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Author(s): L. C. Stuart

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The Environment of the Central American Cold-blooded Vertebrate Fauna

L. C. STUART

Biological Central America includes political Central America, the lowlands of southern México, and northwestern Colombia (Chocó). Ninety per cent of the region lies north of the Nicaraguan Depression, and only 25% of the area rises above the 600-m contour. Owing to the Pacific position of the continental divide most of the lowlands lie on the Caribbean versant, and the major drainage basins are so located. Pliocene uplift, erosion, and Tertiary and Quaternary volcanism are responsible for the high relief of the highlands, which are discontinuous above about 1,500–2,000 m.

Temperature is largely a function of altitude, and annual range is slight. The Caribbean versant receives 2–3 times as much rainfall as do the Pacific lowlands and the highlands. The low sun period is the dry season, and the rainfall displays a double maximum with peaks during the early and late portions of the high sun period. Rainfall varies from less than 500 mm annually to more than 7,000 mm. As a generalization rainforest clothes the lowlands of the Caribbean versant and dry forests the Pacific. The northern highlands support a cover of oak–pine up to about 3,000 m above which are pine–fir forests and meadows. In the south, wet forests are characteristic of the highlands with patches of páramo above 3,100 m. Protected valleys support savannas and scrub forests.

In the north Nuclear Central America has remained positive since the Cretaceous. To the south between southern Nicaragua and Colombia open, island-studded seaways persisted, with the possible exception of the Paleocene interval, up to the Pliocene.

INTRODUCTION

TO essay a brief description of the environment, both past and present, of the Central American cold-blooded vertebrate fauna is not only difficult but downright presumptive. Though dealing with somewhat more terrain than will be considered herein, the environmental volume of the recently published Handbook of Middle American Indians (Wauchope and West, 1964) devoted almost 400 pages to the same subject. That this account may be held to reasonable length, therefore, only such features as are salient to an understanding of cold-blooded vertebrate distribution within the region will be considered, and these at only the geographic or chorographic levels. Soils, because their direct effects upon vertebrate distribution are still but poorly explored, will not be considered. Neither will consideration be given to causal agents since they lie outside the province of the biologist.

Though this account will present in sum-

mary form much the same data as are covered in the "Handbook," some more recent materials are included. Manuscripts for the "Handbook" were submitted as early as 1959, and seven of the ten environmental articles included therein made no effective use of literature that has appeared since 1961.

EXTENT (Fig. 1)

Inasmuch as zoogeographic patterns are continuums through both time and space, interpretation of them within any general region involves consideration of extralimital conditions and events. Here it is first necessary to distinguish between political Central America and biological Central America. Political Central America encompasses the terrain between the southern border of México and the northern border of Colombia, though Panamanians would exclude their country from the region. However, the lowlands of southern México support a fauna with a decided Central American "flavor."

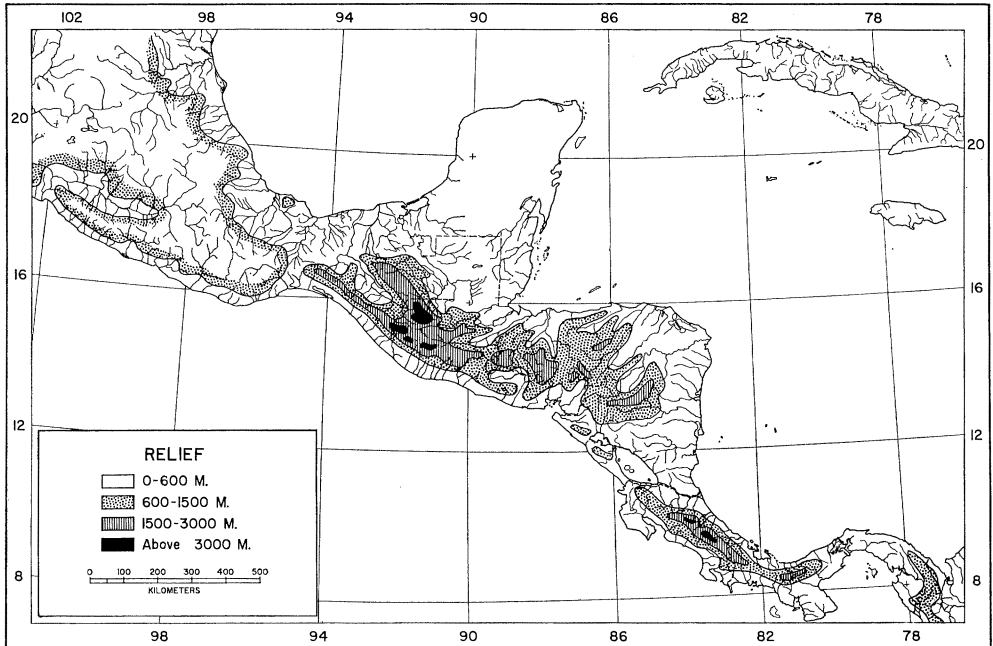


Fig. 1. Relief Map—Central America.

Similarly, many of the faunal elements occurring in lower Central America are shared with northwestern (Pacific) Colombia. Thus biological Central America, as considered herein, includes not only political Central America but also the lowlands of southern México north to the ríos Pánuco (east) and Balsas (west), northwestern Colombia, and all adjacent coastal waters.

This region extends over 20° of latitude (roughly 2300 km) all within the tropics. It has a length of something over 3000 km, attains its greatest width (about 1000 km) through central Guatemala and northern Honduras, and is narrowest through the Panama Canal Zone (60 km). In all it encompasses about 10⁶ km², of which nearly 90% lies north of the Nicaraguan Depression at lat 12° N.

SURFACE CONFIGURATION (Figs. 1 and 2)

Though noted for its mountainous character, only about 25% of the region lies above the 600-m contour, the level utilized herein to distinguish between topographic "highlands" and "lowlands." In view of the tremendous diversity of rocks comprising the

land area of Central America, the great differences in their ages, and the variety of internal and external forces to which they have been subjected, generalization regarding the surface configuration of the region is difficult. General geological summaries have been presented in the works of Sapper (especially 1937) and more recently by Weyl (1961), but detailed studies on the geomorphology of specific regions have only just begun to appear.

The bulk of the lowlands lies to the east of the continental divide which, south of the Isthmus of Tehuantepec, is situated much closer to the Pacific than to the Caribbean except in eastern Panamá. Though almost pinched out in several areas, notably in northern Honduras, the lowlands are continuous along both coasts from north to south. The most extensive lowland block is the limestone platform of the Yucatán Peninsula, northern Guatemala, Belice, and the adjacent Grijalva-Usumacinta lowlands. Here somewhat more than 200,000 km² lie, with the exception of a small area in Belice, below the 500-m contour and most of them below 200 m. The second most extensive lowland area is the Caribbean coastal plain

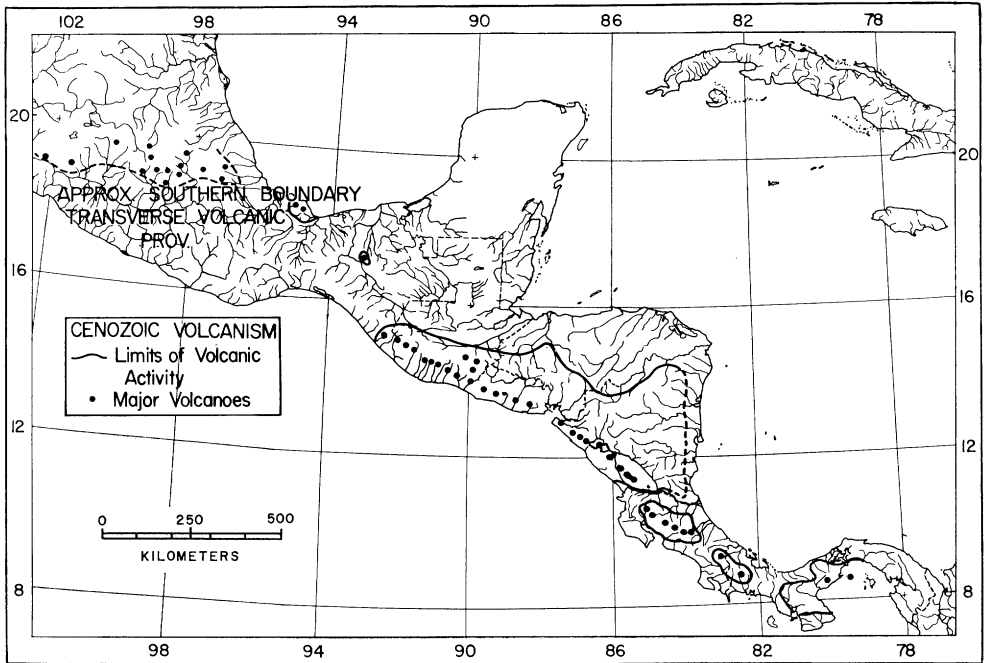


Fig. 2. Cenozoic volcanism—Central America.

of eastern Honduras and Nicaragua. On the Pacific side the lowlands attain their greatest width (120 km) locally on the Anzuero Peninsula of Panamá, but throughout most of their extent along the Pacific they are less than half that width.

The surface configuration of the lowlands is extremely varied. Throughout most of the region they are flat to gently undulating. In contrast, portions of the Yucatán platform and of northern Guatemala are in the mature stage of karst development, and local relief is extremely high. Similarly it is impossible to generalize on the drainage patterns of the lowlands. In some regions, the Pacific coastal plain of Guatemala for example, the lowlands are well drained. Owing to its 1% gradient the numerous streams that cross it are well entrenched, and even during the rainy season, except in the immediate proximity of the coast, there is no flooding, and the porous alluvium insures complete drainage. In regions of low gradient or where extensive hardpans developed, flooding may be extensive during the rainy season. The distributaries of the ríos Grijalva and Usumacinta, for example, flood northern Tabasco as far inland as 80 km, and many

parts of the Yucatán platform with its residual soils become great morasses (*bajos*) during the wet season.

The highlands of Central America occur as two major blocks. In the north the Mesa Central of Chiapas, the highlands of central and southern Guatemala, and those of Honduras, El Salvador, and northern Nicaragua, which together comprise 80% of the Central American uplands, constitute a mass frequently referred to as "Nuclear Central America." In the south the highlands are formed by the narrow backbone of the isthmus and extend from just south of Lake Nicaragua, through Costa Rica, and into western Panamá. A third minor upland area occurs still farther south, the Serranía del Darién and the annectant Serranía de Baudó of eastern Panamá and northwestern Colombia, respectively. The two major blocks are separated by the 200-km break of the Nicaraguan Depression, while the highlands of western and of eastern Panamá are intervened by about 175 km of lowlands. In general these highlands are bordered by narrow piedmonts, and their surfaces are slashed by streams and rivers flowing through youthful valleys separated by interfluves,

many of which are still in the youthful stage.

Although the two major highland blocks are each continuous above the 600-m level, there is little continuity in terrain above about 1500 m south of Guatemala City. To the north and west of the graben within which Guatemala City is located there is a highland mass of some 30,000 km² above 1500 m that extends unbroken almost to the Isthmus of Tehuantepec. The general level of the highland surface west of the Guatemala City graben lies at about 2000 m, and it is surmounted by isolated blocks that attain elevations in excess of 3000 m. The most continuous area above 3000 m occurring in Central America is the high plain of the Sierra de los Cuchumatanes of northwestern Guatemala which encompasses some 1500 km². East and south of Guatemala City the highland surface of Nuclear Central America lies at about 1000 m, and elevations above 2000 m are encountered only as isolated peaks. The southern block is continuous at the 600-m level, but above the 1500-m contour the Cordillera Central and the Cordillera de Talamanca alone form a continuous highland mass. Only some of the volcanic peaks and the Chirripó area of the Cordillera de Talamanca, which encompasses some 400 km², rise above 3000 m. Elevations above 1500 m in the eastern Panamá and northwestern Colombian complex are restricted to a few peaks.

In the north, owing to extensive faulting, volcanism, and the effects of erosion, the highlands present a picture of extremely high relief. Practically all the streams flow through youthful valleys, and in areas deeply overlain with pumice, *barrancas* with sheer walls are frequently encountered. The interfluves are in a stage of early maturity, or in regions of more recent volcanic deposits they may have retained their youthful characteristics. In areas that have not been subjected to volcanism, the limestone Mesa Central of Chiapas for example, high relief has resulted from karst development. In the south, the volcanic Cordillera Central of Costa Rica and especially the Cordillera de Talamanca, streams plunge through youthful valleys separated by maturely dissected interfluves, and here occurs some of the most rugged terrain encountered within Central America.

The most conspicuous physiographic features of Central America are those associated

with volcanism. Between the Chiapas-Guatemalan border and the Panamá Canal Zone roughly 100 "grosser" volcanos are listed by Weyl (1961: Table 9). Of these about 25 retain signs of activity. The volcanic peaks are highest in the north, where two in Guatemala attain 4000 m—Tajumulco is the highest at 4220 m—and 13 others reach 3000 m or more. In Nicaragua no peak rises above 2000 m, while in Costa Rica and Panamá only 3 of 17 exceed 3000 m, with Irazú the highest at 3432 m. On the lowlands of Veracruz there are several regions of Quaternary volcanism, the most extensive of which is the Tuxtlas south of Veracruz city.

Volcanic activity through the Cenozoic has not been restricted to the major volcanic axis facing the Pacific. At least 50% of the highlands of northern Central America are overlain with extrusives. In the south, with the exception of the Cordillera de Talamanca (a batholith), extrusives similarly cover the highlands. The most extensively distributed extrusives were thrown out during the late Tertiary, whereas Quaternary deposits are restricted largely to the vicinity of the present axis.

The effects of volcanism upon the distribution of cold-blooded vertebrates cannot be overestimated. Not only does such activity keep the environment "off balance," but the damming of rivers by glowing avalanches and the heavy loads such as contribute to the streams would certainly have a detrimental effect upon the aquatics. Charcoal recovered from beneath 300 m of avalanche materials on the Guatemalan highlands between Volcán Atitlán and Volcán Fuego (both active during the past century and a quarter) has been dated at $24,000 \pm 3000$ yr (Crane and Griffin, 1958), thus giving some idea of the temporal extent of volcanic activity.

HYDROGRAPHY (Fig. 3)

Inasmuch as students of continental fish faunas deal with both primary and secondary division fishes, some consideration should be given to coastal waters in addition to that accorded inland waters. As a matter of fact, a great deal more is known of the former than of the latter. However, such presentation would unduly lengthen this account, and, except for a few brief statements, coastal waters will not be considered herein. For

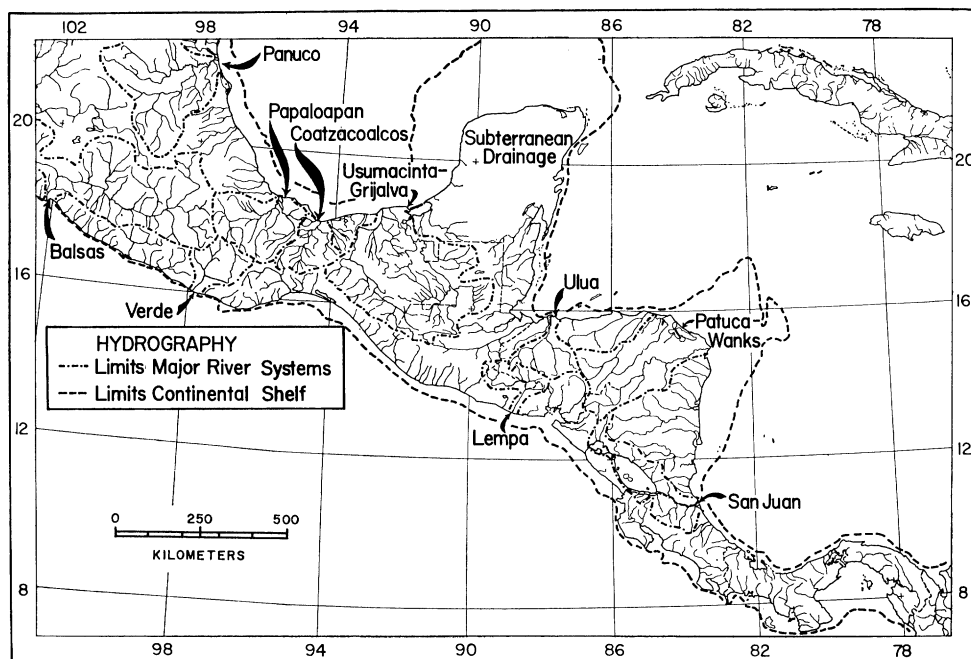


Fig. 3. Hydrography—Central America.

an excellent summary of these, the reader is referred to the articles by Collier (1964) and by Hubbs and Roden (1964) in the aforementioned "Handbook." In the same volume Tamayo and West (1964) present an excellent summary of inland waters.

With three exceptions the continental shelf along both coasts is less than 50 km in width, and along Pacific México north of the Isthmus of Tehuantepec it is less than one-tenth that wide. The Campeche and Miskito Banks, however, extend out from the shoreline to a distance of 250 km, while the Gulf of Panama lies entirely over the shelf and has a width of 150 km.

The coasts and coastal waters of the Atlantic and Pacific sides present several interesting and important contrasts. The mean tidal range along the Pacific amounts to from one to four meters, whereas along the Gulf-Caribbean coast it is less than one meter. The Pacific shores are washed by north-flowing currents between the Panama Bight and the Gulf of Tehuantepec (Cape Corrientes in summer). The Caribbean shore, in contrast, is washed by south-flowing currents between Honduras and South America. As a generalization the Gulf-Caribbean

side may be characterized as a depositing shore, while the Pacific presents an eroding shore except between the Gulf of Fonseca and the Gulf of Tehuantepec, the Pacific Central American Faunal Gap of Springer (1959:483). The Atlantic side, especially in the north, has extensive regions of coral reefs, as opposed to the Pacific shoreline along which coral growth is limited. Such chemical differences as exist need not be noted here. These appear to be associated with such factors as upwellings along the Pacific coast and with river discharge, which is much greater on the Atlantic side than on the Pacific. Associated with this latter factor is also lagoon or estuary formation, which is far better developed along the Atlantic side.

Very little is known of the physicochemical features or of the hydrology of the inland waters south of México. The distribution and the hydrology of the rivers and streams mirrors the distribution of landform types and of climatic factors. Of especial significance is the position of the continental divide. Except on the plateau of southern México and in extreme eastern Panamá the divide lies much closer to the Pacific than to

the Atlantic. Probably as much as 80% of Guatemala, all Belice, over 90% of Honduras, and about 90% of Nicaragua drain into the Atlantic. Furthermore, as a generalization, the Atlantic side receives about twice the rainfall that the Pacific side does. As a result of these conditions drainage basins of any size are restricted to the Atlantic slopes. By far the largest basin within the region is that of the Usumacinta—Grijalva which encompasses an area of over 100,000 km² and has a mean annual discharge of over 10¹¹ m³ (Tamayo and West, 1964: Table 1). The largest basin on the Pacific side is that of the Río Balsas, which approaches that of the Usumacinta—Grijalva in terrain encompassed, but which has a mean annual discharge of only about one-ninth that of the latter (Tamayo and West, *loc. cit.*). South of the San Juan basin of Nicaragua and Costa Rica no large basins have developed, but the streams, though short, are numerous. Tamayo and West (1964:98, 109) stated that there are 153 streams in Panamá discharging into the Caribbean and 325 which discharge into the Pacific. The karsted Yucatán Peninsula is an anomalous area encompassing almost 90,000 km² with practically no surface streams.

The rivers of the two sides, especially in the north, contrast strongly. Those flowing to the Caribbean display a "textbook" profile. The Motagua in Guatemala, for example, through its lower course to a point roughly 100 km inland has an air-line gradient of 0.01%. Through this section it shows all the characteristics of old age, meandering, bordered by oxbows, and with natural levees. Through its middle course of some 150 air-line km the air-line gradient increases to 0.04%, while over the 85 km of its upper course the river has an air-line gradient of 2.5%. In contrast, streams along the Pacific in the north plunge precipitously down the narrow watershed. The Samalá, for instance, leaves the plateau of Guatemala at about 2400 m and falls down a 6.0% air-line gradient to the inner edge of the coastal plain 40 km to the south. Even across the 40 km of coastal plain the Samalá maintains a 1.0% air-line gradient and retains the characteristics of youth almost to its mouth. Translated into velocity, a 1.0% gradient would mean that water flowing through a 3-m semicircular flume brimfull would move at a speed of about 25 kmph (15 mph). Since the current

of but 4 kmph can move egg-sized pebbles and since the transporting power of running water varies as the sixth power of the velocity, we gain some idea of the load that can be transported and the molar action in a stream such as the Samalá. Most Pacific streams taking their origins in the highlands of the region are broken by falls above the 1000-m level.

Owing to the pronounced seasonal distribution of rainfall, great seasonal variation in discharge characterizes the rivers. At Boca del Cerro where the Usumacinta breaks through a ridge and floods out onto the lowlands of Tabasco, for example, the September discharge is 20 × that of May (Tamayo and West, 1964:93). During the wet season the streams carry tremendous loads of silts and clays, and through their middle and upper courses the movements of boulders produce tremendous molar action. Further complicating velocity and load variations are tidal ranges, especially in the cases of rivers flowing across low-lying coastal plains along the Pacific. Tidal influence extends some 70 km upstream on the Río Tuira of eastern Panamá, and 50 km upstream the tidal cycle occurs twice daily producing as much as 3 m difference in water level. Salinity is likewise subject to daily variations. At the head of the estuary of the same river the salinity (NaCl only) at about 6 m depth varies from 600 ppm at low tide to 1500 ppm at high tide (data from Finch, 1964).

Incidence and location of stream capture throughout the region has not been well studied. It is generally accepted that Pacific—Atlantic interchange has taken place in the case of the Pánuco—Lerma systems of México and that Lake Nicaragua, formerly draining to the Pacific, has been captured by the San Juan system (Atlantic). Examination of maps of Honduras and of northern Nicaragua suggests that capture may have occurred in several instances in those countries. There is also biological evidence to indicate possible faunal interchange, though not necessarily through stream capture, between tributaries of the Río Motagua and headwaters of the Río Lempa (pers. comm., R. R. Miller) and between the Río Tuira of eastern Panamá and the Río Atrato of Colombia (Hildebrand, 1938:225). Capture of the upper course of the Río Polochic by the Río Negro in Guatemala has been authenticated (Sapper, 1937:107), but in this case both flow

to the Atlantic side though their mouths are far apart. Similarly faunal interchange between the ríos Bayano and the Chuquinaque in Darién (both Pacific) may have occurred (Terry, 1956:18), while the extensive flooding of the *bajos* at the base of the Yucatán Peninsula during the wet season could conceivably act as a corridor for aquatics moving from the Usumacinta to streams flowing through Belice.

There are few lakes of any size in the region under discussion. Tamayo and West (1964:Fig. 2) list only 17 worthy of notice, and these, with the exception of artificial Gatún, lie north of Costa Rica. By far the largest is Lake Nicaragua, with a surface area of some 8000 km² and a maximum depth of 70 m. Lake Managua is a poor second and Izabal in Guatemala third, with surface areas of about 1000 and 600 km², respectively. The only other lakes of any size include Petén and Atitlán (both without surface outlets) in Guatemala, Ilopango in El Salvador, and Yojoa in Honduras. Practically nothing is known of the limnological aspects of these waters, and such as is known has been summarized by Deevey (1957).

CLIMATE

Considering the control that climate exercises over landforms, hydrography, soils, and biota, it is unfortunate that we are familiar with only the grosser climatic features of Central America. Though rainfall stations are numerous throughout the region—Guatemala has almost 200 with records of 10 yr or more—instrumentation for other climatic parameters is practically nil. Isotherms are extrapolated largely from altitudinal data, and instrumentation for such features as atmospheric pressure, wind movement, or relative humidity is restricted largely to major air- and seaports and the national observatories.

With a latitudinal extent of but 20° and all within the tropics, temperature variation is largely a function of altitude. As a generalization the lapse rate in Central America is computed at roughly 1° C/150–200 m (Sapper, 1932:13). Below about 1200 m the average annual temperature remains above 20° C. Sea-level stations along the Gulf-Caribbean show a decrease in the mean annual temperature from south to north of less than 3° C (Cristóbal, C. Z. 27.0, Bluefields 27.0, Belice 26.3, Coatzacoalcos 25.2,

and Tampico 24.2° C). The mean annual range, however, increases considerably northward (Cristóbal 1.2 as compared with Tampico 9.0° C), but only north of the Isthmus of Tehuantepec does it exceed 5° C. Along the Pacific lowlands the latitudinal differences are similar both with respect to mean annual temperatures (Balboa, C. Z. 27.0, Salina Cruz 26.6, and Manzanillo 25.5° C) and to mean annual ranges. In general the warmest months fall during June, July, and August and the coldest during December, January, and February, with a tendency for both to arrive earlier in the south than in the north. Maximum daily temperatures rarely exceed 35° C even at low elevations (all data from Sapper, 1932:Table 1; Ward, Brooks, and Conner, 1936:Table 1).

Temperature data for elevations above 1200–1500 m are few and scattered. A major climate dependent factor of possible biological significance appears to be the lower limit of occasional frosts. This isopleth, depending upon humidity, lies between 1200–1500 m and coincides roughly with the A/C boundary of the Koeppen System. Between about 1200 m and 2000 m the mean annual temperature lies between 15 and 20° C. Above 2000 m it falls below 15 and above 3000 m below 10° C (Sapper, 1932:12). At 3000 m frosts are frequent, and night temperatures are not uncommonly below 5° C. Snow falls occasionally on the higher peaks in the north (Tacaná and Tajumulco). The mean annual range of temperature and the march of temperature on the uplands parallel conditions encountered on the lowlands. During late fall, winter, and spring occasional cold fronts are deflected southward bringing unseasonably cold weather to eastern México and northern Central America.

The rainfall pattern of Central America is extremely complex and renders generalization difficult with regard to both total annual precipitation and seasonal distribution. Portig (1965) has recently shown that the causal agents are far more complex than was formerly supposed. In general the Northeast Trades provide the major moisture source, but local air movements such as mountain-valley winds and fronts contribute to the patchy rainfall pattern.

Total annual precipitation varies from as little as 500 mm in the middle Motagua valley of Guatemala to more than 6000 mm in southeastern Nicaragua (both facing into

the Trades) and more than 7000 mm locally in the Chocó of northwestern Colombia. As a generalization the Gulf-Caribbean lowlands receive about twice the precipitation as do the Pacific lowlands, but there are many exceptions. Along the Gulf coast from Tampico southward the average annual rainfall increases from about 1100 mm to over 3000 mm in southern Veracruz. The same situation prevails through the Yucatán Peninsula and northern Guatemala. Progreso on the north coast receives less than 500 mm, Flores at the base of the peninsula 2000 mm, while still farther south several stations in the foothills of Alta Verapaz record more than 5000 mm. The lowlands of eastern Guatemala and northern Honduras in general record 2500–3000 mm annually except in protected valleys such as that of the Río Aguán of Honduras and of the Río Motagua mentioned previously. In such valleys annual precipitation is well under 1000 mm. Along the broad lowlands of eastern Honduras and Nicaragua mean annual precipitation increases from about 3000 mm in the north to over 6000 mm in the San Juan del Norte region in the south. The Caribbean lowlands of Costa Rica and Panamá display a patchy pattern of total annual rainfall, but, except for several very local departures, the figure lies between about 2700 and 3300 mm.

Along the Pacific there is a gradual increase in the mean annual precipitation over the lowlands from Cape Corrientes south to the Nicoya Peninsula. Though there are local departures throughout that entire region, from Manzanillo to the Isthmus of Tehuantepec the rainfall averages 900–1300 mm, and the figure gradually climbs to about 2000 mm in eastern El Salvador and through Nicaragua and to 3000 mm in northwestern Costa Rica. From there to the Azuero Peninsula in Panamá most of the lowlands receive in excess of 3000 mm annually. The lowlands surrounding the Gulf of Panamá are somewhat drier, and the annual rainfall figure drops below 2000 mm only to increase rapidly through southeastern Panamá and northwestern Colombia to over 7000 mm in the Chocó.

As is to be expected, piedmonts and mountain slopes are subjected to much heavier precipitation than are the adjacent lowlands. The situation on the Yucatán Peninsula and northern Guatemala has been noted previously. In southern Guatemala, Champerico

(coastal), Retalhuleu (base of piedmont), and *fincas* on the mountain slopes receive roughly 1000 mm, 2000 mm, and over 4000 mm, respectively. Incidentally, the region of highest rainfall on the entire Pacific versant of Central America is, unexplainably, the mountain slopes of eastern Chiapas and western Guatemala. Similarly, on the Caribbean side of Costa Rica, coastal Pto. Limón receives about 3000 mm annually while Siquirres, 15 km inland and at the base of the mountains, receives almost 5000 mm.

Owing to the topographic complexity of the highlands the rainfall pattern of the uplands, especially in the north, is extremely broken. In general, the plateaus of Chiapas, Guatemala, Honduras, and Nicaragua receive about the same annual rainfall as do the Pacific lowlands of those countries, i.e., 1500–2000 mm. However, where rain-shadow conditions occur the mean annual precipitation may fall well under 1000 mm. I have described such an area of considerable extent through Chiapas and Guatemala (Stuart, 1954), and Portig (1965:Fig. 1) maps similar areas in Honduras and Nicaragua. On high unprotected peaks and plateaus in the north, though no rainfall figures are available, extremely humid conditions exist, but such are probably owing more to the mist and cloud banks in which they are enshrouded than to actual precipitation. In the south, owing to narrowing of the isthmus, the highlands are exposed to moisture-bearing winds to a far greater extent than in the north. Over most of these highlands the mean annual precipitation exceeds 3000 mm, and Portig (*loc. cit.*) maps more than 4000 mm in the Cordillera de Talamanca. It may be noted, however, that records for the two highest stations in the Cordillera, Villa Mills at 3000 m and Volcán Chiriquí, record only 2800 and about 3200 mm, respectively. As in the north, local enclosed basins are drier than the surrounding exposed mountains, e.g., San José, Costa Rica, 1868 mm. Most of the above data on precipitation are taken from Sapper (1932), Ward, Brooks, and Conner (1936), and Portig (1965).

There are insufficient long-term records to permit any very detailed analysis of year-to-year variability in annual rainfall. Escoto (1964:Fig. 13), however, indicated that in general on the Atlantic watershed south of the Isthmus of Tehuantepec and on the Pacific watershed south of the Nicoya Pe-

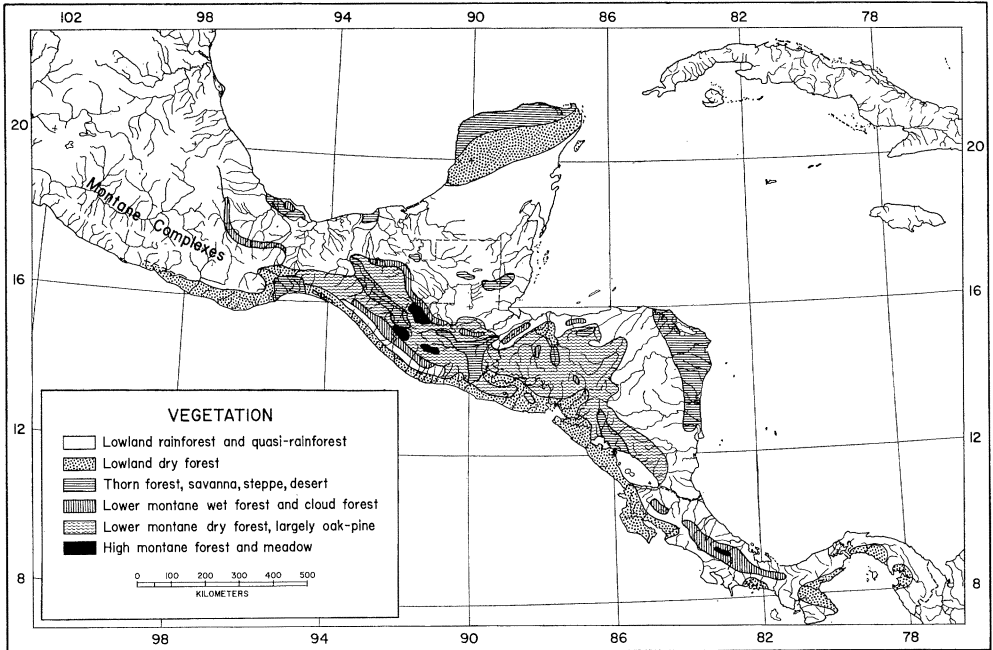


Fig. 4. Vegetation—Central America.

ninsula variability amounts to about 20%. In contrast, along the Gulf coast north of the Isthmus of Tehuantepec and on the entire Pacific watershed north of the Nicoya Peninsula the figure lies between 20 and 40%.

The rainfall regime through the region is uniform and is characterized by a double maximum during the high-sun period. In general January, February, March, and April constitute the dry season. Depending upon latitude and position with reference to watershed, May, June, or July, or combinations thereof witness a first maximum peak. During July or August there is a slacking off of the rains, the "little summer" or *Veranillo de San Juan* or *caniculas* as it is called. A second high peak, generally the primary maximum, occurs during September, October, or November. There is, of course, a narrowing of the two rainfall maxima from south to north. From this general scheme there are, however, many local departures.

Mean annual relative humidity is high throughout the region and is generally in excess of 70% (Escoto, 1964: Figs. 8-9). Windward slopes, especially in the north, may be especially humid between the 1500- and 2000-m levels and usually support "cloud forest."

VEGETATION (Fig. 4)

Three recent efforts have been made to classify the vegetation of Central America *in toto* (Wagner, 1964; Holdridge, 1957; and Lauer, 1959). Owing to the fact that so little is known of the ecology of the bulk of the fauna, none is particularly well suited to the needs of the zoogeographer working at the chorographic level. The Holdridge system (summarized 1964) defines vegetation types but does not describe them. According to the system 12 vegetation types characterizing 12 life zones occur within the region under discussion. Lauer's classification also includes 12 types, and it also emphasizes vertical zones. Wagner utilizes the system of Beard (1955) with the addition of vegetation types that fall outside the limits of the Beard system. At the "formation" level the classification of Wagner is the most useful. The system presented herein takes Wagner as a starting point, and that is about all that can be claimed for it. I have found it useful in dealing with the herpetofauna of the region. It may be outlined as follows:

- Lowland formations (below about 1000 m)
 - Rainforest and quasi-rainforest
 - Dry forest
 - Thorn forest, savanna, steppe, and desert
- Montane formations (above about 1000–1200 m)
 - Lower montane wet forest and cloud forest
 - Lower montane dry forest
 - High montane forest and meadow

Where best developed, as on the piedmonts and most of the coastal plain of Caribbean Central America, the canopy of the rainforest may attain a height of 60 m, with 3–4 understories, and with less than one-third of its components deciduous. Though this formation is continuous on the Atlantic side from Veracruz to Colombia, there are numerous savanna openings scattered through it. Rainforest and quasi-rainforest cover roughly 50% of the entire region. Though largely restricted to the Atlantic side, there are disjunct areas of rainforest along the Pacific, notably the wet piedmont of eastern Chiapas and western Guatemala, southeastern Costa Rica, and eastern Panamá. The rainforest has suffered extensively at the hands of man, especially during the last century. Already it has largely disappeared from southern Veracruz, and large tracts through Tabasco have recently been cleared for agricultural *colonias*. Commercial fruit plantations and poorly regulated lumbering practices are also taking their toll.

Lowland dry forest are lower than the rainforest types, attaining a maximum height of about 30 m, support fewer understories, and are more than 30% deciduous. They are particularly characteristic of the coastal plains of Pacific Central America south to the Nicoya Peninsula, and they occur also as disjunct stands interspersed with savanna around the Gulf of Panamá. This vegetation type also forms the broad belt of transition between the scrub of the outer end of the Yucatán Peninsula and the rainforest farther inland. Like the rainforest, they have suffered extensively from the cultural activities of man. Many have been cleared for agriculture, especially for corn, cotton, and sugar, while others have been felled to provide pasture for the grazing industry.

Thorn forest, savanna, steppe, and desert are grouped together since they provide an "open" environment as opposed to the

"closed" environment of the rainforest and dry forest. Within this broad category there occurs, as is to be expected, a tremendous variety of cover. For want of a better name, very low (generally under 10 m in height) dry forests are here referred to as "thorn," though they may not necessarily be predominantly thorn. It is characterized by a dense tangle of low deciduous trees and shrubs with a ground cover of short grasses. True thorn forest is composed of an impenetrable jungle of thorny bushes and low trees intermixed with cacti, and is frequently referred to as *espinal*. This forest type is apparently restricted to the northern part of Central America. I am familiar with it on the outer end of the Yucatán Peninsula, in eastern Oaxaca, northwestern Guatemala, and along the outer edge of the Pacific coastal plain of Guatemala. Carr (1950) has described it as "mixed scrub" and "thorn scrub" in Honduras.

Although it is customary to classify savannas on the basis of the physiognomy of the grass cover (*e.g.*, Beard, 1953), a more striking feature is the tree cover. On the basis of the latter, there are two major types of savannas in Central America, the broadleaf-savanna and the pine-savanna. Lundell (1937) has given an excellent description of the former in northern Guatemala and Parsons (1955) has done the same for the latter in Nicaragua. The broadleaf-savanna type is characterized by expanses of moderately tall grasses over which are scattered low trees (*Byrsonima*, *Curatella*). It is broken by small wooded "islands" surrounding depressions, and low, gallery-like forest borders the streams. In contrast, the pine-savanna type supports extensive groves of pine (*Pinus caribaea*) and is park-like in appearance. Beneath these, low broadleaf trees, occurring either singly or in clumps and bordering streams, form an understory. Broadleaf-savanna is patchily distributed over the Pacific coastal plains southward to the Nicoya Peninsula and in the Gulf of Panamá region. On the Atlantic side this savanna type occurs in chainlike fashion through the rainforest from Veracruz into north central Guatemala and in interior Honduras (Johannessen, 1963). Isolated pine-savanna is found in northeastern Guatemala and adjacent Belice, and some 23,000 km² of such pine-lands broken by hardwood stands extend along the Miskito Coast of eastern Honduras

and Nicaragua (Parsons, 1955). There is no agreement among the authorities noted above as to whether the savannas of Central America constitute an edaphic climax or are sustained by fire, grazing, and similar factors.

Whether or not true desert occurs within the region is debatable. If it exists any place, it is to be found in the middle valley of the Río Motagua. Here, with less than 500 mm of rainfall and a surface underlain with coarse gravels which accentuate aridity, the valley floor does not support a continuous sod cover, and desert shrubs and *Cereus*-like cacti give it all the aspects of desert terrain (Stuart, 1954:Pl. 4). Holdridge (1957:152) believed it was originally a deciduous forest of hardwoods, and Carr (*op. cit.*: Pl. 28) referred similar cover in the Honduranian Depression to "thorn scrub."

Depending upon elevation, precipitation, slope, and other factors, wet forests of the lower montane series are extremely varied. Where best developed the canopy may attain 40 m with several understories. In the lower part of this belt much of the original forest has been cleared to provide for coffee cultivation. At higher levels, generally above 1500 m, exposed slopes are bathed in almost perpetual fog and support the "cloud forest." In such, the understories are rich in tree-ferns, while epiphytes are particularly abundant, and the trunks and limbs of trees support a thick growth of moss. In the Talamanca range of Costa Rica there occur magnificent stands of oak which fall within this wet forest category. These forests are characteristic of the Caribbean slopes of Chiapas and Guatemala and of isolated peaks in Honduras at roughly 1000–2800 m elevation. Along the Pacific in the north the very wet mountain slopes of eastern Chiapas and western Guatemala, mentioned previously, support this forest type. Where the isthmus narrows through Costa Rica and Panamá they constitute the major cover of the highlands.

Dry montane forests are those in which pines and oaks comprise the most conspicuous elements. These occur as mixed stands, but groves of pure oak or pine with an understory of shrubs are frequent. Forests of this type do not occur south of central Nicaragua, which is also the southern limit of pine both upland and lowland. Over the plateaus of Nuclear Central America, however, such forests provide the dominant cover. Because

of the large population of the highlands this vegetation type suffers considerably from the impact of man. Forest floors, more often than not, are remarkably clean, as even the smallest twigs are gathered for firewood. Pine is used extensively as a building material and for a variety of wooden products, and oak is cut for charcoal, the standard source of heat for cooking.

As the 3000-m level is approached the terrain becomes increasingly more exposed to the northeasterlies, and cold, humid conditions prevail. This is the zone of high montane forest and meadows. At these high elevations two major vegetation types occur in the north. Forests composed largely of pine, cypress, and fir, cloaked in dense fog much of the time, extend up to forest-line at about 3200 m (Lauer, *op. cit.*:350–351). At similar elevations and higher in the same region meadows supporting a cover of short grasses or bunchgrass, over which are scattered stunted bushes, occasional pines, and juniper, are also present. Tree-line in the north lies at 3700–3900 m (Lauer, *loc. cit.*). In Costa Rica oak forests extend up to about 3100 m above which level they are replaced by *paramo* (Weber, 1959). As previously indicated, such areas are neither extensive nor continuous in their distribution.

PALEOGEOGRAPHY (Figs. 5, 6)

In view of the fact that paleogeography provides the basic key to an understanding of extant zoogeographic patterns, it is unfortunate that there is no general agreement among geologists on even the tectonic history of Central America, let alone on other paleogeographic events such as paleoclimatology. Lloyd (1963:99), author of the most recent review of the tectonic history of lower Central America, stated that "opinions are as numerous as they are varied." The following account, therefore, will essay nothing more than a "consensus" based entirely upon geological evidence.

We may inquire first, however, just what sort of a paleogeographic picture is requisite for an explanation of the extant geographic pattern of cold-blooded vertebrates within the region. This question poses problems, for it appears that ichthyologists and herpetologists have, in part, conflicting requisites. For example, herpetologists demand a land connection between North and South

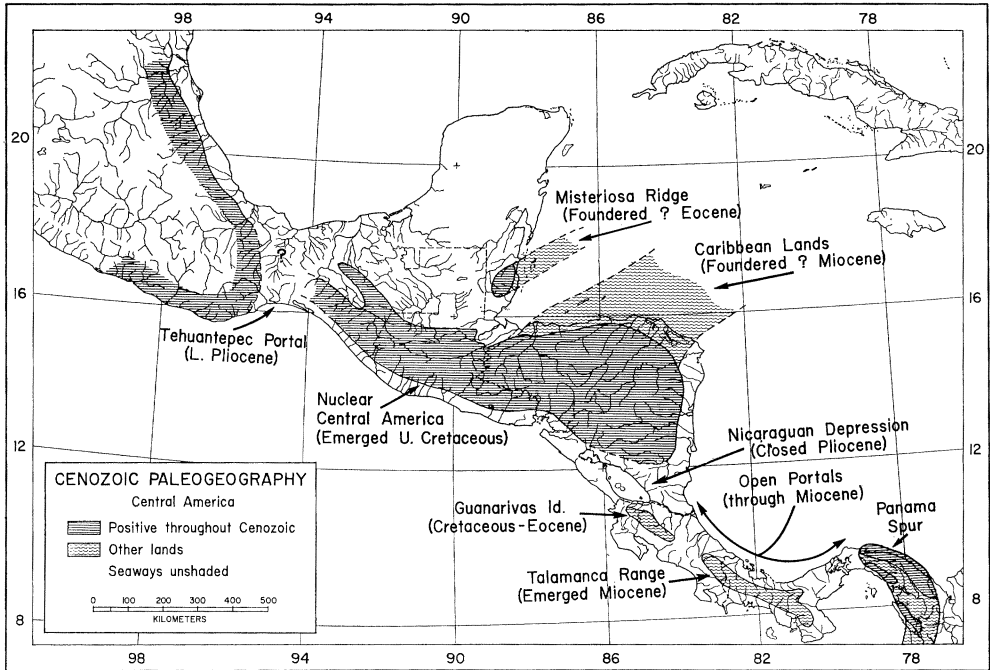


Fig. 5. Cenozoic paleogeography—Central America.

America prior to the opening of the Eocene (see Savage, 1966). Ichthyologists, in contrast, on the basis of primary ostariophysan distribution in Central America, would find such a connection prior to the late Tertiary embarrassing (see Myers, 1966). There are, however, a number of points of agreement between the two.

First, both demand a landmass of some size in northern Central America and southern México which has remained emergent since the close of the Mesozoic. Such a landmass should also have retained connection, except for minor temporal breaks, with North America. Second, both require a fairly effective barrier to animal movements between the indicated landmass and northern South America from Eocene through Miocene. Third, all vertebrate zoogeographers demand an emergent South America since the Jurassic. Fourth, such barriers as are required between North and South America need not necessarily have been open marine portals, but could have been climatic or competition. Furthermore, these should not have been impassable to all cold-blooded vertebrates but, rather, should have operated as "filter routes" permitting move-

ment of the more tolerant (in a very broad sense) elements of the several faunas. With these major requisites as a goal, we may examine the picture as presented by the geologists.

In the north the geological history is relatively clear. Though a borderland lying to the south and west of most of what was to become the Sierra Madre del Sur of México and Nuclear Central America persisted into the Cretaceous (Schuchert, 1935:11-17, Fig. 4, Pls. 1-6; Vinson and Brineman, 1963: Figs. 4-7), our story is initiated with the Laramide revolution at the close of the Cretaceous. At that time the Sierra Madre del Sur and Nuclear Central America were uplifted to form a landmass which has remained emergent up to the present. This upland may have extended northeastward as the "Caribbean Land" to include the Greater Antilles, but if such existed, it foundered probably no later than the Miocene (Maldonado-Koerdell, 1964:18). In addition to Nuclear Central America there was also emergent at that time the extant Maya Mountains of Belice and the long-since foundered Misteriosa Ridge which also extended northeastward into the Caribbean.

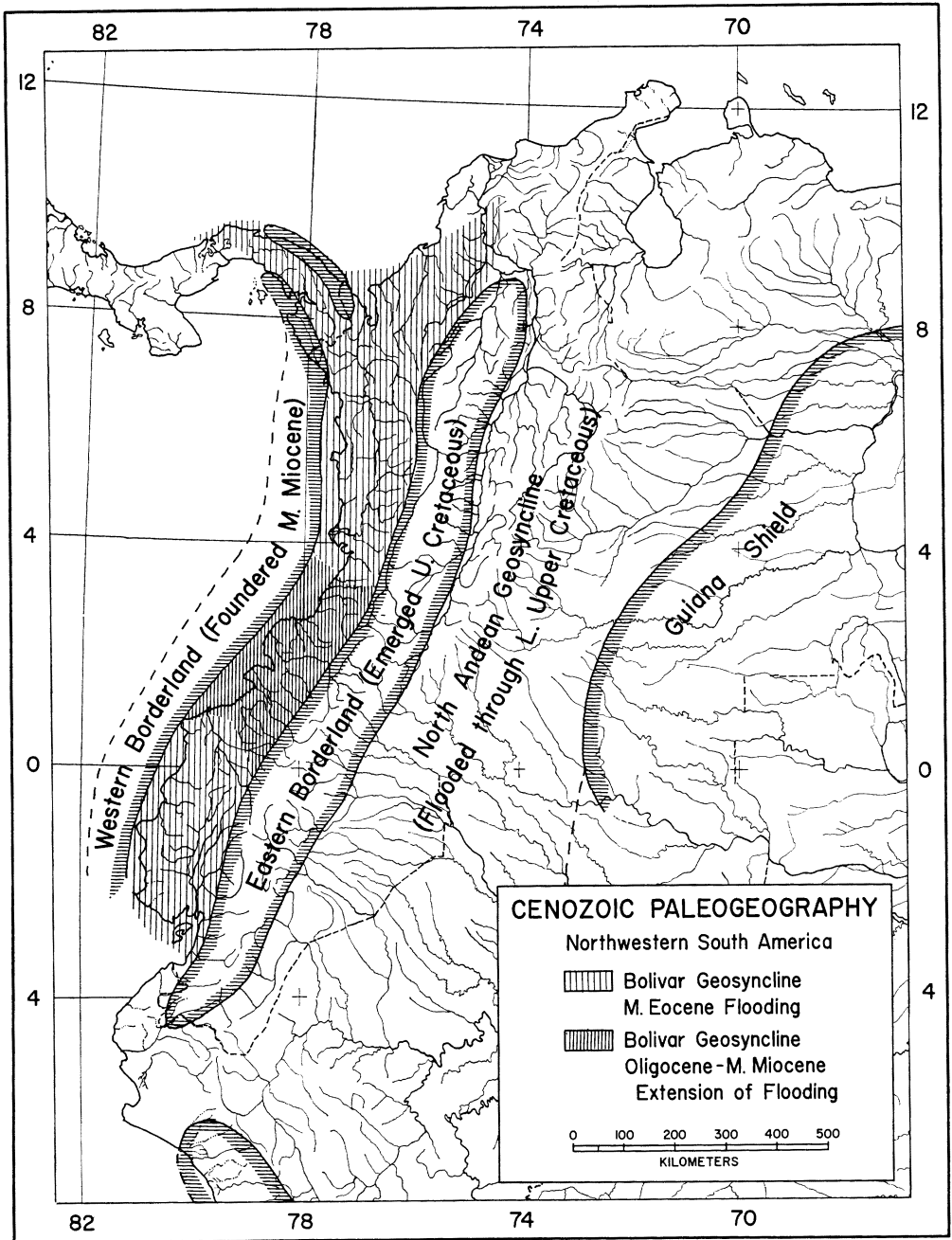


Fig. 6. Cenozoic paleogeography—Northwestern South America.

The former, however, was not joined to Nuclear Central America prior to the Miocene when the entire Yucatán platform began to emerge (Vinson and Brineman, *op. cit.*:104). The present high elevation of

Nuclear Central America is the result of uplift that was initiated in the Pliocene and the widespread volcanism of the late Tertiary and Quaternary.

Though the bulk of South America has

remained emergent since the opening of the Mesozoic, the northwestern section, through which intercontinental faunal exchange had to occur, has been extremely unstable. The tectonic history of this region has been particularly well summarized in three papers, Nygren (1950), Harrington (1962), and Jacobs, Bürgl, and Conley (1963). To the east of this region the Guiana (Guyana) Shield has remained a stable, positive unit since the Middle Precambrian (Harrington, *op. cit.*:1775). West of this, extant upland northwestern South America was flooded from late Jurassic until late Cretaceous when the present Cordillera Central of Colombia emerged. Yet between the emerging Cordillera Central and the Guiana Shield the North Andean geosyncline connecting the Caribbean with the Pacific off northern Peru remained flooded until the Danian (variously placed in the late Upper Cretaceous or Paleocene). In the Pacific, west of the present shoreline of Colombia and Ecuador, there existed a landmass which extended into eastern Darién, this last the "Panama Spur" of Lloyd (*op. cit.*:89). According to Harrington (*op. cit.*:1780) this western borderland may have persisted from the Paleozoic until the Pliocene (mid-Miocene, according to Nygren, *op. cit.*:2003). Between this western borderland and the emerging Andes the Bolívar geosyncline was initiated during the Eocene. This channel, extending from the Caribbean to the Gulf of Guayaquil, was completely flooded, with the exception of occasional emergent "bridges" between the Cordillera Central and the western foreland, from lower Oligocene until middle Miocene when sediments from the now-high western Andes began filling it (Nygren, *op. cit.*:2003-2005).

The most controversial portion of the region under discussion is, of course, the "isthmian link" of lower Central America, i.e., the 1000-km stretch between the southern terminus of Nuclear Central America and the lands of northwestern South America. The most recent review marshaling strictly geological evidence is that of Lloyd (*op. cit.*).

According to Lloyd at the end of the Jurassic the bed of the channel between northern Central America and northwestern South America was folded into a series of submarine ridges striking northwest to southeast. The most westerly of these ridges

ruptured, and a chain of volcanic islands was thrown up extending from the lands of northern Central America southward to south of the Panama Spur. During the Cretaceous this island chain was subjected to erosion and with the Laramide revolution a second volcanic archipelago emerged farther to the northeast. The northern terminus of this archipelago was marked by a fairly extensive island, the "Guanarivas Island" of Lloyd, which was situated in the approximate position of northwestern Costa Rica and southwestern Nicaragua.

Just what conditions prevailed during the Paleocene is not clear. Nygren (1950:2005) stated that the isthmian link was emergent from upper Cretaceous to middle Eocene and suggests that the time was ideal for faunal interchange but cites no evidence to support his conclusion. Lloyd is remarkably vague on this point. Certainly no marine sediments of Danian-Landenian age have been recognized in lower Central America. Whether during the Paleocene there existed an emergent landmass through the isthmian region or whether there remained open a shallow, island-studded portal swept by scouring currents that left no evidence of itself remains to be answered.

There is general broad agreement regarding the tectonic history of lower Central America through the Cenozoic. The Guanarivas chain persisted up to the upper Eocene when subsidence in the channel appears to have resulted in the disappearance of Guanarivas Island and portions of the Panama Spur. Renewed activity during the middle Oligocene witnessed the growth of the Talamanca ridge. By middle Miocene the Talamanca Range had emerged, but an open portal to the north persisted. The isthmian land bridge was finally completed during the Pliocene. During the Quaternary the link attained its present form. Thus, with the possible exception of a Paleocene bridge, geologists can provide biologists with not more than ephemeral volcanic archipelagos rising above shallow seas between the two continents prior to the Pliocene.

There remains still the problem of a late Tertiary barrier between Nuclear Central America and the lands to the north. A sea barrier is not necessary, but such would certainly be convenient. The Balsas portal north of the extant Sierra Madre del Sur of México closed during the upper Cretaceous,

thus leaving the Tehuantepec region as the only possible site for an Atlantic-Pacific portal. On the basis of their studies in this region Durham, Arellano, and Peck (1955) concluded that no such portal could have existed during the Cenozoic. But again, there is always the possibility that a shallow channel washed by scouring currents may not have left any evidence of itself.

Concerning the climate and vegetation of the entire region since the Cretaceous little is known. It is reasonable to assume that at lower elevations humid, tropical conditions prevailed over much of the area up to the present. It is also reasonable to assume that the Madro-Tertiary geoflora had extended southward along the Pacific by the Pliocene. Olson and McGrew (1941:1238) suggested rainforest and forest-margin (? wooded grasslands) as an environment-type in central Honduras during the Pliocene, and Whitmore and Stewart (1965:184) believed similar conditions were probably present in Panamá during the middle Pliocene. On the basis of his analysis of the probable flow of ocean currents along the northwestern coast of South America during Miocene-late Pliocene, Nygren (*op. cit.*:2006) suggested that the adjacent mainland was at that time cooler and drier than at present. Lundell (1937:49) believed that much of the Yucatán Peninsula was considerably drier in the "past" (? Pleistocene) than at present. In view of the fact that extant zoogeographic patterns in Central America developed in post-Miocene times, it is unfortunate that there exist no palynological data to provide us with some hint of the march of climates through that span of time. Vertical zonation must have been well marked through the Pleistocene. Weyl (1955, cited from Weyl, 1961) found evidence of glacial boundaries at the 3500-m level on Cerro Chirripó in Costa Rica. In the north on Iztaccihuatl, White (1962:952) was of the opinion that glaciers may have descended to 2450 m, roughly 2400 m below the present limit of ice fields. To what extent the various zones were lowered or compressed during the height of Pleistocene glaciation, is, however, pure speculation.

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