thorns (MA2004, char. 15): (0) absent; (1) present.
- (53) Clasper length (MA2004, char. 66): (0) short; (1) long.