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The Late Jurassic ray *Kimmerobatis etchesi* gen. et sp. nov. and the Jurassic

radiation of the Batoidea.

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ABSTRACT

The laminated marine mudstones of the Late Jurassic of Kimmeridge, southern England, yield two exceptionally well-preserved partial skeletons of a previously unrecognised species of early batoid. These are described as a new genus and species, *Kimmerobatis etchesi* gen. et sp. nov. which has a general "guitarfish" bauplan as in all other batoids known from the Jurassic. This species possesses a combination of primitive characters such as centra present within the majority of the synarcual and antorbital cartilages that fail to reach the pectoral skeleton along with more derived characters, such as the lack of fin spines. Until now, little study has been carried out on the affinities of Jurassic batoids, despite their key role in understanding batoid evolution. Results from parsimony and likelihood phylogenetic reconstruction indicates that the whole-bodied Jurassic batoids *Spathobatis*, *Belemnobatis*, and *Kimmerobatis* gen. nov. form their own clade, Spathobatidae, and do not lend support to a monophyletic "Rhinobatidae". Among Jurassic batoids, *Kimmerobatis* gen. nov. is most derived, but with derived characters being independently acquired compared to modern batoids (e.g., presence of a postpelvic process). The inclusion of whole bodied Jurassic fossils have generated a more resolved hypothesis of batoid evolution throughout the Cretaceous and into the Cenozoic.

Key Words: Kimmeridgian, phylogeny, ray, guitarfish, evolution

1. Introduction

The Batoidea (skates, stingrays, electric rays, and sawfish) comprise over half of living chondrichthyans (cartilaginous fishes) and are present in virtually all marine, and some freshwater, environments. All of the main clades of batoids are known, or predicted, to have appeared prior to the end of the Cretaceous (e.g. Claeson et al., 2013). Despite their variations of body form, the batoids are clearly monophyletic (e.g. Aschliman et al., 2012 a, b) and are united by a number of unambiguous characters such as a unique (Euhyostylic) jaw suspension, pectoral fins attached to the head anterior of the gill openings, and a synarcual (an elongate tube of continuous crust of tessellated cartilage on the anterior part of the vertebral column). Although fossil batoids are known largely from isolated teeth, several species of batoids are known from the Late Jurassic on the basis of well preserved skeletons within Lagerstätten such as Solnhofen (e.g. Kriwet and Klug, 2004). Unlike the batoids of the Cretaceous and Cenozoic, these Jurassic forms are morphologically conservative and all fit within the "guitarfish" or "rhinobatid" body plan. The relationship between these Jurassic "guitarfish" and modern forms, as well as with each other, is poorly understood. Modern and Cretaceous "guitarfish" are now recognised as polyphyletic (Aschliman et al. 2012, a, b; Claeson et al., 2013), but to date no one has tested whether or not Jurassic taxa belong within one or more of the extant clades, form a basal sister clade to all other batoids, or represent a paraphyletic group of basal batoids sharing plesiomorphic characters.

Whilst the Late Jurassic was evidently an important time in batoid evolution, with a well-represented fossil record, until now batoid fossils from the Kimmeridge Clay of the UK have been limited to isolated teeth (Underwood, 2002). Thus, the discovery of two exceptionally well preserved partial batoid specimens from the

Kimmeridge Clay Formation (Kimmeridgian to Lower Tithonian) of Kimmeridge, southern England represents the first examples of non-dental Mesozoic batoid fossils from Britain, and also the first Late Jurassic batoid skeletons worldwide from offshore mudstone facies. The specimens represent a previously unknown taxon and have allowed us to test the hypothesis that Late Jurassic batoids are more closely related to one another than modern batoids, and to investigate their relationship to other batoids, both extinct and extant.

2. Geological Setting

Late Jurassic sediments are well exposed along the coast of Dorset, southern England. Both of the specimens described here were collected from the Upper Kimmeridge Clay Formation (Early Tithonian) East of Kimmeridge Bay. The holotype specimen was collected from foreshore ledges of the *Pectinatus* Zone at Encombe, whilst the paratype was recovered from a fallen block originating from the *Hudlestoni* Zone near Rope Lake Head. Both specimens are from dark laminated mudstones, typical of the mid part of the Kimmeridge Clay. See Morgans-Bell et al., (2001) for a summary of the stratigraphy of the Kimmeridge Clay Type area. The facies and associated faunas of the Kimmeridge Bay succession are rather different from the silty, shallower water mudstones of the lowest part of the Kimmeridge Clay, which have yielded batoid teeth in the past (Underwood, 2002).

3. Material and Methods

The two specimens described here were collected and prepared by Steve Etches from the Kimmeridge Clay Type area, and form part of the extensive collection now housed in the Etches Collection, Kimmeridge, UK. Both specimens are in dark laminated mudstones without obvious signs of associated benthos. The mudstones are hard and contain no significant carbonate content, and as a result both fossils have been prepared using mechanical methods and air abrasion. The mudstone matrix is unsuitable for isolating individual small elements such as teeth and denticles and so these are not as readily studied as they are in approximately coeval batoid skeletons from Plattenkalk facies (e.g. Thies and Leidner, 2011).

4. Systematic palaeontology

The morphological terminology used here follows that of Cappetta, (1987) and Nelson, Grande, and Wilson, (2016).

Euselachii Hay, 1902

Neoselachii Compagno, 1977

Batomorphii Cappetta, 1980

Spathobatidae Underwood, 2006

4.1. Remarks

Jurassic genera were referred to the extant "Rhinobatidae" by Cappetta (1987; 2012), despite noting the "primitive characteristics of their skeletons". In contrast, Underwood et al., (1999) considered *Spathobatis, Belemnobatis*, and probably *Squatirhina* to form a clade of stem group batoids, later informally considering them

as forming the 'Spathobatidae' due to shared (presumed primitive) characters of an incomplete synarcual (segmented basiventral cartilages) and possession of fin spines (Underwood, 2006). Cione, (1999) considered a Jurassic ray from Argentina, as Batomorphii indet., noting differences from modern clades. Based on the results of the present phylogenetic analyses, which included direct accounts of *Spathobatis*, *Belemnobatis* and the new Kimmeridgian taxon, the family Spathobatidae is formalised. The Argentinian specimen could not be analysed at present.

5. Genus *Kimmerobatis* gen. nov.

5.1. Derivation of name.

From the type, and as yet only, locality at Kimmeridge, Dorset.

5.2. Type species.

Kimmerobatis etchesi gen. et sp. nov. from the Upper Jurassic of the UK.

5.3. Apomorphy based differential diagnosis.

Batoid like *Spathobatis* (Thiollère, 1854) and *Belemnobatis* (Thiollère, 1854) characterised by "guitarfish" like form. *Kimmerobatis* possesses a depressed body, caudal region large in proportion to disk, tail distinct from disk, fins aplesodic; hyomandibula with broad medial articulation with chondrocranium; unsegmented propterygia; no pectoral radials that articulate directly with scapulocoracoid between mesopterygium and metapterygium; synarcual short with vertebral centra nearly reaching neurocranium. Unlike *Spathobatis,* but like *Belemnobatis,* in having pectoral

fins not extending to overlap pelvic fins and lacking enlarged placoid scales. Unlike *Spathobatis* and *Belemnobatis* in having subtriangular rostrum that fails to reach end of snout; no rostral appendix; incipient lingual uvula on teeth; post-pelvic process; neural spines of caudal region longer than centra; no fin spines; rugose axial cartilage of clasper.

5.4. Remarks

There are a number of "guitarfish-like" batoid taxa known from well preserved skeletal remains from the Kimmeridgian and Tithonian, but all differ from *Kimmerobatis* gen. nov.. The best known of these are *Belemnobatis sismondae* Thiollère1854, *Spathobatis bugesiacus* Thiollère1854 and *Asterodermus platypterus* Agassiz, 1843 (*sensu* Kriwet and Klug, 2004) from the Kimmeridgian and Tithonian of France and Germany. All of these species have dorsal fin spines, which are especially large in *B. sismondae,* and robust rostral cartilages, which reach the end of the rostrum. In *S. bugesiacus* and *A. platypterus* the rostrum is far longer than in *Kimmerobatis* gen. nov., whereas in *B. sismondae* it is shorter and gives a convex leading edge to the pectoral fins. Teeth of *A. platypterus* and *B. sismondae* are wide and low, unlike those of *Kimmerobatis* gen. nov., (see Theis and Leidner, 2011), whereas the more equant teeth of *S. bugesiacus* (e.g. Cappetta, 1987) possess a strong occlusal ridge and are larger relative to body size than those of *Kimmerobatis* gen. nov.

"*Spathobatis*" *morinicus* (Sauvage, 1873) is known from a single partial skeleton from the French Tithonian. Reassigned to *Belemnobatis* by Cavin et al., (1995), this specimen differs from any named genus and is difficult to compare directly to *Kimmerobatis* gen. nov., because it is preserved in ventral view. That said, although similar to *Kimmerobatis* gen. nov. in general body shape, "*S.*" *morinicus*

differs in a number of ways. The rostral cartilage of "*S.*" *morinicus* is robust and reached the tip of the rostrum, the teeth are proportionately larger and have a well defined occlusal crest and small cusp, and the propterygium and metapterygium are of similar length to each other and are both far more gracile than in *Kimmerobatis* gen. nov. and exposed ventrally so there is relatively little character overlap with *Kimmerobatis* gen. nov.

An unnamed batoid from the Tithonian of Argentina (Cione, 1999) has a longer synarcual than in *Kimmerobatis* gen. nov. within which centra are only present in the posterior half; this is the only Jurassic batoid known to show this character. In addition it has laterally projecting nasal capsules with an antorbital cartilage bearing a pointed termination, more gracile hyomandibula, larger and more flared mesopterygium and apparently at least one radial articulating directly with the scapulocoracoid.

6. *Kimmerobatis etchesi* gen. et sp. nov.

Figure 1-3.

In press. *Belemnobatis* sp. Underwood.

6.1. Material

Two partial skeletons from the Kimmeridge Clay (Early Tithonian) of Kimmeridge.

6.2. Derivation of name

After Steve Etches, who collected and prepared the specimens.

6.3. Type material.

Holotype, K874; paratype, K1894.

6.4. Diagnosis

See genus above

6.5. Description

Both specimens are highly compacted, however, there is some degree of relief preserved in the more robust parts of the skeleton such as neurocranium, vertebral column and pectoral girdle. The holotype specimen is exposed in dorsal aspect and preserves much of the head and trunk as well as parts of the pectoral fins. It is missing parts of the pectoral fins, much of the pelvic fins, and the mid to distal parts of the caudal region. Dorsal fins are not seen and some parts of the dorsal region of the pectoral girdle are missing. The paratype specimen is seen in ventral view and comprises the pelvic region and claspers as well as the midsection of the caudal region. Again, no dorsal fins are seen.

6.5.1. General body form.

Whilst the full body outline of this species is unknown, much information can be obtained from the specimens, especially the holotype. Note that the outline apparent on the specimen does not represent accurately the original outline, but has been prepared onto the rock as an approximate interpretation and does not form the basis of phylogenetic characters (Fig. 1A). The body shape is typically "guitarfish-like", with a pointed rostrum, each pectoral fin being anteroposteriorly longer than wide and a thick caudal (post-pelvic) region that is longer than the trunk (back of

neurocranium to pelvis). Traces of soft tissue suggest that the proximal part of the caudal region is at least as wide as the neurocranium. Pectoral denticles on the leading edges of the pectoral fins and soft tissue traces suggest that the skin forming the leading edge of the head between the rostrum and pectoral fins formed a straight line and that the rostral tip was sharply angled (Fig. 1). Although the complete shape of the pectoral fins in uncertain, a part of the trailing edge is smoothly convex (Fig. 1B), as are the pelvic fins, so it is likely that the pectoral fins had a curved profile.

6.5.2. Neurocranium

The neurocranium of the holotype is well preserved in dorsal view and is dorsoventrally compacted, but with little distortion. The rostrum is robust and an anterior fontanelle is present on the entire length of the preserved dorsal surface. The rostrum as preserved is longer than the remainder of the neurocranium. The mineralised rostrum does not reach the tip of the rostrum as indicated by the skin outline (Fig. 1A). Whilst it is possible that the tip of the mineralised rostrum has been removed during decay, the preserved cartilage becomes thinner distally, and the fidelity of the skin trace suggests that damage is minimal. It therefore is likely that the tip of the rostral cartilage was unmineralised in life.

There is no posterior fontanelle and the roof of the neurocranium is flat, other than a faint semicircular ridge above the orbital area, representing a weak supraorbital crest (Fig. 1 and 2A). The nasal capsules are oval and somewhat inclined to the anterior. The width of the nasal capsules is less than that of the jaw cartilages. The anterior edge of the nasal capsules is smooth without the horn-like process seen in many other "guitarfish" taxa (see appendices 2 and 3). Antorbital cartilages are roughly triangular in shape and unbranching, with a broad articulation with the posterolateral part of the nasal capsule. The antorbital cartilages reach less than half

of the distance between the nasal capsules and the propterygium of the pectoral fin. The orbital region comprises about half of the length of the neurocranium excluding the rostrum. There is a prominent ridge along the anterior and lateral margins of this region – compression during fossilisation has enhanced the ridge so it appears more robust than when alive. The preorbital process merges into the posterior part of the nasal capsules, where it forms a robust posterior wall (Fig. 1B and 2A). The postorbital processes are short and poorly differentiated. The posterior part of the neurocranium gently widens at the otic region at the articulation with the hyomandibula laterally and synarcual posteriorly. The presence of the jugal arch is evident, but details are unclear (Fig. 2A). The articulation between the neurocranium and synarcual is weakly indented – details about the morphology of the ventral synarcual lip are obscured from view.

6.5.3. *Jaws and branchial skeleton*

The lateral parts of the jaw cartilages are clearly visible, but the medial region and symphysis are not clear because the jaw is largely concealed beneath the neurocranium. The Meckel's cartilage is relatively robust and roughly equal to the palatoquadrate in anteroposterior depth. A moderate dorsal flange of the Meckel's cartilage hooks around the lateralmost part of the palatoquadrate. That dorsal flange is anterolaterally directed, rather than anteriorly as it is in Cretaceous and modern "guitarfish" (Claeson et al., 2013: fig. 6 and MorphoBank Project 749). The mandibular knob is level with the dorsal flange and slightly obscures the articular condyle of the palatoquadrate. The palatoquadrates are robust and have a wide and smoothly tapering articulation with the Meckel's cartilage. The tooth-bearing portion of the Meckel's and palatoquadrate cartilages is broad and the central part of the palatoquatrates has a concave lingual face (Fig. 2A).

The hyomandibulae are short, somewhat plate-like (though not to the extreme as in the Torpedinidae), being less than one and a half times as long as wide, as in modern *Rhinobatos* (see Claeson, 2014). Hyomandibulae are triangular in profile, with a broad articulation to the neurocranium. The articulation with the Meckel's cartilage is rounded and slightly reflexed anteriorly.

The overall shape of the brachial region tapers from the width of the hyomandibulae proximally to about 70% of that width close to the pectoral girdle. Individual elements are not easy to recognise, but the epibranchials are wide and rectangular in shape. Laterally, the epibranchial and ceratobranchial elements articulate to give a "Y" shaped profile. A narrow element close to the hyomandibula appears to represent a pseudohyal cartilage. A robust and smooth, posterolaterally directed element represents the fifth ceratobranchial, which reached the scapulocoracoid, though details of the articulation are unclear.

6.5.4. Vertebral column, synarcual and ribs

The vertebral column comprises cyclospondylic centra that remain a constant size and shape along almost the entire preserved length of the holotype (Fig. 2A and B). Centra are not all readily distinguished due to partial concealment beneath probable soft tissue and neural arch cartilage, but the general shape of most can be broadly recognised. Centra are of slightly greater diameter than length, and have, in side view, thickened rims and a central concavity, each of similar length.

A large and conspicuous synarcual is present, comprising an unsegmented tube of tessellated cartilage, which flanks about 11 vertebral centra, considering the end of the synarcual as the first non-fused neural spine. The preserved synarcual is crushed, but drapes over the vertebral centra allowing their outline to be seen. Large and fully formed centra are present within the synarcual for most of its length, in

contrast to modern batoids. At the anteriormost limit of the synarcual there is a depression, indicating that the centra did not reach the foramen magnum, but was separated by a lip of tessellated cartilage as it is in modern batoids (Fig. 2B). A narrow median crest is present on the dorsal midline of the anterior third of the draped centra. The lateral stays of the synarcual begin to expand laterally about half way down the posterior length of the synarcual and reach their maximum width at about two thirds the length of the synarcual. The lateral stays are posterolaterally directed, with small notches on their distalmost posterior margin. Posterior to the lateral stays, the synarcual flanks the remaining centra before transitioning into segmental neural arches and ribs. A direct articulation between the synarcual and pectoral girdle does not exist. The posterior flanges of the synarcual reach the coracoid bar of the scapulocoracoid; however, in the holotype, the first free neural spine lies anterior of the scapulocoracoid (Fig. 2B).

Neural spines are not preserved in direct articulation with the precaudal vertebral centra, but rather to their left; it is likely that arch elements were poorly mineralised and these are not clear. The dorsal parts of the precaudal neural spines are anteroposteriorly broad and tab-like. The neural spines are caudally inclined and slightly higher than long. There is some variation in the length of adjacent neural spines which is not apparently mirrored in the centra. There are at least 19 precaudal, rib-bearing centra and 19 corresponding neural spines posterior to the synarcual (Fig. 1). Articulated ribs are preserved for some of these precaudal centra. Among them, the posteriormost five of these rib-bearing centra are posterior to the ischiopubic bar of the pelvic girdle in the holotype and paratype (Figs. 1A and 3). From rostral to caudal, the precaudal centra remain relatively similar in size, whereas neural spines become more irregular, which is demonstrated in the caudal region of modern skate development (Criswell et al., 2017). The distalmost preserved neural spine on the

holotype is especially large and about as long as three centra. Among the caudal centra preserved in the holotype, there are 30 centra and 16 corresponding neural spines. Posterior to this point, neural spines are not preserved, but an additional 11 centra are present that taper gradually towards the caudal peduncle.

In the paratype specimen, five of the rib-bearing precaudal centra are posterior to the ischiopubic bar of the pelvic girdle and there are an additional 56 preserved caudal centra. As in the holotype, there are half as many neural spines as centra in the caudal skeleton. More distal neural spines are progressively shorter, and in the posteriormost position are about three times as anteroposteriorly elongate as tall. Hemal arches are present but not clear. They are considerably longer than high and of similar lengths to the neural spines.

Ribs in the holotype and paratype are long and well developed. In the mid part of the thoracic region, only the tips of the ribs are mineralised, and these reach almost to the inner edge of the pectoral fin skeleton. More posterior ribs are completely mineralised and strongly curved posterolaterally. There is no distinction between ribs present anterior and posterior to the ischiopubic bar of the pelvic girdle.

6.5.5. Pectoral skeleton

The pectoral skeleton does not articulate directly with the vertebral column via a suprascapula, although a possible left-unfused suprascapula is present near the proximal point of the scapular process of the scapulocoracoid (Fig. 2B). The scapulocoracoid is largely preserved but dorsoventrally compressed. The scapular process is a short extension off of the posterior corner of the scapulocoracoid. The scapular process tapers and is rounded at its apex, unlike the condition in non-batoid elasmobranchs which is blunt (see Claeson, 2014), and unlike the condition in Cretaceous and extant "guitarfish" which is more angular and would articulate into a

slot-like scapulocoracoid (Aschliman et al., 2012a; Claeson et al., 2013). There is a wide gap in the position predicted to be occupied by the suprascapular cartilage. As in other Jurassic batoids there is no evidence for a point of suprascapular articulation on the synarcual or with the scapulocoracoid. It is unlikely to have been lost taphonomically or during preparation, thus we suggest it was never present or at least unmineralised. The lack of a high posterior part to the synarcual suggests a lack of articulation even if an unmineralised suprascapular cartilage were present. The coracoid bar of the scapulocoracoid is largely concealed but appears to be slender. The lateral aspect of the scapulocoracoid is medio-laterally wide and rather flat, with a faint ridge running across the anterior face. It is somewhat displaced posteriorly but does not flare appreciably. There is direct articulation with the three pterygial cartilages.

The propterygium is broad, robust, and segmented. The first segment comprises over half of the anterior propterygial length and is considerably longer than the anteriormost radials. The mesopterygium is incompletely preserved distally, but is long and widens laterally from a short articulation with the scapulocoracoid. The propterygium has a suture with the mesopterygium that extends for over half of its length. The metapterygium is long and curved. The metapterygial articulation with the scapulocoracoid is longer than the articulation with the other two pterygial cartilages combined. Seven radials articulate with the first segment of the propterygium. About 22 radials articulate with the metapterygium. These radials exhibit crustal calcification (sensu Schaefer and Summers 2005). No radials articulate directly with the scapulocoracoid between the mesopterygium and metapterygium (Fig. 2B). Radial cartilages on the anterior part of the pectoral fin are wide and short. The majority of their length is composed of a single segment; the second segment is very short. Radials attached to the metapterygium are less clear, but the preserved

part, accounting for over three quarters of the width to the fin edge, is composed of a single segment.

6.5.6. Pelvic skeleton and claspers

Although the pelvic skeleton is preserved in both specimens, it is more readily seen in the paratype. The holotype appears to be female and the paratype is male (Figs. 1 and 3). The pelvic fins are more than twice as long as wide (from the basipterygium and excluding the claspers). The ischiopubic bar is about six times as wide as long, straight, and appears to have a minute tab on its posterior margin; the curvature in the central part on the paratype is attributed to compaction. The lateral articular surfaces are not discernable (Fig. 3).

The basipterygium is elongate and slender, straight in the anterior half and gently curved inwards in the posterior half. There are approximately 21 radials; in the paratype four of these are somewhat gracile and parallel to the direction of distal basipterygia the axial cartilage of the clasper. The posterior segments of the slender basipterygia are difficult to discern because they are obscured by the distal pelvic radials.

Both claspers are exposed in ventral aspect of the paratype. The claspers are very long and slender, being about as long as 22 adjacent centra. Much of the exposed surface of the claspers comprises an elongate rugose axial cartilage, similar to the wrinkled surface seen in *Rhinobatos productus* (e.g., USNM 1009; KMC pers. obs.). The axial cartilage is about 10 times as long as wide. Along much of the outer edge of this axial cartilage is a narrow and smooth ventral marginal cartilage (Fig. 3B and C). Much of the terminal part of the clasper glans is covered by an oval ventral covering piece cartilage, with a smooth distal edge but irregular proximally. The homology of this is uncertain, but this may be a ventral extension of the dorsal marginal cartilage.

A small rounded dorsal terminal cartilage is also present, partly concealed beneath other structures, whilst an elongate structure alongside this is considered to represent the ventral terminal cartilage.

6.5.7. Teeth and denticles

The dermal skeleton is not readily observed, much being either removed from the upper surface of the specimens during decay or preparation, or concealed beneath other structures. The mudstone matrix precludes acid extraction of dermal elements as has been carried out in batoid specimens preserved in carbonates. Denticles are seen in relatively few places on the specimens, and there is no evidence of enlarged star-shaped denticles present on some other Jurassic batoids (e.g. Thies and Leidner 2011). Some of the body outline of the holotype is provided by a layer of very small denticles (Fig. 1A). This is especially clear around the rostrum and pectoral fins. These denticles are very small and their shape cannot be discerned. On the leading edges of the pectoral fins, rectangular areas of more prominent denticles are present. These are again small and not readily seen, but appear to be thorn-like, giving the areas a rough texture. Patches of denticles are also present overlying parts of the jaw cartilage and therefore represent the skin covering of the upper lateral parts of the head (Fig. 2C). The denticles are closely packed and irregularly polygonal. The face is smooth and gently domed.

Teeth are seen in the lateral parts of the mouth, but their details are not clear Figs 1 and 2C-D). Teeth are very small, typically about 0.3-0.4 mm wide, deep, and high, being far smaller than adjacent tesserae in the jaw cartilages. Separate lingual and labial crown faces are seen, but there is no clear occlusal crest or cusp separating these. No teeth are preserved with a completely exposed root, but roots appear to be low and a similar width to the crown.

6.5.8. Unmineralised tissues

Large areas of pale brown material are present on both of the specimens, especially in the caudal region (Figs. 1 and 3). This appears to have a vaguely striated texture to it, but lacks structural detail. This is clearly separate from the skin outline as evidenced by denticles, and in places partly overlies cartilages. This appears to be phosphatised muscle tissue, and in the caudal region apparently gives a good representation of original body outline.

A dark area on the dorsal surface of the left palatoquadrate is interpreted as retinal pigment (Fig. 2C). This is in the approximate position and of typical size of the eye of a batoid of this body plan.

7. Phylogeny of early batoids

7.1 Taxonomic Sample

The fossils from Kimmeridge, which represent a new species, are examined and compared with the skeletons of 31 other elasmobranch taxa (12 extinct and 19 extant). Two non-batoid elasmobranchs, *Hexanchus* and *Pristiophorus*, are included as outgroups. Ingroup taxa include the Jurassic batoids, †*Spathobatis* and †*Belemnobatis*, the Cretaceous "sawfish", †*Sclerorhynchus*, and extant batoids *Pristis*, *Torpedo*, *Narcine*, *Myliobatis*, and *Urolophus*. The remaining ingroup taxa are guitarfishes or 'rhinobatoids' (sensu Compagno, 1973), which were analysed by Claeson et al. (2013). 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.

7.2 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 Claeson et al. (2013). The matrix (Appendix 2) was compiled using Mesquite 2.74 (Maddison and Maddison, 2010). No changes to the character matrix were made for the non-Jurassic taxa included by Claeson et al. (2013), only new data were added for the additional Jurassic taxa *Kimmeribatis* n. gen, *Spathobatis*, and *Belemnobatis*. Characters and states for the entire matrix are listed in Appendix 3.

7.3 Phylogenetic methods

We examined the matrix under both parsimony and Bayesian methods. For each method we examined the entire matrix, i.e., no characters were excluded *a priori*. In the parsimony analysis, we treated all characters as unordered and equally weighted. Multistate characters were treated as polymorphic. The character matrix was analysed using PAUP* 4.0b10 (Swofford, 2002) using the maximum parsimony optimality criterion. We employed heuristic searches with 1000 replicates of random stepwise 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 (amb- option); 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).

For the Bayesian analysis, the matrix was examined in MrBayes, with the following parameters: set autoclose=yes nowarn=yes; lset nst=6 rates=invgamma; unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all); prset applyto=(all) ratepr=variable; mcmcp ngen= 10000000 relburnin=yes burninfrac=0.25 printfreq=1000 samplefreq=1000 nchains=4 savebrlens=yes; mcmc; sumt.

7.4 Phylogenetic results

There were 48 of 53 parsimony informative characters and the matrix had 7.19% missing and 1.47% inapplicable data. The heuristic search retained eight trees with 156 steps (CI = 0.4872, HI = 0. 5128, RI = 0.7133, RC = 0.3475). The identical strict consensus and 50% majority rule trees were rooted with Hexanchidae and *Pristiophorus* and are presented in figure 4A. Character transformations are mapped for Jurassic taxa in 4A. The likelihood tree with branch lengths are provided in figure 4B.

The tree topology of the parsimony analysis and the Bayesian analysis are more resolved than the tree presented by Claeson et al. (2013). Relationships among Platyrhinidae and its immediate sister clades remains the same, however, there is more resolution among the sections of the tree where Cretaceous 'guitarfishes' are stem members to the skate and ray lineages. Furthermore, the monophyletic Torpediniformes are recovered as sister taxon to a clade formed by all other batoids including the Jurassic batoids. Jurassic batoids form their own clade, Spathobatidae, where *Kimmerobatis etchesi* gen et sp. nov. is more closely related to *Belemnobatis* than either is to *Spathobatis*.

7.4 Phylogenetic discussion

The Late Jurassic (Kimmeridgian to Tithonian) represents the earliest occurrence of multiple batoid species preserved as articulated skeletons, with six known species, each potentially representing a different genus. The oldest known remains of batoids comprise isolated teeth assigned to several genera from the Toarcian (Early Jurassic), which were not included in the present analysis. Many of these earliest batoids have a tooth morphology very similar to the Late Jurassic genera *Belemnobatis* and *Asterodermus* and an affinity with these genera is considered likely (e.g. Underwood, 2006) while others are considered members of their own family Archaeobatidae (e.g., Delsate and Candoni, 2001). In addition, an as yet undescribed Early Jurassic skeleton from the Posidonia Shale near Holzmaden, Germany, suggests that at least some early batoids ha d a body form rather unlike later Jurassic taxa, particularly features of the axial and clasper skeleton (KMC pers. obs.).

Middle Jurassic batoids also are known exclusively from isolated teeth and not included in this analysis, but a number of taxa have been recognised (e.g. Underwood and Ward, 2004). Occurrence of Middle Jurassic species within different facies suggest a strong palaeoenvironmental preference of different taxa (Underwood 2004). Whilst isolated teeth have been recorded from Cretaceous rocks that may be assigned to genera known from the Jurassic (e.g. Underwood and Rees, 2002, Underwood et al., 1999), skeletal remains from the mid part (Aptian to Turonian) of the Cretaceous (Cappetta 1980, Claeson et al. 2013, Brito and Seret 1996, Brito et al. 2013) all possess derived characters such as the absence of a fin spine, well developed synarcual and propterygium articulating with the antorbital cartilage. The Late Jurassic therefore represents a "window" into batoid evolution, and understanding the phylogeny and relationships of these Jurassic forms is critical to understanding the radiation of the batoids. Indeed, the inclusion of whole bodied

Jurassic fossils have generated a more resolved hypothesis of batoid evolution throughout the Cretaceous and into the Cenozoic.

Of note in the evolution of Batoidea is the morphological variation of the synarcual and the associated pectoral skeleton. The inclusion of Jurassic taxa seems to help explain the early evolution and radiation of batoids, which appears driven by the form and function relationship of the pectoral and axial skeleton. Batoids are diagnosed in part by the presence of a synarcual (see Aschliman et al., 2012a), and within each modern clade of batoids there is a distinct modification to the synarcual morphology (Claeson, 2011; Aschliman et al., 2012; Claeson, 2014).

The Jurassic batoids exhibit a true synarcual, each presenting a short tube of tessellated cartilage. The Jurassic synarcuals present with multiple spinal nerve foramina correlating with multiple vertebral centra. Those centra are bounded anteriorly by tessellated synarcual cartilage and do not articulate directly with the chondrocranium. Outgroups lack this synarcual and centra articulate directly with the chondrocranium.

Secondary to the appearance of a synarcual is the fusion of independent suprascapulae, which is consistent with the bifurcation of the tree between Torpediniformes and all remaining batoids. Torpediniformes have fused suprascapulae (Claeson, 2014), which appears to be an independent acquisition compared to the condition seen in other Cretaceous and Cenozoic taxa, because the suprascapulae in Torpediniformes do not articulate with the vertebral column. Jurassic taxa, distinguished as their own clade, Spathobatidae, are sister taxon to a clade of non-torpediniform Cretaceous and Cenozoic taxa batoids. Suprascapulae in Spathobatidae have never been definitively identified, though based on morphology of the scapular process of the pectoral girdle and the neural spines posterior to the

synarcual, there is no evidence that suprascapulae were fused to each other or articulated with the pectoral girdle, which is plesiomorphic among elasmobranchs.

The clade of non-torpediniform Cretaceous and Cenozoic batoids (including †*Sclerorhynchus*) possesses a fused suprascapula that has a direct relationship to the vertebral column. At the base of this clade and among the stem taxa leading to the skates and stingrays, the suprascapula reflects the plesiomorphic "guitarfish-type" forked-morphology (Compagno, 1977; Claeson, 2011; Aschliman et al., 2012a; Claeson, 2014). This forked suprascapular cartilage articulates with the neural arches of more posterior vertebrae (Garman, 1913; Compagno, 1973; Miyake, 1988; Claeson, 2011; Aschliman et al., 2012a,b). In stingrays, the suprascapulae fuse to both the median crest and a distal component of the lateral stay. The pectoral arch in skates is the fused paired suprascapular cartilages that are incorporated directly into the synarcual (Garman, 1913; Compagno, 1973; Miyake, 1988; Claeson, 2008; Claeson, 2011). Given that the Cretaceous batoids are present at the base of the stingray, skate, and platyrhinid-guitarfish lineages, the fused suprascapulae appears to be the required step for the major radiation in batoid biodiversity.

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FIG. 1.

A. Composite photograph of the more complete holotype specimen. Scale bar is 100mm.

B. Outline drawing of the same specimen; ac- antorbital cartilage, af- anterior fontanelle, bp- basipterygium, br- branchial arches, c- vertebral centra, c5- fifth ceratobranchial, co- coracoid bar, ha- haemal arch, hm- hyomandibula, ib- ischiopubic bar, ls- lateral stay, mc- median crest, mk- Meckel's cartilage, ms- mesopterygium, mt- metapterygium, nc- nasal capsule, ns- neural spine, nse- neural spine, enlarged, pef- pelvic fin outline, pd- pectoral denticles, pf- pectoral fin outline, pm- phosphatised muscle, po- preorbital process, pp- propterygium, pq- palatoquadrate, r- ribs, ro- rostrum, ra- pectoral fin radials, rap- pelvic fin radials, rd- rostral denticle covering, rp- retinal pigment, sc- scapulocoracoid, sp- scapular process, syn-synarcual. Scale bar is 100mm.

FIG. 2.

A. Detail of the cranial region of the holotype. Scale bar is 100mm.

B. Detail of the synarcual and pectoral skeleton of the holotype. Scale bar is 100mm.

C. Part of the mouth of the holotype; de- denticles, rp- retinal pigment, t- tesserae of cartilage, te- teeth. Scale bar is 10mm.

D. Close up view of mouth showing the very small teeth. Scale bar is 5mm.

FIG 3.

A. Photograph of referred specimen. Scale bar is 100mm.

B. Outline drawing of the same specimen; ax- axial cartilage, bp- basipterygium, c- vertebral centra, ha- haemal arch, ib- ischiopubic bar, pm- phosphatised muscle, r- ribs, rap- pelvic fin radials, vc- ventral cartilage plate, possibly dorsal marginal cartilage, vmc- ventral marginal cartilage, vtc- ventral terminal cartilage. Scale bar is 100mm.

C. Detail of the claspers. Scale bar is 100mm.

FIG. 4.

A. Consensus tree based derived from eight most parsimonious trees (156 steps, CI = 0.4872, HI = 0. 5128, RI = 0.7133, RC = 0.3475). B. Likelihood tree. Spathobatidae branches are bold. Apomorphies are mapped on consensus tree for Spathobatidae.

Appendix 1. Materials examined

Fossil Material

†*Asterodermus platypterus*, NHM P10267; †*Belemnobatis sismondus* CM4408; †*Rhinobatos hakelensis*, NHM P4012 paratype; †*Rhinobatos intermedius*; NHM 49516 holotype; †*Rhinobatos maronita*, NHM P10696, NHM P13861, NHM 49511, NHM 49512, NHM 49554, SMNS 12429; †*Rhinobatos tenuirostris*, NHM P4770 holotype; †*Rhinobatos whitfieldi*, AMNH 3703, AMNH 3707, AMNH 3708, AMNH 3709, NHM P9145, NHM P24965, NHM 47519; †*Spathobatis bugesiacus*, NHM P2099, NHM P10934, CM5396

Recent Material

Aptycotrema, AMNH 98512; *Myliobatis* MCZ 1343-s; *Narcine brasiliensis,* AMNH 218276, AMNH 90769, AMNH 92321.a, TNHC 18512_A-C; *Platyrhinoides triseriata,* MCZ 99000, MCZ S895, MCZ S750, MCZ S749; *Pristiophorus japonicus*, MCZ 1045-s, MCZ 1283; *Pristis*, AMNH 55624, MCZ S105; *Raja inornata*, FMNH 2754; *Rhinobatos lentignosus*, MCZ 57799; *Torpedo*, ZMB 33932, ZMB 33933; *Urolophus*, AMNH 214469; *Zapteryx exasperata*, SMF 26135; SMF 30674

Appendix 2. Character Matrix

```
Hexanchidae              0 0 0 0 - - - 0 0    0 0 0 0 0 0 0 0 0 ?    0 0 0 0 0 0 0 0 0 0    0 0 0 0 0 0 0 - 0    0 0 0 0 0 0 0 0 0 0    0 0 0
Pristiophorus            0 0 0 1 1 0 1 0 0 0    0 0 0 0 0 0 1 0 0 ?    1 0 1 0 0 0 ? 0 0      0 0 0 0 0 0 0 0 - 0    0 0 0 0 0 0 0 0 0 0    0 0 0
Spathobatis              0 0 0 0 1 0 0 0 0 0    ? ? ? 0 ? 1 1 0 0 ?    2 0 2 1 0 1 0 0 1 0    0 1 0 0 0 0 0 1 0 0    0 0 0 0 0 0 1 0 0 0    0 1 1
Belemnobatis             0 0 0 0 1 0 0 0 0 0    0 0 0 1 ? 1 1 0 ? ?    2 0 2 1 1 1 0 0 1 0    0 1 0 0 1 0 0 1 0 0    0 0 0 0 0 0 1 0 0 0    1 0 ?
Kimmerobatis             3 1 1 0 1 0 0 0 0 0    0 0 0 1 ? 1 1 0 ? ?    1 0 2 1 ? 1 ? 0 1 0    0 1 0 0 1 0 1 1 0 0    0 0 0 0 0 0 1 0 0 0    0 0 1
Sclerorhychus            0 0 0 1 1 0 0 0 0 0    0 0 0 ? ? 1 1 0 0 ?    1 0 2 1 0 0 ? ? 1 ?    1 1 0 0 0 0 ? 1 1 0    0 0 0 0 0 ? 0 0 0 0    0 0 ?
Pristis                  0 0 0 1 1 0 0 0 0 0    0 0 0 1 0 1 1 0 0 2    2 1 2 1 0 0 0 1 1 1    0 1 0 0 0 0 0 1 0 1    0 0 0 0 0 0 0 0 0 0    0 0 1
Torpedo                  0 0 0 0 1 1 1 0 0 0    1 1 - 0 1 1 1 0 0 0    0 0 2 2 3 1 2 1 1 1    1 1 0 1 1 1 1 1 0 0    1 0 0 0 0 0 0 0 0 0    2 0 0
Narcine                  0 0 0 0 1 1 1 0 0 0    1 1 - 0 1 1 0 0 0 0    0 0 2 2 3 0 2 1 1 1    1 1 0 1 1 1 0 1 1 0    1 0 0 0 0 ? 0 0 0 0    2 0 0
Narke                    0 0 0 0 1 1 1 0 0 1    1 1 - 0 1 1 0 0 0 0    0 0 2 2 3 0 2 0 1 1    1 1 0 1 1 1 0 1 1 0    1 0 0 0 0 ? 0 0 0 0    2 0 0
Iansan                   0 0 ? 0 1 0 0 0 0 0    0 0 0 1 1 1 1 0 0 ?    2 2 2 1 0 0 0 1 1 1    1 1 0 1 1 0 0 1 1 1    0 0 2 0 0 0 0 0 0 0    0 1 ?
Rhynchobatus             0 0 1 1 1 0 0 0 1 0    0 0 0 1 1 1 0 1 0 0    2 0 2 1 0 0 0 1 1 1    1 1 0 0 0 0 0 1 1 1    0 0 0 0 0 1 0 0 0 0    0 1 1
Rhinobatos tenuirostris  0 0 1 0 1 0 0 0 1 ?    0 0 0 ? ? 1 ? 0 ? ?    2 2 2 1 0 0 ? ? 1 1    1 1 0 0 ? 0 0 1 ? 1    0 0 ? ? ? ? 0 0 0 ?    0 1 ?
Rhinobatos maronita      0 0 1 0 1 0 0 0 1 0    0 0 0 ? ? 1 ? 0 ? ?    1 0 2 1 ? 0 ? ? 1 1    1 1 0 0 0 0 0 1 0 1    0 0 0 1 0 0 0 0 0 0    0 1 ?
Aptychotrema             0 0 1 0 1 0 0 0 0 0    0 1 0 1 1 1 1 0 0 1    2 1 2 1 0 0 ? 1 1 1    1 1 0 1 1 0 ? 1 1 1    0 0 1 0 0 ? 1 0 0 0    0 1 ?
Zapteryx                 0 0 1 0 1 0 0 1 0 0    0 0 0 1 1 1 1 0 0 0    2 1 2 1 0 0 0 1 1 1    1 1 1 2 1 0 0 1 1 1    0 0 1 0 0 0 1 0 0 0    0 1 1
Trygonorrhina            0 0 1 0 1 0 0 1 0 0    0 0 0 1 1 1 ? 0 0 0    2 1 2 1 0 0 0 1 1 1    1 1 1 2 1 0 0 1 1 1    0 0 1 0 0 0 1 0 0 0    0 1 1
Rhinobatos hakelensis    0 0 1 0 1 0 0 1 0 0    0 0 0 1 ? 1 ? 0 0 ?    1 0 2 1 ? 0 ? ? 1 1    1 1 2 1 0 0 1 1 1       0 0 1 1 0 0 1 0 0 0    0 1 ?
Raja                     1 0 1 0 1 0 0 1 0 0    0 0 0 1 1 1 1 0 1 0    1 0 2 1 3 0 0 1 1 1    1 1 2 1 0 0 1 1 2       0 0 1 0 0 1 1 1 0 0    1 1 1
Rhombopterygia           0 0 1 0 1 0 0 1 0 0    0 0 0 ? 1 ? 1 ? 0 0    1 0 2 1 ? 0 ? ? 1 1    1 1 2 1 0 0 1 ? 1       0 0 1 0 0 1 0 0 0 0    0 1 ?
Rhinobatos whitfieldi    0 0 1 0 1 0 0 1 0 0    0 0 0 1 ? 1 ? 0 0 ?    1 0 2 1 ? 0 ? ? 1 1    1 1 2 1 0 0 1 1 1       0 0 0 1 1 1 1 0 0 0    0 1 ?
Zanobatos                2 2 0 0 1 0 0 1 0 0    0 0 0 1 1 1 ? 0 0 2    1 0 2 2 0 0 1 1 1       1 1 2 2 1 0 1 1 1 1    0 0 0 1 1 2 0 0 0 0    0 1 0
Myliobatis               2 2 0 0 1 0 0 1 0 1    0 0 3 0 1 1 1 0 2 3    0 0 3 2 3 0 2 1 1 1    1 1 2 2 0 0 0 1 0 2    0 1 3 1 1 2 2 0 0 1    2 0 0
Urolophus                2 2 0 0 1 0 0 1 0 1    0 0 2 0 1 1 1 0 0 2    0 0 2 2 3 0 0 1 1 1    1 1 2 2 0 0 0 1 0 2    0 1 2 1 1 1 0 0 0 0    2 0 0
Rhinobatos               0 0 1 0 1 0 0 1 0 0    0 0 0 1 1 1 0 1 0 2    1 0 2 1 0 0 0 1 1 1    1 1 0 1 1 0 0 1 1 1    0 0 1 0 0 0 1 0 0 0    0 1 1
Rhinobatos latus         0 0 1 0 1 0 0 1 1 0    0 0 0 ? ? 1 ? 0 ? ?    1 0 2 1 0 0 ? ? 1 1    1 1 1 1 0 0 1 0 1       0 0 0 0 0 0 1 0 0 0    0 1 ?
Rhinobatos intermedius   0 0 1 0 1 0 0 1 1 ?    0 0 0 ? ? 1 ? 0 ? ?    1 0 2 1 0 0 ? ? 1 1    1 1 1 1 0 0 1 ? 1       0 0 0 0 0 0 1 0 0 0    0 1 ?
Britobatos               0 0 1 0 1 0 0 1 1 0    0 0 0 0 ? 1 0 0 0 ?    2 2 2 1 0 0 ? ? 1 1    1 1 2 1 0 ? 1 0 1       0 0 1 1 0 0 0 0 1 0    0 1 ?
Tethybatis               3 1 ? ? ? - - 0 0      ? 0 0 ? 1 1 ? 0 - -    - - - - 0 ? ? ? ?      1 1 2 2 1 0 0 1 0 1    ? 0 ? 0 0 0 0 0 0 0    0 1 1
Platyrhina               3 1 0 0 1 2 0 1 1 0    0 0 0 1 1 1 0 0 0 2    2 2 2 1 2 0 0 1 1 1    1 1 2 2 1 0 1 1 ? 1    0 0 0 1 0 0 0 0 1 0    0 1 1
Platyrhinoidis           3 1 0 0 1 2 0 1 1 0    0 0 0 1 1 1 1 0 0 2    2 1 2 1 2 0 0 1 1 1    1 1 2 2 1 0 1 1 0 1    0 0 0 1 0 0 0 0 1 0    0 1 0
Tingitanius              3 ? 0 0 1 2 0 ? 1 0    0 0 0 1 1 1 1 0 0 ?    2 1 2 1 1 0 - - 1 -    - 1 - - - 0 1 1 0 1    0 0 1 1 0 0 0 0 1 0    0 1 1
```

Appendix 3. Characters and states

1. Rostral cartilage Shape (BD2004, char1)

    0 stout

    1 filamentous

    2 absent

    3 subtriangular: a tapered rostrum that fails to reach the anterior margin of the snout

2. Rostral cartilage (MA2004, char24)

    0 complete

1 fails to reach tip of the snout

2 absent

3. Rostral appendix (MA2004, char25)

    0 absent

    1 present

4. Precerebral fossa (BD2004, char11)

    0 present as a circular ovoid concavity

    1 extending anteriorly and roofed to form a tube

5. Antorbital cartilage (BD2004, char2)

    0 absent

    1 present

6. Antorbital cartilage shape

    0 unbranched and narrow, tapering distally

    1 long and branched

    2 plate-like

7. Antorbital cartilage projection direction

    0 postero-laterally

    1 anteriorly

8. Antorbital-propterygium connection (BD2004, char4; MA2004, char7)

    0 free

1 directly jointing

9. Nasal capsules (BD2004, char5)

   0 with a straight and or blunt anterior margin

   1 witha horn-like anterior process

10. Nasal capsule (MA2004, char27)

   0 laterally expanded

   1 ventrolaterally expanded

11. Supraorbital crest (BD2004, char6; MA2004, char30)

   0 present

   1 absent

12. Postorbital process (BD2004, char7; MA2004, char32)

   0 present

   1 absent

13. Location of postorbital process (MA2004, char32)

   0 narrow and in otic region

   1 absent

   2 broad and shelflike and in otic region

   3 broad and shelf like in orbital region

14. Jugal arch (MA2004, char35)

   0 absent

1 present

15. Basal angle of neurocranium (BS1996, char 12; MA2004, char28)

   0 present

   1 absent

16. Relation between palatoquadrate and neurocranium (BD2004, char8; MA2004,

   char2)

   0 articulated

   1 loss of orbital articulation

17. Labial cartilages (MA2004, char38)

   0 present

   1 absent

18. Jaw shape

   0 straight

   1 with sigmoidal curvature

19. Osteodentine in tooth root (MA2004, char17)

   0 absent

   1 present in roots of large teeth only

   2 widespread occurence in tooth roots

20. Pulp cavity of tooth root (MA2004, char16)

   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 vascularisation

0 multiple, irreular (anaulacorhizous)

1 single paired opening (hemiaulacorhizous)

2 open or secondarily roofed (holoaulacorhizous)

3 fused teeth that are polyaulacorhizous

24. Lingual projection of root lobe 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, char39)

0 narrow

1 expanded

27. Basihyal and first hypobranchial (MA2004, char43)

0 both present and unsegmented

1 basihyal is segmented

2 basihyal is absent

3 basihyal and first hypobranchial cartilages are absent

28. Ceratohyal (MA2004, char44)

0 fully developed

1 reduced or absent

29. Distal tip of last ceratobranchial (BD2004, char9; MA2004 char4)

0 independent of scapulocoracoid

1 articulating with scapulocoracoid

30. Pseudohyoid bar (BD2004, char10; MA2004, char3)

0 absent

1 present

31. Paired fins (BD2004, char13 and char19; MA2004, char60)

    0 aplesodic

    1 plesodic

32. Form of pectoral fin (BD2004, char14)

    0 not elongated anteriorly

    1 anteriorly elongated

33. Pectoral propterygium (BD2004, char15; MA2004, char55)

    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, char16)

    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, char17)

    0 not reaching the pelvic fin

    1 extending to the pelvic fin origin

36. Electric ampullae on the pectoral fins (BD2004, char18)

    0 absent

    1 present

37. Postpelvic process (BD2004, char20)

   0 absent

   1 present

38. Synarcual (BD2004, char23;

   0 absent

   1 present

39. Extent of Synarcual Lip (new)

   0 short

   1 long

40. Suprascapulae (BD2004, char24+25; MA2004, char6; new observations)

   0 free of vertebral column

   1 articulated with vertebral column

   2 Fused to vertebral column (new)

41. Scapular process (BD2004, char26;MA2004, char49)

   0 long

   1 short

42. Ball and socket articulation (MA2004, char46)

   0 absent

   1 present

43. Mesocondyle (MDM1996, char48)

    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, char56)

    0 does not extend posterior to procondyle

    1 extends behind procondyle

45. Mesoptergium (MA2004, char58)

    0 present and single

    1 fragmented or absent

46. Shape of puboischadic bar (MA2004, char62)

    0 platelike

    1 narrow and strongly arched without distinct prepelvic processes

    2 narrow, strongly arched with a triangular medial prepelvic process

    3 narrow, moderately arched with barlike medial prepelvic process

47. Pectoral radials (BD2004, char28; MA2004, char57)

    0 all articulating with the propterygium, mesopterygium, and metapterygium

    1 some articulating directly withteh scapulocoracoid, between the meso and the

    metapterygium

    2 many articulating iwth the scapulocoracoid due to the lack of mesopterygium

48. Alar thorns (BD2004, char21, MD1998)

    0 absent

    1 present

49. Parallel rows of enlarged thorns over the posterior part of the disc and tail

    (BD2004, char22)

    0 absent

    1 present

50. Serrated tail spine (MA2004, char13)

    0 absent

    1 present

51. Placoid scales (MA2004, char14)

    0 uniformly present

    1 sparsly to densly covered with placoid scales on the dorsal surface only

    2 free of denticles
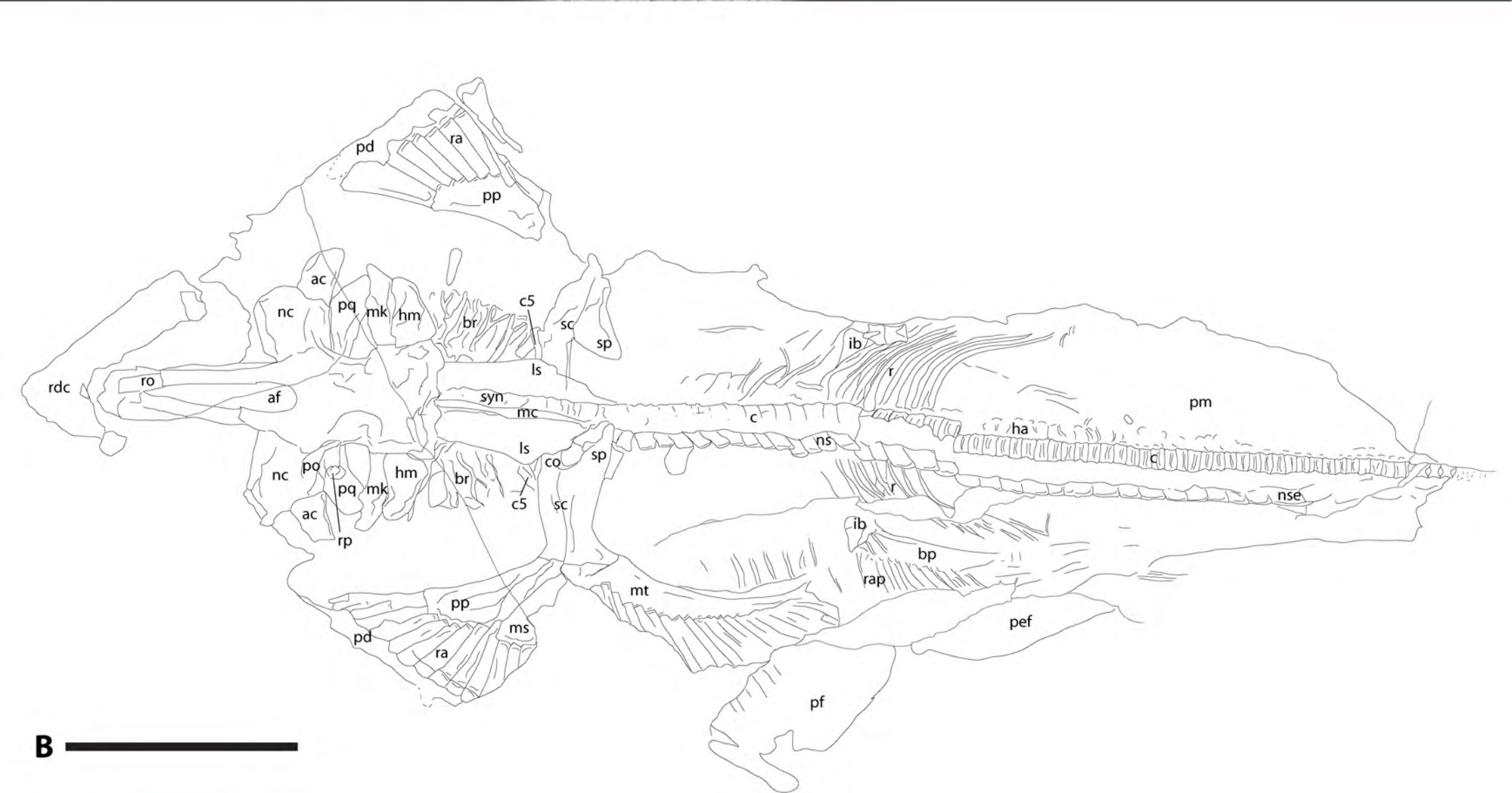

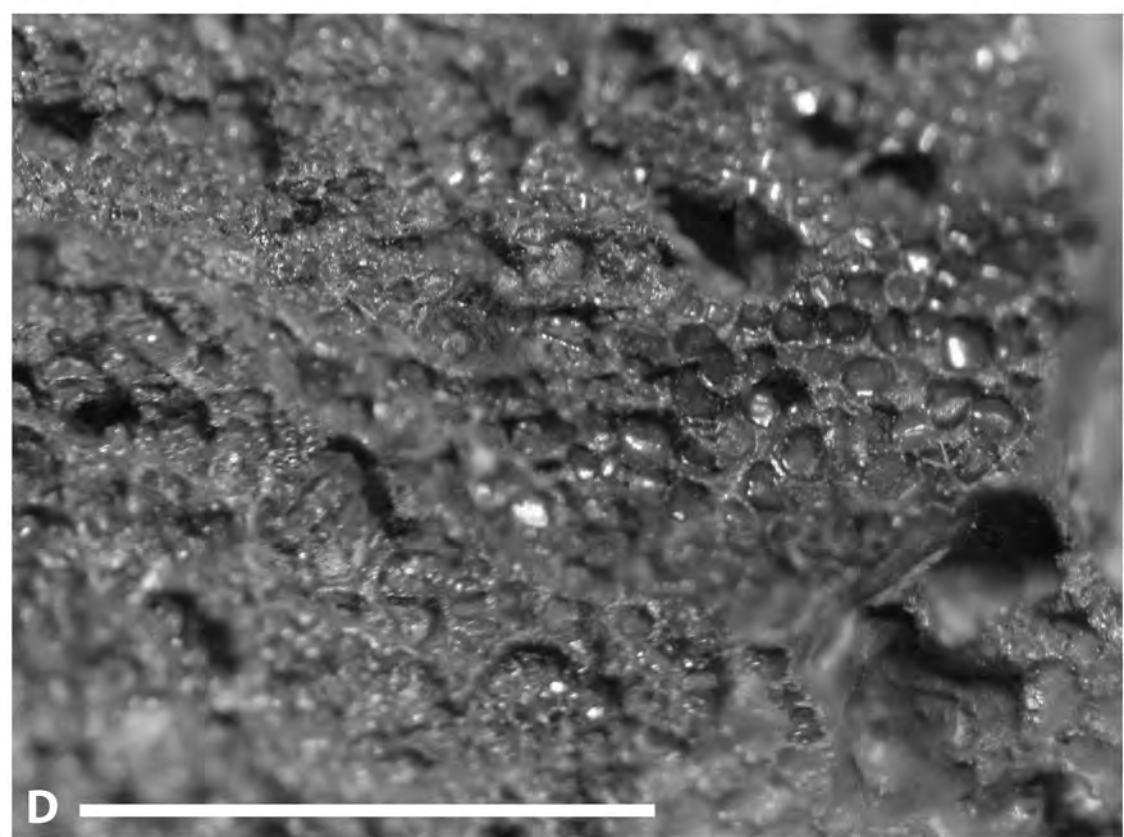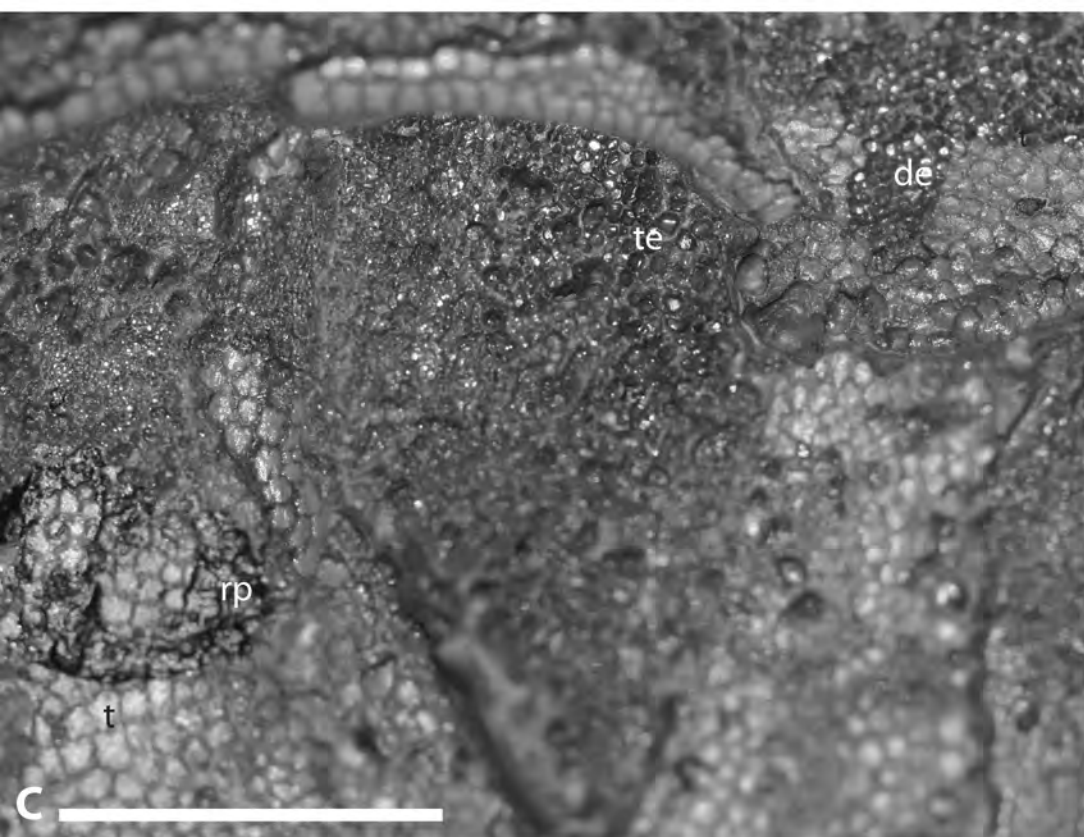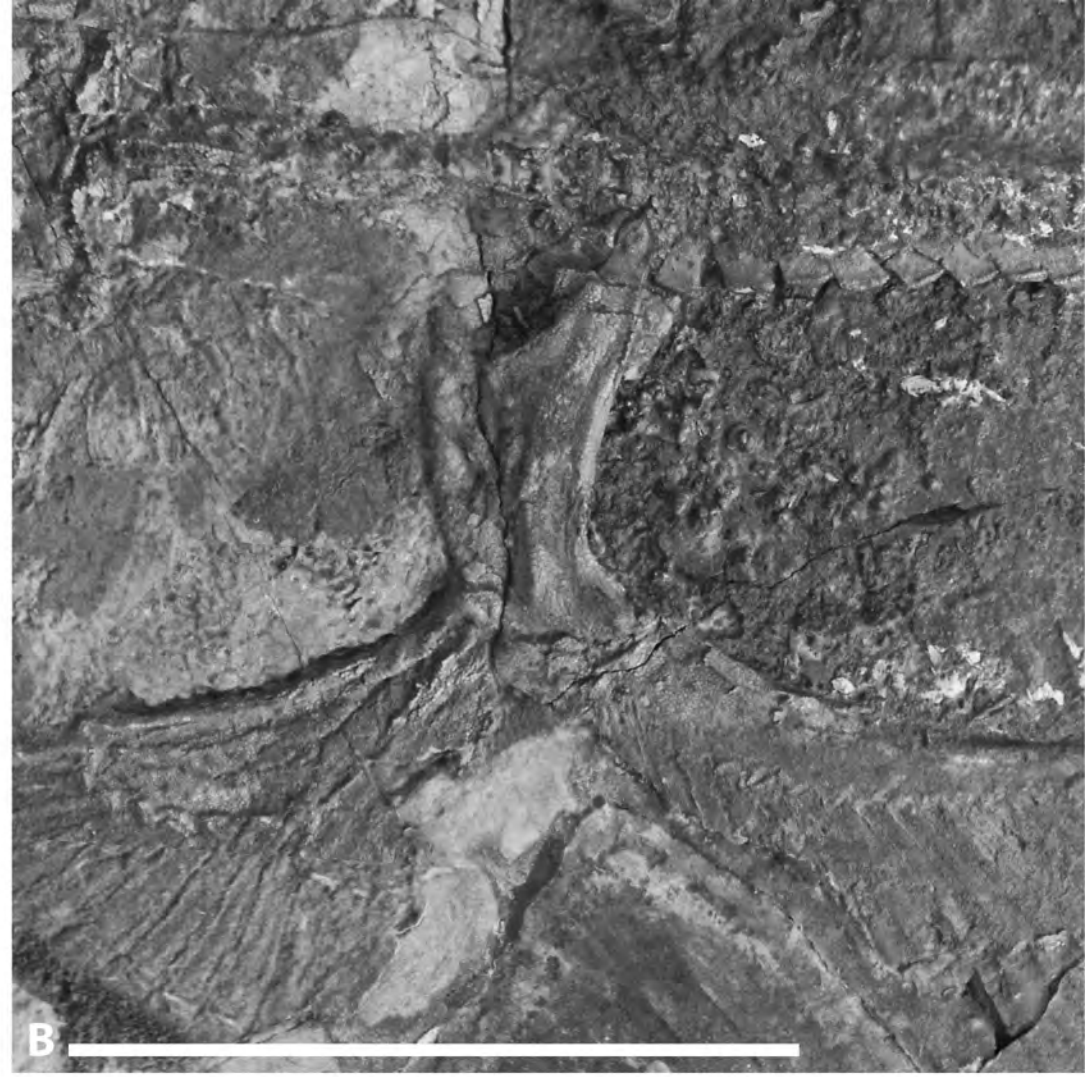52. Large placoid scales or thorns (MA2004, char15)

    0 absent

    1 present

53. Clasper length (MA2004, char64)

    0 short

    1 long

A

B

A

B

C

Character–taxon matrix (columns numbered 1–53; scale marks at 10, 20, 30, 40, 50).

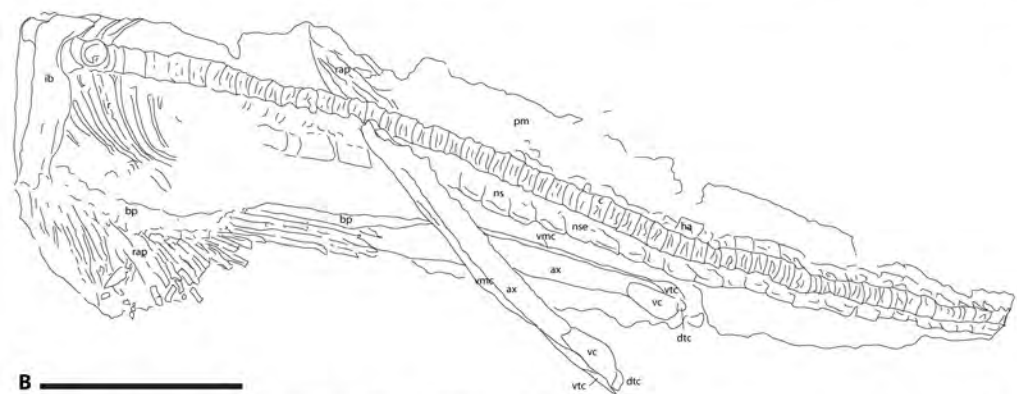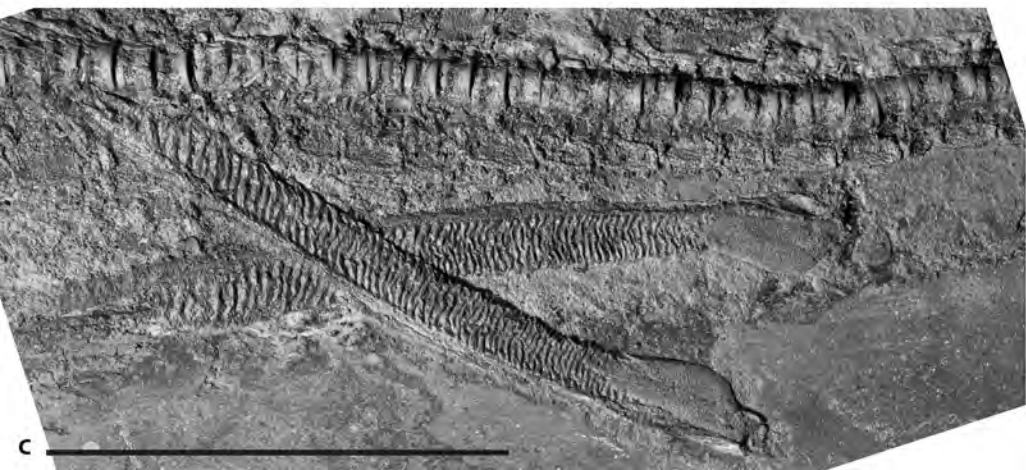| Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Hexanchidae	0	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pristiophorus	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	?	1	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spathobatis	0	0	0	0	1	0	0	0	0	0	?	?	?	0	?	1	1	0	0	?	2	0	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Belemnobatis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	?	1	1	0	?	?	2	0	2	1	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	?
Kimmerobatis	3	1	1	0	1	0	0	0	0	0	0	0	0	1	?	1	1	0	?	?	1	0	2	1	?	1	?	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Sclerorhychus	0	0	0	1	1	0	0	0	0	0	0	0	0	?	?	1	1	0	0	?	1	0	2	1	0	0	?	?	1	?	1	1	0	0	0	0	?	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	?
Pristis	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	2	2	1	2	1	0	0	0	1	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Torpedo	0	0	0	0	1	1	1	0	0	0	1	1	-	0	1	1	1	0	0	0	0	0	2	2	3	1	2	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0
Narcine	0	0	0	0	1	1	1	0	0	1	1	1	-	0	1	1	0	0	0	0	0	0	2	2	3	0	2	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0
Narke	0	0	0	0	1	1	1	0	0	1	1	1	-	0	1	1	0	0	0	0	0	0	2	2	3	0	2	0	1	1	1	1	0	1	1	1	0	1	1	0	1	0	0	0	0	?	0	0	0	0	2	0	0
Iansan	0	0	?	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	?	2	2	2	1	0	0	0	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0	2	0	0	0	0	0	0	0	0	1	?
Rhynchobatus	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	2	0	2	1	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1
Rhinobatos tenuirostris	0	0	1	0	1	0	0	0	1	?	0	0	0	?	?	1	?	0	?	?	2	2	2	1	0	0	?	?	1	1	1	1	0	0	?	0	0	1	?	1	0	0	?	?	?	?	?	0	0	0	0	1	?
Rhinobatos maronita	0	0	1	0	1	0	0	0	1	0	0	0	0	?	?	1	?	0	?	?	1	0	2	1	?	0	?	?	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	?
Aptychotrema	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	2	1	2	1	0	0	0	1	1	1	1	1	0	1	1	0	?	1	1	1	0	0	1	0	0	0	?	1	0	0	0	1	?
Zapteryx	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	2	2	1	2	1	0	0	0	1	1	1	1	1	1	2	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1
Trygonorrhina	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	?	0	0	0	2	1	2	1	0	0	0	1	1	1	1	1	1	2	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1
Rhinobatos hakelensis	0	0	1	0	1	0	0	1	0	0	0	0	0	1	?	1	?	0	0	?	1	0	2	1	?	0	?	?	1	1	1	1	1	2	1	0	0	1	1	1	0	0	1	1	0	0	1	0	0	0	0	1	?
Raja	1	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	2	1	3	0	0	1	1	1	1	1	1	2	1	0	0	1	1	2	0	0	1	0	0	0	1	1	0	0	1	1	1
Rhombopterygia	0	0	1	0	1	0	0	1	0	0	0	0	0	?	1	1	?	0	0	?	1	0	2	1	?	0	?	?	1	1	1	1	1	2	1	0	0	1	?	1	0	0	1	0	0	1	1	0	0	0	0	1	?
Rhinobatos whitfieldi	0	0	1	0	1	0	0	1	0	0	0	0	0	1	?	1	?	0	0	?	1	0	2	1	?	0	?	?	1	1	1	1	1	2	1	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	1	?
Zanobatos	2	2	0	0	1	0	0	1	0	0	0	0	0	1	1	1	?	0	0	2	1	0	2	2	0	0	0	1	1	1	1	1	2	2	1	0	1	1	1	1	0	0	0	1	1	1	2	0	0	0	0	1	0
Myliobatis	2	2	0	0	1	0	0	1	0	1	0	0	3	0	1	1	1	0	2	3	0	0	3	2	3	0	2	1	1	1	1	1	2	2	0	0	0	1	0	2	0	1	3	1	1	2	2	0	0	1	2	0	0
Urolophus	2	2	0	0	1	0	0	1	0	1	0	0	2	0	1	1	1	0	0	1	0	0	2	2	3	0	0	1	1	1	1	1	2	2	0	0	0	1	0	2	0	1	2	1	1	1	0	0	0	1	2	0	0
Rhinobatos	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	0	1	0	2	1	0	2	1	0	0	0	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1
Rhinobatos latus	0	0	1	0	1	0	0	1	1	0	0	0	0	?	?	1	?	0	?	?	1	0	2	1	0	0	?	?	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	?
Rhinobatos intermedius	0	0	1	0	1	0	0	1	1	?	0	0	0	?	?	1	?	0	?	?	2	0	2	1	0	0	?	?	1	1	1	1	1	1	1	0	0	1	?	1	0	0	0	0	0	0	0	0	0	0	0	1	?
Britobatos	0	0	1	0	1	0	0	1	1	0	0	0	0	0	?	1	0	0	0	?	2	2	2	1	0	0	?	?	1	1	1	1	1	2	1	0	?	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1	?
Tethybatis	3	1	?	?	?	-	-	-	0	0	?	0	0	?	1	1	?	0	-	-	-	-	-	-	-	0	?	?	?	?	1	1	2	2	1	0	0	1	0	1	?	0	?	?	0	0	0	0	0	0	0	1	1
Platyrhina	3	1	0	0	1	2	0	1	1	0	0	0	0	1	1	1	0	0	0	2	2	2	2	1	2	0	0	1	1	1	1	1	2	2	1	0	1	1	?	1	0	0	0	1	0	0	0	0	1	0	0	1	1
Platyrhinoidis	3	1	0	0	1	2	0	1	1	0	0	0	0	1	1	1	1	0	0	2	2	1	2	1	2	0	0	1	1	1	1	1	2	2	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
Tingitanius	3	?	0	0	1	2	0	?	1	0	0	0	0	1	1	1	1	0	0	?	2	1	2	1	1	0	-	-	1	-	-	1	-	-	-	0	1	1	0	1	0	0	1	1	0	0	0	0	1	0	0	1	1