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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] *Plesiaceratherium gracile* YOUNG, 1937 [illegible] *Brachypotherium* [illegible] *Plesiaceratherium* [illegible] *Dromoceratherium* [illegible] *Plesiaceratherium* [illegible]

[illegible] *Plesiaceratherium* [illegible]:

P. gracile YOUG, 1937

P. platyodon (MERMIER, 1895)

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

P. fahlbuschi (HEISSIG, 1972)

[illegible] *"Aceratherium" tetradactylum* (LARTET, 1839) [illegible] *Alicornops simorrensis* (LARTET, 1848) [illegible]。

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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 "*Aceratherium*" *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 *Aceratherum* 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 & Virft, 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 posteranials 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)

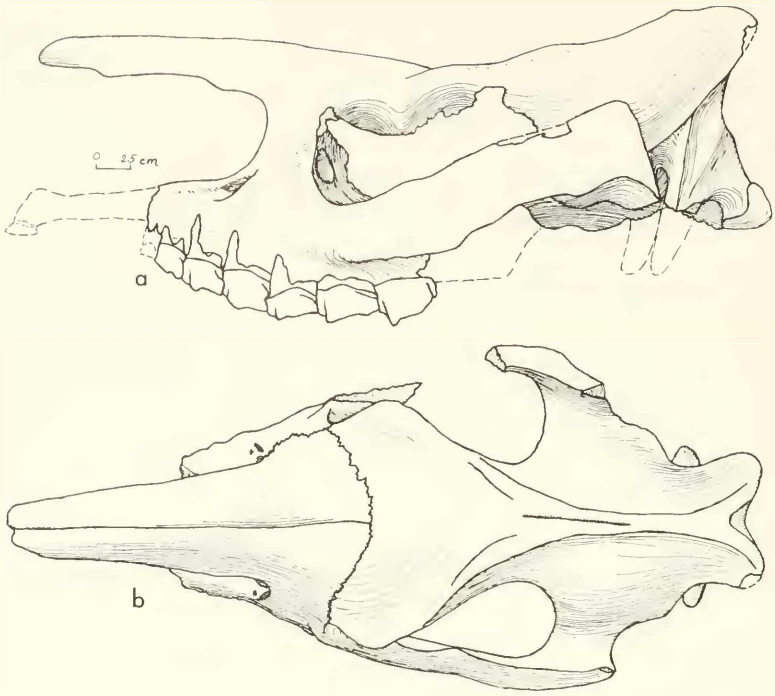

Fig. 1: *Plesiaceratherium fahlbuschi* (HEISSIG 1972) Holotype, BSP Munich 1959 II 400. a, left lateral view. b, dorsal view.

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.symph. 3003	3093	0293	type	male	female	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)

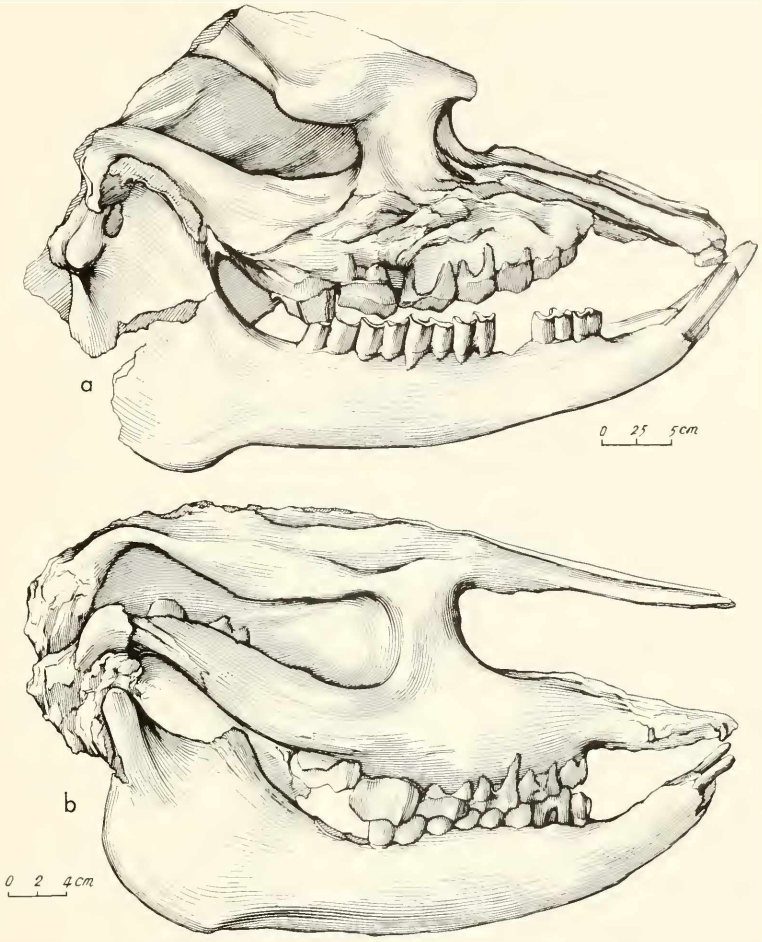

Fig. 2: *Plesiaceratherium gracile* YOUNG 1937. a, adult skull with mandible, right lateral view. b, juvenile skull with mandible, right lateral view. (Both IVPP, Beijing).

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 Rhincerotidae, 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	"*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)

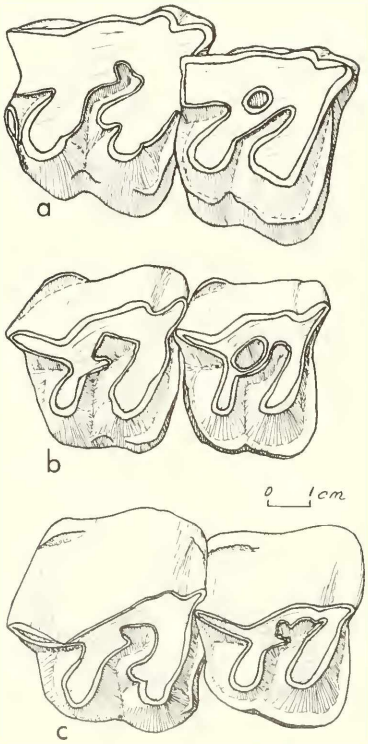

Fig. 3: Right P^4 – M^1 of *Plesiaceratherium*. a, c, *P. gracile*, middle Miocene, Shanwang. b, *P. fahlbuschi*, middle Miocene, Sandelzhausen, f.nr. 1572.

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." tetradactylum*		*A.simorrensis*	*A.incisivum*	
	V.6880	V.6884	401	3003	3093	type	Georgensgmünd	type l	type r	Baigneaux	male	female	type	Senck 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.

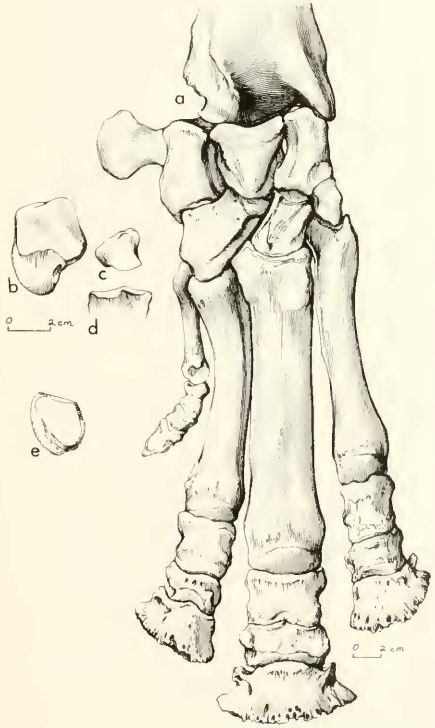

Fig. 4: *Plesiaceratherium gracile* YOUNG, middle Miocene, Shanwang. a, right fore foot. b, Carpal 1, lateral view. c, Metacarpal V, proximal view. d, Metacarpal IV, lateral view. e, *Plesiaceratherium fahlbuschi* (HEISSIG), middle Miocene, Sandelzhausen, Carpal 1, lateral view.

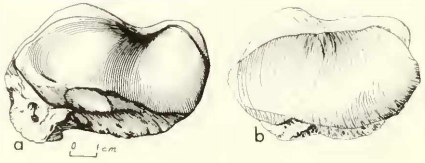

Fig. 5: Right radius, distal view, dorsal surface upside. a, *Plesiaceratherium gracile*, middle Miocene Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Voggersberg, Bavaria.

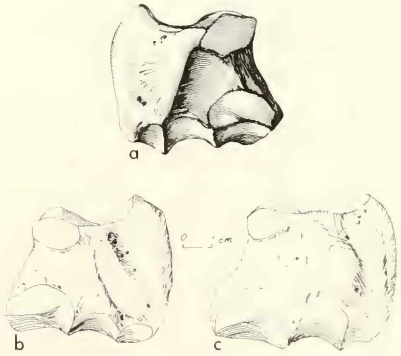

Fig. 6: Radial, laterovolar view. a, *Plesiaceratherium gracile*, middle Miocene Shanwang, left. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, Bavaria, right, BSP Munich, field nr. 475. c, "*Aceratherium*" *tetradactylum*, middle Miocene, Sansan, France, right, BSP Munich 1961 XVII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

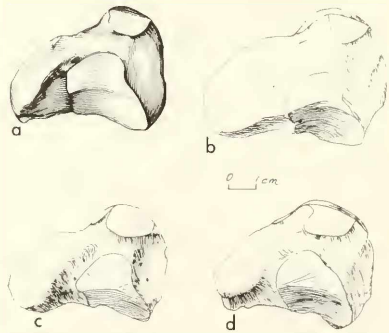

Fig. 7: Right intermedium, lateral view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium mirallesi*, lower Miocene, Can Julia. c, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen. d, *"Aceratherium" tetradactylum*, middle Miocene, Sansan.

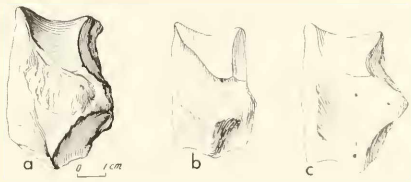

Fig. 8: Left ulnar, lateral view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen. c, *"Aceratherium" tetradactylum*, middle Miocene, Sansan.

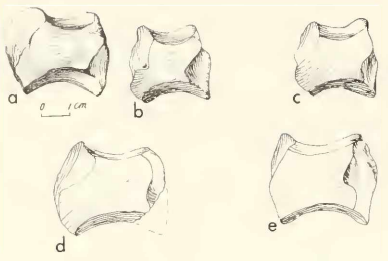

Fig. 9: Right carpal 2, lateral view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 9-L. c, same species, field nr. 21 N. d, *Plesiaceratherium mirallesi*, early Miocene, Can Julia. e, "*Aceratherium*" *tetradactylum*,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

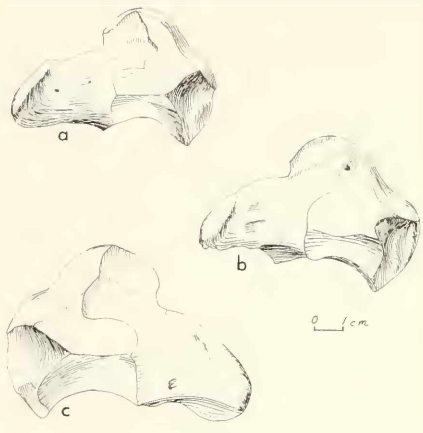

Fig. 10: Carpal 3, medial view. a, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen. b, *"Aceratherium" tetradactylum*, left, middle Miocene, Sansan. c, *Plesiaceratherium mirallesi*, right, early Miocene, Vallés-Penedés.

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.

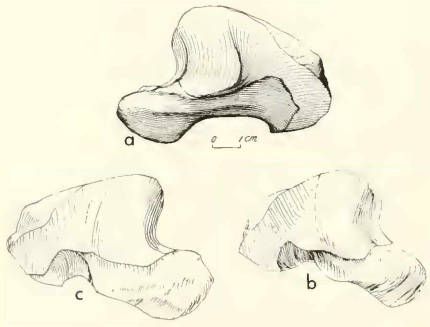

Fig. 11: Carpal 4, distal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang, right. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, left. c, *"Aceratherium" tetradactylum*, middle Miocene, Sansan, left.

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

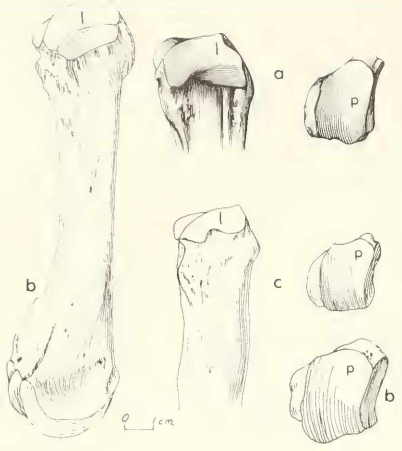

Fig. 12: Right metacarpal II, l – lateral, p – proximal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *"Aceratherium" tetradactylum*, middle Miocene, Sansan. c, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen.

This however is flat in *P. gracile*, strongly concave in *P. fahlbuschi* and slightly concave in *P. mirallesi*, as in *"Ac." tetradactylum*.

Metacarpus (Fig. 4)

In *Plesiaceratherium* the primitive four-toed foot of the Aceratherini is preserved even if the fifth metacarpal is in some respects a little more reduced than in *"Ac." tetradactylum*. There are nearly no distinctive characters except the proportions. The retention of high autopodials is a primitive feature of this genus. In the two smaller species the metapodials are exceptionally slender, in *P. gracile* a little broader and in *P. fahlbuschi* somewhat deeper.

Metacarpal II (Fig. 12, Table 11): There are some specimens of *P. gracile*, but only fragments of *P. fahlbuschi*, that allow a reconstruction of the length. A single specimen from the lower Miocene (Sables de l'Orléanais) of Chilleurs (Museum Orleans) may be referred to *P. platyodon* because it differs from *P. fahlbuschi* by its length and massive proportions distally, but it is too slender to be *P. mirallesi*.

Table 10.

CARPAL 4 OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	dorsal surf. of bone width	height	max. depth lateral	max. diagonal extension	ulnar facet width	depth
P. gracile ex. 1	56	43	48	70	31	27
ex. 2	–	41	–	–	–	–
ex. 3 right	56	46	52	69	29	28
left	55	43	–	–	32	28
P. fahlbuschi f. nr. –	58	46	54	74	31	29
f. nr. 525	55	40	52	72	30	28
f. nr. 7-C	52	40	50	63	27	25
f. nr. 686	50	40	50	68	27	29
Thannhausen, Bav.	52	41	44	62	26	23
P. mirallesi type ser.	(63)	53	–	–	34	28
"Ac." tetradactylum min.	56	46	50	70	32	27
Sansan (Mus. Paris) max.	63	49	61	74	36	35
A. simorrensis Steinheim (Senck. Mus., M 3882)	62	51	53	66	36	29

Table 11.

METACARPAL II OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	max. length (lat.)	proximal basis width	depth	shaft minimal width	depth	distal capitulum width	depth
P. gracile ex. 1	156	37	27	27	16	31	33
ex. 2	154	38	28	27	16	30	32
P. fahlbuschi f. nr. 649	(155)	33	26	31	13	(30)	(35)
f. nr. 2347	–	36	28	28	–	–	–
f. nr. 8-M	–	34	25	(30)	–	–	–
f. nr. 2318	–	35	23	29	13	–	–
P. platyodon? Chilleurs	167	35	28	32	14	35	36
"Ac." tetradactylum min.	143	42	32	33	15	34	37
Sansan (Mus. Paris) max.	156	44	33	40	18	42	42
A. simorrensis, Sansan	144	–	–	33	14	35	36
(M. Basel, Sth 353) Steinheim	139	42	28	31	15	36	34

The proximal facet has a transverse concave curvature that is medially replaced in *P. fahlbuschi* by a weak convexity that is absent in *P. gracile*. Its outline is narrow and oval in *P. gracile*.

Plesiaceratherium lacks a facet for carpal 1 whereas in *"Ac." tetradactylum* it is frequently present.

The carpal-3-facet forms with the carpal-2-facet an acute angle in front as in all Aceratherini. In *P. gracile* there is also an acute angle on the backside whereas *P. fahlbuschi* agrees with the other Aceratherini in having an obtuse angle. The carpal-3-facet is situated vertically. In *P. fahlbuschi*, however, in some specimens the facet is inclined and directed more upward as in *"Ac." tetradactylum* and younger Aceratherini. The metacarpal-III-facet is generally small and not always clearly delimited from the carpal-3-facet.

Table 12.

METACARPAL III OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	max. length	proximal basis width	proximal basis depth	width carp. 3 facet	minimal shaft width	minimal shaft depth	distal capitulum width	distal capitulum depth
P. gracile ex. 1	178	45	38	33	34	18	47	36
ex. 2	–	45	38	33	–	–	46	36
P. fahlbuschi f. nr. 1944	173	45	40	34	35	–	47	33
P. mirallesi type ser.	–	53	48	40	–	–	–	–
"Ac." tetradactylum min.	167	51	41	36	41	17	48	38
Sansan (Mus. Paris) max.	175	56	48	39	44	19	53	45
A. simorrensis Steinheim								
(Mus. Basel Sth 350)	148	44	36	31	34	14	45	34
(Senck. Mus. M 3847)	153	50	44	31	39	17	48	40

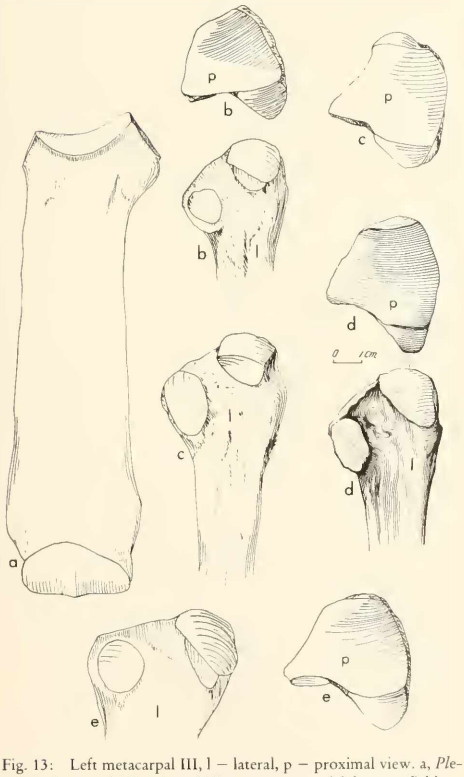

Fig. 13: Left metacarpal III, l – lateral, p – proximal view. a, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 1944, dorsal view. b, same species, field nr. 10-N. c, *"Aceratherium" tetradactylum*, middle Miocene, Sansan. d, *Plesiaceratherium gracile*, middle Miocene, Shanwang. e, Opposite side, *Plesiaceratherium mirallesi*, early Miocene, Can Julia.

The shaft is more strongly curved than in *"Ac." tetradactylum*. The distal trochlea has a normal form in *P. fahlbuschi*: on both sides of a weak keel the side parts of the roll, standing at different levels, are slightly constricted. In *P. gracile* the keel and the constrictions are reduced. The keel is replaced by a median slope that separates the two cylindrical halves of the roll.

Metacarpal III (Fig. 13, Table 12): The situation of the proximal facets in relation to the shaft axis is different in the species of *Plesiaceratherium*. In the smaller species the proximal facets have shifted a little laterally compared with *P. mirallesi* and other Aceratherini. The medial facet for metacarpal II is generally in one line with the medial edge of the shaft. In *P. fahlbuschi*, however, it is set back a little laterally. The high point between the proximal facets is situated about the prolongation of the lateral edge of the shaft. In *P. fahlbuschi* it deviates a little laterally and in *P. mirallesi* medially.

The proximal main facet for the carpal 3 is very deep, especially in *P. mirallesi*. Its hind part is turned medially without changing the curvature.

The carpal-4-facet in *P. gracile* and *P. fahlbuschi* is narrow and not curved transversely as in *"Ac." tetradactylum*. In *P. mirallesi* it is very broad. The dorsal metacarpal-IV-facet is in all species considerably narrower than in *"Ac." tetradactylum*. In *P. mirallesi* it is also shortened and shifted dorsally.

The dorsal surface bears two flat rugosities proximally, the tuberositas os metacarpi. They are separated by a wide depression in *P. gracile* and *P. mirallesi* whereas in *P. fahlbuschi* they are united or separated only by a narrow groove. In *"Ac." tetradactylum* the tuberosities often project far forward.

A rugosity that crosses the front side of the shaft diagonally farther down lies within the variability of most primitive

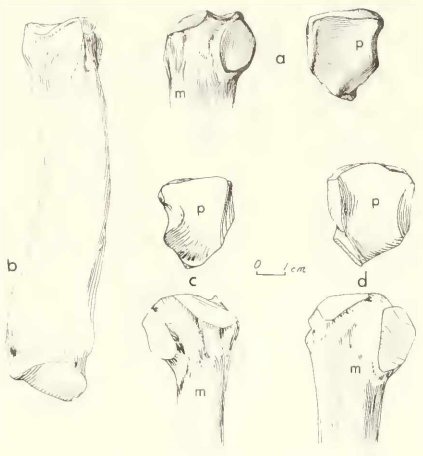

Fig. 14: Metacarpal IV, m – medial, p – proximal view. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang.- b, *Plesiaceratherium fahlbuschi*, right, middle Miocene, Sandelzhausen, field nr. 5-F, dorsal view. c, Same species, left, field nr. 476. d, *"Aceratherium" tetradactylum*, right, middle Miocene, Sansan.

Aceratherini. It is always present in *P. gracile* but only in some specimens of *P. fahlbuschi*.

The distal trochlea is sharply curved and reaches with its dorsal end a vertical inclination in *P. fahlbuschi*. In *P. gracile* it exceeds even the vertical and is slightly turned upwards. In *"Ac." tetradactylum* it does not reach a vertical plane.

Metacarpal IV (Fig. 14, Table 13): This long slender bone in *Plesiaceratherium* is more strongly curved in the proximal half than in the distal, whereas in *"Ac." tetradactylum* the curvature is constant. The proximal facet for the carpal 4 has in all primitive Aceratherini the same pentagonal outline, modified more or less by a notch avove the lateral metacarpal-V-facet. Behind the notch or point the facet is bent down strongly in *P. fahlbuschi*, less in *P. gracile*, whereas in other genera this sloping is even less marked. The metacarpal-V-facet is small and lies dorsally in *P. gracile* and farther back in *P. fahlbuschi*.

The two medial facets for the metacarpal III form a less obtuse angle in *P. gracile* than in *P. fahlbuschi* and *"Ac." tetradactylum*. The volar one is often not in contact with the proximal facet, but the variability is very high in this character. The same is true for the inclination of the dorsal matacarpal III facet.

Above the laterovolar edge of the distal trochlea there is a thickened pillar that is higher in *Plesiaceratherium* than in *"Ac." tetradactylum*.

Metacarpal V (Figs. 4c, 15, Table 14): As in all organs affected by reduction, the variability of this bone is very high. In *P. gracile* the proximal base is displaced a little laterally, a character found only in one specimen of *P. fahlbuschi* and variable in *"Ac." tetradactylum*. It is bent to the rear in both species of *Plesiaceratherium*, but less than in *"Ac." tetradactylum*. The proximal facet is sharply angled in *P. gracile*, more or less sharp in *P. fahlbuschi* and curved in *"Ac." tetradactylum*. Size and proportion of the medial metacarpal IV facet are variable in all species.

Table 13.

METACARPAL IV OF MIDDLE MIOCENE ACERATHERINI

	max. length	proximal basis width	proximal basis depth	minimal shaft width	minimal shaft depth	distal capitulum width	distal capitulum depth
P. gracile ex. 1	148	27	33	20	16	31	33
ex. 2	–	27	33	22	16	31	33
P. fahlbuschi f. nr. 2945	152	29	34	26	16	30	33
f. nr. 568	141	25	30	25	14	30	31
f. nr. 5-F	136	26	30	26	15	33	31
"Ac." tetradactylum min.	142	31	40	29	17	35	38
Sansan (Mus. Paris) max.	146	37	41	32	20	39	42
A. simorrensis Steinheim							
(Mus. Basel, Sth 354)	132	29	37	28	15	37	32
(Senck. Mus. M 3874)	143	35	36	32	15	37	37

Table 14.

METACARPAL V OF MIDDLE MIOCENE ACERATHERINI

	max. length of bone	proximal basis width	proximal basis depth	minimal shaft width	minimal shaft depth	distal capitulum width	distal capitulum depth
P. gracile ex. 1	74	24	23	14	11	22	19
ex. 2	73	22	19	12	10	22	20
ex. 3	68	23	20	13	11	20	17
P. fahlbuschi f. nr. 576	(71)	17	21	13	10	19	–
f. nr. W	–	17	28	12	7	–	–
f. nr. 11-F	–	15	18	–	–	–	–
"Ac." tetradactylum min.	68	16	21	14	10	24	20
Sansan (Mus. Paris) max.	77	20	28	18	13	28	24

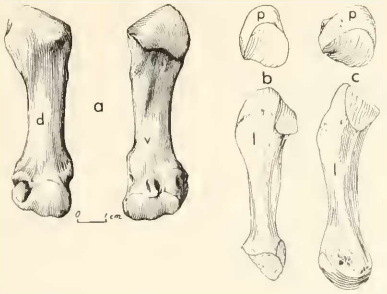

Fig. 15: Metacarpal V. a, *Plesiaceratherium gracile*, right, d – dorsal, v – volar view, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, l – lateral, p – proximal view, middle Miocene, Sandelzhausen. c, *"Aceratherium" tetradactylum*, left, l – lateral, p – proximal view, middle Miocene, Sansan.

The distal keel is weaker than in *"Ac." tetradactylum* which has the bone less reduced. The front side of the trochlea as in other metapodials ascends the highest in *P. gracile*, just reaches a vertical inclination in *P. fahlbuschi*, and is less high in *"Ac." tetradactylum*.

Tarsus (Fig. 16)

Like the carpus the tarsus is exceptionally high in *Plesiaceratherium* and slender in its smaller species, the hind foot of the larger one being nearly unknown. As in Rhinocerotidae generally, the hind foot shows mainly characters of family grade. Only some rare characters are of specific value. A lateral shifting of the matatarsus against the tarsus as in *Chilotherium* is not known in *Plesiaceratherium*.

Astragalus (Fig. 17, Table 15): Corresponding to the high and narrow proportions of the astragalus its fibular facet is inclined steeply and not transversly curved in *P. gracile*. In *P. fahlbuschi*, where the astragalus is not so high, the facet is less inclined and transervsely concave showing that the fibula contributed to body support. In *P. mirallesi* and *"Ac." tetradactylum* this condition is even more accentuated. In most primitive Aceratherini there is a gap formed by the hind margin of the trochlea, the fibula facet and the proximal calcaneal facet. It is present but variable in size in *P. fahlbuschi*, but absent in *P. gracile*.

The configuration of the three calcaneal facets is very variable. The second, sustentacular, facet may fuse with the third, the distal, in *"Ac." tetradactylum* sometimes, in *P. fahlbuschi* rarely, and not in *P. gracile*. A contact of this facet with a posterior cartilaginous seam occurs in one specimen of *P. gracile*.

The second facet seldom unites with the first one in *P. fahlbuschi* and *"Ac." tetradactylum*. It comes in contact with the base of the postero-medial rugosities in single specimens of all *Plesiaceratherium* species. The angle formed between the calcaneal facet 1 and the hind margin of the trochlea is generally acute, but obtuse in some specimens of *P. fahlbuschi*.

Both distal facets include an obtuse edge in *P. gracile* that may be flattened or replaced by a groove in some specimens of *P. fahlbuschi* and *P. mirallesi*. It is generally flattened and disappearing in *"Ac." tetradactylum*. This edge or boundary line may be upturned at the backside to a distally projecting point in some specimens of *P. fahlbuschi* and *"Ac." tetradactylum*. In most specimens of these species it is only very low as in *P. gracile*.

In all primitive Aceratherini the axis of the trochlea is somewhat inclined so that the collum is higher laterally than medially. The cylindrical and convex tarsal-4-facet has no transverse curvature. Behind, it is a little deflected distally to take part in the formation of the weak distal point.

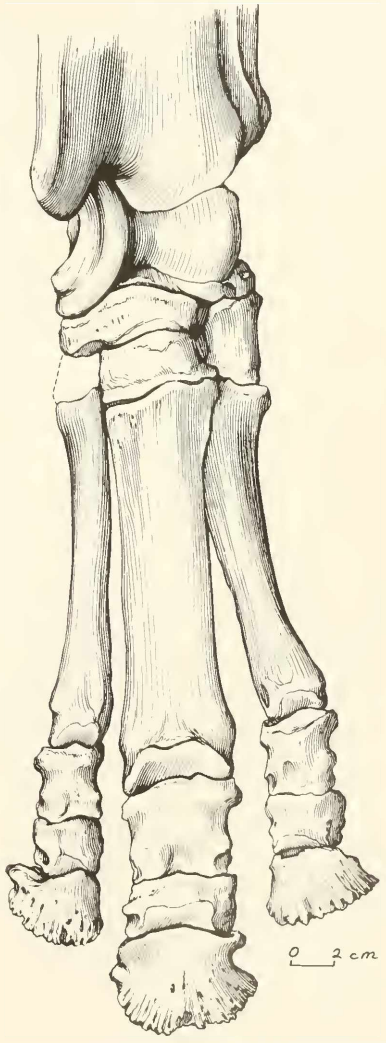

Fig. 16: *Plesiaceratherium gracile* Young, left hind foot, dorsal view, middle Miocene, Shanwang.

Table 15.

ASTRAGALUS OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	height of bone med.	height of bone lat.	width of trochlea	distal width	calcaneus facet 1 height	calcaneus facet 1 width
P. gracile ex. 1 right	57	58	58	63	39	32
left	–	59	58	62	40	33
ex. 3	57	61	62	64	38	27
P. fahlbuschi f. nr. 2235	65	60	64	67	34	32
f. nr. 3058	59	58	66	64	34	33
	58	58	68	64	39	38
	64	61	69	66	34	34
Voggersberg	58	62	70	68	33	34
P. mirallesi type ser. (Senck. Mus. M 4198)	67	–	80	–	33	47
Georgensgmünd	63	62	74	73	37	39
"Ac." tetradactylum min.	64	65	70	–	43	34
(Mus. Paris) Sansan max.	74	74	82	–	53	39
A. simorrensis Steinheim						
(Senck. Mus. M 3865)	55	57	63	64	31	33
(Senck. Mus. M 3867)	54	59	68	69	44	40

Table 16.

CALCANEUS OF MIDDLE MIOCENE ACERATHERINI

	total height	sustentacular width	depth over fac. 1	tuber calcanei width	tuber calcanei depth	collum proc. calc. width	collum proc. calc. depth
P. gracile ex. 1	111	58	52	35	57	29	49
P. fahlbuschi f. nr. 368	102	60	50	39	54	27	44
f. nr. 3125	97	58	50	38	50	28	42
f. nr. 792	100	58	51	41	53	30	47
f. nr. 99	93	55	46	38	48	31	43
"Ac." tetradactylum min.	105	67	53	39	59	29	48
Sansan (Mus. Paris) max.	113	73	60	42	61	34	55
P. mirallesi type ser.	(128)	(65)	52	46	–	36	47

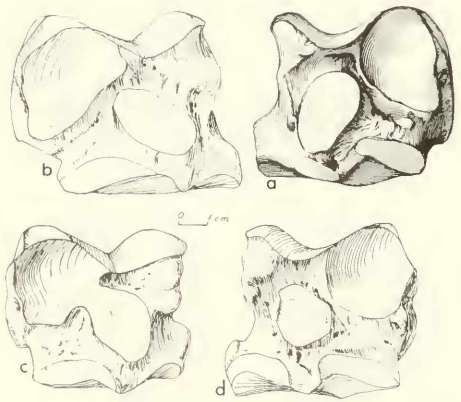

Fig. 17: Astragalus, plantar view. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang. b, *"Aceratherium" tetradactylum*, left middle Miocene, Sansan. c, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen, field nr. 3058. d, Same species and locality, field nr. 2235, right.

Calcaneus (Fig. 18, Table 16): *Plesiaceratherium gracile* and *P. fahlbuschi* agree well in the characters of the calcaneus. Even *"Ac." tetradactylum* differs only slightly. The processus calcanei is longer in *Plesiaceratherium* than in other Aceratherini. Its proximal tuber calcanei forms a dorsally projecting point, surmounted by a helmet-shaped hump farther back that is situated medial from the middle. From the point, situated on the epiphyseal suture, there are on both sides rugosities along the suture. The lateral ones are confluent with the rugosities of the backside in *P. gracile*, but only in some specimens of *P. fahlbuschi*. The stronger medial rugosities end in *P. gracile* at their junction with the medioplantar edge of the tuber; in *P. fahlbuschi* they gradually merge with the posterior rugosities.

The sustentaculum is rather thick and projects with a ledge dorsally and medially over the sustentacular facet. The sulcus muscularis is united in *P. gracile* with a long groove that extends distally to the medial incision of the tarsal-4-facet. In *P. fahlbuschi* this groove is situated farther back and not united with the sulcus. The distal end of the rough backside is marked by a thick tuberosity of varying shape.

The occurrence of small facets for the tibia and fibula is not constant. In *P. gracile* both are present, in *P. fahlbuschi* a fibular facet is frequent and a tibial facet is rarely developed. Behind the fibular facet there is a hollowed horseshoe-shaped process that is very strong in *Plesiaceratherium* when compared with other Rhinocerotidae.

The three facets for the astragalus include a rough surface. The variable distal prolongation of the facet I is sunk a little in this surface. This facet in *P. fahlbuschi* passes dorsally over the facet 2 sometimes. In *"Ac." tetradactylum* this character is found in nearly all specimens. In *P. gracile* it is unknown. The tarsal-4-facet has a medial pit in all primitive Aceratherini. This pit is medially opened by an incision in *P. gracile*. In *P. fahlbuschi* the incision is less deep, so that the medial rim is partly preserved. *"Ac." tetradactylum* has only a slight depression and resembles the more modern Aceratherini in this respect.

Central (Navicular) (Fig. 19, Table 17): This bone is variable in shape and inclination of the distal facets, but hardly in proportions. It retains the normal Aceratherini type being nearly as broad as deep, whereas in *"Ac." tetradactylum* this bone is semilunar in shape and very narrow.

The proximal astragalus facet is saddle-shaped, but the transverse convex curvature in *P. fahlbuschis* weaker than in *"Ac." tetradactylum* and even weaker in *P. gracile*. Its outline is rhombic, corresponding with the general outline of the

Table 17.

CENTRAL IN LOWER AND MIDDLE MIOCENE ACERATHERINI

	max. width	max. depth	dorsal height	plantar height	tarsal 3-facet width	tarsal 3-facet depth
P. gracile ex. 1 right	45	47	22	26	32	37
left	45	47	21	26	30	35
ex. 3	–	–	(21)	27	–	38
P. fahlbuschi f. nr. 40-M	45	51	21	24	32	35
f. nr. 3060	45	49	19	23	32	32
f. nr. 2986	47	51	21	(24)	32	34
f. nr. 2554	38	42	18	19	32	33
f. nr. 2354	48	47	21	25	35	31
f. nr. 36-P	47	47	22	24	32	34
f. nr. 44-N	36	43	21	24	28	35
f. nr. 0101	43	44	23	27	30	34
P. mirallesi type ser.	–	–	27	–	–	44
"Ac." tetradactylum min.	35	47	20	24	34	37
(Mus. Paris) Sansan max.	46	55	27	31	38	45
A. simorrensis Steinheim (Mus. Basel)	37	47	20	25	37	38

bone, with a more or less concave lateral border. The medial margin is straight, with angular edges in *P. gracile* and rounded edges in *P. fahlbuschi*. Sometimes there is a feeble notch in the backside, corresponding with a groove between the plantar rugosities. Medially from the notch, the backside is high, laterally shorter and often somewhat depressed. These features are lacking in some specimens of *P. gracile*. In *P. fahlbuschi* and *"Ac." tetradactylum* it is generally present.

On the lateral side there are two facets, both for the tarsal 4. The proximal one forms a long band that is almost vertically inclined. The distal one is confined to the posterior half of the side and faces obliquely distally. Both facets meet in a twisted edge in *P. gracile* that is more rounded in *P. fahlbuschi*. In *"Ac." tetradactylum* both facets are more or less vertical and may form only a slight convexity at their junction; the proximal band is broadened dorsally.

Distally the largest facet is that for tarsal 3. It is generally triangular with a wavy surface. In *P. fahlbuschi* there is a lateral incision so that the lateral margin is somewhat projecting distally. In *P. gracile* there is no incision, but the projection is marked. This type agrees with *"Ac." tetradactylum*.

The surface is curved around this projection in all these species, forming a flat cone with concave flanks. The posterior

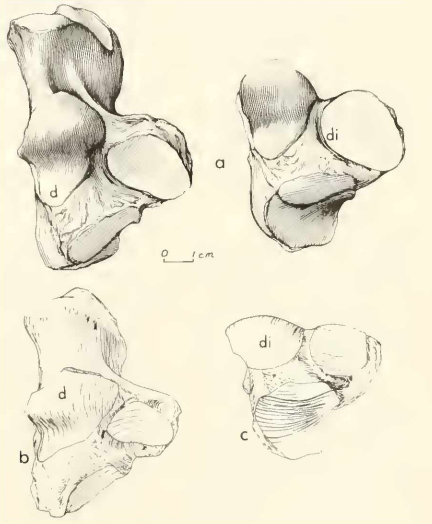

Fig. 18: Left calcaneus, d – dorsal, di – distal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 3125. c, Same species and locality, field nr. 2368.

part of the facet is long in *P. gracile*, shorter in *P. fahlbuschi* and variable in *"Ac." tetradactylum*. The tarsal-2-facet has an oval outline in *P. fahlbuschi*, whereas it is triangular in *P. gracile* and *"Ac." tetradactylum*. It is slightly convex in dorsoplantar direction and lacks a transverse curvature in *Plesiaceratherium*, whereas in *"Ac." tetradactylum* it has a weak transverse concavity and a wavy dorsoplantar curvature. The tarsal-1-facet varies much in shape and curvature. It is bent a little medially and forms an edge with the tarsal-2-facet.

The dorsal surface is more or less smooth. Near the medial edge begin some rugosities along the medial side that are very variable. They normally form a band that terminates with a backwards-projecting and bulbous tuberosity that may be flattened medially in *P. gracile* and *P. fahlbuschi*. On the backside it is limited by a vertical groove. The tuber distally bears the tarsal-1-facet in most individuals of *P. fahlbuschi* and in some of *P. gracile* and *"Ac." tetradactylum*. The groove is crossed in some specimens of *P. fahlbuschi* and *"Ac." tetradactylum* by a ledge connecting the tuber with the base of the distal tarsal-4-facet. This ledge may be somewhat swollen. In *P. fahlbuschi* there may also arise a second smaller tuber on this ledge.

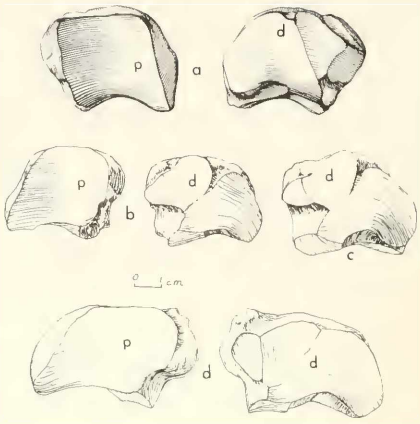

Fig. 19: Central, p – proximal, d – distal view, medial side up. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen, field nr. 264. c, Same species and locality, left, field nr. OH. d, *"Aceratherium" tetradactylum*, left, middle Miocene, Sansan.

Table 18.

TARSAL 2 OF MIDDLE MIOCENE ACERATHERINI

	max. width	max. depth	dorsal height	plantar height	diagonal width of dorsal surf.
P. gracile	15	29	14	16	21
P. fahlbuschi f. nr. 11-P	18	27	14	15	20
f. nr. 9-K	18	24	15	15	20
f. nr. 44-0	16	25	13	13	17
f. nr. 8-H	17	28	15	14	19
f. nr. 4-M	18	26	14	15	20
f. nr. 12-M	19	25	14	14	19
f. nr. 36-P	19	25	14	15	20
"Ac." tetradactylum, Sansan	17	29	15	17	20

Tarsal 2 (Mesocuneiform) (Fig. 20, Table 18): This small bone forms a narrow triangle, its oblique medially-directed dorsal surface forming an acute angle with the lateral side. In *P. fahlbuschi* the dorsal side is less oblique than in *P. gracile*. In both species the bone is narrower and deeper than in *"Ac." tetradactylum*. The proximal facet is concave in dorsoplantar direction. The transverse curvature is feeble and in *P. gracile* is totally absent. In *P. fahlbuschi* it changes from convex to concave whereas in *"Ac." tetradactylum* it is convex. In contrast to *"Ac." tetradactylum*, there is but one medial facet that is situated far back and forms a sharp rectangular edge with the proximal facet. It has an approximately semicircular outline and is slightly concave in both species as well as in *"Ac." tetradactylum*. On the lateral side the facet for tarsal 3 forms a narrow band along the proximal facet that broadens slightly to the rear. In *P. fahlbuschi* and *"Ac." tetradactylum* the facet is shorter and restricted to its hind part. The distal facet is transversely convex whereas the curvature in dorsoplantar direction is inconstant or lacking. A convex deflection medially that occurs in *"Ac." tetradactylum* is absent in *Plesiaceratherium*. The dorsal surface is lower than the hind point. It is rugose and ends medially with a flat tuberosity that may be more prominent in some specimens of *P. fahlbuschi*.

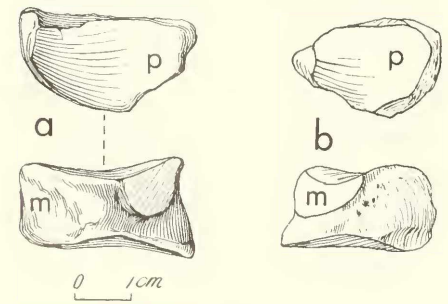

Fig. 20: Tarsal 2, p – proximal, m – medial view. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen.

Tarsal 3 (Entocuneiform) (Fig. 21, Table 19): The bone is a triangular block, relatively higher than in *"Ac." tetradactylum* and most other Aceratherini, with a lateral notch that is less deep than in other tribes of rhinoceroses and even than in some other Aceratherini. The proximal facet forms a very flat funnel-like concave triangle with the centre of the funnel in the shallow notch. The notch is not deeper than the notch of the bone itself, so that there is no synovial pit. The backside of the facet is cut off obliquely by the plantar tarsal-4-facet in *P. gracile*. In *P. fahlbuschi* and *"Ac." tetradactylum* this form occurs too, but in most specimens the facet is cut off more transversely.

On the medial side there are three facets. The proximal one for the tarsal 2 is short and broad, situated far back in *P. gracile*. In *P. fahlbuschi*, as in *"Ac." tetradactylum*, it is longer and narrower and extends farther forward. The two distal facets for the metatarsal II are widely separated and circular in outline, forming sharp edges with the dorsal facet. The dorsal one is vertical and slightly concave, the plantar one planar and bent slightly downwards and to the rear. Laterally there are two facets for the tarsal 4. The proximal one is situated far back and is inclined at an angle of about 45° in *P. gracile* and *P. fahlbuschi*. In *"Ac." tetradactylum* and ex. 3 of *P. gracile* it is somewhat steeper. The distal facet in front of the lateral side is vertical and somewhat concave. It may form with the distal facet a small oblique triangle that may have contacted the metatarsal IV. It is known only in *P. fahlbuschi*. Both lateral facets are semicircular in *P. gracile*, considerably higher in *"Ac." tetradactylum* and variable in *P. fahlbuschi*.

The distal facet is nearly planar with a slight dorsoplantar concavity and a transverse convexity. The notch is more marked than on the proximal facet. There are no differences separating the species. The dorsal surface is roughened and bears a proximally directed ledge which increases medially. In one specimen of *P. gracile* and some of *"Ac." tetradactylum* it is medially enlarged to form a projecting tuberosity.

Tarsal 4 (Cuboid) Fig. 22, Table 20): The carpal 4 is rich in valuable characters, especially the shape and outline of the proximal and distal facets as well as the plantar tuberosity. It

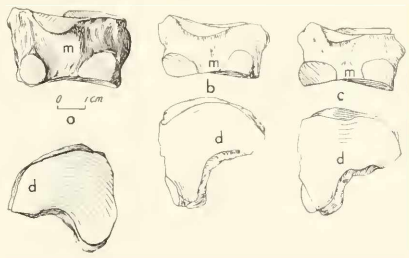

Fig. 21: Tarsal 3, d – distal view, m – medial view, front side up. a, *Plesiaceratherium gracile*, left above and right below, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen, field nr. 13-P. c, same species and locality, field nr. 1967 M.

is high and narrow in front, broad and even higher behind. The dorsal surface is nearly rectangular. It shows in its upper half a somewhat deepened scar that is situated medially in *P. gracile* and near the middle in *P. fahlbuschi*, where it may be flat or even project somewhat. In *"Ac." tetradactylum* it is absent. Deep on the dorsal surface there are two small tuberosities, that may lack in single specimens of *P. fahlbuschi*. The medial one is directed dorsally and the lateral one laterally where it continues to the irregular rugosities on the dorsal half of the lateral surface. These rugosities may be bordered proximally by a narrow groove, running backwards and disappearing gradually. Behind they are separated from the plantar tuber by a deep notch that extends downward behind the distal facet.

The plantar tuber is massive, expanded laterally and to the rear but not very much distally. In *P. gracile* and *"Ac." tetradactylum* its distal component is even smaller than in *P. fahlbuschi*. It is generally oval-shaped and flattened laterally. Above its main distal point there may be a groove on the lateral plate separating two upper tubercles, the lateral one pointing upwards and the plantar one to the rear. This point is placed higher in *P. fahlbuschi* than in *P. gracile*. The deep groove separating the tubercle from the central facet is crossed by a

Table 19.

TARSAL 3 OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	max. width	max. depth	dorsal height	plantar heigth	lateral depth to notch	plantar width to notch
P. gracile ex. 1 right	39	42	23	25	20	11
left	39	40	23	25	20	13
ex. 3	(38)	41	23	25	19	15
P. fahlbuschi f. nr. 13-P	39	42	20	22	22	13
f. nr. 67-M	39	40	21	22	21	14
f. nr. 382	36	38	19	-	22	14
f. nr. 2742	37	42	18	24	20	15
f. nr. 13-K	34	36	21	19	22	14
f. nr. 3184	36	40	21	20	22	17
f. nr. 1864	37	37	20	-	23	17
f. nr. 554	37	37	21	21	22	16
"Ac." tetradactylum min.	42	42	23	21	20	12
Sansan (Mus. Paris) max.	47	49	27	31	26	20
P. mirallesi type ser.	-	-	28	-	24	20

low ridge in *P. fahlbuschi* that is high and strong in *P. gracile*. These elements are similarly developed in *"Ac." tetradactylum* but more variable.

The proximal facets for the astragalus and calcaneus form one unbroken plane that is slightly inclined medially. It is divided only by a shallow groove that may occasionally be absent. In *"Ac." tetradactylum* the facets are slightly angled and in *A. simorrensis* considerably angled. In *A. simorrensis* only the median groove is replaced by an obtuse edge. The posterior margin is rather low when compared with *"Ac." tetradactylum*, both facets being deflected together, whereas in *"Ac." tetradactylum* there is no flexion. Laterally the calcaneus facet is strongly convex with a narrow deflected rim that broadens behind. It is broader and sharply deflected in *P. fahlbuschi* and *A. simorrensis* whereas it is short in *P. gracile* and nearly lacking in *"Ac." tetradactylum*. Except for its plantar deflection, it is concave in dorsoplantar direction, as in all Aceratherini.

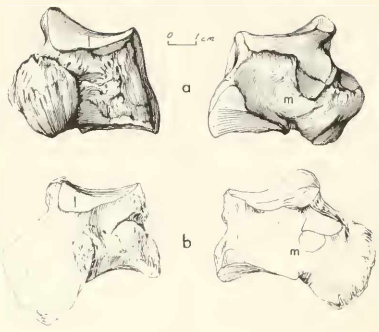

Fig. 22: Right tarsal 4, l – lateral view, m – medial view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, field nr. GR, middle Miocene, Sandelzhausen.

Table 20.
TARSAL 4 OF MIDDLE MIOCENE ACERATHERINI

	dorsal surface height	dorsal surface width	max. height	max. width	max. depth	distal facet width	distal facet depth
P. gracile ex. 1 right	39	29	48	39	54	29	30
left	38	29	47	38	57	29	29
P. fahlbuschi f. nr. 3270	38	29	51	34	61	26	33
f. nr. 2974	36	28	51	39	62	26	32
f. nr. 600	37	26	49	37	58	23	30
f. nr. 545	34	27	45	32	57	–	30
f. nr. Gr	35	29	53	35	58	25	29
f. nr. 066	34	27	46	34	52	22	27
"Ac." tetradactylum min.	39	33	49	52	58	28	32
Sansan (Mus. Paris) max.	45	42	59	64	69	34	37
A. simorrensis Steinheim 364	34	38	46	38	52	31	34
(Mus. Basel) Sth 365	34	40	46	40	56	29	33
P. mirallesi Georgensgmünd	41	–	–	–	66	–	36

On the medial side there is a narrow band-shaped facet proximally that continues behind in a broad spoon-shaped appendix that is sharply angled and deeply concave in its upper part. The lower part is expanded and directed upwards and slightly inclined medially. In *P. fahlbuschi* this appendix is narrower proximally and may rarely separate from the proximal band. In *"Ac." tetradactylum* it is very variable including both extremes. The medial rim of this facet forms a sharp rectangular edge with a semicircular and small facet for the tarsal 3 that faces distomedially. It is very short in *P. gracile*, a little longer in some specimens of *P. fahlbuschi* and variable in *"Ac." tetradactylum*. The dorsal and distal tarsal-3-facet is vertical and simicircular in *P. gracile*. In *P. fahlbuschi* it is deeper and somewhat lower and in *"Ac." tetradactylum* it is much higher.

The distal facet for the metatarsal IV is variable in outline and curvature but not in proportions. It is as wide as deep in *P. gracile*. The depth exceeds the width in nearly all other forms: slightly in *A. simorrensis*, more strongly in *P. fahlbuschi* and very strongly in *"Ac." tetradactylum*. It is nearly even in dorsoplantar direction and may be slightly concave. Its transverse curvature changes from a feeble concavity medially to a strong convex deflection laterally, sometimes again followed by a concave marginal basin. In some specimens of *"Ac." tetradactylum* the convex curvature covers the entire facet.

METATARSUS

Metatarsal II (Figs. 16, 23, Table 21): Both species of *Plesiaceratherium* have high and slender metatarsals. In *P. gracile* the proximal base and the shaft are a little deeper than in *P. fahlbuschi* in which, however, they are a little broader. This difference is even clearer in the shape of the proximal facet. The proportions of *"Ac." tetradactylum* are intermediate between these two types. Therefore, the distance of the lateral facets for the metacarpal III is wider in *P. gracile* than in *P. fahlbuschi*. In *"Ac." tetradactylum* the variability covers both types.

The medial tuber supports the tarsal-1-facet in *P. gracile*, whereas in *P. fahlbuschi* (as in other Aceratherini) the tuber is separated from this facet by a groove. The proximal tarsal-2-

facet is generally cylindrical and concave without dorsoplantar curvature. Its outline is deeply oval but very variable. One specimen of *P. fahlbuschi* shows a dorsally shortened facet (Fig. 23c).

The lateral facets are both divided into a proximal part for the tarsal 3 and a distal one for the metatarsal III. The dorsal facet is separated from the proximal one and shows no clear separation of the two parts. The plantar one is nearer to the proximal facet or may come in contact with it (Fig. 23b). Its proximal and distal halves form an angular edge that is more acute in *P. gracile* and less acute and somewhat variable in *P. fahlbuschi*. In other primitive Aceratherini this edge is never developed, but it is present in some modern forms.

The backside of the bone is rough proximally in *Plesiaceratherium;* in other Aceratherini it is smooth. Its hind edge in *P. gracile* is longer than in *P. fahlbuschi*. Above the middle of the trochlea there rises a keel on the backside in *P. gracile* that is replaced by a scar in *P. fahlbuschi* and *"Ac." tetradactylum*. The lateral edge is interrupted far distally as in most primitive Aceratherini. The distal capitulum shows no special characters. Its dorsal margin ends below the vertical inclination.

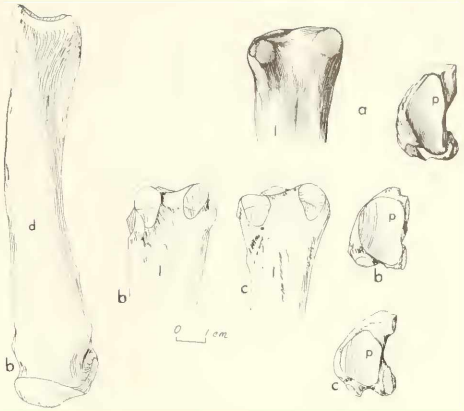

Fig. 23: Right metatarsal II, l – lateral, p – proximal view, dorsal side up, d – dorsal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi,* middle Miocene, Sandelzhausen, field nr. 2367. c, same species and locality, field nr. 12-K.

Table 21.

METATARSAL II OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	max. length	proximal width	proximal depth	minimal shaft width	minimal shaft depth	distal capitulum width	distal capitulum depth
P. gracile ex. 1 right	147	22	34	17	19	25	31
left	146	23	35	17	19	26	32
P. fahlbuschi f. nr. 2367	143	21	31	17	17	25	30
f. nr. 2338	131	18	32	23	–	–	–
f. nr. 3037	(153)	21	34	21	18	–	–
"Ac." tetradactylum min.	131	24	33	23	17	31	36
Sansan (Mus. Paris) max.	141	28	37	30	23	37	41
A. simorrensis Steinheim	144	26	36	25	22	32	35
P. mirallesi type ser.	154	(28)	47	(17)	(30)	–	43

Metatarsal III (Figs 16, 24, Table 22): It is mainly the proportions that distinguish the third metatarsal from that of other Aceratherini, both species being nearly identical. The proximal facet is broader than deep, but more expanded backwards than in *"Ac." tetradactylum*. Its lateral notch is, corresponding with the tarsal 3, obtuse and shallow, whereas it is deep and right-angled in other Aceratherini. In *P. gracile* the angle varies somewhat. The slight curvature of the facet is, as in all Aceratherini, concave in both directions dorsally and dorsoplantar convex behind.

There are two medial facets, the posterior one being small, not completely vertical and facing some degrees more upwards. The distance between the lateral facets is somewhat shorter in *P. gracile* than in *P. fahlbuschi* which is more similar to other Aceratherini. Here the dorsal one is smaller and in contact with the proximal facet. There may occur a small intermediate stripe in between these facets, indicating a faint contact of tarsal 4 and metatarsal III. A corresponding facet was also observed in tarsal 4. As tarsal 3 shows a similar facet for metatarsal IV, there must have been some inconstancy of the serial arrangement of tarsal element in *P. fahlbuschi*.

The lateroplantar facet is somewhat deeper and more widely separated from the proximal facet. It is larger in *P. gracile* than in *P. fahlbuschi* where it is variable in size and may form the most backwards projecting point of the bone. The rough edges of the shaft end about two-thirds down the shaft. On the medial side the smooth interruption of their swelling is shorter in *P. gracile* than in *P. fahlbuschi*. In other primitive Aceratherini these interruptions mostly are even shorter. The dorsal surface shows a flat medial tuberosity as in all Aceratherini. A shallow groove, descending along the shaft from the lateral side of the tuberosity to meet the distal end of the medial swollen edge is found in specimens of both species. In other Aceratherini it may occur, but it is generally weaker and often hardly visible.

On the backside there is a pillar supporting the lateroplantar facet that is strong in *P. gracile* and weaker in *P. fahlbuschi*. It is absent in most other Aceratherini.

In both species the distal trochlea is prolonged upwards, so that it passes over the vertical to face slightly upwards. In other Aceratherini it maximally reaches a vertical inclination.

Table 22.

METATARSAL III OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	max. length	proximal width	proximal depth	minimal shaft width	minimal shaft depth	distance of lateral facets
P. gracile ex. 1 right	161	43	39	30	21	8
left	161	43	(37)	30	20	6
P. fahlbuschi f. nr. 2249	(159)	-	40	30	19	-
f. nr. 2984	167	41	(38)	-	-	-
f. nr. 7-0	-	36	34	30	18	10
P. mirallesi type ser.	170	(55)	-	43	(17)	-
"Ac." tetradactylum min.	146	42	36	36	18	10
Sansan (Mus. Paris) max.	152	47	42	39	21	15
A. simorrensis Steinheim	137	38	-	34	16	-

Table 23.

METATARSAL IV OF MIDDLE MIOCENE ACERATHERINI

	max. length	proximal basis width	proximal basis depth	proximal facet width	proximal facet depth	distal capitulum width	distal capitulum depth
P. gracile ex. 1 right	147	36	34	28	28	26	32
left	-	35	33	27	28	-	32
P. fahlbuschi f. nr. 3018	153	34	36	24	29	24	32
f. nr. 2366	145	29	33	27	24	26	31
f. nr. 30-M	-	33	32	26	31	-	-
f. nr. 220	-	27	28	21	22	-	-
f. nr. 0198	-	30	31	26	25	-	-
P. mirallesi Georgensgmünd	-	37	36	32	33	-	-
"Ac." tetradactylum min.	126	33	34	27	30	24	34
Sansan (Mus. Paris) max.	144	40	40	31	35	32	41
A. simorrensis							
(Mus. Basel, Sth 351)	119	35	35	29	31	29	31
(Senck. Mus., M 3883)	126	36	35	29	32	29	35

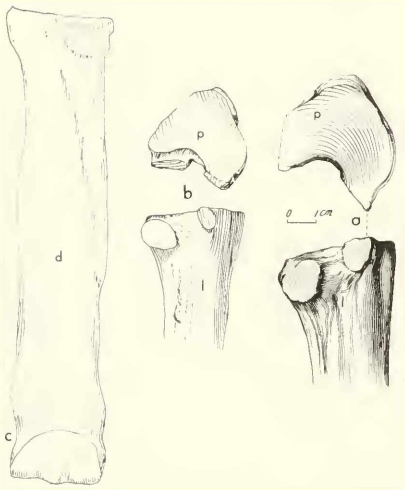

Fig. 24: Right metatarsal III, p – proximal view, l – lateral view, d – dorsal view, mediodorsal side up. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. *b*, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 2242. c. same species and locality, field nr. 2960.

Metatarsal IV (Figs. 16, 25, Table 23): Length and proportions of the distal capitulum are nearly equal in both species. The proximal base is broader than deep in *P. gracile*, and as deep as broad in *P. fahlbuschi*. The specimen from Georgensgmünd, referred to *P. mirallesi*, exceeds both species in size and has a proximal end with equal depth and width. In *"Ac." tetradactylum* the bone is shorter, broader in the shaft and deeper at the proximal and distal end.

The large swollen lateral tuberosity is not only expanded laterally but also considerably to the rear in *P. gracile* where it supports the plantar medial facet. It mostly is weaker in *P. fahlbuschi*. In both species it extends considerably downwards, whereas in *P. mirallesi* it forms only a plate-like rim, extending as far laterally and backwards as in other species, but not distally. The distal extension of this tuberosity is generally reduced during evolution in primitive Aceratherini. Often this tuberosity is divided by a groove in *"Ac." tetradactylum*. This groove is present in *P. mirallesi* and some specimens of *P. fahlbuschi*, but is absent in *P. gracile*. On the proximal and distal side of the tuberosity in *P. gracile* are found well defined scars that are known otherwise only from the most robust specimens of *P. fahlbuschi* (the proximal scar also is present in *P. mirallesi*). They are unknown in *"Ac." tetradactylum* and *A. simorrensis*.

The outline of the proximal facet is rounded in *P. gracile*. It is an irregular oval in *P. fahlbuschi* where sometimes there is a tendency to develop an incision on the lateral margin. This incision occurs also in *P. mirallesi* and *A. simorrensis*, but not in *"Ac." tetradactylum*, even if it occurs in its later relative *"Ac." bavaricum*. The facet is slightly convex in dorsoplantar direction in *P. gracile*. In *P. fahlbuschi* the curvature is a little stronger and begins to turn backwards to a slight concavity. In *P. mirallesi*, as in other primitive Aceratherini, this double curvature is fully developed. The transverse concavity in all primitive Aceratherini is more accentuated when a lateral incision is present. In these specimens the lateral margin is very high and the facet is curved conically around the incision.

The medial facets are in general widely separated. The dorsal one is semicircular and forms a rectangular edge with the proximal facet. A small intermediate facet for the tarsal 3 may occur in *P. fahlbuschi*. The plantar facet is deeper and separated from the proximal one. It is oval in outline and faces slightly downwards whereas the dorsal facet is vertical. The angle between the planes of both facets is less obtuse in *P. gracile* and *P. fahlbuschi* than in *P. mirallesi*, *"Ac." tetradactylum* and *A. simorrensis*.

The dorsomedial edge is acute and split up by a long groove that runs from the front side to the distal interruption of the rough and swollen medial edge. The edge is proximally most acute in *P. gracile*, less so in *P. fahlbuschi* and *P. mirallesi* and obtuse in other primitive Aceratherini. On the lateral side a ledge originates at the proximal tuberosity and runs distally towards the front side. It is strong in *P. gracile*, variable in *P. fahlbuschi* and weak in *P. mirallesi*. It may occur also in other Aceratherini. The distal trochlea is rather uniform.

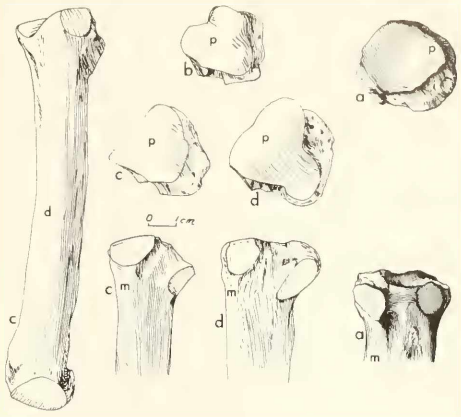

Fig. 25: Left metatarsal IV, p – proximal view, m – medial view, d – dorsal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. *b, Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 0198. c, same species and locality, field nr 2366. d, Plesiaceratherium mirallesi, middle Miocene, Georgensgmünd, Bavaria (BSP Munich A. S. 38).

CONCLUSIONS

It is mainly in the skull where the divergent lines of the Aceratherini show distinctive characters. This is true also for the incisors, but not for the cheek teeth. *Plesiaceratherium* remained primitive in most characters and died out before evolving its own modernisations. Nevertheless, there are some characters which may be derived and changed from the primitive condition of the Aceratherini stock. The small terminal nasal horn is lost (it is thought to be a common primitive feature because it is found also in the Teleoceratini). The upper incisors are somewhat reduced and have partly lost their contact with the lower ones. The lower incisors are flattened and lost their upward curvature to a certain degree.

The second and third characters are in contrast to *Mesaceratherium pauliacense* which may represent the most primitive type in these features. Its modernisations are partly shared with *"Ac." tetradactylum*. This species has rounded and more strongly curved, but nearly horizontally implanted, lower incisors that are greatly enlarged. This is a different path of incisor evolution. The upper incisors are totally lost, and this may have been preceeded by a loss of their shearing function, as in *Plesiaceratherium*. This loss is characteristic of all upper Miocene Aceratherini, except some survivours, and may have evolved independently in different lines. Besides this modern character, *"Ac." tetradactylum* has retained its terminal horn. For these reasons, *"Ac." tetradactylum* may not be included in *Plesiaceratherium*. It is also rather different from *Aceratherium incisivum*, the type species of *Aceratherium*. The creation of a new genus is necessary, but should include the detailed study of this species and its relatives.

Another, less known species, that is contemporaneous with *"Ac." tetradactylum* and therefore younger than all *Plesiaceratherium* species, is *Alicornops simorrensis* (Lartet, 1848). The skull is only partly known and it is not absolutely certain (though highly probable) that it possessed a large upper incisor. The lower incisors are strongly upturned and not extremely enlarged. The diastema is very short. In this feature, and in the retention of a shearing function of the incisors, it resembles the primitive *Mesaceratherium*.

The upper Miocene Aceratherini have shortened nasals without horns. Besides the normal type of facial skull that is slowly tapering, there occurs another type, rapidly narrowing just in front of the orbits, represented by *Aceratherium* and *Acerorhinus*. The genus *Chilotherium* belongs to the first type.

Not all species of *Plesiaceratherium* are completely known. Only the smaller two are represented by skulls and postcranials. Thus, some of their distinctive characters may only reflect their smaller sizes. These species are excluded from the ancestry of any later form by their special characters: the type of incisors is unique; the horn is lost too early for an ancestry of *"Ac." tetradactylum*, and the incisors are too small and too

straight for *A. simorrensis*. The earliest *Chilotherium* is contemporaneous in Asia. The upper Miocene forms with preorbital constriction have stronger and more curved incisors.

Plesiaceratherium platyodon is also of medium size. Its nasals are in fact unknown, but the skull is similar to the other species in front of the orbits. The braincase, however, is broadened and this is a very modern feature for a time, as early as Burdigalian. The rather long diastema is another modern feature. It is therefore not easy to believe that both characters are only the extremes of variability. So, these features exclude the species from the ancestry of *P. fahlbuschi*, even if *P. lumiarense* of intermediate age shows intermediate features in the molarisation.

The least known species is *P. mirallesi* from the Burdigalian of Vallés-Penedés. It is very large compared with other Aceratherini. It may, therefore, not be the ancestor of one of the smaller species. The upper incisor is reduced but more functional than in the other species of *Plesiaceratherium*. The lower incisors are thicker and less flattened. Their type may be intermediate between *Plesiaceratherium* and *"Ac." tetradactylum*. The angle of implantation and the form of the symphysis are unknown. If the specimens from the middle Miocene of Georgensgmünd really belong to this species this fact may argue against an evolutionary line age leading to *"Ac." tetradactylum* because the locality of Sansan is of about the same age as Georgensgmünd.

The only distinctive character of the cheek teeth, the rugosity and flattening of the outer wall of the lower premolars, is still the strongest argument for placing the species *mirallesi* into *Plesiaceratherium*. On the other hand, this feature is mostly absent in the type species *P. gracile*, where it occurs only in some specimens.

The foot structure is as homogenous within the primitive Aceratherini as the tooth structure. Nevertheless, the primitive conditions in *Plesiaceratherium* are a key to the single derived characters in other species. All later species have somewhat shorter foot bones than *Plesiaceratherium*, but in the Burdigalian there are different types of foot bones of equal length that connot be identified with *Plesiaceratherium* or other known species.

Single distinctive characters are more useful, for progressive shortening may occur in different lines. The most characteristic bone is the central of *"Ac." tetradactylum* that is half-moon-shaped instead of the rhombic form of other Aceratherini. This type is found also as early as the Burdigalian of the "Sables de l'Orleanais" in Thenay (Basel Museum) and may prove that some of the long and massive bones belong to unshortened ancestors of this species.

The only species of *Plesiaceratherium* that can be traced over a long time is *P. mirallesi*. The metatarsal IV from Georgensgmünd that is slightly younger than *P. fahlbuschi* from Sandelzhausen is not only larger, especially in the size of its proximal facet, but it has a "modern" lateral projection that is flattened and reduced distally. The change from the primitive, rather high tuberosity in *P. fahlbuschi* would be too sudden within a conservative genus. So it is more probable that this large animal is a late successor of *P. mirallesi*. The few bones represented in both the early and middle Miocene show no trace of shortening. Their size is almost the same in some specimens but in others the younger ones are smaller, indicating that the type of the species was at the upper end of the size range.

Also *P. fahlbuschi* is represented from some localities in Bavaria and France. All these single specimens are teeth or mandible fragments and most bones are rolled. These remains cover a rather short time roughly contemporaneus with the type locality of Sandelzhausen. Nevertheless, some of the dentitions exceed the size range of those from the type locality considerably.

Within the genus the well represented species *P. gracile* and *P. fahlbuschi* are the nearest relatives, as indicated by the different skull form in *P. platyodon* and the different size and incisor type in *P. mirallesi*. It is therefore important to note that in the foot bones there are faint but, at least in the metapodials also constant differences that may prove specific separation even if the size variability overlaps broadly. In the metapodials, *P. gracile* has a little deeper and *P. fahlbuschi* a little broader proximal ends.

It would be impossible yet to separate bones of the two species of the genus if mixed together. For some bones the still unsolved problem is to distinguish foot bones of *"Ac." tetradactylum* and *A. simorrensis* from the same locality (Sansan). Nevertheless, the impossibility of determining a single bone is no argument against specific separation.

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