Intraspecific variation of Eolophiodon laboriense, a basal Lophiodontidae (Mammalia, Perissodactyla) from the early Eocene of Southern France

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✡ Corresponding editor: Gilles Escarguel.

Abstract

The Lophiodontidae is an emblematic and well-documented Eocene family of perissodactyls from Western Europe. However, after more than a century and a half of studies, lophiodontids still display a complex systematics associated with blurry intraspecific variation and a poorly known early radiation. The locality of La Borie, located near the city of Toulouse, France, has yielded numerous remains of *Eolophiodon laboriense*. This abundance of remains allows for the first time the study of the intraspecific variation of a basal lophiodontid. The variation has been investigated for dental and cranio-mandibular characters, notably dental polymorphism, size variation and sexual dimorphism. The intraspecific variation of *E. laboriense* is high with more than 20 polymorphic characters of the dentition, including many additional crests and conules. This dental polymorphism is similar to the one observed in the Bartonian lophiodontid *Lophiodon lautricense*. *Eolophiodon laboriense* also displays an important degree of sexual dimorphism, with male specimens having broader and longer mandibles with

larger canines than females. Despite this high intraspecific variation, the low size variation of teeth and the consistency of diagnostic characters strengthen the validity of the genus *Eolophiodon* and does not impact the previous lophiodontid phylogeny.

Keywords:
Ypresian
Lophiodontid
Perissodactyl
Western Europe
Dental morphology
Polymorphism
Sexual dimorphism

1. Introduction

The Lophiodontidae is an iconic group of Perissodactyla from the Eocene of Europe, known from the Ypresian to the Bartonian (European Mammal Paleogene levels MP7 to MP16; Escarguel et al., 1997; BiochroM'97, 1997*)*. At its origin, the family appears to be endemic to the Southern France/Iberic peninsula bioprovince (Depéret, 1910; Cuesta Ruíz-Colmenares, 1994, 1996; Checa Soler, 1997*)*, and dispersed and diversified through Western Europe during the late Ypresian (~MP10; Stehlin, 1903; Jaeger, 1971; Sudre, 1971; Holbrook, 2009). Lophiodontids have a significant place in the biostratigraphy of the European Eocene (Depéret, 1910; Jaeger, 1971; Franzen, 1993; Labarrère and Montenat, 2011), despite a low taxonomic diversity (4 genera and 21 species; Remy, 2015) and a highly complex systematics (Cuesta Ruíz-Colmenares, 1994). Indeed, since Cuvier (1822), the accumulation of studies has brought unreliable characters, misinterpretations of diagnoses and many synonymies (Franzen, 1993). This problem is certainly correlated with the high degree of intraspecific variation, already mentioned by authors (e.g., Filhol, 1888; Cuesta Ruíz-Colmenares, 1994), but so far only carefully described in *Lophiodon lautricense* from Robiac (MP16; Sudre, 1971). In addition, the basal radiation of the group remains poorly documented. Early species are often known by few specimens, thus precluding intraspecific studies: *Lophiaspis maurettei* Depéret, 1910 (MP7-MP10), *Lophiaspis baicheri* Depéret, 1910 (MP8+9-MP10), *Lophiaspis occitanicus* Depéret, 1910 (MP10-MP15), *Lophiodon baroensis* Checa Soler, 1997 (MP10), *Lophiodon corsaensis* Checa Soler, 1997 (MP10), and *Eolophiodon laboriense* Robinet et al.,

2015 (MP 8+9).

Among these species, *Eolophiodon laboriense* was described based on one skull discovered from La Borie (MP8+9; Robinet et al., 2015). Since then, the type-locality has yielded more than 100 remains, allowing a description of the intraspecific variation of this basal lophiodontid. We therefore analyze hereafter the variation of *E. laboriense* through the analysis of polymorphic dental characters, biometric variation of teeth, and sexual dimorphism through a statistical approach including principal component analysis of the mandibles and comparisons with the variation of other lophiodontids to test the validity of *E. laboriense.* In addition, we test the impact of this variation on previously published lophiodontid phylogenetic analysis.

2. Geological setting

Fossil material has been excavated from the clay quarry of La Borie at Saint-Papoul, near the city of Carcassonne in Southern France (Laurent et al., 2010). Seven fossiliferous levels noted SP0 to SP6 belong to the formation of the “argiles rutilantes d'Issel”. These levels correspond to sandstone beds (SP0-1-5) or thin layers of grey clays rich in organic matter (Level SP2-3-4-6) intercalated within thick ochre clay layers (Laurent et al., 2010). The vertebrate remains include fresh and saltwater fishes, crocodiles, turtles (Claude and Tong, 2004), birds (Bourdon et al., 2016) and numerous mammals which indicate an early Eocene age close to the MP8+9 level (Laurent et al., 2010). The mammal fauna consists of chiropterans, primates, a condylarth, a tillodont, a creodont and a mesonychid (Laurent et al., 2010; Solé et al., 2016). The perissodactyls are represented by three species, among them two lophiodontids. *Eolophiodon laboriense* is the largest and most abundant herbivorous mammal of the locality (Robinet et al., 2015); another, new lophiodontid is also present and currently under study.

3. Material and methods

3.1. Material

The material, collected over the last ten years, mostly consists of dental remains. The material presented in this study consists of 48 specimens including 13 mandibles, with 2 complete and 6 fragmentary crania. The material illustrated in this paper belongs to the collections of the Museum d’Histoire Naturelle de Toulouse (MHNT) and University of Montpellier (UM). The rest of the specimens belong to five private collections; casts of all these specimens are deposited at the UM collection. The complete material is listed in Table

1. The material from the APSO (Association Paléontologique du Sud Ouest) collection follows the denomination APSO.20XX.SPX-X; these specimens are here abbreviated as A.XX.SPX-X. Specimens from the other amateur collections are abbreviated as STP-XX.

3.2. Methods

We refined the dental terminology, illustrated in Fig. 1, by naming some cristae never or rarely described such as those proposed by Boisserie et al. (2010) for Artiodactyla. We use this terminology to avoid some ambiguous terms (e.g., the pseudometaloph; Dedieu, 1976) and for a better understanding of homology within lophiodontids. This terminology is consistent with the terminology of Hooker (1989) with some exceptions. On upper teeth the mesostyle is renamed ectostyle. The term preparaconule crista is shortened in preparacristule. On lower molar, the cristid obliqua is renamed as prehypocristid, the paracristid as preprotocristid, and the mesostyle as postectometacristid. Further details are provided in the caption of Fig. 1.

Cranio-mandibular measurements are illustrated in Fig. 2. We calculate an unbiased coefficient of variation (CV) for each of the dental and mandibular measurements in order to test the homogeneity of size distribution (Gingerich, 1981; Table 2). We describe each polymorphic character with its frequency, based at least on eight specimens. We gather specimens in age classes to estimate how ontogeny impacts variation. These age classes are based on tooth eruption and wear pattern as has been done for rhinoceroses (Hitchins 1978) and artiodactyls (Lihoreau et al., 2014). We use canine and mandibular size to sex a priori the individuals; then we apply statistical approaches to confirm putative dimorphism. Such an analysis to sex fossil perissodactyls has already been done using Student t-tests (Chen et al., 2010; Mead, 2000). However, considering the low number of specimens, we use here a non-parametric Wilcockson test to discriminate males and females. In addition, we perform a principal component analysis (PCA) with the Spearman method to discriminate male and female morphospaces on mandibular characters. The Dimorphic Ratio (mean male/mean female) is then calculated on mandibular characters (Table 3). The dimorphic ratio is calculated with the “method-of-moments” technique (Josephson et al., 1996, Missiaen et al., 2012) on dental characters (Table 2). Differences in body masses between males and females were estimated using size estimation equations based on molar lengths and areas (Legendre, 1989; Damuth, 1990; Janis, 1990) and mandibular measurements (Janis, 1990; Table 3).

Finally, we perform a cladistic analysis to test the impact of polymorphism on an already known lophiodontid phylogeny. This analysis is based on the matrix of Robinet et al. (2015)

with inclusion of the polymorphism observed in *Eolophiodon laboriense* and *Lophiodon lautricense*. The polymorphism has been coded as (0+1) in 27 characters for *E. laboriense* and 14 characters for *L. lautricense,* for a total of 32 characters (Appendix A). We analyze the matrix using heuristic search option in Paup* 4.0α162 (Swofford, 2002) with 1000 replications. The consistency and retention indices, as well as Bremer indices for each node are compared to previously published results (Robinet et al., 2015).

4. Results

The exhaustive description of the holotype (the only known specimen until this study) is available in Robinet et al. (2015). Based on new specimens, we complete the description of the species, emphasizing dental character variation (Figs. 3, 4) and cranio-mandibular morphology. A synthesis of dental morphology is provided on Fig. 3. By comparing the unbiased coefficients of variation (CV), the sexual dimorphism ratios (DR) and discrete sample variations samples from each stratigraphic levels, we observe homogeneity between intra- and inter-level variations.

4.1. Variation in upper teeth

The unbiased coefficients of variation (CV) for the upper teeth measurements are low. All the dental loci display a CV lower than 10 for width and length, except P2 width (CV = 11.13; Table 2).

P2 bears several discrete characters that are present in few specimens (Fig. 3). Lingual to the paracone, half of the specimens (4/8) lack the endocrista which is present in the holotype (Figs. 3, 4(D, E)). A round, small and blunt paraconule is present in 25% (2/8) of P2s (Figs. 3, 4(E, F)). Moreover, 25% (2/8) of P2s bear a small and curved postprotocrista (e.g., MHNT.19.3.1; Fig. 4(A, F)).

P3 is the most variable upper tooth (Fig. 3). The variation mostly concerns the presence or absence of a supplementary crista (Figs. 3, 4). Lingual to the paracone, 20% (2/10) of P3s lack the endoparacrista (Fig. 4(D, F)). The absence of this crest is not linked to wear, as older individuals have a still visible endoparacrista (MNHT.PAL.19.3.1, STP-V1, STP-V3, MHNT.PAL.2018.3.4; Fig. 4(E, G)). In contrast to the holotype (Fig. 4(D)), 80% (8/10) of P3s display a postprotocrista. This crista is straight and salient in young specimens; on older specimens, it is worn on its middle-part. In 50% (5/10) of the specimens, the endometacrista contacts the postprotocrista (Figs. 3, 4(B-F)) and forms a metaloph. The protocone is extended distally by an endoprotocrista in 50% (5/10) of the specimens (Fig. 4(F)). Moreover,

20% (2/10) of the specimens bear a blunt paraconule on the preprotocrista (MHNT.PAL.2018.3.4, STP-L12; Fig. 4(F)).

P4 is less variable than P3 (Fig. 3). Contrary to P3, all teeth bear an endometacrista and a salient postprotocrista (Fig. 4(B, E-G)). On unworn P4s, the two crista are salient and form a metaloph. This contact is lacking in the holotype due to wear (Robinet et al., 2015). The endoprotocrista is present in two specimens (STP-V4, MHNT.PAL.2018.3.5; Fig. 3(F)). Furthermore, only two specimens (STP-V1, A.08SP1-82) have a small paraconule.

Upper molars of *E. laboriense* are less variable than P2 and P3. All M1s and M2s are both quadrangular and present the typical bilophodont structure of lophiodontids. Some specimens (e.g., MHNT.PAL.2018.3.2, MHNT.PAL.2018.3.4, STP-V1) show a labial convexity of the metacone (Fig. 4(C-E)) instead of being flat (Fig. 4(F, G)). Most M3s have a triangular outline, but some specimens (e.g. MHNT.PAL.2018.3.3) are more trapezoidal with a longer metaloph (Fig. 4(D)).

Variation of the upper molars mostly concerns the presence or absence of the endoparacrista and the presence of the ectostyle between the paracone and metacone. The endoparacrista can be long and salient (e.g., STP-V8, STP-V1) or broad and faintly bumped (e.g., A.16.SP0-15, STP-V4). However, 30% (3/10) of M1s lack the endoparacrista, whatever the wear stage (Fig. 4(D, E)). The endoparacrista is also absent in 22% (2/9) of M2s and in 10% (1/10) of M3s (Fig. 4(C)). The ectostyle is low, small and does not reach the paracone and metacone. In 36% (4/11) of M1s, 20% (2/10) of M2s, and 40% (4/10) of M3s, the labial cingulum is reduced and does not bear any ectostyle (Fig. 4(C, D)). There is no significant cingulum variation. The cingulum does not bear any trace of accessory conule. The only noticeable variation is a slight thickening of the labial cingulum on premolars (e.g., STP-V8) and on the mesial and/or distal cingula on molars (e.g., MHNT.PAL.2018.3.4; Fig. 4(C, G)).

4.2. Variation in lower teeth

The unbiased coefficients of variation for the lower teeth measurements are low. All the dental loci display a CV < 10 for width and length, excepting for p2 and p3 measurements (Table 2).

Lower premolars are slightly polymorphic (Fig. 3). The p2s vary in prehypocristid height. On the holotype, the prehypocristid is not prominent and below the protoconid mid-height, whereas 55% (6/11) of the specimens display a salient and higher cristid. This variation is not linked to the stage of wear, as some young individuals (STP-V16, STP-V3, STP-V19) display low cristid and some old individuals retain a salient one (e.g., MHNT.PAL.2018.3.10). The

paraconid on p2s occurs in 40% (4/10) of the specimens (Fig. 5(A, J)). The paraconid is present in half of the p3s (8/16; Fig. 4(C, D)). As shown by the specimens STP-S3, STP-V24 or MHNT.PAL.2018.3.10, the presence or absence of the paraconid on p3 is independent to its presence or absence on p2. The paraconid is always absent on p4s. The lower premolars also vary on talonid width. In some specimens, the talonid is slightly larger than the trigonid. The trigonid/talonid width ratio varies from 1 to 1.25 for the p3s and from 1 to 1.15 for the p4s.

All lower molars follow the same bilophodont pattern. The m1s and m2s are quadrangular, while m3s are more elongated due to the presence of a large hypoconulid lobe. Lower molars present great variation on the postectometacristid and preentocristid (Fig. 3). On most specimens, the postectometacristid is small but salient (Fig. 5(G, H)). In other specimens, the postectometacristid is blunt and less visible or absent (Fig. 5(I, J)). The postectometacristid is present in 77% (10/13) of m1s, 88% (15/17) of m2s, and 87% (13/15) of m3s. The preentocristid is generally short, straight and forms an acute angle with the hypolophid (Fig. 5(G, J)); in some specimens (e.g., MHNT.PAL.19.3.2), it is broad and blunt (Fig. 5(I)) or absent (Fig. 5(H)). This cristid can be partially erased by wear, but its basis is still observable (Fig. 5(J)). However, the character could not be observed in most worn teeth. The preentocristid is present in 73% (11/15) of m1s, 89% (16/18) of m2s, and 94% (15/16) of m3s where it can be seen. Presence of both cristids is independent of the other (Fig. 5(H, I)). On m1 and m2, the prehypocristid typically reaches the base of the protolophid; this connection is less distinct on m3s. Indeed, in 37.5% (6/16) of the m3s, the prehypocristid is short and there is no contact with the protolophid (Fig. 5(J)). In lower teeth the cingulid shows no remarkable variation except a slight thickening on the labial side on some specimens.

4.3. Variation in canines

Upper canines are not preserved on the holotype. New canine specimens are mesiodistally long and labiolingually compressed. They are slenderer and less conical than lower canines (Fig. 4(A)). There is no cingulum at the base of the crown and no sharp mesial and distal crests. The root is long and broad mesiodistally. The upper canines display a great mesial wear surface due to contact with their lower counterparts. The specimens do not show any notable size variation.

The lower canines are broad, conical and are curved like a fang. There is size and morphological variations (Figs. 6, 7) between male and female specimens. Whereas males have more curved canines with higher crown and broader roots (Fig. 6(A); Table 3), females have smaller and straighter canines (Fig. 6(B); Table 3). Unfortunately, the number of

specimens is too low to estimate meaningful unbiased coefficients of variation and to run statistical tests (Table 3). However, the two sexes occupy clearly distinct morphological spaces well separated on the first and second axes of the PCA, altogether explaining 89.7% of the overall variation (Fig. 7). The primary axis is principally composed of the width and the mesio-distal length of the canine (ctr = 54% and 37.8%, respectively); the second axis is dominated by the crown height (ctr = 72%).

4.4. Variation in mandibles

Mandibles of *E. laboriense* are sexually dimorphic (Figs. 6, 8). Male mandibles, including the holotype, are broad and massive (Robinet et al., 2015). Indeed, males (Fig. 6(A)) have a great mandibular height below the cheek teeth and bear large canines. The angle of the mandible is enlarged caudo-ventrally. It shows a broad margin with prominent insertion marks for the masseter muscle. In comparison, female mandibles (Figs. 6(B), 8(A, B)) are slenderer and significantly shorter ($p < 0.05$), with a shorter diastema ($p < 0.05$; Table 3). They also have a significantly lower mandibular corpus ($p < 0.03$; Table 3). The angle of the mandible is less extended ventrally with a significantly lower depth ($p = 0.01$; Table 3). Also, the muscular insertions of the masseter are less marked on females (Fig. 6). Finally, female mandibles also bear smaller canines.

The PCA in Fig. 8 shows a clear distinction of the morphological spaces occupied by each sex. The distinction occurs primarily on the first axis, which explains 45.1% of the overall observed variation. The variables which contribute the most to this axis are the length of the mandible (ctr = 25.8%), the depth of the mandibular angle (ctr = 27.4%), the length of the mandibular angle (ctr = 13.9%), and the height below the molars (ctr = 12.6%).

We also observed variation independent of the sex. Most of the mandibles are indeed thin rostrally, with a lateral post canine constriction. However, 45% of the specimens present a laterally enlarged post-canine diastema. The coronoid process of the holotype is slanted rostrally and partially overhangs the m3 (Fig. 6(A)). In other specimens, the process is more vertical and never overhangs the molars (Fig. 6(B)).

4.5. Variation in the cranium

All crania share similar proportions and do not present a great variation in total length. However, the canine-P2 diastema length shows a slight metric variation. The maxilla is slightly concave above the diastema in all the specimens and does not present variation in width in contrast to the mandibles.

Caudally, the specimens which preserve the parietal region (MHNT.PAL.19.3.1, MHNT.PAL.2018.3.4, A.07.SP2-79, A.09.SP5-45 and A.13.SP2-276) present high sagittal crests and broadly extended nuchal crests. The specimens MHNT.PAL.2018.3.4, A.07.SP2-79, A.09.SP5-45 and A.13.SP2-276, which are both better preserved than the holotype for this cranium area, present nuchal crests which form a flat angle.

The two most complete specimens (MHNT.PAL.19.3.1 and MHNT.PAL.2018.3.4) present great metric variations on their jugals. The holotype presents high and narrow zygomatic arches (Robinet et al., 2015), whereas MHNT.PAL.2018.3.4 has narrow but dorsoventrally thinner arches. On their maximal height, the zygomatic arch of MHNT.PAL.2018.3.4 is two times smaller than in the holotype (Table 4).

MHNT.PAL.2018.3.4 presents also a rounder and broader glenoid cavity than the holotype (Table 4). Furthermore, the postglenoid process of MHNT.PAL.2018.3.4 is laterally and caudally thicker and ventrally two times longer (Table 4) that in the holotype. In ventral view, MHNT.PAL.2018.3.4 and the holotype share the same morphology.

4.6. Cladistic analysis

The analysis of Robinet et al's (2015) dataset with inclusion of the polymorphism observed in *Eolophiodon laboriense* and *Lophiodon lautricense* (Appendix A) returned three most parsimonious trees of 422 steps (CI = 0.45; RI = 0.52). The consensus topology is identical to that proposed by Robinet et al. (2015; Fig. 9). However, the value of Bremer indices for 9 nodes out of 13 differ from this latter. These indices are higher on most of the nodes within Lophiodontidae, but are weaker for the nodes grouping *Eolophiodon* with *Lophiodon* and *Paralophiodon*, Lophiodontinae with Ancylopoda, and *Cardiolophus* with *Phenacodus* (Fig. 9).

4.7. Systematic paleontology

Perissodactyla Owen, 1848

Tapiromorpha *sensu* Hooker, 1984

Tapiroidea Gray, 1825

Lophiodontidae Gill, 1872

Lophiodontinae Gill, 1872

Genus ***Eolophiodon*** Robinet, Remy, Laurent, Danilo et Lihoreau, 2015

Type and only species: *Eolophiodon laboriense* Robinet, Remy, Laurent, Danilo et Lihoreau, 2015

Diagnosis: same as the type and only species.

Eolophiodon laboriense Robinet, Remy, Laurent, Danilo et Lihoreau, 2015

Holotype: complete skull from La Borie (collections of the Natural History Museum of Toulouse): MHNT.PAL.2010.19.3.1, cranium with right P2-M3 and left P3-M3, incisors and canines missing; MHNT.PAL.2010.19.3.2, mandible with p2– m3 on both sides, incisors and left canine missing.

Hypodigm: see Table 1.

Type and only locality: La Borie (Aude Department, Southern France), ‘‘argiles rutilantes d’Issel’’ Fm. (MP8-9; Ypresian, early Eocene) (Laurent et al., 2010).

Emended diagnosis: small Lophiodontidae with a relatively narrow braincase and reduced preglenoid process on the cranium. No metacone on P2; endometacrista on P3; paracone and metacone close together but not fused on P4; incomplete protoloph and metaloph on P3 and P4; entoconule missing on P4. No distinct paraconule but ectostyle present on upper molars. Prehypocristid directed to the middle of the protolophid on lower molars; wide hypoconulid on m3 surrounded by a complete cingulum.

Emended differential diagnosis: Larger than *Lophiaspis* and smaller than known *Lophiodon* and *Paralophiodon*, except for *L. baroensis*. Differs from *Lophiaspis* in having a paraconule of moderate size on upper molars, a prehypocristid directed to the middle of the protolophid, and a wide hypoconulid on lower molars. Differs from *Lophiodon* and *Paralophiodon* in having only one labial cusp on P2, a postglenoid foramen, a torus surrounding the choanae and a mandibular symphysis ending at the level of p2. Differs from *Lophiodon* in lacking an entoconule on P4. Differs from *Paralophiodon* and *Lophiodon* in possessing an incomplete protoloph on P3.

Remarks: Despite the high dental variation observed, all the specimens from La Borie display the following diagnostic characters of *E. laboriense* (Robinet et al., 2015): a unique labial cusp on P2; paracone and metacone close together but not fused on P4; incomplete protoloph on P3 and P4; no labial furrow on P3; no entoconule on P4; paraconule present on the protoloph; and wide hypoconulid on the m3. However, two diagnostic characters are variable in the sample: the prehypocristid of m3 that can join the protolophid, and the vertical process of the mandible that is not slanted rostrally on most of the specimens. Nevertheless, most of the variation of *Eolophiodon* occurs on characters that differentiate *Lophiodon* from *Paralophiodon*, and not those that define the genus *Eolophiodon*. Moreover, the low unbiased coefficient of variation of each tooth locus (Table 2) and the homogeneity of the intra- and

inter-level variation is consistent with the presence of only one species in the sample (Gingerich, 1981; Sudre, 1971). Thus, despite the high variation observed, all specimens can be attributed to *E. laboriense*. The status of the genus is not impacted by the variation, and *E. laboriense* remains valid.

Furthermore, many characters used by Robinet et al. (2015) in the differential diagnosis now appear to be variable. It is the case for most of the characters that differentiate *Eolophiodon* to *Lophiodon* and *Paralophiodon*: presence of the endometacrista on P3, presence of an ectostyle on molars, contact of the prehypocristid with the protolophid on m3. Last, the variable presence of ectostyle in *Eolophiodon* upper molars and the incomplete metaloph on P4 cannot be used in the differential diagnosis to differentiate *Eolophiodon* from *Lophiaspis*.

5. Discussion

5.1. Comparison of dental variation within the Lophiodontidae

The variation observed in *E. laboriense* is important, with more than 20 dental variable characters and a strong variation of mandible morphology between sexes. Given the high intraspecific variation of lophiodontids known since Filhol (1888), these results are not surprising. Because of the lack of revision of Ypresian/Lutetian lophiodontids, we will focus our comparisons on a younger species, *Lophiodon lautricense*. The following comparison is based on an intraspecific variability study of *L. lautricense* (Sudre, 1971) and newly available specimens from the UM collection (measurements in Table S1, Appendix B).

The unbiaised coefficients of variation for each tooth locus of *Eolophiodon* are similar to that observed in *L. lautricense* (Sudre, 1971). These coefficients are not high (almost always < 10) and are characteristic of a homogeneous size distribution, which is common for most mammal species (Gingerich, 1981; Sudre, 1971).

The polymorphism observed in *E. laboriense* teeth is similar to that of *L. lautricense* present in the UM collection. Both taxa have highly polymorphic teeth and most of the characters are homologous between *E. laboriense* and *L. lautricense*. The upper dentition is more variable than the lower dentition in *L. lautricense*, as in *E. laboriense.* The upper premolars are the most polymorphic teeth, with the majority of the variable characters located on the distal crest. In *L. lautricense,* this crest is formed labially by the endometacrista, and lingually by the prehypocrista. As in *E. laboriense*, both parts of the distal crest can be present, reduced or totally absent. However, P4s of *L. lautricense* bear more polymorphic characters than in *E. laboriense* and are more variable. The endometacrista is absent in 28%

(7/29) of the P2s, 17.5% (6/40) of the P3s, and 12.5% (3/24) of the P4s. The prehypocrista is less frequent than the postprotocrista of *E. laboriense*, and is present in only 20.5% (8/39) of the P3s and 21% of the P4s (5/24). The paraconule is totally absent in P2s and P3s, but is still present in one P4 specimen (Sudre, 1971). As in *E. laboriense*, the endoprotocrista is still present in a few specimens which lack the hypocone. However, the endoprotocrista is less frequent in *L. lautricense*, and occurs on only 2.5% (1/41) of the P3s and 4% (1/23) of the P4s.

The variation of the upper molars is even more similar between the two taxa, *L. lautricense* displaying the same polymorphic characters as *E. laboriense*. The endoparacrista is less salient in *L. lautricense* but is still present in the majority of the M1s and M2s. However, in contrast to *E. laboriense*, the endoparacrista is less present on M2s (71%, 15/21) than in M1s (96%, 22/23), and totally absent on M3s. The ectostyle has the same morphology in *L. lautricense*, where it is always present on M1s, contrary to *E. laboriense*, but still polymorphic on M2s and M3s. The proportion of M2s with an ectostyle is identical on both taxa (83%, 19/23), however the majority of *L. lautricense* M3s (71%, 29/41) lacks the ectostyle.

The variations of the lower teeth of *L. lautricense* are also very similar to that of *E. laboriense.* The lower premolars of *L. lautricense* are also molarized, and display an entoconid, except on some p2s (Sudre, 1971). As in *E. laboriense* the lower premolars of *L. lautricense* are much less variable than their upper counterparts. As in *E. laboriense*, the premolars are only slightly polymorphic. The paraconid is less variable in each dental locus. The paraconid is high and always present in p2s, but is small and present in only 10% (2/20) of the p3s and is totally absent on p4s.

The lower molars of *L. lautricense* present the same polymorphism on the postectometacristid than in *E. laboriense*. This crest is present in fewer m1s than in *E. laboriense* (64%, 16/25) and with equal proportion for m2s (87%, 20/23) and m3s (91%, 21/23). In addition, *L. lautricense* always presents a long preentocristid, more salient than in *E. laboriense* and a short prehypocristid that never join the protolophid. As such, this species lacks polymorphism on both characters unlike *E. laboriense*. Furthermore, *E. laboriense* lacks some polymorphic characters that are present in younger lophiodontids, such as the entoconule on molars, the hypocone and the entoconid on molarized premolars (Savage et al., 1966; Sudre, 1971), and other accessory conules.

5.2. Sexual dimorphism

The variation observed on canines and mandibles of *E. laboriense* is consistent with the sexual dimorphism observed in other fossil Perissodactyls (Chen et al., 2010; Gingerich, 1981; Mead, 2000; Mihlbachler, 2007). As in *Teleoceras major* and *Chilotherium wimani,* males of *Eolophiodon* tend to have more massive mandibles with a higher corpus height and an extended angle of the mandible (Chen et al., 2010; Mead, 2000). The lower canines of *E. laboriense* are significantly larger in males, as in *Xenicohippus osborni* (Gingerich, 1981). The upper canines of *E. laboriense* do not show variation, but the sample is relatively small, and the intraspecific variation could not be observed. With a dimorphic ratio between 1.1 and 1.3 (Table 3), the sexual dimorphism of the mandible of *E. laboriense* is slightly smaller than in *Xenicohippus osborni* but is higher than in *Teleoceras major* and in modern perissodactyls (Mead, 2000; Gingerich, 1981). When using equations based on mandibular characters, males have an average body mass estimated at 130 kg, whereas females average *ca*. 90 kg, which is 30% lighter than males (Table 3). As in most dimorphic perissodactyls, males of *E. laboriense* tended to be heavier than females (Mead, 2000). However, the sexual dimorphism is less visible on dental characters. The unbiased coefficients of variation are low and the dimorphic ratio calculated by the "method-of-moments" are almost always < 1.2 (Table 2). The size distribution of male and female teeth strongly overlaps and the size dimorphism is moderate. Only the p3 and p4 display higher ratios due to their variable talonid morphology, independently of the sex of the specimen. Accordingly, the body mass estimates based on dental characters do not show significant differences between males and females (Table 5).

Sexual dimorphism is known in lophiodontids, especially in *Paralophiodon leptorhynchum* (Depéret, 1907). The cranium of *P. leptorhynchum* presents classic variation related to sexual dimorphism, notably a higher sagittal crest on males and a longer canine-premolars diastema. Unfortunately, no sexual variation on mandibles has been reported (Depéret, 1907). Thus, the sexual dimorphism of *P. leptorhynchum* cannot be compared with that of *E. laboriense.*

The lower canines of *L. lautricense* from the UM collection display similar dimorphism as in *E. laboriense.* The dimorphic ratios are similar for the height and width of the canine. The length of the canine is more dimorphic in *L. lautricense* (Table 6). However, the mandibles of *L. lautricense* present in the UM collection are too fragmentary to observe a sexual dimorphism. Most of the specimens display only a part of the mandibular corpus below the cheek teeth. The canine and the mandibular angle are often absent and thus the sex of the specimen could not be determined. Moreover, when present, the mandibular angles are mostly broken and cannot be measured. The lack of complete data prevents a principal

component analysis and therefore a comparison with *E. laboriense*. Variation of the height of the mandibular corpus is observed on adult specimens of *L. lautricense* but cannot be linked to sexual dimorphism.

5.3 Implications of cladistic analysis

The introduction of polymorphism in the cladistic analysis did not modify the resulting topology but greatly affects the reliability of the inferred relationships. Even if the retention and consistency indices are similar to those in Robinet et al. (2015), the robustness (Bremer index) of the different nodes is clearly different. The node grouping *Eolophiodon* and other lophiodontines is greatly weakened (Fig. 9). The Bremer index is 4 points lower as many unambiguous synapomorphies supporting that node in Robinet et al. (2015) (e.g., presence of endoparacrista and ectostyle in upper molars) are now considered as variable in *E. laboriense*. In consequence, those characters become ambiguous synapomorphies of the *Lophiodon-Paralophiodon* clade. As a consequence, this latter clade is strengthened, with a Bremer index 2 points higher (Fig. 9). In the same way, the clades corresponding to the three genera *Lophiaspis*, *Paralophiodon* and *Lophiodon* are more robust due to the implementation of intraspecific variation in *E. laboriense*. This analysis is only a premise of a broader cladistic analysis as the polymorphism has only been coded for two taxa. Many lophiodontids have been described as displaying important morphological variation as *L. tapirotherium* (Filhol, 1888), and the inclusion of their polymorphism will possibly impact the topology and robustness of future cladistic results. Furthermore, many new characters have been highlighted in this study, that should be included in future phylogenetic analysis (e.g., the postprotocrista of the upper premolars, or the difference in crown heights of the canine between males and females).

Therefore, the phylogenetic matrix of lophiodontids must be entirely reshaped to incorporate the variation observed in this taxon. Most of the dental characters need to be re-encoded, with the creation of new character states to include polymorphism into the analysis. Future work on lophiodontids must integrate intraspecific variation as a first step towards a systematic reevaluation of this family. Unambiguous definition of lophiodontid species together with the implementation of clear phylogenetic relationships within the family remains necessary to describe the complete evolutionary history of the largest ungulates from the Western European Eocene.

6. Conclusions

The reassessment of the basal lophiodontid *E. laboriense* reveals an important degree of intraspecific variation. The polymorphism observed is similar to that known in the latest lophiodontid, *Lophiodon lautricense*. Polymorphic characters are often homologous between the two species, or occur on the same part of the teeth, notably on the upper premolars. The low variation of the molars is remarkable. The sexual dimorphism on mandibles (size, canine morphology, mandibular angle morphology) is strong in *E. laboriense* and is similar to that observed in other fossil perissodactyls. Despite the variation, most of the diagnostic characters are constant and so the validity of the genus *Eolophiodon* is strengthened.

Ongoing studies of the basalmost lophiodontid *Lophiaspis* and other new Ypresian specimens from Southern France could confirm this high intraspecific variation in basal lophiodontids. Intraspecific variation will also be investigated on formerly described lophiodontid species in order to propose a new phylogenetic hypothesis for the family taking into account polymorphism. This is a prelude of the complete systematic revision of the lophiodontids.

Acknowledgments

We thank the APSO volunteers and also Bruno Soumeille, Henri-Pierre Labarrère, Eric Lopez and Dominique Teodori for loaning us original material of *E. laboriense* specimens found during the excavations at La Borie. We also thank the Terreal Society, especially Lionel Nathan who kindly provided permits, help and support for palaeontological research at La Borie. We are grateful to Marc Godinot, Jean Remy, Jean Sudre and Céline Robinet for their invaluable discussions on lophiodontids. We are indebted to Suzanne Jiquel (Université de Montpellier, France), Christine Argot (Muséum National d'Histoire Naturelle, Paris, France), Emmanuel Robert (Université Claude Bernard Lyon 1, France) and Loïc Costeur (Naturhistorisches Museum Basel, Switzerland) who gave us access to collections in their care. We also thank Margery C. Combs and Luke T. Holbrook for their constructive reviews that improved the quality of this paper. This is publication ISEM 2018-210.

Appendix A

Coding of *Eolophiodon laboriense* and *Lophiodon lautricense* with inclusion of polymorphic characters in the matrix of Robinet et al. (2015).

'Lophiodon lautricense' 1111111(01)11 1010110(01)11 0(01)(01)110-111 (01)(01)(01)1110-10 11111(01)01-1 111110011(01) 0(01)11210000 -(01)01111100 10011011(01)0 00011(01)00-0 11(01)00--111 11???1?001 0?0111??11 ??01000?01 012100111

'Eolophiodon laboriense' 100-111(01)01 0(01)00000001 0(01)000(01)-011 01001(01)1011 111(01)0(01)1011 1(01)(01)1111(01)0(01) 0(01)(01)120011(01) (01)(01)011(01)00(01)0 1(01)000(01)01(01)0 101(01)0(01)-101 (01)0(01)-(01)-0111 1100110011 1010111111 1010100001 (01)1110100?

Appendix B. Supplementary information

Supplementary information (including Table S1) associated with this article can be found, in the online version, at:

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Table and Figure captions

Table 1. List of material used in this study. F: female; M: male; Ind: Indeterminate.

Table 2. Measurements (in mm) of *E. laboriense* teeth. DR: dimorphic ratio calculated by the method of moments (Josephson et al., 1996; Missiaen et al., 2012); CV: unbiased coefficient of variation; L: length; W: width; N: number of specimens.

Table 3. Measurements (in mm) of *E. laboriense* mandibles. N: number of specimens; HP/2: height below p2; HM/2: height below m2; DL: diastema length; LM: mandible length; DMA: depth of mandibular angle; WMA: width of the mandibular angle; PML: posterior mandibular length; EM: estimation of mass made on mandible measurement (Janis 1990); LC: canine length; WC: canine width; HC: canine height; SD: Standard deviation; CV: unbiased coefficient of variation; DR: dimorphic ratio = mean male/mean female ; F: female; M: male; T: total.

Table 4. Cranial measurements (in mm) of *E. laboriense*. DL: diastema length; I3/P2 L: I3-P2 length; DW: diastema width; HP2: height at P2; HM1: height at M1; HM3: height at M3; PW: postorbital width; CL: cranium length; DNF: distance nasal-frontal; OC: occipital length; CZ: cranium width at the zygomatic; HZ: height of the zygomatic arches; WZ: width of the zygomatic arches; PGW: post-glenoid width; PGH: post-glenoid height; GCW: glenoid cavity width; GCL: glenoid cavity length.

Table 5. Body mass estimation of *E. laboriense* and *L. lautricense*. m1 Legendre: ln body mass (in g) = 1,5133×ln(L×W m1) + 3.6515; m1 Janis: log body mass (in kg) = 3.26×log(m1 length) + 1.337; m2 Janis: log body mass (in kg) =3,2×log(L×W m2) + 1,13; M2 Janis: log body mass (in kg) = 3.18×log(m2 length) + 1.091; mandible Janis: log body mass (in kg) = 2.448×log(DMA) – 0.331; m2 Damuth: log body mass (in kg) = 3.07×log(L×W m2) + 1.07; M2 Damuth: log body mass (in kg) = 3.03×log(m2 length) + 1.06.

Table 6. Canine measurements (in mm) of *L. lautricense*. N: number of specimens; SD: Standard deviation; CV: unbiased coefficient of variation; DR: dimorphic ratio = mean male/mean female; LC: canine length; WC: canine width; HC: canine height; F: female; M: male; T: total; P-value: Wilcockson test p-value.

Figure 1. Dental terminology used for p2 (**A**), p4 (**B**), m3 (**C**), P4 (**D**) and M1 (**E**). The junction of two cristae or cristids forms a loph or a lophid. The junction between the preprotocrista and the preparacristule forms the protoloph. The connection of the postprotocristid and the postmetacristid forms the protolophid, and the connection between the postentoconid and the posthypocristid form the hypolophid. We name the distolingual cusp of the upper molars hypocone due to historical arguments. However, it must be noted that this cusp is surrounded by a cingulum. We prefer the denomination ectostyle to mesostyle on the upper molars, as the style is located in the distal part of the teeth. Abbreviations: EcHylid: Ectohypocristulid; EdMec: Endometacrista; EdPac: Endoparacrista; EdPrc: Endoprotocrista; Hy: Hypocone; Hyd: Hypoconid; Hylid: Hypoconulid; Me: Metacone; Med: Metaconid; Pa: Paracone; Pad: Paraconid; Pal: Paraconule; Pas: Parastyle; PEcd: Preentocristid; PHyc: Prehypocrista; PHycd: Prehypocristid; PHylid: Prehypocristulid; PMec: Premetacrista; PMecd: Premetacristid; PoEcd: Postentocristid; PoectoMecd: Postectometacristid; PoectoPrcd: Postectoprotocristid; PoHycd: Posthypocristid; PoHylid: Posthypocristulid; PoMec: Postmetacrista; PoMecd: Postmetacristid; PoPrcd: Postprotocristid; PoPac: Postparacrista; PoPasc: Postparacristyle; PoPrc: Postprotocrista; PPac: Preparacrista; PPacd: Preparacristid; PPalc: Preparacristule; PPasc: Preparacristyle; PrPrcd: Preprotocristid; Pr: Protocone; Prd: Protoconid.

Figure 2. Cranio-mandibular terminology and measurements. **A**. Cranium in dorsal view. **B**. Cranium in lateral view. **C**. Mandible in lateral view. Cranium and mandible modified from Robinet et al. (2015). Abbreviations: DMA: Depth of mandibular angle; PML: Post-mandibular length; WMA: Width of mandibular angle.

Figure 3. Dental variation of *Eolophiodon laboriense.* **A**. Upper tooth row. **B**. Lower tooth row. Variable characters are colored; character frequency: Black: 100%; Red: [75%-99%]; Yellow: [50%-74%]; Green: [25%-49%]; Blue:]0%-24%].

Figure 4. Upper teeth of *Eolophiodon laboriense*. **A**. Canine, MHNT.PAL.2018.3.1, lateral view. **B**. Left P2-P4, UM BRI-5. **C**. Left M1-M3, MHNT.PAL.2018.3.2. **D**. Right P2-M3, MHNT.PAL.2018.3.3 (reversed). **E**. Left P2-M3, MHNT.PAL.2018.3.4. **F**. Right P2-M3, MHNT.PAL.2018.3.5 (reversed). **G**. Left P2-M3, MHNT.PAL.19.3.1, occlusal view. Scale

bar: 10 mm.

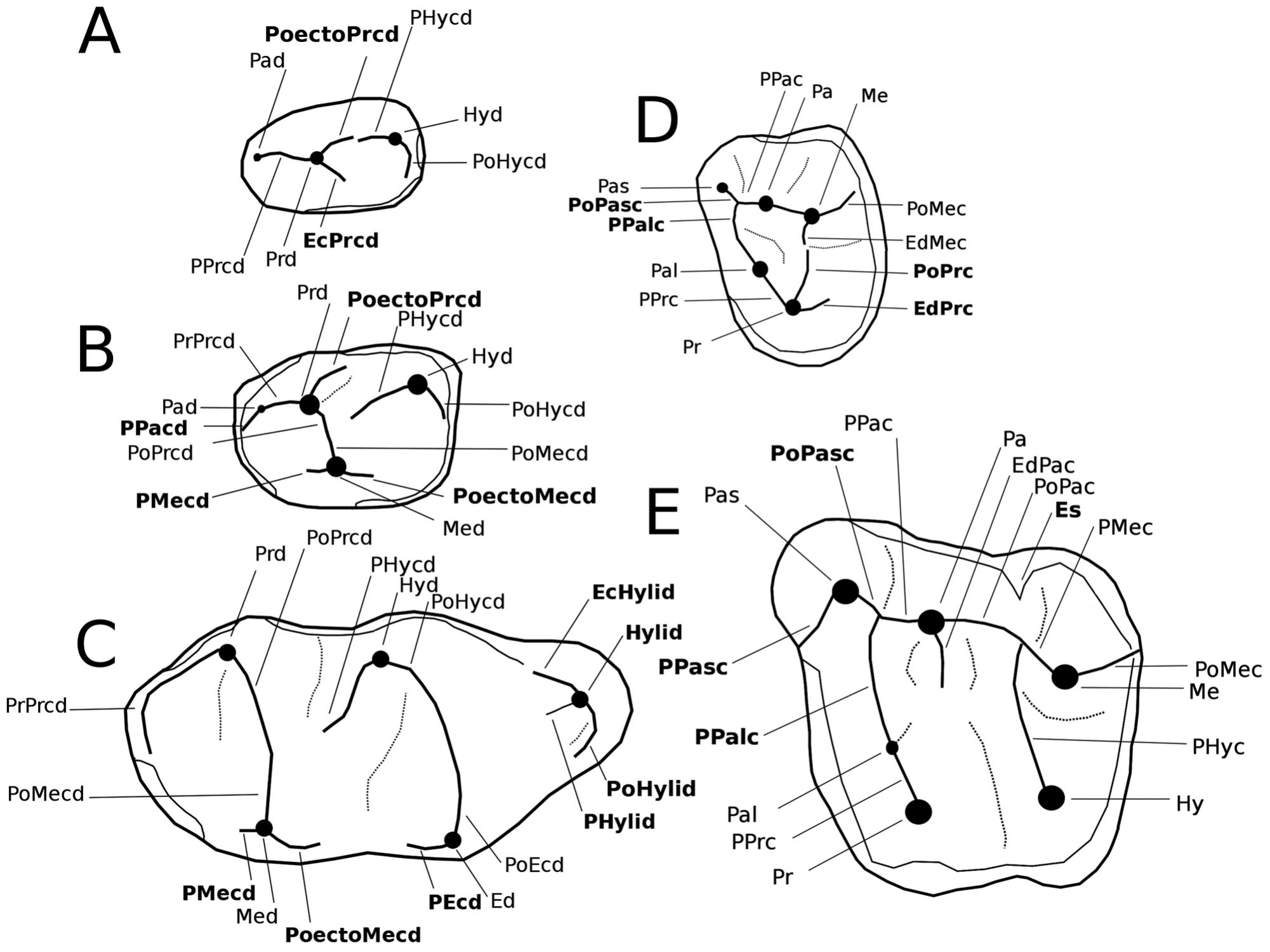
Figure 5. Lower teeth of *Eolophiodon laboriense*. **A, B**. Left p2, MHNT.PAL.2018.3.10, occlusal and lateral views. **C, D**. Left p3, MHNT.PAL.2018.3.6, occlusal and lateral views. **E, F**. Right p2-p3, MHNT.PAL.2018.3.7, occlusal and lateral views. **G**. Left m2 (reversed), MHNT.PAL.2018.3.6, occlusal view. **H**. Right m2, UM BRI-7, occlusal view. **I**. Right m1-m3, UM BRI-6, occlusal view. **J**. Right p2-m3, MHNT.PAL.2018.3.8, occlusal view. Scale bar: 10 mm.

Figure 6. Mandibles of *Eolophiodon laboriense*. **A**. MHNT.PAL 19.3.1, lateral view. **B**. UM BRI-6, lateral view. Scale bar: 5 cm.

Figure 7. Principal Component Analysis of canine measurements of *Eolophiodon laboriense.* **A**. First principal plane. **B**. Correlation circle related to the first principal plane. Abbreviations: F: Female; M: Male; Ind: Indeterminate; LC: canine length; WC: canine width; HC: canine height. The large symbols represent the centroid for each sex in the morphospace.

Figure 8. Principal Component Analysis of mandibule measurements of *Eolophiodon laboriense*. **A**. First and second principal components. **B**. First and third principal components. **C, D**. Correlation circles related to A and B, respectively. Abbreviations: F: Female; M: Male; Ind: Indeterminate; HP/2: height below p2; HM/2: height below m2; DL: diastema length; LM: mandible length; DMA: depth of mandibular angle; WMA: width of the mandibular angle; PML: posterior mandibular length. The large symbols represent the centroid for each sex in the morphospace.

Figure 9. Strict consensus tree of the three most parsimonious topologies obtained by heuristic search on PAUP* 4.0α162. Tree length L = 422, CI = 0.39, RI = 0.51. Node values are Bremer indices; for clarity, the Bremer index values different from Robinet et al.'s (2015) topology are in red, with the original values within parenthesis in black.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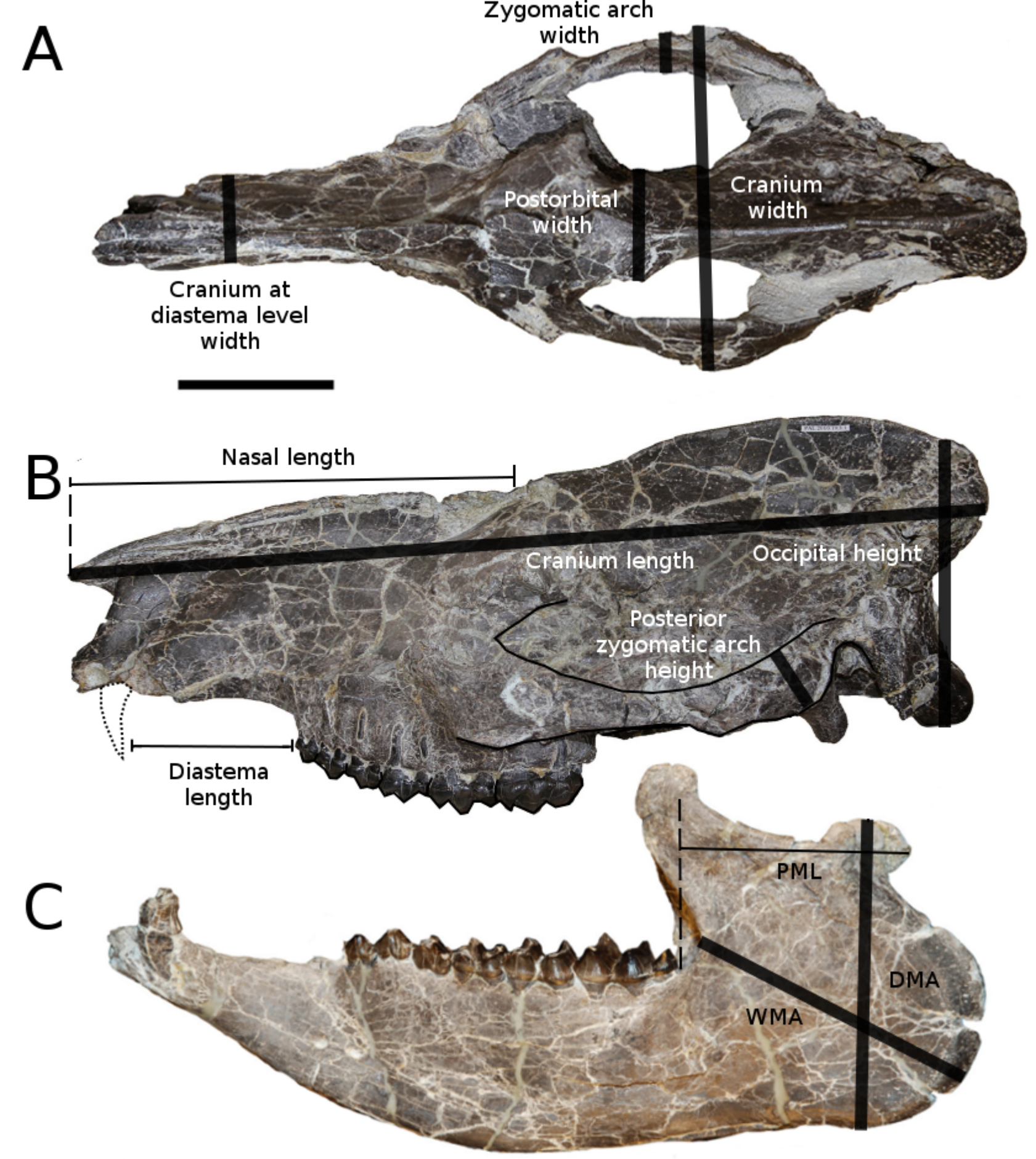
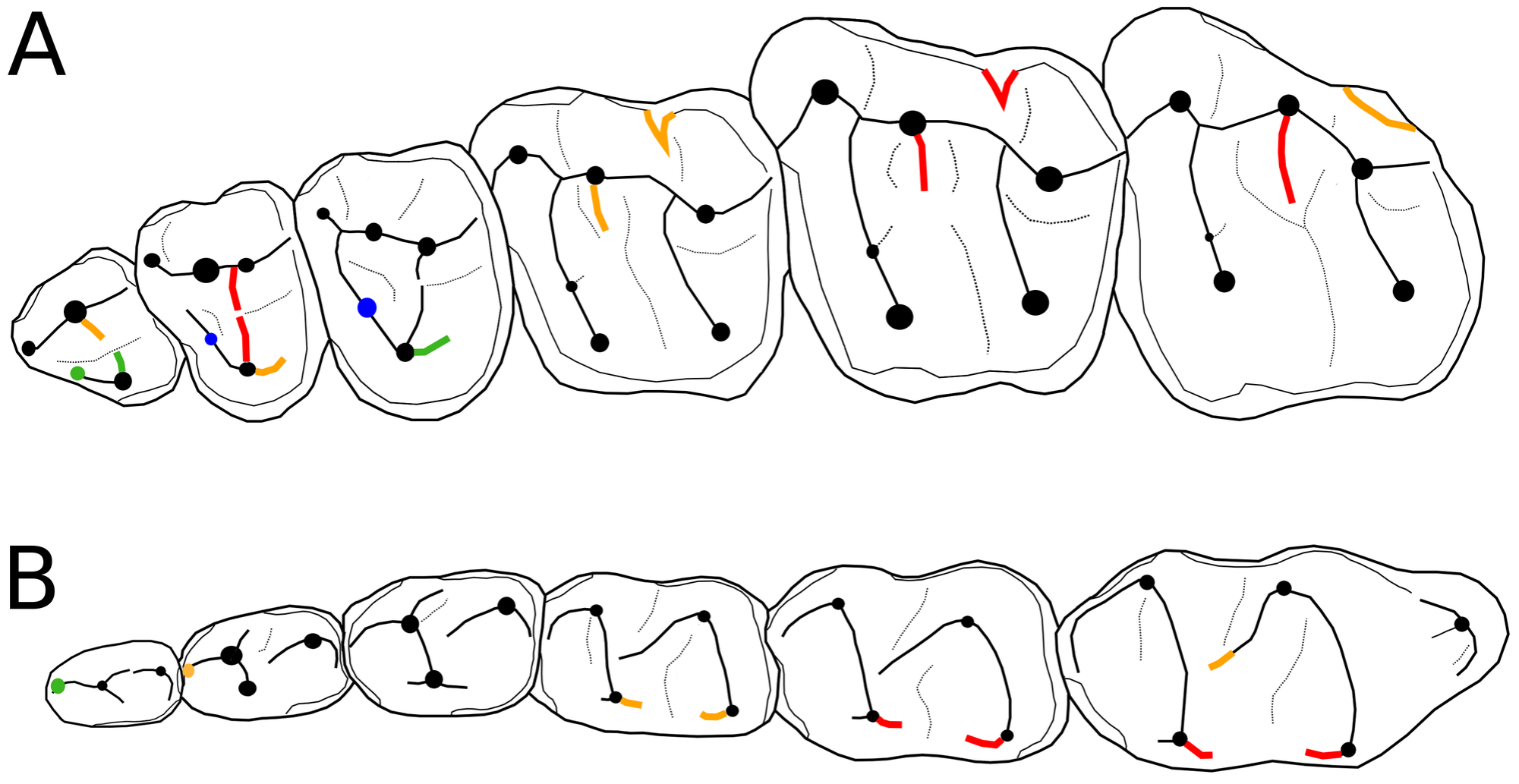
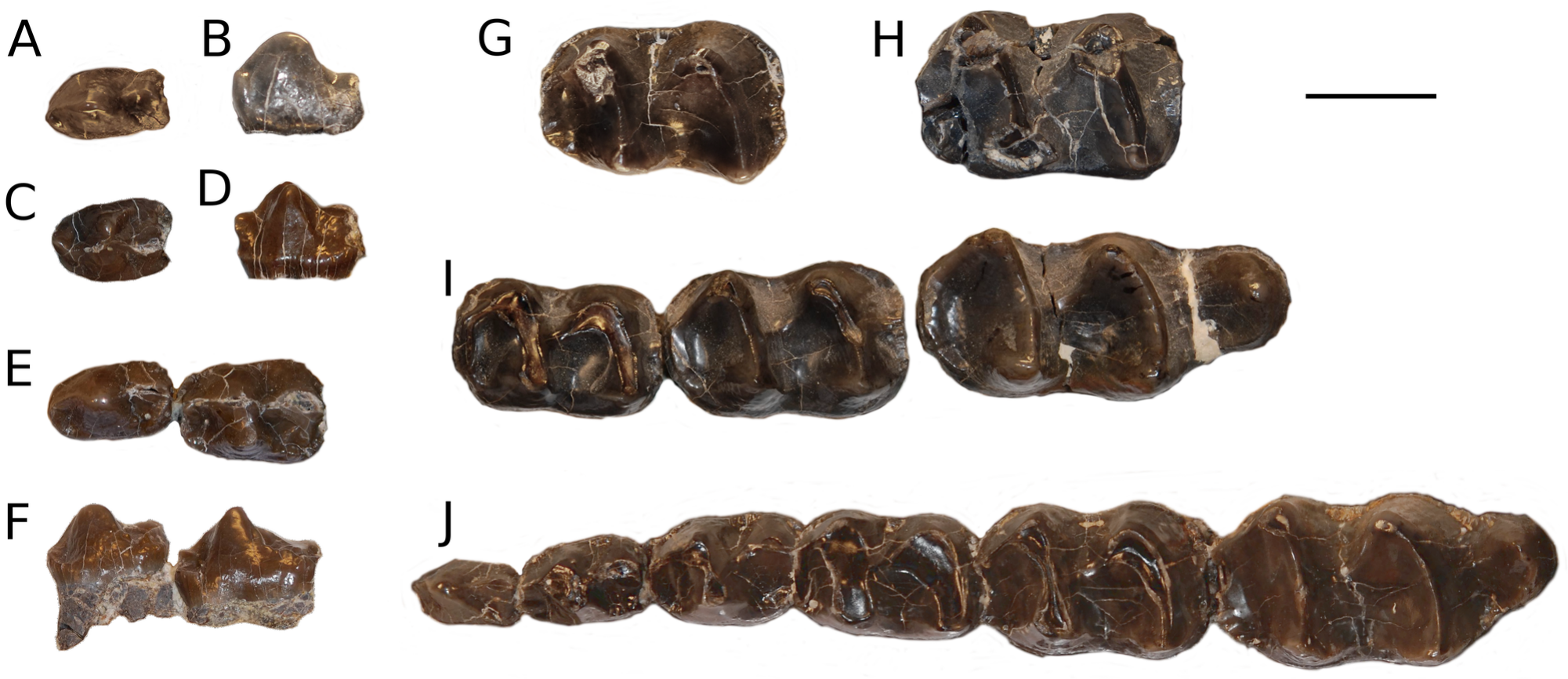
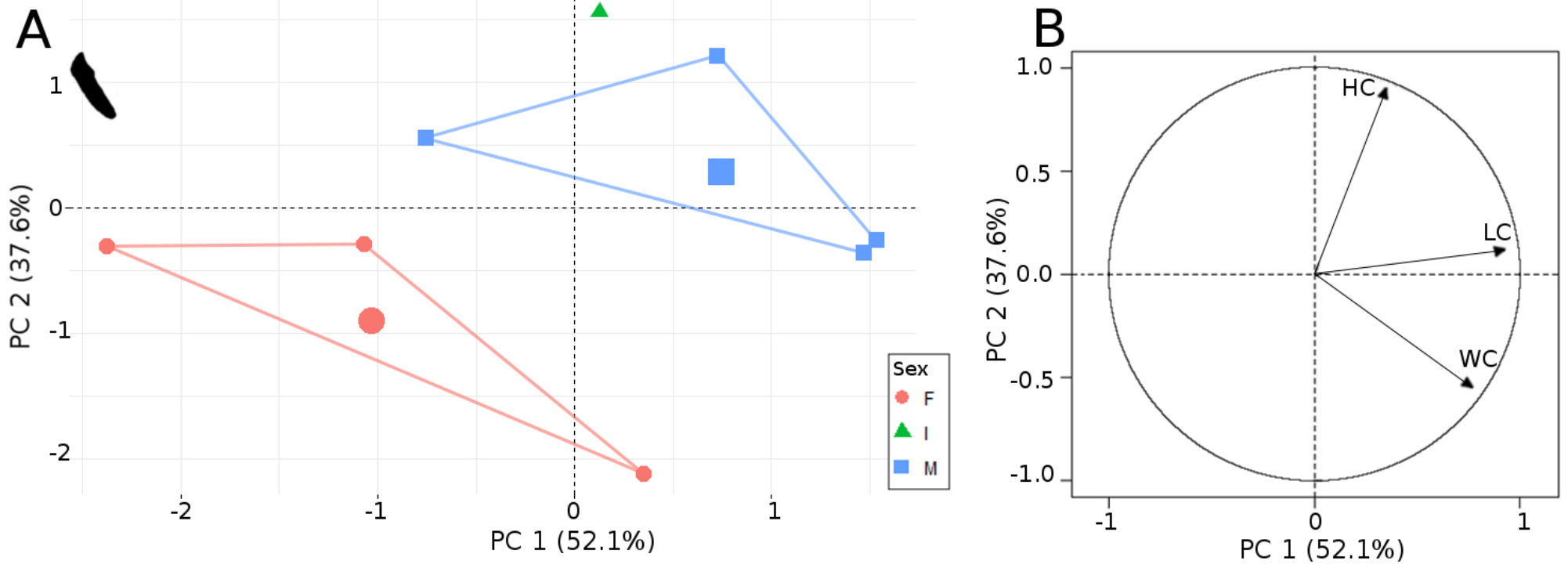

A
Zygomatic arch width
Postorbital width
Cranium width
Cranium at diastema level width
B
Nasal length
Cranium length
Occipital height
Posterior zygomatic arch height
Diastema length
C
PML
DMA
WMA

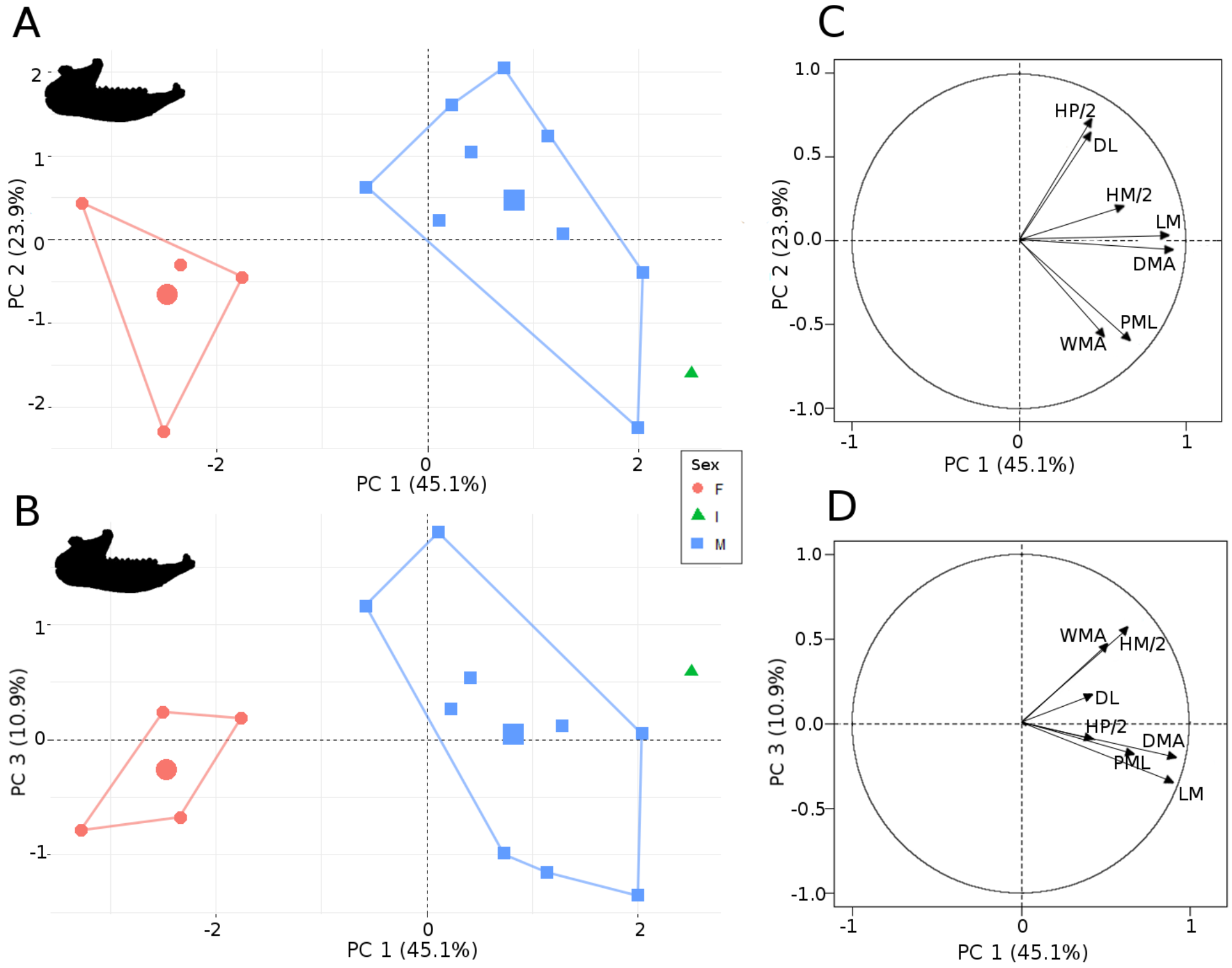

A
B


A
B
C
D
E
F
G


A
B
C
D
E
F
G
H
I
J


A
♂
B
♀


A
1
0
-1
-2
PC 2 (37.6%)
-2
-1
0
1
PC 1 (52.1%)
Sex
F
I
M
B
1.0
0.5
0.0
-0.5
-1.0
PC 2 (37.6%)
HC
LC
WC
-1
0
1
PC 1 (52.1%)


A
B
C
D
PC 1 (45.1%)
PC 2 (23.9%)
PC 3 (10.9%)
Sex
F
I
M
HP/2
DL
HM/2
LM
DMA
PML
WMA

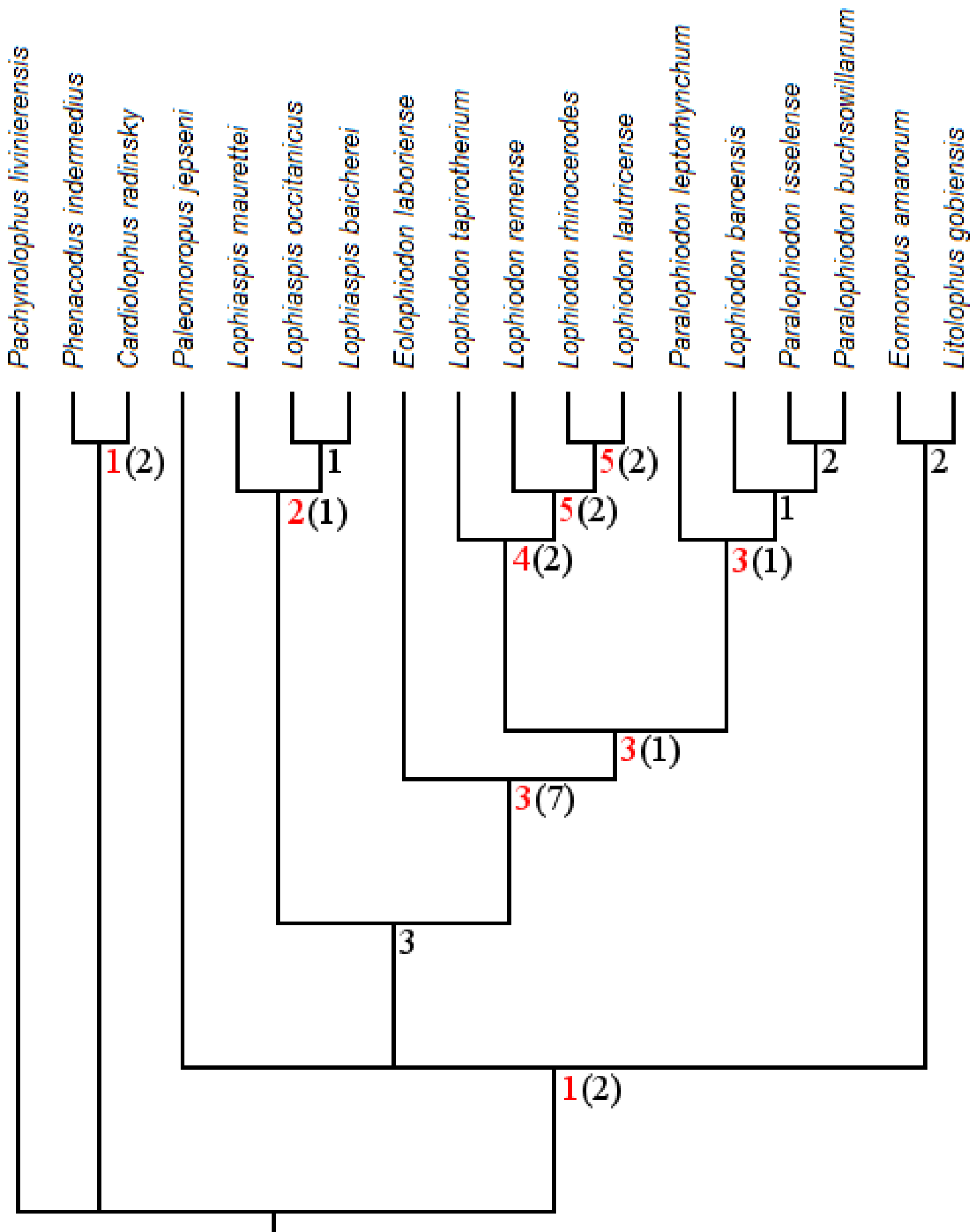

Pachynolophus livinierensis
Phenacodus indermedius
Cardiolophus radinsky
Paleomoropus jepseni
Lophiaspis maurettei
Lophiaspis occitanicus
Lophiaspis baicherei
Eolophiodon laboriense
Lophiodon tapirotherium
Lophiodon remense
Lophiodon rhinocerodes
Lophiodon lautricense
Paralophiodon leptorhynchum
Lophiodon baroensis
Paralophiodon isselense
Paralophiodon buchsowillanum
Eomoropus amarorum
Litolophus gobiensis
1 (2)
1
2 (1)
5 (2)
5 (2)
4 (2)
1
3 (1)
2
2
3 (1)
3 (7)
3
1 (2)

Table 1.

Specimen	Nature	Age classes	Sex
MHNT.PAL.2010.19,3,1	Cranium (Holotype) (Robinet et al.,2015)	7	M
MHNT.PAL.2010.19,3,2	Mandible (Holotype) (Robinet et al., 2015)	7	M
MHNT.PAL.2018.3.1	Canine	?	?
MHNT.PAL.2018.3.2	Maxillar M1-M3	7	?
MHNT.PAL.2018.3.3	Maxillar P2-M3	8	?
MHNT.PAL.2018.3.4	Cranium and fragment mandible	6	M
MHNT.PAL.2018.3.5	Cranium	7	?
MHNT.PAL.2018.3.6	Mandible p3-m3	5	F
MHNT.PAL.2018.3.7	Mandible p2-m3	6	M
MHNT.PAL.2018.3.8	Mandible c-m3	7	F
MHNT.PAL.2018.3.9	Mandible p4-m3	8	M
APSO.2013.SP2-276	Fragment of cranium	?	?
APSO.2006.SP2-12	Fragment of mandible with m3	6_7	?
APSO.2007.SP2-102	Mandible Dp3-M1	3	Ind
APSO.2007.SP2-73	Canine	?	?
APSO.2007.SP2-40	Canine	?	?
APSO.2007.SP2-166	Canine	?	?
APSO.2007.SP2-109	p3	?	?
APSO.2008.SP5-15	Mandible p2-m3	8	M
APSO.2008.SP5-04	Mandible p3-m1	6	F
APSO.2009.SP5-45	Fragment of cranium	?	?
APSO.2016.SP0-15	M3	6	?
UM BRI-5	Maxillar P2-P4	7_8	?
UM BRI-6	Mandible C-m3	5	F
UM BRI-7	Mandible p4-m3	6	M
STP-S3	Mandible C-P/4	7	M
STP-V1	Maxillar P2-M3, P2-M1	7	?
STP-V3	Maxillar P2-M1	6	?
STP-V4	Maxillar P4-M3	7	?
STP-V5	Maxillar DP2-M1	3	?
STP-V7	Maxillar P4-M3	6	?
STP-V8	Maxillar P2-M3	6	?
STP-L9	Maxillar M1-M3	8	?
STP-L10	M1	4	?
STP-V11	P3	>7	?
STP-L12	P3	6	?
STP-T13	M2	8	?
STP-V15	Teeth row p4-m3	5_6	?
STP-V16	Mandible P/2-M/3	5	M
STP-V18	Teeth row p4-m2	7	?
STP-V19	Mandible m1-m2	5	?
STP-V21	Teeth row p2-m2	8	?
STP-V22	Teeth row p2-m3	8	?
STP-V23	Teeth row p2-m3	4_5	?
STP-V24	Teeth row p2-m3	4_5	?
STP-T18	Teeth row C-m3	6	M

Table 2.

Tooth		N	Min	Max	Mean	SD	CV	DR
P2	L	10	8.9	10.6	9.73	0.54	5.71	1.11
	W	10	5.4	7.8	6.74	0.73	11.13	1.20
P3	L	14	10.2	12.8	11.70	0.85	7.42	1.16
	W	14	12.6	15.6	14.20	0.87	6.26	1.11
P4	L	12	11.9	14.5	13.15	0.80	6.19	1.11
	W	12	15.2	18.7	17.03	1.06	6.37	1.12
M1	L	14	15.6	20.4	18.69	1.41	7.66	1.10
	W	14	17.4	22.5	20.05	1.09	5.52	1.00
M2	L	12	19.2	24.1	22.59	1.61	7.27	1.11
	W	12	20.4	25.3	23.71	1.42	6.09	1.00
M3	L	13	18.5	24.7	22.18	1.85	8.49	1.13
	W	13	22.9	28.0	25.98	1.56	6.13	1.00
P/2	L	11	8.2	11.6	9.71	1.03	10.85	1.20
	W	9	4.6	5.9	5.26	0.47	9.18	1.20
P/3	L	17	9.1	13.4	11.36	1.40	12.51	1.25
	W	17	5.6	8.9	7.24	0.91	12.75	1.24
P/4	L	20	11.8	14.3	13.12	0.76	5.87	1.11
	W	19	8.0	10.9	9.35	0.84	9.10	1.32
M/1	L	21	14.6	17.7	16.42	0.88	5.40	1.09
	W	20	9.6	12.1	11.01	0.76	7.03	1.13
M/2	L	20	16.2	24.2	20.13	1.98	9.94	1.12
	W	21	11.2	14.2	13.16	0.86	6.58	1.00
M/3	L	14	25.4	34.7	29.60	2.43	8.35	1.13
	W	17	12.5	15.5	14.23	0.86	6.16	1.10

Table 3.

Measurement	Sex	N	Mean	Min	Max	SD	CV	P-value	DR
HP/2	F	5	37.04	30.80	45.90	5.63			
	M	4	45.58	38.50	50.30	4.61			
	T	9	41.31	30.80	50.30	6.62	16.46	0.02	1.23
HM/2	F	4	42.28	38.50	50.10	5.29			
	M	6	51.70	39.60	57.80	6.71			
	T	10	48.27	38.50	57.80	7.32	15.54	0.06	1.22
DL	F	5	36.86	33.80	41.20	3.10			
	M	4	41.70	36.50	49.10	4.67			
	T	9	38.98	33.80	49.10	4.69	12.37	0.05	1.13
LM	F	4	227.68	216.80	242.20	10.59			
	M	4	255.47	245.50	261.20	8.66			
	T	8	239.59	216.80	261.20	17.37	7.48	0.03	1.10
DMA	F	4	85.33	75.30	91.30	7.29			
	M	5	100.34	96.50	105.00	3.80			
	T	9	93.67	75.30	105.00	9.84	10.79	0.01	1.18
WMA	F	3	87.50	81.10	93.60	6.26			
	M	4	90.93	90.70	92.30	1.64			
	T	7	89.46	81.10	93.60	4.21	4.88	0.20	1.04
PML	F	3	6.81	62.00	73.10	5.64			
	M	5	6.97	63.30	73.60	4.35			
	T	8	68.56	62.00	73.60	4.50	6.76	0.39	1.02
EM	F	4	89.63	65.37	104.77	17.93			
	M	5	132.23	119.98	147.53	12.32			
	T	9	111.57	65.37	147.53	27.44	25.28	---	
LC	F	3	14.00	12.50	14.90	1.31			
	M	3	13.97	12.50	15.90	1.75			
	T	6	13.98	12.50	15.90	1.38	10.28	---	1.00
WC	F	3	10.10	8.70	12.60	1.98			
	M	2	12.35	11.90	12.80	0.64			
	T	5	11.23	8.70	12.80	1.77	16.55	---	1.22
HC	F	3	26.23	24.70	27.90	1.60			
	M	2	33.40	33.00	33.80	0.57			
	T	5	29.10	24.70	33.80	4.10	14.78	---	1.27

Table 4.

Measurement	MHNT.PAL.2010.19,3,1	MHNT.PAL.2018.3.4	MHNT.PAL.2018.3.5	UM BRI-5	STP-S3	STP-V1
DL	48.8	37.8	47.4	44.0	39.6	36.5
I3/P2 L	>87.9	94.1				
DW	41.2	35.7	32.7			38.5
HP2	96.5					
HM1	110.3					
HM3	122.8					
PW	37*2					
CL	316.7	362.9				
DNF	198.1	199.0				
OC	77.8	67.7				
CZ	141.2	176.0				
HZ	41.4	26.6				
WZ		9.9	8.3			
PGW	18.4	29.9				
PGH	14.8	21.4				
GCW	43.1	47.8				
GCL	32.4	30.5				

Table 5.

	E. laboriense	*L. lautricense*
m1 Legendre	101.86	1819.76
m1 Janis	112.32	1921.03
m2 Janis	130.69	2854.48
M2 janis	167.18	3319.56
mandible Janis	111.57	439.79
m2 Damuth	103.60	2000.10
M2 Damuth	158.56	2000.10
Mean estimate	126.54	2050.69

Table 6.

Measurement	Sex	N	Mean	Min	Max	SD	CV	P-value	DR
LC	F	32	29.07	22.70	36.20	3.35			
	M	15	37.57	29.00	42.80	3.82			
	T	47	31.78	22.70	42.80	5.30	16.76	2.3×10^{-7}	1.29
WC	F	32	22.44	19.20	27.10	1.77			
	M	16	28.29	25.30	31.50	1.98			
	T	48	24.39	19.20	31.50	3.33	13.72	2.0×10^{-8}	1.26
HC	F	13	45.71	37.30	55.10	5.51			
	M	5	60.52	47.10	70.80	11.42			
	T	18	49.82	37.30	70.80	9.94	20.22	3.3×10^{-3}	1.32