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Source: American Museum Novitates, 2024(4013) : 1-32

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/4013.1

AMERICAN MUSEUM NOVITATES

Number 4013, 31 pp. May 8, 2024

A Composite Section of Fossiliferous Late Cretaceous–Early Paleogene Localities in Senegal and Preliminary Description of a New Late Maastrichtian Vertebrate Fossil Assemblage

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ABSTRACT

We describe new macro- and microfossils recovered on a field expedition to the North Quarry of Poponguine, a locality in western Senegal that spans the Late Cretaceous through the Early Paleogene, albeit with a likely unconformity at the base of the Danian. Newly discovered macrovertebrates from the Maastrichtian Cap de Naze Formation include pycnodonts, dyrosaurids, and chelonians, the latter two the oldest and first Cretaceous representatives of these clades from Senegal. Screenwashing of this deposit revealed that the matrix also consists of abundant microscopic biological clasts comprising osteichthyan vertebrae, spines, and cranial fragments, shark dermal denticles, invertebrates, and numerous ovoid coprolites among other fragments. These microfossils document a much less conspicuous portion of the paleobiodiversity. We describe the stratigraphy of this new locality and incorporate it into a new correlated section that ties together three other Late Cretaceous–Early Paleogene fos-

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ISSN 0003-0082

siliferous localities of the Senegalese-Mauritanian Basin. The presence of fossiliferous Danian rocks, which are notably rare in West Africa, is elucidated in our section, which synthesizes prior geological and paleontological work around Poponguine and in the nearby coastal region of Ndayane. Primarily dated using the biostratigraphy of ostracods and foraminiferans, the correlated rock units include the Paki and the Cap de Naze Formations of the Late Cretaceous Diass Group and the Ndayane and the Poponguine Formations of the Paleocene Cap-Vert Group, deposits that capture ancient near shore marine environments. The localities described, although separated by only a few kilometers, exhibit dramatic differences in thickness across faulted blocks of the Diass Horst. Dyrosaurids, which are common fossils in nearshore marine outcrops of West Africa, have been hypothesized to be of African origin and to have dispersed to South America in the Late Cretaceous. This dyrosaurid specimen, although fragmentary, documents a western extreme in the geographic range of African dyrosaurids where the clade would have been well situated for broader trans-Atlantic dispersal.

INTRODUCTION

For nearly a century, Late Cretaceous and Early Paleogene rocks of western Senegal have been known to yield fossil vertebrates, invertebrates, plants, and microfossils (e.g., Malavoy, 1935; Tessier, 1952; Apostolescu, 1961). An integrated picture of how these deposits relate to each other, however, is only beginning to emerge. Recent publications have reported new discoveries of this kind from the region or have more fully described older finds, including a fairly complete Paleocene dyrosaurid (Malavoy, 1935; Jacquet, 1936; Martin et al. 2019), fragmentary Late Cretaceous pycnodont fishes (Capasso, 2019), neoselachian sharks (Cuny et al., 2012) and fossil decapod crustaceans (Hyžný et al., 2016a, 2016b).

The North Quarry of Poponguine (figs. 1–3) is a previously undescribed locality in the Senegalese-Mauritanian Basin that yields vertebrate fossils (Sarr, 1995). Situated near the town of Poponguine, rocks of the North Quarry span the Late Cretaceous through the Early Paleogene albeit with an unconformity at the base of the Danian inferred from microfossil stratigraphy as described below. As part of a joint 2010 collaborative expedition between the Cheikh Anta Diop University and Stony Brook University, we recovered several new Late Maastrichtian vertebrate fossils including dyrosaurs, pycnodonts, and chelonians. A new microfauna discovered through screenwashing includes osteichthyan bones, coprolites, and invertebrates that are significantly smaller than the macrofossils from the same locality. Along with a section of the new locality, we present the first composite section tying together three other fossiliferous localities in the area. Our composite builds on the lithostratigraphic framework of Roger et al. (2009) and the biostratigraphic framework developed by Sarr and colleagues for the Formations of the Senegalese-Mauritanian Basin, specifically, the areas of Thiès and the central basin region (Sow, 1992; Sow et al., 1994; Sarr, 1995; 1998; Sarr and Ly, 1998; Cuny et al., 2012; Sarr, 2012; 2013; 2015). Our work complements new synthetic studies of fossil vertebrate localities in Africa such as recent descriptions of the Early Paleogene of the Congo Basin (Solé et al., 2019) and the Cretaceous-Paleogene boundary in Morocco (Bardet et al., 2017).

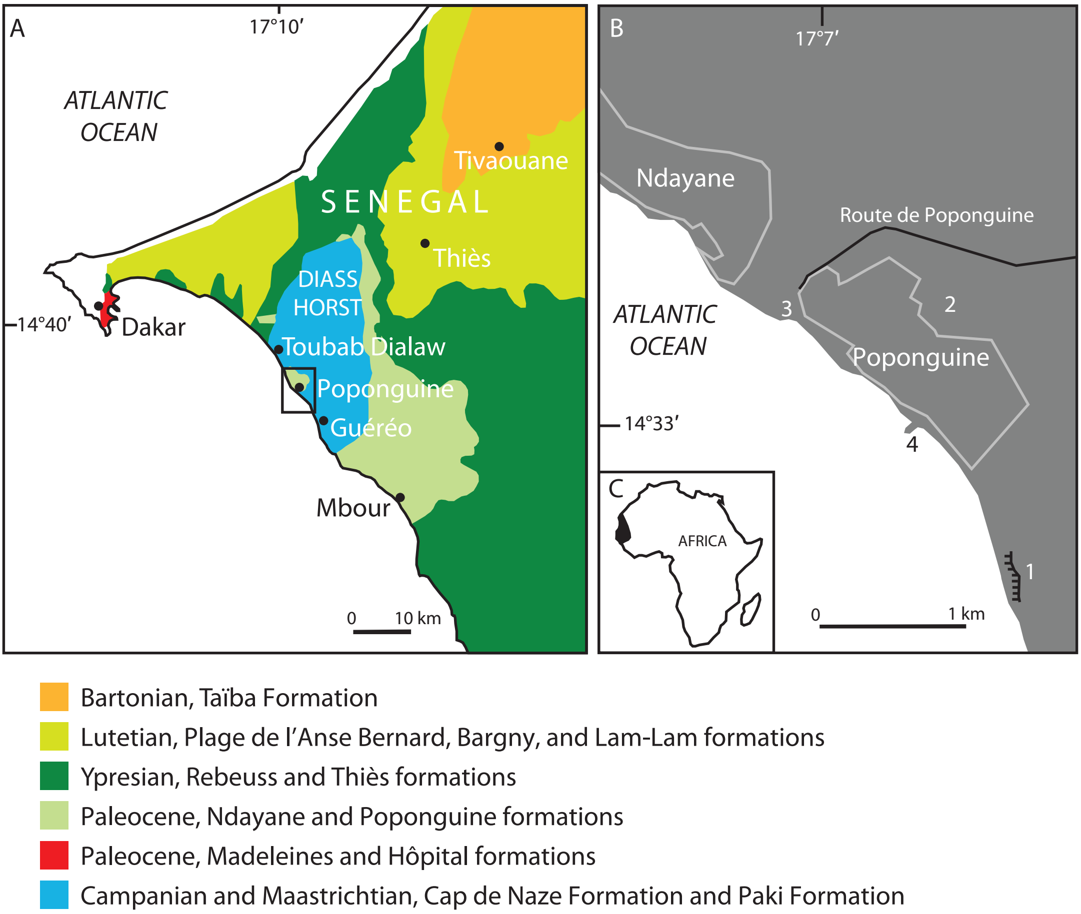

FIGURE 1. **A,** Regional geologic map of western Senegal indicating names and ages of geologic formations exposed (after Roger et al., 2009), with black box indicating area under study (expanded in B). **B,** Positions of the four localities of the Ndayane/Poponguine area described in this paper: **1,** Cap de Naze; **2,** North Quarry of Poponguine; **3,** Ndayane Cliff at Poponguine; and **4,** Islet of Poponguine. All are in close proximity despite the variation in lithology among them. **C,** Position of field area in the Senegalese–Mauritanian Basin in western Senegal, West Africa.

Units integrated into the composite section are the Late Cretaceous Diass Group with the Paki and the Cap de Naze Formations, and the Paleocene Cap-Vert Group with the Ndayane and the Poponguine Formations. The Late Cretaceous beds, particularly the Cap de Naze Formation, are well exposed on the coast of western Senegal (Cuny et al., 2012: fig. 2), however, exposures of other rocks that cross the Cretaceous-Paleogene boundary or that represent Paleogene outcrops are far less extensive and sometimes accessible only as the byproduct of commercial excavations. The North Quarry of Poponguine is the most inland of the four localities in the composite section (fig. 1) and is of special interest because it preserves an additional unit of the Cap de Naze Formation that is younger and different in lithology than the four units of this Formation exposed at the Cap de Naze Cliff.

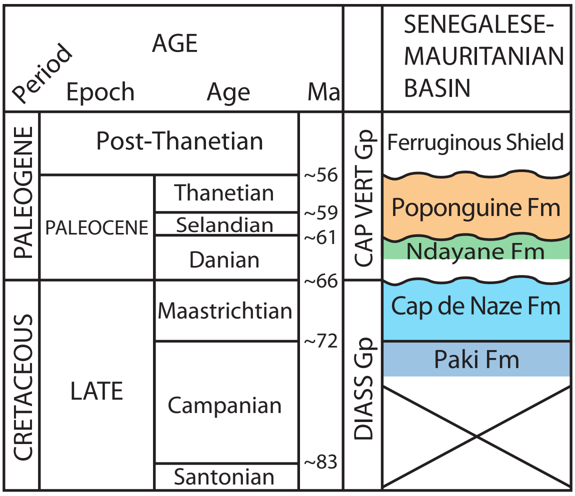

FIGURE 2. Composite of formation names for Late Cretaceous–Early Paleogene rocks of western Senegal.

REPOSITORY AND INSTITUTIONAL ABBREVIATIONS

Specimens collected on the 2010 joint expedition of Cheikh Anta Diop University–Stony Brook University are part of the Collection of the Cheikh Anta Diop University (UCAD), Dakar, Senegal. Abbreviations: CAD-SBU, Cheikh Anta Diop University–Stony Brook University 2010 expedition and collection; M, MorphoBank; SEN, University of Cheikh Anta Diop (UCAD) collection, Dakar, Senegal.

MATERIALS AND METHODS

Fossil collection and manual preparation: At the North Quarry of Poponguine the team collected matrix from the exposed outcrop where bone was first observed on the surface. These rocks were later prepared in the vertebrate fossil preparation laboratory at Stony Brook University. Macrovertebrates were prepared using manual preparation; microfossils were prepared using acid baths that captured specimens in 300 μm sieves. After sieving, microfossils were collected onto filter paper and adhered using thin, water-based glue. Filter papers were inspected under a dissecting microscope and specimens were selected for description based on their completeness and to demonstrate the breadth of taxa present.

Digital preparation of fossils: Micro-CT scanning was performed at the NYIT Visualization Center, Old Westbury, New York. Twenty microfossil specimens were loaded into individual gelatin capsules and packed with polystyrene foam and imaged using micro-CT to visualize their internal features and external surfaces. Scans were taken with a Bruker SkyScan 1173 (USA). Microfossils were scanned at a voltage of 35kV. The number of images varied depending on the size of each specimen, but all were taken with an exposure time of 525 ms each. Voxel size was 25 μm for all specimens. Datasets were three-dimensionally rendered and segmented with Dragonfly version 2022.2 for Windows, Object Research Systems (ORS) Inc, Montreal, Canada, 2022. Images were rendered with Blender 3.10 (Blender Online Community, 2017).

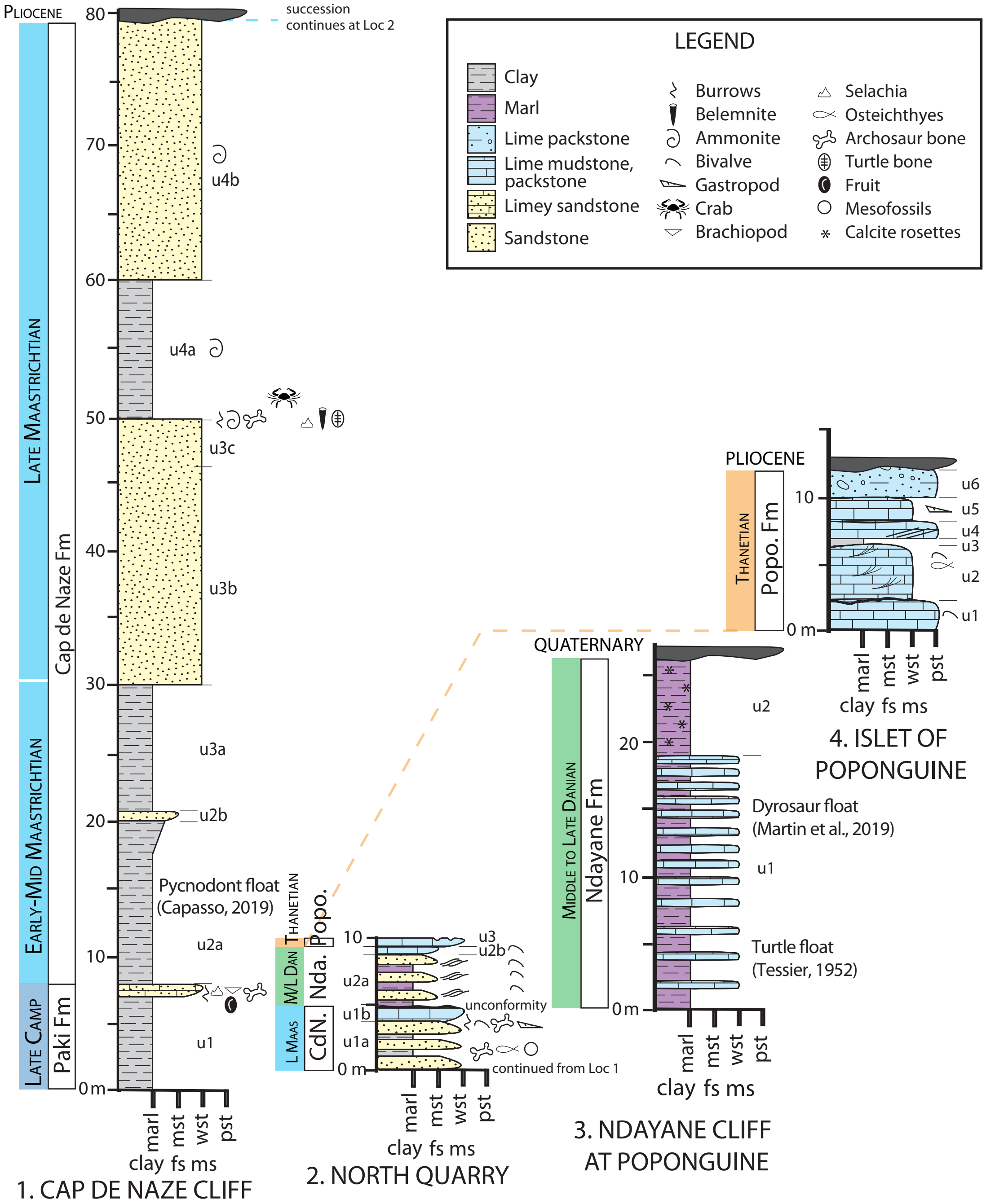

FIGURE 3. Composite stratigraphic section correlating four fossiliferous Late Cretaceous–Early Paleogene localities of Western Senegal. Units are unique to each locality (i.e., unit 2 of the Ndayane Formation at the North Quarry locality is not necessarily the same as unit 2 of the Ndayane Formation at the Ndayane Cliff at Poponguine locality). Abbreviations: **Camp**, Campanian; **CdN.**, Cap de Naze; **Dan**, Danian; **Fm**, formation; **fs,** fine sand; **ms,** medium sand; **L**, late; **M/L**, Middle to Late; **Maas**, Masstrichtian; **Mid**, middle; **mst,** mudstone; **Nda.**, Ndayane Formation; **Popo.**, Poponguine; **pst**, packstone; **u**, unit; **wst**, wackestone. Gray caps on three of the localities are Plio-Pleistocene ferruginous rocks.

Digital Repository: Additional 2D and 3D images of fossil specimens are archived online at http://morphobank.org/permalink/?P4480 (Morphobank Project P4480).

LATE CRETACEOUS–EARLY PALEOGENE LOCALITIES IN THE POPONGUINE-NDAYANE AREA

The study area is located at the western edge of the Senegalese-Mauritanian Basin to the south of the Diass Horst (fig. 1), a faulted anticline where mostly Campanian and Maastrichtian rocks crop out that is surrounded by late Paleocene to early Eocene beds (Sarr, 1998; Tabuce et al., 2020). The Paleogene sedimentary units lie between Toubab Dialaw and Poponguine and correspond to a collapsed southern segment of the Diass horst. The terminal Cretaceous and the Paleocene crop out in the region of Poponguine-Ndayane (figs. 1, 2). Oligo-Miocene volcanic pipes composed of basalt and early Eocene flinty attapulgite intrude into the sedimentary units, as part of the Cap de Naze diatreme. Four localities in this region are described below along with the fossils they have yielded. Discoveries from the North Quarry of Poponguine collected on the 2010 CAD-SBU expedition are further described in Systematic Paleontology below. The localities are in close proximity at only several kilometers apart but nonetheless exhibit dramatic differences in thickness: the Ndayane Formation doubles in thickness over approximately one kilometer.

Throughout this paper we use units that are unique to each locality. For example, unit 2 of the Ndayane Formation at the North Quarry locality is not necessarily the same as unit 2 of the Ndayane Formation at the Ndayane Cliff at Poponguine locality. We describe the four localities from stratigraphically oldest to youngest.

Cap de Naze Cliff

Figures 3–4

On the Atlantic coastline of Poponguine, the Cap de Naze cliff, which ultimately reaches 80 m high, extends to the north of the town of Guéréo. The locality, its macro- and microfossils and its age as dated by biostratigraphy, have been described in a number of studies (Tessier, 1952; Castelain, 1965; Faye, 1983; Khatib et al., 1990; Sow et al., 1994; Sarr, 1995; Cuny et al., 2012; Hyžný et al., 2016a, 2016b). Spanning from the Late Campanian through Late Maastrichtian, the Cap de Naze Cliff consists of alternating clayey-silty sandstones that dip to the southeast toward the diatreme, and the beds are cut in several places by volcanic pipes. Cuny (2012: fig. 2) most recently described the well-exposed cliff and its four major geomorphologic units. We further detail subdivisions of those units as part of the composite section.

Coordinates of locality: N 14° 32′ 21.5; W 17° 06′ 17.0″, base of locality at sea level.

Total thickness of exposure: 80 m.

Formations: Paki and Cap de Naze Formations, Diass Group.

Age: Late Campanian–Late Maastrichtian with a Pliocene capping.

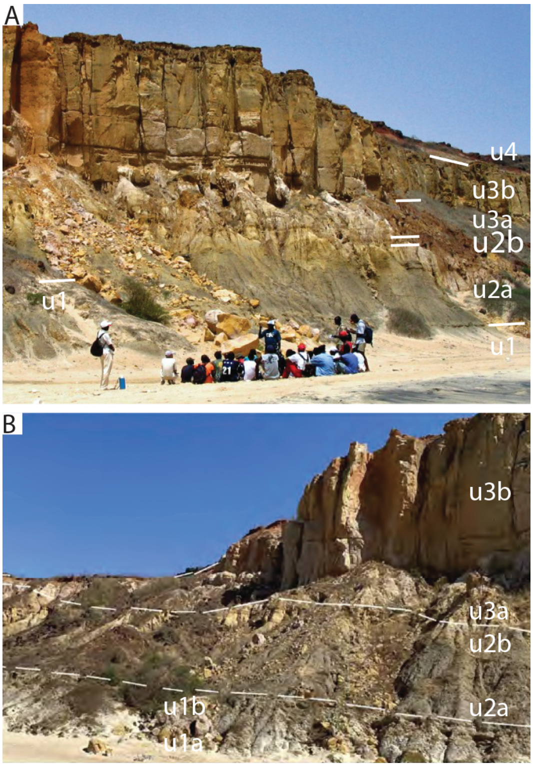

FIGURE 4. The four units visible at the Cap de Naze Cliff locality with the end Campanian Paki Formation and the Late Maastrichtian Cap de Naze Formation cropping out under a Pliocene capping. **A,** units 1–4 (figure modified from Cuny et al., 2012: fig. 2) and **B,** units 1–3.

UNIT 1, PAKI FORMATION, BASE OF THE DIASS GROUP, LATE CAMPANIAN: Unit 1 of the Cap de Naze Cliff sequence is represented by the Paki Formation which is dominated by gray clays cut by small pipes of recrystallized gypsum running in different directions (Sow, 1992; Cuny et al., 2012). The Paki Formation terminates as a bank of yellow siltite with a gray calcareous sandstone at the summit that is both indurated and bioturbated. The sandstone contains a condensed fossiliferous level with brachiopod internal molds (Sarr, 1995), and has also yielded a spine and a tooth of a rajiform (Cuny et al., 2012). At a locality other than Cap de Naze known as the Paki quarry near Diass City, remains of a pterosaur (Monteillet et al., 1982) and fossil fruits (Monteillet and Lappartient, 1981) have been recovered and assigned to the Paki Formation.

The base of the Paki Formation is dated as late Campanian by a planktonic foraminiferan assemblage previously described (Khatib et al., 1990; Sow, 1992; Sarr, 1995). According to Khatib et al. (1990) it contains the following planktonic foraminiferans: *Globotruncanella petaloidea*, *Globigerinelloides praeriehellensis*, *Globigerinelloides subcarinatus*, *Globotruncana stuartiformis*, *G. aegyptiaca*, *Heterohelix striata*, *H. globulosa*, *Pseudoguembelina costulata*, *Rugoglobigerina* cf. *hexacamerata*, *Rugoglobigerina macrocephala*, *Rugoglobigerina. milamensis*, *Rugoglobigerina rugosa*, and, additionally, in the bioturbated massive yellow limestone, *Globigerinelloides multispira*, *Güembelitria cretacea*, *Heterohelix striata*, *Pseudotextularia costulata*, *P.* aff. *deformis*, and *Radotruncana* cf. *calcarata*. *Radotruncana* (formerly *Globotruncanita*) cf. *calcarata* is the index taxon that dates the beds to the terminal Campanian (Khatib et al., 1990; Sow, 1992; Cuny et al., 2012). The following ostracods have been recovered only at the top of the unit (Sow et al., 1994; Sarr, 1995): *Cytherella gambiensis*, *C. sarakundaensis*, *Paracosta warriensis* and *Veenia velata*, and are known only from Campanian and Maastrichtian rocks of the Nigeria and Senegal basins (Apostolescu, 1961; Reyment, 1963; Sarr, 2015). Ostracod taxa *Paracypris jonesi* and *Bythocypris* sp. have also been recovered.

Unit 2, Cap de Naze Formation, lower Diass Group, Early-Middle Maastrichtian: Unit 2 at the Cap de Naze locality marks the first appearance of the Cap de Naze Formation. Its first division, unit 2a, consists of a clayey siltite that transitions to a sandy siltite at the top. That layer is capped by unit 2b, a yellow, fine-grained sandstone. In unit 2a, most of the planktonic foraminiferan species previously seen in the underlying Paki Formation disappear with the exception of *Heterohelix globulosa*, *Globigerinelloides praeriehellensis*, *Globotruncana aegyptiaca*, *Globotruncana stuartiformis*, *Pseudotextularia* aff. *deformis*, *Rugoglobigerina macrocephala*, *R. rugosa*, whereas *Rugoglobigerina* gr. *reicheli* appears. Khatib et al. (1990; see also Cuny et al., 2012) dated this microfaunal association to the early-middle Maastrichtian. The following benthic foraminiferans are present in these Cap de Naze Formation units 1 and 2 and are known in the Campanian and Maastrichtian of the Gabon and Senegal basins (de Klasz and Rérat, 1962; Ly and Kuhnt, 1994; Sarr, 1995): *Anomalinoides* cf. *pinguis*, *Haplophragmoides biauriculata*, *Neobulimina subregularis*, *Orthokarstenia ewaldi*, *O. bramletti*, *Praebulimina crassa*, *P. fang*, and *Vaginulina navarroana*.

Unit 3, Cap de Naze Formation, middle Diass Group, Late Maastrichtian: The Cap de Naze Formation continues as unit 3 with unit 3a beginning with 8 m of mottled, clayey siltites. The siltites of unit 3a are covered by unit 3b, which consists of 16 m of fine, silty sandstones. Finally, at the top, unit 3c forms a bioturbated massif, which is very fossiliferous having yielded belemnites, internal molds of ammonites (not yet described) and decapod crustaceans, namely, the crabs *Costacopluma mamethioupami* and *Paracapsulapagurus poponguinensis* (Cuny et al., 2012; Hyžný, 2016a, 2016b). In addition, unit 3c of the Cap de Naze Formation yields vertebrate fossils such as mosasaurs and turtles along with numerous teeth and vertebrae of neoselachians have been identified by Cuny et al. (2012) including: *Cretalamna* cf. *C. biauriculata*, *Serratolamna serrata*, *Carcharias* cf. *C. heathi*, ?*Carcharias* sp., *Squalicorax pristodontus*, *Schizorhiza stromeri*, *Parapalaeobates* sp., *Rhombodus binkhorsti*, *Rhombodus andriesi*, and *Rhombodus* spp. Unit 3c does not contain foraminiferans; however, Cuny et al. (2012: 114) hypothesized that in aggregate the selachian assemblage dates to the Late Maastrichtian because of the presence of Late Maastrichtian taxa *Serratolamna serrata*, *C. heathi*, and *R. andreisi* and Maastrichtian taxon *R. binkhorsti*.

Unit 4, Cap de Naze Formation, upper Diass Group, Late Maastrichtian: The highest Cap de Naze unit, unit 4, consists of two distinct subunits. Unit 4a is formed of clayey, whitish siltites with ammonites. To the south near the town of Guéréo the siltites are capped by fine-grained, massive sandstone, unit 4b, of varying thickness reaching a maximum of 30 m. Planktonic foraminiferans are absent and the very rare benthic foraminiferan, *Haplophragmoides* spp. (various undescribed species), has not provided reliable temporal data (Sarr, 1995; Cuny et al., 2012). Castelain (1965) related the top of the Cap de Naze locality to the base of deposits on the beaches at Poponguine, the locality we refer to here as the Ndayane Cliff at Poponguine (see also Cuny et al., 2012: 108). There, ammonites (i.e., *Daradiceras gignouxi* and *Spenodiscus corroyi*) were discovered by Tessier (1952) providing Late Maastrichtian index taxa for the top of the Cap de Naze Formation (see also Cuny et al., 2012). We have not included the Cap de Naze deposits in our composite section for our locality 3, Ndayane Cliff at Poponguine (described below), because we have not directly measured those beds.

Ferruginous shield, Pliocene: This 2–3 m thick bed caps the Cap de Naze cliff displacing the underlying sandstone. It lies unconformably on the geologic formations of the Diass Group. Additionally at the Cap de Naze cliff locality Miocene volcanic pipes (Catagrel et al., 1976; Crévola et al., 1994) cut the Diass Group causing contact metamorphism with the sedimentary units. The pipes are altered basalts of phreatomagmatic origin (Tessier, 1952).

Additional Paleontological notes: A pycnodont dentition and isolated tooth have been reported from the Cap de Naze locality, however, it is not known from which part of the section they derive (Capasso, 2019).

Depositional environment: The microfauna suggests a middle platform that underwent a transition to a littoral milieu.

North Quarry at Poponguine

Figures 3, 5, 6

Numerous quarries exist between the towns of Poponguine and Ndayane for commercial exploitation of the deposits of aggregated marly limestones of Danian age. Geological and paleontological work has been possible as a byproduct of this commercial mining. The North Quarry at Poponguine is the only one of the four localities we describe that is located inland; its lithology and ostracod fauna were first described by Sarr (1998: fig. 3). Thanetian shelly limestones of the Poponguine Formation formerly covered areas to the east and north of the town of Poponguine (Tessier, 1952; Sarr, 1998). They no longer exist except to the east of the town and around the civic landmark known as the Basilica of the Marial Sanctuary. The locality we call the North Quarry of Poponguine (termed locality CAD-SBU 2 by us on our 2010 expedition) is located between two additional civic landmarks: the Poponguine Secondary School and a station of the Water Distribution Society (fig. 5). One can observe in this quarry the transition from the Maastrichtian Cap de Naze Formation to the Danian Ndayane Formation capped by the Thanetian Poponguine Formation. In different areas the Poponguine Formation lies unconformably on either the Ndayane Formation or on the top of the Cap de Naze Formation (fig. 5E; 6).

Coordinates of locality: N 14° 33′ 29″; W 17° 06′ 34″; 21 m elev.

Total thickness of exposure: 7.5 m.


A
B
u2b
u2a
u1b
u1a
C
u2b
u2a
u1b
D
u2a
u1b
E
u3
u1b

FIGURE 6. Contact between the Danian Ndayane Formation and the overlying Thanetian Poponguine Formation in the North Quarry of Poponguine locality.

Formations: Cap de Naze Formation, Upper Diass Group and Ndayane and Poponguine Formations, Cap Vert Group.

Age: Maastrichtian-Thanetian.

Unit 1, Cap de Naze Formation, upper Diass Group, Late Maastrichtian: The Cap de Naze Formation crops out at the base of the North Quarry locality in chaotic and partially vaulted blocks with a quick succession of layers in relatively low relief. The base the of Cap de Naze Formation, unit 1a, has blocks of reddish, calcareous conglomeritic sandstone separated by thin, lenslike beds of fine-grained ochre sand and mottled clays extending approximately 4 m. The mottled clays evoke those at the base of unit 3 of the Cap de Naze Formation at the Cap de Naze Cliff locality. This highly indurated sandstone yielded a number of vertebrate fossils on the 2010 CAD-SBU expedition including dyrosaurs and turtles. The matrix also consists of biological clasts that record a microfauna, including vertebrates, that is significantly smaller. These vertebrate and microfauna specimens are described below.

At the North Quarry of Poponguine the summit of unit 1a is a vaulted, thick bank (0.7–0.8 m) of shelly limestone, unit 1b, that has a hard-ground surface. As observed in the field, this part of the Cap de Naze Formation is rich in mollusks in life positions (bivalves, gastropods, and much rarer nautiloids) associated with occasional bones and teeth of vertebrates (these have yet to be collected systematically or described) and burrows from bioturbation. Unit 1 has

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FIGURE 5. North Quarry of Poponguine locality where the Late Maastrichtian–Thanetian Cap de Naze, Ndayane, and Poponguine formations are exposed. Contact between the Cap de Naze Formation and the Ndayane Formation is unconformable. **A,** Panoramic view of the locality with the Poponguine Secondary School visible at the top of the section; **B,** north part of the locality showing prospecting of fossiliferous calcareous sandstone; **C**, detail of the north part of the quarry showing the 20° southwest dip of the beds; **D,** limestones and marls of the Ndayane Formation (unit 2a) onlapping the vaulted bank of shelly limestone of the Cap de Naze Formation (unit 1 b); and **E,** massive shelly limestones of the Poponguine Formation (unit 3) lying unconformably on the shelly limestone of the Cap de Naze Formation (unit 1b). Units are as follows: Cap de Naze Formation: unit 1a, conglomeritic calcareous sandstone with clay lenses, and unit 1b, vaulted bank of shelly limestone; Ndayane Formation: unit 2a, thick blocks of calcareous sandstone with alternating beds of marls, and unit 2b, alternating limestones and marls; and the Poponguine Formation: unit 3, massive shelly limestone banks with local karst.

not yielded foraminiferans but does contain rare ostracods including the species *Jubatocythere casamancea* and *Paracypris* sp., which have previously been found at the base of the Danian at the locality Ndayane Cliff at Poponguine (Sarr, 1998, 2015).

By its lithology unit 1a of the Cap de Naze Formation of the North Quarry of Poponguine corresponds to a similar unit described by Tessier (1952) at his "brachyanticline" locality several hundred meters to the south on the Poponguine beach, near our Ndayane Cliff at Poponguine locality (fig. 3). This brachyanticline, a short, broad anticlinal structure, is now covered by homes, and consists of fine limey sand with thin beds of varicolored clays and limey, reddish sandstone and yields cnidarians, crinoids, and ammonites (Tessier, 1952). At the top is a bank of reddish, ochre calcareous sandstone with a hardground dated by the Maastrichtian ammonites *Daradiceras ginouxi*, *Sphenodiscus corroyi* and *Libycoceras* sp. (Tessier, 1952). This unit covers unit 4b of the Cap de Naze Formation at the Cap de Naze Cliff and dates to the Late Maastrichtian based on the ammonites. Thus, unit 1a of the North Quarry of Popoguine and similar exposures at the brachyanticline of the Ndayane Cliff at Poponguine (not shown in fig. 3) preserve an additional fifth unit of the Cap de Naze Formation that is younger than and different in lithology from the four units of this formation exposed at the Cap de Naze Cliff locality.

Unit 2, Ndayane Formation, lower Cap Vert Group, Danian: At the North Quarry of Poponguine, the Ndayane Formation lies with an erosive contact on the Cap de Naze Formation (fig. 5D). The Ndayane Formation consists of two distinct lithologic units, units 2a and 2b, which contain foraminiferans and ostracods. The base of unit 2a consists of thick blocks of calcareous sandstone with shells and hummocky cross-stratification alternating with beds of marls. These features suggest deposition at storm wave base, and a potential deepening of facies above the Cap de Naze Formation.

Planktonic foraminiferans are scarce, although *Subbotina triloculinoides*, which characterizes biozone P1b of Berggren et al. (1995), has been recovered indicating a middle Danian age. *Globigerina fringa* is also present. At the North Quarry of Poponguine, unit 2b, representing the younger part of the Ndayane Formation consists of alternating limestones and marls with the following planktonic foraminiferans: *Globoconusa daubjergensis*, *Praemurica inconstans*, *Praemurica* cf. *trinidadensis*, *Chiloguembelina morsei*, *Globanomalina compressa*, *Parasubbotina pseudobulloides*, *Morozovella uncinata*, and *Subbotina triloculinoides*. This association indicates biozones P1c to P2 of the late Danian (Berggren et al., 1995).

The ostracods are diverse in units 2a and 2b attributable to the Ndayane Formation (Sarr, 1998) consisting of 30 species: *Bairdia ilaroensis*, *Buntonia issabaensis*, *Bythocypris olaredodui*, *Bythocypris* sp., *Cytherella sylvesterbradleyi*, *Cytherelloidea saharaensis*, *Cytheropteron poponguinensis*, *Cytherura cayorensis*, *Dahomeya alata*, *Eocytheropteron devius*, *Hermanites angulocostata*, *Jubatocythere casamancea*, *Leguminocythereis lagaghiroboensis*, *Looneyella cheikhantai*, *Loxoconcha safeni*, *Loxoconchella thiandoumi*, *Neonesidea elongatoilaroensis*, *Nigeroloxoconcha ndayanensis*, *Orthonotacythere mamethioupani*, *Paijenborchellina lyi*, *Paracypris sokotoensis*, *Paracypris* sp., *Pondoina ndofanensis*, *Quadracythere lagaghiroboensis*, *Reticulina sangalkamensis*, *Soudanella laciniosa triangulata*, *Uroloberis glabella*, and *Xestoleberis senegalensis*. There are also reworked and damaged carapaces of Late

Cretaceous ostracods such as *Cytherella gambiensis* and *Nanocythere vitilis*. This faunal association includes species restricted to the Danian ostracod zone H1a *Bythocypris* sp., *Cytheropteron poponguinensis*, *Cytherura cayorensis*, *Cytherura toubabdialawensis*, and *Looneyella*? *cheikhantai* that are (Sarr, 1995, 1998: fig. 3; 2012: figs. 2, 3). Elsewhere, approximately 200–300 m to the north of the North Quarry of Poponguine, the shelly limestones of the Poponguine Formation lie directly on the vaulted limestone bank of the Cap de Naze Formation (fig. 5E).

Unit 3, Poponguine Formation, upper Cap Vert Group, Thanetian: This Formation lies unconformably on the Ndayane Formation at the North Quarry of Poponguine locality and, as just noted above, to the north of the North Quarry, on the Cap de Naze Formation. The Poponguine Formation crops out in massive shelly limestone banks with local karst (fig. 5E), which has local "swallow" holes. These beds are less extensive to the north where they taper resulting in the appearance of the underlying Ndayane Formation and then the top of the Cap de Naze Formation. The Poponguine Formation dates to the Thanetian at the Islet of Poponguine (see below).

Depositional environment: The Cap de Naze Formation preserved in the North Quarry at Poponguine indicates a depositional environment that was littoral-infralittoral with frequent submersions that stopped at a shelly limestone bank with hardground. Regional transgression during the mid-Danian records a deepening to storm wave base in the Ndayane Formation, followed by a shallowing to a littoral environment in the abbreviated deposits of Poponguine Formation at this locality (Tessier, 1952; Castelain, 1965; Monciardini, 1966; Martin, 1967; Brancart, 1977; Ndiaye et al., 2015).

NDAYANE CLIFF AT POPONGUINE

Figures 3, 7

This cliff (also called simply the "Falaise de Poponguine" (Sarr, 1998: fig. 2; Toumarkine et al., 1984: fig. 5) starts at Toubab Dialaw, is interrupted near Ndiongop, and reemerges between Ndayane and Poponguine to the southwest (figs. 1, 7). It is cut by faults and rarer volcanic veins. It measures just short of 10 m high at Poponguine, but the thickness of the formation is actually 27 m because the beds dip 10° to the southwest. The tallest part of the Ndayane cliff is inaccessible because it extends into the Presidential Residence (a civic landmark) and is currently hidden by a wall. A portion of the Cap de Naze Formation underlies the Ndayane Cliff at Poponguine (fig. 7; Tessier, 1952; Castelain, 1965; Cuny et al., 2012) with an erosive, angular contact that suggests an unconformity. Because we have not directly measured these beds they are not included in our composite section (fig. 3).

Coordinates of locality: 17° 07′ 11.3″; W 14° 33′ 27.1″ N

Total thickness of exposure: 27 m (Martin et al., 2019; 2019; Sarr, 1998).

Formation: Ndayane Formation, lower Cap Vert Group.

Age: Middle to late Danian.

Ndayane Formation, Lower Cap Vert Group, Danian: The section that is most complete consists of a succession as follows. Unit 1 of the Ndayane Formation has gray marls with lenses of calcareous marls covered by a concrete wall, followed by limestones with wavy beds

FIGURE 7. Ndayane Cliff locality at Poponguine with the middle-late Danian Ndayane Formation cropping out. Buildings now cover the brachyanticline (upper right). The Maastricthian Cap de Naze Formation consisting of calcareous sandstone with hard ground underlies the Ndayane Formation unconformably. As seen in the center of the photograph, the beach of Poponguine obscures part of unit 1 of the Ndayane Formation. Unit 1 consists of calcareous sandstone with beds of marls and unit 2 of marls with calcite rosettes.

of marly limestones that become increasingly fine and discontinuous. Unit 2 consists of marls with intercalated calcite rosettes and thin banks of limestone at the base. This section is the stratotype of the Ndayane Formation (Roger et al., 2009), the regional facies of which are characterized by the presence of a Pleistocene ferruginous cap (Toumarkine et al., 1984: fig. 5).

Ndayane Formation beds are rich in foraminiferans and ostracods (Sarr, 1998; Sarr and Ly, 1998) and calcareous nannofossils (Toumarkine et al., 1984). Rare macrofaunal taxa are also known, including a dyrosaur skeleton discovered in 1934 but not described in detail until recently (Malavoy, 1935; Jacquet, 1936; Martin et al., 2019). Additionally, Tessier (1952) described gastropods *Lucina dachelensis* and *Acrilla* cf. *desertorum*, and turtle bones from the locality. The exact level that yielded the latter is unknown.

Martin et al. (2019) studied the microfauna of this locality and concluded that it is middle-late Danian (Castelain, 1965; Faye, 1983; Toumarkine et al., 1984; Sarr, 1995, 1998; Sarr and Ly, 1998). Planktonic foraminiferans are known from the locality several of which are present in the middle shelf of the Tunisian Midway fauna described by Aubert and Berggren (1976): *Chiloguembelina morsei*, *Globigerina fringa*, *Globoconusa daubjergensis*, *Subbotina triloculinoides*, *Parasubbotina pseudobulloides*, *Praemurica* cf. *trinidadensis*, *Praemurica uncinata*, *Globanomalina compressa*, and *Praemurica inconstans* are of Danian to early Selandian age. Benthic foraminiferans comprise 34 species including *Alabamina midwayensis*, *Allomorphina* cf. *trigona*, *Anomalinoides* cf. *midwayensis*, *Bulimina* cf. *kugleri*, *Cibicidoides dayi*, *Dentalina* cf. *catenula*, *Eponides plummerae*, *Lenticulina degolyeri*, *Loxostomoides applinae*, *Marginulina* cf. *gardnerae*, *Osangularia plummerae*, *Quadrimorphina globulosa*, *Siphogenerinoides eleganta*, *Tristix* cf. *excavata*, and *Vaginulinopsis* cf. *longiforma*.

The ostracods comprise 24 species all cited in the Danian level of the Ndayane Cliff North Quarry of Poponguine (Sarr, 1998: fig. 2). Among them three species are limited to the Danian biozone H1a: *Cytheropteron poponguinensis*, *Cytherura cayorensis*, and *Cytherura toubabdialawensis*. Calcareous nannofossils of the grey marls *Cruciplacolithus edwardsii*, *C. primus*, *Ericsonia cava*, *Neochiastozygus primitivus*, *Placozygus sigmoides*, *Prinsius dimorphosus*, and *Toweius petalosus* are of Danian age (Toumarkine et al., 1984: fig. 5).

Depositional environment: The section represents a middle to external platform, which Sarr (1998) and Martin et al. (2019: 345) interpreted as having had a water depth of 100–150 m.

Islet of Poponguine

Figures 3, 8

The locality was described in Sarr (1998: fig. 5) as part of a study of the ostracods it yields. At the time of this writing, it is situated below the landmark known as the Kisito Center. We note this because the localities we describe are situated in populated urban areas.

Coordinates of locality: 17° 06′ 40.2″; W 14° 33′ 03.1″ N.

Total thickness of exposure: 12 m.

Formation: Poponguine Formation, Upper Cap Vert Group.

Age: Thanetian.

Poponguine Formation, Thanetian. The outcrop consists of banks of karst-filled limestone dipping strongly to the southwest. It constitutes the reference type section for the Poponguine Formation and exhibits the following sequence (fig. 8): unit 1: yellowish, crystalline limestone with shells; unit 2: fine coquina with small cross-stratifications and bones of Clupeidae; unit 3: poorly indurated, clayey limestone with planktonic and benthic foraminiferans and ostracods; unit 4: thick coquina with oblique stratifications dominated by

FIGURE 8. The Islet of Poponguine locality where the Thanetian beds of the Poponguine Formation crop out. **A,** Overview of locality showing units 2–5 (see text for lithology); **B,** detail of fine coquina limestone (unit 2) with small cross stratification; **C,** detail of thick coquina limestone (unit 4) with oblique stratifications dominated by lamellibranches; **D,** detail of thick coquina limestone (unit 5) with turritellids; and **E,** detail of limestone breccia (unit 6).

bivalves; unit 5 thick coquina dominated by turritellids; and unit 6, limestone breccia that gouges the preceding layer and encloses limestone blocks from it. At the top there are scraps of discordant ferruginous shield.

Planktonic foraminiferans are very scarce with *Subbotina velascoensis*, *Morozovella acuta*, and *Pseudohastigerina wilcoxensis* of late Thanetian age (Sarr, 1995). Associated benthic species *Anomalinoides ammophilus*, *Cibicides* cf. *westi*, *Pararotalia hensoni*, *P. calcariformis*, and *Rosalina brotzeni* are characteristic of littoral to inner shelf carbonate platforms of the Tethyan carbonate fauna described in the Paleocene of Libya and Mali (Berggren, 1974) and of the Sokoto Basin of Nigeria (Ficarelli, 1976).

Ostracods are abundant, with *Jubatocythere casamancea*, *Orthonotacythere mamethioupani*, and *Buntonia issabaensis* that indicate littoral to inner shelf deposit (Sarr, 1998).

This unit has not yet produced vertebrate fossils.

Depositional environment: Sedimentologic and microfaunal data for the Islet of Poponguine indicate a transition from an inner shelf environment to a littoral environment that had alternating submersions and emersions until the final withdrawal of the sea at the end of Paleocene (Sarr, 1998).

NOTE ON SYSTEMATICS

The fossils described below include microfossils (fig. 9), trace fossils (figs. 9, 10), and macroscopic vertebrate and invertebrate body fossils (figs. 11–14), all of which were recovered from the same horizon, locality, and depositional environment. The microfossils, which comprise coprolites, vertebrate bones, and invertebrate fragments, are aggregated by the thousands and essentially make up the matrix in which much larger macrofossils are embedded. SEN 082 (fig. 9M) is a sample of this aggregate that demonstrates the variety and proportion of coprolites (by far the most abundant elements), as well as spine fragments and other vertebrate bones (less abundant). Many thousands more of these microfossils are collected and cataloged as SEN 070. Although beyond the scope of this study, we hypothesize that the concentration of microfossils resembles a carbonate grainstone, whereby water currents flush away mud-sized sediments, leaving a winnowed framework-supported sediment. We have not uncovered evidence in the literature of similar deposits. Together, these microfossils constitute a diverse, small-bodied component of the paleofauna that stands in contrast to the larger invertebrate and vertebrate remains. Below, we describe all the macroscopic fossils discovered, along with individual microfossils selected for their anatomical completeness or taxonomic coverage to which the following locality data apply.

Horizon in Study Area and Age: Unit 1, Cap de Naze Formation, Upper Diass Group, Senegal, Maastrichtian.

Locality: North Quarry at Poponguine, CAD-SBU 2.

Depositional Environment: Reddish, calcareous, highly indurated conglomeritic sandstone capped by a shelly limestone bank that we interpret as an ancient littoral-infralittoral environment that experienced frequent submersions.

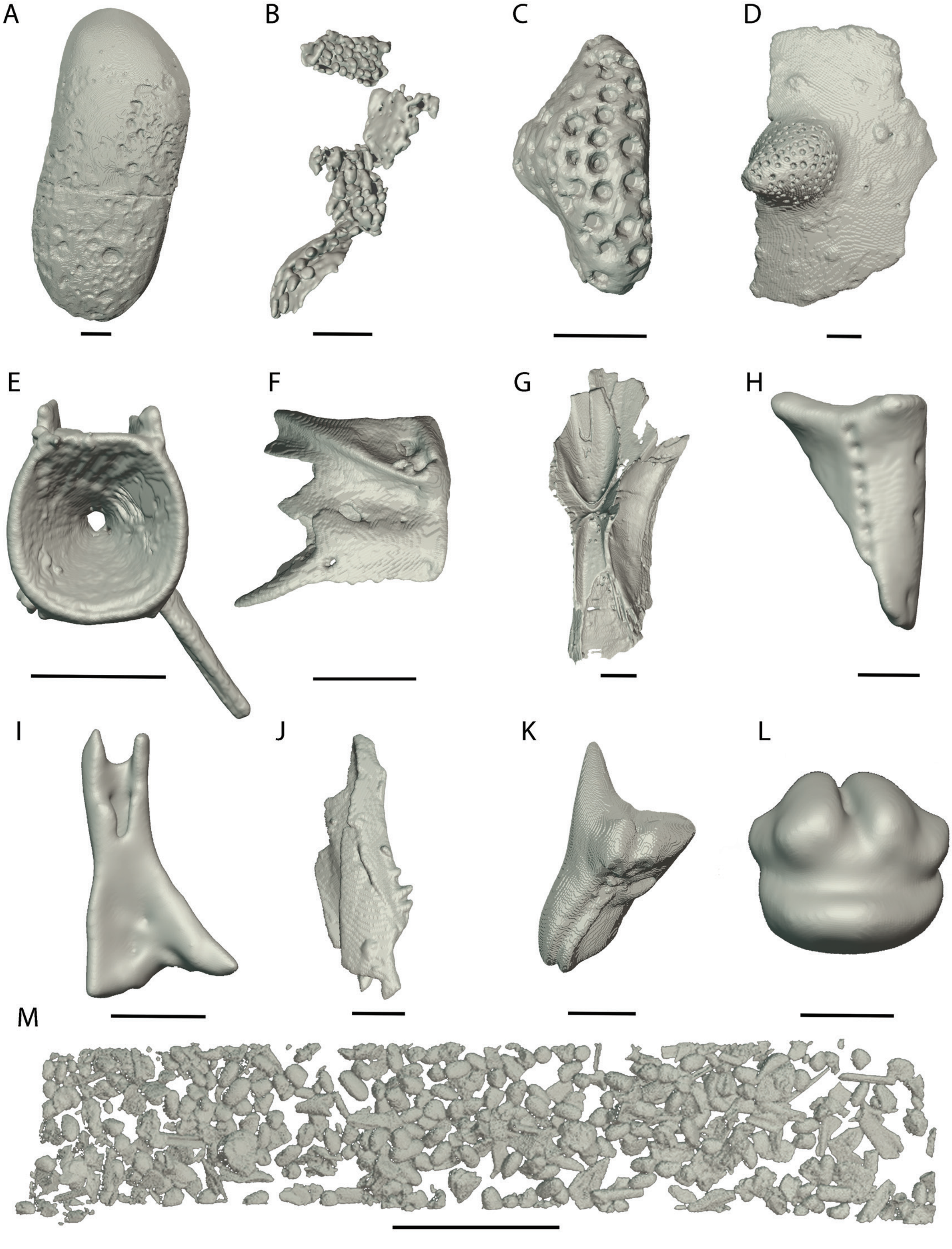
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FIGURE 10. Ovoid vertebrate coprolite (SEN 075). Scale = 1 cm.

SYSTEMATIC ICHNOLOGY

COPROLITES

Figures 9A, B, 10

Referred Material: SEN 075, 099, 100.

Description: SEN 075 (fig. 10) is a simple, ovoid coprolite that resembles vertebrate coprolite Morphotype 2 of Tapanila et al. (2008). These coprolites are characterized by their straight, wide morphology and their size ranging from 100–350 mm (O'Leary et al., 2019). Abundant ovoid coprolites that are similar in morphology to SEN 075, but an order of magnitude smaller, are also found in the bioclastic matrix. SEN 099 (fig. 9A) exemplifies this morphology, exhibiting a straight (nonspiral) form that is nearly cylindrical with rounded ends. SEN 100 comprises part of a branched surface covered with tiny (<0.2 mm) perpendicularly oriented pellets.

Discussion: While the producers of these coprolites are unknown, a conservative hypothesis based on the prior work of Tapanila et al. (2008) in West African sediments of similar ages and depositional environment is that the shape of the coprolites indicates that the maker of SEN 075 was a small marine vertebrate. SEN 100 bears similarities to the ichnospecies *Ophiomorpha peurilis* (Gibert et al., 2006), which has been interpreted as representing the fecal casts of juvenile thalassinidean crustaceans.

FIGURE 9. 3D surface reconstructions of microfossils discovered after acid preparation of the rock matrix from the Late Maastrichtian Cap de Naze Formation, unit 1a, at the locality North Quarry of Poponguine. **A,** Coprolite (SEN 099); **B,** fecal casts (peloids), likely invertebrate (SEN 100); **C,** ?Scleractinia, encrusting coral fragment SEN (094); **D,** Elasmobranchii, dermal denticle, superficial view (SEN 090); **E,** Osteichthyes, partial vertebra, axial view (SEN 088); **F,** Osteichthyes, fragmentary cranial element (SEN 085); **G,** Osteichthyes, fragmentary ?parasphenoid in ventral view (SEN 101); **H,** ?Osteichthyes, indeterminate bone (SEN 084); **I,** Siluriformes, dorsal spine base, caudal view (SEN 093); **J,** Siluriformes, pectoral spine, ?dorsal view (SEN 096); **K, L,** possible osteichthyan otoliths (SEN 097 and 098); **M,** aggregate sample of microfossils showing relative abundance of coprolites, spines, and vertebrate and invertebrate fragments (SEN 082). Scales = 1 mm except M, which is 5 mm.

SYSTEMATIC PALEONTOLOGY

CNIDARIA Hatschek, 1888

ANTHOZOA Ehrenberg, 1834

SCLERACTINIA Bourne, 1900

Figure 9C

Referred Material: SEN 094.

Description: Several of the microfossils resemble encrusting scleractinian corals, with polyp cups of approximately 0.1 mm in diameter.

MOLLUSCA Linnaeus, 1758

GASTROPODA Cuvier, 1795

CERITHOIDEA Fleming, 1822

TURRITELLIDAE Lovén, 1847

TURRITELLINAE Lovén, 1847

cf. *Mesalia* Gray, 1847

Figure 11A

Referred Material: SEN 060.

Description: A single concretion with a partial cast (formed in situ) of a turritellid. Six whorls are visible, becoming increasingly inflated as they are added, as in *Mesalia* (see O'Leary et al., 2019). Each whorl is perforated by four rows of tiny, evenly spaced pits. The specimen has been subject to some diagenetic flattening and evidence of the aperture is obscured by matrix.

Discussion: Extant turritellids are mollusks inhabiting warm water, nearshore marine environments. Fossil turritellids are documented from other ancient, shallow seaways in West Africa (e.g., Mali; O'Leary et al., 2019).

NATICOIDEA Guilding, 1834

NATICIDAE Guilding, 1834

Naticidae indet.

Figure 11B

Referred Material: SEN 071.

Description: Cast (formed in situ) of a naticid shell.

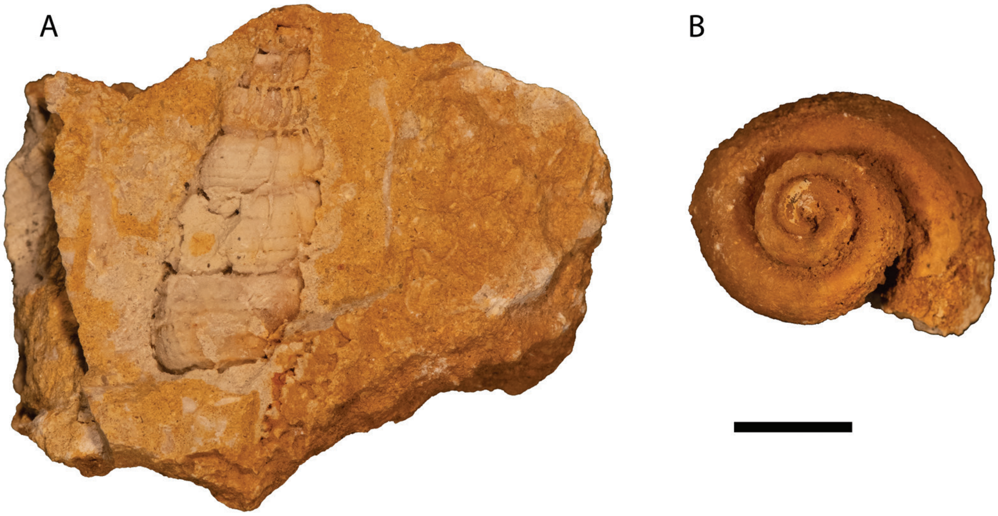

FIGURE 11. Maastrichtian invertebrates (internal molds formed in situ) of the Cap de Naze Formation discovered at the North Quarry of Poponguine. **A,** Turritellidae cf. *Mesalia* (SEN 060) natural cast in ?abapertural view; and **B,** Naticidae indet. (SEN 071), natural cast in apical view. Scale = 1 cm.

Discussion: This specimen preserves an internal cast of a globose shell with three whorls. The cast is broken off such that the full extent of the body whorl cannot be discerned; however, the cross section of this break is semilunar, suggesting a semilunar aperture morphology. The overall morphology is similar to that for specimens tentatively attributed to *Euspira* by O'Leary et al. (2019).

VERTEBRATA Lamarck, 1801
CHONDRICHTHYES Huxley, 1880

ELASMOBRANCHII Bonaparte, 1838

Elasmobranchii indet.

Figure 9D

Referred Material: SEN 090.

Description: Isolated dermal denticle.

Discussion: SEN 090 is tentatively identified as an elasmobranch dermal denticle. It is semicircular with a maximum dimension of 7 mm and possesses a conical spine centered along the edge. The spine is densely ornamented with small, uniform, circular pits. Surrounding the spine on three sides, there is a flat region ornamented with round, sparsely distributed tubercles.

FIGURE 12. *Pycnodus jonesae* (SEN 056) from the Late Maastrichtian Cap de Naze Formation discovered at the North Quarry of Poponguine. Left prearticular in occlusal view. Scale = 1 cm.

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Woodward, 1901

NEOPTERYGII Regan, 1923

PYCNODONTIFORMES Berg, 1937

PYCNODONTIDAE Agassiz, 1833–1844

Pycnodus Agassiz, 1833–1844

Pycnodus jonesae Longbottom, 1984

Figure 12

Referred Material: SEN 056.

Description: The specimen is a partial left prearticular preserving a coronoid process and part of the lower dentition. The teeth have the bluish-white preservation elsewhere described for *P. jonesae* (O'Leary et al., 2019). The medial toothrow preserves three mediolaterally wide teeth with concave wear facets. The first lateral toothrow preserves 10 teeth, all wider than long. The tooth crowns of the medial and first lateral rows are similar in size; however, they become smaller anteriorly. The next lateral row preserves three rounded, buttonlike teeth.

Discussion: Pycnodonts are an extinct clade of largely marine neopterygian fishes with deep, rounded bodies hypothesized to have inhabited ancient reefs and lagoons (Kriwet and Schmitz, 2005). They existed from the Late Triassic through the Eocene and are known for their characteristic durophagous dentitions, which are relatively common elements of shallow marine Cretaceous through Paleogene deposits in West Africa localities in Mali (Longbottom, 1984; Kriwet and Schmitz, 2005; O'Leary et al., 2019). The specimens recovered here represent only the second report of pycnodonts from Senegal (Capasso, 2019). These individuals would have inhabited a paleoenvironment closer to the open ocean than their relatives in the Trans-Saharan Seaway of Mali.

Pycnodontidae gen. et sp. indet.

Referred Material: SEN 076, 077, 081. These specimens are figured as 2D media on MorphoBank as follows, MorphoBank Project P4480: SEN 076 (M902030), SEN 077 (M902027, M902028), SEN 078 (M902029), SEN 081 (M901999).

Description: Isolated teeth.

Discussion: These specimens have similarities to other pycnodonts but are too fragmentary to assign to species (images of them have therefore been included only in the supplementary online material at MorphoBank P4480).

SILURIFORMES Cuvier, 1817

Siluriformes indet.

Figure 9I, J

Two specimens compare closely with spines of Siluriformes. SEN 093 (fig. 9I) is the base of a dorsal spine, characterized by a flared proximal end and a triangular cross section. SEN 096 (fig. 9J) is likely the middle portion of a pectoral spine, missing both the base and tip and subject to some crushing. It bears several triangular denticles along the presumed cranial border of the bone.

Osteichthyes indet.

Figure 9E–H, K–L

Referred Material: SEN 084, 085, 088, 097, 098, 101.

Description: Isolated sub-macroscopic osteichthyan elements and fragments, discovered as part of bioclastic matrix.

Discussion: SEN 088 (fig. 9E) is one of numerous fish vertebrae preserved in the sample. This element is just over 1 mm in diameter, and preserves the centrum, notochordal canal, the base of the neural arch, and a ventral rib.

In addition to fish vertebrae, there are several fragmentary elements that we refer to Osteichthyes based on their resemblance to fish cranial elements. SEN 085 (fig. 9F) is a flat, roughly square element, with oblique ridgelike processes extending from two corners. Two foramina enter the bone surface and communicate with an expanded chamber between bony laminae. This may represent a partial skull element or vertebra. SEN 101 (fig. 9G) is likely a partial parasphenoid, preserving part of the ventral keel and one anterolateral process. SEN 084 (fig. 9H) is an indeterminate bone fragment that may also be a fish cranial element.

We tentatively interpret two additional bones as otoliths. SEN 097 (fig. 9K) is tetrahedral overall, with a deep excavation between three of the vertices. A shallow groove runs along one side of the element. SEN 098 (fig. 9L) is rounded, with a groove that nearly encircles the entire element. On one side of this groove, the element is smooth and hemispherical. On the other side, an orthogonal sulcus and two shallower, oblique sulci separate the other half of the bone symmetrically into four tubercles.

CROCODYLIFORMES Hay, 1930, sensu Benton and Clark, 1988

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

DYROSAURIDAE de Stefano 1903

Gen. et sp. indet.

Figure 13

Referred Material: SEN 057 (M902033), base of tooth crown; SEN 059, proximal end of right metatarsal II; SEN 062, caudal vertebra with partial neural arch and right transverse process; SEN 062 and SEN 064, proximal caudal vertebrae; SEN 065, midcaudal vertebral centrum; SEN 067, tooth crown; SEN 068 (M902036), fragmentary tooth crown; SEN 069, proximal half of right metatarsal II; SEN 073, distal caudal vertebra; SEN 074 (M902040), fragmentary distal caudal vertebral centrum; SEN 079 (M902026), two fragmentary tooth crowns. Material that is figured only in the database MorphoBank have MorphoBank numbers in parentheses.

Description: The fragmentary crocodyliform material is tentatively referred to Dyrosauridae on the basis of vertebral morphology. The caudal vertebrae in the sample are ventrally concave in lateral view and nearly amphiplatyan, with only shallow median depressions on their cranial and caudal surfaces. This morphology closely resembles that described for hyposaurine dyrosaurids by Schwarz et al. (2006).

Five caudal vertebrae are preserved. SEN 062 is a large caudal centrum with an articulated neural arch and a nearly complete right transverse process (caudal rib). The cranial and caudal articular surfaces are very shallowly concave. The ventral surface of the vertebral body is gently concave in lateral view. The downcurved caudal border bears worn facets for the articulation of the hemal arch. Caudodorsally the neural arch is observed to articulate with the body along an undulating suture, indicating the closure if not complete fusion of the neural arch. In dorsal view the right transverse process curves caudally. The details described above are all consistent with an anterior (first through fourth) caudal vertebra of a hyposaurine dyrosaurid (Schwarz et al., 2006).

SEN 064 is another caudal vertebra, also likely from the anterior part of the series. It has a complete neural arch, articulating with the centrum along a very faint suture, and the stump of the broken right transverse process. Both the cranial and caudal faces of the centrum bear articular facets for the hemal arch. The ventral margin is strongly concave in lateral view. SEN

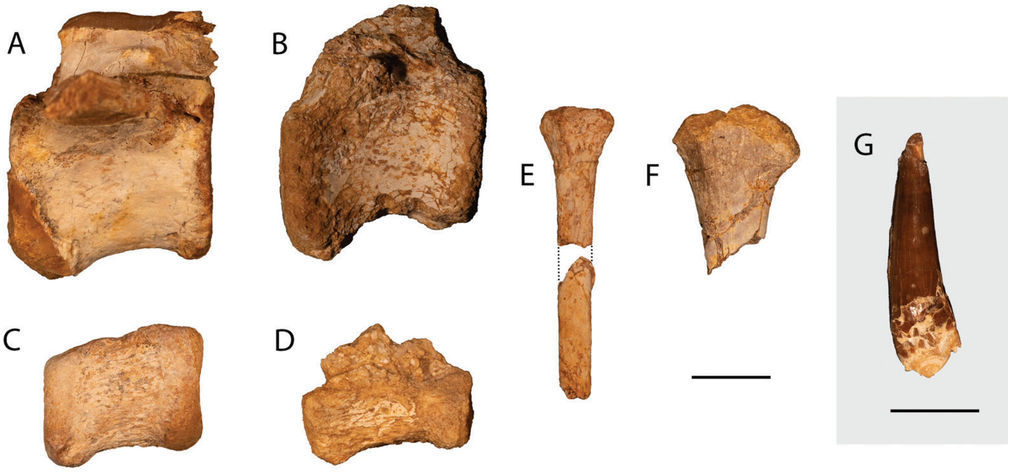

FIGURE 13. Late Maastrichtian dyrosaurid crocodyliforms of the Cap de Naze Formation discovered at the North Quarry of Poponguine. **A, B,** Caudal vertebrae (SEN 062 and 064) from proximal region of tail in right lateral view; **C,** caudal vertebra (SEN 065) from middle of tail in right lateral view; **D,** distal caudal vertebra (SEN 073) in right lateral view; **E,** proximal right metatarsal II (SEN 069) in dorsal view; **F,** proximal right metatarsal II (SEN 059) from a larger individual; and **G,** isolated tooth crown (SEN 067) in labial view. Scalebars: A–F = 2 cm; G =1 cm.

065 is a small, heavily weathered and preserves only the centrum. There is a strongly concave ventral margin in lateral view.

SEN 073 is a caudal centrum with a badly damaged neural arch. Unlike the caudal vertebrae described above, this one is more than twice as long as it is wide, indicating a position as the 14th caudal vertebra or very likely well beyond as it compares closely with the 31st caudal vertebra described by Schwarz et al. (2006). This vertebra has prominent articular surfaces for hemal arches both cranially and caudally. SEN 074 is an extremely weathered centrum that appears to bear a short hypapophysis.

Appendicular remains attributable to crocodyliformes include two proximal metatarsal fragments. Both represent the right metatarsal II, indicating the presence of more than one individual. The proximal articular surfaces possess the offset morphology that allows for imbrication of the metatarsals (Turner and Gatesy, 2021). The two bones are morphologically indistinguishable; however, SEN 059 is about twice the size of 069. Crocodyliform metatarsals are morphologically conservative (Turner and Gatesy, 2021); thus the presence of two similar bones differing only in size suggests either different species or different developmental stages, both plausible alternatives.

Broken tooth crowns (SEN 057 and 068) preserve only the base of the crown, and SEN 079 preserves only the apex. The most complete tooth is SEN 067, a nearly complete crown that compares closely with known dyrosaurid dentition. This tooth is long and slightly recurved, with a lentiform cross section. The subtle mesial and distal carinae are smooth, lacking any denticles.

Discussion: A relatively complete dyrosaurid specimen was collected by French geologists in the 1930s during geological exploration of western Senegal but only recently described in detail (Malavoy, 1935; Jacquet, 1936; Martin et al., 2019). The specimen was found in

Paleocene rocks of the Ndayane Formation in the vicinity of the Ndayane Cliff at Poponguine locality in our composite section (fig. 3) and assigned only to Dyrosauridae for lack of diagnostic skull material (Martin et al., 2019). Our new records from the North Quarry at Poponguine are Late Cretaceous and thus the oldest dyrosaurids known from Senegal. Dyrosaurids, which are common fossils in nearshore marine outcrops of West Africa, are hypothesized to be of African origin and to have dispersed to South America in the Late Cretaceous (Hastings et al., 2011). This new and relatively ancient specimen from Senegal was present at one of the most westerly parts of the African continent and thus well situated to have been part of a larger trans-Atlantic dispersal.

Testudines Linnaeus, 1758

Pleurodira Cope, 1864

Pelomedusoides Cope, 1868

Figure 14

Referred Material: SEN 054, partial shell preserving left epiplastron, hyoplastron, and axillary buttress (bridge), and peripheral carapace fragment; SEN 055 (M902031) and SEN 066 (M900945, M900946), fragmentary plastral elements; SEN 080, partial neural bone. Material that is figured only in the database MorphoBank have MorphoBank numbers in parentheses.

Description: SEN 054 preserves most of the left anterior portion of the plastron. The epiplastron is broken medially, but its suture with the hyoplastron is clearly discerned. A sliver of the entoplastron is preserved, demonstrating a curved caudolateral border. The epiplastron-hypoplastron suture meets the entoplastron far caudally, in contrast to most fossil Pelomedusoides described by Gaffney et al. (2006). The bone surface is too weathered to discern any scale sulci. The carapace fragments include a peripheral element likely from near the cranial end. The margin of the shell is thickened and upturned. The suture with the adjacent costal bone is preserved. A partial neural is preserved, recognized by the incorporated vertebral arch in internal (ventral) view. It is unclear whether this bone was pentagonal or hexagonal as well as from where in the shell it originated.

Discussion: Most West African pelomedusoids from the Late Maastrichtian–Early Paleogene have been assigned to Taphrosphyini, however, this new Maastrichtian specimen is too fragmentary for such refined assignment. The specimen is nonetheless significant because Pelomedusoides from the Maastrichtian are relatively rare compared with those from the Paleogene and it remains an open question whether the clade underwent a post-Cretaceous-Paleogene boundary radiation or if this pattern is a preservational artifact.

DISCUSSION

We report a new, Late Maastrichtian vertebrate fossil-producing locality from western Senegal, the North Quarry of Poponguine, and tie it to a composite Cretaceous through Paleogene

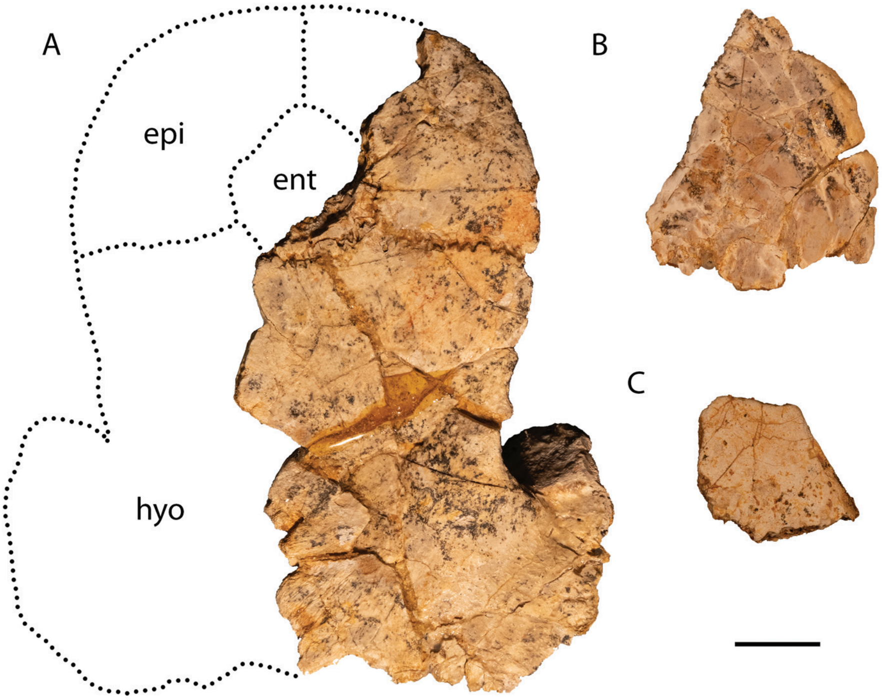

FIGURE 14. Late Maastrichtian Testudines from the Upper Cap de Naze Formation of the North Quarry of Poponguine. **A,** Partial plastron in ventral view (SEN 054). Dotted lines mirrored to show extent of preservation. **B,** Peripheral carapace fragment in dorsal view (SEN 054). **C,** Partial neural bone in dorsal view (SEN 080). Abbreviations: **ent,** entoplastron; **epi,** epiplastron; **hyo,** hyoplastron. Scale = 2 cm.

section together with three other nearshore marine fossiliferous localities. The North Quarry of Poponguine is situated relatively inland from the other three localities, and with the exception of the locality Cap de Naze Cliff, three of the localities in our composite are of relatively limited exposure. The North Quarry of Poponguine has yielded new macrofossils including gastropods, Osteichthyes, dyrosaurid archosaurs, testudines, and vertebrate coprolites, as well as a microfossil fauna of Osteichthyes, Chondrichthyes, vertebrate coprolites, and fragmentary invertebrates.

The Paleogene rocks of these localities are currently dated by biostratigraphy of Foraminifera and Ostracoda that suggests that rocks of the middle to late Danian are preserved in at least two places: the North Quarry of Poponguine and the Ndayane Cliff at Poponguine. This discovery is noteworthy considering Solé et al. (2019), in a recent comprehensive study of Paleogene marine margin sediments of sub-Saharan Africa, stressed that Danian age rocks are not preserved in the Landana section of Angola and tend to be rare in West Africa in general. In Senegal, Danian rocks have yielded rare fossil vertebrates (dyrosaurs), in particular at the Ndayane Cliff at Poponguine. These vertebrates may ultimately form an important point of comparison with Late Maastrichtian vertebrates of the nearby North Quarry of Poponguine following more systematic collecting. The fossils presented here represent the findings of a short reconnaissance mission; more systematic collecting has the potential to assess the density and diversity of fossils in the quarry. Further work, including systematic collecting at each locality, study of the latest Maastrichtian layer of the Cap de Naze Formation, application of more diverse chronostratigraphic methods for the dating of the rocks, and detailed stratigraphic work to standardize the units among localities will be important for better understanding of the fossil discoveries.

ACKNOWLEDGMENTS

For assistance in the field we thank A. Diakite, C. Lepre, R. Malou, M. Sanogo, and E-H. Sow. V. Heisey prepared the fossils and V. Mendizábal photographed them. For helpful discussions and assistance with photography we thank J.B. Bennington and W. Hart. The field expedition was supported by the National Geographic Society and the National Science Foundation. K. Hurdle of the NYIT Visualization Center provided micro-CT scanning services supported on NSF grant 1828305 to the NYIT College of Osteopathic Medicine. We thank two anonymous reviewers and the journal editors for improving an earlier version of this manuscript.

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