Dental and tarsal morphology of the European Paleocene/Eocene “condylarth” mammal *Microhyus*

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New dental and postcranial remains of the alleged louisinine hyopsodontid “condylarth” *Microhyus* from the European Paleocene/Eocene transition are described, and prompt a reevaluation of the genus. New specimens belonging to *Microhyus musculus* from Dormaal (MP7, Belgium) provide the first evidence of the lower dentition of the type species. We describe *M. musculus*? from Pourcy (MP7, France) and cf. *Microhyus* sp. from Berru (MP6a, France). A rich original assemblage of *M. reisi* from Silveirinha (MP7, Portugal) allows a detailed description of the morphological dental variation within that species. Well-preserved astragali and calcanei from Silveirinha can be confidently attributed to *Microhyus reisi*. Functional analysis of these elements suggests that *Microhyus* was a terrestrial mammal capable of rapid running or jumping. The pedal morphology of *Microhyus* is very similar to that of *Paschatherium*. These louisinines share some derived characters with the hyopsodontids *Apheliscus* and *Haplomylus* (e.g., the occurrence of a cotylar fossa on the astragalus) but they differ from *Hyopsodus*. Therefore, in view of the pedal morphology alone, the hyopsodontids may be polyphyletic. Given the dental similarities between *Microhyus* and the early representatives of the order Macroscelidea, we compared the tarsal morphology of louisinines with that of modern macroscelidids (Paleogene tarsal remains are currently unknown for this group). Macroscelidids and louisinines present some similarities in their astragalar morphology; however, the macroscelidid astragalus appears to be too specialized to be compared with that of *Microhyus* and *Paschatherium*.

Key words: Eutheria, “Condylarthra”, Louisininae, *Microhyus*, Paleocene, Eocene.

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Introduction

The mammal *Microhyus musculus* was originally described (Teilhard de Chardin 1926) and named (Teilhard de Chardin 1927) on the basis of a single upper molar collected in the locality of Dormaal, Belgium (reference level MP7 in Europe, Tienen Formation, earliest Eocene). The species has also been reported from two other early Eocene European sites: Pourcy, France (Louis and Michaux 1962) and the Suffolk Pebble Beds (Hooker and Insole 1980; Hooker 1998). In discussing the systematic status of the genus, Sudre and Russell (1982) described, but did not figure, two additional upper teeth from Dormaal. Knowledge of the genus was considerably enhanced with the discovery of numerous dental remains of a new species, *M. reisi*, from the locality of Silveirinha (MP7, Portugal; Antunes et al. 1987). More recently, Lopez-Martinez and Pelaez-Campomanes (1999) described *M.* cf. *musculus* from the late Paleocene Tremp Formation (MP6b, south-central Pyrenees, Spain).

Since its formal description, *Microhyus* has been variously interpreted. It was initially regarded as a hyracoid (Teilhard de Chardin 1926, 1927), then considered as an artiodactyl (Louis and Michaux 1962), a meniscotheriid (Van Valen 1971), and a hyopsodontid (Russell et al. 1975). *Microhyus* was afterward associated with the European genera *Louisina*, *Dipavali*, *Paschatherium*, and *Monshyus* in a new subfamily of hyopsodontids, the Louisininae (Sudre and Russell 1982). This subfamily constituted one of the principal components of European mammalian faunas during the Paleocene and early Eocene. *Microhyus* represents around 45% of the assemblage at Silveirinha (Estravis 1992, this paper) and *Paschatherium* makes up more than 70% of the assemblage from Dormaal (Smith 1999) and the fossiliferous localities of the Tremp Formation (Lopez-Martinez and Pelaez-Campomanes 1999). The louisinine subfamily has not been universally accepted by specialists. On the basis of dental characters, Collinson and Hooker (1987) considered *Paschatherium* to be an adapisoricid insectivore, whereas Godinot et al. (1996) argued that the tarsus of *Paschatherium* shows affinities with that of *Hyopsodus* (but see Hooker 2001). Finally, Tabuce et al. (2001) weakened the hyopsodontid status of the louisinines *Louisina*, *Dipavali* plus *Paschatherium*; and proposed *Microhyus* as a sister group of macroscelidids.

New specimens from Dormaal and Silveirinha belonging to *Microhyus musculus* and *M. reisi*, respectively, are described in this paper; they allow a reassessment of both species. We also describe *M. musculus*? from Pourcy (MP7, France) and cf. *Microhyus* sp. from Berru (MP6a, France). The dental remains from Dormaal significantly improve our understanding of *M. musculus* by providing the first evidence of the lower dentition of the type species of *Microhyus*. *Microhyus reisi* is documented by an important new collection that includes more than 300 new dental specimens. The specimens are well preserved, providing several fragments of lower and upper jaws. *Microhyus reisi* shows considerable dental variability, in both size and morphology. This variability is analyzed in order to confirm the presence of only one species of *Microhyus* at Silveirinha, to remove variable characters of the intrageneric comparison, and to discuss the relative ages of the Dormaal and Silveirinha faunas. In the new collection from Silveirinha, *M. reisi* is also represented by pedal elements (astragali and calcanei). Their morphology is compared to that of *Paschatherium*, other condylarths and extant macroscelidids to assess the validity of the louisinine subfamily and to explore their macroscelidean affinities.

Institutional abbreviations.—UNLSV, Universidade Nova de Lisboa, Lisbon, Portugal, Silveirinha collection; UNLSNC, Universidade Nova de Lisboa, Lisbon, Portugal, Silveirinha new collection; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MNHN, Muséum National d'Histoire Naturelle, Paris, France.

Other abbreviations and dental terminology.—Dental terminology follows that of Bown and Kraus (1979) (see also Fig. 1). To analyze variation in tooth size of *Microhyus reisi*, premolars and molars were measured using a binocular microscope equipped with a scaled reticle. Only teeth not damaged or worn in the parts relevant to measurement were measured. Repeated measurements were taken to reduce intraobserver error. The reading on the reticle was translated into metric measurements according to magnifications. The measurements of *Microhyus reisi* (UNLSV only) are from Estravis (1992). Tooth measurements and statistics used in this paper are as follows: L, maximum mesiodistal length of tooth; W, maximum labiolingual width of tooth; P, parameter; N, sample size; OR, observed range; M, mean; SD, standard deviation; CV, coefficient of variation. All measurements are given in millimeters.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Infraclass Eutheria Gill, 1872

Order "Condylarthra" Cope, 1881

Family ?"Hyopsodontidae" Trouessart, 1879

Subfamily Louisininae Sudre and Russell, 1982

cf. *Microhyus* sp.

Locality: Berru, France.

Age: MP6a (Thanetian, Paleocene).

Material and measurements.—MNHN L-3-BR right M1, L = 2.8, W = 3.2.

Description (Fig. 1A).—This upper molar is sub-square in outline. The four main cusps are bunodont, very close to the center of the crown and they are separated by shallow valleys. The paracone is larger than the metacone and the protocone is lower than the hypocone. The hypocone and the protocone are very labially situated and their lingual walls are sloping toward the base of the crown. The paraconule and metaconule are small and twinned with the protocone and hypocone respectively. A short postprotocrista is directed toward the metaconule. Both the mesial and distal cingula are thick and bear a blunt ectocone and an incipient hypostyle respectively. There is no salient parastyle on the mesial aspect of the tooth. A cingulum can be detected on the damaged labial part of the crown.

Comparisons.—The morphology of MNHN L-3-BR is similar to that of other louisinines in exhibiting the following traits: the outline is sub-square, the four main cusps are low and bunodont, the paracone is larger than the metacone, the parastyle is reduced, the metastyle is absent and a robust cingulum runs around the mesial, labial and distal sides of the tooth. The development and the position of the hypocone indicate possible affinities with the species *Monshyus praevius* and *Louisina mirabilis* as well as with the genus *Microhyus*. *Monshyus praevius* from the early Paleocene of Hainin, Belgium (reference level MP1-5) is the earliest representative of the louisinines and has been interpreted as being the most derived species of the subfamily (Sudre and Russell 1982); it is documented by only one tooth, an M1(or M2) that recalls the specimen from Berru by the labial position of both the protocone and the hypocone. *Monshyus* differs, however, in lacking conules, and in having a longer preprotocrista, a hypocone connected with the distal cingulum, a salient parastyle, and a less robust mesial cingulum. Upper molars of *Louisina mirabilis* from Cernay, France (reference level MP6a; Russell 1964) also differ from MNHN L-3-BR by several characters: the cusps are less bulbous; the pre- and postprotocrista are long and linked with more prominent paraconules and metaconules; and the hypocone is smaller and connected with the distal cingulum. On the basis of all these characters, MNHN L-3-BR is similar to first upper molars of *Microhyus*. However, *M. musculus* and *M. reisi* are notably smaller, the outline of their M1s is relatively labiolingually shorter, the four main cusps are less closely positioned in the center of the crown, the valleys are deeper, the hypocone is larger and the mesial cingulum is weaker. The species from Berru thus appears to be less derived than the

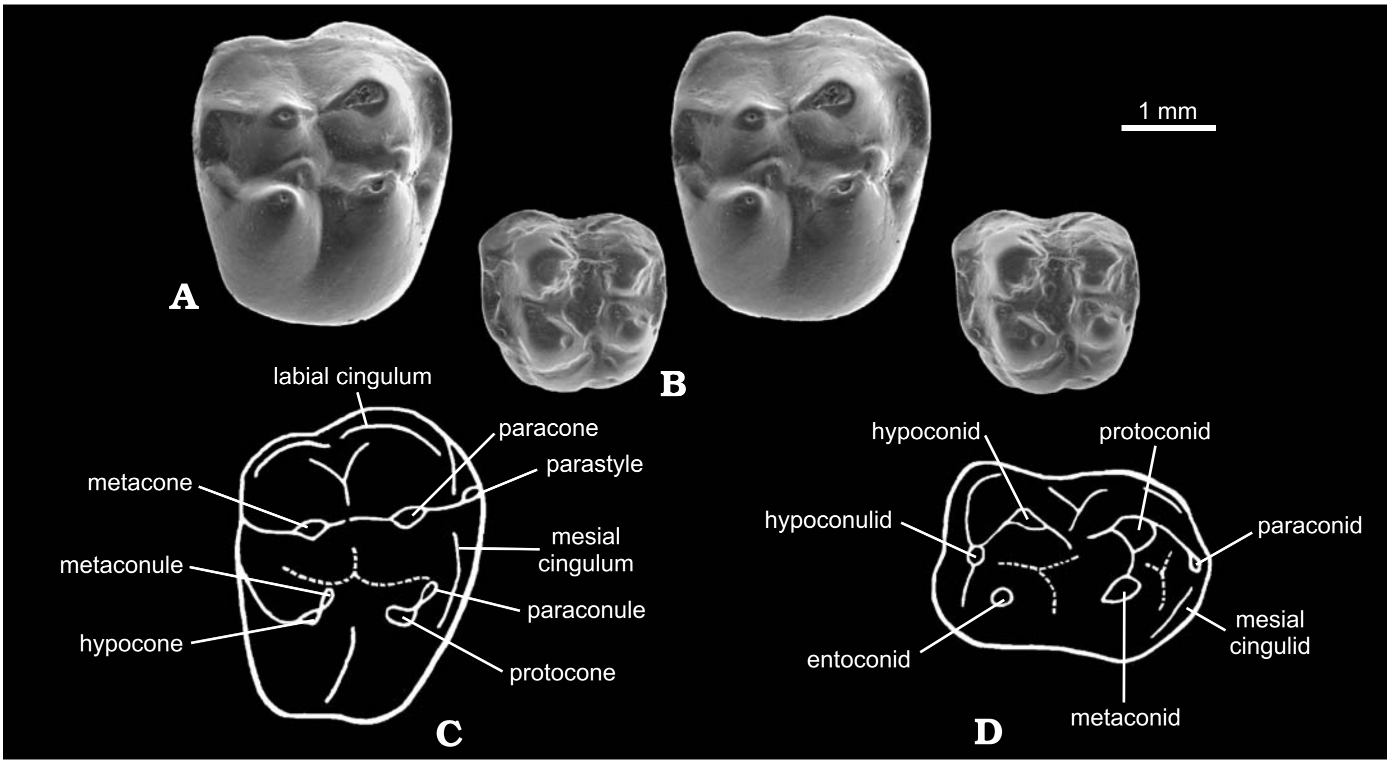

Fig. 1. **A**. cf. *Microhyus* sp., Thanetian, Berru, France, right M1 MNHN L-3-BR. SEM stereophotographs of epoxy resin casts. **B**. *Microhyus musculus*?, early Ypresian, Pourcy, France, left M1 MNHN PYL57. **C**. Schematic drawing with dental terminology of the M2 UNLSV3-10 of *Microhyus reisi*, Silveirinha, Portugal. **D**. Schematic drawing with dental terminology of the m2 UNLSV3-246 of *Microhyus reisi* Antunes, Estravis, and Russell, 1987, Silveirinha, Portugal.

two known species belonging to *Microhyus* by the slight transverse development of the crown and the relative small size of the hypocone; but it is more derived in being larger with centrally positioned, more bulbous cusps. MNHN L-3-BR certainly represents a new taxon, likely a new species of *Microhyus*; this form is, however, still insufficiently documented to be formally defined.

Microhyus Teilhard de Chardin, 1927

Type species: *Microhyus musculus* Teilhard de Chardin, 1927, earliest Ypresian, Dormaal, Belgium.

Microhyus musculus Teilhard de Chardin, 1927

Holotype: IRSNB M115, left M1.

Localities: Dormaal (type locality), Belgium; Suffolk Pebble Beds, England; ?Tremp, Spain.

Age: ?MP6b and MP7 (late Thanetian to early Ypresian, Paleocene–Eocene).

Referred material from Dormaal.—IRSNB M1340 (= DI-2077RS) left p2; DIIC2037RS, right p2; IRSNB M1336, left p4; DIIA1905RS, left p4; IRSNB M1337 (= DIII794RS), left m1; D62, right m2; IRSNB M1338, right m2; IRSNB M1339, left m3; IRSNB M1341, right DP4; D61, left M1 (or M2); DIIA1280RS left ?M2; DIIC1934RS, right M3; IRSNB M1342 (= DIIC623RS), right M3.

Measurements.—IRSNB M115, L = 2.4, W = 2.8; DIIC 2037RS, L = 2.1, W = 1.3; IRSNB M1340, L = 1.85, W = 1.2; IRSNB M1336, L = 3.0, W = 2.0; DIIA1905RS, L = 2.75, W = 1.85; IRSNB M1337, L = 2.6, W = 2.2; D62, L = 2.9, W = 2.35; IRSNB M1338, L = 3, W = 2.3; IRSNB M1339, L = 2.7, W = 2.1; IRSNB M1341, L > 2.6, W = 2.55; D61, L = 2.6, W > 2.7; DIIA1280RS, L = 2.55, W = 3.0; DIIC1934RS, L = 2.6, W = 2.3; IRSNB M1342, L = 2.55, W = 2.45.

Revised diagnosis.—*M. musculus* differs from *M. reisi* by its more exodaenodont p4; both the protoconid and hypoconid of p4 are sharper, forming a blade-like structure. On p4 to m3, *M. musculus* shows an ectostylid. On m1–m2, *M. musculus* differs from *M. reisi* by more pronounced exodaenodonty, a shorter cristid obliqua, the cusps are more bulbous and closely appressed to one another in the center of the crown. On upper teeth, *M. musculus* differs from *M. reisi* in having a more prominent mesial cingulum bearing an ectocone, and lingual cusps that are less peripheral and more concentrated at the center of the crown.

Description of the new specimens from Dormaal (Fig. 2).—The p2 (IRSNB M1340, Fig. 2E) is biradiculate, exodaenodont, and relatively broad. The protoconid is rather central on the crown and pointed; it bears a well developed mesial crest. The talonid is represented by a small hypoconid. On DIIC2037RS, a possible p3, this cusp is larger and relatively well defined.

The p4 (Fig. 2A) is rectangular in outline, very robust, longer than m1–m2, high-crowned, and shows a considerable

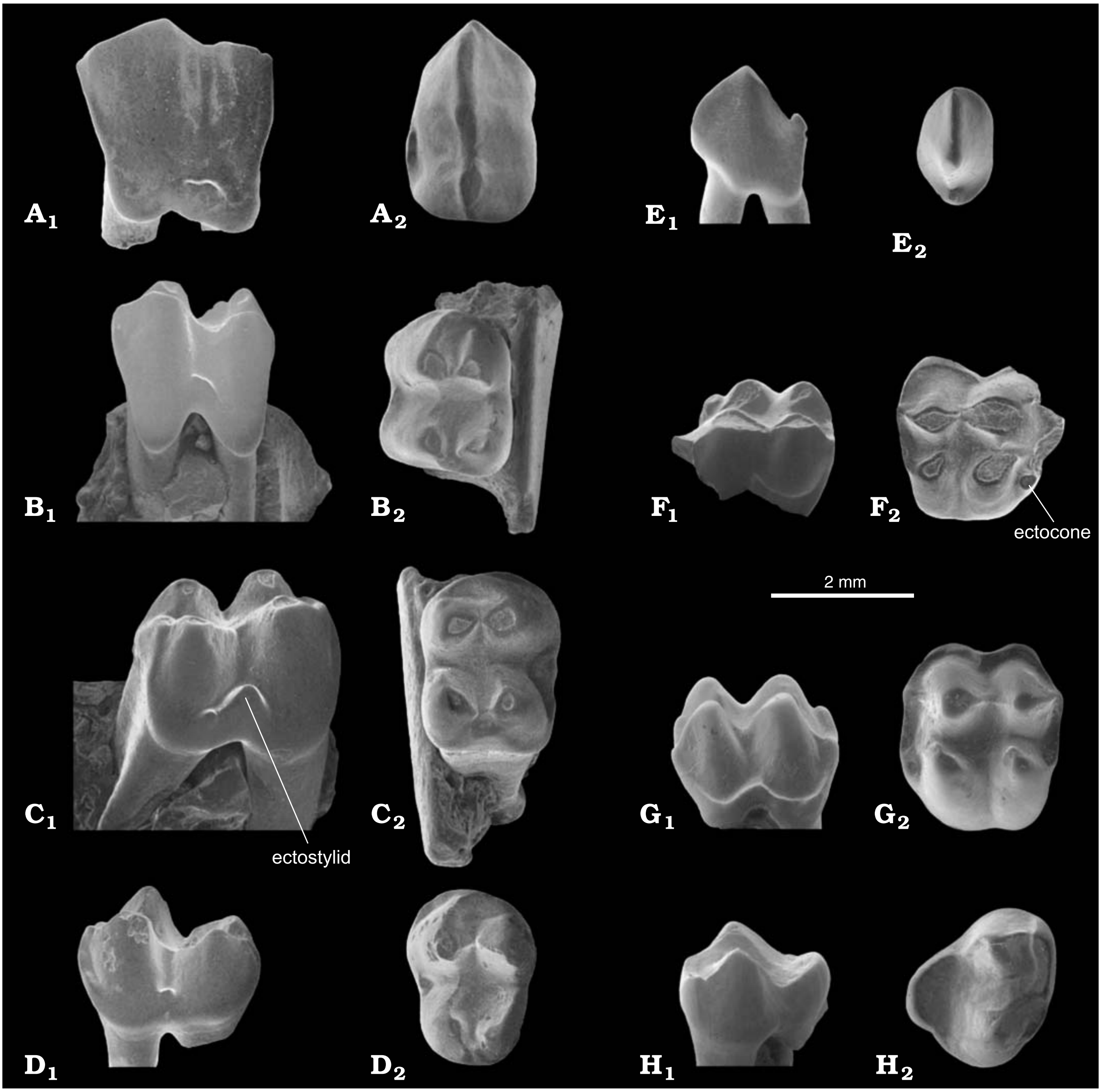

Fig. 2. *Microhyus musculus* Teilhard de Chardin, 1927, earliest Ypresian, Dormaal, Belgium (SEM micrographs). **A**. Left p4, IRSNB M1336 in labial (A_1) and occlusal (A_2) views. **B**. Left m1, IRSNB M1337 in labial (B_1) and occlusal (B_2) views. **C**. Right m2, IRSNB M1338 in labial (C_1) and occlusal (C_2) views. **D**. Left m3, IRSNB M1339 in labial (D_1) and occlusal (D_2) views. **E**. Left p2, IRSNB M1340 in labial (E_1) and occlusal (E_2) views. **F**. Right DP4, IRSNB M1341 in labial (F_1) and occlusal (F_2) views. **G**. Holotype, left M1, IRSNB M115 in labial (G_1) and occlusal (G_2) views. **H**. Right M3, IRSNB M1342 in labial (H_1) and occlusal (H_2) views.

exodaenodonty. The only two differentiated cusps are connected by a longitudinal shearing crest which bears clear apical serration. The protoconid constitutes about two-thirds the tooth length. An incipient paraconid can occur (DIIA1905RS) on the long paracristid. There is no cingulid or trigonid basin.

The lower molars are characterized by swollen crowns and bulbous cusps. The lingual cusps are clearly higher than the labial ones. The four principal cusps are positioned relatively close to the long axis of the teeth. The trigonid and talonid are equal in length, and the trigonid is slightly higher. A mesial cingulid is present; the labial one is absent, but an ectostylid is visible. On the m1 IRSNB M1337 (Fig. 2B), the labial exodaenodonty is well developed, the paraconid is crestiform and mesially positioned. The protoconid and the metaconid are subequal in size and transversely aligned; these cusps are connected by a short, notched protocristid. The metaconid bears a long premetacristid and a reduced postmetacristid. On the talonid, the cristid obliqua is very short; the entoconid and hypoconid are transversely aligned; the entoconid is more developed than the hypoconid and displays an entostylid. There is a notch between the metaconid and the entoconid, and the hypoconulid is lacking. On the m2, the four main cusps are more bunodont, the exodaenodonty is less pronounced, the trigonid is mesiodistally shorter, the paraconid is absent, the paracristid surrounds the mesial border of the tooth and forms a paralophid, the ectostylid is large, and the hypoconulid is distinct between the hypoconid and entoconid at the distal margin of the crown. The m3 is reduced, the paraconid and hypoconulid are lacking, the two talonid cusps are crestifom and smaller than those of the trigonid, the talonid basin is extended.

Of the upper premolars, only a DP4 is documented (Fig. 2F). This tooth was identified as an M1 by Sudre and Russell (1982), because it is essentially molariform and the four cusps are relatively close to the center of the crown as in molars. The large parastylar region is broken, but the crown appears clearly trapezoidal in shape being longer than wide, with the labial margin longer than the lingual one. The paracone is larger than the metacone; there is no preparacrista; the ectoflexus is deep. The metastyle is reduced but the metastylar region is expanded labially. The metacone is compressed labio-lingually. The mesial cingulum is robust and bears an ectocone. This cusp appears well-developed in lingual view. The protocone is larger than the hypocone. The posthypocrista descends to form the distal cingulum, continuing labially to the metastyle. There are no conules.

The holotype IRSNB M115 (Fig. 2G), a probable M1, was described by Sudre and Russell (1982). The three M1s (or M2s) present both ectocone and incipient hypostyle. The hypocone is taller than the protocone. Except for the holotype, the paraconule and metaconule are small but perceptible and twinned with the protocone and hypocone respectively. DIIA 1280RS could be an M2 due to the minor labial expansion of the paracone; the ectocone is strong on this specimen.

The M3 is the smallest of the molars (Fig. 2H). The distal part of the tooth is particularly simplified by the lack of hypocone and the crestiform metacone, which forms a distal lobe. The protocone is bulbous and bears a preprotocrista that reaches the mesial cingulum.

Microhyus musculus? Teilhard de Chardin, 1927

Locality: Pourcy, France.

Age: MP7 (early Ypresian, Eocene).

Material and measurements.—MNHN PYL57 left M1, L = 2.0, W = 2.0.

Discussion (Fig. 1B).—The enamel is chemically eroded on most of the crown. The observed morphology is, however, characteristic of *Microhyus* and reminiscent of that of *M. musculus* in the following diagnostic characters of that species: the mesial cingulum is large and bears an ectocone, both the hypocone and protocone are labially positioned, and the hypocone is higher than the protocone. We assign the tooth from Pourcy to *M. musculus* tentatively because of the paucity of the material and because comparisons with lower molars and premolars of *M. musculus* and *M. reisi* are not possible.

Microhyus reisi Antunes, Estravis, and Russell, 1987

Holotype: UNLSV3-3 (partial left dentary with p3–m1 and alveoli of p1–p2) (Fig. 3D).

Type and only known locality: Silveirinha, Portugal.

Age: MP7 (early Ypresian, Eocene).

Referred material.—446 complete teeth, documenting all molars and premolars (deciduous teeth included), except P1. Astragali (UNLSNC-671, 672, 673, and 674). Calcanei (UNLSNC-675, 676, 677, 678, 679, 680, 681, 682, 683).

Measurements of teeth.—(See Table 1).

Description of new specimens (Figs. 3–6).—The teeth of *Microhyus reisi* were adequately described by Antunes et al. (1987). We describe here the mandible, the dp4 and fragments of maxilla before discussing the dental variability of the species.

The holotype UNLSV3-3 (Fig. 3D) and the specimens UNLSV3-418 (partial left dentary with p3–m2 and p2 alve-

Table 1. Measurements and descriptive statistics for the dentition of *Microhyus reisi*, early Ypresian, Eocene, Silveirinha, Portugal.

Element	N	P	OR	M	SD	CV
p1	11	L	1.38–1.75	1.58	0.11	7.19
		W	0.68–1.0	0.92	0.11	11.56
p2	12	L	1.61–2.05	1.82	0.12	6.55
		W	1.0–1.33	1.11	0.09	8.07
p3	14	L	1.91–2.25	2.1	0.1	4.78
		W	1.07–1.43	1.29	0.1	7.49
p4	26	L	2.21–2.75	2.54	0.12	4.67
		W	1.24–2.0	1.61	0.16	9.88
m1	40	L	2.06–2.55	2.28	0.12	5.46
		W	1.56–2.0	1.77	0.12	6.75
m2	41	L	2.25–3.17	2.64	0.2	7.57
		W	1.84–2.42	2.11	0.15	7.32
m3	30	L	2.06–2.64	2.35	0.15	6.36
		W	1.35–1.88	1.63	0.13	8.27
P2	8	L	1.75–2.0	1.87	0.08	4.46
		W	1.58–2.0	1.84	0.12	6.46
P3	14	L	1.84–2.33	2.06	0.13	6.45
		W	2.18–2.7	2.44	0.18	7.18
P4	30	L	1.84–2.5	2.12	0.15	7.08
		W	2.44–3.45	2.8	0.23	8.16
M1	65	L	1.91–2.63	2.28	0.16	7.02
		W	2.33–3.33	2.71	0.19	7.09
M2	47	L	2.18–2.92	2.47	0.16	6.64
		W	2.74–3.93	3.23	0.26	8.04
M3	39	L	1.73–2.58	2.1	0.17	7.98
		W	1.83–2.55	2.13	0.16	7.32

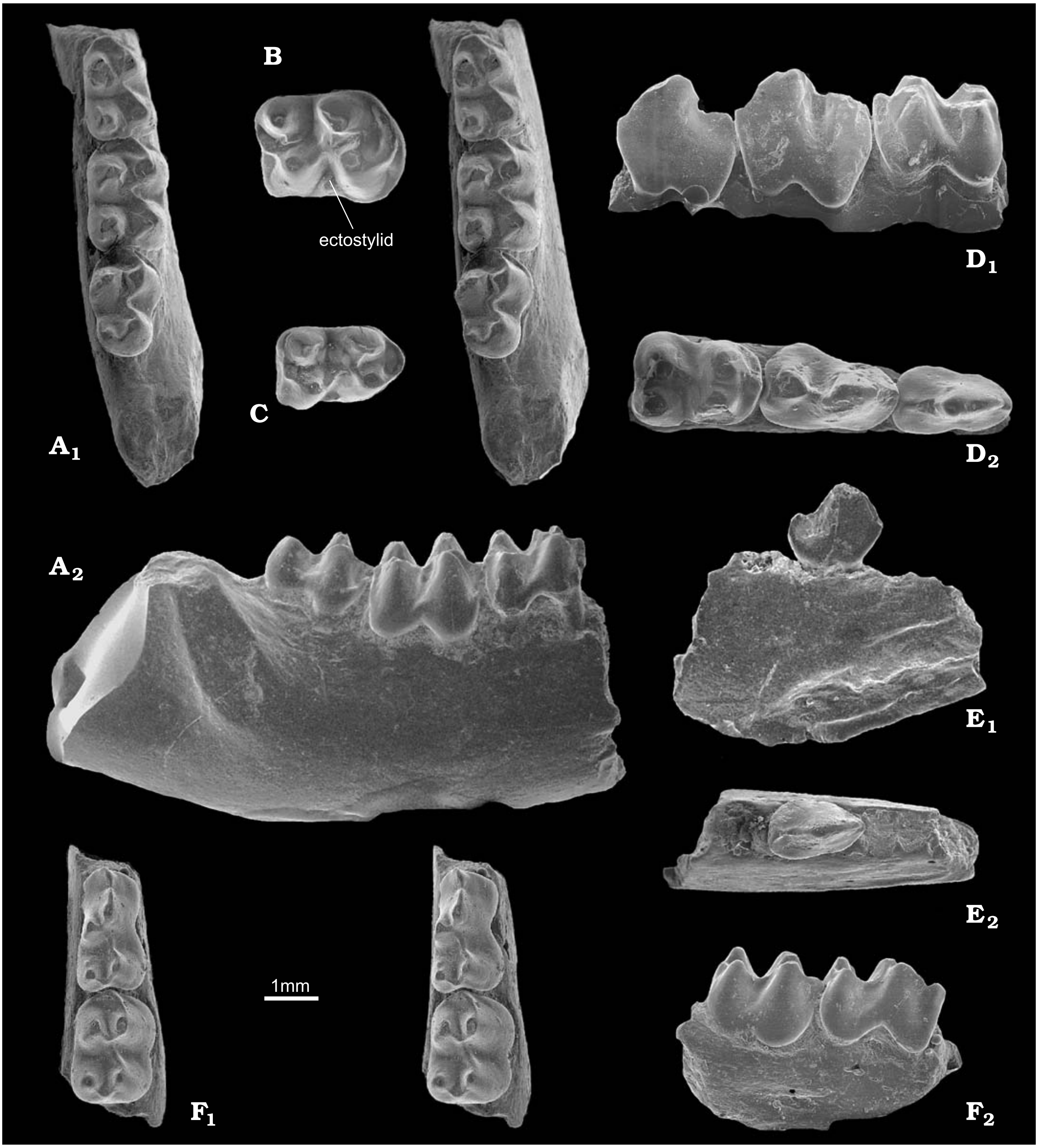

Fig. 3. *Microhyus reisi* Antunes, Estravis, and Russell, 1987, early Ypresian, Silveirinha, Portugal (SEM micrographs of epoxy resin casts). **A**. Right m1–m3, UNLSNC-11 in occlusal (A_1, stereophotographs) and labial (A_2) views. **B**. Right m2, UNLSNC-216 in occlusal view. **C**. Right m1, UNLSNC-35 in occlusal view. **D**. Holotype, left p3–m1, UNLSV3-3 in labial (D_1) and occlusal (D_2) views. **E**. Left p2, UNLSNC-153, with c, p1 and p3 alveoli in lingual (E_1) and occlusal (E_2) views. **F**. Right Dp4–m1, UNLSNC-155, in occlusal (F_1, stereophotographs) and labial (F_2) views.

oli), UNLSNC-11 (partial right dentary with m1–m3) (Fig. 3A), UNLSNC-87 (partial right dentary with p4 and p2–p3 alveoli), and UNLSNC-153 (partial left dentary with p2 plus c-p1 and p3 alveoli) (Fig. 3E) provide evidence of the mandibular morphology of *M. reisi*. A composite construction of the mandible is given in Fig. 4. In lateral view, the horizontal

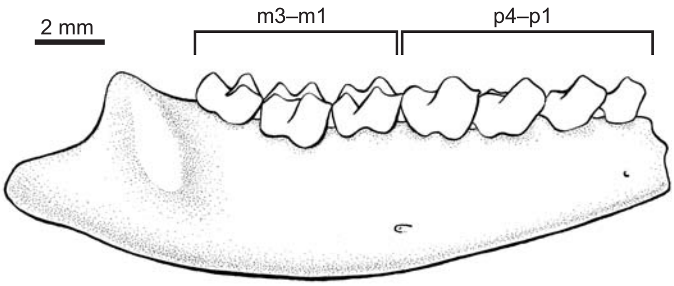

Fig. 4. Reconstruction of the mandible of *Microhyus reisi* based primarily on UNLSV3-3, UNLSV3-418, UNLSNC-11, UNLSNC-87, and UNLSNC-153.

ramus appears relatively robust and increases in depth distally. The c-m3 form a continuous series without diastema. The elongate and strongly ankylosed symphysis extends distally to p2. Two mental foramina are present, one beneath the mesial root of p1 and another beneath the mesial root of m1. The masseteric crest and fossa are well developed.

The specimen UNLSV1-65 of the original collection is interpreted here as a dp3; the dp4 being represented in the new material by the specimen UNLSNC-155 (partial right lower jaw with dp4–m1 (Fig. 3F). This tooth is exodaenodont, longer than the m1, and 8-shaped in outline. The crown is narrow under the metaconid and relatively broad under both the paraconid and talonid. The trigonid represents more than half the length of the crown. The three cusps of the trigonid are labio-lingually compressed, the paraconid is particularly crestiform. The paracristid is long and rectilinear. The metaconid is lower than the protoconid and distally offset, and both cusps are separated by a deep notch. The talonid is similar to that of m1 of *M. musculus*.

The specimens UNLSNC-14 (a right maxilla fragment with P4–M2) (Fig. 5A), UNLSNC-205 (a right maxilla fragment with P4–M3) (Fig. 5C), and UNLSNC-283 (a left maxilla fragment with P4–M2) uphold the identifications of isolated upper cheek teeth made by Antunes et al. (1987). As P4 is molariform (i.e., the hypocone is present, the conules are bulbous and larger than those of the molars), this tooth might have been identified as a molar of another taxon. The zygomatic process of the maxilla arises between M1 and M2.

Dental variability of *Microhyus reisi*

Morphological analysis.—The p4 metaconid is extremely variable. According to Antunes et al. (1987), it varies from being absent to being rather voluminous. It is absent on the eleven specimens of the new material, and is only represented by a broadening distal to the protoconid on UNLSNC-141 and 638. In lateral view, the hypoconid can appear very acute when the prehypocristid-postmetacristid notch is very deep (see UNLSNC-206). Exodaenodonty can be well-marked (UNLSV3-3, UNLSV3-417, UNLSV3-89).

On m1–m2, the depth of the protocristid notch and the distance between cusps is variable; on UNLSNC-35 protoconid

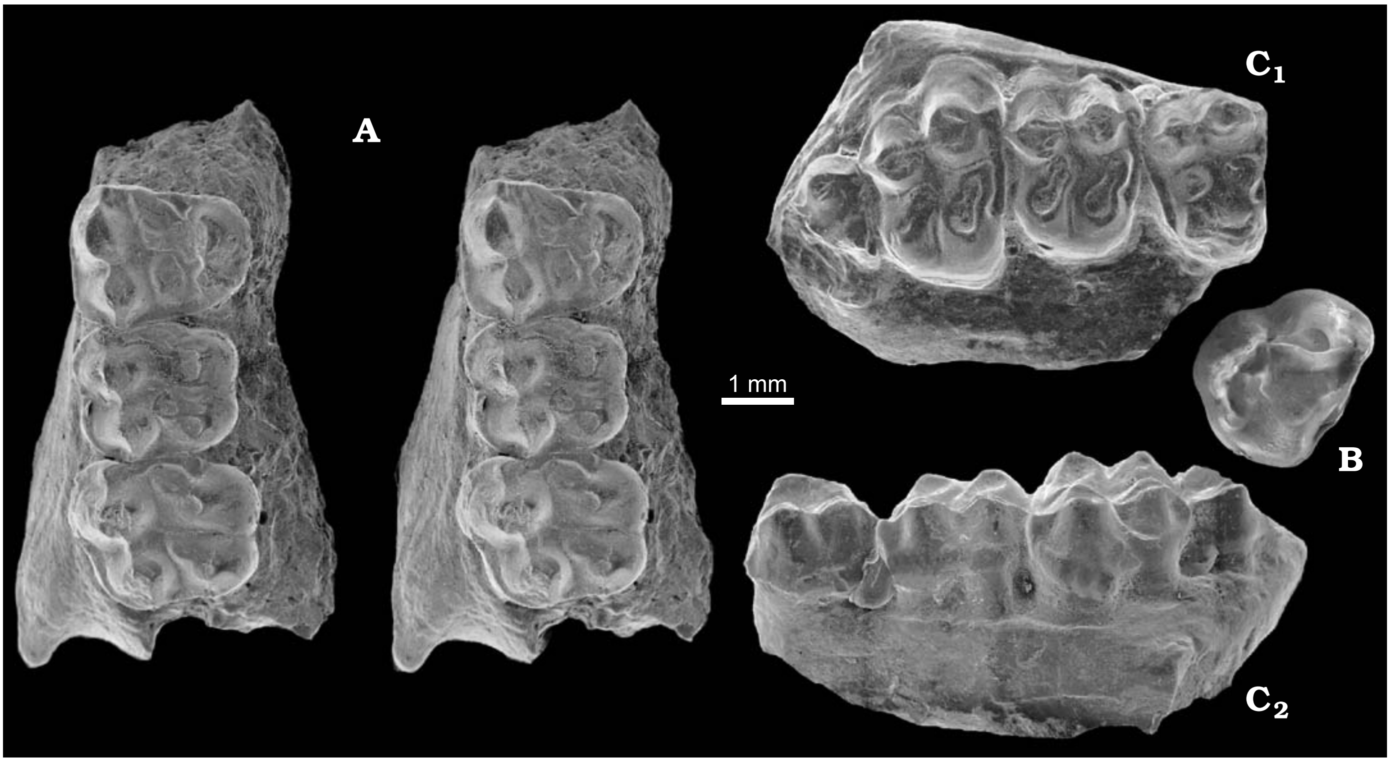

Fig. 5. *Microhyus reisi*, Antunes, Estravis, and Russell, 1987, early Ypresian, Silveirinha, Portugal (SEM micrographs of epoxy resin casts). **A**. Right P4–M2, UNLSNC-14 in occlusal view (stereophotographs). **B**. Right M3, UNLSNC-626. **C**. Right P4–M3, UNLSNC-205 in occlusal (C_1) and labial (C_2) views.

and metaconid are particularly well separated (Fig. 3C). A small ectostylid is common (UNLSNC-137, 345, 315, and 216; Fig. 3B) and a entostylid can occur (UNLSNC-146). A metastylid is usually present, it is particularly well-developed on UNLSNC-137. The m2 UNLSNC-216 presents a marked relief with high crests and deep basins. The cristid obliqua typically joins the trigonid wall below the protocristid notch, but it can be slightly labially offset or linked to the top of the protoconid (UNLSNC-57, 216; Fig. 3B). The paraconid is small to crestiform; the length of the paracristid is irregular and varies in orientation, the trigonid is thus less (UNLSV3-3; Fig. 3D) or more elongate (UNLSNC-35; Fig. 3C).

On m3, the metaconid is often posterolabialy compressed, the hypoconulid is cuspate, small or absent, and a mesoconid can arise on the cristid obliqua (UNLSNC-487). The morphology of the entoconid is very variable on m3: a tiny entostylid can occur (UNLSNC-499), a smooth crest tends to join the cristid obliqua (UNLSNC-13 and 482), or a deep and long notch separates the entoconid and the metaconid (UNLSNC-486). The cristid obliqua usually rises on the labial side of the protoconid. A neomorphic crest can emerge lingually from the cristid obliqua to join the metaconid defining a triangular basin behind the trigonid wall (UNLSNC-499, 482); or the cristid obliqua ends at the top of the protoconid describing a very curved crest (UNLSNC-11, Fig. 3A$_1$), in this case the protocristid notch is very deep.

On P3, the paraconule is always large, an incipient metaconule can be present (UNLSNC-473, 368 and 132), and the postparacrista can bear a sharp metacone (UNLSNC-475 and 132).

The P4 shows a great variability in size and morphology. UNLSNC-111 (Fig. 6D) and 252 are particularly large with a paracone twice the size of the metacone, a huge hypocone and bulbous conules. The paraconule of UNLSNC-118 presents a strong preparaconulecrista that joins the parastyle (Fig. 6E). Specimen UNLSNC-118 is half the size of UNLSNC-111. The hypocone varies from a small cusp not separated from the protocone (UNLSNC-14; Fig. 5A) to a robust, swollen cusp completely separated from the protocone (UNLSNC-111) (Fig. 6D). On UNLSNC-335, the hypocone is also strong, its mesiolingual part is linked to the distal cingulum, and it is connected to the protocone by a narrow crest. On UNLSNC-604, the hypocone bears a third crest that joins the distolabial part of the cusp to the distal cingulum.

On M1–M2, the labial cingulum is absent to robust and continuous (UNLSNC-197, 342, and 139) (Fig. 6K). It can be connected to the centrocrista (UNLSNC-171 and 187), and small cuspules can arise from it (UNLSNC-168). The parastyle is small (UNLSNC-254) to strong (UNLSNC-266). The paraconule and metaconule are generally bunodont, subequal in size, and connected to the protocone and the hypocone, respectively, by short crests (protoloph and hypoloph). The conules can be isolated, reduced to enlarged, rather V-shaped or crestiform. All the morphological intermediates are observed concerning the morphology of these conules. On UNLSNC-267, the conules are small and isolated from the lingual cusps. On UNLSNC-254, the paraconule is in V-shaped and smaller than the metaconule which is isolated from the hypocone. On UNLSNC-476, 319 and 143, the paraconule is bunodont and the metaconule is incorporated into the hypoloph. On UNLSNC-156, the paraconule is connected to the protocone by a short crest and the metaconule is isolated (Fig. 6G). On UNLSNC-256, the conules are absent and both the protoloph and hypoloph are very short.

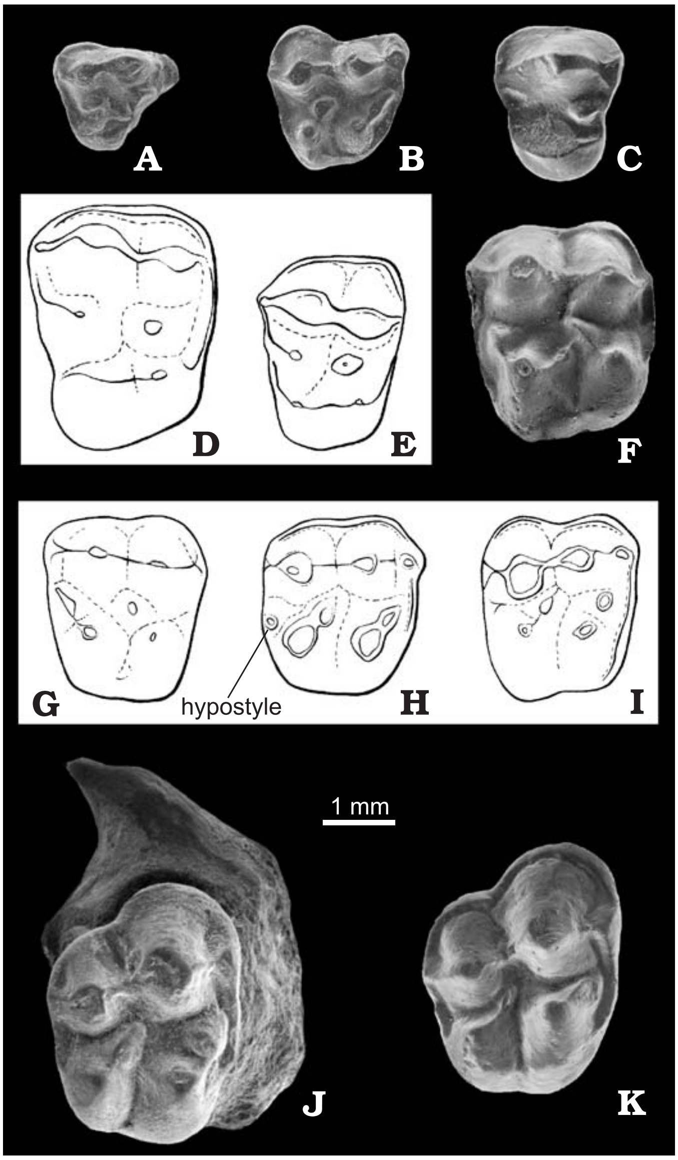

Fig. 6. *Microhyus reisi*, Antunes, Estravis, and Russell, 1987, early Ypresian, Silveirinha, Portugal (SEM micrographs of epoxy resin casts and interpretative drawings showing some aspects of the variability of the species); all teeth in occlusal view. **A**. Right DP3, UNLSNC-122. **B**. Right DP4, UNLSNC-346. **C**. Right P3, UNLSNC-80. **D**. Left P4, UNLSNC-111. **E**. Left P4, UNLSNC-118. **F**. Left M1, UNLSNC-199. **G**. Left M1, UNLSNC-156. **H**. Right M1, UNLSNC-465. **I**. Right M1, UNLSNC-194. **J**. Right M2, UNLSNC-8. **K**. Right M2, UNLSNC-139.

On M1, an ectocone (UNLSNC-266) and hypostyle (UNLSNC-465; Fig. 6H) can occur. UNLSNC-199 is very peculiar by the occurrence of a long postprotocrista joining

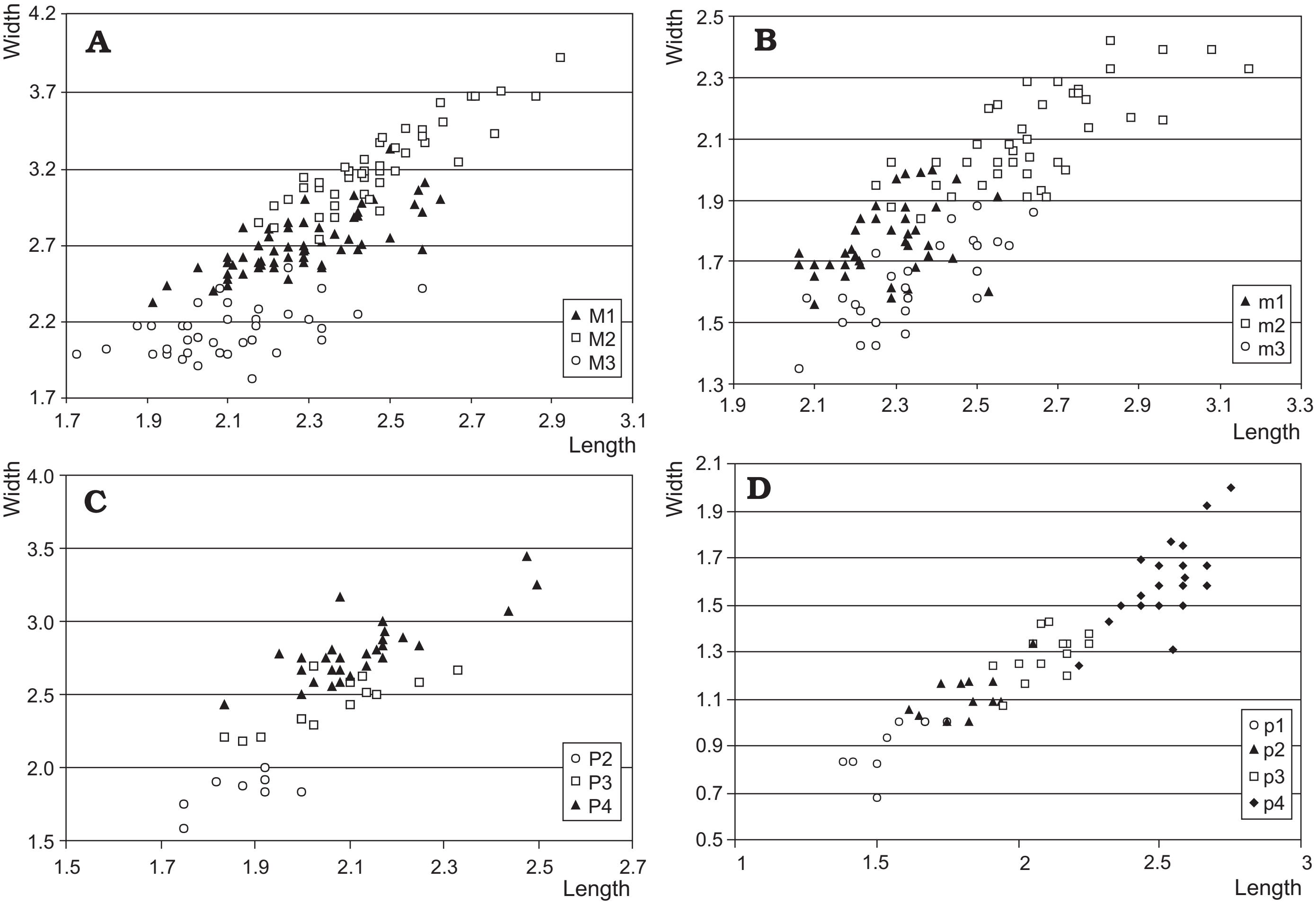

Fig. 7. Bivariate plot of width versus length (in mm) of upper (**A**) and lower (**B**) molars and upper (**C**) and lower (**D**) premolars of *Microhyus reisi*.

the metaconule (Fig. 6F). UNLSNC-194 is characterized by a large hypocone higher than the protocone and displaying a lingual expansion (Fig. 6I). The M2s vary in occlusal outline, because of the more (UNLSNC-228, 319, and 139; Fig. 6K) or less (UNLSNC-14; Fig. 5A) marked labial development of the paracone. On UNLSNC-319 and 139 (Fig. 6K), two very large M2s, the four main cusps tend to be closely appressed to one another in the center of the crown and the conules are completely included in the lophs. On M3 the metacone can be small, crestiform or duplicate (UNLSNC-490); an incipient paraconule and metaconule can occur. On UNLSNC-626, the metaconule is strong (Fig. 5B). The variability of the conules also affects DP3–4. On DP4, the metacone and the cingulum beneath this cusp may form a marked labial expansion (UNLSNC-346; Fig 6B). On the DP3 UNLSNC-602, an incipient hypocone occurs.

Biometric analysis.—Synthetic data and standard statistics on the measurements of the teeth of *M. reisi* are given in Table 1. Bivariate plots of width *versus* length of lower and upper premolars and molars are illustrated in Fig. 7. The scatter plots exhibit an homogeneous distribution pattern for each dental class; however, for the M2/2 the scatter plot shows a relative dispersed distribution, and for the P4s, the largest

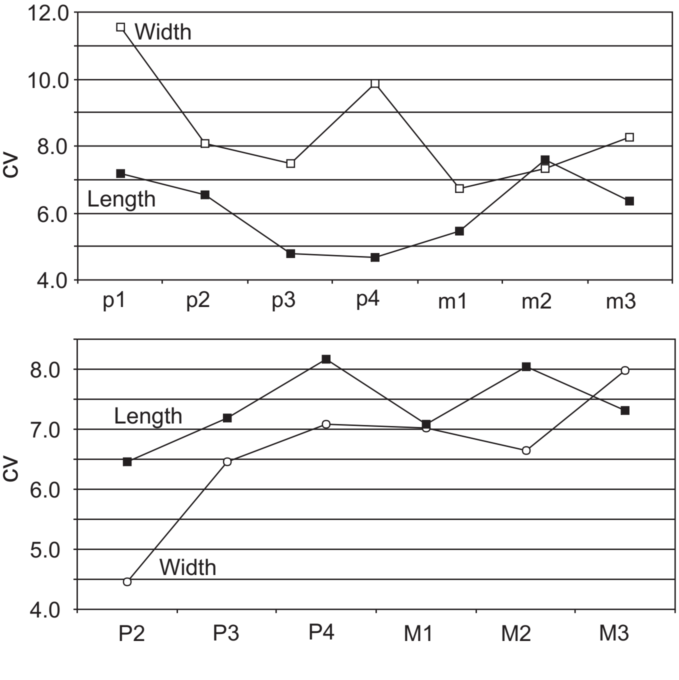

Fig. 8. Coefficients of variation of length and width measurements of premolars and molars of *Microhyus reisi*.

specimens (UNLSNC-111 and 252, UNLSV3-253) seem to be isolated from the other specimens.

The coefficients of variation of length and width dimensions from P2/p1 to M3/m3 are shown graphically in Fig. 8. Studies have shown that large samples of living mammals have coefficients ranging from 3.5 to 8.0 for distal premolars and molars (e.g., Simpson et al. 1960; Gingerich 1974, 1981; Polly 1998). *M. reisi* presents patterns of size variation well within this range for its molars and premolars (except for the width of p4, where v = 9.9). The great labial exodaenodonty of some p4s could explain this high coefficient of variation. In agreement with Gingerich (1974), the m1 is the least variable molar and follows the general mammalian pattern. The same is true for the M1, except for the length of its crown, which is slightly more variable than that of the M2.

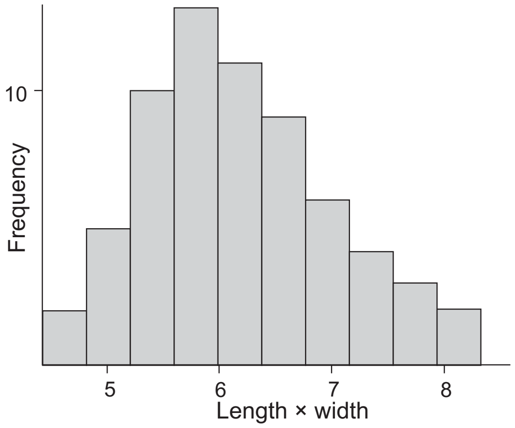

Fig. 9. Histogram of the area (length × width) of M1 of *Microhyus reisi*.

For the most abundantly represented tooth, the M1, a Kolmogorov-Smirnov test (D = 0.09, p-value = 0.62) indicates normality for the distribution of the areas (length × width) of the 65 specimens. The histogram of these areas for the M1 shows a unimodal distribution and confirms that only one species of *Microhyus* exists at Silveirinha (Fig. 9). For other teeth, in particular the lower ones, this unimodal pattern is less evident and reflects the difficulty of measuring with precision the width of the crown when exodaenodonty is prevalent. In conclusion, the dental variability of *M. reisi* affects lower and upper distal premolars and molars. However, the variable characters have a mosaic pattern and they do not define distinct groups.

Comparisons and dental adaptation of *Microhyus*

Comparisons between *M. reisi* and *M. musculus*.—Sudre and Russell (1982), and Antunes et al. (1987) have compared *Microhyus* with other members of the Louisininae. Antunes et al. (1987) discussed an interesting feature of *M. reisi*, the apparent disparity between the upper and lower cheek teeth, which show different stages of evolutionary change. The lower premolars are relatively simple in that the crown is narrow, elongate, and the talonid is reduced; whereas the upper premolars are more complex with both a hypocone and strongly developed conules. Antunes et al. (1987) suggested that the simple p4 represents a reversal, a specialized condition relative to the more molarized morphology of the p4 seen in *Louisina* and *Dipavali* (strong metaconid and well-developed talonid basin, some of which are bicuspate). The new available material belonging to *M. musculus* confirms this hypothesis. Relative to *M. reisi,* this species presents a more advanced condition for the p4 in that it shows a more developed labial exodaenodonty and both higher and sharper protoconid and hypoconid that form a blade-like structure.

From p4 to m3, all specimens of *M. musculus* bear an ectostylid. On m1–m2, *M. musculus* exhibits more pronounced exodaenodonty, a shorter cristid obliqua, and cusps that are more bulbous and closely appressed to one another in the center of the crown. On the upper teeth, *M. musculus* differs from *M. reisi* in having a better prominent mesial cingulum that bears an ectocone. The absence of conules in the holotype of *M. musculus* was cited by Antunes et al. (1987) as another derived trait. The observed variability of conules in the new specimens of the two species suggests that this character should not be given too much weight in arguing that *M. musculus* is more derived than *M. reisi*. Moreover, the oldest louisinine, *Monshyus* from the Paleocene of Hainin (MP1–5), already presents a quadrituberculate upper molar without any trace of conules; the polarity of this dental trait is thus difficult to establish.

Antunes et al. (1987) assumed that the primitive morphology of *M. reisi*, with respect to *M. musculus*, is evidence that the Silveirinha fauna is older than that from Dormaal. The M3/3s of *M. musculus* are bunodont, the crests are blunt, the conules are lacking. *M. reisi* can appear more primitive by its M3/3s bearing conules, sharp crests, and a metacone in several specimens. However, the more pronounced reduction in size of the M3/3s in *M. reisi* is clearly derived. The M3 represents 73% of the area of the M1 in *M. reisi* (86% in *M. musculus*) and the m3 represents 95% of the area of the m1 (99% in *M. musculus*). These traits suggest that *M. musculus* and *M. reisi* belong to two different lineages. Moreover the apparent occurrence of *M. musculus* in the late Paleocene Tremp Formation (Lopez-Martinez and Pelaez-Campomanes 1999) suggests that this genus has little biochronological value for determining the relative ages of the Silveirinha and Dormaal faunas. The position of Silveirinha relative to the Paleocene/Eocene boundary remains uncertain. Lacking complementary data, we maintain the locality in the early Ypresian and we correlate it with the reference level MP7.

Dental function of *Microhyus*.—In *M. reisi*, due to the reduction of the m3 and the enlargement of p3–p4, the length of p2–p4 is greater than the length of m1–m3. We can assume an important role of the premolars during the chewing process. The exodaenodont and blade-like p4 of *Microhyus* (especially in *M. musculus*) works against the enlarged and flattened P4. The two large conules on P4 constitute a third row of cusps between the paracone-metacone and the protocone-hypocone. Even if the sectorial p4 is not completely plagiaulacoid (absence of both the neomorphic apical cusps and serrated cutting edges), this shearing complex is evocative of the independently evolved blade-like teeth in several groups of mammals such as some multituberculates and carpolestid plesiadapiforms (Krause 1982; Biknevicius 1986; Kielan-Jaworowska et al. 2004). The paraconule can present a strong preparaconulecrista that joins the cingulum labially (UNLSNC-118). This structure is also very similar to that observed in the P3–P4 of carpolestids in which the conule develops a crescentic ridge that stretches labially toward the mesial side of the tooth (Smith et al. 2004). The quadrituberculate and bunodont molars of *Microhyus* suggest a frugivorous diet; such a dietary class is also proposed for *Louisina* and *Dipavali* (Hooker 1998). The wear pattern of the teeth exposes dentine on the tops of the cusps, and the teeth seem to have a crushing function. Moreover, the crescentic pattern developed in numerous specimens of *M. reisi* (e.g., UNLSNC-155; Fig. 3F) and the P4/p4 morphology also suggests a high fiber diet, perhaps supplemented by some insects (*Microhyus reisi* and *M. musculus* are small species with a body weight of less than 500 g).

Comparisons with Paleogene Macroscelidea.—Tabuce et al. (2001) compared in detail *Microhyus* with the Herodotiinae, the basal North African elephant-shrews. *Microhyus* and herodotiines share a molariform P4, exodaenodont p4, tetratuberculate M1–2/1–2, and small M3/3. On the upper molars, the shared characters also include a short hypoloph and protoloph, a large hypocone at least subequal in high with the others cusps, and a trend toward the reduction of both paraconule and metaconule. On lower molars, the paraconid is incipient and the hypoconulid is either very reduced or absent. We improve the comparison by two additional dental characters. Numerous M2s belonging to *M. reisi* (e.g., UNLSNC-139, 228, and 319) are very similar to the M2 of *Metoldobotes* (early Oligocene, Egypt) by the extreme labial development of the paracone. The peculiar M1 UNLSNC-194 is also similar to the M1 or M2 of *Nementchatherium* (late middle to late Eocene, Algeria) in having a large hypocone higher than the protocone and in displaying a lingual expansion (Fig. 6I).

Tarsal morphology of *Microhyus reisi*, and its implications for the phylogenetic position of Louisininae

Generic attribution.—In the Silveirinha collection, ten relatively well preserved placental astragali are known, and six morphs are documented. Two of these morphs, represented by one specimen each, can be easily identified as belonging to the orders Perissodactyla and Artiodactyla. According to the identified genera from the site, these astragali belong to *Pachynolophus* (see Hooker 1998: 433) and *Diacodexis*. A small astragalus is similar in morphology to, but smaller than, that of *Paschatherium dolloi* from Dormaal (Godinot et al. 1996); this specimen is thus attributed to the *Paschatherium* species from the site (*Paschatherium marianae*). The most abundant morph is represented by four specimens. As for calcanei, fourteen specimens document six different types. Most of them cannot be identified with precision. One morph is represented by nine specimens that fit well, in size and morphology, with the most abundant type of astragalus. This type is documented by 40% of the astragali and 65% of the calcanei. We attribute this morph to *Microhyus reisi*. This attribution is supported by compatible size and similar level of relative abundances for dental specimens (more than 45% of the latter belonging to *M. reisi*).

Morphology.—The right astragalus (UNLSNC-671) is well preserved and quite complete (Fig. 10). Measurements are given in Table 2. This bone appears robust in outline due to a mediolaterally broad body and neck. The astragalar trochlea, for articulation with the distal tibia, is well defined, wider than long, and proximally prominent. There is no extension of the trochlea onto the neck. On UNLSNC-672 and UNLSNC-674 (Fig. 10B), the trochlea is more deeply grooved and clearly pulley-shaped. On all specimens, the groove is medially offset. The neck forms an angle of 15° with the trochlea. The distinctly asymmetrical trochlea bears moderately sharp borders, and the lateral crest is more expanded and longer than the medial one (lateral crest length is 2.2 mm, medial crest length is 1.7 mm). Both crests are semicircular describing an arc of 180°, the lateral crest having a greater radius of curvature. In proximal view, the crests are nearly parallel, the lateral one is only slightly medially curved, the trochlea is thus plantarly narrower. The fibular facet is wide and helical. A semicircular depression for the attachment of the fibuloastragalar ligament

Table 2. Measurements for the astragalus UNLSNC-671 and calcaneus UNLSNC-682 of Eocene *Microhyus reisi*, Silveirinha, Portugal.

astragalus	proximal width of astragalar body	2.7
	lateral length of astragalar body	2.4
	maximum width of astragalar body	2.0
	proximal width of astragalar trochlea	1.7
	length of neck parallel to long axis	1.2
	maximum length of astragalar parallel to long axis	4.2
	long axis of astragalar head	1.8
	short axis of astragalar head	1.1
calcaneus	minimum width of calcanei tuber	1.2
	minimum height of calcanei tuber	2.5
	proximodistal length of the peroneal process	2.2
	maximum width of the peroneal process	0.9
	maximum length of calcaneum parallel to long axis	8.7
	dorsoplantar height of cuboid facet	2.4
	dorsoplantar height of distal plantar tubercle	0.9

occurs plantar to the fibular facet. On UNLSNC-671, the lateral process of the astragalus is broken; on other specimens it is present but reduced. On the medial side of the bone, the tibial facet is prolonged by a distinct, small concave depression (= cotylar fossa) for articulation with the tibial malleollus, which is dorsomedially delimited by a small tuberosity. The neck is proximodistally short and very broad mediolaterally. In plantar view, the groove for the tendon of m. flexor fibularis continues onto the plantar side of the astragalar trochlea. The proximomedial plantar tuberosity is prominent. The two astragalocalcanear articular surfaces are separated by the deep-grooved sulcus astragali. There is no sign of an astragalar foramen either plantarly or dorsally. The ectal facet occupies one-third of the plantar side of the body, is moderately concave, obliquely oriented to the long axis, and approximately triangular in outline; it is wide medioproximally and narrow laterodistally. The flat sustentacular facet occupies most of the plantar side of the neck and has an irregular outline, being oriented proximodistally with respect to the ectal facet. The sustentacular facet exhibits two incipient proximomedial and distolateral expansions; the latter is not confluent with the navicular facet. The astragalar head is dorsoplantarly compressed and deep laterally, and the navicular facet is kidney-shaped in distal view. This articular surface extends far onto the medial side of the neck to the cotylar fossa. There is no apparent contact for the cuboid.

The right calcaneus UNLSNC-682 is well preserved and complete (Fig. 10). Measurements are given in Table 2. On UNLSNC-675 the peroneal process is broken; other specimens are more fragmentary. Like the astragalus, the calcaneus is robust, and proximodistally elongated; the tuber calcanei makes up half of the length of the bone. The tuber calcanei is compressed mediolaterally and expands dorsoplantarly, and its proximal edge bears two rounded processes which are particularly well preserved on UNLSNC-681 and UNLSNC-680. The convex and crescentic ectal facet is proximodistally elongated, representing one-third of the calcaneus length, and it is situated about midway along the length of this bone. The long axis of the ectal facet forms an angle of 25–30° with the long axis of the tuber calcanei. There is no fibular facet on the lateral side of the calcanear protuberance. The sustentaculum astragali strongly projects on the medial side of the calcaneus; the sustentacular facet is flat and ovoid. The peroneal process is wide, distolaterally tilted, and very distally situated, but it does not reach completely the distal edge of the calcaneus. The peroneal process is broken on UNLSNC-675, but judging from the morphology of its medial part, which is still visible, it is certain that it had the same characters observable on UNLSNC-682. The cuboid facet is evenly and slightly concave, with its major axis mediolateral and oriented at an acute angle (~70°) to the long axis of the calcaneus. In distal view, the cuboid facet is subelliptical in outline and wide mediolaterally. Its medial edge projects by a crest that joins the sustentaculum; on UNLSNC-675, this crest is well developed. On the plantar side of the calcaneus, the distal tubercle is robust and does not reach completely the distal side of the calcaneus, it is separated from the cuboid facet by a short longitudinal groove for the plantar calcaneocuboid ligament. In distal view, a distal plantar tubercle is medially offset to the midline of the cuboid facet.

Functional interpretation.—The upper ankle joint of *Microhyus* is characterized by the pulley-shaped astragalar trochlea with semicircular crests that tend to limit tibio-astragalar motion to flexion/extension. The deep-grooved trochlea, with moderately sharp crests, is indicative of increased lateral stability and dynamic movements such as those observed in cursorial and/or saltorial mammals (Lewis 1989). The loss of the fibular facet of the calcaneus also points to lateral stability (Szalay 1977). Moreover, the complete obliteration of the astragalar foramen allows a slightly greater arc of rotation of the astragalus on the tibia. The calcaneus of *Microhyus* is elongated both proximally and distally to subtarsal joints, a morphology also characteristic of cursorial and/or saltorial mammals. In addition, the relatively small and similar size of the sustentacular facet on the astragalus and calcaneus indicates very little lateral movement of the foot (eversion and inversion) in the lower ankle joint.

The asymmetrical tibial trochlea on the astragalus, with the lateral edge higher than the medial one, is known to be a mechanism for facilitating some degree of inversion (Prasad and Godinot 1994). The curved and longitudinally oriented facets between the astragalus and calcaneus also suggest possible lateral motion. On the transverse tarsal joint, according to Szalay and Decker (1974), a laterally deep and dorsoplantarly compressed astragalar head is indicative of habitual inversion. The very extensive navicular facet of the astragalus suggests an unusually great range of mobility of the transverse tarsal joint (Szalay 1977). The absence of a cuboid facet on the astragalus also indicates flexibility. Finally, the prominent peroneal process on the calcaneus indicates enhanced eversion and adduction by increasing the mechanical advantage of the peroneal musculature.

Nevertheless, considering the functional inference of the deep-grooved astragalar trochlea, we may infer that *Microhyus* was a terrestrial mammal capable of rapid running or jumping. The morphology of both lower ankle and transverse tarsal joints, which allows significant inversion and eversion abilities, may be adequate for a foot adjusting to terrestrial conditions.

Comparisons.—Most of the “condylarth” groups (arctocyonids, periptychids, mioclaenids and phenacodontids) are distinct from *Microhyus* in their tarsal morphology. *Phenacodus* presents some similarities in its astragalar trochlea (dissymmetry, deep groove); but it appears that these similarities are biomechanical convergences, in view of the several observed differences (e.g., astragalar foramen present, extreme reduction of the peroneal process and occurrence of a fibular facet on the calcaneus). The tarsus of some primitive eutherians is more evocative of that of *Microhyus*. The cimolestid *Procerberus* and leptictids (Szalay 1977, 1985) share with *Microhyus* the combination of primitive (peroneal and sustentacular

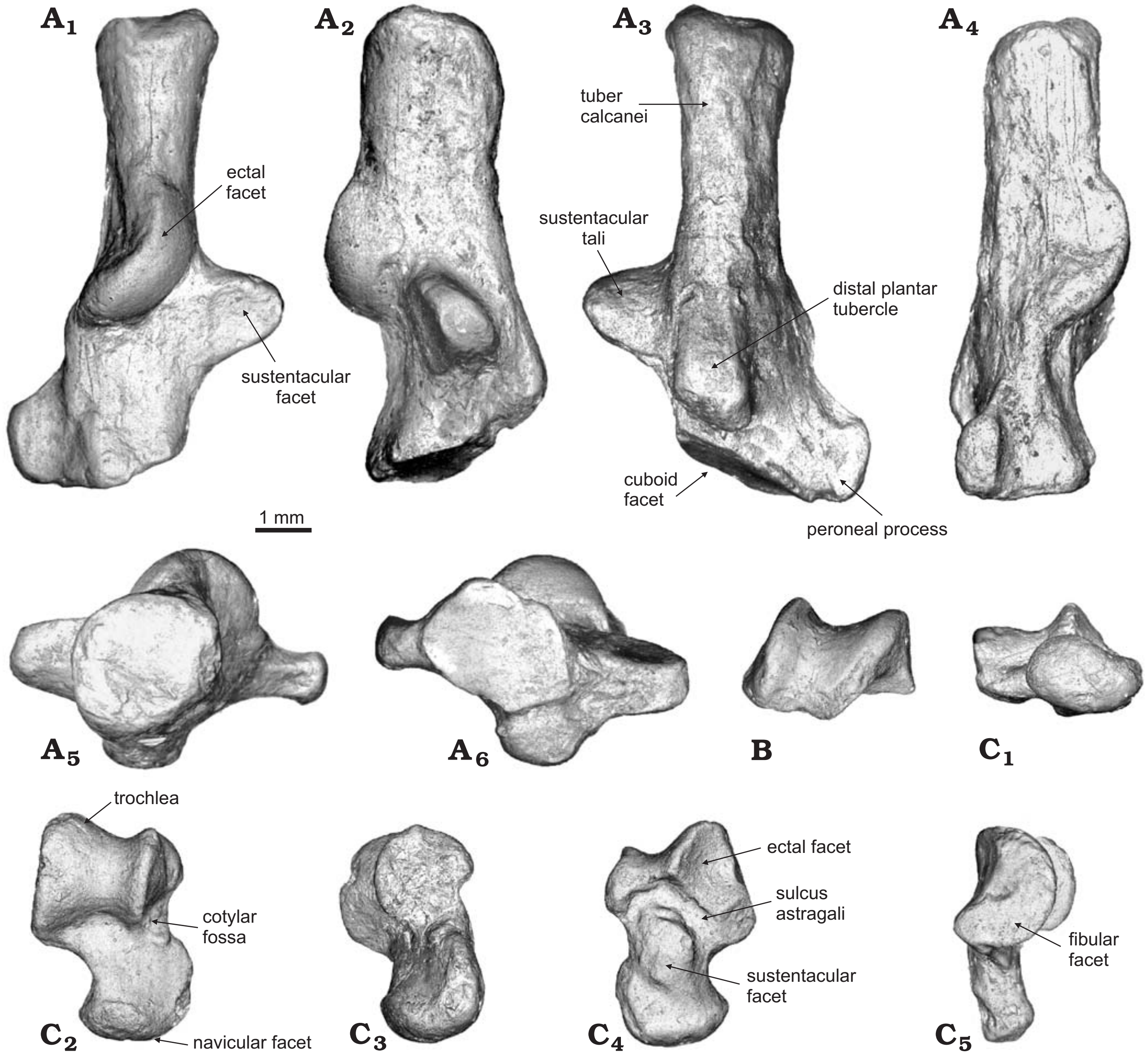

Fig. 10. *Microhyus reisi*, Antunes, Estravis, and Russell, 1987, early Ypresian, Silveirinha, Portugal (inverse SEM micrographs of epoxy resin casts). **A**. Right calcaneus UNLSNC-682 in (A_1) dorsal, (A_2) medial, (A_3) plantar, (A_4) lateral, (A_5) proximal, and (A_6) distal views. **B**. Right astragalus UNLSNC-674 in proximal view. **C**. Right astragalus UNLSNC-671 in (C_1) distal, (C_2) dorsal, (C_3) medial, (C_4) plantar, and (C_5) lateral views.

processes transversally developed, dissymmetrical astragalar trochlea, and mediodistal orientation of the cuboid facet on the calcaneus) and derived characters (deep-grooved trochlea and lack of foramen on the astragalus, short tuber calcanei and absence of fibular facet on the calcaneus).

Hyopsodontids known by tarsal remains are rare. Those of *Hyopsodus* were described by Gazin (1968); Godinot et al. (1996) described those of *Paschatherium*, and more recently Zack et al. (2005) described those of *Apheliscus* and *Haplomylus*. In their calcanei, *Hyopsodus* and *Microhyus* are very similar and differ from *Paschatherium* by the long body and the less distal position of the peroneal process. In its astragalus, *Hyopsodus* differs from *Paschatherium* and *Microhyus* by the longer and narrower neck, the less well grooved trochlea with no medial crest, the lack of cotylar fossa, the occurrence of both a cuboid facet and foramen on the plantar side, and by the more transverse orientation of the ectal facet. Godinot et al. (1996) argued that the differences in the astragalus of *Paschatherium* and *Hyopsodus* are the result of a marked adaptive divergence and that the similarities in the calcanei are the result of close phylogenetic relations between the two genera. However, as Hooker (2001) assumed, we suspect that most of the calcanear characters shared by *Paschatherium* and *Hyopsodus* are primitive placental traits. The astragalus of *Paschatherium* differs from that of *Microhyus* by its smaller size, a less symmetric trochlea with a higher lateral crest, a larger cotylar fossa with a robust distal process, and a greater angle between the trochlea and the long axis of the neck. The calcaneus of *Paschatherium* differs from *Microhyus* in having a shorter body (the distance between the ectal and cuboid facets is shorter), a more distal peroneal process, and by the orientation of the distal edge of the sustentaculum tali; the latter trait being variable in *Microhyus*. Both genera have a number of unifying features such as the large ectal facet that represents one-third of the calcaneus length, the angle between the ectal facet and the tuber is equivalent, the fibular facet is lacking, the sustentaculum is medially prominent, the sustentacular facet has the same weak concavity, and the cuboid facet is similarly dorsoplantarly compressed in outline. On astragalus, *Microhyus* shares with *Paschatherium* a short and wide neck, deep-grooved trochlea that continues onto the plantar side, lack of an astragalar foramen, similar development, and same orientation of the ectal, sustentacular and navicular facets. Consequently, although on the basis of dental characters Tabuce et al. (2001) suggested that *Microhyus* should be removed from the louisinine subfamily, similarities in both the astragalus and calcaneus of *Microhyus* and *Paschatherium* undoubtedly point to a close phylogenetic relationship between both genera within the louisinines. Most of the shared characters between *Microhyus* and *Paschatherium* are also observed in *Apheliscus* and *Haplomylus*; the development of the cotylar fossa on the astragalus is particularly significant. *Apheliscus* and *Haplomylus* differ, however, from louisinines by the occurrence of a cuboid facet on astragalus, and by the reduction of the peroneal process plus the presence of a fibular facet on calcaneus.

Godinot et al. (1996) proposed that the occurrence of the cotylar fossa, the lack of foramen and the deep-grooved astragalar trochlea seen in *Paschatherium* is suggestive of possible relationship with hyracoids. Zack et al. (2005) considered also the cotylar fossa of *Apheliscus*, *Haplomylus*, and *Paschatherium* as a derived character shared with macroscelidids. Considering the supposed *Microhyus*-macroscelidids relationship (Tabuce et al. 2001), the astragali and calcanei of louisinines and macroscelidids need to be compared. The oldest tarsal remains attributed to macroscelidids are known from the East African Miocene (Stromer 1926; Patterson 1965; Butler 1984), and their morphology is very similar to that of living macroscelidids. On the astragalus, macroscelidids and louisinines share the lack of a plantar foramen, the occurrence of a cotylar fossa, and the deeply grooved trochlea with well-marked crests. Moreover, the neck forms a similar angle with the trochlea. In macroscelidids, however, the trochlea is narrower, the medial crest is longer and surrounds the wider and deeper cotylar fossa (the tibial medial malleolus forms a ball-and-socket articulation with the astragalus), the neck is longer and slender, and the navicular facet is flatter (*Myohyrax*) or pivot-like (*Petrodromus*). On the calcanei, two major differences distinguished macroscelidids from louisinines: the lack of peroneal process and the medio-lateral orientation of the calcanear protuberance that bears a fibular facet; on other traits, both groups are more reminiscent. These comparisons indicate that recent and living macroscelidids are distinct from louisinines in their tarsal anatomy. Nevertheless, these differences could be explained by the great chronological divergence between these groups. The recent discovery of tarsal remains belonging to basal (Eocene) macroscelidids would be more adequate to discuss the possible macroscelidid-louisinine relationship.

Conclusion

The study of the pedal anatomy of *Microhyus* allows us to confirm the monophyly of the louisinine subfamily. In dental morphology, two representatives of this subfamily, *Paschatherium* (Denys and Russell 1981) and *Microhyus* (this paper), are very variable. Godinot et al. (1996) advocated a scansorial mode of locomotion for louisinines, similar to that of sciurid rodents. However, the astragalus and calcaneus of louisinines show similar size of the sustentacular facet, which indicates little transverse movement of the foot in the lower ankle joint. In sciurids, the sustentacular facet on the astragalus is much larger than its counterpart on the calcaneus, and allows intense transverse movement. Considering the deeply grooved astragalar trochlea, which indicates extensive flexion-extension movement of the foot, we argue that louisinines were terrestrial mammals capable of rapid running or jumping.

The tarsal bones of the louisinines present no affinity with any group of condylarths except for *Haplomylus* and *Apheliscus*. As *Microhyus* and *Paschatherium* are very distinct from *Hyopsodus*, we suggest that Hyopsodontidae, as defined on the basis of dental morphology, may be polyphyletic. In this way, according to Novacek (1985: 17), "[...] the hyopsodontids are so poorly defined that any small mammal with a rather generalized, nonsectorial dentition may find itself dispatched to this group". Moreover, Cifelli (1983: 33) argued that the family served as wastebasket taxon for "generally primitive ungulates not clearly specialized enough to warrant allocation to other, more advanced suprageneric groups". Only two characters could be apomorphic for the hyopsodontids: the trend toward molarization of the p4 and the labial shift and eventual reduction of the molar paraconid (Archibald 1998). As these characters are widespread in herbivorous mammals, they are not a strong argument to support the monophyly of the hyopsodontid clade. A complete revision of the family is clearly needed.

Based on dental morphology, *Microhyus* and Paleogene macroscelidids show clear similarities, and similarities are also evident in the astragalar morphology of macroscelidids and louisinines. However, in details, the astragalus of modern macroscelidids appears too specialized to be effectively compared with that of *Microhyus* and *Paschatherium*. Finally, we agree with Godinot et al. (1996), who considered that louisinines exhibit some derived characters with the hyracoids in their astragalus. Considering the afrotherian clade (e.g., Murphy et al. 2001), which unifies hyracoids and macroscelidids within the same supraordinal clade, the louisinines could have played a crucial role in the origin of this group. Afrotheria is an odd mixture of living species from Ungulata, Macroscelidea and Lipotyphla, which have no apparent morphological traits to unite them. The Paleocene–Eocene louisinine clade, which also includes an insectivore-like genus (*Paschatherium*) and derived herbivorous ungulate-like genera, appears as a potential archetypical placental ancestor for some afrotherians.

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