# Tooth Size in the European Badger (Meles meles) with Special Reference to Sexual Dimporhism, Diet and Intraspecific Aggression

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Length of the first molar in the upper jaw (M¹) was compared with condylobasal length in 40 skulls of adult badgers (20 of each sex). In addition, the length, width, and height of all teeth except the vestigial first premolar were measured in 24 skulls of juvenile badgers (12 of each sex). All skulls originated in Switzerland. M¹ length was weakly but positively correlated with condylobasal length in adult skulls of both sexes. There was a significant sex difference in condylobasal length but not in M¹ length. Juvenile skulls showed a rostro-caudal gradient in tooth size in both jaws and both sexes within the incisor row (including the canine) and within the cheek teeth row. The size gradient in the cheek teeth was more expressed in the upper jaw. A strong sexual dimorphism in tooth size existed in the canines but not in the cheek teeth. We suggest that sexual dimorphism in canine size is more related to sexual and social behaviour than to feeding.

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### 1. INTRODUCTION

The most striking structure in the dentition of the European badger Meles meles (Linnaeus, 1758) is the first molar in the upper jaw (M1). This tooth is conspicuously larger than any other tooth in the premolarmolar tooth row and it possesses a complex multicusped surface not typically found in carnivore dentition. M1 forms a close functional occlusion with the talidonid of the lower-jaw molar M1 and also with M2. Occlusion is assisted by the peculiarly rigid hinge joint characteristic of the badger skull (Long & Killingley, 1983), and also by the massive character of the masticatory apparatus involving a pronounced sagittal crest, wide zygomatic breadth and strong jaw muscles (musculus temporalis). In addition, M1 is rarely lost intra vitam and is more likely than any other tooth to be present in badger skulls recovered from prehistoric sites or found in spoil heaps at the entrances of existing sets (Lüps, unpublished). This suggests that M<sup>1</sup> is unusually firmly rooted in the jaw, not only by comparison with the badger's other teeth but also by comparison with the carnassials of other carnivores. Taken together,

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these exceptional characteristics of M¹ suggest that it may be an especially important tooth in relation to feeding.

Few quantitative data have been published concerning the badger's dentition, and in this paper we report measurements of tooth size in adult and juvenile skulls. We give special attention to the size of M¹ for the reasons given above; and we consider tooth size not only in absolute terms but also in relation to skull size and with reference to sexual dimorphism. Our primary aim was to relate variation in tooth size to the presumed function of the teeth in question.

### 2. METHODS

#### 2.1. Animals

All skulls were collected between 1967 and 1982 in the canton of Berne, Switzerland (see Lüps, 1984, for further details) and are presently stored in the Natural History Museum, Bern. Two separate series of skulls were measured:

- (1) Length of M<sup>1</sup> was compared with condylobasal length in 20 adult skulls of each sex. The animals from which the skulls were taken were aged between 25 and 50 months, based on inspection of tooth cementum annuli (L ps et al., 1987). The purpose of this series of measurements was to correlate variation in M<sup>1</sup> size with variation in skull size, in adult animals of each sex.
- (2) Tooth measurements were taken from 12 juvenile skulls of each sex, from animals aged between 6 and 12 months. All teeth were measured with the exception of P1, which is very small and which often fails to erupt or is lost during preparation of the skull (Hancox, cited in Neal, 1986; Lüps & Wandeler, in press). The purpose of this series of measurements on juvenile skulls was to obtain data on tooth size at an age when the permanent dentition has completely erupted (Lüps, 1983; Neal, 1986) but when tooth wear, tooth loss, and deposition of tartar are not significant sources of error. It would not have been meaningful to compare tooth size with condylobasal length in juvenile skulls since the skull is not fully grown at age 12 months (Lüps, 1983).

# 2.2. Measurements

Tooth measurements (length, width, and crown height) were taken to 0.1 mm using a caliper under a binocular microscope (Fig. 1). The surface area of each tooth (Gould, 1975) was then estimated by calculating the logarithm of the product of length and width  $[\ln (1 \times w)]$  (see Gingerich & Winkler, 1979). In some teath crown height was not well defined, especially when the border of the alveoles was not flat. Thus, data on crown height should be interpreted with caution.

In the subadult skulls teeth were measured on both sides of each jaw. However, of a total of 2448 possible measurements only 2383 were actually taken owing to a few cases in which teeth were absent (N=16 skulls) or damaged (N=11). No significant left-right difference was found in any measurement in any tooth in either jaw (t-tests, p < 0.05). Each measurement (length, width, or height) was therefore averaged across the left and right tooth in a particular jaw prior to calculating the mean across individuals for that measurement.

In addition there was no significant difference in the length of M1 between

the 20 adult and 12 juvenile skulls in either sex (t-tests, p=0.39 for males, p=0.34 for females). Thus data on size of  $M^1$  can be meaningfully compared across the two series of skulls.

### 3. RESULTS

### 3.1. Adult Skulls

Comparison of  $M^1$  length with condylobasal length in adult badgers (see Fig. 2) showed a marginally significant positive correlation between

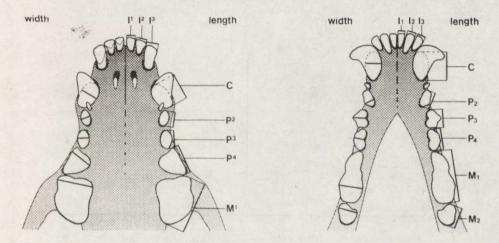


Fig. 1. Dentition in the upper jaw (left) and lower jaw (right) showing how the width and length of each tooth was measured.

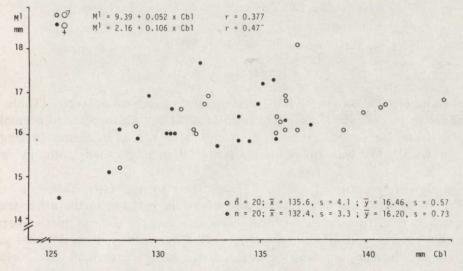


Fig. 2. M¹ length plotted against condylobasal length in adult badgers of both sexes. Open circles: males. Closed circles: females.

the two measurements in each sex (males, r=0.377, p=0.05 one-tailed; females, r=0.477, p<0.05 one-tailed). The sex ratio (male: female) was 1.02 both for  $M^1$  length and for condylobasal length; *i.e.*, both measurements were on average slightly larger in males than in females, though as Fig. 2 shows there was considerable overlap between the sexes. A significant difference between males and females was found only for condylobasal length (t-tests:  $M^1$  length, p=0.11; condylobasal length, p=0.009).

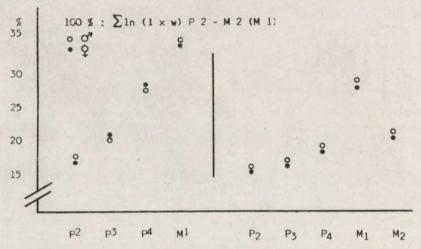


Fig. 3. Surface area [ln  $(l \times w)$ ] of each cheek tooth as a percentage of the total surface area of all cheek teeth in each jaw and each sex. Each point is the mean over 12 skulls. Left side: upper jaw. Right side: lower jaw.

## 3.2. Sub-adult Skulls

# 3.2.1. Size of Teeth

Data on the length, width, and height of sub-adult teeth (Table 1) show an increase in incisor size from I1 to I3 and an increase in premolar size from P2 to P4, in both jaws and both sexes. In terms of length and width, M1 was substantially larger than any other tooth, in each jaw.

Data on estimated surface area [ln  $(1 \times w)$ ] (see Table 2 and Fig. 3) confirm the exaggerated size of M1 in relation to the other teeth in each jaw. In terms of surface area  $M^1$  was the largest tooth overall in both sexes, and  $M^2$  the second largest. Furthermore, since  $M^1$  possesses in reality a complex multicusped surface, measurement of true surface area by morphometric means would demonstrate even more convincingly the difference in size between  $M^1$  and other teeth. In addition Table 2

and Fig. 3 show a tendency for surface area to increase from I1 to I3 and from P2 to P4 and M1 in both jaws and both sexes. This concentration of material towards M1 is less expressed in the lower jaw than in the upper.

Finally, Table 2 shows that the estimated surface area of most upper jaw teeth was greater than that of their lower jaw counterparts. Exceptions were C and P2, which were marginally larger in the lower jaw counterparts.

### 3.2.2. Variation in Tooth Size

In order to investigate variation to tooth size between individuals and sexes, coefficient of variation (v) was calculated for each measurement of each tooth (see Table 1). Coefficient of variation ranged from 3.1

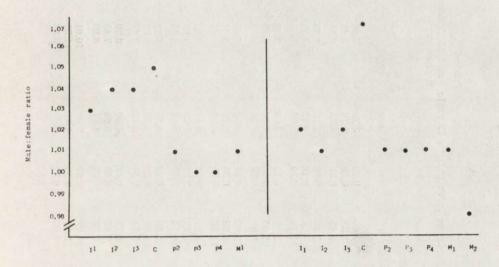


Fig. 4. Male:female ratio in tooth surface area (mean over 12 skulls of each sex) for each tooth in the upper jaw (left) and lower jaw (right). Values greater than 1.00 indicate larger tooth area in males; values less than 1.00 indicate larger tooth area in females.

( $C^1$  height in females) to 11.0 ( $I_1$  height in males), but 58% of all measurements showed moderate values of v between 4.5 and 6.5. Variation tended to be especially great in the height of the lower-jaw incisors, probably because the very thin bone on the labial side of the alveole was often damaged, making exact measurement of tooth height im-

Table 1

Tooth measurements (average left/right) in 12 male and 12 female juvenile badgers (mm); l=length, w=width, h=height.

Pooth	Measure		0,0			0+		C	
		IX	s	a	IX	S	a	\$ = 1.00	d
11	1	3.04	0.10	3.29	2.96	0.12	4.05	1.03	0.091
	W	3.53	0.19	5.38	3.42	0.15	4.39	1.03	0.130
	h	6.43	0.31	4.82	6.33	0.42	6.64	1.02	0.515
1 <sub>2</sub>	1	3.36	0.16	4.76	3.25	0.17	5.23	1.03	0.117
	W	4.00	0.19	4.75	3.75	0.27	7.20	1.06	0.016 *
	Ч	7.14	0.36	5.04	7.02	0.39	5.56	1.02	0.44
I3	1	3.67	0.15	4.09	3.42	0.23	6.73	1.07	0.005 **
	W	5.03	0.31	6.16	4.89	0.30	6.13	1.03	0.273
	h	8.69	0.59	6.79	8.39	0.39	4.65	1.04	0.158
C	1	7.69	0.44	5.72	7.09	0.33	4.65	1.09	0.001
	W	5.85	0.34	5.81	5.34	0.20	3.75	1.10	0.000 **
	Ч	15.92	0.85	3.54	14.81	0.46	3.11	1.08	0.001 **
P2	1	4.61	0.30	6.51	4.58	0.28	6.13	1.01	0.938
	W	3.12	0.18	5.77	3.05	0.23	7.54	1.02	0.416
	h	4.62	0.30	6.49	4.61	0.27	5.86	1.00	0.932
P3	1	5.85	0.39	6.67	5.82	0.27	4.64	1.01	0.829
	W	4.00	0.25	6.25	4.04	0.26	6.44	66.0	0.705
	h	5.55	0.34	6.12	5.47	0.19	3.47	1.02	0.486
P4	1	8.75	0.42	4.80	8.79	0.32	3.64	1.00	0.796
	W	7.45	0.42	5.63	7.40	0.29	3.92	1.01	0.738
	h	6.26	0.28	4.47	00.9	0.27	4.50	1.04	0.030 *
$M^1$	1	16.19	76.0	5.99	16.01	99'0	4.12	1.01	0.601
	W	12.01	0.53	4.41	11.57	0.58	5.01	1.04	0.065
	h	5.05	0.27	5.35	5.03	0.36	7.16	1 00	0 879

ĭ	- ≽ t	2.47	0.11 0.15 0.54	4.45 5.47 11.04	2.41 2.68 4.88	0.16	6.64 6.34 9.63	1.03	0.298 0.369 0.962
Is	: - > c	2.63	0.12	4.56 6.27 9.79	3.27	0.14	5.26 6.12 8.62	0.99	0.579 0.350 0.036
$I_{3}$	: - > c	3.95 3.16 5.94	0.20	5.38	3.85	0.15	3.56 8.52	1.03	0.181 0.246 0.376
O	: , <b>\$</b> .c	8.18 6.68 15.18	0.35	5.84 5.84 5.80	7.61 5.55 13.91	0.34 0.41 0.57	4.47	1.08	0.001 ** 0.000 ** 0.000 **
P	. ⊢≽.¤	5.13	0.19	3.70 3.20 4.07	4.98 3.13 5.17	0.26 0.16 0.29	5.22 5.11 5.61	1.03	0.122 1.000 0.033 *
Рз	- ≽ q	5.56 3.34 5.65	0.23 0.19 0.31	4.14 5.69 5.49	5.52 3.29 5.30	0.23	4.17 4.26 5.66	1.01 1.02 1.07	0.914 0.472 0.010 *
P4	- <b>₽</b> ₽	6.85 3.85 6.01	0.38	5.55 5.97 6.82	6.86 3.74 5.61	0.31 0.23 0.31	4.52 6.15 5.53	1.00 1.03 1.07	0.944 0.254 0.014 *
M,	h & l	16.66 7.63 6.35	0.93 0.47 0.29	5.58 6.16 4.57	16.20 7.61 6.23	0.86	4.94 4.21 4.49	1.03	0.222 0.904 0.314
$\mathrm{M}_2$	n	5.56 5.93 3.90	0.42 0.39 0.33	7.55 6.58 8.46	5.83 6.03 3.82	0.30 0.31	5.83 4.98 8.12	0.95 0.98 1.02	0.098 0.489 0.547
* p<0.05;	** p\$0.005.								

possible. Coefficients of variation for M1 were moderate, being within the range 4.1 to 7.2 across both jaws and both sexes.

Taking all the teeth of the lower jaw together, the average value of v for length and width was 5.3 in males and 5.2 in females; in the upper jaw the averages were 5.4 in males and 5.2 in females. Thus overall degree of variation was very similar in both jaws and both sexes. In comparing the pattern of individual variation it should be borne in mind that the accuracy of measurements may decrease with decreasing tooth size. However, no significant correlation was found between coefficient of variation and tooth size for any measurement in either jaw or either sex.

Table 2
Surface area [ln (length×width)] in the teeth of badgers.

			S. Calm IV	Market Ber	The Res Line			
II -	12	13	C	P2	P3	P4	M1	M2
		Upp	er jaw					
2.37	2.60	2.92	3.81	2.67	3.15	4.18	5.27	
2.31	2.50	2.82	3.67	2.64	3.16	4.18	5.28	In 15 15
1.03	1.04	1.04	1.05	1.01	1.00	1.00	1.01	-
		Low	er jaw					
1.91	2.18	2.52	4.00	2.78	2.92	3.27	4.85	3.50
1.87					2.90			3.56
1.02	1.01	1.02	1.07	1.01	1.01	1.01	1.01	0.98
	2.37 2.31 1.03	2.37 2.60 2.31 2.50 1.03 1.04 1.91 2.18 1.87 2.16	Upp  2.37	Upper jaw 2.37 2.60 2.92 3.81 2.31 2.50 2.82 3.67 1.03 1.04 1.04 1.05  Lower jaw 1.91 2.18 2.52 4.00 1.87 2.16 2.48 3.74	Upper jaw  2.37	Upper jaw  2.37	Upper jaw  2.37	Upper jaw  2.37

# 3.2.3. Sexual Dimorphism

Sex differences in absolute tooth size (length, width, and height) are shown in Table 1 together with the male:female ratio for each measure (females=1.00). For most teeth all three measures were greater in males than in females, but only marginally so (that is, the male:female ratio was close to 1.00 in most cases). In each jaw the most conspicuously dimorphic tooth was the canine, which was significantly greater in males with respect to all three measurements (t-tests, p < 0.001).

Male:female ratio for estimated surface area showed a similar pattern in that the greatest degree of sexual dimorphism occurred in the canines (Fig. 4). Within the canines, dimorphism was greater in the lower jaw than in the upper (male:female ratios 1.07 and 1.05 respectively), a difference which is attributable to the relatively greater width of the male tooth in the lower jaw (see Table 1). Fig. 4 also suggests a tendency for sexual dimorphism to be more pronounced in the incisors than in the cheek teeth, especially in the upper jaw.

### 4, DISCUSSION

### 4.1. Premolars and Molars

The overall picture emerging from our results is that the size of the cheek teeth (length, width, height, and surface area) increases from P2 to M1, resulting in a concentration of material towards M1. This trend is especially evident in the upper jaw. Thus M¹ is the largest tooth of all in terms of surface area and width, and is second only to M₁ in terms of length. Its surface may be more than double that of the carnassial P⁴ and may be larger than the combined surface of all the other teeth in the upper jaw (Pocock, 1920; Petter, 1971). M¹ has evolved from much smaller teeth to result in a large tooth, unusually firmly rooted in the jaw and bearing a complicated multicusped surface (Kurtén, 1967; Thenius, 1969; Petter, 1971). However, the function of the complex cusped surface is unclear since it often becomes flattened, especially on the lingual side (Ognev, 1962; Stubbe, 1965), as a consequence of wear during the badger's relatively long lifetime (Graf & Wandeler, 1982; Neal, 1986).

Corresponding with the concentration of material towards M1, P1 is greatly reduced in size or absent altogether. Again this trend is slightly more marked in the upper jaw,  $P^1$  being more often absent than  $P_1$  (Hancox, cited in Neal, 1986; Lüps, 1986). Similar trends in tooth size, together with loss of peripheral vestigial teeth, have been reported in other mammals (Gingerich & Schoeninger, 1979; Gingerich & Winkler, 1979; Wolsan et al., 1985) and probably reflect a concentration of material towards the point of maximum masticatory force (Petter, 1971). The existence of a West-East cline in the frequency of occurrence of P1 (Heptner & Naumov, 1974) suggests that the dentition of the badger is still evolving in the direction of further specialisation, particularly in the upper jaw. In addition, the occurrence of some degree of overlap between the teeth (especially  $P^3/P^4$  and  $P_2/P_3/P_4$ ) suggests evolution towards an overall reduction in jaw size, possibly in conjunction with a reduction in body size.

Our results suggest a tendency for variation in tooth size to decrease from P<sup>2</sup> to M<sup>1</sup>. This is not simply a consequence of the gradient in absolute tooth size, because overall we found no significant negative correlation between tooth size and coefficient of variation (cf. Pengilly, 1984). M<sup>1</sup> length increased with condylobasal length in adult skulls of both sexes, and a similar relationship has been reported between carnassial and skull length in other carnivores (Kurtén, 1953, 1967). But whereas skull length differed significantly between males and females

(see also Wiig, 1986) there was no significant sexual dimorphism in  $M^1$  length.

Wiig (1986) inferred from sexual dimorphism in various measures of skull size and shape that male badgers probably have a stronger bite than females at the carnassials and molars when the jaw is almost closed; but he was unable to explain this difference in terms of sex differences in diet. Previous work has shown no sex difference in the extent to which M¹ suffers loss, wear or damage (Lüps, 1986) and no sex difference in the amount or type of food consumed by adult badgers as determined from stomach contents (Lüps et al., 1987). Thus while sexual dimorphism in skull morphology remains unexplained, the relative lack of size variation in M¹ may mean that for some functional reason, presumably related to feeding, the absolute size of the tooth is important.

### 4.2. Incisors and Canines

A conspicuous feature of the anterior dentition, by comparison with the cheek teeth, was the degree of sexual dimorphism, especially in I¹, I⁰ and C. In particular, the canine in both jaws was significantly larger in males than in females, not only in absolute measurements and estimated surface area but also in relation to skull size. Similar observations have been made on other carnivores (e.g., Gordon & Morejohn, 1975; Parsons et al., 1978; Fuller et al., 1984; Wolsan et al., 1985) but none of the latter authors has commented on the ecological or ethological significance of their findings.

Since there is no evidence that male and female badgers differ in their feeding habits (see above) it is unlikely that sexual dimorphism in the anterior teeth is related to dimorphism in diet. In any case, it seems unlikely that the canines are frequently used in capturing or despatching prey since *M. meles* feeds mainly on invertebrates and on small items of plant material which are seized with the incisors and swallowed more or less whole (e.g., Kruuk, 1978; Macdonald, 1976). Small vertebrates such as voles, baby rabbits, amphibians and hedgehogs are occasionally eaten but most vertebrate material is probably ingested in the form of carrion (for refs. see Neal, 1986; Lüps & Wandeler, in press).

An alternative explanation is that the canines and possibly also the incisors have evolved at least partly in conjunction with aggressive or defensive behaviour. Badgers are acknowledged to be formidable fighters when attacked by other carnivores, especially domestic dogs and foxes (Neal, 1986; Meyer, 1986); but since this applies as much to females as to males, the sexual dimorphism in tooth size is unlikely to stem from a sex difference in anti-predator behaviour.

A more likely hypothesis is that the anterior dentition, especially the

canines, functions in intraspecific conflict. Badgers are strongly territorial and fierce fights between the members of adjacent social groups occur at territory boundaries (Kruuk, 1978; Roper et al., 1986). Fighting mainly takes the form of reciprocal chasing in which bites are directed towards the opponent's rump, and this can lead to serious injury or even death (Gallagher & Nelson, 1979). Punctures inflicted by the canines are often visible on captured badgers together with nips probably inflicted by the incisors. Such injuries occur in both sexes but are about three times as frequent in males as in females (Gallagher & Nelson, pers. comm.; Wilesmith, pers. comm.).

Whether all intraspecific fighting is attributable to territorial boundary disputes remains to be determined. Few fights have been observed between individuals of known sex, but anecdotal reports and radiotracking studies suggest that boundary fights are largely (perhaps exclusively) confined to males (Kruuk, 1978; Neal, 1986). Females, on the other hand, have been reported to fight other members of their own group in defence of their litters (Ahnlund, 1980; Neal, 1986). The essential point, however, is that data on bite wounding show that fighting (for whatever reason) is more common amongst males; and this offers an explanation of the sexual dimorphism in canine and incisor size. In a similar way, intrasexual competition has been used as an explanation of sexual dimorphism in canine size in some species of cervids (Ralls et al., 1975), in Sus scrofa (Gundlach, 1968; Beuerle, 1975) and in primates (Harvey et al., 1978). On the other hand, the hypothesis that sexual dimorphism in canine size is related to intraspecific competition is to some extent at variance with Wiig's (1986) conclusion that male badgers (unlike other mustelids) do not have a stronger bite than females when the jaws are fully opened and the canines are in use.

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ROZMIARY ZĘBÓW BORSUKA (MELES MELES) ZE SZCZEGÓLNYM ODNIESIENIEM DO DYMORFIZMU PŁCIOWEGO, POKARMU I AGRESJI WEWNĄTRZGATUNKOWEJ

### Streszczenie

Sprawdzono zależność między długością pierwszego trzonowca (M¹) a długością kondylobazalną 40 czaszek dorosłych borsuków (po 20 każdej płci) (Ryc. 1). Dodatkowo u 24 czaszek młodych borsuków (po 12 każdej płci) pomierzono długość, szerokość i wysokość wszystkich zębów (Tabele 1 i 2). Wszystkie okazy pochodziły ze Szwajcarii. Długość M¹ była słabo, dodatnio skorelowana z długością kondylobazalną czaszek dorosłych zwierząt obu płci (Ryc. 2). Dymorfizm płciowy był bardzo wyraźny w długości CB, natomiast nie występował w długości M¹.

U zwierząt młodych stwierdzono gradient wielkości zębów w kierunku przedniotylnym zarówno w szczęce jak i w żuchwie obu płci (Ryc. 3). Dymorfizm płciowy był znaczny w wielkości kłów, nieistotny natomiast w wielkości zębów policzkowych (Ryc. 4). Autorzy interpretują dymorfizm w wielkości kłów jako związany z zachowaniem socjalnym i reprodukcyjnym raczej, niż z pożywieniem.