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The youngest record of metriorhynchid crocodylomorphs, with implications for the extinction of *Thalattosuchia*

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RUNNING HEAD: Youngest evidence of metriorhynchid crocodylomorphs

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ABSTRACT. Here we describe an isolated tooth of a metriorhynchid crocodylomorph from the Hybla Formation (Aptian, Lower Cretaceous) of Rocca Chi Parra quarry (Montagna Grande, Calatafimi, Trapani Province), Sicily, Italy. The specimen shares with the Upper Jurassic taxon *Plesiosuchus manselii* a mediolaterally compressed conical tooth crown, noticeable lingual curvature, mesial and distal carinae with microscopic, rectangular contiguous denticles, strong distal curvature of the mesial margin, and the presence of weak 'carinal flanges' on the labial and lingual surfaces (which are preeminent at the mid-crown). This suite of morphologies is also present in an unnamed Valanginian (Lower Cretaceous) plesiosuchinan from France. However, the Sicilian tooth differs from these taxa in having more pronounced carinae, and faint apicobasally aligned enamel ridges. It also differs from *P. manselii* in having more extensive 'carinal flanges' on the labial surface. The specimen extends the known geological range of Metriorhynchidae and Thalattosuchia by approximately 7-8 million years. This overturns previous hypotheses of Metriorhynchidae becoming extinct early in the Early Cretaceous.

Key words: Aptian – Cretaceous – Plesiosuchina – Sicily – Hybla Formation.

INSTITUTIONAL ABBREVIATIONS

BRSMG, Bristol City Museum and Art Gallery, Bristol, England, United Kingdom;

JJCC, Jean-Jacques Cornée personal collection, Fontvieille, France;

MJML, Museum Jurassic Marine Life, Kimmeridge, England, United Kingdom;

MSNC, Museo di Storia Naturale di Comiso (Comiso Natural History Museum), Comiso, Italy.

NHMUK, Natural History Museum, London, England, United Kingdom.

SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

1. INTRODUCTION

Metriorhynchids were a highly successful group of crocodylomorphs that returned to a marine lifestyle during the Mesozoic. This clade evolved extensive osteological and soft tissue adaptations to a marine existence, including hydrofoil-like forelimbs, a hypocercal caudal vertebral column, loss of osteoderms and enlarged salt glands with a neomorphic opening for excess salt excretion (Fraas, 1902; Andrews, 1913; Fernández and Gasparini 2000, 2008; Gandola et al. 2006; Fernández and Herrera, 2009; Young et al. 2010; Leardi et al. 2012). During the Jurassic and Lower Cretaceous, metriorhynchids were exceptionally diverse in lagoonal, coastal and open-shelf ecosystems (e.g. Eudes-Deslongchamps, 1863–1869; Fraas, 1902; Andrews, 1913; Gasparini et al. 2006; Lepage et al. 2008; Pierce et al. 2009; Pol and Gasparini, 2009; Young et al. 2010, 2011, 2012, 2013a, 2014a; Cau and Fanti, 2011; Foffa and Young, 2014; Herrera et al. 2015). When and how this peculiar group of oceanic crocodylomorphs became extinct is still controversial (Young et al. 2010).

Two studies postulated distinct two-phase extinction hypotheses for Metriorhynchidae (Steel, 1973; Young et al. 2010). Steel (1973) suggested that the radiation of teleosts during the Early Cretaceous may have detrimentally affected both metriorhynchids and ichthyosaurs, with the evolution of mosasaurids being (Steel, 1973:41): "an influential factor in precipitating the extinction of the metriorhynchids and ichthyosaurs". At present, there is no evidence to suggest metriorhynchids and mosasaurids co-occurred. Young et al. (2010) suggested that the regional marine regressions at the Jurassic-Cretaceous Boundary resulted in a biodiversity crash for Metriorhynchidae (as did Pierce et al. 2009), while the combination of rapid climate change (formation of polar ice-caps and lowering of sea surface temperatures) and the resultant marine biota distribution shifts at, and across, this boundary killed off an already stressed clade. The two-phase hypothesis of Young et al. (2010) was recently refuted with the re-description of a poorly known lower jaw of a *Plesiosuchus*-like

taxon from the Valanginian of France (Young et al. 2014a). It demonstrated that at least four lineages of metriorhynchid crossed the Jurassic-Cretaceous Boundary in the Sub-Boreal realm of Europe, thus the regional marine regression at the Jurassic-Cretaceous Boundary did not result in an extinction event for the European metriorhynchids.

Here we provide evidence that refutes the second phase of the two-phase extinction hypothesis postulated by Young et al. (2010). We describe a long known, but little studied, specimen from the Hybla Formation (Lower Cretaceous, Upper Hauterivian-Albian, Rio and Sprovieri, 1986; Martire and Pavia, 2004) of Sicily, Italy. Although an isolated tooth crown is not enough to establish a new taxon, the specimen is of critical importance due to its unusual morphology and geological age. The dental morphology indicates a close relationship to the Kimmeridgian-Tithonian taxon *Plesiosuchus manselii*. This tooth crown suggests the presence of an unknown *Plesiosuchus*-like metriorhynchid in the Tethys Sea during the Aptian (Lower Cretaceous). Thus, at least one lineage of metriorhynchid survived the Valanginian-Hauterivian Boundary event and continued into the Aptian.

2. MATERIAL AND METHODS

MSNC 4475, an isolated tooth crown still partially embedded in matrix found in Rocca Chi Parra quarry, Montagna Grande area, Hybla Formation (Upper Hauterivian-Albian, Calatafimi, Trapani), Sicily, Italy. MSNC 4475 was found by a private collector (Giacomo Sicali) at Rocca Chi Parra, Montagna Grande (Trapani Province, Sicily; Fig. 1) and was donated to the Natural History Museum in Comiso (Ragusa, Sicily), for which Gianni Insacco is the scientific curator. Photographs were taken with a Panasonic Lumix DMC-TZ35EB-K Compact Camera with a 16.1 MP 20x Optical Macro lens Zoom Leica DC 24mm Wide Angle. SEM images were taken with a Tescan Vega II Lum (active area 10 mm²) and processed with a Vega TC software.

3. RESULTS

3.1. *SYSTEMATIC PALAEOLOGY*

CROCODYLOMORPHA HAY, 1930 (*SENSU* WALKER, 1970)

THALATTOSUCHIA FRAAS, 1901 (*SENSU* YOUNG AND ANDRADE, 2009)

METRIORHYNCHIDAE FITZINGER, 1843 (*SENSU* YOUNG AND ANDRADE, 2009)

GEOSAURINAE LYDEKKER, 1889 (*SENSU* YOUNG AND ANDRADE, 2009)

GEOSAURINI LYDEKKER, 1889 (*SENSU* CAU AND FANTI, 2011)

PLESIOSUCHINA YOUNG *ET AL.* 2014A

cf. PLESIOSUCHINA

3.2. *Specimen*

MSNC 4475 (Fig. 2), an isolated tooth crown.

3.3. *Locality*

Rocca Chi Parra quarry, Montagna Grande area, Hybla Formation (Upper Hauterivian-Albian, Calatafimi, Trapani), Sicily, Italy.

3.4. *Horizon and age*

MSNC 4475 is partially embedded in matrix (Fig. 2A), thus it was possible to perform thin section analysis of the rock sample by preparing a piece of the matrix as smear slide (Bown and Young, 1998) for the study of calcareous nannofossils. The recovered nannofossil assemblage allowed the identification of a precise biostratigraphic horizon inside the Hybla

Formation (Fig. 1C). The identified horizon is the Aptian NC6 Zone of Roth (1978), this is based on the presence of *Assipetra infracretacea* (Thierstein, 1973), *Assipetra infracretacea larsonii* (Tremolada and Erba, 2002), *Rucinolithus terebrodentarius* (Applegate et al. 1987; Tremolada and Erba, 2002), *Rucinolithus terebrodentarius youngii* (Tremolada and Erba, 2002), *Nannoconus steinmanni steinmanni* (Kamptner, 1931), *Nannoconus steinmanni minor* (*Nannoconus truittii*, Brönn, 1955), *Nannoconus* sp. (Kamptner, 1931), *Helenea chiastia* (Worsley, 1971), *Cyclagelosphaera margerelii* (Noël, 1965), *Zeughrabdotus embergeri* (Noël, 1958) and *Watznaueria* spp. (Reinhardt, 1964). In addition, the lack of *Eprolithus floralis* (Stradner, 1962; Stover, 1966), fossil markers of the NC7 Zone, strongly constrains the fossil to the lowermost Aptian within the NC6 Zone.

4. DESCRIPTION

The morphology of MSNC 4475 (Fig. 2) is similar to the dental morphology of *Plesiosuchus manselii* (Hulke 1869, 1870; Young et al. 2012) and *Plesiosuchina* indeterminate (Young et al. 2014a). The crown is 20 mm long apicobasally and its base is 13 mm wide mesiodistally and 9 mm labiolingually. The crown lacks the apical-most part of the apex. The tooth has a caniniform morphology, is labiolingually compressed, and slightly lingually curved in the middle section.

The basal section of the crown is wider mesiodistally, creating a sub-circular to slightly ovoid cross-section (Fig. 2F). Overall, the tooth crown is robust (i.e. retaining its labiolingual width along most of its apicobasal length). No constriction is present at the crown-root junction, but the boundary is evident through colour and texture changes. The tooth is broken below the crown-root junction.

The labial and lingual surfaces of the crown have superficial enamel ridges that are apicobasally aligned (Fig. 3A-D). However, these are of very low relief and require optical

aids to be seen. The lingual surface has more of the ridges, and they are more prominent ~~that~~ than those of the labial surface. This differs from the teeth of *Geosaurus* and *Dakosaurus maximus* (Andrade et al. 2010) and *D. andiniensis* (Pol and Gasparini, 2009), which lack apicobasal ridges. It also differs the tooth from the dentition of *Torvoneustes*, which are heavily ornamented with numerous apicobasal ridges in the basal and mid-regions and an anastomosed pattern in the apical region (Andrade et al. 2010; Young et al. 2013a, 2013b).

The carinae are formed by a carinal keel (raised ridge) and true denticles (Fig. 3B-C). The carinae are enlarged in MSNC 4475 (but not as pronounced as in *Dakosaurus* teeth, see Pol and Gasparini, 2009; Young et al. 2012, in press) as the external surface of the tooth crown becomes concave immediately adjacent to the carinae (Fig. 3A). In most other metriorhynchids the external surfaces of the tooth crowns are still convex/straight when they approach the carinae (*Metriorhynchus superciliosus*, *Gracilineustes leedsi*, *Geosaurus* sp. and *G. grandis*, *Torvoneustes carpenteri* and *T. coryphaeus*; Andrade et al. 2010; Young et al. 2012, 2013b, Young et al. in press). In *Plesiosuchus manselii* (Young et al. 2012) and Plesiosuchina indeterminate (Young et al. 2014a) the carinal concavities are much more subtle. In these taxa, the carinal concavities are better, or only seen, on the lingual surface, and are only present in the mid-crown region (the lingual surface being convex at the base and apex).

The only macroscopic wear visible is the broken apex (Fig. 1), although SEM images show an irregularly fractured surface of the enamel, probably for diagenetic reasons.

5. DISCUSSION

5.1. *Metriorhynchid* affinities of MSNC 4475

The conical shape of the tooth crown, noticeable lingual curvature, presence of mesial and distal carinae, and microscopic denticles along the carinae, readily identifies the tooth as a

geosaurine metriorhynchid (e.g. Andrade et al. 2010; Young et al. 2012, 2013a, in press; Foffa and Young, 2014). Within Geosaurinae (Fig. 4), the rectangular shape of the denticles, the strong distal curvature of the mesial margin, and the presence of weak 'carinal flanges' that are preeminent at the mid-crown, place MSNC 4475 in Plesiosuchina (Young et al. 2014a, in press). Denticles appear as a contiguous series of homogeneous and distinct serrations along both mesial and distal carinae, a trait only found in the geosaurine genera *Plesiosuchus* and *Dakosaurus* (e.g. Pol and Gasparini, 2009; Andrade et al. 2010; Young et al. 2012). The denticles of *Geosaurus*, although forming a mostly contiguous series, can form double-denticles and the interdenticular spacing can vary considerably (Andrade et al. 2010). In *Torvoneustes*, the denticles can be hard to discern due to the superficial enamel ornamentation contacting the carinae (Andrade et al. 2010; Young et al. 2013a).

Within Plesiosuchina, MSNC 4475 differs from *Plesiosuchus manselii* in that the tooth has: 1) 'carinal flanges' on the labial surface, and that they extend further apically; 2) the apicobasal enamel ridges can only be reliably observed using optical aids, whereas *P. manselii* has more numerous but low-relief enamel ridges; and 3) the more pronounced carinae (Young et al. 2012, in press). MSNC 4475 differs from the Valanginian plesiosuchinan from France by 1) the having apicobasal enamel ridges only reliably observable using optical aids (these ridges are more numerous and are pronounced in the French specimen), and 2) by having more pronounced carinae (Young et al. 2014a). Unfortunately the dentition of the Valanginian plesiosuchinan from France (Fig. 4B-C) is poorly preserved, with every tooth crown being either incomplete or broken (Young et al. 2014a), thereby hindering detailed comparison. Compared to other plesiosuchinans, MSNC 4475 has more pronounced carinae (especially along the labial surface), due to the more strongly concave surfaces immediately adjacent to the carinae.

5.2. Comparison to other vertebrate taxa

While MSNC 4475 can be referred to Geosaurinae, based on morphological evidence, it is important to exclude the possibility that it may pertain to another clade more commonly found in Early Cretaceous strata. Any attribution to a fish taxon can be excluded based on the overall morphology of the specimen, which is conical in shape, and has two cutting edges (carinae) bearing serrations. Among the Cretaceous fish taxa that are characterised by large teeth, there are at least four lineages with dentition that is some ways reminiscent to MSNC 4475, including pachycormiforms, ichthyodectiforms, pachyrhizodontids and aulopiforms.

The species of the pachycormiform genus *Protosphyraena* have large teeth that clearly differ from the tooth described herein, in being laterally compressed and without serrations along the carinae (see Friedman, 2012). Several ichthyodectiforms taxa also have large jaw tooth crowns, which were usually conical, and always without serrations (e.g. Bardack, 1965; Patterson and Rosen, 1977). As far as the pachyrhizodontids are concerned, some species of the genus *Pachyrhizodus* are characterised by strong conical teeth that, in some cases, have been erroneously referred to mosasaurids (Stewart and Bell, 1994). However, *Pachyrhizodus* teeth are subcircular in cross section, lack carinae and are also characterised by the presence of thick swollen bony collars around their base (Friedman, 2012). Moreover, the teeth of some *Pachyrhizodus* species have a posteriorly recurved apex (see Forey, 1977). Finally, the aulopiform genus *Apateodus* also was characterised by robust jaw and pterygoid teeth similar in size to the Rocca Chi Parra quarry tooth (see Goody, 1969); the *Apateodus* teeth also bear serrations along the carinae but clearly differ from MSNC 4475 in being remarkably laterally compressed (Friedman, 2012).

Among tetrapods, an assignment to Ichthyosauria can be ruled out. Ichthyosaurian teeth are usually conical and devoid of serrations, with the rare exception of macrophagous Lower Jurassic taxa like *Temnodontosaurus* and *Suevoleviathan* (McGowan and Motani,

2003). However, their teeth show moderate labiolingual compression, although not to the extent seen in archosaurs. While serrations have been reported in *Temnodontosaurus* (Conybeare, 1822, Lydekker, 1889; McGowan, 1994), their height to mesiodistal length ratio does not match that of MSNC 4475. Even though ichthyosaurian teeth may vary widely according to their different feeding specializations, they usually share a peculiar external ornamentation of the enamel, characterized by apicobasal ridging interspaced with furrows, coated in enamel, a dental feature called plicidentine, considered synapomorphic for Ichthyosauria (Maxwell et al. 2011b). The Lower Cretaceous Ophthalmosauridae (such as the Aptian *Platypterygius australis* Zammit et al. 2010 and *Platypterygius hercynicus* Fischer, 2012), also have this coarse ornamentation, textured by numerous longitudinal ridges (Maxwell et al. 2011a; Fischer, 2012; Fischer et al. 2012). No such heavy ornamentation is present in MSNC 4475, which shows an almost completely smooth external surface of the enamel.

The attribution to Sauropterygia can also be excluded. While, at first sight, MSNC 4475 may resemble a plesiosaurian tooth, no known plesiosaurian taxon has dentition with the combination of features seen in MSNC 4475. Among plesiosaurians, the single pliosaurid clade that survived in the Cretaceous (Benson and Druckenmiller, 2013) – Brachaucheninae – shows considerably large, conical teeth, strongly ornamented and lacking carinae (Schumacher et al. 2013). Furthermore, the only pliosaurid taxon bearing weakly convex labial sides on teeth is *Pliosaurus* (which became extinct by the end of Jurassic; Benson et al. 2013). However, *Pliosaurus* teeth are also strongly ornamented, with coarse widely spaced striations extend to the apex, lack carinae and carinal flanges, and are not mediolaterally compressed (Welles and Slaughter, 1963; Cruickshank, 1997; Kear and Barrett, 2011; Benson et al. 2013). Among plesiosauroids, only two lineages survived the Jurassic-Cretaceous boundary: Cryptoclididae and Xenopsaria (the latter including Elasmosauridae

and Leptocleidia; Benson and Druckenmiller, 2013). Plesiosauroid teeth are considerably slender, with a high crown high-length ratio, are more conical and rounded in cross section, strongly curved in labiolingual view, uncarinated and normally ornamented with numerous parallel – sometimes branching or inclined – apicobasally oriented ridges (O'Keefe, 2008; Schumacher et al. 2013; Hampe, 2013). Thus, we can exclude a plesiosaurian origin for MSNC 4475.

Mosasauroid affinities can also be excluded for both biostratigraphical (no mosasauroids are reported prior to the Cenomanian; Dutchak and Caldwell, 2009) and morphological reasons. First of all, mosasauroid teeth are characterized by a distinct 'collar' near the root-crown junction, absent in MSNC 4475. Denticulated mosasauroid teeth are more mediolaterally compressed and mesiodistally wider at their base (Polcyn et al. 1999) than MSNC 4475. Although derived mosasaurine teeth are usually reported as “serrated”, these teeth are better described as bearing carinae with transverse ribs on them, resulting in “serrated cutting edges” (Massare, 1987) that differs from “true” serration (i.e. presence of distinct denticles). This “pseudo-serrated” pattern (*sensu* Andrade et al. 2010: conspicuous ornamentation on the carinae but absence of distinct denticles) is also confirmed by SEM analysis (e.g. Fanti et al. 2014). Furthermore, when apicobasal ridges are present in mosasauroid teeth, they are more distinct than in the Sicilian specimen (Ishikawa et al. 1997; Sakurai et al. 1999; Caldwell, 2007).

Other than crocodylomorphs, predatory dinosaurs are the other Cretaceous archosaur clade which have ziphodont teeth. Amongst most theropods the crown curvature (along the mesiodistal axis) of lateral teeth (i.e. maxillary and non-symphyseal dentary teeth) is more marked than in MSNC 4475 (e.g. Madsen, 1976; Currie, 1995). Lateral teeth of spinosaurines and some maniraptoriforms show the apex placed perpendicularly to the basal plane of the crown (Sues et al. 2002; Zanno and Makovicky, 2011), comparable to this tooth. However,

these theropod taxa lack serrations on at least the mesial carina, if not on both carinae, and bear less labiolingually compressed crowns. Although the presence of an apicobasally oriented concave area adjacent to the mesial carina is shared by some averostran theropods (e.g. Abelisauridae, see Smith, 2007), the overall morphology of the specimen – in particular in serration shape – differs substantially with any of these groups. Therefore, a referral of the specimen to a lateral tooth of a theropod is dismissed.

Rostral teeth (i.e. premaxillary and symphyseal dentary teeth) of many theropods show a degree of basiapical curvature of the crown comparable to our specimen (see Hendrickx and Mateus, 2014). The presence of a serrated mesial carina dismisses the referral to Spinosaurinae, compsognathid-grade basal coelurosaurs, most maniraptorans, coelophysoids and some ceratosaurians (Sues et al. 2002; Hendrickx and Mateus, 2014). The lanceolate, symmetrical outline of the crown in apical view, with the carinae aligned along the mesiodistal axis of the crown, markedly differs from most averostran theropods, the latter bearing asymmetrical outline of the crown cross section, usually due to lingual migration of the carinae (Smith, 2007; Hendrickx and Mateus, 2014). In Baryonychinae, the teeth show finely serrated carinae that roughly recall the condition in the Sicilian specimen. Nevertheless, our specimen differs from baryonychines (and most spinosaurids) in lacking the anastomosing pattern of deeply veined enamel ornamentation that curves basally close to the carinae (Charig and Milner, 1997; Sereno et al. 1996). Furthermore, spinosaurid (including baryonychine) crowns are usually ornamented by distinct flutes oriented apicobasally (Charig and Milner, 1997; Sues et al. 2002), which are absent in the MSNC 4475. Therefore, since no theropod taxon fits with the combination of features present in this specimen, any referral to a subclade of Theropoda is considered as unlikely.

In conclusion, we can preclude MSNC 4475 from pertaining to any of the above-mentioned groups (other than Plesiosuchina). Among Early Cretaceous taxa, the tooth crown

suite of morphologies only matches Plesiosuchina, a subclade of geosaurine metriorhynchids (Young et al. 2014a). The presence of Plesiosuchina in the lowermost Aptian of Sicily (Fig. 1C) has some intriguing palaeobiogeographic and macroevolutionary implications for metriorhynchids.

5.3. CRETACEOUS METRIORHYNCHIDS

It is clear that the fossil record of Metriorhynchidae in the Cretaceous is exceptionally poorly known. Previous generalisations, like metriorhynchids in the Cretaceous being a “dead clade walking”, were premature (see Young et al. 2010). There is now no evidence that metriorhynchids were affected by an extinction at the Jurassic-Cretaceous (*contra* Pierce et al. 2009; Young et al. 2010), in contrast to the other thalattosuchian clade, Teleosauridae, which seemingly went extinct at this boundary (Young et al. 2014a, 2014b). At least four metriorhynchid lineages are known to have crossed the Jurassic-Cretaceous boundary: *Cricosaurus*, *Dakosaurus*, *Geosaurus* and Plesiosuchina (Young et al. 2014a).

While much of the metriorhynchid Cretaceous fossil record is fragmentary, there are three (possibly four) time-spans that reveal information on their diversity and evolution. From the upper Tithonian-lower Berriasian levels of the Vaca Muerta Formation of Argentina, *Cricosaurus* sp., *Dakosaurus andiniensis* and *Purranisaurus potens* are known (Gasparini et al. 2006; Pol and Gasparini, 2009; Herrera et al. 2015). The Valanginian-earliest Hauterivian is the best-known Cretaceous time-span for metriorhynchids. In France and Germany, *Geosaurus lapparenti*, *Cricosaurus macrospondylus*, *C. schroederi*, the *nomen dubium* *Neustosaurus gigondarum*, and an indeterminate Plesiosuchina are known (Raspail, 1842; Koken, 1883; Debelmas, 1952, 1958; Debelmas and Demians D'Archimbaud, 1956; Debelmas and Strannoloubsky, 1956; Hua et al. 2000; Karl et al. 2006; Young et al. 2014a); while cf. *Cricosaurus* is known from Colombia (Larsson et al. 2012). From the Barremian of

Spain there is a poorly preserved skull, which may pertain to a metriorhynchid, or possibly another marine crocodylomorph clade (see Parrilla-Bel et al. 2012). Here, we add an indeterminate specimen from the lowermost Aptian of Sicily.

In the Valanginian, we find the first unambiguous morphological evidence of mesopelagic metriorhynchids. These include: *Cricosaurus macrospondylus* with a divided external ~~naris~~ naris which was significantly posterodorsally retracted (Hua et al. 2000); *Cricosaurus schroederi* with very large orbits which had very large and robust sclerotic rings (see Karl et al. 2006); and *Neustosaurus gigondarum* which had almost half of the total number of caudal vertebrae contributing to the tail fluke (Raspail, 1842). It has been suggested that these taxa represent sustained and/or mesopelagic swimmers (Hua et al. 2010; Young et al. 2010). This shows that Cretaceous metriorhynchids were still diversifying, and exploiting new niches.

This high diversity of metriorhynchids in the Early Cretaceous, and the high number of lineages which passed through the Jurassic-Cretaceous boundary, is mirrored by ichthyosaurs. Recent studies have shown that not only did multiple (possibly as many as eight) ophthalmosaurid lineages and at least one basal thunnosaurian lineage cross the Jurassic-Cretaceous boundary, but the Early Cretaceous taxonomic and morphofunctional diversity of ichthyosaurs remained high, even up to the late Albian (e.g. see Fischer *et al.* 2011, 2012, 2013, 2014). As more long-held museum specimens are re-described and studied, as it is the case with MSNC 4475, it is looking increasingly that the same is true for metriorhynchids.

6. CONCLUSIONS

Here we describe an indeterminate metriorhynchid crocodylomorph specimen (an isolated tooth crown) from the Hybla Formation near Calatafimi (Trapani province), Sicily. We show

that the combination of ornamentation, carinae and denticle morphologies is incompatible with any large fish, plesiosaur, mosasauroid, ichthyosaur or theropod taxon. The tooth crown (MSNC 4475), is characteristic of a derived geosaurine metriorhynchid, specifically a *Plesiosuchus*-like taxon of the subclade Plesiosuchina – a subclade already known from Early Cretaceous strata. As this fossil is Aptian in age, it extends the known geological range of Metriorhynchidae (and Thalattosuchia) by approximately 7-8 million years. The presence of a *Plesiosuchus*-like taxon in the Aptian means that the two-phase extinction hypothesis of Young et al. (2010) that metriorhynchids became extinct at, or just after, the Valanginian-Hauterivian Boundary must be discarded. However, it is possible that the Valanginian-Hauterivian Boundary event resulted in the extinction of the European Sub-Boreal metriorhynchids, or forced a range shift towards the warmer environments nearer the equator. Alternatively, as suggested by the presence of geosaurines in the Rosso Ammonitico Veronese Formation (Northern Italy) since the earliest phase of metriorhynchid evolution (i.e. *Neptunidraco*, Cau and Fanti, 2010; Cau, 2014), this clade permanently inhabited the Western Tethys for the large majority of its history. These questions will only be answered by new discoveries from Europe and North Africa, and equatorial deposits. Moreover, indeterminate specimens from the Hauterivian and Aptian stages will also need to be examined with a critical appraisal.

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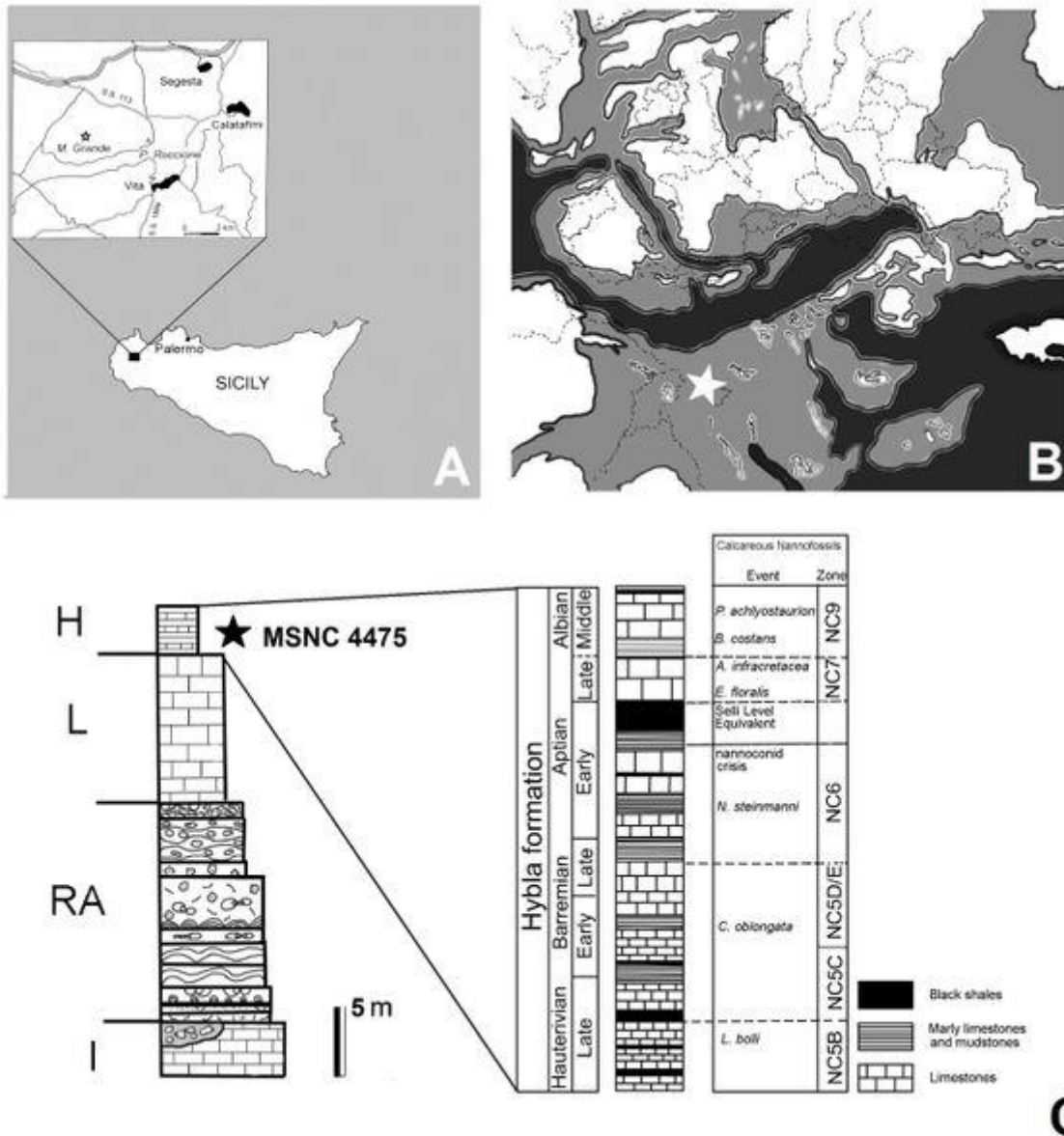


Figure 1: Geographical and geological context of MSNC 4475; A, close-up map of the locality where MSNC 4475 was found (modified from Martire and Pavia, 2004); B, Aptian palaeogeography of the Mediterranean Tethys showing the hypothesized location of MSNC 4475 (modified from Ron Blakey, Colorado Plateau Geosystems); C, stratigraphic column showing the position of MSNC 4475 among the Hybla formation (modified from Roth, 1978 and Pavia et al. 2002). Abbreviations: H: Hybla formation; I: Inici formation; L: Lattimusa formation; RA: Rosso Ammonitico formation.

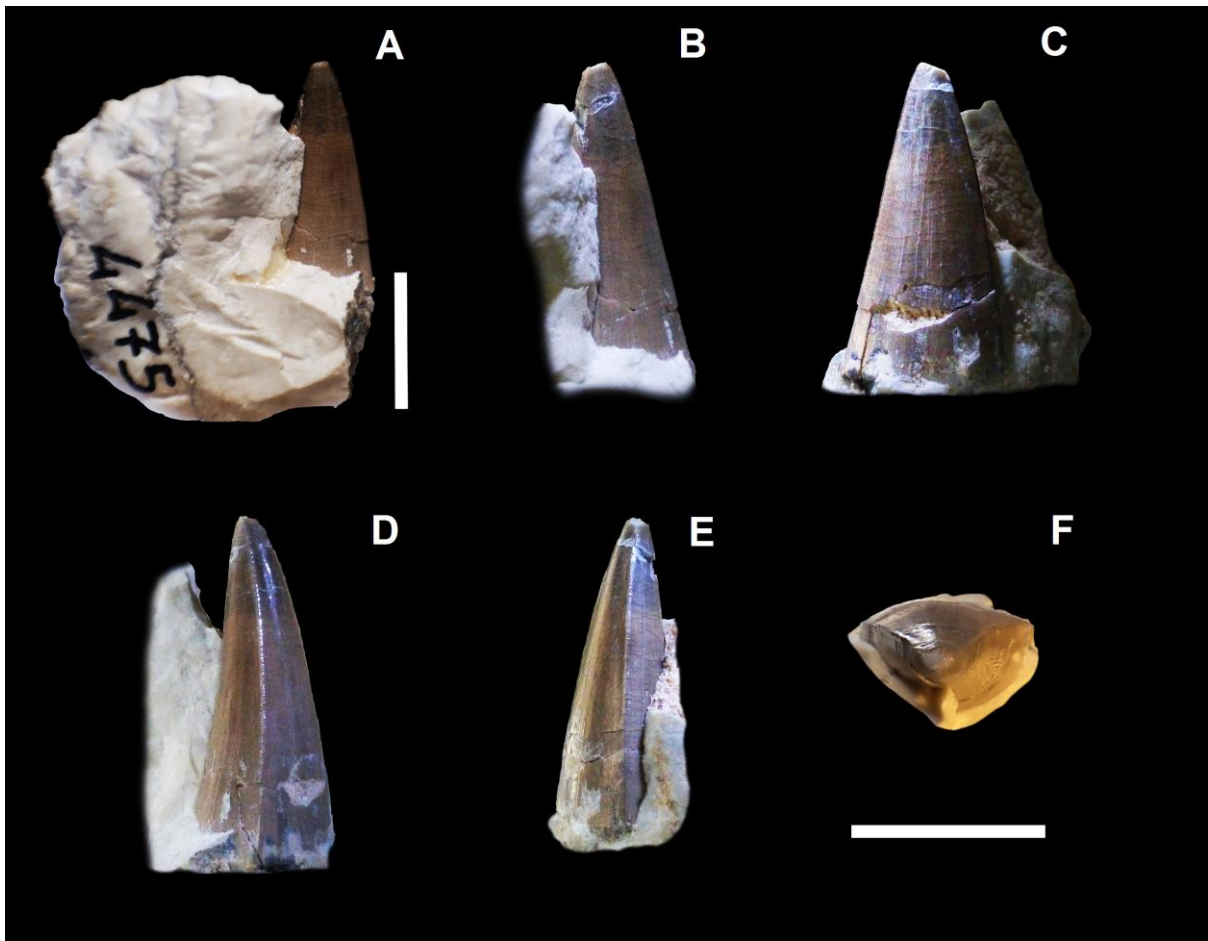


Figure 2: MSNC 4475, cf. *Plesiosuchina*; A, MSNC 4475; B, lingual view; C, labial view; D, distal-carinal view; E, mesial-carinal view; F, apical view; Scale bar: 1 cm.

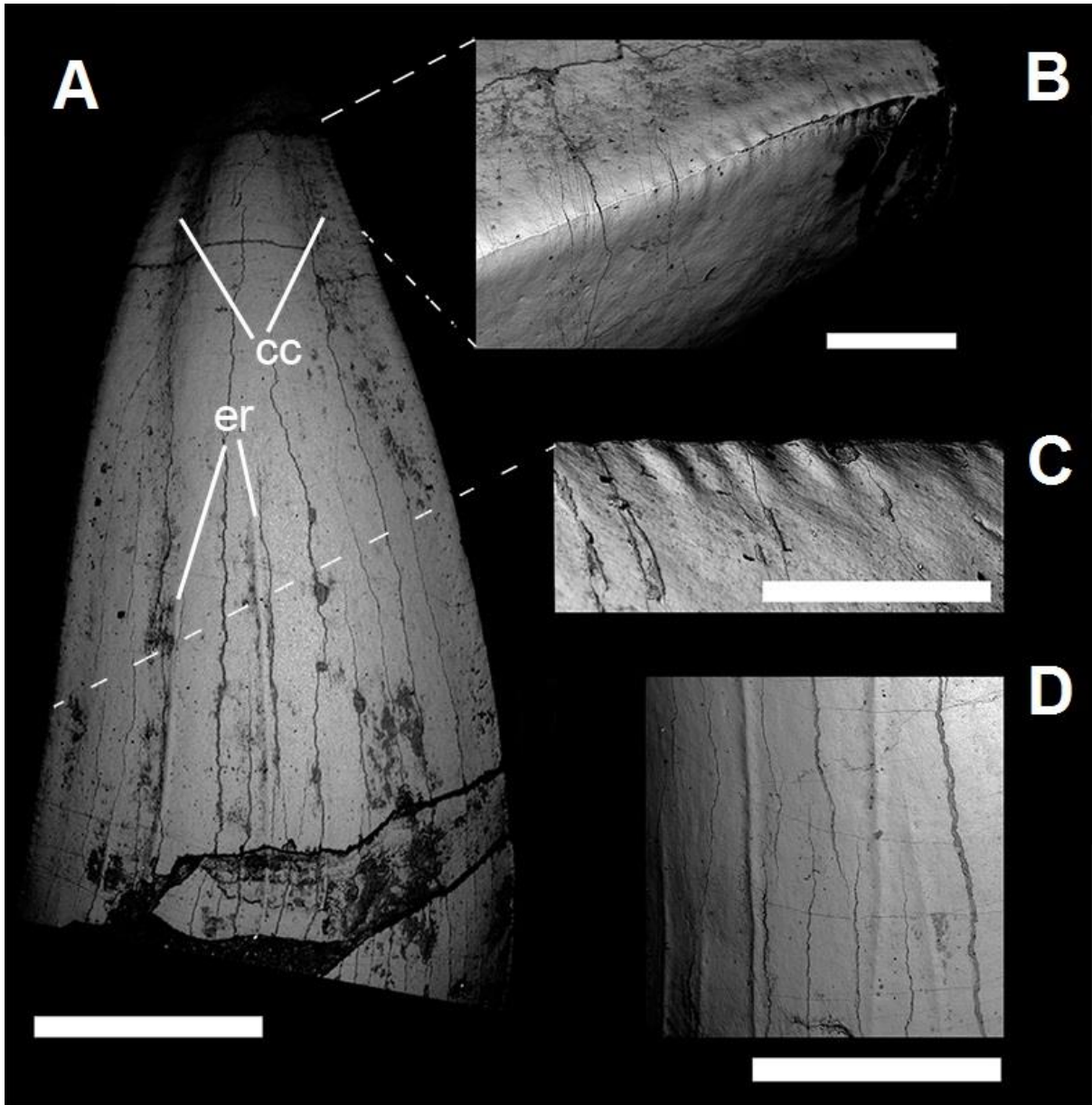


Figure 3: SEM images of MSNC 4475; A, details from the labial surface of the crown showing concavities adjacent to the carinae and surface ornamentation (scale bar: 0.5 cm); B, details from the apical portion of distal carina showing the denticles (scale bar: 1 mm); C, details from basal section of the mesial carina showing serrations (scale bar: 500 μ m); D, details from lingual surface of the crown showing surface ornamentation (scale bar: 1 mm). Abbreviations: cc, carinal concavity; er, apicobasally aligned enamel ridges.

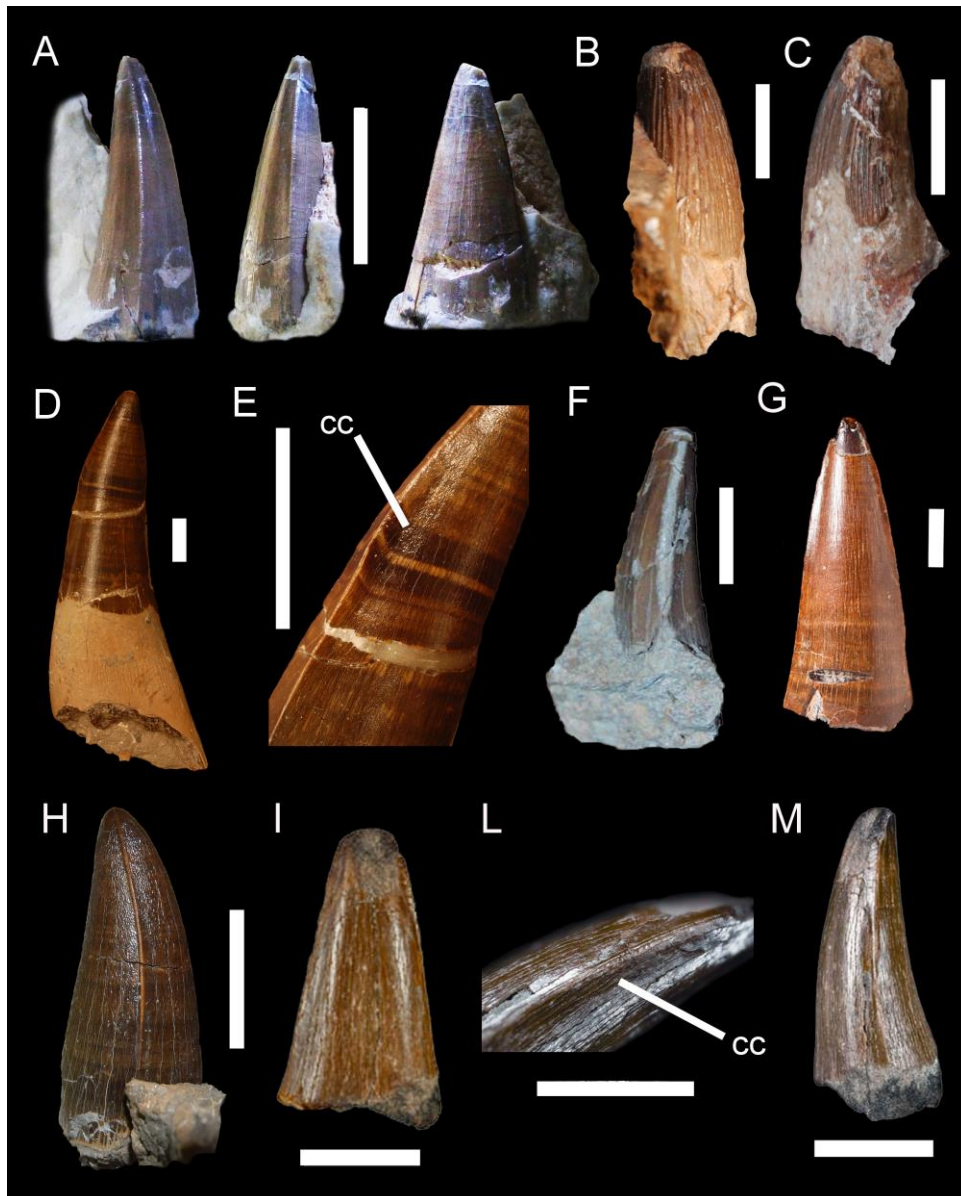


Figure 4: Comparison among Geosaurini teeth; A, MSNC 4475, cf. *Plesiosuchina*; B, JJCC 1, *Plesiosuchina* indet. in lingual view; C, JJCC 1, *Plesiosuchina* indet. in labial view; D, MJML K434, *Plesiosuchus manselii*; E, detail from MJML K434 showing concavities adjacent to the carinae (cc); F, SMNS 91425, isolated tooth of *Dakosaurus maximus*; G, NHMUK PV R36717, isolated tooth of *Dakosaurus maximus*; H, BRSMG CD 7203, isolated tooth from *Torvoneustes carpenteri*; I, NHMUK PV R36638, isolated tooth of *Geosaurus* sp. in labial view; L, detail from NHMUK PV R36638, isolated tooth of *Geosaurus* sp. showing concavities adjacent to the carinae (cc); M, NHMUK PV R36638, isolated tooth of *Geosaurus* sp. in labial/carinal view; Scale bar: 1 cm.