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New material of the ziphodont mesoeucrocodylian *Iberosuchus* from the Eocene of Languedoc, southern France

Nouveau matériel du crocodylomorphe ziphodonte *Iberosuchus* de l'Eocène du Languedoc, sud de la France

[with 6 figures]

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ABSTRACT—Skull fragments and osteoderms assigned to *Iberosuchus* sp. are described from three middle Eocene localities: Aumelas, Robiac and Saint-Martin-de-Londres in Languedoc, southern France. These remains expand the anatomical knowledge of this poorly known taxon, notably on the morphology of the premaxilla, maxilla, postorbital and jugal and allow a comparison with other non-eusuchian ziphodont mesoeucrocodylians. A close relationship of the genus *Iberosuchus* with narrow/elevated-snouted Baurusuchidae or Peirosauridae from the Cretaceous of South America and Africa appears unlikely. Affinities between *Iberosuchus* and Sebecidae, a group reported from the Cenozoic of South America; are suspected but require further testing. The record of *Iberosuchus* is limited to the European middle Eocene (Lutetian and Bartonian) and it is currently known from Portugal, Spain and France.

RÉSUMÉ—Des morceaux crâniens et des osteoderms sont décrits en provenance de trois gisements de l'Eocène moyen du Languedoc, sud de la France : Aumelas, Robiac et Saint-Martin-de-Londres, et assignés au crocodylomorphe ziphodonte *Iberosuchus* sp.. Bien que fragmentaires, ces restes élargissent les connaissances sur l'anatomie de ce taxon mal connu, notamment sur la morphologie du prémaxillaire, du maxillaire, du postorbital et du jugal et autorisent une comparaison avec d'autres mesoeucrocodyliens ziphodontes non-eusuchiens. Le genre *Iberosuchus* ne ressemble à aucun crocodylomorphe à museau étroit et surélevé du Crétacé d'Amérique du Sud ou d'Afrique, tels les Baurusuchidae ou les Peirosauridae. En revanche, des similarités sont notées entre *Iberosuchus* et les Sebecidae, un groupe connu dans le Cénozoïque d'Amérique du Sud, évoquant un lien possible entre ces deux taxons mais qui requiert de futures études. *Iberosuchus* n'est connu que dans l'Eocène moyen (Lutétien et Bartonien) d'Europe et est mentionné au Portugal, en Espagne ainsi qu'en France.

Keywords: Comparative anatomy, Sebecosuchia, Eocene, France

1. Introduction

Amidst the rich mammalian faunas, Eocene continental assemblages of Europe contain ziphodont mesoeucrocodylians with serrated and labiolingually compressed teeth. Europe is unique at that time for hosting two distantly related lineages with convergent cranial morphologies. On one hand, the eusuchian *Pristichampsus rollinati*, recently moved into the genus *Boverisuchus* (Brochu, 2013), is known from French and German Lutetian deposits and is represented by well-preserved skeletons from Geiseltal (e.g. Brochu, 2013). The affinities of the second lineage, possibly related to the Sebecosuchia, remain obscure due to the scarcity of specimens. Sebecosuchia comprise the Sebecidae and the Baurusuchidae,

primarily reported from South America (e.g. Colbert, 1946; Buffetaut and Hoffstetter, 1977; Buffetaut, 1982; Turner and Sertich, 2010; Pol et al., 2012). Distinguishing *Pristichampsus* and Sebecosuchia on the basis of tooth morphology has not proved conclusive yet (Antunes, 1986; Legasa et al., 1993; Brochu, 2013) and their identification will have to rely on the identification of cranial and postcranial elements.

Berg (1966) first recognized 'aff. *Sebecus*? n. sp.' for a fragmentary rostrum and a lower jaw from the Lutetian of Messel pit in Germany, suggesting the first referral to Sebecosuchia in Europe. Two ziphodont 'mesosuchians' were then named from the Eocene of Europe: *Bergisuchus dietrichbergi* Kuhn 1968 for the aforementioned german specimen, and *Iberosuchus macrodon* Antunes 1975 for a rostrum from the Lutetian of Vale Furado, Portugal. Unsurprisingly, the anatomy and affinities of these animals remains poorly known. *Bergisuchus* and *Iberosuchus* have been interpreted as members of the Sebecosuchia and more precisely to be part of the Baurusuchidae (Antunes, 1975; Buffetaut, 1980; Buffetaut, 1982). Then, both taxa were viewed as European members of the family Trematochampsidae (Buffetaut, 1988) or closer to *Sebecus* than to Trematochampsidae for *Bergisuchus* (Rossmann et al., 2000). Gasparini (1984) concluded that the affinities of *Iberosuchus macrodon* were uncertain because the premaxilla combines characters of the Baurusuchidae and Sebecidae (such as the recess for reception of the hypertrophied mandibular fourth tooth), but that contrary to these groups, the premaxilla bears five alveoli instead of four.

The first phylogenetic explorations found *Iberosuchus* as a possible member of the Sebecosuchia and recovered a polyphyletic trematochampsid clade (Ortega et al., 1996). A sebecosuchian affinity was confirmed in Turner and Sertich (2010), and *Iberosuchus* and *Bergisuchus* were considered non-sebecid sebecosuchians in other phylogenetic analyses that included other baurusuchid and sebecid taxa (Ortega et al., 2000; Pol and Powell, 2011; Kellner et al., 2013; Pol et al., 2014). Therefore, *Bergisuchus* and *Iberosuchus* seem to belong

to the Sebecosuchia ((Sebecidae + Baurusuchidae) according Pol et al., 2012). However, the phylogenetic position of Sebecidae is debatable, and they have been allied with Peirosauridae (Larsson and Sues, 2007). More recently, Pol et al. (2014) highlighted that sebecids together with *Iberosuchus* and *Bergisuchus* share derived similarities with baurusuchids and with peirosaurids. Therefore, the placement of *Bergisuchus* and *Iberosuchus* has yet to be explored.

Here, I report new specimens from three Eocene localities in Languedoc, southern France, which despite their fragmentary nature can be attributed to *Iberosuchus* sp. Their description provides a basis for comparing the genus *Iberosuchus* to other non-eusuchian ziphodont mesoeucrocodylians from Europe and Gondwana and although the new material does not add a sufficient number of characters for a phylogenetic analysis, its affinities are preliminary discussed with a focus on the Sebecosuchia (Sebecidae + Baurusuchidae sensu Pol et al., 2012) with which it has previously been allied (Ortega et al., 2000; Turner and Sertich, 2010; Kellner et al., 2013) as well as the Peirosauridae, which are allied to the Sebecidae under the phylogenetic hypothesis of Larsson and Sues (2007).

All the specimens presented here are housed in ISEM, Institut des Sciences de l'Évolution de Montpellier, Université de Montpellier, France, and bear the following acronyms: RBN, Robiac Nord, Gard, France; SMF, St-Martin de Londres, Hérault, France; AUM, Aumelas, Hérault, France.

2. Geological setting

The material described herein comes from three localities of the Languedoc in southern France. All the localities correspond to Eocene continental deposits, whose ages were established according to the European Mammal Paleogene (MP) zonation (Biochro'M,

1997). Aumelas (Hérault) is considered to be the oldest of the three and is attributed a MP13 age according to Escarguel et al. (1997), therefore possibly Lutetian. The outcrop consists of a lacustrine limestone and acid-preparation is therefore necessary to free specimens from their carbonate matrix (Sudre, 1980). Saint-Martin-de-Londres (Hérault) assigned to MP15 (Escarguel et al., 1997) could either be late Lutetian or Bartonian in age. The locality consists of a fossiliferous lens located at the base of limestones containing the freshwater gastropod *Australorbis pseudoammonius* (Crochet et al., 1988). Bones are included in a carbonaceous mud and the site yielded a diverse mammalian fauna together with yet indeterminate remains of birds and a herpetofaunal assemblage (Crochet et al., 1988). Finally, the locality of Robiac (Gard) (Sudre, 1969) assigned to MP16 (Escarguel et al., 1997) might be considered Bartonian in age. Several ziphodont teeth from this locality, housed in the Muséum National d'Histoire Naturelle, Paris have been attributed to the genera *Pristichampsus* (= *Boverisuchus*) and to *Iberosuchus* by Antunes (1986).

3. Systematic Palaeontology

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

SEBECOSUCHIA Simpson, 1937

Genus ***Iberosuchus*** Antunes, 1975

Iberosuchus sp.

Figs. 2–6

Referred Specimens. AUM 466, AUM 474, AUM 477, SMF 203: premaxillae; RBN 2026, SMF 181: maxillae; AUM 465: left postorbital; AUM 472: left jugal; SMF 206: a large

isolated tooth; RBN 201, 2012, 2014, 2018, 2019, 2020, 2021, 2023, 2816; AUM 458, AUM 459: osteoderms.

4. Description

Skull:

Premaxilla - Three specimens come from Aumelas and include an almost complete right element (AUM 474, Fig. 2A, B), a fragment of a right element (AUM 466, Fig. 2C-F), and a pair of premaxillae pressed against each other (AUM 477). Ornamentation of the external surface of these premaxillae is vermiculate. The morphology of AUM 477 corresponds to that described for AUM 466 and AUM 474 in displaying a marked concave notch visible on both elements for the reception of the dentary tooth, as well as the posterior premaxillary foramen visible on the palatal surface of the right element. The size of AUM 477 is about three times larger than the other specimens described below. A right complete premaxilla bearing one tooth in the last alveolus comes from Saint-Martin-de-Londres (SMF 203, Fig. 3A-C) and is the largest of all specimens.

AUM 474 is almost complete and only misses its premaxillary dorsal process. AUM 466 is more fragmentary being represented by the posterior area and the premaxillary dorsal process. In all cases, the premaxilla is taller than long. The external nares face anteriorly and according to AUM 466, which preserves the suture for the nasal, this bone participates in the posterodorsal margin of the external nares as in the holotype (Antunes, 1975). The ornamented lateral surface of the premaxilla consists of a distinct bony ridge that makes the vertical lateral margin of the naris. The anterior end of the premaxilla makes the ventral margin of the naris, is devoid of ornamentation and is visible in dorsal view. This area is flush

against the anterior margin of the premaxilla, where a few foramina open above the tooth row. The lateral border of the naris is marked internally by a narrow and vertical incision or narial recess, obvious in AUM 474 and SMF 203 (Figs. 2F, 3A). In ventral view, the suture for the maxilla is visible and forms the ventral margin of the narial canal, thus the maxilla attains the level of the last premaxillary alveolus. The complete premaxillary tooth row of AUM 474 and SMF 203 presents five alveoli (Figs. 2E, 3C), all of them subcircular in outline as in the holotype (pl. VII in Antunes, 1975). All the alveoli are separated from each other. They increase in diameter until the fourth, which is the largest. The last alveolus is of the same size as the third and is not in line with the other alveoli; it opens more dorsally, near the level of the premaxillary notch. Two excavated and deep pits are located immediately lingual to the tooth row between the second and third, then between the third and fourth alveoli. Anterior to the suture with the maxilla, the ventrolateral margin of the premaxilla bears a deep concave notch for reception of the largest dentary tooth as in the holotype (Antunes, 1975). In ventral view, this notch is delimited medially by a bony ridge, which stands out from the palatal surface of the premaxilla. Medial to this ridge, the palatal surface of the premaxilla is not flat but is deeply concave. Posteriorly along this concavity, a foramen opens ventrally on the premaxillary-maxillary suture as in *Pabwehshi pakistanensis* (Wilson et al., 2001) and *Hamadasuchus rebouli* (Larsson and Sues, 2007). This foramen is visible in AUM 474, AUM 466, SMF 203 and seems visible but broken in the holotype (pl. VII in Antunes, 1975).

Maxilla -Two fragments of maxillae are recognized from Robiac (RBN 2026) and Saint-Martin-de-Londres (SMF 181; Fig. 3). RBN 2026 represents a posterior fragment of a right maxilla hosting two broken ziphodont tooth crowns. SMF 181 is a larger portion of a right maxilla. In both specimens, the lateral surface of the bone is vermiculate. The maxilla RBN 2026 has a vertical lateral surface; however, as seen in anterior view, the lateral margin close to the tooth row is not vertical but is beveled and faces lateroventrally. Alveoli are

mediolaterally compressed. Medially, no palatal process of the maxilla is present but the suture for the ectopterygoid is visible. SMF 181 is a right element from the anterior region of the maxilla. The lateral surface of this maxilla is completely vertical being twice as tall as the complete associated tooth crown. Six alveoli are visible, which are all mediolaterally compressed and their long axis has an oblique direction. The largest of all may correspond to the third alveolus. Antunes (1975) reported that the second maxillary alveolus could be the largest but he observed that the third is incomplete. The collars of all alveoli are indented and in medial view, the alveolar walls are clearly individualized and run for most of the height of the maxilla. Foramina are visible dorsal to the alveoli along the medial maxillary surface. The palatal shelf is not well preserved but can be located far dorsally, at about mid-level of the maxillary height. In anterior view, the internal alveolar wall of the broken alveolus reveals a net of more or less vertical furrows.

Nasal -A fragment of the paired nasals is preserved from Aumelas (AUM 471; Fig. 2O, P). The dorsal surface of the nasal is slightly convex. In dorsal view, the vermiculate ornamentation is too dense to allow discerning the median suture as in the holotype (Antunes, 1975). The suture between the nasals consists of a straight line only visible in the ventral surface. Here, the nasals merge into a thin ridge following the suture. Opening ventrally, a pair of foramina is centered on each nasal. Each nasal is ventrally concave and their lateral wall is oblique. Laterally, the nasal accommodates a dorsoventrally high suture for the maxilla. Although the preserved portion of the nasals is short, the nasals narrow in their anterior portion.

Postorbital - A nearly complete left isolated postorbital comes from Aumelas (AUM 465; Fig. 2G-K) and closely resembles the postorbital of the Spanish *Iberosuchus macrodon* from Aldealengua (Ortega, 2004, unpublished). The dorsal surface is vermiculate. The postorbital has a distinct anterolateral process, the dorsal surface of which is demarcated from

the dorsal surface of the postorbital by a concave notch. Possibly, this process or facet would accommodate a palpebral bone (arrow in Fig. 2H, I, K). The sutures with the frontal and the squamosal are not preserved and it is thus impossible to assess the participation of the postorbital to the infratemporal fenestra. The postorbital builds the anterolateral margin of the supratemporal fenestra but does not overhang this fenestra. Medially, the posterior region of the supratemporal wall of the postorbital presents a wide sutural area for the reception of a lamina (stipple line in Fig. 2G). It is unknown whether this sutural area accommodates a medial contribution of the squamosal or a process of the laterosphenoid. Two small foramina are observed just anterior to this lamina. The postorbital is vertical and triangular in cross section, and slightly concave on each side. No foramen is detected on the bar. The postorbital suture for the jugal is strongly indented and is visible in lateral view. Accordingly, the jugal ascends far dorsally on the lateral margin of the bar whereas the postorbital reaches far ventrally on the medial side of the bar. Dorsally, the posterior margin of the postorbital is deeply inset into a concave and smooth structure. The postorbital bar is roofed by the anterolateral process of the postorbital.

Jugal - A left isolated jugal is identified from Aumelas (AUM 472; Fig. 2L-N). Its anterior process and part of the posterior process are not preserved. Its lateral surface bears faint vermiculate ornamentation as in other bones, rather than pits. The jugal is mediolaterally compressed, with an ovoid section in posterior view. The jugal process of the postorbital bar has the shape of a pillar, is mesiodistally compressed in cross section and devoid of ornamentation. In lateral view, the postorbital bar is nearly perpendicular, albeit slightly bent posteriorly to the posterior process of the jugal. The lateral margin of the postorbital bar is not inset from the lateral rugose surface of the bone but is flush against it. The postorbital bar described in the ziphodont ‘mesosuchian’ from La Livinière, Hérault, France is also not inset medially (Buffetaut, 1986). However, the two jugal specimens from La Livinière are

fragmentary and further comparison with the jugal from Aumelas is limited to the similar sculpturing pattern on the external surface. On the anterior corner of the bar of AUM 472, a bony ridge separates the bar from the lateral surface of the bone. Here, a small circular perforation (diameter = 2 mm) of the jugal is visible. In medial view, the large sutural area for the ectopterygoid indicates that the ectopterygoid posterior process is short, reaching at about the same level as the jugal bar. Dorsally, the entire medial surface of the bar accommodates a sutural area that could correspond to the descending process of the postorbital. Ventrally, the jugal presents a transverse trough bearing a set of equally spaced foramina. This trough is bordered by a thick ridge, delimiting the lateral surface from the ventral surface. In lateral view, the ventral margin of the jugal is not straight with the anterior region curving ventrally. However, the presence of a notch at the level of the ectopterygoid suture (see Pol et al., 2014) could not be assessed with confidence.

Dentition - All of the teeth, including those preserved in premaxillae and maxillae are ziphodont (Figs. 4, 5). They are labiolingually compressed with clearly individualized denticles on the mesiodistal carinae. The premaxilla AUM 466 hosts a replacement tooth, visible in the broken fourth alveolus (Fig. 5C). The tooth displays individualized denticles on the mesial carina. The distal carina is not visible. The denticles spread for the whole crown length. AUM 477 also hosts two replacement teeth with the same morphology; one in the last alveolus of the left premaxilla, another one is heavily damaged and occurs in a break of the bone. As an example of a large isolated tooth, SMF 206 (Fig. 4) shows that the crown is not symmetrical but the apex is distally curved. The crown is thick and flat compared to the mesial and distal margins, which gradually become thinner before merging along the carina.

Postcranial Skeleton:

Osteoderms - A number of osteoderms are preserved in Robiac (Fig. 6) and are identical to osteoderms reported from other localities in Spain (Martín de Jesús et al., 1987; Ortega, 2004). They display a tall ridge of variable extent surrounded by smaller ridges radiating around it. For example, in a series of small osteoderms (RBN 2018, 2020, 2019, 2021, 2012, 2023), one ridge runs for almost the entire length of the osteoderm and culminates into a spine near the anterior or posterior edge of the osteoderm where two lateral accessory processes join, so that in dorsal view, the ridge has the shape of a cross. This morphology of the ridge is also observed in larger osteoderms, but the main body of the osteoderms is flat, ovoid or rectangular in outline (RBN 2816, 2014, 2013). The whole outline of the osteoderm is strongly indented. The ventral surface is flat in large osteoderms and concave in small ones. Two osteoderms (AUM 458 and AUM 459, Fig. 6X-C1) are longer than wide with a nearly rectangular outline as reported in Buffetaut (1986) and Martin (2015). They bear a shallow median ridge associated to radiating vermiculate smaller ridges. Their long margin is serrated and the anterior margin is smooth and convex whereas the posterior margin is beveled in dorsal view.

4. Discussion

4.1. Assignment to the genus Iberosuchus

The record of non-eusuchian ziphodonts from the Eocene of Europe consists of fragmentary remains (Berg, 1966; Antunes, 1975; Buffetaut, 1986, Ortega et al., 1996). Since the first mention of Berg (1966), only two taxa have been formally erected, *Bergisuchus dietrichbergi* Kuhn 1968 and *Iberosuchus macrodon* Antunes 1975. Additional skull material from the Eocene of Tosalet del Morral, Lerida province, Spain has been considered to be reminiscent of *Iberosuchus macrodon* (Buffetaut, 1982; 1988; Ortega, 2004). Ortega et al.

(1996) reassigned to cf. *Iberosuchus* historical specimens consisting of mandibular remains, from the Eocene of Issel, France and Caenes, Spain based on tooth morphology and mandibular characters. Rossmann et al. (2000) reported two mandibles that were referred to *Bergisuchus* cf. *dietrichbergi* from the middle Eocene of Geiseltal, Germany. Other remains of uncertain affinities were reported by Buffetaut (1986) and consist of a jugal, vertebrae and isolated teeth from La Livinière, Hérault, France. Ortega et al. (1993) reported a fragmentary skull and mandibular elements from the Eocene of el Cerro de El Viso, Zamora, Spain. These later remains have been described in Ortega (2004) and they represent the most complete remains attributable to *Iberosuchus*.

Antunes et al. (1975) advanced that the material they described from Vale Furado could not be referred to *Bergisuchus dietrichbergi* because that taxon is characterized by a denser ornamentation of the premaxilla, by the absence of a notch for reception of the fourth mandibular tooth, and by smaller and possibly more numerous maxillary teeth. Ortega et al. (1996) also noted differences between cf. *Iberosuchus* and *Bergisuchus*, notably in the sculpturing, tooth count, shape of the dentary, and in the diameter of the fourth enlarged dentary tooth. At least based on sculpturing, the specimens from Aumelas, Robiac and Saint-Martin-de-Londres cannot be allied to *Bergisuchus dietrichbergi*. Buffetaut (1982; 1988) briefly reported a rostrum from the Eocene of Tosalet del Morral, Spain as being very similar to *Iberosuchus* but also bearing similarities with *Bergisuchus*. This important specimen was also discussed by Ortega (2004), and matches the morphology of the herein described material from southern France and Portugal in: 1) the same tooth counts and dental arrangement in the premaxillae; 2) similar tooth proportions in the maxilla, with a large third tooth followed by smaller fourth and fifth teeth; 3) teeth slightly compressed; 4) the presence of a notch at the level of the premaxillary-maxillary suture. The premaxillae from Aumelas and Saint-Martin-de-Londres closely match the holotype of *Iberosuchus macrodon* in

300 presenting the same alveolar count, a recess along the posterior and ventral narial borders, the
301 subcircular contour of the alveoli, and in being taller than wide. The largest maxillary
302 alveolus in the specimen of Saint-Martin-de-Londres is the third as in the specimen from
303 Tosalet del Morral. The presence of a palatal foramen at the premaxillary-maxillary suture is
304 attested in the premaxillae of Aumelas, Saint-Martin-de-Londres, Tosalet del Morral and Vale
305 Furado. Furthermore, the postorbital from Aumelas is comparable to the postorbital of
306 *Iberosuchus* from Salamanca, Spain (Ortega, 2004, Fig. 5.6) in presenting a notch that may
307 accommodate a palpebral. Finally, osteoderms described here from Languedoc with their
308 peculiar crested or vermiculate ornamentation (Fig. 6) have previously been reported from
309 Spain (Martín de Jesús et al., 1987; Ortega, 2004) or from France (Buffetaut, 1986; Martin,
310 2015) and provide additional evidence for a referral to the genus *Iberosuchus*.
311 Because they are directly comparable to the material from Portugal and Spain, the
312 specimens described here from the French middle Eocene localities of Aumelas, Saint-
313 Martin-de-Londres and Robiac are ascribed to *Iberosuchus* sp.. Although comparative
314 material is extremely limited, the jugal from Aumelas is similar to that of La Livinière
315 (Buffetaut, 1986). Both share the same sculpturing pattern, and a postorbital bar, which is not
316 inset from the lateral surface. It appears plausible that the material from La Livinière can be
317 ascribed to the genus *Iberosuchus* but until more material becomes available it is referred to
318 cf. *Iberosuchus*.
319
320 *4.2. Comparison with other ziphodont mesoeucrocodylians*
321 Although there is presently not enough characters to attempt a phylogenetic analysis,
322 the strong similarities between the specimens from Languedoc and *Iberosuchus* allow
323 comparisons with the three relevant groups with close affiliates to *Iberosuchus*:
324 Baurusuchidae, Peirosauridae, and Sebecidae (Ortega et al., 2000; Turner and Sertich, 2010;

Pol and Powell, 2011; Kellner et al., 2013; Pol et al., 2014). Baurusuchidae is a taxon restricted to the Cretaceous of Brazil, Argentina and possibly India (e.g. Montefeltro et al. 2011). Peirosauridae, which are mostly from the Cretaceous of Argentina and Brazil, includes seven species (see Martinelli et al., 2012) as well as a taxon from the Cretaceous of Morocco (Turner and Sertich, 2010) referred as *Hamadasuchus rebouli* by Larsson and Sues (2007). Sebecidae are exclusively known in the Cenozoic of South America (Colbert, 1946; Busbey, 1986; Buffetaut and Marshall, 1991; Gasparini et al., 1993; Paolillo and Linares, 2007; Pol and Powell, 2011; Kellner et al., 2013; Pol et al., 2014).

In *Iberosuchus*, the ziphodont dentition, the oreinirostral morphology, the presence of an enlarged third maxillary tooth (see also Buffetaut, 1988 for the specimen from Tosalet del Moral, Spain), the conical cross section of the premaxillary dentition, the presence of an antorbital fenestra (Ortega, 2004), the presence of a palpebral, and the excavated notch at the premaxillary-maxillary suture for reception of the enlarged fourth dentary tooth, all indicate a suite of shared characters with members of the Baurusuchidae, Peirosauridae and Sebecidae. In fact, among mesoeucrocodylians, the presence of labiolingually compressed and serrated teeth - the ziphodont condition of Langston (1975); see also Legasa et al. (1994) - arose in distantly related lineages, some with a possible terrestrial habit such as *Araripesuchus wegeneri* (Prasad and de Lapparent de Broin, 2002) and in some eusuchians (e.g. Rossmann, 1999). *Iberosuchus* shares other characters with Baurusuchidae, Peirosauridae and Sebecidae in possessing a palatal foramen on the premaxillary-maxillary suture as occurs in the following sebecids: *Lorosuchus nodosus* from the Paleocene of Argentina (Pol and Powell, 2011) and possibly in *Sebecus icaeorhinus* from the Eocene of Argentina (see plate 12 in Colbert, 1946) and *Ayllusuchus fernandezi* from the Eocene of Argentina (see fig. 2 in Gasparini, 1984). Such a palatal foramen is also present in the peirosaurid *Hamadasuchus rebouli* from the Cretaceous of Morocco (Larsson and Sues, 2007) and finally in *Pabwehshi*

pakistanensis from the Cretaceous of Pakistan, a taxon interpreted as a baurusuchid (Wilson et al., 2001). Among the Baurusuchidae, Peirosauridae and Sebecidae, the presence of an antorbital fenestra is variable and does not preferably indicate a particular affinity. For example, the antorbital fenestra is preserved in the peirosaurids *Pepesuchus deseae*, *Montealtosuchus arrudacamposi*, *Uberabasuchus terrificus*, *Hamadasuchus rebouli* and *Lomasuchus palpebrosus* (Campos et al., 2011; Carvalho et al., 2004; 2007; Larsson and Sues, 2007; Gasparini et al., 1991). The baurusuchids *Baurusuchus salgadoensis* and *Campinasuchus dinizi* possess an antorbital fenestra whereas *Stratiotosuchus maxhechti* and *Pissarrachampsa serra* lack this feature (Riff and Kellner, 2011; Montelfreto et al., 2011). An antorbital fenestra has not been identified in the Sebecidae, although two equivocal members *Zulmasuchus querejazus* (Buffetaut and Marshall, 1991) and *Bretesuchus bonapartei* (Gasparini et al., 1993) display a depression on the lacrimal, corresponding to the likely position of this fenestra. In addition, the antorbital fenestra has been tentatively identified in *Sahitisuchus fluminensis* (Kellner et al., 2013). The area is otherwise unknown in other sebecids such as *Ayllusuchus fernandezi* (Gasparini, 1984) or *Langstonia huilensis* (Langston, 1965). The anterolateral corner of the postorbital of *Iberosuchus* possesses a facet, possibly for the accommodation of a palpebral. A palpebral facet on the postorbital has been reported in the baurusuchid *Campinasuchus dinizi* (Carvalho et al. 2011), in the peirosaurid *Hamadasuchus rebouli* (Larsson and Sues, 2007) and in *Pepesuchus desea* (Campos et al., 2011). Complete palpebrals are known in the baurusuchids *Baurusuchus albertoi*, *Baurusuchus salgadoensis*, *Gondwanasuchus scabrosus* (Marinho et al., 2013), *Stratiotosuchus maxhechti* (Riff et al., 2011) and *Pissarrachampsa serra* (Montelfreto et al., 2011), and also in the peirosaurids *Lomasuchus palpebrosus* and *Montealtosuchus arrudacamposi* (Carvalho et al., 2007). Colbert (1946) described a triangular palpebral attached to the anterior margin of the orbit in the sebecid *Sebecus icaeorhinus* (possibly, a

375 posterior palpebral was present). Considering all those evidences, the presence of a ziphodont
376 dentition, a palatal foramen, an antorbital fenestra and palpebral, are widely distributed
377 characters among Baurusuchidae, Peirosauridae and Sebecidae. Nevertheless, *Iberosuchus*
378 also presents characters found in each of these three families and these are reviewed below.
379 With Peirosauridae, *Iberosuchus* displays two synapomorphies based on the
380 framework of Larsson and Sues (2007, p. 552): the presence of five premaxillary teeth and the
381 anterior two premaxillary alveoli nearly confluent. These characters are clearly visible in the
382 specimens from Aumelas (Fig. 2B, 2E) and Saint-Martin-de-Londres (fig. 3C), in the rostrum
383 from Tosalet del Morral (Buffetaut, 1982, fig. 1) and in the holotype of *Iberosuchus*
384 *macrodon* (Antunes, 1975, pl. VII, fig. 17) and relying on such characters would indicate a
385 peirosaurid affinity for *Iberosuchus*. However, the recently described peirosaurid
386 *Montealtosuchus arrudacamposi* does not have confluent premaxillary teeth and the specimen
387 assigned to *Hamadasuchus rebouli* (Larsson and Sues, 2007) possesses four premaxillary
388 alveoli only. Turner and Sertich (2010, p. 208) coded *Iberosuchus macrodon* on the basis of
389 the datamatrix of Ortega et al. (2000) and found that this genus shares with Peirosauridae the
390 extremely large perinarial fossa (also present in Baurusuchidae, e.g. Riff et al., 2011) and the
391 wedge-like process of the maxilla in lateral view at the premaxillary-maxillary suture.
392 However, comparing *Iberosuchus* with the best-represented members of the Peirosauridae
393 reveals several differences including: the premaxilla of *Iberosuchus* is much taller and
394 rostrocaudally shorter than in any known peirosaurid (i.e., *Montealtosuchus*, *Pepesuchus*
395 *desae*, *Peirosaurus*, *Uberabasuchus terrificus* or *Hamadasuchus rebouli*) and the pattern of
396 ornamentation differs with vermiculation versus pitted ornamentation in Peirosauridae. Also,
397 the dentition of Peirosauridae is conical to sub-conical in cross section but is never extremely
398 compressed, unlike in the maxilla of *Iberosuchus*. *Iberosuchus* also differs in the morphology
399 of the postorbital bar from any peirosaurid (e.g., *Hamadasuchus rebouli* in Larsson and Sues,

2007) because it is not even slightly inset but flushes along the lateral ornamented surface of the jugal (Fig. 2L). Unlike any peirosaurids, *Iberosuchus* sp. possesses an elevated rostrum and cf. *Iberosuchus* shows a small number of dentary alveoli (fourteen alveoli according to Ortega et al., 1996). Among peirosaurids, the dentary alveolar count attains eighteen alveoli (Larsson and Sues, 2007; Carvalho et al., 2007; Campos et al., 2011; Martinelli et al., 2012). As for postcranial elements, osteoderms have recently been reported in the peirosaurid *Montealtosuchus arrudacamposi*. Such osteoderms are unlike those described for *Iberosuchus* in presenting a quadrangular outline and an external ornamentation with cupules (Tavares et al., 2015). Therefore, no characters support an affinity of *Iberosuchus* with the Peirosauridae.

Iberosuchus resembles the Baurusuchidae in sharing the elevation of the rostrum, a vermiculate ornamentation, mediolaterally compressed maxillary teeth, an enlarged third maxillary alveolus and dentary dentition, a vermiculate pattern of ornamentation and osteoderms with a tall ridge and a rugose aspect. An autapomorphy of the Baurusuchidae is the extreme reduction of the number of premaxillary and maxillary alveoli (e.g., Montelfreto et al., 2010; Riff et al., 2011). In *Iberosuchus*, the presence of five premaxillary alveoli, more than five alveoli in the maxilla and a premaxillary palatal foramen discard a referral to the Baurusuchidae or to *Bretesuchus bonapartei* (Gasparini et al., 1993). *Pabwehshi pakistanensis* has been tentatively allied to the Baurusuchidae (Wilson et al., 2001) and is comparable to *Iberosuchus* in sharing a palatal foramen at the level of the premaxillary-maxillary suture, the morphology of the perinarial fossa, the elevated rostrum and the notch for reception of an enlarged dentary tooth. As with *Iberosuchus* or *Bergisuchus*, the affinities of *Pabwehshi pakistanensis* are only tentative because of the fragmentary nature of the material. However, the premaxillary tooth count and maxillary alveolar size precludes further affinities of *Iberosuchus* with *Pabwehshi pakistanensis*. The morphology of the postorbital bar in the baurusuchid *Pissarachampsa serra* is different from *Iberosuchus macrodon* from

Aldealengua, Spain (Ortega, 2004 unpublished) and from *Iberosuchus* sp. from Aumelas (Fig. 2G-K) in being slightly inset (Montefeltro et al., 2011). Although evidence to ally *Iberosuchus* to the Baurusuchidae on the basis of cranial elements is not supported, Martin (2015) highlighted the morphological similarity of European sebecosuchian osteoderms with those of *Baurusuchus* (Nascimento and Zaher, 2010; de Araújo Júnior and da Silva Marinho, 2013). Nevertheless, osteoderms have not been reported in the Sebecidae and similar osteoderms do also exist in non-sebecosuchian notosuchians, which may indicate that this morphology might be widespread within Notosuchia (Martin, 2015).

With the Sebecidae, *Iberosuchus* shares a vermiculate ornamentation, a vertical maxilla, an enlarged third maxillary alveolus, strongly compressed ziphodont teeth as well as characters exclusively found in the Sebecidae. The premaxilla of *Iberosuchus*, *Lorosuchus nodosus* and *Sebecus icaeorhinus* bear subconical premaxillary alveoli matching the subcircular outline of the opposing dentary alveoli (Colbert, 1946; Pol and Powell, 2011). The dentary is unknown in *Ayllusuchus fernandezi* but the premaxillary alveoli are also subcircular (fig. 2 in Gasparini, 1984). The postorbital bar of *Iberosuchus* is similar to that of *Sebecus icaeorhinus* (fig. 7 in Colbert, 1946) in presenting a vertical postorbital bar that is almost in line with the ornamented lateral surface of the bone. The postorbital bar of *Lorosuchus nodosus* has a similar position but unlike *Iberosuchus macrodon* or *Sebecus icaeorhinus*, it is ornamented at its base (Pol and Powell, 2011). The area of interest is not preserved in *Ayllusuchus fernandezi*, *Zulmasuchus querejazus*, *Barinasuchus arveloi* or *Langstonia huilensis*. Although the remains from Languedoc do not preserve a frontal, Pol et al. (2014) noted that a sagittal crest is present on the dorsal surface of the frontal of *Iberosuchus*, as in sebecids (Pol and Powell, 2011). Finally, the only difference to be detected is the premaxillary alveolar count, which is smaller in *Ayllusuchus fernandezi*, *Barinasuchus arveloi*, *Langstonia huilensis*, *Lorosuchus nodosus* and *Sebecus icaeorhinus* all possessing

four premaxillary alveoli (Gasparini, 1984; Paolillo and Linares, 2007; Langston, 1965; Pol and Powell, 2011; Colbert, 1946) versus five alveoli for *Iberosuchus*.

The relationships of *Iberosuchus* with other non-eusuchian ziphodont mesoeucrocodylians remain unsolved and more complete material is needed to allow testing a proper phylogenetic hypothesis. Nevertheless, limited clues available from the fragmentary specimens discovered from southern France hint at a possible affinity with the Sebecidae. This is in good agreement with previous phylogenetic results that recovered *Iberosuchus* and *Bergisuchus* as non-sebecid sebecosuchians (i.e., more derived than Baurusuchidae and close to the Sebecidae) (e.g. Ortega et al., 2000; Pol and Powell, 2011; Kellner et al., 2013; Pol et al., 2014). The quality of the European material is at the moment insufficient to clarify previous questions on the biogeographic origin of *Iberosuchus* (Buffetaut, 1982a; 1986; 1989). This matter could be further refined with a detailed update on *Iberosuchus* remains from Spain (Ortega et al., 1993; Ortega, 2004), with future discoveries from other European localities or from Paleogene deposits of North Africa, where another poorly known taxon with a ziphodont dentition, *Eremosuchus elkoholicus* was described (Buffetaut, 1982b; 1989).

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644

Figure captions.

Fig. 1. Map of southern France with localities (stars) yielding remains of *Iberosuchus* sp.: Aumelas, Saint-Martin-de-Londres, Hérault, and Robiac, Gard (this paper); and La Livinière, Hérault (Buffetaut, 1986) and Issel, Aude (Ortega et al., 1996). [planned for column page width]

Fig. 1. Carte du sud de la France montrant les localités (étoiles) ayant fournies les restes d'*Iberosuchus* sp.: Aumelas, Saint-Martin-de-Londres, Hérault, et Robiac, Gard (ce papier); et La Livinière, Hérault (Buffetaut, 1986) et Issel, Aude (Ortega et al., 1996).

Fig. 2. Skull remains of *Iberosuchus* sp. from the Lutetian of Aumelas, Hérault, France. Right premaxilla (AUM 466) in A, lateral and B, ventral views; right premaxilla (AUM 474) in C, lateral; D, dorsal; E, ventral; F, anterior views. Left postorbital (AUM 465) in G, medial; H, lateral; I, anterior; J, posterior; K, dorsal views. Left jugal (AUM 472) in L, lateral; M, medial; N, ventral views. Nasals (AUM 471) in O, dorsal; P, ventral views. In I, H and K, the arrow points to the palpebral articulation of the postorbital. In L and N, the arrows indicate the anterior direction. Abbreviations: en, external nares; fo, foramen; f pr, fossa on anterior face of premaxilla; nr, narial recess; on, occlusion notch; pr na, premaxillary process for nasal. [planned for page width]

Fig. 2. Restes crâniens d'*Iberosuchus* sp. du Lutétien d'Aumelas, Hérault, France. Prémaxillaire droit (AUM 466) en vues A, latérale et B, ventrale ; prémaxillaire droit (AUM 474 en vues, C, latérale, D, dorsale, E, ventrale et F, antérieure. Jugal gauche (AUM 472) en vues L, latérale, M, médiale et N, ventrale. Nasals pairs (AUM 471) en vues O, dorsale et P, ventrale. En I, H et K, la flèche indique l'articulation du palpébral sur le postorbitaire. En L et N, les flèches sont orientées vers l'avant. Abréviations: en, narines externes; f pr, fosse sur la

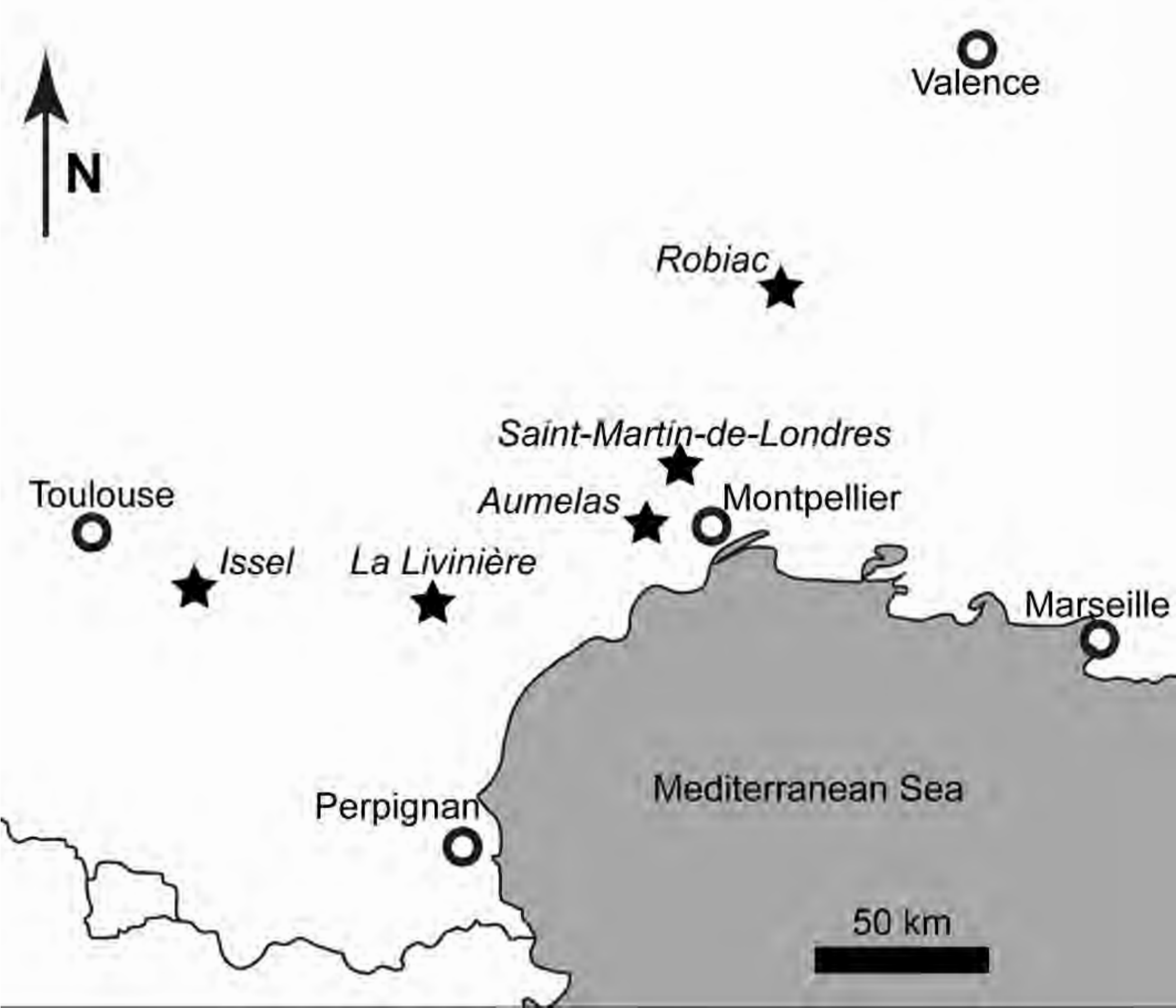
669 surface antérieure du prémaxillaire; nr, incision sur le bord de l'ouverture des narines ; on,
670 depression occlusale; pr na; processus du prémaxillaire pour le nasal.
671
672 **Fig. 3.** Skull remains of *Iberosuchus* sp. from the Lutetian-Bartonian of Saint-Martin-de-
673 Londres, Hérault, France. Right premaxilla (SMF 203) in A, anterior; B, dorsal; C, ventral
674 views. Right maxilla (SMF 181) in D, lateral; E, anterior; F, medial; G, ventral views.
675 Abbreviations: en, external nares; fo, foramen; f pr, fossa on anterior face of premaxilla; nr,
676 narial recess; pr na, premaxillary process for nasal; t, tooth. [planned for page width]
677 **Fig. 3.** Restes crâniens d'*Iberosuchus* sp. du Lutétien-Bartonien de Saint-Martin-de-Londres,
678 Hérault, France. Prémaxillaire droit (SMF 203) en vues A, antérieure, B, dorsale et C,
679 ventrale. Maxillaire droit (SMF 181) en vues D, latérale, E, antérieure, F, médiale et G,
680 ventrale. Abréviations : en, narines externes; fo, foramen; f pr, fosse sur la surface antérieure
681 du prémaxillaire ; f pr, fosse sur la surface antérieure du prémaxillaire ; pr na ; processus du
682 prémaxillaire pour le nasal ; t, dent.
683
684 **Fig. 4.** Isolated tooth of *Iberosuchus* sp. (SMF 206) from the Lutetian-Bartonian of Saint-
685 Martin-de-Londres, Hérault, France. A, labial; B, mesial; C, lingual; D, occlusal views.
686 [planned for page width]
687 **Fig. 3.** Dent isolée d'*Iberosuchus* sp. (SMF 206) du Lutétien-Bartonien de Saint-Martin-de-
688 Londres, Hérault, France en vues A, labiale, B, mésiale, C, linguale et D, occlusale.
689
690 **Fig. 5.** Details of the dentition of *Iberosuchus* sp. from the Lutetian of Aumelas, Hérault,
691 France. A, unnumbered isolated tooth in lingual view with inset view of the mesial carina
692 shown in (B) and bearing individualized denticles; C, close-up view of the mesial denticulate

carina of the broken tooth preserved in the fourth alveolus of the premaxilla AUM 466. [planned for column width]

Fig. 5. Détails de la dentition d'*Iberosuchus* sp. du Lutétien d'Aumelas, Hérault, France. A, Dent isolée sans numéro en vue linguale avec une vue détaillée de la carène mésiale (B) montrant les denticules individualisés; C, détail de la carène mésiale denticulée de la dent cassée préservée dans le quatrième alvéole du prémaxillaire AUM 466.

Fig. 6. Osteoderms attributed to *Iberosuchus* sp.. A–D (RBN 2019; E–H: RBN 2021; I–L: RBN 2013; M–P: RBN 2001 and Q–T: RBN 2002) from the Bartonian of Robiac, Gard, France ; dorsal, lateral, posterior and ventral views from left to right. U–W (SMF 188; X–Z: SMF 187); from the Lutetian-Bartonian of Saint-Martin-de-Londres, Hérault, France , dorsal, lateral and ventral views from left to right in. A1–C1 (AUM 459) from the Lutetian of Aumelas, Hérault, France, dorsal, lateral and ventral views.. [planned for page width]

Fig. 6. Ostéodermes attribués à *Iberosuchus* sp.; les cinq premiers proviennent du Bartonien de Robiac, Gard, France (A–D: RBN 2019; E–H: RBN 2021; I–L: RBN 2013; M–P: RBN 2001 and Q–T: RBN 2002) et sont présentés, de gauche à droite, en vues dorsale, latérale, postérieure et ventrale ; deux spécimens proviennent du Lutétien-Bartonien de Saint-Martin-de-Londres, Hérault, France, (U–W: SMF 188; X–Z: SMF 187) et sont présentés, de gauche à droite, en vues dorsale, latérale et ventrale. Un spécimen provient du Lutétien d'Aumelas, Hérault, France, également présenté en vues dorsale, latérale et ventrale (A1–C1: AUM 459).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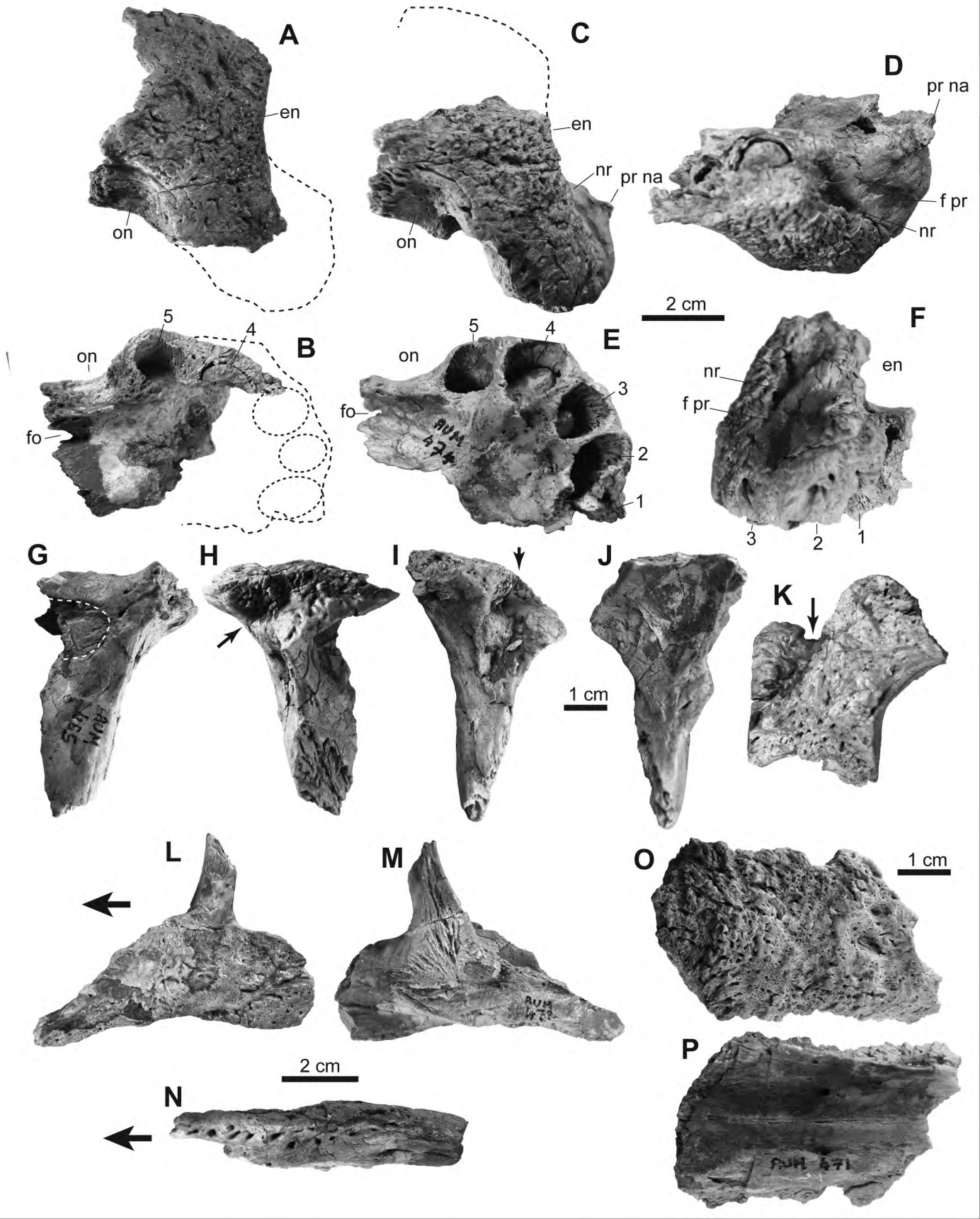
Valence
Robiac
Saint-Martin-de-Londres
Toulouse
Aumelas
Montpellier
Issel
La Livinière
Marseille
Mediterranean Sea
Perpignan
50 km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pr na
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pr na
f pr
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B
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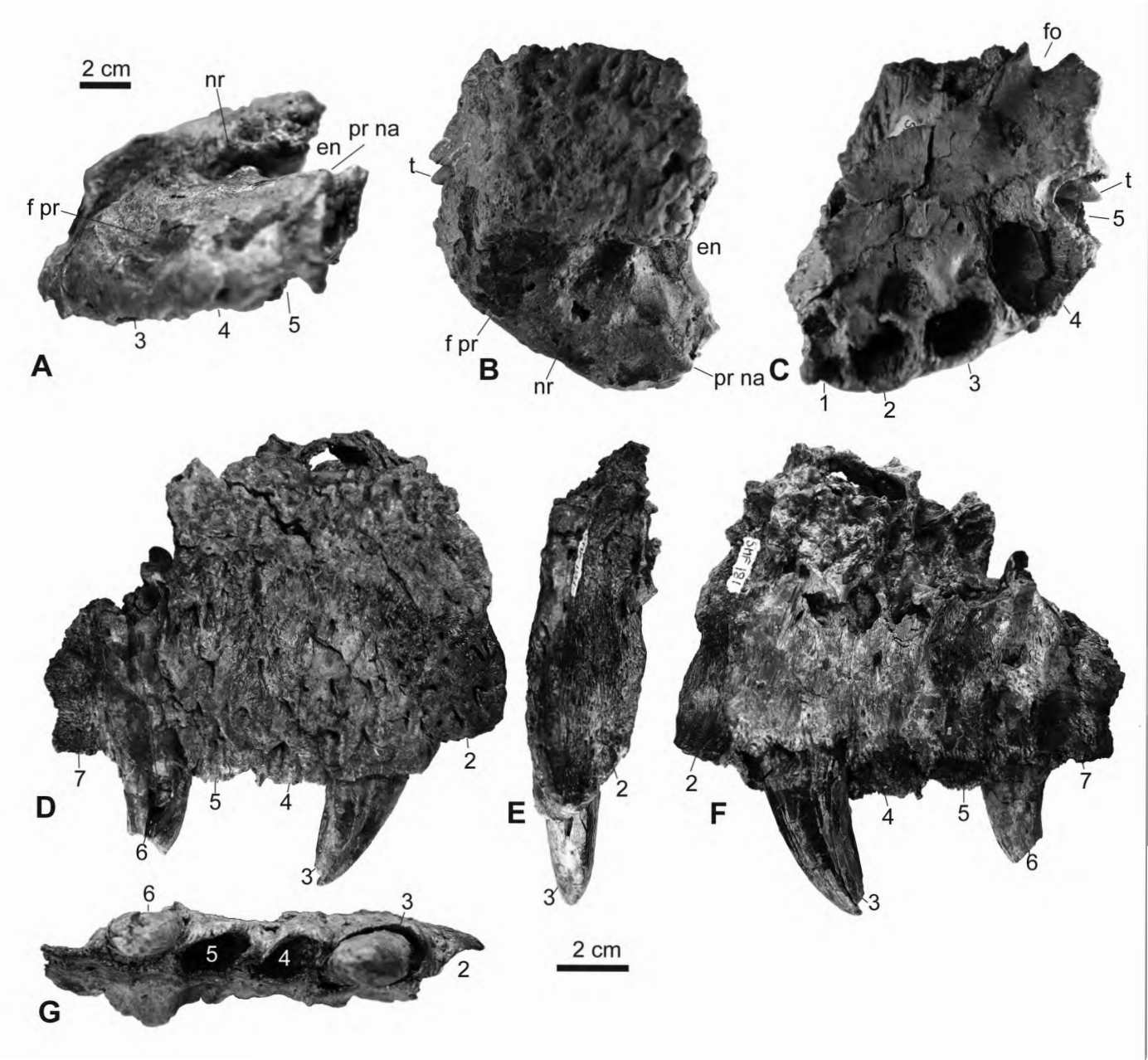
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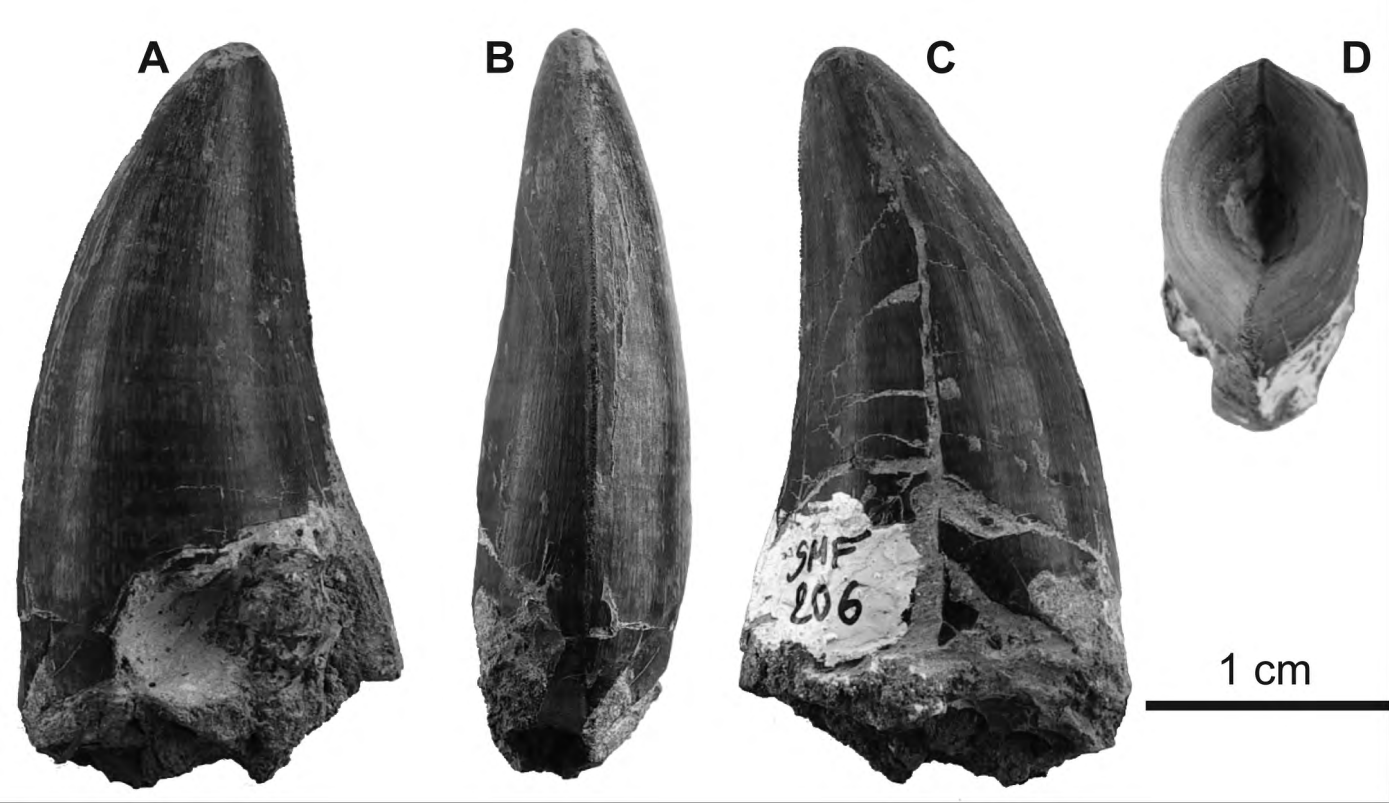
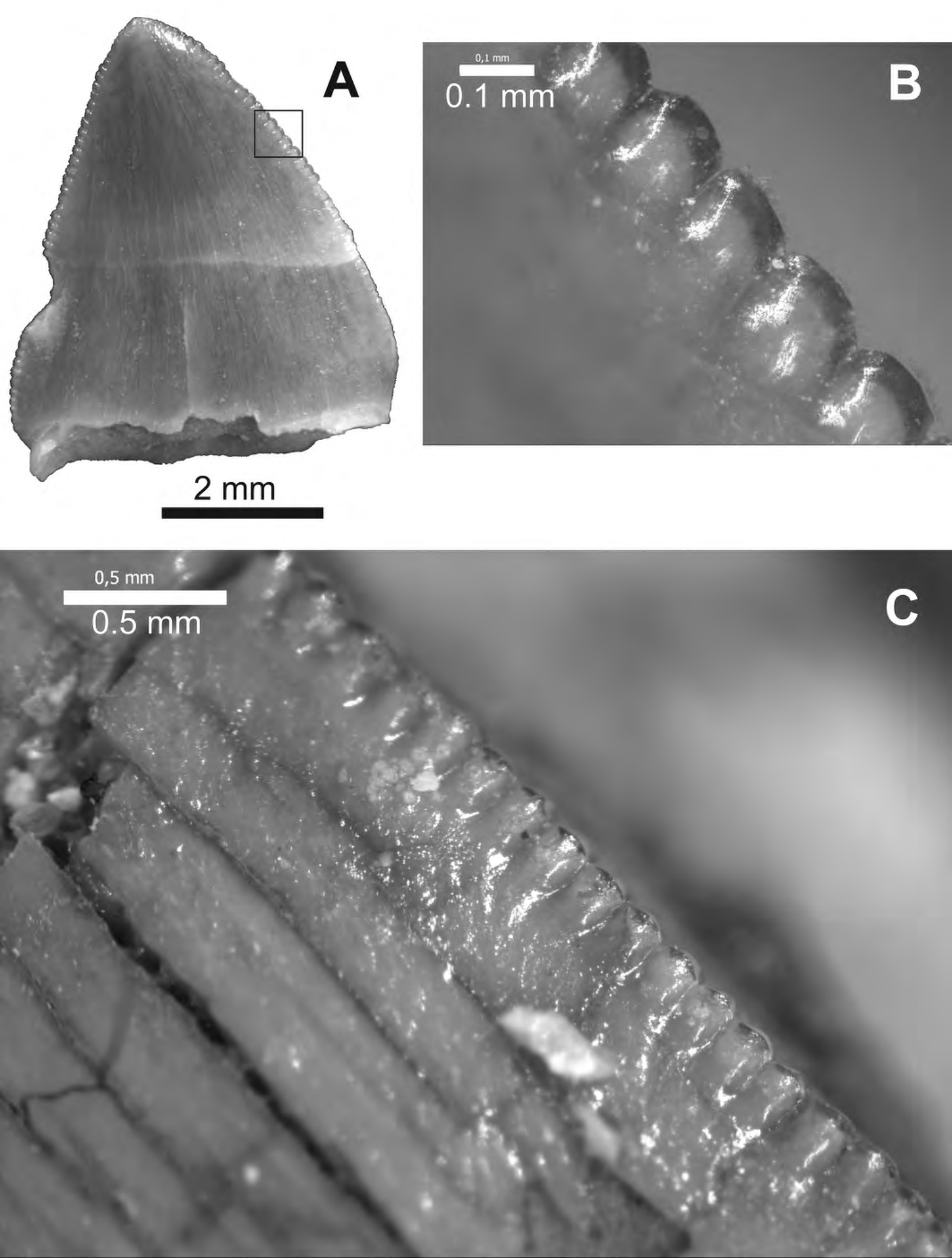

A
B
C
D
SMF
206
1 cm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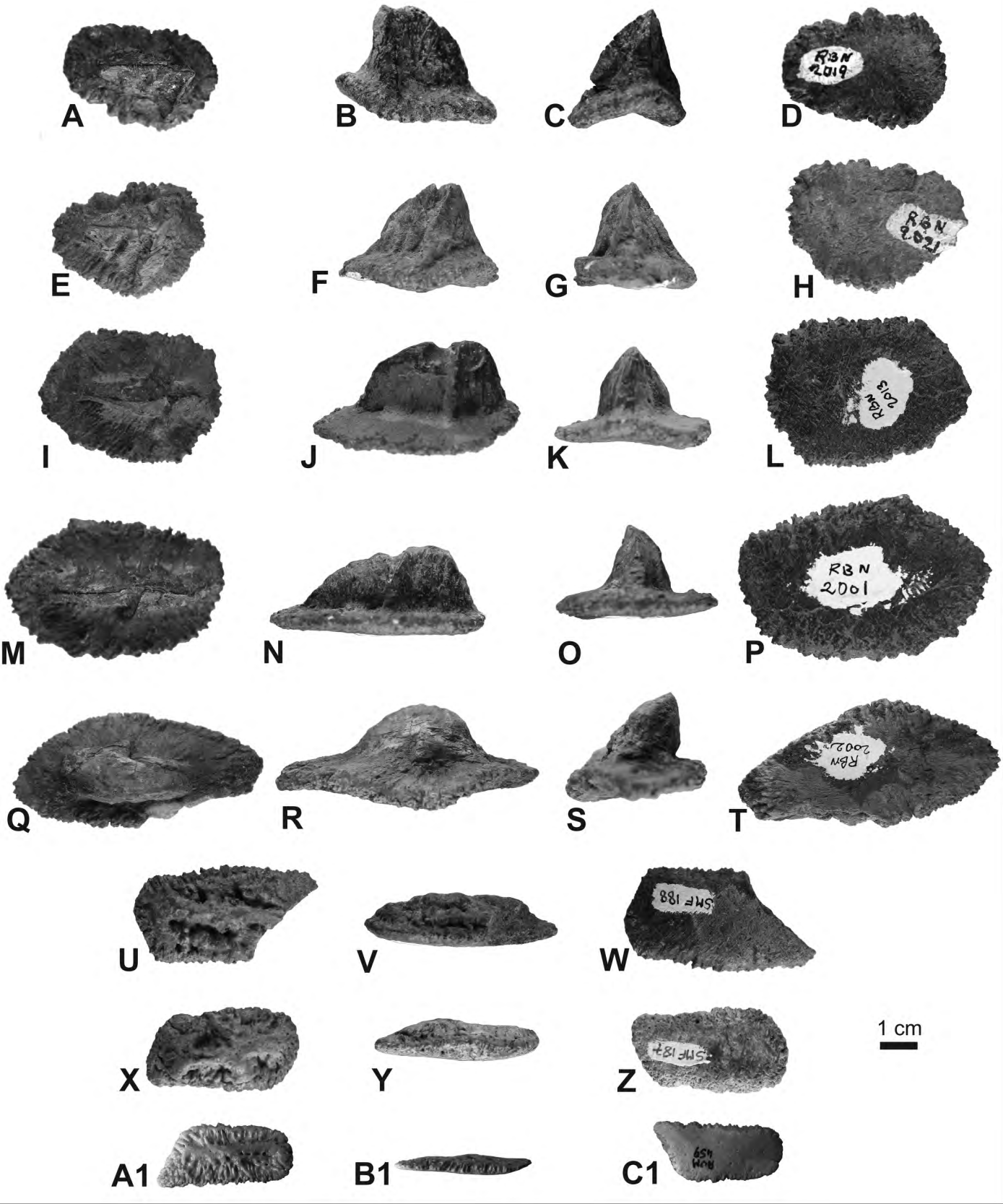
B
0,5 mm
0.5 mm
C


A
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SMF 187
1 cm
A1
B1
C1
RUM 459