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Revision and Autopodial Morphology of the Chinese-European Rhinocerotid Genus *Plesiaceratherium* YOUNG 1937

By

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With 25 figures in the text and 23 tables

ABSTRACT

A reinvestigation of the type material of *Plesiaceratherium gracile* YOUNG 1937 in the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China) revealed that this comprises two species of rhinoceroses, one belonging to the genus *Brachypotherium* and another, the main part of the series, for which the name *Plesiaceratherium* should be retained. This species shows strong affinities with some European species hitherto assigned to *Dromoceratherium*. This younger generic name falls into the synonymy of *Plesiaceratherium*. Thus, the genus *Plesiaceratherium* is composed of the following species: *P. gracile* YOUNG 1937, *P. platyodon* (MERMIER 1895), *P. lumiarense* (ANTUNES & GINSBURG 1983), *P. mirallesi* (CRUSAFONT, VILLALTA and TRUYOLS 1955) and *P. fahlbuschi* (HEISSIG 1972). Skulls, teeth and autopodial morphology of these species are compared with one another and with the well known species *"Aceratherium" tetradactylum* (LARTET 1839) and, as far as possible, with the lesser known species *Alicornops simorrensis* (LARTET 1848).

中文摘要

[illegible] 保存在中国科学院古脊椎动物与古人类所的 *Plesiaceratherium gracile* YOUNG, 1937 正型标本的再研究，表明这些材料包括两种犀，一种属于 *Brachypotherium* 属，而另一个（大部分材料）则属于 *Plesiaceratherium*。这一归入 *Dromoceratherium* 的一些欧洲的种和这个种均相似，*Dromoceratherium* 应该是 *Plesiaceratherium* 晚出同物异名。

我们认为 *Plesiaceratherium* 应包括下列四个种：

P. gracile YOUG, 1937

P. platyodon (MERMIER, 1895)

P. mirallesi (CRUSAFONT, VILLALTA and TRUYOLS, 1955)

P. fahlbuschi (HEISSIG, 1972)

这些种的头骨、颊齿和肢骨的形态变异的范围以及它们之间的区别，以及 *"Aceratherium" tetradactylum* (LARTET, 1839) 和 *Alicornops simorrensis* (LARTET, 1848) 进行了对比。

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KURZFASSUNG

Die Neuuntersuchung des Typusmaterials von *Plesiaceratherium gracile* YOUNG 1937 im Institute of Vertebrate Paleontology and Paleoanthropology (Peking, China) ergab, daß darin zwei Arten fossiler Nashörner enthalten waren. Eine konnte zu *Brachypotherium* gestellt werden; für den anderen, größeren Teil der Serie muß der Name *Plesiaceratherium gracile* beibehalten werden. Diese Art zeigt enge Verwandtschaft mit einigen europäischen Arten, die bisher zu *Dromoceratherium* gestellt wurden. Dieser jüngere Gattungsname ist als Synonym von *Plesiaceratherium* zu betrachten. Danach umfaßt die Gattung *Plesiaceratherium* folgende Arten: *P. gracile* YOUNG 1937, *P. platyodon* (MERMIER 1895), *P. lumiarense* (ANTUNES & GINSBURG 1983), *P. mirallesi* (CRUSAFONT, VILLALTA & TRUYOLS 1955) und *P. fahlbuschi* (HEISSIG 1972). Schädel, Gebiß und die Morphologie der Autopodien dieser Arten werden untereinander und mit der bekannten Art *"Acerathe-rium" tetradactylum* (LARTET 1839) und, soweit möglich, mit der weniger gut bekannten *Alicornops simorrensis* (LARTET 1848) verglichen.

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INTRODUCTION

In 1937, YOUNG described some remains of rhinoceroses from the diatomite quarry of Shanwang near Linqü, Shandong province. Even though the figures were of good quality, the relationships of the species to other primitive Aceratherini remained obscure. The reason is the uniformity of tooth-pattern, not only in this tribe, but in the whole family Rhinocerotidae. The discovery of laterally crushed but complete skeletons in the same quarry was one reason for resuming the investigation of the genus. The first glance at the newly found skulls showed clearly the strong affinities of *P. gracile* to *Dromoceratherium fahlbuschi* from the gravel pit of Sandelzhausen, Bavaria, of approximately the same age. The relatives of this species were also included in the investigations.

The material of *Plesiaceratherium gracile* consists of some complete skeletons that were only superficially studied because of their preparation as a whole, and their housing in the local museums of Linqü and Jinan. In the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing there are some fragmentary skulls an some feet, representing mainly two individuals, but also a number of separate single bones.

The material of *Plesiaceratherium fahlbuschi* comes, with some exceptions, from the locality Sandelzhausen in Bavaria and is housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich (BSP). The specimens, one only nearly complete, uncrushed skull and numerous isolated bones, teeth and mandibular fragments, are not definitely numbered and are referred to by their field numbers for identification. The catalogue number is 1959 II.

The material of *Plesiaceratherium lumiarense* from Portugal is housed in the Universidade nueva de Lisboa, the material from Bézian in the Muséum national d'historie naturelle, Paris. It was not studied by the authors, because it was published after their visit in Paris.

The material of *P. platyodon*, only the skull with mandible, was studied in Lyon, the referred bones in Orléans. The material of *P. mirallesi* is housed in the museum of Sabadell, near Barcelona. The species compared with *Plesiaceratherium* were studied in the museums of Paris, Basel and Frankfurt (Museum National d'Histoire Naturelle Paris, Naturhistorisches Museum Basel, Senckenberg Museum Frankfurt). For explanation of dental morphology and the measurement points of bones, see HEISSIG (1972). The bulk of the specimens from Beijing, Linqü, Jinan, Munich, Paris, Basel and Frankfurt was studied by both authors within an exchange programme between the Academia Sinica and the Max Planck Society.

THE HISTORY OF THE FAMILY RHINOCEROTIDAE AND THE PRIMITIVE ACERATHERINI

The early history of the true rhinoceroses is still unknown. Most of the rhinoceros-like forms of the late Eocene are assigned to the Indricotheriidae, specifically to the Forstercooperiinae. The first undoubted rhinoceroses are found in the Lower Oligocene both in Eurasia and North America, but the relationship of these early forms to the later tribes are unknown. Only the short-lived Diceratherini can be traced back to an American genus such as *Trigonias*. The others appear later, the Rhinocerotinae as late as the so-called Proboscidean datum in the Burdigalian and may have evolved in Africa.

Both tribes of the Aceratheriinae start in the uppermost Oligocene as immigrants to Europe. The Aceratherini began with *Mesaceratherium pauliacense* (RICHARD), a form with strongly curved lower incisors and molarised premolars, but with a shortened metaloph. It is still a moot-point whether this genus continues into the Middle Miocene with *Alicornops simorrensis* (LARTET).

A second wave of immigrants to Europe brought another type of primitive Aceratherini with flat-lying incisors and lingually rounded upper premolars. They seem to belong to at least two well separated lines. One of them, with thick incisors with rounded cross sections, leads to *"Aceratherium" tetradactylum*. It is scarce in the Burdigalian. The other one begins with *Plesiaceratherium platyodon* and *P. mirallesi*, both with flattened incisors. Both genera have long, slowly tapering nasals, which are very broad at their base.

The third time of immigration to Europe and Asia brings the modern types of Aceratherini with shortened nasals an edentulous premaxillae: *Chilotherium* and *Acerorhinus* in Asia, *Aceratherium* in Europe. This group is excluded from the present study, as is *Mesaceratherium*, which shows no affinities with *Plesiaceratherium*.

It is possible that the history of the Aceratherini is far more complicated. The short-legged, horned *Chilotheridium* from Africa is quite isolated and the scattered remains of Aceratherini from western and middle Asia are not well understood. It is therefore necessary to start from one point, *Plesiaceratherium*, of which two species are well represented.

TAXONOMY

Genus *Plesiaceratherium* YOUNG

1937 *Plesiaceratherium* YOUNG, p. 214, Text-figs. 4 (2–6), 5–9; Pls.1, 2.
1937 non *Plesiaceratherium:* YOUNG 1937, Text-fig. 4(1).
1955 *Dromoceratherium* CRUSAFONT, VILLALTA & TRUYOLS, p. 152, Text-figs. 33–37; Pl. 2, fig. 4–5, Pls. 3–5.
1965 non *Plesiaceratherium* (YOUNG, 1937): WANG, B., p. 109, Pl. 1.

Diagnosis: Medium-sized to large Aceratherini with primitive type of skull and dentition. Upper incisors faintly developed but still shearing against lower ones in some species. Lower I_2 flattened, in a lying position and faintly curved. Skull hornless, with deep nasal notch and narrow brain-case. Upper cheek teeth with clumsy paracone and faint constrictions of the inner cusps. Premolars with outer cingulum high above base. Lower premolars long and narrow, with shallow outer groove and flattened outer edge of protoconid. Vertical rugosities on the outer wall are common. Limbs high and slender, mainly in the distal segments. Manus tetradactyle.

Remarks: The type series figured by YOUNG (1937) comprises also the upper premolar series of *Brachypotherium*. All the other specimens belong to the same species of Aceratherini. YOUNG'S diagnosis mentions no premolar characters. So we can restrict YOUNG'S name without hesitation to the majority of his specimens, even if a holotype was not designated.

Plesiaceratherium gracile YOUNG 1937

1937 *Plesiaceratherium gracile* YOUNG, p. 214, Text-figs 4 (2–6), 5–9, Pls. 1, 2.
1937 *non Plesiaceratherium gracile:* YOUNG, Text-fig. 4 (1).

Revised diagnosis: Medium-sized species of *Plesiaceratherium* with narrow skull, flattened and moderately curved incisors and very slender limbs. Mostly no rugosities on the outer wall of the lower premolars. Mandibular symphysis relatively long.

Remarks: It is necessary to designate a lectotype. We propose the complete fore foot illustrated by YOUNG (1937, Text-fig. 7, Pl.1).

Plesiaceratherium fahlbuschi (HEISSIG)

1972 *Aceratherium (Dromoceratherium) fahlbuschi* HEISSIG, p. 59, Text-figs. 1, 2; Pl. 3.

Revised diagnosis: Smaller species of *Plesiaceratherium* with very narrow skull, flattened, faintly curved lower incisors and slender limbs. Rugosities on the outer wall of the lower premolars generally present. Proximal facets of the metapodials narrow and deep.

Remarks: This species is represented by the largest number of specimens. It is most closely related to *P. gracile*. Because the type species of *Dromoceratherium, D. mirallesi* is now included in *Plesiaceratherium*, its earlier classification needs no further discussion.

Plesiaceratherium platyodon (MERMIER)

1895 *Acerotherium platyodon* MERMIER, p. 188, Text-fig. 5; Fl.1.
1896 *Acerotherium platyodon:* MERMIER, p. 255, Pl. 1, fig. 4; Pl. 2.
1896 non *Acerotherium platyodon:* MERMIER, p. 257.
1900 *Aceratherium platyodon* MERMIER: MAYET, p. 268, Text-fig. 85.
1911 *Acerotherium platyodon* MERMIER: ROMAN, p. 5, 84.
1934 non *Aceratherium* aff. *platyodon* MERMIER: ROMAN & VIRET, p. 29, Text-figs. 11–12; Pl. 8, figs. 1–6, Pl. 9, figs. 1–7; Pl. 11, figs. 8–10.
1959? *Aceratherium platyodon* MERMIER: GINSBURG, p. 2891.
1965 *Aceratherium platyodon* MERMIER 1895: BALLESIO, BATTETTA, DAVID & MEIN, p. 51, Text-fig. 1; Pls. 1–6, Pl 7, figs. 1–2.

Revised diagnosis: Medium-sized species of *Plesiaceratherium* with large braincase and separated parietal ridges. Upper premolars with weak molarisation, short metaloph and short postfossette. Lower incisors flattened. Symphysis mandibulae long and curved upwards; diastema rather long. Lower premolars with external rugosities.

Remarks: The holotype comprises only the depressed skull with mandible. The form of the nasals is unknown, and the premaxillaries are lacking. Some other specimens from the Burdigalian of France, mainly teeth, are assigned to this species, but no limb bones could be assigned with certainty. Even if the dentitions from La Romieu, assigned here to *P. lumiarense*, exhibit some intermediate characters, the skull form and mandible of *P. platyodon* seems to indicate a divergent line.

Plesiaceratherium lumiarense (ANTUNES & GINSBURG 1983)

1934 *Aceratherium* aff. *platyodon* MERMIER, partim: ROMAN & VIRET, p. 29, Text-figs. 11, 12; Pl. 8, figs. 1, 2, 5, 6,; Pl. 9, figs. 1, 2, 5, 7; Pl. 11, figs. 8–10.
1934 non *Aceratherium* aff. *platyodon* MERMIER, partim: ROMAN & VIRET, Pl. 8, figs. 3–4; Pl. 9, figs. 3, 4, 6.
1934 *Ceratorhinus tagicus* ROMAN, partim: ROMAN & VIRET, p. 36, Pl. 9, fig. 10.
1934 *Ceratorhinus* sp.: ROMAN & VIRET, Pl. 9, fig. 12.
1972 *Aceratherium (Dromoceratherium) fahlbuschi* n. sp., partim: HEISSIG, p. 60
1983 *Aceratherium lumiarense* nov. sp.: ANTUNES & GINSBURG, p. 28, Textfigs. 8–11, 21, 22; Pl. 4, fig. 4; Pl. 5; Pl. 9, figs. 3–9.
1984 *Plesiaceratherium lumiarense* (ANTUNES et GINSBURG): GINSBURG & BULOT, p. 354, Pl. 1, 2.

Diagnosis: see ANTUNES & GINSBURG 1983, p. 28

Remark: Neither skull nor symphysis are known from this species. The upper premolars exhibit a stage of molarisation intermediate between *P. platyodon* and *P. fahlbuschi*. As the authors have not studied the postcranials in detail the species is not compared with the others in the following text.

Plesiaceratherium mirallesi (CRUSAFONT, VILLALTA & TRUYOLS 1955)

1929 *Aceratherium tetradactylum* (LARTET) partim: WANG, p. 185, Pl. 7, figs. 1, 2, 4–6.
1955 *Dromoceratherium mirallesi* CRUSAFONT, VILLALTA & TRUYOLS, p. 152, Text-figs. 33–37; Pl. 2, figs. 4–5; Pls. 3–5.

Revised diagnosis: Large species of *Plesiaceratherium* with long and less flattened lower incisors and high, but massive, limb-bones. Lower premolars with vertical rugosities on the outer wall but less flattened protoconid edge and deeper external notch.

Remarks: The type specimen consists of the lower dentition and some limb-bones of one individual. It is set apart from the other species by its massive incisors, but their slight flattening and weak curvature are quite unlike *"Ac." tetradactylum*. Also, the more massively-built bones seem to reflect only the larger size of the animal.

The Aceratherini from Georgensgmünd, Bavaria, are provisionally assigned to this species, even if they show similarities to some larger specimens of *P. fahlbuschi*. The morphology of the lower premolars prevents identification as *"Ac." tetradactylum*. Unfortunately, the skull fragment from this locality was destroyed in the war and the figures of WANG (1929) do not show sufficient details.

MORPHOLOGY

Skull (Figs. 1–2, Table 1)

Skulls are known from the species *P. gracile*, *P. fahlbuschi* and *P. platyodon*. WANG (1929, p. 187) reports only some characters of the skull fragment from Petersgmünd, assigned here to *P. mirallesi*, and gives a rough sketch of the frontal outline corresponding approximately with the general characters of the genus. No specimen, including some certainly of the male sex, shows any trace of a horn base. This is in sharp contrast to the evolutionary line of *"Ac." tetradactylum*,, including *"Ac." bavaricum* (STROMER, 1902), where at least the male individuals have a marked swelling at the tips of the nasals, divided by the unossified middle fissure of the nasals. The nasals are long, broad to the rear and narrow gradually to their tips. The deep nasal notch is separated from the orbits only by a short distance. This narrow bar seems to be constant in size even if there is a considerable variability in the position of the orbit and nasal incision relative to the molar series. The distance is shorter than in all comtemporaneous Aceratherini and far inferior to that of *A. incisivum*. Therefore, the infraorbital foramen does not lie clearly behind the nasal notch as in *A. incisivum*, but below or on the edge of this incision.

The nasals are not fused along the midline. As in *"Ac." tetradactylum*, both nasals are vaulted separately, so that there is a median groove on the upper surface. The frontal plate is flat or slightly concave. Its maximum width just behind the middle of the orbits is caused by supraorbital swellings. From these points the skull tapers gradually to the front, whereas in *A. incisivum*, it narrows abruptly.

P. platyodon is separated from other species by a somewhat broader brain-case, indicated by the separation of the temporal lines. This character may be subject to individual variation as in *A. incisivum*, but in the other smaller species there is always a parietal crest. Nevertheless, the occiput is narrow in all three species, narrower than the external width of the condyles. The zygomatic arches project much more when compared with the frontal width.

The premaxillae are preserved only in the type species and bear an incisor of moderate size with a somewhat reduced shearing function.

Mandible (Fig. 2, Table 2)

The mandibles are usually crushed in the symphysis or broken behind it. Also, the diagnostic parts of the ramus are normally missing. BALLESIO, BATTETTA, DAVID & MEIN (1965) have given a good reconstruction of the mandible of *P. platyodon*, but in the other species the angle of the symphysis to the corpus mandibulae is known only approximately. The symphysis is short as in all Aceratherini, rising and curving not far to the front. In *P. gracile* and *P. platyodon*, however, it is a little longer and more strongly curved. The weakest curvature occurs in *P. fahlbuschi*. The ramus mandibulae is rather low.

Table 1.

SKULL PROPORTIONS OF PRIMITIVE ACERATHERINI

(Measurements in mm)

	P.gracile V.6880	V.6884	*P.fahlbuschi* type	nr.3903	*P.platyodon* type	*"Ac." tetradactylum* Paris skull	*Aceratherium incisivum* type cast	smaller specimens Din 1930	Din 1927
length of tooth row incl. P^1	-	-	-	-	220	-	260	-	-
length of tooth row excl. P^1	217	233	196	(202)	203	219	245	-	-
naso-occipital length	590	598	516	-	(550)	530	605	495	-
zygomatic width	258	265	(270)	-	(205)	320	370	255	-
upper width of occiput	-	-	(98)	83	97	141	150	130	-
frontal width	182	186	175	-	178	193	188	(170)	169
basal width of nasals	85	87	90	(100)	(100)	135	91	81	90
length of free nasals	184	191	185	-	(215)	180	176	120	132
distance orbit - nasal notch	66	67	43	35	58	55	80	50	50
foramen infraorbitale above:	$P3m^+$	$P3r^+$	P3/P4	-	P4r	P2/P3	P4/M1	M1r	M2f
nasal notch ends above:	$M1f^+$	-	P4f	P4r	P4r	P4f	P4f	M1f	M1f
orbit begins above:	$M1r^+$	$M2r^+$	M2f	M1m	M1/M2	M1m	M2f	M2m	M2r

(f front, m middle, r rear, + taken from another specimen, () imprecise or estimated)

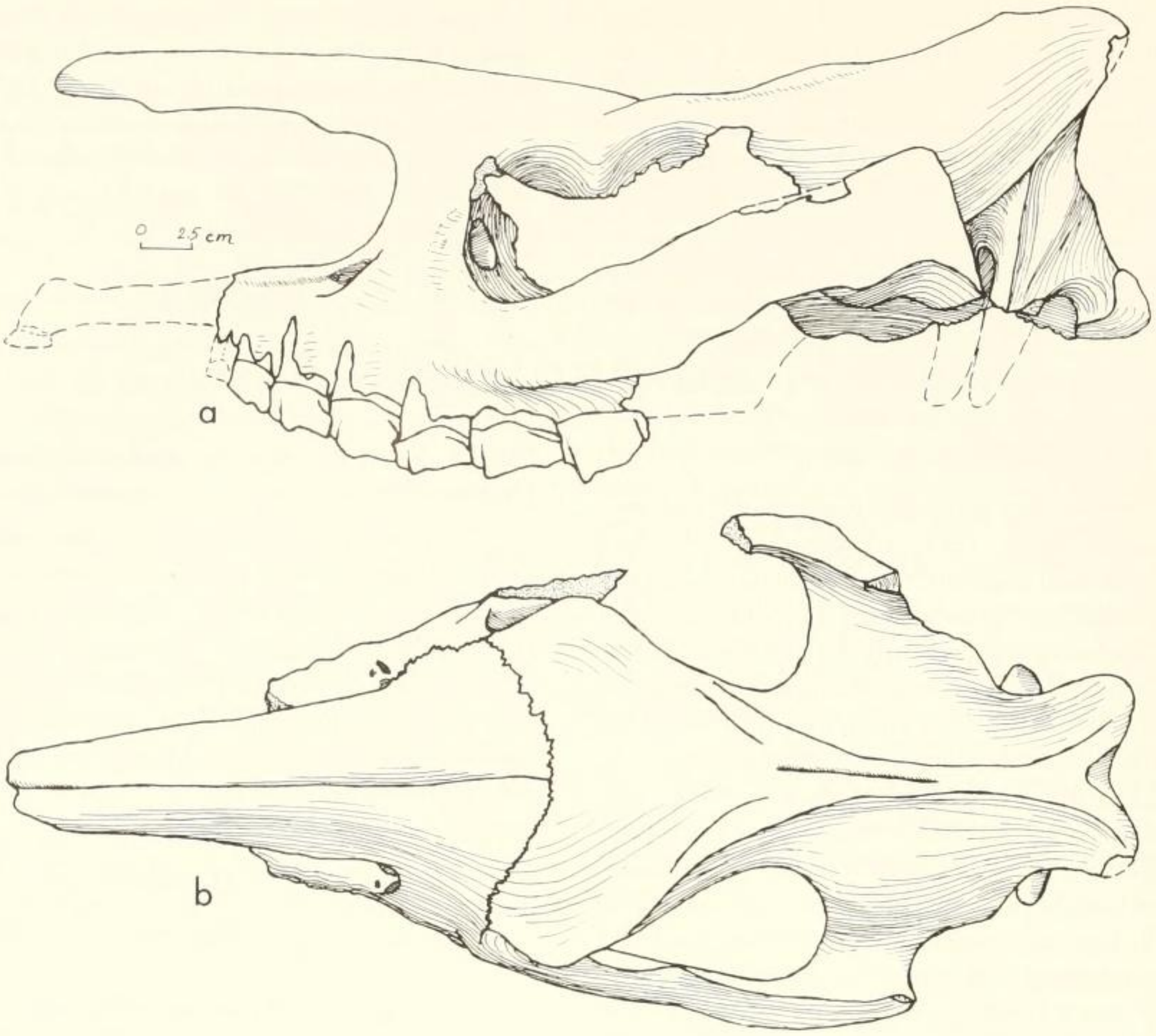

Fig. 1: *Plesiaceratherium fahlbuschi* (HEISSIG 1972) Holotype, BSP Munich 1959 II 400. a, left lateral view. b, dorsal view.

Table 2.

MANDIBULAR PROPORTIONS OF PRIMITIVE ACERATHERINI

(Measurements in mm)

	P.gracile		*P.fahlbuschi*			*P.platyodon*	*"Ac." tetra-dactylum*		*A.simorrensis*	*A.incisivum*		
	V.6880	V.6884	half mand. 3003	symph. 3093	0293	type	male	female	type	type cast	M6811	Din 1928
length symphysis-angulus	435	443	435	-	-	455	520	(500)	420	513	498	517
length P_2 - M_3	208	214	195	189	-	207	-	242	200	230	235	208
diastema P_2 - I_2	79	81	57	-	(56)	76	(80)	(60)	43	83	78	90
length of symphysis	89	96	(108)	-	(80)	96	146	-	(75)	(140)	115	133
width of symphysis	78	76	-	-	(70)	79	-	-	96	100	74	110
ramus height at incision	204	215	(175)	182	-	(176)	197	(170)	185	205	201	220
ramus minimal length	112	120	(120)	-	-	(105)	127	124	110	125	113	122
corpus height at M_3	79	88	85	77	-	85	91	83	83	98	92	88
corpus minimal height	(56)	(72)	(70)	67	-	65	70	78	-	-	78	74
corpus width at M_3	19	21	35	-	-	34	44	44	38	43	42	43
corpus minimal width	-	-	(25)	-	-	29	41	42	-	-	33	42
for. mentale below:	P2f	P2f	P2m	-	P2r	P2f	P2/P3	P3f	P3f	P2/P3	P2r	P2r
end of symphysis below:	-	P1	P2r	-	P2r	P2m	P2/P3	P3f	P2r	P2r	P3f	P2r

(f front, m middle, r rear)

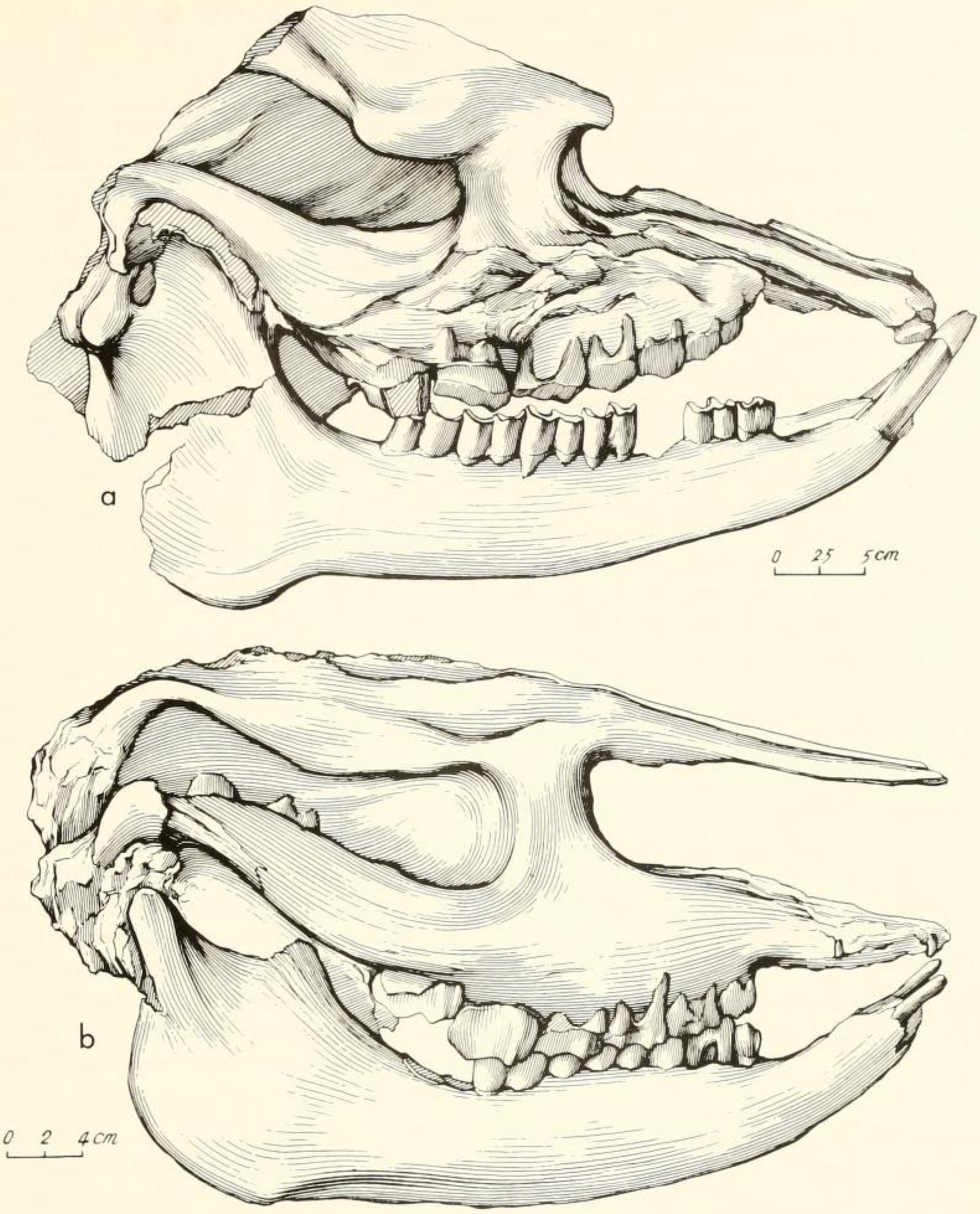

Fig. 2: *Plesiaceratherium gracile* YOUNG 1937. a, adult skull with mandible, right lateral view. b, juvenile skull with mandible, right lateral view. (Both IVPP, Beijing).

Incisors

The weakness of the upper incisors can be understood as an incomplete reduction initiated by a reduction of shear function. So, the genus is different from *Mesaceratherium* (and *Alicornops?*) which have strong unreduced incisors and *"Ac." tetradactylum* and possibly A. *incisivum*, which have edentulous premaxillae.

The existence of upper incisors is positively known from *P. gracile* and *P. mirallesi*. In *P. fahlbuschi* it is indicated by traces of wear on the lower ones. Some weakly worn single teeth from Sandelzhausen may belong to this species.

The lower incisors (I_2) are flattened. Even in the less flattened teeth of *P. mirallesi*, the root has an oval section. So, it is different from *"Ac." tetradactylum* with its thick incisors, that have a rounded crown section, even though the crown may be expanded lingually. The curvature is weak, more outwards than upwards, differing strongly from *Mesaceratherium* and *Alicornops*, which have upturned incisors.

The distance of the I_2 is so narrow, that the small I_1 are displaced labially. They are well developed in *P. gracile* and unknown in the other species. In *P. fahlbuschi* there are sometimes traces of small alveoli in this position. *"Ac." tetradactylum* sometimes has an I_1. The diastema is rather short as is the symphysis. In *P. fahlbuschi* it is even shorter than in other species.

Upper premolars (Fig. 3, Table 3)

Generally speaking, it is difficult to identify cheek teeth of the Rhinocerotidae, especially within tribes or even smaller

Table 3.

UPPER CHEEK TEETH OF ACERATHERINI

(Measurements in mm)

	P.gracile V.6880	V.6884	*P.fahlbuschi* type 1572	3093		*P.mirallesi* Georgensgmünd r	l	*P.platyodon* type Baig- r	l	neaux	*"Ac." tetradactylum* skulls, Mus.Paris		*A.simorrensis* type	*A.incisivum* type
length P^2 - P^4	110	108	87	93	-	102	-	91	91	-	-	-	92	112
length M^1 - M^3	121	131	109	116	-	126	124	115	112	-	126	(103)	(111)	139
P^1 length	-	-	-	-	-	21	24	20	20	-	25*	-	-	24
width	-	-	-	-	-	19	21	18	18	-	24*	-	-	21
P^2 length	31	32	24	28	-	-	29	30	30	-	-	28	25	34
width	36	33	33	34	-	-	36	35	35	-	-	41	33	47
P^3 length	34	37	29	33	29	35	35	28	30	31	35	33	35	47
width	42	41	39	41	39	44	45	43	43	43	53	50	38	55
P^4 length	37	38	32	35	32	37	39	34	34	34	-	38*	36	41
width	43	45	43	44	42	48	49	45	46	47	53	52*	42	60
M^1 length	46	48	32	38	40	41	43	35	36	-	-	-	36	48
width	48	48	44	45	42	47	47	43	43	-	-	-	45	60
M^2 length	48	50	36	43	44	45	46	38	38	43	44	44	38	49
width	50	51	47	47	45	51	51	46	45	47	57	-	45	62
M^3 length	43	46	41	39	39	41	43	37	36	45	45	-	39	49
width	45	47	42	42	44	45	45	42	42	48	52	-	42	58

(* taken from another specimen)

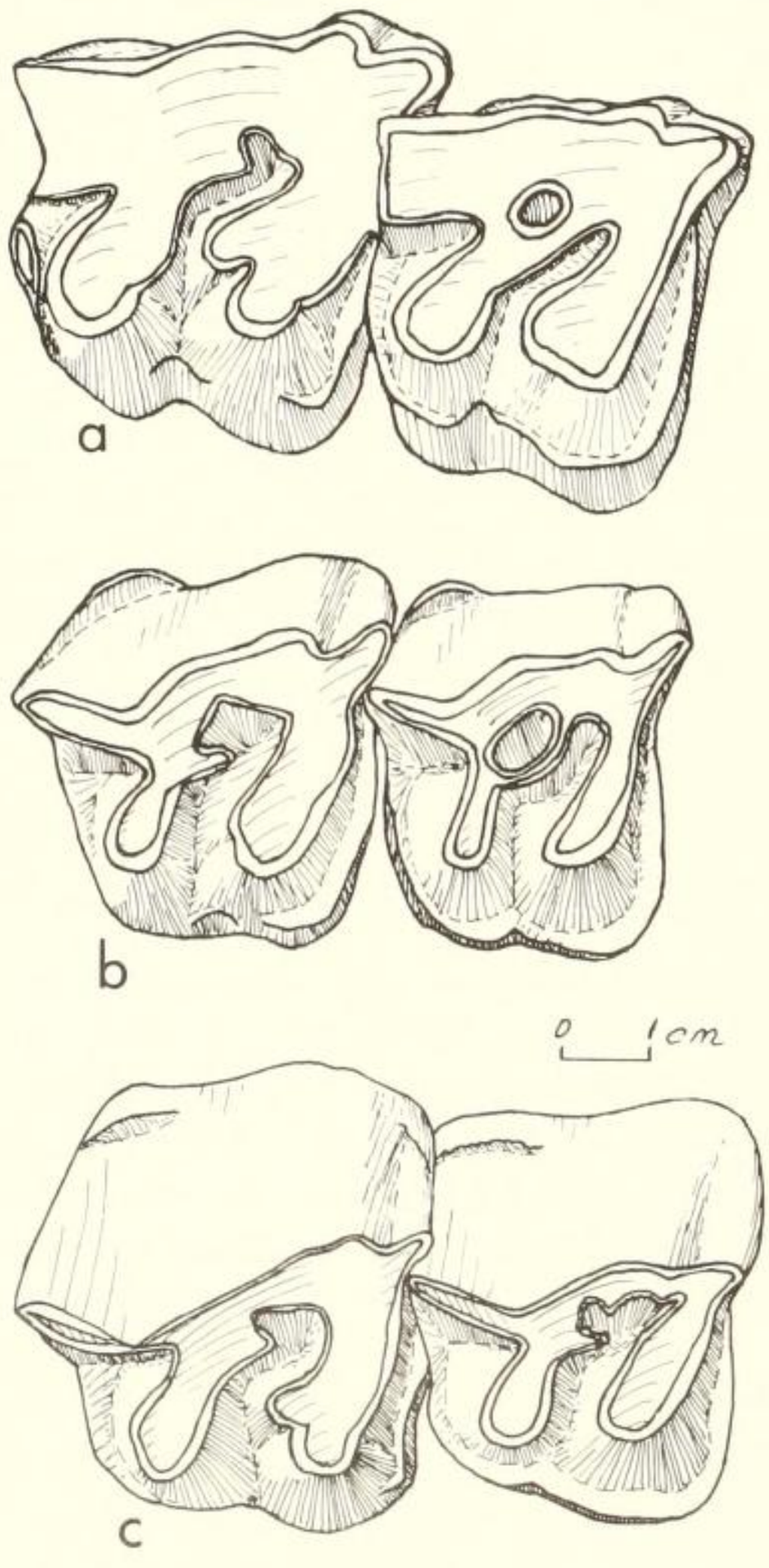

Fig. 3: Right P^4 – M^1 of *Plesiaceratherium*. a, c, *P. gracile*, middle Miocene, Shanwang. b, *P. fahlbuschi*, middle Miocene, Sandelzhausen, f.nr. 1572.

groups. Within the primitive Aceratherini, the upper premolars of *Plesiaceratherium* show strong cingula and weak molarisation. This cingulum forms a broad rim along the lingual side, high above the crown base, not going up and down as in most Aceratherini. It is with only few exceptions, uninterrupted lingually, but does not cross the outer wall, where its posterior part is high as in *"Ac." tetradactylum*. In this species, the inner cingulum is much weaker. *Alicornops simorrensis* has a weaker cingulum which, during evolution, descends to the base of the crown.

Characters allowing the separation of different evolutionary lineages are found mainly in the outer wall. *Plesiaceratherium* agrees here with *"Ac." tetradactylum* in the weakly elaborate mesostyle and metacone ribs. The paracone, however, in *"Ac." tetradactylum* is large and obtuse and has no clear posterior borderline. In *Plesiaceratherium* it is narrower, sometimes flattened and broadens downwards. Its inclination to the rear ist strong on P^2 and weak on P^4. The parastyle fold is sharper than in *"Ac." tetradactylum*, but the posterior borderline of the paracone is variable within the species.

Alicornops simorrensis, on the contrary, has a narrow paracone and the mesostyle and metacone ribs are stronger. The lingual cusps are faintly constricted as in other primitive Aceratherini. The strongest constrictions occur in *P. mirallesi* from Georgensgmünd, the weakest in *P. platyodon* where it occurs, however, also on P_2, which is less reduced than in the other species. The weak molarisation of the premolars of *P. platyodon* is mainly expressed by the short metaloph and the strong lingual bridge connecting the lingual cusps. This bridge, however, is highly variable in all species of *Plesiaceratherium*. Also, a variable character is the connection of crista and crochet, occuring rather frequently not only in *Plesiaceratherium* but also in other Aceratherini.

The first upper premolar is very variable. The outer wall is strongly curved in *"Ac." tetradactylum*. The parastyle is long in *P. platyodon* and *P. mirallesi* and shortened and turned inwards in *P. fahlbuschi*. The lingual structures depend on the relative length of the tooth. Less reduced types exhibit a lingual bridge between two complete lophs, both forming a right angle with the ectoloph. Metaloph and post-fossette persist but the protoloph may be reduced to a short ridge, not reaching the interior margin of the tooth. A medifossette may be formed by the union of crista and crochet. The prefossette is large and triangular.

Upper molars (Fig. 3, Table 3)

The paracone of the upper molars is narrower mainly in *P. fahlbuschi* and *P. mirallesi* than in other genera. Its posterior borderline is best marked in the specimens from Georgensgmünd, but also slightly visible in the other species. The paracone of M^1 is slightly inclined to the rear. The parastyle is rather long, separated from the paracone by a deep and acute parastyle fold. In *A. simorrensis,* the parastyle is shorter, and in *"Ac." tetradactylum* it is thicker and less constricted. There is no metacone rib.

The crochet is feeble, mainly in *P. platyodon*, where it is sometimes lacking. A crista is found only in a few specimens and is never fused to the crochet to form a medifossette. The antecrochet is large; in the last molar it is somewhat flattened.

The protocone constriction is sharp, but less deep than in *"Ac." tetradactylum*. Its posterior furrow is united basally with the narrow groove along the medisinus on M^1 and M^2. It does not reach this groove on M^3. In *P. mirallesi* and *P. gracile* a low ridge sometimes separates the protocone furrow from this groove on M^2 and very seldom on M^1. This ridge is a basal apendix of the antecrochet and contains no cingular elements. The hypocone furrow is commonly weak and falls steeply down into the medisinus. On the M^3, however, it sometimes reaches the lingual side separately behind the inner cingulum. This may also occur on M^1 and M^2 of *P. gracile*, if the medisinus is wide enough to be bridged lingually by a short cingulum.

The hind cingulum of M^3 forms a high and massive ridge, that diverges far from the ectoloph labially. Very often its labial end supports a well marked point, that slopes down labially with a sharp crest.

Sometimes the lingual edge of the protocone is flattened and in *P. gracile* and *P. mirallesi* there may also occur a furrow that notches the cingulum lingually.

Upper milk molars

The variability of mild molars exceeds the high variability of the other cheek teeth. So it seems not worth giving measurements. With the exception of DM^2, the upper milk teeth are smaller and longer equivalents of the true molars. Generally, they have a stronger mesostyle and a stronger metacone rib. The paracone is broader, conical and more strongly inclined to the rear. The crochet is longer and often clubshaped. The crown is lower, and the enamel is thinner than in the molars. The constrictions of the inner cusps in DM^3 are weaker than ind DM^4 and the molars. In most DM^4 a constriction groove runs approximately along the base of the crown parallel to the growth lines.

Milk molars are known from *P. gracile* and *P. fahlbuschi.* The milk molars of *P. mirallesi* from Georgensgmünd were lost in the War. Species differences are masked by variability.

DM^2 is very different from both the molars and premolars. It is even more variable than the other milk molars. Its function within the milk molar series parallels that of later premolars. So, its cingulum corresponds in strength to that of the premolars. In *Plesiaceratherium* it is normally continuous on the lingual side.

Crista and crochet are commonly united and may send a crest to the protoloph that separates a second fossette from the medisinus. If the crista is doubled, there exists a series of three fossettes. In *P. mirallesi* the prefossette is longer, but the protoloph is sometimes not united with the crista. In *"Ac." tetradactylum* the prefossette is even longer and the protoloph may be united with the ectoloph only by means of the crista. Lingually there may be secondary conules on the cingulum or at the base of the protocone. The metaloph may exhibit some secondary folds lingual to the crochet. The middle of the ectoloph is marked by a broad conical paracone. In front is a long flat or slightly convex parastyle, afterwards a flattened metacone rib and occasionaly a weak metastyle. This scheme may be complicated by the splitting up of the paracone. The parastyle fold is shallow but may be sharp in some specimens. In *"Ac." tetradactylum* and its relatives the paracone is narrower and situated in front of the middle.

Lower premolars (Table 4)

Besides the skull and the lower incisors the most characteristic elements of *Plesiaceratherium* are the lower premolars. The flattening of the protoconid edge and the resulting shallowing of the nevertheless sharp outer notch are best marked on P_2 and P_3, whereas in P_4 of the larger species the protoconid is rounded and the notch deep. Most species exhibit in all specimens vertical rugosities on the outer wall that originate from an outer cingulum high above the base, if it is suppressed by the general flattening. The rugosities may spread out over the whole outer wall but are normally restricted to the trigonid.

The species differ a little in these characters. *P. gracile* shows external rugosities only in some specimens. On the other hand, the flattening of the outer wall is best marked in this species. The rugosities are strong in all European species. *P. mirallesi* has only a slightly flattened protoconid edge and a rather deep outer notch. In *P. platyodon* the flattening is more marked, but the notch is still deeper than in *P. fahlbuschi,* which exhibits both characters nearly as strong as in *P. gracile*. The flattening may occasionally begin also on the outer surface of the talonid and may occasionally there produce a shallow groove, that was found in all species.

The outer cingulum is very variable, but is concentrated in different regions that are specifically different. In *P. gracile* and *P. platyodon* the cingulum runs from behind along the talonid to the outer notch. In *P. gracile* it is weaker and lacking

Table 4.

LOWER CHEEK TEETH OF ACERATHERINI

(measurements in mm)

	P.gracile		*P.fahlbuschi*			*P.mirallesi*		*P.platyodon*			*"Ac." tetra-dactylum*		*A.simor-rensis*	*A.incisivum*	
	V.6880	V.6884	401	3003	3093	type	Georgens-gmünd	type l	type r	Baig-neaux	male	female	type	Mainz	Senck Mus.
length P_2 - P_4	86	94	86	85	80	105	-	94	92	-	-	114	89	104	102
length M_1 - M_3	118	123	-	111	107	135	-	116	116	122	126	128	117	129	137
P_1 length	-	-	-	14	-	-	-	-	-	-	-	-	-	16	-
width	-	-	-	8	-	-	-	-	-	-	-	-	-	14	-
P_2 length	28	27	26	21	22	32	-	27	28	-	-	26	26	29	30
width	19	18	16	15	15	18	-	17	18	-	-	19	18	23	20
P_3 length	31	32	30	30	29	35	36	33	31	-	-	32	30	37	38
width	20	22	19	19	18	21	22	23	24	-	-	24	23	28	25
P_4 length	35	36	32	32	33	39	39	33	34	37	(33)	36	35	38	38
width	26	25	22	22	23	25	25	24	24	27	28	28	22	31	28
M_1 length	38	38	32	33	32	43	-	35	35	40	37	36	37	42	44
width	28	27	22	21	22	23	-	24	24	26	-	26	23	31	28
M_2 length	40	40	37	38	36	46	-	38	36	44	41	41	38	46	45
width	26	27	22	24	23	24	-	24	26	28	27	27	24	32	28
M_3 length	43	44	-	39	42	47	44	40	38	42	42	42	42	42	43
width	27	26	-	23	23	25	27	23	23	26	26	27	23	29	25

on P_4. In *P. fahlbuschi* and *P. mirallesi*, on the other hand, it is concentrated on the trigonid, but normally crosses the outer notch. The thick hind cingulum of *P. platyodon* is similar to that in "*Ac.*" *tetradactylum*, which exhibits neither a flattening nor vertical rugosities on the outer wall.

Lingually there are no important characters. The talonid basin gently slopes lingually and may even be flat on some very broad P_4. It is steeper on the narrow P_3 of *P. fahlbuschi*. The hypolophid is sharply inflected in all European species. In *P. gracile* the somewhat weaker inflection may indicate progressive molarisation. The trigonid groove is normally steep and shallow. Both depressions end lingually at the cingulum, but this varies considerably in strength. On the lingual side of the trigonid it normally forms a steeply descending ledge ending in a short hook around the base of the trigonid groove. In the lingual exit of the talonid basin there may occur also short ledges forming a "v", but they may be totally absent or unite to form a high massive crest. Only in one very feeble specimen of *P. fahlbuschi* this structure is similar to the modern Aceratherini: a very faint v-shaped cingulum deep below the exit of the talonid basin.

The second premolar is most distinctive for the species. It is distinguished from other Aceratherini not only by the shallow outer groove, but also by the shallowing of the anterior external groove, which is shallower than the trigonid groove. The paraconid pillar is lengthened in comparison to other Aceratherini.

Within the genus *Plesiaceratherium* the P_2 of *P. gracile* is comparatively short and broad. In *P. platyodon* and *P. mirallesi* the talonid basin has a nearly horizontal floor, which lies in *P. platyodon* at the same level as the lingual end of the trigonid groove; in *P. mirallesi* it is high above that level. In *P. fahlbuschi* the tooth looks somewhat reduced, but always is long and slender; its talonid basin is funnel-shaped. On the outer wall the protoconid is elaborated conically, long in *P. mirallesi* and short in *P. platyodon*.

The lower P_1 is very variable in size. Its single root is rounded in section in smaller specimens, oval and sometimes has a lingual constriction in larger specimens. The crown exhibits more morphological elements than in other Aceratherini. In front of the protoconid is a well formed anterior pillar, limited on both sides by shallow grooves, a faint cingulum running around its base from one groove to the other one. This pillar is connected with the conical main cusp by a high continous longitudinal crest. This crest splits up on top of the main cusp into two short folds, the outer protoconid edge labially and the metaloph lingually. A little deeper between these folds there arises the steeply falling hypolophid, first running somewhat labially, then bending inwards around the funnel-shaped talonid basin. The entoconid may be marked as a thikkening of the ridge or even as a small pillar.

There are some vertical rugosities on the lingual side, from the anterior cingulum to the entoconid. On the outer side similar but weaker rugosities are restricted to the outer groove.

Lower molars (Table 4)

Lower molars are generally poor in significant characters. In the genus *Plesiaceratherium* the external rugosities may be found sometimes on the molars too. The outer cingulum is normally restricted to the outer groove and to the anterior half of the trigonid. On the inner side there is only seldom a cingulum at the talonid basin. It occurs mainly on the front edge of the trigonid.

Lower milk molars

Milk molars of *Plesiaceratherium* may be easily determined by the elongation and flattening of the protoconid edge and,

in the European species, also by their external rugosities. On the contrary, the outer groove remains deep and sharp, especially in the DM_2, where it is overhung by the protoconid edge. The outer cingulum is mainly developed on the talonid, in contrast to the premolars of *P. fahlbuschi*, where it is restricted to the trigonid. On the DM_4 the cingulum on the trigonid and talonid is approximately of the same size.

Trigonid and talonid basins are only slightly inclined because of the lesser crown height. They have flat floors without sharpened grooves. A weak swelling projects from the protoconid into the trigonid basin. The paralophid is split up on DM_3 but there is only a narrow space between the two feeble crests. This splitting up is slightly indicated also on DM_2, but there are no inflected elements.

The interior cingulum is feebly developed at the talonid. At the front edge of the trigonid it forms a strong ledge that barely descends and blocks the interior entrance of the trigonid basin. On DM_2 a strong ridge runs forward from the entoconid and may meet the posterior edge of the metalophid to close the talonid basin. Also, the lingual side may be covered by vertical rugosities that reach forward to the protoconid swelling on DM_2 and to the metaconid fore edge on DM_3.

Carpus (Fig. 4)

Beyond the postcranials it is mainly the autopodials that are well represented. So we shall try first to find out the more important characters of carpals, tarsal, metatarsals and metacarpals, sparing the rest of the skeleton for monographical studies on the individual species.

The main character of the well documented species *P. gracile* and *P. fahlbuschi* is that all autopodial elements are high and narrow. In some bones that is the only difference from other primitive Aceratherini that is not hidden by variability. *P. mirallesi* has more massive foot bones so it is not always easy to distinguish its remains from these of other massive forms. Bones that may be assigned to *P. platyodon* with certainty are not known.

As in all Aceratherini, the radius also articulates with the ulnar, and therefore the ulna lacks an articulation with the intermedium. An articular facet is visible on the radius, but not on the ulnar, where the articulation is confluent with that of the ulna. A general character of the tribe is also the absence of an articular contact between the volar processes of the proximal carpal bones. Rare exceptions may be atavisms.

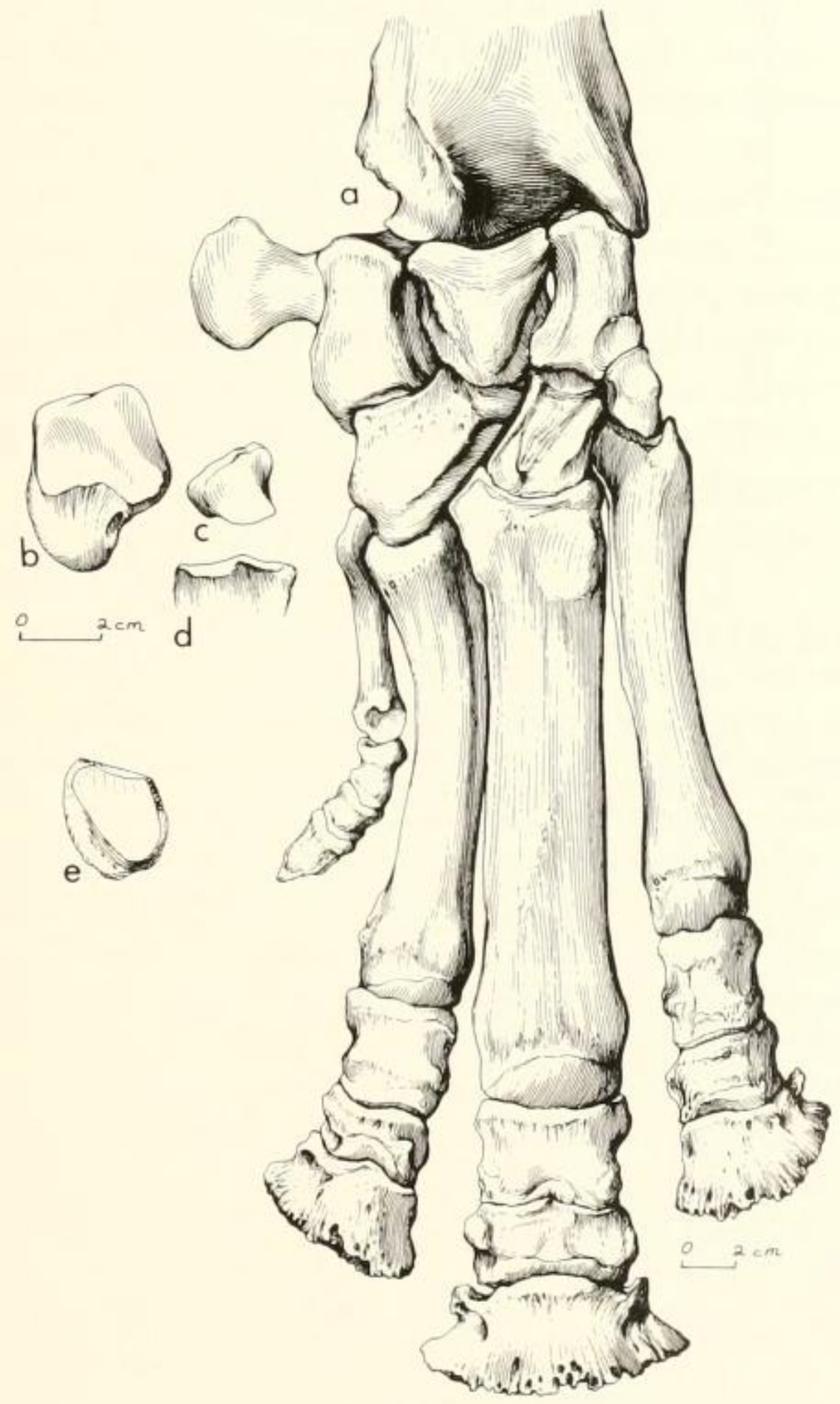

Fig. 4: *Plesiaceratherium gracile* YOUNG, middle Miocene, Shanwang. a, right fore foot. b, Carpal 1, lateral view. c, Metacarpal V, proximal view. d, Metacarpal IV, lateral view. e, *Plesiaceratherium fahlbuschi* (HEISSIG), middle Miocene, Sandelzhausen, Carpal 1, lateral view.

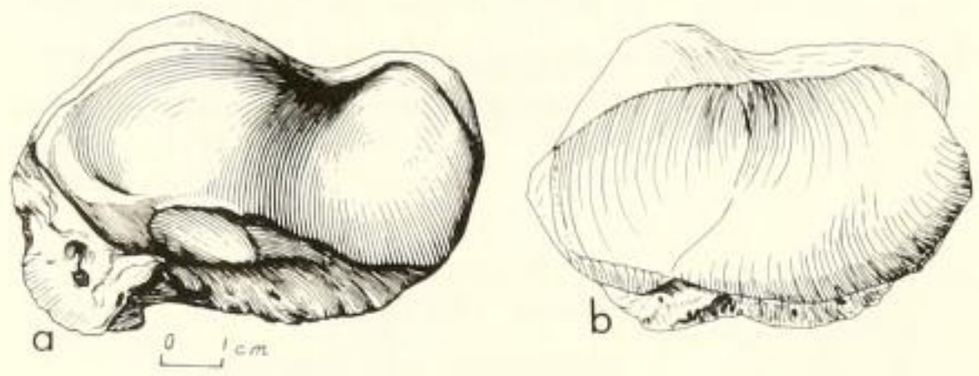

Fig. 5: Right radius, distal view, dorsal surface upside. a, *Plesiaceratherium gracile*, middle Miocene Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Voggersberg, Bavaria.

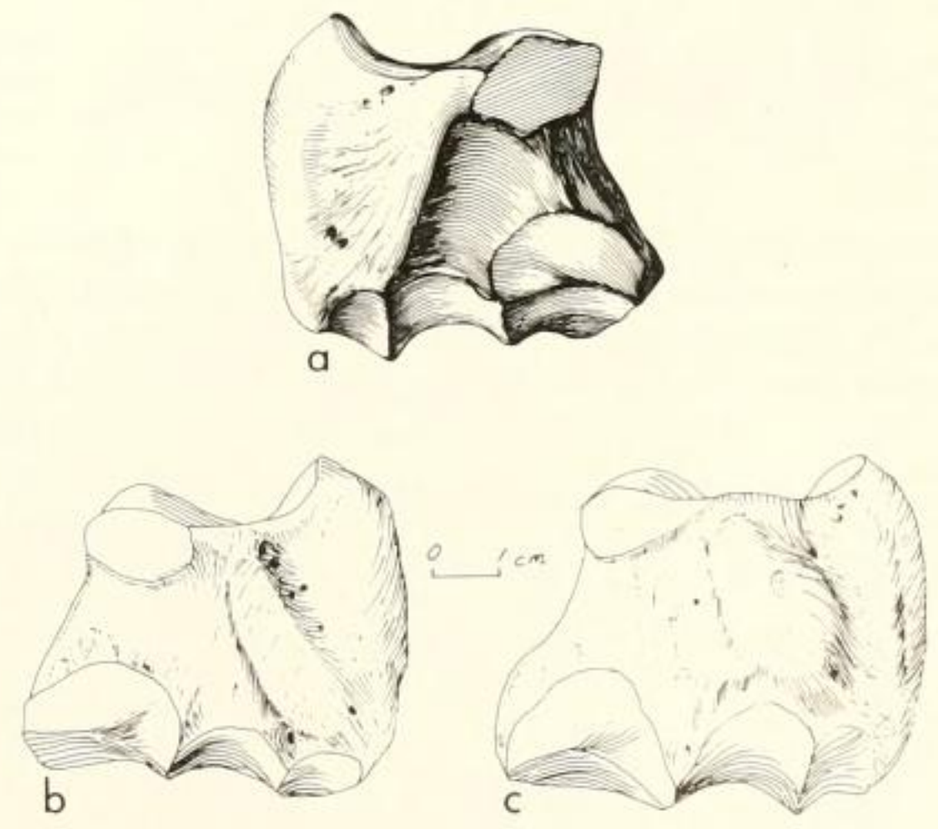

Fig. 6: Radial, laterovolar view. a, *Plesiaceratherium gracile*, middle Miocene Shanwang, left. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, Bavaria, right, BSP Munich, field nr. 475. c, *"Aceratherium" tetradactylum*, middle Miocene, Sansan, France, right, BSP Munich 1961 XVII 46.

Radial (Scaphoid) (Figs. 5–6, Table 5) The radial is a very characteristic bone. According to other primitive Aceratherini except *"Ac." tetradactylum* its medial height exceeds the lateral one considerably. The lateral convexity of the proximal surface is narrow, like in *A. simorrensis*, but in some specimens of *P. fahlbuschi* it is broader, like *"Ac." tetradactylum*. The saddle-shaped proximal facet has a prominent point projecting to the rear and thus is deeper than in other primitive Aceratherini.

There are two lateral facets for the intermedium. The distal one is small and plane. In one specimen of *P. gracile* there exists a third, volar facet for the intermedium whereas in all other specimens there is only a narrow and long projection of the bone without any trace of articulation. In *"Ac." tetradactylum* this projection is thick and rounded.

Distally, *P. fahlbuschi* is characterised by a broad, cylindrical concave facet for the carpal 1, whereas it is narrower and saddle-shaped in other Aceratherini. In *P. gracile*, on the other hand, the facet for the carpal 3 is concave in both directions, whereas the dorsovolar curving is lacking in other Aceratherini or even replaced by a convexity. A deep groove on the dorsal surface above tha carpal-2-facet is stronger than in other Aceratherini.

Table 5.

RADIAL OF MIDDLE MIOCENE ACERATHERINI

			max. breadth of bone	medial height of bone	middle height of bone	max. depth of bone	carpal-3-facet width	carpal-3-facet depth
P. gracile	ex. 1		56	53	39	36	22	19
Shanwang	ex. 2		-	50	39	37	-	-
(IVPP)	ex. 3	left	-	56	39	37	-	-
		right	57	50	39	37	23	24
P. fahlbuschi	f. nr.	739	57	53	37	34	18	18
Sandelzhausen	f. nr.	2336	55	55	38	-	17	18
(BSP)	f. nr.	2219	55	54	37	37	20	20
	f. nr.	223	52	50	37	31	17	-
	f. nr.	475	61	56	39	40	24	24
"Ac." tetradactylum	min.		65	59	42	45	23	18
Sansan (Mus.Paris)	max.		73	66	47	49	27	20
Alicornops simorrensis								
Sansan (Mus.Basel)	min.		60	56	40	40	26	28
	max.		66	57	41	48	27	30
Steinheim (M.Basel)	393		71	55	41	47	24	23
	394		60	49	35	40	20	29

Table 6.

INTERMEDIUM OF LOWER AND MIDDLE MIOCENE ACERATHERINI

			max. depth of bone	max. breadth of bone	frontal height of bone	prox. facet depth	carpal-4-facet width	carpal-4-facet depth
P. gracile	ex. 1		-	41	47	28	-	-
	ex. 2		56	40	45	30	-	-
	ex. 3	right	57	41	45	31	20	20
		left	58	41	44	27	21	30
	ex. 4		56	40	46	28	21	29
	ex. 5		57	(39)	44	30	24	31
P. fahlbuschi	f. nr.	436	56	44	44	25	(23)	-
	f. nr.	2577	50	35	41	20	17	24
	f. nr.	3319	51	35	45	23	17	25
	f. nr.	25-P	50	36	42	24	20	27
	f. nr.	104	55	39	44	27	23	25
	f. nr.	2171	52	38	43	27	18	-
	f. nr.	67-M	54	37	43	-	19	28
	f. nr.	2926	59	40	45	27	22	28
	f. nr.	79	51	36	42	32	20	29
	f. nr.	8-L	58	43	44	26	23	27
P. mirallesi	type ser.		68	-	53	32	27	28
(Senck. Mus.)	Georgensgmünd		-	-	52	37	26	30
"Ac." tetradactylum	min.		58	38	44	28	22	28
(Mus. Paris) Sansan	max.		64	47	50	35	28	32
Alic. simorrensis								
(Mus. Basel Sth 366) Steinheim			61	40	52	33	27	30

Table 7.

ULNAR OF LOWER AND MIDDLE MIOCENE ACERATHERINI

		frontal height of bone	max. depth of bone	max. width of bone	distance of medial facets	carpal-4-facet width	carpal-4-facet depth
P. gracile ex. 1		47	42	(39)	13	34	25
ex. 2		48	39	(39)	-	-	-
ex. 3	right	49	38	36	8	31	26
	left	49	39	38	10	31	29
P. fahlbuschi f. nr. 8-G		50	36	42	11	28	28
f. nr. 32-N		-	35	39	7	27	-
(juvenile) f. nr. 1864		42	35	38	11	24	27
f. nr. 2487		42	32	33	9	23	26
f. nr. 651		45	37	36	7	23	27
f. nr. 14		46	37	35	7	23	26
f. nr. 2758		49	34	40	7	27	28
P. mirallesi type ser.		52	38	48	14	26	(27)
(Senck. M.) Georgensgmünd		(53)	36	44	12	32	26
"Ac." tetradactylum	min.	53	36	47	9	33	28
Sansan (Mus. Paris)	max.	58	46	48	18	40	31
A. simorrense	min.	46	35	43	6	31	27
Sansan (Mus. Paris)	max.	50	45	46	17	37	30
Steinheim (M.Basel)		50	42	44	8	34	26

Intermedium (Lunar) (Fig. 7, Table 6): The volar process is remarkably long in *P. gracile*, *P. fahlbuschi* and *P. mirallesi*. The rare occurrence of a volar articulation with the radial was already mentioned. In most characters the bone is formed by the configuration of its neighbours and therefore has few constant characters.

The dorsal surface narrows downwards more than in other Aceratherini, except the primitive *Mesaceratherium*. The carpal-4-facet narrows considerably to the rear in *P. gracile* but does so only in some specimens of *P. fahlbuschi*. In *P. mirallesi* its breadth decreases only slightly. So in this character we find all types known in the Aceratherini.

Compared with *"Ac." tetradactylum*, the carpal-4-facet is more distally inclined. The distance between the lateral facets for the ulnar is larger.

Ulnar (Cuboid) (Fig. 8, Table 7): The articular facet for the radius is not visible in *P. gracile* and *P. mirallesi* as in other Aceratherini. Only in *P. fahlbuschi* in some specimens traces of its separation from the main proximal facet have been found. The angle included by the ulna and accessorium (pisiforme) facets is more acute in *Plesiaceratherium* than in other Aceratherini. *P. mirallesi* is more like the other forms in having a more obtuse angle when compared with *P. gracile* and *P. fahlbuschi*. The scar below the lateral tuberosity is roofed by two ledges, forming together a broad angle in *P. fahlbuschi* and *P. mirallesi* as in other Aceratherini. In *P. gracile* this scar is framed also from below with similar ridges, forming altogether a rhombic figure. As in middle Miocene Aceratherini in general, the medial hind ledge is well developed. In the smaller species of *Plesiaceratherium* it may bear one or two smaller projections.

The proximal facet for the ulna is flattened medially; laterally it becomes strongly concave dorsovolar and is bent downwards laterally to reach a vertical inclination in *P. gracile* and *P. mirallesi* as in most other Aceratherini. In *P. fahlbuschi* it is shorter and not so steep. In *P. mirallesi* the medial flattening is absent, the surface being steadily curved as in *"Ac." tetradactylum*. The distal carpal-4-facet is normally wide in comparison to its depth. Only in *P. fahlbuschi* and the type specimen of *P. mirallesi* does the depth equal or exceed the width. Its outline is a triangle with curved sides that form

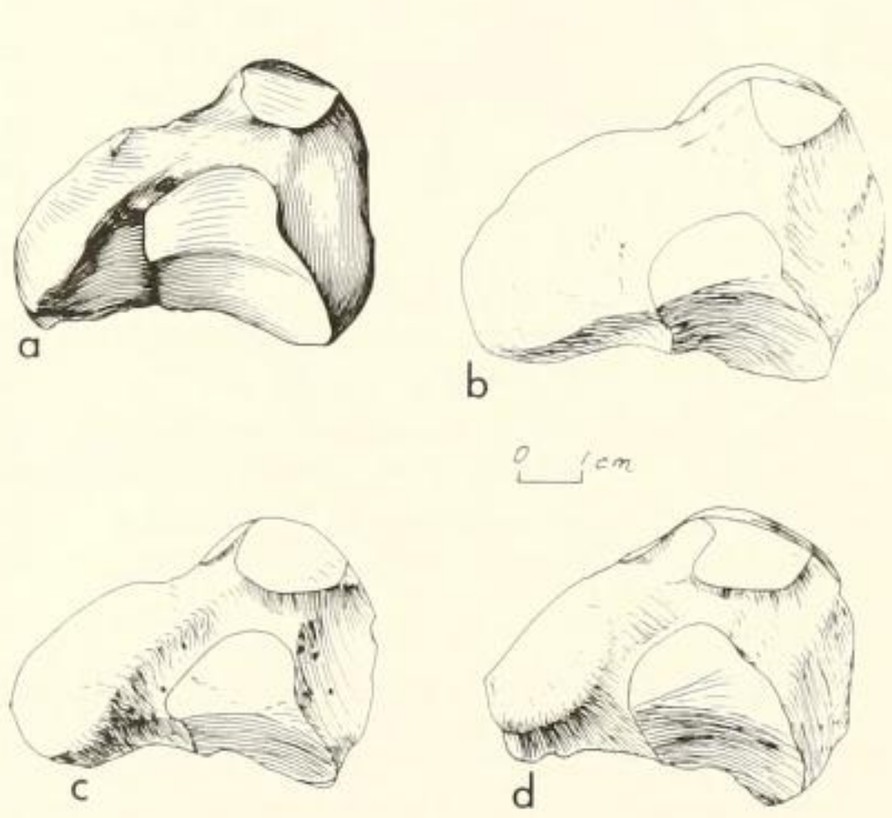

Fig. 7: Right intermedium, lateral view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium mirallesi*, lower Miocene, Can Julia. c, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen. d, *"Aceratherium" tetradactylum*, middle Miocene, Sansan.

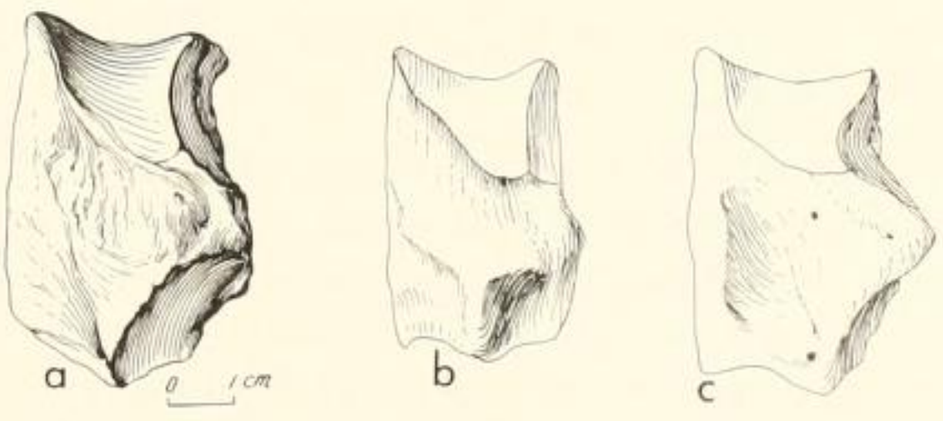

Fig. 8: Left ulnar, lateral view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen. c, *"Aceratherium" tetradactylum*, middle Miocene, Sansan.

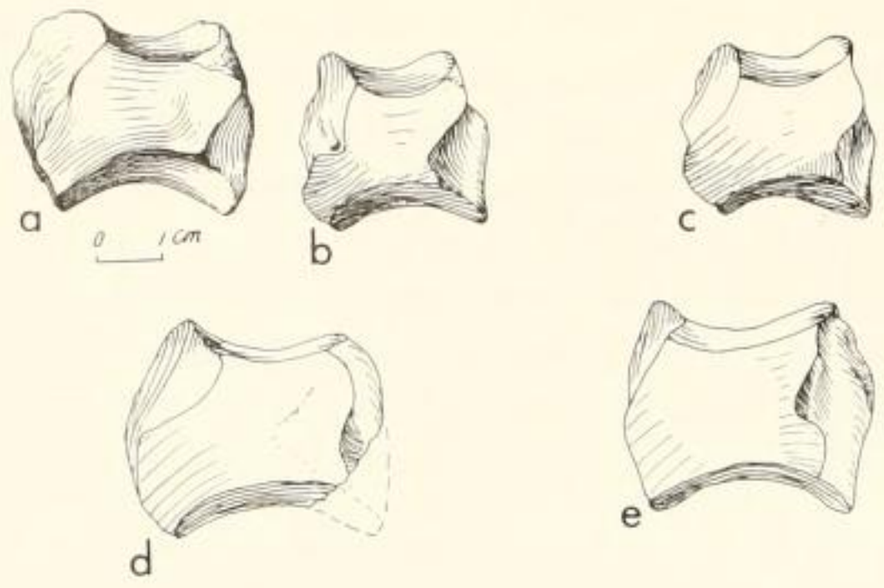

Fig. 9: Right carpal 2, lateral view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 9-L. c, same species, field nr. 21 N. d, *Plesiaceratherium mirallesi*, early Miocene, Can Julia. e, *"Acerathe-rium" tetradactylum*, middle Miocene, Sansan.

a mediovolar right angle in *P. gracile*, and an obtuse angle in *P. mirallesi* as in *"Ac." tetradactylum*. In *P. fahlbuschi* it is subject to great variability so that there are doubts about the constance of this character in other species.

The accessorium (pisiforme) and carpal 1 (trapezium) are omitted here. The first shows no distinctive characters, and the other is only represented by some isolated specimens (Fig. 4a, e) that give no impression of variability. It is unknown in most Aceratherini.

Carpal 2 (Trapezoid) (Fig. 9, Table 8): The second carpal is narrow in *P. gracile* and *P. fahlbuschi* and about as high as deep whereas it is lower in most Aceratherini and *P. mirallesi*. Like other Aceratherini, this species lacks a clear delimitation of the front side because the carpal-3-facet is shifted a little backwards and the medial edge is rounded. In *P. gracile*

Table 8.

CARPAL 2 OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	max. breadth of bone	max. depth of bone	height of bone front	mid.	hind	max. depth of lateral facets
P. gracile ex. 1	22	31	28	20	28	30
ex. 2	22	32	30	20	28	27
ex. 3 left	21	32	32	22	30	29
P. fahlbuschi f. nr. 312	22	30	32	23	28	27
f. nr. 15-K	21	32	31	22	29	30
f. nr. 8-L	23	32	33	23	31	31
f. nr. 8-Ls	21	32	29	23	31	28
f. nr. 94	23	35	35	24	32	30
f. nr. 30-L	-	33	33	24	33	27
f. nr. 9-L	23	33	33	24	31	30
f. nr. 21-N	20	30	28	22	26	28
f. nr. 13-J	20	29	28	20	28	27
f. nr. 9-Lb	22	30	28	23	29	28
P. mirallesi type ser.	-	(40)	-	25	33	40
(Senck. Mus.) Georgensgmünd (M 4215)	25	36	38	30	(35)	32
"Ac." tetradactylum min.	23	38	32	23	32	32
Sansan (Mus. Paris) max.	29	41	34	26	36	35
A. simorrensis min.	27	39	24	18	25	33
Sansan (Mus. Paris) max.	29	39	39	24	34	34

and *P. fahlbuschi* on the other hand, the carpal-3-facet forms the lateral edge of the dorsal surface and in most individuals this surface is also flanked by a medial ridge.

The proximal surface is saddle-shaped, the dorsovolar concavity being inverted in front to form a slight convexity or a flattening as in most other Aceratherini. The transverse convex curvature is much stronger. The narrow and vertical carpal-1-facet is situated far behind and resembles other Aceratherini. In one specimen of *P. fahlbuschi* it is separated from the distal facet.

The lateral carpal-3-facet has in some specimens of *P. gracile* an almost vertical edge. In others, as in *P. fahlbuschi*, it may be notched distally. This incision is situated higher up, near the middle in *P. mirallesi* and *"Ac." tetradactylum*. The distal part of this common facet for the carpal 3 and metatarsal III is greatly expanded to the rear. It is bent downwards and medially, so that the lower backside of the bone narrows distally. This narrowing is expressed less in *P. gracile* and even less in *"Ac." tetradactylum*. The oval-shaped distal facet is also saddle-shaped, but lacks the flattening in front. The convex transverse curvature is weaker than in the proximal facet and irregular, forming a slight keel. This keel is situated medially in *P. gracile*, near the midline in *P. mirallesi* and laterally in *"Ac." tetradactylum*. In *P. fahlbuschi* the variability comprises all these types, so that there are some doubts about the value of this character.

Carpal 3 (Magnum) (Fig. 10, Table 9): This complicated bone is very variable because it is influenced by all of its neighbours. It projects far back and is broader than high on its dorsal surface as in other primitive Aceratherini.

The most useful characters are found in the carpal-2-facet. It is triangular as in *"Ac." tetradactylum*, its upper part extending high up on the hump of the bone. Its upper edge is notched from behind in the figured specimens, a character also occurring sometimes in *"Ac." tetradactylum*. In all other Aceratherini this notch separates the carpal-2-facet completely from the backward prolongation of the radial facet and restricts the contact of the two facets to their fore part.

A deep incision is formed in front between the carpal 2 and the metacarpal II facets. The carpal-2-facet projects strongly above the incision, whereas in *"Ac." tetradactylum* the incision is less marked and the carpal 2 does not project. The angle between both facets is obtuse in *"P. gracile* and *P. fahlbuschi;* in *P. mirallesi*, as in *"Ac." tetradactylum* it is nearly flattened.

The radial facet has a narrow appendix along the intermedium facet until the top of the hump. It is bent upwards from the main facet in all Aceratherini, but the bending is less marked in *P. gracile.* The width of the intermedium facet is correlated with size. So, it is narrow in *P. gracile* and *P. fahlbuschi* and broad in *P. mirallesi.*

The metacarpal-II-facet is always almost vertical. Its hind margin is separated from that of the carpal-2-facet by a sharp angled notch in *P. gracile* that is absent in other Aceratherini. In the fore half of the facet there is sometimes found a faint groove near the upper margin, that may delimit the lower part really used for articulation. It was observed in all specimens of *P. gracile* and some of *P. fahlbuschi.*

The distal metacarpal-III-facet is mainly concave dorsovolar. It has in front a short and feeble inverse curve; at the backside it is only flattened. Its constriction by incisions from both sides is less marked than in other Aceratherini.

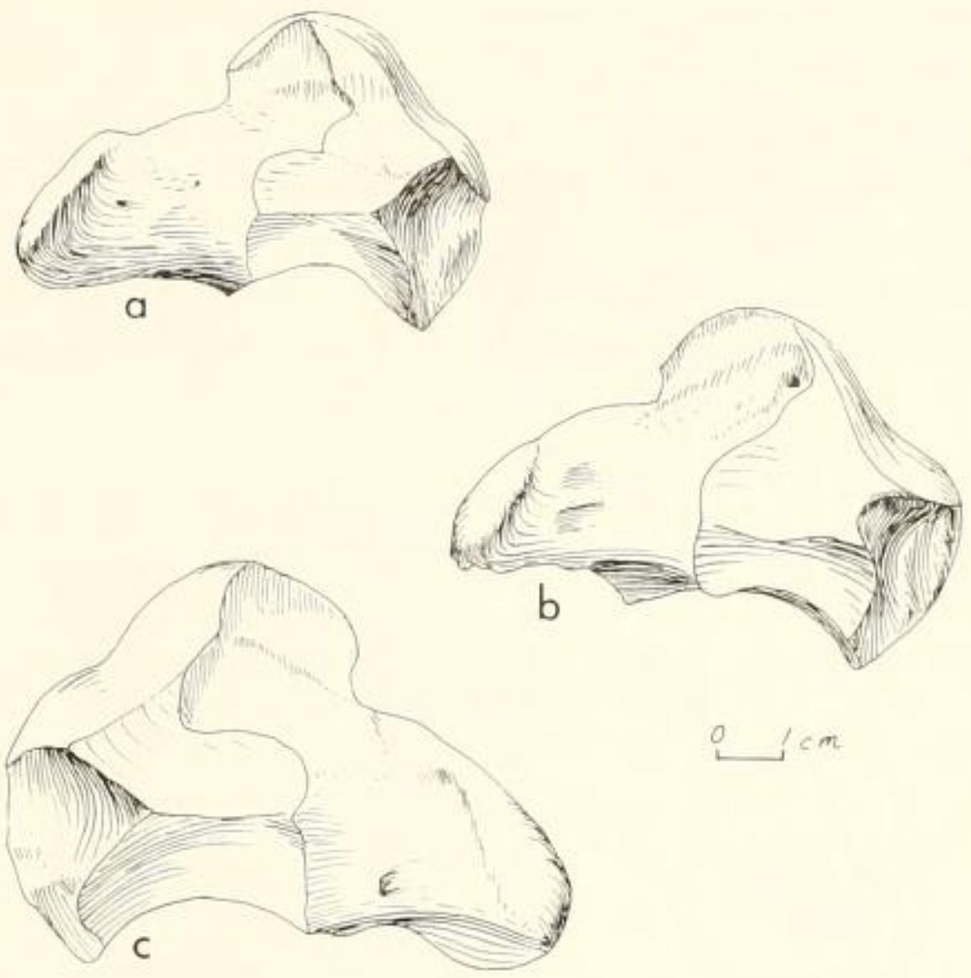

Fig. 10: Carpal 3, medial view. a, *Plesiaceratherium fahlbuschi,* left, middle Miocene, Sandelzhausen. b, *"Aceratherium" tetradactylum,* left, middle Miocene, Sansan. c, *Plesiaceratherium mirallesi,* right, early Miocene, Vallés-Penedés.

Carpal 4 (Unciform) (Fig. 11, Table 10): All primitive Aceratherini have a large articular facet for the metacarpal V. Even in the few forms where this bone is reduced, this facet may persist until the definite loss of the last rudiment. This facet is strongly concave in dorsovolar direction and shows as an odd feature an extension around the corner to the lateral side in *P. gracile* and in some specimens of *P. fahlbuschi.* In *"Ac." tetradactylum, A. simorrensis* and *A. incisivum,* this facet is separated from the metacarpal-IV-facet by a broad groove that is always absent in *Plesiaceratherium.*

The proximal ulnar facet is cylindrically convex and has an appendix that projects laterally from its backside. It is very variable but never attains the metacarpal-V-facet. It is concave where it existst as in *"Ac." tetradactylum.* The metacarpal-IV-facet is constant in width in *P. gracile*, whereas it is broadened in front in *P. fahlbuschi* and *P. mirallesi* as in *"Ac." tetradactylum.* Its transverse curvature is strongly convex, steeply deflected medially to the metacarpal-III-facet.

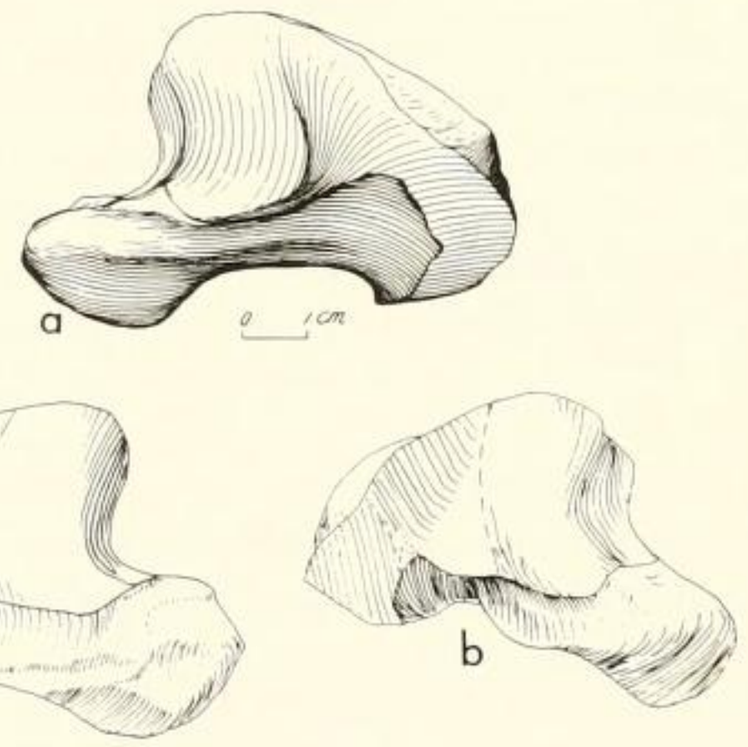

Fig. 11: Carpal 4, distal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang, right. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, left. c, *"Aceratherium" tetradactylum*, middle Miocene, Sansan, left.

Table 9.
CARPAL 3 OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	dorsal surf. of bone height	dorsal surf. of bone width	max. height of bone	max. depth of bone	metacarpal-III -facet width	metacarpal-III -facet depth
P. gracile ex. 1	31	36	-	-	31	36
ex. 2	33	39	-	-	-	-
P. fahlbuschi f. nr. 38-P	-	42	54	80	32	43
f. nr. 201	30	35	48	-	29	35
f. nr. 2160	27	40	48	74	32	37
f. nr. 219	31	36	50	74	31	38
f. nr. 6-M	32	39	48	-	33	-
f. nr. 3053	35	46	56	(79)	38	-
P. mirallesi type ser.	36	41	60	91	37	47
"Ac." tetradactylum min.	31	37	51	79	35	41
Sansan (Mus. Paris) max.	39	45	64	90	42	47