MOSASAURINE MOSASAURS (SQUAMATA, MOSASAURIDAE) FROM NORTHERN ITALY

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ABSTRACT—A review of the remains of mosasaurine mosasaurs from the upper Campanian–Maastrichtian of Italy is provided. The first discoveries of mosasaur material from Italy are represented by a series of isolated teeth from the Scaglia Rossa Formation north of Vittorio Veneto (late Campanian). These teeth show some similarities to Prognathodon, Liodon, and Eremiasaurus, but are not identical and probably represent a new taxon. A partial mosasaur skull found south of Reggio Emilia in 1886 is potentially a new species of Mosasaurus, although more material is needed to support this possibility. This specimen is temporarily referred to M. cf. hoffmanni. A second fragmentary mosasaur skull was accidentally discovered in 1892 north of Verona during the demolition of a school (inside one of the building stones). Based on its general morphology, size, and dentition, this second specimen can be considered as very closely related to M. hoffmanni, but its older age (early–middle Maastrichtian) suggests that it likely represents a new species of Mosasaurus. We refrain from erecting new taxonomic names for these specimens pending the discovery of new, more complete material upon which satisfactory diagnoses can be based. The paleobiogeographic distribution of Mosasaurus hoffmanni, M. cf. hoffmanni, M. beaugei, Liodon, and Prognathodon is reviewed briefly.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Mosasours are large marine lizards that lived in oceans and epicontinental seas during the Late Cretaceous, from about 95–65 million years ago (Russell, 1967; Carroll, 1988; Bell, 1997; Lindgren et al., 2011). Their fossil remains are widely distributed, and in many cases locally very abundant, within the Upper Cretaceous marine deposits on every continent including Antarctica (Russell, 1967; Bell, 1997; Caldwell et al., 2008; Fernández and Martin, 2009; Fernández and Gasparini, 2012). Their success as marine predators was likely due to the acquisition of anatomical adaptations to an active aquatic lifestyle, which included a streamlined body and a heterocercal tail in the most derived forms (Lindgren et al., 2011, 2012; Konishi et al., 2012).

The first discovery of mosasaur material from Italy comprising six teeth (NHMP 5534–5539), recovered near Santa Croce Lake (La Secca, about 15 km north of Vittorio Veneto) in northern Italy (Fig. 1), dates back to the second half of the 19th century (De Zigo, 1883). De Zigo (1883) tentatively attributed these teeth to a genus very close to Mosasaurus or Liodon (= Liodon Agassiz, 1846; Agassiz proposed the name Liodon after noting that Liodon was preoccupied and so we use Liodon here), an attribution later supported by Leonardi (1946). However, neither of these authors could match the material to any known mosasaur species and so decided to leave these fossils in open nomenclature (i.e., Mosasaurus cf. hoffmanni or Liodon cf. anceps).

Shortly after this first discovery, a partial mosasaur skull (IPUM 30200) was found in a creek (Rio del Marangone) close to the small village of San Valentino (Castellarano municipality, about 15 km south of Reggio Emilia; Fig. 1). This specimen was first classified as a crocodile by Uzielli (1887), and later named ‘Capelliniosuchus mutiensis’ by Simonelli (1897), who considered it a close relative of the metriorhynchids. More recently, Sirotti (1990) referred this specimen to Mosasaurus hoffmanni.

In 1892, only 6 years after the discovery of the mosasaur from San Valentino, a new specimen (NHMV V1001) was accidentally discovered during the construction of a school in Marzana (about 6 km north of Verona; Fig. 1). This specimen was recovered during the demolition of a wall, when one of the building stones fell to the ground and split apart revealing the partial mosasaur skull inside (Nicolis, 1900). This skull, represented by very fragmentary material, was attributed to Mosasaurus by Nicolis (1900) and Leonardi (1946).

Despite the fact that mosasaur remains have been reported from the Italian Peninsula since the end of the 19th century, these findings have only rarely been cited in the recent literature. Probably this is in part due to the lack of a precise taxonomic assignment for the materials and also because the original reports are published in old and hard-to-find journals. We believe that these specimens merit brief redescription in order to make these data more readily available to contemporary workers.

We begin with a description and taxonomic placement of the fossils, and then provide a discussion of the paleobiogeographic implications that these specimens have on our present knowledge of mosasaurine mosasaur distribution across the Tethys in the Campanian–Maastrichtian.

Institutional Abbreviations—IPUM, Palentology Museum of the University of Modena and Reggio Emilia, Modena, Italy; IRSB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; NHMP, Natural History Museum of Padua, Padua, Italy; NHMUK, Natural History Museum, London.
DESCRIPTION OF THE SPECIMENS

Teeth from La Secca (NHMP 5534–5539 and NHMP unnumbered)

The specimens consist of seven isolated teeth now curated in the Natural History Museum of Padua (Fig. 2). Six are numbered NHMP 5534–5539, and were recovered at the same locality (La Secca, north of Vittorio Veneto) and same time at the end of the 19th century; a single tooth (unnumbered specimen) was collected later at the same locality. Most of these teeth probably belong to the same taxon, because they share a number of features. All but NHMP 5537 show a very unusual combination of characters: (1) distinct apical beading (or minute anastomosing ridges) on the lingual side; (2) extremely well-developed carinae set off by longitudinal excavations; and (3) well-developed ‘serrations’ or ‘crenulations’ (we prefer the second term, because this feature appears like a series of small scale wrinkles along the edge of the carina, not as a series of sharp cutting edges).

NHMP 5539 (Fig. 2A) consists of a robust tooth crown with shallow labial grooves at its base, distinct trenchant carinæ with crenulations, subequal lingual and labial sides, and some degree of enamel ornamentation on the lingual side towards the missing tip (beading). This tooth is slightly recurved posteriorly. NHMP 5535 (Fig. 2B) is a fragment of tooth crown that lacks part of its base. It shares most features with NHMP 5539, except for the labial grooves, which were probably confined to the missing portion closer to the root. NHMP 5534 (Fig. 2C) is a well-preserved tooth crown with a very well-developed posterior carina that bears a distinct crenulation and is slightly offset labially. An anterior carina is absent. This tooth is strongly mediolaterally compressed and distinctly recurved posteriorly. Shallow grooves on the labial side run from the base of the crown up to about its midheight. NHMP 5537 (Fig. 2D), the smallest tooth in the series, lacks the tip and part of its base: its posterior edge is eroded away. A series of shallow grooves are visible on the labial side. A weakly developed carina is present on the anterior edge. No beading can be observed. NHMP unnumbered (Fig. 2E) is a large tooth crown with smooth lingual and labial sides, well-developed trenchant carinæ, and apical beading. Interestingly, the carinae of this tooth are symmetrical in mediolateral view (i.e., the tooth crown shows no posterior recurvature, so that its anterior and posterior margins are mirror images when the tooth is observed in lateral view), an unusual feature that, as far as we know, has not been reported in any mosasaur. Labial grooves are absent, but this could be because the most basal portion of the crown is missing. NHMP 5536 (Fig. 2F) is very similar to NHMP unnumbered; it shares the same symmetry of the trenchant carinæ, presence of crenulation along their edges, the apical beading, and the lack of distinct grooves on the labial side (although, again, this may be because the basal portion of the crown is missing). NHMP 5538 (Figs. 2G, 3) is a crown with well-developed trenchant carinæ and distinct crenulations. Apical beading is very coarse. Labial grooves are present and extend upwards almost to the tip. The base of the crown is missing.

Although the stratigraphic occurrence of these teeth is uncertain, the only Upper Cretaceous rocks that crop out in the area of their discovery belong to the Scaglia Rossa Formation, dated as late Campanian–Maastrichtian (Costa et al., 1996). We analyzed the rock matrix of two of these teeth (NHMP 5535–5536) in order to obtain more precise dating based on nanofossils. The nanofossil association indicates a late Campanian age (76.82–72.54 Ma) (see Supplementary Data).

The Mosasaur from San Valentino (IPUM 30200)

This specimen (Fig. 4), identified as Mosasaurus hoffmanni by Sirot (1990) (but see Discussion), belongs to the collection of the Paleontology Museum of the University of Modena and Reggio Emilia (IPUM 30200). It consists of a poorly preserved anterior portion of a mosasaur skull, including the premaxilla, left and right maxillæ, left and right dentaries, and the anterior-most portions of the frontal and right prefrontal. Some of the palatal bones are probably preserved, but this is difficult to ascertain because the jaws are preserved in a closed position.

This specimen lay for some time in a riverbed and was subjected to a considerable amount of physical erosion. As a result, the bone surface is heavily abraded, and most of the teeth are badly preserved and broken. However, it is clear that when complete, the teeth were large and robust, and that their external (labial) surfaces possessed some beading towards the base. No grooves (i.e., fluting) are present, but a weak prismatic faceting can be observed on at least two of the best-preserved teeth, which show three faint longitudinal facets on their labial surface (note: we consider as ‘facets’ flat prismatic surfaces that divide the surface of the tooth crown into longitudinal sections, not to be confused with ‘grooves’ or ‘flutes’, which are much narrower and concave). Weak striations present on the enamel are almost certainly the result of diagenetic alteration (cracking). The carinae can barely be observed due to either poor preservation or general lack of exposure, but no serrations/crenulations seem to be present. The two anterior teeth on the premaxilla were slightly procumbent, as can be inferred from the orientation of their preserved roots. The suture line between premaxilla and maxilla extends posteriorly to a position above the posterior edge of the 5th maxillary tooth. The external nares extends posteriorly to a point beyond the posterior margin of the 9th tooth position. Two small teeth preserved in isolation within the matrix that fills the external nares probably represent displaced pterygoid teeth.

Given the area of provenance of this fossil, and considering the stratigraphic range (upper Campanian–Maastrichtian) of M. hoffmanni and closely related taxa (M. cf. hoffmanni) (Jagt, 2005; Jagt et al., 2006; Bardet, 2012), this specimen probably originated either from the Argille di Viano Formation (early Palaeocene–middle Eocene, but containing reworked boulders coming from the Flysch di Monte Cassio Formation, late Campanian–late Maastrichtian) or from the Argille Varicolore di Cassio Formation (late Cenomanian–late Campanian). Both formations are constituted mainly by clays and breccias (Gasperi
FIGURE 2. Mosasaurine mosasaur from the Scaglia Rossa Formation north of Vittorio Veneto (La Secca, S. Croce Lake). A, NHMP 5539 in anterior (A1), labial (A2), lingual (A3), and occlusal (A4) views; B, NHMP 5535 in labial (B1), occlusal (B2), lingual (B3), and anterior (B4) views; C, NHMP 5534 in labial (C1), lingual (C2), posterior (C3), and anterior (C4) views; D, NHMP 5537 anterior (D1), labial (D2), and lingual (D3) views; E, NHMP unnumbered in lingual (E1), labial (E2), and anterior(?) (E3) views; F, NHMP 5536 in labial (F1), lingual (F2), and anterior(?) (F3) views; G, NHMP 5538 in labial (G1), occlusal (G2), lingual (G3), and posterior (G4) views. All scale bars equal 1 cm.
et al., 2005). Unfortunately, the specimen was preserved in a calcisphere packstone that is devoid of foraminiferans and calcareous nannofossils.

The Mosasaur from Marzana (NHMV V1001)

This specimen is now in the collections of the Natural History Museum of Verona. It consists of a partial skull of a fairly large mosasaur (the complete skull was likely about 1 m long). Only portions of the lower jaws, left maxilla, right pterygoid, and a fragment of the left jugal are preserved (Fig. 5). The generally good quality of preservation of this fossil suggests that it was part of a more complete skeleton; the cleanly severed edges that were created when the block that contains the specimen was cut to size as a building stone support this hypothesis.

This specimen was first described by Nicolis (1900), who attributed it to *Mosasaurus* based mainly on the opinion of the eminent palaeontologist Louis Dollo, to whom an image of the specimen had been sent. However, neither Dollo nor Nicolis provided a list of anatomical characters to support their conclusions.

The tooth crowns (Fig. 5C) are anteroposteriorly expanded and have almost straight posterior margins. Two distinct facets are visible on the labial side of some of the teeth. The left pterygoid is only partially preserved, but its general morphology (e.g., tooth size and orientation of the ectopterygoid process) resembles that of *Mosasaurus hoffmanni*. Only five tooth sockets are preserved, and because its anterior part is broken and missing, it is impossible to ascertain whether the original number of pterygoid teeth was comparable to the range of 8–9 reported in the above-mentioned species (Lingham-Soliar, 1995; A.P., pers. observ.).

The lithological features of the rock in which this fossil is preserved (lithotype, texture, color, thickness of the layer) allow its referral to the Scaglia Rossa Formation (Turonian–Maastrichtian; Bosellini et al., 1967). The rock encasing the specimen has been analyzed in order to obtain a more precise age range based on planktonic foraminifera and nannofossils. The age inferred from the microfossil assemblages is lower–middle Maastrichtian (see Supplementary Data).

FIGURE 3. Detail photographs of crenulated carinae and beading on the apex of NHMP 5538. A, labial view of tip of the crown; B, posterior view of tip of the crown. Both scale bars equal 1 mm.

DISCUSSION AND CONCLUSIONS

The teeth from La Secca likely belong to a mosasaurine mosasaur, with the closest affinities lying with the genera *Mosasaurus, Eremiasaurus, Liodon*, and *Prognathodon*. Their age range is consistent with the stratigraphic occurrence of all of the above-mentioned genera except *Eremiasaurus*, which so far has been reported only from the late Maastrichtian of Morocco (Russell, 1967; Lingham-Soliar, 1993; Jagt, 2005; Konishi et al., 2011; LeBlanc et al., 2012).

All teeth (except NHMP 5537) show a unique combination of distinctive features (Table 1): (1) The carinae are extremely

FIGURE 4. *Mosasaurus cf. hoffmanni* (IPUM 30200). A, photograph of skull, dorsal view; B, interpretative drawing of skull, dorsal view; C, photograph of skull, right lateral view; D, interpretative drawing of skull, right lateral view. Abbreviations: De, dentary; Fr, fragment of anterior part of frontal; Max, maxilla; Nar, external nares; Pmx, premaxilla; Prf, fragment of right prefrontal. Scale bar equals 5 cm.
FIGURE 5. *Mosasaurus cf. hoffmanni* (NHMV V1001). A, photograph; B, interpretative drawing; C, detail of the marginal dentition. Abbreviations: A, angular; C, coronoid; De, dentary; J, jugal; Max, maxilla; Pt, pterygoid; S, splenial; Sa, surangular. Both scale bars equal 5 cm.
| Characters                      | Mosasaurus hoffmanni | Liodon                  | Prognathodon         | Eremiasaurus | Mosasaurine from La Secca |
|--------------------------------|----------------------|-------------------------|----------------------|--------------|---------------------------|
| Enamel beading/anastomosis     | May be present       | May be present (e.g., in forms from Morocco, Poland, The Netherlands; see text) | Present             | Absent       | Present                   |
| Trenchant carinae (i.e., set off by longitudinal excavations) | Absent               | Present in all species except *L. mosasauroides* | Generally absent, but present in some species, e.g., *P. solvayi* and *P. giganteus* | Present (on posterior teeth) | Present                   |
| Crenulated carinae             | May be present       | Present                 | May be present       | Absent       | Present                   |
| Presence of symmetrical carinae (i.e., bilaterally symmetrical teeth) | Absent               | Absent, except for *L. sectorius*, where the teeth may show one shallow groove from the base to the middle of the crown | Generally absent, but present in *P. solvayi* and *P. waiparensis* | Present | Present |
| Labial grooves                 | May be present, but in this case they are also on the lingual side | Absent, except for *L. sectorius*, where the teeth may show one shallow groove from the base to the middle of the crown | Present             | Present       | Present                   |
| Crown facets                   | Facets may be weak, but are always present | Absent                 | Absent               | Absent       | Absent                   |
| Posterior margin of the crown  | Never straight and vertical | Straight and vertical from middle to posterior part of jaw rami | Never straight and vertical | Never straight and vertical | Never straight and vertical |
| Labial and lingual sides       | All teeth have a flatter labial side ("U"-shaped cross-section) | Subequal labial and lingual sides on all teeth except in *L. mosasauroides* and *L. sectorius*, where the labial side is flatter | Subequal labial and lingual sides | Subequal labial and lingual sides | Some teeth have a flatter labial side, others have subequal sides |
| Anterior carina on pterygoid teeth | Present               | Unknown                 | Absent               | Absent       | Absent                   |

Data for *Mosasaurus* are from Lingham-Soliar (1995), Jagt et al. (1996), Machalski et al. (2003), Bardet et al. (2004), and A.P., pers. observ.; data for *Liodon* are from Gaudry (1892), Russell (1967), Lingham-Soliar (1993); data for *Prognathodon* are from Lindgren and Schulp (2005), Konishi et al. (2011), and J. Lindgren, pers. comm. (February 2013); data for *Eremiasaurus* are from LeBlanc et al. (2012) and A.P., pers. observ.

*In *P. giganteus*, the trenchant carinae are variably present in the teeth belonging to the same dentigerous element. Moreover, in some species of *Prognathodon*, their presence may be variable ontogenetically, as suggested by two specimens of *P. overtoni* (T. Konishi, pers. comm. April 2013).
well developed and trenchant, i.e., they protrude sharply from the round, almost swollen, surface of the crown. This is a feature seen in *Liodon* (except *L. mosasauroides*), *Eremiasaurus* (posterior teeth), and *Prognathodon* (e.g., *P. giganteus* and *P. solvayi*; J. Lindgren, pers. comm.), but not in *Mosasaurus*. (2) There are well-developed crenulations along the margin of the carinae, a feature present in *Liodon*, *Mosasaurus*, *Prognathodon*, and to a lesser extent *Eremiasaurus*. (3) The labial surface of the crowns is not faceted (i.e., prismatic), in contrast with *M. hoffmanni* (*M. maximus* is likely a junior synonym of *M. hoffmanni* and shares the same dental features; Mulder, 1999), *M. beauegi*, and *M. missouriensis* (see Bardet et al. [2004] for a review of the tooth morphology of these taxa). The whole shape of the crown is different and much stouter than that of *M. leon-neri* (*M. conodon* shows the same tooth morphology, and has been considered a junior synonym of *M. leonneri* by some authors, e.g., Baird and Case [1966], and Russell [1967]), which is characterized by slender, subconical teeth that bear longitudinal grooves both labially and lingually (e.g., IRSB 3131, IRSB 3201, IRSB 3751, IRSB 4670/R28 [type]). The absence of facets agrees with the tooth morphology of *Liodon*, *Prognathodon*, and *Eremi- asaurus* (Gaudry, 1892; Konishi et al., 2011; LeBlanc et al., 2012). (4) The largest teeth show a series of wide and shallow grooves at the base of the labial side. Similar grooves can be observed also in some specimens attributed to *M. hoffmanni* (e.g., IRSB 3189, IRSB R12), but in these Belgian specimens the grooves are present also on the lingual side (based on tooth morphology, we believe that these specimens may actually represent large speci mens of *M. leonneri*). *Eremiasaurus* heterodontus shows similar grooves on the labial side of its largest teeth (A.P., pers. observ.). Labial and lingual grooves are also observed in some speci mens of *Prognathodon* (e.g., *P. solvay*, IRSB 4565), where they can extend for almost the entire length of the tooth crown. (5) All teeth with preserved tips show some sort of beading (anastomosing ridges) on the lingual side of the apical region, and to a lesser extent on the labial side (Fig. 3). This beading can extend towards the base in some of the teeth, but is always more evident close to the tip. Enamel beading can be present in *Mosasaurus* hoffmanni, but it is usually not so strongly developed and occurs mostly at the base of the tooth crowns and not on the tips (Jagt et al., 2006). Enamel beading has also been reported in *Prognathodon* (Bell, 1997; Konishi et al., 2011). (6) Some teeth have an asymmetrical cross-section like that of the teeth belonging to *Mosasaurus* hoffmanni (i.e., with a flatter labial side), but some others are more symmetrical with respect to their sagittal plane (e.g., NHMP 5539, NHMP 5535, NHMP 5538; Fig. 2A, B, G). (7) Some teeth have carinae that are symmetrical in medi olateral view (e.g., NHMP unnumbered, Fig. 2E; NHMP 5536, Fig. 2F), this feature has never been reported in *M. hoffmanni*, *Eremiasaurus*, *Liodon*, nor *Prognathodon*. (8) One tooth of the series (NHMP 5534) is strongly asymmetrical (with an almost flat labial side), has a mediolaterally compressed cross-section, and is strongly curved posteriorly. Moreover, in contrast with all other teeth in this series, it has only the posterior carina and must therefore represent a pterygoid tooth. This morphology is similar to that of the pterygoid teeth in *Prognathodon* and possibly *Eremia- asaurus* (which lacks an anterior carina on its pterygoid teeth, but the presence or absence of a posterior carina in this taxon cannot be determined), whereas the pterygoid teeth of *Mosasaurus hoff- manni* have both an anterior and a posterior carina (A.P., pers. observ.). In NHMP 5537, both the anterior and the posterior mar gins are broken, and the tip is missing. It shows a small remnant of a faint, non-serrated posterior carina, and is the smallest in the series. Because of its fragmentary nature, it is not possible to know whether or not it belongs to the same mosasaur species as all the other teeth from La Secca.

Some of the peculiar features listed above (i.e., apical beading, well-developed carinae set off by longitudinal excavations, marked crenulations, facets very weak to absent) can also be observed in other isolated mosasaur teeth from adjacent regions of the Cretaceous Tethys and neighboring areas (e.g., Morocco, The Netherlands, and Poland), and which have been referred to the nomen nudum ‘*Liodon* cf. *anceps*’ Owen, 1845 [LeBlanc et al. [2012] provide an excellent review of the taxonomic problems associated with this taxon, its type material, and the diagnosis for the taxon]. Arambourg (1952) described some unusual isolated teeth from the Maastrichtian deposits of Morocco and considered it to be a new species endemic to the North African region. He tentatively named it ‘*Mosasaurus* (Liodon) cf. *anceps*’ (note that Arambourg considered *Liodon* to be a subgenus of *Mosasaurus*, but to avoid confusion, here we will refer to this taxon simply as *Liodon* cf. *anceps*). However, a recently described species from Morocco, *Eremiasaurus heterodontus* LeBlanc, Caldwell, and Bardet, 2012, possesses teeth bearing a striking resemblance to those described by Arambourg (1952) (see also Bardet et al. [2010] and Bardet [2012], who attribute the most gracile tooth form of ‘*Liodon* cf. *anceps*’ to *Eremias- asaurus* and the most robust one to a new unnamed species of *Prognathodon*); the only differences between these specimens of *Liodon* cf. *anceps* and *Eremiasaurus* consist of the presence of shallow labial grooves and lack of enamel ornamentation (i.e., anastomosing ridges or beading) in the teeth of the latter. Teeth similar to those described by Arambourg (1952) have also been reported from the same geologic strata in Poland (Machalski et al., 2003) and The Netherlands (Kuypers et al., 1998). All these teeth share well-developed carinae set off by longitudinal excavations, labial grooves very weak to absent, mediolateral compression, and beading/anastomosis that is better developed at the tip rather than at the base of the teeth. The Italian teeth can be distinguished from the *Liodon*-like teeth found in Poland, Morocco, and The Netherlands by the presence of a series of shallow grooves on the labial side of their crowns and the absence of subvertical posterior margins.

The very well-developed trenchant carinae and their crenulation are reminiscent of the tooth crowns of *Liodon* (Owen, 1845), but as already noted by Machalski et al. (2003), the well-developed beading of the enamel seems to set apart this kind of teeth from those of any known species of *Liodon*, whose tooth crowns are smooth (see Gaudry [1892] and Lingham-Solar [1993] for a complete review of the tooth morphology in *Liodon*, but see also Lindgren [2005] for an alternative identification of some of the teeth described by the latter author). However, the largest teeth of *Liodon* are strongly convex anteri or margin and bear shallow labial grooves extending from the base to the middle of the crown (shallow labial and lingual grooves are visible at the base of the crown of two teeth from the English Chalk [NHMUK OR42937 and NHMUK OR48943] that were assigned to *Liodon anceps* [J. Lindgren, pers. comm.], but we wish to point out that these teeth may as well belong to a species of *Prognathodon*). For these reasons, we believe that the material from La Secca, although bearing some resemblance with the teeth from Poland, Morocco, and The Netherlands, should be placed either within *Eremiasaurus* or *Prognathodon*. Furthermore, we believe that their morphology indicates a closer affinity with the latter genus (enamel beading is shared with *Prognathodon* but not with *Eremiasaurus*; Table 1), and the stratigraphic age of the teeth (late Campanian) supports this conclusion.

Dealing with the problematic taxonomic issues surrounding the genus *Liodon* is beyond the scope of this study. However, we want to point out that the differences between *Mosasaurus* and *Liodon* seem small (mostly tooth morphology), and are possibly
consistent with differentiation at the species level only (LeBlanc et al., 2012). Smith-Woodward (1889) suggested synonymizing Liodon with Mosasaurus, and the same view was later held by Dollo (1893, 1924). On the other hand, Schulp et al. (2008) argued that Liodon anceps (the type species of the genus) is a nomen dubium, and that the three remaining species of Liodon (i.e., L. sectiorius, L. compressidens, and L. mosasauroides) be reassigned to the genus Prognathodon. The long suture line between the maxilla and premaxilla, which spans the space of five tooth positions, is a feature shared by Liodon and Mosasaurus (Gaudry, 1892; Lingham-Soliar, 1993, 1995; LeBlanc et al., 2012), and suggests that these two taxa are likely more closely related to each other than either is to Prognathodon. In Prognathodon, this suture line extends above only three tooth positions (Konishi et al., 2011) (Lindgren and Schulp [2010] describe a longer suture line in P. waiparensis, but we consider their material too poorly preserved to be certain). The lack of procumbent premaxillary dentition in Liodon is another feature that makes the synonymization of this genus with Prognathodon problematic (Gaudry, 1892; Lingham-Soliar, 1993).

Given the above-mentioned set of distinctive features present in the teeth from La Secca (especially the presence of symmetrical carinae in some of the teeth), it could be argued that they represent a new mosasaur taxon (i.e., a new species of Prognathodon). However, even if we strongly suspect that they represent a new species, we agree with Machalski et al. (2003:398)

FIGURE 6. Paleogeographic map of the central Tethys and neighboring areas in the latest Cretaceous (Campanian–Maastrichtian) showing the distribution of Mosasaurus hoffmanni (inclusive of M. cf. hoffmanni), Mosasaurus beaugei, Prognathodon, Liodon, and Eremiasaurus, as well as the location of the Prognathodon sp. from La Secca (map modified from Dercourt et al., 2000).
who state: “...identification of mosasaur taxa on the basis of isolated teeth and tooth crowns is fraught with difficulties [...]. The taxonomic potential of teeth in many mosasaurid species remains to be evaluated on the basis of detailed descriptions of teeth belonging to more complete, diagnostic skeletal remains.”

Moreover, it is also relevant to note that a certain amount of intraspecific variation can be observed in the tooth morphology of some living squamates as a result of aging and adaptation to a different diet (Estes and Williams, 1984). Thus, in the total absence of skeletal material we refrain from erecting a new taxon, at least until more anatomical data are available, and will refer to this mosasaur taxon as ‘Prognathodon sp. from La Secca’ in the remainder of this study.

With regard to the taxonomic placement of the mosasaur from San Valentino (IPUM 30200), the extent of the suture between the maxilla and premaxilla (up to the posterior margin of the 5th maxillary tooth), the tooth morphology (stout crowns, ‘U’-shaped cross-section, broad faceting, beading at the base of the crowns), the posteriorly expanded and dorsoventrally compressed internarial bar, and the slightly procumbent teeth of the premaxilla (which are truncated anteriorly in a slanting position) constitute a series of features that allow referral of this specimen to *M. cf. hoffmanni* (Lingham-Soliar, 1995). The lack of distinct facets and the possible absence of serrations on the carinae do not invalidate a close affinity with *Mosasaurus hoffmanni*, because the serrations are only variably present in the above-mentioned mosasaur species (Jagt et al., 2006). There is also the possibility that IPUM 30200 may represent a new species of *Mosasaurus*; however, we refrain from erecting a new taxon based only on minor differences in tooth morphology, especially in the absence of statistical studies on the intraspecific variability of the dental features that are observed in *Mosasaurus*.

As regards the mosasaur from Marzana (NHMV V1001), the straight posterior margins of its tooth crowns suggest a closer affinity to *Liodon* than to *Mosasaurus*; however, the presence of a pair of distinct facets on the labial side of the crowns of NHMV V1001 distinguishes this specimen from any known species of *Liodon*. Labial prismatic facets are typical of the largest species of *Mosasaurus* (*M. hoffmanni*, e.g., IRSB 3189, IRSB R12) and *M. beaugei*. A closer affinity with *M. hoffmanni* can be established on the basis of the limited lateral exposure of the splenial (in *M. beaugei*, the splenial is visible laterally along half of the length of the dentary; Bardet et al., 2004), and also because in *M. beaugei* the facets on the labial surface of the teeth are more numerous (3–5; Bardet et al., 2004). Given the similarities and differences noted above, we agree with Nicolis (1900) in his placement of this specimen in the genus *Mosasaurus* and further suggest an assignment to *Mosasaurus cf. hoffmanni*, the specimen being late Maastrichtian in age like *M. hoffmanni sensu stricto* (Jagt, 2005).

The material described here is informative with regards to the paleobiogeographic distribution of *Mosasaurus hoffmanni* and closely related forms (i.e., *M. cf. hoffmanni* and *M. beaugei*), and the paleobiogeographic distribution of *Prognathodon*. In terms of the biostratigraphic distribution of *M. hoffmanni* and closely related taxa, generally referred to in the literature as *M. cf. hoffmanni*, these forms have been reported as occurring from late Campanian to late Maastrichtian. The Italian data provide evidence for the presence of these forms in the central regions of Tethys where they had not been reported before, and the list of countries where remains of *M. cf. hoffmanni* are present can be extended to include Belgium, northwest Bulgaria, Denmark, France, northern Germany, northern Italy, The Netherlands, central Poland, and northern Turkey (Fig. 6) (Gaudry, 1892; Bardet and Tunoglu, 2002; Reich and Frenzel, 2002; Machalski et al., 2003; Lindgren and Jagt, 2005; Jagt et al., 2006; Tunoglu and Bardet, 2006; Bardet, 2012; this work). Possible remains of *M. cf. hoffmanni* have also been reported from Argentina (Fernández and Gasparini, 2012) and African countries such as the Democratic Republic of Congo and Niger (Lingham-Soliar 1991, 1994; Bardet, 2012). If Mulder’s (1999) proposal to synonymize *M. hoffmanni* with *M. maximus* is accepted, then the overall geographic distribution of this taxon is even wider, including many localities in the U.S.A. (e.g., Alabama, Missouri, New Jersey, Tennessee, and Texas). From this very wide distribution, it is evident that *M. hoffmanni*, *M. cf. hoffmanni*, and *M. beaugei* were part of the radiation of a group of very opportunistic mosasaurs capable of exploiting different marine environments regardless of proximity to the coastline. The same seems to hold true for *Prognathodon*, which occurs on both sides of the Atlantic (Europe and North America; Russell, 1967; Bardet, 2012) and in different areas of the Tethys that were divided by stretches of relatively deep waters (i.e., between the Chalk Basin and the central Tethys) (Leonardi, 1946; Kuypers et al., 1998; Machalski et al., 2003; Lindgren, 2004; Jagt, 2005; Bardet et al., 2012; Buffetaut and Bardet, 2012: Fig. 6). Interestingly, the genus *Liodon*, although showing an intercontinental distribution (*L. aniceps*, *L. compressidens*, and *L. mosasauroides* from Europe, *L. cf. aniceps* from Morocco, and *L. sectorius* from North America), seems to have been more constrained to epicontinental waters, as suggested by its absence within deposits that correspond to the open marine environments of the central Tethys (Gaudry, 1892; Lingham-Soliar, 1993; Bardet, 2012). This distribution could reflect the food preferences of this taxon, which in turn could have made it dependent on particular relatively shallow-water habitats. Alternatively, if as suggested by Bardet et al. (2010) and Bardet (2012) the isolated teeth of *Liodon cf. aniceps* from Morocco are to be referred to a different genus (or genera), then the distribution of *Liodon* proper may be explained more in terms of latitudinal, and hence temperature, preferences, with *Liodon* being a genus whose distribution was confined to northern, relatively cooler, latitudes.

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