Changes in Bat Fauna During the Middle and Late Holocene as Exemplified by Thanatocoenoses Dated with 14C AMS from Kraków-Częstochowa Upland Caves, Poland

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Changes in bat fauna during the Middle and Late Holocene as exemplified by thanatocoenoses dated with ^{14}C AMS from Kraków-Częstochowa Upland caves, Poland

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Fossil material from 12 caves situated in the Kraków-Częstochowa Upland (southern Poland) was studied. In 17 samples of osteological material, 8,275 individuals (Minimal Number of Individuals, MNI = 4,571) of 12 bat species were identified. Thirteen separate thanatocoenoses were found (R × C test) from which bone material was dated using the ^{14}C AMS method; 13 dates from 6,725 to 820 ^{14}C yr BP (yr BP) were obtained. Correspondence analysis for thanatocoenoses from the Atlantic and Subboreal periods distinguished two bat species groups and two thanatocoenosis groups: 1) pontic-mediterranean species with a higher frequency during the Atlantic period, e.g., *Rhinolophus hipposideros* which reoccurs more abundantly at the end of the Subboreal period and *Myotis emarginatus*, which is absent in earlier sediments with the exception of one episode; 2) *Myotis daubentonii*, *Plecotus auritus*, and *Myotis dasycneme* which increase in frequency during humid and cool periods (5,500–4,200 and 3,000–2,700 yr BP); 3) thanatocoenoses from the Holocene climatic optimum (6,000–5,500 yr BP) characterized by a dominance of *Myotis nattereri*; a decrease in its frequency occurred during the cooler end of the Atlantic period; 4) thanatocoenoses from the Subboreal period (4,100–3,500 yr BP) characterized by a dominance of *Myotis bechsteinii*. The maximum frequency of *M. bechsteinii* correlates with an increasing share of *Fagus* and *Carpinus* in forest ecosystems, while its decrease was probably caused by disease and was independent of human activity. *Myotis myotis* was found in assemblages from the Atlantic period, while the remains of a nursery colony in Nietoperzowa Cave (820 ± 25 yr BP) indicate that reproduction of this species occurred to the north of the Carpathians before the appearance of houses with attics. The presence of mass concentrations of *Pipistrellus pipistrellus* (s.l.) in caves was confirmed for the Subatlantic period (2,325 ± 30 yr BP), which shows its independence from both thermal balance and human influence on contemporary ecosystems. The low frequency of *Barbastella barbastellus* in thanatocoenoses prevents reconstructions. Reconstructions for the Atlantic and Subboreal periods show that the composition of the bat fauna depends on changes in climate and vegetation, while human activity seems to have marginal impact. A comparison of paleozoological and radiocarbon datings revealed large differences in age estimation of the thanatocoenoses.

Key words: Kraków-Częstochowa Upland, Poland, Holocene, bat fauna, ^{14}C AMS, cave, climate, vegetation change, human activity

INTRODUCTION

After the Pleistocene Vistulian glaciation, the contemporary warm period of the Quaternary, Holocene, had begun. Its beginning is dated from 10,250 ^{14}C yr BP in Poland and continues to this day (Starkel, 1999). As the climate warmed to the north of the Carpathian and Sudetes Mountains, the contemporary flora and fauna began to

form. Its gradual return from southern refugia took place through the Morawska Gate and through the Carpathian and Sudetes depression (Pawłowski, 1999; Ralska-Jasiewiczowa, 1999). The origin of the bat fauna and bats' migration routes are the subject of intensive research including molecular techniques (e.g., Ruedi and Castella, 2003). The main sources of information on the Holocene bat fauna are cave thanatocoenoses formed mostly during hibernation (Wołoszyn, 1970). Sufficiently numerous osteological material is a major indicator of the relative frequencies of species during certain periods (Gilinsky and Bonnington, 1994). The distribution of fossil localities coincides to a large degree with the occurrence of karstic areas. In Poland, the Kraków-Częstochowa Upland, with over 1,000 known caves (Szelerewicz and Górny, 1986), is the best known and most investigated region. During interdisciplinary archeological and paleozoological research, material from dozens of objects containing the remains of bat bones have been investigated to date (e.g., Bocheński *et al*., 1983; Nadachowski *et al*., 1989, 1991; Wołoszyn, 1989; Dagnan-Ginter *et al*., 1992). Nevertheless, typical thanatocoenoses from the hibernation period containing mostly bat remains were investigated only in a few cases (Skalski and Wójcik, 1968; Wołoszyn, 1976*a*, 1988; Ochman and Wołoszyn, 2000). Numerous sediments were investigated also for the Western Tatra Mts. (Piksa and Wołoszyn, 2001), but only a few are known from caves of the Sudetes Mts. (Hajduk and Ogorzałek, 1968; Bosák and Horáček, 1982; Wołoszyn, 1989), Pieniny Mts. (Alexandrowicz *et al*., 1985; Wołoszyn, 1995; Ochman and Wołoszyn, 2003), Holy Cross Mts. (Kowalski, 1972; Wołoszyn 1976*b*; Ochman, 2003), and karstic cracks on the Roztocze (Kowalski *et al*., 1963) and Bieszczady Mts. (Postawa, 2003). For the Western Carpathians and

foothills of the Sudetes, the possible refugia, over 30 thanatocoenoses were investigated from the Slovak Republic (Obuch, 1994, 1995), the Czech Republic and Slovak Republic (Horáček, 1976, 1995), and Hungary (Kordos, 1982). Similarity in frequency of thanatocoenoses resulted in the description of five separate groups in the Western Carpathians (Obuch, 1995) and three in the Western Tatra Mts. (Piksa and Wołoszyn, 2001), which differ in the share of the most abundant species. The sequence in which species appeared and changes in their frequencyduring the Holocene were correlated with thermal balance (Horáček, 1984; Zahn, 1999), human activity (Horáček, 1984; Wołoszyn, 1989) and vegetational changes (Kordos, 1982; Obuch, 1995). The age of all investigated thanatocoenoses from this region was calculated by paleozoological dating. The large discrepancies between the dates of groups with similar bat fauna by particular authors indicates that this method is imperfect and, in consequence, enables the reconstruction of the sequence in which species appeared. The ^{14}C AMS (Accelerator Mass Spectrometry) dating method for small samples enables age estimation of bone remains directly from thanatocoenoses and prevents inaccuracy in layer dating. The AMS method was used to assess the absolute age of thanatocoenoses from the Austrian Alps, which allowed specification of the period when *M. bechsteinii* had been a dominant species (Baagøe, 2001).

The abundance of numerous caves with well preserved Holocene osteological material was the reason for choosing the Kraków-Częstochowa Upland as a research area. In spite of its small length (120 km), the modern edges of distribution of a few species can be found here, such as *R. ferrumequinum*, *R. hipposideros* and *M. emarginatus*. Small differences in altitude allow for the omission of the vertical aspect of

species' distribution. Changes in the natural environment during the Holocene have been reconstructed for the Upland and surrounding areas, including Holocene temperature and humidity (Pazdur *et al.*, 1988; Dobrowolski *et al.*, 2002), vegetation (Ralska-Jasiewiczowa and Starkel, 1999), human activity (Godłowski, 1995; Kruk *et al.*, 1996) and its influence on vegetational changes (Ralska-Jasiewiczowa *et al.*, 2003).

The following assumptions have been made: i) caves used for hibernation today were also used for hibernation in the early Holocene; ii) thanatocoenoses far from the entrances of caves were accumulated during hibernation; iii) the frequency of species in thanatocoenoses reflects environmental conditions which existed while it was forming.

The aim of this study is to reconstruct changes in the relative frequency of bat species using ^{14}C AMS dating and to describe the most important parameters which influenced the fauna. Also, an assessment of the effectiveness of previous paleozoological dating was made.

Materials and Methods

The Kraków-Częstochowa Upland is a region with an area of 2,600 km², which is the part of the Śląsko-Krakowska Upland. It is a thin belt with a width from 12 km to 50 km and length of 120 km, which extends from 50º50'N to 49º48'N. It is built from a uniform limestone slab of Upper Jura 400 m wide. In the northern part of this area, the altitude reaches about 300 m a.s.l., while the southern part is up to 450 m (the highest hill is 512 m a.s.l.) and surpasses the neighbouring areas by 100 m. The annual rainfall is between 650 and 700 mm, mean temperature is 7.5ºC and is lower than in neighbouring areas by about 0.5–1.0ºC. The winter lasts about 100 days, snow cover lasts for an average of 80 days, although in shaded places up to 100 days (Kondracki, 2001). Karstic elements like caves, over 1000 of which were investigated so far (Szelerewicz and Górny, 1986), are common in the Upland. About 100 caves have a zone with a stable microclimate, with temperature equal to mean annual temperature at ground level, which permits bat hibernation (Kowalski, 1954).

The characteristic forest vegetation is composed of *Dentario glandulosae-Fagetum* on northern slopes of valleys and hills, *Dentario enneaphyllidi-Fagetum* on dry, southern slopes and *Stellario-Carpinetum*. In shaded and chilly localities, fragments of *Lunario-Aceretum* have persisted. On sandy soils *Peucedano-Pinetum* dominates, mostly artificially planted. Besides forest vegetation, there is also thicket-like vegetation with *Corylus avellana* and *Cerasus fruticosa,* and semi-natural dry grasslands. Nevertheless, segetal and ruderal vegetation predominates in the Upland. For the research, 30 caves in the Kraków-Częstochowa Upland were chosen (Fig. 1): Brzozowa, Ciesenć, Dzwonnica-Towarna, Kamiennego Gradu, Kryształowa, Łabajowa, Koralowa, Księdza Borka, Maurycego, Na Biśniku, Na Tomaszówkach Dolnych, Na Świniuszce, Niedźwiedzia, Nietoperzowa, Olsztyńska-Wszystkich Świętych, Ostrężnicka, Piętrowa Szczelina, Pod Sokolą Górą, Psia, Racławicka, Studnisko, Sucha, Trzebniowska, Urwista, Wielkanocna, Wiercica, Wierna, W Straszykowej Górze, W Zielonej Górze, Zegar. The main criterion for selection was the existence of a static microclimate zone in which bats could hibernate. Objects with exploited sediments or where archeological and paleontological studies were conducted at the turn of the XIX and XX centuries (Kowalski, 1951) were not included from this study.

The collection of material took place during the years 1998–2001. Osteological material was picked up directly from the surface of sediments or from the crevices between rocks on the bottom of caves. To assess the homogeneity of material in a cave, samples were collected from several places within each cave. The zone near the entrance was omitted in order to exclude material other than that accumulated during hibernation, e.g., owl pellets (Bocheński *et al.*, 1983; Obuch, 1995). Additionally, bone material available at the collection of the Institute of Animal Systematics and Evolution, Polish Academy of Sciences, in Kraków (ISEA PAS), from caves Małotowa (leg. A. Górny) and Wierzchowska Górna (leg. B. W. Wołoszyn) was investigated. Bat remains were segregated and identified to the species level. In calculations, only mandibles were included due to the small amount of skulls (to 1%) and their bad condition. The frequencies of species were calculated according to MNI [minimal numbers of individuals — the number of the most abundant mandible (left or right)]. A pair of difficult to identify species, *Myotis mystacinus* and *M. brandtii*, were treated as one species. Similarly, the recently separated species *Pipistrellus pipistrellus* and *P. pygmaeus* (Jones and Barrat, 1999) were combined into the category *P. pipistrellus* s.l.
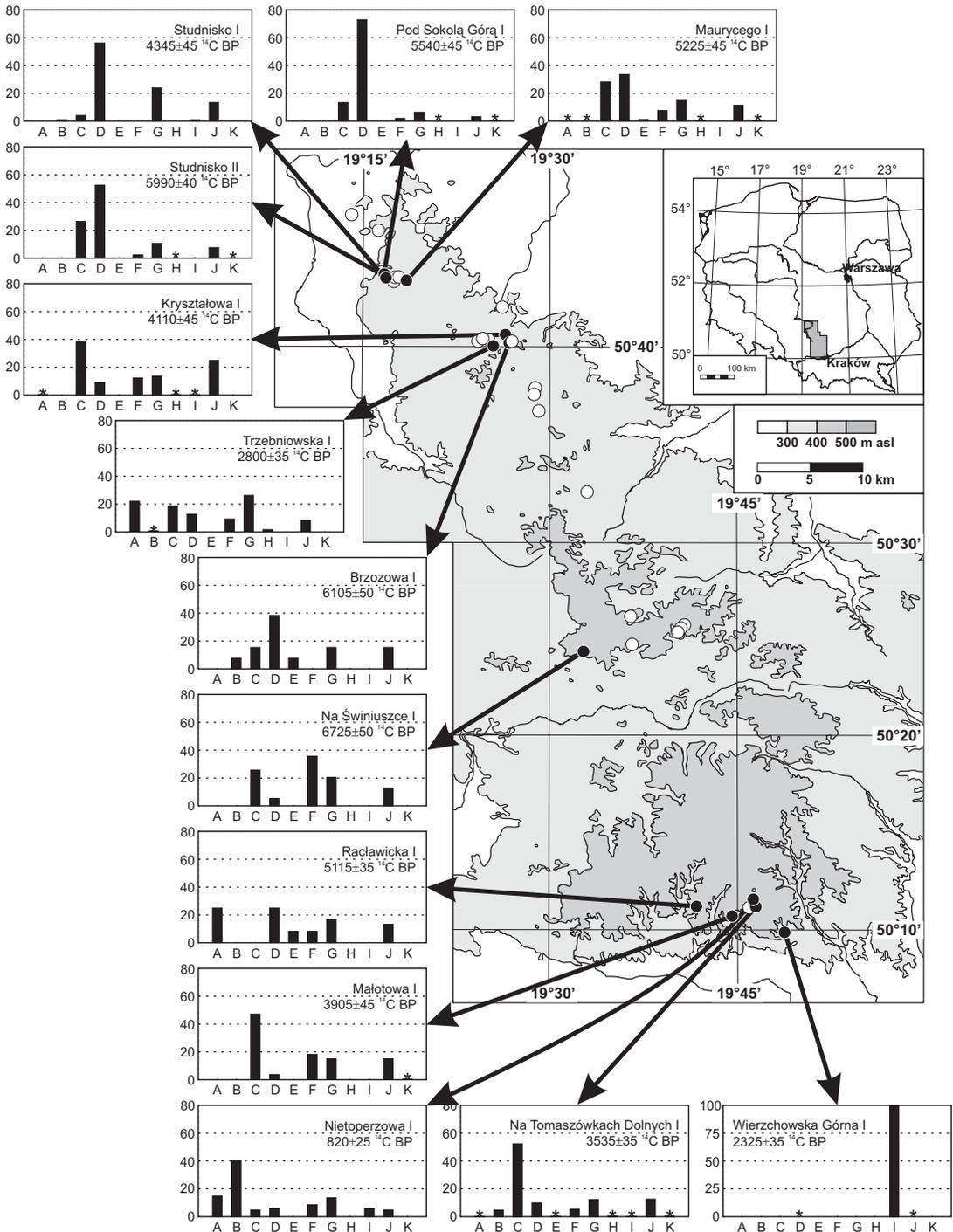
FIG. 1. The distribution of the studied caves in the Kraków-Częstochowa Upland (southern Poland) and frequency (%MNI) of bat species in the obtained thanatocoenoses. ○ – lack of Holocene or older material; ● — Holocene material; taxa: A — *Rhinolophus hipposideros*; B — *Myotis myotis*; C — *M. bechsteinii*; D — *M. nattereri*; E — *M. emarginatus*; F — *M. mystacinus/brandtii*; G — *M. daubentonii*; I — *Pipistrellus pipistrellus* s.l.; J — *Plecotus auritus*; K — *Barbastella barbastellus*; * — frequency of the species ≤ 1%

The naming of samples is as follows: e.g., Brzozowa I_A: Brzozowa — name of the cave, I — site of collection of material within the cave, $_A$ — subsequent collection of material within one site. Osteological material collected several times from the same site in the cave was pooled in calculations.

In order to assess the similarity in species frequency between samples collected within one cave, the R × C test with Williams' correction (G_{adj}) was used (Sokal and Rohlf, 1989). When differences between samples were statistically important, they were treated separately; if not, they were grouped together.

From thanatocoenoses chosen for radiocarbon dating, 1 to 3 grams of unidentified bone (finger bones) were picked. Collagen extraction and preparation of samples for dating was performed in the Radioisotope Department of the Physics Institute in the The Silesian University of Technology in Gliwice. The absolute age of the material was investigated with the accelerator technique ^{14}C AMS (Accelerator Mass Spectrometry) in Leibniz-Labor für Altersbestimmung in Kiel (Germany) according to standard procedure (Goslar and Czerniak, 2000). In this paper, dates are expressed as uncalibrated radiocarbon years before present (yr BP). The names of thanatocoenoses used in the analyses are derived from those that were radiocarbon dated. The paleogeographic divisions of the Holocene are according to Starkel (1999). The graphs illustrating frequency changes are prepared on the basis of the obtained thanatocoenoses.

For describing the relationship between frequency of species and age of thanatocoenoses, correspondence analysis was used. Pearson's r-correlation was used to quantify qualify the similarity of thanatocoenoses dated by the author with available literature data. The calculations were done in Statistica, version 5. In evaluating the influence of factors on bat populations, reconstructions of the environmental background for southeastern Polish uplands were used (Pazdur *et al*., 1988; Godłowski, 1995; Kruk *et al*., 1996; Starkel *et al*., 1996; Ralska-Jasiewiczowa *et al*., 1998, 1999, 2003; Ralska-Jasiewiczowa and Starkel, 1999; Dobrowolski *et al*., 2002).

RESULTS

Taphonomy and Chronology of Investigated Sediments

Fossil remains of bats were collected in 10 caves (33% of all caves), additionally, material from two thanatocoenoses was investigated. Fossils from 6, 1 and 5 caves came from the northern, central and southern part of the Upland, respectively (Fig. 1). Altogether, in 17 samples of osteological material, 8,275 individuals were identified to species level, MNI = 4,571 (Table 1). In all, 12 bat species were found: *Rhinolophus hipposideros* (Bechstein, 1800), *Myotis myotis* (Borkhausen, 1797), *M. bechsteinii* (Kuhl, 1817), *M. nattereri* (Kuhl, 1817), *M. emarginatus* (Geoffroy, 1806), *M. mystacinus* (Kuhl, 1817)/*M. brandtii* (Eversmann, 1845), *M. daubentonii* (Kuhl, 1817), *M. dasycneme* (Boie, 1825), *Plecotus auritus* (Linnaeus, 1758), *Barbastella barbastellus* (Schreber, 1774), and *Pipistrellus pipistrellus* s.l.

The 17 samples were assigned to 13 thanatocoenoses. In nine caves (Brzozowa I, Małotowa I, Maurycego I, Na Tomaszówkach Dolnych I, Nietoperzowa I, Pod Sokolą Górą I, Racławicka I, Trzebniowska I, Wierzchowska I), material came from one collection site, so every site was treated as a separate thanatocoenosis.

In Kryształowa, Na Świniuszce and Studnisko material was collected in two or more sites within an object. The following samples were combined: Kryształowa $I_{A,\,B,C}$ with $II_{A,\,B}$ into thanatocoenosis Kryształowa I (G_{adj} = 7.65, *d.f.* = 5, *P* > 0.05); Na Świniuszce I_A with II_A into thanatocoenosis Na Świniuszce I (G_{adj} = 4.48, *d.f.* = 4, *P* > 0.05); Studnisko II_A, III_A, IV_A into thanatocoenosis Studnisko II (II_A and III_A: G_{adj} = 2.95, *d.f.* = 4, *P* > 0.05; II_A and IV_A: G_{adj} = 1.78, *d.f* .= 4, *P* > 0.05; III_A and IV_A: G_{adj} = 2.44, *d.f.* = 4; *P* > 0.05). Samples Studnisko $I_{A,\,B}$ were treated as separate thanatocoenoses, Studnisko I ($I_{A,\,B}$ and II_A: G_{adj} = 15.996, *d.f.* = 4, *P* < 0.01; $I_{A,\,B}$ and III_A: G_{adj} = 12.14, *d.f.* = 4, *P* < 0.02; $I_{A,\,B}$ and IV_A: G_{adj} = 12.42, *d.f.* = 4, *P* < 0.02). For all thanatocoenoses, 13 dates between 6,725 ± 820 yr BP were obtained (Table 2, Fig. 1).

The thanatocoenoses cluster into two periods: 6,100 ± 5,100 yr BP from which

TABLE 1. Minimal number of individuals (MNI) and total number of specimens (Total) of bat species in the collected osteological samples. Acronyms: Rhip — *Rhinolophus hipposideros*; Mmyo — *Myotis myotis*; Mbec — *M. bechsteinii*; Mnat — *M. nattereri*; Mema — *M. emarginatus*; Mmsb — *M. mystacinus/brandtii*; Mdau — *M. daubentonii*; Ppip — *Pipistrellus pipistrellus* s.l.; Paur — *Plecotus auritus*; Bbar — *Barbastella barbastellus*

Thanatocoenose	Rhip	Mmyo	Mbec	Mnat	Mema	Mmsb	Mdau	Mdas	Ppip	Paur	Bbar	MNI	Total
Brzozowa I$_A$		1	2	5	1		2	1		2		13	19
Krzyształowa I$_{A, B, C}$			122	29		40	45	1		76		313	550
Krzyształowa II$_{A, B}$	2		15	4		4	4	1	2	13		45	63
Małotowa I$_A$			75	6		29	24			24	1	159	294
Maurycego I$_{A, B}$	2	2	255	303	11	70	140	6		104	7	900	1,680
Na Świniuszce I$_A$			21	3		19	13			5		61	103
Na Świniuszce II$_A$			13	4		28	14			12		71	125
Na Tomaszówkach Dolnych I$_{A, B, C}$	2	28	310	59	3	31	73	4	2	75	4	591	1,040
Nietoperzowa I$_A$	12	33	4	5		7	11		5	4		81	126
Pod Sokolą Górą I$_A$			109	591		17	53	1		33	6	810	1,466
Racławicka I$_A$	3				1	1	2			2		12	16
Studnisko I$_{A,B}$			4	54			23		1	13		96	175
Studnisko II$_A$		1	26	60		2	8			3		99	184
Studnisko III$_A$			130	217		8	58	1		43	2	459	874
Studnisko IV$_A$			41	115		8	14			12		190	344
Trzebniowska I$_{A, B, C, D}$	26	1	22	15		11	31	2		10		118	185
Wierzchowska I$_A$				1					547	5		553	1,031
Total	47	66	1,149	1,474	16	275	515	16	557	436	20	4,571	8,275

TABLE 2. Radiocarbon dates ^{14}C AMS (uncalibrated yr BP; $\bar{x} \pm$ calibration error) of obtained thanatocoenoses and characteristics of studied caves (Kraków-Częstochowa Upland, S-Poland). MNI — minimal number of individuals

Cave	Geographic coordinates	Altitude	Thanatocoenose	MNI	Age (yr BP)	Lab. no.
Brzozowa	19°26'48"E, 50°40'10"N	400	I$_A$	13	6,105 ± 50	GdA-164
Kryształowa	19°26'38"E, 50°40'45"N	325	I$_{A, B, C}$	313	4,110 ± 45	GdA-129
			II$_{A, B}$	45		
Małotowa	19°43'26"E, 50°08'18"N	384	I$_A$	159	3,905 ± 45	GdA-133
Maurycego	19°18'09"E, 50°43'37"N	340	I$_{A, B}$	900	5,225 ± 45	GdA-139
Na Świniuszce	19°32'38"E, 50°22'26"N	450	I$_A$	61	6,725 ± 50	GdA-143
			II$_A$	71		
Na Tomaszówkach						
Dolnych	19°46'57"E, 50°09'28"N	435	I$_{A, B, C}$	591	3,535 ± 35	GdA-156
Nietoperzowa	19°46'41"E, 50°09'18"N	447	I$_A$	81	820 ± 25	GdA-163
Pod Sokolą Górą	19°16'28"E, 50°43'44"N	330	I$_A$	810	5,540 ± 45	GdA-155
Racławicka	19°40'05"E, 50°09'11"N	446	I$_A$	12	5,115 ± 35	GdA-165
Studnisko	19°16'31"E, 50°43'41"N	346	I$_{A, B}$	96	4,345 ± 45	GdA-134
			II$_A$	99	5,990 ± 40	GdA-142
			III$_A$	459		
			IV$_A$	190		
Trzebniowska	19°25'32"E, 50°39'41"N	410	I$_{A, B, C, D}$	118	2,800 ± 35	GdA-144
Wierzchowska Górna	19°48'39"E, 50°08'26"N	388 & 399	I$_A$	553	2,325 ± 35	GdA-149

five dates were obtained (Atlantic period), 4,500 ± 3,500 yr BP from which four dates were obtained (Subboreal period), and a further four differing in ages between 470 and 1,500 years ^{14}C. Most material comes from the Atlantic and Subboreal periods. Studnisko I and Nietoperzowa I contain remains of juveniles (mandibles with milk teeth) indicating that sediments accumulated also during reproduction. In case of Studnisko I, there are only four mandibles not identified to species level, while in Nietoperzowa I there are up to 40%, which suggests regular reproduction in the latter. In Wierzchowska I, only one species was identified, and the sample does not contain any juvenile remains, which indicates that it accumulated during hibernation periods.
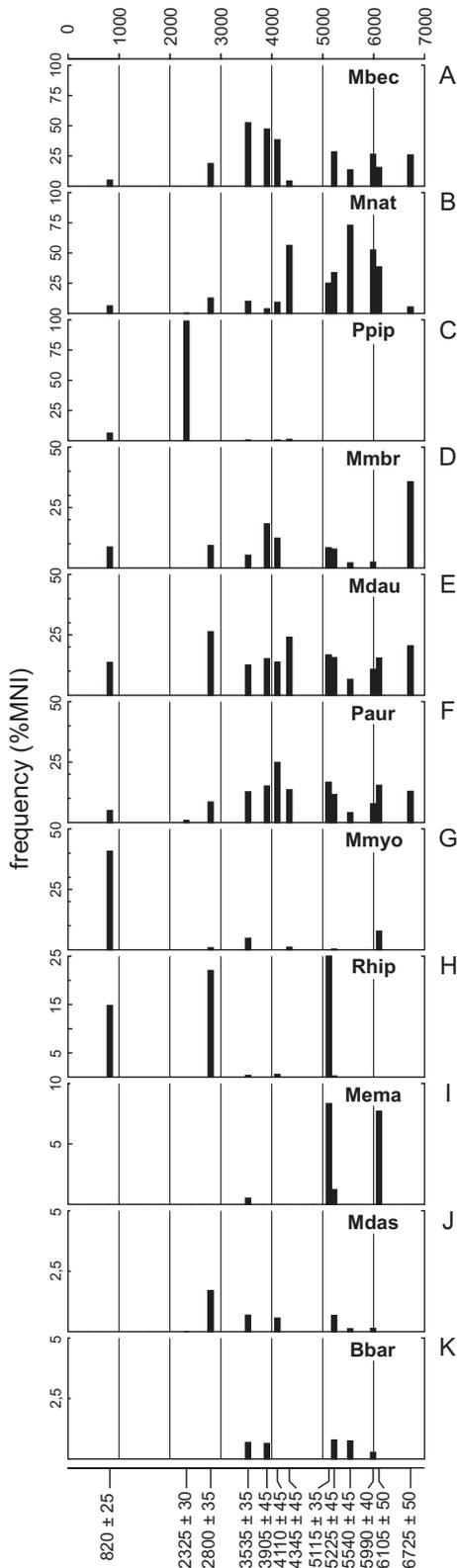
The Frequency of Bat Species in the Dated Thanatocoenoseses

Myotis bechsteinii. Present in 11 thanatocoenoses (Fig. 2A). During the period 6,725–5,200 yr BP, the frequency of this species varied from 14–28% without any trends. Between 4,300 and 3,500 yr BP, it increased up to 52%, while in earlier thanatocoenoses it decreased below 10%. Małotowa I (3,905 ± 35 yr BP) contains about 40% of mandibles with evident teratological changes on bones and teeth caused by an undiscribed illness (Fig. 3). In Na Tomaszówkach Dolnych I (3,535 ± 35 yr BP) this kind of damage was found in 5% of individuals.

Myotis nattereri. Present in 13 thanatocoenoses (Fig. 2B). From 6,700 to 5,500 yr BP, the frequency of this species increased from 5% to 70%. However, in assemblages dated to 5,100 yr BP, it decreased to 30%. With the exception of Studnisko I, in earlier thanatocoenoses, the share of *M. nattereri* did not exeed 13%.

Pipistrellus pipistrellus s.l. Present in five thanatocoenoses (Fig. 2C). Noted in assemblages from 4,300–3,500 yr BP with a frequency up to 1%. In the exceptional thanatocoenosis, Wierzchowska Górna I

FIG. 2. Frequency of bat species (%MNI) in thanatocoenoses dated by AMS ^{14}C yr BP from caves of the Kraków-Częstochowa Upland (S-Poland; see Table 1 for abbreviations)

$(2{,}325 \pm 35$ yr BP), its frequency reaches up to 98%.

Myotis mystacinus and *M. brandtii*. Present in 10 thanatocoenoses (Fig. 2D). Between 6,000–3,900 yr BP, their frequency slowly increased from 2% to 18%. In earlier assemblages it did not exceed 10%. The sample from Na Świniuszce I ($6{,}725 \pm 50$ yr BP) differs from other early thanatocoenoses with a high frequency of these species (35%).

Myotis daubentonii. Present in 12 thanatocoenoses (Fig. 2E). From 6,725 to 5,900 yr BP, its frequency decreased from 20 to 6.5%, and later in a period between 5,900–5,100 yr BP, its frequency increased up to 16% and stayed at this level in earlier assemblages. An exceptional increase in its frequency took place about 2,800 yr BP.

Plecotus auritus. Present in 13 thanatocoenoses (Fig. 2F). From 6,700 to 5,900 yr BP, its frequency decreased from 13–15% to 6,5%, and then increased to a maximum value of 25% at 4,100 yr BP. In thanatocoenoses from 3,900 to 820 yr BP, its frequency decreased to 5%.

Myotis myotis. Present in six thanatocoenoses (Fig. 2G). In sediments dated to 5,200–2,800 yr BP, it is not numerous and exceeds 5% in only one locality; however, the low sample size makes this frequency questionable. The highest frequency of *M. myotis* was noted in Nietoperzowa I, dated to historical times. The presence of young individuals (> 40%) indicates the existence of a large nursery colony of the species in this cave.

Rhinolophus hipposideros. Present in six thanatocoenoses (Fig. 2H). The first record comes from $5{,}225 \pm 45$ yr BP and is the northernmost and the oldest Holocene locality of this species with unquestionable
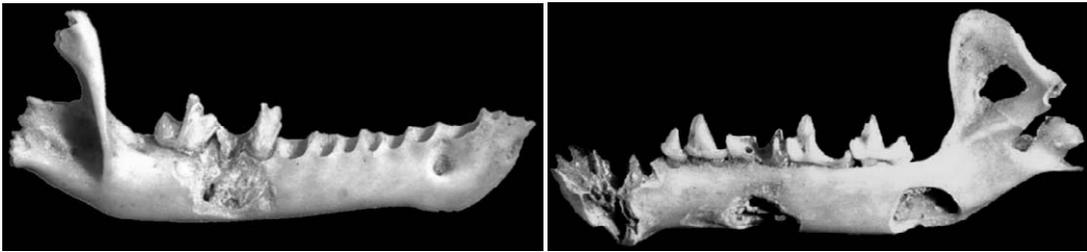
FIG. 3. Mandibles of *M. bechsteinii* with teratological changes of bones and teeth (Małotowa I; 3,905 ± 45 yr BP)

dating in Poland. With the exception of thanatocoenosis Racławicka I, the frequency of this species until about 3,000 yr BP did not exceed 0.56%. From 2,800 to 820 yr BP, it represents 14–20% of remains in assemblages.

Myotis emarginatus. Present in four thanatocoenoses (Fig. 2I). In thanatocoenoses between 6,100 and 5,100 yr BP, it represents up to 8% of individuals. However, the small number of specimens in two of four thanatocoenoses may overestimate its actual frequency, which could be up to 1% as in Maurycy I. In earlier assemblages it is present in only one thanatocoenosis with a frequency of 0.5%.

Myotis dasycneme. Present in six thanatocoenoses (Fig. 2J). Found in assemblages from 6,000 to 2,800 yr BP. The frequency of this species oscillates at a level of 0.5% and is higher only in Trzebniowska I (2,800 ± 35 yr BP; 1.6%).

Barbastella barbastellus. Present in five thanatocoenoses (Fig. 2K). Occurs between 6,000 and 5,100 yr BP, and between 3,900 and 3,500 yr BP. In both periods its frequency did not exceed 0.8%.

Correspondence Analysis

In the correspondence analysis, 11 dated thanatocoenoses from the Atlantic period were included: Na Świniuszce I, Brzozowa I, Studnisko II, Pod Sokolą Górą I, Maurycego I, Racławicka I, and from the Subboreal period: Studnisko I, Kryształowa I, Małotowa I, Na Tomaszówkach Dolnych I, Trzebniowska I. Two thanatocoenoses from the Subatlantic period were omitted: Wierzchowska Górna I with only one species and Nietoperzowa I with a large amount of young individuals. Total variance of the correspondence analysis was 0.72, its two dimensions describe 72.8% ($\chi^2 = 796.7$,

TABLE 3. Share of bat taxa on axes (F_1 and F_2) of the correspondence analysis for thanatocoenoses from the Atlantic and Subatlantic periods

Taxon	F_1 (%)	Taxon	F_2 (%)	Taxon	$F_1 \times F_2$ (%)
M. nattereri	87.54	*R. hipposideros*	95.10	*M. nattereri*	95.89
M. mystacinus/brandtii	62.99	*B. barbastellus*	28.46	*R. hipposideros*	95.58
M. bechsteinii	53.47	*M. emarginatus*	27.17	*M. bechsteinii*	78.64
P. auritus	19.11	*M. daubentonii*	26.77	*M. mystacinus/brandtii*	64.05
M. emarginatus	9.97	*M. bechsteinii*	25.16	*M. emarginatus*	37.14
M. dasycneme	4.75	*M. dasycneme*	10.16	*M. daubentonii*	29.93
M. daubentonii	3.15	*M. nattereri*	8.35	*B. barbastellus*	28.46
P. pipistrellus s.l.	1.83	*P. pipistrellus* s.l.	5.52	*P. auritus*	20.51
M. myotis	1.74	*M. myotis*	1.87	*M. dasycneme*	14.91
R. hipposideros	0.48	*P. auritus*	1.39	*P. pipistrellus* s.l.	7.35
B. barbastellus	0.00	*M. mystacinus/brandtii*	1.06	*M. myotis*	3.61

d.f. = 100, *P* < 0.001). Axes F_1 and F_2 contain 39.3% and 33.5% of main variances, respectively (Table 3).

F_1 is characterized by a contrast between *M. nattereri* and *M. mystacinus/brandtii, M. bechsteinii* and *P. auritus* and it shows a gradient between the Atlantic and Subboreal periods. Species which influence this axis are the most numerous ones and are always present in the sediments. F_2 contrasts *R. hipposideros* and *M. emarginatus* from *B. barbastellus*, *M daubentonii* and *M. bechsteinii* and indicates a gradient between pontic-mediterranean species and eurytopic species. Among the species which have the largest influence on this axis, *M. daubentonii* and *M. bechsteinii* are the most frequent and constantly present, *M. emarginatus* and *R. hipposideros* are the most frequent in only a few periods while *B. barbastellus* was never numerous.

Diagram $F_1 \times F_2$ represents several separate groups (Fig. 4.):

(1) *R. hipposideros* and *M. emarginatus* are species that have a higher frequency during the Atlantic period;

(2) *M daubentonii, P. auritus, M. dasycneme* are species that are characterized by having their highest frequency in the middle and end of the Atlantic period and the oldest part of the Subboreal period;

(3) thanatocoenoses with high frequency of *M. nattereri* from the Atlantic (Brzozowa I, Studnisko II, Pod Sokolą Górą I) and Subboreal periods (Studnisko I). The age of Studnisko I is questionable and should not be taken into account in reconstructions of changes in fauna;

(4) thanatocoenoses with a high frequency of *M. bechsteinii* from the Subboreal period (Na Tomaszówkach Dolnych I, Kryształowa I, Małotowa I). Na Świniuszce I is similiar to these, differing by a high frequency of *M. mystacinus/brandtii*.

The thanatocoenosis Maurycy I, from the end of the Atlantic period, is characterized by intermediate values between the *M. nattereri* and *M. bechsteinii* groups.

Others species do not form groups (*B. barbastellus*) or have a small share in $F_1 \times F_2$ (*M. myotis, P. pipistrellus* s.l.).
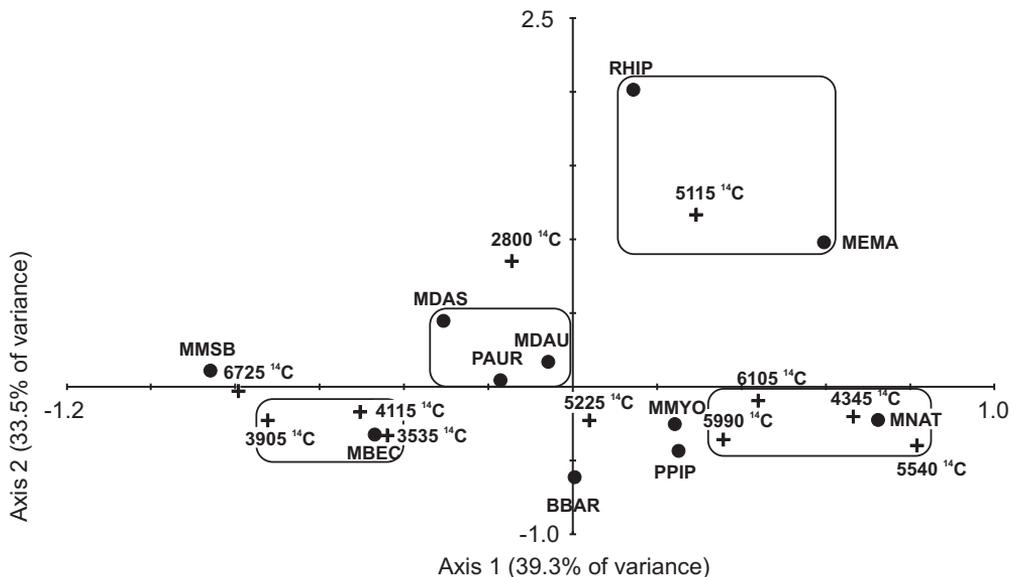

FIG. 4. Projection of thanatocoenoses (dots with dates) and species (black dots, see Table 1 for abbreviations) on graph $F_1 \times F_2$ of correspondence analysis

DISCUSSION

The Holocene thanatocoenoses in Polish caves do appear in surface horizon of cave sediments witch as a rule does not exceed a few centimeters (Wołoszyn, 1989). The use of AMS method allows to determine a radiocarbon age despite little amount of available material. This assay evaluates carbon, a component of collagen, which is accumulated until an animal's death. This principle reduces the possibility of the sample contamination and improves the accuracy of age dating.

The thanatocoenoses that originated in parts of caves far from their entrances are formed by individuals that died during winter (hibernation), or during summer (in nursery colonies; Wołoszyn, 1970). Bone remains deposited during the reproductive period contain remains of young individuals with underdeveloped dentition so the identification of these thanatocoenoses is not difficult. The single juvenile from Studnisko I (4,345 ± 45 yr BP) and more frequent ones from Nietoperzowa I (820 ± 25 yr BP) indicate these caves were used as reproduction sites during the Holocene. Until now there was no evidence for the existence of nursery colonies in caves in Poland except for few (see below). This fact was explained by faster decomposition of less-calcified bones of young bats (Wołoszyn, 1989). The species composition of nursery colonies in caves in this area is also important. In Central European assemblages, cave reproduction was recorded for *M. myotis*, *M. emarginatus*, and *R. hipposideros*. Due to the fact that these species occurred to the north of the Carpathians in different stages of the Holocene and that their reproduction depends on thermal balance (Horáček, 1984; Zahn, 1999), finding thanatocoenoses can be difficult. The possibility of more frequent cave reproduction is confirmed by the exploitation of cave sediments containing bat guano at the end of the XIX century in dozens of objects in the southern Upland (where guano mining was conducted on an industrial scale — Kowalski, 1951, 1954). The total exploitation of these sediments makes an assessment of absolute age impossible, and also impedes the identification of the species which occurred in the sediments in the first place.

All other studied bats remains were accumulated during hibernation. No differences between samples from one cave (Kryształowa, Na Świniuszce) indicates the homogeneity of sediments from this locality. Sediments from Studnisko Cave are exceptional, where the material from Komora Wejściowa (Studnisko Ia) differs from the other three samples both in species frequency and radiocarbon age. This sample comes from the entrance area where mining activity was conducted, so the possibility of mixing these sediments with earlier ones is plausible.

The dated assemblages are spread throughout 6,000 yr BP — from the middle of the Atlantic to the earlier Subatlantic period. The absence of sediments older than 6,725 yr BP is difficult to interpret and requires further investigations. Studies in these reopened caves may shed light on material from the older Holocene periods. During the Holocene, changes in bat fauna were due to climatic factors (Horáček, 1984; Zahn, 1999), changes in vegetation (Kordos, 1982; Obuch, 1995) and human activity (Horáček, 1984; Wołoszyn, 1989). Some of these parameters occur at a large scale, others — e.g. human interference — at a local scale. As a reference, a reconstruction of the environmental background for the Uplands of southeastern Poland was implemented (Fig. 5).

Thanatocoenoses with the most abundant osteological material indicate the existence of large conglomerations of bats.

These come from two periods divided by an expanse without sediments:

The first includes the end of the Mesolithic and first half of the Neolithic (6,105–5,115 yr BP — the Atlantic optimum). The temperature was higher than today (Fig. 5C). During the Mesolithic, anthropogenic pressure on the environment was marginal and limited to hunting and gathering (Godłowski, 1995), while during the Neolithic colonization attained the so called 'digging stick type', which never encompassed great areas (Fig. 5B). Settlements were set up in river valleys, rarely on their terraces, and large scale deforestation did not occur (Kruk *et al*., 1996) and ecosystems remained in a natural state (Fig. 5F).

An interval from which no information is available lasted about 770 yr BP (5,115–
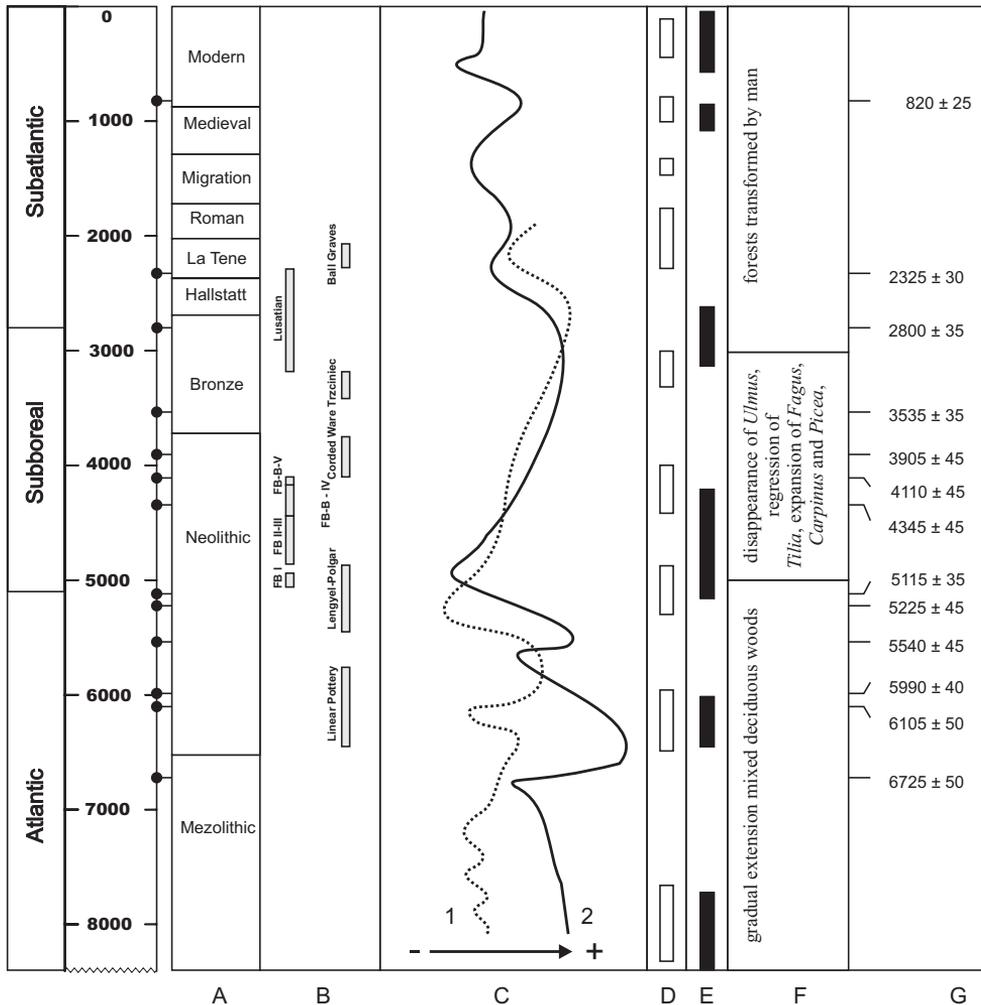

FIG. 5. Human activity and changes in environmental parameters during the middle and early Holocene for southern and central Poland. Paleography of Holocene after Starkel (1999); periods (A) and cultures (B) after Godłowski (1995), Kruk *et al*. (1996), Ralska-Jasiewiczowa *et al*. (1998); temperature (C): 1 — after Pazdur *et al*. (1988), 2 — after Dobrowolski *et al*. (2002); phase with high frequency of floods (D) phases with erosion processes (E) after Ralska-Jasiewiczowa and Starkel (1999); forest communities (F) after Ralska-Jasiewiczowa (1999) and Ralska-Jasiewiczowa *et al*. (2003); radiocarbon dates of the studied thanatocoenoses (yr BP) (G)

4,345 yr BP). The beginning coincides with a strong and sudden decrease in temperature on the change from the Atlantic to the Subboreal period (Fig. 5C). After the cold episode, together with a rise in temperature, slash and burn cultivation developed (Fig. 5B). The population density increased and settlements were gradually set up in terraces and higher ground (Kruk *et al*., 1996). Forest in the vicinity of settlements was transformed for agricultural use, and grazing by large herds further established these changes. This is reflected by the appearance of erosion processes that were caused only by climatic factors during earlier periods of the Holocene (Fig. 5E). These large changes concern the Upper Vistula valley and loess uplands (Kruk *et al*., 1996), while the central and northern part of the Kraków-Częstochowa Upland remained unchanged (Godłowski, 1995). At the end of this phase agriculture declined, while the role of animal breeding increased considerably.

The second period with abundant material in thanatocoenoses corresponds to the end of the Neolithic (so called 'shepherd's phase') and the beginning of the Bronze Age (4,345–3,535 yr BP — Subboreal optimum) (Fig.5B). The temperature was higher than today, and great changes occurred in the forest environment (Fig. 5). During the shepherd's phase, human lifestyle changed from settled to seminomadic or nomadic; herding was still practiced. At the beginning of the Bronze Age the population was much lower than in the Neolithic, and permanent settlement is missing (Kruk *et al*., 1996).

The periods corresponding to the groups of sediments with abundant osteological material differ in the degree of human activity. In the first, human activity is minimal while in the second drastic anthropogenic changes occurred. However, large conglomerations of bats occurred in both periods — human activity did not limit the number of bats. The common feature of

these two periods is a mean annual temperature higher than the contemporary value (Pazdur *et al*., 1988; Dobrowolski *et al*., 2002).

The large hibernacula indicate a higher number of bats than today. Conglomerations were made mostly by eurytopic species (*M. bechsteinii*, *M. nattereri*, *M. daubentonii*, *P. auritus*), with a small share of pontic-mediterranean species (*R. hipposideros*, *M. emarginatus*). Natural localities with over a few hundred hibernating bats are scarce in contemporary Poland (Wołoszyn, 1996), while in regions with a milder climate (Eastern and Western Carpathians) up to 55,000 bats hibernate in some caves (Nagy and Szanto, 2003). This may indicate that population size depends in general on mean annual temperature in particular periods; in warmer times insect biomass may be higher than in colder periods, which in turn could sustain greater numbers of bats. A shortening of the hibernation period may also have some influence, but reconstructions of temperature changes according to oxygen isotopes points only to mean annual temperature and does not inform about conditions during particular months (e.g., Alfano *et al*., 2003).

In order to confirm the alternative relationship: long deposition time — large accumulation of bat bones, the dating of several layers from one thanatocoenosis is required. However, the small thickness of fossil deposits excludes such a possibility and therefore does not allow unequivocal interpretation.

Bats use artificial sites for hibernation in northern Poland because of the lack of natural shelters, and their numbers in similar winter conglomerations often surpass the number of bats in caves. The largest hibernaculum in Central Europe is the Międzyrzecki Fortified Region, where up to 20,000 bats hibernate (Urbańczyk, 1989). For some species such as *M. myotis* and

M. daubentonii, it is a hibernaculum for bats inhabiting an area withina 200 km radius (Urbańczyk, 1991). This indicates a correlation between size of winter conglomerations and availability of hibernacula.

Intervals in sediment accumulation from the turn of the Atlantic and Subboreal periods and from the early Subatlantic period (2,800–2,500 yr BP) correlates with climate coolings (Fig. 5C). These coolings could slow down the accumulation of bat skeletal remains by lowering the number of bats hibernating in caves, which is hard to observe in paleontological data due to the smaller thickness of sediments. More importantly, a lower insect biomass probably decreased the number of bats (opposite to the situation during warmer periods). A dependence of reproduction in some species on temperatures and thermal balance has also been recognized (Horáček, 1984; Zahn, 1999). During cold periods, changes in thermal conditions in caves also occurred: the temperature in static microclimate zones equals the mean annual temperature on the ground (Kowalski, 1954). Lower temperatures in hibernacula and/or a lengthening of the hibernation period could force migration of some species to warmer or more stable hibernacula. Sediments from these time ranges are needed in order to solve this problem.

Thanatocoenoses between 3,535–2,800 yr BP were not registered, although higher temperatures were prevalent and anthropogenic pressure was minimal (Fig. 5C). At about 3,200 yr BP the climate became wetter and the frequency of floods caused by torrential rainfalls increased (Ralska-Jasiewiczowa and Starkel, 1999; Fig. 5DE). This phenomenon explains the demise of the Lusatian culture (Niewiarowski, 1978). A lack of sediments could be the effect of fossil erosion due to increased water input, but as in the case of older thanatocoenoses, further research is needed.

Records of changes in bat fauna during the Subatlantic period are incomplete. Two thanatocoenoses, one which accumulated during the reproductive period (Nietoperzowa I), and another with an unusual species composition (Wierzchowska Górna I) cannot form the bases of reconstructions. The paucity of sediments from this period could be due tothe effect of intensification of environmental transformation and direct devastation of surface sediments due to uncontrolled human visitation (tourism) and contemporary cave exploration.

Reconstruction of Frequency Changes of Bat Species

The most complete scenario of changes in bat fauna was obtained for a period beginning during the middle of the Atlantic and continuing to the end of the Subboreal. Correspondence analysis revealed groups which correspond to a large extent with the ecological demands (species) or age ranges (thanatocoenoses; Fig. 4). Among the 11 analyzed thanatocoenoses, only Studnisko I has values different from the general trends reflected in the other 10 thanatocoenoses. These sediments were probably mixed during calcite exploitationor cave exploration and surely did not come from a single-aged layer.

The first group obtained by correspondence analysis is composed of *R. hipposideros* and *M. emarginatus*. The contemporary distribution of these two species in Poland is restricted to mountains and uplands in the south of the country (Wołoszyn, 2001a, 2001b). Both species, as ponticmediterranean elements, are assumed to colonize Central Europe in the early Holocene. (Horáček, 1984). In cave assemblages from the Kraków-Częstochowa Upland, the presence of *R. hipposideros* was noted from the Atlantic or Subboreal periods (Dagnan-Ginter *et al.*, 1992) or during

historic times (Wołoszyn, 1989), but in the Pieniny Mountains this species was found in thanatocoenoses dated to the early Holocene (Alexandrowicz *et al.*, 1985; Wołoszyn, 1995). Dating results indicate that, at the end of the Atlantic period and during the Subboreal period, this species was a permanent although rare element of the fauna. It shows that migration to the Upland area took place at least during the later Atlantic, and that its population remained stable in spite of further climate change and environmental transformations. Most probably, this species hibernated more frequently in southern but not northern parts of the Upland, which is confirmed by its frequency in assemblages. Due to this species' preference for an environmental mosaic (Schober and Grimmberger, 1997) it is possible that changes in forest ecosystems in the Atlantic period that led to open canopy complexes with a dominance of deciduous species in the Subboreal period (Ralska-Jasiewiczowa *et al.*, 2003) resulted in its dispersal into formerly unoccupied areas. A small number of samples and large variance in their age precludes interpretation and requires further studies.

The presence of *M. emarginatus* in sediments is dated to the Subatlantic period for the Western Carpathians and Sudetes Mts. (Obuch, 1994, 1995; Horáček, 1984), and to the Subboreal period for areas to the north of the Carpathians (Ochman and Wołoszyn, 2000; Ochman, 2003). In the studied material, this species was most frequently found in thanatocoenoses from the Atlantic period, where it reached up to 8%. In the early Holocene its appearance had a short-term character during the Subboreal warming (Na Tomaszówkach Dolnych I). Except for the thanatocoenoses from caves of the Kraków-Częstochowa Upland, it was found only in the Holy Cross Mts. with a relatively large frequency of 8% (Ochman, 2003), although it is not an element of the contemporary

fauna. The absence of this species in assemblages from the earlier Holocene (Subboreal and Subatlantic) indicates its withdrawal to the south with climate cooling at the end of the Atlantic period. Zahn and Henatsch (1998) considered minimal temperatures during the reproductive period as a factor limiting the distribution of *M. emarginatus,* which explains the absence of this species in cool periods of the Holocene.

Myotis bechsteinii and *M. nattereri* are species with a similar hunting strategy; they belong to the group known as 'gleaning bats' (Fenton and Bogdanowicz, 2002). Insects picked from leaf surfaces predominate in the diet of *M. bechsteinii*, while insects captured next to trunks and leaves are the mainstay of *M. nattereri* (Beck, 1995). Apart from these similarities, the two species dominated different periods of the Holocene and are strongly differentiated by correspondence analysis.

Myotis bechsteinii rarely hibernates in caves in the present day, it amounts up to 0.9% of the modern fauna (Postawa and Zygmunt, 2001). The high frequency of this species in Holocene assemblages was interpreted as an indicator of the Holocene climatic optimum (Atlantic period) (Wołoszyn, 1989; Ochman and Wołoszyn, 2000) or as a 'forest optimum' (the transition from the Atlantic to Subatlantic periods; e.g., Obuch, 1994, 1995; Horáček, 1995; Piksa and Wołoszyn, 2001). Thanatocoenoses from Alpine caves (up to 900 m a.s.l.) dated by ^{14}C AMS show the dominance of this species in sediments from the beginning of the Subboreal period (Baagøe, 2001). In the studied thanatocoenoses, the maximum frequency of *M. bechsteinii* was reached also during the Subboreal period between 4,000 and 3,500 yr BP. This coincides with changes in the Neolithic culture and in forest ecosystems. About 4,000 yr BP a great decrease in human population and the regression of slash and burn cultivation

occurred, and instead the sheperds' culture emerged which had a minimal influence in forested areas (Kruk *et al*., 1996). In the uplands belt new tree species appeared: *Carpinus betulus* (about 4,000 yr BP) and *Fagus silvatica* (3,500 yr BP), and the widespread *Corylus avellana* slowly retreated (Ralska-Jasiewiczowa *et al*., 2003). A correlation between human influence and the appearance of the mentioned tree species has also been shown (Ralska-Jasiewiczowa, 1999; Ralska-Jasiewiczowa *et al*., 2003). A larger relative proportion of *M. bechsteinii* coincides with an increase in significance of *F. silvatica* and *C. betulus* in forest ecosystems. The contemporary distribution of this bat species in general coincides with the range of deciduous forests with a substantial share of the two mentioned tree species (Baagøe, 2001). A high frequency, 15–20%, in the oldest assemblages (Atlantic period) indicates an early appearance of *M. bechsteinii*. Baagøe (2001) pointed to the presence of this species from 9,000 yr BP, which emphasizes its pioneering character (Horáček, 1995). The cause of the drastic decline of this species may be reflected in increased human pressure during the Subboreal and Subatlantic periods (e.g., Wołoszyn, 1989). In the dated thanatocoenoses, the decline of *M. bechsteinii* occurred between 3,500–2,800 yr BP. During this period, human influence was much lower than in the Neolithic (Kruk *et al*., 1996), when this species dominated. In slightly older assemblages pathological changes on bones and mandibles were recorded: in Małotowa I about 40% of individuals were pathological, while in Na Tomaszówkach Dolnych I about 5% were pathological. Pathological changes to teeth and neighbouring areas of bone, with signs of paradontosis, can be seen in 2% of bats (Vierhaus, 1981). The high share of pathological changes indicates an epidemic and could have resulted in a drastic decline of the population. The cause

of these changes is unknown, although it could be indirectly connected with changes in climatic parameters. The decrease in the proportion of *M. bechsteinii* in assemblages from the end of the Subboreal period in Poland is not directly caused by human activity, however, the pathologies require further investigations.

The high frequency of *M. nattereri* — up to 70% — corresponds to the Subboreal period (Ochman and Wołoszyn, 2000). This age reflects a tolerance to low temperatures during hibernation in this species (Harmata, 1969; Gaisler, 1970), and low temperatures during the Subboreal period. In Tatra caves with colder temperatures than in the studied localities, the share of *M. nattereri* in thanatocoenoses does not exceed 3% (Obuch, 1995; Piksa and Wołoszyn, 2001). Similar values were found in thanatocoenoses in Sudetes caves (Bosák and Horáček, 1976; Horáček, 1995). Therefore, the higher frequency does not have to be correlated with lower temperatures in hibernation sites. Thanatocoenoses with a similar frequency of this species are unknown except for the Kraków-Częstochowa Upland, which indicates that ecosystems preferred by this species were present in the studied region. The highest frequency of *M. nattereri* in thanatocoenoses falls between 6,000–5,500 yr BP, a time of climatic optimum in the Holocene (Fig. 5C). A dramatic decline in this species correlates with the cooling and and moistening of the climate by the end of the Atlantic period at 5,500–5,000 yr BP. During this time, the frequency of *M. bechsteinii* did not show fluctuations caused by thermal conditions. Because *M. nattereri* is much more widely distributed than *M. bechsteinii* (Schober and Grimmberger, 1997), it seems that changes in thermal balance were not associated. With the exception of Studnisko I with uncertain dating, greater fluctuations in frequency did not occur in earlier sediments, apart from

the cool/warm climate episodes. A probable reason may involve changes in insect fauna comprising the diet of this species. Climate alterations at the turn of the Atlantic and Subboreal periods caused transformations in the forest environment — a decline of the proportion of *Fraxinus* sp. and *Tilia* sp. and almost complete elimination of *Ulmus* sp. (e.g., Ralska-Jasiewiczowa, 1999). This entailed great changes in insect fauna associated with trees and may have resulted in a decline of *M. nattereri*.

Another group isolated by correspondence analysis is comprised of *M. daubentonii* and *M. dasycneme* — two species that are closely connected with water — and *P. auritus*, from the 'gleaning bats' group. *Myotis daubentonii* and *P. auritus* are numerous in sediments (up to 20%), while *M. dasycneme* rarely exceeds 1%. Such a high frequency of *M. daubentonii* is characteristic for the Upland, in others regions of Poland and the Western Carpathians it does not exceed 3% (Piksa and Wołoszyn, 2001; Bosák and Horáček, 1982; Wołoszyn, 1988). The food of *M. daubentonii* is insects captured in the littoral zone from and over the surface of the water (e.g., Bogdanowicz, 1994); while *M. dasycneme* prefers open areas of reservoirs (Swift and Racey, 1983). Obuch (1994, 1995) ascribed a higher frequency of *M. dasycneme* to assemblages from cooler caves and dated them to the Subboreal period.

A higher frequency of the mentioned species coincides with cool and humid periods 5,500–4,200 yr BP and 3,000–2,700 yr BP, while a lower frequency coincides with warmer ones: 6,000–5,500 yr BP. An excess of evaporation over precipitation in warmer periods caused lake levels to drop, which was reflected in a decrease of the rate of peat bog growth (Ralska-Jasiewiczowa and Starkel, 1988, 1999). Through modification of the food base, the lower water level could indirectly influence the number of

M. daubentonii and *M. dasycneme*. The low frequency of the second species might be the result of a poorly developed river system in the Kraków-Częstochowa Upland. Because of *M. dasycneme's* regular seasonal migrations over 300 km (Horáček and Hanák, 1989), remains found in sediments can come from populations with feeding grounds at a considerable distance from the area.

Plecotus auritus is not closely associated with water and its high frequency in cave assemblages is often interpreted as an indication of cool periods (Wołoszyn, 1989; Ochman and Wołoszyn, 2000). In thanatocoenoses from caves of the Polish Tatra, despite their cooler microclimate, this species frequency does not exceed 11% with an average of 2.5% (Piksa and Wołoszyn, 2001). This can be related to the diverse trophic conditions in forest ecosystems. *Plecotus auritus* tolerates great temperature fluctuations while hibernating and often chooses places near entrances (e.g., Harmata 1969; Gaisler, 1970). In warmer periods it uses less isolated shelters and because of this it is less numerous in sediments from inside a cave. Hence the similarity in frequency of this species to species related to water environments.

A similar frequency distribution is shared by a pair of species that are indistinguishable in sediments: *Myotis mystacinus/ M. brandtii*. This species pair is not included in the previous group because of discrepancies in frequency during the Atlantic period. The high frequency of *M. mystacinus/M. brandtii*, up to 95% in some caves, is interpreted as an indication of the early phase of colonization of a particular area by bats and is ascribed to assemblages dated to the early Holocene (Obuch, 1995; Piksa and Wołoszyn, 2001). According to this assumption, thanatocoenoses from caves in the Sudetes (Bosák and Horáček, 1982) and in the Western Carpathians (Obuch, 1994,

1995) are dated to the Boreal period. The poor condition of the remains does not allow for correct identification of *M. mystacinus* and *M. brandtii,* which in turn precludes the monitoring of frequency changes for each species separately. It is possible that in different Holocene periods they dominated interchangeably as suggested by Piksa and Wołoszyn (2001)**.** According to thanatocoenoses from Tatra caves, assemblages dated to the Boreal period containing *M. brandtii* showed that it dominated in Alpine and forest zones, while in subsequent periods it moved to lower locations and *M. mystacinus* took its place. In the studied thanatocoenoses, the frequency of *M. mystacinus*/*M. brandtii* increased at about 5,500 yr BP which may be related to a slight cooling and moistening of climate which took place at the end of the Atlantic and during the Subboreal periods. This pattern is analogous to those of *M. daubentonii* and *P. auritus*. A second maximum frequency for *M. brandtii* was at 4,000 yr BP. This coincides with the reconstruction of forest complexes during high temperatures and could be related with food availability as in the case of *M. bechsteinii.* High alititudes above sea level in most of the described localities from the Tatra (Piksa and Wołoszyn, 2001) and Sudetes Mountains (Bosák and Horáček, 1982), and in effect, lower temperatures in caves, suggest that sediments from these caves might come from earlier Holocene periods. Such an assumption is supported by the share of *M. mystacinus*/*M. brandtii,* up to 35%, in Na Świniuszce I ($6,725 \pm 50$ yr BP). This high frequency coincides with a short-term temperature decrease in the Atlantic period (Dobrowolski *et al.*, 2002), but its absence in older assemblages makes it difficult to explain these changes.

Three others species, *M. myotis*, *B. barbastellus* and *P. pipistrellus* s.l*.,* are poorly represented in assemblages and were excluded from groups in the correspondence analysis.

Myotis myotis was rare in all Holocene thanatocoenoses from Poland studied up to now. Its presence in cave assemblages from the Kraków-Częstochowa Upland was dated to the Subboreal (Ochman and Wołoszyn, 2000) or Subatlantic period (Wołoszyn, 1976*a*). Thanatocoenoses dated in this study indicate that *M. myotis* was present in the Upland at least during the middle of the Atlantic period. At first probably rare, it was more numerous during the Subboreal period. It is thought that *M. myotis* could appear to the north of the Carpathians by migrations from southern Europe via the northern edge of the Alps and foothills of the Sudetes (Ruedi and Castella, 2003), by the Morawska Gate (Wołoszyn, 1989), or by depressions in Beskid Niski (Dukielska Pass). The first hypothesis was based on a greater similarity in mitochondrial DNA between populations from western Poland and southern Spain than between southern Italy; while the second was based on results of bandings of females from nursery colonies from the Carpathian foothills that migrate to hibernacula in Slovakia (Krzanowski, 1960). It is possible that both routes were used independently by different populations of this species. The lack of warm caves hinders reproduction and is considered a factor limiting the migration of *M. myotis* to the north of the Carpathians during the Holocene. Only their adaptation to attics about 200 years ago may have allowed this species to become independent from underground shelters (Horáček, 1984; Zahn, 1999). Harmata (1973) described the reproduction of *M. myotis* in Nietoperzowa Cave at a temperature of 8–10°C, while Pandurska (1998) gave a range of 11–22 °C for Bulgarain caves, which suggests that temperature is not the only factor limiting migration. The thanatocoenosis from Nietoperzowa Cave (820 ± 25 yr BP), a nursery colony,

indicates that reproduction of this species was possible to the north of the Carpathians in spite of the absence of attics. Observations since the last half of the XIX century (Taczanowski, 1854; Waga, 1855), and guano deposits many meters thick speak for the existence of a nursery colony for at least 900 years. The 'Little Ice Age' — the cool period lasting from the XIV to the middle of the XIX century (Maruszczyk, 1999) — most likely did not cause the disintegration of this colony. In spite of the availability of attics — thermally most convenient (Zahn, 1999) — two contemporary underground nursery colonies of *M. myotis* are known from Poland: Nietoperek Reserve, known since the 1970s (Urbańczyk, 1991), and Studnisko Cave, formed in 1998 (Gas and Postawa, 2001). It seems that an additional factor limiting the expansion of this species was the lack of underground shelters with a stable microclimate enabling hibernation. *Myotis myotis* is considered a sedentary species, rarely migrating over 100 km (Güttinger *et al.*, 2001). Until the Middle Ages, its distribution probably coincided with the accessibility of natural hibernacula. Subsequent adaptation to attics allowed expansion of its range for 100–200 km. Underground fortification development permitted this species to become independent from natural hibernaculas in recent years. In the 1950s the distribution of *M. myotis* in Poland was limited to the Uplands belt (Kowalski, 1953), while now the species is distributed all over the country (Wołoszyn, 1996). This indicates a slow shift of its distribution with the acquisition of new hibernation sites and supports the proposed hypothesis.

Barbastella barbastellus prefers lower temperatures during hibernation, and like *P. auritus,* often hibernates near the entrances of its shelters; it is also more often found in artifical shelters (Bagrowska-Urbańczyk and Urbańczyk, 1983; Rydell and Bogdanowicz, 1997). Assemblages containing only this species are known from Western Carpathian caves (Slovakia), (Obuch, 1995). Because this kind of thanatocoenosis was found at different altitudes and not only in caves but also in underground tunnels, Obuch (1995) supposed that they are not characteristic for an area or period. The share of *B. barbastellus* in the studied samples is low, not exceeding 1%, and also does not change through time. Because of its tendency to hibernate near entrances, the real frequency of this species may be underestimated. This is indicated by the higher frequency of this species (up to 13%) in thanatocoenoses from smaller caves that often freeze (Nadachowski *et al.*, 1989).

The presence of huge winter groups of *P. pipistrellus* s.l. in caves was attributed to favorable conditions during the climatic optimum of the Holocene (Atlantic period) Ochman and Wołoszyn (2000) explained this favorability by the presence of ecosystems unaltered by humans, while Horáček (1984) attributed it to deforestation and higher temperatures. Contemporary winter groups of this species are absent north of the Carpathians, but several cases of hibernation are known in artificial underground shelters (Bagrowska-Urbańczyk and Urbańczyk, 1983; Bernard, 1995; Gólski, 1992) and also in building crevices (Wojtowicz and Duszczyk, 2001). The closest mass underground hibernaculum of over 1,000 individuals is known from Slovakia (Uhrin, 1995; Pčola, 1997; Matis, 2000), and the largest is in a cave called Sura Mare (Southern Carpathians, Romania) and reaches 32,000–34,000 individuals of *P. pipistrellus* (Nagy and Szanto, 2003). Wierzchowska Górna I, with a 98% frequency of *P. pipistrellus* s.l.*,* is from the older Subatlantic period (2325 ± 30 yr BP). A few hundred years ago (2,800-2,500 yr BP), a cooling and moistening of climate took

place (Pazdur *et al*., 1988) coinciding with the regression of the Lusatian culture (Godłowski, 1995), after which the regeneration of vegetation began (Ralska-Jasiewiczowa, 1999; Ralska-Jasiewiczowa *et al*., 2003). The next settlement phase began its slow expansion about 2,200 yr BP, and deforestation on a larger scale is dated to the Roman period (about 2,000 yr BP — Ralska-Jasiewiczowa and Starkel, 1999; Ralska-Jasiewiczowa *et al*., 2003). The presence of winter conglomerations of *P. pipistrellus* s.l. in caves seems to be independent from both settlements and a higher thermal balance. Many winter conglomerations in central Europe can be found in shelters with a dynamic microclimate, including the possibility of temperatures falling below zero (Uhrin, 1995; Pčola, 1997; Matis, 2000; Nagy and Szanto, 2003). Racey (1974) also discusses hibernation below 0ºC. Hibernation in shelters with a dynamic microclimate probably doesn't increase mortality during warmer periods, however, it could have brought about the extinction of entire colonies during cool periods. Wierzchowska Górna I is indicative of this scenario; its genesis is dated to a period of rapid and drastic coolings (Fig. 5C). Its fossil material came out of crevices running in the direction of the surface. The appearance of winter conglomerations of this species in caves is hard to explain on the basis of one thanatocoenosis and necessitates the radiocarbon dating of other assemblages from the Western Carpathians.

The results indicate that changes in climate, and consequently in vegetation, were crucial in shaping the bat fauna of the Atlantic and Subboreal periods for the uplands of southern Poland. A markedly lower influence can be ascribed to human activity, which up to now was considered as one of the most important factors. This influence may be present during the Subatlantic period, and especially in the Roman period,

although the small amount of sediments precludes drawing any inferences.

Paleozoological and Radiocarbon Dating

The age of selected thanatocoenoses, calculated according to paleozoological dating, was compared with radiocarbon dating performed by the author. Assemblages with numerous osteological remains from caves of the Kraków-Częstochowa Upland, Roztocze, Holy Cross Mts. and Sudetes were included (see Fig. 6). The well studied Holocene fauna from Tatra (Piksa and Wołoszyn, 2001) was excluded because the frequency of the species may be related to altitude.

The similarity of species composition of thanatocoenoses (Pearson's *r*) indicates the approximate age of assemblages dated paleozoologically:

(1) Assemblages from Cave Duża in Mączna Skala dated from the Atlantic period to historical times (Dagnan-Ginter *et al*., 1992) are included in the group of thanatocoenoses from the Subatlantic period (SA);

(2) The thanatocoenosis from Józefów on Roztocze, dated to the Atlantic period (Kowalski *et al*., 1963) is included in the group from the Subboreal period (SB);

(3) The Atlantic period group (AT) contains assemblages from Zbójecka in Łagów (Ochman, 2003), Pod Sokolą Górą (Ochman and Wołoszyn, 2000) and Studnisko (Wołoszyn, 1976) — all dated to the Subboreal period. The thanatocoenosis Pod Sokolą Górą (5,540 yr BP) comes from the same site as material studied by Ochman and Wołoszyn (2000), which is also reflected in the diagram. Studnisko I (4,345 yr BP) and assemblages studied by Wołoszyn (1976), show a greater similarity to assemblages from the Atlantic period than to the group from the Subatlantic, indicated by radiocarbon dating;
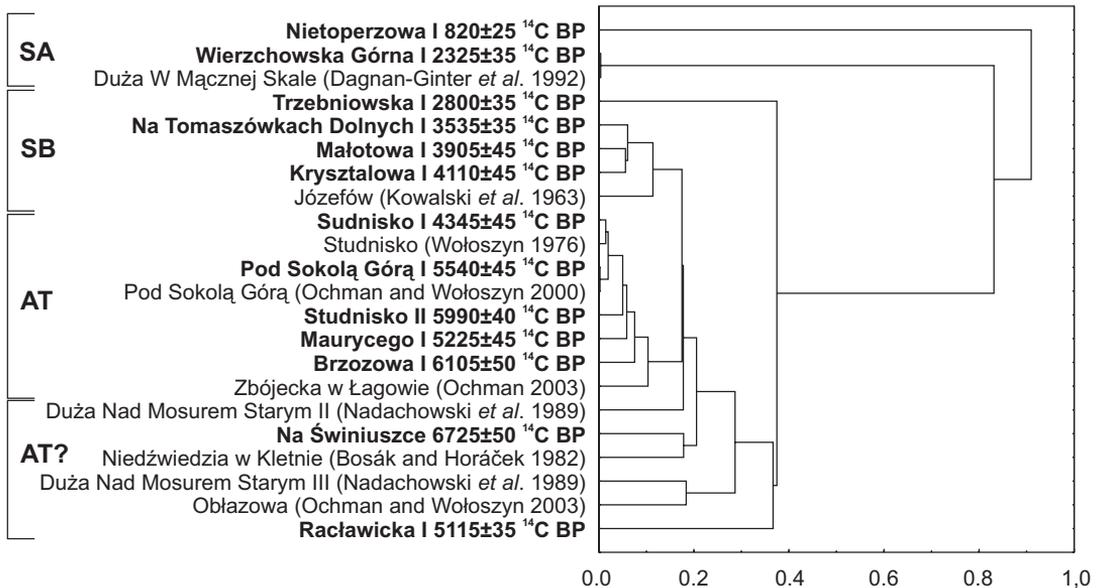
FIG. 6. Hierarchical diagram of similarities of cave thanatocoenoses from southern Poland (Pearson's correlation coefficient) dated by author (name of thanatocoenoses and its age, in bold) and based on literature data. SA — Subatlantic period; SB — Subboreal period; AT — Atlantic period; AT? — probably Atlantic period

(4) The group with uncertain stratigraphy (AT?) contains assemblages dated both to the early Holocene — Niedźwiedzia Cave in Kletno (Bosák and Horáček, 1982) and Obłazowa Cave (Ochman and Wołoszyn, 2003), and to the Subboreal period — Duża Nad Mosurem Starym II and III Cave (Nadachowski *et al.*, 1989). Two radiocarbon dated thanatocoenoses may have an Atlantic origin: Na Świniuszce I and Racławicka I, however, further interpretation is impossible due to a lack of older sediments with certain dates.

Occasionally, the performed comparisons indicate a considerable divergence among so far analyzed thanatocoenoses and bone fossils dated by the author by means of AMS method. This prompts a need for further research with the use of radiocarbon methods, especially for the thanatocoenoses supposedly typical for certain periods, e.g. the assemblage with high proportion of *M. mystacinus*/*M. brandtii* ascribed to early Holocene.

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