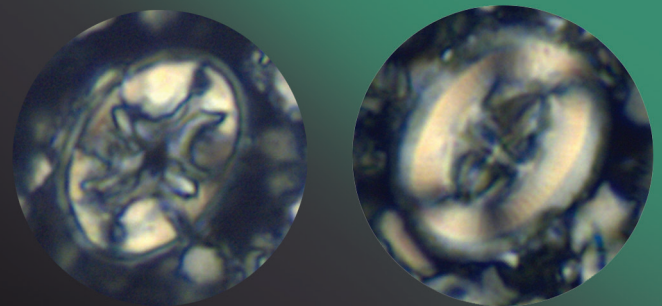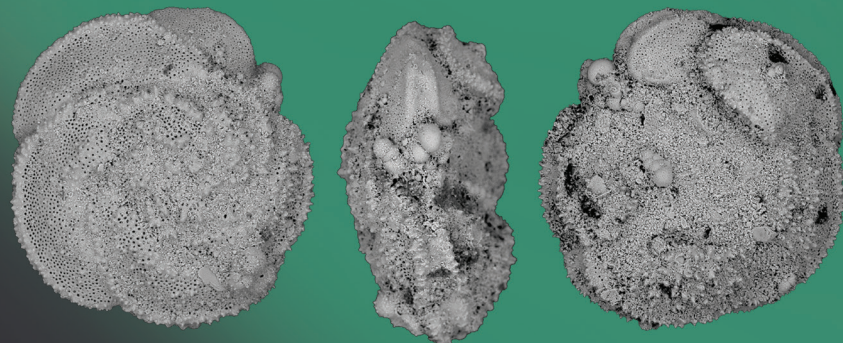# Rediscovery of "*Liodon*" *asiaticum* Répelin, 1915, a Mosasaurini (Squamata, Mosasauridae, Mosasaurinae) from the Upper Cretaceous of the vicinity of Jerusalem – Biostratigraphical insights from microfossils

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Rediscovery of "*Liodon*" *asiaticum* Répelin, 1915, a Mosasaurini (Squamata, Mosasauridae, Mosasaurinae) from the Upper Cretaceous of the vicinity of Jerusalem – Biostratigraphical insights from microfossils

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ABSTRACT

Briefly mentioned in 1915 by the palaeontologist Répelin, the mosasaurid *Liodon asiaticum* Répelin, 1915 was found by a missionary to Africa, Father Ruffier, in Late Cretaceous strata near Jerusalem (without further details on the exact provenance). This material was never described in detail, figured, or revised and was recently rediscovered in the collections of the Muséum d'histoire naturelle of Marseille (Provence, southern France). Here we describe and figure for the first time this material, which now includes more specimens than the original lot mentioned by Répelin, and we propose new systematic assignments for the identified specimens. First of all we demonstrate that the five original vertebrae briefly described by Répelin represent a composite assemblage and are not diagnostic at the specific level. Thus *Liodon asiaticum* should be considered a *nomem dubium*. The most complete and diagnostic specimen belongs to a Mosasaurini (Mosasaurinae) *incertae sedis*, close to *Mosasaurus* Conybeare, 1822 and *Plotosaurus* Camp, 1951, as shown by the unique configuration of its frontal-parietal-postorbitofrontal complex. The two other specimens are identified as indeterminate Mosasaurinae. The study of several groups of microfossils (calcareous nannofossils, planktonic foraminifera and palynomorphs) found in the white chalk preserved with most of the bones constrains the age of these mosasaurid remains to the lower part of the middle Campanian (*C. plummerae* (Gandolfi, 1955) / *G. rosetta* (Carsey, 1926) and CC18 / UC14-15a Zones). This corresponds to the local Mishash Formation that crops out extensively East of Jerusalem (Mount of Olives and surroundings). Father Ruffier probably collected these bones in one of the outcrops of this formation, possibly not very far from where he worked and lived (Saint-Anne Community in Jerusalem). These chalky levels, common in the Middle East, represent a shallow and rather open marine environment, possibly near-shore.

KEY WORDS
Upper Cretaceous,
Israel,
Mosasauridae squamate,
calcareous nannofossils,
planktonic foraminifera,
palynomorphs.

RÉSUMÉ

Redécouverte de "Liodon" asiaticum *Répelin, 1915, un Mosasaurini (Squamata, Mosasauridae, Mosasaurinae) du Crétacé supérieur des environs de Jérusalem – Éclairage biostratigraphique grâce aux microfossiles.*
Brièvement mentionné en 1915 par le paléontologue Répelin, l'espèce de mosasauridé *Liodon asiaticum* Répelin, 1915 fut trouvée par un missionnaire d'Afrique – le Père Ruffier – dans le Crétacé supérieur des environs de Jérusalem (sans plus de précision). Ce matériel ne fut jamais décrit en détails, ni figuré, ni révisé et a été récemment retrouvé dans les collections du Muséum d'histoire naturelle de Marseille (Provence, Sud de la France). Ici nous décrivons et figurons pour la première fois ce matériel qui comprend maintenant bien plus de spécimens que le lot originel mentionné par Répelin, et proposons une nouvelle attribution systématique pour les différents spécimens identifiés. Tout d'abord, nous démontrons que les cinq vertèbres originelles brièvement décrites par Répelin représentent un assemblage composite et n'étant pas diagnostiques au niveau spécifique, *Liodon asiaticum* doit être considéré comme un *nomem dubium*. Le spécimen le plus complet et le plus diagnostique appartient à un Mosasaurini *incertae sedis* (Mosasaurinae), proche de *Mosasaurus* Conybeare, 1822 et *Plotosaurus* Camp, 1951, comme le montre la configuration unique de son complexe frontal-pariétal-postorbitofrontal. Les deux autres spécimens sont attribués à des Mosasaurinae indéterminés. L'étude de plusieurs groupes de microfossiles (nannofossiles calcaires, foraminifères planctoniques et palynomorphes) présents dans la craie blanche encore préservée avec la plupart des os, permet de contraindre l'âge de ces restes de mosasauridés à la partie inférieure du Campanien moyen (Zones *C. plummerae* (Gandolfi, 1955) / *G. rosetta* (Carsey, 1926) et CC18 / UC14-15a). Ceci correspond à la formation locale Mishash, qui affleure largement à l'Est de Jérusalem (Mont des Oliviers et alentours). Le Père Ruffier a probablement récolté ces ossements dans un des affleurements de cette formation, possiblement non loin de l'endroit où il travaillait et vivait (Communauté Sainte-Anne de Jérusalem). Ces niveaux crayeux, fréquents dans tout le Proche-Orient, représentent un environnement marin peu profond et ouvert, possiblement proche du rivage.

MOTS CLÉS
Crétacé supérieur,
Israël,
squamate Mosasauridae,
nannofossiles calcaires,
foraminifères
planctoniques,
palynomorphes.

INTRODUCTION

In 1915, the geologist and palaeontologist Joseph Répelin briefly mentioned in the *Comptes rendus Sommaires de l'Académie des Sciences* the occurrence of a new species of mosasaurid in the "Late Cretaceous around Jerusalem". Nothing more concerning the geographical and stratigraphic provenances of the specimen was mentioned.

The specimen was found by Father Jules Ruffier (1861-1948), a member of the Missionaries of Africa (also called the White Fathers), a Roman Catholic society of apostolic life founded in 1868 that still exists today. He spent many years, from 1884 to 1914 and from 1918 to 1926, in the Saint-Anne Community of Jerusalem located in the northeastern part of the Old City of Jerusalem (Fig. 1A), and was in charge of the Small Seminary of this community (Anonymous 1949; Father F. Richard, pers. comm.).

Répelin (1915) wrote in his short note that he was expecting details about the discovery from Father Ruffier, but that the increasingly difficult relationships with Syria and Palestine prevented that. As a result, he decided to give a preliminary description of the material already sent to him – five vertebrae – and intended to publish more details in a future paper. He thus very briefly described these five vertebrae and compared them to some vertebrae of *Liodon* described by Cope (1875). He concluded that the size differences observed between these vertebrae and those of several species of *Liodon* (which were not

specified) demonstrated that the mosasaurid of Jerusalem did not belong to any known species of this genus. As a result, he proposed the new species *Liodon asiaticum*, without however specifying the holotype / type series or proposing a diagnosis for it, a common situation at that time.

No additional article was ever written by Répelin on this subject and, since that time, the specimen was never studied, described in detail or figured, so it fell into oblivion. Recently, however, it was rediscovered during storage and inventory work in the collections of the Muséum d'histoire naturelle of Marseille (MHNM, Provence, southern France) (S. Jouve, pers. comm.).

Today, the material comprises the five original vertebrae mentioned by Répelin, plus 32 additional unpublished skull bones and vertebrae, for a total of 37 bones kept under the global collection number MHNM.0.419.0 and with an old label indicating the whole material as being the holotype of Répelin's (1915) new species (see details in Part "Origin and composition of the material" and Table 1).

The unpublished additional specimens were probably sent to Répelin (or to someone else at the MHNM) later at an unknown date. Unfortunately, neither additional information nor letters from Father Ruffier, which could have mentioned details of the geographical provenance of the material and when it was sent to Marseille, were found in the Museum of Marseille (S. Jouve, pers. comm.), nor in the archives (in Paris and Jerusalem) of the Missionaries of Africa (Fathers F. Richard and F. Bouwen, pers. comm.).
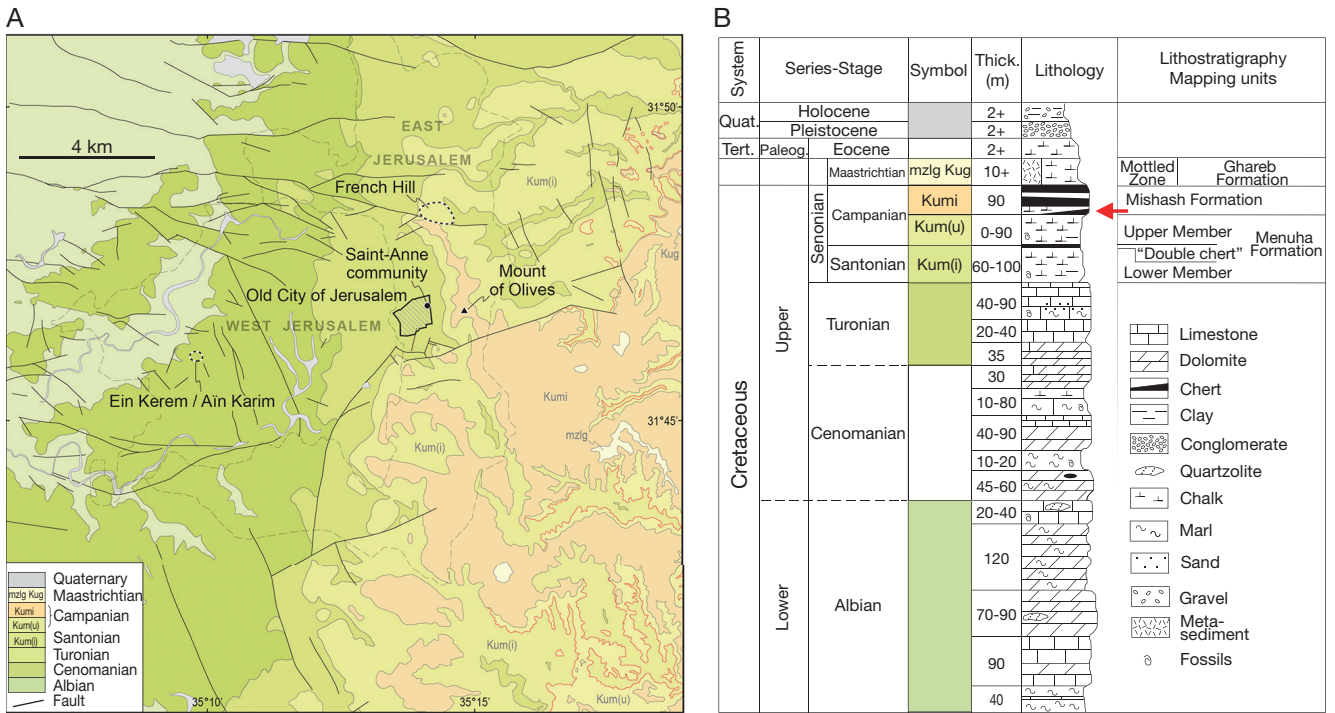
Fig. 1. — Possible geographical (**A**) and stratigraphical (**B**) provenance of the mosasaurid remains. The fossil remains come from the lower part of the Middle Campanian, probable Mishash Formation (red arrow), possibly of a zone located northeast of Jerusalem, between the Saint-Anne Community and the French Hill. Saint-Anne Community is the place where Father Ruffier lived, Ain Karim/Ein Kerem and French Hill the two properties the Saint-Anne Community had (see details on text). Map and log modified from Sneh & Avni (2011).

The aims of this paper are: 1) to describe and figure for the first time this material as a whole, then to discuss and propose a systematic assignment; 2) to determine its stratigraphic setting by studying the micropalaeontological remains in the matrix attached to most of the bones; and 3) to circumscribe as best as possible the geographic provenance of these mosasaurid remains by stratigraphic (age obtained from micropalaeontological analyses), geological (outcrops of corresponding age around Jerusalem) and historical (Father Ruffier's life and habits in Jerusalem) data.

MATERIAL AND METHODS

MOSASAURID REMAINS
Origin and composition of the material
37 bones are preserved under the single number MHNM.0.419.0, including the five original vertebrae described by Répelin (1915) on which he erected the new species *Liodon asiaticum*, as well as 32 unpublished additional bones (see details below) (Table 1). The material as a whole is labelled as follows: "Gift of Father Ruffier – *Mosasaurus asiaticus* (sic) Rep. – Large Pythonomorph – Fragments of skull and vertebrae – Around Jerusalem – Holotype" (translated from French). The fact that all these bones are preserved and labeled together could imply

that they – at least – come from the same outcrop and represent the complete set of bones discovered by Father Ruffier.

Several arguments reinforce this hypothesis. First, all these isolated bones clearly belong to mosasaurid squamates. Second, the material as a whole exhibits the same preservation (see section "Preservation"). Third, a similar matrix (used for the microfossil analyses – Parts "Microfossils" and "Stratigraphic and possible geographic provenances of the mosasaurid remains") is preserved on most bones. Finally, most bones, though isolated, are of comparable size and exhibit a concordant suite of characters (Part "Anatomical and nomenclatural comments on the material").

As a result of these observations, it is here hypothesized that: 1) all bones have the same geographical and stratigraphical provenances, one of the purposes of this work being to determine both as best; and 2) most bones belong to a single large individual composed of skull bones as well as dorsal and caudal vertebrae, whereas a few others are attributed to two other specimens (Part "Anatomical and nomenclatural comments on the material"). It should be noted that the same method has already been applied to discriminate morphotaxa based on isolated specimens occurring in the same outcrop (e.g. Houssaye *et al.* 2011; Makádi *et al.* 2012).

Preparation and cladistic analysis
The bones were first mechanically prepared, using a pneumatic micro-engraver to remove the matrix preserved with most bones and used for micropalaeontological analyses (Parts

TABLE 1. — MHNM 0.419.0: Mosasaurid squamate, Campanian, Jerusalem. List of remains with their anatomical identification and assignment to the different identified specimens.

Reference	Collection no.	Material	Specimens
Répelin (1915)	1	Dorsal	Specimen 1
	2	Median caudal	
	3	Terminal caudal	
	4	Median caudal	Specimen 2
	5	Median caudal	Specimen 3
Unpublished up to now	6	Frontal	Specimen 1
	7	Postorbitofrontal	
	8	Parietal	
	9	Jugal	
	10	Basioccipital complex	
	11	Dentary	
	12	Dorsal	
	13	Dorsal	
	14	Pygal	
	15	Median caudal	
	16	Median caudal	
	17	Median caudal	
	18	Median caudal	
	19	Median caudal	
	20	Median caudal	
	21	Terminal caudal	
	22	Terminal caudal	
	23	Terminal caudal	
	24	Terminal caudal	
	25	Terminal caudal	
	26	Terminal caudal	
	27	Terminal caudal	
	28	Terminal caudal	
	29	Terminal caudal	
	30	Terminal caudal	
	31	Terminal caudal	
	32	Terminal caudal	
	33	Median caudal	Specimen 2
	34	Median caudal	Specimen 3
	35	Indeterminate caudal	Other specimen(s)
	36	Indeterminate caudal	
	37	Indeterminate bone	

"Microfossils" and "Stratigraphic and possible geographic provenance of the mosasaurid remains"), then chemically (10% concentrated acetic acid), finally consolidated with synthetic resin (Plexigum®PQ611) diluted in acetone.

Using the characters found on the most diagnostic material (Part "Systematic Paleontology"), a phylogenetic analysis was performed using a taxon-character matrix from a recent cladistic analysis of mosasauroid squamates (Makádi *et al.* 2012) including 32 taxa and 135 characters, a matrix itself based on those of Bell (1997) and Bell & Polcyn (2005). The analysis was performed using PAUP version 4.0b10 (Swofford 1999). The same tests used by Makádi *et al.* (2012) were applied: all multistate characters were unordered and unweighted, and the data matrix was analyzed using heuristic search algorithms. The ACCTRAN optimization was favored.

MICROFOSSILS

In order to determine the age of the mosasaurid remains, the chalky matrix preserved around most of the bones and recovered during their mechanical preparation was used for micropalaeontological studies, more especially that of calcareous

nannofossils, planktonic foraminifera and palynomorphs. The respective methods of preparation of these taxa are presented below.

Calcareous nannofossils
Calcareous nannofossils were studied using both light and SEM microscopes. For biostratigraphy and the optical microscope observations, the chalky matrix was processed to prepare a simple smear-slide using standard techniques. For the SEM analysis, a chip of fresh, raw matrix sediment was fixed on a stub with carbon scotch and observed through a Hitachi table top TM 3000.

Planktonic foraminifera
Following standard procedures, the chalky sediments were soaked overnight in a dilute solution of hydrogen peroxide and subsequently washed over 63 μm and 1 mm sieves. The microfossils were extracted from the 63 μm-1mm fraction.

Palynomorphs
The sample was treated with HCl and HF (70%), in order to remove the carbonate and silica fractions of the sediment. The residue was then sieved with a 10 μm nylon mesh. The organic residue was mounted on microscope slides with glycerine jelly. Observations were carried out with an Axioplan2 Imaging Zeiss microscope under transmitted light. The slides were entirely scanned along non-overlapping traverses using a 63 × objective lens. Morphological study of palynomorphs was performed using a 100 × objective lens. The observations and determinations noted herein are mainly based on light microscope examination, and fluorescent mode was used sporadically (UV excitation was carried out with a Zeiss HBO 100 Microscope Illuminating System, mercury short-arc lamp).

STRATIGRAPHIC AND POSSIBLE GEOGRAPHIC PROVENANCE OF THE MOSASAURID REMAINS

STRATIGRAPHICAL OCCURRENCE
Calcareous nannofossils
Overall, calcareous nannofossils are moderately well preserved; no severe etching or overgrowth affects the specimen diagnosis; only a pervasive fragmentation, typical of the compaction in chalk sediments, is observed.

The assemblage is abundant, diverse (list of key species in Table 2) and of Tethyan affinity. *Prediscosphaera* Vekshina, 1959, *Retacapsa* Black, 1971, and *Watznaueria* Reinhardt, 1964 are among the most abundant genera comprising the assemblage. *Kamptnerius magnificus* Deflandre, 1959 is also relatively common.

The frequent occurrence of *Arkhangelskiella cymbiformis* Vekshina, 1959, *Aspidolithus parcus parcus* (Stradner, 1963) Noël, 1969, *A. parcus constrictus* (Hattner *et al.*, 1980) Perch-Nielsen, 1984, *Ahmuellerella regularis* (Górka, 1957) Reinhardt & Górka, 1967, *Lithastrinus grillii* Stradner, 1962, *Eiffellithus eximius* (Stover, 1966) Perch-Nielsen, 1968, *Reinhardtites anthophorus* (Deflandre, 1959) Perch-Nielsen, 1968,
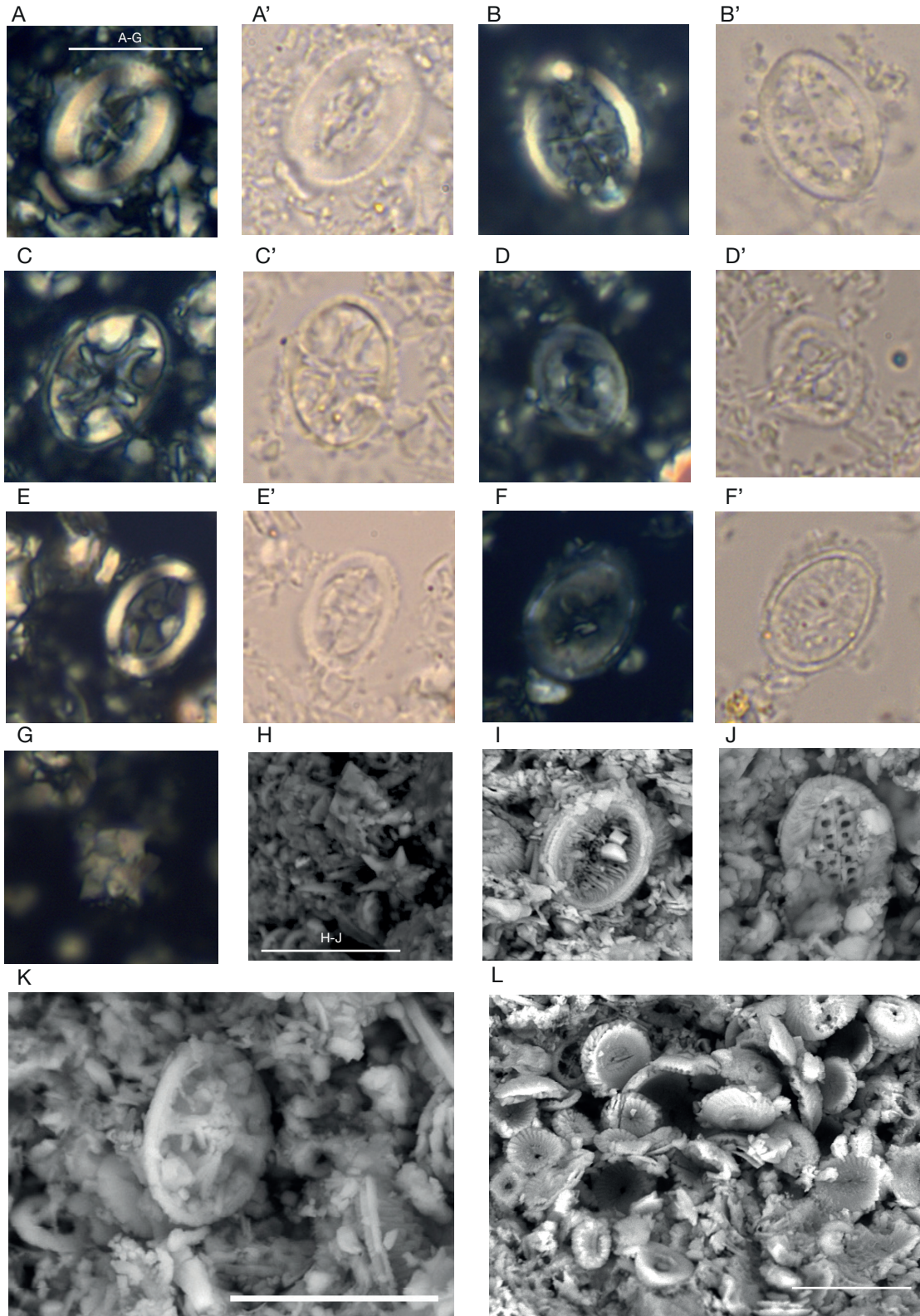
Fig. 2. — *Calcareous nannofossils*, Campanian, Jerusalem: **A**, *Aspidolithus parcus parcus* (Stradner, 1963) Noël, 1969, crossed nicols; **A'**, same specimen, natural light; **B**, *Arkhangelskiella specillata* Vekshina, 1959, crossed nicols; **B'**, same specimen, natural light; **C**, *Eiffellithus eximius* (Stover, 1966) Perch-Nielsen, 1968, crossed nicols; **C'**, same specimen, natural light; **D**, *Reinhardtites anthophorus* (Deflflandre, 1959) Perch-Nielsen, 1968, crossed nicols; **D'**, same specimen, natural light; **E**, *Arkhangelskiella cymbiformis* Vekshina, 1959, crossed nicols; **E'**, same specimen, natural light; **F**, *Kamptnerius magnificus* Deflflandre, 1959, crossed nicols; **F'**, same specimen, natural light; **G**, *Lithastrinus grillii* Stradner, 1962; crossed nicols; **H**, *Lithastrinus grillii* Stradner, 1962, SEM micrograph; **I**, *Kamptnerius magnificus* Deflflandre, 1959, SEM micrograph; **J**, *Aspidolithus parcus parcus* (Stradner, 1963) Noël, 1969, SEM micrograph; **K**, *Eiffellithus eximius*, SEM micrograph; **L**, Chalky nannofacies showing a well preserved, broken coccospheare of *Watznaueria barnesiae* (Black in Black & Barnes, 1959) Perch-Nielsen, 1968. Scale bars: **A-G**, 10 µm; **H-J**, 10 µm; **K**, **L**, 10 µm.

TABLE 2. — Calcareous nannofossils, Campanian, Jerusalem.

List of cited taxa

Ahmuellerella regularis (Górka, 1957) Reinhardt & Górka, 1967
Aspidolithus parcus parcus (Stradner, 1963) Noël, 1969
Aspidolithus parcus subsp. *constrictus* (Hattner, Wind &
  Wise, 1980), Perch-Nielsen, 1984)
Arkhangelskiella cymbiformis Vekshina, 1959
Arkhangelskiella specillata Vekshina, 1959
Bukryaster hayi (Bukry, 1969) Prins & Sissingh *in* Sissingh, 1977
Ceratolithoides aculeus (Stradner, 1961) Prins & Sissingh *in*
  Sissingh, 1977
Eiffellithus eximius (Stover, 1966) Perch-Nielsen, 1968
Kamptnerius magnificus Deflandre, 1959
Lithastrinus grillii Stradner, 1962
Misceomarginatus pleniporus Wind & Wise in Wise & Wind, 1977
Prediscosphaera Vekshina, 1959
Reinhardtites anthophorus (Deflandre, 1959) Perch-Nielsen, 1968
Reinhardtites levis Prins & Sissingh *in* Sissingh, 1977
Retacapsa Black, 1971
Uniplanarius sissinghii (Perch-Nielsen, 1986) Farhan, 1987
Watznaueria Reinhardt, 1964
Watznaueria barnesiae (Black in Black & Barnes, 1959) Perch-
  Nielsen, 1968

TABLE 3. — Planktonic foraminifera, Campanian, Jerusalem.

List of cited taxa.

Contusotruncana fornicata (Plummer, 1931)
Contusotruncana morozovae (Vasilenko, 1961)
Contusotruncana plummerae (Gandolfi, 1955)
Globigerinelloides asper (Ehrenberg, 1854)
Globigerinelloides prairiehillensis Pessagno, 1967
Globotruncana bulloides Vogler, 1941
Globotruncana hilli Pessagno, 1967
Globotruncana mariei Banner & Blow, 1960
Globotruncana orientalis El Naggar, 1966
Globotruncana rosetta (Carsey, 1926)
Muricohedbergella holmdelensis (Olsson, 1964)
Planoheterohelix globulosa (Ehrenberg, 1840)
Rugoglobigerina rugosa (Plummer, 1927)
Whiteinella aprica (Loeblich &Tappan, 1961)

together with rare specimens of *Bukryaster hayi* (Bukry, 1969) Prins & Sissingh in Sissingh, 1977 (Fig. 2) and the absence of *Ceratolithus aculeus* (Stradner, 1961) Prins & Sissingh in Sissingh, 1977, *Reinhardtites levis* Prins & Sissingh in Sissingh, 1977 and *Uniplanarius sissinghii* (Perch-Nielsen, 1986) Farhan, 1987, allow us to confidently assign an age not older than Early Campanian (Zone CC18 according to Sissingh (1977) and Perch-Nielsen (1983); Zone UC14-15a according to Burnett (1998)) and not younger than Late Campanian (Zone CC19). *Misceomarginatus pleniporus* Wind & Wise in Wise & Wind, 1977, a marker of Zone UC15 (Burnett 1998) has not been encountered but this marker is rarely found in the Tethyan domain. It is important to stress that this biostratigraphic analysis based on only one sample should be interpreted with a large confidence interval.

The age – most probably late early to Middle Campanian (*A. parcus* Zone) – as well as the composition of the assemblage, match identical findings in the same area reported by previous literature (Moshkovitz 1987; Gvirtzmann *et al.* 1989; Eshet & Moshkovitz 1995).

Planktonic foraminifera
The assemblage (Table 3) is dominated by small globular planktonic foraminifera. *Globigerinelloides* Cushman & Ten Dam, 1948 are particularly abundant. *Planoheterohelix* Georgescu & Huber, 2009, *Muricohedbergella* Huber & Leckie, 2011 and *Rugoglobigerina* Brönnimann, 1952 are well represented. Keeled forms are in low abundance. *Globigerinelloides* is represented by *Globigerinelloides asper* (Ehrenberg, 1854) (Fig. 3) and *Globigerinelloides prairiehillensis* Pessagno, 1967. High percentages of shallow dwellers (globigerinelloids, muricohedbergellids and planoheterohelicids) associated with diversified hyaline benthic foraminifera and ostracods indicate a shallow marine environment with meso-eutrophic conditions.

The presence of globular meridionally costellated *Rugoglobigerina rugosa* (Plummer, 1927) (Fig. 3) is consistent with a Campanian age. Some muricohedbergellids show weak costellated structures (Fig. 3). *R. rugosa* usually occurs within the former *Globotruncana ventricosa* White, 1928 planktonic foraminifera Zone. Although the index species *G. ventricosa* has been shown to be diachronous (Petrizzo *et al.* 2011) in the Tethyan domain, it does not occur in the basal Campanian (Petrizzo *et al.* 2011). Anyway, it has already been emphasized that *G. ventricosa* only occurs sporadically in Israel's formations (Almogi-Labin *et al.* 1986) and so it is difficult to use. Thus, unsurprisingly, no specimens of *G. ventricosa* have been found in the matrix residues. For this reason, Almogi-Labin *et al.* (1986) defined the *Globotruncana rosetta* (Carsey, 1926) Zone, nearly coeval with *G. ventricosa*. Following the recent biostratigraphic scheme proposed by Petrizzo *et al.* (2011), it would correspond to the Middle Campanian (*Contusotruncana plummerae* (Gandolfi, 1955) Zone).

Among keeled forms (Fig. 3), *Contusotruncana* Korchagin, 1952 is the most common with several specimens of *Contusotruncana morozovae* (Vasilenko, 1961), some *Contusotruncana fornicata* (Plummer, 1931) and rare *Contusotruncana plummerae*. The presence of *C. morozovae* and *C. plummerae* indicates that the sediment comes from the Middle Campanian *C. plummerae* Zone. *Globotrucana* is mainly represented by species with a long stratigraphic range (first occurrences within the Santonian Stage – last occurrences within the Maastrichtian Stage): *Globotruncana bulloides* Vogler, 1941, *Globotruncana hilli* Pessagno, 1967, *Globotruncana mariei* Banner and Blow, 1960 and *Globotruncana orientalis* El Naggar, 1966. One specimen of *G. rosetta* has been found (Fig. 3).

Thus, in accordance with the absence of marginotruncanids, with the occurrence of *C. plummerae* and *G. rosetta*, and with the accompanying fauna already described in the area (Almogi-Labin *et al.* 1986; Honigstein *et al.* 1987), we conclude the sample comes from the *C. plummerae* Zone, Middle Campanian in age.

Palynomorphs
Overall, organic matter particles are poorly preserved. The optical microscopy revealed that the organic matter assemblage is strongly dominated by filamentous fungal hyphae. Other constituents of the organic matter assemblage like opaque phytoclasts, cuticles and palynomorphs are very rare.

Fig. 3. — Planktonic foraminifera, Campanian, Jerusalem: **A**, *Contusotruncana morozovae* (Vasilenko, 1961); **B**, *Contusotruncana fornicata* (Plummer, 1931); **C**, *Contusotruncana plummerae* (Gandolfi, 1955); **D**, *Globotruncana hilli* Pessagno, 1967; **E**, *Globotruncana bulloides* Vogler, 1941; **F**, *Globotruncana orientalis* El Naggar, 1966; **G**, *Globotruncana rosetta* (Carsey, 1926); **H**, *Globotruncana mariei* Banner and Blow, 1960; **I**, *Whiteinella aprica* (Loeblich & Tappan, 1961); **J**, *Muricohedbergella holmdelensi* (Olsson, 1964); **K**, *Rugoglobigerina rugosa* (Plummer, 1927); **L**, Weak costellated muricohedbergellid; **M**, *Globigerinelloides asper* (Ehrenberg, 1854); **N**, *Planoheterohelix globulosa* (Ehrenberg, 1840). Scale bars: **A-L"**; **M-N**, 50 µm; **L"'**, 300 µm.

Concerning palynomorphs, only four dinoflagellate cysts and three spores were observed. The poor state of preservation of palynomorphs complicates their taxonomic identification. Fungal hyphae cells, sometimes septate, have sinuous lateral walls; often the hyphae appear undulating. Lateral sac-shaped cells, possibly hyphopodia, are abundant. These characteristics suggest affinity with the epiphyllous fungus *Meliolinites anfractus* (Dilcher, 1965) (Kalgutkar & Jansonius, 2000).

The use of the florescent mode on some of the observed cuticles revealed stomata distribution and structure. The cyclocytic stomata structure and the presence of papillae suggest a Cheirolepidiacean (Alvin 1982) affinity for some of the observed cuticles. Because of the xeromorphic characters in most cheirolepidiaceans, they are generally considered adapted to rather dry, saline or disturbed habitats (Vakhrameev 1970; Watson 1977, 1988; Upchurch & Doyle 1981; Alvin 1982; Francis 1983, 1984; Zhou 1983; Archangelsky & Taylor 1986; Thévenard *et al.* 2000; Du *et al.* 2014) as may be the case for coastal habitats.

*Age and possible stratigraphical
provenance of the mosasaurid remains*

Although performed on only one sample, the results gathered from two microfossil groups provide coherent and concordant results on the age of the chalky matrix of the mosasaurid remains: the sample, included in the *A. parcus* / CC18 / UC14-15a calcareous nannofossils Zones and the *C. plummerae* / *G. rosetta* planktonic foraminifera Zone, constrains an early Middle Campanian age. When looking at the distribution of the local formations of this age around Jerusalem, there are only two possibilities: the upper part of the Menuha Formation (Kum(u) Formation on geological maps) and the lower part of the Mishash Formation (Kumi Formation on geological maps) (Fig. 1B) (Reiss 1988; Sneh & Avni 2011; Z. Lewy, pers. comm.).

The chalky matrix of the mosasaurid does not appear to be phosphatic, which is confirmed by the very good preservation of the microfossils as a whole (microfossils and invertebrates are generally badly preserved in phosphatic deposits: pers. obs. of the authors). Phosphatic levels occur both in the top of the Menuha and in the Mishash formations (e.g. Reiss 1988), but in different biozones (Eshet & Moshkovitz 1995, fig. 3) than the ones determined in the present work. Finally, the occurrence of *C. plummerae* and the lack of *C. aculeus* in the matrix sample restricts the most probable stratigraphic provenance to the chalks just below the local "Chert Member" of the Mishash Formation (see Eshet & Moshkovitz 1995, fig. 3; see red arrow on Fig. 1B).

POSSIBLE GEOGRAPHIC PROVENANCE
Knowing now the exact age and the probable stratigraphic level in which the mosasaurid remains were found, a hypothesis was made to determine their possible geographic provenance. For this, we first located outcrops of this age around Jerusalem, using the 1/50.000 geological map of the area (Sneh & Avni 2011) and discussions with geologist colleagues in Jerusalem (Z. Lewy, pers. comm.). Then these data were

compared to historical accounts of Father Ruffier's life during his stay in the Missionaries of Africa Saint-Anne Community of Jerusalem (Anonymous 1949; Fathers F. Richard and F. Bouwen, pers. comm.).

On the 1/50.000 geological map of Jerusalem's surroundings (Sneh & Avni 2011), the Mishash formation crops out widely only in the hills – including the famous Mount of Olives – east of Jerusalem (Fig. 1A), so we can hypothesize that the remains were possibly found in this area. The areas located west of Jerusalem and the rocks below Jerusalem city itself are composed of Albian to Turonian rocks (Fig. 1).

Father Ruffier used to walk a lot around Jerusalem with his students from the Small Seminary of the Saint-Anne Community (located in the northeastern part of the Old City of Jerusalem [Fig. 1A]) and it was probably during one of his trips that he found the mosasaurid bones (Father F. Bouwen, pers. comm.). At that time, the Saint-Anne Community owned two properties in the countryside around Jerusalem, where Father Ruffier frequently went to take care of the orchard and vegetable gardens (Anonymous 1949). One was a vacation home called "Montagne Saint-Jean" (the place was so named because it corresponds to the birthplace of the Apostle Saint-John-the Baptist) in Aïn Karim/Ein Kerem (in Arabic and Hebrew), about 4-5 km west to Jerusalem; the other was a vineyard named "Haloué" located about 3.5 km north of the Old City, in a place now called "French Hill" (Anonymous 1949; Father F. Bouwen, pers. comm.) (Fig. 1A).

Considering the Campanian age of the mosasaurid remains, it can be excluded that they come from outcrops located west of Jerusalem – including the Aïn Karim/Ein Kerem place (Cenomanian underground) – where only Albian to Turonian levels crop out (Fig. 1A). On the contrary, considering that the Saint-Anne Community where Father Ruffier lived and worked is located very close to the outcrops of the Mishash Formation, it is possible that the mosasaurid remains were found anywhere in this wide area east of Jerusalem, that at the time was much less urbanized than today and where outcrops were more numerous. Finally, it can be hypothesized – with extreme caution – that the remains could have been found more precisely during one of Father Ruffier's paths between the Saint-Anne Community and French Hill (where the "Haloué" property was located, on Santonian basement), where a large tongue of the Mishash Formation crops out between both places (Fig. 1A).

SYSTEMATIC PALEONTOLOGY

PRESERVATION
All bones exhibit the same mode of preservation, implying that they could all come from the same deposit. Their surface is well preserved, with anatomical details such as sutures (for example on the frontal-postorbitofrontal-parietal complex) still clearly observable. However, some vertebrae are strongly abraded, showing their internal spongious microanatomy, which indicates that they were probably exposed to weathering at the surface. Moreover, some show signs of alteration due

to root systems, also indicating that they were preserved in a layer near the soil surface. Some bones, especially the caudal vertebrae, also bear some typical nail-shaped marks of predation, generally attributed to selachian scavenger activity (e.g. Corral *et al.* 2004). Some vertebrae are also slightly laterally crushed. None of the vertebrae preserves the neural or haemal arches, which were broken either during the fossilization process or, in the case of "fresh" breaks, probably during collection.

ANATOMICAL AND NOMENCLATURAL
COMMENTS ON THE MATERIAL
The five original vertebrae (numbered from MHNM.0.419.1 to MHNM.0.419.5) on which Répelin (1915) erected the new species *Liodon asiaticum*, were neither described in detail measured, figured, nor specifically designated as holotype or type, and no diagnosis was provided. Because of the extremely vague descriptions and brief comparisons with plates 30 and 34 of Cope (1875) that he made, and though these vertebrae bear numbers (from 1 to 5 – written on them in pencil and that are supposed to refer to their order of description in the text), a clear and definitive correspondence with those of Cope's plates is difficult to establish, except the dorsal vertebra (no. 1). As we will never know if these vertebrae were correctly numbered (and by whom), they are here respectively reinterpreted as: no. 1, a dorsal; no. 2, a large median caudal; no. 3, a terminal caudal; no. 4, a large median caudal; no. 5, a small median caudal (see Description). Moreover, by comparing their respective size and morphology, it is noteworthy that these vertebrae belong to at least 3 different individuals and possibly different taxa (Table 1). Finally, in addition to representing a composite assemblage, these 5 vertebrae are not diagnostic at the specific level. For all these reasons, *Liodon asiaticum* should be considered a *nomem dubium*, in order to respect ICZN rules and recommendations (ICZN 2001).

The rest of the unpublished material consists of 32 bones, including 6 cranial elements, 25 vertebrae and an indeterminate bone (Table 1). Also considering size and character concordances and similarities, this material can be divided into four distinct lots that belong to at least three different specimens: a large individual (represented by most of the bones preserved), another large one (represented by one median caudal vertebra) and a much smaller one (represented also by one median caudal vertebra). It should be noted that these three specimens match very well with the three already recognized among Répelin's original material (Table 1). Finally, two damaged caudals remain indeterminate, as well as a fragment of bone that could belong to one or the other of these individuals, or even to another one.

To sum up, we consider the best and most parsimonious hypothesis that the complete set of bones MHNM.0.419.0 has the same geographic and stratigraphic provenances and includes at least four specimens that are (Table 1):

1) A large individual including bones MHNM.0.419.1-3 (Répelin 1915) and MHNM.0.419.6-32 (unpublished until now), here referred to as "Jerusalem Specimen 1";

2) Another large specimen including bones MHNM.0.419.4 (Répelin 1915) and MHNM.0.419.33 (unpublished until now); here referred to as "Jerusalem Specimen 2";

3) A smaller specimen including bones MHNM.0.419.5 (Répelin 1915) and MHNM.0.419.34 (unpublished until now); here referred to as "Jerusalem Specimen 3";

4) Indeterminate mosasaurid bones (bones MHNM.0.419.35-37).

These four lots are separately described and systematically assigned below.

DESCRIPTION AND COMPARISON

REPTILIA Laurenti, 1768
Order SQUAMATA Oppel, 1811
Superfamily MOSASAUROIDEA Gervais, 1852
emend Camp, 1923
Family MOSASAURIDAE Gervais, 1852
Subamily MOSASAURINAE Gervais, 1852
(*sensu* Williston, 1897)
Tribe MOSASAURINI Gervais, 1852
(*sensu* LeBlanc *et al.,* 2012)

Genus and species *incertae sedis*
Jerusalem Specimen 1

MATERIAL. — MHNM.0.419.1-3, and MHNM.0.419.6-32: 30 bones including 3 vertebrae described by Répelin (1915): a dorsal (no. 1), a large median caudal (no. 2), a terminal caudal (no. 3); 27 up to now unpublished bones: 6 cranial bones including incomplete frontal (no. 6), parietal (no. 7) and postorbitofrontal (no. 8) fused and preserved in three fragments, a fragmentary left jugal (no. 9), an incomplete basicranium (no. 10) and a dentary fragment (11), as well as 21 vertebrae, including 2 dorsals (no. 12, 13), one pygal (no. 14), 6 median caudals (no. 15 to 20) and 12 terminal caudals (no. 21 to 32) (Figs 4-6; Table 1).

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCES. — Lower part of the Middle Campanian, probably Mishash Formation, possibly northeastern part of Jerusalem (see Fig. 1).

DESCRIPTION
Cranium (Fig. 4)
Several cranial bones are preserved, including an incomplete frontal-postorbitofrontal-parietal sutured complex, an incomplete occipital unit, and fragmentary jugal and dentary.

Frontal (MHNM.0.419. 6, Fig. 4A)
The frontal is incomplete but from the portions preserved on left and right sides, its complete morphology can be reconstructed.

In dorsal view it is a long, flat, triangular bone almost twice as long as wide. The anterior extremity is broken so it is impossible to know if the bone is invaded by the internarial bar of the premaxillae and by the narial openings. The lateral borders are almost straight, exhibiting only a very slight sigmoid shape and converge only slighty anteriorly, giving the bone its elongated triangular shape. The posterolateral margin is slightly concave and terminates in laterally diverging cornua

that are large and rounded tongues of bones. The dorsal midline anteriorly bears a low and blunt longitudinal crest marked only on the anterior third of the bone. Posteromedially, there are two long and thin flanges of bones embracing the parietal foramen that extend beyond it by around half its length. Lateral to these flanges, the posterior margin of the frontal is deeply excavated and concave, forming an inverted "V". As a result, the frontal-parietal suture is very intricately undulated, precluding mesokinetic movements (LeBlanc *et al.* 2013).

In ventral view, the midline of the bone is occupied anteriorly to posteriorly by a blunt and massive ridge flanked by two large oval grooves, then a large elongated oval concave depression for the olfactory bulbs, followed by a long and narrow olfactory tract that opens posteriorly into a large triangular depression for the cerebral hemisphere. The floor of all these structures lies roughly at the same level. Laterally and raised from this median zone are very large and smooth sutural surfaces for the prefrontal anteriorly and the postorbitofrontal posteriorly. They are almost coalescent, only a thin transversal sheet of bone being present between them, showing that the prefrontal and postorbitofrontal probably almost meet. The surface occupied by the postorbitofrontal is very expanded (see below).

Parietal (MHNM.0.419. 7, Fig. 4A)
Only the right anterior part of the parietal fused to the frontal is preserved. It is a massive ala of bone contacting the frontal anterolaterally into the previously mentioned inverted V-shaped suture. The parietal foramen is of moderate size and oval, and its anterior border contacts the frontal-parietal suture. It is embraced by the long and thin tongues of the frontal. Laterally, a large vertical transversely oriented sutural zone bearing strong horizontal ridges and furrows is present. It shows that the medial wing of the postorbitofrontal was posteromedially expanded. Ventrally, the anterior part of the parietal is hidden by the expanded ala of the postorbitofrontal and the parietal foramen is surrounded laterally by two ridges that seem to converge posteriorly.

Postorbitofrontal (MHNM.0.419. 8, Fig. 4A)
Both incomplete postorbitofrontals are preserved, the right one being better preserved both in dorsal and ventral views. It surrounds the posterolateral corner of the frontal in a regularly convex suture. The anterior branch is dorsally narrow, tapers anteriorly and disappears just before the orbit. Though the postorbitofrontal almost meet the prefrontal ventrally on the frontal, this dorsal morphology indicates however that these two bones do not form a continuous band of bone laterally to the frontal. Ventrally, this branch expands into a wide thin ala of bone that covers most of the posteromedial ventral surface of the frontal into a sigmoid suture, more than half the distance from the corner of the frontal to the midline. This indicates that the postorbitofrontal was firmly attached to the frontal, limiting also mesokinetic movements. The posterior branch is short and narrow, transversely oriented, and medially contacts the parietal into a simple interdigitating suture. The posterolateral corner is broken but judging from the part

preserved it was probably sharp and expanded laterally. The descending branch for the jugal as well as the posterior one for the squamosal are not preserved.

Jugal (MHNM.0.419. 9, Fig. 4B)
An incomplete left jugal bearing a typical L-shape is preserved. Both horizontal and vertical rami are broken distally. The dorsal ramus is stout and elliptical in cross-section whereas the ventral one is laterally flattened. The angle between these two rami is notably very open, about 120°. A well-marked posteroventral process is present. In medial view, there is a shallow ventral surface just anterior to the tuberosity, possibly for loose contact with the ectopterygoid.

Basicranium (MHNM.0.419.10, Fig. 4C)
The incomplete occipital unit preserved most of the basioccipital and basisphenoid, as well as some ventral parapets of the exoccipital-opisthotic and prootic surrounding the foramen magnum. All bones are fused and because this complex is eroded, most of the sutures are not visible. This complex is thus described as a whole, with highlighting of the visible structures in each view.

In dorsal view, the medular canal is relatively wide and deep. At the median part of the complex, probably around the basioccipital-basisphenoid suture, it is laterally constricted. The medial internal suture with the exoccipital-opisthotic is elongated and slightly curved whereas the transverse basioccipital-basisphenoid suture is visible on the floor and lateral sides of the medullary canal. There is no trace of a basilar artery foramen.

In ventral view, the basal tubera are mostly broken but their preserved bases indicate they were probably large. Just anteriorly to them, the posteroexternal tongues of the basisphenoid are not preserved. The suture between the two bones is V-shaped and located in the bottom of an also V-shaped bowl, the tip of the V facing forward for both. Laterally, this V-shaped depression is flanked by two elongated oval depressions. Anteriorly, the basipterygoid processes are not preserved.

In posterior view, the basioccipital condyle is reniform, regularly convex ventrally and excavated dorsally by both the almost flat exoccipital articulations and the concave foramen magnum floor. This condyle is separated from the shaft of the bone by a large convex neck. Its dorsolateral corners are lateroventrally oriented and articulate with the exoccipitals (only the condyle of the left one is preserved). This view shows that the basal tubera of the basioccipital were lateroventrally oriented, with an angle of about 30° from the horizontal axis.

The anterior view reveals the V-shaped morphology of the basisphenoid and the suture with the ventro-anterior part of the prootic. None of the foramina present normally on this anterior surface of the basisphenoid are preserved.

The lateral views are abraded so that the lateral flanges of both the exoccipital-opisthotic and prootic, especially the areas bearing the otosphenoidal crest and all the nerve foramina, are not preserved. The sulcus is only visible in left lateral view below the partly broken ala of the basisphenoid where the jugular vein must pass.

Fɪɢ. 4. — MHNM 0.419.1-2 and MHNM 0.419.6-20 ("Jerusalem Specimen 1"), Mosasauridae, Mosasaurini incertae sedis, Campanian, Jerusalem: Frontal-Parietal-Postorbitofrontal complex (no. 6, 7, 8 respectively) in dorsal (**A**) and ventral (**A'**) views; left jugal (**B**) in medial view; basicranium (no. 10) in right lateral (**C**), dorsal (**C'**) and posterior (**C"**) views; dentary (no. 11) in left lateral (**D**) and dorsal (**D'**) views; dorsal vertebrae (no. 12, 1, 13) respectively) in anterior (**E-G**), dorsal (**E'-G'**) and left lateral (**E"-G"**) views; pygal vertebra (no. 14) in anterior (**H**), ventral (**H'**) and left lateral (**H"**) views; median caudal vertebrae (15, 1, 16 to 20 respectively) in anterior (**I-O**), ventral (**I'-O'**) and left lateral (**I"-O"**) views. Some right lateral views were prefered when better preserved and illustrated in mirror. Scale bars: 5 cm.

Dentary (MHNM.0.419. 11, Fig. 4D).
A small fragment of the dentary (L × W × H = 6.9 / 2.7 / 3.3 cm) is preserved. It is broken both anteriorly and posteriorly. Its longitudinal axis is straight. In occlusal view, it bears three oval dental alveoli as well as smaller round ones for replacement teeth located, as usual, posteromedially to the main ones. The main teeth are all broken at the base of the crown and no tooth apices are visible in the replacement alveoli, so the morphology of the teeth remains unknown. The roots are firmly anchored in the dentary as usual in mosasaurids. Both medial and lateral parapets are of similar height. The lateral one exhibits a small rounded and shallow interdental pit for the accommodation of the corresponding upper jaw tooth apex during occlusion. The lateral surface is gently concave and bears a median row of nutritive foramina – the best preserved being a long narrow oval – and a second ventral one in which only one foramen is observable, due to the poor preservation of the ventral surface of the bone. The medial surface is eroded; it bears a long and narrow ventrally located horizontal Meckelian canal (about 8 mm wide) that slightly narrows anteriorly. Because of the occurrence of a narrow Meckelian canal and of two rows of nutritive foramina, this fragment probably belongs to the anterior third of the dentary.

Axial skeleton (Figs 4; 5)
All the vertebrae are procoelous. The preserved vertebral series, though admittedly incomplete, probably represents the posteriormost part of the dorsal series and an incomplete tail (including pygal, median caudal and terminal caudal vertebrae) of a single individual.

Dorsal vertebrae (MHNM.0.419. 1, 12, 13, Fig. 4E-G)
Three dorsal vertebrae are preserved, including the one numbered no. 1 originally described by Répelin (1915) (Fig. 4F). They are of similar size, morphology and proportions (L~ 2 × W-H), indicating that they probably come from the same portion of the vertebral column and were possibly adjacent. They are slightly distorted, being laterally compressed. The neural arches and transverse processes are broken, only their bases are preserved.

In anterior and posterior views, the articular surfaces are vertically oriented and markedly concave/convex, the cotyle being slightly larger than the condyle. Both are roughly circular in axial view, being slightly higher than wide, but this could be due to the lateral compression above mentioned. The dorsal surface is excavated by the floor of the foramen magnum, which bears a median sharp ridge bordered by two lateral furrows and numerous foramina. The lateral surface bears anteriorly at mid-height large dorsoventrally compressed ovoid transverse processes with large bases that occupy almost half the length of this surface. The ventral surface is gently convex and bears two symmetrical foramina located anteriorly, just ventral to the transverse processes, as well as one median, located approximately ventral to the posterior border of the base of the transverse processes. The base of the neural arch preserved on vertebra no. 1 is fused to the centrum. It shows that its anterior and posterior peduncles are large and lenticular but does not allow us to determine if zygapophyses

were present, nor the shape and orientation of the neural spine. The anteromedian position of the transverse processes permits to identify these vertebrae as posterior dorsals (or lumbars), as defined by Russell (1967: 77). As such, we can hypothesize that the longest of these three vertebrae is the anteriormost and the shortest is the posteriormost, and that these vertebrae could represent some of the last lumbars.

Pygal vertebrae (MHNM.0.419.14, Fig. 4H)
One pygal is preserved. It is much shorter than the dorsals (about one-third), showing that a gap probably exists between them. It is slightly distorted and slightly longer than high and wide. Its articular surfaces are subtriangular. As for the dorsals, the cotyle is slightly larger than the condyle and both are poorly concave/convex, almost flat. In dorsal view, the neural canal is deep and narrow. The ventral surface is gently convex, and bears a median longitudinal low ridge bordered on each side by two shallow depressions. The lateral surface bears large dorsoventrally compressed transverse processes forming narrow alae located ventroanteriorly and projecting ventrally, making an angle of 35-38° from the horizontal. The roughly triangular shape of the articular surface and the ventrally located transverse processes indicate that this pygal was probably an anterior one.

Median caudal vertebrae
(MHNM.0.419. 2, 15-20, Fig. 4I-O)
Seven median caudal vertebrae are preserved, including the no. 2 originally described by Répelin (1915) (Fig. 4J). They all have the same shape, size and proportions with L-H = W (around 35 × 34 × 34 mm), indicating that they were possibly adjacent or near-adjacent vertebrae from the same portion of the tail. The articular surfaces, as on the pygal, are only slightly concave/convex, and the cotyles are slightly larger and flatter than the condyles. Both are sub-hexagonal and the lateral margins are larger than the dorsal and ventral ones. In dorsal view the neural canal is narrow and deep. The neural arches are not preserved but their base shows that they were probably straight narrow blades, with no indication of postzygapophyses. The lateral surfaces are large and almost flat. Anteroventrally, they bear transverse processes that are large, dorsoventrally compressed and posteriorly oriented alae that occupy about ⅔ of the surface length. They also project ventrally with an angle comparable to that observed on the pygal vertebra. The ventral surface is almost flat and bear nutritive foramina. Posteroventrally, these vertebrae bear large fused haemal arches. Though all are broken, their oval or round basal sections show that they were only slightly posteriorly oriented. Because of their subhexagonal articular surfaces and their large transverse processes, these vertebrae are interpreted as anterior median caudals. Their size and proportion are consistent with those of the previously described dorsal and pygal vertebrae, suggesting that they probably belong to the same individual (see also "Anatomical and nomenclatural comments on the material").

Terminal caudal vertebrae (MHNM.0.419.3, 21-32, Fig. 5)
Thirteen terminal caudals are preserved, including the no. 3 originally described by Répelin (1915) (Fig. 5I). As for the
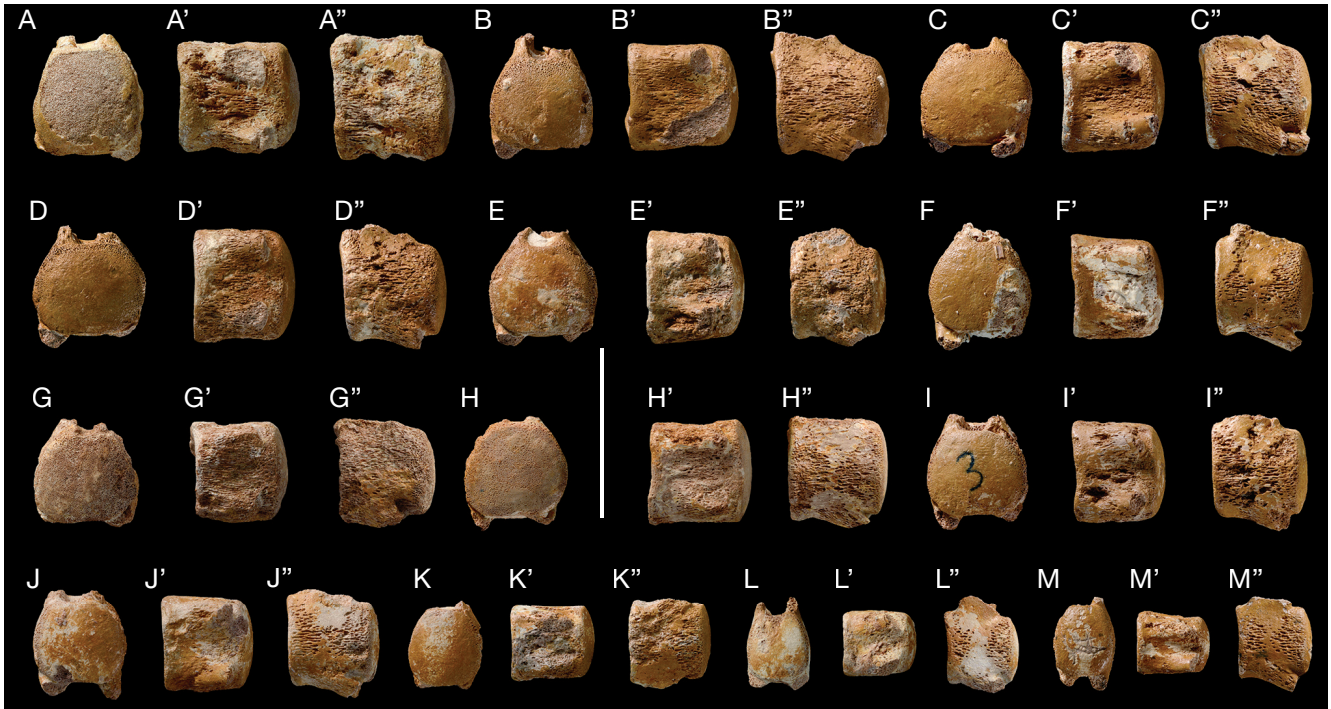
Fig. 5. — MHNM 0.419.3 and MHNM 0.419.21-32 ("Jerusalem Specimen 1"), Mosasauridae, Mosasaurini incertae sedis, Campanian, Jerusalem: Terminal caudal vertebrae (no. 21 to 28, 3, 29 to 32 respectively) in anterior (**A-M**), ventral (**A'-M'**) and left lateral (**A"-M"**) views. Some right lateral views were prefered when better preserved and illustrated in mirror. Scale bar: 5 cm.

median caudals, they show *grosso modo* the same shape and proportion and their size gradually decreases, so they could also represent near adjacent vertebrae from the same portion of the tail, though some gaps are obviously present, especially between the first ten and the three posteriormost. The vertebra interpreted as the anteriormost of this series are longer and wide than high (about 35 × 34 × 32 mm), then they exhibit the same proportions (about 30 × 30 × 25 mm), and finally are as long as high but laterally compressed (about 20 x 20 x 18 mm). As a result, their articular surfaces are first vertically oval with reminiscences of the subhexagonal shape of the previous median caudals, then become horizontally oval to subrectangular, and finally vertically oval. These articular surfaces as a whole are only slightly concave/convex, almost flat as in the previous median caudals. The neural canal is very narrow and deep. None of the neural arches is preserved but from their bases as for the median caudals, it can be deduced they were narrow vertical blades. The lateral surfaces of the centra are regularly convex from side to side and no longer bear transverse processes. The ventral surface is flat to concave and small, being limited to a reduced area between the chevrons, which are fused to the centrum. All are broken proximally but bear a round. Strongly posteriorly oriented basal cross-section, making an angle of less than 10° to the horizontal. The smallest vertebra of this terminal caudal series shows on its cotyle, and especially on its condyle, typical traces of selachian scavenger activity (e.g. Corral *et al.* 2004). Because of the occurrence of haemal arches and the lack of transverse processes, these vertebrae are interpreted as terminal caudals. They are however probably not the posteriormost of the tail, and a gap exists also with more anterior caudals as no posterior median caudals have been identified.

Comparison

As a whole, the "Jerusalem Specimen 1" exhibits a mosasaurine suite of characters including the invasion of the parietal by posteromedian flanges of the frontal, no basal artery canal on the basioccipital floor, vertical vertebral condyles, long trunk vertebrae and fused chevrons (Russell 1967; Bell & Polcyn 2005). These characters, however, have also been reported in the basal taxon *Dallasaurus* Bell & Polcyn, 2005; they could be plesiomorphic for mosasaurines instead of synapomorphies as usually considered (Bell & Polcyn 2005). The specimen has been compared to mosasaurines in which homologous bones are known, such as *Clidastes* Cope, 1868, *Kourisodon* Nicholls & Meckert, 2002, *Moanasaurus* Wiffen, 1980, *Eremiasaurus* LeBlanc *et al.*, 2012, *Prognathodon* Dollo, 1889, *Globidens* Gilmore, 1912, *Plesiotylosaurus* Camp, 1942, *Mosasaurus* Conybeare, 1822 and *Plotosaurus* Camp, 1951.

The "Jerusalem Specimen 1" differs from: 1) *Clidastes,* which has a narrow frontal with nearly straight lateral margins that converged anteriorly and a weak median dorsal ridge, a straight fronto-parietal suture, a small parietal foramen located entirely on the parietal, prefrontal and postorbitofrontal widely separated above the orbit, and a jugal without any ventroposterior process (Russell 1967); 2) *Kourisodon,* which has basal tubera of the basioccipital that are oriented at 45° from the horizontal, and circular to pentagonal articular surfaces on the pygal vertebrae (Nicholls & Meckert 2002); 3) *Moanasaurus,* in which the

frontal is a large triangular bone and the parietal foramen is small, circular and located on the parietal (Wiffen 1980, 1990); 4) *Eremiasaurus*, in which the frontal is a large and short triangle with a median ridge developed on the anterior two-thirds of the bone, and the jugal bears branches oriented at 90° (LeBlanc *et al.* 2012); 5) *Prognathodon*, which has a large, short triangular frontal with a straight suture with the parietal, a parietal foramen only on the parietal, a jugal with branches forming an angle of 75° and no posteroventral process, basioccipital with a small foramen on its floor, posterior dorsal vertebrae with vertical, long, oval articular surfaces, pygals with round articular surfaces, and other caudals with articular surfaces passing from horizontally oval to circular (Dollo 1889; Russell 1967; Lingham-Soliar & Nolf 1989; Schulp *et al.* 2008; Konishi *et al.* 2011); 6) *Globidens*, which has a massive triangular frontal with strongly diverging lateral margins, several dorsal ridges, a strong prefrontal-postorbitofrontal contact above the orbits, a suture with the parietal that is straight on its median part without no invading tongues and that runs strongly anteriorly, a parietal foramen on the parietal, a basioccipital with no distinct neck anterior to the condyle, so that it does not extend farther posteriorly than the basal tubera, which make a shallow angle in posterior view relative to other mosasaurines, a jugal with an extremely small posteroventral process, and a bowed and wide dentary (Russell 1975; Polcyn *et al.* 2010; LeBlanc *et al.* 2019); and 7) *Plesiotylosaurus*, which has a very robust triangular frontal with a weak anterior dorsal ridge, a prefrontal-postorbitofrontal strongly in contact laterally with the frontal above the orbit, a stout and wide postorbitofrontal dorsal surface, and a very small parietal foramen (Camp 1942; Lindgren 2009). To sum up, the "Jerusalem Specimen 1" greatly differs from basal Mosasaurinae such as *Clidastes* and from Globidensini.

On the contrary, it shares several similarities with Mosasaurini (= Plotosaurini of Bell (1997) – see LeBlanc et al (2012) and Madzia & Cau 2017 for nomenclatural details) that include an intricately undulated frontal-parietal suture with posteromedian flanges of the frontal embracing the parietal foramen, a frontal with strongly developed posterolateral alae, laterally and ventrally expanded postorbitofrontal (at least in *Mosasaurus*, see Street & Caldwell 2017). All these characters imply a loss of movements along the mesokinetic axis (Russell 1967; LeBlanc *et al.* 2013). It shares also no basal artery canal on the basioccipital, dorsal vertebrae with circular articular surfaces, triangular pygals and fused chevrons. Some similarities and differences with both *Mosasaurus* and *Plotosaurus* have been observed, making the "Jerusalem Specimen 1" intermediate between these two taxa.

The "Jerusalem Specimen 1" has a fronto-parietal suture comparable to that of *Mosasaurus*, with thin and sharp posteromedian flanges of the frontal embracing the parietal foramen and no extensive prefrontal-postorbitofrontal contact above the orbit, at least in "gracile" species like *M. lemonnieri* Dollo, 1889 and *M. conodon* (Cope, 1881); the contact is broader in larger species like *M. hoffmanni* Mantell, 1829 and *M. missouriensis* (Harlan, 1834), forming a robust bar of bone lateral to the frontal (Lingham-Soliar 2000; Caldwell & Bell 2005; Konishi *et al.* 2014; Harrell & Martin 2015; Ikejiri & Lucas 2015; Street & Caldwell 2017). Unfortunately, the

frontal-parietal complex and postcranial skeleton of *Mosasaurus beaugei* Arambourg, 1952 from the latest Cretaceous southern Tethys Margin (Middle-East, northwestern Africa and Brazil) (see Bardet *et al.* 2004; Bardet 2012a; see "Discussion") is currently unknown, precluding any comparison. It differs in general from the genus *Mosasaurus*, which has a wide triangular frontal with strongly converging margins ending in a rectangular anterior part, a strongly developed dorsal median ridge, and only slightly emarginated posterolateral margins lateral to the median flanges, which are more developed posterior to the parietal foramen (a distance at least its length), a generally circular parietal foramen located on the parietal at some distance from the frontal-parietal suture, branches of the jugal that form an angle of 90°, and basioccipital basal tubera that form an angle of 80% to the horizontal.

The "Jerusalem Specimen 1" shares with *Plotosaurus* a narrow and long frontal bearing very emarginated concave posterolateral margins lateral to the median flanges (Camp 1942; Lindgren *et al.* 2008; LeBlanc *et al.* 2013). However, it differs from this genus, which has less anteriorly converging lateral margins (as a result the frontal remains broad anteriorly), no median dorsal ridge, stout rectangular posteromedian flanges, a very large parietal foramen located very near but not in contact with the suture, a broad prefrontal-postorbitofrontal lateral contact above the orbit, the ventroposterior process of jugal nearly absent, very short posterior dorsal vertebrae (L = W = H), and median caudals triangular to subhexagonal with H>W (Camp 1942; Lindgren *et al.* 2008; LeBlanc *et al.* 2013). It should be noted that *P. bennisoni* Camp 1942, the only currently recognized species of the genus, is probably a juvenile specimen (LeBlanc *et al.* 2013). In the largest probably adult specimens of the genus, previously referred to *P. tuckeri* Camp 1942 (now considered a synonym of *P. bennisoni*, Lindgren *et al.* 2008), the frontal is wider and more triangular, approaching the condition observed in *Mosasaurus*. It could thus be possible that the width and length of the frontal of *Plotosaurus* is ontogenetically controlled (M. Polcyn, pers. comm.), a condition already observed in *M. hoffmanni* (Harrell & Martin 2015). This could also apply to the relative development of the prefrontal-postorbitofrontal bar above the orbit, more developed in larger than in smaller species of *Mosasaurus*. In this case, however, this character could be size – but not necessarily ontogenetically – dependent, because smaller *Mosasaurus* species are currently recognized as valid and not considered juvenile of the larger ones (Street & Caldwell 2017). However ontogenetic growth or relative size of taxa are concerned, both are related to absolute size (small *versus* large). This hypothesis however cannot be confirmed nor rejected here and is beyond the scope of this paper.

To sum up, the "Jerusalem Specimen 1" appears to be clearly a member of the Mosasaurini clade. However, its frontal-parietal-postorbitofrontal configuration, despite being intermediate between *Mosasaurus* and *Plotosaurus*, is unique in bearing a long narrow frontal with long narrow postero-medial flanges embracing a large oval parietal foramen in contact with the fronto-parietal suture, deeply emarginated posterior margins lateral to the median flanges, broad and large posterolateral cornua, a median dorsal ridge extended
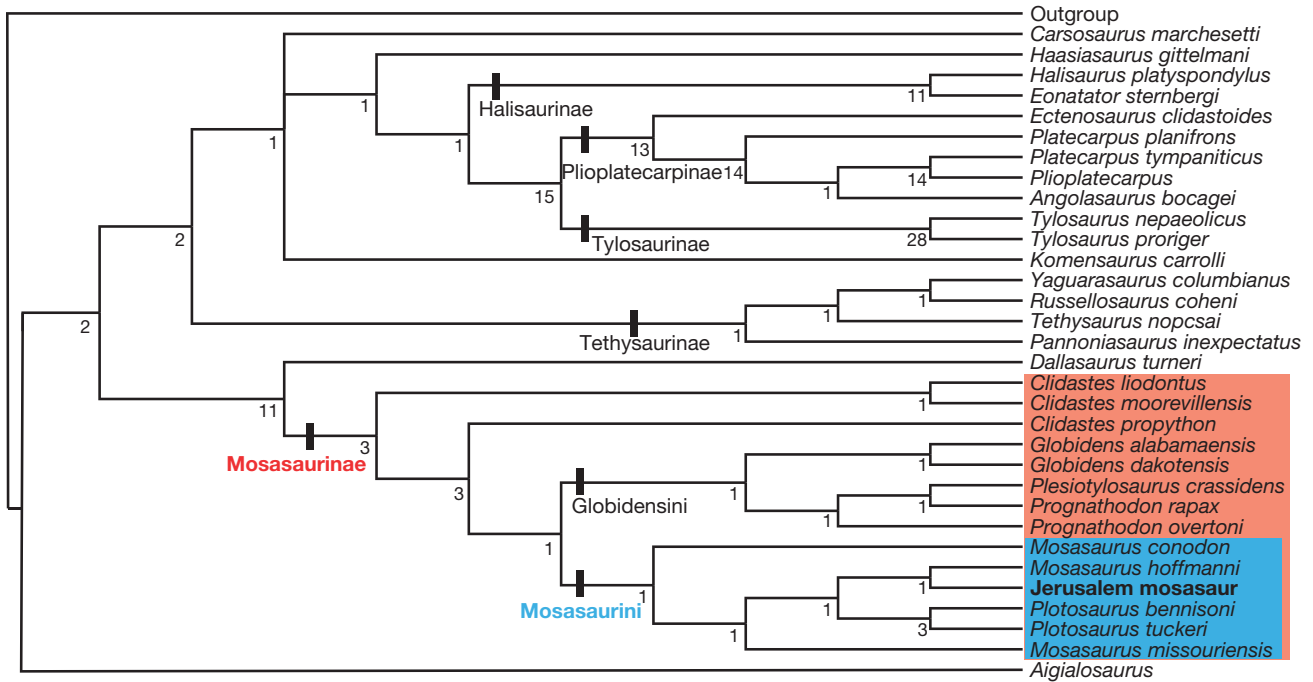
Fig. 6. — Phylogenetical analysis. Strict consensus tree from three most parsimonious trees (**length** = 363 steps, **CI** = 0.4628, **RI** = 0.7310, **HI** = 0.5372) based on a matrix including 135 morphological characters and 32 taxa of mosasauroids (modified from Makádi *et al.* 2012). The different clades as well as the Bremer indices are indicated at the base of the branches. The Jerusalem Specimen 1 is a Mosasaurini, sister-group of *Mosasaurus hoffmanni* Mantell, 1829 from which it differs however by several characters.

only onto the anterior third of the bone, and a short anterior branch of the postorbitofrontal that probably does not contact the prefrontal anteriorly (no bar above orbit). This combination of characters also clearly indicates reduction of cranial movements on the mesokinetic axis, characteristics of derived mosasaurines (LeBlanc *et al.* 2013).

Despite this unique suite of characters that could be suitable to erect a new taxon, due to the scarcity of the material and pending: 1) the discovery of homologous skeletal elements of *Mosasaurus beaugei* (including notably the frontal-parietal complex) for comparison, and because this species is the only one known from the latest Cretaceous Southern Tethys Margin and thus potentially present in Israel; 2) a review of *Mosasaurus* that appears paraphyletic in most recent phylogenetic analyses (e.g. Bell & Polcyn 2005; Madzia & Cau 2017; Simoes *et al.* 2017); and 3) a subsequent comprehensive review of the Mosasaurini and the understanding of the *Mosasaurus* / *Plotosaurus* relationships, this specimen is conservatively referred here to Mosasaurini *incertae sedis*.

PHYLOGENETIC AFFINITIES (Fig. 6)
In order to test the systematic assignment proposed above and provide additional support to the mosasaurine affinities of the "Jerusalem Specimen 1", a phylogenetic analysis using the previous one of Makádi *et al.* (2012) was performed (see Part "Preparation and cladistic analysis" for methodological details and Table 4). Note that *Eremiasaurus* was not included in this analysis because the paper of LeBlanc *et al.* (2012) appeared in the same year (but it has been shown above that the "Jerusalem Specimen 1" is clearly different from this taxon).

The analysis generated three most parsimonious trees, each having 363 steps (CI = 0.4628, RI = 0.7310, HI = 0.5372). The strict consensus tree (Fig. 6) shows the same topology – beyond the scope of this paper to comment – as that reported by Makádi *et al.* (2012).

The analysis confirms the affinities of the "Jerusalem Specimen 1" within the Mosasaurini as the sister-group of *Mosasaurus hoffmanni*, both being sister-groups of *Plotosaurus*. As previously mentioned in the comparison part, the "Jerusalem Specimen 1" differs from *Mosasaurus*, especially the largest species of the genus such as *M. hoffmanni*, by several characters of its frontal-parietal-postorbitofrontal configuration.

REPTILIA Laurenti, 1768
Order SQUAMATA Oppel, 1811
Superfamily MOSASAUROIDEA Gervais, 1852
emend Camp, 1923
Family MOSASAURIDAE Gervais, 1852
Sub-family MOSASAURINAE Gervais, 1852 (Williston, 1897)

Genus and species indet.
Jerusalem specimen 2

MATERIAL. — MHNM.0.419.4, 33: a posterior median caudal vertebra described by Répelin (1915), and another posterior median caudal (Fig. 7A, B; Table 1).

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCES. — Same as "Jerusalem Specimen 1" (see Fig. 1).

DESCRIPTION AND COMPARISON (Fig. 7A, B)
These two median caudal vertebrae bear both transverse processes and haemal arches. They are large, and the length (30 mm) is smaller than the width (35 mm) and height (36 mm). They are of exactly the same size and match one to another, so they could belong to adjacent or near-adjacent vertebrae of the same individual. The articular surfaces are regularly concave and convex, and both the cotyle and the condyle are almost rounded. The condyle is surrounded laterally by a ridge of bone that forms a slight constriction with the rest of the centrum. The neural canal is small and triangular. Though broken, the neural arches were likely laterally narrow and only slightly posteriorly oriented. The transverse processes are small and horizontally oval, located on the anteroventral part of the centrum. The ventral surface of the centrum is rather flat and bears fused chevrons that are strongly posteriorly oriented.

The small size and position of the transverse processes on the lateral surface of the centrum indicate that they are rather posterior median caudals. Because the haemal arches are fused to the centrum, these vertebrae clearly belong to the Mosasaurinae clade (Russell 1967; Bell & Polcyn 2005). Though of similar size, the rounded articular surfaces of these vertebrae differ from those of "Jerusalem Specimen 1" which bear rather triangular articular surfaces, so they probably correspond to another mosasaurine taxon, though this cannot be determined. On the contrary, they are similar in shape to those of the "Jerusalem Specimen 3" described below but stand out by being twice their size.

REPTILIA Laurenti, 1768
Order SQUAMATA Oppel, 1811
Superfamily MOSASAUROIDEA Gervais, 1852
emend Camp, 1923
Family MOSASAURIDAE Gervais, 1852
Sub-family MOSASAURINAE Gervais, 1852
(Williston, 1897)

Genus and species indet.
Jerusalem Specimen 3

MATERIAL. — MHNM.0.419.5, 34: an anterior median caudal described by Répelin (1915) and another anterior median caudal (Fig. 7C, D; Table 1).

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCES. — Same as "Jerusalem Specimen 1" (see Fig. 1).

DESCRIPTION AND COMPARISON (Fig. 7C, D)
These two median caudal vertebrae bear both transverse processes and haemal arches. They are much smaller than Specimens 1 and 2, with length equal to height (about 24 mm) and slightly larger than wide (22 mm) but this could be due to a slight lateral compression. They are of exactly the same size and match one another, so they could belong to adjacent or near-adjacent vertebrae of the same individual. The articular surfaces are slightly concave, the cotyle being almost

rounded, whereas the condyle is very slightly vertically oval. As for the vertebrae of the "Jerusalem Specimen 2", there is a small constriction between the condyle and the lateral surface of the centrum. The neural canal is very narrow but its shape cannot be determined. The transverse processes are large, occupying about ⅔ of the lateral surface of the centrum and located anteroventrally on it. The ventral surfaces of the centrum are regularly convex and bear small median nutritive foramina, as well as chevrons that are large compared to the centrum size and located posteroventrally. Though broken, they were clearly fused to the centrum and from their rounded cross-section of the preserved base, it could be deduced that they were strongly posteriorly oriented.

The position of the transverse processes on the lateral surface of the centra and their large size indicate that they are anterior median caudals. By comparison, the comparable ones of specimens 1 and 2 are twice this size. This animal was thus small, probably no more than 2-3 meters long.

Because the haemal arches are fused to the centrum, these vertebrae clearly belong to the Mosasaurinae clade (Russell 1967; Bell & Polcyn 2005). These two vertebrae, except their small size and slightly different position on the median part of the tail (anterior versus posterior), are rather similar to those of "Jerusalem Specimen 2", especially in their almost rounded articular surface, differing clearly from the roughly triangular ones of "Jerusalem Specimen 1". They could belong to a juvenile individual of the same taxon as "Jerusalem Specimen 2".

REPTILIA Laurenti, 1768
Order SQUAMATA Oppel, 1811
Superfamily MOSASAUROIDEA Gervais, 1852
emend Camp, 1923
Family MOSASAURIDAE Gervais, 1852

Genus and species indet.
Other Jerusalem specimens

MATERIAL. — MHNM.0.419. 35-37: two badly preserved caudals whose position remains unclear (possibly median caudals), and an indeterminate bone that could be either part of a neural arch or crushed skull fragments (Fig. 7E-G; Table 1).

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCES. — Same as "Jerusalem Specimen 1" (see Fig. 1).

DESCRIPTION AND COMPARISON (Fig. 7E-G)
Two very damaged caudal vertebrae are preserved. They both bear subhexagonal articular surfaces. However, on one the ventral surface is not preserved so it is not possible to see if it is a pygal or a median caudal. The other one bears chevrons but its lateral surfaces are eroded so it is not possible to see if it is a median or a posterior caudal. Because of its subhexagonal articular surfaces, it could be a median caudal. A mass of entangled broken bones cannot be determined. It could belong either to a badly preserved neural spine of a cervical or dorsal vertebra, or to agglutinated fragments of skull, possibly from around the prefrontal-maxillary-frontal region.
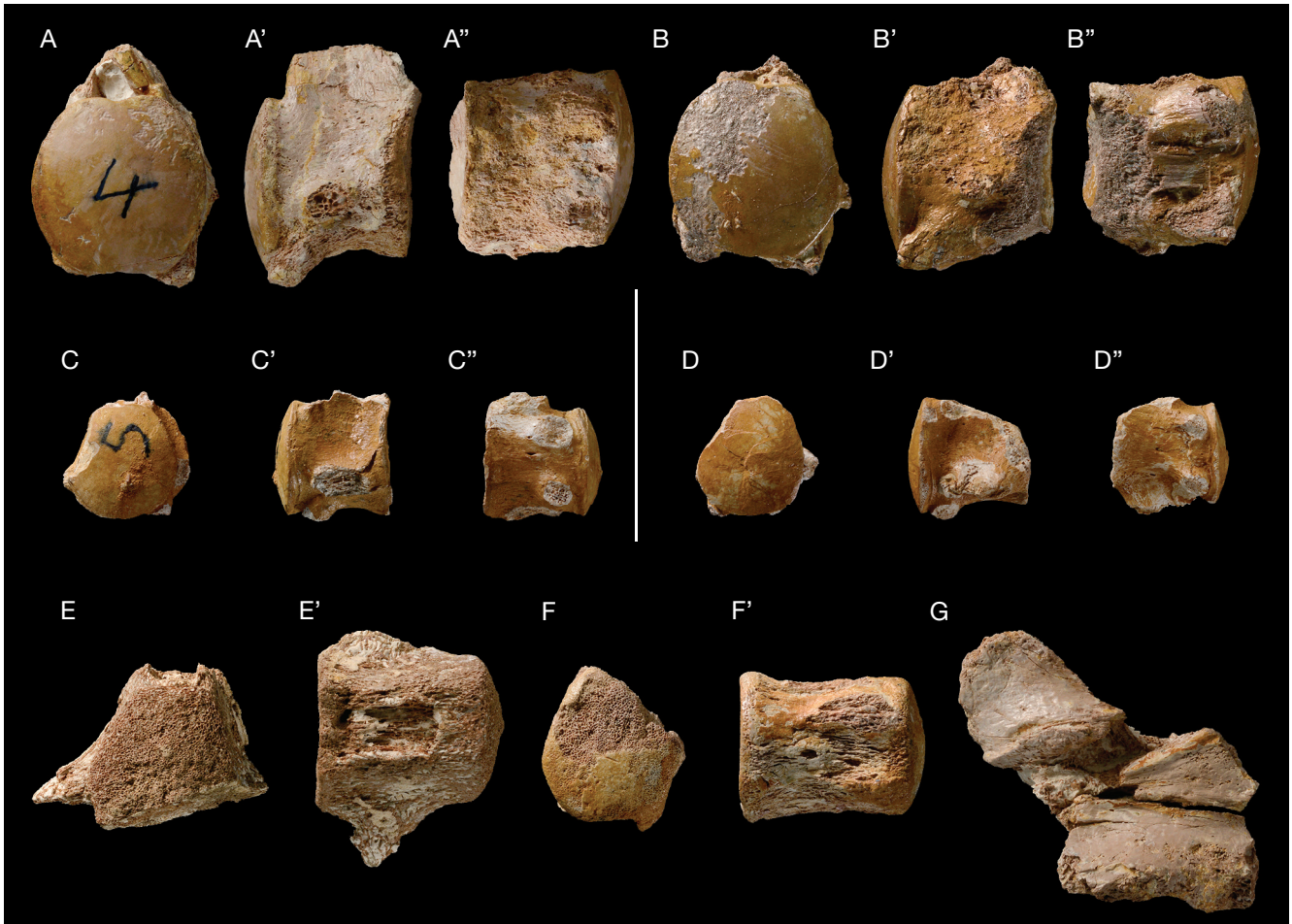
Fig. 7. — HNM 0.419.4 and MHNM 0.419.33 ("Jerusalem Specimen 2"), Mosasauridae, Mosasaurinae indet., Campanian, Jerusalem: Terminal caudal vertebrae no. 4 and 33 respectively in anterior (**A**, **B**), right lateral (**A'**, **B'**) and ventral (**A"**, **B"**) views. MHNM 0.419.5 and MHNM 0.419.34 ("Jerusalem Specimen 3"), Mosasauridae, Mosasaurinae indet., Campanian, Jerusalem: Terminal caudal vertebrae no. 5 and 34 respectively in anterior (**C**, **D**), right lateral (**C'**, **D'**) and ventral (**C"**, **D"**) views. MHNM 0.419.35-37, Mosasauridae indet., Campanian, Jerusalem: Indeterminate caudal vertebrae no. 35 and 36 respectively in anterior (**E**, **F**) and ventral (**E'**, **F'**) views, and indeterminate bone no. 37 (**G**). Scale bar: 5 cm.

DISCUSSION

Late Cretaceous mosasaurids from the Afro-Arabian Platform

Most of the marine reptiles from the Late Cretaceous of the Arabo-African Platform (Southern Tethys Margin), and more especially from the Middle East, come from the Maastrichtian phosphatic deposits of Syria, Jordan, Iraq, Israel and Egypt (see Bardet 2012a). Though classically considered as a whole Campanian in age, all these phosphatic deposits are probably lithostratigraphically equivalent, forming a major phosphatic belt extending from Iraq to Egypt, but not necessarily contemporaneous (e.g. Lucas & Prévôt-Lucas 1996). They most probably range from the Late Campanian to the Early Maastrichtian (see discussion in Bardet *et al.* 2000). Scarce older marine reptiles have been described in the Santonian of Syria (chelonioid turtles and elasmosaurid plesiosaurs, Al Maleh & Bardet 2003) and in the Campanian of Saudi Arabia (*Prognathodon* sp., Kear *et al.* 2008).

The mosasauroid faunas of Israel include several noteworthy taxa, ranging from the Cenomanian to the Maastrichtian, such as the basal *Haasiasaurus* Polcyn *et al.*, 1999, the oldest mosasauroid found up to now from the famous "Ein Yabrud outcrop (Bet-Meir Formation, Cenomanian), to derived Globidensini such as *Prognathodon currii* Christiansen & Bonde, 2002 from the Negev desert (Upper Mishash Formation, Maastrichtian and not upper Campanian, see Lewy & Cappetta 1989), one of the largest and stoutest mosasaurs ever found (Christiansen & Bonde 2002; Polcyn *et al.* 1999).

The first mosasaurid remains from Israel were however described much longer ago by Raab (1963) and come from the Maastrichtian phosphates. A recent bibliographic review of this material permitted us to recognize the following mosasaurid association: *Prognathodon giganteus* Dollo, 1889, *Platecarpus* (?) *ptychodon* Arambourg, 1952, *Halisaurus arambourgi* Bardet & Pereda Suberbiola, 2005 (see Bardet *et al.* 2005a), *Globidens phosphaticus* Bardet & Pereda Suberbiola, 2005 (see Bardet *et al.* 2005b), and *Eremiasaurus heterodontus* LeBlanc *et al.*, 2012 (see Bardet 2012a for details). As a whole, these Maastrichtian mosasaurid faunas are typical of the southern margin of the Mediterranean Tethys – that include also the taxa *Mosasaurus beaugei* Arambourg, 1952 and *Carinodens*

TABLE 4. — Character coding. Autapomorphies of the "Jerusalem Specimen 1", as well as synapomorphies shared with others Mosasaurini, using the data matrix of Makádi *et al.* (2012).

?????	??01?	11001	?11??	011??	??1?1	0????	?11??	?????	?????	????0	110??
?2???	?????	?????	?????	1????	??1?0	1?00?	?????	1????	?????	?????	?????
?????	?????	???0?									

Autapomorphies "Jerusalem Specimen 1":

Unambiguous 9(1), 30(1), 37(1, reversal from 2), 55(0), 57(1)
9: Frontal with intermediate dimensions
30: Postorbitofrontal wide
37: Jugal angle between horizontal and vertical branch about 120º
55: Basisphenoid pterygoid process narrow and facing anterolaterally
57: Basioccipital tubera elongate

Synapomorphies "Jerusalem Specimen 1" + *M. hoffmanni*:

Unambiguous 8(0), 11(1), 38(1); Ambiguous 50(1), 87(1), 94(0)
8: Frontal with sinudoisal sides
11: Frontal with low and fairly inconspicuous midline dorsal keel
38: Jugal with posteroventral process
50: Quadrate conch (not applicable)
87: Synapophysis height on posterior cervicals and anterior dorsals (not applicable)
94: No vertebral synapophysis dorsal ridge on posterior dorsals

Synapomorphies "Jerusalem Specimen 1" + *M. hoffmanni* + *Plotosaurus*:

Unambiguous 105(2); Ambiguous 36(1)
105: Scapula width (not applicable)
36: Maxilla posterodorsal extent (not applicable)

minalmamar Schulp *et al.*, 2009 (see Bardet *et al.* 2004; Schulp *et al.* 2009), unknown up to now in the Middle East – and are globally similar to the ones described from contemporaneous outcrops from Syria, Jordan, Morocco, Egypt, etc. (see Bardet 2012a for details).

The "Jerusalem Specimen 1" is referred here to an *incertae sedis* Mosasaurini, but it differs from all these mosasaurid taxa. However, with the frontal-parietal complex of *Mosasaurus beaugei* remaining currently unknown, it cannot be excluded that it could belong to this species. It is also noteworthy that the mosasaurid remains described here, coming from chalky levels of Middle Campanian age well below the phosphatic deposits in Israel, are much older. With the exception of *Haasiasaurus* (Cenomanian), these mosasaurid remains are thus the oldest ones known from Israel.

CAMPANIAN MOSASAURIDS FROM
THE NORTHERN TETHYS MARGIN
In Europe, mosasaurids have been reported in both the early and late Campanian in Spain (Bardet *et al.* 1997), France (e.g. Bardet 2012b; Bardet & Galoyer 2015), Belgium and The Netherlands (e.g. Jagt 2005), Sweden (e.g. Lindgren & Siverson 2004, 2005), Germany (e.g. Sachs *et al.* 2015, 2018; Honung *et al.* 2018) and Poland (e.g. Jagt *et al.* 2005). They are however less abundant, both in terms of specimens found (generally isolated teeth and vertebrae) and systematic diversity, than those of the Maastrichtian faunas from Belgium, The Netherlands and Morocco (see Bardet 2012b; Bardet *et al.* 2015). The main mosasaurid clades have however been recognized, including halisaurines (*Halisaurus* Marsh, 1869, *Eonatator* Bardet & Pereda Suberbiola, 2005 (see Bardet *et al.* 2005a)), tylosaurines (*Hainosaurus* Dollo, 1885, *Tylosaurus* Marsh, 1872), plioplatecarpines (*Platecarpus* Cope, 1869) and mosasaurines (*Clidastes*, *Prognathodon*, *Globidens* and

Mosasaurus). Noteworthy is the predominance in this European Campanian mosasaurid faunas of mosasaurine taxa, as previously noted for Maastrichtian ones (see Bardet *et al.* 2015). Also of importance is a major faunal turnover among mosasaurids occurring at the Early/Late Campanian boundary both in North America (Russell 1967; Kiernan 2002) but also possibly in Europe from data obtained from Sweden (Lindgren 2004; Lindgren & Siverson 2003, 2004, 2005) that shows the replacement of mosasaurid faunas dominated by *Clidastes-Tylosaurus-Platecarpus* by ones dominated by *Mosasaurus-Prognathodon-Plioplatecarpus*. The mosasaurids described here from the Middle Campanian remain too poorly preserved to test if this scenario could also apply to Middle East faunas. It is simply noteworthy that the "Jerusalem Specimen 1" differs from all the taxa mentioned above.

MOSASAURINI PALAEOBIOGEOGRAPHIC DISTRIBUTION
Currently, Mosasaurini (*sensu* LeBlanc *et al.* 2012) include only the genera *Mosasaurus*, which had a worldwide distribution during the Campanian-Maastrichtian interval, and *Plotosaurus*, known with certainty only from the Maastrichtian of California (e.g. Bardet *et al.* 2014; González-Ruiz *et al.* 2019). The occurrence of mosasaurini remains in the Middle East argues rather in favor of closer affinities with *Mosasaurus* than to *Plotosaurus*, as also supported by the phylogenetic analysis performed here.

CONCLUSIONS

The present work is the first comprehensive study, including anatomical description and systematic assignment, as well as stratigraphic and possibly geographic provenance determination, of mosasaurid remains found in the Late Cretaceous near

Jerusalem more than a century ago and briefly mentioned by the French paleontologist Répelin (1915).

The remains are mosasaurid as a whole and mainly belong to the Mosasaurini clade but a more precise systematic attribution is not possible, although the most diagnostic specimen could be a closer relative of *Mosasaurus*, on the basis of anatomical, phylogenetic and palaeobiogeographic arguments. It however differs by its frontal-parietal-postorbitofrontal configuration from any known species referred to this genus.

Thanks to the integrated study of several microfossil groups (calcareous nannofossils, planktonic foraminifera and palyno-morphs) contained in the white chalk still surrounding the bones, the mosasaurid remains can be constrained to the lower part of the Middle Campanian (*C. plummerae* / *G. rosetta* and CC18 / UC14a Zones) that locally corresponds to the Mishash Formation that crops out widely east of Jerusalem (Mount of Olives vicinity). It is possible that the mosasaurid remains were found by Father Ruffier in one of the outcrops of this formation, possibly not very far from where he worked and lived (Saint-Anne Community in Jerusalem). These chalky levels, common in the Middle East and located below the famous phosphatic deposits, represent a shallow and rather open marine environment, possibly near-shore.

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