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Sclerorhynchus atavus and the convergent evolution of rostrum-bearing chondrichthyans.

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Abbreviated title: *Sclerorhynchus atavus*

Abstract: The description of a partial but well preserved head of the sclerorhynchid batoid *Sclerorhynchus atavus* Woodward, 1889 gave the first clear indication of the presence of a puzzling group of extinct rostrum-bearing rays that resembled both the Pristidae (rays) and the Pristophoridae (sharks). Despite recognizing similarities and differences to these extant groups, Woodward suggested that *Sclerorhynchus* be assigned to the Pristidae, although acknowledging that the rostra are very different. Woodward did note similarities of *Sclerorhynchus* rostrum saw-teeth to those of the Pristiophoridae, including the location of these along the margin of the rostrum, rather than in deep sockets as seen along the pristid rostrum. In addition, the type specimen of *Sclerorhynchus* has very distinct saw-tooth denticles not only along the rostrum, but modified denticles along the sides of the head, as in the Pristiophoridae. The

enlarged rostral denticles of *Sclerorhynchus* also appear to rotate into position, another feature seen in the pristiophorids but not in the pristids and in other sclerorhynchids such as *Libanopristis*. Although individual fossil rostral tooth-like denticles had been earlier described, Woodward's (1889) description of a rostrum and associated rostral tooth-like denticles meant that for the first time a fossil rostrum could be compared to living forms.

Whilst the possession of rigid rostra projecting anteriorly from above the mouth is widespread within vertebrates (such as within the paddlefishes *Polyodon* and *Psephurus* and several clades of teleosts), it is especially common within the chondrichthyans. Within extant forms alone, an anteriorly extended nasal region is present in holocephalans (e.g. *Rhinochimaera*), squalean sharks (e.g. *Deania*), galean sharks (e.g. *Mitsukurina*), and many batoids (e.g. many Rajidae and many 'rhinobatids'). These rostra, however, differ only from the nasal region of non-rostrate relatives in terms of their length. In one family of sharks, the sawsharks (Pristiophoridae) and one family of rays, the sawfish (Pristidae) the rostrum is not only especially large, but bears enlarged rostral denticles along its lateral margins (e.g. Wueringer *et al.* 2009, Welton *et al. in press*). An additional extinct group of rays, the sclerorhynchids, bore rostra similar to those of the pristiophorids and pristids.

There are nine recorded extant species of pristiophorid sharks within two genera, (*Pristiophorus* and *Pliotrema*). All are small with none exceeding 150cm in length (Compagno et al. 2005). All species inhabit either deep seas within the tropics or shallow, temperate waters. Fossils are likewise largely restricted to deep water facies or high palaeolatitudes. Fossils of pristiophorids are known from the Late Cretaceous (Santonian) onwards, but are relatively uncommon.

In contrast to the small and cool water dwelling pristiophorids, pristids are large and tropical. There are between four and seven living species (the species level taxonomy is poorly understood) in two genera, *Pristis* and *Anoxypristis* (e.g. Last and Stevens 1994). All species are known to exceed 300 cm in length, with some reportedly reaching over 700 cm (e.g. Last and Stevens 1994). Pristids are restricted to tropical

and subtropical waters, and are largely found in shallow and coastal regions. Most species enter, or may inhabit, fresh water. Pristids have a good fossil record, first appearing near the base of the Eocene.

Both small and large species of sclerorhynchids are known, and they are known from deep and shallow marine facies, as well as coastal plain fluvial deposits. They are an exclusively Cretaceous group and fossils may be both common and diverse in palaeotropical deposits (e.g. Cappetta 2012)

Rostra with marginal tooth-like structures are thus known from at least three groups of neoselachians (modern-type sharks and rays). Despite the repeated occurrence of rostra within vertebrates, only neoselachians are known to possess these strongly denticulated rostra.

The sclerorhynchid fossil record

Fossils of sclerorhynchid batoids are widespread in rocks of Cretaceous age and are present in both marine and non marine deposits. They appear to have been largely restricted to the Tethyan Realm, but within shallow marine, nearshore sediments deposited in palaeotropical areas, fossils are typically abundant and represent a diverse suite of species.

As with other chondrichthyans, the preservation potential of the endoskeleton of sclerorhynchids is generally poor, and the majority of species are known from isolated oral teeth and enlarged rostral denticles or saw-teeth (also commonly referred to as "teeth"). Of these, oral teeth are typically very small and often rather conservative in morphology, so the more conspicuous rostral denticles are rather better known. The first sclerorhynchid remains to be described were isolated rostral denticles of *Onchosaurus* Gervais 1852 and *Ischyrhiza* Leidy 1856, but the affinities of these were uncertain. In 1889, Woodward described the first articulated specimens of sclerorhynchids and discussed their affinities. The holotype of *Sclerorhynchus atavus* comprises a partial, but well preserved, head from the Santonian of Lebanon (Fig. 1A). Whilst the holotype was recognized as a batoid, other specimens lacking the distinctive rostrum were described at the same time but were assigned to the shark

genus *Squatina* (Woodward 1889). Subsequent finds of *S. atavus* included some more complete skeletons (Cappetta 1980) that allowed Woodward's specimens to be synonymized and demonstrated that between Woodward's specimens much of the skeleton was represented. Other specimens are less complete, but still yield valuable data (e.g. see Fig. 2). Additional sclerorhynchid species, *Libanopristis hiram* (Hay 1903) and *Micropristis solomonis* (Hay 1903) were subsequently discovered in Cenomanian rocks of Lebanon and are also represented by well preserved, articulated, skeletons (Hay 1903, Cappetta 1980). These three Lebanese taxa remain the only sclerorhynchids currently described from articulated skeletons, but all of the skeletons have undergone intense taphonomic flattening. All three of the species known from complete skeletons are small (mostly under 100 cm in total length) and have relatively similar shaped teeth and rostral denticles. Whilst other species are known largely from isolated teeth and rostral denticles, partial rostra are known from *Onchopristis* Stromer 1917 (e.g. Arambourg 1940, Cappetta 1980), *Ischyrhiza* (David Ward, pers. comm.) and the errant form that has typically been included in the sclerorhynchids, *Schizorhiza* Weiler 1930 (e.g. Kirkland and Aguillon-Martinez 2002). These rostra suggest that some sclerorhynchids were very large in comparison to the Lebanese taxa. Other sclerorhynchids are known only from isolated teeth and rostral denticles, although these are variable in morphology and suggest that the sclerorhynchids were a highly diverse group.

More complete fossils of some additional sclerorhynchid taxa are known but have yet to be fully described. A partial skull and jaws of *Onchopristis numidis* Haug 1905 is known (Didier Dutheil pers. comm.) and several specimens of at least two undescribed sclerorhynchid species are known, but have yet to be described, from the Turonian of eastern Morocco (Fig. 3A; Claeson *et al.* 2013).

Rostral denticles on NHMUK specimens of *Sclerorhynchus atavus*

The holotype of *S. atavus* (NHMUK PV P4776) is a partial head preserved in dorsal aspect. The anterior part of the chondrocranium is preserved with about half of the rostrum. The surface preservation of the mineralized cartilage is good, but large parts of cartilage, as well as many of the rostral denticles, have been lost, presumably during collection or preparation of the specimen. The only other specimen in the same

collection preserving part of the rostrum is an incomplete head partly concealed below the remains of two fish (NHMUK 88663; Fig. 2A). The latter specimen was not mentioned by Woodward (1889) and presumably was obtained subsequently by the NHMUK.

Observable characters

NHMUK PV P4776 clearly shows the overall morphology of the proximal part of the rostrum, even though part of the rostral cartilage has broken away and is missing. The rostral cartilage is widest just anterior to its origin. At the widest point on the rostral cartilage, a flange of skin extends posteriorly, merging into the anteriormost edge of the pectoral fin. This forms a wide flange lateral to the sides of the head.. The lateral margin of this cephalic flange is also covered in enlarged lateral cephalic denticles (as noted by Hay 1903). The rostral denticles are irregularly spaced in a single row and are weakly attached to the rostral cartilage, with most seemingly displaced to some extent. By contrast, the lateral cephalic denticles are smaller and present in several poorly ordered rows, with the bases of additional, more medial denticles, indicating that other rows of similar denticles are present on the ventral surface of the cephalic flange. The presence of both erect and recumbent rostral denticles demonstrated that additional (and/or replacement) rostral denticles formed parallel to the edge of the rostral cartilage, before rotating into position (Wueringer *et al.* 2009, Welton *et al. in press)*. There is little detail of the remainder of the skull, and only the lateral extremities of the jaw cartilages can be seen. Few features can be seen on NHMUK 88663 due to poor preservation and obscuring by other fossils, although some rostral denticles can be seen close to, but not attached to, the rostral cartilage.

Features revealed by μCT scanning

Both NHMUK PV P4776 and NHMUK 88663 were scanned at the NHJMUK using the Metris X-Tek HMX ST 225 CT system. Scan data was rendered in VG Studio MAX and features of interest were highlighted in postwork in Photoshop. Segmentation of the data prior to rendering was not carried out as the images were

clear without this and it was considered that there was an elevated risk of acquiring artifacts by omission or addition of high density elements associated with the fossils.

Whilst µCT scanning has become a standard method for study of vertebrate fossils, it has rarely been used on fossils that have undergone high degrees of compaction. Both of the specimens of *S. atavus* yielded considerable additional data when µCT scans were rendered, allowing features concealed within the rock to be studied. In NHMUK P4776 the bulk of additional information was on the concealed ventral surface of the specimen (Fig. 1B). Although the jaw cartilages (Meckel's cartilage and palatoquadrate) were visible on the exposed surface, no details could be seen. Rendering of these allowed both of the jaw elements to be seen in some detail, and the dentition to be observed; this could readily be related to that seen in one of the referred specimens (the holotype of *Squatina crassidens* of Woodward 1889) confirming the synonymy of these specimens. The rostrum and rostral and lateral denticles were clearly resolved, with the arrangement of the lateral cephalic denticles being especially well demonstrated. The development of rostral denticles and their rotation during formation could be confirmed, and a similar developmental style could be seen for the first time in the lateral cephalic denticles (Welton *et al. in press*). The rendered scans also showed, for the first time, several rows of small pointed denticles on the ventral side of the rostral cartilage (Fig 1C). There is a double row near the midline of the rostrum and two additional pairs of rows close to, and at the lateral margin of the rostrum. These appear to show a far more regular spacing than seen in any of the other denticles.

In NHMUK 88663 jaws and teeth were also rendered, but these were seen to be close to the edge of the slab and not well preserved, so little detail could be seen. The rendered ventral view of the specimen allowed the parts of the specimen concealed beneath the fish remains to be seen for the first time (Fig 2B). Whilst it was not clear on the exposed surface whether the lack of large rostral denticles was due to taphonomic loss associated with burial or loss during collection or preparation of the specimen, it was evident from the CT-scan renders that the former is the case and rostral denticles are still associated with, but not articulated on, the rostrum. A number of rostral denticles are visible, but all are disarticulated and scattered through

the rock. In comparison, the lateral cephalic denticles are articulated and demarcate the edge of the cephalic flange.

Despite not being the best preserved or most complete specimens of *Sclerorhynchus atavus*, μCT scanning has revealed a number of features not previously recognized. The rows of ventral rostral denticles have not previously been recognized in this species or any other sclerorhynchid. There is also a clear differentiation in the rostral and lateral cephalic denticles. Not only is there a difference in denticle morphology and density, but there is a consistent pattern in the degree of taphonomic disruption. This would strongly suggest that the rostral denticles were only weakly attached, and were readily disarticulated during decay, whilst the lateral cephalic denticles were strongly embedded in the skin and were not rapidly shed *post mortem*.

Comparison to other sclerorhynchids

The Lebanese specimens of *Libanopristis hiram* and *Micropristis solomonis* show many of the same characters as seen in *Sclerorhynchus atavus*. Whilst the rostral denticles are proportionally smaller than in in *Sclerorhynchus atavus*, their arrangement on the rostrum is similar. As in *Sclerorhynchus* additional rostral denticles can be seen to develop parallel to the rostral cartilage, and subsequently rotating into position. There is also a clear differentiation between the denticles on the rostrum and on the lateral cephalic flange (Fig. 4A). The small ventral denticles have not been observed on either of these additional species; in specimens preserved in ventral aspect it is these are likely to have been lost on the counterpart slab if they were originally present, are concealed in dorsally exposed specimens. The dentitions of all three species are also similar (Cappetta 1980), with teeth of similar shape and arrangement within the jaws, differing largely in the ornamentation on the teeth.

Whilst far less is known about sclerorhynchids other than the three Lebanese taxa, the clade is clearly far more diverse than shown by taxa known from skeletal remains. Rostral denticles of different species vary tremendously in size (from 0.2 cm to over 7 cm high) and also in shape, with considerable variation in the form of the basal region (root) and in the presence or absence of barbs on the crown. Partial rostra of a range

of genera (*Onchopristis* Stromer 1917, *Ischyrhiza* (David Ward, pers. comm.) and possibly *Schizorhiza* Weiler 1930) suggest that the rostra in some taxa reached over two metres in length. Whilst the total length of the individuals cannot readily be assessed, it is likely (by comparison with other rostrate chondrichthyans) that the rostrum comprised 20% to 30% of the total body length. It is not known whether these larger sclerorhynchids possessed lateral cephalic or ventral rostral denticles. Although morphologically relatively conservative, there is considerable variation in shape, but not size, in oral teeth. Some sclerorhynchid-type teeth do not appear to be associated with rostral denticles (e.g. Cappetta 2012), and it therefore seems likely that some sclerorhynchid lineages underwent secondary loss of the rostral denticles. Whilst there is no direct evidence of the mode of addition of rostral denticles in these other sclerorhynchids, some rostral denticles of *Onchopristis* are incompletely mineralized, with an open pulp cavity and poorly mineralized root (Fig. 4B, C). This suggests that these developing denticles were originally hollow, with the root and pulp cavity mineralising after the tooth has been erected into position, as in the pristiophorids (Wueringer *et al.* 2009; Welton *et al.* in review). It is likely that the variation in rostral denticle histology recorded by Cappetta (2012) is due to sampling of denticles at differing developmental stages with a gradual infilling of the pulp cavity during development. It is possible that the rate of infill of the pulp cavity was not consistent between species, giving rise to an apparent divergence in histology within congeneric taxa (e.g. Slaughter and Steiner 1968).

Despite the diversity recorded within the sclerorhynchids, there are some errant species that fall outside the normal range of diversity. *Ctenopristis* Arambourg 1940 has rostral denticles that have a very slender crown orientated at an angle to the root with a well developed basal flange (e,g, see Cappetta 2012). Despite these unique characters, the rostral denticles are in other respects similar to those of sclerorhynchids, as are the oral teeth. This is probably best considered a rather derived but true sclerorhynchid.

Schizorhiza possesses rostral denticles that are unique in both their morphology and mode of replacement (Figs 3B, 4D). The crown is low and triangular and lies above a high root with two, strongly denticulate, lobes. The rostral denticles are closely packed in an alternate pattern along the rostrum, and replacement denticles develop

between the root lobes of the preceding denticle (Kirkland and Aguillon-Martinez 2002). This denticle morphology, and particularly mode of development, is so different from that of other sclerorhynchids that this genus is probably best considered to form an unrelated clade within which the denticulate rostrum has evolved convergently.

Comparison with other rostrate chondrichthyans

Whilst the diversity of the sclerorhynchids is not in doubt, their affinities are less certain, and there have been few attempts at placing them within a phylogeny of the Batoidea (e.g. Kriwet 2004). They possess few synapomorphies that would allow their position within the Batoidea to be assessed with respect to other taxa in the group, whilst issues regarding coding convergent characters in sclerorhynchids and the distantly related pristiophorids are likely to prove problematic. The rostrum and rostral denticles of sclerorhynchids are structurally very different from those of the Pristidae (e.g. Wueringer et al. 2009), and these characters cannot be considered as homologous; Kriwet (2004) considered the three rostrate groups to be closely related but having independently evolved denticulate rostra. Whilst appearing very well preserved, the crushing of the Lebanese specimens obscures many potentially useful characters in the neurocranium, synarcual and claspers. Further study of the affinities of the sclerorhynchids is probably best considered premature until specimens with additional characters are available.

Rostra superficially similar to those in the sclerorhynchids are present in the Pristiophoridae and Pristidae. Of these, the pristids are more closely related to the sclerorhynchids, both being rays, as opposed to the Pristiophoridae which are squalean sharks (e.g. Naylor et al. 2005). Woodward (1889, 1892) suggested that *Sclerorhynchus* be assigned to the Pristidae, although he acknowledged that the rostrum was rather different from any pristids and could equally be placed in the Pristiophoridae (Woodward 1889). Woodward did note similarities of *Sclerorhynchus* rostrum saw-teeth to those of the Pristiophoridae, including the location of these in shallow embayments along the rostrum. Despite both *Sclerorhynchus* and pristids being within the Batoidea, there are few similarities in the structure and development of the rostrum. The rostrum of pristids has large rostral denticles embedded within

sockets in the sides of the rostral cartilage (Fig 3C). The denticles are retained throughout life, and grow continuously from their base, in part counteracted by wear near the denticle tip. Other than these larger lateral rostral denticles, the rostrum is covered in minute denticles similar to those covering the rest of the body, with no additional enlarged or modified denticles on the ventral surface of the rostrum or sides of the head (lateral cephalic denticles; e.g. Welton *et al. in press*). Denticulated rostra of sclerorhynchids and pristids, and possibly also *Schizorhiza*, are thus likely to have evolved convergently, and similarities are purely superficial.

The rostra of sclerorhynchids are in many ways far more comparable to those of pristiophorids than pristids, despite their more distant phylogenetic relationship. As in sclerorhynchids, in pristiophorids the rostral denticles are added through life, forming parallel to the margin of the rostral cartilage before rotating into position (Fig 3D, E). Pristiophorids also possess lateral cephalic denticles, although there are morphologically rather different from those of *Sclerorhynchus*, and a double row of small ventral rostral denticles. These similarities indicate a very strong degree of convergence between the two distantly related clades.

Conclusions

Sclerorhynchids, first described by Woodward in 1889, are now known to represent one of the most successful and diverse clades of extinct neoselachian chondrichthyans. Despite the large number of species identified, and the presence of well preserved skeletons of several taxa (including material from Lebanon studied by Woodward), the group remains relatively poorly understood. Restudy of the holotype and other material of *Sclerorhynchus atavus* using μCT scanning has allowed more information to be obtained. This has allowed additional sets of rostral denticles to be recognised for the first time, and the development and replacement of rostral denticles to be studied in more detail. The rostra of sclerorhynchids are superficially similar to those of the extant pristids and pristiophorids, but there is no evidence to suggest that this is due to any cause other than convergence. It is thus evident that rostra with marginal tooth-like denticles have evolved on at least three occasions within the neoselachians. Unique characters of the rostra of the supposed sclerorhynchid

Schizorhiza Weiler 1930 suggest that this taxon may not be closely related to sclerorhynchids, representing a fourth occurrence of rostra of this type. Even though living chondrichthyan species comprise only about 1.25% of all vertebrates, they are the only clade within which this form of rostrum is known. In addition, if extinct chondrichthyans are included, denticle bearing rostra are only known amongst the Neoselachii. The reasons for both this repeated evolution of denticle bearing rostra, their diverse morphologies, and the apparent restriction of these rostra to a single clade are uncertain. Neoselachians possess skin covering denticles somewhat unlike those present in other chondrichthyan, or other vertebrate, clades. It is therefore possible that these skin denticles have an inbuild propensity to develop into a wide range of morphologies, including rostral denticles as well as other modified forms such as stingray tail spines.

References

ARAMBOURG, C. 1940. Le groupe des Ganopristinés. *Bulletin de la Société Géologique de France*, **10**, 127-147.

Cappetta, H. 1980. Les Sélaciens du Crétacé supérieur du Liban. II. Batoïdes. *Palaeontographica, Abt. A*, **168**, 149-229.

Cappetta H. 2012. Chondrichthyes: Mesozoic and Cenozoic Elasmobranchii. Chondrichthyes II. *In:* Schultze, H. P. (ed) *Handbook of Paleoichthyology*, 3E, 1-512. Verlag Dr. Friedrich Pfeil, München, Germany.

Claeson, K. M., Underwood, C. J. & Ward, D. J., 2013, †*Tingitanius tenuimandibulus*, a new platyrhinid batoid from the Turonian (Cretaceous) of Morocco and the Cretaceous radiation of the Platyrhinidae. *Journal of Vertebrate Paleontology*, 33, 1019-1036.

Compagno, L. J. V., Dando, M., and Fowler S. 2005. *A Field Guide to the Sharks of the World*. HarperCollins Publishers Ltd., London. 368 pp.

Ebert, D.A. & Wilms, H.A. 2013. *Pristiophorus lanae* sp. nov., a new sawshark species from the Western North Pacific, with comments to the genus *Pristiophorus* Müller & Henle, 1837 (Chondrichthyes: Pristophoridae). *Zootaxa*, **3752**, 86-100.

Gervais, P. 1852. *Zoologie et Paléontologie Française (animaux vertébrés)*, **1**, 1-271. Arthus Bertrand, Paris.

Hay, O.P. 1903. On a collection of upper Cretaceous fishes from Mount Lebanon, Syria, with descriptions of four new genera and nineteen new species. *Bulletin of the American Museum of Natural History,* **19**, 395-452.

Herman, J. 1977. Les Sélachians néocrétacés et paléocénes de Belgique et des contrées limitrophes eléments d'une biostratigraphie intercontinentale. *Mémoires pour server a l'Explication des Cartes Géologiques et Miniéres de la Belgique*, **15**, 1-450.

Kirkland, J.I. & Aguillon-Martinez, M.C. 2002. *Schizorhiza*: a unique sawfish paradigm from the Difunta Group, Coahuila, Mexico. Revista Mexicana de Ciencias Geológicas, **19**, 16-24.

Kriwet, J. 2004. The systematic position of the Cretaceous sclerorhynchid sawfishes (Elasmobranchii, Pristiorajea). *In* Arratia, G. & Tintori, A. (eds). *Mesozoic Fishes 3 Systematics, Paleoenvironment and Biodiversity*: 57-74; Verlag Dr. Friedrich Pfeil, München.

Last, P.R & Stevens, J.D. 1994. Sharks and rays of Australia, CSIRO, Australia. 513pp.

Leidy, J. 1856. Notice of remains of extinct vertebrated animals of New-Jersey, collected by Prof. Cook of the State Geological Survey under the direction of Dr. W. Kitchell. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **8**, 220-221.

Naylor, G. J. P., Ryburn, J. A., Fedrigo, O., and López, A. Phylogenetic relationships among the major lineages of modern Elasmobranchs. *In* W. Hamlett W. & Jamieson B. (eds). *Reproductive Biology and Phylogeny of Chondrichthyes*: 1-15: University of Queensland Press.

Slaughter, B.H. & Springer, S. 1968. The replacement of rostral teeth in sawfishes and sawsharks. *Copeia*, **968**, 499-506.

Stromer, E. 1917. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharaje-Stufe (Unterstes Cenoman). 4: Die Säge des Pristiden *Onchopristis*. *Abhandlungen der Bayerischen Akademie der Wissenschaften / Mathematisch-Naturwissenschaftliche Klasse / N.F.*, **28**, 1-21.

Weiler, W. 1930. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. VI. Beschreibung von Wirbeltier-Resten aus dem nubischen Sandsteine Oberägyptens und aus ägyptischen Phosphaten nebst Bemerkungen über die Geologie der Umgegend von Mahamid in Oberägypten. *Abhandlungen der Bayerischen Akademie der Wissenschaften / Mathematisch-Naturwissenschaftliche Klasse / N.F.*, **1**, 1-42.

Welton, M., Smith, M.M, Underwood, C.J. & Johanson, Z. Teeth outside the mouth? Evolution and development of the sawfish and sawshark rostral dentitions (Elasmobranchii; Chondrichthyes). *Royal Society Open Science*, *in review.*

Woodward, A.S. 1889. *Catalogue of the fossil Fishes in the British Museum. Part 1*. British Museum (Natural History), London. 474pp.

Woodward, A.S. 1892. Description of the Cretaceous saw-fish *Sclerorhynchus atavus*. *Geological Magazine*, **9**, 529-534.

Wueringer B.E, Squire Jr. L, & Collin S.P. 2009. The biology of extinct and extant sawfish (Batoidea: Sclerorhynchidae and Pristidae). *Reviews in Fish Biology and Fisheries, 2009,* **19**, 445-464.

Figure captions.

Figure 1.
Holotype specimen of *Sclerorhynchus atavus* Woodward 1889 (NHMUK P4776)
A. Photograph of the specimen with the dorsal surface exposed showing rostral denticles (RD), lateral cephalic denticles (LCD) and poorly preserved jaws (J).
B. Rendered μCT scan showing the ventral surface of the specimen. Rostral denticles (blue, RD) and lateral cephalic denticles (red, LCD) are clearly seen as are the jaws (J) and teeth (T).
C. Rendered oblique ventral view showing two rows of lateral ventral denticles (green, LVD) and a centrally positioned pair of rows of median ventral denticles (green, MVD). Rostral denticles (blue, RD) and lateral cephalic denticles (red, LCD) can also be seen.

Figure 2.
Additional specimen of *Sclerorhynchus atavus* Woodward 1889 (NHMUK 88663).
A. Photograph of the specimen with the dorsal surface of the rostrum partly exposed showing only a single fragmentary rostral denticle (RD).
B. Rendered μCT scan showing the ventral surface of the specimen, with the fish specimens partly removed. Disarticulated rostral denticles (blue, RD) and articulated lateral cephalic denticles (red, LCD) are clearly seen.

Figure 3.

Additional rostrate specimens.

A. Near complete specimen of an undescribed sclerorhynchid from the Turonian of Asfla, Morocco (NHMUK PV P 73630). Photograph taken under Ultraviolet light to enhance the difference between rock (pale), fossil (dark) and resin (dark, speckled).

B. Rostrum of the enigmatic taxon *Schizorhiza stromeri* Weiler 1930 (NHMUK PV P 73625).

C. Rendered μCT scan of a rostrum of a juvenile sawfish (*Pristis* sp.). The translucency of the render allows the rostral denticles to be seen embedded in sockets in the rostral cartilage.

D. Rendered μCT scan of the ventral view of head and rostrum of a Philippines Sawshark (*Pristiophorus lanae* Ebert and Wilms 2013). Rostral denticles (RD) and lateral cephalic denticles (LCD) are superficially similar to those in *Sclerorhynchus*.

E. Detail of the same specimen, rendered in dorsal view. Rostral denticles (RD) and lateral cephalic denticles (LCD) are clearly shown.

Figure 4.

Sclerorhynchid rostral denticles.

A. Detail of the rostrum of *Libanopristis hiram* (Hay 1903) (NHMUK P13858) showing rostral denticles (RD) and lateral cephalic denticles (LCD). Note that some rostral denticles are not fully formed and lie parallel to the edge of the rostral cartilage and lack a root.

B. Longitudinal section of a rostral denticle of *Onchopristis numidus* (Haug 1905) (NHMUK PV P 73628) showing the lack of a pulp cavity.

C. Longitudinal section of a rostral denticle of *Onchopristis numidus* (NHMUK PV P 73629) showing a large pulp cavity and very poorly mineralized root. Few specimens show this low degree of mineralization and it is likely that this denticle is incompletely developed.

D. Articulated rostral denticles of *Schizorhiza stromeri* Weiler 1930 (NHMUK PV P 73625). The morphology and mode of packing of these denticles is unlike that seen in any 'true' sclerorhynchid.