THE MICROSTRUCTURE OF TOOTH ENAMEL IN MULTITUBERCULATE MAMMALS

by G. FOSSE, Z. KIELAN-JAWOROWSKA *and* S. G. SKAALE

ABSTRACT. The enamel microstructure of single teeth and teeth *in situ* in whole jaws of late Jurassic, late Cretaceous, and Palaeocene multituberculates belonging to the Plagiaulacoidea, Taeniolabidoidea, Ptilodontoidea, and *Meniscoessus* (Cimolomyidae, suborder indet.) is examined by incident light microscopy, scanning electron microscopy (SEM), and polarized light microscopy. For comparison one docodont tooth and some single late Cretaceous and Recent eutherian teeth are included. The enamel of the Plagiaulacoidea like that of the docodont tooth is not prismatic, but consists of radially arranged, closely packed 5 μm thick columns of crystals, which diverge from the central axis of each column towards the outer enamel surface. The Asian as well as the North American Taeniolabidoidea have gigantoprismatic enamel, the numerical density of prisms per unit area being four to five times lower than in the Ptilodontoidea and Eutheria. In most taeniolabidoid jaws the prism density is somewhat higher in the molars than in the incisors. The oldest gigantoprismatic enamel was found in some undescribed multituberculate teeth from the early Cretaceous of Asia. As *Meniscoessus* (suborder indet.) has gigantoprismatic enamel, it is suggested that this feature may be useful in establishing the taxonomic position of some multituberculate groups.

THIS paper examines the tooth enamel of multituberculate mammals from the upper Jurassic, Kimmeridgian to the late Palaeocene, in order to discover differences in enamel microstructure among the suborders Plagiaulacoidea, Ptilodontoidea, and Taeniolabidoidea, to elucidate their relationships.

Moss (1969) found that multituberculate enamel was a non-prismatic, continuous structure, and that it contained tubules which followed a zigzag course. Fosse *et al.* (1973) confirmed the presence of these zigzag tubules but challenged Moss' view on the non-prismatic enamel structure on the basis of six unidentified multituberculate teeth from the late Cretaceous in which the enamel was discontinuous and prismatic, the prisms being extremely large in comparison with those of other mammals. Subsequently Fosse *et al.* (1978) investigated the teeth of four identified multituberculate species, *Catopsalis joyneri* and *Stygimys kuszmauli* (Taeniolabidoidea) and *Mesodma thompsoni* and *M. formosa* (Ptilodontoidea). The number of prisms per mm^2 ranged from 3650 to 5860 in the members of the Taeniolabidoidea and from 26 600 to 27 200 in the Ptilodontoidea. The taeniolabidoid prism density was the lowest observed in any group of mammals.

Sahni (1979) studied the enamel microstructure in several late Cretaceous North American Ptilodontoidea and Taeniolabidoidea, as well as Eutheria (from the Hell Creek Formation of Montana, Sloan and Van Valen (1965)) and found large prisms in all the multituberculate genera. According to Sahni the prism density per mm^2 in *Mesodma* and *Meniscoessus* (suborder indet.—see Hahn and Hahn 1983) was 9000 and 7400 respectively, while in *Catopsalis* and *Stygimys* it was 8700 and 4500. The data for *Mesodma* differ considerably from those obtained by Fosse *et al.* (1978). Using the scales given on the *Mesodma* micrographs in Sahni's paper we calculated a mean prism density of 21 400 per mm^2.

In view of the differences between the results obtained by Fosse *et al.* (1978), by Sahni (1979, Table 1), and by us on Sahni's micrographs, concerning *Mesodma*, we decided to examine once more isolated teeth of *Mesodma* sp. and to compare them with a molar of *Meniscoessus* sp. (Cimolomyidae, suborder indet.), all from the late Cretaceous of North America, and with various taeniolabidoid teeth from the late Cretaceous of Asia (Kielan-Jaworowska 1970, 1974a), the Late Palaeocene of Asia (Matthew and Granger 1925), and the late Cretaceous of North America (Sloan

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and Van Valen 1965). All the North American late Cretaceous material comes from the Hell Creek Formation of Montana (Clemens *et al.* 1979). The late Cretaceous Asian material which forms the bulk of the material comes from the Djadokhta and Barun Goyot formations, or the stratigraphic equivalent of the latter: the red beds of Khermeen Tsav. We tentatively accept, after Gradzinski *et al.* (1977) that the Djadokhta Formation belongs to the upper Santonian and/or lower Campanian Stage, while the Barun Goyot Formation (and the red beds of Khermeen Tsav) belong to the middle Campanian Stage.

We also examined the enamel microstructure of isolated teeth from the early Cretaceous of Asia, which are at present being studied by Kielan-Jaworowska, Dashzeveg, and Trofimov. Some of these teeth (genus *Arginbaatar*) were assigned to the Taeniolabididae by Trofimov (1980), while Hahn and Hahn (1983) erected the family Arginbaataridae within the Plagiaulacoidea. Consequently at present we assign all the early Cretaceous Mongolian multituberculates to a suborder indet.

The earliest multituberculate teeth examined by us belong to the suborder Plagiaulacoidea and come from the late Jurassic, Kimmeridgian, of Portugal (Hahn 1969, 1971, 1978). From the same location we also included an unidentified docodont tooth for comparison, as well as teeth of late Cretaceous and Recent eutherian mammals.

ABBREVIATIONS

GI Institute of Geology, Academy of Sciences of the Mongolian People's Republic, Ulan Bator.
IAUB Institute of Anatomy, University of Bergen, Bergen.
PIFU Palaeontologishes Institut, Freie Universität, Berlin.
UM University of Minnesota, Minneapolis, U.S.A.
ZPAL Institute of Palaeobiology, Polish Academy of Sciences, Warsaw.

I incisor dp deciduous premolar P permanent premolar M molar.

MATERIAL

Docodonta
Docodontidae
gen. et sp. indet., Kimmeridgian, Portugal, Leiria, Guimarota: PIFU no number (a molar)
Multituberculata
Plagiaulacoidea
Family, gen. et sp. indet., Kimmeridgian, Portugal Leiria, Guimarota: PIFU no number (a molar)
Paulchoffatidae (all from the Kimmeridgian of Portugal, Leiria, Guimarota):
Paulchoffatia sp.: PIFU VJ 270-155 (dp^1); PIFU VJ 272-155 (P^1); PIFU VJ 273-155 (P^1)
Kuehneodon sp.: PIFU VJ 303-155 (P^5); PIFU VJ 308-155 (P^5)
Suborder indet. (all from the ?Aptian or Albian Guchin beds of Mongolia, Guchin Us):
Arginbaataridae
Arginbaatar dimitrievae Trofimov: GI PST 10/11 (P_4); GI PST 10/13(P_4)
Family, gen. et sp. indet.: GI PST 10/29 (I^1); GI PST 10/23 (P_4)
Taeniolabidoidea
Eucosmodontidae
(*Chulsanbaatar*, *Nemegtbaatar*, and *Kryptobaatar* are from the upper Cretaceous of Asia, Gobi Desert, *Stygimys* from the upper Cretaceous, Hell Creek Formation, North America, Montana, Bug Creek):
Chulsanbaatar vulgaris Kielan-Jaworowska, Barun Goyot Formation, Khulsan: ZPAL MgM-I/62 (I_1, M_1); ZPAL MgM-I/157 (I_1, P_4, M_1); Barun Goyot Formation, Nemegt: ZPAL MgM-I/111 (I_1); red beds of Khermeen Tsav, Khermeen Tsav II: ZPAL MgM-I/108 (I_1); ZPAL MgM-I/109 (I_1, P_4)
Nemegtbaatar gobiensis Kielan-Jaworowska, red beds of Khermen Tsav, Khermen Tsav II: ZPAL MgM-I/81 (I_1, M_1); ZPAL MgM-I/82 (I_1, P_4, M_1)
Kryptobaatar dashzevegi Kielan-Jaworowska, Djadokhta Formation, Bayn Dzak: ZPAL MgM-1/7 (P_4); ZPAL MgM-I/9) (P_4, M_1); ZPAL MgM-I/37 (I_1, M_1); ZPAL MgM-I/53 (I_1, P_4, M_1)
Stygimys kuszmauli Sloan and Van Valen, Hell Creek Formation, Bug Creek: UM no. 5 (I_1, M_2)

Taeniolabididae (all from Asia, Gobi Desert):
Kamptobaatar and *Catopsalis* are from the upper Cretaceous, *Prionessus* from the Upper Palaeocene
Kamptobaatar kuczynskii Kielan-Jaworowska, Djadokhta Formation, Bayn Dzak: ZPAL MgM-I/38 (P_4)
Catopsalis catopsaloides (Kielan-Jaworowska), red beds of Khermeen Tsav, Khermeen Tsav II: ZPAL MgM-I/78 (I_1, M_1); ZPAL MgM-I/80 (M_1)
Prionessus lucifer Matthew and Granger, Naran Bulak: ZPAL MgM-II/67 (I_1, M_1, M_2)
Ptilodontoidea
Neoplagiaulacidae (all from the upper Cretaceous Hell Creek Formation, North America, Montana, Bug Creek):
Mesodma thompsoni Clemens: UM no. 3 (P_4)
Mesodma sp.: ZPAL MK-I/7 (P_4); ZPAL MK-I/8 (P_4); ZPAL MK-I/3 (M^1); ZPAL MK-I/6 (M^1)
Suborder indet.
Cimolomyidae, Bug Creek, Montana, Hell Creek formation:
Meniscoessus sp.: ZPAL MK-I/9 (M_2)
Eutheria
Proteutheria
Kennalestidae, Djadokhta Formation, Gobi Desert, Bayn Dzak:
Kennalestes gobiensis Kielan-Jaworowska: ZPAL MgM-I/3 (P^3)
Rodentia
Muridae, Recent, Europe:
Rattus norvegicus (Berkenhout): IAUB no number (I_1, M_1)
Primates
Hominidae, Recent, Europe:
Homo sapiens L.: IAUB no number (P^2).

METHODS

The Asian multituberculate material investigated in Warsaw consisted of whole mandibles with teeth *in situ*. The right or left mandible was positioned in plasticine on a microscope slide under a dissection microscope in such a way that a selected region of enamel on the tooth to be studied was the highest point of the whole dentition. This region was then carefully planed horizontally by hand using 0/2 and then 0/4 grit emery paper (Buehler Ltd., Evanston, Ill., U.S.A.), each grade having been glued and trimmed to either of the two long, narrow sides of a $10 \times 2 \times 0{\cdot}3$ cm rectangular, planed wood stick. The horizontal, tiny but relatively flat enamel surface, less than 1 mm in diameter formed in this way was then etched with a very small amount of 0·37 N HNO_3 applied by a fine-pointed brush. The etching was interupted after 5 sec with plain water, using a similar brush. Next, to micrograph the etched surface, the microscope slide with the specimen still in the original position on it was transferred to a Leitz Laborlux microscope equipped with camera, an Ultropak incident light condensor and a U-O-11 objective. A Leitz microscale with 10 μm divisions was micrographed with the same magnification.

At IAUB the films of the etched surfaces with cross-cut enamel prisms were copied on 23×30 cm film sheets with a standard magnification.

The smallest unit that describes the number of cross-sectioned prisms per mm^2 (numerical prism density) is a triangle consisting of central distances between three adjacent prisms. Determining the prism density in the enamels consisted of measuring the distances between centres of adjacent prisms in several such triangular units within each micrographed enamel area (Fosse, 1968*a*).

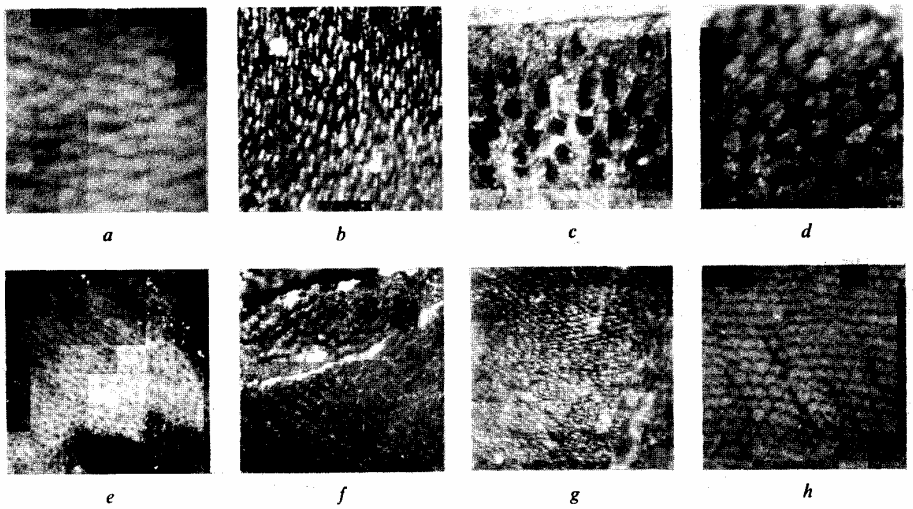
Table 1 presents prism densities (a), mean central distances between adjacent prisms (D), and the new parameter A which signifies the theoretical mean cross-sectional area in μm^2 of the enamel producing end of the ameloblasts (Fosse 1968*d*; Fosse *et al.* 1973, *et al.* 1978). The prism density values presented were calculated from incident light micrographs of superficially planed and etched natural outer enamel surfaces which are nearly planoparallel with an original layer of ameloblasts (Fosse *et al.* 1973). As it is still generally believed that each prism rod is produced by one ameloblast (Fosse *et al.* 1978), the number of prisms per mm^2 in such planes should reflect the number of original enamel producing ameloblasts per mm^2 in that plane, irrespective of its angle with the prism rods underneath (Fosse 1968*c*).

Two multituberculate lower jaws, *Chulsanbaatar vulgaris* Kielan-Jaworowska, ZPAL MgM-I/62, and *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/53, as well as docodont and plagiaulacoid single teeth

(gen. et sp. indet.), and five plagiaulacoid single teeth determined at generic level, all from the Kimmeridgian, Leiria, Guimarota, Portugal, were sectioned by a wire string saw (Fosse *et al.* 1974) to obtain cut surfaces or thin sections for transmitted light microscopy. For the SEM micrographs a Jeol T-200 instrument was used. The specimens were covered by gold-palladium before SEM micrography. A Leitz Ortholux Pol microscope was used for transmitted light micrographs of thin tooth sections.

RESULTS

In the material in Warsaw, clusters of prisms were usually quickly recognized in the planed and etched enamel surfaces. Text-fig. 1*a* represents P_4 of *K. dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/7. With the same magnification text-fig. 1*b*, *c*, and *d* respectively show the prism densities in *Mesodma* sp. (P_4), *Stygimys kuszmauli* (I_1), and *Meniscoessus* sp. (M_2) enamels, all three from the late Cretaceous, Lancian (Maastrichtian), North America, Montana, Bug Creek. In incident light planed and etched enamel surfaces of Kimmeridgian plagiaulacoid and docodont teeth showed regularly packed structures in a pattern resembling cross-cut prism rods, (text-fig. 1*e*, *f*). Their numerical density and mean interproximate central distance were of a magnitude between those of the eutherians: late Cretaceous *Kennalestes gobiensis* and Recent *Rattus norvegicus*, (text-fig. 1*g*; Table 1). Human enamel had considerably larger prisms than *R. norvegicus*. The prism density near the cusp on the outer surface of a human premolar was about the same as that of *Mesodma* sp.,



TEXT-FIG. 1. Incident light micrographs of planed and etched surfaces of various enamels reproduced with the same magnification, × 250. *a* represents the enamel surface of a tooth micrographed *in situ*, *c* and *f* represent the cut and etched enamels of sectioned teeth, all the others represent superficially planed and etched outer enamel surfaces of teeth embedded in plastic blocks. *a*, *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/7, P_4, occlusal edge above. *b*, *Mesodma* sp., ZPAL MK-I/8, P_4, occlusal edge above. *c*, *Stygimys kuszmauli* Sloan and Van Valen, UM no. 5, I_1, showing longitudinal section through medial enamel facet seen in the lingual direction, dentine below. *d*, *Meniscoessus* sp., ZPAL MK-I/9, M_2, occlusal surface above. *e*, *Paulchoffatia* sp., PIFU VJ 273-155, P^1, showing prism-like pattern of structures without distinct borders, occlusal surface to right. *f*, docodont molar (gen. et sp. indet.), PIFU no number, obliquely cut through one of the cusps, showing prism-like pattern, montage. *g*, *Rattus norvegicus* (Berkenhout), IAUB no number, M_1, occlusal surface above. *h*, *Homo sapiens* L., IAUB no number, P^2, occlusal surface above.

TABLE 1. The number of prisms per mm² (a), the mean central distance in microns between adjacent prisms (D), and the theoretical mean cross-sectional area in μm^2 of the enamel producing cells (A) (see Methods) in the enamel of some specimens of European, Asian, and North American multituberculates from different ages, of one undetermined docodont molar, one Cretaçeous, and two recent eutherian species. The ZPAL specimens were represented by whole jaws from which the enamel parameters of more than one tooth were usually available, see Material.

Species/specimen	a	D	A	
Docodont, gen. & sp. indet.				
PIFU no number	34 514	5·78	28·9	M
Paulchoffatia sp.				
PIFU VJ 273-155	43 080	5·17	23·2	P^1
PIFU VJ 272-155	59 987	4·38	16·6	P^1
Kuehneodon sp.				
PIFU VJ 303-155	50 983	4·75	19·6	P^5
Arginbaatar dimitrievae Trofimov				
GI PST 10/11	7123	12·73	140·3	P_4
GI PST 10/13	5426	14·58	184·2	P_4
Multituberculata subord. fam. gen. and sp. indet.				
GI PST 10/29	4891	15·36	204·4	I^1
GI PST 10/23	11 365	10·07	87·9	P_4
Chulsanbaatar vulgaris Kielan-Jaworowska				
ZPAL MgM-I/62	5812	14·09	172·0	I^1
	10 001	10·74	99·9	M_1
ZPAL MgM-I/157	4960	15·25	201·5	I_1
	5734	14·18	174·3	P_4
	11 623	9·96	86·0	M_1
ZPAL MgM-I/111	6519	13·30	153·4	I_1
ZPAL MgM-I/108	7219	12·64	138·5	I_1
ZPAL MgM-I/109	6258	13·58	159·7	I_1
	9520	11·01	105·0	P_4
Nemegtbaatar gobiensis Kielan-Jaworowska				
ZPAL MgM-I/81	5399	14·62	185·1	I_1
	12 133	9·75	82·4	M_1
ZPAL MgM-I/82	5435	14·57	183·9	I_1
	4241	16·49	235·7	P_4
	8271	11·81	120·9	M_1
Kryptobaatar daszevegi Kielan-Jaworowska				
ZPAL MgM-I/7	6314	13·52	158·3	P_4
ZPAL MgM-I/9	3379	18·48	295·9	I_1
	6349	13·48	157·4	P_4
ZPAL MgM-I/10	4464	16·08	223·9	I_1
	5271	14·79	189·6	P_4
ZPAL MgM-I/21	3705	17·65	269·8	I_1
	4908	15·33	203·7	P_4
	3980	17·03	251·2	M_1
ZPAL MgM-I/37	4292	16·40	232·9	I_1
	3753	17·53	266·4	M_1
ZPAL MgM-I/53	3415	18·38	292·7	I_1
	5812	14·09	172·0	P_4
	6039	13·82	165·5	M_1
Stygimys kuszmauli Sloan and Van Valen				
UM no. 5	3860	17·29	259·0	I_1
Kamptobaatar kuczynskii Kielan-Jaworowska				
ZPAL MgM-I/38	6776	13·05	147·5	P_4

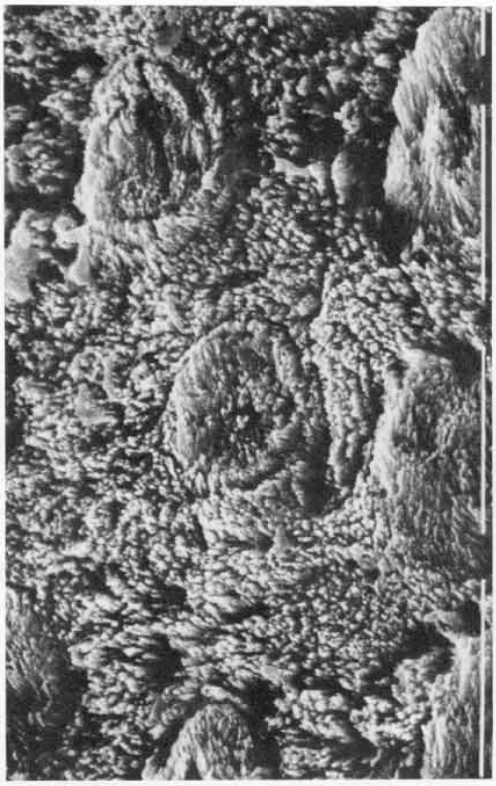
TABLE 1 (*cont.*)

Species/specimen	a	D	A	
Catopsalis catopsaloides (Kielan-Jaworowska)				
ZPAL MgM-I/78	4740	15·60	210·9	I_1
	6650	13·17	150·3	M_1
ZPAL MgM-I/80	6063	13·79	164·9	M_1
Prionessus lucifer Matthew and Granger				
ZPAL MgM-II/67	6440	13·38	155·2	I_1
	5776	14·13	173·1	M_1
	6138	13·71	162·9	M_2
Mesodma sp.				
ZPAL MK-I/7	28 627	6·35	34·9	P_4
ZPAL MK-I/8	26 321	6·62	37·9	P_4
ZPAL MK-I/3	26 694	6·58	37·5	M^1
ZPAL MK-I/6	21 557	7·32	46·4	M^1
Meniscoessus sp.				
ZPAL MK-I/9	4088	16·80	244·5	M_2
Kennalestes gobiensis Kielan-Jaworowska				
ZPAL MgM-I/3	31 599	6·04	31·6	P^3
Rattus norvegicus (Berkenhout)				
IAUB no number	65 703	4·19	15·2	I_1
	67 095	4·14	14·9	M_1
Homo sapiens L.				
IAUB no number	25 335	6·75	39·5	P^2

(text-fig. 1*b*, *h*; Table 1). In most ZPAL taeniolabidoid jaws with more than one tooth micrographed, the prism density of the incisor was lower than that of P_4 or M_1, see Table 1. The higher density in the molars apparently is caused not so much by smaller prisms as by less interprismatic enamel (Pl. 48, figs. 1 and 2). The great difference between the microstructure of taeniolabidoid and *Mesodma* enamels is demonstrated in Plate 48, figs. 1–4, where it is also seen that the crystal structure of the *Kryptobaatar* enamels was coarser than that of the *Mesodma* enamels. Near the outer surface of human enamel there is very little interprismatic substance (Pl. 48, fig. 5). The human prism diameters

EXPLANATION OF PLATE 48

Figs. 1–5. SEM micrographs of superficially planed and etched outer enamel surfaces reproduced with the same magnification, ×2900, documented by the automatically recorded scale divisions of 10 μm having been retained in the micrographs. 1, *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/53, I_1, showing that the prisms are widely separated by interprismatic enamel consisting of crystals being normal to the surface and that the crystals of the prism cores are obliquely orientated relative to the surface and inclined in an incisal direction above. 2, M_1 from the same dentition as I_1 in fig. 1, showing that the spatial arrangement of the crystals in the prisms and interprismatic enamel is less distinct and that the prisms are nearly of the same size but more closely packed than in I_1. 3, *Mesodma* sp., ZPAL MK-I/8, P_4, showing that the prisms are smaller and their numerical density per unit area considerably lower than in *Kryptobaatar* enamel, also that the crystals are more delicate and densely packed. In the interprismatic enamel the crystals are normal to the surface, while those of the prism cores are inclined in a cuspal direction to the left. 4, *Mesodma* sp., ZPAL MK-I/3, M^1, not belonging to the same individual as P_4 in fig. 3, but showing similar prism size, numerical density of prisms, and crystal orientation. Cuspal direction is to the left. In the upper half are some openings of enamel tubules. 5, *Homo sapiens* L., IAUB no number, P^2, showing that prisms are nearly as large as in *Kryptobaatar* enamel (fig. 1), but that their numerical density approximates that of the *Mesodma* enamels (figs. 3 and 4). Cuspal direction is to the right.



1

2

3

4

5

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are about as large as those of the *Kryptobaatar* (Pl. 48, figs. 1 and 2) and *Chulsanbaatar* enamels (Pl. 49, fig. 3), whereas the distances between centres of adjacent prisms equal those of the *Mesodma* enamels (Pl. 48, figs. 3 and 4; Table 1). Thus there is no interdependence between prism diameters and number of prisms per unit area.

Longitudinal and transverse sections of taeniolabidoid incisors showed cross-cut prisms; in longitudinal sections when they passed through the medial enamel facets where the prism rods were inclined in a dorsomedial (mesiolingual) direction in a transversal plane relative to the incisors, in transversal sections in the ventrolateral facets where the prism rods were inclined in an anterior (incisal) direction in a sagittal plane relative to the tooth. Regardless of the orientation of the enamel surfaces represented by Plate 48, figs. 1–4 and Plate 49, figs. 1 and 3, they all demonstrate that the crystals in the interprismatic enamel are orientated with their long axis nearly normal to the natural outer enamel surface. The crystals of the prism cores are parallel with the prism rods, and the apices of the arcades are pointing in the direction of the acute angle between prism rods and the dentine enamel junctional surface.

In the SEM discrete enamel prisms in the Kimmeridgian enamels could not be discerned. Plate 49, figs. 2 and 5 show plagiaulacoid and docodont enamels at the same magnification. A certain regular pattern in the crystal orientation may be observed. This pattern seemed to consist of 5 μm thick, closely packed columns of crystals, the latter diverging from the central axis of each column towards the external enamel surface. In Table 1 are given the values for three plagiaulacoid teeth and one docodont molar from the Kimmeridgian, Portugal, based on measurements in incident light micrographs.

Longitudinal sections, about 80 μm thick, were prepared from three plagiaulacoid teeth of which two were determined on the generic level, and one docodont molar (gen. et sp. indet.) from the Kimmeridgian. In the microscope one of the plagiaulacoid enamels (gen. et sp. indet.) showed large black spots along lines that might correspond to the course of growth lines (striae of Retzius, Pl. 50, fig. 1). In polarized transmitted light with crossed polars and the dentine enamel junction at

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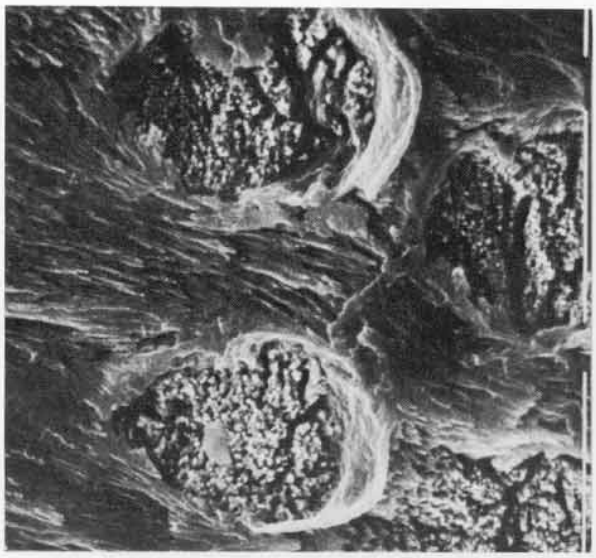
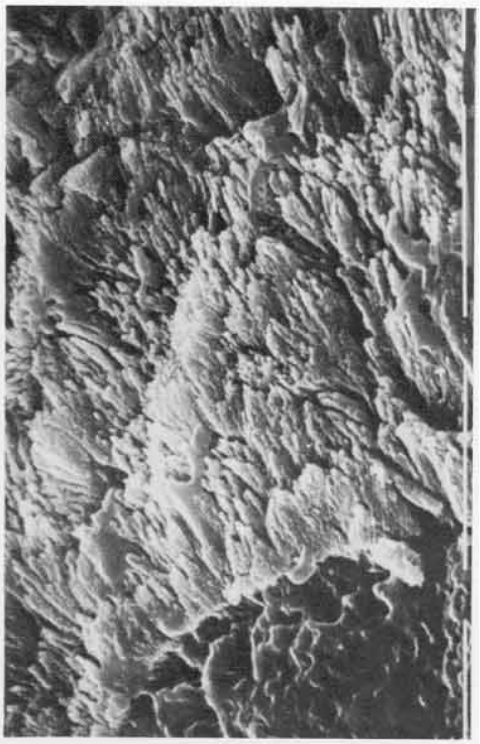
EXPLANATION OF PLATE 49

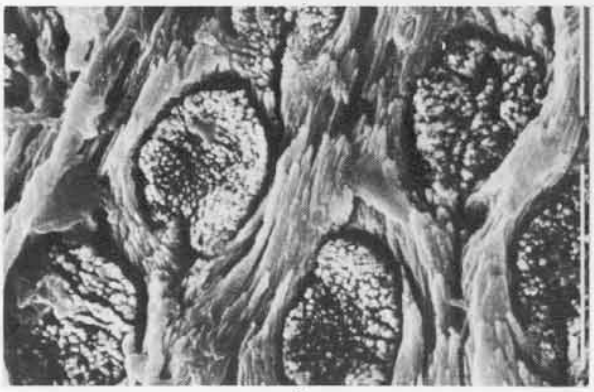
Figs. 1–5. SEM micrographs of various multituberculate enamels reproduced with the same magnification, × 2900, documented by the automatically recorded scale divisions of 10 μm having been retained along the right margins of the micrographs. Figs. 1, 2, and 3 represent sectioned and etched enamel surfaces, figs. 4 and 5 superficially planed and etched outer enamel surfaces. 1, *Stygimys kuszmauli* Sloan and Van Valen, UM no. 5, I_1, enlargement of the same enamel surface as figured in text-fig. 1*c*, but rotated 90°, dentine enamel border at right. The prisms are large and widely separated by interprismatic enamel where the crystals are orientated with their long axes in the figured plane, from left to right, e.g. perpendicularly to the outer enamel surface, while the crystals of the prisms are normal to the figured surface. Towards the dentine at right the borders of two prisms consist of an amorphous material. 2, *Paulchoffatia* sp., PIFU VJ 270-155, dp^1, showing oblique section through cusp where the enamel consists of crystals without preferential orientations in prisms and interprismatic material. In some places it may be seen that the crystals are arranged in fan-shaped clusters. Dentine in lower left corner. 3, *Chulsanbaatar vulgaris* Kielan-Jaworowska, ZPAL MgM-I/62, I_1, showing transversal section through ventrolateral enamel facet. The prisms are somewhat smaller and their numerical density higher than in *Kryptobaatar* (Pl. 48, fig. 1) and *Stygimys* (fig. 1) enamels. The interprismatic enamel consists of crystals orientated with their long axes in the figured plane from top to bottom, e.g. normal to the outer enamel surface while the crystals of the prism cores are nearly normal to the figured plane. Arcade shaped grooves surround the prisms, the apices of which point towards the dentine at top. 4, *Meniscoessus* sp., ZPAL MK-I/9, M_2, showing arcade shaped grooves surrounding the large prisms, the apices of which point in the cuspal direction at left. Crystals of interprismatic enamel are generally normal to the figured surface, while the crystals of the prisms are inclined to the left. 5, docodont molar (gen. et sp. indet.), PIFU no number. There is no organization of crystals in prisms and interprismatic enamel, but the uneven appearance of the etched surface indicates the presence of crystal clusters about 5 μm wide.



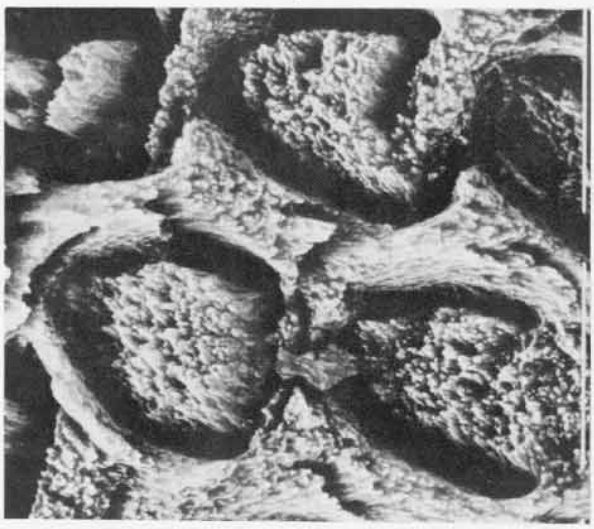
1



2



3



4

5

FOSSE, KIELAN-JAWOROWSKA and SKAALE, multituberculate enamel

a small angle with the polarizer axis, poorly defined band-like 5–6 μm thick structures could be seen in plagiaulacoid as well as docodont enamels, running radially from the inner to the outer surface (Pl. 50, figs. 2–5). Enamel tubules were very scarce. In polarized light the longitudinally cut *Chulsanbaatar*, *Kryptobaatar*, and *Stygimys* enamels showed discrete broad and straight bands of a regular width, running at an angle of approximately 45° to the outer enamel surface. Enamel tubules were abundant, coursing from the dentine enamel junction along the bands for short distances, but mostly crossing them, running mainly in a radial direction (Pl. 50, figs. 6–8). Longitudinally sectioned *Mesodma* premolar enamel like that of the taeniolabidoid enamels showed discrete bands of a regular but much narrower width. A few enamel tubules were seen (Pl. 50 fig. 9). Black spots like those seen in the plagiaulacoid enamel, but irregularly arranged, were observed in some sections of taeniolabidoid enamels. The bands of the docodont and plagiaulacoid enamels were most distinctly seen when their long axes were parallel with one of the polarizer planes. They were negatively birefringent when positioned with their long axes diagonally in the field of vision; in this position these enamels seemed structureless. The bands of the taeniolabidoid and *Mesodma* enamels shown in Plate 50, figs. 6–9, were also negatively birefringent with respect to their length, and most distinctly seen by maximum prism extinction which occurred when they were inclined a little, relative to one of the polarizer planes; from 0° to 20° for the different sections and different enamel areas within each section. This maximum extinction was obtained by rotating the stage with the section in the direction of the prism inclination towards the cusp from the position where the prisms were parallel with one of the polarizer planes.

DISCUSSION

Poole (1956) found that tooth enamel in synapsid reptiles was non-prismatic as the crystals were arranged in closely packed cylindrical groups that were normal to the enamel surface. They were called pseudo-prisms. Poole (1957) stated that prismatic enamel generally originated in primitive mammals. Moss (1969) studied fossil therapsid, non-therian and therian enamels, including the enamel of fossil marsupials and placentals, and concluded that therapsid and *all* non-therian enamels are continuous, but with a banded appearance in longitudinal thin sections when viewed in the polarizing microscope. According to the same author true prismatic enamel which is characteristic

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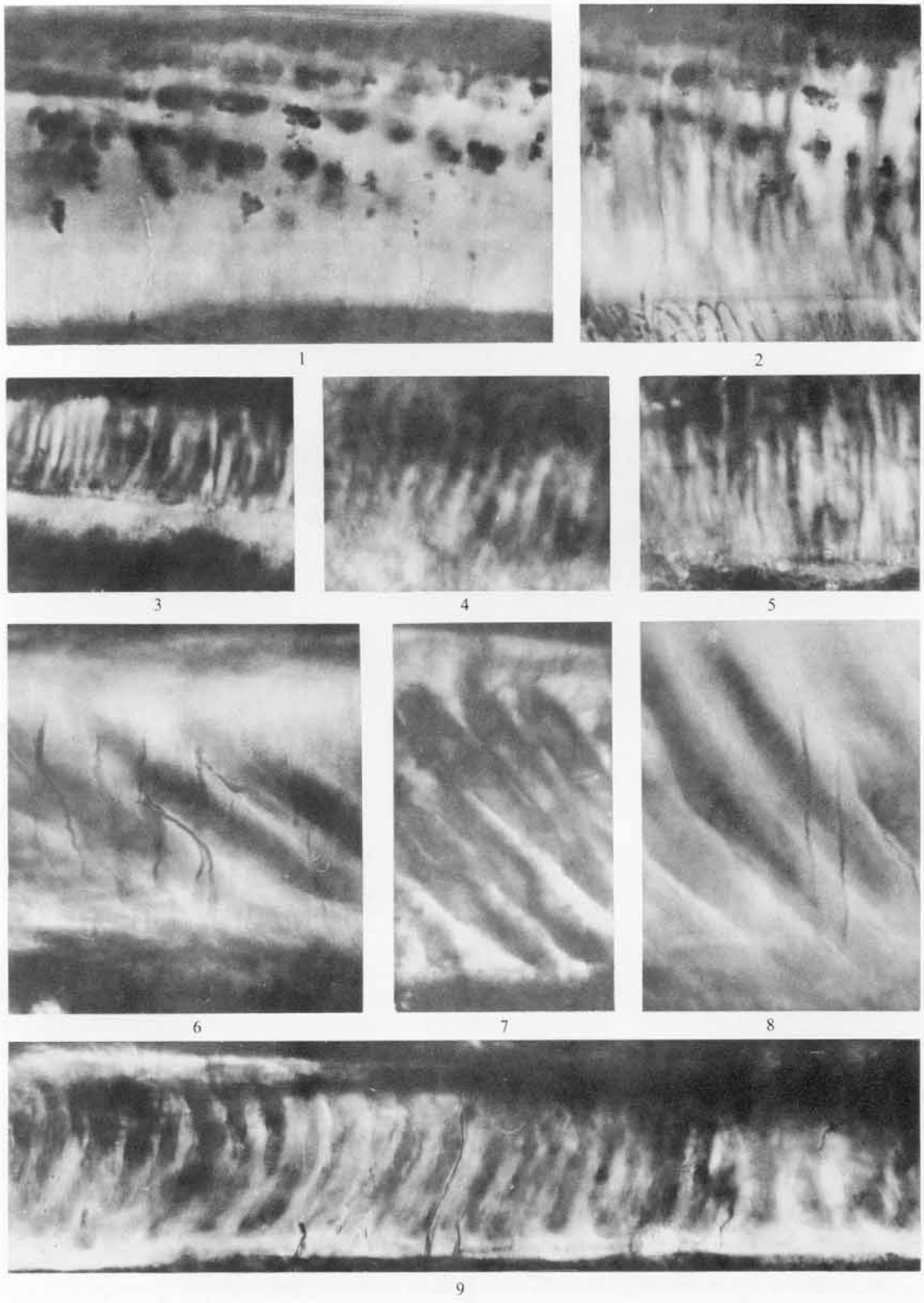
EXPLANATION OF PLATE 50

Figs. 1–9. Thin sections of enamel of longitudinally sectioned teeth micrographed in transmitted light with the same magnification, × 875. Excepting fig. 1 where normal light was used, the sections were micrographed in polarized light with crossed filters. The incisal/cuspal direction is to the left, dentine below. 1, late Jurassic, Kimmeridgian plagiaulacoid molar (gen. et sp. indet.). Black spots within the enamel lie in rows probably along growth lines (striae of Retzius). A few enamel tubules are seen, section thickness 60 μm. 2, the same section showing indistinct band-like structures of irregular width normal to the dentine where hair-pin bends of dentinal tubules are seen. 3, late Jurassic, Kimmeridgian docodont molar (gen. et sp. indet.), showing band-like structures normal to the dentine enamel junction, section thickness 55 μm. 4, *Paulchoffatia* sp., PIFU VJ 273-155, P^1, showing band-like structures nearly normal to the dentine, section thickness 90 μm. 5, *Kuehneodon* sp., PIFU VJ 308-155, P^5, showing band-like structures normal to the dentine, section thickness 90 μm. 6, *Chulsanbaatar vulgaris* Kielan-Jaworowska, ZPAL MgM-I/62, I_1, showing distinct, broad bands of regular width inclined about 45° to the dentine enamel junction, enamel tubules cross the bands, section thickness 80 μm. 7, *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/53, P_4, showing distinct bands of similar width and orientation as in fig. 6, section thickness 90 μm. 8, *Stygimys kuszmauli* Sloan and Van Valen, UM no. 5, M_2, showing slightly broader bands but of similar orientation as in figs. 6 and 7, enamel tubules crossing bands, section thickness 60 μm. 9, *Mesodma thompsoni* Clemens, UM no. 3, P_4, showing distinct curved bands, but of a narrower width than in figs. 6, 7, and 8, a few enamel tubules are seen, section thickness 50 μm.



FOSSE, KIELAN-JAWOROWSKA and SKAALE, multituberculate enamel

only for Theria first appeared in the early Cretaceous (Albian) forms. Poole (1971) studying Jurassic dryolestids, suggested that prismatic enamel originated in Theria. Poole and Cooper (1971) found prismatic enamel in the extant agamid *Uromastix* however, and concluded that enamel prisms are not confined to mammals. Osborn and Hillman (1979) studied by polarizing microscopy the enamel of the pelycosaur *Dimetrodon*, the therapsids *Thrinaxodon*, *Probainognathus*, *Probelesodon*, *Diademodon*, and *Massetognathus*, the early Jurassic primitive triconodont *Eozostrodon* (? = *Morganucodon*), a late Cretaceous dryolestid, and therian mammals. They found that prismatic enamel only appeared in the Cretaceous non-therian and therian mammals. In the Permian *Dimetrodon* the enamel was micromorphologically homogeneous with regard to crystal orientation, whereas all Triassic–early Jurassic enamels are characterized by 'an arrangement of close-packed hexagonal columns of crystals (Osborn and Hillman 1979, p. 58). In a longitudinal section of *Diademodon* enamel a column of crystals was about 5 μm wide. There was no interprismatic enamel. These observations concerning crystal orientation in Triassic–early Jurassic enamels are consistent with the results of our light and SEM microscopic study of the late Jurassic plagiaulacoid and docodont enamels as radially orientated bands about 5 μm wide were seen in longitudinal sections (Pl. 50, figs. 2–5) and prism-like structures with interproximate central distances of about 5 μm in tangential planes (text-fig. 1*e*, *f*). In SEM the late Jurassic enamels studied by us showed crystals spraying out towards the outer enamel surface from the centre of 5 μm thick closely packed 'columns' (Pl. 49, figs. 2 and 5).

Grine *et al.* (1979) by SEM studies found discrete prisms with interprismatic enamel between them in *Eozostrodon* teeth. Grine and Vrba (1980) also demonstrated prismatic enamel in the cynodont *Pachygenelus*. Interprismatic central distances according to magnifications were about 5 μm. Frank *et al.* (1984) described 'preprismatic' enamel in late Triassic haramiyids and so did Sigogneau-Russell *et al.* (1984) in the early Jurassic therian *Kuehneotherium*. Preprismatic enamel according to these latter authors consists of radially arranged columns of crystals similar to those described by Osborn and Hillman (1979) and by us in this paper. Excepting the results of Grine *et al.* (1979) and Grine and Vrba (1980), it may be concluded at present from the reports cited above that prismatic enamel originated in non-therian mammals and not before the Cretaceous as stated by Osborn and Hillman (1979), whereas preprismatic enamel where crystals are arranged in 5 μm thick closely packed columns originated in cynodonts, therapsids, and persisted in some non-therians and therians from the Triassic through the late Jurassic. In light of this the findings of Grine *et al.* (1979) and Grine and Vrba (1980) are perplexing and should encourage further studies on enamel microstructure of non-therian forms of pre-Cretaceous age.

Our findings support the hypothesis of Fosse *et al.* (1978) that the multituberculate suborder Taeniolabidoidea was characterized by remarkably large and widely separated enamel prisms. Osborn and Hillman (1979) have confirmed the existence of such large prisms in *Catopsalis* sp. and *Stygimys* sp. Carlson and Krause (1982) with a few exceptions found large prisms in Taeniolabidoidea. The oldest ZPAL multituberculates derive from the late Cretaceous, Gobi Desert, Djadokhta Formation, which is of ?late Santonian and/or ?early Campanian age (see Material). However, due to the courtesy of Dr. Demberlyin Dashzeveg we were able to examine by incident light microscopy the enamel microstructure of two identified and two unidentified multituberculate teeth from the early Cretaceous (?Aptian or ?Albian) of Guchin Us, Gobi Desert, Mongolian People's Republic (see Clemens *et al.* 1979). They are the specimens GI PST 10/11, GI PST 10/13, GI PST 10/29, and GI PST 10/23 housed in the Institute of Geological Sciences of the Mongolian Academy of Sciences in Ulan Bator. These teeth show the same size and numerical density of prisms as do the Taeniolabidoidea from late Cretaceous of Asia (Table 1). The Guchin Us multituberculates are currently being investigated by Kielan-Jaworowska, Dashzeveg, and Trofimov and if it can be demonstrated that the Early Cretaceous Asian multituberculates are close to the ancestors of late Cretaceous Taeniolabidoidea, which the enamel structure indicates, it may be concluded that this peculiar prismatic enamel structure was established and persisted in Taeniolabidoidea through a time span ranging from Aptian or Albian to late Palaeocene.

Our finding that *Mesodma* (suborder Ptilodontoidea) enamel had a mean prism density of 25800

per mm² agrees with the results of Fosse *et al.* (1978), but disagrees with the conclusion of Sahni (1979) with regard to *Mesodma* enamel. By our method we calculated the densities 24120, 22300, and 19840 respectively in his figured *Mesodma* enamels (Sahni 1979, pl. 1, figs. 2, 3, and 6), which represent cross-cut prisms in *Mesodma* enamel in his paper. Therefore, we submit that in *Mesodma* enamel, there is a significantly higher prism density and smaller prisms than in the representatives of Taeniolabidoidea. Carlson and Krause (1982) in other ptilodontoid taxa also found prism diameters similar to those we observed in *Mesodma* enamels. It seems that Ptilodontoidea do not differ significantly with respect to numerical prism density from many recent representatives of Eutheria (Fosse 1968*b*, *d*) and Metatheria (Fosse *et al.* 1973), nor from the late Cretaceous eutherians *Protungulatum donnae* (Fosse *et al.* 1978) and *Kennalestes gobiensis* (Table 1 in this paper). Thus the enamel in Taeniolabidoidea is gigantoprismatic, meaning that the prism density per unit area is four to five times lower than in the ptilodontoid *Mesodma* sp. and in all other known mammals. Poole (1956) suggested that during amelogenesis each column in pseudoprismatic enamel may be the product of one ameloblast. Assuming that columns in preprismatic enamel and prisms in 'normal' as well as gigantoprismatic enamel are the products of single ameloblasts, the present documentation concerning the range of column and prism dimensions, see text-fig. 1, demonstrates the enormous diversity in ameloblast diameters in mammals. It may be speculated that each prism and half the thickness of interprismatic enamel surrounding it were formed by more than one ameloblast in taeniolabidoid enamel. Considering the similarity of crystal orientation in prisms and interprismatic material between gigantoprismatic and 'normal' enamel (Pl. 48, figs. 1, 3, and 4), this seems improbable and would represent a very unique and special organization of the active ameloblasts in Taeniolabidoidea compared with Ptilodontoidea and other extinct and all Recent mammals.

Fosse *et al.* (1973, Figs. 1, 12, and 13) in the medial facet (not explicitly named so) of a multituberculate incisor from the Hell Creek Formation, Montana, later identified as belonging to the Taenilabidoidea (Fosse *et al.* 1978), observed that the prism rods deviated in a transversal plane relative to the tooth. In the ventrolateral facet (named buccodistal, Fosse *et al.* 1973) of the same tooth the prism rods in the inner two thirds of the enamel deviated towards the tip of the crown. In the present study the same general arrangement of prism rods was observed in sections of the incisors of *Chulsanbaatar vulgaris*, ZPAL MgM-I/62 (Pl. 49, fig. 3), and *S. kuszmauli*, UM no. 5 (Pl. 49, fig. 1), and we tentatively suggest that this prism rod orientation in incisor enamel may be common to all late Cretaceous Taeniolabidoidea.

Fosse *et al.* (1973, Fig. 6) described the crystal orientation in multituberculate enamel, stating also that the prisms are arcade shaped in cross-section, and that the apices of the arcades point in the direction of the inclination of the prism rods relative to the dentine enamel junction. The same orientation of the crystals and the same morphology of the cross-cut prism rods were found in the present study of taeniolabidoid and ptilodontoid late Cretaceous enamels by SEM (Pls. 48 and 49). Polarized light microscopy indicated that the c-axes of the crystals in the prisms are inclined slightly in a cervical direction relative to the long axes of the prism rods, as the acute angle between prism rods and polarizer plane in the extinction position was cervically positioned relative to the prism rods.

In twelve mandibles from the ZPAL collection we were able to compare the prism density of incisors, premolars, and molars and in ten of them the numerical density was lower in incisors than in premolars or molars; in two of these it increased as much as twofold from incisor to molar (Table 1). It should, however, be stressed that the lowest prism densities of *Mesodma* or other mammalian teeth studied were about twice as high as the highest in taeniolabidoid molars.

Like Sahni (1979, Table 1 and pl. 3, fig. 6) we found gigantoprismatic enamel in the late Cretaceous North American *Meniscoessus*. If other genera of Cimolomyidae are distinguished by gigantoprismatic enamel this may indicate a relation of that family to Taeniolabidoidea, although the lower incisors in Cimolomyidae (Archibald 1982) are completely covered by enamel, a feature characteristic of Ptilodontoidea.

In view of the documented large difference between the microstructure of taeniolabidoid and ptilodontoid enamel, we believe that future studies of enamel microstructure may assist in

establishing the systematic position and phylogenetic relationships of some poorly known multituberculate groups regarded at present as *incertae sedis*.

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G. FOSSE

S. G. SKAALE

Institute of Anatomy
University of Bergen
5000 Bergen, Norway

Z. KIELAN-JAWOROWSKA

Zaklad Paleobiologii
Polska Academia Nauk
al. Zwirki i Wigury 93
02–089 Warszawa
Poland

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