

for Janes Moller. Success in the Guajira! *Mike Adams*

THE MONTANE FAUNA OF THE SIERRA NEVADA DE SANTA MARTA:

A THEORY OF ITS ORIGINS AND HISTORY.

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INTRODUCTION

Colombia, a country of great ecological diversity and richness, has on its Caribbean coast one of the most interesting regions on earth - the Sierra Nevada de Santa Marta. Because of its inaccessibility - there are no macadamized roads within it - this mountain range has received little attention. Barely more than a handful of scientists have made serious studies in it. Much of the literature on the region is misleading, from exaggerated portraits of its unhealthy climate, myriads of sandflies and scarcity of animal life (Wollaston 1925), to assertions that only one valley in the entire range is forested (Simons 1879). The Colombian Minister in London remarked after the reading of Wollaston's (1925) paper to the Royal Geographical Society, that "compared with the Andes, the Sierra Nevada is a very small hill". The fact that the Sierra Nevada was uplifted in recent geological times (as mentioned by Vuilleumier 1971, who, by the way, refers to the "Sierra Nevada de Santa Marta, Venezuela"!!) has misled other scientists into suggesting that its faunal history began only recently (e.g. Howden & Campbell, in press). Other more minor errors have included the statement that its highest summit is Pico Simón Bolívar (Hunsaker 1972). Before going on to discuss our theories concerning the origins and history of the montane fauna of the Sierra Nevada, we take this opportunity of putting some of the facts straight.

Firstly, the highest summit in the Sierra Nevada, Pico Cristóbal Colón (5775 m.), is the highest point between the Canadian Yukon and Ecuador. No other Colombian mountain is so high. Indeed, the range is the highest coastal mountain massif on earth (Cabot 1939).

Secondly, a very large proportion of its slopes are clothed in forest. In the north and west, there are large areas of unbroken forest from the foot of the mountains to the tree-line, covering a range of more than 3000 m. In the south-east and east, conditions are drier and forest is largely confined to moist valley-bottoms and sheltered hollows; but even there continuous cloudforest occurs in many places above 1700 m. The dry forests of the foothills (except in the north) are semi-deciduous, and abundance of animal life varies with the seasons.

Although it is true that the Sierra Nevada has an impoverished fauna (in terms of numbers of species), as a result of the combination of its geological and climatic history and its insular character, this fact has been exaggerated by taxonomists examining poor collections. For example, Godman & Salvin (1880) were disappointed with the low total of 80 species of butterflies collected by Simons, but failed to realise that Simons was more a surveyor than a collector; he had, in fact, ample opportunity for collecting 500 species. It is probable that there is little difference between population densities in the Sierra Nevada and the Colombian Andes.

In contrast to the relatively low numbers of species in the Sierra Nevada, the proportion of endemics among them is probably higher than in any other comparable area in the New World. Thirty-two out of the total of 104 bird species belonging to the life-zones above 1350 m. are endemic (31%) (Todd & Carricker 1922). Thirty-five of the 115 montane butterfly species obtained by one of us (M.J.Adams) are endemic (also 31%). Thirty of 73 mammals known to Allen (1904) were peculiar to the range (41%). The relationship between the area of the Sierra Nevada and its endemicity is astonishing: the world-famous table-top mountains of southern Venezuela have 29 endemics among the 96 resident subtropical bird species (Mayr & Phelps 1967), an endemicity very similar to that in the Sierra Nevada (30%); but the total area of the subtropical zone (above 1500 m.) in these mountains is more than twice as great as the combined totals of the subtropical, temperate and páramo zones in the Sierra Nevada (10,000 compared to 4,300 sq. km.).

The faunal impoverishment of the Sierra Nevada cannot be ascribed to lack of suitable habitats, although habitat size is of course restricted because of the small area of the range. Adams (1973) has split the range into eight distinct ecological zones, one of which (the semi-deciduous foothills forest mentioned above) does not occur in the Sierra de Perijá. Below 1000 m., four zones are recognised, together covering an area of about 7800 sq. km.; they include the surrounding plains, either arid or supporting tropical rainforest; the peculiar isolated region of tropical rainforest in the north; and

the dry forests of the rest of the foothills, continuous in the west and south, and mainly confined to valley-bottoms in the east and south-east. Between 1000 and 1800 m. are the two montane rainforest zones, that in the south-east being confined to valley-bottoms, covering about 2700 sq.km. Cloudforest occurs from 1500 m. up to the tree-line at 3000 - 3200 m. right around the range, occupying an area of 2200 sq.km.; and the páramo zone covers just over 1300 sq.km. Todd & Carriker's (1922) zones are based on those given by Chapman (1917) for the Colombian Andes, and are altitudinal only: tropical (0 - 1550 m.), subtropical (1550 - 2700 m.), temperate (2700 - 3300 m.), and páramo (3300 - 4500 m.). An overall survey of plant communities in the range is required to establish more exactly the extent of its life-zones.

The Sierra Nevada de Santa Marta is truly a taxonomists' paradise, but its interest is much more far-ranging than that. It has the prerequisites for a multi-disciplinary approach to its biology: its well-defined borders and the small sizes of its ecological zones mean that the results of all work done within it, whether by geologists, glaciologists, palaeontologists, botanists, zoologists, evolutionary biologists, ecologists or biogeographers, must overlap to a large extent. This, in turn, means that with a relatively small degree of effort and cooperation between scientists in these different fields, its flora and fauna could become the best-known and, more importantly, the best-understood in the neotropics.

In this paper, we collate the evidence accumulated independently in many fields to give an overall picture of one aspect of the biology of the Sierra Nevada: the origins and subsequent history of its montane fauna. Our theories were formed during two three-month visits to the range, in 1971 and 1972, on which we obtained 580 species of butterflies, and during the biogeographical analysis we carried out at the British Museum (Natural History) in London on certain sections of this collection.

We sincerely hope that the ideas put forward here may stimulate work in the Sierra Nevada on as many groups of animals and plants as

possible. Not only is such work necessary for a fuller understanding of the biology of this extraordinary region, but also a greater amount of information on the range is required before detailed plans for its conservation can be made and converted into action. That it deserves to be conserved, and to be conserved quickly, there can be no doubt. Destruction of its unique forests, with their unique fauna, would be a loss not only to Colombia, but to the world of science.

GEOLOGICAL HISTORY OF THE REGION

Tertiary

The Sierra Nevada de Santa Marta has a Precambrian metamorphic core, at least 1300 million years old. Bounded to the west by the Santa Marta - Bucaramanga fault, to the north by the Oca fault, and the south-east by an inferred Cesar lineament, it has always behaved as an independent rigid block (Tschanz *et al* 1974). Early orogenies took place in the Precambrian and Palaeozoic; and volcanic activity in the Mesozoic, ceasing in the early Cretaceous, forced igneous rocks through the core to give rise to batholiths and parallel dyke intrusions. Strong erosion in the Cretaceous weakened the relief of the massif, but it already stood so high that the seas never covered it, leaving calcareous deposits only in its foothills (Gansser 1955).

During the Tertiary, the period of the Andean foldings, the Sierra Nevada underwent little vertical movement. It rose to its present height during the Pleistocene, and there is evidence that the process ended only 30-50,000 years ago (see below).

The topography of the land surrounding the massif has experienced very large changes since the end of the Mesozoic. ^(see Fig 1) It is only since the end of the Pliocene that the Sierra Nevada has been as isolated from mountainous regions to its east and south as it is today. There is a strong possibility that the Cordillera Central (first uplifted before the Cordilleras Occidental and Oriental, in the Mesozoic) extended northwards to the region of Santa Marta, and beyond through the Guajira peninsula, perhaps as far as Aruba in the Dutch Antilles; since the Oligocene the regions of this system north and north-east of El Banco have not been affected by Andean tectonic forces (Alvarez 1971).

The Venezuelan Cordillera de la Costa is made up largely of a Cretaceous batholith, which has slid southwards under the influence of gravity, and so steadily reduced the height of the range (Bell 1971). The islands off the north coast of Venezuela, from Curacao eastwards to Margarita and Trinidad, are all probably parts of this system, which may

have been topographically connected to the Cordillera Central/Sierra Nevada/Guajira system to the west, and to the Lesser Antillean island arc northwards from its easternmost point.

Thus there may have been a nearly continuous chain of mountains, in the Tertiary, extending from the Central Andes to a north coastal range including the Sierra Nevada and the Cordillera de la Costa, thence up the Lesser Antilles, and even perhaps as far as Central America via the Greater Antilles.

Topographically, the Venezuelan Cordillera de Mérida is connected in the north-east to the Cordillera de la Costa, and in the south-west to the Colombian Cordillera Oriental. De Cizancourt (1933) suggested a very plausible theory to explain the apparent "splitting" of the Eastern Andes into the Perijá and Mérida chains. His belief was that the Mérida chain already existed by the late Tertiary, when the Eastern Andes of Ecuador and Colombia were folded. The folding took place "en echelon" from the south-west, and meeting with the obstacles of the Cordillera de Mérida and a hypothetical "median mass" in what is now the Maracaibo basin, it was forced to change direction to the north. It therefore seems likely that when the Mérida chain was uplifted at some time in the Tertiary, it became connected only at its north-eastern end, to the Caribbean chain.

Pleistocene

The folding of the Cordillera Oriental was completed at the Plio-Pleistocene border, at about the same time as large-scale subsidence took place to the south and east of the Sierra Nevada, isolating it from the rest of the Caribbean chain (itself already fragmented by that time) and from the Cordillera Central. Geological evidence in its own is not adequate for explaining the order of these two events, nor the period of time that elapsed between them. But there is ample ~~pxxxmf~~ biogeographical evidence to suggest that the subsidence took place after the meeting of the Cordilleras Oriental and de Mérida (see below).

It is no accident that in spite of an "en echelon" northwards folding in the Pliocene of the Sierra de Perijá, its northern regions are higher and steeper than its central and southern parts. North of Jurispicciones (3850 m.), the range extends for 200 km. before again reaching 3000 m., but opposite the Sierra Nevada it contains several peaks above that altitude, and the western slopes are very steep and not at all indicative of an origin by folding. Krause (1971) believes that subduction of the complex Caribbean Plate under the coast of Colombia was responsible for the most recent orogeny of both the Sierra Nevada and the northern Sierra de Perijá. It was Gansser (1955) who first suggested that this uplift took place in the Pleistocene. Both he and Burgl (1961) assume that the uplifts of the Sierra Nevada and the Colombian Eastern Andes were simultaneous. Finding evidence for a Pleistocene orogeny in the Nevada, Gansser suggested that the Andes rose at the same time; while Burgl, proposing that the Andean orogeny had been completed at the Plio-Pleistocene border, tried to explain away the evidence of Gansser (1955) and Raasveldt (1957) for the Nevada. In fact, since the pressures exerted on the Andes and the Sierra Nevada have been independent since the Oligocene (see above), a simultaneous uplifting of both would be purely coincidental.

From glaciological studies, Gansser (1955) and Raasveldt (1957) independently showed that of the three levels of glacial deposits in the Nevada, the highest represents a minor temperature drop in the Holocene, and the others represent two temperature minima in the Wurm ice age. There are no remnants of any earlier glaciations. Burgl's (1961) attempt to correlate the lower two levels with the Riss I and the Wurm breaks down because van der Hammen & Gonzalez (1960) find three Wurm levels in the Andes at Boyacá. Where are the three levels in the Sierra Nevada? It is more reasonable to suppose that the moraines down to 3300 m. represent the late Wurm extension, and the diffuse remains at 2800 m. the main Wurm, which was colder (Emiliani 1961). Before the main Wurm, the massif was still being uplifted, and if the early Wurm or Riss glaciations left any deposits, these would have been obliterated as they rose in altitude by the later glacial extensions.

A date can therefore be set for the completion of the Sierra Nevada's uplift - between the early and main Wurm glacial extensions, that is (according to Emiliani 1961) 30-50,000 years ago. In the north and west of the range, the topography is very youthful up to almost 3000 m., which suggests that it stood at least 2775 m. high before this uplift. We cannot know when the orogeny began, but at a rate of uplift of 10 m. per 1000 years (as in British Holocene mountain-building), we can guess that it did so about 350,000 years ago, more than one and a half million years after the isolation of the range. The upheaval of the northern part of the Sierra de Perijá was probably synchronous, and of the same extent. Since it now stands at a maximum height of 3750 m., it may have been only 750 m. high in its highest parts, and little above sea-level elsewhere.

This means that the Sierra Nevada was completely isolated from other mountains above 1000 m. in height from the time of the subsidence of the adjoining high land, about two million years ago, until the Sierra de Perijá reached that altitude late in the Pleistocene. The nearest high mountains were in the Cordillera Central (225 km. away) and the Cordillera de Mérida (275 km. away).

THE ORIGINS OF THE MONTANE FAUNA

The taxonomic status of the endemic fauna of an isolated region can give an indication of the relative ages of the elements. Mayr & Phelps (1967) surmised that, because there is a continuous spectrum of bird taxa in the southern Venezuelan (Pantepui) mountains, from endemic superspecies ~~through~~^{to} endemic subspecies of non-endemic species and the resident non-endemics, birds have been immigrating into these mountains continuously. The endemic species and superspecies are the oldest inhabitants, and the more recent invaders have at most only diverged to the subspecific level. In spite of their great distance from the nearest regions supporting subtropical forests (500 km.), the Pantepui highlands have been receiving a virtually steady stream of bird immigrants, and so the origin of their fauna is a composite one.

Similar evidence from the bird fauna of the Sierra Nevada (from Todd & Carriker 1922) shows that it too has diversified origins. But birds, with their great powers of flight, are perhaps not the best biogeographical subjects. Concentration on the continuity of immigration into an area tempts one to overlook the fact that certain periods may have existed when immigration was particularly common; other, less dispersable, animal groups may have been able to colonise the region only during these periods.

We have made a special study of the butterflies in the Sierra Nevada belonging to the family Satyridae, ~~which~~ many of which are among the most sedentary and specialised species that we know of. It is mainly this study that has led us to formulate the theories elaborated in this paper. A great deal of further work is required, not only in the Satyridae and other butterflies, but in all groups of animals and plants in the Sierra Nevada and the neighbouring mountains.

Fifteen species of endemic Satyridae have so far been recorded from the Sierra Nevada. All of them are montane. At least 2 (perhaps 3) comprise 2 or 3 endemic subspecies. The list of known montane non-endemic species numbers 14. There are no endemic subspecies belonging to non-endemic species.

Comparison of the age spectra of the Sierra Nevadan Satyridae and the Pantepui birds demonstrates how large the gap is in the Satyridae, in the category endemic subspecies of non-endemic species:

	Sierra Nevada montane Satyridae	Pantepui birds
Endemic species	15	29
Non-endemic species - with endemic subspecies	0	55
- without endemic subspecies	14	12
	—	—
	29	96

Even allowing for subequal rates of evolution between genera and species-groups, this gap is good evidence that a period existed when the Sierra Nevada was altogether cut off from successful immigration of Satyridae, and that the family's entry into the region took place during two very widely separated periods. Immigrants of the first "invasion" are now represented only by endemic species; those of the second "invasion" have none of them yet evolved to the subspecific level, and so must be of very recent origin. However, in the references below to "Eastern Andean invasions" it must be remembered that the Sierra Nevada was never totally isolated from all groups of animals and plants, and that attempts at colonisation probably took place continuously, but at a much lower rate, during the intervening span of time. (There are 22 endemic subspecies of non-endemic bird species in the Sierra Nevada (Todd & Carriker 1922) - see Table).

Not all the endemic species in the range are necessarily derived from the first invasion. There is some evidence that, as one would expect, it supported a montane fauna before this invasion.

Caribbean Chain

The majority of montane butterfly groups in Latin America are derived from Peruvian and Bolivian centres of diversification, and are best represented in those countries. Any superspecies, particularly one that contains weak-flying, highly sedentary members, which is restricted to northern South America and/or Central America, or which is concentrated there with other members not occurring further south than Ecuador, may be assumed to have originated in the mountains of the Caribbean chain. Of the satyrid fauna of the Sierra Nevada, three superspecies of Lymanopoda and the genus Sabatoga belong in this category, as does one group of the genus Actinote (Nymphalidae: Acraeinae). Others probably remain to be found, and many have disappeared. Todd & Carriker (1922) cite five examples of endemic bird species which have no known relatives outside the Sierra Nevada, and suggest that they may have evolved in the region when the Caribbean chain existed (in the Tertiary). They correctly point out that this chain already stood before the Tertiary diversification of birds (and butterflies), and the first montane species must have derived from lowland forms, subpopulations of which became cut off at higher altitudes, and speciated.

Colombian Cordillera Central

The Tertiary connection with the Cordillera Central must have provided access for Central Andean species to enter the Sierra Nevada. Many groups of animals today have distinct representatives in the Central (and Western) Andes and the Eastern Andes (e.g. the Aulacorhynchus sulcatus species-groups of toucans cited by Haffer 1970). Many satyrid butterfly superspecies are restricted to the Central Andes, and at least two of these have members in the Sierra Nevada - Stereomnia, and a section of Catargynnis. Such a distribution strongly suggests a Central Andean origin for these Sierra Nevadan montane endemics.

First Eastern Andean Invasion

The remainder of the endemic Satyridae in the Sierra Nevada have relatives in the Eastern Andes, between Venezuela and Colombia, and Argentina; they belong to montane genera best represented in Perú and Bolivia. The avifauna shows a similar picture. If these endemics are of Eastern Andean origin, it would seem at first sight that the Sierra de Perijá must have been the source area (the 1000-metre contours in Perijá and the Nevada are only 30 km. apart at their closest point). But we have already shown that the Sierra de Perijá reached its present altitude only 30-50,000 years ago. And if it were the source area, why has there been a long period of much-reduced immigration? Why indeed are there any endemics at all in the Sierra Nevada?

Todd & Carriker's (1922) theory of the origins of the subtropical and temperate avifaunas of the Sierra Nevada appears to us to be basically correct. Their comparative analysis of the bird faunas demonstrated that the fauna of the Sierra Nevada has greater affinities with that of the Venezuelan Andes than with that of the Colombian Cordillera Oriental (see Table). They therefore suggested that the majority of the montane endemics in the Nevada today are derived from progenitors which managed to enter the range from the Cordillera Oriental, via the Venezuelan Andes and the coastal connection between the Cordillera de la Costa and the Sierra Nevada. That there are so many endemics of obvious Andean origins testifies to the fact that the subsidence of this coastal connection must have taken place after the junction of the Cordillera Oriental and the Cordillera de Mérida. Subsidence occurred at the end of the Pliocene, so these endemics must have been isolated in the Sierra Nevada for the whole of the Pleistocene, that is for about two million years.

The only criticisms of their theory are:

1. They believed that the Mérida range rose with the Cordillera Oriental; but, as we have shown, it most probably already existed at the time of the folding of the latter range. This means that it must have already supported its own flora and fauna, derived largely from the Caribbean chain to which it became attached at its north-eastern end. Indeed,

speciation almost certainly took place in it, as a result of the wealth of new, unoccupied habitats made available to the immigrating Caribbean animals and plants. It is no coincidence that many of the inferred Caribbean species-groups have relict species in the Cordillera de Mérida as well as in the Sierra Nevada, ^{nor} ~~and~~ that a new genus of the tribe Lymanopodini has recently been found there (R.I.Vane-Wright, pers. comm.), a tribe that seems to have several Caribbean superspecies.

2. They postulated that in order to explain the presence in the Sierra Nevada of páramo endemics, the coastal connecting range must have stood 3500 m. high. It is extremely unlikely that this was the case, and during the period of the first invasion the Sierra Nevada itself was probably too low to support páramo. We show below that the páramo fauna is probably of more recent origin.

Second Eastern Andean Invasion

During the Pleistocene, there have been four main glacial periods, beginning (according to Emiliani 1961) about 300,000 years ago. The Sierra Nevada and the northern Sierra de Perijá may have begun their recent uplifts about 350,000 years ago. Assuming an uplift of 5000 m. at a steady rate of 10 m. every 1000 years, the two ranges would have stood about 3525 and 1500 m. at the height of the Gunz glaciation, 4475 and 2450 m. at the height of the Mindel, 5175 and 3150 m. at the Riss temperature minimum, and 5725 and 3700 m. at the early Wurm minimum, respectively. By the main Wurm minimum, about 15,000 years ago, the ranges had reached their present heights of 5775 and 3750 m.

As the Sierra de Perijá rose in altitude, so did the diversity of its montane fauna (spreading northwards from the southern parts of the Cordillera Oriental), and so did the rate of immigration of montane species into the Sierra Nevada. But immigration depended not only on the species and population diversities in Perijá, but also on the nature of the intervening land, its height and its vegetation.

Today, a ridge of relatively high land separates the two mountain ranges, between the Ranchería and Cesar valleys. At its lowest point, this ridge reaches an altitude of 350 m. It is made up largely of Pleistocene alluvial sediments (Gansser 1955), and lies directly across the path of the north-east tradewinds, which here are dry and hot because of their passage over the Guajira peninsula. It seems likely, therefore, that the ridge was higher when the two ranges completed their uplifts, and that it has undergone severe erosion since that time.

Van der Hammen & Gonzalez (1960) have shown that the glacial periods of the Pleistocene corresponded, in northern South America, with periods of high humidity and rainfall, and that the interglacial periods corresponded with drier conditions. At the same time, of course, the glaciations brought down mean temperatures, especially at the higher elevations; temperatures at sea-level may have been 3°C lower than today's, while those at 2-3000 m. were about 8°C lower. If the connecting ridge stood 600 m. high during the Wurm glaciation, conditions on it would have been similar to those at 1000 m. today, and the higher rainfall probably would have allowed it to support rainforest.

Although some Andean montane species may have entered the Sierra Nevada during earlier glaciations (mainly through chance dispersal by wind), and evolved to the specific level since (see below), the montane non-endemic species most probably crossed the forested connecting ridge during the main and/or late Wurm glacial periods, either by simple spread, or by chance dispersal in freak storms. A comparison of the montane satyrid faunas of the two ranges would almost certainly show that many species in Perijá failed to reach the Sierra Nevada (or failed to settle in it). Simons found 12 species of tropical Satyridae at Manaure (840 m. in the Sierra de Perijá) in the 1870's (Godman & Salvin 1880), of which only five occurred in the Sierra Nevada. Not one of the other seven appears to have succeeded in crossing the 35-km. expanse of dry, mostly deforested, land between Manaure and the Sierra Nevada in the last 100 years. Since the last glacial extension, the Nevada has become steadily more isolated once again, as the land between it and Perijá has been weathered down and its rainforest replaced by dry forest and open land.

Because the species of the second Eastern Andean invasion entered the Sierra Nevada so recently (about 15,000 years ago), not one of them (at least in the Satyridae) has even diverged to form a distinct endemic subspecies. Maybe closer examination will show slight structural differences between populations of these species in the Sierra Nevada and the Sierra de Perijá.

Table

	<u>Subtropical</u>	<u>Temperate</u>	<u>Páramo</u>	<u>Total</u>
Common to all three ranges	19	5	2	26
Identical with Venezuelan form only	13	0	1	14
Identical with Cord. Oriental form only	4	4	0	8
Distinct species - no close relatives	8	0	1	9
Distinct species - relatives in other two ranges	9	7	1	17
- relatives in Venezuela only	2	0	0	2
- relatives in Cord. Oriental only	2	4	0	6
Distinct subspecies - relatives in other two ranges	12	1	1	14
- relatives in Venezuela only	5	0	0	5
- relative in Cord. Oriental only	1	1	1	3
	—	—	—	—
	75	22	7	104

The representative distribution of the montane avifauna of the Sierra Nevada, with respect to those of the Venezuelan Andes and the Colombian Cordillera Oriental, compiled from Todd & Carriker 1922. (In those cases where the Sierra Nevada has a distinct form with relatives in both the other ranges, the Sierra Nevada form is more closely related with the Venezuelan than the Colombian form)

THE HISTORY OF THE MONTANE FAUNA

First Eastern Andean Invasion

It is difficult to imagine the ecology of the Sierra Nevada two million years ago. Mean temperatures were similar to today's (Emiliani 1961), but the height and topography of the massif were very different. Before the invasion of Eastern Andean species, the flora and fauna would have comprised a mixture of species of Caribbean and Central Andean origins. It is possible that by that time, continued immigration of Central Andean species had already severely reduced the original Caribbean stock.

The numbers of Andean montane species that colonised the range depended on the ability to reach it - for the high montane species, this may have involved chance dispersal from mountain to mountain as well as simple spread where habitats were suitable - and the ability to survive in it. Survival depended on the presence of suitable habitats for breeding and feeding, and the ability to compete successfully with species favouring similar habitats. So long as the populations in the Sierra Nevada were reinforced by continuing immigration from the Eastern Andes, competition would be more likely to lead to niche partitioning of closely-related species than to extinction of one or another of them. But as soon as the connections with the Andes were broken, the range became an island, and island effects came to play.

Isolation and Island Effects

The isolation of the Sierra Nevada in the late Pliocene or at the Plio-Pleistocene border was analogous to the formation of an oceanic island by the subsidence of the land or the rising of the sea-level between it and the mainland. The ecological and evolutionary effects of insularity are discussed by MacArthur & Wilson (1967) and MacArthur (1972). The history of the montane fauna of the Sierra Nevada has been

strongly influenced by these effects.

Obviously a mountain range is not altogether insular. Its foothills and surrounding plains are not nearly so isolated as its higher slopes. In the case of the Sierra Nevada, its south-eastern and eastern foothills are in direct contact with ecologically similar land eastwards into Venezuela, and the forests of its lower slopes in the west and south are connected with the whole Cauca/Magdalena complex of tropical rainforest. Only the arid scrub around Santa Marta, and the tropical rainforests in the north, are ecologically isolated today (see Todd & Carriker 1922 for a discussion of the origins of the lowland bird fauna).

The higher up the mountain, the less will the composition of the fauna be affected by species of wide altitudinal distributions, which are not isolated in the region because of their ability to spread through the lowlands. Fig. 1 shows how the proportion of endemic species of Satyridae (subfamily Satyrinae) at each 100-metre level rises with increasing altitude. It can be assumed that the montane fauna of the Sierra Nevada was sufficiently insular to have been influenced by effects usually associated with oceanic islands.

Immigration

Vuilleumier (1970) surveyed the bird faunas of the páramo "islands" in northern South America, and found that they supported more species than their size and distance from the Ecuadorean "source area" merited, according to calculations based on oceanic island faunas. He pointed out that immigration into these regions of páramo is higher than into comparable oceanic islands, because birds can rest and feed in the intervening lowlands, and therefore have a greater chance of travelling further. Species density on an island is determined by a balance between immigration and extinction, and always tends towards an equilibrium density, which is lower than in similar areas of mainland. This density is expected to be higher on continental than on oceanic islands because of greater immigration and only a negligible reduction in extinction.

Extinction

An island cut off from the mainland soon loses many of its species, some of which never recolonise it (see the example of the Archipiélago de las Perlas south of Panamá, in MacArthur 1972). The chance of extinction is greater on an island than on the mainland, particularly for populations of few individuals. MacArthur & Wilson (1967) calculate that a population of 100 individuals, with a per capita birth rate of 2 per year, and a death rate of 1.82 per year, has a survival expectancy of only 860 years. This effect is due partly to chance fluctuations in numbers in the absence of replacement by immigration, and partly to the much greater influence of competition on islands. And it is augmented by the fact that small-island populations tend to exist at smaller densities than their large-island and mainland counterparts, because of their greater intrinsic inefficiency (Diamond 1970b).

Todd & Carriker (1922) refer to the depauperate nature of the bird fauna of the Sierra Nevada above 1350 m. While 318 montane species had been recorded from the Colombian Cordillera Oriental, the list from the Sierra Nevada numbered only 104. Although this low total is surely due in part to the failure of many species to ever enter the Sierra Nevada, extinction must have also played its part.

Competition

Competition between the species from the first Andean invasion was probably partly responsible for the impoverishment of the fauna during its isolation. The greater richness of the bird fauna of the Cordillera Oriental is contributed to not so much by a greater number of genera, but rather by a greater number of species within each genus (that is, congeners). Below 1350 m. in the Sierra Nevada, there are 140 congeners, making up 41% of the total tropical bird fauna; but above 1350 m., only 14 congeners (7 pairs) exist, merely 14% of the total montane fauna (above 2700 m., there are no congeners at all). In only one of these 7 pairs are both members endemic; in the other cases it is probable that either one (3 cases) or both (3 cases) of the congeners entered with the second Andean invasion, and have not yet

diverged from the parent populations. Of the 15 endemic species of Satyridae in the Sierra Nevada, only one species-group is represented by more than one member.

If one assumes that greater numbers of congeners entered the range with the first invasion, then the intrageneric impoverishment must have been caused by competition between closely-related species, and extinction of all but the most successful within each genus or species-group.

Restriction of habitat during Pleistocene climatic fluctuations

Another cause of extinction of species may have been the changes in the patterns of vegetation, and its composition, during the glacial and interglacial periods of the latter part of the Pleistocene.

The decrease of mean temperatures in the glacial periods was greater with increasing altitude, so that the altitudinal extent~~um~~ of each ecological zone was reduced. The tree-line descended to 1700 m. in the Riss glaciation (at least in the Sabana de Bogotá - van der Hammen & Gonzalez 1960). The area of forest must have been severely cut back, by about 2000 sq.km. (or by 15% of the total), in the Sierra Nevada. The resultant decrease in population densities may have led to extinctions.

The effects of the warm and dry interglacial periods were probably more disastrous. The presence of a dry, semi-deciduous forest in the western foothills of the Sierra Nevada, where rainfall is the highest in the region (see Adams 1973), is good evidence that such forest was more widespread previously, and is a relic of recent much drier conditions. This forest today attains altitudes of almost 1000 m. on exposed ridges, and may have extended on ridges to the tree-line in the interglacials. At the montane elevations, rainforest would have been restricted to the moist valley-bottoms, separated from one another by the ridges, which in the most part of the range are very steep and long, radiating outwards and downwards from the tree-line. At the lower altitudes, rainforest would most probably have been altogether absent.

Those species of animals unable to cross from one region of forest to the next were faced with a suddenly much stronger chance of extinction, because population numbers were greatly reduced, and competition became fiercer. Decrease in niche space may have meant that even distantly related species occupying the same habitat came into conflict because of niche overlap. As a result, therefore, of the peculiar topography of the Sierra Nevada, with its absence of broad montane valleys and flood-plains, more of the original early Pleistocene fauna became extinct.

Another result of the fragmentation of montane forest during the interglacials was autochthonous subspeciation and perhaps even full speciation among the endemic fauna (see below).

The replacement of tropical rainforest with dry, open forest during the dry interglacials must have caused widespread extinctions of tropical species restricted to moist forest. The nearest pockets of lowland rainforest were probably the "Nechí" and "Catatumbo" refuges, immediately north of the Cordilleras Central and Occidental, and in the region between the Sierra de Perijá and the Cordillera de Mérida, respectively (Haffer 1969). Some of the Sierra Nevada tropical endemics may have reached these refuges as the rainforest retracted, and may later have recolonised the range as non-endemics. It is interesting in this context that there are no tropical endemics among the Satyridae of the Sierra Nevada; Morpho rhodopteron Godman & Salvin descends at least to 700 m., but is most abundant at 1500 m., and of the subfamily Satyrinae, Lymanopoda caeruleata Godman & Salvin descends the lowest, to 1100 m. The other 14 endemics are found only from 1300 m. upwards.

Second Eastern Andean Invasion

The invasion of Eastern Andean montane species from the Sierra de Perijá into the Sierra Nevada during the Wurm glacial period increased the species diversity in the latter range, but most probably further reduced the stock of original endemics.

The theory that species from diversified environments are compet-

itively superior to those from smaller, restricted environments has been proposed, and substantiated, several times (see Mayr 1963: p.75). A simple explanation is that evolution for maximum fitness in individuals of a species which exist in a variety of different habitats imparts adaptability to the species' gene pool. In those cases when a species from a large area colonises a new smaller area already occupied by a congener, and both species must undergo niche displacements in order to coexist, the newcomer's greater plasticity gives it the greater chance of survival.

During the second invasion of the Sierra Nevada, it is likely that several closely-related species-pairs came into contact for the first time. Where these pairs had similar ecological requirements, the newcomer species was at an advantage. Just how relatively less adaptable were the residents, we cannot know, but we can suggest that the profound effects of the climatic fluctuations discussed above may have added a large amount of variability into their gene pools. Given some degree of plasticity in the residents, and a considerable amount of empty niche space into which they and the newcomers could shift, the destructive effect of the second Eastern Andean invasion on the endemic stock was probably less than might be expected;

Now, just as species of Caribbean descent doubtless entered the Cordillera de Mérida when it was uplifted and came into close contact with the coast range during the Tertiary, should not endemic species in the Sierra Nevada have crossed into the Sierra de Perijá at the time of the second invasion? Actually there is a major difference between these two processes: in the first, the newly-formed mountain chain was poorly represented with animal life, and invading species from the coast range met with little competition or predation. In the latter case, the Sierra de Perijá was certainly rich in species - probably richer than the Sierra Nevada. Niche space within it was restricted. Secondly, the zone of physical contact stood higher above sea-level in the former case, allowing a greater ease of spread by montane forms. Thirdly, a result of adaptation to insular life by a newcomer from a richer environment is often loss of or reduction in its powers of dispersal (MacArthur & Wilson 1967).

The combination of these three factors make it likely that the second invasion was not counteracted by an equal spread of montane species in the opposite direction. Two cases of butterfly species that may have left the Sierra Nevada for the first time during the Wurm are Lymanopoda maso Godman and L. albifasciatus (Rober), both first described from the Sierra Nevada, and both now found down the Cordillera Oriental as far as Ecuador only.

Speciation and Subspeciation

Cut off from gene flow from the parent populations in the Andes, the Sierra Nevadan populations were able to evolve along their own lines, until they had diverged morphologically and reproductively to such an extent that taxonomists now rate them as distinct species.

We have so far been talking in terms of two widely-separated invasions into the Sierra Nevada, implying that all colonisation ceased between them. Now MacArthur (1972) writes: "the length of time it normally takes for a species to split and diverge sufficiently to be regarded as two species is a small, uncertain, number of thousands of years"; and Haffer (1969) proposes that the great diversity of Amazonian bird species is a result of large-scale speciation in forest refuges during the Pleistocene interglacials, the longest of which lasted about 80,000 years (Emiliani 1961). Haffer even postulated generic divergence during these periods. As the montane Sierra Nevada was isolated for about two million years, one should perhaps expect endemic genera and species-groups among its fauna, yet it is remarkable in many cases how little divergence has taken place between daughter populations in the Sierra Nevada and the Cordillera de Mérida.

If it were not for two lines of evidence, one might be led to suggest that the entire stock of first Andean invaders had perished, and that all the endemics are derived from much more recent immigrants.

1. The first line of evidence has already been discussed. It is the significant gap in the taxonomic spectrum of the Satyridae in the Sierra Nevada. The absence of endemic races of non-endemic species is taken to

show that a period existed prior to the second immigration of Andean species when colonisation of satyrids was so low that no immigrants succeeded in establishing themselves. Colonisation of bird species, however, appears to have continued between the two invasions, and 22 Andean species have endemic subspecies in the Sierra Nevada (Todd & Carricker 1922), and see Table). This difference no doubt reflects the greater powers of dispersal of birds.

2. Certain pairs of montane butterfly species in the Sierra Nevada and the Cordillera de Mérida are remarkably similar, have no close relatives in the Sierra de Perijá, and are slow-flying, sedentary, and ecologically restricted species. Dalla merida Evans (Hesperiidae) is conspecific in the two ranges, and absent from the Sierra de Perijá; Actinote naura Druce and an unnamed species from the Sierra Nevada are very similar, and the superspecies has no representative in Perijá. For perhaps the last 350,000 years, the latter range has been a substantial mountain chain lying directly between the other two ranges, and during its uplift it developed a diversity of habitats as great as in the others. If dispersal from Mérida during the Pleistocene is taken to account for these species' presence in the Sierra Nevada, how did they cross the Perijá range without colonising it too? And if they are such able dispersers, why have they not spread around via Cúcuta into the Sierra de Perijá? It is much more likely that their separate populations are relictives of parent populations distributed throughout the Caribbean coast range and the Cordillera de Mérida, and that they have been unable to spread or disperse any significant distance at all.

It seems to us, therefore, that species living at higher elevations, in an isolated region, speciate much more slowly than those occupying the tropical lowlands. The Amazonian birds probably diverged from one another more quickly at the beginning of each glacial period, when close relatives became sympatric and strong selection acted against hybridisation, ~~rather~~ than during the interglacials themselves. Such selection has only acted on some of the Sierra Nevada endemics since the second invasion, when close congeners came into contact with them for the first time.

There is very little evidence that adaptive radiation of the original endemics has taken place in the Sierra Nevada. This is hardly surprising, because of the compact nature of the massif and the strength of intrageneric competition. But the fragmentation of the montane forests in the interglacials did allow some divergence, particularly among the most sedentary species. At least three endemic species of Satyridae possess two or more distinct autochthonous subspecies within the range, even though there are now no ecological barriers between them at the altitudes at which they fly. One of them, Sabatoga nevada (Kruger), seems to contain three distinct races, in the north, west and south-east, all in the very uppermost forest around the tree-line. The others, Pedaliodes tyrrheus Godman & Salvin, and an unnamed species of Catargynnis, have at least two each, in the west and south-east. P. tyrrheus is more fully discussed below. These races doubtless evolved in separate pockets of forest during the interglacials and have failed to merge with one another since.

Full autochthonous speciation appears to have been rarer than subspeciation. Apart from the example of Pedaliodes tyrrheus and P. "cebolleta" elaborated below, the only other possible example among the Satyridae is given by Lymanopdda maso and L. albifasciatus. We believe that they were endemics until the Wurm, when they left the Sierra Nevada against the current of the second invasion. They are morphologically very similar, and fly in the same area of the range (in the north).

Ecological Displacements

When two or more closely-related species meet one another in the same habitat, niche overlap means immediate competition, and selection will favour those mutants which can cope successfully with an alteration in their niche requirements such that overlap is reduced. This niche displacement first occurs by force of circumstance, and later may become fixed in the gene pool of the species. In Hutchinson's (1965) terminology, the species' "fundamental niche" is altered to become its "realised niche" under competition.

Certain species in the Sierra de Perijá exist today without very closely-related competitors, while their entry into the Sierra Nevada has brought them into direct contact with close endemic congeners. The butterflies of the Sierra de Perijá are little known, and it would make a fascinating study to compare the niches realised by such species in the two ranges.

Two endemic satyrid species still survive in the presence of close allies derived from the second invasion in the Sierra Nevada. The first, Pedaliodes symmachus Godman & Salvin, belongs in the same species-group, and occupies the same habitats between the same range of altitudes, as P. manis Felder, a widespread Andean species. Presumably the two species have succeeded in partitioning their niche spaces so that as little overlap occurs as possible. P. symmachus is everywhere the commoner of the two, in the Nevada. We would not be surprised if manis were more abundant in the Sierra de Perijá, nor if it occupied a wider range of ~~nizquez~~ habitats.

The other example is more interesting: an unnamed species of Pronophila, "julianoi"; flies abundantly in many places between 1800 and 2700 m.; its Andean relative in the Sierra Nevada, P. thelebe Doubleday, occurs rather less commonly between 1400 and 2300 m. It seems that in the region of overlap (1800 - 2300 m.), the two species avoid competition (in the larval stage, where it has the greatest effect) by temporal separation. While both sexes of "julianoi" were flying at 2700 m. in early August 1972, only males flew at 2000 m., along with both sexes of thelebe; in late August 1971 at the same locality at 2000 m., both sexes of "julianoi" flew with only females of thelebe (see Fig.2). More detailed observation is required, but it seems that where they overlap, ~~xxxxxxxxxxxxxx~~ "julianoi" emerges later than it does above this zone, and thelebe has its main emergence before this time, so that the larvae do not reach maximum densities simultaneously.

The re-expansion of montane forest after each interglacial period also brought together very closely-related species, in those (probably few) cases where speciation had occurred in separate pockets of forest.

The only example of such autochthonous speciation that we know of (other than that of Lymanopoda maso and L. albifasciatus, mentioned above) involves Pedaliodes tyrrheus and an unnamed species of the same superspecies, "cebolleta". P. tyrrheus possesses two distinct races, typical tyrrheus in the south-east, and the unnamed "tairona" in the west. It is probable that the two species evolved in isolation during an early interglacial, and that the two subspecies of tyrrheus appeared in a more recent one.

P. "cebolleta" flies in the west in a very narrow range between 2900 and 3000 m., and tyrrheus "tairona" flies below it from 2200 to 2900 m. In the south-east, typical tyrrheus occurs right up to 3000 m., and there is no sign of "cebolleta". Perhaps "cebolleta" and tyrrheus diverged in the west and south-east, respectively; the two species spread with the expansion of forest, and tyrrheus was competitively superior, except in the very uppermost part of their range, where the other species was able to hold its own. P. "cebolleta" perhaps never managed to spread around into the south-east, but survived in the west through the later interglacial(s) during which tyrrheus split into two subspecies^(see Fig. 3). The facies of the two species are very similar, but their male genitalia are remarkably different, suggesting that when they came into contact, selection acted on the reproductive machinery to avoid hybridisation. They are now most probably sexually incompatible, as evidenced by our finding a male of tyrrheus "tairona" flying within a colony of "cebolleta" at 2900 m., and no traces of any hybrids. The fundamental niche of tyrrheus probably includes the range of altitudes now occupied by "cebolleta", but the competitive superiority of the latter species within that range forces the western race of tyrrheus to restrict its niche space.

Finally, the páramo fauna of the Sierra Nevada is of interest because, as already suggested, it is unlikely that the range was high enough at the time of the first Eastern Andean invasion to have supported true páramo species. Therefore the endemic species living above the tree-line must either have entered since the start of the Pleistocene uplift from Andean páramo, or shifted upwards from lower elevations.

Two of the seven páramo butterfly species known to us are probably descendants of the second invasion, and were already páramo species at that time. The first, an unnamed species of "Thecla" (Lycaenidae), closely resembles a páramo species from Perú, and as far as we know no similar forms occur in the intervening regions. One can only assume that the parent species spread northwards during the glacial periods when páramo was almost continuous from Perú to the Sierra de Perijá, and has since disappeared except in Perú and the Sierra Nevada, where the daughter populations have diverged slightly in appearance. The second species is Tatochila xamphodice Lucas (Pieridae), which is found also in other páramo regions in Colombia, and has probably a similar history to the thecline, except that it has apparently not diverged from the Andean pattern.

Two other species recorded from the páramo of the Sierra Nevada are often blown above the tree-line; but almost certainly breed only below it.

The remaining three are Nathalis iole Boisduval, an unnamed species of Tatochila (both Pieridae), and Pedaliodes oculata Kruger. The two latter species are endemic. N. iole's presence in the páramo is extremely interesting, as it is a widespread species at sea-level in northern Central America, the West Indies, and North America. It probably represents a relic population from a time when the species occurred in southern Central and northern South America (a glacial period?), which has survived in the Sierra Nevada by making an enormous altitudinal shift of 3000 m. Judged by its abundance, it is a highly successful páramo species. Explanation of the presence of the endemic Tatochila and Pedaliodes is not so easy; and one can only guess that the former ~~entered~~ entered during an early glacial period, by dispersal, and diverged from its parent (which was perhaps T. xamphodice) to the species level; when xamphodice entered with the second invasion, competition between them forced further divergence, particularly in the male genitalia, which are very distinct. (It would be interesting to compare the genitalia of Andean and Sierra Nevadan individuals of xamphodice, to see whether this species also was forced

to alter its reproductive niche). P. oculata belongs to a superspecies that, as far as we know,, has no other páramo representatives, suggesting that its presence above the tree-line is the result of an altitudinal shift, perhaps to avoid competition with other species of the genus. The páramo bird Troglodytes monticola may represent an analogous situation: according to Todd & Carriker (1922), its closest relatives outside the Sierra Nevada are T. sostitialis and T. solitarius, which are montane, but not páramo, species.

SUMMARY

Geological evidence suggests that the Sierra Nevada was at the western end of a chain of mountains, perhaps almost encircling the Caribbean Sea during the Tertiary, to which the Cordillera de Mérida became attached; and that there was also a mountainous connection between the Cordillera Central and the Sierra Nevada. The earliest fauna of the Sierra Nevada was of Central Andean and Caribbean origins, of which there are some remnants today.

The folding of the Cordillera Oriental at the end of the Tertiary allowed species from the main Peruvian and Bolivian centres of diversification to enter the Cordillera de Mérida, and from there some succeeded in reaching the Sierra Nevada. Soon afterwards, subsidence isolated the Nevada, which then stood almost 2800 m. high.

About 350,000 years ago, in the Pleistocene, the Sierra Nevada and the northern Sierra de Perijá (previously less than 1000 m. high) began to be uplifted by pressure from the subduction of the Caribbean Plate, and they reached their present heights 30-50,000 years ago. A second invasion of Eastern Andean species entered the Nevada from the Sierra de Perijá during the last glacial period.

The depauperate montane fauna of the Sierra Nevada is a result of island effects due to its isolation for about two million years. Immigration, particularly of sedentary species, was very low during this period, and extinction was high. The causes of extinction were competition between congeneric species, especially during the interglacial periods when montane forest was restricted to isolated valley-bottoms, and the replacement of lowland rainforest by a dry, semi-deciduous forest unsuitable to many species. The second Andean invasion further reduced the original stock of endemics because of the competitive superiority of the more adaptable invading species.

The high degree of endemism in the Sierra Nevada is ascribed to the long period during which the survivors of the first Andean invasion,

and the earlier inhabitants, were isolated from their parent populations. The great majority of the endemics have existed in the range for two million years, but a few evolved more recently by autochthonous speciation and subspeciation in the interglacial periods, and others have diverged since their arrival during the late Pleistocene glacial periods.

Niche partitioning between some closely-related pairs of endemic species, and of endemic and recently invaded species, has allowed co-existence, and a few forms have undergone niche shifts from lower altitudes into the páramo, whose fauna is late Pleistocene in origin.

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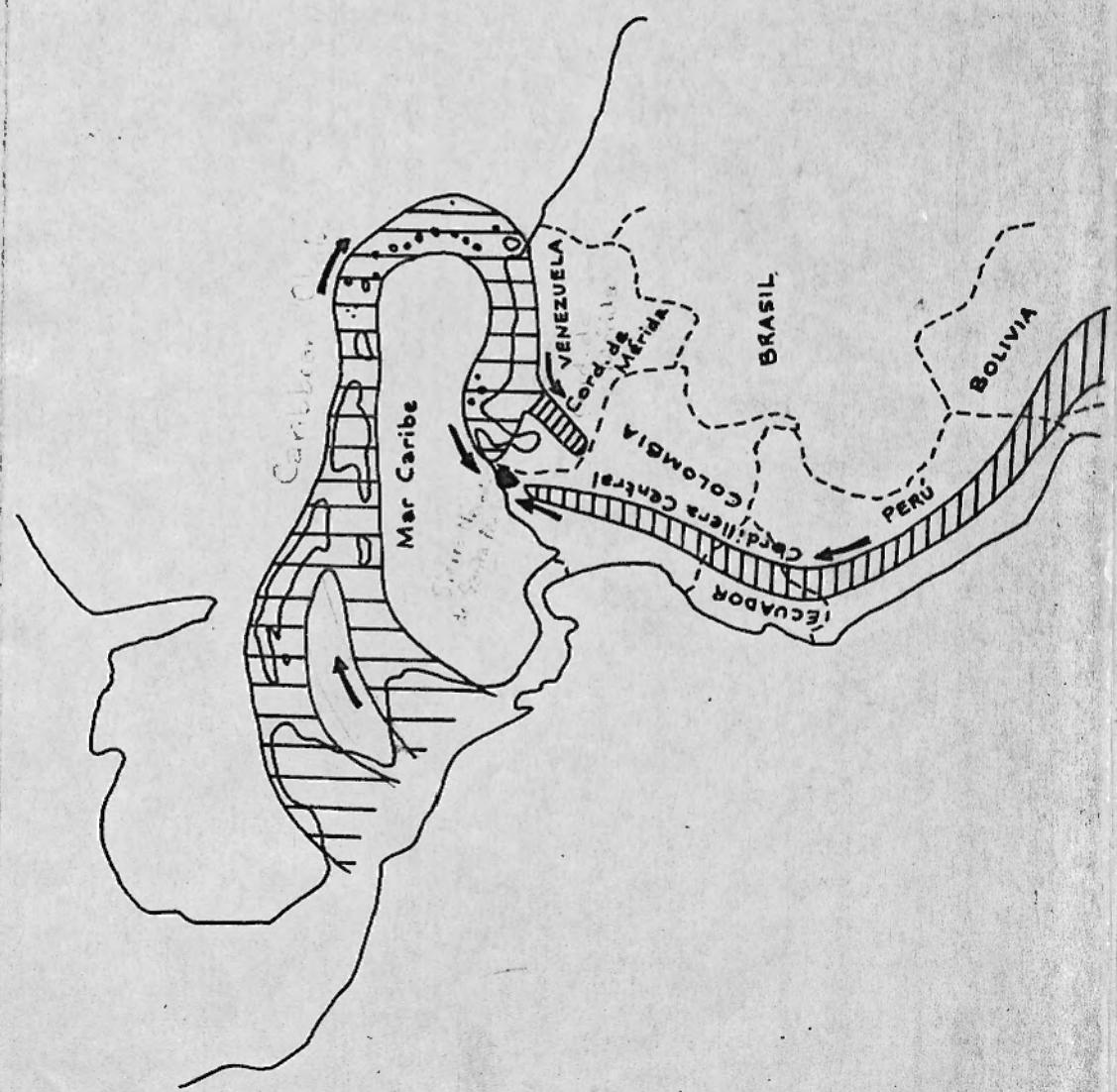
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Fig. 1a. TERTIARY movement of montane animals



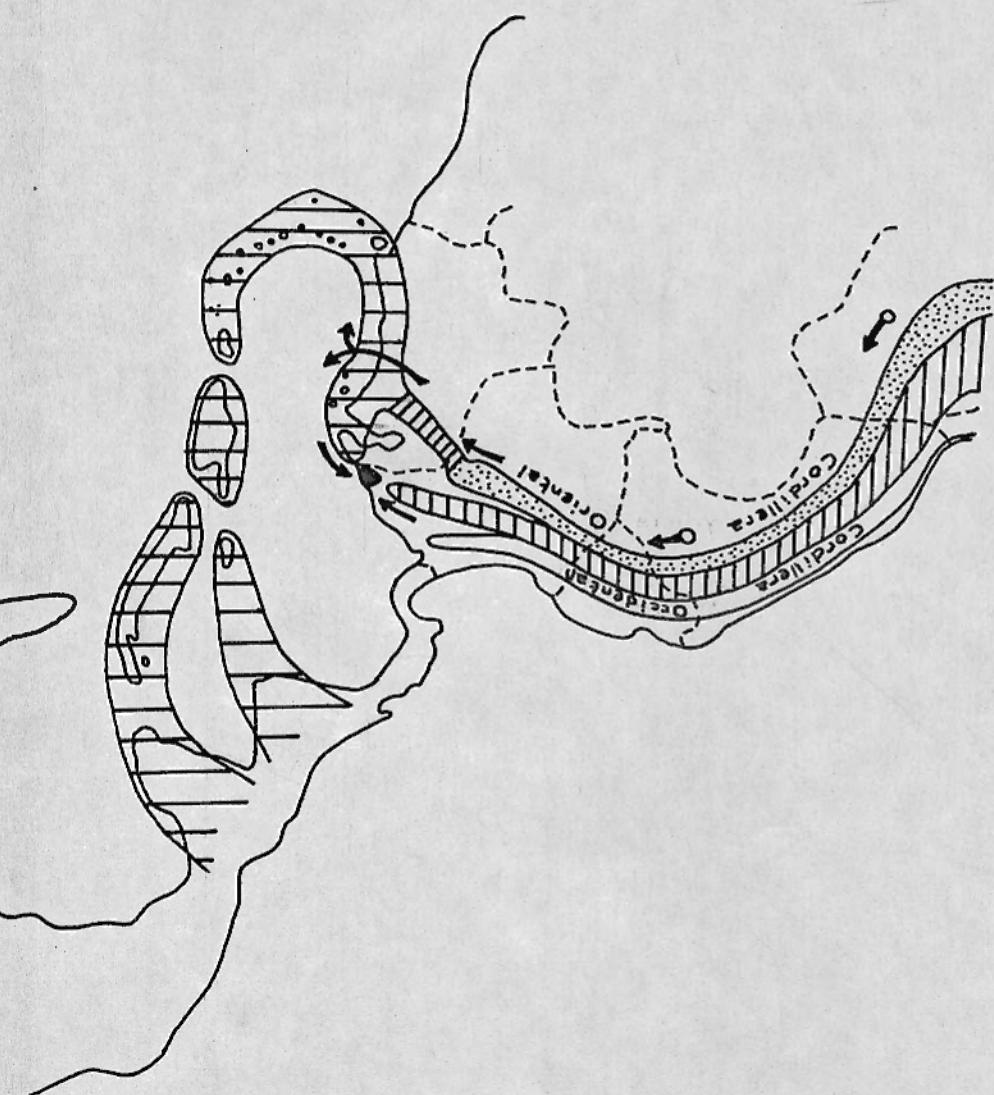


Fig 16. Plio-Pleistocene BORDER.

→ centre of diversification of montane animal life

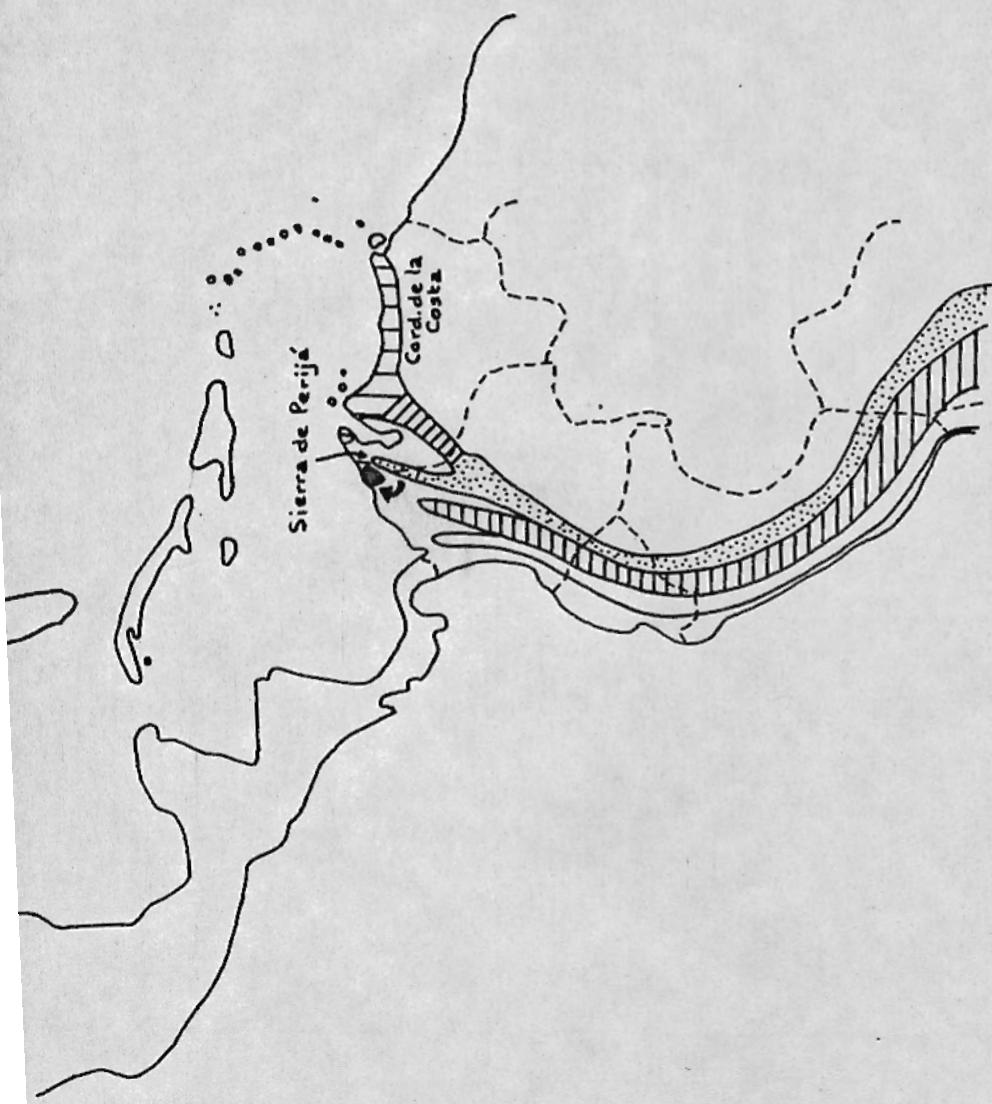


Fig 1c. Wium GLACIATION

Fig. 2
SATYRIDAE of Sierra Nevada

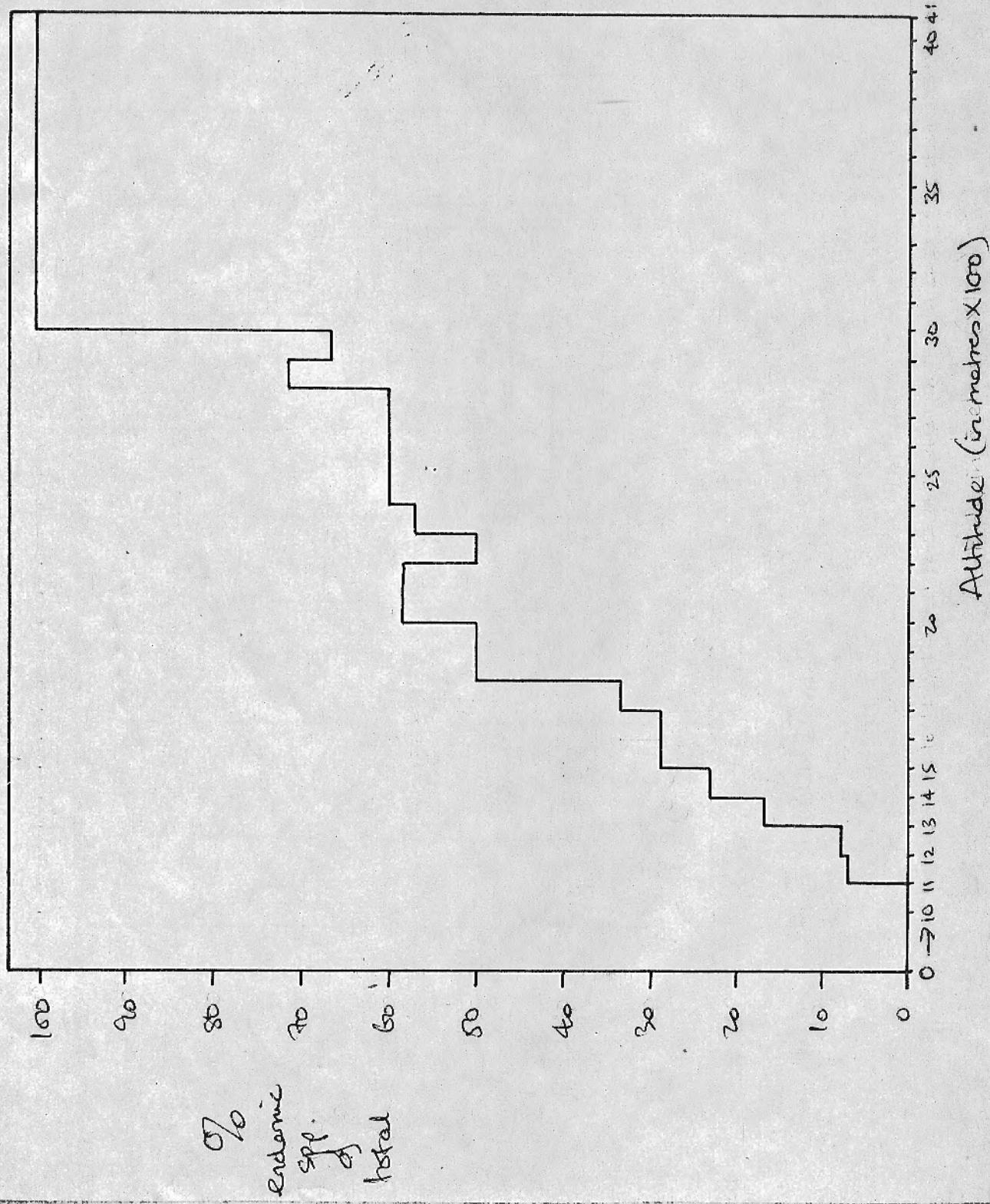
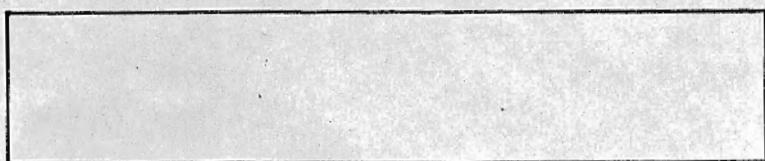
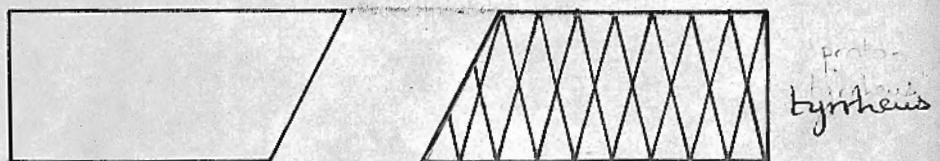


Fig. 3. Schematic history of Pedetes "cebolleta", P. tyrrheus tyrrheus
 & P. tyrrheus "tavona"

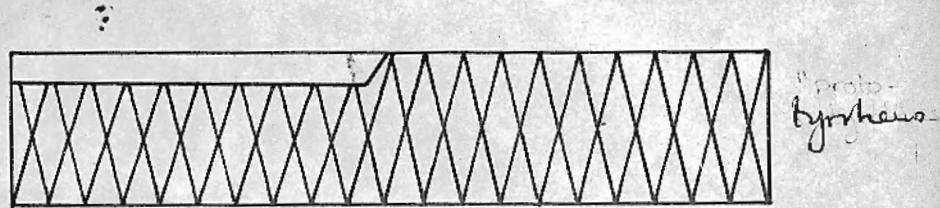
1. Prototype



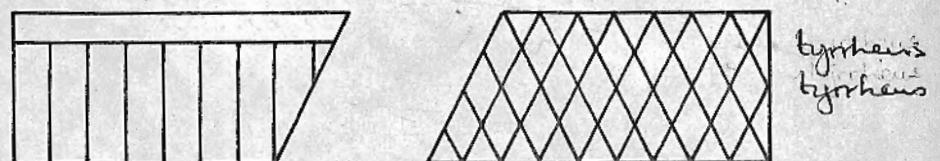
2. Interglacial
 cebolleta



3. Glacial
 cebolleta
 tyrrheus



4. Interglacial
 cebolleta
 tyrrheus
 tavona



5. Today

