

BIOGEOGRAPHIC FEATURES OF THE PYRENEAN RANGE

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ABSTRACT The general biogeographic features of the Pyrenean range are reviewed with particular reference to the distribution of flowering plants, amphibians, and reptiles. The role of the Pyrenees in the past, as a barrier to, or as a channel for, the migration of species between Europe and the Iberian Peninsula is described. The present distribution of species can be related to past climates, especially glacial and interglacial periods. When conditions were inhospitable mountain plants, reptiles, and amphibians achieved physiological adaptations, and in many cases mountain habitats became important refuges. Today the Pyrenean reptiles and amphibians are controlled to a large degree by altitude, especially as it determines climatic variability and temperature ranges.

RÉSUMÉ *Caractéristiques biogéographiques de la chaîne des Pyrénées.* Les caractéristiques biogéographiques générales de la chaîne des Pyrénées sont passées en revue, en particulier en ce qui concerne la distribution des plantes à fleurs, des amphibiens et des reptiles. Le rôle des Pyrénées dans le passé, en tant que barrière ou passage pour la migration des espèces entre l'Europe et la Péninsule ibérique, est examiné. La distribution actuelle des espèces peut être rapportée au climat du passé, en particulier les périodes glaciaires et interglaciaires. Quand les conditions étaient défavorables, les plantes de montagne, les reptiles et les amphibiens se sont adaptés physiologiquement, et dans beaucoup de cas les habitats montagnards sont devenus des refuges importants. De nos jours, les populations de reptiles et d'amphibiens des Pyrénées sont en grande partie sous la dépendance de l'altitude, principalement du fait que celle-ci détermine la variabilité climatique et les amplitudes thermiques.

ZUSAMMENFASSUNG *Die biogeographischen Merkmale der Pyrenäenketten.* In dieser Veröffentlichung werden allgemeine biogeographische Merkmale der Pyrenäenketten untersucht, besonders im Hinblick auf Verteilungen von Blütenpflanzen, Amphibien und Reptilien. Die Rolle der Pyrenäen in der Vergangenheit als Schranke gegen und als Wegweiser für Artenmigrationen zwischen Europa und der Iberischen Halbinsel wird beschrieben. Die heutige Artenverteilung entwickelte sich aus vergangenen Klimata, besonders während der glazialen und interglazialen Perioden. Wenn unwirtliche Bedingungen herrschten, paßten sich die Gebirgspflanzen, Reptilien und Amphibien physiologisch an und in vielen Fällen waren Gebirgshabitate wichtige Schutzplätze. Die derzeitige Verteilung von Reptilien- und Amphibienarten in den Pyrenäen ist hauptsächlich durch die Höhenlage bestimmt, insbesondere da diese klimatische Variationen und Temperaturbereiche bestimmt.

RÉSUMÉ *Caractéristiques biogéographiques de la chaîne des Pyrénées.* Les caractéristiques biogéographiques générales de la chaîne des Pyrénées sont passées en revue, en particulier en ce qui concerne la distribution des plantes à fleurs, des amphibiens et des reptiles. Le rôle des Pyrénées dans le passé, en tant que barrière ou passage pour la migration des espèces entre l'Europe et la Péninsule ibérique, est examiné. La distribution actuelle des espèces peut être rapportée au climat du passé, en particulier les périodes glaciaires et interglaciaires. Quand les conditions étaient défavorables, les plantes de montagne, les reptiles et les amphibiens se sont adaptés physiologiquement, et dans beaucoup de cas les habitats montagnards sont devenus des refuges importants. De nos jours, les populations de reptiles et d'amphibiens des Pyrénées sont en grande partie sous la dépendance de l'altitude, principalement du fait que celle-ci détermine la variabilité climatique et les amplitudes thermiques.

INTRODUCTION

The Pyrenees constitute an extremely interesting mountain range for biological research because of the great variety of environments. They have also played an important role throughout a long period of geological time as a barrier between the Iberic and Atlantic provinces of the great Palearctic biogeographic region. Furthermore, they have experienced several major climatic changes which have modified the regional flora and fauna; the most recent and most important are the glacial and interglacial epi-

sodes of the Late-Cenozoic, including the Holocene and Recent periods. In this paper no attempt is made to produce a detailed study of each of these aspects of the Pyrenees: each are worthy of far more extensive treatment than time or space allows. We shall attempt, therefore, to give emphasis to some of the more important and general features of the mountain biogeography as a means of complementing the other topics considered in this special issue. The authors, a botanist (P. Montserrat Recoder) and a

zoologist (J. P. Martinez Rica), by preparing the paper together, have sought to provide an overview rather than a specialized and technical treatment.

To achieve the stipulated objectives, this paper introduces the major issues with illustrations from two special disciplines: one involving amphibians and reptiles, to represent the animal kingdom; the other, selections from flowering plants, to represent the plant kingdom. Although amphibians and reptiles are mobile, they are tied to local

habitats that do not extend for large distances. They confer specific characteristics upon the communities within which they belong in a manner almost as strictly controlled as that of the flowering plants. Both groups integrate climatic variables directly; thus herpetocenoses and phytocenoses are alike in that they are functioning entities that clearly reflect and synthesize their surrounding conditions. They are, therefore, extremely useful as environmental indicators.

GENERAL FEATURES OF THE PYRENEES

As with many of the great Eurasian mountain ranges, the main orientation of the Pyrenees is east-west. Those mountain chains with similar orientation in Eurasia have a common origin: pressure of the African and Indian tectonic plates against the Eurasian plate. This factor, originating in remote geologic time, has important consequences for the biogeography of today. Thus, the east-west orientation, especially in the temperate zone, results in a strong contrast between south-facing slopes, which receive much more direct solar radiation, and north-facing slopes, which are colder and, under natural conditions, covered in dense forest. In the context of traditional French alpine geography, this had produced the familiar terms *adret* and *ubac* respectively. The Spanish equivalents are *solanas* and *umbrías*.

Other Pyrenean features are not common to all east-west oriented mountain ranges. One important Pyrenean characteristic is proximity to large bodies of water; thus the mountain chains close to seas and oceans (including the Alps and Caucasus) have climates clearly distinctive from the more continental mountain ranges. In the Pyrenees, for instance, the moist Atlantic air readily penetrates the northern slope, while the southern valleys become increasingly drier toward the east. The southern valleys of the Central Pyrenees experience a distinctively dry continental climate, since they are distant both from the Atlantic and the Mediterranean (Dupiaz, 1985; Izard, 1985).

The primary consequence of the east-west orientation of the Pyrenean axis on plant distributions relates to the barrier role that the range has played since its formation. Many species of Euro-Siberian origin reach their southern limit close to the mountain divide, while species of Iberian or Ibero-African origin do not extend northward of the crestline. Examples of northern plants are *Potentilla montana* and *Echinops spheroccephalus*, while *Veronica triphyllos* and *Valeriana longiflora* are Iberic species whose northern limit coincides with the Pyrenean crestline (Montserrat Marti, 1984). Northern species of amphibians and reptiles include *Rana dalmatina* and *Lacerta agilis*, while Iberic species include *Psammotromus algirus* and *Vipera latasti*, which are very rare, or entirely absent, in France.

Similar situations occur in other mountain ranges. The Alps, for instance, provide the southern limit for a number of reptilian and amphibian species (for example, *Bufo calamita* and *Lacerta agilis*) and the northern limit for others (for example, *Bufo viridis* and *Chalcoides chapsides*).

When mountain ranges are large enough they act as

major barriers and may become the boundaries of the major biogeographical regions (for example, the Himalaya). In the case of a mountain barrier of moderate proportions the species separation between both slopes is not complete. The line of the crest can be regarded as an open or permeable fence through which many species have penetrated by using low passes. The Pyrenees have many such corridors that have allowed a restricted diffusion of many individual species. Most important from a biogeographic point of view are the main passes at either end of the range: the western pass, between the mountains and the Atlantic in Basque country, serves as a passage for European species into the Iberian peninsula (for example, *Betula verrucosa* and *Triturus alpestris*); the eastern passage has the reverse direction, allowing Mediterranean forms access into France (for example, *Genista scorpius* and *Psammotromus algirus*).

There is a third Pyrenean pass of biogeographic interest which connects Mediterranean areas in both France and Spain (the valleys of the Têt and Segre) at the mid-altitude level of about 1,100 m. Some European species such as *Lacerta agilis* have taken this route to enter Spain, although they have not penetrated far from the crestline.

Another evident result of the east-west orientation of the Pyrenean chain is the structure of the areas occupied by different animal and plant species, forming parallel, alternate bands. On both sides of the chain, but mainly on the southern side, there is a series of minor ranges (sierras) which are oriented parallel to the main Pyrenean axis. There is a sharp contrast in these ranges between the northern slopes (*umbrías*) and the southern ones (*solanas*), reproducing a contrast similar to that found in the main chain. The "solanas" provide habitats for thermophilous species, which sometimes extend to fairly high altitudes and which very nearly approach the crestline through the southern valleys. Thus, typically Mediterranean species, such as *Lavandula latifolia* and *Malpolon monspessulanus*, occur not far from the crestline at an altitude of over 1,200 m.

The hygrophilous species, in contrast, occupy the symmetrically opposite conditions. In the southern Pyrenean ranges the crests of the sierras make a clear separation between both kinds of species: this separation is so pronounced that very different forms occur within a few meters of each other (for instance, *Fagus sylvatica* and *Thymus vulgaris* on each side of the crest, very near the divide).

Among Pyrenean reptiles there are several pairs of similar species belonging to the same genus, but with different ecological requirements. These species occupy the southern and northern slopes of the ranges; they are well separated but nevertheless very close to their congeneric species. Among these pairs of thermophilous-hygrophil-

ous species are: *Coronella girondica*-*Coronella austriaca*; *Lacerta lepida*-*Lacerta viridis*; *Podarcis hispanica*-*Podarcis muralis*; *Vipera latastei*-*Vipera aspis*; and others. All of them are distributed in the Prepyrenean mountains according to the model just described.

CLIMATIC CHANGES IN THE PYRENEES

To understand the actual distribution of plants and animals in the Pyrenees we also need some knowledge of the past climatic conditions in the area, for these conditions have influenced the establishment and differentiation of species. The progression of glacial and interglacial phases of the Late-Genozoic (Pleistocene Ice Ages) has been particularly important in this respect.

In the Pyrenees is evidence of all five classic European glaciations, Donau, Gunz, Mindel, Riss, and Würm. Only the traces of the last two are preserved well enough to allow a detailed study. The Riss glaciation seems to have been the most intensive with a maximum ice extension; the latest glaciation (Würm) has been fairly well studied, including its different phases and subphases, although, of course, there are still many unknowns (Alimen, 1964), and major shifts in interpretation are to be expected now that the entire classic system is under review.

The extension of Pyrenean glaciers was dependent on two main factors: the amount of snowfall, and the persistence of the snow as related to ablation season temperatures, together with other secondary factors. The snowfall was, and is still, heavier in the western part of the chain which is open to the flow of moist Atlantic air masses. During some periods of the last glaciation the Atlantic flow appears to have been reduced and a very cold, continental climate developed (Ruddiman and McIntyre, 1981). The persistence of the snow depends mainly on the altitude, which is greatest in the Central Pyrenees. These circumstances allow us to visualize a complex pattern of long glacier tongues running down the northern Pyrenean valleys between the Gave de Pau and the Arige rivers, and a set of very short glaciers in almost all the valleys of the southern slope. The glaciers filled valley floors, but the watershed divides between them and the surrounding areas were exposed to periglacial processes. These areas, snow covered only in winter and spring, were extensive on the southern slope, reaching even to the Ebro valley. The widest part of that periglacial belt was the southern exposure of the Central Pyrenees; the presence of many small mountain ranges south of the Pyrenean axis and the strong continental character of the area resulted in intense periglacial activity.

During the interglacial or interstadial periods glaciers retracted, or even disappeared, and traces of periglacial activity were scarce below 2,000 m. Under these conditions, very similar to those of today, thermophilous species advanced, mainly through the valleys in the Pyrenean chain, while other species, more tolerant to cold, were driven out and their habitats were more and more diminished. As the Iberian Peninsula was a refuge for cold species during glacial phases, and as there are several mountain ranges on the southern side, it is not surprising to find today several isolated populations of mountain species near the summits of these mountains. They have been reduced in area to the higher altitudes by the advance of thermophilous species during the warm phases.

For instance, the sierras of Montseny, Montsech, Guara, and San Juan de la Peña support isolated populations of Pyrenean endemics, such as *Merendera pyrenaica* and *Euproctus asper*, and of species coming from the north, such as *Drosera rotundifolia* and *Lacerta viridis*. Isolated plant populations, even small ones, are often resilient and able to persist for millennia, but that is not so frequent in animal populations, which easily become extinct. This is the case, for instance, for *Euproctus asper*, an endemic amphibian from the Pyrenees which reached the Cantabrian mountains at the end of the Würm glaciation, and which disappeared from there during the postglacial period (Sanchiz, 1977).

The glacial periods, of course, produced a reverse process. Then, species adapted to cold advanced to the Ebro valley while Mediterranean species were driven far to the south. As in the other case, these species found some warm refuges, which became the habitat of isolated populations of thermophilous species. These refuges are steep, south-facing slopes. Although close to the Pyrenean divide, these slopes were connected with fluvial valleys trending south so that Mediterranean species could penetrate during the Atlantic thermal maximum, about 7,000 years ago. Subsequently they were isolated from their mother populations. Several isolated areas of this kind are found here and there on the south side of the Pyrenees, with species such as *Thymus vulgaris*, *Colutea arborescens*, *Podarcis hispanica*, and *Lacerta lepida* (Martinez Rica, 1983; Dupiaz, 1985).

EVOLUTION IN MOUNTAIN AREAS

Mountain areas harbor pioneer and unstable ecosystems, not only because of the pronounced annual oscillations, but also because the environmental conditions are severe. Opportunistic animal species occupy such ecosystems and have a high reproductive rate and high genetic

plasticity. Even so, these species must pay the price of high mortality to be able to persist in mountain environments.

The high reproductive rate and mortality, the genetic plasticity, and the strong selection pressures combine to speed the evolution of populations and to allow rapid dif-

ferentiation of form in the lower taxonomic levels. That differentiation displays itself through adaptive features which animals and plants use in response to environmental stress and, through the birth of new species, give rise to the high percentage of endemics so common in mountain areas.

In the Pyrenees, species differentiation has been intense because of the many geologic and climatic contrasts. For instance, the geologic complexity (a very old and ruptured basement under the Cenozoic Pyrenees, which were folded and thrust over Triassic marls) induces an environmental diversification which, together with the climatic factors, aids in the persistence of past ecologic structures. Braun-Blanquet (1948) points to the persistence of old orophytic subtropical elements in the Pyrenees, in contrast to the situation in the Alps. The Boltaña anticlinal, with an approximate north-south direction along the Greenwich meridian, marks a barrier of the past which persists today and influences the dynamics of distribution areas (Montserrat Marti, 1984).

Adaptations of plants and animals to mountain conditions are well known. Among amphibians and reptiles they are mainly modifications to the biological cycle, allowing the animals to make effective use of the short vegetative season (ovoviviparism, parthenogenesis). There are also other adaptive features although less clear; for instance, hibernation reversibility, or the lowering of thermopreferendum. Even at the intraspecific level, mountain populations show subtle physiologic adaptations (Grossenbacher, 1980). Several mountain species, such as *Coronella austriaca* and *Vipera aspis*, have an adaptive ovoviviparism. Other species, such as *Rana temporaria* and *Lacerta monticola*, are very tolerant to cold and they remain active even when temperatures fall close to 0°C.

There is much that is known about the adaptive features of mountain reptiles and amphibians. Perhaps the most surprising ones are the internal metamorphosis in *Salamandra atra* and the natural parthenogenetic reproduction of four species of Caucasian lizards (Darevsky, 1966), although both, like ovoviviparism, are found in non-mountain ecosystems. Among the plants, there are many species which show features adaptive to mountain conditions; one Pyrenean genus is *Gentiana*, with species such as *Gentiana alpina* and *G. verna*, which have floral buds already prepared in winter, ready to flourish immediately when the snow disappears at the beginning of spring.

The process of birth of many endemic species can be related to glacial periods. During cold periods the Pyrenean barrier between Europe and the Iberian Peninsula was stronger, and this induced the formation of isolated nuclei (shelter for Mediterranean species) as noted above. The populations in these nuclei evolved separately, achieving some degree of differentiation. In fact, all Mediterranean lands constituted a large refuge for species driven out from Europe by the cold; every peninsula or large island was a part of this refuge, playing the role of an independent center of differentiation. De Lattin (1967) names nine

centers of this kind in the Mediterranean, the largest being the Ibero-Atlantic refuge, which included the whole Iberian Peninsula, the north coast of Morocco and Algeria, and the south coasts of France. The Pyrenees, therefore, were not a complete limit for that refuge, but isolation of the Iberian Peninsula was sufficient to allow the formation of several known endemics, such as *Triturus boscai* and *Chalcides bedraigai*, whose differentiation began, of course, long before the Pleistocene.

The Pyrenean barrier favored the formation of endemics in another way also. As is generally understood, mountain ranges are similar to island environments: archipelagoes of summits surrounded by a sea of lowlands. The lowland areas are, of course, more permeable than an actual sea for the passage of animals. Moreover, their limits are not clear and change with climatic fluctuations. Nevertheless, mountains have many isolated areas suitable for the differentiation of endemics and for the application of the theoretical frame developed by island biogeography. In the Pyrenees there are three kinds of such habitats. All form isolated areas with fairly permanent conditions, with some independence from climate change; all of them serve, therefore, as refuges.

The first of these habitats are the crests and summit areas. Many remain uncovered by snow or ice because snow is blown off by the wind, and was even during glacial times. Some localities with fairly mild microclimates (shelters, crevices) allow the persistence of a number endemic taxa, sometimes since very remote epochs.

Among the Pyrenean amphibians and reptiles, the small lizard *Lacerta monticola bonnali* is an example of such an endemic. This subspecies belongs to a species that originated during the Miocene in the Ibero-Atlantic refuge; it is restricted now to high altitudes of the Iberian mountain systems, and was fragmented by glaciations into several subspecies. The Pyrenean subspecies lives today at an altitude in excess of 2,000 m.

Another type of refuge includes the warm localities sheltered by relief features. Mainly on the south Prepyrenean slopes, there are several rocky formations, large rock precipices facing south (Riglos, Rodellar, Collegats) that are warmed, not only because they are directly exposed to the sun but also because of ascending thermal air currents. Such precipices are not suitable for populations of amphibians or reptiles, but are inhabited by endemics of other animal groups (for instance Gasteropoda) and, of course, by interesting endemic plants.

The third type of stable refuge in the Pyrenees are the caves; although no Pyrenean cave harbors endemic reptiles or amphibians, there are endemics from other groups. Only a few species, such as the Pyrenean newt (*Euproctus asper*) and the salamander (*Salamandra salamandra*), can form stable underground populations, very small and lasting only for a few generations. These populations, therefore, do not reach the stage of genetic differentiation, although they show some interesting physiological adaptations.

ALTITUDE DISTRIBUTION OF AMPHIBIANS AND REPTILES

It has been already pointed out that the biogeographic importance of reptiles and amphibians is almost as great as that of plants; the similarity of both groups reveals itself in the altitudinal structure of their distribution areas; these form belts of specific composition around the mountain blocks. The altitudinal distribution of Pyrenean amphibians and reptiles has been studied in detail, although the results have not yet been published. Different species show marked preferences for some altitude ranges, mainly because of their thermic needs. In the Pyrenees there are six groups of species that occur at mean altitudes ranging from 320 to 2,350 m. Although the range of each group overlaps, the species within a particular group show an altitudinal conformity. Three of these groups include true mountain forms.

The first group includes *Coluber viridiflavus*, *Alytes obstetricans*, *Triturus helveticus*, *Salamandra salamandra*, and *Podarcis muralis*. These species occur normally between 600 and 1,600 m, with a mean altitude of 1,100 m. The second group occurs between 800 and 1,800 m (mean altitude 1,350 m) and includes the following species: *Coronella austriaca*, *Vipera aspis*, *Lacerta vivipara*, *Euproctus asper*, *Lacerta agilis*, and *Rana temporaria*. The last group has only one species, *Lacerta monticola*, living between 1,850 and 2,950 m, with a mean altitude of 2,350 m.

The number of species occurring at high elevations is smaller than the number at lower altitudes, not only because of the more severe environments but also because

at high altitudes the available area is small. In the Pyrenees, the number of amphibian and reptile species at the lowest altitudes is about 40, and this decreases to 0 at 3,000 m. The relationship between species richness and altitude is linear, of the type:

$$y = ax + b$$

A linear relationship holds also for other vertebrate groups and other mountain ranges (Diamond, 1973) and for Spanish reptiles in other mountains (Bas, 1982).

The functional relationship between species richness and altitude depends on the topographic and climatic features of each range; it differs from place to place. In the southern Spanish mountains, for instance, the relationship for reptiles is of a log-exponential type, such as

$$y = P/(1 + a \exp bx)$$

calculated from data in Pleguezuelos (1986) while in the Pyrenees the relationship

$$y = ax/(b + x)$$

is more accurate. Nevertheless, an approximate linear relationship holds fairly well for several animal groups and mountain areas, and that is sufficient for most purposes.

MOUNTAIN HERPETOLOGY AND CLIMATIC VARIABLES

The influence of temperature in the life of amphibians and reptiles is so great that these animals have been taken as models for the study of autoecologic problems (Huey *et al.*, 1983). Of course, there are several other environmental factors in addition to temperature (such as rainfall, sunlight, and thermic oscillation), the influence of which is also paradigmatic.

In the Pyrenees the annual isotherm of 10-12°C, following approximately the 1,200 m contour on southern slopes and the 800 m contour on northern slopes, can be taken as delimiting the true "mountain" area. Using that line Pyrenean amphibians and reptiles can be divided into two groups: the thermophilous species and the cryophilous species. These groups overlap widely, although their normal distribution structure is composed of "island" populations where species forming a group live within the area of another. A better separation is obtained by using the March isotherm of 6°C; during that month thermophilous species reach the peak of their reproductive activity.

Relative humidity and other related factors (such as total rainfall, number of rainy days, potential evapotranspiration, and so on) are also important indicators for delimitation of the area of a species. These factors, however, do not relate so closely to altitude as does temperature. Humidity

increases not only with altitude, but also from east to west. To select a useful isohyet to discriminate between xerophilous and hygrophilous species, therefore, is difficult. Perhaps the best approximation for that purpose is the use of the March isohyet of 80 mm in the eastern half of Pyrenees and of 100 mm in the western half. Both lines clearly mark the two corridors that allow the hygrophilous European species to pass into Spain, and the xerophilous Mediterranean species to pass to France.

The location of the Pyrenees, as noted above, is responsible for some interesting features, and perhaps one of greatest biogeographical importance is climate variability. As in other mountain ranges, the windward side is rainy, while the leeward side, especially if far from the sea, has a continental climate. Several papers discuss the biogeographic consequences of Pyrenean continentality; that of Montserrat (1981) is the most significant one. It discusses many kinds of continentality that act upon plants and indicates the complex effect on plant communities. Here we are not able to provide a detailed treatment, and we consider all different classes of continentality (macroclimatic, oroclimatic, edaphic, geologic, and so on) under a single heading.

The main environmental factor useful to express conti-

mentality is thermic oscillation, measured as the difference of the mean maxima and the mean minima for every month. The isopleths of monthly maps of these differences (Font, 1983) depict the yearly evolution of continentality. The winter development of a continental nucleus in the Ebro valley extends to Ribagorza. During the year other Prepyrenean areas may acquire continental features, although Ribagorza (near the center of the southern half of the Pyrenees) is always the most continental one.

Distribution of rainfall throughout the year is another useful measure of continentality. Fillat (1983) has shown that in the Spanish Pyrenees continentality is linked with a summer rainfall maximum. This criterion allows delimitation of a continental area that coincides with the distribution of several Prepyrenean plants of steppe origin, such as *Artemisia alba*, *Nepeta latifolia*, *Adonis vernalis*, and *Odontites luteus*.

While these and other plants are good indicators of continentality, amphibians and reptiles are not very useful for this purpose. Some species, such as *Bufo bufo*, *Alytes obstetricans*,

and *Psammotromus algirus*, are common in continental areas but this is because of their general tolerance to variable environmental factors. In addition, they are also common near the sea. Euryoic species, of course, are well adapted to thermic oscillations. To obtain a good measure of the thermal tolerance of a species, its altitudinal range would be best suffice: species with a restricted altitudinal range would be stenothermic, the others eurythermic. Unfortunately, altitudinal range is correlated with the mean altitude of a species. The high mountain species can be found also in cold places of low altitude, while species from the plains have less opportunity to survive in mountains.

If we consider only lowland species, then it is not difficult to point out those with wide altitudinal ranges: *Bufo calamita*, *Bufo bufo*, *Alytes obstetricans*, *Coronella girondica*, and *Lacerta lepida*; all of them are, of course, thermophilous species, with some resistance to cold. Herpetocenoses made only by these species, or by these and other lowland forms (*Pelodytes punctatus*, *Psammotromus algirus*) often coincide with the ranges of continental plant communities.

CONCLUSIONS

The Pyrenees offer much interest for biogeographic research. The complex structure and history of the area, together with its relatively small size, offer the possibility of many significant findings when studied in depth. Very few mountain chains in the northern hemisphere (Sierra Nevada of California, Cascaus, Taurus) have so many different landscapes and perhaps no other has such a great variety for its size as the Pyrenees. This is the main conclu-

sion of our study. Biogeographic research in the Pyrenees, both from a historic viewpoint and from a comparative one, is worthy of much more extensive effort than has been accomplished so far. But first we need an objective basis for such research. The geographic distribution of Pyrenean species must be known in detail and paleoclimatic features must be ascertained from the results of many palynologic and sedimentologic studies still waiting to be undertaken.

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