Riv. It. Paleont. Strat.	v. 98	n. 3	pp. 353-370
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ON DORCATHERIUM NAGRII (TRAGULIDAE, MAMMALIA) - WITH A **REVIEW OF SIWALIK TRAGULIDS**

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Key-words: Mammals, Dorcatheres, Systematic review, Siwalik, India, Neogene.

Riassunto. Frammenti mascellari e mandibolari ben conservati di Dorcatherium nagrii provenienti dal Middle Siwalik di Haritalyangar (India) permettono una diagnosi più completa della specie. Sulla base di confronti dettagliati, di analisi statistiche e della revisione di varie specie di Dorcatherium di Siwalik vengono suggeriti cambiamenti nelle attribuzioni specifiche di parte del materiale di Dorcatherium descritto in precedenza. Il peso corporale stimato dei Dorcatheri di Siwalik si distribuisce approssimatamente tra 4 kg e 41 kg.

Abstract. Well-preserved maxillary and mandibular fragments of Dorcatherium nagrii described in this paper from the Middle Siwaliks of Haritalyangar (India) provide a more complete diagnosis of D. nagrii. On the basis of detailed comparison, statistical analysis and review of various Dorcatherium species from Siwaliks, changes in the specific affiliations of some of the Dorcatherium material described earlier are suggested. The estimated body weight of Siwalik dorcatheres ranges from approximately 4 kg to 41 kg.

Introduction.

The Siwalik deposits of the Haritalyangar area, Bilaspur District, Himachal Pradesh, India are known all over the world for their rich and varied mammalian fauna (Prasad, 1970; Chopra, 1983; Vasishat, 1985). In the present paper the author describes additional material of the tragulid taxon Dorcatherium nagrii Prasad (1970) from the Nagrii Formation of Middle Siwaliks exposed about 0.5 km northeast of Talyangar Village (Fig. 1). These beds, which in the past yielded many hominoid and adapoid primates, have been investigated magnetostratigraphically and an age of between 7.5 to 7 MA has been assigned to them (Johnson et al., 1983). The present collection, which includes many maxillary and mandibular fragments, probably represents the best preserved and the most complete specimens of Dorcatherium nagrii described so far from the Siwaliks. The P2 and P3 of D. nagrii are described here for the first time. The relative completeness of the material has also enabled the author to

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update the specific diagnosis of *D. nagrii*. In addition to the amended diagnosis and systematic descriptions, detailed comparison, variation, zoogeography and statistical analysis of *D. nagrii* material are presented here for the first time. The paper also includes a brief review of the genus *Dorcatherium*.

Systematic palaeontology

Order Artiodactyla Owen, 1848 Family *T r a g u l i d a e* Milne Edwards, 1864 Genus *Dorcatherium* Kaup, 1833 *Dorcatherium nagrii* Prasad, 1970 Pl. 24, fig. a-k

Revised specific diagnosis.

A small species of *Dorcatherium*, about 30 to 40% smaller than *D. minus* (Lydekker, 1876), 50 to 60% smaller than *D. majus* (Lydekker, 1876) and about 30 to 35% larger than *D. minimus* (West, 1980) in length and width dimensions of the teeth. Upper molars with very strong mesostyle and strong anterior rib; cingulum weakly developed. Basal internal pillar (entostyle) on upper molars absent and in this respect differs from *D. majus* and *D. minus*. M 1/1 comparatively small. P² bicuspid. Mandible thin and slender; deepest below M₃. Molars less hypsodont than *D. minus*; small anterior and posterior cingular developments on lower molars. Basal internal pillar on lower molars absent or vestigial. Double-fold on the distal side of protoconid and paraconid well-developed (Revised from Vasishat, 1985).

New material. VPL/AS/H/100, left maxillary fragment with P^4 - M^3 ; VPL/AS/H/101, right mandibular fragment with P₂-P₃; VPL/AS/H/102, right mandibular ramus, with DM₄, M₁-M₃; VPL/AS/H/104, right M³; VPL/AS/H/103, left maxillary fragment with M¹-M³; VPL/AS/H/105, right mandibular fragment with M₁-M₃; VPL/AS/H/106, left mandibular fragment with M₁ and M₂; VPL/AS/H/107, left mandibular fragment with M₂.

Horizon. All specimens are from Nagrii Formation of Middle Siwaliks.

Locality. About 0.5 km northeast of Talyangar Village, Bilaspur District, Himachal Pradesh, India.

Repository. The specimens are in the collections of Prof. Ashok Sahni, Laboratory of Vertebrate Palaeontology (VPL), Centre of Advanced Study in Geology, Panjab University, Chandigarh.

Description.

Maxilla. The left maxilla (VPL/AS/H/100) with P⁴, M¹, M², and M³ also pre-



Fig. 1 - Locality map of the area.

serves the alveolar process and a portion of the palate (Pl. 24, fig. a, b). P^4 is bicuspid with a lingual and a labial cusp. The paracone is very prominent, more than in the molars. The parastyle and mesostyle are well-developed and display a prominent rib between them. The protocone is broken.

 M^1 is the smallest of the three molars with a strong mesostyle and a very weak metastyle. The anterior rib is more prominent than the posterior rib. The protocone does not form a complete crescent due to the weak development of its posterior wing. A moderate cingulum surrounds the base of the protocone.

The cingulum becomes weaker from M^1 to M^3 . Basal internal pillar is absent in all the three molars. M^2 is similar to M^1 in its crown morphology, except for its larger size. The crown details of M^3 are similar to M^1 and M^2 with small differences, viz. slightly stronger parastyle and metastyle, larger size, transverse diameter of distal lobe less than the mesial lobe, and the absence of cingulum.

Mandible. The right mandibular fragment (VPL/AS/H/101) with P₂ and P₃ is laterally compressed (Pl. 24, fig e-g). P₂ is bucco-lingually compressed with a strong and medial principal cuspid and a comparatively small and distally placed accessory cuspid, arranged in a mesio-distal direction. Lingually P₂ has two shallow valleys, one between the principal cuspid and the distal accessory cuspid, the second behind the distal accessory cuspid. But for its larger size, P₃ is similar to P₂.

Another right mandibular half (VPL/AS/H/102), which gradually thickens distally, preserves DM4, M1, M2, and M3 (Pl. 24, h-j). DM4 is elongated and laterally compressed with a proximal, a middle, and a distal lobe. Each lobe is defined by a deep notch in profile. The mesial lobe consists of labial and lingual cuspids, both showing transverse flattening but neither is developed as a true crescent. The middle and distal lobes agree closely in morphology with those of M1 and M2. The middle lobe shows traces of "Dorcatherium fold" and a small "Palaeomeryx fold" at its base on

MAXILLA

Sp.	$M^{1} + M^{2} + M^{3}$	I	2 2	Р	3	P	1	М	1	М	2	М	3
No.	L	L	В	L	В	L	В	L	В	L	В	L	В
VPL/AS/H/100	20.8	-		-	-	6.0	5.8	6.3	6.7	7.5	8.0	8.0	8,4
VPL/AS/H/103	21.0	-	-	-	-	-	-	6.2	6.6	7.5	7.9	8.1	8.9
VPL/AS/H/104	-	-	-	-	-	-	-	-	-	-	-	8.0	8.9

MANDIBLE

Sp. No.	$M_1 + M_2 + M_3$	Р	2	P ₃		P	ł	М	1	М	2	M	3
	L	L	В	L	В	L	В	L	В	L	В	L	В
VPL/AS/H/102	24.0	-	-	-	-	8.2	3.3	5.8	3.4	7.1	4.2	11.0	4.3
VPL/AS/H/101	-	5.2	2.3	7.0	2.6	-	-	-	÷	E	-	-	-
VPL/AS/H/105	-	-		-		-	-	-	-	7.4	3.8	11.5	4.7
VPL/AS/H/106	-	-	-	ж	ч.	-	-	5.9	3.6	6.7	3.9	-	- 1
VPL/AS/H/107	-	-	-	-	-	-	-	-	-	7.0	4.5	-	-

L=Mesio-distal diameter; B=Transverse diameter.

Tab. 1 - Measurements (mm) of the dentitions of D. nagrii from Haritalyangar.

Dorcatherium nagrii

the labial cuspid between the middle and distal lobes. Faint labial cingulum can be seen at the base of DM4.

 M^1 shows crown features similar to other species of *Dorcatherium*. The protoconid and paraconid show an enamel fold each on the distal side. The anterior cingulum is well-developed. There is only a slight trace of the external basal pillar between the protoconid and the hypoconid. M_2 is slightly larger than M_1 and its anterior cingulum is well-developed. The folds on the posterior aspect of the protoconid and paraconid of M_2 are stronger than in M_1 , and there is no external basal pillar. \dot{M}_3 is much more elongated than M_1 and M_2 due to the addition of a strong hypoconulid. There is no external basal pillar on M_3 . The measurements of the present material are given in Tab. 1.

Comparison.

The family *Tragulidae* is represented in the Siwaliks by two genera, viz. *Dorcabune* and *Dorcatherium*. The present material clearly differs from *Dorcabune* by its much smaller size. It also differs from *Dorcabune* in the presence of a smooth and thin enamel. In *Dorcabune* the enamel is heavy and wrinkled (Colbert, 1935). The present specimens further differ from *Dorcabune* by the absence of an isolated parastyle, mesostyle and backwardly directed labial ridge on the protocone of upper molars. The lower molars of *Dorcabune* are broad with a wide hypoconulid on M₃. In the present material, the lower molars are narrow and the hypoconulid on M₃ is small and narrow. The present specimens are, therefore, very much different from *Dorcabune* and are congeneric with *Dorcatherium*.

The present specimens are on an average about 50 to 60 per cent smaller in linear dimensions than *Dorcatherium majus* and about 35 to 40 per cent smaller than *Dorcatherium minus*. Besides size, the present material differs from *D. minus* and *D. majus* by the presence of a very strong mesostyle and mesial rib on upper molars. It also differs from *D. majus* and *D. minus* in the presence of a weak cingulum on upper molars and the absence of an external basal pillar on lower molars. In *D. majus* the cingulum on upper molars is well-developed, the mesostyle and mesial rib on upper molars relatively less strong, and the lower molars have a prominent external basal pillar. The present material can be further differentiated from *D. minus* by its comparatively less hypsodont molars. The M^3 in the present collection differs from that of *D. minimus* by its 30 to 35 per cent larger size and the presence of a relatively strong mesial rib. The present material differs from *D. birmanicus* by its small size. In size, the specimens in the present collection come very close to *Dorcatherium nagrii*.

Figures 2 to 5 represent the plots of the length and breadth of upper and lower molars of some species of *Dorcatherium* from the Indian subcontinent and Africa, in addition to the material described here. For dimensional and other details of the *Dorcatherium* material used for these plots, besides the present material, reference may be



Fig. 2 - Scatter diagram of the length and breadth of M^1 and M_1 of some Dorcatherium species.

Dorcatherium nagrii

made to the following works: Lydekker (1876), Colbert (1935), Prasad (1970), Hamilton (1978), Gaur et al. (1980, 1983), Sahni et al. (1980), West (1980), Sankhyan (1981), Vasishat et al. (1983, 1985) and Vasishat (1985). These plots clearly demonstrate the metric affinities of the present material with *D. nagrii* (Fig. 2-5). The present material also shares with *D. nagrii* a number of dental characters, such as less hypsodont molars, very strong mesostyle and mesial rib on upper molars, weak to no internal cingulum on upper molars, and the absence of external basal pillar on lower molars. In view of their similarity in size and crown morphology with *D. nagrii*, the specimens in the present collection are assigned to this species.



Fig. 3 - Scatter diagram of the length and breadth of M^2 of some species of Dorcatherium.



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Fig. 4 - Scatter diagram of the length and breadth of M³ of some species of Dorcatherium.

Statistical analysis.

The dentitions of *Dorcatherium nagrii* were subjected to some elementary statistical analysis. The results are presented in Tab. 2. The limitations of the sample size restricted the application of these tests to the molars only. As can be seen in Tab. 2 and Fig. 6, the coefficient of variation (CV) of lower molars is greater than the upper molars pointing towards greater size variation among lower molars. The combined length of M 1/1, M 2/2, M 3/3 shows the least variation and is therefore a better



Fig. 5 - Scatter diagram of the length and breadth of M2 and M3 of some Dorcatherium species.

character for identification than the lengths of individual molars. Among the upper molars, the transverse diameter is a very variable character, as is evident from its high CV values (Tab. 2; Fig. 6). It follows that the length of upper molars of *D. nagrii* is a more stable character than the breadth and is therefore more reliable for the purposes of identification. The length of M^2 shows the least CV among upper molars and is therefore the second most stable character after the combined length of upper molars. As in the case of upper molars, the transverse diameter of lower molars, except M₃, too shows higher CV values than the length (Tab. 2; Fig. 6) and is hence more varia-

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Measurement		N	x	Range	SD	CV
UPPER MOLAF	lS I I I I					
Combined length	of $M^1 + M^2 + M^3$	3	20.96	20.80-21.10	0.12±0.04	0.60
	L	10	6.40	6.00-7.00	0.36±0.03	5.70
M ¹	В	10	6.51	5.70-7.50	0.54±0.05	8.35
	Ι	10	102.16	93.80-108.70	5.05 ± 0.50	4.95
	L	9	7.24	7.00-7.50	0.23±0.02	3.26
M ²	В	8	6.87	6.00-8.00	0.73±0.09	10.61
	Ι	9	93.45	82.60-106.60	8.61±0.96	9.22
	L	4	7.80	7.10-8.10	0.41±0.10	5.20
M ³	В	4	8.30	7.00-8.90	0.77±0.19	9.36
	1	4	106.17	98.60-111.20	4.96±1.24	4.67
LOWFR MOLA	RS					
Combined length	of $M_1 + M_2 + M_3$	5	24.62	24.00-26.10	1.17±0.23	4.77
	L	10	6.29	5.30-7.10	0.69±0.06	11.02
M_1	В	10	3.68	3.00-4.30	0.48±0.05	13.11
	I	10	59.94	42.80-78.63	11.20 ± 1.12	18.69
	L	15	7.45	6.60-8.60	0.60±0.04	8.09
M ₂	В	15	4.28	3.00-5.10	0.53 ± 0.03	12.49
	Ι	15	57.09	37.50-64.30	6.51±0.43	11.41
	L	13	10.46	9.00-12.40	1.01±0.08	9.69
M3	В	13	4.66	4.00-5.30	0.39±0.03	8.45
	I	13	44.79	39.10-51.20	4.53±0.35	10.10
			1	1		1

L=Mesio-distal diameter; B=Transverse diameter; I=Index (B/L x 100).

Tab. 2 - Statistical analysis of upper and lower molars of Dorcatherium nagrii.

ble. Indices of both upper and lower molars, in general, have high CV values and show greater variation, and are therefore least reliable for identification purposes. One reason for the high CV values, particularly that of breadth, could be the wear-related change as most often the measurements are taken at the occlusal level. Some of the high CV values could partly be also due to the collation of measurements taken by different workers.

Estimated body weight of Siwalik Dorcatherium species.

Body size is a very useful parameter to understand the natural history and ecology of mammals (Western, 1979). Many of the demographic and behavioural



Fig. 6 - Histograms of the coefficient of variation of length, breadth and index of upper and lower molars of *Dorcatherium nagrii*.

aspects such as relative abundance, diversity, longevity, social organization, locomotion, home range, etc. are to a certain extent related to body size. The teeth of fossil mammals provide useful estimates of body weight. In this paper, the author has followed Gingerich et al. (1982) who devised a fairly easy and reliable method of predicting body weight from tooth crown area and suggested the use of lower molars, particularly M₁, for this purpose. According to Gingerich et al. (1982), "the area of M₁ and M₂ are most highly correlated with body size, and measurements of these teeth are consequently the best to use in predicting body weight from tooth size". Since M₁ of various Siwalik *Dorcatherium* species shows greater variation in dimensions (Tab. 2), the M₂ area was employed for estimating body weight, except in the case of *D. minimus* which is known only by a M³. The estimated body weights of different *Dorcatherium* species known from the Siwaliks of the Indian subcontinent are presented in Tab. 3.

Zoogeography of *Dorcatherium* in the Indian subcontinent, with particular reference to *D. nagrii*.

Dorcatherium is a widespread genus and is known from the Miocene deposits of Asia, Africa and Europe. In the Palaearctic region the tragulids, however, disappeared in the Miocene and their niche was probably occupied by a cold-loving musk deer, *Moschus* (Gentry, 1978). Today we have only two survivors, viz. the tropical Asian chevrotain, *Tragulus*, and the west African, *Hyemoschus*, of the once widespread and varied family *Tragulidae*. In the Indian subcontinent, *Dorcatherium* ranges from lower Middle Miocene to Lower Pleistocene. The oldest record of *Dorcatherium* is in the Basal Manchar Formation, Sind, Pakistan (Raza et al., 1984), and the youngest record in the Pinjor Formation of Upper Siwaliks near Chandigarh (Gaur et al., 1980). The Basal Manchar Formation (15 to 16 MA old) is considered older than the Chinji Formation of Lower Siwaliks (Raza et al., 1984). *Dorcatherium* was distributed over the Indian subcontinent from Pakistan in the west to Nepal, India and Burma in the east. In China, two species of *Dorcatherium*, *D. minus* and *D. progressus*, occur in the Late Miocene deposits at the hominoid site of Lufeng, South China (Chuan Kuei et al., 1984).

Dorcatherium nagrii ranges from the Chinji Formation of Lower Siwaliks to Dhokpathan Formation of Middle Siwaliks and questionably even up to Tatrot Formation of Upper Siwaliks. The fossil record available up to now reveals that geographically the species was distributed from Chinji and Hasnot (Pakistan) in the west to Kalagarh (Utter Pradesh) in the east. The distribution of *D. nagrii* during the Neogene is presented in Fig. 7. The occurrence of this tragulid probably indicates roughly similar ecological conditions prevailing in the Siwaliks basin stretching between Hasnot and Chinji in Pakistan to Kalagarh in India, during the Neogene (Gaur & Vasishat, 1989).

Dorcatherium nagrii

Sr.	Species	Locality	Ν	Estimated ⁽¹⁾ Weight (Kg)	95% ⁽²⁾ Confidence Interval (Kg)
1.	D. nagrii	Siwaliks (India)	15	4.7	4.4 - 5.0
2.	D. minus	Siwaliks (India)	4	18.5	16.5 - 20.5
3.	D. majus	Siwaliks (India)	4	41.1	35.7 - 47.3
4.	D. minimus	Siwaliks (Pakistan)	1	4.4	4.0 - 4.8
5.	D. pigotti	Africa	1	6.3	5.9 - 6.8
6.	D. chappuisi	Africa	1	16.8	15.2 - 18.5

N = Number of specimens.

- The weight was calculated following Gingerich et al. (1982) using the equation, X=1nb + a 1nY (X=body weight, Y=tooth crown area, a and b are constants).
- (2) The 95% confidence interval was calculated using the following formula given by Gingerich et al (1982):

$$\ln X = \ln X \pm 1.96 V C_1 + (\ln X - C_2)^2 (C_3)$$

(C1, C2, C3 are constants).

Tab. 3 - Comparative table of estimated weight of some Dorcatherium species from India and Africa.



Fig. 7 - Geographical distribution of *Dorcatherium nagrii* during the Neogene. 1) Chinji; 2) Hasnot; 3) Udhampur; 4) Ramnagar; 5) Bhapral; 6) Haritalyangar; 7) Nurpur; 8) Kalagarh.

Brief review of Siwalik fossil tragulids.

As mentioned earlier, Dorcabune and Dorcatherium are the two tragulid genera represented in the Siwaliks. A third species, Tragulus sivalensis, created by Lydekker (1882) on a molar from the Middle Siwalik of Hasnot (Pakistan), was considered to be "of very doubtful value "by Colbert (1935, p. 314). Dorcabune is more primitive than Dorcatherium and shows many primitive characters such as very bunodont molars, thick and rugose enamel, well-developed cingular shelves, etc. In many respects Dorcabune resembles primitive anthracotheres. The possibility that Dorcabune is in fact an anthracothere has not yet been eliminated (Gentry, 1978, p. 578). The extant genera of tragulids, Tragulus and Hyemoschus, are very similar to Dorcatherium in some of their characters and they may eventually be synonymised under Dorcatherium (Gentry, 1978). In the Indian subcontinent, the genus Dorcatherium is known by four species, viz. D. majus, D. minus, D. nagrii and D. minimus. Dorcatherium sp. of Colbert (1935) was included under the newly erected species, D. nagrii, by Prasad (1970). The plots of the molar dimensions of various Dorcatherium species from the Indian subcontinent (Fig. 2-5) display three distinct clusters referable to three species, viz. D. nagrii, D. majus, and D. minus. The fourth species, D. minimus, is poorly known. Except for its relatively small size, it is not much different from D. nagrii in morphology and, therefore, needs further investigations.

A major character commonly employed to distinguish between the Siwalik Dorcatherium species is most often the difference in size. However, besides size, there are variations in the degree of development of various dental characters, such as presence or absence of basal pillars, degree of development of basal cingulum, degree of hypsodonty, etc., which help to differentiate Siwalik dorcatheres.

If we take into consideration presence or absence of primitive and advanced characters, then *Dorcatherium nagrii* would appear to be the most advanced among the Siwalik dorcatheres and *D. majus* the most primitive. *Dorcatherium nagrii* displays many advanced characters, such as the absence of internal basal pillars in upper molars and its absence or vestigial nature in lower molars, the reduction of internal cingulum, presence of strong styles, etc. *D. nagrii* is also known from relatively younger deposits than other Siwaliks *Dorcatherium* species. On the basis of the presence of advanced characters and its occurrence in younger deposits it can be surmised that *D. nagrii* was probably on a line leading to the extant Asian chevrotain, *Tragulus*.

An examination of Fig. 2-4 reveals some interesting facts. Specimen number AM 19306 (Colbert, 1935; Prasad, 1970) of *D. nagrii* is larger than the average *D. nagrii* and comes much closer to *D. minus*. It would be appropriate therefore to remove this specimen from the species *D. nagrii* and include it under *D. minus*. Similarly specimen number AM 19517 (Colbert, 1935) would seem to fit better in size with M^1 of *D. majus* than *D. minus*.

A comparison of the Indian *Dorcatherium* species with those from Africa shows that *D. majus* is much larger than some large African species, e.g., *D. chappuisi* Aram-

Summary.

Dorcatherium nagrii is probably the most advanced species among the Indian fossil tragulids and ranges from Chinji Formation of Lower Siwaliks to Tatrot Formation of Upper Siwaliks. It may probably be on a line leading to the extant Asian chevrotain Tragulus. Upper molars of D. nagrii are less variable in size than the lower molars. Length of molars is a more stable character and the index the most variable. The combined length of molar series shows the least variation. The oldest record of Dorcatherium, as yet, in the Indian subcontinent is from the Basal Manchar deposits, Pakistan and the youngest from the Pinjor Formation of Upper Siwalik near Chandigarh, India. In the Indian subcontinent, three well-defined species of Dorcatherium, viz., D. majus, D. minus and D. nagrii can be recognised. D. minimus is poorly known and needs further investigations. D. majus was the heaviest of the Siwalik dorcatheres and D. minimus the lightest. The geographic distribution of dorcatheres suggests the presence of similar ecological conditions in the Middle and Late Miocene Siwalik deposits of India, Pakistan and Nepal, and the Latest Miocene Baodean deposits of South China at Lufeng.

Acknowledgements.

The author is grateful to Prof. Ashok Sahni, Center of Advanced Study in Geology, Panjab University, Chandigarh for providing the fossil material for the present work and also for some very useful suggestions. Thanks are also due to Prof. A. Azzaroli, Museo di Geologia e Paleontologia, dell'Università di Firenze, Firenze, Italy, for going through the manuscript and some valuable suggestions.

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- Fig. a, b Left maxillary fragment (VPL/AS/H/100) with P^4 -M³ (a = occlusal view; b = buccal view).
- Fig. c, d Left maxillary fragment (VPL/AS/H/104) with M¹-M³ (c= occlusal view; d= buccal view).
- Fig. e-g Right mandibular fragment (VPL/AS/H/101) with P2-P3 (e= lingual view; f= occlusal view; g=
 - buccal view).
- Fig. h-j Right mandibular fragment (VPL/AS/H/102) with DM4, M1-M3 (h= occlusal view; i= buccal view; j= lingual view).
- Fig. k Occlusal view of a right mandibular fragment (VPL/AS/H/105) with M1-M3.

(Bar represents 10 mm)

