SEX DIMORPHISM AND SIZE TRENDS IN THE CAVE BEAR, URSUS SPELAEUS ROSENMÜLLER AND HEINROTH

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INTRODUCTION

Almost since the first description of the cave bear as a separate species, many observations have been published on the extraordinary variation found in that species, and numerous explanations have been brought forward. For a historical account, the reader is referred to ERDBRINK (1953, pp. 473—482). In general, the following possibilities have been suggested:

(a) Purely individual variation (apparently first suggested by ROSEN-MÜLLER in 1804);

(b) Sexual dimorphism (ROSENMÜLLER, *op.cit.*; also many later authors, and notably KOBY, 1949).

(c) The existence of »dwarf» races (apparently first suggested by G. CUVIER in 1806, repeated in various forms by later authors, and including the concept of a »degeneration», developed by ABEL and his collaborators, especially in ABEL and KYRLE, 1931).

This is a problem which may be definitely illuminated only by means of careful quantitative analysis. Conflicting statements have been issued with such an emphasis that it is quite clear that subjective judgment must be more or less fallacious in this case. The biometric method does not wholly abolish the role of subjective judgment, but it certainly narrows down the range, within which such judgment must be executed, to a very great extent.

Not only the answers, but the questions asked, have often been wrong. To an important extent the conflict derives from confusion of concepts which are logically and biologically separate, and from the use of terms without clear definition of their meaning. The attempt in the present contribution is to show which questions should be asked, and to indicate the way in which answers may be obtained.

Sex dimorphism is mainly treated in the first part of this paper, and size trends in the second. The topics are, however, so closely interwoven that many problems, such as individual, spatial and temporal variation, are considered in both parts, though sometimes from different aspects.

MATERIAL AND METHODS

The study is mainly based on the following samples.

Ursus arctos L., recent. Collections from Finland and Sweden in the following institutions: Zoological and Anatomical Institutes of Helsingfors University, Finland; Zoological Institute of Uppsala University and Zoological Department of Naturhistoriska Riksmuseet in Stockholm, Sweden.

Ursus maritimus Phipps, recent. A collection from Greenland in the Zoological Museum, Copenhagen, Denmark.

Ursus spelaeus Rosenmüller and Heinroth, Pleistocene. (a) Collections from the Drachenhöhle at Mixnitz in Styria, Austria; from the Schreiberwand Cave of the Dachstein Massif, Austria; and from the Slouper Cave in Moravia, Czechoslovakia; all of these in the Paleontological Institute of Vienna University.

(b) The Nordmann collection from caves at Odessa and Nerubaj, Ukraine, Soviet Union, in the Geological Institute of Helsingfors University.

(c) A collection from the Trosketa Cave, Guipúzcoa, Spain, in the possession of Dr. M. CRUSAFONT PAIRÓ, Sabadell, Spain.

(d) Further data on the Slouper bear, and data on the bear from the cave of Sundwig in Westphalia, Germany, published by VON REICHENAU (1906).

(e) Data on *U. spelaeus hercynica* published by RODE (1935).

The size of these samples will appear from the tables and graphs. Some additional sources of data will be acknowledged in the text.

Mensuration was carried to .1 mm. for teeth and 1 mm. for the other skeletal dimensions treated in this paper. In calculation, secondary grouping was used, except for very small samples. The statistical handling of the data will be commented upon to some extent in the text, insofar as it goes beyond the basic procedures of calculating means, standard deviations, and coefficients of variation, explained in all elementary texts (the book most suitable to the paleontologist is, of course, SIMPSON and ROE, 1939).

SEX DIMORPHISM

DISCUSSION AND DEFINITION

RODE (1935), in a study of the covariation of crown length and crown width of the lower canines in cave bears and brown bears (see Rode's figs. 4 and 5), found bimodal frequency distributions in both recent and extinct populations, and concluded that this represented sexual dimorphism. More recently, KOBY (1949) made a study of 682 canines of cave bears (a much larger sample than that of Rode) and obtained, similarly, a bimodal frequency distribution for their widths, the modes occurring at about 16 mm. and 22 mm. respectively. Moreover, Koby studied material of recent *U. arctos*, which had been sexed on other criteria, and showed that the means for males and females differed in both populations considered (one sample from the

Pyrenees, and another from Central Europe, the latter, however, containing numerous zoo specimens). Analysis for significance of Koby's data shows the differences to be indubitably significant. ERDBRINK (1953), however, subjected the results to severe criticism. While admitting that the figures might indicate the existence of a »limited sexual dimorphism in separate (more or less isolated?) regions», he does not consider the result valid, apparently because Koby's samples represent temporally and spatially circumscribed populations[1]. Erdbrink refers to the works by MIDDENDORFF (1953) and SCHÄFF (1889), in which it was established that female bears may be as powerfully developed as male ones, even from the same geographic region, in the recent *U. arctos*[2].

The disagreement seems to me to have its source, partly in a conflicting use of the term »dimorphism», and partly in confusion of intergroup and intragroup variation. By dimorphism, ERDBRINK apparently understands a complete separation of the ranges of variation for both sexes, valid for the whole species and making it possible to determine the sex of a single specimen from any locality and any stratigraphic level. Significant as it might be, this definition appears to me, if not impracticable, at least impractical.

In the first place, it fails to discriminate between inter- and intrapopulation variation. Thus, in a species with wide geographic range, where local populations differ in average gross size — as is the case with the recent *U. arctos* — thorough sexual differences might exist in each single population, and yet they would be obliterated if the species as a whole were considered. The first prerequisite for any intelligent study of quantitative sex dimorphism must be the narrowing down of the sample so as to obtain a material representing a single population or a closely-knit structure of populations agreeing in average characters.

Even so the demand for complete dichotomy appears to be impractical. It would exclude most cases where males and females differ in average characters, even where this difference is quite pronounced. Thus we would face the necessity of creating a new term for the description of such phenomena. This would lead to unnecessary confusion, and it appears to me more practical to qualify the term »dimorphism» for such instances.

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[1] ERDBRINK also states that »everything depends on the number of measured specimens», but insofar as this might be interpreted as a reflection on the adequacy of KOBY's cave bear sample, I am bound to express emphatic disagreement. Koby's sample is more than adequate to establish a bimodal frequency distribution beyond doubt.

[2] MIDDENDORFF cites three instances in which one male and one female skull from the same region are of equal size. He gives no data on the canines. All of SCHÄFF's skulls are from a single territory, but the material is not sexed, and for most specimens data on canines are not given. Likewise, most of Middendorff's skulls are not sexed.

I propose the following definitions:

Quantitative sex dimorphism is shown to exist in a population when the means for fully developed males and females differ in a statistically significant way. The dimorphism is *partial* when the standard ranges[1] of males and females overlap, and *complete* when they do not.

DIMORPHISM IN THE LOWER CANINES

Mensuration.

The datum used is the width (transverse diameter) of the canine at the base of the enamel (table 1). This datum has the advantage of being more easily determined than the length (antero-posterior diameter), and may often be determined even on material in advanced stages of wear, as well as on some anlages. This same measurement was used, and recommended, by KOBY (1949).

Ursus arctos, *recent.*

Out of a sample of 55 adult specimens, on which this measurement could be taken, from Finland and Sweden, 9 were sexed males and 15 sexed females. The frequency distribution is given in fig. 1. The ranges of sexed males and females are shown to overlap; but the means are significantly different, the male canines averaging about 2.3 mm. broader than the female. Calculation shows that the odds against this difference being accidental are far more than a million to one, being thus vastly beyond the border of statistical significance. It must be considered a definitely proven fact that a partial sex dimorphism exists in the lower canines of the brown bear population in Fennoscandia.

What is the practical possibility of sexing unsexed material on this basis? In order to settle that question, we need a measure of the extent to which male and female individuals show overlap in the character mentioned. In the first place, we may desire a measure of the range of variation to be expected in both sexes. The observed range is a more or less meaningless datum in this respect, as in most others; the best approximation is the standard range of SIMPSON, measuring the expected range of variation in a »standard population» of 1000 individuals. It is

$$(1) \qquad S.R. = M \pm 3.24 \ \sigma$$

This formula gives a female standard range between 9.49 and 14.11 mm., and a male standard range between 10.86 and 17.42 mm. The overlap is about 3.25 mm.

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[1] SIMPSON, 1941; also discussed later on in the present paper.

This sounds discouraging; but now it should be remembered that most samples are far smaller than 1000 specimens, and consequently are very unlikely to show the extreme limits of variation. A more realistic and practical datum would give the amount of overlap in percentage of the sample; that is, how many per cent of the sample in hand may equally well represent either males or females.

Fortunately, the required figure may be fairly easily approximated to by means of a method the outlines of which are given by MAYR et al. (1953). It should be noted that the majority of specimens will cluster around the male and female means respectively, whereas the distal variants that form the »tails» of the two distributions are in minority. The procedure is to calculate a »coefficient of difference» (C.D.) according to the formula

$$(2) \qquad C.D. = \frac{M \male - M \female}{\sigma \male + \sigma \female}$$

In the present case, $M \male - M \female = 2.34$, and $\sigma \male + \sigma \female = 1.72$; consequently, C.D. $= 1.36$. The corresponding amount of joint overlap may be obtained through a simple calculation from any table giving areas of the normal curve, or from specially prepared tables (MAYR et al. give a table for a limited series of C.D. values). In the present case, the percentage of joint overlap is about 9; that is, in any sample of brown bears from Fennoscandia, about 9 per cent of the males will be indistinguishable from about 9 per cent of the females. In other words, 91 per cent of the males, and 91 per cent of the females may be sexed according to width of lower canines.
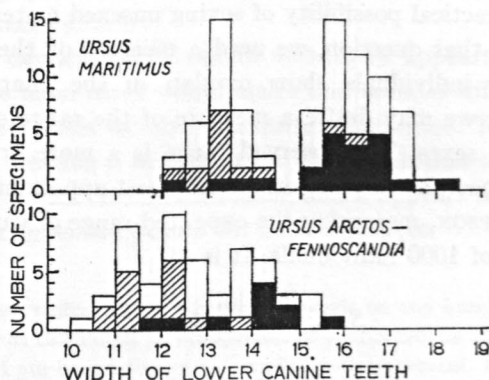

Fig. 1. Frequency distributions for width of lower canines in samples of recent *Ursus maritimus* from Greenland and recent *U. arctos* from Finland and Sweden, as labelled. Originally sexed specimens: cross-hatched, females; black, males. Some of the *U. maritimus* specimens can be shown almost surely to be wrongly sexed (see text, also p. 40). Original data.

The procedure, therefore, has certain limitations. It does suffice, if the object is, for instance, to determine the sex ratio in a sample. The nine-tenths of the population that may be sexed will give reliable enough values, and discrepancies such as an excess of either sex may be readily found and further evaluated by means of the special statistical methods available for such problems (which will be briefly indicated later on in this paper). It does not, on the other hand, suffice for exact calculations of means and dispersions in other characters. Tentative estimates of such parameters may be formed, but it will then be necessary to divide the unsexed portion of the sample *pro rata* among males and females. With the joint overlap being of such a magnitude as in the present case, the procedure is not recommended. It may however be noted that part of the indeterminate sample may be sexed by other methods, to be discussed later on. In the present case, however, I have used only the definitely sexed specimens for further calculation, because the samples are large enough for the purpose.

Ursus maritimus, *recent*[1].

Out of a sample of 89 specimens from Greenland, 35 were sexed, 13 females and 22 males. The ranges overlap, but the means differ with the highest order of significance. A partial sex dimorphism is certainly demonstrated.

When the unsexed specimens are included, the result is two separate distributions, each one of a normal type (fig. 1). A discrepancy is, however, noted in the distribution of a minority of the sexed individuals. Some very small specimens are labelled males, and two fairly large ones females. Some (though not all) of these are very far outside the standard ranges of distribution, and the chances are, hence, less than one in a thousand for their being correctly sexed. When the coefficients of variation are calculated with inclusion of the sexed specimens only, they rise to values not seen in other bear populations, and indicating almost certain heterogeneity. The discrepancy might, of course, result from sampling out of several populations differing slightly in modal size. This should, however, be reflected in a tendency to platykurtosis in the frequency distributions. No very marked tendency in that direction is found, and all the evidence thus indicates that most of the disputed specimens are wrongly sexed[2]. I include them, however, in the further analysis, with the exception of one juvenile specimen, labelled a male, but almost certainly a female.

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[1] ERDBRINK (op.cit.) has shown that *Thalarctos* and several other proposed genera of the Ursidae should be reduced to subgeneric status. This is a very welcome simplification of an unnecessarily top-heavy taxonomy, and I agree thoroughly with his procedure on most points.

[2] See also pp. 39—41.

TABLE 1.

Width of lower canines (at base of enamel) in bear populations, males and females separately.

		N	M	σ	S.R.
Ursus arctos, recent	♂	9	14.14 ± .34	1.01 ± .24	10.86—17.42
Fennoscandia	♀	15	11.80 ± .18	.71 ± .13	9.49—14.11
U. maritimus, recent	♀	56	16.05 ± .17	1.01 ± .10	12.76—19.34
Greenland	♀	32	13.37 ± .14	.82 ± .10	10.73—16.01
U. spelaeus, Pleistocene, ...	♂	8	18.58 ± .23	.65 ± .16	16.47—20.69
Dachstein	♀	9	14.09 ± .20	.61 ± .14	12.11—16.07
U. spelaeus, Pleistocene	♂	32	21.57 ± .18	1.02 ± .13	18.26—24.88
Odessa	♀	28	16.52 ± .18	.97 ± .13	13.39—19.65
U. spelaeus, Pleistocene	♂	160	21.84 ± .09	1.14 ± .06	18.15—25.53
Mixnitz	♀	124	16.75 ± .09	1.01 ± .06	13.48—20.02

N, number of specimens; M, mean; σ standard deviation; S.R., standard range of variation.

The standard ranges would overlap if the separate distributions were sexually homogeneous, and the dimorphism is certainly partial only. But the percentage of joint overlap, established in a similar way as described above for *U. arctos* (but in this case on the basis of the whole sample, unsexed specimens being sexed according to canine width), is much lower than in that latter case, being on the order of 2.2 per cent. Thus almost 98 per cent of a sample in hand may be sexed. The remaining fraction is so small that a distribution of these intermediate specimens *pro rata* in the male and female groups will have an exceedingly slight effect on the measures of central tendency and dispersion. Results based on such grouping will be valid in all essentials, and are used in this study; but the sexing has been checked from other criteria, to be discussed below.

These data for recent populations have certainly established a partial sex dimorphism in the size of the lower canine. In the fossil populations, distributions of precisely the type seen in the polar bear are encountered, as has already been shown by KOBY. My results are in perfect agreement with Koby's.

Ursus spelaeus, *Mixnitz.*

The distribution (fig. 2) is strongly bimodal. There are a number of intermediate specimens (in particular, the 6 between 19.0 and 19.4 mm. in width) which may be apportioned *pro rata* between the two distributions. The result is a grouping into 160 male and 124 female specimens with a highly significant
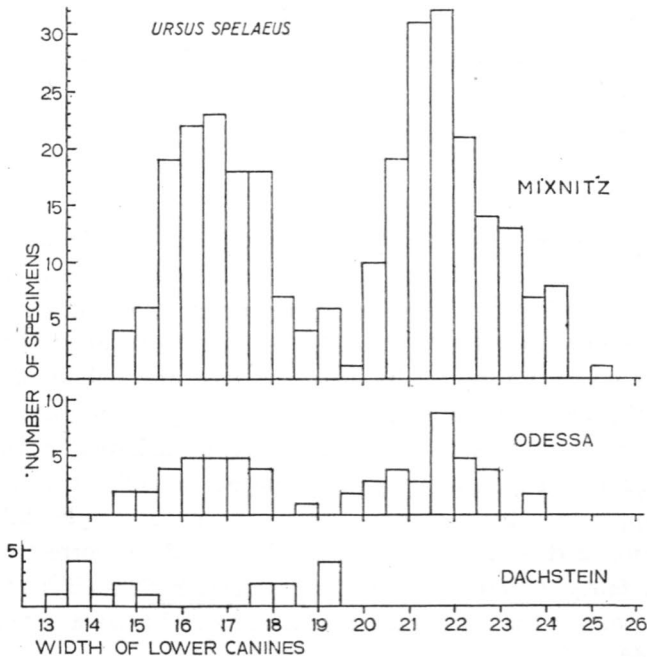
Fig. 2. Frequency distributions for width of lower canines in samples of Pleistocene *Ursus spelaeus* from Mixnitz, Odessa and Dachstein. Original data.

mean size difference of more than 5 mm. The standard ranges overlap to some extent, and the sex dimorphism is partial.

The coefficient of difference in this case is as high as 2.37, which corresponds to a joint overlap of less than 1 per cent. Thus more than 99 per cent of a sample of the Mixnitz population, or of a population with similar characters could be sexed on this basis. This agrees well with the actual number of intermediate specimens, which constitute about 2 per cent of the sample. The slight excess is accounted for by the grouping; moreover it lacks statistical significance.

The sexing was checked by other methods, discussed below, except, of course, in the case of isolated canines.

Ursus spelaeus, *Odessa.*

The data are somewhat fewer in this case (fig. 2), but the distributions show precisely the characters of the Mixnitz sample. The means and dispersions for the males and the females, respectively, are practically identical in both cases. In the present case, one specimen only takes an intermediate position, and in analogy with the Mixnitz sample, this one should be classed as a female. The dimorphism is partial.

The coefficient of difference is 2.54, and the corresponding joint overlap .5 per cent. Thus about 99.5 per cent of a sample from Odessa would be sexable on this basis. The figure is on the same order of magnitude as that for the Mixnitz bear.

Ursus spelaeus, *Dachstein.*

The small sample from the Schreiberwand Cave of Dachstein (fig. 2) shows completely disjunct distributions. In analogy with our previous results, these may be confidently classed as representing males and females. Standard ranges do not overlap; this would, then, be a population with complete sex dimorphism. But the difference between the upper limit of the female range, and the lower limit of the male range, is only .4 mm.; and in a sample of this relatively small size, this interval is overshadowed by the standard errors of the means and the standard ranges. Actually, the coefficient of variation appears to be spuriously low in the male sample (table 1). The standard error of this coefficient is rather high, and the correct value would probably be fairly similar to that for the females. Both coefficients are somewhat lower than in the cave bears from Mixnitz and Odessa, a feature which may be valid.

As the standard ranges do not overlap, it may be expected that the coefficient of difference will show less than .1 per cent joint overlap. In fact, it gives a value of less than .02 per cent. With more data in hand, this figure would probably be somewhat modified towards the datum given for the Odessa bear. At any rate it may be concluded that some 99 per cent, or more, of a sample from the Schreiberwand Cave may be confidently sexed.

Both males and females from Dachstein average much smaller than the corresponding samples from Mixnitz and Odessa. The differences are of indubitable significance throughout, and the Dachstein cave bear is certainly a representative of a »dwarf» population. This will be discussed in greater detail in the section on size trends.

UPPER CANINES

The results from a similar study of the upper canines are analogous in most respects, and it does not seem necessary to go into similar detail regarding them. Table 2 summarizes the main results, giving also the theoretical percentages of joint overlap.

It is clear that the upper canines show a somewhat greater joint overlap throughout, and thus are somewhat less reliable in sexing.[1] Only for *U. arctos*

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[1] Such was also the case with KOBY's cave bear sample.

TABLE 2.

Variation in sexed samples of fossil and recent bears, and percentage of joint overlap between sexes.

			N	M	σ	Joint overlap per cent
Ursus arctos,	Width C^s	♂	10	13.70 ± .27	.84 ± .19	} 8
recent		♀	15	11.67 ± .18	.69 ± .13	
Fennoscandia	Length M$_2$	♂	13	24.55 ± .39	1.39 ± .27	} 17
		♀	11	22.11 ± .36	1.18 ± .25	
	Skull, prosthion-	♂	9	292.6 ± 3.8	11.4 ± 2.7	} 4
	basion	♀	11	260.6 ± 2.4	8.0 ± 1.7	
U. maritimus,	Width C^s	♂	58	16.99 ± .14	1.08 ± .10	} 11
recent		♀	38	14.20 ± .20	1.16 ± .14	
Greenland	Length M$_2$	♂	54	20.76 ± .14	1.05 ± .10	} 23
		♀	39	19.29 ± .14	.86 ± .10	
	Skull, prosthion-	♂	34	350.4 ± 2.9	17.1 ± 2.1	} 4
	basion	♀	21	310.3 ± 3.0	13.9 ± 2.1	
U. spelaeus,	Width, C^s	♂	27	21.87 ± .25	1.32 ± .18	} 1.7
Pleistocene		♀	11	16.34 ± .39	1.28 ± .27	
Mixnitz	Length M$_2$	♂	79	32.44 ± .12	1.09 ± .09	} 13
		♀	52	29.85 ± .16	1.18 ± .12	
	Skull, prosthion-	♂	27	435.1 ± 3.4	17.4 ± 2.4	} 7 ½
	basion	♀	11	377.9 ± 6.7	22.1 ± 4.7	
	Jaw, C-condyle	♂	33	326.8 ± 2.3	12.9 ± 1.6	} 2.2
		♀	21	280.1 ± 2.2	10.2 ± 1.6	
— Odessa	Jaw, C-condyle	♂	5	321.4 ± 1.9	4.2 ± 1.3	} .3
		♀	3	280.0 ± 6.2	10.8 ± 4.4	
— Dachstein	Length M$_2$	♂	4	30.08 ± .50	.99 ± .35	} 2.9
		♀	6	26.28 ± .42	1.02 ± .29	

are the percentages of joint overlap equal for upper and lower canines. The joint overlap in the upper canines seems to be wider in *U. maritimus* than in *U. arctos*, an impression that may be spurious, because the data are of the same order of magnitude. It is much lower in the cave bear from Mixnitz than in any of the recent forms, in analogy with our previous result regarding the lower canines.

LOWER SECOND MOLAR

The joint overlap of the cheek teeth (as exemplified by the M$_2$; table 2) is much higher than that of the canines. It is clear that the cheek teeth pro-

vide a relatively poor basis for sexing; yet there is a significant dimorphism in every sample of sufficient size that I have studied (table 2 and unpublished; see also fig. 3). The cheek teeth may give some clues in the sexing of specimens indeterminate from the size of the canine teeth, but this possibility is restricted to some extent by the fact that canines and cheek teeth are generally correlated in size (KURTÉN, 1953, p. 23), and thus intermediate canines are quite likely to be associated with intermediate cheek teeth.

It has been claimed that slender cheek teeth are generally female, and thick-set cheek teeth male (see EHRENBERG, 1935 a). This is not necessarily true, though it may be so in some instances. In M^1, width is positively allometric to length (unpublished data), and thus smaller teeth tend to be somewhat more slender, in relation to length, than larger teeth. The allometric correlation is not absolute, and so the proportions of this molar cannot give important evidence. In some other teeth, width is isometric to length, and here the relative robustness has apparently no significance for sexing at all. In the hyaenid species *Ictitherium hyaenoides* Zdansky, the width of the lower fourth premolar is negatively allometric to length, and the allometry is quite strong (KURTEN, 1954). If there is a sexual dimorphism in this species (which is not unlikely), the males would be characterized, on an average, by relatively more slender P_4.

LENGTH OF LOWER JAW

The length of the lower jaw was measured from the anterior border of the canine alveolus to the midpoint of the hind border of the condyle. Only adult jaws were used, i.e. specimens with teeth in permanent position and somewhat worn. Data for *U. spelaeus* from Odessa and Mixnitz are given in table 2.

The dimorphism is rather strong, though partial, and the overlap is slight. This is especially true for the Odessa sample, but here the number of individuals is so low that the percentage figure may be spurious. This is certainly indicated by the extremely low coefficient of variation for the male jaws. Coefficients under 3 do not appear to be reliable for bear material, and it is probable that the sample does not give valid indication of the amount of variation actually present in the population. This is borne out by a comparison with the figure for the females, which is comparable with those found in the Mixnitz sample.

The correlation between jaw and canine size is weak; hence the size of the adult jaw is a valuable character for sexing specimens indeterminate on the score of the canines.

Sexing in practice

The first prerequisite for sexing of a specimen is that we have access to the population background, i.e. that a sample including both sexes, and preferably several representatives of each, is present. As we have seen, the modal size of cave bears may be different in different populations (more data on this subject will be presented in the section on size trends), and a single specimen from any locality may be completely indeterminate as to sex, unless it corresponds to the male series in the large, »normal» form; in that latter case it may, with little hesitation, be classed a male.

The sexing should begin with the canines, which show the strongest dimorphism in the dentition. If there remain specimens indeterminate on this score, isolated canines may be distributed *pro rata* (if the percentage is very small), but specimens showing other characters besides canine size may be studied further. If the size of the skull or mandible is ascertainable, such data are preferable for further determination, because these characters are weakly correlated with canine size; hence intermediate canines will very rarely be associated with intermediate adult skulls or jaws. Regarding juveniles, or damaged specimens that do not show jaw or skull length, clues may be found in the incisors or cheek teeth. The length of the diastem might be a useful character, but I have not compiled any data on it.

If any fraction remains indeterminate after the application of these methods, the specimens in question should be distributed *pro rata* if the aim is to establish parameters of central tendency and dispersion, or be left out totally, if the sex ratio is the object of inquiry. If the fraction is large, as is quite likely for *U. arctos* and smaller forms, the results may be valid for establishing sex ratios, but not for the study of means and dispersions.

Reliability of the method

Strictly said, the reliability of the method is a topic outside the scope of this paper, because it would involve the reliability of the application of statistical methods and concepts to organisms. It has been shown that, in most cases where large-sized forms such as cave bears are involved, application of quantitative method may lead to positive results for upwards of 99 per cent of a sample, or more. In some instances (well preserved material) the collateral study of several variates may increase this percentage so as to include virtually the whole sample. Thus the fraction on which subjective judgment must be executed may be narrowed down to such an extent that its further handling will have no particular significance for the results. Equally important, the *limitations* of the method are clearly indicated, and thereby also the type of problem that may be solved.

It might be objected that measurements cannot be taken with the necessary precision. This is, however, not true. In the case of the canine width, for instance, I have used .5 mm. groups; the original measurements were taken to .1 mm., and the variates are clearcut and easily measured, so that the error can under no circumstances, except for gross carelessness, exceed the group limit.

It might, perhaps, be further objected that the method is laborious. There is little basis for that objection, except insofar as the passing of subjective judgment is easier than the making of a detailed inquiry. The scientific study of a material always includes — or should include — the taking of a number of routine measurements; and with the help of a biometry text, a simple statistical evaluation of the data can be performed in little time. The precision in expression and conclusions thereby permitted is a gain which far outweighs the labour.

SEX RATIOS

The significance of the sex ratios found in the samples under discussion is easily evaluated by means of standard statistical procedures. Thus, for instance, the sexed recent specimens of *U. arctos* in my sample from Finland and Sweden comprise 9 males and 15 females. The ratio is 37.5 per cent males and 62.5 per cent females. Is this deviation from the expected ratio (which is, of course, 50—50) significant? The deviation (d) is 12.5 per cent. The standard error of the deviation is

$$\text{(3)} \qquad \sigma_d = \sqrt{\frac{pq}{n}}$$

where p and q are the expected percentages (50 and 50) and n the size of the sample, 24 in the present case. σ_d is 10.2 and $d/\sigma_d = 1.23$, a figure corresponding to a probability value of about .2, as will be found on consulting a table giving corresponding values of d/σ_d and P. The deviation has no significance, and there is no evidence for a preponderance of females in the Fennoscandian population.

A similar study of the *U. maritimus* collection shows the excess of males to be of probable statistical significance. The probability that this deviation from the expected ratio is due to chances of collecting only are about 2 ½ per cent. Whether this represents an actual excess of males in the population, or whether it represents selection in killing (e.g. females being more shy or cautious), must remain an open question.

Of the total of upper and lower canines from Odessa, 69 could be sexed as males, and 79 as females. The difference is not significant.

Regarding the Mixnitz bear, BACHOFEN VON ECHT (in ABEL and KYRLE) called attention to the fact that the male canines were in considerable excess at certain levels, a result stressed by many later workers. Only a very limited part of the total amount of canines from Mixnitz has been available to me. Bachofen von Echt states that the total number of canines that went through his hands exceeded ten thousand. It may probably be judged that the samples available to me — e.g. about 300 lower canines — represent a fairly unbiassed cross-section of that total. The sample is sufficient to establish the deviation from the expected ratio on a statistically wholly significant basis. The males are considerably in excess, the ratio being on the order of 160 males to 124 females; the odds for the deviation being accidental are one to a hundred.

The ratio is, of course, far from that given in various connexions for the uppermost levels of the Mixnitz series (3 : 1 or even 4 : 1), but the sample studied by me represents the whole series, and so the discrepancy would naturally be less pronounced. Unfortunately, the material is not thoroughly labelled, and so I find it impossible either to corroborate or reject the statement that the proportion of males increased from about 1 : 1 in the lower deposits to the high values mentioned in the upper strata. As far as it goes, the evidence in hand shows the discrepancy to exist, and there is little reason to doubt BACHOFEN VON ECHT's contention; most specimens show the sex character very clearly.

I have sexed 38 adult skulls, 27 of which are male and 11 female. The deviation is notable and of probable statistical significance $(P = .01)$.

In contrast, the large sample studied by KOBY shows a marked excess of females. According to Koby's own estimate, 281 specimens may be sexed as males, and 345 as females, the remainder being indeterminate. The excess of females is probably significant $(P = .01)$. The sample represents several different sites, and the sex ratios vary between the subsamples. If the intermediate 19-mm.-class (in which the frequency is always low) is left out, the subsamples show the following sex ratios.

Gondenans (Doubs, France): 201 males and 255 females, or about 1.3 females per male. The excess is probably significant $(P \backsim .01)$. Montolivot (Doubs): 18 males and 36 females, or 2 females per male; this excess is probably significant $(P = .014)$. Vaucluse (Doubs): 16 males and 28 females, or 1.75 females per male; the excess is not significant, though it may be valid. Saint-Bras (Jura of Berne): 21 males and 55 females, or 2.6 females per male — the strongest deviation in favour of females recorded, and on the highest order of significance $(P = .0001)$. Finally, a composite sample from many different sites shows the ratio of 25 males and 22 females; the slight preponderance of males has no significance.

2

For other caves, the following estimates may be cited. Hastière, Belgium (EHRENBERG, 1935 a): a ratio of 3 males per 2 females in a sample of 76 canines. The deviation, though quite likely valid, is of little statistical significance. Trou du Sureau, Belgium (EHRENBERG, 1935 b): 1.7 males per 1 female in a sample of 94 canines. The deviation is probably significant. Salzofen Cave, Austria (EHRENBERG, 1950): 2 males per female in a sample of 107 individuals (minimum estimate of number of individuals represented). The deviation is almost surely significant. A sample of normal-type *U. spelaeus* from many localities in Germany, Poland, Czechoslovakia, and Hungary, published by RODE (1935): 32 males and 49 females; the excess of females has little statistical significance $(P \sim .05)$ but may nevertheless be valid.

A splitting of the composite sample of RODE might show similar differences in sex ratios at different sites and levels.

As to the evaluation of these interesting data, it should be noted that there are several possibilities. They may actually reflect a disproportion between the sexes in the living population, a conclusion reached by ABEL (1929) and granted by several other authors, e.g., SOERGEL(1940). In my opinion, there is much to say for another possible conclusion, viz., that the disproportion may represent different ecological preferenda in both sexes; that is, that some caves — notably that of Mixnitz — might be suitable for the requirements of solitary males, but rejected by females, for some reason or other, whereas others might have been preferred by females with their young. The fact that this ratio may have changed in the Drachenhöhle would not be wholly inexplicable either; the cave itself evolved through time, and may have been more suitable for bear »family life» at an earlier stage. Juvenile remains appear, of course, to be numerous through the Mixnitz series, but the claim is not that the site was completely avoided.

On the whole, an ecological explanation seems to me somewhat more probable than the conclusion that the numbers represent actual excess in the population. A few cases are known, for instance in some shore birds, where the homogametic sex (males) is in excess; for instance in *Agelaius phoeniceus* (322 males and 98 females, according to McILHENNY, 1940). »Sex ratio» genes are known; but they reduce the number of the heterogametic sex. An excess of males in a mammal species would be difficult to understand on this basis[1].

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[1] See also KOBY, p. 687. His suggestion that the preponderance of males in the Mixnitz collection may be due to bias in sampling must, however, be rejected. The discrepancy is also found in the sex ratio of the skulls (and jaws), and surely a female cave bear skull or jaw is too large an object to be overlooked by a collector. The evidence from other sites strengthens the case; the conclusion that the sex ratio varied at different sites appears to me unavoidable.
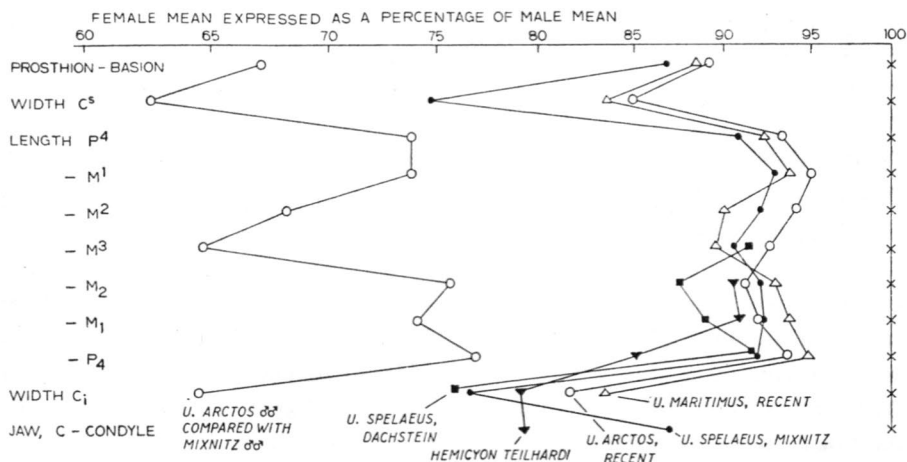
Fig. 3. Ratio diagram, showing sex dimorphism in dimensions of skull and dentitions in various bear populations. Standard (100 per cent), mean for males; mean for females expressed as a percentage of corresponding standard. Left, males of *Ursus arctos* (Recent, Fennoscandia) as compared with male cave bears from Mixnitz. Data on *Hemicyon teilhardi* from Colbert; other data original.

Some differences in mortality probably exist between the sexes in most or all mammals, but the tendency appears, in this case also, to favour the homo-gametic sex.

INTERSEXUAL VARIATION

The ratio diagram, fig. 3, indicates the pattern of intersexual variation in various ursid species, by showing the divergence of male and female means for various characters.

There is a basic similarity in the pattern of all populations: the dimorphism is strongest in the size of the canine teeth; next come the dimensions of the head, as expressed by skull length (prosthion to basion) or jaw length (canine to condyle); and last the cheek teeth, where the dimorphism is relatively weak. Some minor irregularities may be noted, but not all of them are signi-ficant, and they all concern details in the dimorphism of the cheek teeth.

The main difference between the cave bears and the recent species is that the dimorphism generally is stronger in the former. This holds especially for the canines, but also for most other characters. To avoid cluttering of the picture, I have not represented the Odessa population; it agrees, however, in all essentials with the two forms represented in the graph (Mixnitz and Dach-stein).

The usual impression of extreme variability in the cave bear appears to me to be determined, to a great extent, by this uncommonly strong sex di-morphism. Even if the intrasexual variation were slight, the pronounced

dichotomy between males and females would lead to a very broad range of size variation.

As a generalization it might be said that the dimorphism appears to become more accentuated with increasing size; it becomes relatively stronger in the series *U. arctos - maritimus - spelaeus*[1]. Exceptions occur for some details, and the dimorphism in the Dachstein bear is stronger than expected; in this latter case, however, the data are not very numerous.

It is interesting to note that a greatly similar dimorphism seems to have existed in such primitive bears, or dog-bears, as *Hemicyon* (exemplified by *H. teilhardi* Colbert). The data are from COLBERT (1939)[2]. They are not numerous (the sample contains two male and three female jaws, most of them fragmentary) but suffice to establish a basic similarity of pattern. The dimorphism in jaw length may appear spuriously great; actually the comparison is based on two specimens only, one male and one female.

The pattern of sex dimorphism may be compared with the deviation between two species. In the ratio diagram, I have represented *U. arctos* (means for male sample) as compared with *U. spelaeus* from Mixnitz (means for male sample). The difference greatly exceeds that between the sexes in any population, but otherwise the pattern shows somewhat similar features. Again, the greatest difference is seen in the size of the canine teeth; that in skull length is somewhat smaller; and that between the cheek teeth, smallest of all. There is, however, an exception in the hindmost molars of both upper and lower series; M^2 and M_3 are both much more elongated, relative to the other cheek teeth, in *U. spelaeus* than in *U. arctos*.

The presence of such marked dimorphism in large bears is of some importance in practical taxonomy. Single finds from different localities may belong to different sexes and thus tend to differ strongly in size, though belonging to one species or even one subspecies.

INTRASEXUAL VARIATION

In contrast with the strong sex dimorphism, the intrasexual variation in the cave bear is remarkably low. In view of the fact that so many students have stressed the »enormous variability» of the species, this result must be considered in some detail.

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[1] Dr. D. A. HOOIJER (*in verbis*) informs me that he finds a somewhat similar relation between dimorphism and gross size in some Primates.

[2] Colbert noted the great size differences and discussed the possibility of their being due to sex dimorphism, but pointed out that the circumstances of association of the finds made this somewhat improbable (odds eight to one against that interpretation). The evidence now available seems to back the interpretation to an extent that forces us to accept these odds, the statistical significance of which is slight enough to be overruled by the striking analogy with conditions in other bear populations.

TABLE 3.

Coefficients of variation for sexually homogeneous bear samples.

		Ursus spelaeus			U. arctos	U. maritimus
		Mixnitz	Odessa	Dachstein		
Length prosthion-basion	♂	4.00 ± .54			3.90 ± .92	4.87 ± .59
	♀	5.86 ± 1.25			3.07 ± .65	4.48 ± .69
Jaw, C — condyle	♂	3.96 ± .49	1.32 ± .42			
	♀	3.62 ± .56	3.86 ± 1.58			
Width, C^s	♂	6.05 ± .82			6.11 ± 1.37	6.32 ± .59
	♀	7.82 ± 1.67			5.94 ± 1.08	8.14 ± .76
Length, P^4	♂	5.76 ± .56			8.22 ± 1.94	4.38 ± .41
	♀	4.20 ± .58			4.21 ± 1.94	5.02 ± .55
Length, M^1	♂	5.12 ± .46			4.62 ± 1.09	4.75 ± .43
	♀	3.84 ± .56			4.24 ± 1.00	4.08 ± .43
Length, M^2	♂	4.76 ± .40			4.58 ± 1.08	7.40 ± .69
	♀	4.11 ± .58			5.62 ± 1.32	7.48 ± .82
Width, C_i	♂	5.95 ± .38	4.75 ± .59	3.51 ± .88	7.16 ± 1.69	6.32 ± .60
	♀	5.21 ± .29	5.85 ± .78	4.35 ± 1.02	6.03 ± 1.10	6.10 ± .76
Length, P_4	♂	6.66 ± .65	4.99 ± 1.33		6.99 ± 1.65	5.35 ± .51
	♀	5.91 ± .64	4.91 ± 1.31	6.73 ± 1.80	8.27 ± 1.95	3.77 ± .42
Length, M_1	♂	3.27 ± .28	4.15 ± .85		4.22 ± 1.06	4.90 ± .52
	♀	3.70 ± .41	4.37 ± .89	4.28 ± 1.01	3.38 ± 1.13	4.08 ± .46
Length, M_2	♂	3.36 ± .27	3.28 ± .70	3.30 ± 1.17	5.67 ± 1.11	5.06 ± .49
	♀	3.94 ± .39	4.79 ± 1.02	3.87 ± 1.12	5.32 ± 1.13	4.46 ± .50
Length, M_3	♂	6.53 ± .70	5.92 ± 1.48		5.60 ± 1.32	6.98 ± .68
	♀	6.93 ± .55	4.81 ± 1.13		6.55 ± 1.54	7.38 ± .89
Average, teeth ...		5.17	4.76	4.34	5.71	5.67

It will be shown later that interpopulation variation was considerable in the cave bear, populations at different sites differing more or less strongly in modal characters. But at any single locality, discounting the intersexual variation, the population appears to be remarkably homogeneous. The coefficients of variation for sexually homogeneous samples (table 3) show that the cave bear populations were actually less variable, in most characters, than the two recent populations with which they are compared. Yet the recent U. arctos population is certainly very homogeneous (the coefficients are based on the Finnish population only). The coefficients of variation have been averaged for dental dimensions; for both recent species, this average is on the order of 5.7; but all cave bear samples show lower averages. The differ-

ences, for any single character, are rarely of statistical significance; but the evidence is cumulative, and the conclusion that local cave bear populations were less variable than most recent populations, seems to be well founded.

The impression of unusual variability stems, in my opinion, partly from the sex dimorphism, and partly from the simple fact that these cave bear populations are represented by uncommonly large samples — in such, distal variants of course do turn up more frequently than in the relatively small recent samples usually available to the student. I have had the good fortune to have access to fairly large recent samples, and as could be expected, such distal variants did turn up in them as well.

It seems necessary to stress once more that conclusions on the basis of the observed range of variation of a quantitative character, unless by a student well versed in statistical concepts, will almost inevitably be wrong. This is also true for any transformation of the observed range, such as expressing it as a percentage of the mean (see criticism by Simpson, 1947 a).

On the whole, the coefficients of variation for these bear populations are not unusually high (almost all falling between the »normal» values 4 to 7), and the notion that bear populations are unusually variable in quantative characters must be rejected. To avoid misunderstanding, I wish to stress that this conclusion concerns the quantitative characters only. There can be no doubt that bears are very variable, perhaps even exceedingly so, in many morphological features such as cusp patterns and outlines of teeth. In some matters of covariation peculiar traits are shown especially by the cave bear, a feature to which I hope to return in another connexion.

Some trends in variability appear to recur in most or all of the samples. Thus the canine teeth tend, on an average, to be more variable in size than the cheek teeth. The difference is slight but may have some significance. It is interesting to note that the canines also show the greatest interspecific and intersexual variation. There is thus some suggestion that canine size may be positively allometric to the other characters considered here — a suggestion put forward by Rensch (1947) in an analogous case.

The variation in functionally relatively unimportant teeth seems generally to be somewhat higher than in others. For P_4, the coefficients are higher than average both in *U. spelaeus* and *U. arctos*, but not in *U. maritimus*; in the latter, more strictly carnivorous species, this tooth would appear to have greater functional importance. On the other hand, the M^2 and M_3 of the polar bear are exceptionally variable; both teeth, apparently, have lost much of their functional importance, and are quite clearly in the process of being reduced.

SIZE TRENDS

THE SUPPOSED DWARFING OF THE MIXNITZ BEAR

One spectacular result of great interest, brought forth by the studies of ABEL and his collaborators on the Mixnitz cave bear population, was the conclusion that a marked dwarfing had taken place during the final phase of the bear's existence at that site. The main basis for this conclusion is formed by the very thorough and careful study by MARINELLI (in ABEL and KYRLE) of the skull of the Mixnitz cave bear. The impression during collection was, as Professor EHRENBERG (*in verbis*) has kindly informed me, that the small skulls were generally found in the latest deposits of the cave bear strata.

The study of the sex dimorphism in the lower jaws of the Mixnitz bear (*vide supra*) appears to me to throw important light on the theory of dwarfing at this site. It was shown that the male and the female jaws form two very slightly overlapping series (the overlap being about 4 per cent for the adults). I have made a study of all the skull material available at the Paleontological Institute of Vienna University, which includes 38 fully adult skulls that could be sexed on the basis of the canine teeth, and on which the prosthion-basion length could be determined with sufficient accuracy. Of 5 other good skulls, 4 are probably male and 1 is probably female, but the canines are either lacking or badly damaged. There is also a number of fragmentary skulls, which may be sexed according to canine size, but where the length of the skull cannot be accurately determined.

The skulls sexed as females on the basis of the canine teeth are identical with those classed as »small skulls» by MARINELLI, and interpreted as »dwarfs» by ABEL, with the following exceptions: 3 of them are comparable with the smallest specimens of the »large skull» series, and one specimen, classed as a »small skull» by Marinelli, is actually a juvenile male (No. 90). The prosthion-basion length of this specimen is somewhat short of 400 mm.; this is in the upper part of the female series, and close to the lower limit of the observed range in the male series. Some sutures are beginning to close, others are open; there is little doubt that the skull would have grown into »normal» male size in maturity.

On the other hand, the skulls classed as male on this same basis, all belong to the »large» series of Marinelli (except the juvenile specimen mentioned above, which has not at all been included in my computations).

A minor part of the material studied by Marinelli was not accessible to me, being in the Museum at Graz.

Statistical data on skulls and jaws are given in table 2; the corresponding frequency distributions are shown in fig. 4.
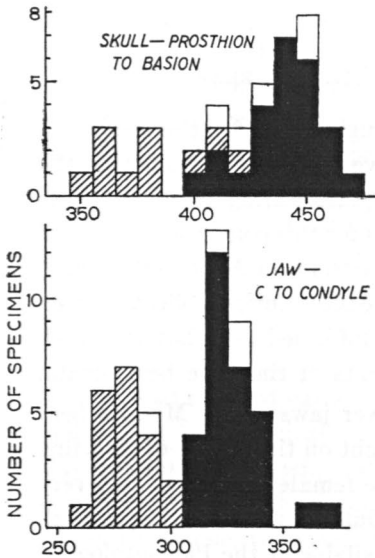
Fig. 4. Frequency distributions for lengths of skull and jaw, as labelled, of *Ursus spelaeus* from Mixnitz. Specimens sexed according to size of canines: cross-hatched, females; black, males. Original data.

It is of particular interest to note that the mean length of the lower jaws classed as females, in per cent of the mean length of the male ones, is the same as the corresponding figure for the prosthion-basion lengths, or 85.8 per cent for the jaws and 86.9 per cent for the skulls. The difference of 1.1 per cent has, of course, no significance. There can be no doubt that the »small» skulls were associated with the female jaws, and the »large» skulls with the male jaws. It is concluded that the former represent females, and the latter males.

Other large bears show quite similar relations. The cave bear from Odessa shows a sex dimorphism in the lower jaw which is equivalent to that of Mixnitz, the females averaging 87.1 per cent in length of the males. Only one Odessa skull permits determination of the prosthion-basion length; it agrees perfectly with the modal females in the Mixnitz series, and may also be unhesitatingly classed a female from canine size. The skull of the polar bear shows a similar dimorphism, the length of the females averaging 88.6 per cent of the length of the males. In *U. arctos* the corresponding figure is 89.1 per cent (Finnish population); in *Hemicyon teilhardi* (jaws) on the order of 80 per cent.

The skull and jaw length distributions are, within such limits as are set by the number of specimens, of a quite normal type in each case, including the Mixnitz samples (but not, of course, the *Hemicyon*, where only two good jaws are known). They give no evidence whatever for the supposition of heterogeneity within either sex sample.

The strongest argument against the contention that the small skulls *and* small jaws represent a dwarf variety or race is that the canine width distributions (where the material is fairly large) are of a quite normal type, too, and do not show any secondary dichotomy or tendency to multimodality. Such a tendency would necessarily have existed and been strong enough to be detected, at least in the form of skewing or other irregularities, unless there was a total lack of sex dimorphism in both the »normal» and the »dwarf» races. Such a lack would be improbable in the extreme, in view of the marked dimorphism shown to exist in all larger bears, including a true »dwarf» cave bear, that from Dachstein.

It has been supposed that the »dwarf» was characterized by less marked sex dimorphism, and that sexing would be more difficult than for the »normal» form. As the present results show, the only possibility would be that males and females of the dwarf race would be precisely similar in secondary sex characters, and moreover identical with the female of the normal form. Such a contention appears to me extremely far-fetched; there is no evidence in favour of it, and every other item of evidence appears to negate it.

The apparent preponderance of small skulls in the latest part of the Mixnitz cave bear sequence may conceivably be spurious, on account of the difficulties of correlation in a cave of the type of the Drachenhöhle. If valid, it would apparently denote a secondary »female optimum» in the ecological development of the cave.

In this connexion it may be mentioned that the Mixnitz series illustrates another trend — the evolution of the full-fledged cave bear from an ancestor much similar to the form described as *Ursus deningeri*[1] from the Middle Pleistocene deposits of Mosbach and Mauer by VON REICHENAU (1906). The single skull is from the basal part of the Mixnitz series and has been extensively described in the Mixnitz monograph. The size of the single extant, but badly mauled canine, is about intermediate between that of the typical males and females in later strata. The same holds for the length of the skull. These size features are associated with »arctoid» characters, such as flat profile of the skull, definitely noted at excavation (though this part was damaged in the process). The simultaneous presence of such a number of aberrant characters in the single representative of a population makes it most improbable that the specimen was drawn from the typical Mixnitz population. The specimen certainly represents a population of quite different modal characters[2]. It is more probable that it is a male of a smaller type of bear than a female of a gigantic bear form. Very likely it represents a population ancestral to the true cave bear, and illustrates the process of phyletic growth, the final stage of which appears in the true cave bear.

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[1] ERDBRINK (*op.cit.*) calls the true cave bear *Ursus spelaeus* Rosenmüller and Heinroth, and the large Pleistocene brown bears that approximated to the cave bear in size and other features, *U. arctos spelaeus* (Rosenmüller and Heinroth). This is of course not permissible under the rules of nomenclature, the latter designation being a homonym of the former. The type of *U. spelaeus* (from Gailenreuth) is a true cave bear, and the name is valid for that species only. The large brown bears in question are generally called *U. deningeri*. I agree with Erdbrink that they should be given subspecific status under *U. arctos*, and am going to use the name *deningeri* provisionally, recognizing, however, the possibility that some one out of the welter of earlier names bestowed on fossil bears may have priority.

[2] SPAHNI (1954), apparently, considers the specimen an *U. arctos*.

TABLE 4.

Percentages of joint overlap in dimensions of different local populations of *Ursus spelaeus.*

	Percentage of joint overlap between population from Dachstein and population from:				
	Mixnitz	Odessa	Trosketa	Sundwig	Slouper
Length P⁴	11	13	23	—	18
Length M¹	19	11	>25	—	18
Length M²	9	10	23	—	24
Width Ci ♂	3.5	3.6	—	—	—
— ♀...............	15	6	—	—	—
Length P₄	18	11	—	>25	17
Length M₁	20	18	>25	>25	>25
Length M₂	18	16	>25	>25	>25
Length M₃	16	10	>25	18	21

THE DACHSTEIN BEAR

The bear from the Schreiberwand Cave at Dachstein certainly represents a population differing strongly in modal size from the large cave bear of Mixnitz and Odessa. The differences in quantitative characters are of an order that sometimes exceeds the conventional limit of subspecific differentiation, as defined by Mayr et al. (1953). ahis limit is drawn at 10 per cent joint overlap in a dimension, which means that 90 per cent of a sample may be classified. The percentages of joint overlap are given in table 4; only for canines the material has been divided on the basis of sex.

However, the Dachstein population differs less strongly from other cave bear populations. Those from the Spanish Trosketa Cave, the German cave of Sundwig, the Salzofen cave (see SPAHNI, 1954) and other sites, and particularly the Einhornhöhle (RODE, 1935) exemplify bears of relatively small modal size; thus the Dachstein form does not stand isolated, though being among the smallest of them all (*hochalpine Kleinformen*; see EHRENBERG and SICKENBERG, 1929). The ratio diagram, fig. 5, shows how modal dimensions vary in different local populations. It also shows that the dimensions and general proportions of the Dachstein bear are very closely approximated to by those of the Einhornhöhle form, which was described as *Ursus spelaeus hercynica* by RODE (op.cit.).

From this, it would appear most probable that the Dachstein bear was not contemporary with the »normal» form of other sites, but that it belonged to the same population as the German *hercynica*. The high elevation of the site shows that this form lived during part of an interglacial or interstadial
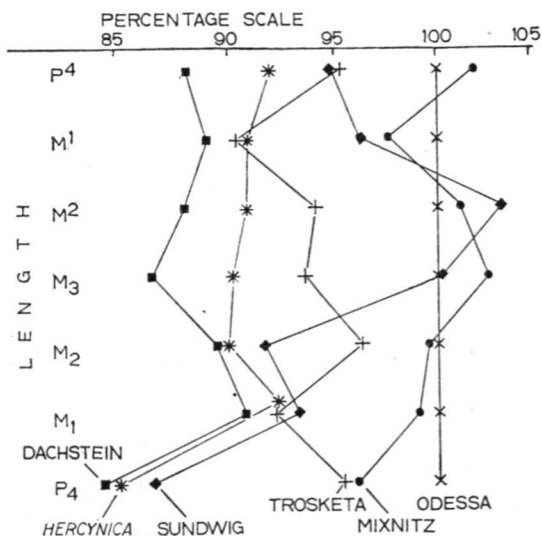
Fig. 5. Ratio diagram, comparing mean dental dimensions of cave bear demes from different sites, as labelled (both sexes combined). Standard (100 per cent), Odessa mean. Data on *U. spelaeus hercynica* (Einhornhöhle) from Rode (actually medians, not means); other data original and from von Reichenau.

spell; it is tempting to explain its small size in accordance with Bergmann's rule.

On the other hand, if these forms were contemporary and represent parts of a single widespread population, we might expect to find similar small cave bears at some sites in the interjacent lowlands as well. Dimensions vary, but no lowland cave bear is quite so small as these alpine forms — the Krasnodar bear, mentioned by SPAHNI in this connexion, is almost certainly not a true *U. spelaeus* (ERDBRINK, 1953). On the contrary, we seem to find a very close negative correlation between mean size and altitude (fig. 6), as regarding the Austrian cave bears at any rate. The problem, however, is apparently not quite so simple as suggested by this interrelationship; I shall return to it later on.

Most probably, the Dachstein bear and its allies are dwarfed true cave bears, and not primitively small forms. This appears from many considerations, among which may be mentioned the fact that the Dachstein bear shows the typical cave bear allometry in M^1, and only that (see KURTÉN, in press); the cave bear allometry should not be optimal for a bear of the average size of the Dachstein form, and its being retained most probably results from complete loss of genes present in populations ancestral to the cave bear.
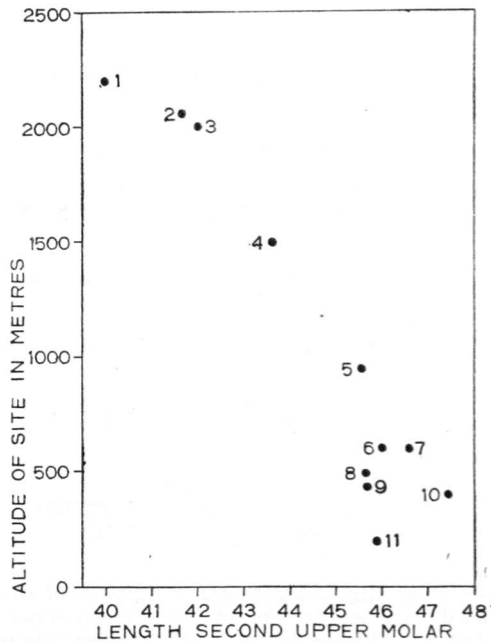
Fig. 6. Mean length of M² in cave bear samples, plotted against altitude of site. 1, Schreiber-wand Cave, Dachstein; 2, Salzofen, Bad Aussee; 3, Schottloch, Gosau; 4, Gamssulzen Cave, Windischgarten; 5, Drachenhöhle, Mixnitz; 6, Frauenloch, Stübing; 7, Tischofer Cave, Kufstein; 8, Badl Cave; 9, Merkenstein Cave, Vöslau; 10, Lettenmayr Cave, Krems-münster; 11, Winden Cave. Data from Spahni (1954).

INTERGROUP VARIATION AND SIZE GRADIENTS

Some features of intergroup variation were brought forth in the ratio diagram, fig. 5. It appears that different samples generally differ in absolute and relative lengths of the teeth, and in most cases it can be shown that the differences, small though they often are, are statistically significant. They are certainly not large enough to warrant subspecific splitting on a grand scale; the samples may be thought of as representing imperfectly isolated demes. The only form which may really merit subspecific distinction would seemingly be RODE's *U. spelaeus hercynica*, which probably should include the *hochalpine Kleinformen* of Austria.

Within most of the demes, the variation is quite low, indicating homogeneity of sample; but the presence of morphological gradients in space and/or time, during the existence of the species in Europe, is evident.

The question to what extent these gradients were spatial or temporal may, to some extent, be illuminated by means of a comparative study of gradients in the brown bear and cave bear populations. The *Ursus arctos* samples used

TABLE 5.

Length of second upper molar in one subfossil and seven recent samples of *Ursus arctos*.

	N	M	σ	V	S.R.
Subfossil, Denmark ...	9	38.24 ± .80	2.40 ± .57	6.27 ± 1.48	30.47—46.01
Recent, Norway	25	32.22 ± .46	2.29 ± .32	7.09 ± 1.00	24.82—39.62
Recent, Sweden	20	31.98 ± .42	1.86 ± .29	5.82 ± .92	25.95—38.01
Recent, Finland	44	31.93 ± .32	2.13 ± .23	6.68 ± .71	25.03—38.83
Recent, Fennoscandia .	89	32.00 ± .22	2.12 ± .16	6.63 ± .50	25.11—38.89
Recent, Central European U.S.S.R.	35	34.40 ± .36	2.12 ± .25	6.15 ± .74	27.54—41.26
Recent, Caucasus	5	32.10 ± 1.06	2.37 ± .75	7.40 ± 2.34	24.41—39.79
Recent, Okhotsk	7	36.50 ± .59	1.56 ± .42	4.27 ± 1.14	31.45—41.55

in this study are as follows: Recent: 44 Finnish and 20 Swedish specimens (original data); 25 Norwegian (data from DEGERBØL, 1933); 35 specimens from the central part of European U.S.S.R. (data from SCHÄFF, 1889); 5 from Caucasus and 7 from the territory around the Sea of Okhotsk (data from VON MIDDENDORFF, 1853); subfossil: 9 specimens from Denmark and 3 from Prussia (DEGERBØL, *op.cit.*). The variate selected is the length of the second upper molar. The statistics for these samples appear from table 5. As regarding the cave bear, I have used original data and the sources credited in the introduction, and, in addition, means for Austrian samples published by SPAHNI (1954).

Gradients in space.

The three Fennoscandian populations do not differ significantly in any parameter, and it may be concluded that the recent *U. arctos* populations of Norway, Sweden and Finland agree well as regarding the length of M². The sample from central U.S.S.R., on the other hand, shows greater mean dimensions; the difference is significant beyond doubt (d/σ_d being no less than 5.7). The Okhotsk form is still larger, and differs from the central U.S.S.R. form with high significance ($d/\sigma_d = 3.15$). Of course it is also significantly different from the Fennoscandian form ($d/\sigma_d = 7.4$). Finally, the Caucasian form is smaller than that from central U.S.S.R., the difference being probably significant ($d/\sigma_d = 2.05$), but agrees in size with the Fennoscandian bear.

These are samples out of an almost continuous population (breaks in the range are of very recent date), and thus permit some tentative conclusions on the size gradients within it. The clines are diagrammatically represented in fig. 7, the abscissa giving the approximate distances between the centres from which the samples were drawn, and the ordinate giving length (on a log scale). Naturally, the geographic distances must remain approximations only,
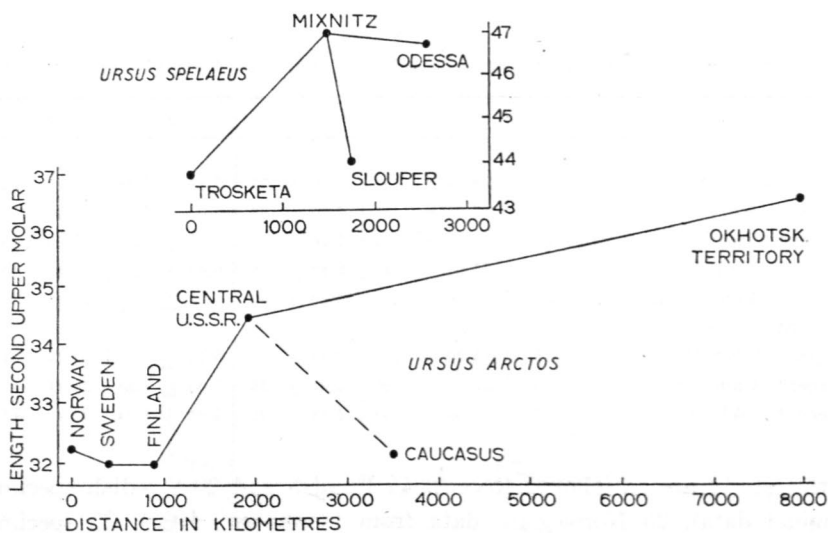
Fig. 7. Clines in bear populations. Bottom, geographic variation in length of M², recent *Ursus arctos*, showing west-east gradient (Norway to Okhotsk) and north-south gradient (Central European U.S.S.R. to Caucasus). Inserted, gradients for cave bear samples, showing steep cline between Mixnitz and Slouper caves; contemporaneity doubtful. Original data, partly (on *U. arctos*) from table 5.

since the precise geographic location of the centre of each sample is impossible to determine.

There is, apparently, no gradient at all through the Fennoscandian part of the range (the slight rise towards Norway cannot be shown to be significant). Between Finland and central European U.S.S.R., on the other hand, the gradient is very steep. It averages .24 mm. per 100 km., or .75 per cent change over that same distance. From central U.S.S.R. to the east, the gradient is much reduced, averaging only .035 mm., or .10 per cent, per 100 km. Of course a study of interjacent populations would give more detailed information; on the other hand it has been repeatedly stated that the largest brown bears occur in the Bering Straits region, and so it is probable that the peak of the cline would not occur west of Okhotsk (see also below, fig. 9). The data now in hand suggest that the main change in average size, in the northern part of the range of the species, occurs rather far to the west.

Proceeding southward from central European U.S.S.R. to Caucasus, we find another steep gradient, with an average change of .14 mm., or .44 per cent, per 100 km.; this gradient is comparable to the Russian-Fennoscandian.

These data may be compared with some estimates for the cave bear. If it is assumed that the populations of Mixnitz, Slouper, Odessa and Trosketa were roughly contemporaneous — which is, to be sure, a rather daring assumption — the following gradients are found (see fig. 7).

Mixnitz to Slouper: 1.2 mm., or 3 per cent, per 100 km.

Mixnitz to Odessa: .03 mm., or .05 per cent, per 100 km.

Mixnitz to Trosketa: .21 mm., or .5 per cent, per 100 km.

The gradient between Mixnitz and Slouper is steeper than any one found in the recent population. The terrain between the two sites is partly mountainous, and other data suggest rather limited migration in the cave bear population; thus such gradients might, possibly, be built up and maintained between contemporary demes. On the other hand, some interjacent populations (e.g., Vöslau and Winden, according to SPAHNI, 1954) show dimensions equalling or exceeding those of the Mixnitz bear.

Between Mixnitz and Trosketa the gradient is of the same order as those between central U.S.S.R. and Caucasus or Fennoscandia in the recent population, if the small bears from the Dachstein area are ignored; but a study of interjacent populations may give a different picture. Finally, no gradient at all appears between Mixnitz and Odessa, a feature which may be spurious.

Gradients in time.

The dwarfing of *U. arctos* in postglacial time is a well-known instance of a temporal size gradient. A comparison between the subfossil Danish sample and the recent Fennoscandian one shows a reduction in size of more than 16 per cent during a period on the order of 8000 years[1]. This gives a minimum average of about 2.0 per cent per 1000 years. In the terminology of HALDANE (1949), this is an evolutionary rate of 20 darwins; the corresponding value for some changes in horse dentitions are only 40 millidarwins (see below).

This dwarfing is apparently a result of adjustment to environmental change. But it is of such a magnitude and rapidity that it is unlikely to have occurred in a self-contained population. The change in mean is no less than 2.4 times the standard deviation of the subfossil population, and the joint overlap between the two populations is less than 9 per cent, a figure giving some indication of the necessary replenishing of genetic materials (even though the dwarfing to some extent might result from modification). It is, however, probable that part of the genetic material was supplied by gene flow from adjacent populations. A subfossil Prussian sample shows considerably smaller dimensions; the spatial gradient between this population and the Danish one would be on the order of 2.4 per cent per 100 km. The steepness of this gradient is probably somewhat in excess of what may be maintained in perfectly contemporaneous populations, and there is probably some difference in age, but at any rate it seems clear that there was a potentially available supply of genes in adjacent populations.

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[1] The subfossil finds span several thousand years, mainly from the Mullerup and Ertebölle periods; the average age should, however, be on the order of 8000 years.
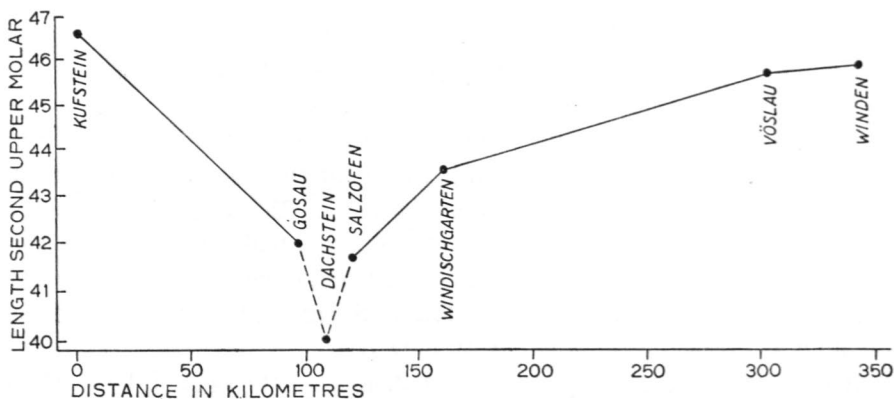
Fig. 8. Lengths of M^2 in Austrian cave bear samples, arranged on a west-east »pseudo-cline». The populations considered are almost certainly not all contemporary. Data on M^2 from Spahni (1954).

The difference between the *hochalpine Kleinform* of Dachstein and the »normal» cave bear is not so great as that between the Danish subfossil and the recent *U. arctos*. However, if we analyse the spatial gradients between the Dachstein dwarfs and the surrounding normal populations, we arrive at almost fantastic figures. Fig. 8 shows such a »cline» from west (Kufstein) to east (Winden) in Austria, based on SPAHNI's data. The gradient between the Tischofer Cave of Kufstein and the Schottloch at Gosau, for instance, would be on the order 4.4 mm., or almost 10 per cent, per 100 km. It seems to me very improbable that such an enormously steep gradient could have been maintained between contemporary populations. On the other hand, a dwarfing of this magnitude (a reduction of about 13 percent in the case of the Dachstein bear) is quite likely to have occurred in a geologically short time, especially if a part of the necessary variability was supplied by gene flow from other demes. In the unusually low coefficients of variation for the Dachstein bear (see table 3) we may possibly see an indication that the selection was actually severe and that the variation may not have been replenished to the rate that it was expended. On the other hand, the low variation may result from gene loss due to small size of population; thirdly, it may result from short duration in time, so that mean dimensions did not change perceptibly during deposition.

Notes on subspecies of Ursus arctos.

Though this analysis is not detailed enough to permit definite conclusions as to the subspecific differentiation within *U. arctos*, a brief discussion of its bearing on that question may be warranted, the topic having been approached from rather different points of view in recent years (e.g., ERDBRINK, 1953; COUTURIER, 1954). As ERDBRINK notes, the creation of subspecies, species and even genera of cave bears and brown bears has been the fashion for more

than a century. Most of them are, of course, a meaningless encumbrance to taxo-
nomy, and have no validity whatever. Erdbrink proposes to abolish them all,
thus lumping, for instance, all recent brown bears (and most fossil ones, except
his »*U. arctos spelaeus*») into a single subspecies; but I do not consider his
reasons for doing so more valid than the procedures of the earlier splitters[1].

Applying the joint overlap test to the recent populations, we find that
the Fennoscandian, Caucasian, and central U.S.S.R. populations all show
mutually more than 25 per cent joint overlap in the length of the second
upper molar, and thus are not entitled to subspecific distinction on this basis.
The two populations that differ most are those from Fennoscandia and the
Okhotsk territory. Here the percentage of joint overlap is about 11; or, in
other words, these two populations are on the verge of subspecific differentia-
tion, according to the test. Now, of course, this test is not a fiat, and was
not so intended by MAYR et al.; the decision must follow from other con-
siderations as well. One of these is the study of clines; the end points of a
cline may represent populations showing much less joint overlap, and yet not
entitled to subspecific distinction because no break or »step» in the gradient
indicates where the borderline should be drawn.

As far as the present incomplete data show, such a break or stepped-up
gradient occurs only between the central U.S.S.R. and the Fennoscandian
populations. If anywhere, the borderline between two subspecies should be
drawn here — in fact, in a place where such a boundary has not earlier been
placed even by some extreme splitters.

A body of quantitative data on the Old World *U. arctos* has been compiled
by COUTURIER (1954, pp. 295—321), mainly from works by OGNEV and
POCOCK. I have selected the total length of the skull (prosthion to opisthion)
in males[2]. The means were plotted at the approximate centre of distribution

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[1] For instance, ERDBRINK refuses the grizzly bear subspecific distinction, on the
grounds that isolated Old World specimens may show similar characters (light fur, large
size, white claws, etc.). This is another instance of his insistence on absolute dichotomy.
I do not have the data necessary for a full evaluation, but it seems highly probable that
the 90 per cent rule of MAYR et al. gives sufficient reason for considering the grizzly sub-
specifically different from the European form. It must again be emphasized that the modal
conditions of populations in nature are what count in this connexion, not the quandaries
of an investigator finding a few specimens out of a large suite difficult to classify. To declare
(a) that such intermediate specimens represent a different taxonomic group, or (b) that
they represent a transition between two taxonomic groups, and therefore prove the in-
validity of these groups, are both examples of typological approach, and equally prove its
complete bankruptcy.

[2] Couturier gives the mean values, or data from which means may be computed. For
the Asia Minor population, only a female mean could be obtained. In other populations,
the female mean averages 87 per cent of the male mean, and a hypothetical value was
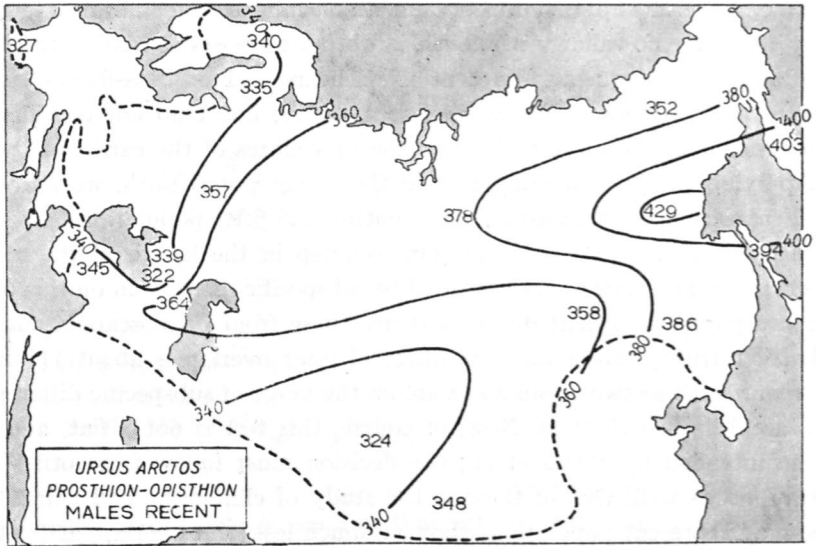computed on this basis.

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Fig. 9. A preliminary isophene system for prosthion-opisthion length of males in recent
Ursus arctos population of the Old World (contour lines connecting equal mean values).
The isophenes are here represented as smooth curves, but should probably in many cases
be influenced by geographical features. Information lacking for many areas, particularly
the centre of the range. Data from Couturier (1953) and original.

of the population concerned, and a system of isophenes was tentatively
drawn on this basis (fig. 9).

Each of the values is determined from a comparatively small number of
observations (N being on the order of 5 to 10 in most cases), and the signi-
ficance of deviations can not be studied in all cases. Also, the interpretation in
terms of isophenes may vary. In particular it should be noted that the
isophenes probably, more often than not, coincide with, or run parallel to,
such major obstacles as mountain ridges etc.; a feature which is however
difficult to take into account as long as the available data are so scattered,
and the gaps so wide, as in the present case.

The interpretation shows a maximum on the coast of the Sea of Okhotsk,
and two minima, one in Tibet, and the other in western Europe. Along the
west-east cline considered above (Fennoscandia to Okhotsk), a major break
is shown, again, to occur far to the west; moreover, the present data seem to
indicate a stepped-up gradient in eastern Siberia as well. In most other cases,
except for Caucasus where the bears on the northern and southern slopes
seem to differ considerably in size, the gradients are not pronounced. This
picture is surely over-simplified, and a study of intervening populations will
probably reveal the existence of other zones with steep clines; at any rate

it does not justify the extensive splitting into ten or more subspecies practised by some students[1].

The erection by DEGERBØL (1933) of a subspecies *U. arctos nemoralis* for the subfossil Danish population was severely criticized by ERDBRINK. In my opinion there is much to say for considering that form subspecifically distinct from the recent nominate form, i.e., the Fennoscandian. The fact that the joint overlap is less than 9 per cent is not in itself decisive; here, too, a study of gradients is necessary. The boundaries between temporal subspecies should preferably be drawn where temporal gradients are the steepest, in analogy with the procedure for spatial subspecies. As will be shown below, the gradient *U. arctos nemoralis* — *U. arctos arctos* is actually much steeper than the average in bear evolution, and so a taxonomic distinction would seem proper. On the other hand, the relations between *U. a. nemoralis* and large late glacial bears are by no means clear, and it is quite possible that some earlier name out of the almost endless synonym lists may actually have precedence.

As a conclusion it may be said that, for the time being, it seems more important and urgent to extricate the valid subspecific names than to create new ones; and that this should be done by means of quantitative analysis, the typological method being worthless in that task.

Chronoclines in the ancestry of the cave bear.

Whereas the minutiae of size trends at the population level are as yet somewhat obscure, a study of the evolution of size in the ancestry of the cave bear is perfectly feasible. The information on evolutionary rates so obtained appears to be of some general interest.

I have selected the length of the first upper molar as a suitable variate for such a study. The length of the second molar appears to be less well suited for a study of that kind, since a relative elongation of this molar is one of the characteristics of ursid evolution from *Ursavus* to *Ursus*. M¹ is more approximately (though not exactly) similar in shape and relative length throughout the sequence.

The samples considered are: *Ursavus elmensis* Stehlin from the Burdigalian of Wintershof-West in Germany (see DEHM, 1950; the data used here are original, taken by me in the Paleontological Institute of the university, Munich); *Ursavus brevirhinus* (Hofmann), Sarmatian, various locs.; *Ursavus depereti*

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[1] It may be noted that the isophenes show partial agreement with isolines for continentality (differences between winter and summer temperatures), skull length, then, being positively correlated with temperature amplitude. It is suggestive that there is some evidence for increased continentality during the postglacial »Boreal» phase, from which part of the subfossil Danish material is derived.

TABLE 6.

Length of first upper molar in a phylogenetic bear sequence from Miocene to Pleistocene, with approximate ages in terms of million years.

	N	M	σ	V	S.R.	Age
Ursavus elmensis, Burdigalian	16	10.80 ± .14	.55 ± .10	5.11 ± .91	9.01—12.59	22
Ursavus brevirhinus, Sarmatian	7	12.99 ± .32	.84 ± .23	6.49 ± 1.73	10.26—15.72	15
Ursavus depereti, Pontian	3	16.60				10
Ursus etruscus, Villafranchian ...	11	22.32 ± .36	1.20 ± .26	5.40 ± 1.15	18.42—26.22	.9
Ursus arctos dening-eri, Günz-Mindel	8	25.69 ± .55	1.56 ± .39	6.08 ± 1.52	20.63—30.75	.5
Ursus spelaeus, Würm	118	29.89 ± .13	1.46 ± .10	5.07 ± .33	25.15—34.63	.1

Schlosser, with *U. ehrenbergi* (Brunner)[1], Pontian (data on both of these culled from various sources, e.g., ZAPFE, 1950, and WEITZEL, 1952); *Ursus etruscus* Cuvier (Villafranchian; data from ERDBRINK); *Ursus arctos deningeri* (Reichenau), Mosbach (Middle Pleistocene; original data); *Ursus spelaeus* Rosenmüller and Heinroth, Odessa (Late Pleistocene; original data).

The statistics appear from table 6. Approximate ages are given, in terms of million years; regarding the Tertiary epochs I have followed SIMPSON (1947 b). The chronoclines are represented in fig. 10, which also shows the corresponding rates of change in HALDANE's units, millidarwins (1 darwin being equal to an increase of 1/1000, or .1 per cent, in 1000 years — or, alternatively, a decrease by 1/1001; 1 millidarwin = .001 darwin).

The size trends are highly uniform during the Miocene and Pliocene epochs, being always on the average order of 40-50 millidarwins. It should be noted, of course, that these are average trends, and the data do not suffice to demonstrate absence of »steps» or steeper gradients in the gaps. It seems, however, as if interjacent records would tend to fall approximately on the chronocline thus determined, as far as may be judged from the condition in *Ursus böckhi* Schlosser (Middle Pliocene; see fig. 10). This figure is rather uncertain, because Schlosser's material does not include upper dentitions, but the length of M[1] would apparently be about the same as in *Ursus edensis* (Frick), where it is on the order of 17—18 mm.

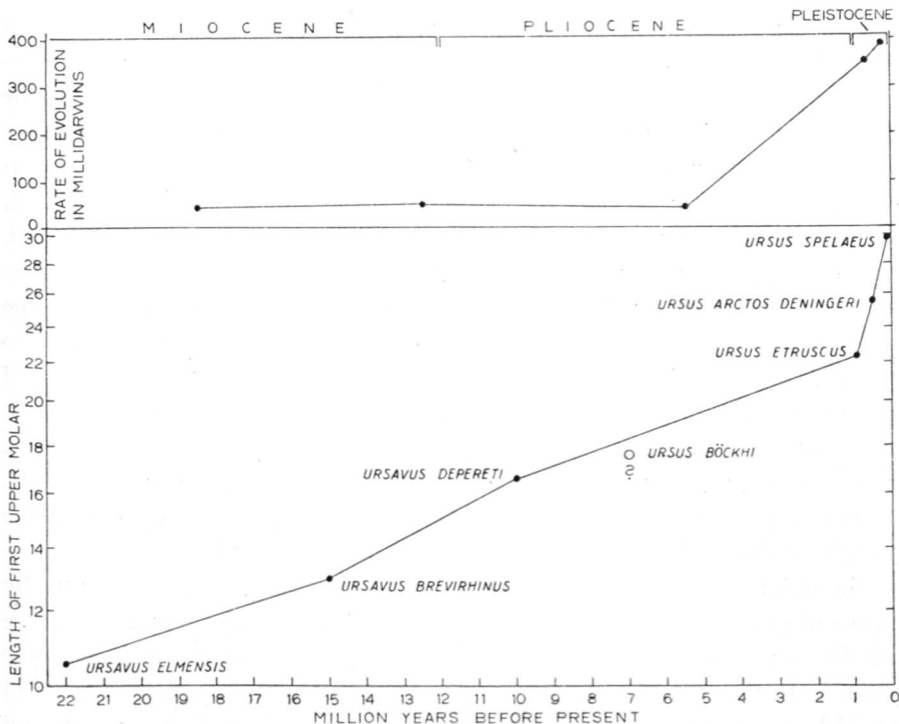[1] Probably synonymous (ERDBRINK, 1953, p. 545).

Fig. 10. Chronoclines and rates of phyletic growth (in millidarwins) for length of M^1 in the ancestry of the cave bear; data from table 6. In the chronocline representation, a tentative datum for *Ursus böckhi* (Middle Pliocene) is shown to agree with expectation.

These evolutionary rates are comparable with those found by SIMPSON (see Simpson, 1953) for Tertiary horses. Expressed in millidarwins, the rates for paracone heights of upper molars vary between 24 and 76 millidarwins, and those for ectoloph lengths of upper molars between 6 and 33 millidarwins. Of these dimensions, the length of the ectoloph is more closely related to body size, and thus most suitable for a comparison with the data for bears. It may be concluded that the rates in bears, during the Tertiary, averaged slightly higher than the rates in horses.

In the Pleistocene, however, there occurs an abrupt change in the bear sequence. The rate of change suddenly increases, averaging some 350 millidarwins for the transition *U. etruscus* — *U. arctos deningeri*, and about 390 millidarwins in the final evolution of *U. spelaeus*. This remarkable change would almost certainly appear to be connected, in some way, with the rapid climatic changes of the Pleistocene, as contrasted with the slower evolution of the environment during the Tertiary. To conclude that it represented *only* the effect of Bergmann's rule through time would seem to me an undue simplifi-

cation. Many discussions of size trends during and after the Pleistocene seem to imply that the Ice Age represents a single glaciation with a peak somewhere in the middle — an idea which, of course, everybody knows to be wrong, but which somehow seems to persist in many applications of Bergmann's rule to temporal sequences. The penultimate (or Mindel-Riss) interglacial is well known to have been many times as long as the Holocene; and, to take another instance, the gigantic subfossil Danish bear must have lived, during part of its existence at least, in a climate as warm as that of the present day. The factors involved in the high evolutionary rates of the Pleistocene bears, thus, must certainly be more complex than a simple adjustment to heat-loss. Quite likely, the rapid oscillations of the climate acted as a powerful stimulus to evolution, regardless of their direction (see ZEUNER, 1953, p. 390); they may have led to considerable spatial differentiation, thus forming a supply of geographic variability making rapid evolutionary change possible.

The only instance of still more rapid evolution that I have found is the postglacial dwarfing of *U. arctos*, discussed above. This extraordinary rate — on the order of 20,000 millidarwins[1] — was probably made possible only by means of gene flow from adjacent populations. The maximum rate of change possible for a self-contained, normally variable population, such as these bears (note the essential stability of the coefficients of variation in table 6) would be interesting to know. Apparently it lies somewhere between 390 and 20,000 millidarwins.

DISTRIBUTIONS AND SIZE TRENDS

A detailed study of the properties of the frequency distributions throws some additional light on the size trends in the cave bear. The properties of especial interest in this connexion are kurtosis, skewness, and changes correlated with age. All these topics necessitate the study of fairly large samples. Kurtosis and skewness, in particular, show rather erratic trends in small samples. In the present case it was necessary to study the behaviour of several different variates, and to average the trends. For the study of kurtosis and skewness, I have selected the lower dentitions and M^2 of the Mixnitz cave bear and the recent *U. maritimus*, and the lower canines of the Odessa bear.

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[1] Given here in millidarwins to facilitate comparison. SIMPSON (1953) thinks the use of darwins as rate units unnecessarily complicated, and prefers to express rates as percentage increase (or decrease) during 1 million years. In the present case, such figures would be extremely cumbersome. Phyletic growth at a rate of 20,000 millidarwins would lead to an increase of 48,500 million per cent during 1 million years; phyletic dwarfing at the same rate would reduce the bear to a submicroscopic animal. These figures, though awe-inspiring, have no relevance in nature, and the use of darwins is to be preferred.

Kurtosis.

Kurtosis occurs when the distribution is either flatter (platykurtosis) or more peaked (leptokurtosis) than the normal curve.[1] A platykurtic distribution may, for instance, be formed when two normal distributions differing slightly in mean are added together. Thus it is natural that any variate showing sex dimorphism will give a platykurtic distribution, if not a bimodal one, when the sexes are not separated; actually, either one or the other alternative was found in all cave bear variates, from all samples, which I have studied.[2]

A leptokurtic distribution, on the other hand, may be obtained e.g. by adding together two normal distributions with equal means but different standard deviations. Extreme instances (though clearly not due to the mentioned sort of bias) are seen in fig. 1 (the originally sexed males and females of *U. maritimus*).

The coefficients of kurtosis are given in table 7. As might be expected from the relatively small size of the samples, the trends are somewhat erratic. However, as regarding the Mixnitz sample, only two variates out of twelve show positive coefficients, male lower canines and male M_2; and of these, the former does not differ significantly from 0. The general trend is quite clearly towards platykurtosis, rather slight but probably significant.

This is not unexpected. The sampling represents a fairly long temporal sequence (see, e.g., SOERGEL, 1940), probably characterized by marked secular changes in environment — notably climate. Slight changes in average size would probably have occurred during this time, and would be reflected in a tendency to platykurtosis. The data, of course, indicate minor changes only, very far from the order of the extreme »dwarfing» previously discussed. Incidentally, the fact that the coefficients of variation are relatively low in spite of this platykurtosis, shows that the variation at any one level or point in time must have been very restricted.

The Odessa bear shows a similar platykurtosis, which may probably be interpreted in an analogous way.

The data for *U. maritimus* appear, at first sight, to present a completely incongruous picture. The canines show extreme leptokurtosis, whereas the distributions for most other variates are platykurtic. This result appears to

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[1] The coefficient of kurtosis is

$$K = \frac{m^4/N}{\sigma^4} - 3,$$

where m^4 is the fourth moment around the mean. Positive values indicate leptokurtosis, negative values platykurtosis.

[2] This was implicitly stated by EHRENBERG (1928), relating to the Mixnitz sample.

TABLE 7.

Coefficients of kurtosis (K) and skewness (S_k) for distributions in sexed samples of bears.

| | Ursus spelaeus | | | | | | U. maritimus | | |
| | Mixnitz | | | Odessa | | | Recent | | |
	N	K	S_k	N	K	S_k	N	K	S_k
Ci, width ......♂	160	+.02	+.34	32	—.46	—.32	56	+3.9	—.03
♀	124	—.37	+.15	28	—.44	—.09	32	+5.2	+.47
P_4, length ...♂	52	—.42	+.30				53	— .54	+.47
♀	43	—.52	+.27				40	— .13	+.45
M_1, length ...♂	67	—.53	—.06				55	— .78	—.15
♀	41	—.06	+.44				40	— .13	+.26
M_2, length ...♂	79	+.85	—.06				54	+ .99	—.09
♀	52	—.18	—.03				39	— .50	+.80
M_3, length ...♂	80	—.40	+.70				50	— .14	+.08
♀	43	—.29	—.18				34	— .67	—.52
M^2, length ...♂	71	—.59	—.26				60	— .06	—.62
♀	21	—.29	+.53				44	— .01	+.07
Average		—.23	+.18					(+ .59)	(+.10)

me to be wholly inexplicable unless it is assumed that some of the originally sexed specimens were wrongly sexed (see above, p. 9). In that case, however, the result agrees with expectation. The leptokurtosis of the canine distributions, of course, would be due to the inclusion of a few specimens of the opposite sex, widely outside the standard range of distribution, and tending to »stretch out» one of the tails of the distribution. In the case of the other variates, where the dimorphism is slight, the wrongly sexed specimens would not fall outside the standard range, and the result will be that of adding together two distributions differing slightly in mean, or platykurtosis. Thus the data for *U. maritimus,* as here presented, do not permit any final conclusion of biological value, and I have included them in order to indicate the necessity of critical evaluation of the raw data, and to demonstrate methods suitable for detecting sampling errors of this kind.

Skewness.

Skewness occurs when a distribution is not symmetric, i.e., one of its »tails» is longer than the other, and falls away slower from the mode[1]. As has been observed by SIMPSON and ROE (1939), a slight skewing to the right

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[1] The coefficient of skewness is S = (Mean — Mode)/σ. Positive values indicate skewness to the right, negative skewness to the left.

(i.e. the right tail is longer) is the normal condition in most zoological distributions.

The average trend for the Mixnitz cave bear (table 7) is, actually, a slight skewness to the right, perhaps more pronounced than the expected trend. If valid, it might indicate that the population mean tended to remain at a slightly lower level than the sample mean during the main part of the time represented by deposition. The Odessa canines show the opposite tendency; but in both cases the samples are somewhat too small, and the deviations too slight, to form any basis for valid conclusions.

In *U. maritimus*, the tendency for the males is skewing to the left, and for the females skewing to the right; a result in perfect agreement with the conclusion that some specimens are wrongly sexed.

Age and variation.

Variates not subject to change from growth or use, such as certain dimensions of teeth, may be used for the evaluation of differential mortality. By this method light can be thrown on the processes of natural selection which underlie the size trends.

The variates selected are the lengths of the upper and lower cheek teeth, and the width of the lower canines, in the sexed Mixnitz samples. The lengths of the cheek teeth are usually somewhat affected by wear from the tooth in front and/or behind. For a student well acquainted with the dental morphology of the cave bear, it is usually possible to determine the (initial) length of the tooth within the limits I have used in the secondary grouping (.5 mm.), as long as the interstitial wear is slight. Specimens on which this measurement could not be ascertained with sufficient accuracy have, of course, been discarded in computation.

The samples were split into two age groups, teeth not touched by wear being grouped as »young» and teeth with perceptible wear as »old». Different teeth begin to wear at somewhat different times, and they often wear unevenly; thus the groups for different teeth are not always fully equivalent. All comparisons are, however, between homologous teeth; the wear may start at slightly different ages in different individuals, but this slight inconsistency is probably of little importance.

The data are given in table 8. The changes in mean size of the teeth appear from the column giving increase or decrease in per cent of the mean for the »young». A slight decrease is almost universal (also for teeth not generally affected by interstitial wear of the dimension measured: canines and P_4), though, in such small samples, the trend is somewhat erratic and a minority show increase.

TABLE 8.

Parameters for unworn (U) and worn (W) teeth of *Ursus spelaeus*, Mixnitz, sexed samples, to show changes in mean and variation, and their significance (P)[1].

		N	M	Change in %	P	σ	Change in mm.	P
Males:	Width, C_i, ... U	58	21.87 ± .14	− .2		1.06 ± .10	+.12	
	W	102	21.82 ± .12			1.18 ± .08		
	Length, P_4, ... U	38	16.56 ± .20	−1.2		1.22 ± .14	−.54	.005
	W	14	16.36 ± .18			.68 ± .13		
	Length, M_1, ... U	25	32.22 ± .20	−1.6	.06	.98 ± .14	+.17	
	W	42	31.72 ± .18			1.15 ± .13		
	Length, M_2, ... U	37	32.44 ± .20	− .3		1.22 ± .14	−.25	.06
	W	42	32.32 ± .15			.97 ± .10		
	Length, M_3, ... U	38	30.13 ± .32	−3.0	.06	1.97 ± .23	+.17	
	W	33	29.22 ± .37			2.14 ± .26		
	Length, P^4, ... U	25	21.40 ± .31	+ .1		1.53 ± .22	−.55	.03
	W	27	21.42 ± .19			.98 ± .13		
	Length, M^1, ... U	28	29.90 ± .28	− .5		1.49 ± .20	−.01	
	W	35	29.74 ± .25			1.48 ± .18		
	Length, M^2, ... U	35	48.54 ± .40	− .2		2.35 ± .28	−.08	
	W	36	48.42 ± .38			2.27 ± .27		
Females:	Width, C_i, ... U	46	16.97 ± .17	−2.0	.09	1.15 ± .12	+.18	
	W	78	16.63 ± .11			.97 ± .08		
	Length, P_4, ... U	32	15.27 ± .14	+ .7		.81 ± .10	+.29	
	W	11	15.38 ± .33			1.10 ± .24		
	Length, M_1, ... U	12	29.74 ± .44	−1.5		1.53 ± .31	−.73	.02
	W	29	29.30 ± .15			.80 ± .11		
	Length, M_2, ... U	23	29.96 ± .26	− .3		1.25 ± .18	−.05	
	W	30	29.85 ± .22			1.20 ± .16		
	Length, M_3, ... U	17	27.85 ± .29	−5.3	.002	1.19 ± .20	+.57	.20
	W	21	26.37 ± .38			1.76 ± .27		
	Length, P^4, ... U	17	19.33 ± .21	+2.0		.87 ± .15	−.09	
	W	9	19.71 ± .26			.78 ± .18		
	Length, M^1, ... U	7	26.91 ± .66	+3.9	.13	1.75 ± .47	−.38	
	W	16	28.01 ± .34			1.37 ± .24		
	Length, M^2, ... U	10	45.65 ± .52	−3.9	.007	1.65 ± .37	−.12	
	W	15	43.87 ± .40			1.53 ± .28		

[1] Values for P entered only for possibly significant or apparent border-line cases.

The significance of these deviations is given under P. In most instances, it does not reach the 5 per cent level $(P>.05)$. In two cases, however, the decrease of the means is surely significant: for M_3 and M^2 in females. In the former case, the length is reduced by 5.3 per cent, and the odds for this being purely accidental are only 1 to 500. In the latter case, the decrease is 3.9 per cent, and the corresponding odds less than one to a hundred. In the male groups, the mean lengths of M_3 and M_1 are reduced from »young» to »old» by 3 and 1.6 per cent respectively, the probability in both cases being about 6 percent (odds about 1 to 17).

No instance of increase has any significance at all. The highest positive value (for M^1 in females) is 3.9 per cent increase, but the corresponding P-value (13 per cent) is not significant. Out of 16 variates, only 4 show increase in mean size from »young» to »old».

If these changes in mean dimensions were caused by differential mortality, which appears probable, they should be accompanied by a depletion of variability in the »old» age group. As might be expected, such is the case. The trend is, of course, somewhat erratic in this case also; in 6 cases out of 16, the standard deviation is higher in the »old» group than in the »young». The difference is usually slight in these instances, however, and it is never significant. On the other hand, the decrease is probably or almost surely significant for several variates, in particular male P_4 and P^4, and female M_1. The averaged coefficients of variation are 5.18 for the »young» and 4.78 for the »old». Thus it appears probable that differential mortality led to a depletion of variation within the cohort, favouring, at the same time, variants slightly below the mean. The former trend illustrates the »centripetal» or »stabilizing» component of selection; the latter indicates the existence of a directional component.

Whether this latter trend was local or general in the cave bear population, for how long time it persisted, and what were its evolutionary results, is of course impossible to judge at present; but the results indicate that these questions may be further illuminated by future study of other large samples.

The cave bear population and Wright's model.

The results of the present investigation suggest some tentative conclusions regarding the structure of the cave bear population. The fairly low variation within single demes, as contrasted with the considerable intergroup variation, suggests a limited intermigration between the local population units. In an animal as large as the cave bear, this could hardly have been realized by means of any other factors than a highly developed *Ortstreue* (possibly associated with territoriality). The low variation would, then, be the natural expression of gene loss and fixation in small populations. It may be noted that

this picture (of a relatively large total population divided into small pan-mictic units with limited migration) has been considered optimal for rapid evolution by WRIGHT. It is interesting to compare the model of Wright (I use the review in SIMPSON, 1953, p. 123) with what is known, or may be inferred, regarding the cave bear.

In the first place, according to Wright, the total effective breeding popul-ation should be of the minimum order of 100,000 to 1,000,000. In fact, an estimate of the probable abundance of the cave bear within all of its range (see map in ERDBRINK, p. 471) would reasonably fall somewhere between these values. The second prequisite is a division into local demes with effective breeding populations on the order of 100 — that is, the population should be split into about 1,000 to 10,000 demes. This cannot, of course, be proved regarding the cave bears; but it would seem not to be a wholly unrealistic estimate. Territories with suitable caves have a decidedly patchy distribution, the intervening territory being often mountainous, or else forming more or less wide plains, apparently less suitable for the species; the scantiness of *U. spelaeus* records from open-air sites seemingly indicates that the species was highly dependent on the presence of caves (see SOERGEL, 1940).

Finally, the transfer of genetic materials from one deme to another should be low, on the order of .01 to .001, but not completely barred. As SIMPSON (*loc.cit.*) notes, such situations are probably not very common in nature. Many data on cave bears do suggest limited intermigration, but its scale would be very difficult to estimate. One possibility might be a study of the number of polygenes determining size (in some related form) and, on that basis, an estimate of the maximum value of m (gene flow) which is possible without levelling down the size gradients between adjacent demes.

Inconclusive and speculative as these comparisons are, they suggest that conditions resembling the model of WRIGHT may occur in nature, and may actually be coupled with high rates of evolution.

In this connexion, the possibility of crossing with the Pleistocene *U. arctos* should be mentioned. EHRENBERG (1929) has described two very remarkable skulls from caves at Winden in Austria, which unite the characters of both species in a way differing considerably from that seen in *U. arctos deningeri*. It does not appear unlikely that the two species were in marginal contact, and that the gene flow between them, perhaps, was not entirely broken. A survey of allometries in the dentitions of the two species (KURTÉN, in press and unpublished) shows that their genetic constitutions differed considerably, but that some allometry determinants may be homologized in both.

In concluding, I wish to express my agreement with ABEL's (1929) opinion that study of the history of the cave bear may give most important data for the theory of evolution (though I disagree with many features in his inter-

pretation). As SIMPSON (e.g., 1953) has observed, the great majority of paleontological data pertain to continuously large, and relatively slowly evolving, populations. Data on small and rapidly evolving populations are usually scanty. The cave bear is a remarkable exception: few fossil or living mammals, if any, are represented by greater collections available to science, or better suited for quantitative study. Yet this species evolved rapidly (its range in time being limited to the late Pleistocene) and had a relatively small population (its range in space being more or less wholly limited to the continent of Europe[1]). The abundant information on the species is due to its preferring a biotope which is ideal for fossilization.

Moreover, the ancestors of the cave bear are well known from large samples, and are conspecific with a living form. Thus many different features contribute to the possibility of a study in evolution, unique in breadth of scope and precision of procedure and conclusions. If the present paper has contributed towards that goal, and towards shaping the methods to be used, its main purpose will be fulfilled.

CONCLUSIONS

A significant partial sex dimorphism in various quantitative characters was found in all the bear populations here studied (of the species *Ursus spelaeus*, *U. arctos* and *U. maritimus*). The relative magnitude of the difference between means for males and females varies in different populations, but it appears to some extent to be positively correlated with size. Smaller forms than the recent *U. arctos* have not been considered; the trend suggests that the dimorphism is slighter in such species.

The dimorphism is especially strong in the size of the canines, somewhat less pronounced in skull dimensions, and still less in the cheek teeth.

Sexing should be done through study of frequency distributions. The width of the lower canines is the best variate for sexing unsexed specimens. The procedure may be checked, and part of the residual specimens sexed, by analogous study of other variates.

Sex ratios in cave bear samples from different sites may differ significantly and strongly from each other and from the expected ratio, 1 : 1. These deviations may probably be explained on ecological grounds.

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[1] The small Caucasian race described by BORISSIAK, 1932, appears not to be a true cave bear, as has been noted by ERDBRINK. Erdbrink also shows that the bear described as *Ursus spelaeus* var. by PEI (1934) from Choukoutien is a relatively large *U. arctos*.

The so-called dwarf form from the site of Mixnitz represents, like many other »dwarfs», normal females of the cave bear. True »dwarfs» or small forms are represented by e.g. the cave bears from Dachstein and Trosketa.

The intrasexual variation within single cave bear demes is lower than in corresponding recent populations. Apart from the sex dimorphism, thus, local populations of cave bears are certainly not more variable than local populations of recent bears. On the other hand, different demes may differ significantly and strongly in mean quantitative characters. The differences do not warrant subspecific splitting as yet, but may do so in future, when spatial clines and chronoclines have been studied in more detail. There is a possibility that spatial clines in the cave bear may have been steeper than the clines of the recent brown bear population. The brown bear clines show few areas of stepped-up gradients and do not warrant the recognition of more than 2—4 recent subspecies, at most, in the Old World.

Evolution in size of the bears was relatively slow and uniform from the Middle Miocene to the end of the Tertiary, but extremely rapid in the Quaternary. This should probably be interpreted as resulting from changes in intensity and direction of selection, and in population structure, in conjunction with the more extreme climatic oscillation and zonation of the Quaternary. Simple adaptation by phyletic growth to cold climate was certainly not the sole factor involved; the record does not show size oscillations in rapport with the climatic ones. The most rapid change in size recorded is that from subfossil Danish bears to recent Fennoscandian ones, a change that would not be expected from climatic conditions. The rapid rate was probably made possible, in this case, by means of gene transport from neighbouring populations.

The intrasexual variation in the Mixnitz cave bear is characterized by slight platykurtosis and slight skewing to the right, perhaps reflecting minor evolutionary changes during time of deposition. The effect of selection, in the form of differential mortality, is revealed in reduction of mean size and variation in old age groups as compared to young.

The structure of the cave bear population appears to have had some affinity with a model stressed in Wright's population-genetical studies.

The cave bear permits study of a rather rapidly evolving and small population on the basis of extremely abundant material, a very unusual situation in paleontology.

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