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The Upper Cretaceous elasmobranch fauna from Senegal

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Abstract. Three successive horizons were sampled by bulk-sampling across the Campanian–Maastrichtian marine succession at the Cap de Naze cliff, South of Popenguine, Senegal. The material collected includes several hundreds of elasmobranch micro-remains as well as surface-collected specimens that are described in the present work. Twenty-six species are recorded, including three new genera and eight new batomorph species (*Ptychotrygon nazeensis* sp. nov., *Terangabatis thiami* gen. et sp. nov., '*Rhinobatos*' *popenguinensis* sp. nov., *Atlantobatis acrodonta* gen. et sp. nov., *Sowibatos minimus* gen. et sp. nov., '*Dasyatis*' *reticulata* sp. nov., *Coupatezia casei* sp. nov., *Phosphatodon cretaceus* sp. nov.). These new samplings complement previous records based on surface collection of the Cape de Naze section and bring the number of elasmobranch species for this fauna to 31. Increasing elasmobranch taxonomic diversity throughout the three successive assemblages indicates a transition from restricted marine to open coastal settings. This high-diversity fauna is dominated by necto-benthic batomorphs and is similar in its structure to other Tethyan and Eastern Atlantic Maastrichtian faunas. The high number of species apparently endemic to the studied area suggests high habitat differentiation in corresponding marine Maastrichtian settings. The presence of typical Maastrichtian species in the top of Unit 1 argues against a Campanian age previously proposed for this unit, while our data support a middle–late Maastrichtian age for the ferruginous sandstone bed of Unit 3.

Key words: chondrichthyans, micro-vertebrates, Maastrichtian, Western Africa, biostratigraphy, palaeoecology.

1. Introduction

The latest Cretaceous (Campanian-Maastrichtian) represents an all-time diversity peak in the elasmobranch evolutionary history (Guinot and Cavin, 2016). Campanian-Maastrichtian elasmobranch assemblages are known from a variety of depositional environments and geographical areas, although most of the fossil record of this group is based on faunas from North America, Northern Europe, and Northern Africa. In the eastern Atlantic and southern Tethys, knowledge on Maastrichtian elasmobranch assemblages is strongly dominated by samplings from Morocco (e.g. Arambourg, 1952; Noubhani and Cappetta, 1997) and the Middle East (Bardet et al., 2000; Cappetta, 1991a; Cappetta et al., 2000; Lewy and Cappetta, 1989; Signeux, 1959), although the latter often consists of faunal lists lacking thorough descriptions of the reported taxa. In contrast, records of sub-Saharan African faunas are scarce. These are restricted to sporadic accounts from Angola and Democratic Republic of Congo (Antunes and Cappetta, 2002; Darteville and Casier, 1959, 1943) as well as from Senegal (Cuny et al., 2012), Niger and Nigeria (Cappetta, 1972; Vullo and Courville, 2014; White, 1934). These reports are mainly based on surface-collections that overlooked micro-remains and do not allow a clear picture of the regional diversity distribution of Maastrichtian elasmobranchs in this area.

When reporting on the surface-collected elasmobranch macro-remains from the Late Campanian-Maastrichtian section of Popenguine (Senegal), Cuny *et al.* (2012) found strong similarities between the Senegalese assemblages and others from Morocco and the Near East, and underlined the potential of this West African section for sampling of elasmobranch micro-remains. Here, we present a detailed account of the elasmobranch fauna from the Popenguine section based on bulk-sampling and additional surface prospections from three successive horizons. Biostratigraphic implications and geographic distribution of the elasmobranch communities in the eastern Atlantic and southern Tethys areas are discussed in light of the newly described fauna.

2. Geological and Geographical Settings

Sedimentary levels producing marine vertebrates described here crop out in the area surrounding the village of Popenguine along the Atlantic coastline of Senegal (Figure 1A), and span the uppermost Cretaceous–early Paleocene interval (Cuny et al., 2012; Jacquet, 1936; Martin et al., 2019; Sarr, 1995; Sow, 1992). The Cap de Naze cliff, located South of Popenguine is a topographic height, which consists of a stack of Late Cretaceous argilites and siltstones from the Paki and Cap de Naze Formations from the Campanian-Maastrichtian interval that is subjected to the weathering action of the waves. Detailed geological information is available from Tessier (1952), Khatib et al. (1990), Sow

(1992), Sarr (1995) and has recently been summarized in Cuny *et al.* (2012). A slight southward dipping of the lithographic succession allows access to the oldest, mostly argillaceous, levels (Units 1 and 2) in the northern area of the section, whereas younger levels dominated by siltstones (Units 3 and 4), are located in the cliff area (Figure 1B-C). Unit 1 (Paki Formation) comprises grey silty argillites (12.50 m thick) underlying yellow siltstone (30 cm thick) that is topped by a yellow calcareous sandstone bed (20 cm thick). Within the Cap de Naze Formation, Unit 2 is composed of a 12 m thick series of argillites and siltites topped by a fine sandstone level, while Unit 3 is thicker (24 m) and includes basal variegated clayey siltstones (8 m) overlain by a massive set of medium-fine sandstones (16 m) with variegated siltstone. The top of Unit 3 comprises a fine to medium silty sandstone with ferruginous cement and has produced a diverse assemblage of surface-collected invertebrate and vertebrate remains (Cuny *et al.*, 2012; Hyžný *et al.*, 2016b, 2016a). This is no longer accessible due to the recent collapse of parts of the cliff. Planktonic foraminifera were used to establish the chronostratigraphic succession for the lower units at Cap de Naze with Unit 1 corresponding to the uppermost Campanian and Unit 2 to the lower to middle Maastrichtian (Khatib *et al.*, 1990; Sarr, 1995; Sow, 1992). Units 3 and 4 are devoid of foraminifera. However, the elasmobranch taxa reported by Cuny *et al.* (2012) from Unit 3 support a Maastrichtian age for this unit. Unit 4 yielded an ammonite assemblage reported by Tessier (1952) from the calcareous sandstone at the base of this unit on the Popenguine beach, which suggests an upper Maastrichtian assignment.

FIGURE 1 HERE

3. Material and Methods

The specimens reported here were bulk-sampled and surface-collected from three horizons within the Paki and Cap de Naze Formations. In Unit 1 of the Paki Formation, one sample (sample 1; Figure 1B-C) consisted of 9.7 kgs from the grey silty argillites (about 8 meters below the calcareous sandstone), which were processed using diluted (3%) hydrogen peroxide. Another sampling within Unit 1 consisted of 6.5 kgs of rock from the yellow calcareous siltstone (sample 2; Figure 1B-C) and was acid processed using diluted (7%) formic acid buffed with 30% of calcium formate solution. Sampling from the summit of Unit 3 within the Cap de Naze Formation (sample 3; Figure 1B-C) consisted of about 20 kgs of ferruginous sandstone that were processed using diluted (7%) formic acid buffed with 30% of calcium formate solution. All residues were sieved down to 0.35 mm mesh size. In total, 331 identifiable isolated elasmobranch specimens were studied (of which only 18 were surface-collected from sample 2), along with several fragmentary teeth and isolated scales. Sample 2 produced abundant isolated actinopterygian remains (teeth, vertebrae) and scarce fragmentary

decapod remains, while sample 1 yielded a few bivalve fragments and no associated fauna was recovered in sample 3.

The specimens described here are currently under study at the University of Montpellier and will be housed in the Laboratoire de Sédimentologie et de Biostratigraphie, Département de Géologie, Université Cheikh Anta Diop, Dakar, Senegal.

The present work is registered in ZooBank under the following Life Science Identifier (LSID): urn:lsid:zoobank.org:pub:2E7AEE55-E41D-440B-82EB-5CFFFB0755D, and the LSIDs of new species names are provided in the Systematic Palaeontology section, below.

4. Systematic Palaeontology

The systematics and terminology used here largely follow those of Cappetta (2012).

Order Orectolobiformes Appelgate, 1972

Family Hemiscylliidae Gill, 1862

Genus *Chiloscyllium* Müller & Henle, 1837

Chiloscyllium sp.

Fig. 2A-B

Material. Two teeth (SN2012-41-42) from Unit 3, Cap de Naze Formation.

Description. The crown is smooth and less than 1.2 mm high. The main cusp is triangular, biconvex and slightly inclined toward the commissure. The main cusp is flanked by a pair of low, broad and triangular cusplets with the mesial one being more reduced than the distal one. The faint cutting edges are observable in the lower third of the main cusp and run continuously until the base of the cusplets. The cusplets are diverging and located more labially than the main cusp. The apron is developed and broad with a narrow medio-labial concavity. The labial face of the cusplets displays a slight bulge that runs over the labial outline of the apron and only tapers near its median concavity. The median uvula and root are missing on both specimens.

Remarks. Dental remains of *Chiloscyllium* have been so far reported from the Maastrichtian of the Tethys (Bardet et al., 2000; Cappetta et al., 2014; Cappetta and Corral, 1999) but these were not illustrated and it is therefore impossible to compare our specimens with them. The teeth described

here differ from those reported as *Chiloscyllium* sp. from the Maastrichtian of New Jersey (Case et al., 2001) by their less developed cusplets and apron with narrower labial concavity. The Senegalese specimens can be differentiated from *C. frequens* Guinot, Underwood, Cappetta and Ward, 2013 known from the Santonian and Campanian of France, England and Germany (Guinot et al., 2013) by their smaller size, bulged labial outline of the cusplets and apron, less developed cutting edges and narrow medio-lingual concavity in the apron. Teeth of *C. salvani* Noubhani and Cappetta, 1997 from the Paleocene of Morocco display a convex labial crown face and an apron demarcated by marginal convexities in labial view.

Genus *Hemiscyllium* Müller & Henle in Smith 1837

Hemiscyllium sp.

Fig. 2C-D

Material. One tooth (SN2012-43) from Unit 3, Cap de Naze Formation.

Description. The single tooth found is about 0.6 mm wide and lacks the apex of the main cusp and most of the root. The labial crown face is flat whereas the lingual face of the main cusp is convex. The apron is wide with a regular and curved lower edge with no demarcation. Very faint cutting edges are present at the base of the main cusp, in labial position, and taper when reaching the heels. The distal heel is horizontal in labial view, whereas the mesial heel is oblique. The margino-lingual crown faces are high and abrupt, the distal one being less laterally expanded and is overhung by the heel in labial view. The uvula is rather wide, broadly united to the margino-lingual face and is slightly mesially oriented.

Remarks. Teeth of *Hemiscyllium* are known from several Maastrichtian and Paleocene assemblages including *H. hermani* Müller, 1989 from the Campanian and Maastrichtian of Germany (Herman, 1982; Müller, 1989) as well as from the Maastrichtian and Danian of Denmark (Adolfssen and Ward, 2015, 2014) and a few unnamed species (Kriwet et al., 2007; Noubhani and Cappetta, 1997). The tooth described here differs from those of other *Hemiscyllium* species in being of smaller size and not mesio-distally expanded with a weakly demarcated apron.

Family Ginglymostomatidae Gill, 1862

Genus *Plicatoscyllium* Case & Cappetta, 1997

Fig. 2E-M

1997 *Plicatoscyllium youssoufiaense* Noubhani & Cappetta; p. 43, pl. 16, figs 1-10.

2014 *Plicatoscyllium youssoufiaense* Noubhani & Cappetta; Cappetta et al., Table 1.

Material. Four teeth (SN2012-44-47) and several crown fragments from Unit 3, Cap de Naze Formation.

Description. Anterior teeth (Fig. 2F-H) are higher than wide and not exceeding 1.5 mm high. The crown comprises of a triangular and rather developed main cusp with a broad lower region that is flanked by a pair of elongate and weakly divergent cusplets as well as a second external pair of low and incipient cusplets. The cutting edges run continuously from the main cusp to the marginal angles of the crown although notches separate the main cusp and cusplets. The lower region of the labial crown face displays a rather short, weakly developed and bifid apron with slightly concave marginal edges. The labial crown face bears ornament made of a single vertical ridge on the main cusp that bifurcates in its lower region where it is accompanied by several irregular vertical ridges of variable sizes that occupy a triangular area on the apron, but do not reach the cusplets nor the lower edge of the apron. The lingual crown face is smooth and concave in profile view and displays a developed lingually-projected uvula. The hemiaulacorrhize root projects lingually and is heart-shaped in basal view with nearly flat to concave basal face that is pierced by a large central foramen. The root branches are oriented labially and the moderately developed lingual protuberance displays a rather large median foramen in basal position. A pair of large oval-shaped margino-lingual foramina is present in the concavities between the marginal faces and the lingual protuberance. Some teeth display a second, smaller foramina on the mesial marginal face, in a more labial position than the other. Teeth from lateral and latero-posterior files (Fig. 2E, I-M) are strongly asymmetrical, the main cusp and cusplets being bent toward the commissure. There are two pairs of cusplets of decreasing size marginally as well as a third incipient mesial cusplet that is reduced to a protuberance. The apex of the cusplets is bent toward to main cusp. The apron is short and weakly bifid. The labial crown ornament consists of a vertical ridge on the main cusp that does not divide before reaching the base of the cusp where several subvertical folds of various sizes are present. The density of the labial ornament decreases towards the posterior files where it is limited to few large and short folds below the cusplets. The root is strongly asymmetrical with a longer mesial branch and the medio-lingual foramen is narrower than in anterior teeth.

Remarks. The teeth described here display typical features of members of the genus *Plicatoscyllium*, which included seven species so far, all represented in the Maastrichtian. The Senegalese specimens differ from those of *P. globidens* (Cappetta and Case, 1975) from the Maastrichtian of the USA and of *P. lehneri* (Leriche, 1938) from the Maastrichtian of Morocco, the Democratic Republic of Congo, Trinidad and Tobago, and Spain by the presence of well-developed main cusp and cusplets. Among species represented by teeth with developed cusplets, teeth of *P. antiquum* Case and Cappetta, 1997, *P. derameei* Case and Cappetta, 1997 and *P. gharbii* Noubhani and Cappetta, 1997 can be separated from the Senegalese specimens by their much weaker labial ornamentation. *Plicatoscyllium youssoufiaense* Noubhani and Cappetta, 1997 from the Maastrichtian of Morocco and *P. minutum* (Forir, 1887) from the Maastrichtian of Morocco, Netherlands, and Belgium are species with moderate to strong labial crown ornamentation, respectively. The specimens described here are much closer to *P. youssoufiaense* in that they display characteristic features of the species: small size, two to three cusplets, short but wide apron that is bifid in anterior teeth, and moderately developed lingual root protuberance. Some anterior teeth from Senegal present a slightly more developed labial ornament than in the specimens from the type series (Upper Maastrichtian of the Ganntour Basin) that is attributed to intraspecific variability.

[FIGURE 2 HERE]

Order Lamniformes Berg, 1958

Family Anacoracidae Casier, 1947

Genus *Squalicorax* Whitley, 1939

Squalicorax pristodontus (Agassiz, 1843)

Fig. 3A-B

For synonymy, see Hoganson et al. (2019), and add:

2012 *Squalicorax pristodontus* (Agassiz); Cuny et al., p. 111, Fig. 3P-R, V-X.

2014 *Squalicorax pristodontus* (Agassiz); Cappetta et al., p. 221, fig. 7F-I.

2017 *Squalicorax pristodontus* (Agassiz); Case et al., p. 70, fig. 3G.

Material. A single incomplete tooth (SN2012-48) from the yellow calcareous sandstone bed of Unit 1, Paki Formation.

Description. This robust lateral tooth is triangular in labial view with straight distal and convex mesial cutting edges. The mesial heel is reduced and inclined basally while the distal heel is incipient.

Serrations are strong and deep, being coarse in the upper half of the crown and decreasing in size toward the heels. The labial crown face is flat to slightly concave in its centre and overhangs the root in the areas situated below the heels. Several coarse vertical folds are present above the crown/root edge, being more developed in the centre of the crown. The lingual crown face is strongly convex. The lingual crown/root edge is triangular with a marked collar. The basal root face displays a wide medio-central foramen. Numerous oval-shaped foramina are present on the labial face, immediately below the crown. The root lobes are lacking.

Remarks. The crown morphology, size, and serration pattern comply with those of *S. pristodontus* (see Darteville and Casier, 1943 and Arambourg, 1952 for illustrations). This species has a worldwide distribution, is common in early Campanian to late Maastrichtian faunas, and was previously reported from Senegal by Cuny et al. (2012) from the Unit 3 of the Cap de Naze Formation.

Family Carchariidae Müller & Henle, 1838

Genus *Carcharias* Rafinesque, 1810

Carcharias sp.

Fig. 3C-F

Material. Two anterior teeth (including SN2012-50) from the yellow calcareous sandstone bed of Unit 1, and one (SN2012-49) from the grey silty argillites of Unit 1, Paki Formation.

Description. The teeth are higher than wide and can reach up to 30 mm in total height. The main cusp is elongate, smooth, and bent lingually. The lingual crown face is strongly convex, whereas the labial face is flatter and bears a marked vertical convexity that broadens towards its basal crown edge. A short collar is present at the base of the lingual crown face. In labial view, the heels are elongate and strongly oriented basally. The basal edge of the labial crown face strongly overhangs the root from the medio-labial region towards the extremities of the heels. The medial overhang is narrow and triangular and can bear enameloid folds. A pair of triangular cusplets is present, lingually oriented with sharp and developed cutting edges. The main cusp bears well-developed cutting edges that taper before reaching the cusplets, from which they are separated by a marked notch. The root displays a marked and somewhat wide lingual protuberance, which bears a nutritive groove where a large central foramen opens. The root branches are elongate and thin, with compressed extremities. Several small foramina are present below the lingual collar as well as immediately below the labial crown bulge, and reach larger sizes in the medio-labial area.

Remarks. These anterior teeth resemble those of *Odontaspis samhameri* Cappetta & Case, 1975 but differ from the latter in the morphology of the cusplets, their more elongate crown heels and labial crown face with strong and narrow labial bulge. The same characteristics differentiate the Senegalese specimens from *Odontaspis holmdelensis* Cappetta and Case, 1975 and *Odontaspis hardingi* Cappetta and Case, 1975, along with their smooth lingual face. The specimens described here also bear resemblances with anterior teeth of *Serratolamna serrata* (Agassiz, 1843) (see Arambourg, 1952), but differ from the latter in being more symmetrical and gracile with more slender and elongate root branches. The three anterior teeth reported here most closely resemble those of *Carcharias heathi* Case and Cappetta, 1997. However, the latter differ in being more robust with a flat labial crown face, while the Senegalese specimens display a marked vertical convexity. Cuny et al. (2012) reported two teeth as *Carcharias cf. heathi*, but these show no marked labial crown bulge and display a flat labial crown face.

Family Otodontidae Glickman, 1964

Genus *Cretolamna* Glickman, 1958

Cretolamna maroccana (Arambourg, 1935)

Fig. 3G-J

For synonymy, see Case and Cappetta (1997), and add:

2014 *Cretolamna maroccana* (Arambourg); Cappetta et al., fig. 6I-K.

2017 *Cretolamna maroccana* (Arambourg); Case et al., p. 69, fig. 3E.

Material. Two teeth (SN2012-51-52) from the yellow calcareous sandstone bed of Unit 1, Paki Formation.

Description. The lower anterior tooth (Fig. 3G-H) displays a triangular main cusp flanked by a pair of lateral cusplets and an additional outer pair of incipient cusplets. The main cusp is biconvex, the lingual face being more developed. The apical region of the main cusp is missing. Strong sharp cutting edges are present on the main cusp and are separated from the less marked cutting edges of the cusplets by a deep but narrow notch. The cusplets are broad, triangular and diverging, the distal one being more bent marginally. The pair of incipient outer cusplet is poorly separated from the inner cusplets by a shallow notch. The cusplets are positioned in a more labial position than the main cusp and extend over the basal end of the cutting edges of the main cusp, forming a large notch in labial view. The base of the labial crown face shows a bulge that is more marked in the central region,

where the basal outline of the crown is concave and bears numerous short vertical folds. The root is robust with root branches oriented labially. The distal branch is slightly shorter and thinner than the mesial one. A shallow and short nutritive notch is present but damaged in the area of the central foramen. Numerous oval foramina of varying sizes are present immediately below the basal bulge of the labial crown face. The lower lateral tooth (Fig. 3I-J) differs from the anterior in being lower, more robust, and more mesio-distally developed. The root is mesio-distally expanded, labio-lingually compressed in its mesial and distal extremities, and the surface of the basal face is irregular. The margino-labial angle of the root is slightly acute in basal view and oriented lingually.

Remarks. This species is restricted to the Maastrichtian and was reported from Morocco (Arambourg, 1952, 1935; Cappetta et al., 2014; Noubhani and Cappetta, 1997), the Democratic Republic of Congo (Darteville and Casier, 1943), United States (Case et al., 2017; Case and Cappetta, 1997; Welton and Farish, 1993), and Madagascar (Gottfried et al., 2001). Among previous records, those based on fine stratigraphic framework suggest that this species might be restricted to the Upper Maastrichtian (Case and Cappetta, 1997). Its occurrence in the lower Maastrichtian of Israel as *Cretalamna biauriculata maroccana* is not supported by illustrations (Lewy and Cappetta, 1989).

Family Serratolamnidae Landemaine, 1991

Genus *Serratolamna* Landemaine, 1991

Serratolamna serrata (Agassiz, 1843)

Fig. 3K-T

For synonymy, see Hoganson et al. (2019), and add:

? 2012 *Cretalamna* cf. *C. biauriculata* (Wanner, 1902); Cuny et al., p. 108, Fig. 3A-I.

Material. Seven teeth (including SN2012-53-57) from the yellow calcareous sandstone bed of Unit 1, Paki Formation.

Description. Anterior teeth (Fig. 3M-N) are higher than broad and can reach 25 mm in total height. The main cusp is triangular and biconvex, although this convexity is more marked in the lingual face. A pair of broad, triangular, and diverging cusplets is present, separated from the sharp cutting edges of the main cusp by a narrow notch. The basal edge of the lingual crown face displays a distinct collar. The basal edge of the labial crown face is developed and strongly overhangs the root, especially in the medio-labial area where the depression of the basal edge is acute. The root is strongly asymmetrical with the distal lobe being broad and distally oriented with squared extremity,

whereas the mesial lobe is short, basally oriented with an acute extremity. Both lobes are separated by a broad concavity of the basal root edge. Several foramina open below the labial bulge, the largest and most oval-shaped one being restricted to the medio-labial region. The lingual root face is low and can overhang the crown at the level of the cusplets in basal view. A moderate lingual protuberance is present with a distinct nutritive groove. Teeth from lateral files (Fig. 3K-L, O-T) are more mesio-distally developed and more asymmetrical than anterior ones. Up to three pairs of cusplets can be observed, the distal ones being more developed and more diverging. The root lobes are mesio-distally oriented with squared extremities. A notch is frequently present near the distal and mesial extremities of the basal edge of the lingual face.

Remarks. This species has a wide palaeogeographical range but is restricted to the Maastrichtian (Hoganson et al., 2019). In Senegal, *S. serrata* was previously reported from Unit 3 of the Cap de Naze Formation based on a single tooth (Cuny et al., 2012) and the specimens described here extend the stratigraphic range of this species to Unit 1 (Paki Formation). However, some additional specimens reported by Cuny et al. (2012) from Unit 3 were tentatively assigned to juvenile individuals of *Cretolamna* cf. *biauriculata*, although the authors noted the strong resemblances with *S. serrata*, differing only in being more symmetrical with a less slender main cusp. Arambourg (1952; pl. 16, figs 31-32, 37-40) illustrated small-sized *S. serrata* specimens from Morocco that display similar morphologies and symmetry to the specimens from Senegal reported by Cuny et al. (2012). It is therefore likely that the small teeth reported from Unit 3 by Cuny et al. (2012) actually represent juvenile teeth of *S. serrata*.

[FIGURE 3 HERE]

Super-order Batomorphii Cappetta, 1980

Order Rajiformes Berg, 1940

Sub-Order Sclerorhynchoidei Cappetta, 1980

Family Sclerorhynchidae Cappetta, 1974

Genus *Dalpia* Checchia-Rispoli, 1933

Dalpia stromeri Checchia-Rispoli, 1933

Fig. 4A-J

1902 *Problematicum*, Quaas, p. 320, pl. 28, fig. 15.

340 1933 *Dalpiazia stromeri* Checchia-Rispoli, p. 7, pl. 1.

341 1935 *Onchosaurus maroccanus* Arambourg, p. 421, pl. 19, fig. 8.

342 1940 *Onchosaurus maroccanus* Arambourg; Arambourg, p. 143, pl. 3, figs. 2-5.

343 1943 *Onchosaurus manzadinensis* Darteville & Casier, p. 166, pl. 14, figs. 1-8, text-fig. 55.

344 1952 *Onchosaurus (Ischyrhiza) maroccanus* Arambourg; Arambourg, p. 191, pl. 19, figs. 34-43.

345 1972 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 198, pl. 4, fig. 8 and pl. 13, figs. 11-12.

346 1987 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 147, p. 148, fig. 125.

347 1991a *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 23, pl. 4, fig. 1-8.

348 1997 *Dalpiazia stromeri* Checchia-Rispoli; Noubhani & Cappetta, p. 138, Tab. 4 (name only).

349 1999 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta & Corral, p. 362, pl. 3, fig. 9.

350 2000 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta et al., p. 85 (name only).

351 2000 *Dalpiazia stromeri* Checchia-Rispoli; Bardet et al., p. 273, Tab. 1 (name only).

352 2012 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 375, fig. 363.

353 Material. Eight teeth (including SN2012-58-60) from Unit 3, Cap de Naze Formation.

354 Description. Teeth of this species are higher than wide, not exceeding 0.7mm in height and show a

355 strong degree of heterodonty. Possible anterior teeth (Fig. 4A-D) are symmetrical and strongly

356 cuspidate. The crown bears a wide and strongly linguallly-oriented main cusp bearing incipient cutting

357 edges that become more marked in its basalmost region and run continuously over the heels until

358 the marginal angles. The heels are rather developed laterally, linguallly oriented and only slightly

359 inclined basally. The labial crown face displays a marked but somewhat narrow vertical medio-labial

360 protuberance that develops basally below the basal edge of the heels and overhangs the crown/root

361 edge in occlusal view. The medio-labial protuberance bears a vertical ridge that originates in the

362 lower half of the main cusp and tapers before reaching the basal edge of the labial crown face. The

363 lingual crown face is smooth and slightly protrudes medially where it is nearly flat. The crown/root

364 edge is narrow but the basal region of the root is flared at all points in occlusal view. The crown is

365 high and labio-linguallly elongated. In basal view, the root lobes are separated by a groove that is

366 partially closed in the median region but broadens towards the lingual and labial edges, forming a

367 wide triangular notch in the latter. A wide central foramen opens linguallly at the bottom of the

368 nutritive groove. In basal view, the root lobes are more mesio-distally developed in their labial half

than in their lingual region. In the latter, the basal face is inclined basally whereas this inclination only involves the margino-labial edges of the labial region, which is otherwise flat. The medio-lingual root protuberance is moderate and wide. Both the labial and lingual root faces are concave. Up to two foramina are present on the flared area of each margino-lingual face, the foramina placed in lingualmost position being larger. Teeth from supposed more lateral files (Fig. 4E-J) are smaller with a shorter triangular main cusp. The heels are less laterally expanded, more strongly inclined basally and broadly united to the main cusp. The medio-labial protuberance of the crown is absent or residual and the medio-lingual crown protuberance is faint. Labial crown ornament is stronger and consists of several vertical ridges that originate at the base of the main cusp and do not reach the basal crown edge. The root has a wider mesial lobe in basal view and wider nutritive groove.

Remarks. The genus *Dalpiazia* includes the Maastrichtian type species *D. stromeri* as well as *D. indica* (Chiplonkar and Ghare, 1977), which is known from a single rostral denticle from the Cenomanian–Turonian Bagh Beds of NW India. Although *D. stromeri* is common in Tethyan and Eastern Atlantic deposits (RDC, Niger, Morocco, Libya, Egypt, Jordan, Syria, Spain), these occurrences are mostly based on rostral denticles. Some of these were referred to different species (*Onchosaurus maroccanus* Arambourg, 1935 and *Onchosaurus nzadinensis* Darteville and Casier, 1943), but these should be considered junior synonyms of *D. stromeri* (Cappetta, 2006, 1972). Oral teeth have only been described in detail by Cappetta (1991a) based on specimens from the Maastrichtian of Egypt and on the co-occurrence of oral sclerorhynchiform teeth with *D. stromeri* rostral denticles in a lower Maastrichtian assemblage from Oued Erguita (Morocco). Cappetta (1991a) noted that the crown morphology of teeth from Egypt display a stronger variability (medio-lingual protuberance present or absent and varying degree of labial ornament) than the specimens from Morocco, which constantly bear a medio-lingual protuberance and no labial folds. In addition, the lingual crown face of specimens from Egypt is characterized by a pair of short but sharp vertical ridges on each sides of the base of the main cusp, a feature that is not present in the Moroccan specimens, according to Cappetta (1991a). The specimens reported here, albeit few, comprise some teeth with a smooth crown and marked medio-lingual protuberance bearing a single vertical ridge as well as teeth devoid of a medio-lingual crown protuberance and numerous vertical folds of the labial face. This suggests that the variation observed among and between the populations from Egypt, Morocco, and Senegal correspond to a single species with high variation in tooth morphology. However, no rostral denticles were recovered in our samplings and therefore we cannot confirm the attribution of the oral teeth of the morphology described here and in Cappetta (1991a) to *D. stromeri*, although the arguments provided by Cappetta (1991a) are convincing and are followed here pending additional data.

403 Genus *Ctenopristis* Arambourg, 1940

404 *Ctenopristis nougareti* Arambourg, 1940

405 Fig. 4K-L

406 1940 *Ctenopristis nougareti* Arambourg, p. 137, fig. 11, p. 138, fig. 12, pl. 4, figs 4-5, 7.

407 1952 *Ctenopristis nougareti* Arambourg; Arambourg, p. 194, pl. 29, figs 3-11.

408 1959 *Ctenopristis nougareti* Arambourg; Darteville & Casier, p. 324, pl. 32, figs 1-4.

409 1959 *Ctenopristis nougareti* Arambourg; Signeux, p. 237, pl. 9, fig. 16.

410 1987 *Ctenopristis nougareti* Arambourg; Cappetta, p. 147, fig. 124.

411 2012 *Ctenopristis nougareti* Arambourg; Cappetta, p. 373, fig. 362.

412 Material. Four incomplete rostral denticles (including SN2012-61) from Unit 3, Cap de Naze
413 Formation.

414 Description. The less damaged specimen preserves a cap lacking most of the cusp that bears
415 numerous silica grains embedded in the enameloid. The cap is strongly posteriorly oriented and
416 dorso-ventrally compressed. The crown base is antero-posteriorly elongated with triangular dorsal
417 and ventral margins in apical view, which confer a lozenge shape to the crown in apical view. The
418 edges of the basal dorsal and ventral margins are irregular and markedly curved apically to form
419 ridges, especially in the anterior region. Their posterior, uncurved, region can display a few slight
420 enameloid protuberances. The anterior angle of the basal crown edge is sharp and connects the
421 anterior face of the cusp by a very salient cutting edge that is straight to slightly convex in
422 ventral/dorsal view. The posterior edge of the crown is concave in ventral/dorsal view.

423 Remarks. Although incomplete, these rostral denticles are identical to the type specimens of *C.*
424 *nougareti* described by Arambourg (1952, 1940) from the Maastrichtian of Morocco. This species has
425 also been reported from Maastrichtian localities in the Democratic Republic of Congo and Cabinda
426 enclave (Darteville and Casier, 1959). Although original description and subsequent reports were
427 based on rostral denticles, teeth were subsequently attributed to this species based on samplings
428 from Morocco (Herman, 1973). The genus *Ctenopristis* also includes the species *C. jordanicus*
429 Mustafa, Case and Zalmout, 2002, which was described from the Santonian of Jordan and
430 subsequently reported from the Coniacian-Santonian of Turkey (Yilmaz et al 2018). This species is
431 only known by teeth and it is therefore impossible to compare the rostral denticles of *C. nougareti*.
432 Numerous other reports of *Ctenopristis* rostral denticles and/or teeth have been made, especially

from the Maastrichtian (Bardet et al., 2000; Cappetta, 1991a; Cappetta et al., 2000; Signeux, 1959) and Campanian (Lewy and Cappetta, 1989) of the Middle East. However, these reports did not provide illustrations of the specimens and it is therefore impossible to compare them with the type series of Arambourg (1940).

[FIGURE 4 HERE]

Subfamily Schizorhizinae Kirkland & Aguillón-Martinez, 2002

Genus *Schizorhiza* Weiler in Stromer & Weiler, 1930

Schizorhiza stromeri Weiler in Stromer & Weiler, 1930

Fig. 5A-O

1930 *Schizorhiza stromeri* Weiler in Stromer & Weiler, p. 20-23, pl. 2, figs. 1-8, pl. 4, figs 2-4.

1933 *Schizorhiza weileri* Serra, p. 103-108, figs 1-7.

1934 *Schizorhiza stromeri* Weiler; White, pl. 3, figs 2-4 *non* figs 5-6.

1940 *Schizorhiza* aff. *weileri* Serra; Arambourg, p. 143, pl. 3, fig. 10-12 et p. 132, fig. 6.

1943 *Schizorhiza stromeri* Weiler; Darteville & Casier, p. 168, pl. 14, figs 10-16.

1948 *Schizorhiza* cf. *weileri* Serra; Dunkle, p. 174-175, fig. 2.

1952 *Schizorhiza stromeri* Weiler; Arambourg, p. 193-194, pl. 29, figs 12-20.

1959 *Schizorhiza stromeri* Weiler; Signeux, p. 237, pl. 9, fig. 17.

1972 *Schizorhiza stromeri* Weiler; Cappetta, p. 199, pl. 4, figs 9-10

1987 *Schizorhiza stromeri* Weiler; Cappetta, p. 155, fig. 133.

1991a *Schizorhiza stromeri* Weiler; Cappetta, p. 24, pl. 5, figs 1-6.

1991b *Schizorhiza* aff. *stromeri* Weiler; Cappetta, p. 436, fig. 1.

1993 *Schizorhiza* aff. *stromeri* Weiler; Gayet et al., fig. 6E.

1993 *Schizorhiza* cf. *weileri* Serra; Welton & Farish, p. 145, figs 1, 2.

2000 *Schizorhiza stromeri* Weiler; Cappetta et al., p. 85 (name only).

2000 *Schizorhiza stromeri* Weiler; Bardet et al., Tab. 1 (name only).

459 2002 *Schizorhiza stromeri* Weiler; Kirkland & Aguillon-Martinez, p. 22, figs 2, 5-11.

460 2006 *Schizorhiza* cf. *stromeri* Weiler; Becker et al., p. 709, figs 4.17-4.19.

461 2007 *Schizorhiza stromeri* Weiler; Knight et al., p.88, fig. 1A-B.

462 2012 *Schizorhiza stromeri* Weiler; Cappetta, p. 388, figs 376-377.

463 2012 *Schizorhiza stromeri* Weiler; Cuny et al., p. 111, fig. 3Y-AA.

464 2014 *Schizorhiza stromeri* Weiler; Cappetta et al., p. 224, tab. 1 (name only).

465 Material. Three fragmentary rostral denticles and eight teeth (including SN2012-62-65) from Unit 3,
466 Cap de Naze Formation, and one rostral denticle (SN2012-66) from the yellow calcareous sandstone
467 bed of Unit 1, Paki Formation.

468 Description. The teeth are higher than broad, do not exceed 2 mm high and show some degree of
469 heretodonty. The cuspidate crown is triangular in labial view and strongly bent lingually. In anterior
470 teeth (Fig. 5A-D), the labial crown face slightly overhangs the root and is strongly convex in profile
471 view. The basal region of the labial crown face can bear a pair of slight oblique folds situated below
472 the marginal angles or a single median vertical ridge. The lingual crown face is smooth and strongly
473 concave in profile view. The cutting edges are variably present in the upper half of the main cusp but
474 are consistently present in its lower part where they diverge and become more developed to form
475 incipient and abrupt heels. The heels of one specimen display a pair of short and broad incipient
476 cusplets with the distal one being slightly more developed. The root is moderately high with strongly
477 convex basal face and flared lingual and marginal regions, whereas the labial face is nearly flat. The
478 root is anaulacorhize with a very shallow nutrient canal except near the labial and lingual edges of
479 the basal face. The nutrient canal opens labially into a wide circular median foramen and lingually
480 into a large oval-shaped and rather high median foramen. Lateral teeth (Fig. 5E-J) are less mesio-
481 distally compressed, with cutting edges of regular development from the apex to the base of the
482 cusp and no demarcated heels. These teeth further show a less marked constriction of at the
483 crown/root edge and less marked bulge of the labial crown face.

484 The rostral denticle displays a strongly dorsoventrally compressed and lozenge-shaped crown in
485 dorsal/ventral view. The crown is lower than the root, with sharp and rectilinear cutting edges. The
486 root is bilobate with lobes (one lacking) separated by a deep V-shaped notch. The root is narrower in
487 its upper region below the crown than in its lower region, where vertical undulations are present.

488 Remarks. *Schizorhiza* is a monospecific genus that was only known by its highly characteristic rostral
489 denticles until Cappetta (1991a, 1991b) associated teeth of *S. stromeri* to rostral denticles based on

material from Bolivia and Egypt. Since then, rostral denticles of *S. stromeri* have been reported from numerous Maastrichtian localities worldwide but teeth were not recorded. Additionally, Kirkland and Aguilón-Martínez (2002) reported a fragmentary rostrum with associated denticles from the Uppermost Campanian Cerro de Pueblo Formation, Mexico. The morphology of the teeth described here complies with that of teeth reported from Egypt and only differ in the presence of incipient cusplets on one tooth, which probably falls within the intraspecific morphological variation of this species. Two rostral denticles were reported by Cuny et al. (2012) from the Unit 3 of the Cap de Naze Formation. The teeth reported here from the Unit 3 add to the description of the Senegalese population of this species from Unit 3, and the rostral denticle from Unit 1 extends the stratigraphic distribution of this species lower in the Cap de Naze series.

Family Ptychotrygonidae Kriwet, Nunn and Klug, 2009

Genus *Ptychotrygon* Jaekel, 1894

Ptychotrygon nazeensis sp. nov.

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Fig. 5P-T

Derivation of name. After the Cap de Naze, the name of the type locality.

Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper Maastrichtian.

Diagnosis. Ptychotrygonid species with sub-oval to triangular teeth not exceeding 2 mm in width. Crown low, mesio-distally elongated and devoid of main cusp. Wide and high transverse crest separating the lingual and labial faces and not reaching the marginal angles. Coarse secondary crest in the middle of the labial face not reaching the marginal angles nor the extremities of transverse crest. Acute and triangular labial crown edge with narrow and rounded apron projecting labially and basally. Few short and coarse ridges between secondary crest and labial crown edge. Upper region of lingual crown face concave and inclined; flat and abrupt lower region. Marked horizontal lingual ridge not reaching marginal angles. Wide and rather short uvula with rounded lower edge. Root holaulacorhize, moderately high with triangular, inclined and slightly flared basal lobe faces. Wide nutritive groove with central foramen. Pair of margino-lingual foramina and slightly scalloped basal edge lingual root face.

Material. One tooth (SN2012-67, holotype) from Unit 3, Cap de Naze Formation.

Description. This low-crowned tooth is mesio-distally elongated with a sub-oval and slightly asymmetrical outline in occlusal view. The crown overhangs the root at all points and displays a wide and high transverse crest that separates the lingual and labial faces. The extremities of the transverse crest are slightly curved labially towards the wide marginal angles, where they taper. A secondary crest is present on the middle of the labial face and is curved labially towards the apron in occlusal view. The extremities of the secondary crest do not reach the marginal angles and taper before reaching the extremities of the transverse crest. The labial crown edge is acute and triangular in occlusal view. A narrow and rounded apron projects labially and basally. Few short and coarse ridges connect the secondary crest with the labial crown edge. In profile view, the lingual crown face is divided into a concave and inclined upper region and a flat and abrupt lower region by a marked horizontal ridge that does not reach the marginal angles. The lower region of the lingual crown face bears a wide but rather short uvula with a rounded lower edge that is slightly oriented distally. The uvula is only slightly demarcated from the rest of the crown with wide and shallow concavities in lingual view. The holaulacorhize root is moderately high with triangular and slightly flared basal faces of the root lobes, which are somewhat inclined. The lobes are separated by a wide nutritive groove in the middle of which opens a foramen. The margino-lingual faces bear a foramen and the basal edge of the lingual root face is slightly scalloped. Several foramina open on the basal root face, close to the labial edge and marginal-angles.

Remarks. *Ptychotrygon* is a genus of sclerorhynchiform skates with denticle-free rostra (Villalobos-Segura et al., 2021, 2019) that includes over 20 named species and ranges from the Albian to the Maastrichtian of Europe, Africa and the Near East as well as N. America, where most Campanian-Maastrichtian records originate. Teeth of *Ptychotrygon nazeensis* sp. nov. differ from those of other *Ptychotrygon* and ptychotrygonid taxa (*Texatrygon* Cappetta & Case, 1999, *Asflapristis* Villalobos-Segura, Underwood, Ward and Cleason, 2019, *Ptychotrygonoides* Landemaine, 1991, *Iberotrygon* Kriwet, Nunn and Klug, 2009) in exhibiting the following combination of characters: non-cuspidate crown with low and flat labial face and very weakly ornamented crown. Teeth of *Erguitaia misrensis* Cappetta, 1991a from the Maastrichtian of Egypt display resemblances with *Ptychotrygon nazeensis* sp. nov. but differ in having a much higher uvula, a more developed apron, more ornamented lingual and labial crown faces and no secondary crest. The Cenomanian species *Libanopristsis hiram* (Hay, 1903) is known from articulated skeletons with denticle-bearing rostra from Lebanon (Cappetta, 1980), and its teeth display several similarities with those of *Ptychotrygon nazeensis* sp. nov. However, teeth of the Lebanese species are more cuspidate with a blunt labial crown edge, whereas it exhibits a ridge in *Ptychotrygon nazeensis* sp. nov. The genus *Ptychotrygon* has been reported from Maastrichtian deposits of Morocco, Jordan and Egypt (Cappetta, 1991a; Cappetta et al., 2000;

Noubhani and Cappetta, 1997) but corresponding specimens have not been illustrated. However, *Ptychotrygon nazeensis* sp. nov. is likely present in the Upper Maastrichtian assemblage from Imin Tanout, Morocco (GG pers. obs.).

[FIGURE 5 HERE]

Order Rhinopristiformes Naylor, Caira, Jensen, Rosana, Straube & Lakner, 2012

Suborder Rhinobatoidei Fowler, 1941

Family Rhynchobatidae Garman, 1913

Genus cf. *Rhynchobatus* Müller & Henle, 1837

cf. *Rhynchobatus* sp.

Fig. 6A-B

Material. One tooth (SN2012-68) from Unit 3, Cap de Naze Formation.

Description. This tooth preserves the crown and a small part of the root. The crown is 2 mm wide and displays a large and slightly convex labial face with an abrupt labial edge in profile view. The labial face is separated from the lingual one by a rather wide and shallow transverse crest. The crest is lingually convex and reaches the marginal angles of the crown. Below the crest, the upper region of the lingual crown face is triangular flat and oblique. The lower region of the lingual crown face is concave in profile view and made of a wide and moderately elongate median uvula and rather high margino-lingual faces. In lingual view, the mesial and distal edges of the margino-lingual faces are slightly concave. The median uvula is triangular and projects lingually relatively to the margino-lingual faces. A pair of margino-lingual foramina is present.

Remarks. Although incomplete, this tooth displays a combination of crown characters that is typical of teeth of living and fossil *Rhynchobatus* species: convex labial face, transverse crest, triangular oblique and flat upper lingual face region, lower region with moderately developed median uvula, no marginal uvulae. However, the tooth described here departs from those of *Rhynchobatus* species by its much wider uvula and absence of crown ornament, whereas *Rhynchobatus* teeth display a typical ornamentation on the labial and upper lingual region. This specimen likely represents a new rhynchobatid genus and species. This taxon would represent the oldest record of the family Rhynchobatidae, which was so far unknown prior to the Ypresian (Cappetta, 2012), although the

genus *Rhynchobatus* has been reported without illustrations from the Maastrichtian of Morocco (Noubhani and Cappetta, 1997).

Family Rhinobatidae Garman, 1913

Genus *Terangabatis* gen. nov.

Type species. *Terangabatis thiami* gen. et sp. nov.

Derivation of name. From the Wolof word “Teranga” (hospitality in Wolof, a word that is often used to define the Senegalese lifestyle and philosophy) and *batis* (ray/skate in ancient Greek).

Diagnosis. Rhinobatid with teeth showing moderate degree of monognathic heterodonty. Non-cuspidate teeth broader than long; crown with transverse crest separating lingual and labial crown faces. Transverse crest slightly convex lingually reaching the marginal angles. Crown bulged in the median area of the crest. Labial crown face concave near the transverse crest, convex near the developed labial crown margin. No apron differentiated. Marginal angles wide and obtuse. Lingual crown face very abrupt; reduced margino-lingual faces; slightly lingually protruding median region extended basally into a uvula. Median region of lingual crown face with vertical depression bordered by bulged and V-shaped margins of uvula. Uvula wide and triangular not reaching the basal root face. Root holaulacorhize, less than half the total tooth height and overhung by the crown. Pair of large oval margino-lingual foramina; additional foramina occasionally present.

Remarks. The tooth morphology of this taxon can be separated from that of other rhinoprists and rhinopristsiforms by the following combination of characters: mesio-distally elongate and labio-lingually compressed crown, non-cuspidate crown, flat to concave lingual crown face, median uvulae wide with vertical concavity and broadly attached to marginal faces (no notches), reduced margino-lingual faces with no developed marginal uvulae.

Terangabatis thiami gen. et sp. nov.

LSID: urn:lsid:zoobank.org:act:FF66D7CE-641F-4A75-BDEF-5B789CC486D0

Fig. 6C-K

Derivation of name. After Dr. Mouhamadou Moustapha Thiam (Institut des Sciences de la Terre, Cheikh Anta Diop University, Dakar) for his participation in the fieldwork.

613 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper
614 Maastrichtian.

615 Diagnosis. As for genus.

616 Material. Four teeth (SN2012-69-72) from Unit 3, Cap de Naze Formation.

617 Description. Teeth from anterior jaw positions (Fig. 6C-I) are broader than long and do not exceed 2
618 mm in width. The crown exhibits a transverse crest that separates the lingual and labial crown faces
619 and reaches the marginal angles. The transverse crest is slightly convex lingually in labial view and
620 the crown is bulged in the median area of the crest. In profile view, the labial crown face is concave
621 in the vicinity of the transverse crest and convex near the labial margin of the crown, which is devoid
622 of apron. The labial crown edge is rounded and strongly overhangs the root in profile view. The
623 marginal angles are wide and obtuse in labial view. The lingual crown face is overall abrupt and made
624 of reduced margino-lingual faces and a slightly lingually protruding median region extended basally
625 into a uvula. The lateral edge of the margino-lingual faces is convex, while their lower margin is
626 straight to slightly convex in lingual view. The median region of the lingual crown face displays a
627 vertical depression that is bordered by bulged and V-shaped edges of the uvula, which diverge and
628 taper towards the margino-lingual faces. The uvula is wide and triangular and does not reach the
629 basal root face. The uvula is separated from the lower edges of the margino-lingual faces by wide
630 and shallow concavities. The root is holaulacorhize and accounts for less than half the total height of
631 the tooth. The root is positioned lingually and is overhung by the crown at all points in occlusal view.
632 The marginal root edges are straight and slightly diverging basally in lingual view. In basal view, the
633 root lobes are L-shaped with lingually and labially developed branches, with concave margino-lingual
634 faces. The basal face of each root lobe is flat to lightly convex and oblique. The lobes are separated
635 by a large nutritive groove, which hosts a central foramen. Each margino-lingual root faces are
636 pierced by a large and oval foramen situated below the concavity of the lower crown edge.
637 Additional small margino-lingual foramina can be present below the margins of the uvula. Teeth from
638 more lateral jaw positions (Fig. 6J-K) display a similar morphology but show a more convex transverse
639 crest with a less bulged median region.

640 Remarks. The teeth of this taxon exhibit a peculiar morphology, which makes their identification
641 easy. Some superficial resemblances can be noted with teeth of species of the Cenomanian genus
642 *Rhombopterygia* Cappetta, 1980. However, species of the latter genus differ in having a more
643 lingually protruding and convex medio-lingual crown region, a moderately developed cusp as well as
644 a convex labial crown face and incipient lateral uvulae. Teeth of some species of the mid to late
645 Cretaceous *Squatirhina* Casier, 1947 can be easily separated from those of *T. thiami* gen. et sp. nov.

by their stronger heterodonty, developed main cusp, ornamented crown and developed apron.
Terangabatis thiami gen. et sp. nov. is so far restricted to the type locality.

[FIGURE 6 HERE]

Genus *Rhinobatos* Link, 1790

'Rhinobatos' popenguinensis sp. nov.

LSID: urn:lsid:zoobank.org:act:62E0D86F-1855-45F8-AD59-6991ADF88B58

Fig. 7

Derivation of name. After Popenguine, a locality close to the Cape de Naze cliff.

Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper Maastrichtian.

Diagnosis. Small rhinopristiform species showing a weak degree of monognathic and possibly sexual dimorphism. Teeth slightly higher than wide. Crown lozenge-shaped in occlusal view with acute marginal and medio-labial angles. Transverse crest convex lingually, reaching the marginal angles and projecting lingually above median uvula. Occasional presence of incipient cusp. Margino-lingual faces reduced. Short and lingually protruding lateral uvulae. Median uvula strongly lingually projected not reaching the basal root edge. Profile of median uvula convex medially and near its basal tip; concave profile below the transverse crest and between the two convexities. Median uvula triangular with convex lateral margins and a sharp lower extremity; slight flaring of the media uvula below the notches separating the lateral uvulae in some teeth. Labial visor strongly overhanging the root with strong and rounded median process. Margino-labial crown edges straight to slightly concave in occlusal view. Root lingually projected and narrower than the crown. Basal face of root lobes convex and L-shaped with short marginal projections. Wide nutritive groove with large labial foramen.

Material. Twenty-six teeth (including SN2012-73-78) from Unit 3, Cap de Naze Formation.

Description. Teeth of this species are slightly higher than wide and do not exceed 1 mm. The crown is rather low and comprises a developed labial face, a developed median uvula, and reduced lateral uvulae. The crown is lozenge-shaped in occlusal view with acute marginal and medio-labial angles. A marked transverse crest separates the lingual and labial crown faces. The crest is convex lingually, reaches the marginal angles and can project in its median region into an incipient cusp in putative male individuals. The margino-lingual faces are reduced with oblique marginal edges converging

basally as well as very short and lingually protruding lateral uvulae. The lateral uvulae are separated from the median uvula by a broad notch. The median uvula is strongly lingually projected and does not reach the basal root edge. In profile view, the median uvula displays a marked medial convexity separated from the convex basal region by a concavity. The region immediately below the transverse crest and the medial convexity is also markedly concave in profile view. The median uvula is triangular in lingual view with convex lateral margins and a rather sharp lower extremity. In some teeth, there is a slight flaring of the uvula just below the notches separating the lateral uvulae. Most of the labial crown face is slightly concave in profile view, except its labial visor, which is flat to convex. The labial visor strongly overhangs the root and displays a strong and rounded median process that projects both basally and labially. The margino-labial crown edges are straight to somewhat concave in occlusal view. The root is lingually projected and narrower than the crown. The labial root face is oblique and the convex basal face of the root lobes is L-shaped with short marginal projections. The root lobes are separated by a wide nutritive groove at the labial edge of which a large foramen opens. The depressed margino-lingual root faces host a moderately wide and rounded foramen. Anterior teeth tend to display a more marked lingual projection of the median uvula, whereas lateral teeth are slightly lower and more mesio-distally expanded.

Remarks. A number of Campanian-Maastrichtian species have been referred to the genus *Rhinobatos*. However, the tooth morphology of living rhinopristiform species is imperfectly known (Guinot et al., 2018) and many Cretaceous species included in this genus might belong to new genera (Cappetta, 2012). Among described *Rhinobatos* species, teeth of '*R. popenguinensis* sp. nov.' are morphologically close to those of *R. ibericus* Cappetta and Corral, 1999 from the Maastrichtian of Spain but differ from the latter by their more acute marginal angles of the crown, sharper and more protruding apron as well as broader and more triangular uvula. '*Rhinobatos*' *popenguinensis* sp. nov. differs from *Rhinobatos echavei* Cappetta and Corral, 1999 from the Maastrichtian of Spain by its teeth with more acute marginal angles of the crown, transverse crest with short cusp, sharp apron, marginal edges of margino-lingual faces oblique and converging basally, and smaller size. Teeth of the new Senegalese species can be separated from numerous *Rhinobatos* species with developed lateral uvulae (e.g., *R. casieri* Herman in Cappetta and Case, 1975; *R. ladoniaensis* Cappetta and Case, 1999) by their reduced lateral uvulae, triangular labial crown edge and much smaller size. Teeth of *R. craddocki* Case and Cappetta, 1997 differ in having a lower lingual crown face with shorter uvula that is more broadly united to the margino-lingual faces, more flared and labially oriented margino-lingual crown faces, more mesio-distally developed crown, less lingually projected medio-lingual region. Teeth of *R. uvulatus* Case and Cappetta, 1997 can be separated from those of '*R. popenguinensis* sp. nov.' by their uncuspidate crown with more rounded marginal angles and labial crown edge, and less

protruding central uvula with a rectilinear profile. *Rhinobatos mariannae* Bor, 1983 differs by its teeth with higher margino-lingual faces, less marked transverse crest with convex extremities near the marginal angles, less acute and oblique marginal angles, presence of lingual ornament and more rounded extremity of uvula. Teeth of '*R.*' *popenguinensis* sp. nov. differ from those of *Rhombopterygia* in having a lozenge-shaped labial face, straight margino-labial crown edges, convex medio-lingual region in profile view, acute marginal angles of the crown. '*Rhinobatos*' *popenguinensis* sp. nov. is possibly closely related to *R. ibericus* and probably belongs to a new rhinobatid genus, but more knowledge is needed on living rhinobatid taxa before drawing such conclusions.

[FIGURE 7 HERE]

Rhinopristiformes *incertae familiae*

Genus *Atlantobatis* gen. nov.

Derivation of name. After the geographic distribution of species of this genus.

Type species. *Hamrabbatis weltoni* Case & Cappetta, 1997.

Diagnosis. Same as for type species.

Remarks. *Hamrabbatis weltoni* was described from the Late Maastrichtian (Navarroan), Kemp Clay Formation in Texas (South Sulphur River, near Commerce, Hunt County). This species was referred to the genus *Hamrabbatis* based on superficial resemblances with *H. ornata* Cappetta, 1991a, the type species of the genus. However, the morphology of the type specimens of *Hamrabbatis weltoni* departs from that of *H. ornata* teeth in having a more developed labial protuberance of the labial crown margin, a higher crown, much higher occlusal face, higher lingual crown face, crown with irregular ornament not reticulate nor alveolate, less acute marginal angles, more constricted root near the crown, and no margino-lingual foramina. Teeth of *Archingeayia* Vullo, Cappetta and Néraudeau, 2007 share similar crown characters with *Atlantobatis* gen. nov., but differ by the absence of labial ornament, different lingual ornament, lingual occlusal region and lingual crown faces abrupt and in the same plane in profile view, lingual face much shorter and restricted to a bulge-like lingual crest, and more developed cusp. The genus *Hamrabbatis* should now be restricted to the type species from the Maastrichtian of Egypt and *H. bernardezi* Vullo, Cappetta and Néraudeau, 2007 from the Cenomanian of France and Spain. A putative additional, unnamed *Hamrabbatis* species with a weakly ornamented crown is probably present in the Maastrichtian of Syria (Bardet et al., 2000). The genus

Atlantobatis gen. nov. described here includes the type species as well as a new species described below, and is so far restricted to the Maastrichtian of the Atlantic Ocean.

Atlantobatis acrodonta gen. et sp. nov.

LSID: urn:lsid:zoobank.org:act:4D98EAFD-1DCA-4D59-A339-A3691C6FB81F

Fig. 8

Derivation of name. After the high-crowned teeth of this species.

Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper Maastrichtian.

Diagnosis. Teeth broader than high; triangular crown in occlusal view with elliptical occlusal crown face. Thick transverse crest, sub-horizontal or convex in its medial region, situated below the marginal angles in lingual view. Lingual crown face high, abrupt, and concave in profile view with marked median articular concavity and faint median uvula. Occlusal face is high, labio-lingually compressed, and triangular in lingual view. Sharp and lingually-projected occlusal crest connecting the transverse crest lingually and separating the occlusal face into lingual and labial areas. Lingual area concave with light irregular ornament. Labial area of occlusal face convex with short and rather coarse vertical folds near basal edge. Coarsely ornamented labial crown face separated from occlusal face by an irregular secondary crest. Labial crown face with very developed median protuberance. Root low, bilobate and narrower near the crown. Root lobes triangular with rounded angles in basal view. Root lobes varying from as broad as long to mesio-distally expanded. Nutritive groove wide and rather deep with central foramen in labial position.

Material. Forty-one teeth (including SN2012-79-86) from Unit 3, Cap de Naze Formation.

Description. These teeth are broader than high and do not exceed 1.5 mm in width. In occlusal view, the crown is triangular and overhangs the root at all points. The occlusal crown face is elliptical and bordered lingually by a marked and thick transverse crest situated below the marginal angles in lingual view. The crest can be sub-horizontal or convex in its medial region, and its marginal extremities are oblique as they reach the marginal angles. This crest is in continuity with the sharp ridge that runs along the labial crown edge. The marginal angles are rounded and rather wide. Below the transverse crest, the lingual crown face is well developed, abrupt, and concave in profile view. A marked median articular concavity is present and the basal edge of the lingual crown face is triangular with a faint uvula that is individualized from the rest of the basal edge by broad

771 concavities. The occlusal face is very high, labio-lingually compressed, and triangular in lingual view.
772 The occlusal face bears a sharp and lingually-projected occlusal crest that is slightly lingually
773 positioned. The extremities of the occlusal crest are lingually oriented and connect the transverse
774 crest on the lingual face, just before the marginal angles. The occlusal crest separates the occlusal
775 face into two areas linguo-labially. The lingual area is concave in profile view, excepted medially
776 where it is flat, and bears light irregular ornament that tend to arrange into apico-basally oriented
777 wrinkles near the basal edge. The labial area of the occlusal face is convex in occlusal view and
778 displays short and rather coarse vertical folds in its basal edge. This ornament is coarser on the labial
779 crown face, which can be separated from the occlusal face by an irregular secondary crest. This
780 secondary crest, when present, bifurcates from the labial ridge that runs along the labial crown edge.
781 In occlusal view, the labial crown face is weakly inclined basally and weakly developed in its marginal
782 areas but bears a very developed median protuberance. The median protuberance is well
783 demarcated from the rest of the crown by concave margino-labial edges in occlusal view. The median
784 protuberance is developed both labially and basally. The labial crown edges are blunt with no
785 articular facets. The root is rather low and constricted near the crown. In basal view, the root lobes
786 are triangular with rounded angles. The basal face of the root lobes is flat to slightly convex and
787 inclined towards the nutritive groove. The root lobes vary from being as broad as long to mesio-
788 distally expanded. Some teeth display a short lingual projection of the root lobes. The nutritive
789 groove is wide and rather deep and bears a central foramen in labial position. There are no margino-
790 lingual foramina.

791 Remarks. Teeth of this species are morphologically close to those of *A. weltoni* comb. nov. This
792 species was described based on two illustrated specimens from the Late Maastrichtian of Texas (Case
793 and Cappetta, 1997), which did not provide a complete overview of the intraspecific morphological
794 variation. Study of numerous specimens of *A. weltoni* comb. nov. from the type locality housed in the
795 collections of the University of Montpellier (G.G. perso. obs.) and comparison with the specimens
796 from Senegal allowed the identification of several differences between teeth of *A. weltoni* comb.
797 nov. and those of the Senegalese species. Teeth of the latter display a less marked lingual ornament,
798 denser and finer labial ornament, presence of a marked labial crest, and less high lingual crown face.

799 **[FIGURE 8 HERE]**

800

801 Genus ? *Microbatis* Cappetta, 1993

802 ? *Microbatis* sp.

803

Fig. 9A-J

804 Material. Four teeth (SN2012-87-90) from Unit 3, Cap de Naze Formation.

805 Description. Teeth of this species are higher than broad and minute-sized (less than 1 mm wide). The
806 crown is asymmetrical, smooth and cuspidate. The labial crown face is flat to slightly concave in
807 profile view, with a convex labial edge strongly overhanging the root. The labial visor is convex and
808 connects the labial crown face in a sharp angle in profile view. The marginal angles are blunt in
809 anterior teeth, while more lateral teeth have a more marked distal marginal angle. The lingual crown
810 face displays a moderately developed conical cusp that is oriented lingually. Blunt and thick cutting
811 edges originate at the base of the main cusp, in labial position, the mesial one being more developed.
812 The cutting edges taper just before reaching the marginal angles. The lingual crown face is strongly
813 concave in profile view. A short and rather wide median uvula is present below the main cusp and
814 separated from the margino-lingual faces by wide concavities. The margino-lingual faces are reduced,
815 abrupt and labially oriented. The marginal uvulae are very short, being reduced to fine blades
816 oriented mesio-distally and more marked mesially. The root, although incomplete in all specimens, is
817 very low, bilobate, and lingually positioned. A wide nutritive groove is present where a broad central
818 foramen opens.

819 Remarks. The combination of characters present in teeth of this taxon and their size compare well
820 with those of *Microbatis sabatieri* Cappetta, 1993, which was described from the Thanetian of
821 Morocco and is the only known species of the genus *Microbatis*. However, the specimens described
822 here differ from in having a more demarcated, although short, median uvula, very reduced and more
823 labio-lingually oriented margino-lingual faces, and by the presence of very short marginal uvulae.
824 *Microbatis sabatieri* is supposedly moderately heterodont and most specimens from the type series
825 lack the root. Considering the small number and poor preservation of the specimens sampled
826 described here, they cannot be assigned to the genus *Microbatis* with certainty.

827

828 Genus *Sowibatos* gen. nov.

829 Derivation of name. After Prof. El Hadji Sow, who greatly facilitated the organization of the field
830 sessions.

831 Type species. *Sowibatos minimus* gen. et sp. nov.

832 Diagnosis. Teeth broader than high not exceeding 0.8 mm wide. Crown lozenge-shaped in occlusal
833 view; labial visor strongly overhanging the root with median labial expansion separated by straight to

834 concave margino-labial edges. Marginal angles wide and bevelled labially. Transverse crest high,
835 wide, and acute, separating the lingual and labial faces. Transverse crest straight to curved labially,
836 tapering before reaching the margino-lingual edges, anterior to the marginal angles. Occlusal region
837 flat and oval to triangular in shape. Lower lingual region abrupt, moderately developed and concave
838 in profile view with flared basal edge. Median uvula short, wide and triangular, demarcated from
839 margino-lingual faces by a slight concavity. Holaulacorhize root low and lingually positioned with
840 concave lingual face and flat to convex and oblique labial face. Root lobes with triangular basal faces;
841 wide nutritive groove with rounded central foramen positioned slightly labially.

842
843 *Sowibatos minimus* gen. et sp. nov.

844 LSID: urn:lsid:zoobank.org:act:3950016E-24C0-4F95-81AF-4417ED802685

845 Fig. 9K-U

846 Derivation of name. After the small size of teeth of this species.

847 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper
848 Maastrichtian.

849 Diagnosis. As for genus.

850 Material. 37 teeth (including SN2012-91-94) from Unit 3, Cap de Naze Formation.

851 Description. Teeth of this species are broader than high and do not exceed 0.8 mm in width. The
852 crown is smooth, low and more developed mesio-distally than labio-lingually. In occlusal view, the
853 crown is lozenge-shaped, although the lingual edge tends to be less developed than the labial one in
854 some specimens. The lingual edge is convex, whereas the labial visor strongly overhangs the root and
855 displays a wide median labial expansion, which is demarcated by margino-labial edges that vary from
856 being slightly concave in anterior teeth to more strongly concave in laterals. The marginal angles are
857 rather wide and blunt, except in their labial region where the concavity of the margino-labial edges
858 confers an acute outline to this area, especially in lateral teeth. The labial face is convex, both labio-
859 lingually and mesio-distally. The labial and lingual faces are separated by a high, wide, and acute
860 transverse crest. This transverse crest varies from being strongly curved labially to nearly straight in
861 anterior teeth. The crest orientates slightly labially and tapers before reaching the margino-lingual
862 edges, slightly anterior to the marginal angles. The lingual crown face is separated into two regions.
863 One, on occlusal position, is delimited labially by the transverse crest and lingually by the angle with
864 the lower and oblique lingual region. This occlusal region is oval to triangular in shape and flat. The

abrupt, lower lingual region is moderately developed and concave in profile view. The basal edge of this face is slightly flared and flanked by obtuse margino-lingual angles that are overhung by the marginal angles, which they join by a slightly concave edge in lingual view. No individualized marginal uvulae are present but a short and wide triangular median uvula is demarcated from the margino-lingual faces by a slight concavity. The median uvula can be slightly bent distally in lateral teeth. The crown is devoid of ornamentation, but its surface can be irregular on the occlusal region of the lingual face and on the labial face. The holaulacorhize root is low and positioned lingually. In profile view, the lingual root face is strongly concave, whereas the labial face is flat to concave, and oblique lingually. The basal edge of the lingual crown face is flared with an irregular outline and is as developed as the lingual crown face in profile view. A pair of margino-lingual foramina is present below the concavities separating the median uvula from the margino-lingual crown faces. The basal face of the root lobes is triangular with a slight projection of the median region, close to the nutritive groove, which is wide, circular in cross section, and more open in its labial part. The large circular central foramen opens in the nutritive groove, in labial position. One tooth, probably originating from a parasymphyseal file, differs from the morphology described above in being much more mesio-distally compressed and more asymmetrical with straight mesial marginal angle, more developed margino-lingual crown faces and more elongate median uvula.

Remarks. Teeth of this species differ from those of species referred to the genus *Hamrabatis* (see above) including *H. ornata* and *H. bernardezi* in having a smooth crown, thicker transverse crest, no lingual crest, less concave lower lingual crown face, more mesio-distally developed root lobes, and no labial foramina. The crown morphology of *S. minimus* gen. et sp. nov. tends to superficially resemble that of some rhynchobatids but the Maastrichtian species differs by its smooth and more mesio-distally elongate crown, shorter median uvula, no or incipient lingual projection of the root and more marked transverse crest not reaching the marginal angles.

[FIGURE 9 HERE]

Order Myliobatiformes Compagno, 1973

Superfamily Dasyatoidea Whitley, 1940

Family Dasyatidae Jordan & Gilbert, 1879

Genus '*Dasyatis*' Rafinesque, 1810

'Dasyatis' reticulata sp. nov.

898 Derivation of name. After the reticulate ornamentation on the crown of teeth of this species.

899 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper
900 Maastrichtian.

901 Diagnosis. Dasyatid showing gradient monognathic and possibly gynandric heterodonty. Non-
902 cuspidate teeth higher than wide (anterior) to wider than high (laterals/posterior). Crown with fine
903 reticulate ornamentation on occlusal face and upper part of labial face, occasionally on basal region
904 of labial face. Occlusal face bulged in anterior, flat in laterals/posterior. Labial face concave in
905 profile view; labial visor strongly flared with a developed, convex, and smooth lower face. Lingual
906 crown face high, smooth, with depressed margino-lingual faces separated by a broad medio-lingual
907 crest; marked transverse depression on lingual crown face; margino-lingual faces concave; lingual
908 visor developed and triangular. Cuspidate teeth high and labio-lingually developed. Cusp strongly
909 bent lingually with blunt and curved margins reaching the marginal angles. Median vertical
910 depression on labial crown face from the apex to the labial visor. Labial visor flared with concave
911 margins. Lingual face high with two concave and basally flared margino-lingual faces separated by
912 broad medio-lingual crest. Elongated and strongly lingually-projected lingual visor. Reticulate crown
913 ornament on labial face and occasionally on upper part of lingual face. Root holaulacorhize, lingually
914 positioned. Root lobes triangular in basal view and lingually-projected. Developed labial root face
915 with several foramina.

916 Material. 74 teeth (including SN2012-95-107) from unit 3, Cap de Naze Formation.

917 Description.

918 *Non-cuspidate morph (Fig. 10A-A')*. Anterior teeth are higher than wide and do not exceed 2mm in
919 height. In occlusal view, the crown outline is overall lozenge-shaped with sharp marginal and medio-
920 lingual angles, but with a blunt medio-lingual angle. The occlusal face is strongly bulged in profile
921 view, and bears a marked and fine reticulate ornamentation. The marginal angles are marked and
922 reach the labial visor by a labially inclined and thick bulge. The labial crown face displays two
923 depressed margino-labial faces separated by a wide medio-labial bulge originating from the occlusal
924 face toward the medio-labial angle of the visor. In profile view, this median bulge can be straight and
925 oblique to convex. In occlusal view, the marginal edges of the labial visor are straight to slightly
926 concave. The labial crown face is generally devoid of ornamentation, excepted in its upper region
927 where the reticulate ornament of the occlusal face tapers. Some specimens occasionally bear coarse

but shallow ridges in the lower region of the labial crown face. The labial visor is strongly flared with a developed, convex, and smooth lower face. The lingual crown face is high and smooth with depressed margino-lingual faces separated by a broad medio-lingual crest. No marked transverse crest is observable. In profile view, a strong transverse depression separates the vertical upper region of the lingual face from the oblique lower region. Both the upper and lower regions display a convex profile. The margino-lingual edges are oblique and the lingual visor is triangular with a rounded lower extremity. The holaulacorhize root is positioned lingually and shows a constriction just below the crown/root edge. The root lobes are triangular in basal view and project lingually where they barely overtake the basal edge of the lingual visor of the root in profile view. The lingual and labial root faces are transversally convex. The nutritive groove is wide and bears a broad central foramen. Several labial foramina of varying sizes open below the crown/root edge, whereas there are no lingual foramina. Teeth from more lateral jaw positions are lower and generally broader than high, with some lateral teeth being very large (Fig. 10E-H). Posterior teeth are very low-crowned. The occlusal face gradually becomes flat and the lingual crown face is reduced with a more marked transverse depression. A blunt transverse crest marks the limit between the occlusal and lingual crown faces. The lingual visor is proportionally shorter than in anterior teeth. The medio-lingual and medio-labial angles are blunt or absent in posterior-most teeth. The labial depression of the crown is present and can bear a reticulate ornament similar to that of the occlusal face. The marginal angles are blunt in posterior teeth. The root displays similar features to those observed in anterior teeth, but differ in being lower with wider root lobes.

Cuspidate morph (Fig. 10B'-S'). Teeth of this morph are of similar size to those of the non-cuspidate morph but differ in being higher, more labio-lingually developed, and in bearing an elongate but broad cusp. In profile view, the cusp is strongly bent lingually with blunt and curved margins reaching the marginal angles. The labial crown face displays a median vertical depression that runs from the apex of the cusp to the labial visor, which is bifid in its median region. In some teeth, the vertical depression bears a broad median vertical ridge, which connects a medio-labial angle. In profile view, a transverse depression separates the convex labial face of the cusp from the flared labial visor, which is demarcated from the rest of the labial face by concave edges in basal view. The lower face of the labial visor is very developed, smooth, and convex. The lingual face is high with two concave margino-lingual faces separated by a broad medio-lingual crest, which is concave in profile view. The lingual visor is elongated and strongly projects lingually. The basal edges of the margino-lingual crown faces are markedly flared. The extent of the crown ornamentation is variable, but is generally present as a reticulate pattern on the labial face of the main cusp and often develops over the labial

visor. Some teeth bear such an ornamentation on the upper half of the lingual crown face as well (Fig. 10Q'-S'). The root displays the same features as in teeth of the non-cuspidate morph.

Remarks. The general morphology and heterodonty of these teeth agree with those of extant and extinct dasyatids. Fossil dasyatid species have been commonly assigned to the genus '*Dasyatis*' as their tooth morphology was closer to that of some extant *Dasyatis* species than to other dasyatid genera, but knowledge on tooth morphology of extant dasyatid species is very limited (Guinot et al., 2018). However, the systematics of extant dasyatids has been deeply modified (Last et al., 2016) and while the genera *Himantura* and *Dasyatis* used to gather most dasyatid species, the latter have been split into several genera. Therefore, considering the lack of knowledge on the tooth morphology of extant dasyatids and uncertainties on the systematic position of fossil representatives of this clade, it is preferred to refer the species described here to '*Dasyatis*'. Several *Dasyatis*-like fossil species have been reported from various Campanian-Maastrichtian and Paleocene localities. Among them, few display the reticulate crown ornamentation observed in teeth of the new Senegalese species. Comparable crown ornamentation occurs in teeth of the Maastrichtian *D. commercensis* Case and Cappetta, 1997 and of the Danian *D. martini* Noubhani and Cappetta, 1997, *D. tetraedra* Arambourg, 1952, *D. hexagonalis* Arambourg, 1952, *D. ponsi* Noubhani and Cappetta, 1997, *D. alveolata* (Leriche, 1942), *Palaeodasyatis hermani* Halter, 1989 (pl. 1-2 non pl. 3) and *D. puerensis* Williamson and Lucas, 1993. Teeth of '*D.*' *reticulata* sp. nov. differ from these species excepted *D. commercensis* and *D. hexagonalis*, by the combined presence in non-cuspidate teeth of a strongly bulged occlusal face, developed and markedly depressed margino-labial crown faces, and high lingual crown face. The new species described here further differs from *D. commercensis* by the absence of marked transverse crest, more developed labial crown face, longer lower face of the labial visor, and more marked transverse depression of the lingual crown face. Teeth of *D. hexagonalis* and *P. hermani* are larger with finer and denser crown ornamentation, and display labio-lingually developed, non-triangular root lobes that characteristically separate these species from '*D.*' *reticulata* sp. nov. In addition, teeth of *D. hexagonalis* possess a median vertical depression on the lingual crown face bordered by two vertical wrinkles that further differentiates this species from '*D.*' *reticulata* sp. nov. Large lateral teeth of the non-cuspidate morph of '*D.*' *reticulata* sp. nov. might suggest the presence of protrusions in the dentition of this species, as seen in some modern dasyatids (e.g., *Urogymnus*, *Hypanus*).

[FIGURE 10 HERE]

Family Dasyatoidea incert. fam.

Genus *Coupatezia* Cappetta, 1982

Coupatezia casei sp. nov.

994 LSID: urn:lsid:zoobank.org:act:85FE70A4-C1A9-47BB-88B7-40862262D7C4

995 Fig. 11

996 Derivation of name. After Gerard R. Case, for his contribution to the knowledge on Cretaceous
997 elasmobranchs.

998 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper
999 Maastrichtian.

1000 Material. 86 teeth (including SN2012-108-126) from Unit 3, Cap de Naze Formation; two teeth from
1001 the yellow calcareous sandstone bed of Unit 1, Paki Formation.

1002 Diagnosis. Dasyatoid species with moderate degree of monognathic heterodonty and strong sexual
1003 heterodonty. Teeth varying from broader than high to as high as broad, not exceeding a maximum
1004 size of 1.5 mm. Holaulacorhize root low and wider than the crown but constricted below the crown.
1005 Root lobes triangular projecting lingually with flat and strongly inclined basal face. Broad and deep
1006 nutritive groove wider in its central region with wide central foramen. Labial root face sub-vertical
1007 with one to three large foramina. Non-cuspidate anterior teeth of trapezoidal occlusal outline,
1008 broader labially than lingually; rectangular in laterals. Marginal angles are obtuse and blunt. Margino-
1009 labial angles very developed, acute and strongly projecting labially as well as laterally in anteriors.
1010 Marked median concavity of the labial crown edge between the margino-labial angles. Oblique and
1011 lingually-protruding transverse region separating the lingual and labial faces with oval to rectangular
1012 depression. Labial edge of transverse depression weakly convex with irregular crest of varying
1013 sharpness. Lingual edge of transverse depression with granulose enamelled ornament that can form
1014 a sharp irregular crest. Crest on labial face that may or may not reach the marginal edges of the base
1015 of the margino-labial angles. Fine and irregular transverse ridge between the crest and the labial
1016 crown edge. Labial ornament coarse and irregular represented by tubercles, short ridges or cupulas.
1017 Lingual face is high and concave in profile view, divided into two depressed margino-lingual faces by
1018 a wide hourglass-shaped vertical ridge. Marginal edges of lingual crown face vertical and straight.
1019 Lower edge of lingual crown face concave in its centre. Cuspidate teeth cordiform in occlusal view
1020 with concave labial edge. Rounded, broad and both labially and laterally (in anteriors) projected
1021 margino-labial angles. Labial crown face oblique and bordered labially by a sharp ridge. Base of labial
1022 crown face depressed, upper profile convex. Very coarse labial ornament of broad tubercles
1023 occasionally arranged into vertical ridges. Main cusp short, narrow, triangular, and lingually curved.
1024 Lingual crown face high with weakly depressed margino-lingual faces and vertical medial convexity.
1025 Lingual face with concave marginal and lower edges.

1026 Material. 85 teeth (of which nine belong to the cuspidate morph) from Unit 3, Cap de Naze
1027 Formation; two uncuspidate teeth from the sandstones of Unit 1, Paki Formation.

1028 Description.

1029 *Non-cuspidate morph (Fig. 11A-C')*. Anterior teeth are as high as broad or slightly broader than high
1030 with a trapezoidal occlusal outline that is broader labially than lingually. The margino-labial angles
1031 are very developed, acute and strongly project both labially and laterally. The margino-labial angles
1032 are separated by a marked median concavity of the labial crown edge in occlusal view. The marginal
1033 angles are obtuse and blunt and connect the margino-labial angles by slightly concave, sharp, and
1034 diverging edges. The transverse region separating the lingual and labial faces is oblique, protruding
1035 lingually and occupied by an oval to rectangular depression in lingual view. In occlusal view, the labial
1036 edge of this transverse depression is weakly convex, almost straight and can bear in its central region
1037 a blunt and irregular crest. The lingual edge of the transverse depression is made of a blunt and
1038 concave projection that reaches the marginal angles and bears irregular and granulose enamelled
1039 ornament that can join each other to form a sharp but irregular crest. The labial face displays a crest
1040 that may or may not reach the marginal edges of the base of the margino-labial angles. Another very
1041 fine and irregular crest can be present between the latter and the labial crown edge. The labial
1042 ornament is coarse and irregular in the concave area between the labial crest and the transverse
1043 depression, where it can be represented by tubercles, short ridges or cupulas. The lingual face is high
1044 and concave in profile view and is overhung by the transverse region. The lingual face is divided into
1045 two strongly depressed margino-lingual faces by a wide hourglass-shaped vertical ridge that connects
1046 the basal edge of the lingual face and the lingual edge of the transverse depression. The marginal
1047 edges of the lingual face are vertical and straight as is its lower edge, excepted below the hourglass-
1048 shaped vertical ridge where it is concave. The root is positioned lingually, low and wider than the
1049 crown in lingual view. A strong and somewhat high constriction of the root is present below its
1050 contact with the crown. The lobes are triangular in basal view and project lingually with a flat basal
1051 face that is strongly inclined. The lobes are separated by a broad and deep groove that tends to be
1052 wider in its central region and at the bottom of which a wide central foramen opens. The labial face
1053 is sub-vertical and generally displays from one to three large foramina. Other small labial foramina
1054 can be present just below the crown. Teeth from more lateral jaw positions display the same general
1055 morphology but differ in being more labio-lingually compressed and broader than high with a
1056 rectangular outline in occlusal view. The margino-labial angles are wider and developed labially but
1057 not laterally. The labial ornament displays the same pattern as in anteriors but is generally sharper.
1058 Both the upper and lower edges of the transverse depression are sharper, although irregular. The
1059 lingual face is wide with a less marked vertical separation between the margino-lingual faces. The

root is of comparable morphology to that of anteriors, but is lower with more labio-lingually compressed and mesio-distally developed lobes.

Cuspidate morph (Fig. 11D'-V'). Anterior teeth of this morph are cordiform in occlusal view with a strongly marked concavity of the labial crown edge separating the rounded margino-labial angles. The margino-labial angles are broad and projected both labially and laterally. The labial crown face is oblique and bordered labially by a sharp ridge that can be very developed in some teeth. The lower edge of the labial crown face is thick and convex in profile view. The labial crown face is depressed between this basal labial ridge and the rest of the labial crown face, which is mainly convex in profile view. The labial ornament is very coarse and consists of broad tubercles that tend to be arranged into vertical ridges in some teeth. The main cusp is rather short, narrow, triangular, and curved lingually. The marginal angles are wide and faint and bear a fine ridge that runs continuously from the labial edge of the margino-labial angles to the base of the cusp. The lingual crown face is high with weakly depressed margino-lingual faces separated by a vertical medial convexity. The margino-lingual faces are concave in lingual view as is the lower edge of the lingual face. The root is of similar morphology to that of non-cuspidate teeth. Lateral cuspidate teeth are more mesio-distally developed and more asymmetrical, with less deep and broader concavity of the basal edge of the labial face.

Remarks. Teeth of *Coupatezia casei* sp. nov. differ from those of most congeneric species by their strong, coarse and non-reticulated labial ornament, which is also present in teeth of *C. ambroggii* Noubhani and Cappetta, 1997 and *C. reniformis* Noubhani and Cappetta, 1997 from the Maastrichtian of Morocco (Noubhani and Cappetta, 1997). Teeth of *Coupatezia casei* sp. nov. can be separated from those of *C. ambroggii* by their higher lingual face, presence of transverse depression between lingual and labial faces, less numerous transverse ridges on labial face, granular ornament on lingual face, no secondary reticulate ornament in cupulas, and large labial foramina. The Senegalese species differs from *C. reniformis* by its teeth with less oblique labial face in profile view, stronger labial ornament, wider and more oblique transverse depression, lower root, less flared basal root lobe face, and wider nutritive groove less constricted lingually. This is the sixth nominal Maastrichtian *Coupatezia* species known so far.

[FIGURE 11 HERE]

? *Coupatezia* sp.

Fig. 12A-C

Material. One tooth (SN2012-127) from Unit 3, Cap de Naze Formation.

Description. This tooth is broader than high and roughly triangular in occlusal view. The transverse region separating the lingual and labial faces is devoid of crest but bears a marked bulge that is thicker and nearly rounded in its median region. Several faint and irregular vertical folds originate from the lingual side of this bulge. The lingual crown face is divided into an upper, oblique region situated below the transverse bulge and a lower, abrupt region. The upper area is concave in profile view and separated from the lower region by a faint ridge made of fine reticulate ornament that reaches the transverse bulge on the margino-lingual angles. The lower part of the lingual face is mostly damaged but appears made of concave margino-lingual faces separated by a flat vertical band of enameloid. The basal edge of the lingual crown face is convex. The labial crown face is concave in profile view and displays wide margino-labial angles connected to the margino-lingual angles by oblique and irregular marginal edges. The labial crown edge is wider than the lingual and the former shows a median convexity delimited from the margino-labial angles by shallow and broad convexities. The labial crown ornament is made of irregular and finely anastomosed ridges that are mainly situated near the labial edge of the labial face. The root is damaged but is at the holaulacorhize stage with a central foramen and margino-labial foramina.

Remarks. This tooth, although incomplete, bears crown characters typical of the genus *Coupatezia* but differ in having a marked transverse bulge that is nearly rounded in its median region. However, teeth of the Thanetian species '*Dasyatis russelli* Cappetta, 1972, which should most likely be assigned to the genus *Coupatezia*, tend to develop such a median bulge, although they differ from the specimens described here by a much stronger crown ornament

Superfamily Myliobatoidea Compagno, 1973

Family Rhombodontidae Cappetta, 1987

Genus *Rhombodus* Dames, 1881

Rhombodus binkhorsti Dames, 1881

Fig. 12D-H

Material. Four teeth (including SN2012-128) from the yellow calcareous sandstone bed of Unit 1, Paki Formation.

Description. Teeth of this species are large, reaching up to about 15 mm in total width. The crown is thick, lozenge-shaped in occlusal view, and much higher than the root. The occlusal surface is flat and bears a shagreened ornament observable on teeth with a low degree of wear. The margino-labial

faces are slightly concave in profile view and bear vertical to sub-vertical folds and grooves that are mainly located on their lower two-thirds. These margino-labial faces bear a shagreened ornament that is comparable to that of the occlusal face, but can change to a honeycombed ornamentation in their upper part. A very prominent ridge marks the limit between the margino-labial faces and the lower edge of the labial visor. The latter is smooth, oblique and concave in profile view. The margino-lingual faces are abrupt, sometimes slightly convex in profile view, and bear large sub-vertical folds and grooves that are smooth and bifurcating in the upper third of the lingual face. A strong bulge borders the basal edge of the margino-lingual faces and is separated from the rest of the margino-lingual faces by a deep but narrow transverse depression. This bulge is smooth, slightly concave on the margino-lingual faces but convex in the medio-lingual region although not developing into a marked uvula. The marginal angles are blunt, forming narrow marginal faces with weaker ornament than on the margino-lingual faces. The root is robust, slightly narrower than the crown, and somewhat offset lingually. The lobes are trapezoidal in basal view and separated by a wide and deep furrow where foramina of variable number and position open. Short branches bordering the furrow develop lingually, which confers a concave outline of the lingual crown face in basal view. The labial face is slightly higher than the lingual. The labial and lingual root faces are abrupt to slightly oblique towards the basal face. Several small round to oval foramina are aligned just below the crown on all root faces, and additional larger foramina are present on the margino-labial root faces. The basal root face also bears numerous foramina of variable size and shape.

Remarks. Teeth reported here can be attributed to the genus *Rhombodus* by the lozenge-shaped occlusal outline of the crown, the holaulacorhize root of lozenge-shape basal outline with deep and large median notch separating large root lobes. Seven valid nominal species of *Rhombodus* are known so far, spanning the Campanian-Maastrichtian interval (see Cicimurri and Ebersole, 2020). The specimens reported here display a combination of characters (crown much higher than the root with strong labial and lingual vertical wrinkles, flat occlusal crown face, moderately developed basal bulge on lingual crown face with median convexity, slightly concave labial crown face in profile view) reminiscent of teeth of *R. binkhorsti*, the type species of the genus. This species has a large geographical range (North and South America, Western Europe, Northern and Western Africa, and Middle East), but is restricted to the Maastrichtian (Cicimurri and Ebersole, 2020). *Rhombodus binkhorsti* has been reported from the Unit 3, Cap de Naze Formation (Cuny et al., 2012), but is reported from Unit 1 for the first time.

Rhombodus sp.

? 2012 *Rhombodus* sp.; Cuny et al., p. 113, fig. 5.

Material. One tooth (SN2012-129) from the yellow calcareous sandstone bed of Unit 1, Paki Formation.

Description. This tooth does not exceed 1 mm in width and 6 mm high, the (worn) crown being much lower than the root. The crown is rhombic in occlusal view. The margino-lingual faces are low with thick residual vertical folds. A well-developed and smooth basal bulge is present on the lingual crown face, with a straight margino-lingual outline and reduced median convexity. The margino-labial faces are very low and smooth. The lower edge of the labial visor is strongly oblique and slightly concave in profile view. The marginal angles are blunt. The root is high and narrower than the crown. The root lobes are trapezoidal in occlusal view and separated by a deep and wide furrow where several large foramina open. The margino-lingual root faces are convex and slightly oblique basally. The margino-labial root faces are concave in profile view. Large foramina are present below the labial visor, whereas only few small foramina open just below the lingual crown bulge.

Remarks. This tooth differs from the co-occurring teeth of *R. binkhorsti* by its more developed basal bulge on the lingual crown face with straight margino-lingual outline, less developed median convexity of the bulge, higher and more oblique lower edge of the labial visor, absence of labial crown ornament, higher root, absence of incipient lingual root branches, and concave margino-labial root faces. The specimen described here further differs from the Maastrichtian species *R. andriesi* Noubhani and Cappetta, 1994 reported from Unit 3 of Cap de Naze Formation by Cuny et al. (2012) by its higher root, basal bulge with straight margino-lingual outline and reduced median convexity, and more labio-lingually developed root. A specimen (SN235) reported as *Rhombodus* sp. by Cuny et al. (2012) from the same horizon in Unit 1 of the Paki formation displays similarities in both size and morphology with the tooth described here. However, both SN235 and the tooth described here are imperfectly preserved and there are no basal views available for SN235, which precludes detailed comparison of crown ornament and root morphology. Nevertheless, SN235 displays higher margino-lingual crown faces, possibly less ornamented lingual crown face, and less robust root branches showing an oblique labial face while it is vertical in the specimen described here. Although both specimens might be conspecific, the above-mentioned differences suggest that more material is needed to better assess this tooth morphology.

Cuny et al. (2012) reported a myliobatiform caudal spine from Unit 3 that was assigned to *Rhombodus* arguing that this genus was the only myliobatiform present in Unit 3, although the size of the spine was considered very small in comparison to teeth of *Rhombodus*. Our new samplings

1188 indicate that at least four myliobatiform genera were present in Unit 3 (*Dasyatis*, *Coupatezia*,
1189 *Rhombodus*, and *Phosphatodon*). Consequently, the generic attribution of the caudal spine reported
1190 in Cuny et al. (2012) is unknown.

1191

1192 *Myliobatiformes incertae familiae*

1193 *Phosphatodon* Cappetta, 2012

1194 *Phosphatodon cretaceus* sp. nov.

1195 LSID: urn:lsid:zoobank.org:act:C97061D2-C44F-447E-BA31-E6DF5ECA9E5F

1196 Fig. 12N-Q

1197 Derivation of name. From the Cretaceous occurrence of this genus, which was previously restricted
1198 to the Paleogene.

1199 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper
1200 Maastrichtian.

1201 Diagnosis. Teeth very high with crown broader than root. Lingual face abrupt and concave in profile
1202 view. Margino-lingual faces slightly depressed, separated by a wide and faint central vertical bulge
1203 the upper region of lingual face. Central uvula wide, short, and triangular, separated from the
1204 margino-lingual faces by shallow and broad concavities. Occlusal face inclined lingually and convex
1205 both. Lingual crown edge of occlusal face convex, labial outline with concave margino-labial edges
1206 and marked medio-labial bulge. Labial crown face is as high as lingual face with labially projected
1207 median region. Margino-labial faces flat to slightly concave. Lower edge of labial crown face
1208 scalloped with broad and triangular medio-labial protuberance. Crown not ornamented although of
1209 irregular surface or rough lingually. Root very high, narrow, and oval in cross-section and constricted
1210 above the deep nutritive groove. Root lobes moderately high and mesio-distally compressed. Medio-
1211 lingual foramen in a depression located labially to the groove. Several margino-lingual and labial
1212 foramina below the crown/root edge and above the root constriction.

1213 Material. One tooth (SN2012-130, holotype) from Unit 3, Cap de Naze Formation.

1214 Description. The holotype is an anterior tooth that is much higher than broad and about 3 mm high.
1215 The crown only slightly overhangs the root in occlusal view and is as high as broad. The lingual face is
1216 abrupt and somewhat concave in profile view with straight marginal edges in lingual view. The
1217 margino-lingual faces are slightly depressed and separated by a wide and faint central vertical bulge

restricted to the upper region of the lingual face. The lower edges of the margino-lingual faces are oblique and straight, although irregular. These converge medially into a wide, short, and triangular central uvula that is separated from the margino-lingual faces by shallow but broad concavities. The lingual face is not ornamented, although its surface is irregular and weakly rough. The occlusal face is inclined lingually and convex both mesio-distally and labio-lingually. The lingual crown edge of the occlusal face is convex and blunt due to functional wear, whereas the labial outline displays concave margino-labial edges that connect into a marked medio-labial bulge with a straight edge. The marginal angles are rounded and about 90°. The labial crown face is as high as the lingual face. The median region of the labial face is broad and labially projected, whereas the margino-labial faces are flat to slightly concave. The lower edge of the labial crown face is scalloped and develops medially into a broad, triangular, and rather long medio-labial protuberance that is somewhat depressed in its median region. The surface of the labial crown face is irregular but devoid of ornament. The root is very high, relatively narrow, and oval in cross-section. A constriction is present at mid-height of the crown, above the nutritive groove. Below the constriction, the margino-labial root faces are flat. The root lobes are moderately high, mesio-distally compressed and separated by a wide groove. A foramen is present in a depression located labially to the groove. Several margino-lingual and labial foramina are present just below the crown/root edge, others scarce foramina open lingually and labially above the constriction.

Remarks. The morphological features observed in this new species include a very high and narrow root, crown with high lingual and labial faces bearing broad and short median uvula and marked labial bulge, constriction of the root and mesio-distally compressed root lobes. These dental features are uncommon among elasmobranchs and are unique to the genus *Phosphatodon* (originally *Prosopodon*, see Cappetta, 2012). So far, the genus *Phosphatodon* was restricted to a single species, *P. asafai* (Noubhani and Cappetta, 1995), known from the Danian of Morocco and Europe. Teeth of this species show a strong degree of monognathic heterodonty with a decrease in tooth height towards lateral files, where teeth have lower lingual and labial crown faces, a reduced median uvula and no medio-labial protuberance. This morphology led Noubhani and Cappetta (1995) to include the genus *Phosphatodon* in the Dasyatoidea. Considering its extremely derived morphology, this genus might be better regarded as Myliobatiformes of uncertain affinities. Despite the strong resemblances between the Paleocene and the Maastrichtian species, anterior teeth of *P. cretaceus* sp. nov. can be separated from those of *P. asafai* by the following characters: no marked crown ornament, scalloped basal crown edge of labial face, wider labial bulge of the crown that is more developed labially, concave lingual face, convex labial face with no demarcated labial visor, more developed medio-labial protuberance that almost reaches the level of the lower edge of the median

uvula, convex profile of the labial face, lower constriction of the root, and smaller size. The species described here extends the stratigraphic range of the genus back into the Mesozoic.

Batomorphii incertae sedis

Batomorphii indet. 1

Fig. 12R-V

Material. One tooth (SN2012-131) from Unit 3, Cap de Naze Formation.

Description. This tooth is as high as broad and displays a hexagonal outline in occlusal view. The labial crown face is separated from the lingual face by a wide and blunt transverse crest that is sharper near the acute marginal angles. This crest projects lingually and overhangs the lingual crown face in occlusal view. The margino-labial regions of the labial face are strongly depressed and concave in labial view. These depressed area do not reach each other labially and are separated by a thin labial band of occlusal surface projecting labially, which ends into a short and flat labial visor. The margino-labial edge of the crown is straight. The lingual crown face is concave in profile view and separated into a median and two margin-lingual faces that are flat. The broad and moderately long median uvula is weakly demarcated from the margino-lingual edges by shallow and wide concavities. The root is worn but shows two labio-lingually compressed lobes placed lingually and separated by a nutritive groove where a central foramen opens. A strong constriction of the root is present, immediately below the crown.

Remarks. The overall crown morphology of this specimen is reminiscent of that of some extant and extinct dasyatoids such as *Aturobatis* and *Pastinachus*. The labial crown morphology is particularly close to that of anterior teeth of the extant *Pastinachus sephen* (see Cappetta 2012), which display a marked degree of tooth interlocking. Nonetheless, the Senegalese specimen differs from anteriors of *P. sephen* in the presence of a uvula basal edge of lingual crown face. However, teeth of some rhinobatoid taxa (e.g., *Atlantobatis* gen. nov. and, to a lesser extent *Phosphatobatis*) have comparable lingual crown face morphology. In the absence of knowledge on its heterodonty and tooth histology, the taxon represented by the specimens described here cannot be positively assigned to any higher taxonomic rank

Batomorphii indet. 2

Fig. 12W-Z

1283 Material. One tooth (SN2012-132) from Unit 3, Cap de Naze Formation.

1284 Description. This tooth is labio-lingually compressed (0.5 mm) and mesio-distally expanded (1 mm).

1285 The crown is low and oval-shaped in occlusal view. A rather wide and blunt transverse crest

1286 separates the labial and lingual faces. The transverse crest is rectilinear in occlusal view but its

1287 extremities are slightly oriented lingually when reaching the rounded marginal angles. The labial face

1288 is oblique and concave in profile view and bounded labially by an incipient but broad and irregular

1289 ridge that follows the labial edge of the labial face. The labial visor overhangs the root in occlusal

1290 view and displays a basally projected median process, which is triangular in labial view. The upper

1291 third of the lingual face is flat and oblique, and demarcated from the lower part, which is abrupt and

1292 concave in profile view. The basal edge of the lingual crown face bears a wide but short and rounded

1293 median uvula. The uvula is separated from the rest of the crown by faintly concave margins. The

1294 whole crown has an irregular surface made of very fine pits. The holaulacorhize root is high and

1295 strongly labio-lingually compressed. In basal view, the root lobes are mesio-distally developed with

1296 straight to slightly convex labial and lingual margins with their mesial and distal edges are rather

1297 wide and rounded. The basal faces of the lobes are flat and strongly oblique. The nutritive groove is

1298 deep and relatively wide, in the centre of which opens a labio-lingually compressed median foramen.

1299 The root displays no lingual or labial foramina.

1300 Remarks. The morphology of this tooth recalls that of some dasyatoid or rhinoprismid taxa with

1301 crushing dentition but the combination of crown and root characters observed in the Senegalese

1302 specimen have not been reported previously. Additional material is needed to better assess the

1303 systematic position of this probable new taxon.

1304

1305 Batomorphii indet. 3

1306 Fig. 12A'-B'

1307 Material. Two teeth (SN2012-133-134) from Unit 3, Cap de Naze Formation.

1308 Description. These teeth are less than 1 mm high and are roughly as broad as high. The crown is high

1309 with a flat labial face. The lingual face is abrupt and high and slightly project lingually in its median

1310 region at the base of which a variably developed median uvula is present. One of the specimens is

1311 damaged on its basal edge of the lingual crown face but seems devoid of marginal uvulae, whereas

1312 another specimen shows notches separating short marginal uvulae from the central one. The labial

1313 face displays a curved labial edge and a triangular lingual edge that connect into broad and blunt

1314 marginal angles. The margino-lingual edges are straight to slightly convex and gently converge

1315 medially. None of the specimens have a preserved root but the preserved elements indicate labio-
1316 lingually compressed root lobes separated by a notch that bears a central foramen in labial position.

1317 Remarks. These teeth resemble those of the late Cretaceous hypsobatid species *Angolabatis*
1318 *benguelaensis* (Antunes and Cappetta, 2002) but differ in their rounded labial crown edge, whereas
1319 this is markedly angular in *A. benguelaensis*. Teeth of the Cenomanian rajoid *Rajorhina epansa*
1320 (Davis, 1887) show a comparable overall crown morphology but are cuspidate (although less marked
1321 in lateral teeth) with less developed uvulae. More material is needed to provide a more accurate
1322 identification and higher taxonomic rank assignment of this taxon.

1323 **[FIGURE 12 HERE]**

5. Discussion

5.1. Biostratigraphical implications

The geological section and biostratigraphy of the Cap de Naze cliffs were previously studied by Tessier (1952), Khatib et al. (1990), Sow (1992), and Sarr (1995). While the oldest works suggested a Maastrichtian age for the Cretaceous series (Faye, 1983; Tessier, 1952), Khatib et al. (1990) reported samplings made in the marls of Unit 2, just above the calcareous sandstone bed of Unit 1, which yielded the species *Globotruncanita* cf. *calcarata* (Cushman). According to Khatib et al. (1990), this, along with other taxa that would suggest the presence of the biozones *G. calcarata* to *G. aegyptiaca*, would indicate the uppermost Campanian. However, the assemblage of planktonic foraminifera from the calcareous siltstone bed of Unit 2 (*Globotruncana aegyptiaca* and *Gansserina gansseri* biozones) suggests an early to middle Maastrichtian age (Khatib et al., 1990). Consequently, Khatib et al. (1990) placed the Campanian-Maastrichtian boundary at the base of Unit 2, one meter above the calcareous sandstone bed of Unit 1 (sampling 2, here), and assigned a Campanian age to the gypsum-rich clays of the base of Unit 1 (sampling 1, here).

The gypsum-rich clays yielded a single elasmobranch tooth attributed here to *Carcharias* sp., which does not provide any valuable biostratigraphic information. However, eight elasmobranch taxa were recovered from the calcareous sandstone bed of Unit 1 (Table 1): one (*Rhombodus* sp.) reported by Cuny et al. (2012) and seven reported in the present work (*Squalicorax pristodontus*, *Carcharias* sp., *Cretolamna maroccana*, *Serratolamna serrata*, *Schizorhiza stromeri*, *Coupatezia casei* sp. nov., and *R. binkhorsti*). Among the nominal elasmobranch species sampled in this work, a single one (*S. pristodontus*) spans the Campanian-Maastrichtian interval. However, this horizon yielded three geographically widespread and exclusively Maastrichtian elasmobranch species (*C. maroccana*, *R. binkhorsti*, and *S. serrata*). The presence of these species strongly argues against a Campanian age for the calcareous sandstone bed, and rather suggests that this horizon is Maastrichtian in age. These new findings potentially have important implications because this calcareous sandstone bed may be laterally equivalent to the one that yielded fossil remains of diverse groups including bivalves, brachiopods, fruits (Monteillet and Lappartient, 1981), fish teeth, and remains of a pterosaur (Monteillet and Lappartient, 1982) in the Paki area.

Unit 3 is devoid of microfossils but has been assigned a middle to late Maastrichtian age due to its position between the underlying early to middle Maastrichtian Unit 2 and overlying Unit 4, which was assigned a late Maastrichtian age based on ammonites (Tessier 1952). This middle-late Maastrichtian age was supported by the elasmobranch fauna reported from the ferruginous sandstone bed of Unit 3 by Cuny et al. (2012), who described several exclusively Maastrichtian, and

possibly late Maastrichtian, taxa (Table 1). Cuny et al. (2012) reported the species *Cretolamna* cf. *biauriculata* from Unit 3, which would argue against an Upper Maastrichtian age, since this species seems restricted to the early Maastrichtian. However, this material should rather be considered juveniles of *S. serrata* (see above, Systematics section), which is common in late Maastrichtian faunas. Additional elasmobranch species described here (*Plicatoscyllium youssoufiaense*, *Dalpiazia stromeri*, and *Ctenopristis nougareti*) further support the proposed middle-late Maastrichtian age for the ferruginous sandstone bed of Unit 3.

5.2. Palaeoenvironmental and palaeogeographical implications

Previous works on the geological section at Cap de Naze provided sedimentological and micropalaeontological arguments that suggest several successive short-term regressive cycles, which make part of a long-term transgressive phase (Khatib et al., 1990; Sow et al., 1994). The gypsum-rich clays of Unit 1 (sample 1) represent the base of a regressive cycle reaching a lowstand located in the sandstones of Unit 1. This is followed by a transgressive event right above the yellow calcareous sandstone bed (sample 2), at the top of Unit 1. The ferruginous sandstone (sample 3) would correspond to a lowstand that follows the second regressive event recorded in the lower siltstones of Unit 3. Both sampled horizons 2 and 3 were interpreted as representing nearshore palaeoenvironments (Khatib et al., 1990; Sow et al., 1994).

The elasmobranch assemblage from the yellow calcareous sandstone bed contains exclusively lamniforms (*S. pristodontus*, *Carcharias* sp., *C. maroccana*, and *S. serrata*) and batomorphs (*S. stromeri*, *Coupatezia casei* sp. nov., *Rhombodus* sp., and *R. binkhorsti*). The assemblage from the ferruginous sandstone differs in its much higher taxonomic diversity (28 species). Only two species among those recorded in the lower yellow calcareous sandstone bed (the lamniforms *Carcharias* sp. and *C. maroccana*) were not recovered in the Unit 3, which instead yielded the species *Carcharias* cf. *heathi* and *Carcharias* sp. 1 reported by Cuny et al. (2012). The sampled assemblage from Unit 3 further differs from that of the yellow calcareous sandstone in the presence of three orectolobiforms (*Chiloscyllium* sp., *Hemiscyllium* sp., and *Plicatoscyllium youssoufiaense*) and much more diverse batomorphs (21 species). The increasing species diversity toward the top of the section (one species in sample 1, eight in sample 2, and 28 in sample 3) suggests a transition from restricted marine (Sample 1) to more open coastal conditions (Sample 3), and is in line with an increasing opening of the marine setting reported previously (Khatib et al., 1990).

The fauna reported here is typical of Cretaceous nearshore tropical/sub-tropical settings and the dominance of sclerorhynchoids, rhinopristiforms, myliobatiforms, lamniforms, and orectolobiforms

compares well with other Maastrichtian Tethyan and Eastern Atlantic faunas known so far from Morocco (Noubhani and Cappetta, 1997), Egypt (Cappetta, 1991a), Niger (Cappetta, 1972), Syria (Bardet et al., 2000), Jordan (Cappetta et al., 2000), and Spain (Cappetta and Corral, 1999; Corral et al., 2016). It also contrasts with other Maastrichtian assemblages from the Western Interior Seaway (Case and Cappetta, 1997; Cook et al., 2014; Estes, 1964), NW Atlantic (Cappetta and Case, 1975), as well as with assemblages from Niger and Algeria in the absence of hybodonts, despite the coastal palaeoenvironment of the Senegalese assemblages. Most of the previously known species recorded from the Popenguine fauna are represented by cosmopolitan taxa (*S. pristodontus*, *C. maroccana*, *S. serrata*, *D. stromeri*, and *R. binkhorsti*) as well as *S. stromeri*, a species largely distributed in sub-tropical Tethyan and Eastern Atlantic neritic environments in the Maastrichtian (Cappetta, 2012). Some species with a more restricted distribution include *P. youssoufiaense* (Unit 3) previously limited to the Maastrichtian of Morocco (Noubhani and Cappetta, 1997), *R. andriesi* (Unit 3) known from the Maastrichtian of Morocco and Spain (Cappetta and Corral, 1999; Noubhani and Cappetta, 1997), and possibly *C. heathi* previously reported from Morocco, Spain, and the USA (Cappetta and Corral, 1999; Case and Cappetta, 1997; Noubhani and Cappetta, 1997). Although similarities with the Maastrichtian Moroccan fauna are expected, these are few. More striking, however, is the large number of new taxa recorded in the Popenguine fauna. These newly described taxa are mainly represented by necto-benthic species and suggests a strong degree of endemism in marine coastal vertebrate assemblages from eastern Atlantic environments, as these taxa were not reported from Niger (Cappetta, 1972), Morocco (Noubhani and Cappetta, 1997), or Angola (Antunes and Cappetta, 2002), where fine sieving for micro-vertebrates was carried out. Although several published Maastrichtian faunas from the Tethys have not been formally described (Cappetta et al., 2000; Lewy and Cappetta, 1989), some known assemblages (e.g., from Egypt, Syria) indicate a similar degree of endemism (Bardet et al., 2000; Cappetta, 1991a). This strong degree of endemism among necto-benthic species likely reflects high habitat differentiation in tropical to sub-tropical marine Maastrichtian settings, which probably mediated the all-time diversity peak in the elasmobranch evolutionary history (Guinot and Cavin, 2016) that preceded the Cretaceous/Paleogene extinction event.

6. Conclusions

Additional fieldwork was carried out in the late Cretaceous geological section at Cap de Naze near Popenguine. Surface collecting and bulk-sampling allowed to largely complement the previous report on the elasmobranch fauna (Cuny et al., 2012) by the addition of 22 species and to improve

knowledge on the stratigraphic distribution of the elasmobranch taxa along the section. Three new genera and eight new species are described, all being represented by small-sized teeth, which highlights the importance of bulk-sampling and fine sieving techniques in the understanding of past elasmobranch communities. Our findings suggest a Maastrichtian age for the calcareous siltstone at the top of Unit 1 (Paki Fm.), based on the presence of three exclusively Maastrichtian elasmobranch species (*C. maroccana*, *R. binkhorsti*, and *S. serrata*). This challenges previous works based on microfossil analysis. Samplings from Unit 3 (Cap de Naze Fm.) is in agreement with the middle-late Maastrichtian age proposed based on the previous account on elasmobranchs (Cuny et al., 2012). Increasing taxonomic diversity throughout the three successive assemblages indicates a transition from restricted marine to open coastal settings. This high-diversity fauna is dominated by necto-benthic batomorphs and is similar in its structure to other Tethyan and Eastern Atlantic Maastrichtian faunas. The high number of species apparently endemic to the studied area suggests high habitat differentiation in corresponding marine Maastrichtian settings.

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Author contributions

LH, RS, JM and GG conceived the study; LH, JM, RS, and BS did the fieldwork and sampling; GG drafted the manuscript and illustrations with inputs from all authors; all authors reviewed the manuscript.

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1719 **Figure Captions**

1720 **Figure 1.** Geographical and geological setting of the sampled locality. **A)** geographical situation of the
1721 Cap de Naze cliffs (black star), the grey-shaded area represents the extent of Campanian-
1722 Maastrichtian series. **B)** geological section at the Cap de Naze cliffs (after Khatib *et al.* 1990), stars
1723 indicate the sampled horizons. **C)** view of the northern part of the Cap de Naze area (November
1724 2018), showing the three sampled horizons (stars).

1725 **Figure 2.** Orectolobiform sharks from the Unit 3, Cap de Naze Fm. **A-B: *Chiloscyllium* sp.** A: tooth
1726 (SN2012-41) in labial view; B: tooth (SN2012-42) in labial view. **C-D: *Hemispyllium* sp.** tooth (SN2012-
1727 43) in C, labial and D, lingual views. **E-M: *Plicatoscyllium youssoufiaense*.** E: latero-posterior tooth
1728 (SN2012-44) in labial view; F-H: anterior tooth (SN2012-45) in F, labial, G, lingual and H, basal views;
1729 I: lateral tooth (SN2012-46) in labial view; J-M: lateral tooth (SN2012-47) in J, lingual, K, labial, L,
1730 oblique basal and M, basal views. Scale bars 500 μ m (AB and C-D) and 1mm (E-M).

1731 **Figure 3.** Lamniformes from the Unit 1, Paki Fm. **A-B: *Squalicorax pristodontus*** tooth (SN2012-48) in
1732 A, lingual and B, labial views, yellow sandstone (Unit 1). **C-F: ? *Carcharias* sp.** C-D: anterior tooth
1733 (SN2012-49) in C, labial and D, lingual views, argillites (Unit 1); E-F: anterior tooth (SN2012-50) in E,
1734 labial and F, lingual views, yellow sandstone (Unit 1). **G-J: *Cretalamna maroccana*,** yellow sandstone
1735 (Unit 1). G-H: anterior tooth (SN2012-51) in G, lingual and H, labial views; I-J: lower lateroposterior
1736 tooth (SN2012-52) in I, lingual and J, labial views. **K-T: *Serratolamna serrata*,** yellow sandstone (Unit
1737 1). K-L: upper lateral tooth (SN2012-53) in K, lingual and L, labial views; M-N: anterior tooth (SN2012-
1738 54) in M, lingual and N, labial views; O-P: anterolateral tooth (SN2012-55) in O, labial and P, lingual
1739 views; Q-R: lateral tooth (SN2012-56) in Q, lingual and R, labial views; S-T: lateral tooth (SN2012-57)
1740 in S, labial and T, lingual views. All scale bars equal 1cm.

1741 **Figure 4.** Sclerorhynchiforms from the Unit 3, Cap de Naze Fm. **A-J: *Dalpiazia stromeri*.** A-D: anterior
1742 tooth (SN2012-58) in A, labial, B, basal, C profile and D, lingual views; E-H: lateral tooth (SN2012-59)
1743 in E, labial, F, basal, G, profile and H, lingual views; I-J: posterior tooth (SN2012-60) in I, lingual and J,
1744 labial views. **K-L: *Ctenopristis nougareti*,** rostral denticle (SN2012-61) in K, anterior and L, profile
1745 views. Scale bars equal 1mm.

1746 **Figure 5.** Sclerorhynchiforms from the Paki and Cap de Naze Fm. **A-N: *Schizorhiza stromeri*** teeth
1747 from the Unit 3, Cap de Naze Fm. A-B: anterior tooth (SN2012-62) in A, labial, B, lingual and C, profile
1748 views; D-G: anterior tooth (SN2012-63) in D, labial, E, lingual, F, profile, and G, basal views; H-K:
1749 anterior tooth (SN2012-64) in H, labial, I, profile, J, lingual, and K, basal views; M-N: juvenile anterior
1750 tooth (SN2012-65) in M, labial and N, occlusal views. **O: *Schizorhiza stromeri*** rostral denticle
1751 (SN2012-66) from the Unit 1 (yellow sandstone), Paki Fm. **P-T: *Ptychotrygon nazeensis* sp. nov.,**

1752 tooth (SN2012-67, **holotype**) from the Unit 3, Cap de Naze Fm. in O, lingual, P, occlusal, Q, basal, R,
1753 profile, and S, labial views. Scale bars equals 1 mm, excepted O (5 mm).

1754 **Figure 6.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-B: cf. *Rhynchobatus* sp.**, tooth
1755 (SN2012-68) in A, lingual and B, profile views. **C-K: *Terangabatis thiami* gen. et sp. nov.** C-D: anterior
1756 tooth (SN2012-69) in C, lingual and D labial views; E-I anterior tooth (SN2012-70, **holotype**) in E,
1757 occlusal, F, lingual, G, labial, H, profile, and I, basal views; J: lateral tooth (SN2012-71) in lingual view;
1758 K: posterior tooth (SN2012-72) in occlusal view. All scale bars equal 1mm excepted K (500 μ m).

1759 **Figure 7.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-Q: '*Rhinobatos*' *popenguinensis* sp.**
1760 **nov.** A-D: tooth (SN2012-73) in A, lingual, B, occlusal, C, profile, and D, labial views; E: tooth (SN2012-
1761 74) in lingual view; F-H: tooth (SN2012-75) in F, lingual, G, basal, and H, profile views; I-J: tooth
1762 (SN2012-76) in I, occlusal and J, lingual views; K-M: tooth (SN2012-77) in K, labial, L, lingual, and M,
1763 occlusal views; N-Q: tooth (SN2012-78) in N, lingual, O, occlusal, P, profile, and Q, basal views. All
1764 scale bars equal 500 μ m.

1765 **Figure 8.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-Y: *Atlantobatis acrodonta* gen. et sp.**
1766 **nov.** A-E: tooth (SN2012-79, **holotype**) in A, lingual, B, basal, C, occlusal, D, profile, and E, labial
1767 views; F-G: tooth (SN2012-80) in F, labial and G, lingual views; H-J: tooth (SN2012-81) in H, occlusal, I,
1768 lingual, and J, profile views; K-N: tooth (SN2012-82) in K, lingual, L, occlusal, M, profile, and N, basal
1769 views; O-Q: tooth (SN2012-83) in O, lingual, P, lingual, and Q, basal views; R-T: tooth (SN2012-84) in
1770 R, lingual, S, occlusal, and T, basal views; U-W: tooth (SN2012-85) in U, labial, V, occlusal, and W,
1771 lingual views; X-Y: tooth (SN2012-86) in X, lingual and Y, basal views. Scale bar equals 1mm.

1772 **Figure 9.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-J: ? *Microbatis* sp.** A-D: anterior tooth
1773 (SN2012-87) in A, lingual, B, labial, C, profile, and D, basal views; E-F: anterolateral tooth (SN2012-88)
1774 in E, lingual and F, basal views; G-H: anterolateral tooth (SN2012-89) in G, lingual and H, labial views;
1775 I-J: anterolateral tooth (SN2012-90) in I, lingual and J, labial views. **K-U: *Sowibatos minimus* gen. et**
1776 **sp. nov.** K-L: tooth (SN2012-91) in K, occlusal and L, lingual views; M-O, tooth (SN2012-92) in M,
1777 lingual, N, basal, and O, occlusal views; P: tooth (SN2012-93) in lingual view; Q-U: tooth (SN2012-94,
1778 **holotype**) in Q, occlusal, R, basal, S, profile, T, labial, and U, lingual views. Scale bar equals 500 μ m.

1779 **Figure 10.** Myliobatiforms from the Unit 3, Cap de Naze Fm. **A-A': '*Dasyatis*' *reticulata* sp. nov., non-**
1780 **cuspidate morph.** A-D: tooth (SN2012-95) in A, lingual, B, profile, C, occlusal, and D, basal views; E-H:
1781 tooth (SN2012-96) in E, lingual, F, occlusal, G, profile, and H, basal views; I-L: tooth (SN2012-97) in I,
1782 lingual, J, profile, K, occlusal, and L, basal views; M-P: tooth (SN2012-98) in M, lingual, N, profile, O,
1783 occlusal, and P, basal views; Q-T: tooth (SN2012-99) in Q, lingual, R, profile, S, occlusal, and T, basal
1784 views; U-W: tooth (SN2012-100) in U, lingual, V, basal, and W, occlusal views; X-A': tooth (SN2012-

1785 101) in X, lingual, Y, profile, Z, occlusal, and A', basal views; **B'-S': 'Dasyatis' reticulata sp. nov.,**
 1786 **cuspidate morph.** B'-C': tooth (SN2012-102) in B', profile and C', occlusal views; D'-F': tooth (SN2012-
 1787 103) in D', profile, E', lingual, and F', basal views; G'-I': tooth (SN2012-104) in G', occlusal, H', profile,
 1788 and I', lingual views; J'-L': tooth (SN2012-105) in J', occlusal, K', profile, and L', basal views; M'-P':
 1789 tooth (SN2012-106) in M', lingual, N', profile, O', occlusal, and P4, basal views; Q'-S': tooth (SN2012-
 1790 107) in Q', profile, R', lingual, and S', labial views. Scale bar equals 2mm.

1791 **Figure 11.** Myliobatiforms from the Unit 3, Cap de Naze Fm. **A-C': Coupatezia casei sp. nov., non-**
 1792 **cuspidate morph.** A-D: anterolateral tooth (SN2012-108, **holotype**) in A, lingual, B, basal, C, profile,
 1793 and D, occlusal views; E-F: anterior tooth (SN2012-109) in E, lingual and F, labial views; G-I:
 1794 anterolateral tooth (SN2012-110) in G, lingual, H, profile, and I, basal views; J-L: anterior tooth
 1795 (SN2012-111) in J, lingual, K, basal, and L, occlusal views; M-P: anterolateral tooth (SN2012-112) in
 1796 M, lingual, N, labial, O, basal, and P, occlusal views; Q-R: anterior tooth (SN2012-113) in Q, lingual
 1797 and R, occlusal views; S-U: anterolateral tooth (SN2012-114) in S, lingual, T, basal, and U, occlusal
 1798 views; V-W: anterolateral tooth (SN2012-115) in V, lingual and W, occlusal views; X: lateral tooth
 1799 (SN2012-116) in occlusal view; Y: lateral tooth (SN2012-117) in occlusal view; Z-A': anterolateral
 1800 tooth (SN2012-118) in Z, lingual and A', occlusal views; B'-C': lateral tooth (SN2012-119) in B', lingual
 1801 and C', occlusal views. **D'-V': Coupatezia casei sp. nov., cuspidate morph.** D': lateral tooth (SN2012-
 1802 120) in occlusal view; E'-H': lateral tooth (SN2012-121) in E', lingual, F', labial, G', occlusal, and H',
 1803 basal views; I'-J' : anterior tooth (SN2012-122) in I', lingual and J', labial views; K': anterior tooth
 1804 (SN2012-123) in occlusal view; L'-N': anterior tooth (SN2012-124) in L', lingual, M', occlusal, and N',
 1805 labial views; O'-Q': anterior tooth (SN2012-125) in O', occlusal, P', lingual, and Q', labial views; R'-U':
 1806 anterolateral tooth (SN2012-126) in R', occlusal, S', labial, T', lingual, and U', basal views. Scale bar
 1807 equals 1mm.

1808 **Figure 12.** Myliobatiforms and Batomorphii *incertae sedis* from the Paki and Cap de Naze Fm. **A-B: ?**
 1809 **Coupatezia sp.** tooth (SN2012-127) from the Unit 3, Cap de Naze Fm. in A, occlusal, B, lingual, and B,
 1810 profile views. **D-H: Rhombodus binkhorsti**, tooth (SN2012-128) from yellow sandstone (Unit 1) of the
 1811 Paki Fm. in D, occlusal, E, labial, F, lingual, G, profile, and H, basal views. **I-M: Rhombodus sp.,** tooth
 1812 (SN2012-129) from yellow sandstone (Unit 1) of the Paki Fm. in I, occlusal, J, labial, K, lingual, L,
 1813 profile, and M, basal views. **N-Q: Phosphatodon cretaceus sp. nov.** tooth (SN2012-130, **holotype**)
 1814 from the Unit 3, Cap de Naze Fm. in N, occlusal, O, lingual, P, labial, and Q, profile views. **R-V:**
 1815 **Batomorphii indet. 1** tooth (SN2012-131), from the Unit 3, Cap de Naze Fm. in R, labial, S, profile, T,
 1816 lingual, U; occlusal, and V, basal views. **W-Z: Batomorphii indet. 2** tooth (SN2012-132) from the Unit
 1817 3, Cap de Naze Fm. in W, occlusal, X, lingual, Y, labial, and Z, basal views. **A'-B': Batomorphii indet. 3.**

1818 A', tooth (SN2012-133) from the Unit 3, Cap de Naze Fm. in lingual view; B', tooth (SN2012-134, Unit
1819 3) in lingual view. All scale bars 1mm, excepted D-H (5mm).

1820 **Table 1.** Faunal list from the Cape de Naze section including previous report of Cuny et al. (2012)
1821 indicated by letter C, and the news records reported in the present work indicated by letter P. S1
1822 refers to Sampling 1 (grey silty argillites of Unit 1), S2 refers to Sampling 2 (yellow calcareous
1823 siltstone of Unit 1), S3 refers to Sampling 3 (ferruginous sandstone of Unit 3).

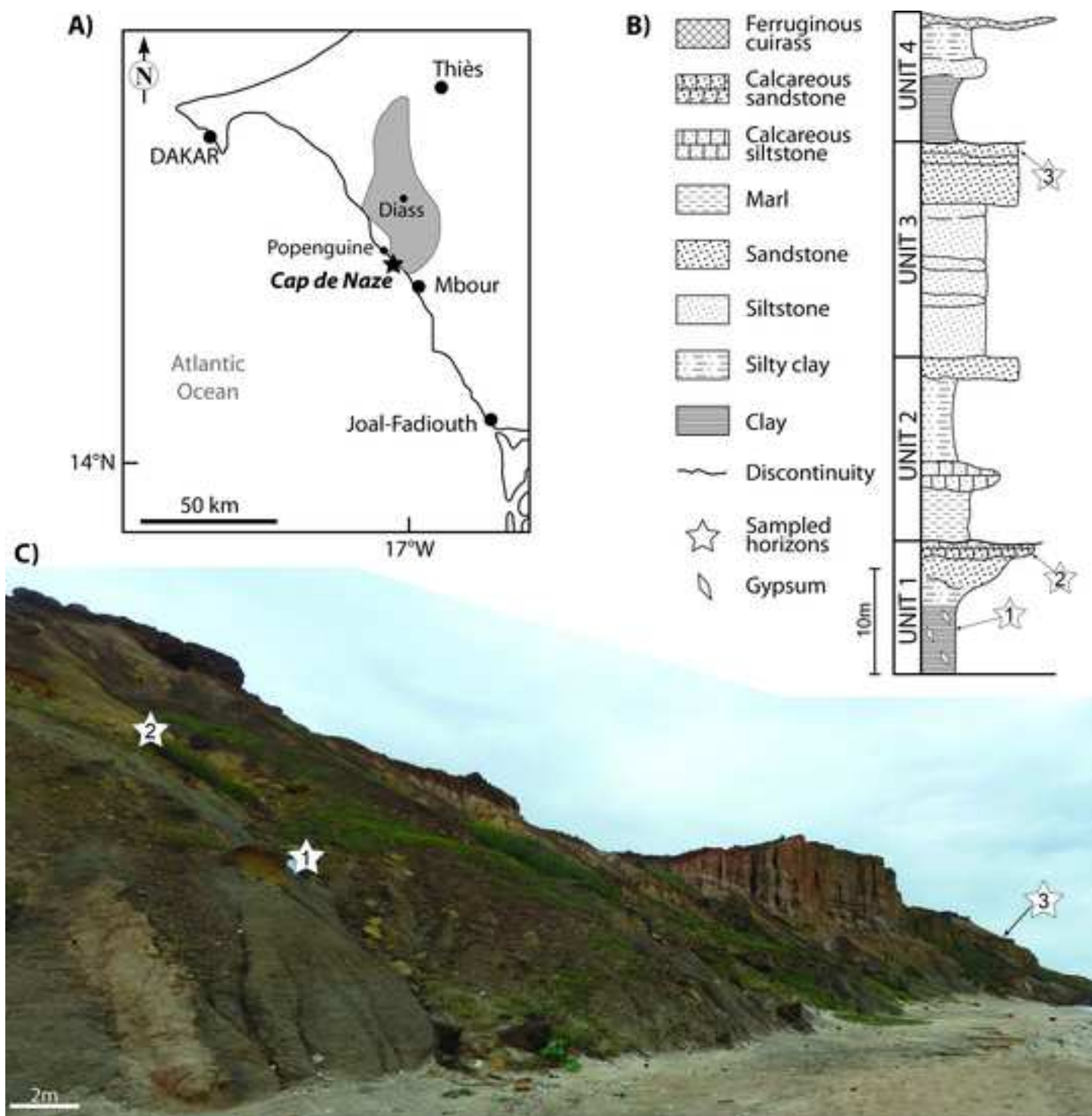


Figure 2

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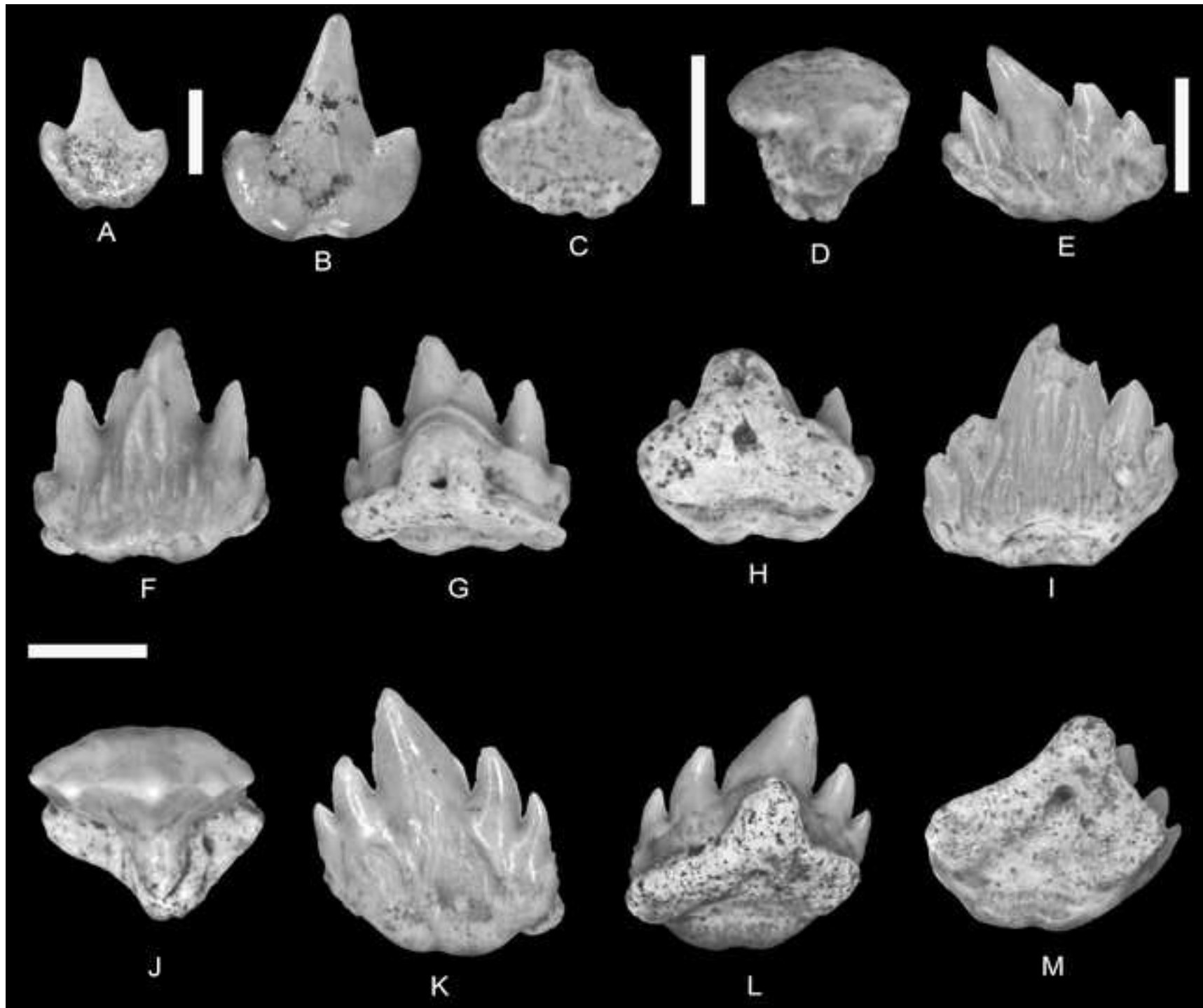


Figure 3

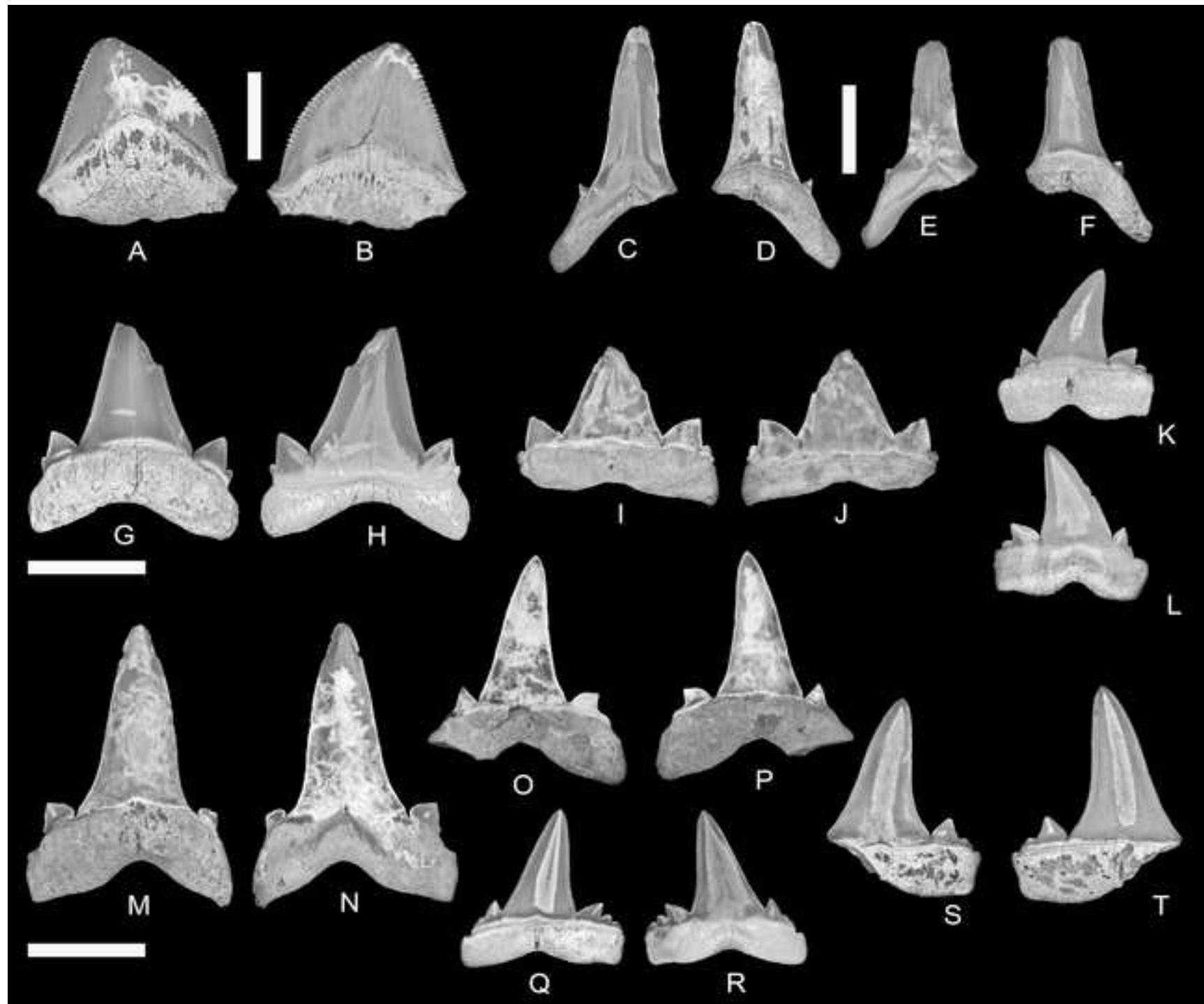
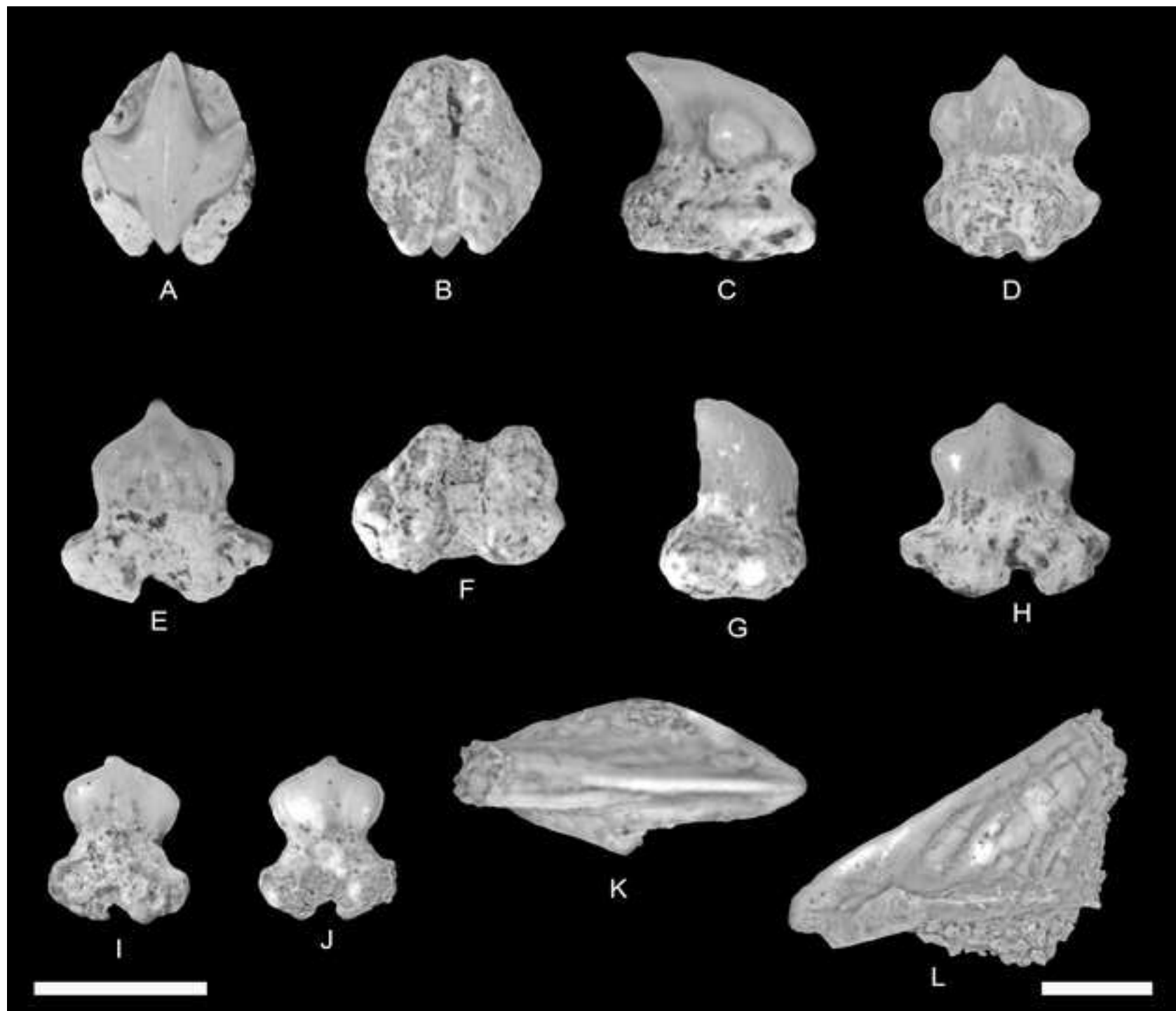
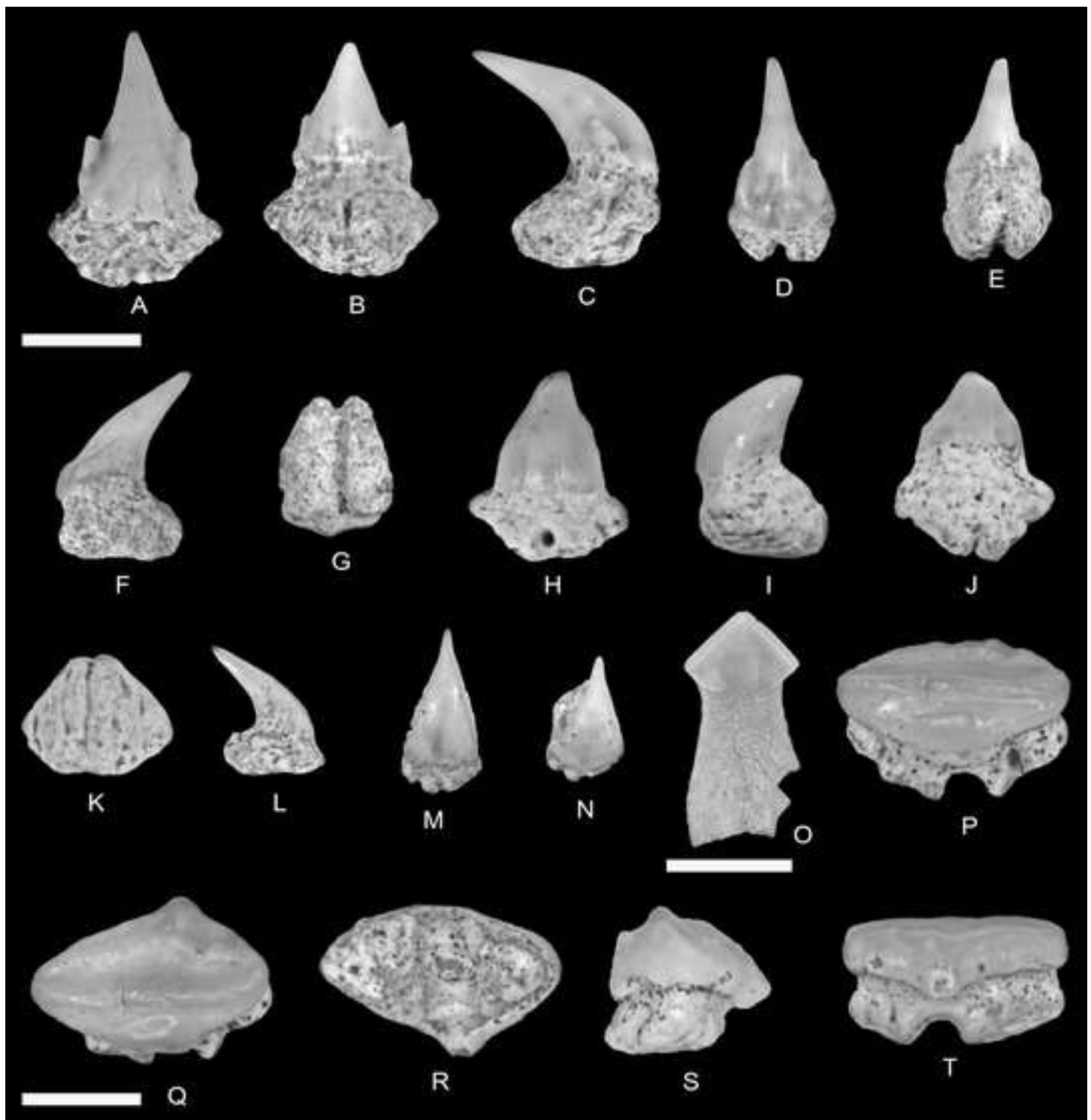
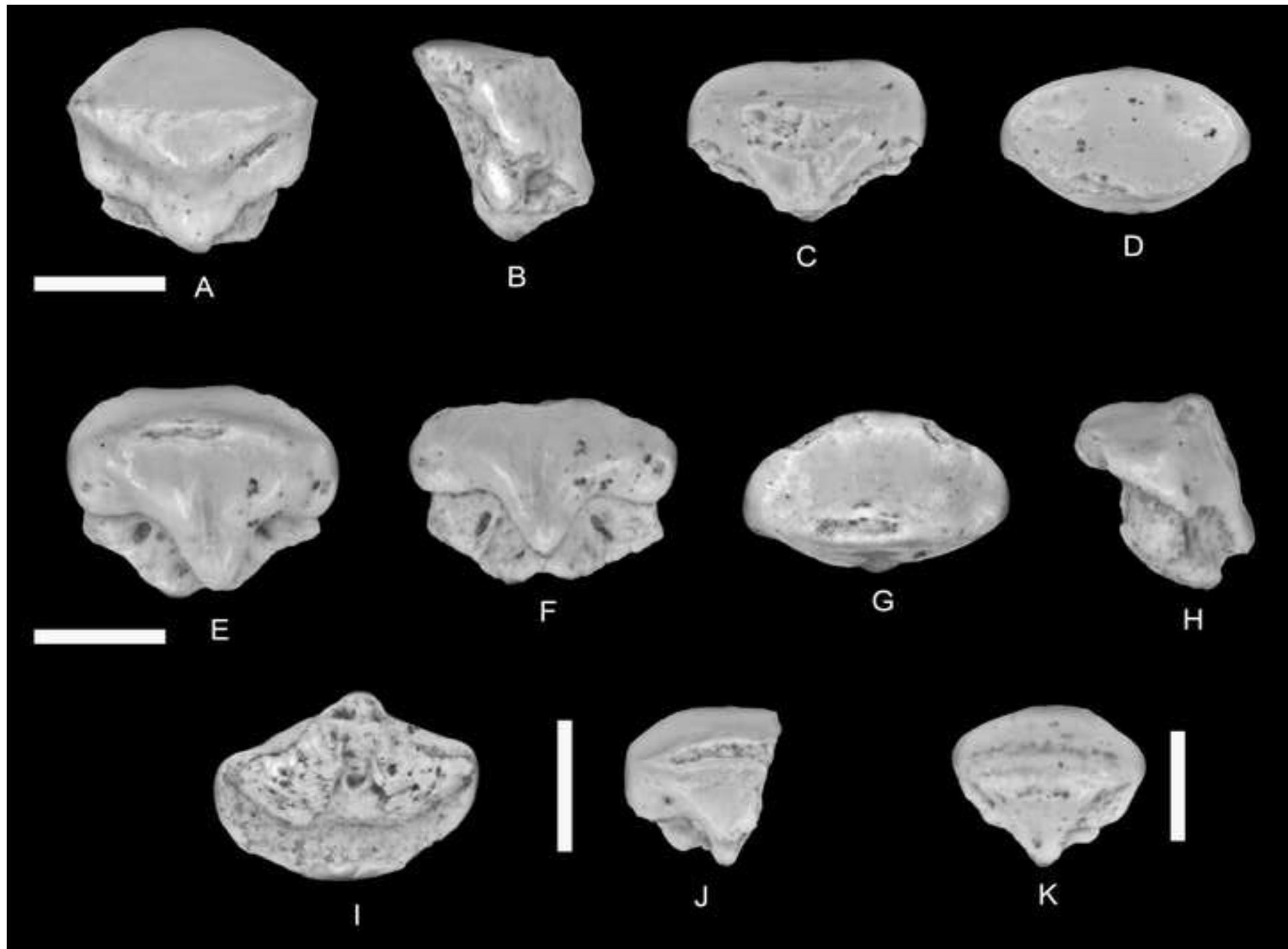
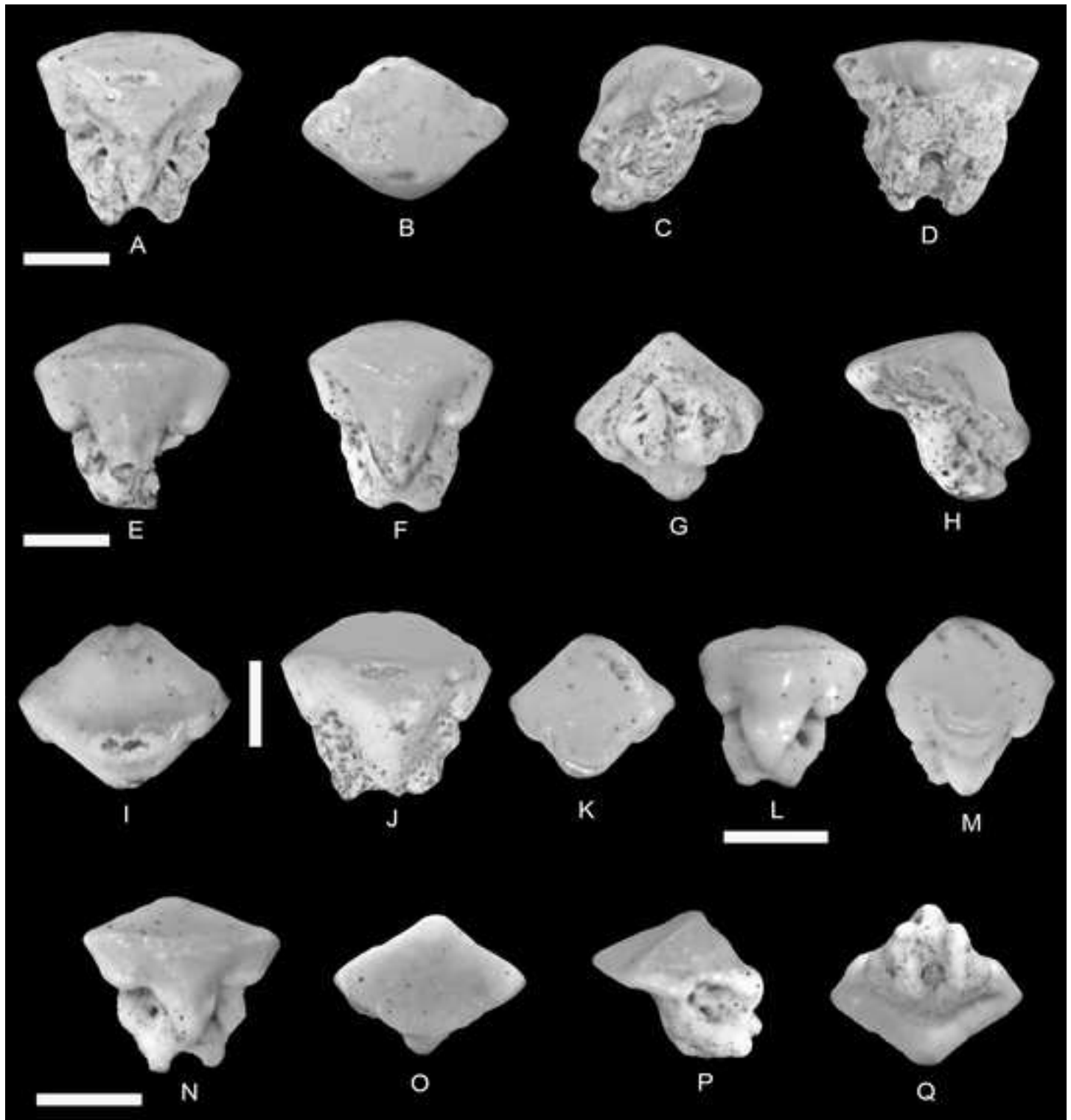


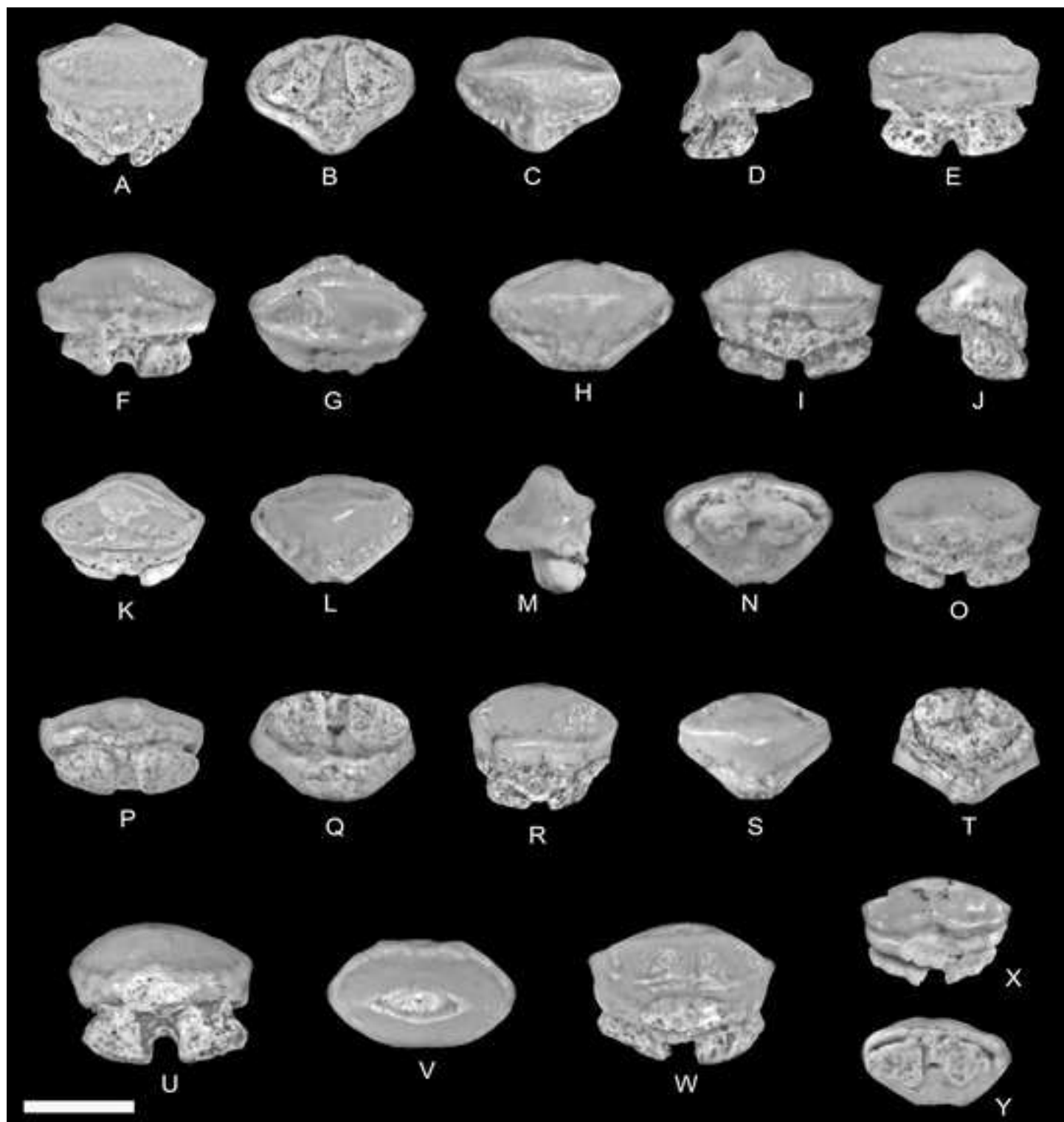
Figure 4

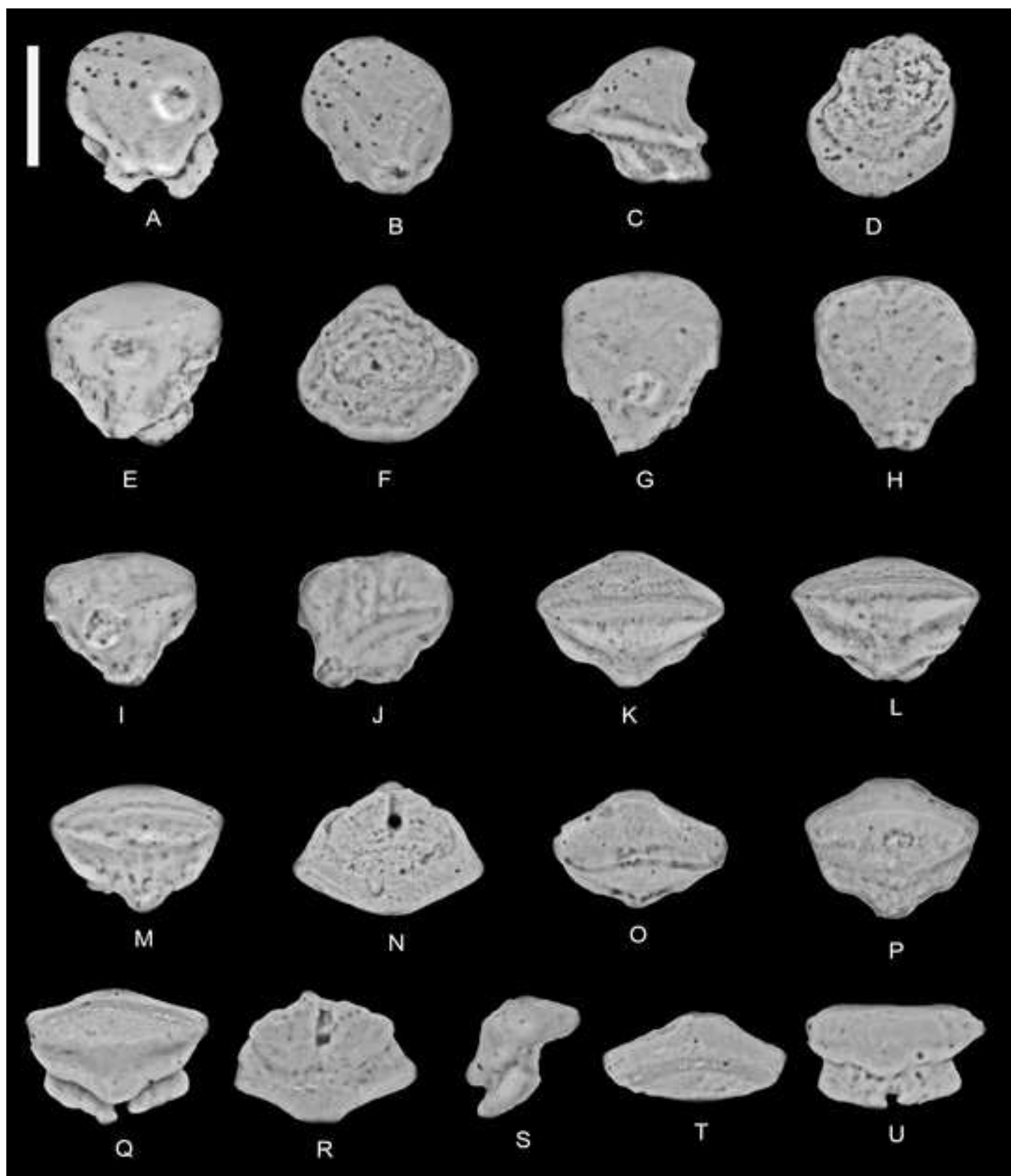


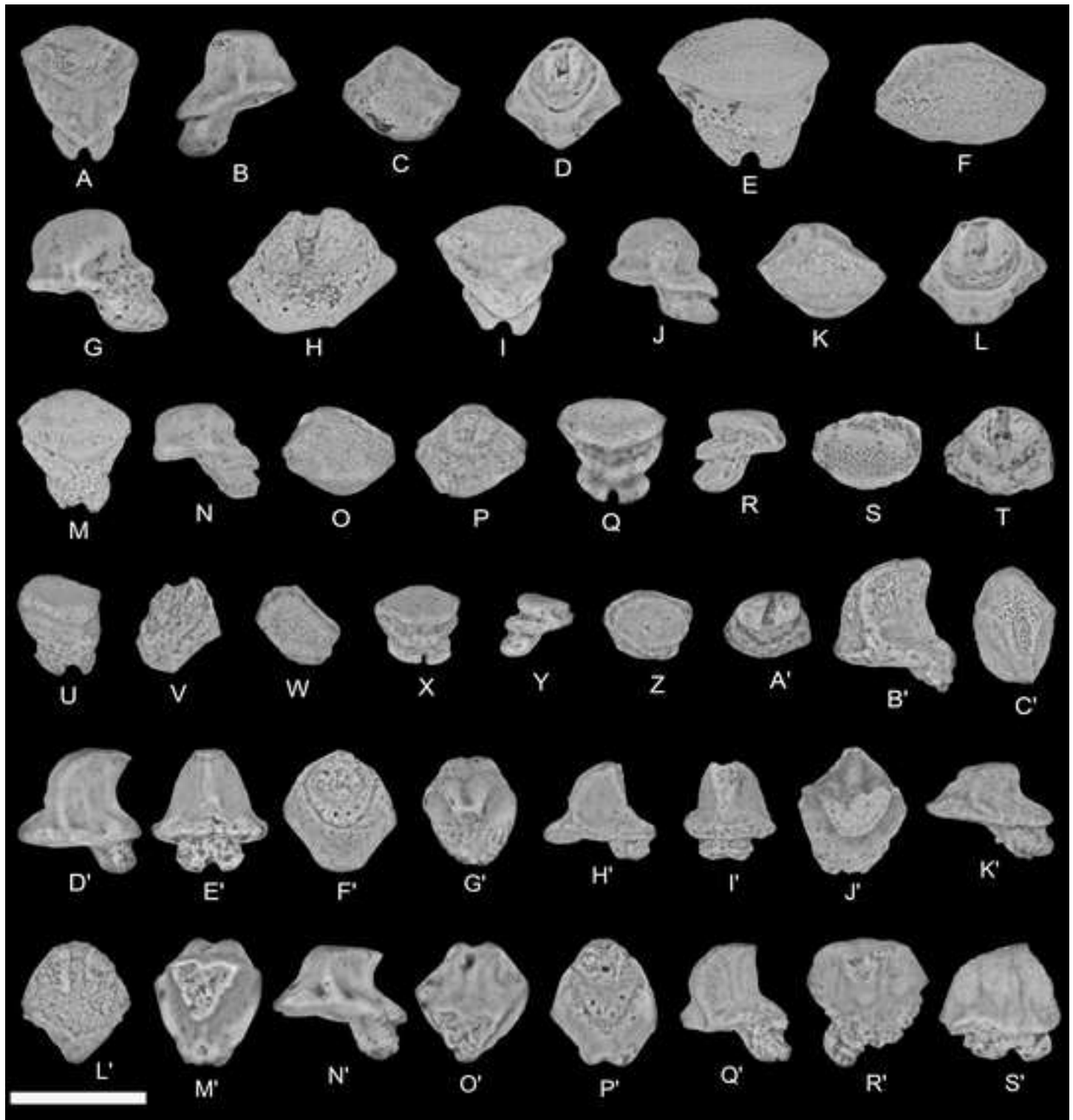


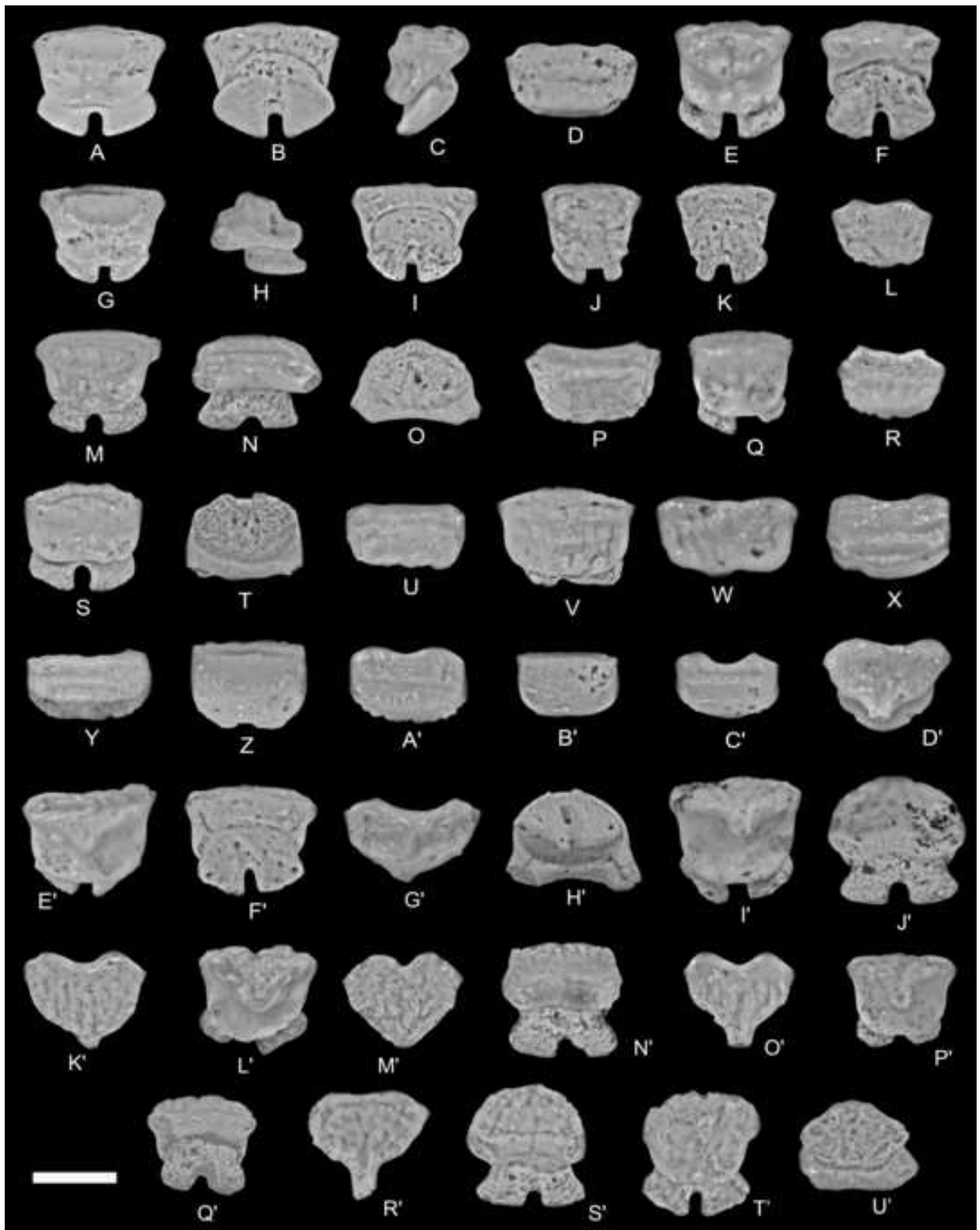












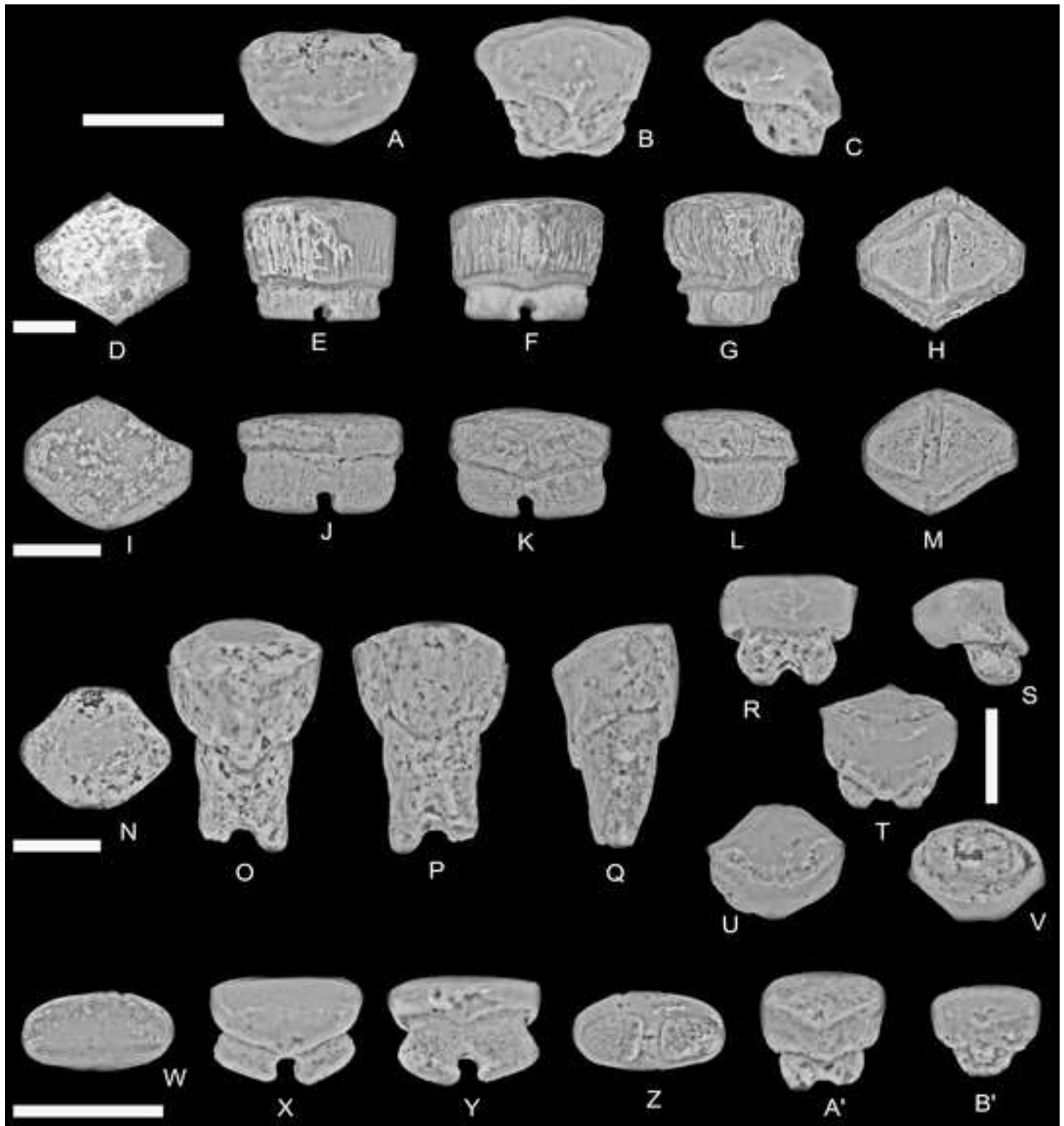
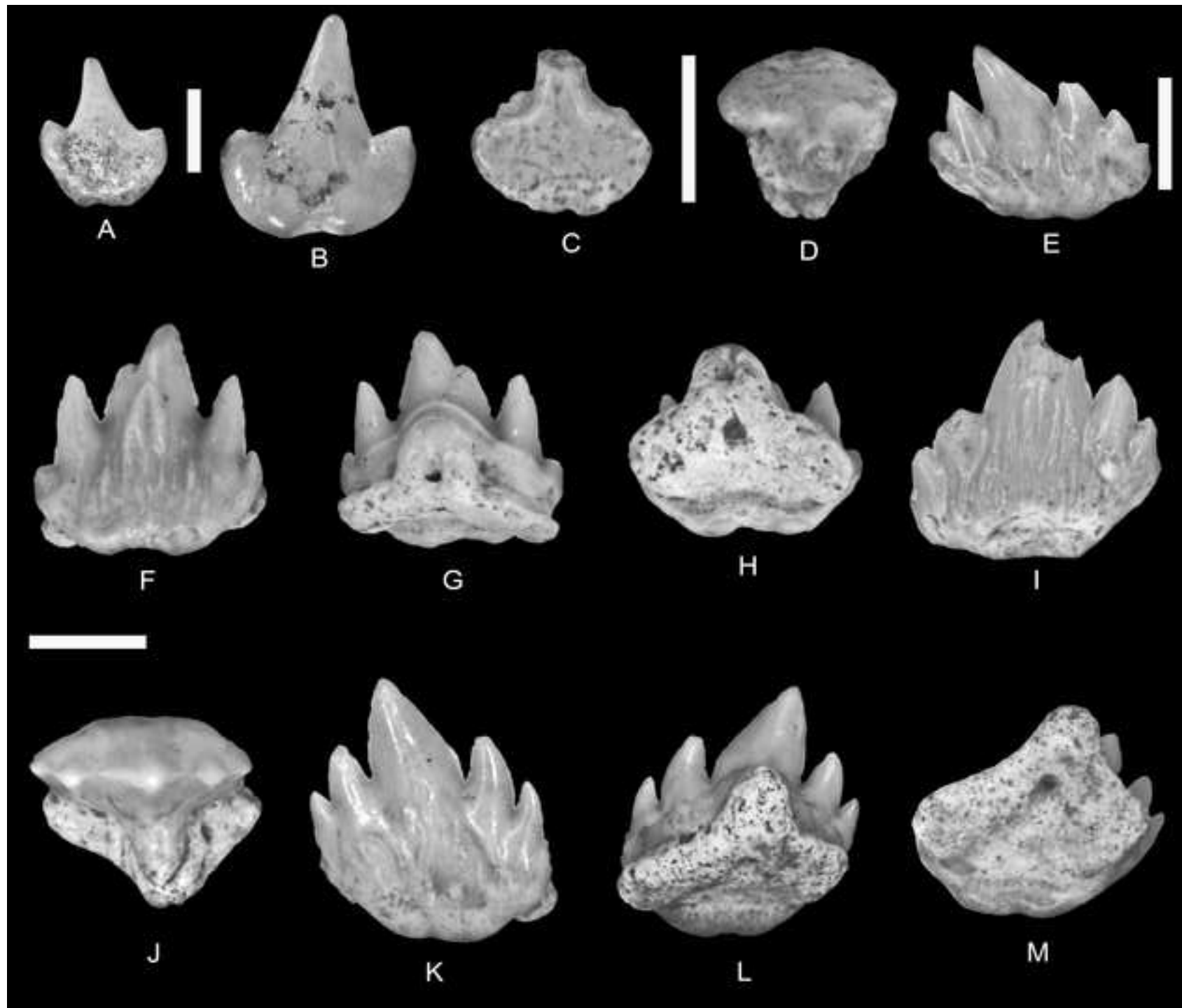


Figure 2

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Order	Family	Taxon
Orectolobiformes	Hemiscylliidae	<i>Chiloscyllium</i> sp. <i>Hemiscyllium</i> sp.
Lamniformes	Ginglymostomatidae	<i>Plicatoscyllium youssoufiaense</i>
	Anacoracidae	<i>Squalicorax pristodontus</i>
	Carchariidae	<i>Carcharias</i> cf. <i>heathi</i> <i>Carcharias</i> sp. 1 <i>Carcharias</i> sp. 2
Rajiformes	Otodontidae	<i>Cretalamna maroccana</i>
	Serratolamnidae	<i>Serratolamna serrata</i>
	Sclerorhynchidae	<i>Dalpiazia stromeri</i> <i>Ctenopristis nougareti</i> <i>Schizorhiza stromeri</i>
	Sclerorhynchidae	<i>Ptychotrygon nazeensis</i> sp. nov.
	Ptychotrygonidae	<i>Parapalaeobates</i> sp.
Rhinopristiformes	Parapalaeobatidae	cf. <i>Rhynchobatus</i> sp.
	Rhynchobatidae	<i>Terangabatis thiami</i> gen. et sp. nov. <i>Rhinobatos' popenguinensis</i> sp. nov. <i>Atlantobatis acrodonta</i> gen. et sp. nov. ? <i>Microbatis</i> sp. <i>Sowibatos minimus</i> gen. et sp. nov.
	Rhinobatoidei incert. fam.	<i>Dasyatis' reticulata</i> sp. nov.
Myliobatiformes	Dasyatidae	<i>Coupatezia casei</i> sp. nov.
	Dasyatoidea incert. fam.	? <i>Coupatezia</i> sp.
	Rhombodontidae	<i>Rhombodus binkhorsti</i> <i>Rhombodus andriesi</i> <i>Rhombodus</i> spp.
	Myliobatiformes incert. fam.	<i>Phosphatodon cretaceus</i> sp. nov.
Batomorphii incert. sed.	Batomorphii incert. sed.	Batomorphii indet. sp. 1 Batomorphii indet. sp. 2 Batomorphii indet. sp. 3

* reported as *Cretalamna* cf. *biauriculata* by Cuny *et al.* (2012)

S1 (Unit 1)	S2 (Unit 1)	S3 (Unit 3)
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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

LH, RS, JM and GG conceived the study; LH, JM, RS, and BS did the fieldwork and sampling; GG drafted the manuscript and illustrations with inputs from all authors; all authors reviewed the manuscript.