

## PROSANTORHINUS, THE SMALL TELEOCERATINE RHINOCEROTID FROM THE MIOCENE OF WESTERN EUROPE

ESPERANZA CERDEÑO

CERDEÑO E. 1996. *Prosantorhinus*, the small teleoceratine rhinocerotid from the Miocene of Western Europe. [*Prosantorhinus*, le petit rhinocérotidé téléocératine du Miocène d'Europe occidentale]. GEOBIOS, **29**, 1 : 111-124. Villeurbanne, le 29.02.1996.

Manuscrit déposé le 27.12.1993 ; accepté définitivement le 19.10.1994.

### ABSTRACT

*Prosantorhinus* HEISSIG, 1974 material from 19 Spanish, Portuguese, French and German localities is studied and described. Four different forms of this genus are present in the Lower and middle Miocene of Western Europe. The type species *P. germanicus* (WANG, 1929) was defined on German material and it is here recognized at Savigné (France). *P. douvillei* (OSBORN, 1900) is a larger species which appears in France, Portugal and Spain. The anatomical study has evidenced that differences between both species are greater in postcranial skeleton than in dental remains, and mainly concern to size and proportions. Material previously classified as *Diceratherium douvillei* and *Gaindatherium rexmanuelli* ANTUNES & GINSBURG, 1983, as well as some ascribed to *Diceratherium aurelianense* (NOUEL, 1866) from the Lisbon area, is here considered as *P. douvillei*. The sample from Baigneaux, previously referred to *P. germanicus*, is also recognized as *P. douvillei*. The brachypothere rhinoceros from Buñol (Spain) is specially robust, and it is considered as *Prosantorhinus* sp. A. Similarly the brachypothere from La Grive-Saint-Alban (France), classically ascribed to *Brachypotherium*, is here classified as *Prosantorhinus* sp. B, having the particularity of a greater size and robustness. However, in both cases, the scarcity of material does not enable, at this moment, a more accurate determination. Both appear closer to *P. douvillei* than to *P. germanicus*, but they seem to exceed its intraspecific variation. The biostratigraphic distribution of the genus *Prosantorhinus* ranges from the Ramblian to the upper Aragonian, that is from the MN3 to the MN7/8 biozone.

KEYWORDS : *PROSANTORHINUS*, RHINOCEROTIDAE, LOWER-MIDDLE MIOCENE, WESTERN EUROPE.

### RÉSUMÉ

Le matériel de *Prosantorhinus* HEISSIG, 1974 provenant de 19 gisements d'Espagne, Portugal, France et Allemagne est ici révisé. Quatre formes différentes de ce genre sont présentes dans le Miocène inférieur et moyen de l'Europe occidentale. L'espèce type *P. germanicus* (WANG, 1929), décrite dans plusieurs localités allemandes, est aussi reconnue en France, à Savigné. *P. douvillei* (OSBORN, 1900) est une espèce plus grande qui apparaît en France, Espagne et Portugal. L'étude anatomique a mis en évidence que les différences entre ces deux espèces sont plus grandes pour le squelette post-crânien que pour la denture et sont principalement référées à la taille et aux proportions. Du matériel dénommé *Diceratherium douvillei* et *Gaindatherium rexmanuelli* ANTUNES & GINSBURG, 1983, ainsi que quelques os attribués à *Diceratherium aurelianense* (NOUEL, 1866), du Miocène de Lisbonne, sont ici rapportés à *P. douvillei*. Nous déterminons aussi comme *P. douvillei* l'échantillon de Baigneaux, précédemment attribué à *P. germanicus*. Le rhinocéros brachypotère de Buñol (Espagne) apparaît particulièrement trapu et il est considéré comme *Prosantorhinus* sp. A. Egalement, le matériel français de la Grive-Saint-Alban, classiquement attribué à *Brachypotherium*, est ici identifié comme *Prosantorhinus* sp. B, plus grande et trapue que toutes les autres. Cependant, dans ces deux cas, les restes sont trop rares actuellement pour une meilleure détermination. Ils sont plus proches de *P. douvillei* que de *P. germanicus*, mais ils semblent dépasser sa variation intraspécifique. La distribution biostratigraphique de *Prosantorhinus* est pourtant étendue du Ramblien à l'Aragonien supérieur, c'est-à-dire de la biozone MN3 à la biozone MN7/8.

MOTS-CLÉS : *PROSANTORHINUS*, RHINOCEROTIDAE, MIOCÈNE INFÉRIEUR-MOYEN, EUROPE OCCIDENTALE.

## INTRODUCTION

The genus *Prosantorhinus* was defined by Heissig (1974) based on the species *Brachypodella germanica* (WANG, 1929), changing this previous generic name, *Brachypodella* HEISSIG, 1972, since it became an invalid name. *Prosantorhinus* is a small brachypothere included in the tribe teleoceratini within the subfamily Aceratheriinae (Heissig 1989 ; Cerdeño 1995), contrary to the current classification in Prothero & Schoch (1989), where they consider this tribe within Rhinocerotinae. Heissig (1972) established two evaluative lines of *Prosantorhinus* : one of them with *P. tagicus* (ROMAN, 1907) and *P. germanicus*, and the other with *P. douvillei* (OSBORN, 1900). *P. tagicus* was definitely ascribed to the genus *Protaceratherium* by Antunes & Ginsburg (1983), and even the species became synonymous of *Protaceratherium minutum* (CERDEÑO, 1989). Within *Prosantorhinus germanicus*, Heissig (1972) included a part of the French material described by Mayet (1908) for the species *Diceratherium douvillei* defined by Osborn (1900) at Beaugency. This ascription to the genus *Diceratherium* has been maintained with doubts, but the species has been reported at several French Miocene sites (Ginsburg 1974), although a clear description has never been done. On the other hand, Antunes & Ginsburg (1983) stated the presence of *Prosantorhinus* cf. *germanicus* in the Lisbon area (Portugal) from a few dental remains of smaller size than *P. douvillei*. At the same time, they also emphasized the abundance of the former at Baigneaux-en-Beauce (France).

I recently established the presence of *Prosantorhinus* sp. in Spain (Cerdeño 1989, 1992) at the site of Buñol (Valencia) - modifying the previous report of *Brachypotherium aurelianense* (SANTAFÉ & BELINCHON, 1988) - *Prosantorhinus* cf. *douvillei* at la Artersilla (Zaragoza) (Cerdeño 1993 ; Azanza *et al.* 1993). The former determination was mainly based on a McIV from Buñol which was very similar to the homologous bone of "*Gaindatherium rexmanueli*" from Lisbon ; this fact led me to consider that this latter form was actually a synonym of *Prosantorhinus* (CERDEÑO, 1989). On the other hand, the remains classified as *Prosantorhinus* sp. from Montredon (French Upper Miocene ; Guérin 1980, 1988) were later identified as *Alicornops alfambrense* (CERDEÑO & ALCALA, 1989 ; as genus *Aceratherium*), restricting the temporal distribution of *Prosantorhinus* to the Lower and Middle Miocene. With occasion of the recent revision of a lot of French material of the teleoceratine species *Diaceratherium aurelianense* and *Brachypotherium brachypus* (CERDEÑO, 1993), I could also verify the presence of a

		AGE	FRANCE	GERMANY	SPAIN/PORTUGAL
M I O C E N E	A S T A R A G O N I A N	MN 7/8	La Grive ** Malartic		
		MN 6		Georgensmünd * Sandelzhausen *	
L.	O R L E A N A I S	MN 5	Pontlevoy Savigné * Bézian La Romieu Beaugency Baigneaux Chevilly		Ch. Lumiar
		MN 4		Langenau I *	Q. Pedreiras Q. Narigao Buñol ** Artesilla
M I O C.	R A M B L I A N	MN 3	Neuville	Hessler *?	
		MN 2			

Table 1 - Chronostratigraphic distribution of the European localities with *Prosantorhinus* (after de Bruijn *et al.* 1992).\* *P. germanicus* ; \*\* *Prosantorhinus* sp. ; others with *P. douvillei*. *Distribution chronostratigraphique des localités européennes à Prosantorhinus* (d'après De Bruijn *et al.* 1992).\* *P. germanicus* ; \*\* *Prosantorhinus* sp. ; d'autres à *P. douvillei*.

small brachypothere coexisting at most sites with one of the two other species. This was a good opportunity to attempt a general revision of *Prosantorhinus* to bring up-to-date the knowledge on this genus. The chronostratigraphical distribution of all considered Miocene sites ranges from the upper Ramblian to the upper Aragonian, this is from the MN3 biozone to the MN7/8 (Tab. 1).

## MATERIAL AND METHODS

The *Prosantorhinus* material directly revised is listed below for each locality and the institution where it is stored :

### Spain

- Buñol (Valencia), Museo paleontológico de Valencia : FBC166, r. D<sup>2</sup> ; BUR4, l. pyramidal ; PAN832, l. uniform fragment ; pan75, r. McIV.  
- Artesilla (Zaragoza), University of Zaragoza (material provisionally loaned to the Museo Nacional de Ciencias Naturales, CSIC, Madrid) : MPZ-6485, r. D<sup>1</sup> ; MPZ-6486, r. D<sup>3</sup> ; MPZ6487, l. D<sub>3</sub>-D<sub>4</sub> ; MPZ-6491, r. astragalus ; MPZ-16510, l. astragalus fragment. Milk molars have been ascribed with doubts to *Prosantorhinus* (AZANZA *et al.*, 1993).

### Portugal

Different sites in the Lisbon area, Dept. de Paleobiologia, Universidade Nova de Lisboa. Material classified by Antunes & Ginsburg (1983) as : *Prosantorhinus* cf. *germanicus* : 12, hemimandible with D<sub>2</sub>-D<sub>4</sub> ; 85, l. P<sup>3</sup> ; 84 and 143 l. P<sup>4</sup> ; 144, r. P<sup>4</sup>. *Gaindatherium rexmanueli* : 112, l. maxillary with P<sup>1</sup>-P<sup>3</sup> (holotype) ; 104, l. maxilla with D<sup>2</sup>-D<sup>4</sup> and M<sup>1</sup> ; 59, r. P<sup>2</sup> ; 94, 97 and 102, l. M<sup>1</sup> ; 99 and 105, l./r. M<sup>2</sup> ; 91, 93, 95 and 96, l. M<sup>3</sup> ; 103, juv. hemimandible with D<sub>1</sub>-D<sub>2</sub> ; 163, l. hemimandible with P<sub>3</sub>-M<sub>3</sub> ; 141, mandibular fragment with P<sub>3</sub>-P<sub>4</sub> ; 142, l. mandibular fragment with P<sub>4</sub>-M<sub>1</sub> ; 286, r. P<sub>4</sub> ; 67, frag. scaphoid ; 62, r. trapezoid ; 61 and 122, McIII ; 121, r. McIV ; 118 and 119, l. cuboids ; 123, MtII ; 115 and 126, MtIII ; 65, 120, 124 and 125, MtIV ; and *Diaceratherium*

*aurelianense* : 44, r. scaphoid ; 46, r. pyramidal ; 53 and 55, l. McII ; 52, l. McIII ; 49 and 50, l. McIV ; 57, l. MtII.

### France

Muséum National d'Histoire Naturelle, Paris (except expressed indication) :

- Neuville (Universitäts-Institut für Paläontologie und historische Geologie, Munich, Germany) : cast 1968 XIV, 192, l. MtIII.

- Baigneaux-en-Beauce : Ba 1664, r. maxillary with P<sup>4</sup>-M<sup>2</sup>; Ba 1667, l. maxillary with P<sup>2</sup>M<sup>3</sup> ; Ba 1668, r. maxillary fragment with M<sup>1</sup>-M<sup>2</sup> ; Ba 1672, l. P<sup>3</sup>, P<sup>4</sup>, M<sup>1</sup>, M<sup>2</sup> and M<sup>3</sup> (different individuals) ; Ba 1674, l. P<sup>2</sup>, P<sup>4</sup> and M<sup>1</sup> ; Ba 3045, 2324, 2330 and 2327, 31./1r. P<sup>2</sup> ; Ba 2317, 2314 and 2316, 1r./2l. P<sup>3</sup> ; Ba 1676, l. mandible with P<sup>2</sup>-M<sup>3</sup> ; Ba 2689, l. scapula ; Ba 2695, 2697, 2698, 2699, 2700, 2701, 2702 and 2703, humeri ; Ba 2722, 2723, 2724, 2725, 2728, 2739 and 2740, 5l./2r. ulnas ; Ba 2710 and 2718, l. radii ; Ba 2769, r. femur ; Ba 2795, r. tibia ; Ba 2810 and 2814, l. fibulae ; Ba 2505, r. astragalus ; Ba 2518, 2521, 2522 and 2523, r. calcanei ; Ba 2517, l. calcaneum ; Ba 2550, 2551, 2552 and 2553, r./l. ectocuneiforms ; Ba 2986, l. McII ; Ba 2591, 2592 and 2593, 1l./2r. McIII ; Ba 2598 and 2624, r. McIV ; Ba 2603, r. MtII ; Ba 2614, 2615, 2616, 2619 (juv.) and 2620, l. MtIII ; Ba 2617 and 2618, r. MtIII ; Ba 2634, first central phalanx ; Ba 2643, third central phalanx.

- La Romieu (Centre Sciences de la Terre, Université Claude Bernard, Lyon) : 320542, l. humerus fragment ; 320532, l. radius ; 320506, l. unciform ; 320509, r. McII ; 320531, r. tibia ; 320219, r. MtIII.

- La Motte-Fanjas (Centre Sciences de la Terre, Université Claude Bernard, Lyon) : 99998, r. P<sup>2</sup> ; 99999, r. P<sup>4</sup>.

- Chevilly : CHE 81, l. D<sup>4</sup> ; CHE 104, r. P<sub>4</sub> ; CHE 102, r. M<sub>1</sub> ; CHE 106, r. McIII ; CHE 107, l. astragale.

- Beaugency-Tavers (type locality of *P. douvillei*): TAV 81, l. P<sup>2</sup>-M<sup>3</sup> ; TAV 82, l. maxillary with P<sup>2</sup>-M<sup>2</sup> (holotype ; Osborn, 1900) ; TAV 110, r. P<sup>3</sup> ; TAV 122 and 124, l. M<sup>1</sup> ; TAV 76, l. M<sup>1</sup> ; TAV 105, r. M<sup>2</sup> ; TAV 108, r. M<sup>3</sup> ; TAV 84, l. mandible with D<sub>4</sub>-M<sub>1</sub> ; TAV 80, r. mandible with P<sub>2</sub>-P<sub>4</sub> and M<sub>2</sub>-M<sub>3</sub> ; cast 3903, r. mandible with P<sub>2</sub>-M<sub>1</sub> ; TAV 36, mandible with r. P<sub>2</sub>-M<sub>3</sub> and l. P<sub>3</sub>-M<sub>2</sub> ; TAV 116 and 117, r./l. P<sub>2</sub> ; TAV 118, l. M<sub>2</sub> ; TAV 123, l. McII fragment ;

- Pontlevoy-Thenay : FP 1784, r. P<sup>2</sup>-P<sup>4</sup> ; FP 582, r. mandible with P<sub>4</sub>-M<sub>1</sub> ; FP 581, l. mandible with D<sub>4</sub>-M<sub>2</sub> and P<sub>2</sub>, P<sub>3</sub> and M<sub>3</sub> erupting.

- Savigné-sur-Lathan (Museo Nacional de Ciencias Naturales, Madrid, Spain) : cast of a left astragalus.

- Malartic : SML 868, l. astragalus (cast).

### Germany

Universitäts-Institut für Paläontologie und historische Geologie (Munich).

- Sandelzhausen (very abundant ; material described by Heissig 1972).

- Georgensgmünd (type material of *P. germanicus*; same reference).

- Langenau I : 1980 126, cast of r. mandible with I<sub>2</sub>-P<sub>2</sub>-M<sub>3</sub>.

- Hessler : cast of l. P<sup>3</sup>-M<sup>4</sup> ;

- Kutaenhausen : cast of a mandible with l. P<sub>3</sub>-M<sub>3</sub> and r. P<sub>3</sub>-M<sub>1</sub>.

Data from Bézian (France) are after Ginsburg & Bulot (1984) ; the presence of *Prosantorhinus* at La Grive-Saint-Alban (France) was recently proposed by the author (Cerdeño 1993), data from Depéret (1887) and Guérin (1980).

The morphometrical comparison of the samples is presented. The Statgraphics program has been used to deal with the numerical data.

*Abbreviations* : l. = left ; M = molar ; Mc = metacarpal ; Mt = metatarsal ; P = premolar ; r. = right. Dimensions in tables : APDDIA = antero-posterior diameter of the diaphysis ; APDD=distal antero-posterior diameter ; APDI = internal antero-posterior diameter ; APDP = proximal antero-posterior diameter ; DL = distance between lips of the trochlea ; DTD = distal transversal diameter ; H = height ; L = length ; TDD = distal transversal diameter ; TDDIA = transversal diameter of the diaphysis ; TDP = proximal transversal diameter ; W = width.

## DESCRIPTION AND DISCUSSION

The comparative study of the dental and postcranial material listed above shows the existence of two main groups concerning size and proportions, corresponding to *Prosantorhinus germanicus* and *P. douvillei*. Both share the same morphological characters, with minor differences on articular surfaces.

A few **cranial** fragments have been recovered only from Sandelzhausen (*P. germanicus* : a crushed adult skull-not numbered ; 3165, another distorted adult skull ; 3124, an infantile specimen; and 3306, anterior portion of the nasal bones). The cranial characteristics that could be observed are the following : thickened, enlarged and roughened nasal extremity, which would support a small horn ; slightly concave dorsal profile ; short sagittal crest ; high and narrow zygomatic arches ; and postglenoid and posttympanic processes in contact.

Concerning **dental morphology** (Pl. 17, 18), upper premolars of *Prosantorhinus* are characterized by the crochet which usually presents two or more folds. The crista is well developed on milk molars, but its presence is rare on permanent teeth (e.g. P<sup>3</sup> from Baigneaux). Lingual cingulum is present, more frequently simply developed as a tubercle between protoloph and metaloph. Labial cingulum is often present on P<sup>4</sup> and M<sup>1</sup>. Protocone constriction increases from P<sup>3</sup> to M<sup>2</sup>. A small "bridge" between protoloph and metaloph has been observed on several specimens (e.g. P<sup>3</sup> Ba 2321 and Ba 2316 from Baigneaux ; P<sup>3/4</sup> from Beaugency-Tavers and Pontlevoy ; P<sup>2</sup> 99998 from La Motte-Fanjas ; P<sub>2</sub>-P<sub>3</sub> of the holotype of "*Gaindatherium rexmanueli*" from Lisbon). Some teeth of the studied sample show cement remains on the ectoloph.

Dentition of *P. germanicus* from Sandelzhausen and Georgensgmünd gathers in size together with the remains from Baigneaux, these latter being closer to the largest German specimens (tabl. 2-3 ; Fig. 1). A second group corresponding to *P. douvillei* is somewhat greater, even if some teeth are quite similar to the largest ones of the first group (Fig. 1). Upper tooth dimensions from

	LP1	WP1	LP2	WP2	LP3	WP3	LP4	WP4	LM1	MM1
P.g.										
N	4	4	20	20	18	18	22	22	23	23
X	16.1	13.9	23.7	28.9	28.6	36.8	31.6	41.7	36.2	40.7
Min.	15.0	12.7	20.4	26.0	26.2	33.0	28.0	39.3	31.0	37.0
Max.	17.5	14.7	28.6	34.7	30.5	40.8	35.4	45.6	39.3	45.6
C.v.	6.6	6.2	10.0	9.7	3.9	5.6	5.9	4.2	5.8	5.3
C	-	-	29.4	33.7	33.3	41.5	36.6	47.8	41.9	48.6
C	-	-	29.8	35.6	-	-	-	-	-	-
D	24.0	20.3	33.2	33.9	37.7	40.3	-	-	50.8	-
D	-	-	32.1	40.8	-	-	-	-	-	-
E	-	-	-	-	35.8	47.7	33.0	48.8	-	-
E	-	-	-	-	-	-	37.3	46.8	-	-
E	-	-	-	-	-	-	39.2	46.8	-	-
F	-	-	25.6	32.2	28.2	36.6	33.0	41.0	41.3	43.4
F	-	-	-	-	-	-	33.0	46.5	41.4	43.0
F	-	-	24.8	30.2	29.6	36.8	36.5	43.7	39.5	41.1
F	-	-	-	-	30.9	36.7	33.1	40.6	42.7	45.8
F	-	-	24.2	30.2	29.3	39.7	-	-	36.1	46.2
F	-	-	26.2	31.3	25.4	34.2	-	-	-	-
F	-	-	26.6	31.5	-	-	-	-	-	-
G	-	-	29.4	35.7	34.9	42.4	39.0	50.2	46.6	49.9
G	-	-	-	-	34.0	40.5	-	-	46.2	48.0
G	-	-	29.4	39.6	37.4	47.8	41.7	54.5	40.0	45.6
H	-	-	31.4	37.9	35.6	44.6	38.3	50.9	-	-
I	-	-	26.0	32.5	-	-	37.0	48.0	-	-

Table 2 - Comparative dimensions of the upper teeth of *Prosantorhinus*. P.g. = *P. germanicus* from Sandelzhausen and Georgensgmünd ; N = sample size ; X = average ; Min. = minimum ; Max. = maximum ; C.v. = coefficient of variation. C = Hessler ; D = "Gaidatherium", Lisbon ; E = *Prosantorhinus*, Lisbon ; F = Baigneaux ; G = Beaugency ; H = Pontlevoy ; I = La Motte-Fanjas. *Dimensions comparées des dents supérieures de Prosantorhinus*.

Lisbon ("Gaidatherium"), Beaugency and Pontlevoy are always greater than those of *P. germanicus*. With regard to lower teeth this difference in size is not so clear for Beaugency (Fig. 2).

The **postcranial skeleton** of *Prosantorhinus* (Pl. 18, 19) is well represented at Sandelzhausen, Baigneaux and Lisbon area (material described as *G. rexmanueli*). The broadest comparison concerns astragali and metapodials (Tab. 4-6), since they appear within most of the studied populations. In general all bones are wide and short as typical teleoceratines, with smaller size than the best known species *D. aurelianense* and *B. brachypus*. Epiphyses are large (both transversal and antero-posterior diameters) with respect to the diaphysis, and there are usually well developed tuberosities. The distal epicondyle of the

	LP2	WP2	LP3	WP3	LP4	WP4
P.g.						
N	14	14	18	18	19	19
X	19.3	14.1	25.6	19.1	28.9	22.0
Min.	16.3	13.3	22.0	17.0	25.6	18.5
Max.	25.0	15.5	32.0	23.0	35.7	24.0
C.v.	10.7	4.1	10.3	9.5	9.4	6.2
C	21.7	14.9	26.7	18.0	-	-
D	-	-	34.5	23.2	34.1	25.9
D	-	-	34.0	25.4	37.3	27.0
D	-	-	-	-	40.0	30.6
F	-	-	-	-	30.0	22.5
F	22.1	16.3	29.3	21.2	30.0	24.0
G	19.6	16.6	27.0	21.5	31.0	22.8
G	23.7	16.1	31.8	22.1	32.9	25.2
G	26.3	19.5	-	-	-	-
G	28.9	19.7	-	-	-	-
H	26.9	18.6	32.5	24.5	30.5	25.0
H	25.0	18.0	-	-	-	-
J	-	-	29.9	22.0	31.6	24.0
J	-	-	30.1	22.1	31.4	23.3
K	21.6	15.2	29.2	19.0	33.0	22.7
U	-	-	-	-	32.0	23.2

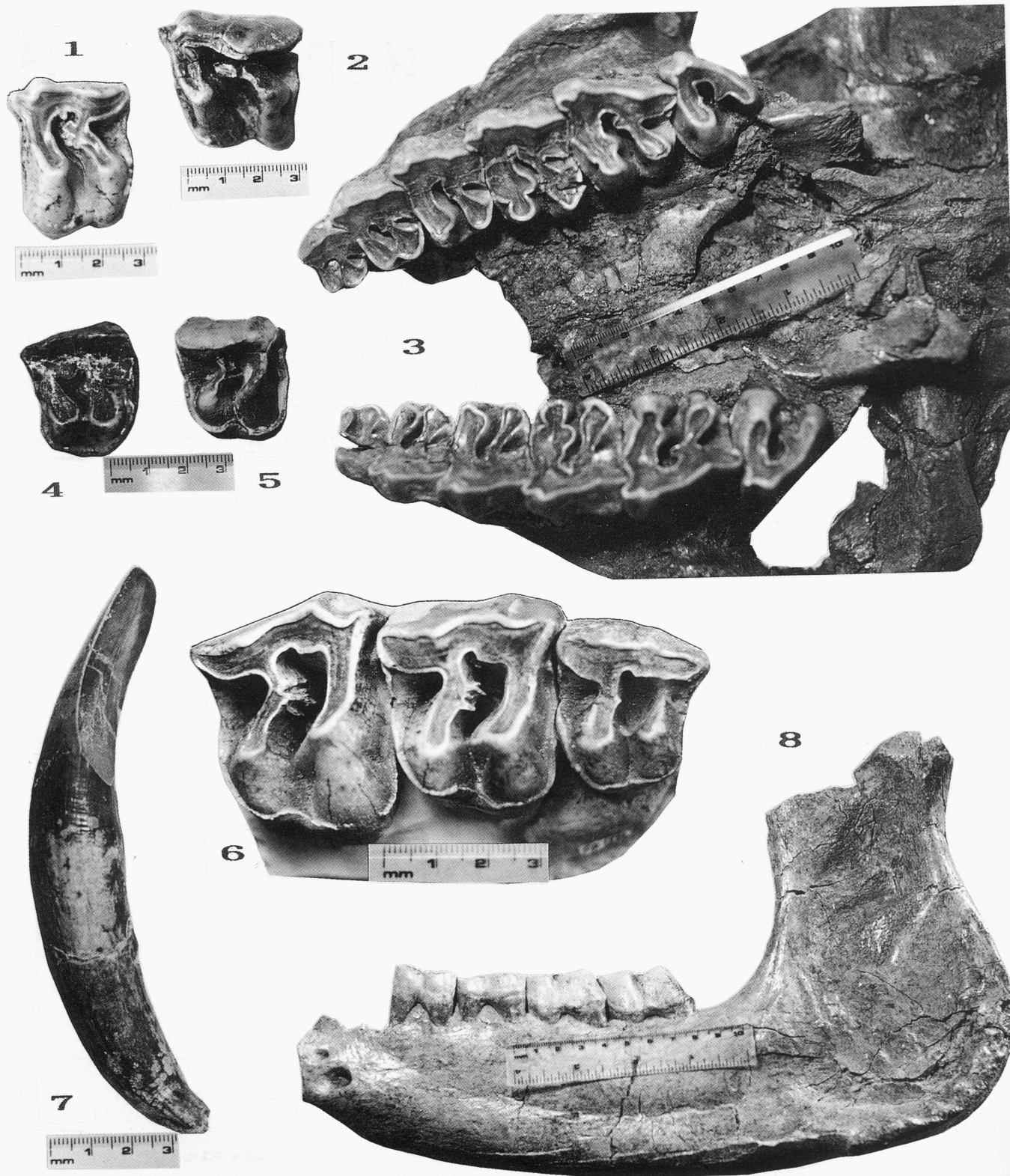
Table 3 - Comparative dimensions of the lower premolars of *Prosantorhinus*. Legends in table 2, and J = Kutaenhausen ; K = Langenau I ; U = Bézian. *Dimensions comparées des prémolaires inférieures de Prosantorhinus*.

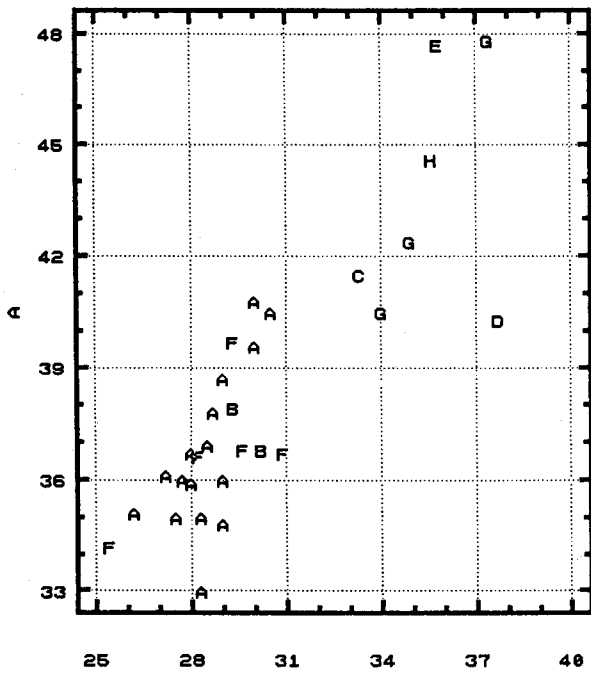
humerus is high but little laterally developed. The posterior articular facets of the radius are fused. The tibia has a relatively wide anterior tibial groove. The scaphoid has a third posterior medial facet for the semilunate. This latter bone do not have proximal ulna-facet. The McII has a trapezium-facet, and the McV is a fully developed metapodial. The calcaneum shows a short tuber, with strong unevenness ; the sustentaculum is disposed at a right angle ; and both fibula and tibia facets are present on the calcaneum. The astragalus has the facet-1 (postero-external) rather flattened, and the development of its distal projection is variable. Little differences concern the outline of the isolated facet-2 (postero-internal) of

## PLATE 17

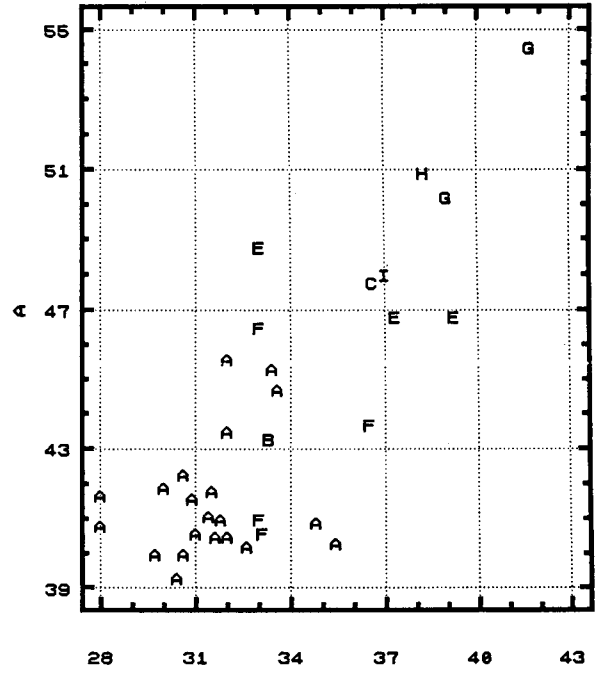
Fig. 1-3, 7-8 - *Prosantorhinus germanicus*. 1, Sandelzhausen, left  $P^4$  (1431). 2, Sandelzhausen, left  $M^2$  (801). 3, Sandelzhausen, palatal fragment with right and left  $P^2-M^3$  (not numbered). 7, Sandelzhausen, right  $I_2$  (PQ 422). 8, Sandelzhausen, left mandibular ramus with  $P_4-M_3$  (2490). 1,  $P^4$  gauche (1431). 2,  $M^2$  gauche (801). 3, fragment de palais avec  $P^2-M^3$  droites et gauches (sans numéro). 7, droite  $I_2$  (PQ 422). 8, demi-mandibule gauche avec  $P_4-M_3$  (2490).

Fig. 4-6 - *Prosantorhinus douvillei*. 4, Baigneaux, left  $P^3$  (Ba 2321). 5, Baigneaux, right  $P^2$  (Ba 2330). 6, Pontlevoy, right  $P^2-P^4$  (FP 1784). 4,  $P^3$  gauche (Ba 2321). 5,  $P^2$  droite (Ba 2330). 6,  $P^2-P^4$  droites (FP 1784).



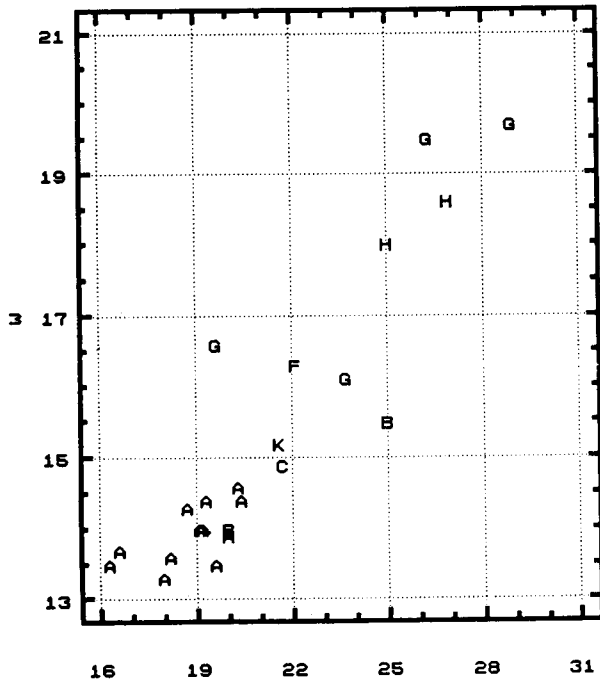


UPPER P3-L

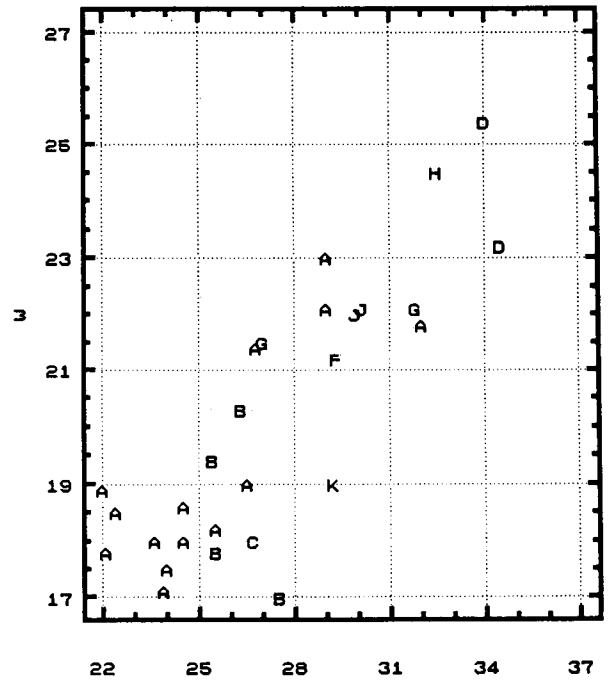


UPPER P4-L

Figure 1 - Length/width relationship of upper P3 and P4 of *Prosantorhinus* A = Sandelzhausen ; B = Georgensgmünd ; C = Hessler ; D = Lisbon ("*Gaidatherium*") ; E = Lisbon (*Prosantorhinus*) ; F = Baigneaux ; G = Beaugency ; H = Pontlevoy ; I = La Motte-Fanjas. *Relation longueur/largeur des P3 et P4 supérieures de Prosantorhinus.*



LOWER P2-L



LOWER P3-L

Figure 2 - Length/width relationship of lower P2 and P3 of *Prosantorhinus*. Legends in figure 1 and J = Kutaenhausen ; K = Langenau I. *Relation longueur/largeur des P2 et P3 inférieures de Prosantorhinus.*

	MTD	H	DTD	DL	APDI
P.g.					
N	14	14	14	14	14
X	65.6	47.9	54.5	39.7	34.1
Min.	61.6	45.3	48.8	36.6	31.1
Max.	69.9	52.2	59.2	42.0	36.2
C.v.	4.4	4.7	5.1	4.5	4.7
L	76.0	59.0	67.0	50.0	-
M	73.0	59.7	67.5	49.3	-
F	71.7	57.3	59.7	45.0	37.7
Q	68.2	55.3	59.3	47.5	-
H	71.3	58.3	61.0	44.3	40.6
H	82.4	66.0	67.6	52.7	44.0
H	79.5	69.1	71.0	51.8	46.4
H	85.0	71.4	75.7	56.0	53.4
P	67.0	52.5	56.0	43.5	42.2
R	86.0	57.0	74.0	59.0	43.5
R	91.0	-	80.5	-	56.0

Table 4 - Comparative dimensions of the astragalus of *Prosantorhinus*. Legends in table 2-3, and L = Artesilla ; M = Chevilly ; P = Savigné ; Q = Malartic ; R = La Grive. *Dimensions comparées des astragales de Prosantorhinus*.

the astragalus ; it is more or less rounded or semilunate, in contrast to the much more transversely elongated facet-2 of *D. aurelianense* and *B. brachypus*. The antero-posterior diameter of this bone is great such it is in these species.

Figure 3 shows how the astragali are grouped by size. There are three "medium-sized" astragali from Pontlevoy which are difficult to be interpreted (Cerdeño 1993). As I stated then, they possibly represent greater specimens of *Prosantorhinus* rather than smaller ones of *B. brachypus* (among other remains from Pontlevoy, one astragalus clearly corresponds to *Prosantorhinus* and another one to *B. brachypus*), since proportions are closer to *Prosantorhinus*. These three bones (FP 1791, FP 1792 and FP 1795) are also close to the specimens of *D. aurelianense* from Neuville and Chilleurs ; however, considering them as this last species would suppose the co-existence of three brachypothere forms, and specially of *D. aurelianense* and *B. brachypus* ; this is not very plausible taking into account the age of Pontlevoy, and that latter two species are not present together anywhere else (further discussion in Cerdeño 1993).

The astragalus from Savigné is very close to the assemblage from Sandelzhausen. On the contra-

McIII	L	TDP	APDP	TDDIA	APDDIA	TDD	APDD
P.g.							
N	5	7	7	7	7	5	4
X	92.5	40.5	29.5	37.2	13.5	44.5	27.0
Min.	89.0	38.2	26.9	35.5	11.6	42.5	26.0
Max.	96.7	42.8	31.5	38.5	15.4	47.5	28.2
C.v.	3.6	5.1	5.6	2.7	8.7	5.0	3.5
F	111.5	46.1	34.3	40.0	16.3	51.0	32.7
F	118.5	52.0	35.9	39.5	17.2	-	31.2
F	107.8	46.0	-	40.7	14.5	53.0	34.8
M	113.7	55.0	35.8	47.0	16.9	49.3	35.0
E	112.7	52.8	37.2	46.5	17.0	54.7	35.5
E	114.0	46.0	43.2	46.0	21.7	55.5	42.3

McIV	L	TDP	APDP	TDDIA	APDDIA	TDD	APDD
P.g.							
N	4	4	4	4	4	3	4
X	75.1	27.1	29.4	25.7	12.7	32.0	25.6
Min.	73.1	25.4	28.0	25.0	12.2	30.6	24.0
Max.	76.5	28.6	30.7	27.0	13.0	32.8	27.1
C.v.	2.1	4.9	4.3	3.4	3.1	3.9	5.5
D	-	37.0	46.0	32.4	20.6	-	-
E	92.7	37.4	40.2	31.0	18.3	43.6	32.6
E	95.5	38.0	-	30.3	18.4	43.1	-
F	90.8	32.2	34.7	29.0	14.4	36.3	29.9
F	89.1	31.3	37.2	27.1	15.0	35.0	29.0
T	78.0	31.6	36.0	32.3	18.7	39.0	35.0

Table 5 - Comparative dimensions of the metacarpals of *Prosantorhinus*. Legends in table 2-4, and T = Buñol. *Dimensions comparées des métacarpiens de Prosantorhinus*.

ry, that from Baigneaux closes to Pontlevoy, Malartic, Artesilla and Chevilly. The astragalus from La Grive-Saint-Alban is greater but relatively shorter than all others of *Prosantorhinus* (Fig. 3). Classically considered as *Brachypotherium*, this rhinoceros seems actually to be closer to *Prosantorhinus* as already proposed (Cerdeño 1993). It could correspond to a final form of this genus, larger and stronger than *P. douvillei*, and I classify it tentatively as *Prosantorhinus* sp. B., probably also different from the *Prosantorhinus* sp. A from Buñol.

When comparing metapodials (Fig. 4) the first thing to be detached is that the sample from Baigneaux is well separated from *P. germanicus* from Sandelzhausen, as it was for the astragalus and in contrast to what happened to dental remains. This difference is greater for metacarpals (McIII and McIV) than for metatarsals (MtIII).

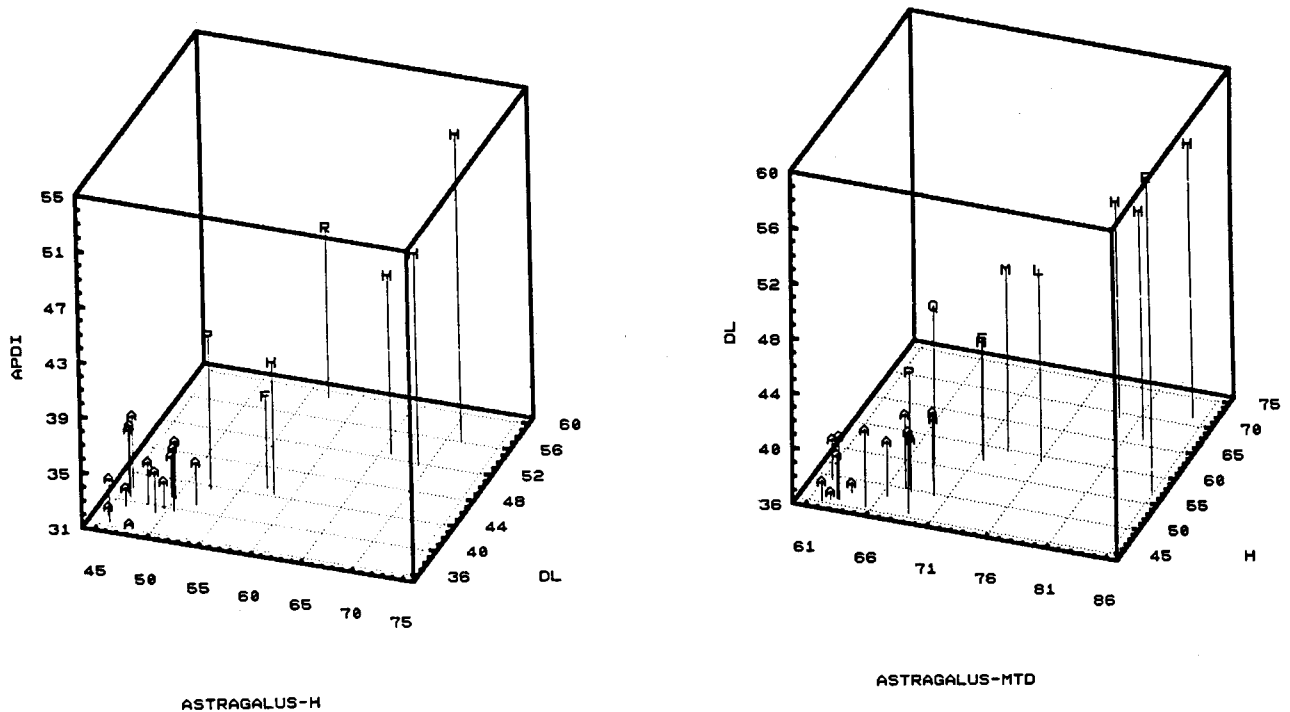


Figure 3 - Tridimensional scatterplot of the astragalus of *Prosantorhinus*. Legends in figure 1 and **L** = Artesilla ; **M** = Chevilly ; **P** = Savigné ; **Q** = Malartic ; **R** = La Grive. **APDI** = internal antero-posterior diameter ; **DL** = distance between lips of the trochlea ; **H** = maximal height ; **MTD** = maximal transversal diameter. *Représentation tridimensionnelle de l'astragale de Prosantorhinus.*

The cluster analysis realized for metapodials shows that the sample from Baigneaux is grouped together with the greatest specimens, and all of them keep apart from Sandelzhausen.

The McIV from Buñol is hardly longer than those from Sandelzhausen but much more stronger (Fig. 4). On the other hand, I have compared the gracility index (TD diaphysis x100/L) of the McIII and MtIII, as well as the ratio DLx100/H of the astragalus (Fig. 5). It becomes evident that *P. germanicus* from Sandelzhausen, with a smaller size, has a proportionally broader and shorter astragalus and stronger metapodials than *P. dou-*

*villei*. Only the great astragalus from La Grive presents the same index than the strongest specimen from Sandelzhausen. Two McIII of *P. douvillei* from Lisbon and Chevilly are comparable in gracility to *P. germanicus*, but those from Baigneaux are clearly more slender than those from Sandelzhausen.

In a general view the German MtIII are also stronger. However, there is a very slender specimen which keeps far away from the other MtIII from Sandelzhausen. Baigneaux also presents a rather wide range, with a MtIII even more slender than that one. Even greater gracility is veri-

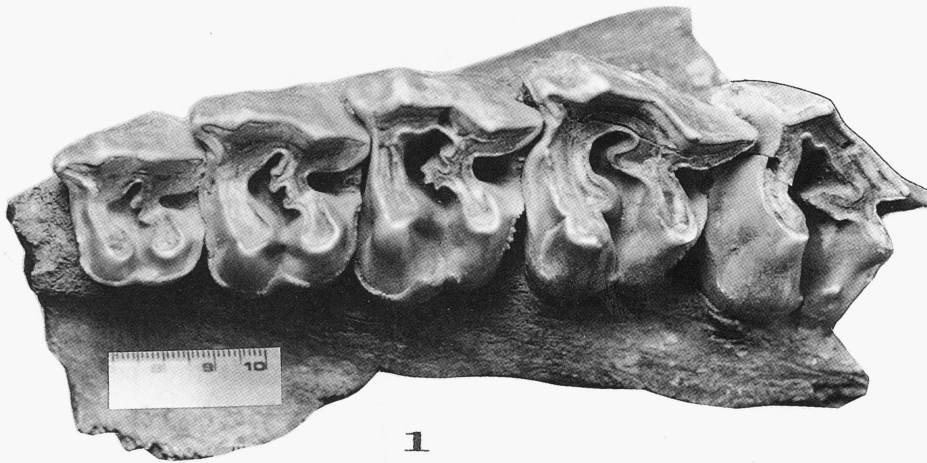
## PLATE 18

Fig. 1-2 - *Prosantorhinus douvillei*. **1**, Beaugency-Tavers, left  $P^2-M^2$  (Tav 82), holotype. **2**, Beaugency-Tavers, right mandibular fragment with  $P_2-P_4$ , and  $M_2M_3$  (Tav 80). **1**,  $P^2-M^2$  gauches (Tav 82). **2**, fragment mandibulaire droit avec  $P_2-P_4$ , et  $M_2M_3$  (Tav 80).

Fig. 3-9, 11 - *Prosantorhinus germanicus*. **3**, Sandelzhausen, right unciform (0139), proximal view. **4**, Sandelzhausen, left semilunate (460), lateral view. **5**, Sandelzhausen, right pyramidal (2818), postero-medial view. **6**, Sandelzhausen, right astragale (1234), posterior view. **7**, Sandelzhausen, left calcaneum (3368), medial view. **8**, Sandelzhausen, right MtIII (781), anterior view. **9**, Sandelzhausen, left McIV (13J), anterior view. **11**, Sandelzhausen, right McV (37M), anterior view. **3**, *onciforme droit* (0139), *vue proximale*. **4**, *semilunaire gauche* (460), *vue latérale*. **5**, *pyramidal droit* (2818), *vue postero-médiale*. **6**, *astragale droit* (1234), *vue postérieure*. **7**, *calcaneum gauche* (3368), *vue médiale*. **8**, *MtIII droit* (781), *vue antérieure*. **9**, *McIV gauche* (13J), *vue antérieure*. **11**, *McV droit* (37M), *vue antérieure*.

Fig. 10 - *Prosantorhinus A*, Buñol, right McIV (PAN 75), anterior view. *McIV droit* (PAN 75), *vue antérieure*.

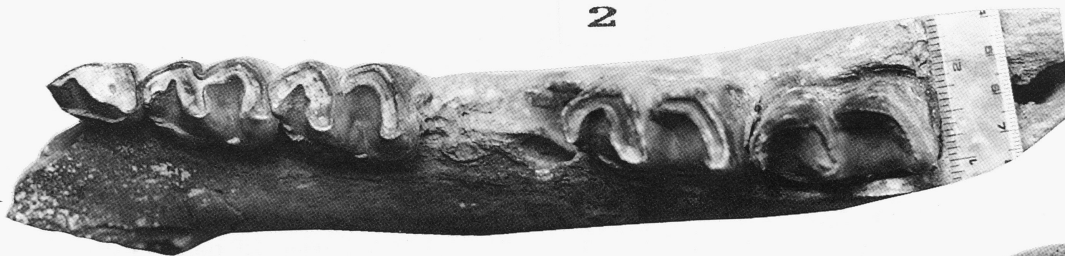




1



3



2



4



5



6



7



8



9



10



11

MtIII	L	TDP	APDP	TDDIA	APDDIA	TDD	APDD
P.g.							
N	8	8	8	7	8	8	7
X	80.1	34.0	30.0	32.2	14.5	41.6	28.8
Min.	74.5	31.4	27.1	30.5	12.5	38.4	26.6
Max.	86.4	36.4	39.1	34.0	15.9	44.6	31.0
C.v.	5.6	5.6	13.1	3.8	7.2	4.9	4.6
F	95.0	41.0	34.0	37.1	17.1	45.2	34.2
F	95.8	37.0	35.0	36.9	15.3	46.8	34.9
F	-	42.4	36.6	37.4	19.4	-	-
F	-	40.0	36.0	-	17.1	-	-
F	-	32.8	33.2	30.0	11.1	-	-
F	-	41.5	34.0	-	-	-	-
F	96.2	36.9	33.4	33.2	16.0	45.0	32.6
O	100.0	44.5	36.4	42.2	20.5	55.0	41.3
D	101.8	41.5	38.0	40.5	21.3	50.3	34.0
D	101.3	42.3	33.5	40.0	17.4	48.5	37.0
S	101.0	39.0	33.6	39.0	-	48.2	37.6
R(X)	111.5	51.8	-	45.5	22.3	61.0	41.5

MtIV	L	TDP	APDP	TDDIA	APDDIA	TDD	APDD
P.g.							
N	1	3	3	2	2	1	1
X	67.0	26.4	28.4	23.1	13.1	31.0	26.3
Min.		25.4	25.8	22.3	12.4		
Max.		28.0	30.0	24.0	13.8		
C.v.		5.3	8.0	5.2	7.5		
D	87.7	36.0	39.4	29.0	22.2	36.5	40.2
D	89.4	35.2	37.0	29.2	20.0	34.7	40.2
D	-	35.6	34.0	28.7	18.4	-	-
E	79.7	35.9	41.2	28.4	21.6	36.3	38.3
R	90.5	(40.0)	(38.0)	31.5	19.5	45.0	40.0

Table 6 - Comparative dimensions of the metatarsals of *Prosantorhinus*. Legends in tables 2-5. *Dimensions comparées des métatarsiens de Prosantorhinus*.

fied for the specimens from La Romieu. It is interesting to notice that the *Brachypotherium* from this last site is also more slender than the same species from other localities (Cerdeño 1993). Data from Neuville, Lisbon and La Grive are closer to most values from Sandelzhausen (Fig. 5). The remains from Baigneaux are worthy of special comments. The teeth from this site are hardly different from the sample of *P. germanicus* from Sandelzhausen, being closer to the greater specimens. However, the postcranial elements from Baigneaux keep clearly apart from those from Sandelzhausen, specially the metapodials

which are grouped with *P. douvillei* in the cluster analysis. Even for the other samples of *P. douvillei*, differences among teeth are not so great with respect to Sandelzhausen (e.g., P<sub>4</sub> from Baigneaux ; Tab. 2), what would reveal a lesser variation for dentition than for postcranial skeleton. So it seems coherent to support taxonomic differentiation with postcranial characteristics, and therefore I gather the sample from Baigneaux with *P. douvillei*.

Special robustness is observed for the McIV from Buñol ; the homologous bones from Lisbon are similar to it, but they remain more slender. By now it seems better to maintain the species from Buñol as *Prosantorhinus* sp. A. On the other hand, the greater and stronger remains from La Grive are considered as a final form of *Prosantorhinus*, but the scarcity of data does not enable by the moment more taxonomical precision, and they are tentatively determined as *Prosantorhinus* sp. B.

When considering the studied populations altogether, different kind of analyses (one sample analysis ; one-way ANOVA) always reveal the presence of at least two different samples whatever variable is checked, what supports the validity of both species *P. germanicus* and *P. douvillei*. The scarce representation of both forms of *Prosantorhinus* sp. does not allow an adequate statistical treatment to support their taxonomic differentiation of *P. douvillei*, though present data point to that.

## CONCLUSIONS

Different European populations of *Prosantorhinus* have been compared each other. There is a well defined group corresponding to *Prosantorhinus germanicus*, the small and robust species from the Lower (?) and Middle Miocene of Germany (Heissig 1974), here also recognized at Savigné (France). Its better representation corresponds to Sandelzhausen (Germany). Numerical data from Georgensmünd (type locality) and Sandelzhausen gather with those from Langenau I, Hessler, Kutaenhausen, and Savigné. However, data from Hessler and Kutaenhausen show high values among the group, and the P<sup>3</sup> from Hessler reaches the greatest forms. Lacking other remains known to me from this latter site, I keep doubts about its assignment to *P. germanicus*.

The second group of larger forms, mostly ascribed to *P. douvillei*, is more scarcely represented at each locality. It includes the small teleoceratine