A giant mosasaur (Reptilia, Squamata) with an unusually twisted dentition from the Argille Scagliose Complex (late Campanian) of Northern Italy

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ABSTRACT

A snout of a large-sized mosasaur from the Upper Cretaceous pelagic-turbiditic deposits of the Argille Scagliose Complex of Northern Italy is described. Nannofossil assemblages from the immediately over-lying strata belong to the late but not latest Campanian calcareous nannofossil standard zone CC22, based on the presence of *Uniplanarius trifidus* and *Eiffellithus eximius*. The specimen includes a broken pre-maxilla, the anterior part of the maxillae and dentaries in articulation: preserved teeth show distinctive characters previously unreported in other mosasaurs. Although the marginal teeth show a posterior migration of the labial carina along the jaw length — diagnostic of derived mosasaurines — they are unusual in the combination of features, including anteriormost teeth with asteroid cross section followed by teeth with crowns twisted labioposteriorly from one-third to one-half of their height toward the apices. A comparison between the new specimen and *Mosasaurus hoffmanni* skulls suggests an estimated skull length comparable with some of the largest known mosasaurids. Consequently, the new specimen represents the largest mosasaur and the largest fossil reptile found in Italy to date. Several lines of dental evidence also support the interpretation of the Italian mosasaur as a macrophagous generalist predator. Paleogeographic reconstruction for the Argille Scagliose Complex as well as the occurrence of typical low- to mid-latitude nannofossils support a southern Tethyan margin affinity of the taxon.

1. Introduction

The Italian fossil record of mosasauroids is poorly represented and consists of occasional discoveries of fragmentary material restricted to the northern regions. The first mosasauroid specimens from Italy were collected during the nineteenth century in the Venetian Prealps (Cigala Fulgosi et al., 1980; Dalla Vecchia et al., 2005); a few decades later, a fragmentary rostrum of a large predatory reptile was collected from the Argille Scagliose deposits near the Gavardo locality (San Valentino, Reggio Emilia province) in 1886. Simonelli (1896) interpreted the specimen as a new crocodile,

and erected *Capelliniosuchus mutinensis* as a member of Metrio-rhynchidae. However, the specimen was re-examined by Sirotti (1989), who referred it to *Mosasaurus* cf. *hoffmanni* based on overall morphology, preserved sutural pattern of bones, and tooth shape. To date, it has not been possible to refer the latter specimen to a specific stage of the Cretaceous, although the local geological setting is indicative of lower Upper Cretaceous (Sirotti and Papazzoni, 2002): in addition, the attribution of the Gavardo specimen to *M.* cf. *hoffmanni* is questionable due to the absence of autapomorphies (see discussion below). Leonardi (1946) described isolated teeth and a partial skull from the Senonian deposits of the Scaglia Rossa and Scaglia Cinerea formations of Veneto, all referred to *Mosasaurus* sp. Additional mosasauroid remains were collected in 1972 in Veneto (Dalla Vecchia et al., 2005). In 1980, Cigala Fulgosi et al., provided the first list of the mosasauroid specimens collected in Veneto, including material from the Turonian—lower Santonian Scaglia Rossa Veneta Formation of the Lessini Mountains: such material, housed in the Natural History Museum in Verona and the Paleontological Museum in Sant'Anna d'Alfaedo, has been recently
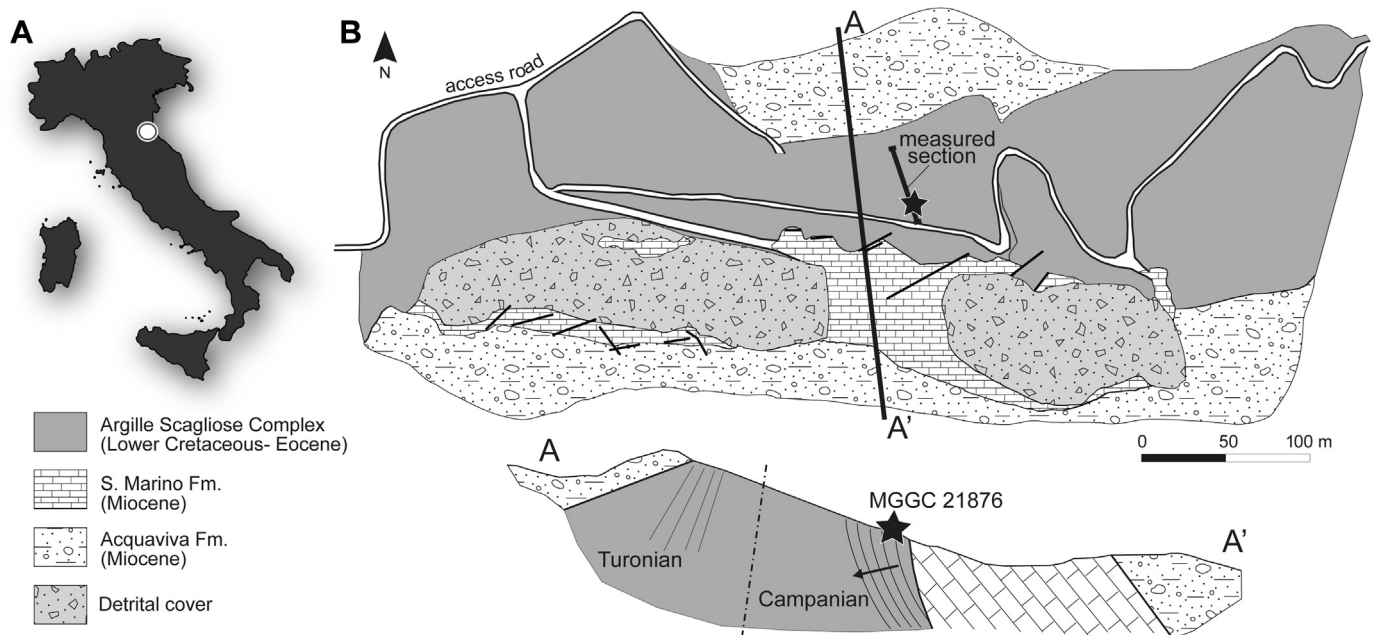
Fig. 1. A, locality map showing the Monte Ceti locality in the romagnolo Apennine of north-eastern Italy; B, simplified geological map of the quarry, showing the position of MGGC 21876 and measured sections discussed in the text. The black arrow indicates the way-up of the strata sampled for nannofossil analyses. The dashed line indicates the tectonic contact between Campanian and Turonian deposits.

referred to a new genus and two new species, *Romeosaurus fumanensis* and *R. sorbinii* (Palci et al., 2013). Similarly, Roghi (1995) reported on isolated mosasauroid teeth from Veneto. Thus, with the notable exception of the Gavardo specimen from the Northern Apennine chain, all known Italian mosasauroid discoveries are restricted to the Turonian–Santonian deposits of the Veneto Region (north-eastern Italy). It is also noteworthy that a relatively rich mosasauroid fauna is known from the Cenomanian–Turonian deposits that crop out near the city of Komen in western Slovenia (Caldwell et al., 1995, Caldwell and Palci, 2007, and references therein).

In this study we describe a partial snout of a very large-sized mosasauroid collected from the uppermost Cretaceous Argille Scagliose Complex in the Romagna Apennine of Italy. We discuss its taxonomic affinities and briefly compare the specimen with the possibly coeval Emilian Apennine mosasaur (i.e., the Gavardo specimen). In addition, we provide a detailed biostratigraphic analysis of the pelagic deposits of the Argille Scagliose Complex, which has been previously nearly exclusively dated on the basis of geometrical and indirect evidence. The Romagna taxon represents the first vertebrate collected from the Argille Scagliose from the area. Further investigation at the locality did not yield any additional vertebrate element, suggesting a complex burial history of the specimen. However, in addition to the mosasauroid from Gavardo and the specimen reported in this study, an increasing number of ichthyosaur and pliosaur cranial and postcranial remains have been reported from the Argille Scagliose deposits that crop out extensively along the Apennine chain in Emilia-Romagna and southern Lombardia (Capellini, 1889; Simonelli, 1910; Renesto, 1993; Rompianesi and Sirotti, 1995; Sirotti and Papazzoni, 2002). Lacking diagnostic biostratigraphic markers, all these findings have been questionably referred by the authors to the Aptian–Turonian interval. Recently, Garassino et al. (2012) reported on the first polychelid lobster from the Argille Scagliose, referring the type specimen to the upper Lower Cretaceous on the basis of rare foraminifera.

2. Geological setting

The new mosasauroid specimen was found in 2010 by Mr. P. Giordani, an amateur collector, at the Monte Ceti active quarry near the village of Secchiano (Novafeltria, Rimini), on the west bank of the Marecchia River (Fig. 1). The Marecchia valley is characterized by a complex assemblage of lithostratigraphic units that encompass the entire Lower Cretaceous–Eocene interval (Conti, 2002), with a structural pattern made up of imbricated, NE-verging slices. At the Monte Ceti locality, a large overthrust is responsible for the juxtaposing of Upper Cretaceous pelagic successions of the Argille Scagliose Complex (and specifically the Argille Varicolori Formation) on top of the Miocene limestone of the San Marino Formation (Fig. 1B). The term 'Argille Scagliose' has been widely used in the Italian geological literature to indicate structural units, tectonosedimentary units or highly deformed sedimentary bodies characterized by an apparent chaotic appearance in outcrop and a certain degree of rock mixing (we refer the readers to Pini, 1999 for a detailed revision of the unit). Some of the Argille Scagliose, including the Monte Ceti deposits, have been recognized as sedimentary bodies inside layered sequences of normal, pelagic, marine strata. These deposits originated on the vast oceanic domains of the Ligurian palaeo-ocean and therefore belong formally to the Ligurian structural nappes (Vai and Castellarin, 1992; Camerlenghi and Pini, 2009, and references therein). The overall maximum thickness is estimated as 600–700 m: the age of the whole Argille Scagliose Complex, however, is still controversial and encompasses a substantial stratigraphic interval from the Aptian–Albian to the lower Eocene (Conti, 1994; Cerrina Ferroni et al., 2002; Garassino et al., 2012). It should be noted that a number of regional studies on the Argille Scagliose have documented a significant transition in the depositional facies at the Campanian–Maastrichtian boundary in the northern Apennines. The Aptian–Campanian deposits, in fact, are largely dominated by clay beds intercalated with minor siliciclastic and calcareous turbidites; this interval is capped by the Helminthoid Flysch marker unit, characterized by carbonate-

dominated, turbitic deposits and rare clay beds (Parea, 1965; Bortolotti and Malesani 1967; Fontana, 1991; Vai and Castellarin, 1992, and references therein).

2.1. Lithostratigraphy

At the Monte Cety quarry, two distinct litho- and chronostratigraphic intervals occur (Fig. 2). The lower sequence consists of an alternation of sub-vertical, dark grey to green and red argillaceous pelagic beds, calcareous turbidites up to 50 cm thick, and minor, coarse-grained, siliciclastic turbidites. The stratigraphic interval exposed at the Monte Ceti quarry shows no indication of reversed strata as the pelagic deposits show typical fining-upward graded bedding and flute/groove casts at the base of the turbidites. The turbiditic deposits are also characterized by tubular Planolites-like feeding traces at the base, whereas rare Zoophycos traces are found on the interbedded, pelitic, hemipelagic deposits. The mosasaur snout described here was preserved as a subnodular, oval, carbonate concretion within a pelitic, siliciclastic turbidite in the lower deposits of this interval. The overlying deposits consist exclusively of light grey, argillaceous pelagic beds with rare, centimetre-thick marl beds and calcareous turbidites.

3. Nannofossil biostratigraphic analyses

In order to provide a reliable age for the specimen, the pelitic matrix in which MGGC 21876 was embedded has been tested for calcareous nannofossil analyses but proved to be barren.
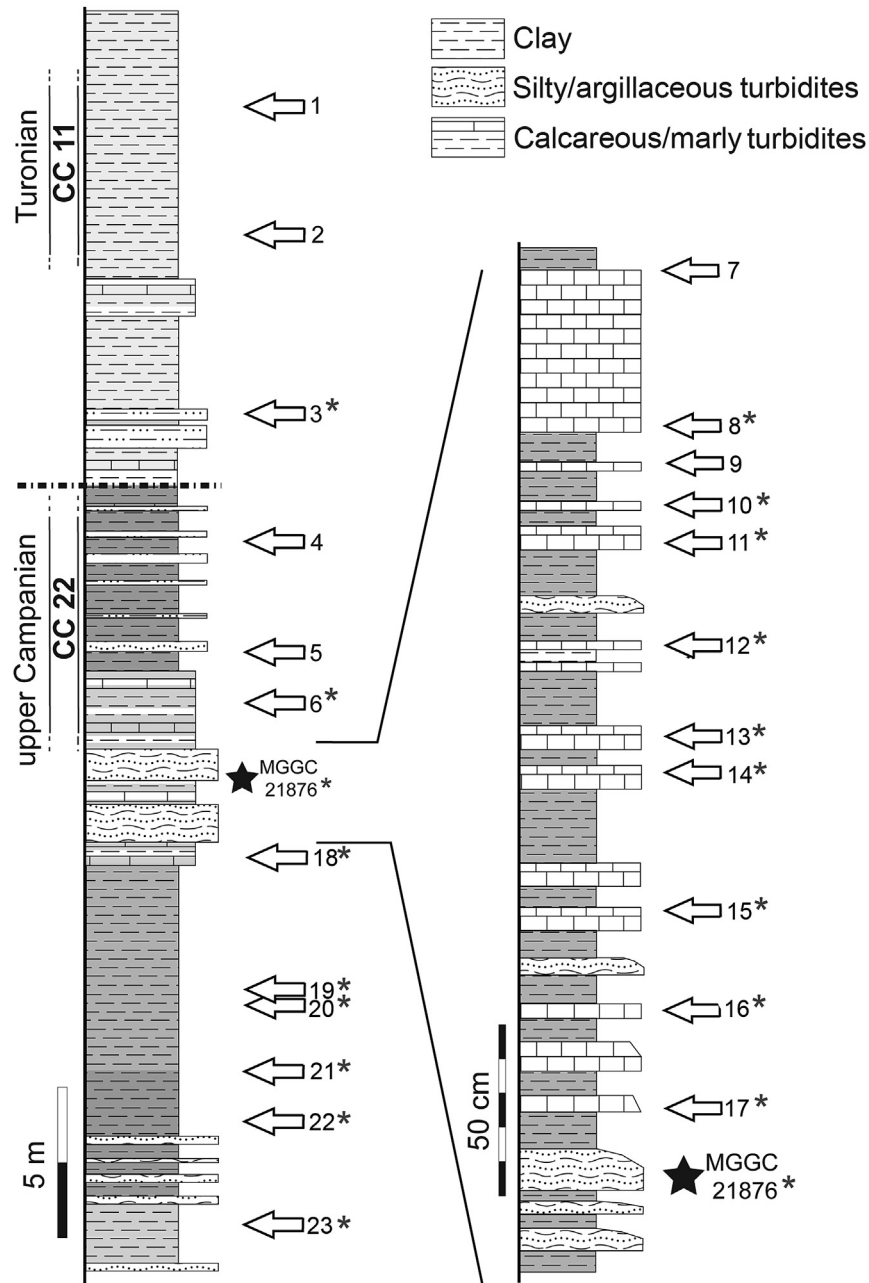

Fig. 2. Measured stratigraphic columns of the Monte Ceti locality showing the samples collected for nannofossil biostratigraphic zonations and the occurrence of MGGC 21876, approximately 10 m below the tectonic contact between Campanian and Turonian deposits indicated by the dashed line. Samples marked with an asterisk proved barren of nannofossil.

Table 1
Nannofossil vertical distribution along the measured section. Abbreviations: Am abundant, 10–50 specimens per field of view (FOV); C, common, 1–10 specimens per 11–50 FOV; F, few, 1 specimen per 1–10 FOV; R, rare, 1 specimen per 11–50 FOV; B, barren. Preservation estimate abbreviations: G, good preservation of specimens; M, moderate implying that specimens exhibit some etching or overgrowth or dissolution, primary morphological characteristics are sometimes altered, however most specimens are identifiable at the species level.

Species (Sissingh 1977)	1	2	3	4	5	6	7	8	9	10
Sample zone	CC 11 Turonian	CC 11 Turonian		CC 22 Upper Campanian	CC 22 Upper Campanian		CC 22 Upper Campanian		CC 22 Upper Campanian	
Abundance	R	A	B	A	A	B	A	B	C	B
Preservation	G	G		M	G		G		G	
Biscutum sp.										
Retecapsa angustiforata		R								
Calculites obscurus				R	R		R		R	
Cretarhabdus crenulatus		R								
Cretarhabdus surirellus		R		F	F		F		F	
Cribrosphaerella ehrenbergii	C	C		F	C		C		C	
Eiffellithus turriseiffelii	C	F		F	F		C		F	
Eprolithus floralis				F	F					
Eprolithus octopetalus	R									
Eiffellithus eximius				R	R		R		R	
Manivitella pemmatoidea		R		R	R		R		R	
Micula staurophora				C	C		C		C	
Zeugrhabdotus embergeri	R	R		R	R		R		R	
Zeugrhabdotus diplogrammus	R	R		R	R		R		R	
Zeugrhabdotus bicrescenticus				R	R		R		R	
Zeugrhabdotus erectus	R	R		R	R		R		R	
Reinhardtites anthophorus				R	R		R		R	
Prediscosphaera sp. round	R	R		R	R		R		R	
Tranolithus phacelosus	R	R		R	R		R		R	
Tegumentum stradneri	R	R		R	R		R		R	
Tegumentum lucidum				R	R		R		R	
Discorhabdus ignotus	R	R		R	R		R		R	
Microrhabdulus decoratus				R	R		R		R	
Quadrum gartneri		R								
Gartnerago obliquum	R	R								
Percivalia imperforata	R	R								
Kamptnerius magnificus		R								
Broinsonia parca parca				C	C		C		C	
Broinsonia parca constricta				C	C		C		C	
Lithraphidites carniolensis		R		R	R		R		R	
Ceratolithoides aculeus				R	R		R		R	
Lucianorhabdus maleformis		R								
Lucianorhabdus cayeuxii				R	R		R		R	
Uniplanarius trifidus				C	C		C		C	
Uniplanarius sissinghii				F	F				F	
Watznaueria sp.	C	C		C	C		C		C	

Fossilization processes most likely altered the original mineralogical composition of the sediments, dissolving and re-depositing them as different forms of carbonates, resulting in the complete disappearance of any original calcareous nannofossil assemblage. Therefore, a total of 23 sediment samples were collected along a measured section at the Monte Ceti quarry (Fig. 2): 12 samples have been used to date the entire exposed stratigraphic section (Fig. 2, left-hand log), whereas 11 more densely collected samples were used to constrain the fossiliferous bed to a specific stage (Fig. 2, right hand log). A number of nannofossil biostratigraphic zonations for the Late Cretaceous have been proposed (Cepek and Hay, 1969; Thierstein, 1976; Manivit et al., 1977; Sissingh, 1977; Verbeek, 1976; Roth, 1978; Crux, 1982; Perch-Nielsen, 1985, Burnett, 1998); for this study, we refer to Sissingh (1977) as reported in Perch-Nielsen (1985) (see also Appendix 2). Samples were analysed for calcareous nannofossil content by A.N. at the lab of Stratigraphy and Paleoecology of the Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche (Ancona, Italy), and the smear-slide preparation was kept simple (e.g., no concentration or centrifugation of the sediment), in order to retain the original composition of the nannofossil assemblages, and was performed on the same samples used for geochemical analyses. Estimates of calcareous nannofossil totals and species abundance were carried out using a polarized light microscope at a magnification of ×1250. A minimum of 300 fields of view were observed in random traverses for each smear-slide. Calcareous nannofossil total abundance and species abundance were semiquantitatively evaluated and expressed (see Table 1). The preservation estimate was recorded after close inspection of dissolution and overgrowth, and was coded according to the Ocean Drilling program standards.

3.1. Biostratigraphic results

Only six out of the 23 samples collected at the Monte Ceti quarry yielded enough nannofossils to permit age determination: as previously stated, the matrix associated with MGGC 21876 proved barren of nannofossils. Samples 1 and 2 at the top of the low-resolution section (Fig. 2, left-hand log) show moderately to well preserved assemblages with common *Watznaueria barnesae*, and are barren of tiny and delicate forms such as *Biscutum*; *Cretarhabdus* spp., *Eiffellithus turriseiffelii*, *Gartnerago obliquum*, *Lithraphidites carniolensis*, *Lucianorhabdus maleformis*, *Tranolithus phacelosus*, *Z. diplogrammus* and *Zeugrhabdotus embergeri*, are subordinate (see Table 1). *Helenea chiastia* and *Corollithion kennedyi* are not present. One specimen of *Quadrum gartneri*, whose first occurrence marks the base of the CC11 Biozone, is recorded in sample 2, whereas taxa such as *Micula* sp. and *Eiffellithus eximius* are rare or absent. *Eprolithus octopetalus* is present in sample 1, and *Kamptnerius magnificus* in sample 2. The latter taxon is reported approximately 9 m above the Cenomanian–Turonian boundary, marked by the Bonarelli level, at the Bottaccione type section (Gubbio, Italy) (Tremolada, 2002). Therefore, samples 1 and 2 can be confidently referred to the CC11 Biozone of Sissingh (1977), thus indicating a Turonian age for this part of the section. Samples 4,5, 9 and 11 show a moderately to well preserved and diversified nannofossil assemblages: *Watznaueria barnesae* is common to abundant and other co-occurring species include *Broinsonia parca parca*, *Broinsonia parca constricta*, *Ceratolithoides aculeus*, *Cretarhabdus crenulatus*, *Cribrosphaerella ehrenbergii*, *Eiffellithus turriseiffelii*, *Lithraphidites carniolensis*, *Lucianorhabdus cayeuxii*, *Micula staurophora*, *Prediscosphaera* sp., *Reinhardtites anthophorus*, *Retecapsa angustiforata*, *Zeugrhabdotus embergeri*, *Zeugrhabdotus diplogrammus*, *Uniplanarius sissinghii* and *Uniplanarius trifidus* (see Table 1) This assemblage allows referral of the sediments to the late but not latest Campanian calcareous nannofossil standard zone CC22 of Sissingh (1977), defined by the

first occurrence of *Uniplanarius* (*Quadrum*) *trifidus* and the continuous presence of *R. anthophorus* (see Burnett, 1998, figs. 6.5 and 6.7). It must be emphasized that the presence of *Reinhardtites anthophorus* and *Eiffellithus eximius* (both species disappear at the CC22/23 boundary) at the top of the normal, pelagic basal deposits completely exclude a Maastrichtian age of the sediments containing MGGC 21876. According to Wagreich et al. (2012), typical low- to mid-latitude "Tethyan" nannofossils such as *Ceratolithoides aculeus*, *Uniplanarius trifidus* and *U. sissinghii*, together with a relatively high occurrence of *Watznaueria* spp., support a Tethyan character of the nannofossil assemblage. The nannofossil analyses indicate a late Campanian age for the interval from sample 4 to sample 9, whereas on top of this interval light grey, argillaceous pelagic beds with rare, centimetre-thick marl beds and calcareous turbidites of Turonian age occur. The juxtaposition of these units is interpreted as the result of local, tectonically-driven deformation of the Argille Varicolori Formation. Finally, no evidence of the Helminthoid Flysch marker unit is observed at the Monte Ceti quarry, indicating the absence of the highest Campanian strata.

4. Material

In this study we describe a partial but well preserved snout of a large-sized mosasaur, catalogued by the Soprintendenza per i Beni Archeologici dell'Emilia Romagna as ST 249811. The specimen, however, has been prepared at the Museo Geologico Giovanni Capellini (MGGC) in Bologna where it is permanently stored and catalogued under the accession number MGGC 21876. Therefore, in this study the specimen will be referred to as MGGC 21876. Three tooth fragments

have been recovered with the snout and have been included in this study: in particular, the distal portion of the second right premaxillary tooth has been used in order to obtain SEM images of the carinae and microscopic wear patterns. MGGC 21876 measures 66 cm in length, and 34 cm at its maximum width at the distal end.

5. Methods

In order to evaluate the phylogenetic affinities of MGGC 21876, we entered an operational taxonomic unit based on the new Italian mosasauroid in the phylogenetic analysis of Palci et al. (2013). An additional character, describing the absence/presence of anterior snout dentition including very small premaxillary teeth and larger and tightly interlocked anterior marginal teeth (a synapomorphy of Mosasaurini, LeBlanc et al., 2012), was included in the data set (see Appendix 1 for character coding). The data matrix was analysed with TNT vers. 1 (Goloboff et al., 2008). The following heuristic search settings were used to generate the most parsimonious trees (MPTs): hold 10,000 trees, 1000 Wagner builds with tree bisection and reconnection (TBR) as the search strategy. Mosasauroid taxonomy follows LeBlanc et al., (2012). *Mosasaurus* species taxonomy follows Bardet et al., (2004) and Lindgren and Jagt (2005).

Tooth parameters terminology and tooth morphology guilds for the mosasaur follow Massare (1987, 1997) and Ross (2009). Dental wear terminology follows Young et al., (2012).

SEM secondary electron images of selected tooth characters were acquired using a Scanning Electron Microscope Philips 515b (operating voltage 3 kV) on uncoated specimens at the Dipartimento di Scienze Biologiche, Geologiche e Ambientali in Bologna.
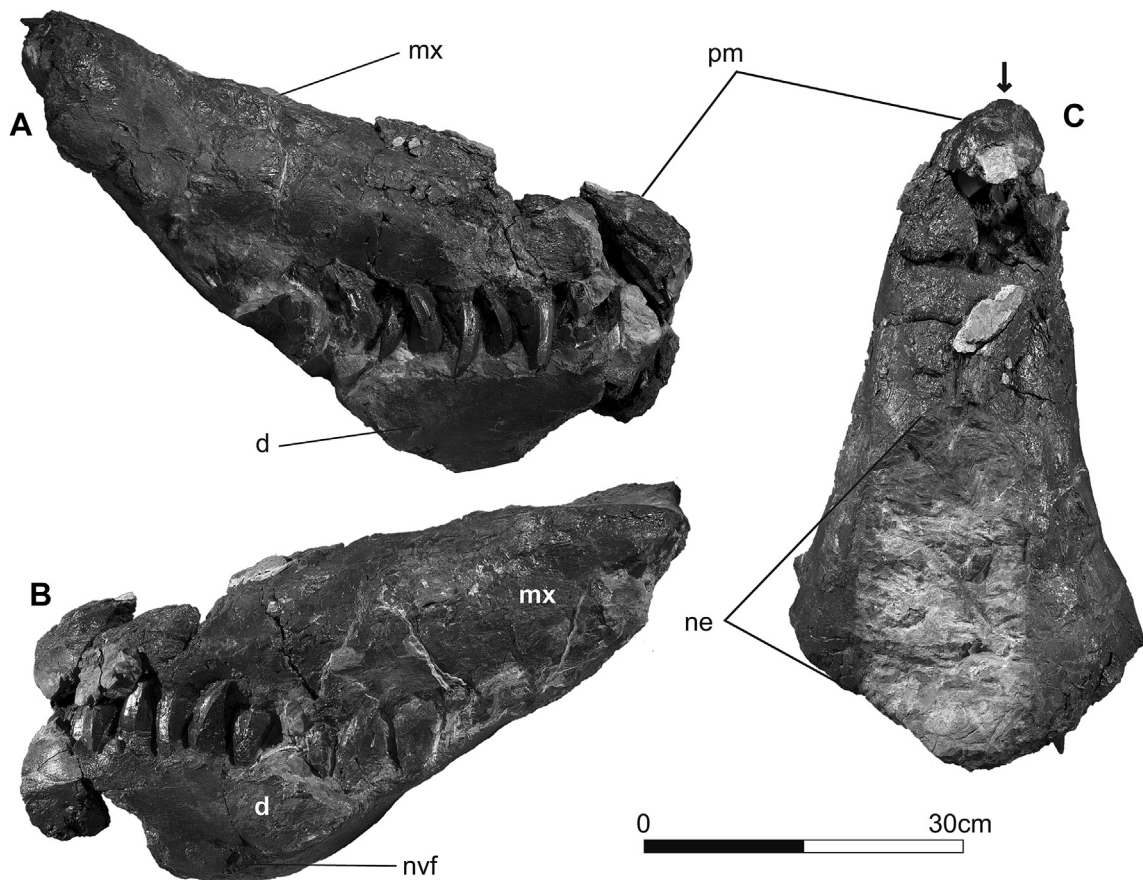

Fig. 3. Specimen MGGC 21876 in A, right lateral, B, left lateral, and C, dorsal views. Abbreviations: d, dentary; mx, maxilla; ne, narial emargination; nvf, neurovascular foramen; pm, premaxilla. The arrow indicates an obtusely angled, round predental rostrum of the premaxilla.
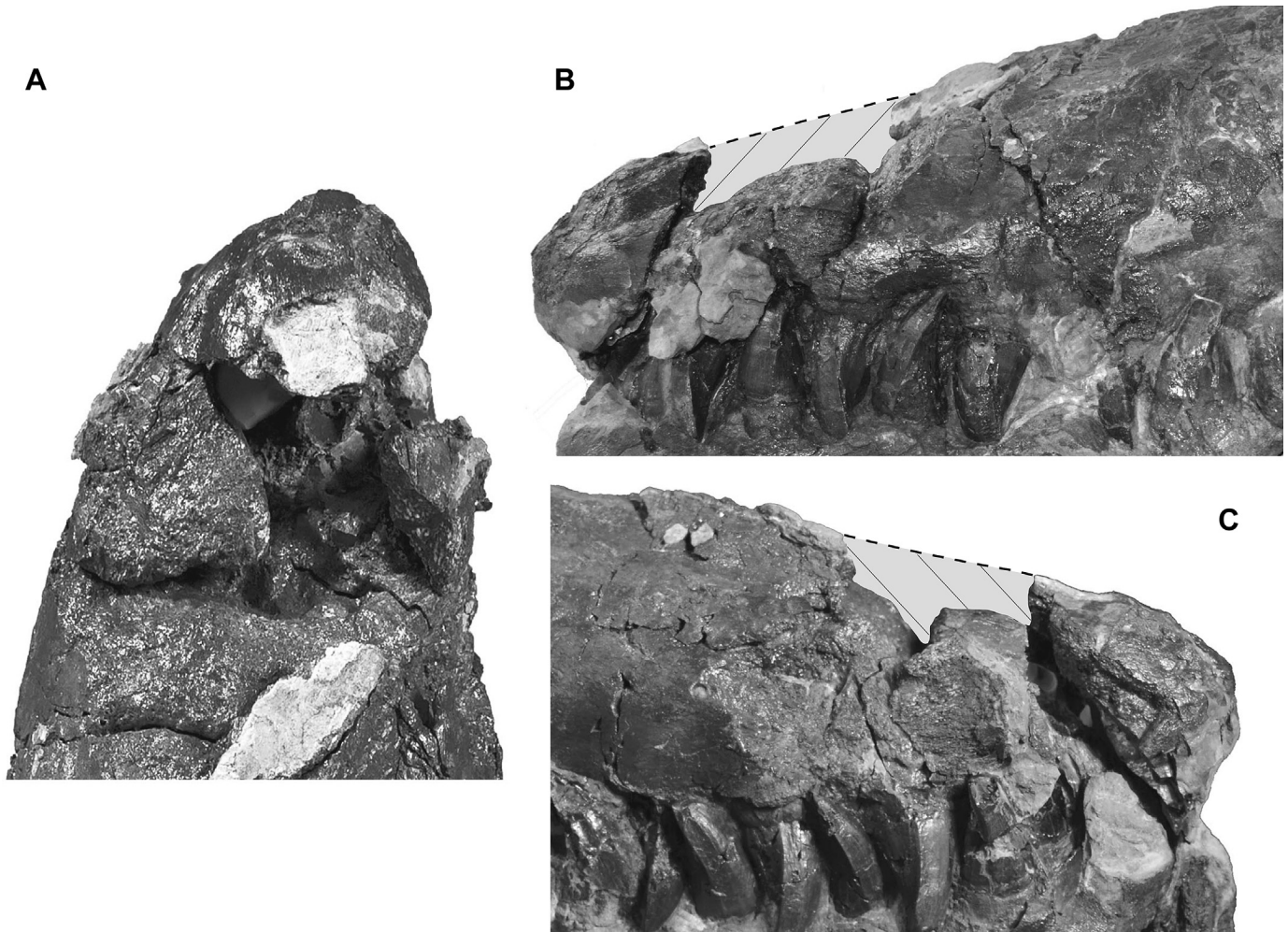
Fig. 4. Rostrum of MGGC 21876 in A, dorsal view; B, left lateral view; and C, right lateral view.

6. Systematic palaeontology

Class Reptilia Linnaeus, 1758
Order Squamata Oppel, 1811
Family Mosasauridae Gervais, 1852
Subfamily Mosasaurinae Gervais, 1852
Tribe Mosasaurini (Gervais, 1852) *sensu* LeBlanc, Caldwell and Bardet, 2012
Genus *Mosasaurus* Conybeare, 1822
Mosasaurus sp. indet.
Figs. 3–9
Specimen. MGGC 21876, premaxilla, anterior portion of maxillae and dentaries, anterior marginal teeth.
Locality and horizon. Monte Ceti, Novafeltria Municipality, Rimini Province, Italy. Argille Varicolori Formation, late Campanian (this study).

7. Description

7.1. General features

MGGC 21876 is the rostral portion of a large-sized mosasaur skull, comprising a dorsally incomplete premaxilla, the anterior section of the maxillae and dentaries with their teeth in occlusion (Figs. 3 and 4). The specimen preserves the anteriorly expanded portion of the external nares: based on this, we estimate that approximately the anterior half of the maxillae are preserved. The specimen is stocky and massive, with robust maxillae and dentaries gradually deepening posteriorly. The preserved posterior portion of the right maxilla, however, was most likely deflected laterally post-mortem, exhibiting a greater degree of posterior rise in lateral view and a lateral bulge in dorsal view in comparison to the left counterpart (Fig. 3). While the premaxilla suffered considerable damage on its dorsal side, its largely intact anterior end shows a parabolic outline in dorsal view, with a broadly rounded, short rostral projection and posterolaterally diverging lateral sides. The anterior border of the narial emarginations begins at the level of the fourth maxillary tooth and the emarginations extend posteriorly for the whole preserved specimen. Most of the marginal teeth are preserved *in situ* and fully erupted, showing a tightly interlocking tooth row formed between opposing jaws (Figs. 4 and 5): in addition, a few small crowns are preserved inside the narial cavities.

7.2. Premaxilla

The anterior dentigerous body is deeper than long in lateral view. A short, obtuse rostrum is present in front of the first premaxillary teeth (Fig. 3C). The rostral end is completely preserved (Fig. 4) and indicates a short dome-like bony projection less developed than the cone-like projection present in some *Mosasaurus* species (Russell, 1967, Lingham-Soliar, 1995; Bardet et al.,
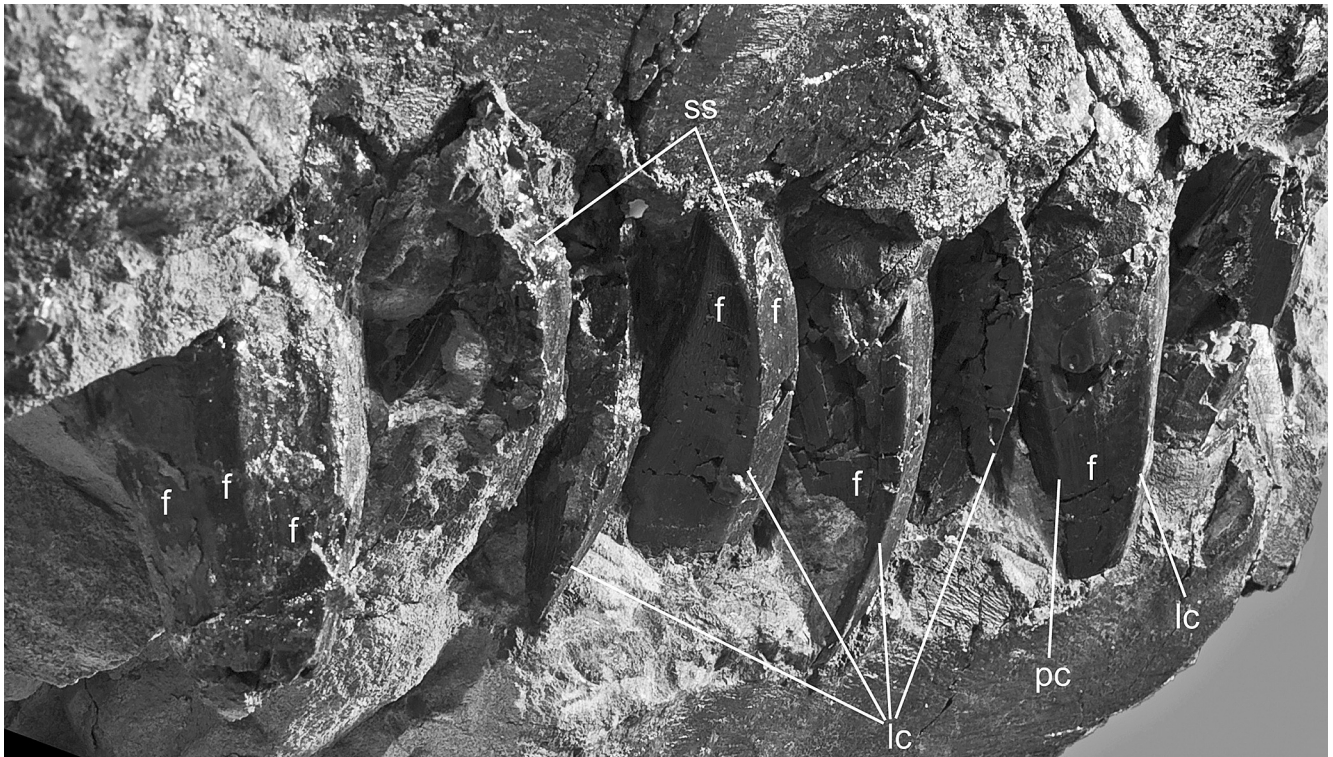
Fig. 5. Detail of marginal dentition of MGGC 21876 in right posterolateral view. Abbreviations: f, facet; lc, labial carina; pc, posterior carina; ss, spalled surface. Note that the facets on most of the anterior tooth crowns are unusually broadly concave posterior to labial carina.

2004). The only intact dorsal surface of the anteriormost of the dentigerous rostrum is smooth. Otherwise, the dorsal surface of the element is too poorly preserved to warrant further description.

7.3. Maxilla

The maxillae are deeper than the tooth crowns, suggesting deeply socketed roots. The outer wall of the element consists of the sub-vertical, ventrolateral surface and the dorsolaterally facing dorsal half. A series of neurovascular foramina (the exits for the fifth cranial nerve) occurs along the junction between these surfaces (Fig. 3A).

7.4. Dentary

The worn, anteriormost margin of the dentary may indicate that a short projection anterior to the first teeth was present. A large ovoid exit for the fifth cranial nerve is present on the ventrolateral surface of the dentary at the level of the fourth dentary tooth on both sides. Otherwise, the cortical surface of the lower jaw is smooth as preserved.

7.5. Dentition

The premaxillary teeth are smaller than the maxillary teeth, and show prismatically-faceted crowns with finely crenulated carinae ('false serration' of de Andrade et al., 2010: presence of conspicuous ornamentation on the carina but absence of distinct denticles) (Fig. 7). In cross section, the premaxillary crowns show a sub-triangular outline near the base, where all facets are comparably planar. The maxillary and dentary teeth exhibit more robust crowns with uniquely labioposteriorly twisted carinae, and are moderately compressed labiolingually (Figs. 6 and 8). Unexpectedly, the carinae lack evidence of the crenulation seen in the premaxillary teeth. The anteriormost couple of dentary teeth are poorly preserved, with only the first left dentary tooth preserving the highly worn apex. The latter shows a uniquely asteroid-pentagonal cross section (Fig. 9A, B). The labial surfaces of the anterior crowns bear from three to five flat prismatic facets. In both the maxillary and dentary crowns, the number of labial prisms increases toward the rear of the mouth. Throughout the preserved maxillary and dentary teeth, the labial surface anterior to the labial carina is convex; however, the one posterior to the carina is concave distally, except for that on the posteriormost preserved teeth where the surface is gently convex. In the anteriormost teeth the labial carinae are more developed and placed labially, whereas they are less prominent and shift to a more posterior position in the posteriormost preserved teeth.

The twisted nature of the marginal teeth is extreme at the level of the third dentary tooth, which shows a prominent labial carina, shifting posteriorly towards the apex and bounds the convex anterior half and the concave posterior half of the crown surface (Fig. 6C). Some crowns (e.g., the second left dentary tooth) show a distinct pattern of transversally oriented enamel bands running along the labial surface, a feature not common in mosasaurs but reported in other marine reptiles (e.g., *Geosaurus*; de Andrade et al., 2010). The enamel bands are closely spaced and most developed basally (Fig. 8A).

A few small, isolated crowns are preserved inside the narial cavity: they are subtriangular, labiolingually compressed and bear distinct carinae running anteroposteriorly. Lacking a strong curvature and their isolated nature preclude confident identification of these teeth as pterygoid teeth. It is more likely that small, erupting marginal teeth were dislocated post-mortem and floated into the current position.
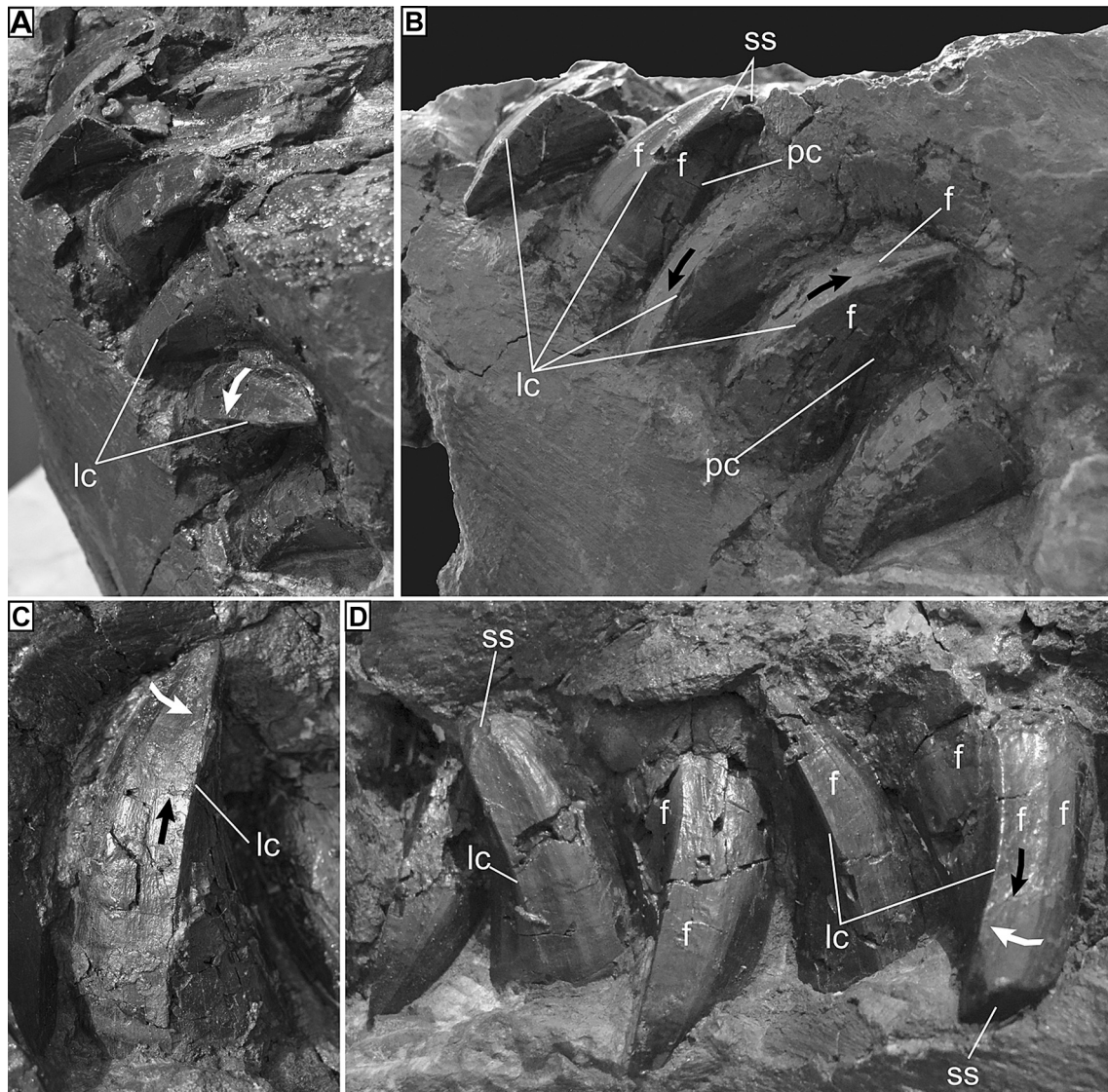
Fig. 6. Close-up photographs of the marginal dentition of MGGC 21876. A, B, left lateral series in dorsolateral view; C, third left dentary tooth in lateral view; D, right lateral series in lateral view. Abbreviations: lc, labial carina; pc, posterior carina; ss, spalled surface. White arrows indicate labioposterior twisting of crowns, and black arrows indicate the same of labial carinae.

7.5.1. Dental wear

Both macroscopic and microscopic wear patterns are present in the teeth. The most abundant macroscopic wear pattern is represented by apical spalling (Young et al., 2012). The second right premaxillary crown shows a moderate spalling in form of an ovoid facet running apicobasally along the lateral carina (Fig. 7). In the first left dentary tooth, spalling is so extensive that the crown apex is reduced to a bluntly rounded surface (Fig. 9A, B). Compared to the wear pattern present in the dentition of extant and extinct odontocetes, in which apical spalling is an even plateau (e.g., *Orcinus citoniensis* holotype MGGC-1COC17; see also Young et al., 2012, fig. 7A), that of the first left dentary tooth is an uneven surface, suggesting that the apex first broke off by violent impact and subsequently wore down. Apical spalling is also present in most of the well preserved maxillary and posterior dentary crowns. In these teeth, the worn surfaces are planar and consistently restricted to the anterolabial margins of the crowns, producing a characteristic blunt apex in side view.

The microscopic wear pattern was observed in the carina of the premaxillary tooth analysed with SEM. The carina ornamentation is badly abraded, with most of the crenulation apices worn away (Fig. 7).

8. Phylogenetic analysis

Heuristic searches recovered 192 shortest trees of length 428 (Consistency Index = 0.3808, Retention Index = 0.6926). The strict consensus of the shortest trees placed the Italian specimen among the included *Mosasaurus* species (Fig. 10A). When *Mosasaurus conodon* is pruned from the resulted topologies, MGGC 21876 results as sister taxon of the 'M. hoffmanni – M. missouriensis' node (Fig. 10B). Characters supporting the placement of the new Italian mosasauroid among Mosasaurini are the absence of coarsely textured crowns, and the combination of small premaxillary teeth and tightly interlocked anterior marginal teeth (LeBlanc et al., 2012). Among Mosasaurini, the Italian taxon shares with other species of *Mosasaurus* the combination of a dentary with a bony projection in front of the first tooth, and not inflated marginal tooth crowns bearing elevated carinae. The absence of a distinctly cone-shaped premaxillary
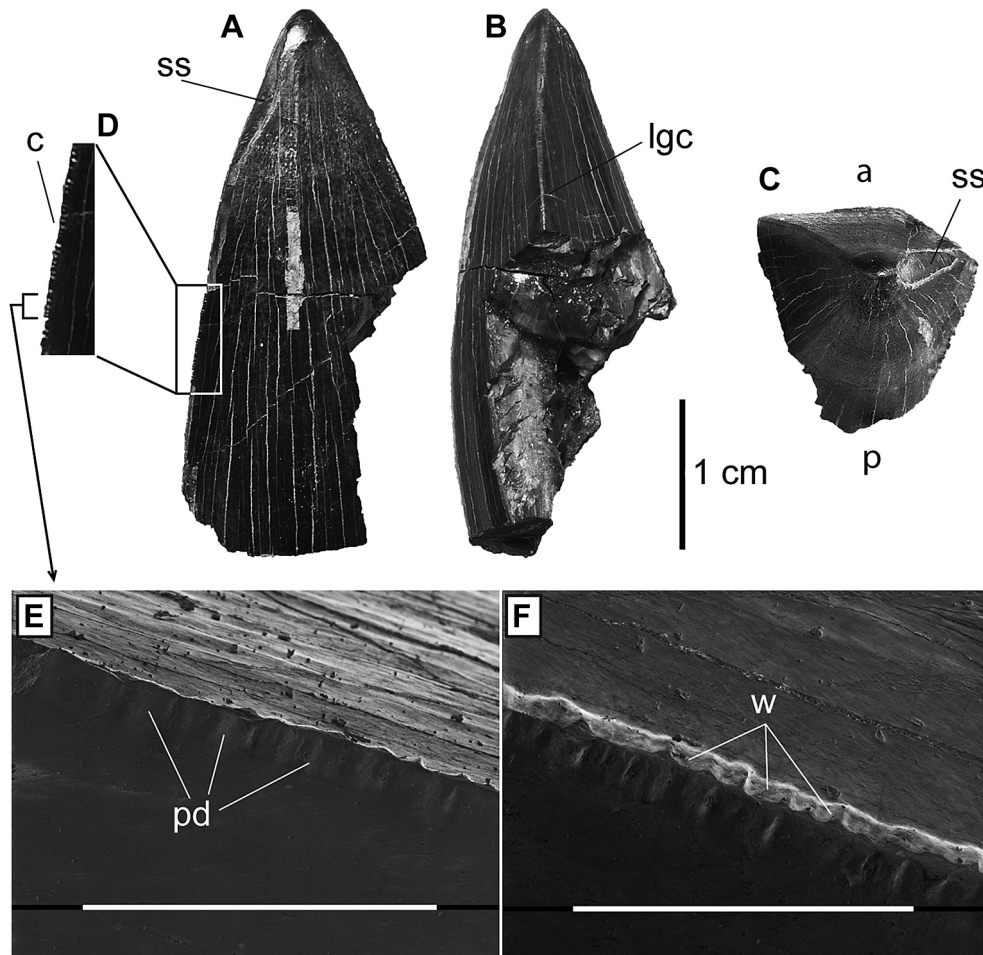
Fig. 7. Second right premaxillary tooth crown in anterior (A), lingual (B), and apical (C) views. D, detail of the crenulated carina. E–F, SEM photographs of the carina (scale bar 1 mm). Abbreviations: a, anterior; c, carina; lgc, lingual carina; p, posterior; pd, pseudo-denticle; ss, spalled surface; w, worn surface along the carina.

rostrum excludes MGGC 21876 from the least inclusive clade containing *M. hoffmanni* and *M. missouriensis*.

9. Discussion

Using the diagnosis provided for Mosasaurini by LeBlanc et al. (2012), MGGC 21876 can be referred to this tribe based on the combination of the following characters: broadly convex dorsal profile of premaxilla, premaxillary teeth much smaller than lateral dentition, and tightly interlocking anterior marginal teeth. However, some of these characters in combination can readily characterise a globidensine *Prognathodon* as well (Konishi et al., 2011: figs. 2–4), and may represent mosasaurine homoplastic features. Nevertheless, the posterior migration of labial carinae along the length of the jaw is a feature that is shared by members of the subfamily Mosasaurinae (Russell, 1967; Lingham-Soliar, 1995; Bardet et al., 2004), with the possible exception of *Clidastes* (YPM 40350, T. Konishi pers. comm., 2012). In non-mosasaurine plio-platecarpine and tylosaurine taxa, the carinal position does not change along the jaw margin (e.g., Lindgren 2005; Konishi and Caldwell 2011; Konishi pers. comm., 2012). Based on overall morphology, the Italian specimen is referable to *Mosasaurus* (Russell, 1967), although the loss of most of the skull (in particular, the fronto-parietal region and the suspensorium) precludes a more precise placement among the known *Mosasaurus* species (Lingham-Soliar, 1995; Bardet et al., 2004). Although the massive dentary of MGGC 21876 is reminiscent of *Prognathodon* (Lingham-

Soliar and Nolf, 1990; Dortangs et al., 2002), large specimens of *Mosasaurus* (e.g., BMNH R1224, *M. hoffmanni*) exhibit massive dentaries with a bowed ventral margin as well, and the Italian mosasaur lacks the smooth and swollen marginal teeth character-istic of the former genus (Lingham-Soliar and Nolf, 1990; Christiansen and Bonde, 2002; Caldwell and Bell, 2005; Konishi et al., 2011). Regardless, what is unusual about MGGC 21876 is that the marginal teeth are consistently and considerably twisted distal to one-third to one-half of the crown height labioposteriorly along with the carinae, which is a character hitherto unknown in any mosasaur or other marine reptile taxon (e.g., Massare, 1987; see Figs. 6 and 7). Furthermore, the facets on each crown are broad, due to the presence of only three to five ridges (Fig. 9A). Such facets are known in a number of mosasauroid taxa, but are typically much narrower and much more numerous than in *Mosasaurus*, as seen in plioplatecarpines. Among *Mosasaurus* species, the unusual dental morphology observed in MGGC 21876 may fall under three possible interpretations: 1. apomorphic characters diagnostic for a new taxon; 2. pathological condition; or 3. post-mortem deformation due to taphonomic conditions. Accurate analyses of the dentition of MGGC 21876 enable a pathological condition to be excluded: in fact, the discussed characters are not atypical in their distribution but follow a progressive modification along the tooth row that in-cludes variation in overall dimensions, crown cross section, and number and position of carinae. This pattern is present along both upper (premaxilla-maxilla) and lower (dentary) tooth series, and symmetrically along left and right sides of the mandible. In
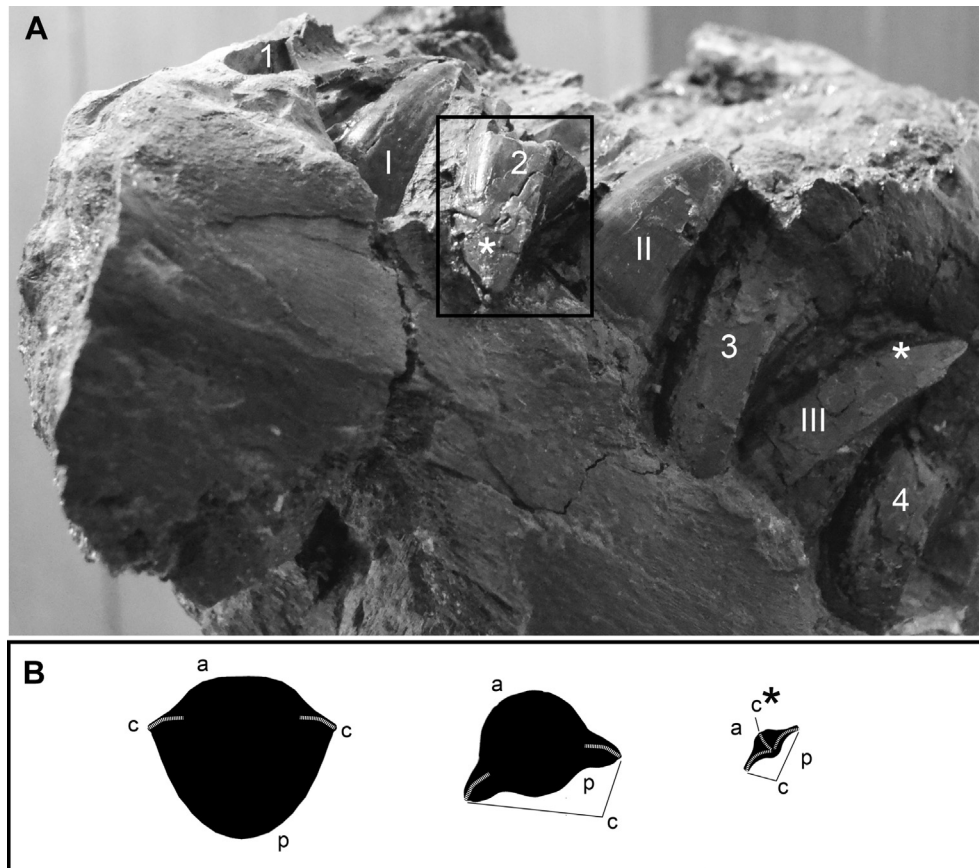
Fig. 8. A, marginal dentition of MGGC 21876 in left lateroventral view. B, cross sections of second left maxillary tooth taken at (from left) the basal end, mid-height, and the apical end of the crown. Note the twist. Abbreviations: a, anterior; p, posterior; c, carina.

particular, the labial carinal placement in the anterior marginal teeth is indeed atypical if compared with the fossil record but their function can be referred to specific predatory habits of a large-bodied generalistic predator (discussed below). The morphology of the dentition is one of the most widely mentioned features in mosasauroid taxonomy (e.g., Russell, 1967; Bardet et al., 2004, 2006; Lindgren, 2005; Lindgren and Siverson, 2002; Schulp 2005; LeBlanc et al. 2012). In particular, heterodonty involving progressive modifications of tooth morphology along the oral series is reported in some mosasaurine taxa, where it is both taxonomically and ecologically significant (e.g., Schulp 2005; LeBlanc et al. 2012). Similarly, available data in the literature do not provide any examples of major ontogenetical variations in the dentition of mosasaur species. Although the latter hypothesis cannot be entirely ruled out, we suggest that the characters discussed may eventually prove to be diagnostic for a new taxon. Nevertheless, due to the absence of information from taxonomically relevant regions of the skull, and the complete absence of postcranial elements, we have decided not to refer the Italian specimen to a previously named species, or to erect a new taxon. Pending additional specimens from the Argille Varicolori sharing the unique dentition pattern of MGGC 21876 that may elucidate its taxonomic interpretation, it is provisionally referred to an indeterminate species of *Mosasaurus*.

Sirotti (1989) first recognised the mosasauroid affinities of "*Capelliniosuchus mutinensis*" and referred it to *Mosasaurus hoffmanni*. After examination of the specimen housed in the palaeontological collection of the University of Modena, we concur concerning its mosasauroid affinity, but disagree in detail with Sirotti's (1989) reconstruction and interpretation. Sirotti (1989)

identified both prefrontals and frontal bones along the posterior half of the dorsal surface of the specimen. We disagree, since the skull block only continues posteriorly to the level immediately posterior to the posterior end of the narial emargination, and the external bone surface in this area is mostly worn away. We note that the reconstruction of the sutural surfaces in the skull made by Sirotti (1989, fig. 2B) is unique when compared with most mosasaurid skull reconstructions (e.g., Russell, 1967; Lingham-Soliar, 1995) in having the prefrontal narial emargination longer than the maxillary narial emargination, the prefrontal emargination forming the whole posteriormost narial margin with limited posteromedial frontal participation, and the frontal forming the posterior third of the internarial bar. If confirmed, such morphology would be highly autapomorphic for "*C. mutinensis*" as this would make this specimen a mosasaur with a disproportionately short muzzle. Accordingly, we consider Sirotti's (1989) reconstruction unsupported, and his reference of the "*Capelliniosuchus mutinensis*" specimen to *Mosasaurus hoffmanni* without basis. MGGC 21876 differs from "*C. mutinensis*" in being larger and stouter (although we cannot dismiss that these differences may be ontogeny related), in showing the narial emargination starting from the level of the fourth maxillary tooth (sixth on "*C. mutinensis*" holotype), and in possessing labioposteriorly twisted tooth crowns with broad facets.

10. Size estimation and feeding ecology

The preserved upper right dentigerous margin of MGGC 21876 includes seven consecutive tooth positions (two premaxillary and five maxillary) and is about 40 cm long. In an articulated

Mosasaurus hoffmanni skull about 145 cm long (Lingham-Soliar, 1995, fig. 5) the same region is about 36 cm long. Assuming the skull of MGGC 21876 closely followed the skull proportions of *M. hoffmanni* (Lingham-Soliar, 1995, fig. 4), we estimate that it was of comparable size when complete. In articulated mosasaurid skeletons, the total body length is about 7–10 times the skull length although it is more likely that a mosasaurine body length was about seven times skull length, based on a nearly complete specimen of *Prognathodon overtoni* (Russell, 1967; Konishi et al., 2011). Therefore, we estimate that at the time of death the complete body length of the animal that the new Italian specimen belonged to was at least 11 m long and possibly greater, comparable to the largest known mosasaurids (Christiansen and Bonde, 2002; *Tylosaurus proriger* KU 5033, Konishi pers. comm., 2012). Using the mass estimate method in Motani (2001), such a mosasaur would weigh close to 10^4 kg.

Several lines of evidence support the interpretation of the Italian mosasaur as a macrophagous hypercarnivorous predator, analogous to extant Orcinidae among aquatic amniotes. As in killer whales, in fact, MGGC 21876 shows a robust set of jaws with robust interlocking dentition showing extensive wear facets (Young et al., 2012 and references therein). The apical spalling facets have been commonly observed in various globidensine mosasaurines; in particular, *Prognathodon overtoni* preyed upon not only large osteichthyans but was also capable of crunching large turtle shells (Konishi et al., 2011). Some of the features in the unique combination of mandibular and dental specialisations present in *P. overtoni* and MGGC 21876 were convergently acquired by distinct lineages of large bodied predatory reptiles. For example, as in tyrannosaurid theropod dinosaurs, *P. overtoni* and MGGC 21876 show a combination of deep and robust mandible, broadly rounded rostrum with premaxillary dentition smaller than maxillary teeth, and large, robust and 'incrassate' maxillary teeth (Brochu, 2003). As in pliosaurid plesiosaurians, the Italian mosasaur shows a large head and tooth crowns with a characteristic subtriangular cross section (Massare, 1987: fig. 10). In crown morphology, MGGC 21876 shows an unique combination of features independently evolved among geosaurine crocodylomorphs: the presence of 'pseudoserrated' carinae as in *Torvoneustes*, faceted crowns as in *Geosaurus*, and a stout rostrum with robust interlocking dentition and extensive crown wear as in *Dakosaurus* (de Andrade et al., 2010; Young et al., 2012). We therefore suggest that this mosasaur frequently if not always fed on abrasive, large bodied prey items, as suggested for the above mentioned non-mosasaurid taxa, and also in *Prognathodon* (Massare, 1987; Konishi et al., 2011; Bardet, 2012a).

A number of studies have focused on habitat partitioning of large mosasaurs based on hypothesized swimming capabilities, histology, and predator-prey relations (Massare, 1988; Sheldon, 1997; Rothschild and Martin, 2005). Paleogeographic reconstructions for the western Tethyan domain at the end of the Campanian indicate a fully oceanic environment for the deposition of the Argille Scagliose Complex (Fig. 11), as documented by the repeating sequences of pelagic and turbiditic deposits from which MGGC 21876 was collected. Therefore, unlike the well-known taxa from the Western Interior Basin of North America and from northwestern Europe, MGGC 21876 extends the mosasaur record outside shallow marine and epicontinental-sea environmental settings (Bernard et al., 2010; Bardet, 2012b; Houssaye et al., 2013; Polcyn et al., in press).

11. Conclusions

In this study, we describe a new mosasaurid specimen from the Campanian of the Argille Varicolori Formation of the Northern Appenine. It represents the largest fossil reptile found in Italy to date, with an estimate body length of more than 10 m. Based on overall morphology, including dental features, the Monte Ceti specimen is referred to the genus *Mosasaurus*. The Italian mosasaur was a formidable predator with robust jaws and robust, twisted teeth equipped with equally twisted, well-developed cutting edges: a jab from such a tooth is predicted to have torn through the prey tissues in multiple planes as it penetrated the flesh. Although the large size of the specimen, the massively built mandible and some dental features present in MGGC 21876 may support its referral to *Mosasaurus hoffmanni*, most of the autapomorphies of the latter species (see Lingham-Soliar, 1995) cannot be determined in the Italian specimen. Furthermore, according to the biostratigraphic analysis presented here, we refrain from referring it to
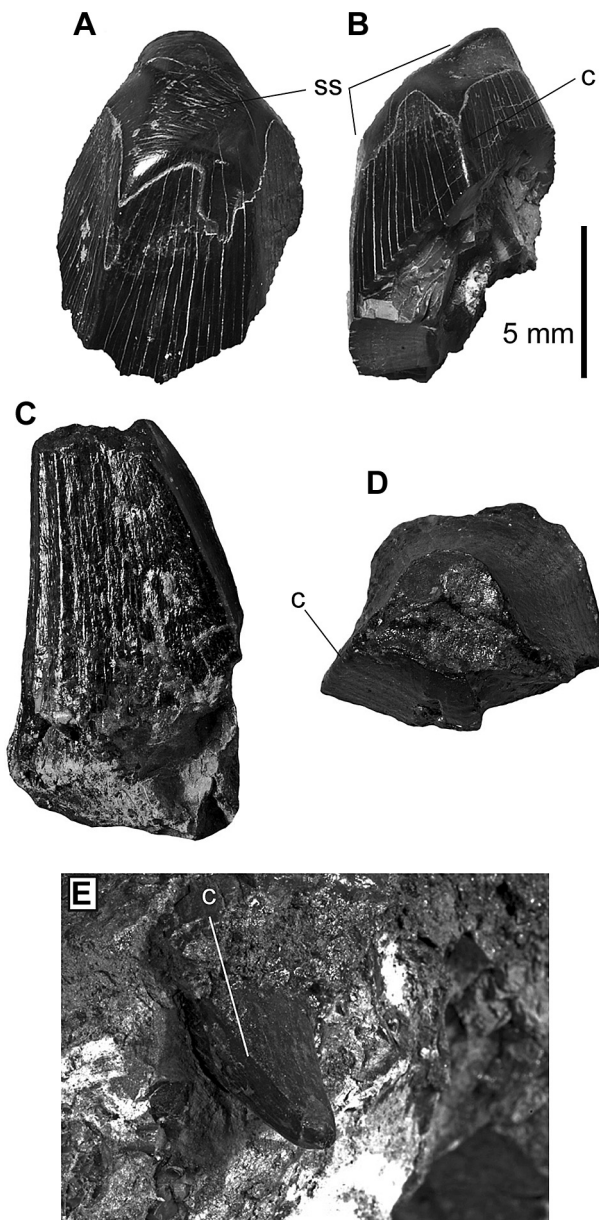
Fig. 9. A, B, first left dentary tooth crown apex in antero-apical (A) and labial (B) views. C, isolated tooth recovered in the narial region in labial, and D, apical view. E, *in situ* tooth located in the right, posterior margin of the dentary (see also Fig. 4). Abbreviation: c, carina; ss, spalled surface. Note in A that this first dentary tooth bears a total of five, semi-evenly-spaced, shallowly concave facets, making the cross-section somewhat asteroid shaped. Such a tooth is not known in any other mosasaur taxon known to date.
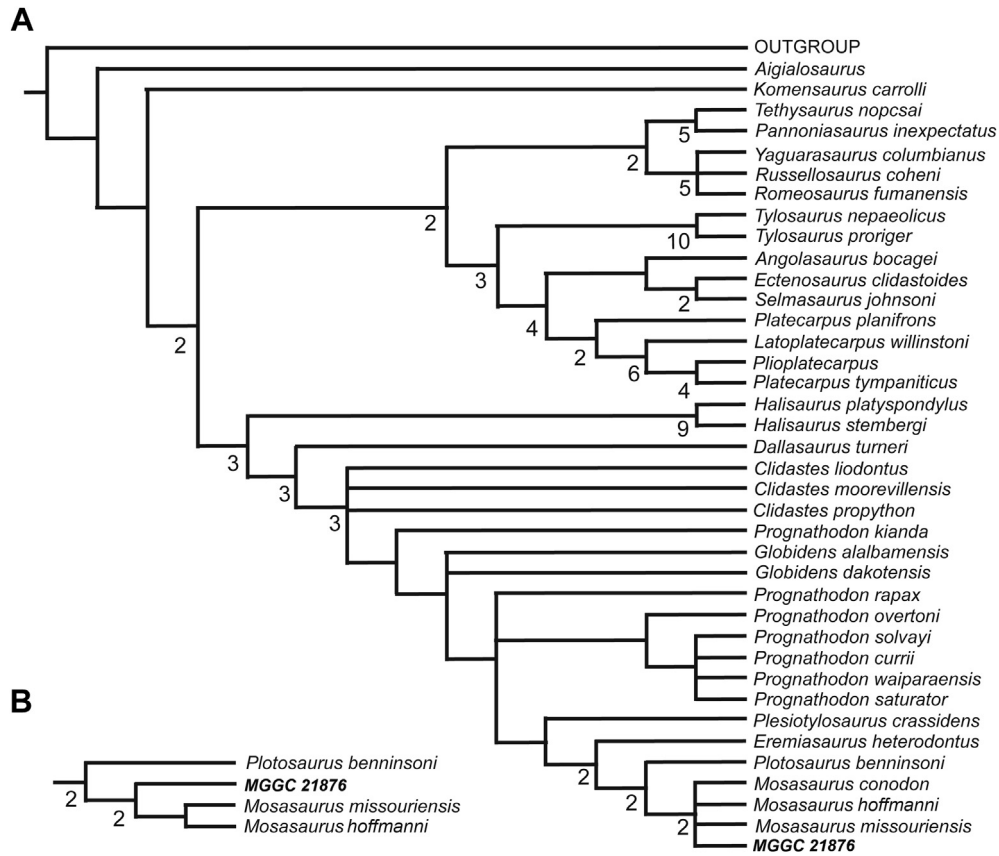
Fig. 10. Phylogenetic relationships of MGGC 21876. A, strict consensus of the shortest trees found. B, details of the topology among Mosasaurini after the *a posteriori* pruning of *Mosasaurus conodon*. Number adjacent to nodes indicate decay index values >1.
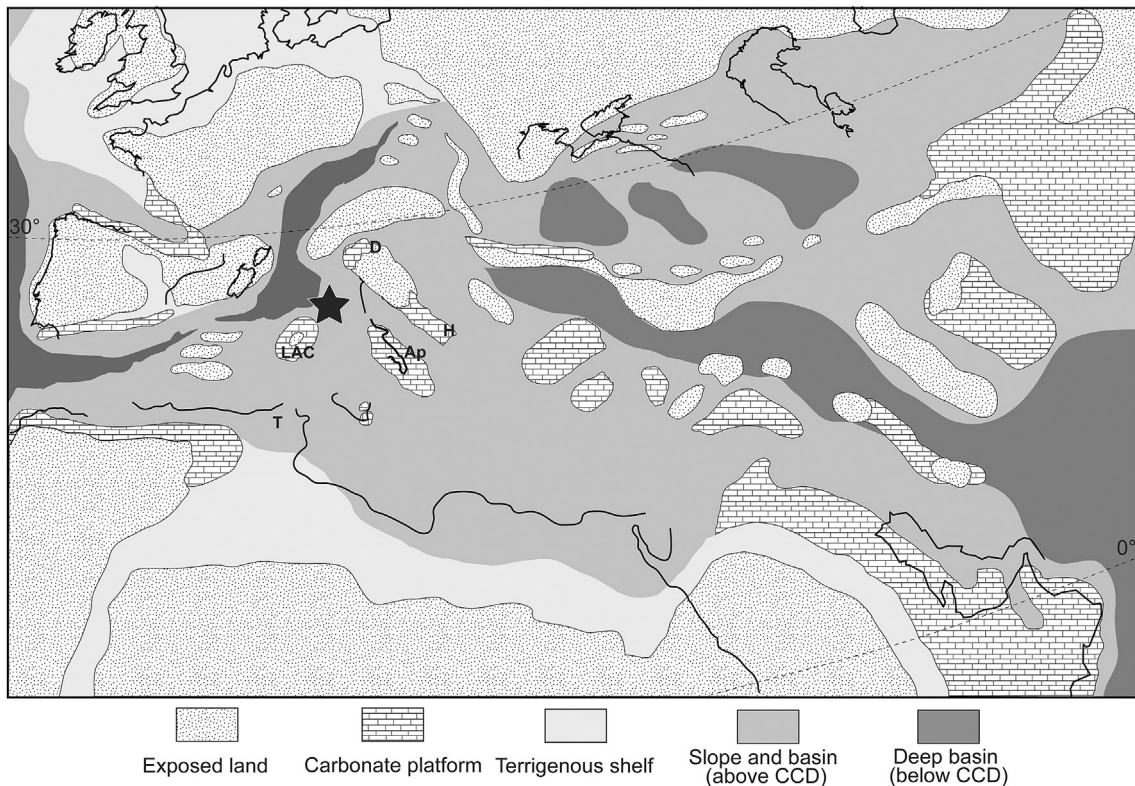
Fig. 11. Campanian-Maastrichtian palaeogeography of the Mediterranean Tethys showing the hypothesized location of MGGC 21876, after Steuber and Schluter (2012). Abbreviations: Ap, Apulian Carbonate Platform; D, Dinaric Platform; H, Hellenic; LAC, Lazio-Abruzzi-Campania Carbonate Platform; T, Tunisia.

M. hoffmanni, since the latter is not documented from the Campanian of Europe (Bardet, 2012b). The referral of the Italian specimen to *M. hoffmanni*, although not implausible, would extend the European record of that species prior to the Maastrichtian, an implication that we prefer not to endorse based on the limited diagnostic data observed in the Monte Ceti specimen. Pending further studies on laterally equivalent deposits, this study provides important new biostratigraphic data for the Argille Scagliose Formation, which represents one the most important sources of Late Cretaceous marine vertebrate remains in Italy.

Acknowledgements

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Appendix 1

New character added to the data set of Palci et al. (2013).
Character #132. Anterior marginal dentition formed by small premaxillary and rostralmost dentary teeth and larger anterior maxillary and dentary teeth with tightly interlocking occlusion pattern: absent (0); present (1). (LeBlanc et al., 2012).

The character is scored as "0" in the outgroup, Clidastes propython, Globidens dakotensis, Latoplatecarpus willistoni, Pannoniasaurus inexpectatus, Platecarpus planifrons, Platecarpus tympaniticus, Plesiotylosaurus crassidens, Prognathodon currii, Prognathodon overtoni, Prognathodon rapax, Prognathodon saturator, Prognathodon solvayi, Tylosaurus nepaeolicus, Tylosaurus proriger, and Yaguarasaurus columbianus.

The character is scored as "1" in Eremiasaurus heterodontus, MGGC 21876, Mosasaurus hoffmanni, Mosasaurus missouriensis, and Plotosaurus bennisoni.

The remaining taxa are scored as "?".

Character states of the additional OTU included in the data matrix of Palci et al., (2013).

MGGC 21876
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Appendix 2

Calcareous nannofossil discussed in the manuscript

Biscutum Black in Black and Barnes, 1959
Broinsonia parca parca (Stradner, 1963) Bukry, 1969
Broinsonia parca constricta (Stradner, 1963) Bukry, 1969
Ceratolithoides aculeus (Stradner, 1961) Prins and Sissingh in Sissingh 1977
Corollithion kennedyi Crux, 1981
Cretarhabdus Bramlette and Martini, 1964
Cribrosphaerella ehrenbergii (Arkhangelsky, 1912) Deflandre and Piveteau, 1952
Eiffellithus turriseiffelii (Deflandre in Deflandre and Fert, 1954) Reinhardt, 1965
Eiffellithus eximius (Stover, 1966) Perch-Nielsen, 1968
Eprolithus octopetalus Varol, 1992
Gartnerago obliquum (Stradner, 1963) Noel, 1970
Helenea chiastia Worsley, 1971
Kamptnerius magnificus Deflandre, 1959
Lithraphidites carniolensis Deflandre, 1963
Lucianorhabdus cayeuxii Deflandre, 1959
Lucianorhabdus maleformis Reinhardt, 1966
Micula Vekshina, 1959
Micula staurophora (Gardet, 1955) Stradner, 1963
Quadrum gartneri Prins and Perch-Nielsen in Manivit et al., 1977
Prediscosphaera Vekshina, 1959
Retecapsa angustiforata Black, 1971
Retecapsa crenulata (Bramlette and Martini 1964) Grün in Grün and Alleman, 1975
Tranolithus phacelosus Stover, 1966
Uniplanarius sissinghii Perch-Nielsen, 1986
Uniplanarius trifidus (Stradner in Stradner and Papp, 1961) Hattner and Wise, 1981
Watznaueria barnesae (Black, 1959) Perch-Nielsen, 1968
Zeugrhabdotus diplogrammus (Deflandre in Deflandre and Fert, 1954) Burnett in Gale et al., 1996
Zeugrhabdotus embergeri (Noel, 1958) Perch Nielsen, 1984

Crocodylomorph genera discussed in the manuscript

Dakosaurus Quenstedt, 1856
Geosaurus Cuvier, 1824
Torvoneustes Andrade, Young, Desoio and Brusatte, 2010

Mosasaur species discussed in the manuscript

Clidastes propython Cope, 1869
Eremiasaurus heterodontus LeBlanc, Caldwell and Bardet, 2012
Globidens dakotensis Russell, 1975
Latoplatecarpus willistoni Konishi and Caldwell, 2011
Mosasaurus conodon Cope, 1881
Mosasaurus hoffmanni Mantell, 1829
Mosasaurus missouriensis Harlan, 1834
Pannoniasaurus inexpectatus Makádi, Caldwell and Osi, 2012
Platecarpus planifrons Cope, 1874
Platecarpus tympaniticus Cope, 1869
Plesiotylosaurus crassidens Camp, 1942
Plotosaurus bennisoni Camp, 1942
Prognathodon currii Christiansen and Bonde, 2002
Prognathodon overtoni Williston, 1897
Prognathodon rapax Hay, 1902
Prognathodon saturator Dortangs, Schulp, Mulder, Jagt, Peeters and Graaf, 2002
Prognathodon solvayi Dollo, 1889
Tylosaurus nepaeolicus Cope, 1874
Tylosaurus proriger Cope, 1869
Yaguarasaurus columbianus Paramo, 1994