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Primates and Plesiadapiformes from Cos (Eocene, Quercy, France)

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Abstract

A new fauna has been collected from a fissure filling named Cos in the Quercy region, South-West France. It includes four primate species and a plesiadapiform. The cercamoniine adapiform *Protoadapis andrei* Godinot and Vidalenc nov. sp. is represented by a material which completes our knowledge of the genus *Protoadapis* for upper canine, upper molar and other details of morphology. It appears more primitive than *P. brachyrhynchus* from the Old Quercy Collections. The other cercamoniine *Pronycticebus cosensis* Godinot and Vidalenc nov. sp. completes our knowledge of the genus, including data on intraspecific variations. Both species suggest a bushy evolution within these genera. Two teeth document the presence of a third cercamoniine, *Anchomomys* sp. indet. The new microchoerid *Quercyloris eloisae* Godinot and Vidalenc nov. gen. nov. sp. has very primitive characters and seems to document a primitive member of the *Pseudoloris* clade. A poorly documented paromomyid plesiadapiform is distinct enough to be named *Arcius moniquae* nov. sp.. It represents the first discovery of a plesiadapiform in the Quercy fossil record and makes a link with paromomyids surviving until the Lutetian MP 13 level. The primates indicate a broad age interval between MP 10 and MP 12. The identification of the same species of *Pronycticebus* and of the new genus in the Vielase fauna suggests more precisely the MP 10 – MP 11 interval.

Keywords: Adapiformes, Microchoeridae, Paromomyidae, Lutetian, Europe

1. Introduction

Fossil primates were found very soon after the beginning of the industrial exploitation of phosphatic deposits known as Phosphorites du Quercy. Quercy is a limestone plateau south-west of the French Central Mountain. Its name refers to abundant oak forests (*Quercus*) which covered the region in historical time. At the end of the XIXth Cenury, fissure-fillings rich in phosphatic deposists were exploited, and during industrial exploitation remains of fossil vertebrates were discovered and soon made the region famous for them. Fossils primates found at that time plaid a role in science. A cranium found in Beduer revealed that the enigmatic mammal described by Cuvier (1822) as *Adapis* indeed was a primate, something that had not been realized before (Delfortrie, 1873). Further fossil primates were described by Filhol (e.g. 1874), among others by Grandidier (1904), Schlosser (1907), and a major contribution was given in two steps by Stehlin (1912, 1916). Fossil primates found in the XIXth or early XXth Centuries had sometimes no precise provenance, sometimes were located with a village name. However, most of these village names are useless because a number of fissures were exploited in their vicinity. A few exceptions are large fissures which were given a name, e.g. Mémerlein, Prajoux. All the early finds are labelled Old Quercy Collections.

A large number of the fissures were emptied by industrial exploitation. However, a systematic search for fossil remains was started in the 1960s by paleontologists from Montpellier, Poitiers and Paris. It was discovered that mounds of clay residues were sometimes left at close proximity of the exploited fissures, which in a few cases allowed the collecting of a small vertebrate fauna coming from that fissure. More importantly, there are still remnants of pockets, sometimes deep in underground galleries, sometimes closer to the surface. Some of them still contain filling without phosphatic deposit and often without fossils (pure red clay). However, others yielded vertebrate fossils, collected by washing and screening. A few entirely new untouched pockets were even found. The number of fossil localities progressively increased, allowing the building of a new vertebrate record, known as New Quercy Collections. Steps in the building and study of this record can be found in paleontological syntheses (Crochet et al., 1981; Rémy et al., 1987; Mourer-Chauviré, 2006; Rage, 2006; Sigé and Crochet, 2006; Sigé & Hugueney, 2006). Field work in the Quercy continues, in large part in the context of a geological reserve in the Lot Department, where the fossiliferous deposits now are protected.

Paleontological studies also continue in many groups, including plants, insects, lower vertebrates, birds and mammals. Concerning primates, some well-dated material was published (Godinot, 1984a, 1985, 1988, 2003), some postcranials were published (Dagosto, 1983, Godinot and Dagosto, 1983; Godinot, 1992; Bacon and Godinot, 1998). The systematics of large adapines was revised (Godinot and Couette, 2008) and adapine locomotion continues to be discussed (Boyer et al., 2013; Marigo et al., 2019). Until now, some of the primates found in the XIXth Century had never been found again, e.g. *Necrolemur zittelli, Pronycticebus gaudryi, Protoadapis (Cercamonius) brachyrhynchus, P. angustidens*, etc… In this context, the new fauna of Cos provides crucial new evidence which at the same time completes earlier finds and yields entirely unsuspected forms. The whole underlines that our knowledge of Quercy primates still is far from complete. It is worth noting that the Cos fissure was the very first to be discovered by Jean André Poumarède in 1865. This eclectic scholar observed that wheat was exceptionally vigorous in the area, and discovered that the soil was rich in nodules containing a high proportion of tricalcic phosphate. He then started the first exploitation, for fertilizer, of what soon became famous as Phosphorites du Quercy (Pulou, 1980).

2. Geological setting

The fissure, with its fossiliferous content, lies within marine limestones of the Cajarc Formation, dated late Bajocian/Bathonian. It is a large excavation, almost empty, of around 80 x 50 m, elongated in a N110°E direction, which is one of the major directions of fracturation for the Quercy plateaux. The bottom of the excavation is filled by a water body known as the

Lac de Cos. At its South-East are remnants of exploitation, which make a mound of ~65 x 60 m. The rims of the fissure are covered by vegetation, except in the small area cleaned by one of us (D.V.) for quarrying in search of fossils (Fig. 1), during several decades.

The sedimentary unit, with the fossiliferous remains, is composed by small beds of granular and porous limestones punctually alternating with red clays sometimes rich in small pisoliths. The limestones are stratified, folded, probably affected by gliding (Fig. 1), and their relations with the red clays remains unclear. There are fossils scattered all through the section, not abundant, however concentrations of bird shells were found toward the top, and micromammals were found in one bed. Toward the bottom is a 20 cm bed with complete bird bones. This filling is unlike those found in other remnant pockets in the Quercy region, and a more elaborated sedimentological study has been undertaken, which will be published elsewhere.

3. Material and methods

All the fossils described here were excavated, prepared and catalogued by one of us (D.V.). They are housed in the collections of Montpellier University. One exception is an M3/ from an amateur collection, of which a cast is deposited in the University collection. Geological observations were done on the site by the crew, especially the geologists (C.L. and T.P.). Measurements were done with a digital caliper for the larger specimens (more than 1 cm), and with a Nikon Measuring Microscope MM – 400/SL with electronic lecture on a Heidenhain screen for smaller specimens, i.e. almost all teeth. When there is no special indication, two successive measurements related by an x mean Length x Width; they are given in mm. Photographs of specimens were taken with a digital camera with computer control (Canon EOS 5D, Mark III camera and EOS Utility software). Most comparisons of the fossils were done under a binocular using high quality expoxy casts for the comparative material of middle sized species, and sometimes original fossils when they were available (e.g. for *Europolemur mancyi* from the Paris basin). One exception is *Protadapis weigelti*, for which only the description and figures in Thalmann (1994) could be used. For the very small microchoerid, a cast of the type specimen of *P. isabenae* was available, and the first author was able to take excellent macro photographs of *P. saalae* during a visit in Halle. For the paromomyid, casts were available for *Arcius rougieri* and *A. ilerdensis*, and excellent illustrations of the other species are provided in Aumont (2003). Dental nomenclature follows usual terms for primate dentitions (see Szalay and Delson, 1979), with the addition of two terms: for upper molrs, centrocrista is used for postparacrista + premetacrista; for lower molars and p/4, postvallid is used for the valley situated between protoconid and hypoconid.

4. Systematic Paleontology

Class Mammalia Linnaeus, 1758

Order Primates Linnaeus, 1758

Suborder Strepsirrhini Geoffroy Saint-Hilaire, 1812

Infraorder Adapiformes Hoffstetter, 1977

Family Notharctidae Trouessart, 1879

Subfamily Cercamoniinae Gingerich, 1975

Genus *Protoadapis* Lemoine, 1880

4.1. Protoadapis andrei Godinot and Vidalenc nov. sp.

Figures 2 and 3

Derivation of the name: dedicated to Mr André Boutié, in recognition of his continuous support of field work to one of us (D. V.).

Holotype: the right mandible Cos 253 bearing p/3 to m/3 (Montpellier University collection)

Referred material: a left jaw bearing the p/3 Cos 254; isolated teeth, m/3 Cos 246, upper canine Cos 753, P4/ Cos 77, M2/ Cos 247, M3/ Cos 248; two lower incisors are referred with less confidence, i/1 Cos 252 and i/2 Cos 249.

Type locality: Cos, fissure-filling in the Quercy region (South West France);

Occurrence: type locality only;

Measurements: type mandible Cos 253: p/3, 5.76 x 3,48; p/4, 5.55 x 3.87; m/1, 5.82 x 4.10; m/2, 6.03 x 4.47; m/3, 7.14 x 3.98; p/3 Cos 254, 5,51 x 3.66; m/3 Cos 246, 6.98 x 4.14; P4/ Cos 77, 4.59 x 5.75; M2/ Cos 247, 5.83 x 7.47; M3/ Cos 248, 4.66 x >= 5.94. Canine Cos 753, length at the cervix measured in profile, 6.30; perpendicular width, 4.71; height in the middle, 11.80 on the labial side, 11.65 on the lingual side; i/2 Cos 249, 2.23 (mesio-distal) x 2.38 (labio-lingual); i/1 Cos 252, 1.94 x 1.90. Measurements of mandibles are given in the descriptions.

Diagnosis: Large *Protoadapis* species, which differs from *P. weigelti* by its very high p/3, posteriorly broader p/4, and m/1 with a broader trigonid, a paraconid and a lingually open trigonid basin. Differs from *P. angustidens* by its much broader p/4, especially in its posterior part, and by an m/2 which is not much broader than m/1 and m/3. Differs from *P. (Cercamonius) brachyrhynchus* by the presence of a p/1 and a double-rooted p/2 instead of only a single-rooted p/2 in the latter; by a p/4, which has a larger and higher placed metaconid, and is posteriorly broader, having a broader talonid basin and a larger hypoconid; by a slightly longer paralophid on m/1 and m/2.

4.1.1. Description

Description of mandibles.

The right mandible Cos 253, which is the type-specimen, is incomplete and somewhat deformed (Fig. 2A-B). The corpus of the mandible is broken in several regions. Below and posteriorly to m/3, and at the anterior extremity, fissures and small displacements are due to taphonomic processes. In the middle of the corpus, a large fissure starting between m/1 and m/2 and running anteroventrally, which was accentuated or produced when the specimen was found, is repared with plaster. In its present state, the mandible gives the impression of an increase in height of the corpus from m/2 onward, however the height below p/4 is exaggerated by the plaster reconstruction. Parts of the corpus are intact enough below the anterior root of p/3 and below the posterior root of m/2 to permit measurement of corpus height in these two places. Measurements give, below p/3, 14.6 mm in labial view and 15.8 in lingual view; and below m/2 13.5 in labial view and 14.6 in lingual view. These measurements show that there was a slight anterior increase in height between m/2 and p/3. The maximum thickness of the corpus is 7.75 below p/3 and 7.0 below m/2.

The posterior part of the mandible is well preserved from its ventral rim to the level of the articular condyle. The coronoid process is broken away. The condyle is well preserved on its labial side, and slightly deformed on its lingual side by erosion of the dorsal surface and breakage and repair of a small piece of bone. Continuity of the ventral and lingual surfaces shows the deformation to be small. In dorsal view, the condyle is salient lingually. Its total labiolingual extension is 9.6 mm. The dorsal articular surface seems to have been slightly convex anteroposteriorly and almost flat mediolaterally. Judging from the posterior part of the mandible as seen in lingual view, it seems that the condyle was relatively low, close to the level of m/2-3. The angular process is preceded anteriorly by a marked dorsal concavity. It is ventrally convex, hook-like with its extremity directed slightly dorsoposteriorly, and its whole body is deflected posterolingually (Fig. 2B). Anteriorly, the symphyseal surface of Cos 253 starts below the posterior border of the posterior alveolus for p/2. Its limit is not sharply defined, due to some erosion. The anterior part of the mandible is very well preserved on the next specimen.

Cos 254, a left lower mandible bearing p/3, is not at all deformed (Fig. 2C-E). The p/3 of this specimen is very similar in size and morphology to the preceding one, however there are differences in the size of the mare anterior premolars and diastemae. On Cos 253, the alveoli for p/2 are large, the posterior being of similar size to the anterior alveolus of p/3. They are separated from p/3 by a substantial diastema, as long as the posterior alveolus of p/2. The crown of p/2 must have been as broad as the anterior part of p/3 but much shorter than the latter, and slightly offset posterolingually. A small diastema separates p/2 from the alveolus for p/1, which is again large (almost the size of the anterior root of p/2). The p/1 alveolus is close to the posterior border of the large canine alveolus. On Cos 254, the alveoli for p/2 are smaller than those of Cos 253 and the posterior one is appressed against the anterior border of p/3, without any diastema. The alveolus for p/1 is also smaller than on Cos 253, separated from the alveoli for p/2 by a longer diastema, and from the canine alveolus also by a slightly longer and ventroposteriorly inclined diastema. The canine alveolus is large. In dorsal view, it has an almost anteroposteriorly straight lingual rim. The labial rim is convex and shows an oval and elongated outline in dorsal view, however in labial view it appears ventrally curved (with a height slightly exaggerated by breakage of a small chip of the ventral border). This suggests that a relatively large canine was anteriorly and labially inclined (the posterior inclination of the canine root can be seen on Cos 253 through the posteroventral inclination of the posterior border of its canine alveolus). On Cos 254, the curvature of the anteroventral border of the jaw, anterodosally inclined, suggests that little bone is missing. What remains of the incisor alveoli shows that there was a small i/1 (root close in size to the root of p/1 but more compressed) and a large i/2 (compressed, root length close to p/2 alveoli length, root breadth similar to p/1 root breadth).

The mandibular corpus of Cos 254 shows a broad ventral convexity from below m/2 to the anterior part. The symphyseal region is very well delineated by a salient dorsal rim starting below the p/2-p/3 limit and a ventral rim more extended posteriorly (below p/3). The symphyseal surface is long and high, only slightly anterodorsally inclined (angle difficult to estimate because the alveolar rim is not preserved on enough length, the ventral border is curved – possibly around 30°). The salient posterior extremity of the ventral symphyseal rim underlines the presence, just behind, of a pit for the insertion of the geniohyoid muscles.

Description of lower teeth.

On Cos 253, the p/3 is a simple and high tooth (Fig. 3F,H). It is clearly higher than p/4. In profile view, the preprotocrista is slightly curved, convex anteriorly; the postprotocrista is straight in its first quarter below the summit, and after a point of inflexion it becomes slightly more abrupt and very slightly concave posteriorly. Its base is lowered by wear. The lingual cingulum is thin, continuous with a low dorsal convexity in its middle. The labial cingulum is thinner, interrupted on a short length in its middle. On its posterior part, a large wear facet with the dentine covered by black manganese cuts the base of the postprotocrista and a part of the posterior cingulum. Thin wear surfaces are preserved along the enamel rims, ascending until midheight of the protoctristid. The p/3 of Cos 254 is very similar in its global shape, its height and its slightly convex anterior profile (Fig. 3G). It is in fact slightly shorter. Its cingula are less differentiated, clear only at the anterolingual extremity. On the upper part of the protoconid, there is no slope change visible in lingual view, however on the posterior face, at a similar level, a posterolingual crest is starting, which descends until the base of the protoconid and curves into a brief posterolingual cingulum, which isolates a vertical lingual groove. From the same high point on the protoconid, a median postprotocristid was probably st arting, however it is affected by a long wear facet, fine at its departure and progressively broadening downward and hollowing out the base of the crown (presumably having worn out a small cingular talonid point).

The p/4 of Cos 253 is partly dorsally offset from the tooth row, and an unusual sheet of bone around the anterior root prevents to put it back in a normal place (Fig 3.F,H). The tooth might have been accidentally displaced during the life of the animal? In occlusal view, the crown of p/4 is clearly broader posteriorly than anteriorly. Its protoconid is much lower than that of p/3. A posterolingual protocristid joins its summit with a well formed metaconid. In dorsal view, the protocristid is only slightly curved around the anterolingual groove which separates the metaconid body from the protoconid. There is no corresponding groove on the posterior side of the protoconid. Despite wear of the summit of the metaconid, in anterior or posterior view one can see that the protocristid made only a shallow groove between the two cusps. A short anterolingual cingulum is ascending along the base of the protoconid, its summit making a cuspule, a small paraconid situated well above the base of the lingual cingulum. On the labial side, the anterior cingulum vanishes at the base of the small paraconid. The labial cingulum is continuous, thick at the level of an incipient postvallid. This cingulum was presumably reducing along the base of the hypoconid, because tiny grooves behind the hypoconid suggest an incipient posterior cingulum. However, the exact morphology is lost due to a relatively large wear facet which affects the summit and the labial slope of the hypoconid. In occlusal view, the summit of the hypoconid is situated labially. The main postprotocristid starts below the summit of the protoconid, descends and curves slightly labially toward the hypoconid until the groove which separates the latter. A secondary crest branches off the postprotocristid, descending posterolabially, thickening ventrally, making a prominent relief on the labial side between the protoconid and hypoconid walls. The lingual crest starting from the hypoconid summit forms a long curve until a low summit, a crestiform entoconid, and then curves anteriorly and ventrally until it ascends dorsally along the base of the metaconid. The relatively vast talonid basin, mainly oriented labiolingually and slightly sloping ventrolingually, is lingually closed by the latter crest.

The three lower molars are quite similar to each other (Fig. 3F,H). In occlusal view they have a massive outline and a slight ectoflexus on m/1 and m/2 (barely on m/3). In labial view, they have protoconids of similar height and volume from m/1 to m/3 (very slightly more voluminous on m/2), and hypoconids slightly lower than the protoconids. The cristid obliqua seems more abrupt on m/1, however this is due to the wear affecting the back of its trigonid. On m/3, the cristid obliqua joins the posterior wall of the trigonid between the notch of the protocristid and the protoconid summit in dosal view, and clearly below the level of this notch in posterior view. On m/2, the cristid obliqua curves along the trigonid wall until a point closer to the protoconid notch. On m/1, this junction is unclear due to wear, however the worn zone clearly shows that the cristid was directed toward the protocristid notch, and not toward the metaconid summit as occurs on some genera. In posterior view, the metaconid appears as broad and lower than he protoconid on m/1, quite similar to the protoconid on m/2, and narrower and as high as the protoconid on m/3. On the thee molars, the notch of the protocristid is deep I posterior view, close to a V on m/3 (it is shallower in many species). The entoconid is low and small on m/3, well formed on m/2 and m/1. The pre-entocristid and the postmetacristid are continuous on m/1 and m/2, closing the talonid basin. On m/3, the base of the postmetacristid is more abrupt, making a deep notch which almost opens the talonid basin lingually. On m/2 and m/3, the preprotocristid descends, curves into a subhorizontal and transverse paralophid, which at its lingual end diminishes, curves dorsally in merging into the base of the metaconid. On m/1, a cuspidated paraconid is well isolated from the base of the metaconid b a groove. The labial part of the paralophid is inclined, slightly inflated, and isolated from the protoconid base by a lingual groove. The labial cingulum is well formed on the anterior half of the molars, faint on their posterior part, even on m/3 (it is highly placed on the hypoconid of m/1). The third lobe of m/3 is moderate in size, simple, lingually placed, limited in dorsal view by a very shallow lingual concavity, a deep labial concavity, and there is no deep groove in these regions.

The isolated m/3 Cos 246 is broadly similar to that of Cos 253, however it also differs in a series of characters (Fig. 3E). Its trigonid is relatively smaller, slightly anteroposteriorly shorter, with a protoconid slightly shifted lingually in occlusal view and markedly lower in labial view, and in anterior view a protoconid much smaller than on Cos 253, which is accentuated by wear of its summit and of its preprotocristid, and a slightly lower metaconid. It has a shorter paralophid, better isolated from the metaconid base lingually, less separated in its lingual part due to the lack of groove. In occlusal view, the outline presents a less quadrangular anterolabial corner. The third lobe is smaller, more triangular, less rounded posteriorly and limited by a lesser labial concavity. In lingual view, the hypoconulid summit is slightly lower, and the entoconid is almost no more distinguishable (minuscule swelling). The labial cingulum is present around the hypoconid and continues below the anterior part of the hypoconulid, instead of ascending between the two cusps.

Description of upper teeth.

A large upper canine, Cos 753, is interpreted as a left one, having one face more bulging and more deeply grooved which is identified as its lingual face (Fig. 3A1-2). Crown and root present a slight global anterior curvature. Its enamel is slightly wrinkled. Two salient crests link the pointed summit to the base, joining the anterolingual cingulum anteriorly, and the two cingula posteriorly. On the lingual face, there are two vertical and shallow grooves, one close to the anterior crest and the second, deeper, slightly more distant from the posterior crest. The lingual cingulum is almost continuous, ascending toward the tip at the level of the posterior groove, and ascending at both extremities toward the anterior and the posterior crests. The labial face is more flattened, showing only a very shallow posterior groove and only a posterior basal cingulum, ascending at its extremity toward the posterior crest.

The P4/ Cos 77 is a robust and simple primate P4/, with a lingual part narrower than the labial part (Fig. 3B). From the tip of the paracone, a preparacrista and a postparacrista, straight in occlusal view, join the preprotocrista and the posterior cingulum, respectively. Parastyle and metastyle can be recognized but are not cuspidated. The postparacrista is continuous with the labial cingulum, and a metastyle is detectable only in labial view, isolated by a very shallow groove. The preparacrista joins but does not merge into the continuous crest formed by the extremity of the preprotocrista and the labial cingulum. The parastyle is made only by a thickening of the curving cingulum, labially to the junction. The protocone is massive and high, having at least three quarters of the paracone height in anterior or posterior views. Its lingual slope is abrupt. The preprotocrista is salient, straight in occlusal view, strongly deepening and curving again upward toward its junction with the labial cingulum in anterior view. A postprotocrista is present, directed posteriorly, abrupt, not salient and interrupted before the groove limiting the posterior cingulum. The posterior cingulum is well formed and long, reaching the lingual border lingually and the postparacrista labially. The faint anterior cingulum is much shorter, reaching less far lingually, and interrupted labially well below the preprotocrista.

The M2/ Cos 247 is very simple in its morphology, quadrangular with its lingual part slightly narrower than its labial part (Fig. 3C). Its enamel is slightly wrinkled. The metacone is slightly lingually shifted in comparison with the paracone. The posterior part of the tooth also is narrower than its anterior part. The protocone, almost central, is in fact slightly anteriorly placed. The preprotocrista is continuous until the labial border; it bears a small paraconule. A swelling similar to a tiny postparaconule-crista joins the base of an hypoparacrista; the latter is not salient, however well formed as the edge between two faces having different orientations. The postprotocrista takes a posterior direction before curving toward the metacone; this way, it surrounds a vast trigon basin, anteroposteriorly broad. There is no metaconule (a minuscule remnant can be detected at high magnification). The postprotocrista ascends along the metacone wall and stops, continued through an edge issued from the summit (almost an hypometacrista). The link between protocone and metacone is subcontinuous. The labial cingulum is continuous, well-formed and limited by a groove in its median part, thinner on both sides. No style is present (a minuscule cuspule at the place of a metastyle can be detected at high magnification). The anterior cingulum is interrupted labially below the paraconule; lingually it is continuous with the lingual cingulum, which is subcontinuous: interrupted only by three tiny grooves at the lingual base of the protocone. In occlusal or in lingual view, the impression is that the lingual cingulum is almost continuous. There is a small crestiform hypocone, barely visible in occlusal view, forming a low summit in lingual or in posterior view. The posterior cingulum is thick, continuous, interrupted only just at the junction with the base of the postmetacrista.

The M3/ Cos 248 is incomplete in its basal part, however its triangular outline is exact (Fig. 3D). Small remnants of cingulum show that it must have possessed a continuous lingual cingulum, a labial cingulum, and that the posterior cingulum is labially interrupted well before reaching the postmetacrista, which is labially curved. The metacone is moderately reduced. The trigon basin is vast and the enamel is slightly wrinkled, as on the M2/. One difference with the M2/ is that the protocone is lower. There is no paraconule, however the preprotocrista is broad and thick until the groove surrounding the base of the paracone. The postprotocrista is well formed and reaches until the base of the metacone. The lingual edge of the metacone is blunt, nevertheless a continuity between protocone and metacone is visible in anterior or posterior view. The M3/ is neither reduced nor transversally elongated as found in many species.

A small tooth, Cos 252, has the right size to be an i/1 of this species. Its root is laterally compressed and would fit in size with the remnant of alveolus on Cos 254. The crown is heavily worn, no details can be seen. The outline in occlusal view is very circular, somewhat flattened on the labial side, where the crown slope is abrupt. The outline is somewhat salient lingually, with a more inclined surface making the usual broad lingual bulging of lower canines. No cingulum is visible on the lingual part. The wear surfaces are inclined, one mesially, the other distally, and they join in a very blunt labiolingual edge.

A larger incisor, Cos 249, has a compressed root compatible in size with the alveolus for i/2 of Cos 254. Its crown is better preserved, the labial outline is curved, the lingual side is more expanded, without lingual cingulum. The tip of the crown is an elongated mesiodistal wear facet, parallel to the labial face, thick in its mesial and median parts, narrowing in its curving distal part, which continues as a slightly worn distal crest. A very shallow groove can be followed from midheight at some distance of the mesial border, going upward, turning to follow just along the wear facet, and turning downward and following the salient distal crest, which is vertical.

4.1.2. Remarks

Comparisons

Comparisons are made only with fossils that have been described as large *Protoadapis* species. *P. weigelti* differs from *P. andrei* through the loss of p/1 and the absence of diastema between p/2 and the canine, p/3 strongly anterolabially implanted on the mandible, p/3 by far not as pointed and as elevated, p/4 more elongated and narrower in its posterior part, m/1 with a narrow trigonid, a short paralophid curving toward the metaconid, rendering the trigonid basin “almost closed” according to Thalmann (1994), m/1 with a cristid obliqua directed toward the metaconid and apparently reaching high on its posterior wall (fig. e on plate VIII of Thalmann, 1994). All these differences show *P. weigelti* to be quite distinct from all other Quercy *Protoadapis* species, including *P. andrei*. Its relatively low p/3 is a difference with all species ascribed to *Protoadapis* until now, and the reduction of the trigonid of m/1 indicates a derived stage of evolution.

Comparison with the type specimen of *P. angustidens* is made through the photographs published by Teilhard de Chardin (1922). The latter shows an m/1 much smaller than the m/2, whereas these teeth are close in size in *P. andrei* (such a size difference exists on *P. brachyrhynchus*, however much less exaggerated). There might have been differences on the trigonid of m/2 and m/3, possibly slightly reduced, narrower on *P. angustidens*, however this is difficult to appreciate from the sole photograph. Conspicuous differences concerns p/4, which is more elongated and narrower on *P. angustidens* than on *P. andrei* (and *brachyrhynchus*), added in lingual view to a horizontal paraconid shelf (instead of ascending) and a lower talonid. The p/3 of *P. angustidens* appears also very high. Several of these characters could be explained by intraspecific variations, as has been found for the two m/3 of *P. andrei*. However the differences on the p/4 clearly exceed the intraspecific variations found in some cercamoniine assemblages (e.g. Godinot et al., 2018), and we consider *P. angustidens* as probably representing a different *Protoadapis* species different from *P. andrei* and *P. brachyrhynchus*.

The mandible PLV-35, referred by Gingerich (1977) to the same species as the type specimen of *P. angustidens* (renamed by him *P. "filholi"*, a new name that cannot be accepted because there is no synonymy among *Protoadapis* species), was figured in profile view by Gingerich (1977) and its two molars are beautifully illustrated in Tattersall and Schwartz (1983). The mandible is more gracile than those of *P. angustidens* and *P. andrei*. Its two molars are very close in overall morphology to those of *P. andrei*. The third lobe is smaller than on Cos 243 but similar to Cos 246. Several details separate them: the extremity of the paralophid of m/2 and m/3 does not merge into the base of the metaconid but instead shows a slightly ventrally oriented narrowing extremity; the paralophid bears a small paraconid medially situated on m/2 and a tiny remnant cuspule on m/3; on m/3 the cristid obliqua is ascending further dorsally, coming close to the protocristid notch, on m/3, whereas this crest meets the posterior trigonid wall at a lower level on the two m/3 from Cos. The strongest difference on the molars is the clearly stronger cingulum on PLV-35 molars, the latter being even continuous on the labial side of the m/3. These differences on m/2 and m/3 could be significant or could be accounted for by intraspecific variations. The anterior part of PLV-35 is well preserved, and very similar to Cos 254. Alveoli for i/1, i/2 and the canine have similar shapes and dimensions. However, there is a clear shortening around the anterior premolars. The alveoli for its p/2 are quite large (around as large as on Cos 253, larger than on Cos 254). The p/2 was just against p/3 as on Cos 254, however anteriorly a small alveolus shows that he p/1 was small, markedly smaller than on Cos 254 (itself smaller than on Cos 253). This small p/1 sits between two small diastemae, that with p/2 very small, that with p/1 slightly larger, however still smaller than on Cos 254. If one compares, beyond differences in p/1, p/2 and diastemae, the distance between the canine and the p/3, one can see that this distance is clearly shorter on PLV-35 than on the two mandibles from Cos. For this shortening, PLV-35 is intermediate between *P. andrei* and *P. brachyrhynchus*. Comparing the anterior part of PLV-35 with the photograph of *P. angustidens*, it appears clearly that the latter has a much larger p/1 and a longer diastema between p/1 and p/2, showing that it belongs with *P. andrei* to the group of *Protoadapis* species having a large p/1 and long diastemae, very likely primitive.

The mandible of *P. (Cercamonius) brachyrhynchus* is slightly higher and more robust than those of *P. andrei*. Its preserved teeth, p/4 to m/2, are overall very similar to those of *P. andrei*, however a few differences can be observed. Despite some wear on the summit of the protoconid and the anterior slope of the trigonid, one can see that a paraconid is present, slightly smaller than on *P. andrei*, and the paralophid is slightly curving posterolingually, shifting the paraconid slightly closer to the metaconid. A slight degree of trigonid basin closing has occurred on the m/1 of *P. brachyrhynchus*. On m/2 also, the paralophid appears slightly shorter and meeting the metaconid wall at a higher level. On p/4, the protocristid joining the summits of the protoconid and metaconid has the same length and orientation in occlusal view. However in profile or posterior views, it appears that the metaconid is markedly smaller, and more ventrally placed, in *P. brachyrhynchus*. Differences on the paraconid shelf cannot be observed because the anterior part of the p/4 is eroded in *P. brachyrhynchus*. Their p/4s markedly differ in their posterior part: the hypoconid is much smaller on *P. brachyrhynchus*, associated with a much narrower talonid basin, and it did not possess the supplementary labial fold described on *P. andrei*. Their p/4s therefore have a different outline in occlusal view, posteriorly narrower in *P. brachyrhynchus*. In the anterior part of the mandible, the two species differ markedly: there is only a single rooted p/2 on *P. brachyrhynchus,* and no diastema on both sides of the tooth, showing a marked reduction in anterior premolars and length of the anterior part of the jaw.

Discussion

This new species has p/4 to m/2 overally similar to the same teeth in *P. brachyrhynchus*, differing only in details of the paralophid of m/1 and m/2 and differing more in their p/4s, showing that the two species must be closely related. Strong differences occur in the anterior part of the mandible, with only a single rooted p/2 and no diastema between p/3 and the canine in *P. brachyrhynchus*. The surprise is to have *P. andrei* so primitive in its anterior dentition, and so morphologically close to typical *Protoadapis* species by many characters, particularly the high and pointed p/3. This confirms the interpretation of Stehlin (1916), who described the specimen as a derived species of *Protoadapis*. The new material is important because it completes our knowledge of large Quercy *Protoadapis* species, with for the first time associated upper P4/ and molars, and an upper canine. Relatively unexpected is to find an upper molar of such a large species with only an incipient crestiform hypocone. When we extend the comparison to other large *Protoadapis* species, *P. weigelti* is the species which appears the most divergent in its molar morphology. It was interpreted by Gingerich (1977) as intermediate with *Caenopithecus*, something we doubt, however this proposition is consonant with our interpretation of a diverging lineage for *P. weigelti*.

Among the large *Protoadapis* species found in the Quercy, we have seen that if details of molar morphology and the gracility of PLV-35 could be accounted for by intraspecific variabilities, the reduction of the anterior premolars and jaw would be the major evolutionary trend, allowing the proposition of a *P. andrei* – PLV-35 – *P. brachyrhynchus* specific lineage. One might even suspect *P. angustidens*, with its elongated p/4, to represent an even more primitive evolutionary stage. If its p/4 and peculiar proportions of molars could be accounted for by intraspecific variabilities, one could even suspect *P. andrei* to be a junior synonym of *P. angustiens*, and the picture would be one lineage *P. angustidens* – PLV-35 – *P. brachyrhynchus*. However, more information on intraspecific variations is needed to strengthen such an interpretation. The material at hand seems to indicate a more bushy picture of *Protoadapis* species: *P. angustidens* might be early specialized by its p/4, PLV-35 might belong to a more gracile branch with slightly different molars, and *P. andrei* seems advanced over *P. brachyrhynchus* in its p/4 morphology, which would imply two different specific lineages or an unlikely reversal in p/ evolution. Clearly we do not have enough material, not enough information about intraspecific variability, to favor one specific lineage over a more complex history, which is suggested by the variety of p/4 morphologies. When comparing with more distant *Protoadapis* species, it is striking that the early Eocene *P. curvicuspidens*, the type species of the genus, has an already shortened anterior dentition, with a relatively small and single-rooted p/2. Our Quercy species must be rooted in a more primitive stock. It might be tempting to propose those species leading to *P. brachyrhynchus* as the *Cercamonius* lineage, however we cannot identify significant characters which would separate its earlier species from other *Protoadapis* species. As we have seen, the most divergent species of the genus would be *P. weigelti*, and for this species as for earlier ones, upper teeth are unknown. Our knowledge is still insufficient to allow a systematic reappraisal of all *Protoadapis* species.

Genus *Pronycticebus* Grandidier, 1904

4.2. *Pronycticebus cosensis* Godinot and Vidalenc nov. sp.

Figures 4, 5 and 6

Derivation of the name: from the type locality, Cos;

Holotype: left mandible Cos 271 bearing i/2, C, broken p/1, p/2 to m/3, University of Montpellier collection.

Referred material: right fragment of mandible bearing m/3, Cos 269; juvenile anterior part of mandible with unerupted p/3, Cos 275; mandible fragment bearing p/4 and m/1, Cos 270; maxillary fragment with P4/ and alveoli of P3/, P2/, and a more anterior part, Cos 265; maxillary fragment with M1/ and M2/, Cos 258; and 26 isolated teeth (see Table 1).

Type Locality: Cos fissure-fill (Quercy region, South West France);

Occurrence: the type locality, possibly Vielase (Quercy);

Measurements: for all teeth, see Table 1 for Length and Width; complementary measurements are: for the lower canine of Cos 271, length and height in labial view, 1.96 and 3.54 mm; for the upper canines, height is 3.78 for Cos 863 and >3.45 for Cos 864. Measurements of the type mandible Cos 271 are: total length of mandible without the incisor, 5.25 cm; length p/4-m/3, 1.72 cm; height below p/2, 6.17 mm; height below m/2, 7.53 mm; width at the level of m/2, 2.98 mm. Maxillary fragment Cos 265, length and height in labial view are 12.51 and 8.01 mm. Some complementary measurements are given with the descriptions.

Diagnosis: Species of *Pronycticebus* which differs from *P. gaudryi* by its smaller p/2, p/3s having more complicated posterior cresting, a main posterolingual crest and varying secondary crests often suggesting an incipient metaconid; p/4s with a larger and better isolated metaconid; m/2 and m/3 with thinner paralophid, without bulge, and shorter m/3 paralophid; P3/ to M1/ have a smaller parastyle, and a less salient posterolabial corner (straight postparacrista on P3-4/, less elongated and curved postmetacrista on M1/, no metastylar expansion); P3/ has a more reduced protocone, M1/ is much less waisted, and M2/ has a continuous or subcontinuous lingual cingulum. Differs from *P. neglectus* by its smaller size, presence of first premolar above and below, higher and more pointed entoconid on m/1, continuous lingual cingulum on M2/. *P. neglectus* further differs from the two others by the complete absence of metaconid on p/4, the thin paralophid joining the base of the metaconid on m/1 and m/2 (long and posteriorly curved on m/1), and a smaller hypocone at least on M2/.

4.2.1. Description

Mandibles

The type specimen Cos 271 is a left mandible, very well preserved in its anterior half, partly damaged in its part posterior to m/3 (Fig. 4A1-3). The corpus is relatively thin and elongated anteriorly. Its ventral border is regularly convex. Some damage of its anterior extremity is present on its labial side, probably causing a slight labial protrusion at the level of the canine root. On the lingual side, the bone is intact, the symphyseal surface is very anteriorly inclined, and extends posteriorly until below the space between p/2 and p/3 (Fig. 4A2). The corpus shows a slight increase in height posteriorly until below m/3; posteriorly, the ventral border makes a dorsal concavity followed by a ventral convexity. In labial view, the posterior appears affected by two large cracks, one ventroposterior starting behind m/3, and a second dorsoposteriorly oriented starting after the latter. Despite these large cracks and the dorsal displacement of the m/3, one can see in lingual view that the ventral parts are almost joined; their junction is masked by a calcite deposit, which shows that the breakages were natural, due to taphonomical processes. The ventral border of the posterior convexity appears irregular in labial view, due to some calcite still covering this side. However, in lingual view, that border appears intact, and the whole outline of this mandible is almost not deformed when seen in lingual view. Only at the posterior extremity is bone missing. The articular condyle is not preserved, however the broadening of the bone just below the condyle is there, and in fact the line below the condyle, which is very steep and slightly posteroventrally inclined, is intact. It curves on the top of the angular process. Because the ventral line is curved, it seems that very little of the angular process is missing, just its posterior border, which must have been curved. The angular process must have resembled in smaller that of *Notharctus* (Gregory, 1920: Fig. 76). In ventral view, a slight displacement of the posterior part can be detected.

The mandibular fragment Cos 275, which bears a germ of p/3 in place (Fig. 4C1-2), appears quite similar to Cos 271: p/2 of similar size, diastemae on both sides of p/1, the alveolus of which is similar in size to that of Cos 271. Small differences between the two specimens are: the height below p/2 is smaller on Cos 275, the symphyseal surface appears less grooved; in labial view, a mental foramen is present below the anterior border of p/2, whereas on Cos 271 a small mental foramen is present below p/1 and a larger one below the anterior root of p/3. Measurements of Cos 275 are: height of mandible below p/1 alveolus, 4.02 mm, height below p/2, 4.72, width of mandible at p/1 alveolus, 2.81, and at the middle of p/2, 2.73 mm; length of canine alveolus ~2.49 mm, alveolus for p/1, 1.35 x 1.11; roots of p/2, 1.70 x 1.19 mm.

A posterior part of mandible, Cos 269, bears its m/3. It is fragmented by taphonomical processes. It gives some complementary information. A space is present between the m/3 and the ascending ramus, which is steep. The ventral border appears less sinuous than on Cos 271. At the posterodorsal extremity of the fragment, a part of the posterior rim is preserved, which shows that the coronoid process was anteroposteriorly short. The base of this rim curves posteriorly and becomes thicker, thus indicating the upper level of the articular condyle. The latter appears to have been high, far above the tooth row.

Dentition of the type mandible Cos 271 (Fig 5A1-2, L-P).

The anterior extremity of the specimen is lacking only very little bone. The space for the i/1 alveolus cannot be directly observed because it is still covered with a sheet of calcite (and some glue?), however it must have been very small, and i/1 was certainly very small. The i/2 is still in place, in front of the canine, partly out of its alveolus. Its root is close in size to the root of p/1. Its crown is spatulate. Its anterodorsal rim is almost straight, linguolabially oriented, showing only a slight irregularity of its middle (a very slight anterior groove). Its lingual half is intact; its labial half is affected by a deep wear surface, a broad labial groove having an anteroventral orientation.

The canine of Cos 271 is not large. It is only slightly higher than p/3 and p/4. In occlusal view it appears oval, somewhat laterally compressed. Three main crests can be seen, however they are blunt, not salient: 1, the anterior crest, arcuate, underlined by a slight lingual concavity; 2, the posterior crest, very straight, affected by a moderate vertical wear facet in its dorsal half, smooth in its ventral half; 3, a posterolabial ridge bordering an almost flat posterolabial face. A faint basal cingulum can be seen only on both sides of the posterior crest. There is a sizable diastema, as long as the canine length, between the p/1 and the canine. The small p/1 is incomplete; the lingual part of its crown is broken away. Its labial part is still covered by a thin layer of calcite. From what remains of this labial side, it appears difficult to predict its crown height. However, its length in occlusal view is less than half the length of p/2, hence it must have been quite small. p/2 is a small biradiculated tooth, with a simple crown. The main cusp is high, its anterior crest is arcuate; its posterior crest is straight, with an irregularity, a slight bulge above its mid-height, visible in lingual view. A basal cingulum, not salient, is present on its posterior face. It fades on both sides, on which it can be detected as very faint, incipient.

The p/3 of Cos 271 is abnormal: its presents a labial expansion of its crown, above a third labial root situated in the middle of the labial side. In lingual view, the tooth is slightly higher than p/4, however this is due to the dorsally expanded anterior root. If the sole crowns are compared, taking into account the fact that the tip of p/4 is worn, the crowns of p/3 and p/4 appear subegal in height. In lingual view, p/3 has a classic shape, with an anteriorly arcuate preprotocristid; the lingual cingulum presents two concavities separated by a broad and high dorsal convexity in its middle (Fig.). Two crests descend posteriorly from just below the tip of the protoconid. In posterior view, the most salient of them descends and curves gently lingually to join the lingual cingulum at a point just posterior to its rounded summit; in lingual view, this crest shows a thickening below its midheight, which evokes a low placed incipient metaconid. The second posterior crest issued from the the tip of the protoconid takes a more labial course; it is blunt and continuous until it reaches the posterolabial cingulum; it seems to correspond to the postprotocristid, labially displaced in relation with the abnormal labial expansion of the crown. The continuous labial cingulum has its lowest point above the supplementary root and is ascending on both sides, being more weakly expressed in its anterior part. There is a talonid, well developed in lingual view, however not basined.

The p/4 of Cos 271 has a more usual aspect with its horizontal crown. The anterolingual cingulum is thick, subhorizontal; posteriorly it vanishes in ascending at the base of the metaconid. The metaconid is well formed, relatively acute in lingual view, isolated from the protoconid by a deep groove; the protocristid makes a notch in posterior view despite the fact that the tips of the protoconid and metaconid are partly worn out. A postmetacristid descends lingually and curves into a lingual cingulum surrounding a small talonid basin. A postprotocristid descends below the notch of the protocristid and at its posterior extremity curves again dorsally, forming a low cingular hypoconid. A blunt posterolabial crest joins the tip of the protoconid to the posterolabial cingulum. The labial cingulum appears nevertheless subcontinuous, well-formed anteriorly, faint in the middle, thicker in its posterior part joining the low hypoconid.

The three lower molars share an outline in occlusal view which is slightly narrower in the anterior half than in the posterior one. Their trigonids are labiolingually narrower than their talonids. They all have a relatively wide talonid basin. Some aspects of their proportions are obscured by wear, which affects most strongly the protoconid of m/1, still strongly the metaconid of m/1 and the protoconid and metaconid of m/2, and moderately the hypoconid and entoconid of m/1 and the entoconid of m/2. Despite this inconveniency added to the fact that the m/3 is no more aligned with the other teeth, it is recognizable in labial view that protoconid volume and height decreased from m/1 to m/3; also, the hypoconid is clearly higher on m/2 (and probably m/1) than on m/3. On the three molars, the paralophid is relatively short, not reaching the lingual rim in occlusal view. On m/2 and m/3 it is subrectilinear, with a slightly posterolingual orientation. On m/1, it is curved and more anteriorly directed (the trigonid of m/1 is much more mesiodistally extended than those of m/2 and m/3); it bears a bulging in its middle, which is a very small median paraconid. On all molars, the lingual extremity of the paralophid tapers and is isolated from the base of the metaconid by a groove (there is no premetacristid and no tendency toward a fusion of the paralophid into the metaconid). The protocristid is not salient, very low, pushed under the mesiodistal groove separating protoconid and metaconid. It is still recognizable on m/2 and m/3, making the dorsal limit of the posterior wall of the trigonid (in posterior view, it makes a very open V, almost a broad dorsal concavity, on m/3). It is present on m/1 as the edge separating the mesiodistal trigonid groove from the postvallid extremity. The cristid obliqua is low on m/3, curved, anteriorly and slightly lingually oriented, reaching the posterior trigonid wall well below the protoconid summit. On m/2 it strongly lowers and curves more lingually, reaching the posterior trigonid wall well below the protocristid notch. On m/1 the cristid obliqua lowers less strongly than on m/2, it goes up again toward the mesiodistal groove of the trigonid (very slightly lingually to it); it is not directed toward the metaconid summit, however it joins the base of the wear facet labially descending from the latter's summit. The crest joining the metaconid to the entoconid is continuous, little salient; it lingually closes the talonid basin, at a level very slightly above the lowest point of the talonid. The entoconid is slightly more anterior on m/2 than on m/1, and correlatively the postcristid is more posteriorly arched on m/2. The entoconid was probably lower on m/3 than on the others, however this cannot be precised because its summit is worn. The m/3 hypoconulid is broad. The crest which links it to the entoconid is subcontinuous, whereas the crest which links it to the hypoconid is interrupted by a deep groove, exaggerated on the specimen by a deep wear facet hollowing the posthypocristid. The labial cingulum is well developed around the base of the protoconid, lacking at the base of the hypoconid (slightly incipient there on m/1); in labial view, it makes a broad dorsal convexity, subhorizontal on m/1; this convexity is more accentuated and anterodorsally inclined on m/2, and even more on m/3; the latter seems to have a deformed crown, with its base strongly ascending anteriorly.

Variations in the lower teeth

A small and simple tooth, Cos 278, is close in size to the P/1 of Cos 271 (Fig. 5B). It has a robust root, and in occlusal view its outline is a broad oval, not far from circular. The single cusp is very sligthly procumbent. Its anterior side is a broad wear facet, pointed at its summit (crest) and quickly broadening ventrally. It would well correspond to wear produced by the upper canine. The posterior crest of the cusp is well formed. At its base, it is continuous with a weak and blunt cingulum curving along the lingual side.

An unerupted right p/3 in its mandibular fragment Cos 275, is incomplete at its distal extremity due to breakage. In lingual view its preprotocritid is markedly arcuate, its anterolingual cingulum shows an anterior concavity shallower than on Cos 271, and this cingulum is interrupted before joining the postprotocristid. In posterior view, the latter descends with a slight lingual inclination; it makes below the midheight a lingual projection more accentuated than on Cos 271 (better expressed incipient metaconid). Just labial to this projection, a salient posterior crest descends toward the cingulum (broken); a salient postmetacristid descends below the projection, and the posterior face appears broadly grooved between these two crests (on Cos 271, only a very faint short crest can be detected below the incipient metaconid). The right p/3 Cos 276 is slightly different (Fig. 5D1-2). In occlusal view it appears narrower in its posterior part, with a slight labial concavity underlying this narrowing. Its postprotocristid is very salient, descends posteriorly until a turn where it goes ventrolingually and slightly anteriorly, continuing until it reaches the lingual cingulum. Close to the turn point, slightly labially, a posterior crest continues descending, almost in prolongation of the postprotocritid but less abrupt. In labial view the turn point appears as a salient angle, again suggesting an incipient metaconid. Between the posterior crest and the lingual cingulum, a small talonid basin is grooved. The p/3 Cos 277 is broad in its posterior part (Fig. 5C1-2). It is the simplest of all p/3s. It has a posterolingual postprotocristid continuous until it joins the posterolingual cingulum, without any projection evoking a metaconid. Well below the midheight, a posterior crest starts at some distance of the preceding crest; it joins the posterior cingulum, which is circular, without any summit: there is no hypoconid, no talonid. The p/3 Cos 280, which is narrow in its posterior part, is again different in its cresting. Its very salient postprotoconid is directed posterolingually in occlusal view. It descends until a point where it divides in two branches: the most salient, posterolabial, reaches the small posterior talonid point (salient, a true tiny hypoconid); the less salient branch continues a posterolingual descent until the samall talonid basin, without interrupting it, without reaching the lingual cingulum. The lingual cingulum, very salient, has a peculiar morphology. Its anterior half is made of two lines starting from a low ventral point; the anterior ascending crest is thick (incipient paraconid shelf); the posterior crest is first ascending, then subhorizontal until it divides in two parts: the main branch descends as a well formed posterolingual cingulum, dorsally concave, and the minor branch ascends dorsally and fades, disappearing into the lingual wall of the protoconid. On the labial side, the cingulum is well formed in the posterior half of the tooth, then missing along the labial wall of the protoconid, and again present only at its anterior extremity.

The mandible Cos 270 bears p/4 and m/1 (Fig. 5F). Its p/4 is very similar to that of Cos 271. In occlusal view, its talonid basin is very slightly shorter. In posterior view, the metaconid seems somewhat more distant from the protoconid, however the latter is worn, making this difficult to appreciate. The posterior crest starts slightly labially to the protocristid notch (on Cos 271 it starts just below). The lingual view confirms that the metaconid is slightly lower on this p/4 than on Cos 271. In this view, the preprotocristid is less abrupt, slightly more anteriorly directed; it joins an anterolingual cingulum which is more salient anterolingually than on Cos 271; the latter cingulum is shorter than on Cos 271, but it ascends slightly anterodorsally, it is thick and evokes an incipient paraconid. An isolated p/4 with two roots, Cos 860, is anteriorly very short, and quite worn (Fig. 5E). It is very similar to the others, with the same type of metaconid and simple posterior crests. Its talonid is more extended than on Cos 270, and in occlusal view, it appears quite broad in its posterior part (broader than Cos 271). It is moderately worn in its posterior part: broad facet at the base of the postprotocristid, with both anterior and posterior prolongations, hollowing of the posterolabial cingulum. It is extremely worn in its anterior part, with a broad wear surface lowering the protoconid and continuing through a long anterior vertical wear surface, descending until the base of the crown; the anterior extremity of the crown is worn away. This is a very unusual type of wear. Another p/4 bearing only one root, Cos 859, is quite similar to the others (Fig. 5G1-2). It shows wear facets along the postprotocristid and on the posterior face of the metaconid. A small wear facet hollows the cingulum at its posterolabial extremity. The enamel on the other surfaces is less shiny than on the other teeth, suggesting some kind of chemical erosion. Its notable character is a basal paraconid even better formed and developed than on Cos 270. The m/1 of the Cos 270 mandible is very similar to that of Cos 271: same kind of paralophid anteriorly salient, thickening of its labial part, the wear of which suggests the presence of a small paraconid (Fig. 5F). It is less worn, so that one can well see the deep notch in V of the protocristid; the cristid obliqua is directed toward this notch, but in posterior view it does not reach it, being below and under its labial side; only a narrow wear facet joins this crest to a broader wear facet descending from the tip of the metaconid. Two isolated lower molars are important because they are unworn. They are interpreted as m/1 because they are narrow in their anterior part and their cristid obliqua is directed as on the others or more lingually. The first, Cos 272 (Fig. 5I), gives the impression that the protoconid and the metaconid are closer than on Cos 271, and its trigonid slightly narrower (however the strong wear on Cos 271 might be misleading). The cristid obliqua has the same way than on Cos 271; as there is very little wear, one can see the groove extending the hypoflexid, which reaches exactly the bottom of the protocristid notch, and the cristid obliqua which ascends just next, lingually, and at its extremity turns toward the tip of the metaconid, fusing into that part of the protocristid. The paralophid is quite thick in occlusal view. Its extremity, which tapers abruptly, is much closer to the lingual rim than on Cos 271. In anterior view, the preprotocristid is subvertical (slightly curved), then it curves into the paralophid, which presents a summit (slightly labial to the midline) and then descends ventrolingually, making again a small bump at its extremity. In occlusal view, only two low bulges can be detected. Despite there is no well-formed cusp, one can describe the paralophid as made of two successive bulges, a larger labial one (paraconid equivalent) and a smaller lingual one. The other m/1, Cos 755 (Fig. 5H1-3), has the same kind of paralophid, descending ventrolingually and well isolated from the base of the metaconid, made of two bulges, a larger labial (paraconid) and a smaller lingual and more ventral. This m/1 is striking through its cristid obliqua ascending directly toward the tip of the metaconid (Fig. 5H1). The postvallid groove ascends and joins in continuity the mesiodistal groove separating the metaconid from the protoconid. The protocristid has completely disappeared.

The m/2 Cos 273 is identified through its cristid obliqua, which at its anterior extremity ascends below the summit of the protoconid, clearly more labially than on all m/1s (Fig. 5J). Its anterolabial outline is rounded in occlusal view. Its paralophid is thick in its labial part, narrower in its lingual part; it does not present the irregularities (bulges) present on the m/1s. At its extremity, the paralophid is not isolated from the base of the metaconid by a groove; it comes against, and the base of the metaconid presents there a blunt ridge, not salient, vertical in anterior view; this makes an incipient link between paralophid and metaconid.

The m/3 still present on the mandibular fragment Cos 269 is very similar to that of Cos 271 (Fig. 5K). It differs from the latter through the lack of a labial groove separating hypoconid and hypoconulid. Its paralophid is shorter, presenting a bulge along the base of the protoconid. Lingually, a tiny low bulge unites the paralophid to the base of the metaconid, on which a blunt ridge descends, becoming visible near the base through a small wear facet on its surface. This weak ridge and the small bulge again makes an incipient continuity between paralophid and metaconid, as on the m/2 Cos 273.

The DP/4 Cos 274 is much narrower and more elongated than the M/1s (Fig. 6R). As on Cos 755, the cristid obliqua is continuous from the hypoconid to the tip of the metaconid. It differs from the latter by the strongly anteriorly shifted protoconid relative to the metaconid, and a further anterior shifting of the paraconid, which is pointed, cuspidated but not inflated. There is a wide space between the metaconid and the paraconid, each bordered by a vertical groove, the two grooves (somewhat converging ventrally) being separated by the protoconid lingual wall. The three anterior cusps are acute, and the pre- and the postprotocristid are salient. The talonid is similar to that of the M/1s, being only smaller.

Maxilla and upper dentition

Maxillary fragment

A fragment of right maxilla, Cos 265, bears the P4/, posteriorly the alveolus for the anterolabial root and half of the alveolus for the lingual root of M1/, and anteriorly it shows three alveoli for P3/, two alveoli for P2/, one for P1/ and a part of the canine alveolus (Fig. 6A1-2). Breakage of the anterior part starts at the wall between the two alveoli of P2/, so that the more anterior alveoli are seen only at a deeper level. The most anterior space, filled with matrix (hard calcite), is probably a part of the canine alveolus, at a level relatively distant from the palate surface. Compression of this space is congruent with the strong compression of the two upper canines described below. No precise statement can be made concerning the size of the canine root present in this fragment beyond the fact that it seems compatible with the sizes of the roots of those canines. In occlusal view, the rim of the fragment curves outward anteriorly. This curvature is exactly similar to the same region on the cranium of *Pronycticebus gaudryi*, where it surrounds the base of the canine root. In lateral view, a large infraorbital foramen is present just above the anterior root of the P4/, which is similar to that seen on *P. gaudryi* (height of the foramen at its opening, 1.67 mm). Above, a short part of the anterior orbital rim is present. In dorsal view, one can see a short part of the anterior orbital floor; an anterior cavity seems to correspond to the opening of the infraorbital canal.

Upper canines

The upper canine Cos 863 is well-preserved (Fig. 6B1-2). Due to its slight curvature, its anterior and posterior sides are easily recognizable. The posterior side presents a salient vertical crest, whereas the anterior side is rounded and presents a shallow crest only at its base, where it joins the lingual cingulum. If we identify the lingual side as the one presenting the best developed cingulum, the tooth appears as a left canine. In occlusal view, the lingual face is more extended than the labial. It bears a posterior vertical groove, deeply hollowed, and an anterior part flattened (very slightly grooved in occlusal view). The labial side presents only a flattening of its posterior part, with a very shallow groove visible in labial view. A thin cingulum runs around the base of the crown, ascending in low summits under the crests and making shallow concavities under the grooves; it completely disappears on the anterolabial side. The second upper canine, Cos 864, is broken at its tip and eroded. It presents two deep posterior grooves, one lingual and one labial. The crown outline is affected by a broad vertical wear surface, which extends on the root; this surface is lateral to the blunt anterior crest, which is recognizable through the faint ascending cingulum. Because the basal cingulum is better developed on the other side, the latter would appear as lingual, and the wear surface would be anterolabial. The tooth would thus also be a left canine, however the strange fact is that in occlusal view its labial side is more extended than the lingual one (relative to the anterior and posterior crests), which is the reverse of the other canine. The identification of both canines as left is still unsecure.

Upper premolars

A small and simple tooth, Cos 279, is oval in outline in occlusal view, very slightly more elongated than the (incomplete) presumed p/1 Cos 278. It is higher and more pointed than the latter in lingual view; its posterior crest is more salient and slightly longer than the anterior one. The labial side is entirely convex, whereas on the lingual side a slight flattening is observed anteriorly, and a shallow grooving is present all along the posterior crest, which gives to the tooth a premolar stamp (Fig. 6C). It is interpreted as a left P1/.

The premolar Cos 281 is interpreted as a left P2/ (Fig. 6D1-2). A part of its posterior root is preserved, whereas the breakage of its anterior root cannot be seen. The presence of a space between the two roots can be seen on the labial side. The crown is expanded above the roots. These roots seem compatible in size with the two alveoli for a P2/ that are incompletely preserved on Cos 265. In occlusal view, the crown has an oval outline, broader than that of the lower P/3-4. The main cusp is high, pointed. Its anterior crest is very abrupt and blunt; its posterior crest is very salient and slightly posteriorly extended (very slightly less abrupt than the anterior one). Two vertical grooves are present, one on each side of the posterior crest, the lingual being deeper than the labial one. A thick cingulum is present on the posterior part, short on the labial side, making a small summit in front of the posterior crest (which does not join it), longer on the lingual side, on which it ascends anteriorly along the posterior side of the main cusp. It seems that there was a thin and short anterior cingulum, however it is very difficult to distinguish from the breakage and glue of this zone. The line visible on the base of the anterolingual side is a breakage, not a cingulum. This tooth is almost as high as the P3/ Cos 858, and these two teeth would well fit in the same tooth row. However, in this case P2/ appears unreduced, in contrast with the lower P/2, which is much smaller than P/3. Such a discrepancy has been sometimes observed.

Two P3/, Cos 264 and Cos 858, have a main cusp (paracone) elevated and pointed, with a lingual wall more expanded than the labial, a salient posterior crest and no anterior one (rounded wall). Both have a protocone lobe, which is small, very short and broad on Cos 264, more elongated, narrow and underlined by a deeper concavity of the posterior rim on Cos 858. Cos 264 has a protocone very low, crestiform, integrated in the rounded cingulum (Fig. 6F1-2). Cos 858 has a clearly higher protocone, whose summit and posterolingual slope are worn;

on the anterior side, the protocone shows a vertical crest which joins the irregular anterior cingulum at right angle (Fig. 6E1-2). The notch which separates the protocone and the paracone is deep and narrow, between a short crest at the base of the paracone and the vertical anterior wall of the protocone. The anterior cingulum is continuous on both P3/s, without summit or thickening (no parastyle). On Cos 264, the posterior cingulum, continuous, broadens and ascends in a crestiform metastyle, very low. The labial cingulum is interrupted in its middle. The posterolingual face of the paracone presents a broad and shallow groove, which descends until the base, just above the cingulum, on Cos 264. On Cos 858, there is no grooving of the posterolingual face of the paracone, neither a crest at the base of the paracone on the lingual side; the labial cingulum is slightly more developed, however it is still incipient in its central part, subcontinuous. On the posterior side, the outline of the crown is more angulated in occlusal view, as if there were a more projected metastyle, however in posterior view its cingulum summit is even less marked than on the other tooth, being low and rounded. Three P4/s show the same basic and common plan, with a large paracone, a protocone with an anterolabial preprotocrista joining the anterior cingulum near the parastyle, and a more abrupt postprotocrista, posteriorly directed and joining the posterior cingulum close to the lingual border, a continuous labial cingulum (Fig. 6G-I). However, they also show strong character variations, including in the proportions of the main cusps. In occlusal outline, Cos 263 is narrower anteroposteriorly, at the level of the paracone as well as at the level of the protocone, than Cos 262. Their anterior and posterior rims have weak concavities in occlusal view, more expressed on Cos 262 due to the more expanded stylar regions. The P4/ present on the maxillary fragment Cos 265 contrasts with the two others through its strongly narrower protocone relative to the paracone, resulting in an accentuated waisting of the crow (exaggerated in occlusal view by a small broken fragment on its posterior side). In anterior view, the protocone of Cos 262 is almost as high as its paracone (Fig. 6G2), whereas on Cos

265 the protocone is much lower than the paracone (Fig. 6I2); clearly Cos 265 has the smallest protocone of the three P4/s. The lingual edge of the paracone becomes crested near its base, limited by a groove, on Cos 262 and Cos 263, or it starts to build a continuity with a blunt labial bulging of the protocone on Cos 265. There are a few variations of the styles. The parastyle is round, crestiform and isolated by a groove in occlusal view on all; in anterior view, it is low on Cos 262, and has a well formed summit on Cos 263 and Cos 265, which have a cuspidated parastyle. There is no metastyle at all on Cos 265, and it is very weak, incipient on the two others, with in labial view a cingulum ascending posteriorly on Cos 262, but horizontal on Cos 263. On the latter, the postparacrista has a slight posterior orientation in occlusal view, which is absent on the two others. On the anterior side, below the preparacrista, a narrow cingulum is present on Cos 263, which is more extended lingually on Cos 262, on which it turns around half of the protocone. This anterolingual cingulum is very faint, barely incipient, on Cos 265.

Upper molars

A M1/ and a M2/ are present on the fragment of maxilla Cos 258 (Fig. 6M). The two molars differ: M2/ is transversely more elongated, which gives more space between the paraconule and the base of the paracone. The metacone is smaller than the paracone on M2/, something conspicuous in posterior view. Its anterior cingulum is more extended lingually than on M1/. Its hypocone is smaller, however its posterolingual hypocrista is much more extended than on M1/, closing the hypocone groove, leaving only a short space on the lingual base of the protocone without cingulum. In contrast, M1/ has no lingual cingulum. The two molars have a slight entoflexus, that of M1/ being more accentuated in relation with its larger hypocone. On M2/, the bottom of the large notch of the centrocrista is shifted labially, a character present but less expressed on M1/. M1/ has a more accentuated concavity of its posterior side than

M2/, which gives it a more waisted outline. Both molars share many details, as a distinct small parastyle, no metastyle, the postmetacrista directed posterolabially, a small thickening of the labial cingulm in its middle, a relatively voluminous paraconule with an abrupt preparaconule-crista, and no metaconule at all. There is a marked angle (in posterior view) between the end of the postprotocrista and the blunt edge descending lingually from the tip of the metacone (hypometacrista, not salient).

The smaller M1/ Cos 832 (Fig. 6L) differs from the preceding one by: an ectoflexus and a posterior concavity more accentuated (more waisting of the crown), a slightly smaller paraconule, a small metaconule which is only a small elevation of the postprotocrista, and which is followed labially by an ascending crest on the metacone, making an increased continuity between the postprotocrista and the tip of the metacone (not far from a continuous crista obliqua). The hypocone seems not to be larger than on the preceding M1/, however it is more lingually placed, which produces a posterolingual extension of the crown outline, absent on the other. Its enamel is smooth and there is no parastyle. Another small M1/ with marked waisting and smooth enamel is Cos 861 (Fig. 6J), which has a big hypocone, and posterolingual extension of its outline, underlined by a small entoflexus. Its hypocone is larger than that of Cos 832 and it is isolated by a groove which extends until the lingual rim. Its posthypocrista is blunt, difficult to recognize. It has a parastyle and a well formed metaconule (bulging on both sides of the postprotocrista). The M1/ Cos 257 (Fig. 6K1) is even smaller, waisted; its enamel is slightly irregular, not smooth. It is transversally short and its labial cusps appear very high and pointed (e.g. a very abrupt slope of the metacone in posterior view, Fig. 6K2). Its hypocone appears small, especially because the groove which separates it from the protocone is shallow and interrupted by the small posthypocrista, which is in a high position; the groove has no lingual prolongation at all. However, the base of the hypocone is voluminous, producing some posterolingual extension of the crown as on most M1/s. It bears a small parastyle, close to the preparacrista, little salient in occlusal view but well formed; there is also a thickening of the cingulum forming a metastyle. The posterior part of the labial cingulum curves lingually in the middle of the labial rim, to reach the bottom of the notch of the centrocrista (which is slightly labially shifted); on the point of curvature, a small summit makes a true tiny mesostyle, underlined by a small groove separating it from the anterior half of the ectocingulum. Cos 257 has no preparaconule-crista. It has a tiny metaconule visible only in anterior or posterior view as a small summit; in occlusal view it has no bulging but makes a slight turn of the postprotocrista, which further labially curves slightly posteriorly in ascending toward the metacone tip. A labial half of tooth, Cos 862, probably respresents an M1/, because paracone and metacone have the same height; the paraconule helps recognizing the anterior side. There is a small parastyle not well separated from the preparacrista; the postemetacrista is more labially directed than on the other teeth; it presents a marked thickening, a metastyle. This fragmentary tooth is interesting because it presents the most isolated and the most inflated metaconule, well isolated lingually and labially by grooves, posteriorly bulged into a thick ridge descending until the posterior cingulum, which is thin at its level.

The M2/ Cos 255 is very close in size to the M2/ of Cos 258, however it is narrower in its lingual part, which gives it a transversally more elongated appearance (Fig. 6N1). They are close in overall shape, however in the details, Cos 255 differs through its metacone lingually shifted, its slightly smaller hypocone; its anterior cingulum ends at its lingual extremity with a bulging, a small pericone, which is separated only by a groove from the lingual cingulum prolonging the posthypocrista; the lingual cingulum is subcontinuous. The paraconule of Cos 255 is more deeply separated from the preprotocrista than on Cos 258. The lingual edge issued from the tip of the paracone is salient, forming a conspicuous hypoparacrista (much less expressed on Cos 258). There is a bulging metaconule, which on its posterior side is related to the posterior cingulum through a small crest, labially curving near the cingulum. Labially to the metaconule, a small groove separates it from the sharp crest wich ascends high on the metacone edge, which is also sharp (well expressed hypometacrista). Except for the small groove limiting the metaconule, the crista obliqua is continuous from protocone to metacone (Fig. 6N2). In the middle of the labial cingulum, the thickening of the cingulum is broader than on Cos 258 and it is accompanied by a small elevation: it is a very small mesostyle. A very small parastyle is close in size to that of Cos 258, however it is closer to the preparacrista, not isolated by a groove. The upper molar Cos 256 is interpreted as a M2/ because it is transversally elongated, with a large space between the paraconule and the paracone, it has a metacone smaller than the paracone, and its lingual cingulum is continuous (Fig. 6O). It has a big crestiform parastyle, an enormous paraconule deeply separated from the protocone by grooves, no metaconule. The place of the metaconule can be localized through the small groove interrupting the continuity of the postprotocrista, by a small crest ascending from the posterior cingulum in its direction, and in occlusal view through a slight curvature of the postprotocrista, however there is no bulging, no real metaconule. This tooth has strongly crenulated enamel. It is remarkable by two characters: it is the upper molar showing the maximum labial shift of the centrocrista, the bottom of its notch coming close to the ectocingulum; and it presents an enormous hypocone with a base bulging far lingually; this hypocone is isolated from the protocone by a deep groove, interrupted lingually by the cingulum, which is continuous with the low posthypocrista. This hypocone produces such a strong deformation of the crown outline that it seems anomalous, especially for an M2/, knowing that the others have hypocones smaller than the M1/s.

The M3/s are known through a labial fragment (Cos 261) and casts of two M3/ present in a private collection. The best preserved, the Cos 259 cast (Fig. 6P), is a triangular tooth, transversely elongated, with a metacone much smaller than the paracone but well-formed and distant. Its postprotocrista is cut in two parts by a groove, the first part issued from the protocone is posterior and abrupt (incipient protocone fold?), the second part slightly shifted labially, directed toward the metacone, borders a trigon basin as broad as on the other upper molars. The lingual cingulum ascends along the protocone and forms a lingual cusp with a low summit close to the cingular groove and the protocone wall, however with a broad bulging base. Its location is almost lingual to the protocone (only slightly posterior). By comparison with the M2/ Cos 256, which has a tiny pericone, it seems more appropriate to call this cusp a hypocone (it being a pericone might be discussed).

The DP4/ Cos 266 differs from the M1/s in being transversally shorter, the protocone base being much less lingually expanded (Fig. 6Q). It is narrower in its lingual part relative to the labial, with an accentuated concavity of the posterior border, resulting in a more triangular outline. The base of the hypocone is posterolingually salient as on several M1/s. The protocone is anteriorly shifted, and the postprotocrista has a strong sloping which is posterior instead of posterolabial in occlusal view. The two conules are more cuspidated and pointed than on most other M1/s. The hypocone has a size similar to that of Cos 257, however it is more deeply separated from the protocone base, and it appears less crestiform. There is a small and well formed parastyle which, as the weak metastyle, enters the variations seen in the upper molars. The labial cingulum is more irregular than on all upper molars, being completely interrupted along the paracone posterolabial base; posterior to this interruption, a marked swelling makes a real small mesostyle; further posteriorly, the labial cingulum is faint, visible in occlusal view but not isolated by a groove.

4.2.2. Remarks

Variability, pathology and function

The differences existing between some teeth are so large that the question must be raised: does all this material represents one or several species? First, two specimens show variations that we consider pathological. The case is obvious for the p/3 present on the type mandible, with its three roots. It seems also the case for the M2/ Cos 256, with its enormous hypocone whereas other M2/s have a much smaller one; it looks as if a very large hypocone as that of some M1/ had developed on a M2/, making such a huge bulge lingually that the tooth seems deformed, its lingual extremity probably being excluded from any significant function against the lower molars. The question also was raised if the m/3 of the type mandible might be in part abnormal through its anterolingual crown excessive elevation. It is not common o have in such a limited sample two clear cases of pathology, and a possible third one. Apart from the latters, among the most striking differences are those seen among the four M1/s. If one places side to side under the binocular the M1/ of Cos 258 (associated with its M2/) and the smallest Cos 257, one would tend to place them in two distinct species, because there is a strong size difference added to a series of other differences. However, the other M1/s appear intermediate in size between them, and all the characters of the upper molars appear to vary independently, in a mosaic way: hypocone size, lingual bulging and posterior cresting, conules size, bulging and cresting, labial shifting of the centrocrista, presence of a mesostyle, enamel crenulation. It does not seem possible to separate two groups, or one specimen wich would be clearly outside the rest of the group. A similar situation exists, more simple, with the three P4/s: Cos 263 is narrower than Cos 262 and one could wonder if they can belong to the same species; however the third one, Cos 265, is lingually narrow and labially broad, being an intermediate which differs in its own way, having the smallest protocone. Separation in two groups appears difficult. With the P/3s, the variations are also strong. Most of them have crest sinuosities and/or bifurcations at the level of a presumptive metaconid, but one of them, Cos 277, which is the broadest, has none at all and has the simplest and shortest talonid. Should we place it apart? Considering the series, it does not seem necessary to distinguish it, to take it out of the sample, especially when considering the important variations existing between the others (e.g. narrow posterior part present or not, variable paraconid shelf, …), and the fact that Cos 277 still has two posterior crests; it is not a completely simple p/3, it has a first step in its posterior complication. Other notable variations were mentioned on the paralophid and cristid obliqua (with the protocristid which can be lost) of the m/1s, the size of the protocone on the P3/s and P4/s. In fact, all along our descriptions, notable variations occurred on all teeth for which we have several specimens. All this suggests that we are dealing with one dentally variable species.

Several observations present in our descriptions deserve a functional comment. On the small i/2 preserved in front of the type specimen, the peculiar labial wear does not show a clear wear facet. Hence it was not caused by contact with a superior tooth, and probably is due to food pieces grasped between the anterior teeth during biting. A large and high wear facet was described on the p/4 Cos 860. The latter tooth is moderately worn on the back of the metaconid and on the talonid, and the vertical anterior wear, starting obliquely on the protoconid summit, which is lowered, and continuing until it affects the base of the crown, appears enigmatic. It hardly seems of taphonomical origin. Had the preceding p/3 been accidentally lost? Was an occluding upper premolar too high? Was some pathology present? Last, the tooth identified as a P2/, Cos 281, would be quite unreduced, as high as a P3/, whereas the p/2 of the mandible is a very reduced tooth (reduced in length and breadth, however still quite high). Is this congruent? Close examination of Cos 281 reveals that it presents a wear facet, not yet extensive, high on the labial side of its main cusp. And close examination of the p/2 of the type mandible also reveals a short zone of wear on its posterior crest, at around two thirds of its height. It is not a vertical wear facet as would produce the wear facet of the upper P2/, however this p/2 is extremely fresh, unworn at first glance, and the small facet indicates that contact with the occluding tooth did exist; therefore, there is no objection from occlusion to the identification of the P2/.

Comparisons

Comparison of the lower teeth and jaws from Cos with the mandible of *Pronycticebus gaudryi* shows that the latter was slightly larger. From the base of the crown, it appears that its p/2 was less reduced. *P. gaudryi* had a very simple p/3, bearing only a median postprotocristid reaching the tiny talonid in its middle. In contrast, all the p/3s from Cos have some complication of the posterior crests, the simplest of them, Cos 277, having its main posterior crest clearly posterolingual in occlusal view, and a second crest starting from the latter at a high level (level of a presumptive metaconid) and joining the middle of the posterior rim of the tooth. The four p/4s from Cos have a metaconid larger and better isolated from the protoconid than the p/4 of *P. gaudryi*. None of the p/4 from Cos has a paraconid shelf as transversally extended as it is on *P. gaudryi*, and none has a small paraconid as cuspidated as it is on *P. gaudryi*. On the available m/2s and m/3s from Cos, the paralophid is more attenuated than on *P. gaudryi*, none of them having the labial bulge present on the m/2 and m/3 of *P. gaudryi*, and the two m/3s having a paralophid shorter than on the m/3 of *P. gaudryi*. No clear difference occurs on m/1, as Cos 755 has a paralophid extremely similar to that of *P. gaudryi*. Concerning the upper dentition, the two P3/s from Cos have a postparacrista straight, posteriorly directed, simple; on the cranium of *P. gaudryi*, this crest has a slight labial inclination and its base joins the cingulum which goes labially around a “metastylar lobe” which is completely absent on the P3/s of Cos. The protocone of P3/ is smaller on the right P3/ than on the left on *P. gaudryi*. However, even the P3/ from Cos which has the largest protocone, Cos 858, has one which is even narrower and lower; and the second p3/ has almost no more protocone, only an elevation of its lingual cingulum. There is clearly a reduction of the protocone of P3/ in *P. cosensis* in comparison with *P. gaudryi*.

On the P4/s also, there is a difference in the postparacrista, which on the three P4/s of Cos is never as labially curved as on *P. gaudryi*, and is never associated with a labial stylar expansion. On P3/ and P4/ of *P. gaudry* there is a large salient paratsyle, never present on these teeth at Cos.

On the M1/s, we have seen variations in the degree of waisting of the crown. However, even the small Cos 257, which has the highest waisting at Cos, is less waisted than the M1/ of *P. gaudryi*. The latter has a long labial part, with an extended postmetacrista within a somewhat triangular posterolabial corner, whereas this part is more squared on the M1/s from Cos, which have a less extended postmetacrista. The M1/s of *P. gaudry* also seem to have a more developed parastyle than on those from Cos. All this results in a triangular aspect more expressed in *P. gaudryi* than on all the M1/s from Cos. It is possible that the M1/s of *P. gaudryi* would have had a hypocone smaller than on *P. cosensis*, however the strong degree of wear of the specimen makes this very unsecure (there is no groove of the lingual border in *P. gaudryi*), and the variations in hypocone size are quite strong in *P. cosensis*.

The three M2/s from Cos have a lingual cingulum which is continuous or subcontinuous, whereas it is really absent on the M2/s of *P. gaudryi*.

All these differences taken together show that the species from Cos is distinct from *P. gaudryi* and deserves a new species name. The most significant differences are summarized in the diagnosis of the new species. If we try to place these differences in a phylogenetic context, it appears that these species seem to belong to two divergent lineages. In *P. cosensis*, the reduction of P/2, the complication of the posterior part of p/3, the development of the lingual cingulum on M2/, are certainly apomorph characters in comparison with cercamoniines in general. Likewise, the development of the posterolabial corner of P3/, P4/ and the M1/s, with long curved postparacrista or postmetacrista, are apomorph in *P. gaudry*i, so that even without any precise statement concerning more ambiguous characters (as the size of the metaconid on P/4, or the size of the protocone of P3/), these two species show divergent specializations, and thus cannot be placed in one hypothetical specific lineage. It is very possible that the larger p/4 metaconid, the reduction of the P3/ protocone (also starting on P4/) and a larger hypocone would be further advanced traits in *P. cosensis*, however more assemblages of *Pronycticebus* are needed to further elaborate likely character polarities.

Comparison with *P. neglectus* is first made with the mandible ascribed by Thalmann (1994) to this species. It is slightly larger than *P. gaudryi*, resulting in being significantly larger than the specimens of Cos. In its molars, it has long and narrow paralophids, which are closer to those at Cos (those without swellings), however on m/2 the paralophid joins the base of the metaconid, which has a slight premetacristid and realizes more continuity than at Cos, and this link with the metaconid base is present on m/1, where the paralophid curves slightly posteriorly, whereas such a closing is never observed on the m/1s of Cos. In lingual view, the m/1 of *P. neglectus* has an entoconid lower and less pointed than on the m/1s of Cos. In occlusal view, the m/3 of *P. neglectus* has an entoconid salient lingually, which is not the case on the two m/3s from Cos. For premolars, *P. neglectus* differs more strongly by the absence of p/1 and complete absence of metaconid on p/4. Its p/3 has a beginning of posterior cresting with two crests, one of them becoming posterolingual in occlusal view, recalling those of Cos, however the posteriorly directed crest is till the dominant one, recalling the primitive morphology present on *P. gaudryi*. The p/3 also has no lingual cingulum, and on p/3 and p/4 the anterior cingula are simpler, without any swelling in the paraconid shelf region. The description of the type skeleton by Thalmann (1994) confirms what is suspected from the examination of the mandible: this species had lost the first premolar, both in the upper and lower dentition. M1/ and M2/ had no lingual cingulum. From the illustrations by Thalmann and our own observations of the type specimen, we estimate that the hypocone is smaller on M1/ and M2/ than on the upper molars of *P. cosensis*. On the whole, the species of Cos is also clearly different from that of the Geiseltal, which is also divergent in its own way (loss of p/1/, no metaconid on p/4, narrow paralophid curving posteriorly on m/1. Again none of them would appear as a likely ancestral state in a specific lineage.

A last comparison must be done with the very scanty material mentioned in Vielase as *Pronycticebus* cf *gaudryi* (Legendre et al., 1992). Comparisons were limited at that time because the upper teeth are highly worn on the cranium of *P. gaudryi*. The M2/ VIE 141 appears to be extremely similar to the M2/s described above (Fig. 6S). Small differences concern a very slight flexus on the anterolingual border of the tooth, not observed in Cos, the lingual cingulum which appears slightly less complete: the prehypocrista is very short, leaving the groove between protocone and hypocone lingually open (as on some M1/s from Cos), whereas this crest is longer on the two well preserved M2/ of Cos, almost completing the lingual cingulum (on the pathological one, the crest is very low and the groove quite open). Another difference is the complete absence of paraconule on this tooth, whereas it is well formed on the M2/s from Cos. However, the difference is very small with the M2/ of Cos 258, which has the smallest paraconule in the Cos assemblage. The centrocrista is straight on VIE 141, as on the M2/ of Cos 258. The M2/ from Vielase has strongly crenulated enamel, and its mesostyle is larger than in all the teeth from Cos, accompanied by a low crest joining the bottom of the notch of the centrocrista. Polarities appear opposed for these morphological differences. The M2/ from Vielase could appear more primitive through its less complete lingual cingulum, and more derived through the complete loss of the paraconule and the larger mesostyle. Because there are strong variations among lingual cingular characters, may be that the two others are a first indication of the Vielase species being slightly more advanced? Clearly, this hypothesis needs more quantitative data to be strengthened. Another fragmentary tooth from Vielase, VIE 142, is an incomplete m/2 or m/3, which has a paralophid thin and straight as on Cos 271 (Fig. 6T). The tooth seems to posteriorly broaden as would an m/3, and the reach of the cristid obliqua on the trigonid wall, relatively low and labial, also fits with an m/3. This tooth does not add any difference with those of Cos. Pending the recovery of more specimens, the species from Vielase is best be referred to the new species *P. cosensis*.

Genus *Anchomomys* Stehlin 1916

4.3.*Anchomomys* sp.

Material: One incomplete M2/, Cos 290 and one upper canine, Cos 297.

Measurements: C sup Cos 297, 1.50 x 1.14; M2/ Cos 290, > 2.20 x >= 3.10.

Description and remarks

This M2/ Cos 290 is very close in morphology to the M2/ of the type specimen of *Anchomomys gaillardi* from Lissieu, described by Stehlin (1916) and Szalay (1974). The main differences are: a significantly larger size, a slightly larger hypocone, more cuspidated, associated with a slightly more quadrangular lingual border of the crown. The tooth seems to be slightly more transversally elongated, which is corroborated by the slope of the paracone, which is extremely steep in anterior view in *A. gaillardi*, whereas the same slope is more lingually extended on the tooth of Cos. These differences are enough to consider this specimen as belonging to a different species, however from the available evidence also a very close one. Because it is more transversally elongated, it might be primitive in relation to *A. gaillardi*. However, upper molars in the *Anchomomys* clade are quite conservative. This tooth is also very close to one upper molar of *A. frontanyensis* from Sant Jaume de Frontanyà (Marigo et al., 2011). The hypocone is closer in size in the latter species, however the tooth seems to be also more transversely short in *A. frontanyensis*, with a paracone not lingually extended (see Figure 1J in Marigo et al., 2011). More teeth are needed to further elaborate the significance of the Cos *Anchomomys*.

The small tooth Cos 297 is not easy to identify. It is relatively simple, moderately longer than broad, and it seems very slightly procumbent (Fig. 7B). On its lingual side, a cingulum is present, weak anteriorly, more salient posteriorly, absent in-between. The root is complete and in posterior view somewhat labially shifted at its extremity, which fits with an upper, and not with a lower canine. The global shape is not far away from the upper canines which were described for *A. frontanyensis* and *Mazateronodon endemicus* (Marigo et al., 2010, 2011), however it differs from them in being less pointed and much smaller in relation to the upper molars. Nothing else in the fauna would suggest the presence of a second smaller species of *Anchomomys*. We consider more likely that these two teeth belong to the same species, which in turn suggests that a marked evolution in upper canine size took place within *Anchomomys* lineages.

Infraorder Omomyiformes Schmid 1982

Family Microchoeridae Lydekker 1887

4.4. Genus *Quercyloris* Godinot & Vidalenc, nov. gen.

Figure

Derivation of name: from the Quercy region and the living genus *Loris*, a small insectivorous strepsirrhine fromAsia

Type species: *Quercyloris eloisae* Godinot & Vidalenc, nov. sp.

Included species : the type species only

Occurrence and diagnosis: see type species

Quercyloris eloisae Godinot & Vidalenc, nov. sp.

Figure 7

Derivation of name : in honor of Eloïse Lande-Zoukouba, in recognition of her dedication to sorting small fossils in washing and screening residues of Quercy localities during many years.

Holotype: the right M1/ Cos 288;

Paratypes: two other upper molars, the right M1/ Cos 287 and the left M2/ Cos 289;

Material: one upper incisor Cos 304, one upper canine Cos 294, three upper premolars left P4/ Cos 291, Cos 292 and right P4/ Cos 293, one p/3 Cos 298, an m/2 Cos 295, and an incomplete m/1 Cos 301.

Type Locality: Cos in the Quercy region, France.

Occurrence: the type locality only;

Measurements: I1/ Cos 304, length perpendicular to the root (H in Godinot 2003, Fig 2), 1.31, width 0.92, length along the crown base in lingual view, 1.88; upper canine Cos 294, length 1.35 x width 0.89 x height 0.78; P4/ Cos 291, 1.48 x 2.12; P4/ Cos 292, 1.37 x 1.86; P4/ Cos 293, 1.49 x 1.94; M1/ Cos 287, 1.76 x 2.43; M1/ Cos 288, 1.65 x 2.38; M2/ Cos 289, 1.53 x 2.26; p/3 Cos 298, 1.20 x 0.91 x 0.59; m/1 Cos 301, 1.55 x 1.33; m/2 Cos 295, 1.75 x 1.44.

Diagnosis: Small microchoerid with transversely elongated upper molars, without hypocone or *Nannopithex*-fold, and with a long postmetaconule crista and variably elongated premetaconule crista forming a crescent around the metacone base; P4/ with an elongated and narrow lingual lobe, low protocone, and isolated metastylar swelling; upper incisor elongated, with a strongly bulging posterolingual eminence, and a crown without the global curvature present in *Pseudoloris*; lower molars with relatively low relief, big cuspidated paraconid isolated from the metaconid by a groove, making a lingually open trigonid on m/1-2.

4.4.1. Description

The p/3 Cos 298 is typical of small microchoerid premolars, single rooted with the crown markedly anteriorly inclined, having in lingual view an elongated and rectilinear cingulum (see Godinot, 2003, Figure 1a,h,i); anteriorly, the protoconid is not high above the cingulum, a character accentuated here by a strong wear of the protoconid summit (Fig. 7K1). In occlusal view, the posterior part of the crown is very broad, producing a subtriangular outline, despite a long vertical wear facet has affected the posterolingual border and slightly diminished the posterior breadth. This posteriorly broad outline is the reason to consider this tooth a p/3 instead of a p/2. There is only one posterior crest on the posterior side of the protoconid, which is median and not salient; it joins the posterior cingulum. In posterior view, the cingulum extends only on the lingual side of this junction, until it is interrupted by the above mentioned wear facet.

The two lower molars are uneasy to identify, because the best preserved, with its large paraconid resembles m/1s and the other is incomplete, its entirely broken away protoconid rendering its interpretation difficult. However, because they have similar talonids and similar low relief in lingual view, we place them in the same species. The slightly smaller one, Cos 301, despite its broken away protoconid, has a well preserved paraconid, which is very salient anteriorly, median instead of lingual on the other; also what remains of its outline shows the anterior half of the crown to be much narrower than the posterior half (Fig. 7L1). For these reasons, Cos 301 is probably an m/1, and the complete one, Cos 295, is probably an m/2. Both share in posterior view a low entoconid and a much higher hypoconid, with enamel more ventrally extended (some exodaenodonty); this explains why the labial slope of the protoconid is extended on Cos 295, as is often the case in microchoerids (Fig. 7M1). Both have a similar cristid obliqua joining the back of the trigonid, clearly below the protoconid summit on Cos 295. They also have similar metaconids, that of Cos 301 being slightly worn, with a wear facet extending on its side of the protocristid. The paraconid of the m/1 Cos 301 is cuspidated, slightly more crestiform than on Cos 295; it is anteriorly placed, median, and isolated from the metaconid by a deep valley (Fig. 7L2). On Cos 295, the paraconid is more bulbous, more lingually placed, also isolated from the metaconid by a groove, however a shallower one. Both paraconid and metaconid have on Cos 295 blunt edges directed toward each other in occlusal view, however they do not meet, the groove between them is continuous, the overall appearance is still of two bulbous cusps and a lingually open trigonid basin (Fig. 7M2). On the labial side, there is no cingulum around the hypoconid (a crack in the crown just below could be misleading); a rounded cingulum starts at the opening of the postvallid, with a small bulge, an interruption just in front of the valley, and a cingulum extending forward, then strongly dorsally curving, and then interrupted by the breakage of the antero-ventrolabial part of the crown. On Cos 301, one sees only an unusual rounded bulge of enamel toward the opening of the postvallid, and anteriorly the crown is damaged.

The right I1/ Cos 304 has a convex and smooth labial face, and a flatter lingual face entirely surrounded by a crest (Fig. 7C1): anterior and posterior crests on both sides of the protoconid, continuous on both sides with the cingulum, which forms two ventrally inflated parts separated by a concavity; the anterior part first follows an almost straight line, then it fades through the concave part, possibly due to some degree of wear (difficult to recognize), then the posterior part is shorter and strongly bulging lingually; the tip of this bulging is affected by a lingual wear facet, which prevents to know if it would have made a salient summit (which would have been analogous with a small plesiadapid posterocone). The crown is on the whole somewhat extended, recalling the extension of lower premolars as seen in lingual view.

Another isolated tooth, Cos 294, has an overall similarity with the p/3 described above (Fig. 7D1-3). However, it differs by its crown more perpendicular to its root, an outline in occlusal view more rounded, less posteriorly broadened, a lingual cingulum limited to its anterior part, a posterior cingulum more cusp-like, round, isolated from the protocone by a transverse groove. On the whole, it was a less procumbent tooth, less modified to fit into a closely packed series, it may have been slightly higher, however wear of its summit also obscures that aspect. It is best interpreted as an upper canine.

The three P4/ Cos 291, Cos 292 and Cos 293 (Fig. 7E-G) are transversely elongated, with a narrow protocone lobe, a well isolated metastylar crest, a preprotocrista continuous with the anterior cingulum (less continuous, thinner and sinuous, on Cos 293), reaching a cingular parastyle, a more abrupt postprotocrista quickly joining he posterior cingulum, also continuous until the metastyle. The labial cingulum is only incipient in the middle of the labial side (not visible on Cos 291 due to breakage of the base of the crown). They differ in some details. Cos 292 has a lingual lobe slightly shorter and broader than the others, giving it a more quadrangular outline, with a postprotocrista directed posteriorly. Cos 291 has a postprotocrista directed posterolingually, as Cos 293, which has a narrower protocone lobe, rounded in outline, with a slight flexus of its anterior border. There is a faint anterior cingulum below the preprotocrista on Cos 291, not on the others. The metastylar crest makes an angle with the postparacrista on Cos 291, visible in occlusal as in posterolingual view; this crest is more continuous on Cos 293, which has a slightly more inflated metastyle.

The three upper molars Cos 287, Cos 288 and Cos 289 are quite similar to each other (Fig. 7H-J). They are simple, transversely elongated, narrower lingually than labially. Cos 289 has a metacone smaller than the paracone, a protocone slightly lower than the two others, with a less extended lingual protocone slope; it is likely an M2/. Cos 287, with its slight waisting, is a likely M1/. Cos 288 is more ambiguous, however because it shares with Cos 287 a high protocone and long lingual slope, we identify it as a second M1/. Cos 287 and 288 have a slight ectoflexus, whereas Cos 289 has a straight labial border. All have a postmetacrista somewhat labially oriented, they have cingular parastyle and metastyle, not cuspidated. The posterior cingulum is well formed on Cos 289, being continuous and staying low in its lingual part. On the two others, the posterior cingulum moderately ascends lingually, the crown becomes salient beyond it in occlusal view, which gives the impression of an incipient hypocone. Cos 287 and Cos 288 have a distinct paraconule, with a summit visible in anterior or posterior view, Cos 289 has no real paraconule, only a very faint broadening of the base of the preprotocrista. All have a paracone which has a long lingual edge, which becomes more crested toward its base (and is slightly longer on Cos 289); this extension (hypoparacrista not salient) is always separated from the preprotocrista or preparaconule-crista by a groove; none of them has a post-paraconule crista which would make the link between paraconule and paracone often encountered in *Nannopithex* species. The metaconule is only crestiform on Cos 287, crestiform with a low summit on Cos 289, and crestiform with a well formed summit, that is cuspidated, on Cos 288. It has a long postmetaconule crista joining the posterior cingulum when there is one (and still continuing until the metastyle when the posterior cingulum is interrupted, as on Cos 287). The premetaconule crista is broadly divergent from the latter, lowering and going around the metacone base on Cos 287; on Cos 288, the premetaconule crista is less divergent, it turns and joins the base of the metacone; and on Cos 289, the premetaconule crista goes more toward the metacone; it is also much less abrupt, realizing a continuity between the metaconule and the metacone lingual edge.

4.4.2. Remarks

These new fossils do not fit in any of the microchoerid genera described until now. They would most closely compare with the most primitive species of the family, *Melaneremia* from the early Eocene and early *Nannopithex*. The upper molars are close, however the sole M1/described in *Melaneremia* has a small metaconule and a direct link from protocone to metastyle (Hooker, 2007); it does not present the strong metaconule with crescentiform crests of *Quercyloris*. The lower molars also would appear close, however the p/3s are markedly different. Whereas *Melaneremia* still has a two-rooted p/3 relatively similar to p/4, as in primitive omomyids (Hooker, 2012), *Quercyloris* has a single-rooted one with the anterodorsally oriented crown typical of more advanced microchoerids (Fig. 7K1). This reflects a higher degree of premolar compaction, clearly indicating a different genus. The most primitive species of *Nannopithex*, *N. zuccolae* from Prémontré, has transversely elongated upper molars and P4/, and no hypocone (Godinot et al., 1992). However, here again there are differences: the postprotocrista presents a more or less expressed *Nannopithex*-fold, the M2/ is lingually more dissymmetrical, and the metaconule does not present the long postmetaconule crista present at Cos as on the upper molars of *Pseudoloris* species. Furthermore, the tendency of the two labial metaconule cristae to make a crescent around the metacone base, as in *Pseudoloris,* is well expressed on Cos 287, less on Cos 288, not on Cos 289, which is more similar to *Nannopithex* for this character. On the paraconule side, the upper molars of Prémontré frequently have the link between paraconule and hypoparacrista usually present in *Nannopithex* species, whereas all the upper molars from Cos have a groove separating the paraconule from the hypoparacrista. Differences also occur on the lower molars. The m/2s of Prémontré have much more acute crests than Cos 301. They also have a much deeper protocristid notch and a deeper trigonid basin; the trigonid crests are higher, there is a true premetacristid, the paraconid is less lingually placed, and the trigonid crests are starting to lingually close the trigonid basin (in the way which is more advanced on the m/3s, with their narrow triangular trigonid typical of *Nannopithex*). In contrast, the trigonid basin is shallower, lingually open, and the paraconid more lingual on Cos 301. In sum, the molars from Cos resemble those of *N. zuccolae* by their primitive proportions and characters (large paraconid on the lower molars, lack of hypocone on the uppers), however they belong to a different lineage which did not develop a *Nannopithex*-fold and a crest linking paraconule and paracone on the uppers, which did not develop the closing of the trigonid in the *Nannopithex* way on the lowers, and which shares with *Pseudoloris* the tendency to build a metaconule crescent on the upper molars. It is very probably a primitive member of the *Pseudoloris* clade. It cannot be ascribed to a primitive species of *Pseudoloris* because there are still too many differences in major characters between them: *Pseudoloris* lower molars never have a large cuspidated paraconid, they have a high pointed entoconid in lingual view; its upper incisors have a different shape, being more pointed and curved; added to the fact that *Pseudoloris* upper molars and premolars are transversely shorter, all these differences justify the erection of a new genus. Its only known species, *Quercyloris eloisae* gen. nov. sp. nov., appears primitive relative to *Pseudoloris* in many of its known characters, so that it could represent an early member of the *Pseudoloris* lineage. This will have to be tested by further discoveries (e.g. intermediate I1/ morphology, intermediate trigonid shapes, etc.).

Another poorly documented genus, *Pivetonia*, often has been considered a synonym of *Pseudoloris* (e.g. Szalay & Delson, 1979; Godinot, 1983; Minwer-Barakat et al., 2010, 2012). However, we consider it as a valid genus, represented by its type species *P. isabenae* from Capella (Crusafont-Pairo, 1967), and by *P. saalae* from the Geiseltal (Thalmann, 1994). *Pivetonia* has also been mentioned as possibly present in Lissieu (Godinot, 1983), Cuzal (Marandat et al., 1992), and Vielase (Legendre et al., 1992). The teeth of the type specimen of *P. isabenae*, a mandible bearing p/3 to m/2, show a remarkable overall similarity with the teeth of *Q. eloisae*. Their p/3s are similar; their lower molars have the same size and low relief. However, on the m/1 of *Pivetonia*, a lingual crest joins the paraconid to the metaconid, lingually closing the trigonid basin; on m/2, the difference is strongly accentuated because the paraconid, more crestiform but still voluminous, is shifted labially, and the closing of the trigonid basin is more complete. The trigonid is made of a triangle, the paraconid summit being closer to the protoconid than to the metaconid. This means that *P. isabenae* is advanced in a process of a trigonid closing. This process is more advanced on *P. saalae* from the Geiseltal, which has on m/2 and m/3 a trigonid made of three crests in triangle. Such a process appears apomorphic, and difficult to reconcile with the morphology of an early assemblage of *Pseudoloris* as illustrated in Le Bretou (Godinot, 1988). On the latter's m/1 and m/2, the trigonid is lingually open, and we think that such a morphology is unlikely to be derived from a closed trigonid morphology. In the different processes of trigonid evolution, *Pivetonia* is already advanced toward a triangular trigonid closing, which distantly recalls the trigonid closing found among *Nannopithex* species. We consider as unparsimonious, unlikely, a secondary loss of the lingual crest joining the paraconid to the metaconid, i.e. a secondary reopening of the trigonid basin in the *Pseudoloris* lineage. In this view, *Pivetonia* is evolving in its own way, divergent from *Pseudoloris*, whereas *Quercyloris* is still a candidate for a morphology possibly ancestral to that of *Pseudoloris*. More material will help to test these hypotheses. For example, *P. saalae* has an enlarged p/4 which also recalls *Nannopithex* and might be associated with enlarged anterior incisors. A p/4 of *Quercyloris* would help to test this scenario, as would an m/3 (posteriorly broadened as in *Nannopithex*, or not, as in *Pseudoloris*?).

In this context, the significance of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà (MP 14-15; Minwer-Barakat et al., 2010) will be important. On one hand, its incompletely lingually closed trigonid and its variations might appear intermediate between those of *Pivetonia* and *Pseudoloris*. On the other hand, the lower incisors attributed to this species, as those attributed to *P. cuestai* (Minwer-Barakat et al., 2012) are so different from those of *P. parvulus* and from those of microchoerids in general, that they would indicate a different lineage (*Pivetonia*?) or be misattributed to those species. Further analyses are requested to better settle these questions.

Comparisons also must be made with the two fragmentary teeth from Vielase previously mentioned as *Pivetonia* n. sp. (Legendre et al., 1992). The trigonid of m/1 VIE 144 appears very similar to the parts preserved in the incomplete m/1 from Cos. The cusps are low and it possesses a very large paraconid separated from the metaconid by a wide space. It resembles a lot the m/1 of *Quercyloris moniquae*, despite a small difference in paraconid shape. However the fragmentary M1/ VIE 143 is transversely shorter than the upper molars form Cos, it is markedly narrower in its lingual than in its labial part, and it has cingula, especially the posterior one, which are much stronger than on the teeth from Cos. This M1/ cannot belong to the same species as in Cos. Nevertheless, we can list *Quercyloris* as present in Vielase in replacement of *Pivetonia*, which is not there.

Order Plesiadapiformes Simons and Tattersall, in Simons 1972

Family Paromomyidae Simpson, 1940

Genus *Arcius* Godinot, 1984b

4.5. *Arcius moniquae* Godinot & Vidalenc, nov. sp.

Figure 8

Derivation of the name : in honor of our colleague Monique Vianey-Liaud, in recognition of her magnificent research on fossil rodents from the Quercy.

Holotype: the left M2/ Cos 300, University of Montpellier collection.

Material: The P4/ Cos 299, the m/3s Cos 305 and Cos 306, the i/1 Cos 302.

Type Locality: Cos, Quercy region, France.

Measurements: P4/ Cos 299, 1.82 x 2.15 mm; M2/ Cos 300, holotype, 1.95 x 2.57; m/3 Cos 305, > 1.95 x 1.40; m/3 Cos 306, 2.63 x 1.39; lower incisor Cos 302, total length, 7.41, height at the base of the crown, 2.58, width (in occlusal view) in the middle of the crow, 1.35.

Diagnosis: Species of *Arcius* which differs from all previously described species of the genus by its reduced labial cingulum and complete absence of paraconule on the upper molars; very reduced trigonid on its m/3, without any remnant of paralophid, and with a low vestigial protocristid making the trigonid broadly open posteriorly. In addition, the upper molars are relatively transversely short and have a vast posteriorly extended posterior fossa.

4.5.1. Description

The partial i/1 Cos 302 is broken at its tip and at its base (Fig. 8A1-2). The remaining part is long and characteristic enough to be identified: in its preserved part, it is exactly similar to the i/1 of *Arcius rougieri*, as described in Godinot (1984) and again figured in Lopez-Torres and Silcox (2018, Figure 1). This part does not need to be described again. Breakage at the tip allows to see that the enamel is thicker on the labial and ventral side, thinner on the dorsal side and lingually above the thin crest which curves and posteriorly quickly reaches the dorsal side (Fig. 8A1). Two m/3, Cos 305 (Fig. 8D) and Cos 306, are very similar. Their trigonid is anteroposteriorly very short; no trace of paralophid can be distinguished. Their protocristid is extremely reduced: very low and blunt on the protoconid side, no more discernible on the metaconid side. The trigonid is no more a transverse wall, it is mainly an anteroposterior broad valley. Their hypoconid is low and its crests are almost anteroposterior. The third lobe is broad, the entoconid low and very little lingually salient.

The P4/ Cos 299 and the M1-2/ Cos 300, the type specimen, are quite similar in overall shape, with a subquadrangular outline, weak labial cingulum, straight preprotocrista directly reaching the parastyle, postprotocingulum surrounding a vast posterior fossa, a low postprotocrista (Fig. 8B-C). They differ by the outline transversely more extended and posteriorly shortened in Cos 300, which is similar to most M1-2/ described in *Arcius* species. In labial view, the paracone and metacone summits are slightly closer, and the paracone is higher, on Cos 299, which prompts us to identify it as a P4/. The notch of the centrocrista as seen in labial view is deeper on Cos 299, extremely low on Cos 300 on which it makes a very open V and the crest appears highly situated. The trigon fossa is deeper on Cos 300 than on Cos 299, which may also confirm our identification. The paracone lingual extension is a blunt edge on Cos 299, it is more lingually extended and more crested on Cos 300 (hypoparacrista). On both teeth, a groove separates these crests from the preprotocrista; on the latter, a paraconule is completely lacking on Cos 300, and vestigial, visible only in anterior view as a very low summit of the crest on Cos 299. The labial cingulum is poorly differentiated, not isolated by grooves. In labial view, a very shallow relief allows the delineation of a paratsylar and a metastylar low relief; in the middle of the labial border, there is no cingulum on Cos 299, whereas on Cos 300, even if the cingulum is poorly crested, the presence of a small fossa anterolabially to the metacone underlines its presence.

4.5.2. Remarks

When compared with all the species of *Arcius* described until now, the small material from Cos presents several original characters. Its cusps and crests are relatively low, less acute than in several species as *A. rougieri* and *A. fuscus*. In most *Arcius* species, the notch of the centrocrista is deep, whereas it is especially shallow on the M2/ of Cos. The two upper teeth also are less transversely elongated than in the primitive species of the genus, *A. zbyszewskii* and *A. fuscus*. In occlusal outline, they are close to some of the upper molars of *A. lapparenti* figured by Aumont (2003, 2004). However, the upper molars of *A. lapparenti* have a more differentiated labial cingulum, and for some of them a less posteriorly extended posterior fossa. More important, all the upper molars of these species, and *A. ilerdensis*, have a distinct paraconule and a link between the paraconule and the hypoparacrista. This is also true of the P4/s of *A. fuscus* and *A. lapparenti*. The loss of the paraconule and groove isolating the preprotocrista from the hypoparacrista, on M2/ and possibly on P4/, appears as unique to the species of Cos. If our identification of Cos 299 as a P4/ is correct, then this P4/ seems transversely shorter than the P4/s of most other *Arcius* species; it may also have the paracone and metacone the closest in size among the species of *Arcius*, which would be one more derived character relative to the others. On the lower m/3s, the species of Cos also appears at the end of a morphological trend, the reduction and posterior opening of the trigonid. All the figured m/3s of *Arcius* have a more or less reduced paralophid, and some kind of anterior extension of either the preprotocristid (e.g. *A. lapparenti* in Aumont 2004) or the premetacristid (*A. ilerdensis*); a paralophid crest is lacking on the m/3s of Cos. Furthermore, all the m/3s of other species have a well differentiated protocristid, whereas this major transverse crest is highly reduced on the m/3s of Cos, broadly posteriorly opening the trigonid. For all these reasons, despite the paucity of the material recovered until now in Cos, this *Arcius* material needs to be recognized as a new species, which appears apomorph relative to previously described species for several of its distinctive characters. An evolutionary trend toward more bunodont teeth has already been identified in *Arcius* and in other genera of paromomyids (Lopez-Torres et al., 2017). Morphological quantifications may be done in the future to test if this new species really is an advanced stage in this trend among *Arcius* species.

The m/3s of Cos lead to comment the two m/3s from Bouxwiller which have been described by Aumont (2003) as *A. lapparenti*, and excluded from this genus and considered as possibly belonging to a *Nannopithex* by Lopez-Torres et al. (2018). Among the reasons to question their attribution to *Arcius* was the extremely short trigonid and very broad talonid basin. These characters are present on the new species from Cos, and moreover on the figures of Aumont (2003, Plate 15) the protocristid appears as reduced as it is on the m/3s from Cos. There is no doubt that the two m/3s from Bouxwiller belong to an *Arcius*, and they may best be referred to *A.* cf *moniquae* pending the recovery of more material from both localities. The m/3 figured by Aumont (2003) appears slightly anteroposteriorly shorter than the m/3s from Cos, and the talonid basin this way seems to be broader, however these differences are very small; they do not exceed the strong intraspecific variations illustrated in large assemblages of *Arcius* by Aumont (2003), and they do not justify to exclude the m/3s from Bouxwiller of the genus *Arcius*. These m/3s appear closer to *A. moniquae* nov. sp. than to any other *Arcius* species.

5. Discussion

The new fauna of Cos has a very original composition. It does not include any perissodactyl nor any artiodactyl. It is rich in rodents and bats, and also in bird remains. Bones of some large prey birds have been recovered, which suggest that the assemblage may result from the accumulation of preys by raptors. The other elements of the fauna are under study.

The fauna of Cos being new, it would be important to propose for it an age, which will be given by the fossil content because it is a fissure filling. However, the primates are new species and the plesiadapiform belongs to a poorly documented lineage. The biochronological considerations which follow therefore will not be precise. The fauna does not content any primate species found in Bouxwiller. The *Protoadapis* has a remarkably primitive M2/ without hypocone, whereas the *Europolemur* and a possible other cercamoniine from Bouxwiller have very large hypocones. These elements suggest that the fauna is probably older than Bouxwiller, i.e. older than MP 13. If we consider that *P. brachyrhynchus*, absent in Bouxwiller, is probably older than MP 13, then *P. andrei*, which must be older than *P. brachyrhynchus*, would be even older, which would point toward MP 12 or before. The only species of *Pronycticebus* known outside of the Quercy is *P. neglectus* from the Geiseltal, MP 12 level. No simple lineage of *Pronycticebus* has been identified, the genus seems to have had a bushy evolution, however its presence in the MP 12 reference-level is an important indication. As seen above, the presence of *P. cosensis* in the MP 10-11 fauna of Vielase, even if they have a slight difference in evolutionary stage, suggests a close age for Cos. The absence of these primates from the relatively well sampled faunas from the MP 10 level suggests that it is likely later than MP 10. The new species of *Arcius*, which seems more advanced than the MP 10 common species *A. fuscus* and *A. lapparenti*, would confirm this indication. It is very difficult to go further. Rouzilhac, which is not very far away, has different middle-sized cercamoniines and no micromammals. It is placed in the MP 10 – MP 11 interval, which is broad (Godinot et al., 2018). In conclusion, the absence of well delineated lineages prevents strong biochronological statements, however many indirect arguments point toward a MP 10 – MP 12 bracket, and the presence of *P. cosensis* and a *Quercyloris* species in Vielase suggest an age close to that ascribed to this locality, in the MP 10 – MP 11 interval. Based on the differences on one upper molar of *Pronycticebus* and the presence of a larger species of *Quercyloris* in Vielase, a preliminary conjecture would propose the Cos fauna as possibly older than Vielase. This first indication needs confirmation by other evidence.

6. Conclusion

The four new species described in this paper are a significant addition to our knowledge of European Eocene primates and plesiadapiformes. The new *Protoadapis andrei*, close to *P. (Cercamonius) brachyrhynchus*, is documented by more complete material than the latter, including p/3, p/4, m/3, and more importantly for the first time upper canines, a P4/ and an M2/ which can confidently be attributed to a *Protoadapis* species. This will be very important for future phylogenetical analyses. Concerning the new *Pronycticebus*, the material also presents for the first time a lower incisor, a lower canine in place, p/2, and unworn teeth from third premolar to last molar above and below, with variations. Documenting the intraspecific variability is crucial to a sound appreciation of the value of characters in phylogenetic analyses. Our comparisons have shown us that, on isolated lower molars, it may be difficult to distinguish *Pronycticebus* from *Europolemur* species. This is illustrated by the proposal of Tattersall & Schwartz (1983) to consider the mandible from Mancy previously ascribed to *Protoadapis curvicuspidens* (Russell et al., 1967) as a new species of *Pronycticebus, P. mancyi*. This attribution was not followed by us, and we lately thought that this species should be considered as *Europolemur mancyi*. The new material of *Pronycticebus* confirms this choice in making clear a difference between the two genera: *Europolemur* species have large canines, whereas *Pronycticebus* species have much smaller canines, above and below. Also, unworn teeth reveal that *Pronycticebus* molars are much less bunodont than those of *Europolemur*. These new characters will be crucial to enhance our understanding of the genera *Protoadapis, Europolemur* and *Pronycticebus*, which until now have unresolved phylogenetic relationships, in large part due to insufficient documentation. Interestingly, in both *Protoadapis* and *Pronycticebus*, our preliminary phylogenetic observations seem to point toward a bushy evolution and not to simple specific lineages easily traceable through time. It is possible that the two species *P. brachyrhynchus* and *P. andrei* will fit in a well-defined genus *Cercamonius*, however this would necessitate a good understanding of *Protoadapis* species and their evolution, which is not the case.

The new genus and species *Quercyloris eloisae* is an important addition to our knowledge of the small microcheorids because it documents a very primitive form which seems closely related to *Pseudoloris*. Until now, we had only two species of *Pivetonia*, without upper dentitions, as possible relatives of *Pseudoloris*. The new form found at Cos documents a new lineage which at the same time appears as suitably ancestral for *Pseudoloris* and leads to place aside the species of *Pivetonia* in a lineage parallel to *Nannopithex* instead of directly ancestral to *Pseudoloris*. More material of these tiny forms will be needed to complete the scenario, and confirm or invalidate our hypothesis. Nevertheless, the new species demonstrates a very early separation between a *Nannopithex* clade, including later *Necrolemur* and *Microchoerus*, and the clade leading to *Pseudoloris*.

The new species of *Arcius* is the first discovery of a plesiadapiform in the Quercy fossil record. Its large incisor is exactly similar to those found in the earliest Eocene, showing the remarkable stability of this tooth in the genus *Arcius*. Furthermore, it illustrates an evolutionary trend in *Arcius*, an increasing bunodonty, linking the early Eocene forms to the latest occurring European plesadapiform in Bouxwiller, late Lutetian (MP 13). This confirms the relatively late survival of paromomyids in Europe, which was recently questioned by Lopez-Torres et al. (2018).

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Figure captions

Figure 1. Left, view of the Cos fossiliferous outcrop, at the rim of a large fissure covered with vegetation; it shows the superposition of beds. Right, a closer view after some excavation; the beds appear affected by sliding; hammer and bag give the scale.

Figure 2. Mandibles of *Protoadapis andrei* nov. sp. A-B, the right mandible Cos 253, the type mandible, in occlusal (A) and lingual (B) views; C-E, the left mandible Cos 254 in occlusal (C), lingual (D) and labial (E) views. Scale bar is 1 cm.

Figure 3. Teeth of *Protoadapis andrei* nov. sp. A1-2, the upper canine Cos 753 in lingual (A1) and labial (A2) views; B-E, occlusal views of the P4/ Cos 77 (B), the M2/ Cos 247 (C), the M3/ Cos 248

(D), and the m/3 Cos 246 €; F, H, p/3 to m/3 of the type mandible Cos 253 in occlusal (F) and lingual (H) views; G, the p/3 Cos 254 in lingual view. Scale bar is 1 cm.

Figure 4. Mandibles of *Pronycticebus cosensis* sp. nov. A1-3, type mandible Cos 271 in labial (A1), lingual (A2) and occlusal (A3) views; B1-2, posterior fragment bearing m/3 Cos 269 in lingual (B1) and labial (B2) views; C1-2, fragmentary juvenile mandible with anterior alveoli and p/3 germ in place in lingual (C1) and occlusal (C2) views. Scale bar is 5 mm.

Figure 5. Lower teeth of *Pronycticebus cosensis* nov. sp. The type specimen Cos 271 is on A1-2 and L-P. A1-2, L, , anterior teeth, i/2 to p/4 of Cos 271 in labial (A1), lingual (A2) and occlusal (L) views; B, p/1 Cos 278 in lingual vie; C1-2, p/3 Cos 277 in occlusal (C1) and lingual (C2) views; D1-2, p/3 Cos 276 in occlusal (D1) and lingual (D2) views; E, p/4 Cos 860 in occlusal view; F, p/4 and m/1 of Cos 270 in occlusal view; G1-2, p/4 Cos 859 in occlusal (G1) and lingual (G2) views; H1-3, the m/1 Cos 755 in Occlusal (H1), labial (H2), and lingual (H3) views; I-K, m/1 Cos 272 (I), m/2 Cos 273 (J), m/3 Cos 269 (K) all in occlusal views; M-P, posterior teeth of Cos 271 in occlusal (M-N), labial (O), and lingual (P) views. Scale bar is 5 mm.

Figure 6. Maxillary fragment and upper teeth of *Pronycticebus cosensis* nov. sp. A1-2, maxillary fragment bearing P4/ cos 265 in occlusal (A1) and labial (A2) views (scale bar 5 mm); B1-2, upper canine Cos 863 in lingual (B1) and labial (B2) views; C, P1/ Cos 279 in lingual view; D1-2, P2/ Cos 281 in lingual (D1) ad labial (D2) views; E1-2, P3/ Cos 858 in anterior (E1) and occlusal (E2) views; F1-2, P3/ Cos 264 in occlusal (F1) and anterior (F2) views; G1-2, P4/ Cos 262 in occlusal (G1) and anterior (G2) views; H, P4/ of Cos 265 in occlusal view; I1-2, P4/ Cos 263 in occlusal (I1) and anterior (I2) views; J, M1/ Cos 861 in occlusal view; K1-2, M1/ Cos 257 in occlusal (K1) and posterior (K2) views; L, M1/ Cos 832 in occlusal view; M, M1/ and M2/ on a fragment of maxilla Cos

258 in occlusal view; N1-2, M2/ Cos 255 in occlusal (N1) and posterior (N2) views; O-P, M2/ Cos 256 and M3/ Cos 259 (cast) in occlusal view; Q-R, milk teeth, DP4/ Cos 266 and dp/4 Cos 274 both I occlusal views; S-T, two teeth from another Quercy locality, Vielase, the M2/ VIE 141 (S) and the anterior part of a right m/2 or m/3, both in occlusal views. Scale bar for all teeth from B1 to T is 5 mm.

Figure 7. Teeth of *Anchomomys* sp. (A-B) and of *Quercyloris eloisae* nov. gen. nov. sp. (C1-M2). A, incomplete M1-2/ Cos 290 in occlusal view; B, Upper canine Cos 297 in lingual view; C1-2, upper anterior incisor Cos 304 in lingual (C1) and posterior (C2) views; D1-3, upper canine Cos 294 in lingual (D1), posterior (D2) and labial (D3) views; E-G, three P4/s in occlusal views, Cos 291 (E), Cos 292 (F), and Cos 293 (G); H-J, three upper molars in occlusal views, M1/ Cos 287 (H), M1/ Cos 288, type specimen (I), M2/ Cos 289 (J); K1-3, p/3 Cos 298 in lingual (K1), posterolingual (K2), and posterolabial (K3) views; L1-2, incomplete m/1 Cos 301, missing its protoconid, in occlusal (L1) and lingual (L2) views; M1-2, m/2 Cos 295 in occlusal (M1) and lingual (M2) views. Scale bar is 2 mm.

Figure 8. Teeth of *Arcius moniquae* nov. sp. A1-2, Lower anterior incisor Cos 302 in lingual (A1) and labial (A2) views; B, P4/Cos 299, C, M2/ Cos 300, type specimen, and D, m/3 Cos 305, all in occlusal view. Scale bar is 2 mm.

Table caption

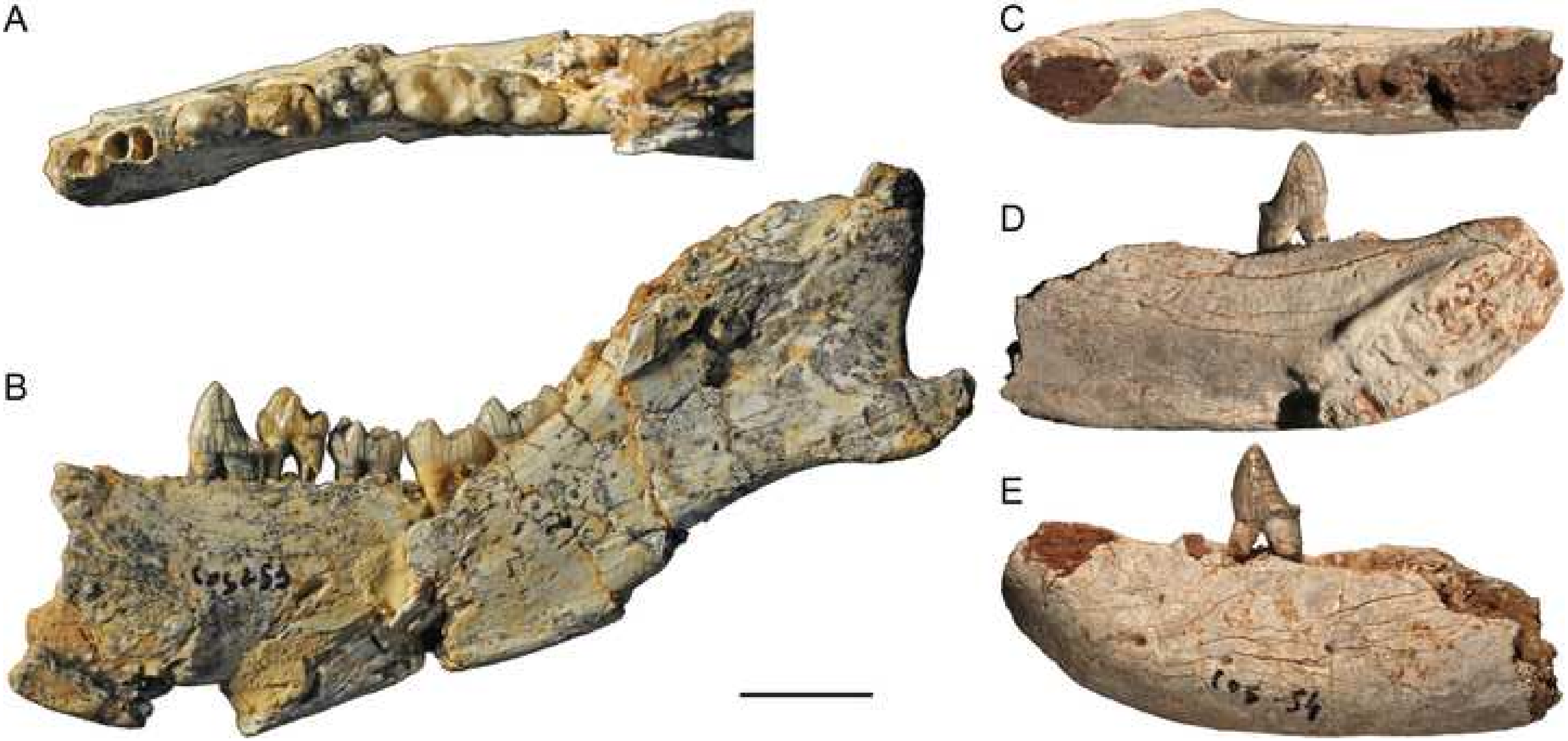
Table 1. Measurements of the teeth of *Pronycticebus cosensis* nov. sp., all in mm.

1781

1782

Table 1

Tooth	Length	Width	Tooth	Length	Width	Tooth	Length	Width
Cos 271 C	2.07	1.61	p/4 Cos 860	3.02	2.23	P4/ Cos 262	3.14	4.21
--- p/1	1.30	1.06	Cos 270 p/4	3.21	2.15	P4/ Cos 263	2.62	3.73
--- p/2	1.83	1.20	--- m/1	3.66	2.52	P4/ Cos 265	3.03	3.89
--- p/3	2.86	2.44	m/1 Cos 272	4.05	2.87	M1/ Cos 257	3.35	4.00
--- p/4	3.25	2.41	m/1 Cos 755	3.99	2.79	M1/ Cos 832	3.59	4.43
--- m/1	3.69	2.73	m/2 Cos 273	3.39	2.36	M1/ Cos 861	3.56	4.51
--- m/2	3.71	2.97	m/3 Cos 269	4.82	2.73	M1/ Cos 862	3.69	--
--- m/3	4.79	2.80	dp/4 Cos 274	3.07	2.84	Cos 258 M1/	3.92	5.00
p/1 Cos 278	1.43	1.34	C sup Cos 863	2.46	1.93	--- M2/	4.00	5.43
p/3 Cos 275	> 2.46	1.69	C sup Cos 864	2.51	1.83	M2/ Cos 255	3.89	5.20
p/3 Cos 276	2.84	1.72	P1/ Cos 279	1.43	1.09	M2/ Cos 256	3.67	5.08
p/3 Cos 277	2.73	1.85	P2/ Cos 281	2.26	1.68	M3/ Cos 259	3.20	4.78
p/3 Cos 280	2.99	>= 1.80	P3/ Cos 264	2.75	2.65	M3/ Cos 261	3.31	--
p/4 Cos 859	3.30	1.98	P3/ Cos 858	2.89	2.91	DP4/ Cos 266	3.53	3.64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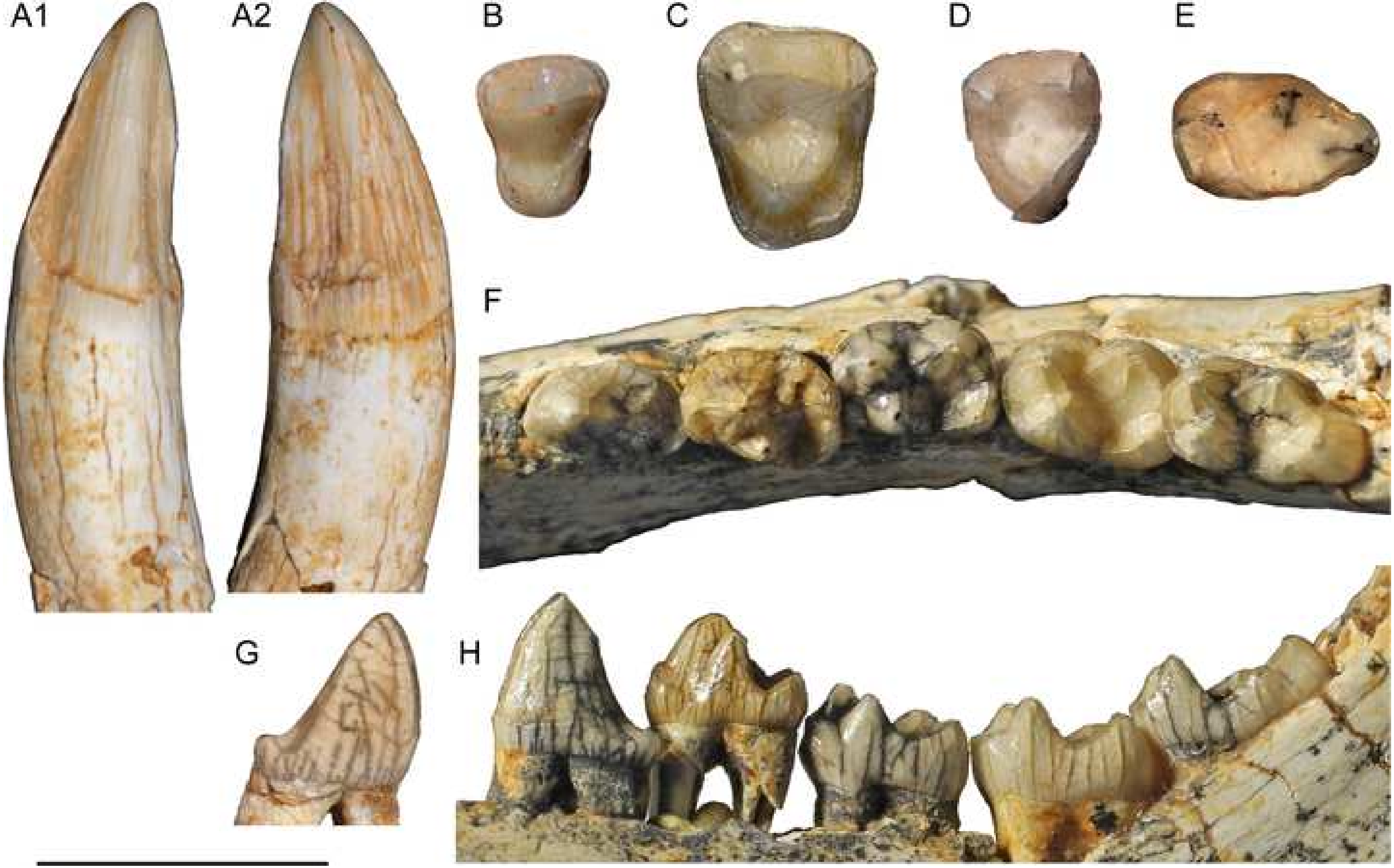
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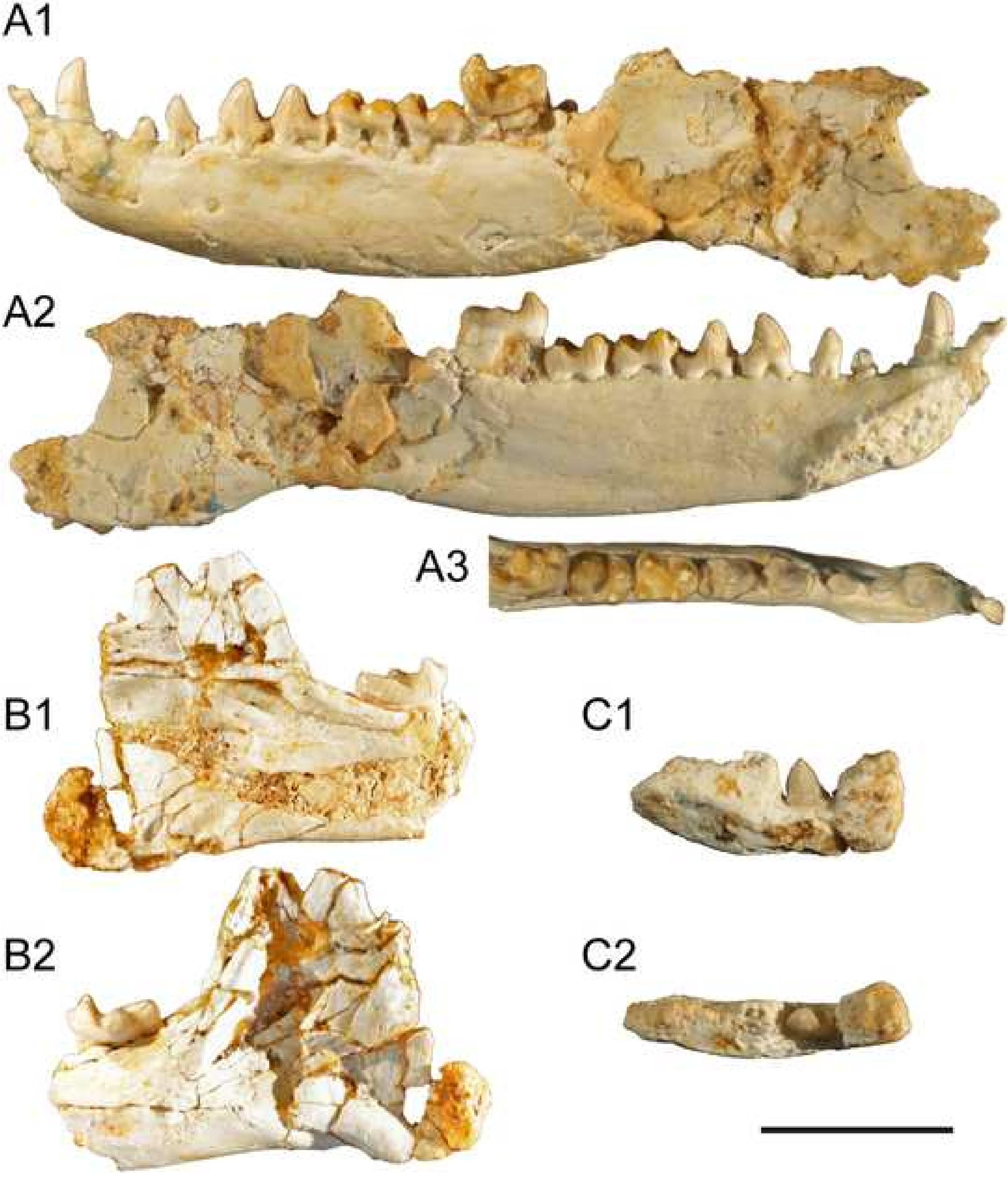
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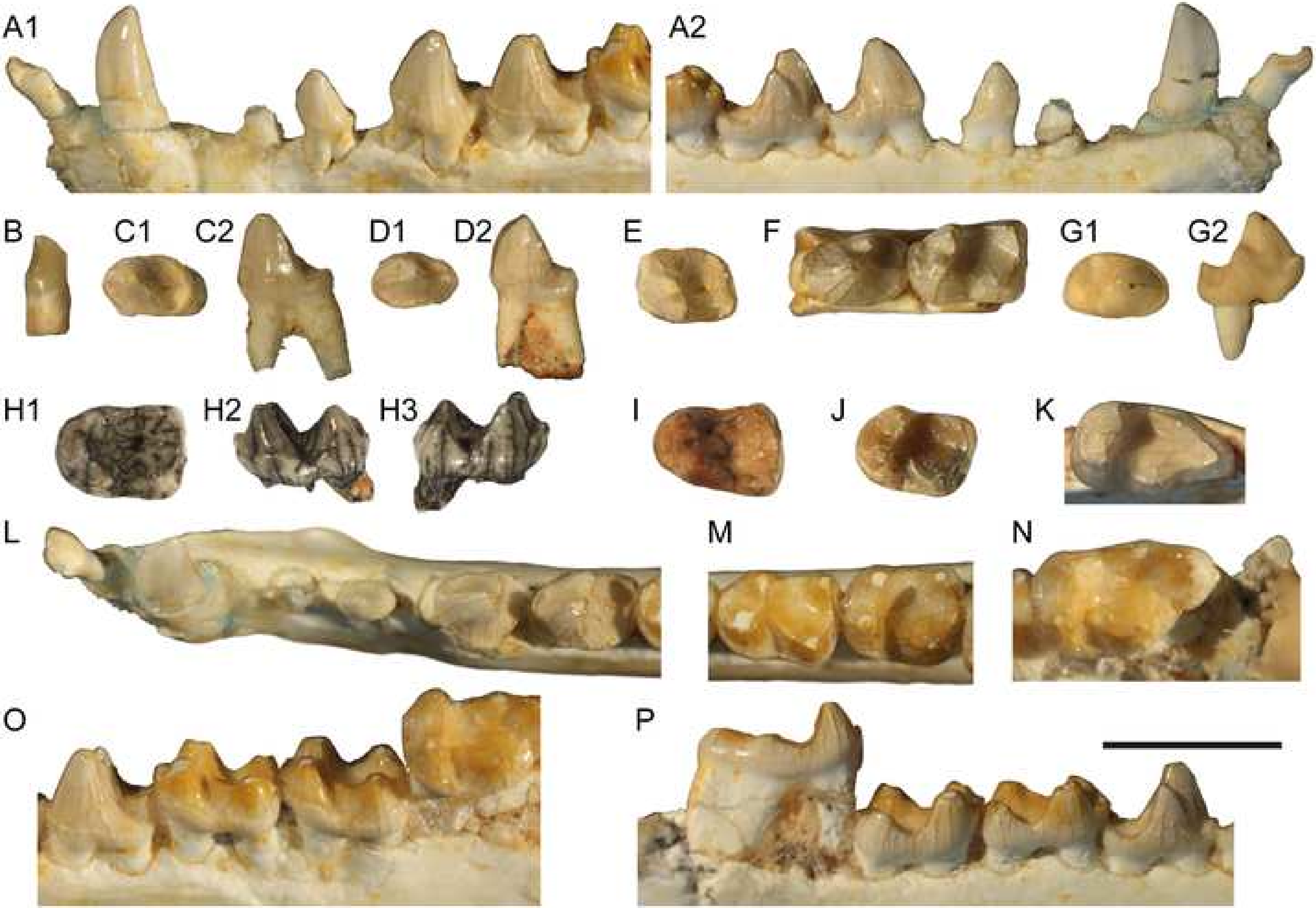
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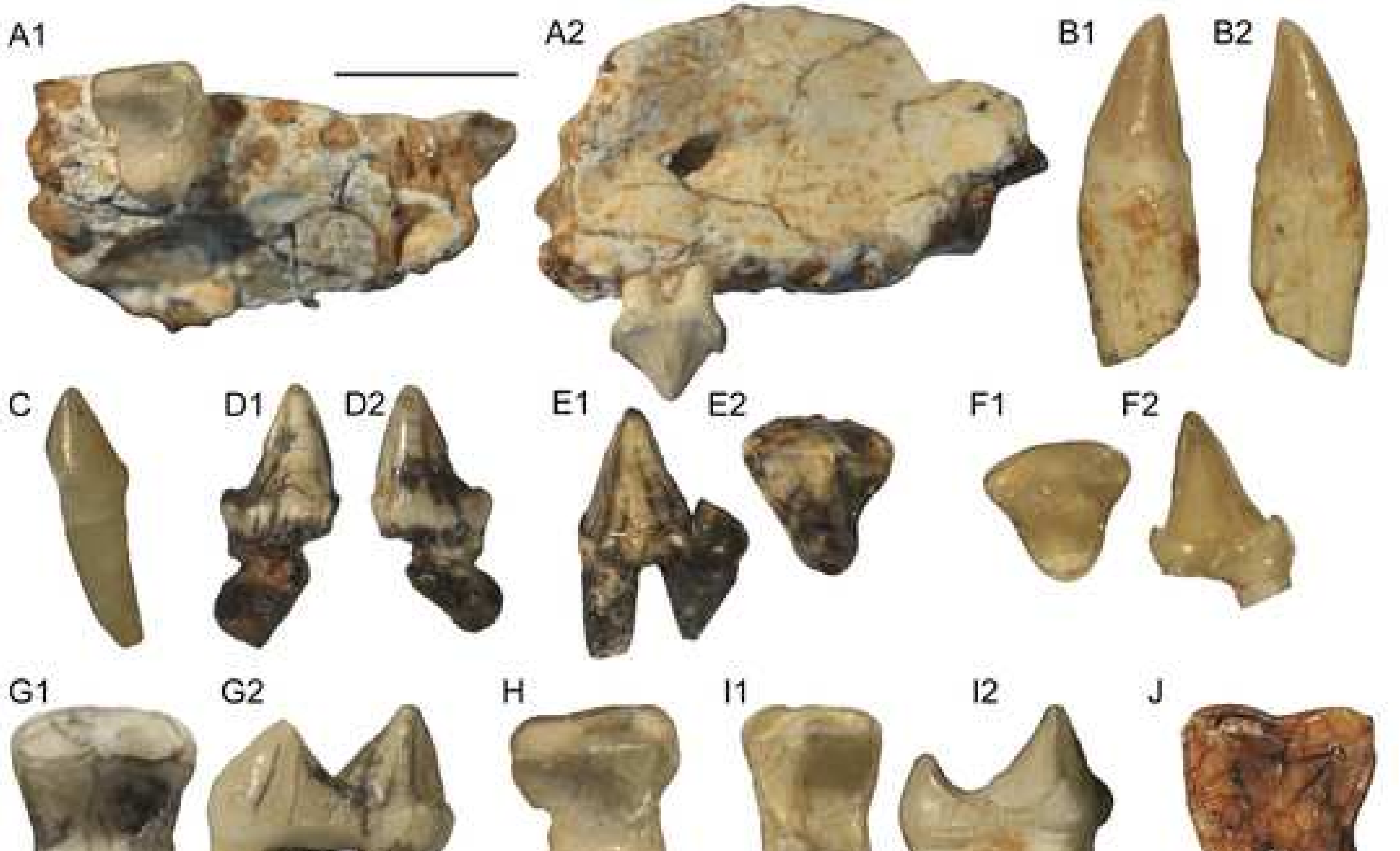
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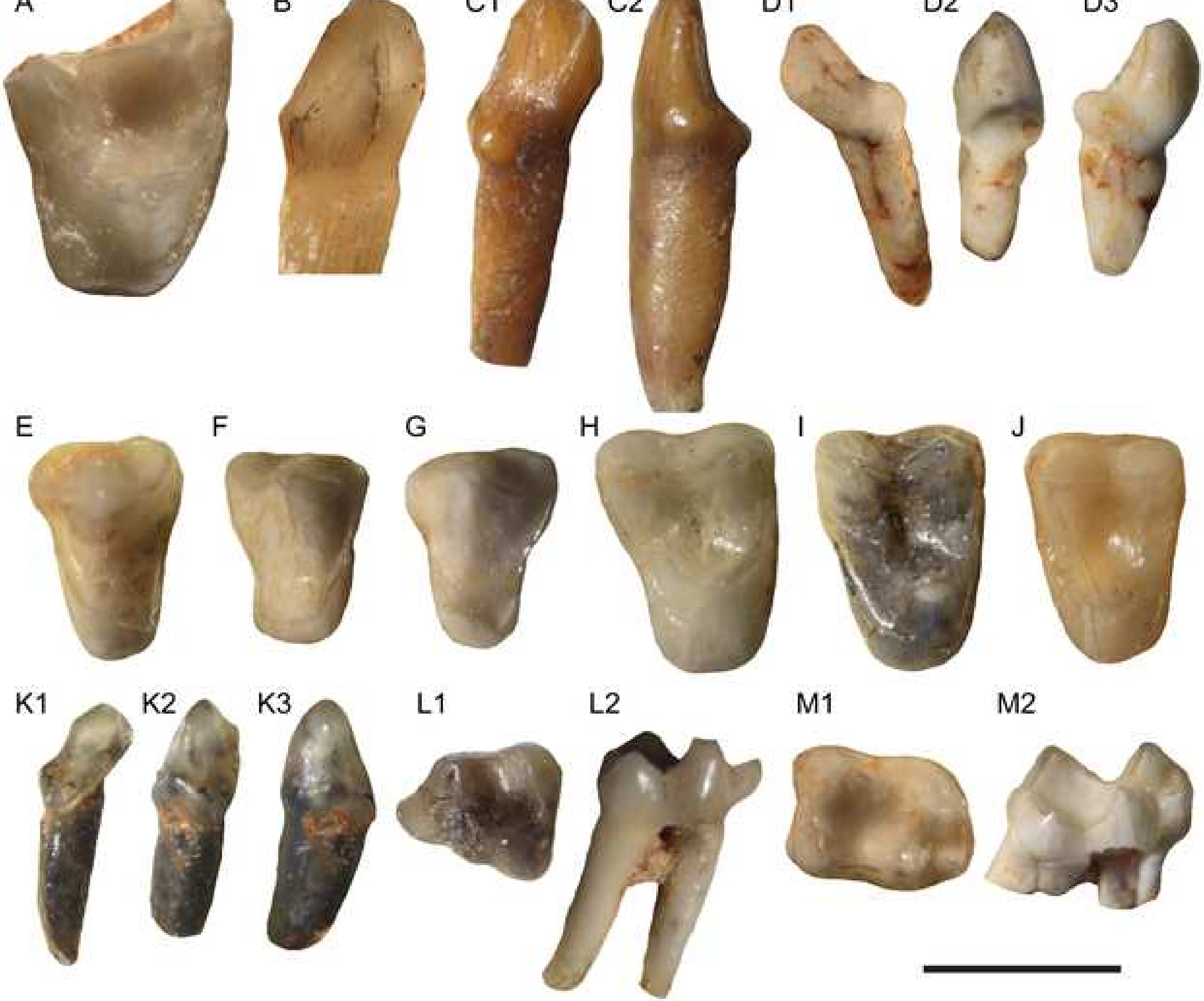
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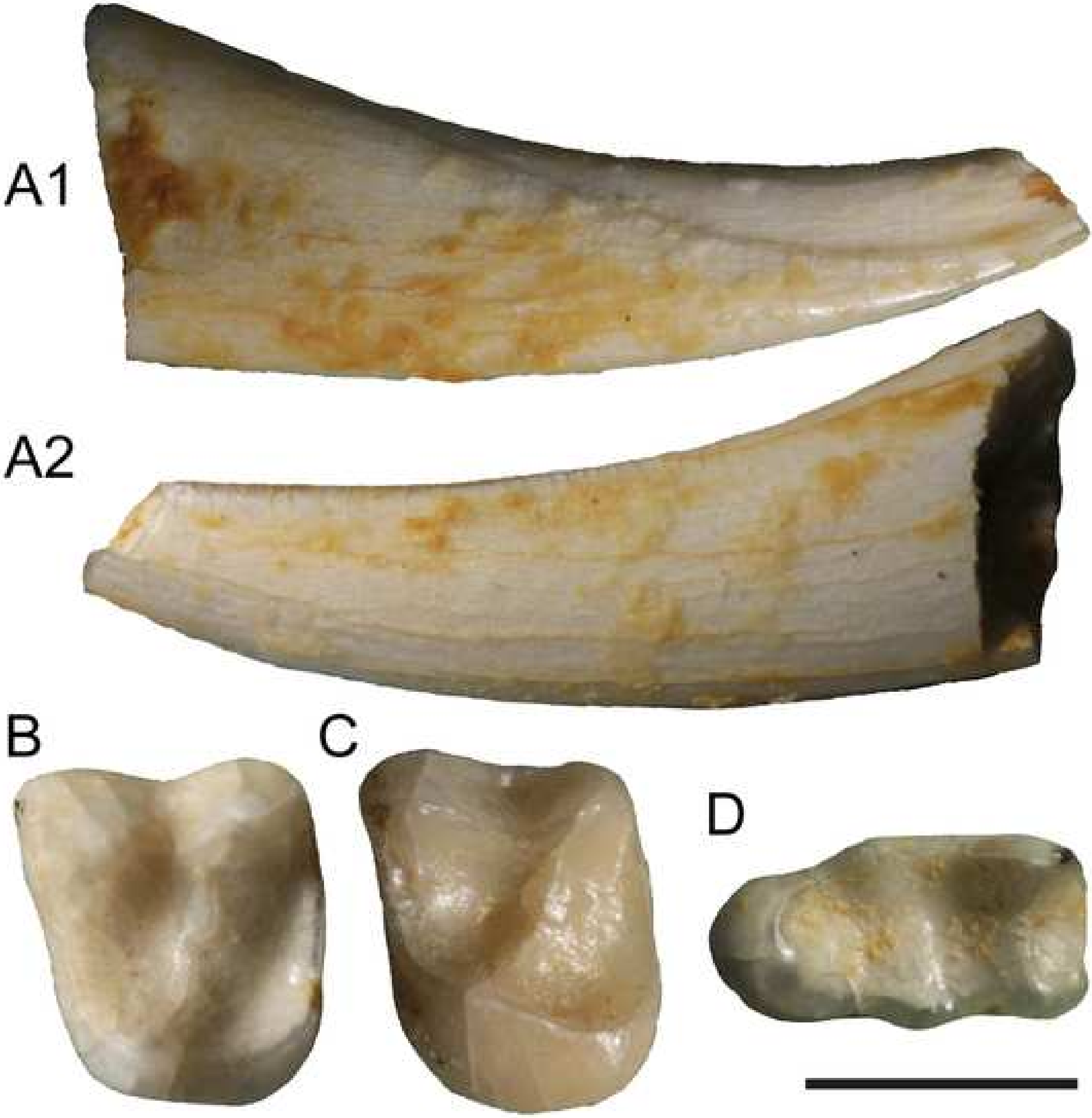
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