

Fig. 25. Rotation of the mandible about the contralateral postglenoid process in a skull of *Rhinoceros unicornis* (UZ unnumbered). Occlusal surfaces on working side are shown in black, and the 'occlusal sector' of the upper tooththrow is marked by broken lines. Sectors of circles with centres at the fulcrum indicate the path of travel and its extension in both directions. Between skull and mandible is shown a lateral view of the occipital region. - Abbreviations: a.m. = auditory meatus, g.f. = glenoid fossa, p.g.p. = postglenoid process. Drawn from photographs, mandible reversed.

loses contact. The hypoconid of M_2 reaches passing facet 10 contact with the hypocone of M^2 . The last phase II contact is facet 9 between the hypoconid of M_3 and the protocone of M^3 .

The above illustrates how the anterior teeth are the last to reach and the first to lose occlusal contact during the power stroke, which corresponds to their role as puncture-crushing rather than chewing or-

gans. It also supports the idea that in forms with partly molarized premolars a relatively smooth anteroposterior gradient from puncture-crushing to chewing exists, involving perhaps gradual transport of food from front to back during mastication. Note also how small and restricted the phase II facets are in rhinoceroses; it is difficult to believe that they have any crucial role in food comminution.

4. Patterns

4.1. Tooth size and body size

4.1.1. Introduction: allometry

Pilbeam & Gould (1974) and Gould (1975) proposed that postcanine occlusal area in mammals should scale to the metabolic requirements of the animal according to 'Kleiber's Law', i.e., as body

mass to the exponent $3/4$ (Kleiber 1947). Since for objects of the same shape and density area scales to mass at the exponent $2/3$, the 'metabolic' scaling proposed by Pilbeam & Gould represents positive allometry of tooth size to body size. However, they were only able to document significantly positive allometry of tooth size to body size in a single case: the

South American hystricomorph rodents (see Table 2). Many investigators since have found that postcanine occlusal area is nearly isometric to body size in most mammals (see below and Table 2).

It is undeniable that the energy which drives the animal's metabolism comes (at the very least mainly) from its food, which is comminuted between the postcanine teeth. (Exceptions such as toothless forms are irrelevant to the discussion of the scaling of tooth size.) Relationships must exist between tooth size, comminution performance, body size and metabolism, so the discrepancy between theory (positive allometry) and empirical data (isometry) is therefore unsatisfactory. In this section I will attempt to resolve this apparent paradox, which may be due to a simple misconception.

Simpson (1953) already considered allometry a concept familiar to all biologists, and there is no need to discuss its general significance here, although it must be noted that the issue is still far from unproblematic. In this text I treat allometric relations as empirical generalizations, not as the expressions of laws, but it cannot be denied that the high incidence of exponents close to 1/4 and 3/4 relating physiological variables to body mass is suggestive of some general underlying law(s) (see e.g. Peters 1983 for examples and a discussion). There are several methodological problems, some of which are particularly relevant in the present context (for more general discussions see e.g. Reeve & Huxley 1945, White & Gould 1965, Gould 1966, 1971, Harvey 1982, Harvey & Mace 1982, R.D. Martin 1983, Peters 1983 and Schmidt-Nielsen 1984).

First, although an allometric function of the form $Y = aW^b$ (where a and b are empirical constants) can be fitted to practically any two size or size-dependent variables W and Y , the underlying biological relationship is not always the same. Thus allometric ontogenetic growth (heterauxesis) is not the same biological phenomenon as 'static' allometry (allomorphy) between adults of different size or between taxa (of which several kinds may be distinguished), and neither is the same as allometric change in an evolving lineage (Simpson 1953). The last case is particularly problematic, since it includes components of morphological change as such, and also change related to trends of increasing or decreasing size (Gould 1966, R. D. Martin 1983). Much confusion has arisen from this in the past, but the difficulties are now generally recognized.

Second, dimensionality creates problems of several kinds. Relevant here are two: (a) that the relationship proposed by Pilbeam & Gould (1974) relates an area to a mass, and (b) that either or both often have to be estimated from linear dimensions. Let V be a volume (substituted for mass), A an area and L a linear dimension: for geometrically similar objects $V \propto A^{3/2} \propto L^3$. In this text I will use the term 'isometry' of relationships described by these expo-

nents, regardless of the dimensionality of the variables actually compared (i.e., regardless of how body size and tooth size have been estimated in a particular case).

Allometry between the size of two organs may theoretically occur even when both organs are geometrically similar at all sizes, if their rates of size change are unequal (e.g. the tooththrow might increase in size relative to the skull but both might retain their proportions). In such a case simple arithmetical manipulation gives the expected allometric exponent at any combination of dimensions. For example, the relation $A_y \propto V_w^{3/4}$ can be transformed into

$$A_y \propto L_w^{3 \times 3/4} = L_w^{9/4}, L_y \propto L_w^{1/2 \times 9/4} = L_w^{9/8},$$

and so on. It is clear that this ideal situation is rarely if ever encountered in reality, and that allometry usually involves changes in shape that make it impossible to exactly estimate one dimension from another (cf. Hills & Wood 1984). Nevertheless, these transformed relations give estimates of the exponents expected from direct metabolic scaling of postcanine occlusal area as proposed by Pilbeam & Gould. They can not be regarded as exact 'null hypotheses', but they are given in the tables as a guideline.

Third, several curves may be fitted to the data to give the constants a and b . The problem of which one should be used has been subject to some discussion recently. I follow Gould (1975) and Harvey & Mace (1982) in using logarithmically transformed variables and the ('unreduced') major axis. This gives a linear relationship $\log Y = b \log W + \log a$, in which the variance in both variables is treated equally (Model II regression; Sokal & Rohlf 1981). Recent criticism of the empirically justified use of log-transformed variables appears to have been adequately met by Harvey (1982). Major axis regression analysis is really bivariate principal components analysis, and it might be argued that multivariate analysis should be used instead. However, the problem of how tooth size scales to body size is essentially bivariate, and multivariate analysis also presents unsolved problems of interpretation which are undesirable in this context (Harvey & Mace 1982). For these reasons bivariate analysis appears to be more appropriate here. All calculations were executed according to the procedure suggested by Sokal & Rohlf (1981) (see also App. 8).

Fourth, the relationship between two variables is not the same at all taxonomic levels. The species of a genus, the genera of a family or the families of an order often give different lines, and it is not always obvious which one is the most relevant to the problem at hand. Plots including several hierarchic levels (e.g. the species of an order) often show several linear clusters (e.g. families), usually with nearly identical slopes but different intercepts (Fig. 26). As recognized at least by Kurtén (1954), Meunier (1959) and Gould (1971), this offsets the effect of lower-

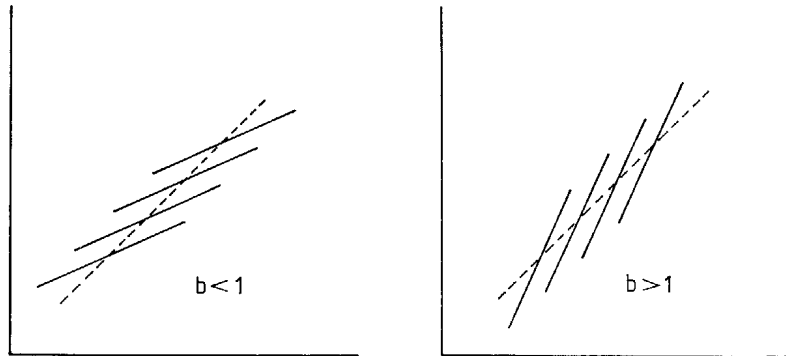


Fig. 26. How transposition may result in overall isometry, based on Gould (1971).

level allometry at higher levels. Meunier, who considered intra- versus interspecific relations, introduced the term Transposition for this phenomenon: "Die kompensierende Transposition ... hebt die im Zuge der innerartlichen Allometrie eingetretene Gestaltverzerrung wieder auf." (1959:347). Gould (1971) noted that this is true for both positive and negative allometry (see Fig. 26), and gave examples.

For all these and other reasons (see Harvey & Mace 1982) it is difficult to choose the appropriate taxonomic level for analysis, although it is obvious that it should be one pertaining to the problem under study. Many orders contain few families, many families few genera and many genera few species, so the choice is often a compromise between statistical (sample size) and biological considerations. In this investigation I have used species means as data points at all levels except the intraspecific. This is a relatively minor problem as the higher level relationships are all nearly isometric (see below).

4.1.2. Tooth size and body size: data

This section deals with the published data on tooth size body size relationships, and with original data collected for this study (App. 1 & 2). Most of the data suffer from two faults; they are based on few individuals and the body mass data are from different individuals than are the cranial and dental measurements. Use of some cranial or skeletal dimension as an estimate of body mass eliminates the second problem but introduces the complication that this dimension may itself be allometric to body mass. However, better data are simply not available, and the overall pattern is sufficiently uniform to suggest that these problems may not be too serious at the level of general comparison. For clarity this section is divided into five parts: (i) interspecific allometry at the family level and higher (most ungulate genera include only one or two species), (ii) intraspecific allometry between adults, (iii) ontogenetic dentition allometry, (iv) dwarfing, and (v) sex.

Higher level relationships

The first person to challenge the hypothesis of direct metabolic scaling of occlusal area as proposed by Pilbeam & Gould (1974) was probably Kay (1975). He presented data to show that the area of crushing surfaces on second lower molars of various primates scales at exponents significantly lower than 0.75 to body weight, and that postcanine tooth area also scales at such exponents in non-cercopithecooid primates and in bovids (Table 2). Kay (1978) presented further evidence that among the Cercopithecidae, five different dimensions on M_2 (crown length, hypoconid height, metaconid height, area of crushing surfaces, and cristid oblique length) scale isometrically with body weight in both sexes, separately as well as pooled. In the male and pooled samples the width of M^2 scaled at significantly negative allometry and entocristid length with significant positive allometry. Kay concluded that the hypothesis of 'metabolic scaling' was in disagreement with his data. Lucas (1980) presented data on postcanine tooth area for anthropoids and bovids (Table 2), and reached a similar conclusion. Creighton (1980) presented data for M_1 area and head-and-body length for a large sample of 'all mammals', and for selected orders and families. He found isometry except in Mammalia, Insectivora, Rodentia and Felidae, in which significant negative allometry was found (Table 2). Prothero & Sereno (1982) likewise found isometry of postcanine tooth area to body weight in suine artiodactyls and ceratomorph perissodactyls. Gingerich et al. (1982) showed that the central teeth (P_4 , M_1) scale at lower than isometric and the terminal teeth at higher than isometric exponents in primates. This result gives some support to the argument of Pilbeam & Gould (1974, 1975) and Gould (1975), that the entire postcanine area must be used, not just single teeth. However, Gingerich et al. (1982) found that total postcanine area scaled approximately isometrically with body weight in the primate sample (Table 2).

Table 2. Tooth size (Y) – body size (W) relationships at and above the family level. Selected data from the literature. Slope estimates are generally closer to the isometric than the "metabolic" value. Abbreviations see p. 75.

Taxon	W	Y	N	r	Slope used	Slope value	Isom. slope	'Metab' slope	Source
Mammalia	HBL	M ₁ A	288	0.952	r.m.a.	1.82	2.00	2.25	4
Insectivora	HBL	M ₁ A	20	0.897	r.m.a.	1.59	2.00	2.25	4
Erinaceidae	MAL	MRUL	30	–	l.sq.	0.87	1.00	1.12	9
Primates	HBL	M ₁ A	14	0.909	r.m.a.	1.75	2.00	2.25	4
Primates	AWT	TRUA	78	0.949	m.a.	0.62	0.67	0.75	7
Primates	AWT	TRUA	77	0.964	m.a.	0.69	0.67	0.75	7
Lemuroidea, males	BL	TRUA	11	0.945	m.a.	2.18	2.00	2.25	1
Ceboidea, males	BL	TRUA	14	0.975	m.a.	2.18	2.00	2.25	1
Cercopithecoidea, males	BL	TRUA	14	0.953	m.a.	1.95	2.00	2.25	1
Cercopithecoidea, females	AWT	TRUA	10	0.971	m.a.	0.80	0.67	0.75	1
Cercopithecoidea, females	BL	TRUA	11	0.931	m.a.	2.19	2.00	2.25	1
Cercopithecoidea	MAL	MRUL	59	0.990	l.sq.	0.75	1.00	1.12	9
Cercopithecoidea, males	AWT	M ₂ A	49	0.926	l.sq.	0.70	0.67	0.75	3
Cercopithecoidea, females	AWT	M ₂ A	49	0.900	l.sq.	0.65	0.67	0.75	3
Cercopithecoidea	AWT	M ₂ A	49	0.889	l.sq.	0.62	0.67	0.75	3
Rodentia	HBL	M ₁ A	136	0.927	r.m.a.	1.73	2.00	2.25	4
Hystricomorpha	MAL	MRUL	50	0.974	l.sq.	1.05	1.00	1.12	9
S.Amer. Hystricomorpha	BL	TRUA	34	0.967	m.a.	2.49	2.00	2.25	1
S.Amer. Hystricomorpha	AWT	TRUA	14	0.971	m.a.	0.72	0.67	0.75	1
S.Amer. Hystricomorpha	HBL	M ₁ A	17	0.921	r.m.a.	2.01	2.00	2.25	4
Sciuridae	HBL	M ₁ A	47	0.905	r.m.a.	1.88	2.00	2.25	4
Muridae	HBL	M ₁ A	13	0.884	r.m.a.	1.75	2.00	2.25	4
Cricetidae	HBL	M ₁ A	40	0.845	r.m.a.	1.96	2.00	2.25	4
Carnivora	HBL	M ₁ A	74	0.859	r.m.a.	1.99	2.00	2.25	4
Mustelidae	HBL	M ₁ A	17	0.883	r.m.a.	2.25	2.00	2.25	4
Canidae	HBL	M ₁ A	18	0.707	r.m.a.	2.45	2.00	2.25	4
Felidae	HBL	M ₁ A	15	0.960	r.m.a.	1.59	2.00	2.25	4
Viverridae	HBL	M ₁ A	18	0.910	r.m.a.	1.79	2.00	2.25	4
Ceratomorpha	TRUA	AWT	7	0.969	l.sq.	1.59	1.50	1.69	6
Ceratomorpha	CPL	TRUA	7	0.976	l.sq.	1.99	2.00	2.25	6
Equidae (fossil hyps.)	BRCL	TRUL	13	0.977	r.m.a.	1.26	1.00	1.12	8
Equidae (fossil brach.)	BRCL	TRUL	12	0.972	r.m.a.	1.01	1.00	1.12	8
Artiodactyla	HBL	M ₁ A	12	0.852	r.m.a.	2.01	2.00	2.25	4
Suina	BL	TRUA	9	0.953	m.a.	2.31	2.00	2.25	1
Suina	CPL	TRUA	9	0.926	l.sq.	2.24	2.00	2.25	6
Suina	TRUA	AWT	8	0.926	l.sq.	1.52	1.50	1.69	6
Cervidae	FEL	TRUA	17	0.962	m.a.	2.17	2.00	2.25	1
Bovidae	AWT	TRUA	10	–	l.sq.	0.52	0.67	0.75	2
Bovidae males	AWT	TRUA	7	0.992	l.sq.	0.59	0.67	0.75	5
Bovidae females	AWT	TRUA	7	0.991	l.sq.	0.63	0.67	0.75	5

Sources:

1. Pilbeam & Gould 1974, 2. Kay 1975, 3. Kay 1978, 4. Creighton 1980, 5. Lucas 1980, 6. Prothero & Sereno 1982, 7. Gingerich et al. 1982, 8. Radinsky 1984, 9. Williams 1955.

An inspection of Table 2 reveals only one case of distinct positive allometry of tooth size to body size in addition to the South American hystricomorph rodents of Pilbeam & Gould (1974). This is the sample of fossil hypsodont equids investigated by Radinsky (1984). However, Radinsky used braincase length as a standard in his investigation (which was about skull proportions, not tooth size body size relationships), and it may scale with negative allometry to body mass, as does brain mass. Martin (1981) gave the

slope 0.76 for brain/body mass allometry in placental mammals ($N = 309$ species). Assuming braincase length to scale isometrically with brain size, we might compensate for the negative allometry by simply multiplying Radinsky's slopes by 0.76. This would give the slope 0.96 for the hypsodont horses, but it would also lower the slope for brachyodont horses to 0.77. The 'correction' is of course very crude and may be quite unwarranted, and the matter is further complicated because the material contains a factor of

Table 3. Bivariate relationships between adult body weight and cranial and dental dimensions in a sample of ungulates (App. 1-2). Note general isometry. * = value outside 95 % CL (*b*). Abbreviations see p. 75.

W-variable	Y-variable	<i>N</i>	<i>r</i>	<i>b</i>	95 % CL (<i>b</i>)	log <i>a</i>	Isom. slope	'Metab.' slope
Adult body weight	CBL	46	0.981	0.31	0.294-0.331	4.260	0.33	0.38*
	WZY	46	0.965	0.31	0.284-0.335	4.371	0.33	0.38*
	SKA	46	0.984	0.62	0.590-0.658	2.135	0.67*	0.75*
	UL	44	0.967	0.31	0.289-0.340	4.376	0.33	0.38*
	TRVA	43	0.965	0.65	0.595-0.708	2.883	0.67	0.75*
	M ¹ L	42	0.964	0.32	0.296-0.353	4.091	0.33	0.38*
	M ¹ W	46	0.952	0.34	0.308-0.374	4.610	0.33	0.38*
	M ¹ A	42	0.961	0.67	0.611-0.734	3.340	0.67	0.75*
	M ² L	42	0.965	0.32	0.296-0.352	4.584	0.33	0.38*
	M ² W	44	0.954	0.33	0.300-0.365	4.616	0.33	0.38*
	M ² A	42	0.965	0.66	0.606-0.721	3.301	0.67	0.75*
	M ³ L	41	0.928	0.33	0.287-0.373	4.556	0.33	0.38*
	M ³ W	41	0.950	0.32	0.282-0.350	4.595	0.33	0.38*
	M ³ A	41	0.952	0.66	0.590-0.727	3.301	0.67	0.75*
	∑M ¹⁻³ L	40	0.966	0.33	0.298-0.355	4.407	0.33	0.38*
	∑M ¹⁻³ A	40	0.966	0.66	0.605-0.721	2.986	0.67	0.75*
	TRLL	42	0.960	0.30	0.273-0.328	4.433	0.33	0.38*
	TRLL×M ² W	42	0.964	0.62	0.564-0.674	3.106	0.67	0.75*
	M ₁ W	46	0.962	0.34	0.310-0.369	4.671	0.33	0.38*
	M ₂ W	42	0.953	0.31	0.278-0.341	4.691	0.33	0.38*
M ₃ W	40	0.946	0.31	0.273-0.342	4.678	0.33	0.38*	
Skull length	WZY	53	0.956	0.98	0.894-1.063	0.385	1.00	1.12*
	TRUL	50	0.907	1.08	0.941-1.233	0.319	1.00	1.12
	TRUA	49	0.949	2.09	1.898-2.311	-4.270	2.00	2.25
	M ¹ L	48	0.944	1.02	0.922-1.135	1.221	1.00	1.12
	M ¹ W	53	0.933	1.09	0.979-1.218	1.125	1.00	1.12
	M ¹ A	48	0.942	2.16	1.950-2.412	-2.788	2.00	2.25
	M ² L	48	0.948	1.03	0.928-1.134	1.154	1.00	1.12
	M ² W	50	0.932	1.06	0.951-1.194	1.123	1.00	1.12
	M ² A	48	0.945	2.13	1.927-2.370	-2.915	2.00	2.25
	M ³ L	47	0.921	1.09	0.958-1.236	1.047	1.00	1.12
	M ³ W	47	0.928	1.00	0.889-1.133	1.219	1.00	1.12
	M ³ A	47	0.937	2.14	1.922-2.407	-2.953	2.00	2.25
	∑M ¹⁻³ L	46	0.952	1.04	0.939-1.143	0.652	1.00	1.12
	∑M ¹⁻³ A	46	0.948	2.13	1.927-2.363	-3.859	2.00	2.25
	TRLL	48	0.963	0.96	0.884-1.046	0.563	1.00	1.12*
	TRLA	48	0.962	1.99	1.835-2.175	-3.661	2.00	2.25*
	M ₁ W	53	0.955	1.09	1.000-1.193	1.312	1.00	1.12
	M ₂ W	48	0.947	1.00	0.904-1.108	1.375	1.00	1.12*
	M ₃ W	46	0.942	1.00	0.895-1.113	1.387	1.00	1.12*
	Skull length × skull width	TRUA	49	0.968	1.05	0.972-1.131	1.212	1.00
TRLA		48	0.977	1.01	0.989-1.080	1.495	1.00	1.12*
M ¹ A		48	0.969	1.08	0.989-1.177	1.967	1.00	1.12
M ² A		48	0.965	1.06	0.982-1.156	1.899	1.00	1.12
M ³ A		47	0.962	1.07	0.981-1.162	1.883	1.00	1.12
∑M ¹⁻³ A		46	0.970	1.06	0.987-1.150	1.411	1.00	1.12
TRUL	TRLL	48	0.987	0.97	0.926-1.021	0.050	1.00	
M ¹ A	M ² A	48	0.994	0.99	0.957-1.020	-0.065	1.00	
M ¹ A	M ³ A	46	0.967	0.99	0.914-1.073	-0.088	1.00	
M ² A	M ³ A	46	0.984	1.00	0.947-1.059	-0.019	1.00	

phylogenetic change. I only mention these complications here to indicate that the case can not be cited as unambiguous evidence of positive allometry of tooth size to body size. On the other hand, the number of cases of considerably lower exponents than the estimates of direct metabolic scaling is considerable (Table 2), and one might be tempted to reverse the argument of Pilbeam & Gould (1974:898) that "the pattern begins to convince by its unerring repetition".

To investigate the scaling of tooth size specifically in ungulates in more detail, I measured various dimensions on ungulate skulls and dentitions, as detailed in Appendix 2. Selected results are presented in Tables 3 and 4. Table 3 compares the relationships between different pairs of variables in the whole hyrax-to-elephant sample, while Table 5 compares selected taxa.

Table 3 may be summarized as follows:

1. No cranial or dental dimensions are significantly allometric (in the sense of deviation from isometry) to body weight except skull length times width and lower postcanine toothrow length, which are barely negatively allometric ($P < 0.05$). All the dental slopes are significantly lower than predicted by the hypothesis of direct metabolic scaling ($P < 0.05$).

2. No dental dimensions are significantly allometric to skull length, but correlations tend to be lower than for body weight and confidence limits are correspondingly wider. The best estimate in all cases but three suggests very weak positive allometry. Only four dimensions have slopes significantly lower than predicted by direct metabolic scaling (M^3L , $TRLL$, M_2W , M_3W).

3. No tooth areas are significantly allometric to skull length times width, but only lower postcanine area scales at a slope significantly lower than the direct metabolic. All slope estimates are very slightly above unity (isometric).

4. Dental dimensions are not significantly allometric to each other.

Thus a very extensive geometric similarity is observed, with a possible weak negative allometry of skull size to body size.

In comparing the relationships within different taxa (Table 4) sample size becomes a problem, as confidence limits expand with decreasing sample size. Despite this difficulty some taxa may be compared. (Particularly for selenodont artiodactyls many more species are potentially available, but I simply did not have access to more.) Using both upper toothrow area and M^1 area gives some extra confidence, since these parameters do not share any measurements, yet in all cases behave similarly.

1. *Ceratomorpha*. Prothero & Sereno (1982) used data from the five extant rhino and two extant tapir (of the four available) species to investigate dwarfism in Miocene rhinoceroses. My results largely reproduce theirs: there is a (non-significant) negative allometry of skull size to body size, and a correspond-

ing positive allometry of tooth size to skull size, while tooth size is more nearly isometric to body size. However, this seems to be an artefact of mixing groups of different design, since excluding the tapirs changes the result (see below under "Dwarfing", p. 44).

2. *Rhinocerotidae*. There is no evidence of allometry. Correlations are lower than for the *Ceratomorpha* because the range is much smaller.

3. *Suina*. There is a weak (non-significant) indication of negative allometry of skull size to body size and a corresponding positive allometry of tooth size to skull size. Prothero & Sereno (1982) obtained a statistically significant result to the same effect.

4. '*Selenodont artiodactyls*'. Pooling bovids, cervids, tragulids, the giraffe and a camel results in this assemblage. Correlations are high, reflecting the great size range, and perhaps similarity of design. There are no significant departures from isometry, but there is a suggestion that skull size is slightly negatively allometric to body size and that tooth size is slightly negatively allometric to both.

5. *Cervidae*. My sample is rather heterogeneous (see App. 2), but such as it is it suggests general isometry. There is no evidence of the positive allometry of skull size to body size expected by Gould (1973, 1975), nor of the positive allometry of tooth size to body size found by Pilbeam & Gould (1974) (but their sample was larger and more homogeneous).

6. *Bovidae*. This sample is also heterogeneous, but correlations are all higher than 0.97, which is evidence that a similar design applies to all the species included. Slopes are not significantly different from isometry, but the pattern of negative allometry of skull to body and of teeth to both is again suggested. Kay (1975) and Lucas (1980) have presented data to show that postcanine tooth area is negatively allometric to body weight in bovids (Table 2).

In summary, there is no compelling pattern of allometry generally or in any ungulate group, but there is some indication that isometry is less dominant at lower taxonomic levels, with deviations in both directions. This confirms Meunier's (1959) and Gould's (1971) suggestion that the transposition of lower taxa in allometric plots serves to maintain overall geometric similarity. If the conclusion that geometric similarity equals functional similarity through size-related changes in rates is accepted, it follows that departures from isometry at lower levels may not be generally related to function. Instead, they may reflect growth constraints or similar factors, as suggested by Meunier (1959). This does not preclude the possibility that allometry may be functionally adaptive in specific cases, of course. It would, for example, be interesting to know why the lower carnassial tooth scales with positive allometry to body size in mustelids and canids, but with negative allometry in felids and viverrids (Creighton 1980).

Table 4. Bivariate relationships between adult body weight and cranial and dental dimensions in selected ungulate groups (App. 1–2). Note general isometry. * = value outside 95 % CL (*b*). Abbreviations see p. 75.

Taxon	W	Y	N	r	b	95 % CL (<i>b</i>)	log <i>a</i>	Isom.	'Metab.'
Suina	AWT	SKA	6	0.950	0.59	0.366–0.859	2.27	0.67	0.75
	AWT	TRUA	6	0.922	0.70	0.374–1.168	2.76	0.67	0.75
	AWT	M ¹ A	6	0.886	0.66	0.273–1.250	3.46	0.67	0.75
	SKA	TRUA	8	0.919	1.16	0.751–1.871	0.92	1.00	1.12
	SKA	M ¹ A	8	0.895	1.11	0.655–1.954	2.03	1.00	1.12
	CBL	TRUA	8	0.964	2.62	2.031–3.584	-6.06	2.00*	2.25
Selenodont Artiodactyla	AWT	SKA	24	0.988	0.62	0.578–0.663	2.06	0.67*	0.75*
	AWT	TRUA	23	0.968	0.58	0.513–0.650	3.06	0.67*	0.75*
	AWT	M ¹ A	22	0.973	0.60	0.536–0.669	3.45	0.67	0.75*
	SKA	TRUA	25	0.974	0.95	0.862–1.053	1.55	1.00	1.12*
	SKA	M ¹ A	24	0.981	0.98	0.895–1.069	2.23	1.00	1.12*
	CBL	TRUA	25	0.962	1.83	1.624–2.076	-3.21	2.00	2.25*
Cervidae	AWT	SKA	7	0.974	0.65	0.489–0.843	1.84	0.67	0.75
	AWT	TRUA	6	0.932	0.59	0.317–0.951	2.96	0.67	0.75
	AWT	M ¹ A	6	0.911	0.56	0.256–0.970	3.51	0.67	0.75
	SKA	TRUA	7	0.969	0.96	0.710–1.298	1.54	1.00	1.12
	SKA	M ¹ A	7	0.955	0.90	0.614–1.289	2.45	1.00	1.12
	CBL	TRUA	7	0.965	1.76	1.309–2.506	1.48	2.00	2.25
Bovidae	AWT	SKA	13	0.988	0.63	0.566–0.678	2.07	0.67	0.75*
	AWT	TRUA	13	0.983	0.62	0.548–0.623	3.00	0.67*	0.75*
	AWT	M ¹ A	12	0.974	0.62	0.526–0.729	3.44	0.67	0.75*
	SKA	TRUA	14	0.985	0.99	0.889–1.112	1.45	1.00	1.12*
	SKA	M ¹ A	13	0.985	0.99	0.883–1.115	2.20	1.00	1.12*
	CBL	TRUA	14	0.970	1.90	1.633–2.241	-3.45	2.00	2.25*
Ceratomorpha	AWT	SKA	7	0.990	0.58	0.493–0.683	2.90	0.67	0.75*
	AWT	TRUA	7	0.980	0.72	0.563–0.905	3.03	0.67	0.75
	AWT	M ¹ A	7	0.974	0.97	0.736–1.270	2.76	0.67*	0.75
	SKA	TRUA	7	0.988	1.24	1.039–1.486	0.21	1.00*	1.12
	SKA	M ¹ A	7	0.978	1.67	1.320–2.169	-0.27	1.00*	1.12*
	CBL	TRUA	7	0.967	2.72	2.071–3.854	-8.22	2.00*	2.25
Rhinocerotidae	AWT	SKA	5	0.991	0.64	0.488–0.815	2.74	0.67	0.75
	AWT	TRUA	5	0.903	0.62	0.104–1.573	3.55	0.67	0.75
	AWT	M ¹ A	5	0.877	0.54	-0.004–1.535	4.26	0.67	0.75
	SKA	TRUA	5	0.898	1.01	0.232–4.457	1.10	1.00	1.12
	SKA	M ¹ A	5	0.852	0.88	-	2.23	1.00	1.12
	CBL	TRUA	5	0.804	2.00	-	5.58	2.00	2.25

Adult intraspecific allometry

There is less data on intraspecific allometry of tooth size and body size published than one would perhaps expect. Klatt (1913), working with domestic dogs, published data on tooth size and skull length, and Williams (1955), also using dogs, gave an allometric equation relating molar row length to mandible length (Table 5). Although other published data presumably do exist, I have not been able to find any except those of Radinsky (1984) giving the relationship between upper toothrow length and braincase length in the domestic horse. My own material is of limited usefulness because tooth size is difficult to measure with sufficient accuracy in most ungulates because the crown bases are exposed only late in life. In many bovids I have actually found a weak negative correlation between skull size and tooth size (unpub-

lished data), presumably because the youngest individuals which have the least erupted and least worn teeth (with maximum length dimensions) have not yet reached maximum skull size. My sample sizes tend to be small for species unaffected by this complication. Data for three such species are given in Table 5. The bear data are from the unpublished records of Björn Kurtén.

Ignoring the horse for a moment, there is a clear distinction between the two carnivores and the three ungulates; carnivores have negatively allometric teeth and ungulates positively allometric ones. Although correlations are weak (except for the domestic forms with their artificially expanded size ranges), the 95 % confidence limits exclude isometry in all cases when they are given or can be calculated. (The slope 5.44 for *Sylvicapra grimmia* goes with the very

Table 5. Intraspecific tooth size allometry in selected cases. Note difference between carnivores and ungulates. Abbreviations see p. 75.

Species	W	Y	N	r	b	95 % CL (b)	log a	Isom.	Source
<i>Canis familiaris</i>	CBL	P ¹ AL	37	0.967	0.63	0.573–0.688	1.030	1.00	3
<i>Canis familiaris</i>	MAL	MRUL	42	0.971	0.75	–	–0.062	1.00	4
<i>Ursus arctos</i>	BL	M ¹ L	81	0.439	0.42	0.235–0.634	1.887	1.00	2
<i>Diceros bicornis</i>	SKA	TRUA	24	0.648	2.19	1.368–4.329	–3.914	1.00	1
<i>Diceros bicornis</i>	SKA	M ² A	24	0.674	2.50	1.626–4.695	–3.532	1.00	1
<i>Equus caballus</i>	BRCL	TRUL	18	0.952	0.69	–	0.463	1.00	5
<i>Hyaemoschus aquaticus</i>	SKA	M ² A	31	0.525	1.95	1.081–4.880	–0.010	1.00	1
<i>Sylvicapra grimmia</i>	CBL	M ² L	79	0.249	5.44	2.810–46.225	–3.550	1.00	1

Sources: 1. = original data, 2. = Björn Kurtén unpublished, 3. = data from Klatt (1913), 4. = Williams (1955), 5. = Radinsky (1984).

low correlation coefficient of +0.25, and is almost certainly much too high.)

Radinsky's horses display strong negative allometry (exponent 0.69 of toothrow length against braincase length). If braincase length is negatively allometric to body size, as suggested above, the allometry becomes even more pronounced. But the domestic horse sample differs from the other ungulate samples in that it includes dwarfs, and this may account for the apparent anomaly. This point will be discussed in connection with dwarfism.

In no case does the intraspecific allometry correspond to the observed interspecific isometry, but it is premature to generalize from such limited data. It would be particularly interesting to know how tooth size scales with actual body mass within species, and whether the strong patterns of allometry perhaps reflect the scaling of skull size rather than the scaling of tooth size itself. A thorough study of the intraspecific scaling of tooth size might be rewarding. At present we may note that the observed intraspecific isometry is certainly not a trivial result of isometric scaling within species, and that it therefore would seem to reflect some higher-order constraint, such as functional or ontogenetic restrictions.

Ontogenetic relationships of the dentition

Tooth growth can be studied as a conventional problem of ontogenetic allometry, but that aspect is irrelevant here. Teeth do not begin to function until they have reached their final size, and the dentition can only grow by addition of whole teeth. However, one may consider the actual size of the row of erupted teeth as a function of body size during individual growth. A sample of 11 juveniles of *Diceros bicornis* gives the slope 0.85 (95 % confidence limits 0.305 to 2.054, $r = 0.71$, $\log a = 0.734$) for erupted toothrow length against condylobasal length. This is different from the positive allometry of the adults (Table 5), but the significance is unclear.

Radinsky (1984) demonstrated a very similar on-

togenetic scaling of the distance between the last erupted cheek tooth and the first upper incisor to braincase length in domestic horse (slope 0.80). In this case, however, the scaling between adults was practically identical (slope 0.86). In the fossil horse sample these dimensions scaled at exponent 1.24. Discussion of this is in the next section.

Dwarfing

Gould (1975) suggested, based on the hypothesis of positive allometry of tooth size to body size, that dwarf forms might have relatively larger teeth than their full-sized ancestors. He investigated the living and two extinct species of pygmy hippo (the living *Hippopotamus amphibius* acting as a substitute ancestor) using skull length as an estimate of body size, and found that the dwarfs indeed had relatively larger tooth area than *H. amphibius*. The exponent of postcanine tooth area against basicranial length for *H. amphibius*, *H. lemerlei*, *H. minutus* and *Choeropsis liberiensis* was 1.75. Gould also cited Maglio's (1972) observation that the dwarf *Elephas falconeri* had relatively larger molars than its ancestor *Elephas namadicus*.

Prothero & Sereno (1982) wanted to 'test' this 'prediction' on Miocene dwarf rhinos from the Gulf coast of Texas and Florida, and claimed that their results falsified it both for the rhinos and the hippos, and that Gould had been misled by negative allometry of skull size to body size. Their results do not warrant such a conclusion, however. What they demonstrated was that skull size is negatively allometric to body size in suine artiodactyls and the 'Ceratomorpha'; i.e., the five living rhinos plus two living tapirs. As discussed above, the latter conglomerate may not be very relevant biologically since tapirs are rather inadequate models of small rhinos in terms of cranial and dental design. Similarly, pigs may not be satisfactory as models of dwarf hippos. Their suggestion that dwarfs have relatively smaller skulls rather than relatively larger teeth is interesting but not demonstrated.

Table 6. Tooth size – skull size allometry in the Rhinocerotidae and ‘Ceratomorpha’, according to different data sets. Abbreviations see p. 75.

Taxon	W	Y	r	b	95 % CL (b)	log a	b'	Isom.
Ceratomorpha (P&S)	CPL	AWT	0.970	3.44	2.656–4.811	–18.03	3.26	3.00
	TRUA	AWT	0.969	1.67	1.263–2.300	–5.58	1.59	1.50
	TRUA	CPL	0.976	2.07	1.626–2.761	–6.50	1.99	2.00
Rhinocerotidae (P&S)	CBL	AWT	0.864	3.54	1.551–44.701	–19.35	2.71	3.00
	TRUA	AWT	0.868	2.62	1.073–44.731	–11.78	2.06	1.50
	TRUA	CPL	0.927	1.35	0.596–4.071	–3.46	1.23	2.00
Rhinocerotidae (From Table 4)	CBL	AWT	0.974	2.80	1.920–4.796	–14.40	2.67	3.00
	TRUA	AWT	0.903	1.62	0.636–9.654	–5.75	1.40	1.50
	TRUA	CBL	0.804	2.00	–	–	–5.58	1.42

P&S = Prothero & Sereno (1982); b = major axis slope, b' = least squares slope

Table 6 gives the relevant relationships for the ‘Ceratomorpha’ and for the Rhinocerotidae, calculated from the data given by Prothero & Sereno (1982) and from data taken from Table 4. No meaningful confidence limits may be given, but the best estimate for the rhinos is that (i) tooth area is isometric to skull length, and (ii) tooth area is slightly negatively and skull length slightly positively allometric to body weight. Since Prothero and Sereno do not give the appropriate measurements for their single complete dwarf rhino skull, it is impossible to say whether or not it would plot significantly off the line for the Rhinocerotidae.

Although it has not been mentioned in the recent literature, the idea that dwarfs have relatively larger teeth is of old standing. Indeed, it was “eine bekannte Tatsache” to Antonius (1922:254). Quantitative data in support of it concern tooth size relative to skull size, and isometry has usually been the implicit null hypothesis. Traditionally the problem was seen as one of domestication rather than of dwarfing, and it is conceivable that several factors are indeed involved (see below).

The first to suggest that dwarfs have relatively larger teeth may have been Leche (1904), who gave data for wild versus domestic yak and goat. Klatt (1913) gave data for domestic dog and Lundholm (1947) for domestic horse and insular versus mainland red deer. As noted above, Williams (1955) also gave data for domestic dogs and Radinsky (1984) for a domestic horse sample with a wide size range, including “a very small Shetland pony” of 36 cm skull length. In each case the smaller forms had relatively larger teeth. However, Leche (1904) also noted that domestic camels have relatively (and absolutely) larger molars than wild camels, although they are not themselves smaller. The possibility that domestication per se somehow causes relatively larger teeth (better nutrition?) cannot be ruled out, and more than one factor may well be involved. Lundholm (1947) showed that early (Bronze Age) horses had relatively the largest teeth, and that relative tooth size later decreased.

Radinsky’s (1984) data suggest that in domestic horses ontogenetic and adult allometries of tooth size to skull size are identical; i.e., that adult horses of different sizes may be considered as points on an ‘ontogenetic trajectory’ describing changes in size and shape during individual growth (Alberch et al. 1979). However, the case is complicated by the problem mentioned above, that teeth do not grow continuously but are formed at a given size long before the skull has reached its final dimensions. In *Diceros bicornis* the relationship is apparently different from that of the domestic horse, and it would be valuable to know the situation in a wild horse population.

In view of the complexity of the problem and the almost total lack of data one should not jump to conclusions, but nevertheless two points suggest themselves: (i) domestic forms with artificially extended size ranges may not be applicable to problems of scaling in wild mammals, and (ii) positive allometry of tooth size to skull size between adults and negative allometry during ontogeny combined with large teeth in dwarfs suggest a phenomenon analogous to paedomorphism (retention of a juvenile state in the adult; see Gould 1977) as the cause of dwarfism. However, nothing requires that all dwarfism should be due to the same ontogenetic modification, and indeed such a situation appears highly unlikely. Roth (1984) found a mixture of paedomorphic and peramorphic (Gould 1977) traits in dwarf elephants.

Sexual dimorphism in tooth size and body size

In sexually dimorphic mammals cheek tooth size differs less between the sexes than body size (c.g. Gingerich 1981). Kay (1978) for primates and Lucas (1980) for various primates and bovids showed that smaller females have relatively larger teeth than larger males (see Table 7 for another example: *Kobus defassa*). Kay (1978) suggested that this might be due to higher energy requirements of females during pregnancy, but Lucas (1980) pointed out that

Table 7. Sexual dimorphism of skull size and tooth size in two bovid species. *Kobus* males are larger than females, while in *Ourebia* the reverse is true. In both cases tooth size is less dimorphic than skull size. Skulls from TE (App. 2). Abbreviations see p. 75.

	Sex	N	Mean	SD	95 % CL (mean)	% dimorphism
<i>Kobus defassa</i>						
CBL	♂	61	382.8	11.5	379.8–385.7	
	♀	38	362.3	8.86	359.4–365.2	105.6
M ² L	♂	61	22.34	1.27	22.02–22.67	
	♀	38	21.99	1.16	21.61–22.38	101.6
<i>Ourebia ourebi</i>						
CBL	♂	46	154.9	5.68	153.2–156.5	
	♀	15	162.6	3.62	160.6–164.6	95.3
M ² L	♂	46	11.8	1.18	11.50–12.20	
	♀	15	11.7	0.91	11.22–12.22	100.8
M ² W	♂	46	8.9	0.61	8.71–9.07	
	♀	15	9.0	0.44	8.74–9.23	98.9

males are known to possess higher metabolic rates for their weight than females (Benedict 1938, Morrison & Middleton 1965, Altman & Dittmer 1974 and Dale et al. 1970, all cited in Lucas 1980). Moreover, when the sexes are of equal size there is no dimorphism of tooth size, as might otherwise be expected (e.g. Gingerich & Ryan 1979). Lucas (1980) also suggested that when females are larger, the males are the ones with relatively larger teeth, and showed this for *Ateles geoffroyi*. My data for *Ourebia ourebi* (Table 7) support this suggestion.

It thus seems to be fairly well established that there is no one-to-one relationship between metabolic requirements and tooth size between the sexes, and that sexual dimorphism displays a similar intriguing negative allometry of tooth size to body size as dwarfing. Whether or not this means that processing capacity is unrelated to energy requirements at this level depends on the unknown sexual scaling of other relevant variables (see below).

4.1.3. Tooth size, body size and food comminution

Pilbeam & Gould (1974) were not the first to consider the scaling of tooth size in mammals in terms of food processing and metabolism. Simpson (1944, 1953) discussed hypsodonty in relation to body size in horse evolution and concluded that the two were independent although spuriously correlated because both increased (independently) in the same lineage. In this view, hypsodonty evolved in response to increased dental wear caused by grass eating. Huxley (1953), however, thought that the increased life span (and thus increased period of tooth use and wear) of the larger animals made higher teeth necessary, and this assumption is common in the literature.

Van Valen (1960) suggested that 'functional hypsodonty' (in principle, any adequate measure of a tooth's ability to tolerate wear while maintaining its

functional efficiency) would scale with metabolic rate as $M^{3/4}$ (where M is body mass). Pilbeam & Gould (1974) and Gould (1975), who considered momentary rather than life-long metabolic requirements of food processing, suggested that post-canine occlusal area should scale similarly as $M^{3/4}$. As nothing requires that tooth shape remain constant there is no contradiction between the two statements. Since an area scales to a volume as $A = V^{2/3}$, Pilbeam's & Gould's $3/4$ exponent signifies positive allometry of occlusal area to body mass. Van Valen's 'functional hypsodonty' is not fixed dimensionally, which means that no particular allometric relationship can be specified. If it were determined only by height, strong positive allometry ($M^{3/4}$ against isometry $M^{1/3}$) would be predicted. But if it is determined by volume, the predicted relationship is actually negative allometry ($M^{3/4}$ against M^1). If different mechanical properties of the dental tissues are involved, the relationship may take almost any form. It is clear, however, that Van Valen thought that hypsodonty would scale with positive allometry to body size when he wrote that "It would be of interest to know ... whether hypsodonty ... [is] largely involved in the necessary compensation for increasing size..." (Van Valen 1960:531). It is clear from the above that 'tooth size' may be several different things, depending on which aspect of the morphology of the tooth or biology of the animal is considered.

Gould (1975:361) described his paper as "an unabashed plea for the entrance of more talent into an exciting and unexplored field". A decade later one notes that the paper has been much quoted and discussed, chiefly by authors presenting data which seem to falsify the hypothesis of direct metabolic scaling of tooth area. As noted in the previous section, the accumulating empirical evidence now strongly suggests that isometry of tooth size to body size is the rule. It is, then, all the more surprising that

theoretical discussion has been almost nil, and that no functional hypothesis explaining the widely observed isometry has been offered. Perhaps it has been felt that isometry requires no explanation, but one must agree with Gould that there is no compelling a priori reason to expect that particular relationship on theoretical grounds. Now that not only basal metabolic rate but a whole host of other physiological rates, including that of ingestion, are known to scale approximately as $M^{3/4}$ (Peters 1983), the need to explain the discrepancy between Van Valen's and Pilbeam & Gould's predictions on one hand and the empirical data on the other seems rather pressing.

A potential solution is offered by consideration of other biological correlates of size. To start with a simple case, Huxley's (1953) statement that the increased life span of large animals requires tooth height to scale with positive allometry to body size is, of course, testable. Peters (1983) compiled data from the literature to show that life span scales approximately as $M^{1/4}$ in mammals, which is less than the isometric relation of a linear measurement (height) of $M^{1/3}$. If life span alone is considered, negative allometry of tooth height to body size would thus be expected; the opposite of what Huxley thought.

The above conclusion is of obvious relevance to Van Valen's (1960) discussion of hypsodonty and life-long food requirements, since both metabolic rate and life span influence these. That is, an animal will need energy at a certain rate for a certain length of time, which defines the total amount of energy (and food) needed. This presumably in turn determines the total sum of tooth wear. If just metabolic rate and life span are considered, 'functional hypsodonty' would be expected to scale as $M^{3/4} \times M^{1/4} = M^1$; i.e., isometrically with body mass. This is consistent with Simpson's (1944, 1953) view that hypsodonty has evolved independently of body size.

As to the more complicated matter of tooth size and processing capacity, it is useful to recall the essentials of food comminution (Sect. 3.2.1.). For each food there exists a critical stress at which it breaks, and stress is independent of absolute size (since it is determined by load proportional to muscular (physiological) cross sectional area and by occlusal area, both scaling approximately as $M^{2/3}$). Breakage is thus in principle independent of absolute tooth size. Breakage also appears to be independent of particle size for the range involved in chewing (Lucas & Luke 1983a).

Selection decreases with decreasing particle size and beyond a lower size limit chewing no longer pays (Lucas & Luke 1983a). As discussed above (Sect. 3.2.1.), this may be interpreted in terms of relative rather than absolute particle size; i.e., as a limit in the ratio of particle size to the size of the occlusal surface (the comminuting equipment). If this is correct, selection, too, would be effectively independent of absolute size. Testable predictions can be derived

from the above. For example, for a given dental design and food, the number of chews before swallowing should be constant and independent of absolute tooth size, and particle size at corresponding stages (for example at swallowing) should be isometric to tooth size.

Gould (1975) assumed that the volume processed per chew would scale as occlusal area, for isometric teeth as $M^{2/3}$. Since this assumption is crucial to the whole hypothesis of direct metabolic scaling of tooth size, it is worth examining in some detail. Consider a body of food trapped between upper and lower tooththrows. When the teeth move into occlusion, the food is first deformed and then separated into a number of smaller portions, some of which end up between blades or at other 'comminuting locations'. If all such selected particles break, the volume comminuted will depend on selection; i.e., area. But consider the entire system in several sizes: is there any reason to suppose that the shape of the body of food between the teeth will change as the teeth become larger or smaller? I believe not, except for foods that consist of particles that must be treated as individuals (for example, nuts). For foods that can be shaped into a bolus in the mouth and manipulated as a plastic mass during chewing it is reasonable to assume that, for a given occlusal morphology, the body of food placed between the occlusal surfaces before each power stroke will be of a constant shape. If so, and if particle size at corresponding stages of comminution is isometric to tooth size as suggested above, it is difficult to see how the volume comminuted per stroke could be proportional to area. A more reasonable assumption is that it is proportional to the volume placed between the teeth, which for isometric teeth will scale as M^1 .

If the volume comminuted per chew scales as M^1 , larger animals will need relatively fewer chews per unit time to satisfy their metabolic requirements scaling as $M^{3/4}$. They might spend less time during the day chewing, or they might chew more slowly, or both. These hypotheses are testable. Since it is a matter of common knowledge that small animals chew faster than large animals, it may be a reasonable hypothesis that the compensation occurs mainly via chewing rate. All else being equal, chewing rate should scale as $M^{-1/4}$ for comminution rate to scale with metabolic rate and ingestion rate as $M^1 \times M^{-1/4} = M^{3/4}$. Chewing cycle duration should then scale inversely as $M^{1/4}$.

The durations of various biological phenomena, for example, heartbeats and breaths, do in fact scale as $M^{1/4}$ in mammals (Peters 1983), but chewing cycle durations do not appear to have been investigated in this respect. Hiimäe (1978) compiled a table of data then available, and concluded that no relationship exists between chewing rate and body size. However, her data were for mammals diverse in their taxonomy and diet, and any relationship might well

Table 8. Major axis regression of chewing cycle duration (ms) on body weight (kg). Log-transformed data from App. 6 (A) and Hendrichs 1965 (H).

Group	<i>N</i>	<i>r</i>	<i>b</i>	95 % CL (<i>b</i>)	log <i>a</i>
Fresh chewing (A)	12	0.91	0.23	0.16–0.31	1.15
Fresh chewing (A ¹)	10	0.85	0.19	0.10–0.29	1.44
Fresh chewing (H)	16	0.79	0.13	0.07–0.19	1.67
Cud chewing (A)	12	0.91	0.22	0.15–0.29	1.46
Cud chewing (H)	16	0.86	0.16	0.10–0.21	1.58

¹ Rabbit and pig omitted.

be masked by factors unrelated to size. Even in single individuals, chewing cycle durations are influenced by the kind of food eaten, the time of day etc. (Hendrichs 1965, De Vree & Gans 1975). Hendrichs (1965) presented data on chewing rates for a wide range of ruminants, but about half of his larger species chew the cud at precisely one chew per second, suggesting that his data may not be sufficiently accurate for the present purpose. Analysing his data gives positive correlations of 0.79–0.86 between chewing cycle duration and body weight, and major axis slopes of 0.13–0.16 (Table 8).

Data on chewing cycle durations collected by myself at the Zoo of Helsinki (App. 6) give both higher correlations and higher slopes (Table 8). If data for rabbit and miniature pig taken from the literature are included, fresh chewing gives a correlation of +0.91 and a slope of 0.23. If rabbit and pig are omitted, lower values are obtained ($r = +0.85$, $b = 0.19$). Rumination probably helps to standardize conditions of chewing, and it is interesting that cud chewing gives a correlation of +0.91 and a slope of 0.22. (Table 8). Except for the data from Hendrichs (1965), which may not be sufficiently accurate, all the data sets give 95 % confidence intervals for the slope that contain the predicted value of 0.25. Considering that so many other factors must be involved, this is almost surprising. Certainly the hypothesis can not at present be rejected.

It is interesting to calculate that if processing capacity per stroke would scale as $M^{3/4}$, as predicted by Pilbeam & Gould (1974), and chewing rate as $M^{-1/4}$, volume processed per unit time would scale as $M^{1/2}$, leading to an immediate energy crisis in large animals with a metabolic rate scaling as $M^{3/4}$. This seems to falsify the hypothesis that volume comminuted per stroke scales with occlusal area, and thus the foundation of the hypothesis of direct 'metabolic' scaling of post-canine tooth area.

It seems, then, that isometry of occlusal area to body size is in fact also true metabolic scaling, and an acceptable 'null hypothesis' for comparisons. In the form in which it is presented here it is clearly distinct from the naive misconception criticized by Gould (1975), that geometric similarity as such would imply

functional similarity. Geometric similarity prevails for reasons which may or may not be related to function (see below), and functional similarity is achieved through other than morphological means, as in this case through rates. It follows that it is impossible to consider the problem in terms of morphology and size alone, since that excludes a major part of the relevant information. The same applies to predictions, which may be quite specific, derivable from the present model. For example, one may predict that non-isometric scaling will be found when the diet of the animal consists of foods which cannot be manipulated as a plastic mass during chewing, or when the timing of the feeding is very restricted and/or chewing rate does not scale as $M^{-1/4}$. It would be interesting to investigate intraspecific scaling of chewing rate to find out whether or not it is related to the observed tooth size allometry. In particular it might be rewarding to study chewing in carnivores and ungulates, to see whether the difference in tooth size allometry (negative in carnivores, positive in ungulates) tentatively noted in the previous section, corresponds to differences in chewing rate. Such a difference might, for example, reflect differences in mechanical properties of plant and animal foods.

3.1.4. Why is isometry so common?

Since ratios between parameters of different dimensionality change with isometric size change, isometry in the sense of geometric similarity can not be generally equivalent with functional similarity. For this reason, Gould (1971:129) considered it "a problem, not an expectation". I have tried to show above that functional similarity of isometrically scaled systems can be obtained by changes in the time dimension, and that this applies at least to the masticatory apparatus. In this section I will offer some speculation as to why isometry is so general in mammalian design.

Gould (1971) suggested two reasons for why isometric scaling would be common. First, that proportional size changes are commonly associated with simple genetic and hormonal changes which might

permit rapid evolution of size in response to environmental change. Second, that it might improve functional performance, for example when functional similarity requires 'only' negatively allometric size increase of an organ (e.g. the brain). This second argument obviously cuts both ways since isometric size increase (or decrease) may equally well result in impaired function. In the brain, isometric size increase will improve 'encephalization', while isometric size decrease will impair it. If one accepts that animals are well designed as a rule, it seems unlikely that isometric size change would improve net overall functional performance.

D'Arcy Thompson (1917) pointed out that absolute jumping height in animals of similar design is independent of absolute body mass. Similarly, occlusal stress is independent of absolute size for isometrically scaled teeth and jaw muscles (Sect. 3.2.1). Given that required critical stress is determined by the food, it would seem that isometric scaling of the whole masticatory apparatus is to be expected, at least unless there is a systematic size-dependence of food strength. Such does not appear to be the case; grazers, for example, are found in all size classes. On the other hand, energy requirements (metabolic rate) would, *ceteris paribus*, require a negatively allometric scaling of tooth area. This points to a general problem of considerable theoretical importance: functional similarity in one sense (breakage) has different scaling requirements from functional similarity in another sense (rate of comminution). In other words, there is *no* scaling that will result in functional similarity at different sizes. In the case of food comminution, breakage requires a certain stress, and changes in timing can not alter this fundamental fact. In contrast, the rate of comminution can be altered by a changed chewing rate, and this is what is observed. It is conceivable that the principle could be generalized to cover size-dependent rates and durations in general, such as life span and metabolic rate, but that is not within the bounds of the present investigation.

The principle of nested growth, or the "production of parts in existing parts" (Woodger 1945:100), is another reason why general isometry in animals sharing a basic 'Bauplan' is to be expected. Spatial constraints during growth (and related phenomena such as the diameters of exit apertures) do not allow changes in proportions that would make the part nested inside another part relatively much larger. For surfaces, the well-known increase of folding offers an escape, but no such possibility is available for volumes. It follows that major size changes must be nearly isometric for nested organs (unless it is allometric in the other direction, which may then cause problems due to empty space). Of course, this principle would not apply to structures growing outside the body, such as horns and antlers, which do seem to be positively allometric to body size as a rule.

Growth and function of individual organisms is not so tightly constrained, however, as can be seen in the considerable variation in populations. One needs only to think of perfectly viable three-legged dogs or one-legged birds, or the variety of foods that can be successfully consumed by many animals, to realize that a considerable functional buffering or overcapacity is the rule during relaxed environmental circumstances, both among wild and captive animals. The constraints on proportions discussed above apparently apply to much greater size ranges than those normally covered by species or even genera. If the relationship exists at these levels it is obscured by other factors and by individual variation.

In summary, I propose that isometry at high taxonomic levels reflects two main circumstances. First, that *no* scaling of size alone will necessarily result in functional similarity at different sizes. Factors such as stress, which are ratios between equidimensional parameters (e.g. areas), are similar only with isometric scaling, while factors involving time can be altered by changing rates and durations. Second, that nested growth of organs precludes major changes in proportions without producing cascading effects on the whole body plan. (Such changes have probably occurred, but we may not recognize them as 'allometric'. Perhaps some morphological discontinuities between taxa correspond to this type of reorganization?) These principles apply to the higher taxonomic levels, or, perhaps more properly, to wide size ranges. The occurrence of proportional dwarfs due to simple mutations would result in isometric scaling, too (Gould 1971), but that mechanism predicts isometric scaling at lower levels also, which is not observed.

4.1.5. *Body size and spatial constraints on growth*

From fertilized ovum to full-grown adult, an elephant clearly has a longer way to grow than a mouse. This applies both to absolute mass increase and the number of mitoses (see e.g. Thompson 1917). It is also known that large mammals tend to have relatively smaller young than small mammals (Leitch et al. 1959). Peters (1983) compiled data from the literature giving least squares slopes between 0.71 and 0.95 for birth weight to adult body weight for mammals in general. For a sample of 21 species of ungulates taken from the literature, a major axis slope of 0.80 is obtained, significantly lower than the isometric 1.00 (Table 9). Since tooth size is isometric to adult body size, it should be positively allometric to birth size, and this is what is observed. Positive (though statistically insignificant) allometry is indeed found for all dental dimensions studied (Table 9). The same is true for skull size, which is interesting, since the brain grows with nega-

Table 9. Relationships between birth weight, adult weight, skull size and tooth size in a sample of ungulates (App. 1–2). Larger species have relatively smaller young, but adult skull size and tooth size is positively allometric to birth size. This presumably accounts for the isometry observed in adults. Abbreviations see p. 75.

W	Y	N	r	b	95 % CL (b)	log a	Isom.
AWT	BWT	21	0.939	0.80	0.671–0.958	2.060	1.00*
BWT	CBL	22	0.950	0.35	0.299–0.408	3.007	0.33
BWT	SKA	22	0.926	0.72	0.595–0.826	0.450	0.67
BWT	TRUL	21	0.909	0.35	0.273–0.426	3.139	0.33
BWT	TRUA	21	0.901	0.77	0.606–0.969	1.250	0.67
BWT	M ¹ A	20	0.912	0.82	0.651–1.021	1.719	0.67
BWT	M ² A	20	0.903	0.81	0.633–1.020	1.676	0.67
BWT	M ³ A	20	0.853	0.77	0.559–1.042	1.795	0.67

tive allometry to the body. Positive allometry of skull size to birth size suggests that the growth of the face and jaws is scaled to that of the teeth. Functional teeth are needed at weaning at the latest, and weight at weaning scales to adult weight at least squares slope 0.73 in mammals (Peters 1983).

One could thus hypothesize that the teeth of large mammals begin to grow in relatively smaller jaws than those of small mammals, and this might constitute a general constraint on the proportions of the dentition. A plausible specific hypothesis is that the teeth that begin to form first in the largest mammals should be most affected and the ones that begin to form last in the smallest mammals should be least affected, all else being equal. Thus, early forming teeth should be negatively allometric to late forming teeth in a sample of sufficient size range and unity of design for the constraint to have a measurable influence.

As noted above (Table 3), at the level of 'all ungulates' no such allometry is detected, nor is it within the bovid sample (unpublished data). But the data are not conclusive since they do not include height, which may be the critical dimension. Gingerich et al. (1982) found that in primates M1 is negatively and M3 positively allometric to body size, but did not consider growth constraints as a possible explanation.

If large mammals have relatively smaller young with relatively smaller jaws, this should affect the proportions between milkteeth and the premolars which replace them. Few researchers have bothered to measure milkteeth systematically, but Guérin (1981) gives data for six species of Plio-Pleistocene European rhinoceroses (see Table 10; "*Dicerorhinus etruscus etruscus*" and "*D. e. brachycephalus*" are perhaps distinct enough to be treated as species). Six species is too small a sample to allow great confidence, but the correlations are high and the major axis estimates plausible. Table 10 can be summarized as follows:

1. Taken as blocks the milkteeth are negatively allometric to the premolars ($b = 0.81$). The larger the animal, the relatively larger the premolars.

Table 10. Allometry between deciduous molar and premolar size (length \times width) in six species of Plio-Pleistocene rhinoceroses: "*Dicerorhinus megarhinus*", "*D. etruscus etruscus*", "*D. e. brachycephalus*", "*D. hemitoechus*", "*D. kirchbergensis*", *Coelodonta antiquitatis*. Data from Guérin 1980.

Teeth (W:Y)	r	b	95 % CL (b)	log a
Premolars:milk molars	0.98	0.81	0.59–1.08	0.84
P ² :D ²	0.61	0.98	–	0.10
P ³ :D ³	0.93	0.59	0.30–0.97	1.12
P ⁴ :D ⁴	0.85	0.78	0.15–2.40	0.78
D ⁴ :D ³	0.90	0.91	0.38–2.01	0.42
P ⁴ :P ³	0.99	1.23	0.99–1.54	–0.67

2. P², which is a small, incompletely molarized terminal tooth, is isometric to dm².

3. dm³ is strongly (and even at this sample size significantly) negatively allometric to P³ ($b = 0.59$), whereas dm⁴ is much less ($b = 0.78$) negatively allometric to P⁴. As noted above (Sect. 3.4.2), the first cheek teeth to erupt in rhinoceroses are dm³ and dm²; dm⁴ erupts distinctly later and grows in a larger jaw.

4. dm³ is slightly negatively allometric or isometric ($b = 0.90$) to dm⁴, which suggests that the growth constraint on the milkteeth is not strongly size dependent.

5. P³ is positively allometric to P⁴ ($b = 1.23$), indicating that the main change involved is an increase in the size ratio P³/P⁴ relative to dm³/dm⁴. Why P³ should be more constrained in smaller forms than in larger ones is unclear, and this result is in conflict with the prediction. It must be noted, however, that the sample includes part of what is either a lineage or a series of closely related forms, and other interpretations are possible.

It is not necessary to postulate a general size relationship for spatial constraints on growth. Kingdon (1979) has argued persuasively that the increase in relative size of M3 from brachydont to hypsodont in

the pigs *Potamochoerus porcus*, *Hylochoerus meinertzhageni* and *Phacochoerus aethiopicus* is related to growth constraints. Gould (1975) noted the greatly enlarged last molar of the capybara (*Hydrochoerus hydrochoeris*), and suggested that it was large in order to produce "enough tooth area". The pattern seems to be fairly common among hypsodont ungulates, suggesting that relative tooth size (height) is a more important factor than absolute size. A strong subjective impression (which I share with many colleagues) is that sheep and goats have relatively large third molars; in the fossil record a more obvious example is the stenomyline camels (see e.g. Frick & Taylor 1968). The small, hypsodont toxodontid notoungulate *Nesodon ovinus* also had relatively very much enlarged third molars compared with the larger, less hypsodont and better known *N. imbricatus*. The hypsodont equids are apparently a counterexample, and the principle, if it applies, is clearly less than universal.

An example involving a strong size factor would be the Ursidae, which have unusually small neonates (e.g. Eisenberg 1981), and wide teeth set in narrow jaws. Kurtén (1976) illustrated the relative increase in size of M_3 in the morphological series *Ursavus elmensis* – *Ursavus depereti* – *Ursus etruscus* – *Ursus arctos* – *Ursus spelaeus*, which corresponds to a marked increase in absolute size. Kurtén favoured the functional interpretation of increased herbivory, but the ontogenetic explanation is an alternative possibility. Nothing, of course, precludes that both are involved. Within the species *Ursus spelaeus* M_3 is strongly positively allometric to M_2 , with a reduced major axis slope of 1.62 (Kurtén 1967). The similarity of ontogenetic and phylogenetic relationships could be read as evidence that ontogenetic constraints have influenced evolution.

I argued previously (Fortelius 1982) that hypsodont rhinoceroses have relatively larger last molars than brachyodont ones because the last molars are better positioned for "grinding" grass, but the positional argument has been shown to be geometrically suspect by Greaves (1978), and I would now favour the ontogenetic explanation of growth constraints affecting the anterior molars more than the posterior ones.

4.2. Relative tooth width and functional categories

4.2.1. Rationale

Given that opposing surfaces are required for food comminution, one can predict that the greater the component of lateral movement is during the power stroke, the greater will be the difference in width between upper and lower teeth. In principle, either the upper or the lower teeth might be wider, but in prac-

tise it is almost always the uppers. This probably ultimately reflects the functional demand to keep the mandible as light as possible, although other explanations are conceivable (for example in terms of food circulation).

Recall that relationships exist between the path of movement during the power stroke and the proportions of muscle masses (Sect. 3.3). Thus the possibility exists that simple relative width of teeth might distinguish quantitatively not only between dental morphological categories but also, or perhaps primarily, between functional categories in the design of the whole masticatory apparatus.

4.2.2. Materials and methods

In order to investigate this possibility, I obtained width data for upper and lower molars from a sample of 483 species of recent and fossil 'herbivorous' mammals (details in App. 5). In order to be able to use data from the literature, I had to use maximum basal width, which is clearly not an ideal estimate of occlusal width. Yet for two reasons it may be better than might at first appear. First, in many ungulates at least, occlusal width is clearly related by gradual wear to basal width. Second, the widest parts of serially homologous teeth tend to occlude with each other. For example, in a typical rhinoceros such as *Diceros bicornis*, the upper molars are widest over the protoloph and the lower molars over the talonid, which are roughly the parts that occlude. In the case of M_3 this second point is not always true, however. I did not use relative widths of premolars for this preliminary study because the varying degree of molarization introduces complications which would be difficult to handle at this stage. I chose M_2 rather than M_1 simply because the number of samples was larger. For macropod marsupials I used M_3 , which has the analogous position to M_2 in placentals. (Sometimes I had to substitute M_2 when data for M_3 were not given.) For proboscideans I used M_3 because very few data were available for other teeth. For manatees I used the last erupted tooth but one. I do not consider that this will affect the results in any relevant way.

The relative width of upper and lower teeth can be expressed as a simple index, obtained by dividing upper with lower width. I propose to call this the 'index of anisodonty' (*ADI*). Thus:

$$ADI = W_u / W_l,$$

where W is maximum tooth width and the subscripts refer to upper (u) and lower (l) serially homologous teeth, respectively. The derivation of the name is by analogy with anisognathly, which refers to unequal spacing of upper and lower toothrows (see below). Surprisingly enough, the term does not appear to be

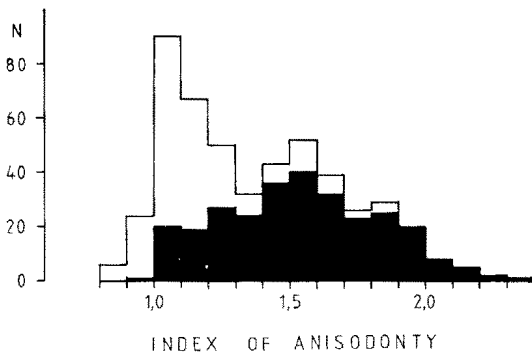


Fig. 27. Distribution of the index of anisodonty (ADI) in the whole sample. The distribution in the ungulate subsample is shown in black. N = number of species. See Table 11 for taxa included.

in earlier use. Anisodonty thus signifies unequal width of upper and lower teeth. The special case of equal width can be called isodonty ($ADI = 1$), while wider upper teeth will be referred to as positive anisodonty ($ADI > 1$) and wider lower teeth as negative anisodonty ($ADI < 1$). Because of the nature of the data one cannot expect any particular distribution of ADI , so statistical testing is difficult. However, the results are, on the whole, sufficiently unambiguous for interpretation even without the support of statistics.

4.2.3. Relative tooth width

Fig. 27 shows the distribution of $ADI(M2)$ in the whole sample, and separately for ungulates. The whole sample has a trimodal distribution, with peaks at the 1.00–1.09, 1.50–1.59 and 1.80–1.89 classes. The same three peaks are distinguishable in the ungulate sample, and in addition there is a fourth peak at the 1.20–1.29 class. The distribution of ADI within selected groups shows that these peaks correspond to recognized morphological categories (Fig. 28). Thus the 1.00–1.09 peak mainly consists of forms that have molars with distinct transverse cutting edges and palinal chewing (Group I in Fig. 28). The 1.20–1.29 peak includes a considerable range of bunodont and bilophodont forms (Group II in Fig. 28). The two are not separated by ADI , and indeed in the whole material the first two peaks are united, showing that in terms of translation the bilophodont-bunodont group and its modifications are one complex. In contrast, the third peak at 1.50–1.59 stands out clearly and is shown to consist largely of selenodont artiodactyls (Group III in Fig. 28). The fourth peak, at 1.80–1.89, is made up of the various trilophodont and ectolophodont forms (Groups IV and V in Fig. 28). It is possible to distinguish subgroups: the equids

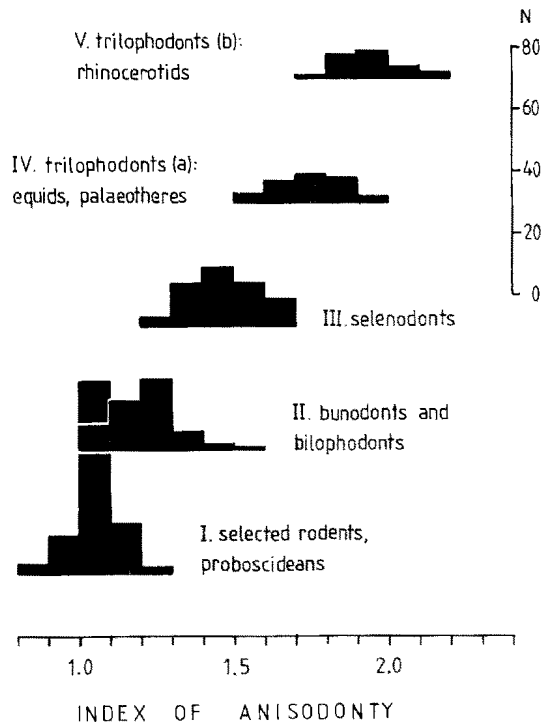


Fig. 28. The distribution of the index of anisodonty (ADI) in selected groups. N = number of species. The taxa included in the different groups are:

- I. Heteromyidae, Cricetidae, Muridae, Proboscidea
- II. Macropodidae, Diprotodontidae, Ursidae, Suidae, Tayassuidae, Tapiriidae, Dinocerata, Sirenia
- III. Camelidae, Giraffidae, Cervidae, Bovidae
- IV. Equidae, Palaeotheriidae
- V. Rhinocerotidae

and palaeotheres, which tend towards seleno-lophodonty, peak at 1.70–1.79, while the ectolophodont rhinocerotids (Group V) peak at 1.90–1.99.

Table 11 gives the mean values of $ADI(M2)$ for the taxa included in this analysis. Readers familiar with the groups will note several interesting features. Thus the most primitive forms (the 'condylarths' and the microsypid, plesiadapid and adapid primates) have values clustering about 1.4–1.6. The strongly ectolophodont forms (rhinocerotoids, astrapotheres and some of the subungulate families) all have high values, at about 1.8–2.1. The trilophodont tapiroids (Lophiodontidae, Helaletidae) have an ADI -mean in the 1.7 region (together with chalicotheres, palaeotheres, equids, litopterns and procaviid hyraxes), while the bilophodont Tapiridae have a mean at 1.4 (corresponding to that of indriid primates, various suiform families, coryphodonts and sirenians). It is probably prudent to be conservative about interpretation of details at this stage, however.

Table 11. The index of anisodonty for second molars, ADI(M2), for selected taxa. N = number of species. Data see App. 5.

	N	ADI	CV		N	ADI	CV
Marsupialia (ADI(M2,3))	19	1.22	6.5	"Condylarthra"	14	1.52	9.1
Macropodidae	13	1.18	4.5	Arctocyoniidae	7	1.51	8.2
Diprotodontidae	6	1.29	6.4	Phenacodontidae	2	1.44	—
Primates	42	1.43	15.8	Hyposodontidae	3	1.54	1.9
Microsyopidae	5	1.61	3.9	Meniscotheriidae	2	1.63	—
Plesiadapidae	10	1.54	2.4	Tillodontia			
Adapidae	5	1.60	4.3	<i>Esthonyx</i>	2	2.02	—
Indriidae	8	1.29	11.5	Tubulidentata			
ibid. excl. <i>Archaeolemur</i>	5	1.36	3.9	<i>Orycteropus</i>	3	1.00	0.6
Hominoidea s.l.	10	1.14	7.8	Litopterna	8	1.70	8.8
<i>Australopithecus</i> + <i>Homo</i>	3	1.06	0.9	Protheroheriidae	6	1.72	5.7
Rodentia	147	1.06	8.7	Macraucheniiidae	2	1.67	—
Paramyidae	8	1.14	2.7	Notoungulata	16	1.81	22.7
Ischyromyidae	6	1.15	9.1	Oldfieldthomasiidae	3	2.19	14.7
Sciuridae	12	1.12	6.0	Isotemnidae	2	2.14	—
Castoridae	3	0.90	4.0	<i>Homalodotherium</i>	1	1.89	—
Heteromyidae	18	1.01	9.9	Leontinidae	2	2.14	—
Theridomyidae	6	1.19	7.7	Notohippidae	2	1.52	—
Gliridae	10	1.11	5.0	Toxodontidae	2	1.30	—
Cricetidae	33	1.03	3.9	Hegetotheriidae	2	1.33	—
Muridae	24	1.08	5.4	Astrapotheria	2	2.11	—
Hystriidae	6	0.94	6.8	Perisodactyla	75	1.79	9.6
Carnivora				Tapiroidea excl. Tapiriidae	14	1.70	6.7
Ursidae	7	1.20	5.1	Tapiriidae	3	1.44	5.6
Artiodactyla	108	1.41	5.1	Hyracodontidae	2	1.73	—
Dichobunidae	3	1.48	4.9	Rhinocerotidae	24	1.94	5.3
Leptochoeridae	2	1.50	—	<i>Amynodon</i>	1	2.11	—
Entelodontidae	3	1.45	4.3	Equidae	17	1.72	4.7
Anthracotheriidae	2	1.58	—	Palacotheriidae	11	1.77	7.7
Hippopotamidae	4	1.32	6.8	Chalicotheriidae	2	1.77	—
Suidae	12	1.23	6.4	Pantodonta	8	1.82	10.6
Tayassuidae	9	1.12	8.0	Pantolambdidae	2	1.88	—
Agriochoeridae	3	1.60	1.3	Barylambdidae	5	1.88	4.5
Merycoidodontidae	2	1.47	—	<i>Coryphodon</i>	1	1.40	—
Oromerycidae	4	1.72	12.3	Dinocerata			
Camelidae	11	1.38	6.9	<i>Tinoceras</i>	1	1.27	—
Protoceratidae	5	1.53	4.6	Sirenia			
Tragulidae	2	1.60	—	<i>Trichechus</i>	2	1.30	—
Hypertragulidae	2	1.58	—	Proboscidea (ADI(M3))	19	1.07	4.6
Leptomerychidae	2	1.61	—	Gomphotheriidae	3	1.08	1.9
Cervidae	13	1.46	10.0	<i>Zygodon</i>	1	1.04	—
Giraffidae	2	1.41	—	Stegodontidae	2	1.14	—
Bovidae	28	1.44	5.6	Elephantidae	13	1.06	4.8
				Hyracoidea			
				Procaviidae	10	1.61	6.6
				<i>Kvabebihyrax</i>	1	2.00	—

4.2.4. Anisodonty and chewing mechanics

In chewing it is of course the movement in three dimensions that is of interest, rather than the component of lateral movement resolved into the horizontal plane. A major distinction exists between forms in which the occlusal surfaces dip towards buccal all the way (corresponding to a continuously dorsally plunging path of the power stroke), and forms in which such is not the case (Fig. 13). As discussed by Becht (1953) and Greaves (1980), the reason is that when the occlusal surfaces dip towards buccal the

animal can use both working- and balancing-side masseters throughout the power stroke (see above Sect. 3.3.2). When the surfaces are horizontal, and particularly when there are lingually dipping phase II surfaces, this is not the case, and the pterygoids assume a crucial function. For the latter group the point beyond which the mandible cannot be pulled further towards mediad must be determined by the working angles of the pterygoids, but no similarly distinct limit needs to exist in the former (essentially selenodont artiodactyls plus *Equus* of the living ungulates). It follows that increased lateral movement

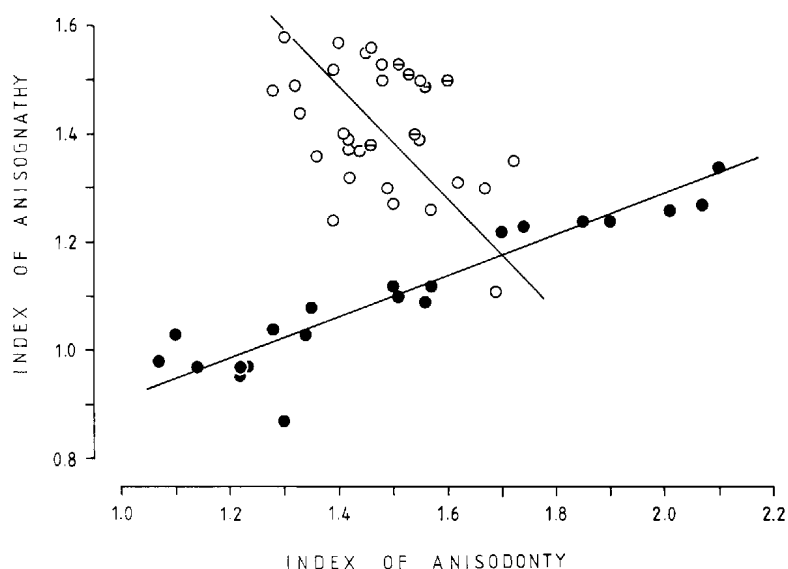


Fig. 29. Major axis regression of the index of anisognathy (AGI) on the index of anisodonty (ADI) for two groups of ungulates. Black circles are bunodont forms and lophodont forms with a two-phase occlusal morphology. Empty circles are selenodont artiodactyls. Split circles are *Equus*. Discussion in text.

can come about in different ways in the two groups: whereas the 'unlimited' group can expand the upper tooth either buccally or lingually, the 'pterygoideus-limited' group can only expand the upper tooth towards buccal to increase lateral movement. A specific prediction is that a strong positive correlation between anisodonty and anisognathy (the relative spacing of the toothrows) will be found in the latter, but not in the former group.

To test this prediction we need a measure of anisognathy. To measure spacing independently of tooth width we may take the distance between the buccalmost parts of left and right teeth, and subtract one (= two halves) toothwidth from that. The index of anisognathy (AGI) is the ratio of upper to lower spacing of serially homologous teeth. Formally:

$$AGI = D_u - W_u / D_l - W_l,$$

where D is buccal-to-buccal distance between left and right teeth, W is tooth width and the subscripts refer to upper (u) and lower (l) jaws and teeth. I used first molars, which are usually the most widely spaced teeth in the upper toothrows of ungulates, but other molars ought to give a similar result if the hypothesis is correct.

Fig. 29 shows a plot of $ADI(M1)$ against $AGI(M1)$ for a sample of ungulates (App. 2). It is immediately obvious that the prediction is gloriously fulfilled: the correlation for the heterogeneous group excluding selenodont artiodactyls and *Equus* is +0.92 ($P < 0.001$), while the selenodont plus horse group has a correlation of -0.44 ($P < 0.05$) (Table 12). None of the four dimensions included in ADI and AGI is significantly allometric to any of the others, nor to skull size or body size (unpublished data), and

the result is unlikely to reflect some trivial relationship external to the argument. Neither can it be an artefact of incorrectly measured spacing of lower teeth in forms with an unossified mandibular symphysis, since the horses and camels plot with the other selenodonts. If the negative correlation in this group is a real phenomenon it has interesting implications beyond the original hypothesis (see below).

To understand the result in more detail, it is useful to consider the influence of the 'correction term' (i.e. tooth width) included in AGI . If this term is eliminated and the 'uncorrected' buccal-to-buccal distances are used as such, the negative correlation is decreased to insignificance in the selenodont-plus-horse group, while the positive correlation is somewhat increased in the other group (Table 12). The most parsimonious explanation of this pattern is that anisodonty changes by buccal expansion or reduction in the bunodont-lophodont forms, but by lingual expansion or reduction in the selenodont-plus-horse group. Increased ADI thus leads to increased AGI in the former (the ratios between distances and between widths both increase), but to decreased AGI in the latter (buccal-to-buccal distance remains unchanged but the ratio between the 'correction terms' is increased).

As in the case of tooth size relationships, the strong correlation between ADI and AGI in lophodonts is a phenomenon of extended size ranges and/or higher taxonomic levels. An intraspecific plot of ADI against AGI for *Diceros bicornis* gives no significant correlation ($N = 28, r = -0.29$). The nature of the pterygoideus-vector hypothesis, used above to explain the observed relationships, is such that it must exist at all taxonomic levels. Either individual

Table 12. Relationships between relative width and spacing of upper and lower molars in ungulates. ADI = index of anisodonty, AGI = index of anisognathy. See discussion in text.

Group/index	N	r	P(r)	b	95 % CL (b)
Bunodonts and lophodonts (excluding <i>Equus</i>)					
AGI:ADI	21	0.92	<0.001	0.38	0.31–0.46
'buccal-to-buccal':ADI	21	0.96	<0.001	0.50	0.44–0.57
Selenodonts plus <i>Equus</i>					
AGI:ADI	32	-0.44	<0.05	-0.98	-2.58– -0.37
'buccal-to-buccal':ADI	32	-0.24	–	-0.35	-1.54– -0.33

variation occurs within limits which are wide enough to obscure the functional pattern that is apparent at higher levels, or the hypothesis is false. The present data are not sufficient to decide between these alternatives.

4.2.5. Evolutionary significance

It is possible to use the results discussed above to interpret evolutionary changes in dental morphology in relation to chewing mechanics.

The cheek teeth of primitive representatives of most placental orders were quite similar, not far removed from the tribosphenic type but with some beginning differentiation between carnivores with more vertical wear facets and herbivores with more horizontal ones (Butler 1972). One of the latter is the Late Cretaceous condylarth *Protungulatum*, which is probably close to the origin of all ungulates, at least morphologically. Later condylarths and early representatives of at least artiodactyls and perissodactyls have basically similar cheek teeth, with varying stages of development of a hypocone. The molars are brachydont, with more or less separate cusps partly connected by ridges, and with both phase I and phase II wear facets present. ADI values cluster about 1.5 (Table 11). Occasionally they are referred to as bunodont, but they are not bunodont in the same sense as those of later suiforms and hominoids, for example, which have ADI values in the 1.0–1.3 range and reduced buccal facets (see below). Later lophodont, selenodont and bunodont teeth must have evolved from such an ancestry.

The artiodactyls apparently arose from arctocyonid or hyopsodontid condylarths (discussion in Van Valen 1971), and the 'stem artiodactyl' *Diacodexis* is not much different from either. ADI is in the region of 1.5–1.6 in both these condylarths and the early artiodactyl families (Table 10). Later selenodont families have slightly lower ADI, about 1.4–1.5, which may relate to increased crown height and correspondingly less prominent basal projection of the lingual cusps of the upper teeth. The basic plan

of the molars, with longitudinally flattened cusps, is little changed, but primary is replaced by secondary occlusal morphology. Apparently in this process the phase II facets are lost and the single-phase occlusal surfaces which dip gently towards buccal are developed. It is interesting to consider that present-day selenodont artiodactyls all ruminate, and that rumination affects the structural and mechanical properties of foods but cannot reduce wear due to inorganic inclusions. In other words, one rather expects to find differences in crown height, but not in occlusal morphology, as noted in Sect. 3.2.2.

The derivation of bunodont teeth in artiodactyls seems to proceed via a bunoselenodont stage such as is seen in anthracotherids, for example (Thenius 1976), by reduction of the distance between buccal and lingual cusps in the upper tooth. A basin between buccal and lingual cusps of the upper tooth is required for steeply dipping anteroposteriorly striking phase I facets. If it is lost the lower tooth cannot move into it and more horizontal contact surfaces result. It was suggested (and perhaps demonstrated) above, that the buccal cusps are displaced towards lingual rather than vice versa, presumably because the limit of movement towards lingual is set by the angle of the pterygoideus vector. A bilophodont condition (as in *Listriodon splendens* or various peccaries) can evolve from a bunodont one by secondary development of basins between pairs of anterior and posterior cusps. This makes possible a high occlusal relief without changing the anatomy of jaws and muscles.

The radiation in molar morphology seen in the Perissodactyla can be similarly understood. The earliest representatives of equoids, tapiroids and chalicotheroids are all similar to each other, although with characteristic differences in detail (Radinsky 1969). Of these, the equoid, *Hyracotherium*, is closest to the ancestral phenacodontid condylarths, and is generally considered the most primitive (Radinsky 1966). The mean ADI of phenacodontids in Table 11 is 1.44, but the sample is small, so a true value of about 1.5 may be more likely.

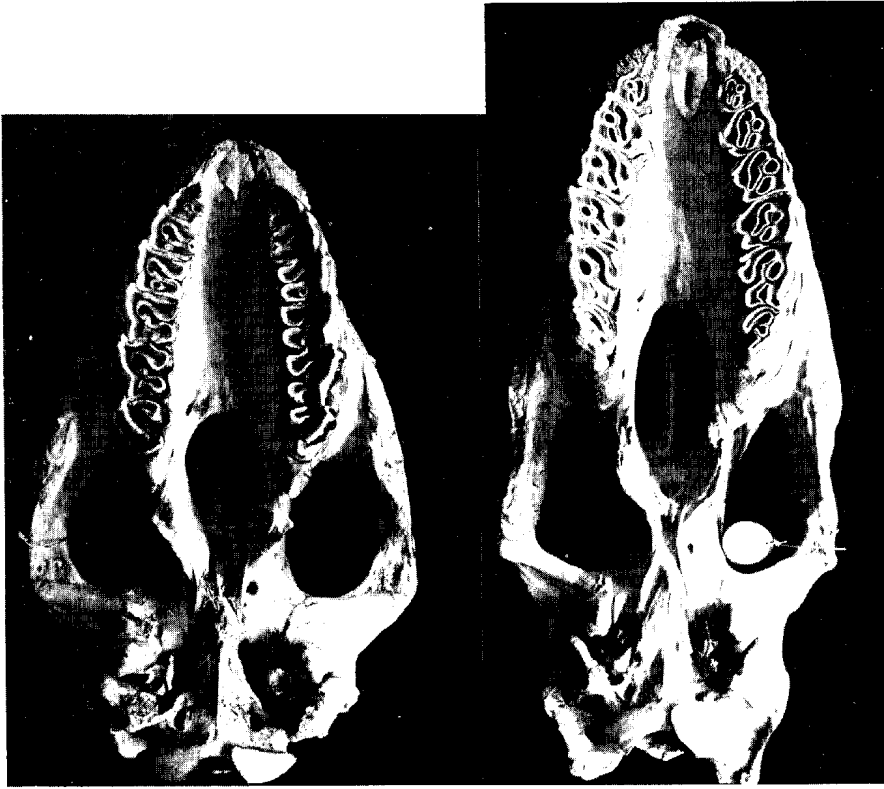


Fig. 30. Ventral views of skulls of *Diceros bicornis* (left) and *Ceratotherium simum* (right). Note the widely spaced zygoma of the ectolophodont *Diceros* and the narrow zygoma of the plagiolophodont *Ceratotherium*. Both skulls from TE.

Hyracotherium can be called bunio-lophodont, with phase I facets both buccally and across the cross lophs, and phase II faces in the usual positions (Butler 1952a). The molars of later perissodactyls are modifications of this type, involving (at least initially) a stronger development of lophs and increased occlusal relief. From various trilophodont forms more specialized bilophodont and ectolophodont types are derived. From the latter plagiolophodont teeth with serial anteroposteriorly striking cutting edges and secondarily reduced occlusal relief occasionally evolve. The purest bilophodonty is found in the tapiroid families Tapiridae and Deperetellidae. Other tapiroids are variously trilophodont, and rhinocerotoids presumably arose from such forms, perhaps paraphyletically (Radinsky 1969). In the Ceratomorpha (tapiroids and rhinocerotoids) the cusps are suppressed and the lophs are smooth. This is in contrast to the Hippomorpha (equoids, chalicotheroids, brontotheroids), in which cusps tend to retain more of their individuality. This is probably related to the tendency towards dilambdodonty (with a W-shaped ectoloph) in the latter group, but the differences are not clearly reflected in *ADI*.

Rhinocerotids and amynodontids, however, have *ADI* values that are distinctly higher than those of other trilophodont perissodactyls, which probably reflects the extreme ectolophodonty of these hypsodont forms. To maintain a secondary two-phase occlusal morphology a wide 'basin' between the buccal and lingual edges of the upper tooth is required. To load the buccally displaced phase I facets, the masseter vectors must have a marked component towards lateral, which probably is why rhinoceroses have such widely spaced zygomatic arches. In plagiolophodont forms this does not apply, and it is striking that in such rhinoceroses (*Coelodonta*, *Ceratotherium*) the zygoma are much narrower (Fig. 30).

Plagiolophodonty seems to require anteroposteriorly striking medial and lingual cutting edges (seleno-lophodonty), and the functional morphology is analogous to selenodonty. In the modern equids this is observed as a lack of the positive correlation between *ADI* and *AGI*, but *Ceratotherium* still plots with the other rhinoceroses. Perhaps this is because *Ceratotherium* developed plagiolophodonty very recently and is still very much like a 'typical' rhinoceros in its anatomy?

4.3. Tooth shape and enamel structure

4.3.1. Introduction

The patterns of stress distribution must be different in differently shaped teeth, and the differences in shape must reflect differences in development. Similarly, the fine structure of the dental tissues, particularly enamel, directly reflect developmental processes on one hand and affect the mechanical properties of the teeth on the other. It is thus reasonable to expect that relationships will exist between morphology, development, function and evolution, although these relationships need not be simple.

An outline of the relationships between enamel development and structure was given in Section 3.1.2., and the relationships between enamel structure and wear properties were discussed in Section 3.4.1. In this section I will deal with relationships at one particular level of organization, namely that of the orientation of the zones of decussating enamel prisms or Hunter-Schreger bands (HSB:s). This question has received little attention until recently, and a comprehensive synthesis is not within reach (Rensberger & von Koenigswald 1980, Rensberger 1983, Fortelius 1984, Boyd & Fortelius in press). A discussion of the problem is nevertheless clearly required in the present context.

Technical problems loom large. Particularly, there is no method available to image the HSB:s over more than small areas of the crown at a time, which makes mapping tedious and uncertain. Nevertheless, these problems do not affect the theoretical issues. A discussion of materials and methods as well as technical data are given in Appendix 7.

4.3.2. Hunter-Schreger bands and wear relief

Historically, the discovery of vertically oriented Hunter-Schreger bands with vertical prism decussation is due to the striking effect this arrangement has on wear relief. Rensberger & von Koenigswald (1980), in their original description of the phenomenon, stated that they wished to know how the curious tiny ridges and valleys observed on rhinoceros enamel came about. They found that the relief corresponds to radially arranged vertical HSB:s, one set of bands forming ridges separated by valleys corresponding to the other set.

As a matter of fact, all HSB:s are potentially capable of producing such a relief. Ordinary horizontal HSB:s with horizontal decussation frequently give rise to a concentric wear relief, as for example in the suid *Potamochoerus porcus* or the desmostylian *Desmostylus hesperus* (Fig. 31). The relationship involved is simply that prisms of different HSB:s are intercepted by the wear surface at different angles, and

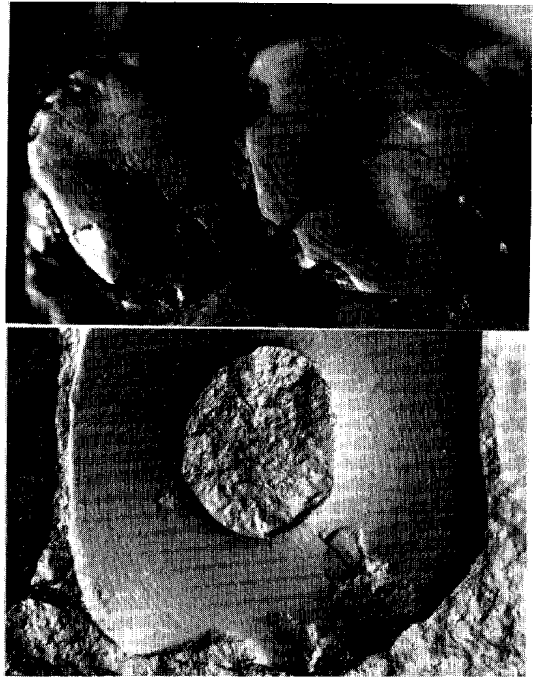


Fig. 31. Concentric wear relief in thick-enamelled forms with horizontal decussation. – Above: *Potamochoerus porcus*, entoconid and hypoconid of second lower molar (ST 130a, Cameroun). Field width 11 mm. – Below: *Desmostylus japonicus*, one cusp on holotype specimen (TO). Field width 18 mm. Light micrographs of transparent epoxy casts (App. 7.1).

are consequently unequally resistant to wear (see Sect. 3.4.1.). Vertical decussation maximizes this difference for horizontal wear surfaces, and consequently gives rise to a higher relief. It is also highly probable that relief is more distinct when decussation is between distinct zones (i.e., involves little gradual transition in prism direction) than when zones intergrade into each other, although this has not been investigated.

The relief on true facets is relatively low, and the highest relief develops where occlusal contact does not occur (Fig. 18). Why this is so is not entirely clear, but it indicates that the differential wear is mainly due to low energy processes of food 'polish' rather than to events associated with high stress. The relief developed on one facet may cause a distinct relief on the facet with which it occludes. For example, on the buccal phase I facets in rhinoceroses or astrapotheres, where the ridges on the ectoloph edge wear troughs into the buccal facets of the lower teeth (which are situated mainly on outer enamel with little decussation) (Fig. 32).

One might argue that such wear-induced ridging is a functional feature associated with cutting tough

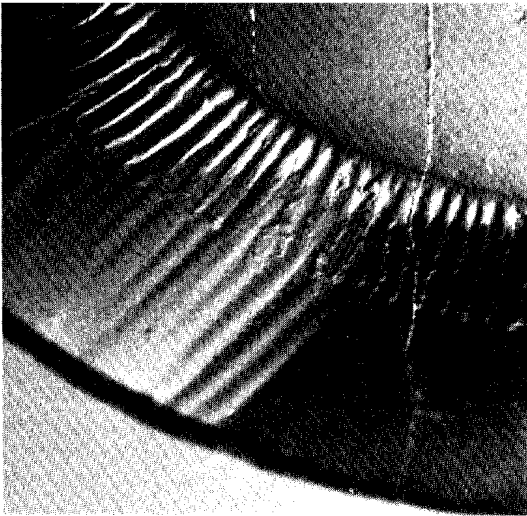


Fig. 32. Wear relief due to two different causes on *Rhinoceros sondaicus* lower premolar buccal edge (facets 3 and 4). The relief on the upper part (inner enamel) is due to differential wear resistance (vertical decussation), while the relief in the lower part (outer enamel) is due to the relief on the antagonist (which in turn is again due to vertical decussation). Light micrograph of transparent epoxy cast (App. 7.1). Field width 5 mm.

food materials, just as the crenellated canines of sabre tooth cats are said to have been designed to cut through tough skin. The weakness of this argument is that the relief (unlike on the canines) is developed parallel to the direction of relative movement, at least at the main cutting edges. Because of this they cannot function as stress concentrators, which is the functional principle involved in all crenellated and saw-toothed cutting devices (which are usually single blades, not blade pairs).

Rensberger & von Koenigswald (1980) argued that the relief, as such, is of little functional relevance, and that the functional advantage of vertical decussation is that it increases overall wear resistance. They described an experiment in which two pieces of rhinoceros enamel were glued together with the HSB:s vertical in one piece and horizontal in the other, and abraded by sandblasting. Under these experimental circumstances the piece with vertical HSB:s was the most resistant one. This result, however, is easily explained in terms of prism (rather than HSB) orientation (see Sect. 3.4.1.). When a portion of enamel with vertical prism decussation is turned on its side and cut parallel with the HSB direction, all the prisms are exposed longitudinally; i.e., in the orientation of least wear resistance. This is not the case when it is cut transverse to the HSB direction, when (depending on the angle of decussation) at least one, and in all but one orientation both

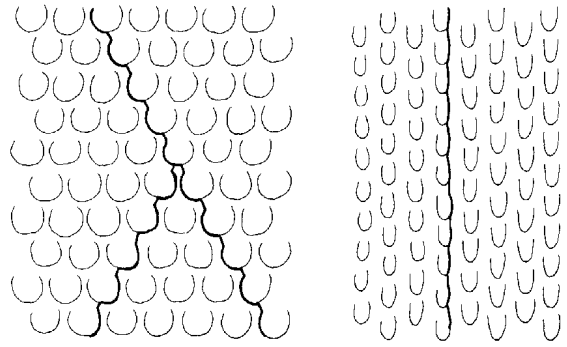


Fig. 33. Crack propagation in enamel with different prism packing patterns. Cracks 'jump' from one prism boundary discontinuity to the next. Based partly on Boyde 1976b and partly on personal communication with Alan Boyde (1983—84). The directions shown are typical but not the only ones that occur.

sets of bands have prisms cut at an angle. Nor is it the case in real horizontal decussation, where prisms in both left- and rightslanting zones apparently always have an inclination towards occlusal and are therefore intercepted at an angle by a horizontal surface.

Thus there are no grounds for regarding vertical decussation as increasing wear resistance. Indeed, if only wear resistance is considered, non-decussating enamel is the ideal. Hardness of enamel is proportional to density (Karlström 1931), and for simple geometrical reasons parallel prisms can be more closely packed than decussating prisms. It is indeed the case that the outer, little-decussating enamel of rhinoceroses is more resistant to wear than the inner, strongly decussating enamel (Boyde & Fortelius in press).

4.3.3. Hunter-Schreger bands and crack propagation

Enamel is not an isotropic material, and cracks are preferentially propagated from one prism boundary discontinuity to the next at locations where crystals are stressed transverse to their c-axes (i.e., separated from each other rather than broken in tension) (Boyde 1976b). Such crack propagation is determined by the prism packing pattern, but cracks may also follow the boundaries of zones of decussating prisms, at least when the change in prism orientation is abrupt, as in rhinoceroses (Boyde & Fortelius in press). At least two levels of structural organization thus influence crack propagation: prism pattern and HSB orientation.

Pattern 3 enamel cracks preferentially in such a way that prism boundary discontinuities are joined diagonally across the rows (Boyde 1976b), while Pattern 2 enamel cracks along the rows (along the 'inter-row sheets') (Alan Boyde, pers. comm. 1984) (see

Fig. 34. Hypothetical scheme to show advantage of vertical decussation when enamel is loaded away from the dentine. The vertically 'laminated' structure prevents massive cleavage in planes parallel to the prism boundaries and occlusal surfaces. See text.

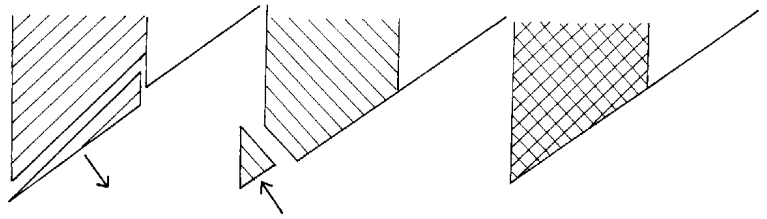


Fig. 33). Pattern 3 enamel cracks diagonally across the HSB:s; Pattern 2 enamel along them. Both may presumably crack between HSB:s at sharp zone boundaries. Irrespective of prism pattern, vertical decussation would thus reduce the tendency of the enamel to flake off parallel to horizontal surfaces. This would be particularly critical when the enamel is stressed in shear in a direction away from the supporting dentine, as on the steeply dipping buccal and lingual facets of trilophodont teeth (Fig. 34).

Composite materials with fibres (or whiskers) in a matrix are stronger in tension along rather than across the fibres (see e.g. Gordon 1968). von Koenigswald (1980) discussed the enamel structure of rodent molars in terms of tensile and compressive stress, and it may be that the aspect is important. Conditions of prolonged tensile stress are probably rare in teeth, but might occur during chewing of very sticky foods. More important is perhaps elastic deformation and rebound during and after compression, which may induce local tension and cracking. If such deformation is mainly along an axis normal to the occlusal surface (which is reasonable if load is normal to that surface), enamel with prisms (more properly: crystals) parallel to the surface will crack more easily than enamel with prisms normal to it. Again, the steeply dipping buccal and lingual facets of trilophodont upper teeth are the ones where prisms are most parallel to the surface in non-decussating and horizontally decussating enamel (in which all prisms are inclined towards occlusal) (Fig. 34). Vertical decussation means that the prisms in alternate bands are nearly normal and nearly parallel to the surface in both upper and lower teeth. If decussation patterns are functionally important and if they are related to crack propagation, one would thus expect vertical decussation primarily in association with a pronounced two-phase occlusal morphology (high relief transverse to the direction of the power stroke).

4.3.4. The occurrence of decussation modes

Among living ungulates, vertical decussation is found only in rhinoceroses, while all others have horizontal decussation (in which the zone boundaries may be abrupt or gradual). In the fossil record, how-

ever, vertical decussation is not a rare phenomenon, but is commonly found in large lophodont forms, though apparently never in bunodont or selenodont ones. Horizontal HSB:s can, however, be variously bent and tilted, and it is necessary to make explicit distinctions between decussation modes. Table 13 summarizes prism packing patterns and decussation modes in the lophodont forms considered in this investigation.

Horizontal decussation

Horizontal decussation develops as concentric zones about the origin(s) of enamel secretion, usually the cusp tip(s), and usually but not always parallel to the developing front (Boyde & Fortelius in press, and below). The pattern usually resembles a spiral, and spirals are extremely common in structures formed by incremental growth (Thompson 1917). I assumed earlier (Fortelius 1984) that it is in fact a spiral and still consider that likely, but the question has not been properly investigated. In any case the arrangement is concentric.

On flat, high cusps which join to make a loph there is a tendency of the HSB:s to bend towards the loph crest between cusp tips (Fig. 35A). The same pattern results if one squeezes plasticine model cusps flat,

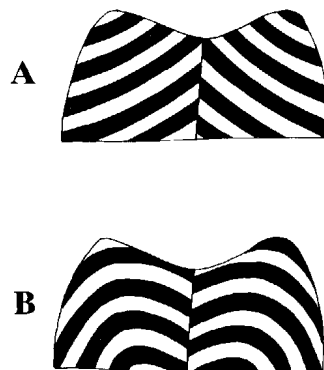


Fig. 35. Modified horizontal decussation patterns: Concave horizontal decussation (above), where HSB's bend towards the loph crest between cusps, and convex horizontal decussation (below), where the HSB's follow the occlusal relief. Highly schematic.

Table 13. Decussation and prism packing patterns (PP) in some lophodont ungulates. See App. 7 for methods.

	Species studied	HSB orientation	PP	Methods
Pantodonta				
Pantolambdidae	<i>Pantolambda bathmodon</i>	none (vertical?)	1,3	TSRLM, LM
Coryphodontidae	<i>Coryophodon</i> sp.	vertical (irregular)	3	TSRLM, LM, SEM
Dinocerata				
Uintatheriidae	<i>Uintatherium</i> sp.	vertical (irregular)	3	TSRLM, LM
Litopterna				
Macraucheniiidae	<i>Macrauchenia patachonica</i>	horizontal (convex)	2	TSRLM, LM
Notoungulata				
Toxodontidae	<i>Nesodon imbricatus</i>	horizontal	2	TSRLM, LM, SEM
	<i>Toxodon platensis</i>	horizontal	2	TSRLM, LM, SEM
Astrapotheria				
Astrapotheriidae	<i>Astrapotherium</i> sp.	vertical (regular)	3	TSRLM, LM, SEM
Pyrotheria				
Pyrotheriidae	<i>Pyrotherium</i> sp.	vertical (irregular)	3	TSRLM, LM, SEM
Perissodactyla				
Lophiodontidae	<i>Lophiodon rhinoceros</i>	horizontal (concave)	?	LM
Helaletidae	<i>Hyrachys</i> sp.	horizontal (concave)	?	LM
?Helaletidae	<i>Chasmotherium minimum</i>	horizontal (concave)	?	LM
Deperetellidae	<i>Deperetella</i> sp.	vertical (regular)	2	TSRLM, LM
Tapiridae	<i>Tapirus indicus</i>	horizontal (concave)	3(2)	TSRLM, LM
Hyracodontidae	<i>Hyracodon nebrascensis</i>	vertical (regular)	?	LM
Rhinocerotidae	many species	vertical (regular)	3	TSRLM, LM, SEM
Amyndodontidae	<i>Amyndodon</i> sp.	vertical (regular)	?	LM
Equidae	<i>Meshippus bairdi</i>	horizontal (convex)	3,2	TSRLM, LM, SEM
	<i>Anchitherium aurelianense</i>	horizontal (convex)	3,2	TSRLM, LM, SEM
	<i>Merychippus primus</i>	horizontal	2	TSRLM, LM
	<i>Equus caballus</i>	horizontal	2	LM, SEM
Palaeotheriidae	<i>Palaeotherium magnum</i>	horizontal (concave)	2(3)	TSRLM, LM, SEM
	<i>Plagiolophus</i> sp.	horizontal	3	TSRLM, LM
Brontotheriidae	<i>Lambdaotherium</i> sp.	horizontal (concave)	?	LM
	<i>Menodus prouti</i>	horizontal (concave)	?	LM
	<i>Titanotherium</i> sp.	horizontal (concave)	3	LM, SEM
Chalicotheriidae	<i>Nestortherium sivalense</i>	horizontal (concave)	?	LM
	<i>Schizotherium pilgrimi</i>	horizontal (concave)	?	LM
	<i>Chalicotherium goldfussi</i>	horizontal (concave)	?	LM
Artiodactyla				
Suidae	<i>Listriodon splendens</i>	horizontal (concave)	2	TSRLM, LM
Proboscidea				
Dinothereiidae	<i>Prodinotherium</i> sp.	irregular	3	LM, SEM
Hyracoidea				
Geniohyidae	<i>Titanohyrax ultimus</i>	horizontal	3(2)	TSRLM, LM
Embrithopoda				
Arsinoitheriidae	<i>Arsinoitherium zitteli</i>	vertical (irregular?)	2	TSRLM, LM, SEM

and the pattern may at least partly be a simple mechanical consequence of flattening. However, it means that HSB:s are intercepted nearly transversely along the loph crest, and wear relief similar to that in genuine vertical decussation is developed. This situation, which I will refer to as 'horizontal concave' HSB:s, is found in palaeotheres, brontotheres, and in many tapiroids. The HSB:s in this arrangement are parallel to the perikymata.

A curious modification of horizontal decussation is what appears to be the reverse of the above, namely that the HSB:s curve down along cusp walls. This arrangement is found along the buccal enamel of upper teeth in selenodont artiodactyls, on the ectoloph of

equids (Fig. 35B) and possibly also in *Macrauchenia*. The orientation of the HSB:s is nearly transverse to the perikymata; i.e., they are curved in opposite senses. I have been unable to reconstruct the three-dimensional arrangement of the HSB:s in this mode, which I will refer to as 'horizontal convex' HSB:s.

In all horizontal decussation the HSB:s are sectioned in a basically concentric pattern by a horizontal wear surface, but inclined bands and/or surfaces may cause varying degrees of radial orientation and corresponding wear relief. Such relief is maximized when the HSB:s are concave and minimized when they are convex (Fig. 35).

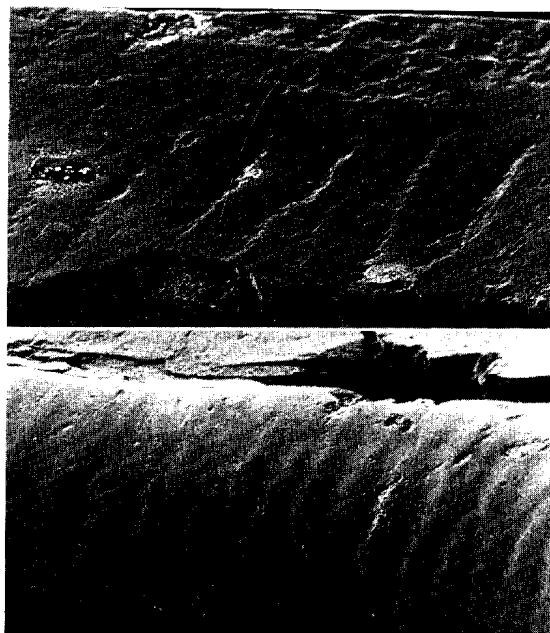


Fig. 36. Wear surfaces of forms with irregular vertical decussation. The grooves correspond to narrow zones of prisms parallel with the occlusal surface; on these inclined surfaces these are either occlusal- or cervical-slanting prisms. – Above: *Coryphodon* sp. (Pantodonta, Eocene) protoloph (facet 1) of M^3 (HP P1109). – Below: *Uintatherium* sp. (Dinocerata, Eocene) premolar protoloph wear surface (non-facet) (BM M3815). The enamel-dentine junction is towards the bottom (above) or towards the top (below). SEM images of epoxy casts, field width of both images 1.7 mm.

Vertical decussation

In rhinoceroses, at least, vertical decussation develops radially; i.e., transverse to the formative edge from the beginning of enamel secretion (Boyde & Fortelius in press). It is thus transverse to the perikymata, and the HSB:s do not depart from their vertical course at or between cusps. Two grades of organization can be distinguished, which I will refer to as 'irregular' and 'regular'.

In irregular vertical decussation many prisms have horizontal inclinations, but the strongly inclined prisms are inclined vertically (towards occlusal or cervical). Focussing up through such enamel (with the TSRLM; see App. 7.3) in a surface-parallel view one can see prisms feeding in from both sides to join a vertical zone of steeply inclined prisms. The developmental situation must have been that in a field of more or less random, moderate translatory movement, some groups of ameloblasts translated rapidly through the 'crowd' in vertical directions. The result is an enamel which is not neatly divided into adjacent HSB:s, but in which vertical zones exist in a less de-

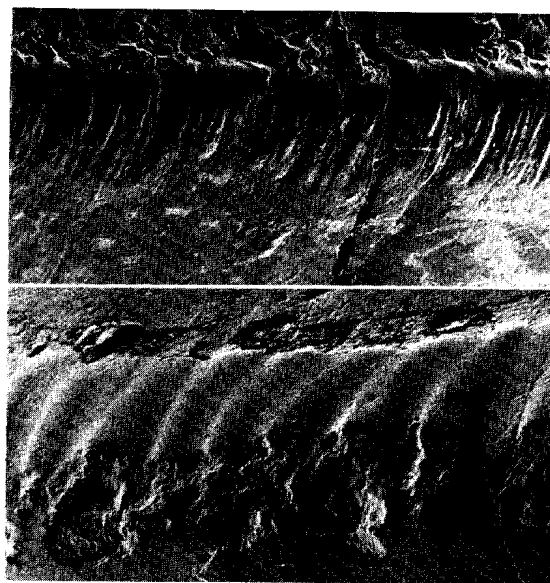


Fig. 37. Wear surfaces of forms with (irregular?) vertical decussation more pronounced than of those in Fig. 36. Grooves and valleys are of about equal width. – Above: *Arsinoitherium zitteli* (Embrithopoda, Oligocene), hypolophid (facet 4) of lower molar (HP P788). – Below: *Pyrotherium* sp. (Pyrotheria, Oligocene), cross loph of (upper?) molar (HP P868). Enamel-dentine junction towards top in both. SEM images of epoxy casts, field width of both images 2.1 mm.

cussating 'matrix'. This kind of arrangement is found in coryphodontids and dinocerates (Fig. 36). More documentation is needed to decide whether the irregular vertical decussation seen in *Pyrotherium* and *Arsinoitherium* (Fig. 37) is of the same nature.

Regular vertical decussation is found in rhinocerotoids, deperetellid tapiroids, and in astrapotheres (Figs. 38, 40). The (inner) enamel is entirely divided into HSB:s, and decussation is purely vertical. The bands may divide around each other to form 'Y-junctions' in both the surface-parallel and transverse senses (Boyde & Fortelius, in press), but are in principle continuous (Fig. 39).

4.3.5. Evolutionary relationships

The primitive mammalian condition is non-decussating, and probably non-prismatic, enamel (see Kozawa 1984 for a brief review and references), and it appears highly likely that decussation evolved independently several times. Until more is known

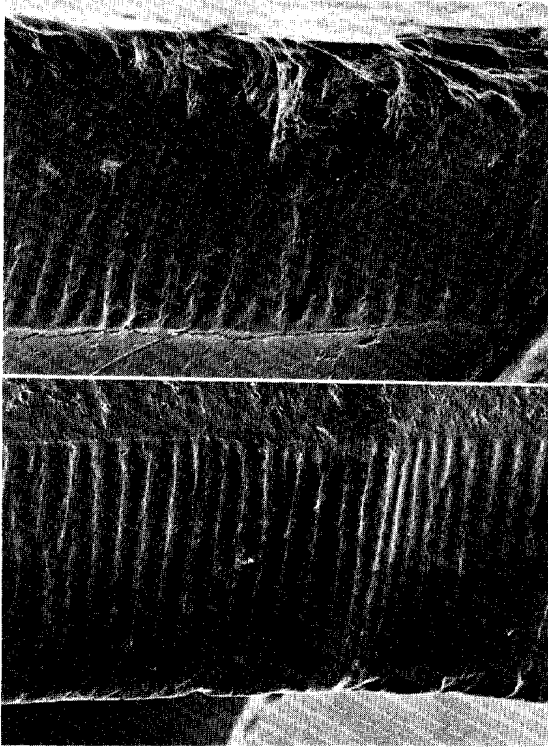


Fig. 38. Wear surfaces of forms with regular vertical decussation. – Above: *Dicerops bicornis* ectoloph of M² (HZ 647/1960). SEM image of epoxy cast, field width 3.9 mm. – Below: *Astrapotherium* sp. (Astrapotheria, Miocene) ectoloph of upper molar. SEM image of epoxy cast, horizontal field width 3 mm. Enamel-dentine junction towards top in both. (For corresponding lower teeth see Figs 18 & 32).

about the organization of enamel in fossil ungulates evolutionary scenarios must remain speculative.

True vertical decussation seems to unite the rhinocerotoids with the deperetellids (Fig. 40). The condition in the supposed helaletid ancestors of rhinocerotoids has not been sufficiently well studied, but the HSB distribution appears to be concave horizontal. The same appears to be the case in lophiodontids (Fig. 41). The data are very incomplete at the moment, and more documentation is needed before their significance can be evaluated. They do, however, lend some support to the proposal of Rensberger & von Koenigswald (1980) that vertical decussation in rhinocerotoids evolved by modification of a concave horizontal pattern. For ontogenesis this requires the destruction of the relationship between the decussation and the developing front: ameloblasts must move transverse rather than parallel to the front. The breaking-up is complete in rhinoceroses, and the very beginning of decussation is vertical with the HSB:s radial from the cusp tip (Boyde & Fortelius in press).



Fig. 39. Y-junctions of HSB's on polished and airpolished (App. 7.2) protoloph enamel of *Astrapotherium* sp. (HP unregd. fragm.). Horizontal section, enamel-dentine junction towards bottom. SEM (BSE+SE) image, field width 1000 μ m.

An alternative scenario, which is attractive ontogenetically but lacks phylogenetic support, is that vertical decussation arose directly out of non-decussation. It does not appear to be known whether the wholly irregular decussation of proboscideans (Boyde 1969) is primitive or derived, but irregular vertical decussation could easily arise from such a state by simple emphasizing of ameloblast movement in the vertical directions. Similarly, regular vertical decussation could be derived from irregular vertical decussation by a further increase in dominance of vertical movement to the exclusion of all other directions. At the moment the evolutionary sequence does not appear to have been established for a single lineage, and speculation beyond this point is of little avail. Nothing requires that the same sequence apply in all cases.

4.3.6. Causal relationships

In the absence of other options it is defensible to discuss possible causal relationships in terms of correlation, although it must be recognized that associations between factors may reflect relationships which are not included in the analysis. The main correlation between HSB orientation and crown shape is clearly the actual orientation of the HSB:s to occlusal surfaces on one hand and the height of occlusal relief on the other. In the buccal enamel of upper teeth where enamel is loaded in a direction away from the enamel-dentine junction, there is a particularly suggestive pattern.

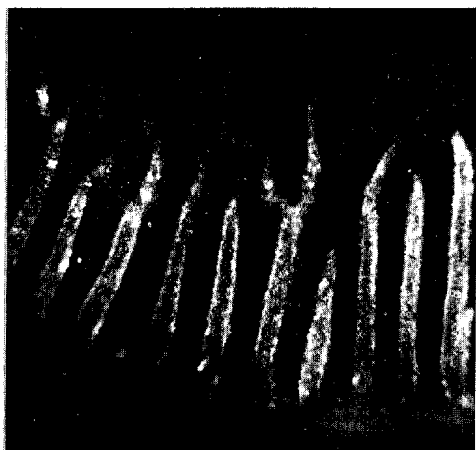


Fig. 40. Vertical decussation in *Deperetella* sp. (Tapiroidea, Eocene). Occlusal (horizontal) surface of M_3 hypolophid (BM M12756). The light bands are due to reflection from prism sheaths lying more parallel to the surface (transverse to the light path) than those in neighbouring zones. The enamel-dentine junction is towards the bottom of the field; note how the light bands gradually disappear towards the non-decussating, outer enamel. This suggests that the light bands are zones of cervically inclined prisms, since all prisms in the outer enamel are inclined towards occlusal (at least in rhinoceroses and astrapotheres). TSRLM image (App. 7.3), field width 570 μm .

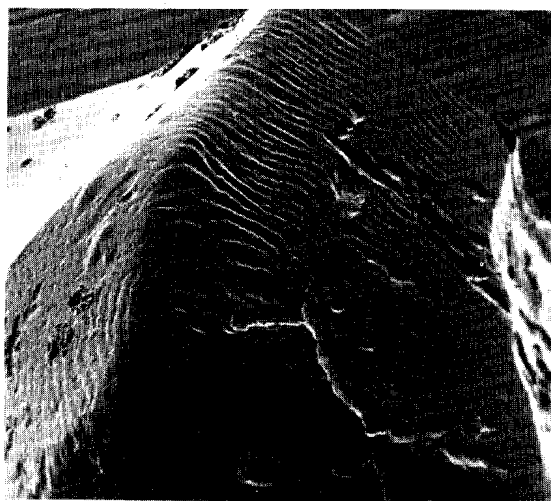


Fig. 41. Wear relief on M^3 protoloph (facet 1) of *Lophiodon lauricense* (Tapiroidea, Eocene; BM M8331). The appearance is much as in vertical decussation, but is apparently due to concave horizontal decussation (see text). SEM image of cut epoxy cast, field width 8.5 mm.

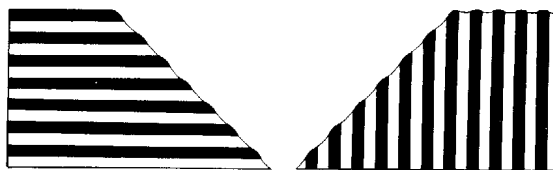


Fig. 42. How inclined facets intercept HSB's, irrespective of whether these are horizontal or vertical.

If there is no transverse occlusal relief (i.e., parallel to the direction of occlusal movement), then vertical HSB:s will be intercepted transversely and horizontal HSB:s longitudinally by the wear surface (Fig. 42). If transverse relief is present, the angle of interception will depend on the orientation of the HSB:s and that of the wear facet. Bands inclined in one direction will be intercepted more transversely and bands inclined in the other direction more longitudinally. In an idealized case of wear facets inclined 45 degrees, both straight vertical and straight horizontal decussation result in the same angle of the bands to the facets (Fig. 42). It is quite striking that high transverse relief accompanies concave horizontal decussation that produces the characteristic radial ridging in palaeotheres and titanotheres. True vertical decussation is found in forms with low transverse relief, such as rhinocerotoids, astrapotheres and arsinotheres. In both cases the longitudinal occlusal relief (transverse to the direction of movement) is pronounced.

Of the lophodonts, equids are the ones which seem to have the lowest longitudinal occlusal relief (the least distinction between the phases of the power stroke). It is very suggestive that the arrangement of the HSB:s at the ectoloph in lophodont horses (e.g. *Anchitherium*) is convex horizontal, as it is in selenodont artiodactyls. This arrangement minimizes the angle between facets and HSB:s. A common feature of horses and selenodonts is also the relatively thin enamel with Pattern 2 prism packing (at least at the buccal facets concerned). The litoptern *Macrauchenia* seems to have the same structure, and toxodontid and homalodontid notoungulates have thin enamel, little transverse relief and straight horizontal bands, which also results in parallel orientation of bands and facets. These forms also have Pattern 2 enamel.

In other cases the relationship is less clear, but I know of no actual counterexample to the principle that HSB:s tend to be parallel to occlusal facets in thin-enamelled forms with Pattern 2 prism packing and low longitudinal relief. HSB:s transverse to occlusal facets are, on the whole, found in association with relatively thicker enamel and higher longitudinal relief, but with both Pattern 2 and Pattern 3 prism packing. Depending on transverse relief, the HSB:s may be either straight or concave horizontal. In other words, the prediction made above (Sect.

4.3.3.) is fulfilled; that vertical decussation, or more properly transversely intercepted HSB:s, would occur in association with high longitudinal relief.

It is much more difficult to suggest any unifying principle, however speculative, for crown shape and true ontogenetic decussation mode. This proves nothing, of course, and may simply reflect lack of imagination, but one might interpret it as evidence that decussation modes reflect functional demands rather than ontogenetic constraints. At the same time, if the

functional relationships proposed are correct, an ontogenetic constraint is strongly implied at a secondary level. The decussation mode is the same over the whole crown, and in upper as well as lower teeth, although the functional advantage only applies to one (important but limited) set of facets. In other words, ameloblasts behave in one way or another, but not in several ways simultaneously in the same dentition.

5. Thesis: adaptations, exaptations, constraints and evolution

There can be no reasonable doubt that teeth function well because their evolution has been largely adaptive; i.e., under the control of natural selection. Dental morphology is highly heritable, and both natural and artificial selection do result in altered morphology (see review by Butler 1983). However, selection for other than morphological properties may also result in morphological change (Paynter & Grainger 1962, cited in Butler 1983), so all observed change in dental dimensions (for example, in successive age classes) is not necessarily a result of selection directed at the dimensions studied. This is true, for example, in cases where variance has been shown to decrease with increasing age (Kurtén 1953 and several papers since; see Butler 1983). The actual demonstration of selection is consequently problematic. After careful sifting of the evidence, Butler (1983) concluded that major differences between groups are related to specific functional demands (and hence are presumably adaptive), but that minor differences between closely related taxa may well be due to chance, and this conclusion appears plausible. Major functional types of (more or less interdependent) dentitions, muscular systems and jaw designs exist and can be identified (Sect. 4.2 above).

That teeth function well is not proof, however, that their evolution has been entirely adaptive. Gould & Vrba (1982) pointed out that there has been no term for functionally 'good' (aptive) features which are not the result of natural selection for their present purpose. They proposed the term 'exaptation' for features which 'happen to be' fit (aptus) by reason of (ex) their form; such exaptations have incidental effects, as opposed to adaptations which have functions resulting from selection. Both are 'aptations', and what has usually been known as preadaptations should be called 'preaptations'; i.e., potential but unrealized exaptations. Features which do not contribute to fitness are 'nonaptations'. I will adopt

this terminology here despite the disadvantage of using unfamiliar terms, since I think that Gould & Vrba correctly identify the lack of appropriate terms as one reason for the ignoring of other features than 'adaptations' 'preadaptations' and 'nonadaptations'. Such other features clearly exist and appear important in evolution.

When attention is shifted from current function and evolutionary past to the evolutionary potential in the future, it becomes immediately clear that many aptations are also constraints; i.e., limit the adaptability of the functional system for new or altered tasks. Viewed from a hypothetical future functional state before any adaptation for the future function has occurred, only exaptations and nonaptations exist, and these determine the potential for change: current aptations are constraints on the future. (Constraints obviously have no specified relation to current functional performance, and may equally well be 'strengths' as 'weaknesses'. Thus both aptations and nonaptations may be constraints.)

The 'alveolar area hypothesis' (Sect. 3.4.2), if correct, is an example of this. Relative eruption pressure (and hence relative wear rate) of adjacent teeth is a function of the number of fibroblasts present in the periodontal ligament; i.e., approximately of the area of unerupted tooth left in the alveolus. This relationship follows from a general physiological principle and is thus an exaptation, not an adaptation. It has the functional effect of causing teeth of unequal height to wear at rates proportional to their height, so that the dentition wears out evenly. However, this levelling has only a limited effect, because the eruption pressure is only a fraction of the total occlusal pressure. Hence the mechanism can only compensate for moderate size differences, and may be said to act as a constraint on size gradients.

Similarly, the inclination of enamel prisms towards occlusal, which causes lower teeth to be more wear-

resistant than upper at buccally dipping buccal facets and lingually dipping lingual facets (Sect. 3.4.1) is an exaptation (if it is an adaptation at all), for it is present in all kinds of teeth, even non-occluding ones. It is difficult to come to grips with this problem, but the arrangement is perhaps best viewed as a constraint, a nonadaptation that has been co-opted (Gould & Vrba 1982) into a functional system. In other words, it has partly channelled the evolution of that system. It is clear, however, that several adaptations also affect the relative dimensions of upper and lower teeth (particularly between chewing mode and occlusal relief), which makes theoretical analysis difficult.

A somewhat more simple case is the unequal wear resistance of the dental tissues which makes possible occlusal surfaces with proud enamel edges (blades) separated by hollowed-out areas of dentine and cement. It is almost certain that they have undergone adaptive evolution since first occlusion and later hypsodonty (and hence secondary occlusal surfaces) evolved (Sect. 4.3.6), but the original difference in wear resistance antedates both, and is clearly an exaptation with respect to them.

Because teeth begin to form at their tips and are finished at their bases increased crown height can evolve easily (Sect. 3.1.1), and this presumably constrains change in other directions. However, hypsodont (and hypselodont) teeth are only functionally meaningful with secondary occlusal surfaces. When the primary occlusal morphology cannot be replaced by a functionally similar secondary morphology (as in bilophodonts) hypsodonty is of little avail. No bilophodonts have ever become truly hypsodont (at least not while maintaining a high-relief occlusal surface); instead, at least in two cases (*Trichecus*, *Peradorcas*) they have evolved continuous replacement when faced with heavy dental wear. This seems to be a case of adaptations acting as constraints, since bilophodonty and trilophodonty (the latter is possible with secondary occlusal surfaces) arose from emphasis on different sets of facets. Because bilophodonty and trilophodonty have different muscular requirements, the two systems diverge by a process that might be called 'functional autocanalization': two components (occlusal surface morphology, musculature) of a functional system (the masticatory apparatus) constrain change in each other and thus of the whole system. In one case the extreme is continuous replacement, in the other continuous growth (hypsodonty).

The synchronization of the ontogenies of future antagonists and the resulting buffering of the system against malocclusion due to genetic variation or environmental disturbance (Sect. 3.1.1), must greatly affect the evolutionary potential of the dentition. Changes will tend to result in altered but occluding dentitions, and such changes that do not will be strongly selected against. Until the matter is

better understood it is useless to speculate on the evolutionary origin of this synchronization. At present it may be equally regarded as an adaptation to prevent malocclusion or as an exaptation with the same effect.

Tooth classes (whether due to intrinsic or extrinsic ontogenetic control) appear in many ways as the most distinct morphological and functional units of the dentition (Sect. 3.1.1). The differences between single teeth in a class are often small and gradual along the series, while the whole dentition in mammals rarely if ever can be regarded as one morphological or functional unit. Tooth classes may become very similar morphologically (particularly 'molarization' of premolars), but even in an extreme case such as *Equus*, isolated molars and premolars can generally be distinguished by specialists. In contrast, separation of P3 from P4 or M1 from M2 is difficult or impossible in many ungulates, for example, rhinoceroses which have much less uniform tooththrows than that of a horse. It also appears that increasing hypsodonty of the molars may be associated with increasing hypsodonty of the premolars, as in most ungulates, but also with premolar reduction as in pigs.

Kurtén (1953) applied correlation analysis to the problem of the genetic control of dental morphology, and found that: (i) adjacent molars tend to have more highly correlated dimensions than more distant molars, and (ii) that occluding teeth show the highest correlations of all. In many of his diagrams (particularly Kurtén 1953, figs. 37) there is a suggestion of separate correlation maxima for occluding teeth which belong to the same class. However, in carnivores with well developed carnassials (*Vulpes*, *Felis*) the highest correlation in the cheek tooth row is between the carnassials, which belong to different classes (P^4 , M_1). I suggested above (Sect. 3.1.1) that the carnassials of carnivores have 'escaped' from their classes, which might explain this obviously aptive feature. If this is true, then their strong correlation would seem to be an adaptation rather than an exaptation. It is a reasonable guess that the proximate cause of correlation patterns is synchronized ontogeny where several teeth share a substantial amount of genetic information. It is difficult, however, to decide whether this represents an adaptation or a constraint which has become co-opted into the functional system as an exaptation.

As shown above (Sect. 4.1.3), previous attempts to relate tooth size to body size via metabolic rate have failed to take into account the relevant time parameters (chewing rate, life span), and have therefore resulted in predictions at variance with the empirically observed data. If the time dimension is properly considered, predictions and observations largely coincide, but the problem as such becomes more complex. The isometric scaling of tooth size to body size results in 'metabolic scaling' of tooth per-

formance and durability when chewing rate and life span are scaled to body size as they are, but whether the temporal scaling is cause or effect of the spatial scaling is impossible to decide. Perhaps one should see the whole pattern as a reflection of some basic physiological consequences of body size; i.e., (again) as interacting constraints co-opted into the functional system as exaptations?

This admittedly speculative review thus suggests that much of what might appear as obvious adaptations to the naive observer are either certainly or pos-

sibly exaptations, which can equally well be regarded as one-time constraints. These have determined the basic lines of evolution of the system, while modifications within the portion of morphospace defined by them may be largely adaptive (although minor variations may again be nonadaptations due to drift rather than natural selection). Stated thus in the abstract, this conclusion sounds rather trivial, but it is worth noting that these different levels and features can at least partly be identified and investigated empirically, as shown above.

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References

- Alberch, P., Gould, S. J., Oster, G. F. & Wake, D. B. 1979: Size and shape in ontogeny and phylogeny. – *Paleobiology* 5(3):296-317.
- Altman, P. L. & Dittmer, D. S. (eds.) 1974: *Biology Data Book*. 2nd ed. Vol. III. – Federation of American Societies for Experimental Biology. Bethesda, Maryland.
- Antonius, O. 1922: *Grundzüge einer Stammesgeschichte der Haustiere*. – Jena.
- Atkins, A. G. & May, Y. W. 1979: On the guillotining of materials. – *J. Materials Science* 14:2747-2754.
- Becht, G. 1953: Comparative biological-anatomical researches on mastication in some mammals. I & II. – *Proc. Ned. Akad. Wet. Ser. C* 56:508-527.
- Benedict, F. G. 1938: *Vital energetics: A study in comparative basal metabolism*. – Carnegie Inst. Washington, Washington.
- Bhaskar, S. N. (ed.) 1980: *Orban's oral histology and embryology*. 9th ed. – The C.V. Mosby Company, St. Louis.
- Boule, M. & Piveteau, J. 1935: *Les fossiles*. – Masson & CIE, Paris.
- Boyde, A. 1964: *The structure and development of mammalian enamel*. – Ph.D. Thesis, Faculty of Medicine, University of London.
- » – 1967: The development of enamel structure. – *Proc. R. Soc. Medicine* 60(9):1318.
- » – 1969a: Electron microscopic observations relating to the nature and development of prism decussation in mammalian dental enamel. – *Bull. Group. Int. Rech. Stomat.* 12:151-207.
- » – 1969b: Correlation of ameloblast size with enamel prism pattern: use of scanning electron microscope to make surface area measurements. – *Z. Zellforsch.* 93:583-593.
- » – 1976a: Amelogenesis and the structure of enamel. – In: Cohen, B. & Kramer, I. R. (eds.), *Scientific Foundations of Dentistry*: 335-352. Heinemann, London.
- » – 1976b: Enamel structure and cavity margins. – *Operative Dentistry* 1(1):1328.
- Boyde, A. & Fortelius, M. (in press): Development, structure and function of rhinoceros enamel. – *Zool. J. Linn. Soc.*
- Boyde, A. & Martin, L. B. 1982: Enamel microstructure determination in hominoid and cercopithecoïd primates. – *Anat. Embryol.* 165:193-212.
- Boyde, A., Petran, M. & Hadravsky, M. 1983: Tandem scanning reflected light microscopy of internal features in whole bone and tooth samples. – *J. Microscopy* 132(1):17.
- Brown, R. W. 1956: *Composition of scientific words*. – Smithsonian Institution Press, Washington D.C.
- Butler, P. M. 1939: Studies on the mammalian dentition. Differentiation of the post-canine dentition. – *Proc. Zool. Soc. Lond. (B)* 109:136.
- » – 1946: The evolution of carnassial dentitions in the Mammalia. – *Proc. Zool. Soc. Lond.* 116:196-220.
- » – 1952a: The milk-molars of *Perissodactyla*, with remarks on molar occlusion. – *Proc. Zool. Soc. Lond.* 121(4):777-817.
- » – 1952b: Molarization of the premolars in the *Perissodactyla*. – *Proc. Zool. Soc. Lond.* 121:819-843.
- » – 1956: The ontogeny of the molar pattern. – *Biol. Reviews (Cambridge)* 31:3070.
- » – 1972: Some functional aspects of molar evolution. – *Evolution* 26(3):474-483.
- » – 1978a: Molar cusp nomenclature and homology. – In: Butler, P. M. & Joysey, K. A. (eds.), *Development, function and evolution of teeth*: 439-453. Academic Press, London.
- » – 1978b: The ontogeny of mammalian heterodonty. – *Jour. Biol. Buccale* 6:217-227.
- » – 1979: Some morphological observations on unerupted human deciduous molars. – *Ossa* 6:233-8.
- » – 1980: Functional aspects of the evolution of rodent molars. – *Palaeovertebrata (Mem. Jubil. R. Lavocat)*: 249-262.
- » – 1982: Directions of evolution in the mammalian dentition. – In: Joysey, K. A. & Friday, A. E. (eds.), *Problems of phylogenetic reconstruction*: 235–244. Academic Press, London.
- » – 1983: Evolution and mammalian dental morphology. – *Jour. Biol. Buccale* 11:285–302.
- Covert, H. H. & Kay, R. F. 1981: Dental microwear and diet: implications for determining the feeding behaviors of extinct primates, with a comment on the dietary pattern of *Sivapithecus*. – *Am. J. Phys. Anthropol.* 55:331–336.
- Creighton, G. K. 1980: Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. – *J. Zool. Lond.* 191:235–243.
- Crompton, A. W. & Hiiemäe, K. 1969a: Functional occlusion in tribosphenic molars. – *Nature* 222:678–679.
- » – 1969b: How mammalian molar teeth work. – *Discovery* 5(1):23–34.
- » – 1970: Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. – *Zool. J. Linn. Soc.* 49:21–47.
- Cuvier, G. 1815: *Essay on the theory of the earth*. 2nd ed. – R. Jameson trans., William Blackwood, John Murray and Robert Baldwin, London. – The relevant chapter ('Of the difficulty of distinguishing the fossil bones of Quadrupeds') reprinted as pp. 25–40 in: Scoch, R. M. (ed.), *Vertebrate Paleontology*. Van Nostrand Reinhold, New York 1984.
- Dale, H. E., Shanklin, M. D., Johnson, H. D. & Brown, W. H. 1970: Energy metabolism of the chimpanzee. – In: Bourne, G. H. (ed.), *The chimpanzee*. Vol. 2:100–122. Karger, Basel.
- De Vree, F. & Gans, C. 1976: Mastication in pygmy goats "*Capra hircus*". – *Ann. Soc. R. Zool. Belg.* 105:255–306.
- Dietrich, W. O. 1942: Zur Entwicklungsmechanik des Gebisses der afrikanischen Nashörner. – *Zbl. Min. Geol. Paläont. B* 1942:297–300.

- » - 1950: Stetigkeit und Unstetigkeit in der Pferdegeschichte. - N. Jb. Min. Geol. Paläont. 91:121—148.
- Domning, D. P. 1982: Evolution of manatees: a speculative history. - J. Paleont. 56(3):599—619.
- Eisenberg, J. F. 1981: The mammalian radiations. An analysis of trends in evolution, adaptation, and behaviour. - Univ. of Chicago Press, Chicago.
- Epstein, B. 1947: The mathematical description of certain breakage mechanisms leading to the logarithmic-normal distribution. - J. Franklin Inst. 244:471—477.
- Flower, S. S. 1931: Contributions to our knowledge of life in vertebrate animals. V. Mammals. - Proc. Zool. Soc. London 1931:145—234.
- Forstén, A. 1968: Revision of the Palearctic Hipparion. - Acta Zool. Fennica 119:1—134.
- Fortelius, M. 1981: Functional aspects of occlusal cheek-tooth morphology in hypsodont, non-ruminant ungulates. - Inter. Symp. Concept. Meth. Paleont. Barcelona 1981 Contr. Pap. 153—162.
- » - 1982: Ecological aspects of dental functional morphology in the Plio-Pleistocene rhinoceroses of Europe. - In: Kurtén, B. (ed.), Teeth: form, function, and evolution: 163—181. Columbia Univ. Press, New York.
- » - 1984: Vertical decussation of enamel prisms in lophodont ungulates. - In: Fearnhead, R. W. & Suga, S. (eds.), Tooth enamel IV: 427—431. Elsevier.
- » - 1985: The functional significance of wear-induced change in occlusal morphology of herbivore cheek teeth, exemplified by *Dicerorhinus etruscus* upper molars. - Acta Zool. Fennica 170:157—158.
- Frick, C. & Taylor, B. E. 1968: A generic review of the stenomyeline camels. - Am. Mus. Novitates 2353:1—51.
- Gardner, R. P. & Austin, L. G. 1962: A chemical engineering treatment of batch grinding. - In: Rumpf, H. (ed.), Zerkleinern Symposium: 217—248. Verlag Chemie, Düsseldorf.
- Gingerich, P. D. 1981: Cranial morphology and adaptations in Eocene Adapidae I. Sexual dimorphism in *Adapis magnus* and *Adapis parisiensis*. - Am. J. Phys. Anthrop. 56:217—234.
- Gingerich, P. D. & Ryan, A. S. 1979: Dental and cranial variation in living Indriidae. - Primates 20(1):141—159.
- Gingerich, P. D., Smith, B. H. & Rosenberg, K. 1982: Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. - Am. J. Phys. Anthrop. 58:81—100.
- Gordon, K. D. 1982: A study of microwear on chimpanzee molars: Implications for dental microwear analysis. - Am. J. Phys. Anthrop. 59:195—215.
- » - 1984: Pitting and bubbling artifacts in surface replicas made with silicone rubbers. - J. Microscopy 134(2):183—188.
- Gordon, K. D. & Walker, A. C. 1983: Playing 'Possum': A microwear experiment. - Am. J. Phys. Anthrop. 60:109—112.
- Gordon, S. E. 1976: The new science of strong materials. 2nd ed. - Penguin Books, Middlesex.
- Gould, S. J. 1966: Allometry and size in ontogeny and phylogeny. - Biol. Reviews (Cambridge) 41:587—640.
- » - 1971: Geometric similarity in allometric growth: A contribution to the problem of scaling in the evolution of size. - Am. Naturalist 105:113—136.
- » - 1973: Positive allometry of antlers in the "Irish Elk", *Megaloceros giganteus*. - Nature 244:375—376.
- » - 1975: On the scaling of tooth size in mammals. - Am. Zoologist 15:351—362.
- » - 1977: Ontogeny and phylogeny. - Harvard Univ. Press, Cambridge Mass.
- » - 1980a: The promise of paleobiology as a nomothetic, evolutionary discipline. - Paleobiology 6(1):96—118.
- » - 1980b: Is a new and general theory of evolution emerging? - Paleobiology 6(1):119—130.
- » - 1984: Morphological channelling by structural constraint: convergence in styles of dwarfing and gigantism in Cerion, with a description of two new fossil species and a report on the discovery of the largest Cerion. - Paleobiology 10(2):172—194.
- Gould, S. J. & Eldredge, N. 1977: Punctuated equilibria: the tempo and mode of evolution reconsidered. - Paleobiology 3(2):115—151.
- Gould, S. J. & Lewontin, R. C. 1979: The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. - Proc. R. Soc. Lond. 205 B:581—598.
- Gould, S. J. & Vrba, E. S. 1982: Exaptation — a missing term in the science of form. - Paleobiology 8(1):4—15.
- Greaves, W. S. 1978: The jaw lever system in ungulates: a new model. - J. Zool. Lond. 184:271—285.
- » - 1980: The mammalian jaw mechanism — the high glenoid cavity. - Am. Naturalist 116(3):432—440.
- Groves, C. P. 1982: The skulls of African rhinoceroses: Wild and captive. - Zoo Biology 1:251—261.
- Guerin, C. 1980: Les rhinoceros (Mammalia, Perissodactyla) du Miocene terminal au Pleistocene superieur en Europe Occidentale. Comparaison avec les especes actuelles. - Docum. Lab. Geol. Lyon 79 (1,2,3):1—1184.
- Harvey, P. H. 1982: On rethinking allometry. - J. Theor. Biol. 95:37—41.
- Harvey, P. H. & Macc, G. 1982: Comparisons between taxa and adaptive trends: problems of methodology. - In: King's College Sociobiology Group (ed.), Current problems in sociobiology: 343—361. Cambridge Univ. Press, Cambridge.
- Havers, C. 1689: Osteologia nova. - Smith, London.
- Hendrichs, H. 1965: Vergleichende Untersuchung des Wiederkauerverhalten. - Biol. Zbl. 84:651—751.
- Heptner, V. G., Nasimovich, A. A. & Bannikov, A. G. 1966: Die Säugetiere der Sowjetunion. Band I. Paarhufer und Unpaarhufer. - Gustav Fischer, Jena.
- Herring, S. W. & Scapino, R. P. 1973: Physiology of feeding in miniature pigs. - J. Morphology 141:427—460.
- Hershkovitz, P. 1971: Basic crown patterns and cusp homologies of mammalian teeth. - In: Dahlberg, A. (ed.), Dental morphology and evolution. Univ. of Chicago Press, Chicago.
- Hills, M. & Wood, B. A. 1984: Regression lines, size, and allometry. - In: Chivers, D. J., Wood, B. A. & Bilsborough, A. (eds.), Food acquisition and pro-

- cessing in primates: 557—567. Plenum Press, New York.
- Hiiemäe, K. M. 1978: Mammalian mastication: a review of the activity of the jaw muscles and the movements they produce in chewing. — In: Butler, P. M. & Joysey, K. A. (eds.), *Development, function and evolution of teeth*: 359—398. Academic Press, London.
- Hooijer, D. A. 1972: A Late Pliocene rhinoceros from Langebaanweg, Cape Province. — *Ann. S. Afr. Mus.* 59(9):151—191.
- » — 1981: How do elephants replace their teeth? — *J. Anat.* 133(1):129.
- Hooijer, D. A. & Patterson, B. 1972: Rhinoceroses from the Pliocene of Northwestern Kenya. — *Bull. Mus. Comp. Zool.* 144(1):1—26.
- Hulbert, R. C., Jr. 1982: Population dynamics of the three-toed horse *Neohipparion* from the late Miocene of Florida. — *Paleobiology* 8(2):159—167.
- Hunter, J. 1839: Treatise on the natural history and diseases of the human teeth, explaining their structure, use, formation, growth and diseases. — Haswell, Barrington, and Haswell, Philadelphia.
- Huxley, J. 1953: *Evolution in action*. — Chatto & Windus, London.
- Janis, C. M. 1976: The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. — *Evolution* 30:757—774.
- » — 1979: Mastication in the hyrax and its relevance to ungulate dental evolution. — *Paleobiology* 5(1):50—59.
- » — 1983: Muscles of the masticatory apparatus in two genera of hyraxes (*Procavia* and *Heterohyrax*). — *J. Morphology* 176:61—87.
- Jones, S. J. & Boyde, A. 1974: Coronal cementogenesis in the horse. — *Archs. Oral Biol.* 19:605—614.
- Jørgensen, K. D. 1956: The deciduous dentition. A descriptive and comparative anatomical study. — *Acta odont. Scand. suppl.* 20:1—202.
- Karlström, S. 1931: Physical, physiological and pathological studies of dental enamel with special references to the question of its vitality. — A.B. Fahlcrantz' Boktryckeri, Stockholm.
- Kawai, N. 1955: Comparative anatomy of the bands of Schreger. — *Okajimas Folia Anat. Japon* 27:115—131.
- Kay, R. F. 1975: (Comment on Pilbeam & Gould 1974). — *Science* 169:63.
- » — 1977: The evolution of molar occlusion in the Cercopithecidae and early catarrhines. — *Am. J. Phys. Anthropol.* 46:327—352.
- » — 1978: Molar structure and diet in extant Cercopithecidae. — In: Butler, P. M. & Joysey, K. A., *Development, function and evolution of teeth*: 309—339. Academic Press, London.
- Kay, R. F. & Covert, H. H. 1983: True grit: a microwear experiment. — *Am. J. Phys. Anthropol.* 61:33—38.
- Kay, R. F. & Hiiemäe, K. M. 1974: Jaw movement and tooth use in recent and fossil primates. — *Am. J. Phys. Anthropol.* 40:227—256.
- Kingdon, J. 1971: *East African mammals. I*. — Academic Press, London.
- » — 1979: *East African mammals. III B. Large Mammals*. — Academic Press, London.
- » — 1982: *East African Mammals III C—D. Bovids*. — Academic Press, London.
- Klatt, B. 1913: Über den Einfluss der Gesamtgrösse auf das Schädelbild. — *Archiv für Entwicklungsmechanik der Organismen* 36:387—471.
- Kleiber, M. 1947: Body size and metabolic rate. — *Physiol. Reviews* 27:511—541.
- von Koenigswald, W. 1977: *Mimomys cf. reidii* aus der villafranchischen Spaltenfüllung Schambach bei Treuchtlingen. — *Mitt. Bayer. Staatsllg. Paläont. hist. Geol.* 17:197—212.
- » — 1980: Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). — *Abh. Senckenb. Naturforsch. Ges.* 539:1—129.
- » — 1982: Zum Verständnis der Morphologie der Wühlmausmolaren (Arvicolidae, Rodentia, Mammalia). — *Z. Geol. Wiss. Berlin* 10(7):951—962.
- Kollar, E. J. & Lumsden, A. G. S. 1979: Tooth morphogenesis: the role of the innervation during induction and pattern formation. — *Jour. Biol. Buccale* 7:49—60.
- Korenhof, C. A. W. 1982: Evolutionary trends of the inner enamel anatomy of deciduous molars from Sangiran, Java. — In: Kurten, B. (ed.), *Teeth: form, function, and evolution*: 350—365. Columbia Univ. Press, New York.
- Korvenkontio, V. A. 1934: Mikroskopische Untersuchungen an Nagerincisiven. — *Annales Zool. Soc. Zool.-Bot. Fennicae 'Vanamo'* 2(1):1—274.
- Kozawa, Y. 1984: The development and evolution of mammalian enamel structure. — In: Fearnhead, R. W. & Suga, S. (eds.), *Tooth enamel IV*: 437—441. Elsevier.
- Krause, D. W. 1982: Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*. — *Paleobiology* 8(3):265—281.
- Kurtén, B. 1953: On the variation and population dynamics of fossil and recent mammal populations. — *Acta Zool. Fennica* 76:1—122.
- » — 1954: Observations on allometry in mammalian dentitions: its interpretation and evolutionary significance. — *Acta Zool. Fennica* 85:1—13.
- » — 1963: Return of a lost structure in the evolution of the felid dentition. — *Comment. Biol. Soc. Sci. Fennica* 26(4):1—12.
- » — 1967: Some quantitative approaches to dental microevolution. — *J. Dental Res.* 46(5):817—828.
- » — 1976: *The cave bear story*. — Columbia Univ. Press, New York.
- » — 1983: Variation and dynamics of a fossil antelope population. — *Paleobiology* 9(1):62—69.
- Laurie, A. 1982: Behavioural ecology of the Greater One-horned Rhinoceros (*Rhinoceros unicornis*). — *J. Zool. Lond.* 196:307—341.
- Laws, R. M. 1968: Dentition and ageing of the hippopotamus. — *E. Afr. Wildlife J.* 6:19—52.
- Leitch, I., Hytten, F. E. & Billewicz, W. Z. 1959: The maternal and neonatal weights of some Mammalia. — *Proc. Zool. Soc. Lond.* 13:11—28.
- Leche, W. 1904: *Zoologie*. — In: Hedin, S. (ed), *Scientific results of a journey in Central Asia 1899—1902. Vol. 6. (1)*:1—69.
- Levins, R. 1968: *Evolution in changing environments*. — Princeton Univ. Press, Princeton.
- Lucas, P. W. 1979: The dental-dietary adaptations of mammals. — *N. Jb. Paläont. Mh.* 8:486—512.
- » — 1980: Adaptation and form of the mammalian dentition with special reference to primates and the

- evolution of man. – Ph.D. Thesis, University of London.
- Lucas, P. W. & Luke, D. A. 1983a: Methods for analysing the breakdown of food in human mastication. – *Archs Oral Biol.* 28(9):821–826.
- » – 1983b: Computer simulation of the breakdown of carrot particles during human mastication. – *Archs Oral Biol.* 28(9):821–826.
- » – 1984: Chewing it over: basic principles of food breakdown. – In: Chivers, D. J., Wood, B. A. & Bilsborough, A. (eds.), *Food acquisition and processing in primates*: 283–302. Plenum Press, New York.
- Lumsden, A. G. S. 1979: Pattern formation in the molar dentition of the mouse. – *Jour. Biol. Buccale* 7:77–103.
- Lumsden, A. G. S. & Osborn, J. W. 1977: The evolution of chewing: a dentist's view of paleontology. – *J. Dentistry* 5:269–287.
- Lundholm, B. 1947: Abstammung und Domestikation des Hauspferdes. – *Zool. Bidrag från Uppsala* 27:1–287.
- Maglio, V. J. 1972: Evolution of mastication in the Elephantidae. – *Evolution* 26:638–658.
- Marshall, P. M. & Butler, P. M. 1966: Molar cusp development in the bat, *Hipposideros beatus*, with reference to the ontogenetic basis of occlusion. – *Archs. Oral Biol.* 11:949–965.
- Martin, L. B. 1983: The relationships of the later Miocene Hominoidea. – Ph.D. Thesis, University of London.
- » – 1985: Significance of enamel thickness in hominid evolution. – *Nature* 314:260–263.
- Martin, R. D. 1981: Relative brain size and basal metabolic rate in terrestrial vertebrates. – *Nature* 293:57–60.
- » – 1983: Human brain evolution in an ecological context. Fifty-second James Arthur Lecture on the evolution of the human brain, 1982. – American Museum of Natural History, New York.
- Mayhall, J. T., Shelley, R. S. & Belier, P. L. 1982: The dental morphology of North American whites: a reappraisal. – In: Kurten, B. (ed), *Teeth: form, function, and evolution*: 245–258. Columbia University Press.
- Maynard Smith, J. & Savage, R. J. G. 1959: The mechanics of mammalian jaws. – *School Science Review* 40:289–301.
- McCandless, E. & Dye, J. A. 1950: Physiological changes in intermediary metabolism in various species of ruminants due to functional development of the rumen. – *Am. J. Physiol.* 162:434–446.
- Meunier, K. 1959: Die Größenabhängigkeit der Körperform bei Vögeln. – *Zeitschr. wissensch. Zool.* 162:328–355.
- Miller, F. L. 1974: Biology of the Kaminuriak population of barren-ground caribou. Part 2. – *Canadian Wildlife Service Report Series* 31:1–87.
- Mills, J. R. E. 1955: Ideal dental occlusion in the primates. – *Dent. Practitioner (Bristol)* 6:47–61.
- » – 1978: The relationship between tooth patterns and jaw movements in the hominoidea. – In: Butler, P. M. & Joysey, K. A. (eds.), *Development, function and evolution of teeth*: 341–353. Academic Press, London.
- Morrison, P. & Middleton, E. H. 1968: Body temperature and metabolism in the pigmy marmoset. – *Folia Primatol.* 6:70–82.
- Osborn, H. F. 1903: The extinct rhinoceroses. – *Mem. Amer. Mus. Nat. Hist.* 1(3):75–164.
- » – 1907: Evolution of mammalian molar teeth. – *Biological studies and addresses I.* London, Macmillan.
- » – 1918: *The origin and evolution of life*. – G. Bell and sons, London.
- Osborn, J. W. 1973: The evolution of dentitions. – *Am. Scient.* 61:548–559.
- » – 1978: Morphogenetic gradients: fields versus clones. – In: Butler, P. M. & Joysey, K. A. (eds.), *Development, function and evolution of teeth*: 171–201. Academic Press, London.
- Osborn, J. W. & Lumsden, A. G. S. 1978: An alternative to "thegosis" and a re-examination of the ways in which mammalian molars work. – *N. Jb. Geol. Paläont. Abh.* 156:371–392.
- Owen, R. 1845: *Odontography*. – London.
- Paynter, K. J. & Grainger, R. M. 1962: Relationship of morphology and size of teeth to caries. – *Internat. Dent. J.* 12:147–160.
- Peters, R. H. 1983: *The ecological implications of body size*. – Cambridge Univ. Press, Cambridge.
- Pilbeam, D. & Gould, S. J. 1974: Size and scaling in human evolution. – *Science* 186:892–901.
- » – 1975: (Reply to Kay 1975.) – *Science* 189:64.
- Pocock 1917: *Field (London)* 130:871 (cited by Flower 1931).
- Prothero, D. R. & Sereno, P. C. 1982: Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf coastal plain. – *Paleobiology* 8(1):16–30.
- Putnam, W. C. & Bassett, A. B. 1971: *Geology*. – Oxford Univ. Press, London.
- Radinsky, L. 1963: Origin and early evolution of North American Tapiroidea. – *Peabody Mus. Nat. Hist. Yale Univ. Bull.* 17:1–106.
- Radinsky, L. B. 1966: The adaptive radiation of the phenacodontid condylarths and the origin of the Perissodactyla. – *Evolution* 20(3):408–417.
- » – 1967: *Hyrachyus*, *Chasmotherium*, and the early evolution of helaeletid tapiroids. – *Am. Mus. Novitates* 2313:1–23.
- » – 1969: The early evolution of the Perissodactyla. – *Evolution* 23(2):308–328.
- » – 1984: Ontogeny and phylogeny in horse skull evolution. – *Evolution* 38(1):1–15.
- Reeve, E. C. R. & Huxley, J. S. 1945: Some problems in the study of allometric growth. – In: I.e Gros Clark, W. E. & Medawar, P. (eds.), *Essays on growth and form presented to D'Arcy Wentworth Thompson*: 121–156. Oxford University Press, Oxford.
- Rensberger, J. M. 1973: An occlusion model for mastication and dental wear in herbivorous mammals. – *J. Paleont.* 47(3):515–528.
- » – 1975: Function in the cheek tooth evolution of some hypsodont geomyoid rodents. – *J. Paleont.* 49(1):10–22.
- » – 1978: Scanning electron microscopy of wear and occlusal events in some small herbivores. – In: Butler, P. M. & Joysey, K. A. (eds.), *Development, function and evolution of teeth*: 413–438. Academic Press, London.

- » - 1983: Effects of enamel structure on wear. - *Am. J. Phys. Anthropol.* 60:343—344.
- Rensberger, J. M. & von Koenigswald, W. 1980: Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. - *Paleobiology* 6(4):447—495.
- Rensberger, J. M., Forstén, A. & Fortelius, M. 1984: Functional evolution of the cheek tooth pattern and chewing direction in Tertiary horses. - *Paleobiology* 10(4):439—452.
- Retzius, A. 1836: Mikroskopiska undersökningar öfver tändernas, särdeles tandbenets, struktur. - *Kongl. Vetensk. Akad. Handl.* 52—140 (Stockholm).
- Ringström, T. 1924: Nashörner der Hipparion-Fauna Nord-Chinas. - *Palaeontologica Sinica Scr. C* 1(4):1—156.
- Romcr, A. S. 1945: Vertebrate paleontology. 2nd ed. - The Univ. of Chicago Press, Chicago.
- » - 1970: The vertebrate body. 4th ed. - W. B. Saunders, Philadelphia.
- Rudwick, M. J. S. 1972: The meaning of fossils. - Macdonald, London.
- Ryan, T. A., Joiner, B. L. & Ryan, B. F. 1982: Minitab reference manual. - Minitab Inc., 215 Pond Laboratory, University Park, Pa. 16802, U.S.A.
- Sakai, T. 1982: Morphogenesis of molar cusps and tubercles in certain primates. - In: Kurten, B. (ed.), *Teeth: development, function, and evolution*: 307—322. Columbia Univ. Press, New York.
- Sanson, G. D. 1983: Nabarlek, *Peradorcas concinna*. - In: Strahan, R. (ed.): *The Australian Museum complete book of the Australian mammals*. Angus & Robertson, London.
- Schmidt-Nielsen, K. 1979: Animal physiology. Adaptation and environment. 2nd ed. - Cambridge Univ. Press.
- » - 1984: Scaling: why is animal size so important? - Cambridge Univ. Press, Cambridge.
- Schultz, W. 1979: Magen-Darm-Kanal der Monotremen und Marsupialier 3. - *Handbuch der Zoologie* 8(2—3):1—117. Walter Gruyter & Co., Berlin.
- Sheine, W. S. & Kay, R. F. 1977: An analysis of chewed food particle size and its relationship to molar structure in the primates *Chirogaleus medius* and *Galago senegalensis* and the insectivoran *Tupaia glis*. - *Am. J. Phys. Anthropol.* 47:15—20.
- Siivonen, L. 1976: Pohjolan nisäkkäät (Mammals of Northern Europe). - Otava, Helsinki.
- Simpson, G. G. 1944: Tempo and mode in evolution. - Columbia Univ. Press, New York.
- » - 1953: The major features of evolution. - Columbia Univ. Press, New York.
- Slavkin, H. C., Snead, M. L., Zeichner-David, M., Bringas, P., Jr. & Greenberg, G. L. 1984: Amelogenin gene expression during epithelial-mesenchymal interactions. - In: *The role of extracellular matrix in development*: 221—253. Alan R. Riss, Inc., New York.
- Sokal, R. R. & Rohlf, F. J. 1981: Biometry. 2nd ed. - W. H. Freeman, San Francisco.
- Stockler, L. 1957: Trigeminusmuskulatur und Kiefergelenk von *Elephas maximus* L. - *Morph. Jahrb.* 98:35—76.
- Strahan, R. (ed.) 1983: *The Australian Museum complete book of the Australian mammals*. - Angus and Robertson, London.
- Taylor, R. M. S. 1982: Aberrant maxillary third molars, morphology and developmental relations. - In: Kurten, B. (ed.), *Teeth: development, function, and evolution*: 64—74. Columbia Univ. Press, New York.
- Teaford, M. F. 1982: Differences in molar wear gradient between juvenile macaques and langurs. - *Am. J. Phys. Anthropol.* 57:323—330.
- Teaford, M. F. & Walker, A. 1983: Dental microwear in adult and still-born guinea pigs (*Cavia porcellus*). - *Archs Oral Biol.* 28(11):1077—1081.
- » - 1984: Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. - *Am. J. Phys. Anthropol.* 64:191—200.
- Thenius, E. 1969: *Stammesgeschichte der Säugetiere*. - *Handbuch der Zoologie* 8(47—48):1—722. Walter Gruyter & Co., Berlin.
- Thompson, D. W. 1917(1961): On growth and form. (Edited by J. T. Bonner, Cambridge Univ. Press, Cambridge.)
- Tobien, H. 1978: Brachyodonty and hypsodonty in some Palaeogene Eurasian lagomorphs. - *Mainzer Geowiss. Mitt.* 6:161—175.
- Turnbull, W. D. 1970: Mammalian masticatory apparatus. - *Fieldiana, Geol.* 18:147—356.
- Van Valen, L. 1960: A functional index of hypsodonty. - *Evolution* 14(4):531—532.
- » - 1964: Nature of the supernumerary molars of *Otocyon*. - *J. Mammalogy* 45(2):284—286.
- » - 1966a: Deltatheridia, a new order of mammals. - *Bull. Amer. Mus. Nat. Hist.* 132:1—126.
- » - 1966b: Nearly rooted incisors in an abnormal rat, and control of tooth growth. - *Evolution* 20(3):428—430.
- » - 1970: An analysis of developmental fields. - *Developmental Biol.* 23:456—477.
- » - 1971: Towards the origin of artiodactyls. - *Evolution* 25(3):523—529.
- Van Valen, L. M. 1982: Homology and causes. - *J. Morphology* 173:305—312.
- Vincent, J. F. V. 1982: The mechanical design of grass. - *J. Materials Sci.* 17:856—860.
- Vorontsov, N. N. 1967: *Evolychia pichchevaritel'noij sistemi grizunov (Mishedobraznie)*. (Evolution of the alimentary system of myomorph rodents). - Nauka, Novosibirsk.
- Walker, A. C. 1980: Functional anatomy and taphonomy. - In: Behrensmeier, A. K. & Hill, A. P. (eds.), *Fossils in the making*: 182—196. Univ. of Chicago Press, Chicago.
- Walker, A., Hoeck, H. N. & Perez, L. 1978: Microwear of mammalian teeth as an indicator of diet. - *Science* 201:908—910.
- Webb, S. D. 1983: The rise and fall of the late Miocene ungulate fauna in North America. - In: Nitecki, M. H. (ed.), *Coevolution*: 267—306. Univ. of Chicago Press, Chicago.
- Weijjs, W. A. 1980: Biomechanical models and the analysis of form: a study of the mammalian masticatory apparatus. - *Am. Zool.* 20(4):707—719.
- Weijjs, W. A. & Dantuma, R. 1981: Functional anatomy of the masticatory apparatus in the rabbit (*Oryctolagus cuniculus* L.). - *Netherlands J. Zool.* 31(1):99—147.
- Westergaard, B. 1980: Evolution of the mammalian denti-

- tion. – Mem. Soc. Geol. Fr. N.S. 139:191–200.
 – » – 1983: A new detailed model for mammalian dental evolution. – Z. f. Systematik u. Evolutionsforschung 21(1):68–78.
 White, J. F. & Gould, S. J. 1965: Interpretation of the coefficient in the allometric equation. – Am. Naturalist 44:5–18.
 White, T. E. 1959: The endocrine glands and evolution, no. 3: os cementum, hypsodonty, and diet. – Contr. Mus. Paleont. Univ. Michigan 13(9):211–265.

- Williams, G. 1955: The relationship between the length of the jaw and the length of the molar series in some eutherian mammals. – Proc. Zool. Soc. London 126:51–64.
 Woodger, J. H. 1945: On biological transformations. – In: Le Gros Clark, W. E. & Medawar, P. (eds.), Essays on growth and form presented to D'Arcy Wentworth Thompson: 94–120. Oxford University Press, Oxford.

Appendices

Appendix 1. Body weight data

All the data on body weight were taken from the literature. This was necessary because weight data were not recorded for the museum specimens on which skull and tooth measurements were taken. I used the following sources, in the order of preference: Kingdon (1979–1982), Siivonen (1982), Eisenberg (1981), Heptner et al. (1966). The weight data for the Rhinocerotidae were taken from Kingdon (1979), Groves (1982) and Laurie (1982). A list of species and sources is given after the next section (App. 2.).

For sexually dimorphic mammals the mean of the means for the sexes was used except when the cranial and dental measurements were only for one sex. In such cases the value for the appropriate sex was used. When only ranges were given, range midpoints were used as a substitute for means.

Birth weights were obtained from the same literature, particularly from Eisenberg (1981).

For body weights used in the chewing rate analysis see App. 6.

Appendix 2. Cranial and dental measurements

The material was accumulated from several different collections. For most species only a few complete specimens were available, and it would not have been worth while to measure large samples in the few cases when this would have been possible, particularly as the weight data had to be taken from other sources anyway. Thus the data are at best only approximate, and insufficient for more refined analysis, but it would have been beyond my powers to collect much better data for this investigation.

Material was used from the following collections:

- CA Museum of Zoology, University of Cambridge (UK)
 GB Naturhistoriska Muset, Gothenburg (Sweden)
 HZ Zoologiska Museet, Helsinki (Finland)
 KO Zoologisk Museum, Copenhagen (Denmark)
 LE Rijksmuseum van Natuurlijke Historie, Leiden (The Netherlands)
 ST Naturhistoriska Riksmuset, Stockholm (Sweden)
 TE Koninklijk Museum voor Midden-Afrika, Tervuren (Belgium)
 UZ Zoologiska Institutionen, Uppsala (Sweden)

The measurements were taken with large calipers (when available) or steel tape for dimensions exceeding 160 mm. Smaller dimensions were measured with small dial calipers. Depending on how accurately the endpoints of the dimension could be determined, the small calipers were read to the nearest mm or the nearest 1/10 mm. Large calipers and tape were always read to the nearest mm.

Data for the following species were used in this investigation (*N* refers to number of specimens, occasionally one or several measurements could not be obtained from one or more specimens; species marked (*) were only used in the tooth width analysis; BW refers to body weight source: Eis = Eisenberg 1981, Gro = Groves 1982, Hep = Heptner et al. 1966, Kin = Kingdon 1971–1982, Lau = Laurie 1982, Sii = Siivonen 1976):

Species	<i>N</i>	Coll.	BW
PERISSODACTYLA			
Equidae			
<i>Equus grevyi</i>	2	KO	Kin
<i>E. burchelli</i>	2	KO	Eis
<i>E. caballus</i>	2	HZ	-
<i>E. hemionus</i> (*)	1	HZ	-
<i>E. asinus</i> (*)	1	HZ	-
<i>E. onager</i> (*)	1	HZ	-
Tapiridae			
<i>Tapirus terrestris</i>	3	ST	Eis
<i>T. indicus</i>	1	ST	Eis
Rhinocerotidae			
<i>Dicerorhinus sumatrensis</i>	2	KO	Gro
<i>Rhinoceros sondaicus</i>	3	KO	Gro
<i>R. unicornis</i>	2	KO,UZ	Gro
<i>Diceros bicornis</i>	24	TE,KO,ST,GB,LE	Kin
<i>Ceratotherium simum</i>	11	TE,KO	Lau
ARTIODACTYLA			
Suidae			
<i>Sus scrofa</i>	1	HZ	Sii
<i>Potamochoerus porcus</i>	4	ST	Kin
<i>Hylochoerus meinerzhageni</i>	2	ST	Kin
<i>Phacochoerus aethiopicus</i>	2	ST	Kin
<i>Babirussa babirussa</i>	4	ST	-
Tayassuidae			
<i>Tayassu peccari</i>	3	ST	Eis
<i>T. tajacu</i>	3	ST	Eis

Hippopotamidae			
<i>Hippopotamus amphibius</i>	2	ST	Kin
Camelidae			
<i>Camelus dromedarius</i>	2	HZ,ST	Eis
Tragulidae			
<i>Tragulus</i> spp.	6	ST,KO	Eis
<i>Hyaemoschus aquaticus</i>	2	ST,KO	Kin
Cervidae			
<i>Moschus mosciferus</i>	4	ST,KO	Eis
<i>Muntiacus muntjak</i>	3	ST,KO	Eis
<i>Hydropotes inermis</i>	3	ST,GB	-
<i>Dama dama</i>	1	HZ	Sii
<i>Odocoileus virginianus</i>	1	HZ	Sii
<i>Rangifer tarandus</i>	4	HZ	Sii
<i>Alces alces</i>	1	HZ	Sii
<i>Capreolus capreolus</i>	1	HZ	Sii
Giraffidae			
<i>Giraffa camelopardalis</i>	2	ST	Kin
Bovidae			
<i>Litocranius walleri</i>	1	ST	Kin
<i>Sylvicapra grimmia</i>	4	KO,ST	Kin
<i>Madoqua saltiana</i>	3	ST,UZ	Kin
<i>Ourebia ourebi</i>	1	KO	-
<i>Rhaphicercus campestris</i>	2	KO	Kin
<i>Tragelaphus scriptus</i>	2	KO	Kin
<i>Beatragus hunteri</i>	1	KO	Kin
<i>Alcelaphus buselaphus</i>	2	KO	Kin
<i>Connochaetes taurinus</i>	1	KO	-
<i>Bos grunniens</i>	2	ST	-
<i>Syncerus caffer caffer</i>	1	TE	Kin
<i>S. c. nanus</i>	1	TE	Kin
<i>Taurotragus oryx</i>	1	GB	Kin
<i>Oryx beisa</i>	1	KO	Kin
<i>O. gazella</i>	1	GB	Kin
<i>Hippotragus equinus</i>	2	ST,GB	Kin
<i>H. niger</i>	1	GB	Kin
PROBOSCIDEA			
Elephantidae			
<i>Elephas maximus</i>	1	HZ	Eis
SIRENIA			
Trichechidae			
<i>Trichechus inunguis</i> (*)	1	UZ	-
<i>T. senegalensis</i> (*)	1	UZ	-
HYRACOIDEA			
Procaviidae			
<i>Procavia capensis</i>	3	ST,GB	Kin
<i>P. habessinica</i>	3	ST	Kin
<i>Heterohyrax</i> spp.	3	ST	Kin
<i>Denrohyrax dorsalis</i>	1	ST	Kin
<i>D. spp.</i> (small)	4	ST,GB	Kin

Appendix 3. Fossil material

The fossil material mentioned in this paper is housed in the following institutions:

BM British Museum (Natural History), London (UK)
 HP Paleontologiska Museet, Helsinki (Finland)
 KO Zoologisk Museum, Copenhagen (Denmark)
 MU Staatliche Sammlung für Paläontologie und historische Geologie, Munich (German Federal Republic)
 ST Naturhistoriska Riksmuseet, Stockholm (Sweden)
 TO National Science Museum, Tokyo (Japan)
 UP Paleontologiska Institutionen, Uppsala (Sweden)

Appendix 4. Sectioned casts

For a qualitative illustration of the plunge of occlusal movement during the phases of the powerstroke, epoxy casts (see App. 7.1) of upper and lower teeth were sectioned in one vertical plane, the horizontal direction of which was determined by sighting along occlusal facets and/or striae. An example showing both the occlusal surface and the sectioned surface is Fig. 43. The sectioned surfaces were polished smooth and camera lucida drawings were prepared (Figs 14–16).



Fig. 43. An example of a sectioned molar replica (*Equus grevyi* M³), showing both the occlusal surface and the profile.

Appendix 5. Tooth width data

Maximum basal tooth widths of fossil and recent 'herbivorous' mammals were taken from the ungulate sample (App. 2, 3), but mainly from the literature. All the relevant monographs, journals and reprints in the public and private libraries in the Division of Geology and Paleontology, Department of Geology, University of Helsinki were used. Data used met the minimum requirements of: (1) upper and lower teeth of at least one individual, or (2) at least three isolated specimens of each tooth from one locality. However, most species are represented by samples well above these minimum requirements (up to >100 specimens). Only M1 and M2 were used in this investigation, but the widths of all cheek teeth were recorded (see text). The species and sources are not listed here, but are available from the author. A family-level summary is given in Table 11.

In the analysis of anisodonty and anisognathly I used data from the ungulate sample (App. 2 above). The following species were included:

1) Bunodonts and lophodonts (excl. *Equus*):

Diceros bicornis, *Ceratotherium simum*, *Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*, *R. unicornis*, *Tapirus terrestris*, *T. indicus*, *Sus scrofa*, *Potamochoerus porcus*, *Hylochoerus meinertzhageni*, *Phacochoerus aethiopicus*, *Babirusa babirusa*, *Tayassu peccari*, *T. tajacu*, *Hippopotamus amphibius*, *Procavia habessinica*, *Heterohyrax* spp., *Dendrohyrax dorsalis*, *D. spp.*

2) Selenodonts plus *Equus*:

Equus grevyi, *E. burchelli*, *E. caballus*, *E. hemionus*, *E. onager*, *E. asinus*, *Camelus dromedarius*, *Tragulid spp.*, *Hyaemoschus aquaticus*, *Giraffa camelopardalis*, *Moschus moschiferus*, *Muntiacus muntjak*, *Hydropotes inermis*, *Dama dama*, *Odocoileus virginianus*, *Rangifer tarandus*, *Alces alces*, *Capreolus capreolus*, *Litocranius walleri*, *Sylvicapra grimmia*, *Madoqua saltiana*, *Rhaphicerus campestris*, *Tragelaphus scriptus*, *Beatragus hunteri*, *Alcelaphus buselaphus*, *Syncerus caffer caffer*, *S. c. nanus*, *Taurotragus oryx*, *Oryx beisa*, *O. gazella*, *Hippotragus equinus*, *H. niger*.

Appendix 6. Chewing rate measurements

The data were obtained at the Helsinki Zoo in March 1984. The chewing rates were calculated from timed sequences of rhythmic chewing (I used a stopwatch and counted until the animal stopped chewing). This was much easier for cud chewing than for fresh chewing, which in ruminants tends to consist of short bouts of about a dozen cycles. Depending on availability, between 20 and 500 cycles were timed for each species (mean 209, *SD* 125). Comparison of values obtained from different chewing bouts suggests that there is little variation in one individual but that individuals differ markedly in ways not obviously related to body size.

The body weights were estimated with the help of zoo records and the literature, particularly Eisenberg (1981). It is obvious that they are only rough approximations but nothing else was available. The data obtained are listed below (CD = chewing cycle duration in milliseconds, BW = body weight in kilograms):

Species, sex	CD	BW
I. Fresh chewing		
<i>Capra ibex</i>	597	40
<i>C. falconeri</i>	581	64
<i>Hemitragus jemlahicus</i>	471	50
<i>Oreamnos americanus</i>	780	60
<i>Ammotragus lervia</i>	584	66
<i>Bos grunniens</i>	872	250
<i>Bison bonasus</i>	793	300
<i>Camelus bactrianus</i>	912	500
<i>Equus hemionus</i>	797	210
II. Cud chewing		
<i>Capra ibex</i> , subadult	821	40
<i>C. falconeri</i>	657	64
<i>Hemitragus jemlahicus</i>	628	50
<i>Oreamnos americanus</i>	846	60
<i>Ovibos moschatus</i>	1169	400
<i>Bos grunniens</i>	880	250
<i>Bison bonasus</i>	1145	500
<i>Rangifer tarandus</i>	864	125
<i>Alces alces</i>	1072	450
<i>Odocoileus virginianus</i>	779	80
<i>Camelus bactrianus</i>	1172	500

III. In addition, the following data from the literature were used (D&G = De Vree & Gans 1975, H&S = Herring & Scapino 1973, W&S = Weijts & Dantuma 1981):

Fresh chewing		
<i>Oryctolagus cuniculus</i> (W&D)	267	1.8
<i>Sus scrofa</i> (dwarf) (H&S)	330	22.3
<i>Capra hircus</i> (dwarf) (D&G)	520	20
Cud chewing		
<i>Capra hircus</i> (dwarf) (D&G)	500	20

Appendix 7. Preparation of samples for microscopy and imaging techniques

App. 7.1. High resolution replication and study of worn tooth surfaces

Replication

The teeth were cleaned with water and detergent, ethanol, acetone, or various combinations of these, depending on the circumstances. If facilities were available the teeth were rinsed in distilled water and air dried, but more often they were wiped dry with soft tissue. Two-stage silicone rubber molds were made of the cleaned teeth (Optosil hard and Xantopren blue, Bayer Dental, D-5090 Leverkusen, BRD). The molds were transported to Helsinki, cleaned when necessary and poured with a clear epoxy resin (UH Products, Porvoo 15, Finland). Bubbles were removed mechanically with a blunt needle, and the epoxy was allowed to set at room temperature and pressure. A useful discussion of replication problems and artefacts is given by Gordon (1984).

Light microscopy

Clear epoxy replicas are particularly suitable for light microscopy, as they (unlike the teeth themselves) can be illuminated by transmitted light so that surface reflections are eliminated. For low magnification study and documentation of wear surfaces, an ordinary stereo light microscope is thus a good alternative to a scanning electron microscope.

In this investigation I used a Wild M7 stereomicroscope with a fibre optics lightsource. The casts were placed on a transparent plastic box directly below the objective lens, and illuminated by light reflected obliquely from a white paper card underneath the box. The illumination thus achieved is either lightfield or darkfield, depending on the relative positions of light source, reflective surface and specimen. By adjusting these, a suitable illumination could generally be achieved without difficulty. It should be noted that this technique primarily resolves structures transverse to the direction of illumination, which may confuse the unwary.

Scanning electron microscopy

Epoxy replicas can, of course, be coated and examined in a scanning electron microscope. Depending on the quality of the replica, magnifications up to several thousand times can be used (see Gordon 1982). In this investigation the replicas were sputter-coated with gold and examined in the secondary electron mode at 10 kV acceleration voltage (see below).

App. 7.2. Enamel samples for scanning electron microscopy (SEM)

Minimum damage strategies in preparation of tooth samples for the SEM are discussed by Boyde & Martin (1982). Most of the samples used in this investigation were prepared by rather destructive techniques, since I was unaware of alternatives at the time. The specimens were cut in defined planes, polished, etched and coated. Polishing was variously on abrasive paper, on a glass plate with abrasive powder of successively finer grain, on 'jeweller's rouge' paper or on a soft lap with diamond paste. Chemical etching was with H_3PO_4 , typically but not invariably 0.5 % for 60 seconds. For physical etching an 'airpolishing' unit (Dentsply/Cavitron Prophy-Jet, Dentsply International, York, PA 17405, USA) was used (at the Department of Anatomy and Embryology, University College London). Various working distances and treatment times were used, but an approximate norm was 2–3 mm and 60 secs. These and other preparation procedures are discussed in Boyde & Fortelius (in press).

The specimens were sputter coated with gold or gold-palladium and investigated in secondary (SE) and/or backscattered (BSE) electron modes at 10–20 kV acceleration voltage (depending on imaging mode). The microscopes used were Cambridge Stereoscans 1 and S4-10 (at the Department of Embryology and Anatomy, University College London), the latter with a 4 sector solid state backscattered electron detector, and a JEOL 135-C (at the Department of Electron Microscopy, University of Helsinki).

App. 7.3. The tandem scanning reflected light microscope (TSRLM)

The technical details of this optical scanning microscope are given in Boyde et al. (1983) and references cited therein. The microscope is able to focus on a very narrow optical plane, and to exclude any reflections from above or below this plane (including the strong reflection from the surface of the specimen, which is otherwise a major problem of reflected light microscopy). By moving the focal plane up and down through the specimen, one can obtain information about the three-dimensional structure of the tissue. Unfortunately this information is difficult to record in a form that could be published in a journal, and at the moment static light micrographs and verbal description have to suffice.

The microscope used in this study is one housed in the Department of Anatomy and Embryology, University College London (Prof. Alan Boyde); as of this writing (Dec. 1984) it is the only operational TSRLM outside Czechoslovakia. This particular instrument is designed to take standard light microscope objective lenses. For investigations of enamel structure, oil immersion lenses were found to be most suitable, but dry lenses and water and glycerin immersion lenses could also be used successfully.

The depth of penetration (i.e., the greatest depth from which enough light is reflected to form an image) varies, but 100 microns is not unusual for fossil enamel and visible light. A practical limit (which was occasionally reached) is set by the free working distance of the objective lens. For standard oil immersion lenses of 100 times magnification this is in the region of 200 microns. The thickness of the

non-decussating outer enamel of many larger ungulates exceeds the depth of penetration, so that it is not possible to study the more 'diagnostic' or otherwise more interesting, decussating inner enamel from the surface. However, the problem can be partly overcome by inspecting occlusal and interstitial wear facets or broken surfaces which expose the inner enamel.

Despite some technical difficulties with TSRLM, it has several features which make it a most promising tool for paleontological fine structure research. No preparation of the specimen is required, very large specimens (on the instrument used in this study up to one metre in diameter) can be examined intact, and the specimens are not submitted to anything more drastic than intense visible light. Thus complete specimens (including holotypes!) can be examined without undue risk of damage. Any part of the specimen (within the limits of accessibility) can be examined, not just the fragments that happen to be available. It is to be hoped that this microscope will become part of the standard equipment of palaeontological museums and laboratories. It would drastically reduce the drain on irreplaceable material now lost in destructive ultrastructure research involving cutting and etching.

Appendix 8. Statistical calculations

All more demanding calculations were performed on a Burroughs B7800 computer, located at the Computing Centre, University of Helsinki, using the 'Minitab' program system (Minitab Inc., 215 Pond Laboratory, University Park, Pa. 16802, U.S.A.). The major axis slopes, intercepts and confidence limits were calculated according to Sokal & Rohlf (1981); all other statistics according to programmes extant within the 'Minitab' system (Ryan et al. 1982).

Appendix 9. Abbreviations

Variables

AWT	adult body weight
BL	basal skull length
BRCL	braincase length
BWT	birth weight
CBL	condylobasal skull length
CPL	length of skull from condyles to anterior margin of second premolar
FEL	femur length
HBL	head and body length
M ¹ A, M ² A, M ³ A	area (L × W) or upper molars
M ₁ A, M ₂ A, M ₃ A	area (L × W) of lower molars
M ¹ L, M ² L, M ³ L	length of upper molars
M ₁ L, M ₂ L, M ₃ L	length of lower molars
M ¹ W, M ² W, M ³ W	width of upper molars
M ₁ W, M ₂ W, M ₃ W	width of lower molars
MAL	length of mandible
MRUL	length of upper molar row
P ⁴ AL	alveolar length of P ⁴

SKA	skull "area" (CBL × WZY)	m.a.	major axis slope
TRLA	area of lower postcanine tooththrow (except for Table 2 calculated as $TRLA \times M_2W$)	N	number of data points
		P	probability of rejection of null hypothesis
TRLL	length of lower postcanine tooththrow	r	coefficient of correlation
TRUA	area of upper postcanine tooththrow (except for Table 2 calculated as $TRUA \times M_2W$)	r.m.a.	reduced major axis slope
		SD	standard deviation
TRUL	length of upper postcanine tooththrow	W	(independent) variable
WZY	greatest zygomatic width (of skull)	Y	(dependent) variable

Statistical parameters

a, b	empirical constants of the allometric equation $Y = aW^b$; b is slope and $\log a$ is intercept of the line $\log Y = b \log W + \log a$
CL	confidence limits
CV	coefficient of variation
l.s.q.	least squares slopes

Other abbreviations

ADI	index of anisodonty (def. p. 51)
AGI	index of anisognathy (def. p. 54)
HSB	Hunter-Schreger band

For crown morphology see caption of Fig. 2. Abbreviations of museum collections are given in App. 2–3. Further occasional abbreviations are given in the relevant figure and table captions.