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## The late Miocene mammals from the Konservat-Lagerstätte of Saint-Bauzile (Ardèche, France)

*Conservation exceptionnelle de mammifères du Miocène supérieur à Saint-Bauzile (Ardèche, France)*

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## ARTICLE INFO

## Article history:

Received 9 October 2016

Accepted after revision 10 May 2017

Available online 23 June 2018

Handled by Didier Néraudeau and Sylvain Charbonnier.

## Keywords:

Konservat-Lagerstätten

Diatomites

Mammals

Late Miocene

France

## ABSTRACT

Diatomite deposits of Saint-Bauzile near Privas (Ardèche) in southern France have been known since more than two centuries for abundant and extremely well-preserved fossils of plants and animals. The radiometric dating brackets fossil-bearing horizons between 7.2 and 7.6 Ma, which is consistent with the biochronologic age given by fossil mammals, which are characteristics of the late MN11 zone, i.e. the second part of the late Miocene. The main interest of this site for mammals is that they are preserved almost “in the flesh”, as entire skeletons with bones in their anatomical connection, and often with skin and fur charred and forming a halo around the body. In this work, we studied the remains of a lagomorph, two rodents, an equid, a suid, a bovid and a rhino. The mode of preservation of mammals as entire bodies suggests sudden death and rapid burial of individuals.

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## R É S U M É

Les dépôts de diatomites de Saint-Bauzile près de Privas (Ardèche, France) sont connus depuis plus de deux siècles par des restes de végétaux et animaux fossiles qu'on y trouve en abondance et dans un exceptionnel état de préservation. Les datations radiométriques donnent un âge entre 7,2 et 7,6 Ma pour les niveaux fossilifères, ce qui est conforme à l'âge biochronologique indiqué par les mammifères fossiles qui caractérisent la zone MN11 tardive, c'est-à-dire la deuxième partie du Miocène supérieur. L'intérêt principal de ce site pour la paléontologie des mammifères est que des animaux, à la fois de petites et de grandes tailles, y sont préservés comme presque « en chair et en os », c'est-à-dire avec leur squelette entier et en connexion, des restes carbonisés de leur peau et de leur chair, voire le contenu stomacal, la trace de leur nourriture en forme de halo autour du corps. Dans ce travail, nous

## Mots clés :

Conservation exceptionnelle

Diatomites

Mammifères

Miocène supérieur

France

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avons pu étudier les restes d'un lagomorphe, de deux rongeurs, d'un Equidae, d'un Suidae, d'un Bovidae et d'un Rhinocerotidae. Le mode de préservation des mammifères en cadavres entiers suggère la mort subite et l'enfouissement rapide des individus.

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## 1. Introduction

Extraordinarily well-preserved fossils (Konservat-Lagerstätten) provide unusual morphologic and potential molecular information of ancient life. Among various sedimentary environments that favour soft tissue preservation, lacustrine deposits are renowned for their exceptional fossils (Allison and Briggs, 1991). In the case of such rare preservations, the specimen is represented not only by its skeleton, but also by its body shape, fur characteristics, stomach content and exceptionally the foetus of a pregnant female. Such specimens are known from only a few sites, the most famous of them being Messel (middle Eocene; Franzen, 1985; Schaal, 1992) and Willerhausen (late Pliocene; Rietschel and Storch, 1974) in Germany, Las Hoyas Quarry in central Spain (Early Cretaceous; Martin et al., 2015), the localities of Daxigou (Middle Jurassic; Luo et al., 2011) and Dawangzhangzi (Early Cretaceous; Ji et al., 2002) of northeastern China. Fossils in such a state of preservation are generally found on slabs of laminated sediments and they appear more or less compressed.

The diatomite accumulation often reflects a favourable sedimentary environment for preserving exquisite fossils, including articulated skeletons and soft tissues (Esperante et al., 2015; Harding and Chant, 2000). The diatomite is formed by the accumulation of siliceous frustule of diatoms, a single-celled, free-floating or attached golden-brown algae belonging to the Class Bacillariophyceae of the Phylum Chrysophyta (Fig. 1 D–E; Flower, 2007). Diatomite deposits have a worldwide distribution and can be either freshwater or marine in origin, ancient or extant, and can usually be identified in the field as grey sediment (friable when dry) with low specific density. In shallow lakes, benthic diatom production requires that the sediment surface lies within the photic zone and that the diatoms are growing in clear water with only small amounts of terrigenous material entering the system (Flower, 2007). Generally, shallow freshwater diatom deposits are closely associated with volcanic activity (basalts, tephros, and volcanic deposits) that can supply abundant dissolved silica for diatom growth. Because of their great economic interest (e.g., filtration and pharmaceuticals), the diatomites are extracted by quarrying, which also allows discoveries of extraordinary preserved fossil assemblages.

The site of Saint-Bauzile near Privas, Ardèche, France, is renowned for the variety and completeness of its late Miocene fauna and flora (Demarcq et al., 1989; Riou, 1995). About 50 m thick sequence of lacustrine diatomite has yielded a rich flora (diatoms, pollens, foliar prints, seeds) and fauna (insects, fish, amphibian, reptiles and mammals). The earliest written record about the fossils from

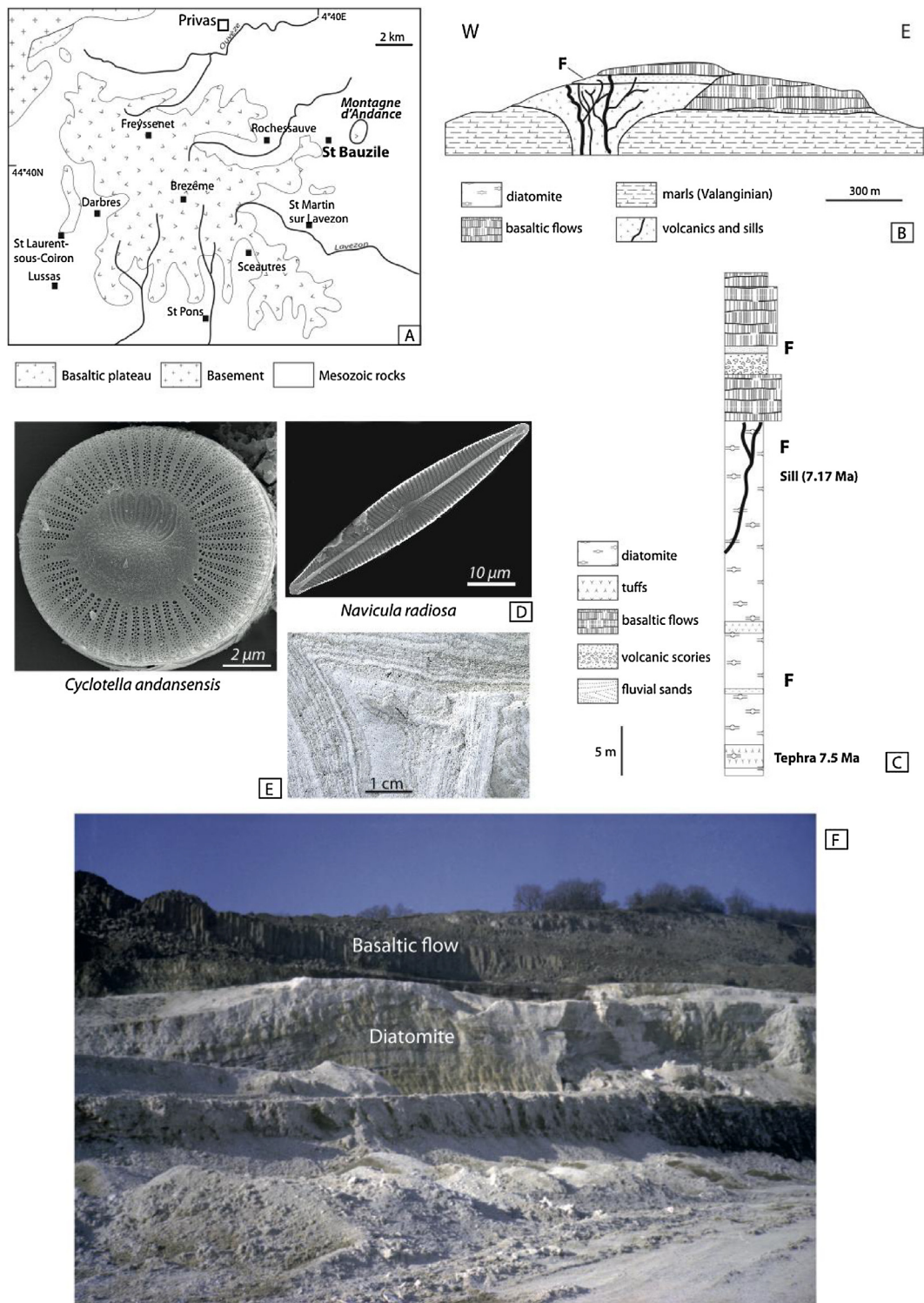
the diatomite of la Montagne d'Andance (Ardèche) dates back to the 18th century when Faujas de Saint Fond (1778) noticed abundant fossil plants, and later the presence of fishes and insects (Faujas de Saint Fond, 1815). Boulay (1887) first reported fossil mammals, and most subsequent scientific studies focused on plants microfossils and pollen grains (Grangeon, 1960; Iskandar, 1988), and the assemblage of diatoms (Ehrlich, 1966; Kuehlthau-Serieyssol, 1993; Fig. 1D–E). A detailed faunal list of vertebrates is produced by Mein et al. (1983), and detailed taxonomic studies have been carried out on glirid rodents (Mein and Romaggi, 1991), on a lagomorph (Mein et al., 1983) and on boselaphine bovids (Romaggi, 1987). However, the rest of mammal taxa preserved in Saint-Bauzile are still undescribed, and for most of them never been figured in the literature. Moreover, there is little information available in English on this unique, at the scale of Europe, late Miocene Konservat-Lagerstatt. The fossils from Saint-Bauzile not only provide details of the postcranial skeleton, but also an amazing preservation of the soft body outline and hairs. In addition, gut contents are apparently preserved (to be confirmed).

Our objective here is to provide geological, palaeontological, and taphonomical information about the fossil mammals of that locality, with a focus on the taxonomic diversity and the style of preservation. All the figured specimens of large mammals are housed at the National Museum of Natural History, Paris (Nos. MNHN-FMCF 60, MNHN-FMCF 61, MNHN-FMCF 62) and the collections of the University of Lyon (No. 212-996), while the remains of small mammals are dispersed in several private and public collections.

## 2. Geological setting and age of diatomitic beds

The “Montagne d'Andance”, near Saint-Bauzile, is an isolated hill that lays on the northeastern margin of the vast basaltic plateau of Coiron (Fig. 1A). Stratigraphically, the diatomitic unit lies beneath the volcanic plateau, and it is exploited for industry since the 1960's (Champreux and Euvrard, 1993). The stratigraphic sequence exposed in the Montagne d'Andance is summarized in Fig. 1B–C. According to Grangeon (1960), the lacustrine sedimentation could be related to a lava flow dam, located in the eastern part of the site, thus infilling of a maar-crater (Champreux and Euvrard, 1993; Demarcq et al., 1989).

The diatomite was primarily considered lower Turolian (MN11, ca. 7.5–8.5 Ma, Agusti et al., 2001) based on the co-occurrence of the murine rodent *Parapodemus lugdunensis*, the equid *Hipparion tuyolsi*, and the primitive boselaphine *Graecoryx andancensis* (Demarcq et al., 1989). The main



**Fig. 1.** A. Simplified geological map showing the extension of the Coiron Basaltic Plateau and Montagne d'Andance near the village of Saint-Bauzile. B. Schematic cross-section of the Montagne d'Andance (from Grangeon, 1960; Pastre et al., 2004); F indicates the location of the diatomaceous unit in which fossil vertebrates were collected. C. Synthetic log of the Montagne d'Andance; the dating of the basal tephra and sill is from Pastre et al., 2004. D. The fresh water diatom *Cyclotella andansensis* and *Navicula radiosa*, the most common diatom species accumulated at Saint-Bauzile during the late Miocene (from <https://westerndiatoms.colorado.edu>); 114 species of diatoms have been identified at St-Bauzile (Kuehlthau-Serieysso, 1993). E. Close-up of the diatomitic rock showing the grey-whitish infra-millimetric thin layers alternating with 2 millimeters thick white layers. This cyclicity of diatom blooming might be related to moon cycles and/or local volcanic activity (Esperante et al., 2015). F. Photo of the outcrops of the Montagne d'Andance showing the diatomite sequence (white) capped by the basaltic plateau (dark in the back).

diatomitic unit (~50 m in thickness) that has yielded fossil vertebrates is sandwiched between Miocene volcanic breccia (Fig. 1B) and the Coiron basaltic lava flows that is now dated to  $7.13 \pm 0.06$  Ma (Pastre et al., 2004; Fig. 1F). Moreover, the deposition of diatomite necessarily predates the intrusive basaltic sills dated to  $7.17 \pm 0.06$  Ma (Pastre et al., 2004). Furthermore, the trachytic tephra identified in the lower part of the sequence (levels C and D of Pastre et al., 2004), where most vertebrates were recovered, provide a reliable chronostratigraphic marker to date the diatomitic beds yielding fossils. The  $^{40}\text{Ar}/^{39}\text{Ar}$  age of this tephra is  $7.54 \pm 0.06$  Ma (Pastre et al., 2004). Consequently, the large part of the diatomite deposited during an interval from 300 to 400 ky, with probable intervals of non-sedimentation. Pastre et al. (2004) estimated that the diatomitic lake functioned during ~100 ky. The volcanic activity at the origin of tephra deposits is related to a peak of volcanism near 8 Ma in the area (Nehlig, 1999). Finally, it is worth noting that the top of the diatomitic sequence is incised by channelized conglomerates that have yielded a mammal assemblage taxonomically very close to that of diatomites, suggesting a sub-contemporaneous age (Demarcq et al., 1989).

### 3. The mammal fauna

Studies of mammalian palaeobiology can contribute to an understanding of the environment of ancient palaeolakes, most often through taphonomic investigations, and also through a comparative approach that utilizes taxonomic and functional analogues from extant mammals. Extant taxonomic and functional analogues may provide interpretations of physical and ecological limiting factors, behaviour and trophic dynamics of fossil mammals, as inferred from presumed functional relationships between morphology and habitats or feeding modes. However, the reliability of such inferences decreases with increasing geological age, and with increasing phyletic distance between fossils and extant equivalents. The fossil mammals from the diatomite of Saint-Bauzile are moderately diversified taxonomically, but they offer a large spectrum of size, locomotor adaptation, and feeding habits.

#### 3.1. Small mammals

All the small mammals from the diatomite of Saint-Bauzile are preserved on slabs, and they represent complete individuals (except breakages in the slab) having various parts of the body in natural position and without any part disarticulated (Figs. 2–3). Each individual of small mammals is preserved as imprints of the skin in black or dark-brown, surrounded by a light halo of bristles, particularly around the body and tail. The skin

being disappeared, the bones are visible generally in their anatomical position or slightly displaced, and their proportions are preserved. As Rietschel and Storch (1974) demonstrated, such preservation is only possible if the individuals are drowned, flooded with water that wets the coat and fills the stomach and lungs, immersed quickly and consequently embedded into sediment in presumable nearshore shallow waters. The preservation of a complete body with imprints of skin and fur supposes incomplete degradation of organic matter. This is the case for all specimens of small mammals that we examined from the diatomites of Saint-Bauzile. They all preserved, in addition to their skeleton, the remains of their skin and fur, which became a structureless carbonaceous crusts, and the imprint of the body as a halo around the skeleton.

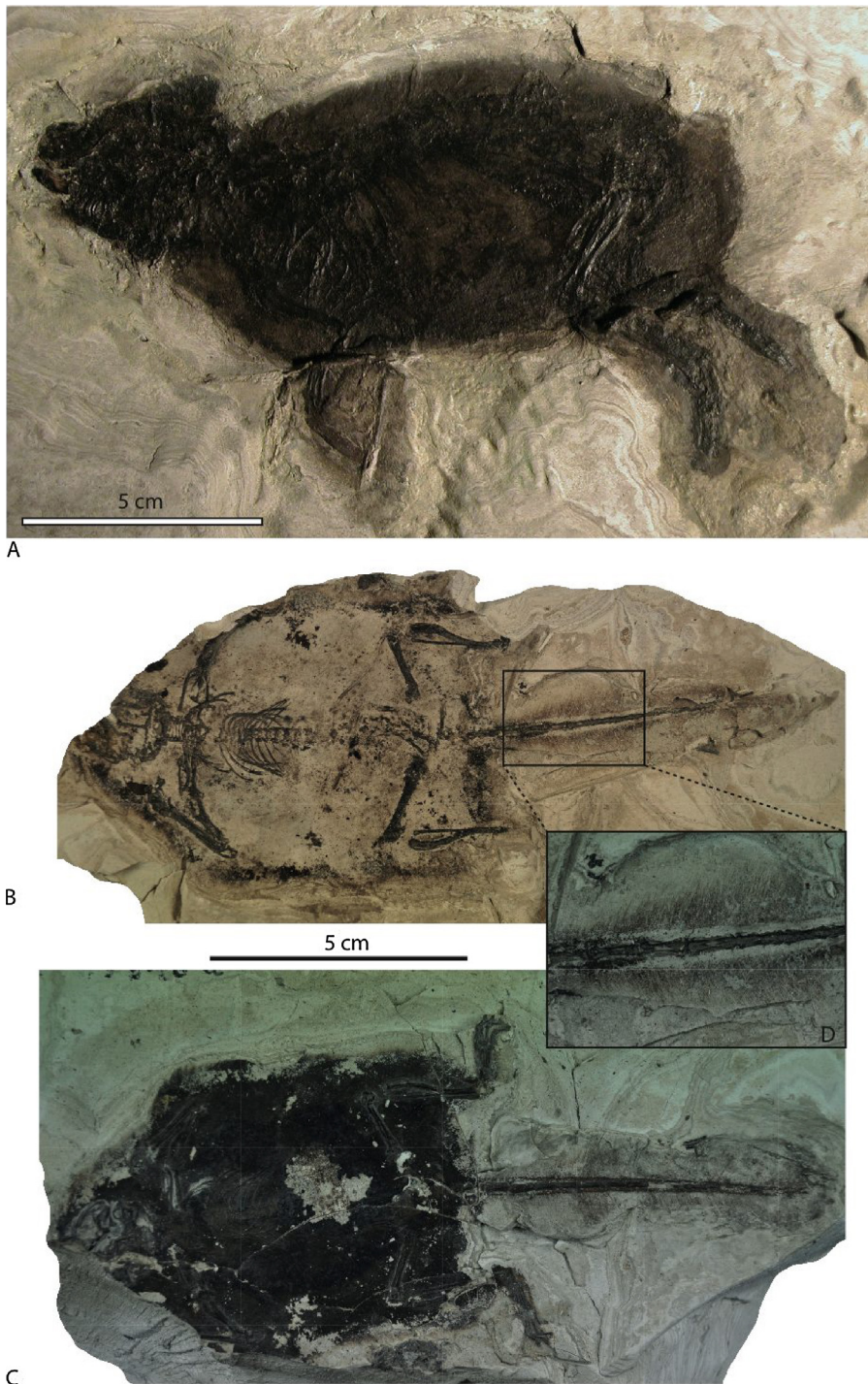
Systematics of fossil small mammals is mainly based on their dentitions, sometimes completed by the characters of upper and lower jaws or skulls, and very exceptionally by their skeleton. The list given by Demarcq et al. (1989) and reported by Riou (1995) enumerates six species of small mammals to be found in the diatomites of Saint-Bauzile: *Prolagus crusafonti*, *Parapodemus lugdunensis*, *Parapodemus aff. barbarae*, *Valerimys* sp., *Dipoides problematicus* and *Glirulus aff. lissiensis*. Among these species, we have at our disposal the specimens or high definition photos referred to *P. crusafonti*, *P. lugdunensis* and *P. aff. lissiensis*.

##### 3.1.1. *Prolagus crusafonti* Lopez-Martinez, 1975

According to Mein et al. (1983), five skeletal remains of an ochotonid lagomorph have been discovered at Saint-Bauzile, all dispersed in private collections. Mein et al. (1983, pl. 1, fig. 1; see also López Martínez, 2001, fig. 4 for the same specimen) described and illustrated one of them, Riou (1999, figure in p. 255) illustrated a second one, and we have the picture of a third specimen given to us by B. Riou in the 1980s. As far as we know from the literature, these specimens are the only complete skeletal imprints known for the whole family Ochotonidae. The three specimens mentioned here above are complete skeletons with fur imprint on diatomite slabs. Mein et al. (1983) and López Martínez (2001) described some morphological characters of limb bones, skull and dentition, and discussed the systematics of the Saint-Bauzile ochotonid to identify it as *Prolagus crusafonti*, which we agree.

The imprint of the dark organic matter shows that the total length (nose–tail base) is between 15.5–19 cm, the length of the head about 4.5 cm, and the maximum body height behind the shoulders is about 7 cm. The imprint of the fur beyond the body imprint is short (less than 10 mm), indicating that this species of *Prolagus* had a rather thin fur cover on its dorsal body (Fig. 2A). The head is rather massive and its roof is gently convex, the ears are short and

**Fig. 1.** A. Carte géologique simplifiée montrant l'extension du plateau basaltique de Coiron et de la montagne d'Andance près du village de Saint-Bauzile. B. Coupe schématique de la montagne d'Andance (d'après Grangeon, 1960 ; Pastre et al., 2004) ; F indique l'emplacement de l'unité diatomitique dans laquelle les vertébrés fossiles ont été récoltés. C. Coupe synthétique de la montagne d'Andance ; les datations du téphra basal et du sill sont issues de Pastre et al., 2004. D. Des diatomées d'eau douce *Cyclotella andancensis* et *Navicula radiosa*, les espèces les plus communes à Saint-Bauzile au Miocène supérieur (<https://westerndiatoms.colorado.edu>) ; 114 espèces de diatomées ont été identifiées à Saint-Bauzile (Kuehlthau-Serieyssel, 1993). E. Gros plan de la roche diatomitique de Saint-Bauzile montrant les couches minces gris-blanchâtre infra-millimétriques alternant avec des couches blanches épaisses de 2 mm. Cette cyclicité de la floraison de diatomées pourrait être liée aux cycles de la lune et/ou à l'activité volcanique locale (Esperante et al., 2015). F. Photo des affleurements de la montagne d'Andance, montrant la séquence de diatomites (blanche) coiffée par le plateau basaltique (sombre en arrière-plan).

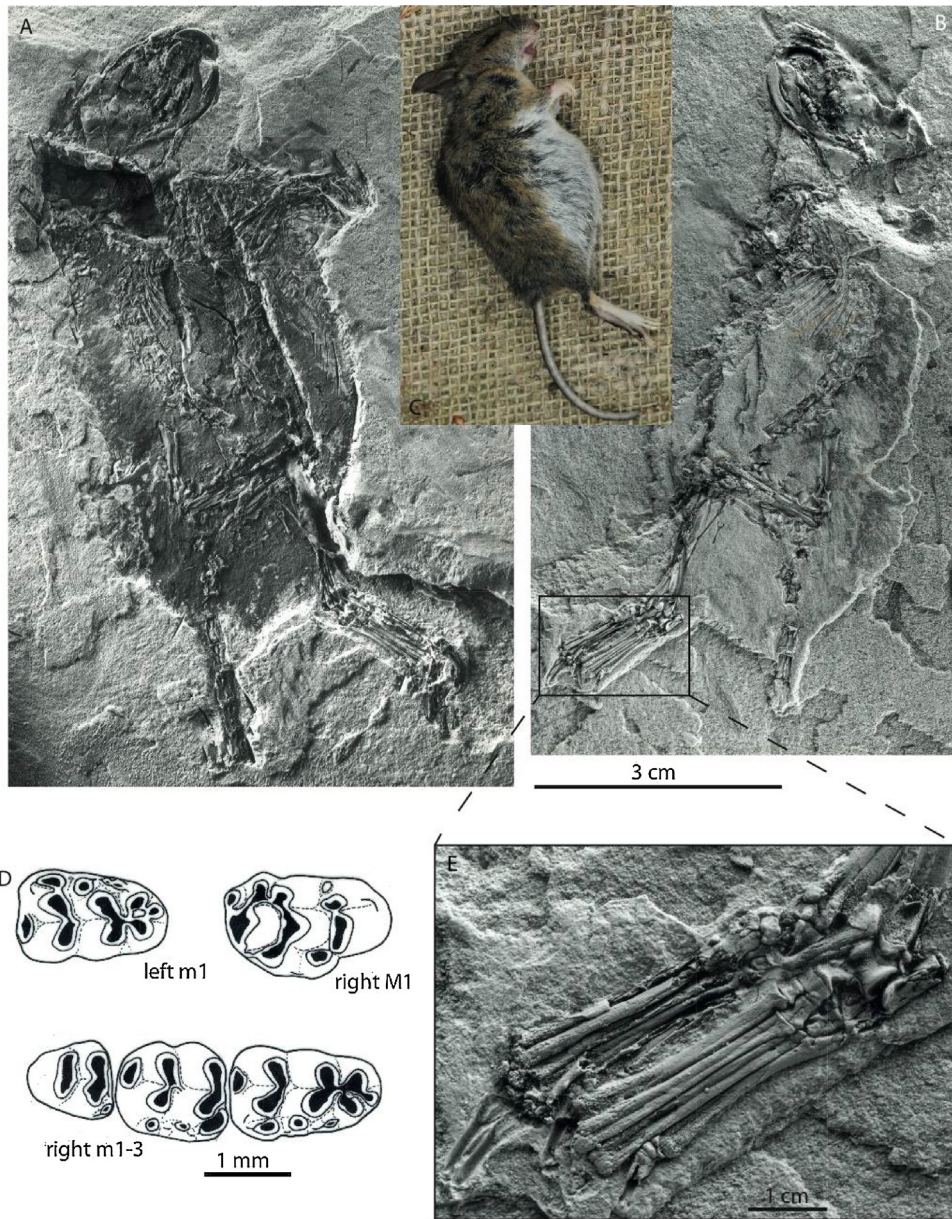


**Fig. 2.** Small mammals from the late Miocene of Saint-Bauzile, Ardèche, France. A. *Prolagus crusafonti* (specimen from Bernard Riou's collection). B and C. *Paraglitirulus aff. lissiensis* (specimen FSL 69916), both side of the same individual as seen on two slabs. D. Detail of the tail of the same individual.

**Fig. 2.** Les petits mammifères du Miocène supérieur de Saint-Bauzile, Ardèche, France. A. *Prolagus crusafonti* (spécimen de la collection de Bernard Riou). B et C. *Paraglitirulus aff. lissiensis* (spécimen FSL 69916), les deux côtés du même individu vus sur deux dalles. D. Détail de la queue du même individu.

their tip is apparently rounded, and the neck is short. On the body, the vertebral column is strongly curved at the shoulders and on the dorsal region, but the lumbar vertebrae curve is weaker, or even rather flat. The preserved

curvature of Saint-Bauzile skeletons on their slabs is astonishingly similar to that of *Prolagus sardus*, as reconstructed by Dawson (1969). Mein et al. (1983) noted that *P. crusafonti* of Saint-Bauzile has 13 vertebrae, instead of 14 in the



**Fig. 3.** Small mammals from the late Miocene of Saint-Bauzile, Ardèche, France. A and B. *Parapodemus lugdunensis* on two slabs showing both sides of the same individual (Bernard Riou's collection). C. A natural dead body of the woodmouse *Apodemus sylvaticus* at the same attitude as the fossil specimen of Saint-Bauzile. These two species have close phylogenetic relationships. D. Upper and lower molars of the Saint-Bauzile individual. E. Detailed view of the right and left feet to show the remarkable lengthening of the metatarsals, probably indicative of jumping abilities of the species.

**Fig. 3.** Les petits mammifères du Miocène supérieur de Saint-Bauzile, Ardèche, France. A et B. *Parapodemus lugdunensis* sur deux dalles montrant les deux côtés du même individu (collection de Bernard Riou). C. Un cadavre naturel d'*Apodemus sylvaticus* dans la même attitude que le spécimen fossile de Saint-Bauzile. Ces deux espèces ont des rapports phylogénétiques proches. D. Molaires supérieures et inférieures de l'individu de Saint-Bauzile. E. Vue détaillée des pieds droit et gauche pour montrer l'allongement remarquable des métatarsiens, probablement indicatifs de la locomotion par saut de l'espèce.

extant *Ochotona*. According to its halo, the fur covers all the head and body, except around the mouth, and on the hand and foot. It is thicker around the neck, on the chest and on the back of the body than elsewhere.

The limb bones clearly show that the hind limb is longer than the forelimb. The proportions of limb elements are considered informative of cursorial adaptations of mammals. On the specimen illustrated by Mein et al. (1983), the

length of the humerus is 28 mm, of the radius 26 mm, of the femur 33 mm, and of the tibia 40 mm. On the other specimen (Fig. 2A), the same measures are 25, 23, 33 and 37 mm, respectively. These proportions may have been slightly modified with flattening of the bodies.

Among the extant lagomorphs, the pikas (genus *Ochotona*) are known as having less cursorial ability than the rabbits and hares (family Leporidae). Dawson (1969)

compared the limb bones of *Prolagus sardus* from Sardinia Island with that of *Ochotona princeps* from North America, and observed that several characters of scapula and humerus indicate a greater muscular development than in *Ochotona*. She also noted that the proportions of limb bones suggest for *P. sardus* more cursorial locomotion than in *Ochotona*. To demonstrate this, she provided several indices that are used in Table 1 to compare several lagomorph species. *P. crusafonti* of Saint-Bauzile has radius, compared to humerus, longer than in *Ochotona*, *P. sardus* and *Romerolagus*, but shorter than all *Lepus* species. The tibia/femora and the humerus/femora proportions do not seem any significant difference from one species to another. The proportions of humerus plus radius compared to that of femur plus tibia clearly show that the forelimb is longer in *Prolagus*, *Ochotona*, *Romerolagus* and *Oryctolagus* compared to the proportions in all *Lepus* species. From this comparison, it appears that *P. crusafonti* from Saint-Bauzile has intermediate values between *Ochotona* (less cursorial) and *Lepus* (more cursorial), and similar in that to *Prolagus sardus* and *Oryctolagus cuniculus*. Young et al. (2014) also investigated on the cursorial abilities of some North American extant lagomorphs using several parameters on the limb bones, such as bone robustness, bone mineral density, bone bending strength index, and relative limb segment lengths. The specimens from Saint-Bauzile being crushed skeletons on slabs, only the relative lengths of limb bones can be used, as previously did by Dawson (1969) to evaluate the cursorial abilities of *C. crusafonti*, and compared to some other lagomorphs, as given here in Table 1, while the other parameters used by Young et al. (2014) cannot be applied in the case of Saint-Bauzile ochotonid.

### 3.1.2. *Glirulus aff. lissiensis* Hugueny and Mein, 1965

Mein and Romaggi (1991) described an exceptionally preserved specimen of *G. aff. lissiensis* from Saint-Bauzile. Both sides of a dorsoventrally compressed body are preserved on two slabs. They display all details related to the skeleton and body shape. The imprint of the dark coloured organic matter shows the extension of the skin on the slab. The skin is enlarged at the level of thorax (about 60 mm) and the neck (about 27 mm), and stretched between the

forelimbs and hind limbs (Fig. 2B–C). Such a preservation of soft tissues indicates the presence of a patagium suggesting an adaptation to gliding, a lifestyle that is not observed in extant glirids. In addition, the great difference between the widths of the chest cavity (maximum width 17 mm) and the skin at the level of thorax (about 60 mm) favours this interpretation, as did Mein and Romaggi (1991). This specimen is the first evidence that *G. aff. lissiensis* had gliding adaptations. The limb bones are all preserved in their anatomical positions. Taking into account the measurements of the humerus (13 mm) and radius-ulna (16.2 mm) on the forelimbs and femora (14.7 mm) and tibia (16.3 mm) on the hind limbs, it can be concluded that the hind limbs are slightly longer than the forelimbs. Such a proportion is unusual for Gliridae and is only seen in arboreal and gliding species. On the other hand, the metacarpals are short while the phalanges are rather elongated and dorsoventrally curved.

The total length of the head plus body is 71 mm and the tail is 77 mm. The latter is composed of at least 22 vertebrae. One of the interests of this specimen is the preservation of the fur imprint (Fig. 2B–C). Outside the skin border, it is represented by a brown halo that can be seen all around the head, body, limbs and tail. Its thickness around the body does not exceed 5 mm, but around the tail the fur is much thicker, almost 10 mm. On the body, the bristles are not well distinguished but on the tail, it is possible to distinguish almost every bristle and they are directed backward with an angle of about 70° to the longitudinal axis. The diameter of the skin at the thorax measures 55 mm, while the chest cavity is not wider than 17 mm. This skin almost draws a straight line between the wrists and ankles, parallel to the axis of the body. The skin still wide at the neck is tightening its normal position on the skull.

### 3.1.3. *Parapodemus lugdunensis* Schaub, 1938

Several specimens on slabs have been referred to this species, without however a reliable description of its anatomical and dental characteristics. Riou (1995, pl. 2, fig. 8) illustrated a slab with a complete individual from nose to the end of tail, lying on the left side. In another paper, Riou (1999, figure in p. 256) illustrated another complete

**Table 1**

Proportions of the main limb bones in some species of Ochotonidae and Leporidae in comparison with that of two specimens from Saint-Bauzile. Measurements used for *Romerolagus* are from Dawson (1969), for *Prolagus sardus* from Tobien (1935), for *Ochotona princeps* and *Lepus californicus* from Young et al. (2014) and for *Oryctolagus* and *Lepus* from De Marfà y Taillefer (2009).

**Tableau 1**

Proportions des principaux os des membres dans certaines espèces d'Ochotonidae et de Leporidae en comparaison avec celles de deux spécimens de Saint-Bauzile. Les mesures utilisées pour *Romerolagus* sont celles de Dawson (1969) pour *Prolagus sardus* de Tobien (1935), pour *Ochotona princeps* et *Lepus californicus* de Young et al. (2014) et pour *Oryctolagus* et *Lepus* de De Marfà y Taillefer (2009).

Species	Radius/humerus	Tibia/femur	Humerus/femur	Humerus + radius/femur + tibia
<i>Prolagus crusafonti</i> (specimen B. Riou)	92	112	76	69
<i>Prolagus crusafonti</i> (Mein et al., 1983)	93	121	85	74
<i>Prolagus sardus</i> -Sardinia	89	113	81	72
<i>Ochotona princeps</i> , North America	76	114	95	65
<i>Romerolagus diazi</i> , Mexico	87	120	81	72
<i>Oryctolagus cuniculus</i> , Europe	95	113	77	70
<i>Lepus californicus</i> , North America	120	122	79	78
<i>Lepus timidus</i> , Europe	102	117	80	76
<i>Lepus europaeus</i> , Europe	91	111	80	80
<i>Lepus granatensis</i> , Spain	114	102	74	78

individual lying on the left side, without any comment or size information for both specimens. We have at our disposal one slab of an individual lying on left side (MNHN.FMCF 63) and the pictures of another one that Bernard Riou allowed one of us to study in mid 1980s (Fig. 3). The shape of the skull and mandible, as well as some preserved molars allow identification of these remains as *Parapodemus lugdunensis* Schaub, 1938. On the MNHN specimen, the head measures 24 mm, the body without tail 69 mm, and the tail is preserved on 42 mm. On the Riou's specimen (Fig. 3), the head measure 24 mm, the body length is 60 mm and from the tail there are only five vertebrae measuring 18 mm. On both individuals, the hind limb is much more developed than the forelimb, and the length of metatarsals is particularly remarkable. The height of the skull between the roof and the angular process of mandible is 17 mm on the MNHN specimen and 18.5 mm on the other. The body height at the end of the thorax cavity is 31 mm on the Riou's specimen and approximately 32 mm on the other.

Both specimens at our disposal are preserved in their natural death position as compared to dead individuals of woodmouse *Apodemus sylvaticus* (Fig. 3C), i.e. the front legs bent beneath the breast, while the hind legs stretched backwards, and the fingers of the hand and the foot bent backwards. The vertebrae column is broken on Riou's specimen and displaced ventrally. Despite this, the original shape of the body is apparently preserved as the outline of the halo around the skeleton (Fig. 3A). The thickness of the fur is difficult to appreciate on both specimens. The MNHN specimen is partly embellished by adding black ink on the body, and on the specimen that B. Riou lent us, the imprint of the skin and fur forms a halo of carbonaceous matter in which it is not possible to distinguish the boundary between the skin and fur. It is obvious that the front legs are shorter than the hind legs. However, it is not possible to measure them accurately because of numerous breakages and stacking of bones.

### 3.2. Large mammals

Large mammals are well documented in the diatomite of Saint-Bauzile. Several complete skeletons including gravid females have been figured in different academic works, but most of them are not published (e.g., Romaggi, 1987), and housed in private collections. A detailed review of the large mammals from Saint-Bauzile would be necessary but it is out of the scope of the present work. Here we provide a short description of large to medium-sized mammals from Saint-Bauzile based on the material housed in the MNHN collections (plus high definition photos of the skull referred to *Miotragocerus andancensis*), with remarks on the styles of preservation, the taxonomic status of fossils, and the palaeobiological inferences that can be provisionally made.

#### 3.2.1. *Miotragocerus andancensis* (Romaggi, 1987)

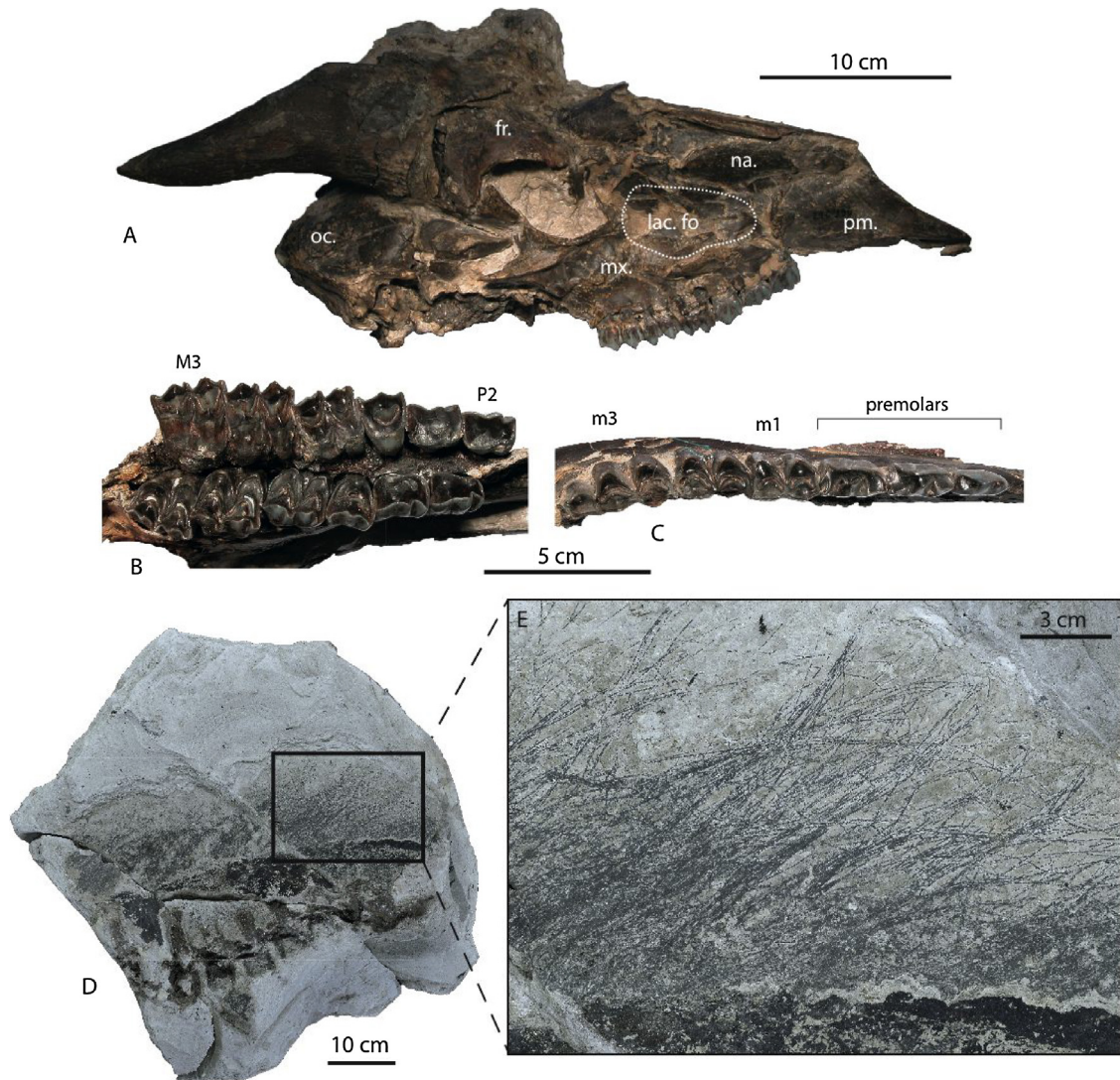
This boselaphine bovid is documented by an abundant material that comprises both flattened complete skeleton with body outline, and skeleto-dental remains preserved in 3D. This fossil material was studied in detail by Romaggi (1987) who erected a new species of the

genus *Graecoryx*, *G. andancensis* from the material from Saint-Bauzile. The taxonomic status of *Graecoryx* is controversial, since the material referred to as *Graecoryx* would actually represent an artificial assemblage of juvenile-subadult individuals of different species (Bouvrain, 1988), and consequently should not be used. Spassov and Geraads (2004) proposed to restrict the use of the name *Graecoryx* to the type specimen of *G. valenciennesi* from Pikermi (MN12), and to consider the other species referred to *Graecoryx* (including *G. andancensis*) as belonging to the '*Miotragocerus-Tragoportax* complex'. Here we have chosen to refer the bovid material to *Miotragocerus* Stromer, 1928 because of the priority on *Tragoportax* Pilgrim, 1937. The fossil material from Saint-Bauzile includes juveniles, males and females, and one of the female is gravid (Romaggi, 1987). This antelope was about 2 m long for the male, and female and male display a pair of horn-cores (Fig. 4A). This presence of individuals of various ages suggests that this antelope lived in herds by the palaeolake. This is consistent with the elongation of phalanges similar to those of the extant cervid *Rangifer tarandus*, an adaptation to walk on soft substrate under humid conditions (Romaggi, 1987). The low-crowned molars of *M. andancensis*, and its lower premolars barely molarized (Fig. 4C) unlike most bovinds of the late Miocene suggest a diet based on leaves and soft vegetation although more abrasive food in their diet cannot be ruled out, and would require further studies. Moreover, the morphology and size of the bony horn core indicates a sexual dimorphism (Romaggi, 1987). Unfortunately, the skull of the male adult (Fig. 4A) is slightly crushed dorsoventrally, preventing the observation of the fronto-parietal postcornual area. The lachrymal fossae are well developed; the occipital is slightly concave posteriorly and shows a prominent crest suggesting powerful nuchal muscles. The anterior rim of the orbit is above M2. Imprints of hairs are preserved on some specimens, and the presence of a 10-cm-long goatee has been observed, like it is on the extant goat (Romaggi, 1987).

#### 3.2.2. *Microstonyx* sp.

The slab preserves six cervical vertebrae, the skin impression, and the dorsal guard hair and overhair (Fig. 4D). The vertebrae are longitudinally broken, and the internal spongy structure is visible. The skin impression is dark, and the thickness of skin plus underlying fat layers between the apex of the neural apophysis of vertebrae and the outer skin surface is about 5 cm. The hairs are matted with frayed ends (Fig. 4E). The internal structure of guard hairs varies between suids and tayasuids, and hair size, shape and colour are sufficient to give indications about identity (Hess et al., 1985). These structures are visible by SEM, and further investigations should be made to determine whether or not these structures were destroyed during the compaction of diatomitic sediments. Pickford (2016) reported dental remains of the suid *Hippopotamodon major* from Saint-Bauzile without specifying whether they come from the diatomites or the fluvialite fossiliferous sandstones that lay above the diatomites.





**Fig. 4.** Fossil artiodactyls from the late Miocene of Saint-Bauzile, Ardèche, France. A–C. *Miotragocerus andancensis* (specimen 212-996 Coll. Université de Lyon); skull of a male in dorsolateral-right side view (A), the left and right upper tooth rows of the same individual with P2–M3 in occlusal view (B), the left lower jaw with p2–m3 in occlusal view (C). D–E. *Microstonyx* sp., (MNHN.FMCF 62), (D) slab of the diatomite preserving part of the vertebral column (5 cervical vertebrae are visible) and dorsal guard hairs and overhairs, (E) close-up of the hairs and dorsal overhairs. Anatomical abbreviation used for the skull: fr: frontal; lac. fo: lacrimal fossa; mx: maxillary; na: nasal; pm: premaxillary; oc: occipital.

**Fig. 4.** Artiodactyles fossiles du Miocène supérieur de Saint-Bauzile, Ardèche, France. A–C. *Miotragocerus andancensis* (spécimen 212-996 Coll. Université de Lyon) ; crâne d'un mâle en vue dorsolatérale, côté droit (A), rangées dentaires supérieures P2–M3 gauche et droite du même individu en vue occlusale (B), mâchoire inférieure gauche avec p2–m3 en vue occlusale (C). D–E. *Microstonyx* sp., (MNHN.FMCF 62), (D) dalle de diatomite portant une partie de la colonne vertébrale (5 vertèbres cervicales sont visibles) et poils dorsaux. (E) Détail de l'organisation des poils. Abréviations anatomiques utilisées pour le crâne : fr : frontal ; lac. fo : fosse lacrymale ; mx : maxillaire ; na : nasal ; pm : prémaxillaire ; oc : occipital.

### 3.2.3. *Dihoplus schleiermacheri* (Kaup, 1832)

This taxon is mostly documented by the specimen MNHN.FMCF 60. It consists of both undeformed skeletal elements preserved in 3D and part of the ribcage in 2D (Fig. 5). This latter is found flat in the bedding planes, and with well-preserved soft tissues and body outline. The slab of diatomite (Fig. 5A) displays the dorsal part of the vertebral column with ten vertebrae preserved in three dimensions (although flattened). The ribs are also preserved and slightly flattened.

#### 3.2.3.1. Description of the specimen MNHN.FMCF 60 (elements preserved in 3D).

Mandible (Fig. 5B–C; height under the anterior border of m1: 7.6 cm; height under the anterior border of m3: 8.8 cm; height of the mandible between its lower border and the articular condyle: 21.6 cm)—The left incomplete mandible (Fig. 5B–C) preserves p3–m3 and the ascending ramus with the articular process (the coronoid process is damaged), but lacks the rostral part of the symphyseal region. The ventral border of the body is nearly straight and becomes slightly convex from m3 to the notch



**Fig. 5.** The rhinocerotine *Dihoplos shleiermachi* from the late Miocene of Saint-Bauzile, Ardèche, France (MNHN.FMCF 60). A. Slab of diatomite preserving part of the vertebral column (9 dorsal vertebrae are visible) and associated costal ribs on both sides. B–D. Left lower jaw preserving p3–m3 in medial (B), lateral (C), and occlusal (D) views. E–F. Right femur in posterior (E), and anterior (F) views. G–I. Right second metacarpal (Mc-2) in posterior (G), anterior (H), and lateral (I) views. The main articulation facets with the carpal bones are indicated.

**Fig. 5.** Le rhinocéros *Dihoplos shleiermachi* du Miocène supérieur de Saint-Bauzile, Ardèche, France (MNHN.FMCF 60). A. Dalle de diatomite portant une partie de la colonne vertébrale (9 vertèbres dorsales sont visibles) et des côtes des deux côtés associées. B–D. Mandibule gauche préservant p3–m3 en vues interne (B), externe (C), et occlusale (D). E–F. Fémur droit en vues postérieure (E) et antérieure (F). G–I. Deuxième métacarpien droit (Mc-2) en vues postérieure (G), antérieure (H), et médiale (I). Les principales facettes articulaires avec les os du carpe sont indiquées.

that marks the boundary with the angular process. The p3 and p4 are heavily worn, and the m1 is affected by a longitudinal crack. The m2 is worn and the m3 is barely worn, just erupted. The m2 is rectangular in occlusal view. The

paralophid is narrow, mesiolingually-oriented whereas the metalophid and hypolophid are almost parallel which is not the case on the m3 where the two crests form an acute angle. In the latter, the protoconid is angular and

displays a shallow expansion into the anterior valley. The metaconid and the entoconid are about the same size. The metalophid is straight and the metaconid seems to be anteriorly constricted on m3. The talonid forms an obtuse angle in occlusal view. There is an anterior cingulid, but no posterior cingulid.

Femur (Fig. 5E–F; maximum length: 48.0 cm; transverse diameter of the proximal epiphysis: 19.6 cm; transverse diameter of the distal epiphysis: 14.4 cm)—The right femur has a wide proximal epiphysis. The head is rounded, asymmetrical, and occupies less than half of the proximal surface. The greater trochanter is wide, obliquely oriented, and lower than the head of the femur, and its lateral surface is thick, flat and inclined medially (~45° with respect to the major axis of the shaft). There is a deep trochanteric fossa. The lesser trochanter, on the medial side, is restricted to a long and narrow oblique ridge with a straight medial border, and it extends up to slightly above the level of the upper side of the third trochanter. The latter is strong and is situated at about mid-length of the diaphysis. It is laterally expanded, and its lateral border is curved cranially. The distal limit of the third trochanter is well differentiated from the shaft. The diaphysis is short and stout, with a curved medial border. The distal epiphysis is transversely large, and the distal trochlea is almost symmetrical. The medial epicondyle is well marked, and rounded.

Mc II (Fig. 5G–I; maximum length: 15.2 cm; transverse diameter at mid-diaphysis: 3.4 cm)—The right Mc II is complete, although the distal half of the diaphysis is slightly damaged laterally. In proximal view, the proximal trapezoid facet has a ‘crescent’-shaped outline. This facet is almost flat, antero-posteriorly convex, transversally concave, and it forms a V in posterior view. There is no facet for the trapezium. The proximal border of the lateral side is occupied by the facet for the magnum. The section of the shaft is oval. The diaphysis is antero-posteriorly flattened, and it has a concave medial border and a convex lateral one. The medial process for the collateral ligament is well developed and rounded.

#### 4. Discussion

The material described above is consistent with the definition of ‘*Dicerorhinus*’ *shleiermachi* given by Guérin (1980). The species initially referred to the genus *Rhinoceros* by Kaup (1832) is now the type species of the genus *Dihoplus* (Giaourtsakis and Heissig, 2004). The specific attribution of isolated postcranial remains of rhinos is sometimes difficult, and the systematic history and definition of the species attached to *Dihoplus* fairly complex (Pandolfi et al., 2015). *Dihoplus schleiermachi* Kaup, 1832 is based on a complete skull and mandible of an adult from Eppelsheim (MN9). The height of the corpus of the mandible under the anterior border of m3 (8.8 cm) and the length m1–m3 (13.2 cm) of the mandible from Saint-Bauzile (Fig. 5B–D) are lower than in *D. schleiermachi* from Eppelsheim (MN9), *Dihoplus pikermiensis* from Pikermi (MN12), and *Ceratotherium neumayri* from Maragha (MN11) (see Giaourtsakis et al., 2006, tables 4 and 5). The key differences between the *Dihoplus pikermiensis* and *D. schleiermachi* concern the strength of the symphysis

and the anterior dentition, two features that are not observable on the available specimens from Saint-Bauzile. The preliminary identification of the rhino material proposed here needs to be tested with further morpho-anatomical studies that would include the fragmentary vertebrae preserved on the slab (Fig. 5A). The biostratigraphic range of *D. schleiermachi* extends from the lower Vallesian (MN9) to the lower Ruscinian (MN14) (Montoya et al., 2006).

The bones are not compacted at all; some of them are fractured but we do not know whether these cracks result from syn- or post-collecting (Mc II in Fig. 5G–I). The bones are light; the spongiose bone is not filled with sediment (Fig. 5E–F). The wear facets on teeth or articular facets on bones are as in extant animals; the notches or tubercles for insertion of muscles are visible in most skeletal elements preserved in 3D.

##### 4.1.1. *Hipparion tuyolsi* Sondaar, 1961

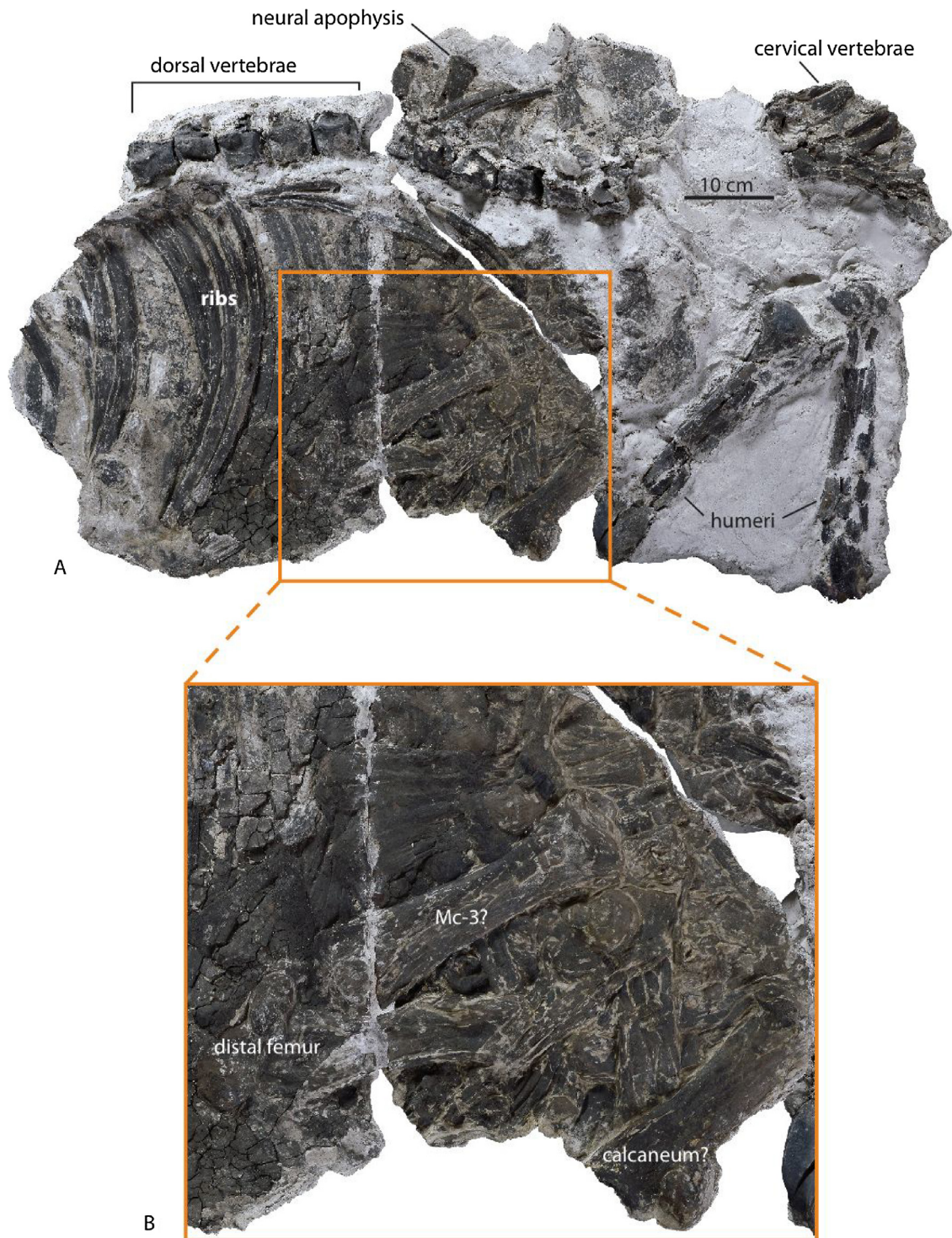
This equid is documented by complete skeletons, including a gravid female belonging to the private collection of B. Riou to which we did not get access (see Riou, 1999, figures on pp. 257–259). The mode of preservation is similar to that of other large mammal taxa, but unlike *Microstonyx*, there is no trace of hair and skin. The slab (Fig. 6A–B) preserves a ribcage with possible stomach content. Eleven dorsal vertebrae are preserved, in addition to three cervical vertebrae, which are not in anatomical connection with dorsal vertebrae. Below the cervical vertebrae, the two humeri are preserved complete but cracked (Fig. 6A). The interior of the ribcage is made of brown-dark deposits that would need further detailed studies (pollen, geochemistry) to determine if the stomach content is undamaged. The outline of long bones is visible in this area (Fig. 6B). The size of the metacarpal (the only bone than can be safely identified) falls in the expected size range of the metacarpal of the same individual, and this bone was removed from the forelimb to the ribcage during the dismantlement of the skeleton, before the burial. The two other bones are hardly identifiable due to the compression that greatly affected their outline and shape. The tangle of bones in the abdomen indicates important syn- or post-mortem displacement of bones, which might be related to taphonomic parameters such as scavenging, or decomposition of soft tissues (tendons and ligaments) with possible feeble bottom currents in the palaeolake that favoured the dislocation.

#### 5. Discussion

##### 5.1. Style of preservation

Two styles of preservations are distinguishable for the fossils from Saint-Bauzile:

- complete or sub-complete skeletons usually suffered compaction and are preserved at two dimensional levels because of compressional flattening in the bedding planes. Most fossil mammals are preserved as articulated skeletons with soft tissues or skin impressions (Figs. 2–4 and 6). Generally, the vertebrate skeletons



**Fig. 6.** The equid *Hipparion tuyolsi* from the late Miocene of Saint-Bauzile, Ardèche, France. A. MNHN.FMCF 61, slab of diatomite preserving part of the vertebral column (11 dorsal vertebrae, and 3 cervical vertebrae are visible), costal ribs, and the two humeri. B. Close-up of the abdomen with additional bones of the same (?) individual, which are tentatively identified.

**Fig. 6.** *Hipparion tuyolsi*, équidé du Miocène supérieur de Saint-Bauzile, Ardèche, France. A. MNHN.FMCF 61, plaque de diatomite portant une partie de la colonne vertébrale (11 vertèbres dorsales et 3 vertèbres cervicales sont visibles), les côtes et les deux humérus. B. Gros plan de l'abdomen, avec des os supplémentaires du même (?) individu, avec identification provisoire.

have a dark-brown colour, sometimes with brownish-coloured skin, and the bones distinctly marked in the body by a darker coloration. Several specimens show detailed skin patterns around the skeletons, and brownish hair impressions. Further studies are needed to see whether or not the ultrastructure of hair is preserved. Likewise, the stomach content is potentially preserved, but further analyses would be needed to confirm this point;

- three-dimensional fossils are found, but always disarticulated. They are isolated postcranial bones, mandibles or skull; some of them show a slight lateral flattening, but generally fossils are three-dimensional and perfectly preserved. Bones are brownish to dark, and show neither trace of transport or breakage nor evidence of bioerosion by macro- or micro-invertebrates (Figs. 4–5). These isolated and three-dimensional fossils clearly resulted from a distinct taphonomical process that prevented them from being compacted. Microscopic decay organisms caused separation of connective tissue before burial, probably during decomposition when the floating carcass was still full of gas, and before it sank straight into the lake by gravity.

## 5.2. Origin of preservation

Exceptional preservation of lacustrine fossil biota is a combination of various limnologic and taphonomic factors. Fossil skeletons can potentially be a rich source of information about temperature, depth, hydraulic energy, scavengers and oxygen concentration of ancient lakes (Yang and Yang, 1994). The diatomite slabs bearing fossil skeletons show no macroscopic scavenger disturbance, indicating that macroscopic scavengers were absent between the time of death and burial. The absence of scavengers suggests either that burial was extremely rapid or that the environment did not usually support the presence of macroscopic scavengers, such as in anoxic bottom waters (Chen, 2000). The latter hypothesis is consistent with the absence of benthic invertebrate fossils and the lack of any signs of bioturbation. Moreover, Decho (2000) has shown that when bacteria and microalgae are associated in the photic zone, they can secrete a matrix of mucilaginous extracellular polymers (extracellular polymeric secretions, EPS) to form a microbial biofilm. This biofilm produces a strong protective effect of fossils before burial, and prevent them from any kind of post-mortem damages (O'Brien et al., 2008). These parameters are consistent with toxic or anaerobic conditions in bottom waters of the palaeolake that favoured the exceptional preservation of fossils.

## 5.3. Cyclic sedimentation and seasonal environmental variation

The diatomite of Saint-Bauzile is mostly formed of the accumulation of the diatom *Cyclotella* (Ehrlich, 1966; Kuehlthau-Serieysson, 1993), and it is clearly laminated with an alteration of whitish and greyish laminae (Fig. 1E). The thickness of these laminae or varves is irregular and varies from a millimetre to a tenth of millimetres. The diatom production in lakes is almost invariably cyclic with a

strong annual or bi-annual signal, depending on the number of blooms. Consequently, the diatomite is made of a succession of infra-millimetric laminae (Fig. 1E) indicating seasonality (Simola, 1979). During the spring and summer, the humid-warm climate, high precipitation rate and intermittent water supplies resulted in suspended mud particles and made the lake water turbid. It was during this phase that the dark grey or dark-brown organic-rich layers were deposited. During the autumn and winter, the lake had little or no surface water supply, and diatoms died massively owing to the changes of insolation affecting primary production (Flower, 2007). These dead diatoms were deposited on the calm lake bottom, forming the light-coloured diatom-rich layers. Under warm, subtropical climate, there can be two blooms of diatoms per year, and thus a double-couplet lamina (Flower, 2007).

Each couplet of varves represent in theory one year. However, the post-depositional compaction has certainly averaged this annual cyclicity. The complete skeletons although highly flattened are generally embedded within dozens of laminae, and there seems to be no specific lamina supporting the hard tissue of fossils. However, soft tissues generally occur on light-coloured, less organic lamina, which is consistent with the burial of animal closely related to diatom blooms. The relatively large (~1 mm) band of light laminae in which grey bands are very thin or absent (Fig. 1E) would correspond to the proliferation of diatoms and possibly biofilm. This short interval may also indicate a dry and warm climatic phase as evidenced by pollen assemblage (Iskandar, 1988).

## 5.4. Possible causes of death of the mammals

The limited sample of mammals does not allow detecting periodicity and timing of mortalities, related for example to a seasonal signal. Moreover, the cause(s) of deaths of mammals is not necessarily the same as it is for invertebrates or plants that are fossilized in the palaeolake. The presence of gravid females, young and old adult individuals does not suggest a selection by age classes that could have been related to a specific behavioural feature. Instead, we are inclined to advance that the cause of mass and sudden mortality events was probably related to volcanic eruption and toxic gas emission, a phenomenon that can cause mass terrestrial vertebrate kills and exceptional preservation (Spencer et al., 2003).

## 6. Conclusion

The Miocene epoch was a time of particularly extensive diatomite formation (marine and lacustrine), and Kidder and Gierlowski-Kordesch (2005) suggest that the nonmarine Miocene diatomite deposits are associated with the rise of grasslands and changes in the silica cycle. The Lake of Saint-Bauzile documents this late Miocene interval corresponding to a critical shift within terrestrial ecosystems (Strömberg, 2011). This palaeolake is renowned for the superb condition of fossil specimens of various groups of animals and plants preserved in its diatomaceous deposits. The Saint-Bauzile Miocene biota offers an excellent example of deposits preserving fossils with soft tissue, and

formed in a volcanically influenced small lake under a warm temperate climate (Demarcq et al., 1989; Iskandar, 1988; Riou, 1995, 1999). The quality and quantity of the Saint-Bauzile biota set it apart from other known non-marine Konservat-Lagerstätten, and both palaeoecological and geologic evidences suggest that the extraordinary preservation of the fossil biota was caused by a combination of various limnologic and taphonomic factors. Besides systematic studies of fossils, new analyses such as SEM analyses of the hair (in rodents and in the pig for instance), pollen analyses of the purported stomach content, or CT-scans to access 3D data of teeth and limb bones will certainly bring new insights into the paleobiology of mammals from Saint-Bauzile. Finally, further research on taphonomic processes in relation to sedimentological and geochemical parameters of the palaeolake as well as comparisons with other similar lake deposits will further illuminate the palaeoenvironmental conditions required for the formation and preservation of lacustrine Konservat-Lagerstätten.

### Acknowledgments

We are indebted to Simona Saint Martin who has shared with us her vast knowledge on diatoms, and provided us with important literature. We thank Philippe Loubry, and Lilian Cases for most photos of this paper, Denis Geraads for the photo of the skull of *Miotragocerus andancensis*, specimen housed in the collection of the University Claude-Bernard, and Emmanuel Robert (University of Lyon, France) for the photos of *Glirulus* aff. *lissiensis* housed in the collection of the University Claude-Bernard. We are grateful to Bernard Riou who allowed one of us studying some small mammals from his collection and provided the picture of the Saint-Bauzile quarry and *Prolagus* specimen. We thank Guillaume Billet and Vincent Pernègre for access to the MNHN collection, the editors of the thematic volume “Exceptional Preservations”, Oscar Sanisidro for the help with bibliography, and Christine Argot (Paris) and Loïc Costeur (Basel, Switzerland) for their constructive comments on a previous version of the manuscript.

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