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A sebecosuchian in a middle Eocene karst with comments on the dorsal shield in Crocodylomorpha

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Isolated elements comprising a set of ziphodont teeth and osteoderms from the middle Eocene karst deposit of Lissieu, France are assigned to either *Iberosuchus* sp. or *Bergisuchus* sp., poorly known crocodylomorphs of possible sebecosuchian affinities. A general survey of dorsal osteoderm variability among Crocodylomorpha points to the similarity between the osteoderms from Lissieu and those of some Cretaceous notosuchians, notably the sebecosuchian *Baurusuchus*. Such isolated osteoderms represent a useful tool for identifying non-eusuchian crocodylomorphs in post-Cretaceous deposits. Relying on the distinctive morphology of these osteoderms might help augmenting the extremely scant fossil record of Paleogene sebecosuchians in Europe, thus improving the spatiotemporal resolution of this group. At least three types of predators coexisted in the ecosystem of Lissieu, which indicates that in the middle Eocene of Europe, carnivorous mammals were not the exclusive predators in terrestrial habitats and shared resources with a ground bird and a sebecosuchian. This faunal composition is comparable to contemporaneous ecosystems in South America.

Key words: Crocodylia, Sebecosuchia, Paleogene, Eocene, France.

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Introduction

Sebecosuchians primarily occur in Paleogene and Neogene continental deposits of South America, where the first species, *Sebecus icaeorhinus* Simpson, 1937 was erected. Although recovered specimens are extremely fragmentary, authors recognise on the basis of recent phylogenetic analyses (e.g., Pol et al. 2012) that Sebecosuchia or a taxon closely related to them also occur in Paleogene continental deposits of Europe. But the Paleogene radiation of Sebecosuchia in Europe is poorly understood because these possibly terrestrial crocodylomorphs have been reported from extremely fragmentary material limited to a few localities in Portugal, Spain, France and Germany (Berg 1966; Antunes 1975; Buffetaut 1986, 1988; Ortega et al. 1993; Rossman et al. 2000). Reasons for their persistence after the end-Cretaceous mass extinction, then of their extinction later in the Cenozoic, are unknown. Perhaps, a terrestrially inclined adaptation (e.g., Buffetaut 1986; Busbey 1995) allowed them to fill ecological niches later occupied by other predators, raising questions of habitat competition with mammals. Although this is perplexing, a better framework for the sebecosuchian spatial and temporal distribution needs to be realised.

Here, I report isolated teeth and osteoderms assignable to a sebecosuchian based on material recovered from a well-dated karstic bone accumulation (middle Eocene MP 14 mammal reference level of Lissieu, Rhône, France). This report is biostratigraphically significant because Lissieu is younger than Messel (MP 11) where the first European sebecosuchian *Bergisuchus dietrichbergi* Kuhn, 1968 was reported (Berg 1966). A checklist of European localities with Sebecosuchia is provided (Table 1).

Institutional abbreviations.—MHNL, Musée des Confluences, Lyon, France; UCBL-FSL, Université Claude Bernard Lyon 1, Faculté des Sciences Lyon, Villeurbanne, France.

Systematic palaeontology

The ordinal taxonomy follows the view of Martin and Benton (2008) although Brochu et al. (2009) expressed strong disagreement with it. As a side note, Gmelin (1789) coined the name Crocodili, hence Crocodylia, not Crocodylia, should be used. Indeed, I acknowledge that the view of Brochu et al. (2009), in which Crocodylia is used to refer to the crown group, is currently followed by the majority of workers in the

Table 1. Known Paleogene European occurrences of sebecosuchians, the youngest on top (note that the localities from Sables du Castrais and Argenton, France, are not included, the material needing revision).

Taxon or denomination	Occurrence	Age	Remains	Source
<i>Iberosuchus macrodon</i>	Vale Furado, Nazaré, Leiria Province, Portugal	ante-Bartonian	cranial remains	Antunes 1975
cf. <i>Iberosuchus</i>	Caenes, Salamanca Province, Spain	Bartonian, MP16	mandibular elements	Ortega et al. 1996
? <i>Iberosuchus</i>	La Livinière, Hérault, France	Bartonian, MP15	postcranials, jugal, isolated teeth	Buffetaut 1986
cf. <i>Iberosuchus</i>	Issel, Aude, France	Lutetian, MP14	mandibular elements	Ortega et al. 1996
cf. <i>Iberosuchus</i> sp.	Lissieu, Rhône, France	Lutetian, MP14	osteoderms	present work
<i>Iberosuchus macrodon</i>	Cuenca del Duero, Spain	Lutetian, MP13-14	teeth, osteoderms	Martin de Jesus et al. 1987; Santiago and Andrés 2009
<i>Bergisuchus</i> cf. <i>dietrichbergi</i>	Geiseltal, Sachsen-Anhalt, Germany	Lutetian, MP13	snout fragment, dentaries	Rossmann et al. 2000
<i>Bergisuchus dietrichbergi</i>	Messel, Hessen, Germany	Lutetian, MP11	maxilla, nasals, lacrimal, dentary	Berg 1966; Kuhn 1968; Buffetaut 1988
cf. <i>Iberosuchus macrodon</i>	Tosalet del Morral, Lerida province, Spain	Lutetian	snout fragment	Berg and Crusafont 1970; Buffetaut 1982
“cocodrilos Iberoccitanos”	El Cerro de El Viso, Zamora, Spain	middle Eocene	cranial remains	Ortega et al. 1993

community, but I use Crocodylia to refer to a more exclusive clade here.

Superorder Crocodylomorpha Hay, 1930

Order Crocodylia Gmelin, 1789

Suborder Sebecosuchia Simpson, 1937

Family et genus indet.

Material.—UCBL-FSL 530863a–c, three isolated teeth; MHNL 341, a set of isolated osteoderms including 5 complete and 6 fragmentary dorsal elements. The label accompanying these specimens reports the date 1895. Material from MP 14 (Mammal Paleogene reference level, Biochro'M 1997) of Lissieu, Rhône, France. Information on this locality is presented in Rage and Augé (2010).

Description.—Three teeth including the apex of a crown and two complete crowns are preserved (Fig. 1). They are of the ziphodont type, i.e., their mesiodistal carinae bearing denticles from the base of the crown to the tip of the apex. These denticles consist of plication of the enamel (Fig. 1A₃, B₂, C₃). The two best-preserved teeth have different general morphologies that reflect a different position in the tooth row. The smallest tooth (apicobasal length is 11 mm) is sub-conical and its crown is curved. This type of morphology was described in the premaxillary dentition of *Iberosuchus macrodon* by Antunes (1975). The other complete crown is much larger (apicobasal length is 23 mm) and is labiolingually compressed with the tip of the apex bent in a posterior direction. The labial or lingual surface of that tooth has two ridges running from the apex to the base of the crown. Teeth attributed to a mesosuchian from La Livinière (Buffetaut 1986) superficially resemble the teeth described here in being slightly labiolingually compressed. Nevertheless, the teeth from La Livinière do not show individualised denticles on the mesiodistal carinae, but as highlighted by Buffetaut (1986) present crenulations of the enamel.

Eleven unusual osteoderms are preserved, six of them being complete (Fig. 2). The osteoderms are dorsoventrally thin and at least three times longer than wide with a roughly rectangular outline. Their ornamentation does not show the cupular pattern observed in aquatic forms. Instead, these osteoderms have a vermiculate ornamentation as observed in the skull elements of *Iberosuchus macrodon* Antunes, 1975. All osteoderms reported here possess a tall longitudinal ridge surrounded by fine ridges radiating perpendicularly to it. In one specimen (Fig. 2D₁), one of the perpendicular ridges is thick, giving to the osteoderm a cross-like shape in dorsal view. The longitudinal ridge runs for almost the entire length of the osteoderm and gradually merges with the anterior border, but finishes abruptly with the posterior border. Although the margins of the largest specimen seem eroded (Fig. 2A), the long margins of the other specimens are finely indented. The anterior margin is smooth and convex. In all specimens, the ventral surface is nearly flat to slightly convex and bears an interwoven pattern produced by the attachment of the epaxial musculature.

Remarks.—The material described above is assigned to the Sebecosuchia (including Sebecidae + Baurusuchidae; e.g., Pol et al. 2012) on the basis of the following synapomorphies: mediolaterally compressed teeth with mesiodistal carinae possessing denticles (the ziphodont condition of Langston 1975); anteroposteriorly elongated dorsal osteoderms possessing a central median prominent keel running for most of the length; rugose ornamentation devoid of pits and cupules; anterolateral process of osteoderms absent. Under an alternative hypothesis allying Sebecidae with Peirosauridae (the Sebecia of Larsson and Sues 2007), the synapomorphies highlighted here would not be valid anymore and would be considered as homoplastic. Moreover, the Peirosauridae do not share the characters mentioned above for *Iberosuchus* or *Bergisuchus*. Indeed, the postcranial skeleton of peirosaurids is largely unknown, but if ornamentation of their osteoderms

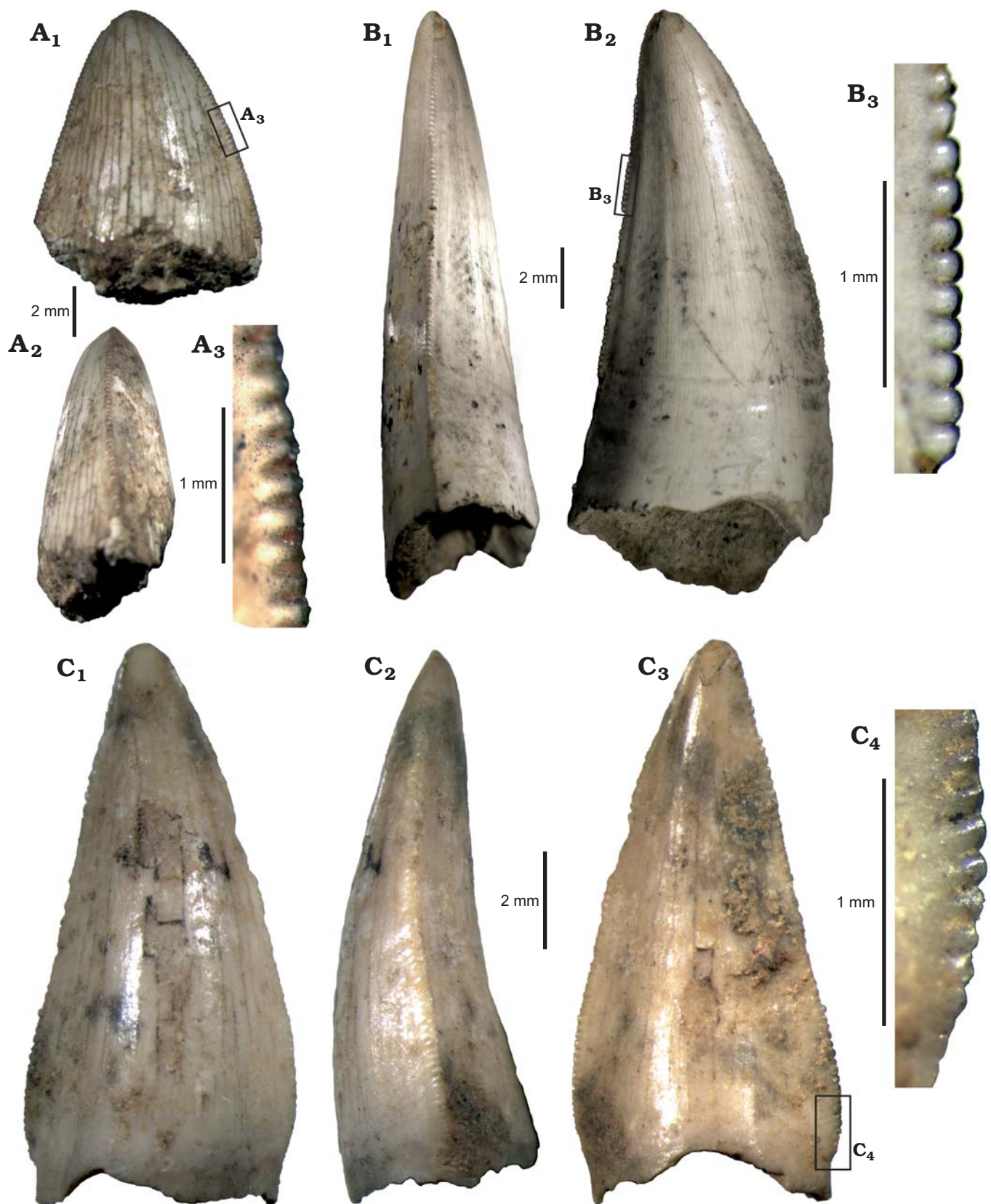


Fig. 1. Isolated ziphodont teeth of *Sebecosuchia* indet. from the middle Eocene of Lissieu, France. **A.** Isolated apex (UCBL-FSL 530863a) in labial (A_1), mesial or distal (A_2) views, detail of the denticles (A_3). **B.** Isolated crown (UCBL-FSL 530863b) corresponding to a maxillary or mid-position in the dentary distal (B_1), labial or lingual (B_2) views, detail of the denticles (B_3). **C.** Isolated crown (UCBL-FSL 530863c) nearly circular in cross section corresponding to a premaxillary or anterior position in the dentary tooth row in labial (C_1), mesial or distal (C_2), lingual (C_3) views, detail of the denticles (C_4).

reflects that of the skull, they should present pits and cupules. Moreover, the presence of serrations or true denticles in the dentition of all Peirosauridae remains unclear (compare for example *Hamadasuchus* [Larsson and Sues 2007] and *Pepesuchus* [Campos et al. 2011]).

Discussion

Dorsal osteoderms in Crocodylomorpha.—The above-described osteoderms have no morphological equivalent among eusuchians recovered from Cenozoic deposits and are thus easily recognizable (e.g., compare with eusuchians in Salisbury and Frey 2000; Salisbury et al. 2006). The osteoderms reported for *Boverisuchus* (formerly *Pristichampsus*, see Brochu 2013) *rollinati* are of the general eusuchian morphology, i.e., rectangular, flat and ornamented with large circular pits (Rossmann 2000) and cannot be mistaken with those described here from Lissieu. On the other hand, the osteoderms from Lissieu are comparable to crocodylomorphs outside Eusuchia (see also Ortega 2004). It is reminded that the presently described osteoderms are isolated and cannot be precisely positioned along the dorsal shield (although the articulated nature of the material described for *Baurusuchus albertoi* Nascimento and Zaher, 2010 provides a reliable approximation of the shield in the sebecosuchian from Lissieu). Consequently, only a general comparison is made, focusing on isolated elements of the dorsal armour, highlighting similarities and differences. Few complete articulated shields are known in the fossil record of non-eusuchian crocodylomorphs, and the most remarkable are mentioned below. The topology of Crocodylomorpha follows recent hypotheses uniting Sebecidae and Baurusuchidae into Sebecosuchia, although it should be noted that an alternative hypothesis uniting Sebecidae with Peirosauridae was also proposed (see discussion in Pol et al. 2012).

Among basal crocodylomorphs, the paramedian shield of the spheosuchians *Dromicosuchus grillator* and *Dibothrosuchus elaphros* present elongate osteoderms (Wu and Chatterjee 1993; Sues et al. 2003) reminiscent of the morphology and ornamentation described here for the osteoderms from Lissieu. But contrary to those, the osteoderms of *Dromicosuchus grillator* are described as possessing an anterolateral process articulating beneath the preceding osteoderms (Sues et al. 2003). In *Gobiosuchus kielanae*, the dorsal osteoderms are quadrangular and ornamented with a pattern “en fleur de lys” (Osmólska et al. 1997: fig. 5F). In *Protosuchus richardsoni* (Brown 1933), osteoderms forming the dorsal shield are rectangular, being wider than long, ornamented with a pattern of furrows on their dorsal surface, somehow comparable to those of *Gobiosuchus kielanae*. They articulate with the preceding osteoderms through an articulation facet and possess an anterolateral process. A dorsal shield was reported in *Hsisosuchus chunkingensis* by Li et al. (1994) and in *Hsisosuchus chowi* by Peng and Shu (2005). The osteoderms are arranged in a double row

of quadrangular osteoderms ornamented with numerous pits and lacking a keel. Peng and Shu (2005) mention that contrary to *Protosuchus*, *Sunosuchus*, and *Sichuanosuchus*, the osteoderms of *Hsisosuchus* lack the anterolateral process.

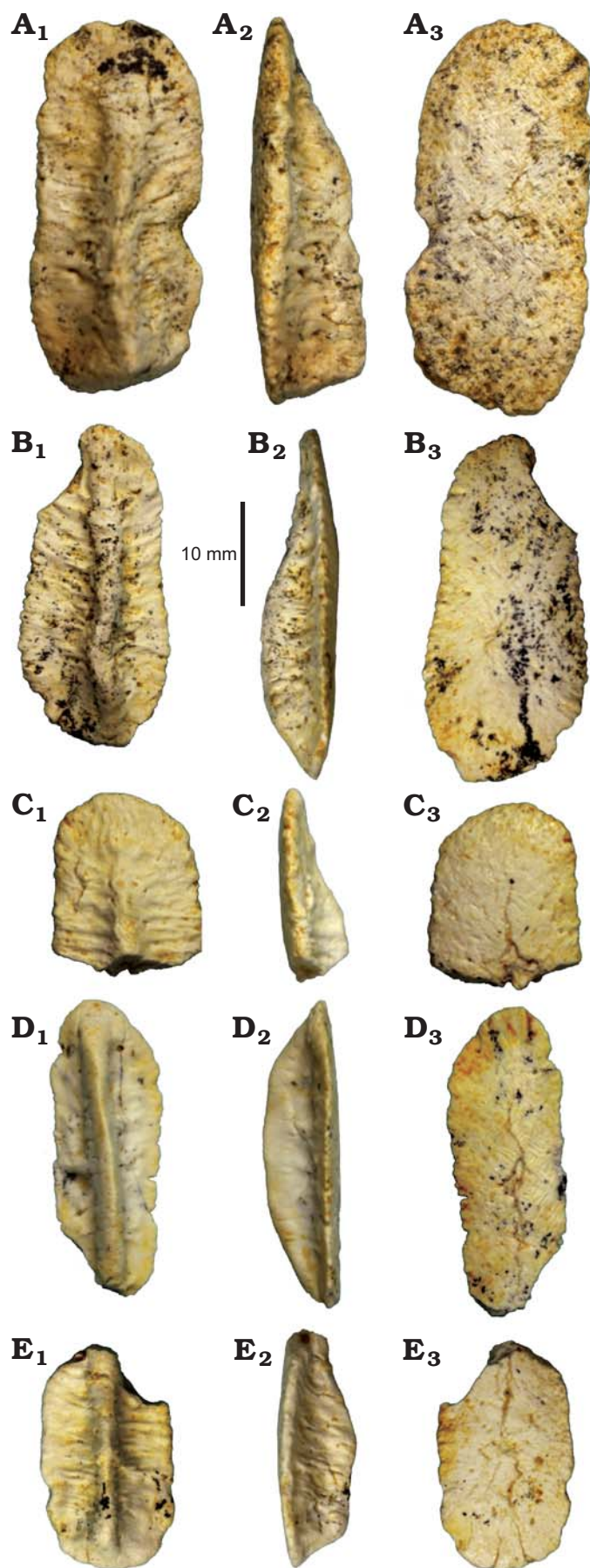
Among thalattosuchians, the dorsal armour is well preserved in *Pelagosaurus typus* showing subrectangular, unkeeled osteoderms (Pierce and Benton 2006). The dorsal shield of teleosaurids is represented by numerous articulated skeletons. Osteoderms are square to rectangular possessing a spiny anterolateral process. A keel is often present on the dorsal surface as a continuity of this process and large ovoid pits cover most of the dorsal surface (e.g., Westphal 1962). On the other hand, the dorsal armour is completely lost in metriorhynchids (e.g., Young et al. 2010).

Among atoposaurids such as *Montsecosuchus*, *Alligatorrellus* or *Alligatorium*, the dorsal shield is made of subtrapezoidal units (Buscalioni and Sanz 1988) with a keel in lateral position. In the genus *Theriosuchus*, dorsal osteoderms are transversely more elongated than in the above-mentioned atoposaurids and possess an anterolateral process (e.g., Schwarz and Salisbury 2005: fig. 7K). In all these taxa, the dorsal osteoderm surface is ornamented with small circular pits.

In Dyrosauridae, the dorsal shield is known from a few species (Jouve et al. 2006; Schwarz et al. 2006). Each osteoderm is square to rectangular in outline, ornamented with ovoid pits and is nearly flat and does not bear any ridge. In some cases, the dorsal osteoderms show a laterally projecting facet (Jouve et al. 2006).

In Coelognathosuchia, which includes Goniopholididae and Pholidosauridae (Martin et al. 2014), the dorsal shield is represented by distinctly rectangular osteoderms, being much wider than long and possessing a long and pointed anterolateral process (e.g., Wu et al. 1996: fig. 12). The presence of an articulation facet for the preceding osteoderms is variable but sculpture always consists of large circular pits. The dorsal surface of the osteoderms is rather flat and a keel is running close to the lateral edge of the scute.

There are a number of notosuchians in which the dorsal shield is preserved, some of them showing a shield comparable to that described above for the Lissieu specimens. None of the osteoderms referred here possess an anterolateral process, and this may represent an apomorphy for Notosuchia. Pol (2005) described osteoderms found associated with a specimen of *Notosuchus terrestris*. These are pentagonal, possessing a smooth anterior facet for articulation with the preceding osteoderms, have a dorsal keel and do not have an anterolateral process. Their dorsal surface is slightly ornamented with ridges and grooves. The dorsal shield of *Simosuchus clarki* is made of a double row of paramedian osteoderms joined laterally by several rows of accessory osteoderms with similar shapes and sizes. The osteoderms are all keeled, slightly longer than wide, sutured to each other and finely sculptured with faint grooves and foramina; no anterolateral process occurs (Hill 2010). In all species of *Araripesuchus* preserving a dorsal shield, osteoderms have the following morphology: they are rectangular



with an anterior smooth facet, a shallow dorsal keel, and are finely ornamented with small pits and grooves (Ortega et al. 2000; Turner 2006; Sereno and Larsson 2009). However, the osteoderms from Lissieu are more similar to those described in the following notosuchians. In *Mariliasuchus amarali* (Nobre and Carvalho 2013), a double row of osteoderms was found articulated to the thoracic and lumbar region. These osteoderms are ovoid in outline, possess a median keel and their ornamentation is rugose with accessory keels. The osteoderms from Lissieu are most similar to the anteroposteriorly elongate osteoderms in the articulated paramedial shield of two notosuchians from Africa: *Malawisuchus mwakasyungutiensis* (see Gomani 1997: fig. 5) and *Pakasuchus kapilimai* (see O'Connor et al. 2010: fig. 1). But the most striking resemblance is found when comparing the osteoderms from Lissieu with the articulated series in *Baurusuchus* (Nascimento and Zaher 2010; de Araújo Júnior and da Silva Marinho 2013). All these osteoderms bear a tall ridge and are ornamented with a set of accessory crests and furrows giving to the dorsal surface a rugose aspect. They are elongated in the anterior trunk area, and become wide in the thoracic and pelvic region indicating that the elongated osteoderms from Lissieu might correspond to the anterior region of the dorsal shield.

This peculiar elongated morphology of the dorsal osteoderms is therefore present in two distantly related lineages within Notosuchia: *Malawisuchus/Pakasuchus* and sebecosuchians. O'Connor et al. (2010) proposed that such longitudinally expanded osteoderms represent only the central primary ossification as is observed in the early stages of osteogenesis (Vickaryous and Hall 2008). It is therefore plausible that this morphology repeatedly occurred independently within different lineages of notosuchians for developmental reasons. In any case, this peculiar morphology has not been reported outside Notosuchia yet, (the closest resemblance being those of some spheosuchians) and the absence of an anterolateral process associated to a rugose elongated morphology bearing a long median keel might be a characteristic of all sebecosuchians as well as some other members of the Notosuchia.

Taxonomic assignment of the Lissieu crocodylomorph.—

In Paleogene continental deposits of Europe, labiolingually compressed teeth with serrated or denticulate carinae (the ziphodont condition of Langston 1975) are easily recognizable from the conical teeth of freshwater eusuchians. Nevertheless, the attribution of these ziphodont teeth to either a planocraniid eusuchian (see Brochu 2013) or to a non-eusuchian is equivocal despite one previous attempt to distinguish them on the basis of denticle count (Antunes 1986). On the other hand, the morphology of osteoderms found associated with these ziphodont teeth provides a reliable criterion to assess the higher-level taxonomy of fragmentary remains: the

Fig. 2. Selected sebecosuchian osteoderms (MNHL 341) from the middle Eocene of Lissieu, France, in dorsal (A_1 – E_1), lateral (A_2 – E_2), and ventral (A_3 – E_3) views.

rationale behind this assignment is the vermiculate ornamentation, which matches the ornamentation of cranial elements of *Iberosuchus macrodon* Antunes, 1975. Moreover, these osteoderms have previously been found in an Eocene locality in southern France in association with specimens then referred to a mesosuchian (Buffetaut 1986) and were also found associated with elements attributed to *Iberosuchus macrodon* from various localities in Spain (Martín de Jesus et al. 1987; Ortega 2004). Reports of such osteoderms, identical to those recovered from Lissieu, are limited to the middle Eocene (MP 15) of La Livinière, Hérault, France (Buffetaut 1986: pl. 1), the middle Eocene of the Duero Basin, Spain (Martín de Jesus et al. 1987: pl. 3), the middle Eocene of Salamanca, Spain (Ortega 2004) and the middle Eocene (MP 13-14) of Corrales del Vino, Zamora, Spain (Santiago and Andrés 2009: fig. 16). Although such osteoderms have not yet been described from Paleogene deposits of South America where sebecosuchians are diverse, two osteoderms of similar morphology were briefly described but not figured with the type material of the ziphodont *Eremosuchus elkoholicus* Buffetaut, 1989 from the late early Eocene of Algeria, then identified as a trematochampsid.

Therefore, based on the morphology of the osteoderms (matching that of Cretaceous sebecosuchians), their ornamentation (recalling the skull surface of *Iberosuchus macrodon*) and their association with ziphodont teeth (same as *Iberosuchus macrodon*), the isolated specimens described above from Lissieu are assigned to a sebecosuchian, possibly *Iberosuchus* or *Bergisuchus*.

Distribution of European sebecosuchians.—Occurrences of *Iberosuchus macrodon* and *Bergisuchus dietrichbergi* in the Paleogene of Europe are based on fragmentary cranial material (Table 1), and although they have been assigned to the Sebecosuchia in recent phylogenetic works (e.g., Pol et al. 2012), it is worth remembering that more complete material is necessary to validate this hypothesis.

The oldest European report of a Cenozoic “mesosuchian” appears to be from late Paleocene continental deposits of Vinalmont in Belgium (Groessens-Van Dick 1982) on the basis of a single amphicoelous vertebra. Then, a temporal gap in the fossil record of the group is observed between the Thanetian and the Lutetian, lasting more than 8 million years. Whether this Paleocene amphicoelous form is related to the later sebecosuchians of the middle Eocene is unknown and could only be tested if more material arises from formations corresponding to that 8 million years gap. The vast majority of sebecosuchian occurrences in Europe are concentrated in Lutetian deposits of Portugal, Spain, France and Germany. The youngest occurrences are known from two records, one in France (Buffetaut 1986) and one in Spain (Ortega et al. 1996), both Bartonian in age. There are no proven records of sebecosuchians in Europe after the MP 16 mammal reference level. During a relatively narrow timeframe (MP 13-14), sebecosuchians were geographically distributed across Spain (Ortega et al. 1996), southern France (Buffetaut 1986),

southeastern France (this study) and Germany (Rossmann et al. 2000). It can be expected that coeval sites of the Lutetian, such as Egerkingen in Switzerland (MP 14; Biochro'M 1997) may yield contemporaneous sebecosuchian remains.

Very few reports of crocodylomorphs from karstic deposits exist and notable exceptions consist of infrequent finds in comparison to other vertebrate remains, largely represented by mammal bones. For example, the alligatorine *Arambourgia gaudryi* (de Stefano, 1905) is exclusively known from the late Eocene phosphorites of Quercy, France and is represented by a single skull only. Rare remains of *Diplocynodon* sp. and maybe a pristichampsine (now referred as Planocraniidae, Brochu 2013) were also reported from the phosphorites of Quercy (see review in Rage 2006).

Out of the large collection of vertebrates from Lissieu screened both in the Musée des Confluences and in the Université Lyon 1, very few elements are identified as sebecosuchians. The rarity of sebecosuchian remains in Lissieu may be due to their low abundance, which might be linked to their ecological position as predators and/or the under-representation of their habitat in this fossil assemblage. That sebecosuchians occupied a carnivorous niche in a terrestrial habitat is corroborated by the morphology of their ziphodont dentition and their possible land-dwelling habits. Buffetaut (1986) discussed that the morphology of the postcranial elements of the ziphodont mesosuchian from La Livinière probably reflected terrestrial habits. More recently, examination of the postcranial skeleton of baurusuchids (close in morphology and affinities to European sebecosuchians) led to the conclusion that these animals had an erect posture (Nascimento and Zaher 2010) consistent with a terrestrially inclined type of locomotion. Nevertheless, the precise ecological interactions of sebecosuchians with mammalian herbivores or even with other predators cannot be assessed for the moment. All that can be observed is that the locality of Lissieu contains a non-negligible number of medium-sized terrestrial (or possibly terrestrial for the sebecosuchian) predators: a flightless phorusrhacid bird (Angst et al. 2013), creodont and carnivorous mammals (Lange-Badré and Haubold 1990) and finally the sebecosuchian reported here. Body size plays a major role in ecological hierarchy (Farlow and Pianka 2002) but establishing body size from isolated remains is tentative. However, the largest osteoderms from Lissieu are about 3 cm long and would point to an animal no smaller than a metre in total length. The Lutetian carnivorous mammals, with a small to intermediate weight of 1–30 kg (Morlo 1999) and the phorusrhacid bird with a height of about 1.5 m (Angst et al. 2013) are therefore comparable in body size to the rough approximation of the sebecosuchian from Lissieu. Indeed, these estimates are far from being precise but suggest that at least three distinct predatory clades coexisted with overlapping body size. Because of their similar body size, these taxa may have competed for the same resources (Farlow and Pianka 2002). However, it is reasonable to assume that segregation (either spatial or temporal) took place because of the different feeding strategies implied by the

distinct morphologies of these three predator clades (beak and claws for the bird; ziphodont teeth for the sebecosuchian; caniniform and molariform teeth for the mammals). This type of ecological structure is comparable to the situation in South America during the Cenozoic (e.g., Gasparini et al. 1993). In conclusion, such trophic structure composed of a bird, several mammals and a crocodylomorph as terrestrial predators no longer exists in post-Eocene continental ecosystems of Europe, which eventually became dominated by mammals. Reasons for this ecological shift remain to be evaluated.

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