HAL
open science

The skeletal remains of the euryhaline sclerorhynchoid †Onchopristis (Elasmobranchii) from the 'Mid'-Cretaceous and their palaeontological implications

Eduardo Villalobos-Segura, Jürgen Kriwet, Romain Vullo, Sebastian Stumpf, David J Ward, Charlie J Underwood

▶ **To cite this version:**

Eduardo Villalobos-Segura, Jürgen Kriwet, Romain Vullo, Sebastian Stumpf, David J Ward, et al.. The skeletal remains of the euryhaline sclerorhynchoid †Onchopristis (Elasmobranchii) from the 'Mid'-Cretaceous and their palaeontological implications. Zoological Journal of the Linnean Society, 2021, 193 (2), pp.746-771. 10.1093/zoolinnean/zlaa166 . insu-03134850

HAL Id: insu-03134850

https://insu.hal.science/insu-03134850v1

Submitted on 8 Feb 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

by Eduardo Villalobos-Segura[1], Jürgen Kriwet[2], Romain Vullo[3], Sebastian Stumpf[2], David J. Ward[4] and Charlie J. Underwood[1].

[1] School of Earth Sciences, Birkbeck College, Malet Street, London, WC1E 7HX, UK

[2] University of Vienna, Department of Palaeontology, Geozentrum, Althanstraße 14, 1090 Vienna, Austria.

[3] UMR CNRS 6118 Géosciences, Université Rennes 1, Campus de Beaulieu263 avenue du Général Leclerc, 35042 Rennes, France.

[4] Department of Earth Sciences, The Natural History Museum, London SW7 5BD, UK;

Running head: Skeletal remains of †*Onchopristis*

Corresponding author: Eduardo Villalobos-Segura, elasmo177@gmail.com

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*). Aiming to determinate a phylogenetic relations of †*Onchopristis* within sclerorhynchoids a cladistic analysis carried out based on the remains described here, its results suggest a new taxonomic arrangement within sclerorhynchoids.

INTRODUCTION

†*Onchopristis* Stromer, 1917 is a puzzling Cretaceous batoid taxon, with most of its fossil record being recorded from many 'mid' Cretaceous sites in coastal and fluvial settings. 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 †*Squatina aegyptiaca* 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.

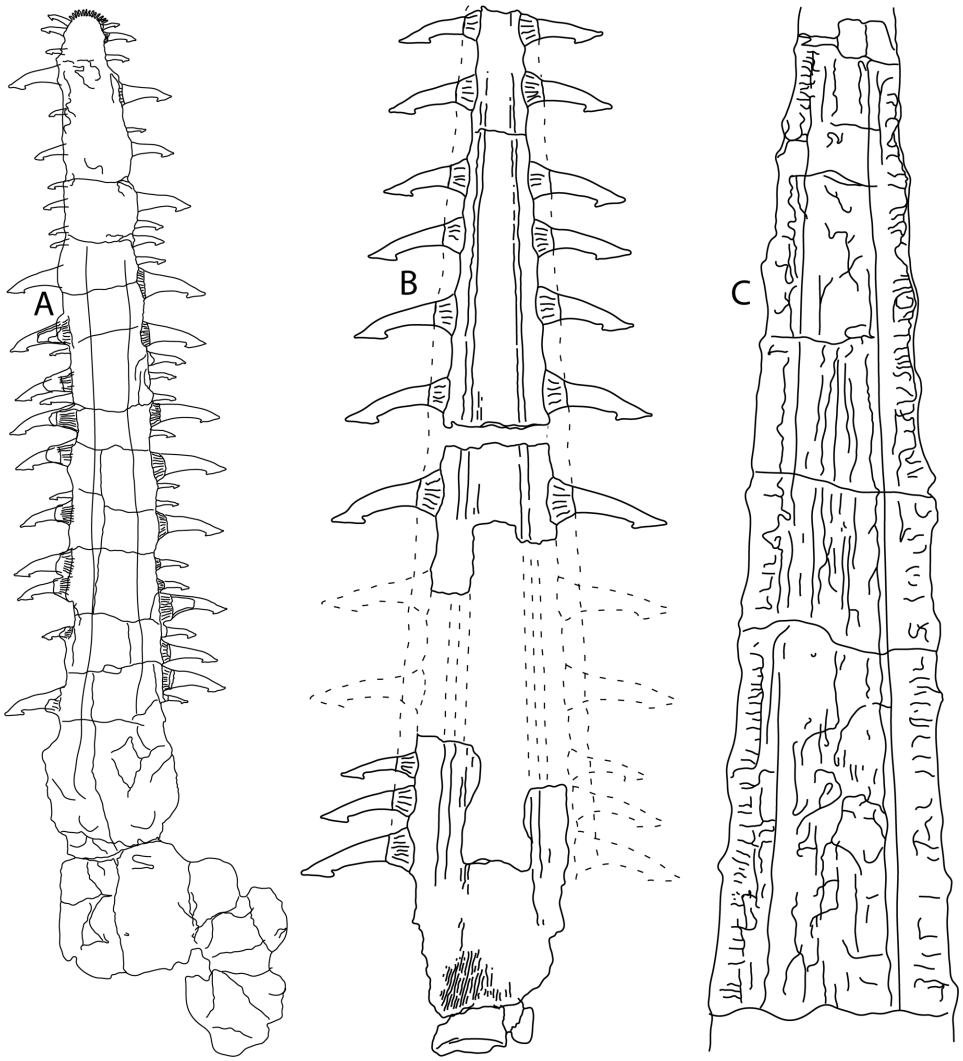

Figure 1. A. Rostral remains figured in Stromer (1925; TL 1450 mm). B-C. Rostral remains figured in Stromer (1917; B, TL. 260 mm. C, TL. 520 mm).

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. However, the specimens 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.* †*Onchopristis dunklei* is also reported from the Albian of Tunisia, although this 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). 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)
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, the 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.

To determinate the phylogenetic implications of these newly discovered remains of †*Onchopristis* and to test their phylogenetic relations within sclerorhynchoids, a matrix of 14 taxa and 29 characters based on previous works (Aschliman *et al*., 2012; Claeson *et al.,* 2013;

235 Underwood & Claeson, 2017; Villalobos *et al.,* 2019a; b) with modifications to account for the
236 morphological variation added by the specimens described here was assembled in Mesquite
237 3.31 (Maddison & Maddison, 2018) (Supplementary materials) and analysed. As batoids
238 monophyly is well-established by molecular and morphological analyses (e.g. Douady et al.,
239 2003; Naylor et al., 2012 McEachran & Aschliman, 2004; Aschliman *et al*., 2012), and not
240 being the objective of the present study to test this, the selection of the outgroups included only
241 batoids. To properly test the affiliation of †*Onchopristis* within sclerorhynchoids and the
242 monophyly of sclerorhynchoids, the outgroup was composed by taxa that have been previously
243 found in a sister relation to sclerorhynchoids by other phylogenetic analyses (e.g. *Pristis* by
244 Kriwet, 2004 and Underwood & Claeson, 2017, *Spathobatis* by Claeson *et al.,* 2013, and
245 rajoids (*Raja* and *Bathyraja*) by Villalobos *et al.,* 2019a; b). It is worth mention that the
246 proximity of these taxa to sclerorhynchoids variates depending on the analysis (i.e. they are not
247 always in immediate proximity to sclerorhynchoids). The outgroup also
248 included *Anoxypristis* to contain all Pristidae genera (Fricke *et al*., 2020), and *Rhinobatos* a
249 genus that no previous analysis has placed in proximity to sclerorhynchoids, but present
250 similarities with the other outgroup taxa in the analysis.

251 As the specimens described here are mostly composed of rostral and neurocranium
252 remains, the selection of character was focused heavily on these structures, trying to avoid the
253 uncertainty associated with the extensive inclusion of missing data. However, some postcranial
254 skeletal features like the enlargement and shape of the proximal pectoral elements were kept
255 (Char. 1, see supporting information for character discussion), as they provide key features that
256 distinguish sclerorhynchoids from other batoids. For the comparison of the specimens
257 described here, eight sclerorhynchoid genera from which skeletal remains are known are
258 included and compose the ingroup in the analysis. Some tooth features were used, although not
259 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)

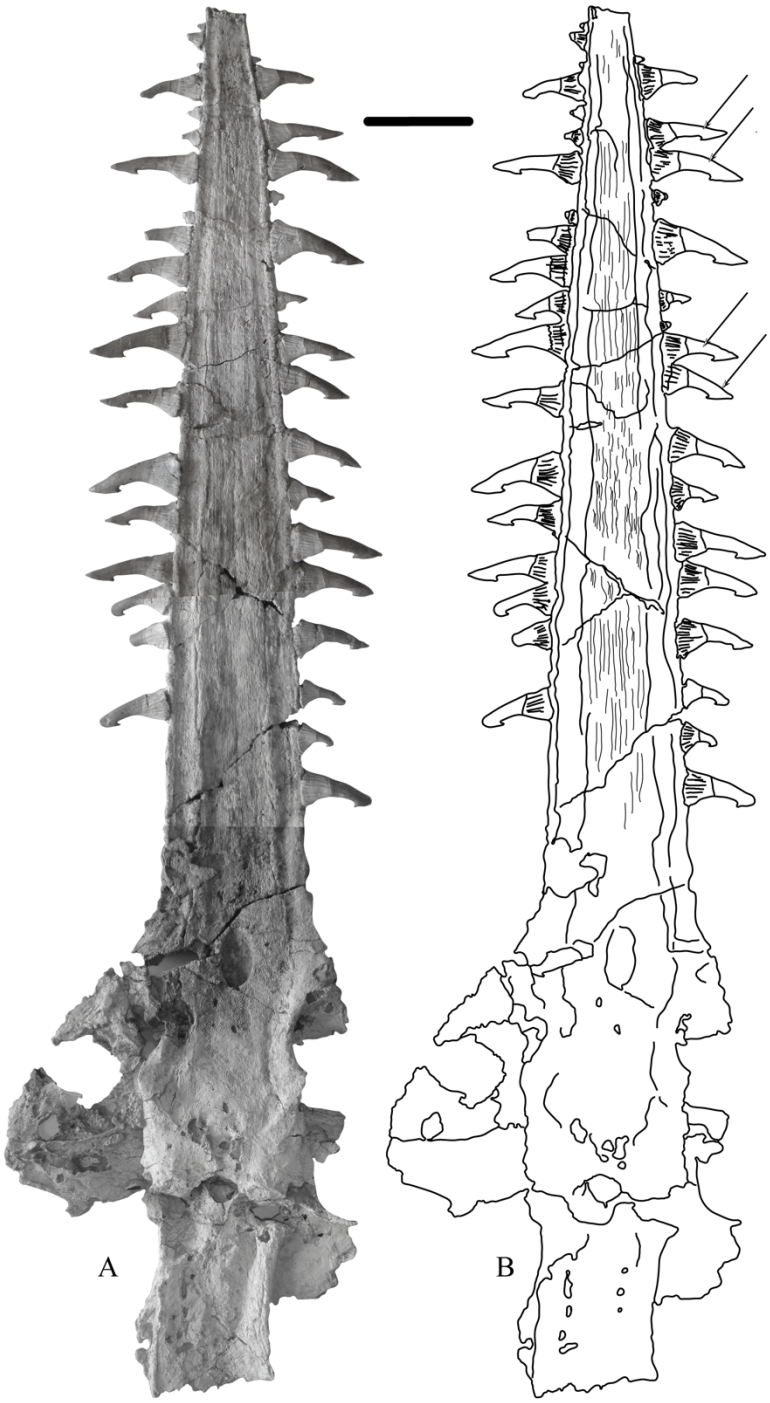

Figure 2. A, Cranial and rostral remains of †*Onchopristis numidus* (IPUW 353500). B, Interpretative line drawing of the specimen remains. Denticles in pair arrangement marked with an arrow. Scale bar: 5cm.

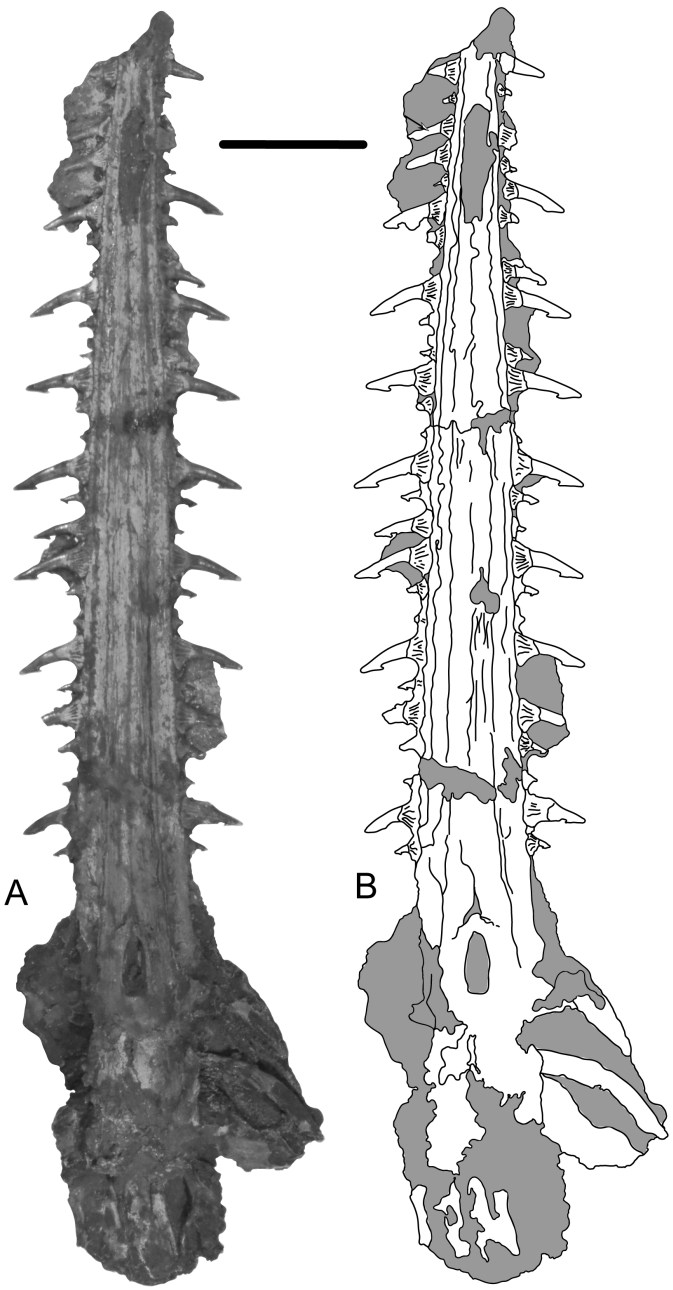

Figure 3. A, Cranial and rostral remains of †*Onchopristis numidus* (IGR 2818). B, line drawing of the specimen remains (darken areas represent rock matrix). Denticles in pair arrangement marked with an arrow. Scale bar: 10 cm.

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.

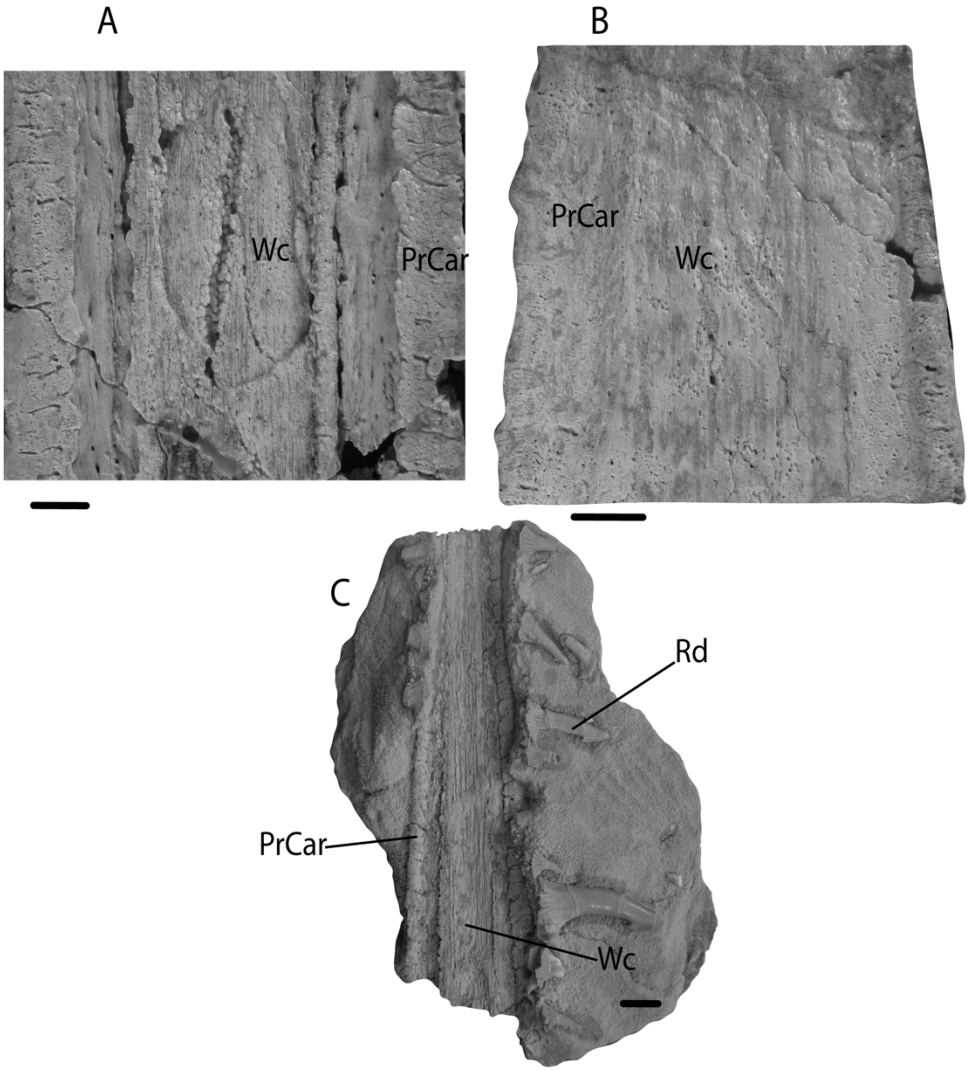

Figure 4. A-C, Rostrum of †*Onchopristis numidus*. A, Ventral surface of IPUW 353500. B, Dorsal surface of IPUW 353500. C, NHMUK PV P 75502. Scale bar:1cm.

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.

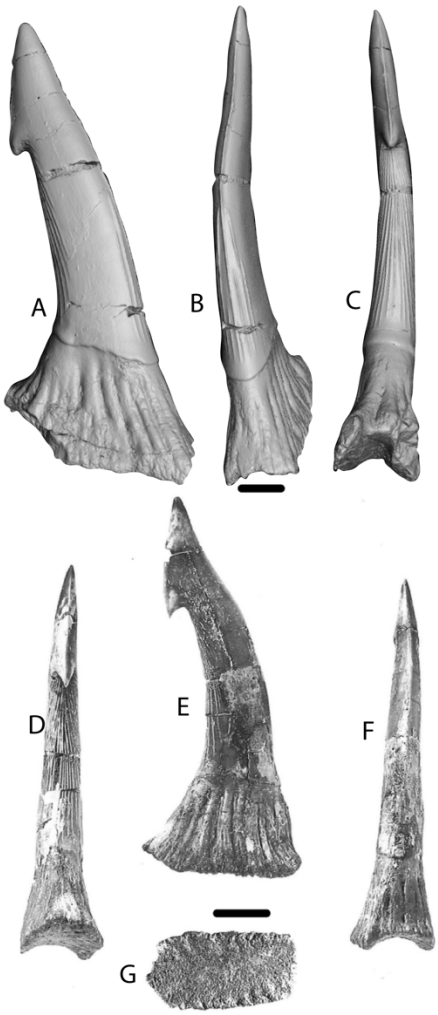

Figure 5. Enlarged rostral denticles of †*Onchopristis*. A–C, micro-CT-based volume rendering of denticle collected along with the specimen IPUW 353500 from Morocco: (A) dorsoventral, (B) anterior, and (C) posterior view. D–G, denticles collected Egypt (Werner, 1989; plate 19, figs. 2a-d): (D) posterior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

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).

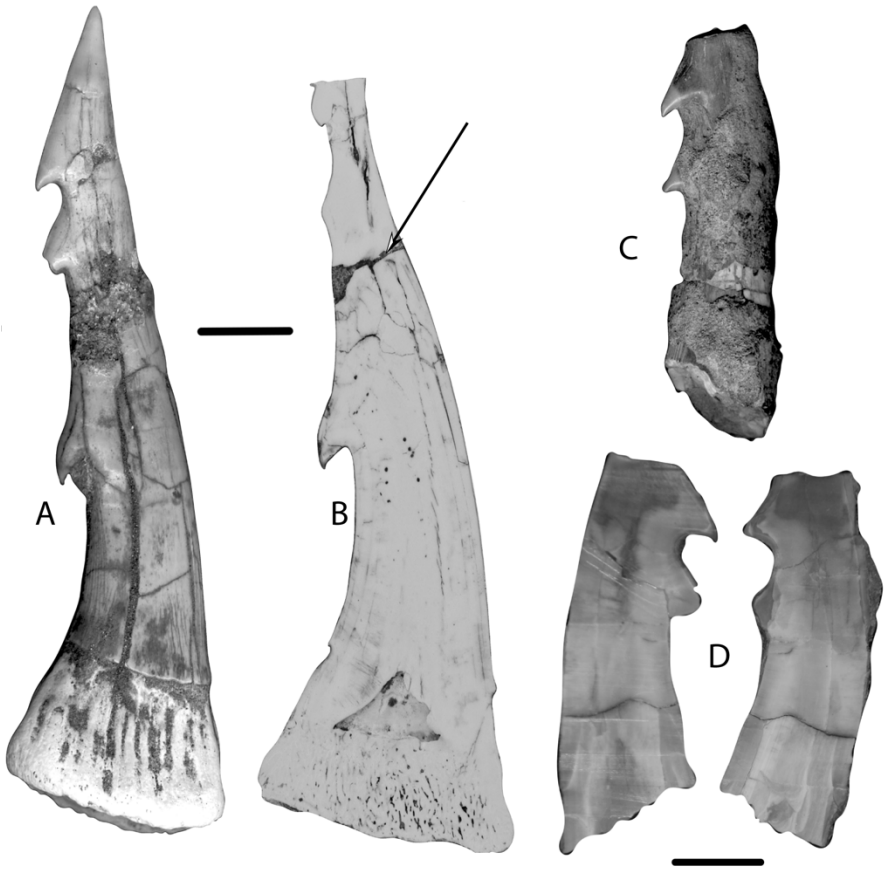

Figure 6. A and C Rostral denticles with multiple barbs bought in Morocco. A, Denticle composed of two different denticles brought from a fossil dealer in Morocco NHMUK PV P74053. B, Sagittal section of denticle, the section where the denticles were glued marked with

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.

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).

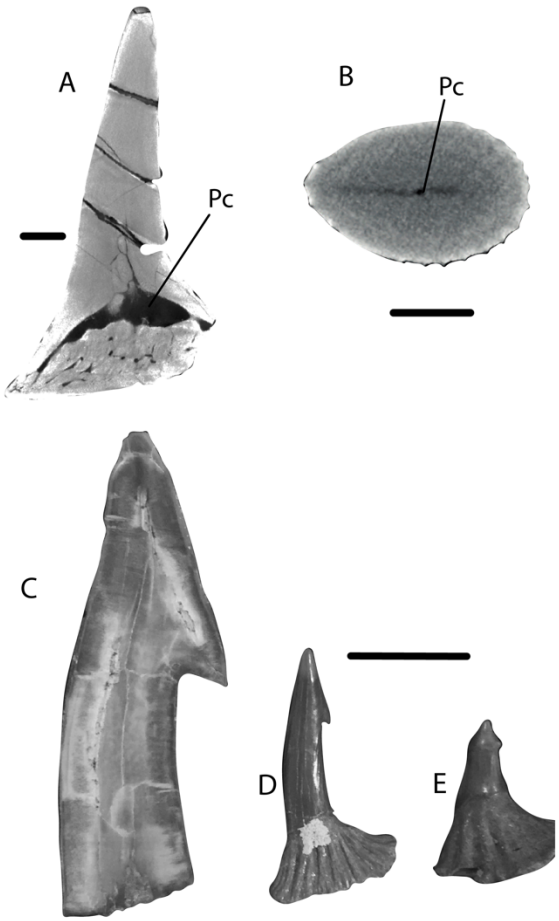

Figure 7. Rostral denticles of †*Onchopristis numidus* found in the "Kem Kem Beds" NHMUK PV P74045. A, CT scan of denticles (scale bar: 1mm). B, Transverse section of denticle (scale

bar: 2 mm). C Lateral section of the tip of rostral denticles. D-E, Smaller denticles with different barb sizes (scale bar: 1cm).

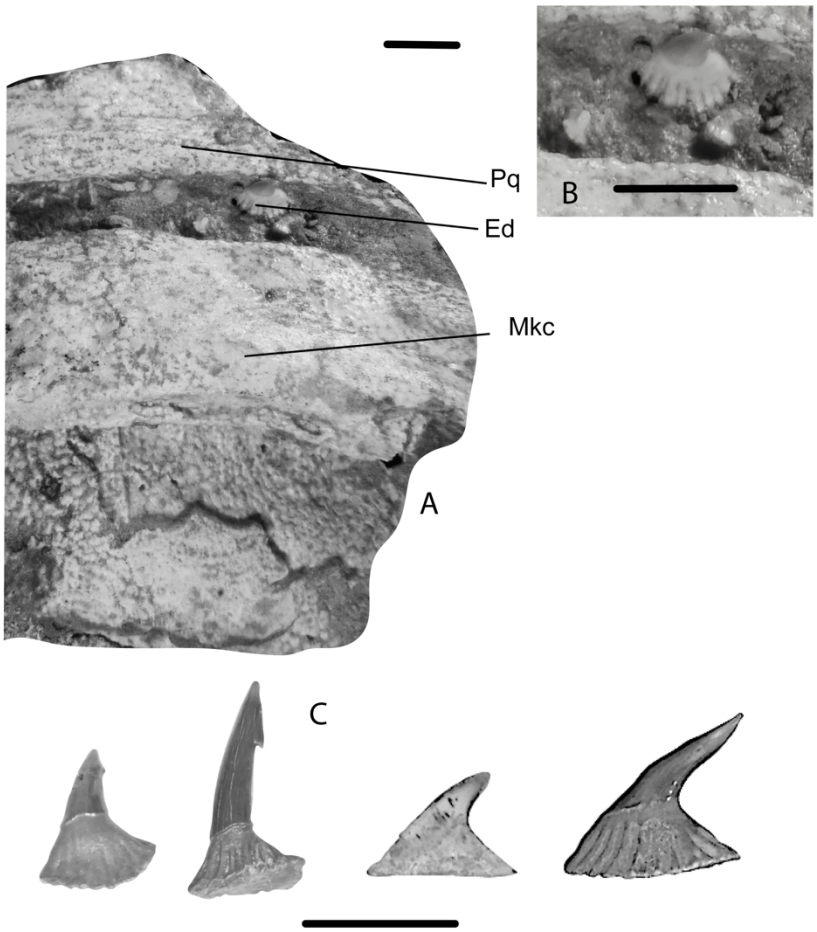

Figure 8. A, Mouth of †*Onchopristis numidus* (IPUW 353500). B, Close up view of enlarged denticle in the mouth. C, Disarticulated denticles with similar morphology found in the "Kem Kem Beds" collection sites: KK1 (easting: 382819, northing: 3501936 UTM) and KK3 (easting: 416828, northing: 3418567 UTM).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

Enlarged denticle series: Different morphologies of enlarged denticles possibly 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 barbless and curved denticle between the jaws of specimen IPUW 353500 (Fig. 8A) and its morphological similarities with the lateral rostral denticles (i.e. a narrow base

427 composed of osteodentine with several ridges on the sides, well differentiates from the
428 orthodentine filled cap) confirms the presence of multiple series of enlarged denticles in
429 †*Onchopristis numidus*. Its placement in the mouth indicates displacement of the denticle
430 during the taphonomic process (i.e. not preserved in situ). However, from its position and the
431 comparison with those of †*Sclerorhynchus atavus* NHMUK PV P 4776 and *Pristiophorus*
432 *lanae* (see Welten et al. 2015 figs. 6c and 8e) we hypothesise that this denticle corresponds the
433 lateral cephalic series.

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

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

451 Based on the presence of highly porous cartilages along the sides of the rostrum, and
452 the presence of fully functional denticles of different size classes in †*Onchopristis numidus,* we
453 hypothesise that in this species the denticles are periodically added across the rostrum as it
454 grows and develops over time (Fig. 9). The presence of fully erect small denticles followed by
455 larger ones, as observed in specimen IPUW 353500 and IGR 2818, suggests a seriated
456 appearance of the rostral denticles beginning with smaller denticles and subsequently followed
457 by larger ones (Fig. 9A-B). The three-size cluster of rostral denticles with a mirrored
458 arrangement (i.e. similar-sized denticles placed on opposite sides in dorsal view) recognised in
459 IGR 2818, is interpreted to be the result of synchronised development on both sides of the
460 rostral denticles. This mirroring pattern is unnoticeable or less conspicuous at the tip of the
461 rostrum, probably because it is a more fragile region and denticles in this area could be more
462 susceptible to fracture due to taphonomic processes. The presence in both specimens (IPUW
463 353500; IGR 2818) of small denticles (G1) and larger denticles (G2 and G3) with fully
464 enamelled caps suggest that denticles do not gradually grow, but instead that larger denticles
465 are periodically added as the animal grows (Fig. 9C). Both the arrangement and addition
466 sequence are different from other sclerorhynchoids (e.g. Sternes & Shimada, 2019; Welten *et*
467 *al.,* 2015; Underwood *et al.,* 2016; Smith *et al.,* 2015).
468 Overall this arrangement is somewhat similar to that observed in *Pristiophorus* (Welten
469 et al., 2015 and Underwood et al., 2016). With some notable differences: In †*Onchopristis*
470 *numidus* both small and large rostral denticles seems to lack a differentiated degree of
471 mineralisation and present a cap densely filled with orthodentine, whereas rostral denticles in
472 *Pliotrema warreni* differ in the mineralisation pattern between older (larger) and younger
473 (smaller) denticles (Welten et al., 2015). In addition, the triplet arrangement observed in the
474 rostral denticles of *Pliotrema warreni* is not always present in †*Onchopristis numidus* in which
475 denticles of the same size as those of the functional generation replace or occupy the available

space. This arrangement is similar organisation to that reported for other sclerorhynchoid species (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)".

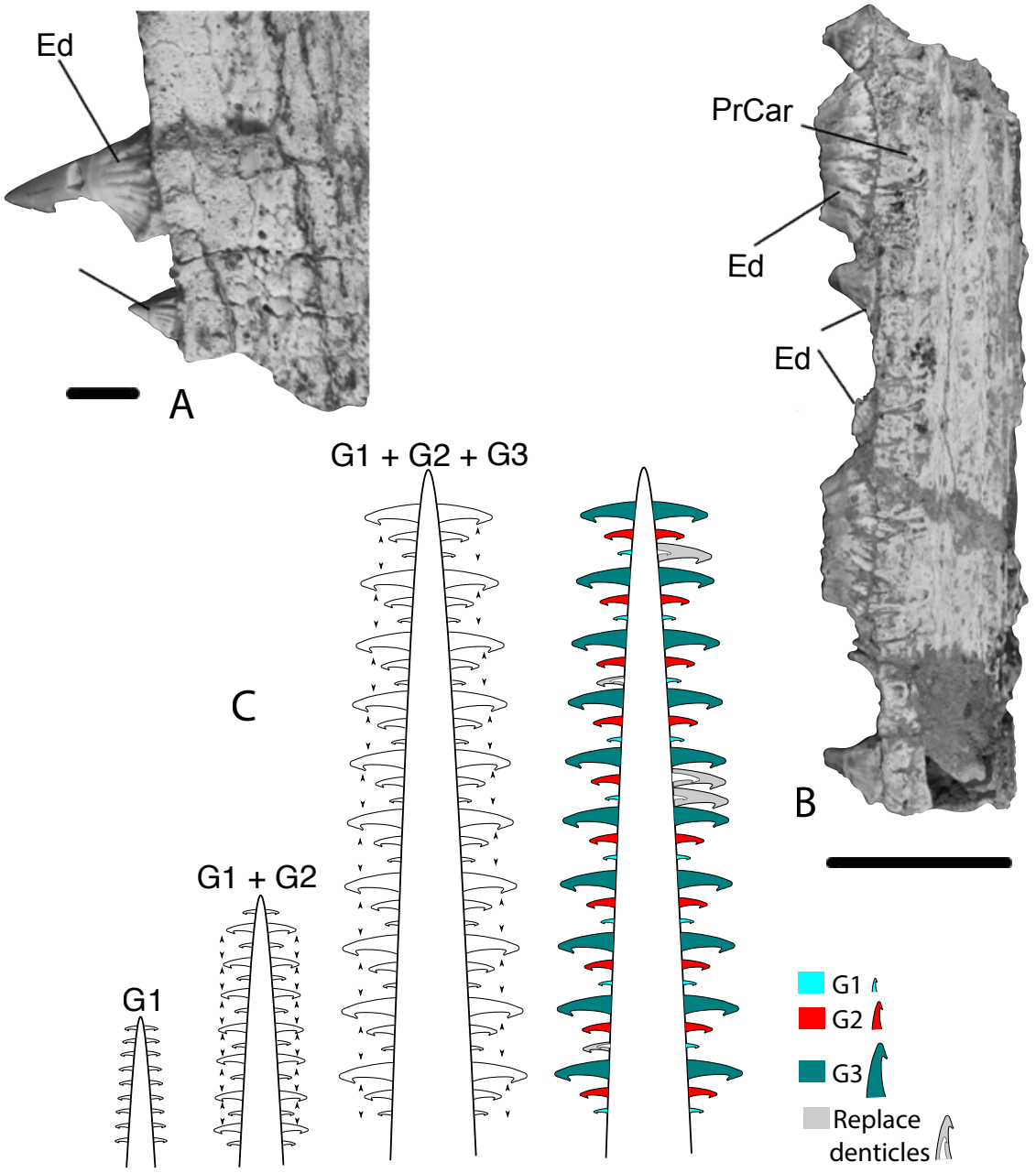

Figure 9. Fragment of the rostrum of †*Onchopristis numidus*. A, IPUW 353500 (scale bar: 1cm). B, NHMUK PV P 75503 (scale bar: 5cm). C, Hypothetical scheme of the growth and

addition of rostral denticles in †*Onchopristis*. Denticles in grey in figure C are larger denticles replacing smaller ones that fell.

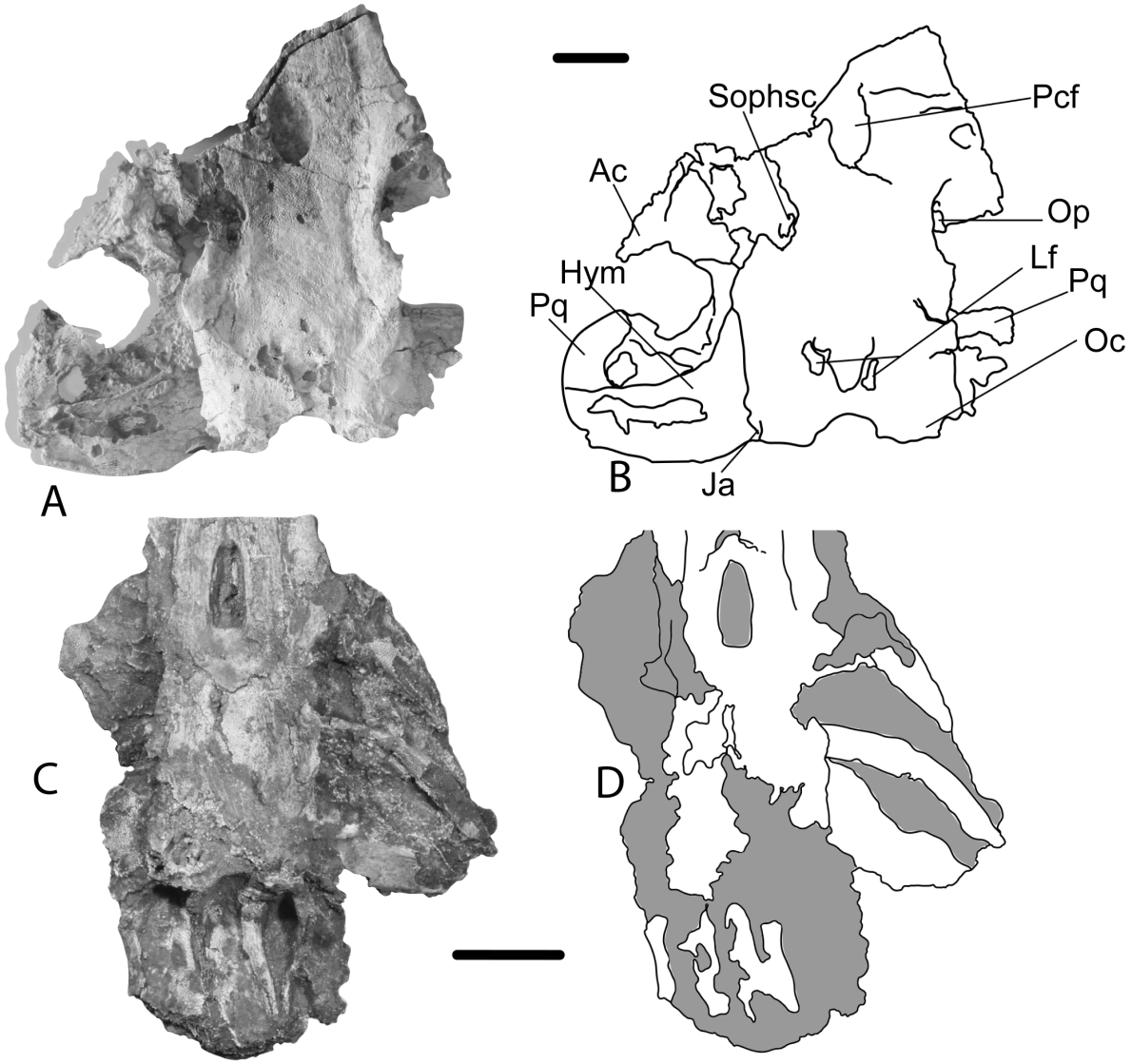

Figure 10. A-B, Neurocranium of †*Onchopristis numidus*. A, picture of IPUW 353500. B, line drawing. C, picture of IGR 2818. D, line drawing. Scale bar 4 cm. Note: darken areas on drawing represent sediments.

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

Hyomandibula

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

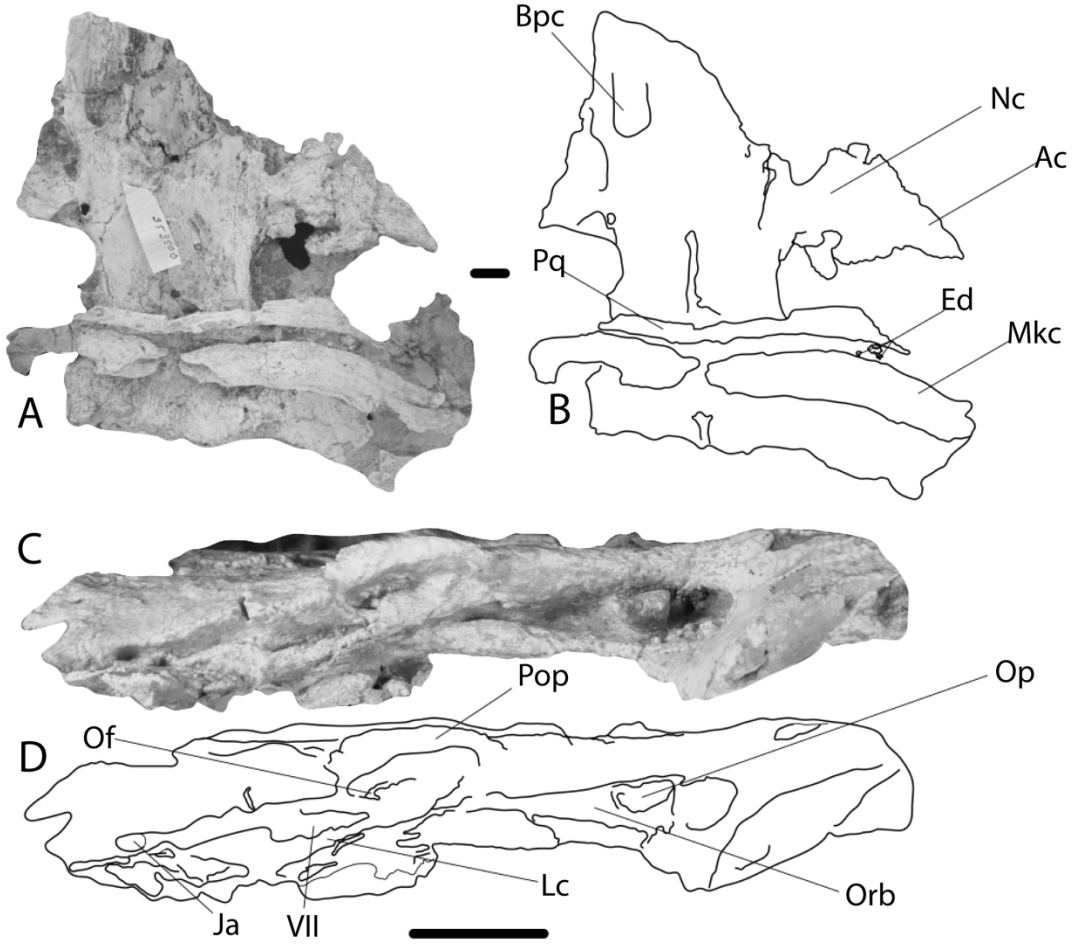

Figure 11. Neurocranium of †*Onchopristis numidus* (IPUW 353500). A, Ventral view. B, Line draw. C, Lateral view. D, Line draw. (A-B, scale bar: 2 cm). (C-D, scale bar: 5 cm).

Jaw cartilages

Only part of the Meckel's and palatoquadrate cartilages are observable in ventral view (Fig. 11 A-B). The palatoquadrate is thin and narrows progressively towards the symphysis (Fig. 11 A-B). In ventral view, there is no clear articulation with the neurocranium, the

Meckel's cartilage and palatoquadrate are present, and both jaw elements seem to be supported by the hyomandibula. The palatoquadrate and Meckel's cartilage antimeres are not fused and connected at the symphysis. The Meckel's cartilage is wider than the palatoquadrate but also becomes narrower towards the symphysis (Fig. 11 A-B).

Oral teeth: Teeth of †*Onchopristis numidus* have been figured multiple times (e.g. by 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.).

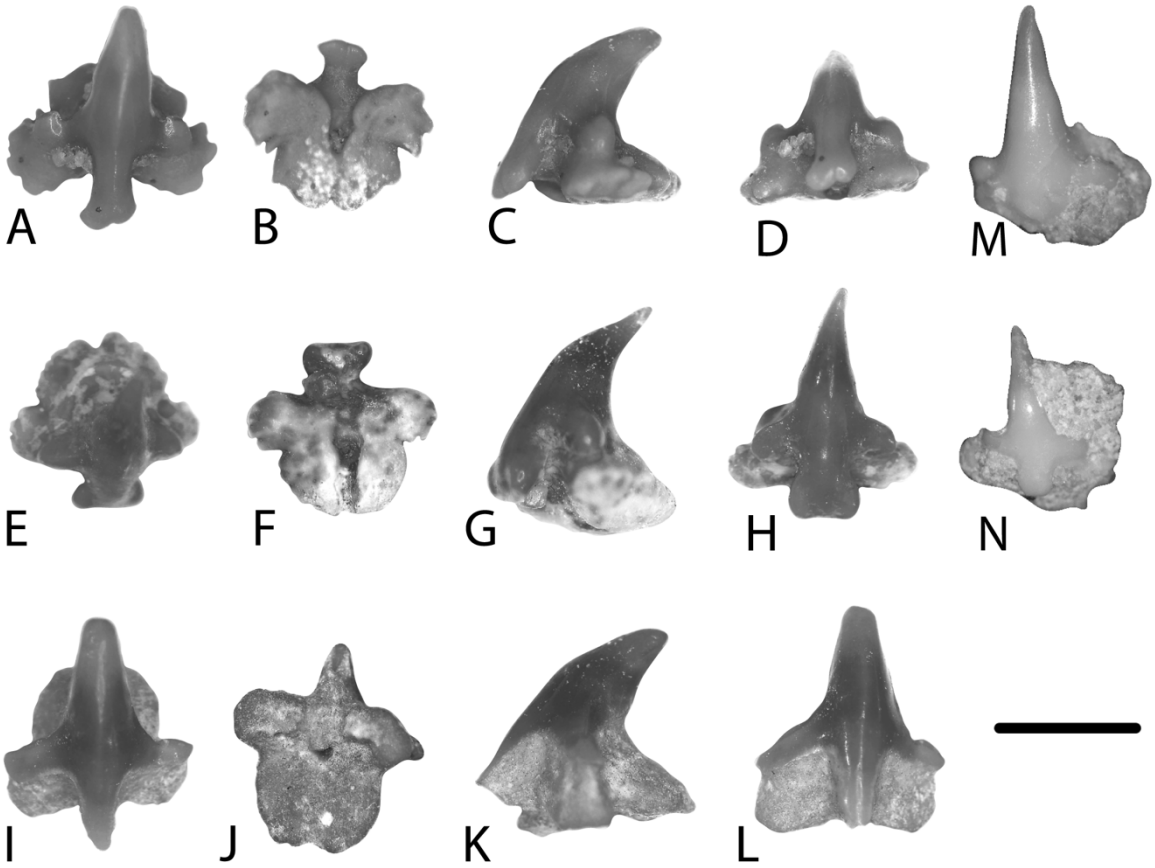

Figure 12. A-L. Oral teeth of †*Onchopristis numidus* found in the "Kem Kem Beds", collection site Boulalou (KK5: easting: 418413, northing: 3479178 UTM, zone: 30) NHMUK PV P 74050. M-N Teeth extracted from the preparation of specimen IPUW 353500. (A, E, I, D, H, L, M and N) Labial face. (B, F and J)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

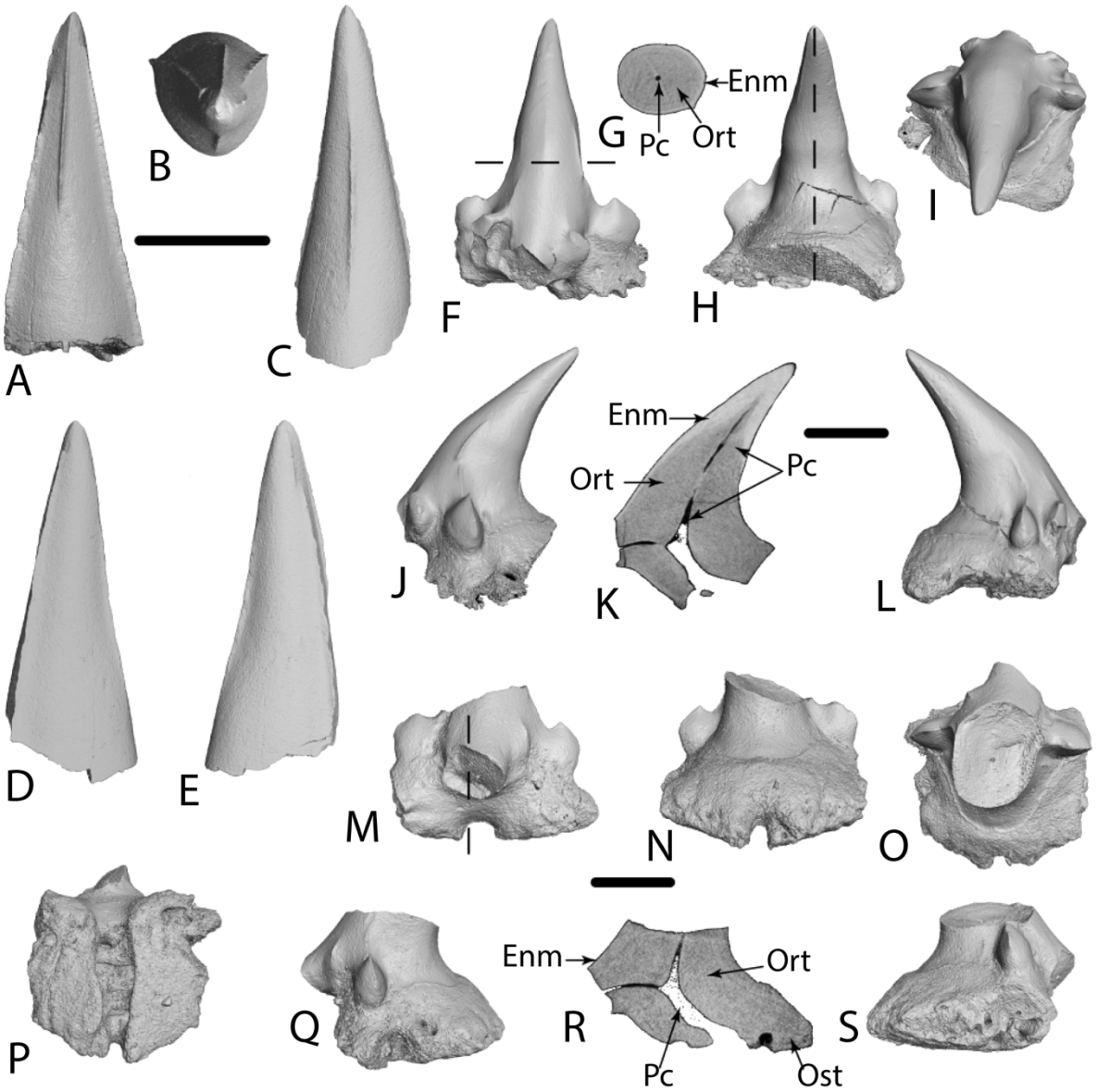

Figure 13. Micro-CT-based volume renderings and virtual sections of oral teeth of †*Onchopristis numidus* found associated with IPUW 353500. A–E, broken main cusp in (A) labial, (B) occlusal, (C) lingual, (D) medial, and (D, E) profile views. F–L, incomplete tooth lacking part of the labial apron and 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).

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)

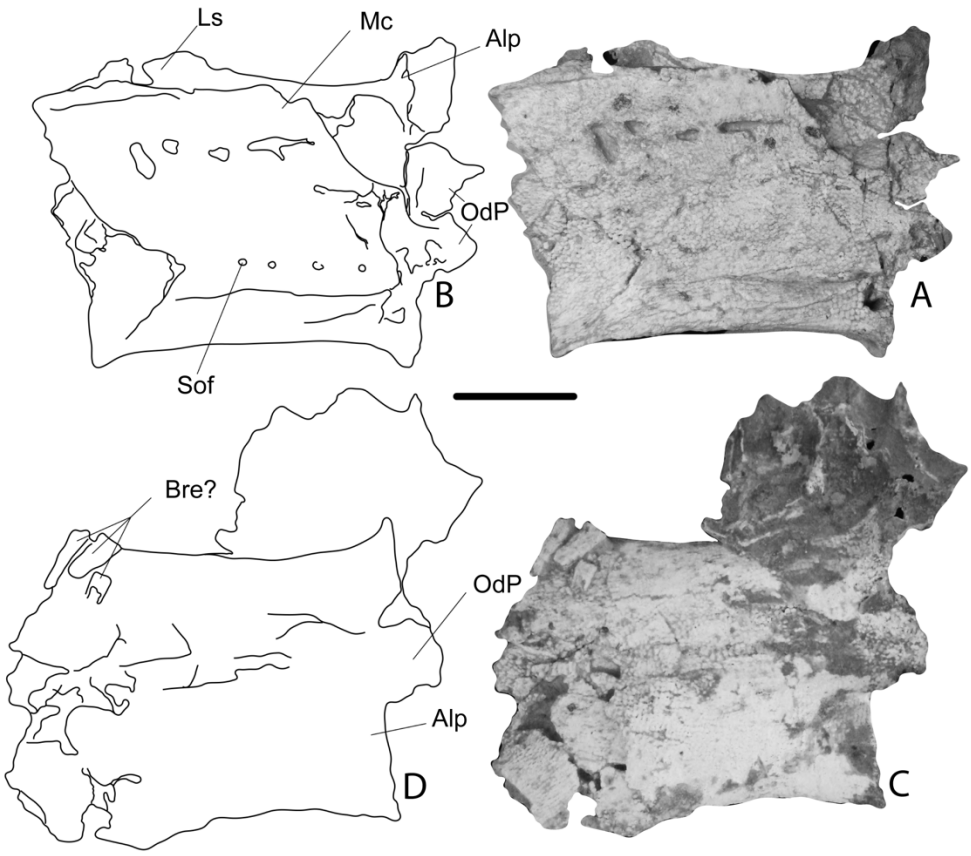

Figure 14. Synarcual of †*Onchopristis numidus* (IPUW 353500). A, dorsal view. B, line draw. C, ventral view. D, line draw. Scale bar: 5 cm.

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).

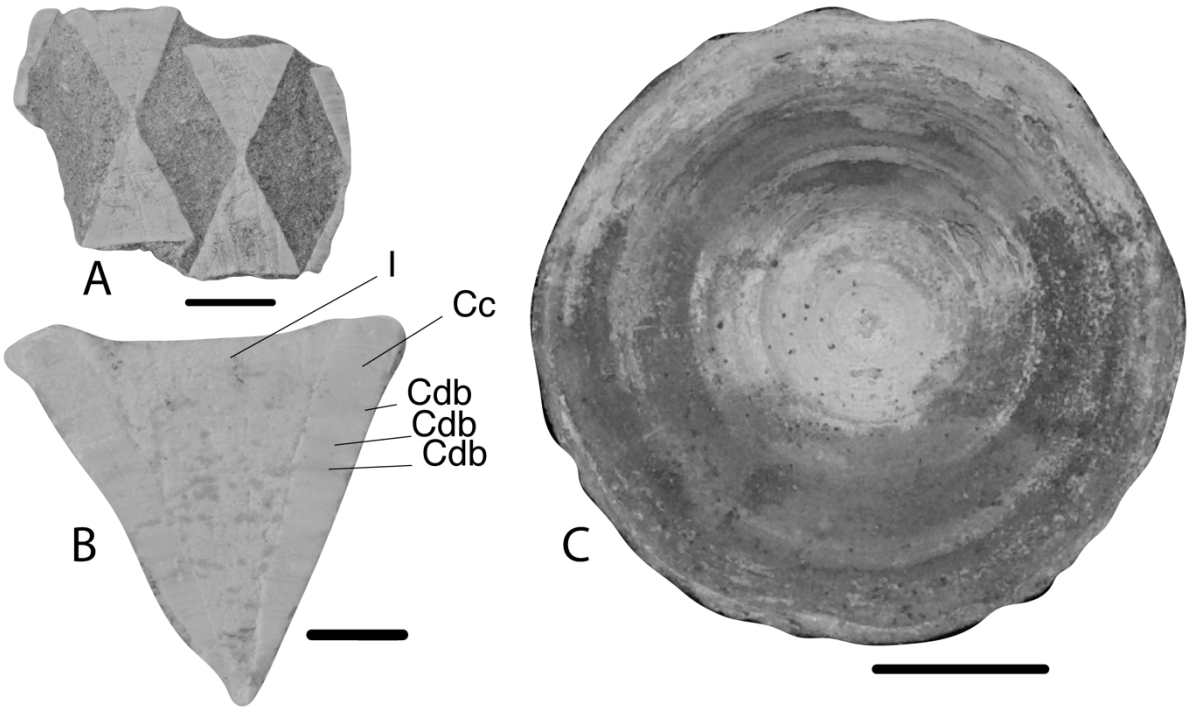

Figure 15. A-B. Vertebral centra of †*Onchopristis numidus* from the "Kem Kem Beds" Collection sites Boulalou (KK5: easting: 418413, northing: 3479178 UTM) NHMUK PV P 74052. (A-B) Sagittal section of vertebra. (C) Articulation surface of the vertebra. Scale bars: 1 cm.

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).

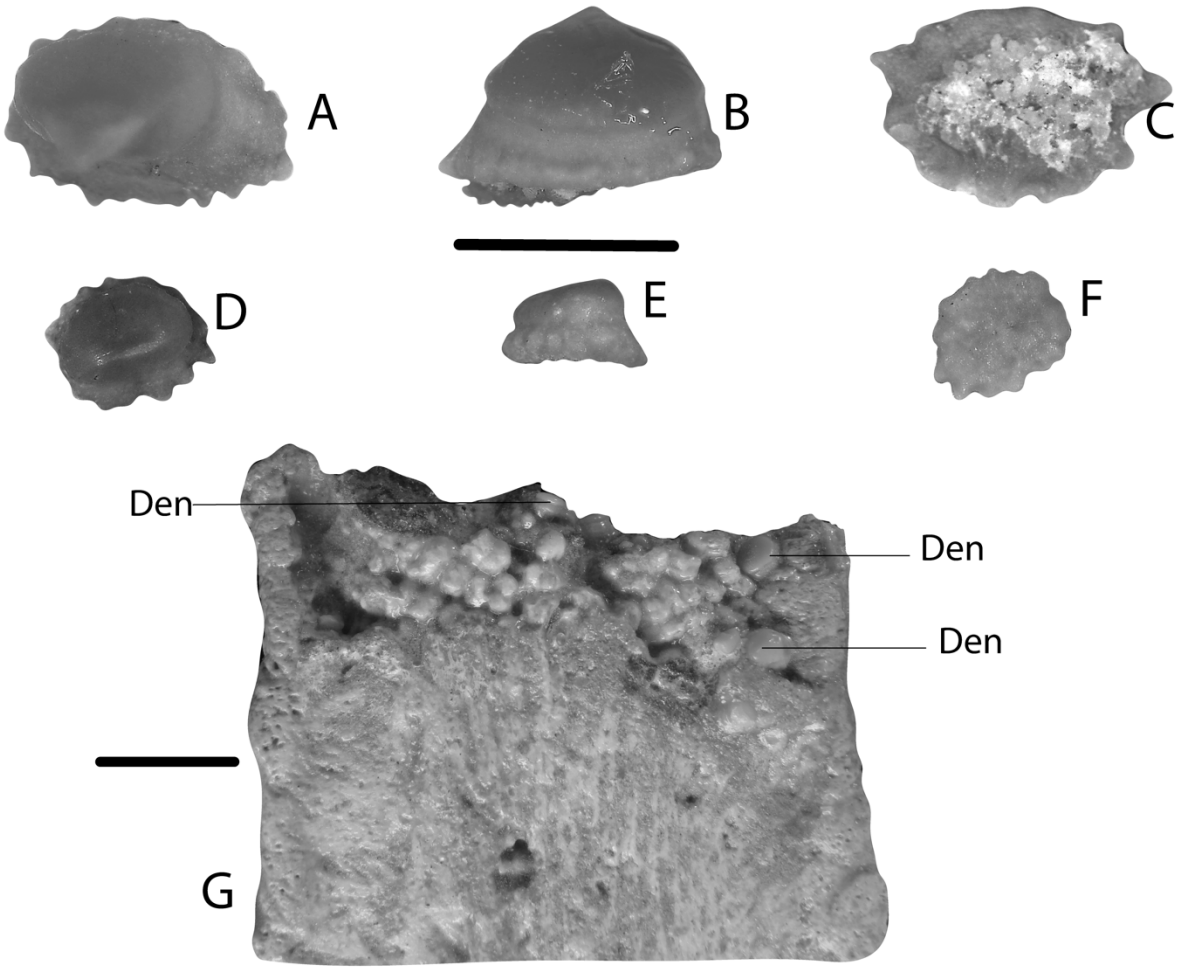

Figure 16. A-F Ventral rostral denticles from the section of the rostrum of †*Onchopristis numidus* (NHMUK PV P 75502). A-C, Morpho 1. D-F, Morpho 2 (scale bar: 2mm) NHMUK PV P 74051. G, anterior part of the ventral surface of IPUW 353500 rostrum (scale bar: 1cm).

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).

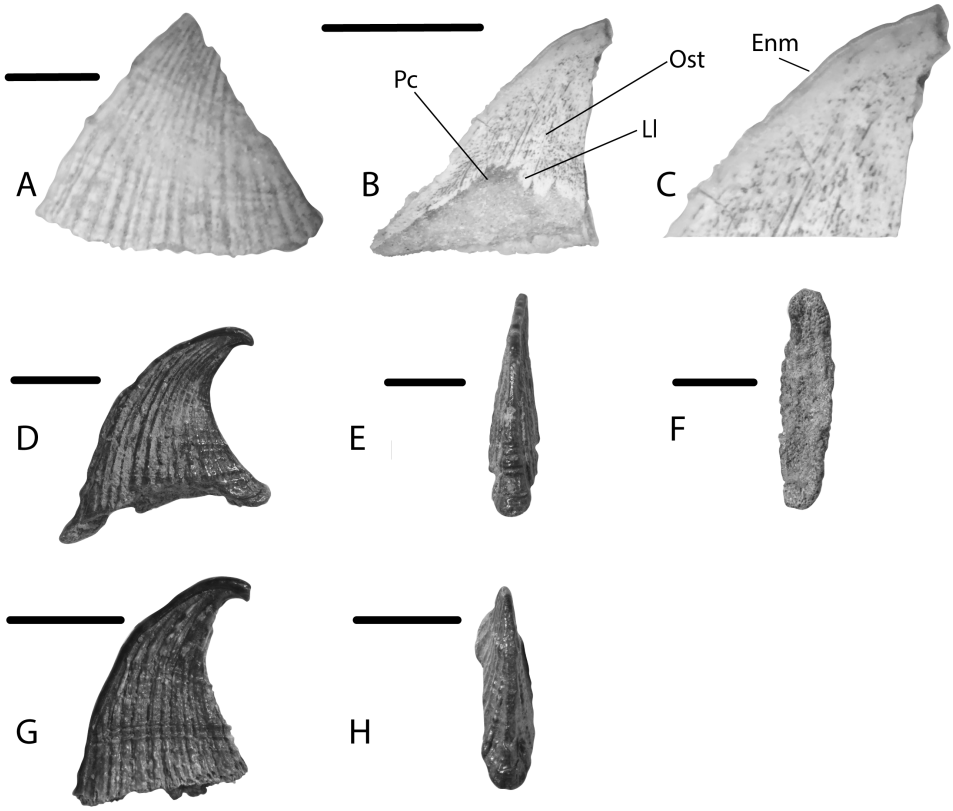

Figure 17. Enlarged dermal denticles of †*Onchopristis numidus* from the "Kem Kem Beds". A-C. B-C, C.U personal collection, longitudinal section and close-up of the enameloid layer

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.

PHYLOGENETIC ANALYSIS

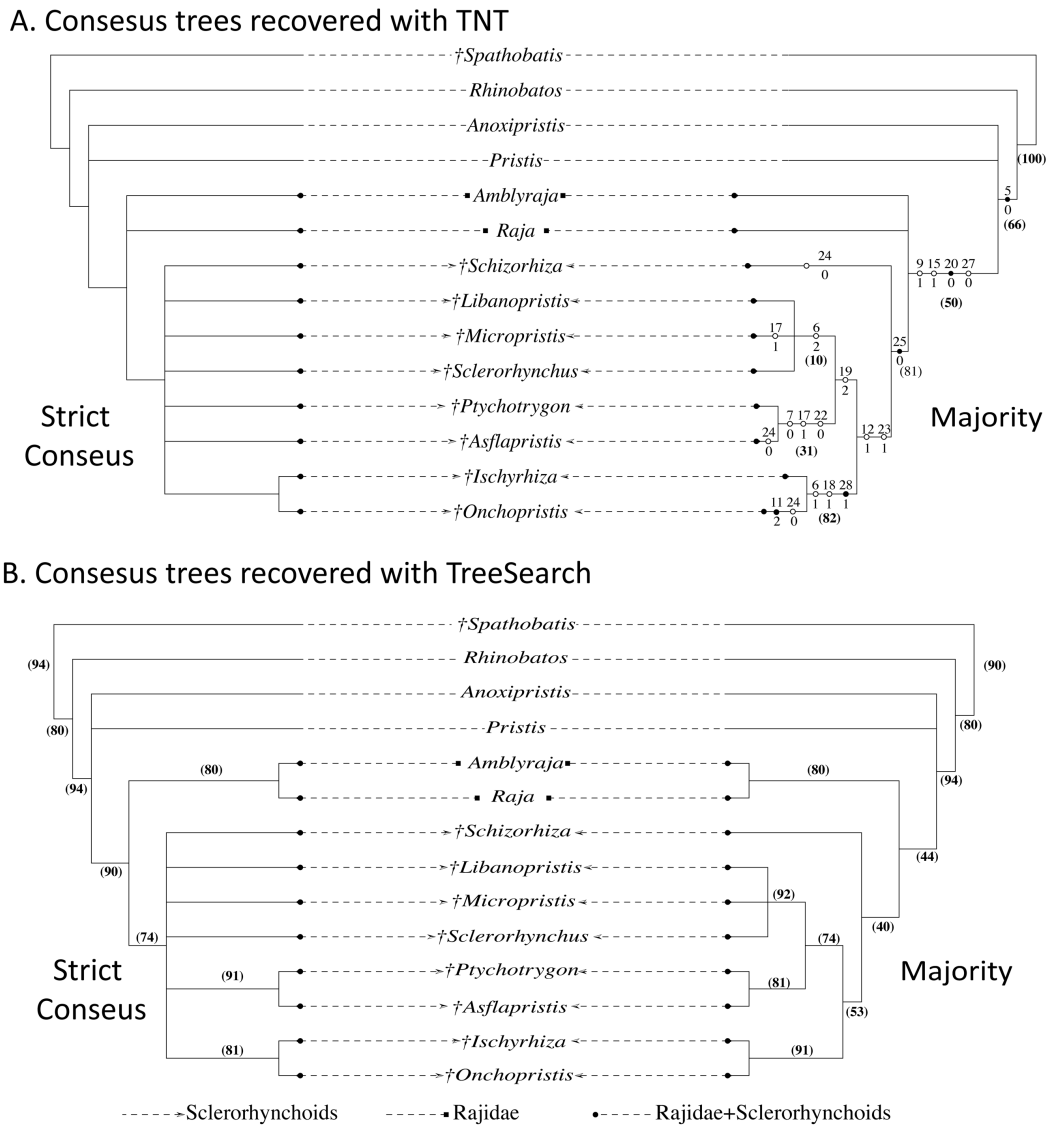

Figure 18. Phylogenetic trees recovered by the different analysis used in the present study. (A) strict consensus and majority rule trees produced by the TNT analysis. (B) strict consensus and majority rule trees produced by the TreeSearch analysis: Clade support values from the Jackknife analysis displayed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

630 majority rule tree (MRT): Black circles characters recovered by both consensus methods;
631 White circles characters recovered only by MRT.
632
633 The character matrix for the phylogenetic analysis used here is a modified version from
634 that used by Villalobos *et al.* (2019b). The main changes include recoding of the polymorphic
635 characters 5, 6 and 9, which were changed for *Raja* and *Amblyraja* (see supplement material;
636 Character discussion). These features refer to the absence/presence of malar thorns, which are
637 developed only in male rays (Aschliman *et al.,* 2012). Three different coding schemes were
638 considered for these characters, that included removing those characters, leaving them as a
639 polymorphic character and coding them as presence, small topological changes resulted from
640 these different codifications (supplement material). However, we consider that regardless of
641 the sexual dimorphism link of these characters, the malar thorns are features that correspond
642 to the genera and should be coded as present.
643 Character 20 (absence/presence of a differentiated lateral uvula on the teeth), was
644 changed for *Anoxypristis* to present as its teeth show a variably developed lateral uvula (e.g.
645 Underwood *et al.,* 2011; Cappetta, 2012), but in general, seems to be present.
646 Character 24 (absence/presence of a lingual uvula in the teeth) was changed for
647 †*Ptychotrygon*, following the observations made on †*Ptychotrygon rostrispatula* by
648 Villalobos *et al*. (2019b) and four characters were included (Chrs. 25-29) to increase the
649 morphological variance observed within sclerorhynchoids.
650 The TNT analysis recovers 13 most parsimonious trees of 41 steps with a consistency
651 index of 0.78 and a retention index of 0.85, whereas the TreeSearch analysis recovered a 41
652 steps tree. Both strict consensus trees (Treesearch and TNT) place all sclerorhynchoids taxa,
653 including †*Schizorhiza* into a polytomy (Fig. 18 A-B, clade support Cs (strict) = 74%, Cs
654 (majority) = 40%). In both strict consensus and majority rule trees this clade is supported by

655 one shared feature, the lack of a rostral appendix (Fig. 18 A, Character (Chr.) = 25, 0,
656 Consistency index (Ci) = 1) which refers to the absence of thin cartilage attached to the rostrum
657 (see, character discussion in supplementary material). However, the compared anatomy of the
658 process occurring within sclerorhynchoids is unique. In Myliobatiformes, the rostral appendix
659 is polymorphic, some groups present it (e.g. *Urotrygon* and *Potamotrygon*) and others do not
660 (e.g. *Rhinoptera* and *Zanobatus*). The development of this structure in Myliobatiformes
661 corresponds to the anteromedial growth of the trabecula (i.e. the rostral shaft or rostral
662 cartilage) (Miyake *et al*., 1992). In platyrhinoids the trabecula does not present mid growth, as
663 a result the appendix is absent, also these taxa develop as similar structure which is referred as
664 a rostral process by McEachran & Aschliman (2004) and Aschliman *et al*. (2012). Within
665 torpedinids, the development of the rostrum varies with different embryonic cartilages
666 participating in its formation (e.g. In *Torpedo* the rostral cartilages develop from the lamina
667 orbitonasalis, whereas in *Narcine* the rostral cartilages derive from the trabecula, which also
668 presents different chondrification periods) (Miyake *et al*., 1992). In comparison, the
669 development of rostral cartilages in sclerorhynchoids appears simpler, as they present a good
670 anteromedial growth with no apparent rostral appendix (similar to that of sawsharks),
671 suggesting a convergence between sclerorhynchoids and sawsharks, considering the
672 anatomical differences between these shark and batoid groups (i.e. presence of synarcual and
673 antorbital cartilages). The sclerorhynchoid clade is placed in a sister relation to the Rajidae
674 (*Amblyraja* and *Raja*, Fig. 18 A-B, Cs = 80%). The monophyletic group Rajidae +
675 Sclerorhynchoids (Fig. 18 A-B, Cs (strict) = 90%, Cs (majority) = 44%), is supported by four
676 shared features in the majority rule tree and one in the strict consensus (Fig. 18 A). Both trees
677 place the lack of differentiated lateral uvula in teeth (Fig. 18 A, Character (Char.) = 20, 0, Ci =
678 1) as a shared synapomorphy (see, character discussion in supplementary material). It is worth
679 mention that sclerorhynchoids are not the only batoids lacking these projections. All

680 sclerorhynchoids dentitions reviewed here lack these structures, suggesting more than just a
681 diet adaptation.

682 Within the sclerorhynchoids clade, two monophyletic groups are recovered by the strict
683 consensus tree estimated with TreeSearch and one with TNT analyses (Fig. 18 A). Both
684 analyses coincide in the grouping of †*Onchopristis*, and †*Ischyrhiza* as a monophyletic group
685 (Fig. 18 A-B, Cs (strict) = 81%, Cs (majority) = 91%). This relation is supported by one
686 common synapomorphy in both strict consensus and majority rule trees, that is the presence of
687 smaller denticles with a round cap associated with the base of the enlarged rostral denticles
688 (Fig. 18 A, Character (Char.) = 28, 1, Ci = 1). The majority tree rule recovered two more shared
689 features for the †*Onchopristis* and †*Ischyrhiza* clade, the reason why these characters are not
690 considered a synapomorphy and do not appear in the strict consensus tree (Fig. 18 A) is the
691 presence of ambiguity; for character 18 (Ci = 1) the coding of †*Schizorhiza* (?) creates
692 ambiguity. While, for character 6 (Ci = 1) the uncertainty comes from the collapse of the
693 †*Libanopristis*, †*Micropristis*, †*Sclerorhynchus*, †*Ptychotrygon* and †*Asflapristis* clade (Fig.
694 18 A-B, Cs (majority) = 74%). Of the features, the presence of large denticles associated with
695 the body (Char. 18, 1) is significant as †*Onchopristis* and †*Ischyrhiza,* as they are currently the
696 only sclerorhynchoids presenting this feature, supporting the closer relationships found
697 between these taxa by the present analysis.

698 The strict consensus tree estimated with the TreeSearch analysis is better resolved than
699 that of the TNT analysis, recovering another monophyletic group that includes †*Asflapristis* +
700 †*Ptychotrygon* (Fig. 18 B, Cs (strict) = 91%, Cs (majority) = 81%). Three features support the
701 relation (see MRT, Fig. 18 A); (1) lack of enlarged denticle series associated to the rostral
702 cartilages (Char. 7, 0, Ci = 1), (2) presence of a transversal crest on teeth (Char. 17, 1, Ci = 1)
703 and (3) lack of calcified suprascapula (Char. 22, 0, Ci = 0.5) (see, character discussion in
704 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). However, while there is a strong phylogenetic support for accommodating †*Onchopristis* and †*Ischyrhiza* in a single family (i.e. †Ischyrhizidae Cope, 1875), we argue for the formation of the family †Onchopristidae, as resurrecting Cope's (1875) †Ischyrhizidae would be taxonomically risky because the genus with the most complete fossil record is †*Onchopristis*. Consequently, it is expected that both taxa would be differentiated if more complete material of †*Ischyrhiza* turns up resulting in excluding †*Onchopristis* from the family it diagnoses. As such †Onchopristidae is diagnosed by the presence of the following characters: (proposed 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); and (5) two series of enlarged denticles with acute cap associated with the latera regions of the rostrum and head (Char 6, 1, Ci = 1); (6) a symmetric addition of rostral denticles with denticles of different sizes being periodically added (Char = 11, 2, Ci = 1); and (7) rostral denticles with a cap of filled with orthodentine (Char = 24, 0, Ci = 1). This combination of characters is unique compared to other sclerorhynchoids and differentiates †Onchopristidae from any other taxon tentatively assigned to it (†*Schizorhiza* and †*Ischyrhiza*). Therefore, the

754 similarities in rostral morphology similarities (e.g. wood-like mineralization and the presence
755 of a lateral layer of porous cartilage on the sides of the rostrum) seems more likely to be a
756 convergent development since the addition and replacement of their rostral denticles seems
757 radically different (Character 11) and requires more complete material of †*Ischyrhiza* to
758 evaluate the status of this character in more detail.

759 There are some other uncertainties concerning the taxonomic hierarchy of the
760 ptychotrygonoids. Villalobos *et al*. (2019b) suggest a placement within the Sclerorhynchidae
761 family, based on similarities in their tooth morphology with those of †*Libanopristis* (i.e.
762 present transverse crests in the labial apron, see Cappetta, 1980b, text-fig 7 B; 2012, text-fig.
763 368 I, in present analysis character 17). However, the teeth of †*Libanopristis* present a more
764 prominent cusp, and the labial apron is less ornamented than that of ptychotrygonoids. In
765 †*Ptychotrygon* there is a deep central interlocking depression. Cappetta (1980) also indicated
766 a lingual depression for some teeth of †*Libanopristis hiram*, but there are no clear illustrations,
767 and we were unable to determinate if he refers to the lingual profile of the cusp below the apex
768 or a region on the lingual uvula. Considering the present results, where ptychotrygonoids form
769 a monophyletic group in by the strict consensus of TreeSearch with relatively high support
770 (Fig. 18 B, Cs (strict) = 91% and Cs(majority) = 81%), a similar arrangement to
771 †Onchopristidae is proposed for the †*Ptychotrygon* and †*Asflapristis* clade resurrecting the
772 family †Ptychotrygonidae *sensu* Kriwet *et al*. (2009). The TNT majority rule tree and the clade
773 support analysis corroborates this placement (Fig. 18 A Cs = 31). Members of
774 †Sclerorhynchidae are differentiated form †Ptychotrygonidae in the presence of enlarged
775 denticle series associated with the rostrum (lateral and both ventral (lateral and central) series
776 (Char = 7, Ci = 1, Char = 8, Ci = 1) and the presence of highly ornamented teeth with transversal
777 crests in members of †Ptychotrygonidae, (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 clades form part different groups which shares no immediate ancestor with †Sclerorhynchidae. 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 genera †*Schizorhiza* and †*Ischyrhiza* 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 their rostrum suggests its classification within †Onchopristidae. However, considering that no cranial remains are known for both genera and that no enlarge body denticles are known for †*Schizorhiza*, and its highly specialised replacement pattern of the lateral series of rostral denticles, their phylogenetic relationships within Sclerorhynchoidei remain uncertain for the moment.

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 canals covered with an external layer of "wood-like". Two series of enlarged denticles with acute cap associated with the lateral regions of the rostrum and head, of which the lateral rostrum series shows smaller denticles with a round cap associated with their base. Symmetric addition of rostral denticles with denticles of different sizes being periodically added. Rostral denticles with a cap of filled with orthodentine. Large denticles are associated with the body (also see, Sternes & Shimada, 2019 for †*Ischyrhiza*).

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 but are 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 peculiar neurocranial and rostral anatomy of the †*Onchopristis* remains described here, with their rectangular shape of the post-nasal region, a reduced post-orbital process, an anterior fenestra located at the base of the rostral cartilages, and the lack of foramina or cavities at the base of the rostral cartilages for the supra ophthalmic nerve, confirm previous hypotheses

that include the placement of †*Onchopristis* within the Sclerorhynchoidei (Cappetta, 1987; 2006; 2012). However, previous genus affiliations to the family Sclerorhynchidae are doubtful and not supported here, as the rostral anatomy and the 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*. Following the phylogenetic analysis, three monophyletic clades are recognised within Sclerorhynchoidei, which based on their differences in their rostral cartilages and dental morphologies are interpreted as families by the present study: †Sclerorhynchidae, †Onchopristidae and †Ptychotrygonidae. Recognising a new group within the Sclerorhynchoidei, the family †Onchopristidae that includes a single the genus †*Onchopristis*.

ACKNOWLEDGEMENTS

We thank the NHMUK for the use of their facilities and equipment for the preparation of the specimens, and M. Graham for the training in the use of the equipment. We also thank Emma Bernard at the NHMUK for her help with access to and curation of fossil specimens. We also thank the preparation team at the Institute of Palaeontological Research at the University of Vienna for their curation work. We are particularly indebted to Brahim Tahiri, Moha Ouhouiss, Hamad and Moha Segaoui who let us purchase the specimens at very reasonable prices and guide us through the localities. We also thank Bernard Hogrel kindly providing the Rennes specimen and Damien Gendry for the photographs of the Rennes specimen. We also want to thank Tyler Greenfield for his observation regarding the taxonomic classification proposed here. Thanks to the CONACYT for the PhD Scholarship. Finally, we want to thank Todd Cook, an anonymous reviewer and editor for their comments and guidance on the early draft of this paper.

LITERATURE CITED

Aschliman NC, Claeson KM, McEachran JD. 2012. Phylogeny of Batoidea. In: Carrier JC, Musick JA, Heithaus MR, eds. *Biology of Sharks and Their Relatives*. Florida: CRC Press, Boca Raton, 57–95.

Belvedere M, Jalil NE, Breda A, Gattolin G, Bourget H, Khaldoune F, Dyke GJ. 2013. Vertebrate footprints from the Kem Kem Beds (Morocco): A novel ichnological approach to faunal reconstruction, *Palaeogeography, Palaeoclimatology, Palaeoecology* **383:** 52–58.

Bernardez E. 2002. *Los dientes de seláceos del Cretácico de la Depresión Central Asturiana*. Unpublished D. Phil. Thesis, University of Oviedo.

Brazeau, MD. 2011. Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society* **104**: 489–498.

Brazeau MD, Guillerme T, Smith MR. 2019. An algorithm for Morphological Phylogenetic Analysis with Inapplicable Data, *Systematic Biology* **68:** 619–631.

Cappetta H. 1980. Les sélaciens du Crétacé supérieur du Liban. II. Batoïdes, *Palaeontographica, Abteilung A* **168:** 149–229.

Cappetta H. 1987. *Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. Handbook of Paleoichthyology, Volume 3B*. Gustav Fisher Verlag, Stuttgart.

Cappetta H. 2006. *Fossilium Catalogus, I: Animalia.* Backhuys Publishers, Leiden, Netherlands.

Cappetta H. 2012. *Chondrichthyes: Mesozoic and Cenozoic Elasmobrachii: Teeth, Volume 3E*. Gustav Fischer Verlag. München.

Cavin L, Forey LP. 2004. New mawsoniid coelacanth (Sarcopterygii: *Actinistia*) remains from the Cretaceous of the Kem Kem Beds, Southern Morocco. In Arriatia G, Tintori A, eds. *Mesozoic fishes Systematics Paleoenvironments and Biodiversity, Volume 3*. München: Verlag Dr. Friedrich Pfeil, 101–109.

Cavin L, Tong H, Boudad L, Meister C, Piuz A, Tabouelle J, Aarab M, Amiot R, Buffetaut E, Dyke G. 2010. Vertebrate assemblages from the Early-Late Cretaceous of southeastern Morocco: an overview, *Journal of African Earth Sciences* **57:** 391–412.

Claeson KM, Underwood CJ, Ward DJ. 2013. †*Tingitanius tenuimandibulus*, a new platyrhinid batoid from the Turonian (Cretaceous) of Morocco and the Cretaceous radiation of the Platyrhinidae, *Journal of Vertebrate Palaeontology* **33:**1019–1036.

Cope ED, 1875. The vertebrata of the Cretaceous formations of the west: Report of the United States Geological Survey of Territories, **2:** 1–303.

Cuny G, Ouaja M, Srarff D, Schmitz L, Buffetaut E. 2004. Fossil sharks from the Early Cretaceous of Tunisia. *Revue de Paléobiologie* **9:** 127–142.

De Lapparent AF, Gorce F. 1960. The dinosaurs of the "Continental Intercalaire" of the central Sahara. *Memoirs of the Geological Society of France* **39:** 1–57.

Douady CJ, Dosay M, Shivji MS, Stanhope MJ. 2003. Molecular phylogenetic evidence refuting the hypothesis of Batoidea (rays and skates) as derived sharks. *Molecular phylogenetics and evolution* **26**: 215–221.

Dutheil BD. 1999. An overview of the freshwater fish fauna from the Kem Kem Beds (Late Cretaceous: Cenomanian) of Southeastern Morocco. In: Arratia G, Schultze HP, eds. *Mesozoic Fishes Systematics and Fossil Record*, *Volume 2.* München: Verlag Dr. Friedrich Pfeil, 553–563.

Ettachfini EM, Andreu B. 2004. Le cénomanien et le turonien de la plateforme préafricaine du Maroc. *Cretaceous Research* **25:** 277–302.

Fricke R, Eschmeyer WN, van der Laan R. 2020. Eschmeyer's catalog of fishes: genera, species, references at: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp, accessed 9 June 2020.

Goloboff PA, Farris J, Nixon K. 2013. TNT: Tree Analysis Using New Technology. Updated at: http:// www.lillo.org.ar/phylogeny/tnt/, accessed 12 January 2019.

Haug E. 1905. Paléontologie. Documents scientifiques de la Mission saharienne (Mission Foureau-Lamy). Publication de la Société de Géographie **1905:** 751–832.

Huxley TH. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London. Zoological Society of London* **1880:** 649–662 pp.

Ibrahim N, Sereno PC, Varricchio DJ, Martill DM, Dutheil DB, Unwin DM, Baidder L, Larsson HCE, Zouhri S, Kaoukaya A. **2020.** Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. ZooKeys 928: 1–216. https://doi.org/10.3897/zookeys.928.47517

Keyes IW. 1977. Records of the northern hemisphere Cretaceous Sawfish genus Onchopristis (order Batoidea) from New Zealand. *New Zealand Journal of Geology and Geophysics* **20**:263-272.

Kilian C. 1931. Des principaux complexes continentaux du Sahara. *Comptes Rendus Sommaires de la Société Géologique de France* **9:** 109–111.

Kirkland J, Aguillón-Martínez, M. 2002. *Schizorhiza*: a unique sawfish paradigm from the Difunta group, Coahuila, México. *Revista Mexicana de Ciencias Geológicas* **19**(1):16–24.

Kriwet J. 1999. Neoselachier (Pisces, Elasmobranchii) aus der Unterkreide (unteres Barremium) von Galve und Alcaine (Spanien, Provinz Teruel). *Paleo Ichthyologica* **9:** 113–142.

Kriwet, J. 2004. The systematic position of the Cretaceous sclerorhynchid sawfishes (Elasmobranchii, Pristiorajea). In: Arratia G, Schultze HP, eds. *Mesozoic Fishes Systematics and Fossil Record*, *Volume 3.* München: Verlag Dr. Friedrich Pfeil, 57-73.

Kriwet J, Kussius K. 2001. Paleobiology and paleobiogeography of sclerorhynchid sawfishes (Chondrichthyes Batomorphii). *Revista Española de Paleontología* **16:** 35-46.

Kriwet J, Nunn EV, Klug S. 2009. Neoselachians (Chondrichthyes, Elasmobranchii) from the Lower and lower Upper Cretaceous of north-eastern Spain. *Zoological Journal of the Linnean Society* **155:** 316–347.

Läng E, Boudad L, Maio L, Samankassou E, Tabouelle J, Tong H, Cavin L. 2013. Unbalanced food web in a Late Cretaceous dinosaur assemblage. *Palaeogeography, Palaeoclimatology, Palaeoecology* **381:** 26–32.

Leidy J. 1856. Notice of some remains of fishes discovered by Dr. John E. Evans. *Proceedings of the Academy of Natural Science of Philadelphia* **8:** 256–257.

Maddison WP, Maddison DR. 2018. Mesquite: A Modular System for Evolutionary Analysis. Version 3.51 Available at http://mesquiteproject.org.

Mannion PD, Barrett PM. 2013. Additions to the sauropod dinosaur fauna of the Cenomanian (early Late Cretaceous) Kem Kem Beds of Morocco: Palaeobiogeographical implications of the mid-Cretaceous African sauropod fossil record. *Cretaceous Research* **45:** 49–59

Martill DM, Ibrahim N. 2012. Aberrant rostral teeth of the sawfish *Onchopristis numidus* from the Kem Kem Beds (? early late cretaceous) of Morocco and a reappraisal of *Onchopristis* in New Zealand. *Journal of African Earth Sciences* **64:** 71–76.

McEachran JD, Aschliman N. 2004. Phylogeny of Batoidea. In*:* Carrier JC, Musick JA, and Heithaus MR, eds. *Biology of sharks and their relatives*. Florida: CRC Press, Boca Raton 79–113.

McNulty CL, Slaughter BH. 1962. A new sawfish from the Woodbine Formation (Cretaceous) of Texas. *Copeia* **1962:** 775–777.

Miller W. 1974. Observations on the Developing Rostrum and Rostral Teeth of Sawfish: *Pristis perotteti* and *P. cuspidatus*. *Copeia* **1974**: 311-318.

Morgan DL, Whitty JM, Phillips NM, Thorburn DC, Chaplin JA, McAuley R. 2011. North-western Australia as a hotspot for endangered Elasmobranchs with particular reference to sawfishes and the Northern river Shark. *Journal of the Royal Society of Western Australia* **94:** 345–358.

Miyake T, McEachran JD, Walton PJ, Hall BK. 1992. Development and morphology of rostral cartilages in batoid fishes (Chondrichthyes: Batoidea), with comments on homology within vertebrates. *Biological Journal of the Linnean Society* **3:** 259–298.

Naylor GJ, Caira JN, Jensen K, Rosana KA, Straube N, Lakner C. 2012. Elasmobranch phylogeny: A mitochondrial estimate based on 595 species. In: Carrier JC, Musick JA, Heithaus MR, eds. *Biology of Sharks and Their Relatives*. Florida: CRC Press, Boca Raton, 31–56

Néraudeau D, Vullo R, Gomez B, Vincent P, Videt B. 2005. Stratigraphie et paléontologie (plantes, vertébrés) de la série paralique Albien terminal–Cénomanien basal de Tonnay-Charente (Charente-Maritime, France). *Compte Rendus Palevol* **4**: 79–93.

Pereira AA, Mdeiros MA. 2008. A new Sclerorhynchiform (Elasmobranchii) from the middle Cretaceous of Brazil. *Revista Brasileira de Paleontologia* **11**: 207–212.

Rage JD, Dutheil DB. 2008. Amphibians and squamates from the Cretaceous (Cenomanian) of Morocco. A preliminary study, with description of a new genus of pipid frog. *Palaeontographica Abteilung A* **285:** 1–22.

Sereno PC, Dutheil DB, Iarochène M, Larsson HCE, Lyon GH, Magwene PM, Sidor CA, Varricchio DJ, Wilson JA. 1996. Predatory Dinosaurs from the Sahara and Late Cretaceous Faunal Differentiation. *Science* **272:** 986–991.

Slaughter BH, Steiner M. 1968. Notes on Rostral Teeth of Ganopristine Sawfishes, with Special Reference to Texas Material. *Journal of Paleontology* **42:** 233–239.

Slaughter BH, Thurmond JT. 1974. A Lower Cenomanian (Cretaceous) ichthyofauna from the Bahariya Formation of Egypt. *Annals of the Geological Society, Egypt* **4:** 25–40.

Smith MM, Riley A, Fraser GJ, Underwood CJ, Welten M, Kriwet J, Pfaff C, Johanson Z. 2015. Early development of rostrum saw-teeth in a fossil ray tests classical theory of the evolution of vertebrate dentitions. *Proceedings of the Royal Society B: Biological Sciences* **282:** 20151628.

Sternes PC, Shimada K. 2019. Paleobiology of the Late Cretaceous sclerorhynchid sawfish, *Ischyrhiza mira* (Elasmobranchii: Rajiformes), from North America based on new anatomical data. *Historical Biology* **31:** 1323–1340.

Stromer E. 1917. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wiisten Agyptens. 11. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 4: Die Sage des Pristiden *Onchopristis*. *Abhandlungen de Bayerischen Akademie der Wissenchaften, Mathematish-naturwissenschaftliche Abteilung* **28:** 1–31 pp.

Stromer E. 1925. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wiisten Agyptens. 11. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 8. Ein Skelettrest des Pristiden *Onchopristis numidus* Haug sp. *Abhandlungen de Bayerischen Akademie der Wissenchaften, Mathematish-naturwissenschaftliche Abteilung* **30:** 1–22.

Stromer E. 1927. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wiisten Agyptens. 11. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 9. Die Plagiostomen mit einem Anhangiiber kano und mesozoische Riickenflossenstacheln von Elasmobranchiern. *Abhandlungen de Bayerischen Akademie der Wissenchaften, Mathematish-naturwissenschaftliche Abteilung* **31:** 1–67.

Thurmond JT. 1971. Cartilaginous fishes of the Trinity Group and related rocks (lower Cretaceous) of north central Texas. *Southeastern Geology* **13:** 207–227.

Underwood CJ, Claeson K. 2017. The Late Jurassic ray *Kimmerobatis etchesi* gen. *et* sp. nov. and the Jurassic radiation of the Batoidea. *Proceedings of the Geologists Association* **30:** 345–354

Underwood CJ, Smith MM, Johanson Z. 2016. *Sclerorhynchus atavus* and the convergent evolution of rostrum-bearing chondrichthyans. *Geological Society, London, Special Publications* **430:** 129–136.

Underwood CJ, Ward DJ, King C, Antar SM, Zalmout IS, Gingerich PD. 2011. Shark and ray faunas in the Middle and Late Eocene of the Fayum Area, Egypt. Proceedings of the Geologists' Association **122:** 47–66.

Villalobos-Segura E, Underwood CJ, Ward DJ, Claeson KM. 2019a. The first three-dimensional fossils of Cretaceous sclerorhynchid sawfish: *Asflapristis cristadentis* gen. et sp. nov., and implications for the phylogenetic relations of the Sclerorhynchoidei (Chondrichthyes). *Journal of Systematic Palaeontology* **17:** 1847–1870

Villalobos-Segura E, Underwood CJ, Ward DJ. 2019b. The first skeletal record of the Cretaceous enigmatic sawfish genus *Ptychotrygon* (Chondrichthyes: Batoidea) from the Turonian (Cretaceous) of Morocco. *Papers in Palaeontology* **2019:** 1–24

Vullo R, Néraudeau D, Videt B. 2003. Un faciès de type falun dans le Cénomanien basal de Charente-Maritime (France). *Annales de Paléontologie* **89:** 171–189.

Welten M, Smith MM, Underwood CJ, Johanson Z. 2015. Evolutionary origins and development of saw-teeth on the sawfish and saw shark rostrum (Elasmobranchii; Chondrichthyes). *Royal Society Open Science* **2:** 1–19.

Welton BJ, Farish RF. 1993. *The collector's guide to the fossil sharks and rays from the Cretaceous of Texas*. USA: Before Time.

Werner C. 1989. Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Agypten. *Palaeo Ichthyologica* **5:** 1–112.

Whitty JM, Phillips NM, Thorburn DC, Simpfendorfer CA, Field I, Peverell SC, Morgan DL. 2014. Utility of rostra in the identification of Australian sawfishes (Chondrichthyes: Pristidae). *Aquatic Conservation: Marine and Freshwater Ecosystems* **24:** 791-804.