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# ANTERIOR PREMOLAR VARIABILITY IN PLEISTOCENE CAVE AND BROWN BEARS AND ITS SIGNIFICANCE IN SPECIES DETERMINATION

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**Abstract:** The current study deals with the anterior premolar pattern in the cave and brown bear lineage, and its significance in species determination. The occurrence of single premolars and its combinations in skulls and mandibles is recorded for various chronological and regional groups.

Both lineages stay more "conservative" in the upper than in the lower dentition, but show contrasting reduction tendencies. Brown bears tend to retain the first premolar, while in the cave bear lineage, third premolars prevail.

Exclusively diagnostic for brown bears is the occurrence of a single P1, as well as a complete dentition in skulls. With caution, the combination of P1 and P3 is characteristic for the Deninger bear/cave bear lineage. This pattern was not observed in the current brown bear sample, but has been mentioned in literature. In mandibles, evidence of a single p1 (and its combinations) and a complete dentition is exclusively found in brown bears.

A single lower p3 is diagnostic for Deninger bears in completely preserved diastema. The absence of all three anterior premolars as typical for the cave bear lineage is occasionally reported for brown bears in literature, but was not observed in the studied material. Other premolar combinations stay scarce in both lineages, and may partly be influenced by early or pathological tooth loss.

Brown bears reveal no evolutionary trend in premolar reduction. All possible patterns and a similar frequency of complete dentition is found in modern and fossil representatives.

No evidence was found for high variability in the premolar pattern of *U. deningeri*, as is suggested in literature. The already moderate presence of anterior premolars declines further in Late Pleistocene cave bears. Nonetheless, already the bears of the Cromerian Forest-Bed lack all anterior premolars in mandibles, and hence imply partly evolutionary tendencies in the cave bear lineage, but also populational differences in the occurrence of premolars anterior the P4/p4.

**Key words:** Mammalia, Ursidae, Pleistocene, dentition, premolar pattern, *Ursus spelaeus*, *Ursus arctos*

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## Introduction

The Pleistocene of Europe is rich in remains of ursids. Rare evidence of *Ursus thibetanus* Cuvier, 1823 (e.g. Crégut-Bonnoure 1996) was assumed for the Early and Middle Pleistocene, while recently Wagner et al. (2012) could show that there is no clear evidence of *U. thibetanus* in Europe before MIS 15. Different phylogenetic traits have taken the scene since the end of the Early Pleistocene (Villafranchian). Traditionally, and very briefly, two lineages are proposed (Kurtén 1976, Torres Pérez-Hidalgo 1992, Argant 2001, 2009, Vila Taboada and Grandal d'Anglade 2001): one led from *Ursus etruscus* Cuvier, 1823 towards *Ursus deningeri* von Reichenau, 1904 and ended in *Ursus spelaeus* Rosenmüller, 1794 at the onset of the Last Glacial Maximum (Pacher and Stuart 2009). Some authors summarize *U. deningeri* and *U. spelaeus* within the genus or subgenus *Spelearctos* Geoffroy Saint Hilaire, 1833 (Baryshnikov and Foronova 2001, Musil 2005, Baryshnikov 2007). The other branch still exists today, and is represented by *Ursus arctos* Linnaeus, 1758, respectively the closely related *Ursus maritimus* Phipps, 1774.

In earlier times, no less than eight subspecies of Deninger bear were established (Temmel 1996: 235), and up to 232 synonyms for modern brown bears are listed (Erdbrink 1953: 324), as well as several species and subspecies of cave bears (see compilation in Baryshnikov 2007). Even hybrids between cave and brown bear were speculated (e.g. Ehrenberg 1938), a topic recently reinforced by genetic studies (Barlow et al. 2015). Predecessors of the two lineages with partly arctoid traits (García and Arsuaga 2001, Musil 2001, 2005), such as *Ursus dolinensis* García et Arsuaga,

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2001 from Atapuerca, Spain and *Ursus rodei* Musil, 2001 from Untermaßfeld, Germany were described. Based on genetics and morphogical studies, several evolutionary lines of the Late Pleistocene cave bear (*Ursus spelaeus*) are proposed (Rabeder and Nagel 2001, Rabeder and Hofreiter 2004, Rabeder et al. 2004).

All these approaches reveal one fact – distinguishing between members of the two branches based on paleontological material, very often teeth and tooth-bearing parts, is not always straightforward, due to the high morphometrical variability encountered in bears, and often exaggerated by a small sample size. Especially with some Middle Pleistocene assemblages, half-hearted, halting solutions are presented, suggesting intermediate forms between cave and brown bears, like *U. arctos deningeri* (Kurtén 1957), *U. a. spelaeus* (Erdbrink 1953), or morpholometrical variants like *U. deningeroides* Mottl, 1964 (Mottl 1964: 52), or simply omitting a determination on the species level. In a more recent approach, morphometrical data from cheek teeth of Middle Pleistocene assemblages were used to solve taxonomic questions (Wagner and Čermák 2012). In studying material from Early and Middle Pleistocene sites, such as West Runton (Lewis et al. 2010), Bad Deutsch-Altenburg (Rabeder et al. 2010) and Repolust cave (Pacher 2014), the author faced this problem as well. Therefore, a comprehensive study on bear remains in order to distinguish variability from true diagnostic differences between these two lineages has been started, commencing with a comprehensive examination of the premolar pattern.

## Occurrence of anterior premolar

In early studies of modern brown bears, their varying premolar pattern was recognized early on (e.g. Schäff 1889, Reynolds 1906, and compilation in Erdbrink 1953: 371–375). Studies show that first and third premolars occur frequently, and asymmetry in left and right halves of mandibles and maxillae are quite frequent.

The number of premolars in fossil ursids is variable as well. It is generally concluded that in *Ursus etruscus*, all premolars prevail (e.g. Mazza and Rustioni 1994, García and Arsuaga 2001), although Torres Pérez-Hidalgo (1988: 207) mentions a few examples of missing premolars in these Early Pleistocene bears. Two out of eight maxillae and two out of eleven mandibles are missing one premolar.

The reduction of premolars is commonly related to an evolutionary process, leading from the initial pattern to a more evolved dentition, and the nearly complete absence of anterior premolars in *Ursus spelaeus* populations (e.g. Altuna 1973: 134, Torres Pérez-Hidalgo 1988: 208, Mazza et al. 1995, Rabeder et al. 2000: 29, Quiles 2003: 48), whereas Erdbrink (1953: 375) coupled the loss to a size increase in bears.

A reduction sequence starting with the loss of lower p2, upper P2, lower p3 and finally upper P1 is assumed (according to Hensel 1876: 49, see also in Erdbrink 1953: 374). This evolutionary process leaves a dentition with upper P3 – P4 and lower p1 – p4 as the most common stage in brown bears. The final stage following this model would be P4/p4, which has not yet been reached in brown bears, but was in cave bears. The rare occurrence of additional premolars is subsequently seen as atavistic trait in the latter.

As a consequence, the premolar pattern is further used to differentiate between specimens of cave and brown bears, yet the distinguishing criteria given stay vague. Freudenberg (1914: 575), based on material from Hundsheim concluded *U. deningeri* possesses a P1, while the P2 is indicated by a furrow, and the P3 is either developed or lost during life. Torres Pérez-Hidalgo (1988: 207) refers also to high variability in Deninger bears, while Quiles (2003: 48) summarizes the pattern as follows: "cave bears lack premolars anterior the P4 in their upper dentition, and retain a lower p1 only exceptionally. Evidence of a lower p3 is also rare, while the first premolar is scarce in *U. deningeri*, and the third more frequent".

The following study, based on personal observations compared against compilations in literature aims to establish a more precise pattern of premolar occurrence in various brown bear and cave bear populations, in order to test their reliability in species determination, and the proposed assumption of an evolutionary process.

## Material and methods

This study is based on a comprehensive comparison of regional and chronological compiled samples of brown bears, Deninger bears and cave bears. The sample size is rather small in each group, hence personal observations are supplemented by records from the literature.

Eleven groups of brown bears are distinguished, consisting of four modern samples from Kamchatka (Ua-A1), North America (Ua-A2), south-eastern Europe (Ua-A3) and the Near East/Africa (Ua-A4), two Holocene samples from caves of the Alps (Ua-B1) and Spain (Ua-B2), three Late Pleistocene pools from the Central European loess area (Ua-C1), Great Britain (Ua-C2), and a compilation from various sites (Ua-C3), as well as the Eemian bears from Taubach (Ua-D1) and a mixed group from Middle to Early Pleistocene sites (Ua-D2). The latter comprises brown bears from Gray's Thurrock, as well as material with controversial taxonomic assignments, such as bears from Atapuerca, Süssenborn, Untermaßfeld and Bad Deutsch-Altenburg (see Discussion and conclusion).

For Deninger bears, material from Mosbach, Germany (Ud-D1), the Repolust cave, Styria, Austria (Ud-D2), the Cromerian Forest Bed, Great Britain (Ud-D3) and a compilation of several sites (Ud-D4) are available.

For cave bears, the material from Schwabenreith cave (Us-C1) and Herdengel cave (Us-C2), both in Lower Austria have been studied. A detailed list of examined specimens and included references are given in Appendix.

The following approaches were applied: first, the simple presence or absence of each of the three anterior premolars was recorded by teeth, respectively alveoli. Second, the pattern of premolars was analyzed in complete diastema. Third, differences between left and right halves were observed, when pairs were available. The fossil samples consist mainly of single halves of mandibles, or parts of maxillae. Hence, left and right halves of maxillae and mandibles were counted separately. Results were then compared between the established regional and chronological groups of cave

and brown bears. Since premolars in this study were not consistently measured, no metrical analyses were possible.

**Abbreviations of collections**

AZS – Archäozoologische Sammlung der Universität Tübingen, Germany
IQW – Forschungsstation für Quartärpaläontologie der Senckenbergischen Naturforschenden Gesellschaft, Weimar, Germany
IPUW – Institut für Paläontologie der Universität Wien, Wien, Austria
LDfH – Landesamt für Denkmalpflege Hessen, Wiesbaden, Germany
LMJ – Landesmuseum Joanneum, Graz, Austria
MZM – Moravské zemské muzeum (Moravian Museum), Brno, the Czech Republic
MWNH – Museum Wiesbaden, Naturhistorische Sammlungen, Wiesbaden, Germany
NHMW – Naturhistorisches Museum Wien, Wien, Austria
NM – Naturmuseum, St. Gallen, Switzerland
NMB – Naturhistorisches Museum, Basel, Switzerland
NHML – Natural History Museum, London, Great Britain
nhmMainz – Naturhistorisches Museum, Mainz, Germany
NÖLM – Landesmuseum Niederösterreich, St. Pölten, Austria
NWHCM – Cromer Museum, Norwich and Gressenhall, Great Britain
OG – Oddelek za geologijo Univerza v Ljubljani, Ljubljana, Slovenia
SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany
UCBL – Université Claude Bernard Lyon 1, Lyon, France
VMU – Veterinärmedizinische Universität, Wien, Austria
WKL – Wasserkluster Lunz, Lunz am See, Austria

## Observed premolar patterns

The results of the current study show certain variability in the premolar pattern (Tabs 1–4), but also specific tendencies in cave and brown bears. Unfortunately, the analyses of fossil material were hampered by a rather high degree of fragmentation. Complete tooth-bearing parts were rarely observed. Despite the small sample size in fossil brown bears, the pattern for fossil and modern brown bears from various regions is similar (Tabs 1–2).

### Upper dentition

In brown bears, both the P1 and the P3 occur regularly, with a high frequency, ranging from 76% to 100% for the P3, and 84.6% up to 100% for the P1 (Tab. 1, Text-figs 1, 2). The large sample by Dittrich (1961) and Sládek (1989) gave very similar results, with 88% and 86% for the P1 and 90% respectively 93% for the P3. These and additional results for modern brown bear populations are compiled in Korablev et al. (2000: 200, tab. 3). The lower abundance of P1, with 42% in the sample from Taubach (Ua-D1) is caused by a rather high fragmentation of maxillae. If a P1 is assumed in the

**Table 1. Number of premolars encountered in maxillae. n = number of maxillae, left and right maxillae counted separately, + = presence, - = absence, ~ = part of maxilla missing, % = percentage of observed premolars or alveoli.**

| Groups | n | P1 | P2 | P3 | P1% | P2% | P3% |
|---|---|---|---|---|---|---|---|
| ***U. arctos*** | | **+ / - / ~** | **+ / - / ~** | **+ / - / ~** | | | |
| Ua-A1 (Kamchatka) | 202 | 191/11/0 | 26/176/0 | 197/5/0 | 94.6 | 12.9 | 97.5 |
| Ua-A2 (N-America) | 25 | 21/4/0 | 0/25/0 | 19/5/1 | 84.0 | – | 76.0 |
| Ua-A3 (SE-Europe) | 20 | 18/2/0 | 6/14/0 | 20/0/0 | 90.0 | 30.0 | 100.0 |
| Ua-A4 (NearEast-N-Africa) | 13 | 13/0/0 | 2/10/1 | 11/0/2 | 100.0 | 15.4 | 84.6 |
| Ua-B1 (Alps-Holocene) | 40 | 38/2/0 | 8/32/0 | 39/0/1 | 95.0 | 20.0 | 97.5 |
| Ua-B2 (Spain-Holocene) | 23 | 23/0/0 | 6/17/0 | 23/0/0 | 100.0 | 26.1 | 100.0 |
| Ua-C1 (Loess-UP) | 4 | 1/0/3 | 0/3/1 | 4/0/0 | – | – | – |
| Ua-C2 (GBrit-UP) | 11 | 11/0/0 | 5/6/0 | 11/0/0 | 100.0 | 45.5 | 100.0 |
| Ua-C3 (varia-UP) | 19 | 15/3/1 | 4/15/0 | 18/0/1 | 78.9 | 21.1 | 94.7 |
| Ua-D1 (Taubach) | 14 | 6/4/4 | 3/11/0 | 12/0/2 | 42.9 | 21.4 | 85.7 |
| Ua-D2 (varia-OM)[1] | 7 | 2/1/4 | 4/2/1 | 6/0/0 | – | – | – |
| ***U. deningeri*** | | | | | | | |
| Ud-D1 (Mosbach) | 48 | 3/37/8 | 1/44/3 | 27/14/7 | 6.3 | 2.1 | 56.3 |
| Ud-D2 (Repolust) | 37 | 1/33/2 | 0/36/0 | 14/22/0 | 2.7 | – | 37.8 |
| Ud-D3 (Forest-Bed) | 5 | 1*/4/0 | 0/5/0 | 2/3/0 | – | – | – |
| Ud-D4 (varia-DB) | 32 | 3/26/3 | 0/31/1 | 15/11/6 | 9.4 | – | 46.9 |
| ***U. spelaeus*** | | | | | | | |
| Us-C1 (Schwabenreith) | 55 | – | – | 11/44/0 | – | – | 20.0 |
| Us-C2 (Herdengelh.) | 47 | – | – | 2/45/0 | – | – | 4.3 |

[1] results unclear due to high fragmentation
* shallow depression (Bacton, NHML-M17964)

**Table 2. Combination of premolars in complete maxillae. n = left and right maxillae counted separately, no = number of observed anterior premolars, diff:eq = number of different pattern versus equal pattern on left and right side from the same individual.**

| Group | n | P1 + 2 + 3 | P1 + 2 | P1 + 3 | P2 + 3 | P1 | P2 | P3 | no | diff:eq |
|---|---|---|---|---|---|---|---|---|---|---|
| ***U. arctos*** | | | | | | | | | | |
| Ua-A1 (Kamchatka) | 201 | 24 | 1 | 161 | 1 | 4 | – | 10 | – | 19:82 |
| Ua-A2 (N-America) | 24 | – | – | 17 | – | 3 | – | 2 | 2 | 3:8 |
| Ua-A3 (SE-Europe) | 20 | 6 | – | 12 | – | – | – | 2 | – | 6:4 |
| Ua-A4 (NearEast-N-Africa) | 11 | 1 | – | 10 | – | – | – | – | – | 0:5 |
| Ua-B1 (Alps-Holocene) | 39 | 8 | – | 29 | – | – | – | 2 | – | 0:12 |
| Ua-B2 (Spain-Holocene) | 23 | 6 | – | 17 | – | – | – | – | – | 3:7 |
| Ua-C1 (Loess-UP) | 1 | – | – | 1 | – | – | – | – | – | – |
| Ua-C2 (GBrit-UP) | 11 | 5 | – | 6 | – | – | – | – | – | 0:5 |
| Ua-C3 (varia-UP) | 17 | 3 | – | 11 | 1 | – | – | 2 | – | 1:5 |
| Ua-D1 (Taubach) | 8 | 1 | – | 5 | 1 | – | – | 1 | – | 1:0 |
| Ua-D2 (varia-OM)[1] | 2 | – | – | 1 | – | – | – | 1 | – | 1:0 |
| ***U. deningeri*** | | | | | | | | | | |
| Ud-D1 (Mosbach) | 34 | – | – | 3 | 1 | – | – | 20 | 10 | 5:6 |
| Ud-D2 (Repolust) | 35 | – | – | 1 | – | – | – | 13 | 21 | 0:14 |
| Ud-D3 (Forest-Bed) | 5 | – | – | 1* | – | – | – | 1 | 3 | 1:1 |
| Ud-D4 (varia-DB) | 23 | – | – | 1 | – | – | – | 11 | 11 | 0:5 |
| ***U. spelaeus*** | | | | | | | | | | |
| Us-C1 (Schwabenreith) | 55 | – | – | – | – | – | – | 11 | 44 | – |
| Us-C2 (Herdengelh.) | 47 | – | – | – | – | – | – | 2 | 45 | – |

[1] results unclear due to high fragmentation

* shallow depression of p1-alveoli (Bacton NHML-M17964)

missing anterior parts, their frequency corresponds to that from other brown bear samples. The P2 is far less frequent, ranging from a total absence up to 30%, with exception of fossil brown bears from Great Britain (Ua-C2) that show a P2 frequency of 45.5%. Dittrich (1961) and Sládek (1989) show a consistent low frequency of P2, with 13.9% and 13.3%. Similar results are added in Korablev et al. (2000: 200, tab. 3).

Hence, the most frequent combination in *U. arctos* is that of **P1 + P3**. Its percentage based on numbers in Table 2 ranges from 91% to 60%. In modern bears from Norway studied by Degerbøl, sixteen skulls out of 25 retain these two premolars, resulting in a similar frequency of 64% (ex Erdbrink 1953: 373).

Other premolar combinations remain rare. The **P1 + P2** as well as **P2 + P3** are observed in one side of two different skulls from Kamchatka (Ua-A1). Degerbøl (ex Erdbrink 1953: 373) gives one example of a P2 + P3 combination for bears from Norway, and Korbalev et al. (2000: 199, tab. 2) another from Russia. One fossil example of a P2 + P3 combination comes from Taubach (Ua-D1) and one from Caverne du Mars (Ua-C3), according to Bonifay (1971).

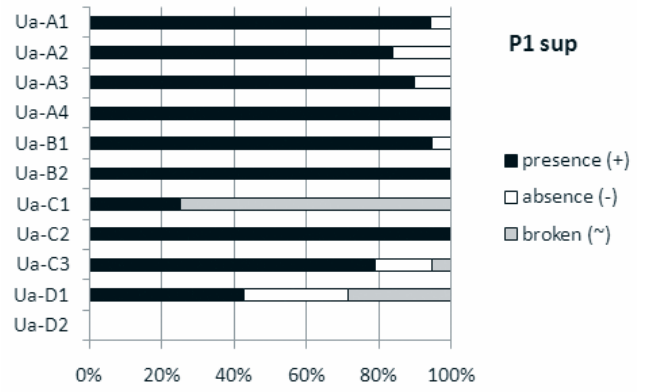
Similarly scarce is the occurrence of a single anterior premolar. The **P1** alone is only found in both sides in one skull from Kamchatka (Ua-A1), and three times in the North American sample (Ua-A2). Hall (ex Erdbrink 1953: 372) mentioned one example out of 81 skulls from Alaska. One out of 44 skulls retains the P1 in the sample studied by von Middendorff (ex Erdbrink 1953: 371).

The presence of a single **P3** in modern and fossil samples is scarce as well (Tab. 2). Ten out of 201 maxillae from Kamchatka (Ua-A1) show this pattern, which still results in a very low percentage of 5%. In other brown bear samples, one or two times a single P3 is recorded. Von Middendorff (ex Erdbrink 1953: 371) listed seven modern skulls with a single P3.

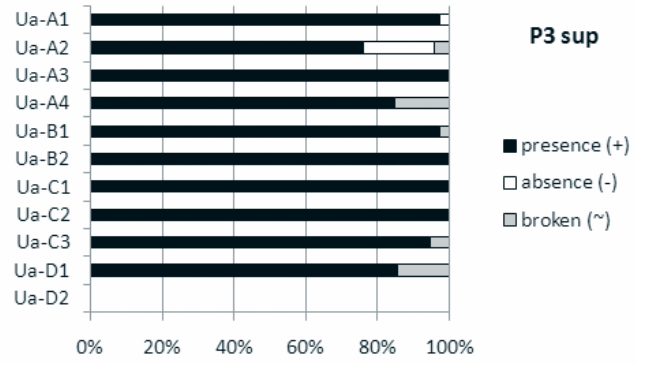
Interestingly, all three anterior premolars (**P1 + P2 + P3**) are rather common in nearly all brown bear groups. The large sample from Kamchatka (Ua-A1) results in a frequency of 11.9%. Degerbøl mentions eight skulls out of 25 from Norway with complete dentition, and von Middendorff gives eleven examples, while Hall listed four skulls with all four premolars (all ex Erdbrink 1953: 371–373). Among eight skulls from Croatia, one retained all anterior premolars, while in one only a single P3 occurred, and in six cases the P1 + P3. All skulls showed the same pattern on both sides (pers. comm. Jan Wagner)

The **loss of all three anterior premolars** was not observed in the studied brown bear material. References come only from the literature. Hall mentioned a brown bear skull from North America, and von Middendorff listed two skulls from Siberia (ex Erdbrink 1953: 371–373). A fossil skull from Rancho La Brea (Kurtén 1960: 4, fig. 2) and a skull from Malarnaud (Couturier 1948) complete the record.

The number of premolars is usually low in Deninger bears, and decreases even further in cave bears (Tab. 1, Text-figs 3, 4). In *U. deningeri*, the P3 is the most common anterior premolar, ranging from 37.8% to 46.9%, but is missing in the




**Text-fig. 1. Occurrence of P1 in maxillae from brown bears, data after Table 1 (presence = P1 or alveoli observed, absence = no P1 developed, broken = rostral part of maxilla broken).**




**Text-fig. 2. Occurrence of P3 in maxillae from brown bears, data after Table 1 (presence = P3 or alveoli observed, absence = no P3 developed, broken = caudal part of maxilla broken).**

Cromerian Forest-Bed sample (Ud-D3). The occurrence of a P1 is a rare feature, and observed in less than 10% in several samples. A P2 was only confirmed once, at Mosbach (Ud-B2).

Compared to previous studies, the results for Mosbach differ. Two examples of a P1 given by von Reichenau (1906) could not be confirmed. There is no P1 in the large skull (von Reichenau 1906: pls I, II). It shows P3 and P2 alveoli in the middle of the diastema, about 35 mm from the canine. Also, the rostrum from the museum Wiesbaden (von Reichenau 1906: pl. IV, fig.1) lacks the P1. Hence, based on studied material and additional remains figured in von Reichenau (1906), the frequency of the first anterior premolar for Mosbach sums to 6.3%, based on 48 maxillae (Tab. 1), which is still far less than the 21% value proposed by Schütt (1968: 53), based on 19 specimens.

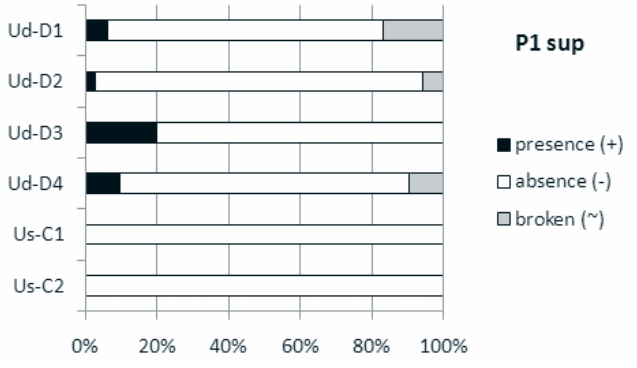
The P3 occurred with a frequency of 56.3% in this study, which is again considerably lower than the value of 79% given by Schütt (1968: 53). The difference could be based on varying sample size, counting method and preservation. In the available sample from Mosbach, eight maxillae are partly broken or allow no decision on the occurrence of anterior premolars.

Nonetheless, the tendencies in premolar reduction are similar in all the Deninger bear groups, with a moderate occurrence of the P3 and rare examples of a P1. P3 occurs with a frequency of 37.8% to 46.9%, and in two specimens from the Cromerian Forest-Bed (Ud-D3), while anterior premolars are absent in Deninger bears from Hundsheim (Ud-D4).

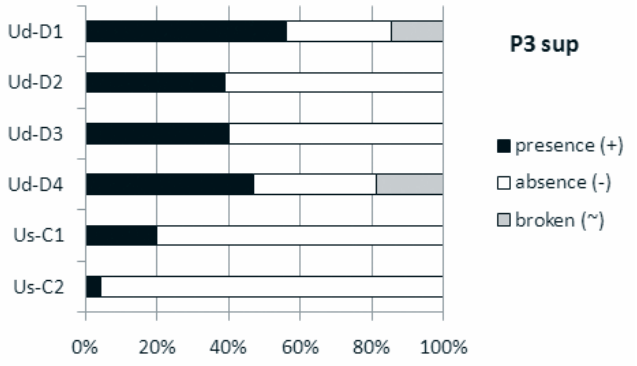
P1 is even less abundant, with frequencies from 2.7% to 9.4%. In the small sample from the Cromerian Forest-Bed (Ud-D3), the P1 occurs probably once. The specimen from Bacton shows only a small depression, which could represent a shallow alveolus.

The *U. deningeri* material from Westbury analyzed by Bishop (1982: 36) retains a P3 in all three available maxillae. According to Schütt (1968: 53), 11% of the bears from Scharzfeld (Einhornhöhle) possess the P3, based on 18 specimens. Additional examples of a persisting P1 or P3 in Deninger bears is mentioned by Quiles (2003: 161, tab. 91), from Arago. Of 5 maxillae, one retains the P1 and one the P3. A single rostral fragment from Koněprusy caves showed the P3 alveoli on both sides (Wagner and Čermák 2012: 476).

Subsequently, the possible patterns in Deninger bears are restricted, too. 59% of complete maxillae from Mosbach reveal a single P3, while a P1 + P3 combination is confirmed three times, and the P2 + P3 combination was only found in




**Text-fig. 3. Occurrence of P1 in maxillae from Deninger bears and cave bears, data after Table 1 (presence = P1 or alveoli observed, absence = no P1 developed, broken = rostral part of maxilla broken).**




**Text-fig. 4. Occurrence of P3 in maxillae from Deninger bears and cave bears, data after Table 1 (presence = P3 or alveoli observed, absence = no P3 developed, broken = caudal part of maxilla broken).**

the left side of one skull (nhmMainz 1939-1093). The right side lacks all anterior premolars. In the other analyzed groups, the combination of P1 and P3 occurs only once (Tab. 2).

The presence of a P3 is regarded as an atavistic trait in cave bears (e.g. Schlosser 1910: 413, Rabeder et al. 2000, Quiles 2003: 161), which is supported by the low frequency of P3 in two Austrian sites. At Schwabenreith cave, eleven maxillae out of 64 (7.04%) possess a P3. At Herdengel cave, only one out 45 maxillae retain the third premolar (0.45%).

Torres Pérez-Hidalgo (1988: 208) studied 55 maxillae of cave bears from various Spanish sites, and encountered 13 with upper P3, which results in a relative high frequency of 23.6%, although eight of these maxillae came from a single site – the cave Troskaeta, from which Torres et al. (1991) describes the new small-sized subspecies *U. s. parvilatipedis*. Quiles (2003: 161, tab. 91) mentioned three P3 (18.8%) in 16 maxillae from Fate, Italy, and no anterior premolars from Crouzade and Tournal, France and Basura, Italy, based on six maxillae.

### Lower dentition

The lower dentition again shows diagnostic tendencies (Tabs 3, 4). In modern brown bears, the p1 is the most common anterior premolar, with a frequency of 88.9% to 100% in modern and Holocene brown bear samples (Tab. 3, Text-fig. 5). Its occurrence varies in fossil samples, mostly caused by preservation conditions, but may also reach 100% in Late Pleistocene brown bears from Great Britain (Ua-C2).

The p3 occurs regularly, but with varying frequency (Text-fig. 6), from 4.5% up to 53.9%. The p2 occurs in several populations, and reaches a maximum of 16.7% in the modern North American sample (Ua-A2), but is absent in others.

Giving the combination of lower anterior premolars, the presence of a single **p1** is the most common pattern encountered, followed by a combination of **p1 + p3** (Tab. 4). This sequence is in accordance with the results from von Middendorff (ex Erdbrink 1953: 371). He listed the p1 in 22 individuals (50.0%), and p1 + p3 in 12 individuals (27.3%), out of 44 modern brown bears. According to Degerbøl, bears from Norway retain the p1 + p3 more often than a single p1. He encountered the p1 alone in 10 cases, and p1 + p3 in 12 out of 25 individuals (ex Erdbrink 1953: 373). Also, Torres Pérez-Hidalgo (1988: 210) shows a predominance of single p1 in brown bear populations from North America (53 out of 59 mandibles). Four times a p1 + p3 pattern is mentioned.

Additional combinations of anterior lower premolars, like **p1 + p2** are mainly found in four modern and the Holocene groups, ranging from 2.5% to 13.6% (Tab. 4). Von Middendorff and Degerbøl give evidence of two respectively four individuals with a p1 + p2 combination (ex Erdbrink 1953: 371, 373). One example from Russia is listed in Korablev et al. (2000: 199, tab. 2), and one out of eight individuals from Croatia showed this pattern on the left and right side as well (pers. comm. Jan Wagner).

Like in skulls, **all anterior premolars** mainly occur in modern brown bears, namely in samples from Kamchatka (Ua-A1) with 3.6% and North America (Ua-A2) with 11.1%. Also, von Middendorff mentioned four individuals with complete premolar row (in Erdbrink 1953: 371), while

**Table 3. Number of premolars encountered in halves of mandibles. n = number of mandibles, left and right mandibles counted separately, + = presence, - = absence, ~ = part of mandible missing, % = percentage of observed premolars or alveoli.**

| Group | n | p1 | p2 | p3 | p1% | p2% | p3% |
|---|---|---|---|---|---|---|---|
| ***U. arctos*** | | **+ / - / ~** | **+ / - / ~** | **+ / - / ~** | | | |
| Ua-A1 (Kamchatka) | 198 | 198/0/0 | 12/185/1 | 73/124/1 | 100% | 6.1% | 36.9% |
| Ua-A2 (N-America) | 18 | 16/2/0 | 3/15/0 | 5/13/0 | 88.9% | 16.7% | 27.8% |
| Ua-A3 (SE-Europe) | 22 | 22/0/0 | 3/19/0 | 1/21/0 | 100% | 13.6% | 4.5% |
| Ua-A4 (NearEast-N-Africa) | 13 | 13/0/0 | 0/13/0 | 0/12/1 | 100% | – | – |
| Ua-B1 (Alps-Holocene) | 46 | 45/0/1 | 3/38/5 | 14/28/4 | 97.8% | 6.5% | 30.4% |
| Ua-B2 (Spain-Holocene) | 16 | 15/0/1 | 0/16/0 | 6/9/1 | 93.8% | – | 37.5% |
| Ua-C1 (Loess-UP) | 13 | 7/1/5 | 0/9/4 | 7/4/2 | 53.9% | – | 53.9% |
| Ua-C2 (GBrit-UP) | 14 | 14/0/1 | 0/14/1 | 4/9/2 | 100% | – | 28.6% |
| Ua-C3 (varia-UP) | 26 | 23/0/3 | 2/24/0 | 8/16/2 | 88.5% | 7.7% | 30.8% |
| Ua-D1 (Taubach) | 38 | 34/0/5 | 0/37/2 | 4/21/14 | 89.5% | – | 10.5% |
| Ua-D2 (varia-OM)[1] | 26 | 17/3/7 | 4/21/2 | 10/17/0 | 65.4% | 15.4% | 38.5% |
| ***U. deningeri*** | | | | | | | |
| Ud-D1 (Mosbach) | 52 | 0/46/6 | 0/48/4 | 5/44/3 | – | – | 9.6% |
| Ud-D2 (Repolust) | 57 | 0/53/4 | 0/55/2 | 4/53/0 | – | – | 7.0% |
| Ud-D3 (Forest-Bed) | 25 | 0/24/1 | 0/24/1 | 0/25/0 | – | – | – |
| Ud-D4 (varia-DB) | 42 | 0/40/2 | 3/39/0 | 1/40/1 | – | 7.1% | 2.4% |
| ***U. spelaeus*** | | | | | | | |
| Us-C1 (Schwabenreith) | 118 | 0/118/0 | 0/118/0 | 0/118/0 | – | – | – |
| Us-C2 (Herdengelh.) | 60 | 0/60/0 | 0/60/0 | 0/60/0 | – | – | – |

[1] results unclear due to high fragmentation

**Table 4. Combination of premolars in mandibles with complete diastema. n = left and right maxillae counted separately, no = no anterior premolars observed, diff:eq = number of different pattern versus equal pattern on left and right side from the same individual.**

| Group | n | p1 + 2 + 3 | p1 + 2 | p1 + 3 | p2 + 3 | p1 | p2 | p3 | no | diff:eq |
|---|---|---|---|---|---|---|---|---|---|---|
| ***U. arctos*** | | | | | | | | | | |
| Ua-A1 (Kamchatka) | 197 | 7 | 5 | 66 | – | 119 | – | – | – | 15:68 |
| Ua-A2 (N-America) | 18 | 2 | 1 | 3 | – | 10 | – | – | 2 | 1:8 |
| Ua-A3 (SE-Europe) | 22 | – | 3 | 1 | – | 18 | – | – | – | 1:10 |
| Ua-A4 (NearEast-N-Africa) | 12 | – | – | – | – | 12 | – | – | – | 0:5 |
| Ua-B1 (Alps-Holocene) | 40 | – | 3 | 12 | – | 25 | – | – | – | 1:12 |
| Ua-B2 (Spain-Holocene) | 14 | – | – | 5 | – | 9 | – | – | – | 2:4 |
| Ua-C1 (Loess-UP) | 6 | – | – | 3 | – | 3 | – | – | – | – |
| Ua-C2 (GBrit-UP) | 12 | – | – | 4 | – | 8 | – | – | – | – |
| Ua-C3 (varia-UP) | 21 | 1 | – | 7 | – | 13 | – | – | – | 0:4 |
| Ua-D1 (Taubach) | 20 | – | – | 4 | – | 16 | – | – | – | 0:5 |
| Ua-D2 (varia-OM)[1] | 19 | 3 | – | 7 | – | 6 | – | – | 3* | 1:4 |
| ***U. deningeri*** | | | | | | | | | | |
| Ud-D1 (Mosbach) | 43 | – | – | – | – | – | – | 4 | 39 | 0:2 |
| Ud-D2 (Repolust) | 53 | – | – | – | – | – | – | 3 | 50 | 0:2 |
| Ud-D3 (Forest-Bed) | 24 | – | – | – | – | – | – | – | 24 | – |
| Ud-D4 (varia-DB) | 42 | – | – | – | – | – | 3 | 1 | 38 | 1:4 |
| ***U. spelaeus*** | | | | | | | | | | |
| Us-C1 (Schwabenreith) | 118 | – | – | – | – | – | – | – | 118 | – |
| Us-C2 (Herdengelh.) | 60 | – | – | – | – | – | – | – | 60 | – |

[1] results unclear due to high fragmentation,

* one specimen is probably influenced by pathological tooth loss (Süßenborn IQW 1305-5840)

Torres Pérez-Hidalgo (1988: 210) found no such pattern in 59 mandibles from North America.

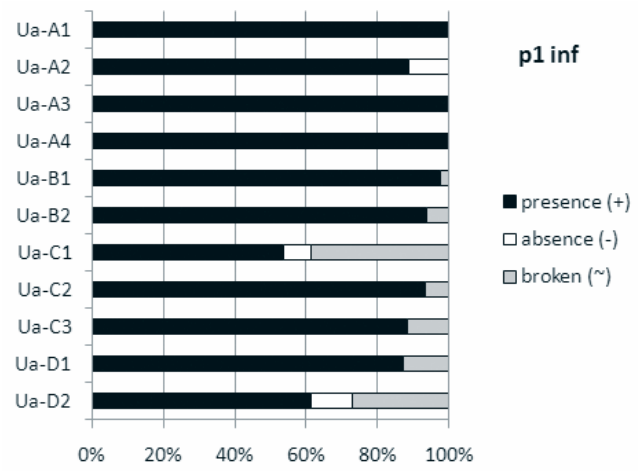
The only possible chronologically older find with a complete dentition is encountered in a right mandible from Hundsheim. The specimen is included in the Late Pleistocene sample (Ua-C3), although the brown bears from Hundsheim lack detailed stratigraphic information (e.g. Zapfe 1948). Two cases are reported from Untermaßfeld (Musil 2001), and one from Atapuerca (García and Arsuaga 2001), included in the mixed brown bear sample (Ua-D2).

A single **p3** was neither encountered in the current brown bear sample nor mentioned in the compilation by Erdbrink (1953: 371–373). Only Torres Pérez-Hidalgo (1988: 210) refers to one case from North America, and Korablev et al. (2000: 199, tab. 2) to one from Russia. Quiles (2003: 167, tab. 100) mentioned a single p3 in the fossil specimen from Fate. Evidence of a complete **absence of the three anterior premolars** in brown bear mandibles is scarce, too. One case each is reported from Kamchatka (von Middendorff ex Erdbrink 1953: 371), North America (Torres Pérez-Hidalgo 1988: 210) and Russia (Korablev et al. 2000: 199, tab. 2). Among the mixed sample (Ua-D2), one mandible from Süssenborn (IQW 5840) lacks all three anterior premolars, but is heavily influenced by pathological tooth loss. The p4 and m3 are also lost. In addition, two corresponding mandible halves from Untermaßfeld (Ua-D2) lack all three anterior premolars, according to Musil (2001: 638, tab. 119). Hence, absence of anterior premolars stays exceptional in brown bears, and might be partly caused by pathological tooth loss.

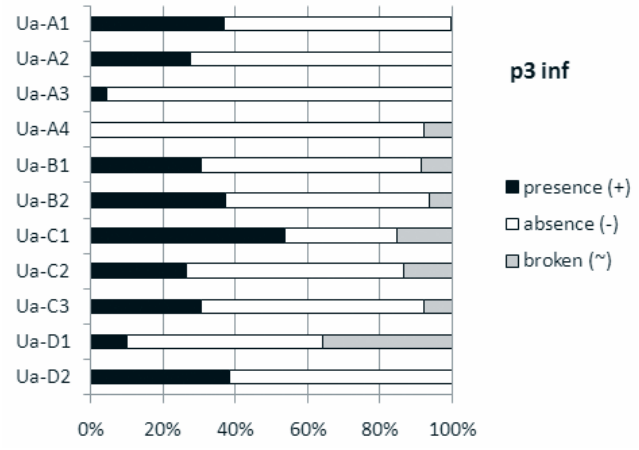
The cave bear lineage shows different preferences. The majority of examples from Deninger bears lack all three premolars. The only exception is a subordinate evidence of the p3 (Table 3, Text-figs 7, 8), which reaches 11.3% in Mosbach (Ud-D1), including one specimen from the collection in Hildesheim, figured by von Reichenau (1906: pl. IX, figs 1–2). The value is considerable higher than the 4.5% frequency given by Schütt (1968: 53). In the other Deninger bear samples, the frequency stays lower, with 7.0% (Ud-D2) and one evidence from Bilzingsleben (Musil 1991) included in the mixed Deninger bear sample (Ua-D4). The bears of the Cromerian Forest-Bed (Ud-D3) show no evidence of the anterior three premolars, and hence anticipate the situation in Late Pleistocene cave bears from Herdengel cave (Us-C2) and Schwabenreith cave (Us-C1).

The Westbury bears retain the p3 in four cases out of 32 mandibles, resulting in 12.5% (not 13.5% as in Bishop 1982: 43, tab. 16), and hence show a frequency comparable to the Deninger bear samples in this study. In addition, a single p2 alveolus is encountered twice, and surprisingly also one case of a p1 alveolus is mentioned (Bishop 1982: 36 and 43, tab.16).

A similar situation is given for the bears from Scharzfeld (Einhornhöhle). The p3 occurs with a frequency of 7.0%, In addition, 5.5% show a p2, and the p1 occurs in 3% of the material, according to Schütt (1968: 53). In the current samples, evidence of a single p2 is missing. Three examples are found in the literature. Musil (1991: 82) mentions two cases from Bilzingsleben (Ud-D2), and Rode (1933: 74,




**Text-fig. 5. Occurrence of p1 in mandibles from brown bears, data after Table 3 (presence = p1 or alveoli observed, absence = no p1 developed, broken = diastema fragmented).**

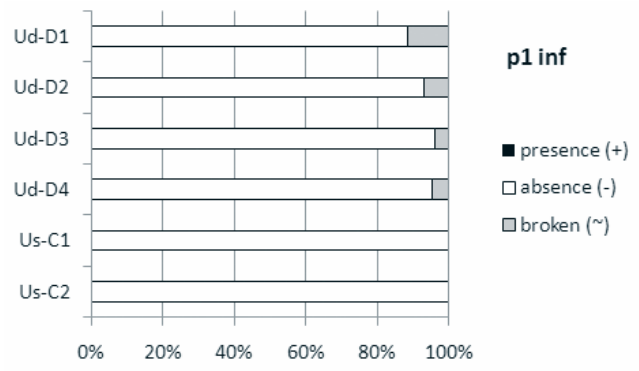



**Text-fig. 6. Occurrence of p3 in mandibles from brown bears, data after Table 3 (presence = p3 or alveoli observed, absence = no p3 developed, broken = diastema fragmented).**

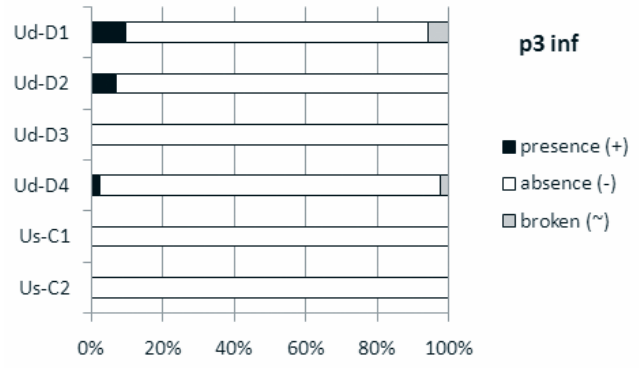
pl. XII, figs 1–2) refers to one mandible from Steinheim (Ud-D2).

In addition, Quiles (2003: 167, tab. 100) found one p3 in nine mandibles from Arago, and the site Petralona revealed one out of five mandibles with a two-rooted p3 (Kurtén and Poulianos 1977: 84).

None of the analyzed Late Pleistocene cave bear mandibles from Schwabenreith cave and Herdengel cave show evidence of anterior premolars. Quiles (2003: 167, tab. 100), on the other hand, mentioned four mandibles out of 42 from Fate, and the single specimen from Badalucca caves with a p3 alveolus. These specimens are erroneously listed in the p1 column in Quiles (2003: 167, tab. 100). 41 mandibles from Basura and 13 from Portel, Hortus and Tournal showed no additional anterior premolars (Quiles 2003: 167, tab. 100). Torres Pérez-Hidalgo (1988: 208) found in 180 mandibles from Spanish sites, 3 mandibles with a p1 alveolus, another three with a p2 alveolus and one example with p1 and p2 alveoli, although stating the possibility that the p2 alveoli might represent remaining alveoli of milk teeth.




**Text-fig. 7. Occurrence of p1 in mandibles from Deninger bears and cave bears, data after Table 3 (presence = p1 or alveoli observed, absence = no p1 developed, broken = diastema fragmented).**




**Text-fig. 8. Occurrence of p3 in mandibles from Deninger bears, data after Table 3 (presence = p3 or alveoli observed, absence = no p3 developed, broken = diastema fragmented).**

The presence of a p1 in Deninger and cave bear mandibles seems rather unlikely, based on results of the current study. Nonetheless, a higher frequency of anterior premolars was mentioned for the material from Odessa (see Nordmann 1858: 52–55, Mottl 1964: 50). Nagel (2005: fig. 5b) published a mandible with a p1 alveolus on the left side. Hence, homogeneity of the material and species determination of these finds mentioned in literature need to be revised.

## Variability in halves of mandibles

Variability of premolar patterns does not only occur in different specimens, but also between the left and right body side of the same individual. This phenomenon is regularly observed in several analyzed groups, although at varying frequency (Tabs 2, 4). It indicates high flexibility in a part of the dentition that lost most of its function in both bear lineages. In certain cases, remaining alveoli of milk teeth in the middle of the diastema obscure clear identifications of premolar patterns (e.g. Torres Pérez-Hidalgo 1988: 209, Musil 1991: 82). Certain patterns, especially the rare ones might also be influenced by early tooth loss, like in the mandible from Steinheim (Rode 1933: 73, pl. XII, figs 1–2). It lacks even the p4 on the left side, which probably either

never developed, or the alveoli became overgrown. On the broken right side, the p4 seems to occur. Another example is the mandible from Süssenborn (IQW 1305-5840), that lost all premolars and the m3.

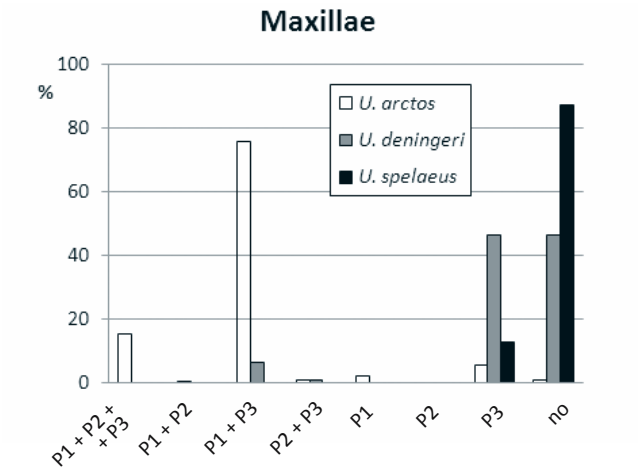
In addition, the number of roots in the anterior lower premolars varies. The studied material shows examples of two-rooted P3/p3 alveoli in skulls and mandibles. The brown bear mandible from Schussenquelle (SMNS 4815-1) in the Late Pleistocene sample (Ua-C3) shows a two-rooted p3 alveolus on the left side, and Kurtén and Poulianos (1977) mentioned one case in *U. deningeri* from Petralona. One skull from Repolust cave (LMJ-59500) retains a two-rooted P3 on both sides (Mottl 1964: fig. 2), and a brown bear mandible from Hundsheim (NHMV-GP 1909-II-73) showed even a two-rooted p2 alveolus.

## Discussion and conclusion

As already stated by several authors, major tendencies in the number of premolars are diagnostic for the various groups of bears. Nonetheless, results are partly different from former assumptions, especially concerning *U. deningeri*. The great variability proclaimed for Deninger bears, and the occurrence of first premolars in the cave bear lineage could not be confirmed, which is due to a more detailed methodological approach and a different species assignment for the mixed material in the Ua-D2 group. In this study, I follow Rabeder et al. (2010), who assign the bear populations from Bad Deutsch-Altenburg, Austria and Süssenborn, Germany to the brown bear group, while others argue for an occurrence of Deninger bears in these assemblages, too (Wagner and Čermák 2012, Baryshnikov and Puzachneko 2017). The rather clear and distinctive premolar pattern obtained in this study seems to argue in favor of the suggested group assignment. Nonetheless, the question of early cave and brown bears is not resolved, and if *U. etruscus* is seen as their common ancestor, very early cave bears and brown bears could probably also retain a more similar pattern. However, this is an assumption, which can only be resolved by clear species determination. The rather variable pattern described for cave bears from Odessa also remains unclear. It could reveal a true more diverse pattern in a distinct cave bear population, or it could be caused by mixed material.

From the results of this study, no evolutionary sequence in the reduction of premolars can be observed, and premolar stages of brown and cave bears are not steps on a common evolutionary ladder, but show distinctive tendencies in the loss of anterior premolars (Schütt 1968: 54).

In general, both lineages show a more pronounced reduction of anterior premolars in the lower than in the upper dentition. The teeth most frequently reduced are the P2/p2, although in brown bears they occur more often than in the cave bear lineage, mainly caused by a high frequency of complete premolar rows in mandibles and maxillae. The reason for the early loss of the P2/p2 could be the concave appearance of the post-canine area, therefore the premolars in the middle of the concavity were the first missing the capability for occlusion (G. Baryshnikov pers. comm. in 2017). Given the few examples of premolar loss in *U. etruscus*, they are not the



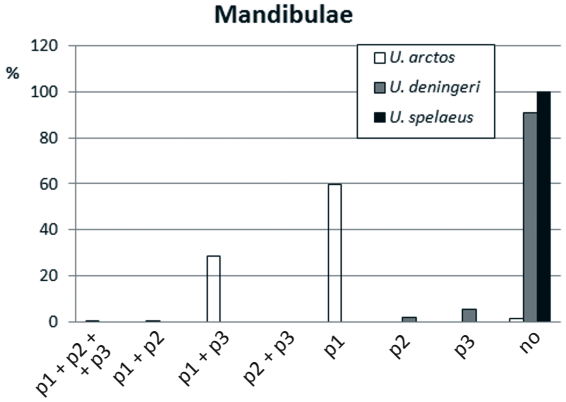

**Text-fig. 9. Frequencies of anterior premolar patterns in maxillae (data after Tab. 2).**

regular first tooth to be reduced. Torres Pérez-Hidalgo (1988: 207) mentioned only one maxilla in *U. etruscus* that lacks the P2, another lacks the P1. The lower p1 is missing in one mandible and the p3 in another.

The reduction of anterior premolars is more pronounced in the cave bear lineage than in brown bears, and contrasting patterns are observed. If at all, Deninger and cave bear tend to retain the P3/p3, while in brown bears, the P1/p1 is the most frequent anterior premolar.

In the **upper dentition**, the most common pattern in brown bears is a combination of P1 and P3. Although less frequent, all three premolars occur regularly in brown bear populations (Text-fig. 9). A single P1 is only slightly more frequent than a single P3. The observation of a single P3 in different brown bear population is noteworthy, despite its rarity, since it is typical in Deninger bears, and still sometimes observed in cave bears. Also, the loss of all anterior premolars in brown bears, the most common stage in Deninger and cave bears, is mentioned in literature, but not confirmed in the available samples. The P1 + P3 pattern occurs with low frequency in Deninger bears. All other patterns remain extremely scarce.

In the **lower dentition** (Text-fig. 10), evidence of a single p1 is the most common feature in brown bears, followed by a combination of p1 + p3. Other combinations, like p1 + p2 are




**Text-fig. 10. Frequencies of anterior premolar patterns in mandibles (data after Tab. 4).**

scarce, and encountered so far only in modern and Holocene samples. A complete premolar row occurs in modern as well as in fossil samples. Total absence of all anterior premolars in brown bears has been mentioned in the literature, but might also be influenced by pathological tooth loss, as suggested by one example in the current study. The complete lack of anterior premolars is the most common feature in Deninger bears. Occurrence of a p3 is scarce, and presence of a single p2 is assumed in three cases. Late Pleistocene cave bears lack all anterior premolars in mandibles.

Hence, the occurrence of a first premolar in skulls and mandibles (alone or in combination) is diagnostic for brown bears, as well as the occurrence of complete tooth rows in the upper and lower dentition. The P1 + P3 combination in skulls is more frequent in brown bears, but may also occur in Deninger bears. The opposite situation is found regarding a single P3 pattern. Most likely, the absence of all three anterior premolars is diagnostic for the cave bear lineage, since the loss of all anterior premolars in brown bears is not well confirmed. Nonetheless, they are not exclusively diagnostic for distinguishing between cave and brown bears. As with other rare patterns, they might also be partly influenced by pathological tooth loss.

In the cave bear lineage, the number of possible combinations is restricted, probably due to a higher specialization. The previously assumed high variability in Deninger bears could not be confirmed, and was probably caused by misidentification or mixed samples of Deninger bears and brown bears. A clear decrease in the P3/p3 frequency from rather high values in certain Deninger bear samples up to very low rates of retaining P3 in Late Pleistocene cave bear maxillae and a complete absence in mandibles is observed, implying an evolutionary trend. On the other hand, already the bears of the Cromerian Forest-Bed lack all anterior premolars in the lower tooth row. As in brown bears, even chronologically older members of the lineage are able to exhibit the whole observed range of premolar patterns, also suggesting the influence of a different factor rather than an evolutionary process.

The results suggest a certain evolutionary trend in specialization in the cave bear lineage, besides differences in populations. Brown bears, on the contrary, may retain all anterior premolars, like its predecessor *U. etruscus* throughout time. Hence, the loss of anterior premolars does not follow any evolutionary tendency in brown bears. The greater range of possible patterns and their varying frequency in different populations might be correlated with the more general mode of life of the brown bear lineage.

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**Appendix. Material and references included in the samples from various regions and chronological units.**

**A. Brown bears**

Ua-A1: Kamchatka
NHMW-Zoology (Inv.No.: 40598-40605, 40609-40623, 40625-40626, 40629-40640, 40642-40687, 40690-40697, 40700-40706, 40713-40715, 40718-40730).

Ua-A2: North America
NHMW-Zoology (Inv.No.: 2570, 3158, 7793, 31596, 41251), NMB (Inv.No.: 2470), AZS (Inv.No.: UR7); data after Reynolds (1906), Kurtén (1960), Green (1962), Spiess and Cox (1976), Mustoe and Carlstadt (1995), Czaplewski and Willsey (2013).

Ua-A3: SE-Europe
NHMW-Zoology (52, 166, 21491, 44213, 67301, 67919), IPUW (2220), VMU(Urs 3), OG (3c175, no number), private collection (one specimen).

Ua-A4: The Near East and Northern Africa (modern and fossil)
NHMW-Zoology (1282, 4220), IPUW (1401), VMU (Urs7), data after Couturier (1948), Hooijer (1961), Auboire and Gillon (1995), Ouchaou and Amani (2002).

Ua-B1: Alps (Holocene – Late Glacial)
NHMW-Zoology (3724, 19991, H72-50-5, H76-20-1, H77-18-2, H81-26-7, H83-47-1, H85-6-1, H86-170-9, H86-178-1, H87-64-1, H89-27-1, H89-31-2, H90-31-4, H90-62-1a, H90-62-1b,H90-148-1, H93-12-12A, H93-12-12B, H98-31-2), NHMW-Geology (Tauernlucke 1962), NÖLM (F/3225, F/3048), IPUW (GS-max), 2842-1, 2842-2, 2702g, Mh), NMB (B.U.1, B.U.4, B.U.5), NM (skeleton Wildenmannlisloch), LMJ3068, 3070, 16472, 236644), private collection (one specimen), data after Döppes and Frank (1997), Withalm (1999)
Ua-B2: Spain (Holocene – Late Glacial)
Data after Altuna (1973), Torres Pérez-Hidalgo (1988).

Ua-C1: Loess sites (Late Pleistocene)
Dolní Věstonice (MZM 3285, 149), Pavlov (MZM 169-c13, 169-c35, 170), Předmostí (MZMa, b, c, c, e, f, g, i and no number, IPUW-no number), Spitz-Mieslingstal (NHMW-Geology 73642-two specimen).

Ua-C2: Great Britain (Late Pleistocene)
Brixham Cave (NHML 48752, 48787), Crayford (NHML-M5041), Coygan Cave (NHML-2507), Magdalen College (NHML-12358), North Cave (NHML-82734), Ravenscliff (NHML-9584), Torbryan Cave (NHML-M4603), Tornewton (NHML-41804, 40702-40703, 41797, TN XVIIC 58), Windy Knoll (NHML-2005, 2097) and data after Reynolds (1906: 31).

Ua-C3: varia-UP (Late Pleistocene)
Winden (IPUW-Wi1), Jaurens (UCBL 301183-301184, 301191-301193), Hundsheim (NHMW-Geology 1909-II-71, -72, -73), Frauenloch (LMJ2037, LMJ3471, LMJ3470), Josefinengrotte (LMJ3070), Schussenquelle (SMNS4815-1), Hohle Fels (SMNS7624-08, SMNS1786), Devil's Tower (NHML13405), Genista Cave (NHML47070, NHML47678a, b), Zoolithenhöhle (NHML O.C.1), data from Blanot 2 (Argant 1991), Pinilla del valle (Alférez et al. 1985), Grotte du Prince and Caverne de Mars (Bonifay 1971), Maspino (Couturier 1948).

Ua-D1: Taubach (Eemian)
IQW (444, 446, 448, 454-455, 460-461, 463-464, 602, 604, 10091, 10094, 10097-10099, 10102, 10105, 10368, 10683, 10689, 10999, 11001-11004, 11007-11008, 11287, 11448, 11715, 11743, 11823, 12342, 12718, 12776, 12954, 13006, 13064-13066).

Ua-D2: varia-OM (Early and Middle Pleistocene)
Atapuerca, Trinchera dolina, lowermost level (data after García and Arsuaga 2001), Süssenborn (IQW 5840, 6999, 9282-9283, 9574), Sontheim cave (SMNS), Bad Deutsch-Altenburg (IPUW-4B/18/14, 4B/18/36, 4B/18/37 and Rabeder etal. 2010), Gray's Thurrock (NHML18756, 22029-22030, 23138, 21651, 28079) and Untermassfeld (data after Musil 2001).

**B. Deninger bears and cave bears**

Ud-D1: Mosbach
NHMW-Geology (C3907), SMNS (32854-1, -5, -7, -8), MWNH (167-172, 174, 176, 180, 561-562, 620, 802, 933-935, 943), nhmMainz (1939-1093, -1094, -1095; 1950-688; 1951-395; 1953-119, -213, -257; 1954-181, -457, -577; 1955-11, -762, -818; 1956-310, -669, -1000; 1957-126, -127, -390; 1958-241, -261, -313, -736; 1959-298, -399 skull and mandible, -784, -867; 1961-682, -865; 1962-332; 1965-354; 1966-207a+b, -208b, -1513; 1964-182, -448, -480, -644, -692; 1972-120; 1974-282, -290, -295; 1975-44a, -185, -187, -692, -710, -1031; 1984-9), LDfH (95-22, 33-7, 15-1, 72-95) and data after von Reichenau (1906).

Ud-D2: Repolust cave
LMJ (57495, 58084, 59026-59032, 59194-59195, 59252, 59500-59505, 59508-59013, 59915, 59893-59897, 59899-59900, 74495, 76120-76121, 76125-76127, 76130-76134, 76137, 76139-76142, 76171-67172, 76194-76195, 76213, 200092, 201077-201081, 201083-201094, 201096-201098, 201100).

Ud-D3: Forest-Bed
Bacton (NHML-6186, 6186-1245, 6186-1248, 6187, 16448, 17906, 17910-17920, 17864, NWHCM-50951a and b), Palling (NWHCM-370), Overstrand (NHML-6079, 6188), Pakefield (NHML-BM2016), Sidestrand (NHML-6190), Mundesley (NHML-6191), Forest Bed, Norfolk (NWHCM-17983, 379).

Ud-D4: varia-DB
Bilzingsleben (data after Musil 1991, 2005), Ehringsdorf (IQW1966-4088, -4943, -4945, -4946, -4954,-4988 -6444, -6552, -7927, 1993-24261), Steinheim (SMNS 16293, 16558, 17281, 17567, 17767 and Rode 1933), Swanscombe (NHML-18923, 49696, skull-April 1943), Kent's Cavern (NHML-M800, 1008, 1011, 1028, 1030, C529, no number) and Hundsheim (IPUW-1889/5/300, 404+405, 406, 410-414, 104, Hundsheim II; NÖLM-typusskull, Hm2).

Us-C1: Schwabenreithhöhle
WKL (118 mandibles and 55 maxillae).

Us-C2: Herdengelhöhle
WKL (60 mandibles and 47 maxillae).