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ARACHNOLOGICAL EVIDENCE FOR GLACIAL REFUGIA IN THE BAVARIAN ALPS

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Abstract

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According to geomorphological conclusions some regions of the Bavarian Alps remained free of ice during the Pleistocene glaciations. The current concepts of phytogeography acknowledge plant survival during cryocratic periods in Bavarian massifs de refuge as well as on the nunatak system. Hitherto in zoogeography, little proof has been offered in support of these assumptions. According to recent investigations the distribution areas of the arachnids *Cryphoeca lichenum nigerrima* (Hahniidae) and *Megabunus lesserti* (Phalangiidae) suggest continuous inhabitation of Bavarian refugia since interglacial times. Especially in the Ammergau refugium the persistance of animal life during the last glaciation could be confirmed.

Introduction

At the beginning of our century it became more and more evident, that the occurrence of endemics and disjunct populations of organisms is concentrated in certain peripheral regions of the Alps. In addition, biogeographers recognized that specific types of disjunction have been encountered regularly, even in unrelated taxa. They ascertained that the distribution of these species is restricted to areas which were free of ice, at least during the Würm glaciation. In the 1950s, this knowledge was summarised in phyto- and zoogeography by MERXMÜLLER (1952, 1953,1954) and HOLDHAUS (1954), respectively. The term "massif de refuge" was introduced for a peripheral region in the Alps in which organisms were able to survive the Pleistocene glaciations, thus becoming inter- or preglacial relicts (CHODAT, PAMPANINI, 1902; HOLDHAUS, 1906, 1954). Four important peripheral refugia in the Alps are known: Southwestern, Southern, Southeastern and Northeastern refugium (see Fig. 3). Subsequently glacial survival on the nunatak system of the Central Alps has been proved as well (MERXMÜLLER, POELT, 1954; JANETSCHEK, 1956; SCHMÖLZER, 1962). Nunataks are summits which rose above the ice shield. They were free of snow due to their exposed position and their steep slopes.

In the present literature, the terms massif de refuge and nunatak are often confused, because no exact definitions are available. Certainly the delimitation is sometimes problematical, but nevertheless distinguishable phenomena are involved. I propose to fix the differentiation by the position of the refugia according to the Pleistocene snow-line. Nunataks are located above that level. They remained snowless due to their position and structure. In general, nunataks are of small size and allowed the survival of an azonal vegetation (rock vegetation in favourable exposure) and a few psychrophilic animal species only. Massifs de refuge originated in regions, where due to geomorphological and climatic conditions, the upper limit of glaciation did not meet the Pleistocene snow-line. Usually this situation occurred only in peripheral parts of the Alps, but under special circumstances such refugia could develop and be surrounded by glaciated areas (e.g. in the Ammergau Alps, see also JANETSCHEK, 1960). Massifs de refuge can reach considerable extension and were able to bear at least fragments of zonal communities, even in the Northern Alps (e.g. Caricetum firmae, EGGENSBERGER, 1994).

1. Glacial refugia in the Bavarian Alps

According to the harsh climatic conditions, the fauna and flora of the Northern Alps, which extends from the Swiss Jura in the west to the river Traun in the east, has been regarded as extensively devastated by the Pleistocene glaciations (HOLDHAUS, 1954). Due to the low extent of endemism, biogeographers call this region the Bavarian gap (i.e. “Bayerische Lücke”) (SCHMID, 1936; MERXMÜLLER, 1952). In certain regions of the Bavarian Alps, however, there are plant taxa aggregates which occur, elsewhere, in the Southern or Northeastern Alps only (MERXMÜLLER, 1953, 1954). These relicts are enriched in those local refugia which were close to the northern borderline of glaciation, e.g. in the Berchtesgaden and Chiemgau Alps, although MERXMÜLLER (s. l.) also assumed glacial survival in isolated massifs de refuge, e.g. the Ammergau Alps. The locations of these sites obviously coincide with areas free of ice in the Würm glaciation (KLEBELSBERG, 1935). Recent botanical publications emphasize nunatak survival in the German Alps (URBAN, MAYER, 1996).

Distribution areas of beetles support the assumption of four important massifs de refuge in the Bavarian Alps: namely, Chiemgau Alps around Traunstein/Ruhpolding, Tegernsee and Kochelsee area, Ammergau Alps (HOLDHAUS, 1954; Fig. 1). Apart from that, zoology provides little evidence of the persistence of pre- or interglacial relicts in the Bavarian Alps. This lack of information has already been pointed out by JANETSCHEK (1974).

Within the arachnids the false scorpion *Neobisium dolomiticum* BEIER (Neobisiidae) shows a remarkable north-south disjunction which may be interpreted as an interglacial

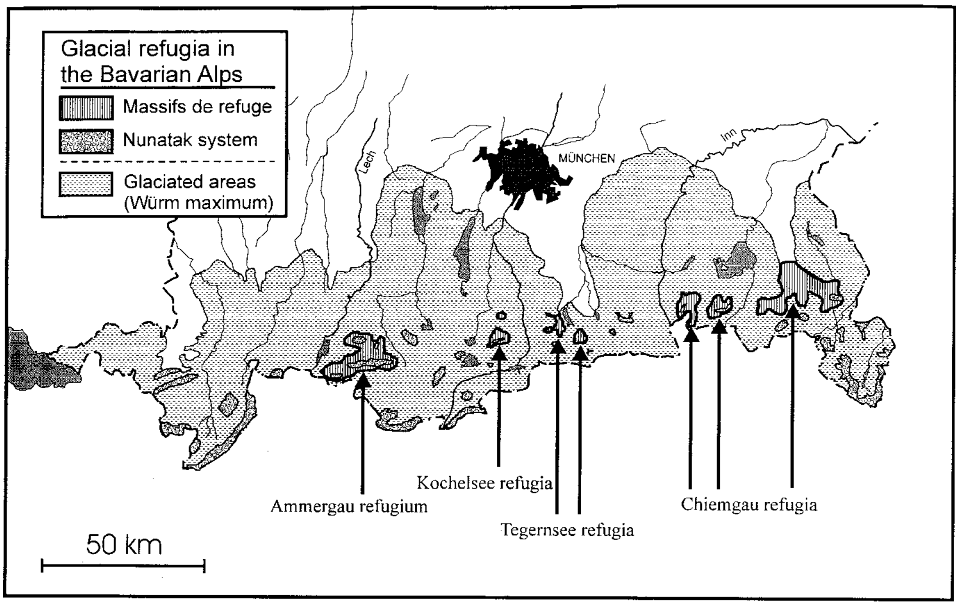

Fig. 1. Glacial refugia in the Bavarian Alps.

relict (THALER, KNOFLACH, 1997). In Bavaria this species was first recorded by SCHAWALLER (1982) from the Allgäu Alps. So far the only two local endemics of the Northern Calcareous Alps west of the river Inn, *Cryphoeca lichenum nigerrima* and *Lepthyphantes severus* (Linyphiidae), have been described by THALER (1978, 1990) from Tyrol/Austria. Survival on the nunatak system is assumed for these spider taxa. *C. lichenum nigerrima* has recently been recorded from Bavaria (MUSTER, LEIPOLD, 1999).

2. New arachno-faunistic arguments on glacial refugia in the Bavarian Alps

According to recent investigations in the Bavarian Alps two arachnid taxa suggest local survival in isolated glacial refugia. *Cryphoeca lichenum nigerrima* probably persisted on the nunatak system and *Megabunus lesserti* SCHENKEL in the Ammergau massif de refuge.

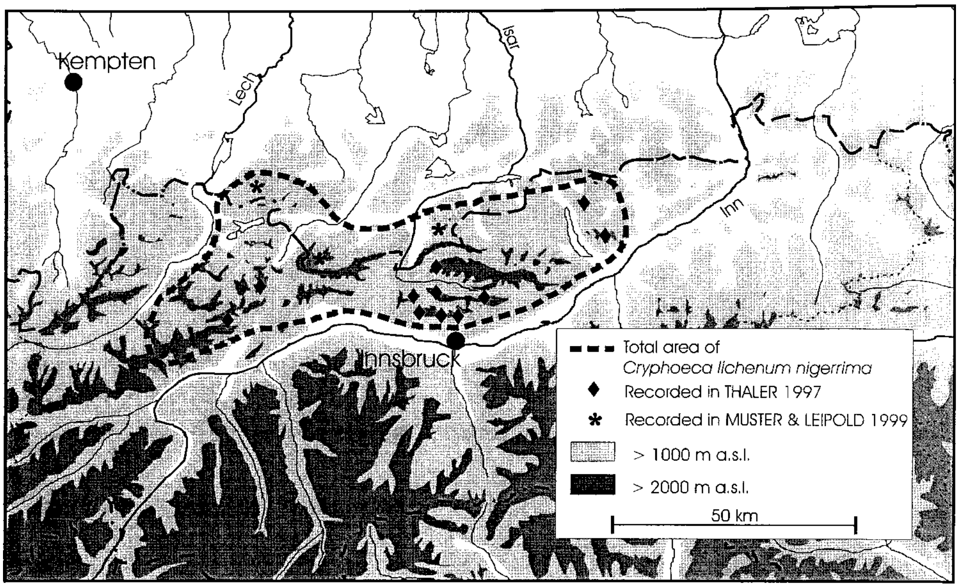

Fig. 2. Distribution of *Cryphoeca lichenum nigerrima* in Bavaria and Tyrol (total area).

2.1 Cryphoeca lichenum nigerrima Thaler **(Hahniidae)**

2.1.1 General distribution

In the Alps five taxa of the genus *Cryphoeca* occur. Their affinities and distribution patterns are of considerable interest for zoogeography, as they seem to be highly influenced by the Pleistocene glaciations (Thaler, 1978, 1980). *Cryphoeca l. lichenum* L. Koch from the Eastern Alps and the eurosiberean *C. silvicola* (C. L. Koch) both inhabit biotopes below the timber line. They occupied their present areas in postglacial re-immigration from arboreal refugia outside the Alps. *Cryphoeca brignolii* Thaler is distributed discontinuously along the southern border of glacial influence. In the Italian Alps it is restricted to peripheral massifs de refuge. The high-alpine taxa *C. nivalis* Schenkel and *C. lichenum nigerrima* are local endemics of the Swiss and the Northern Calcareous Alps, respectively. They evolved in glacial isolation, presumably on the nunatak system. The taxonomic status of *C. l. nigerrima* in relation to its parental form *C. l. lichenum* needs further examination (Thaler, Knoflach, 1997).

Hitherto *C. lichenum nigerrima* was only known from the mountain ranges of Karwendel, Rofan and Lechtal Alps in Tyrol (Thaler, Knoflach, 1997; Thaler, 1998)[1]. Local endemics

[1] The records of *Cryphoeca lichenum* from the Allgäu Alps and the Silvretta in Kreuels, Lückmann (1998) belong to *C. silvicola* according to recent re-examination.

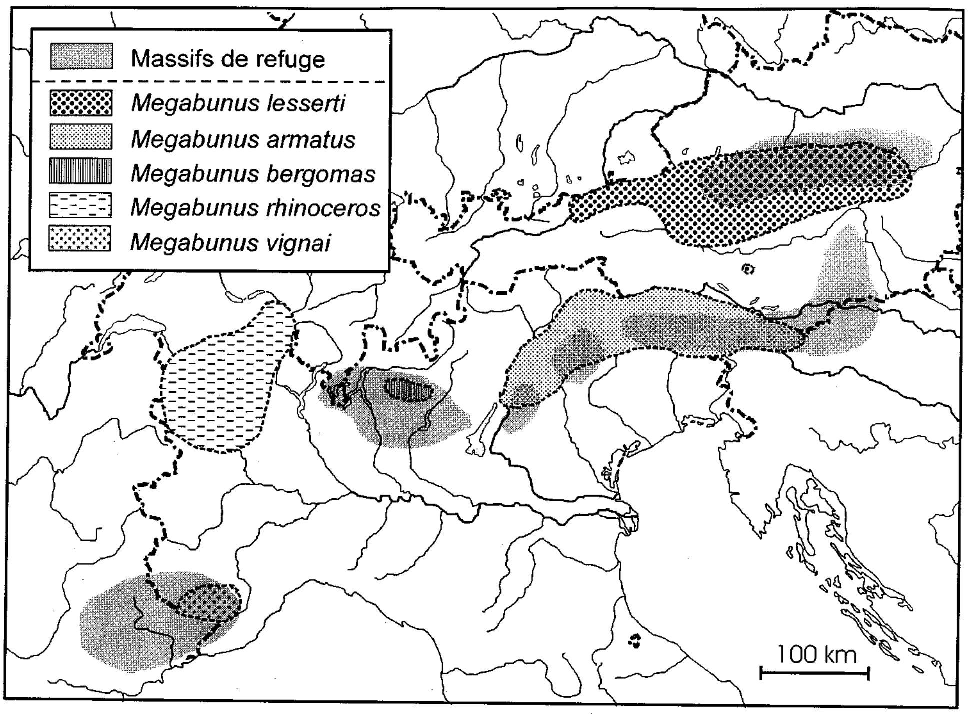

Fig. 3. Distribution of the genus *Megabunus* in the Alps, in relation to important massifs de refuge (according to REISIGL, 1991).

in the fauna of the Northern Calcareous Alps west of the river Inn are rare exceptions (see section 1).

2.1.2 *Cryphoeca lichenum nigerrima* in Bavaria

In 1997/98 three populations of *C. l. nigerrima* were discovered in the Bavarian Alps by pitfall-trapping: Ammergau Alps (3 ♂♂, 2 ♀♀, 1920 m a.s.l., leg. Muster), Wettersteingebirge (1 ♀, 2050 m a.s.l., leg. Voith), Karwendel (11 ♂♂, 3 ♀♀, 2160 m a.s.l., leg. Muster). For details see MUSTER, LEIPOLD (1999).

From this new information it can be inferred that this subspecies occupies nearly all massifs > 2000 m a.s.l. limited by the river Inn in the South and East, by the river Lech in the West and by the northern margin of the Alps (Fig. 2). However, the inhabitable area of adequate elevation comprises less than 1000 sq. km (MUSTER, LEIPOLD, 1999). This fact has serious implications and is of considerable relevance to conservation policies.

The assumption of nunatak survival is suggested by the actual restriction to the upper alpine zone. As shown in Fig. 2, all collecting sites are situated near elevations > 2000 m a.s.l., which were according to KLEBELSBERG (1935) Würm nunataks. This distribution

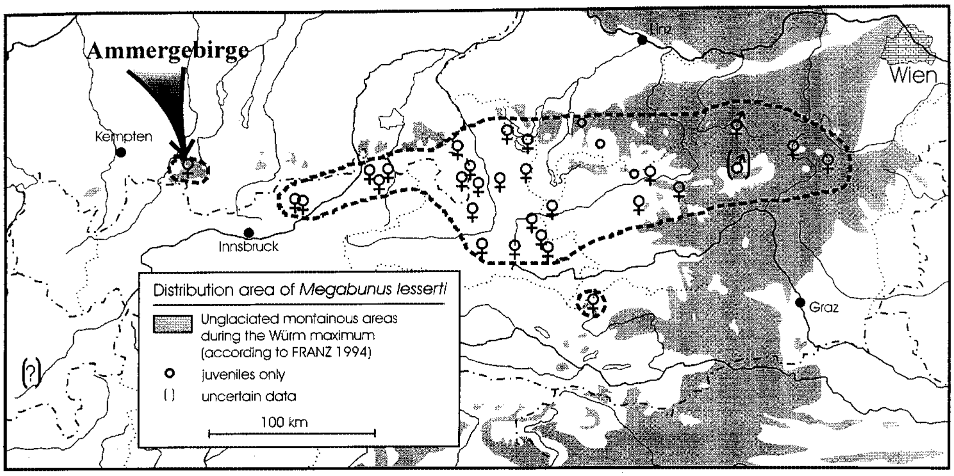

Fig. 4. Distribution pattern of parthenogenetic and bisexual populations of *Megabunus lesserti*, in relation to glacial history.

pattern implies minimal postglacial range expansion. Low dispersal tendency may be assumed for all local relicts and has also been noted in other species of this genus (THALER, 1980). Taxa which are not able to adapt to the conditions prevailing outside the refugia were designated "conservative relicts" by UDVARDY (1969). Further arguments on nunatak survival are provided by the ecology and associates of *C. l. nigerrima*. It shares the habitat preference for stony debris with the majority of locally-endemic spiders of the Alps (THALER, 1990). The concentration of endemics in such biotopes is explained by their greater resistance to climatic oscillations compared with climax communities which, in turn, results in high continuity (PAWLOWSKI, 1969).

2.2 *Megabunus lesserti* SCHENKEL (Phalangiidae)

2.2.1 General distribution

The genus *Megabunus* in the Alps is represented by five endemic species (MARTENS, 1978; CHEMINI, 1985) which occur allopatrically. Without exception their distribution areas are associated with glacial refugia (Fig. 3). *Megabunus armatus* (KULCZYŃSKI), *M. bergomas* CHEMINI and *M. vignai* MARTENS are restricted to the southeastern, southern and southwestern massifs de refuge, respectively. For *M. rhinoceros* (CANESTRINI), which occurs in high altitudes between 1600 and 3000 m a.s.l. (MARTENS, 1978), survival on the nunatak system of the Western Alps has to be assumed.

T a b l e 1. Sex ratios of *Mitopus morio* – populations at different altitudes of the Northern Alps (A- Allgäu Alps, AM- Ammergau Alps, K- Karwendel, MG- Mangfallgebirge).

habitat	altitude	A			AM			K			MG			sum		
		♂	♀	♀ (%)	♂	♀	♀ (%)	♂	♀	♀ (%)	♂	♀	♀ (%)	♂	♀	♀ (%)
subalpine spruce forest	1400-1490 m	17	22	**56**	1	2	**67**	1	5	**83**	5	12	**71**	24	41	**63**
alpine pasture	1450-1600 m	0	3	**100**	38	40	**51**	4	2	**33**	30	34	**53**	72	79	**52**
prostrate pine forest	1650-1800 m	1	46	**98**	2	15	**88**	5	40	**89**	0	50	**100**	8	151	**95**
alpine grassland	1780-1900 m	24	117	**83**	10	71	**88**	8	62	**89**	42	120	**74**	84	370	**81**
rocks and screes	1820-2150 m	4	33	**89**	5	29	**85**	0	6	**100**	8	33	**80**	17	101	**86**

Megabunus lesserti is probably endemic to the Northern Calcareous Alps. Since its original description from the Engadin (Schenkel, 1927) this species has only been recorded east of lake Achensee (Martens, 1978; Thaler, 1998). New and revised records in the eastern part of its range are given in Komposch (1998), together with the information about a disjunct population in an isolated calcareous massif of the Central Alps. Males have been found so far in the easternmost parts of its distribution area (Komposch, l. c.; see discussion below). In Bavaria, this opilionid hitherto has been recorded only once from the Berchtesgaden Alps (Hammelbacher, 1987).

2.2.2 *Megabunus lesserti* in the Ammergau Alps

Megabunus lesserti in the Ammergau Alps was discovered by pitfall-trapping (2 ♀♀, 18 June – 20 July 1998, leg. Muster). The pitfalls were installed in south-exposed alpine grassland (Seslerio-Caricetum sempervirentis, 1920 m a.s.l.) of moderate inclination (38°) near the summit of the Hochplatte (2082 m a.s.l.). The collecting site is at a distance of 40 m from the east-west ridge of that mountain. Towards the north, the massif descends 300 meters almost vertically. According to the literature (Ausobsky, 1987; Thaler, 1994), *M. lesserti* inhabits, stenotopically, steep calcareous cliffs. Thus, the north-exposed rocky slopes of the Hochplatte massif will presumably be the favoured habitat of this opilionid in the Ammergau Alps. Geologically this tract consists of Wetterstein limestone (Bgl, 1967).

According to the data available at present, the Ammergau population is isolated from the main population by a distance of approximately 70 km (Fig. 4). Of course the occurrence of this species in intervening sites cannot be totally excluded. However, Thaler, (in litt.) has searched in vain for this species in the southern ridges of the Karwendel as well as in the adjacent Lechtal Alps. Also recent pitfall trapping in the separating Wetterstein mountains and the German Karwendel has never yielded this harvestman (Muster, unpubl.). In general, faunistic knowledge about opilionids is quite advanced compared with other groups of invertebrates. Thus, a postglacial reimmigration to the Ammergau Alps from the east seems unlikely for *Megabunus lesserti*.

Clearly the question arises whether *M. lesserti* survived the Würm glaciation multi-locally on the nunatak system or in selected massifs de refuge only. Under present climatic conditions its vertical distribution ranges from 850 to approximately 2000 m a.s.l., records at higher altitudes being rare exceptions (Komposch, 1998). Hence this species is absent in the upper alpine and subnival zones, where, predominantly, well-documented nunatak survivors occur. Furthermore, absence in the Karwendel, where nunatak survival is demonstrated for several species (Thaler, 1978, 1990), contradicts the nunatak hypothesis. Therefore, *M. lesserti* has to be regarded as a relict of the massifs de refuge.

The assumption of continuous inhabitation of the Ammergau massif de refuge since interglacial times is supported by the following arguments:

(1) In the Ammergau Alps an area of approximately 150 sq. km below the snow line was not covered by Pleistocene ice during the Würm maximum. For details see the glaciation map in Eggensberger (1994).

(2) The aggregation of widely isolated populations of numerous taxa in the Ammergau Alps cannot be explained by present ecological conditions alone. Eggensberger (1994) mentions at least 7 relicts in the Ammergau flora whose disjunctions originate in glacial events. Some species inhabit widely separated sites in glacial refugia of the Alps: *Pedicularis oederi* Vahl, *Helictotrichon parlatorei* (Woods) Pilger, *Ranunculus hybridus* Biria and *R. parnassifolius* L., *Asperula cynanchica* s. l., *Saussurea pygmaea* (Jacquin) Sprengel. *Carex baldensis* L. has its distribution centre in the southern massifs de refuge, with an isolated occurrence in the Northern Alps in the Ammergau refugium. The distribution of *Soldanella minima minima* Lüdi resembles this type of disjunction (Merxmüller, 1953). Holdhaus (1954) associates an isolated area of the apterous weevil *Otiorhynchus azaleae* Penecke (Curculionidae, now regarded as subspecies of *O. subcostatus* Stierlin) with the Ammergau massif de refuge.

(3) Similar disjunction patterns occur with regularity in non-related taxa. Thus, the distribution of *Megabunus lesserti*, together with its sibling *M. armatus* from the Dolomites, matches the south-north-northeast disjunction type sensu Merxmüller (1954). In the flora of the Ammergau Alps, the distribution of *Ranunculus hybridus, Saussurea pygmaea and Soldanella minima* s. l. characterise this category.

(4) According to Niklfeld (1972) relicts in the montane floras of the Northeastern Alps are typically restricted to azonal communities. This concept may also be generally applicable to animal species, at least it is true in the stenotopical *Megabunus lesserti*. The preferred habitat of this opilionid, almost vertical cliffs, can only be occupied by organisms with special adaptations. Within montane communities, rock vegetation could persist, throughout cryocratic periods, further to the north (Niklfeld, l.c.). In precipitous biotopes, life could most likely escape eradication by Pleistocene glaciations. Life could persist under favourable microclimatic conditions in advantageous exposed situations. Decreased interspecific competition in extreme habitats seems to be important for the survival of glacial relicts in postglacial times as well.

(5) Characteristic differences in the modes of reproduction between glacial refugia and postglacial invasion areas have been observed in some plant (EHRENDORFER, 1949, 1962; POLATSCHEK, 1966) and insect species (SEILER, 1961). Parthenogenesis in *Megabunus lesserti* will be discussed in more detail.

2.3.3 Parthenogenesis and glaciation

Several authors assume that parthenogenetic reproduction occurs in the western part of the range of *M. lesserti* (MARTENS, 1978; THALER 1994, 1998; KOMPOSCH, 1998). No males have yet been found in the counties Salzburg, Tyrol and Bavaria (Styria ?). The distribution of parthenogenetic and bisexual populations (Fig. 4) reveals within the European arachnids a remarkable example of peripheral parthenogenesis (sensu ENGHOFF, 1994). This distribution pattern has not been correlated to glacial history, although glaciation was considered by CUELLAR (1977) to be the ecological driving force behind parthenogenesis in certain species. He revealed that parthenogenesis predominates throughout the world in regions which have experienced disclimax conditions. The early postglacial periods certainly provided an ecological unstable situation in Central Europe. In postglacial recolonization, parthenogenetic organisms were able to invade and occupy open habitats faster than bisexuals, due to their double intrinsic rate of increase and their ability to establish a new colony from one individual (see CUELLAR, 1977). In alpine zoogeography SEILER (1961) found that parthenogenetic populations of the moth *Dahlica triquetrella* (HÜBNER) (Psychidae) in Switzerland mainly inhabit areas previously covered by the Würm glaciation, whereas the bisexual races occupy the nonglaciated areas. Considering the known distribution of *Megabunus lesserti* (Fig. 4), the similarity is striking. Thus, *M. lesserti* presumably survived the last glaciation in the Northeastern refugium (sensu MERXMÜLLER) where a bisexual population occurs (THALER, 1963). Postglacial range extension towards the west apparently led to establishment of parthenogenetic populations.

In this regard, the sex ratio of the Ammergau population is of special interest. Since only two females have been found as yet, no conclusions can be drawn. If males were found, it would be an additional argument on glacial survival in the Ammergau refugium. If this population proves to be parthenogenetic, one could assume postglacial re-immigration according to the theory stated above. But it must be emphasised that all assumptions are speculative, as long as the origin of the parthenogenetic race remains unknown. Two hypotheses are proposed: (1) parthenogenesis in *Megabunus lesserti* evolved postglacially as a result of low population densities in new available habitats at the margins of the refugia. In this way SEILER (1961) deduces thelytoky in *Dahlica triquetrella*. A late glacial or postglacial origin of parthenogenesis is also assumed for the millipede *Nemasoma varicorne* C. L. KOCH (Nemasomatidae, see ENGHOFF, 1976). Since only one bisexual *lesserti* population of small range is known, a single origin for the parthenogenetic race has to be favoured in this case. (2) The parthenogenetic form of *M. lesserti* evolved during the Pleistocene glaciations. This hypothesis is supported by the greater tolerance of females to severe environmental conditions in many species, e.g. *Nemasoma varicorne* (see ENGHOFF, 1976). In the harvestman *Mitopus morio* (FABRICIUS)

(Phalangiidae), recent investigations by the author in the Northern Calcareous Alps yielded significantly reduced percentages of males at high altitudes (Table 1). Therefore, harsh environmental conditions might favour an increased proportion of females and, during the extremes of the Würm maximum, selection pushed the species towards a thelytokous form. In this case, a multi-local origin is plausible, and even parthenogenetic populations may be interglacial relicts. An example of this conception is given by DAREVSKY (1966) in *Lacerta*. He states that in glacial refugia, populations which had become parthenogenetic survived, whereas the bisexual populations either died out or were pushed further south under the influence of the glacier.

Further investigations on the population structure of *M. lesserti* are required, especially in the isolated parts of its distribution area (Ammergau, Gurktal and Engadin Alps). They may result in a better understanding of parthenogenesis as a consequence of the geophysical history and elucidate time scales in Quaternary speciation. Bisexual populations in the fragmented areas would point to a postglacial origin of the parthenogenesis, otherwise the parthenogenetic races probably evolved earlier, during a cryocratic period.

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