A contribution to the evolutionary biology of *Conohyus olujici* n. sp. (Mammalia, Suidae, Tetraconodontinae) from the early Miocene of Lučane, Croatia

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ABSTRACT

We describe here the topotypic series of *Conohyus olujici* n. sp. from the Croatian locality of Lučane. This sample was originally collected by local lignite miners in the 1930's, who conveyed the sample to the parish's Franciscan monk Dr. Josip Olujić. The Lučane *Conohyus* sample includes seven lower jaws and jaw fragments; no upper cheek teeth have yet been recovered. Our use of bivariate statistics, log10 ratio diagrams and a cladistic analysis all reveal that *C. olujici* n. sp. is the most primitive member of the *Conohyus* clade. The analyses reveal that: of the sample considered, only two species are referable to *Parachleuastochoerus*, *P.* sp. and *P. crusafonti*; *Parachleuastochoerus* is the sister-taxon to *Conohyus*; *Conohyus* is a clade, and *C. olujici* n. sp. is the sister-taxon of the *C. steinheimensis-C. simorrensis* and *C. sindiensis* clades. *Conohyus olujici* n. sp. would appear to have occurred at a time when the genus enjoyed a relatively continuous geographic range that extended from southern Europe to South Asia. *Conohyus olujici* n. sp. was evidently adapted to swamp forest habitats. Its paleodiet, as evidenced by its thick molar enamel and labiolingually expanded posterior premolars, likely included hard object frugivory.

KEY WORDS
Mammalia,
Suidae,
Tetraconodontinae,
Conohyus,
Lučane,
Croatia,
phylogeny,
paleobiology.

RÉSUMÉ

Contribution à la biologie évolutive de Conohyus olujici *n. sp. (Mammalia, Suidae, Tetraconodontinae) du Miocène inférieur de Lučane (Croatie).*
Nous décrivons ici la série du topotype de *Conohyus olujici* n. sp. de la localité de Lučane en Croatie. Ce spécimen a été trouvé dans les années 1930 par des mineurs locaux qui apportèrent l'échantillon au Dr Josip Olujić, un moine franciscain de la paroisse. Le *Conohyus* de Lučane comprend sept mâchoires inférieures et des fragments de mâchoires ; aucune dent supérieure n'est connue. Les méthodes utilisées, tant statistiques que cladistiques, convergent pour placer *C. olujici* n. sp. comme le taxon le plus primitif du clade *Conohyus*. Nos analyses montrent aussi que dans l'échantillonnage taxonomique choisi, seules deux espèces peuvent être rapportées à *Parachleuastochoerus, P.* sp. et *P. crusafonti* ; que *Parachleuastochoerus* est le groupe frère de *Conohyus* ; que *Conohyus* est un clade ; et que *C. olujici* n. sp. est le groupe frère du clade composé par *C. steinheimensis-C. simorrensis* et *C. sindiensis. Conohyus olujici* n. sp. aurait existé à une époque où le genre avait une extension géographique continue depuis l'Europe méridionale jusqu'à l'Asie du Sud. *Conohyus olujici* n. sp. était à l'évidence adapté aux habitats forestiers marécageux. Comme le montre l'émail épais de ses molaires et l'expansion labiolinguale des prémolaires postérieures, son régime alimentaire devait inclure des fruits durs.

MOTS CLÉS
Mammalia,
Suidae,
Tetraconodontinae,
Conohyus,
Lučane,
Croatie,
phylogénie,
paléobiologie.

INTRODUCTION

The vertebrate paleontology of Croatia is poorly appreciated despite the fact that there is a local scientific literature. The locality of Lučane is found in one of the more important Croatian Neogene basins. It is located in Dalmatia, southern Croatia, just 35 km north of Split and at the western edge of the Sinjsko polje (Fig. 1). The Sinjsko polje is a typical karst polje surrounded by thick carbonate massifs. The Lučane beds initially drew the scientific interest of a local Franciscan monk, Dr. Josip Olujić in the 1930's. Although never trained as a paleontologist, Dr. Olujić made remarkably sophisticated interpretations of the local gastropod biostratigraphic succession and correlation. The Lučane vertebrate fauna, which besides *Conohyus* also includes *Gomphotherium* and *Brachypotherium*, was discovered in the 1930's by laborers exploiting the local lignite. These fossil remains were given to Dr. Olujić, and retained until recently in the Franciscan Friary of the town of Sinj. In March, 2003, Franciscan authorities approved the transfer of this collection to the Geological and Paleontological Department of the Croatian Natural History Museum (Hrvatski Prirpodoslovni, Muzej [HPM-GP]).

In the Summer of 2000, a joint Croatian-American research group undertook renewed investigations of the Croatian Neogene. These included a new scientific study of Lučane's existing vertebrate fauna, as well as exploration of its geologic sections for fossil plant, invertebrate and vertebrate remains, and the chance to obtain contextual information on the local sedimentary environments, paleoecology and age. We describe here a new species of primitive tetracanodont suid, *Conohyus olujici* n. sp. (HPM-GP 10767), from the upper levels of the Lučane section. We further undertake both a statistical and cladistic analysis of *C. olujici* n. sp. in comparison to two hyothere and seven tetraconodont taxa to better ascertain *C. olujici* n. sp. phylogenetic relationships, biochronologic correlation and biogeographic relationships.

FIG. 1. — Geographic location of Sinj (where the locality of Lučane is situated), Croatia.

MATERIALS AND METHODS

We compare the Lučane suids with two hyotherine, and seven tetraconodont taxa that occur in Europe, Asia and North Africa. These taxa range from the earliest Miocene of Western Europe (*Hyotherium meissneri*) to the latest Miocene of North Africa. The continuous variables used follow the conventions set forth previously by Bernor & Fessaha (2000). This includes up to eight measurements for a single tooth (third molars have the most measurements) and characterization of wear stages (WS; see legend for Table 1).

The Lučane specimens included in our analyses are listed in Table 1. The material is housed in the Croatian National Museum, Zagreb. Bivariate plots and log10 ratio diagrams have been calculated with Excel 2000 using the *Hyotherium meissneri* sample from Westtangente (early Miocene, MN2) as the standard. The taxa which we have studied and that are included in our comparative analysis include:
Hyotherium meissneri: a well known, primitive hyotherine typical for the latest Oligocene-basal Miocene (MN1-2) of Europe, which we have sampled from Westtangente, Germany

TABLE 1. — Measurements and wear stages (**WS**) on Lučane *Conohyus olujici* n. sp. Abbreviations: measurements (M1-8) (in mm): **M1**, basal length; **M2**, occlusal length; **M3**, width across anterior pillar pair; **M4**, height of lingual cusp on lower cheek tooth; **M5**, width across second pillar pair; **M6**, height of second (from mesial-to-distal) pillar pair; **M7**, width across third pillar pair (in advanced tetraconodonts; talonid here); **M8**, height of third (from mesial-to-distal) pillar pair (in advanced tetraconodonts; talonid here) ; wear stages (WS0-6): **0**, unworn; **1**, enamel wear facets developed; **2**, dentine slightly exposed; **3**, dentine highly exposed but no occlusal flattening; **4**, dentine highly exposed and occlusal flattening; **5**, confluence of adjacent enamel basins; **6**, crown completely worn; sex designations: **M**, male; **F**, female; **UK**, unknown; side: **r**, right; **l**, left.

Spec-Id	Sex	Tooth	Side	M1	M2	M3	M4	M5	M6	M7	M8	WS
HPM-GP 10767	M	c	r	17.1	15.3	7.1						
HPM-GP 10767	M	p2	r	14.9	14.6	6.8						
HPM-GP 10767	M	p3	r	16.9	17.8	10.1	13.8					1
HPM-GP 10767	M	p4	r	16.0	15.7	11.8	10.8					2
HPM-GP 10767	M	m1	r	14.4	15.5	12.4	9.1	12.7	8.0			2
HPM-GP 10767	M	m2	r	17.4	18.0	14.6	9.8	14.4	8.4			1
HPM-GP 10767	M	m3	r	22.9	19.8	14.0	10.9	12.8	9.5	12.5	8.3	1
HPM-GP 10768	M	p4	l	15.0	14.7	11.0	9.9					2
HPM-GP 10768	M	m1	l	14.7	14.7		6.5		7.6			3
HPM-GP 10768	M	m2	l	16.6	17.1	12.9	10.0	12.2	8.6			1
HPM-GP 10768	M	m3	l	22.4	19.5	13.3	9.2	11.8	9.0	9.9	7.2	1
HPM-GP 10769	F	c	r	9.9	6.3	14.1						
HPM-GP 10769	F	i3	r	5.2	10.9	19.1						
HPM-GP 10769	F	p3	l	18.8	16.9		13.3					1
HPM-GP 10770	UK	p4	r	15.7	14.1	11.4	11.8					2
HPM-GP 10770	UK	m1	r	14.4	15.1	12.0	7.9	11.9	9.4			4
HPM-GP 10770	UK	m2	r	15.8	17.0	13.3	10.7	12.3	10.5			1
HPM-GP 10770	UK	m3	r	22.1	19.4	13.2	9.5	11.4	8.6	9.8	6.4	1-
HPM-GP 10771	UK	m1	r	14.1	14.0	12.2	8.5	12.3	6.9			3
HPM-GP 10771	UK	m2	r	16.6	16.6	14.3	12.1	13.6	9.5			2
HPM-GP 10771	UK	m3	r	23.8	22.8	14.4	11.0	12.5	10.0	11.1	8.0	1
HPM-GP 10772	UK	m1	l	14.6	14.3	12.9	8.7	13.6	7.1			2
HPM-GP 10772	UK	m2	l	17.6	17.9	15.0	10.2	14.3	8.2			1
HPM-GP 10773	UK	m1	l	13.8		14.4		14.9				
HPM-GP 10773	UK	m2	l	17.0	18.5	15.5	12.0	14.0	11.2			1
HPM-GP 10774	UK	m3	l	23.7	21.9	14.2	11.5	12.4	9.7	10.4	7.2	1

(Hellmund 1991; SMNS [see definition of acronyms below, this section]). This species is characterized by small size, P1/p1 much smaller and lower crowned than P2/p2; P3 with tall pointed principal cusp and well defined distolingual shelf; P4 with two distinct buccal cusps, a single lingual cusp and virtually continuous cingulum; M1-M3 with small, low bunodont cusps and cingulum on all but the lingual margin; M3 with short talon; p4 has a principal cusp that is moderately bifurcated lingually; mandibular molars with cingulum variably expressed on the buccal surface; m1-m2 rectangular shaped; m3 elongate/triangular shaped with decreased width from mesial to distal extent.

Hyotherium shanwangense: a new primitive species of hyothere recently described from the late early Miocene of Shanwang, China (Liu *et al.* 2002; IVPP). The authors have diagnosed this species as (Liu *et al.* 2002: 156): "A medium sized species of the genus. Distinguished from other known species by p1 incisiform, p4 uni-

cuspid and somewhat inflated in the manner of tetraconodonts, with a posterobuccal bulge, upper molars lacking buccal cingulum. The cheek tooth series is continuous from P1 to M3 and p2 to m3, with no gaps between adjacent surfaces of occluding teeth". Dr. Liu has graciously provided us with casts of this material to facilitate our comparisons.

Parachleuastochoerus sp. (to be published as a new species): a primitive, small tetraconodont from the early Vallesian (late MN9) of Rudabánya, Hungary (MAFI). This taxon is characterized as: "A species larger than the genotypic species *Parachleuastochoerus crusafonti*; with generally broader proportions of the maxillary and mandibular posterior premolar and molar teeth; cingulum generally not as strongly developed as in *P. crusafonti* and diminishing with tooth wear; P1 and P2 small, elongate, with low principal cusp and well developed blades mesially and distally; P3 with high principal cusp, buccolingually inflated at its base, and with a distolingual shelf lacking a cusp; P4 as in *P. crusafonti*, with two buccal cusps closely positioned but not as completely fused as in *Conohyus* sp.; maxillary molars with broadly spaced, tall cusps; M3's with variably shaped talon; mesial mandibular premolars small with pointed apices; p3 with tall principal cusp that exhibits slight buccal inflation; p4 with tall principal cusp, slightly developed innenhügel and tall distal heel, with greater buccal and lingual swelling of the base, but still maintaining some "waisting" between distal aspect of the principal cusp and distal heel; m2-m3 relatively broad compared to *P. crusafonti* and *P*. sp. 2 from Rudabánya".

Parachleuastochoerus crusafonti: a taxon which we restrict here to specimens from Vallesian age levels (MN9/10) of Can Llobateres, Spain (Pickford 1981; IPS). This is the smallest tetraconodont species known. Morphologic characteristics include: cheek teeth generally more elongate than in Rudabánya *Parachleuastochoerus* sp., cingulum is well developed on the cheek teeth, anterior premolars small and more slightly built than posterior premolars which are

buccolingually slender; P4 with two buccal cusps incompletely fused along their interfacing margins; molar enamel relatively thin compared to *Conohyus*. We believe that the nomen *Parachleuastochoerus* is appropriately applied to the two taxa defined here: *P. crusafonti* (Spain, MN9) and *Parachleuastochoerus* sp. (Hungary, MN9). There is some evidence that *Parachleuastochoerus* is known from MN8 of Spain, but this requires further study. Liu & Pickford (2001) have described a species of early late Miocene *Parachleuastochoerus*, *P. sinensis*, which we have not been able to study which we discuss further below.

Conohyus sindiensis: a species of Indian Subcontinent *Conohyus* (here, YPM). This species has its oldest occurrence in the Potwar Plateau of 14.5 m.y., and it occurs earlier to the south in Sind at Sehwan locality HGSP-8114, which has been correlated with the 16 m.y. levels of the Potwar Plateau (Bernor *et al.* 1988a, b). *Conohyus sindiensis* is a moderate sized member of the genus that precociously realizes fusion of maxillary P4 paracone and metacone and expansion of mandibular p3 and p4 buccal wall. Anterior premolars are elongate, blade-like structures like all other members of the genus. Molars are more squarish in their outline than in European members of the genus and have thick enamel teeth (see Pickford 1988). In South Asia, *Conohyus* is replaced by the larger tetraconodont lineage *Sivachoerus*, which has plausible affinities with African *Nyanzachoerus*, and forms with gigantic posterior premolars, *Tetraconodon minor* and *T. major*. While we do not necessarily agree with all the conclusions of Van der Made (1999), we acknowledge the importance of this work as essential background to the study of the Tetraconodontinae.

Conohyus steinheimensis: this species has recently been transferred to the genus *Parachleuastochoerus* (e.g., Fortelius *et al.* 1996; [here, SMNS]). Our analysis here suggests that this referral is unwarranted and that *C. steinheimensis* is a bonafide *Conohyus*. *Conohyus steinheimensis* is one of the smaller species of the genus from the

Astaracian (MN7+8) of Central Europe (Chen 1984). This species is still considerably larger than any known *Parachleuastochoerus*, with P1 relatively smaller, P2 somewhat longer, P3 and P4 proportionally much wider than *Parachleuastochoerus*. Maxillary P4 has greater fusion of the two buccal cusps and p4 with greater fusion of the principal cusp and innenhügel than seen in *Parachleuastochoerus*, but still not as advanced in these characters as more derived Indo-Pakistan members of *Conohyus sindiensis*. Molar teeth are elongate with buccal and lingual cingulum generally not as prevalent as in *Parachleuastochoerus*.

Conohyus simorrensis: a species of West Asian and European *Conohyus* that is less well known than *C. steinheimensis*. *Conohyus simorrensis* is more derived than *C. steinheimensis* in its development of the conical posterior premolars, having a mandibular p3 which often is very large and elongate. Mandibular p3 and p4 are not as buccally expanded as in *C. sindiensis*. *Conohyus simorrensis* has a reported stratigraphic range of late Orleanean-early Vallesian (MN5-9) of Europe and West Asia. The sample that we analyse here is derived from Göriach, Austria (NHMW and LMJ) and Paşalar, Turkey (University of Ankara).

Conohyus huenermanni: a small species of European *Conohyus* (*contra* Fortelius *et al.* 1996) from the early Vallesian (MN9) of southern Germany (Heissig 1989; BSP). This species has a small, yet buccally bulging mandibular p4 characteristic of *Conohyus*, not *Parachleuastochoerus*. Molars are as in other European *Conohyus*. Our statistical analysis below confirms *C. heunermanni*'s likely relationship to other European *Conohyus*. We further reject Van der Made's (1999) referral of the Rudabánya small tetraconodont suid (our *Parachleuastochoerus* sp. here) to *Parachleuastochoerus huenermanni*: the Rudabánya form is different at the genus level from *C. huenermanni*, and *C. huenermanni* is not, in our opinion, a parachleuastochoere.

There are a number of species previously referred to *Parachleuastochoereus* and *Conohyus*

that we have not analysed here because of the lack of primary data, or because of taxonomic issues. We provide a brief reference to these taxa below: *Parachleuastochoerus sinensis*: a species of *Parachleuastochoerus* described by Liu & Pickford (2001). We have not seen either the original material, nor casts of this collection, and must rely on the authors' description and their figures for what follows here. This taxon is reported as being the largest parachleuastochoere. The holotype (V.8092.1, MAFI) is a right mandible with part of the canine root and p2-m3. Mandibular p2 and p3 are simple, pointed-conical teeth, with p3 exhibiting no discernable labial bulge. The authors cite the p4 as being triangular in lateral view, and having a weak bifurcation of the main cusp. This bifurcation provides a bucco-lingually aligned pair of cusps unlike any tetraconodonts that we have studied. When the principal cusp and innenheugel are not fused in tetraconodont p4's, we have observed the innenheugel to be offset slightly linguo-distally. The molar teeth would appear to be relatively thin enamelled compared to all *Conohyus* species recognized, and particularly *C. olujici* n. sp. On the type mandible, the m1 has broadly exposed dentine at the cuspid apices, while m2 has slight exposure of dentine on the mesial and distal pairs of cuspids. The maxillary dentition has P3 triangular shaped, with a prominent distolingual cusp and an expanded fovea between the distolingual cusp and the remainder of the crown. This fovea is more strongly developed, both absolutely and relatively, than seen in our sample of *Parachleuastochoerus* sp. and *P. crusafonti*. There is no P4 reported, and this is unfortunate because it can prove to be an extremely diagnostic tooth for the Tetraconodontinae, with fusion of the paracone and metacone, and heavy wrinkling of the buccal enamel wall being expected. Referral of this hypodigm to *Parachleuastochoerus* would appear to be warranted, but not absolutely conclusive.

Conohyus chinjiensis: this species of Siwalik (Indo-Pakistan) *Conohyus* was initially recognized by Pilgrim (1926). It was subsequently synonymised into *C. sindiensis* by Pickford (1988). We follow this synonymy here.

Conohyus indicus: this species was initially recognized by Pilgrim (1926) and was retained by Pickford (1988: 43). Pickford (1988) diagnosed this species as: "A large species of *Conohyus* in which the upper molar row is longer than 60 mm". It should be added that Pickford (1988: 38) has diagnosed the other Siwalik species of *Conohyus* that he has recognized, *C. sindiensis*, as: "A small species of *Conohyus* in which the upper molar row is less than 60 mm long". The holotype of *C. indicus* is a lower premolar, GSI D57 (Pickford 1988: 43). The hypodigm listed by Pickford (1988: 43) includes no complete maxillary molar tooth row, and in fact except for a mandibular p3-m3 and two maxillary P3-4s, Pickford's hypodigm of *C. indicus* is restricted to individual teeth. Most specimens in Pickford's hypodigm have an indefinite stratigraphic provenance. Given the limited information on this hypodigm, and lack of any discrete characteristics, this taxon cannot be analysed by the methods employed here. It should be noted that J. Barry (Harvard University) did show Bernor a partial maxillary fragment that he supposed may be referable to *C. indicus*, but this specimen simply has too little morphologic information to be useful for our analysis.

Conohyus prasadi: this taxon was originally recognized by Verma *et al.* (1981). Van der Made (1999) has recently placed this species in *Conohyus giganteus*, which includes Pilgrim's (1926) *Sivachoerus giganteus* and Azanza's (1986) *Conohyus ebroensis*. Van der Made (1999) recognizes BMNH15835 as the lectotype (Falconer & Cautley 1847: pl. 69, fig. 1). There is little agreement that this hypodigm belongs to a single species of *Conohyus* (see Van der Made 1999: 212 for a discussion). Van der Made bases his referral on maxillary P3, P4 and M3 morphology, but it is unclear how this taxon differs from the large, younger aged *Sivachoerus*, and for that matter, *Nyanzachoerus* (Van der Made 1999). We believe that this taxon is taxonomically too ambiguous to allow any meaningful analysis in this study.

Conohyus ebroensis: this species was initially recognized by Azanza (1986). The type specimen, DPZ-2001, is a right mandible with a portion of the symphysis, alveoles for p2-3, an unerupted p4 and m1-m2 (Azanza 1986: pl. 2, fig. 1). The type originates from the late middle Miocene (MN8) locality of El Buste, Spain. As cited above, Van der Made (1999) refers this to the Siwalik species, *C. giganteus*. The type material is limited, and we have not seen it. Van der Made (pers. comm.) further recognizes a maxillary molar, probably an M1 (DPZ-2010), from the MN8 locality of La Ciesma (Azanza 1986).

ABBREVIATIONS AND CONVENTIONS

BMNH	The Natural History Museum, London;
BSP	Bayerisches Staatssamlung Paläontologie, München;
DPZ	Departamento de Paleontologia, Zaragoza;
GSI	Geological Survey of India;
HGSP	Howard-Geological Survey of Pakistan Project;
IPS	Institut de Paleontologia "M. Crusafont", Sabadell, Spain;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
LMJ	Natural History Museum, Graz;
MAFI	The Museum of the Hungarian Geological Institute, Budapest;
NHMW	Naturhistorisches Museum für Naturkunde, Wien;
Paşalar Collection	specimens housed at the University of Ankara, numbers have no institutional acronym;
SMNS	Staatliches Museum für Naturkunde, Stuttgart;
YGSP	Yale-Geological Survey of Pakistan Collection, currently housed at Harvard Peabody Museum, Cambridge, Massachusetts;
YPM	Yale Peabody Museum, New Haven.

ANATOMICAL DESCRIPTIONS

In addition to standard dental nomenclature (e.g., Fortelius 1985: 4-8) we use the following terms describing suid teeth:

Innenheugel	the lingual cusp (usually relatively distally placed in tetraconodonts) of the twinned main cusp found on p4 (Stehlin 1899-1900; see also Schmidt-Kittler 1971);
Principal cusp	in the P1-3 and p1-3, the most prominent, usually central cusp of the premolar main axis;
Mesial ridge (or blade)	the ridge (or blade) descending on the mesial surface of the mandibular premolar principal cusp to the base of the crown;

Distal ridge	the ridge descending on the distal surface of the mandibular premolar cusp to the base of the crown;
Furche	any one of the deep enamel folds or grooves that partition molar cusps in a regular pattern (Furchenmuster) as recognized by Hünermann (1968; see also Pickford 1986, 1988). These are not to be confused with the shallow enamel wrinkles that are also commonly found on the surface of suid teeth.

For molar cusps we use the following pragmatic nomenclature:

Maxillary molars	mesiobuccal cusp (= paracone), mesiolingual cusp (= protocone), distobuccal cusp (= metacone), distolingual cusp (= hypocone), talon (= expanded distal shelf, usually with a well developed cusp on M3);
Mandibular molars	mesiobuccal cusp (= protoconid), mesiolingual cusp (= metaconid), distobuccal cusp (= hypoconid), distolingual cusp (= entoconid), talonid (= expanded distal shelf, with one to several distinct cuspids).

SYSTEMATICS

Order ARTIODACTYLA Owen, 1848
Family SUIDAE Gray, 1821
Subfamily TETRACONODONTINAE Lydekker, 1876
Genus *Conohyus* Pilgrim, 1926

Conohyus olujici n. sp.

HOLOTYPE. — HPM-GP 10767, male right mandible fragment with canine, p1 roots, base crown and roots of p2 and complete p3-m3.

ETYMOLOGY. — Species name assigned after Dr. Josip Olujić, the Franciscan monk who collected and studied the rich molluscan collection of the Lučane geological section in the 1930's.

HYPODIGM. — HPM-GP 10768, left p4-m3 (plausibly the same individual as the holotype); HPM-GP 10769, female mandible fragment with right canine, right i2, roots preserved of right i1, and i3 left i1 and i2, associated with a left mandibular fragment with broken p3; HPM-GP 10770, right mandibular fragment with p4-m3; HPM-GP 10771, right mandibular fragment with m1-m3; HPM-GP 10772, left mandibular fragment with m1-m2; HPM-GP 10773, left mandibular fragment with broken m1 and m2; HPM-GP 10774, left m3.

AGE. — Early Mammal Neogene Unit 5 (MN5) or possibly older, near the early/middle Miocene boundary.

DIAGNOSIS. — A smaller sized species of *Conohyus*. Maxillary teeth unknown. Mandible with canines not robustly built, but strongly sexually dimorphic so that in males, canine is vertically inplanted and in females it is splayed buccalward; p3 with flat lingual wall, slightly bulging buccal wall and elongate, nearly concave mesial blade and principal cusp placed distally over the tooth's posterior root; p4 moderately elongate, with slight lingual bulge and moderate buccal bulge and innenheugel fully fused to the principal cusp; m1 and m2 slightly rectangular; m3 relatively short and narrow, tapering distally; all mandibular molars with thick enamel accompanied by lavishly developed furchen and modestly developed buccal cingulum.

DESCRIPTION

There are eight mandibular specimens, including jaw fragments and teeth, that constitute the Lučane topotypic series of *Conohyus olujici* n. sp. The MNI is 3 based on the number of right m3's, and at least one male and one female is represented in the sample.

The holotype HPM-GP 10767 was originally represented by two specimens, however these two specimens preserved a good contact that allowed conjoining them into the type right mandible specimen (Fig. 2). This specimen is a right male mandible with canine, roots of p1, most of p2 and p3-m3 complete. A left mandibular fragment, HPM-GP 10768 (Fig. 3), has p4-m3 and because of identical preservation, size and wear stage, we believe that it may well be the same individual as the holotype.

The type specimen has a large, nearly vertically implanted canine that has its mesial margin rotated outward. The canine has a broad, flat lingual surface and a buccal surface that is unequally divided into a lesser mesial portion, separated from a greater distal portion by a distinct
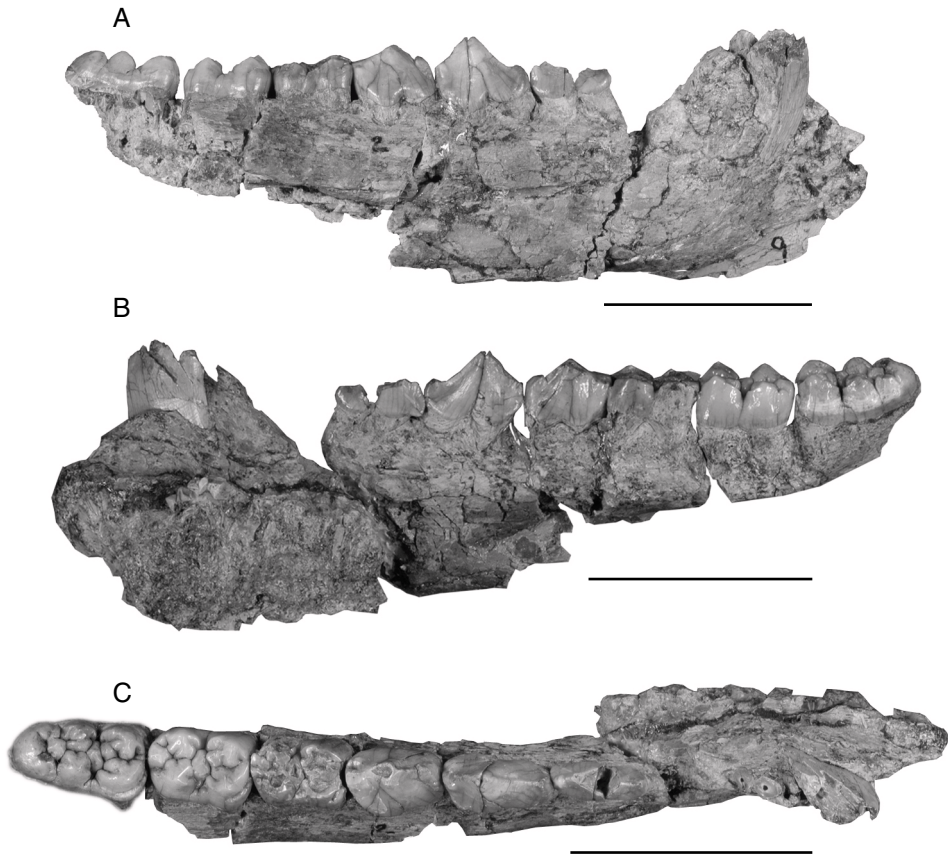
Fig. 2. — *Conohyus olujici* n. sp., holotype (HPM-GP 10767), male right mandible fragment with canine, broken p2 and complete p3-m3; **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bars: 4 cm.

vertical ridge. The p1 lacks its crown, but has its two roots clearly preserved and separated from p2 by a substantial diastema. The p2 has an elongate blade missing the apical cusp. The p3 is perfectly preserved and preserves the following salient characters: the apex of the principal cusp is placed posteriorly over the anterior aspect of the posterior root; the lingual wall is flat and the buccal wall is only slightly convex; the mesial blade is long, sloping at a 45° angle, and terminates in a distinct cusp; when viewed from the lingual side, the p3 mesial blade takes on a nearly concave-anterior morphology; in contrast, p3's distal blade is shorter, having a

cusp that terminates higher than the mesial one. The p4 is rather short, has a relatively flat lingual wall, and modestly bulging buccal wall; there is a distinct vertical furrow posterobuccal to the principal cusp; the principal cusp is worn, but it is clear that the innenheugel is completely fused with it; the mesial blade is short and terminates in a distinct, mesiodistally flattened cusp flanked on either side by a strongly developed cingulum; the blade coursing distalward from the principal cusp terminates in a furrow flanked by two, worn narrow cusps; there is a distinct buccal cingulum immediately lateral to these cusps and flanking the distovertical furrow described
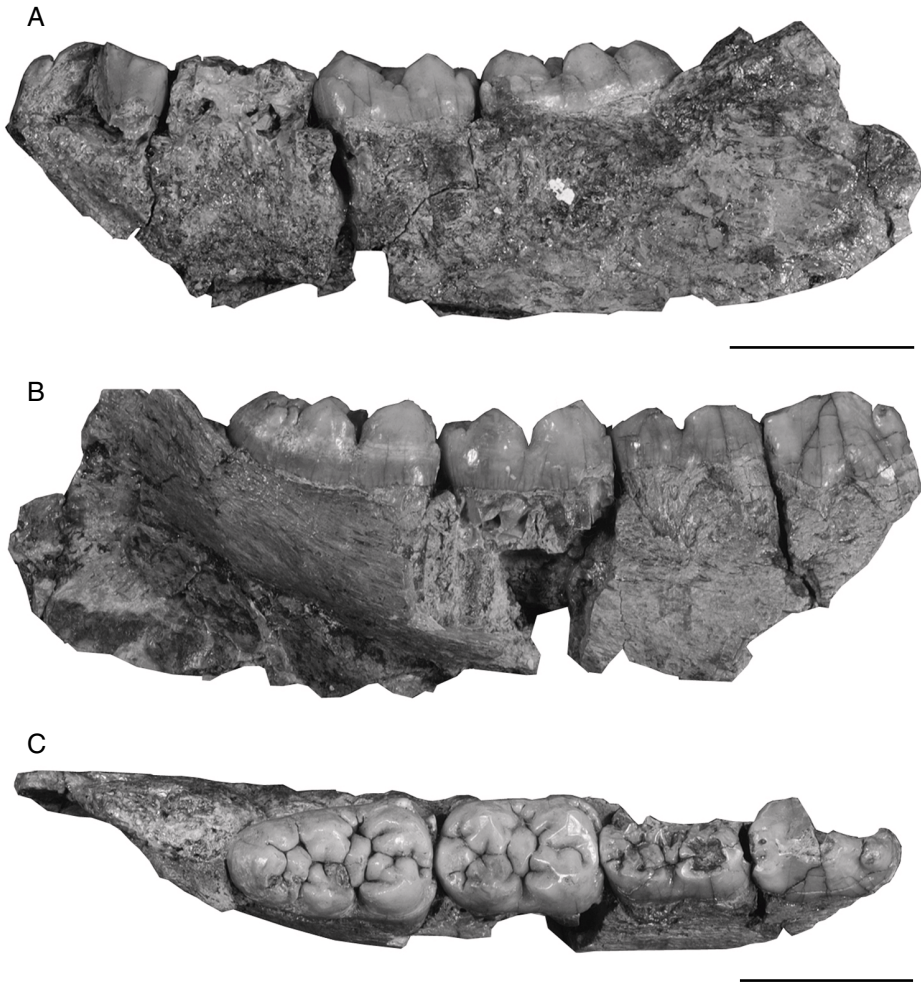
Fig. 3. — *Conohyus olujici* n. sp. (HPM-GP 10768), left p4-m3 (plausibly the same individual as the holotype); **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bars: 2 cm.

above. The m1 is characterized as follows: crown outline resembles a short rectangle; crown relief is relatively low; enamel is thick with limited exposure at the cusp tips and in the center of the central pillar; furchen are apparent between the cusps and central and distal pillars; cingulum is well developed on the mesiobuccal border and extends weakly approximately halfway distally on the buccal surface. The m2 is similar in its shape to m1, but substantially larger, and is characterized as follows: cingulum is

developed as in m1; the mesial pair of cuspids are elevated above the crown's central basin and inclined mesialward; enamel is thick with no visible penetration of the dentine; the central pillar has a broad, labiolingually directed oval shape; the distal pillar is distinct and round in shape. The m3 has the following morphological characteristics: it is elongate, tapering distally; there are four principal cuspids, a broad central pillar and a narrow talonid composed of four distinct, albeit subequal sized cuspids; cingulum

A

B
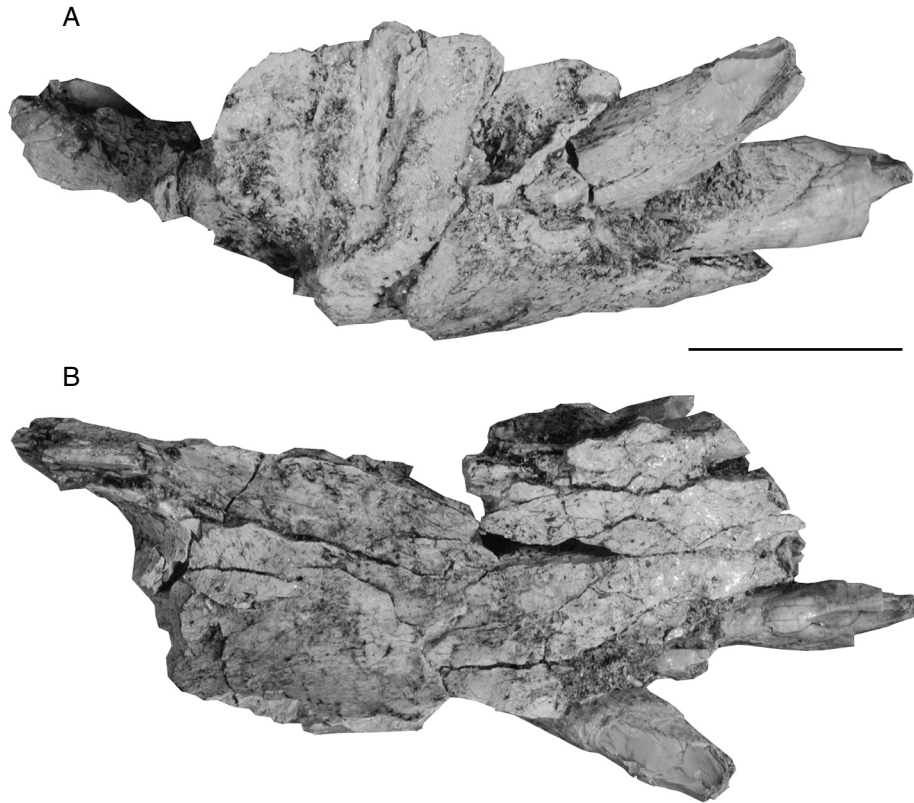
Fig. 4. — *Conohyus olujici* n. sp. (HPM-GP 10769), female mandible fragment with right canine, right i2, roots preserved of right i1, right i3 and left i1, left mandibular fragment with broken p3; **A**, labial view; **B**, occlusal view. Scale bar: 2 cm.

is distinct on the mesial half of the buccal margin, only; furchen are apparent.

The left mandibular fragment specimen, HPM-GP 10768 (Fig. 3), also preserves p4-m3. Much of the ventral margin of the mandibular corpus is broken away, along with the buccal walls of p4 and m1. This specimen is the same size, has the same preservation, tooth length and width proportions and all essential morphological details of the type and may in fact be the same individual as the type. As would be expected, the teeth are in the same stage-of-wear as the holotype.

HPM-GP 10769 (Fig. 4) includes two anterior mandibular fragments derived from a single female individual. The right fragment preserves the mandibular symphysis, canine and i2, roots of right i1 and i3 and roots of left i1 and i2. The canine is much smaller than its male counterpart (HPM-GP 10767), being a peg-like structure with an oval contour, and being splayed sub-horizontally buccalward. Mandibular i2 like-wise has an oval outline, and the lingual surface of the crown's base has a very distinct, sharply raised keel. The symphysis is markedly shallo-wer than the male specimen, due to the much smaller canine. The left side of this mandible preserves a fragmentary m3, whose buccal wall is broken away. This p3 however does preserve all the essential morphological details of the holotype, but would appear to have a slightly more vertically directed mesial blade.
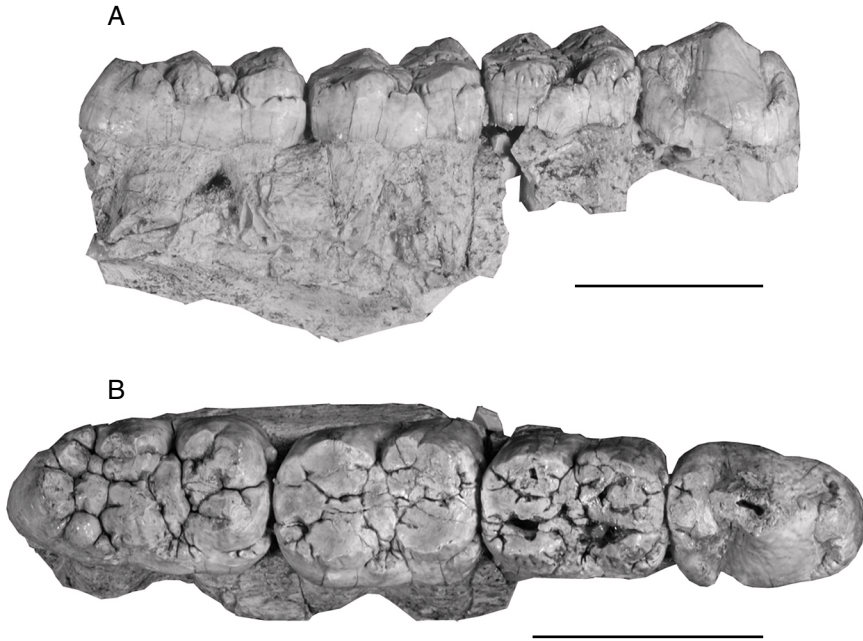
Fig. 5. — *Conohyus olujici* n. sp. (HPM-GP 10770), right mandibular fragment with p4-m3; **A**, labial view; **B**, occlusal view. Scale bars: 2 cm.

HPM-GP 10770 (Fig. 5) is a right mandibular fragment of unknown sex with p4-m3. Much of the mandibular corpus has been lost, but the dentition is in excellent condition. The p4 has the following characteristics: it is rather short, the lingual wall is relatively flat; the buccal wall bulges modestly, and has a distinct vertical furrow posterobuccal to the principal cusp; the principal cusp is worn and has the innenheugel completely fused with it; the mesial blade is short, slanting and terminates in a distinct, mesiodistally flattened cusp flanked on either side by a strongly developed cingulum; the posterior blade terminates in a small, worn cusp flanked buccally by a large cusp which itself has a thick cingular ridge coursing downward on the distobuccal margin. The m1 is characterized as follows: the crown outline is rectangular-shaped; cusp relief is relatively low; enamel is thick with limited penetration of the dentine cavity; furchen are abundant and lavishly distributed over the crown's surface; the crown's four principal cuspids are not clearly delineated; there is a small cingular conule on the mesiolingual border, and a more extensive cingulum that wraps around the mesiobuccal cuspid extending midway along the buccal margin; the central pillar is elaborate with distinct, elongate arms extending buccally and lingually. The m2 is similar in its shape to m1, but substantially larger: the cingulum is developed in the same manner as found in the m1; the crown relief is low, with four broad cuspids; enamel is thick with no visible penetration of the dentine; the central pillar has a broad, labiolingually directed oval shape; the distal pillar is distinct and round in shape; furchen are apparent, deeply incised, but not as lavishly developed as in m1. The m3 is elongate and has the following characteristics: the crown surface is deeply incised by furchen; the talonid is composed of seven distinct, albeit subequally sized cuspids; cingulum is distinct on the mesial half of the buccal margin, only.
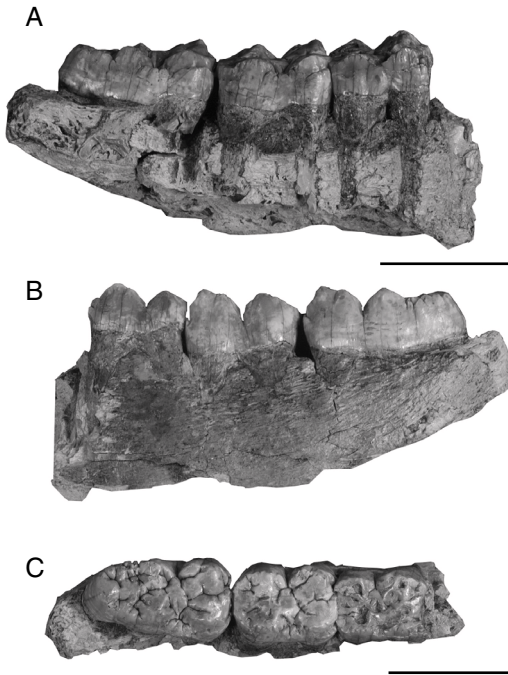
FIG. 6. — *Conohyus olujici* n. sp. (HPM-GP 10771), right mandibular fragment with m1-m3; **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bars: 2 cm.
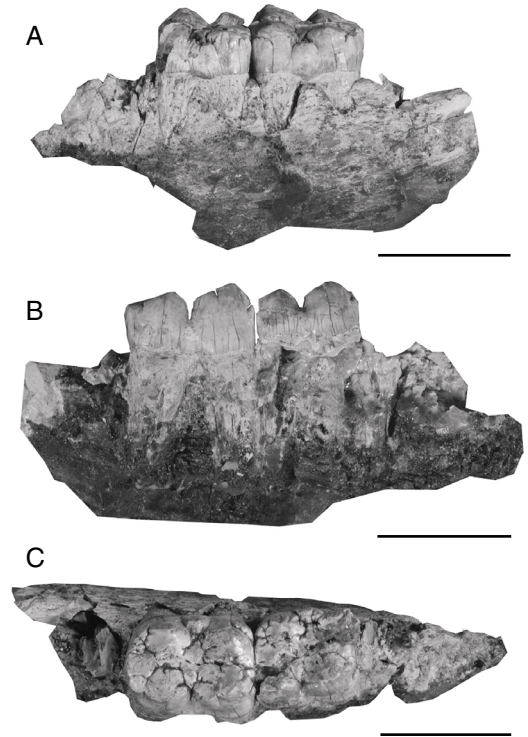

FIG. 7. — *Conohyus olujici* n. sp. (HPM-GP 10772), left mandibular fragment with m1-2; **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bars: 2 cm.

HPM-GP 10771 (Fig. 6) is a right mandibular fragment with m1-m3. This specimen is similar in its size and morphology to HPM-GP 10770. Mandibular m1 and m2 are short-rectangular shape, while m3 is elongate. The m1 is worn and has the dentine exposed at the apices of all four principal cuspids. The m2 and m3 have the same size and morphology as found in HPM-GP 10768. Although in slightly more advanced wear than HPM-GP 10768, m1-m3 furchen and cingula are very similarly developed.

HPM-GP 10772 (Fig. 7) is a left mandibular fragment with slightly worn m1 and m2. The m1 has its mesiobuccal margin broken, but is otherwise complete. Despite its wear, m1 has only its mesiolingual cuspid beginning to have its dentine exposed at the cuspid's apex. The morphol-

ogy of these teeth are as described above for other m1's and m2's.

HPM-GP 10773 (Fig. 8) is a left mandibular fragment with m1 and m2. Most of m1's crown is broken away, disallowing description. The m2 is large and in an early stage-of-wear. The lingual cuspids in this specimen are distinctly much higher than the buccal ones. Cingulum is composed of four distinct accessory cuspids on the mesiobuccal margin, and two accessory cuspids on the buccal margin between the mesiobuccal and mesiodistal cuspid. The central pillar is round and beginning to wear into a more oval-shaped structure. The distal pillar is mesiodistally extensive, forming the appearance of a small talonid.

HPM-GP 10774 (Fig. 9) is a single left m3 differing in no essential details from the other four m3's in the sample.
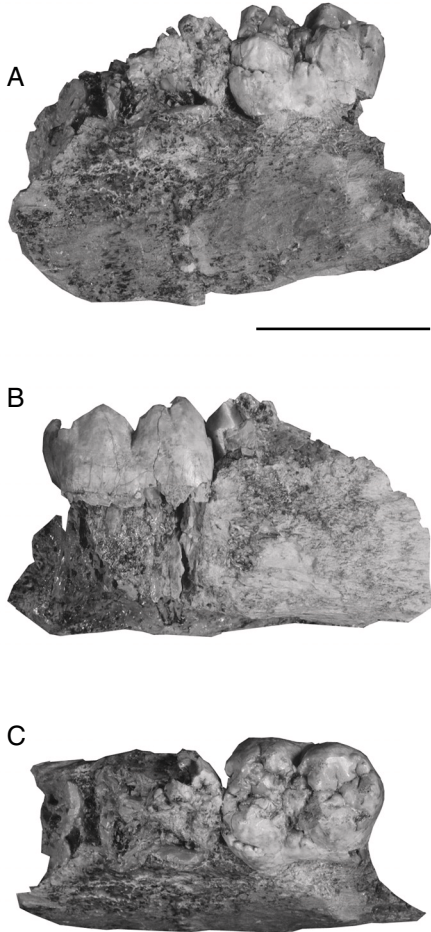
FIG. 8. — *Conohyus olujici* n. sp. (HPM-GP 10773), left mandibular fragment with broken m1 and m2; **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bar: 2 cm.
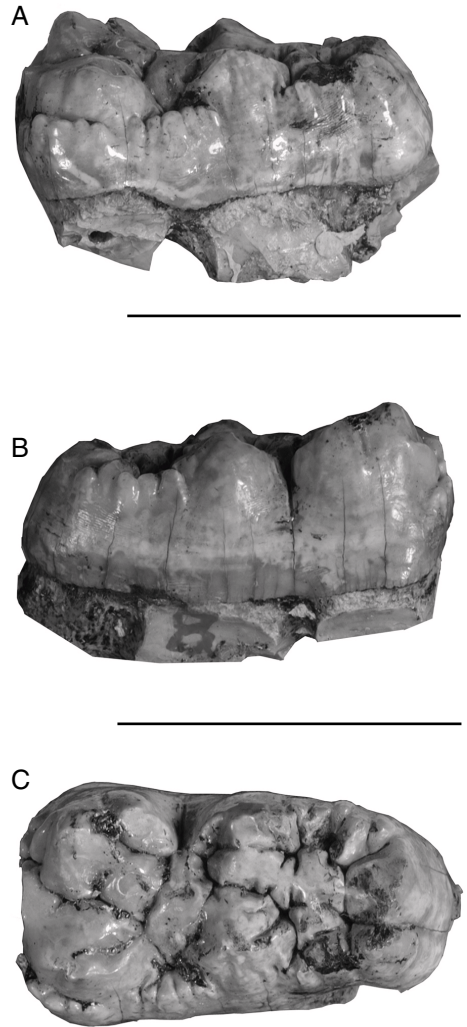

FIG. 9. — *Conohyus olujici* n. sp. (HPM-GP 10774), left m3; **A**, labial view; **B**, Lingual view; **C**, occlusal view. Scale bar: 2 cm.

STATISTICAL ANALYSES

BIVARIATE PLOTS

Figure 10A is a bivariate plot of mandibular p3 basal length versus width. This plot sorts four size categories. There is a group of small taxa that includes six specimens of *Parachleu-astochoerus crusafonti* (IPS), and one each of *Parachleuastochoerus* sp., *Hyotherium meissneri* (SMNS) and *H. shanwangense* (IVPP). The next size group includes all three specimens of *Conohyus steinheimensis* (Steinheim) and the single, complete p3 from Lučane. There is a specimen from Göriach in this scatter also which we are confident is not plotted here due to a measurement error; there is a distinctly smaller

morph in the Göriach sample most plausibly referable to *C. steinheimensis*. The sample of *Conohyus sindiensis* (YPM) constitutes the third largest group. This group is characterized by considerable variability, particularly in width, and three of the five specimens have relatively short and wide dimensions for p3; the buccal bulge is prominent on four of these specimens. One individual, with the greatest length dimension and shortest width dimension, falls on the length versus width slope of *C. olujici* n. sp. and *C. steinheimensis.* The largest group includes a broadly distributed sample of *Conohyus simorrensis* from Göriach, which clearly has the longest p3's in our sample. It does not have the same short length versus broad width proportions as the majority of the *C. sindiensis* sample does. The Göriach sample overlaps the *C. sindiensis* sample only slightly.

Figure 10B is a bivariate plot of mandibular p4 basal length versus basal width. This plot does not segregate our sample into as distinct size groups as did the p3 plot. There is a relatively clear and consistent grouping of the smallest taxa in the lower left hand corner of the plot: *H. meissneri* (six specimens), *H. shangwangense* (one specimen only), *Parachleuastochoerus* sp. (two specimens only), and *P. crusafonti* (10 specimens). In the lower middle portion of the plot we have the three specimens of the *C. olujici* n. sp. rendered with very close measurements to one another. Overlapping *C. olujici* n. sp. is a specimen of *C. steinheimensis*. The single known specimen of the type *C. heunermani* is as wide, but slightly shorter than the *C. olujici* n. sp. hypodigm. The remaining three specimens of *C. steinheimensis* are longer and mostly wider (but on the same slope as) *C. olujici* n. sp. There are three specimens of Göriach *Conohyus* that plot within or close to this group. *Conohyus sindiensis* has three specimens with proportionately shorter-wider measurements, while a fourth individual is still wider, but substantially more elongate than the other three specimens of *C. sindiensis*. Once again, the larger Göriach *Conohyus* has an extended length range, and its length versus width is greater than three out of

the four *C. sindiensis* individuals in our sample. We take this as being biologically representative of this morph. There are two specimens of Paşalar *Conohyus* that plot within the range of the larger Göriach *Conohyus*.

Mandibular m1 is subject to great length reduction due to its heavy wear in even young adult suids. This often results in extensive metric ranges within-species and extensive inter-species overlap when closely related species are plotted. We do not present a plot of mandibular m1 here for these reasons.

Figure 10C is a plot of mandibular m2 basal length versus width. *Parachleuastochoerus crusafonti* is represented by 13 specimens, plots at the lowest left extent of this figure, and has the narrowest dimensions of our sample. Whereas width varies relatively little, the length dimension is highly variable due mostly to changes with the degree of interstitial wear. *Hyotherium meissneri* is the next largest form and is represented by nine specimens. Whereas *P. crusafonti* is more variable in its length dimensions than its width dimensions, length and width seem to co-vary proportionally with one another in the *H. meissneri* sample. We find that Rudabánya *Parachleuastochoerus* sp. plots midway within the length range of *P. crusafonti* and just above the upper part of the width range of *P. crusafonti.* The single specimen of *Hyotherium shanwangensis* is plotted at the uppermost limit of *H. meissneri* range, and on *H. meissneri* slope. *Conohyus heunermani* single m2 is substantially wider than both parachleuastochoeres, and at the upper part of *H. meissneri* range. There are 6 m2's of *C. olujici* n. sp. The two smallest individuals plot only slightly longer and wider than *C. heunermanni*, while the remaining four plot within a group that includes most of the *C. steinheimensis* and *C. sindiensis* sample. *Conohyus steinheimensis* includes four specimens that plot longer than *C. olujici* n. sp., and this can be taken as a characteristic separating these two taxa. The Siwalik sample of *C. sindiensis* is variable, overlapping at its smallest extreme *C. heunermanni*. Most of the Paşalar and Göriach (large morph only) samples
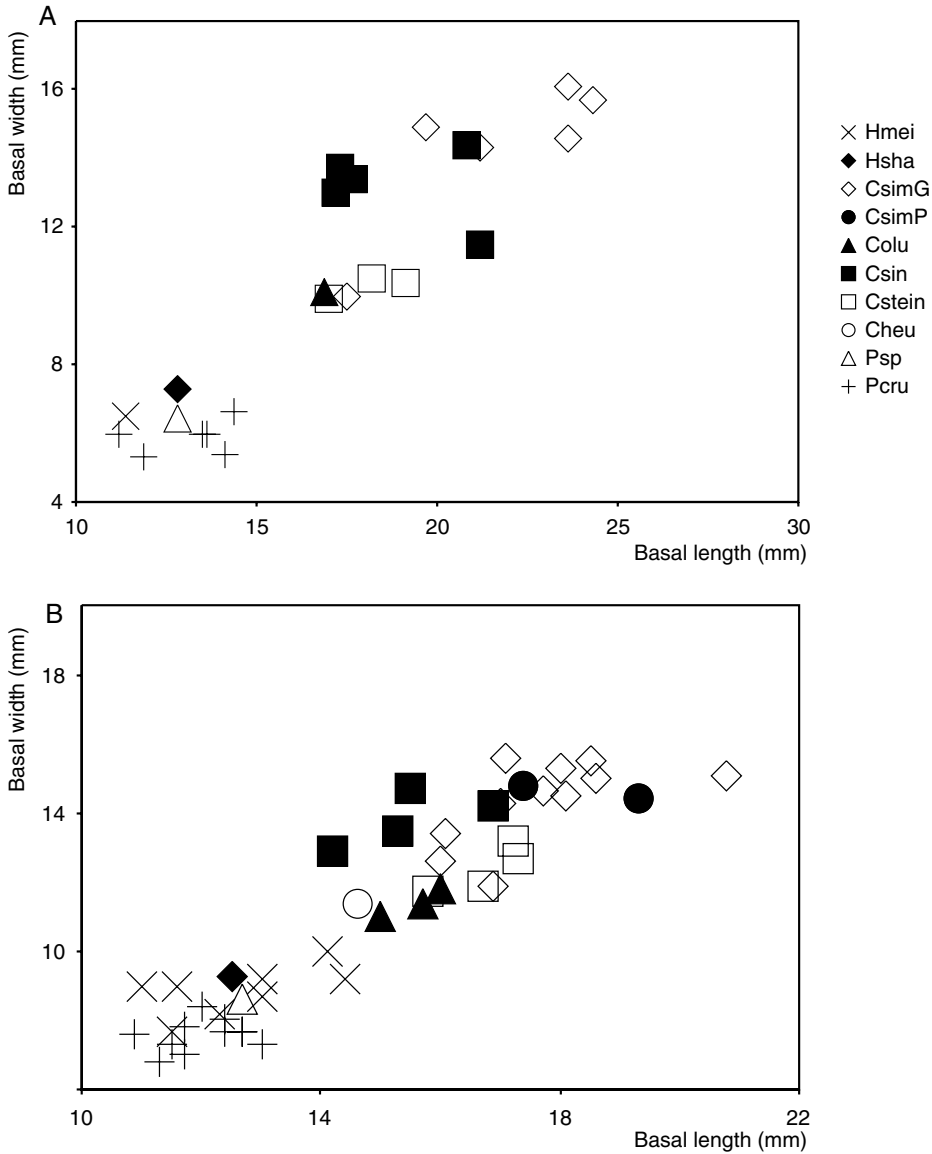
FIG. 10. — Bivariate plots; **A**, mandibular p3 basal length vs. width on selected hyotheres and tetraconodonts; **B**, mandibular p4 basal length vs. width on selected hyotheres and tetraconodonts; **C**, mandibular m2 basal length vs. width on selected hyotheres and tetraconodonts; **D**, mandibular m3 basal length vs. width on selected hyotheres and tetraconodonts. Abbreviations: **Cheu**, *Conohyus hunermanni*; **Colu**, *Conohyus olujici* n. sp.; **CsimG**, *Conohyus simorrensis* Göriach; **CsimP**, *Conohyus simorrensis* Paşalar; **Csin**, *Conohyus sindiensis*; **Cstein**, *Conohyus steinheimensis*; **Hmei**, *Hyotherium meissneri*; **Hsha**, *Hyotherium shangwangense*; **Pcru**, *Parachleuastochoerus crusafonti*; **Psp**, *Parachleuastochoerus* sp. Rudabánya.

of *C. simorrensis* overlap with *C. steinheimensis*. A single Göriach specimen overlaps with a small individual of *C. olujici* n. sp. There is a sharp contrast between European and Turkish *Conohyus* and Siwalik *C. sindiensis*: *C. steinheimensis* and *C. simorrensis* have relatively elongate m2's while *C. sindiensis* has relatively short and wide m2's. There is a single Göriach

C

D
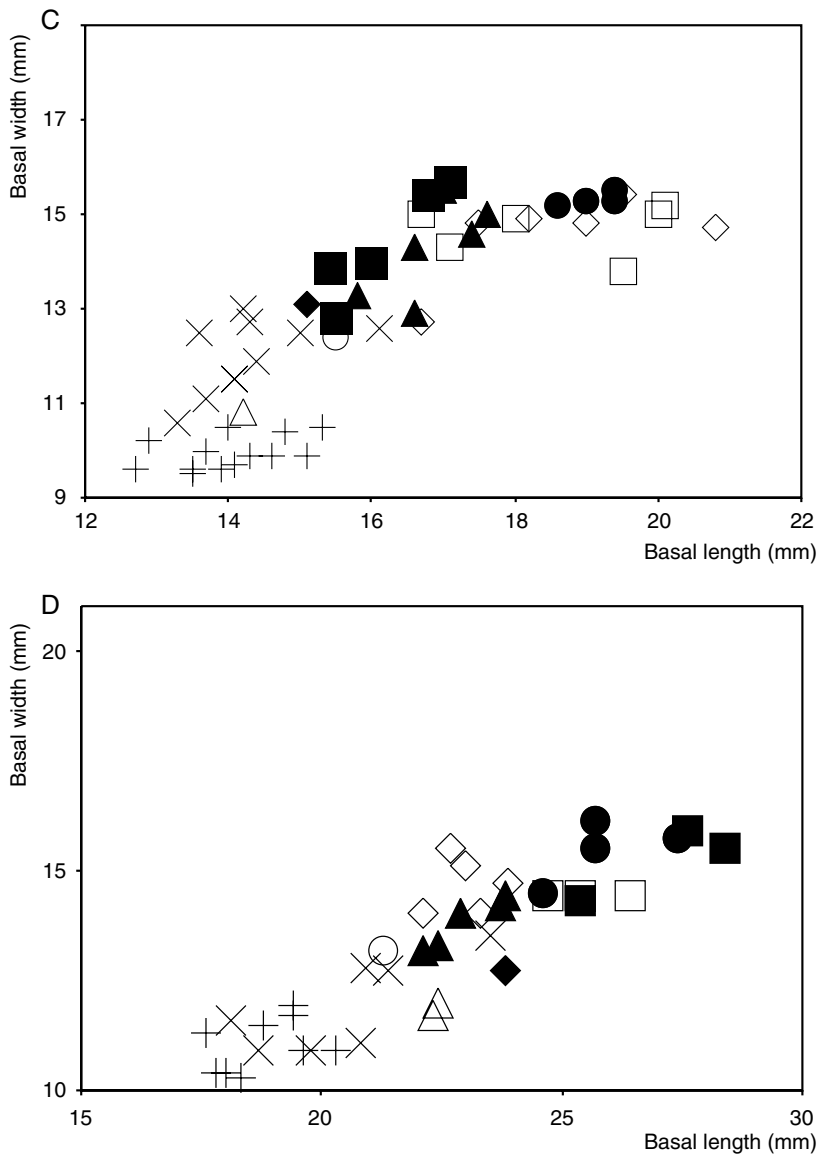
Conohyus that plots far to the right of the graph, exhibiting the great size range in Göriach *Conohyus simorrensis*. The Lučane *Conohyus* exhibits no evidence of either particularly elongate or short m2's: it would appear to fall on the same length versus width slope as *H. meissneri*. We believe that *C. olujici* n. sp. length versus width shape is underived; *C. steinheimensis* and

C. simorrensis are for the most part derived in their relative lengthening of m2, whereas *C. sindiensis* is derived in its relatively short and wide m2. Figure 10D is a bivariate plot of m3 basal length versus basal width. Once again, *P. crusafonti*, represented by nine specimens, plots as the smallest suid in the sample. It does overlap extensively however the *H. meissneri* sample of
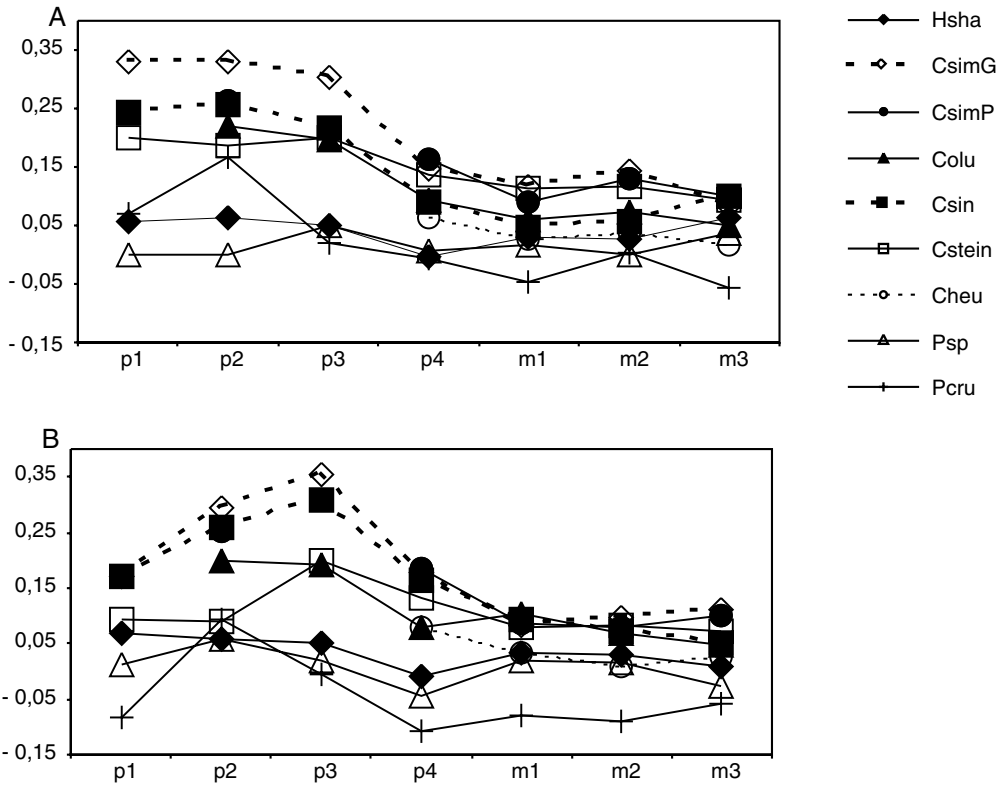
FIG. 11. — Log10 ratio diagrams; **A**, log10 ratio diagram of length (M1) on selected hyotheres and tetraconodonts, *Hyotherium meissneri* STD; **B**, log10 ratio diagram of width (M3) on selected hyotheres and tetraconodonts, *Hyotherium meissneri* STD. Abbreviations: **Cheu**, *Conohyus huenermanni*; **Colu**, *Conohyus olujici* n. sp.; **CsimG**, *Conohyus simorrensis* Göriach; **CsimP**, *Conohyus simorrensis* Paşalar; **Csin**, *Conohyus sindiensis*; **Cstein**, *Conohyus steinheimensis*; **Hsha**, *Hyotherium shangwangense*; **Pcru**, *Parachleuastochoerus crusafonti*; **Psp**, *Parachleuastochoerus* sp. Rudabánya.

six specimens. *Hyotherium meissneri* itself has a great length and width range. *Conohyus huenermanni* has the shortest m3 of all *Conohyus* species considered here, and is closest in its length versus width measurements to *C. olujici* n. sp. and the larger specimens of *H. meissneri.* The Lučane sample does not exhibit great variability, and overlaps the largest *H. meissneri* and smallest Göriach *Conohyus* specimens. The *C. steinheimensis* sample has the same width as most of the *C. olujici* n. sp. sample, but has greater length dimensions than *C. olujici* n. sp. *Conohyus sindiensis* has mostly larger m3's than *C. steinheimensis*, with one out of three of these overlapping *C. steinheimensis*. The Göriach *Conohyus simorrensis* sample has uniformly

shorter m3's than all the Paşalar sample of the same species, and the Steinheim sample of *C. steinheimensis.*

RATIO DIAGRAMS

Figure 11A is a log10 ratio diagram of lower cheek tooth length on those taxa considered above for which we have information. The two *Parachleuastochoerus* species group together. They visibly differ in this plot only in relative p3 length: *P. crusafonti* exhibits a relatively longer p2 than *Parachleuastochoerus* sp. from Rudabánya. Also, *H. shanwangense* plots most similarly with these two parachleuastochoere species being most similar to *Parachleuastochoerus* sp. for p3 length and m2 length. The

Lučane *Conohyus* plots between *C. steinheimensis* and *C. sindiensis* for p2 length, the three taxa overlap for p3 length, and then Lučane tracks very closely to *C. sindiensis* in its p4-m2 length, while *C. steinheimensis* clearly exhibits relative lengthening in its p4-m2 dimensions. *Conohyus huenermanni* tracks *C. olujici* n. sp. and *C. sindiensis* for p4-m2 very closely, but is smaller than all *Conohyus* species recognized here. *Conohyus huenermanni* m3 has the shortest length of all *Conohyus* species. Only the Göriach sample of *Conohyus simorrensis* (the large form in this sample) has p1-p3 and these plot distinctly longer than the previously cited *Conohyus* and *Parachleuastochoerus*. Both Göriach and Paşalar *C. simorrensis* are represented by p4-m3, which overlap extensively with the other *Conohyus* species in our sample. Figure 11B is a log10 ratio diagram of lower cheek tooth width. The two species of *Parachleuastochoerus* do not plot as closely as they did for the length measurements. Except for the p2, *P. crusafonti* has relatively narrower teeth than Rudabánya *Parachleuastochoerus* sp., and for that matter, all species under consideration. *Conohyus steinheimensis* has the relatively narrowest p1 of our *Conohyus* sample. The Lučane *Conohyus* p2 has a greater relative width than *C. steinheimensis*, the parachleuastochoeres and hyotheres. *Conohyus olujici* n. sp. closely overlaps *C. steinheimensis* for p3 width, is narrower than *C. steinheimensis* for p4 width (but has the same relative width as *C. huenermanni*), and has very similar values as *C. sindiensis*, *C. steinheimensis* and *C. simorrensis* (both Göriach and Paşalar) for m1 and m2 width. The Lučane *Conohyus* has a narrow m3 width measurement overlapping *C. huenermanni* and *C. sindiensis*. *Conohyus huenermanni* exhibits a relatively wide p4 compared to the two parachleuastochoere species and *H. shanwangensis*, and overlaps *C. olujici* n. sp. in its dimension. *Conohyus simorrensis* is remarkable for its relatively wide p2 and p3, however, its p4-m2 tracks very closely to other *Conohyus* species, and in particular *C. sindiensis*. *Conohyus simorrensis*' m3 is marginally wider than other species of *Conohyus*.

CLADISTIC ANALYSIS

Our cladistic analysis is presented in Figure 12. Tetraconodont ingroup taxa include: *Parachleuastochoerus crusafonti*, *Parachleuastochoerus* sp., *Conohyus olujici* n. sp., *C. steinheimensis*, *C. simorrensis* and *C. sindiensis*. *Conohyus heunermanni* was excluded from our analysis because the material is too scanty for this analysis (type specimen only, p4-m3). *Hyotherium meissneri* is a primitive member of the hyotheriinae. *Hyotherium shanwangensis* is a slightly more derived hyothere which may or may not be closely related to the Tetraconodontinae (Liu *et al.* 2002). Both hyotheres were used as outgoups, with *Hyotherium meissneri* having been used to root the cladogram.

Eleven characters (1-11, Table 2) scored from eight taxa were analysed in NONA (Goloboff 1993). Multicharacters were treated non-additively (unordered). The character states are arranged onto the branch under the DELTRAN option (Fitch 1971). After we used the hold 1000; hold/500 and mult*200; command, a single most parsimonious tree with a length of 16 steps was constructed with a Consistency Index (CI) of 0.93, and a Retention Index (RI) of 0.94.

This analysis suggests that the Eurasian tetraconodonts are characterized by the following synapomorphies: 2.1 (mandibular p3 lingual cingular collar lacking); 3.1 (mandibular p3 labial bulge slight); 4.1 (mandibular p4 lingual cingular collar lacking); 7.1 (mandibular m2 shape elongate rectangle); 10.1 (enamel morphology on P4 labial/lingual walls with wrinkles).

The genus *Conohyus* is demonstrated to be a monophyletic group. Within the genus *Conohyus*, *C. sindiensis* lies in the crown group with the sister taxa *C. simorrensis* and *C. steinheimensis*, supported by 9.1 (P4 paracone and metacone fully fused). Whereas Fortelius *et al.* (1996) transferred *C. steinheimensis* to the genus *Parachleuastochoerus*, this analysis supports our hypothesis that *C. steinheimensis* is a member of the *Conohyus* clade, forming a subgroup with *C. simorrensis*. *Conohyus olujici* n. sp. lies at the base of the *Conohyus* clade, united with other
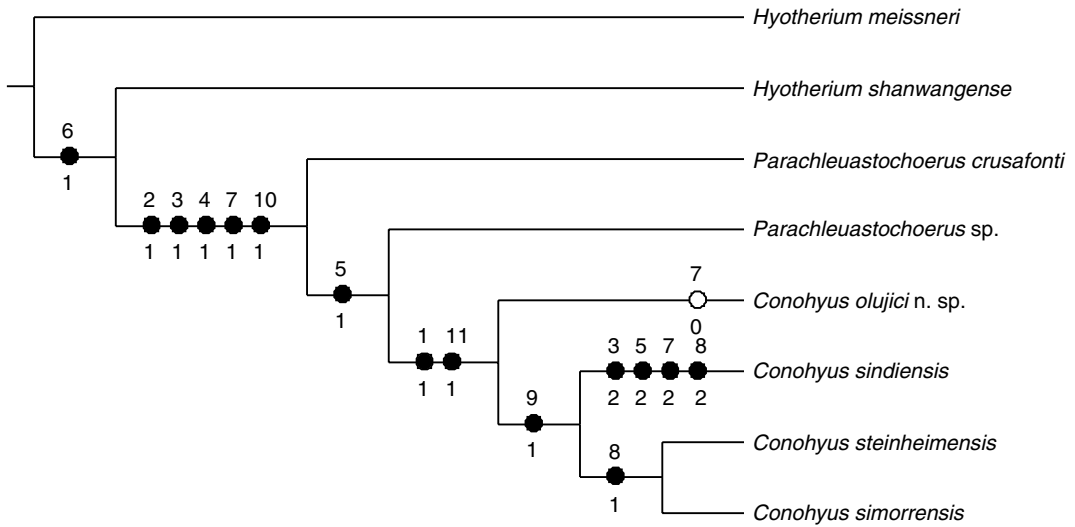
Fig. 12. — Cladistic analysis of selected hyothere and tetraconodont taxa. See Appendix for character diagnostics.

TABLE 2. — Data matrix for cladistic analysis. Character states: **1**: mandibular p1 and p2 crown shape: (0) tall and short; (1) low and long; **2**: mandibular p3 lingual cingular collar: (0) faint; (1) lacking; **3**: mandibular p3 labial bulge: (0) lacking; (1) slight; (2) great; **4**: mandibular p4 lingual cingular collar: (0) faint; (1) lacking; **5**: mandibular p4 labial bulge: (0) convex; (1) slight; (2) great; **6**: mandibular p4 innenheugel: (0) distinctly separate from principal cusp; (1) fused [completely or incompletely] to the principal cusp; **7**: mandibular m2 shape: (0) short, rectangular; (1) elongate rectangle; (2) square; **8**: postero-lingual shelf and fossa in P3: (0) both present; (1) relictual shelf only; (2) both absent; **9**: P4 paracone-metacone fusion: (0) not completely fused, with two cusps closely apposed, but distinguishable; (1) cusps fully fused; **10**: enamel morphology on P4 labial/lingual wall(s): (0) lacking wrinkles; (1) with wrinkles; **11**: enamel thickness: (0) thin; (1) thick.

	12345	67891 0	1 1
Hyotherium meissneri	00000	00000	0
Hyotherium shanwangense	00000	10000	0
Parachleuastochoerus sp.	01111	11001	0
Parachleuastochoerus crusafonti	01110	11001	0
Conohyus olujici n. sp.	11111	10???	1
Conohyus steinheimensis	11111	11111	1
Conohyus simorrensis	11111	11111	1
Conohyus sindiensis	11212	12211	1

members of *Conohyus* by characters 1.1 (mandibular p1 and p2 crown shape low and long) and 11.1 (enamel thickness thick). *Parachleuastochoerus* is a paraphyletic group. *Parachleuastochoerus crusafonti* and *Parachleuastochoerus* sp. are more primitive and were placed outside *Conohyus* clade. Compared to *Parachleuastochoerus crusafonti*, *Parachleuastochoerus* sp. is more closely related to *Conohyus*, sharing synapomorphy 5.1 (mandibular p4 labial bulge slight) with the members of *Conohyus*.

DISCUSSION

Lydekker (1876) originally recognized the family Tetraconodontidae based on fossil collections from the Indian Subcontinent. Simpson (1945) lowered the tetraconodont rank to a subfamily within the Suidae, Tetraconodontinae. Tetraconodonts are first known to occur in the late early Miocene, and range through the Miocene in Eurasia and Africa, becoming restricted to Africa in the Pliocene. Recent revisions and summaries include Pickford (1988) for the

Indian Subcontinent, Fortelius *et al.* (1996) for Western Eurasia and Van der Made (1999) who has attempted a revision of the entire subfamily. The Siwalik tetraconodont record is the most diverse, and Pickford (1988) has recognized the following taxa: *Conohyus sindiensis*, *C. indicus*, *Lophochoerus nagrii*, *Tetraconodon majus*, *T. minor* and *Sivachoerus prior*. Of these taxa, *C. sindiensis* and *S. prior* are relevant to our analysis.

Fortelius *et al.* (1996) reviewed the taxonomy, evolution, biogeography and paleoecology of the Suoidea from Central Europe and the Eastern Mediterranean. There was a single major taxonomic revision recommended by Fortelius *et al.* (1996): *Conohyus steinheimensis* and *Conohyus huenermanni* were transferred into the genus *Parachleuastochoerus* along with *P. crusafonti* based on their greater resemblance to *Parachleuastochoerus crusafonti* than *Conohyus simorrensis*. Along with this transfer was the synonymy of the Rudabánya para-chleuastochoere into "*P.*" *heunermanni*. Our current results do not support these taxonomic rearrangements. These taxonomic changes were subsequently followed by Van der Made (1999), who initially proposed them in Fortelius *et al.* (1996).

Van der Made's (1999) revision of the Tetra-conodontinae was based on a morphometric analysis of the group. He did not consider many discrete characters, and did not analyze incisors, anterior premolars or skulls. His analysis was largely restricted to calculating ratios between M1/m1 length and width and posterior premo-lar lengths and widths. His revision of the Tetraconodontinae resulted in the recognition of three tribes: Tetraconodontini, taxa with extremely enlarged P3/p3 and P4/p4 and includ-ing species of *Conohyus*, *Sivachoerus* and *Nyanzachoerus*; the Nyanzachoerini, including *Conohyus simorrensis*, *C. giganteus*, *Nyanza-choerus kanamensis*, *Nyanzachoerus cookei*, *Nyanzachoerus jaegeri*, *Notochoerus euilus*, *Notochoerus scotti*, *Notochoerus harrisi* and *Lophochoerus*; Parachleuastochoerini, taxa with narrow and relatively small premolars, including

Parachleuastochoerus steinheimensis, *P. huener-manni* and *P. crusafonti*. The result of this revi-sion has been a major reshuffling of genera and species between tribes. Harris & Leakey (2003) did not accept the transfer of *Nyanzachoerus* species to *Sivachoerus*, and expressed the view that Van der Made's analysis of teeth only was too limited because skull and mandible morpho-logy have proven important for sorting African tetraconodont species into lineages. Our analy-sis also does not support several of the taxono-mic reallocations suggested by Van der Made (1999).

Our analysis suggests that *Parachleuastochoerus* should be restricted to the Spanish species *P. crusafonti*, Rudabánya (Hungary) *Para-chleuastochoerus* sp., and perhaps *P. sinensis* of Liu & Pickford (2001). All three species are cor-related with the Vallesian. There may well be an MN7+8 *Parachleuastochoerus*, but the material that we have studied thusfar is too limited to determine which species. We do not include *Conohyus steinheimensis* or *C. huenermanni* within *Parachleuastochoerus* for the reasons cited below.

Our bivariate plots (Fig. 10) consistently show that the parachleuastochoeres are hyotherine size, with *P. crusafonti* having remarkably elongate and narrow cheek teeth. *Parachleu-astochoerus* sp. is less derived than *P. crusafonti*, and overall morphologically closest to *Hyothe-rium* of the sample under consideration. *Conohyus olujici* n. sp. is a small *Conohyus* and exhibits neither the bucco-lingual inflation of p3 and p4 exhibited in *C. sindiensis* (essentially, labial bulge), nor the cheek tooth lengthening of *C. steinheimensis* and *C. simorrensis*. As such, it is intermediate between these groups. *Conohyus huenermanni* is small, approaching *Para-chleuastochoerus* sp. in its size and proportions, but its p4 has an expanded bucco-lingual dimen-sion characteristic of *Conohyus*. The log10 ratio diagrams (Fig. 11) support these interpretations, and strengthen the distinction between the para-chleuastochoere species and *Conohyus* species. In addition to those characters already cited immediately above, all species of *Conohyus* have

elongate, narrow and low anterior premolars, whereas hyotheres and parachleuastochoeres have short, pointed anterior premolars. As shown in Figure 11, species of *Conohyus* are clearly distinct from the hyotheres and parachleuastochoeres in their p2-4 log10 ratio values and p3-4 bivariate values. The exception to this observation is the relatively, but not absolutely large p2 found in *Parachleuastochoerus crusafonti*. All other bivariate and log ratio values of *P. crusafonti* securely position it within the parachleuastochoeres. *Conohyus olujici* n. sp. is close in size to *C. heunermanni*, and a viable intermediate in cheek tooth proportions to *C. sindiensis* and *C. steinheimensis*. The *Conohyus "simorrensis"* sample shows great morphologic variability, with the smaller specimens overlapping extensively with *C. steinheimensis*; this particularly for p3 and p4 length versus width dimensions. We believe it likely that two *Conohyus* taxa occur at Göriach: *C. steinheimensis* (relatively rare) and *C. simorrensis* (more common). Resolution of this issue requires further study.

Our cladistic analysis finds congruence with the statistical analysis and supports our phylogenetic hypotheses. Our analysis does not support the monophyly of *Parachleuastochoerus*, but it does support the hypothesis that parachleuastochoeres are primitive tetraconodonts. "*Parachleuastochoerus*" is small sized with simple, underived anterior premolars, minimally inflated posterior premolars, maxillary P4's with wrinkling and fused paracone-metacone, and mandibular p4 with innenheugel at least partially fused to the principal cuspid. Of these two species analysed here, *Parachleuastochoerus* sp. is the least derived in its size, morphology, cheek tooth proportions and dimensions. Rather than postulating a substantial reversal of *Parachleuastochoerus* through a *C. steinheimensis* stage-of-evolution, we hypothesize that *Parachleuastochoerus* sp. is a primitive European offshoot of *Hyotherium*. If this were to prove to be the correct phylogenetic interpretation, we propose that MN7+8 *Parachleuastochoerus*, and subsequent MN9 *Parachleuastochoerus* sp. and

P. crusafonti represent a "ghost lineage" of considerable duration between its first (unknown occurrence, MN4/5?) and its actual first stratigraphic record (MN7+8). It is distinctly possible that fragmentary middle Miocene specimens of *Parachleuastochoerus* reside in museum collections today and have been misidentified as "*Hyotherium*" s.l.

Our analysis supports *Conohyus* monophyly. *Conohyus olujici* n. sp. is the most primitive member of this clade and is the sister taxon of the *C. steinheimensis*-*C. simorrensis* and *C. sindiensis* clades. Bivariate and log10 ratio analyses support the cladistic results in this regard. Our analysis *does not* support the extensive character reversal implied by the hypothesis that *Parachleuastochoerus* evolved by progressive size reduction through a *C. steinheimensis*-*C. heunermanni*-*Parachleuastochoerus crusafonti* succession, and that this succession explicitly includes Rudabánya *Parachleuastochoerus* sp. in a "*Parachleuastochoerus huenermanni*" hypodigm.

There has been substantial controversy about the first appearance of tetraconodonts in Europe and Asia. This controversy centers on the chronologic ambiguity of MN units, which are currently undergoing major revision for the MN4-MN6 temporal interval. Much of the most pertinent current information remains unpublished. Pickford (1989) cited the first European occurrence of *Conohyus* in MN4, *c.* 16 m.y. Van der Made (1999) argued that this correlation was too old, claiming an MN5 FAD, *c.* 13.8 m.y. Bernor & Tobien (1990) argued that Paşalar, with *C. simorrensis*, was best correlated with MN6 and *c.* 15 m.y. of age. Van der Made (1999) has stated that the oldest *Conohyus* on the Indian Subcontinent is 16.5 m.y. John Barry (pers. comm.) cites the earliest evidence of *Conohyus* in the Potwar Plateau (Pakistan) sequence as being 14.5 m.y. The HGSP program has discovered material of *Conohyus sindiensis* from Sind (locality HGSP-8114), Pakistan, which correlates with the 16.1 m.y. levels of the Potwar Plateau (Bernor *et al.* 1988a). This would be, as far as we know, the oldest correla-

tion of *Conohyus* on the Indian Subcontinent. In any case, the Lučane *Conohyus* is more primitive than both the MN5 *Conohyus* species from Göriach and the 16.1 m.y. specimens of *Conohyus sindiensis* from Sind, Pakistan. This concurs with our current hypothesis that the Lučane fauna is late Orleanean age, or late MN4-early MN5 correlative, *c.* 17-16 m.y.

Biogeographically, the earliest members of the *Conohyus* clade likely ranged from Croatia in the west to Indo-Pakistan in the east. By the beginning of the middle Miocene, the *Conohyus* clade would appear to have diverged into a western clade that included *C. steinheimensis* and *C. simorrensis*, and an eastern clade that included *C. sindiensis*. Our review and analysis leads us to the hypothesis that *Parachleuastochoerus* had a broad Eurasian middle-early late Miocene geographic distribution, but is extremely rare being identified only in Vallesian age horizons. However, there are isolated teeth in the YGSP collection that compare closely in size and morphology with *Parachleuastochoerus* (Bernor pers. obs.). The lack of material ascribed to *Parachleuastochoerus* from MN6 horizons (but occurring in MN7+8) suggests a sampling problem.

Thenius (1952) made early interpretations of European *Conohyus* paleoecology. He argued based on faunal and sedimentological considerations that *C. simorrensis* inhabited marshy forests, while *C. steinheimensis* was adapted to drier conditions. Pickford (1988) emphasized that *Conohyus* was characterized by inflated posterior premolars and thick enamel on the molar teeth. Fortelius *et al.* (1996) suggested that the combination of thick dental enamel and conical premolars with hyaena-like macrowear might indicate that cracking hard food items such as seeds was an important component of tetraconodont feeding behavior. Amongst the tetraconodonts we have analysed here, *Parachleuastochoerus crusafonti* actually has more slender cheek teeth (except p2) than *Hyotherium meissneri*, meaning that there is likely a reversal away from the *Hyotherium* stage-of-evolution. Rudabánya *Parachleuasto-*

choerus sp. is very similar to both *Hyotherium meissneri* and *Hyotherium shanwangensis* in its log10 ratio values, and together with the cladistic analysis presented here appears to be morphologically representative of a primitive tetracondont. *Conohyus olujici* n. sp. has modestly inflated p3 and p4 buccal margins. Moreover, *C. olujici* n. sp.'s p3 would appear to have a piercing principal cusp and talonid, while having a distinctly slicing mesial blade. *Conohyus olujici* n. sp.'s p4 has a distinctly inflated buccal margin and crushing function. Its molars have markedly thickened enamel over the *Hyotherium* and *Parachleuastochoerus* sp. stages-of-evolution that would have resisted premature wear. The fact that m3 was fully emergent before m1's apical cusp dentine was exposed through the enamel, is fundamentally different from other Miocene and recent suines (Armour-Chelu *et al.* 2003), and undoubtedly adapted for masticating tough foods. *Conohyus huenermanni* is in our view, simply a late occurring small European *Conohyus* that differs little from *C. steinheimensis*. *Conohyus steinheimensis* diverges from both *C. olujici* n. sp. and *C. sindiensis* in its more slender-elongate posterior cheek teeth that probably had a paleodietary background: *Conohyus steinheimensis* probably was adapted to eating seeds and fruits with a less hard endocarp than *C. sindiensis*.

CONCLUSIONS

Conohyus olujici n. sp. is an early member of the *Conohyus* clade. This species would appear to have occurred at a time just prior to this clades' radiation into European and South Asian radicles: *C. steinheimensis* and *C. simorrensis* in Europe; *C. sindiensis* in South Asia. *Conohyus olujici* n. sp. was recovered from lignite deposits which were derived from warm, subtropical swamp forests that likely supported fruits with tough endocarps. Its posterior premolars are primitive and lacking the degree of buccolingual inflation found in more derived forms, especially *Conohyus sindiensis*. The Lučane

Conohyus has proven to be of additional importance for correlating the local Croatian section with other Eurasian localities of late early Miocene age, and for striking hypotheses of biogeographic connections between South Asia and Europe. Future radioisotopic and biochronologic analyses of the Lučane section will provide rigorous tests of the stratigraphic correlations and biogeographic interpretations we make here.

Acknowledgements

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APPENDIX

Character diagnostics for Fig. 12. Abbreviations: **CI**, Consistency Index; **RI**, Retention Index. Note: character 6 in *Hyotherium shanwangensis* is biologically informative in that it is an apparent synapomorphy with the all Tetraconodontinae as cited in the text.

Character	Steps	CI	RI
1	1	100	100
2	1	100	100
3	2	100	100
4	1	100	100
5	2	100	100
6	1	uninformative	
7	3	66	50
8	2	100	100
9	1	100	100
10	1	100	100
11	1	100	100