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The fossil assemblage from Pontils, a middle Eocene primate-bearing locality from Northeastern Spain

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RH: MINWER-BARAKAT ET AL.—MIDDLE EOCENE FOSSILS FROM PONTILS (NE SPAIN)

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ABSTRACT—The Pontils fossil site (middle Eocene, Ebro Basin, Spain) includes several vertebrate-bearing levels situated in a sequence recording a continental to marine transition. Although the locality has been known since the 1980s and scarce mammal remains have been already documented, an intensive sampling has not been developed until now. This work presents the first results of the recent field campaigns carried out at this site. Seven levels have yielded significant vertebrate remains, revealing a diverse assemblage which includes chondrichthyans, actinopterygians, amphibians, crocodilians, squamates, metatherians, eulipotyphlans, apatotherians, chiropterans, rodents, artiodactyls, perissodactyls and primates, besides other non-vertebrate fossils. The Pontils assemblage indicates a mangrove swamp environment with warm and humid conditions and increasing marine influence towards the top of the sequence. Among mammals, primates are particularly diverse, including abundant remains of a minuscule, still undetermined omomyiform, and scarce teeth of *Pseudoloris*, *Necrolemur* and an undetermined anchomomyin. The occurrence of larger benthic foraminifera allows the assignment of Pontils to Shallow Benthic Zone 17 (Bartonian), solving the debate about the age of the locality, previously assigned either to the Bartonian or the Lutetian. These data, together with previous magnetostratigraphic analyses, allow correlation to chrons C18r or C18n.1r, constraining the age of Pontils to between 39.58 and 41 Ma. Therefore, the Pontils site represents a new reference section for the correlation of marine and continental biostratigraphy during the middle Eocene.

INTRODUCTION

The Eocene begins with some of the warmest temperatures of the Cenozoic, followed by a gradual cooling trend, punctuated by several hyperthermal events, and culminating in a rapid shift to icehouse conditions at the Eocene-Oligocene boundary (Westerhold et al., 2020). Several of the climatic changes within this epoch are associated with major events in vertebrate evolution. Many modern mammal orders (such as chiropterans, artiodactyls, perissodactyls, and euprimates) appeared and rapidly diversified during the Paleocene-Eocene Thermal Maximum (PETM, Domingo et al., 2009; Hooker, 2015; Smith et al., 2006), whilst at the Eocene-Oligocene boundary there is a major faunal turnover known as the *Grande Coupure*, during which a great number of taxa went extinct (Godinot, 2015; Hooker, 1986, 2010; Speijer et al., 2020; Stehlin, 1910). More specifically, during the Bartonian age, a global warming event known as the Middle Eocene Climatic Optimum (MECO) occurred between 40.5 and 40 Ma, during which sea surface temperatures rose by about 3–6 ºC (Bohaty and Zachos, 2003; Henehan et al., 2020; Speijer et al., 2020). This event has been well studied and is associated with marked changes in marine biota (Boscolo-Galazzo et al., 2015; Cramwinckel et al., 2019; D'Onofrio et al., 2021). In contrast, the effects of the MECO on terrestrial vertebrate faunas have not been analysed in detail, although it is assumed that this climatic optimum coincided with a peak in mammal diversity (Antoine et al., 2012; Bai et al., 2020; Figueirido et al., 2012). Specifically, Bartonian land mammal faunas are poorly known in Europe, due to the scarcity of vertebrate fossil sites of that age. In fact, the Mammal Paleogene Reference Levels (MP) are not adequately described for the Bartonian, and the age of some sites such as La Livinière-2, previously proposed as the reference locality for

MP15, remains controversial (Bonilla-Salomón et al., 2016; Comte et al., 2012; Speijer et al., 2020). In this context, the description of new Bartonian terrestrial faunas is important to evaluate the effects of the MECO on vertebrate diversity.

The locality of Pontils represents an unusual example of a middle Eocene terrestrial vertebrate site in contact with marine sediments. Located in the Ebro Basin, province of Tarragona, NE Spain (Fig. 1), the Pontils section consists of alternating limestones, marls and lignite, which represents a transitional continental to marine sequence. This locality was first noted by Anadón (1978) and Anadón and Feist (1981), who described a charophyte assemblage including *Raskyella vadaszi, R.* aff. *vadaszi, Harrisichara* aff. *brevipes, H. gigantea, Nitellopsis (Tectochara) major* and *Maedleriella leiostachys*, and briefly mentioned the presence of rodent remains. Soon after, Anadón et al. (1983) focused on the nannoplankton and benthic foraminifera from the upper levels of that section, pointing out the exceptional potential of the site for correlating continental and marine biochronological timescales. Regarding vertebrates, Anadón et al. (1983) referred to the presence of several taxa from two different levels, Pontils-26 and Pontils-38. From PO-26, these authors described a small collection of rodents (15 teeth), erecting a new species (*Pseudoltinomys cosetanus*) and documenting the occurrence of *Paradelomys* sp., *Elfomys* sp. and *Suevosciurus* cf. *romani*. They also mentioned the presence in this level of undetermined crocodilian and lipotyphlan remains. From PO-38, Anadón et al. (1983) mentioned the presence of very scarce remains of undetermined insectivores (Lipotyphla indet.) and primates (Omomyidae indet.), although they did not provide any description or illustration of these taxa.

The age of the Pontils fossil site has been discussed since its discovery in the 1980s, although the scarce mammal remains recovered from this locality did not allow detailed correlations with other well-dated vertebrate sites, and thus most interpretations were based on other fossil groups. The first works describing this locality (Anadón and Feist, 1981; Anadón et al., 1983) assigned the continental levels of the Pontils section (Bosc d'en Borràs Formation) to the upper Bartonian on the basis of the recovered charophyte and rodent remains; the overlying marine levels of the Collbàs Formation were also assigned to the late Bartonian in age, being correlated to the P14-15 zone of planktonic foraminifera and to the NP17 zone of calcareous nannoplankton (Cavalier and Pomerol, 1977; Hardenbol and Berggren, 1978). However, later works (Cavagnetto and Anadón, 1996) considered that the continental levels of the Pontils section corresponded to the early Bartonian, whereas the overlying marine levels were assigned to the middle Bartonian on the basis of their foraminifera and nannoplankton assemblages.

Later on, Lévêque (1993) published a correlation of the main European Eocene and Oligocene vertebrate localities with the geomagnetic polarity time scale. Although this work did not include any paleomagnetic analysis developed at the Pontils section, this author correlated the Pontils fossil site with chron C18n based on previously reported planktonic foraminifera and calcareous nannoplankton from the marine deposits overlying the vertebrate bearing levels, and assigned an age between 38.5 and 40 Ma to the Pontils fossil site. However, paleomagnetic analyses carried out in this section some years later (Legendre and Lévêque, 1997) revealed that the continental levels bearing vertebrate remains in the Pontils section (PO-26, PO-38) correspond to a reversed-polarity interval, and must be therefore correlated to chron C18r (early Bartonian), with a slightly older age than previously considered (i.e., between 40 and 41 Ma).

In contrast, Beamud et al. (2003, 2012) and Beamud (2013) correlated the mammal-bearing levels of the Pontils section to chron C19n (late Lutetian) on the basis of new paleomagnetic analyses. Nevertheless, the samples supposedly taken from the Pontils locality do not correspond with the actual location of the fossil site: according to fig. S2.2 of Beamud (2013), the Pontils fossil site is mistakenly placed more than 3 km to the SW of the actual position of the locality. Moreover, in the stratigraphic column represented in fig. S2.4, Beamud (2013) placed the Pontils fossil site close to the base of the Bosc d'en Borràs Formation, whereas the vertebrate-bearing levels from Pontils are near the top of this formation, being just overlain by the marine marls of the Collbàs Formation (see Fig. 2). In addition, the assignment of the Pontils fossil site to a normal-polarity interval (C19n) contradicts the previous data of Legendre and Lévêque (1997), who placed the vertebrate-bearing levels of Pontils in a reversed-polarity interval. Consequently, we cannot consider the correlation of the Pontils site with chron C19n proposed by these authors to be valid.

It is worth noting that the locality of Pontils was assigned the to the MP15 Mammal Paleogene Reference Level by Schmidt-Kittler (1987), and its equivalence in age with La Livinière-2, considered the reference locality of the MP15, has been generally assumed in the literature (Aguilar et al., 1997; Beamud et al., 2003, 2012; Legendre and Lévêque, 1997; Lévêque, 1993). Such a correlation was based on the supposed presence of *Pseudoltinomys cosetanus* at La Livinière-2. However, Comte et al. (2012) questioned the attribution of the material from La Livinière-2 to *P. cosetanus*, and pointed out that the scarce rodent remains from La Livinière-2 are very similar to those from Robiac (MP16). Therefore, these authors argued that La Livinière-2 must no longer be considered as the MP15 reference level, but must be replaced by another fossil site with an age intermediate between Egerkingen and

Robiac, such as Chéry-Chartreuve or some of the fossil-bearing levels from the Sant Jaume de Frontanyà section (see also Bonilla-Salomón et al., 2016). In addition, Comte et al. (2012) also questioned the correlation of the Pontils fossil site with chron C18r reported by Legendre and Lévêque (1997), stating that the reversed-polarity interval recorded at Pontils could either be correlated to chrons C18r or C17r, this latter corresponding to the late Bartonian (c. 38 Ma). To summarize, although most authors agree in correlating the vertebrate-bearing site of Pontils with the Bartonian, previous data are not conclusive enough to provide a precise dating for this locality. Here we present a revised stratigraphy and faunal list for the Pontils section based on new fieldwork, with the additional aim of confirming the age of this site.

During the 1990s, Cavagnetto and Anadón (1995, 1996) studied the marine marls that overlie the vertebrate-bearing levels of the Pontils section, describing a diverse pollen assemblage and providing a first paleoenvironmental reconstruction for this fossil site. These authors inferred the existence of a complex mangrove swamp with different vegetational zones, with plants indicative of an intertidal zone (*Avicennia alba, A. marina*), tidal channel banks (*Aegiceras*), and landward mangrove zone (*Acrostichum, Pelliceria, Brownlowia, Heritiera, Sesuvium*). They also identified *Nypa*, which probably lived further inland. Today, most of these taxa are thermophilous plants restricted to tropical and subtropical climates, which indicates warm and humid conditions for the Pontils site, an interpretation corroborated by the absence of plants typical of temperate regions.

In contrast to these detailed paleobotanical studies, the vertebrate remains from Pontils remained unstudied since the 1980s. Only brief mentions of the mammal fauna appeared in some compilations, these usually highlighting the presence of a small undetermined omomyid primate, or corroborating the attribution of the rodent assemblage to the Bartonian (Antunes et al., 1997; Bonilla-Salomón et al., 2016; Comte et al., 2012; Legendre and Lévêque, 1997; Marigó et al., 2014).

Thirty years after its discovery, we resumed fieldwork at this fossil site, specifically with the aim of recovering vertebrate remains. Field campaigns were carried out in 2012 and 2016, during which large amounts of sediments from different levels across the Pontils section were sampled. After sample processing, abundant vertebrate remains were identified, revealing a much more diverse assemblage than previously known, including chondrichthyans, actinopterygians, amphibians, crocodilians, squamates, metatherians, eulipotyphlans, apatotherians, chiropterans, rodents, artiodactyls, perissodactyls and four different primate species. Here we present the results of these field campaigns, from which only very preliminary observations of the ichthyofauna and herpetofauna have been published to date (Blanco et al., 2017a; Bolet et al., 2017). Although focusing on the vertebrate remains, other fossil groups (charophytes, foraminifera, marine invertebrates) are also here briefly described, especially in order to help establish the age of this fossil site and the paleoenvironmental setting.

GEOLOGICAL CONTEXT

The Pontils section was first described by Anadón (1978) and crops out west of the provincial road T-201, 300 m to the north of the village of Pontils, in Tarragona Province (Catalonia, NE Spain, Fig. 1). The section is located in the SE sector of the Ebro Basin, which is bounded by the Pyrenees to the north, the Iberian Chain to the southwest, and the Catalan Coastal Ranges to the southeast. The infilling of the basin comprises up to 5000 m of marine and continental sediments ranging in age from the Late Cretaceous to the Middle Miocene (Busquets et al., 2003, Garcés et al., 2020). Until the late Eocene, the basin was open to the Atlantic Ocean through the Bay of Biscay. During this time, sedimentation was mainly marine in the northern part of the basin and predominantly continental (with some marine episodes) in the southern sector. The marine connection ended during the Priabonian (~36.0 Ma; Costa et al., 2010). From the late Eocene to the Late Miocene, the Ebro Basin displayed an endorheic drainage system, with distributive alluvial systems fed from the tectonically active surrounding ranges, changing laterally to lacustrine systems (Agustí et al., 1987; Barberà et al., 2001; Sáez et al., 2007). The basin infill corresponding to this continental phase consists of alluvial, fluvial and lacustrine deposits, in which several vertebrate sites have been identified (Agustí et al., 1987; Anadón et al., 1987; Crusafont-Pairó, 1967; Cuenca et al., 1992; Köhler and Moyà-Solà, 1999; Minwer-Barakat et al., 2013, 2016; Vianey-Liaud et al., 2019).

In the studied area, Paleogene deposits are divided into several lithostratigraphic units (Anadón, 1978; Beamud et al., 2012; Cavagnetto and Anadón, 1996; Costa et al., 2013; Fig. 2). The Mediona Formation (upper Thanetian) consists of red mudstones and sandstones with calcareous paleosoils. This unit is overlain by the Orpí Formation, consisting of marine limestones early Eocene in age (early Ypresian). Overlying the Orpí Formation, the continental Pontils Group consists of mudstones, sandstones, conglomerates, limestones and gypsum, up to 870 m thick, which was deposited from the Ypresian to the Bartonian in diverse non-marine environments: fluvial, lacustrine, palustrine and sabkha (Anadón, 1978; Anadón and Feist, 1981; Cavagnetto and Anadón, 1996). In the study area, the Pontils Group is subdivided in several units: the Santa Càndia, Carme, Valldeperes and Bosc d'en

Borràs formations, the latter mainly consisting of palustrine limestones. The Bartonian transgression led to the deposition of a thick sequence of marine deposits (Santa Maria Group), which is subdivided into three formations: the Collbàs Formation (limestones, marls, sandstones and fine conglomerates deposited in a nearshore environment) has been attributed to the middle-late Bartonian on the basis of foraminifera and nannoplankton (Anadón et al., 1983; Ferrer, 1971), whereas the marls of the Igualada Formation and the coralline limestones of the Tossa Formation are assigned to the Priabonian (Beamud et al., 2012; Costa et al., 2013). Above the Santa Maria Group, the alluvial Sant Miquel de Montclar Formation consists of conglomerates with interbedded sandstone and mudstone lenses, changing laterally to the distal alluvial and fluvial facies of the Artés Formation, assigned to the late Eocene and early Oligocene.

The section of Pontils (Fig. 2) consists of a nearly 100 m thick alternation of limestones, marls, clays and lignite (Bosc d'en Borràs Formation). The lowermost 25 m correspond to white, grey and pink massive and nodular limestones. Upwards, 20 to 50 cm thick levels of yellowish/grey marls and lignite alternate with the limestones, among them some of the levels sampled in this study, namely Pontils-19, 20, 22, 23, 25 and 26 (PO-19 to PO-26). Above PO-26, a thick (4.5 m) body of red clays crops out, followed by a new alternation of different colored limestones and marly limestones with some intercalations of thin levels of grey marls (e.g., PO-33). Towards the top of the section, a thick body of lignite and marls, showing centimetric-millimetric lamination, crops out. Its base (lower 40 cm) consists of lignite and dark marls with gastropod shells (PO-38). Towards the top, 40 cm of dark brown marls appear (PO-38 TOP), overlain by 50 cm of light brown marls (PO-39B), which locally show identifiable macrovertebrate remains (PO-39A). This level marks the top of the

Bosc d'en Borràs Formation. The uppermost levels of the section correspond to the marls and marly limestones of the Collbàs formation; only one level was sampled in this unit (PO-40), corresponding to yellowish marls with identifiable marine invertebrates (mainly bivalve shells).

MATERIAL AND METHODS

Fieldwork on the Pontils section focused especially on the recovery of small vertebrate remains, and therefore large amounts of sediments were taken from each relatively thick marl or lignite level suitable for screen-washing treatment. After the preliminary results of the 2012 field campaign, those levels that yielded abundant vertebrate remains were sampled again in 2016. The total amount of sediment recovered from each level is indicated in Table 1. The Pontils section crops out on a slope above a road, and is covered entirely by a metallic net that protects the road from rock falls (Fig. 3). For the purposes of investigating the section, we were permitted by the provincial government to remove the protective net, but only for a short period of time. Therefore, sampling was limited to small patches around selected points and restricted to a few days in each field campaign. A single point was sampled from each level, except for PO-39, from which two points were sampled. PO-39A corresponds to large mammal remains (artiodactyls and perissodactyls) that were identified in situ and recovered manually, while sample PO-39B is a sediment sample taken from a different point within the same stratigraphic level, from which small vertebrate remains were obtained.

Lignite samples (e.g., PO-38) were particularly difficult to break up for screen-washing, and several chemicals (acetic and formic acids, hydrogen peroxide) were tested in small fractions in order to facilitate dissolution. None of these proved effective, and subsequently all samples were screen-washed with only water, using three superposed meshes of 2.0, 1.0 and 0.5 mm gauge. A small fraction (1 kg) of the sample recovered from the marine marls of the Collbàs Formation (PO-40) was screen-washed through 250 and 63 µm sieves to recover microfossils, particularly foraminifera. No secondary treatment was applied to the concentrates resulting from the screen-washing. Fossils were picked from the dry residues with the aid of a binocular microscope.

Micrographs of primates, rodents, metatherians, eulipotyphlans, apatotherians, chiropterans, charophytes, most chondrichthyans and actinopterygians and some crocodyliforms were taken using the Environmental Scanning Electron Microscope (ESEM) Quanta 200 FEI at the Universitat de Barcelona (UB). Images of squamates and some fishes were taken with a Leica stereoscopic binocular with an integrated camera. Most crocodyliform remains were photographed with a Nikon D610 DSLR camera and a Sigma 105 mm macro lens. Artiodactyl and perissodactyl teeth were photographed with a Panasonic LUMIX DC-TZ90 camera with LEICA Optical; in order to enhance the visualization of the fossil morphology due to their dark color, these remains were coated with ammonium chloride before being photographed. To view internal structures, larger foraminifera were sectioned along the equatorial plane and imaged using an Olympus stereomicroscope and camera. Scanning Electron Micrographs (SEM) of smaller benthic foraminifera were taken at the University of Zaragoza. All the described specimens are curated at the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain). Identification of teeth follows conventional nomenclature, with capital letters ‘I’, ‘C’, ‘P’ and ‘M’ for upper incisors, canines, premolars, and molars, respectively, and lowercase ‘i’, ‘c’, ‘p’ and ‘m’ for lower incisors, canines, premolars, and molars, respectively. Deciduous teeth are prefaced with a capital ‘D’ or lowercase ‘d’ for upper and lower teeth, respectively.

Institutional Abbreviations—IPS, Institut de Paleontologia de Sabadell (former name, used until 2006, of the current Institut Català de Paleontologia Miquel Crusafont).

RESULTS

From the levels sampled in the 2012 season, PO-19, 20 and 26 did not yield identifiable vertebrate remains and PO-23 produced only a few fragments of teeth of indeterminate mammals, whereas PO-22, 25, 33, 38, 38 TOP, 39 and 40 yielded significant vertebrate remains. These latter levels were resampled in 2016. Figure 4 summarizes the vertebrate groups identified from each sampled level. Some general trends can be observed, e.g., amphibians are only present in PO-22 (the level with the least marine influence), whereas crocodyliforms have been identified from all levels except PO-33. Chondrichthyan and actinopterygian remains were scarce in PO-38 TOP and abundant in PO-39 and PO-40, pointing to an increased marine influence towards the top of the section. Large mammal remains (artiodactyls and perissodactyls) were only recovered from PO-39 and PO-40 (in the latter level only represented by three artiodactyl teeth). Table 2 provides a list of the vertebrates identified from each of the sampled levels, including determinations from Anadón et al. (1983).

In addition to vertebrates, charophyte gyrogonites were identified from all sampled levels, and they were particularly abundant in PO-25. Scarce larger benthic foraminifera have been found in all levels from PO-19 to PO-38, and were most abundant in PO-39. In PO-40, screen-washing with fine sieves (250 and 63 µm) resulted in the recovery of abundant smaller benthic foraminifera. Finally, marine invertebrate remains (mainly bivalves) were identified principally from PO-40 as well as from PO-39.

Primates

A minimun of four primate species can be recognized at Pontils. The most abundant one is a very small microchoerine omomyid recorded from PO-22, 25, 33, 38, 38 TOP and 39. It is smaller than *Pseudoloris* or any other known European microchoerine (Fig. 5). The m1 and m2 (IPS105623, IPS105592; Fig. 5A, B) have a nearly rectangular outline; the trigonid is open lingually and similar in width to the talonid; the paraconid is distinct, while the hypoconulid is weak or absent. The m3 (IPS105592, IPS105597; Fig. 5B, C) has no paraconid; the paracristid joins the metaconid and closes the trigonid basin, which is very short; the entoconid is weak and the hypoconulid lobe is large and protrudes distally. All the upper molars are triangular and display a simple dental pattern (IPS124931, IPS86811; Fig. 5D, E): they have a very broad stylar shelf, the paraconule and metaconule are feeble or even absent, and there is no trace of a hypocone. This diminutive primate has not been recorded elsewhere, and a more detailed study will permit the description of a new species.

Some dental elements found in the same levels (PO-22, 25, 33, 38, 38 TOP and 39) can be ascribed to the genus *Pseudoloris*, common in middle and late Eocene localities from the Iberian Peninsula, France, Germany, and Switzerland (Crusafont-Pairó, 1967; Godinot, 1983, 1988a; Köhler and Moyà-Solà, 1999; Minwer-Barakat et al., 2010, 2012, 2013, 2015a, 2017a; Thalmann, 1994). The material from Pontils shows features typical of this genus such as lower first and second molars (IPS86802; Fig. 5F) with sharp cuspids, trigonid narrower than the talonid, well-developed buccal cingulid, low paracristid, no distinct tubercular paraconid and a pointed hypoconulid, and an m3 (IPS105527; Fig. 5G) with a narrow and protruding hypoconulid lobe. In the upper molars (IPS105596, IPS86804; Fig. 5H-I) paracone and metacone are similar in size, the paraconule is small, the metaconule is crescentiform and the hypocone is small but distinct and isolated from the protocone. The only recovered upper incisor (IPS105621; Fig. 5J) is buccolingually compressed and has an acute apex and a prominent talon; its buccal side is nearly flat, and the lingual side shows a marked cingulum. The size and morphology of the studied teeth are roughly similar to those of *P. pyrenaicus* from Sant Jaume de Frontanyà-3C (Minwer-Barakat et al., 2010) and *P. parvulus* from Sossís (Minwer-Barakat et al., 2015a). Further study is needed to identify these remains to the species level.

A single m3 of a medium-sized anchomomyin was recovered from PO-38 (IPS105619; Fig. 5K). It is very close in size to the genus *Mazateronodon*, larger than *Anchomomys* and *Nievesia*, and smaller than *Buxella* and *Periconodon* (Godinot, 1988b, 1998; Marigó et al., 2010, 2011, 2013). The metaconid is much higher than the protoconid and a premetacristid encloses the trigonid basin from the lingual side.

There is a hint of a minuscule paraconid where the premetacristid and the paracristid meet. This m3 hypoconulid lobe does not protrude much distally, with a hypoconulid closer to the entoconid than to the hypoconid. The m3 proximal and distal roots are fused at the base of the tooth.

Finally, a fourth primate is represented only by a fragment (trigonid) of a lower molar from PO-33 (IPS105569; Fig. 5L). It could belong either to an m2 or an m3, and shows the enamel wrinkling typical of the microchoerine genera *Necrolemur* and *Microchoerus*. Although its incompleteness prevents taking measurements, direct comparison shows that this tooth is larger than those of *Necrolemur anadoni* from Sant Jaume de Frontanyà-1 (Minwer-Barakat et al., 2015b) and *N.* aff. *anadoni* from La Verrerie de Roches (Minwer-Barakat et al., 2017a), similar in size to *Necrolemur antiquus* from La Bouffie (Godinot, 2003) and smaller than *Microchoerus hookeri* from Sossís (Minwer-Barakat et al., 2017b). This specimen is therefore identified as *Necrolemur* sp.

Rodents

At least five different species are present among the rodent remains obtained in the new sampling of the Pontils section. As was the case of the material from PO-26 studied by Anadón et al. (1983), the predominant taxon in most of the new sampled levels is *Pseudoltinomys cosetanus*, which is present in all levels from PO-22 to PO-39. The type material of this species comprised exclusively molars, and the morphology of the premolars remained unknown. The new material from Pontils includes both permanent and deciduous premolars. These are smaller than the molars and the DP4 is trapezoidal in outline with a complete protoloph with a very small paraconule (IPS105540; Fig. 6A), a long anteroloph that reaches the base of the paracone, a discontinuous mesoloph, and a metalophule that is isolated from the hypocone. The P4 has a reduced anteroloph (IPS105691; Fig. 6B), a protoloph that is not connected to the protocone, a mesoloph that is discontinuous and a metalophule II (for the anatomical terminology, see Bonilla-Salomón et al., 2016) connected to the posteroloph. The lower premolars are narrow anteriorly, with well-developed protoconid and metaconid, a postmetacristid that is always well developed, and a mesolophid that is short in most specimens (IPS105601; Fig. 6F). The molars show generally the same morphology as in the type material. There are no size differences between levels, although there is an increase in the length of the mesoloph and mesolophids from older to younger levels.

A second form is represented by just two specimens from PO-22 (IPS108650) and PO-25 (IPS105546) (Fig. 6J-K). These specimens are significantly larger than *P. cosetanus* and fit within the size ranges of *P. crebrum* from Mazaterón (Peláez-Campomanes, 1996), *P.* aff. *crebrum* from Les Alleveys (Hooker and Weidmann, 2007) and *P. phosphoricus* from Perrière and Lavergne (Comte et al 2012). Morphologically the material is close to *P. cosetanus* and to *P. crebrum* in the poorly developed mesoloph (better developed in *P.* aff. *crebrum*) and mesolophid, and the connection between the sinus and the syncline II (absent in *P. phosphoricus*). The scarcity of the material does not allow a more precise comparison and we therefore assign these specimens to *Pseudoltinomys* sp.

Some teeth found in PO-22 and 38 are assigned to the genus *Paradelomys*. The p4 from PO-22 (IPS105506; Fig. 6L) is similar in size, morphology and enamel wrinkling to the specimen of *Paradelomys santjaumensis* from Sant Jaume de Frontanyà 1 (SJF-1) described by Bonilla-Salomón et al. (2016). However, the entolophid is complete in *P. santjaumensis*, connecting the entoconid to the hypoconulid, whereas the specimen from PO-22 has a posterior protrusion directed to the hypoconulid without reaching it. The m1-2 from PO-38 (IPS105500; Fig. 6M) resembles those of *P. santjaumensis* in size and overall morphology, including the high metaconid, the well-developed anteroconid connected to the protoconid by an anterolophulid, the transverse and well-developed antesinusid, the disconnected lingual and labial branches of the metalophid I, the slightly oblique postprotocristid, connected to the prehypocristid by a short ectolophid, the continuous entolophid, the absence of mesolophid and the crenulated enamel on the synclinid II. The scarcity of the material does not allow the comparison of all dental loci, so we prefer to determine this material as *Paradelomys* sp.

Some teeth from PO-38 TOP (1 M1-2, IPS105635, Fig. 6N; 1 p4, IPS105634, Fig. 6O) and PO-39 (1 M1-2, IPS105681; 1 m1-2, IPS105680, Fig. 6P; 1 m3, IPS106134, Fig. 6Q) can be attributed to *Sciuroides* cf. *romani*. This material is similar in size to that previously described from PO-26 (Anadón et al., 1983). Morphologically, the M1-2 is similar to those previously published, with well-differentiated paraconule and metaconule, and the lower molars show well-developed enamel ornamentation in the synclinids. The material from Pontils resembles that of the genus *Sciuroides* from Mazaterón and Miñana in the Almazán Basin; this material was originally described as *S.* cf. *siderolithicus* (Peláez-Campomanes, 1996), but we consider that it should be also assigned to *S.* cf. *romani*. Both the teeth from Pontils and those from the Almazán Basin are smaller than *S. romani* from Robiac and Le Bretou (Hartenberger, 1973, 1988), and represent the smallest form assigned to the genus *Sciuroides*. The scarcity of material does not allow to evaluate if it could represent a new, more primitive, species of *Sciuroides* or if the differences are due to provincialism, as proposed by Peláez-Campomanes (1996).

The last species recorded in Pontils is a small, hypsodont Remyinae that can be assigned to the genus *Pairomys* based on the absence of the lingual arm of the hypoconid (Vianey-Liaud et al., 1994). Only two specimens of this taxon have been found, an m3 from PO-25 (IPS105538, Fig. 6R) and a P4 from PO-39 (IPS106133; Fig. 6S). Both teeth are slightly larger than those of *P. crusafonti* from its type locality, Sant Cugat de Gavadons, and show better-developed synclines II and IV. The morphology is similar to that of *P. ibericus* from Mazaterón and Miñana (Vianey-Liaud et al., 1994). The P4 is unworn and differs from that of *P. ibericus* from Mazaterón by its larger metaconule, which is not aligned with the metaloph. The m3 shows similar development of the entoconid and the posterior arm of the protoconid than those from Mazaterón and Miñana (Vianey-Liaud et al., 1994). The taxon from Pontils could be interpreted as being more primitive than *P. ibericus* on the basis of its intermediate size between *P.* aff. *ibericus* from Babilafuente and *P. ibericus* from Mazaterón and Miñana. Based on the similarities with this latter species, we assign the material from Pontils to *P.* cf. *ibericus*.

Metatherians, Eulipotyphlans, Apatotherians and Chiropterans

The small invertivore mammal assemblage is mostly represented by fragmented teeth. The few complete dental elements recovered are canines and premolars, which are of little taxonomic value due to their generalistic morphology (i.e., plesiomorphic characters shared by several groups). Nonetheless, some considerations about them can be tentatively provided. With some reservations, metatherians, chiropterans, eulipotyphlans, apatotherians and/or closely related Paleogene counterparts are represented in Pontils.

The group of the metatherians is represented in PO-22 by several fragments of teeth, mostly lower molars (IPS105511, IPS105512, IPS105518; Fig. 7A-C) but also two broken upper ones (IPS105519, IPS105520; Fig. 7D-E). The occurrence of this group in PO-25 is only tentatively evidenced by an incomplete upper molar (IPS105550; Fig. 7F) in which the labial margin is damaged, and the paracone and the metacone are partially missing.

The group of the insectivores (Eulipotyphla) is possibly represented by a nyctitheriid in PO-25 (IPS106193; Fig. 7G) and PO-33 (IPS105571; Fig. 7H). Similarly, Apatotheria are represented by some other dental elements tentatively ascribed to (an) apatemyid-like form(s) of uncertain identification. Such elements have been recovered from layers PO-25 (IPS105551), PO-38 TOP (IPS105636; Fig. 7I) and PO-39 (IPS105705).

Finally, there are two complete canines from PO-22 (IPS106192) and PO-33 (IPS105577) which clearly reproduce the typical morphology found in chiropterans (Fig. 7J-K). These specimens deserve a more detailed analysis, but they are more than likely the oldest evidence of chiropterans in the Iberian Peninsula reported hitherto. Although fossil bats are known since the early Eocene (Jones et al., 2021), there is no record of this mammal order in localities of that age in Spain. This may be simply because most early Eocene localities in the Iberian Peninsula are relatively poor, having yielded in most cases scarce large mammal remains or, more rarely, few rodent or primate dental elements (Antunes et al., 1997; Marigó et al., 2012, 2014).

Any attempt of specific or generic identification of all these forms is rapidly precluded by the absence of diagnostic elements and the scarcity of literature of similarly aged faunas in the Iberian Peninsula. Although the association of early insectivores (mainly nyctitheriids) and apatemyids has been reported from several Spanish Paleogene localities (e.g., Gibert and Agustí, 1979; López-Martínez and Peláez-Campomanes, 1999; Sigé 1997), no references exist about middle Eocene assemblages. The reference works of similar faunas from France, the neighboring country, are based on nicely preserved specimens with rather complete dental series (e.g., Crochet, 1980; Sigé, 1976); unfortunately, the material from Pontils is too scarce to be compared with that from middle Eocene French sites.

Perissodactyls and Artiodactyls

An unworn right M2-3 from PO-39 (IPS106100; Fig. 8A) is provisionally described as cf. *Palaeotherium* sp. (Palaoetheriidae, Equoidea). It is characterized, among other traits, by a flattened and lingually inclined ectoloph, and the absence of paracone and metacone ribs on the labial surface, though prominent styles (especially mesostyle) and stylar ribs (sensu Perales-Gogenola et al., 2021) are present. However, a marked concavity on both sides of the mesostylar ribs, which is typical in many palaeotheriids, is absent and consequently the ectoloph is not markedly W-shaped. IPS106100 therefore corresponds to a palaeotherid equoid, smaller and less hypsodont than the Iberian *Franzenium* and *Cantabrotherium* and the species *Palaeotherium llamaquiquense* and *Palaeotherium giganteum* (see Perales-Gogenola et al., 2022). IPS106100 is larger than *Palaeotherium (F.) lautricense*, *P. duvali* and *P. siderolithicum* but smaller than *P. castrense*, *P. castrense robicense*, *P. ruetimeyeri* or *P.* aff. *ruetimeyeri* (Franzen, 1968; Remy, 1992). The early Priabonian (MP17) species (e.g., *P. medium, P. crassum, P. magnum*) are generally larger than IPS106100. The absence of a marked concavity on both sides of the mesostylar rib is similar to the condition in the early Priabonian (MP17) *Palaeotherium crusafonti* from Roc de Santa, Catalonia (Casanovas-Cladellas, 1975), but this is also larger than IPS106100*.*

More abundant specimens from PO-39 are assigned to the small-sized pachynolophs (Fig. 8B-G). The lack of complete or partial tooth rows hinders a precise determination, but the three upper molars (IPS 106094.2, IPS 106094.1, IPS 106102.1; Fig. 8B-D) are more lophodont and hypsodont than those of the middle Eocene pachynolophines *Lophiotherium, Propalaeotherium* and *"Propachynolophus*". The paraconule and metaconule are weak, hardly differentiated from the continuous and sharp-crested protoloph and metaloph. There is no mesostyle. The dentition of *Pachynolophus* is also lophodont and some species (*P. duvali, P. livinierensis, P. cesserassicus, "P." hookeri, P. boixedatensis*) also lack a mesostyle. Nevertheless, the morphological features of these upper molars seem to better fit with the Anchilophini as proposed by Remy (2012) than with the rest of the pachynolophines, including *Pachynolophus*. Unlike *Pachynolophus*, the studied molars are more lophodont, without intermediate conules, and lack paracone and metacone ribs on the labial surface. This morphology is close to *Paranchilophus* (Casanovas-Cladellas and Santafé-Llopis, 1989), which was described from several middle and late Eocene sites of the Iberian Peninsula, such as Mazaterón (Almazán Basin), Llamaquique (Oviedo Basin) and Zambrana (Miranda-Treviño Basin) (see Badiola et al., 2022). *Paranchilophus* was considered by Remy (2012) to be a subgenus of *Anchilophus*. Accordingly, these three molars are provisionally classified as cf. *Anchilophus* (*Paranchilophus*) sp. They differ from the anchilophine *Metanchilophus* by being more lophodont and hypsodont without well differentiated intermediate conules; M1 and M2 more elongated transversally (almost square in outline); M1-M3 with a more flattened ectoloph, which is not lingually markedly inclined like in *Metanchilophus*, and without a marked metacone rib on the labial wall. IPS106129 is smaller than the other molars (Fig. 8E) and is lophodont, without prominent intermediate conules, with a well differentiated paracone rib and without a mesostyle. Its morphology is close to *Pachynolophus* and *Anchilophus*, and can be referred to the paraphyletic or polyphyletic subfamily “Pachynolophinae” (more details in Badiola et al., 2022 and Danilo et al., 2013). IPS106111 and IPS106157 are both upper premolars, both possibly P2s (Fig. 8F-G). They have an oval outline, a single lingual cusp, and a very narrow lingual wall. They match the size of the molar IPS106129 (Fig. 8E) and could belong to the same pachynolophine species. They are also classified as “Pachynolophinae” indet.

Five specimens from PO-39 (Fig. 8H-L) are assigned to the bunoselenodont anoplotheriids (Erfurt and Métais, 2007 and references therein). They are provisionally classified as Dacrytheriinae indet.. Upper molars (IPS106107, IPS106135; Fig. 8H-I) have crested shaped paracone, metacone and metaconule and the paracone and metacone are included in the W-shaped ectoloph. The P4 (IPS106112.1; Fig. 8J) is triangular in outline with a crescentic lingual cusp like in *Dacrytherium* and *Catodontherium*, but the lack of the complete external wall in molars precludes an accurate observation of some features (e.g., styles, ribs, lingual inclination of the labial wall), hindering a referral to any of these taxa. The m1-2 and lower premolars (IPS106136, IPS106138; Fig. 8K-L) fit the size of the upper teeth. The m1-2 does not have the diagnostic third lingual cuspid (or lingual mediostylid) described in *Dacrytherium*, though other morphological features are similar to those seen in that genus: crescent-shaped labial cuspids (protoconid and hypoconid), bunodont lingual cups (metaconid and entoconid), trigonid closed and talonid open between the metaconid and the entoconid, because the anterior crest of the hypoconid (the prehypocristid) reaches the metaconid. Finally, three isolated lower teeth from PO-40 (IPS105709, IPS105708, IPS105707; Fig. 8M-O) correspond to a small dichobunid artiodactyl with bulbous and bunodont dentition and are provisionally classified as Hyperdichobuninae indet. (Theodor et al., 2007). More material is needed to refine the taxonomic identity of this material.

Squamates and Amphibians

The fragmentary nature of the Pontils amphibians and squamates precludes precise identification at the species or genus level. Gekkotans are identified on the basis of a dentary fragment from PO-22 with a closed Meckelian fossa and small, simple and pointed pleurodont teeth (IPS106035; Fig. 9A), as well as portions of amphicoelous vertebrae from PO-22 (IPS120792) and PO-39 (IPS106047). One fragmentary fused frontal from PO-22 (IPS106034; Fig. 9K) bears poorly developed cristae cranii, its dorsal surface is smooth (no ornamentation), and its overall morphology is reminiscent of that of scincids. Some tooth-bearing bone fragments (maxillae, dentaries or indeterminate) from PO-22 (IPS105523, IPS106033, IPS126358, IPS126359, IPS126360; Fig. 9B-D) and PO-33 (IPS106031) contain bicuspid pleurodont teeth and are thus interpreted as belonging to lacertids. They compare well to other lacertids described in the Iberian late Eocene (Bolet and Evans, 2013), and the different degree of development of the cusplet, as well as the variable presence of striae in the lingual surface of the crown suggest that two different forms might be present. The tricuspid teeth in a few maxillae and dentary fragments from PO-39 (IPS106045, IPS106044; Fig. 9E-F) suggest the presence of an iguanian that compares well with the widely distributed Eocene genus *Geiseltaliellus*; interestingly, in level PO-39 this pleurodont iguanian replaces lacertids. Anguids are represented by two forms according to the shape of the recovered osteoderms. Numerous osteoderms with a vermiculate external ornamentation from PO-22 (IPS120809, IPS126036, IPS126361, IPS126362; Fig. 9G-H), PO-33 (IPS120789) and PO-39 (IPS106046; Fig. 9I) correspond to an unidentified anguine, whereas a single tuberculated osteoderm from PO-25 (IPS120784) is referred to a glyptosaur. Indeterminate anguids are also represented by fragments of skull (IPS120804) with the characteristic vermiculate ornamentation of the group and, tentatively, a fragment of right maxilla (IPS106039a) and one of left dentary (IPS106039b), all from PO-22. Fragmentary vertebrae from PO-22 (IPS120807), PO-25 (IPS120802) and PO-33 (IPS120790) are referred to indeterminate lizards and, tentatively, to indeterminate “scincomorphs” (IPS106038; Fig. 9J) and anguines (IPS106037, IPS120779, IPS120782). The latter are characterized by procoelous vertebrae bearing centra with parallel longitudinal margins in ventral view, and dorsoventrally depressed condyles. The remaining lizard material corresponds to fragments of pterygoid from PO-22 (IPS120773, IPS120783) and PO-38 TOP (IPS106043), maxilla from PO-25 (IPS120780) and PO-40 (IPS106040, IPS106041), dentary from PO-22 (IPS120786) and PO-25 (IPS120801), indeterminate tooth-bearing bones from PO-22 (IPS120775, IPS120796, IPS120810) and PO-25 (IPS120785, IPS120799, IPS120800), and a skull bone from PO-22 (IPS120805) of indeterminate lizards. Moreover, premaxillae from PO-22 (IPS120774) and 38 TOP (IPS106049) and an anterior portion of dentary from PO-25 (IPS106048; Fig. 9L) are assigned to an indeterminate “scincomorph”; it maybe corresponds to a scincid, but the material is extremely fragmentary and does not allow a definitive identification. Fragmentary procoelous vertebrae with rounded condyles and well-developed haemal keels from PO-22 (IPS106032, IPS120776, IPS120806, IPS126363; Fig. 9M), PO-25 (IPS120798), PO-33 (IPS120788) and PO-39 (IPS120778, IPS120781, IPS120787) are assigned to snakes. Regarding amphibians, the scarce available material is comprised of ornamented skull fragments (IPS120793), portions of tooth-bearing bone with pedicelate teeth (IPS120794, IPS120795), and fragments of postcranial bones, including fused tibiofibulae (IPS120777, IPS120797), all from PO-22, referred to indeterminate anurans.

Crocodyliforms

Crocodyliforms are represented exclusively by shed, isolated teeth. The fragmentary nature of the crocodyliform material precludes precise taxonomic identification, but teeth can be grouped in different morphotypes. Within any single morphotype, the shape varies depending on the tooth position (Blanco et al., 2020; Mook, 1921). Teeth from anterior tooth positions are expected to have proportionally larger, thinner and more pointed crowns, whereas posterior or molariform teeth show lower, wider and more blunt crowns.

A total of 3303 teeth were recovered. These were grouped in four different morphotypes. The first morphotype (e.g., IPS126355, IPS126356, IPS126348; Fig. 10A-C) corresponds to conical unornamented teeth. It includes teeth showing smooth enamel on lingual and labial surfaces, without any ridges or grooves. Carinae on mesial and distal margins are unserrated. The second morphotype (e.g., IPS126352, IPS126354, IPS126349; Fig. 10D-F) is composed of conical teeth with parallel apicobasal ridges on the enamel. Both lingual and labial surfaces are ornamented, although ridges are stronger on the lingual side. Mesial and distal carinae occur on teeth from anterior dental positions, but do not contact the apicobasal ridges. The third morphotype (e.g., IPS126357; Fig. 10G) comprises labio-lingually compressed teeth with serrated carinae. The tooth enamel is smooth, lacking ornamentation, and the carinae bear true denticles. Teeth from anterior positions have the apex curved distally and only develop the distal carina. In contrast, teeth from intermediate and posterior positions have both mesial and distal carinae. The fourth morphotype (e.g., IPS126351, IPS126353, IPS126350; Fig. 10H-J) includes conical teeth with enamel ornamented with multiple small and discontinuous ridges. Both lingual and labial surfaces are ornamented, although the lingual ridges are stronger and may contact the carinae, developing false ziphodonty.

Morphotypes 1, 2 and 4 are by far the most abundant and are known from multiple levels (PO-22, PO-25, PO-38, PO-38 TOP, PO-39, PO-40). They are rarest in level PO-40 (only eight teeth of morphotype 1), perhaps because it was deposited in a marine environment. These are generalist teeth with little taxonomic value and are referred to Crocodylia indet. These teeth resemble *Diplocynodon* from the Eocene of the Duero Basin (Martín de Jesús et al., 1987; Ortega et al., 2022), but similar ornamentation has also been seen in other crocodylians (Prasad and de Lapparent de Broin, 2002). Although the occurrence of *Diplocynodon* at Pontils is possible considering the broad European distribution of this taxon from the Selandian to the Miocene (Puértolas-Pascual et al., 2016), this cannot be certainly established at this time. Morphotype 3 is rare (only 7 of 3303 specimens) and has only been recorded from PO-39. The ziphodont teeth of morphotype 3 are characteristic of sebecosuchian notosuchians (Pol et al., 2012, 2014). Despite being considered primarily South American taxa, fossil records of sebecosuchian representatives have been reported from several middle Eocene (Lutetian and Bartonian) localities in Europe: Issel, Lissieu, Saint-Martin-de-Londres, Aumelas, Robiac (France), Geiseltal, Messel (Germany), Vale Furado (Portugal), Tossalet del Morral, Caenes and other sites in the Duero Basin (Spain) (Antunes, 1975; Berg, 1966; Berg and Crusafont, 1970; Kuhn, 1968; Martin, 2015, 2016; Martín de Jesús et al., 1987; Ortega et al., 1996; Rossmann et al., 2000). These European sebecosuchian remains were referred to two different genera: *Bergisuchus* (MP 11-13, Lutetian of Germany) and *Iberosuchus* (MP 13-16, Lutetian and Bartonian of Portugal, Spain and France). The ziphodont teeth from Pontils match the geographic and chronostratigraphic ranges of *Iberosuchus* but, given the fragmentary nature of the material and the lack of diagnostic features, we prefer not to determine these remains at the genus level. In any case, the presence of sebecosuchians at Pontils represents one of the youngest European occurrences of this group.

Chondrichthyans and Actinopterygians

The uppermost levels of the Pontils section record a change from continental to marine conditions. In PO-38 TOP, rare marine fish teeth are present together with terrestrial mammals; in PO-39, both marine fishes and terrestrial mammals are relatively abundant, whereas in PO-40, at the top of the sequence, fishes are the most abundant vertebrates and are associated with abundant marine invertebrate shells. A relatively diverse ichthyofauna has been recognized, mainly from PO-40.

Chondrichthyans include at least three sharks and three rays. Sharks are represented by one unserrated and two serrated tooth morphotypes. The serrated teeth are laterally compressed, with a posteriorly curved apex that bears denticles in the distal carinae (e.g., IPS103636; Fig. 11A). Similar teeth from different middle Eocene localities have been referred to *Hemipristis* (e.g., Adnet et al., 2020; Zouhri et al., 2021). A second serrated morphotype is represented by a single tooth with a low and rounded crown (IPS103637). The crown is lingually inclined and both mesial and distal carinae show denticles (Fig. 11B, C). This tooth resembles those referred to *Nebrius* from several Eocene localities (e.g., Adnet et al., 2020; Case et al., 2015; Trif et al., 2022). The non-serrated morphotype corresponds to teeth with pointed and smooth crowns. The crown is laterally compressed and both mesial and distal carinae are simple (e.g., IPS103664; Fig. 11D). Similar teeth from several Eocene localities have usually been referred to lamniform and carcharhiniform taxa (Adnet et al., 2020; Case et al., 2015; Malyshkina and Ward, 2016; Trif et al., 2019, 2022). We refer this morphotype to Selachii indet., pending more detailed study.

Rays are represented by isolated teeth and dermal denticles. Teeth were grouped in three different morphotypes. The first morphotype corresponds to globular teeth with smooth enameloid and three lingual uvulae (e.g., IPS103627; Fig. 11E). We assign these teeth to cf. *Rhinobatos* sp., given their similarity with this genus. The second morphotype comprises teeth with an elliptical crown in occlusal view, bearing a central groove, with a concave lingual surface, a convex labial surface, and both faces with rugose enameloid towards the occlusal margin (e.g., IPS103616; Fig. 11F). These teeth resemble those of *Coupatezia* (Cappetta, 1987). The third morphotype includes small teeth with globular crowns bearing a transverse crest. The labial surface is flat and smooth (unornamented) (e.g., IPS103645; Fig. 11G).

These teeth are similar to those referred to *Dasyatis* (Cappetta, 1987) or *Himantura* (Adnet et al., 2020), so they are preliminary regarded as Dasyatidae indet.

Actinopterygians are mostly represented by both isolated and stacked rounded molariform teeth, typical of fishes with a durophagous diet (e.g., IPS103613, IPS103609; Fig. 11H, I). Similar teeth from other Eocene localities (e.g., Triff et al., 2019, 2022) have been referred to phyllodontid, pycnodontiform and perciform taxa; therefore, they are here regarded as Actinopterygii indet. Additionally, four stacked triangular flat teeth (e.g., IPS103629; Fig. 11J, K), interpreted as part of the lower dental plate, might belong to a tetraodontiform fish (Dica, 2002; Triff et al., 2022). Finally, some pointed teeth with high crowns, enamel ornamented with apicobasal ridges and an acrodine cap on the apex (e.g., IPS103659; Fig. 11L) can be referred to lepisosteiform fishes (Blanco et al., 2017b; Grande, 2010; López-Arbarello, 2012; Szabó et al., 2016).

Invertebrates

Marine invertebrates are abundant in the samples from PO-39 and, especially, PO-40. Most shells are fragmented due to collecting and screen-washing procedures. Among bivalves, ostreids (*Ostrea*) are the most abundant, followed by pectinids. Remains of echinoids (skeleton plate fragments and spines), bryozoans (Gymnolaemata), balanids and crustaceans are also present.

Benthic Foraminifera

Larger and smaller benthic foraminifera have been identified, but no planktic foraminifera have been observed in the study samples. Larger benthic foraminifera were observed in samples PO-19, 20, 22, 23, 25, 26, 33, 38 and 39. Only 1-3 individuals were found in PO-19, 20 and 26, and the highest abundance (more than 250 individuals) was recorded in PO-39. Specimens are moderately well preserved and infilled with calcite. All specimens are nummulitids, and almost all of *Nummulites. Nummulites garnieri sturi* (= *Nummulites praegarnieri* (Schaub, 1981); Costa et al., 2013; Papazzoni, 1993; Papazzoni and Sirotti, 1995) is the most common form, found in all samples containing larger benthic foraminifera. Externally these have granules and sinuously curved filaments (Fig. 12F). Internally, the specimens show a tight, regular spiral with straight septae, relatively square chambers and a small proloculus of ~ 60 µm diameter (Fig. 12D, E). Two specimens of an A-form (megalospheric), reticulate *Nummulites* with a proloculus diameter (excluding walls) of 100 and 90 µm, but showing clear reticulation, were found in PO-22 and PO-39, respectively (Fig. 12B, C). These belong to the *Nummulites fabianii* lineage and were identified as *N. garganicus* following Özcan et al. (2010, 2019). *Nummulites garganicus* is characterized by a proloculus diameter of 100-140 µm; although the specimens in this study are at the lower limit of this range, they cannot belong to the preceding member of the lineage, *N. bullatus*, as the reticulation is too well developed. Two *Operculina* were found in PO-23 (Fig. 12A). These specimens are evolute with granules across their septa, and relatively straight septa with a high angle where they meet the periphery of the test. They belong to the *Assilina alpina* group (also referred to as *Operculina alpina*). The proloculus diameter in one sectioned individual is 40 µm and therefore it is tentatively assigned to *Assilina (Operculina) schwageri* following Hottinger (1977) and Özcan et al (2019).

Smaller benthic foraminifera were only identified in PO-40, which was processed using fine mesh sieves (250 and 63 µm). These are moderately to poorly preserved, and some tests are broken and partially abraded. The assemblages are dominated by *Protelphidium* (Fig. 13), followed by *Pararotalia* and *Elphidium* (common), then *Patellina* and *Cibicides* (rare). Scarce agglutinated foraminifera such as *Ammodiscus* and trochamminids were also recovered.

Charophytes

Three charophyte species have been recovered from the studied section, all of them already reported from this site by Anadón and Feist (1981). The low species diversity could be related to the mesh apertures of the sieves used during the sediment processing: the smallest mesh size was 0.5 mm for all levels except for PO-40, and therefore the smallest fraction of the gyrogonite population was probably filtered through the meshes.

A few gyrogonites of *Raskyella vadaszi* were extracted from levels PO-22, PO-25 and PO-33 (Fig. 14A-D). Gyrogonites are large, 1090 µm high and 1125 µm wide, with an isopolarity index (ISI) of 96. Normally, the gyrogonite has a sub-ovoidal shape following the taxonomical nomenclature of Feist et al. (2005). The apex is flat, formed by an apical operculum of five triangular to pentagonal cells. The base is rounded or slightly elongated, showing a pentagonal basal pore in some specimens located inside a funnel. Nine or ten convolutions are visible laterally. Spiral cells are slightly convex but become concave near the base. They are highly ornamented. The ornamentation varies from well individualized and prominent tubercules that display the same width as the spiral cells and are spaced in regular intervals and separated by concave part of the cells, to smooth or undulated mid-cellular crest.

Tens of gyrogonites of *Nitellopsis (Tectochara) major* were recovered from levels PO-22, PO-33, PO-38 and PO-39. Hundreds of specimens were picked from sample PO-25 (Fig. 14E-H), and this represents by far the most abundant species at Pontils. However, a large part of the population shows evidence of deformation (flattening) related to diagenetic processes. Gyrogonites are very large, with an average height and width of 1424 µm and 1356 µm respectively, pear-shaped with an ISI of 105. The apex is prominent with apical nodules. The base is elongated with a large pentagonal basal pore located within a marked basal funnel. Spiral cells are flat or slightly convex and form 10 convolutions in lateral view. The apex is Nitellopsioid, i.e., with strong shortening and thinning of spiral cells in the periapical region (Feist et al., 2005). Ornamentation is absent except near the apical zone, where poorly marked nodules occur.

Finally, few gyrogonites of *Madleriella leiostachys* have been recovered from PO-25 (Fig. 14I-K). They are large (910 µm in height and 980 µm in width), suboblate in shape according to Feist et al. (2005). The ISI is 92. The apex is rounded, without periapical modification, sometimes showing poorly marked nodules. The base is rounded, showing a small pentagonal basal pore. Eight convolutions are visible in lateral view. Spiral cells are flat or slightly convex, showing a characteristic ornamentation composed of regularly spaced massive tubercles.

DISCUSSION

Age of the Locality

The new data provided in this work help clarify the temporal duration and age of this locality. Although the Pontils section represents a total thickness of about 70 m (from PO-22 to PO-40) the recovered fauna suggests a relatively short duration. The most relevant taxa from a biostratigraphic point of view, i.e., rodents and foraminifera, do not show differences among the studied levels. *Pseudoltinomys cosetanus*, *Sciuroides* cf. *romani*, *Nummulites garganicus* and *N. garnieri sturi* are identified from levels PO-22 and PO-39, the lowest and uppermost continental levels of the section. Therefore, the age difference between the bottom and the top of the Pontils section is likely not significant. This is consistent with a coastal environment and marine transgressive context, which is likely associated with a high sedimentation rate.

The Pontils rodent assemblage is relatively impoverished in comparison to other Bartonian faunas (Comte et al., 2012; Hooker and Weidmann, 2000, 2007). So far, a minimum of five rodents have been recorded in the Pontils section, among which *P. cosetanus* is the most abundant. A similar situation was described by Peláez-Campomanes (1996) at Mazaterón and Miñana (Almazán Basin), where only three rodent taxa were recorded, among which *Pseudoltinomys crebrum* was the most abundant. Although the Almazán species are probably evolutionarily more advanced than those from Pontils, their morphological similarity indicates a roughly similar age for these sites (Peláez-Campomanes 1996). The section of Sant Jaume de Frontanyà has yielded two rodent assemblages, SJF-3C (Quer and Agustí, 2010) and SJF-1 (Bonilla-Salomón et al., 2016). Compared with Pontils, they represent older faunas, based on the presence in SJF-3C of *Frontanyamys russelli*, which is less hypsodont and lophodont than *Pairomys* cf. *ibericus* from Pontils. *Paradelomys santjaumensis* and *Elfomys catalaunicus* from SJF-1 represent the most primitive species of their genera. The presence of *Paradelomys* sp. from Pontils is in agreement with a younger age than that of SJF-1.

Pontils is likely older than MP16 given the presence of taxa that are considered to be more primitive than those recorded from MP16 localities as Robiac, Le Bretou or Rocourt-Saint-Martin (Vianey-Liaud and Marivaux, 2017). The presence in PO-26 of a DP4 (PONT 002, Anadón et al., 1983, Pl. I, fig. 9) assigned by Comte et al. (2012) to *Protadelomys*, could indicate an age close to Chéry-Charteuve (Comte et al., 2012), which yielded the youngest record of *Protadelomys*. The presence in Les Alleveyes of *Pseudoltinomys* aff. *crebrum*, morphologically very close to the type material from Mazaterón but of larger size (Hooker and Weidmann, 2007), and *Paradelomys* sp., morphologically similar to *P. santjaumensis* (Bonilla-Salomón et al., 2016), also supports a middle Bartonian age for the Pontils section.

The most conclusive data to confirm the assignment of the Pontils section to the Bartonian come from the study of the benthic foraminifera. Though the larger foraminiferal assemblage was not particularly diverse, it contained biostratigraphic indicators within the Shallow Benthic Zonation (SBZ, Costa et al., 2013; Gradstein et al., 2020; Serra Kiel et al., 1998). *Nummulites garnieri sturi* and *Assilina (Operculina) schwageri – alpina* group with a proloculus size below 120 µm have a SBZ17-18 age (Özcan et al. 2019, Papazzoni and Sirotti, 1995; Serra Kiel et al, 1998). The *Nummulites fabianii* lineage is well known for its use in Eocene biostratigraphy, with *N. garganicus* indicating an SBZ17 age (Özcan et al., 2010), which is correlated to chron C18 (Gradstein et al., 2020). Therefore, the reversed polarity at the Pontils fossil site could correspond to chron C18r, with an age between 40 and 41 Ma, as already proposed by Legendre and Leveque (1997). However, an alternate correlation with chron C18n.1r (39.67–39.58 Ma, Speijer et al., 2020) cannot be excluded, and therefore the possible age range of the Pontils fossil assemblage spans from 39.58 to 41 Ma (Fig. 15). The controversy about the age of this fossil site seems finally solved.

Paleoenvironmental Interpretation

The Pontils assemblage is consistent with the global warm conditions inferred for the Bartonian. The age estimated for this fossil site broadly coincides with the Middle Eocene Climatic Optimum (40.5–40 Ma; Bohaty and Zachos, 2003; van der Boon et al., 2021), although a confident correlation is not possible, because the range of possible ages for this locality (41–39.58 Ma) is quite longer than the MECO. The diversity observed in the different levels of Pontils and, particularly, the abundance of some taxa that are typically associated to warm and humid conditions, such as omomyiform and adapiform primates (Gingerich, 2012) would be consistent with their deposition during the MECO. Nevertheless, the scarcity of similar aged vertebrate faunas in Europe does not allow comparing with other localities and establishing trends on the vertebrate diversity along the Bartonian. Furthermore, the unusual diversity of the Pontils assemblage considered as a whole may be partially due to its particular location in a coastal environment, which permits finding together vertebrates typical of terrestrial and marine environments. In any case, there is a marked change in the fossil content from the lowest levels of the Pontils section (which only contain remains of terrestrial organisms, except for scarce foraminifera transported from the sea) to the uppermost level, PO-40 (dominated by sharks, rays, and marine invertebrates with very sparse remains of terrestrial animals, that should be transported from the continent). This change could reflect the sea level rise that occurred in relation to the warm conditions during the MECO (Bohaty and Zachos, 2003; Miller et al., 2020).

The vertebrate assemblage from the lower Pontils section (PO-22 to PO-39) is consistent with a densely forested, warm and humid swampy environment (Cavagnetto and Anadón, 1995, 1996). The two main primate groups recorded in Europe during the Eocene, adapiforms and omomyiforms, are generally interpreted to be arboreal (Fleagle, 2013; Gebo, 2002; Gunnell and Rose, 2002; Silcox et al., 2009), and their presence is consistent with a forested environment. In particular, *Pseudoloris* and *Necrolemur*, both found at Pontils, are believed to have been nocturnal and arboreal leaping primates (Dagosto and Schmid, 1996; Fleagle, 2013; Gunnell and Rose, 2002). While the Pontils anchomomyin adapiform cannot be identified to the genus level, postcranial bones of other members of this group (e.g., *Anchomomys*) indicate that they were arboreal (Marigó et al., 2016, 2020). The habitat preferences of the small omomyid, the most common member of the Pontils primate assemblage, remain unknown.

Crocodilians occur in almost all the continental levels of the Pontils section, (Fig. 4). Their absence from PO-33 is unusual since the rest of the faunal elements from PO-33 do not differ significantly from those recorded in the other continental levels. Interestingly, all the crocodilian teeth found in Pontils, except those referred to *Sebecosuchia*, are small and seem to have belonged to juvenile individuals. The rarity of sebecosuchian remains at Pontils (few teeth at PO-39) may be related to their low abundance in the original community, as expected for their ecological role as top predators. Unlike the other crocodyliforms at Pontils, sebecosuchians were completely terrestrial. Based on the morphology of their teeth and the postcranial bone elements that allowed an erect posture, they are considered cursorial predators whose lifestyle is not connected to water (Nascimento and Zaher, 2010). Thus, such type of predators might have covered a wide home range (Pough et al., 2013) and would have been occasional inhabitants in the swampy and coastal environments recorded at Pontils.

Squamates and amphibians are neither abundant nor diverse at Pontils, which is generally the case at Iberian Eocene localities. The lack of amphisbaenians at Pontils is not surprising because these are lacking from all European localities between the MP11 and MP15. They are present, however, in the slightly younger (MP16) Iberian assemblage from Mazaterón (Bolet, in press), suggesting that Pontils is older than the return of amphisbaenians after the gap that lasted a great part of the middle Eocene. More intriguing is the scarcity of glyptosaurs (a single osteoderm was identified), which are a ubiquitous component of Eocene herpetofaunas across Europe and are usually abundant at all other Iberian Eocene localities yielding squamates (Bolet, 2017; Bolet and Augé, 2014; Bolet and Evans, 2013). Due to the unusual geological setting of the locality, situated in a coastal environment, we suggest that probably this poor record of glyptosaurs might have had a paleonvironmental cause. Additionally, anurans were recovered only from a single level low in the section (PO-22). Since anurans are generally sensitive to increases in salinity, their absence from the upper parts of the Pontils section may be due to the observed marine transgression. Iguanians and lacertids are, however, found together in other Eocene localities without marine influence (e.g., Sossís, Bolet and Evans, 2013), so it is less clear that the apparent replacement of lacertids by iguanids observed in the Pontils section is related to this same change in environment. As a whole, the squamate fauna from Pontils displays transitional features between those from early and late Eocene Iberian localities and, despite the paucity of material, represents a typical European middle Eocene assemblage. Further samplings could help to confirm the patterns of distribution of different taxa and to understand their relationship with paleoenvironmental factors.

The presence of charophytes in all levels except for PO-40 indicates the prevalence of shallow freshwater or oligohaline conditions. Proximity to the sea is also indicated by the occurrence of larger benthic foraminifera in levels PO-22 to PO-38. Nummulitids inhabit the photic zone (Beavington-Penney and Racey, 2004) and are typical of warm shallow marine environments; if the water is cloudy, they tend to occupy shallower settings to compensate for lower light levels. Therefore, they could have been easily transported unto the swamp by water currents, perhaps related to storms. Increasing marine influence towards the top of the section is indicated by the occurrence of chondrichthyan and actinopterygian remains in the upper levels, which are scarce in PO-38 TOP and abundant and accompanied by marine invertebrate shells in PO-39. The uppermost sampled level, PO-40, was deposited in a shallow marine environment, as indicated by the abundance of marine fish, bivalve and other invertebrate remains, and the presence of smaller benthic foraminifera in combination with remains of terrestrial squamates and artiodactyls.

Among the fishes identified at the upper levels of the Pontils section, pycnodontiforms and perciforms occur in a wide range of aquatic habitats, from open marine to freshwater environments (Nelson, 2006). Even batoids can also tolerate brackish and freshwater conditions, especially dasyatoid rays, which include some freshwater species. In contrast, selachians are typical marine fishes (although sharks can make infrequent freshwater incursions; Cappetta, 1987; Nelson, 2006), and tetraodontiform fishes are also nearly exclusively marine (Nelson, 2006), thus pointing to a connection with open marine waters.

Among the marine invertebrates, ostreids can tolerate some fluctuations of salinity, but other elements such as echinoids and bryozoans from PO-39 and PO-40 are stenohaline and indicate saline waters. In PO-40, the presence of *Protelphidium, Pararotalia* and *Patellina* points to an inner shelf environment (Murray, 2006).

CONCLUSIONS

The first intensive sampling of the Pontils section resulted in the recovery of significant diversity of vertebrates and other fossils from seven different levels, including several groups that had not been previously documented from this site. The lowest levels (PO-22, 25, 33 and 38) contain mainly remains of terrestrial organisms, although larger benthic foraminifera are also recorded due to marine influence in the context of a coastal mangrove environment. Levels PO-38 TOP and PO-39 contain both terrestrial and marine fossils, whereas the assemblage from PO-40 is dominated by marine groups with scarce continental fossils. The vertebrate assemblage from Pontils is in agreement with a densely vegetated mangrove with warm and humid conditions, as previously inferred from the pollen assemblage. Further detailed studies of the already available remains, together with new sampling leading to the recovery of additional material, will permit more precise taxonomic determinations (and likely the description of new taxa).

Pontils is unique among middle Eocene European sites mainly in the unusual co-occurrence of marine and terrestrial fossils, which makes possible the correlation of the mammal fauna with marine biostratigraphic scales. In contrast to previous age estimates based on marine fossils recovered from the overlying marls of the Collbàs

Formation, we have identified larger benthic foraminifera from the same levels yielding mammal remains (PO-22 to PO-39), which are assigned to the SBZ17 zone. These data, together with previous paleomagnetic analyses, allow constraining the age of the Pontils section between 39.58 and 41 Ma. This confirms the assignment of Pontils to the Bartonian and solves the debate about the age of this site.

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FIGURE CAPTIONS

FIGURE 1. Location of the Pontils section (Ebro Basin, Tarragona Province, NE Spain). [planned for page width]

FIGURE 2. Stratigraphic column of the Pontils section in the context of nearby Paleogene lithostratigraphic units. Sampled levels (PO-22 to 40) that have yielded significant vertebrate remains are highlighted in bold. Asterisks indicate the position of paleomagnetic samples with reversed polarity (Legendre and Lévêque 1997). [planned for page width]

FIGURE 3. General view of the Pontils section (A) and detail of one of the sampled levels (Pontils-33, indicated by an arrow) during the field campaign carried out in 2016 (B). [planned for page width]

FIGURE 4. Distribution of the vertebrate taxa identified in the fossiliferous levels from the Pontils section (Pontils-22, 25, 33, 38, 38 TOP, 39 and 40). [planned for page width]

FIGURE 5. ESEM images of the primate teeth from Pontils. **A–E**, Omomyidae indet. **A**, left m1-2 from PO-38 TOP (IPS105623) in occlusal (**A1**) and buccal (**A2**) views; **B**, fragment of right mandible with m2 and m3 from PO-38 (IPS105592) in occlusal (**B1**) and buccal (**B2**) views; **C**, right m3 from PO-38 TOP (IPS105597) in occlusal (**C1**) and buccal (**C2**) views; **D**, left upper molar from PO-38 TOP (IPS124931) in occlusal (**D1**) and buccal (**D2**) views; **E**, fragment of left upper molar from PO-33 (IPS86811) in occlusal (**E1**) and buccal (**E2**) views. **F–J**, *Pseudoloris* sp. **F**, left m1-2 from PO-33 (IPS86802) in occlusal (**F1**) and buccal (**F2**) views; **G**, fragment of right m3 from PO-25 (IPS105527) in occlusal (**G1**) and buccal (**G2**) views; **H**, left M1-2 from PO-38

(IPS105596) in occlusal (**H1**) and buccal (**H2**) views; **I**, fragment of right M1-2 from PO-33 (IPS86804) in occlusal view. **J**, right I1 from PO-38 TOP (IPS105621) in medial view. **K**, right m3 of Anchomomyini indet. from PO-38 (IPS105619) in occlusal (**K1**) and buccal (**K2**) views. **L**, fragment of right m2-3 of *Necrolemur* sp. from PO-33 (IPS105569) in occlusal view. Scale bar equals 1 mm. **Abbreviation**: **ESEM**, Environmental Scanning Electron Microscope. [planned for page width]

FIGURE 6. ESEM images of the rodent teeth from Pontils. **A–I**, *Pseudoltinomys cosetanus*. **A**, right DP4 from PO-25 (IPS105540); **B**, left P4 from PO-39 (IPS105691); **C**, left M1-2 from PO-25 (IPS105541); **D**, left M1-2 from PO-33 (IPS105588); **E**, right M3 from PO-38 TOP (IPS106203); **F**, right p4 from PO-38 (IPS105601); **G**, left m1-2 from PO-25 (IPS105535); **H**, right m1-2 from PO-39 (IPS108669); **I**, right m3 from PO-39 (IPS105690). **J–K**, *Pseudoltinomys* sp. **J**, right M1-2 from PO-25 (IPS105546). **K**, right m1-2 from PO-22 (IPS108650). **L–M**, *Paradelomys* sp. **L**, left p4 from PO-22 (IPS105506); **M**, right m1-2 from PO-38 (IPS105500); **N–Q**, *Sciuroides* cf. *romani*. **N**, right M1-2 from PO-38 TOP (IPS105635); **O**, right p4 from PO-38 TOP (IPS105634); **P**, right m1-2 from PO-39 (IPS105680); **Q**, left m3 from PO-39 (IPS106134). **R–S**, *Pairomys* cf. *ibericus*. **R**, left m3 from PO-25 (IPS105538); **S**, right P4 from PO-39 (IPS106133). Scale bar equals 1 mm. **Abbreviation**: **ESEM**, Environmental Scanning Electron Microscope. [planned for page width]

FIGURE 7. ESEM images of the teeth of metatherians, eulipotyphlans, apatotherians and chiropterans from Pontils. **A–F**, Metatheria indet. **A**, trigonid of right lower molar from PO-22 (IPS105511) in occlusal view; **B**, trigonid of left lower molar from PO-22 (IPS105512) in occlusal view; **C**, talonid of right lower molar from PO-22 (IPS105518) in occlusal view; **D**, fragment of left upper molar from PO-22 (IPS105519) in occlusal

view; **E**, fragment of left upper molar from PO-22 (IPS105520) in occlusal view; **F**, fragment of right upper molar from PO-25 (IPS105550) in occlusal view. **G–H**, Nyctitheriidae indet. **G**, left upper incisor from PO-25 (IPS106193) in medial (**G1**) and labial (**G2**) views; **H**, right i3 from PO-33 (IPS105571) in medial (**H1**) and occlusal/labial (**H2**) views. **I**, Apatemyidae indet.: left upper premolar from PO-38 TOP (IPS105636) in occlusal view. **J–K**, Chiroptera indet. **J**, right upper canine from PO-22 (IPS106192) in occlusal view; **K**, left lower canine from PO-33 (IPS105577) in labial view. Scale bar equals 1 mm. **Abbreviation**: **ESEM**, Environmental Scanning Electron Microscope. [planned for page width]

FIGURE 8. Perissodactyl and artiodactyl remains from Pontils. **A**, right M2-3 broken mesio-labially of cf. *Palaeotherium* sp. from PO-39 (IPS106100) in occlusal (**A1**), lingual (**A2**) and labial (**A3**) views; **B–D**, cf. *Anchilophus* (*Paranchilophus*) sp. from PO-39; **B**, left M3 (IPS106094.2) in occlusal (**B1**) and labial (**B2**) views; **C**, left M2 (IPS106094.1) in occlusal (**C1**) and labial (**C2**) views; **D**, right M1 broken disto-labially (IPS106102.1) in occlusal (**D1**) and labial (**D2**) views; **E–G**, “Pachynolophinae” indet. from PO-39; **E**, right M1 (IPS106129) in occlusal (**E1**) and labial (**E2**) views; **F**, right P2 (IPS106111) in occlusal (**F1**) and labial (**F2**) views; **G**, left P2 broken posteriorly (IPS106157) in occlusal (**G1**) and labial (**G2**) views; **H–L**: Dacrytheriinae indet. from PO-39; **H**, left M1-2 incomplete labially (IPS106107) in occlusal view; **I**, fragment of right M1-2 (IPS106135) in occlusal view; **J**, left P4 broken mesio-labially (IPS106112.1) in occlusal view; **K**, right m1-2 (IPS106136) in occlusal view; **L**, right lower premolar (IPS106138) in occlusal (**L1**), lingual (**L2**) and labial (**L3**) views; **M-O**, Hyperdichobuninae indet. from PO-40; **M**, left m1-2 (IPS105709) in occlusal view; **N**, ?p4 (IPS105708) in occlusal view; **O**, ?p-3 (IPS105707) in occlusal view. Scale bars equal 1 cm. [planned for page width]

FIGURE 9. Representative selection of squamate specimens from Pontils. **A**, Gekkota indet., fragment of left dentary from PO-22 (IPS106035); **B–D**, Lacertidae indet. from PO-22; **B**, right maxilla fragment (IPS126358); **C**, left dentary portion (IPS126359); **D**, partial left dentary (IPS126360); **E–F**, Iguanidae indet. (?*Geiseltaliellus*) from PO-39; **E**, partial right dentary (IPS106045); **F**, partial left maxilla (IPS106044) in lingual (**F1**) and labial (**F2**) views; **G-I**, Anguinae indet.; **G**, body osteoderm from PO-22 (IPS126361); **H**, body osteoderm from PO-22 (IPS126362); **I**, body osteoderm from PO-39 (IPS106046); **J**, fragment of vertebra of "Scincomorpha" indet. from PO-22 (IPS106038); **K**, partial frontal of ?Scincidae indet. from PO-22 (IPS106034) in ventral (**K1**) and dorsal (**K2**) views; **L**, anterior portion of left dentary of "Scincomorpha" indet. from PO-25 (IPS106048); **M**, two partial vertebrae in anatomical connection of Serpentes indet. from PO-22 (IPS126363). [planned for page width]

FIGURE 10. Crocodyliform remains from Pontils. **A**, Crocodylia indet. (morphotype 1) from PO-40 (IPS126355) in lingual view; **B**, Crocodylia indet. (morphotype 1) from PO-40 (IPS126356) in lateral view; **C**, Crocodylia indet. (morphotype 1) from PO-22 (IPS126348) in lateral view; **D**, Crocodylia indet. (morphotype 2, anterior tooth) from PO-38 (IPS126352) in lingual view; **E**, Crocodylia indet. (morphotype 2, posterior tooth) from PO-39 (IPS126354) in lingual view; **F**, Crocodylia indet. (morphotype 2, anterior tooth) from PO-22 (IPS126349) in lingual view; **G**, Sebecosuchia indet. (morphotype 3) from PO-39 (IPS126357) in lingual view; **H**, Crocodylia indet. (morphotype 4, anterior tooth) from PO-25 (IPS126351) in lingual view; **I**, Crocodylia indet. (morphotype 4, posterior tooth) from PO-38 (IPS126353) in lingual view; **J**, Crocodylia indet. (morphotype 4, anterior tooth) from PO-22 (IPS126350) in lingual view. **C**, **F** and **J** correspond to ESEM images; the rest of images were taken with a

DSLR camera. **Abbreviation**: **ESEM**, Environmental Scanning Electron Microscope. [planned for page width]

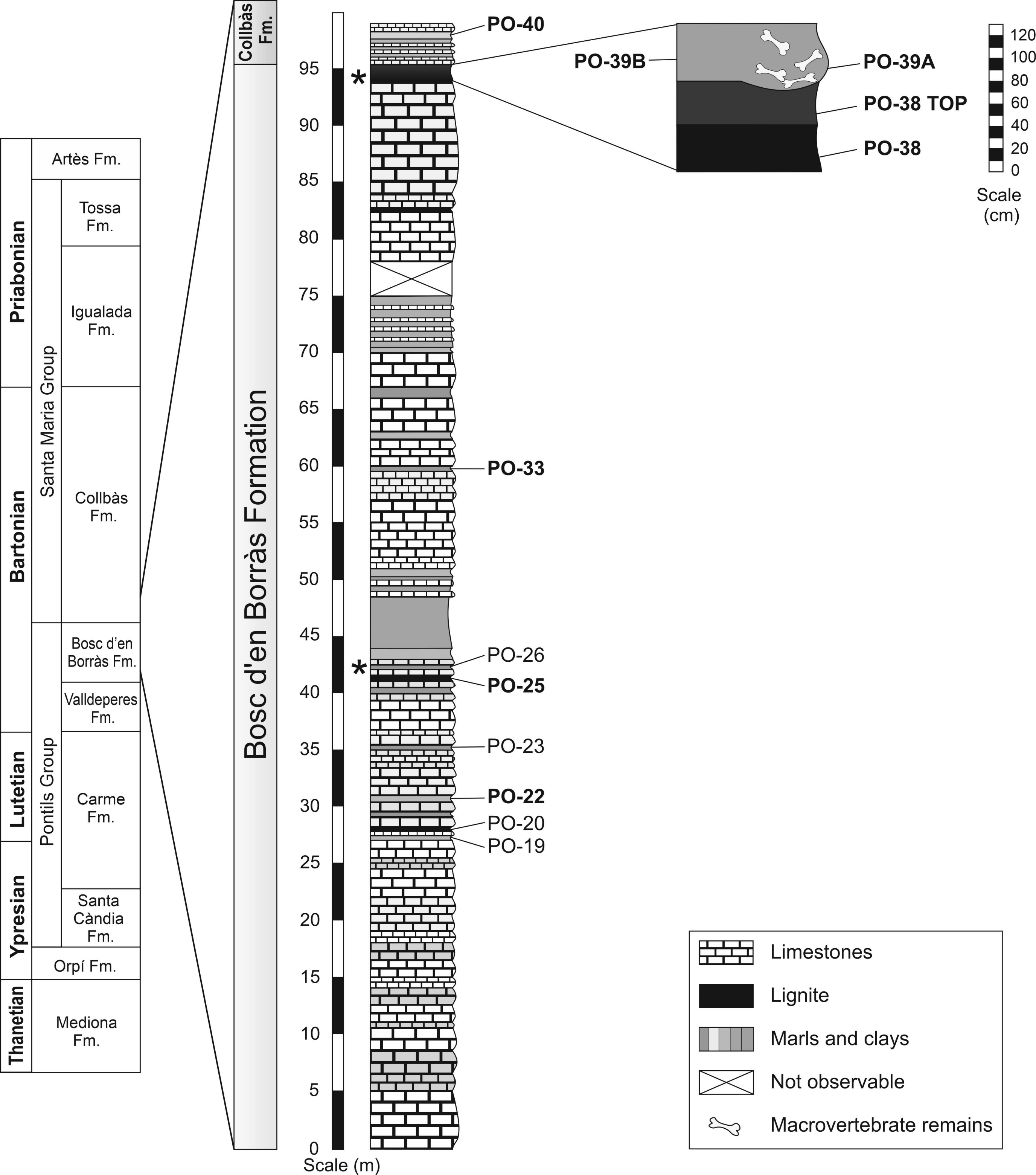
FIGURE 11. Fish remains from Pontils. **A**, selachian morphotype 1 (cf. *Hemipristis* sp.) from PO-40 (IPS103636) in lateral view; **B–C**, selachian morphotype 2 (cf. *Nebrius* sp.) from PO-40 (IPS103637) in labial view (**B**) and detail on the denticles (**C**); **D**, selachian morphotype 3 (Selachii indet.) from PO-40 (IPS103664) in labial view; **E**, batoid morphotype 1 (cf. *Rhinobatos* sp.) from PO-40 (IPS103627) in occlusal view; **F**, batoid morphotype 2 (cf. *Coupatezia* sp.) from PO-40 (IPS103616) in diagonal labial view; **G**, batoid morphotype 3 (Dasyatidae indet.) from PO-40 (IPS103645) in diagonal lingual view; **H**, actinopterygian morphotype 1 (Actinopterygii indet.) from PO-40 (IPS103613) in lateral view; **I**, actinopterygian morphotype 1 (Actinopterygii indet.) from PO-40 (IPS103609) in occlusal view; **J–K**, actinopterygian morphotype 2 (Tetraodontiformes indet.) from PO-40 (IPS103629) in occlusal (**J**) and lateral (**K**) views; **L**, actinopterygian morphotype 3 (Lepisosteiformes indet.) from PO-39 (IPS103659) in lateral view. All the pictures are ESEM images except **B**, **J** and **K**, which were taken with a Leica stereoscopic binocular with an integrated camera. **Abbreviation**: **ESEM**, Environmental Scanning Electron Microscope. [planned for page width]

FIGURE 12. Age-diagnostic larger benthic foraminifera from Pontils. **A**, *Assilina (Operculina) schwageri* (equatorial section) from PO-23; **B**, *Nummulites garganicus* (equatorial section) from PO-22; **C**, *Nummulites garganicus* (equatorial section) from PO-39; **D**, *Nummulites garnieri sturi* (equatorial section) from PO-33; **E**, *Nummulites garnieri sturi* (equatorial section) from PO-39; **F**, *Nummulites garnieri sturi* (external view) from PO-39. Scale bar equals 500 µm. [planned for page width]

FIGURE 13. SEM images of smaller benthic foraminifera from PO-40. **A**, *Elphidium* sp. in side views (**A1**, **A3**) and apertural view (**A2**); **B**, *Protelphidium* sp. in side views (**B1**, **B3**) and apertural (**B2**) view; **C**, *Protelphidium* cf. *hofkeri* in side views (**C1**, **C3**) and apertural view (**C2**); **D**, *Patellina* sp. in dorsal (**D1**), front (**D2**) and ventral (**D3**) views. Scale bars equal 100 µm. [planned for page width]

FIGURE 14. ESEM images of the charophyte gyrogonites from Pontils. **A–D**, *Raskyella vadaszi* from PO-23 in apical (**A**), lateral (**B**, **C**) and basal (**D**) views; **E–H**, *Nitellospis (Tectochara) major* from PO-25 in apical (**E**), lateral (**F**, **G**) and basal (**H**) views; **I–K**, *Madleriella leiostachys* from PO-25 in apical (**I**), lateral (**J**) and basal (**K**) views. Scale bars equal 500 µm. **Abbreviation**: **ESEM**, Environmental Scanning Electron Microscope. [planned for page width]

FIGURE 15. Chronostratigraphic scheme of the Lutetian-Priabonian, showing the Geomagnetic Polarity Timescale, the Shallow Benthic Zonation (SBZ, based on larger benthic foraminifera), the Mammal Paleogene Reference Levels (MP) and the European Land Mammal Ages (ELMA). MP15 is not included because of the uncertain age of the La Livinière-2 fossil site, previously proposed as the MP15 reference level (see Comte et al., 2012). The line with arrowheads indicates the maximum possible age range of the Pontils fossil assemblage. Modified from Speijer et al. (2020). [planned for column width]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Ypresian
Thanetian
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Pontils Group
Bosc d'en Borràs Fm.
Valldeperes Fm.
Carme Fm.
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Orpí Fm.
Mediona Fm.
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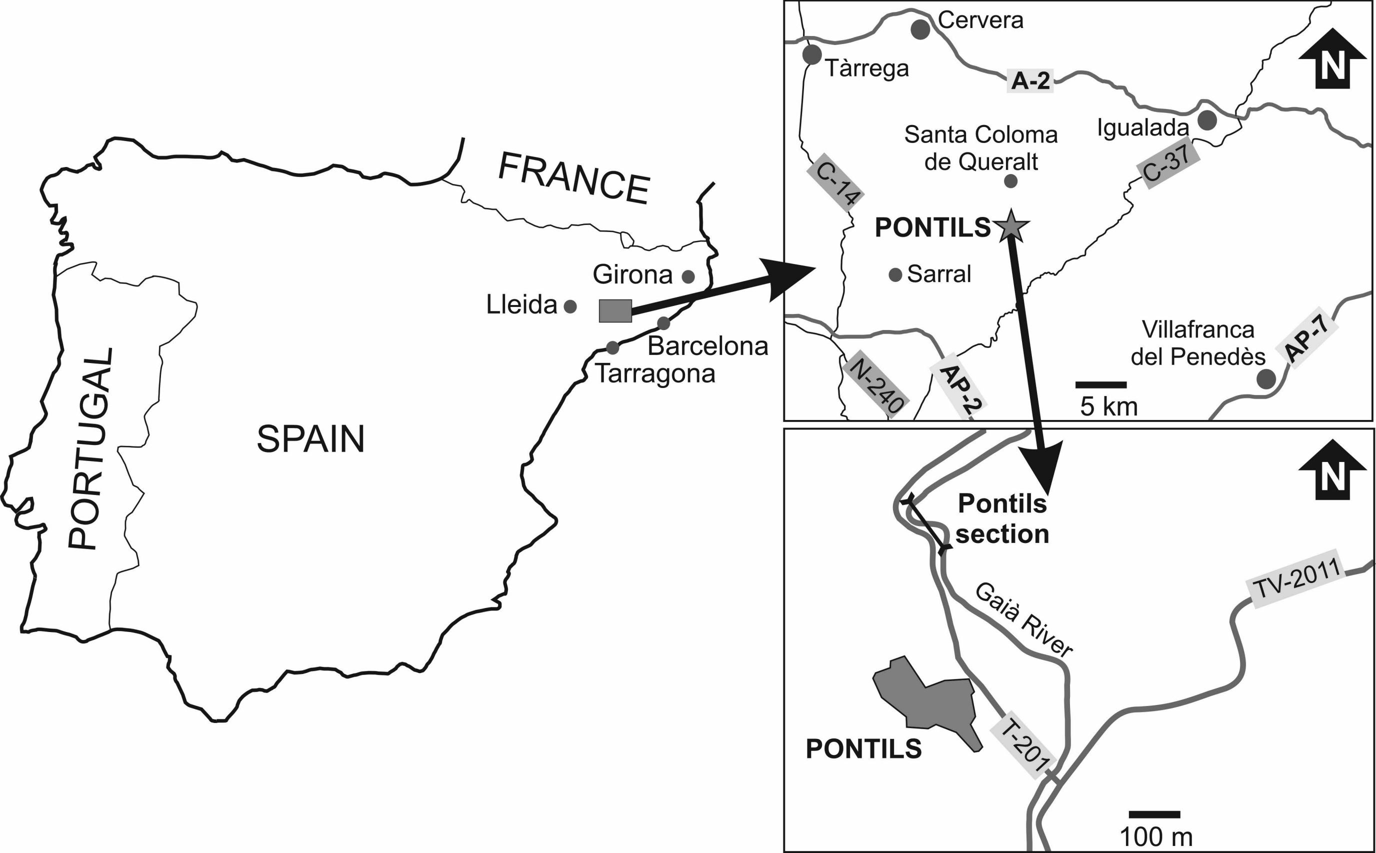
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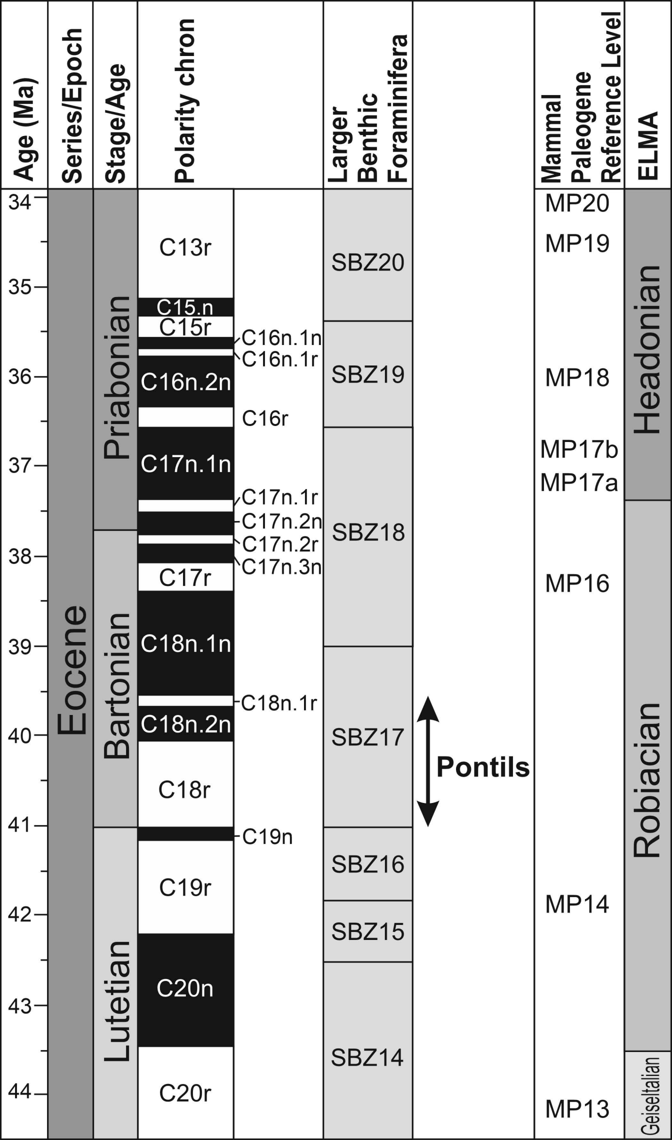
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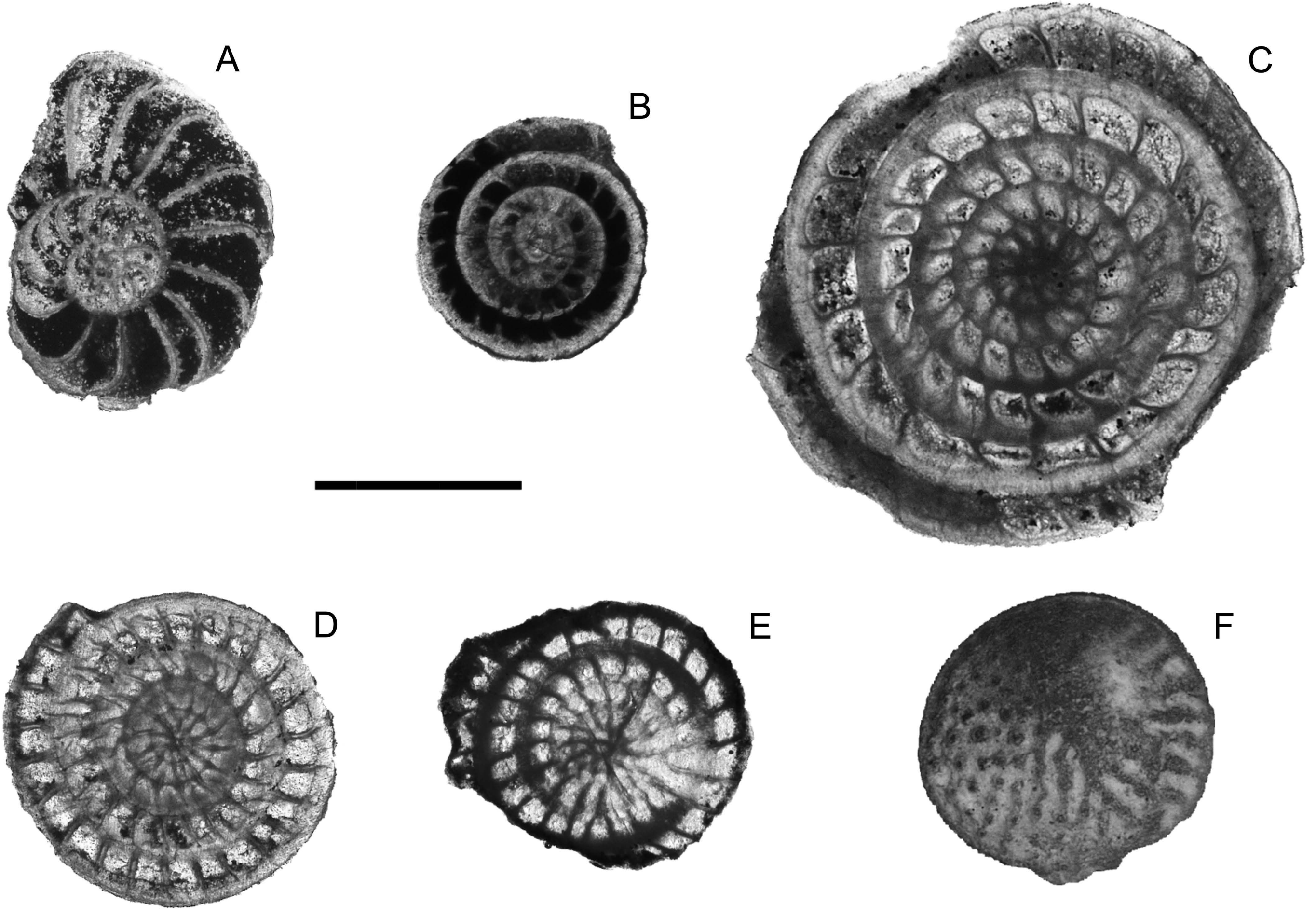
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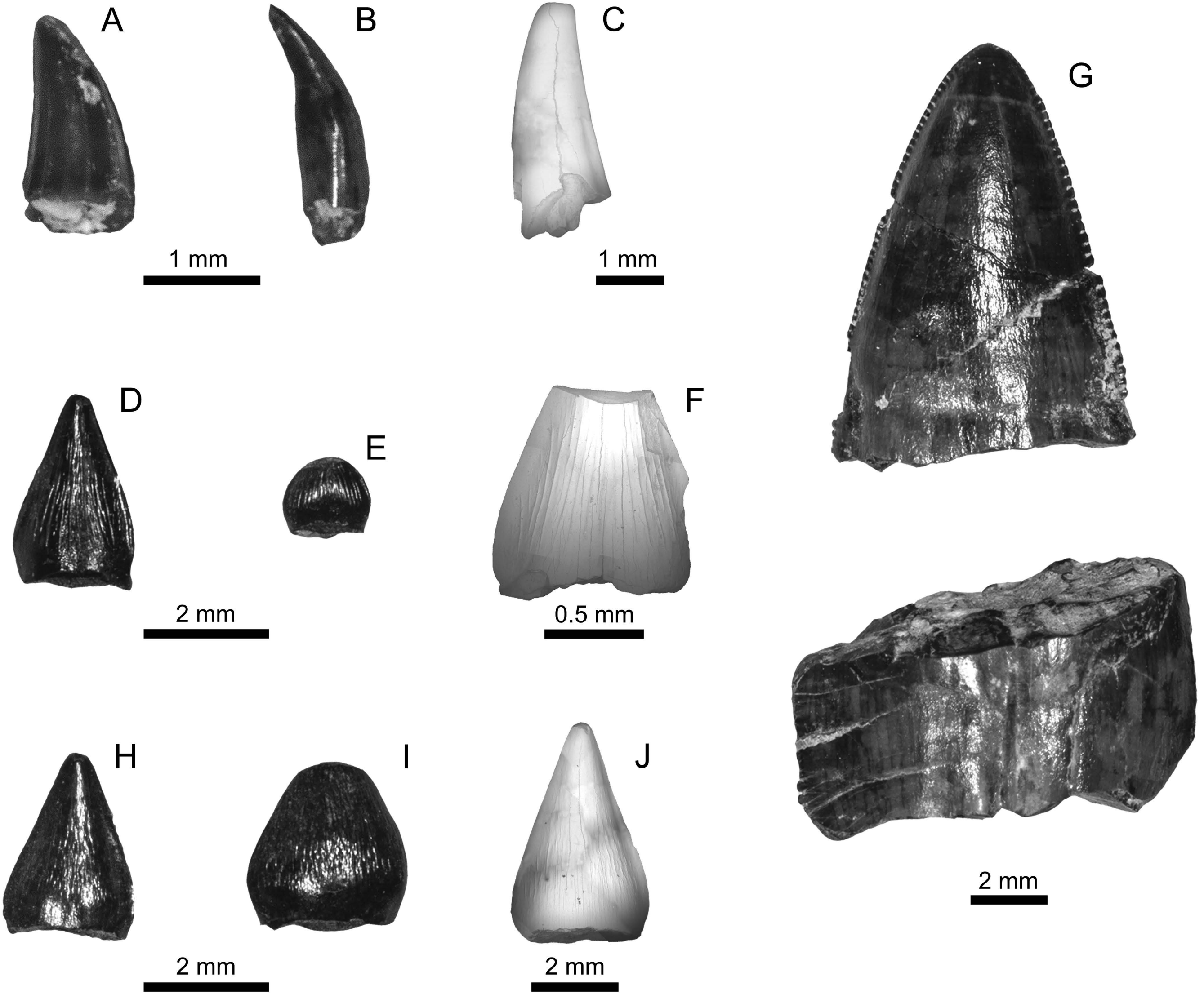
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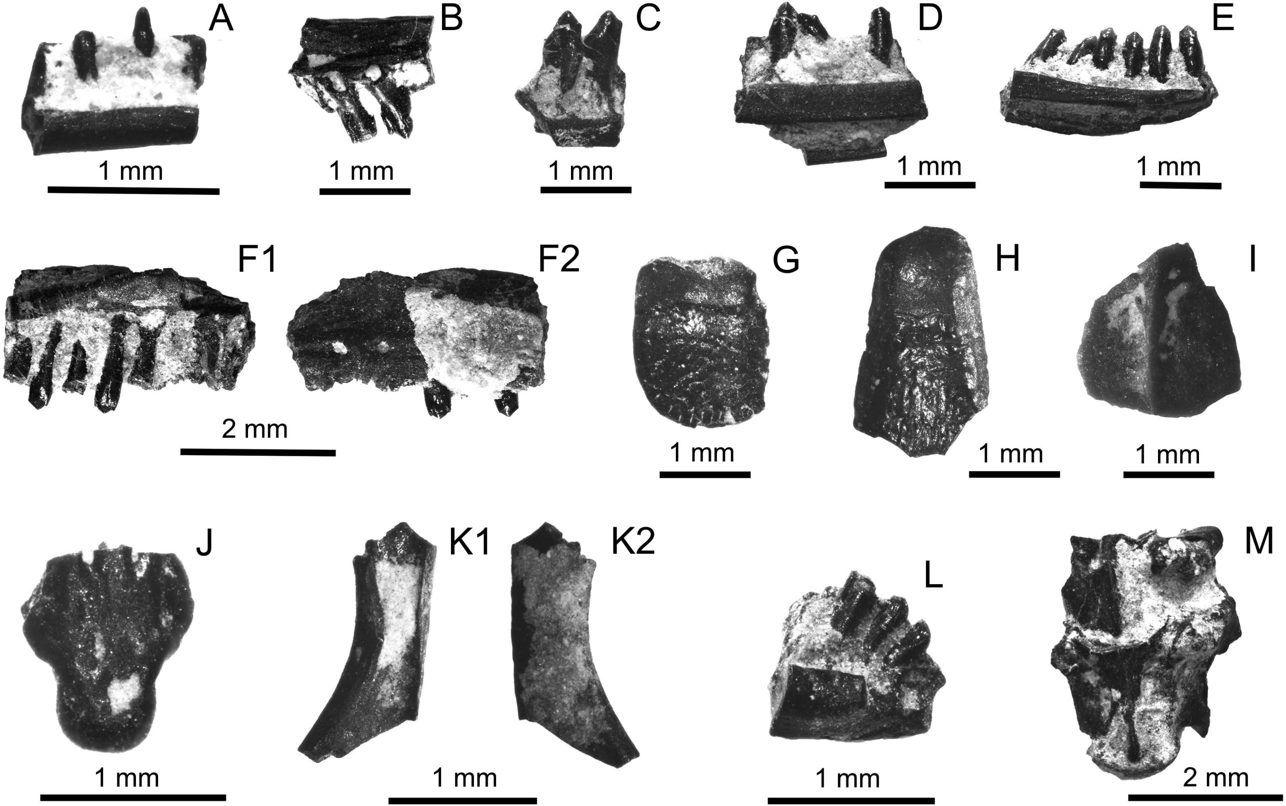
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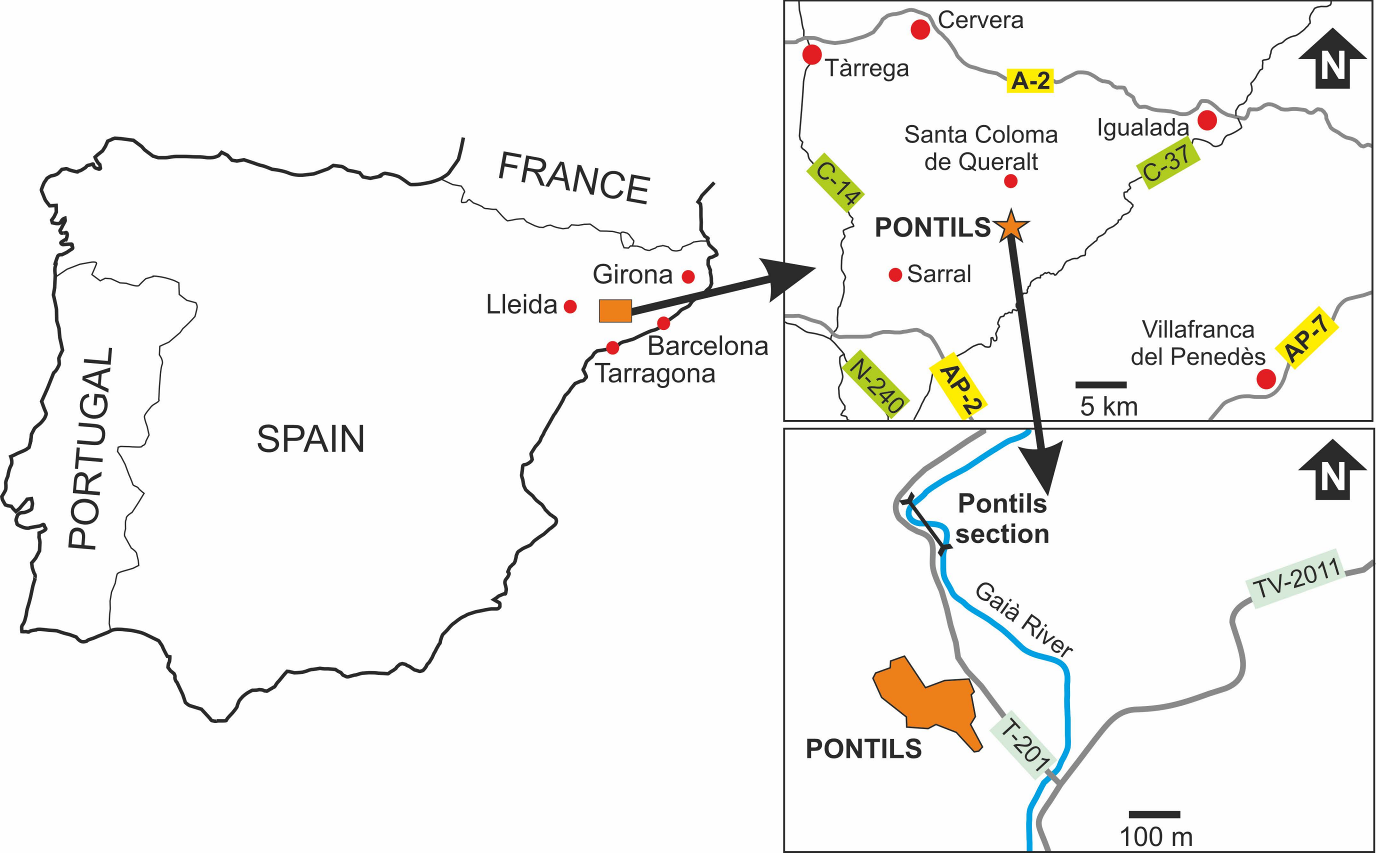
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PONTILS
Sarral
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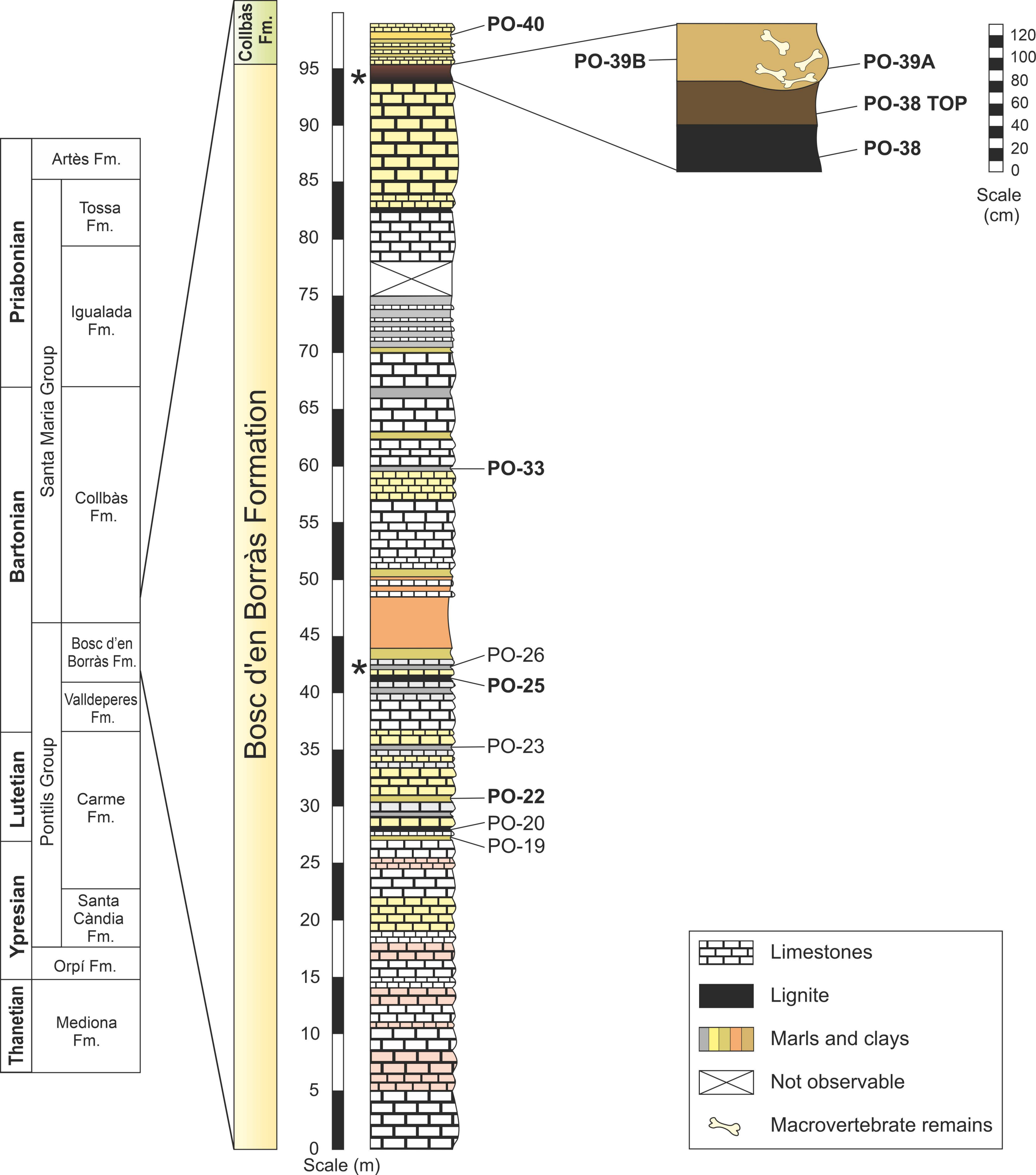
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Scale (cm)
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Marls and clays
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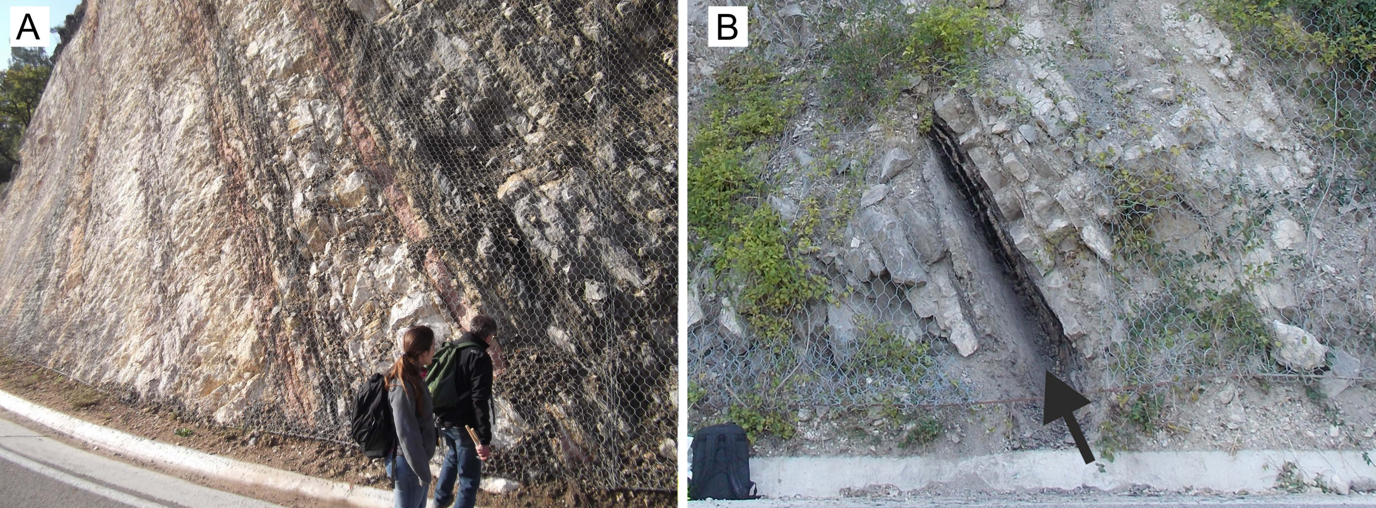
Macrovertebrate remains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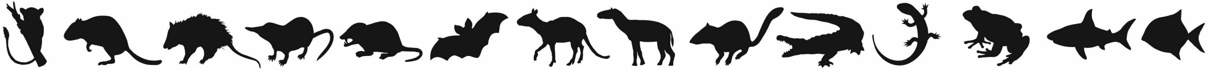
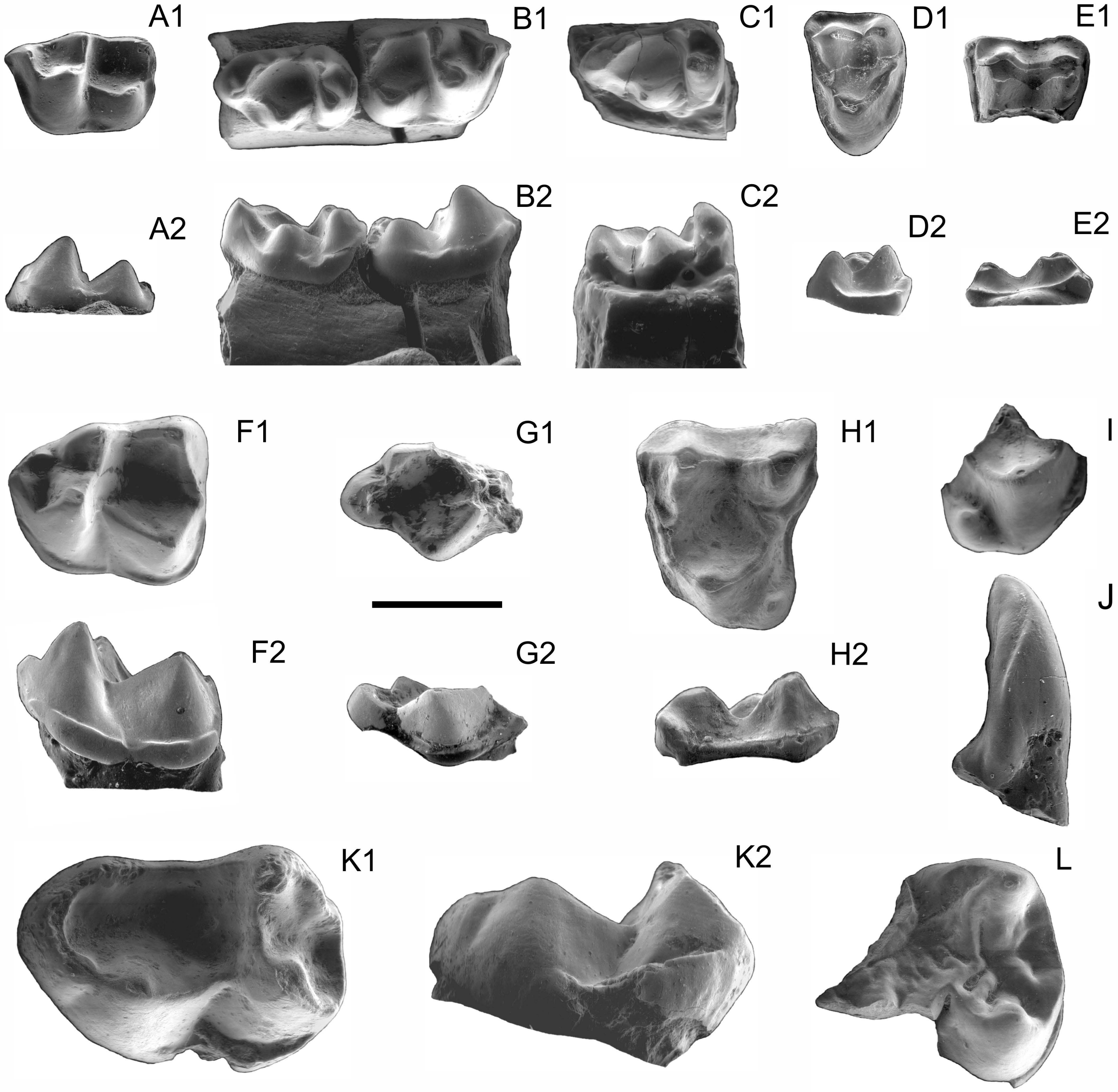


	Primates	Rodents	Metatherians	Eulipotyphlans	Apatotheria	Chiropterans	Artiodactyls	Perissodactyls	Undetermined mammals	Crocodyliforms	Squamates	Amphibians	Chondrichthyans	Actinopterygians
PO-40							■			■	■		■	■
PO-39	■	■			■		■	■	■	■	■		■	■
PO-38 TOP	■	■			■				■	■	■		■	■
PO-38	■	■							■	■				
PO-33	■	■		■		■			■		■			
PO-25	■	■	■	■	■				■	■	■			
PO-22	■	■	■			■			■	■	■	■		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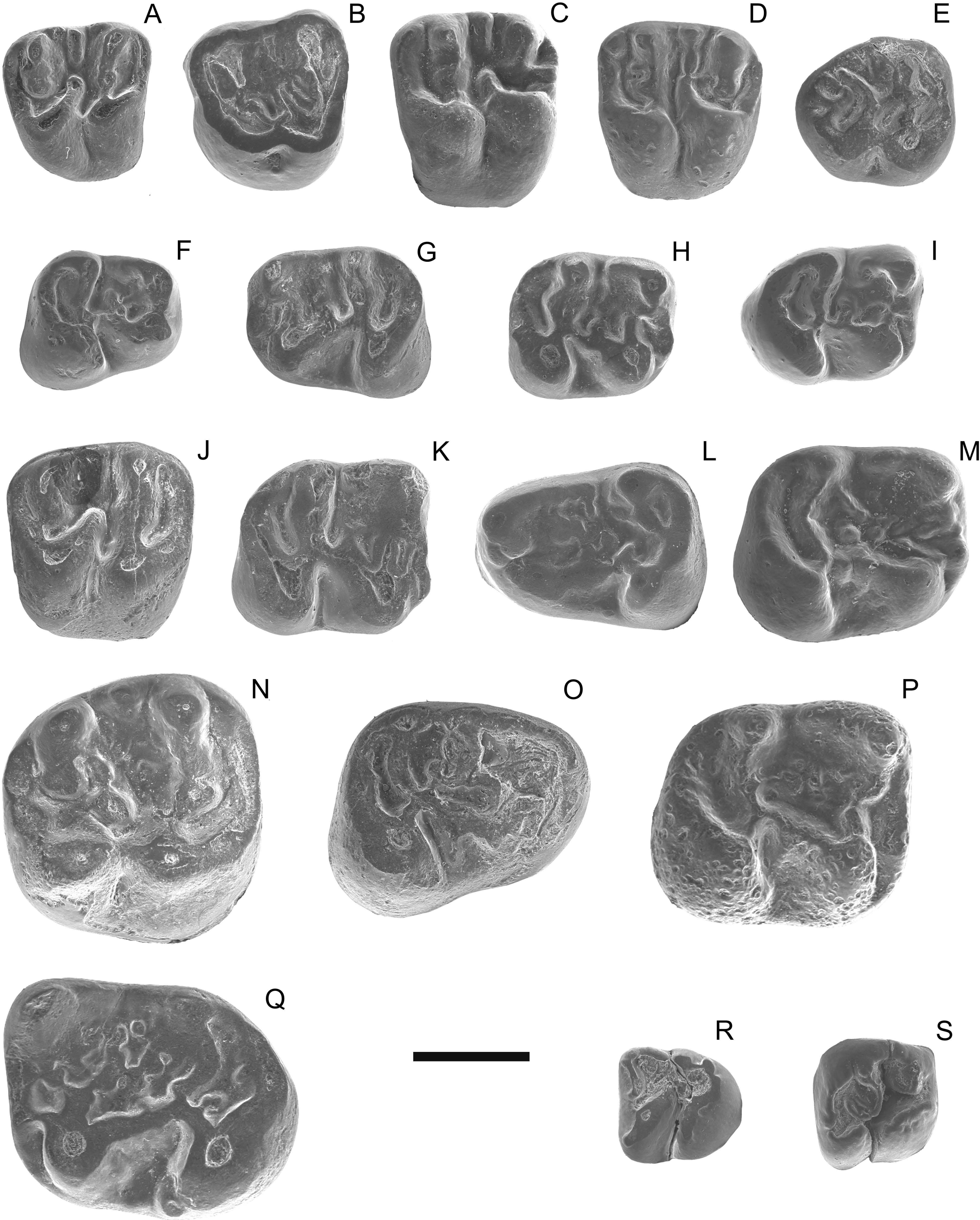
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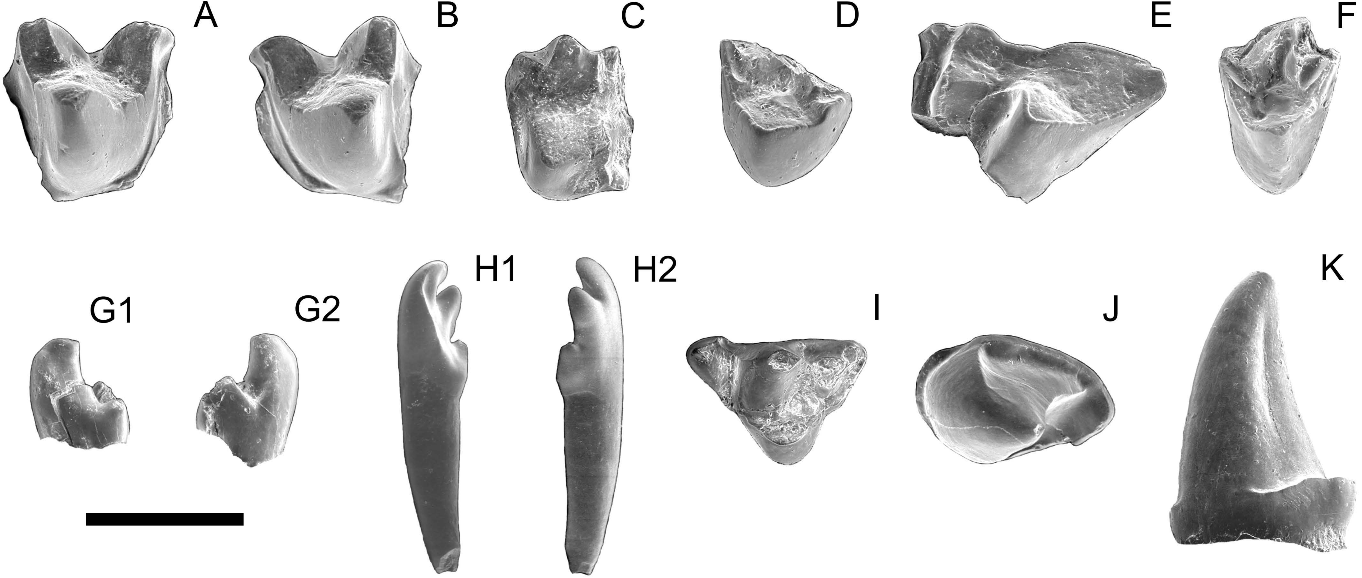
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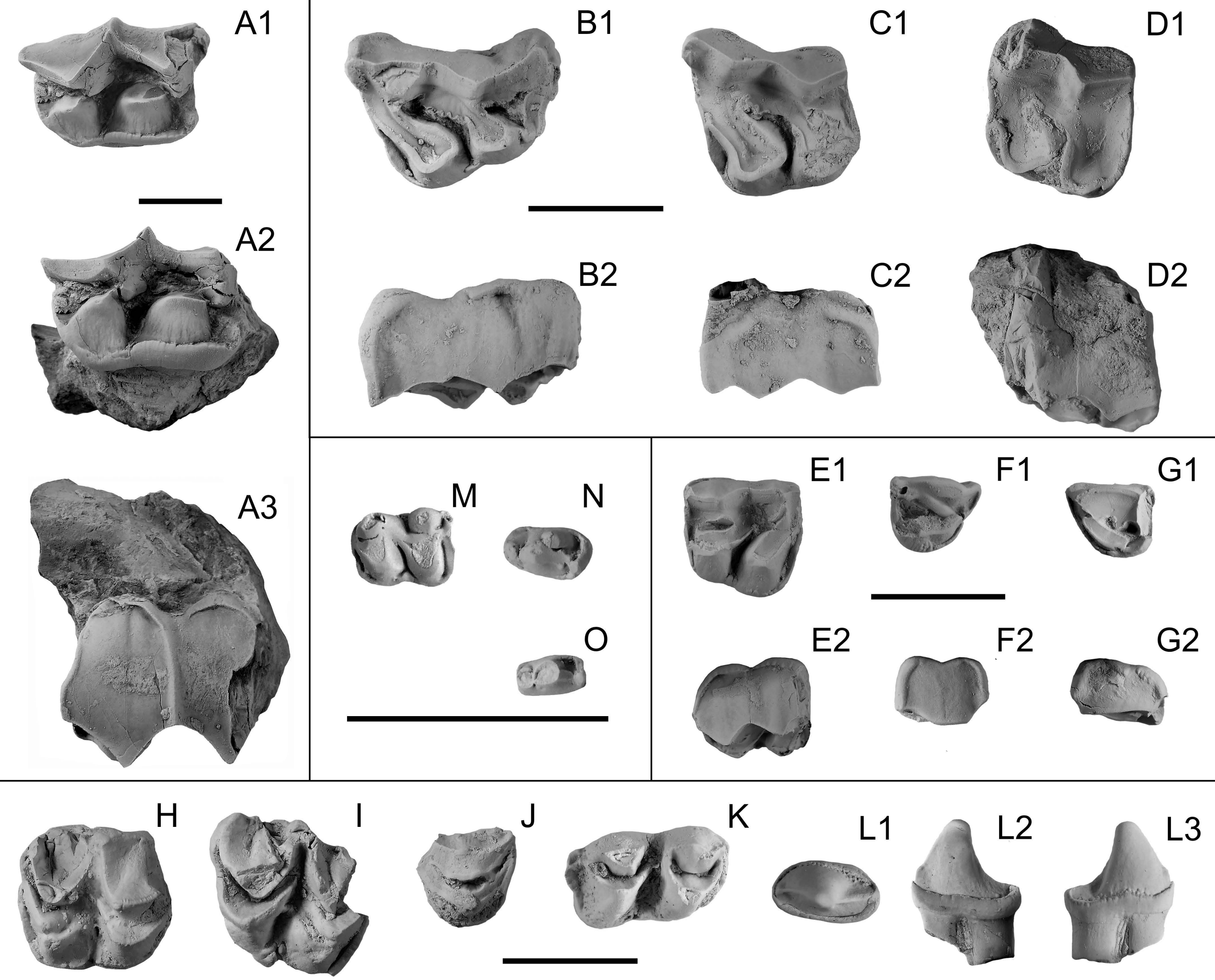
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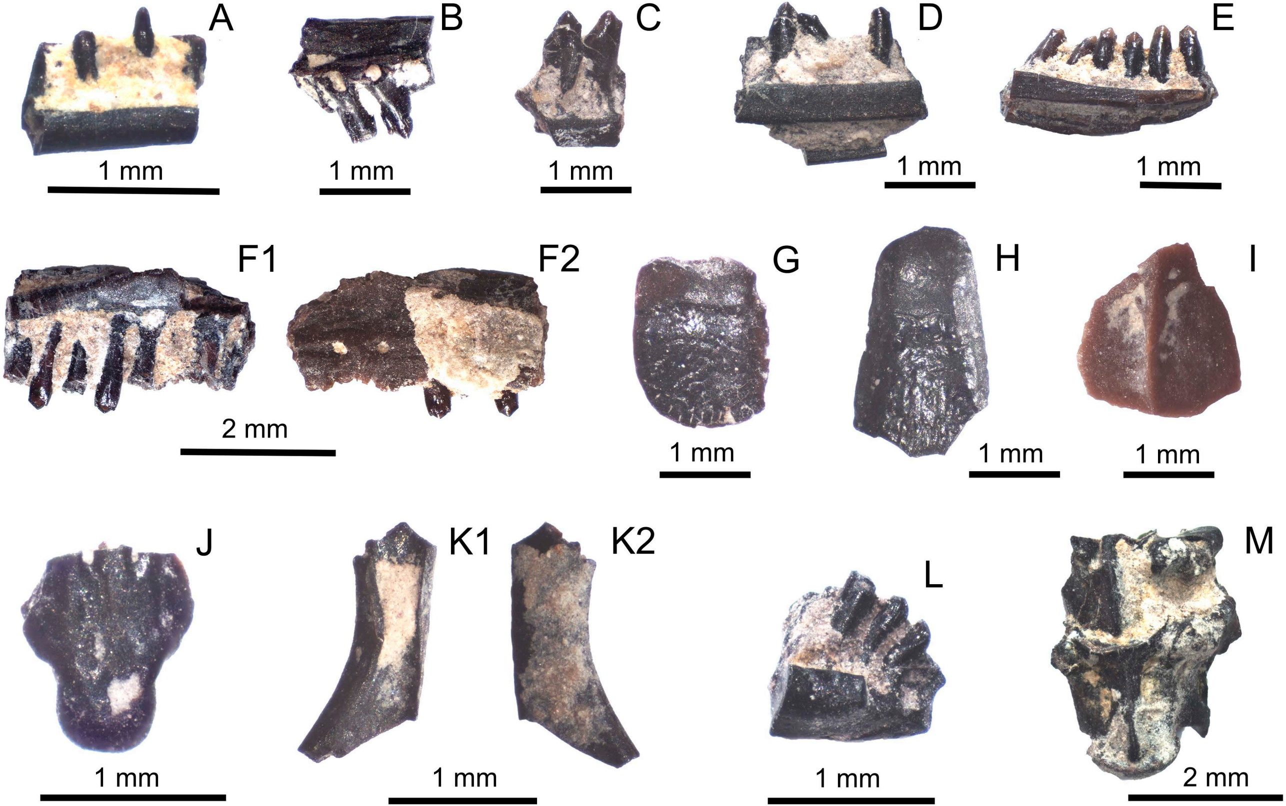
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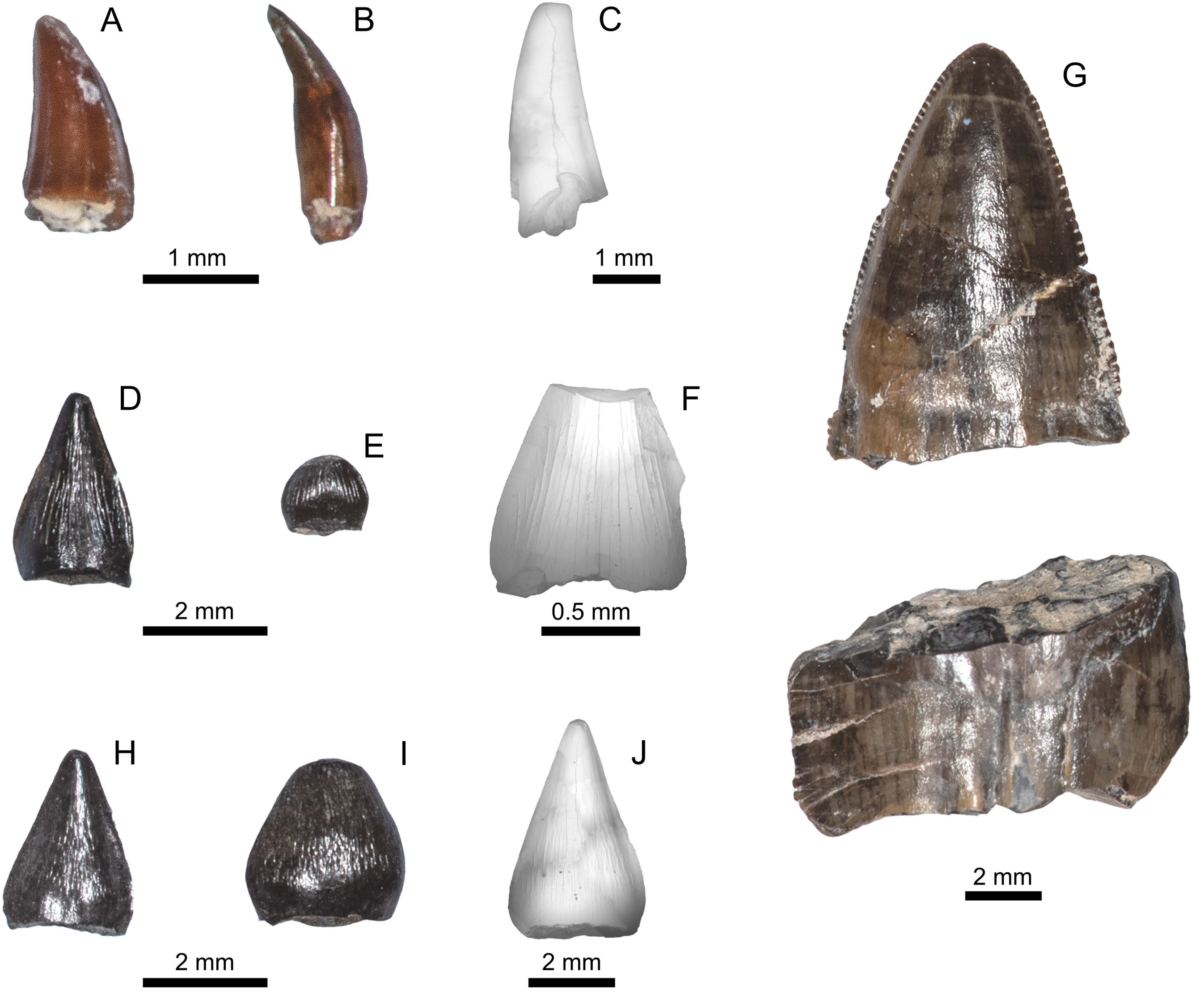
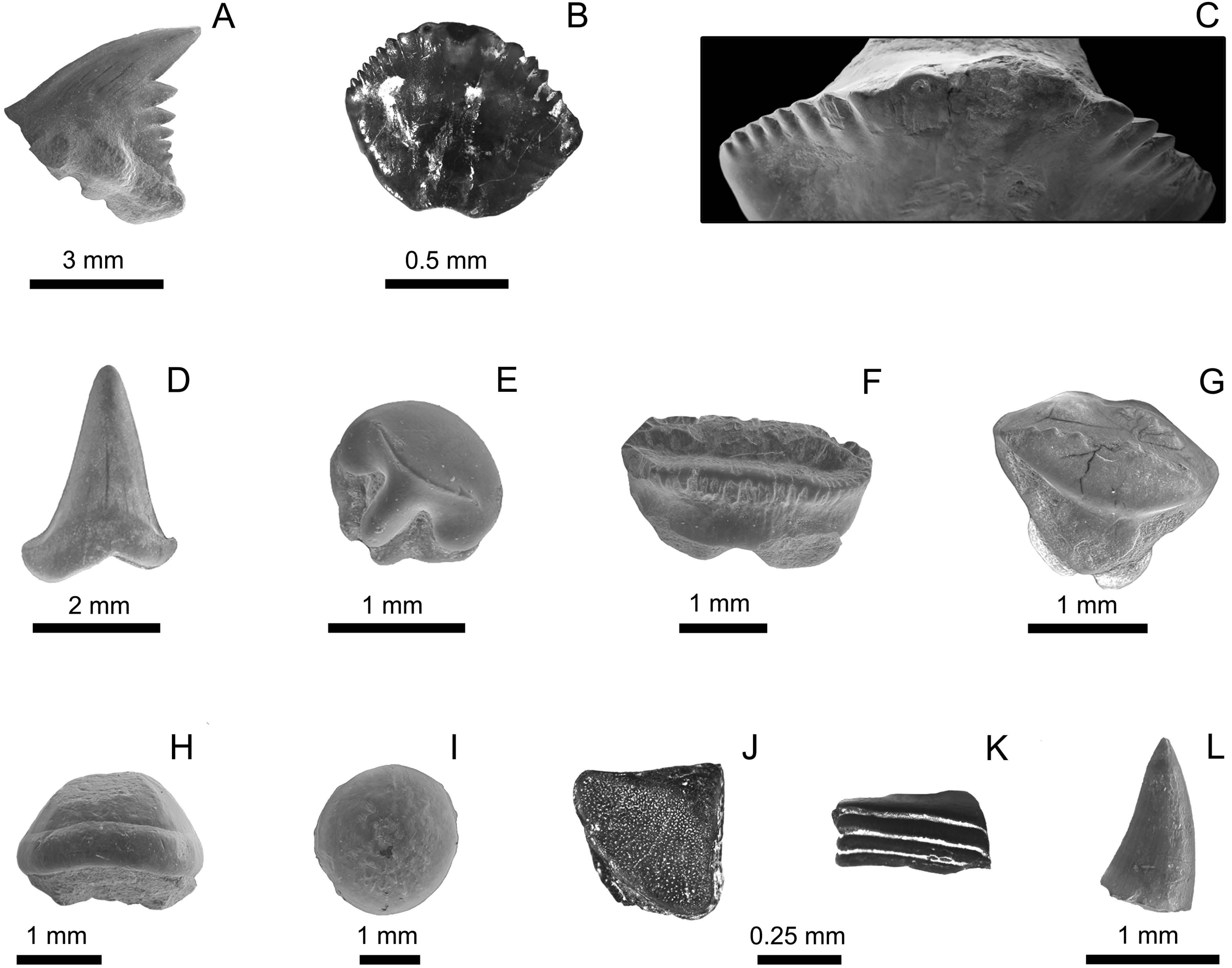
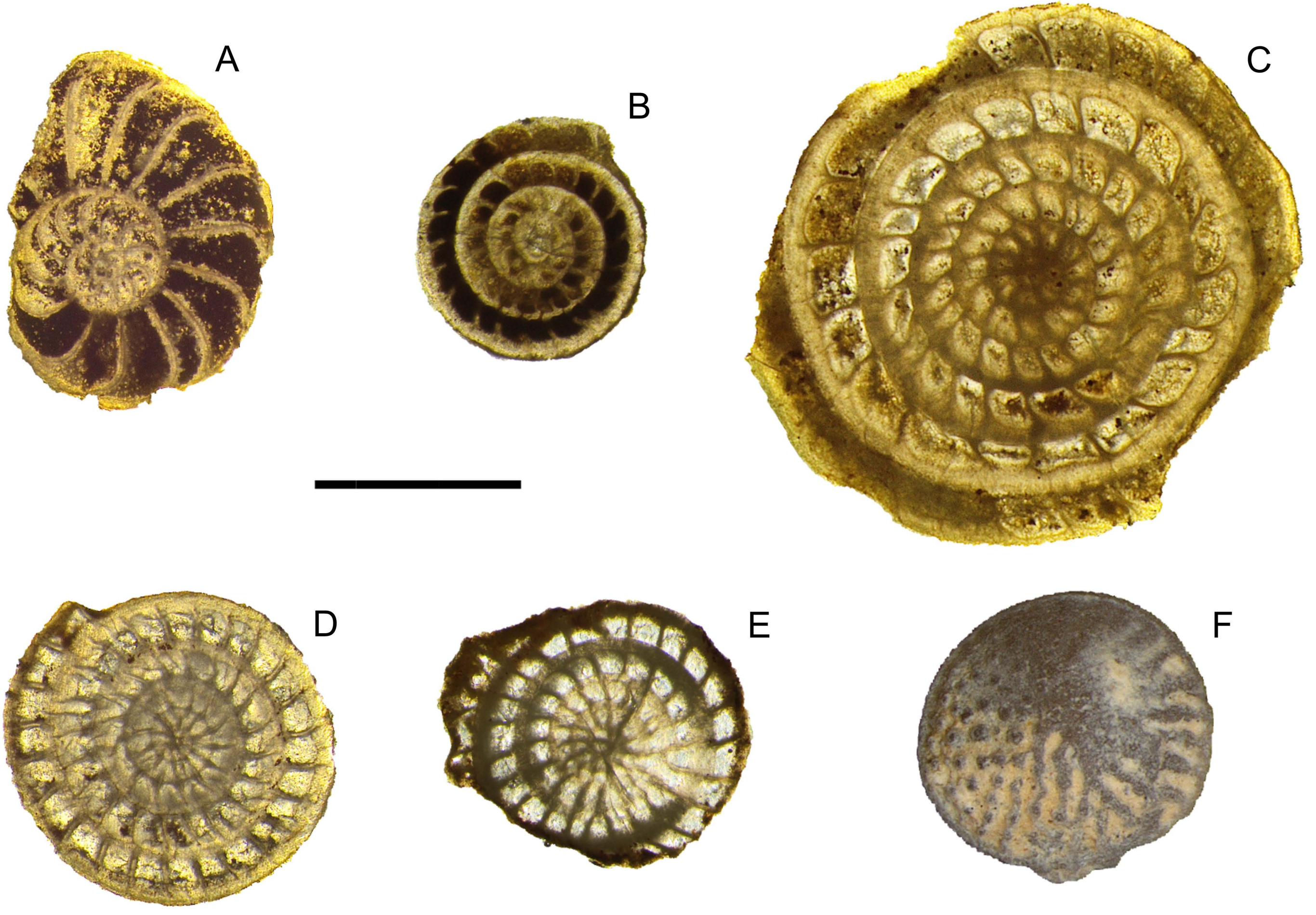
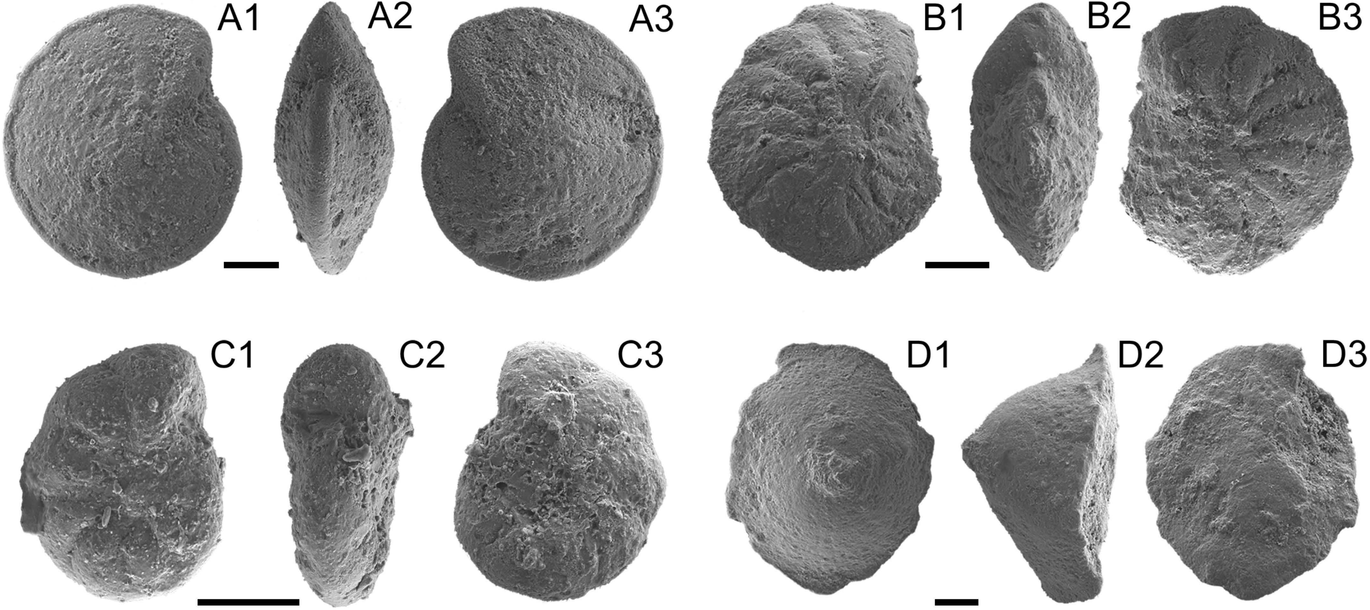
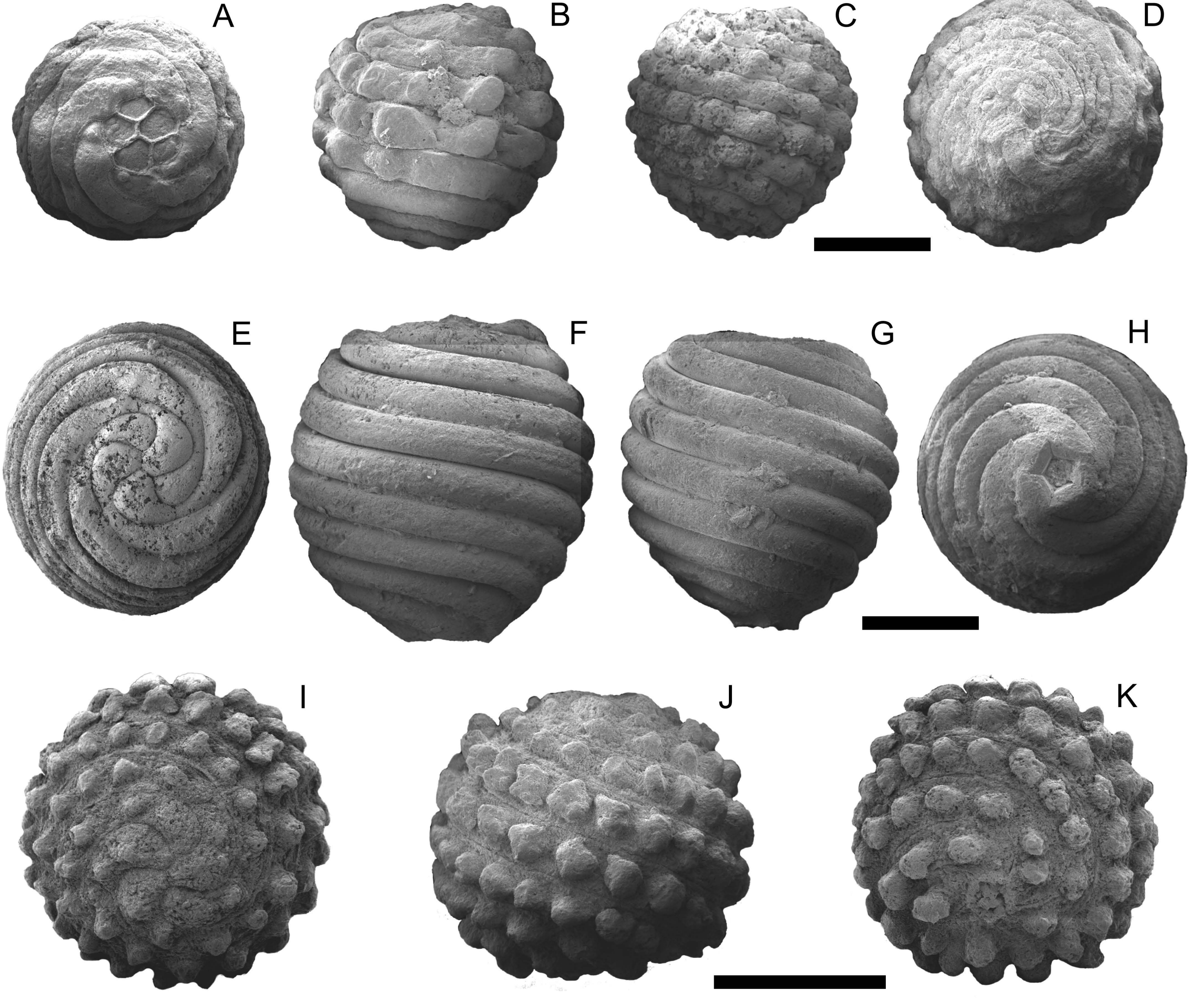
F1
F2
2 mm
G
1 mm
H
1 mm
I
1 mm
J
1 mm
K1
K2
1 mm
L
1 mm
M
2 mm


A
B
C
1 mm
1 mm
G
D
E
F
2 mm
0.5 mm
H
I
J
2 mm
2 mm
2 mm


A
B
C
3 mm
0.5 mm
D
E
F
G
2 mm
1 mm
1 mm
1 mm
H
I
J
K
L
1 mm
1 mm
0.25 mm
1 mm


A
B
C
D
E
F


A1
A2
A3
B1
B2
B3
C1
C2
C3
D1
D2
D3


A
B
C
D
E
F
G
H
I
J
K

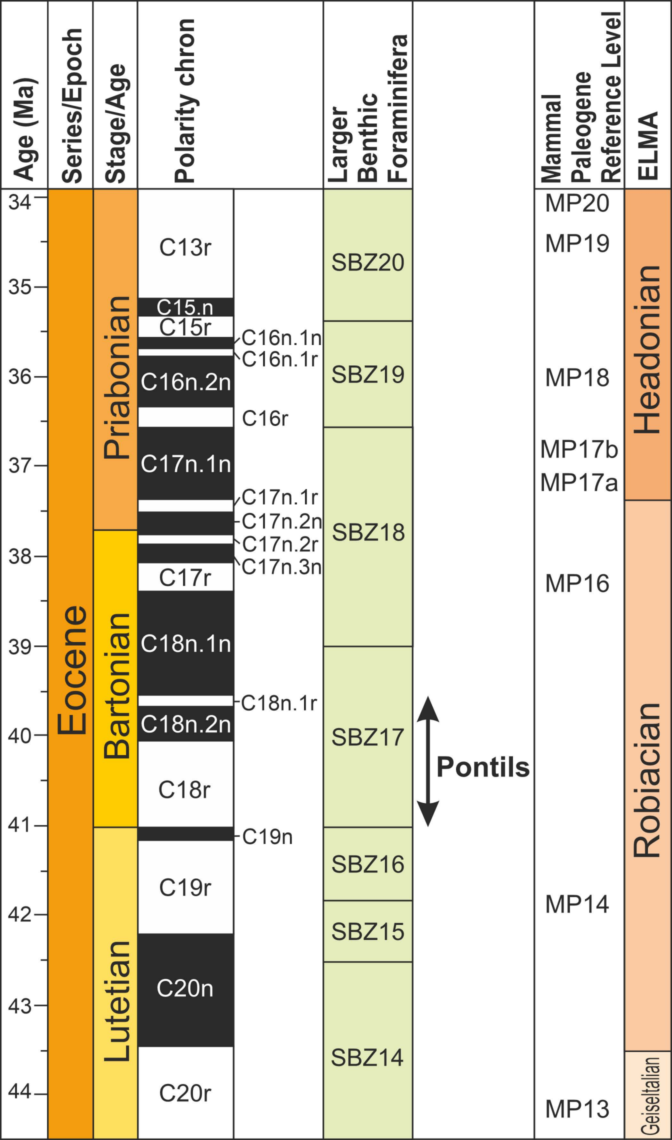

Age (Ma)
Series/Epoch
Stage/Age
Polarity chron
Larger Benthic Foraminifera
Mammal Paleogene Reference Level
ELMA
34
35
36
37
38
39
40
41
42
43
44
Eocene
Priabonian
Bartonian
Lutetian
C13r
C15.n
C15r
C16n.1n
C16n.1r
C16n.2n
C16r
C17n.1n
C17n.1r
C17n.2n
C17n.2r
C17n.3n
C17r
C18n.1n
C18n.1r
C18n.2n
C18r
C19n
C19r
C20n
C20r
SBZ20
SBZ19
SBZ18
SBZ17
SBZ16
SBZ15
SBZ14
Pontils
MP20
MP19
MP18
MP17b
MP17a
MP16
MP14
MP13
Headonian
Robiacian
Geiseltalian

TABLE 1. Sediment weight (in kg) recovered from each sampled level of the Pontils section during the 2012 and 2016 field campaigns.

Level	2012	2016	Total
PO-40	100	200	300
PO-39	840	400	1240
PO-38 TOP	160	500	660
PO-38	540	680	1220
PO-33	180	500	680
PO-26	800	-	800
PO-25	320	440	760
PO-23	200	-	200
PO-22	220	500	720
PO-20	140	-	140
PO-19	40	-	40

TABLE 2. Vertebrate taxa identified in the different levels of the Pontils section studied by Anadón et al. (1983) and in this work.

	Anadón et al. (1983)		This work						
	PO-26	PO-38	PO-22	PO-25	PO-33	PO-38	PO-38	PO-39	PO-40
Mammalia									
Metatheria indet.			X	X					
Primates									
Omomyidae indet.		X	X	X	X	X	X	X	
***Pseudoloris* sp.**			X	X	X	X	X	X	
***Necrolemur* sp.**					X				
Anchomomyini indet.						X			
Rodentia									
***Elfomys* sp.**	X								
Pseudoltinomys cosetanus	X		X	X	X	X	X	X	
***Pseudoltinomys* sp.**			X	X					
***Paradelomys* sp.**	X		X			X			
Pairomys* cf. *ibericus				X				X	
Sciuroides* cf. *romani	X						X	X	
Eulipotyphla									
Eulipotyphla indet.	X	X							
Nyctitheriidae indet.				X	X				

TABLE 2 (CONTINUED)

Apatotheria									
Apatemyidae indet.				X			X	X	
Chiroptera									
Chiroptera indet.			X		X				
Perissodactyla									
cf. *Palaeotherium* sp.								X	
“Pachynolophinae” indet.								X	
cf. *Anchilophus (Paranchilophus*) sp.								X	
Cetartiodactyla									
Dacrytheriinae indet.								X	
Hyperdichobuninae indet.									X
Sauropsida									
Sebecosuchia indet.								X	
Crocodylia indet.	X		X	X		X	X	X	X
Gekkota indet.			X					X	
Scincidae indet.			X						
Lacertidae indet. Morph 1			X		X				
Lacertidae indet. Morph 2			X		X				
cf. *Geiseltaliellus* sp.								X	
Anguinae indet.			X		X			X	
Glyptosaurinae indet.				X					
Serpentes indet.			X	X	X			X	
Indeterminate lizards			X	X			X		X
Amphibia									
Anura indet.			X						

TABLE 2 (CONTINUED)

Chondrichthyes			
cf. *Rhinobatos* sp.			X
cf. *Coupatezia* sp.		X	X
Dasyatidae indet.	X	X	X
cf. *Hemipristis* sp.		X	X
Selachii indet.	X	X	X
cf. *Nebrius* sp.			X
Osteichthyes			
Actinopterygii indet.	X	X	X
Lepisosteiformes indet.		X	
Teleostei			
Tetraodontiformes indet.			X