BEAUFORTIA

INSTITUTE FOR SYSTEMATICS AND POPULATION BIOLOGY
(ZOOLOGICAL MUSEUM) UNIVERSITY OF AMSTERDAM

Vol. 48, no. 8 November 14, 1998

ON THE PRESENCE OF FIRST PREMOLARS IN SKULLS OF BADGERS, *MELES MELES* (LINNAEUS, 1758), MAINLY FROMTHE NETHERLANDS

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Keywords: first premolars, non-functional teeth, Badgers *(Meles meles)*, geographical distribution

ABSTRACT

The Eurasian badger *(Meles meles)* shows much variation in presence of first premolars. In this study a collection of badger skulls, mainly from the Netherlands, was examined for the presence of first premolar elements. The distribution pattern of first premolars, in skulls from the Netherlands, was compaired with data, presented in literature. Our results indicate that there are differences in distribution between different populations and that there might be differences between males and females in presence of first premolars.

From a subset of 50 skulls, several measures were taken to see which factors are highly related with presence of first premolars. The amount of direct space for the first premolar to develop (distance between the canine and the second premolar) seems to be highly related with presence or non-presence of first premolars.

INTRODUCTION

The dental formula of the Eurasian badger *(Meles meles)* has been the cause of some contradiction (Neal, 1948; Lüps & Wandler, 1993; Fullager *et al.*, 1960; Spitten *et al.*, 1985). The source of the confusion has been the number of premolars that a badger is suppose to have. The badger always has three pairs of fully functional premolars and often also has a non-functional small first premolar (Pm1) as well. This has caused many authors to give different dental formulas with three or four premolars. The presence or absence of these Pm1 elements seem to vary between populations. Several authors report different distributions of Pm1 elements in different populations (Hancox, 1988; Ratcliffe, 1970; Stubbe, 1980; Lüps, 1990; Heptner *et al.*, 1974). Geographical variation has already been noted between Middle European badgers and Far Eastern badgers (Heptner *et al.*, 1974), see also Fig. 1 in the section discussion.

Presence or absence, of these kinds of dental anomalies, can vary in different populations of a species due too several processes:

(1) genetic drift within populations can cause a non-functional element, like a first premolar element, to dissappear or be reduced in size.
(2) local adaptations within a species can cause changes in jaw size within a population. These changes can have an effect on the amount of room left for a non-functional small element, such as the first premolar.
(3) local adaptations within a species can cause changes in size of functional teeth, leaving less or more room for first premolar elements to develop.

All these processes can cause different populations to change their first premolar (Pm1) presence/absence distribution in a variety of ways. Variation in Pm1 distribution of separate populations could show that populations have been separated long enough to indicate that these differences have evolved.

Lüps (1990) presented data on Swiss badgers which showed that presence/absence of Pm1 is highly correlated with the distance between the functional second premolar (Pm2) and the canine. The smaller the room between the canine and the Pm2, the less likely it is that a Pm1 will be present. Lüps (loc. cit.) found that distances between the canine and the first molar or the condylobasal length itself did not correlate to presence or absence of Pm1. The lower jaw seems to have more space than the upper jaw and lower jaws have a higher chance of containing Pm1 elements. This may lead to the conclusion that the increase in size of Pm2 is a factor involved in the presence/absence distribution of Pm1. Lüps reports no differences between males and females in Pm1 presence.

Lüps presented data from other authors as well to show the distribution of Pm1 in different Eurasian populations. Unfortunatly, Lüps only gives the precentage of Pm1 present in a population, not how these teeth are distributed in different individuals, for example how many animals have four, three, two one or no first premolars. This could give detailed information about the amount of variation within a population and could show differences in distribution patterns between populations with the same Pm1 percentage.

This article presents data on Pm1 presence / absence of badger skulls predominantly from the Netherlands. Our results are compaired with Pm1 distributions from other populations presented in literature. The badgers in the Netherlands live in a more endangered state than anywhere else in Europe. The populations from the Netherlands are highly isolated and the populations are not very well connected due too fragmentation of suitable habitat. Inbreeding and loss of genetic variation must be a big problem for the populations in the Netherlands. This could show itself in a very peaked distribution pattern of Pm1 elements. Newman (1994) already stated that a peaked distribution of Pm1 elements could be an indication of inbreeding or that the population went through a bottleneck. Comparison of the collection of skulls from the Netherlands with other populations can indicate if this is the case.

Another reason why the Pm1 distribution of the Netherlands might be of interest is the fact that previous research of badger skulls was done with badgers from Britain, Denmark, middle Europe (Germany and Switzerland) and the Far East. The collection from Netherlands and the skulls from France can tell something about the Pm1 numbers on mainland western Europe. If the Pm1 distribution of Western Europe is similar to the Middle European numbers (round 75% presence) than no Pm1 differentation has taken place in the western parts which is an indication that the western populations are more related to one another than they are in the eastern part of their range. If these populations show great variation towards the Middle European numbers than some isolating forces have caused these populations to show differentation. This isolation could have been brought about by natural phenomena (natural barriers) or by human intervention (cultivation/urbanisation).

The skulls from the Netherlands are separated in "Middle Netherlands" and "South Netherlands". The big river systems must be a certain permanent barrier between these two populations.

From a subset of skulls the distance between

Pm2 and the canine were taken together with the length of the lower jaw to see if they had a relation with presence/absence of Pm1, like the data that Lüps presented suggests. This is important because it would allow us to check if the findings that Lüps (1990) did on the Swiss badgers can be extended to other Europian populations and is not merely confined to the Swiss population.

MATERIAL AND METHODS

BADGER SKULLS

348 badger skulls from the collections of the Amsterdam Zoological Museum, the National Natural History Museum at Leiden and the Rotterdam Nature Museum were examined on presence/absence of Pm1 elements. The number of Pm1 elements present in a skull was quantified across a range going from four (a full set of Pm1 elements in the upper and lower jaw) to zero (no Pm1 elements present in a skull). The skulls in the collections were from the following locations:

- 158 skulls from the south of the Netherlands (provinces of Limburg and Noord Brabant).
- 21 skulls from the middle of the Netherlands (provinces of Gelderland and Utrecht).
- 20 skulls from the area around Langon in France (Département Gironde).
- 15 skulls from the Département Loire-Atlantique in France.
- 28 skulls from the eastern slopes of the Cevennes in France.
- 8 skulls from Denmark.
- 7 skulls from Sweden.
- 43 skulls from unknown origin in the Netherlands.
- 2 skulls from the Island of Crete, Greece.

Several measures were taken from a subset of 50 skulls: (1) the distance between the second functional premolar (Pm2) and the canine. This as a measure for the amount of room left for a Pm1 to develop. (2) The length of the lower jaw. This as a measure for the amount of room for teeth to develop in total. (3) The total condylobasal length,which is a measure to standardize the length of the jaw to the total size of the skull. The 50 skulls were taken at random from the Amsterdam collection. It was made sure that males and females were equally represented.

DISTRIBUTION

For each separate population the percentage of Pm1 elements present in the skulls is given. The percentage distribution is given over five categories: no Pm1 elements present in the skulls, one Pm1 element present, two Pm1 elements present, three Pm1 elements present, a full set of four Pm1 elements present. The total percentage of Pm1 presence, like Heptner *et al.* (1974) and Lüps (1990) used, is also calculated.

All the skulls with two Pm1 elements were further separated in three categories: (1) both elements in the upper jaw, (2) both in the lower jaw , (3) unevenly distributed in the upper and lower jaw. This was done to see if the populations have a higher tendency to have elements in the lower jaw and if they are symmetrically distributed in the left and right plane of the skull.

STATISTICS

The T-test for statistical diffences was used on the data gathered from the subset of 50 skulls to see if animals with Pm1 elements differ in these measures from animals without Pm1 elements or a lower number of Pm1 elements.

The upper and lower jaw were analysed separately. For the upper jaw the skulls were subdivided into two groups: a group with no Pm1 elements in their upper jaw and a group with one or two elements in their upper jaw. For the lower jaw the skulls were subdivided into: a group with zero or one Pm1 element and a group with both elements present. The different grouping criteria, between the analyses on the upper and lower jaw, was used to make the two groups compairable in sample size. The T-test was used to check whether the two groups differed in regard too:

- the distance between Pm2 and the canine in the upper jaw
- the distance between Pm2 and the canine in the lower jaw
- length of their lower jaw divided by the total condylobasal length

The 50 skulls were also grouped into males and females to look at differences between the sexes regarding the variables mentioned above. The total group of skulls was separated into males and females as well to look at differences in number of Pm1 presence between the sexes. The T-tests were done for the upper jaw, lower jaw and both jaws together. The same analyses was done on a subset of the skulls which came from one single population in the south of the Netherlands.

RESULTS

DIFFERENCES BETWEEN POPULATIONS

To see if the populations differ in regard to their Pm1 distribution, the data is given for each population separately. The results are presented in Table 1. If possible, the populations have been subdivided into males (M) and females (F). The skulls from the area around Langon (France) were all of unknown sex. Table 1 shows the Pm1 presence distribution, in percentage, for each population, over the five categories from "none" (no Pm1 elements present in the skulls) to "4" (a full set of four Pm1 elements present). The total percentage at the bottom of the table gives the total Pm1 presence percentage for a population (see Heptner *et al.*(1974) and Lüps (1990)). This total percentage is given for males and females combined.

All the skulls with two Pm1 elements were further separated in three categories: both elements in the upper jaw (category "upper jaw"), both in the lower jaw (category "lower jaw") or unevenly distributed in the upper and lower jaw (category "rest"). The results are shown in Table 2.

DIFFERENCES BETWEEN BADGERS WITH DIFFERENT NUMBERS OF PM1 ELEMENTS

This section containes the data on differences between the skulls with Pm1 elements present and those without or a lower number of Pm1 elements present. Table 3 gives the data for the upper jaw and Table 4 gives the data for the lower jaw.

DIFFERENCES BETWEEN SKULLS FROM MALES AND FEMALES

This section deals with the differences between males and females regarding Pm1 presence. The same variables were used as in Tables 3 and 4 only now the differences between the sexes was tested. Table 5 shows the results.

Table 6 presents the average number of Pm1 elements present in the upper, lower and both jaws for males and females, together with the significance level. This analysis was done for all the skulls that were examined.

The same information as in Table 6 is given in Table 7 only for the population from the south of the Netherlands to see if a difference could be found within one single population.

Because of uncertainty about the parametric nature of the data concerning Pm1 numbers, the same data set, as shown in Tables 5 and 6, was tested with the Wilcoxon non-parametric test as well. The results were the same as shown in Tables 5 and 6, only the significance levels for Table 5 were far lower (<0.0001) and for Table 6 they were around the same level.

DISCUSSION

GEOGRAPHIC VARIATION

The geographic variation in teeth number, that caused the confusion in the dental formula of the badger, is certainly present in this study. The skulls, that originate from different locations, have different numbers of first premolars. Variation in Pm1 distribution could be an indicator of populations getting isolated from each other. A map of Eurasia that shows the differences between populations might indicate certain areas with different Pm1 distribution.

Heptner *et al.* (1974) and Lüps (1990) reported percentage data on presence of first premolars. This is helpful to show the difference between badgers from the far east (Siberia, China), having no or very few first premolars and the western badgers having a relative high number of first premolars. The badgers in between these two groups seem to take a middle position.

For easy interpretation, it is advantageous that premolar numbers are shown in a single digit. Fig. 1 gives the same data as given in Table 1 at the bottom (the total percentage). The data is pooled for males and females to make the data comparable with the data from Heptner *et al.* (1974) and Lüps (1990).

Fig. 1 shows that the Western European badgers do not differ that much in percentages of

Table 1. The distribution of Pm1 elements in the different populations that were studied.

	all skulls together		Netherlands (South)		Netherlands middle		France (Nantes reg.)		France (Langon reg.)
	F (n=117)	M (n=110)	F (n=93)	M (n=81)	F (n=12)	M (n=8)	F (n=4)	M (n=10)	F/M (n=20)
none	28%	10%	27%	12%	42%	0%	25%	0%	10%
1	12%	15%	10%	15%	17%	13%	0%	0%	5%
2	33%	38%	38%	42%	42%	75%	0%	0%	25%
3	9%	13%	9%	12%	0%	13%	0%	10%	10%
4	17%	24%	17%	19%	0%	0%	75%	90%	45%
	tot. percentage=50%		tot. percentage=48%		tot. percentage=35%		tot. percentage=91%		tot. percentage=66%

Table 2. The distribution of Pm1 elements in the upper and lower jaw for skulls with two Pm1 elements.

	all skulls together		Netherlands (South)		Netherlands middle		France (Nantes reg.)		France (Langon reg.)
	F (n=39)	M (n=42)	F (n=35)	M (n=34)	F (n=5)	M (n=6)	F (n=0)	M (n=0)	F/M (n=5)
Upper jaw	8%	10%	11%	12%	-	-	-	-	-
Lower jaw	79%	76%	71%	71%	100%	100%	-	-	100%
rest	13%	14%	18%	17%	-	-	-	-	-

Table 3. Differences between badger skulls with no Pm1 element in their upper jaw and the badger skulls with one or two Pm1 elements in their upper jaw. The measures used are: the distance between the canine and Pm2 and the length of the lower jaw divided by the condylobasal length (significance 0.05).

	0 Pm1	1 or 2 Pm1	significance
distance Pm2-canine	1,37	1,64	0,0139
condylobasal/lower jaw	1,45	1,46	0,2013

Table 4. Differences between badger skulls with zero or one Pm1 element in their lower jaw and the badger skulls with both Pm1 elements in their lower jaw. The measures used are: the distance between the canine and Pm2 and the length of the lower jaw divided by the condylobasal length (significance 0.05).

	0 or 1 Pm1	2 Pm1	significance
distance Pm2-canine	2,36	2,75	0,0170
condylobasal/lower jaw	1,45	1,46	0,1310

Table 5. The difference between males and females in: distance between Pm2 and the canine for the upper jaw, distance between Pm2 and the canine for the lower jaw, length of the lower jaw and lower jaw divided by the total condylobasal length (significance 0.05).

	Males	Females	significance
distance Pm2-canine upper jaw	1,320	1,550	0,0690
distance Pm2-canine lower jaw	2,580	2,580	0,4911
length lower jaw	89	91	0,0176
condylobasal/length lower jaw	1,476	1,453	0,0135

Table 6. The difference between males and females in the average number of Pm1 elements present, in the upper jaw, the lower jaw and both jaws together. All skulls that were examined are included (significance 0.05).

	M (n=110)	F (n=117)	significance
upper jaw	0,815	0,570	0,0232
lower jaw	1,445	1,186	0,0223
both jaws	2,245	1,752	0,0059

Table 7. The difference between males and females in the average number of Pm1 elements present, in the upper jaw, the lower jaw and both jaws togehter. Only the skulls from the south of the Netherlands were used (significance 0.05).

	M (n=76)	F (n=85)	significance
upper jaw	0,753	0,615	0,2781
lower jaw	1,383	1,191	0,1439
both jaws	2,099	1,796	0,1319

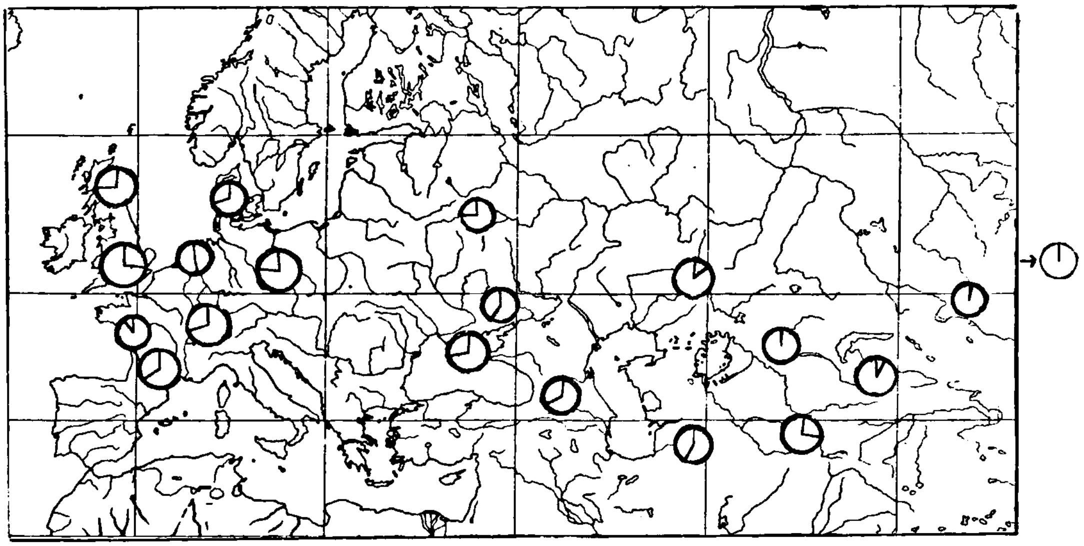

Fig. 1. The percentage of the first premolar presence in the different badger populations.
Scotland (Argyll) (from Ratcliff, 1970), Britain (from Hancox, 1988), Denmark (from Lüps, 1990), Netherlands (present study), France (Nantes) (present study), France (Langon) (present study), Switzerland (from Lüps, 1990), East Germany (Hakel) (Stubbe, 1980), middle Russia, south Russia, Caucasus, Crimea, Turkmenistan, Pamir, south Ural, Siberian Altai, Kazakhstan, Tien Shan, Ussuri (right next to map) (from Heptner *et al.*, 1974).

first premolar presence. Only the population from the Netherlands and the population from Britain seem to have less first premolar elements than other populations. The small sample from Scotland (Ratcliffe, 1970) indicates the "normal" Western European norm of somewhere around 75% presence. If first premolar presence is going to be useful in population studies in Western Europe, less data reduction needs to be done.

Fig. 1 shows that there are geographic differences in presence of Pm1 elements between the different populations. Table 1 shows that the distribution in number of Pm1 elements (five categories from zero to four) is even more distinct between populations. Several other authors have published data on the distribution of Pm1 elements as well.

Fig. 2 shows the data of table 1 together with data found in literature. Fig. 2 clearly shows that there are differences between the populations. Some populations have a rather low sample size (middle of the Netherlands and France (Nantes)). It cannot be concluded for example that badgers from the middle of the Netherlands differ significantly from the badgers of the south of the Netherlands, allthough the figure would suggest this. The fact that males and females differ much in the middle of the Netherlands is probably an artefact as well. If males and females differ significantly in number of Pm1 elements it does not necessarily have to mean that they have totally different distribution patterns.

The data from the south of the Netherlands (the area in the Netherlands below the large rivers) indicates that the badgers start loosing their upper Pm1 elements. 71% of all the badgers with two Pm1 elements had them in their lower jaw (Table 2). Of the badgers with only one Pm1 element, 81% had their element in the lower jaw (males and females pooled together). Of the badgers with three Pm1 elements, 83% had the missing Pm1 element in the upper jaw. The distribution in Fig. 2 also show that two premolars seems to be the norm in the Netherlands. The population in the Netherlands seems to have

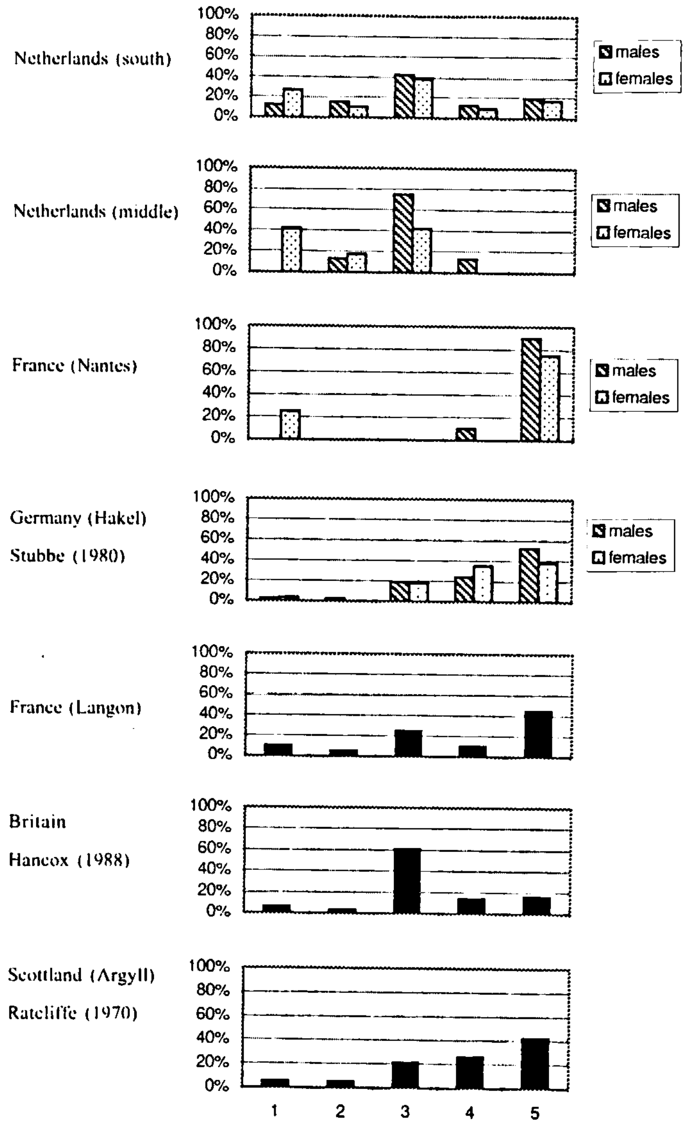

Fig. 2. The distribution from zero Pm1 elements to four Pm1 elements for the different populations. The Y-axis shows the percentage of the total population having no, one, two, three or four Pm1 elements.

a tendency towards symetric first premolar distribution. The number of skulls with one or three Pm1 elements is lower than the other categories and as said before the skulls with two Pm1 elements only had 18% assymetry (table 2 category "rest").

The British population (Hancox, 1988) seems to have a more pronounced norm of two Pm1 elements. A pronounced peak in distribution could be a sign of inbreeding or that the population went through a bottleneck (Newman, 1994). Hancox reports that 57% of the skulls with two Pm1 elements had the elements in their lower jaw. This percentage is lower than the number from the Netherlands. It is unclear if the Hancox data covers Great Britain as a whole or just England. The area that the Hancox data covers is perhaps too large to give single population data. The small sample from Argyll, Scotland (Ratcliffe, 1970) suggests that their is variation within the British populations.

The distribution data of Pm1 elements that Stubbe (1980) presents from Hakel (East Germany) shows that four Pm1 elements is more or less the norm. The numbers slowly go down because the numbers of skulls with three Pm1 elements is second in distribution importance and the ones with two Pm1 elements, third. There is a higher tendency in these badgers as well to loose Pm1 elements from their upper jaw. Of all the skulls with three Pm1 elements, 82% lost an element in the upper jaw. Of all the skulls with two Pm1 elements, 63% had both elements in the lower jaw. The one skull with only one element had the element in the lower jaw. Differences between males and females are not significant in this population allthough males on average have a higher number of Pm1 elements.

Though very interesting, the number of skulls from Sweden, Denmark and the Island of Crete was too small to be used in our present study.

FACTORS INVOLVED IN THE DIFFERENCES IN PM1 PRESENCE

Badgers belong to the family of the Mustelidae, the evolution of this group seems to be characterized by shortening of the jaw. The younger members of this family, like Polecats (*Mustela putorius*) and Stoats (*Mustela erminea*), have relative short jaws and no Pm1 element at all. The reduction in size of the first premolar to a non-functional element in badgers is probably due to this shortening of the jaw compaired to ancestral groups. Shortening of the jaw within present day badger populations is apparently not responsible for further reduction of Pm1 numbers, since there is no difference in lenght of jaw between badgers having Pm1 elements and badgers without Pm1 elements. Only the actual room for Pm1 seemed to give significant results.

The T-tests that were done on the subset of 50 skulls indicate differences in measurements between badgers that have first premolars and badgers that have not got first premolars (or at least a lower number of first premolars than the first group). The differences are in concordance with most of the findings by Lüps (1990).

The skulls from badgers with a relatively large number of Pm1 elements seem to have more space between their Pm2 and the canine, then badgers with less Pm1 elements or no Pm1 elements at all. There is no difference in jaw length between the two groups. One can conclude from this that the amount of space for a Pm1 element to develop is mostly regulated by the direct space (distance between Pm2 and the canine) that is available for a Pm1 to develop and not by the total amount of space present in the jaw. This leads to the conclusion that the size of functional teeth is the most important factor in the proces of the reduction of the number of Pm1 elements just like the data that Lüps presented suggest. The increase of size of functional teeth (the three functional premolars or the molar itself) have led to the reduction of Pm1 in the evolution of the badger (hypotheses number 3 in the introduction).

Lüps (1990) reported no differences between males and females, females tended to have more Pm1 elements than males but this difference did not reach any level of significance. This study however suggests otherwise, as males were found to have a higher number of Pm1 elements and the difference is significant when the entire dataset is used. The difference is not significant for the one population of badgers coming from the south of the Netherlands but the trend points in the same direction. The data that Stubbe (1980) presents for East German badgers points in the same direction. More populations need to be studied to see if the two sexes differ in the number of Pm1 elements.

The difference is not significant but there is a strong trend for males to have less space, between their upper Pm2 and the canine, than females. This combined with the fact that males might have a higher tendency to develop Pm1 elements might suggest that there is some genetic component to the development of the Pm1 element itself, which shows a higher expression in males. Males seem to have smaller jaws as well, relative and in actual length. More populations, with high numbers of skulls of known sex, need to be examined in order to clarify this issue.

It has to be noted that there was a large difference in the size of Pm1 elements and that upper jaws sometimes had extremely small elements which were almost attachted to the canine.

Since the data are simply quantified in presence/absence, further research could show if this possible higher tendency of Pm1 expression in males is related to these small elements.

CONCLUSION

The non-functional nature of the Pm1 element makes it a perfect characteristic to study differences in populations and to answer questions about sub-speciation between badger populations. The percentage method used by Heptner *et al.* (1974) and Lüps (1990) might not be that suitable to look at differences between the western populations. The badgers do not seem to vary that much in western Europe. The badgers from the Netherlands and from Great Britain seem to have a far lower number of Pm1 elements but the rest of the group seems to be around 75% presence (+/- 5%). Still some authors claim that several sub-species exist within the western range, for example *Meles meles danicus* Holten, 1935. The Danish badger does not show a marked difference in Pm1 percentage. Lüps (1990) mentions that 70% of all the Danish skulls that were studied contained four Pm1 elements which is much higher than the Hakel distribution that Stubbe (1980) presented which only had 52% (males) of the population with four Pm1 elements. The badgers from the Netherlands have never been ascribed as a separate subspecies but the deviation from the mainland norm of 75% warrants further investigation. The bottleneck effect, that was mentioned before, could be the cause of the reduction of Pm1 elements in the population in the Netherlands.

One should not think that the Pm1 element can answer all the questions about sub-speciation but it is certainly a good tool to look at differences.

It is to be hoped that a study like this will be done on Mediterranean badgers because there is no information at all from this part of the range. More populations need to be studied with large numbers of skulls. It would also be useful that information is separated between sexes because some of the data suggests that some differences might exist.

ACKNOWLEDGEMENTS

The authors like to thank the following people for their kind help in providing access to some of the badger skulls used in this study: Dr C. Smeenk (National Natural History Museum at Leiden), Drs E. J.O. Kompanje (Rotterdam Nature Museum), Mr F. Chanudet and the management of the Muséum d'Histoire Naturelle at Nantes. The authors like to thank Mr. Matthew Prescott and Dr S. Broekhuizen for reviewing the article and giving useful comments.

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Received: 6 April 1998