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

3

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14 Running head: Skeletal remains of †*Onchopristis*

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27 Abstract. We present the first known cranial remains of the fossil batoid †*Onchopristis*
28 *numidus*. Based on two exceptionally well preserved specimens collected from the “Kem Kem
29 Beds” (Albian-Cenomanian), South-East of Morocco, an almost complete description of the
30 rostral and cranial portions of the genus †*Onchopristis* is provided, together with new
31 observations regarding the development and arrangement of the rostral denticle series for this
32 genus. The comparison between the rostrum length of the specimens of †*Onchopristis*
33 *numidus* with those of extant pristids revealed a relatively large batoid species with an
34 estimated total length between two to four meters. Overall, the cranial morphology of
35 †*Onchopristis* resembles that of other sclerorhynchoids. Its robust hypertrophied rostrum with
36 the characteristic wood-like mineralisation covering the inner layer of tessellate cartilage at the
37 centre of the rostrum, in addition to the thick lateral layers of densely porous cartilage on the
38 sides of the rostral cartilages, resembles that observed in †*Ischyrhiza* and †*Shizorhiza*, and
39 differentiates †*Onchopristis* from other sclerorhynchoid (e.g. †*Micropristis*,
40 †*Sclerorhynchus* and †*Libanopristis*). Aiming to determinate a phylogenetic relations of
41 †*Onchopristis* within sclerorhynchoids a cladistic analysis carried out based on the remains
42 described here, its results suggest a new taxonomic arrangement within sclerorhynchoids.

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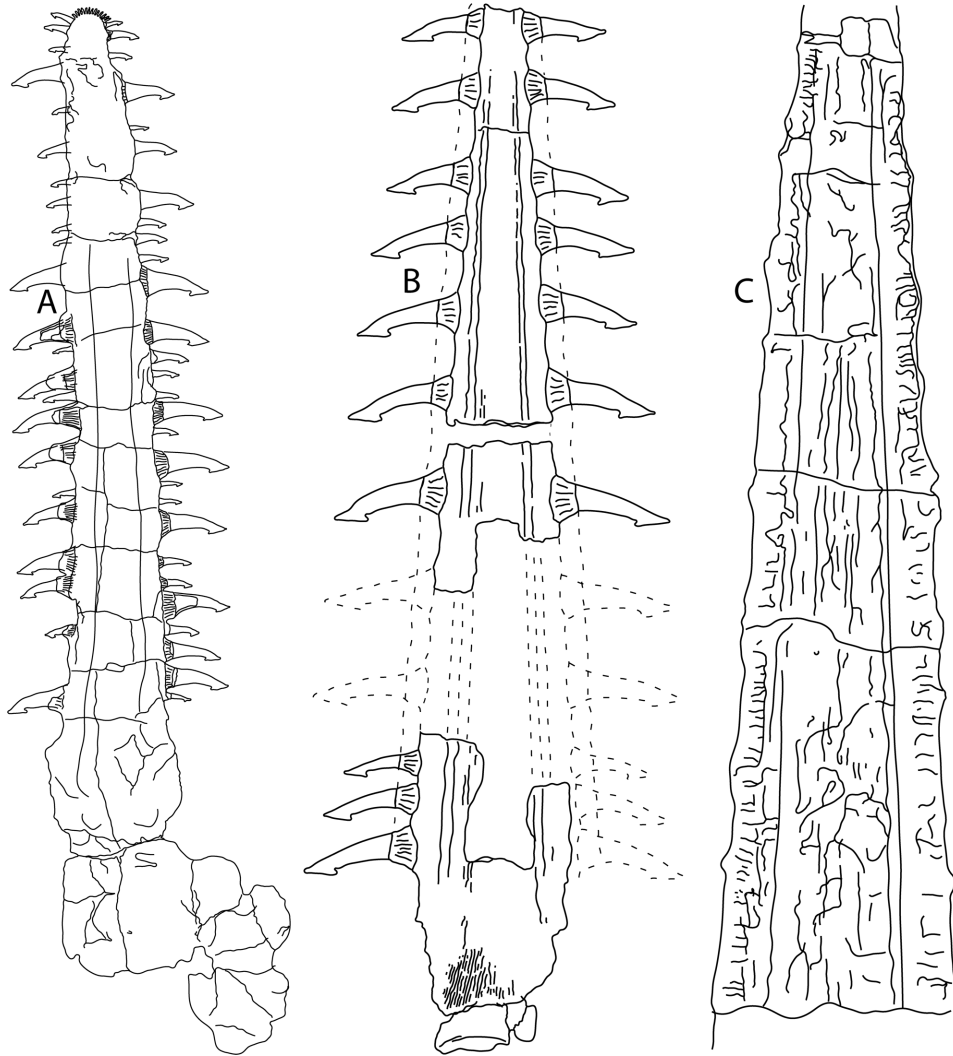
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INTRODUCTION

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47 †*Onchopristis* Stromer, 1917 is a puzzling Cretaceous batoid taxon, with most of its
48 fossil record being recorded from many ‘mid’ Cretaceous sites in coastal and fluvial settings.
49 The taxon was first described based only on rostral fragments and denticles (Haug, 1905;
50 Stromer, 1917; 1925) (Fig. 1) with the teeth being described as †*Squatina aegyptiaca* by
51 Stromer (1927), but later assigned to †*Onchopristis* by Slaughter & Thurmond (1974) (see also
52 Cappetta, 1987). Werner (1989) rejected this interpretation and assigned the teeth associated

53 with †*Onchopristis numidus* erroneously to a new taxon, †*Sechmetia aegyptiaca*. Currently,
54 †*Onchopristis* is placed systematically in the suborder †Sclerorhynchoidei within the family
55 †Sclerorhynchidae (Cappetta, 2012), although this affiliation has not been tested
56 phylogenetically.



57
58 **Figure 1.** A. Rostral remains figured in Stromer (1925; TL 1450 mm). B-C. Rostral remains
59 figured in Stromer (1917; B, TL. 260 mm. C, TL. 520 mm).

60 The genus is restricted to the Barremian-Cenomanian (Kriwet, 1999) and presently
61 includes only two valid species (†*Onchopristis numidus* and †*O. dunklei*, see Table 1).
62 †*Onchopristis numidus* (Haug, 1905) occurs in the Albian of Djoua, Algeria (Cappetta, 1987),
63 the Cenomanian of Egypt (Stromer, 1927; Slaughter & Thurmond, 1974; Werner, 1989), the

64 Albian-Cenomanian of Morocco (Cappetta, 1980). It should, however, be noted that the exact
 65 stratigraphic age of many of the North African sites is still in debate.

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

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

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

Type of remains	Original description	Current taxonomic status
Oral	† <i>Squatina aegyptiaca</i> Stromer, 1927	Syn. † <i>O. numidus</i> (Cappetta, 2006)
Oral	† <i>Sechmetia cruciformis</i> Werner, 1989	Syn. † <i>O. dunklei</i> (Cappetta, 2006)
Oral	† <i>Sechmetia aegyptiaca</i> Stromer, 1927	Syn. † <i>O. numidus</i>
Oral and Rostral	† <i>O. dunklei</i> McNulty & Slaughter, 1962	Valid (Cappetta, 2006)
Vertebra	† <i>Platyspondylus foureaui</i> Haug, 1905	Syn. † <i>O. numidus</i> (Cappetta, 2006)
Oral, Rostral and Cranial	† <i>O. numidus</i> (Haug, 1905)	Valid (Cappetta, 2006)
Rostral	† <i>Onchopristis</i> sp. Werner, 1989	Unknown species

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85 The genus †*Onchopristis* can be differentiated from other sclerorhynchoids in the shape
86 and size of its rostral denticles (reaching 7 cm in length). The presence of barbs (hook-like
87 protuberances directed backwards) situated on the posterior margin, along with numerous
88 rectilinear folds along the posterior and anterior margins of the rostral denticles, are key
89 features for their identification. Currently, the two valid species of †*Onchopristis* are
90 differentiated from each other by the number of barbs associated with their rostral denticles:
91 one in †*O. numidus* and several in †*O. dunklei* (Cappetta, 2012). Numerous hypotheses have
92 been proposed to explain the development of this feature. Slaughter & Steiner (1968) suggested
93 that there is an evolutionary tendency to increase the number of barbs associated with the rostral
94 denticles. However, a secondary loss cannot be discarded (i.e. the plesiomorphic state could be
95 additional (more than one) barbs associated with the rostral denticles). McNulty & Slaughter
96 (1962) proposed that the number of barbs is related to the size of the rostral denticles, and as
97 the denticles grow the number of barbs also increases. The presence of multiple barbed
98 denticles (usually two) in specimens from Morocco and Egypt (Stromer, 1917, plate 1; Martill
99 & Ibrahim, 2012, text-fig. 3A-B and 5) (Fig. 7B) renders the use of the barb numbers as a valid
100 character for species determination within †*Onchopristis* problematic. Despite this, the
101 presence of multiple barbs is typical for North American specimens of †*O. dunklei*, but it is a
102 rare feature observed in North African specimens assigned to †*O. numidus*, where these
103 denticles comprise less than 1% of the rostral denticles.

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

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STUDY AREA AND TAPHONOMY

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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).

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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.

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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

135 Ifezouane Formation in the South of the area rests unconformably on the basement and
136 comprises two channelised sandstone units separated by a major channel base surface. Most
137 fossils are known from the channel lag at the base of the upper unit. In the North, there are two
138 channelised sandstones separated by a heterolithic unit of siltstones and rippled sandstones. A
139 gypsum rich mudstone separates these sandstones from the basement below. Fossils are
140 common in both the channelised sandstones and the heterolithic unit, with the specimens
141 described here being collected from the heterolithic unit.

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

158 Lamniform and other elasmobranch shark teeth are present but rare. Tetrapod bone
159 fragments are also prevalent (especially chelonian carapace fragments, crocodilian bone

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

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

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MATERIAL

176 All specimens described here were obtained from Morocco-based commercial sources,
177 with one of them (NHMUK PV P 75502) brought directly at the site of Boufza (UTM Easting
178 353973, UTM Northing 3509602, Zone 30), which facies are not exploited (i.e. commercially
179 used) elsewhere (pers. observ. C. Underwood). Specimen IPUW 353500 presents an almost
180 complete rostrum and an almost complete neurocranium, with only the left nasal cavity,
181 hyomandibula, and some jaw elements missing. Specimen IGR 2818 shows an almost complete
182 rostrum with only the tip and the complete left side of the rostrum missing. The specimens
183 NHMUK PV P 75502 and 75503 are rostral fragments. Additional small specimens of isolated
184 teeth and denticles were largely collected *in situ*, typically from the weathered spoil of

185 commercial excavations and by sieving of sediment gathered near those sites (e.g. Begaa
186 (KK3): UTM Easting 418421, UTM Northing 3418555, Zone 30 and Boufaddouz (KK7):
187 UTM Easting 373009, UTM Northing 3501097, Zone 30).

188 *Institutional abbreviations*

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

191 *Fossil material*

192 †*Asflapristis cristadentis* (NHMUK PV P 73925, 75428 a-e, 75429 a-d, 75431, 75432,
193 75433). †*Ischyrhiza mira* (Sternes & Shimada, 2019; text-fig. 2 a-I, text-fig. 4 a-f, text-fig 5 a-
194 I; Slaughter & Steiner 1968; text-fig. 4A-C). †*Micropristis solomonis* (Cappetta, 1980, pl. 1,
195 fig. 1-4; pl. 2, fig. 1). †*Libanopristis hiram* (Cappetta, 1980, pl. 1, fig. 4; NHMUK PV P
196 108705, 108706, 13858, 63610, 75075). †*Onchopristis numidus* (NHMUK PV P 75502,
197 75503, 1, 74045, 74047, 74050, 74051, 74052, 74053, 74054; IPUW 353500; IGR 2818, 2819,
198 2820, 2821). †*Ptychotrygon rostrispatula* (NHMUK PV P 73630, 75496, 75496, 75497,
199 75500). †*Sclerorhynchus atavus* (Slaughter & Steiner, 1968, text-fig. 4D; NHMUK PV P 4017,
200 4776, 49546, 49518, 49533, 49547). †*Shizorhiza stromeri* (Smith *et al.*, 2015; text-fig. 1a-l;
201 2a-f; NHMUK PV P 73625). †*Spathobatis bugesicus* (NHMUK PV P 6010, 2099 (2); BSP
202 AS I 505, 1952 I 82).

203 *Abbreviations used in the figures*

204 Ac, antorbital cartilage; Alp, anterior lateral process; Bpc, buccopharyngeal nerve
205 cavity; Bre, branchial elements; Cc, corpus calcareum; Cdb, cyclical deposition bar; Den,
206 dermal denticle; Ed, enlarged denticle; Enm, enameloid; Hym, hyomandibula; I, Intermedialia;
207 Ja, jugal arch; Lc, lateral commissure; Lf, lymphatic foramina; Ll, laminar layer, Ls, lateral
208 stays; Mc, medial crest; Mkc, Meckel's cartilage; Oc, occipital condyle; OdP, odontoid
209 process; Of, orbital foramen; Op, optic pedicel; Orb, orbital cavity; Ort, orthodontine; Ost,

210 osteodentine; Pcf, precerebral fenestra; Pop, postorbital process; Pq, palatoquadrate; PrCar,
211 periphery cartilage; Rd, rostral denticle; Sof, spino-ochipital foramina; Sophc, supra
212 ophthalmic nerve cavity; VII, hyomandibular branch of the facial nerve foramen; Wc, Wood-
213 like cartilage.

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METHODS

216 Smaller specimens were field-collected from several sites along the main Kem Kem
217 escarpment. Despite the extensive outcrops, exposures are restricted, and fossiliferous sites are
218 commercially exploited. Spoil is exposed to wind ablation and (rare) rain exposing fossils
219 therein allowing the surface collection of larger specimens and enabling dry sieving through
220 0.5 or 1mm mesh sieves to collect small specimens. Sieved residues were later additionally wet
221 sieved and picked under a microscope.

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

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

232 To determinate the phylogenetic implications of these newly discovered remains of
233 †*Onchopristis* and to test their phylogenetic relations within sclerorhynchoids, a matrix of 14
234 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

260 specimens within the museums. Contingent or reductive coding (Brazeau, 2011) was used as
261 the coding method. Finally, the matrix was analysed using the recently published algorithm of
262 Brazeau *et al.*, (2019) in the R package TreeSearch and compared with the tree resulted from
263 a heuristic search using TNT 1.5 (Goloboff *et al.*, 2013).

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

276

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RESULTS

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SYSTEMATIC PALAEOLOGY

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CHONDRICHTHYES Huxley, 1880

280

BATOMORPHII Cappetta, 1980

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

282

†SCLERORHYNCHOIDEI Cappetta, 1980

283

†*ONCHOPRISTIS* Stromer, 1917

284

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

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DESCRIPTION

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

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(Figs. 2-15)

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291 *Diagnosis*

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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

311 lingual profile is concave with an almost incipient uvula. The root is more prominent than the
312 crown and protrudes laterally, and its vascularisation is holaulacorhize. Large denticles with
313 an enameloid crest on the anterior surface are associated with the body.

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

318

319 *Temporal and spatial distribution*

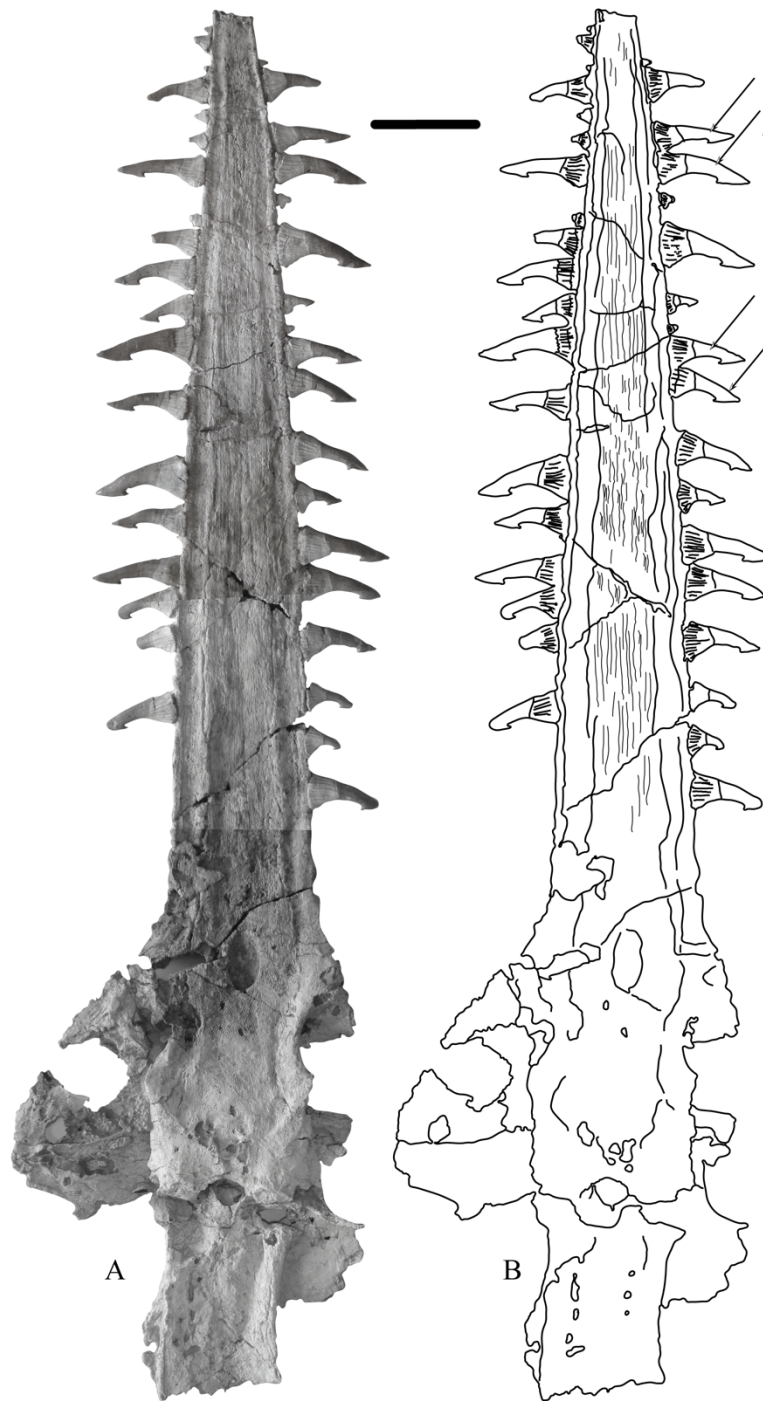
320 Albian- Cenomanian of Africa (Egypt by Werner, 1989: plate 19-20, 23, 35-38) and
321 Morocco by Cappetta (1980) and the present study).

322

323 *Etymology*

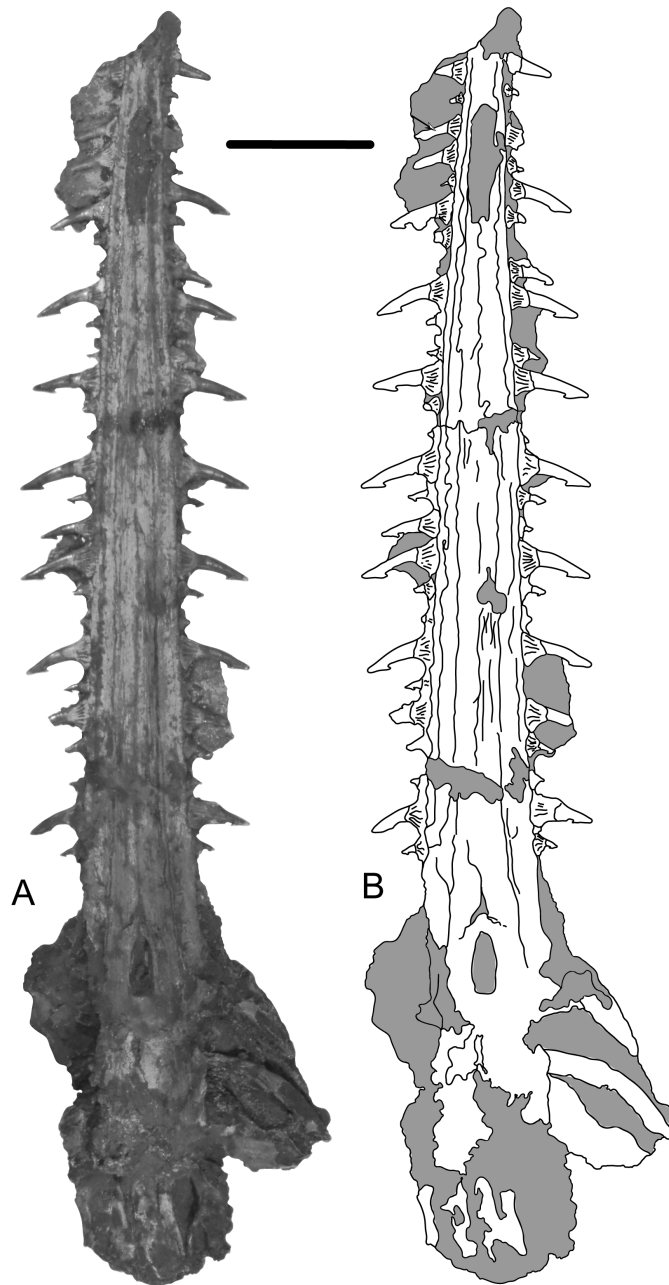
324 Genus: From the Latin ὄγκος (oncos) referring to the protuberance of on the lateral rostral
325 teeth (barb) and πρίστης (pristis) = saw.

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



328

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



332

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

336

337 *Rostrum*

338

339

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

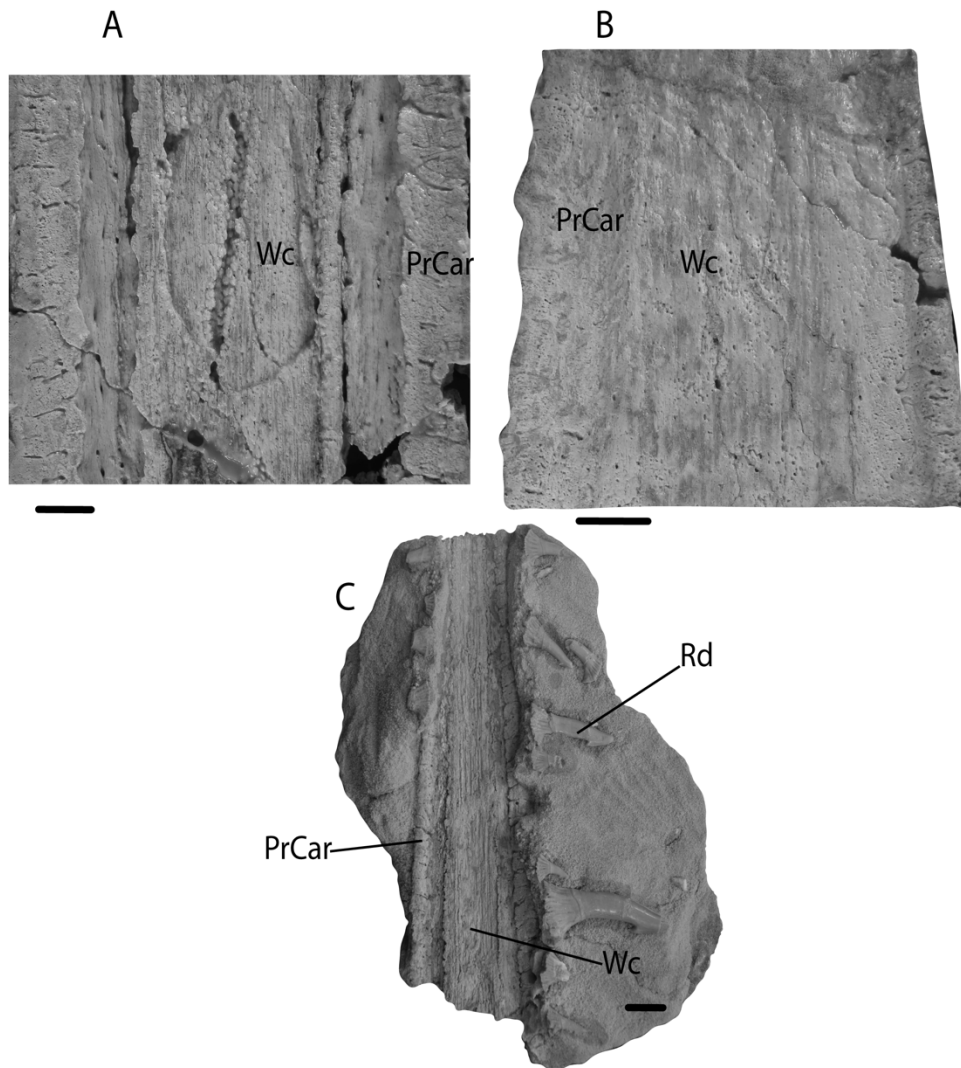
340 base of the rostrum progresses smoothly into the neurocranium. After removal of the sediment,
341 the specimens revealed the presence of a layer of ‘wood-like’ cartilage layer, covering the inner
342 tessellate (mosaic-like) cartilage along the central part of the rostrum. This layer was first
343 observed in †*Onchopristis* by Stromer (1917) and characterised as possible fossilised skin.
344 Later it was described by Cappetta (1980) as the cartilage covering the canals for the
345 ophthalmic nerves in the rostrum. Sternes & Shimada (2019; fig. 2c) describe a similar cartilage
346 type located at the sides of the rostrum of †*Ischyrhiza* next to slight thicker cartilage on the
347 periphery of the rostrum where the lateral rostral denticles are attached.

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

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

362 Towards the centrum of the rostral cartilages and next to the highly porous lateral layer
363 of cartilage, on both the dorsal and ventral surfaces are two canals, one on each side (Fig. 4A-
364 C). The superficial ophthalmic nerve canal runs on the dorsal surface covered by a layer of

365 cartilage and seems to terminate in a cavity next to the supraorbital crest. On the ventral side,
366 the buccopharyngeal nerve canal terminates at the base of the nasal capsules. Both canals
367 become narrower towards the tip of the rostrum, and in several places, are covered by the
368 ‘wood-like’ cartilage suggesting that this cartilage entirely covered the canals.



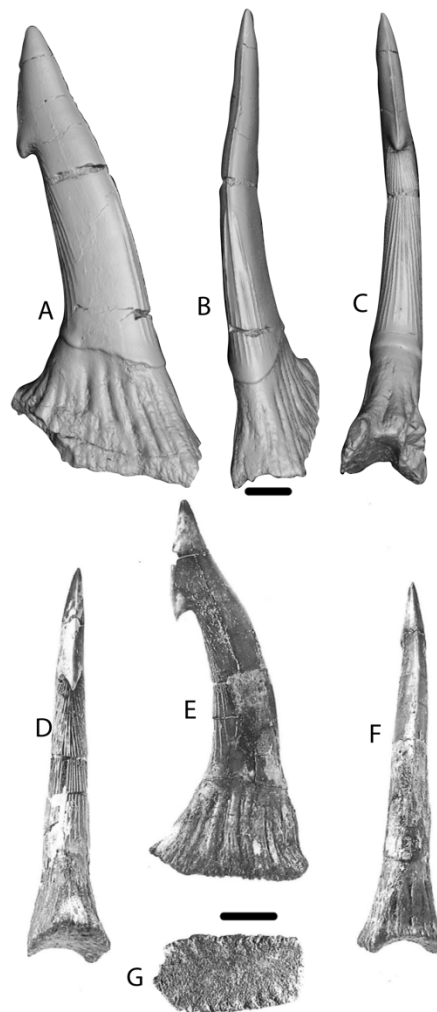
369
370 **Figure 4.** A-C, Rostrum of †*Onchopristis numidus*. A, Ventral surface of IPUW 353500. B,
371 Dorsal surface of IPUW 353500. C, NHMUK PV P 75502. Scale bar: 1cm.

372

373 *Lateral enlarged rostral denticles*

374 All lateral rostral denticles in specimens NHMUK PV P 75502, IPUW 353500 and IGR
375 2818, as well as disarticulated denticles recovered from various sites in the “Kem Kem Beds”,

376 display a small flat base composed mostly of osteodentine and a large-cap composed entirely
377 of orthodentine, with an external layer of enamel, and a characteristic barb on the apical
378 posterior margin of the denticle. Strongly marked cutting edges, accompanied by rectilinear
379 crests, are developed on both anterior and posterior faces of the denticles (Fig. 5). The presence
380 of these cutting edges and the lack of abrasion patterns on the denticles cap suggest that these
381 denticles were not used to probe in the sediment.

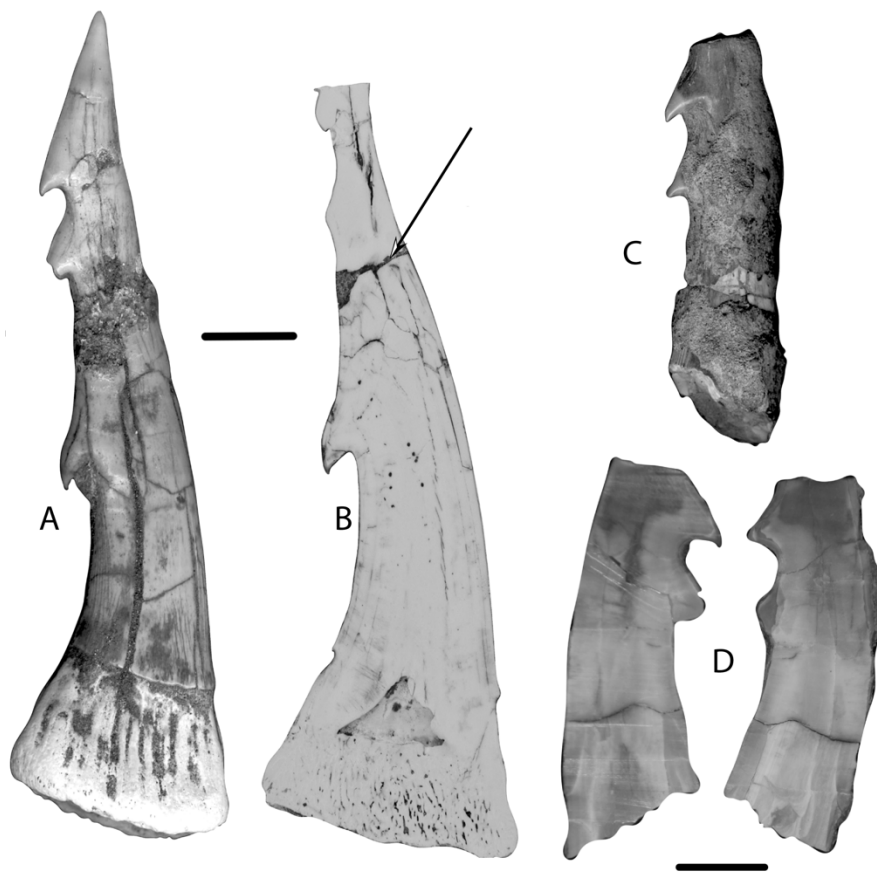


382
383 **Figure 5.** Enlarged rostral denticles of †*Onchopristis*. A–C, micro-CT-based volume rendering
384 of denticle collected along with the specimen IPUW 353500 from Morocco: (A) dorsoventral,
385 (B) anterior, and (C) posterior view. D–G, denticles collected Egypt (Werner, 1989; plate 19,
386 figs. 2a-d): (D) posterior view, (E) dorsoventral, (F) anterior, and (G) base. Scale bar: 1mm.

387

388

389 Denticles with multiple numbers of barbs were sporadically collected in Morocco (Fig
390 6). These denticles have similar dimensions to single barbed denticles, indicating that there is
391 no correlation between denticle size and barb numbers and that the number of barbs is not a
392 function of ontogenetic stages (Fig 6A). The presence of multiple barbed denticles in the
393 Egyptian and Moroccan localities suggests the sporadic development of double and even triple
394 barbed denticles within †*Onchopristis numidus* (Stromer, 1917; plate 1 fig. 9 and 1; Werner,
395 1989; plate 20, fig. 1a and 1b, 3 and 6-7) including a three barbed specimen (Wegner, 1989;
396 plate 20, fig. 5).



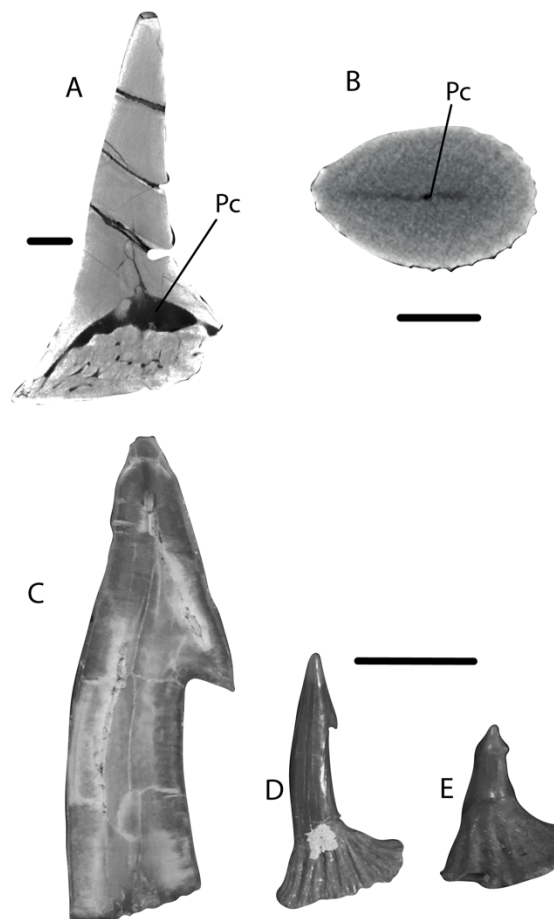
397

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

401 an arrow (single barb base attached to a double barbed tip denticle). D, Sagittal section of
402 denticle in C that revealed no modifications NHMUK PV P74053. Scale bar: 1 cm.

403

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

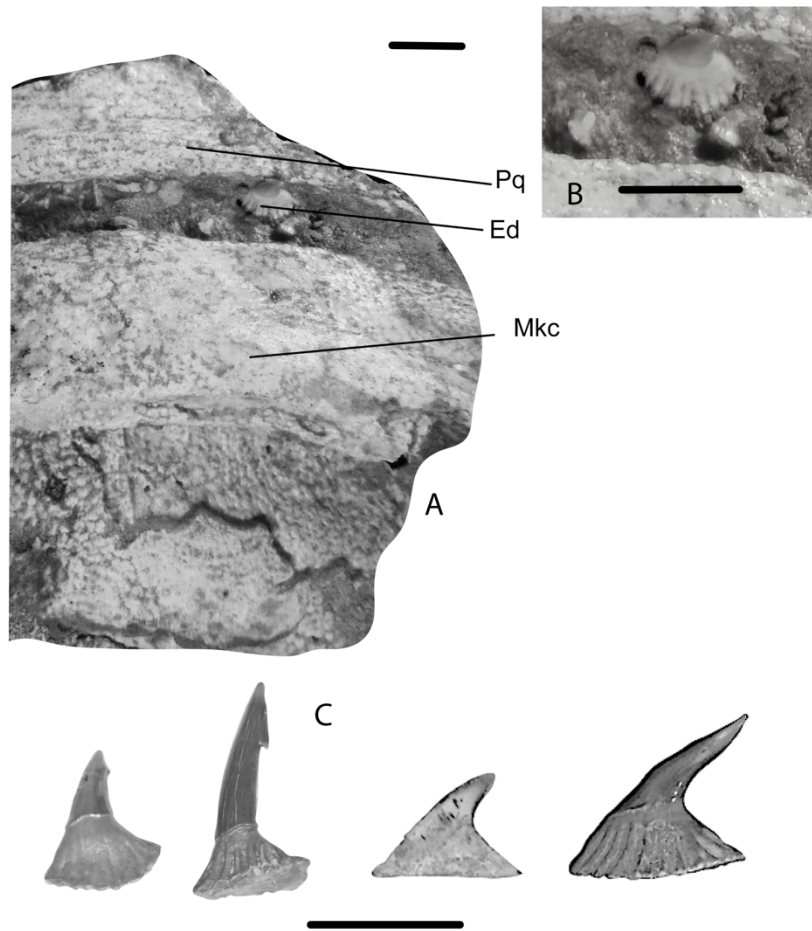


411

412 **Figure 7.** Rostral denticles of †*Onchopristis numidus* found in the “Kem Kem Beds” NHMUK

413 PV P74045. A, CT scan of denticles (scale bar: 1mm). B, Transverse section of denticle (scale

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



416
417 **Figure 8.** A, Mouth of †*Onchopristis numidus* (IPUW 353500). B, Close up view of enlarged
418 denticle in the mouth. C, Disarticulated denticles with similar morphology found in the “Kem
419 Kem Beds” collection sites: KK1 (easting: 382819, northing: 3501936 UTM) and KK3
420 (easting: 416828, northing: 3418567 UTM). Scale bar: 1cm.

421
422 *Enlarged denticle series:* Different morphologies of enlarged denticles possibly
423 attributed to †*Onchopristis numidus* have been reported in Egypt (e.g. Stromer, 1927, plate 1,
424 fig. 30b-32b; Werner, 1989, plate 20, fig 8-9) and were collected in Morocco (Fig. 8A-C) . The
425 presence of barbless and curved denticle between the jaws of specimen IPUW 353500 (Fig.
426 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.

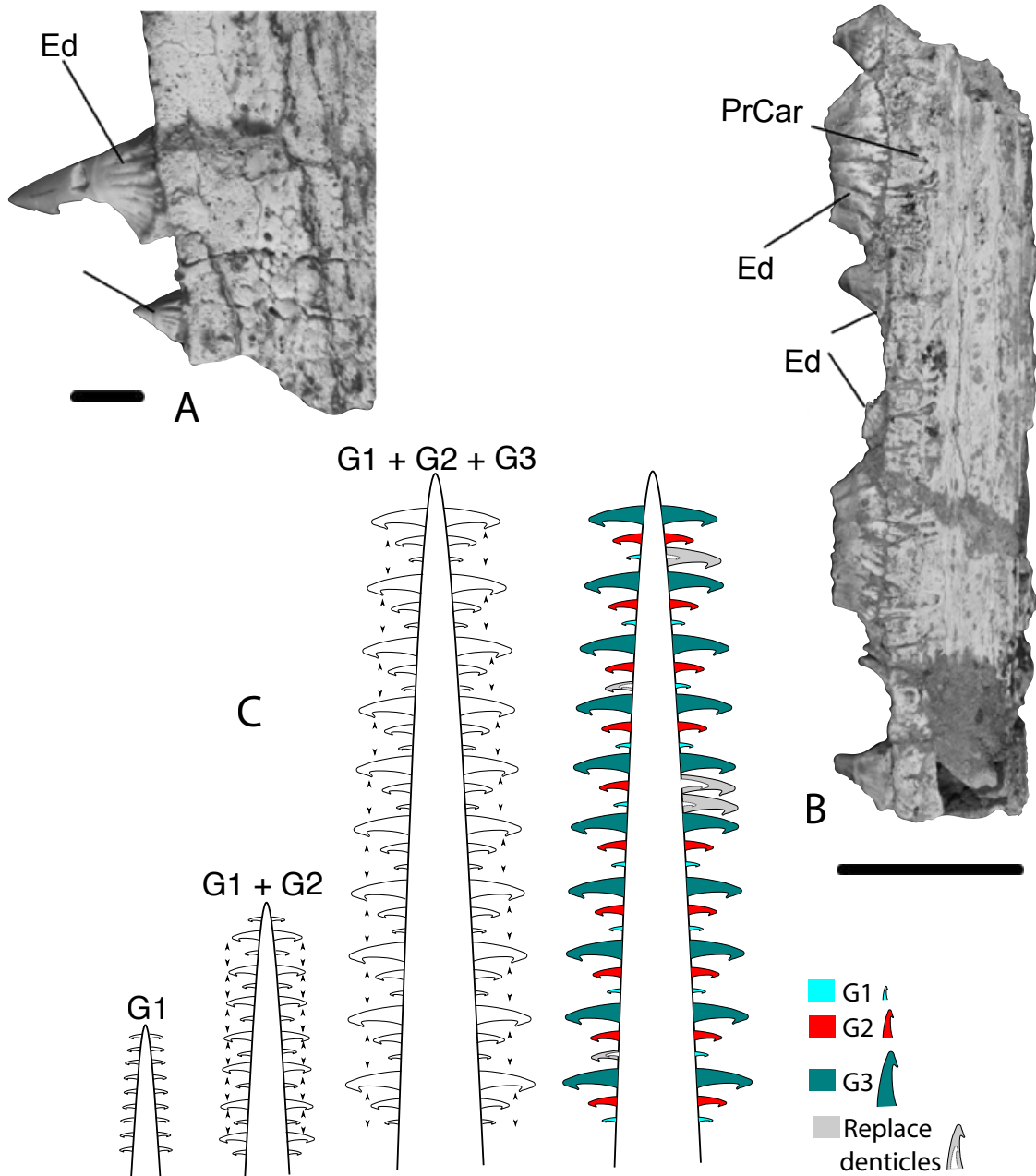
434 The presence of different enlarged series of denticles in †*Onchopristis numidus* that
435 vary according to their position in the rostral and cephalic regions is similar to that of other
436 sclerorhynchoids (e.g. †*Sclerorhynchus* Welten *et al.*, 2015; Underwood *et al.*, 2016).
437 Furthermore, 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

476 space. This arrangement is similar organisation to that reported for other sclerorhynchoid
 477 species (e.g. †*Sclerorhynchus*, Welten et al., 2015), in which some replacement denticles are
 478 so closely associated with the existing functional ones that they seem to appear in pairs (Fig.
 479 2, denticles marked with an arrow)”.

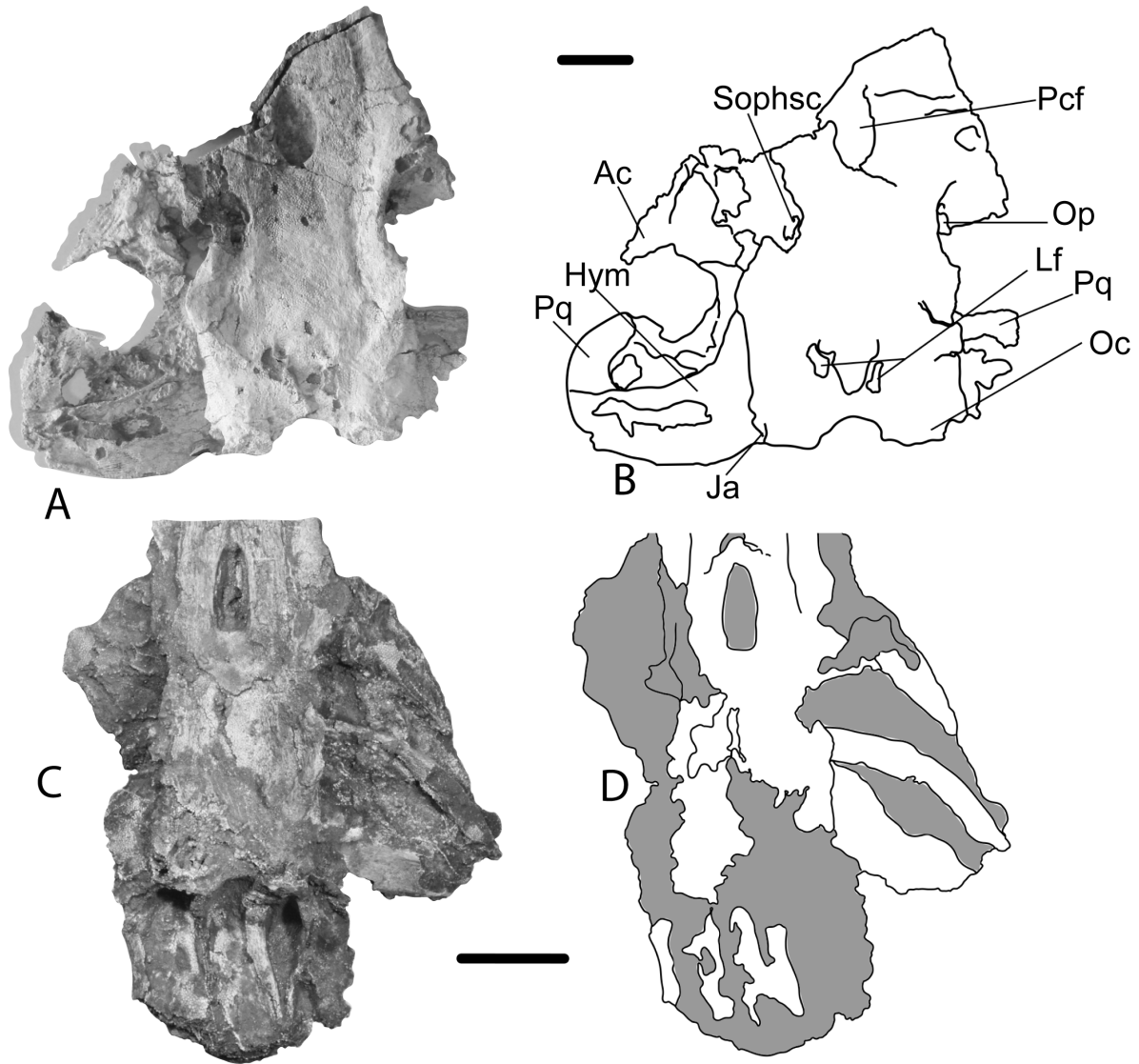


480
 481 **Figure 9.** Fragment of the rostrum of †*Onchopristis numidus*. A, IPUW 353500 (scale bar:
 482 1cm). B, NHMUK PV P 75503 (scale bar: 5cm). C, Hypothetical scheme of the growth and

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

485

486



487

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

491

492 *Neurocranium*

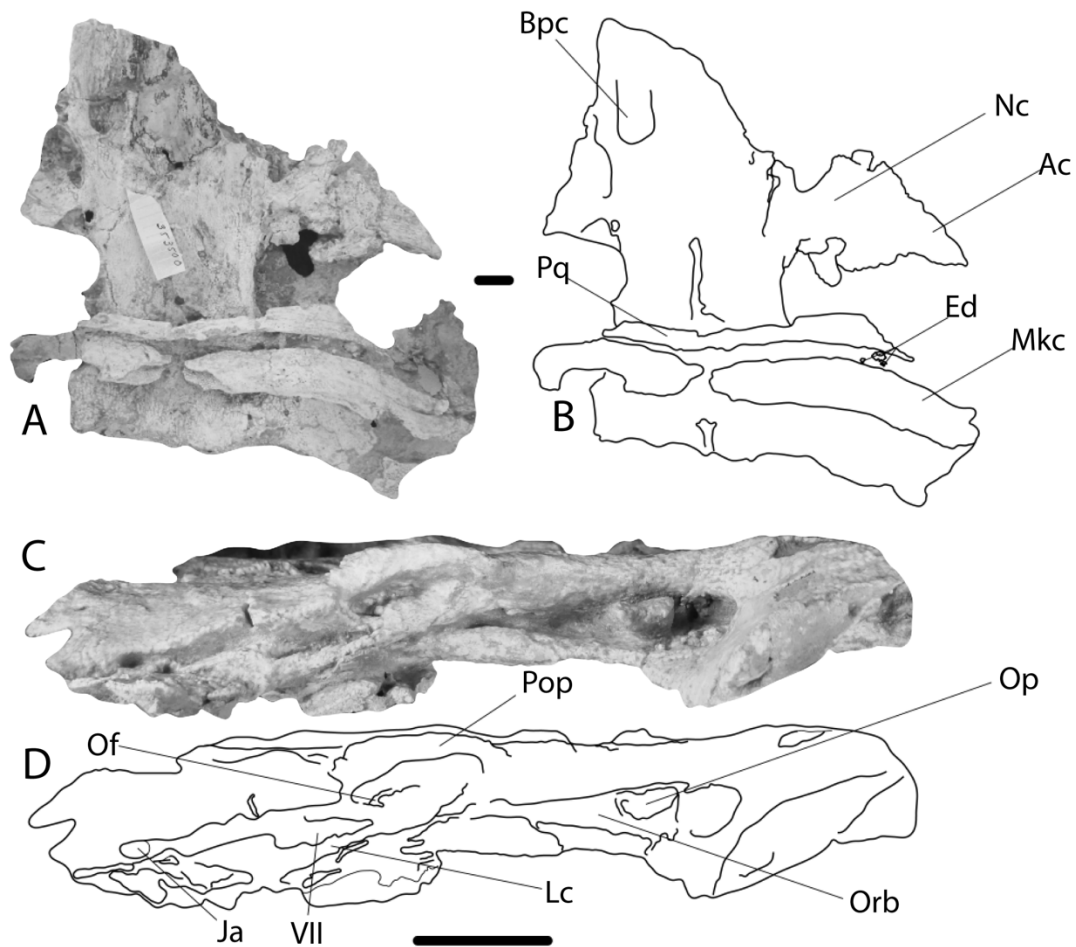
493 Only the postnasal region and part of the posterior edge of the nasal capsules can be
494 addressed here, as the most anterior part of the nasal capsules is missing. The neurocranium is
495 box-like and rectangular shaped, with an oval-shaped precerebral fenestra located near the base
496 of the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

501 The profile of the antorbital cartilage is triangular, with its narrow distal edge pointing
502 posteriorly and its wide proximal edge articulating with the nasal capsule (Fig. 11 A-B). Even
503 though the neurocranium presents some crushing dorsoventrally, the supraorbital crest stands
504 above the dorsal surface of the chondrocranium and does not cover the eye cavity. The orbital
505 cavity is large and houses a well mineralized optic peduncle; additional nerve foramina were
506 not observed (Fig. 11 C-D). Next to the supraorbital crest is the cavity for the superficial
507 ophthalmic nerve (Fig. 10 B). The postorbital region is rectangular and narrow with a small
508 triangular postorbital process. In the otic region, the orbital fissure is above the lateral
509 commissure and below the postorbital crest. The lateral commissure covers part of the
510 hyomandibular branch of the facial nerve foramen (Fig. 11 C-D). The lymphatic foramina are
511 present in the posterior part of the neurocranium. The jugal arches follow the otic region and
512 are located anteriorly to the occipital condyles which are well developed and expanded laterally
513 forming a broad and deep articulation facet for the anterior lateral process of the synarcual
514 (Fig.10).

515

516 *Hyomandibula*

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



522
 523 **Figure 11.** Neurocranium of †*Onchopristis numidus* (IPUW 353500). A, Ventral view. B,
 524 Line draw. C, Lateral view. D, Line draw. (A-B, scale bar: 2 cm). (C-D, scale bar: 5 cm).

525

526 *Jaw cartilages*

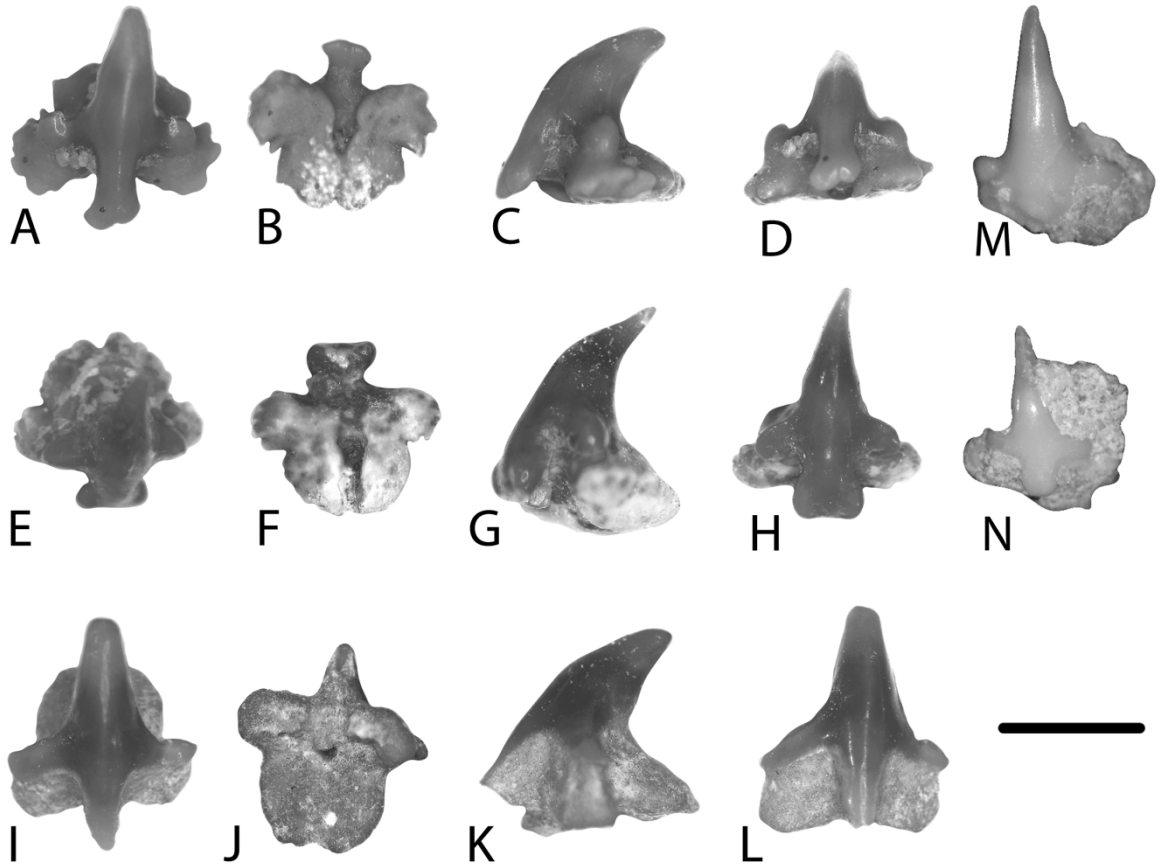
527 Only part of the Meckel's and palatoquadrate cartilages are observable in ventral view
 528 (Fig. 11 A-B). The palatoquadrate is thin and narrows progressively towards the symphysis
 529 (Fig. 11 A-B). In ventral view, there is no clear articulation with the neurocranium, the

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

534 *Oral teeth:* Teeth of †*Onchopristis numidus* have been figured multiple times (e.g. by
535 Stromer, 1927, plate I, figs 1-4, under the name †*Squatina aegyptiaca*; by Werner (1989, plates
536 35-37), under the name †*Sechmetia aegyptiaca*. The teeth figured on plates 21 & 22 by Werner
537 (1989) and described as †*Onchopristis*, probably belong to a different sclerorhynchoid such as
538 †*Renpetia*) and are similar to those of †*O. dunklei* (Welton & Farish, 1993; Kriwet & Kussius,
539 2001, text-fig. 4; Cappetta, 2012; Fig. 370M-R; Vullo *et al.*, 2003: pl. 2, fig. 6).

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

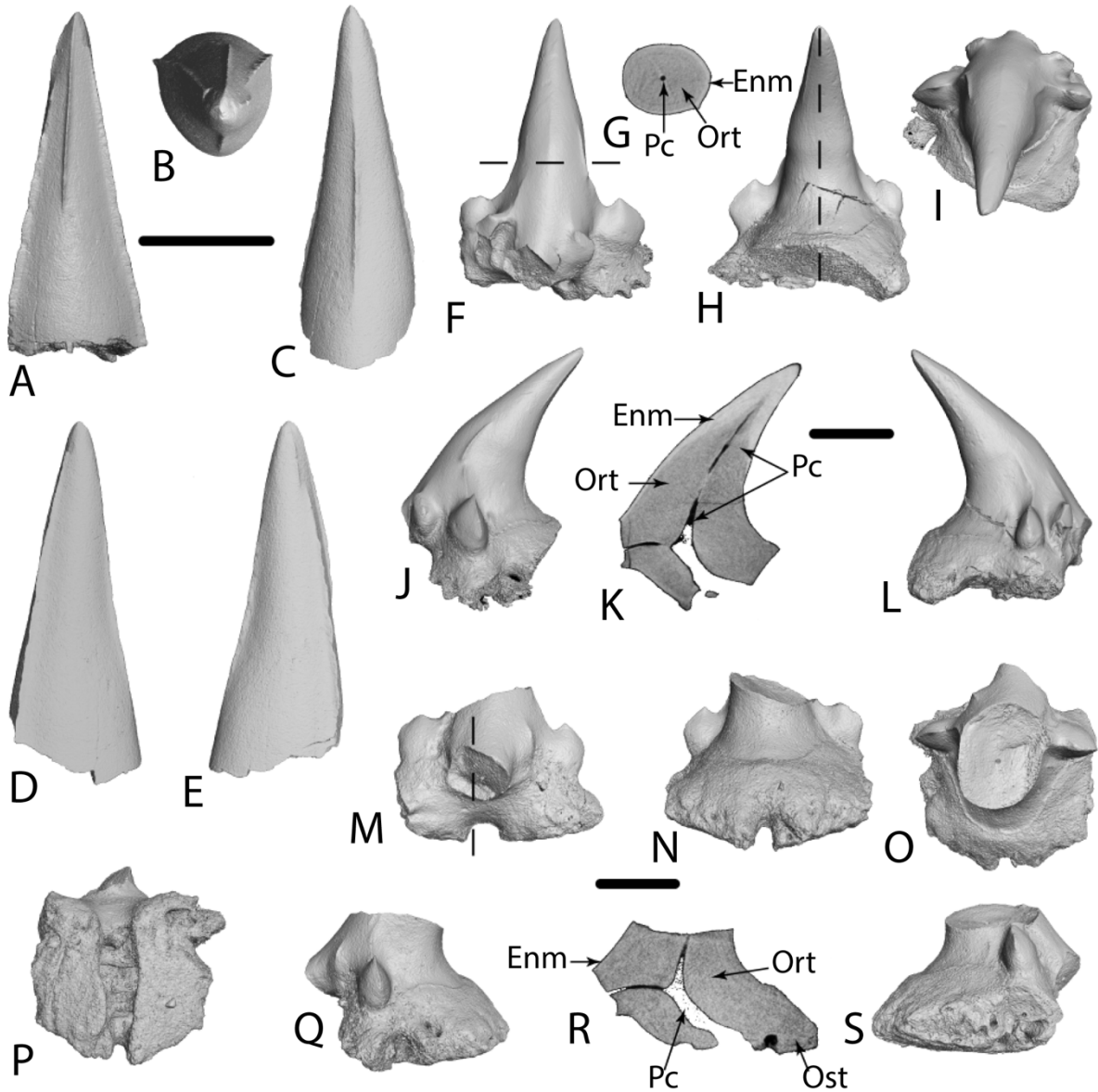
548 Cross-sections of the oral teeth revealed the presence of a large pulp cavity in the root
549 that extends apically into the crown where it becomes narrower as it progresses towards the apex
550 (Fig. 13 G, K, R.).



551

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

556

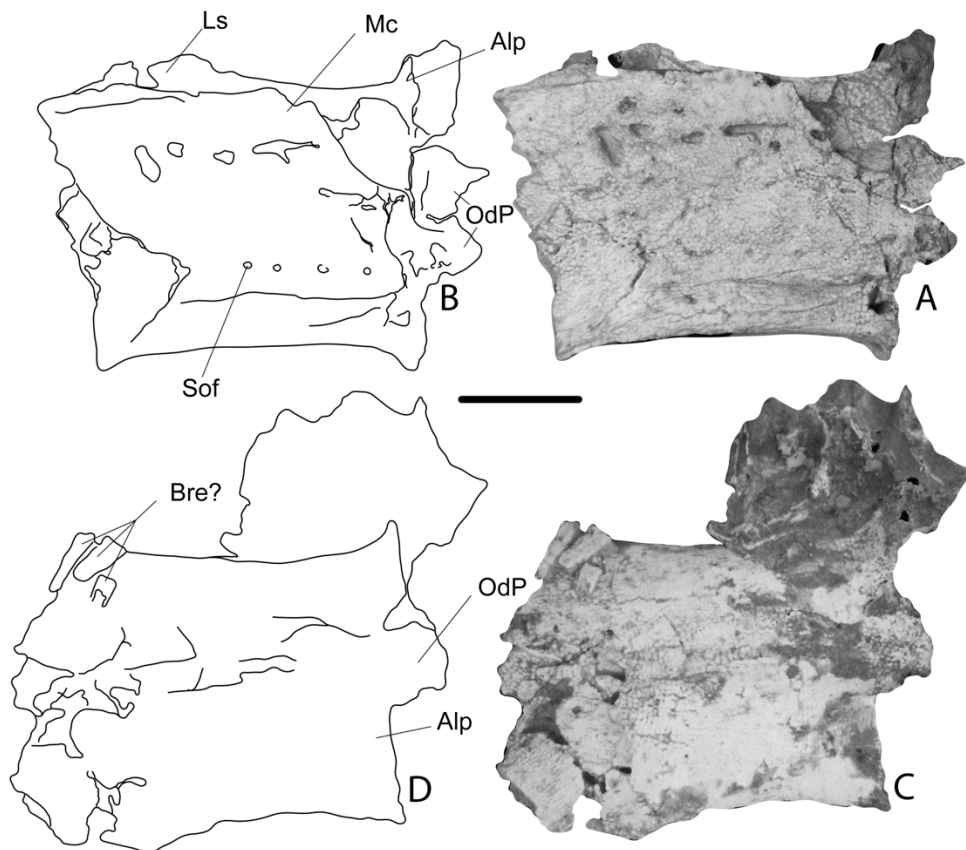


557

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

564 *Synarcual*

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



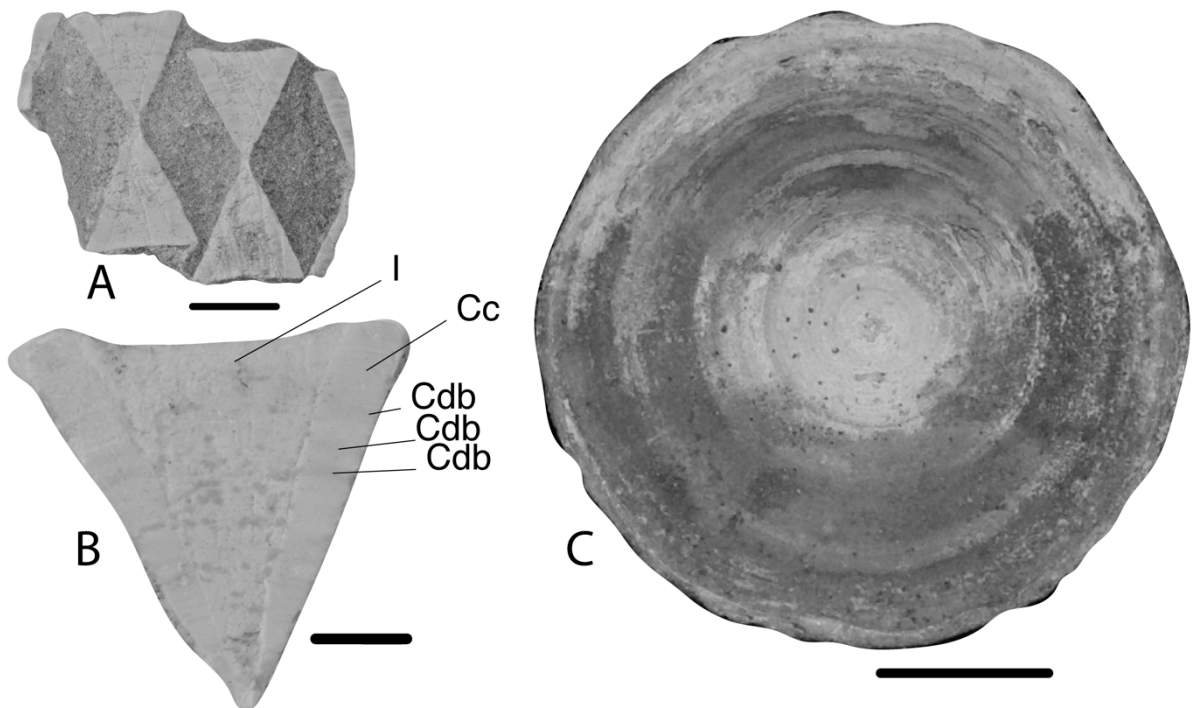
578

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

581

582 *Vertebrae*

583 The vertebral centra of †*Onchopristis* consist of the corpus calcareum and the
584 intermedialia as in other chondrichthyans. The corpus calcareum is well mineralized and
585 shows clear and opaque bands suggesting a cyclical deposition of mineral. Whether this
586 pattern was seasonal as in other chondrichthyans, remain ambiguous for the moment (Fig.
587 15).



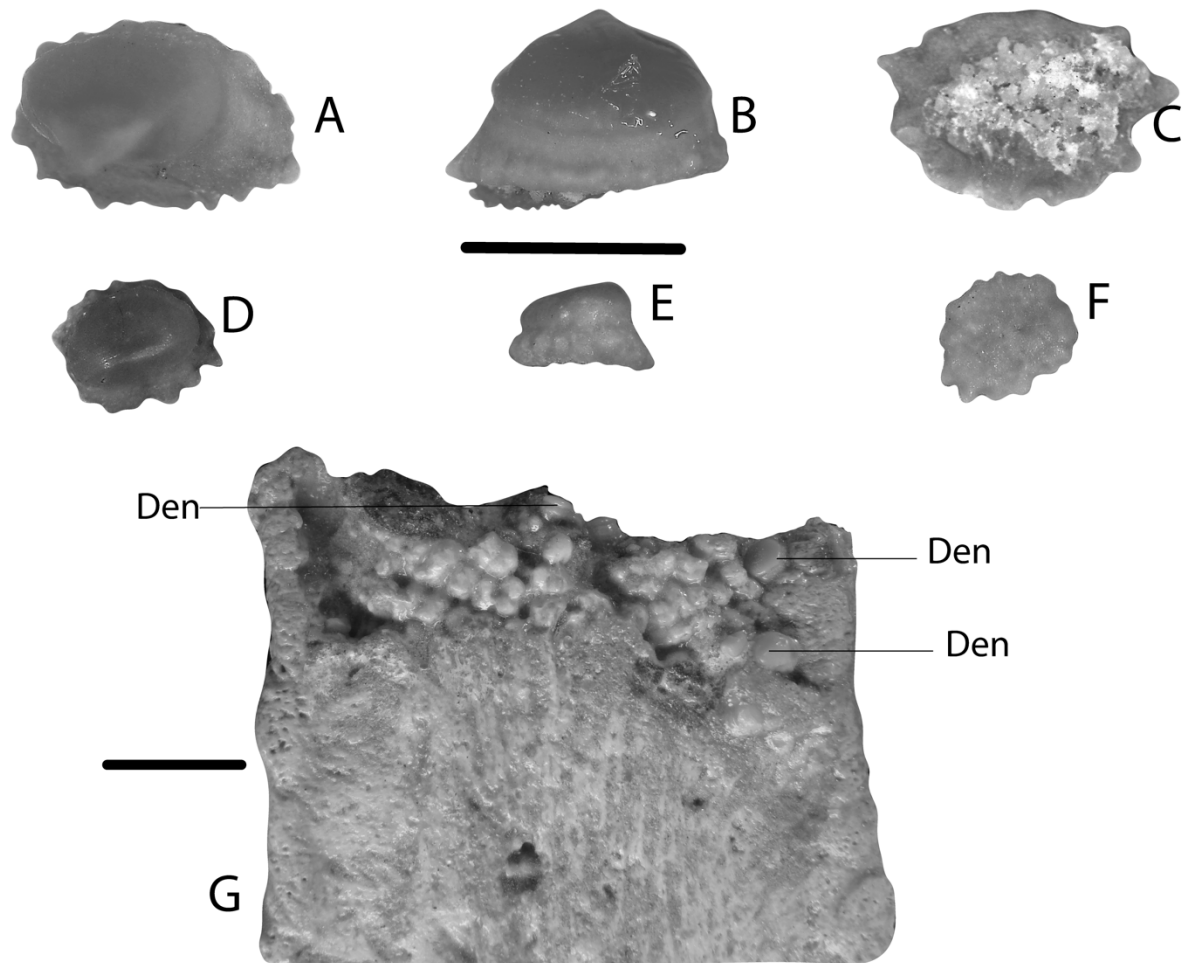
588

589 **Figure 15.** A-B. Vertebral centra of †*Onchopristis numidus* from the “Kem Kem Beds”
590 Collection sites Boulalou (KK5: easting: 418413, northing: 3479178 UTM) NHMUK PV P
591 74052. (A-B) Sagittal section of vertebra. (C) Articulation surface of the vertebra. Scale bars:
592 1 cm.

593

594 *Dermal denticles*

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

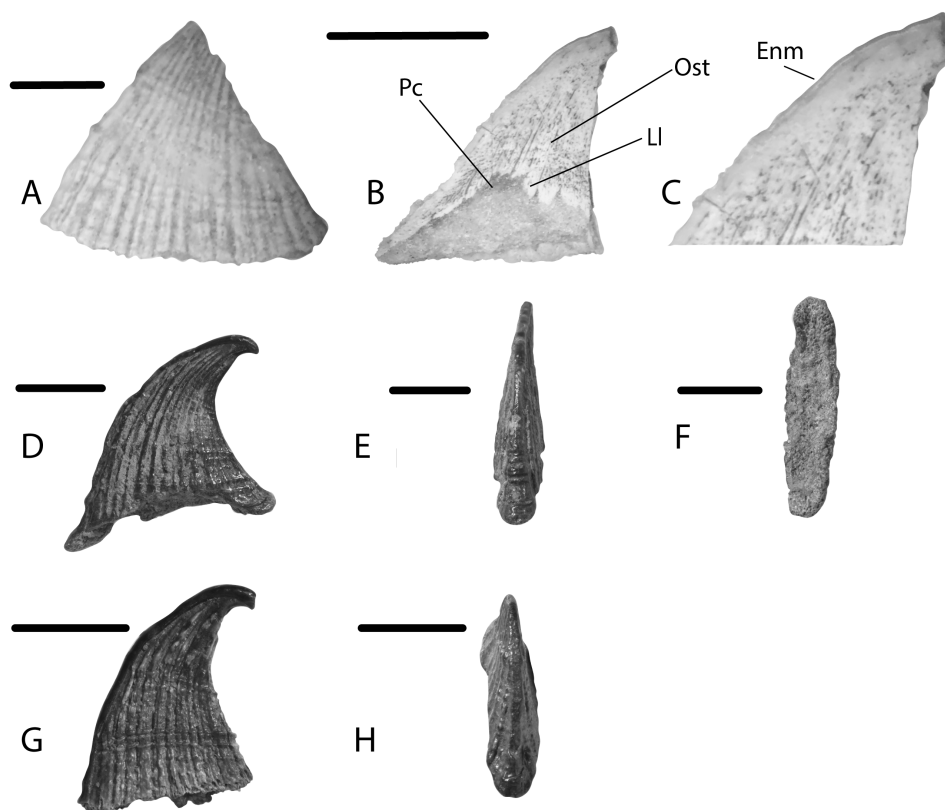


599
600 **Figure 16.** A-F Ventral rostral denticles from the section of the rostrum of †*Onchopristis*
601 *numidus* (NHMUK PV P 75502). A-C, Morpho 1. D-F, Morpho 2 (scale bar: 2mm) NHMUK
602 PV P 74051. G, anterior part of the ventral surface of IPUW 353500 rostrum (scale bar: 1cm).

603
604 As in other fossil assemblages (Werner, 1989), the occurrence of †*Onchopristis* in the
605 “Kem Kem Beds” coincides with that of “*Peyeria*-like” denticles (Fig. 17). Cappetta (2012)

606 noted that these two batoids are commonly found together, proposing that †*Peyeria* Werner,
 607 1989 was, a synonym of †*Onchopristis* and the †*Peyeria* remains were, in fact, dermal
 608 denticles of †*Onchopristis*. Recently, similar enlarged dermal denticles were reported for
 609 †*Ischyrrhiza mira* Leidy, 1856 by Sternes & Shimada (2019) in Campanian–lower
 610 Maastrichtian of Tennessee and Alabama, U.S.A, suggesting that this feature might be even
 611 more common among sclerorhynchoids. The presence of these types of enlarged body denticles
 612 in Morocco agrees with Cappetta (2012) and Sternes & Shimada (2019) interpretations.

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



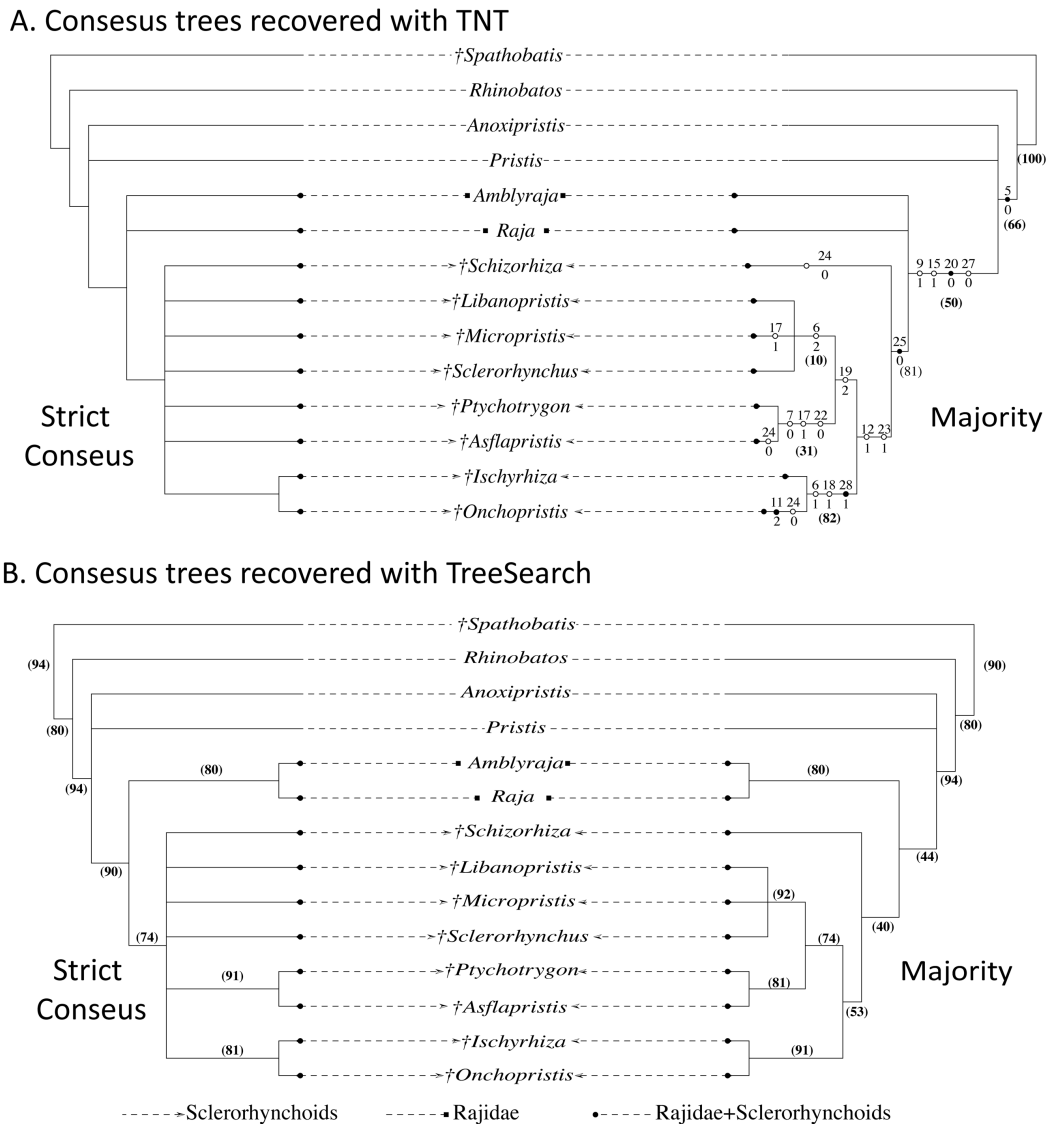
618
 619 **Figure 17.** Enlarged dermal denticles of †*Onchopristis numidus* from the “Kem Kem Beds”.
 620 A-C. B-C, C.U personal collection, longitudinal section and close-up of the enameloid layer

621 C.U personal collection, lateral view. D-F, IGR 2819, lateral, anterior and basal views. G, IGR
 622 2820, lateral view. H, IGR 2821, antero-apical view. Scale bars: 1 cm.

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624

PHYLOGENETIC ANALYSIS



625

626 **Figure 18.** Phylogenetic trees recovered by the different analysis used in the present study. (A)

627 strict consensus and majority rule trees produced by the TNT analysis. (B) strict consensus and

628 majority rule trees produced by the TreeSearch analysis: Clade support values from the

629 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).

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DISCUSSION

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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.

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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*.

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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.

729 The topologies recovered by the present analyses suggest that a different taxonomic
730 affiliation for †*Onchopristis* and †*Ischyrrhiza* could be proposed. Both analyses place these
731 genera previously associated with †Sclerorhynchidae (Cappetta, 2012) in a monophyletic
732 group separated from the remaining sclerorhynchoids with relatively good group support
733 (TreeSearch: Fig. 18 B, Cs (strict) = 81% and Cs (majority) = 91%; TNT: Fig 18 A, Cs = 82)
734 (see, TNT log in supplementary material). However, while there is a strong phylogenetic
735 support for accommodating †*Onchopristis* and †*Ischyrrhiza* in a single family (i.e.
736 †Ischyrrhizidae Cope, 1875), we argue for the formation of the family †Onchopristidae, as
737 resurrecting Cope's (1875) †Ischyrrhizidae would be taxonomically risky because the genus
738 with the most complete fossil record is †*Onchopristis*. Consequently, it is expected that both
739 taxa would be differentiated if more complete material of †*Ischyrrhiza* turns up resulting in
740 excluding †*Onchopristis* from the family it diagnoses. As such †Onchopristidae is diagnosed
741 by the presence of the following characters: (proposed characterised by the following features:
742 (1) a very peculiar rostral morphology with a thick lateral layer of porous cartilage on the sides
743 of the rostral cartilages, where the enlarged denticle lateral series attach (Character (Char) = 4,
744 1, Consistency index (Ci) = 1); (2) an external layer of "wood-like" cartilage in the centre of
745 the rostrum (Char = 2, 1, Ci = 1 and Char = 3, 1, Ci = 1); (3) the presence of large denticles in
746 the body (also see, Sternes & Shimada, 2019) (Char = 18, 1, Ci = 1); (4) the presence of smaller
747 denticles with a round cap associated with the base of the rostral denticles (Char = 28, 1, Ci =
748 1); and (5) two series of enlarged denticles with acute cap associated with the lateral regions of
749 the rostrum and head (Char 6, 1, Ci = 1); (6) a symmetric addition of rostral denticles with
750 denticles of different sizes being periodically added (Char = 11, 2, Ci = 1); and (7) rostral
751 denticles with a cap of filled with orthodentine (Char = 24, 0, Ci = 1). This combination of
752 characters is unique compared to other sclerorhynchoids and differentiates †Onchopristidae
753 from any other taxon tentatively assigned to it (†*Schizorhiza* and †*Ischyrrhiza*). 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 †*Ischyrrhiza* 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).

778 Whether ptychotrygonoids are considered a separate family or not makes no difference
779 phylogenetically. The same could be said for †Onchopristidae, as both clades form part
780 different groups which shares no immediate ancestor with †Sclerorhynchidae. However, their
781 taxonomic identification is needed, as it helps the definition of sclerorhynchoidei, facilitates the
782 approach for future studies, and improves the current understanding of the group. Furthermore,
783 we believe that there is enough evidence to support the taxonomical differentiation of the two
784 groups into two families.

785 According to the present analyses, the genera †*Schizorhiza* and †*Ischyrhiza* should be
786 placed within the Sclerorhynchoidei. The presence of a thick lateral layer of cartilage on the
787 sides and the external layer of “wood-like” cartilage in their rostrum suggests its classification
788 within †Onchopristidae. However, considering that no cranial remains are known for both
789 genera and that no enlarge body denticles are known for †*Schizorhiza*, and its highly
790 specialised replacement pattern of the lateral series of rostral denticles, their phylogenetic
791 relationships within Sclerorhynchoidei remain uncertain for the moment.

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793

TAXONOMIC IMPLICATIONS

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

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CHONDRICHTHYES Huxley, 1880

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BATOMORPHII Cappetta, 1980

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

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†SCLERORHYNCHOIDEI Cappetta, 1980

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†ONCHOPRISTIDAE fam. nov.

804 †*ONCHOPRISTIS* Stromer, 1917

805 †*Onchopristis numidus* (Haug, 1905)

806

807 *Diagnosis of †Onchopristidae:* Sclerorhynchoid group with a very peculiar rostral
808 morphology, that includes a thick lateral layer of porous cartilage on the sides of the rostral
809 cartilages, where the enlarge denticle lateral series attach. Rostral centre and superficial
810 ophthalmic nerve canals covered with an external layer of “wood-like”. Two series of enlarged
811 denticles with acute cap associated with the lateral regions of the rostrum and head, of which
812 the lateral rostrum series shows smaller denticles with a round cap associated with their base.
813 Symmetric addition of rostral denticles with denticles of different sizes being periodically
814 added. Rostral denticles with a cap of filled with orthodentine. Large denticles are associated
815 with the body (also see, Sternes & Shimada, 2019 for †*Ischyrhiza*).

816

817 CONCLUSION

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

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

829 that include the placement of †*Onchopristis* within the Sclerorhynchoidei (Cappetta, 1987;
830 2006; 2012). However, previous genus affiliations to the family Sclerorhynchidae are doubtful
831 and not supported here, as the rostral anatomy and the addition and arrangement of the enlarge
832 rostral denticle series are different from other members of the group (e.g. †*Sclerorhynchus* and
833 †*Libanopristis*) and resembles that of †*Ischyrhiza*. Following the phylogenetic analysis, three
834 monophyletic clades are recognised within Sclerorhynchoidei, which based on their differences
835 in their rostral cartilages and dental morphologies are interpreted as families by the present
836 study: †Sclerorhynchidae, †Onchopristidae and †Ptychotrygonidae. Recognising a new group
837 within the Sclerorhynchoidei, the family †Onchopristidae that includes a single the genus
838 †*Onchopristis*.

839

840

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853

LITERATURE CITED

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

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

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

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

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

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

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

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

873 **Cappetta H. 2012.** *Chondrichthyes: Mesozoic and Cenozoic Elasmobranchii: Teeth, Volume*
874 *3E.* Gustav Fischer Verlag. München.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

914 **Keyes IW. 1977.** Records of the northern hemisphere Cretaceous Sawfish genus *Onchopristis*
915 (order Batoidea) from New Zealand. *New Zealand Journal of Geology and Geophysics*
916 **20**:263-272.

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

919 **Kirkland J, Aguilón-Martínez, M. 2002.** *Schizorhiza*: a unique sawfish paradigm from the
920 Difunta group, Coahuila, México. *Revista Mexicana de Ciencias Geológicas* **19**(1):16–
921 24.

922 **Kriwet J. 1999.** Neoselachier (Pisces, Elasmobranchii) aus der Unterkreide (unteres
923 Barremium) von Galve und Alcaine (Spanien, Provinz Teruel). *Paleo Ichthyologica* **9**:
924 113–142.

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

- 928 **Kriwet J, Kussius K. 2001.** Paleobiology and paleobiogeography of sclerorhynchid sawfishes
929 (Chondrichthyes Batomorphii). *Revista Española de Paleontología* **16**: 35-46.
- 930 **Kriwet J, Nunn EV, Klug S. 2009.** Neoselachians (Chondrichthyes, Elasmobranchii) from
931 the Lower and lower Upper Cretaceous of north-eastern Spain. *Zoological Journal of*
932 *the Linnean Society* **155**: 316–347.
- 933 **Läng E, Boudad L, Maio L, Samankassou E, Tabouelle J, Tong H, Cavin L. 2013.**
934 Unbalanced food web in a Late Cretaceous dinosaur assemblage. *Palaeogeography,*
935 *Palaeoclimatology, Palaeoecology* **381**: 26–32.
- 936 **Leidy J. 1856.** Notice of some remains of fishes discovered by Dr. John E. Evans. *Proceedings*
937 *of the Academy of Natural Science of Philadelphia* **8**: 256–257.
- 938 **Maddison WP, Maddison DR. 2018.** Mesquite: A Modular System for Evolutionary
939 Analysis. Version 3.51 Available at <http://mesquiteproject.org>.
- 940 **Mannion PD, Barrett PM. 2013.** Additions to the sauropod dinosaur fauna of the Cenomanian
941 (early Late Cretaceous) Kem Kem Beds of Morocco: Palaeobiogeographical
942 implications of the mid-Cretaceous African sauropod fossil record. *Cretaceous*
943 *Research* **45**: 49–59
- 944 **Martill DM, Ibrahim N. 2012.** Aberrant rostral teeth of the sawfish *Onchopristis numidus*
945 from the Kem Kem Beds (? early late cretaceous) of Morocco and a reappraisal of
946 *Onchopristis* in New Zealand. *Journal of African Earth Sciences* **64**: 71–76.
- 947 **McEachran JD, Aschliman N. 2004.** Phylogeny of Batoidea. In: Carrier JC, Musick JA, and
948 Heithaus MR, eds. *Biology of sharks and their relatives*. Florida: CRC Press, Boca
949 Raton 79–113.
- 950 **McNulty CL, Slaughter BH. 1962.** A new sawfish from the Woodbine Formation
951 (Cretaceous) of Texas. *Copeia* **1962**: 775–777.

- 952 **Miller W. 1974.** Observations on the Developing Rostrum and Rostral Teeth of Sawfish:
953 *Pristis perotteti* and *P. cuspidatus*. *Copeia* **1974**: 311-318.
- 954 **Morgan DL, Whitty JM, Phillips NM, Thorburn DC, Chaplin JA, McAuley R. 2011.**
955 North-western Australia as a hotspot for endangered Elasmobranchs with particular
956 reference to sawfishes and the Northern river Shark. *Journal of the Royal Society of*
957 *Western Australia* **94**: 345–358.
- 958 **Miyake T, McEachran JD, Walton PJ, Hall BK. 1992.** Development and morphology of
959 rostral cartilages in batoid fishes (Chondrichthyes: Batoidea), with comments on
960 homology within vertebrates. *Biological Journal of the Linnean Society* **3**: 259–298.
- 961 **Naylor GJ, Caira JN, Jensen K, Rosana KA, Straube N, Lakner C. 2012.** Elasmobranch
962 phylogeny: A mitochondrial estimate based on 595 species. In: Carrier JC, Musick JA,
963 Heithaus MR, eds. *Biology of Sharks and Their Relatives*. Florida: CRC Press, Boca
964 Raton, 31–56
- 965 **Néraudeau D, Vullo R, Gomez B, Vincent P, Videt B. 2005.** Stratigraphie et paléontologie
966 (plantes, vertébrés) de la série paralique Albien terminal–Cénomanién basal de Tonnay-
967 Charente (Charente-Maritime, France). *Compte Rendus Palevol* **4**: 79–93.
- 968 **Pereira AA, Mdeiros MA. 2008.** A new Sclerorhynchiform (Elasmobranchii) from the middle
969 Cretaceous of Brazil. *Revista Brasileira de Paleontologia* **11**: 207–212.
- 970 **Rage JD, Dutheil DB. 2008.** Amphibians and squamates from the Cretaceous (Cenomanian)
971 of Morocco. A preliminary study, with description of a new genus of pipid frog.
972 *Palaeontographica Abteilung A* **285**: 1–22.
- 973 **Sereno PC, Dutheil DB, Iarochène M, Larsson HCE, Lyon GH, Magwene PM, Sidor CA,**
974 **Varricchio DJ, Wilson JA. 1996.** Predatory Dinosaurs from the Sahara and Late
975 Cretaceous Faunal Differentiation. *Science* **272**: 986–991.

- 976 **Slaughter BH, Steiner M. 1968.** Notes on Rostral Teeth of Ganopristine Sawfishes, with
977 Special Reference to Texas Material. *Journal of Paleontology* **42**: 233–239.
- 978 **Slaughter BH, Thurmond JT. 1974.** A Lower Cenomanian (Cretaceous) ichthyofauna from
979 the Bahariya Formation of Egypt. *Annals of the Geological Society, Egypt* **4**: 25–40.
- 980 **Smith MM, Riley A, Fraser GJ, Underwood CJ, Welten M, Kriwet J, Pfaff C, Johanson**
981 **Z. 2015.** Early development of rostrum saw-teeth in a fossil ray tests classical theory
982 of the evolution of vertebrate dentitions. *Proceedings of the Royal Society B: Biological*
983 *Sciences* **282**: 20151628.
- 984 **Sternes PC, Shimada K. 2019.** Paleobiology of the Late Cretaceous sclerorhynchid sawfish,
985 *Ischyrhiza mira* (Elasmobranchii: Rajiformes), from North America based on new
986 anatomical data. *Historical Biology* **31**: 1323–1340.
- 987 **Stromer E. 1917.** Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wiisten Agyptens.
988 11. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 4: Die Sage des Pristiden
989 *Onchopristis*. *Abhandlungen de Bayerischen Akademie der Wissenschaften,*
990 *Mathematisch-naturwissenschaftliche Abteilung* **28**: 1–31 pp.
- 991 **Stromer E. 1925.** Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wiisten Agyptens.
992 11. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 8. Ein Skelettrest des
993 Pristiden *Onchopristis numidus* Haug sp. *Abhandlungen de Bayerischen Akademie der*
994 *Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung* **30**: 1–22.
- 995 **Stromer E. 1927.** Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wiisten Agyptens.
996 11. Wirbeltier-Reste der Baharije-Stufe (Unterstes Cenoman). 9. Die Plagiostomen mit
997 einem Anhangüber kano und mesozoische Riickenflossenstacheln von
998 Elasmobranchiern. *Abhandlungen de Bayerischen Akademie der Wissenschaften,*
999 *Mathematisch-naturwissenschaftliche Abteilung* **31**: 1–67.

- 1000 **Thurmond JT. 1971.** Cartilaginous fishes of the Trinity Group and related rocks (lower
1001 Cretaceous) of north central Texas. *Southeastern Geology* **13**: 207–227.
- 1002 **Underwood CJ, Claeson K. 2017.** The Late Jurassic ray *Kimmerobatis etchesi* gen. et sp. nov.
1003 and the Jurassic radiation of the Batoidea. *Proceedings of the Geologists Association*
1004 **30**: 345–354
- 1005 **Underwood CJ, Smith MM, Johanson Z. 2016.** *Sclerorhynchus atavus* and the convergent
1006 evolution of rostrum-bearing chondrichthyans. *Geological Society, London, Special*
1007 *Publications* **430**: 129–136.
- 1008 **Underwood CJ, Ward DJ, King C, Antar SM, Zalmout IS, Gingerich PD. 2011.** Shark and
1009 ray faunas in the Middle and Late Eocene of the Fayum Area, Egypt. *Proceedings of*
1010 *the Geologists' Association* **122**: 47–66.
- 1011 **Villalobos-Segura E, Underwood CJ, Ward DJ, Claeson KM. 2019a.** The first three-
1012 dimensional fossils of Cretaceous sclerorhynchid sawfish: *Asflapristis cristadentis* gen.
1013 et sp. nov., and implications for the phylogenetic relations of the Sclerorhynchoidei
1014 (Chondrichthyes). *Journal of Systematic Palaeontology* **17**: 1847–1870
- 1015 **Villalobos-Segura E, Underwood CJ, Ward DJ. 2019b.** The first skeletal record of the
1016 Cretaceous enigmatic sawfish genus *Ptychotrygon* (Chondrichthyes: Batoidea) from
1017 the Turonian (Cretaceous) of Morocco. *Papers in Palaeontology* **2019**: 1–24
- 1018 **Vullo R, Néraudeau D, Videt B. 2003.** Un faciès de type falun dans le Cénomanién basal de
1019 Charente-Maritime (France). *Annales de Paléontologie* **89**: 171–189.
- 1020 **Welten M, Smith MM, Underwood CJ, Johanson Z. 2015.** Evolutionary origins and
1021 development of saw-teeth on the sawfish and saw shark rostrum (Elasmobranchii;
1022 Chondrichthyes). *Royal Society Open Science* **2**: 1–19.
- 1023 **Welton BJ, Farish RF. 1993.** *The collector's guide to the fossil sharks and rays from the*
1024 *Cretaceous of Texas*. USA: Before Time.

- 1025 **Werner C. 1989.** Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation
1026 (Obercenoman) der Oase Bahariya, Agypten. *Palaeo Ichthyologica* **5**: 1–112.
- 1027 **Whitty JM, Phillips NM, Thorburn DC, Simpfendorfer CA, Field I, Peverell SC,**
1028 **Morgan DL. 2014.** Utility of rostra in the identification of Australian
1029 sawfishes (Chondrichthyes: Pristidae). *Aquatic Conservation: Marine and Freshwater*
1030 *Ecosystems* **24**: 791-804.
- 1031
- 1032
- 1033
- 1034
- 1035
- 1036
- 1037
- 1038
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- 1041
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