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The skeletal remains of the euryhaline sclerorhynchid batoid †*Onchopristis* (Elasmobranchii, Batoidea) from the 'mid' Cretaceous and its palaeontological implications

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Abstract:

We present the first known cranial remains of the fossil batoid †*Onchopristis numidus*. Based on two exceptionally well-preserved specimens collected from the "Kem Kem Beds" (Albian-Cenomanian), South-East of Morocco, an almost complete description of the rostral and cranial portions of the genus †*Onchopristis* is provided, along with new observations regarding the addition and arrangement of the rostral denticles series for this genus. The comparison between the rostrum length of the specimens of †*Onchopristis numidus* with those of extant pristids revealed a relatively large batoid species with an estimated total length between two to four meters. Overall, the cranial morphology of †*Onchopristis* resembles that of other sclerorhynchoids. Its robust hypertrophied rostrum with the characteristic wood-like mineralisation covering the inner layer of tessellate cartilage at the centre of the rostrum, in addition to the thick lateral layers of densely porous cartilage on the sides of the rostral cartilages, resembles that observed in †*Ischyrhiza* and †*Shizorhiza*, and differentiates †*Onchopristis* from other sclerorhynchoids species (e.g. †*Micropristis, †Sclerorhynchus* and †*Libanopristis*). Based on these rostral features, a phylogenetic analysis to establish the phylogenetic position of †*Onchopristis* within sclerorhynchoids is carried out, which results suggest a new taxonomic arrangement for the sclerorhynchoids.

Abstract. We present the first known cranial remains of the fossil batoid †*Onchopristis numidus*. Based on two exceptionally well preserved specimens collected from the "Kem Kem Beds" (Albian-Cenomanian), South-East of Morocco, an almost complete description of the rostral and cranial portions of the genus †O*nchopristis* is provided, together with new observations regarding the development and arrangement of the rostral denticle series for this genus. The comparison between the rostrum length of the specimens of †*Onchopristis numidus* with those of extant pristids revealed a relatively large batoid species with an estimated total length between two to four meters. Overall, the cranial morphology of †*Onchopristis* resembles that of other sclerorhynchoids. Its robust hypertrophied rostrum with the characteristic wood-like mineralisation covering the inner layer of tessellate cartilage at the centre of the rostrum, in addition to the thick lateral layers of densely porous cartilage on the sides of the rostral cartilages, resembles that observed in †*Ischyrhiza* and †*Shizorhiza*, and differentiates †*Onchopristis* from other sclerorhynchoid (e.g. †*Micropristis*, †*Sclerorhynchus* and †*Libanopristis*). Based on these rostral features, a phylogenetic analysis to establish the phylogenetic position of †*Onchopristis* within sclerorhynchoids is carried out, its results suggest a new taxonomic arrangement for the sclerorhynchoids.

INTRODUCTION

†*Onchopristis* Stromer, 1917 is a puzzling Cretaceous batoid taxon, with most of its fossil record recorded from many 'mid' Cretaceous sites in coastal and fluvial settings, and composed of fragmentary remains of rostral cartilages, rostral denticles, and teeth. The taxon was first described based only on rostral fragments and denticles (Haug, 1905; Stromer, 1917; 1925) (Fig. 1) with the teeth being described as a different taxon by Stromer (1927), but later assigned to †*Onchopristis* by Slaughter & Thurmond (1974) (see also Cappetta, 1987). Werner

(1989) rejected this interpretation and assigned the teeth associated with †*Onchopristis numidus* erroneously to a new taxon, †*Sechmetia aegyptiaca.* Currently, †*Onchopristis* is placed systematically in the suborder †Sclerorhynchoidei within the family †Sclerorhynchidae (Cappetta, 2012), although this affiliation has not been tested phylogenetically.

Insert figure 1.

The genus is restricted to the Barremian-Cenomanian (Kriwet, 1999) and presently includes only two valid species (†*Onchopristis numidus* and †*O. dunklei,* see Table 1). †*Onchopristis numidus* (Haug, 1905) occurs in the Albian of Djoua, Algeria (Cappetta, 1987), the Cenomanian of Egypt (Stromer, 1927; Slaughter & Thurmond, 1974; Werner, 1989), the Albian-Cenomanian of Morocco (Cappetta, 1980). It should, however, be noted that the exact stratigraphic age of many of the North African sites is still in debate.

†*Onchopristis dunklei* (McNulty & Slaughter, 1962) is reported from the Cenomanian and middle-upper Albian of Texas and also possibly from the Albian of Tunisia, although the latter record is based on incomplete material (Cuny *et al.,* 2004), and from the Cenomanian of Spain and France (Bernardez, 2002; Vullo *et al*., 2003; Néraudeau *et al*., 2005). The specimens of †*Onchopristis dunklei* collected from the Lower Cretaceous (Aptian-Albian), Trinity Group of Texas, U.S.A. are considered a subspecies by Thurmond (1971), who introduced the name †*Onchopristis dunklei/praecursor*. In addition, an unnamed older species exists, which was recovered from Barremian deposits of north-eastern Spain (Kriwet, 1999).

†*Onchopristis dunklei/praecursor* also occurs in the Upper Cretaceous (Campanian-Maastrichtian) of New Zealand by Keyes (1977). Martill & Ibrahim (2012) revised this taxon and redescribed it as †*Australopristis wiffeni*. Based on the differences between the specimens figured by Keyes (1977) and the teeth of typical †*Onchopristis*, Cappetta (2012) proposed that the sclerorhynchid rostral teeth from New Zealand might be close to †Sclerorhynchus and might have acquired convergently morphologies with posterior barbs resembling that of

†*Onchopristis*. Alternatively, †*Australopristis* maybe a sawshark belonging to Pristiophoridae, similar to †*Pliotrema*.

Table 1. List of species assigned to †*Onchopristis* with their currently accepted taxonomic status.

Type of remains	Original description	Current taxonomic status
Oral	†*Squatina aegyptiaca* Stromer, 1927	Syn. †*O. numidus* (Cappetta, 2006)
Oral	†*Sechmetia cruciformis* Werner, 1989	Syn. †*O. dunklei* (Cappetta, 2006)
Oral	†*Sechmetia aegyptiaca* Stromer, 1927	Syn. †*O. numidus*
Oral and Rostral	†*O. dunklei* McNulty & Slaughter, 1962	Valid (Cappetta, 2006)
Vertebra	†*Platyspondylus foureaui* Haug, 1905	Syn. †*O. numidus* (Cappetta, 2006)
Rostral	†*Australopristis wiffeni Martill & Ibrahim, 2012*	Valid (Martill & Ibrahim, 2012)
Rostral	†*O. dunklei/praecursor* Thurmond, 1971	Syn. †*Australopristis wiffeni* Martill & Ibrahim, 2012
Oral, Rostral and Cranial	†*O. numidus* (Haug, 1905)	Valid (Cappetta, 2006)
Rostral	†*Onchopristis sp.* Werner, 1989	Unknown species

The genus †*Onchopristis* can be differentiated from other sclerorhynchoids in the shape and size of its rostral denticles (reaching 7 cm in length). The presence of barbs (hook-like protuberances directed backwards) situated on the posterior margin, along with numerous rectilinear folds along the posterior and anterior margins of the rostral denticles, are key features for their identification. Currently, the two valid species of †*Onchopristis* are differentiated from each other by the number of barbs associated with their rostral denticles: one in †*O. numidus* and several *in* †*O. dunklei* (Cappetta, 2012). Numerous hypotheses have been proposed to explain the development of this feature. Slaughter & Steiner (1968) suggested that there is an evolutionary tendency to increase the number of barbs associated with the rostral denticles. However, a secondary loss cannot be discarded (i.e. the plesiomorphic state could be additional (more than one) barbs associated with the rostral denticles). McNulty & Slaughter (1962) proposed that the number of barbs is related to the size of the rostral denticles, and as the denticles grow the number of barbs also increases. The presence of multiple barbed denticles (usually two) in specimens from Morocco and Egypt (Stromer, 1917, plate 1; Martill & Ibrahim, 2012, text-fig. 3A-B and 5) (Fig. 7B) renders the use of the barb numbers as a valid character for species determination within †*Onchopristis* problematic. Despite this, presence of multiple barbs is typical for North American specimens of †*O. dunklei*, but it is a rare feature observed in North African specimens assigned to †*O. numidus*, where these denticles comprise less than 1% of the rostral denticles.

Here, we describe previously unknown features for †*Onchopristis numidus* based on several specimens recently collected from the "Kem Kem Beds" (Albian-Cenomanian) of SE Morocco and analysed their characters with those described for †*O. dunklei*. The new "Kem Kem" material reveals a peculiar arrangement of the enlarged lateral rostral denticle series with intercalations of various sizes, as well as the morphology of the synarcual and other cranial remains of the genus †*Onchopristis* for the first time.

STUDY AREA AND TAPHONOMY

Geological setting– In North Africa, the 'Continental Intercalaire' comprises an extensive non-marine succession of fluvial and fluvial-deltaic facies of Late Jurassic to 'middle' Cretaceous age (Kilian, 1931; De Lapparent, 1960; Cavin *et al.*, 2010; Ibrahim *et al.*, 2020). In Morocco, the 'Continental Intercalaire' is informally known as the "Kem Kem Beds" (Sereno *et al.*, 1996); this term subsequently was later restricted to deposits of mid-Cretaceous age Albian and/or Cenomanian age (Cavin *et al.*, 2010). The fluvial sandstone-dominated facies contain an abundant and diverse vertebrate fauna and are the source of extensive small-scale commercial fossil mining operations. The known fauna is dominated by diverse aquatic and semi-aquatic taxa, with facultatively terrestrial forms being rare. These faunas have been the subject of several studies (e.g. Dutheil, 1999; Cavin & Forey, 2004; Rage & Dutheil, 2008; Belverde *et al.*, 2013; Mannion & Barret, 2013; Ibrahim *et al.*, 2020).

The "Kem Kem Beds" are present along an escarpment at the north-eastern, eastern and south-eastern margins of the Moroccan Anti-Atlas, and are underlain by folded Palaeozoic rocks and overlain by Cretaceous marine limestones that also form the top of the escarpments. This unit is typically divided into two units: the sandstone-dominated Ifezouane and the overlying mudstone-dominated Aoufous formations (Cavin *et al.*, 2010; Ettachfini & Andreu, 2004). Most vertebrate fossils from the southern part of the area come from the Ifezouane Formation. In the northern part of the area, close to the mouth of the River Ziz gorge, well preserved fish fossils, and amphibian and squamate remains are known from the Aoufous Formation (Dutheil, 1999). Within the Ifezouane Formation, there is no formalised internal stratigraphy, and there is no stratigraphic control on the fossil assemblages.

Consequently, it is unknown whether the faunas found in the region have the same time age or are an assemblage of multiple ages. Despite this lack of stratigraphic detail, the Ifezouane Formation in the South of the area rests unconformably on the basement and comprises two channelised sandstone units separated by a major channel base surface. Most fossils are known from the channel lag at the base of the upper unit. In the North, there are two channelised sandstones separated by a heterolithic unit of siltstones and rippled sandstones. A gypsum rich mudstone separates these sandstones from the basement below. Fossils are common in both the channelised sandstones and the heterolithic unit, with the specimens described here being collected from the heterolithic unit.

The majority of the publications describing fossils from the "Kem Kem Beds" utilise commercially collected material with relatively few publications dealing with material collected *in situ* (Dutheil, 1999, Rage & Dutheil, 2008). As a result, palaeoecology studies of the unit are biased by collection procedures (e.g. higher value specimens) and taphonomic aspects (e.g. merging of stratigraphically, environmentally and geographically isolated faunas). Some studies have assumed a rather homogeneous palaeoenvironment (Cavin *et al.,* 2010) or noted some stratigraphical variation in the faunas but did not link that to palaeoenvironments (Läng *et al.*, 2013). There is a general dominance of small remains (vertebrae, teeth and scales fish) of actinopterygian fishes at all field sites, although these are of low commercial value and small size and hence are underrepresented in many collections. Lungfish toothplates and remains of coelacanths are found more irregularly. Chondrichthyan remains are common and composed mainly of †*Onchopristis numidus* rostral denticles, along with vertebral centra and fragments of rostral cartilages. †*Onchopristis numidus* teeth and smaller denticles are also common but typically only are recovered by screen-washing due to their small size. Hybodont fin spines are frequent macroscopic finds, with small hybodont teeth of several genera being abundant in many sieved samples.

Lamniform and other elasmobranch shark teeth are present but rare. Tetrapod bone fragments are also prevalent (especially chelonian carapace fragments, crocodilian bone fragments and spinosaurid teeth) and a vast diversity of large and small tetrapods are known. Non-vertebrate remains include multiple gastropod species, small bivalves and carapace fragments of decapod crustaceans, which are rarely recorded. Ferruginised pieces of wood occur in some localities, especially in northern localities of the channel sandstone facies (e.g. Aghanbou). These fossil assemblages and the sedimentology suggest a fluvial association, with little evidence of marine influences. However, the frequent presence of †*Onchopristis numidus* (present within coastal and brackish water facies in Egypt) may suggest a link to coastal facies within which it is known elsewhere (Werner, 1989), and the occurrence of several species of lamniform sharks (typically considered as marine) may suggest a direct and possibly close connection to the marine environments.

The channel structures within the fluvial facies in some localities (e.g. Boufaddouz) are immense, suggesting a considerable extension of the channels, which might have been part of a meandering river system, as very large and sinuous channels persist in both Morocco and Libya, indicating the continuity of an extensive river system.

MATERIAL

All specimens described here were obtained from Morocco-based commercial sources, with one of them (NHMUK PV P 75502) brought directly at the site of Boufza (UTM Easting 353973, UTM Northing 3509602, Zone 30), which facies are not exploited (i.e. commercially used) elsewhere (pers. observ. C. Underwood). Specimen IPUW 353500 presents an almost complete rostrum and an almost complete neurocranium, with only the left nasal cavity, hyomandibula, and some jaw elements missing. Specimen IGR 2818 shows an almost complete rostrum with only the tip and the complete left side of the rostrum missing. The specimens NHMUK PV P 75502 and 75503 are rostral fragments. Additional small specimens of isolated teeth and denticles were largely collected *in situ*, typically from the weathered spoil of commercial excavations and by sieving of sediment gathered near those sites (e.g. Begaa (KK3): UTM Easting 418421, UTM Northing 3418555, Zone 30 and Boufaddouz (KK7): UTM Easting 373009, UTM Northing 3501097, Zone 30).

Institutional abbreviations

IGR: Geological Institute of the University of Rennes 1, NHMUK: Natural History Museum United Kingdom. IPUW: Palaeontological Collections of the University of Vienna

Fossil material

†*Asflapristis cristadentis* (NHMUK PV P 73925, 75428 a-e, 75429 a-d, 75431, 75432, 75433). †*Ischyrhiza mira* (Sternes & Shimada, 2019; text-fig. 2 a-I, text-fig. 4 a-f, text-fig 5 a-I; Slaughter & Steiner 1968; text-fig. 4A-C). †*Micropristis solomonis* (Cappetta, 1980, pl. 1, fig. 1-4; pl. 2, fig. 1). †*Libanopristis hiram* (Cappetta, 1980, pl. 1, fig. 4; NHMUK PV P 108705, 108706, 13858, 63610, 75075). †*Onchopristis numidus* (NHMUK PV P 75502,

75503, 1, 74045, 74047, 74050, 74051, 74052, 74053, 74054; IPUW 353500; IGR 2818, 2819, 2820, 2821). †*Ptychotrygon rostrispatula* (NHMUK PV P 73630, 75496, 75496, 75497, 75500). †*Sclerorhynchus atavus* (Slaughter & Steiner, 1968, text-fig. 4D; NHMUK PV P 4017, 4776, 49546, 49518, 49533, 49547). †*Shizorhiza stromeri* (Smith *et al*., 2015; text-fig. 1a-l; 2a-f; NHMUK PV P 73625). †*Spathobatis bugesicus* (NHMUK PV P 6010, 2099 (2); BSP AS I 505, 1952 I 82).

Abbreviations used in the figures

Ac, antorbital cartilage; Alp, anterior lateral process; Bpc, buccopharyngeal nerve cavity; Bre, branchial elements; Cc, corpus calcareum; Cdb, cyclical deposition bar; Den, dermal denticle; Ed, enlarged denticle; Enm, enameloid; Hym, hyomandibula; I, Intermedialia; Ja, jugal arch; Lc, lateral commissure; Lf, lymphatic foramina; Ll, laminar layer, Ls, lateral stays; Mc, medial crest; Mkc, Meckel's cartilage; Oc, occipital condyle; OdP, odontoid process; Of, orbital foramen; Op, optic pedicel; Orb, orbital cavity; Ort, orthodentine; Ost, osteodentine; Pcf, precerebral fenestra; Pop, postorbital process; Pq, palatoquadrate; PrCar, periphery cartilage; Rd, rostral denticle; Sof, spino-ochipital foramina; Sophc, supra ophthalmic nerve cavity; VII, hyomandibular branch of the facial nerve foramen; Wc, Wood-like cartilage.

METHODS

Smaller specimens were field-collected from several sites along the main Kem Kem escarpment. Despite the extensive outcrops, exposures are restricted, and fossiliferous sites are commercially exploited. Spoil is exposed to wind ablation and (rare) rain exposing fossils therein allowing the surface collection of larger specimens and enabling dry sieving through 0.5 or 1mm mesh sieves to collect small specimens. Sieved residues were later additionally wet sieved and picked under a microscope.

Mechanical preparation was carried out in all larger specimens to remove sediment and reveal features concealed by it, for the smaller disarticulated specimens the lab work involved the sagittal and axial cutting and polishing of rostral denticles in order to check their internal morphological features.

Further histology patterns of isolated rostral denticles and teeth were examined at the Department of Palaeontology of the University of Vienna using a desktop micro-computed tomography (micro-CT) device (Bruker SkyScan 1173). The software packages DataViewer (Bruker, version 1.5.1.2) and Amira (FEI Visualization, version 5.4.g) to generate 3D volume renderings of the generated micro-CT slice file stacks from the fossil material and to digitally dissect it using clipping planes of different angles.

For the phylogenetic analysis, a matrix of 14 taxa and 29 characters based on previous works (Aschliman *et al*., 2012; Claeson *et al.,* 2013; Underwood & Claeson, 2017; Villalobos *et al.,* 2019a; b) with modifications made from the specimens described here was assembled in Mesquite 3.31 (Maddison & Maddison, 2018) and analysed (Supplementary materials). For the selection of the outgroups, several batoid groups previously found in close relation to sclerorhynchoids by other phylogenetic analyses were used (rhinopristoids (e.g. *Pristis*) Kriwet, 2004, Claeson *et al.,* 2013, Underwood & Claeson, 2017 and rajoids (e.g. *Raja*) Villalobos *et al.,* 2019a; b). As the specimens described here are mostly composed of rostral and neurocranium remains, the selection of character was focused heavily on these structures, trying to avoid the uncertainty associated with the extensive inclusion of missing data. However, some postcranial skeletal features like the enlargement and shape of the proximal pectoral elements were kept (Char. 1, see supporting information for character discussion), as they provide key features that distinguish sclerorhynchoids from other batoids. For the comparison of the specimens described here, eight sclerorhynchoid genera from which skeletal remains are known are included and compose the ingroup in the analysis. Some tooth features were used, although not extensively, because they would involve further preparation and possible damage to the specimens within the museums. Contingent or reductive coding (Brazeau, 2011) was used as the coding method. Finally, the matrix was analysed using the recently published algorithm of Brazeau *et al.*, (2019) in the R package TreeSearch and compared with the tree resulted from a heuristic search using TNT 1.5 (Goloboff *et al*., 2013).

For the TNT analysis, the command line was used to perform a heuristic search with unweighted characters, which included TBR (tree bisection and reconnection) as search algorithm and stepwise addition of 1000 random replications (see, supplementary material). While for the TreeSearch analysis a script available at 'https://cran.r-project.org/web/packages/TreeSearch/vignettes/inapplicable.html', was followed (see supplementary material for the R script). The clade support was estimated using Jackknife analysis with 1000 iterations was performed in **TreeSearch** supplementary the group support was also estimated for the TNT analysis using frequency differences (Goloboff *et al*., 2013). Two uninformative characters (Chars. 3 and 11) were kept in the analyses, and although they do not provide grouping information, they were map in the resulting phylogenetic tree as they offer interesting discussion points. All character optimisations were mapped on **TreeSearch** and discussed in the Supplementary material.

RESULTS

SYSTEMATIC PALAEONTOLOGY

CHONDRICHTHYES Huxley,1880

BATOMORPHII Cappetta, 1980

RAJIFORMES *SENSU* Naylor *et al*., 2012

†SCLERORHYNCHOIDEI Cappetta, 1980

†*ONCHOPRISTIS* Stromer, 1917

Type species: †*Onchopristis numidus* (Haug, 1905)

DESCRIPTION

†***ONCHOPRISTIS NUMIDUS*** (Haug, 1905)

(Figs. 2-15)

Diagnosis

Sclerorhynchoids of relatively large size (TL ~ 4 m). Rostrum massive and with reinforcements having a triangular shapes. Rostrum consists of tessellated cartilage formed by a layer of small of prismatic (tessellate or mosaic-like) calcified cartilage blocks covered by a layer of fibrous cartilage similar to wood cortex with several vertical, parallel and well mineralised ridges (i.e. 'wood-like' cartilage layer), along the central part of the rostrum and covering the grooves of the ophthalmic nerves. The periphery of the rostrum presents a thick layer of porous cartilage, where enlarge lateral series of rostral denticles attach. Rostral denticles on the lateral series of the rostrum are slender their caps are larger than the peduncle and its apical posterior region present hook-like projections (barbs). The number of barbs varies for 1-3 (one being the most common). The posterior surface of the enlarged rostral denticles presents several well marked ridges (~11) extending from the base and converging at the base of the barb. The denticles anterior face ornamented with smaller ridges that reach the lower third of the cap. The basal bulge is well marked. The peduncle is small with flat and strongly grooved lateral faces. The denticles on the lateral cephalic series do not present barbs and are smaller and wider than the rostrum series and do not present a pulp cavity. Lateral rostral denticles with a large pulp cavity at their base that becomes extremely narrow almost undetectable at the cap. Tooth crown with a large medial cusp and laterally expanded by the lateral shoulders (cusplets). The acute cusp is triangular-shaped bent lingually. On lateral view the labial profile is convex, and the long apron projects anteriorly surpassing the root. The lingual profile is concave with an almost incipient uvula. The root is more prominent than the crown and protrudes laterally, and its vascularisation is holaulacorhize. Large denticles with an enameloid crest on the anterior surface are associated with the body.

Differential diagnosis: Rostral denticles of †*Onchopristis numidus* have an orthodentine filled cap, with a smaller pulp cavity that extends into the denticle cap, whereas the rostral denticles of †*O. dunklei possess* a larger pulp cavity that extends well into the denticle cap with a thin orthodentine layer.

Temporal and spatial distribution

Albian- Cenomanian of Africa (Egypt by Werner, 1989: plate 19-20, 23, 35-38) and Morocco by Cappetta (1980) and the present study).

Etymology

Genus: From the Latin ὄγκος (oncos) referring to the protuberance of on the lateral rostral teeth (barb) and πρίστης (pristis) = saw.

Species: From Numidia the old kingdom bereber, that comprehended (Algeria and part of Tunisia)

Insert figure 2.

Insert figure 3.

Rostrum

The hypertrophied rostrum is robust and triangular-shaped, reaching its widest point at the base and narrowing towards the tip (length: width at base ratio 0.0186) (Figs. 2-3). The base of the rostrum progresses smoothly into the neurocranium. After removal of the sediment, the specimens revealed the presence of a layer of ‘wood-like’ cartilage layer, covering the inner tessellate (mosaic-like) cartilage along the central part of the rostrum. This layer was first observed in †*Onchopristis* by Stromer (1917) and characterised as possible fossilised skin. Later it was described by Cappetta (1980) as the cartilage covering the canals for the ophthalmic nerves in the rostrum. Sternes & Shimada (2019; fig. 2c) describe a similar cartilage type located at the sides of the rostrum of †*Ischyrhiza* next to slight thinker cartilage on the periphery of the rostrum were the lateral rostral denticles are attached.

From the description of the specimens presented here the presence of this wood-like layer seems to be not restricted only the superficial ophthalmic nerve canals, but rather is more widely extended in the rostrum, similar to that observed in †*Schizorhiza* (see Kirkland & Aguillón-Martínez, 2002; fig 8). All three genera present a thick layer of heavily porous cartilage on the sides of the rostrum supporting the lateral series of enlarged of denticles. However, in †*Schizorhiza,* this layer is much less porous on the rostrum margins.

Based on the presence of fully functional (erect) enlarged denticles of different sizes on the sides of the rostrum of †*Onchopristis,* we hypothesise a constant addition of rostral denticles. While †*Schizorhiza,* a rather peculiar sclerorhynchoid, presents a similar rostral morphology which comprises a thin layer of ‘wood-like’ cartilage and a thick lateral layer of cartilage. The differences in the addition-replacement of lateral rostral denticles and rostral anatomy of †*Onchopristis* and †*Schizorhiza*, suggest differences with other sclerorhynchoids in the use of them (i.e. possibly as a hunting tool or a defence mechanism in †*Onchopristis* and †*Schizorhiza*).

Towards the centrum of the rostral cartilages and next to the highly porous lateral layer of cartilage, on both the dorsal and ventral surfaces are two canals, one on each side (Fig. 4A-C). The superficial ophthalmic nerve canal runs on the dorsal surface covered by a layer of cartilage and seems to terminate in a cavity next to the supraorbital crest. On the ventral side, the buccopharyngeal nerve canal terminates at the base of the nasal capsules. Both canals become narrower towards the tip of the rostrum, and in several places, are covered by the 'wood-like' cartilage suggesting that this cartilage entirely covered the canals.

Insert figure 4.

Lateral enlarged rostral denticles

All lateral rostral denticles in specimens NHMUK PV P 75502, IPUW 353500 and IGR 2818, as well as disarticulated denticles recovered from various sites in the "Kem Kem Beds", display a small flat base composed mostly of osteodentine and a large-cap composed entirely of orthodentine, with an external layer of enamel, and a characteristic barb on the apical posterior margin of the denticle. Strongly marked cutting edges, accompanied by rectilinear crests, are developed on both anterior and posterior faces of the denticles (Fig. 5). The presence of these cutting edges and the lack of abrasion patterns on the denticles cap suggest that these denticles were not used to probe in the sediment.

Insert figure 5.

Denticles with multiple numbers of barbs were sporadically collected in Morocco (Fig 6). These denticles have similar dimensions to single barbed denticles, indicating that there is no correlation between denticle size and barb numbers and that the number of barbs is not a function of ontogenetic stages (Fig 6A). The presence of multiple barbed denticles in the Egyptian and Moroccan localities suggests the sporadic development of double and even triple barbed denticles within †*Onchopristis numidus* (Stromer, 1917; plate 1 fig. 9 and 1; Werner, 1989; plate 20, fig. 1a and 1b, 3 and 6-7) including a three barbed specimen (Wegner, 1989; plate 20, fig. 5).

Insert figure 6.

Isolated denticles present various barb sizes despite the similar size of the denticles (Fig. 7C). The difference in barb size associated with the rostral denticles could be related to their position along the rostrum. Therefore, the barb grows with the denticle during its development. Sections and micro-CT scan of denticles revealed a pulp cavity projecting beyond the base and narrowing significantly to a very thin, almost absent canal when it reaches the barb region, suggesting that the barb could reach a fixed size faster than the remaining portions of the denticle cap (Fig 7A-B).

Insert figure 7.

Insert figure 8.

Enlarged denticle series: Different morphologies of enlarged denticles possible attributed to †*Onchopristis numidus* have been reported in Egypt (e.g. Stromer, 1927, plate 1, fig. 30b-32b; Werner, 1989, plate 20, fig 8-9)and were collected in Morocco (Fig. 8A-C) . The presence of one of these morphologies (a barbless and curved denticle) between the jaws of the specimen IPUW 353500 (Fig. 8A) and its morphological similarities with the lateral rostral denticles (i.e. a narrow base composed of osteodentine with several ridges on the sides, well differentiates from the orthodentine filled cap) confirms the presence of multiple series of enlarged denticles in †*Onchopristis numidus*. Its placement in the mouth indicates displacement of the denticle during the taphonomic process (i.e. not preserved in situ). However, from its position and the comparison with those of †*Sclerorhynchus atavus* NHMUK PV P 4776 and *Pristiophorus lanae* (see Welten et al. 2015 figs. 6c and 8e) we hypothesise that this denticle corresponds the lateral cephalic series.

The presence of different enlarged series of denticles in †*Onchopristis numidus* that vary according to their position in the rostral and cephalic regions is similar to that of other sclerorhynchoids (e.g. †*Sclerorhynchus* Welten *et al*., 2015; Underwood *et al.,* 2016). Furthermore, the subsequent lateral section of differently shaped free denticles found in the localities showed no evidence of any projection on their posterior margins (Fig. 8B-C), suggests that the development of the barb is restricted only to the lateral series of the rostrum.

Replacement of enlarged rostral denticles: We identified three different size classes plus a replacement one in the lateral series of enlarged denticles of the rostrum of †*Onchopristis numidus*. With large denticles intercalated with smaller ones and vice versa (i.e. large denticles intercalated with smaller ones) in a single line. This type of arrangement is new in batoids, including Pristidae, in which the single lateral rostral series is composed of a single line of continuously growing rostral denticles. Miller (1974) observed that the size arrangement and number of rostral teeth are established during the embryological stages in *Anoxypristis cuspidata* and *Pristis pristis* Welten *et al.* (2015) propose a similar observation regarding the arrangement and number of rostral denticles in pristioids. However, this last work suggests that if denticles are added, it will be caudally near the base of the rostrum or closer to the tip, but only more pristioids embryonic material will confirm this.

Based on the presence of highly porous cartilages along the sides of the rostrum, and the presence of fully functional denticles of different size classes in †*Onchopristis numidus,* we hypothesise that in this species the denticles are periodically added across the rostrum as it grows and develops over time (Fig. 9). The presence of fully erect small denticles followed by larger ones, as observed in specimen IPUW 353500 and IGR 2818, suggests a seriated appearance of the rostral denticles beginning with smaller denticles and subsequently followed by larger ones (Fig. 9A-B). The three-size cluster of rostral denticles with a mirrored arrangement (i.e. similar-sized denticles placed on opposite sides in dorsal view) recognised in IGR 2818, is interpreted as the result of synchronised development on both sides of the rostral denticles. This mirroring pattern is unnoticeable or less conspicuous at the tip of the rostrum, probably because it is a more fragile region and denticles in this area could be more susceptible to fracture due to taphonomic processes. The presence in both specimens (IPUW 353500; IGR 2818) of small denticles (G1) and larger denticles (G2 and G3) with fully enamelled caps suggest that denticles do not gradually grow, but instead that larger denticles are periodically added as the animal grows (Fig. 9C). Both the arrangement and addition sequence are different from other sclerorhynchoids (e.g. Sternes & Shimada, 2019; Welten *et al.,* 2015; Underwood *et al.,* 2016; Smith *et al.,* 2015).

Overall this arrangement is somewhat similar to that observed in *Pristiophorus* (Welten *et al.,* 2015 and Underwood *et al.,* 2016). With some differences: we were unable to see a difference in the degree of mineralisation between older and younger denticles observed in *Pliotrema warreni* by Welten et al. (2015) in the rostral denticles of †*Onchopristis numidus* as both small and large denticles present a cap densely fill with orthodentine. Furthermore, the triplet arrangement is no entirely followed in †*Onchopristis numidus* in cases of replacement denticles of the same size as those of the occurring generation are added in the space, giving a similar organisation to that reported in other species of sclerorhynchoids (e.g.

†*Sclerorhynchus*, Welten *et al.,* 2015), in which some replacement denticles are so closely associated with the existing functional ones that they seem to appear in pairs (Fig. 2, denticles marked with an arrow)

Insert figure 9.

Insert figure 10.

Neurocranium

Only the postnasal region and part of the posterior edge of the nasal capsules can be addressed here, as the most anterior part of the nasal capsules is missing. The neurocranium is box-like and rectangular shaped, with an oval-shaped precerebral fenestra located near the base of the rostrum at the centre of the anterior part of the neurocranium (Fig. 10). The dorsal surface of the left nasal capsules is not discernible, because it is heavily crushed. In ventral view, the posterior region of the right nasal capsule is preserved and presents a deep nasal fenestra that smoothly progresses into the rostrum. The buccopharyngeal nerves cavities are located on the ventral surface anterior to the nasal capsules (Fig, 11 A-B).

The profile of the antorbital cartilage is triangular, with its narrow distal edge pointing posteriorly and its wide proximal edge articulating with the nasal capsule (Fig. 11 A-B). Even though the neurocranium presents some crushing dorsoventrally, the supraorbital crest stands above the dorsal surface of the chondrocranium and does not cover the eye cavity. The orbital cavity is large and houses a well mineralized optic peduncle; additional nerve foramina were not observed (Fig. 11 C-D). Next to the supraorbital crest is the cavity for the superficial ophthalmic nerve (Fig. 10 B). The postorbital region is rectangular and narrow with a small triangular postorbital process. In the otic region, the orbital fissure is above the lateral commissure and below the postorbital crest. The lateral commissure covers part of the

446 hyomandibular branch of the facial nerve foramen (Fig. 11 C-D). The lymphatic foramina are
447 present in the posterior part of the neurocranium. The jugal arches follow the otic region and
448 are located anteriorly to the occipital condyles which are well developed and expanded laterally
449 forming a broad and deep articulation facet for the anterior lateral process of the synarcual
450 (Fig.10).

451

452 *Hyomandibula*

453 The hyomandibula is triangular shaped (length: width at base ratio = 0.51, length: width
454 at tip ratio = 0.018), with its proximal end articulating to the neurocranium, and its narrow
455 distal end connected between the palatoquadrate and Meckel's cartilages. A section of the
456 dorsal surface of the hyomandibula is missing; however, the remaining parts are slightly
457 elevated, which could indicate the presence of a process for muscle articulation. (Fig 10).

458

459 Insert figure 11.

460

461 *Jaw cartilages*

462 Only part of the Meckel's and palatoquadrate cartilages are observable in ventral view
463 (Fig. 11 A-B). The palatoquadrate is thin and narrows progressively towards the symphysis
464 (Fig. 11 A-B). In ventral view, there is no clear articulation with the neurocranium, the
465 Meckel's cartilage and palatoquadrate are present, and both jaw elements seem to be supported
466 by the hyomandibula. The palatoquadrate and Meckel's cartilage antimeres are not fused and
467 connected at the symphysis. The Meckel's cartilage is wider than the palatoquadrate but also
468 becomes narrower towards the symphysis (Fig. 11 A-B).

469 *Oral teeth*: Teeth of †*Onchopristis numidus* have been figured multiple times (e.g. by
470 Stromer, 1927, plate I, figs 1-4, under the name †*Squatina aegyptiaca*; by Werner (1989, plates

35-37), under the name †*Sechmetia aegyptiaca.* The teeth figured on plates 21 & 22 by Werner (1989) and described as †*Onchopristis,* probably belong to a different sclerorhynchoid such as †*Renpetia*) and are similar to those of †*O. dunklei* (Welton & Farish, 1993; Kriwet & Kussius, 2001,text-fig. 4; Cappetta, 2012; Fig. 370M-R; Vullo *et al*., 2003: pl. 2, fig. 6).

Both species have teeth with a sharp and acute cusp, that bent lingually (Fig. 12 C, G, K; Fig. 13 J, L). The labial apron is narrow, with a blunt distal edge that projects anteriorly and surpasses the root and present pair of incipient lateral cusplets (Fig. 12 A, E; Fig. 13 O, K, S). Several teeth collected in Morocco present a double-lobed labial apron (Fig. 12 A, E, D, H). Some teeth also have a cutting edge on the labial and lingula crown faces (Fig. 13 A-E). All teeth display well developed cutting edges, which are continuous between the cusp and lateral cusplets (Fig. 12; Fig. 13 J, L). The lingual uvula is absent (Fig 12 C, G), and the root is bilobed and laterally projected (Fig. 12 B, F; Fig. 13 P).

Cross-sections of the oral teeth revealed the presence of a large pulp cavity in the root that extends apically into the crow where it becomes narrower as it progresses towards the apex (Fig. 13 G, K, R.).

Insert figure 12.

Insert figure 13.

Synarcual

Only the anterior part of the synarcual is preserved, which presents a well-developed odontoid process (synarcual lip) that forms part of the articulation surface for the synarcual with the neurocranium along with the extensive anterior lateral process that mirrors the odontoid processes in the neurocranium. This process and the depth of the odontoid process suggest a close and not very mobile articulation with the neurocranium (Fig. 14). The central portion of the synarcual is well developed displays some spino-occipital foramina (the actual number remains unknown as only a portion of the synarcual is preserved). The medial crest anterior part is missing; however, is remaining portions are thin and well developed, and seems to have been folded during taphonomic processes. Only the right lateral stay is visible, and it becomes progressively narrower backwards. Its distal end is well developed and flattened, and it probably was dorsally directed during life (Fig. 14 A-B). In ventral view, no vertebral centra are observable, which suggests that the vertebra centra did not pass the midpoint of the synarcual (Fig. 14 C-D), as in other sclerorhynchoids (Villalobos *et al*., 2019a)

Insert figure 14.

Vertebrae

The vertebral centra of †*Onchopristis* consist of the corpus calcareum and the intermedialia as in other chondrichthyans. The corpus calcareum is well mineralized and shows clear and opaque bands suggesting a cyclical deposition of mineral. Whether this pattern was seasonal as in other chondrichthyans, remain ambiguous for the moment (Fig. 15).

Insert figure 15.

Dermal denticles

The rostrum also presents a small series of denticles at the base of the enlarged rostral denticles and on the ventral surface (Fig. 16 G). Two morphologies are present, both with a rounded well enamelled cap and a stellated base with fringes that projects just out below the cap and can be distinguished by the presence of a central cusp (Fig. 16 A-F).

Insert figure 16.

As in other fossil assemblages (Werner, 1989), the occurrence of †*Onchopristis* in the "Kem Kem Beds" coincides with that of "*Peyeria*-like" denticles (Fig. 17). Cappetta (2012) noted that these two batoids are commonly found together, proposing that †*Peyeria* Werner, 1989 was, a synonym of †*Onchopristis* and the †*Peyeria* remains were, in fact, dermal denticles of †*Onchopristis.* Recently, similar enlarged dermal denticles were reported for †*Ischyrhiza mira* Leidy, 1856 by Sternes & Shimada (2019) in Campanian–lower Maastrichtian of Tennessee and Alabama, U.S.A, suggesting that this feature might be even more common among sclerorhynchoids. The presence of these types of enlarged body denticles in Morocco agrees with Cappetta (2012) and Sternes & Shimada (2019) interpretations.

†*O. numidus* dermal denticles found in Morocco are unique among sclerorhynchoids (Werner, 1989, plate 41, figs. 1-4; Sternes & Shimada, 2019, text-fig. 4e-f). They present a thick enameloid layer on the anterior edge of the denticles. Additional cross-sections revealed a small pulp cavity followed by a thin, not very porous laminar layer, on which a thick layer of highly vascularised osteodentine that reaches the tip of the denticle is deposited (Fig. 17 C).

Insert figure 17.

PHYLOGENETIC ANALYSIS

Insert figure 18.

The character matrix for the phylogenetic analysis used here is a modified version from that used by Villalobos *et al.* (2019b). The main changes include recoding of the polymorphic characters 5, 6 and 9, which were changed for *Raja* and *Amblyraja* (see supplement material; Character discussion). These features refer to the absence/presence of malar thorns, which are developed only in male rays (Aschliman *et al.,* 2012). Three different coding schemes were considered for these characters, that included removing those characters, leaving them as a polymorphic character and coding them as presence, small topological changes resulted from these different codifications (supplement material). However, we consider that regardless of the sexual dimorphism link of these characters, the malar thorns are features that correspond to the genera and should be coded as present.

Character 20 (absence/presence of a differentiated lateral uvula on the teeth), was changed for *Anoxypristis* to present as its teeth show a variably developed lateral uvula (e.g. Underwood *et al.,* 2011; Cappetta, 2012), but in general, seems to be present.

Character 24 (absence/presence of a lingual uvula in the teeth) was changed for †*Ptychotrygon*, following the observations made on †*Ptychotrygon rostrispatula* by Villalobos *et al.* (2019b) and four characters were included (Chrs. 25-29) to increase the morphological variance observed within sclerorhynchoids.

The TNT analysis recovers 13 most parsimonious trees of 41 steps with a consistency index of 0.78 and a retention index of 0.85, whereas the TreeSearch analysis recovered a 41 steps tree. Both strict consensus trees (Treesearch and TNT) place all sclerorhynchoids taxa, including †*Schizorhiza* into a polytomy (Fig. 18 A-B, clade support Cs (strict) = 74%, Cs (majority) = 40%). In both strict consensus and majority rule trees this clade is supported by one shared feature, the lack of a rostral appendix (Fig. 18 A, Character (Chr.) = 25, 0, Consistency index (Ci) = 1) which refers to the absence of thin cartilage attached to the rostrum (see, character discussion in supplementary material). We do not give this character the statue of synapomorphy~~,~~ ~~yet~~ as a comparison within a larger phylogenetic context is needed. However, the compared anatomy of the process occurring within sclerorhynchoids is unique. In Myliobatiformes, the rostral appendix is polymorphic some groups present it (e.g. *Urotrygon* and *Potamotrygon*) and others do not (e.g. *Rhinoptera* and *Zanobatus*) the development of this structure in Myliobatiformes corresponds to the anteromedial growth of the trabecula (i.e. rostral shaft or rostral cartilage) (Miyake *et al*., 1992). In platyrhinoids, the appendix is also absent, but again they lack the mid growth of the trabecula, plus these taxa development of a rostral process (McEachran & Aschliman, 2004; Aschliman *et al*., 2012). Within torpedinoids, the development of rostral cartilages varies with different embryonic cartilages participating in the formation of the rostral cartilages ~~depending on the group~~ (e.g. In Torpedo is the lamina orbitonasalis whereas in *Narcine* is the trabecula with different chondrification periods) (Miyake *et al*., 1992). In comparison, the process seen in sclerorhynchoids seems to be simpler, with rostral cartilages with a good anteromedial growth with no apparent rostral appendix (similar to that of sawsharks). Thus, we consider this feature a convergence between sclerorhynchoids and sawsharks, considering the anatomical differences between these shark and batoid groups (i.e. presence of synarcual and antorbital cartilages). The sclerorhynchoid clade is placed in a sister relation to the Rajidae (*Amblyraja* and *Raja*, Fig. 18 A-B, Cs = 80%). Both sclerorhynchoids and Rajidae from a monophyletic group Rajidae + Sclerorhynchoids (Fig. 18 A-B, Cs (strict) = 90%, Cs (majority) = 44%), which is supported by four shared features in the majority rule tree and one in the strict consensus (Fig. 18 A). Both tress place the lack of differentiated lateral uvula (Fig. 18 A, Character (Char.) = 20, 0, Ci = 1) as a shared synapomorphy (see, character discussion in supplementary material). It is worth mentioning that sclerorhynchoids are not the only batoids which lack these projections. We added this observation as in sclerorhynchoids both durophagous (e.g. †*Asflapristis*), and more generalist (e.g. †*Onchopristis*) taxa lack these projections suggesting more than just an adaptation to a diet as the absence of these projections. Furthermore, one other feature already suggested as synapomorphies for the Rajidae + Sclerorhynchoids clade by previous analysis (Villalobos *et al.,* 2019a) is recovered again by the majority rule tree (MRT) the fusion between the second hypobranchial and basibranchial. However, as in previous analyses, the lack of observations continues to hinder its placement as a synapomorphy for the group (Villalobos *et al.,* 2019a; b).

Within the sclerorhynchoids clade, two monophyletic groups are recovered (Fig. 18 A) supported by the strict consensus tree estimated by the TreeSearch analysis and one by TNT. Both analyses coincide in the placement of †*Onchopristis*, and †*Ischyrhiza* (Fig. 18 A-B, Cs (strict) = 81%, Cs (majority) = 91%) in a monophyletic group, a relation supported by one common synapomorphy in both strict consensus and majority rule tree: The presence of smaller denticles with a round cap associated with the base of the rostral denticles (Fig. 18 A, Character (Char.) = 28, 1, Ci = 1). The majority rule recovered two more possible synapomorphies, the reason why this characters are not considered a synapomorphy and do not appear in the strict consensus tree (Fig. 18 A) is that the ambiguity that rises from the coding in †*Schizorhiza* (?) for character 18 (Ci = 1) and the collapse of the †*Libanopristis*, †*Micropristis*, †*Sclerorhynchus*, †*Ptychotrygon* and †*Asflapristis* clade (Fig. 18 A-B, Cs (majority) = 74%) for character 6 (Ci = 1). Of the features, the presence of large denticles associated with the body (Char. 18, 1) is a significant one a †*Onchopristis* and †*Ischyrhiza,* as they are currently the only sclerorhynchoids presenting this feature, supporting the closer relationships found between these taxa by the present analysis.

The strict consensus tree estimated with the TreeSearch analysis is better resolved than that of the TNT analysis, recovering another monophyletic group that includes †*Asflapristis* +

†*Ptychotrygon* (Fig. 18 B, Cs (strict) = 91%, Cs (majority) = 81%). Three features support the relation (see MRT, Fig. 18 A); (1) lack of enlarged denticle series associated to the rostral cartilages (Char. 7, 0, Ci = 1), (2) presence of a transversal crest on teeth (Char. 17, 1, Ci = 1) and (3) lack of calcified suprascapula (Char. 22, 0, Ci = 0.5) (see, character discussion in supplementary material).

DISCUSSION

Measurements established from other studies on Pristidae (e.g. Morgan *et al*., 2011; Whitty *et al*., 2014) and those made on †*Libanopristis hiram* (NHMUK PV P 75075) and †*Ptychotrygon rostrispatula* (NHMUK PV P 73630, 75496), suggest an approximate proportion between the length of the rostrum and the standard length to range from 21-30% in sclerorhynchoids. This scaling suggests that the specimens of †*Onchopristis* described here had an estimated total body length of 2.94 - 4.25 metres (m) for IPUW 353500 and 2.21-3.15 m for IGR 2818. This size in comparisons to modern Pristidae and Rhynchobatidae of similar post rostral lengths suggest a weight of 70-150 kg.

The present study aimed to evaluate the phylogenetic relations of †*Onchopristis* within sclerorhynchoids. As such, some batoid groups were not included (e.g. torpedinoids, platyrhinoids and myliobatoids). We ignore these groups in the analysis because no previous phylogenetic analysis has established a close relationship between them and sclerorhynchoids (Claeson *et al.,* 2013; Underwood & Claeson, 2017; Villalobos *et al.,* 2019a). However, when interpreting the main features that distinguish †*Onchopristis* and sclerorhynchoids, we include them to give a broader perspective (see, phylogenetic analysis section). The sawsharks were not included in the present analysis, because morphological features like the presence synarcual and antorbital cartilages suggest a clear batoid affiliation for †*Onchopristis.*

As both specimens described here are mainly composed of rostral and cranial characters, the selection of features focused on these structures to avoid uncertainties in the phylogenetic analysis, related to the extensive inclusion of missing characters (?) that will ultimately affect the resolution of the analysis. Thus, the use of other anatomical features (e.g. pelvic and pectoral girdles) was avoided.

The topologies recovered by the present analyses suggest that a different taxonomic affiliation for †*Onchopristis* and †*Ischyrhiza* could be proposed. Both analyses place these genera previously associated with †Sclerorhynchidae (Cappetta, 2012) in a monophyletic group separated from the reaming sclerorhynchoids with relatively good group support (TreeSearch: Fig. 18 B, Cs (strict) = 81% and Cs(majority) = 91%; TNT: Fig 18 A, Cs = 82)(see, TNT log in supplementary material). Based on this, and the combination of characters present by these two genera, we propose the family †Onchopristidae. Which is characterised by the following features: (1) a very peculiar rostral morphology with a thick lateral layer of porous cartilage on the sides of the rostral cartilages, where the enlarge denticle lateral series attach (Character (Char) = 4, 1, Consistency index (Ci) = 1); (2) an external layer of "wood-like" cartilage in the centre of the rostrum (Char = 2, 1, Ci = 1 and Char = 3,1, Ci = 1); (3) the presence of large denticles in the body (also see, Sternes & Shimada, 2019) (Char = 18, 1, Ci = 1); (4) the presence of smaller denticles with a round cap associated with the base of the rostral denticles (Char = 28, 1, Ci = 1); (5) two series of enlarged denticles with acute cap associated with the latera regions of the rostrum and head (Char 6, 1, Ci = 1).

There are some uncertainties concerning the taxonomic hierarchy of the ptychotrygonoids. Villalobos *et al.* (2019b) suggest a placement within the Sclerorhynchidae family, based on similarities in their tooth morphology with those of †*Libanopristis* (i.e. present transverse crests in the labial apron, see Cappetta, 1980b, text-fig 7 B; 2012, text-fig. 368 I, in present analysis character 17). However, the teeth of †*Libanopristis* present a more prominent cusp, and the labial apron is less ornamented than that of ptychotrygonoids. In †*Ptychotrygon* there is a deep central interlocking depression. Cappetta (1980) also indicated a lingual depression for some teeth of †*Libanopristis hiram*, but there are no clear illustrations, and we were unable to determinate if he refers to the lingual profile of the cusp below the apex or a region on the lingual uvula. Considering the present results, where ptychotrygonoids form a monophyletic group in by the strict consensus of TreeSearch with relatively high support (Fig. 18 B, Cs (strict) = 91% and Cs(majority) = 81%), a similar arrangement to †Onchopristidae is proposed for the †*Ptychotrygon* and †*Asflapristis* clade resurrecting the family †Ptychotrygonidae *sensu* Kriwet *et al*. (2009). The TNT majority rule tree and the clade support analysis corroborates this placement (Fig. 18 A Cs = 31). †Sclerorhynchidae and †Ptychotrygonidae, are differentiated from each other by the presence or absence (depending on the group) of enlarged denticle series associated to the rostrum (lateral and both ventral (lateral and central) series (Char = 7, Ci = 1, Char = 8, Ci = 1) and the highly ornamented teeth of †Ptychotrygonidae, which includes the presence of transversal crest on teeth (Char = 17, 1, Ci = 1).

Whether ptychotrygonoids are considered a separate family or not makes no difference phylogenetically. The same could be said for †Onchopristidae, as both groups form part of a monophyletic group. However, their taxonomic identification is needed, as it helps the definition of sclerorhynchoids, facilitates the approach for future studies and improves the current understanding of the group. Furthermore, we believe that there is enough evidence to support the taxonomical differentiation of the two groups into two families.

According to the present analyses, the genus †*Schizorhiza* should be placed within the Sclerorhynchoidei. The presence of a thick lateral layer of cartilage on the sides and the external layer of “wood-like” cartilage in the rostrum suggest its classification within †Onchopristidae. However, considering that no cranial, nor enlarge denticles of the body are known, and the highly specialised replacement pattern of the lateral series of rostral denticles is different, its phylogenetic relations are uncertain for the moment.

CONCLUSION

Currently, two species are assigned to †*Onchopristis*: †*O. numidus* and †*O. dunklei*, both of which seem to be restricted to the Early to 'mid' Cretaceous (Barremian-Cenomanian). These two species possess remarkably similar oral tooth morphologies, differentiated by the internal structure of the enlarge rostral denticles. The rostral denticles of †*Onchopristis numidus* have an orthodentine filled cap, with a smaller pulp cavity that extends into the denticle cap, whereas the rostral of †*O. dunklei* presents a larger pulp cavity that extends well into the denticles cap and a thin orthodentine layer (McNulty & Slaughter, 1962, text-fig. 1c).

The rostral remains described here confirm previous hypotheses to include †*Onchopristis* within the Sclerorhynchoidei (Cappetta, 1987; 2006; 2012), as suggested by its peculiar neurocranial anatomy with a rectangular shape of the post-nasal region, a reduced post-orbital process and anterior fenestra located at the base of rostral cartilages. Previous genus affiliations to the family Sclerorhynchidae are doubtful and not supported here, as the rostral anatomy and addition and arrangement of the enlarge rostral denticle series are different from other members of the group (e.g. †*Sclerorhynchus* and †*Libanopristis*) and resembles that of †*Ischyrhiza*.

TAXONOMIC IMPLICATIONS

Following these results, three families are suggested within Sclerorhynchoidei (†Sclerorhynchidae, †Onchopristidae and †Ptychotrygonidae) based on the differences in their rostral cartilages and dental morphologies. Within this arrangement the family †Onchopristidae is proposed, leaving the taxonomic classification for †*Onchopristis numidus* as follows.

CHONDRICHTHYES Huxley,1880

BATOMORPHII Cappetta, 1980

RAJIFORMES *SENSU* Naylor *et al*., 2012

†SCLERORHYNCHOIDEI Cappetta, 1980

†ONCHOPRISTIDAE fam. nov.

†*ONCHOPRISTIS* Stromer, 1917

†*Onchopristis numidus* (Haug, 1905)

Diagnosis of †Onchopristidae: Sclerorhynchoid group with a very peculiar rostral morphology, that includes a thick lateral layer of porous cartilage on the sides of the rostral cartilages, where the enlarge denticle lateral series attach. Rostral centre and superficial ophthalmic nerve canal covered with an external layer of “wood-like”. Two series of enlarged denticles with acute cap associated with the latera regions of the rostrum and head, of which the latera rostrum series shows smaller denticles with a round cap associated with their base. Large denticles are associated with the body (also see, Sternes & Shimada, 2019 for †*Ischyrhiza*).

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Figures.

Figure 1. [168mm] A. Rostral remains figured in Stromer (1925; TL 1450 mm). B-C. Rostral remains figured in Stromer (1917; B, TL. 260 mm. C, TL. 520 mm).

Figure 2. [168mm] A, Cranial and rostral remains of †*Onchopristis numidus* (IPUW 353500). B, Interpretative line drawing of the specimen remains. Denticles in pair arrangement marked with an arrow. Scale bar: 5cm.

Figure 3. [168 mm] A, Cranial and rostral remains of †*Onchopristis numidus* (IGR 2818). B, line drawing of the specimen remains (darken areas represent rock matrix). Denticles in pair arrangement marked with an arrow. Scale bar: 10 cm.

Figure 4. [168 mm] A-C, Rostrum of †*Onchopristis numidus*. A, Ventral surface of IPUW 353500. B, Dorsal surface of IPUW 353500. C, NHMUK PV P 75502. Scale bar:1cm.

Figure 5. [168 mm] Enlarged rostral denticles of †*Onchopristis*. A–C, micro-CT-based volume rendering of denticle collected along with the specimen IPUW 353500 from Morocco: (A) dorsoventral, (B) anterior, and (C) posterior view. D–G, denticles collected Egypt (Werner, 1989; plate 19, figs. 2a-d): (D) posterior view, (E) dorsoventral, (F) anterior, and (G) base. Scale bar: 1mm.

Figure 6. [168 mm] A and C Rostral denticles with multiple barbs bought in Morocco. A, Denticle composed of two different denticles brought from a fossil dealer in

Morocco NHMUK PV P74053. B, Sagittal section of denticle, the section where the denticles were glued marked with an arrow (single barb base attached to a double barbed tip denticle). D, Sagittal section of denticle in C that revealed no modifications NHMUK PV P74053. Scale bar: 1 cm.

Figure 7. [168 mm] Rostral denticles of †*Onchopristis numidus* found in the "Kem Kem Beds" NHMUK PV P74045. A, CT scan of denticles (scale bar: 1mm). B, Transverse section of denticle (scale bar: 2 mm). C Lateral section of the tip of rostral denticles. D-E, Smaller denticles with different barb sizes (scale bar: 1cm).

Figure 8. [168 mm] A, Mouth of †*Onchopristis numidus* (IPUW 353500). B, Close up view of enlarged denticle in the mouth. C, Disarticulated denticles with similar morphology found in the "Kem Kem Beds" collection sites: KK1 (easting: 382819, northing: 3501936 UTM) and KK3 (easting: 416828, northing: 3418567 UTM). Scale bar: 1cm.

Figure 9. [168 mm] Fragment of the rostrum of †*Onchopristis numidus*. A, IPUW 353500 (scale bar: 1cm). B, NHMUK PV P 75503 (scale bar: 5cm). C, Hypothetical scheme of the growth and addition of rostral denticles in †*Onchopristis*. Denticles in grey in figure C are larger denticles replacing smaller ones that fell.

Figure 10. [168 mm] A-B, Neurocranium of †*Onchopristis numidus*. A, picture of IPUW 353500. B, line drawing. C, picture of IGR 2818. D, line drawing. Scale bar 4 cm. Note: darken areas on drawing represent sediments.

Figure 11. [168 mm] Neurocranium of †*Onchopristis numidus* (IPUW 353500). A, Ventral view. B, Line draw. C, Lateral view. D, Line draw. (A-B, scale bar: 2 cm). (C-D, scale bar: 5 cm).

Figure 12. [168 mm] A-L. Oral teeth of †*Onchopristis numidus* found in the "Kem Kem Beds", collection site Boulalou (KK5: easting: 418413, northing: 3479178 UTM, zone: 30) NHMUK PV P 74050. M-N Teeth extracted from the preparation of specimen IPUW 353500.

(A, E, I, D, H, L, M and N) Labial face. (B, F and J) root. (C, G, and K) profile view. Scale bar: 2mm.

Figure 13. [168 mm] Micro-CT-based volume renderings and virtual sections of oral teeth of †*Onchopristis numidus* found associated with IPUW 353500. A–E, broken main cusp in (A) labial, (B) occlusal, (C) lingual, (D) medial, and (D, E) profile views. F–L, incomplete tooth lacking part of the labial apron and root in (F) labial, (H) lingual, (I) apical, and (J, L) profile views; tooth sections in (G) axial and (K) sagittal aspects; M–S, tooth with a broken main cusp in (M) labial, (N) lingual, (O), occlusal, (P) basal, and (Q, S) profile views tooth section in (R).

Figure 14. [168 mm] Synarcual of †*Onchopristis numidus* (IPUW 353500). A, dorsal view. B, line draw. C, ventral view. D, line draw. Scale bar: 5 cm.

Figure 15. [168 mm] A-B. Vertebral centra of †*Onchopristis numidus* from the "Kem Kem Beds" Collection sites Boulalou (KK5: easting: 418413, northing: 3479178 UTM) NHMUK PV P 74052. (A-B) Sagittal section of vertebra. (C) Articulation surface of the vertebra. Scale bars: 1 cm.

Figure 16. [168 mm] A-F Ventral rostral denticles from the section of the rostrum of †*Onchopristis numidus* (NHMUK PV P 75502). A-C, Morpho 1. D-F, Morpho 2 (scale bar: 2mm) NHMUK PV P 74051. G, anterior part of the ventral surface of IPUW 353500 rostrum (scale bar: 1cm).

Figure 17. [168 mm] Enlarged dermal denticles of †*Onchopristis numidus* from the "Kem Kem Beds". A-C. B-C, C.U personal collection, longitudinal section and close-up of the enameloid layer C.U personal collection, lateral view. D-F, IGR 2819, lateral, anterior and basal views. G, IGR 2820, lateral view. H, IGR 2821, antero-apical view. Scale bars: 1 cm.

Figure 18. [168 mm] Phylogenetic trees recovered by the different analysis used in the present study. (A) strict consensus and majority rule trees produced by the TNT analysis. (B) strict consensus and majority rule trees produced by the TreeSearch analysis: Clade support values

from the Jackknife analysis displayed inside the parenthesis. Character supporting nodes of TNT's majority rule tree (MRT): Black circles characters recovered by both consensus methods; White circles characters recovered only by MRT.

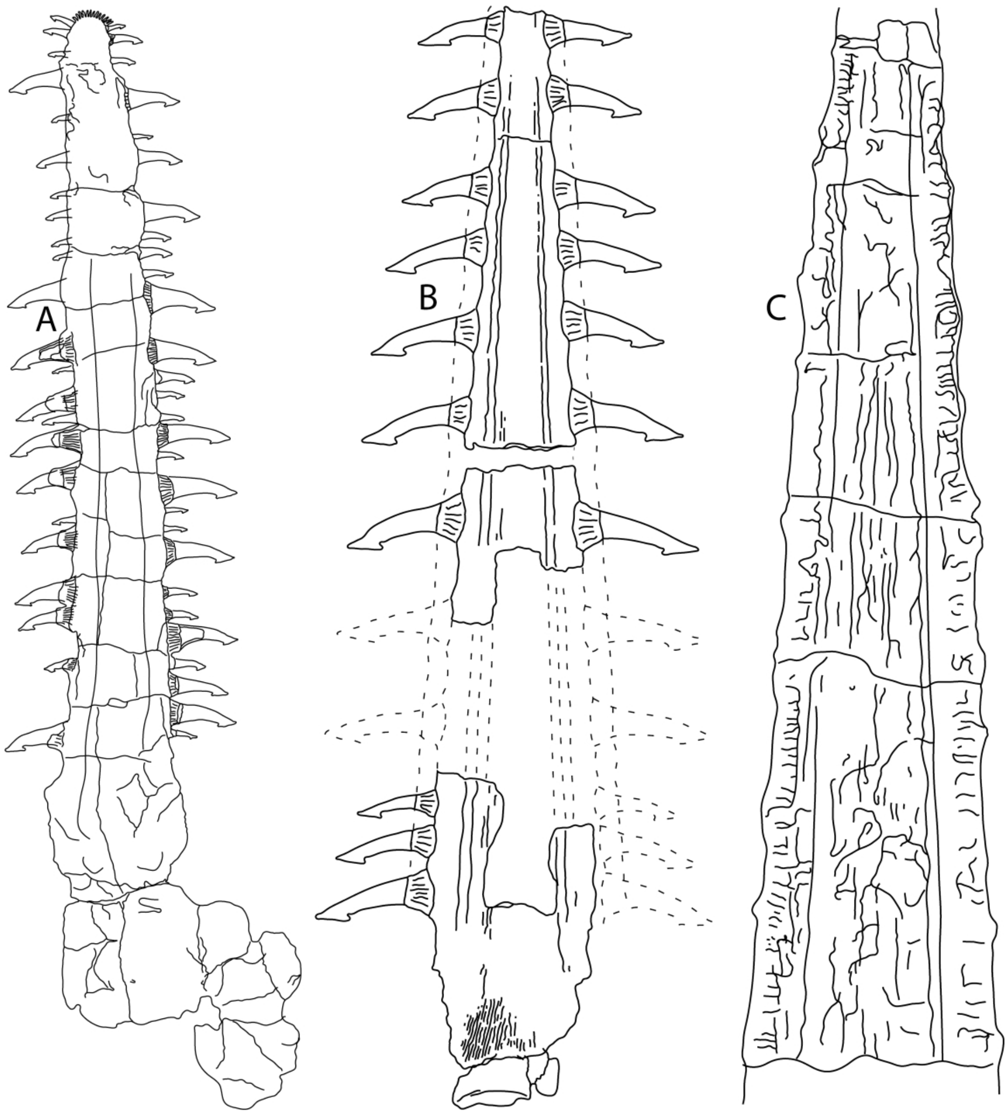

Figure 1. A. Rostral remains figured in Stromer (1925; TL 1450 mm). B-C. Rostral remains figured in Stromer (1917; B, TL. 260 mm. C, TL. 520 mm).

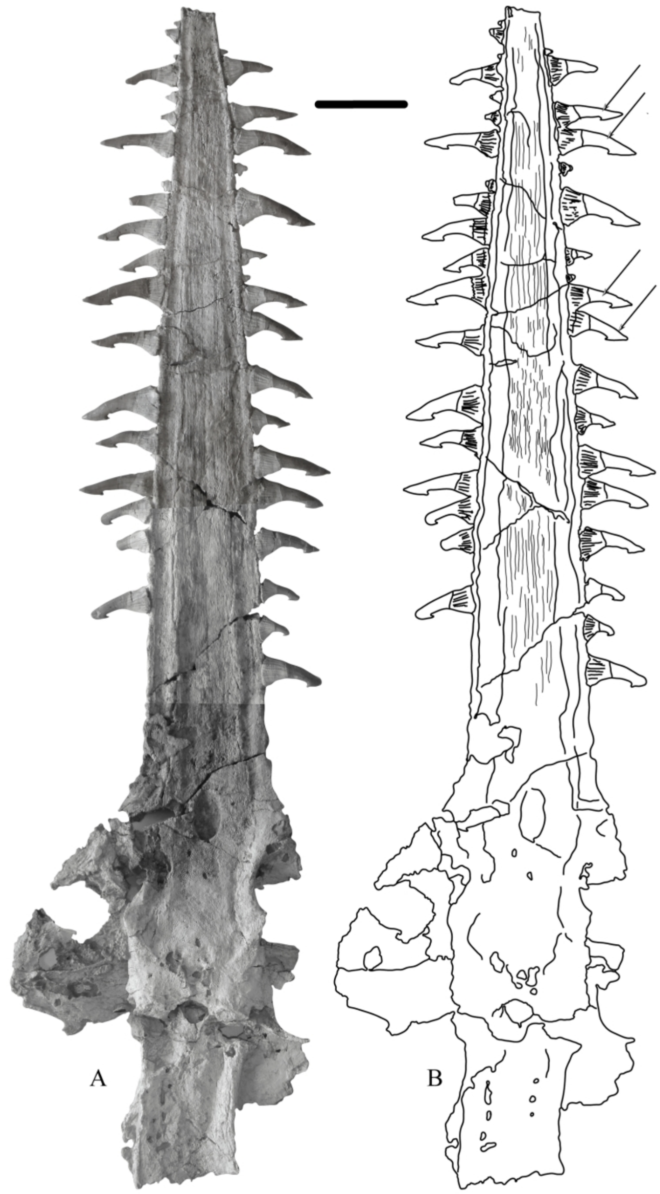

Figure 2. A, Cranial and rostral remains of †*Onchopristis numidus* (IPUW 353500). B, Interpretative line drawing of the specimen remains. Denticles in pair arrangement marked with an arrow. Scale bar: 5cm.

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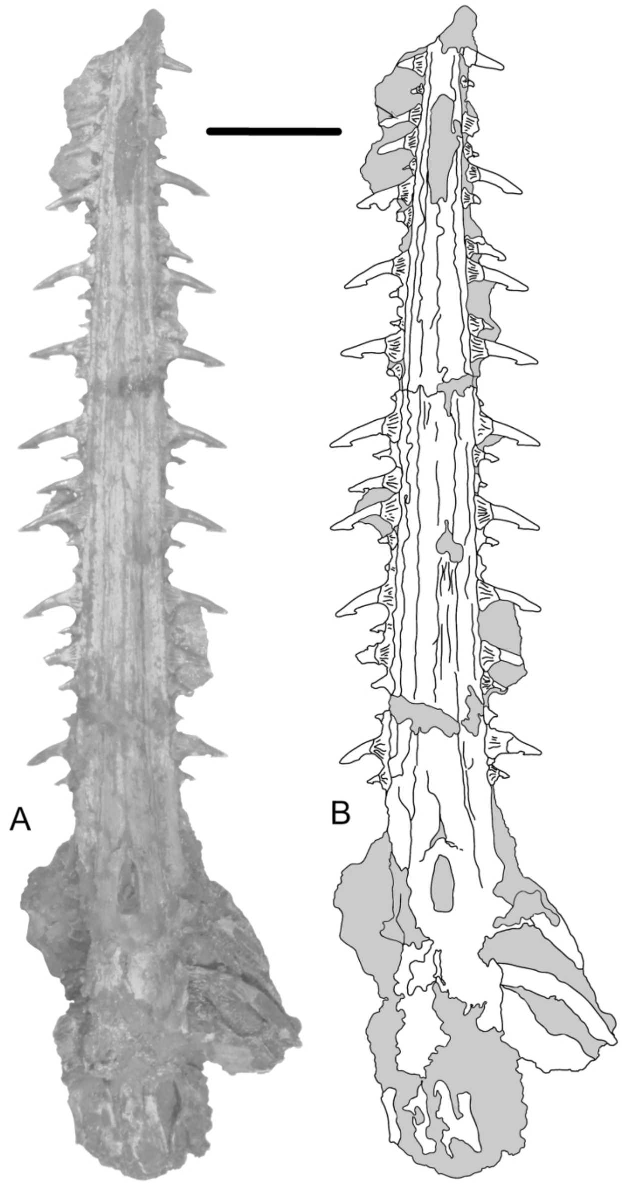

Figure 3. A, Cranial and rostral remains of †*Onchopristis numidus* (IGR 2818). B, line drawing of the specimen remains (darken areas represent rock matrix). Denticles in pair arrangement marked with an arrow. Scale bar: 10 cm.

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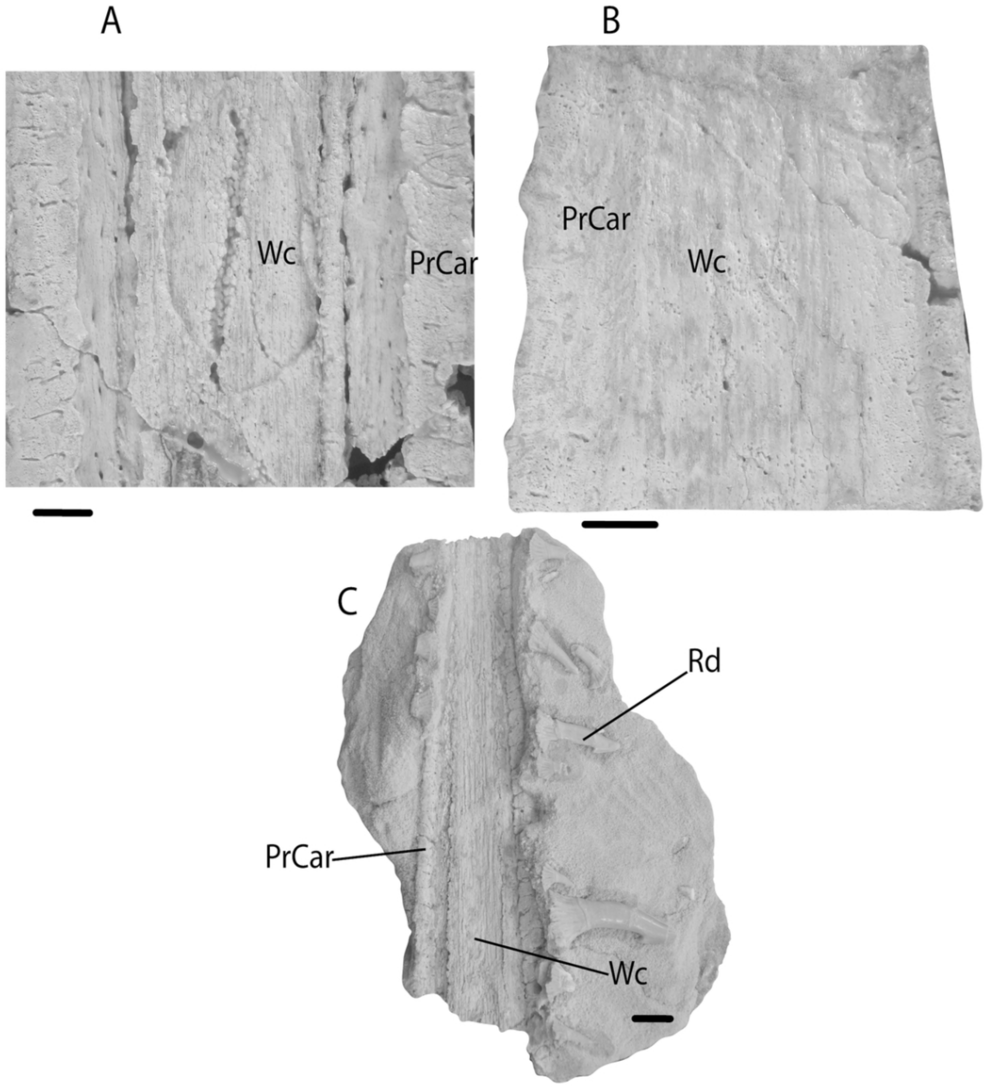

Figure 4. A-C, Rostrum of †*Onchopristis numidus*. A, Ventral surface of IPUW 353500. B, Dorsal surface of IPUW 353500. C, NHMUK PV P 75502. Scale bar:1cm.

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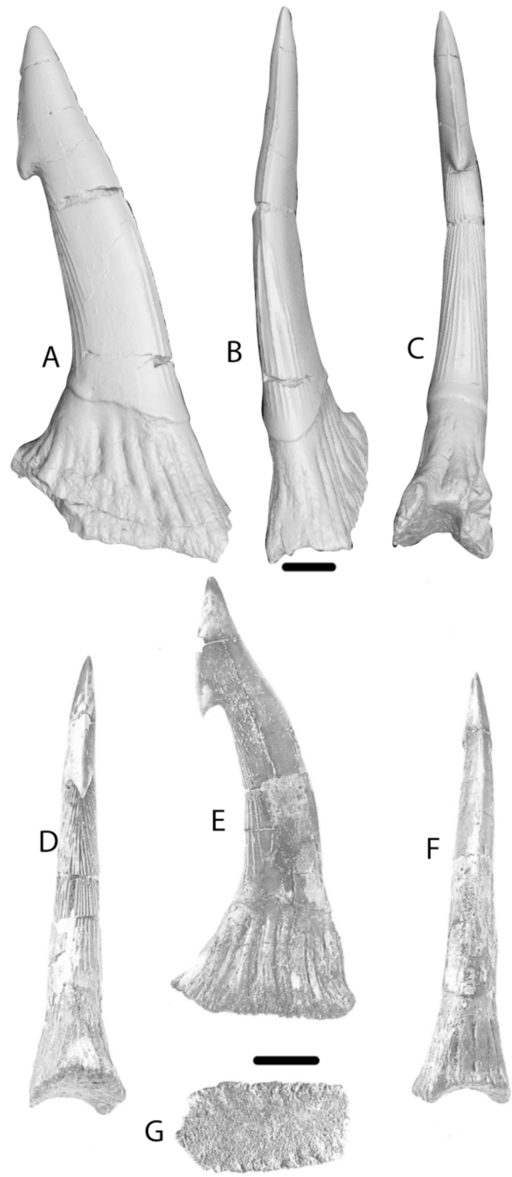

Figure 5. Enlarged rostral denticles of †*Onchopristis numidus*. A–C, micro-CT-based volume rendering of denticle collected along with the specimen IPUW 353500 from Morocco: (A) dorsoventral, (B) anterior, and (C) posterior view. D–G, denticles collected Egypt (Werner, 1989; plate 19, figs. 2a-d): (D) posterior view, (E) dorsoventral, (F) anterior, and (G) base. Scale bar: 1mm.

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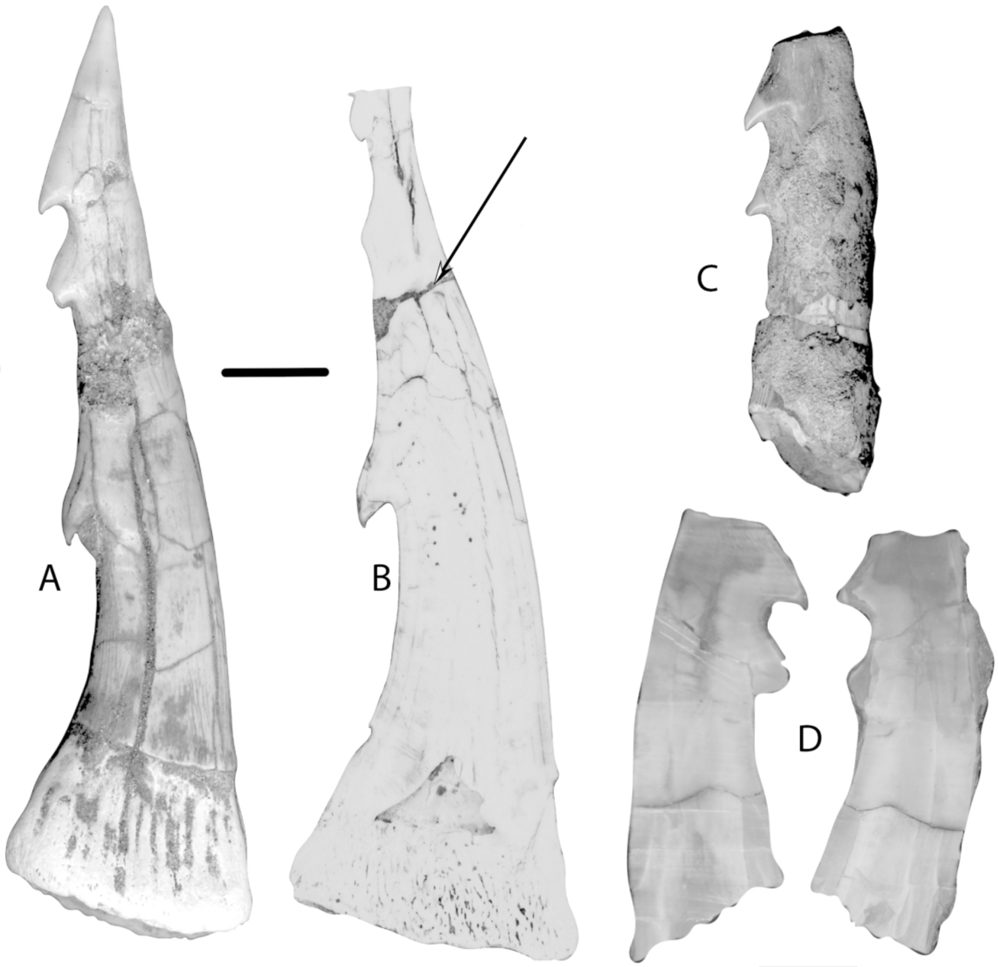

Figure 6. A and C Rostral denticles with multiple barbs bought in Morocco. A, Denticle composed of two different denticles brought from a fossil dealer in Morocco NHMUK PV P74053. B, Sagittal section of denticle, the section where the denticles were glued marked with an arrow (single barb base attached to a double barbed tip denticle). D, Sagittal section of denticle in C that revealed no modifications NHMUK PV P74053. Scale bar: 1 cm.

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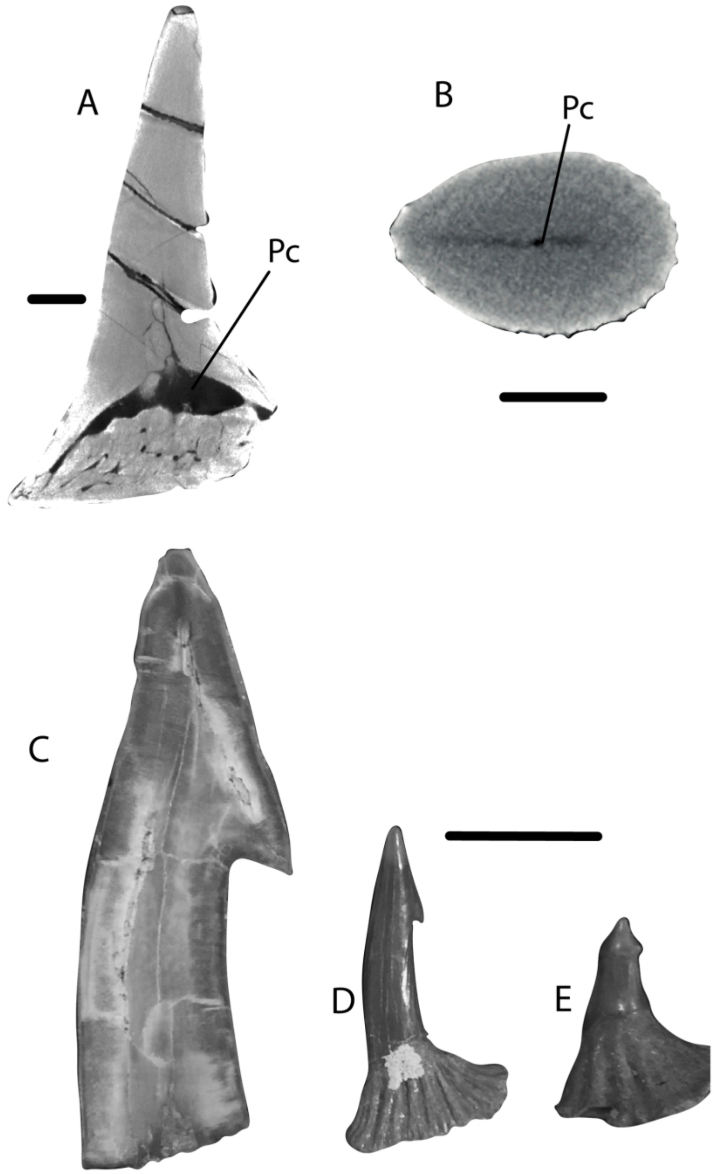

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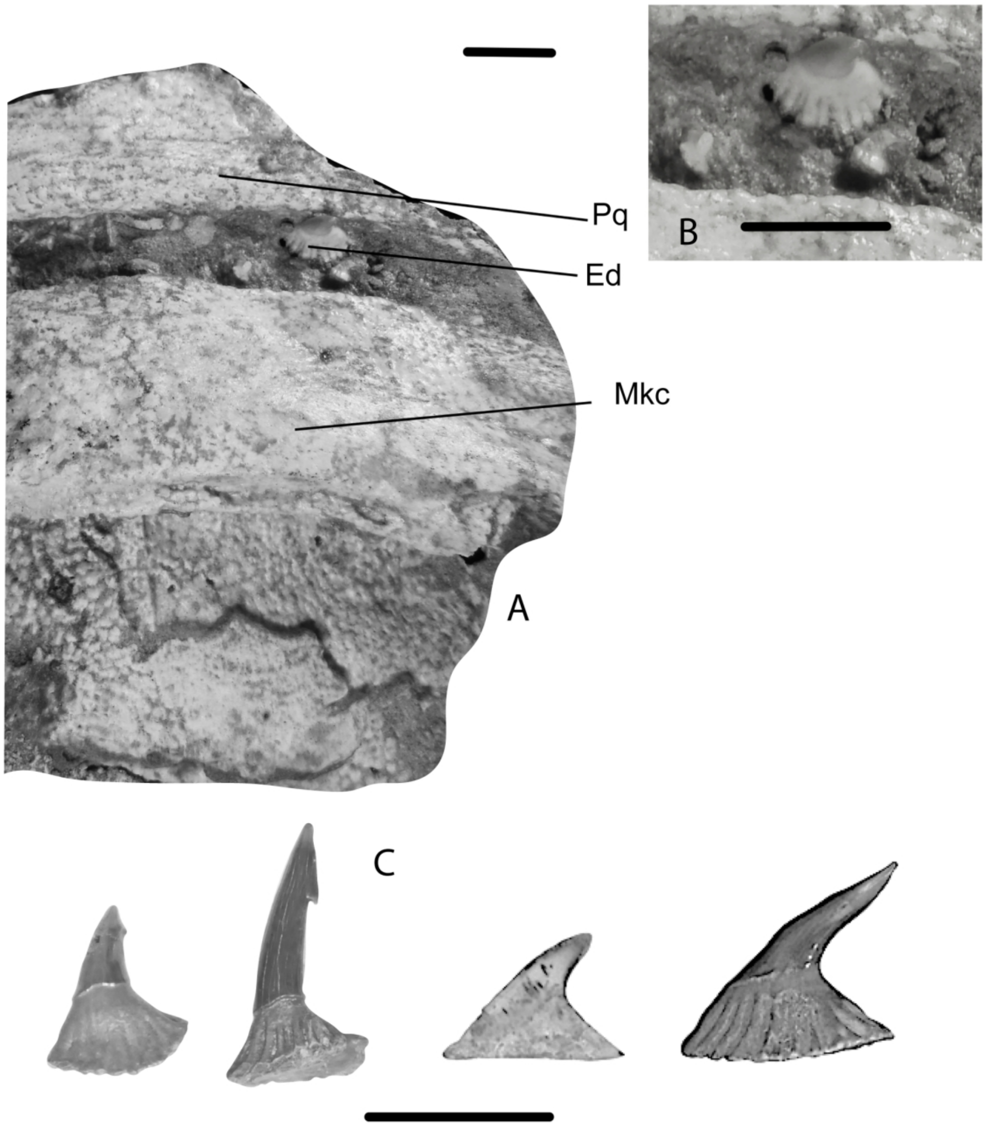

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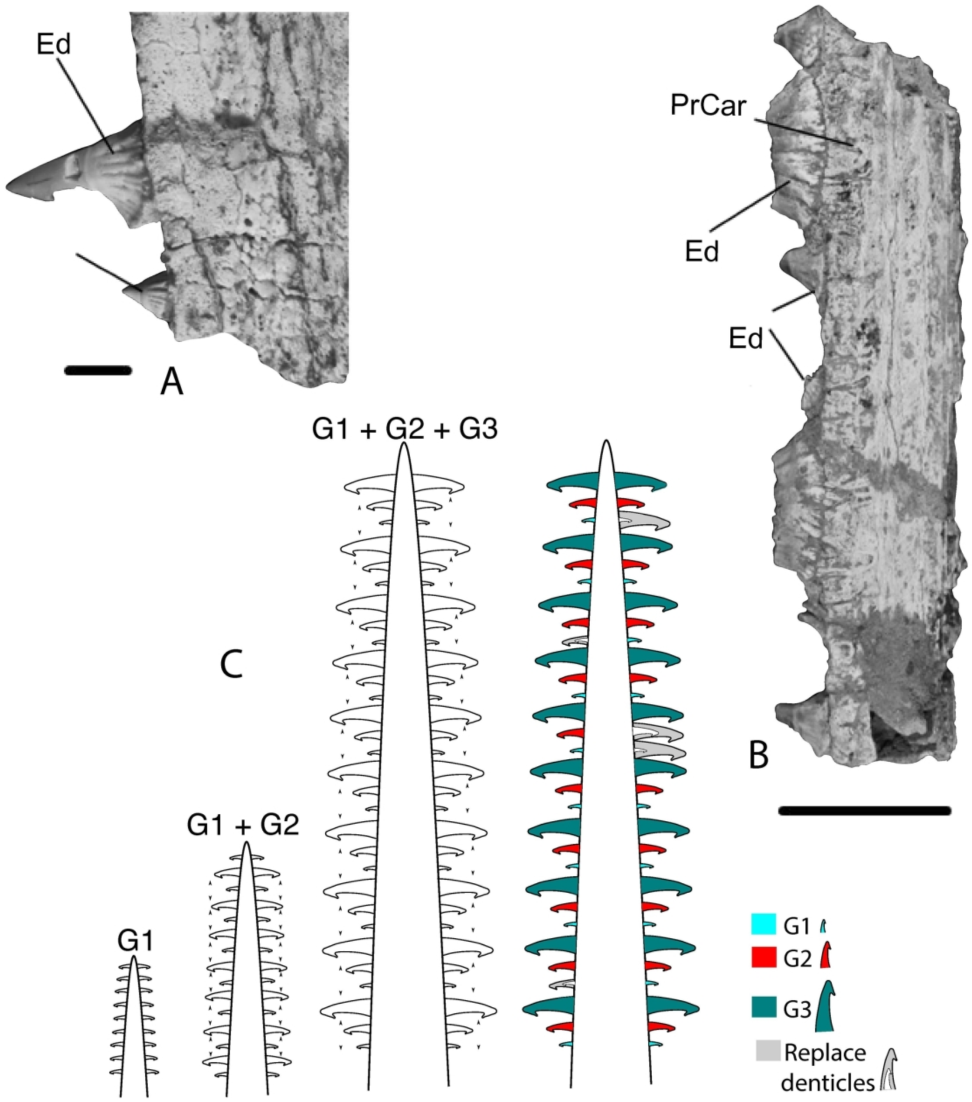
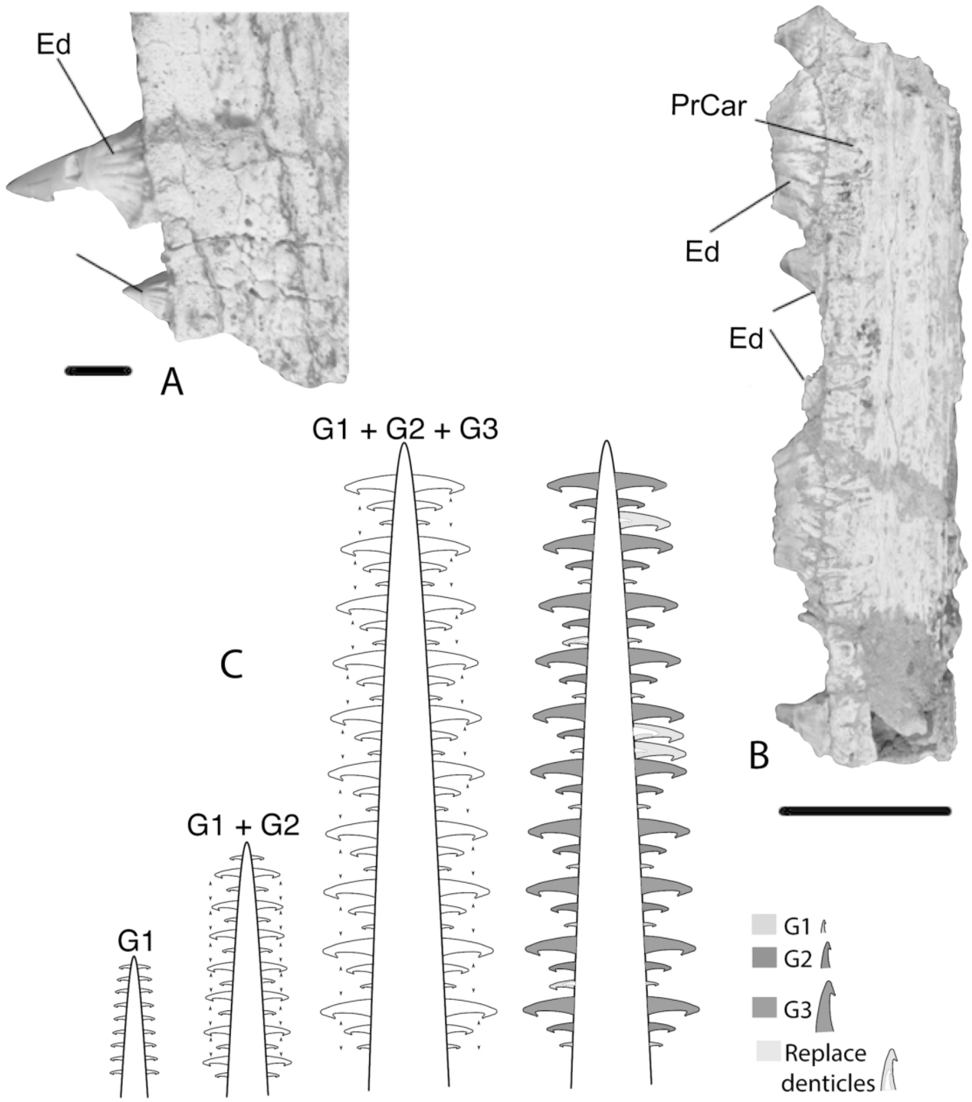


Figure 9. Fragment of the rostrum of †*Onchopristis numidus*. A, IPUW 353500 (scale bar: 1cm). B, NHMUK PV P 75503 (scale bar: 5cm). C, Hypothetical scheme of the growth and addition of rostral denticles in †*Onchopristis*. Denticles in grey in figure C are larger denticles replacing smaller ones that fell.

167x186mm (300 x 300 DPI)



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168x186mm (300 x 300 DPI)

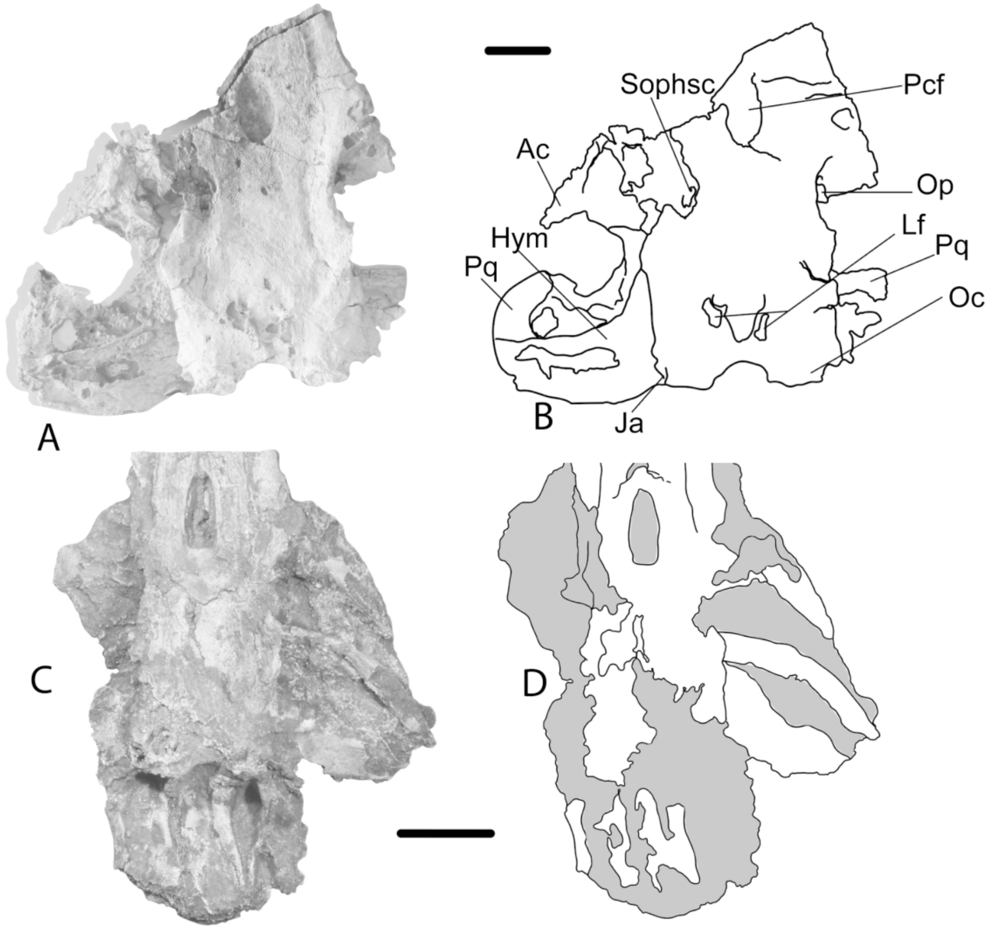

Figure 10. A-B, Neurocranium of †*Onchopristis numidus*. A, picture of IPUW 353500. B, line drawing. C, picture of IGR 2818. D, line drawing. Scale bar 4 cm. Note: darken areas on drawing represent sediments.

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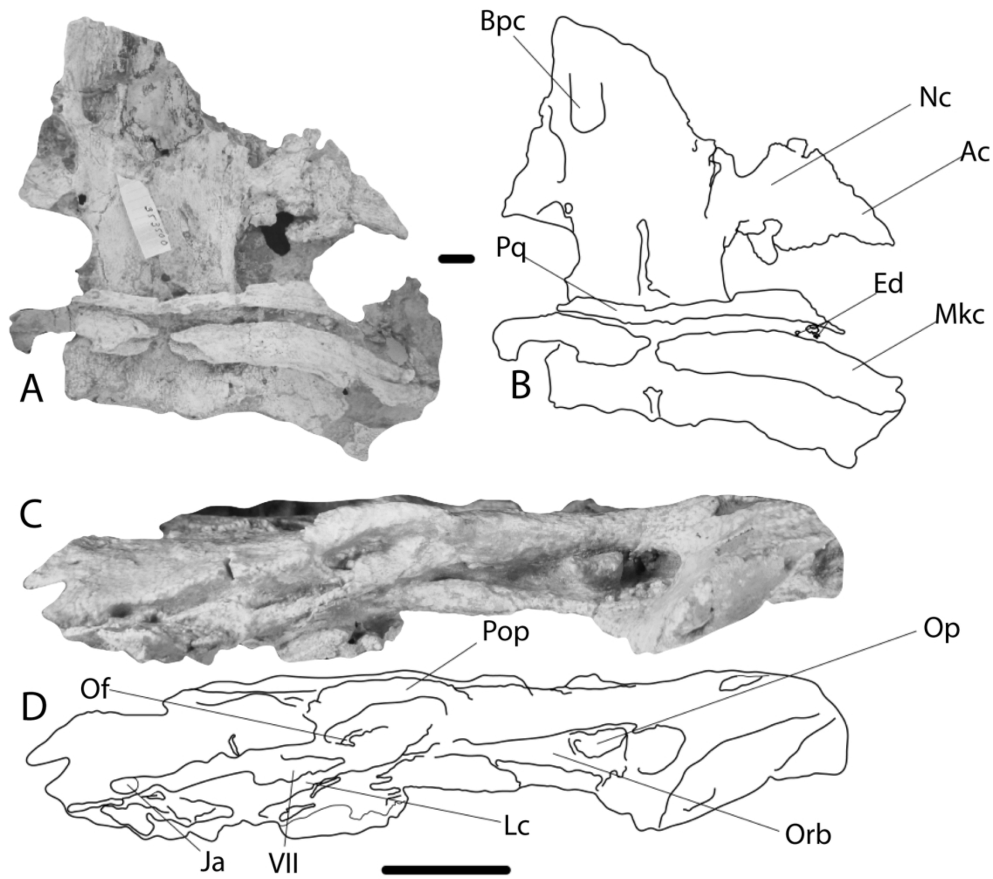

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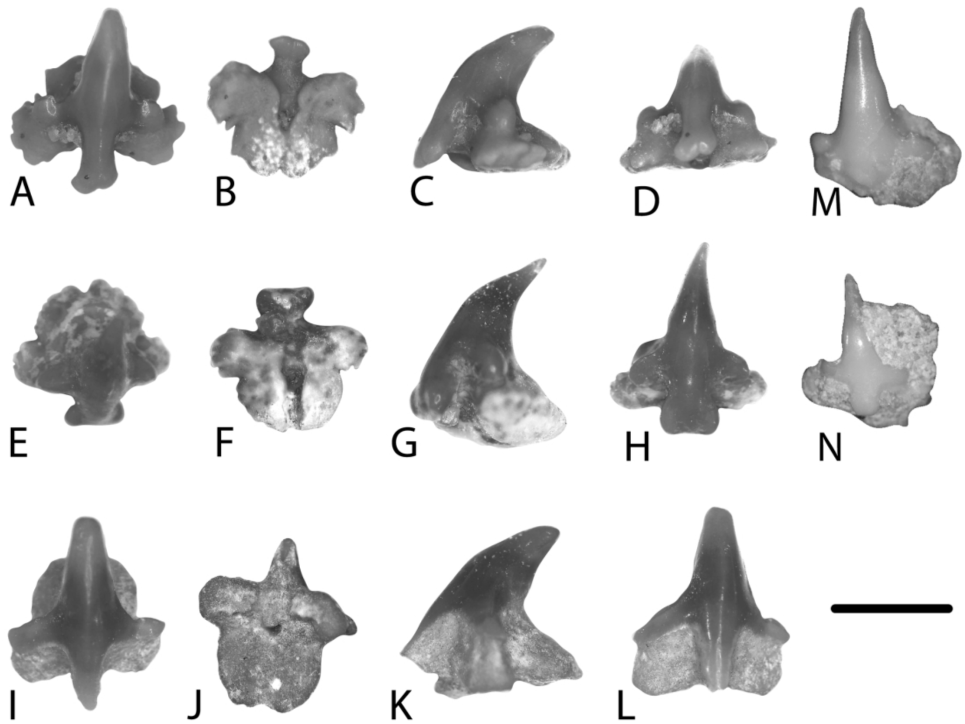

Figure 12. A-L. Oral teeth of †*Onchopristis numidus* found in the "Kem Kem Beds", collection site Boulalou (KK5: easting: 418413, northing: 3479178 UTM, zone: 30) NHMUK PV P 74050. M-N Teeth extracted from the preparation of specimen IPUW 353500. (A, E, I, D, H, L, M and N) Labial face. (B, F and J) root. (C, G, and K) profile view. Scale bar: 2mm.

168x123mm (300 x 300 DPI)

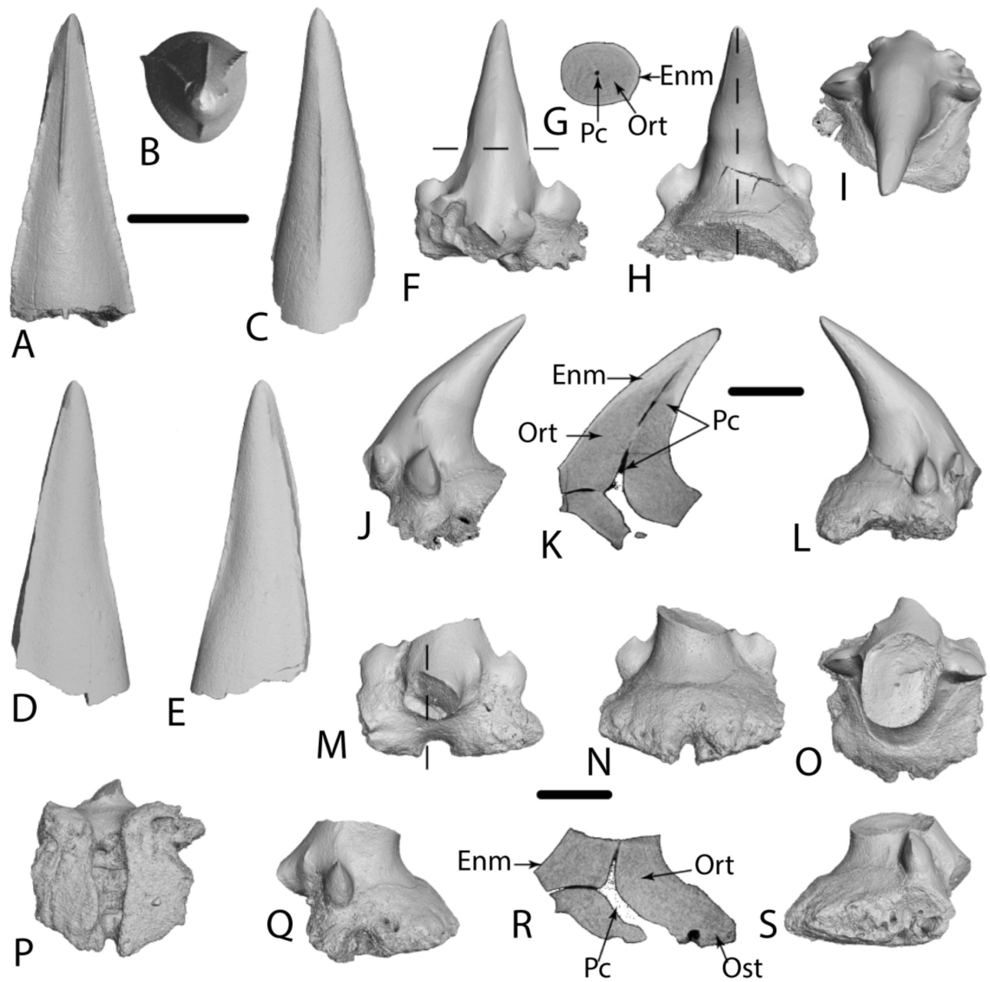

Figure 13. Micro-CT-based volume renderings and virtual sections of oral teeth of †*Onchopristis numidus*found associated with IPUW 353500. A–E, broken main cusp in (A) labial, (B) occlusal, (C) lingual, (D) medial, and (D, E) profile views. F–L, incomplete tooth lacking part of the labial apron and root in (F) labial, (H) lingual, (I) apical, and (J, L) profile views; tooth sections in (G) axial and (K) sagittal aspects; M–S, tooth with a broken main cusp in (M) labial, (N) lingual, (O), occlusal, (P) basal, and (Q, S) profile views tooth section in (R).

168x166mm (300 x 300 DPI)

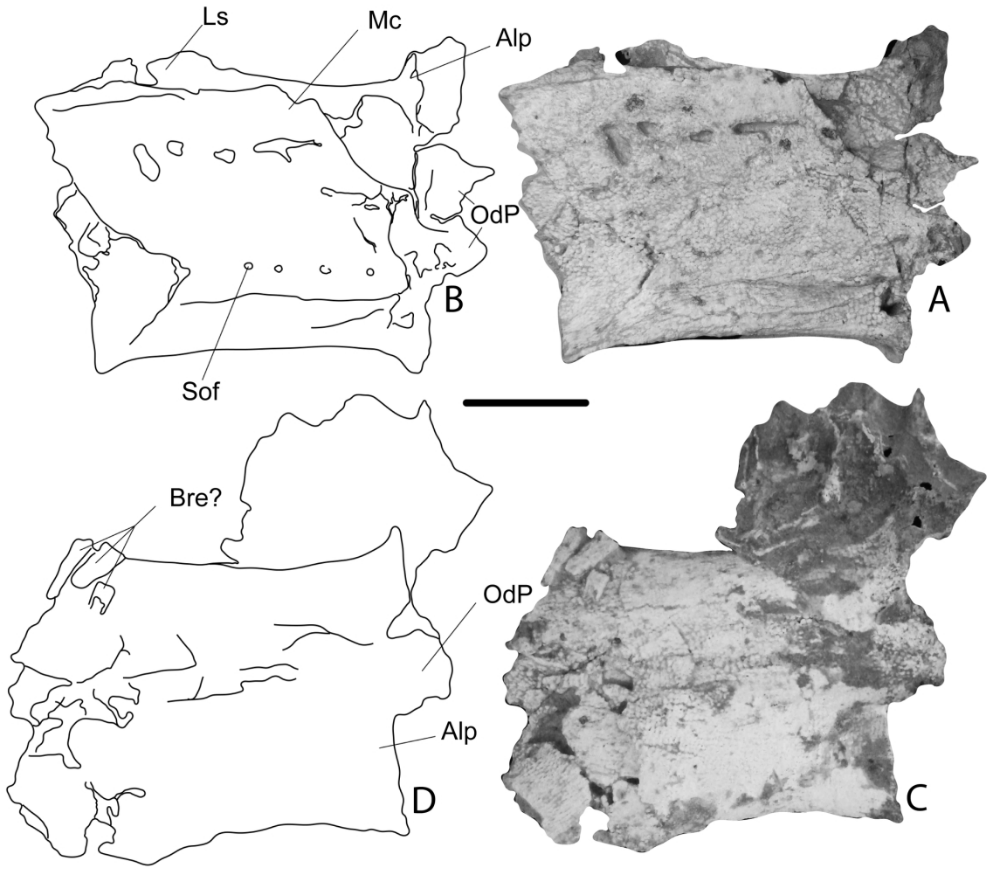

Figure 14. Synarcual of †*Onchopristis numidus* (IPUW 353500). A, dorsal view. B, line draw. C, ventral view. D, line draw. Scale bar: 5 cm.

181x159mm (300 x 300 DPI)

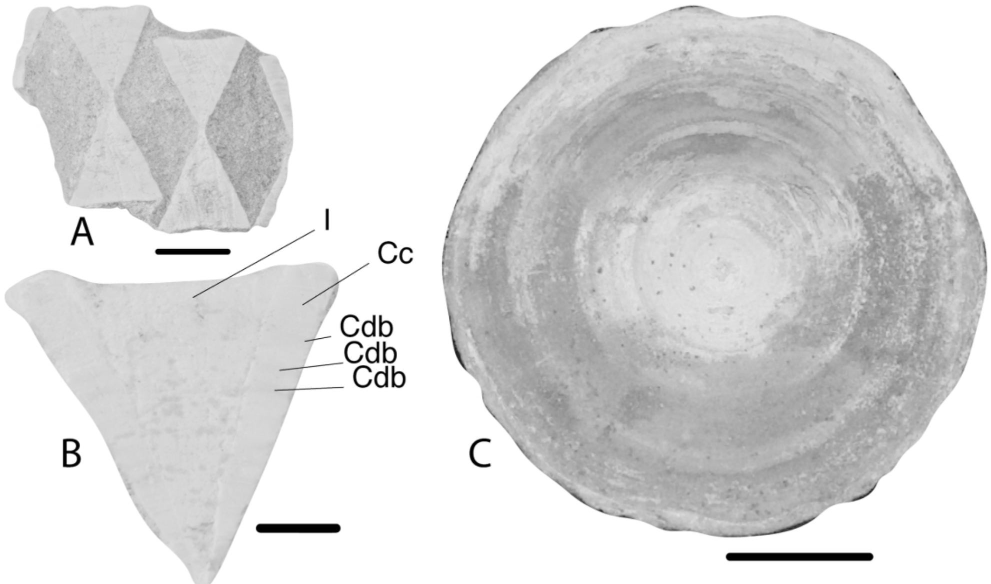

Figure 15. A-B. Vertebral centra of †*Onchopristis numidus*from the "Kem Kem Beds" Collection sites Boulalou (KK5: easting: 418413, northing: 3479178 UTM) NHMUK PV P 74052. (A-B) Sagittal section of vertebra. (C) Articulation surface of the vertebra. Scale bars: 1 cm.

167x108mm (300 x 300 DPI)

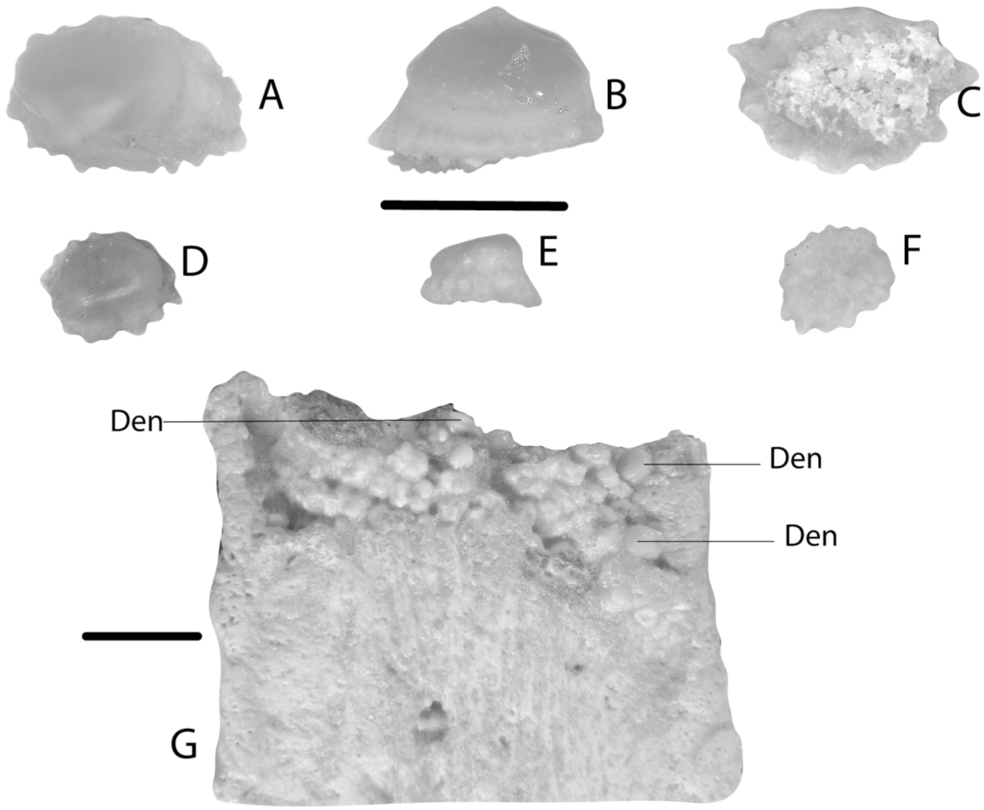

Figure 16. A-F Ventral rostral denticles from the section of the rostrum of †*Onchopristis numidus* (NHMUK PV P 75502). A-C, Morpho 1. D-F, Morpho 2 (scale bar: 2mm) NHMUK PV P 74051. G, anterior part of the ventral surface of IPUW 353500 rostrum (scale bar: 1cm).

158x131mm (300 x 300 DPI)

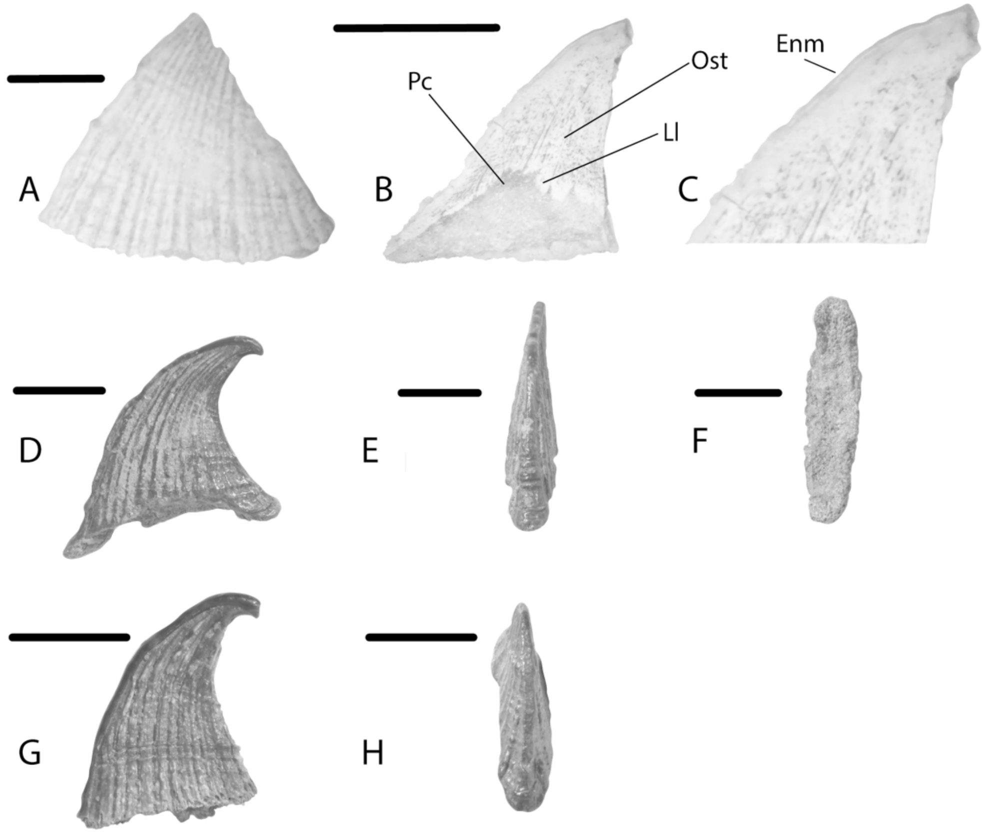

Figure 17. Enlarged dermal denticles of †*Onchopristis numidus* from the "Kem Kem Beds". A-C. C.U personal collection, lateral view. B-C, C.U personal collection, longitudinal section and close-up of the enameloid layer. D-F, IGR 2819, lateral, anterior and basal views. G, IGR 2820, lateral view. H, IGR 2821, antero-apical view. Scale bars: 1 cm.

190x159mm (300 x 300 DPI)

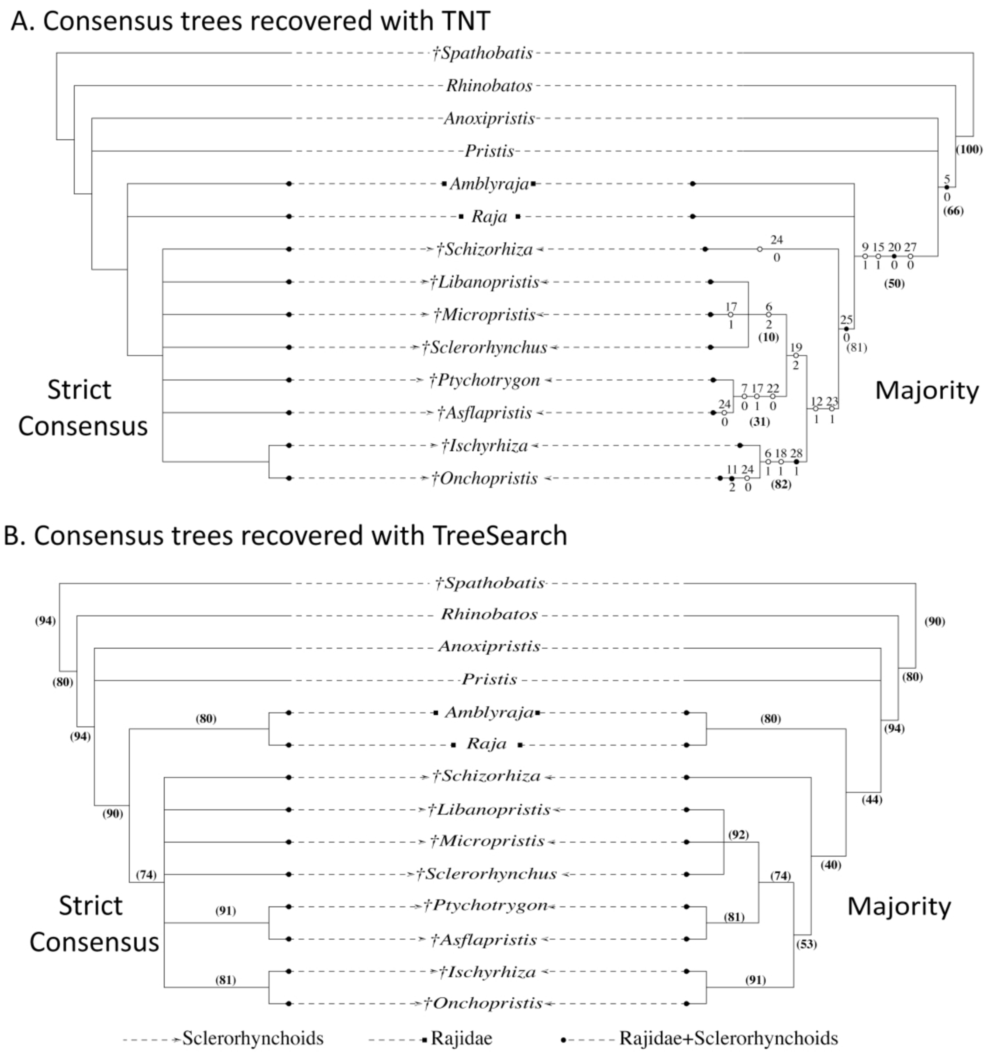

Figure 18. Phylogenetic trees recovered by the different analysis used in the present study. (A) strict consensus and majority rule trees produced by the TNT analysis. (B) strict consensus and majority rule trees produced by the TreeSearch analysis: Clade support values from the Jackknife analysis displayed inside the parenthesis. Character supporting nodes of TNT's majority rule tree (MRT): Black circles characters recovered by both consensus methods; White circles characters recovered only by MRT.

395x427mm (300 x 300 DPI)