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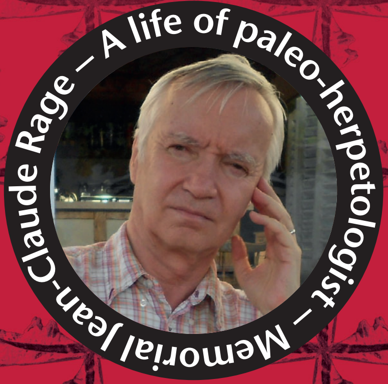

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The lizard (Reptilia, Squamata) assemblage from the Paleocene of Montchenot (Paris Basin, MP6)

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KEY WORDS
Lizards,
Scincoidea,
Lacertoidea,
Amphisbaenia,
Anguimorpha,
Paleocene,
Paris Basin.

ABSTRACT
Here we describe the lizard fauna from the locality of Montchenot (Paris Basin, late Paleocene, MP6). This material can be allocated to five major clades: Scincoidea, Lacertoidea (?Lacertidae), Amphisbaenia, Anguimorpha (?Anguidae and Shinisauridae). The assemblage from Monchenot is dominated by small lizard specimens and appears as highly sorted. Predation could produce such biased assemblages. The composition of the lizard fauna from Monchenot is rather similar to those of Cernay-lès-Reims and Rivecourt, two coeval localities (MP6) in the Paris Basin. However, these faunas sharply contrast (in diversity and composition) with the lizard fauna found in the early Eocene of the same area (Paris Basin and Belgian Basin). These differences highlight the impact of the Paleocene/Eocene transition on the lizard fauna of Europe.

MOTS CLÉS
Lézards,
Scincoidea,
Lacertoidea,
Amphisbaena,
Anguimorpha,
Paléocène,
Bassin de Paris.

RÉSUMÉ
Les lézards fossiles du Paléocène de Montchenot (Bassin de Paris, MP6).
Les faunes de lézards trouvées dans la localité de Montchenot (Paléocène supérieur, MP6, Est du Bassin de Paris) sont décrites. Ce matériel se répartit entre plusieurs groupes : Scincoidea, Lacertoidea (?Lacertidae), Amphisbaenia, Anguimorpha (?Anguidae et Shinisauridae). L'assemblage de Montchenot est dominé par des spécimens de petite taille, certainement le résultat d'un tri sélectif marqué. L'action de prédateurs peut produire de tels assemblages. Les taxons présents à Montchenot sont aussi présents, pour la plupart, dans deux gisements de même niveau (MP6) : ceux de Cernay-lès-Reims et de Rivecourt dans l'Est du Bassin de Paris. D'autre part, la faune de Montchenot diffère nettement (en composition et diversité) de celles reconnues dans les gisements de l'Éocène ancien (MP7) de la même zone géographique (Bassin parisien et belge). Ces différences mettent en relief le fort impact de la transition Paléocène/Éocène sur les faunes de lézards.

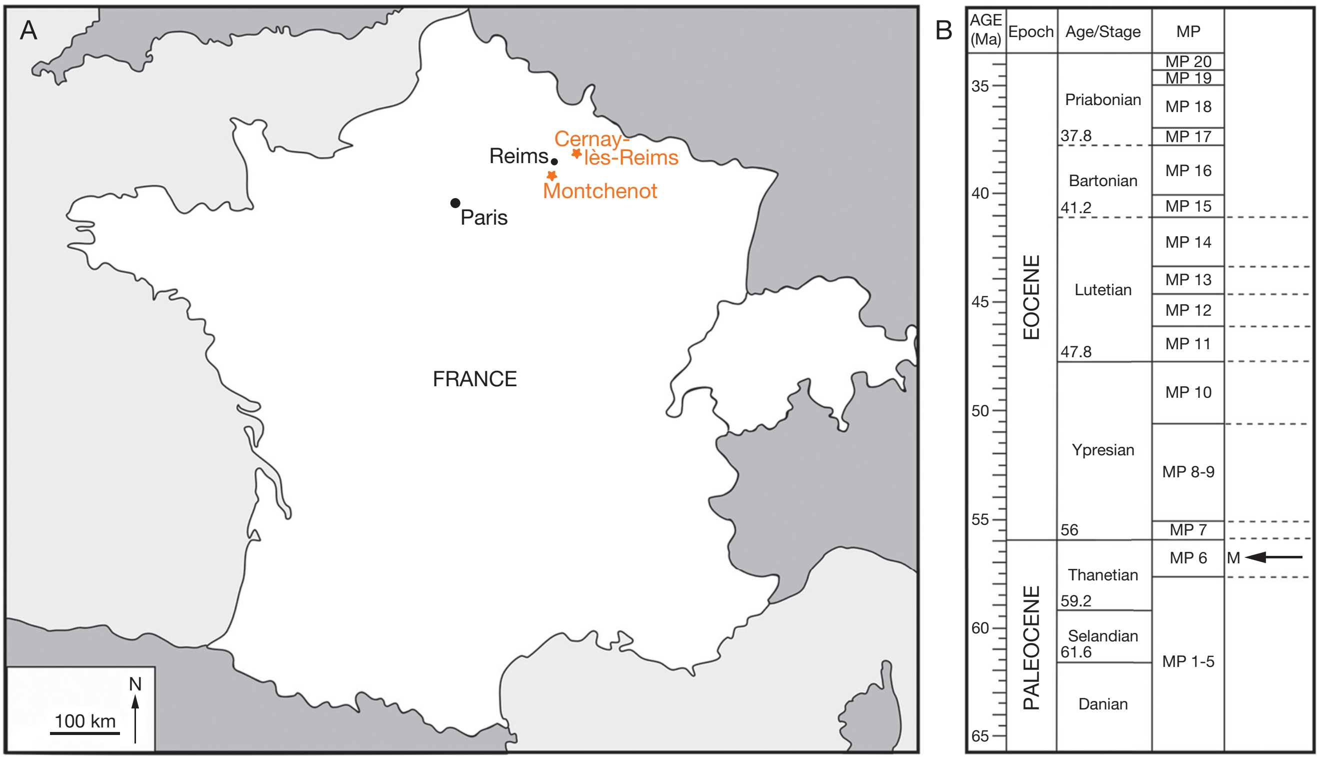

Fig. 1. — **A**, Map showing the two fossiliferous localities studied here; **B**, stratigraphic position of the localities (black arrow).

INTRODUCTION

Herpetofaunal assemblages from Western Europe are relatively well documented in the earliest Eocene, chiefly at Dormaal (Belgian Basin, standard level MP7, e.g. Hecht & Hoffstetter 1962), being the Dormaal member of the Tienen formation correlated with the beginning of the Paleocene-Eocene Thermal Maximum (PETM). In sharp contrast, the late Paleocene European herpetofauna, prior to the Paleocene/Eocene boundary (and thus the PETM) is rather poorly known, a condition that applies to the entire European Paleocene (Rage 2013). However, the occurrence of herpetofauna has been mentioned in several Paleocene localities from the Paris and Belgian Basin: Hainin, Cernay-lès-Reims (called in this article "Cernay")-Berru, Rivecourt Petit Pâtis, Montchenot (Fig. 1) and these localities yielded some new fossil lizard taxa, belonging to diverse groups : Amphisbaenian, Anguimorpha, Scincoidea, ?Lacertoidea (e. g., Augé 2005; Folie 2006; Folie *et al.* 2005, 2013). Herpetofauna from Montchenot have only been listed by J-C Rage in the publication of Jehle *et al.* 2012 (i.e., urodeles, anurans, choristoderes and crocodiles). Otherwise, this publication was mostly devoted to mammal fossils (see also Jehle *et al.* 2019).

Here we describe the lizard assemblage found in the locality of Montchenot. The Paleocene/Eocene boundary (and the PETM) is a global event that stands as one of the most important environmental change in the Cenozoic era. Description of the lizard fauna from Montchenot is an important addition to the fossil record of the immediate pre-PETM period and it may be crucial to interpret the faunal evolution and change in lizard paleodiversity during the Paleocene/Eocene transition.

Mammal fossils found at Montchenot indicate an age close to that of the classic localities of Cernay-Berru (European mammalian reference level MP6; Hooker 1998; Hooker & Millbank 2001; Jehle *et al.* 2012, 2019) . These studies confirm the late Thanetian age previously determined on the basis of mollusc and charophytes (Laurain & Henry 1968; Riveline 1976).

The chronicle of paleontological researchs in the Marnes de Montchenot and more generally in the Paleocene of the Eastern part of the Paris Basin may be consulted in Louis (1996) and Jehle *et al.* (2012). Two outcrops near Montchenot yielded vertebrate fauna, including herpetofauna: an abandoned quarry, Les Monts-Martin and a second locality, in the immediate vicinity of Les Monts-Martin that has been recently exploited, in particular by one of us (DM). The collection made by P. Louis certainly came from Les Monts-Martin. According to Jehle *et al.* 2012: "both localities appear to be closely similar in faunal content and show a comparable lithology".

INSTITUTIONAL ABBREVIATIONS

MNHN.F	Muséum national d'Histoire naturelle, Paris, collection de Paléontologie;
MTC	specimens from Montchenot.

Fig. 2. — Indeterminate Scincoidea, incomplete right dentary, MNHN.F.MTC245: **A**, lingual view; **B**, labial view. Scale bar: 1 mm.

SYSTEMATIC STUDY

Order SQUAMATA Oppel, 1811
Superfamily Scincoidea Oppel, 1811

Scincoidea indet.

Material examined. — Two incomplete dentaries: Dentary, MNHN.F.MTC245 (Fig. 2), bears four tooth loci (the most posterior teeth); Dentary, MNHN.F.MTC244 (Fig. 3), bears four tooth loci.

Description

Dentaries, MNHN.F.MTC245 (Fig. 2)

This robust, right dentary (L = 3.7mm) is strongly arched (concave), its posterior part is deep and it distinctly narrows towards the anterior margin. This specimen preserves three incomplete teeth. On the lingual side the subdental shelf (*sensu* Rage & Augé 2010) is eroded except in the posterior part of the dentary, where it is sub-vertical and meets the dental table nearly at a right angle. It is difficult to assess the

Fig. 3. — Indeterminate Scincoidea, incomplete left dentary, MNHN.F.MTC244 **A**, labial view; **B**, lingual view. Scale bar: 1 mm.

presence of a medial sulcus dentalis along the tooth bases, due to the poor preservation of the subdental shelf. A large posterodorsal process extends behind the level of the last tooth and presents a deep, inclined surface which certainly received the anteromedial dentary process of the coronoide. On that surface, a circular cavity located behind the level of the last tooth may mark the position of the anterior end of this process. Posteriorly, the sulcus Meckeli is widely open medially and it gradually narrows towards the anterior end of the specimen. Under the dental table, there is an intramandibular septum, between the level of the last-penultimate tooth positions. It shows no vertical projection.

In lateral view, no labial foramens are exposed. Posteriorly, there is a well-developed labial coronoid process, which bears no trace of contact with an anterolabial dentary process of the coronoid.

Dentition: The three incompletely preserved teeth are pleurodont and robust (amblyodont). They gradually taper towards the apex, the tooth base is enlarged and medially expanded. Two tooth bases are pierced by a large, central replacement cavity and cement deposits around the tooth bases are poorly developed. Apices are broken in all teeth, except perhaps for the last one which seems to bear a rounded crown.

Specimen MNHN.F.MTC244 (Fig. 3)

Incomplete left dentary (L = 5.1mm) that bears five tooth positions, and two teeth partially preserved. The morphology of dentary MNHN.F.MTC244 is nearly identical to that of specimen MTC245 (described above). The subdental shelf is arched, vertical and moderately deep and it meets the dental table nearly at a right angle. A sulcus dentalis is present. The teeth are better preserved than those of specimen MTC245 and their apex is obtusely pointed and bears neither cusps nor striations.

The labial surface of the two dentaries bears important marks of alteration, certainly caused by digestive process (Andrews 1990). It is worth noting that these processes could be at least partially behind the lack of striations on the teeth (see above).

Comparisons and discussion

On account of the fragmentary nature of these specimens their taxonomic position is difficult to evaluate. In addition, no clear diagnostic features or synapomorphies are present in those dentaries. However, there are some features which, in combination may suggest scincoid relationships: pleurodont dentition, subdental shelf well developed, sub-vertical and forming a nearly right angle with the surface of the dental table, presence of a sulcus dentalis. At this point, it may be objected that those characters are also present in Lacertoidea (and particularly in lacertid lizards). However the first dentary (specimen MNHN.F.MTC245) differs significantly from that of most fossil and extant Lacertoidea in two characters: 1) in lingual view, the presence of a large posterodorsal extension behind the subdental shelf that received the anteromedial dentary process of the coronoid; and 2) in labial view, the dentary has an upwardly directed coronoid process that prevents the extension of the coronoid onto the labial surface of the dentary (Daza *et al.* 2015). In lacertid and teiid lizards this process is reduced and the anterolateral dentary process of the coronoid is expanded anteriorly and covers the posterodorsal part of the dentary, generally leaving a clear mark on it (Augé 2005).

Presence of a mesial and distal crest or of a single longitudinal crest on the tooth crown are certainly primitive within Scincoidea (Kosma 2004; Richter 1994, 1995; Georgalis *et al.* 2017). Accessory cusps on the mesial and distal crests are virtually unknown in Scincoidea and skinks tend to have blunt, chisel-shaped tooth crowns (Smith & Gauthier 2013; Daza *et al.* 2015) while most lacertids have acute cusps; absence of cusps in the dentaries from Montchenot tend to exclude them from lacertoid lizards.

Absence of striae on the tooth crowns and obtusely pointed teeth without longitudinal crest (in dentary MNHN.F.MTC244) are clearly characters that come into conflict with the generalized scincoid dentition (Richter 1994; Böhme 2010) or scincid grade *sensu* Kosma (2004:5). Once again, absence of striae may be du to the poor preservation of these teeth. However, a great number of forms, notably among scincids, depart from this tooth pattern and bear specialized dentitions (Estes & Williams 1984; Kosma 2004; Augé 2005; Nydam *et al.* 2013; Bolet & Augé 2014). In addition, this scincid-grade of tooth morphology is also present in some non-scincid taxa, such as some species of Gymnophthalmidae and Gekkonidae (Nydam *et al.* 2013; Sumida & Murphy 1987). In addition, the lack of striae may be due to taphonomic pocesses (e.g. digestive process) that affected the enamel.

Recently, several scincoid taxa have been described in the European Paleogene, some forms being referred to scincids (e.g. Bolet *et al.* 2015; Augé 2005) others to cordylids s.l. (Bolet & Evans 2013) or to Scincoidea (Weber 2004; Folie *et al.* 2005; Bolet & Augé 2014; Augé & Smith 2009; Čerňanský *et al.* 2016). Most generally, these authors recognized that the distinction between the two families (Scincidae and Cordylidae) is difficult. The tooth shape and the arched dentary suggest that the fossils from Montchenot belong more likely to scincids than to cordylids. Unfortunately, these fossils are too incomplete and thus unsuitable for a more specific assignment.

As a last point, some characters of these dentaries, in combination, may suggest amphisbaenian relationships (e.g. well-developed coronoid process, robust teeth and a probable low tooth count). However, their general shape, in particular their strongly arched (concave) ventral border and subdental shelf clearly exclude this possibility. This morphology sharply contrast with the straight ventral border of the dentary that is shown by nearly all amphisbaenian members (see Gans & Montero 2008). Gans (1974) clearly demonstrates that this morphology is tied to the fossorial habits of these lizards.

? Scincoidea indet.

Material examined. — MNHN.F.MTC242, one incomplete axis (Fig. 4).

Description

Terminology follows Hoffstetter & Gasc 1969 and Čerňanský *et al.* 2014.

The centrum is well-preserved and strongly built but the neural arch is entirely lacking. A posteroventrally oriented intercentrum (second intercentrum) is sutured (not fused) to the base of the centrum and forms a rather short ventral keel in the antero-ventral region of the centrum. A small, slightly anteriorly curved process is fused to the posterior part of the base of the centrum, nearly beneath the condyle articulation. These two reliefs are separated by a deep, rounded trench.

The huge odontoid process covers most of the articulation area in anterior view, it is high (dorso-ventrally elongated) and not markedly expanded anteriorly. In posterior view, the condyle is laterally compressed.

Remarks

According to Čerňanský 2016 the squamate atlas-axis complex may be an important source of new morphological characters that can help to resolve persistent conflicts between morphological and molecular phylogenetic analyses of lizard phylogeny (Losos *et al.* 2012). However, only a handful of morphological studies include detailed anatomy of the atlas-axis complex in lizards (Rieppel 1980, Čerňanský *et al.* 2019, anguimorph lizards; Čerňanský *et al.* 2014 ; Čerňanský 2016; Čerňanský & Stanley 2019 about the atlas-axis in chamaeleonids, Cordyliformes and dibamids respectively; Vaugh *et al.* 2015, geckos). The work of Hoffstetter & Gasc 1969 develops a wide-ranging comparative study of the atlas-axis complex between lizard families.

The axis from Montchenot bears several phylogenetic significant characters: odontoid process dorso-ventrally elongated; condyle laterally compressed (occurs in nearly all Cordyliformes,

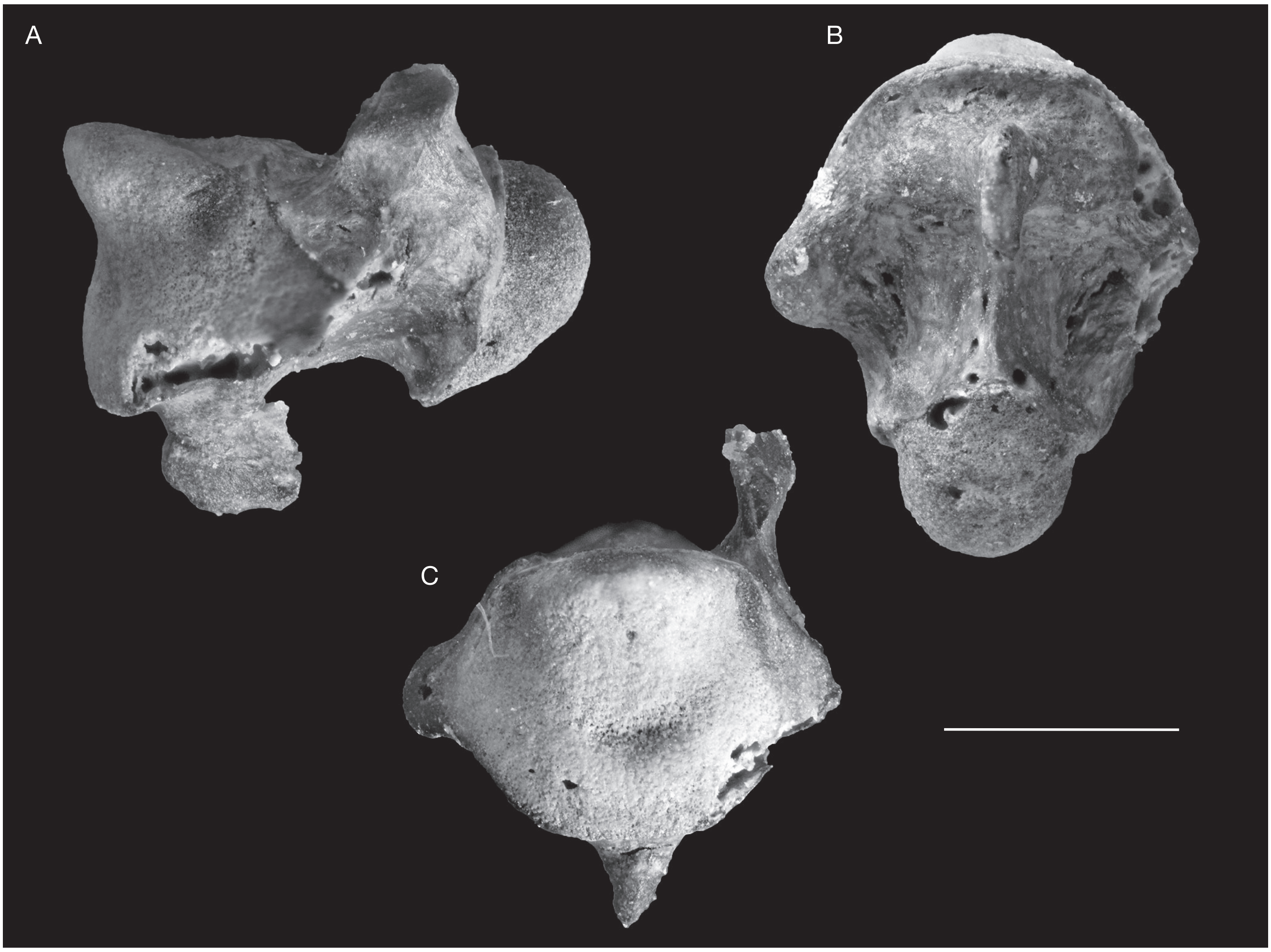

Fig. 4. — ?Scincoidea, incomplete axis, MNHN.F.MTC242: **A**, lateral view; **B**, vental view; **C**, anterior view. Scale bar: 1 mm.

Čerňanský 2016: 22); position and suture of intercentra on the ventral region of the centrum. Among Anguimorpha, the intercentra are fused to the centrum in anguid lizards and in varanids the odontoid process is laterally elongated. The condyle of lacertoid lizards is rather rounded and not laterally compressed and most gekkonids have amphicoelous vertebrae. All characters of this axis suggest scincoid relationships. For example, the morphology of the axis of *Broadleysaurus* (Cordyliformes, Gerrhosauridae) is very similar to that of the axis from Montchenot (Čerňanský 2016: fig. 8). However, this referral is at best tentative due to the incompleteness of MNHN.F.MTC242 and the very limited number of specimens available for comparisons.

Superfamily Lacertoidea Camp, 1923
Family ? Lacertidae Bonaparte, 1831

? Lacertidae indet.

Material examined. — MNHN.F.MTC246, one fragmentary jaw, possibly a dentary (Fig. 5); MNHN.F.MTC239 distal end of a left humerus (Fig. 6).

Description

Fragmentary jaw (L = 2.9 mm) with eight tooth positions that preserve two complete, pleurodont teeth. Tooth shaft sub-cylindrical, nearly columnar, with an incipient medial bulging. The shaft is slightly constricted under the apex which bears two (anterior and posterior) small cutting edges which join up on the tip of the apex. Otherwise, the apex is blunt and bears no cusps. The tooth base is slightly enlarged and is inserted into cementum as well as the labial side of the tooth shaft. Tooth bases are implanted on an horizontal dental table. A central replacement pit pierces the tooth base whose medial side comes near the dorsal margin of the subdental shelf (or supradental shelf) so that there is a reduced sulcus dentalis. The subdental shelf is shallow, rounded and there is no marked angle between it and the dental table.

Discussion and comparisons

Affinities of this specimen are particularly elusive due to its poor preservation and, to our knowledge, the very unusual morphology of the tooth apex bears no resemblance to those seen in any extant lizard families, except in some lacertid lizards (Kosma 2004). This tooth morphology is certainly not the result of wearing or preservational artifacts as several well-preserved

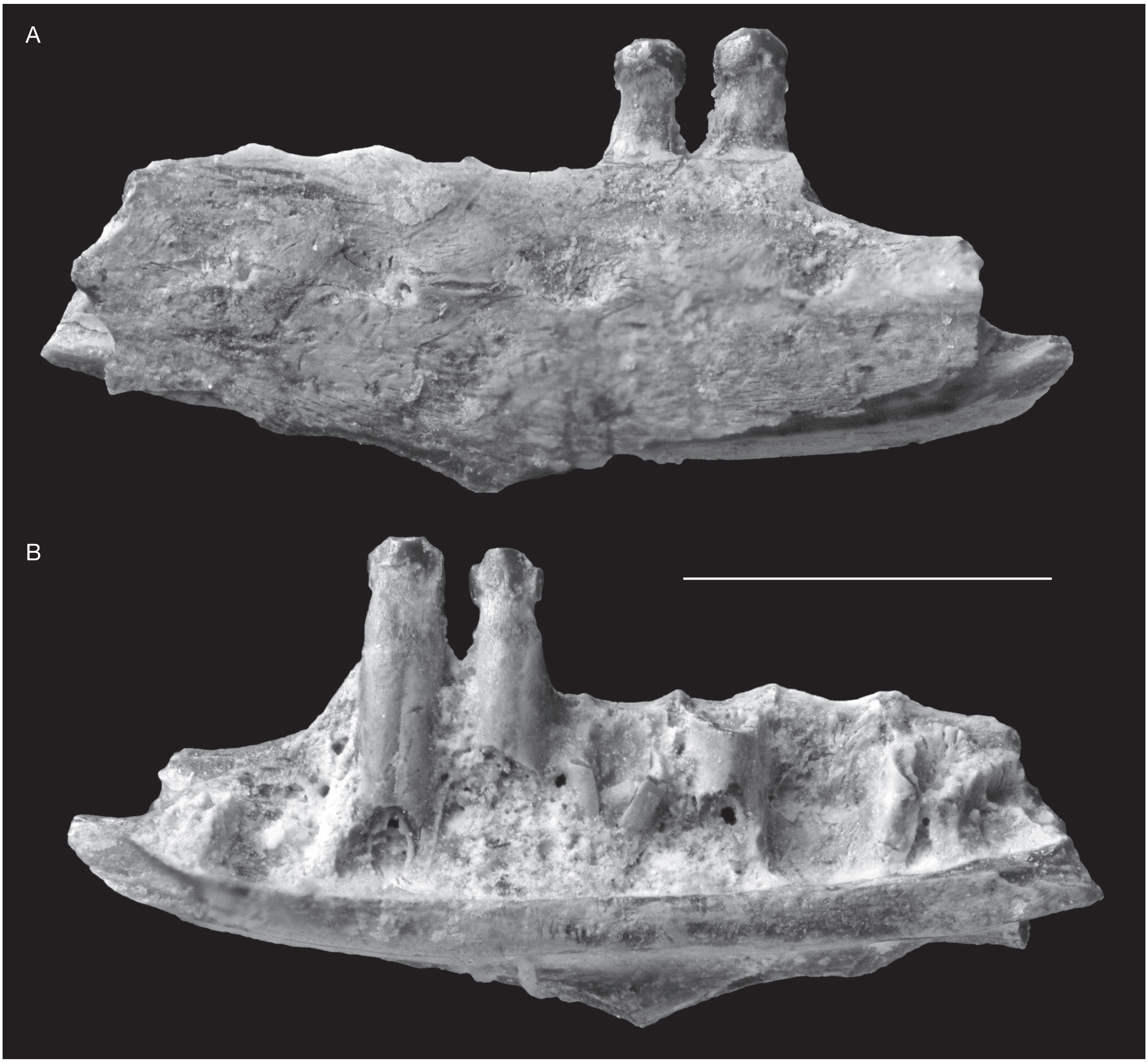

Fig. 5. — ?Lacertidae, fragmentary jaw, possibly dentary?, MNHN.F.MTC246: **A**, labial view; **B**, lingual view. Scale bar: 1 mm.

jaws from the coeval locality of Cernay show the same tooth morphology (see below).

Several characters suggest lacertid affinities: teeth strictly pleurodont, horizontal dental table, posteriorly reduced sulcus dentalis, central replacement pits on tooth bases. However, some of those characters are common to several lizards families, like Iguanidae, Scincidae or Cordylidae and neither is regarded as a possible apomorphy.

Presence of cutting edges on the lateral sides of the rounded apex may suggest anguimorphan (more precisely anguid) affinities, as well as the reduction of the sulcus dentalis. However, the pleurodont implantation of the teeth represents an important conflicting character (anguid lizards have a subpleurodont implantation, *sensu* Hoffstetter 1954). Some features suggest the possibility of referring it to the family Iguanidae (non-acrodont Iguanian, *sensu* Estes *et al.* 1988): iguanid lizards have pleurodont teeth and a reduced sulcus dentalis, mostly in the posterior part of the dental row. However, no iguanid is known to have a tooth apex reminiscent of those of MNHN.F.MTC246.

The localities of Cernay yielded many dentaries that share the same typical dentition with dentary MNHN.F.MTC246 from Montchenot (collection Phélizon, deposited in the MNHN). Cernay is coeval with Montchenot (Paleocene, MP6) and the two localities are in close geographical proximity. These dentaries have not been described yet but they show clear affinities with lacertid lizards: teeth pleurodont, sulcus dentalis reduced posteriorly, absence of a posterodorsal extension of the subdental shelf in lingual view, and reduction of the posterodorsal process of the dentary labially that bears a shallow depression which indicates the contact with the anterior (dentary) process of the coronoid.

Fig. 6. — ?Lacertidae, distal end of a left humerus, MNHN.F.MTC239, ventral view. Scale bar: 1 mm.

Taken at face value, this posterior reduction of the dentary is characteristic of lacertoid lizards (Teiidae and Lacertidae). In contrast, the posterior part of the dentary of iguanid lizards (mainly the posterodorsal pocess) extends widely onto the coronoid. Otherwise, these dentaries lack teiid features (e.g. clearly heterodont dentition, presence of important cement deposit on tooth base) and the tooth morphology of MTC246 (mainly its apex) is reminiscent of those of a Miocene Lacertidae from Sansan, MN6 (*Edlartetia sansaniensis* Augé & Rage, 2000) and even of extant lacertids like *Lacerta agilis grusinica* Peters, 1960 (Kosma 2004: fig. 34) and *Zootoca vivipara* (Lichtenstein, 1823) (Kosma 2004: fig. 51). This attribution is only tentative due to the poor preservation of the teeth and depends on the description of the material of Cernay.

Humerus (Fig. 6)

As the humerus of all full leged lizards, this specimen has an elongated, sub-cylindrical shaft (diaphysis) that forms the middle part of the bone. In lizards, the proximal and distal ends are expanded but the proximal end of specimen MNHN.F.MTC239 is broken off. Ventrally, the distal end presents two obliquely trending radial (lateral, or capitellum *sensu* Romer 1956) and ulnar (mesial) condyles separated by a notch (condylar gutter). A deep radioulnar fossa (*sensu* Tschopp et al 2018) is located proximal to the ulnar condyle.

Mesially, the entepicondyle is moderatelly developed into a knob-like expansion. On the lateral side of the distal extremity, the ectepicondyle is weakly developed, as in most limbed lizards except varanoids that have a marked crest on the distal end of the humerus. The ectepicondylar foramen is certainly visible in ventral view but several cavities due to weathering are also present on the lateral side of the ectepicondyle.

A large triangular depression is present just above the condyles and a rather large foramen (here called supra-condylar foramen) opens on the proximal rim of this depression. This foramen and its associated depression are clearly observed in almost all limbed squamates except varanoids (Smith 2009). It conveys the radial and ulnar nerves branching from the brachial plexus (Lécuru 1968).

What is clear from this description is that the incomplete humerus from Montchenot presents a generalised morphology observed in most limbed lizards, except varanoids (Lécuru 1969; Smith 2009).

Entepycondyles of gekkonid lizards are far more developed (projected mesially) than that of humerus MNHN.F.MTC239 (e.g., Lécuru 1969: fig. 12). Generally, in gekkonids and Scincoidea the supra-condylar foramen opens just above the condyles, while in Lacertoidea, Iguania and Anguimorpha it opens well above the condyles. Hence, humerus MTC239 could belong to a member of those taxa (i.e. Lacertoidea, limbed Anguimorpha different from Varanidae or Iguanidae). The presence of a deep radioulnar fossa and of the large obliquely trending radial condyle suggest the possibility of referring this humerus to the family Lacertidae. Furthermore, observation of the humerus of the extant genus *Timon* (Lacertidae, Lacertinae, Tschopp *et al.* 2018: fig. 20) shows a number of interesting resemblances with the humerus of Montchenot. However, it must be stressed that these observations are limited to only a few specimens and species in each family which casts doubts on their taxonomic value.

Modifications by digestion are evident on the surface of this fossil: in digestion, corrosion is often localized in articular ends, with the epiphyses severely pitted, while the diaphysis is less severely damaged as in the humerus from Montchenot (e.g. Andrews 1990; Fernandez-Jalvo & Andrews 1992; Denys *et al.* 1995).

AMPHISBAENIA Gray, 1844
Family POLYODONTOBAENIDAE Folie, Smith & Smith, 2013

cf. ***Camptognathosaurus parisiensis***
Folie, Smith & Smith, 2013

MATERIAL EXAMINED. — MNHN.F.MTC238 (Fig. 7), posterior part of a left dentary (L = 3.2 mm); it preserves only two tooth positions with one complete tooth.

DESCRIPTION

The sulcus Meckeli (its posterior part) opens widely and faces medio-ventrally. This fossa is divided by a well-developed, subvertical intramandibular septum that separate the alveolar canal from the Meckelian canal; Its ventral margin is fused with the internal, ventral wall of the dentary and the septum terminates at, or near, the level of the posteriormost tooth (see discussion on this position in Čerňanský 2019). Its posterior margin is deeply incised.

Overhanging the Meckelian fossa, the subdental shelf is not arched, its mesial border is nearly vertical and terminates at the level of the last tooth position. Immediately behind this tooth, the dentary bears a strong coronoid process that projects posterodorsally.

The single preserved tooth (certainly the penultimate one) is heavily built, subcylindrical and slightly tapers towards the crown. The tooth base is broad and nearly half of the tooth height projects above the dental parapet. The apex is somewhat eroded and it seems rather rounded. The tooth implantation is pleurodont and a sulcus dentalis may run along the medial side of the tooth raw although the presence of sediment casts some doubts on this observation.

DISCUSSION AND COMPARISONS

Despite the fragmentary nature of this fossil, the presence of a well-developed intramandibular septum fused with the ventral wall of the dentary and of a strongly developed coronoid process are features common to many amphisbaenian lizards, though they may be present in some skinks like *Ophiomorus* (Čerňanský pers. comm.). In addition, the robust tooth shows typical amphisbaenian morphology (Čerňanský *et al.* 2015) with simplification of the tooth crown (Smith 2009), features obviously absent in scincid lizards As a last point, this dentary is very similar to other dentaries from the late Paleocene of Rivecourt Petit Pâtis and Cernay-lès-Reims attributed to the amphisbaenian taxon *Camptognathosaurus parisiensis* (Folie *et al.* 2013). The dentary from Montchenot shares two diagnostic features with this species: teeth bulbous that project above the dental parapet nearly half of their height. However, due to the fragmentary nature and the poor preservation of the specimen, this referral cannot be accepted without some reservations.

Suborder ANGUIMORPHA Fürbringer, 1900
Family ? ANGUIDAE Gray, 1825

Anguidae indet.

MATERIAL EXAMINED. — MNHN.F.MTC241 (Fig. 8). The incomplete left dentary represents the middle and posterior parts of the bone and its ventral margin is broken.

DESCRIPTION

This small dentary (L: 2.9 mm) carries eight rather widely spaced tooth positions, but only one tooth is preserved. In medial view, the subdental shelf and the dental row are slightly concave. The subdental shelf forms a narrow, rounded surface overhanging the sulcus Meckeli. This fossa is rather narrow and faces mostly ventrally, mainly towards the anterior end of the bone. The dentition is subpleurodont (*sensu* Camp 1923; Hoffstetter 1954), that is the teeth tend to be attached to a single plane and the subdental table, as defined by Rage & Augé (2010) becomes an inclined surface. Hence tooth bases are attached to a moderately inclined or concave surface. Moreover, this type of implantation is often associated with a poor

FIG. 7. — Cf. *Camptognatosaurus parisiensis* Folie, Smith & Smith, 2013, posterior part of a left dentary, MNHN.F.MTC238: **A**, labial view; **B**, lingual view. Scale bar: 1 mm.

development or absence of the sulcus dentalis and subdental shelf; effectively the dentary from Montchenot has no sulcus dentalis and a poorly developed, rounded subdental shelf.

The lateral surface is gently convex, smooth and preserves only two labial (mental) foramina. The base of the single preserved tooth is not covered by cementum, except for two small anterior and posterior deposits. It is somewhat expanded, so that the mesial side of the tooth base comes near the dorsal margin of the subdental shelf. The tooth shaft slightly bends posteriorly and it steadily tapers dorsally towards the crown. The apex is rather rounded, with an incipient central bulb and two slight lateral shoulders. The tooth base is excavated by a central replacement pit. The tooth projects about one-half of its height above the parapet of the dentary. There are no striae on the apex of the tooth but they could have been obliterated by weathering.

COMPARISONS AND DISCUSSION

Dentary MNHN.F.MTC241 is referred to an anguimorph lizard because it shows the following combination of characters: 1) Sulcus Meckeli faces ventrally in anterior portion of dentary (Estes *et al.* 1988); 2) narrow and rounded subdental shelf; 3) teeth subpleurodont; 4) absence of sulcus dentalis; 5) crescentis or boat shaped tooth row (Estes 1964); and 6) teeth unicuspid, without lateral cups, not closely spaced (Camp 1923).

Some of these characters are regarded as anguimorphan synapomorphies (e.g. character 1, Estes *et al.* 1988), however several of them are not clear synapomorphies as they are subject to important variability among anguimorph taxa and often they are not unique to anguimorphs (Evans 2008). For example, the narrowness and reduction of the subdental shelf are very different among anguimorph lizards: from a well developed subdental shelf in *Xenosaurus* to a near absence in *Varanus* (see other examples in Bochaton *et al.* 2016).

Conflicting characters that are often cited as anguimorphan synapomorphies are clearly absent in the dentary from Montchenot: tooth apex pointed and tooth replacement alternate or distally displaced replacement pit on tooth bases (McDowell & Bogert (1954). Pointed, canine like teeth indicative of predaceous habits are common in anguimorph lizards but rounded tooth apex occasionally provided with

Fig. 8. — Anguimorpha, ?Anguidae, incomplete left dentary, MNHN.F.MTC241: **A**, lingual view; **B**, labial view. Scale bar: 1 mm.

a cutting edge (Estes 1964) has sometimes been regarded as an anguid synapomorphy (Estes et al 1988). Alternate tooth replacement is a clear feature of some extant and fossil anguimorph taxa, e.g. *Varanus*, *Lanthanotus*, *Heloderma*, *Saniwa*, *Palaeovaranus* (Ex *Necrosaurus*). Otherwise, tooth replacement shows important intra-individual and intraspecific variability among anguid taxa. In some anguids the variability appears along the tooth row: in the genera *Gerrhonotus* and *Diploglossus*, the first tooth bases have a central replacement pit while the others bear a distally displaced replacement pit. The same variability is also evident in the genus *Pseudopus* (Anguinae, see figures in Klembara 2012; Klembara *et al.* 2010, 2014). The presence of these two characters (rounded apex and tooth replacement) may be indicative of anguid affinities but the evidence is at best feeble and further comparisons with more complete material should be carried out.

Many purported terrestrial Anguimorpha have been described from the Mesozoic fossil record in Europe, Asia and North America (e.g. Hoffstetter 1967; Alifanov 2000; Evans 1994; Evans *et al.* 2006; Fernandez *et al.* 2015). In particular, the Cretaceous record includes fossils that bear some resemblances to extant terrestrial anguimorphan families (e.g. ?Xenosauridae, Pérez-García et al 2015; Anguidae, Blain *et al.* 2010; Helodermatidae, Nydam 2000, 2013; Platynotan, Norell *et al.* 2007; Mo *et al.* 2012; Varanoidea, Houssaye *et al.* 2013).

In contrast, fossils attributed to anguimorphan lizards in the early European Paleocene are far more scanty. Lizard extinctions across the K/T boundary may explain this poor record (Longrich *et al.* 2012) but it may also reflect the paucity of fossil lizards described so far in the European Paleocene (table 1). Among them, the incomplete dentary referred to Anguimorpha indet. found in the late Paleocene of Rivecourt (Smith *et al.* 2014, fig. 7) bears some resemblances with the dentary from Montchenot: teeth subpleurodont, rounded subdental shelf, teeth apparently with a central replacement pit but all these features are plesiomorphic within Anguimorpha. Another possibility could be an attribution to another anguimorphan lizard, a pan-shinisaur whose osteoderms are present in the locality. However, except for its anguimorphan relationships, nothing in the morphology of this dentary (particularly its size) is consistent with such an attribution.

Clade PAN-SHINISAURUS Smith & Gauthier, 2013

Pan-Shinisaurus indet.

Material examined. — MNHN.F.MTC240-MTC242, MTC243, nearly fifty osteoderms, a few complete, most more or less severely damaged by digestive processes or post-burial damages (Fig. 9).

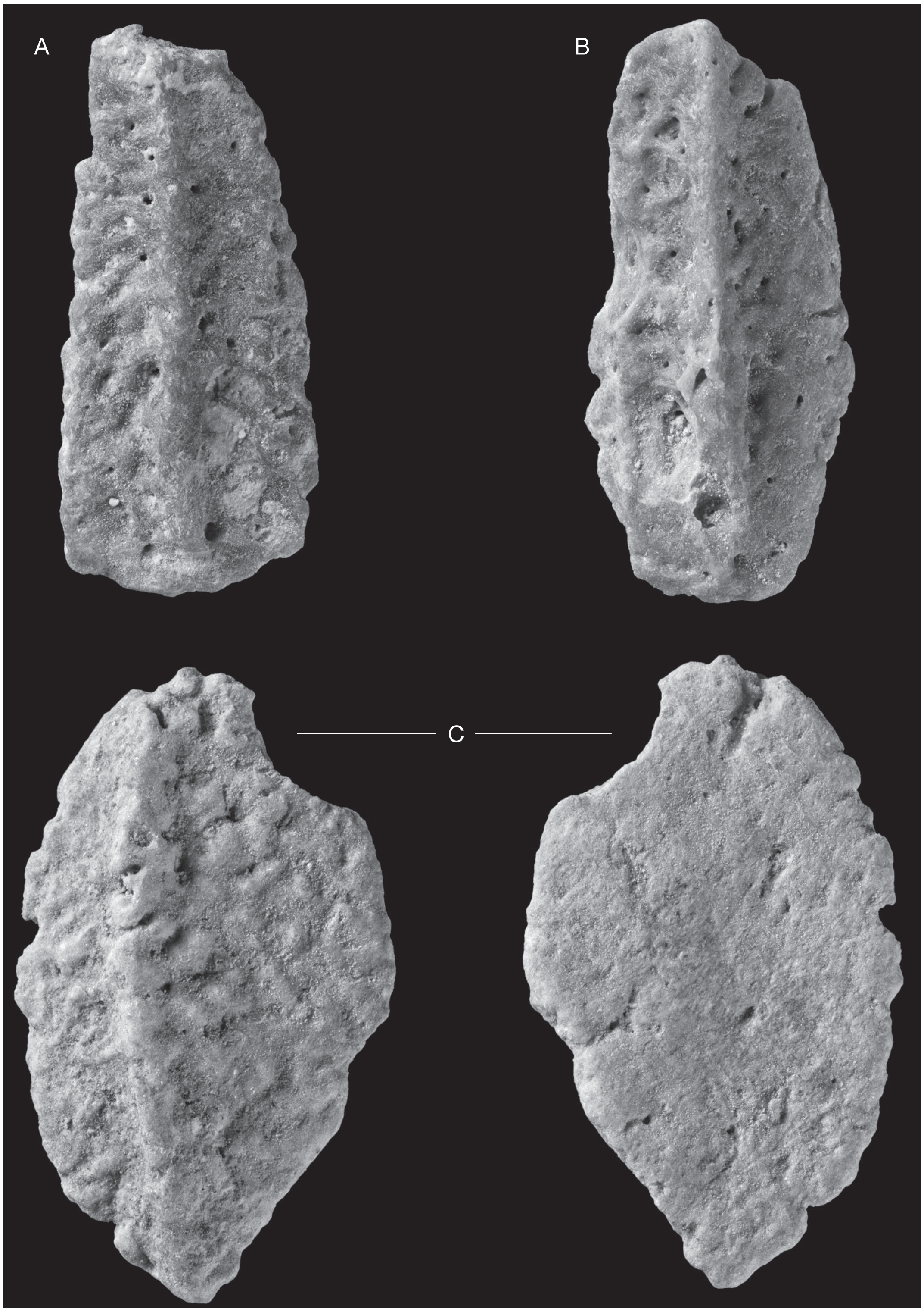

FIG. 9. — Pan-Shinisauridae, osteoderms, MNHN.F.MTC240-MTC242, specimen in: **A**, dorsal view; **B**, dorsal view; **C**, dorsal and ventral views. Scale bar: 1 mm.

DESCRIPTION

Measures (mm): maximum width (w) of osteoderms ranges between 1.1 and 3.9 mm. The osteoderms, when complete, are oval, suboval or subrectangular elements with more or less irregular margins. Gliding surfaces are absent. All bear a prominent medial keel that extends the full length of the osteoderm. A slight concavity on the underside of some osteoderms reflects the form of the keel. From the keel a pattern of deep pits or grooves and marked ridges radiates. The dorsal surface of most osteoderms is flat but a few have a rather strongly vaulted shape which certainly reflect different positions on the body.

COMPARISONS AND DISCUSSION

Some characters are traditionally used to separate anguimorph taxa (and more specifically anguid genera) by their osteoderms (Hoffstetter 1962a; Meszoely 1970; Bochaton *et al.* 2015, 2016), including the presence of a gliding surface and of a keel. For example, Gauthier (1982) considered keeled body osteoderms to be the plesiomorphic state for Anguimorpha. Referral of the osteoderms from Montchenot to Pan-*Shinisaurus* (*sensu* Smith & Gauthier 2013) follows from the combination of the features described above. These osteoderms are similar in shape to those of other fossil pan-shinisaurs, particularly *Provaranosaurus fatuus* Smith & Gauthier, 2013 (Smith & Gauthier 2013, early Eocene of the Wasatch Formation, Wyoming, United States), *Merkurosaurus ornatus* Klembara, 2008 (Klembara 2008, early Miocene, Orleanian, MN3, Bohemia) and an indeterminate pan-shinisaur from Messel (Smith 2017, middle Eocene, Germany). Crocodile-tailed lizards (Chinese crocodile lizard) or shinisaurs are represented by a single living species, *Shinisaurus crocodilurus* Ahl, 1930. It is worth noting that similar osteoderms have already been reported in the European Paleocene and early Eocene, in particular in the localities of Cernay (MP6, Hoffstetter 1943), Dormaal and Le Quesnoy (early Eocene, MP7, Hecht & Hoffstetter 1962; Augé 1990) and perhaps at Rivecourt-Petit Pâtis (Smith *et al.* 2014). Hecht & Hoffstetter (1962) and Augé (2005) suggested that these osteoderms could be attributed to the genus *Necrosaurus* as they are also similar to those of *Palaeovaranus cayluxi* (Ex *Necrosaurus*), see figs. in Rage 1978; Estes 1983; Augé & Smith 2009; Klembara & Green 2010. However, the taxonomic status and phylogenetic affinities of these lizards are a complex matter. Georgalis (2017) pointed out that the name *Necrosaurus*, as established by Filhol (1876) is a nomina nuda and that Zittel (1887-1890) was the first author to make the name *Palaeovaranus cayluxi* available. The phylogenetic affinities of *Palaeovaranus* are a moot point: briefly, McDowell & Bogert (1954) noted significant morphological differences between *Palaeovaranus* and members of the Platynota (*sensu* Pregill *et al.* 1986) and they referred it to xenosaurid lizards, an option first adopted by Hoffstetter (1954). Later this author returned *Palaeovaranus* to the Platynota (Hoffstetter 1962b). Lee (1997) rejected this taxon as paraphyletic. The phylogenetic position of *Palaeovaranus* is still a matter of discussion, although several derived characters suggest Platynotan relationships (see discussion in Smith 2017). In contrast, the attribution of *Provaranosaurus fatuus* and specimen SMF ME 11403 (an autotomized tail) from Messel to pan-shinisaur is a settled matter as they show no Platynotan derived characters (Smith & Gauthier 2013; Smith 2017). The fossils from Dormaal (osteoderms, vertebrae and an undescribed dentary) previously attributed to *Necrosaurus* (*Palaeovaranus*) show no Platynotan features and are nearly identical to the material of *Provaranosaurus fatuus* described by Smith & Gauthier 2013. In particular, *Provaranosaurus* has both rectangular and oval osteoderms, as in the material from Monchenot, while *Palaeovaranus* bears only ovoid osteoderms. On the basis of these resemblances, the osteoderms from Monchenot may be referred to pan-*Shinisaurus* and the presence of rectangular osteoderms seems to exclude an attribution to *Palaeovaranus*.

DISCUSSION AND CONCLUSION

Small lizards dominated the assemblage at Montchenot, a pattern that is also displayed by mammal fauna (Jehle *et al.* 2012). So far, only one rather large-sized taxon (cf. Pan-*Shinisaurus*) has been recovered from the locality. It is worth noting that this anguimorph lizard is represented exclusively by osteoderms, that is by small dermal elements, comparable in size to the other specimens of lizards yielded by the locality. Thus, Montchenot assemblages appear as highly selective (or biased).

As recognized by Andrews (1990), predation produce death assemblages that are highly selective and often lead to preferred preservation of microfossils. Marks of chemical alteration are another possible signature of predation. They are frequent on the fossils of Montchenot (mammals and lizards) and they are probably the result of digestion by predators. Acide induced soil corrosion may also affect bone surface but it has different effects from those observed on digested bones (Andrews 1990; Denys *et al.* 1995). In addition, hydrodynamic sorting can not be excluded, given the presence of relatively large lizards (cf Pan-*Shinisaurus*) in the locality, represented only by small elements (osteoderms).

The lizard assemblage recovered at Montchenot is quite similar to those of Cernay-Berru and Rivecourt Petit Pâtis (see Table 1). This resemblance (also identified for mammals, Jehle *et al.* 2012) confirms the late Thanetian age (MP6) of the locality (Laurain & Henry 1968; Riveline 1976; Jehle *et al.* 2012).

More generally, the composition of lizard assemblages recovered from the European late Paleocene (MP6) appears as rather coherent: all yield scincoids, primitive amphisbaenians (genus *Camptognathosaurus parisiensis*, Folie *et al.* 2013) and anguimorphs (cf Pan-*shinisaurus* and Anguidae). The presence of lacertoid (?Lacertidae) lizards in the European Paleocene (in particular at Cernay-Berru), is a moot point : Augé (2005: 118) described a new lacertid species, *Cernaycerta duchaussoisi* from the Paleocene of Cernay. Sullivan (2007) strongly disagreed with the referral of this fossil and suggests that this taxon is a *nomen dubium.* Folie *et al.* (2005) described a new genus and species, *Scincoideus haininensis* from the middle Paleocene (MP1-5) of Hainin (Mons Basin, Belgium) and they considered this taxon as a basal scincoid lizard. Smith & Gauthier (2013) recognized a new member of the genus, *Scincoideus grassator* in the early Eocene of the Wasatch Fmt., Wyoming, and they suggested that « one plausible hypothesis is that *Scincoideus* is a sister-group to Lacertidae ». Here it is evident that further studies are necessary, notably for the lizard fauna present at Cernay-Berru.

TABLE 1. — Lizard assemblages yielded by the main Paleocene European localities. Data from Augé 2005; Folie 2006; Folie *et al.* 2005, 2013; Smith *et al.* 2014.

Walbeck	**Hainin**	**Cernay-lès-Reims-Berru**	**Rivecourt**	**Montchenot**
MP1-5	MP1-5	MP6 ?Iguanidae	MP6 –	MP6 –
	Scincoidea	Scincoidea	Scincoidea	Scincoidea
	?Lacertoidea	?Lacertoidea	–	?Lacertidae
	Scincoideus	*Berruva* *Cernaycerta*	– –	– –
Amphisbaenidae (1)	Amphisbaenidae	Amphisbaenidae *Camptognathosaurus*	Amphisbaenidae *Camptognathosaurus*	Amphisbaenidae *Camptognathosaurus*
	?Anguimorpha	Anguimorpha ?Shinisauridae	Anguimorpha ?Shinisauridae	Anguimorpha ?Shinisauridae
	?Anguidae (2)	–	Anguidae	?Anguidae

The number of localities prospected and studied in the European Paleocene is low (five for the whole period if we include the German locality of Walbeck whose lizard fauna is currently lost, Estes 1983: 104) and this paucity may hide further lizard diversity in the European Paleocene.

However, the contrast between the rather depauperate lizard faunas from the European Paleocene and their richness in the early Eocene, in particular at Dormaal (MP7, Belgium, Hecht & Hoffstetter 1962; Augé 1990) is striking. These differences highlight the importance of the PETM for the vertebrate fauna in Europe : the early Eocene is a critical period in the history of mammals and it also represents a major turnover in lizard evolution (e.g. Russell 1975; Godinot 1996; Gingerich 2006; Augé *et al.* 2012; Bolet 2017). Widespread dispersals between continents (Europe, Asia, North America) are certainly involved here (e.g. Augé 2003; Godinot & Lapparent de Broin 2003; Beard & Dawson 1999; Beard 2002; Bowen *et al.* 2002; Rage 2012; Smith 2011; Smith *et al.* 2006) and a better knowledge of the Paleocene fauna is a key step in the comprehension of the major diversity changes that takes place across the Paleocene/Eocene boundary in Europe.

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