

CORRELATING GENETIC RESULTS WITH BIOMETRIC ANALYSIS ON METAPODIAL BONES

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S. C. Münzel – K. Athen: Correlating Genetic Results with Biometric Analysis on Metapodial Bones

Abstract: The ancient DNA research from three geographically close caves in the Ach valley, namely Geißenklösterle, Hohle Fels and Sirgenstein, revealed two different cave bear haplogroups, haplogroup 1 (*Ursus spelaeus*) and haplogroup 4 (*Ursus ingressus*). The latter replaced the former around 28,000 years BP (Hofreiter et al., 2002). The goal of this analysis is to find species or taxa defining characteristics using biometrical analysis. Beside teeth (Rabeder, 1999, Baryshnikov et al., 2003; Grandal d'Anglade and Lopez-Gonzalez, 2005), metapodials are one of the most promising elements of the postcranium in respect of evolutionary trends, species distinction and sexual dimorphism. After a preliminary statistical investigation (distribution, variance, correlation) each metapodial was classified and allocated to either species or taxon by discriminant analysis. These results were cross-checked due to stratigraphical provenience of the items correlated with the date of replacement.

Key words: Palaeogenetic Analysis, Biometric Analysis, Metapodial Bones, Cave Bears

INTRODUCTION

The morphological variability of cave bears is one of their characteristics as Ehrenberg stated already in 1922. Very early the 'hochalpine Kleinform' (Ehrenberg, 1929) of cave bears in the Alps were matter of considerable debate, reflecting if either their origin was monophyletic with respect to their mtDNA representing an ancestral state, or if the small size was an adaptation to high-alpine environment but derived from large forms several times, or a third possible explanation suggesting that it represents a seasonal separation of sexes (Hofreiter et al., 2002; Rabeder et al., 2000; Rabeder et al., 2004; Reisinger and Hohenegger, 1998). The high variability was one reason for Hofreiter to study the mitochondrial-DNA of cave bears (Hofreiter, 2002). He differentiated four haplogroups within the cave bear lineage. Quite recently a fifth haplogroup the so called Asian cave bear was sequenced by Knapp et al. (2009).

To palaeontologists and archaeozoologists the question arises, if there are any recognisable morphological differences between the haplogroups at all, respectively between *Ursus spelaeus* and *ingressus*.

The cave bear replacement in the Ach valley happened quite suddenly within the Gravettian occupation (ca. 30,000 and 27,000 BP). Considering the radiocarbon dates, which

show very little overlapping, all specimens older than 28,000 years belong to *Ursus spelaeus* and all specimens younger than this to *Ursus ingressus*.

But a separation of the undated bear remains to either taxon was not possible neither by tooth morphology (Münzel et al., 2007) nor by a clear cut in the stratigraphical sequence, since in the Gravettian horizon IIb (AH IIb) of Hohle Fels both haplogroups are present (Münzel et al., in press). For the stratigraphical cross-checking we thus referred all specimens underlying AH IIb of Hohle Fels and AH It of Geißenklösterle to *Ursus spelaeus*, all specimens above these layers as possible *ingressus*-candidates (fig. 1).

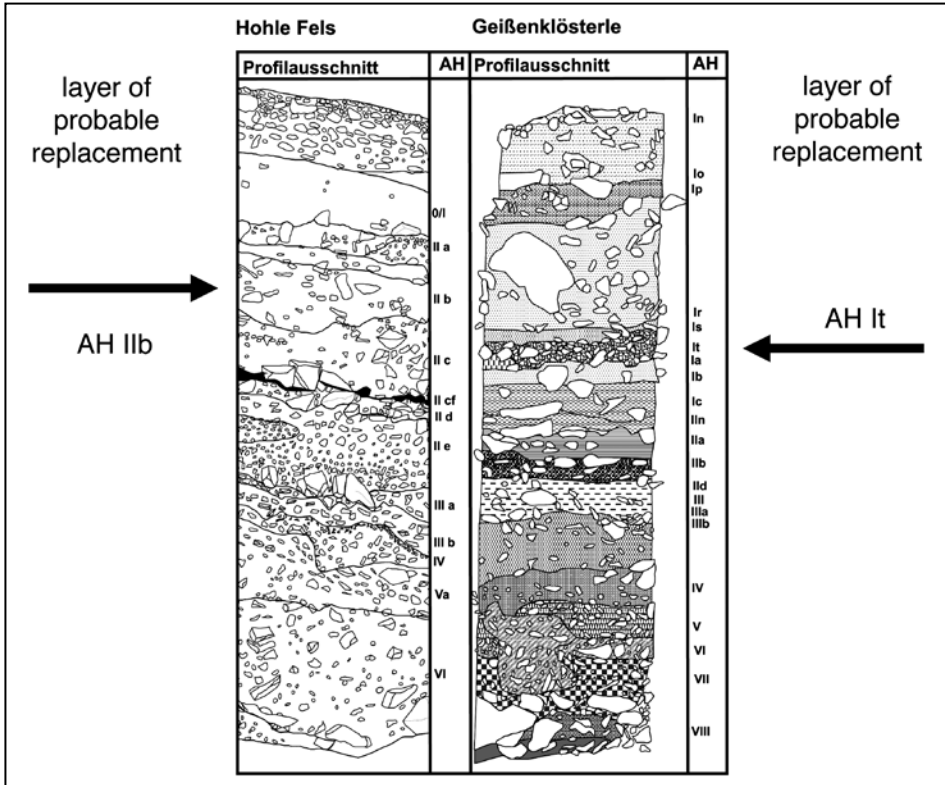


Figure 1: Stratigraphical location of the replacement in the Hohle Fels and Geißenklösterle profiles.

To compare the two taxa at the same locus, namely in Hohle Fels and Geißenklösterle, the material for the time after the replacement was not large enough to be statistically relevant. From the first appearance of *Ursus ingressus* around 28,000 BP to his probably last evidence around 24,000 BP¹, *ingressus* had only 4,000 years to get settled in the Ach valley, which is not very long in geological terms. Meaning, even if one could classify each bear bone, one cannot expect a very large sample of *Ursus ingressus* in the Ach valley caves.

¹ At present the youngest date for cave bear is 23,780±120BP from Vindija cave. The 13,230±130BP (OxA-4,854) date of an *Ursus ingressus* from Geißenklösterle was revised by a second dating in Groningen (GrA-39,687) to 24,210±100BP (Münzel et al., in press). The Swabian Jura was believed to serve as one of the refuge for cave bears, but this and other new dates from the Ach valley confirm that cave bears became extinct before the Last Glacial Maximum. This re-dated sample is consistent with other dates in Europe (Pacher and Stuart, 2009).

Therefore, the biometrical data of Gamssulzen cave bears, the type locality of *Ursus ingressus* in Austria, were included into the analysis as a reference population for this species.

METHODICAL CONSIDERATION

Mitochondrials are inherited by the mother lineage and are not responsible for the phenotypic appearance of an individual. In the case of the Ach valley it means that the mother lineage (*spelaeus*) was replaced by more successful *ingressus*-females. The phenotype respectively the appearance is coded in the nuclear DNA. Knapp et al. (2009, 1234) stated “mitochondrial data alone are insufficient to evaluate the species status and additional nuclear DNA data would be necessary to test the multiple species hypothesis.” In only one known case we possibly deal with species, since there obviously was no mitochondrial gene flow between *Ursus spelaeus eremus* and *Ursus ingressus* during more than 15,000 years in the neighbouring caves of Ramesch and Gamssulzen. Considering this evidence of consistency in palaeontological and genetic results over such a long period, a species status of *U. spelaeus* and *ingressus* in the original biological sense is very possible (Hofreiter, 2005). Consequently Knapp et al. (2009) speak about three main cave bear lineages, as there are *Ursus spelaeus* (including *U. s. spelaeus*, *U. s. eremus* and *U. s. ladinicus*), *Ursus ingressus* and *Ursus deningeri kudarensis*, the Asian cave bear.

The separation of the two ursid lineages *Ursus spelaeus* and *Ursus ingressus* was estimated by Hofreiter (2002) with 660,000 years for the MRCA (Most Recent Common Ancestor), while after Knapp et al. (2009) the *spelaeus* and *ingressus* lineages diverged between 173,000 and 414,000 years ago. In any case, even if there is no direct correlation between ancient DNA and morphological appearance, it is worth trying to find characteristics for the two relevant taxa under consideration. In the following we refer to them as species.

MATERIAL AND METHODS

Only very few biometrical analyses work with postcranial elements, especially for the classification of taxa (Reisinger, 2001; Toškan, 2007). Biometrical and statistical methods revealed distinguishing features characteristic for the species, *Ursus spelaeus* and *Ursus deningeri* (Athen, 2006; 2007). These tools seemed to be promising for the distinction of *Ursus spelaeus* and *ingressus* as well. The goal of the analysis presented here is to find species or taxa defining characteristics of these two groups.

The most promising postcranial bones are metapodials, because they are quite robust and resist weathering better than other skeletal elements. Metapodials do not only show evolutionary trends (Withalm, 2001), they also have a strong sexual dimorphism (Athen, 2009; Josephson et al., 1996; Rabeder, 2001; Reisinger and Hohenegger, 1998; Toškan, 2006) and do have the potential of species defining characteristics.

For the presented statistical analysis *U. deningeri*-data were raised from Hundsheim, Repolust cave, Deutsch-Altenburg from Austria, Westbury-sub-Mendip from the United Kingdom, Château from France and Mosbach Sands from Germany. The *U. ingressus* material came from Gamssulzen cave in Austria. The included *U. spelaeus*-material was from the fossil sites of Erpfingen and of Zoolithen cave in Germany and of Goyet in Belgium. The data sets of Hohle Fels and Geißenklösterle were compared to this data pool. All together 2,202 metapodial bones had been analysed statistically (tab. 1 and 2).

Table 1: Number of metapodials per cave site.

Cave sites this study	number
Hohle Fels	209
Geißenklösterle	30
Gamssulzen	511
Sum	750
Data pool of <i>Ursus deningeri</i> + <i>spelaeus</i>	1452
Total	2202

Table 2: Number of metapodials per element.

Element	Number
Metacarpals	
Mc I	214
Mc II	223
Mc III	231
Mc IV	222
Mc V	235
Metatarsals	
Mt I	187
Mt II	234
Mt III	248
Mt IV	221
Mt V	187
Total	2202

Table 3: Measurements taken after Duerst 1926 and von den Driesch 1976 (see Fig. 2).

GL	greatest lenght
SB	smallest breath diaphysis
GBp	gr. breath proximal
Bd	gr. breath distal
SBdE	sm. breath epicondylus
SD	sm. thickness diaphysis
Dd	gr. depth distal epiphysis
Hd	distal height
SBp	sm. breath prox. epiphysis
Dp	proximal depth
BJp	gr. breath prox. articular facette
DJp	gr. depth prox. articular facette
BdE	gr. breath dist. epiphysis
PCm	distance crista medial
PCI	distance crista lateral

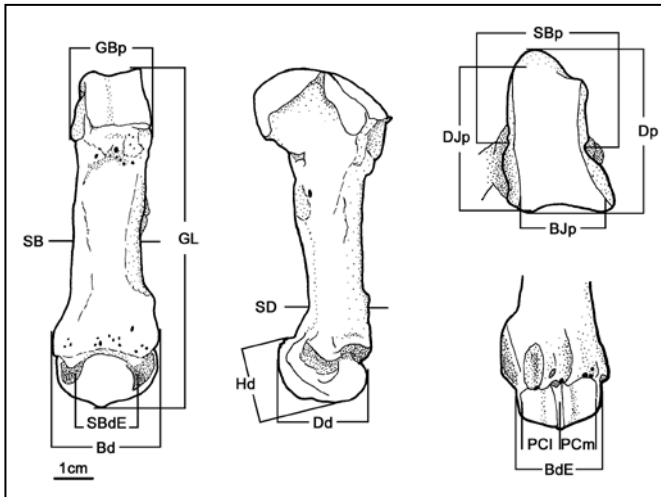


Figure 2: Measurements on metacarpal IV (GPIT-MA-619) taken after Duerst 1926 and von den Driesch 1976 (see Tab. 3).

Additional to the data assemblage of the standard measurements such as greatest length (GL), smallest breadth (SB) and smallest thickness (SD) of the diaphysis, the breadth (Bp, Bd) and thickness (Dp, Dd) proximally and distally (Duerst, 1926; von den Driesch, 1976), also measurements of the articular joint surfaces had been collected (fig. 2, tab. 3). On each skeletal element 15-17 parameters had been gathered, 154 all together. The data investigation was executed with the software program R (R 2.8.1, 2008, originator John Chambers et al. from Bell Laboratories, Bill Venables, David Smith) and SPSS (SPSS Inc., 2005).

First the data were analysed with univariate statistical methods, which revealed differences in the comparison of the species groups. Two-sample tests (*t*-, Welch *t*- and Mann-Whitney *U*-tests) revealed the differences between the

species. The material from Hohle Fels and Geißenklösterle was excluded from this part of the investigation. Afterwards the *alpha*-adjustment after Holm was applied. With this adjustment the *p*-value (*alpha*) of 5 % was adapted to the number of variables (154 measurements), the number of skeletal elements (10 metapodial bones) and to the number of groups (3 species). The adjusted *alphas* indicate whether the results are significant or not.

Following the univariate procedures the data were analysed with the multivariate discriminant analysis. There each specimen was allocated to one of the three species, in a second step also the data from the Ach valley. In this procedure logarithmic data were used to linearise size differences between the groups, because those were no crucial features. It was searched for differences in the proportions of each skeletal element, which could be caused by different nutrition of individuals or sexes. The re-classification of specimens, of which it was known for sure to which of the three species they belong to, was

used as a quality reference. These fossil finds were *a priori* identified and this information included in the discriminant analysis. On the basis of some out of the pool of 154 measurements the *a priori* specification was compared to the *a posteriori* classification. The program output shows the eigen-value, Wilk's Lambda and the *p*-value. Together these quality criteria led to the results of high significance. The allocation to the species had been carried out for each specimen. The statistical program provides a probability of correct classification for each specimen from the Ach valley.

Table 4: Results of the two-sample Welch-*t*-test, examining species differences. Relevant are adjusted *p*-values <0,000016233.

(Mc II = Metacarpal II; n_used = number of cases used in the analysis; n_missing = number of missing data; adj_pWelch_Us.vs.Ui = adjusted *p*-values in the Welch-*t*-tests for species distinction, *U. spelaeus* versus *U. ingressus*; *Ui* = *Ursus ingressus*; *Us* = *Ursus spelaeus*).

Mc II	variable	n_used	n_missing	adj_pWelch_Us vs.Ui
1	GL	128	31	0,219632037186297
2	SB	157	2	0,326099776447185
3	SD	152	7	0,610491905107538
4	GBp	139	20	0,517868260930064
5	SBp	129	30	1,000000000000000
6	Dp	100	59	1,000000000000000
7	BJp	120	39	0,000012619314135
8	DJp	75	84	0,513914064776387
9	Bd	137	22	0,517868260930064
10	SBdE	141	18	1,000000000000000
11	BdE	94	65	0,085821598330856
12	Dd	92	67	1,000000000000000
13	Hd	94	65	0,308847534526504
14	PCm	83	76	0,002807840157268
15	PCI	78	81	0,085821598330856

RESULTS

The tests showed that *U. ingressus* is quite close to *U. spelaeus* and it is almost impossible to statistically distinguish both, especially when *U. deningeri*-material is included in the analysis. Only one parameter could be found in the two-sample tests, which shows a difference between the species (tab. 4, fig. 3 and 4). Relevant is the adjusted *p*-value, which is <0,000016233. Figure 3 shows boxplots of the greatest breadth of the proximal articular facette (BJp) on metacarpal II in millimetre, showing the difference between the species. Figure 4 shows the same parameter, but

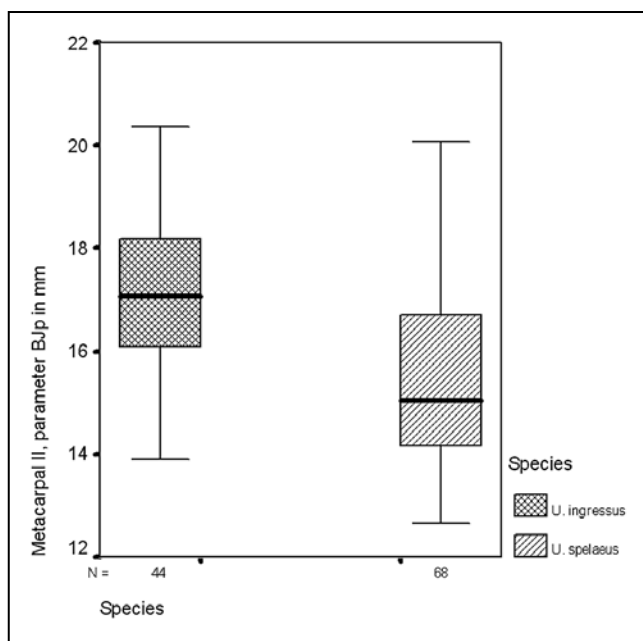


Figure 3: Boxplot of the greatest breadth of the proximal articular facette (BJp) on metacarpal II in millimetre showing the difference between the species (see Tab. 5).

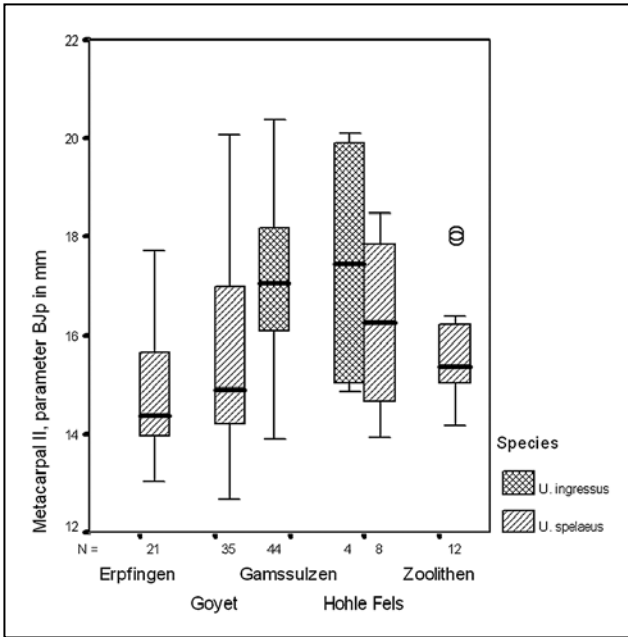


Figure 4: Same as figure 3, but distinguishing the fossil bear sites. The *Ursus spelaeus*-material is from Erpfingen, Goyet, Hohle Fels and Zoolithen cave. The *Ursus ingressus*-material originates from Gamssulzen and Hohle Fels cave. Below the boxplots is a line with the number of specimens included in the graph.

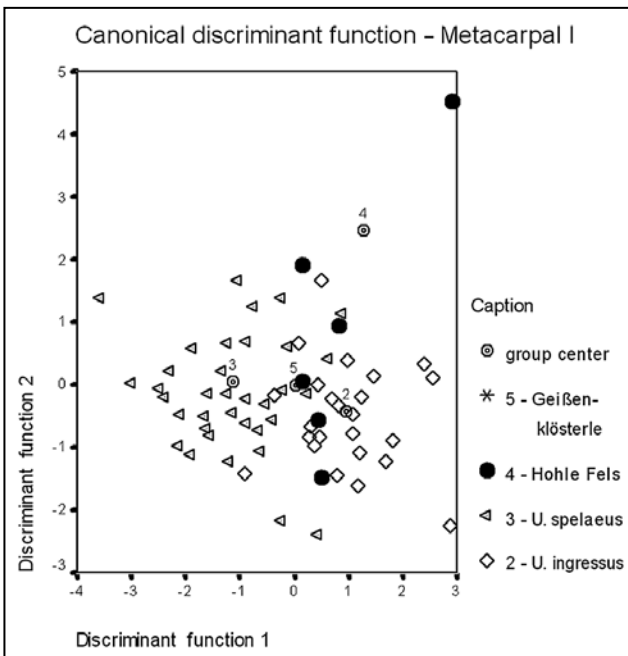


Figure 5: Plot of the discriminant function 1 and function 2 of metacarpal I.

separating the fossil bear sites. *Ursus spelaeus*-material originates from Erpfingen, Goyet, Hohle Fels and Zoolithen cave. *Ursus ingressus*-material has its origin from Gamssulzen cave and *ingressus*-candidates from Hohle Fels. The numbers of specimens are written below the boxplots. This is the result of the univariate tests.

Because of damages on the metapodials, not all measurements could be raised on each specimen of Geißenklösterle und Hohle Fels. Thus, only a part of the data could be included in the discriminant analysis. The results are only partly concurrent with the genetic analyses of the Hohle Fels- and Geißenklösterle-material. The estimation in the discriminant analysis, which specimen belongs to which species, is more often conform with the *a priori* classification for *U. spelaeus* than for *U. ingressus*. Metatarsal III and metatarsal IV play a minor role in the species differentiation, possibly because their structure is too unspecific for the difficult distinction of *U. ingressus* and *U. spelaeus*.

To visualise the results of the discriminant analysis the values of the discriminant functions were plotted to each other, e. g. function 1 to function 2 of metacarpal I (fig. 5). The data of *U. spelaeus* from Erpfingen, Goyet and Zoolithen cave and of *U. ingressus* from

Gamssulzen cave are well grouped showing little overlap, while the values of Hohle Fels (none of Geißenklösterle here) are situated between the two groups of *U. spelaeus* and *U. ingressus*. The results for the other nine skeletal elements are very similar. Nevertheless the results of the discriminant analysis demonstrate the importance of parameters on the proximal and distal joints (BJp, DJp, PCm, PCI) for the distinction of the two species. This visualises that both species are present in Hohle Fels, but at this point are not distinguishable by biometrical methods.

STRATIGRAPHICAL RE-CHECKING

Modern archaeological excavations in Geißenklösterle and Hohle Fels provide differentiated stratigraphical information, which are substantiated by many radiocarbon dates (Conard and Bolus, 2008). In the discriminant analysis the taxa were classified independent of their stratigraphical provenance and this provides the possibility to prove these classifications by cross-checking them with the stratigraphy of Hohle Fels and Geißenklösterle. From the genetic analysis we know that the bear specimens from the older layers (older than 28,000BP) belong to *Ursus spelaeus* and the specimens younger than 28,000BP belong to *Ursus ingressus*. We cross-checked this with the classifications of the discriminant analysis. The results showed that the predicted classifications (*a priori*) of the Hohle Fels- and Geißenklösterle-material do not suit reliably the produced classifications (*a posteriori*) in the discriminant analysis (tab. 5). The high proportion of unclassified metapodials is due to

Table 5: Summary of the biometrical classification with discriminant analysis versus stratigraphical provenience in Hohle Fels.

Layers	Total	without classification	<i>Ursus ingressus</i>	<i>Ursus spelaeus</i>
	n	%	% (n)	% (n)
< 28.000BP	57	70,2	25,9 (14)	7,9 (3)
> 28.000BP	151	50,3	74,1 (40)	92,1 (35)
Total	208	55,8	100,0 (54)	100,0 (38)

incomplete data sets caused by bad preservation. While the distribution of *Ursus spelaeus* is quite possible with some specimens in the upper layers caused by removal of faunal material from the inside of the cave by Oscar Fraas in 1870/71, the large percentage of *Ursus ingressus* in the lower layers is inconsistent with the genetic results of Michael Hofreiter (2002) and Mathias Stiller (Münzel et al., in press).

Considering the geographical range of the cave bear haplogroups in Central Europe, the borderline of distribution for *Ursus ingressus* ends very close to Zoolithen cave (Hofreiter, 2002, fig.18, 71). Surprisingly, the type locality for *Ursus spelaeus* revealed also *Ursus ingressus* (Michael Hofreiter, personal communication). Thus the reference material used is not a pure *spelaeus*-population. Therefore it is quite possible that the results of the classification in the discriminant analysis of *spelaeus* and *ingressus* are so weak because at least one of the reference populations is mixed. There is no such information for Erpfinden so far, but this cave is also situated quite close to the evidenced *ingressus*-caves. Goyet in Belgium might be far enough west not to be undermined by *ingressus*. Even in this cave morphological different cave bears are present, but this material has not been genetically analysed so far (Mietje Germonpré, personal communication).

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KORRELATION GENETISCHER UND BIOMETRISCHER DATEN AN METAPODIEN

Zusammenfassung

In einer vergangenen Untersuchung wurde postkraniales Fundmaterial der Höhlen Geißenklösterle und Hohle Fels aus dem Achat auf DNA untersucht und nun, im Rahmen der vorgelegten Untersuchungen, mit zerstörungsfreien statistischen Analysen verglichen. Die DNA-Analysen legten offen, dass Haplogruppe 1 (*Ursus spelaeus*) und Haplogruppe 4 (*Ursus ingressus*) in beiden Höhlen vorkommen.

Die statistischen Tests zeigen, dass sich *U. ingressus* und *U. spelaeus* sehr ähnlich sind und, dass es fast unmöglich ist, die beiden statistisch voneinander zu trennen. Außerdem stimmen die Ergebnisse nicht durchgehend mit denen der genetischen Tests überein. Die *a priori* angenommene Ursidenspezies stimmt nicht zuverlässig mit der in der Diskriminanzanalyse *a posteriori* berechneten Klassifikation überein. Dies lässt sich z. T. damit erklären, dass die Höhlen, die als Vergleichspopulationen herangezogen wurden, anscheinend nicht mono-spezifisch sind. Das hat möglicherweise die Ergebnisse der Diskriminanzanalyse der biometrischen Merkmale beeinflusst. Nichts desto weniger zeigt die Untersuchung eindrucklich, dass es ein Potential an artspezifischen Merkmalen im Postkranium der Bärenspezies gibt. Für zukünftige Studien sollte allerdings jeder Höhlenfundplatz auf seine genetische Kontinuität oder Diskontinuität überprüft werden, um sicher zu gehen, dass unvermischte Vergleichspopulationen vorliegen. Erst dann werden die Chancen steigen, *U. spelaeus* von *U. ingressus* mit statistischen Methoden zu trennen.

KORELÁCIA GENETICKÝCH ÚDAJOV S VÝSLEDKAMI BIOMETRICKEJ ANALÝZY METAPÓDIÍ

Zhrnutie

Fosilne zvyšky medved'ov z lokalít Geißenklösterle a Hohle Fels v údolí Ach (Nemecko) sa použili už pre výskum fosilnej DNK. Získané výsledky sa porovnali s výsledkami nedeštruktívnych

štatistických metód pre vymedzenie rovnakých jedincov. Predchádzajúce testy DNK odhalili haploidnú skupinu 1 (*Ursus spelaeus*) a haploidnú skupinu 4 (*Ursus ingressus*) na oboch jaskynných lokalitách.

Štatistické testy ukázali, že *U. ingressus* je určite blízko príbuzný druhu *U. spelaeus* a že je takmer nemožné ich navzájom rozlíšiť štatisticky. Výsledky sa len mierne zhodujú s genetickými analýzami z fosilného materiálu z jaskýň Fels a Geißenklösterle. Výsledky ukázali, že predpokladaná klasifikácia (*a priori*) sa nezhoduje veľmi s klasifikáciou v diskriminantnej analýze (*a posteriori*). Lokality, ktoré sa použili ako zdroj populácie *U. spelaeus* v štatistických testoch, nevykazujú ich monošpecifickosť. To by mohlo mať dopad na výsledky z biometrických údajov. Napriek tomu, štúdia demonštruje istý potenciál pre druhové definovanie znakov v postkraniálnom materiále. V budúcnosti by mala byť každá vzorka z jaskynnej lokality analyzovaná z hľadiska genetickej kontinuity alebo diskontinuity, čo je dôležité pre výskum fosilnej DNK v kombinácii s rádiouhlíkovým datovaním. Takto bude potenciál pre klasifikáciu nálezov do druhu *U. spelaeus* alebo *U. ingressus* štatistickými metódami oveľa vyšší.