Int. J. Speleol. 17 (1988): 31-50

Paleoenvironment and speciation in the cave beetle complex Speonomus delarouzeei (Coleoptera, Bathysciinae)

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SUMMARY

In the eastern part of the Pyrenees (France) the author describes a scenario of speciation in the cave species complex *Speonomus delarouzeei* (Coleoptera Bathysciinae); the speciation processes have been initiated by a breakdown of the ecological equilibrium induced during three glacial-interglacial episodes. The scenario is the following: — during the first glaciation (2.3-2.1 MY), psychrophilic populations ancestral to *S. brucki* were selected over the highest elevation of the range, by means of cold effect which produced an adaptive demographic advantage; adaptive characters of troglobitic species (K strategy) take place presumably in relation to colonization of caves and M.S.S.; — during the second glaciation (1.7-1.3 MY) and a more recent, *S. charlottae*, latter *S. emiliae*, diverged from troglobite ancestors of *S. brucki* without further adaptive characters, as result from stochastic and historical events.

M.S.S. generated during erosional period of glacial event provided ways for migration and new niches for colonization.

Bottleneck effect in size population of ancestors, founder effect, and colonization by local population which present genetic and behavioural geographical polymorphism, argue for a rapid speciation, presumably 100,000 years long and 50,000 generations in the case of *S. emiliae*.

The object of the present paper is to present up two models of microspeciation in cave-beetles related to paleoclimatic events in the temperate zone. These models arise from the results of genetical, ethological, ecophysiological, biometrical and ecologi-

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cal studies performed by myself and several authors (1) on the *Speonomus delarouzeei* complex, distributed in the eastern part of the Pyrenees. The first model involves the climatic change of the late Pliocene, during which tropical climate was replaced by temperate and mediterrean climates and is concerned with associated adaptive events. The second model arises from glacial-interglacial Pleistocene events and their impact on mountain slopes, and is mainly concerned with stochastic events without adaptive effect on beetles populations inhabiting cave and M.S.S. (Milieu souterrain superficiel). The two models habitats support the hypothesis of rapid evolution due to founder and bottleneck effects on population size.

In tropical volcanic regions, where the glaciations had no direct effect, Howarth (1980) suggests that climatic fluctuations are not essential in initiating troglobitic colonization and speciation in the Hawaian lava tube cave systems. The recent data on the *Speonomus delarouzeei* complex and on the paleoecology of the southern part of Europe provide a basis to reexamen and discuss the role of glaciation on speciation in cave beetles in the Pyrenean mountains located near the Mediterranean, and to compare with the scenarios of Barr (1968), Barr and Holsinger (1985), Culver (1971, 1982), and Peck (1980, 1981) for United States cave species groups.

RANGE AND DISTRIBUTION OF THE SPEONOMUS DELAROUZEEI COMPLEX

The species of the complex *S. delarouzeei* are distributed in the eastern part of the Pyrenees, in the northeast of the Catalan country, from Mont Canigou to the Rio Ter, a distance of 60 km from north to south, and from Girona to the Rio Llobregat, 100 km from east to west (Fig. 1).

The populations inhabit cave or M.S.S. habitats under different surface climates, from the Mediterranean zone (from 150 m to 500 m in elevation) to the mountain and sub-alpin zone (from 500 m to 2000 m). The first climatic zone is characterized

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(1) This paper gathers data of several authors and teams. Team of Moulis: C. Juberthie, ecology and paleoenvironment, B. Delay, electrophoresis and ecophysiology, L. Juberthie-Jupeau, reproductive isolation. J. Durand, thermobiology. Team of Rome: V. Sbordoni, M. Cobolli Sbordoni, E. De Matthaeis, electrophoresis and population genetics Team of Barcelone: of Barcelone: X. Bellés, taxonomy, O. Escola and M. Blas, taxonomy and faunistic.

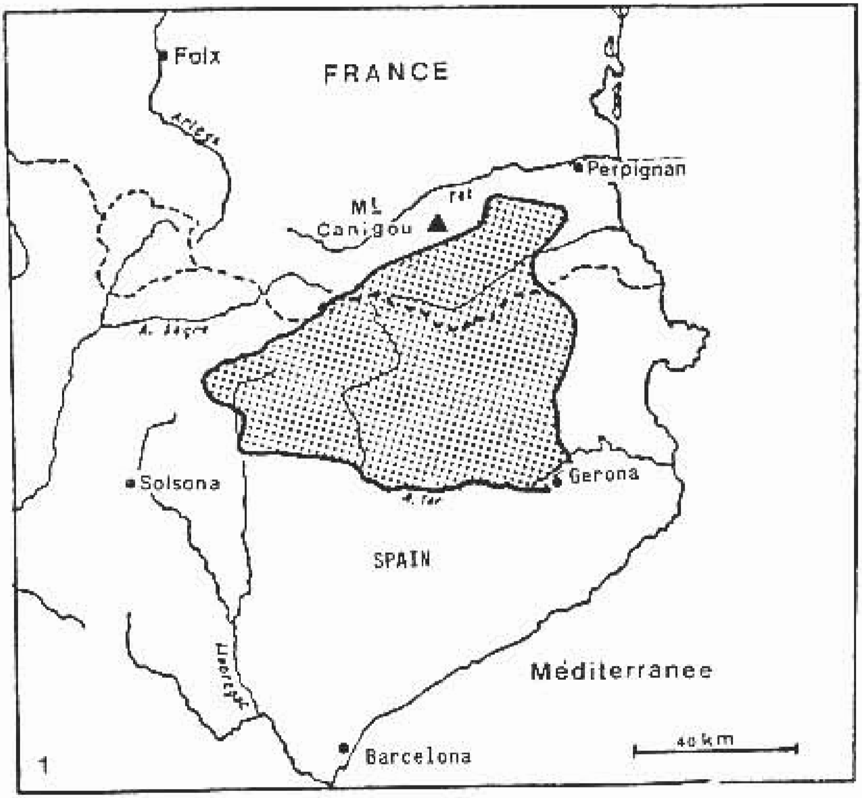
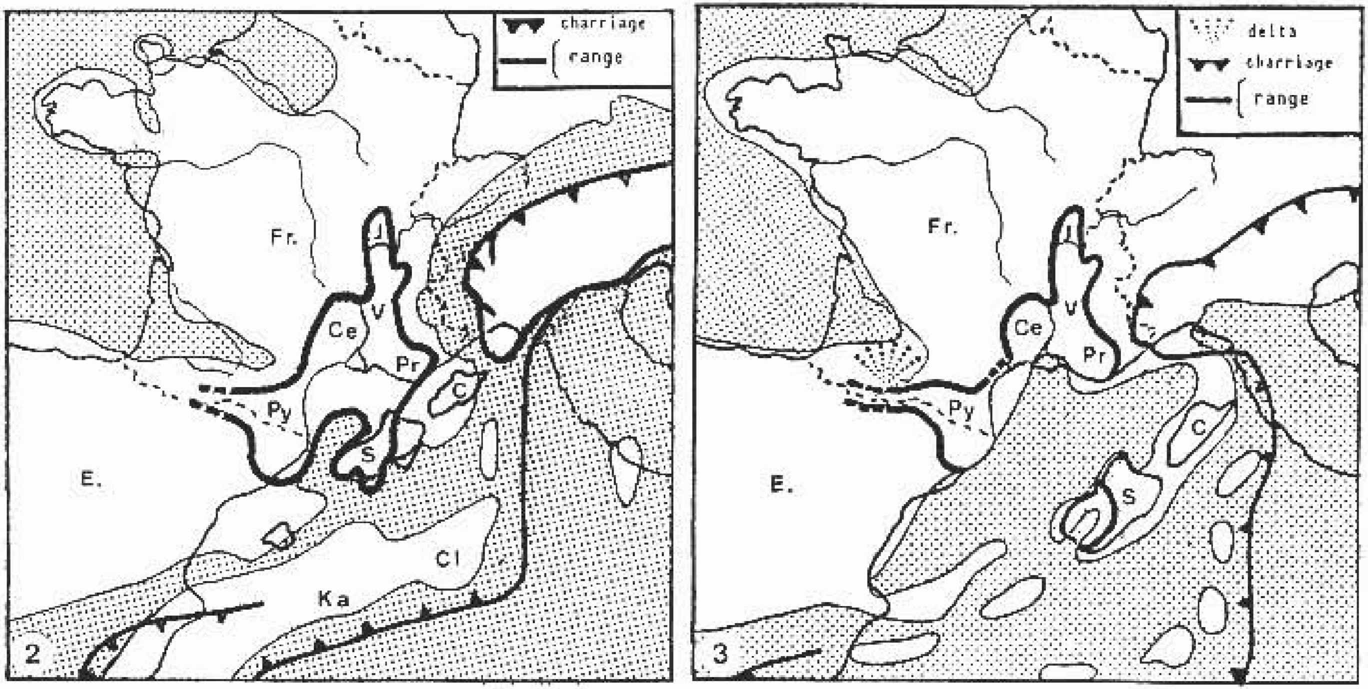


Fig. 1 - Distributional limits of the *S. delarouzeei* complex in eastern Pyrenees. Upper limits: 2,000 m in elevation; lower limits: 150 m in elevation. Southern limit: rio Ter; northern limit: Mont Canigou; eastern limit: Gerona; western limit: near rio Llobregat.

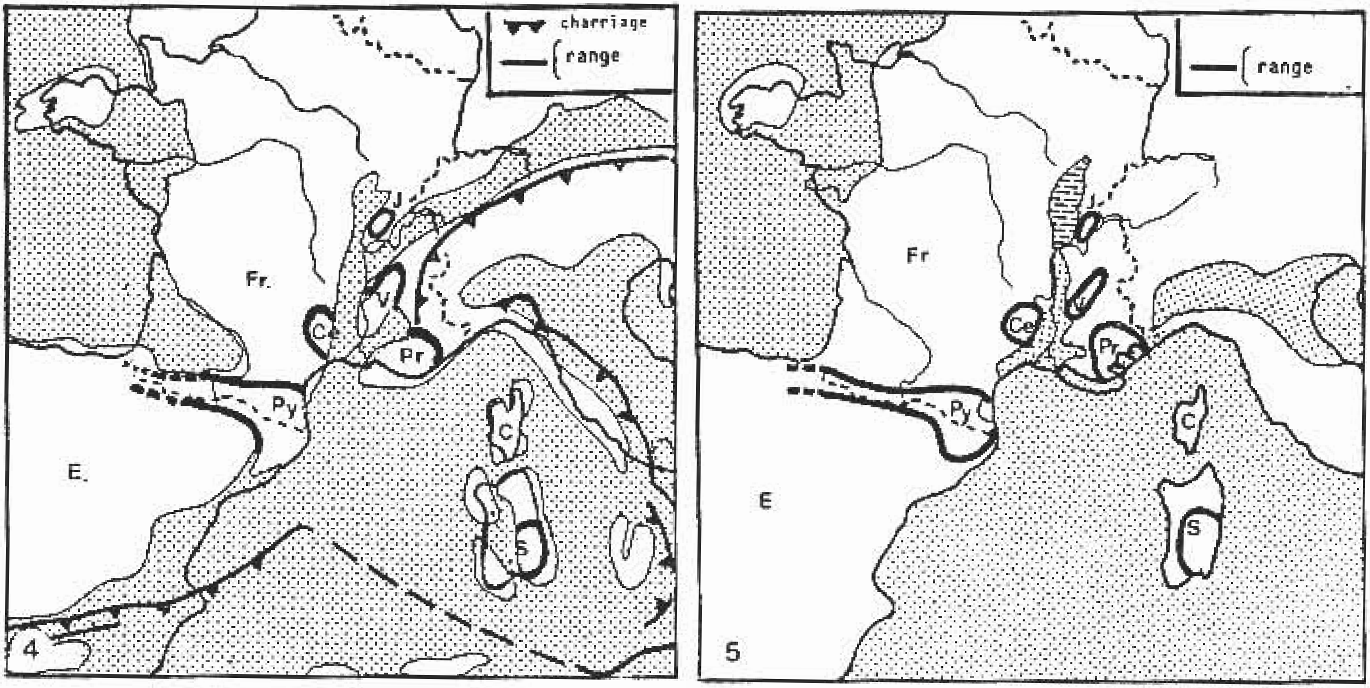
by *Quercus ilex*, the second by forests of *Fagus sylvatica*, and the third by grassland. The changes of climatic zones are rapid along the slopes of mountains.

The paleoecological evolution of climate and vegetation of this range is one of the best known (Jalut, 1977; Jalut et al., 1982; Mardones and Jalut, 1983; Suc, 1986) and the repetitive effects of Pleistocene climatic changes have been drastic.

The fact that *S. delarouzeei* s. l. inhabits M.S.S. as well as caves conduce to very accurate limits of the ranges of the different species, and offers way to the colonization (Juberthie, 1984).



Figs. 2-5 - Four sequential maps showing the reconstructed successive configurations of western Mediterranean, and correlated stages in the break up of the ranges of the cave Bathysciinae and their ancestors. 2 - Oligocene (35 MY); tropical climate; Sardinia and Corsica crustal plate is attached to landmass: Eurasian plate (France and Spain). 3 - Aquitanian (20 MY); tropical climate; reconstruction showing opening of the western Mediterranean correlated to easternward drift of the Sardinia and Corsica crustal plate and isolation of the Sardinian Bathysciinae.



4 - Tortonian (10 MY); tropical climate; reconstruction showing fragmentation of the distribution of Bathysciinae in several isolated ranges, in Jura, Vercors, Provence, Cevennes, which can be attributed to marine invasion in the Rhône and Saône valleys. 5 - Flandrian (5 MY); isolation of alpine Bathysciinae from western Bathysciinae (Cevennes and Pyrenees); C = Corsica; Ce = Cevennes; Cl = Calabre; E = Spain; Fr = France; Ka = Kabylie; Py = Pyrenees; S = Sardina; V = Vercors.

PALEOBIOGEOGRAPHY; THE RANGE AND DIFFERENTIATION OF SPEONOMUS AND S. DELAROUZEEI S. L. ANCESTORS DURING THE LATE TERTIARY AND QUATERNARY

Knowledge of tectonic, paleoclimatic and geologic events is extremely valuable for understanding the ranges of species and for determining the rate of evolution in the group.

According to Jeannel (1952), the oculate or microphthalmic ancestors of Bathysciinae inhabited the soil of tropical forests but I think also limestone caves, cracks and voids of the M.S.S.; indeed, Oromi et al. (1986) discovered M.S.S. under the soil of relict tropical forest in the Canary Islands at an elevation of 1000 m in Tenerife, inhabited by *Pterostichus* which are partly pigmented oculate or microphthalmic. The range of the ancestors of *Speonomus* and others cave genera of Bathysciinae extended into the Jura, southern Alpes, Cevennes, eastern part of the Pyrenees and Sardinia (fig. 2).

Before 25 MY, Corsica and Sardinia and their tectonic plate was connected to the landmass that is to say to the area of present day Catalogne, Languedoc and Provence (Dercourt et al., 1985; Ricou et al., 1985). A chain of mountains has extended from the Pyrenees to Provence since the end of the Cretaceous (Bousquet and Vignard, 1985). The climate was tropical and rain forests covered the range of the ancestors of the troglobitic Bathysciinae at lower altitude. The forest was a Laurisylva, similar to the relict tropical forest in the Canary Islands (Bramvell and Bramvell, 1983) and the rain forest of the southern part of China. It was composed of Taxodiaceae *(Sequoia, Cupressus)*, of Lauraceae, Bamboos, Juglandaceae, and also several typical mediterranean species such as *Quercus ilex, Quercus coccifera*. At medium elevation (about 500 - 600 m) the rain-forest progressively changed into an association composed of *Quercus, Ulmus, Acer, Gingko* and *Cupressus, Juniperus, Pinus* and *Abies*.

About 25-20 MY (early Miocene), the chain of mountains between the Pyrenees and Provence were erodal and break (Golfe du Lion), the southern part of the « Massif Central » rose, the Corsica and Sardinia separated from the landmass with their tectonic plate drifting eastward, so that the occidental Mediterranean basin was opened (fig. 3). This was an early fragmentation of the range of the ancestors, so that Sardinian Bathysciinae were isolated from Pyrenean populations. They ultimately became the new genus *Batinoscelis*. We can estimate the time of genetic divergence between *Batinoscelis* - *Speonomus delarouzeei* by means of electrophoresis; indeed

Sbordoni (1982) gives a genetic distance (Nei) of 2.418 corresponding to approximately 25 MY. So, the times given by tectonic events and isoenzyme analysis are in concordance.

Between about 10 MY (middle Miocene; Tortonian) and 5 MY (Plaisancian), the rotational movement of the Corsica-Sardinia plate ended. The sea invaded the valleys of the Rhône and Saône; the sea transgression presented a barrier between alpin Bathysciinae and « Cevennes » Bathysciinae (fig. 4). The isolation of the ancestors of the alpin genera, *Cytodromus*, *Royerella*, *Troglodromus*, from *Diaprysius* and *Mayeta* in Cevennes was not later than 10 MY; it was perhaps earlier if the species were isolated on mountains by rain forest with compact soil and cracks filled at low altitude in valleys.

The isolation between the ancestors of *Speonomus* and *Diaprysius*, *Mayeta* could be dated from the same period (no later than 10 MY). However, the sea transgression between the Pyrenees and the Massif Central had not been extensive enough to isolate the two groups of Bathysciinae. The most probable scenario is an earlier isolation in M.S.S. and caves of mountains which were surrounded by rainforest at lower elevation. This hypothesis is supported by data on tropical rain forest in Africa and America, where this type of beetle (oculate or microphthalmic) is absent, while it has been collected in high elevation caves of the Sierras in Central America (Barr, 1971) or in forest and glassland on the top of African volcanoes (Jeannel, 1935). The biochemical erosion and laterite which filled cracks, voids and M.S.S., particularly in nonkarstic areas covered by rainforest, can explain their absence. In fact granitic rocks (Montagne noire) and clay sediments (tertiary « molasses ») lie between the present ranges of *Speonomus* and *Diaprysius*.

According to this hypothesis, the three groups of genera (Pyrenean; Cevennes; Alpin) had been isolated no later than 10 MY but presumably earlier in mountain M.S.S. and caves, perhaps at the beginning of the rise of the southern part of the Massif Central, from 10 to 20 MY ago. Studies by means of other methods such as electrophoresis are necessary to test this scenario.

The first climatic event (3.2 MY) at the end of the tertiary, was a period of lower temperature (fig. 6). It induced changes over 200,000 years from tropical hot and wet climate to more temperate conditions.

About 2.3 MY, the main ecological event began. The first true glacial period, which extended for 200,000 years, played a major role in determining the range of *Speonomus delarouzeei* and by acting as a selective factor which differentiate the psychrophilic group of species from the mediterranean group.

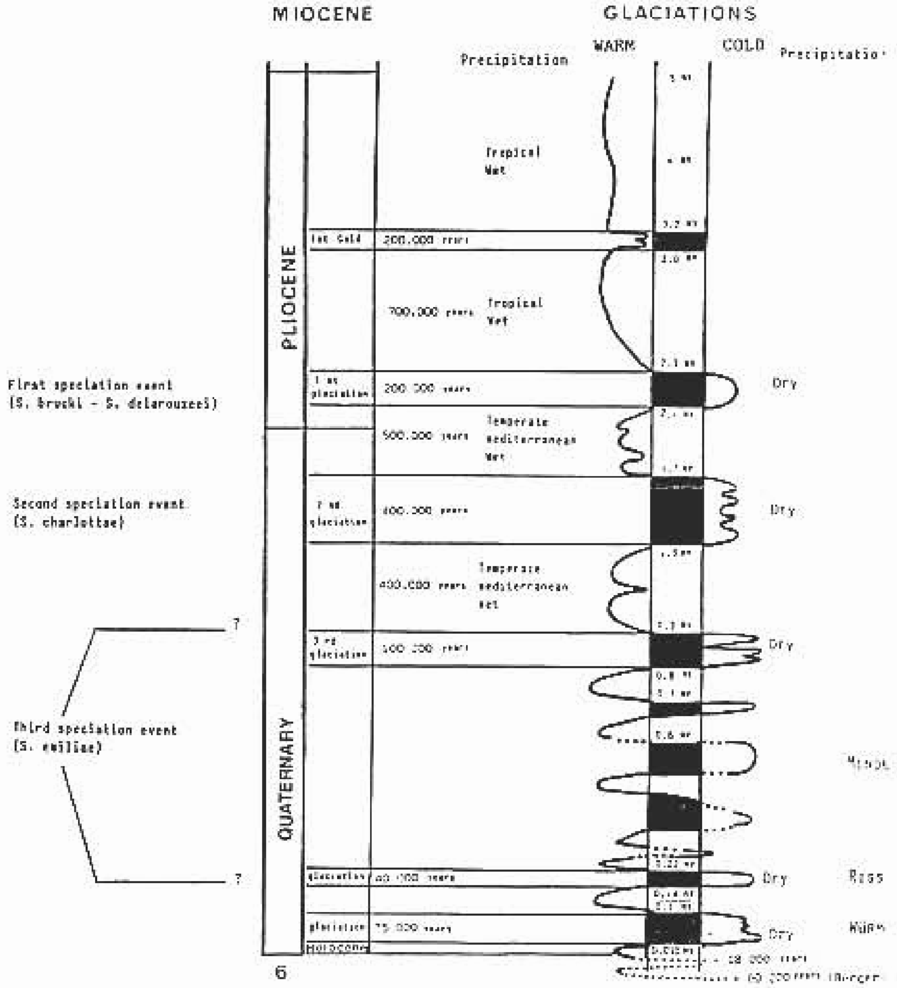


Fig. 6 - Reconstructed temperature variations during Pleistocene and Holocene showing the first glacial period and sequences of glacial and interglacial stages (from H. Zagwijn) corresponding speciation events.

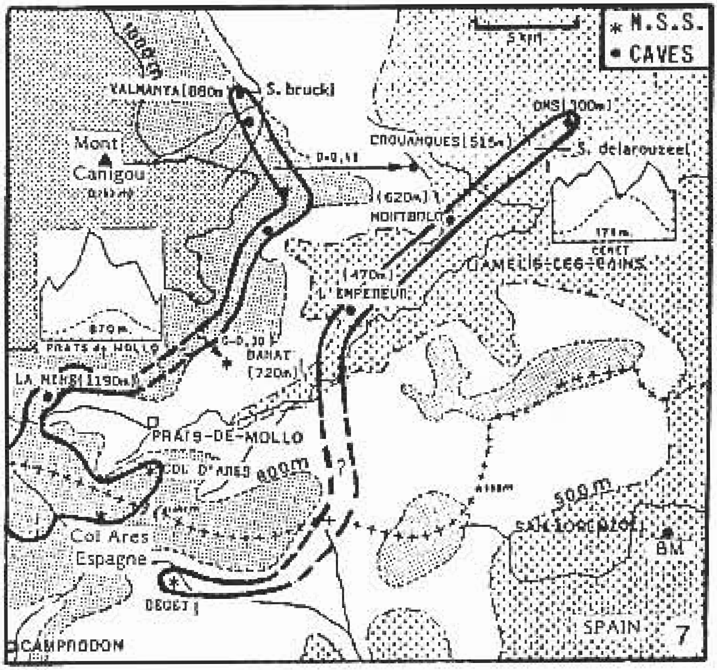


Fig. 7 - Limits of the ranges of *S. delarouzeei* and *S. brucki*; temperature and precipitation at 170 m in elevation (mediterranean vegetation zone), and at 870 m (forest mountain vegetation zone).

FIRST BREAK UP OF THE COMPLEX S. DELAROUZEEI INTO TWO GROUPS

The climate event (2.3-2.1 MY), corresponds to the first true glacial period, which established the mediterranean climate, dry and hot in summer and cold in winter, at the lower elevation of the range of the ancestors of *Speonomus delarouzeei* sensu lato, and established a more temperate and cold climate in mountains. The increased cold temperatures at high latitude induced dryness around the Mediterranean and the spreading of steppes with *Artemisia* (de Beaulieu and Suc, 1985). During the interglacial episode, at low elevation, the tropical rainforest was replaced by persistent deciduous species of which *Quercus ilex* was dominant.

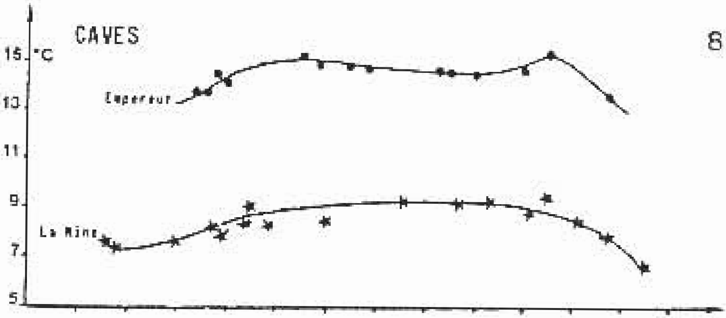


Fig. 8 - Annual temperature fluctuations in two caves: «l'Empereur» habitat of *S. delarouzeei* and «La Mine» habitat of *S. brucki*; C1 = *S. brucki*; C2 = *S. delarouzeei*; j = days; according to Juberthie et al. (1984).

Many data support the hypothesis that the first glacial period generate two basic species in the complex: *Speonomus delarouzeei* Fairm. sensu stricto in the mediterranean zone and *Speonomus brucki* Fairm. in the mountain forest zone.

The actual range of *S. brucki* (fig. 7) extends from 1000 m to 1500 m in elevation, along the slopes of the Mont Canigou, under a forest of *Fagus sylvatica* or at higher elevation grassland, with a maximum of rain at the late spring and more one meter annual of precipitation; the annual temperature range, for example, in the cave of «La Mine», 1190 m in elevation, is 7 - 9° C (fig. 8). *S. delarouzeei* s. stricto inhabits caves and M.S.S. in the mediterranean zone, more dry and hot in summer, with *Quercus ilex* vegetation; the annual temperature fluctuation is, for example, 13 - 15° C in the Cave « Resurgence de l'Empereur » (for more details see Juberthie et al., 1984).

The two species are characterized by:

1 - strongest differences in mating behaviour, *S. brucki* mates in 1 step and *S. delarouzeei* in 3 steps (fig. 10), and breeding experiments demonstrate a complete reproductive isolation (Juberthie-Jupeau and Cazals, 1984 a, b, 1985 a, b);

2 - largest genetic distance (D = 0,75), based on analysis of 12 loci and using Nei's method (Delay et al., 1980) (fig. 9).

There are thermobiological differences between the two main species with regard to fecundity, the speed of development of eggs and larvae. *S. brucki* has higher fecundity and faster development at low temperature (Delay, 1979, in press), and the upper lethal temperature is lower for *S. brucki* (Durand et al., 1984). This suggests that the cold temperatures of the

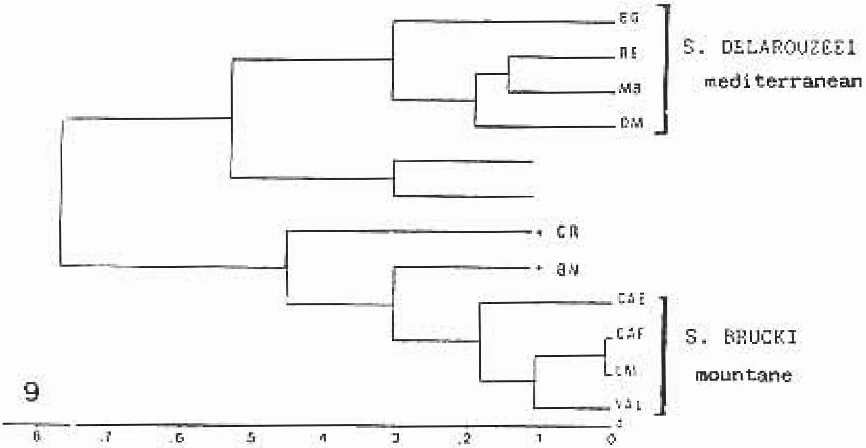


Fig. 9 - Dendrogram of genetic distances (using Nei's method), showing branching of the two main groups: *S. delarouzeei* (mediterranean), *S. brucki* (mountain), BN = M.S.S. Banat; CAE = M.S.S. Col d'Ares Spain; CAF = M.S.S. Col d'Ares France; CR = Crouanques Cave; LM = La Mine; Val. = Valmanya cave; BG = M.S.S. Beget; RE = Résurgence de l'Empereur; MB = Montbolo cave; OM = Oms cave; according to Delay et al. (1980) simplified.

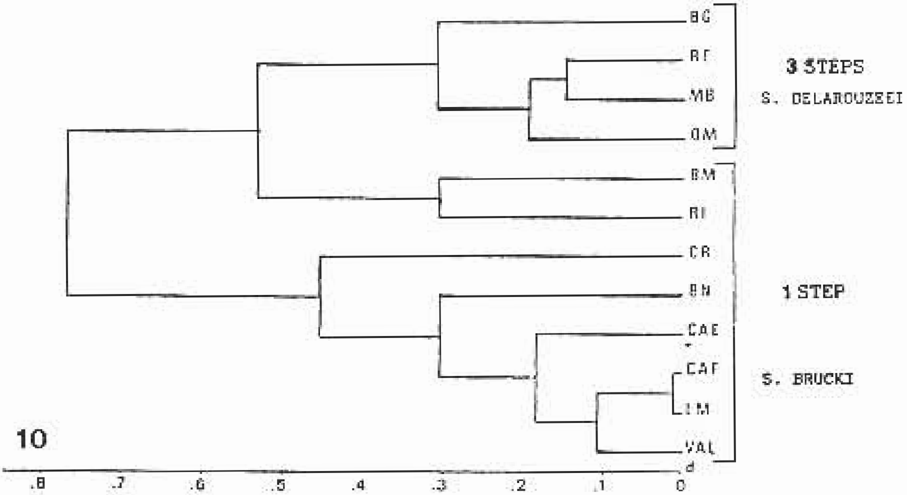


Fig. 10 - Dendrogram of degrees of reproductive isolation, determined by: prezygotic factors (sexual behaviour) and hybridization. BM = Bora Major Cave; RI = Rialb Cave; CR = Crouanques Cave; BN = M.S.S. Banat; according to Juberthie-Jupeau (in litteris).

glacial period could have selected for psychrophilic genotypes, typical of *Speonomus brucki*, in the montane part of the range (on the slopes of Mt Canigou) around 1000 m in elevation, where today the annual range of cave temperature is 8°-10° C. Indeed, the temperature mean has been from 5° to 7° C lower in summer and even more in the winter during the Würm glacial period and presumably during the first glaciation, as well this agrees with the temperature range which produces a demographic advantage (cold effect) for *S. brucki* as Delay demonstrated for the eggs and larvae reared at 5° C (fig. 11). At warmess temperature during interglacial periods the development time difference is very slight and no advantage exists; so during these periods the temperature is a neutral factor and the selection does not occur.

In contrast, in the mediterranean part of the range where inhabited to day by *S. delarouzeei* sensu stricto, caves temperatures average 14° C, the demographic advantage could not be expressed, because temperatures in the glacial period (8° C - 9° C in the summer) were near to the neutral part of the developmental thermic curve (see fig. 11). However in winter the decline of temperature was probably sufficient to select some psychrophilic individuals, from no more half of eggs laid a year. This could explain the thermobiologic polymorphism observed in *S. delarouzeei* s. stricto.

The decline of temperature during the earlier climatic change (3.2 MY) was probably not enough strong to induce cold effect, and separation of the ancestral stock in two species.

The first glacial period of 200,000 years duration, was characterized by extension of steppe vegetation, gelifraction of rocks generating M.S.S. on the slopes of valleys, in both the mediterranean zone and the mountains, summer air and soil dryness in the mediterranean area, erosion of soils. Cold temperatures and changes in vegetation reduced the primary production and the level of organic matters in caves and M.S.S., according to the level of organic matter measured in layers of pollen analysis in glacial period and beginning of warming (Mardones and Jalut, 1983). This could have decreased the size of cave and M.S.S. beetle populations as well as the diversity of communities. These phenomena could had led to the disappearance of r genotypes and species in M.S.S. and cave communities, and selection for K strategist with lower energy requirement.

The fact that *S. brucki*, *S. delarouzeei* and all the species of the complex show the same degree of K strategy, argues for a selection of genotypes adapted to low energy at the same period, presumably during the first glacial period, 2.3 - 2.1 MY,

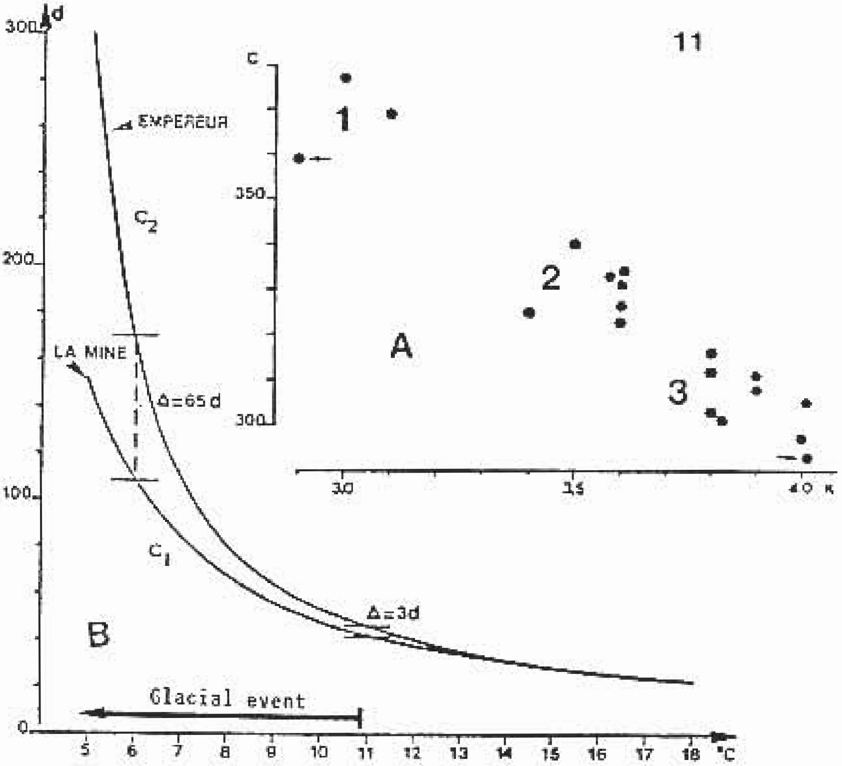


Fig. 11 - Variation of embryonic development time related to temperature. A - Embryonic time development of *S. delarouzeei* from « L'Empereur Cave ». The first group (1) is more psychrophilic (low K and high C values) than the second (2) with medium K and C values and the third (3) with high K values. The value of K indicates the position of the function D = F(T) on the scale of temperatures (from Delay, in press). B - Speed of development of eggs of *S. brucki* (C1) and *S. delarouzeei* (C2) sensu stricto related to temperature. Note: The presence of a neutral temperature zone, from 18 °C to 10 - 9 °C, in which the speed of embryonic development of the two species is similar, and a range of low temperatures where a « cold effect » occurs which induces differences in speed of development with a maximum around 5 °C; at this temperature, the development of *S. brucki* is twice as rapid (150 days) as that of *S. delarouzeei* (300 days); from Delay (1978).

and related to the colonization of M.S.S. and caves. This demographic pattern, typical of other cave beetles, probably has been selected very early in the cave evolution.

The strong correlation between allozymic and behavioural dendrograms suggests that the reproductive isolation and the selection of psychrophilic populations of *S. brucki* have occurred simultaneously.

Hybridization between the two sibling species may also have been suppressed by male-female incompatibility. ♂ try to mate often and randomly with ♀ of their species or of other species of the complex. Male *S. delarouzeei* from cave at 13 - 15° C tend to mate with ♀ of *S. brucki* from cave at 8 °C. Mating attempts result in death of the females of *S. brucki* (Juberthie-Jupeau, in litteris). This could contribute to the separation of the ranges of the two species.

LATTER EPISODES. SPECIATION IN RELATION TO GLACIAL-INTERGLACIAL PLEISTOCENE EVENT WITHIN THE PSYCHROPHILIC AND TROGLOBITIC GROUP S. BRUCKI S.L.

Each glacial episode displaced the forest belt several hundred meters downward in elevation, replaced forests with steppe vegetation due to the cold and dry climate, and was a period of erosion which generated cracks, voids and M.S.S. and provoked a sink phase in caves (fig. 12). Each interglacial period is characterized by warming climate, extension of forests and forest belts, and dominance of biochemical erosion which fills cracks and voids and producing barriers to gene flow.

The three sibling species, *Speonomus brucki*, *S. emiliae* n. sp. (in litteris), *S. charlottae* n. sp. (in litteris) have similar mating patterns (one step; fig. 10), genetic distances (Nei) between them *brucki - emiliae* D = 0.30, *brucki - charlottae* D = 0.46 (fig. 9) (Cobolli Sbordoni et al., 1983); breeding experiments indicate that they represent true species (Juberthie-Jupeau and Cazals, 1985 a, b). This speciation within the complex occurs over a narrow elevational range from 1500 to 500 m on the slope of Mont Canigou. These speciation events correspond with two more recent paleoclimatic glacial-interglacial episodes.

The immediate ancestors of *Speonomus emiliae*, an M.S.S.-dweller in Banat at 720 m in elevation, were probably ancestral populations of troglobitic *Speonomus brucki* that were com-

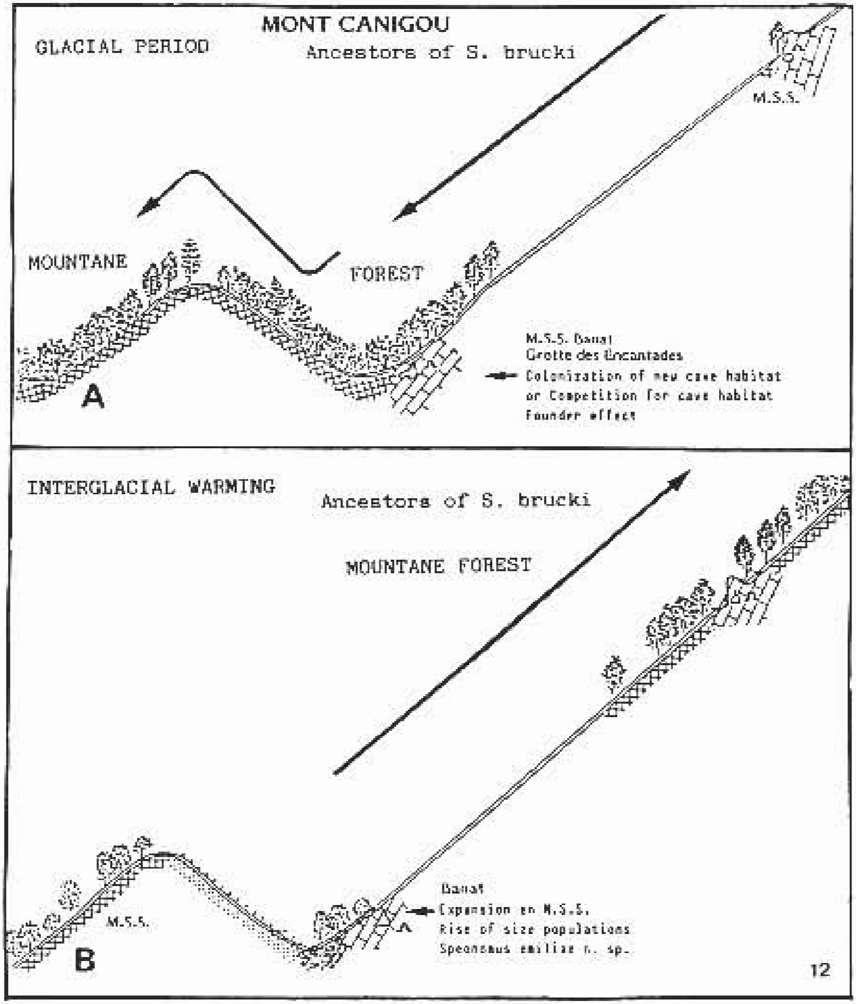


Fig. 12 - Hypothesized colonization-isolation events during a glacial-interglacial period giving rise to the *S. emiliae*. A. - Glacial period. Migration to lower elevation of the forest belt by the ancestors of *S. emiliae* through cracks and micro-voids of the M.S.S.; colonization of a newly generated M.S.S. in Banat. B. - Interglacial warming. Forest belt migrated to upper elevation; isolation and speciation of *Speonomus* in M.S.S. Banat.

pressed downward altitudinally with the forest belt during a glacial period, through the cracks and voids in the M.S.S. They invaded a newly generated and well developed zone of M.S.S. in Banat (fig. 12).

During the beginning of interglacial warming, the mountain forest belt extended up, and the rapid filling of cracks and micro-voids by pedogenesis (geomorphological barriers), isolated a population in empty spaces of the large Banat M.S.S.

Peck (1980) has proposed a similar scenario, with M.S.S. unknown at this time, for the isolation of the arthropod species in Grand Canyon caves and (1981) for *Ptomaphagus hirtus* species group of the southeastern United States.

TIME AND RATE OF SPECIATION

Estimates of divergence times for the speciation events, using Nei's method and electrophoretic data, are 4 MY, 2.5 MY and 1.5 MY for the three events described above. The arguments presented above support more recent divergence times and, therefore, more rapid speciation. For example, the estimate of time since divergence for the two closely species, *S. brucki* and *S. emiliae*, based on Nei's distance is 1.5 MY, that correspond to the second Pleistocene glaciation (fig. 6). This estimate is undoubtedly too old, because a population of *S. charlottae*, from Crouanques cave, as a higher Nei's distance (D = 0,46; fig. 9) indicating that it diverged even earlier from the same ancestors.

So, a reasonable scenario is the following:

— First glaciation, 2.3 - 2.1 MY. Divergence of *S. brucki* and *S. delarouzeei* sensu stricto; psychrophilic populations ancestral to *S. brucki* were selected over the highest elevation of the area, due to the presence of cold climate (cold effect); adaptive characters of troglobitic species (K strategy) take place;

— Second glaciation, 1.7 - 1.3 MY. *S. charlottae* diverged from troglobitic ancestors of *S. brucki*, on the eastern slope of Mont Canigou, due to isolation and divergence rather than an adaptative shift;

— Third glaciation, 0.9 - 0.8 MY or more recent glaciations. *S. emiliae* arosed from troglobitic ancestors of *S. brucki*, on the southern slope of Mont Canigou, through a process of colonization - isolation in lower altitude caves or M.S.S. peripheral to the ancestral population.

The last two speciation events *(S. charlottae, S. emiliae)* presumably were not related to cave adaptation because these new cave species have risen from cave limited ancestral population. This provides an historical and stochastic aspect to the speciation process, as Stanley (1975) has argued for other animals.

In the Mediterranean part of the range, during the second glaciation, the southern populations in Bora Major cave (*S. gimjuani*) and Rialb cave (*S. catalonicus*) diverged from ancestors of *S. delarouzeei* sensu stricto, that to day inhabit caves in Vallespir Valley (Résurgence de l'Empereur, Montbolo, Oms) and Bebet M.S.S. in Spain.

Several factors provide evidence for a rapid speciation:

— a bottleneck in size population of the ancestors due to the decrease of the primary production and the amount of organic resource in cave habitat, induced by the onset of the glacial climate;

— a founder effect (Templeton, 1980) related to the colonization of caves and newly-generated M.S.S., at lower elevation and in peripheral zones, by populations which possessed only a portion of the genetic variability of the parent population·

— a colonization by local elements of a general population characterized by geoghaphical, genetic and behavioural polymorphisms, related to habitat heterogeneity characterized by limestones intercalated between schistous or compact rocks.

The speciation event occurred during a breakdown of the ecological equilibrium related to the instable climates of the glacial and the beginning of the interglacial period; the breakdown of the ecological equilibrium occurred several times within the range of the complex, but produced new species only three times, according to the present data.

In the case of *S. emiliae*, the third and later glaciation were 100,000 years long. With a life-cycle of one year at 11 °C and two years at 6 °C, the species diverged from ancestors of *S. brucki* in no more than 50,000 generations. In the case of *S. charlottae*, the second glacial period was 400,000 years long corresponding to 200,000 generations.

Taxonomy. Morphological characters of the aedeagus (internal sac), distinguish the four species which have close morphological similarity and slight differences (Belles, 1984). The effectiveness of these internal morphological characters is supported by the great genetic distance between species and by the ethological distance as determined by breeding experiments performed by Juberthie-Jupeau et al. (1985b, 1988). In several complexes of troglobitic species of Bathysciinae and Trechinae morphological differences are very slight. Thus, a need arises to use additional biological characteristics (e. g., behavioural and isoenzymatic data) to infer systematic relationships.

CONCLUSIONS

In the eastern part of the Pyrenees in the range of the species complex *S. delarouzeei*, the speciation process appears to have been initiated by a breakdown of the ecological equilibrium, induced by glacial episodes. This process of microspeciation occurred three times during the Quaternary, producing neoendemic cave Bathysciinae.

Two types of speciation occurred successively in the complex.

— The earlier episode presumably related to colonization of the underground habitat, involved an adaptive shift during the first glaciation which produced a cave species with an adaptive demographic advantage under conditions of cold temperature and energy availability;

— The latter episodes arose from stochastic events related to glacial-interglacial episodes producing species which diverged from the previous troglobitic ancestors without further adaptive changes.

Fracturing of rocks and development of M.S.S. during the erosional period of a glacial event, provided ways for migration and colonization of caves and made available a new niche in the newly generated M.S.S.

At low elevation (southern mediterranean part of the range of the complex) the preliminary studies supported hypothesis that species which diverged from ancestors of *S. delarouzeei* s. stricto had been isolated by compact zones generated by biochemical erosion which filled cracks and M.S.S. in the interglacial period. The result is a patchy habitat with geomorphological barriers to gene flow.

ACKNOWLEDGEMENTS

The author would like to thank Thomas Kane for his attentive linguistic corrections and Gisele Ruffat for technical help.

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