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Découverte de Mosasauroidea (Squamata) dans le Crétacé supérieur (Campanien inférieur) continental de Villeveyrac–L'Olivet, Sud de la France

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ABSTRACT

New mosasauroid material from the Villeveyrac-L'Olivet mine (Hérault, southern France) is described. This historical and fossiliferous bauxite mine has yielded from the same stratigraphical level (Early Campanian) diverse continental vertebrates, including fishes (Lepisosteidae and Phyllodontidae), amphibians (Albanerpetondidae and the oldest representative of the Palaeobatrachidae), turtles (Solemydidae and Bothremydidae), squamates (Mosasauroidea), crocodilians (Eusuchia), dinosaurs (Rhabdodontidae, Nodosauridae and Dromaeosauridae), and a possible pterosaur. The mosasauroid specimens represent different individuals of a single taxon, belonging to a large plesiopedal tethysaurine-like form (about 3 meters long). This discovery adds to previous reports of plesiomorphic freshwater mosasauroids in the Late Cretaceous dinosaur-bearing sites of the European archipelago.

RÉSUMÉ

Du nouveau matériel de mosasaures provenant de la mine de l'Olivet à Villeveyrac (Hérault, Sud de la France) est décrit. Cette mine de bauxite historique et fossilifère a livré, dans le même niveau stratigraphique (Campanien inférieur), divers vertébrés continentaux, comprenant des poissons (Lepisosteidae et Phyllodontidae), des amphibiens (Albanerpetondidae et le plus ancien représentant des Palaeobatrachidae), des tortues

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(Solemydidae et Bothremydidae), des squamates (Mosasauroidea), des crocodiles (Eusuchia), des dinosaures (Rhabdodontidae, Nodosauridae et Dromaeosauridae) et un possible ptérosaure. Les spécimens de mosasaures correspondent à différents individus d'un même taxon, appartenant à une grande forme plésiopédale (jusqu'à 3 m de long), possiblement de Tethysaurinae. Cette découverte s'ajoute aux mentions antérieures de mosasauroïdes plésiomorphiques d'eau douce, provenant de sites à dinosaures du Crétacé supérieur de l'archipel européen.

1. Introduction

Most continental reptile assemblages from the Late Cretaceous of southern France come from localities of Late Campanian to Late Maastrichtian age (e.g. Allain and Pereda-Suberbiola, 2003; Buffetaut et al., 1999; Csiki-Sava et al., 2015; Le Loeuff, 1991; Valentin et al., 2012). However, a few occurrences of Early Campanian vertebrates are known, notably in Languedoc (Buffetaut et al., 1997). Early Campanian beds are present and well exposed in the Villeveyrac-Mèze Basin, inside vast Albian-Cenomanian open cast bauxite mines (Berger et al., 1981), defined and called by some authors (Buffetaut et al., 1996, 1997) the Villeveyrac Basin or the Villeveyrac locality. The Villeveyrac-Mèze syncline is filled by 800 m of Upper Cretaceous floodplain and fluvio-lacustrine deposits (Freytet, 1971), containing numerous and distinct dinosaur eggs and eggshells (Garcia and Vianey-Liaud, 2001; Garcia et al., 2000). These Lower Campanian deposits have also yielded mosasauroid remains found in the L'Olivet mine, which are the subject of the present study.

Mosasauroids were large marine squamates that underwent a spectacular radiation during the Late Cretaceous, with 30 genera and 70 species described. They attained a cosmopolitan distribution favoured by marine routes largely opened at this time before disappearing during the K–Pg extinction event (i.e. Bardet et al., 2014, 2015; Polcyn et al., 2014). Mosasauroids are mainly characterised by a large elongated skull and a long 'varanoid' body, as well as by their tooth morphologies (Bardet et al., 2015). They display a large range of ecologies, as demonstrated by considerable variation in their body proportions, sizes and morphology.

During their evolutionary history, they evolved three morphotypes illustrating steps in their gradual adaptation to increasingly open-sea habitats: small (1–2 m long) plesiopedal and plesiopelvic mosasauroids (with terrestrial-like limbs and a sacrum) found from the Early Cenomanian to the Early Turonian in the Mediterranean Tethys and Mexico; medium sized (1.5–3 m long) plesiopedal and hydropelvic mosasauroids (with terrestrial-like limbs but no sacrum) known from the Middle Turonian of Morocco and Texas; and large (3–15 m long) hydropedal and hydropelvic mosasauroids (with flippers and no sacrum), the 'true mosasauroids', cosmopolitan open-sea active swimmers known from the Late Turonian to the end of the Maastrichtian (see Bardet et al., 2014 for details).

Up to now, only 'true mosasauroids' have been described from the Latest Cretaceous. These derived mosasauroids, mainly adapted to an offshore marine life, were particularly widespread in almost all putative Campanian-Maastrichtian marine outcrops worldwide, especially in North America (Western Interior Seaway), Europe (Belgium and The Netherlands), Africa (Morocco, Angola) and New Zealand (see Bardet et al., 2014, 2015).

As a logical result of this marine life, mosasauroids remain very scarce or absent in coeval contemporaneous continental deposits. In Europe, of particular importance is the recent description of *Pannoniasaurus* Makádi et al. (2012) in the Santonian continental outcrop of Iharkút, Hungary (Makádi et al., 2012). *Pannoniasaurus* is not only a plesiomorphic tethysaurine mosasauroid of the plesiopedal/hydropelvic grade (see above), but also the only infrafamilial mosasauroid taxon reported from these Late Cretaceous European continental outcrops. Other indeterminate isolated mosasauroid and/or aquatic varanoid remains, consisting only of largely undiagnostic vertebrae, have been mentioned in several continental outcrops otherwise characterized – like Villeveyrac-L'Olivet – by herpetofaunas including mainly dinosaurs, pterosaurs, crocodyliforms, chelonians and squamates. These are the Late Campanian-Maastrichtian outcrops of Aveiro and Viso in Portugal (Antunes and de Lapparent de Broin, 1988; Bardet et al., 2008; Sauvage, 1897–1898), as well as several Late Campanian outcrops of Languedoc in southern France (E. Buffetaut and L. Makádi, pers. comm; Buffetaut et al., 1999; Csiki-Sava et al., 2015; Laurent et al., 2002).

The mosasauroid remains here described provide important information on the scarcely known and poorly understood invasion of the freshwater environment by mosasauroids.

Abbreviations: UP: Université de Poitiers (France); USTL: Université des Sciences et Techniques du Languedoc, Montpellier (France).

2. Geological context

The L'Olivet mine site is located in the northern part of the Villeveyrac-Mèze Basin (Hérault Department, Languedoc Region, southern France), about 30 km west of Montpellier (Fig. 1A). This historical and fossiliferous bauxite quarry (Fig. 1B) was first reported by Bleicher (1872) and its fossil assemblage (some scattered bones) was first studied by Gervais (1877) and later by Lapparent (1947).

The outcrop comprises a succession of fine sandstones, clays, mostly pedogenized marls and calcretes. The fossiliferous level consists of lignite grey clays at the base of the section (Fig. 1C), which contains an accumulation of transported bones and plant remains, rich in organic matter and ferruginous sulphur crust.

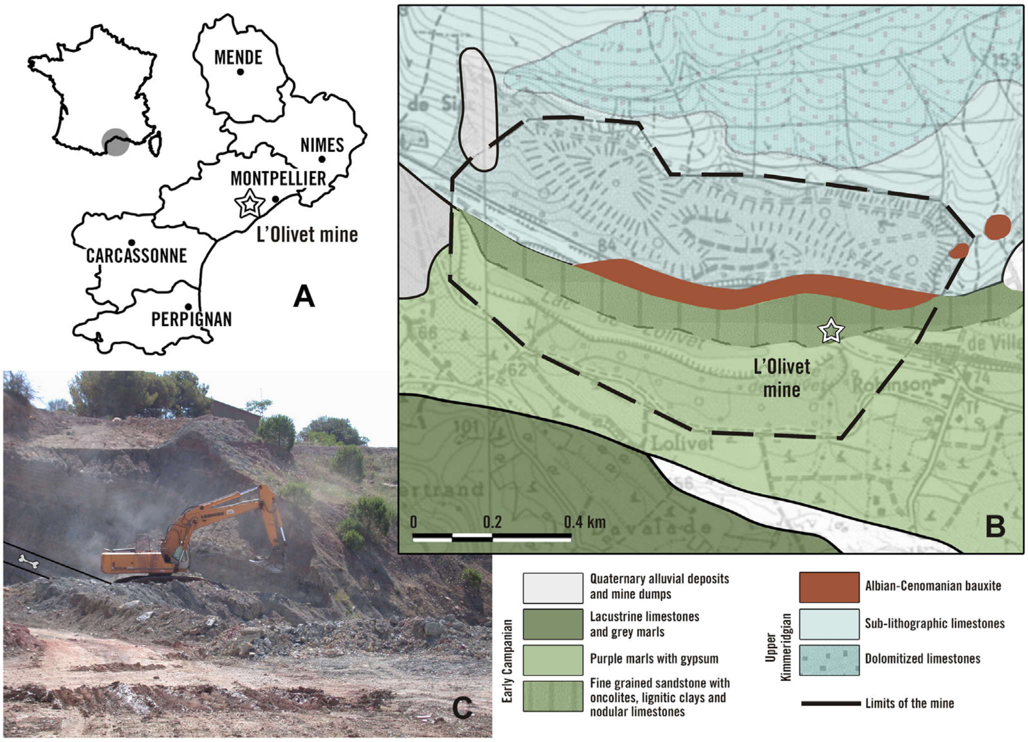

Fig. 1. (Colour online.) Geographical location (A) and geological map (B) of the site "L'Olivet mine" from Villeveyrac, indicated by a star. C. View of the excavation and the stratigraphic section. The fossiliferous level is represented by a bone symbol.

Fig. 1. (Couleur en ligne.) Localisation géographique (A) et carte géologique (B) du site « mine de l'Olivet » à Villeveyrac, indiqué par une étoile. C. Vue des fouilles et de la section stratigraphique. Le niveau fossilifère est représenté par un os.

Field campaigns, first conducted in 1998 by X. Valentin, A. Cabot ('La Plaine des Dinosaures' society), J. Sudre and M. Vianey-Liaud (University of Montpellier II), then directed by the research association 'Palaios' (X. Valentin), excavated numerous well-preserved vertebrate fossils. A faunal list was established by Buffetaut et al. (1996) from historical and private collections (G. Costa and X. Valentin). This list, however, is a composite of the vertebrates found at the different levels of the excavations (called Mas de Siau, Roquemale, Usclades and L'Olivet) in the bauxite mines.

Since then, a faunal list, from diverse specimens collected in the same fossiliferous level, located at the base of the section up to the bauxite one, was completed (Table 1). It includes bony fishes (Lepisosteidae and Phyllodontidae; L. Cavin, pers. comm.), amphibians (Albanerpetondidae and the oldest representative of the Palaeobatrachidae), squamates (the mosasauroid specimens described here), turtles (*Solemys* and *Polysternon provinciale*), crocodylians (the eusuchians *Allodaposuchus* and *Acynodon*), a possible pterosaur, and dinosaurs. The latter includes two ornithopods (the endemic European *Rhabdodon* and an indeterminate small form), one ankylosaur (the nodosaurid *Struthiosaurus languedocensis* Garcia and Pereda-Suberbiola, 2003), and at least one theropod (referred to as Dromaeosauridae indet.).

The fossil reptiles were found in association with plant macro-remains (eudicot angiosperms; B. Gomez, pers. comm.) and mollusks, including bivalves (*Unio* spp., *Corbicula*, *Lucina*, *Tapes*), and numerous gastropods (*Campylostylus*, *Cyclophorus*, *Melania* and *Viviparus*; Freytet, 1971 and X.V. pers. determ.), consistent with a quiet freshwater environment (Freytet, 1971; X.V., pers. obs.). This malacofauna is typical of the lacustrine "Fuvelian" (a regional stratigraphic unit for the continental stage established in southern France; Babinot and Durand, 1980a,b) of Provence.

In addition, the sampling made by Carquet (1977) has led to the recognition of the presence of charophytes, ostracodes and pollen (see Babinot et al., 1983). Charophytes include *Dughiella* sp., *Michochara* sp. and *Peckichara pectinada*. Ostracods are represented by *Paracandona gardanensis* and *Virganocypris*. Finally, the pollen association consists of *Extratriporopollenites* sp., *Heidelbergipollis tilioides*, *Interporopollenites proporus*, *Suemegipollis triangularis* and *Vacuopollis microconcavus*.

The site of L'Olivet mine was inferred to be of Early Campanian age (= "Fuvelian"), based on biostratigraphic arguments, among which is the composition of the vertebrate assemblage (Buffetaut et al., 1997). The gastropods, charophytes and palynomorphs found in equivalent beds elsewhere in the basin provide a consistent age (Feist and Freytet, 1983). In addition, a magnetostratigraphic study made along the whole sequence of the site by Benammi et al. (2006) clearly confirms this Early Campanian age (chron C33.1r corresponding to an age of 83.5 to 79.5 Ma, correlated by Gradstein et al., 2012 to 83.6 to 80 Ma).

Table 1
List of the vertebrate fossils from the lignite bearing bed of the lower part of the series (Early Campanian) in the L'Olivet mine from Villeveyrac (Hérault Department). Established on the basis of newly collected material and after Buffetaut et al. (1996), de Lapparent de Broin and Murelaga (1999), Tong and Gaffney (2000) and Garcia and Pereda-Suberbiola (2003). In bold, the taxon whose fossils are described in this paper.

Tableau 1
Liste des fossiles de vertébrés provenant du niveau ligniteux à la base de la série dans la carrière (Campanien inférieur) de la mine de l'Olivet à Villeveyrac (Hérault). Établie sur la base de nouvelles récoltes de matériel et d'après Buffetaut et al. (1996), de Lapparent de Broin et Murelaga (1999), Tong et Gaffney (2000) et Garcia et Pereda-Suberbiola (2003). En gras, le taxon dont les fossiles sont décrits dans ce travail.

Chondrichthyes
  Hybodontidae indet.

Osteichthyes
  Lepisosteidae: cf. *Atractosteus*
  Teleostei: Phyllodontidae indet.

Lissamphibia
  Allocaudata: Albanerpetontidae indet.
  Anura: Palaeobatrachidae indet.

Squamata
  Mosasauroidea:?Tethysaurinae indet.

Testudines
  Stem Testudines - Solemydidae: *Solemys* aff. *vermiculata*
  Pan-Pleurodira - Bothremydidae: *Polysternon provinciale*

Crocodyliformes
  Eusuchia: *Allodaposuchus* sp.
    Acynodon sp.
    ?Alligatoroidea indet.

Dinosauria
  Theropoda - Dromaeosauridae indet.
  Ankylosauria - Nodosauridae: *Struthiosaurus languedocensis*
  Ornithopoda - Rhabdodontidae: *Rhabdodon* sp.
    Ornithopoda indet.

Pterosauria
  Pterosauria indet.

3. Material and methods

The vertebrate material is housed in part in the collections of the University of Poitiers (UP) under the numbers UP-VIL, VIL corresponding to the name of locality Villeveyrac-L'Olivet. The other part is catalogued and deposited in the University of Montpellier (USTL- OLV CV: coll. Valentin, who donated his collection to this establishment in 1998).

The squamate specimens include a frontal (UP-VIL-10-9), several vertebrae of which ten are here described (UP-VIL-10-03, UP-VIL-10-04, UP-VIL-10-10, UP-VIL-10-11, UP-VIL-10-12, UP-VIL-10-13, UP-VIL-cast 1588, USTL-OLV 3CV, USTL-OLV R 05, USTL-OLV R05 CV), and two limb bones (metacarpal: UP-VIL-10-06; tibia: UP-VIL-10-08). They mostly show the same preservation and colour (dark grey). The fossils were mostly recovered from the same stratigraphical level and in relatively close association. As a result, a comparison of the respective size of the bones has been made (see details in Description and comparisons parts) and indicates that at least some of them could belong to the same individual, for example the frontal, the tibia and possibly also the first metacarpal, as well as some vertebrae. Variation in vertebral centrum length (CL) combined to homogeneous anatomical characters, suggest that, although several individuals are present, only one taxon appears to be represented. Pending the discovery of more complete specimens, the whole material will be described here as a single new taxon, although too little can be established about its anatomy to justify naming it.

4. Systematic palaeontology

REPTILIA Linnaeus, 1758
SQUAMATA Oppel, 1811
MOSASAUROIDEA Gervais, 1853
? TETHYSAURINAE Bardet and Pereda-Suberbiola, 2005 (in Bardet et al., 2005)
Genus and species indeterminate

4.1. Description and comparisons

Skull

Frontal (UP-VIL-10-9; Fig. 2A–B)

The frontal represents the only mosasauroid skull bone found up to now in Villeveyrac-L'Olivet. With the exception of its anterior part, it is almost complete and of relatively large size (preserved length = 80 mm). Both posterolateral corners are broken off but the left one (Fig. 2A–B) permits us to reconstruct their shape and lateral expansion with a relative degree of certainty. The posterior right corner exhibits an oval puncture (about 5 × 10 mm) with sharp and elevated edges (especially the medial one), suggesting a bite mark. As a whole the bone is long and narrow (width above orbits = 29 mm). Posterior to the orbits, although incomplete, the posterolateral corners of the frontal appear to have been sharp and laterally expanded (estimated width at the parietal contact = 50 mm). The margins are almost straight above the orbits, and then curve medially anteriorly (Fig. 2A). Anteriorly, the frontal is incomplete, and its contribution to the narial emargination cannot be assessed. Posteriorly, the suture for the parietal is straight, vertical and with low interlocking ridges (cf. Bell, 1997). The dorsal surface of the frontal bears discrete ornamentations. The area between the posterior corners is slightly concave and lined by transverse longitudinal ridges posteriorly, as well as with discontinuous small ridges converging towards the middle of the bone anteriorly. Anterior to this area that ends around the middle of the orbits, the frontal bears some slight longitudinal ridges and a slight median elevation that in most mosasaurs extends anteriorly onto the internarial bar. In ventral view, the median groove for the olfactory canal is only partly embraced ventrally by a descending process. It is largely open anteriorly, and then narrows at the orbital level. Posteriorly, there is a large surface that cannot be strictly considered a tabular boss (sensu Bell, 1997), inclined at about 45° from the horizontal for the cerebral hemispheres. This surface bears rough striations and two slender notches located posterolaterally to the median groove (Fig. 2B). The sutural surface for the prefrontal is much larger than that for the postorbitofrontal and they are not in contact, indicating that the frontal takes part in the dorsal margin of the orbit. Both represent large horizontal overlapping zones.

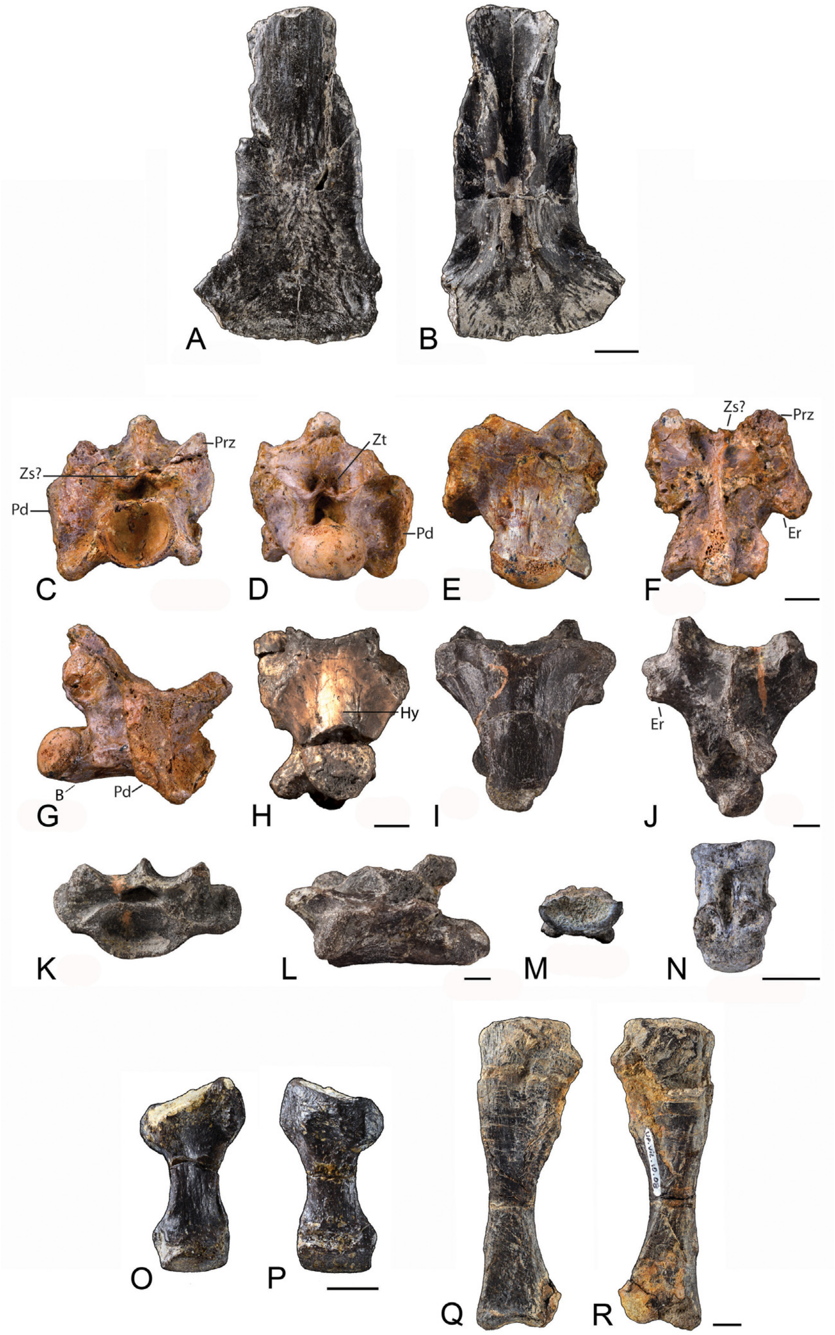

Fig. 2. (Colour online.) Mosasauroid remains,?Tethysaurine indet., Early Campanian of Villeveyrac–L'Olivet, southern France. A–B. Frontal UP-VIL-10-9 in dorsal and ventral views. C–G. Cervical vertebra UP-VIL-10-11. H. Cervical vertebra UP-VIL-cast 1588. I–L. Dorsal vertebra UP-VIL-10-10. M–N. Anterior caudal vertebra UP-VIL-10-03; in anterior (C, K, M), posterior (D), ventral (E, H, I, N), dorsal (F, J), right lateral (G), and left lateral (L) views. O–P. Metacarpal UP-VIL-10-06 in anterior and posterior views. Q–R. Tibia UP-VIL-10-08, in anterior and posterior views. B: bump; Er: epidiapophyseal ridge; Hy: hypapophysis (here only the anterior part originating from the centrum is observable); Pd: paradiapophysis; Prz: prezygapophysis; Zs: zygosphene; Zt: zygantrum. Scale bars equal 1 cm.

Fig. 2. (Couleur en ligne.) Restes de mosasauroïdés,?Tethysaurine indet. du Campanien inférieur de Villeveyrac–L'Olivet, Sud de la France. A–B. Frontal UP-VIL-10-9 en vues dorsale et ventrale. C–G. Vertèbre cervicale UP-VIL-10-11. H. Vertèbre cervicale UP-VIL-cast 1588. I–L. Vertèbre dorsale UP-VIL-10-10. M–N. Vertèbre caudale antérieure UP-VIL-10-03 ; en vues antérieure (C, K, M), postérieure (D), ventrale (E, H, I, N), dorsale (F–J), latérale droite (G), et latérale gauche (L). O–P. Métacarpien UP-VIL-10-06 en vues antérieure et postérieure. Q–R. Tibia UP-VIL-10-08 en vues antérieure et postérieure. B : bosse ; Er : ride épidiapophysaire ; Hy : hypapophyse (ici seulement la partie antérieure originaire du centrum est observable) ; Pd : paradiapophyse ; Prz : prézygapophyse ; Zs : zygosphène ; Zt : zygantrum. Échelles : 1 cm.

Following Bell (1997), the following combination of characters indicates that this frontal belongs to a plesiomorphic mosasauroid: lateral sides sinusoidal (char 9-0), no median dorsal keel (char 12-0), sharp posterior ala (char 13-0), no contact of prefrontal and postorbital sutures ventrally (char 30-0), no tabular boss anterior to the frontal-parietal suture (char 16-0) is straight and simple, frontal suture with parietal opposing and with low interlocking ridges (char 17-0), no frontal invasion of the parietal and parietal foramen considered as located far from the frontal suture (char 24-0). On the contrary, the following character is apomorphic for the studied frontal: frontal-prefrontal contact consisting in a broad horizontal ventral surface (char 15-1). The narial emargination (char 11) cannot be checked as this region is broken. However, contrary to Bell (1997), the olfactory canal partly embraced ventrally by descending processes of the frontal (Bell, 1997, char 14-1) and the long and narrow morphology of the frontal (Bell, 1997, char 10-1) are here considered as plesiomorphic for mosasauroids (when compared with *Varanus*). Especially, the long and narrow morphology of the frontal in general looks like that of plesiomorphic mosasauroid forms, such as *Aigialosaurus*, *Russellosaurus* and *Tethysaurus* (N.B., pers. obs.). This morphology strongly differs from that of derived mosasauroids, which usually possess large triangular frontal tables (Bell, 1997). It differs from that of *Aigialosaurus* from the Cenomanian-Turonian of Croatia (see Dutchak and Caldwell, 2006) in having more sinusoidal lateral margins. It differs from that of *Russellosaurus* from the Turonian of Texas (Polcyn and Bell, 2005), which exhibits more convex lateral borders and a well-defined triangular surface for the cerebral hemispheres. It roughly looks like that of *Tethysaurus* from the Turonian of Morocco (Bardet et al., 2003) in its general morphology, but in *Tethysaurus* (like in *Russellosaurus*) the triangular area for the cerebral hemispheres is much sharper. No frontal has been described for *Pannoniasaurus*, from the Santonian of Hungary (Makádi et al., 2012), the only mosasauroid genus currently known from continental deposits. However, an unpublished specimen from the same outcrop (courtesy of L. Makádi, Budapest) looks similar to that of UP-VIL-10-9 (N.B., pers. obs.). Pending both the description of the Hungarian material and the discovery of additional material in Villeveyrac-L'Olivet, the frontal here described is referred to an indeterminate plesiomorphic mosasauroid, most probably belonging to the Tethysaurine clade sensu Bardet et al. (2005). The size of the frontal, as compared with the *Tethysaurus* holotype, indicates an animal probably about 3 meters long (N.B., pers. obs.).

Vertebrae

General. Ten vertebrae are available for study. Their original positions along the vertebral column were estimated after comparisons with extant lizards and fossil pythonomorphs. The vertebral material consists of two cervical vertebrae (UP-VIL-10-11 being more posterior than UP-VIL-cast 1588; Fig. 2C–H), six dorsal vertebrae (USTL-OLV 3CV, USTL-OLV R 05, USTL-OLV R05 CV, UP-VIL-10-10, UP-VIL-10-12 and UP-VIL-10-13; Fig. 2I–L), one caudal (UP-VIL-10-03; Fig. 2M–N), and one indeterminate vertebra (UP-VIL-10-04). There are important size differences between the specimens. The two cervical vertebrae are of similar size (CL = 44.7 mm in UP-VIL-10-11, CL = 45.7 in 1588), the two dorsal vertebrae USTL-OLV R 05 and UP-VIL-10-10 as well (CL = 61.9 and 60.4, respectively), whereas the others are of various sizes (CL = 50.2 in USTL-OLV 3CV, CL = 41.7 in USTL-OLV R05 CV, CL = 33.0 in UP-VIL-10 12, CL = 20.3 in UP-VIL-10-03, CL = 10.2 in UP-VIL 10 13). Despite size differences, suggesting different individuals (the largest vertebrae are comparable in size to those of *Tethysaurus*), these vertebrae show, beyond natural intracolumnar variability, similar anatomical features suggesting that they belong to the same taxon.

All vertebral centra are procoelous, triangular in ventral view (Fig. 2E, H, I), and clearly lack pachyostosis. They are widened anteriorly because of the lateral extension of the paradiapophyses but are rather straight thereafter. There is no precondylar constriction. In dorsal view, vertebrae are wider anteriorly than posteriorly, especially because of the lateral extension of the paradiapophyses (Fig. 2F, J). Indeed, prezygapophyses are not strongly laterally extended (at less than 45°), although the width between the prezygapophyses is larger than across the postzygapophyses. Prezygapophyses rather strongly project anteriorly, extending well beyond the anterior border of the cotyle (Fig. 2G, L). Prezygapophyses are much inclined on the horizontal and prezygapophyseal facets are elongated (Fig. 2J). The narrowest part of the interzygapophyseal constriction is positioned posteriorly, at about two thirds of the neural arch length (Fig. 2F, J). Zygapophyses lie clearly above the floor of the neural canal and above paradiapophyses (Fig. 2C, K). The epidiapophyseal ridge is sharp posterior to the dorsal border of the paradiapophysis and even seems to protrude posterolaterally, forming a convexity at this place. Only UP-VIL-10-11 displays a well-preserved zygantrum (Fig. 2D), although apparently no zygantral facet is present. Zygosphenes are not preserved although a V-shaped poorly preserved structure in the two cervical vertebrae (Fig. 2C, F) may represent rests of rudimentary notched zygosphenes. The neural canal is subtriangular (with a trilobate aspect) and much smaller than the cotyle, both in height and width (Fig. 2C, K). The cotyle is ovoid (Fig. 2K). The posterior borders of the neural arch are concave. In posterior view, the neural spine is thick and rather short. Only sufficiently well-preserved on vertebrae UP-VIL-10-11, it seems to rise behind the zygosphene, at the level of the posterior limit of the prezygapophyses, in a very gentle slope that increases progressively posteriorly (Fig. 2G). It also markedly widens posteriorly and ends in a large knob. Posteriorly, it does not seem to extend beyond the condyle. Paracotylar, subcentral, lateral, and/or zygantral foramina are present, although their occurrence and number vary. The gently convex ventral surface of the cervical vertebra UP-VIL-cast 1588 suggests that a hypapophysis was present, although the posterior portion of the centrum is incomplete and probably bore only a small peduncle (Fig. 2G). The ventral surface of UP-VIL-10-11 is nearly flat, and probably bore only a small peduncle (like in the varanoid squamate *Pachyvaranus*; Houssaye et al., 2011). All dorsal vertebrae display a shallow sagittal furrow that originates directly posterior to the cotyle, where it is the deepest, and becomes shallower posteriorly to a flat end.

Cervical vertebrae (UP-VIL-10-11, UP-VIL-cast 1588; Fig. 2C–H)

In the cervical vertebrae, the axis of the cotyle-condyle system appears straight. Paradiapophyses extend well below the ventral border of the cotyle (Fig. 2C, G). Observation of the most anterior cervical vertebra (UP-VIL-cast 1588) suggests that the hypapophyseal peduncle is co-ossified with the centrum (Fig. 2H). However, it cannot be described, as the posterior part of the centrum is eroded ventrally (Fig. 2H).

Paradiapophyseal articular facets appear rather posteriorly located in the anterior most (preserved) cervical vertebra (although still in the centrum first half), as compared to the other vertebrae; they gradually move anteriorly, from posterior cervical to posterior dorsal vertebrae. They are located much posteriorly to the posterior limit of the prezygapophyses in cervicals (Fig. 2G), which is not the case in dorsal vertebrae (Fig. 2L). In the posterior cervical, paradiapophyses are dorsoventrally well expanded and their dorsal part bends posteriorly (Fig. 2G).

Dorsal vertebrae (USTL-OLV 3CV, USTL-OLV R 05, USTL-OLV R05 CV, UP-VIL-10-10, UP-VIL-10-12 and UP-VIL-10-13; Fig. 2I–L)

Dorsal vertebrae lack any trace of swelling on the ventral face of the centrum (Fig. 2I, L). The dorsal vertebrae preserved are considered rather posterior ones based on the fact that the ventral border of the paradiapophyses lies well above the ventral base of the cotyle (Fig. 2K). Paradiapophyses are located anteriorly; their dorsal part curves posteriorly (Fig. 2L), as in the cervical vertebrae. However, they are positioned much more dorsally than in cervicals and the paradiapophyseal facet is shorter dorsoventrally. The axes of the cotyles and condyles are inclined, the cotyle facing anteroventrally and the condyle being oriented posterodorsally (Fig. 2L).

Anterior caudal vertebra (UP-VIL-10-03; Fig. 2M–N)

The poorly preserved fragmentary vertebra UP-VIL-10-03 bears both transverse processes and peduncles for articulation with haemal arches; it is thus an anterior caudal. The transverse processes are broken off; their bases show that they are located anteriorly, originate from the dorsal part of the centrum clearly above the level of the cotylar ventral rim. The centrum is much longer than wide and high. The cotyle is ovoid (Fig. 2M). The centrum also displays a sagittal groove in ventral view (Fig. 2N). Two ventral peduncles for articulation with chevron bones are located posteriorly (Fig. 2N).

Discussion. All vertebrae are procoelous, with dorsoventrally depressed cotyles and condyles. The axis of the cotyle-condyle system is oblique in (at least) dorsal vertebrae; the hypapophysis originates from the centrum; there seem to be articulated caudal chevrons; the narrowest part of the interzygapophyseal constriction, as seen in dorsal view, occupies a posterior position. These vertebrae are thus characteristic of the Varanoidea sensu Lee (1997), i.e. the Varanidae, Helodermatidae and Pythonomorpha sensu Lee (1997) following Lee (2009). Intracolumnar variation in the axis of the cotyle-condyle system has already been described in varanoid lizards (e.g. *Arcanosaurus*; Houssaye et al., 2013). The presence of a zygosphene-zygantrum system within these taxa defines the Pythonomorpha (Lee, 1997). The occurrence of a well-developed zygantrum (although articular facets could not be observed) and the possible zygosphene indicate that such a system may have been present. Moreover, the vertebrae differ from those of *Varanus* in e.g., the absence of precondylar constriction, the size and trilobate shape of the neural canal, from Helodermatidae and Lanthanotidae in the triangular shape of the centrum in ventral view (A.H. pers. obs.; Rieppel, 1980).

The general vertebral morphology is clearly distinct from that observed in snakes (e.g. wider across the prezygapophyses than across the postzygapophyses, absence of prezygapophyseal processes and absence of sagittal keel on precloacal vertebrae). The clear absence of pachyostosis distinguishes the present taxon from most stem-ophidiomorphs (sensu Palci and Caldwell, 2007), the pythonomorph *Carentonosaurus* Rage and Néraudeau (2004) and the unnamed "pythonomorph from Touraine" (Houssaye, 2010) (see Houssaye, 2013). The shape of the centrum in ventral view is distinct from the Y-shape (marked by a strong width reduction just behind the paradiapophyses) observed in the non-pachyostotic stem-ophidiomorphs *Dolichosaurus* and *Coniasaurus* (Caldwell, 1999, 2000). In addition, the articulation of the zygapophyses is nearly horizontal in these two taxa (A.H., pers. obs.). Although diagnostic characters for mosasauroid vertebrae are almost lacking, the shape of the centrum, lateral projection and anterior position of the paradiapophyses, the relative size of the neural canal, in accordance with the general size of the vertebrae, strongly suggest a mosasauroid affinity. Prezygapophyses project much more anteriorly and are more strongly inclined on the horizontal than in the plesiopedal and plesiopelvic mosasauroids (sensu Bell and Polcyn, 2005; Caldwell and Palci, 2007; A.H., pers. obs.).

The Villeveyrac-L'Olivet material is distinct from most hydropedal mosasauroids, notably in the relatively long centrum, the obliquity of the cotyle-condyle system in (at least) dorsal vertebrae, and the lack of reduction or vertical orientation of the zygapophyses in the dorsal region. The shape of the centrum in ventral view differs from *Dallasaurus*, where it is more elongated, cylindrical and convex in ventral view (Bell and Polcyn, 2005). The material cannot be distinguished from *Tethysaurus*, based on the original description (Bardet et al., 2003), but also based on the combination of the following observations: prezygapophyses strongly projecting anteriorly and not so much laterally, and much inclined on the horizontal; prezygapophyseal facets elongated; sharp epidiapophyseal ridge posterior to the dorsal border of the paradiapophysis, protruding posterolaterally; dorsal centra flat with a sagittal shallow furrow; and caudal vertebra centrum (at least in anterior caudals) much longer than wide and high. However, the impossibility to determine if a true zygosphene-zygantrum system occurs prevents us from attributing this material to *Tethysaurus*. However, it differs from *Pannoniasaurus* (*Tethysaurus*'s sister taxon) in the occurrence of paracotylar foramina (Makádi et al., 2012).

Limbs

Metacarpal (UP-VIL-10-06; Fig. 2O–P)

The first right metacarpal is a rather large bone (length = 37 mm; proximal width = 22 mm; distal width = 18 mm). It is long and not twisted. The proximal end is expanded into a shallow transverse oval cup for articulation with the distal carpal row. This cup is bordered laterally, medially and posteriorly by large crests. The distal end is more slender that the proximal one. It has a convex hemi-circular rolling surface for articulation with the proximal phalanx. This shape permits great extension and flexion movements but restricted lateral ones. Because of the development of both proximal and distal extremities, both lateral and medial surfaces of the shaft are concave in dorsal and ventral views. Both dorsal and ventral surfaces are almost smooth.

As a whole, this first metacarpal is comparable in shape to that of the extant *Varanus*, though being more robust in general proportions, and of basal mosasauroids for which this bone is known (N.B., pers. obs.). In general, the first metacarpal is more than one third of the tibia length in mosasauroids whereas it is less than 1/3 in *Varanus* (N.B. pers. obs.). The respective length of the first metacarpal and of the tibia (see description below) from Villeveyrac-L'Olivet (MC1: 37 mm; Tibia: 108 mm) indicates that these two bones probably belong to the same taxon and individual (a hypothesis under which the ratio was more than 1/3), suggesting that the MC1 probably belonged to a plesiopedal mosasauroid rather than to a varanoid (sensu Bell and Polcyn, 2005).

Tibia (UP-VIL-10-08; Fig. 2Q–R)

The preserved right tibia is slightly crushed, especially its proximal end. It is a long and narrow bone, its length being approximately three times greater than its proximal width (see Table 2). Though slightly crushed, the shaft was probably almost flat and not bowed in life. Both anterior and posterior margins are slightly concave, the anterior more than the posterior one. The dorsal (extensor) surface of the tibia is flat and bears on its proximo-anterior part the cnemial crest; though broken, it appears slightly developed. The ventral (flexor) surface is also almost flat but, because of the larger condyle expansion it bears a proximo-medial domed relief. The proximal articulation for the femur is larger than the distal one. It is composed of two flat condyles, the posterior being larger than the anterior one, both separated by a slight oblique groove. The distal articulation is saddle-shaped for articulation with the astragalus. Both epiphyses are clearly ossified.

In hydropedal mosasauroids (sensu Bell and Polcyn, 2005), the tibia is generally a short bone, being slightly longer than wide (Russell, 1967). The rather long and narrow morphology of UP-VIL-10-08, in which the proximal extremity represents about 1/3 of the total length of the bone, looks like that of basal mosasauroids (Caldwell, 1996). These proportions differ from those of limbed terrestrial squamates, such as *Varanus*, in which the tibia is a much more elongate and gracile bone, its proximal extremity representing about 1/4 of the total length (see Table 2). More especially, the Villeveyrac-L'Olivet tibia resembles that of plesiopedal/plesiopelvic mosasauroids in which this bone is preserved (*Aigialosaurus*, *Carsosaurus*, *Komensaurus* and *Haasiasaurus*; see references in Table 2). However, UP-VIL-10-08 differs from all these mosasauroids by several characters that could indicate as a whole that it belongs to a more derived mosasauroid, possibly of the plesiopedal/hydropelvic grade. They are:

- clearly ossified epiphyses;
- a proximal width/length ratio (see Table 2) indicating a shorter and wider bone;
- a twice or three times larger size, indicating an animal measuring probably around 3 m long (a size noteworthy in agreement with the one estimated from the frontal).

4.2. Implications

The respective size of the bones and the fact that they have been found in relative close association indicate that at least some of them could belong to the same individual. As well, the anatomical characters of the bones indicate that probably only one squamate taxon is represented in the Villeveyrac-L'Olivet continental assemblage. The combination of characters found on both the frontal, the vertebrae and possibly the tibia, identifies the taxon as a basal mosasauroid probably of the plesiopedal/hydropelvic grade and belonging to the Tethysaurinae clade (sensu Makádi et al., 2012). On the basis of the size estimations made on the frontal, the tibia and the largest vertebrae, the Villeveyrac-L'Olivet mosasauroid was probably a large animal about 3 meters long, with limbs poorly adapted to an aquatic life.

The occurrence of such a basal mosasauroid in the continental outcrop of the Villeveyrac-Mèze Basin, though appearing at first sight surprising, is not so unexpected and, on the contrary, rather reinforces the idea of the occurrence of freshwater mosasauroids, a group until recently considered as strictly marine. Indeed, several reports of mosasauroid remains in comparable Late Cretaceous continental outcrops of Europe have been made in Hungary (Makádi et al., 2012), Portugal (Antunes and de Lapparent de Broin, 1988; Bardet et al., 2008; Sauvage, 1897–1898), and southern France (E. Buffetaut and L. Makádi, pers. comm; see Csiki-Sava et al., 2015). It is not impossible that some large varanoid vertebrae mentioned by Buffetaut et al. (1999) and Laurent et al. (2002) could belong to the same, or at least a closely related mosasauroid.

The ecological implications of the occurrence of such an aquatic taxon in these continental palaeoenvironments remain unresolved, though several hypotheses can be proposed. As noted above, the Villeveyrac-L'Olivet mosasauroid was a rather large animal, about 3 m long. *Pannoniasaurus* of Hungary was larger, probably up to 6 m long (see Makádi et al., 2012) and some vertebrae found in southern France are also relatively large (E. Buffetaut and L. Makádi, pers. comm.). At least in Villeveyrac-L'Olivet, the faunal list (see Table 1) indicates that large aquatic predators are lacking as the crocodyliforms are both poorly represented and of moderate size. The mosasauroid of Villeveyrac-L'Olivet, because of its relatively large size, could represent one of the largest known predators in the aquatic zones of this continental environment, as noted previously for *Pannoniasaurus* (Makádi et al., 2012). Finally, though mosasauroids have acquired ovoviviparity very early in their evolution, indicating that they probably were freed from the terrestrial realm (Caldwell and Lee, 2001) and gave birth in open oceanic habitats (Field et al., 2015), it cannot be ruled out that these relatively

Table 2
Comparison of the tibia size and proportions in plesiomorphic mosasauroids in which this bone is known and in some *Varanus* species (N.B. pers. obs.), with mention of the used references.
Tableau 2
Comparaison de la taille et des proportions du tibia chez les mosasauroïdés plésiomorphes chez lesquels cet os est connu et chez quelques espèces de *Varanus* (N.B. obs. pers.), avec indication des références utilisées.

Taxa	Length (mm)	Proximal width (mm)	Distal width (mm)	Ratio PW/L	Reference
Vallecillosaurus	29	8.7	7.2	0.3	Smith and Buchy (2008)
Haasiasaurus	28–29				Polcyn et al. (1999)
Aigialosaurus dalmaticus	33				Polcyn et al. (1999), Dutchak and Caldwell (2006)
Lauragais bucchichi	36	9		0.25	Kornhuber (1901), Dutchak and Caldwell (2009)
Carsosaurus	50	14	10	0.28	Kornhuber (1893)
Komensaurus	?				Caldwell and Palci (2007)
Varanus varius MNHN AC 1910-12	58.5	14.2	8.9	0.24	This work
Varanus rudicollis MNHN AC 1983-6	66.5	19	12	0.28	This work
Villeveyrac taxon	**108**	**35**	**25**	**0.32**	**This work**

protected freshwater continental environments could have been used by more basal mosasauroids as nurseries.

5. Conclusions

Mosasauroid remains have been discovered in the Upper Cretaceous continental deposits of the L'Olivet mine, in the Villeveyrac-Mèze Basin, near the city of Montpellier (Hérault Department, Languedoc Region, southern France). These remains were found disarticulated but closely associated with the bones of other vertebrates, such as dinosaurs, crocodyliforms, turtles, lissamphibans, osteichthyans, chondrichtyans, and possibly pterosaurs. The presence of plant remains, bivalves and gastropods in the fossiliferous level suggest a quiet freshwater environment. Based on magnetostratigraphic and biostratigraphic (i.e., gastropods, charophytes and the palynomorph association) data, the L'Olivet mine is inferred to be of Early Campanian age. The mosasauroid material consists of a skull (frontal) bone and a dozen postcranial elements, including ten vertebrae and two limb bones (metacarpal, tibia). Several individuals are probably represented in the assemblage; based on the size of the frontal, tibia and some vertebrae, the largest individuals could be about 3 m long. The anatomical characters observed in the bones indicate that probably only one squamate taxon is represented in the site. The combination of characters found on the frontal, the vertebrae and the tibia is typical of a plesiomorphic member of Mosasauroidea. Pending further discoveries, the Villeveyrac-L'Olivet mosasauroid is here tentatively referred to Tethysaurine indet. The vertebrae are indistinguishable from those of *Tethysaurus* from the Turonian of Morocco, and differ from *Pannoniasaurus* from the Santonian of Hungary in having paracotylar foramina. The Villeveyrac-L'Olivet frontal closely resembles that of *Tethysaurus* (this element is unknown in *Pannoniasaurus*). The limb bones (mostly unknown in Tethysaurinae so precluding comparisons) – and especially the tibia, are similar to those of plesiopedal mosasauroids. Despite its fragmentary nature, the Villeveyrac-L'Olivet mosasaurid is considered to be a plesiopedal form of mosasauroid. After Iharkút (Hungary) and Aveiro-Viso (Portugal), this is the third unambiguous report of mosasauroid remains from Late Cretaceous dinosaur-bearing sites of the European archipelago. The occurrence of tethysaurine mosasauroids in close association with terrestrial vertebrates suggests that these animals were probably more abundant in these environments than previously thought, possibly representing predators in these vertebrate communities, and could also indicate that at least plesiomorphic mosasauroids used these freshwater environments as nurseries. It contributes to our knowledge of the currently poorly known and understood invasion of the freshwater environment by the most famous and diversified clade of marine squamates, the mosasauroids.

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