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Abstract

Diacodexeidae are the first representatives of Artiodactyla in the fossil record. Their first occurrence is at the very base of the Ypresian (earliest Eocene, 56.0 Ma) with the genus *Diacodexis*. *Diacodexis* is a well-diversified genus during the early Eocene in Europe, especially during the MP7-MP8+9 interval. However, most of European species are documented by scarce material, retrieved from single localities. In this work, we describe new *Diacodexis* material from ~MP7 and ~MP8+9 localities of Southern Europe including material of *D. antunesi* from Silveirinha, considered as the most primitive European *Diacodexis*, and material from three localities from Southern France (Fordones, Palette, and La Borie). The new material documents *Diacodexis* premolar morphology and deciduous dentition which bear potentially important phylogenetic information, as well as astragali, including a specimen from Silveirinha that constitutes the earliest occurence of an astragalus of the genus *Diacodexis* in the European fossil record. Investigation of the enamel microstructure reveals that early European species had a simple enamel pattern with one-layered Schmelzmuster composed of 'basic' radial enamel only, instead of the two-layered Schmelzmuster (thin radial enamel + thick layer of Hunter-Schreger bands) observed on North American species and so far considered to represent the primitive condition within Artiodactyla. In accordance with previous studies, our observations highlight that *Diacodexis gigasei* from Belgium is morphologically closer to the North American species *D. ilicis* than to *D. antunesi* from Portugal. The latter species, together with *D.* aff. *antunesi* from Fordones, appears to be morphologically closer to the Asiatic taxa *D. indicus* and *D. pakistanensis*. Finally, we found numerous similarities between *D.* cf. *gigasei* from Palette and *D. gigasei*, a result that challenges the intra-European provincialism that characterizes the earliest Ypresian. *Diacodexis gigasei* could be one of the rare species in common between northwestern and southwestern bioprovinces.

Keywords:

Diacodexeidae

Ypresian

Enamel microstructure

Deciduous dentition

Astragalus

1. Introduction

Diacodexeid artiodactyls are the first representatives of even toed hoofed mammals in the fossil record (Rose, 1982, 2006; Theodor et al., 2007). Their first occurrence is found at the very base of the Ypresian (earliest Eocene, 56.0 million years ago) with the genus *Diacodexis* Cope, 1882. Based on this early occurrence in the fossil record and on their very simple tribosphenic molar pattern, Diacodexeidae have been regarded as primitive among Artiodactyla (Cope, 1882; Romer, 1966; Van Valen, 1971; Godinot, 1981; Theodor et al., 2007). Formal phylogenetic analyses show *Diacodexis* as the first offshoot of the order (Geisler and Theodor, 2009) or close to the differentiation of crown artiodactyl groups (Gentry and Hooker, 1988; Geisler, 2001; Orliac and Ducrocq, 2012; Gatesy et al., 2012).

Together with other modern groups of mammals such as primates or perissodactyls, *Diacodexis* makes its first appearance in the fossil record during the Mammalian Dispersal Event (MDE), which coincides with the global climate warming of the Paleocene Eocene Thermal Maximum (or PETM) characterized by a global negative carbon isotope excursion (CIE) (Magioncalda et al., 2004; Gingerich, 2006). Species of *Diacodexis* have been reported from Eocene fossil localities on all continents of the Northern hemisphere, and dental, cranial and postcranial features of the genus are now well documented (e.g., Guthrie, 1971; Godinot, 1981; Russell et al., 1983; Sigogneau-Russell and Russell, 1983; Sudre et al., 1983; Thewissen et al., 1983; Kumar and Jolly, 1986; Gingerich, 1989; Smith et al. 1996; Bajpai et al., 2005; Kumar et al., 2010; Orliac and Gilissen, 2012; Orliac and O'Leary, 2014). *Diacodexis* is known from Asia, Europe, and North America, three places that have been alternatively proposed as center of origin of the genus (Thewissen et al., 1983; Krishtalka and Stucky, 1985; Smith et al., 1996). Europe and North America have housed, among others, the oldest *Diacodexis* (earliest Eocene) whereas the first occurrence of the genus in Asia is a little more recent (early Eocene; Kumar et al., 2010). The oldest North American species is *D.*

ilicis from Wasatchian-*Meniscotherium* (Wa-M) and Wasatchian-0 (Wa-0) biozones of the Wasatchian NALMA (North American Land Mammal Age) (Gingerich, 1989; Rose et al., 2012:92); Wa-M and and Wa-0 faunas are, respectively, coincident with the maximum of the CIE and the main body of the PETM (Bowen et al., 2014).

In Europe, the first occurrence of *Diacodexis* also coincides with the onset of the PETM with *D. gigasei* from Dormaal (MP7 Reference Level) and Erquelinnes, Belgium (Smith et al., 1996; Smith et al., 2006; Missiaen et al., 2013) (Fig. 1). Other MP7 species are *D. antunesi* from Silveirinha, Portugal (Estravis and Russell, 1989), *Diacodexis* sp. from Le Quesnoy, France (Nel et al., 1999), *D. morrisi* from Abbey Wood, UK (Hooker, 2010), *Diacodexis* sp. from Kyson, UK (Sudre et al., 1983), *D. gazini* from Rians, France (Godinot, 1981), and *Diacodexis* cf. *gazini* from Fordones, France (Marandat, 1991). Among these species, Estravis and Russell (1989) and Theodor et al. (2007) considered *D. antunesi* as the oldest, most primitive European *Diacodexis*. Later in the early Eocene, *Diacodexis* is known by two species: *D. corsaensis* from the MP8+9 locality of Corsà 0, Spain (Checa Soler, 2004) and *D. varleti* from several localities from the Paris Basin such as Condé-en-Brie, Mutigny, Avenay (MP8+9 Reference Level), and Pourcy (either MP7 or MP8+9) (Sudre et al., 1983) (Fig. 1). A closely related species, named *D.* cf. *varleti* was described from several MP 10 localities also from the Paris Basin (Saint-Agnan, Cuis, Mancy, Prémontré, and Grauves) (Sudre et al., 1983; Sudre and Erfurt, 1996). The latest occurrence of *Diacodexis* cf. *varleti* dates from the "untere Unterkohle" (MP11) of the Geiseltal, Germany (Erfurt and Sudre, 1996) (Fig. 1). Finally, several *Diacodexis* sp. indet. were mentioned from numerous localities from Spain, correlated with MP10 (Sudre et al., 1983; Antunes et al., 1997)

Diacodexis is therefore a well-diversified genus during the early Eocene in Europe, especially during the MP7-MP8+9 interval. However, most of European *Diacodexis* species are documented by scarce material, retrieved from a single locality. The scarcity of the

material often prevents comparing the same dental loci from two localities. Indeed, some localities yielded upper dentition only, while others yielded lower dentition. Besides, the lack of complete tooth rows makes dental association tricky. Finally, the scarcity of the documented material makes it difficult to apprehend the potential intraspecific variability that exists within *Diacodexis* species.

Here, we describe new material from ~MP7 and ~MP8+9 localities of Southern Europe that greatly increases our knowledge of European *Diacodexis* species. The new material comes from Portugal (Silveirinha), and Southern France (Fordones, Palette, and La Borie) and notably includes a mandible with p3-m3 and an upper cheek tooth row with P3-M3, which represents the most complete *Diacodexis* remains in Europe to date. The new material described also documents *Diacodexis* premolar morphology and deciduous dentition which bear potentially important phylogenetic information, as well as one astragalus from Silveirinha that constitutes the earliest mention of an astragalus of the genus *Diacodexis* in the European fossil record. The enamel microstructure of *Diacodexis* species from Silveirinha and Fordones is also investigated. These new data about European early *Diacodexis* species call into questions features considered as primitive within Artiodactyla, and allow discussion of the distribution and palaeobiogeographic relationships between Northern and Southern Europe near MP7.

2. Material and methods

2.1. Material

2.1.1. New material

The material studied here comes from four localities, one is situated in Portugal (Silveirinha), the others in Southern France (Fordones, Palette, and La Borie) (Fig. 1). Silveirinha, Palette, and La Borie are well-known for having yielded rich mammalian faunas,

the most diversified ones for the early-middle Ypresian period of Southern Europe (e.g., Antunes and Russell, 1981; Antunes et al., 1987; Estravis, 2000; Tabuce et al., 2006, 2009, 2011 for Silveirinha; Godinot, 1984; Godinot et al., 1987; Solé et al., 2017 for Palette; and Laurent et al., 2010; Robinet et al., 2015; Solé et al., 2014 for La Borie). According to the Southern Europe biochronological sequence proposed recently for the beginning of the Eocene (Marandat et al., 2012), Silveirinha would be the oldest Southern European site referred to the MP7 level and Fordones and Palette –also referred to the MP7– would be co-eval and slightly younger than Silveirinha. Interestingly, Fordones and Palette are considered equivalent in age with another Southern French locality (Le Clot); the latter being estimated 1 myr younger than the MP7 reference Dormaal locality (Yans et al., 2014). Finally, as for the locality of La Borie, Laurent et al. (2010) argued for a MP8+9 age. The mandible PAT 159 from Palette was scanned at the CT-Scan facility of the Montpellier University with a resolution of 35 µm and 3D models representing its external surface and a virtual restoration of its ascending ramus are available on MorphoMuseuM (Orliac et al., in press, Models ID: M3#315_ UMPAT159, M3#317_ UMPAT159).

2.1.2. Comparison material

Comparisons are performed with *Diacodexis* species from Europe, Asia and North America. Observation of the European species are based on *D. antunesi* Estravis and Russell, 1989 from Silveirinha, Portugal (direct observation of new material and on casts of the material figured by Estravis and Russell, 1989); *D. gigasei* Smith, Smith and Sudre, 1996 from Dormaal, Belgium (direct observation on casts of the material); *D. morrisi* Hooker, 2010 from Abbey Wood, England (observation from Hooker 2010: fig. 47 and direct observation on casts of M15141); *D. varleti* Sudre, Russell, Louis and Savage, 1983 from Condé-en-Brie, France (direct observation of the original material stored at the MNHN); *D. gazini* Godinot,

159 1981 from Rians, France (direct observation of the original material stored at the MNHN); *D.*
160 *corsaensis* Checa Soler, 2004 from Corsà 0 (observation from Checa Soler, 2004: fig. 2).
161 Observations of the Asian species are based on *Diacodexis pakistanensis* Thewissen et al.,
162 1983 (= *Gujaratia pakistanensis*, see Kumar et al. 2010 p.1249) (known from several
163 localities in India and Pakistan); *D. indicus* (Bajpai et al., 2005) (Vastan, India), *D. parvus*
164 Kumar et al., 2010 (Vastan, India), and *Diacodexis* sp. from Andarak 2, Kyrgyzstan (based on
165 Thewissen et al., 1983; Kumar et al., 2010; and Averianov, 1996 respectively). Finally,
166 observations of the North American species *D. ilicis* Gingerich, 1989 (Bighorn Basin,
167 Wyoming, USA) and *D. secans primus* Krishtalka and Stucky, 1985 (Bighorn and Powder
168 River Basin, Wyoming and Four Mile area, Colorado, USA) are based on Gingerich (1989)
169 and Rose et al. (2012), and Krishtalka and Stucky (1985) respectively.
170

171 *2.2. Methods*

172 *2.2.1. Enamel microstructure*

173 We studied the enamel microstructure of two *Diacodexis* specimens: one m2 from
174 Silveirhina (SNC 3) and one fragmentary upper molar from Fordones (FDN 254). Sample
175 preparation followed the protocol of Tabuce *et al*. (2007a). Casts of the specimens were made
176 prior to preparation for enamel microstructure study. All specimens were embedded in epoxy
177 resin and sectioned horizontally and tangentially. We subsequently performed 37 %
178 phosphoric acid etching of the samples for 30 seconds to make the microstructural details
179 visible. After rinsing with distilled water and drying, the samples were coated with conductive
180 material (gold-palladium). They were observed and studied with two different scanning
181 electron microscopes (SEM): HITACHI S4000 and S4800 (x250 to x500). Several parameters
182 were evaluated in the description of enamel microstructure. Enamel thickness was measured
183 perpendicularely to the Enamel-Dentine Junction (EDJ), and corresponds to the distance

between that plane and the Enamel Outer Surface (EOS). The orientation of the interprismatic matrix (IPM) is the angle between crystallites of the IPM and those of prisms. Each measure has been reproduced ten times.

2.2.2. Abbreviations for institutions and dental nomenclature followed

Institutions: **CEPUNL**, Centro de Estratigrafia e Paleobiologia da Universidade Nova de Lisboa; **MHNT**, Muséum d'Histoire Naturelle de Toulouse, Toulouse, France; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **UCMP**, University of California Museum of Paleontology, Berkeley, USA; **UM**, Université de Montpellier, Montpellier, France.

The dental nomenclature mainly follows Boisserie et al. (2009) and Orliac and Ducrocq (2012).

3. Systematic paleontology

Order Artiodactyla Owen, 1848

Superfamily Dichobunoidea Gill, 1872

Family Diacodexeidae Gazin, 1955

Genus ***Diacodexis*** Cope, 1882

3.1. New material from the locality of Silveirinha Pequena, Baixo Mondego, Portugal

The first mention of *Diacodexis* remains from the early Eocene locality of Silveirinha was made in the faunal list of the locality provided by Antunes and Russell (1981: p. 1101) as *Diacodexis* cf. *gazini*. Estravis and Russell (1989) subsequently revised the material and erected a new species, *Diacodexis antunesi* Estravis and Russell, 1989. In the latter work,

abundant dental remains of *D. antunesi* are described, documenting upper and lower molars, as well as dP4 and p2 or p3 of the species. Part of this *Diacodexis* material is also described and figured in the PhD thesis of Estravis (1992: p. 182-196). Additional material described here comes from field campaigns conducted in Silveirinha in the past 20 years.

Diacodexis antunesi Estravis and Russell, 1989

Fig. 2

Synonymy: 1981. *D.* cf. *gazini* - Antunes and Russell, p. 1101.

Holotype: r. m2 SV3 338 (coll. CEPUNL, in Estravis and Russell, 1989: pl. 1, fig. 2).

Material (coll. CEPUNL): in addition to that published by Estravis and Russell (1989) - SNC 64, dp2 or dp3 (left); SNC 386, p2 or p3 (left); SNC 74, m1-2 (right); SNC 6, m1 (right); SNC 93, m1 (right); SNC 3, m2 (right); SNC 17, m3 (left); SNC 59, m3 (left); SNC 63, m3 (right); SNC 65, m3 (left); SNC 58, P3 (right); SNC 33, P4 (right); SNC 311, P4 (right); SNC 405, P4 (right); SNC 13, dP4 (left); SNC 49, M1 (right); SNC 339, M1 (right); SNC 20, M2 (right); SNC 25, M2 (right); SNC 36, M2 (right); SNC 55, M2 (left); SNC 95, M3 (right); SNC 18, M3 (right); SNC 262, M3 (right); SNC 687, astragalus (right).

Type locality and horizon: Silveirinha Pequena, Baixo Mondego, Portugal; Silveirinha Formation, Rio Mondego Member, early Eocene, ~MP7.

Original diagnosis: see Estravis and Russell (1989 : p. 31).

Emended diagnosis: very small species of *Diacodexis* with high and sharp cusps and cuspids; long and well-marked crests; lower molars with central and low cristid obliqua; hypoconulid small and close to entoconid on m1-2; short or absent labial cingulid; P3 with small lingual lobe; P4 with strong preprotocristid, connected to the antero-labial corner of the tooth, labial margin without ectoflexus; M1-2 with large parastyle protruding anteriorly; lingual lobe of M1-2 clearly slenderer antero-posteriorly than the labial margin of the crown;

M3 triangular in shape compared to M2.

Measurements: Tables 1-2.

Description:

Lower dentition. Two lower premolars (SNC 64 and SNC 386) have been identified in addition to the deciduous premolar published by Estravis and Russell (1989: pl. 2.7) (Fig. 2(A-D)). Both specimens present a low crown. The paraconid is lingually located and distinct from the preprotocristid. The hypoconid is separated from the postprotocristid by a small groove; in labial and lingual views, the hypoconid lies below the level of the paraconid. Based on the very small enamel thickness and on its low, labio-lingually narrow crown, SNC 64 is referred to as dp2 or a dp3. SNC 386 has a thicker enamel and a wider protoconid than SNC 64 and rather documents permanent dentition, p2 or p3.

The new sample includes nine lower molars of *D. antunesi*. As noted by Estravis and Russell (1989), m1 has a large paraconid separated from the metaconid whereas this cuspid is clearly smaller on m2 (Fig. 2(M)). This character, together with the size of the tooth, allows for the m1-2 distinction. The trigonid becomes wider and the entoconid increases in both width and height from m1 to m3. The lower molars of *D. antunesi* present a trigonid with high and pointed cusps. Protoconid and metaconid are of sub-equal height, edges of the trigonid are defined by the preprotocristid and postprotocristid labially, by the postmetacristid, premetacristid, postparacristid lingually, and by the preparacristid anteriorly. The basin of the trigonid is deep; an endometafossid is observed on unworn teeth, as well as a clear postmetafossid. The basin of the talonid is delimited labially by a low cristid obliqua (=prehypocristid). Lingually, the ectoentocristid is short and low and connects a very slight postectometacristid. The postectometacristid is variably absent or very slight in the new sample, a character also observed on the material published by Estravis and Russell (1989). The anterior end of the low cristid obliqua occupies a central position on all lower molars of

our sample: it reaches anteriorly the level of the trigonid notch. On m1-2, the hypoconulid is connected to the entoconid, to the hypoconid and to a long posterior cingulid by high cristids. The hypoconulid is closely apposed to the entoconid. The labial cingulid is short or absent on m1-2. Despite important variations concerning the posterior lobe of m3, in all specimens, the hypoconulid is clearly distinct from the talonid on m3 and a deep groove separates the hypoconulid from the entoconid. A small accessory cusp, labial to the hypoconulid, can occur (Fig. 2(J)).

Upper dentition. The new sample includes five upper premolars, including a decidual one. Two new premolar loci are documented here in addition to the dP4 already described by Estravis and Russell (1989). SNC 58 is broken in its lingual part but its shape indicates a P3 (Fig. 2(S)). Its parastyle is reduced and embedded in the anterior cingulum. The posterior part of the tooth is occupied by a large metastyle. The lingual portion of the tooth is broken and the extension of the lingual lobe cannot be assessed. The P4 is subtriangular in occlusal view (Fig. 2(R)). The protocone is located slightly anterior to the paracone. The paracone is considerably larger and higher than the protocone and bears three cristae, a preparacrista and a postparacrista connected to a large parastyle and a smaller metastyle respectively, plus a clear and sharp endoparacrista, located low in the valley between the paracone and protocone. On both P4 specimens (SNC 405 and SNC 311), the endoparacrista connects to a very small endoprotocrista. The protocone shows a sharp preprotocrista merging anteriorly with the anterior cingulum; there is no postprotocrista. The parastyle is large especially on SNC 311 illustrated in Figure 2(R). There is no ectoflexus. The lingual, anterior and posterior cingula are continuous. The dP4 (SNC 13, Fig. 2(T)) is morphologically very close to that described by Estravis and Russell (1989: pl. 2.5). The tooth is posterolabially elongated, especially in its disto-labial corner. This character, together with its small width (Table 1), indicate that it is a deciduous tooth. DP4 morphology is very close to that of permanent upper molars. The

protocone is big and low, and bears two thick cristae, the preprotocrista and the postprotocrista. They project toward the protoconule and the metaconule respectively but are separated from the latter by grooves. The metaconule and the protoconule are small and pointed. The metaconule bears three cristae: small pre and endometacristule, and a longer postmetacristule, which joins the metastyle at the disto-labial corner of the tooth. The endometacristule connects a small endometacrista, at the base of the metacone. Likewise, the protoconule bears a preprotocristule which joins the parastyle; yet, the endoprotocristule is lacking.

The M1-2 have a rather characteristic morphology (Fig. 2(P-Q)). The cusps are sharp and high, with well-marked cristae. The parastyle is large and projects/protrudes on the anterior edge of the tooth. A pericone is sometimes present (SNC 20, 55 and 74), a small hypocone is observed on some specimens (SNC 25 and 74). The preparacrista and postmetacrista are sharp, often both on the same plane as the centrocrista. The paraconule and the metaconule both present pre-, endo- and postcristae. The endopara and endometacristules connect the endopara and endometacrista respectively. The anterior and posterior cingula are long, thick, but never connect lingually. In occlusal view, the posterior edge of the crown shows an internal angle at the point where the postmetacristule joins the postero-labial corner of the tooth. The labial edge is straight except on the M2 SNC 20. The M1 SNC 49 differs from the other molars collected at Silveirinha by a weak parastyle, weak cingula, and a round shape at the base of the metacone and paracone. However, these observations could be due to a particular taphonomic history. Indeed, the enamel is thin or absent on the labial part of the tooth. The latter could have been digested by a predator. The M3s show a triangular outline. The three M3 of the new sample (SNC 18, SNC 75, and SNC 262) have a more rounded lingual outline than the specimen figured by Estravis and Russell (1989: pl. 2.1; SV3 126). M3s show a crest pattern similar to that of M1-2.

309 Observed variation on dental material. The dental material shows some morphological
310 variability. Variation on lower molars is observed on the length of the cingulids, the presence
311 of the labial cingulid, and the connections of the posterior cristids of the talonid of the m3
312 (Estravis and Russell, 1989). Among the molar sample, variation on the paraconid size is also
313 observed with the m3 SNC 17, which has a smaller paraconid. We interpret these differences
314 as part of the plausible intraspecific variation. Indeed, the case of one specimen with a
315 reduced paraconid within a *Diacodexis* sample has already been reported from other localities
316 (Sudre et al., 1983; Kumar et al., 2010). All the material from Silveirinha is referred here to
317 the species *D. antunesi.*

318 Enamel microstructure. The lower molar SNC 3 presents a 'basic' radial enamel on the
319 whole enamel thickness (Fig. 3). Its thickness varies from 37 to 152 μm, its average is 91 μm.
320 There is no synchronous prism undulation. The prisms have an average diameter of 4 μm.
321 Prisms rise from the EDJ at an angle of 64° and reach EOS with an angle of 78°. The IPM
322 forms a closed coat. The IPM crystallites are at an angle of 27° with those of prisms. The
323 outer aprismatic part represents on average 4.5% of the enamel thickness.

324 Astragalus. In addition to the new dental material, one astragalus was also found at
325 Silveirhina and constitutes the first mention of postcranial remains attributed to *Diacodexis*
326 *antunesi*. The astragalus SNC 687 (Fig. 2(U-W), Table 2) is broken below the sustentacular
327 facet and the distal trochlea is missing. The two crests of the tibial trochlea are separated by a
328 deep groove. They are asymmetric, the lateral condyle being higher than the medial one.
329 There is no fossa for the anterior process of the tibia. The fossa for the tibial malleolus is wide
330 and deep. The fibular sulcus is well marked in posterior view. The sustentacular facet is long,
331 ovoid and its long axis is directed slightly proximomedially. The sustentacular facet is only
332 slightly convex laterally. The ectal facet, separated from the sustentacular facet by a wide
333 sulcus tali, is shrunk in its central part but more extended in its upper half.

Remarks:

Comparison with MP7 and MP8+9 Southern European species. *Diacodexis antunesi* differs from most other species of the genus by its smaller size, especially for the lower molars (Figs. 4-5). Compared to *D. gazini* from the slightly more recent locality of Rians (Marandat et al., 2012), *D. antunesi* shows less massive upper and lower molars, with deeper labial notches in occlusal view between the trigonid and the talonid on lower molars and between the labial and lingual cusps on the upper molars. *D. antunesi* has smaller entoconid and hypoconid on lower molars (Fig. 6). On upper molars, the parastyle of *D. antunesi* is larger and protrudes anteriorly; on M1-2, the postmetacristule and preprotocristule are salient which confers to the crown an hourglass shape, something not observed on *D. gazini* which crown is more rectangular; when present, the hypocone of *D. antunesi* is smaller than that of *D. gazini* on M1-2. *D. antunesi* seems to show a close morphology to the poorly illustrated *D. corsaensis* from the MP8+9 locality of Corsà 0, Spain (Checa Soler, 2004: fig. 2), represented by lower dentition only. All dental remains of *D. corsaensis* are of larger size than *D. antunesi* (Fig. 4).

Comparison with MP7 Northern European species. Lower molars of *D. antunesi* differ from those of *D. gigasei* from Dormaal (Belgium) in having a smaller paraconid (especially on m1), a lower cristid obliqua on m1-2, a hypoconulid on m1-2 situated closer to the entoconid. The fresh lower molars of *D. gigasei* show a distinct endohypocristid (Fig. 6). The upper molars of *D. antunesi* and *D. gigasei* are close morphologically, but the parastyle is bigger in *D. antunesi*. They are also close regarding M3 proportions (Fig. 5). The P4 of *D. gigasei* presents an ectoflexus that is not present in the specimens of *D. antunesi* (Fig. 7(K)). The first lower molar of *Diacodexis antunesi* differs from that of *D. morrisi* (from MP7 of England) by a narrower talonid, and a lower and more central cristid obliqua. The upper molars of *D. morrisi* are more rounded lingually, and present a smaller parastyle; the groove

intersecting the postprotocrista is deeper in *D. morrisi* (Fig. 7(G)). Despite a smaller size, *D. antunesi* is morphologically very close to *D. varleti.* Both species present a hypoconulid of m1-2 situated close to the entoconid, a protoconid almost as high as the metaconid on lower molars, hourglass-shaped upper M1-2 with salient postmetacristule. Morphological differences consist in a smaller parastyle of the upper molars less protruding anteriorly for *D. varleti*; M3s of the latter species also have a greater anteroposterior length (Fig. 5).

Comparison with Northern American species. *Diacodexis antunesi* differs from *D. ilicis* from the Wasatchian of North America in having more pointed cuspids/cusps. The lower molars of North American species have a paraconid located more lingually. In *D. antunesi*, the hypoconulid of m1-2 is situated closer to the entoconid. On upper premolars, the paracone of P3 of *D. antunesi* is larger than that of *D. ilicis* and it does not seem to present the accessory cusp on the postparacrista observed in *D. ilicis* (Rose et al., 2012: fig. 51.D). The protocone lobe of P3 seems to be less distinct in *D. antunesi* (broken on the only available specimen). The P4 of *D. antunesi* presents a straight posterior edge, whereas *D. ilicis s*hows an anterior deflection of the lingual part of the crown. The upper molars of *D. antunesi* and *D. ilicis* are close morphologically with an angular lingual lobe, sharp and salient preprotocristule and postmetacristule, and a parastyle protruding anteriorly. Based on what is preserved of the astragalus, the sustentacular facet seems to be larger in *D. antunesi* than in *D. ilicis*.

Comparison with Asian species. *Diacodexis antunesi* differs from *D. indicus* in being smaller and in having a wider sulcus tali, a very long and posterolabially expanded postmetacrista on dP4, more transverse upper molars with stronger parastyle and metastyle, and more posteriorly deflected postprotocrista on M2; its lower molars have a less elevated and a more labial cristid obliqua and shorter and weaker anterior cingulids. *Diacodexis antunesi* similarly differs from *D. pakistanensis* by its transverse upper molars with strong

parastyle and metastyle; it further differs from this Asian species by a larger paraconid on lower molars. *Diacodexis antunesi* differs from *D. parvus* in having a metacone and paracone of similar size, an incomplete lingual cingulum, a more posterior orientation of the postprotocrista on M2, and an undivided ectal facet on the astragalus. *Diacodexis antunesi* differs from *Diacodexis* sp. from Andarak 2 by more tranverse upper molars with anterior cingulum and sharp endoparacristule.

3.2. New material from the locality of Fordones, Aude, France.

Some specimens of *Diacodexis* from Fordones were described by Marandat (1991) and referred to *Diacodexis* cf. *gazini*. This material includes dp4, m1-2, and P2-3, but only the dp4 and the m1 were figured (Marandat, 1991: pl.4, figs. 10, 12, 14). We provide here additional views of these specimens and figure the loci that were not illustrated in Marandat (1991). Revision of the material referred to *Diacodexis* by Marandat (1991) revealed that the fragmentary m3 FDN 253 is not *Diacodexis* and rather belongs to a primate. Additional material from Fordones was collected in 2009. During screen washing, a P3-M3 series was retrieved in the same sieve and most probably belongs to the same individual, the bone of the maxilla was possibly not preserved during diagenesis and only teeth fossilized. Unfortunately, the M1 is missing.

Diacodexis aff. *antunesi*

Fig. 8

Synonymy: 1991. *Diacodexis* cf. *gazini* – Marandat, pl. 4, figs. 10, 12, 14.

Material (coll. UM): FDN 279, p2 or p3 (right); FDN 122, dp4 (left fragment); FDN 123, dp4 (left); FDN 124, m1 (left); FDN 255, m1 (right); FDN 125, m2 (right); FDN 252, P2 (right); FDN 251, P3 (right); FDN 254, M (fragment); FDN 280, M (left fragment); P3-4 and

M2-3 FDN 283 (right).

Locality and horizon: Fordones, Aude, France; «Grès à nummulitidés» Formation, early Eocene, ~MP7.

Measurements: Table 3.

Description:

Lower dentition. One permanent lower premolar of *Diacodexis* is documented (FDN 279) from Fordones (Fig. 8(D-F)). By its size and morphology, it either represents p2 or p3. Despite wear, a small paraconid is visible. The hypoconulid is central and distinct from the postparacristid. The dp4 (FDN 123) presents a protruding and deeply basined anterior lobe with a high paraconid. The paraconid lies in a central position and slightly extends lingually. The anterior basin is delimited by high and sharp cristids originating from the paraconid and joining the preprotocristid labially and the premetacristid lingually. The cristid joining the protoconid is worn and the lack of a primonid cannot be directly verified; however, there is no swelling of the cristid. The protoconid and metaconid are of equal size, and located on the same transversal plane; both bear postcristids. A small basin is present between the protoconid and metaconid, delimited by incipient endofossids. There is no clear endoproto- and endometa- cristids. The lingual cutting edge of dp4 is composed of high premetacristid, postectometacristid and ectoentocristid. The entoconid also bears a small endoentocristid and a sharp postentocristid. The latter is not connected to the posthypocristid. The cristid obliqua connects the base of the metaconid. There is no hypoconulid. Concerning the root pattern, the dp4 bears only two pillars, there is no trace of third labial pillar (see discussion). A fragmentary dp4 documenting the trigonid (FDN 122) shows the same morphology as FDN 123.

The lower molars are documented by two m1 and one m2. All specimens are worn and the finest structures of the crest and groove pattern have been worn away. The specimens

show a long and thin anterior cingulid; the labial cingulid is absent. Compared to m1, the trigonid of m2 is more compressed due to the posterior position of the paraconid (appressed to the metaconid). On m1-2, the cristid obliqua joins the base of the protoconid (Fig. 8(G-L)). Marandat (1991) considered that the hypoconulid was absent and that the entoconid was connected to the posterior cingulid. However, these observations are related to the wear of the teeth, a small groove and the shape of the exposed dentine indicate that a small hypoconulid was indeed present. The apparent connection of the entoconid to the posterior cingulum is also due to wear. The talonid notch is deep and marked.

Upper dentition. The upper dentition of *D.* aff. *antunesi* is documented by two isolated premolars and by an upper tooth raw comprising P3-4, M2-3 (FDN 283). The P2 (FDN 252) is slightly inflated in its posterolingual part, but its posterior-most portion is broken (Fig. 8(Q)). There are sharp and high pre- and post- paracristae. A very small parastyle lies anteriorly to the preparacrista. The postparacrista and preparacrista are finely crenulated. The P3 is documented by two specimens (FDN 283, FDN 251). It has a triangular outline (Fig. 8(P)) and three well separated roots, one anterior, one posterior and one supporting the lingual lobe. The paracone bears sharp and high pre- and post- paracristae. The parastyle is salient and distinct from the preparacrista. The postparacrista joins the posterior cingulum at the level of the metastyle. The lingual lobe is small and bears no protocone; a small basin is present, lined by a thin lingual cingulum. In both specimens, the lingual cingulum is continuous with the posterior one. The P4 shows a rather small protocone, which summit is more anterior than that of the paracone (Fig. 8(O)). The protocone bears a sharp preprotocrista joining the anterior cingulum, but no posterior crista. There is no endoprotocrista and no endoparacrista. The posterior cingulum is thick, long and joins a small metastyle on the posterolabial corner of the tooth. The cingulum is interrupted lingually at the protocone level. The labial cingulum is thin and continuous. There is no ectoflexus.

459 The M2 (FDN 283) has a trapezoidal outline (Fig. 8(N)). The labial edge is straight
460 and the lingual lobe is antero-posteriorly wide. The anterior cingulum is long and ends
461 lingually at the level of a small pericone whereas the posterior cingulum is less extensive but
462 thicker with a small hypocone. The parastyle is small. Wear does not obscure the presence of
463 the endoproto- and endometa-cristules. The M3 is triangular in shape. It exhibits a
464 pronounced ectoflexus and the paracone is larger than the metacone (Fig. 8(M)). The
465 protocone is smaller than on M2. The anterior cingulum joins lingually a small pericone. In
466 the upper tooth raw, the size of M3 is only slightly smaller than M2, whereas P4 is
467 considerably smaller than the latter (Fig. 8(M-O)).

468 Enamel microstructure. The 'basic' radial enamel of the upper molar FDN 254 from
469 Fordones has the same characteristics as that of *D. antunesi* (Fig. 3). It is slightly thinner (84
470 μm) and the IPM cristallites are directed to 33° relative to the prism direction. Prisms rise
471 from the EDJ at an angle of 65° and reach EOS with an angle of 72°. The aprismatic outer
472 enamel layer is thicker than in *D. antunesi*: it represents on average 20% of total enamel
473 thickness.

474 **Remarks**: *D.* aff. *antunesi* is morphologically very close to *D. antunesi* from the slightly
475 older locality of Silveirinha, Portugal. The upper teeth are generally the same size: upper
476 molars fall in the range of variation observed in *D. antunesi*, the P4 is slightly larger labio-
477 lingually (Fig. 5). However, greater size difference is observed for m1-2, with specimens of
478 *D.* aff. *antunesi* from Fordones larger than those of *D. antunesi* (Fig. 4). Compared to *D.*
479 *antunesi*, m1-2 of *D.* aff. *antunesi* have a larger entoconid that widens the talonid part of the
480 tooth. Both taxa show the same crest pattern and a hypoconulid closely linked to the
481 entoconid, as well as subequal trigonid and talonid, separated by deep labial and lingual
482 notches (Fig. 7(C)). Like *D. antunesi*, the P4 of *D.* aff. *antunesi* has no ectoflexus; however,
483 the parastyle and the paracone are smaller and the endoparacristule is lacking in *D.* aff.

antunesi. The P3 of *D.* aff. *antunesi* differs from that of *D. antunesi* by a slenderer distal part with a weaker cingulum. Because of these differences and of the small number of remains available from Fordones, we decided to refer it to as *D.* aff. *antunesi.*

Marandat (1991) referred the *Diacodexis* remains from Fordones to *Diacodexis* cf. *gazini* based on dimensions of the lower molars slightly larger than *D. antunesi* and on characters he considered also present in *D. gazini*: lack of hypoconulid on lower molars, entoconid small and fused to the posterior cingulid, a paraconid close to the metaconid. Based on our new observations, the absence of hypoconulid in the lower molars of Fordones and in the specimens of *D. gazini* from Rians is due to wear: the hypoconulid has been worn away; the connection of the entoconid to the posterior cingulid and the proximity of the paraconid and metaconid are also characters related to the wear stage of the teeth. Compared to *D. gazini* from the more recent locality of Rians (Marandat et al., 2012), *D.* aff *antunesi* from Fordones has less internal paraconid and metaconid and thinner cingulids on lower molars. Upper molars of *D.* aff *antunesi* have more pointed cusps, the lingual lobe of M2 is proportionally wider in *D. gazini* due to massive cingula. The ectoflexus of upper molars is shallower in *D. gazini* (Fig. 7(C) vs (E)). Like *D. antunesi*, *D.* aff. *antunesi* is morphologically very close to *D. varleti* but shows smaller dimensions of upper and lower teeth. The M2 specimen from Fordones is much smaller, but M3s of both species have the same labio-lingual diameter but they are much longer in *D. varleti* (Fig. 5). The dp4 of *D. varleti* (CB 811) is also mentioned in the literature (Sudre 1983:295) but could not be found in the MNHN collections and is possibly lost. *D.* aff. *antunesi* from Fordones differs from other early Ypresian *Diacodexis* species for the same characters as those mentioned for *D. antunesi*. For additional comments on enamel microstructure and dp4 morphology and comparisons with other *Diacodexis* species, see discussion section.

509 *3.3. New material from the locality of Palette, Bouches-du-Rhône, France*

510 *Diacodexis* material from Palette was mentioned by Godinot et al. (1987) who
511 tentatively referred one astragalus to cf. *Diacodexis*. The dental material of *Diacodexis* from
512 Palette, identified and prepared in 2012, confirms the presence of this genus in this locality.
513

514 *Diacodexis* cf. *gigasei*

515 Figs. 9-10

516 **Referred material** (coll. UM): PAT 159, dentary with p3-m3 and alveoli i1-p2 (left); PAT
517 136, m1 (left); PAT 19, astragalus (left); PAT 168, astragalus (right).

518 **Locality and horizon**: Palette, Bouches-du-Rhône, France; at the top of the «Calcaires de
519 Langesse», early Eocene, ~MP7.

520 **Measurements**: Tables 2, 4.

521 **Description**:

522 Dentary. PAT 159 consists in a left dentary preserving p3-m3 (Fig. 9). The anterior-
523 most part of the mandible is preserved and the alveoli of i1-p2 are visible. The body of the
524 mandible is free from deformation and complete except for a small portion of its ventral edge,
525 broken under p4-m1. The posterior part of the mandible, including the angular apophysis, is
526 missing. The ascending ramus is deformed: its height and width are diminished by fractures
527 and medial sliding of the bone. The 3D model of the originally preserved state specimen as
528 well as a 3D model showing a reconstruction of the ascending ramus based on the preserved
529 fragments are available at MorphoMuseuM.com (Orliac et al., in press; models ID: M3#315_
530 UMPAT159, M3#317_ UMPAT159). PAT 159 constitutes the most complete specimen of
531 European *Diacodexis* to date, and the longest tooth row documented for the same individual
532 for European *Diacodexis* species. The body of the mandible is particularly slender and low,
533 especially in the incisors and canine region, and slightly increases from the incisors to the

molars, but is of constant height between p3 and m2. The body of the mandible is particularly shallow at the level of p1 where it slopes downward (Fig. 9(A-B)). Three mental foramina are present on the labial surface: one below the p1, one below the posterior root of the p2, and one between the p3 and p4. The first mental foramen is the largest. The mandibular symphysis starts from the level of p2. Despite of breakage of the posterior part of the mandible, the coronoid apophysis is complete; it is slightly curved posteriorly and shows a wide plateau at its dorsal extremity. Its dorsal extension is weak: its height is similar to the height of the body of the mandible at the level of m3. This is, to our knowledge, the first documentation of a complete coronoid apophysis for *Diacodexis*, except the conceptual reconstruction provided by Russell et al. (1983: fig. 1) for *D. pakistanensis* in which the dorsal extremity was figured in dotted lines. The anterior part of the mandibular condyle is preserved, separated from the ascending ramus by a wide incisura. The condyle, which was small in size, was situated well above the tooth row. There is a large space between the root of the ascending ramus and the posterior part of m3. Based on the disposition of the alveoli on the anterior portion of the mandible, there were three short diastemata between p3 and p2, between p2 and p1, and between p1 and canine. The canine and the p1 are single-rooted, the p2 is double-rooted and its size was probably similar to that of the p3. The alveolus of p1 and that of the canine are similar in size. Judging from the size of their alveoli, the incisors of *D.* cf. *gigasei* were minute. Alveoli of i1-i2 are coalescent.

Lower tooth row. The p3 has a tiny paraconid connected to the protoconid via the preprotocristid. The postprotocristid joins the posterolingual cingulid but the hypoconid only consists in a bulge of the posterior cingulid. The p3 has no anterolabial cingulid. The p4 is wider than p3, longer, and has a more distinct paraconid and a rather larger hypoconid than p3. Compared to p3, a small anterolingual cingulid is present and the anterior and posterior basins are more elongate. Three posterior crests originate from the protoconid, a long

postprotocristid, and short endoprotocristid and postectoprotocristid. On p3-4, the preprotocristid is labial and is shifted lingually in its anteriormost portion to join the paraconid. The m1 is antero-posteriorly shorter than p3 and p4. The m2 is the widest molar labio-lingually and its length is clearly superior to that of m1 (Table 4). On m1-3, the talonid is larger than the trigonid; the cristids of the trigonid are close together and the trigonid basin is narrow. The paraconid is almost as high as the protoconid, which itself is small and close in size to the metaconid. The protoconid and the metaconid are about the same height. The paraconid is distinct from the metaconid on m1, these two cuspids being less separated on m2-3. In spite of wear, the endoprotofossid and endometafossid are present. The talonid notch is weak and the postectometacristid is absent on m1-3. The entoconid is located lingually and large but smaller than the hypoconid. The cristid obliqua is directed toward the metaconid on m1 and central on m2-3. The anterior cingulid is long and almost continuous with the labial cingulid on m2-3. The hypoconulid is linked to the entoconid, to the hypoconid and to the posterior cingulid except on m3 where it is separated from the labial cingulid by a groove. The posterior lobe of the m3 is massive and bears a large hypoconulid.

Astragalus. Two astragali retrieved in Palette are referred here to the species *D.* cf. *gigasei*. They are identical in terms of size and proportions. The proximolateral part of the tibial trochlea is missing on the astragalus PAT 168 whereas the astragalus PAT 19 is almost complete, with only the tibial trochlea lateral condyle and the distal calcaneal facet partly broken (Fig. 10(A-D)). The two trochlea of the astragalus PAT 19 have the same width. In both specimens, the groove of the tibial trochlea is wide and shallow, and the condyles are nearly symmetrical proximally. The fossa for the anterior process of the tibia is present on PAT 19 (corresponding part broken on PAT 168). On both specimens, the distal trochlea is robust and has a very prominent cuboid facet, which is especially pronounced on PAT 19. The fossa for the tibial malleolus is deep and the sustentacular facet is long and strongly

convex in lateral view. The surface where fits the calcaneo-navicular ligament is wide on both specimens. The ectal facet is shrunk in its center, and its upper part is round. The ectal facet is separated from the sustentacular facet by a narrow sulcus tali. Slight differences are observed between the two specimens: the neck of PAT 19 is narrower than that of PAT 168 (Fig. 10(A) vs (E)) and its lateral cavity is deeper.

Remarks:

Comparison with other known *Diacodexis* dentaries. Dentaries of *Diacodexis* figured in the literature are scarce and, to our knowledge, only available for *D. indicus* (Kumar et al., 2010: fig. 5E), *D. secans* (Krishtalka and Stucky, 1985), and *D. pakistanensis* (Russell et al., 1983: fig. 1; Thewissen et al., 1983). A decent fragment of the mandible of *D. ilicis* is also illustrated in Gingerich (1989). The morphology of the mandible remains undescribed for European taxa so far. The three diastemata observed in *D.* cf. *gigasei* (between p3 and p2, between p2 and p1, and between p1 and canine) are also present in *D. pakistanensis* as figured by Russell et al. (1983: fig. 1). The material illustrated by Thewissen et al. (1983: pl. 2) shows that variability occurs in that species and that the p3-p2 diastema can be present or absent (Thewissen et al., 1983: pl. 2.4 vs 5). Short diastemata between p2 and p1 and p1 and canine are also present in *D. indicus* (Kumar et al., 2010: fig. 5E) and *D. secans* (Krishtalka and Stucky, 1985). The p3-p2 diastema is also observed in *D. secans* (Krishtalka and Stucky, 1985), but does not seem to be present on the specimen of *D. indicus* (Kumar et al., 2010: fig. 5E). Compared to the specimen of *D. pakistanensis* figured by Thewissen et al. (1983: pl. 2.4a), to *D. indicus* (Kumar et al., 2010: fig. 5G) and to *D. ilicis* (although most probably deformed, Gingerich, 1989: fig. 36B) the body of the mandible PAT 159 only slightly increases in height posteriorly between p3 and m3. The downward curve of the anterior part of the mandible, anterior to p2 at the level of p1 (that is of the symphysis) observed on PAT 159 is neither present on the specimen of *D. pakistanensis* illustrated by Thewissen et al.

609 (1983: pl. 2.4a) nor on that of *D. indicus* illustrated by Kumar et al. (2010: fig. 5G). This
610 downward slope of the anterior-most region of the mandible is however perceptible on the
611 occluding tooth row of *D. pakistanensis* (Thewissen et al., 1983: pl. 1.3a) and is observed in
612 other artiodactyls of the Eocene (e.g. *Chorlakkia* Gingerich et al., 1979). The main mental
613 foramina observed on the labial surface of PAT 159 are also present in the other *Diacodexis*
614 species. The space between the root of the ascending ramus and the posterior edge of m3 is
615 superior in PAT 159 than in other *Diacodexis* species for which this character is documented
616 (*D. pakistanensis*, Russell et al., 1983; *D. ilicis*, Kumar et al., 2010).

617 Comparison of the tooth row with other early-middle Ypresian *Diacodexis* species.
618 The dentition of *D.* cf. *gigasei* can only be partially compared to other European *Diacodexis*
619 species because its upper dentition is not documented, and because lower premolars of most
620 of the other *Diacodexis* species are not documented: the p3 can only be compared to *D.*
621 *antunesi*, *D. gazini* and *D.* aff. *antunesi*, the p4 can only be compared to *D. morrisi*. In terms
622 of size, the dental remains of *D.* cf. *gigasei* from Palette are generally larger than those of *D.*
623 *antunesi*, and close in size to other MP7 species from Southern Europe (Fig. 4).

624 *Comparison with Southern European MP7 and MP8+9 species.* The lower dentition
625 of *D.* cf. *gigasei* shows clear differences with that of *D. antunesi*. The p3 has a longer
626 preprotocristid, more curved lingually than the p2/3? of *D. antunesi*, which is also labio-
627 lingually slenderer. These differences can be due to the fact that SNC 64 is in fact a p2 rather
628 than a p3. Concerning the lower molars, compared to *D. antunesi*, *D.* cf. *gigasei* presents a
629 proportionally smaller trigonid that represents less than half of the crown surface. The
630 trigonid basin is slender, and shallower and the paraconid is very close to the metaconid. The
631 postectometacristid is absent in *D.* cf. *gigasei* whereas it is long sharp and connected to the
632 ectoentocristid in *D. antunesi*. The cingulids of *D.* cf. *gigasei* are longer and the anterior
633 cingulid is almost connected posteriorly to the labial one. The hypoconulid is located closer to

634 the median plane of the tooth in *D.* cf. *gigasei*. In this latter taxon, there is a marked
635 difference of height between the protoconid and the lingual cuspids, whereas in *D. antunesi*
636 this difference is weaker. The astragalus of *D.* cf. *gigasei* from Palette is more robust than that
637 of *D. antunesi* (Fig. 2 vs Fig. 10, Table 2). The narrowing at the level of its neck is less
638 pronounced and the tibial trochlea groove is wider and the sulcus tali narrower than in *D.*
639 *antunesi*. Compared to *D.* aff. *antunesi* from Fordones, the p3 of *D.* cf. *gigasei* presents much
640 smaller paraconid and hypoconulid, and a longer preprotocristid, more curved lingually. The
641 lower m1-2 of *D.* cf. *gigasei* are wider with longer cingulids and a more medial position of
642 the hypoconulid. Compared to *D. gazini*, the p3 of *D.* cf. *gigasei* shows a wider protoconid
643 than that of the p2/3? of the former species, a more central/medial position of the paraconid
644 which is fused to the anterior cingulid. The tooth is labio-lingually slenderer in *D. gazini*.
645 These differences might be due to the fact that RI 208 is in fact a p2 rather than a p3. The m2
646 of *D.* cf. *gigasei* differs from that of *D. gazini* by a wider and lower crown; *D. gazini* shows a
647 proportionally slenderer and smaller trigonid relative to the talonid and a longer anterior
648 cingulid. Like in *D. gazini*, *D.* cf. *gigasei* has a paraconid very close to the metaconid.
649 Compared to *D.* cf. *gigasei*, *D. varleti* presents a hypoconulid of m1-2 situated closer to the
650 entoconid, a protoconid almost as high as the metaconid on lower molars, a shorter anterior
651 cingulid, sharper lingual crests (postectometacristid absent in *D.* cf. *gigasei*). The groove
652 separating the metaconid and the paraconid is deeper in *D. varleti* than in *D.* cf. *gigasei*.
653 Finally, *D.* cf. *gigasei* differs from *D. corsaensis* by a smaller size of the p4 and larger size of
654 m3 (Fig. 4).

655 *Comparison with Northern European MP7 species.* The *Diacodexis* material from
656 Palette is close to *D. gigasei* from Dormaal (Belgium) in its size, and morphologically
657 speaking by the presence of: i) a long anterior cingulid on m2, ii) a reduced lingual cutting
658 edge on lower molars (low ectoendocristid and no clear postectometacristid), iii) an

hypoconulid apart from entoconid on m1-2, iv) a postentocristid directed toward the hypoconulid on m3. Lower molars from the two localities differ by their length/width ratios which are smaller for m1-2 of *D.* cf. *gigasei* than in those from Dormaal (Fig. 4). In *D.* cf. *gigasei*, the m3 paraconid also appeared reduced and the molar crown looks slightly more bunodont, but this can be due to difference in wear stages. As a result, despite the good morphological and close metrical correspondence between the material from Palette and that collected from Dormaal, the *Diacodexis* material from the former locality is left under open nomenclature as *D.* cf. *gigasei*. Further discoveries, especially that its upper molars, could clarify this attribution.

The p4 of *D.* cf. *gigasei* differs from that of *D. morrisi* (Hooker, 2010: fig. 47d,g) by a longer preprotocristid, more curved lingually, and by a shorter postectoprotocristid. Both taxa present three posterior crests originating from the protoconid, endoprotocristid, postprotocristid and postectoprotocristid. The m1 of *D. morrisi* shows a more open trigonid basin with a larger paraconid located more lingually than in *D.* cf. *gigasei*. The labial notch, in occlusal view, is deeper on m1 and m3 in *D. morrisi* and a long and sharp postectometacristid is present.

Comparison with Northern American and Asian species. D. cf. *gigasei* is smaller than *D. indicus* and all Northern American species; moreover, it has no postectometacristid in contrast to all North American and Asian species; it differs from *D. parvus* and *D. indicus* by a more central location of the hypoconulid. Finally, *D. indicus* and *D. pakistanensis* have a more labial cristid obliqua. The p4 of *D.* cf. *gigasei* differs from that of *D. ilicis* and *D. secans primus* in lacking a distinct lingual demarcation/inflexion of the paraconid. In *D. ilicis*, the lingual basin on the talonid is deeper and bordered by a thick posterior cingulid. The presence of the three posterior crests on p4 cannot be ascertained based on the low resolution figures provided by Rose et al. (2012) and Krishtalka and Stucky, (1985). There seem to be a stronger

endoprotocristid and no postectoprotocristid on the North American specimens.

3.4. New material from the locality of La Borie, Aude, France.

Diacodexis sp.

Fig. 11

Referred material (coll. UM): BRI 1, P3 (right); BRI 2, P4 (left); BRI 3, M2 (right); BRI 4, M3 (right); MHNT.PAL.2017.21.2, m2 on a fragmentary dentary (left).

Locality and horizon: La Borie, Aude, France; «Argiles rutilantes d'Issel et de Saint-Papoul» Formation, early Eocene, ~MP8+9.

Description: The unique lower molar is much worn; considering the size of its trigonid and the morphology of the preserved roots of the anterior teeth, MHNT.PAL.2017.21.2 is attributed to an m2. No peculiar detail of the crown is visible.

The upper dentition is documented by premolars and molars. The P3 (BRI 1) has a triangular outline (Fig. 11(D)) and three distinct roots (anterior, posterior, lingual). The paracone bears sharp and high pre- and post- paracristae, crenulation cannot be observed because of wear. There is no trace of parastyle, but the corresponding locus is slightly worn; if present, it was very small. There is no metastyle. The lingual lobe is large and protrudes lingually; it bears a small protocone and a small basin. The lingual cingulum is continuous and joins the anterior and posterior cingula. The labial cingulum is very thin. The P4 (BRI 2) has no ectoflexus (Fig. 11(C)). This tooth is remarkably unworn. The unworn paracone is very high. Parastyle and metastyle are present, the metastyle being higher than the parastyle. The P4 has a small protocone which summit is slightly anterior to that of the paracone. It bears anterior and posterior cristae. There are no endoproto- and endopara- cristae, nor anterior and posterior cingula.

The M2 (BRI 3) is only little worn but is broken anterolingually (Fig. 11(B)). It has

round labial corners. The labial edge is straight. The paracone is higher and slightly larger than the metacone. The preparacrista and postmetacrista are both on the same plane as the centrocrista. The endoparacristule and endometacristule are present, but the endoparacristule is very low. There is not a postmetacristule deflection (i.e. postmetacristule protruding on the posterior edge of the tooth, cf. Fig. 7B, F) on the occlusal surface. The styles are limited to cingular swellings. The posterior cingulum is short, there is no clear hypocone. The M3 (BRI 4) is little worn. It has round labial corners and a tilted lingual edge (Fig. 11(A)). The paracone is the highest cusp. The preparacrista and postmetacrista are both on the same plan as the centrocrista. The anterior and posterior cingula are long, thick, but not connected at the protocone level.

Remarks:

Comparison with Southern European MP7 and MP8+9 species. The taxon from La Borie is larger than *D. antunesi* and smaller than *D. morrisi*. It differs from *D. antunesi* and *D. gigasei* in having no postmetacristule deflection on the occlusal surface. It differs from *D. antunesi* in having a P3 with an elongate paracone and more convex labial edge, a reduced parastyle on upper molars. It differs from other species of *Diacodexis* in having a P4 without anterior and posterior cingula. It differs from *D. gigasei* in having a P4 without ectoflexus and upper molars with shorter posterior cingulum (no lingual bulge). It differs from *D. morrisi* in having no endoparacrista and a less important groove intersecting the postprotocrista on upper molars.

The material of La Borie appears close to *D. gazini* in size and morphology. Both species have round labial corners on upper molars, straight labial edge on M2, and similar mesiodistal M2 length. On M3 however, the *Diacodexis* species from La Borie has a less protruding parastyle and strongly round cusps and conules when compared to *D. gazini*. Conversely, the M2 of La Borie does not show bulbous cusps like for the M3 of *D. gazini*.

734 This discrepancy could be explained by the degree of wear (the M2 is almost unworn contrary
735 to the M3). Finally, the M2 from La Borie does not have a long and thick posterocingulum
736 shaping in hypocone while the presence of the latter feature constitutes a diagnosic character
737 of *D. gazini*. Finally, compared to *D. varleti*, the species from La Borie has less pronounced
738 ectoflexus on M2, the parastyle is not protruding, and the conules are reduced with lesser
739 endocristules.

740 Comparison with Northern American and Asian species. The taxon from La Borie is
741 smaller than *D. indicus* and all North American species; it further differs from *D. ilicis* in
742 having no postmetacristule deflection. Among Asian species, *Diacodexis* sp. from Andarak 2
743 and *D. pakistanensis* differ from *Diacodexis* sp. from La Borie by the lack of endoparacristule
744 and postprotocrista on upper molars and P4, respectively; *Diacodexis indicus* has a larger
745 parastyle on M2 and a more reduced metacone on M3.

746

747 **4. Discussion**

748 *4.1. Ancestral morphotype of artiodactyl enamel microstructure*

749 Recent data on artiodactyl enamel microstructures revealed a diversity of patterns
750 relevant to phylogenetic inferences (Alloing-Séguier et al., 2014). From this point of view,
751 *Diacodexis* is crucial to discuss the enamel ancestral morphotype of artiodactyls. Since Maas
752 and Thewissen (1995) and Stefen (1999), *Diacodexis* is thought to have developed a two-
753 layered Schmelzmuster (the spatial arrangement of the different enamel types through enamel
754 thickness): a thin layer (5-10%) of radial enamel close to EDJ and a thick layer of Hunter-
755 Schreger bands (HSB) that generally extends to the EOS; in some parts a very thin layer of
756 radial enamel can occur at the EOS. Our data on *Diacodexis antunesi* and *Diacodexis* aff.
757 *antunesi*, which have a one-layered Schmelzmuster with 'basic' radial enamel only, reveal a

simple enamel pattern. This result implies a surprising interspecific variability among *Diacodexis* species, which is rare among eutherian mammals.

Maas and Thewissen (1995) based their observations on *Diacodexis* on an undetermined North American species represented by a lower molar from the Wa-5 (= '*Bunophorus* Interval Zone' in the original publication). Regarding Stefen (1999)'s analysis, two species were studied based on specimens from the UCMP collections, i.e. *Diacodexis robustus* and an undetermined species. Theodor et al. (2007) now attribute the former species to *Bunophorus*; this diacodexeid genus is thus excluded from the present discussion. As for the undetermined *Diacodexis*, online UCMP database (accessed on September 2017, available at: http://ucmpdb.berkeley.edu/) indicates that the figured specimen comes from the mid-Wasatchian (Wa3-5) (= 'Graybullian' in the database) of the Willwood Formation, Wyoming. Therefore, based on the stratigraphical ranges proposed by Krishtalka and Stucky (1985) for North American *Diacodexis* species, we can assume that the undetermined species studied by Maas and Thewissen (1995) and Stefen (1999) is either *D. secans* (known from the early Wasatchian to the Bridgerian) or less probably *D. gracili*s (rare, known in the mid-Wasatchian, Wa3-5). Importantly, *Diacodexis antunesi* and *Diacodexis* aff. *antunesi* are smaller and have more crestiform, simple molars than *D. secans* and *D. gracili*s. These size and morphological differences could be correlated to the dissimilar enamel microstructure that we observe between *Diacodexis* species.

Actually, according to Koenigswald et al. (1987), HSB characterized almost all large herbivorous mammals since the early Paleocene. Stefen (1999) proposed that convergent evolution of HSB within eutherians result of co-occurring changes in dental morphology, body-size, overall ecology, and chewing pattern. Fundamentally, small insectivorous mammals have 'basic' radial enamel (e.g., eulipotyphlans, chiropterans, small primates, some "condylarths") whereas herbivorous, omnivorous, and mid-sized carnivorous and large

783 mammals have prism decussation such as HSB. Interestingly, our results on *Diacodexis*,
784 would support this trend at the genus level: *D. antunesi* and *D.* aff. *antunesi* are small-sized
785 most likely insectivorous species with tribosphenic, crestiform molars, whereas *D. secans* and
786 *D. gracili*s are putative omnivorous and/or herbivorous, larger species with more
787 quadritubercular, bunodont molars (see also Theodor et al. 2007: p. 37).
788 Interestingly also, the fossil record of placental mammals suggests that the 'basic'
789 radial enamel is the primitive condition (see Tabuce et al. 2017: p. 103). With the exception
790 of odontocetes (due to the simplification of their tooth morphology and piscivorous diet),
791 there are no reversion from HSB to 'basic' radial enamel. In other words, the enamel
792 microstructure (i.e., 'basic' radial enamel) of *Diacodexis antunesi* most likely represents the
793 primitive condition among *Diacodexis* species and most probably represents the ancestral
794 morphotype for Artiodactyla.
795
796 *4.2. Ancestral morphotype of artiodactyl fourth lower deciduous premolar*
797 The new *Diacodexis* material described here includes one dp4 attributed to *D.* aff
798 *antunesi* (Figs. 8A-C, 12A). This specimen from the Ypresian locality of Fordones represents
799 one of the earliest record of dp4 for artiodactyls. Only few specimens of dp4 of *Diacodexis*
800 are documented in the literature. A dp4 of *D. varleti* was reported by Sudre et al. (1983) from
801 Condé-en-Brie, but the specimen was neither figured nor described by the authors, and could
802 not be found in the MNHN collections. In addition to this specimen, a dp4 of *D. morrisi* has
803 been described and figured by Hooker (2010: fig. 48E). This specimen is fresh and allows
804 observing the finest structures of the crown (Fig. 12(B)). In addition to these specimens,
805 several dp4s of early artiodactyls are documented from the French MP10 locality of
806 Prémontré (Aisne, Nothern France). One specimen, SLP-29-PE 637 (Fig. 12(E)), was
807 originally attributed to *D.* cf. *varleti* by Sudre and Erfürt (1996) but it was not figured. Four

other dp4 of artiodactyls from the same locality were referred to Dichobunidae Eurodexeinae by Sudre and Erfürt (1996: pl. 1, fig. 8; Fig. 12(F)). Since the publication of this material, another specimen was retrieved from the sediment from Prémontré. This specimen, UM PRE151, is here attributed to *Diacodexis* sp. (Fig. 12(D)). From Asia, a worn dp4 of *D. indicus* was described by Kumar et al. (2010: fig. 6G-I; Fig. 12(C)) from the Vastan mine in Western India. Luckett and Hong (1998) paid special attention to the morphology of the lower fourth deciduous premolar in extant and fossil artiodactyls. In artiodactyls, the anterior lobe of the trilobed dp4 is described as bearing a mesiolabial and a mesiolingual cusp, forming a third lobe, a character retrieved as a synapomorphy of Artiodactyla (e.g., Gentry and Hooker, 1988; Luckett and Hong, 1998). Luckett and Hong (1998) consider that the paraconid is anteriorly displaced and lingual, and that "*the anterior lobe of the artiodactyl* dP_4 *is characterized by the development of a neomorphic cusp on the paracristid that runs between the protoconid and the paraconid; this new cusp provides a "squaring" of the anterior portion of the tooth*" (Luckett and Hong, 1998: p. 135). Surprisingly, these authors illustrate a specimen they refer to as *Diacodexis* cf. *varleti* from the French locality of Prémontré and numbered SLP 29PR 2122, while this specimen was initially attributed to Eurodexeinae indet. by Sudre and Erfürt (1996). A line drawing of the occlusal surface of the crown of SLP 29PR 2122 (Fig. 12(F)) shows that its general pattern considerably differs from that of dp4 of other *Diacodexis* species and that this specimen might indeed belong to the Eurodexinae. In turn, as illustrated on Figure 12, the MP7 European specimens referred to *Diacodexis* all present only one large cupid on what is generally considered as the anterior lobe or "paraconid lobe" (Hooker, 2010). This cusp is located on the lingual border of the tooth, and bears its own crest pattern with a lingual and a labial crest, touching the premetacristid and the preprotocristid respectively. According to its lingual position, this anterior cusp might be called the paraconid. The anterior part of the tooth rather has a triangular shape and there is no

"squaring" of the anterior portion of the tooth, as described by Hooker (2010: p. 108) based on the specimen of *D. morrisi*. The general shape of the crown is hourglass rather than trilobed, and there is no constriction between the paraconid lobe and the rest of the trigonid. In the specimens of *Eurodexis russelli* from Prémontré (Sudre and Erfürt, 1996: pl. 1, fig. 8), an additional cuspid is present labial to the large paraconid and the anterior part of the tooth is indeed squared; it presents a trilobed outline, like in most other extant and extinct artiodactyls. On the very fresh dp4 of *Diacodexis* sp. from Prémontré (UM PRE151, Fig. 12(D)), a very small accessory cuspid is present on the labial crest originating from the paraconid. The dp4 from the same locality attributed to *Diacodexis* cf. *varleti*, by Sudre and Erfürt (1996) in fact presents a completely different morphology: there is one main cusp which is displaced labially and connected to the protoconid, a series of accessory cuspids are present in a crest-like structure, not mesiolabially, but lingually (Fig. 12(E)). There is no anterior basin. These two specimens illustrate the potential intraspecific variation for dp4.

These observations suggest that the labial anterior cuspid appears after the lingual one, here recognized as the paraconid based on its lingual position. Then it seems logical to recognize the anterior lingual cuspid as the paraconid and the labial one as the primonid, as identified by Luckett and Hong (1998). This nomenclature however contrasts with that used by authors for other artiodactyl groups such as suoids (Made, 1996; Orliac and Ducrocq, 2012; Orliac et al., 2015) where the labial cusp is named the paraconid and the lingual one the primonid. Early European *Diacodexis* dp4s suggest the opposite homology. In the phylogenetic analyses of Theodor and Foss (2005), the dp4 of *Diacodexis* is considered to be six cusped based on observations of *Diacodexis pakistanensis*. In contrast, observations of Ypresian material from Europe indicate that early *Diacodexis* species have only one anterior cuspid on dp4. Besides, the presence of two basins only, and the hourglass outlines of the dp4 of earliest *Diacodexis* species, do not match the trilobed pattern traditionally considered as a

858 synapomorphy for Artiodactyla. Finally, the dp4s of *Diacodexis* bear two pillars only, which
859 contrasts with the three rooted pattern of most more derived artiodactyls. The presence of a
860 two rooted pattern also occurs in other early members of Artiodactyla (Dichobunidae,
861 Cainotheriidae, Choeropotamidae; Orliac pers. obs.) as well as in basal members of Suoidea
862 (Orliac et al., 2012), and might represent the primitive condition within Artiodactyla.
863
864 *4.3. Relationships within* Diacodexis *and paleobiogeographic inferences*
865 Artiodactyls appear rather abruptly in earliest Eocene deposits in the fossil record
866 (Gingerich, 2006). Because of their early occurrence and the simple tribosphenic pattern of
867 their molars, *Diacodexis* has been regarded as a paraphyletic ancestral pool of species near the
868 base of the artiodactyl radiation (Rose, 2006), and was considered as implicated in the origin
869 of some European Eocene endemic groups (Sudre and Erfurt, 1996; Checa Soler, 2004), as
870 well as North American groups (Krishtalka and Stucky, 1985). The position of *Diacodexis*
871 species varies depending of the sample included in phylogenetic analyses (e.g., Theodor and
872 Foss, 2005; Geisler et al., 2007; Orliac and Ducrocq, 2012).
873 *Diacodexis* shows a vast repartition of species, close in terms of morphology and
874 stratigraphic age, despite sometimes huge geographic distances. For several taxa, mostly for
875 European ones, only few specimens are available. On the other hand, species documented by
876 relatively abundant material indicate that intraspecific variation occurs and might affect
877 features used to differentiate species (e.g., morphology of the m3 talonid, of the cingulids).
878 Besides, the absence of complete skull, or even tooth raw preservation, makes association of
879 upper and lower dentition problematic for some taxa (e.g., *Diacodexis* cf. *varleti*; Sudre et al.,
880 1983: p. 302). In addition to these taphonomic/preservation bias, wear degree has a potentially
881 drastic impact on crown morphology and the way it can be described by authors. Several
882 features, such as relative height or size of cusp(id)s, or accessory crest pattern can be affected

883 by wear. To be reliable, comparisons should be performed between specimens showing the
884 same degree of wear, which is not always possible given the scarcity of available material for
885 some taxa.

886 The new material described here shows that premolars, deciduous dentition, as well as
887 enamel microstructure are informative for systematic and phylogenetic purposes. However,
888 these characters are incompletely represented in several *Diacodexis* species, limiting the
889 extent of comparisons. Their rather simple molar morphology, combined to potential
890 intraspecific variation, dental locus association problems, impact of wear on morphology,
891 continuity of most of the characters described (cusp/id bulging, relative size, height, conule
892 location, cingulum/id size, length), and to the incompleteness of the loci documented between
893 localities/taxa, are factors that hinder the implementation of a phylogenetic analysis of
894 *Diacodexis* species so far.

895 Yet, relationships of European *Diacodexis* species have been discussed in the literature
896 based on comparisons between taxa only and not on formal cladistic analyses. *D. antunesi* has
897 been regarded as the most primitive *Diacodexis* species by some authors (e.g. Smith et al.
898 1996; Theodor et al., 2007); Hooker (2010) instead considers that *D. gigasei* from Dormaal
899 (MP 7) represents the most primitive species of the genus. Based on outgroup comparison
900 polarization criterion with hyopsodontid and arctocyonid 'condylarths', Hooker (2010)
901 considers that some characters point to *D. antunesi* being relatively derived within *Diacodexis*
902 species. These characters are: on lower molars, the crown height, the lingual position of the
903 m1-2 hypoconulid, the constriction of the m3 hypoconulid lobe, and the bulging of m1-2
904 entoconid; and on upper molars, the occlusal pattern of distolabially directed M1-2
905 postprotocrista, and a "bowed centrocrista". The lower molars of *D. antunesi* indeed present a
906 hypoconulid closer to the entoconid and located more lingually than what is observed in *D.*
907 *gigasei*. For this character *D. antunesi* is closer to *D. varleti* from Condé-en-Brie, France, but

908 also to *D. indicus* from Vastan, India (Fig. 13). However, based on our observations, the
909 entoconid of *D. antunesi* does not appear to be particularly larger than that of *D. gigasei* on
910 m1 (Fig. 13(B) vs (F)). Smith et al. (1996) propose that *D. gigasei* and *D. antunesi* share a
911 continuous structure uniting the hypoconulid and the hypoconid, a character seen by these
912 authors as plesiomorphic. This continuous structure might result from wear pattern on the
913 specimens, yet, study of fresh teeth indicates that the hypoconulid and the hypoconid are
914 always separated by a groove (Fig. 13). For upper molars, the "bowing of the centrocrista"
915 mentioned by Hooker (2010), is, to us, directly related to the size of the parastyle, which is
916 large in *D. antunesi*; while the orientation of the preprotocrista relies more on the general
917 lingual width of the upper molars (i.e. wide in *D. ilicis* and *D. gigasei*). Again, for these
918 characters, *D. antunesi* is closer to Asian taxa, *D. indicus* and *D. pakistanensis* (Kumar et al.,
919 2010: fig. 8), which present a lingual shift of the preprotocrista on M1, and a relatively
920 narrow lingual lobe on the upper molars. Based on upper molar morphology, we agree that *D.*
921 *gigasei* and *D. morrisi* are closer to *D. ilicis* than to *D. antunesi*. Yet, for now, there is no
922 formal way to affirm that these character state represent the primitive condition.
923 Hooker (2010) uses outgroup comparison as polarization criterion, and compares
924 *Diacodexis* species to hyopsodontids and arctocyonids. Hyopsodontids is a polyphyletic
925 assemblage and might be more closely related to Perissodactyla or some afrotherians, than to
926 Artiodactyla (Zack et al., 2005; Tabuce et al., 2007b; Ladevèze et al., 2010; Tabuce in press)
927 and should be left aside. Arctocyonids show a wide range of morphologies, including a
928 hypoconid closely apposed to the entoconid in lingual position on m1-2, and bulging
929 entoconid (e.g., *Chriacus truncatus* Rose, 1996: fig. 1; *Loxolophus hyattianus* Kondrashov
930 and Lucas, 2012). Arctocyonids also show a wide range of orientation of the M1-2
931 postprotocrista and "centrocrista bowing": *Protungulatum* and other arctocyonids (e.g., Rose,
932 2006: fig. 12.3) exhibit a lingual shift of the preparacrista and a strong parastyle, related to a

933 "bowed centrocrista". This is a plesiomorphic condition at the eutherian scale (e.g., Wible et
934 al., 2009). The generally simple molar crown morphology of most arctocyonids, with high
935 and pointed cusps associated with the primitive tribosphenic-tritubercular pattern, recall a
936 somewhat more "insectivorous" diet. Still, this morphology could as well be secondarily
937 derived within Artiodactyla, but in the general picture of Paleocene/Eocene eutherians, would
938 be consistent with a primitive pattern in *D. antunesi*.

939 The new material described here further documents the premolar dentition of
940 European *Diacodexis* species and provides new morphological characters for comparisons.
941 The P4 of *D. antunesi*, is morphologically close to *D. pakistanensis* with a labial wall with no
942 ectoflexus, and a paracone with salient endoparacristule. This structure is absent in *D. gigasei*,
943 and in the specimen referred to *D.* aff. *antunesi* from Fordones; it is also lacking in *D. ilicis*.
944 The P4 of *D. gigasei* presents an ectoflexus, like North American species like *D. ilicis* (Fig.
945 7), *D. secans-metsiacus* (Krishtalka and Stucky, 1985: fig. 4D-E).), or *D. secans-secans*
946 (Krishtalka and Stucky, 1985: fig. 2A-B). The P3 of European species is rather short
947 anteroposteriorly and bears a wide paracone; the lingual lobe of *D.* aff *antunesi* is small and
948 poorly differentiated, and bears no accessory cusp. This lobe is larger and more individualized
949 in *Diacodexis* sp. from La Borie, with a small accessory cusp. P3 of European species are
950 closer morphologically to the P3 of *D. indicus* from Vastan, than to the P3 of North American
951 species *D. ilicis* and *D. secans metsiacus*, which are longer anteroposteriorly and slenderer
952 bucco-lingually with a more salient lingual bobe and a bigger accessory cusp. Regarding the
953 lower dentition, the p4 of *D.* aff. *gigasei* from Palette is closer to *D. ilicis* than to *D. indicus*.
954 Unfortunately, comparisons with *D. antunesi* are not possible as this locus is not documented
955 yet. The morphology of the dp4 is complex and each documented taxon has its specificity (see
956 above).

Our observations highlight that *D. gigasei* is morphologically closer to *D. ilicis* than to *D. antunesi*, in accordance with Gingerich (1989), Smith et al. (1996), and Hooker (2010). *Diacodexis antunesi*, and *D.* aff. *antunesi* from Fordones appear to be morphologically closer to the Asiatic taxa *D. indicus* and *D. pakistanensis*. As a result, if a cladistic analysis of these taxa appears premature, an interesting conclusion may nevertheless be drawn at this stage: although *D. antunesi* and *D. gigasei* are certainly very close in age, close to the PETM, the preceding comparisons show that these two European species differ widely. This strongly suggests that at least two phases of migration of *Diacodexis* could have occurred in Europe around the Paleocene-Eocene boundary. Asia might be the dispersal centre of these two events (see Beard 1998). Interestingly, an Asian origin of European *Diacodexis* might be supported by the similarities between *D. antunesi* and the Asian species *D. pakistanensis* and *D. indicus*. Such a faunal interchange between Europe and South Asia , but well after the Paleocene-Eocene boundary, is also well-supported by some recent evidence (e.g., Smith et al. 2007; Rana et al. 2008; Rose et al. 2009; Tabuce et al. 2009).

Finally, we found numerous similarities between *D.* cf. *gigasei* from Palette and *D. gigasei* from Dormaal. This result is quite surprising considering the now well-established intra-European provincialism that characterizes the earliest Ypresian: mammals from the northwestern (Anglo-Belgian and Paris basins) and southwestern (south of France and Iberian Peninsula) provinces greatly differ (Marandat, 1997; Marandat et al., 2012; Solé et al., 2017). Along with few species ―such as the herpetotheriid marsupial *Peratherium constans* and the paromomyid plesiadapiform *Arcius fuscus* (see Godinot et al. 1987; López-Torres and Silcox in press)― *D. gigasei* could be one of the rare species in common between northwestern and southwestern bioprovinces.

5. Conclusions

The new material described here considerably increases our knowledge of European *Diacodexis* species, including the earliest representatives of the genus. Documentation of the enamel microstructure of *Diacodexis antunesi* from Silveirinha and *Diacodexis* aff. *antunesi* from Fordones, reveals that those early species had a simple enamel pattern with one-layered Schmelzmuster composed of 'basic' radial enamel only. These observations contrast with those performed on North American species that present a two-layered Schmelzmuster composed of a thin layer of radial enamel and a thick layer of Hunter-Schreger bands. This latter enamel microstructure pattern was so far considered to represent the primitive condition within Artiodactyla. The occurrence of a simple one-layer enamel in earliest European *Diacodexis* species challenges this hypothesis, and rather suggests that this simple pattern represents the primitive condition among *Diacodexis* species and probably among Artiodactyla. Likewise, the crown morphology of the dp4 of earliest *Diacodexis* species indicates a considerable diversity of the tooth occlusal pattern. Some *Diacodexis* species from Europe have only one anterior cuspid, two basins, and present an hourglass outline instead of the trilobed pattern so far considered as a synapomorphy for Artiodactyla. Besides, the dp4 of *Diacodexis* bear two pillars only, which contrasts with the three rooted pattern of other artiodactyls considered to be more derived. Study of earliest *Diacodexis* species therefore questions features considered as primitive within Artiodactyla. A large scale revision of diacodexeid species including North American material, as well as a wide sampling of potential branching groups, would be necessary to discuss the early radiation of Artiodactyla through a formal cladistic analysis, and properly determine character polarization.

In accordance with previous study, our observations highlight that *Diacodexis gigasei* is morphologically closer to *D. ilicis* than to *D. antunesi*. The latter species, together with the new material referred to *D.* aff. *antunesi* from Fordones, appear to be morphologically closer to the Asiatic taxa *D. indicus* and *D. pakistanensis*. Finally, we found numerous similarities

between *D.* cf. *gigasei* from Palette and *D. gigasei* from Dormaal, a result that attenuates the intra-European provincialism that characterizes the earliest Ypresian. *Diacodexis gigasei* could be one of the rare species in common between northwestern and southwestern bioprovinces.

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1257

Table and Figure captions

Tooth	Specimen	L	l	L/l
p	UM SNC 386	2.83	1.05	2.71
p	UM SNC 64	2.91	0.93	3.13
m1	UM SNC 93	2.68	1.74	1.54
m1	UM SNC 6	2.65	1.89	1.40
m1	UM SV3-133	3.05	2.00	1.53
m1	UM SNC 74	2.72	1.76	1.55
m2	UM SNC 74	3.07	2.12	1.45
m2	UM SV3-338	3.43	2.14	1.60
m2	UM SNC 3	3.13	2.44	1.28
m3	UM SV3-129	4.27	2.59	1.65
m3	UM SV3-332	3.50	2.34	1.49
m3	UM SNC 63	3.51	2.02	1.74
m3	UM SNC 17	3.72	2.34	1.59
m3	UM SNC 65	3.71	2.24	1.66
P3	UM SNC 58	3.27	1.79	1.83
P4	UM SNC 33	2.43	2.97	0.82
P4	UM SNC 311	2.49	3.08	0.81
P4	UM SNC 405	2.32	3.38	0.69
dP4	UM SNC 13	3.15	3.24	0.97
dP4	UM SV3-131	2.91	2.58	1.13
M1	UM SNC 49	2.86	4.03	0.71
M1	UM SV3-163	2.72	3.45	0.79
M1	UM SV3-189	2.66	3.40	0.78
M1	UM SV3-128	2.97	3.70	0.80
M1	UM SNC 339	-	3.59 *	-
M2	UM SV3-74	3.07	4.11	0.75
M2	UM SNC 20	3.07	3.79	0.81
M2	UM SNC 25	2.98	3.79	0.79
M2	UM SNC 36	3.15	3.95	0.80
M2	UM SNC 55	3.27	4.11	0.80
M2	UM SNC 95	3.50	4.02	0.87
M3	UM SNC 18	2.38	3.20	0.74
M3	UM SNC 262	2.52	3.34	0.75
M3	UM SV3-126	3.16	3.65	0.87

Table 1. Dental measurements of the new material of *Diacodexis antunesi* from Silveirinha, Portugal described in this work. Abbreviations: L, maximal length; l, maximal width, * corresponds to estimated value on broken material.

Locality	Silveirinha	Palette	Palette
specimen	UM SNC 687	UM PAT 168	UM PAT 19
Length (L)	-	7.08	6.90
Width body (l1)	4.17	4.15	3.76
Width neck (l2)	2.31	2.62	2.57
Width head (l3)	-	3.68	3.68
Length head (L3)	-	2.33	2.05
Length sust. fac. (Ls)	2.85	3.57	3.54
Width sust. fac. (ls)	2.02	2.16	2.42
Width navic. fac. (ln)	-	2.44	2.37

1264

1265 **Table 2**. Measurements of the astragalus from the MP7 localities of Silveirinha and Palette.

1266

tooth	specimen	L	l	L/l
p	UM FDN 279	2.80	1.25	2.25
dp4	UM FDN 123	3.51	1.61	2.18
m1	UM FDN 255	3.19	2.312	1.38
m1	UM FDN 124	3.27	2.20	1.49
m2	UM FDN 125	3.57	2.88	1.20
P2	UM FDN 252	-	1.33	2.07
P3	UM FDN 251	3.30	2.34	1.41
P3	UM FDN 283	2.89	2.03	1.42
P4	UM FDN 283	2.39	2.75	0.87
M2	UM FDN 283	3.12	4.13	0.76
M3	UM FDN 283	2.82	3.71	0.76

1267

1268 **Table 3**. Dental measurements of *Diacodexis* aff. *antunesi* from Fordones, France. .

1269 Abbreviations: L, maximal length; l, maximal width.

1270

tooth	specimen	L	l	L/l
m1-m3	UM PAT 159	11.23	-	-
p4-m3	UM PAT 159	14.93	-	-
p3-m3	UM PAT 159	18.55	-	-
c (alveolus)	UM PAT 159	2.13	0.93	-
p1 (alveolus)	UM PAT 159	2.29	1.02	-
p2 (alveolus)	UM PAT 159	3.42	1.21	-
p3	UM PAT 159	3.74	1.60	2.34
p4	UM PAT 159	3.79	2.04	1.86
m1	UM PAT 159	3.02	2.43	1.25
m1	UM PAT 136	3.23	2.16	1.50
m2	UM PAT 159	3.58	2.96	1.21
m3	UM PAT 159	4.63	2.91	1.59

1271

1272 **Table 4**. Dental measurements of *Diacodexis* cf. *gigasei* from Palette, France. Abbreviations:

1273 L, maximal length; l, maximal width.

1274

tooth	specimen	L	l	L/l
m1	UM APSO.2015.SP2-302	4.20	2.83	1.48
P3	UM BRI1	3.30	2.40	1.37
P4	UM BRI2	2.76	3.04	0.91
M2	UM BRI3	3.69	-	-
M3	UM BRI4	2.67	4.08	0.65

1275

1276 **Table 5**. Dental measurements of *Diacodexis* sp. from La Borie, France. Abbreviations: L,

1277 maximal length; l, maximal width.

1278

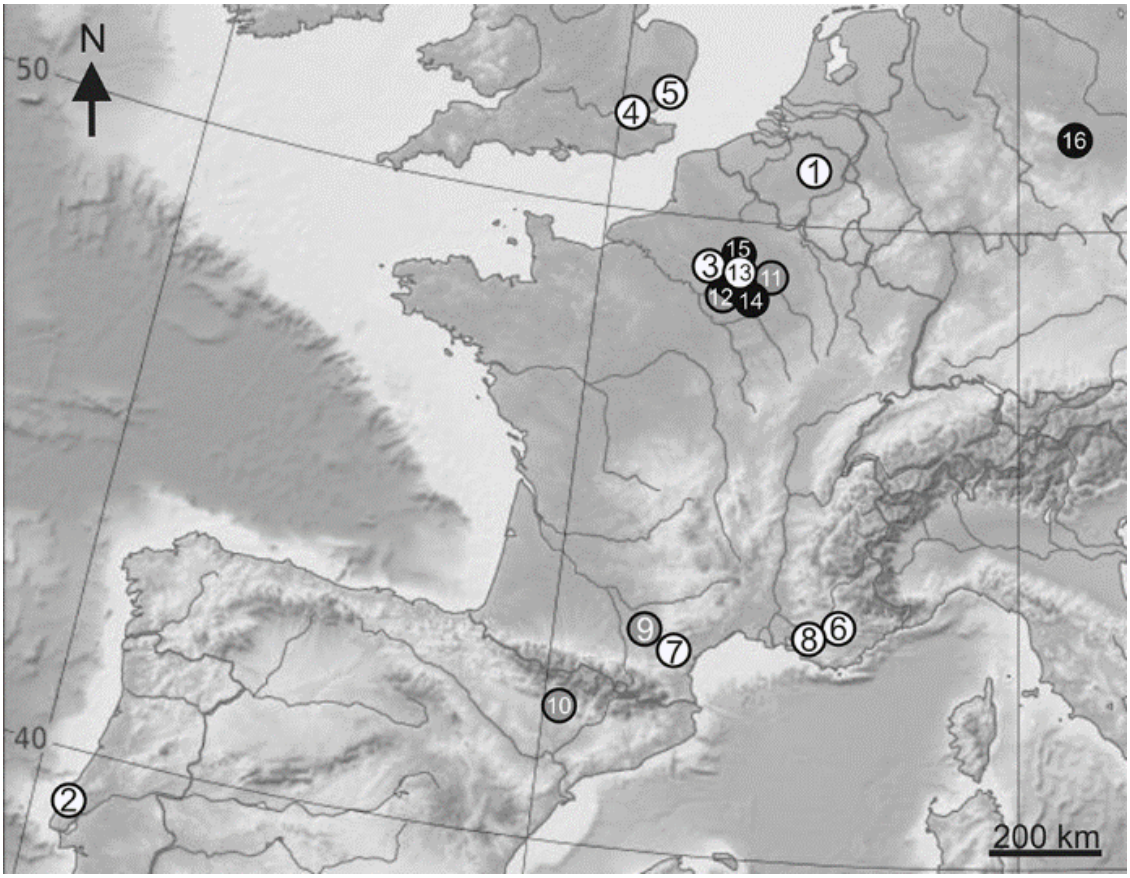
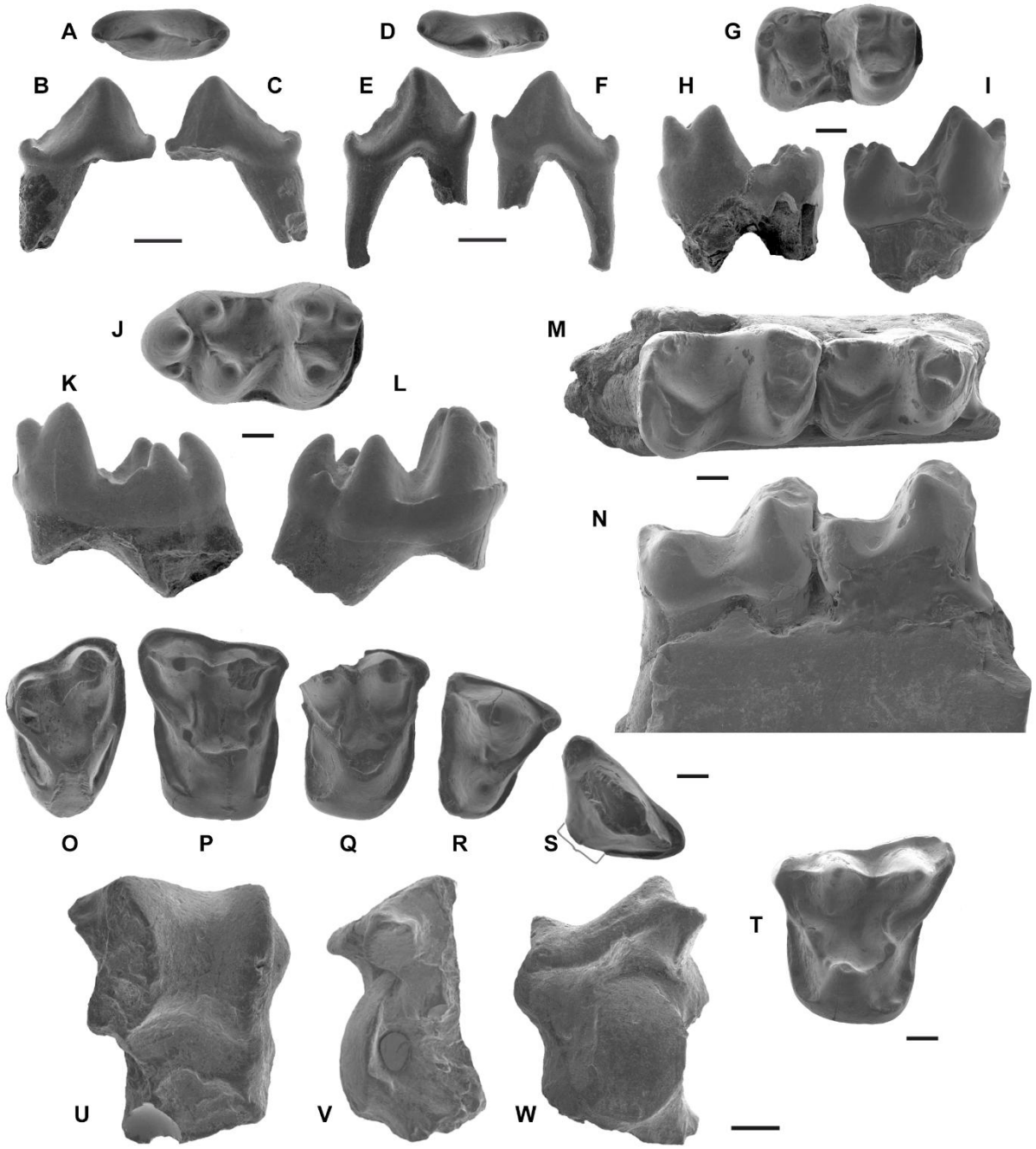


Figure 1. Map showing early Eocene *Diacodexis*-bearing localities in Europe (MP7, MP8+9, and MP10 localities are indicated by white, grey, and black circles, respectively): 1- Dormaal, Belgium; 2-Silverinia, Portugal; 3-Le Quesnoy, France; 4- Abbey Wood, UK; 5-Kyson, UK; 6-Rians, France; 7-Fordones, France; 8- Palette, France; 9-La Borie, France; 10- Corsà 0, Spain; 11-Avenay and Mutigny, France; 12-Condé-en-Brie and Saint-Agnan, France; 13-Pourcy, France; 14-Grauves, Cuis, and Mancy, France; 15-Prémontré, France; 16- Geiseltal, Germany.



1289

1290 **Figure 2**. Dental and postcranial remains of *D. antunesi* from Silveirinha Pequena, Baixo

1291 Mondego, Portugal. A-C, SNC 64, p2/3?; D-F SNC 386, dp2/3?; G-I SNC 93, m1; J-L, SNC

1292 63, m3; M-N, SNC 74, m1-2; O, SNC 18, M3; P, SNC 20, M2; Q, SNC 339, M1; R, SNC

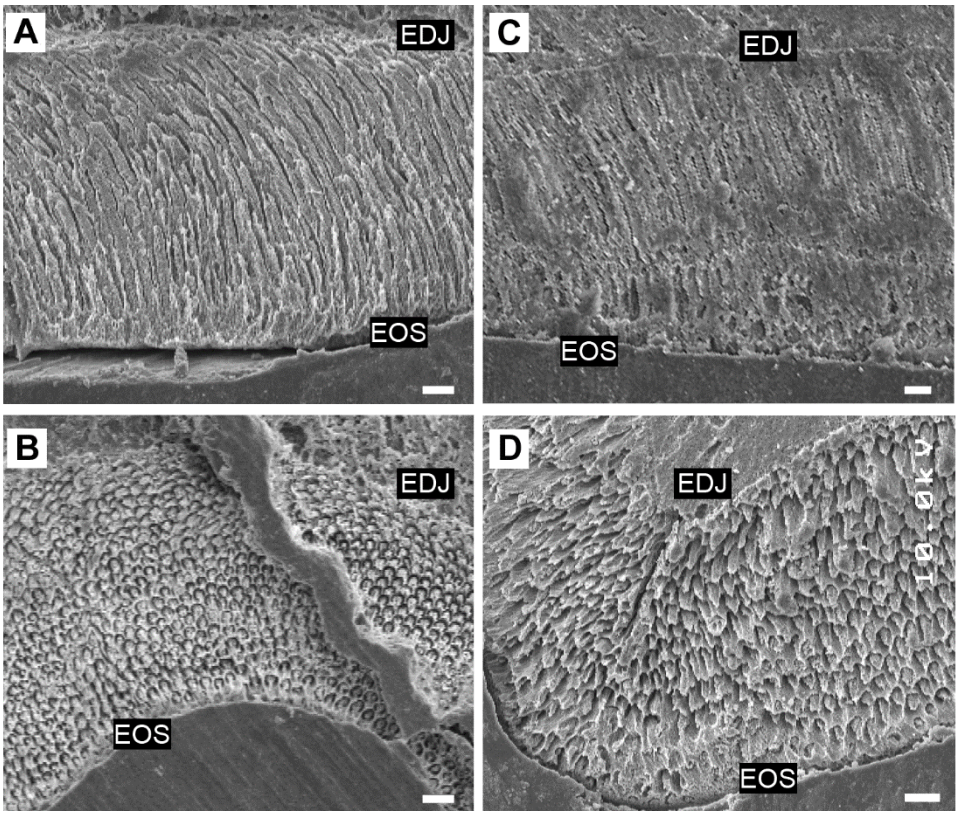
1293 311, P4; S, SNC 58, P3; T, SNC 13, dP4; U-W, SNC 687, astragalus. Views: A, D, G, J, M,

1294 O-T, occlusal; B, E, I, L, N, lingual; C, F, H, K, labial; U, anterior; V, lateral; W, posterior.

1295 Scale bars: A-F=1mm; G-T=0.5mm; U-W=1mm.

1296

1297



1298 **Figure 3**. Enamel microstructure in A-B, *D. antunesi* from Silveirinha Pequena, Baixo

1299 Mondego, Portugal and C-D, *D.* aff. antunesi from Fordones, Aude, France A-C horizontal

1300 plane, B-D tangential plane. Scale bar = 10µm.

1301

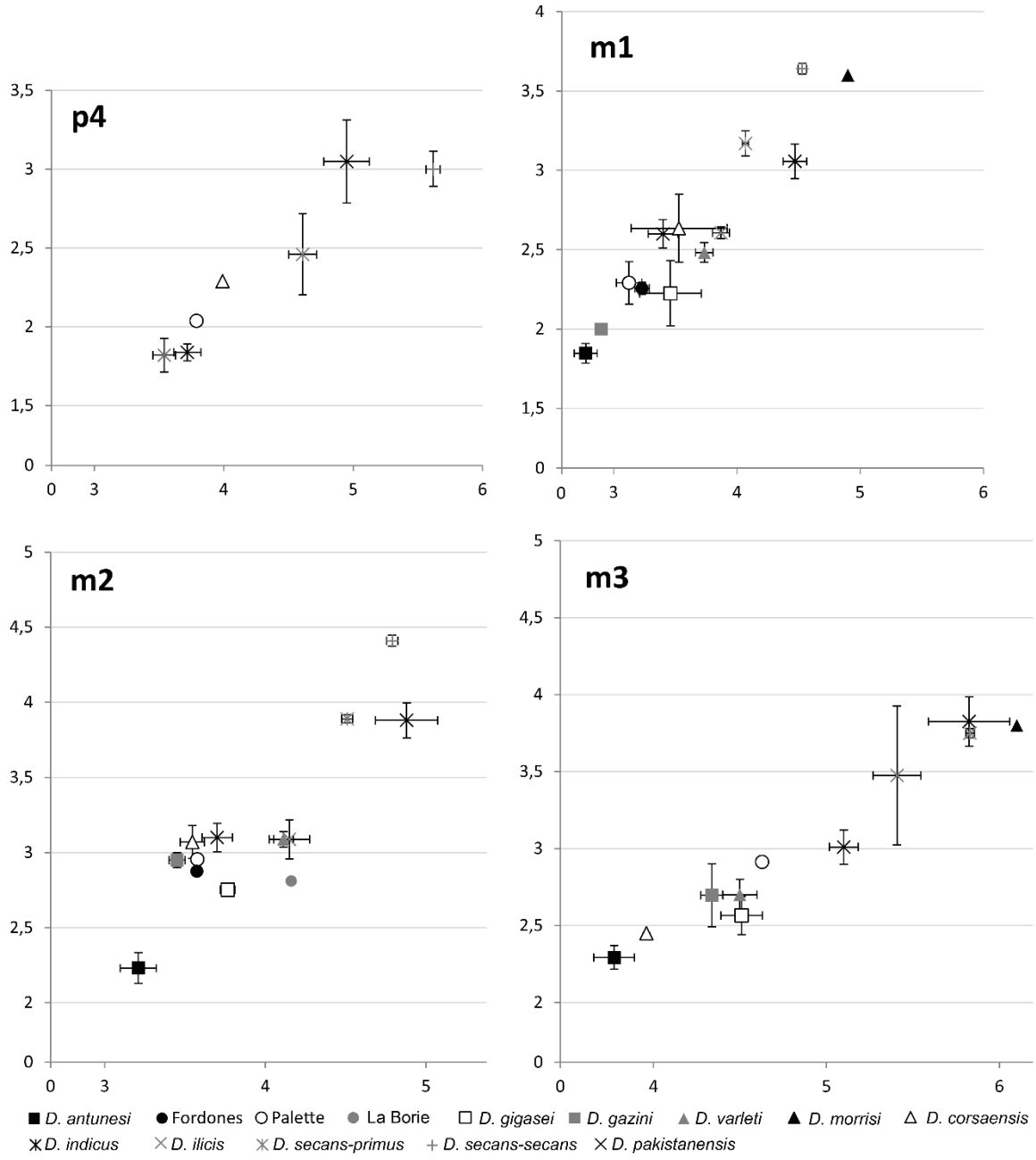
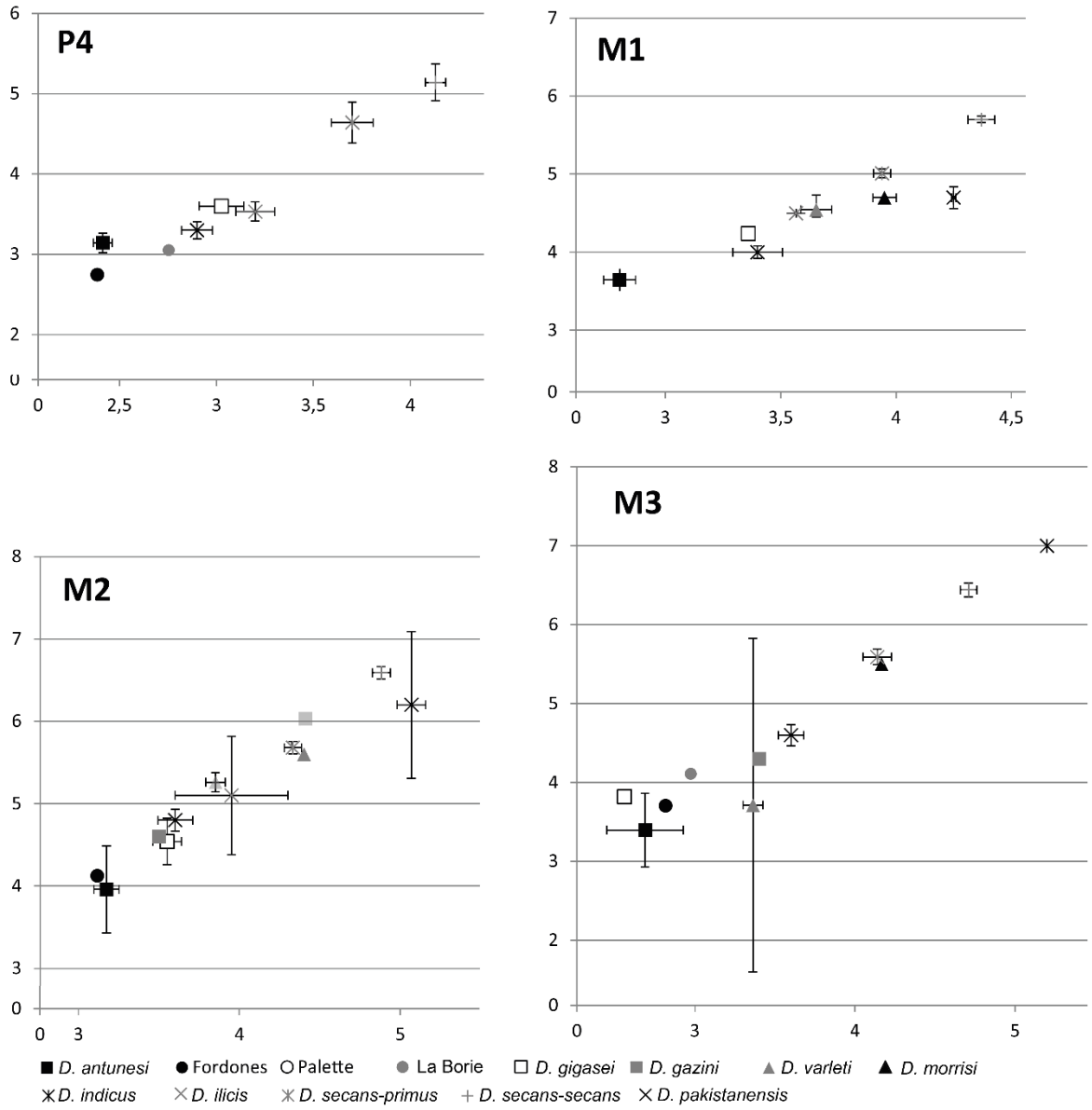


Figure 4. Biplots of lower dentition measurements with standard error. X=length, Y=width. Measurements from: *D. antunesi*, Estravis and Russell (1989) and Table 1; Fordonnes, Marandat (1991) and Table 3; Palette, Table 4; La Borie, Table 5; *D. gigasei*, Smith et al. (1996); *D. gazini*, Godinot (1981); *D. varleti*, Sudre et al. (1983); *D. morrisi*, Hooker (2010); *D. corsaensis*, Checa Soler (2004); *D. indicus*, Kumar et al. (2010); *D. ilicis*, Gingerich (1989) and Rose et al. (2012); *D. secans primus*, Krishtalka and Stucky (1985); *D. secans secans*, Krishtalka and Stucky (1985); *D. pakistanensis*, Thewissen et al. (1983).



1310

1311 **Figure 5**. Biplots of upper dentition measurements with standard error. X=length, Y=width.

1312 Measurements from: *D. antunesi*, Estravis and Russell (1989) and Table 1; Fordonnes,

1313 Marandat (1991) and Table 3; Palette, Table 4; La Borie, Table 5; *D. gigasei*, Smith et al.

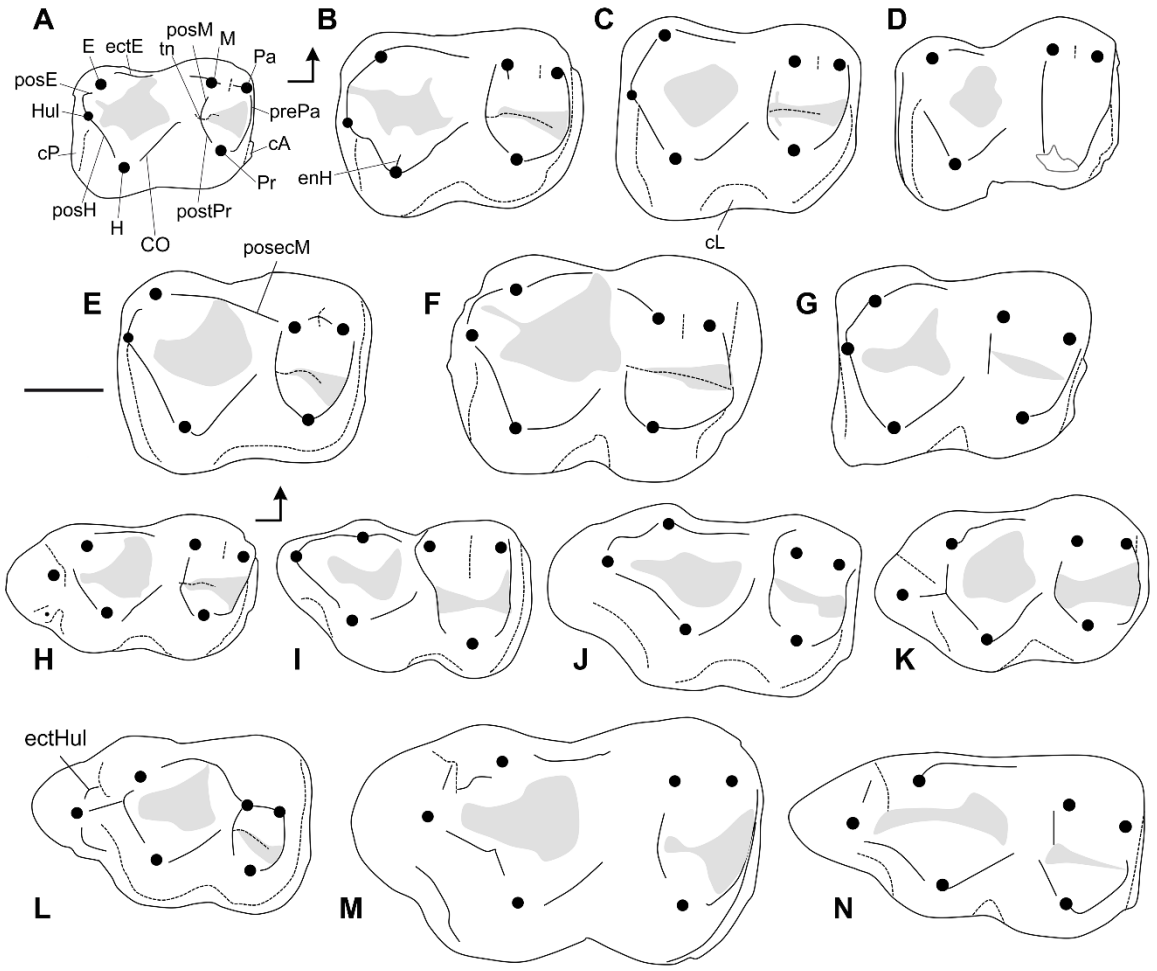
1314 (1996); *D. gazini*, Godinot (1981); *D. varleti*, Sudre et al. (1983); *D. morrisi*, Hooker (2010);

1315 *D. corsaensis*, Checa Soler (2004); *D. indicus*, Kumar et al. (2010); *D. ilicis*, Gingerich

1316 (1989) and Rose et al. (2012); *D. secans primus*, Krishtalka and Stucky (1985); *D. secans*

1317 *secans*, Krishtalka and Stucky (1985); *D. pakistanensis*, Thewissen et al. (1983).

1318



1319

1320 **Figure 6**. Lower dentition of *Diacodexis* species. A-G m2 of: A, *D. antunesi* SV3 338; B, *D.*

1321 *gigasei* IRScNB M 1815; C: *D.* cf. *gigasei* PAT 152; D: *D.* aff. *antunesi* FDN 125; E, *D.*

1322 *gazini* RI 163; F: *D. varleti* CB 1276, G: *D. pakistanensis* HGSP 300 5003. H-N, m3s: H, *D.*

1323 *antunesi* SNC 63; I, *D. gigasei* IRScNB M 116; J, *D.* cf. *gigasei* PAT 152; K, *D. varleti* CB

1324 579; L, *D. gazini* RI 162; M: *D. morrisi* M60060; N, *D. pakistanensis* HGSP 300 5003.

1325 Abbreviations: cP, posterior cingulid; cL, labial cingulid; cM, mesial cingulid; CO, cristid

1326 obliqua (= prehypocristid); ectE, ectoentocristid; ectHul, ectohypocristulid; enH,

1327 endohypocristid; E, entoconid; H, hypoconid; Hul, hypoconulid; M, metaconid; Pa,

1328 paraconid; posecM, postectometacristid; posE, postentocristid; posH, posthypocristid; posM,

postmetacristid; posPr, postprotocristid; prePa, preparacristid; Pr, protoconid; tn, trigonid notch. Modified after Kumar et al. (2010) and Orliac & Ducrocq (2011).

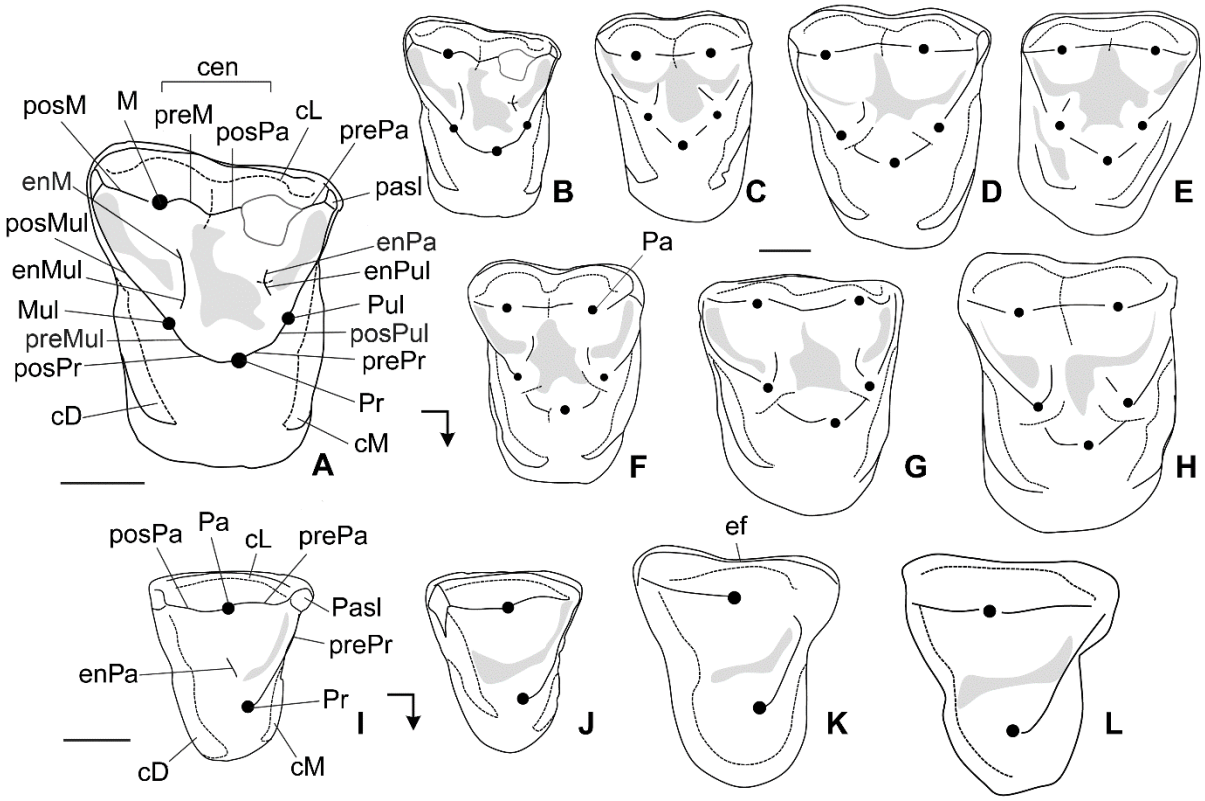


Figure 7. Upper dentition of *Diacodexis* species. A-H: M1 or M2 of: A-B, *D. antunesi* SNC 20; C, *D.* aff. *antunesi* FDN 283; D, *D. varleti* CB 973; E, *D. gazini* RI 168; F, *D. gigasei* IRScNB M 1820; G, *D. morrisi* M44943; H, *D. ilicis* USNM 538412. I-L: P4 of: I, *D. antunesi* SNC 311; J, *D.* aff. *antunesi* FDN 283; K, *D. gigasei* IRScNB M1822; L, *D. ilicis* USNM 538412. Abbreviation: cen, centrocrista; cD, distal cingulum; cL, labial cingulum; cM, mesial cingulum; ef, ectoflexus; enMul, endometacristule; enPr, endoprotocrista; enPul, endoprotocristule; M, metacone; Mul, metaconule; enPul, endoparacristule; Pa, paracone; Pasl, parastyle; posPa, postparacrista; posM, postmetacrista; posMul, postmetacristule; posMuld, postmetacristule deflection; posPr, postprotocrista; prePa, preparacrista; prePr, preprotocrista; preM, premetacrista; prePr, preprotocrista; Pr, protocone; Pul, protoconule. Modified after Kumar et al. (2010) and Orliac & Ducrocq (2011).

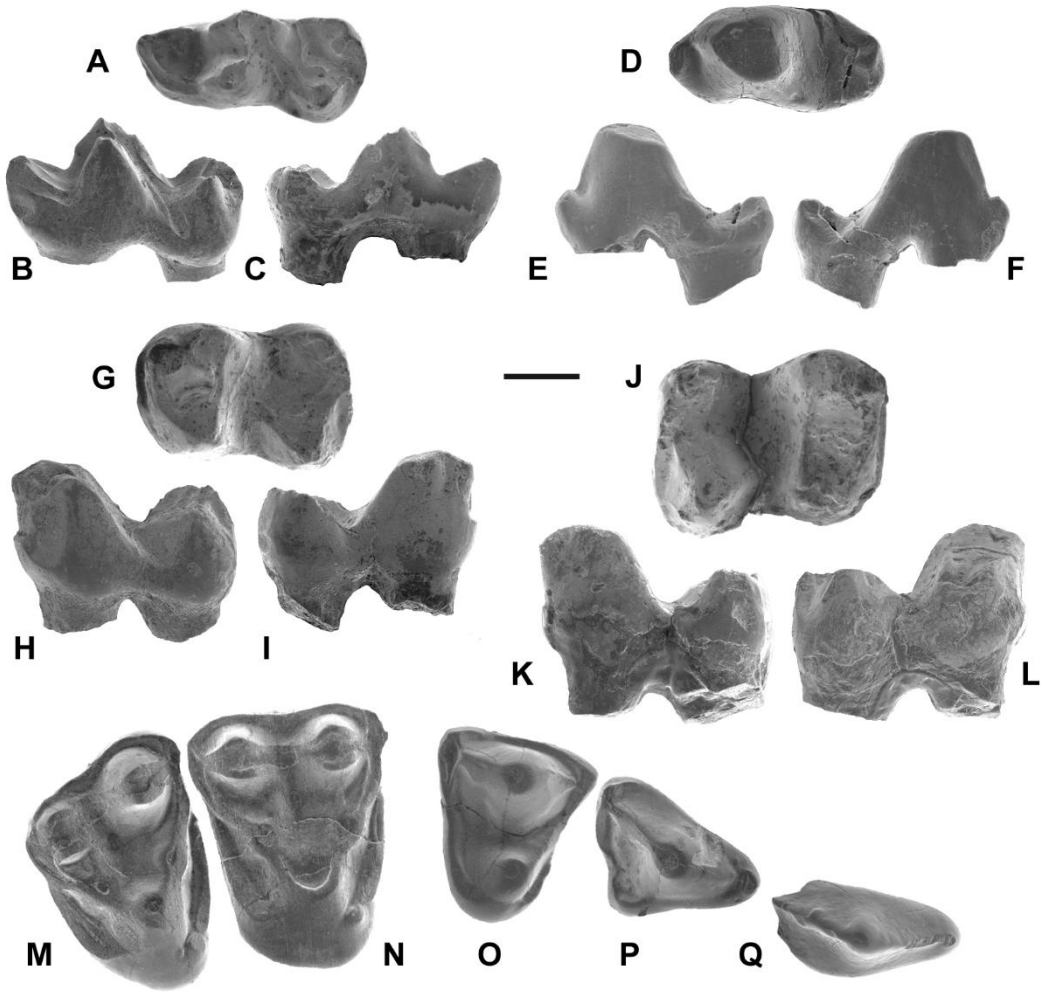
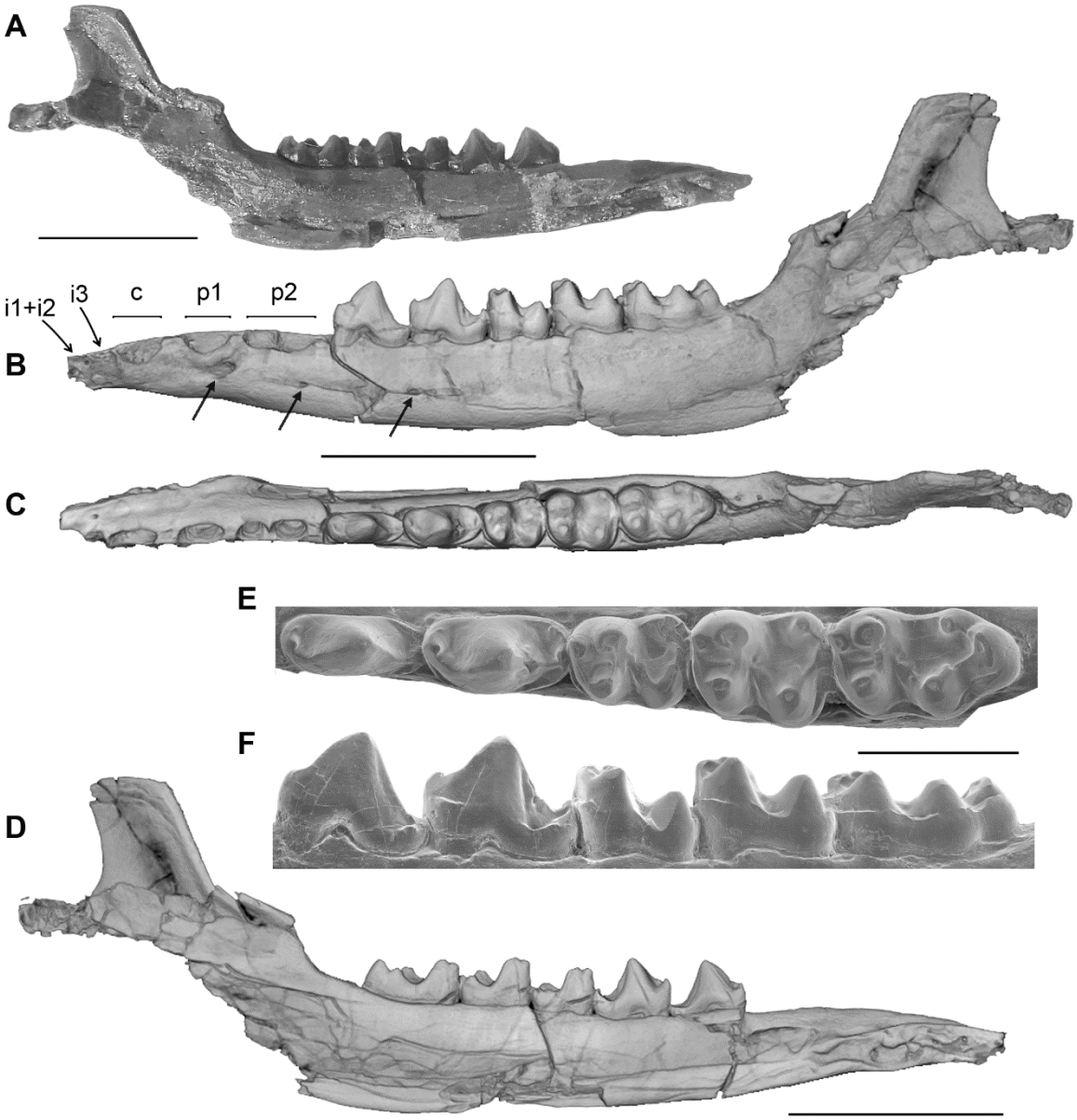


Figure 8. Dental remains of *D.* aff. *antunesi* from Fordones, Aude, France. A-C, FDN 123, dp4; D-F, FDN 279, p2 or p3; G-I, FDN 124, m1; J-L, FDN 125, m2; M-P, associated upper tooth row, from right to left M3, M2, P4, P3 (FDN 283); Q, P2 (FDN 252). All material figured at the same scale. Views: A, D, G, J, M-Q, occlusal; B, F, H, L, labial; C, E, I, K, lingual. Scale bar=1mm.



1351

1352 **Figure 9**. *Diacodexis* cf. *gigasei* from Palette. A, PAT 159 medial view; B-D virtual 3D

1353 model of PAT 159 in B, medial, C, occlusal, D, lateral views; E-F, details of the teeth row in

1354 E, occlusal and F, labial view. Arrows indicate location of mental foramina. Scale bars = 1cm

1355 for A-D, 5 mm for E-F.

1356

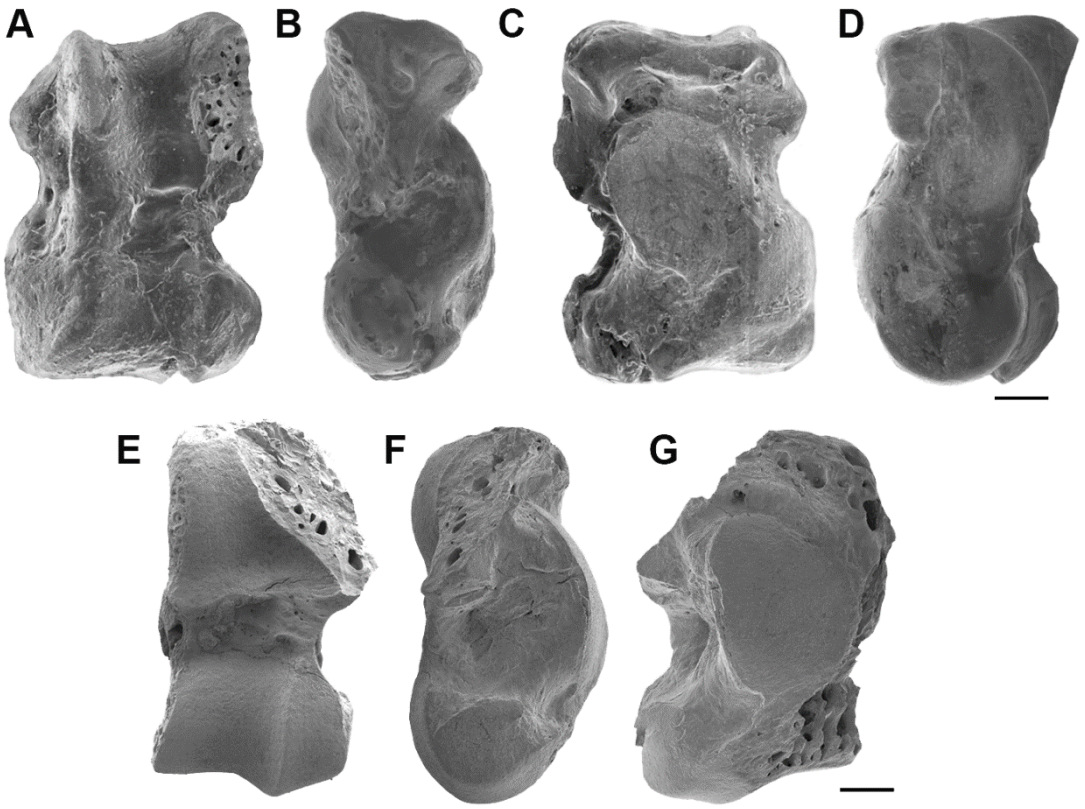


Figure 10. Astragali of *Diacodexis* cf. *gigasei* from Palette. A-D, left astragalus (PAT 19) in A, anterior; B, lateral; C, posterior; D, medial views; E-G, right astragalus (PAT 168) mirror view, in E, anterior; F, lateral; G, posterior views. Scale bars = 1 mm.

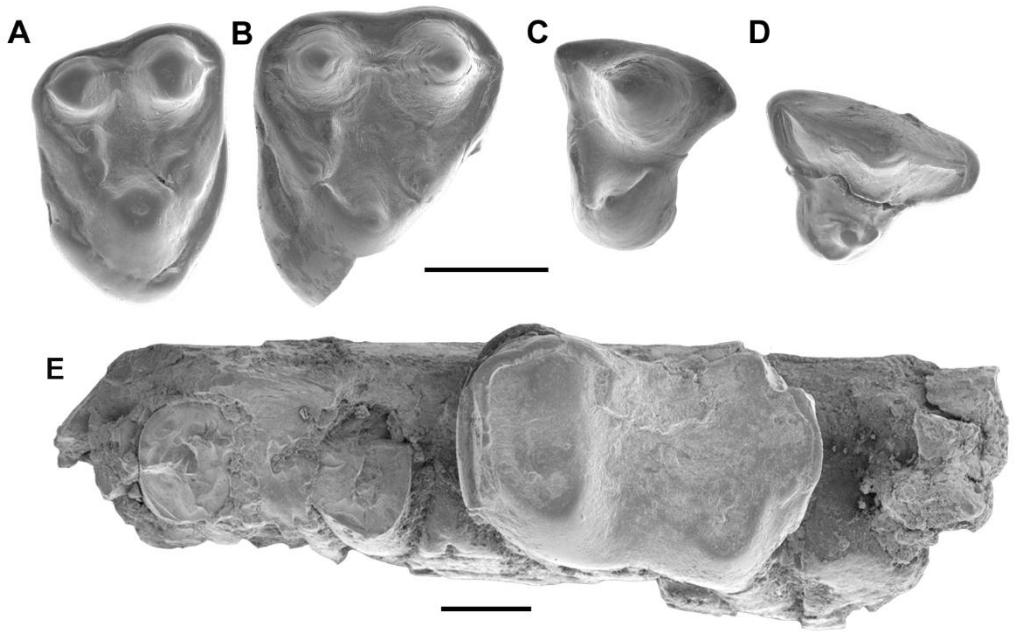


Figure 11. Dental remains of *Diacodexis* sp. from La Borie, Aude, France. A, BRI 4, M3; B, BRI 3, M2; C, BRI 2, P4; D, BRI 1, P3 ; E, MHNT.PAL.2017.21.2, m2 on a fragmentary dentary. Scale bars: A-D = 1.5 mm ; E = 1 mm.

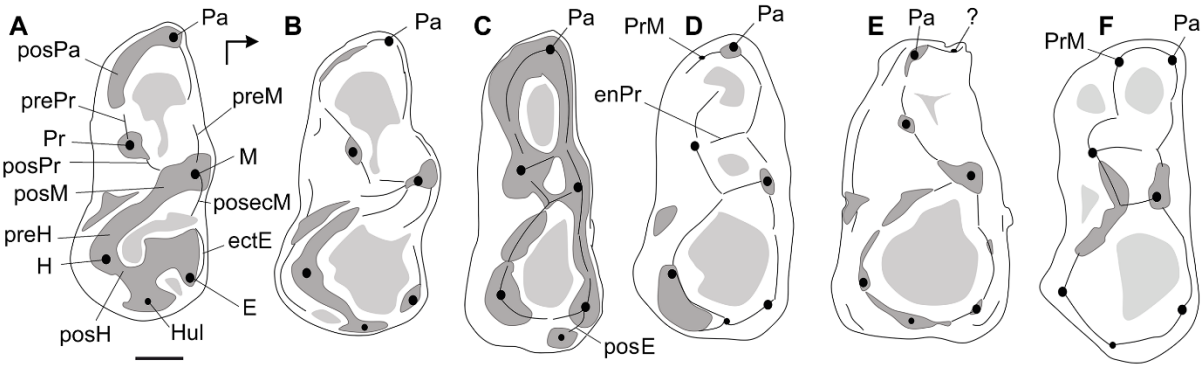


Figure 12. Schematic pattern of grooves and crests of the lower fourth deciduous premolar of Diacodexeinae and Eurodexeinae. A, *D.* aff. *antunesi* (FDN 123); B, *D. morrisi* (M63703; drawn after Hooker 2010:fig.48E); C, *Diacodexis indicus* (Gu 513; drawn after Kumar et al., 2010); D, *Diacodexis* sp. from Prémontré (UM PRE151); E, *D.* cf. *varleti* from Prémontré (SLP-29-PE 637) mentioned by Sudre and Erfürt (1996); F, Eurodexinae indet. from Prémontré (SLP 29PR 2122) according to Sudre and Erfürt (1996). Scale bar = 0.5 mm. Full lines originating from cuspids represent crests; dark grey surfaces represent worn surfaces; light grey surfaces represent basins. Abbreviations: ectE, ectoentocristid; E, entoconid; enPr, endoprotocristid; H, hypoconid; Hul, hypoconulid; M, metaconid; Pa, paraconid; posecM, postectometacristid; posE, postentocristid; posH, posthypocristid; posM, postmetacristid; posPa, postparacristid; posPr, postprotocristid; preH, prehypocristid; preM, premetacristid; prePa, preparacristitid; Pr, protoconid; prePr, preprotocristid; PrM, primonid.

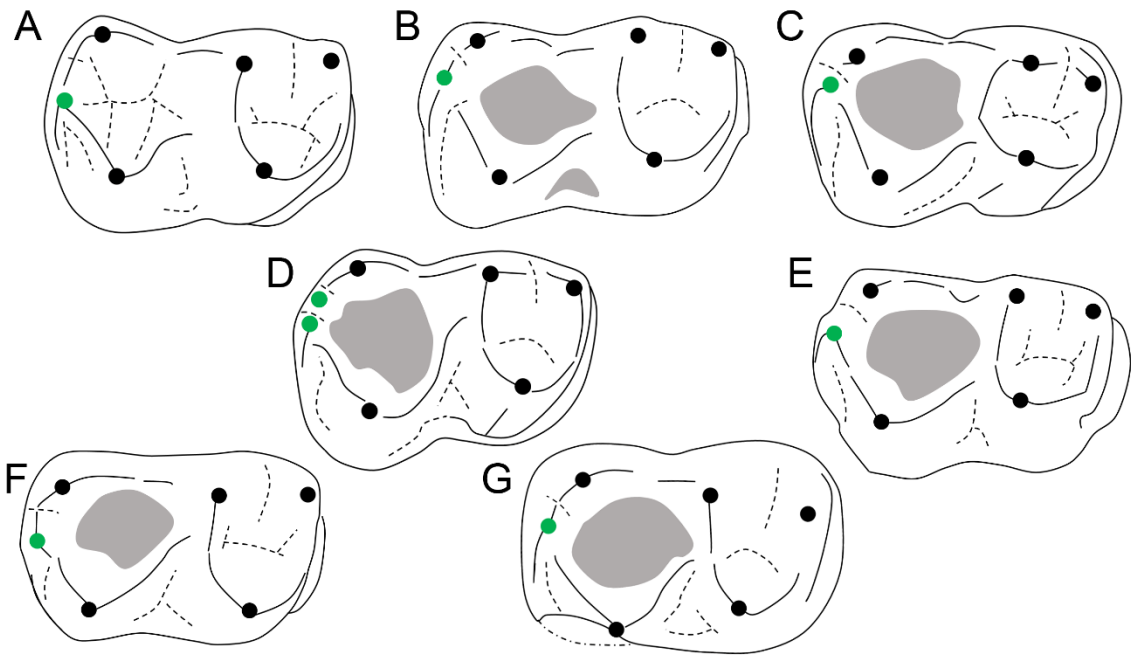


Figure 13. Schematic pattern of grooves and crests of the first lower molar in occlusal view of: A, *D. ilicis* (USNM 538371, after Rose et al., 2012: fig.51G); B, *D. antunesi* (SNC 63); C, *D. indicus* (GU 29, after Kumar et al., 2010: fig.7D, mirror view); D, *D. morrisi* (holotype, M83071, after Hooker, 2010: fig.47e), E, *D. varleti* (holotype, MNHN CB 255); F, *D. gigasei* (IRScNB M 1816, after Smith et al., 1996: pl. 1.2a); G, *D. gazini* (RI 165). Full lines originating from cuspids represent crests, dotted lines represent grooves, grey surfaces represent the basin of the talonid. The hypoconulid is highlighted in green. Not to scale.