

Sexual dimorphism in limb bones of Late Pleistocene cave bear (*Ursus spelaeus*, Carnivora, Mammalia) from three caves in Eastern Alps (Austria and Italy)

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ABSTRACT – The length and width of cave bear (*Ursus spelaeus*) stylo- and zeugopodia were measured. The material comes from three Late Pleistocene alpine caves: Conturines Cave in Northern Italy, Gamssulzen Cave in Upper Austria, and Herdengel Cave in Lower Austria. With the help of hierarchical cluster and discriminant analysis, all of the elements under study may be classified into two groups. Size differences between limb bones are interpreted in terms of sexual dimorphism. Such dimorphism of size may be observed in all recent bear species. This paper argues against a "High-Alpine small form" for the remains of the Conturines Cave as tested by one-way analyses of variance.

ZUSAMMENFASSUNG – [Geschlechtsdimorphismus an Extremitätenknochen jungpleistozäner Höhlenbären (*Ursus spelaeus*, Carnivora, Mammalia) aus drei ostalpinen Höhlen Österreichs und Italiens] – Verschiedene Längen- und Breitenmaße von Stylo- und Zeugopoden des Höhlenbären (*Ursus spelaeus*) wurden vermessen. Das Material stammt aus drei alpinen Höhlen des Jung-Pleistozäns: der Conturineshöhle in Norditalien, der Gamssulzenhöhle in Oberösterreich und der Herdengelhöhle in Niederösterreich. Mit Hilfe hierarchischer Clusteranalysen und Diskriminanzanalysen konnten alle untersuchten Elemente in zwei Gruppen unterteilt werden. Größendifferenzen zwischen den Extremitätenknochen werden als Sexualdimorphismus interpretiert. Ein derartiger Größenunterschied kann bei allen rezenten Bärenarten beobachtet werden. Dieser Artikel wendet sich gegen die in der Literatur angeführte "Hochalpine Kleinform" für die Conturineshöhle.

RIASSUNTO – [Dimorfismo sessuale in ossa articolari di orso delle caverne (*Ursus spelaeus*, Carnivora, Mammalia) da tre caverne delle Alpi orientali (Austria e Italia)] – Sono state misurate la lunghezza e larghezza di stylo- e zeugopodia di orso delle caverne. Il materiale proviene da tre grotte alpine del tardo Pleistocene: Grotta di Conturines in Italia settentrionale, Grotta di Gamssulzen in Austria settentrionale e Grotta di Herdengel in Austria meridionale. Le analisi utilizzate <hierarchical cluster> e <discriminant analysis>, permettono di classificare in due gruppi tutti gli esemplari esaminati. Le diverse dimensioni delle ossa articolari sono interpretate in termini di dimorfismo sessuale. Tale dimorfismo nelle dimensioni può essere osservato in tutte le specie recenti di Orso. Questo articolo pone in discussione la "piccola forma Alto alpina" proposta in letteratura per la Grotta di Conturines.

INTRODUCTION

In the Ursidae the males are always larger than females (Stubbe, 1993, p. 249). Sex-specific size differences can be small (10-20%) in some species, but values may also exceed 50% (Stirling, 1993). Sexual dimorphism is extreme in the polar bear (*Ursus maritimus*) and brown bear (*Ursus arctos*), confirming the correlation with absolute body size (Kurtén, 1967, p. 52). In addition to this sex-determined variation, bears can also show intraspecific spatial size variation. Brown bears in Scandinavia are on average much smaller than the eastern Siberian and Alaskan representatives (Kurtén, 1955). Furthermore, bear fossils may demonstrate evolutionary size increase.

Analyses of size differences in cave bears are numerous. Studies of canines have shown evidence of sexual dimorphism (Bachofen-Echt, 1931; Rode, 1935; Koby, 1949; Kurtén, 1955). In regard to postcranial elements, Kurtén (1976, p. 70) generally remarked that "... the sexual dimorphism in size is, in

fact, seen in all of the body. Almost any skeletal dimension will show a bimodal frequency curve of the same type as the canines (the cheek teeth are an exception)". Size differences in postcranial elements of cave bears were also studied (e.g., Torres Pérez-Hidalgo, 1988; Kunst, 1992; Grandal d'Anglade, 1993). Koby (1950) shows the ranges of some long bone elements and compared them with data discussed in the literature. Generally, the average lengths of male cave bear limb bones are reported to be about 15% longer than female ones. Therefore, the large limb bones as the best indicators of body size are diagnostic for sexual dimorphism (Reisinger, 1995).

Statistical methods offer the possibility to prove differences in body size of fossil animals and demonstrate the extent of variation. Univariate frequency distributions can to a certain degree describe sexual dimorphism as well as the sex ratio. However, the simultaneous comparison of a variable set leads to more accurate interpretations. Multivariate statistical methods are used in palaeontology, biology, and

archaeology in order to ascertain species and determine sex, such as in recent and fossil primates (Hohenegger & Zapfe, 1990). Other applications include the classification of bones in respect to differentiate between wild versus domesticated animals, or between the fore versus back legs of an individual (Benecke, 1987).

LOCATION AND MATERIAL

This study is based on measurements of adult cave bear stylo- and zeugopods (humerus, radius, ulna, femur, tibia, fibula) from the three alpine caves Herdengel (e.g., Rabeder & Mais, 1985), Gamssulzen (Kühtreiber, 1995; Rabeder & Weichenberger, 1995), and Conturines (Rabeder, 1991).

CONTURINES CAVE (CO)

This cave is situated in the Dolomites, 40 km to the east of Bolzano, Italy. It is the highest cave bear site in the Alps (2,775 m). Radiometric dating of bones by the uranium-series method yielded ages from 44,000 to 115,000 years BP (Rabeder, 1995). The identification labels BC and CU depicted in Text-fig. 8/1 to 8/5 mark on the one hand the material belonging to the Office for the Preservation of Historical Monuments in Bolzano, Italy (BC), and on the other the material from excavations by Rabeder (CU). No reports can be found about the stratigraphical layers.

GAMSSULZEN CAVE (GS)

This cave is located 5 km to the west of the village Spital am Pyhrn, Upper Austria (Rabeder, 1995). Radiocarbon data indicate ages from 25,000 to 38,000 years BP (Nagel & Rabeder, 1991; Leitner-Wild & Steffan, 1993). The Gamssulzen Cave contains the smallest amount of long bones from the three caves. Its altitude (1,300 m) is intermediate between the other two caves. No information about stratigraphical layers are available.

HERDENGEL CAVE (HD)

This cave is located 2 km to the west of Lunz am See, Lower Austria, at 780 m above sea level (Rabeder & Mais, 1985). Most of the bone remains have been dated by radiocarbon and uranium-series methods, yielding ages between 36,000 to 67,000 years BP (Leitner-Wild & Steffan, 1993; Leitner-Wild, Rabeder & Steffan, 1994; Rabeder, 1995). However, two long bones (1 humerus and 1 tibia) from the lowest stratigraphical layers show ages between 126,000 to 136,000 years BP according to the uranium-series method, which indicate the Late Riss.

The material from the Herdengel and Gamssulzen Caves is deposited at the Institute of Palaeontology,

University of Vienna, Austria. The cave bear remains from the Conturines Cave are stored at the Office for the Preservation of Historical Monuments in Bolzano, Italy.

METHODS

The main problem in analysing stylo- and zeugopods of cave bears is the small number, together with their fragmentation. Remains from the Herdengel and Conturines Caves are relatively numerous and well preserved, providing an adequate basis for biometrical studies.

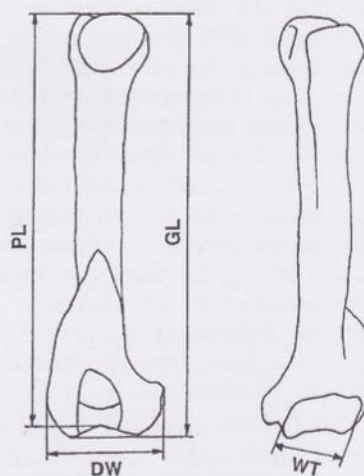
Different lengths and widths were measured on the stylo- and zeugopods of adult cave bears using a dial caliper as indicated in Driesch (1982). The scale is in millimetres. G. K. Kunst (University of Vienna) treated bones from the Gamssulzen and Herdengel Caves, the first author (C.R.) investigated the Conturines remains. Differences in performing measurements were tested and the results correlate.

The following four distances were measured on the **humerus** (Text-fig. 1; abbreviations in parentheses): 'greatest length' (GL), 'physiological length' (PL), 'distal width' (DW), and 'width of trochlea humeri' (WT).

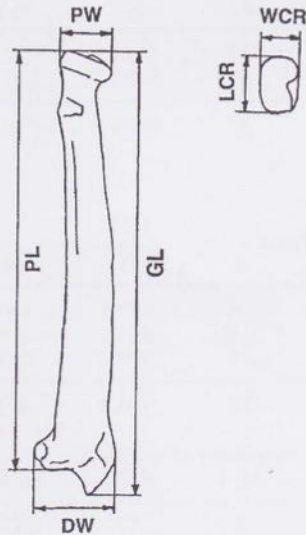
The six distances on the **radius** are (Text-fig. 2): 'greatest length' (GL), 'physiological length' (PL), 'distal width' (DW), 'proximal width' (PW), 'length of caput radii' (LCR), and 'width of caput radii' (WCR).

Seven distances were taken on the **ulna** (Text-fig. 3):

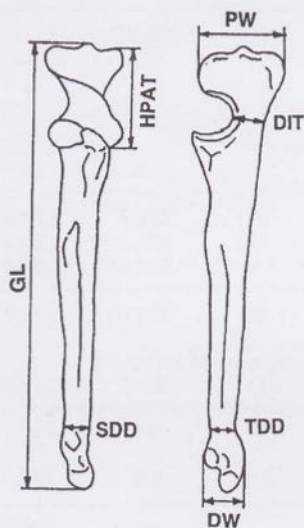
'greatest length' (GL), 'distal width' (DW), 'proximal width' (PW), 'smallest sagittal diaphysis diameter' (SDD), 'smallest transversal diaphysis diameter' (TDD), 'distance between processus anconaeus and tuberculum olecrani' (HPAT), and 'diameter of the incisura trochlearis' (DIT).



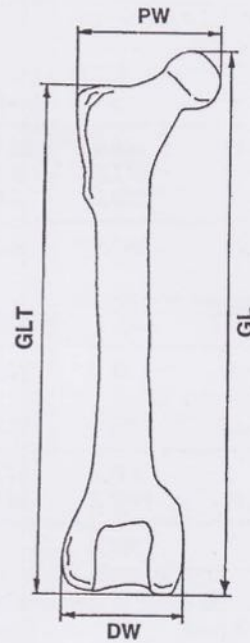
Text-fig. 1 - Humerus measurements.



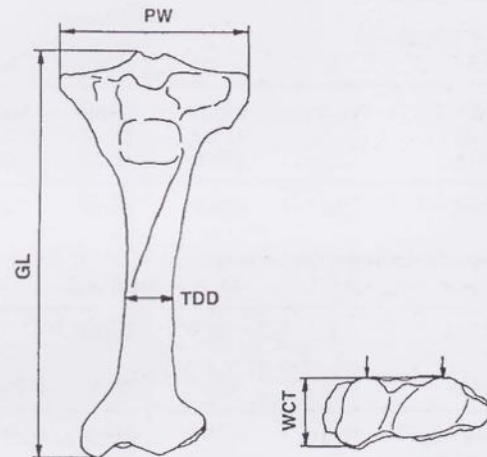
Text-fig. 2 - Radius measurements.



Text-fig. 3 - Ulna measurements.



Text-fig. 4 - Femur measurements.



Text-fig. 5 - Tibia measurements.

Four distances were taken from the **femur** (Text-fig. 4):

'greatest length' (GL), 'length between trochanter major and epicondylus' (GLT), 'proximal width' (PW), and 'distal width' (DW).

The following distances characterise the **tibia** (Text-fig. 5):

'greatest length' (GL), 'proximal width' (PW), 'transverse diaphysis diameter' (TDD), and 'width of cochlea tibiae' (WCT).

Inference statistical methods allow to distinguish whether frequency distributions are factual or accidental (Bortz, 1993; Sokal & Rohlf, 1995). Therefore, the data were treated applying the follow-

ing statistical methods: 'Frequency distribution diagrams' characterise the single variables and inferences were tested using the 'one-way analysis of variance' in the parametric case, and the 'Kruskal-Wallis test' in the nonparametric case. Multivariate frequency distributions were gained by 'hierarchical cluster analysis' as the descriptive statistical method, and inferences were tested by 'discriminant analysis'. Since the chosen classification method (Ward's method on standardized variables) is based on the 'minimum variance criterion', this analysis creates multivariate normal distributed classes, which can be subsequently tested by parametric 'discriminant analysis' based

HUMERUS (female)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	13	365.8	10.74	2.98
GS	5	371.6	2.38	1.06
HD	6	369.3	2.88	1.17
Total	24	367.9	8.30	1.69

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
3.8181	2	21	0.039

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	135.6	67.8	0.3904
Within Grp.	21	1447.2	68.9	
Total	23	1582.8		

Nonparametric test for differences of populations:

Kruskal-Wallis	Chi-Square	d.f.	Sign.
	4.0462	2	0.1322

HUMERUS (male)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	5	423.5	10.87	4.86
GS	3	414.2	15.67	9.05
HD	18	426.8	15.28	3.60
Total	26	424.6	14.63	2.87

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
0.1218	2	23	0.886

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	415.7	207.8	0.3945
Within Grp.	23	4934.3	214.5	
Total	25	5350.0		

RADIUS (female)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	16	286.8	10.68	2.67
GS	9	284.9	8.73	2.91
HD	13	286.8	11.76	3.26
Total	38	286.4	10.41	1.69

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
0.4579	2	35	0.636

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	24.8	12.4	0.8970
Within Grp.	35	3982.0	113.8	

Total 37 4006.9

RADIUS (male)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	5	327.1	6.07	2.71
GS	4	334.1	6.66	3.33
HD	11	330.2	10.54	3.18
Total	20	330.2	8.89	1.99

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
0.7699	2	17	0.479

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	109.7	54.8	0.5246
Within Grp.	17	1391.0	81.8	
Total	19	1500.7		

ULNA (female)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	22	322.2	12.80	2.73
GS	16	328.2	12.10	3.02
HD	6	331.1	4.73	1.93
Total	44	325.6	12.09	1.82

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
3.7830	2	41	0.031

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	537.4	268.7	0.1600
Within Grp.	41	5746.2	140.2	
Total	43	6283.6		

Nonparametric test for differences of populations:

Kruskal-Wallis	Chi-Square	d.f.	Sign.
	3.1663	2	0.2053

ULNA (male)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	8	364.2	21.71	7.68
GS	3	381.2	7.25	4.19
HD	13	376.4	14.84	4.12
Total	24	372.9	17.47	3.57

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
3.4770	2	21	0.050

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	975.0	487.5	0.2082
Within Grp.	21	6048.5	288.0	
Total	23	7023.5		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	975.0	487.5	0.2082
Within Grp.	21	6048.5	288.0	
Total	23	7023.5		

Nonparametric test for differences of populations:

Kruskal-Wallis	Chi-Square	d.f.	Sign.
	2.0275	2	0.3629

FEMUR (female)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	20	390.8	12.40	2.77
GS	3	378.3	5.51	3.17
HD	9	392.8	13.23	4.41
Total	32	390.2	12.53	2.22

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
1.0098	2	29	0.377

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	488.8	244.4	0.2156
Within Grp.	29	4380.0	151.0	
Total	31	4868.8		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	488.8	244.4	0.2156
Within Grp.	29	4380.0	151.0	
Total	31	4868.8		

FEMUR (male)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	3	452.7	19.30	11.14
GS	4	456.2	20.12	10.06
HD	23	464.4	18.71	3.90
Total	30	462.1	18.74	3.42

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
0.0109	2	27	0.989

Statistic	d.f. 1	d.f. 2	2-tail Sign.
0.0109	2	27	0.989

Tab. 1 - One-way analysis of variance. Descriptive statistics. Test of homogeneity of variance. Non-parametric test (Kruskal-Wallis) for three cases only.

on canonical correlation (e.g., Blackith & Reymont, 1971; Bortz, 1993; Everitt, 1993; Sokal & Rohlf, 1995; SPSS, 1983). All calculations and drawings were done using the software package SPSS for Windows (version 6.1.3.).

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	522.3	261.2	0.4913
Within Grp.	27	9661.5	357.8	
Total	29	10183.8		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	522.3	261.2	0.4913
Within Grp.	27	9661.5	357.8	
Total	29	10183.8		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	522.3	261.2	0.4913
Within Grp.	27	9661.5	357.8	
Total	29	10183.8		

TIBIA (female)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	27	264.4	9.26	1.78
GS	7	266.2	12.10	4.57
HD	4	274.4	13.52	6.76
Total	38	265.8	10.40	1.69

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
1.7291	2	35	0.192

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	346.3	173.2	0.2051
Within Grp.	35	3655.0	104.4	
Total	37	4001.3		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	346.3	173.2	0.2051
Within Grp.	35	3655.0	104.4	
Total	37	4001.3		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	2	346.3	173.2	0.2051
Within Grp.	35	3655.0	104.4	
Total	37	4001.3		

TIBIA (male)

Statistical parameters:

Cave	n	$\bar{x}$	sd	se
CO	5	297.9	4.90	2.19
GS	1			
HD	31	303.3	7.58	1.36
Total	37	302.6	7.46	1.24

Levene test for homogeneity of variances:

Statistic	d.f. 1	d.f. 2	2-tail Sign.
0.9035	1	34	0.349

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	1	125.9	125.9	0.1347
Within Grp.	34	1822.5	53.6	
Total	35	1948.4		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	1	125.9	125.9	0.1347
Within Grp.	34	1822.5	53.6	
Total	35	1948.4		

Source	d.f.	S.S.	M.S.	F-Prob.
Between Grp.	1	125.9	125.9	0.1347
Within Grp.	34	1822.5	53.6	
Total	35	1948.4		

RESULTS

UNIVARIATE ANALYSES

The histograms of fore limbs (Text-fig. 6) show clear bimodal distributions for all bones in each cave.

While small (interpreted as female) bones are predominant in Conturines Cave (and partly in Gamssulzen Cave as well), larger (interpreted as male) bones dominate in the Herdengel Cave. The number of humeri ($n = 9$) from Gamssulzen is relatively small, but the histogram fits very well into the common trend visible in the other caves. In particular, the modes in all three histograms prove the extent of dimorphism. Besides the virtually identical position of males the variances within sexes are also congruent. In general, sexual dimorphism of limb bones is best indicated by the greatest length of humerus, radius and ulna.

The situation is less clear in the hind limbs.

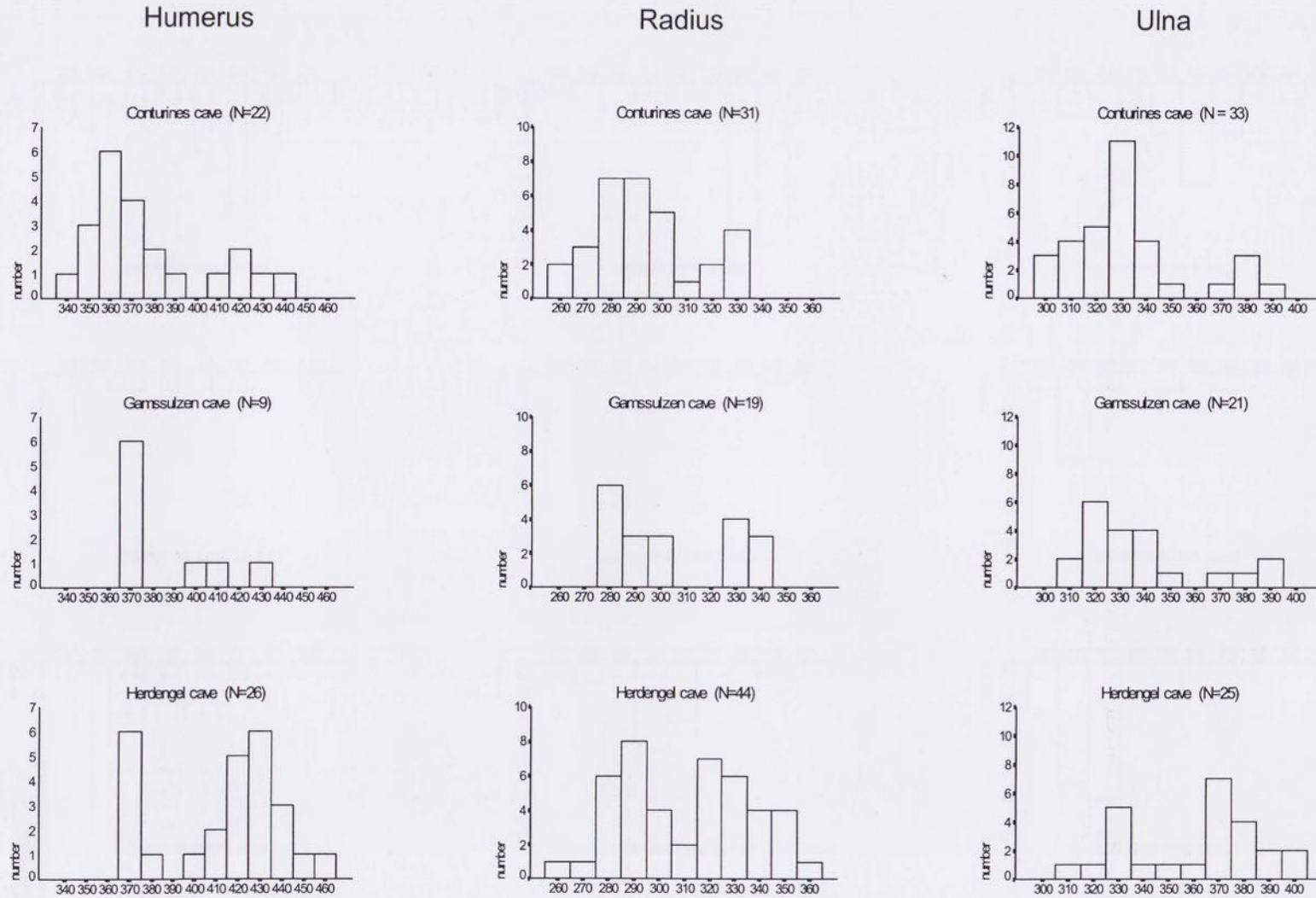
However, the histogram of femora (Text-fig. 7) from the Herdengel Cave clearly shows a bimodal distribution, where the number of male bones is larger. On the other hand, the Conturines and Gamssulzen Caves show fewer male femora. In all histograms from the three caves, however, the comparison of modes indicates clear congruence. Despite the relatively large number of tibiae (except from Gamssulzen Cave), the frequency distribution of their greatest lengths (Text-fig. 7) demonstrates a less clear bimodal distribution than the previous elements. The Conturines and Gamssulzen Caves again show a clear surplus of female tibiae. Complete fibulae are rarer than any other long bones. Owing to

Humerus	Var.	Wilks'	F-test	Signif.
CO, n=18	GL	0.1339	103.46	0.0000
	PL	0.1436	95.41	0.0000
	WT	0.2369	51.53	0.0000
	DW	0.2471	48.76	0.0000
GS, n=8	DW	0.1264	41.47	0.0007
	WT	0.1312	39.72	0.0007
	GL	0.1314	39.67	0.0007
	PL	0.1685	29.61	0.0016
HD, n=24	GL	0.2128	81.36	0.0000
	PL	0.2181	78.86	0.0000
	DW	0.2454	67.63	0.0000
	WT	0.2949	52.60	0.0000
Radius	Var.	Wilks'	F-test	Signif.
CO, n=21	DW	0.2026	74.79	0.0000
	GL	0.2313	63.13	0.0000
	PL	0.2417	59.61	0.0000
	PW	0.3630	33.34	0.0000
	LCR	0.4182	26.43	0.0001
	WCR	0.4683	21.57	0.0002
GS, n=13	WCR	0.0749	135.80	0.0000
	DW	0.0837	120.48	0.0000
	PL	0.0960	103.53	0.0000
	LCR	0.0965	102.98	0.0000
	PW	0.0976	101.76	0.0000
	GL	0.0998	99.22	0.0000
HD, n=24	DW	0.1436	131.17	0.0000
	PW	0.1735	104.81	0.0000
	LCR	0.1735	104.79	0.0000
	GL	0.1976	89.36	0.0000
	PL	0.2594	62.81	0.0000
	WCR	0.2962	52.28	0.0000
Ulna	Var.	Wilks'	F-test	Signif.
CO, n=30	SDD	0.2775	72.91	0.0000
	DIT	0.2983	65.88	0.0000
	PW	0.3299	56.88	0.0000
	TDD	0.3338	55.89	0.0000
	DW	0.3375	54.95	0.0000
	GL	0.3948	42.91	0.0000
	HPAT	0.4425	35.28	0.0000

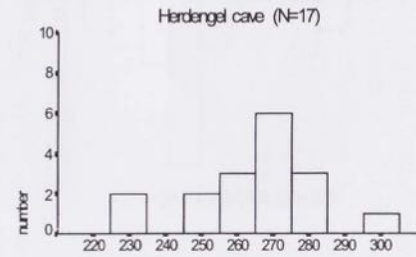
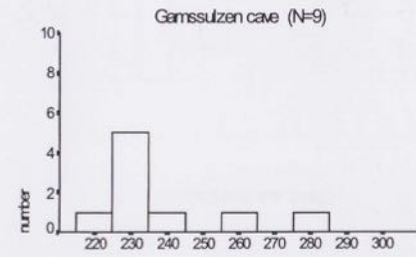
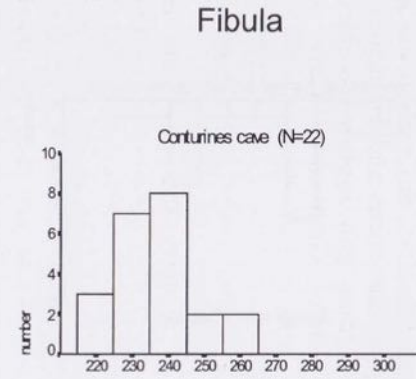
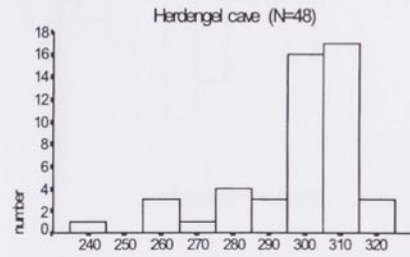
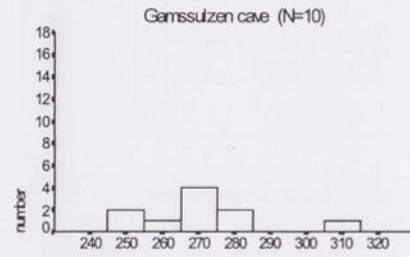
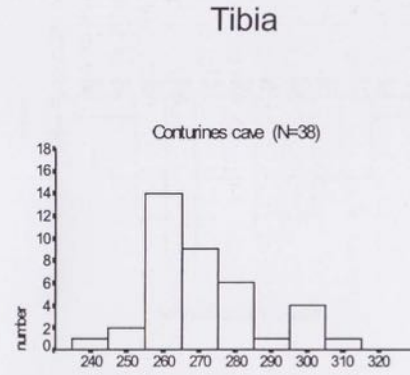
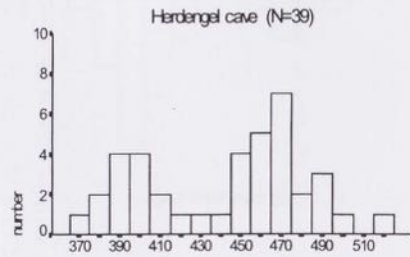
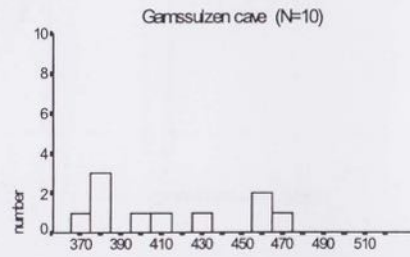
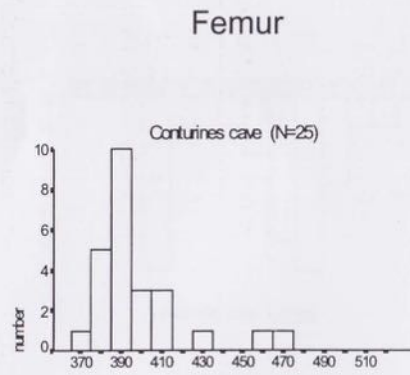
GS, n=19	PW	0.1251	118.86	0.0000
	HPAT	0.1729	81.33	0.0000
	GL	0.2447	52.46	0.0000
	DW	0.2498	51.04	0.0000
	TDD	0.3319	34.21	0.0000
	SDD	0.3866	26.97	0.0001
	DIT	0.4176	23.71	0.0001
HD, n=19	PW	0.1829	75.95	0.0000
	HPAT	0.2177	61.08	0.0000
	DIT	0.2358	55.09	0.0000
	GL	0.2462	52.04	0.0000
	SDD	0.3221	35.78	0.0000
	TDD	0.3240	35.46	0.0000
	DW	0.3460	32.14	0.0000
Femur	Var.	Wilks'	F-test	Signif.
CO, n=23	GL	0.2683	57.27	0.0000
	PW	0.3041	48.06	0.0000
	DW	0.3164	45.38	0.0000
	GLT	0.3428	40.25	0.0000
GS, n=7	GLT	0.0805	57.08	0.0006
	GL	0.1092	40.80	0.0014
	DW	0.1399	30.74	0.0026
	PW	0.1686	24.66	0.0042
HD, n=32	PW	0.1682	148.33	0.0000
	GLT	0.1930	125.43	0.0000
	GL	0.2154	109.28	0.0000
	DW	0.2604	85.19	0.0000
Tibia	Var.	Wilks'	F-test	Signif.
CO, n=32	GL	0.3296	61.03	0.0000
	PW	0.3356	59.40	0.0000
	WCT	0.4072	43.67	0.0000
	TDD	0.5392	25.64	0.0000
HD, n=35	PW	0.4182	45.90	0.0000
	GL	0.4341	43.02	0.0000
	WCT	0.5333	28.88	0.0000
	TDD	0.5984	22.15	0.0000

Tab. 2 - Test for sexual dimorphism in limb bone measurements of 3 cave sites using one-way analysis of variance.

Text-fig. 6 - Histograms of greatest length (GL) of fore limb bones.



Text-fig. 7 - Histograms of greatest length (GL) of hind limb bones.



their rod-shaped design, fibulae tend to fragment more easily than other limb bones. Nevertheless, there are more female bones in Conturines and Gamssulzen, while male fibulae are more numerous in Herdengel. These sex ratios correspond very well to those of the tibiae because fibula length directly correlates with tibia in the same individual.

MULTIVARIATE ANALYSES

All limb bones were examined using hierarchical cluster analysis, except of the fibula. The dendrograms (Text-fig. 8/1 to 8/5) of every site show a clear separation of the five limb bones into two classes, the one is interpretable as female, the other as male individuals. One-way analyses of variance confirm the significant differences between sexes for all limb bones in each cave (Table 2).

According to the dendrograms of **humeri** (Text-fig. 8/1), samples from the three caves differentiate very clearly into two groups corresponding to sex. Even the small sample from Gamssulzen Cave ($n = 8$) follows this trend. Dendrograms of **radii** from Conturines, Gamssulzen and Herdengel Cave also allow a clear separation into two groups. This confirms the conclusion from univariate comparison, that radii are suitable to distinguish sexual dimorphism. The distinction of sexes using the **ulnae** is similar to that of the radii, as the two bones are functionally and positionally connected. Furthermore, ulnae and radii are more common in all sites than other limb bones. The **femora** and **tibiae** dendrograms also allow a clear distinction into sexes. Note that only one male tibia from Gamssulzen Cave can be separated (Text-fig. 8/5) using cluster analyses.

The sex ratio obtained by cluster analysis also corresponds to the results of univariate analysis (Text-figs 6 and 7). Cave bears from Conturines and Gamssulzen Caves clearly show more female limb bones. In Herdengel Cave, male bones are predominant or the sex ratio is relatively balanced (radius).

Discriminant analyses based on the groups obtained by cluster analysis strengthen the clear differentiation into sexes as obtained by univariate analyses. This is well represented by frequency histograms of discriminant scores which are similar to the univariate frequency distributions (Text-fig. 9/1 to 9/3). Additionally, the canonical discriminant functions for each cave and skeletal element are highly significant ($p < 0.05$).

Even the small sample size of humeri at Gamssulzen (e.g., only 5 female and 3 male) or male radii from the same cave (number of 4) still reveals the main trend of a clear classification into 2 groups (Text-fig. 9/1). The number of male ulnae from Gamssulzen ($= 3$), the male femora from Conturines ($= 3$) and the female and male femora from Gamssulzen Cave ($= 3$ and 4, respectively) is also relatively small (Text-fig. 9/2), but discriminant analyses

can be calculated on the basis of at least three individuals per class. Therefore, this analysis was applied for tibiae only at Conturines and Herdengel Caves (Text-fig. 9/3), because only one case was observed in the male subset of Gamssulzen Cave sample. Differences between sexes are very small in the case of ulnae from Conturines and tibiae from Herdengel Cave, but their distinction into two groups is nevertheless clear.

Discriminant analyses also allows to test the results of cluster analysis by positioning each bone to defined classes according to probabilities. This type of classification resulted in a rate of 100% correctly designated skeletal elements, thus misclassification rate is 0% for every long bone at each cave. Additionally, the canonical discriminant function for each cave and skeletal element show no significance ($p = 0.05$).

SEX RATIO

Sex ratios of the five limb bone elements are calculated for each cave by relating the counted numbers between the two classes as obtained by cluster analysis. Differences in sex ratios between the Herdengel and Conturines Cave are obvious. While in the high alpine cave the females dominate, which is confirmed by the range of female/male-ratios between 2.60 and 6.67, the males dominate in the deepest cave (female/male-ratio from 0.17 to 0.64) except the radius, where both sexes are equally represented. The sex ratio for the Gamsulzen Cave bears is similar to that of the Conurines Cave with a dominance of small-sized bones, despite the low content of cave bear remains.

Sex ratios of humerus data:

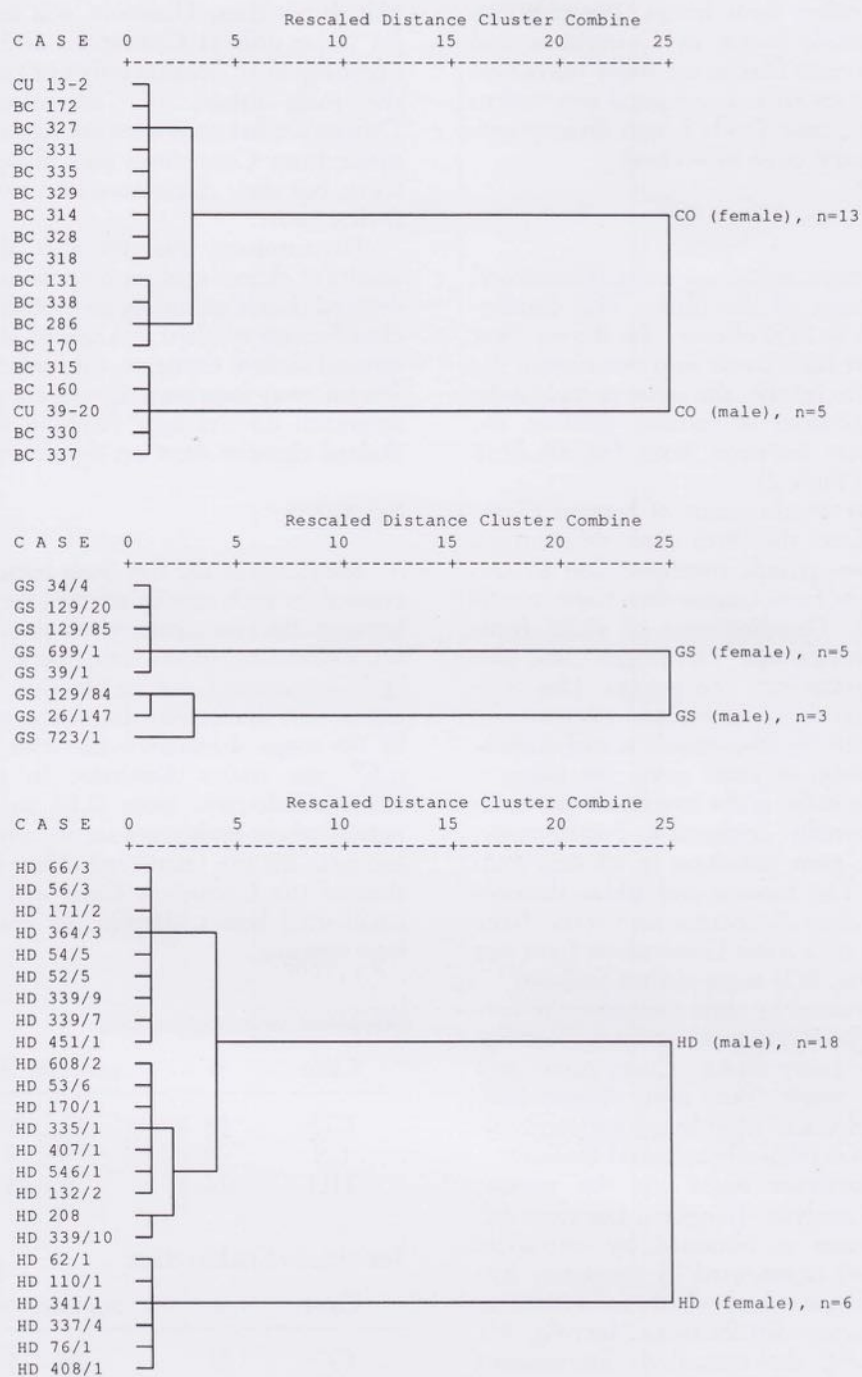
Cave	n	sex ratio (female/male)
CO	18	13 : 5 or 2.60
GS	8	5 : 3 or 1.67
HD	24	6 : 18 or 0.33

Sex ratios of radius data:

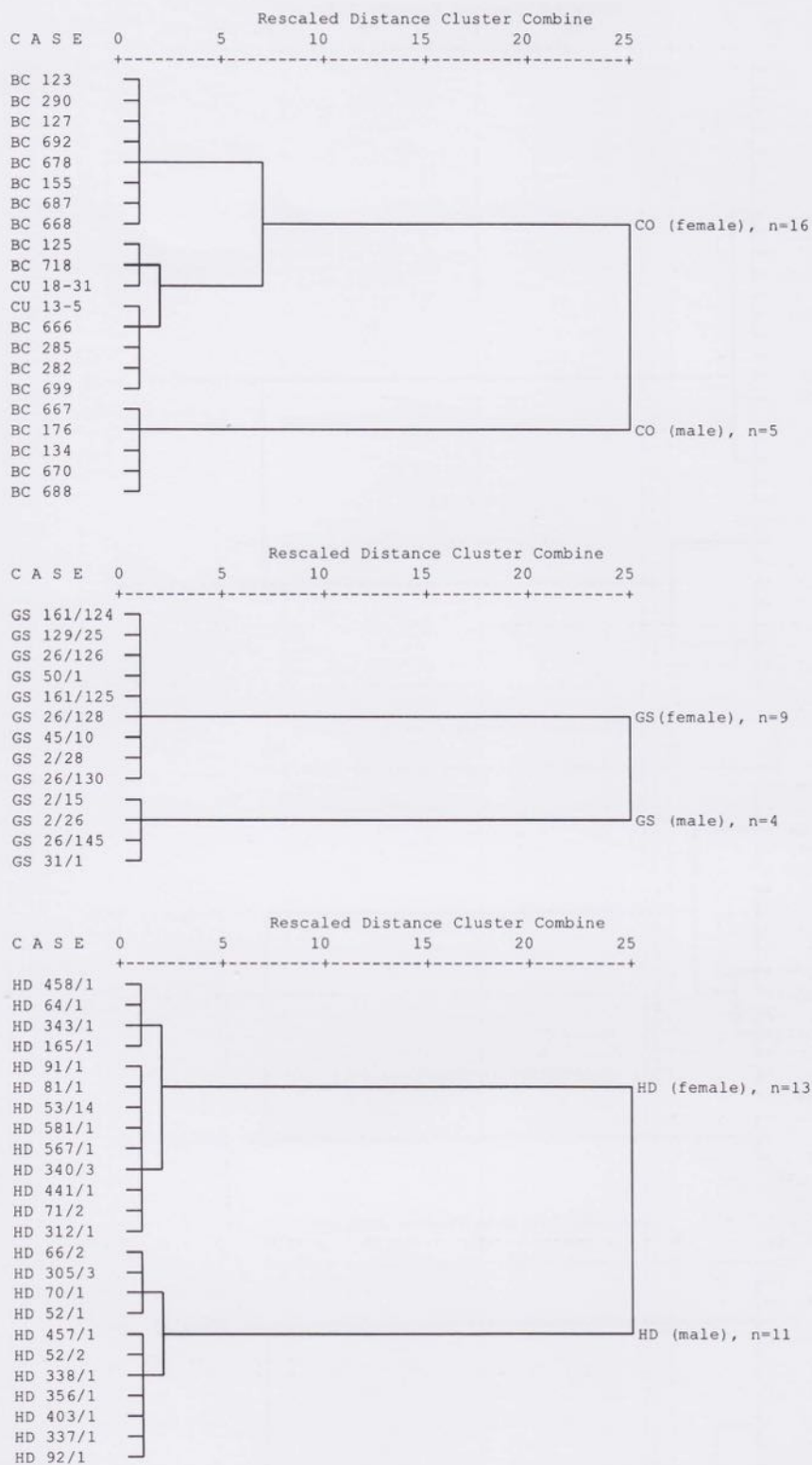
Cave	n	sex ratio (female/male)
CO	21	16 : 5 or 3.20
GS	13	9 : 4 or 2.25
HD	24	13 : 11 or 1.18

Sex ratios of ulna data:

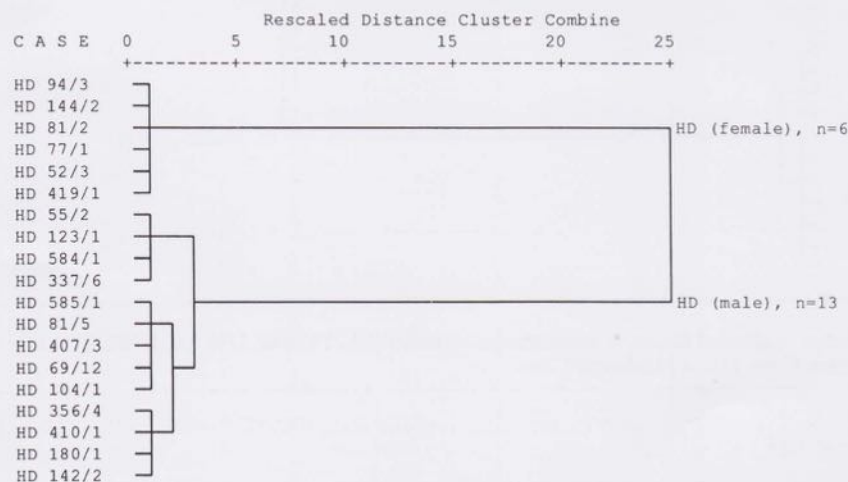
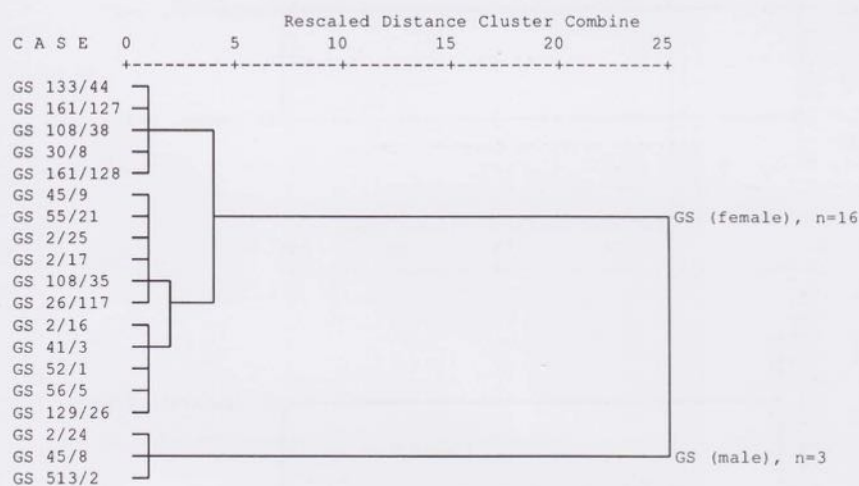
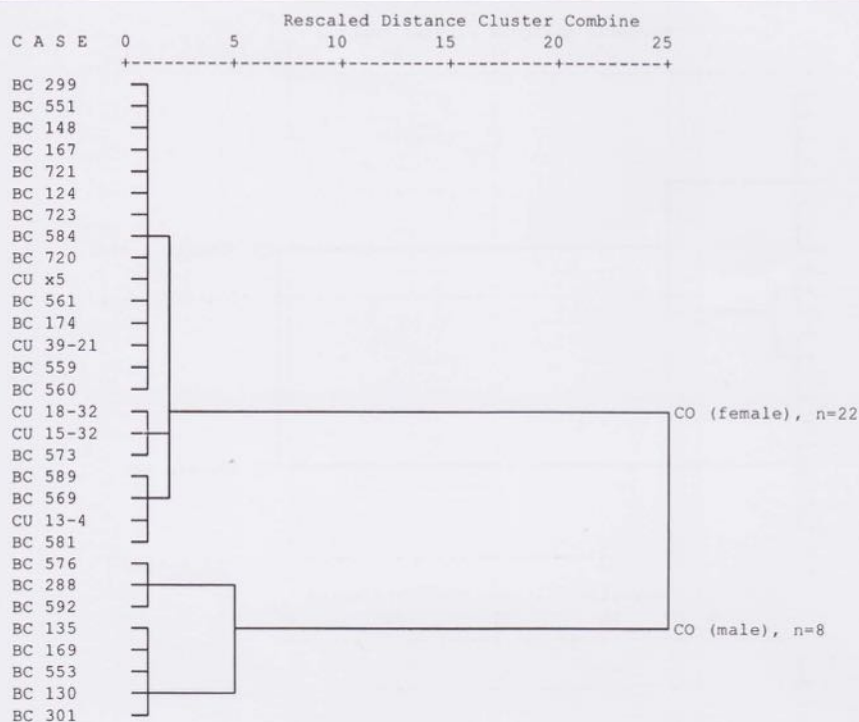
Cave	n	sex ratio (female/male)
CO	30	22 : 8 or 2.75
GS	17	16 : 3 or 5.33
HD	19	6 : 13 or 0.64



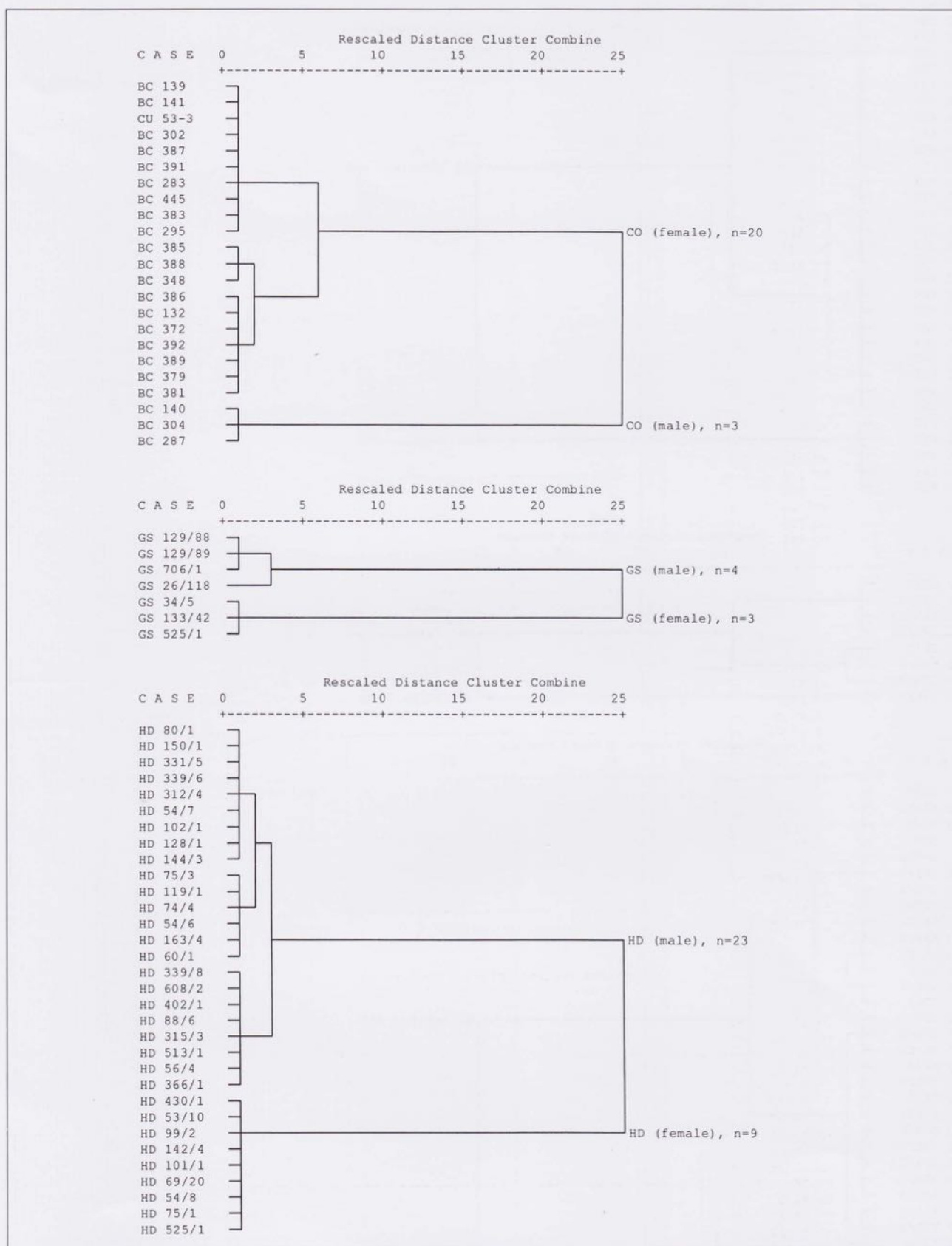
Text-fig. 8/1 - Hierarchical cluster analysis of humerus. 4 measurement variables (GL, PL, WT, DW). CO = Conturines Cave, GS = Gamssulzen Cave, HD = Herdengel Cave.



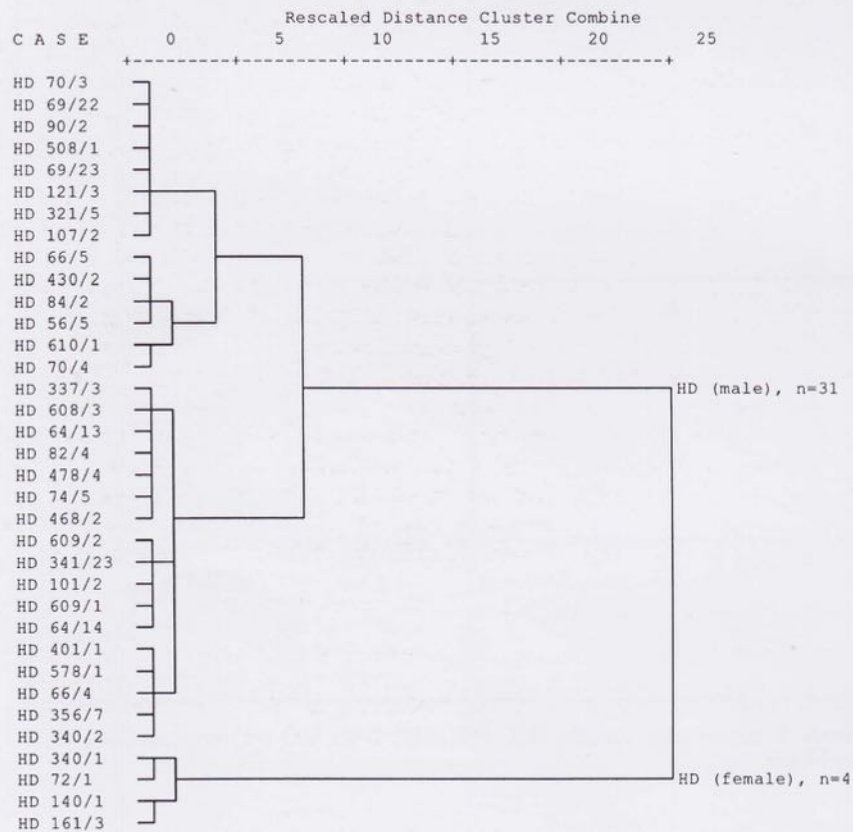
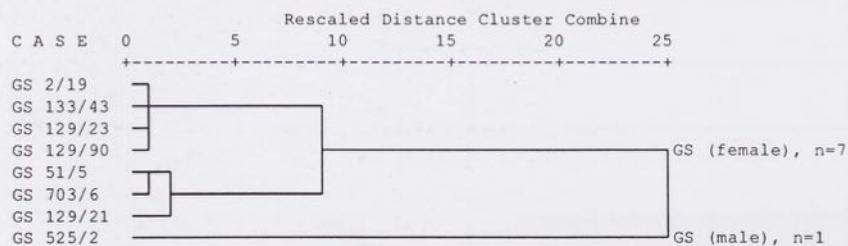
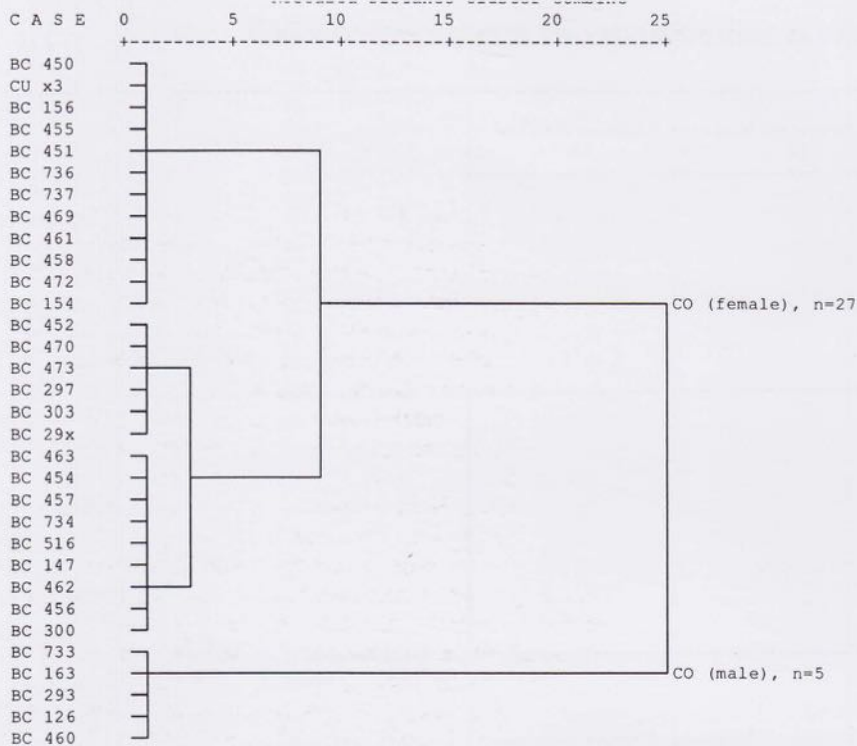
Text-fig. 8/2 - Hierarchical cluster analysis of radius. 6 measurement variables (GL, PL, PW, DW, LCR, WCR). CO = Conturines Cave, GS = Gamssulzen Cave, HD = Herdengel Cave.



Text-fig. 8/3 - Hierarchical cluster analysis of ulna. 7 measurement variables (GL, PW, DW, SDD, TDD, HPAT, DIT). CO = Conturines Cave, GS = Gamssulzen Cave, HD = Herdengel Cave.



Text-fig. 8/4 - Hierarchical cluster analysis of femur. 4 measurement variables (GL, PW, GLT, DW). CO = Conturines Cave, GS = Gamssulzen Cave, HD = Herdengel Cave.



Sex ratios of femur data:

Cave	n	sex ratio (female/male)
CO	23	20 : 3 or 6.67
GS	7	3 : 4 or 0.75
HD	32	9 : 23 or 0.39

Sex ratios of tibia data:

Cave	n	sex ratio (female/male)
CO	32	27 : 5 or 5.40
GS	8	7 : 1 or 7.00
HD	35	4 : 31 or 0.17

On the basis of the three investigated caves from different altitudes, a shift in the sex ratios correlated to altitude can be detected. While larger sized males are numerous at low altitudes, females seem to become more abundant in higher regions. If limb bones are not differentiated according to sex, then the summarised size distributions may show a significant decrease in population means correlated to altitude, which led to the assumption of a small-sized 'high-alpine form' (Rabeder, 1991).

The existence of such a small sized local population must be proven by significant differences within both or even one of the sexes considering the three caves. Parametric and nonparametric analyses of variance were performed for each sex from the three sites using the greatest length of examined limb bones (Table 1). Testing homogeneity of variances as an assumption for parametric one-analysis of variances showed homogeneity, but demonstrated significant differences for only three bones: the female humerus, the female ulna, and the male ulna. The nonparametric Kruskal-Wallis test was additionally performed for these elements. Results of both types of analyses demonstrate the statistically significant homogeneity of all limb bones for each sex. Thus, there are no significant differences in all five skeletal elements between the three caves for each sex. In the following, the assumption of a small-sized form of cave bear from Conturines Cave must be rejected.

DISCUSSION

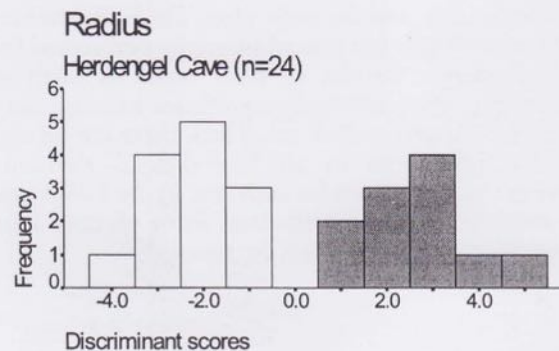
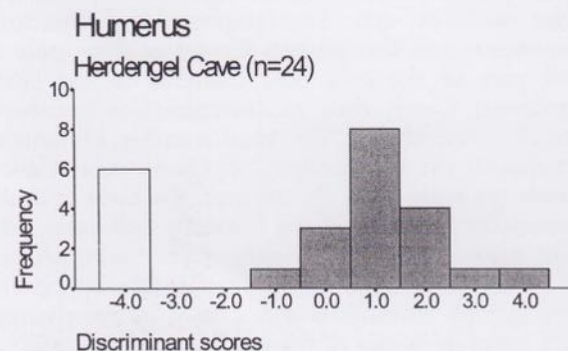
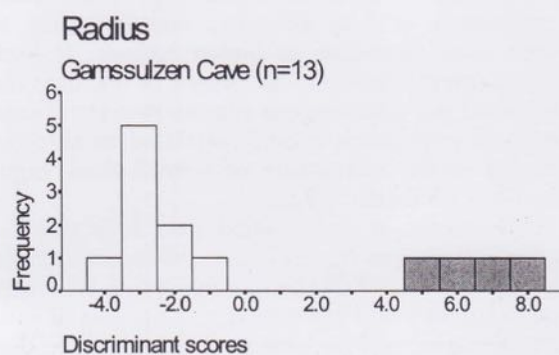
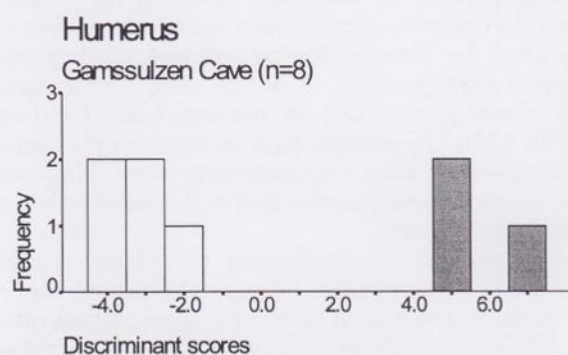
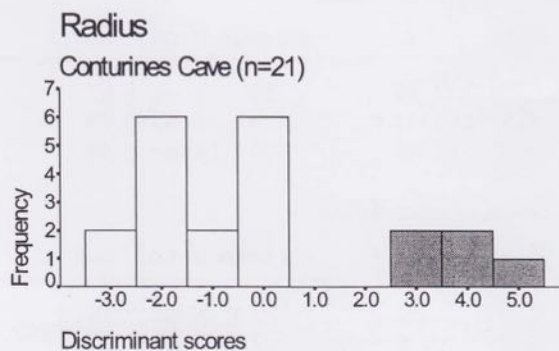
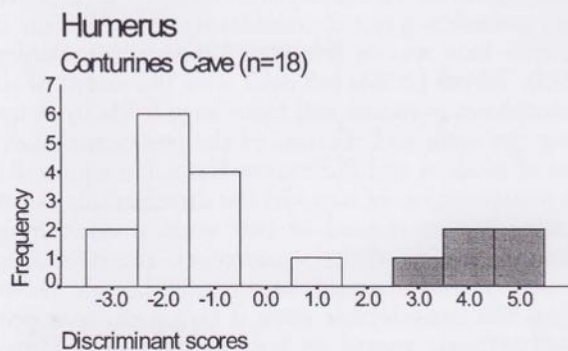
Sexual dimorphism can be expressed as bimodal frequency distributions in long bones of cave bears. Other explanations of bimodality are possible, such as effected by large- and small-sized sympatric species occupying different ecological niches. This interpretation, however, would lead to the assumption that

there was no sexual dimorphism in either species present, a weak argument considering the situation in modern bear species (Kurtén, 1967, p. 56; Stirling 1993). Turner (1984) has dealt with the extent of sex dimorphism in recent and fossil large felids by examining the teeth and remains of the postcranial skeletons of modern and Pleistocene lions. He argues that the interpretation of bimodal size distributions as two distinct species instead of two sexes is misleading. Turner concludes that "... moreover, attempts using the fossil record as a guide to tempo and mode in evolution risk considerable error if taxa have been proposed without regard to sexual variation" (Turner, 1984, p. 8).

Differences in body size of cave bear sexes calls for a biological explanation. The larger body size of males may best be accounted for territorial fights during mating periods, as has been observed in modern bears. In contrast, dimorphism may perhaps also be explained by females having reached fertility and stopped growing earlier than their male counterparts, also a well-known fact in modern bears (Stirling, 1993). Other hypothesis such as food supply shortages argues against a size-increasing trend. However, such developments can also lead to the stabilisation of sexual dimorphism.

Comparison of distribution parameters for all limb bone measurements between the sites of different altitude resulted in constancy for each sex, thus no differences in either males or females correlated to altitude could be detected. The problem with sex ratio of cave bears is that the material often represents a small number of the existing remains. Additionally, the size of caves can change rapidly during some 10,000 years. The investigated skeletal elements are either without any stratigraphical information (Conturines and Gamssulzen Caves) or show only a small part of the cave bear contents of the sites (Herdengel Cave), thus an interpretation becomes difficult. Nevertheless, the total number of female elements in the Conturines and Gamssulzen Caves exceeds the male ones. By contrast, the ratio of limb bones in the Herdengel Cave is mostly well-balanced, while male elements are otherwise predominant. Therefore, the obvious shift to smaller sized specimen living in high altitudes is only caused by the change of sex ratios in favour of the smaller sized females.

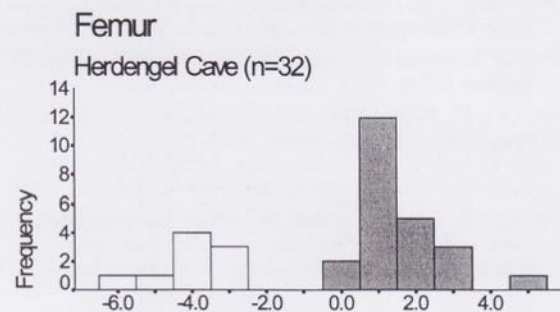
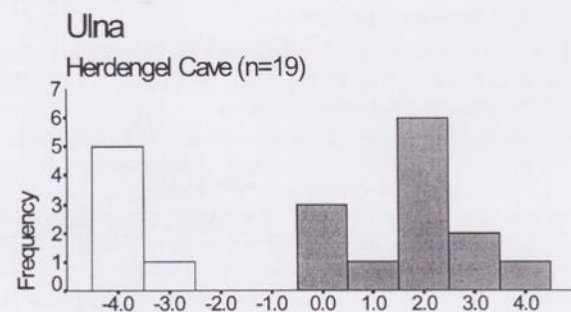
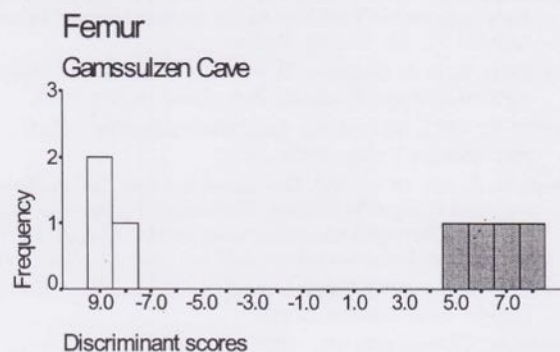
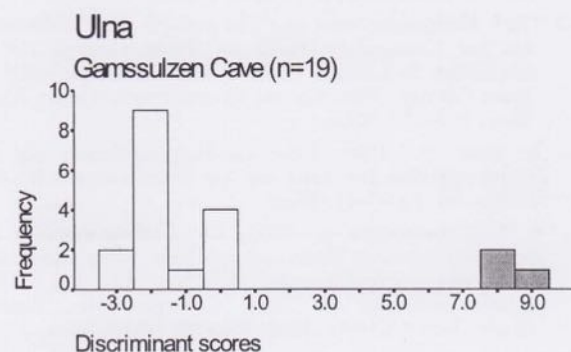
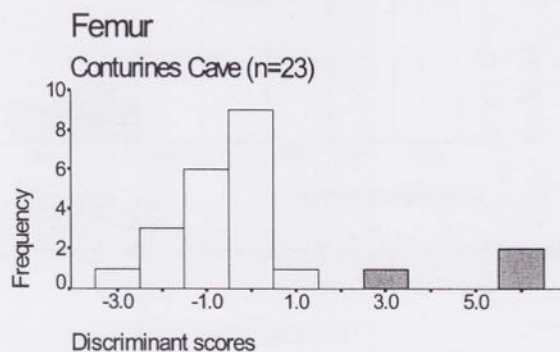
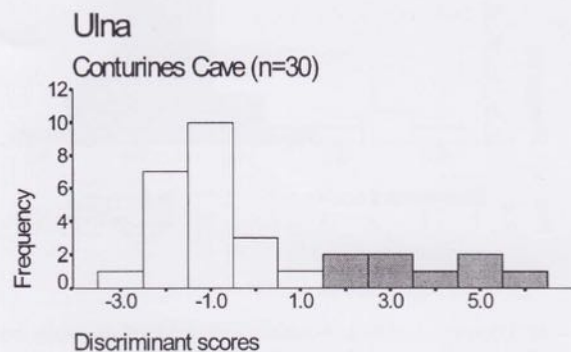
An explanation of female dominance in ecologically extreme regions may be found in hiding cubs against males. For example, Kurtén (1976, p. 77) suggests that female cave bears with cubs show preference for small caves as sleeping places, because they are easier to defend against male intruders.



Text-fig. 9/1 - Frequency histograms of discriminant scores from humerus and radius. Hollow bars represent female elements, shadowed bars male elements. The number in parentheses (beside the subtitle) represents sample size.

A last issue of this investigation is the stability of limb-bone dimensions over a relatively long period of time for both sexes. Such stability is indicated by frequency distributions of the investigated bones, constant over a duration of about 90,000 years (from

25,000 to 115,000 years BP). Only 2 bones from the Herdengel Cave show older ages (from 126,000 to 136,000 years B.P), but both fit well into the dimension range of the younger bones.

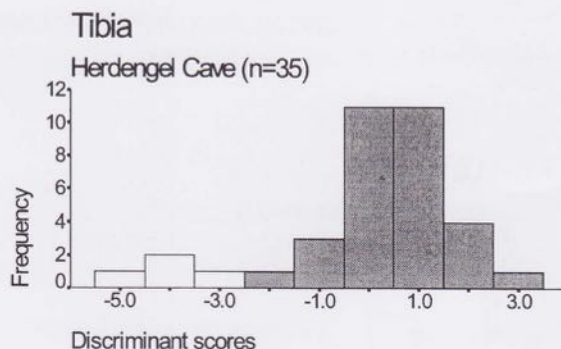
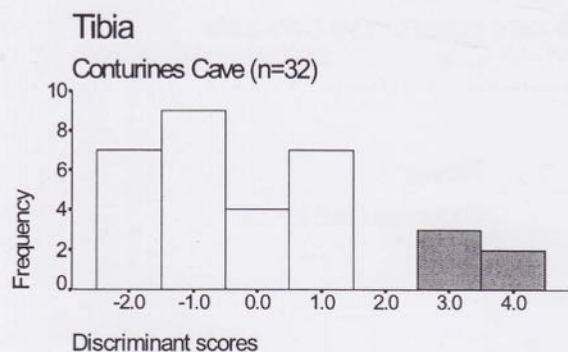


Text-fig. 9/2 - Frequency histograms of discriminant scores from ulna and femur.

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Text-fig. 9/3 - Frequency histograms of discriminant scores from tibia.

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