The floral and faunal succession of "Cueva del Toll", Spain

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Mit 7 Abbildungen im Text

Summary. The deposits of "Cueva del Toll" near Moyá (province of Barcelona, Spain) have been studied pollen analytically. The sequence shows an oscillation between pine forest (up to 80% pine pollen), representing a humid and temperate climate, and open vegetation (only 30% pine pollen), representing phases of dry and warm climate. The same changes appear in the composition of the mammalian fossil fauna, and also in the lithology of the cave deposits. The two temperate and humid phases represented in „Cueva del Toll" are correlated with the Early and Main Würm respectively; the warm and dry oscillations represent the Eem interglacial, the Göttweig interstadial, and the end of Würm. This climatic sequence is in agreement with the Würm sequence of Middle Europe. The leading fossil mammal of the Göttweig phase in this cave is the cave bear; it appears to be most closely akin to the Gailenreuth form in Middle Europe, and differs by its larger size from the Early Würm and interglacial populations.

Resúmen. Los depósitos de la "Cueva del Toll"; situada en las cercanías de Moyá (Província de Barcelona, España) han sido estudiados con el método de los pólenes. El corte demuestra una oscilación entre el bosque de pino (las muestras contienen hasta 80% de pólenes de pino) representando un clima húmedo y templado y la vegetación abierta (las muestras contienen únicamente un 30% de pólenes de pino) que representa un clima seco y caliente. Las mismas variaciones aparecen tanto en la composición de los fósiles de la fauna mamífera como también en la litología de los depósitos de la mentionada cueva. Las faces, templada y húmeda, representadas en la Cueva del Toll están correlacionadas con las épocas principio y medio de Würm. Las oscilaciones calientes y secas representan las épocas del interglacial Eem, la interstadial Göttweig y la parte final de la época de Würm. Este lapso climatológico coincide con el de Würm de Europa Central. En esta cueva el fósil predominante de face Göttweig es el del oso de las cavernas, que parece ser el más proximo forma de Gailenreuth de Europa Central, difiriéndose, sin embargo de fauna de la época temprana de Würm y de la época interglacial, por su gran tamaño.

Introduction

The cave named "Cueva del Toll" lies about 50 km north of Barcelona and some 5 km east of Moyá (c. 750 m above sea-level) in the province of Barcelona, Spain. During a short visit there in the summer of 1956, samples of the cave deposits were taken by DONNER in order to find out if they contain any pollen, and, if they do, whether the pollen composition reflects any vegetational changes in the period during which the cave layers were deposited. The faunal succession, as shown by the remains of different mammalian species, could then be compared with the vegetational succession, and the results used for dating the deposits. Cave layers are probably the most suitable deposits for a study of this kind, as they contain enough remains of mammals for statistical purposes. At the same time, some of the fossil mammals were studied by KURTÉN. The authors wish to express their deeply felt gratitude to the leader of the excavations in the Toll, Dr. J. F. DE VILLALTA COMELLA, and to his associates, for their great generosity in placing all their resources and material at our disposal, for numerous courtesies extended to us, and for important information supplied during the subsequent work.

The work has been supported by grants from the Finnish State Commission of Natural Science.

"Cueva del Toll" and its remains of mammalian species are described by THOMAS & VILLALTA in the guide for the excursions B 2 — B 3 during the V INQUA Congress in Spain in 1957. Notes by SERRA and FUSTÉ on the archaeological finds and human remains respectively are also included in the same guide. The present description of the cave and its stratigraphy is based entirely on the guide. The cave, which is formed in Eocene limestone, has many galleries, but "Galerie Sud" is the only one in which there is cave-earth of some thickness, i. e. up to 9 m. The samples for pollen analysis were taken from section B (fig. 1), about 5 m from the entrance of the cave. The layers and the average thickness of each are shown in fig. 2. The stratigraphy of section B is as follows:

Layer a. Thickness 1.1—1.5 m. Unsorted sand with angular stones. The layer contains Neolithic remains.

Layer b. Thickness 0.2 m. Reddish sandy clay.

Layer c. A thin intercalated layer.

Layer d. Thickness 0.2 m. Sandy clay, lighter than in layer b.

Layer e. Thickness 0.2 m. A clay sediment, mixed with hyena coproliths.

Layer f. Thickness 0.3 m. Compact reddish clay. Less coproliths than in the layer above. In the clay a discontinous intercalation of flat angular stones.

Layer g. Thickness 0.25 m. Varved clay.

Layer h. Thickness 0.35 m. The lithology differs very much from that of the other layers. Layer h consists of a loose breccia with bones and angular stones in a sandy clay matrix.

Layer i. Thickness 0.2 m. Compact reddish clay.

Layer j. Thickness 0.4 m. Compact deep-red clay, with an intercalation of angular stones.

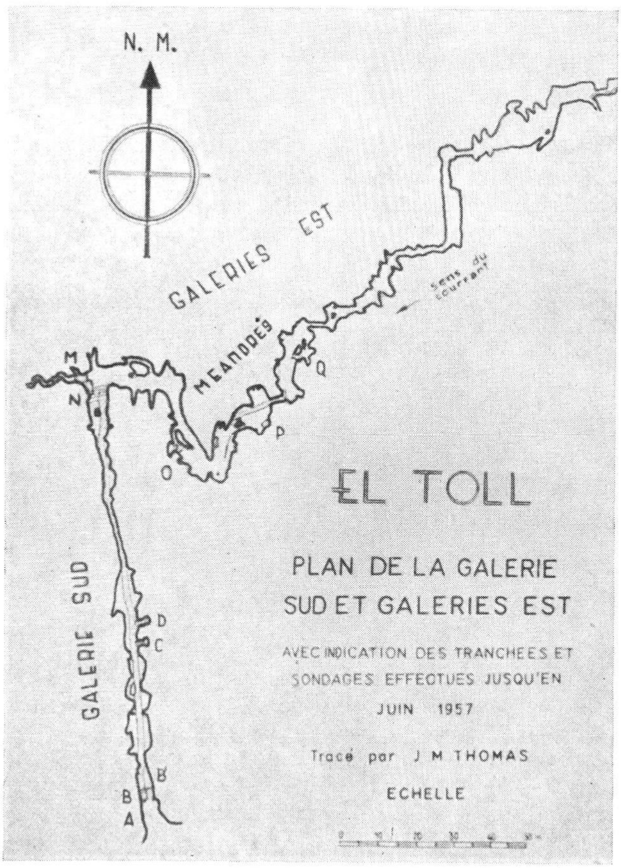

Fig. 1. Plan of „Cueva del Toll", showing Galeries Est and Sud and the location of Section B

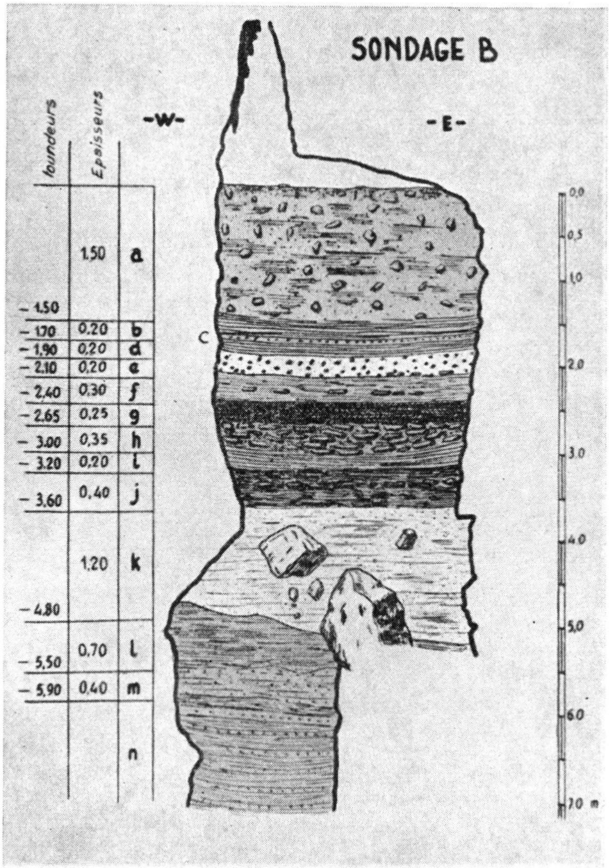

Fig. 2. Section B of "Cueva del Toll". After THOMAS & VILLALTA.

Layer k. Thickness c. 1.2 m. Very sandy loose clay in which big stones, coming from the ceiling, are found.

Layer l. Thickness c. 0.7 m. Sterile clay.

Layer m. Thickness c. 0.4 m. Sandy clay, slightly varved.

Layer n. Excavated down to 2 m. Coarse gravel with layers of clay.

The vegetational succession (J. J. DONNER)

The part of the section which was pollen analytically studied is 185 cm thick. Twelve samples were taken from layers b—j, the interval between the samples being 10—25 cm (see fig. 3). The siliceous matter of the pollen samples was removed by HF treatment (see FAEGRI & IVERSEN 1950). The boiling with HF, followed by HCl treatment, was in most cases done twice. About 4—5 cm^3 material was needed for 1—3 slides, the cover glass being 20 x 40 mm. All the analysed samples contained pollen, but some of the slides were extremely poor in pollen. Therefore the total amount of pollen counted in each sample is only 100. To get this amount up to 280 traverses of 2 cm had to be counted for one sample. Some of the pollen and spores were badly preserved, but most of them could be identified. Only 0—4% of the total amount could not be identified, and they were not included in the counts.

The deposits in "Cueva del Toll" are not ideal for pollen analysis. WELTEN (1956), however, has, in a work dealing with subrecent changes of the pollen rain in the subalpine regions of Spain, demonstrated that even arid soils, like deep-red clay, can be used for pollen analysis. Another factor which must be considered is the location of the section in the cave. van Campo & Leroi-Gourhan (1956) studied the pollen rain in the d'Arcy-sur-Cur caves, and they came to the conclusion that a large amount of pollen are carried by the wind up to 10 m from the entrance provided it is big enough. If an air current goes through the cave pollen are carried further in, up to 30 m from the entrance. Section B in Toll is about 5 m from the entrance, as mentioned above. Thus one would expect the section to be near enough to the entrance to have received a pollen rain reflecting the surrounding vegetation. The exposure to the prevailing winds can also have some influence, as shown by Derville & Firtion (1951) in their study of a rock-shelter in Cantal. They demonstrated a clear difference in pollen sedimentation between different sides of the cave. The sheltered part had almost sterile sediments. The section from which the samples in "Cueva del Toll" were taken lies in the middle of the cave and it has therefore been well exposed to the wind currents.

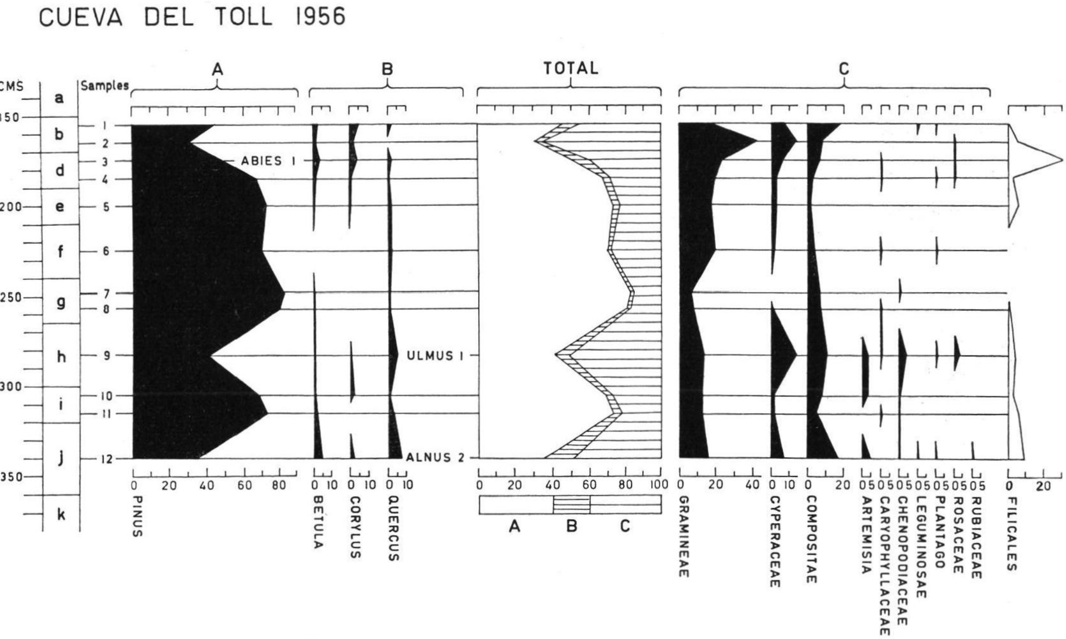

Fig. 3. "Cueva del Toll", pollen diagram, layers j to b.

Taking into account the above-mentioned investigations it seems probable that the sediments in section b of „Cueva del Toll" have received a representative pollen rain. The sediments are not likely to contain any secondary pollen. In the pollen diagram from the Brüggli cave near Neuzlingen (Canton of Bern) Welten (1954) found secondary pollen in one of the two profiles studied. In the pollen diagram, starting with the late-glacial Younger Dryas period, Welten found some pollen which were from the last interglacial period or even older. They were, according to Welten, incorporated in the sediments which had been sliding down a slope. In "Cueva del Toll" the cave layers are horizontal, so disturbances similar to those described by Welten are not likely to occur. It may also be mentioned that Welten did not find any trace of a sinking down of pollen from the surface.

The results from "Cueva del Toll" can be seen in the pollen diagram in fig. 3. During the Bronze Age there was a land-slide which closed "Galerie Sud" (Thomas & Villalta, 1957). Thus a pollen spectrum reflecting the present vegetation is not represented in the diagram. As seen from the diagram *Pinus* is most common of all pollen types. Its percentage varies between 30—80⁰/₀. No size measurements of the *Pinus* pollen were done but most of them are of the *Pinus silvestris* type (see WELTEN 1956). *Betula, Corylus* and *Quercus* are all present. They form discontinuous curves of 1—7⁰/₀. Occasional pollen of *Abies, Alnus* and *Ulmus* were also found. Of the non-tree pollen Gramineae, Cyperaceae and Compositae are the most common, but *Artemisia*, Caryophyllaceae, Chenopodiaceae, Leguminosae, *Plantago*, Rosaceae and Rubiaceae are also present. Filicales, which are not included in the total, are highest in sample 3 (30⁰/₀) and present in all samples except in 6 and 7.

The pollen types were divided into three groups, the relative variations of which are shown separately in the diagram (fig. 3). *Pinus* (and *Abies)* forms group A, *Betula, Corylus* and *Quercus* group B, in which also *Ulmus* and *Alnus* are included, and the non-tree pollen group C. The pollen curves in group B and C and the *Pinus* curve vary inversely. The curves of the diagram suggest changes between forest, dominated by *Pinus silvestris*, and an open vegetation with herbs and a few deciduous trees. Climatically the curves most probably show changes between temperate humid periods and warm dry periods. The *Pinus* values of about 30⁰/₀ in the two uppermost samples, which represent the Neolithic time or a somewhat older period, are probably due to long distance transport. This can be expected to have a strong influence if the local vegetation is open (and the local pollen production is low), as suggested by the high non-tree pollen values. The rather strong influence of *Pinus* outside the pine forests has been demonstrated by WELTEN (1956) in his study of subrecent pollenspectra from Spain, and also in a study of the recent pollen rain in Switzerland (WELTEN 1950). The high *Pinus* value of c. 80⁰/₀ in the Toll diagram must, on the other hand, reflect a strong representation of pine forests in the area. It is difficult to judge how near the pine forests came and how large an area they covered, but they must have been common well outside (below) their present scattered areas higher up in the Pyrenees (see GAUSSEN 1956). At present the Moyá region has no pine, only *Quercus lusitanica* and some *Fagus*.

From the changes in the pollen diagram we may conclude that there were two temperate humid periods interrupted by a warm dry period (layer h) similar to the present one (or at least to that during the Neolithic time). Layer j also represents a warm dry period, but probably only its last stage. It is remarkable how uniform the pollen curves are and how the same value for pine (30⁰/₀) repeats itself in three different layers. In layer f, sample 6, there is a small depression in the *Pinus* curve. To check if this has any significance, a hundred more pollen were counted. After this count the percentage for *Pinus* rose and the depression in the curve disappeared. It is thus only a result of the small number of pollen counted. (The diagram shows the original percentages based on a hundred pollen.)

It is difficult to get a clear picture of the open vegetation when layers j, h and b were formed. It can be noted that the Cyperaceae curve reacts very clearly, and Cyperaceae must in Spain be included in the "steppe" elements. All the other non-tree pollen types also belong to these elements. The deciduous trees show the same changes as the non-tree pollen. They have, however, very low values, and they were probably only present as scattered trees or in small woods in favourable areas. As the pollen diagram from "Cueva del Toll" is the only one from this region, no conclusive results about the vegetational changes can be given. Even if the pollen diagram reflects the main changes, the cave deposits may not give the normal percentages for the various pollen types.

The pollen diagram can not directly be used for dating the layers in "Cueva del Toll". But in obtaining a succession of warm dry periods alternating with temperate humid periods the age of the various layers can be suggested if the faunal succession is also taken into account.

As a summary of the pollen analysis of the layers in "Cueva del Toll" the following table of the vegetational and climatic changes can be given:

Layers	Vegetation	Climate
b	wood-less	warm dry
d, e, f, g	pine forest	temperate humid
h	wood-less	warm dry
i	pine forest	temperate humid
j	wood-less	warm dry

The faunal succession (B. Kurtén)

In a chart given by Thomas & Villalta (1957) the presence and relative abundance of mammalian species is tabulated, layer by layer, as revealed by the preliminary excavations in "Galerie Sud". In future, with a more complete record at hand, and when estimates of the absolute number of individuals at different levels can be made, more detailed and accurate analysis will be possible. At present only a relatively crude analysis is possible, the main purpose being to check whether the vegetation history is compatible with the faunal succession.

Since the pollen diagram indicates an oscillation between pine forest and open country - or, climatically, between temperate-humid and warm-dry conditions - the proper way of grouping the mammalian species would seem to be into (1) sylvan, (2) non-sylvan, and (3) indifferent. This has here been attempted as follows.

Sylvan forms. This group is taken to include *Erinaceus, Talpa,* bats, *Vulpes, Felis silvestris, Meles, Castor, Apodemus, Sus, Capreolus, Cervus, Hippopotamus,* and *Rhinoceros mercki.* Most of these need little comment; *Hippopotamus* is included as an indicator of humid climate rather than as a forest form.

Non-sylvan forms. This group includes the grazers *(Bison, Bos, Equus),* alpine species *(Capra ibex)*[1]), and the species determined as *Rhinoceros tichorhinus.* This last-mentioned determination seems doubtful, as there is no other tundra form in the fauna, and the species occurs at a level (h) which evidently represents a warm and dry phase. It may perhaps be suggested that the rhinoceros in question is actually a steppe grazer, not a tundra grazer.

Indifferent or indeterminate forms. This group includes the lagomorphs, *Microtus,* and all the larger carnivores.

Thomas & Villalta express the abundance of each species in five grades, from single specimens to predominant forms. For the present purpose, these grades were given corresponding scores as follows:

"Une trace" — 1

"Quelques restes" — 2

"Abondant" — 4

"Très abondant" — 8

"Espèce dominant" — 16

Scores for all three groups were added up for each level (but for level a all the domestic forms were left out) and percentages calculated on the total score for sylvan

[1]) The chamois, *Rupicapra rupicapra,* is mentioned by Thomas & Villalta in the text (p. 19) but does not occur in the tabulation.

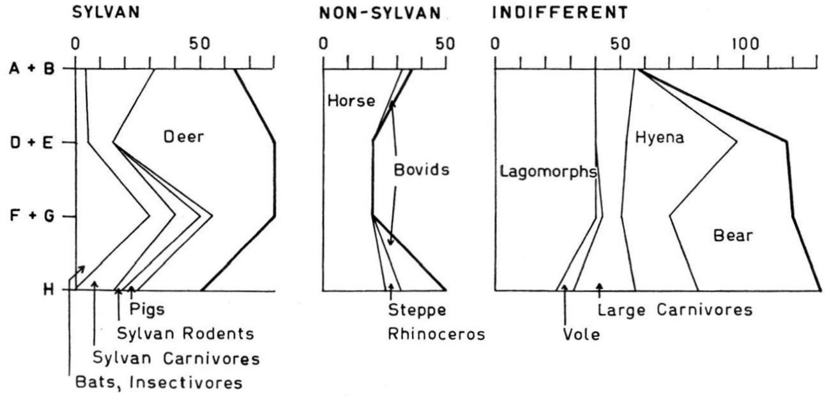

Fig. 4. Faunal succession in layers h to a of "Cueva del Toll", based on scorings for abundance as described in the text.

plus non-sylvan forms. The levels below layer h were too poor to be studied in this way, and the study was limited to the sequence from layer h to layer a. To reduce the chance fluctuations, the levels above layer h were grouped two and two (f+g, d+e, and a+b), a procedure which seems warranted by the stability of the pollen facies for each group.

The results are indicated diagrammatically in fig. 4. From a minimum in layer h, the sylvan elements increase rapidly and stay predominant up to layers d—e, but decrease again in the uppermost layers. The agreement with the vegetation history is patent and will be discussed below, together with its implications.

As to the zones not included in the diagram, it may be noted that layer i, temperate-humid with pine forest according to the pollen data, contains the forest form *Rhinoceros mercki* and such a diagnostic "humid" form as *Hippopotamus*.

Before proceeding to a discussion, it may perhaps once more be emphasized that the percentages are not based on precise estimates of the numbers of individuals, but only on a conventional scoring from very rare (1) to predominant (16), and hence are subject to revision when the total fossil content of the cave is known and more accurate estimates have been made.

Discussion

The region in which "Cueva del Toll" is situated was evidently outside the periglacial zone of the Pleistocene glaciations. The type of climatic oscillation found here is analogous to that found in the Carmel caves (Bate 1937). The humid and temperate oscillations represent glaciations, the warm and dry episodes interglacials or interstadials.

The vegetation history depicts a twofold cool oscillation. In the mammalian fossil record, only the second oscillation can be statistically confirmed at present, since the lower layers are poor in bones. The agreement between the two sequences is clear, however (see fig. 5), and, as previously mentioned, there is a clear suggestion of an earlier forest fauna episode in the presence (in layer j) of Merck's rhinoceros and the hippopotamus. The faunas of these Iberian cool oscillations are, in fact, reminiscent of the interglacial faunas in Middle Europe. This appears quite natural; during glaciations, the temperate fauna of Middle Europe was forced southward into refuge areas, of which the Iberian peninsula apparently is one example. Thus we may expect a fauna of "interglacial" type, by Middle European standards, to characterize the glacial epochs in Spain. The same also holds for the flora.

The lithology also reflects the climatic changes. It may be noted that Thomas & Villalta (op. cit.) mention the presence of wind-blown quartz grains in the material of layer h, which supports the conclusion that this layer was formed during a period with a

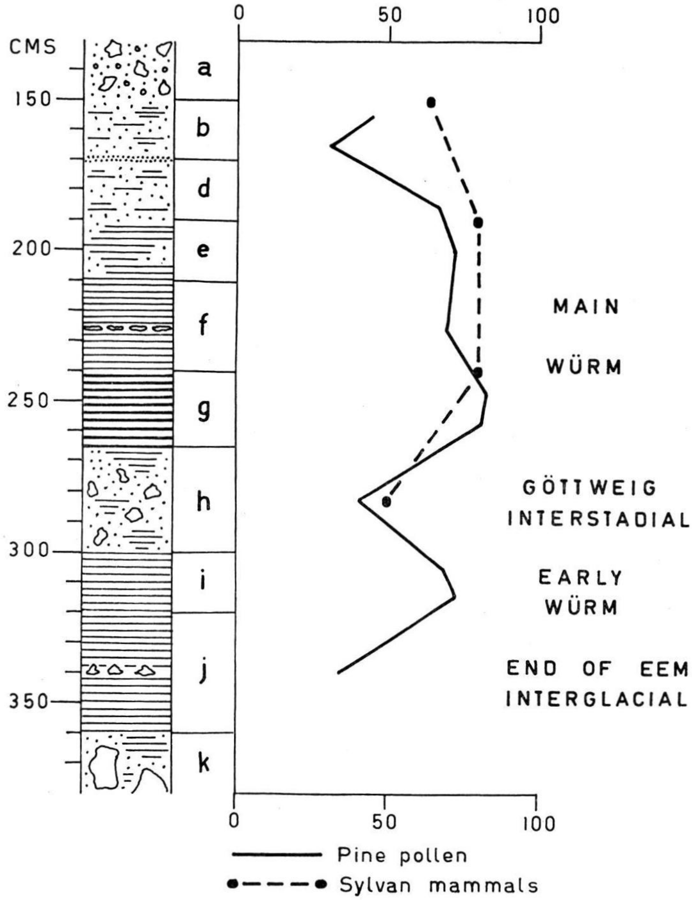

Fig. 5. Profile showing lithology, pine pollen curve (from fig. 3), curve for sylvan mammals (from fig. 4), and suggested dating of the cave sediments in "Cueva del Toll".

dry climate and an open vegetation. It is, however, the alternation of sandy and clayey deposits which gives especially valuable evidence. The most compact and "varved" clays date from the phases of maximum humidity, the sandy deposits from the warm and dry phases. These lithological features are in precise agreement throughout with the inferences based on flora and fauna, but it is interesting to note that the earlier cold (humid) oscillation seems to have begun well before deposition of layer j; the main lithological change is between k and j.

We correlate the two cold oscillations with the Early and Main Würm respectively, the warm episode intervening between them with the Göttweig interstadial, and the layers j and k are considered to have been deposited during the relatively warm and dry conditions at the end of the Eem interglacial. A second interpretation which might be suggested would be to correlate the steppe horizon h with the Eem, and the forest peak of i with the late Riss, but this appears rather improbable for several reasons. The Göttweig is well known to have been a relatively long episode with a marked climatic amelioration very much farther to the north, and it is almost inconceivable that it would have had no effect on the sequence from g to d. The fauna seems also to agree better with this interpretation than with any other; the cave bear mass occurrence is in layer h, and it is known in other regions to be very common in the Göttweig (Gross 1957 b).

The record from "Cueva del Toll" is thus found to be in very good agreement with the outlines of the Würm glaciation, as they heve now emerged elsewhere (Emiliani 1956, Gross 1957 a, 1957 b, and literature there cited). The glaciation is dichotomous, with a shorter and perhaps less intense Early Würm and a long Main Würm, separated by a very well-defined interstadial. On the other hand, the minor interstadials of the Main Würm are not clearly depicted in this record.

If the climatic history found here is in excellent agreement with that of the periglacial zone, it is, on the other hand, definitely at variance with the sequence of the Carmel caves. The Carmel record indicates three cold episodes, the two earlier of about equal strength and the third considerably weaker. This third episode would seem somewhat too weak to represent the Main Würm, and its significance remains obscure.

The results from "Cueva del Toll" also suggest a reconsideration of, for instance, the stratigraphy of the Gorham Cave, Gibraltar (see Zeuner 1953), where it would seem that the sandy layers would represent interstadials or interglacials, not glaciations.

The cave bear of "Cueva del Toll" (B. Kurtén)

The cave bear material from "Cueva del Toll" is of considerable interest. It is one of the few large samples of this species which are exactly datable. The very great majority of the specimens seen by me are from layer h and are thus interstadial in age. The species, however, continues up to layer d. When the excavations are concluded, it may be worthwhile to study the microevolutionary trends of *Ursus spelaeus* in this sequence, and the material of "Cueva del Toll" may well become a standard of comparison for the population history of this species in western Europe. At the present stage some elementary statistical comparison with other samples will serve to indicate the possibilities.

The present investigation is limited to univariate analysis of the lengths of the cheek

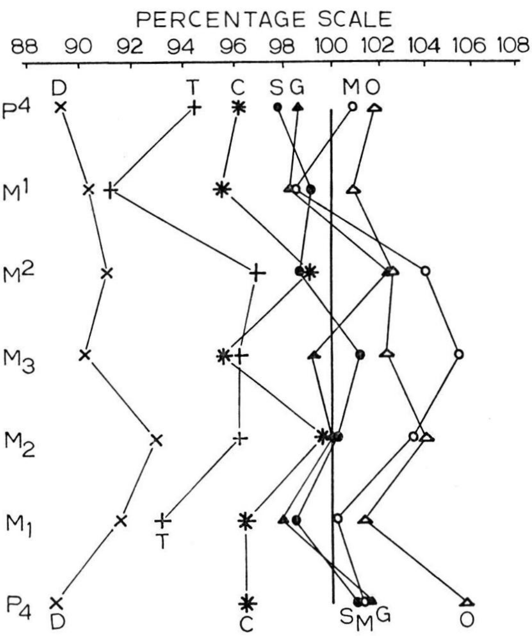

Fig. 6. Ratio diagram, comparing mean lengths of cheek teeth in samples of *Ursus spelaeus;* means expressed as percentages (on a log scale) of the selected standard sample of "Cueva del Toll" (100%). D = Dachstein (Schreiberwandhöhle); T = Trosketa Cave; C = Cotencher, S = Slouperhöhle; G = Gailenreuth; M = Mixnitz (Drachenhöhle); O = Odessa caves.

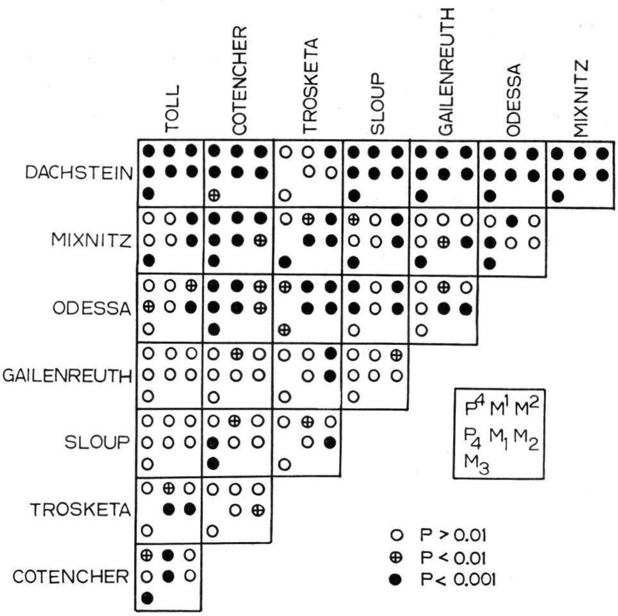

Fig. 7. Significance of differences in means between samples compared in fig. 6. Measurement key in inserted square. Symbols indicate probability values (P) according to key: $P > 0.01$ not significant, $P < 0.01$ probably and $P < 0.001$ highly significant. (Example: Significance of difference between mean lengths of M^2 in Toll and Sloup samples: upper right symbol in the square showing comparison Toll/Sloup indicates $P > 0.01$; the difference is not significant.)

teeth. Sexable remains (jaws, skulls, and isolated canines: see KURTÉN 1955, 1958) indicate equal representation of both sexes, and thus there should be no important bias in the mean values, resulting from sex dimorphism. The means (table 1) have been compared with those for seven other samples: a small sample from another Iberian cave (the Trosketa Cave in Guipuzcoa), the probably interglacial small form from the Schreiberwandhöhle of Dachstein in Austria, the Early Würm population from Cotencher in Switzerland, and the classical populations of Gailenreuth (type locality), Mixnitz, Sloup, and Odessa. At Mixnitz, but seemingly not in any other of these sites, the males outnumber the females, and the means may be slightly higher than true population means. All data used are original.

The mean lengths of the teeth are compared in fig. 6 by means of SIMPSON's (1941) well-known ratio diagram method. The differences between sample means were evaluated by means of t-tests, probability values below 0.01 being considered as probably significant, and below 0.001 as highly significant. Test results are summarized in fig. 7. They suggest a division into three more or less well-defined size groups:

(1) Small forms (Dachstein and Trosketa).

(2) Medium-large (Toll, Gailenreuth, Sloup). The Cotencher sample is somewhat intermediate between (1) and (2).

(3) Very large (Mixnitz and Odessa, but the Mixnitz values may be spuriously high).

Some of these differences probably arise from spatial raciation, but some are almost surely due to chronological differentiation. There is some suggestion of an evolutionary trend from the small forms, like that from Dachstein, through the type of Cotencher into the medium- large forms of group (2).

The cave bear appears to have attained maximum size in some marginal areas of its range, as exemplified by the Odessa form and particularly by the very few specimens of *Ursus spelaeus* known from British deposits. Some of these reach dimensions rarely or never attained in Continental populations.

Studies along the indicated lines, including also bivariate analysis (see KURTÉN 1954), of these and other cave bear samples may become useful both in the evaluation of the evolutionary trends of *Ursus spelaeus* and as a chronological tool. The field work in bear caves should then be up to the highest standard. Many of the classical cave samples, unfortunately, now have a very dubious scientific value; they have frequently been dispersed and broken up. Predatory exploitation of bear caves is, however, the darkest chapter.

Table 1

	N	M	S. D.	V.	S. R.
P^4	33	20.67±0.25	1.41±0.17	6.8	16.11—25.23
M^1	54	29.64±0.20	1.46±0.14	4.9	24.90—34.58
M^2	44	45.19±0.37	2.45±0.26	5.4	37.16—53.12
M^3	62	27.20±0.22	1.75±0.16	6.4	21.54—32.86
M^2	78	30.69±0.17	1.52±0.12	5.0	25.76—35.62
M^1	71	30.98±0.17	1.46±0.12	4.7	26.25—35.71
P^4	23	15.74±0.27	1.28±0.19	8.1	11.10—19.88

N = number of specimens; M = mean; S. D. = standard deviation; V = coefficient of variation; S. R. = standard range of variation (estimate of variation in a population of 1,000 individuals).

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Manuskr. eingeg. 22. 2. 1958.

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