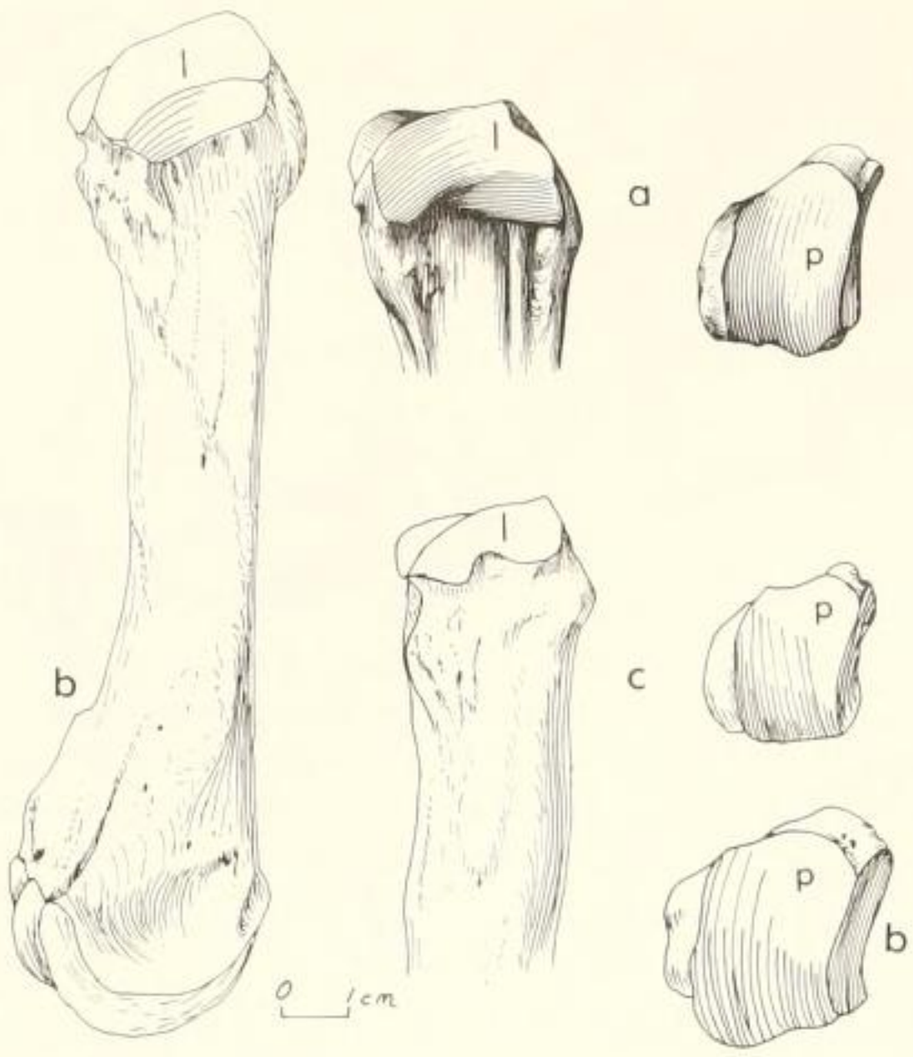

Fig. 12: Right metacarpal II, l – lateral, p – proximal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *"Aceratherium" tetradactylum*, middle Miocene, Sansan. c, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen.

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	dorsal surf. of bone height	max. depth lateral	max. diagonal extension	ulnar facet width	ulnar facet 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	proximal basis depth	shaft minimal width	shaft minimal depth	distal capitulum width	distal capitulum 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

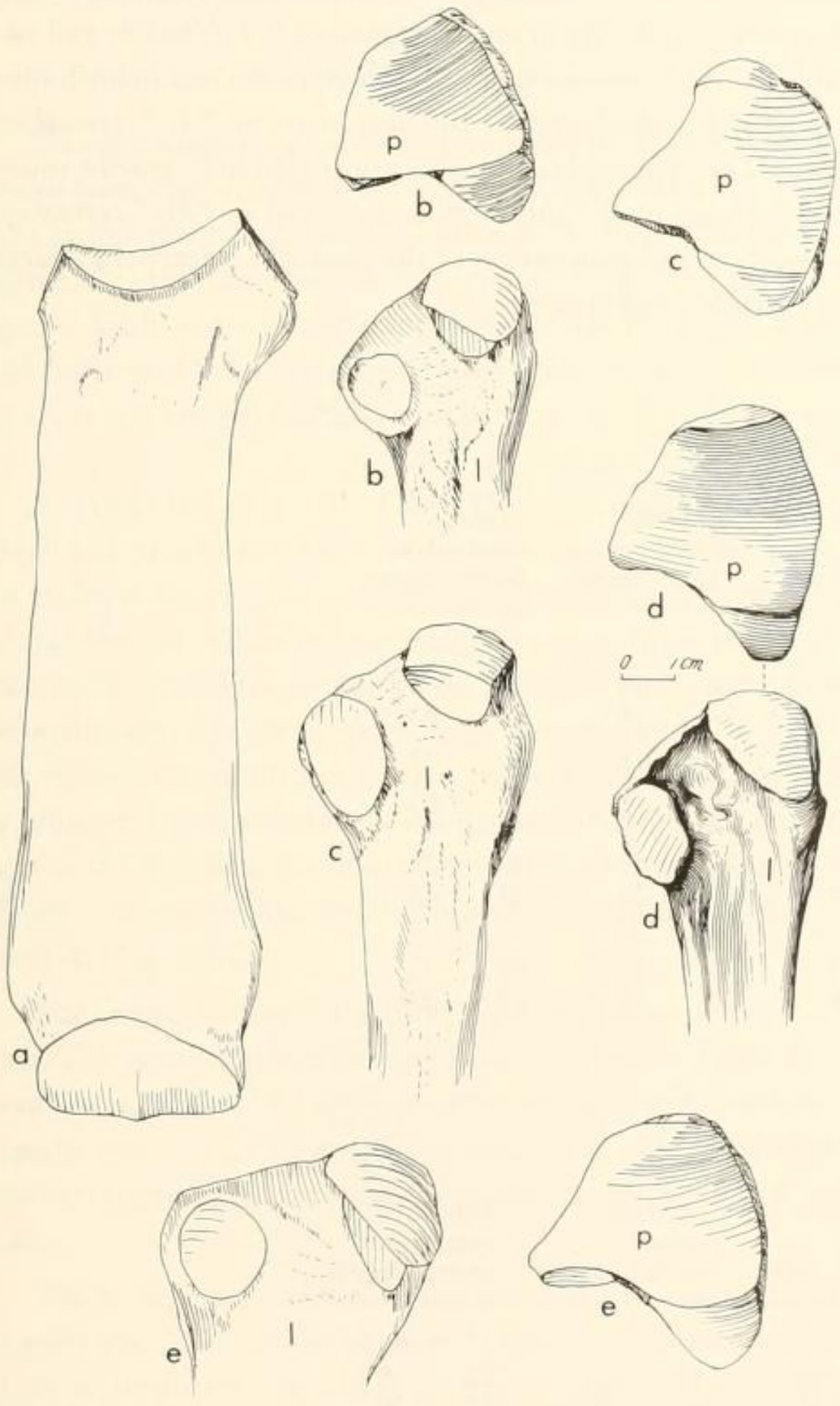

Fig. 13: Left metacarpal III, l – lateral, p – proximal view. a, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 1944, dorsal view. b, same species, field nr. 10-N. c, *"Aceratherium" tetradactylum*, middle Miocene, Sansan. d, *Plesiaceratherium gracile*, middle Miocene, Shanwang.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

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

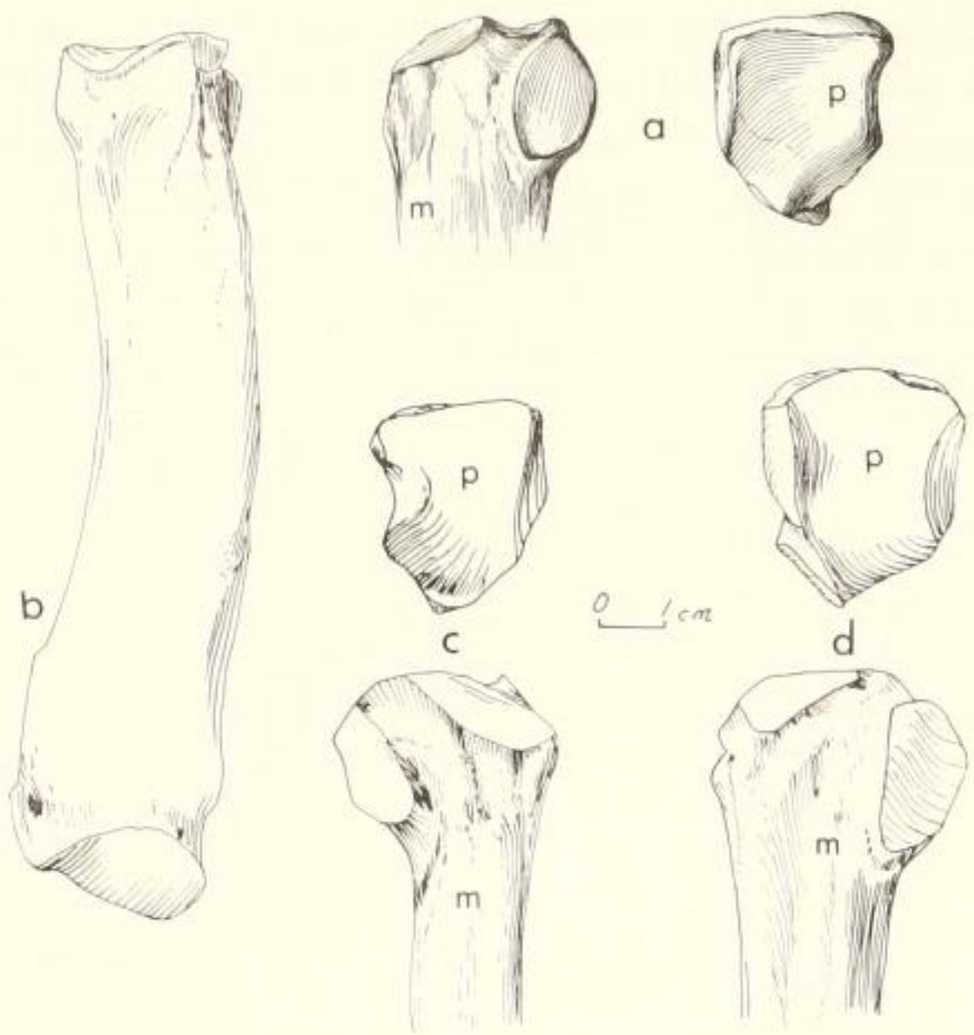

Fig. 14: Metacarpal IV, m – medial, p – proximal view. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang.- b, *Plesiaceratherium fahlbuschi*, right, middle Miocene, Sandelzhausen, field nr. 5-F, dorsal view. c, Same species, left, field nr. 476. d, *"Aceratherium" tetradactylum*, right,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

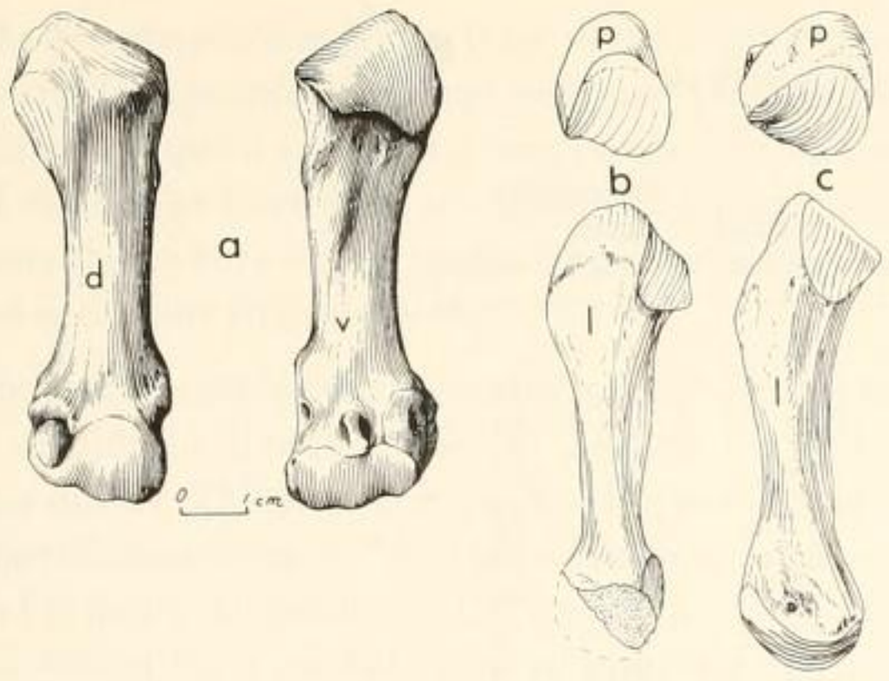

Fig. 15: Metacarpal V. a, *Plesiaceratherium gracile*, right, d – dorsal, v – volar view, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, l – lateral, p – proximal view, middle Miocene, Sandelzhausen. c, *"Aceratherium" tetradactylum*, left, l – lateral, p – proximal view, middle Miocene,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

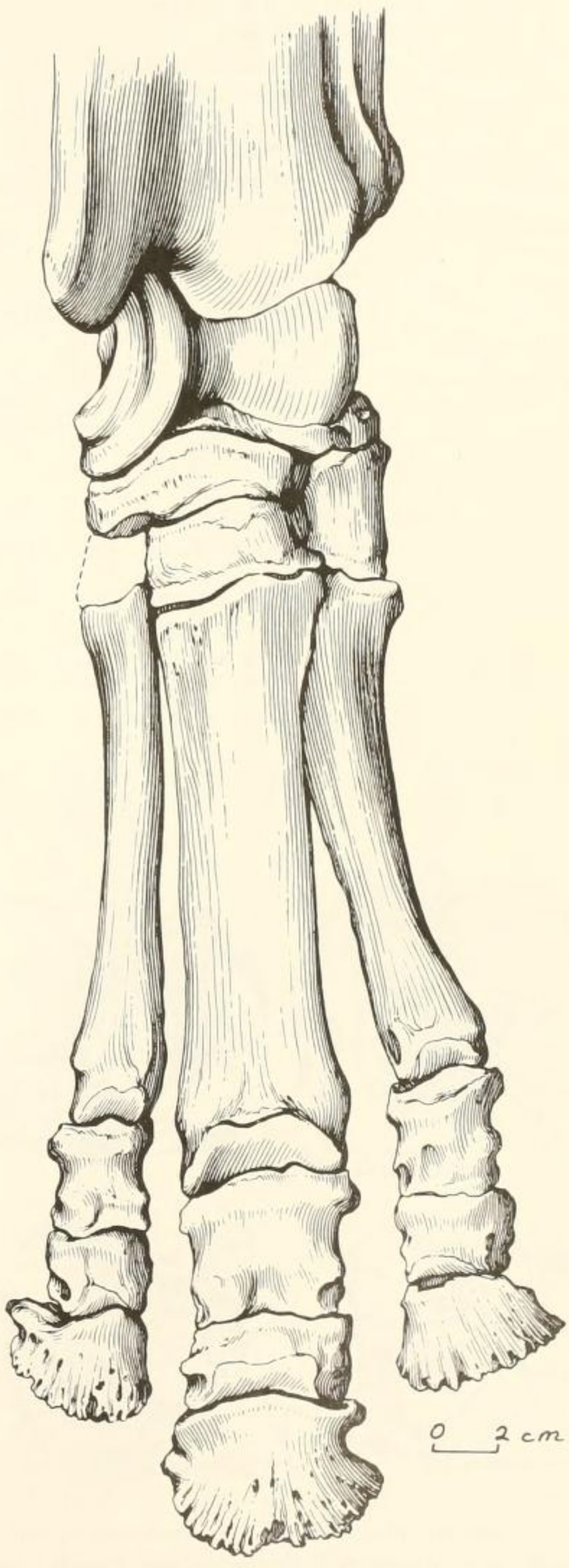

Fig. 16: *Plesiaceratherium gracile* Young, left hind foot, dorsal view, middle Miocene, Shanwang.

Table 15.

ASTRAGALUS OF LOWER AND MIDDLE MIOCENE ACERATHERINI

	height of bone med.	lat.	width of trochlea	distal width	calcaneus facet 1 height	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	depth	collum proc. calc. width	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

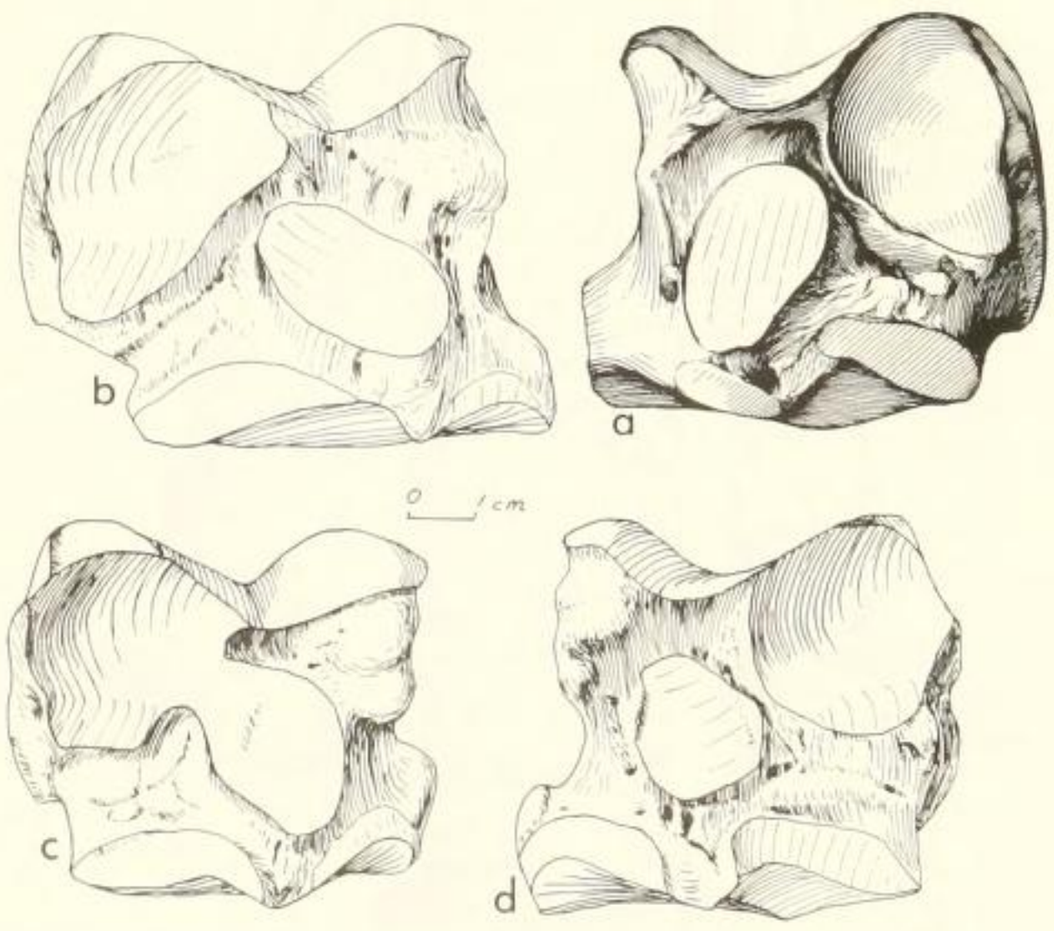

Fig. 17: Astragalus, plantar view. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang. b, *"Aceratherium" tetradactylum*, left middle Miocene, Sansan. c, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen, field nr. 3058. d, Same species and locality, field nr. 2235, right.

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 1 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 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.

Table 17.

CENTRAL IN LOWER AND MIDDLE MIOCENE ACERATHERINI

		max. width	max. depth	dorsal height	plantar height	tarsal width	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 (Mus. Paris) Sansan	min.	35	47	20	24	34	37
	max.	46	55	27	31	38	45
A. simorrensis Steinheim (Mus. Basel)		37	47	20	25	37	38

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

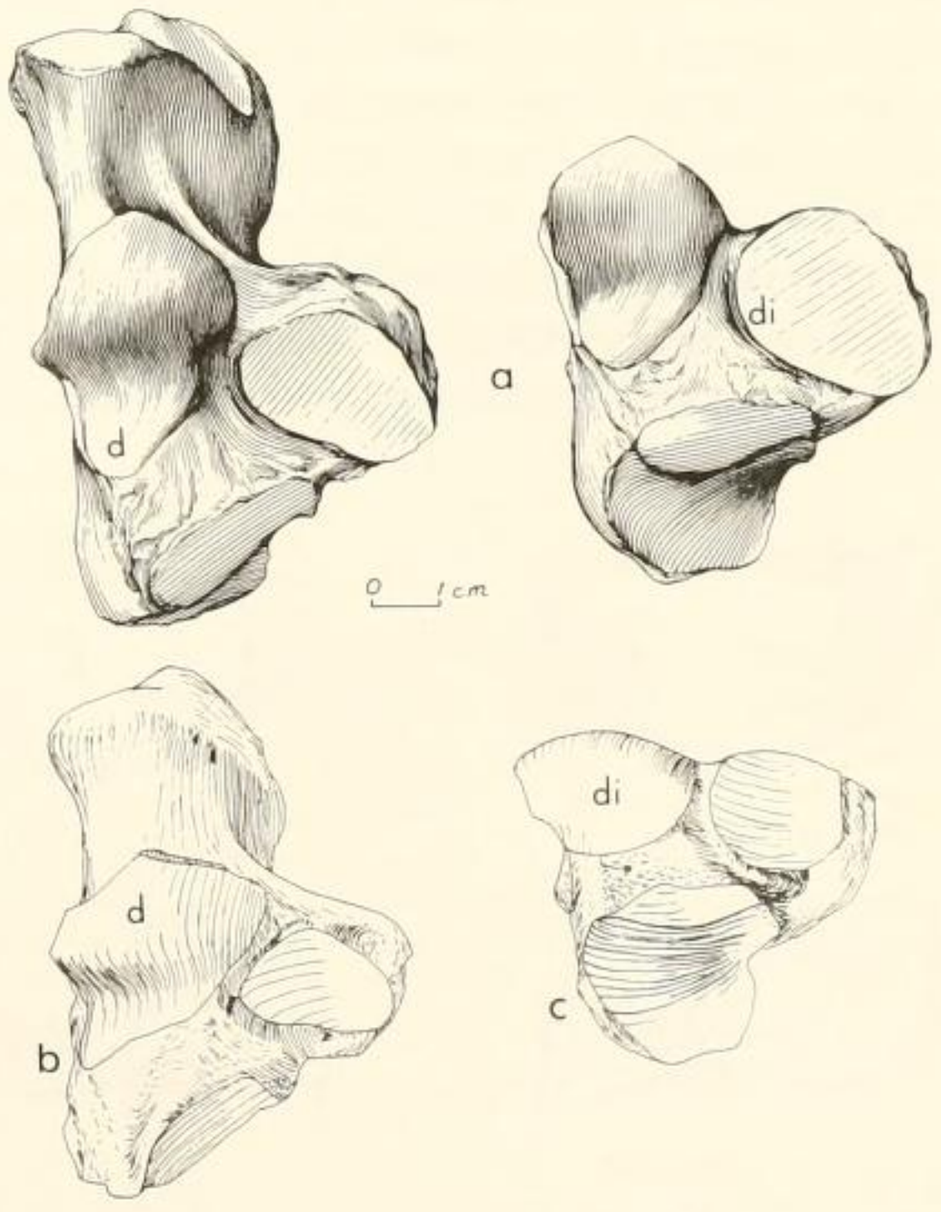

Fig. 18: Left calcaneus, d – dorsal, di – distal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 3125. c, Same species and locality, field nr. 2368.

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.

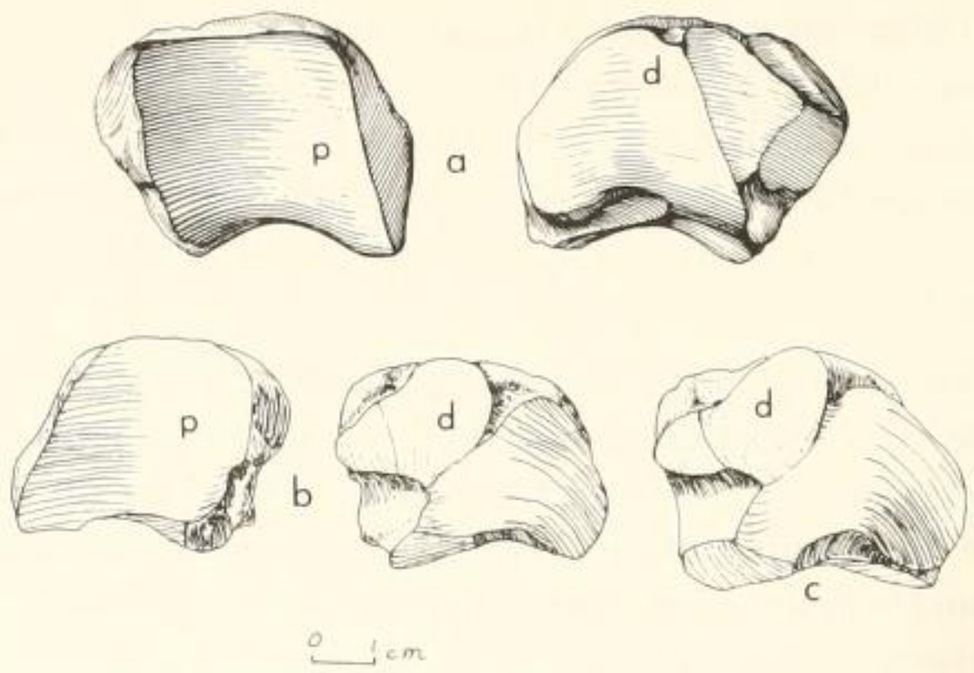

Fig. 19: Central, p – proximal, d – distal view, medial side up. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen, field nr. 264. c, Same species and locality, left, field nr. OH. d, *"Aceratherium" tetradactylum*,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

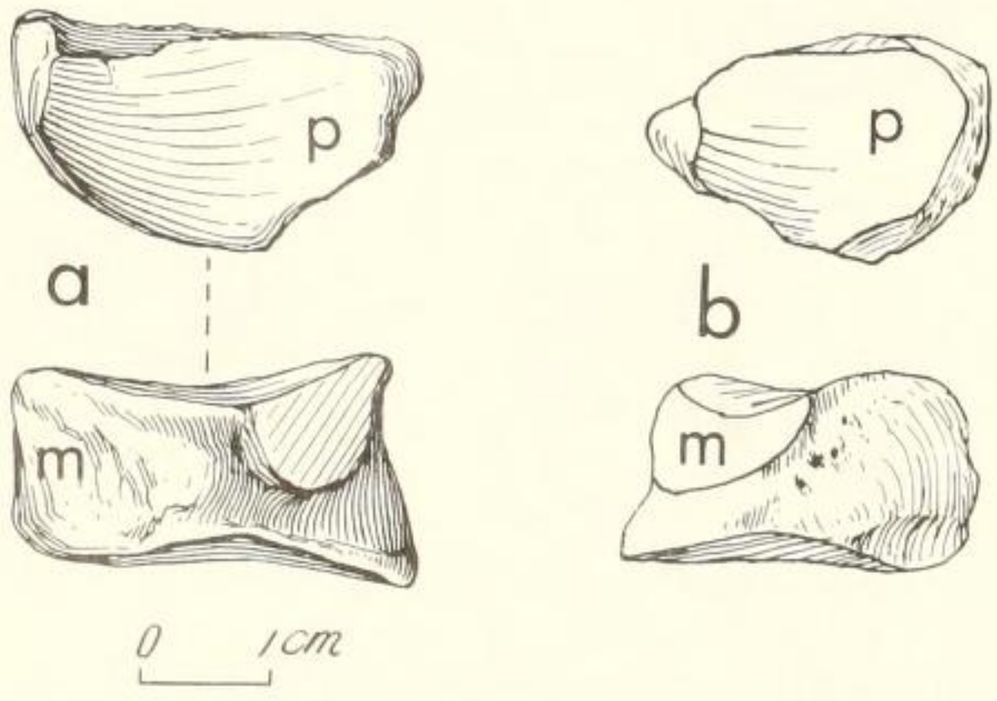

Fig. 20: Tarsal 2, p – proximal, m – medial view. a, *Plesiaceratherium gracile*, right, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen.

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

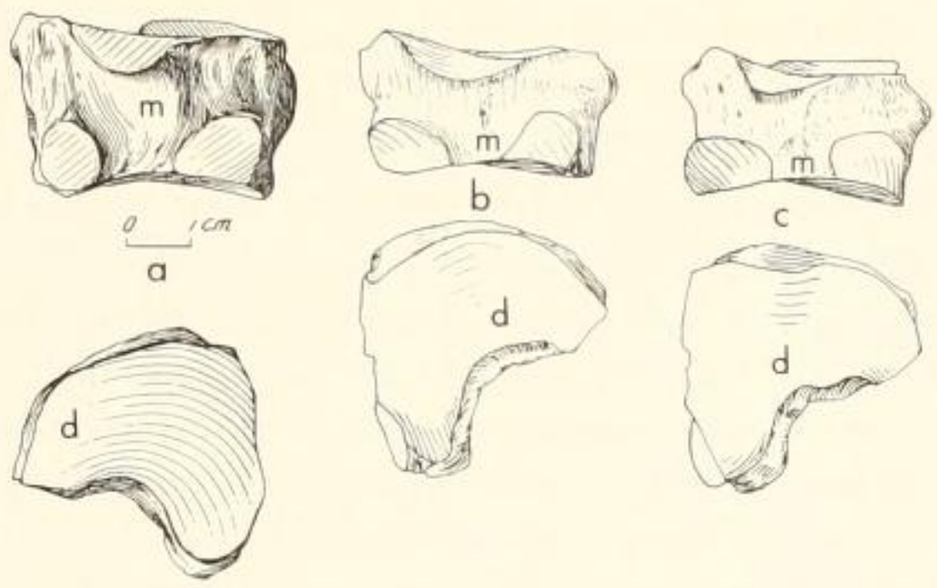

Fig. 21: Tarsal 3, d – distal view, m – medial view, front side up. a, *Plesiaceratherium gracile*, left above and right below, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, left, middle Miocene, Sandelzhausen, field nr. 13-P. c, same species and locality, field nr. 1967 M.

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.

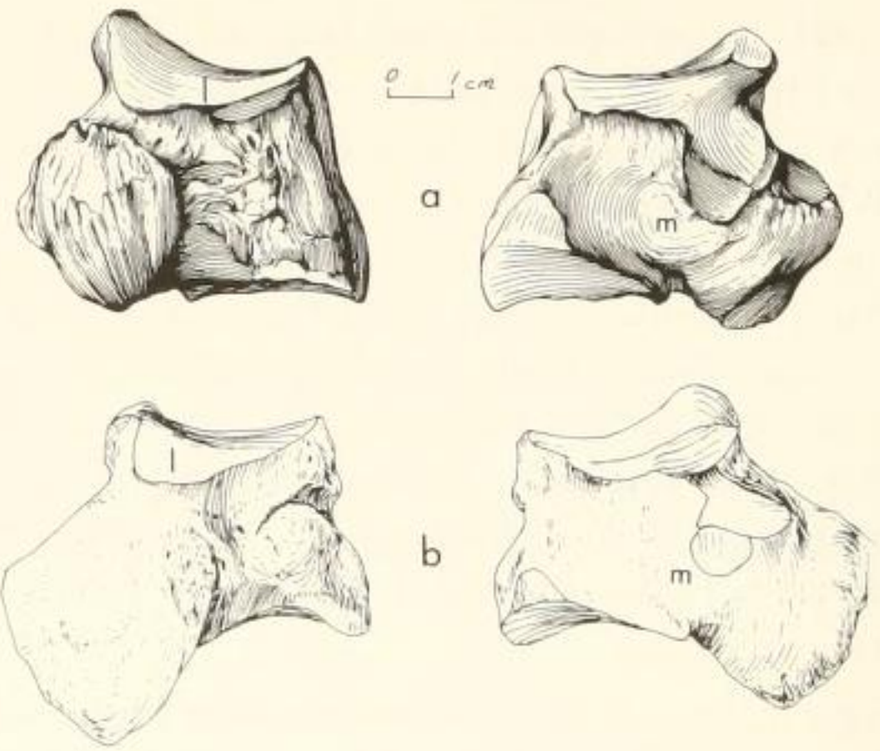

Fig. 22: Right tarsal 4, l – lateral view, m – medial view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi*, field nr. GR, middle Miocene, Sandelzhausen.

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.

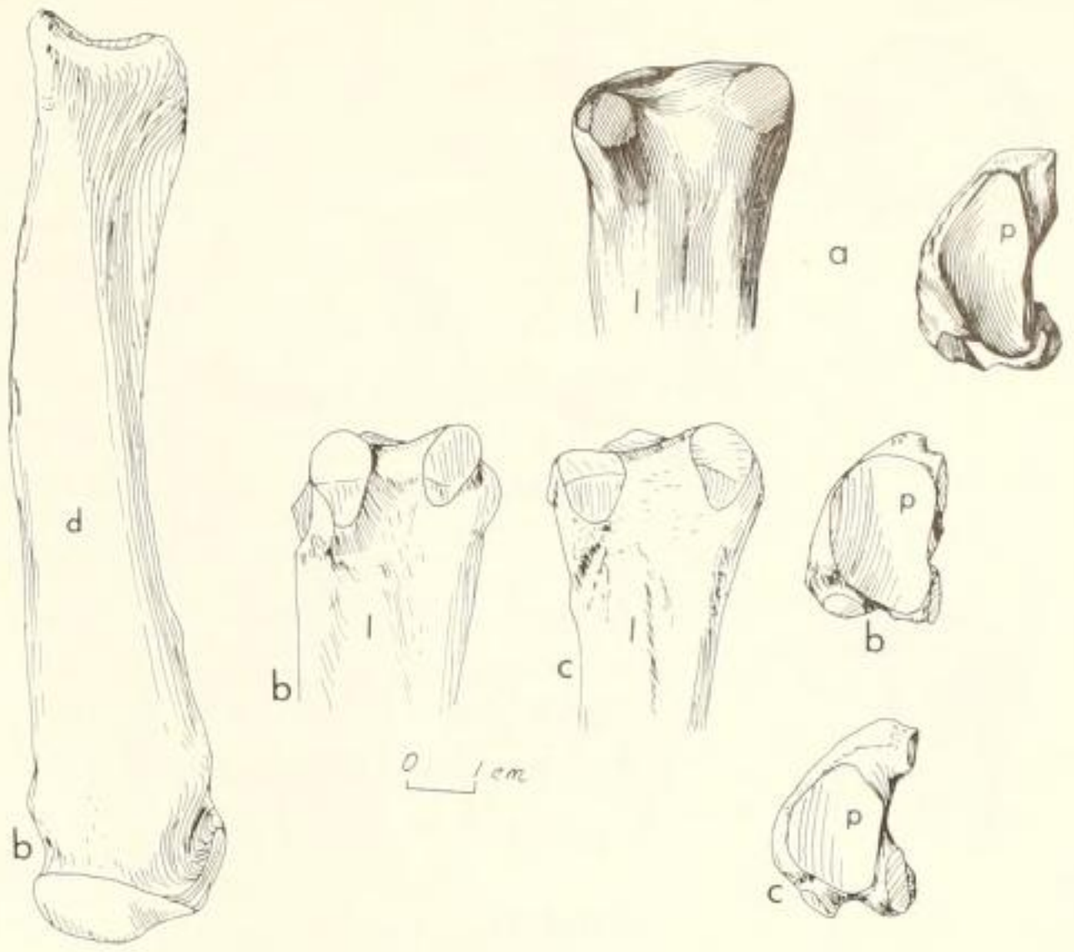

Fig. 23: Right metatarsal II, l – lateral, p – proximal view, dorsal side up, d – dorsal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. b, *Plesiaceratherium fahlbuschi,* middle Miocene, Sandelzhausen, field nr. 2367. c, same species and locality, field nr. 12-K.

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 Sansan (Mus. Paris)	min.	131	24	33	23	17	31	36
	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

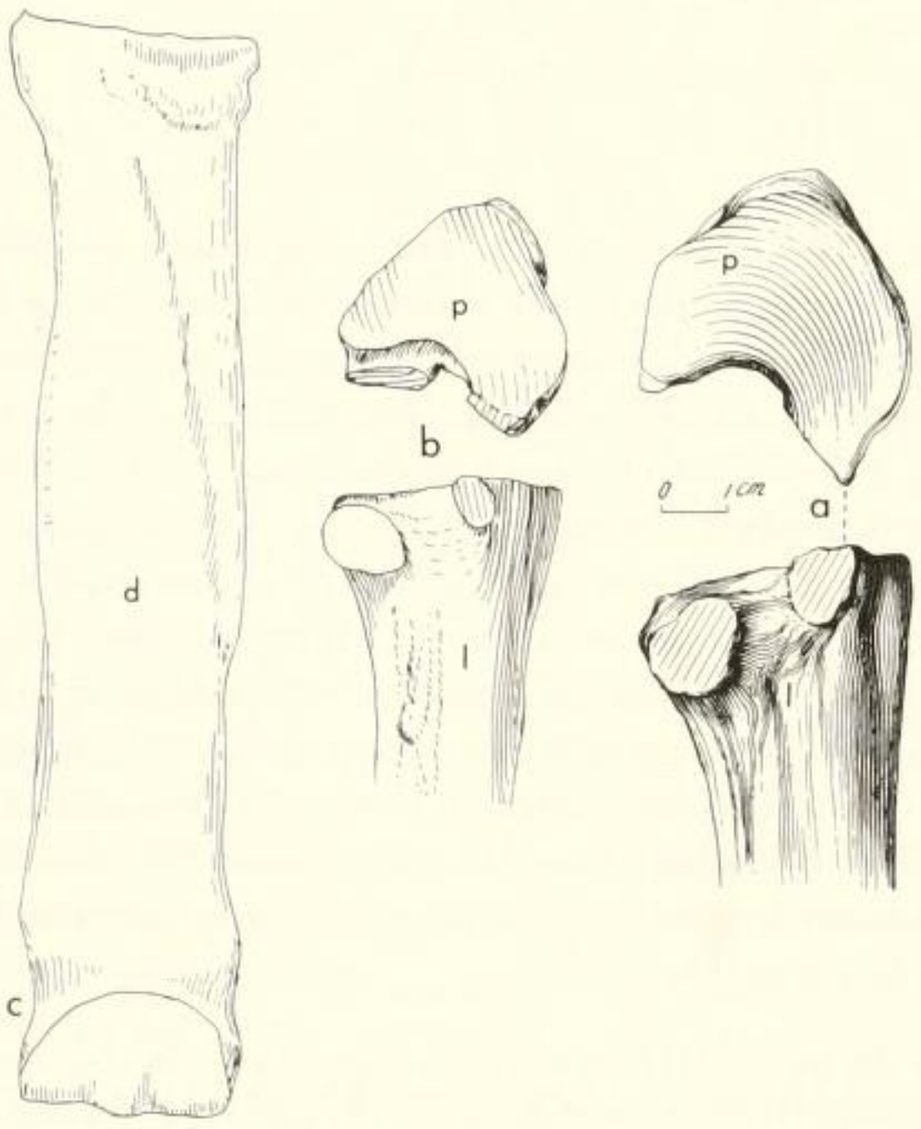

Fig. 24: Right metatarsal III, p – proximal view, l – lateral view, d – dorsal view, mediodorsal side up. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. *b, Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 2242. c. same species and locality, field nr. 2960.

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.

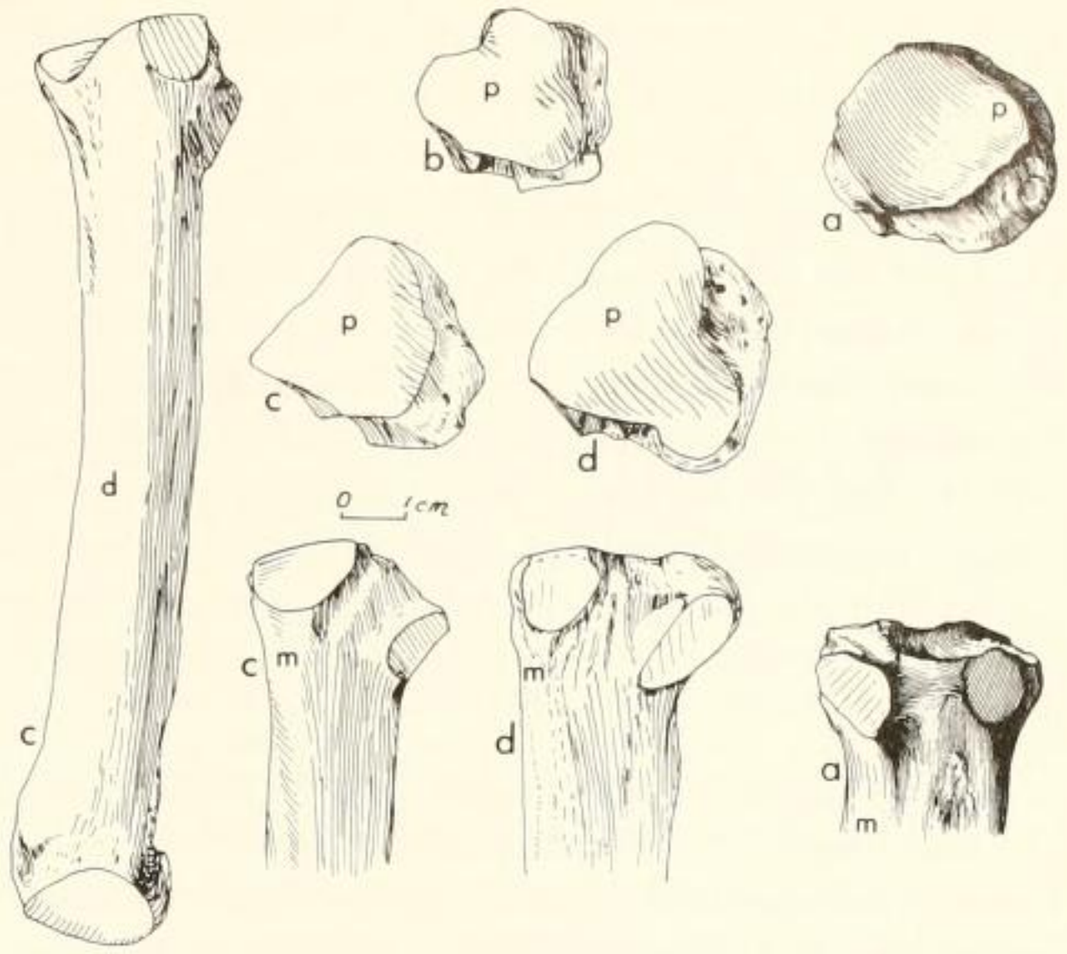

Fig. 25: Left metatarsal IV, p – proximal view, m – medial view, d – dorsal view. a, *Plesiaceratherium gracile*, middle Miocene, Shanwang. *b, Plesiaceratherium fahlbuschi*, middle Miocene, Sandelzhausen, field nr. 0198. c, same species and locality, field nr 2366. d, Plesiaceratherium mirallesi, middle 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 halfmoon-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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