



REVISION OF THE EUROPEAN SPECIES OF *PROSANTORHINUS* HEISSIG, 1974 (MAMMALIA, PERISSODACTyla, RHINOCEROTIDAE)

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Abstract: It is not size that distinguishes the genus *Prosantorhinus* HEISSIG, 1974 from *Diaceratherium* DIETRICH, 1931, but the following characters: a concave dorsal skull profile with upslanting nasals and narrowing on the distal side of the last upper molar.

Using these characters, in addition to the type species *Prosantorhinus germanicus* (WANG, 1929), the following species can be added to the genus: *Prosantorhinus douvillei* (OSBORN, 1900) (Heissig 1972a: 69, Cerdeño 1996:112 ff.), from the Early and Middle Miocene (MN 3–5) of Western Europe, *Prosantorhinus laubei* HEISSIG et FEJFAR, 2007 from MN 3 of northern Bohemia, *Prosantorhinus aurelianensis* (NOUEL, 1866) from MN 3–4a of Western Europe, and with some reservation “*Rhinoceros*” *tagicus* ROMAN et TORRES, 1907 (Heissig 1972a: 69), an enigmatic species from the Early Miocene (MN 3) of Portugal, known only by its upper cheek teeth.

At the beginning of MN 3 (Mein 1989), the metapodials of *Prosantorhinus aurelianensis* were considerably more robust than those of the latest *Diaceratherium* species (Laugnac, MN 2b) (de Bonis 1973: 128 ff.) Within the genus shortening of the distal limb segments and narrowing of the distal side of M3 increased with time. The metapodials of *Prosantorhinus laubei* are less robust but of medium length, in contrast to the Middle Miocene (MN 5) *Prosantorhinus germanicus* in which they are extremely shortened.

No transitional species or co-occurrence of *Diaceratherium* and *Prosantorhinus* are known.

Key words: Teleoceratini, *Prosantorhinus*, *Diaceratherium*, morphology, proportion indices, Early Miocene, Middle Miocene, Central Europe, Western Europe

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Introduction

When Cerdeño (1996) published the first revision of the genus *Prosantorhinus* only two well defined species were known: *Prosantorhinus germanicus* (WANG, 1929), the type species from Georgensgmünd and Sandelzhausen, Germany (both Middle Miocene MN 5) and *Prosantorhinus douvillei* (OSBORN, 1900) from Beaugency-Tavers (MN 5) and many Early Miocene sites in France. These species had been separated mainly based on their difference in size and the proportions of the postcranial skeleton. Cerdeño (1996) added to the well determined bulk of the genus several smaller samples which had been previously determined as *Gaindatherium* (*Iberotherium*) *rexmanueli* ANTUNES et GINSBURG, 1983, “*Diceratherium douvillei*” and even *Diaceratherium aurelianense* (NOUEL, 1866) from Lisbon (Antunes and Ginsburg 1983: 30). She identified them, on the basis of their size, as *P. douvillei* (OSBORN, 1900). This

is correct in particular for the holotype of “*Gaindatherium rexmanueli*” from MN 5, so that this species name is clearly synonymous with *P. douvillei*. She changed the species determination of some collections and recognized two further species, represented by very limited material from Buñol (Spain) and La Grive (France), but not suitable for species definition.

Since that time Heissig and Fejfar (2007: 26) added the species *P. laubei* from Tuchořice (the Czech Republic) (MN 3) to the genus. Later a more comprehensive sample of this species was collected at the locality Ahníkov (Heissig and Fejfar 2013, 2018) by several private collectors, completing the knowledge of its osteology (material now housed in the National Museum, Prague). This early species differs in several remarkable characters from *P. germanicus*, which had nearly the same tooth size, but was considerably smaller in the postcranials. Only a few specimens were cited by Cerdeño (1996: 113 f.) from sites older than the rich faunas

of Neuville and Chilleurs (MN 3b). They are similar in size to *Prosantorhinus douvillei*, but could not be determined with certainty. The inclusion of *P. laubei* made a new diagnosis of the genus necessary but these early occurrences from French sites, probably contemporaneous with *P. laubei*, could not be included in this species.

Material and methods

Museums and collections

BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
CRu	Collection of Dr. M. Rummel, Weißenburg, Germany
CSm	Collection of Ulrich Schmid, Augsburg, Germany
HLMD	Hessisches Landesmuseum Darmstadt, Germany
IPUW	Institut für Paläontologie der Universität Wien, Austria
MHNT	Muséum d'Histoire Naturelle Toulouse, France
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHM	Muséum d'histoire naturelle de Marseille, France
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MSNO	Muséum des Sciences Naturelles, Orléans, France
NHMW	Naturhistorisches Museum Wien, Austria
NMA	Naturmuseum Augsburg, Germany
NMBa	Naturkundemuseum Basel, Switzerland
NMBe	Naturkundemuseum Bern, Switzerland
NMP	Národní muzeum, Praha, the Czech Republic
SMF	Senckenberg Museum und Forschungsinstitut Frankfurt, Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
UCBL	Université Claude Bernard, Lyon, France
UNL	Centro de Estratigrafia e Paleobiologia da Universidade Nova de Lisboa, Monte de Caparica, Lisboa, Portugal

Materials

The characterization of a rhinocerotid species needs a sufficient number of specimens from one site or horizon. Therefore this study concentrates on a restricted number of localities, leaving aside single specimens from other sites. The following collections have been examined in detail and compared generally with other species of *Prosantorhinus*:

Ahníkov (MN 3a): NMP
Tuchořice (MN 3a): NMP, NHMW
Wintershof-West (MN 3): BSPG
Neuville (MN 3b): MSNO
Chilleurs (MN 3b): MSNO, NMBa
Maigreville (MN 3b): MSNO
Artenay (MN 4a): MSNO
Chevilly (MN 4b): MNHN, MSNO
Baigneaux (MN 4b): MNHN, NMBa, MSNO
Langenau (MN 4b): SNMS
Montréal-du-Gers = Béon (MN 4b): MHNT
Rothenstein 16 (MN 3b): NMA

Sandelzhausen (MN 5a): BSPG
 Georgensgmünd (MN 5a) BSPG
 Beaugency-Tavers (MN 5a): MNHN, MSNO
 Pontlevoy-Thenay (MN 5b): MNHN, MSNO

For numbers of specimens see measurement tables in the Appendix.

Morphological and metric basis

The elements of cheek teeth are named after Osborn (1898, 1900) with additions to the terminology in Heissig and Fejfar (2007: figs 6, 7). The osteology of the skull and the postcranial elements are taken from the comparative anatomy standards (Nickel et al. 1992: 67 ff.) in a simplified form (Heissig and Fejfar 2007: 25). Thus “os carpi primum” (= trapezium) is written “carpal 1” etc. Only the names astragalus and calcaneus are preserved in the traditional way.

The length (L) of the upper cheek teeth was measured along the labial wall (ectoloph) at the level of the proximal and distal cingulum. The width (W) was taken at the crown base, perpendicular to the long axis of the tooth row. In some teeth there are two width measurements, anterior (Wa) and posterior (Wp). The length of the lower cheek teeth was taken parallel to the longitudinal axis of the tooth row, and two width measurements perpendicular to the widest parts of the trigonid and the talonid. The height (H) of the upper cheek teeth was defined as the maximal height at the paracone not vertically but parallel to the inclined ectoloph. The height of the lower cheek teeth was taken at the minimal height of the hypolophid, parallel to the inclination of the ectoflexid.

Skull measurements were taken according to Guérin (1980: 46). Unfortunately most fossil skulls are heavily crushed so that a comparison of measurements does not reveal any substantial characteristics of the species.

The distal limb bones are orientated according to their long axis, not to their position in the skeleton. The antero-posterior diameter is perpendicular to the length, the width according to the anatomical position, forms the third dimension. The measurements of the astragalus and most metapodials were taken according to Heissig (1972b: pl. 13), the measurements of single articular facets were taken along their inclined surface. The proximal diameter of metacarpal II and metatarsal II were taken parallel to the medial side facets, the proximal width at a right angle to this side. The measurements of the trochlea in all metapodials follow the plane of its middle ridge. The maximal length of the metapodials is termed L, proximodistal measurements of the astragalus are termed as the height (H). All measurements are given in mm, rounded off to half millimetres, over 100 to whole millimetres.

Anatomical abbreviations and numbering

Where possible the terms are given in their entirety. In the tables and diagrams it was necessary to use abbreviations. These are: a = anterior, D. = anteroposterior diameter, d. or dex. = dexter (right), di. = distal, dist. = distance, drs. = dorsal, fc. = articular facet, H = height, L = length, lt. = lateral, md. = medial, p. = posterior, plm. = palmar, plt. = plantar, px. = proximal, s. or sin. = sinister (left), sh. = shaft (diaphysis), W = width.

Very often museums use a collective numbering system. If a collective number for all specimens from one site is used, this number is added to the collection and the individual number is cited separately, e.g. the collective number for all rhinoceroses from Tuchořice in the Czech National Museum is 7391/Rh, all mammals in the Senckenberg Museum have the collective number SMF M, the collective number for all specimens from Sandelzhausen in the Bavarian State Collection is 1952 II. Specimens from this collection which have not yet been definitely numbered are marked with G, followed by the field number.

Data for several specimens was taken from the literature. These are marked in the tables.

Methods

The details of measurement are given in “Morphological and metric basis”.

The morphological comparison of teeth and skeletal elements follows the terminology and characters, indicated in Heissig (1972b: 9 ff., pl. 13). The size groups are shown in two dimensional scatter diagrams. In addition to the morphological comparison, several metric indices are used to show the differences more exactly. A characteristic trait of the Teleoceratini is the significantly increasing width of the upper premolars from the second to the fourth. Thus the premolar width gradation index ($WpP2 \times 100 / WaP4$) can be used to illustrate this tendency (App. Tab. A19). The length reduction in premolars compared to the molars is another typical feature in Teleoceratini. This can be quantified by the premolar reduction index, ($LP3 \times 100 / LM2$) (App. Tab. A17 for upper teeth and for lower App. Tab. A18).

Most authors characterise a rhinoceros species according to the size of the teeth as either small or large. But the size of skull and postcranials is not always proportional to tooth size. Some species have small teeth and relatively large limb bones compared with other species. This relationship can be expressed by the skeletodental index ($LP3 \times 100 / LMC III$ in upper teeth and $Lm3 \times 100 / LMT III$ in lower; App. Tabs A15, A16). A general trend is the shortening of the limb bones expressed by Cerdeño's (1996: 118) gracility index ($Wsh \times 100 / L$). It is shown for MC III and MT III (App. Tabs A13 and A14).

Systematic palaeontology

Family Rhinocerotidae OWEN, 1848

Subfamily Aceratheriinae DOLLO, 1885

Tribe Teleoceratini HAY, 1902

R e m a r k . The subdivision of the family Rhinocerotidae into subfamilies follows the systematics established by Heissig (1973) on the basis of several key characters.

Genus *Prosantorhinus* HEISSIG, 1974

Type species. *Dicerorhinus germanicus* WANG, 1929.

Other species. *P. douvillei* (OSBORN, 1900), *P. laubei* HEISSIG et FEJFAR, 2007, *P. aurelianensis* (NOUEL, 1866), ? *P. tagicus* (ROMAN et TORRES, 1907).

Occurrence. Early to Middle Miocene (MN 3 – MN 7), Western and Central Europe.

Diagnosis (emended). Small to medium sized brachycephalic Teleoceratini with concave dorsal skull profile and elevated nasals fused near the tips below the subterminal horn base. Nasal incision high and of medium depth. Upper premolars shortened compared with the molars. Last upper molar with triangular outline and short distal cingulum. Incomplete cement layer on the labial tooth walls. Postcranials robust. Manus tetractyl to tridactyl. Second metatarsal with proximal articular facet shortened from the rear by a foramen nutritium.

Comparison. See Table 1. Earlier Teleoceratini of the genus *Diaceratherium* DIETRICH, 1931, include the Oligocene species *D. lamilloquense* MICHEL, 1983 and *D. massiliae* MÉNOURET et GUÉRIN, 2009, as well as the early Miocene species *D. lemanense* (POMEL, 1853). *D. asphaltense* (DÉPÉRET et DOUXAMI, 1902), *D. tomerdingense* DIETRICH, 1931, and probably *D. aginense* (REPELIN, 1917) may be synonyms of the latter (Antoine and Becker 2013: 141). In contrast to most species of *Prosantorhinus* these species are medium sized to large. They had, as far as it is known, a rather long skull (e.g. Depéret and Douxami 1902: pl. 1, figs 1, 2, Duranthon 1990: pl. 1, Becker et al. 2010: fig. 3C), a dorsal profile which is concave only in the posterior part of the frontals and straight or slightly convex at the transition from frontals to nasals (see figures cited above). The nasals are horizontal, and not fused together and therefore bearing a split horn base, which is defined by a roughened bone surface near the tip of the nasals, punctured by many foramina. The nasal incision is deeper and lower. The last upper molar has a trapezoidal outline and a long robust distal cingulum (see figures cited above). The metapodials are less robust than in *Prosantorhinus* (Scherler et al. 2013: fig. 5). The manus is generally tetractyl.

Table 1. Cranial characters of different species of *Prosantorhinus*, compared with *Diaceratherium* and *Brachypotherium*.

Genus/species	<i>Diaceratherium</i>	<i>Pr. aurelianensis</i>	<i>Pr. douvillei</i>	<i>Pr. germanicus</i>	<i>Brachypotherium</i>
Distal limb segments	long	short	short	very short	short
Fronto-nasal profile	straight	concave	concave	concave	straight
Nasal incision	deep	medium	medium	medium	medium
Nasals	long	medium	medium	medium	short
Horn base	small	medium	stronger	very strong	reduced or lacking
Anterior orbit rim above	M2	M1	M1	P4/M1	M1 – M2

The cranial characters are known only in the three best documented species of *Prosantorhinus*. Two others are generically determined by dental characters.

The last genus of the Teleoceratini, *Brachypotherium* ROGER, 1904 immigrated into Europe during MN 4 and was the largest in Europe. It had a tridactyl manus, less shortened premolars, a straight skull profile and short narrow nasals with occasionally a feeble horn or was without a horn.

- 1974 v *Prosantorhinus* nov. nom. *germanicus* – Heissig, p. 37.
- 1993 *Prosantorhinus germanicus* – Cerdeño, p. 65.
- 1996 *Prosantorhinus germanicus* – Cerdeño, p. 111 ff., pl. 18, figs 3–9, 11.
- 1996 v non *Prosantorhinus germanicus* – Cerdeño, p. 113 f., (Kutaenhausen, Langenau 1).

H o l o t y p e . Left maxilla fragment P2 – M3, BSPG A.S.7.

T y p e l o c a l i t y . Georgensgmünd, Southern Germany.

S t r a t u m t y p i c u m . Middle Miocene (MN 5).

O c c u r r e n c e . Middle Miocene (MN 5 – MN 7), Southern Germany, France.

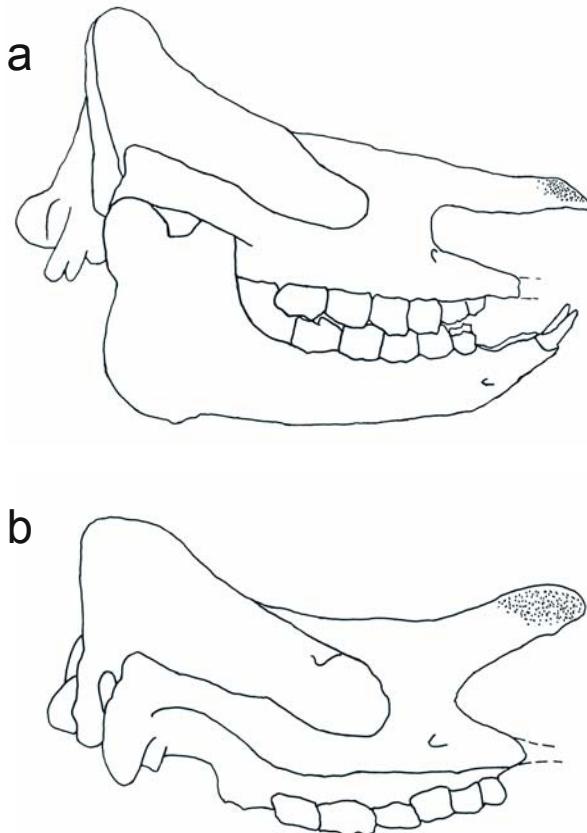
D i a g n o s i s . Type species of the genus *Prosantorhinus* with a strong nearly terminal bulbous horn base and fused nasals. The finger like prolongation of the nasals in front of the horn base is feeble and directed ventrally. Postcranials robust, relatively small compared with tooth size. Manus tetradactyl.

D e s c r i p t i o n . After Cerdeño's (1996) revision, no doubt remained about the taxonomy of this species. The odontology is documented in Peter (2002).

There are several distorted or fragmentary skulls from Sandelzhausen. The general shape is broad and short with flaring zygomatic arches. The temporal lines form a low, short sagittal crest. The occipital crista is broad and the occiput broadens ventrally towards the mastoid processes without any lateral constriction. The nasofrontal surface is deeply concave in profile and faintly convex transversally. The most peculiar structure is that of the horn base. It forms a nearly terminal bulbous, rough protuberance of the nasals, which is hollowed internally due to a pneumatic sinus. In front of this horn base is the very short tip of the nasals and is directed ventrally. The nasal bones arise rostrally and are fused at the tips in adults. They are short, triangular and broad at the base. The nasal incision is of medium depth and very high in front.

The mandibles show a less acute angle between the two halves than in most other rhinoceroses. The lower margin is curved and the branches are comparatively low. The symphysis is massive and slightly upturned with a short diastema. There is no space for the i1 between the large i2 on the narrow rostral side of the symphysis. The large diverging lower incisors show somewhat twisted crowns, which are strongly curved.

The limb bones are generally shortened and smaller than in other species. Its length ratio corresponds to the graviportal type. Carpal and tarsal bones are broad and low, metacarpals and metatarsals robust. Most of their characters are due to their proportions and are similar to the other known species. The fifth metacarpal is fully developed and bears a complete digit. Size and proportions can be seen best in the comparative diagrams in the appendix.



Text-fig. 1. Skull shape in *Diaceratherium* (a) and *Prosantorhinus* (b). a. *Diaceratherium aginense* (REPELIN, 1917), Laugnac (MN 2), Skull B; b. *Prosantorhinus aurelianensis* (NOUEL, 1866), Neuville (MN 3b), holotype.

Prosantorhinus germanicus (WANG, 1929)

N o t e . For earlier synonyms see Heissig (1972a: 65).

- 1929 v *Dicerorhinus germanicus* n. spec. – Wang, p. 191 ff., pl. 8, figs 1–4, pl. 9, figs 1, 2, text-fig. 2 B.
- 1929 v *Diceratherium steinheimense* (Jaeger) – Wang, p. 203, pl. 8, figs 5–7.
- 1929a v non *Dicerorhinus germanicus* nov. spec. – Wang, p. 4, pl. 2, fig. 5.
- 1934 *Ceratorhinus tagicus* ROMAN, partim – Roman and Viret, p. 35, pl. 9, figs 9, 11.
- 1965 *Brachypotherium aurelianense* Nouel – Ballesio et al., p. 75, pl. 7, fig. 3a, b.
- 1970 v *Dicerorhinus sansaniensis-germanicus* Gruppe part. – Mottl, pp. 83, 89, 98, 102.
- 1972a v *Brachypodella* n. gen. *germanica* – Heissig, p. 65 ff.

Prosantorhinus douvillei (OSBORN, 1900)

N o t e . A lot of smaller collections cited from different localities have been omitted in the synonymy list because

the limited amount of material does not allow a clear determination on the basis of the figures and the suggested classification is not different from any other.

- 1900 v *Diceratherium douvillei*, sp. nov. – Osborn, p. 239, fig. 6.
 1907 *Rh. (Diceratherium) Douvillei* Osborn – Stehlin, pp. 527, 530 f.
 1907 *Rhinoceros* sp. III – Stehlin, pp. 527, 531.
 1908 v *Diceratherium Douvillei* Osborn – Mayet, p. 90 ff., fig. 25–27.
 1908 v non *Diceratherium Douvillei* Osborn – Mayet, fig. 28.
 1918 *Ceratorhinus sansaniensis* mut. *Harlei* nob. – Repelin, p. 68.
 1925 *Br. aurelianense* – Stehlin and Helbing, p. 113, footnote.
 1925 “*Rhinoceros turonensis* Bourgeois” – Stehlin and Helbing, p. 114.
 1934 *Rhinoceros* sp. – Roman and Viret, p. 65.
 1948 *Ceratorhinus sansaniensis* mut. *Harlei* – Richard, p. 237.
 1972a *Brachypodella douvillei* – Heissig, p. 70.
 1979 *Prosantorhinus douvillei* – Ginsburg and Antunes, p. 493 f.
 1979 *Gaindatherium* – Ginsburg and Antunes, p. 493 f.
 1983 *Gaindatherium (Iberotherium) rexmanueli* – Antunes and Ginsburg, p. 30 ff., text-figs 12–20, pl. 6, figs 1–8, 10–12, pl. 7, figs 1–4.
 1983 non *Gaindatherium (Iberotherium) rexmanueli* – Antunes and Ginsburg, pl. 6, fig. 9, pl. 7, fig. 5.
 1987 *Gaindatherium (Iberotherium) rexmanueli* – Ginsburg et al., p. 306.
 1996 *Prosantorhinus douvillei* (Osborn, 1900) – Cerdeño, p. 112 ff.
 1997 v *Prosantorhinus germanicus* – Antoine, pp. 400, 412.
 1997 v *Prosantorhinus germanicus* – Antoine and Duranthon, pp. 202, 211.
 1998 v *Prosantorhinus* cf. *douvillei* – Wermelinger, pp. 1–246, figs 5–8, pls 1–40.
 2002 *Prosantorhinus douvillei* (Osborn, 1900) – Antoine, p. 37.

Holotype. Left maxilla fragment with P2 – M2, MNHN, Tav82 (Osborn 1900: 239, fig. 6).

Type locality. Beaugency-Tavers, France.

Stratum typicum. Middle Miocene (MN 5).

Occurrence. Early to Middle Miocene (MN 3b – MN 5), France, Southern Germany.

Diagnosis. Medium sized species of the genus *Prosantorhinus* with subterminal, slightly swollen horn base and partly fused nasals with a rough finger like rostrally directed prolongation of the nasals in front of the horn base. Postcranials robust, relatively large compared with tooth size. Manus variably tetra- or tridactyl.

Description. The most comprehensive material is from Montréal-du-Gers (MN 4b), also known as Béon, the best almost undistorted skull is from Langenau near Ulm

(MN 4b). On the basis of this specimen and the more or less distorted skulls from Montréal-du-Gers, the dental and skull characters can be described as follows. The general shape is broad and short with flaring zygomatic arches. The occiput is generally broad but the temporal lines unite to form a sagittal crest at least in males. The widest part of the occiput lies at the mastoid processes. The nasofrontal surface is concave in profile and convex transversally, more convex at the nasal base than over the frontals. The horn base is very similar in all primitive Teleceratini, but more robust than in *Diaceratherium*. It forms a slightly swollen, rough thickening of the nasals, which is subterminal. In front of this structure each nasal bone terminates in a narrow, finger like, rough process. The nasal bones arise frontally and are fused below the horn base in old animals. They are rather short, narrowing rostrally from the broad frontals and tapering at the end. The nasal incision is of medium depth and widely open rostrally.

The angle between the two halves of the mandibles is wide, similar as in *Prosantorhinus germanicus*. The lower margin of the corpus is curved and the branches are comparatively low. The symphysis is massive, broad and slightly upturned with a short diastema. The large incisors are close to one another. There is no twist on the incisor crowns which are less strongly curved than in the type species.

The limb bones are robust and large compared to the tooth size. Their length ratio corresponds to the graviportal type. Carpal and tarsal bones are broad and short, metacarpals and metatarsals less robust than in the type species. In the Montréal-du-Gers (Béon) collection the fifth metacarpal is generally reduced to a knob, but there is one specimen of a less reduced MC V with an articular facet for the ground phalanx. Unfortunately the most lateral metacarpal is not known from earlier horizons. Size and proportions can be seen best in the comparative diagrams.

There seems to be a problem with the remains from Portugal which have been named as *Gaindatherium (Iberotherium) rexmanueli* (Antunes and Ginsburg 1983: 30). The measurements of the upper molars would better fit the species *P. aurelianensis*, but the morphology, especially of the last molars, is identical with *P. douvillei*. Possibly the rather large size of these teeth, according to the literature, is due to different measuring methods.

***Prosantorhinus laubei* HEISSIG et FEJFAR, 2007**

- 2007 v *Prosantorhinus laubei* n. sp. – Heissig and Fejfar, p. 26 ff.

Holotype. Upper cheek teeth, right P2 – P3, M3-fragment, left P3 and M1-fragment, NMP 7391/Rh-53.

Type locality. Tuchořice, the Czech Republic.

Stratum typicum. Early Miocene (MN 3a; Fejfar 1989).

Other localities. Early Miocene (MN 3a), Ahníkov, the Czech Republic, Wintershof-West, Southern Germany.

Diagnosis. Medium sized species of *Prosantorhinus* with less shortened distal limb segments and very low crowned small cheek teeth. Medisinus of upper premolars

more frequently closed than in other species of the genus. Metacone rib of upper premolars broad and more lingually inclined than paracone rib. Mostly without a distal hypocone furrow in upper molars. Last upper molar with triangular outline, but the short distal cingulum appears as one or two prominent warts. Lower premolars without any trace of a labial cingulum. Limb bones large compared with tooth size.

Description. The material from the type locality is described in Heissig and Fejfar (2007). Additional and more comprehensive material will be described in Heissig and Fejfar (2018).

Prosantorhinus aurelianensis (NOUEL, 1866)

Note. The vast number of specimens and localities of this species makes it necessary to treat the synonymy in a selective way.

- 1866 v *Rhinoceros aurelianensis* – Nouel, p. 10, pl. 1–5.
- 1900 *Teleoceras (R.) aurelianensis* Nouel – Osborn, p. 250 f., text-figs 11, 12D.
- 1907 *Rhinoceros (Teleoceras) sp.* – Roman, p. 44, pl. 3, figs 2, 3.
- 1907 *Rhinoceros (Teleoceras) aurelianensis* Nouel – Stehlin, pp. 526 f., 530 f.
- 1908 *Teleoceras aurelianense* sp. Nouel – Mayet, p. 98 ff., text-fig. 29.
- 1949 *Brachypotherium (Teleoceras) aurelianense* Nouel – Zbyszewski, pp. 14–23.
- 1960 *Brachypotherium aurelianense* Nouel – Antunes, p. 258.
- 1979 *Brachydiceratherium aurelianensis* (Nouel) – Ginsburg and Antunes, p. 493.
- 1981 *Brachypotherium (Diceratherium) aurelianensis* (Nouel, 1866) – Ginsburg et al., p. 355.
- 1983 *Diceratherium aurelianensis* (Nouel 1866) – Antunes and Ginsburg, pp. 24 f., 90 f., text-figs 1–6, pl. 2, figs 4–8, pl. 3, figs 1–10.
- 1983 *Diceratherium cf. aurelianensis* (Nouel 1866) – Antunes and Ginsburg, pp. 23, 90, pl. 1, figs 2–4.
- 1987 non *Brachypotherium aurelianense* – Belinchón, p. 267, pl. 14, figs 1–3.
- 1989 *Diceratherium aurelianense* (Nouel, 1866) – Ginsburg, p. 162.
- 1993 *Diceratherium aurelianense* (Nouel, 1866) – Cerdeño, p. 29 ff.
- 1999 *Diceratherium aurelianense* (Nouel, 1866) – Heissig, p. 182.
- 2007 *Diceratherium aurelianense* – Heissig and Fejfar, p. 38.

Holotype. Skull with mandible and almost complete right side limbs MNHN.

Type locality. Neuville-aux-Bois.

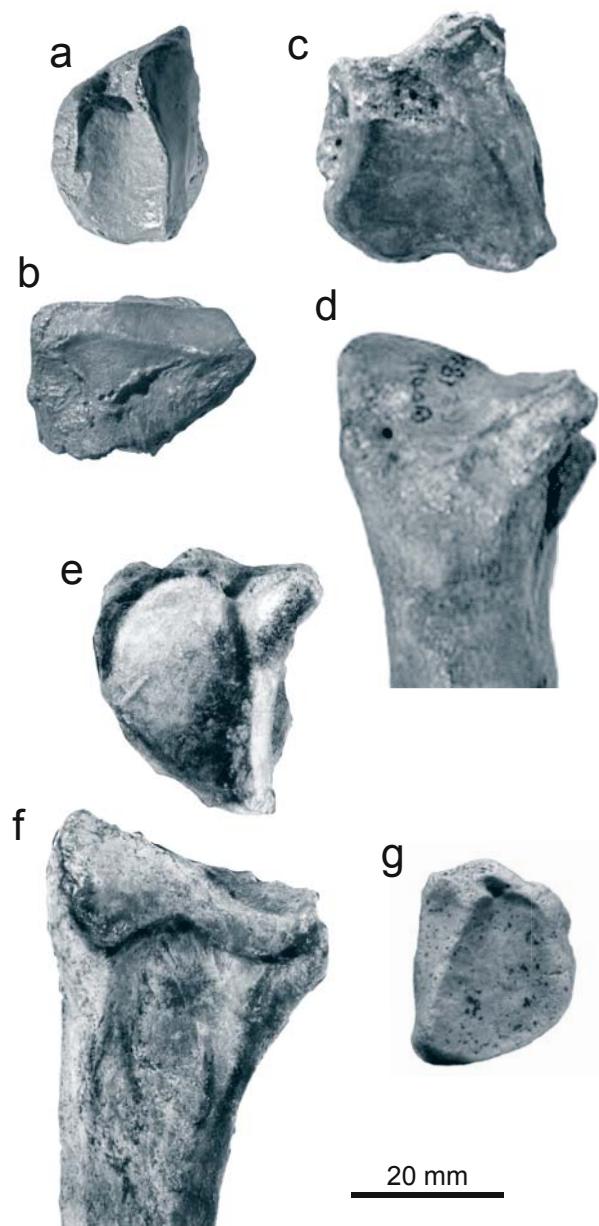
Stratum typicum. Early Miocene (MN 3b).

Other occurrences. Early Miocene (MN 3a – MN 4a), France, Spain, Portugal, Germany.

Remarks. Regardless of size, the combination of some crucial characters corresponds much more to *Prosantorhinus* than to *Diceratherium* where the species *aurelianensis* was

classified because of its size. These characters are: the deeply concave skull profile with upslanting nasals (Text-fig. 1b) a wide nasal incision of medium depth, and the triangular last upper molar. The characters are in contrast to all *Diceratherium* species, in particular to *D. aginense* and *D. lemanense*, the latest representatives of this genus. The size difference between the somewhat smaller *Prosantorhinus aurelianensis* and these largest species of *Diceratherium* makes direct ancestry very improbable.

The shortening of the proximal articular facet of MT II is a character of this species but does not occur in *Diceratherium*.



Text-fig. 2. Metatarsal II of different species of *Prosantorhinus*. a, b. *Prosantrorhinus douvillei*, Montréal-du-Gers, left MT II, a. proximal view, b. lateral view; c, d. *Prosantrorhinus germanicus*, Sandelzhausen, left MT II, c. proximal view, d. lateral view; e, f. *Prosantrorhinus laubei*, Achníkov, left MT II, e. proximal view, f. lateral view; g. *Prosantrorhinus aurelianensis*, Rothenstein 16, juvenile, right MT II, proximal view.

Diagnosis. The largest, moderately brachycephalic species of the genus *Prosantorhinus* with somewhat narrower occipital crest but not fully united temporal lines. Skull profile deeply concave with ascending nasals. Horn base moderately swollen with a rough, finger like prolongation in front. Lower incisors without torsion. Cheek teeth with relatively simple morphology, uppers with shortened premolars compared to the molars. The cross lophs of the premolars are less oblique than in other species. The crochet in the premolars is multiple or branching, less prominent than in other species of *Prosantorhinus*. Premolars and molars with faint to absent metacone ribs. The last upper molar has a triangular outline, but its rather short distal cingulum is somewhat variable in length and thickness. The mandible and the lower cheek teeth show the general characters of the genus. The large incisors show no torsion.

A more specific description and the bone measurements are given in Cerdeño (1993: 29 ff.).

?*Prosantorhinus tagicus* (ROMAN et TORRES, 1907)

Note. All the small rhinocerotids cited with this species name, except the type specimen, turned out to be *Protaceratherium minutum* (CUVIER, 1822). These specimens are omitted here from the synonymy list which concerns only the different citations of the holotype.

- 1907 v *Rhinoceros (Ceratorhinus?) tagicus* nov. sp. – Roman and Torres, p. 42, pl. 3, fig. 1.
- 1960 *Ceratorhinus tagicus* – Antunes, p. 258.
- 1972a *Brachypodella tagica* (Roman 1907) – Heissig, p. 70.
- 1979 *Prosantorhinus tagicus* (Roman) – Ginsburg and Antunes, p. 493.
- 1983 *Protaceratherium tagicum* (Roman 1907) – Antunes and Ginsburg, p. 22, pl. 1, fig. 1.
- 1989 *Protaceratherium minutum* (Cuvier 1822) – Cerdeño, p. 60.
- 1996 *Protaceratherium minutum* – Cerdeño, p. 112.

Holotype. Upper cheek tooth rows, right P2 – M3 and left P3 – M2, partially fragmentary.

Type locality. Lisbon (Horta das Tripas).

Stratum typicum. Early Miocene (MN 3a).

Other occurrences. Unknown.

Diagnosis. Smallest species of the genus *Prosantorhinus* with prominent but not fused crista and crochet in premolars, small crista in molars. Premolars semimolariform with lingual bridge lower than transverse lophs. All teeth except P2 with antecrochet. Posterior protocone furrow in all teeth, anterior one in P4 and the molars. Anterior hypocone furrow only in M1 and M2, in both separated from the medisinus base line by a cingulum cone. A trace of a posterior hypocone fold only in M2. Labial side of P3 with two broad, slightly converging ribs, no mesostyle. Metacone rib also present in M1 and M2, but only in M2 separated from the mesostyle swelling by a small furrow. M3 triangular with short but well developed distal cingulum and a somewhat lingually shifted crochet.

Description. See diagnosis.

Remarks. The smallest and probably earliest species of *Prosantorhinus* may be *P. tagicus* (ROMAN et TORRES, 1907). This species name, originally attached to "Ceratorhinus", was later applied to many small rhinoceroses, which turned out to be *Protaceratherium minutum* (CUVIER, 1822), a species of Aceratheriini, of nearly the same size as *P. tagicus*. The type and only specimen from the type locality Horta das Tripas (Lisbon) (MN 3a), however, has nothing in common with all these specimens except for its small size. The upper cheek teeth show several characters which exclude this specimen from *Protaceratherium minutum* and even from the tribe Aceratheriini. The most important is a posterior hypocone furrow on the second molar, which is typical for many Teleoceratini and excludes the species from the Aceratheriini. This character is also absent in all Early Miocene Elasmotheriini. A strong metacone fold on the ectoloph of the upper premolars, less accentuated but also present in the molars, is similar to that of the small sized *Prosantorhinus germanicus*, but absent in Aceratheriini. In most early Rhinocerotinae it is even more pronounced than in *Prosantorhinus tagicus*, which leads to its superficial similarity to early Elasmotheriini. The lingual side of the upper premolars, however, is fundamentally different from any elasmotherere. The bridge connecting the main lingual cusps remains in a lingual position in elasmothereres (Heissig 1972b: pl. 6, fig. 4), whereas it is more labially positioned in *Prosantorhinus tagicus*, leaving a considerable space between the bridge and the horizontal cingulum. This incomplete cingulum crosses the medisinus entrance, where it is more pronounced than at the bases of the lingual cusps. In elasmothereres it is more or less reduced to steep ledges which do not meet below the medisinus. The forked or multiple crochet of the premolars, and the clearly triangular outline of the last upper molar with a very short distal cingulum on the distolingual corner of the tooth, are more widespread features among rhinoceroses.

In particular *Protaceratherium minutum* shows no similarities with *Prosantorhinus tagicus*. In *Protaceratherium* there is only a faint trace of a metacone rib on the premolars and no trace of it in the molars (Roman 1924: pl. 3, fig. 1, pl. 5, fig. 1, 1a). The lingual cingulum of the premolars is generally complete, at least in some of the premolars. There is no trace of a posterior hypocone furrow in either the molars or milk molars in any Aceratheriini. The last molar is trapezoidal in *Protaceratherium* with a rather long distal cingulum, a character generally present in all Early and Middle Miocene age Aceratheriini. It is triangular with a short distal cingulum in most *Prosantorhinus* species. So the identification by Antunes and Ginsburg (1983: 22) and Cerdeño (1989: 60) of the holotype from Horta das Tripas as a member of *Protaceratherium* is by far less probable than its inclusion in *Prosantorhinus*. The presence of a crista in the premolars, which is used by Antunes and Ginsburg (1983: 22) as an important common character of *Prosantorhinus tagicus* and *Protaceratherium minutum* is a variable character which also occurs in 11% of the P4 and 4% of the P3 of *P. germanicus* from Sandelzhausen (Peter 2002: 35) and in a lot of other rhinoceroses in different tribes.

Unfortunately most isolated specimens of MN 3a age in Western Europe cannot be determined at species level. Therefore we can assign to this species only the

holotype with a rather limited set of characters. The lack of information regarding skull and postcranial characters makes the separation from other small species doubtful. Some characters, e.g. the strong cristae, characterise it as an independent species.

Morphological comparisons

Size and proportions

Comparative tables are given only for dental elements and skeletal elements which are sufficiently represented in the fossil record and therefore also in publications. As most holotype specimens are skulls, mandibles or tooth rows, the teeth are the keystones for all comparisons and the determination of different local collections ascribed to a given species. If individual, sexual and/or local variability cause differences in size or characters, the determination must contain the term aff. If lack of features prevent a clear determination the term cf. is used.

Skulls and cheek teeth

From MN 3b onwards there are two size groups. These groups are clearly separated based on the measurements of P3, P4, and the molars, but in the P2 the measurements are more variable and the ranges of the size groups overlap one another.

The larger group, *Prosantorhinus aurelianensis*, becomes extinct in MN 4a (last occurrence: Artenay; Cerdeño 1993: 64). The smaller group, *Prosantorhinus douvillei*, is relatively long lived and continued until MN 5 (holotype). Some collections contain individuals of nearly the same size as the smaller representatives of *Prosantorhinus aurelianensis*. Both are confined to Western and Central Europe. Beginning at MN 4b there is a third, smaller group, *Prosantorhinus germanicus*, with a more eastern range, surviving until MN 7. Generally all large samples show a wide range of sizes.

The earliest occurrences of the genus, however, show a more puzzling picture. At the time of its first occurrence, in MN 3a, the genus shows its greatest diversity with probably three species in existence, the tiny *Prosantorhinus tagicus*, the medium sized, but dentally small *Prosantorhinus laubei* and the somewhat larger *Prosantorhinus aurelianensis*. The deep concave dorsal profile, a common character of the later species, is known from that time only in *Prosantorhinus aurelianensis*. There are only upper cheek teeth available from *Prosantorhinus tagicus*, showing all the typical characters of the genus and clearly separating it from the same sized *Protaceratherium minutum*. The dental morphology of *Prosantorhinus tagicus* is more similar to that of the much later dwarf species *Prosantorhinus germanicus* than to *Prosantorhinus douvillei* but there are no occurrences known which would bridge the time gap between them.

The Baigneaux collection, contemporaneous with other occurrences of *P. douvillei* is intermediate in tooth size between this species and *Prosantorhinus germanicus*. Its postcranials, however, are identical in size to those of *Prosantorhinus douvillei*.

The size groups in relation to cheek teeth and limb bones do not parallel one another (skeletodental index; App. Tabs

A15 and A16). Therefore it is necessary to have an alternative viewpoint with regard to premolars, molars and some limb bones. The dental or appendicular elements were selected for the calculation of indices according to their significance and availability. The size relationship between the different species can be best illustrated by scatter diagrams. The most represented teeth are the upper M2 and P3. Lower cheek teeth are more uniform concerning their transverse diameter.

As shown in the scatter diagram of P3 (App. Text-fig. A1) *Prosantorhinus laubei* is grouped with the largest specimens of *P. germanicus* and the small sized specimens of *P. douvillei* from Baigneaux. Several specimens from this latter collection are, however, of the same size as *P. douvillei* from Beaugency-Tavers and Chilleurs. There is, on the other hand, a large overlap between the size groups of *P. aurelianensis* and the larger *P. douvillei* from Pontlevoy-Thenay.

In the upper molars, especially in M2 (App. Text-fig. A2) there is a clear separation between the size groups of *Prosantorhinus germanicus* and *P. douvillei*. *P. laubei* and the collection of *P. douvillei* from Baigneaux, however, are intermediate. The main collections of *P. douvillei* show identical molar sizes. Its size group cannot be entirely separated from that of *P. aurelianensis*, but has only a small overlap. The difference is due to the molar/premolar relationship.

In the diagrams it is visible that the size of the two latest species of *Diaceratherium* is equal or even superior to the largest specimens of *Prosantorhinus aurelianensis*.

The scatter diagrams show that the size of the second upper molar clearly separates the species *Prosantorhinus germanicus*, *P. laubei* and *P. douvillei*, whereas the third premolars of these species are very similar in size. That means that the size relationship between premolars and molars is different in these species. This difference is illustrated by the length ratio of P3 to M2 and p3 to m2, the upper and lower premolar reduction index (Premolar reduction index; App. Tabs A17 and A18).

Another character, the relative width of the skull, shows the increasing brachycephaly (App. Tab. A2). The first step is from the dolichocephalic *Diaceratherium* with a high and deep nasal incision with parallel upper and lower margins and a nearly rectangular caudal end to the somewhat brachycephalic *Prosantorhinus aurelianensis* with ascending nasals and a triangular nasal incision opening rostrally. The second step is between this species and *Prosantorhinus douvillei* on one hand and on the other hand *Prosantorhinus germanicus* with its very brachycephalic skull. The skulls of *Prosantorhinus tagicus* and *Prosantorhinus laubei* are unknown.

Metapodials

Considering the metapodials, the size groups of the smaller species of *Prosantorhinus* are clearly separated, the metapodials of Baigneaux where the tooth remains are exceptional small are grouped together with other collections of *P. douvillei*, but widely separated from *P. germanicus*. *P. aurelianensis*, however, has a large overlap with *P. douvillei*. The discrepancy between dental and skeletal groupings is even more accentuated in *P. laubei*, with metapodials the

same size as in *P. aurelianensis*. So it is clear that there is no constant size relation between teeth and limb bones (see the skeletodental index; App. Tabs A15 and A16).

The postcranial bones of *Prosantorhinus laubei* and *Prosantorhinus aurelianensis* exhibit more robust distal limb segments than *Diaceratherium* (see gracility index of MC III and MT III; App. Tabs A13 and A14). A general trait of the Teleoceratini is the tendency towards limb shortening, leading to graviportal proportions. Even when all limb bones are somewhat more robust than in the gracile early Aceratheriini, the shortening is mainly expressed in the distal limb segments, that is in the carpals, tarsals, metapodials and digits. The progressive shortening is most clearly seen in the proportions of the metapodials.

Diaceratherium, the earliest European teleoceratine rhino (Menouret and Guérin 2009) has robust slightly shortened metapodials. The first representatives of *Prosantorhinus*, *P. aurelianensis*, and *P. laubei* are somewhat more robust in proportions (Scherler et al. 2013: fig. 5). The large *Prosantorhinus aurelianensis* is a little more robust than the latest species of *Diaceratherium*, *Diaceratherium lemanense* and *Diaceratherium aginense*. *Prosantorhinus douvillei* and *Prosantorhinus germanicus* show a continuation of this trend, not only in shortening of the limb bones but also in size reduction.

The gracility index (DT shaft $\times 100 / \text{Lmx}$) after Cerdeño (1996: 118) (App. Tabs A13 and A14) indicates that *Prosantorhinus aurelianensis* was rather robust. *Prosantorhinus laubei*, however, was more gracile than all the other species of *Prosantorhinus* and thus did not differ from the *Diaceratherium* species in this respect. The considerably smaller *Prosantorhinus douvillei* has nearly the same gracility index as the larger *Prosantorhinus aurelianensis*. In both diagrams the dwarf *Prosantorhinus germanicus* is clearly set apart from all other species by its more robust metapodials.

Astragalus

Obviously the astragalus is very variable in size so that there is a considerable overlap between neighbouring size groups, especially in *P. douvillei* and *P. aurelianensis*. The clear separation of smaller and larger specimens from Baigneaux, similar to the situation regarding the premolars, is in contrast to its uniformity with respect to the molars and may be due to greater sexual dimorphism.

Morphology

Skull

The skull morphology of *Prosantorhinus* is different from that of *Diaceratherium* from the late Oligocene and the earliest Miocene. This genus has a plesiomorphic rather long skull with a longitudinal profile, which is straight in the fronto-nasal region and concave in the posterior part of the frontals. The nasal incision is deep with parallel upper and lower margins. In *Prosantorhinus* the dorsal profile is deeply concave in the naso-frontal region, accompanied by transversal vaulting. Thus the nasals ascend frontally, are somewhat shorter and therefore provide space for a rostrally wide open nasal incision (see Text-fig. 1)

Within the genus *Prosantorhinus* the most obvious differences occur in the nasal tips. These are plesiomorphic in *Diaceratherium* and therefore of the same type as in early Aceratheriini. Skull remains of only three *Prosantorhinus* species are known. Generally the horn base is more prominent in *Prosantorhinus* than in other genera of European Teleoceratini. In contrast to the more plesiomorphic *Diaceratherium* the nasal bones are fused in the region of the horn base. This structure forms a pillow like swelling with a rough surface. In front of it the nasals may have a narrower, also rough, appendix. In the Montréal-du-Gers collection it is a straight prolongation of the nasals, but is more downwards turned in other specimens, with an angle of about 45° in the type of *P. aurelianensis* but also in the skull fragment of *P. douvillei* from Rebrechien (MN 3b) and the single nasal from Chevilly (MN 3b) of the same species. It is shorter and nearly vertical in the skulls of *P. germanicus* from Sandelzhausen. The line of fusion is marked in all species except *P. germanicus* by a deep dorsal furrow. In the terminal species, *Prosantorhinus germanicus*, the horn base forms a globular bulb which is pneumatised from the interior of the nasal cavity. There is no difference in the mandible within the genus except for size. The lower margin of the corpus is somewhat more curved than in *Diaceratherium*.

Dentition

The upper cheek teeth have the characteristic shortened premolars of Teleoceratini. Their difference in width, calculated according to the premolar width gradation index (App. Tab. A19) is greatest in *P. germanicus* with a score of approximately 1.5 and somewhat lower in *P. douvillei* and *P. aurelianense*, but still higher than in *Diaceratherium aginense*. The difference in premolar shortening is less marked. The premolar reduction index (App. Tabs A17 and A18) is generally about 1.25 in the collection of *P. germanicus* from Sandelzhausen, between 1.25 and 1.5 in *P. douvillei* and *P. aurelianense*, in only two *P. aurelianense* individuals it exceeds 1.5 (App. Tabs A17 and A18).

In addition to these proportional characters the dental traits of the premolars are very variable within the genus. There is very often a conspicuous metacone rib on the outer wall, which is narrow and clearly limited by parallel furrows in the smaller species, but broader and less prominent in medium sized ones. Therefore the rib may be very flat or even lacking, especially in the P4 of *P. douvillei* and *P. aurelianensis*. The more prominent paracone rib is inclined in P2, also sometimes in P3, so that the ribs are apically converging. In P3 and P4 there is, if it exists, only a flat swelling representing the mesostyle. The transversal crests are lingually converging in P2, parallel in P3 and P4, a lingual bridge may occur in all premolars, but it is more frequent in P2 than in the following teeth, except in *P. germanicus*, where it occurs only in a few P4. The transversal crests are oblique to the ectoloph, except in *P. aurelianensis*, where they are nearly perpendicular to it. The crochet is often present in P3 and P4, sometimes also in P2. It is absent in *P. laubei*, short and simple or complex in *P. aurelianensis* and *P. tagicus*, slightly longer, forked or multiple in *P. douvillei* and *P. germanicus*. The crista is the most variable feature.

Very often there is no trace of it, but in rare cases it may unite with the crochet to close a small medifossette in *P. douvillei*. This medifossette is more frequent in all premolar positions of *P. germanicus*. In this species the protocone is constricted at least by a posterior furrow in P3 and P4, whereas in *P. douvillei* and *P. aurelianensis* the anterior furrow is confined to the base of the cusp and the posterior furrow ascends further apically. Sometimes there also occurs a faint anterior hypocone furrow.

The cingulum may be interrupted below one or both lingual cusps, but is always present at the entrance of the medisinus. Labially there is no cingulum in *P. tagicus*, *P. aurelianensis* and *P. laubei*. There may sometimes be one or two short labial ledges, descending steeply from the parastyle and the metastyle in *P. douvillei*, whereas it may be absent to nearly continuous in *P. germanicus*. At the end of the posterior ledge, most frequently present in *P. douvillei*, there may be a swelling, which results in the posterior width of P3 in particular being equal to or exceeding the anterior width.

The molars are less variable. M1 and M2 are similar. Labially the parastyle is short and separated by a deep furrow from the prominent paracone. A flat metacone swelling occurs quite frequently in M1, but rarely in M2. The mesostyle swelling, if present, is broad and not delimited. The postfossette is as deep as the medisinus. It generally has an oval outline with a deep central slit. In *P. tagicus* it is shorter and circular in outline. The crochet is short and simple in *P. laubei* and *P. aurelianensis*, longer and sometimes forked in *P. tagicus*, *P. germanicus* and *P. douvillei*. There is no trace or only the faint trace of a crista. A third fold projecting into the medisinus from the protoloph opposite to the crochet or a little more labially occurs in some M2 of *P. germanicus*. It may also occasionally occur in other species.

The last upper molar has a triangular outline, thus differing from the trapezoidal outline in the earlier *Diaceratherium*. Therefore the distal cingulum was undergoing a process of reduction, generally lacking a projecting labial edge. There are characteristic differences when compared with the more anterior molars. There is neither a postfossette nor a free metastyle. Ectoloph and metaloph form a common distolabial wall, which usually exhibits no other elements than the paracone and parastyle. The crochet is in a more lingual position than in the other molars. The constrictions of the lingual cusps are less pronounced than in the preceding molars. There is no posterior hypocone furrow and its anterior furrow is visible only at the very base. The antecrochet is relatively flat and the anterior protocone furrow is shallow. The medisinus entrance is wide and the furrows remain separate.

There is a clear trend in the development of the distal cingulum. In *P. tagicus* it is a short thick ridge with equal height lingually and labially. In *P. laubei* and *P. aurelianensis* it remains thick, but may be reduced to a pair of blunt cusps. In *P. douvillei* there is wide variation, but generally a less thickened ridge is descending labially more or less steeply from the highest lingual point. Sometimes it seems to be strongly compressed at the posterolingual edge of the tooth. This condition is most frequent in *P. germanicus*, but only in this species it may be extended along the enamel base as far

as the protocone base. There are more misshaped specimens in the last molar than in any other molar.

The lower cheek teeth show only a few diagnostic features, and are relatively uniform within the genus. In most species they are also similar to those of *Diaceratherium*. The lower premolars are generally shorter than the molars (App. Tab. A18). Especially the talonid is short and the hypolophid significantly bent, its transversal part being perpendicular to the axis of the tooth row. The enamel surface shows fine lines parallel to the base.

The molars are very uniform. There is no protoconid fold. There are gradual changes of some characters from m1 to m3. Both lingual grooves are more open in m3 than in m1. Their lingual entrance is in a higher position in m1. The ectoflexid is generally more acute in m1. Labial cingula are more frequent in m1 than in m3. On the lingual side, however, partial cingula are most frequent in m2.

The first lower milk molar (dp1) is reduced. It is single rooted and its crown is simplified to a single pointed or globular cone, in contrast to *Diaceratherium* where it is longer in use and still has a more complete morphology. It erupts late, after dp2 and dp3 in *P. germanicus*, where it is the most reduced. In this species it is a tiny pin which is never used and is shed before the milk molars are replaced by the permanent premolars (Böhmer et al. 2016: 268 f.) The size of this small non-functional tooth and the time of its loss are not known for sure in other species.

The blade-like upper incisors are broad and show a marked sexual dimorphism. They are considerably longer craniocaudally and higher in males, with a short laterally flattened root. In females the crown is lower and very broad.

The lower tusks are curved upwards in one plane in *P. aurelianensis*, *P. laubei* and *P. douvillei*, in *P. germanicus*, however, they show a three dimensional torsion. The enamel cover of the tooth is confined to the labial side in males. In females there is also a thin cover on the lingual side with a basal cingulum which is lacking in males. The root shows a collum at least in females.

Postcranials

Generally, bones are less stable compared with teeth. So they are often fragmentary or strongly affected by transport therefore their features maybe partly veiled. Often the surface structure, crests and the limits of articulation facets are obscured.

Neither morphology nor size of the vertebrae and ribs allow a clear distinction between genera and species within the Teleoceratini. In most cases only fragments are preserved.

The long bones of the extremities are mostly fragmentary. Only a few specimens of each species are complete, therefore the variability in size and characters is not determinable. Only a few of the larger collections give an overview of the size and characters of the carpal and tarsal bones. The differences between collections and between species are not easy to disentangle.

The elements which best give an impression of morphology are the astragalus and the metapodials. These bones contribute a considerable amount of information regarding the characteristics of the genus and its species. Generally the changes in proportions are more significant

than the variation within single characters. The proximal end of MC II in *Prosantorhinus aurelianensis* has a deep dorsopalmar diameter exceeding its width, whereas in *Diaceratherium* the width is greater. In addition, in all smaller *Prosantorhinus* species the dorsopalmar diameter is smaller than the width. The main proximal articular facet is generally narrower than its dorsopalmar extension, with the exception being in *P. douvillei*. In *Prosantorhinus* the facet articulating with the third carpal is generally more proximally facing than in *Diaceratherium*. In *D. lemanense* the width exceeds the dorsopalmar diameter, in *D. aginense* and all species of *Prosantorhinus* this facet is narrower, even in *P. laubei*. The lateral facet articulating with the MC III is very variable in size and cleavage. It may be split into a proximal and distal part by a distal incision as in some specimens of *P. germanicus* or remain undivided without any incision as in some *P. aurelianensis*. Specimens of *P. douvillei* in the different collections exhibit numerous variations between the two options. According to the more or less robust shape of the bone the medial rugosities for the intermetacarpal tendon are of different length. Its thickness is connected with the individual's age. MC III has a proximal facet which is equal or broader transversally than in the dorsopalmar direction in most species of *Prosantorhinus*. In *Diaceratherium* and *P. germanicus*, however, they are narrower. Its saddle shaped curvature varies somewhat in the convex sagittal vaulting. So it is somewhat shorter palmarly in *P. laubei* and *P. douvillei* compared to the other species. The medial facet articulating with MC II has no distal incision in *P. douvillei*, but there is a variable, more or less deep incision in *P. laubei* and *P. germanicus*. On the lateral side the dorsal facet articulating with MC IV is shortened and has no contact with the main proximal facet in both *P. douvillei* and *P. germanicus*. The progressive flattening of the bone brings both lateral facets closer together in these later species, whereas they are widely separated in *P. aurelianensis* and *P. laubei*.

The proximal facet of MC IV is rather broad in *P. douvillei*, but narrower in all other species with a less reduced MC V. The facet articulating with this element is smaller in the stratigraphically higher species, because of the progressive reduction of MC V. The palmar facet articulating with MC III is situated more distally in *P. douvillei* and *P. germanicus* compared with the earlier species. MC V is present in all species. In *P. douvillei*, however, it is very often reduced to a knob without a distal trochlea. A single specimen from Béon shows that the reduction process had not been completed (Wermelinger 1998: pl. 31). All other species are fully tetradactyl, but with MC V having different proportions. It is shorter in *P. aurelianensis* compared with *P. germanicus*.

The astragalus is one of the best and most frequently preserved bones. Its high variability in size and proportions does not allow any clear distinction between the species especially when more than one species is present in the locality. On the other hand there is a clear difference compared to *Diaceratherium*, which has a less depressed astragalus with a comparatively lower medial lip on the trochlea. In most species of *Prosantorhinus* this lip rises considerably higher above the median groove than in *Diaceratherium*. Only in *P. germanicus* it is comparably lower. Most morphological traits of the bone are generally the characters of the tribe.

In *P. germanicus* the sustentacular facet may have a circular outline. If it is oval it is less depressed than in all other species. The proximolateral main facet for the calcaneus does not have or has only a faint distal appendage in *P. aurelianensis* and *P. laubei* whereas the appendage is very variable in both *P. germanicus* and *P. douvillei*. The collum is highest in *P. aurelianensis*, variable in *P. douvillei* and low in adult astragali of *P. germanicus* and *P. laubei*. The facet for the fibula is somewhat oblique and transversally concave in adults of *P. germanicus*, but subvertical and transversally convex in juveniles as is the situation in most of the other *Prosantorhinus* species. All these characters are variable, so that a distinction can be made only in combination with size differences. MT II is the only bone which shows a characteristic feature in the whole genus, but which is not present in *Diaceratherium* and *Brachypotherium*. The palmar side of the proximal articular facet is bound by a large foramen (Text-fig. 2). A specimen of this bone from *Teleoceras fossiger* COPE, 1878, however, shows a similar structure. So the lateral facet articulating with the second tarsal is significantly extended plantarly over the main facet. It is steep in its dorsal region but turns upwards after passing the plantar end of the proximal facet. This turning upwards is gradual in *P. aurelianensis* and *Teleoceras fossiger*. The facet changes its direction with a marked bend in *P. douvillei* and *P. germanicus*. The proportions of the main proximal facet are therefore different in these species. In *Diaceratherium* it is generally narrow and extended plantarly. In *P. laubei* and partly also in *P. aurelianensis* it is approximately square, in *P. douvillei* somewhat narrower and in *P. germanicus* much narrower compared with the dorsoplantar diameter. It is transversally concave in all species except *P. aurelianensis* where it is flat. There is a medial facet present for the short tarsal 1 + MT I in *P. aurelianensis* and *P. laubei*. In *P. douvillei* it is variable and may be absent. In *P. germanicus* it is generally lacking. MT III shows only a few differences in the lateral articulation with MT IV. The plantar facet is quite uniform in morphology. The dorsal facet is relatively high in *Diaceratherium lemanense*, lower in *Diaceratherium aginense* and most species of *Prosantorhinus*, and very low in *P. douvillei*.

MT IV is the shortest of all the metapodials. Most of its characters are variable. The bone is proximally broader in *Diaceratherium* than in most species of *Prosantorhinus*. In *P. germanicus*, however, it is narrow compared with its dorsoplantar diameter. The flat main proximal facet is faintly undulating. Its more or less circular outline is modified in *P. douvillei* by a slight dorsal indentation. In *P. germanicus* the lateral margin of the facet may be somewhat upturned as in most Aceratheriini. In *P. laubei* the lateral tubercle continues as a distal ridge, disappearing distally.

Medially the rough ridges for the attachment of the intermetatarsal ligament are long and are separated from the medial epicondyle by a short distance, the shortest being in *P. douvillei*. In *P. germanicus* the ridge may be fused with the epicondyle. Compared to other metapodials there is weaker sagittal vaulting of the trochlea in all *Prosantorhinus* species, so that the trochlea is more extended dorsoplantarly to allow the same degree of phalangeal movement.

Conclusions

Systematics

The main result of the present study is the inclusion of the large species *P. aurelianensis* (NOUEL, 1866) in the genus *Prosantorhinus*. The most important character for this new generic determination is the dorsal skull profile which is different from that in *Diaceratherium*, to which the species was hitherto assigned. This determination is confirmed by the shortened proximal articulation facies of MT II which is unique among the Teleoceratini.

The generic determination of *P. tagicus* (ROMAN et TORRES, 1907) which had already been suggested by Heissig (1972a: 69), remains doubtful, even though the features of the upper cheek teeth are similar to other *Prosantorhinus* species, especially to *Prosantorhinus germanicus* (WANG, 1929). Several characters of this specimen were also shared with early Elasmotheriini such as e.g. the triangular outline of the last upper molar with a much shortened distal cingulum and the relatively high tooth crowns. On the other hand the large crista and prominent metacone rib, typical for early Elasmotheriini, are lacking and the presence of a lingual cingulum in the premolars also excludes the specimen from this tribe.

The small collections from other Spanish localities, as well as from Artesilla and La Grive are not sufficient for certain species determination, even though most of the specimens are of an intermediate size and may represent *Prosantorhinus douvillei*.

Chronological range

There are no small teleoceratine rhinoceroses in Europe earlier than MN 3. There seems to exist only one genus, *Diaceratherium*, beginning with medium sized species in the late Oligocene (Menouret and Guérin 2009) and ending with the large species *D. lemanense* and *D. aginense* in MN 2. All teleoceratine rhinoceroses in MN 3 are newcomers, members of the genus *Prosantorhinus*, with a size range of very small to large species.

The largest, *P. aurelianense* made its last appearance in MN 4a and was later replaced by the even larger genus *Brachypotherium*. The smaller species *P. douvillei* is relatively long lived and disappears in the Middle Miocene, probably in MN 7–8. There is nothing known about the fate of *P. laabei*, restricted to MN 3a in Bohemia and possibly in Southern Germany. Later, in MN 5 there are collections of *P. germanicus* in Southern Germany, contemporaneous but regionally separated from *P. douvillei*. *P. germanicus* is of unknown origin. It is similar to the smaller *P. tagicus* from MN 3, but as no intermediate finds are known, this phylogenetical connection remains in general improbable.

Paleogeography

The immigration of *Prosantorhinus* to Middle and Western Europe occurs contemporaneously with the immigration of *Anchitherium*. The most probable origin is in Asia, the supposed evolutionary center of the teleoceratine rhinoceroses. There, in Pakistan, the occurrence of a small, short legged rhinoceros which was ranged into *Prosantorhinus* by Antoine et al. (2010: 170, 181) antedates

the occurrence of the genus in Europe. The dominant species in Western Europe in MN 3a is *P. aurelianensis*, which is rare in Central Europe. There we find at the same time *P. laabei*, a medium sized and more gracile species. Also in MN 3, but possibly somewhat later the first rare specimens of *P. douvillei* are known in Western Europe. If we add the doubtful species *P. tagicus*, also from MN 3a, there are at least three species immigrating. The range of *P. douvillei* from Central Europe until the Iberian Peninsula during the Early Miocene is reduced at the beginning of the Middle Miocene (MN 5) when it was replaced by *Prosantorhinus germanicus* in Southern Germany.

Morphology

In the well-known species there is considerable variability in size and characters. This is limited in *P. aurelianensis* and highest in *P. douvillei*, probably caused by the large number of known occurrences and the greater geographical and temporal range of this species. It is expressed in the presence or absence of a fully developed lateral digit and in the tendency towards irregular palmar articular facets especially in the fourth carpal, articulating with the third carpal in *P. douvillei* and with the third metacarpal in *P. germanicus*.

The size relationship between the cheek teeth and the metapodials (skeletodal index; App. Tabs A15, A16) is different in these species. *P. laabei* has comparatively small teeth, *P. aurelianensis* on the other hand, much larger teeth but metapodials of nearly the same length as *P. laabei*.

There is some tendency towards shortening of the distal limb elements, but it is masked by the variability within the species. Nevertheless the latest occurring species, *P. germanicus*, has the shortest metapodials with a relatively low gracility index (App. Tabs A13, A14).

Environment and diet

Most species of *Prosantorhinus* are predominantly browsers, indicated by the low crowned cheek teeth, a character generally suggesting a diet of not abrasive plants with relatively high nutrient content. This is generally confirmed by the form of the wear surface of the upper molars (Mesowear method; see Fortelius and Solounias 2000). The form of the cusps on the outer wall of the upper cheek teeth is mostly sharp in molars, and sharp to slightly rounded in the premolars. The relief is, depending on the stage of wear, medium high in most molars to flat in a rather early stage of wear in the premolars, mainly the second. This points to a somewhat mixed diet, containing only a minor proportion of abrasive plants. The presence of a relatively strong lingual cingulum in the upper premolars protects the gingiva from lesions caused by hard twigs. Thus most species can be characterized as non-selective browsers.

Within the genus some differences can be observed. *P. aurelianensis* has generally larger cheek teeth, corresponding to the overall size of the animal. The premolars are somewhat higher, probably not as an adaptation to a more abrasive diet, but as reserve for a longer life. *P. laabei* is especially low crowned with comparatively small cheek teeth. So we can conclude that its diet was soft with a high nutritive value. *P. germanicus* and *P. douvillei* show somewhat higher crowns and less complete lingual cingula. This can be interpreted

as a sign of a slightly more abrasive diet but not containing any hard twigs. *P. tagicus*, however, exhibits a relatively low relief, combined with strongly rounded cusps. The lingual cingulum of the premolars is significantly interrupted below the protocone. Thus the smallest species was probably a mixed feeder with a greater proportion of abrasive plants in its diet.

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Appendix

Measurements taken from the literature are noted with the following symbols: ⁺ Cerdeño (1993), [#] Duranthon (1989), ^{*} Repelin (1917), ^o de Bonis (1973), [§] Wermelinger (1998).

Abbreviations used in tables

a = anterior, ana = anatomical (= physiological), C 1, 2, 3, 4, = carpal 1 – 4, Calc = calcaneus, Ce = centrale, D. = anteroposterior diameter, dex. = dexter (right), di. = distal, dis. = distance, diag. = diagonal, drs. = dorsal, f. = articular facet, fib. = fibula, H = height, inc. = incision, L = length, lat. = lateral, MC II, III, IV = metacarpal II – IV, MT II, III, IV = metatarsal II – IV, med. = medial, mid. = middle, mx. = maximal, nas. = nasal, p = posterior, plm = palmar, plt = plantar, px. = proximal, sin = sinister (left), sh. = shaft (diaphysis), T 1, 2, 3, 4 = tarsal 1 – 4, tro. = trochlea, W = width.

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Table A1. Skull size in *Prosantorhinus* and *Diaceratherium*.**Measurements**

All measurements are taken in mm.

Species	<i>Diaceratherium</i> sp.	<i>P. aurel.</i>	<i>Prosantorhinus douvillei</i> ♀	<i>Prosantorhinus douvillei</i>	<i>Pros. germanicus</i>
Locality	Engelhalde	Ulm WT	Neuville	Langenau	Sandelzhausen
Collection	NMBE	SMNS	MSNO	MHNT	BSPG 1959 II
Number/Side	D 3193 dex.	4299 sin.	41575 sin. 41575 dex.	sin. 2003 G5 2A dex.	MNHN
P2-P4 L	85.5	98.5	87.0	85.5	Tavers
P2-M3 L	201	228	201	182	G 6606
M1-M3 L	89	134	123	(105)	16501
Diastema II-D1	(73)		51.0	1.32	MNHN
Nasal-Occiput	472		428	435	TAV 82
Premaxilla-Condyle	(510)		563	491	342
L nasal	125		86.0	98.0	381
H nasal incision	70.0		24.0	35.5	(400)
W nasal basis	(75)		96.0	77.0	115
L nasal tip-orbit	(200)			(150)	111
L orbit-nas.-inc.	(71)		85	66.5	(43)
H occiput-foramen			142	(90)	97.5
H occiput-condyle			158	157	362
W occiput top		233	(130)		362
W occiput maximal		269	(190)		54.0
W maximal skull			250	(295)	54.0
W frontal		171		(186)	54.0
H orbit	79.5	(78)	73.5	57.5	52
H jugal maximal	65.0	85.8	60.6	60.4	(47)
W articular facet			91.0	91.0	72.5
W condyle		66.5		27.5	96.0
H condyle		43.5	16.5	49.5	54.5
				46.5	48.0
				37.0	54.5
				39.0	48.0

Table A12. Measurements of the metatarsal IV of *Prosantorhinus* and *Diceratherium*.

Species	Locality	Coll.	Number / side	Measure											
				Lmx	Wpx	Dpx	WT4f	DT4f	HptrT3f	DptrT3f	Wsh	Dsh	Wdi	Wtro	Dtro
<i>Diceratherium aginense</i>	Laugnac*	MHNMM	M1Lg / dex.	106	41.5	43.0	30.0	36.5	14.0	21.5	27.0	18.5	41.3	30.5	41.5
<i>Diceratherium lamilloquens</i>	Castelmaurou#	MHNNT	CAM 11'side unpublished	132	41.0	37.5				25.0	20.0		27.5	27.5	39.0
<i>Diceratherium lemanense</i>	Budenheim	SMB	M 936 / sin.	132	37.0	48.0	33.0	41.5	14.5	12.5	25.0	21.0	35.0	33.0	37.5
<i>Prosantorhinus aurelianensis</i>	Rothenstein 16	NMA	2083 / sin.	87.5	39.0	42.5					31.0	21.0		34.5	39.0
<i>Prosantorhinus aurelianensis</i>	Rothenstein 16	NMA	2083 / sin.	86.0	37.5	39.5	31.0	34.0			29.0	19.0		34.0	38.0
<i>Prosantorhinus aurelianensis</i>	Rothenstein 16	NMA	2083 / dex.	87.0	37.5	37.5	33.5	22.0			31.0	20.0		37.0	39.0
<i>Prosantorhinus aurelianensis</i>	Artenay*	MNHNM	no data published	122	45.5	54.5	28.5	44.5			27.5	29.5	38.0	(37)	(44)
<i>Prosantorhinus laubei</i>	Ahníkov	NMP	Pv 10246 / sin.	102	37.5	33.5	29.5	29.0	13.5	16.5	23.0	17.5	30.5	29.0	34.5
<i>Prosantorhinus</i> sp.	Wintershof-West	BSPG	19337 II 19632 / sin.	96.0	39.5	33.5					31.0	24.0	36.0	(33)	38.0
<i>Prosantorhinus</i> sp.	Wintershof-West	BSPG	19337 II 19642 / dex.	87.5	34.0	32.5					31.5	21.5	37.5		33.5
<i>Prosantorhinus douvillei</i>	Chilleurs	MSNO	878 / sin.	87.0	38.5	36.0	43.0	23.5	15.5	14.5	28.5	20.5			
<i>Prosantorhinus douvillei</i>	Chilleurs	NMBA	6718 / dex.	83.0	37.0	36.5	32.5	30.5	14.0	18.0	25.5	17.0	33.5	29.0	32.0
<i>Prosantorhinus douvillei</i>	Artenay	MSNO	614 / sin.	95.0	36.5	31.5	34.5				35.0	15.0	41.0	35.0	
<i>Prosantorhinus douvillei</i>	Artenay*	MHNT	no data published	95.5	44.0	50.5	37.5	39.0			33.5	23.0	40.0	35.0	46.5
<i>Prosantorhinus douvillei</i>	Béon	MHNNT	G 840 / sin.	77.0	34.0	36.5	32.0	30.5	14.0	15.0	24.5	18.0	32.5	29.5	36.5
<i>Prosantorhinus douvillei</i>	Béon	MHNNT	E2 612 / sin.	83.5	32.5	37.5	30.0	31.5	12.5	11.0	26.0	18.5	32.0	31.0	39.0
<i>Prosantorhinus douvillei</i>	Béon	MHNNT	E 3 616 / dex.	69.0	31.5	33.5	31.5	34.0	11.0	15.0	29.5	18.5	36.0	30.0	35.5
<i>Prosantorhinus douvillei</i>	Béon	MHNNT	F2 980 / dex.	78.0	37.0	35.0	31.0	33.0	10.5	10.5	28.5	18.0	37.5	32.5	38.5
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G 2207 / sin.	61.5	26.0	30.0	24.5	25.5	10.5	11.0	24.5	14.5	28.5	24.0	25.5
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G 3917 / dex.	68.5	26.5	28.0	22.5	24.5	11.5	10.5	21.0	13.0	29.5	24.5	29.0
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G 3240 / dex.	68.5	28.5	26.5	25.5	26.5	10.5	13.5	24.0	13.5		24.5	26.5
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G 13-M. 55-65 / dex.	(65)	25.0	27.5	24.5				22.0	13.5		23.5	26.5

Indices

Table A13. Gracility index of MC III (= Wshaft × 100 / L) of *Diaceratherium* and *Prosantorhinus*.

Species	Locality	Collection. no. / side	Lmx	Wsh	Index	26	28	30	32	34	36	38	40	42	44	46	48
<i>Diaceratherium lamilloquense</i>	Castelnaurou*	MHNT. CAM 10' / side unpubl.	144	38.5	26.7												
<i>Diaceratherium aginense</i>	Laugnac#	MHNM. I.g M / sin.	148	43.5	29.5												
<i>Diaceratherium lemanense</i>	Hessler	SME. 6273a / sin.	161	42	26												
<i>Diaceratherium lemanense</i>	Hessler	SMF. 6271a / dex.	162	43	26.5												
<i>Diaceratherium lemanense</i>	Oberleichtersb.	BSPG cast / dex.	140	45	32.1												
<i>Prosantorhinus aurelianensis</i>	Chilleurs	MHNO. 924 / dex.	130	47	36.2												
<i>Prosantorhinus aurelianensis</i>	Chilleurs	MHNO. 748 / dex.	143	50.5	35.3												
<i>Prosantorhinus aurelianensis</i>	Neuville	MNHN / no data published	124	47.5	38.3												
<i>Prosantorhinus aurelianensis</i>	Artenay	MHNO / 613, dex.	137	47.5	34.7												
<i>Prosantorhinus aurelianensis</i>	Artenay+	MNHN / no data published	134	47.5	35.6												
<i>Prosantorhinus aurelianensis</i>	Artenay+	MNHN / no data published	143	53.5	37.4												
<i>Prosantorhinus laubei</i>	Ahníkov	NIMP. Pv 10255 / sin.	148	42.5	28.7												
<i>Prosantorhinus laubei</i>	Ahníkov	NIMP. Pv 10253 / dex.	139	40	28.8												
<i>Prosantorhinus douvillei</i>	Chilleurs	NMBa.1400 / dex.	118	44.5	37.7												
<i>Prosantorhinus douvillei</i>	Chilleurs	NMBa. 2309 / sin.	116	38	32.8												
<i>Prosantorhinus douvillei</i>	Chevilly	MNHN. Che 106 / sin.	113	44.5	39.4												
<i>Prosantorhinus douvillei</i>	Béon#	MNHT. 1991 F3 SN 50 / dex.	115	45.5	39.6												
<i>Prosantorhinus douvillei</i>	Béon#	MNHT. 89 F1 814 / dex.	115	38	33												
<i>Prosantorhinus douvillei</i>	Béon #	MNHT. G3 503, dex.	117	47	40.2												
<i>Prosantorhinus douvillei</i>	Béon #	MNHT. G3 1049 / sin.	113	43.5	38.5												
<i>Prosantorhinus douvillei</i>	Béon #	MNHT. G3 1018 / sin.	115	45	39.1												
<i>Prosantorhinus douvillei</i>	Béon #	MNHT. E3 142 A / sin.	124	46.5	37.5												
<i>Prosantorhinus douvillei</i>	Béon #	MNHT. F1 538 / sin.	119	45	37.8												
<i>Prosantorhinus douvillei</i>	Langenau	SNMS. 4089 / sin.	108	41	38												
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG.1959 II 17005 / dex.	96	34.5	35.9												
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG. G 46505 / dex.	93	41.5	44.6												
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG.1959 II 12290 / dex.	79	37	46.8												

Table A14. Gracility index of MT III (= Wshaft × 100 / L) of *Diaceratherium* and *Prosantorhinus*.

Species	Locality	Collection, no. / side	Lmx	Wsh	Index
<i>Diaceratherium aginense</i>	Laugnac	MHNMM.M.I.g / d.	106	27	25.5
<i>Diaceratherium aginense</i>	Hessler	SMFM M 737c / dex.	122	41	33.6
<i>Diaceratherium lamilloquense</i>	Castelmauro#	MHNT, CAM 11' / -	132	25	18.9
<i>Diaceratherium lemanense</i>	Hessler	HLMD Aq 24 / dex.	137	33	24.1
<i>Diaceratherium lemanense</i>	Budenheim	SMF, M 4635 / dex.	155	40	25.8
<i>Diaceratherium lemanense</i>	Budenheim	SMF, M 4633 / dex.	148	40	27
<i>Diaceratherium lemanense</i>	Budenheim	SMF, M 4634 / sin.	143	38	26.6
<i>Diaceratherium lemanense</i>	Budenheim	HLMD, Bu 385 / sin.	126	41	32.5
<i>Prosantorhinus aurelianensis</i>	Neuville+	MNHN, no data pub.	117	44	37.6
<i>Prosantorhinus aurelianensis</i>	Neuville cast	BSPG, 1968IV192	119	43	36.1
<i>Prosantorhinus aurelianensis</i>	Neuville+	MNHN, Neu 98	119	42	35.3
<i>Prosantorhinus aurelianensis</i>	Chevilly	MNSQ, 809 / dex.	116	43	37.1
<i>Prosantorhinus aurelianensis</i>	Chilleurs	NIMBa, 226 / dex.	111	42.5	38.3
<i>Prosantorhinus aurelianensis</i>	Chilleurs	NIMBa, 619 / dex.	110	45	40.9
<i>Prosantorhinus aurelianensis</i>	Artenay+	MNHN, no data pub.	117	27.5	22.5
<i>Prosantorhinus aurelianensis</i>	Artenay+	MNHN, no data pub.	113	43.5	38.5
<i>Prosantorhinus aurelianensis</i>	Ahnikov	NIMP, Pv 10246 / sin.	102	23	22.5
<i>Prosantorhinus sp.</i>	Wintershof-West	BSPG, 19632 / sin.	96	31	32.3
<i>Prosantorhinus sp.</i>	Wintershof-West	BSPG, 19642 / dex.	87.5	31.5	36
<i>Prosantorhinus laubei</i>	Chilleurs	MSNO, 878 / sin.	87	28.5	32.8
<i>Prosantorhinus laubei</i>	Chilleurs	NIMBa, 6718 / dex.	83	25.5	30.7
<i>Prosantorhinus douvillei</i>	Chevilly	MSNO, 40 / sin.	96.5	37.5	38.9
<i>Prosantorhinus douvillei</i>	Neuville	MSNO, 176 / sin.	100	42.5	42.5
<i>Prosantorhinus douvillei</i>	Neuville cast	BSPG, 968IV192 / sin.	103	43	41.7
<i>Prosantorhinus douvillei</i>	Baigneaux	NIMBa	102	37	36.3
<i>Prosantorhinus douvillei</i>	Baigneaux	NIMBa	97.5	35	35.9
<i>Prosantorhinus douvillei</i>	Artenay	MSNO, 614 / sin.	95	35	36.8
<i>Prosantorhinus douvillei</i>	Artenay+	MNH, no data pub.	95.5	33.5	35
<i>Prosantorhinus douvillei</i>	Béon	MNHT, G 840 / sin.	77	24.5	31.8
<i>Prosantorhinus douvillei</i>	Béon	MNHT, E2 612 / sin.	83.5	26	31.1
<i>Prosantorhinus douvillei</i>	Béon	MNHT, E 3 616 / dex.	69	29.5	42.8
<i>Prosantorhinus douvillei</i>	Béon	MNHT, F2 980 / dex.	78	28.5	36.5
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG, G 2207 / sin	61.5	24.5	39.8
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG, G 2806 / dex.	84.5	32.5	38.5
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG, G 3917 / dex.	68.5	21	30.7
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG, G 3240 /dex.	68.5	24	35
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG, ohne G. / dex.	(65)	22	33.8

Table A15. Skeletodental index a (= LP3 × 100 / LMC III).

Species	Locality	Collection	Number of individuals	Index
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	4	27.9
<i>Diaceratherium lemanense</i>	Hessler	SMF	2	20.0
<i>Diaceratherium lemanense</i>	Budenheim	HLMD	1	19.4
<i>Prosantorhinus aurelianensis</i>	Neuville	MNHN	2	23.5
<i>Prosantorhinus aurelianensis</i>	Chilleurs	MSNO	1	24.3
<i>Prosantorhinus laubei</i>	Ahníkov	NMP	1	20.9
<i>Prosantorhinus douvillei</i>	Montréal-du-Gers	MHNT	4	26.2
<i>Prosantorhinus douvillei</i>	Chilleurs	NMba	1	29.7
<i>Prosantorhinus douvillei</i>	Langenau	SMNS	2	26.1
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	5	32.7

Table A16. Skeletodental index b (= Lm3 × 100 / LMT III).

Species	Locality	Collection	Number of individuals	Index
<i>Diaceratherium lamilloquense</i>	Castelmaurou	MHNT	2	30.7
<i>Diaceratherium aginense.</i>	Laugnac*	MHNM	2	35.7
<i>Diaceratherium lemanense</i>	Hessler	SMF	2	33.4
<i>Diaceratherium lemanense</i>	Budenheim	HLMD	2	28.9
<i>Prosantorhinus aurelianensis</i>	Neuville	MNHN	3	40.7
<i>Prosantorhinus aurelianensis</i>	Chilleurs	MSNO	2	41.4
<i>Prosantorhinus douvillei</i>	Montréal-du-Gers	MHNT	2	38.7
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	9	24.2

Table A17. Premolar reduction index a (= LP3 × 100 / LM2).

Species	Locality	Coll.	No. / side	Index
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	A / sin.	69.8
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	B / dex.	76.9
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	C / sin.	69
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	D / no data	64
<i>Diaceratherium lemanense</i>	Bérac#	MHNT	? / dex.	50
<i>Diaceratherium lemanense</i>	Hessler	HLMD	Aq 7a / dex.	84.8
<i>Diaceratherium lemanense</i>	Engelhalde	NMBE	D3193 / d.	61.3
<i>Prosantorhinus aurelianensis</i>	Petersbuch 62	CSm	- / sin.	61.1
<i>Prosantorhinus aurelianensis</i>	Neuville+	MNHIN	Type / sin.	55.7
<i>Prosantorhinus aurelianensis</i>	Chilleurs	MSNO	791/716 / d.	57.1
<i>Prosantorhinus aurelianensis</i>	Artenay+	MNHIN	no data	71.6
<i>Prosantorhinus douvillei</i>	Montréal-du-Gers	MHNT	SN 33 / sin.	69.9
<i>Prosantorhinus douvillei</i>	Baigneaux	MHNO	cast / sin.	69.1
<i>Prosantorhinus douvillei</i>	Tavers (type)	MNHIN	Tav 82 / sin.	62.2
<i>Prosantorhinus tagicus</i>	Horta d. Tripas	UNL	1681 / dex.	77.4
<i>Prosantorhinus germanicus</i>	Georgensgmünd	BSPG	AS 7 / sin.	68.9
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G6304 / d.	66.2
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G6606 / s.	80.5
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G2741 / s.	77.4
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	1959II464 /	65.5
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	4566-8 / sin.	70.7

Table A18. Premolar reduction index b (= Lp3 × 100 / Lm2).

Species	Locality	Coll.	No. / side	Index
				60 64 68 72 76 80 84 88 92 96 100 104 108
<i>Diaceratherium lamilloquense</i>	Castelmauro#	MHNT	- / dex.	79
<i>Diaceratherium lamilloquense</i>	Castelmauro#	MHNT	- / sin.	70.3
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	A / sin	76.2
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	B / sin.	73.3
<i>Diaceratherium aginense</i>	Laugnac*	MHNM	D / sin.	72.2
<i>Diaceratherium aginense</i>	Calmont#	MHNT	- / dex.	82.8
<i>Diaceratherium lemanense</i>	Hessler	SMF	? / / dex.	75.6
<i>Diaceratherium lemanense</i>	Budenheim	SMF	M 4639 / sin.	75
<i>Diaceratherium lemanense</i>	Budenheim	SMF	M 6777 / sin.	81.7
<i>Diaceratherium lemanense</i>	Gannat	UCBL	744 / side unpubl.	81.3
<i>Diaceratherium lemanense</i>	St Michel-du-Touch#	MHNT	- / sin.	66.8
<i>Prosantorhinus aurelianensis</i>	Neuville	MSNO	349 / sin.	69
<i>Prosantorhinus aurelianensis</i>	Neuville+	MNHN	side unpublished	63.3
<i>Prosantorhinus aurelianensis</i>	Chilleurs+	MNHN	side unpublished	78.8
<i>Prosantorhinus aurelianensis</i>	Chilleurs+	MNHN	side unpublished	78.6
<i>Prosantorhinus laubei</i>	Ahníkov	MNP	Pv 10203-05 / dex.	81.8
<i>Prosantorhinus laubei</i>	Alníkov	MNP	Pv 10208-10 / sin.	104.5
<i>Prosantorhinus laubei</i>	Tuchořice	NMP	36/42 / sin.	78.9
<i>Prosantorhinus douvillei</i>	Montréal-d.-G.	MHNT	- / sin.	76.6
<i>Prosantorhinus douvillei</i>	Montréal-d.-G.	MHNT	SN 108 / sin. and dex.	83.1
<i>Prosantorhinus douvillei</i>	Beaugency	MHNT	Tav 80 / dex.	72.4
<i>Prosantorhinus douvillei</i>	Beaugency	MHNT	3903 Abg. / dex.	72.4
<i>Prosantorhinus douvillei</i>	Langenau	SMNS	Abg. / dex.	60.7
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	'59 II 406 / dex.	71
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G 6813 / sin. and dex.	64.6
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	1959 II 2251 / sin.	68.9
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	1959 II 2275 / sin.	71.8
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G 6835 / sin.	76.8
<i>Prosantorhinus germanicus</i>	Georgengsmd.	BSPG	1902 I 2 / sin.	71
<i>Prosantorhinus germanicus</i>	Georgengsmd.	NHMW	1877 / dex.	71.8

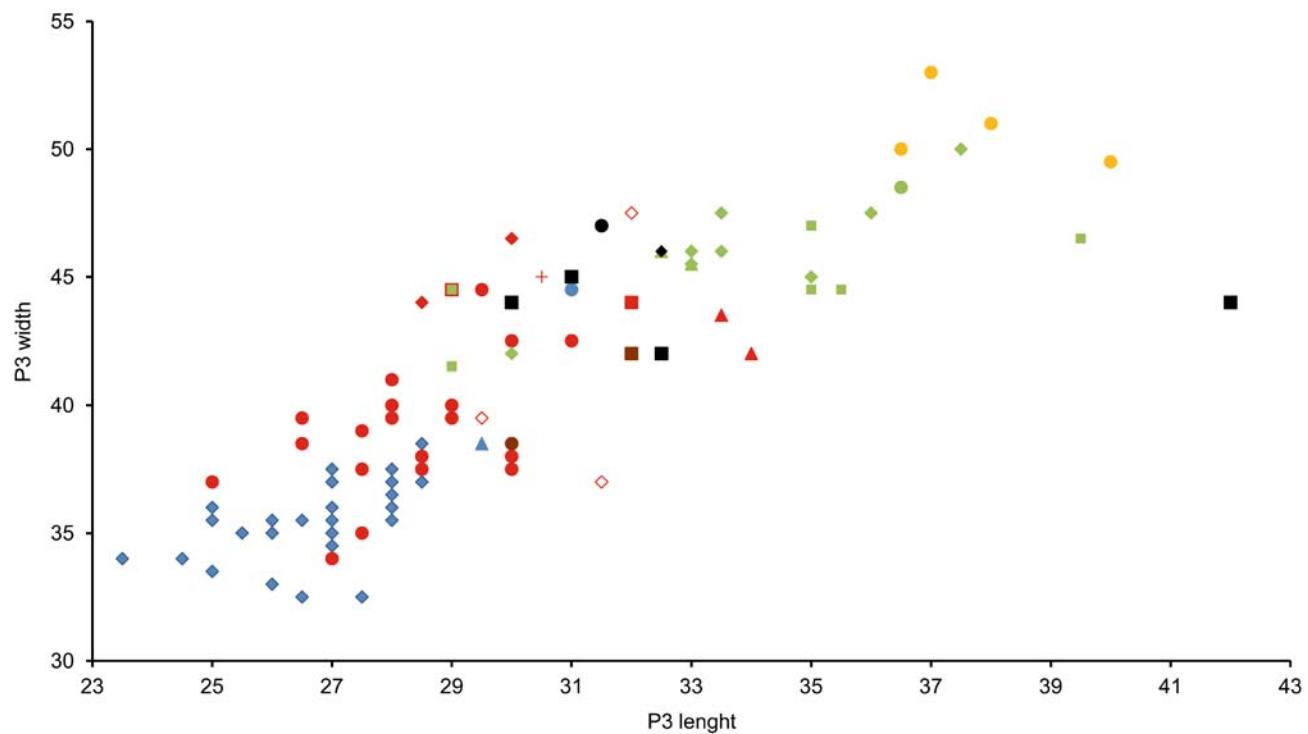
Table A18. Premolar reduction index b (= Lp3 × 100 / Lm2).

Species	Locality	Coll.	No. / side	WpP2	WaP4	Index
<i>Diatherium aginense</i>	Laugnac*	MHNMM	A / sin.	44	56	78.6
<i>Diatherium aginense</i>	Laugnac*	MHNMM	B / dex.	38.5	56	68.8
<i>Diatherium aginense</i>	Laugnac*	MHNMM	C / sin.	43	60	71.7
<i>Diatherium aginense</i>	Laugnac*	MHNMM	D / side not publ.	43	58	74.1
<i>Diatherium lemanense</i>	Bézac#	MHNT	- / dex.	38.5	49	78.6
<i>Diatherium lemanense</i>	Hessler	HLMD	Aq 7a / dex.	37	50	74
<i>Prosantorhinus aurelianensis</i>	Petersbuch 62	CRu	Feb. 62 / dex.	38	53.5	71
<i>Prosantorhinus aurelianensis</i>	Neuville	MNHN	Type / sin.	36.5	43.5	83.9
<i>Prosantorhinus douvillei</i>	Montréal-du-Gers	MHNT	SN 33 / sin.	35	51.5	68
<i>Prosantorhinus douvillei</i>	Montréal-du-Gers	MHNT	F 28 / sin.	39.5	53.5	64.5
<i>Prosantorhinus douvillei</i>	Baigneaux	NMBa	6835 / dex.	34.5	45	76.7
<i>Prosantorhinus douvillei</i>	Baigneaux	MSNO	east / sin.	32.5	41	79.3
<i>Prosantorhinus douvillei</i>	Tavers (type)	MNHN	Tav 82 / sin.	36.5	51	71.6
<i>Prosantorhinus germanicus?</i>	Thenay	MNHN	FP 1784 / dex.	40.5	51	79.4
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G6606 / sin.	23.5	30	78.3
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G6606 / dex.	24.5	30	81.7
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	1959II2917 / dex.	29	40.5	71.6
<i>Prosantorhinus germanicus</i>	Sandelzhausen	BSPG	G 1501 / sin.	26	41	63.4

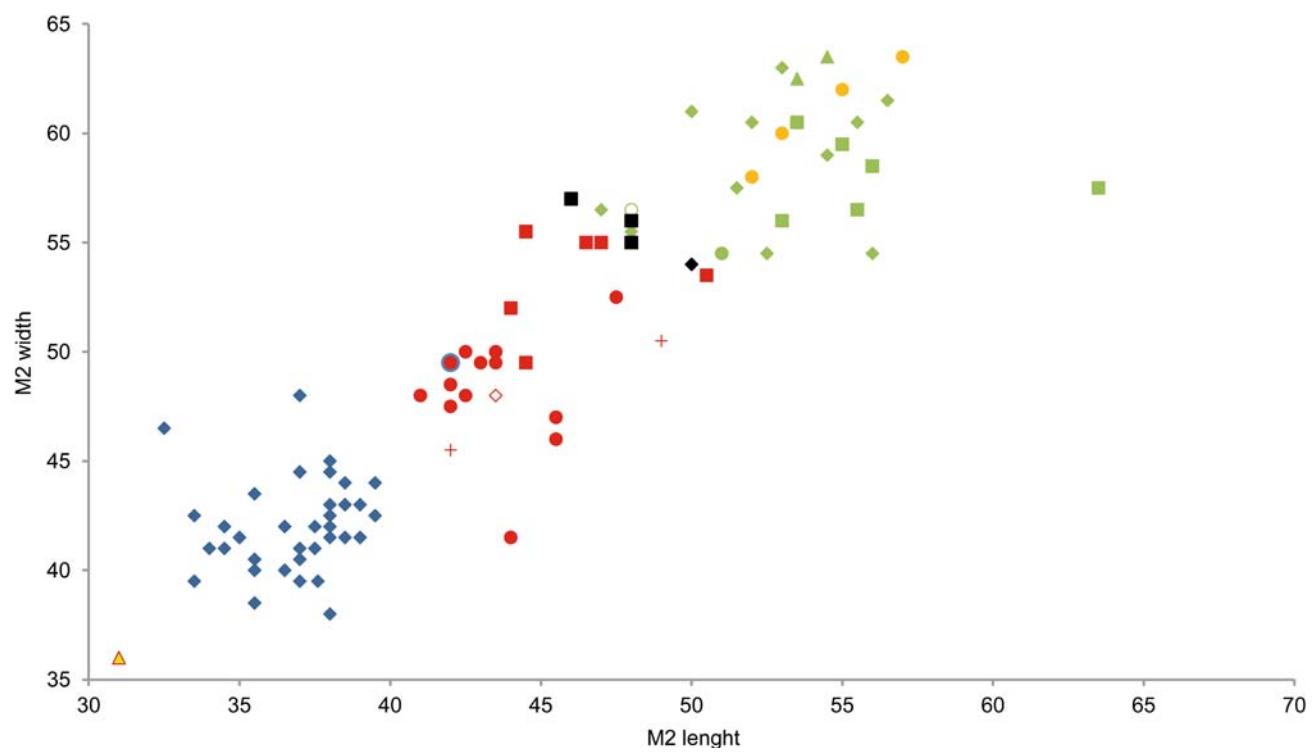
Diagrams

Symbols in diagrams.

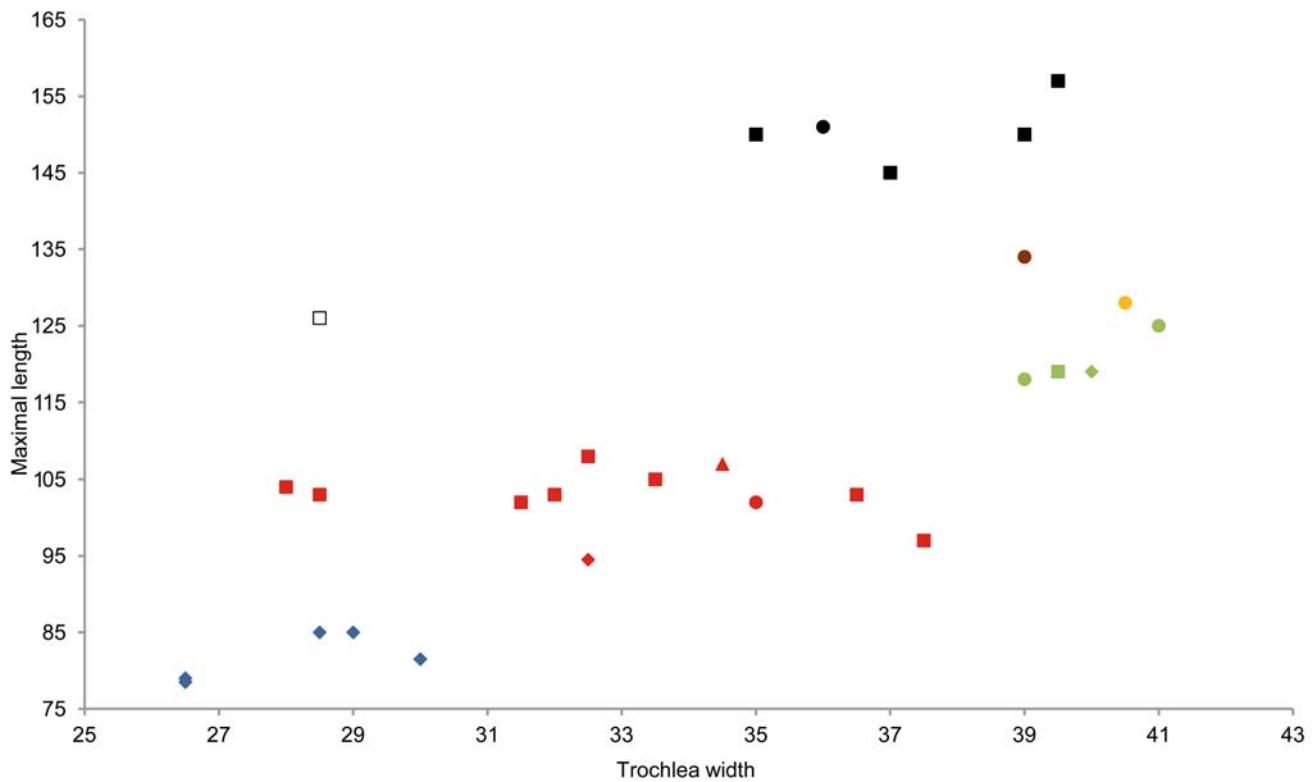
- Diaceratherium aginense*: ▲ Hessler, ● Laugnac
Diaceratherium lemanense: ◆ Bézac, ● Budenheim, ■ Hessler, ▲ Oberleichtersbach, □ Paulhiac
Prosantorhinus aurelianensis: ● Artenay, □ Chevilly, ♦ Chilleurs, ■ Neuville, ▲ Petersbuch 62, △ Rothenstein 16,
○ Wintershof-West
Prosantorhinus laubei: ● Ahníkov, ■ Tuchořice
Prosantorhinus germanicus: ● Georgensgmünd, ♦ Sandelzhausen, ▲ Thenay
Prosantorhinus douvillei: ○ Artenay, ● Baigneaux, ✕ Beaugency-Tavers, + Chevilly, ▲ Chilleurs, ♦ Langenau,
△ Maigreville, ■ Montréal-du-Gers, — Neuville, □ Petersbuch 2, ◇ Pontlevoy-Thenay
Prosantorhinus tagicus: ▲ Horta das Tripas



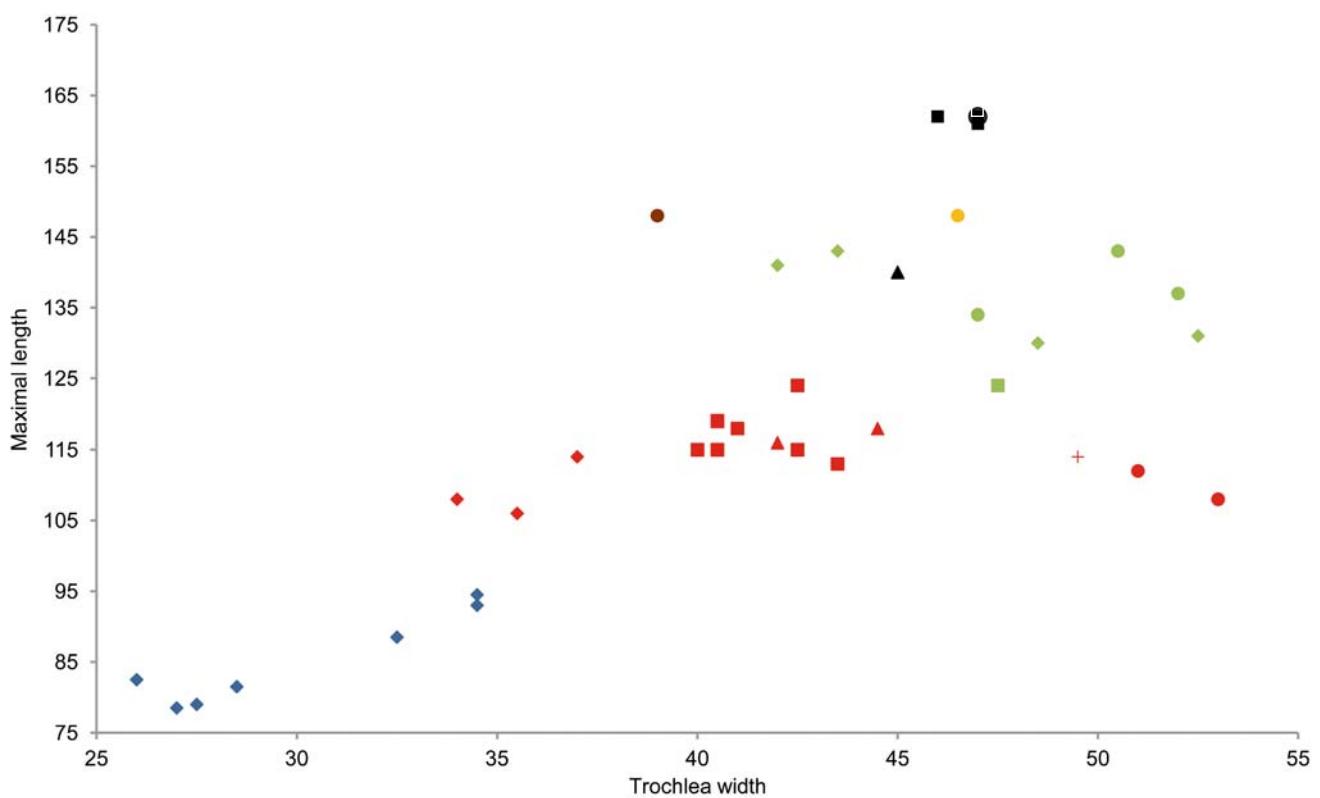
Text-fig. A1. Scatter diagram of P3 sizes of different species of *Prosantorhinus* and *Diaceratherium*.



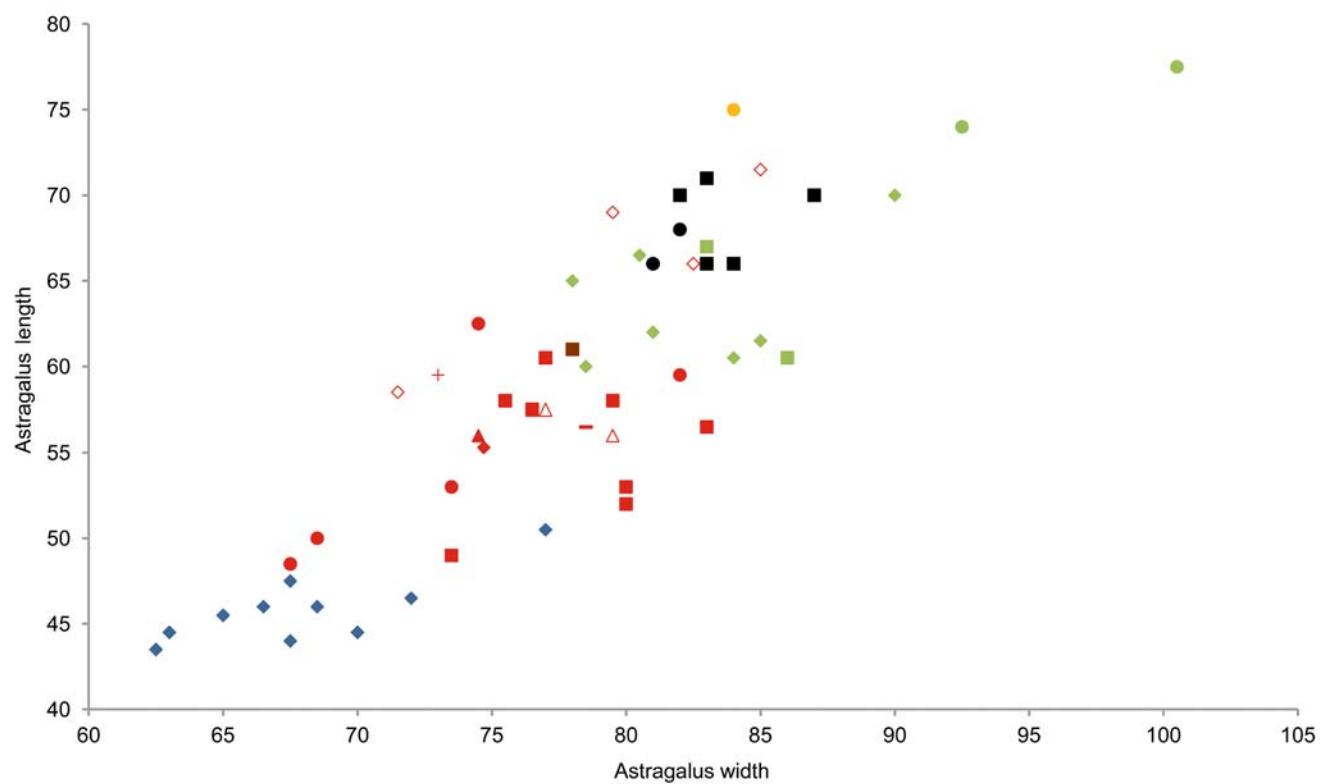
Text-fig. A2. Scatter diagram of M2 sizes of different species of *Prosantorhinus* and *Diaceratherium*.



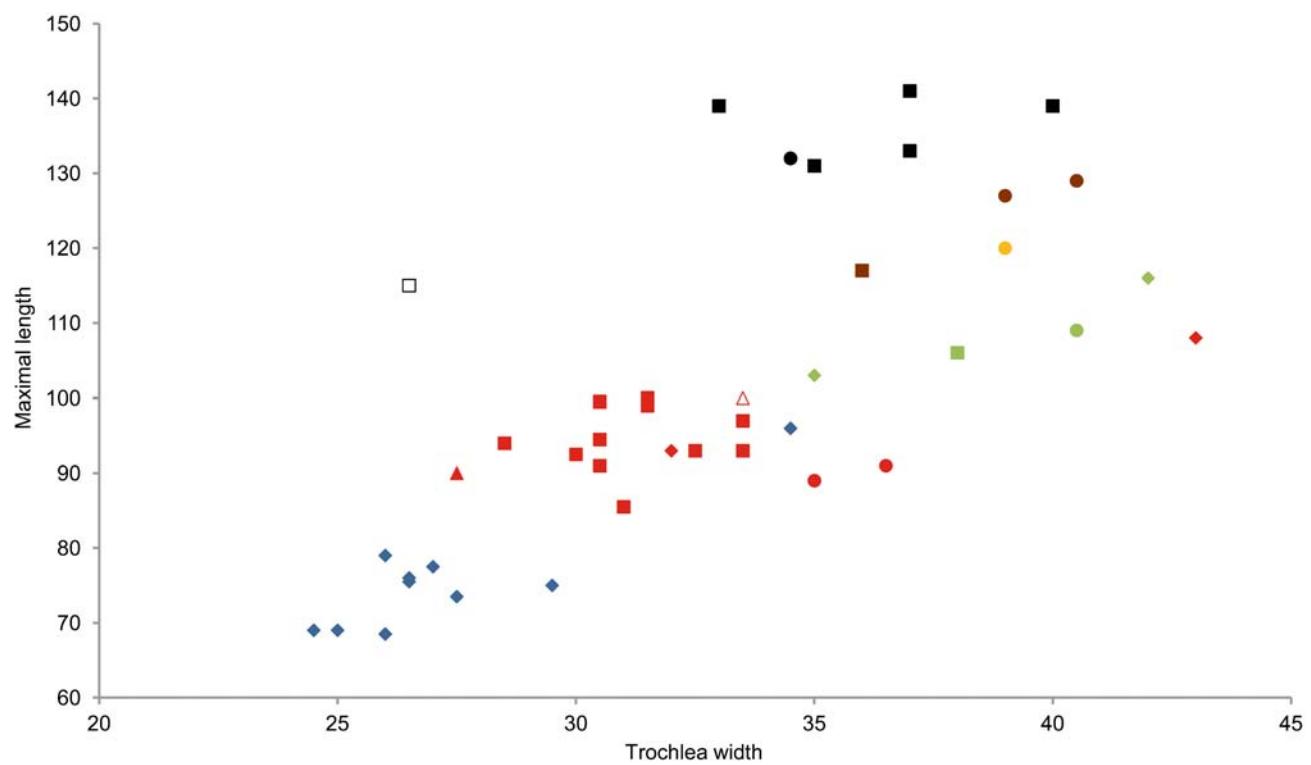
Text-fig. A3. Scatter diagram of the size of MC II of *Prosantorhinus* and *Diaceratherium*.



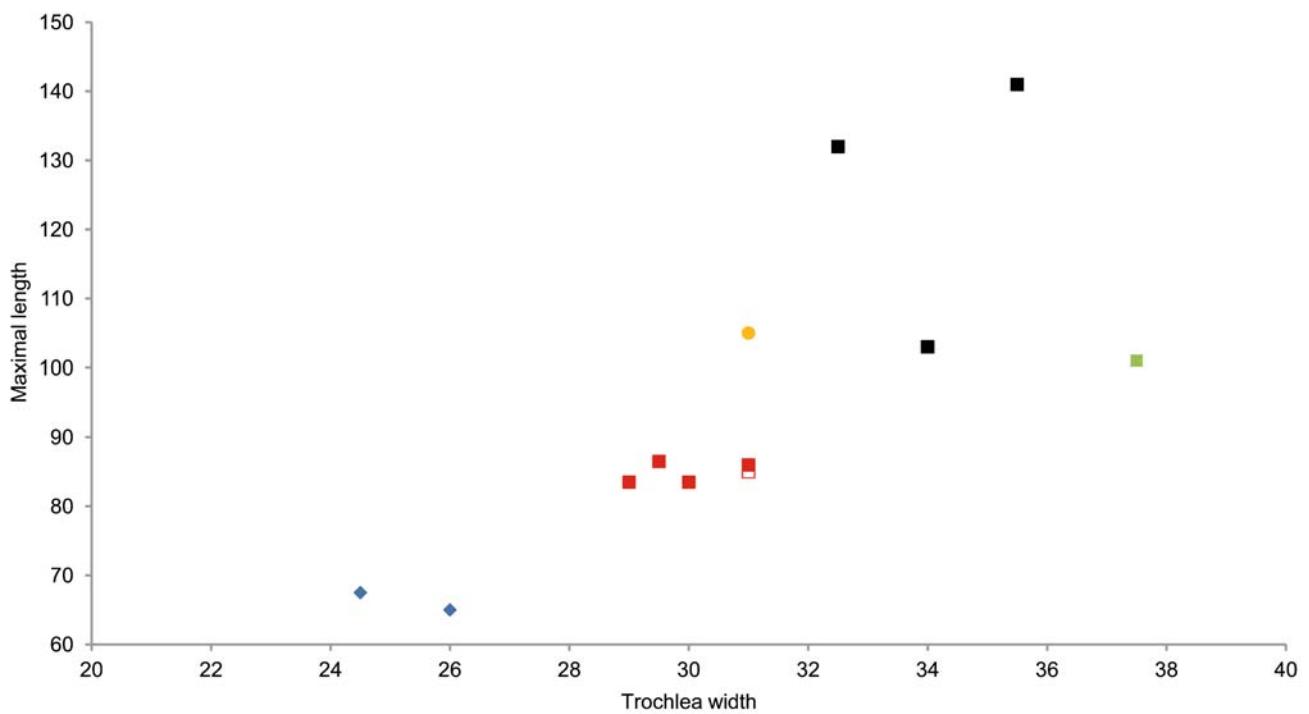
Text-fig. A4. Scatter diagram of the size of MC III of *Prosantorhinus* and *Diaceratherium*.



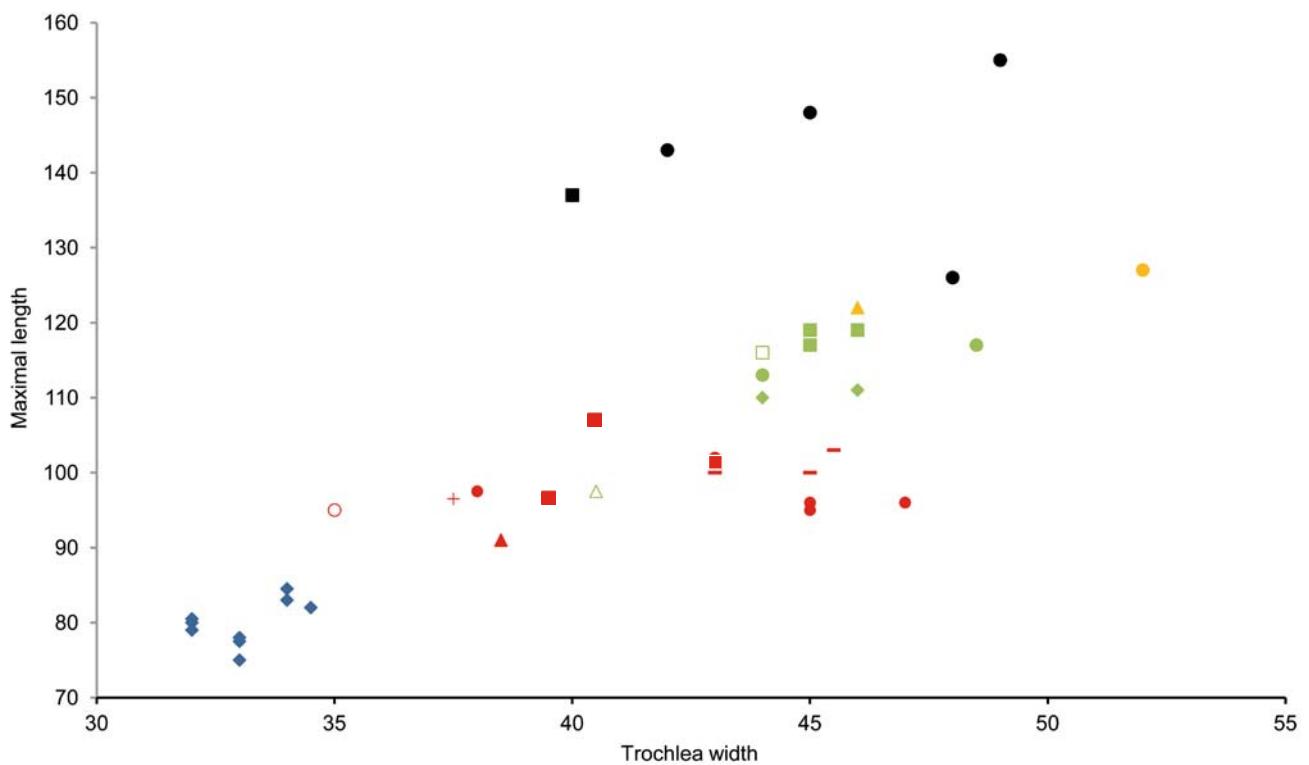
Text-fig. A5. Scatter diagram of the size of MC IV of *Prosantorhinus* and *Diaceratherium*.



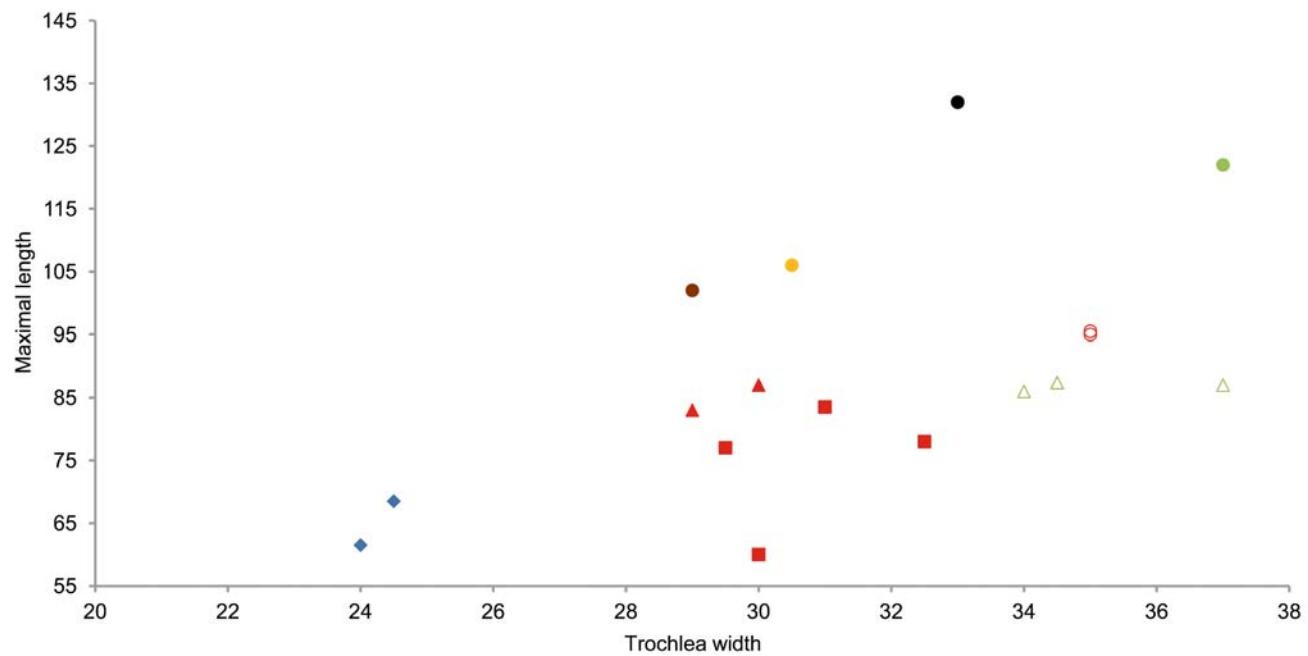
Text-fig. A6. Astragalus size in *Diaceratherium* and *Prosantorhinus*.



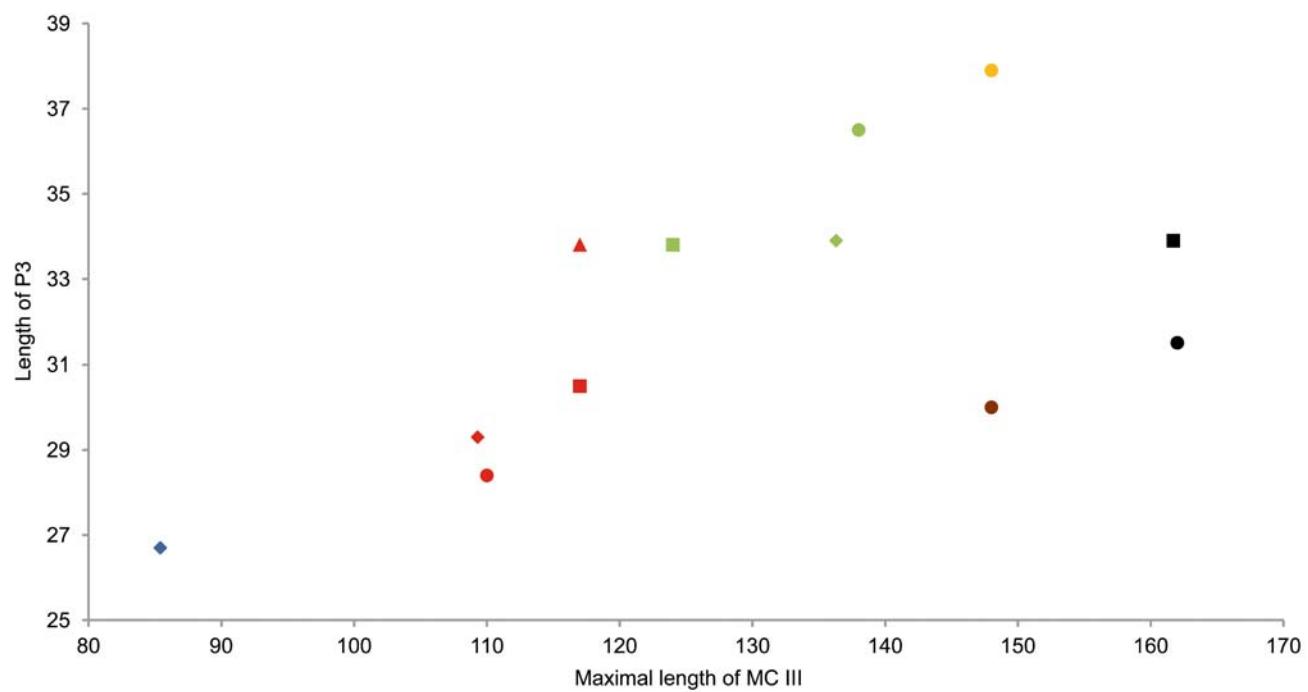
Text-fig. A7. Scatter diagram of the size of MT II of *Prosantorhinus* and *Diaceratherium*.



Text-fig. A8. Scatter diagram of the size of MT III of *Prosantorhinus* and *Diaceratherium*.



Text-fig. A9. Scatter diagram of the size of MT IV of *Prosantorhinus* and *Diaceratherium*.



Text-fig. A10. Size comparison of cheek teeth and metapodial (MC III), means of localities.