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**The first three-dimensional fossils of Cretaceous sclerorhynchid sawfish:
Asflapristis cristadentis gen. et sp. nov., and implications in the phylogenetic
relations of the Sclerorhynchoidei (Chondrichthyes).**

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A new fossil batoid (ray) *Asflapristis cristadentis* gen. et sp. nov. is described from six exceptionally well-preserved, three-dimensional skeletal remains from the Turonian (Late Cretaceous) of Morocco. Mechanical and acid preparation and CT scanning of these specimens reveal details of much of the proximal skeleton, especially the skull, synarcual and pectoral skeleton, with only the more distal parts of the skeleton missing. These fossils represent a relatively large animal (62 cm preserved length, estimated total length to approximately 2 meters) possessing a robust rostrum that lacks enlarged rostral denticles. It has a narrow and small chondrocranium with jaws that are relatively large compared to the rest of the skull and robust with highly ornamented teeth that lack cusps. The branchial skeleton shows a large second hypobranchial without anterior process which was probably fused to the basibranchial as in other sclerorhynchoids. The synarcual is large and lacks centra through its entire length, and with no direct connection to the pectoral girdle was observed. Pectoral fins probably possessed enlarged proximal elements (propterygium, mesopterygium and metapterygium), the reduced articulation facet between the coracoid with the pectoral elements was reduced. A phylogenetic analysis using both parsimony and bayesian methods was performed incorporating this new taxon. Both analyses recovered a phylogenetic topology that places the sclerorhynchoids in a close relation to rajoids and clearly separated from the morphologically similar Pristidae within the Rhinopristiformes. In respect to the extant taxa, the phylogenies generated are similar to that obtained in molecular analysis of

modern batoids. The palaeoecological implication of this discovery suggests that the Asfla assemblage was not from a 'normal' open carbonate shelf but rather a restricted environment favouring a low diversity chondrichthyan fauna.

Key words: Phylogenetic analysis, *Asflapristis cristadentis*, Sclerorhynchoidei, batoids, Morocco, Turonian.

Introduction

The Batoidea (rays and their relatives) form the sister group to sharks within the Elasmobranchii and comprise more than half of living species of chondrichthyans. Whilst modern batoids are very diverse, including skates, sawfish, stingrays, electric rays and guitarfish, there are also a number of extinct clades, especially from the Jurassic and Cretaceous (Cappetta 2012; Maisey 2002). The most palaeontologically diverse of these extinct batoid clades is the sclerorhynchoids, a group of superficially sawfish-like forms that were present through much of the Cretaceous, becoming extinct at the end of the period. Currently there are over 60 sclerorhynchid nominal species, with most known only from isolated oral teeth or their characteristic enlarged rostral denticles (Cappetta 2012).

Sclerorhynchid remains are present in both marine and non-marine deposits, they appear to have been largely restricted to shallow-marine, nearshore, temperate-tropical areas within the Tethyan Realm (Underwood 2006), with sclerorhynchid fossils commonly dominating Cretaceous Tethyan chondrichthyan assemblages (e.g. Welton & Farish 1993). Articulated skeletal remains of all batoids are rare, with sclerorhynchoids being especially poorly represented. Almost all articulated sclerorhynchid material described to date is from the Late Cretaceous (Cenomanian or Santonian) of Lebanon (e.g. Cappetta 1980). From these sites, articulated and in many respects beautifully preserved, remains of the small sclerorhynchoids *Sclerorhynchus*, *Libanopristis* and *Micropristis* are known. Despite preservation of fine skeletal detail, and even traces of soft tissues, these fossils are dorsoventrally flattened and as a result the complex three-dimensional detail of structures such as the neurocranium, branchial elements, synarcual and pectoral girdle are poorly

known. Other non-dermal (teeth and denticle) sclerorhynchid material is restricted to partial to near complete rostra, typically of large species (e.g. Werner 1989), although there are additional records of an articulated cranium of *Onchopristis* (Dutheil & Brito 2009 not yet described).

Despite the lack of uncrushed skeletal remains of sclerorhynchoids, it has been recognised that they form a well-defined and monophyletic clade (Cappetta 1980, 1987; Kriwet 2004; Wueringer *et al.* 2009). However, there has been great uncertainty as to the phylogenetic position, and evolutionary significance, of this clade, with characters of critical parts of the anatomy being obscured by crushing in all known specimens. Currently sclerorhynchoids are typically placed as part of the order Rajiformes and comprising the suborder Sclerorhynchoidei (Cappetta 1987, 2006). Their striking (but superficial) similarity with modern sawfishes (Pristidae) and sawsharks (Pristiophoridae) has complicated phylogenetic placement of the group. Rostrum-associated structures have sometimes been regarded as homologous within these disparate groups, greatly influencing their apparent phylogenetic position, even though there are considerable differences in detail (e.g. Welten *et al.* 2015). As a result, sclerorhynchoids have been considered to reside in different positions in batoid phylogeny (e.g. Kriwet 2004; Claeson *et al.* 2013; Underwood & Claeson 2017) (see phylogenetic implications),

Kriwet (2004) is the direct antecedent for the present study, representing the most extensive review of the phylogenetics of the sclerorhynchoids to date. This analysis proposed several characters that distinguish the sclerorhynchoids from other batoids (e.g. buccopharyngeal and ophthalmic nerves not embedded in the rostral cartilage and lack of connection between the rostral cartilages and rostral denticles). In addition, Kriwet (2004) also included several characters from previous morphological studies (Nishida 1990; Brito & Seret 1996; De Carvalho 1996; Lovejoy 1996; McEachran *et al.* 1996; Shirai 1996) that supported the Hyposqualea hypothesis (Shirai 1992), within which batoids were considered to be derived squalean sharks, which has been extensively refuted by Dunn & Morrissey 1995; Schwartz & Maddock 2002; Douady *et al.* 2003; Winchell *et al.* 2004; Aschliman *et al.* 2012b; Last *et al.* 2016). This study also included several errors in matters of character definitions and coding (Aschliman *et al.* 2012a).

With the recovery of the first three dimensionally preserved skeletal fossils of sclerorhynchoids from the Cretaceous of Morocco, previously unknown morphological details were studied and reviewed allowing the clarification the phylogenetic relations for the group.

Geological setting

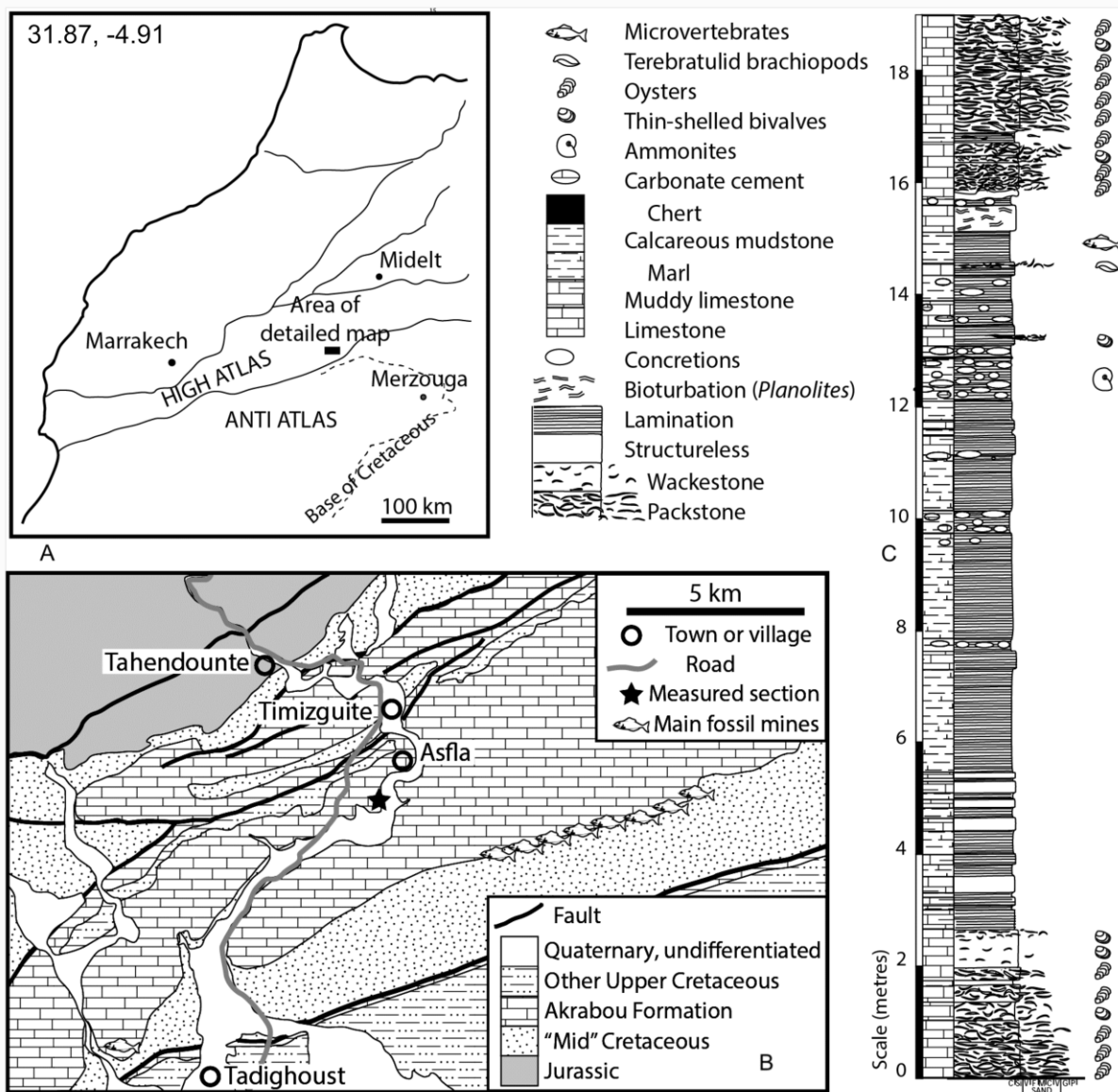


Figure 1. A, Map of the region; B, Locality map; C, Stratigraphic column of the Turonian in Asfla.

The area North of the town of Goulmima, southeast Morocco, is well known for fossils of ammonites (e.g. Cavin *et al.* 2010, Kennedy *et al.* 2008) and vertebrates (e.g. Ettachfini & Andreu 2004). Fossils are commercially collected, with the trade being centred on the village of Asfla. Fossils come from the Akrabou Formation, a unit of platform carbonates that ranges from late Cenomanian to Turonian (Cretaceous) in age, representing the early part of the late Cretaceous. These carbonates overlie the famously fossiliferous 'mid' Cretaceous Kem Kem fluvial facies and are overlain by further non-marine late Cretaceous rocks. The Akrabou Formation, therefore presents a strongly transgressive succession and relatively high sealevel, followed by a regressive episode. More southern outcrops of the Akrabou Formation form a near horizontal foreland area to the South of the High Atlas tectonic belt, with successions North of Goulmima being subject to folding and reverse faulting along the southern margin of the High Atlas (Lezin *et al.* 2012) (Fig.1). Whilst much of the Akrabou Formation comprises very shallow water facies containing monospecific shell beds, microbial laminites and tepee structures, the ammonites and vertebrates are largely known from a deeper water interval comprising marls and impure micrites with ovoid calcareous concretions. These concretions contain a diverse ammonite fauna (Kennedy *et al.* 2008) indicative of the *Mammites nodosoides* biozone of the Early Turonian (Cavin & Dutheil 1999) and mark a point of maximum transgression and relative water depth (Ettachfini & Andreu 2004). The deeper water facies are laterally discontinuous, and pass into shallower water limestones to the east, such as in the Ziz Gorge South of Errachidia (e.g. Ettachfini & Andreu 2004). Whilst the deeper water marls are up to 15 metres thick (close to the village of Asfla), fossiliferous concretions are largely limited to near the top of the unit. Where fossils are actively mined, there are typically two distinct units of concretions. A lower concretion bed, up to one metre thick, is generally poor in macrofossils although some ammonites are present. A second concretion bed, about two metres higher in the succession, is somewhat discontinuous (being absent at this level at Asfla itself) and often highly fossiliferous. It is this level that is commonly mined as a series of adits in the cliff face to extract fossils for sale; where these concretions are absent, there is no systematic mining for fossils. The

concretion-bearing levels are typically finely laminated and trace fossils are limited to rare, fine *Planolites* and other tubular burrows. Benthic fossils are rare other than oval, thin shelled bivalves and very small gastropods. At least some of the bivalves appear to be members of the Lucinidae. Small cirripede plates and comatulid crinoids are common in some commercially obtained concretions, but their provenance is uncertain. Whilst the laminated marls are pale brown or grey in colour, they have been exposed to extensive modern weathering and it is likely that they were originally rather organic-rich and dark in colour, as in unweathered examples of similar facies elsewhere.

Within the concretion beds, fossils are largely restricted to within the concretions themselves, with the only macrofossils in the surrounding rocks being small molluscs. Concretions are typically ovoid and 0.2-0.3 metres long, but when they enclose a vertebrate fossil, typically take on the general shape of the enclosed fossil. Batoid and teleost skeletons collected from the Asfla area are three-dimensional, with skeletal elements occupying several planes within the concretion (Cavin *et al.* 2010; Underwood & Ward 2009; Claeson *et al.* 2013), although there may be some crushing of larger elements (Claeson *et al.* 2013). The most abundant larger fossils within the nodules are relatively large ammonites (Kennedy & Juignet 1981; Kennedy *et al.* 2008). Fish fossils are also abundant, with most comprising partial to near complete skeletons. A large proportion of the fish are *Goulimimichthys arambourgi* (Cavin 1995), with *Ichthyodectes bardacki*, *Osmeroides rheris* and *Araripichthys corytophorus* (Cavin *et al.* 2010) also being frequent; *Enchodus sp.* (Cavin & Dutheil 1999) and indeterminate pycnodonts are also present. Chondrichthyans are far less common and restricted in diversity, with only batoids known from skeletal remains (Cavin, 1995; Claeson *et al.*, 2013; Underwood *et al.*, 2015). Sclerorhynchoids are known from multiple partial to near complete skeletons (e.g. Underwood *et al.*, 2015; fig. 3).

Sampling for microvertebrates suggest a small number of additional chondrichthyan species are present (see below). The marine reptiles include abundant remains of the mosasaur *Tethysaurus nopcsai* Bardet *et al.* 2003a, several plesiosaurs including *Thililua longicollis* Bardet *et al.* 2003b and *Manemergus anguirostris* Buchy *et al.* 2005, and undescribed chelonians (Cavin *et al.* 2010). The overall fossil

composition of the Akrabou Formation, whilst restricted in diversity, contains many of the faunal elements present in other shallow seas of the southern and western Tethys, and shows strong affinities with the South Atlantic and even the Western Interior Seaway in North America (Maisey & Moody 2001; Cavin 2001).

The Akrabou Formation typically forms high and steep escarpments, with the concretion beds often within the upper part of these cliffs. The upper nodule bed is the focus of intense commercial collecting activity, with horizontal adits being driven into the escarpments wherever abundant fossils are present. The most productive fossil sites are along the large escarpment South and East of Asfla; exposures elsewhere either lack the upper concretion bed or are less fossiliferous and are not commercially exploited. As a result, few fossils are seen *in situ* in the field, although ammonites and a skull of *Goulimimichthys* were recorded by the authors, and weathered fossils, including fragments of fish and reptiles, are not uncommon in the natural screes on the lower parts of the escarpments. The softer marls, especially those of the level of the Upper Nodule Bed, are suitable for bulk sampling. As with many Moroccan palaeontological investigations, the presence of commercial collecting has proven critical to this study.

Taphonomy

Whilst fossils of dermal elements of chondrichthyan are often very common in the fossil record, skeletal remains are far less so. Teeth are produced continuously through life and are often conspicuous. In sclerorhynchoids, teeth are small and rarely seen in the field, whereas the rostral denticles are typically large and conspicuous. In both teeth and denticles, the enameloid and dentine composition gives them a high preservation potential. In contrast, the cartilaginous skeleton is less commonly fossilised. Whilst many skeletal elements may be mineralised with apatite tesserae, these form a mineralised outer layer of the skeletal elements and readily disarticulate during decay. As a result, preserved endoskeletal elements of chondrichthyans are largely limited to the most intensely mineralised structures such as vertebral centra, jaw cartilages and rostra. More complete skeletal remains of chondrichthyans are restricted to a small number of konservat lagerstätten (e.g. Solnhofen, Nusplingen (Kriwet & Klug 2004), Monte Bolca (Marramà et al. 2018), Green River Formation (De Carvalho et al. 2004)). Cretaceous sites with well-

preserved batoids are rare and, other than isolated occurrences, largely limited to sites in Lebanon (e.g. Cappetta 1980) and the Santana Formation of Brazil (e.g. Martill 1988). Of these sites, the outwardly spectacularly preserved fossils of Lebanon are highly compressed, whilst the uncrushed batoid fossils of Brazil are restricted to two species (*Iansan beurleni* (Brito & Seret 1996) and *Stahlraja sertanensis* Brito *et al.* 2013).

At Asfla, vertebrate remains are preserved largely uncrushed within large and irregular carbonate concretions. The bony fish are typically preserved with the concretions centred around their trunk, with concretions around smaller fish being ovoid, those around larger skeletons roughly replicating the outline of the enclosed remains. The edges of the concretions rarely reach the extremities of the skeleton, with the caudal area, and often front of the skull, commonly missing. As isolated fish scales, teeth and vertebrae are common in the surrounding matrix marl, it is likely that the loss of these extremities occurs during collection rather than as taphonomic loss of bone outside the concretions. Specimens of *Asflapristis cristadentis* are far less complete than is typical of bony fish. Some specimens like NHMUK PV P 75431 were clearly disarticulated prior to burial whereas others like NHMUK PV P 75433, although incompletely preserved, show a skeleton that extends beyond the edges of the concretions and were complete and articulated at the time of burial. In the cases of these articulated specimens, it is likely that parts of the skeleton outside the concretions were lost at the time of collection, with the collectors not recognising the crushed cartilaginous skeleton outside the concretions. The high degree of articulation of even relatively fragile skeletons of batoids suggests that scavenging on the seafloor was absent or minimal, indicative of a hostile seafloor and/or very rapid burial. Whilst the concretion-bearing units of rock are thin, this does not rule out rapid burial by episodic sedimentation, even if the net sedimentation rate was low. Evidence for rapid burial comes from the fact that some of the elements of the skeletons are articulated even though they do not exist on the same bedding plane of the rock. This is clearly seen in the articulated dentitions of specimens like NHMUK PV P 75432 (Fig. 2 A-B) where parts of articulated dentition are present in their life position relative to jaw cartilages. This can only have been preserved if burial had occurred prior to decay of dermal tissue supporting the teeth. A similar situation exists with the three-dimensional nature of branchial and jaw elements in

some batoid specimens, where connective tissue must have retained the geometry of the skeleton until burial.

The rich biota of the Asfla concretion beds is composed almost entirely of free-swimming taxa, especially ammonites and vertebrates. By contrast, benthos is very limited and largely occurs sporadically, possibly restricted to certain bedding surfaces, whilst infaunal ichnofossils (burrows) are largely absent. A likely explanation of this is that the seafloor was generally hostile to life (e.g. Wignall 1994). The few benthic bivalves appear to be largely limited to lucinids, which possess with their sulphide-oxidising endosymbionts and thus may have found the conditions favourable when other benthos did not. Whilst there is clear no evidence of scavenging of vertebrate remains (such as bite marks), there are suggestions of scavenging by large organisms on at least one of the specimens. In specimen NHMUK PV P 75428 (Fig. 2 C-D), a large piece of sheet-like cartilage with ragged edges is present. The affinity of this is unclear, but it appears to be a partially detached piece of the braincase. This displacement cannot easily be explained by burial processes, and therefore it may represent the damage to the skull caused by feeding by a large (e.g. reptilian) scavenger.

No soft tissue preservation has been recognised in specimens of *Asflapristis cristadentis*, although phosphatised muscle tissue was noted in another batoid taxon (Claeson *et al.* 2013) and may be present but inconspicuous. This, albeit rare, preservation of soft tissue points towards an environment with poor conditions for organisms responsible for decomposing (Lezin *et al.* 2012) associated with microbially-mediated precipitation of apatite being more rapid than complete decay of soft tissues (Martill 1988).

Whilst fossils within the concretions are typically preserved in three dimensions, there is evidence of some degree of compaction prior to carbonate precipitation to form the concretions. There is some degree of crushing of the neurocranium and pectoral girdle of some specimens and shortening of obliquely orientated elements has previously been noted (Claeson *et al.* 2013). The overall taphonomic environment is thus similar to that of the Santana Formation of Brazil (see Martill 1988), despite the lack of similarity of depositional environment, with fully marine

environments of Asfla contrasting with the rather more restricted palaeoenvironments of the Santana Formation which lacks fully marine invertebrates (Martill 1988).

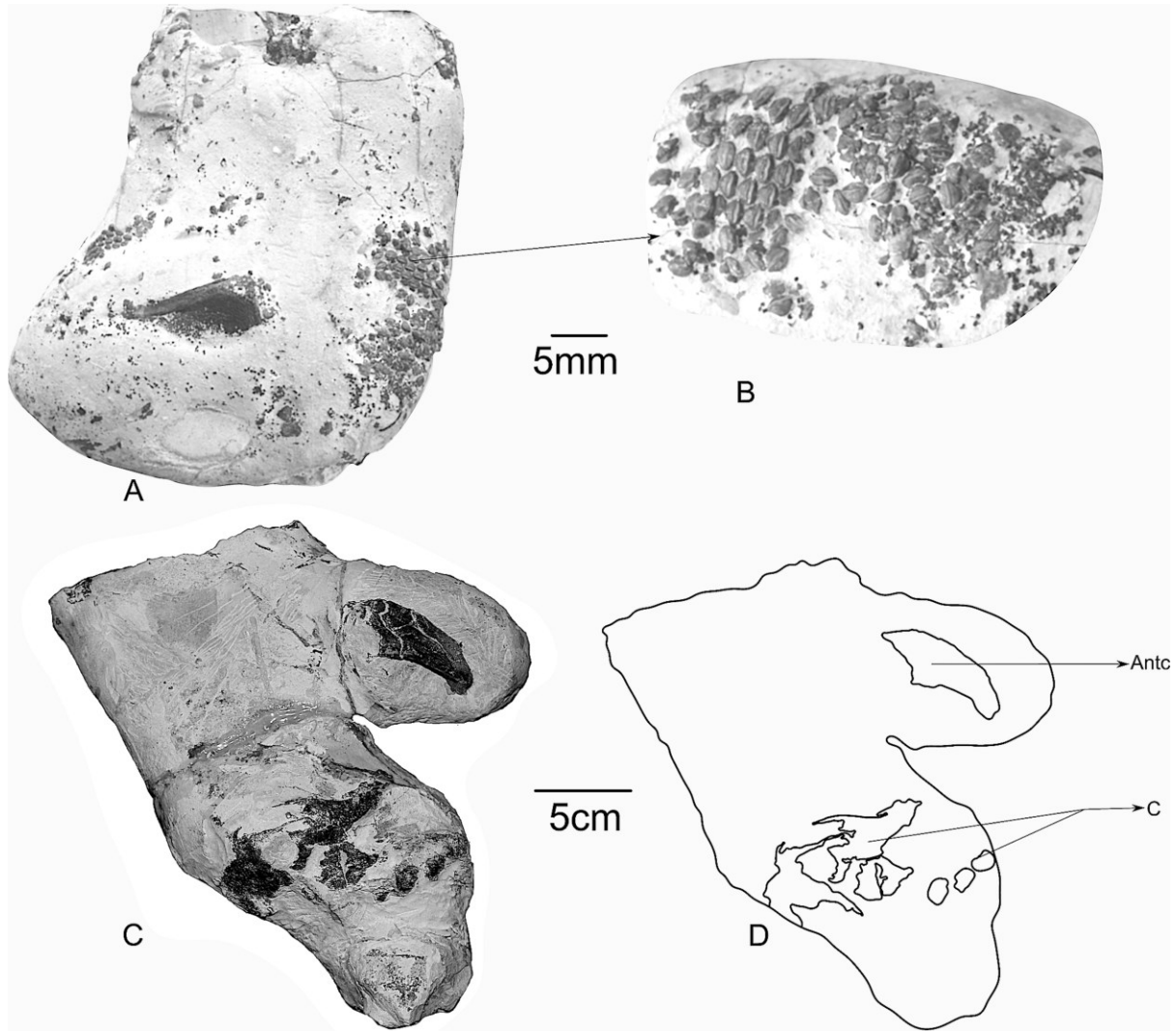


Figure 2. Examples of preservation of specimens of *Asflapristis cristadentis* gen. et sp. nov. found in Asfla. A, B, paratype NHMUK PV P75432; C, D, ventral view of paratype NHMUK PV Pe 75428 a–e. *Abbreviations:* Antc, antorbital cartilage; C, undetermined cartilages.

Material and methods

The specimens described here were obtained by the authors (D.W. and C.U.) from Morocco-based commercial sources, either from fossil collectors in Asfla itself or from larger scale local wholesalers based in Erfoud, Rissani and Rich. Specimens of *Asflapristis* were obtained either totally unprepared, or with only minimal, and

typically rather crude, preparation. In all cases some cartilage with tesserae was showing on the surface of the concretion, sometimes associated with teeth. Additional sclerorhynchid remains associated with a different tooth morphology (referred to here as *Ptychotrygon* sp.) are also present. To prevent incorrect attribution of specimens to *Asflapristis*, only specimens associated with the characteristic teeth were included in this study. Of the skeletally preserved batoid material obtained by the authors, *Tingitanius tenuimandibularis* Claeson *et al.* 2013 was represented by a single specimen, *Asflapristis cristadentis* description is based on six specimens and an additional sclerorhynchid, provisionally referred to *Ptychotrygon* sp. (currently under study), by rather more abundant specimens including a near complete skeleton (see Underwood *et al.* 2015; fig. 3). This general pattern of frequency is somewhat different to assemblages of isolated teeth obtained by sieving marls from levels equivalent to the upper nodule bed; teeth of *Ptychotrygon* are by far the dominant elasmobranch fossils, followed by extremely small teeth resembling those of *Rhinobatos*; *Asflapristis* teeth are relatively rare as are teeth of a small anacoracid shark and *Cretomanta*. Isolated *Tingitanius* teeth have not been recorded in these samples. It is possible that the larger size of skeletal elements of *Asflapristis* favoured both its preservation and collection.

The concretions enclosing the batoid remains are very hard, whilst cartilage elements are often fragile, and tesserae are commonly slightly disarticulated. The somewhat shattered tesserae ruled out acid preparation of the specimens, and mechanical preparation was only carried out where necessary to potentially expose characters not seen elsewhere. Mechanical preparation was performed in the Natural History Museum of the United Kingdom (NHMUK) and involved physical removal of the matrix using air pen, chisel and hammer to expose important characters for the description of the specimen. The preservation of specimen NHMUK PV P 75429 a-d, indicated that any preparation would risk severe damage to the material, and it was left unprepared but studied as rendered CT scan images.

The specimen (NHMUK PV P 75429 a-d) was scanned at the High-Resolution Computed Tomography Laboratory at The University of Texas at Austin (UTCT) using an NSI scanner. GE Titan source, small spot, 370 kV, 1.1 mA, 1 brass filter, Perkin Elmer detector, 2 pF gain, 1 fps (999.911 ms integration time), no binning, no

flip, source to object 853.276 mm, source to detector 1421.23 mm, continuous CT scan, 3 frames averaged, 0 skip frames, 3099 projections, 7 gain calibrations, 15 mm calibration phantom, data range [-2, 15] (rescaled from NSI default). Voxel size = 0.1316 mm, beam-hardening correction = 0.5. Post-reconstruction ring correction applied by Jessie Maisano using parameters oversample = 3, bin-width = 21, sectors = 60. Total slices = 1904. Slice data were further analysed 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.

For the study of microvertebrates, approximately 125 kilogrammes of surrounding marl matrix have been sieved. Very small teeth necessitated the use of sieves down to 0.375mm mesh. Residues were treated in 7.5% formic acid buffered with calcium formate (spent acid) at a pH of 3.2 or above to remove carbonate fragments and yielded abundant teeth, largely of batoids.

For the phylogenetic analysis a matrix of 37 taxa and 95 characters based on Aschliman and collaborators (2012a) analysis and characters from (Brito & Seret 1996; McEachran & Dunn 1998; McEachran & Aschliman 2004; Brito & Dutheil 2004; Kriwet 2004; Claeson *et al.* 2013; Johanson *et al.* 2013; Brito *et al.* 2013; Claeson 2014; Underwood & Claeson 2017) was used. Aschliman's observations were reviewed using extant material from different collections (see Material examined). In cases where extant material was not available, published images (e.g. Nishida 1990; Alfonso & Gallo 2001; Domínguez & González- Isaís 2007; Claeson 2010; Da Silva & De Carvalho 2015) and electronic material (<https://sharkrays.org>, to access this image bank contact Gavin Naylor) were used. In cases where no image was accessible, the coding of Aschliman or of other literature was retained (for discussion over character changes see supplementary material). The matrix was assembled in Mesquite 3.31 (Maddison & Maddison 2017) (supplementary material) using reductive coding (Brazeau 2011) seeking to recover as much information as possible from the characters and analysed on TNT 1.1 (Goloboff *et al.* 2013), PAUP (Swofford 2001), Mr. Bayes (Ronquist & Huelsenbeck 2003) and CIPRES (Miller *et al.* 2010).

For the parsimony analysis in TNT, a similar search protocol to Mannion *et al.* (2013) was used using the menu interface; a first search using the new technology search option within the analyse menu with the following parameters was implemented; search algorithm Ratchet with 10 init. addition sequence, 1000 random starting points, 1000 iterations collapsing trees after the search and a second search using the traditional search option within the analyse menu using the most parsimonious trees (MPT's) found in the first search (trees in RAM) was performed using the tree bisection and reconnection algorithm (TBR) and the following parameters: 1000 random seed, 10000 replications and 10 trees saved per replication collapsing trees after the search.

For the parsimony analysis in PAUP an heuristic search with 1000 replicates of random stepwise addition (branch swapping: TBR) holding one tree at each step was used.

Institutional abbreviations

Institutional abbreviations. **AMNH**: American Museum of Natural History. **BHN**: Muséum d'Histoire Naturelle de Boulogne-Sur-Mer. **BRC**: Birkbeck Reference Collection. **BSP**: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany. **CNPE-IBUNAM**: National Collection of Fishes, Biology Institute, Universidad Nacional Autónoma de México (UNAM). **JM-SOS**: Jura Museum Eichstätt, Germany. **MNHN**: Muséum national d'Histoire naturelle, Paris. **NHMUK**: Natural History Museum United Kingdom, London. **UERJ**: Universidade do Estado do Rio de Janeiro.

Material examined

Fossil material. *Asflapristis cristadentis* (NHMUK PV P 73925, 75428 a-e, 75429 a-d, 75431, 75432, 75433), *Asterodermus platypterus* (NHMUK PV P 12067, 10934, JM-SOS 3647), *Belemnobatis morinicus* (BHN 2P1 Specimen figured in Cavin *et al.* 1995, Figs. 2-6); *Britobatos primarmatus* (MNHN 1946.18.94, NHMUK PV P 4015, 4016, 49517); *Kimmerobatis etchesi* (K874, paratype, K1894. Only the dorsal surface of exposed. Specimen figured in Underwood & Claeson 2017, Figs. 1-3);

Libanopristis hiram (NHMUK PV P 108705, 108706, 13858, 63610, 75075); *Sclerorhynchus atavus* (NHMUK PV P4017, 4776, 49546, 49518, 49533, 49547); *Spathobatis bugesicus* (NHMUK PV P 6010, 2099 (2), BSP AS I 505, BSP 1952 I 82: Only the dorsal surface of exposed, specimen figured in Kriwet & Klug 2004, Fig. 18c). In addition, data is also included from a yet undescribed species of *Ptychotrygon* sp. (NHMUK PV P73630 Specimen figured in Underwood *et al.* 2015 Fig 3A).

Extant material. *Amblyraja radiata* (BRC-Amblyraja, skeleton); *Aptychotrema vincentiana* (CT-Scan available in <https://sharksrays.org>); *Glaucostegus typus* (NHMUK 1967.2.11.3, CT-Scan); *Hydrolagus affinis* (BRC-Hydrolagus, skeleton); *Chimaera cubana* (CT-Scan available in <https://sharksrays.org>); *Gymnura altavela* (CT-Scan available in <https://sharksrays.org>); *Heptranchias perlo* (CT-Scan available in <https://sharksrays.org>); *Hexanchus nakamurai* (CT-Scan available in <https://sharksrays.org>); *Hypnos monopterygius* (CT-Scan available in <https://sharksrays.org>); *Irolita waitii* (CT-Scan available in <https://sharksrays.org>); *Mobula munkiana* (CT-Scan available in <https://sharksrays.org>); *Narcine brasiliensis* (CNPE-IBUNAM 9280, skeleton); *Narcine entemedor* (CNPE-IBUNAM 5807, CT-Scan); *Narcine tasmaniensis* (NHMUK 1961, CT-Scan); *Pristis* (NHUMK 2047483647, CT-Scan); *Platyrrhina* (BRC-Platyrrhina, CT-Scan) *Platyrrhinoidis triseriata* (MNHN 4329); *Raja clavata* (BRC-Raja, CT-Scan); *Raja eglanteria* (CT-Scan available in <https://sharksrays.org>); *Rajella fyllale* (BRC-Rajella, skeleton); *Rhina ancylostoma* (NHMUK 1884, 1925, CT-Scan); *Rhinobatos glaucostigma* (CNPE- IBUNAM 17810, CT-Scan); *Rhinobatos horkelli* (UERJ 1397, skeleton); *Rhinobatos lentiginosus* (CNPE- IBUNAM 17827, CT-Scan); *Rhinobatos leucorhynchus* (CNPE-IBUNAM 1039, X-ray); *Rhinobatos percellens* (UERJ 1240, skeleton); *Rhinobatos productus* (CNPE- IBUNAM 17829, CT-Scan y 17821, X-ray); *Rhinoptera bonansus* (BRC-Rhinoptera, skeleton; CT-Scan available in <https://sharksrays.org>); *Rhynchobatus djiddensis* (MNHN 7850, X-ray); *Rhynchobatus lübberti* (MNHN 50-22-04.80); *Rhynchobatus* sp. (BCR-Rhynchobatus, skeleton); *Tetronarce nobiliana* (CNPE- IBUNAM 9869, CT-Scan); *Torpedo* (NHMUK 72261); *Trygonorrhina fasciata* (MNHN 1372; BRC-Trygonorrhina, CT-Scan); *Urobatis jamaicensis* (AMNH 30385); *Urolophus aurantiacus* (CT-Scan available in <https://sharksrays.org>); *Urotrygon chilensis* (CT-Scan available in

<https://sharkrays.org>) *Zanobatus* sp. (MNHN 1989.12.91 X-ray, CT-Scan available in <https://sharkrays.org>); *Zapteryx brevirostris* (UERJ-PMB 35, skeleton, UERJ 1234, skeleton y 1237, skeleton); *Zapteryx exasperata* (CNPE-IBUNAM 17822, 17823 (1), 17824 (1), 17826 (1), 17825 (1) CT- Scan and skeleton, 20528 (2)); *Zapteryx xyster* (CNPE-BUNAM 16661(1), CT-Scan, and skeleton 19790 (4)).

Systematic palaeontology

Class **Chondrichthyes** Huxley, 1880

Superorder **Batomorphii** Cappetta, 1980

Order **Rajiformes** Berg 1937

Suborder **Sclerorhynchoidei** Cappetta, 1980

Family **Ptychotrygonidae** Kriwet *et al.* 2009

Genus ***Asflapristis*** gen. nov.

Type species. *Asflapristis cristadentis* gen. et sp. nov.

Diagnosis Sclerorhynchid batoid with estimated total length in excess of two meters. Rostrum of uncertain length but robust and apparently lacking enlarged rostral denticles and ‘wood-like’ cartilage. Neurocranium (posterior to nasal capsules) of similar length and width with flattened roof with an anterior fontanelle. Palatoquadrate and Meckel’s cartilages are wide and stout and with a thin outer layer of ‘wood-like’ perichondrium. Second hypobranchial without an anterior process. Synarcual long with well-developed medial crest and dorsally directed lateral stays but does not directly connect to the pectoral girdle. Synarcual lip large and fits within the chondrocranium. Vertebral centra fail to reach the middle of the synarcual. Lateral facet of scapulocoracoid thick and compact and articulate to the pectoral elements. Propterygium, mesopterygium and metapterygium expand distally and paddle-shaped. Dentition relatively homodont, teeth oval in occlusal view and lacking a medial cusp or well-developed uvulae, and with large pulp cavity. Occlusal ornament with a strong transverse ridge with fine and irregular branching ridges, mostly linguo-labial and around margins. A fine ridge along labial edge of occlusal

face is present in many teeth. Root low with widely spaced root lobes with rounded basal face.

Derivation of Name. After the town of Asfla, where the specimens were found.

Asflapristis cristadentis

Material. Holotype: NHMUK PV P 75433, presents most of the dorsal surface neurocranium, the whole synarcual and pectoral girdle, although distal pectoral elements are missing. Paratypes: NHMUK PV P 73925, on dorsal view presents most of the post nasal capsules neurocranium and both hyomandibular cartilages. On the ventral surface both antimeres of the Meckel cartilage, the right antimeres palatoquadrate and anterior part of the right second hypobranchial are exposed. NHMUK PV P 75428 a-e, specimen composed of five fragments, on ventral view shows a small tooth patch close to the mouth region, fragments of the anterior section of the second hypobranchial and antorbital cartilages. NHMUK PV P 75429 a-d, specimen composed of four fragments on its dorsal surface shows most of the middle portion of the neurocranium along with fragments of the rostrum. Most of the anterior portion of the synarcual is preserved and parts of the medial crest and lateral stays exposed. On the ventral surface a patch of teeth is exposed. NHMUK PV P 75431, complete synarcual. It was assigned after preparation work revealed a characteristic tooth. NHMUK PV P 75435, articulated teeth set without associated identifiable skull material.

Diagnosis. As for genus.

Derivation of Name. From the possession of several ridges in the teeth.

Description. Measurements and body proportions are difficult to establish since no complete specimen has been found. Six specimens of skeletal material can unambiguously be referred to *Asflapristis* based on teeth morphology. Between them they provide data on the neurocranium and proximal part of the rostrum, jaws and dentition, synarcual, brachial skeleton, pectoral girdle, proximal part of the pectoral

fins, and the trunk vertebral column. The pelvic girdle and fins, claspers, dorsal fins, caudal skeleton, distal parts of the pectoral fins and tip of rostrum are unknown.

In the holotype, most of the skeletal elements were preserved in a horizontal plane within the nodule, parts of neurocranium and rostrum were broken during the extraction of the specimen. Some of the gill arches are disarticulated but show little damage suggesting that these elements were separated before lithification.

Chondroskeleton. The exposed skeletal elements are composed of a layer of tesserae, prismatic cartilage. Tesserae are visible around all skeletal elements. The mouth of the specimen NHMUK PV P 75433 also shows a small layer or wood-like perichondrium similar to that observed in the rostrum of *Onchopristis* and *Schizorhiza* (Kirkland & Aguillon-Martínez 2002). The wood-like perichondrium is absent in other regions of the skeleton including the rostrum. Its presence in the jaw may be an adaptation of this species to durophagy.

Chondrocranium. This is a rectangular, box shaped structure that seems to lack the characteristic bottle shape of other batoids. It widens slightly towards the nasal capsules, but these structures are themselves missing. Posterior to the nasal capsules the chondrocranium becomes somewhat narrower. Posterior to the postorbital process it slightly widens and progressively narrows until it reaches its posterior face (Figs. 3 A-B). The antorbital cartilages are scythe shaped (curved posteriorly towards the distal end) with a wide base and become narrower towards the tip (Fig. 4 C-D). The supraorbital crests are present and elevated from the rest of the chondrocranium. At the posterior region of the neurocranium there is a deep concave indentation where the synarcual lip (odontoid process) fits. At the sides of the indentation are the occipital condyles which are large and present a broad articular surface for the lateral anterior facets of the synarcual. The lateral and basal faces of the chondrocranium were not clearly visible on any specimen.

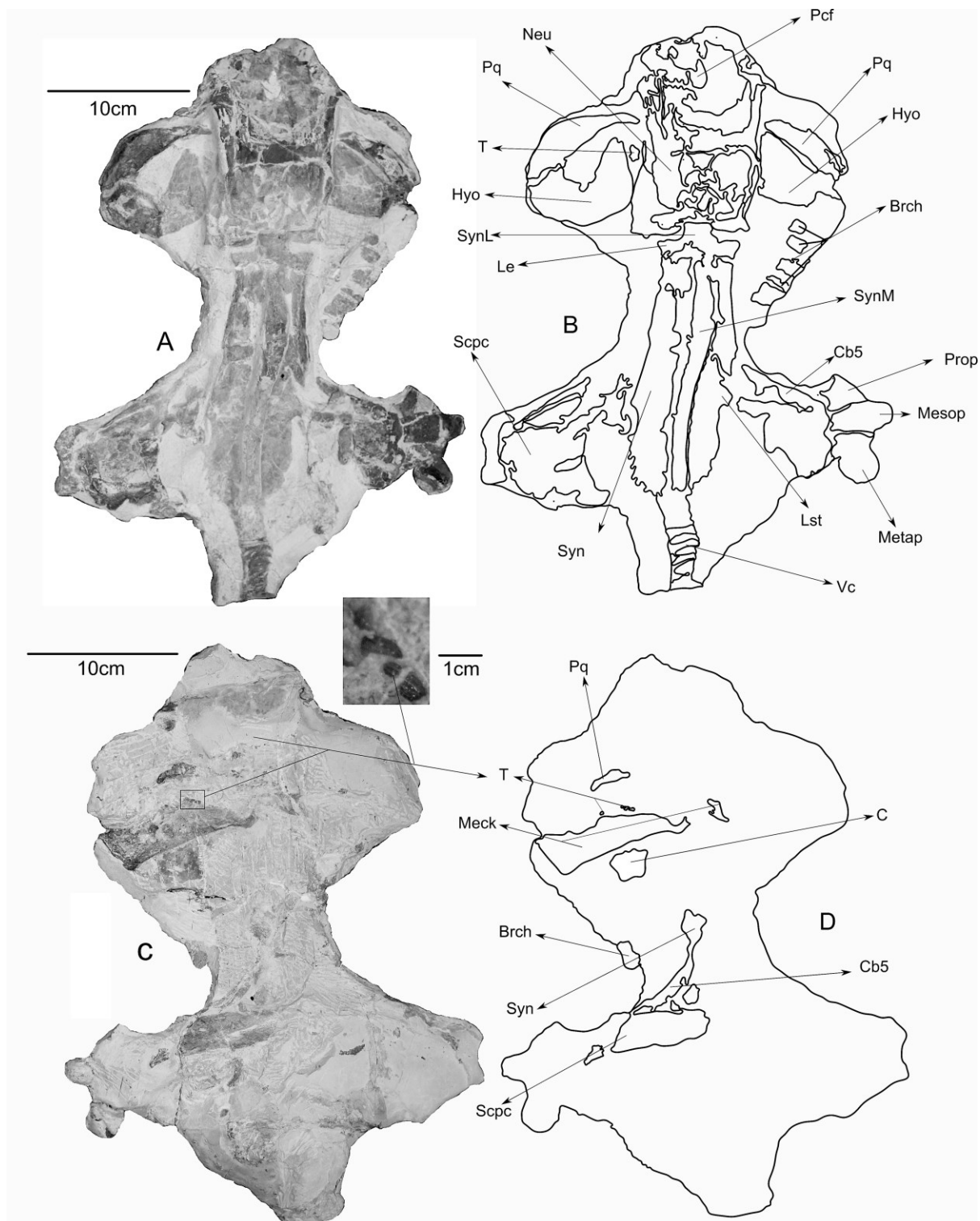


Figure 3. *Asflapristis cristadentis* gen. et sp. nov. holotype NHMUK PV P75433. A, B, dorsal view of the anterior skeleton; C, D, ventral view of the specimen. *Abbreviations:* Brch, branchial elements; C, undetermined cartilages; Cb5, fifth ceratobranchial; Hyo, hyomandibula; Le, lateral extensions; Lst, lateral stays; Meck,

Meckel's cartilages; Mesop, mesopterygium; Metap, metapterygium; Neu, neurocranium; Pcf, precerebral fenestra; Pq, palatoquadrate; Prop, propterygium; Scpc, scapulocoracoid; Syn, synarcual; SynL, synarcual lip; SynM, synarcual medial crest; T, teeth; Vc, vertebra centra.

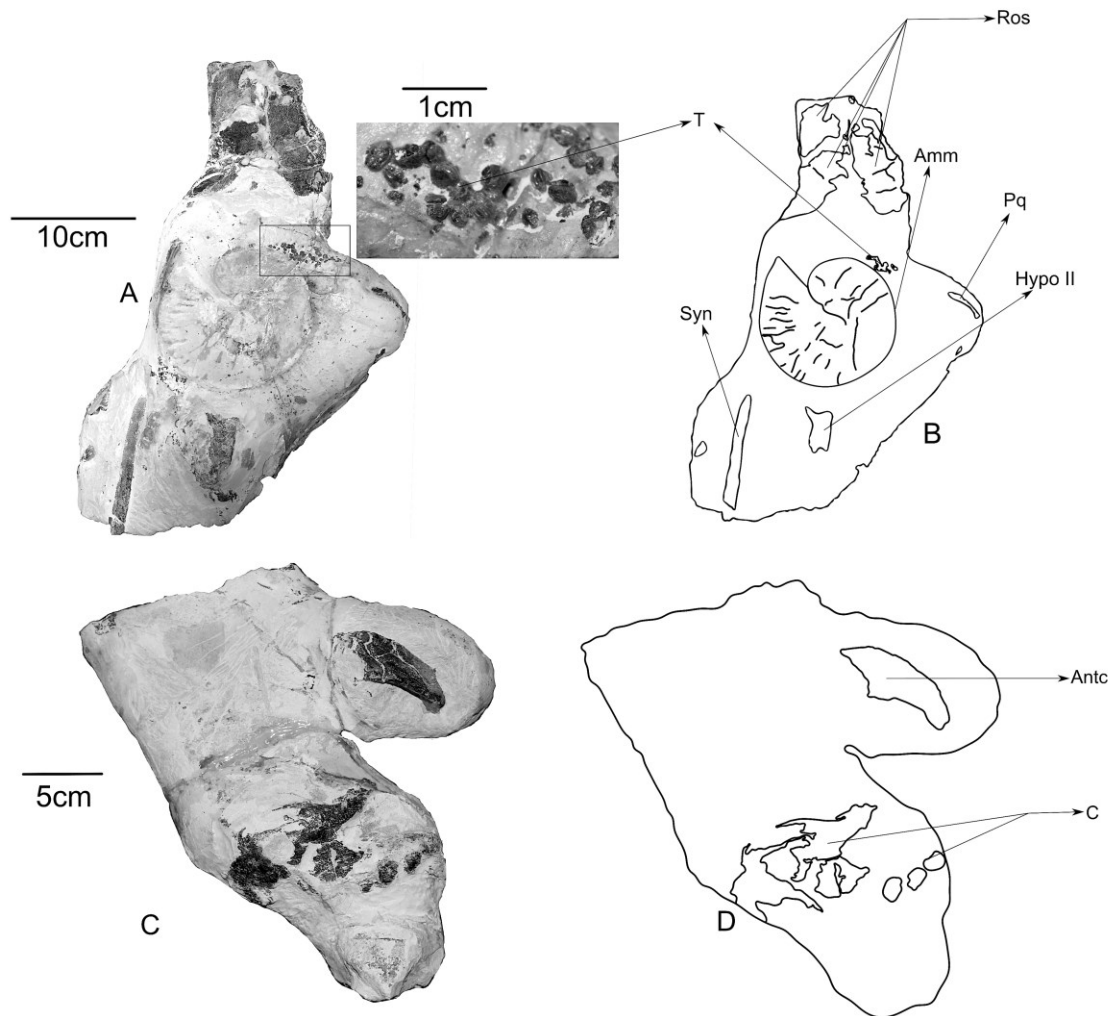


Figure 4. *Asflapristis cristadentis* gen. et sp. nov. paratype NHMUK PV P 75428 a–e. A, B, ventral view of part of the anterior skeleton; C, D, ventral view of another section of the specimen. *Abbreviations:* Amm, ammonite; Antc, antorbital cartilage; C, undetermined cartilages. Hypo II, second hypobranchial; Pq, palatoquadrate; Ros, rostrum; Syn, synarcual; T, teeth.

Rostrum. Despite the lack of a complete rostrum, some specimens preserve fragments of rostrum, showing a basal part with an oval shaped precerebral fenestra (Figs. 3 A-B). The fragmentary remains observed suggest the presence a of stout and hypertrophied rostrum probably over twice as long as the neurocranium (Fig. 5

A-B). It lacks the ‘wood-like’ cartilage seen in other sclerorhynchoids, and there are no obvious longitudinal grooves. There is no evidence of enlarged rostral dermal denticles and no cavities or canals was found internally.

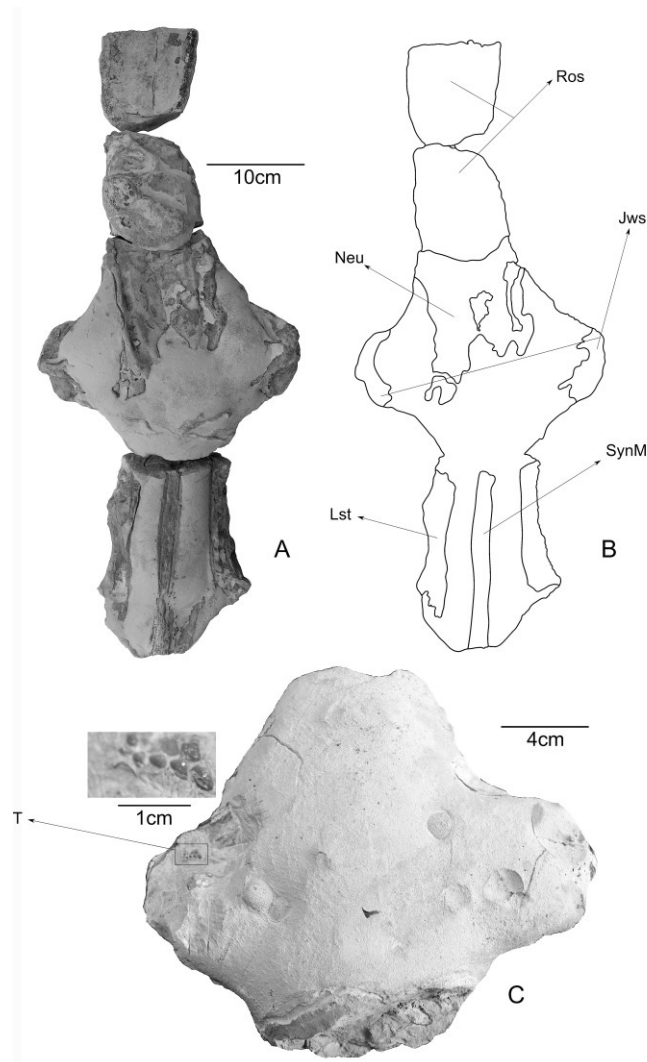


Figure 5. *Asflapristis cristadentis* gen. et sp. nov. paratype NHMUK PV P75429a–d. A, B, dorsal view of the neurocranium and part of the synarcual and of rostral cartilage; C, ventral view of neurocranium. *Abbreviations:* Jws, jaws; Lst, lateral stays; Neu, neurocranium; Ros, rostrum; Syn, synarcual; SynM, synarcual medial crest; T, teeth.

Visceral Skeleton. The mouth cavity is broad; twice the width of the postorbital region. The Meckel’s and palatoquadrate cartilages are straight and broad, and their antimeres are not fused (Fig. 6 C-D). The palatoquadrate width is approximately 22% of the length of the cartilage, while the Meckel’s cartilages width is

approximately 32% of its length. The Meckel's cartilages are twice as deep as the palatoquadrate and have a lateral tab-like process that articulates with the notched distal end of the palatoquadrate (Fig. 7 A). The Meckel's cartilages lack the ventral lateral flange for muscle articulation observed in guitarfishes, rajoids and myliobatoids. The hyomandibular cartilages are triangular and present a strong medial crest for the articulation of muscles. They become slender towards their distal tip which articulates between the palatoquadrate and Meckel's cartilages (Fig. 6 A-B). The basihyal is fragmented in two parts, but still reveals a broad, crescent shape, similar to that found in *Ptychotrygon* sp. (NHMUK PV P73630). The basihyal and first hypobranchial are not in articulation, whether this disarticulation was present in life or occurred during fossilisation is unknown (Fig. 7 C). The first hypobranchial is separated from the pseudohyal and is a roughly arrow shape with an acute proximal edge followed by two process, one dorsal and another ventral. The mid region of the first hypobranchial is narrow and rectangular with an expanded distal edge (Fig. 7 C). The pseudohyal is triangular with its proximal edge wider than its distal edge. Only the anterior part of the second hypobranchial is preserved (Figs. 6 C-D); its distal edge is convex and wide no evidence of articulation with an anterior process.

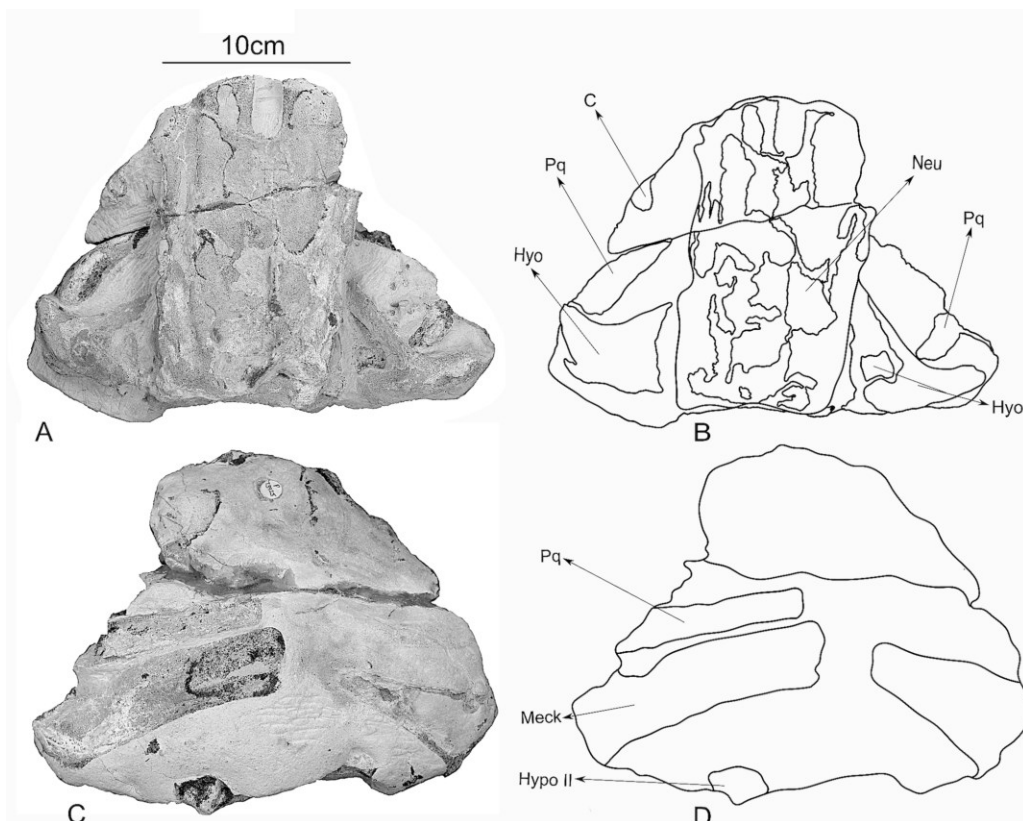


Figure 6. *Asflapristis cristadentis* gen. et sp. nov. paratype NHMUK PV P73925. A, B, dorsal view of chondrocranium; C, D, ventral view of chondrocranium. *Abbreviations:* Hyo, hyomandibula; Hypo II, second hypobranchial. Meck, Meckel's cartilage; Neu, neurocranium; Pq, palatoquadrate.

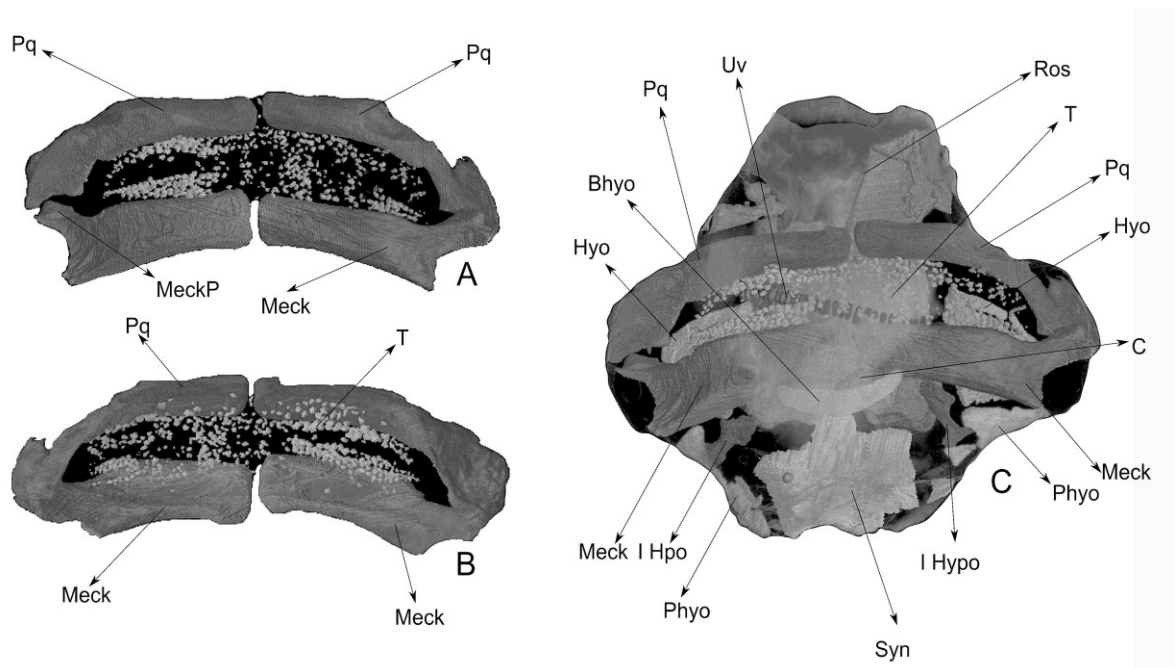


Figure 7. *Asflapristis cristadentis* gen. et sp. nov. CT scan of paratype NHMUK PV P75429b. A, frontal view; B, rear view of the jaw. *Abbreviations:* Bhyo, basihyoid; C, undetermined cartilage; Hyo, hyomandibula; I Hypo; first hypobranchial, Meck, Meckel's cartilage; MeckP, Meckel's tab-like process; Phyto, pseudohyoid; Pq, palatoquadrate; Ros, rostrum; T, teeth; Uv, undetermined vertebrate remains.

Synarcual and vertebrae. The synarcual extends posteriorly and extends well beyond the scapulocoracoid, it is about three times longer than its maximum width and twice the length of the preserved portion of the neurocranium in the holotype specimen. The synarcual lip is long and articulates with the posterior part of the neurocranium. The superior lateral facets of the synarcual are thick and project laterally mirroring the occipital condyles of the neurocranium suggesting a tight interaction between these elements despite being slightly dislocated (Fig. 8 F). The median crest of the synarcual is wide and well developed. There is no evidence for

either fusion or articulation between the synarcual and suprascapula, although whether the suprascapula was present or not remains unknown. The lateral stays of the synarcual are present and dorsally directed (Fig. 8 C-D and F). The first exposed vertebral centrum fails to reach the mid-point of the synarcual cartilage (Fig. 8 A-B). Post synarcual vertebrae are preserved and revealing a dense notochordal centre with appositional rings of areolar cartilage, which is consistent with seasonal growth of elasmobranchs (NHMUK PV P 75431). Neural arches and spines are poorly preserved and yield no useful characters.

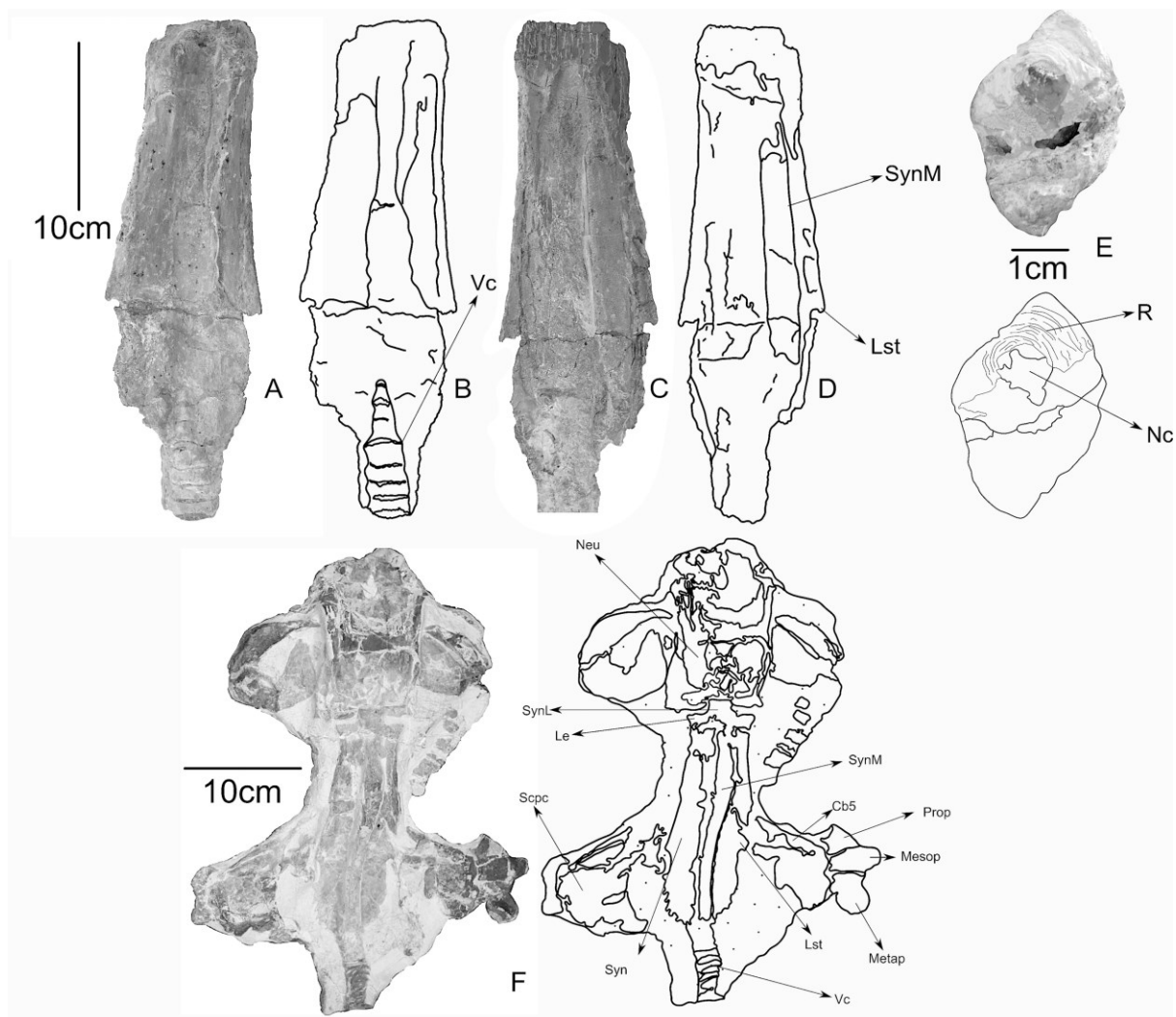


Figure 8. *Asflapristis cristadentis* gen. et sp. nov. A–E, paratype NHMUK PV P75431; A, B, ventral view of the synarcual; C, D, dorsal view of the synarcual; E, vertebra on distal end of synarcual. F, holotype NHMUK PV P75433 in dorsal view. *Abbreviations:* Cb5, fifth ceratobranchial; Le, lateral extensions; Lst; lateral stays;

Mesop, mesopterygium; Metap, metapterygium; Nc, notochordal centre; Neu, neurocranium; Prop; propterygium; R, appositional rings; Scpc, scapulocoracoid; Syn, synarcual; SynL, synarcual lip; SynM, synarcual medial crest; Vc, vertebra centra.

Appendicular skeleton. The scapulocoracoid is thick and short (the same length as the synarcual in holotype specimen). The scapular processes are broken and separated from the basal portion of the scapulocoracoid, regardless they are long, slender and probably dorsally directed (Fig. 8 F). No evidence of a union between the synarcual cartilage and the suprascapula was observed. The lateral facet of the scapulocoracoid is compact and robust with no enlargement between the proximal pectoral elements (procondyle, mesocondyle and metacondyle) and no direct articulation of the pectoral radials. There are three condyles for the articulation of the proximal pectoral elements. Between the procondyle and the mesocondyle is the anterior dorsal fenestra. The posterior dorsal fenestra is located between the mesocondyle and metacondyle. Although most of the distal part of pectoral proximal elements is missing their base is preserved and show the sturdy and paddle-like shape (Fig. 8 F) as those of other sclerorhynchoids.

Teeth. Descriptive tooth terminology largely follows that of Cappetta (1987). The dentition is relatively homodont, with some variation in tooth size and width-depth ratio across the jaw, but the greatest variation occurs within the details of the occlusal ornamentation, with differences appearing to show no systematic variation with jaw position. The teeth are generally robust and up to 5 mm wide (Fig. 9 C). Teeth are oval, or slightly expanded labially, in occlusal view and wider than deep (Fig. 9 A). The tooth crown overhangs the root on all sides and the tooth is (linguo-labially) deeper than high. There is a very weakly developed lingual uvula but no lateral uvulae. The overall form of the tooth occlusal face is flat to weakly domed with no defined cusps; the margins of the occlusal face are rounded except where fine ridges are present at the edge of the occlusal face. The tooth occlusal face is highly ornamented with the ornament being variable in detail, even within adjacent teeth in the dentition. A narrow and sharp-edged transverse ridge bisects the occlusal crown face, with a shorter parallel ridge labial to this. Other ornament is highly variable and not all elements are present in all teeth. A somewhat irregular ridge may be present

at the lingual edge of the occlusal face, and short longitudinal or irregularly orientated ridges may occur across the face but are often concentrated near the crown edge or along the lingual margin. These may bifurcate or break up into tubercles, and rarely join with the main transverse ridges (Fig. 9 B). The root is low with equal sized and well separated root lobes. The basal faces of the root lobes are convex and there is no sharp edge between the lateral and basal faces. Teeth have a very large and well-developed pulp cavity that may occupy over half of the crown height in section (Fig. 10). There is a relatively thin surrounding layer of orthodentine, but the enameloid is rather thick, especially where ornament is present (Fig. 10). There is no osteodentine present in the root with the exception of a thin band observed between the crown and root.

The tooth morphology is highly distinctive and unlike that of other batoids, although the highly ornamented occlusal face bears some superficial resemblance to that of *Rhina*, *Rhynchobatus*, *Pucabatis* and even *Ptychodus*. In all cases, though, the overall tooth shapes and morphology of the root are rather different. Teeth of *Ptychotrygon*, *Texatrygon*, *Micropristis* and *Libanopristis* are considerably more gracile than those of *Asflapristis cristadentis* but show many similarities in detail. In each of these genera, a well-defined transverse ridge is present, with shorter ridges on the labial and/or lingual sides of it. In some species of *Ptychotrygon*, more complex occlusal ornamentation is also present (e.g. Cappetta & Case 1999) but not comparable with that of *Asflapristis*. Roots are similarly low and with rounded edges. Despite this, teeth of *Ptychotrygon*, *Texatrygon*, *Micropristis* and *Libanopristis* all possess a low and triangular main cusp, are diamond shaped to triangular in occlusal view, have a less complex ornamentation, possess a weak labial apron and more distinct uvula, and have root lobes with more flattened bases. Teeth most closely resemble those of *Ptychotrygon gueveli* Cappetta (2004) but can be differentiated by the presence of small crest between the transverse ridges and the lack of a medial cusp suggesting a close relation between these two genera.

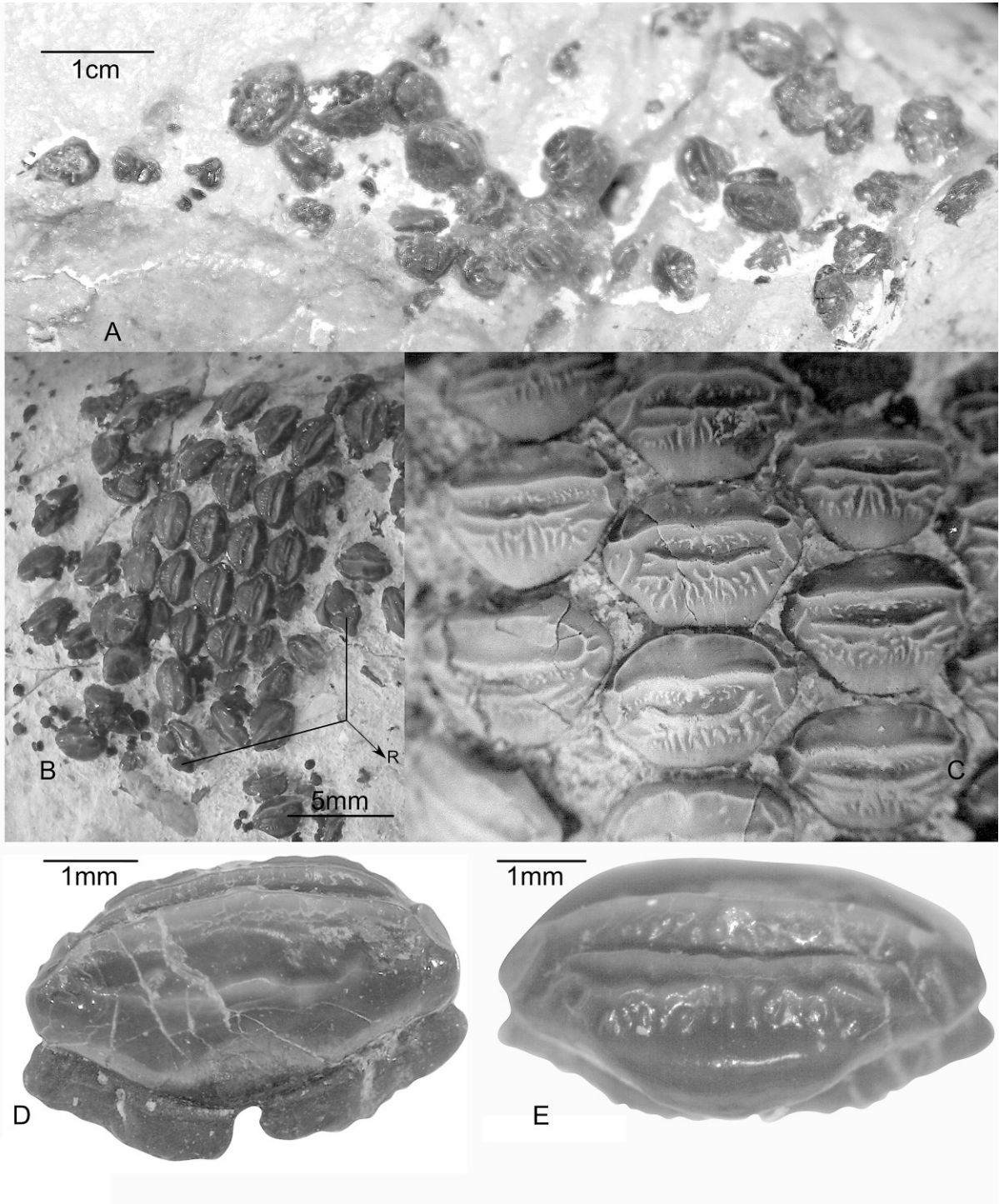


Figure 9. *Asflapristis cristadentis* gen. et sp. nov., tooth sets of different specimens and disarticulated tooth from the preparation of these specimens. A, tooth set of paratype NHMUK PV P75428a–e. B, C, occlusal view of tooth set of paratype NHMUK PV P75432. D, lingual view and E, labial view of separated tooth of NHMUK PV P75432. *Abbreviation:* R, root.

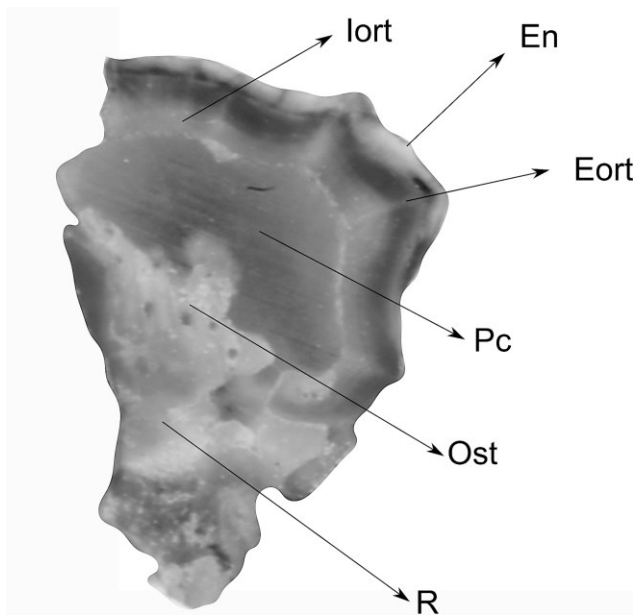


Figure 10. *Asflapristis cristadentis* gen. et sp. nov., lateral section of a tooth found during the preparation of paratype NHMUK PV P75431. *Abbreviations:* En, enameloid; Eort, external orthodontine; lort, internal orthodontine; Os, Osteodentine; Pc, pulp cavity; R, root.

Denticles. No extensive areas of skin with articulated denticles were found associated in any of the specimens. Although the majority of denticles were collected as isolated specimens, after treating the matrix surrounding the specimens with acid, some denticles were found directly associated with the mouth region and could be observed in situ. These denticles were circular with a smooth dorsal surface were found (Fig. 11 A-D). In lateral view these denticles are tall and become narrower in the middle and expand towards the stem. The stem presents several fringes over the margins (Fig. 11 B-C).

Four distinct morphologies of denticles were found: 1) Leaf shaped with a smooth dorsal surface (Fig. 11 E-G); these denticles have irregular terminations on their posterior edge and on lateral view are significantly shorter than the circular denticles (Fig. 11 G). 2) Arrow shaped (Fig. 11 H-J); these denticles possess ridges on the dorsal surface, of similar shape to those found on the dorsal surface of some sharks as well as ‘rhinobatid’ rays. 3) Thorn-like rostral denticles (Fig. 11 K-L); taller than the rest, crown is posteriorly director and are very similar to those found on the ventral surface of the rostrum of *Sclerorhynchus atavus* (Welten *et al.* 2015). 4) a single specimen of a large triangular denticle of unknown provenance was recovered (Fig.

11 N). The large concentrations of denticles found during the preparation of specimens (Fig. 11 M) may suggest that at least parts of *Asflapristis* (such as surrounding the jaws) were uniformly covered with denticles. However, the relatively small number of denticles recovered in acid residues (compared to in *Tingitanius tenuimandibularis* Claeson *et al.* 2013) may suggest incomplete denticle coverage of at least parts of the body.

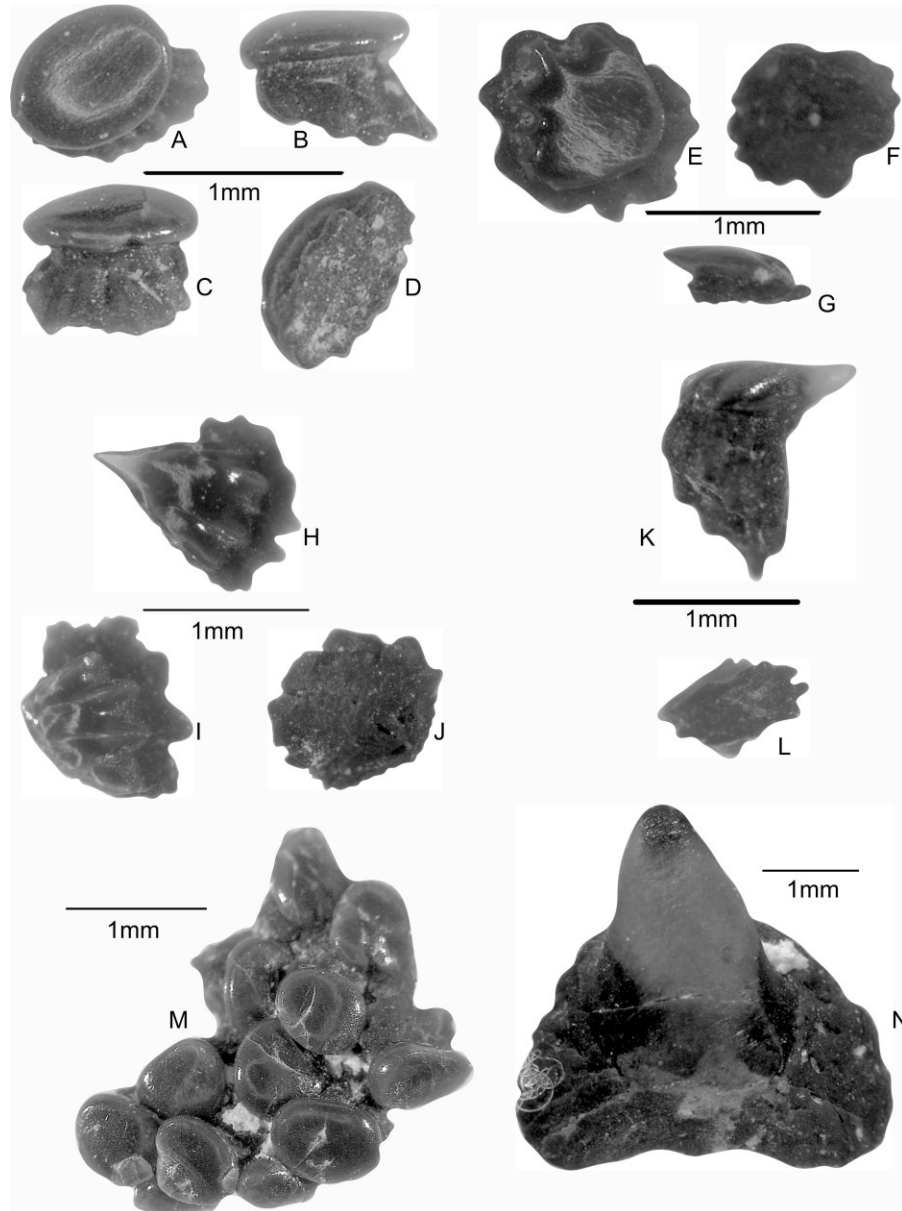


Figure 21. *Asflapristis cristadentis* gen. et sp. nov., dermal denticles from the preparation of NHMUK PV P75432 (A–G and M) and NHMUK PV P75428 (H–L and N).

parenthesis are the nodes. Synapomorphies black points character number is on top and state of character in on bottom.

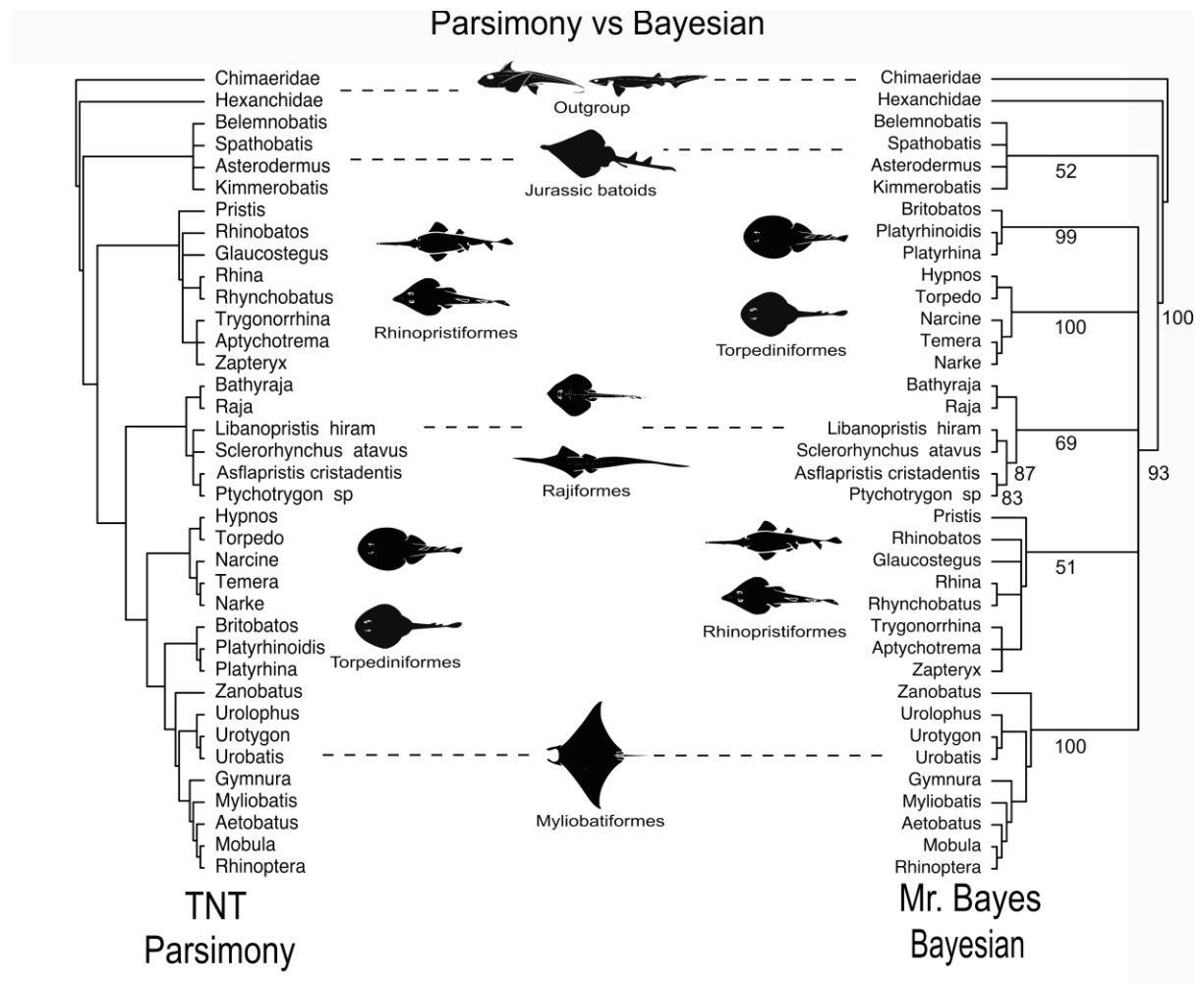


Figure 33. Phylogenetic trees obtained on the different analysis: Strict consensus from parsimony analysis compared to Posterior probability tree from Bayesian inference.

Discussion

Phylogenetic implications

All of the analyses separated the Jurassic genera *Asterodermus*, *Kimmerobatis*, *Spathobatis* and *Belemnobatis* from Rhinopristiformes (Underwood & Claeson 2017) and placed them in a monophyletic clade forming a sister group to all post-Jurassic batoids (Node = 52, Bremer = 1, Bootstrap= 41, Posterior probability (Pp) = 52%) with one unambiguous synapomorphy (Char. 93, similar shape of propterygium and

mesopterygium) (see supplementary information). The present placement differs from previous phylogenies (Claeson *et al.* 2013; Underwood & Claeson 2017), which place the Jurassic batoids within modern batoids in a close relation with Rhinopristiformes. Our results suggest that their similarity with Rhinopristiformes is superficial. All remaining batoids included in the present study are grouped in node 42 (Fig.12), which is characterised by the presence of a calcified suprascapula (Char. 6), reduced Ceratohyal, (Char. 50) and a slightly expanded first pelvic radial, articulating with several segments in a parallel fashion (Char. 68).

The placement of the other groups varied depending on the analysis. These different topologies reflect the variation in the methods of reconstruction (O' Reilly *et al.* 2016). The bayesian analysis found a polytomy that comprises all of the modern orders (*sensu* Last *et al.* 2016) (Fig. 13). Whilst the parsimony analysis the next node forming a sister relationship with the remaining taxa is the Rhinopristiformes (Fig. 13). However, the topology recovered by the Bootstrap analysis (supplementary material) resembles that found by the bayesian analysis and suggests that the placement of Rhinopristiformes as the sister group of other batoids is requires further consideration. In the present analyses this relation is supported, by the presence an anterior projection of the second hypobranchial (Char. 89 (0)). The coding of the character requires further work, as in *Pristis* the hypobranchials are fused in a medial plate (Nishida 1990, fig. 28g), in their ontogenetic development the medial plate is divided in two (Miyake & McEachran 1991, Fig. 5). The anterior process of the second hypobranchial could be involved in the development of the upper plate but this cannot be clearly demonstrated due to the lack of material of a range of ontogenetic stages available. As a result of this, the character was coded as (?) for *Pristis*. As for the remaining batoids, there seem to be different and non-homologous processes leading to the loss of this structure which could be coded as separate characters. In electric rays there seems to be several arranges of the hypobranchials (Miyake & McEachran 1991, Fig. 6) and for Myliobatiformes there seems to be a reduction and fusion of branchial elements (Nishida 1990, Figs. 27-28) and as well for this groups the character was code as a (?).

The placement of *Pristis* with other Rhinopristiformes has only recently been recovered in molecular analysis. Although this grouping is present all the analyses

(Node = 53, Bremer = 1, Bootstrap= 10, Pp = 51%) (Fig. 12), the present analysis did not find an exclusive synapomorphy for Rhinopristiformes, rather this clade is supported by a combination of characters (e.g. Scapulocoracoid is elongated between the mesocondyle and metacondyle with the direct articulation (Char. 59) with the direct articulation of pectoral radials to the scapulocoracoid (Char. 63) and the presence of lateral uvula in teeth (Char. 87) (Fig. 12).

All analyses suggest place sclerorhynchoids as a sister group for living Rajiformes, based on similarities in the branchial skeleton (Node 40). Although being recovered in all parsimonious trees in the present analysis, the support values for the sclerorhynchid-rajoids relationship are relatively low (Bremer = 1, Bootstrap = 4, Pp = 69%), possibly caused by the presence of missing characters and the rather extensive morphological differences between these groups, such as the unique pectoral skeleton of sclerorhynchoids (Char. 92) and the absence in some sclerorhynchoids of a suprascapula (Char. 6). The present placement varies from previous phylogenies Kriwet (2004); places the sclerorhynchoids as an intermediate group between Pristidae and Pristiophoridae; Claeson *et al.* (2013), recovers them as an intermediate group between the Jurassic genus *Spathobatis* and Pristidae and Underwood & Claeson (2017) places them within Rhinopristiformes. In the present study, besides of changes in the coding of some characters (e.g. Char. 6), we included previously unknown data such as the second hypobranchial fused to the basibranchial (Char. 26, Fig. 12) which suggest a close relation, between this two groups. As more specimens of well-preserved sclerorhynchoids are discovered, and more characters made evident, the values of support for this group will change and the relation between these two groups will become clearer.

All analyses place *Asflapristis cristadentis* and *Ptychotrygon sp.* within sclerorhynchoids (Node = 66, Bremer = 2, Bootstrap= 55, Pp = 87%) based on characters like their pectoral fin anatomy with the enlargement and paddle shape of propterygium, mesopterygium and metapterygium (Char. 92) and the reduced postorbital process (Char 38) (Fig. 12). Most of the posterior part of the branchial skeleton of *Ptychotrygon sp.* is preserved and is very similar to that of *Sclerorhynchus atavus* (NHMUK PV P 49546), characterized by the presence of a well-developed second hypobranchial fused, along with the third hypobranchial, to

the basibranchial (Char. 26) and with no evidence of a direct articulation of any branchial element to the second hypobranchial as seen in Rajiformes. In addition, *Asflapristis cristadentis* (NHMUK PV P 73925) and *Ptychotrygon sp.* (NHMUK PV P73630) possess a very similar upper part of the second hypobranchial to that seen in other sclerorhynchoids (e.g. *Sclerorhynchus atavus* (NHMUK PV P 49546)) and this seems to be characteristic of the sclerorhynchoids. *Asflapristis cristadentis* also has a wide and stout basihyal, a large and well mineralized first hypobranchial that subsequently articulates with the pseudohyal similar to that of *Ptychotrygon sp.* This characters in addition with the presence of a transversal crest differentiating the labial crown face and very well-developed labial visor (Kriwet *et al.* 2009), place *Asflapristis* in the family Ptychotrygonidae.

As with other morphological analysis, the placement of Platyrrhinidae (Node = 47, Bremer = 2, Bootstrap = 69, Pp = 97%) (Fig. 12) as a sister group to electric rays (Node = 44, Bremer = 7, Bootstrap = 98, Pp = 100%) (Fig. 12) forming the order Torpediniformes (*sensu* Last *et al.* 2016) was not recovered in the present study, despite some taxa sharing characters like an irregular shape of the antorbital cartilages (Char. 9), laterally to relatively lateral projection of the lateral stays and the separation of the ventral antimeres of scapulocoracoid (Char. 53). The bayesian analysis recovered Platyrrhinidae as part of a polytomy that compromise all modern groups with the exclusion of sclerorhynchoids (Pp = 93), similar to that recovered by Aschliman *et al.* 2012b. While the Parsimony analysis recovered them as the sister group of Myliobatiformes (node = 50), similar to Aschliman *et al.* 2012a. The variation in these results was expected as the relations within Torpediniformes and Rhinopristiformes (*sensu* Last *et al.* 2016) are problematic for morphological based analysis mostly because of the presence of highly derived taxa like *Pristis* and electric rays complicates the identification of synapomorphies between these taxa and the more plesiomorphic ones in their respective orders.

Myliobatiformes is recovered as a monophyletic group (Node = 57, Bremer = 4, Bootstrap = 78, Pp = 100%) and is composition changed little to that recovered by Aschliman *et al.* (2012a) and other molecular studies (Aschliman *et al.* 2012b). This group is easily differentiated as noted by the large number of synapomorphies found in the present study (Fig. 12) of special interest is the placement of *Zanobatus*

(panrays) within this group as a sister group. The present study found similar relations for this genus as those recovered in Aschliman *et al.* (2012a) which places them as a suborder within Myliobatiformes. Naylor *et al.* (2012) reversed the panrays within Rhinopristiformes but as noted by the authors this placement is model dependent and should be addressed carefully. The most current molecular phylogeny places them as part of Myliobatiformes (Last *et al.* 2016) however the authors do not discuss further on this change. We followed Eschmeyer (2018) model for classification at the ordinal level, which is based on Last *et al.* (2016).

Palaeoecological implications

The restricted overall diversity of the Asfla biota suggests that the environment was not that of a 'normal' open carbonate shelf, and as a result the autecology of the organisms themselves may have been somewhat specialised. Large vertebrates are highly mobile and so may have lived, or at least fed, away from the depositional site, but the large number of shed teeth of *Ptychotrygon* in the marl matrix would suggest that it at least spent a significant time in the area of deposition. Whilst sclerorhynchoids are often common and diverse in shallow marine environments of the Cretaceous of Tethys (Kriwet & Kussius 2001), the extreme dominance of the chondrichthyan fauna by two sclerorhynchid species is unusual; elsewhere they are typically associated with diverse 'rhinobatid-grade' batoids (e.g. Cappetta 1987) and often nectobenthic sharks. The rarity of other batoids in particular may be an indication of a hostile seafloor inhibiting nectobenthic taxa (e.g. Underwood & Cumbaa 2010), which would be consistent with the rarity of benthic shelly fossils. If the restriction of most batoids were due to a hostile seafloor, it would suggest that these sclerorhynchoids were more pelagic than other coeval batoids, living largely within the water column along with the co-occurring fish, reptiles and ammonites. Despite this, sclerorhynchoids appear to have had a very small caudal fin (Cappetta 1980) with small and rather rigid pectoral fins containing long, stiff, radial elements. They would therefore be unlikely to have been either fast or powerful swimmers. Most modern batoids, other than planktivorous taxa, feed on relatively small benthic organisms, with many having robust teeth that show considerable wear from processing shelled food. Teeth of *Asflapristis* are likewise robust and some teeth within dentitions show considerable wear, indicating a food source that is strong and

hard. The rostrum of *Asflapristis* appears to have been both long and robust but lacking enlarged rostral denticles. Whilst rostra of modern Pristidae and Pristiophoridae have a range of functions (Wueringer *et al.* 2009), they are highly supplied with sense organs and thus a rostrum without enlarged denticles is still highly functional as a sensory structure (Wueringer *et al.* 2011). Considering the unusual occurrence of *Asflapristis*, its poor swimming and durophagous diet, it may have fed on ammonites; slow moving, pelagic and armoured. It is also possible that the large sensory rostrum allowed hunting of ammonites, which may have relied a lot on sight as in many modern cephalopods, in poor visibility such as at night or in turbid water.

Conclusion

Well preserved partial skeletons of *Asflapristis cristadentis* from the Late Cretaceous of Morocco have provided the first recorded examples of sclerorhynchid batoids with the skeleton preserved in three dimensions, aiding in our understanding of this important but problematic group. This new genus and species present a suite of morphological characters that place it within sclerorhynchoids (e.g. enlarged proximal pectoral elements, lack of suprascapula) but also differentiate it from them and place it as a member of Ptychotrygonidae (e.g. hypertrophied rostrum with no evidence of enlarged dermal denticles a transversal crest differentiating the labial crown face and very well-developed labial visor). Furthermore, this genus presents dental characters that separate it from other *Ptychotrygon* species (e.g. reduced medial crest, with shorter crests on the labial and/or lingual sides and between the transverse ridges and a very large pulp cavity).

With the discovery of *Asflapristis cristadentis* and *Ptychotrygon* sp. certain characters of visceral skeleton, synarcual and pectoral girdle are evident for the first time within sclerorhynchoids (e.g. posterior and anterior fenestra of the lateral facet of the scapulocoracoid, the dorsally directed lateral stays of the synarcual, the shape and interactions of the basihyal with second hypobranchial) and allow us to look for them in other specimens (e.g. *Sclerorhynchus atavus* (NHMUK PV P 49546)). As previously suggested for *Ptychotrygon* (Cappetta & Case 1999), *Asflapristis* lacks

enlarged rostral denticles, and the current remains suggests the presence of a large and flattened rostrum for the family as seen in other sclerorhynchoids which is further corroborated by *Ptychotrygon* sp.

The phylogenetic analyses in the present study suggest a close phylogenetical relation between sclerorhynchoids and rajoids based on similarities on the branchial skeleton. These two groups are the only two known batoids that present no articulation surface between the basibranchial and the second hypobranchial, also none of the sclerorhynchoids included in the present analysis showed evidence of articulation between the second hypobranchial with any other branchial element. The fact that bayesian analysis further differentiates within Sclerorhynchoidei and separates them in two groups, suggests an internal topology for the groups within it worthy of further analyses. The placement of *Asflapristis cristadentis* in the Ptychotrygonidae, with characters different from those recorded in other skeletally-preserved sclerorhynchoids supports the idea that a number of distinct families present within the Sclerorhynchoidei (Kriwet *et al.* 2009; Cappetta 2012).

Our results separate sclerorhynchoids from Rhinopristiformes (Cappetta & Case 1999) and suggest that the similarities with the Pristidae are superficial and convergent. These analyses also show an interesting evolutionary pattern which was previously recognised by Claeson 2010 in which in every batoid order there is a group with a “rhinopristiform” body plan (elongate body form, robust caudal region and enlarged and well-developed rostral cartilages) suggest that this overall body plan is a primitive character within the Batoidea (Fig. 11 grey labelled taxa).

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