Proc. Kon. Ned. Akad. v. Wetensch. 95 (1), 81-95, March 30, 1992

Sanitheres from the Miocene Manchar Formation of Sind, Pakistan and remarks on sanithere taxonomy and stratigraphy

by J. van der Made[1] and S. Taseer Hussain[2]

[1]*Faculteit Geologie en Geofysica, Rijksuniversiteit Utrecht, Posthus 80021, 3508 TA Utrecht, the Netherlands*
[2]*Department of Anatomy, Howard University and Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.*

Communicated by Prof. J.E. van Hinte at the meeting of September 30, 1991

ABSTRACT

Sanitherium schlagintweiti Von Meyer is described from the Lower Manchar Formation. In order to determine and interpret the material, the sanithere classification of Pickford (1984) was revised.

We consider *Diamantohyus* a junior synonym of *Sanitherium* and *S. nadirum* and *S. leobense* junior synonyms of *S. schlagintweiti*. The three remaining sanithere species form a lineage: *Sanitherium jeffreysi* had simple, small premolars, which evolved into the large but simple premolars of *S. africanus* to become large and complicated in *S. schlagintweiti*.

S. jeffreysi (Bugti Beds, Indo-Pakistan Subcontinent) and *S. africanus* (Rusinga Beds and Karungu, Africa) are found in Early Miocene deposits with *Bunolistriodon*. *S. schlagintweiti* has been found in deposits which not only contain *Bunolistriodon*, but also *Conohyus*, or deposits of similar age (Europe: Seegraben-Leoben, Chios; Indo-Pakistan Subcontinent: Lower Manchar Formation) and in younger deposits, which have yielded *Conohyus* only or which are of similar age (Middle and Late Miocene; Indo-Pakistan Subcontinent: Chinji Formation, Kushalgar; Africa: Maboko, Nyakach).

The occurrence of sanitheres on the Indo-Pakistan Subcontinent and in Africa and Europe indicates connections between these areas and a sufficient degree of continuity of favorable habitat.

INTRODUCTION

During 1981-84 fossil material was collected from the Manchar Formation in Sind, Pakistan, by a joint team of the Geological Survey of Pakistan, the Howard University (Washington, D.C.) and the State University of Utrecht. Fossil sanitheres were found in localities from the lower part of the Manchar Formation, which can be correlated with the Kamlial Formation (Lower Miocene) or the lower part of the Chinji Formation (Middle Miocene) (Jacobs et al. 1990).

The material will be filed at the Geological Survey of Pakistan in Islamabad under H-GSP 8209/1124, H-GSP 8209/1145, H-GSP 8321/2076 and H-GSP 8412/3334 (H-GSP means Howard - Geological Survey of Pakistan Project). The sanitheres described in this paper are from H-GSP localities 8209, 8321, 8412 and 8420. Locality 8209 is situated in the Gaj River Area, whereas the remaining three localities are found in the Sehwan Area (figure 1).

At the localities the sanitheres are accompanied by other suiforms, which are listed below:

H-GSP 8209: *Hemimeryx blanfordi* Lydekker, 1883;
H-GSP 8321: *Bunolistriodon* sp., *Anthracotherium silistrense* Pentland, 1828, *Hemimeryx blanfordi*;
H-GSP 8412: *Conohyus* sp., *Bunolistriodon* sp., *Anthracotherium silistrense*, *Hemimeryx blanfordi*, Anthracotheriidae cf. *Anthracotherium bugtiense* Pilgrim, 1907;
H-GSP 8420: *Conohyus sindiensis* (Lydekker, 1884), *Anthracotherium silistrense*, *Hemimeryx blanfordi*.

The *Bunolistriodon* of localities H-GSP 8321 and 8412 is a form close to *B. jeanneli* (Arambourg, 1933), *B. lockharti* (Pomel, 1848) and *B. latidens* (Biedermann, 1873); it is not one of the larger species (we consider all larger Listriodontinae to belong to *Kubanochoerus* Gabunia, 1955).

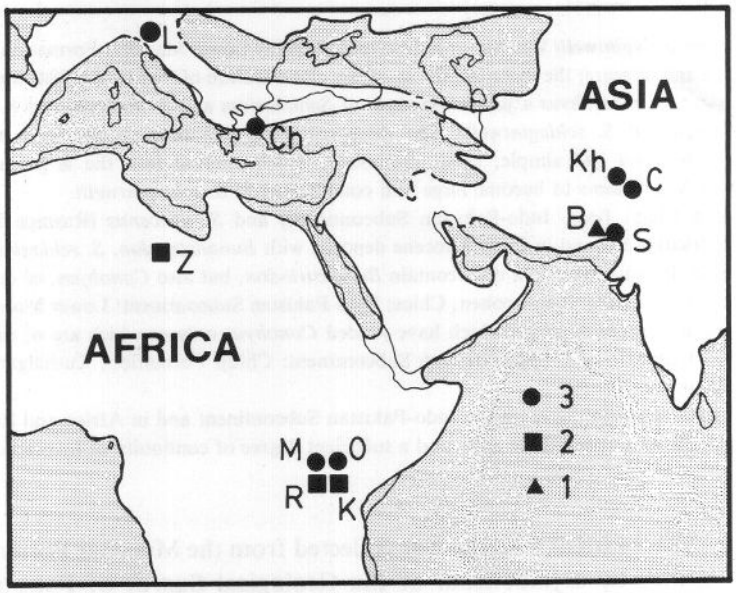


Fig. 1. The geographical distribution of the sanitheres. 1. *Sanitherium jeffreysi*, B: Bugti; 2. *Sanitherium africanus*, K: Karungu, R: Rusinga, Z: Gebel Zelten; 3. *Sanitherium schlagintweiti*, C: Chinji Formation, Ch: Chios, Kh: Khushalgar, O: Ombo, L: Seegraben (Leoben), S: Lower Manchar Formation (Sehwan, Sind). Thin lines indicate actual geography; thick lines and shaded seas indicate mid-Miocene paleogeography (slightly modified after Adams et al., 1983).

HGSP 8209/1124 left M^3 [length 13.1 mm, width of the first lobe 11.6 mm, width of the second lobe 10.1 mm]. Plate 1, figs. 1–3.

The tooth has a somewhat selenodont appearance and the enamel is wrinkled. The paraconule is fused to the protocone and extends forward to the anterior part of the tooth. It is not fused with the cingulum. The cingulum is only present antero-lingually. The lingual cusps have mesial and distal ridges and both have a buccal ridge or "rib" and a postero-lingual ridge. There is a continuous buccal cingulum. The posterior cingulum is widened to form a small talon.

HGSP 8209/1145 left M_1 or M_2 [length >9.3 mm, width of second lobe >6.5 mm]. Plate 2, fig. 1.

The labial cingulum is weakly developed and there is a posterior cingulum. A small cusp at the labial end of the transverse valley is comparable to the "pli-*Palaeomeryx*" indicated by Pickford (1984). The enamel is strongly folded.

HGSP 8321/2076 lef M_3 [width of second lobe 6.9 mm, width of third lobe 5.6 mm]. Plate 2, figs. 2 and 3.

The first lobe is broken and the tooth is much weathered. The labial cingulum is present on the second lobe, which is typical for lower molars in sanitheres. The enamel is wrinkled. The third lobe has one main cusp.

HGSP 8412/3334 left M^1 or M^2 [length 9.7 mm, width first lobe 8.6 mm, width second lobe 8.1 mm]. Plate 1, figs. 4 and 5.

The tooth is much worn in an aberrant way: at the back of the lobes large facets were formed which dip distally. Not much of the tooth structure can be seen in its present form. The lingual roots are fused.

HGSP 8420/3445 left M^1 or M^2 [width of the second lobe is 9.5 mm]. Plate 2, fig. 4.

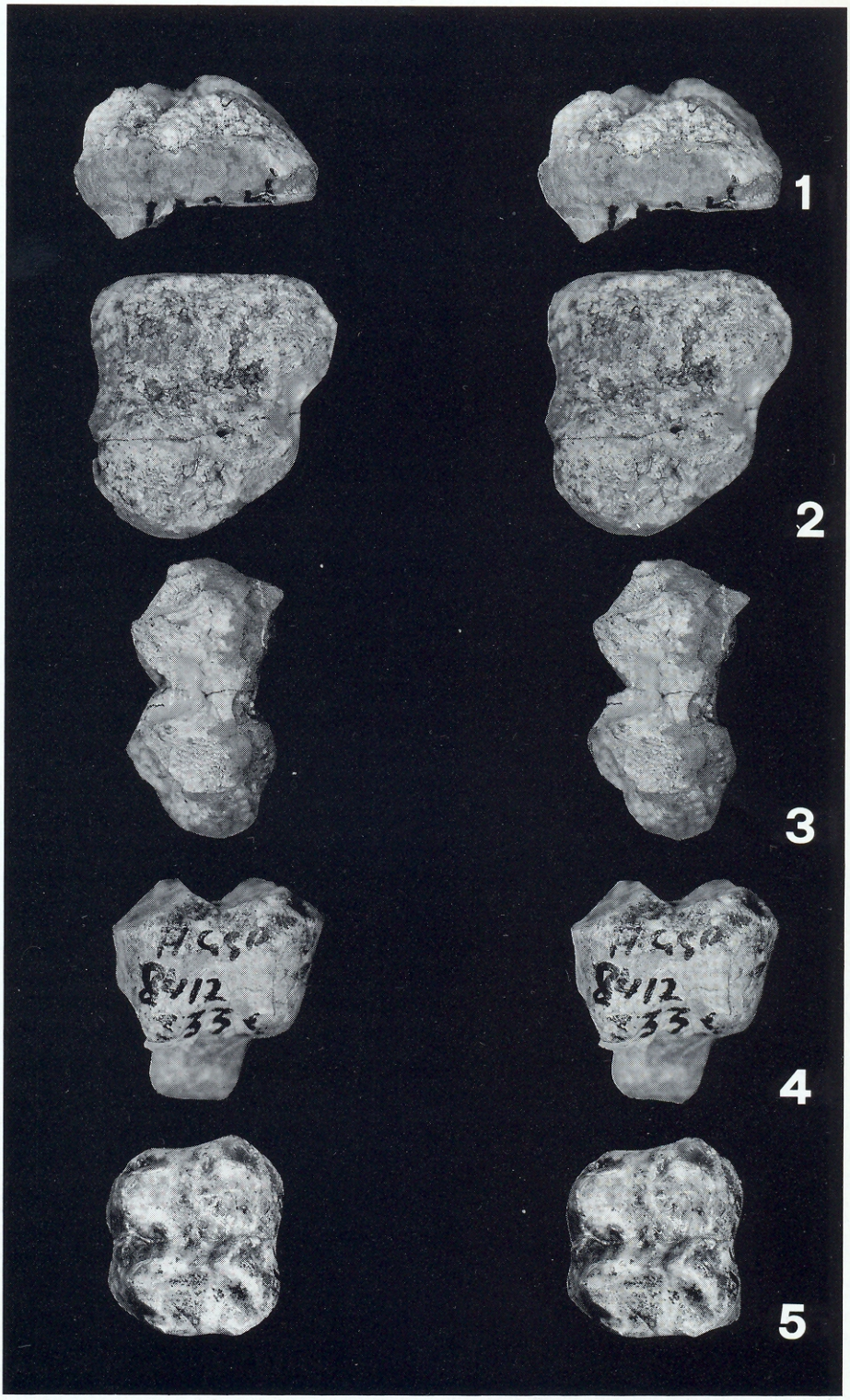
Some parts of the tooth are lost. The paraconule is large and fused to the protocone. It is not fused to the cingulum. The lingual cusps have a somewhat selenodont appearance. The metacone has a strong "rib". A labial cingulum is present.

SANITHERE SYSTEMATICS AND DETERMINATION OF THE H-GSP MATERIAL

The combination of strongly folded enamel, labial cingula in the lower molars, the fused paraconule with the protocone and the "ribs" at the labial sides of the labial cusps indicate that most of the material is sanithere. To properly identify our specimens we have to summarize sanithere systematics.

Recently, Pickford (1984) studied most of the sanithere material and he did not consider it to belong to Suidae. Pickford's (1984) classification is as follows:

Suoidea Cope, 1887
Sanitheriidae Pickford, 1984


1
2
3
4
5

Diamantohyus Stromer, 1926; *D. africanus* Stromer, 1926 (Africa) and *D. jeffreysi* (Forster-Cooper, 1913) (Indo-Pakistan)

Sanitherium Von Meyer, 1866; (including *Xenochoerus* Zdarsky, 1909); *S. schlagintweiti* Von Meyer, 1866 (Indo-Pakistan) (including *Sus pusillus* Falconer, 1868 and *Sanitherium cingulatum* Pilgrim, 1926); *S. leobense* (Zdarsky, 1909) (south-east Europe) (Including *Sanitherium masticum* Paraskevaidis, 1940); *S. nadirum* Wilkinson, 1976 (Africa).

Pickford (1984) gave the following diagnoses for *Sanitherium* (1) and "*Diamantohyus*" (2):

1) "A genus of the family Sanitheriidae in which P^4 has six cusps of subequal size. Lower molars wider than than in *Diamantohyus*."

2) "A genus of the family Sanitheriidae, in which the molarisation of the premolars is not as complete as it is in *Sanitherium*: P^4 with three main cusps and two subsidiary ones; anterior and postero-lingual cusps less developed than in *Sanitherium*; metastylid prominent in little worn lower molars."

The ranges for absolute width (DT) and length/width ratio (I = 100 × length/width) for the molars attributed to "*Diamantohyus*" and *Sanitherium* have a great overlap (table 1). *S. schlagintweiti* is the type species of *Sanitherium*. The lectotype of *schlagintweiti* (selected by Pickford) is a mandible with an M_2 and a partial M_3. The M_2 of the lectotype of *S. schlagintweiti* falls within the ranges of the material attributed to the genus "*Diamantohyus*". The values for another specimen attributed to *S. schlagintweiti* do not indicate a great width either (Pickford, 1984; table 2). The specimens figured by Von Meyer (1866) are well worn; in the M_2 the cusps are completely worn away, the M_3 is also much worn. The figure is too obscure to judge the size of the metastylid; it does not seem to be larger than that of "*D.*" *africanus* as figured

gures 3, 4 & 6). Of Pickford's (1984) diagnoses the remains as the main criterion for separation of the two genera. The only premolar attributed to *S. schlagintweiti* is a P_1, so it is not possible to compare this species to the other sanithere species.

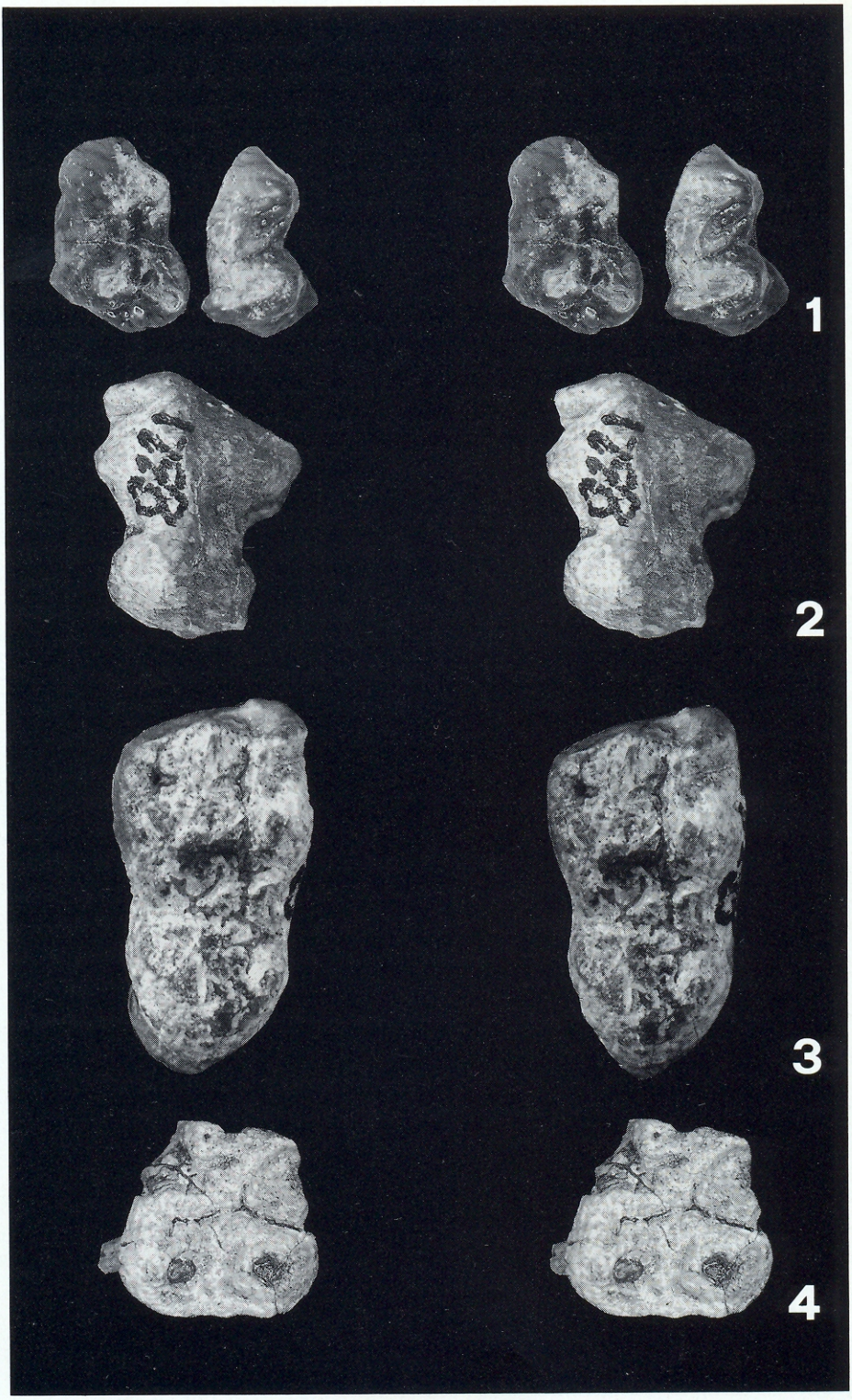
Pickford (1984) did not give a diagnosis for the type species *S. schlagintweiti*, the diagnoses of *S.* "*leobense*" (1) and *S.* "*nadirum*" (2) are respectively:

1) "A species of *Sanitherium* in which the length of the lower M_{1-2} is about 22 mm."

2) "A species of *Sanitherium* with wider molars than *S. schlagintweiti* or *S.* "*leobense*". M_{1-2} length about 22.5 mm."

←

Plate 1. *Sanitherium schlagintweiti* from Sind.
Stereopairs. All figures magnification 3×.
Figure 1 HGSP 8209/1124 left M^3, anterior view.
Figure 2 HGSP 8209/1124 left M^3, occlusal view.
Figure 3 HGSP 8209/1124 left M^3, buccal view.
Figure 4 HGSP 8412/3334 left M^1 or M^2, buccal view.
Figure 5 HGSP 8412/3334 left M^1 or M^2, occlusal view.


1
2
3
4

M_{1-2} length in *S. schlagintweiti* is 21.5 mm (Pickford, table 2). This is 96 % of 22.5 mm. Molar length is about equal in the three species. Average sizes of recent and fossil related sympatric suoid species with similar dentitions differ usually by 15% (V. d. Made, 1990) and size overlap may occur. Size differences for males an females of the same species are 3% (V. d. Made, in press). Differences of 2 to 4% are too small to be used for recognition of species, especially so if the samples are small. The only remaining criterion for distinction is the wider molars in *S.* "*nadirum*", which does not hold either, see the measurements (DT) and indices (I) (table 2).

We recognize two groups of sanitheres, on the one hand *S.* "*leobense*" and *S.* "*nadirum*" (which we cannot separate), with molarised premolars, and on the other hand "*D.*" *jeffreysi* and "*D.*" *africanus*, with premolars with a lesser degree of molarisation, but we do not know to which group *S. schlagintweiti* (the genotype of *Sanitherium*) belongs. Authors who created other sanithere species, failed to show that they are really different from *S. schlagintweiti* and those who proposed other sanithere genera failed to show that they are different from *Sanitherium*. For instance, the genus "*Diamantohyus*" was contrasted with "*Xenochoerus*" Zdarsky, 1909, yet Thenius (1956) synonymized *Xenochoerus* with *Sanitherium*.

Changes in relative lengths and widths (DAP′ and DT′, expressed as percentages of the length, DAP and width, DT of M1) and indices ($I = 100 \times DAP/DT$) of premolars and molars are important in suoid evolution (V. d. Made, 1989). DAP′ and DT′ are preferentially calculated on large samples, but if this is not possible tooth rows of one individual may be used (table 3). DAP′ and DT′ of the upper premolars are smaller in "*D.*" *jeffreysi* than in "*D.*" *africanus* and *S.* "*leobense*". The P^2 in "*D.*" *jeffreysi* is also more elongated. The P_4 in *S.* "*leobense*" is larger and more elongated than that of "*D.*" *africanus*. The M_3 of *S.* "*leobense*" is narrower or smaller than the M_3 in "*D.*" *africanus*, in the M^3 this seems to be the other way around, so there is no clear trend in the last molars. The premolars of "*D.*" *africanus* and "*D.*" *jeffreysi* are less molarised than those of *S.* "*leobense*". On the basis of these data, three forms can be recognized: "*D.*" *jeffreysi* with small and simple premolars, "*D.*" *africanus* with large but still simple premolars and *S.* "*leobense*" with large and complicated premolars.

The premolars seem to have a continuous range from small and simple to complicated and large forms. In the following paragraph it will be shown that,

---

←

Plate 2. *Sanitherium schlagintweiti* from Sind.
Stereopairs. Figures 1, 2 and 4 magnification ×3, figure 3 magnification ×4.
Figure 1 HGSP 8209/1145 left M_1 or M_2, occlusal and buccal views.
Figure 2 HGSP 8321/2076 left M_3, lingual view.
Figure 3 HGSP 8321/2076 left M_3, occlusal view.
Figure 4 HGSP 8420/3445 left M^1 or M^2, occlusal view.

	N	min.	mean	max.	N	min.	mean	max.	N	min.	mean	max.
DT	M_1				M_2				M_3			
Sanitherium	4	6.5	6.7	7.0	6	7.5	8.0	8.5	4	8.1	8.8	9.1
S. schlagintweiti, holotype					1		8					
Diamantohyus	8	6.0	6.3	6.7	6	7.2	8.0	8.6	11	7.0	8.3	9.3
I	M_1				M_2				M_3			
Sanitherium	4	138	151	162	5	138	155	169	3	222	226	231
S. schlagintweiti, holotype					1		138					
Diamantohyus	8	145	156	167	5	135	147	160	8	195	214	238

Table 1. Width (DT) in millimeters and index (I = 100 × length/width) of all molars assigned by Pickford (1984) to the genera *Sanitherium* and "*Diamantohyus*" and of the holotype of *Sanitherium schlagintweiti*. The "genera" cannot be separated on the basis of width of the molars using absolute (DT), nor relative (I) width; the ranges overlap and the averages are close and the holotype of the typespecies *S. schlagintweiti* fits in both "genera". Measurements taken from Pickford (1984).

	N	min.	mean	max.	N	min.	mean	max.	N	min.	mean	max.
DT	M_1				M_2				M_3			
S. nadirum	1		7.0		3	8.0	8.2	8.5	2	8.9	9.0	9.1
S. schlagintweiti												
holotype					1		8					
all material	2	6.5	6.7	6.8	2	7.5	7.8	8	1		8.1	
S. leobense	1		6.5		1		8		1		9	
DT	M^1				M^2				M^3			
S. nadirum	0				1		10.5		2	10.6	11.0	11.4
S. leobense	2	9.4	9.5	9.6	2	11	11.1	11.1	2	11.2	11.6	12
S. schlagintweiti	0				0				0			
100 x (DAP/DT)	M_1				M_2				M_3			
S. nadirum	1		150		2	149	159	169	2	226	229	231
S. schlagintweiti												
holotype					1		138					
all material	2	138	150	162	2	138	153	167	1		222	
S. leobense	1		154		1		150		0			
100 x (DAP/DT)	M^1				M^2				M^3			
S. nadirum	0				1		98		2	114	120	125
S. leobense	2	96	101	106	2	101	103	105	2	108	115	121

Table 2. Width (DT) in mm and index (I = 100 × length/width) of the lower molars of the three species of *Sanitherium*, recognized by Pickford. Measurements from Pickford (1984) of all material he assigned to these species. The small differences are probably not real (considering sample size) and cannot be used for separating the species.

in addition to being more primitive the first two species are also older than the third species: a lineage seems probable. With the degree of molarisation of the premolars changing gradually, all species can be placed in the same genus. The one P_4 specimen known of *S.* "*nadirum*" is complicated and this species may be synonimised with its contemporary *S.* "*leobense*".

Von Meyer (1866) recorded *Hipparion* from the same locality as the holotype of *S. schlagintweiti*. This would imply that the holotype is from Nagri equivalent (or even younger) strata. Although "localities" in those days included often more than one level, he separately described fossils from three different localities in Khushalgar, which indicates that no material from different levels was lumped together. Later workers stated that the types came from Chinji equivalent strata (Pilgrim, 1926; Colbert, 1935; Pickford, 1984), but none of them could substantiate this. On basis of the provenance of the lectotype of *S. schlagintweiti*, we expect that *S. schlagintweiti* to have complicated premolars and that both *S.* "*leobense*" and *S.* "*nadirum*" are junior synonyms of this species.

It may prove that *S. schlagintweiti* has even more complicated premolars than *S.* "*leobense*", in which case, there will be four species, or it may prove to be difficult to separate *S. schlagintweiti* from "*D.*" *africanus* morphologically or from "*D.*" *africanus* and "*D.*" *jeffreysi* biometrically.

Our proposed classification is:

Sanitherium Von Meyer, 1866 with *S. schlagintweiti* Von Meyer, 1866 (including *S. leobense* and *S. nadirum*) (India, Africa, S.E. Europe);
S. africanus (Stromer, 1926) (Africa, ?India) and *S. jeffreysi* (Forster-Cooper, 1913) (India, ?Africa)

Present data do not allow for the distinction of geographical "species" in *Sanitherium*.

Because the H-GSP material does not include premolars, it can be identified to species level only in an indirect way. All four localities have *Conohyus* or have a stratigraphic position above the entry of this genus. We refer the H-GSP specimens to *S. schlagintweiti* because this species occurs together with *Conohyus* (see next section).

The determination of specimen HGSP 8412/3334 is tentative because of the wear of the tooth. The lingual roots are fused as in primitive peccaries and possibly in sanitheres. In Suidae and *Anthracotherium silistrense* these roots are separated. The tooth is smaller than that of *Anthracotherium silistrense* and more elongated. Pickford (1987) included in "*Pecarichoerus sminthos*": *Microbunodon sminthos* (a mandible from Bugti), *Lophochoerus exiguus* (a molar from Chinji) and *Pecarichoerus orientalis* (some teeth from Chinji). The size of the teeth increases with time. The Sehwan molar is intermediate in size, it also matches well the other material described here, it either belongs to *Sanitherium* or to "*P. sminthos*".

PALAEOGEOGRAPHIC AND BIOSTRATIGRAPHIC CONSIDERATIONS

S. jeffreysi and the more progressive *S. africanus* occur in faunas with

	P_2			P_3			P_4			M_1	M_2			M_3		
	DAP'	DT'	I	DAP'	DT'	I	DAP'	DT'	I	I	DAP'	DT'	I	DAP'	DT'	I
Diamantohyus africanus																
Karungu KA 45							103	97	154	145	--	--	--	195	143	197
Karungu KA 12577	88	55	231	94	97	154	103	97	154	145	--	--	--	195	143	197
Rusinga RU 2796										163	--	122	--	160	134	195
Rusinga RU 2807							91	83	164	150						
G. Zelten BU 6416-61							97	95	160	157	--	--	--	191	127	237
Sanitherium leobense																
Seegraben (Leoben)							116	80	179	147	120	120	147	--	114	--
Sanitherium schlagintweiti																
Khushalghar, holotype													138			
	p^2			p^3			p^4			M^1	M^2			M^3		
	DAP'	DT'	I	DAP'	DT'	I	DAP'	DT'	I	I	DAP'	DT'	I	DAP'	DT'	I
Diamantohyus jeffreysi																
Bugti	72	58	129	75	73	107	76	81	87	104	105	115	95			
Diamantohyus africanus																
Langental, holotype										106	127	116	116			
Karungu KA 12577 right	74	69	108	90	80	107	90	101	89	100	102	112	91	128	111	115
Karungu KA 12577 left	78	--	97	94	--	106	94	--	94	--	111	--	--	139	--	--
G. Zelten BU-640-2										99	122	106				
Sanitherium leobense																
Seegraben (Leoben)	78	67	116	86	78	109	92	99	92	99	121	119	101	142	123	114
Chios	76	67	109	85	80	101	101	91	107	96	120	116	99	147	117	121

Table 3. Lengths (DAP') and widths (DT') of sanithere cheek teeth expressed as a percentage of the same dimension in the M1. I stands for length/width × 100. Data were taken from Pickford (1984), except for those on the Seegraben material, which was measured by us.

scheme for correlation	Asia		Africa		Europe	
S. schlagintweiti *Conohyus*	Khushalgar Chinji Formation	*S. schlagintweiti* *Conohyus*	Maboko Nyakach Ombo?	*S. schlagintweiti* (= *S. "nadirum"*) *Conohyus*	MN 6 - 9	*Conohyus*
S. schlagintweiti *Bunolistriodon* *Conohyus*	lower Manchar Fm.	*S. schlagintweiti* *Conohyus* *Bunolistriodon*	Ombo?	*S. schlagintweiti* (= *S. "nadirum"*)	MN 5 Seegraben (Leoben) Chios	*S. schlagintweiti* (= *S. "leobense"*) *Conohyus* *Bunolistriodon*
S. africanus *Bunolistriodon*		*S. africanus?* *Bunolistriodon?*	Gebel Zelten (Set III)	*S. africanus*	MN 4	*Bunolistriodon*
			Rusinga Karungu (Set II)	*S. africanus* *Bunolistriodon*		
S. jeffreysi *Bunolistriodon*	Bugti	*S. jeffreysi* *Bunolistriodon*		*S. jeffreysi?* *Bunolistriodon?*		

Table 4. Schematic distribution of the species of *Sanitherium*. Per area biozones and formations or localities where Sanitheres are found are indicated as well as the presence or absence of *Conohyus* or *Bunolistriodon* in these levels. *Conohyus* has recently been found at Maboko and Nyakach (Pickford, pers. comm.).

Bunolistriodon but no *Conohyus* or faunas of similar age (Bugti, Karungu, Rusinga, Gebel Zelten; Pickford 1984, 1986 and 1987) while *S. schlagintweiti* was found with *Bunolistriodon* and *Conohyus* or with faunas of a similar age (lower Manchar Formation, Chios, Leoben: the last two localities are dated MN 5; V.d. Made, in press; MN = Neogene Mammal Units, Mein, 1977) or in younger faunas (Khushalgar, Von Meyer, 1866; Chinji, Colbert 1935; Maboko, Nyakach, Pickford, 1984). These associations indicate age: 1) the Bugti fauna (or at least a part of it, since the fauna does not seem to be homogeneous; Pickford, 1987) is the oldest fauna (Early Miocene); 2) Karungu, Rusinga and Gebel Zelten form a group of younger localities (Early Miocene) and 3) the localities from the lower Manchar Formation, Chios and Seegraben-Leoben are a still younger group, whyle the Maboko, Nyakach, Chinji Formation and Khushalgar localities are of Middle and Late Miocene age (table 4).

Not only the *Sanitherium* from Rusinga is more primitive than the one from the European MN 5 localities, the same holds for *Bunolistriodon*; *B. jeanelli* from Rusinga having primitive, elongated and relatively large premolars in comparison to the European *B. lockharti* and *B. latidens*. The relative size of the premolars in Indian *Bunolistriodon* is not known.

The presence of the same sanithere species in these three regions is not surprising. During the late Early Miocene and the Middle Miocene, there was a land connection between Africa, Arabia and Asia (Adams et al. 1983; Bernor et al. 1987; Campbell & Bernor, 1976; Rögl & Steininger, 1983). The eastern end of the Mediterranean was closed since the Burdigalian. South-eastern Europe was not well connected to western Europe, but it was connected to the Middle East (see figure 1). Indications for a tropical climate in the Early Miocene of France (Pickford, 1990) suggest that the whole area where *Sanitherium* is found was tropical and that similar biotopes may have occurred in south east Europe, Pakistan and Africa.

Although there have been ecological barriers to certain species, other species could travel. Some examples will show that connections between the three areas existed during the period from which this genus is known.

Conohyus entered Europe in MN 5, at about the same time it entered India ("Kamlial") (Van der Made 1988a & b, 1989, in press). It is present in the Manchar Formation in some of the localities with sanitheres. Also *Giraffokeryx* is found in India, Turkey and south-eastern Europe in MN 5 (Pavlovic, 1969; Gentry, 1990). Earlier the first bovids entered India between the Bugti fauna and the fauna of the lower Manchar Formation. Still earlier, migrations in this area were possible for *Bunolistriodon*, elephants and deinotheres.

ACKNOWLEDGEMENTS

The present study is a contribution to the Howard University-Geological Survey of Pakistan project entitled "Cenozoic Mammals and Biostratigraphy of Pakistan". This project is under the direction of S.T. Hussain (Howard University) and S.M. Ibrahim Shah (Geological Survey of Pakistan). We thank Mr.

A.H. Kazmi, Director General, Geological Survey of Pakistan and his staff for their continuous support of the project.

We are indebted to Dr. Greve of the Joanneum in Graz and to the Director General of the Geological Survey of India for allowing one of us to study the sanithere material in their collections. Prof. J.E. van Hinte and Dr. J. de Vos reviewed the manuscript and made useful comments. We also thank Dr. R.L. Bernor who read an earlier draft of the manuscript.

The field work was supported by several grants from the Smithsonian Institution, current grant number is 7087190000-13.

REFERENCES

Adams, C.G., A.W. Gentry & P.J. Whybrow - Dating the terminal Tethyan event. In: J.E. Meulenkamp ed. Reconstruction of marine paleoenvironments. Utrecht Micropaleontological Bulletins, **30**, 273-298 (1983).

Bernor, R.L., M. Brunet, L. Ginsburg, P. Mein, M. Pickford, F. Rögl, S. Sen, F. Steininger & H. Thomas - A consideration of some major topics concerning old world Miocene mammalian chronology, migrations and paleogeography. Geobios, **20**, 4, 431-439 (1987).

Campbell, B.G. & R.L. Bernor - The origin of the Hominidae: Africa or Asia? Journal of Human Evolution, **5**, 441-454 (1976).

Colbert, E.H. - Siwalik mammals in the African Museum of Natural History. Trans. Am. philos. Soc., New York, **26**, 1-401 (1935).

Forster-Cooper, C. - New anthracotheres and allied forms from Baluchistan - preliminary notice. Ann. Mag. nat. Hist. London, **12**, 514-522 (1913).

Gentry, A.W. - Ruminant artiodactyls of Paşalar, Turkey. Journal of Human Evolution **19**, 529-550 (1990).

Jacobs, L.L., L.J. Flynn, W.R. Downs & J.C. Barry - *Quo vadis, Antemus*? The Siwalik Muroid record. In: E.H. Lindsay et al. European Neogene Mammal Chronology. Plenum press New York, 573-586 (1990).

Made, J. van der - Two *Conohyus* lineages (Tetraconodontinae, Suidae). IV Jornadas de Paleontología, resúmenes de las communicaciones, Salamanca, 58 (1988a).

Made, J. van der - Iberian Suoidea (Pigs and Peccaries). Coloquio Homenaje a Rafael Adrover Bioeventos y Suceciones faunisticas en el Terciario Continental Iberico, Sabadell, Resúmenes, 20-21 (1988b).

Made, J. van der - A *Conohyus* - lineage (Suidae, Artiodactyla) from the Miocene of Europe. Revista Española de Paleontología, **3**, 19-28 (1989a).

Made, J. van der - Relative tooth sizes in Suoidea. V Jornadas de Paleontología. Resúmenes de comunicaciones, Valencia, 83-84 (1989b).

Made, J. van der - A range-chart for European Suidae and Tayassuidae. Paleontología y Evolución, in press.

Mein, P. - Proposition de biozonation du Neogène Mediterraneen à partir des mammifères. In: M.T. Alberdi & E. Aguirre. Actas I Coloquio intenacional sobre biostratigrafía continental del Neogeno Superior y Cuaternario Inferior. Trabajos Sobre Neogeno-Cuaternario 4: 112-113 (1975).

Meyer, H. von - Ueber die Fossilen von Wirbeltieren welche die Herren von Schlagintweit von Ihren Reisen Indien und Hochasien mittgebracht haben. Palaeontographica, Stuttgart, **15**, 1-40 (1866).

Paraskevaidis, I. - Eine Obermiozän Fauna von Chios. Neues Jb. Miner. geol. Palaeont., **83**, 369-442 (1940).

Pavlovic, M.B. - Miozän-Säugetiere des Toplicka-Beckens. Geoloski Anali balk. Poluost., **34**, 269-394 (1969).

Pickford, M. - A revision of the Sanitheriidae, a new family of Suiformes (Mammalia). Geobios, **17**, 2, 133-154 (1984).

Pickford, M. - A revision of the Miocene Suidae and Tayassuidae (Artiodactyla, Mammalia) of Africa. Tertiary Res. Spec. Paper, **7**, 1-83 (1986).

Pickford, M. - Révision des Suiformes (Artiodactyla, Mammalia) de Bugti (Pakistan). Annales de Paléontologie (vert. Invert.), **73**, 4, 289-350 (1987).

Pickford, M. - Dynamics of Old World Biogeographic Realms during the Neogene: Implications for Biostratigraphy. In: E.H. Lindsay et al. European Neogene Mammal Chronology. Plenum press New York, 413-442 (1990).

Pilgrim, G.E. - The fossil Suidae of India. Mem. geol. Surv. India Palaeont. indica, Calcutta, **4**, 1, 68 (1926).

Rögl, F. & F.F. Steinginger - Vom Zerfall der Tethys zu Mediterran und Parathethys. Ann. Naturhist. Mus. Wien, **85A**, 135-163 (1983).

Stromer, E. - Reste Land - und Süsswasser - bewohnenden Wirbeltiere aus den Diamantenfeldern Deutsch Südwestafrikas. In: E. Kaiser. Die Diamantenwüste Südwestafrikas, Berlin, **2**, 107-153 (1926).

Thenius, E. - Die Suiden und Tayassuiden der Steirischen Tertiärs. Beitrage zur Kenntnis der Säugetierreste des Steirischen Tertiärs VIII. Sber. Akad. Wiss. Wien, 1, 165, 337-382 (1956).

Wilkinson, A.F. - The Lower Miocene Suidae of Africa. In R.J.G. Savage & S.C. Coryndon eds. Fossil vertebrates of Africa, **4**, 173-282 (1976).

Zdarsky, A. - Die miozäne Säugetierfaune von Leoben. Jb. K. K. geol. Reichsanst., Wien, **59**, 245-288 (1909).