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Rhinocerotidae from Paşalar, middle Miocene of Anatolia (Turkey)

Rhinocerotid remains from the middle Miocene Anatolian locality at Paşalar are described, and referred to *Begertherium tekkayai*, *Aceratherium* sp. aff. *tetradactylum*, and *Brachypotherium brachypus*. *Begertherium tekkayai* (=*Beliajevina tekkayai* HEISSIG) is only known from this locality. The material of *Brachypotherium brachypus* is similar to that from Sansan and Steinheim am Albuch (MN6–7), rather than to the earlier (informal) species *B. stehlini* known from La Romieu and Baigneaux (MN4), or to described African and Asian species. *Begertherium tekkayai* was probably a grazer, *Aceratherium* sp. a browser and *Brachypotherium brachypus* a mixed feeder. The very high proportion of juveniles in the *Begertherium* sample may point to accumulation by a predator.

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Introduction

The middle Miocene locality Paşalar, near Bursa in Western Anatolia (Turkey) (Becker-Platen *et al.*, 1975) has yielded a rich fauna with 57 species of mammals, including two hominoids (Andrews & Tobien, 1977; Alpagut *et al.*, 1990). The fossiliferous part of the deposit represents a very brief time interval, and the whole fauna seems to be contemporaneous and locally derived (Andrews & Alpagut, 1990; Andrews & Ersoy, 1990; Bestland, 1990). The history of the excavations at Paşalar is given by Alpagut (1990). The present paper describes material collected between 1983 and 1988, with a few important specimens from 1989 added (the letters A, B, C . . . in specimen numbers refer to the year of collection, starting with A = 1983). For descriptions of rhinoceros material recovered earlier, see Heissig (1974, 1975, 1976).

Three species of rhinoceros are represented in the material recovered from Paşalar: *Begertherium tekkayai* (=*Beliajevina tekkayai* HEISSIG), *Brachypotherium brachypus* and *Aceratherium* (sensu lato) sp. aff. *tetradactylum*. *Begertherium tekkayai* is only known from Paşalar and was the only species reported by Heissig (1974, 1975, 1976). It is by far the most common rhinoceros at the locality, and is represented by a few juvenile jaws, a great number of mainly fragmentary milk teeth and a few permanent teeth. *Brachypotherium* is represented by permanent teeth and one milk tooth fragment, while *Aceratherium* is represented only by a few milk teeth and one permanent molar fragment. The posteranial remains of rhinoceroses from Paşalar are few and fragmentary, and have been omitted from this paper.

Measurements

The measurements used here are basal maximum length and width measurements of individual teeth: buccal length (BBL), lingual length (BLL), mesial width (MBB) and distal width (DBB). Widths were measured parallel to and somewhat above the plane of the crown base (at the level giving the highest reading). Lengths of upper teeth were measured similarly, with the level of measurement on the buccal side chosen at the point where the sides of the ectoloph become subparallel. Lengths of lower teeth were measured slightly obliquely, from the level of the anterior cingulum to the posterior basal bulge of the

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enamel immediately above the crown base (this somewhat peculiar measurement gives the most comparable results for isolated teeth and dentitions). The height measurements are given here for unworn teeth only. Buccal height (BUH) is the height along the paracone style of upper teeth and along the protoconid fold of lower teeth. Lingual height (LIH) is the height of the protocone in upper teeth and the height of the metaconid in lower teeth.

Systematics

Order: Perissodactyla Owen, 1848.
Family: Rhinocerotidae Gray, 1821.
Subfamily: Rhinocerotinae Gray, 1821.
Tribus: Elasmotherini Gill, 1872.
Genus: *Begertherium* Beliaeva, 1972.

Begertherium comprises elasmotherine rhinoceroses with hypsodont premolars, subhypsodont molars, and relatively weak deposition of coronal cement. The upper premolars lack a mesostyle, the postfosette is very low and double, with separate pits lingually and buccally of the metaconule. The lower molars and milk molars have cone-shaped hypoconids, demarcated by vertical folds. Incisors are vestigial or absent (see Fortelius & Heissig, 1989).

Begertherium tekkayai (Heissig, 1974)

Synonymy
1974 *Beliajevina tekkayai* Heissig p. 23ff; Plate 2, Figures 1–6.
1975 *Beliajevina tekkayai* Heissig p. 145.
1976 *Beliajevina tekkayai* Heissig p. 13ff; Plate 1, Figures 1–8; Plate 2, Figures 13–19; Plate 3, Figure 8.
1989 *Beliajevina tekkayai* Alpagut *et al.*, 1989.

Material
Ankara Üniversitesi, Paleoantropoloji:
(Letters in specimen numbers refer to year of collection, starting with A = 1983, B = 1984 etc.)
Juvenile left maxillary fragment with dp^1–dp^4: D236
Juvenile right mandibular fragment with dp_2–dp_3: D261
Juvenile left mandibular fragment with dp_3: E290
Juvenile left mandibular fragment with dp_3–dp_4: E290
Juvenile left mandibular fragment with dp_2–dp_4 + M_2: G945
dp^1: sin. D236/1, F455/1, G673
dp^2: dex. A171, E880, F455/2; sin. F474, G576, G876
dp^3: dex. D662/5, F454, F502, G1123; sin. E292, F455
dp^4: sin. D753, F465
dp_1: dex. B593/1, B593/2, C131/2–4, D387/1–3, F468/1–4, G725, G773, G875, G1066/2 sin. B593/2, C131/5–6, D387/4–6, E772, F468/3–9, G/539, G1066/1.
dp_2: dex. D535; sin. A165, C131/7, F460, G1089
dp_3: dex. C131/1, D433, F453, F461, F495, F516, F455/3, G585, G924, G1034;

sin. E759/1–5, G693, G949, G1085
dp_4: dex. D536, E622, F462, F499/1–2
sin. D254, D369, E28, G696, G1028
P sup. dex. fragments (two specimens) G422/1 & G1128.
M^1: dex. D737, sin. C131/8
M^2: sin. D754
M^3: dex. F517
P_2: dex. D59, G1052/1
P_3: dex. F463, F515
M_2: sin. D936
M_2: dex. E28/1, G677
M_3: dex. D57

Maden Tektik ve Arama Enstitüsü, Ankara:
dp_4: dex. BP721, BP722
(more material present but not studied).

Bayerische Staatssammlung für Paläontologie und historische Geoligie, Munich:
See Heissig (1976: 14f).

The list includes only measured or otherwise documented specimens. The previous collection of rhinoceros remains from Paşalar (Heissig, 1976) contained only teeth (8) and tooth fragments (41) of *Begertherium tekkayai*. In both collections the dominance of the milk teeth is striking. The total number of specimens collected between 1983 and 1989 and preserved with other unidentified fragments certainly exceeds one thousand, and milk tooth fragments too small to be useful are among the most common fossils at Paşalar. Such fragments have generally not been collected, but a large number is nevertheless potentially available for studies that require destructive techniques, or for similar purposes. An attempt to fit together more complete specimens from a great number of small fragments was carried out in the field in 1986, but gave a negative result. The number of individuals represented is thus considerably greater than the list would suggest, and the proportion of juveniles higher. By the crude but conservative indicator of the most common repeated element there are 16 individuals (right dp_1). This tooth is commonly retained in rhinoceroses, and may be quite unworn even in adults. For the proportion of adults to juveniles other teeth must be used. By the right dp_3 and several permanent tooth categories there are eleven juveniles and two adults. In other words, here are at least 16 individuals present, over 85% of them juveniles.

Description

Skull. One of the most complete specimens of any species known from Paşalar is a juvenile left maxillary fragment with the full set of milk molars *in situ* (D236), (see Figure 1). Unfortunately, little of the skull morphology can be divined, except that the narial incision probably did not extend beyond dp^2 and that the infraorbital foramen was placed above the anterior half of that tooth. A shallow narial incision in adults seems to be a characteristic of the Elasmotherini, except for the *Ningxiatherium-Sinotherium-Elasmotherium* clade (Kretzoi, 1943, Figure 2; Beliaeva, 1971; Figure 3; Chen, 1977, Plate 1). Both the incision and the infraorbital foramen characteristically migrate

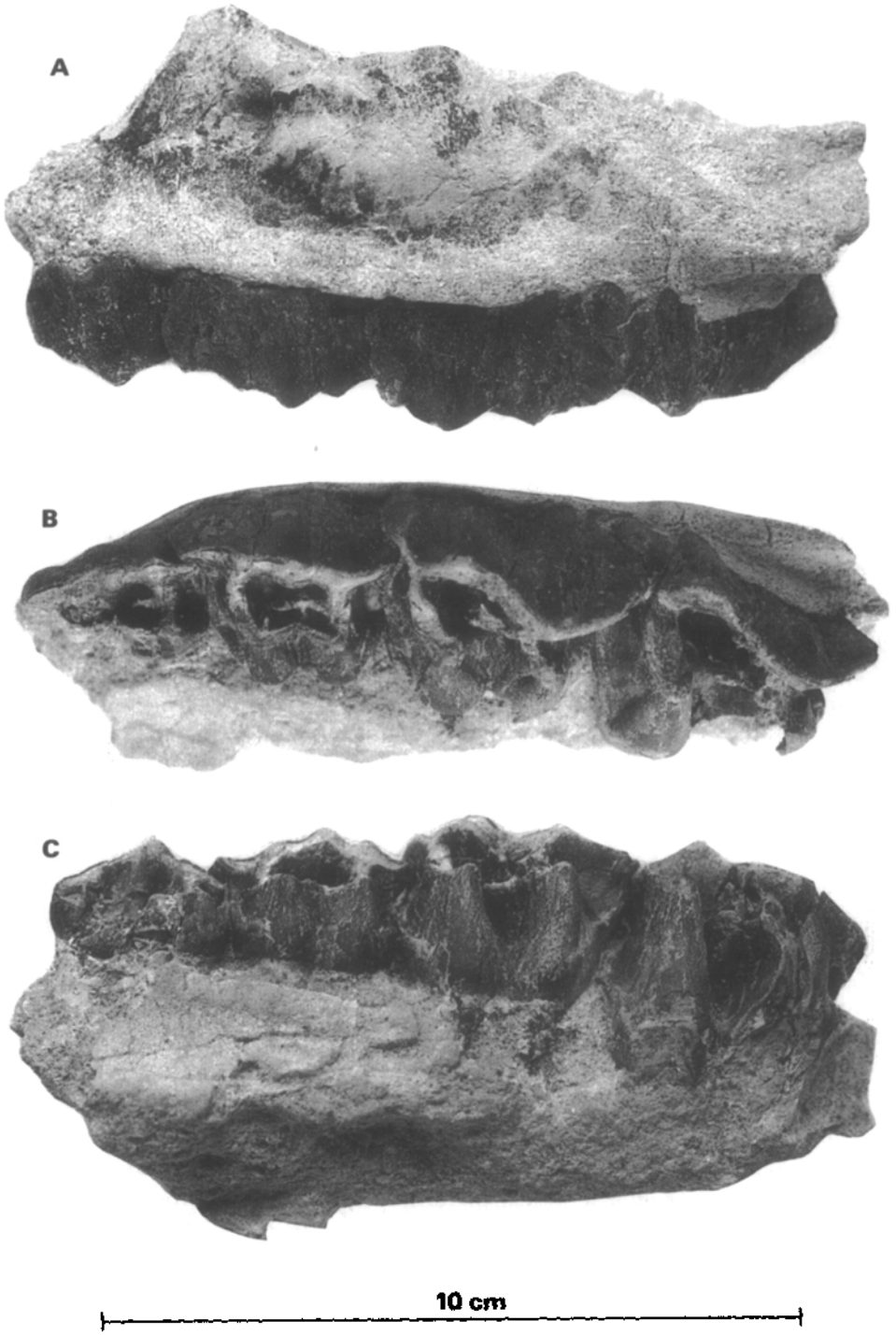


Figure 1. *Begertherium tekkayai*, juvenile left maxillary fragment with dp^1–dp^4 10236, Paşalar A, buccal; B, occlusal; C, lingual.

backwards during growth, however. In the absence of comparable juvenile material of other elasmotherines, the significance of this specimen is somewhat unclear. However, juvenile specimens of *Rhinoceros, Diceros, Ceratotherium* and *Chilotherium* have (in increasing order) deeper incisions and more posteriorly located foramina. It is thus probable that *Begertherium tekkayai* had a shallow narial incision when adult as well.

Deciduous teeth. Milk incisors are unknown and were probably absent.

The complete set of left upper milk molars of the maxillary fragment (D236), and isolated right milk molars obviously from the same individual are available, as well as two mandibular fragments with teeth and several isolated upper and lower complete teeth. As noted by Heissig (1976), most of the milk teeth are little worn.

The milk molars have been adequately described by Heissig (1976: 16ff), mainly from fragments. The following amendments and addenda are based on the much more complete material which is presently available. Measures are given in Table 1. As is evident from Figure 1, dp^1 is a buccally elongated tooth with a strong hypocone and metaloph. The tooth is rather larger than one would expect from the small and simple dp_1. All known examples of dp^2 share the feature seen in Figure 1, having protocone and hypocone united by a symmetrical pair of crests. The mesial crest is probably homologous with the antecrochet, the distal one with a similar bulge seen mesiobuccally of the hypocone on upper molars and other upper milk molars (see description of M^3 below). Such a hypocone bulge is, indeed, seen in other elasmotherines as well, for example in *Begertherium* (="*Hispanotherium*") *grimmi* (HEISSIG) (Fortelius & Heissig, 1989), and fusion of protocone and hypocone is, of course, the rule in elasmotherine upper premolars. Both dp^3 and dp^4 have ordinary, separate proto- and hypocones.

Of the lower milk molars, all except dp_3 are well described by Heissig (1976). dp_3 is a long tooth, with an elongated metalophid and strongly forked paralophid (Figure 2). The metaconid is mesiodistally long, with a tendency to develop accessory cusplets mesially and distally of the main cusp, much as described for dp_2 by Heissig (1976). Between paraconid and protoconid the buccal wall has a pronounced vertical fold ["vordere Aussenfurche" of Heissig (1976)] extending down to a short cingulum a few millimetres above the crown base and parallel to it. A similar feature is seen on dp_2, which also supports a forked paralophid. The hypoconid of dp_3 and dp_4 is demarcated by gentle symmetrical folds, converging towards the cusp tip to form the outline of an elongated cone ["Modellierung" of Borissiak (1935) and Heissig (1976)]. The trigonid basin is steep, continuing without a threshold as a groove onto the lingual crown base. The talonid basin is also steep, but has a distinct threshold and a narrow V-shaped entrance.

Permanent teeth. Permanent incisors are unknown.

No additional upper premolars, apart from two fragments, have been discovered since Heissig (1976), and there is nothing to add to his description. The premolars of *Begertherium* are very hypsodont, more so than the molars (Table 1). The lingual cusps are strong and confluent.

Two first and one second upper molars are now present, along with fragments of a few more specimens. All of the complete specimens are very little worn and quite hypsodont, with a rather short metaloph (Figure 3). The ectoloph was well described by Heissig (1976), who noted the absence of a mesostyle. The lingual cusps are very steep, with almost no basal swellings. About 1 cm above the lingual crown base both first molars have a

Table 1. **Dental measurements of *Begertherium tekkayai* from Paşalar (in mm)**

A: Milk dentition

Tooth	Dimension	*N*	Mean	S.D.	O.R.
dp^1	BBP	1	25		
	BLL	1	13·5		
	MBB	1	20·5		
	DBB	3	19·47	1·150	18·3–19·5
	BUH	1	14·8		
	LIH	1	10·5		
dp^2	BBL	2	29·50	0·707	29·0–30·0
	BLL	4	20·32	1·408	18·8–21·8
	MBB	3	29·70	1·900	27·8–31·6
	DBB	3	29·60	1·908	27·6–31·4
dp^3	BBP	4	32·25	0·759	31·3–33·0
	BLL	5	24·16	2·948	21·2–29·0
	MBB	4	35·22	2·431	32·6–38·4
	DBB	5	34·02	2·159	31·0–37·0
dp^4	BBL	3	36·97	2·684	34·9–40·0
	BBL	2	28·05		27·1–29·0
	MBB	2	40·55		38·1–43·0
	DBB	1	36·6		
	BUH	1	33·0		
	LIH	1	25·6		
dp_1	L	17	13·71	1·345	11·6–16·5
	B	20	8·41	0·878	7·1–9·6
	H	2	12·4		11·8–13·0
dp_2	BBL	4	23·0	1·828	20·4–24·6
	BLL	3	22·67	2·203	20·4–24·8
	MBB	4	11·45	1·156	10·4–13·1
	DBB	5	14·34	1·397	12·1–15·7
	BUH	1	16·7		
	LIH	1	12·2		
dp_3	BBL	9	33·29	2·354	28·2–46·3
	BLL	8	31·61	2·148	27·9–34·0
	MBB	12	16·42	1·220	13·8–18·2
	DBB	9	17·29	1·369	14·2–18·6
	BUH	1	20·8		
	LIH	1	15·2		
dp_4	BBL	12	33·71	1·576	30·5–35·6
	BLL	12	33·32	2·204	28·6–35·8
	MBB	10	18·74	1·301	16·1–21·0
	DBB	12	19·46	1·141	16·8–20·8
	BUH	6	31·80	1·145	29·8–33·0
	LIH	4	24·20	3·691	21·2–29·3
P^2	BBL	1	23·4		
	BLL	1	20·7		
	MBB	1	31·3		
	DBB	1	29·1		
P^3	BBL	1	29·7		
	BLL	1	30·2		
	MBB	1	45·9		
	DBB	1	40·8		
	BUH	1	58·0		
	LIH	1	42·6		
M^1	BBL	2	36·9		34·6–39·2
	BLL	2	30·7		30·5–31·0
	MBB	1	46·7		
	DBB	1	41·9		
	BUH	1	40·5		
	LIH	1	33·0		

Table 1—*continued*

B: Permanent dentition				
Tooth	Dimension	N	Mean	O.R.
M^3	BBL	1	42	
	BLL	1	33·3	
	MBB	1	52	
	DBB	1	50	
	LIH	1	42·0	
P_2	BBL	1	24	
	BLL	1	25	
	MBB	1	14	
	DBB	–	–	
P_3	BBL	2	28·4	28·0–28·9
	BLL	2	15·1	25·0–25·3
	MBB	2	20·1	18·9–21·4
	DBB	2	21·5	21·4–21·7
	BUH	1	44·6	
	LIH	1	34·2	
M_1	BBL	2	34·4	34·2–34·7
	BLL	2	37·0	35·3 38·8
	MBB	2	21·7	21·0 22·5
	DBB	2	24·3	23·5–25·1
	BUH	1	44·6	
	LIH	2	37·7	37·3–38·1
M_2	BBL	2	44·4	42·2–46·7
	BLL	2	43·8	42·5 45·0
	MBB	1	27·6	
	DBB	1	28·1	
	BUH	1	50·5	
	LIH	1	47·0	
M_3	BBL	1	48·0	
	BLL	1	48·9	
	MBB	1	27·3	
	DBB	1	26·4	

cingulum-like groove, which may be a hypoplastic defect. The mesial and distal cingula are low, as consequently is the postfossette.

There are three fragments of a moderately worn right M^3 (F517): most of the ectoloph, the protocone with most of the protoloph, and the hypocone. The ectoloph has a buccal cingulum, extending along the crown base, from the mesial border about halfway towards distal. The protocone has a characteristic trefoil-shape, the main cusp being divided by a vertical fold in the lingual midline into two subequal lobes. The distal lobe is further bilobed, a weaker vertical fold running slightly to the lingual of the distolingual corner of the cusp. Further towards buccal is a well-developed antecrochet (Figure 4). The hypocone is bilobed, with a vertical fold on the mesio-lingual aspect of the cusp.

Coronal cement is present, but definitely less than in most elasmotherines [approximately as in *Caementodon oettingenae* HEISSIG; Heissig (1972)]. The enamel of all permanent teeth is rough, with prominent perikymata and a fine vertical relief corresponding to the vertical Hunter-Schreger bands (Boyde & Fortelius, 1986). Fragments of *Begertherium* teeth are easily distinguished by their enamel surface from those of any other mammal species known from Paşalar.

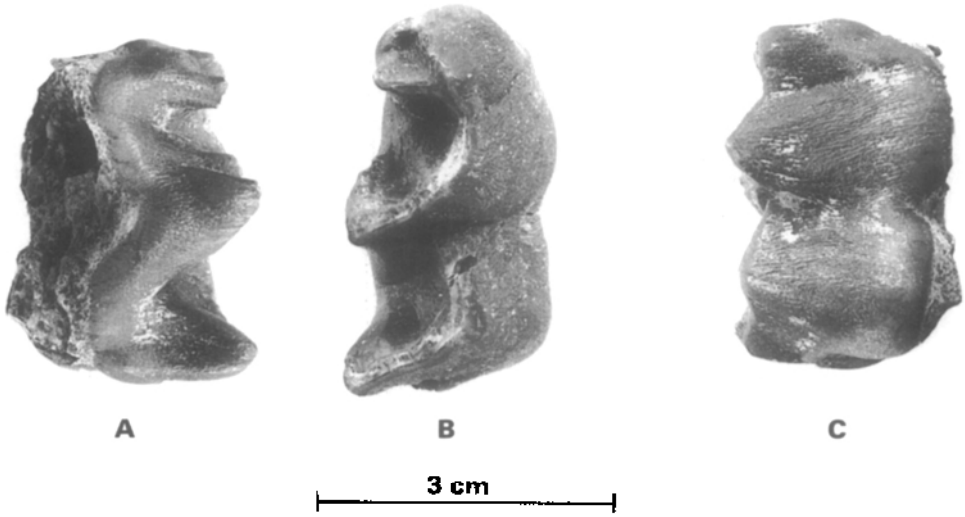


Figure 2. *Begertherium tekkaya*, dp_3 dex. F461, Paşalar. A, lingual; B, occlusal; C, buccal.

Lower premolars were unknown to Heissig (1976), and only three have since been discovered. One is an incomplete, little worn right P_2 (D59). The buccal wall of the tooth is square and rather flat, with a weak buccal fold. The talonid basin is closed off to an almost circular fossettid, and filled with cement. The lingual side of the specimen is damaged. The other two teeth are an unworn and a worn right P_3 or possibly P_4 (F515, F463; Figure 5). As might be expected from the very hypsodont upper premolars, the crown is high and short. The buccal fold is deep, but becomes shallowed towards the base. Both buccally and lingually the cusps have small but distinct basal swellings. The trigonid basin is very steeply angled and basally confluent with the lingual wall of the tooth, so that it has no "bottom" and thus no entrance. The talonid basin is deep, enclosed between the strongly curved hypolophid and the distally extending metaconid base. It is filled with cement basally, and its entrance has a narrow V-shape. The mesial and distal cingula are high, the mesial one extending obliquely towards the crown base on the buccal side. The buccal enamel of the meta- and paralophids has deep, irregular furrows.

As noted by Heissig (1976), the lower molars are much more hypsodont than the milk molars, but not unlike dp_4 in morphological details. The buccal fold is even deeper than on the premolar, but otherwise similar. The trigonid basin is a deep inverted cone with a narrow V-shaped entrance between the lingually flattened, mesiodistally long metaconid and the strongly recurved paralophid. The hypoconid is also lingually flat, and meets the distal projection of the metaconid at the narrow V-shaped entrance of the talonid basin. Mesial and distal cingula are rather low and weak, buccal and lingual cingula are absent.

Discussion

The systematics of the elasmotheres is not well understood, and the taxonomy is rather confused. Fortelius & Heissig (1989) presented a possible classification and phylogeny, recognising as separate the genera *Caementodon*, *Hispanotherium*, *Begertherium* and *Beliajevina*, which have been lumped in *Hispanotherium* by several authors. In this classification, *Begertherium* is seen as the sistergroup of a clade consisting of *Caementodon* and

Figure 3. *Begertherium tekkayai*, M^1 dex. D737 & M^2 sin. D754, Paşalar. A, occlusal; B, lingual.

Hispanotherium. These three genera together form the sistergroup of all other elasmotherines (with *Beliajevina* as the most primitive genus of this second clade). A more detailed revision of the Miocene forms, taking into account all the material currently lying undescribed in museum drawers, would probably change the picture considerably. Meanwhile, *Begertherium* appears as a genus with an Asian known distribution a stratigraphic range

Figure 4. *Begertherium tekkayai*, M¹ dex. F517, protoloph, Paşalar. Occlusal view.

spanning most of the middle and upper Miocene. *Begertherium tekkayai* is the anatomically least derived and stratigraphically oldest member of the genus (Fortelius & Heissig, 1989).

Subfamily: Aceratheriinae Dollo, 1885.
Tribus: Aceratherini Dollo, 1885.
Genus: *Aceratherium* Kaup, 1831 (sensu Heissig, 1976).

Aceratherium sp. aff. *tetradactylum* (Lartet, 1837)

Synonymy
1989 *Aceratherium* sp. (partim) Alpagut *et al.*

Material
Ankara Üniversitesi, Paleoantropoloji:
Juvenile right maxillary fragment with dp^2–dp^3: D1060
dp^2 sin.: D1060/1 (probably same ind. as D1060)
dp_3 dex.: F458
M sup. dex. metacone fragm.: G693/b.

All the little worn milk teeth could well belong to the same individual. The molar is somewhat worn, and must be from a different animal. There is thus evidence of one juvenile and one adult or subadult animal.

Description
The milk teeth are considerably more brachydont than those of *Begertherium*. The enamel is smooth and shiny. Measurements are given in Table 2.

Both the dp^2 are similar to each other and may well belong to the same individual. The crown is rounded in occlusal view, with a curved ectoloph and a moderately projecting parastyle (Figure 6). The paracone style rises from the base at an angle towards distal, reaching the ectoloph crest close to the midline. The mesostyle and metacone style are weak and vertical. There is a continuous buccal cingulum at the base of the crown. The protoloph is continuous but small and recurved, so that the tooth is much broader distally than mesially. The hypocone is strong and conical, the metaloph crest between metacone

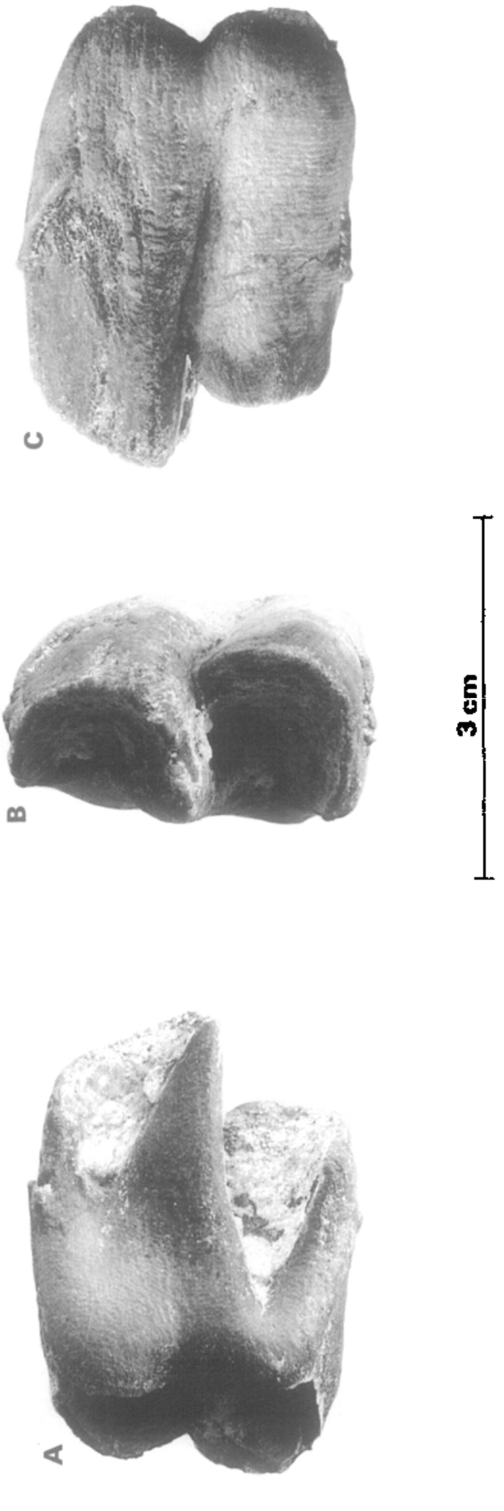


Figure 5. *Begertherium tekkayai*. P_3 dex. F515. Paşalar. A. lingual; B. occlusal; C. buccal.

Table 2 **Dental measurements of *Aceratherium* sp. from Paşalar (in mm)**

Tooth	Dimension	N	Mean	O.R
dp^2	BBL	2	35·2	34·0–36·4
	BLL	2	23·9	23·8–24·0
	MBB	2	28·5	27·6–29·4
	DBB	2	32·0	31·6–32·4
dp^4	BBL	1	34·8	
	BLL	1	24·5	
	MBB	1	35·9	
	DBB	1	32·0	
dp_3	BBL	1	33·5	
	BLL	1	33	
	MBB	1	15·8	
	DBB	1	18·9	

and hypocone short. The well-developed crochet meets almost equally strong cristae from the ectoloph and protoloph, forming a nearly symmetrical triradiate figure in the mediofossette. The lingual cingulum is strong, undulating, elevated above the crown base, and continuous with the mesial and distal cingula.

The dp^3 is molariform, with a well developed, recurved protoloph and a metaloph with a strong crochet (Figure 6). Multiple cristae are present, but do not join up with the crochet or each other. The basal cingula are weaker than in dp^2, but similarly disposed.

The dp_3 is long and narrow, with open V-shaped trigonid and talonid basins. The distolingual corner of the metaconid is quite sharp, as is the mesiolingual corner of the entoconid. A discontinuous buccal cingulum is present, running parallel to the crown base, about 5 mm above it. A weak lingual cingulum is present at the trigon basin entrance.

The molar fragment, essentially the metacone, is too small to be described meaningfully. The identification is based on size, crown height and enamel surface texture.

Discussion

The teeth are generally similar to specimens from other Middle Miocene sites, such as Sansan (Muséum national d'Histoire naturelle, Paris, specimens SA6340, SA6370, SA6359, SA6373). The teeth are too few, however, and comparative material too incomplete, for a definitive specific identification. Moreover, the systematics of the group is badly in need of revision. It is perhaps likely that the Paşalar form is identical with, or close to, the one known from Çandır, assigned to *Aceratherium* aff. *tetradactylum* by Heissig (1976). Certainly the dp_3 figured by Heissig (1976, Plate 4, Figures 4–5) is similar to the tooth from Paşalar.

Tribus: Teleoceratini Hay, 1902.
Genus: *Brachypotherium* Roger, 1904.

Brachypotherium brachypus (Lartet in Laurillard, 1848)

Synonymy

1989 *Brachypotherium* sp. (partim) Alpagut *et al.*

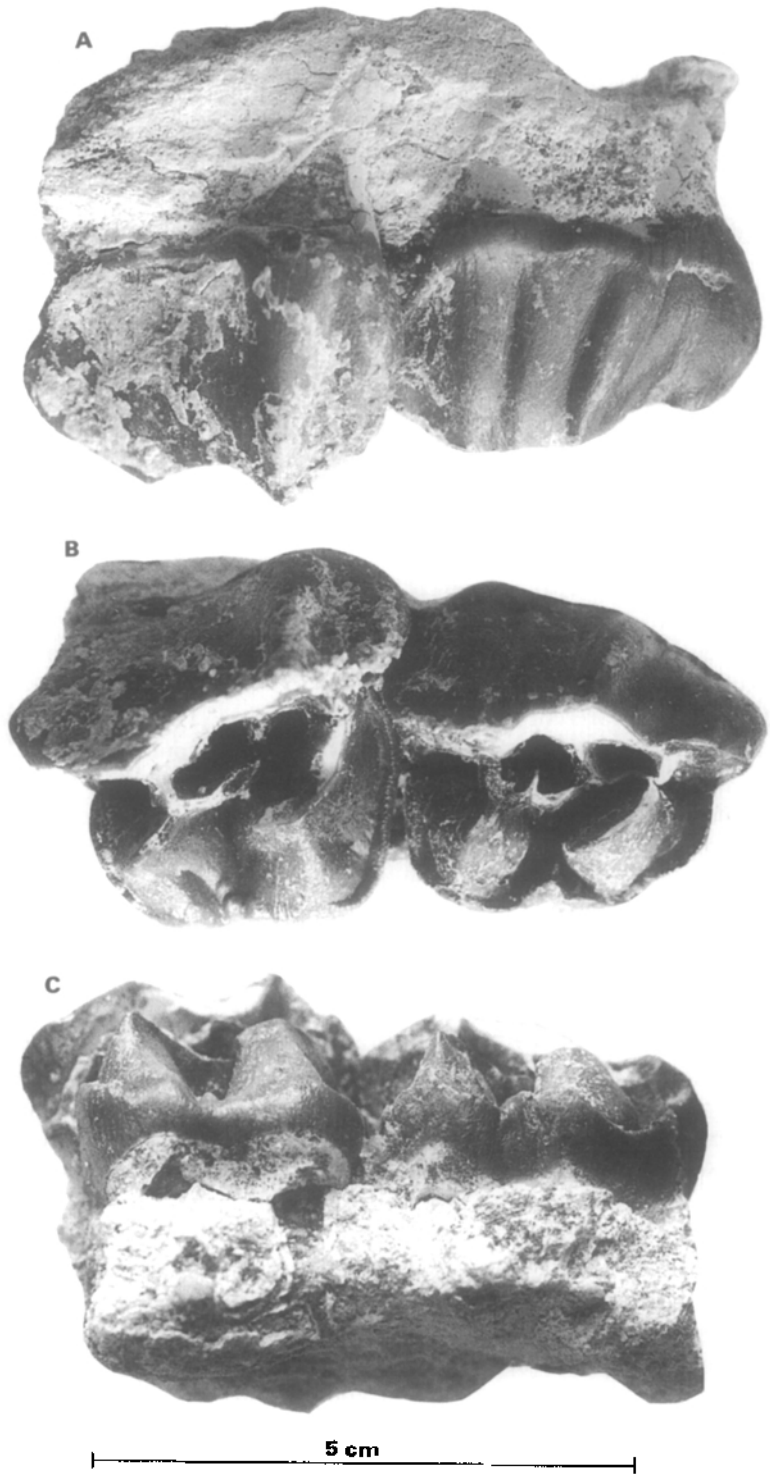


Figure 6. *Acerathertum* sp., juvenile maxillary fragment with dp^2-dp^3 dex. D1060, Paşalar. A. buccal; B. occlusal; C. lingual.

Material
Ankara Üniversitesi, Palcoantropoloji:
$dp_{3 \text{ or } 4}$ dex. fragm.: G659
P^2 sin.: G827
P^4 sin.: D964
$P^{3 \text{ or } 4}$ dex. three fragments of one tooth: E285/1a–c
$P^{3 \text{ or } 4}$ dex. lingual fragment: E285
M^3 dex. in mandibular fragment: G1124
Associated lower dentition with I_2 sin., P_2 dex. et sin., P_4 sin., M_2–M_3 dex. et sin.: C216
I_2 sin.: C133(T1)
P_2 dex.: C132(T1)
M_1 sin.: B599, probably part of C216
M_3 dex. in mandibular fragment G995
The *Brachypotherium* material from Paşalar comes from at least three individuals, one of which is a juvenile.

Description
In contrast to the other two species of rhinoceros from Paşalar, *Brachypotherium* is represented mainly by permanent teeth, most of which are well worn. The enamel is thick, with a shiny, even surface. There is no coronal cement. Measurements are given in Table 3; useful comparative data are not at hand.

The single milk tooth present is the distal half of a $dp_{3 \text{ or } 4}$. It is very brachydont, with characteristically inflated cusps. The protoconid and metaconid approach each other closely.

Skull remains and upper incisors are absent.

Upper premolars are represented by one P^2 and three specimens of P^3 or P^4. The ectoloph is very even, with no ribs additional to the moderately developed paracone style (Figure 6). The lingual cusps are well rounded. The protocone has a distinct fold on the mesial side but only a very weak one on the lingual side. The weak buccal cingulum characteristic of the species is present (Déperet, 1887: 223; Hooijer, 1963: 46). The lingual cingulum is well developed, elevated above the base of the crown, and rises obliquely across the lingual aspect of the hypocone to meet the distal cingulum closing off the rather small postfossette. On all specimens the cingulum has a distinct peak on the lingual aspect of the protocone. There is a well developed crochet and multiple cristae, except on P^2.

Upper molars of *Brachypotherium* are represented by a single right M^3. The tooth is very low crowned, has the broad and short outline characteristic of the genus, a prominent metacone rib on the ectoloph and lacks basal cingula. There is a strong, simple crochet.

There are two left lower tusks (I_2), both rather damaged (C133 and C216). One was found in apparent association with the mandibular dentition (C216) discussed below. Identification is mainly by association and size, although C216 does show traces of the mediobasal flare characteristic of the genus.

An almost complete lower dentition (C216) was discovered upside down in a pothole, with the teeth more or less in their original positions but with no trace of the mandible. A left M_1 (B599) discovered separately during the preceding season could belong to this dentition. All these and the few additional teeth and fragments have the unmistakable *Brachypotherium* characteristics: gentle, "molten" shape with no sharp folds or angles, long hypolophid, open talonid basins with broad V- or U-shaped entrances close to the crown

Table 3 **Dental measurements of *Brachypotherium brachypus* from Paşalar**

Tooth	Dimension	*N*	Mean	O.R.
P^2	BBL	1	28·3	
	BLL	1	24·4	
	MBB	1	34·0	
	DBB	1	36·3	
P^3	BBL	1	45·0	
	BLL	1	40·5	
	MBB	1	62·0	
	DBB	1	58·3	
M^3	BBL	1	68·9	
	BLL	1	50·4	
	MBB	1	63·8	
P_2	BBL	2*	30·0	
	BLL	2*	28·9	
	MBB	2	16·3	
	DBB	2	20·0	
P_4	BBL	1	42·8	
	BLL	1	40·1	
	MBB	1	26·4	
	DBB	1	30·7	
M_1	BBL	1	49·2	
	BLL	1	49·5	
	MBB	1	29·5	
	DBB	1	33·2	
M_2	BBL	2*	54·2	
	BLL	2*	52·8	
	MBB	2*	30·4	
	DBB	2*	32·2	
M_3	BBL	2	53·8	53·1–54·4
	BLL	2	55·8	55·2–56·4
	MBB	2	31·1	29·2–33·0
	DBB	2	31·2	30·5–31.8

* Mean of right and left of one individual.

base, the weak oblique lingual cingulum from the paralophid to the trigonid basin entrance and the corresponding oblique mesiobuccal cingulum. Other buccal and lingual cingula are absent. The trigonid basin is steep, and merges without a distinct entrance with the crown base at the base of the mesiolingual cingulum (Figure 7).

Discussion

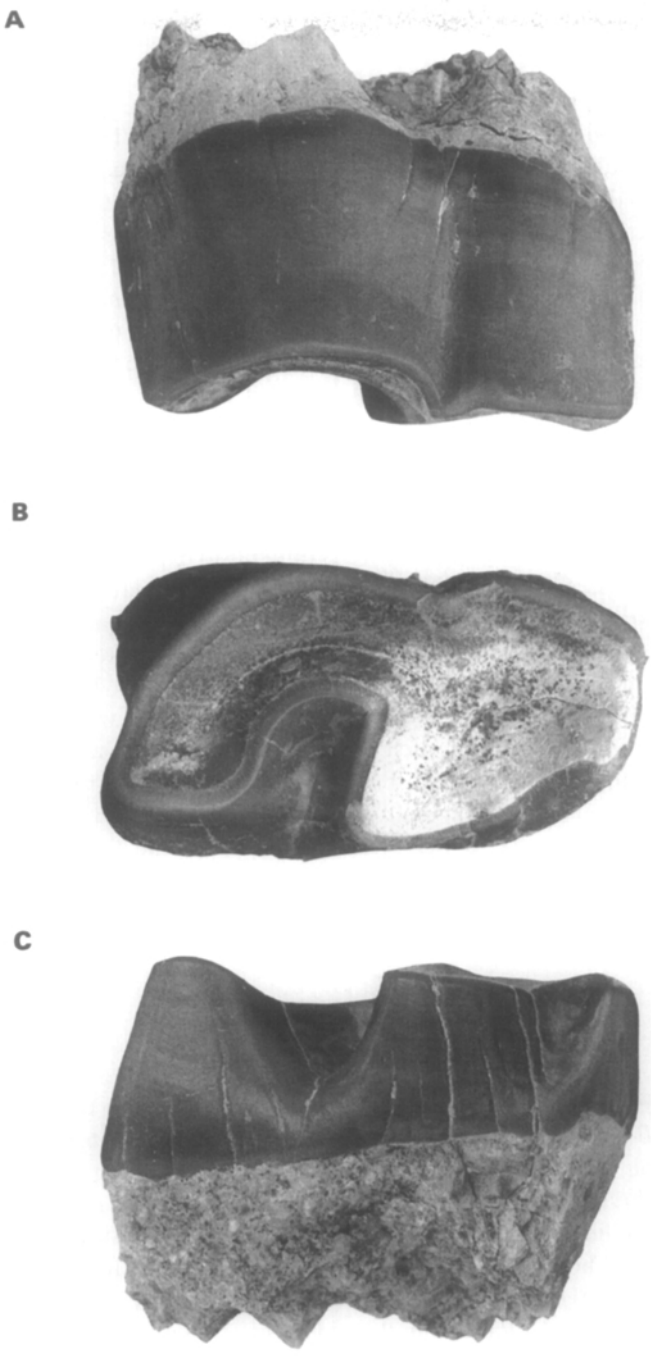
Brachypotherium brachypus from Paşalar is similar to the type material from Sansan (MN6), and to material from such sites as Steinheim am Albuch or Przeworno (MN7). The Paşalar form is not especially similar to any described African and Asian species (Hooijer, 1963, 1966, 1978; Heissig, 1971, 1972), but a revision is clearly overdue. The earlier European form known from La Romieu and Baigneux (MN4) is often referred to as *B. stehlini* (Viret, 1961; Heissig, 1971, 1976; Hooijer, 1978) but the name has never been formally assigned. This form is less hypsodont and has a more angular overall dental shape, stronger development of buccal cingula on the lower molars, less steep trigonid basin and rougher enamel (Roman & Viret, 1934; Mottl, 1969). *B. brachypus* is also known from Çandır, Yeni Eskihisar, and a number of younger Anatolian localities (Heissig, 1976; Andrews *et al.*, 1980; Kavusan & Schultz, 1985).

Figure 7. *Brachypotherium brachypus*, P^1 sin. D964, Paşalar. Occlusal view.

Palaeoecology

A proper palaeoecological evaluation of the Paşalar fauna will have to await the results of detailed studies under way, but some preliminary discussion is not out of place here. Rhinoceroses are ecologically diverse, and were apparently much more so in the Miocene, but their palaeoecology is not well understood and simplistic notions abound in the literature.

The elasmotherini as a group were hypsodont and, as far as is known, long-limbed animals, of probably open habitats (Heissig, 1976). The dental wear of later forms (*Sinotherium*, *Elasmotherium*) shows them to have been specialized grazers: the enamel edges are covered with parallel scratches, and true facets (Rensberger, 1978) are lacking, as in *Cerathotherium simum* (unpublished observations; cf. discussion in Fortelius, 1985: 26ff). *Begertherium* retains true facets on little worn permanent teeth and on milk teeth. The few and rather fragmentary specimens of worn adult teeth suggest that adult facet development was moderate, of a degree approximately comparable to the mainly grazing *Rhinoceros unicornis*. Pending more detailed investigation *Begertherium tekkayai* may be classed as a probable grazer, but it must be emphasized that the food of the numerous juveniles cannot have been mature grass.



ure 8. *Brachypotherium brachypus*, M_2 sin. (T216), Paşalar. A, buccal; B, occlusal; C, lingu

Aceratheres retain very brachydont and generally plesiomorphic teeth, and were certainly browsers.

The teleoceratines were short-legged animals of hippo-like proportions, but the European forms have not usually been regarded as amphibious. Indeed, *Brachypotherium brachypus* is often regraded as a grazer of dry habitats, especially since Thenius (1951*a*, *b*), but the evidence is conflicting and is primarily by association with other presumed grazers (e.g., Kubiak, 1982). The teeth are quite brachydont, but the wear pattern is somewhat intermediate between browser and grazer in the degree of facet development. *Brachypotherium brachypus* is no less hypsodont than the grazing *Hippopotamus*, but clearly less so than unequivocal grazing rhinos, such as the North American teleoceratine *Teleoceras*, for which there is good evidence for grazing in the form of preserved food residues (Voorhies & Thomasson, 1979). Webb (1983) regarded *Teleoceras* as an ecological vicar of *Hippopotamus*, and it is possible that a tendency towards a hippo-like life style was common in this short-legged tribe, including the early, brachydont forms like *Brachypotherium brachypus*. This species is probably best regarded as a mixed feeder, pending more detailed comparisons.

The high proportion of *Begertherium* juveniles is difficult to explain, unless accumulation by a predator is assumed. Of the carnivores present in the fauna at least *Percrocuta* would have been able to take unprotected juveniles, and a pack would perhaps occasionally have been able to separate calves from their mothers in the manner of recent African *Crocuta* (Goddard, 1967; Kruuk, 1972; Kingdon, 1979). The numbers are too high by analogy with living hyaenas, however, and the very high proportion of juveniles would really require a predator specializing in rhino calves, such as a sabertooth. There are indeed very rare (undescribed) sabertooth remains from Paşalar, but no direct evidence of carnivore accumulation. A high proportion (nearly 50%) of juveniles is also seen in the suid *Listriodon* (Fortelius & Bernor, 1990), and a personal impression of the fossil material is that hominoid, proboscidean and giraffid juveniles are relatively common as well.

Biochronology and biogeography

The rhinoceros material will not, at this stage, contribute much to the biostratigraphic dating of Paşalar. *Begertherium tekkayai* is only known from this site, while the genus *Begertherium* [including "*Hispanotherium*" *grimmi*; see Fortelius & Heissig (1989)] has a range that spans most of the middle and upper Miocene (Heissig, 1976). *Aceratherium* sp. aff. *tetradactylum* is also of limited biostratigraphic value, partly because of the imprecise identification, and partly because the form has a long stratigraphic range. The only Paşalar rhinoceros of some biostratigraphic value is *Brachypotherium brachypus*, which would indicate a maximum age around MN6. Paşalar is the oldest site in Turkey with *Brachypotherium*, however, and the possibility must be considered that it extends the known range of the species downwards.

The biogeographic affinities of the rhinoceroses of Paşalar are broadly Eurasian, with *Brachypotherium brachypus* and *Aceratherium* sp. aff. *tetradactylum* representing a western, and *Begertherium tekkayai* an eastern element. There is no evidence of an African influence in the rhinoceros material.

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