ZOOGEOGRAFIA

GEOLOGIC-CLIMATIC HISTORY AND ZOOGEOGRAPHIC SIGNIFICANCE OF THE URABA REGION IN NORTHWESTERN COLOMBIA [1].

By

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The lowlands around the Gulf of Urabá, in extreme northwestern Colombia, connect the isthmus of Panamá with the mainland of South America. This general region is still today only very little known geographically and geologically. Dense tropical forests cover the steep uninhabited slopes of the rugged mountain ranges around the Gulf of Urabá in eastern Panamá and northwestern Colombia. The Atrato River empties into the Gulf and drains the most humid area of South America. The lower part of the Atrato Valley is a large marsh bordered by swampy forests. No map exists today which shows in accurate detail the shape and distribution of the hills and mountain ranges of this region and its vegetation cover. Besides the collecting of birds and mammals no comprehensive regional zoological studies have been carried out, although the zoogeographic significance of this general area was recognized by Simpson (1950) and Mayr (1964 a) who considered eastern Panamá and northwestern Colombia as the most important "filter" or barrier zone for the exchange of the Central and South American faunas during the Tertiary and Pleistocene.

I have conducted geological fieldwork in Colombia from 1958 to 1967, particularly in the northern and northwestern part of the country, and have studied the bird fauna of the Urabá region in some detail (Haffer 1959, 1967 a, b, in press a). In this article I present several maps of the Urabá region and attempt to describe the paleogeographic history and zoogeographic significance of this area.

[1] I am very grateful to Eugene Eisenmann, American Museum of Natural History, New York, who has read the manuscript and offered helpful suggestions.

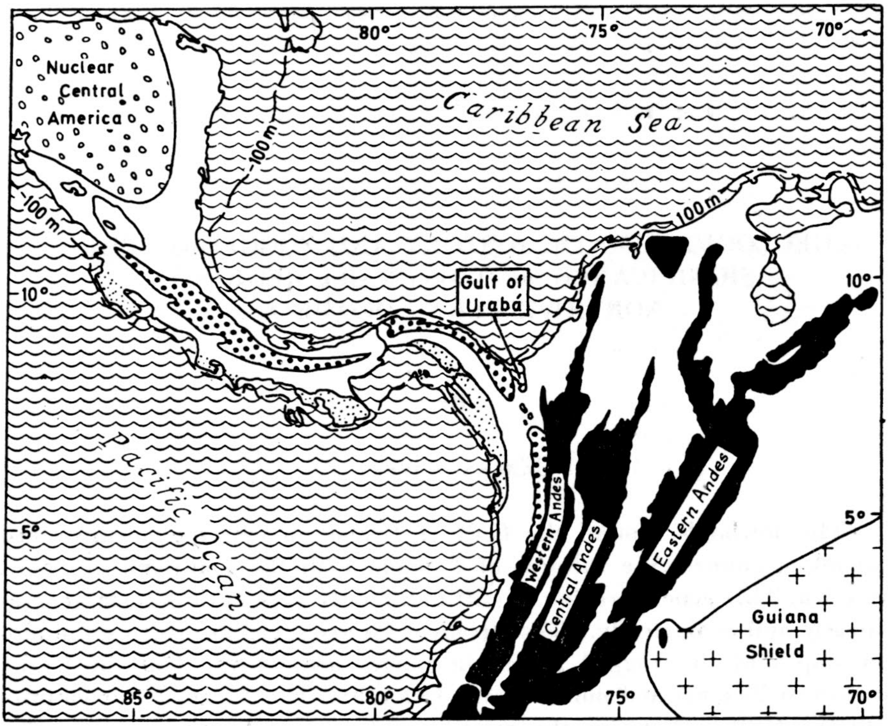

Fig. 1. Geomorphologic units of northwestern South America and southern Central America.

Dotted - Talamanca and Tacarcuna mountains; Stippled mountains of Pacific Costa Rica, Panamá and Colombia.

Topography

The Serranía de Abibe to the southeast of the Gulf of Urabá forms a high northern spur of the Western Andes of Colombia. It reaches 2200 meters elevation at the Alto de Carrizal and drops in a northern direction to 1000 meters east of Chigorodó. Still farther north, in the area east of the Gulf of Urabá between Turbo and the upper Rio Sinú, there are chains of narrow steep ridges, 200 to 700 meters in elevation, which represent the last extensions of the Serranía de Abibe. The elevations given for the Alto de Carepa and Alto de Quimarí in this area on official maps are erroneous, as both peaks are under 1000 meters high.

A rugged basalt range, 100 to 300 meters in elevation, forms the western shore of the Gulf of Urabá and many small islands dot the coas-

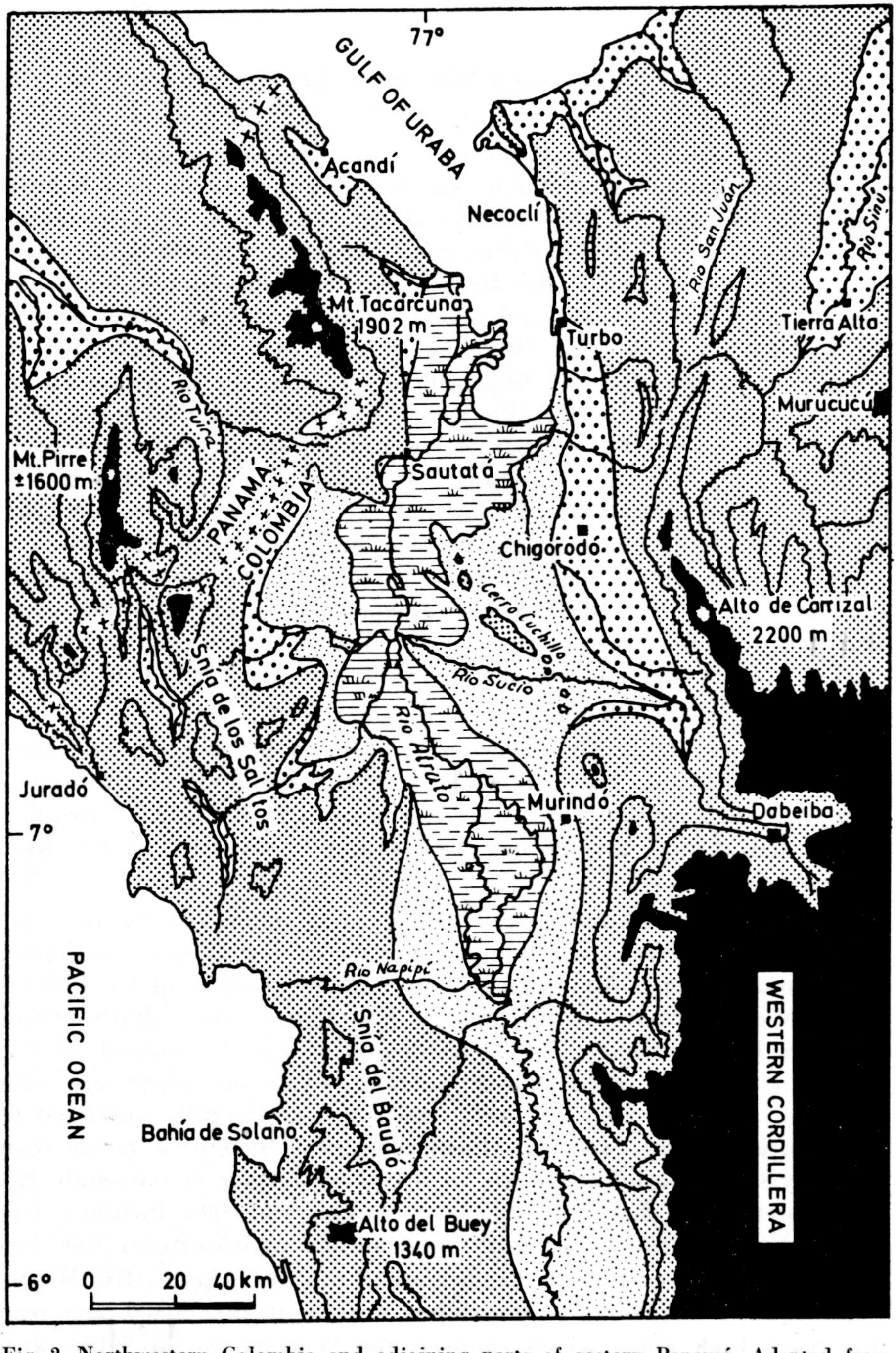

Fig. 2. Northwestern Colombia and adjoining parts of eastern Panamá. Adapted from Mapa topográfico de Urabá (1:100.000), preliminary topographic maps 1:25.000 (Juradó area), Instituto Geográfico Militar, Bogotá; Map of South America, 1:1.000.000, sheets Barranquilla and Bogotá, soil map of the Urabá region (Goosen et al. 1962) and author's observations.

Key: Elevations above 1.000 meters are in black; narrowly stippled — hills and mountains below 1.000 meters (with the 500 meters contour line indicated); dotted — terraces and alluvial plains (partly deforested along the Turbo road, along the Caribbean coast and in the Sinú valley); widely stippled — swampy forest (periodically flooded); dashed — grass and palm swamps, marshes and lagoons.

tal waters. A rough sea beats the rocky coast line during the tradewind season, from December to March. The Serranía del Darién rises farther inland to elevations of 1900 meters at Mt. Tacarcuna. This mountain range forms the Colombian-Panamanian border and terminals abruptly southwest of the Gulf of Urabá. Its geological continuation in a southeastward direction underneath and across the wide swampy lower Atrato Valley (Hubach 1930, Troll 1930, Gansser 1950, Plate V) is indicated by a series of isolated forested hills which rise from the immense Atrato swamps. Cerro Cuchillo ("Knife Ridge") is the highest of these hills (Figure 3 and 4). It has an average elevation of around 600 meters with the highest peak possibly reaching 700 meters. Other low hills to the northwest (Loma Aislada) and southeast of Cerro Cuchillo complete the discontinuous connection of the Serranía del Darién with the Western Andes of Colombia ("Cuchillo bridge"). The size, elevation, number and exact location of these hills are not yet indicated on any published map. The hills stand out very clearly from the densely forested swampy plains of the Atrato Valley and are easily viewed from the foothills of the Serranía de Abibe to the east.

The Atrato river forms an extensive delta on the southwestern shore of the Gulf of Urabá. The delta deposits are carried into the Gulf through numerous small mouths which are blocked by bars of depths of two meters or less. Sandy, mangrove-covered cays line the head of the Gulf north to Turbo.

A series of steep and rugged basalt ranges follow the Pacific coast of Colombia (Serranía del Baudó, Serranía de los Saltos), continuing into eastern Panamá (Mt. Sapo, Mt. Pirre). The elevation of Mt. Pirre is given on official maps as 1615 meters. Ch. Myers' (1966) Lufft pocket altimeter indicated only 1550 meters elevation for the summit of this mountain. The Mt. Pirre massif and the Tacarcuna range are connected by a series of low hills which are geologically unrelated to these basalt ridges. The Mt. Pirre complex is somewhat larger than normally shown on official maps, as it extends farther to the south. Recently published charts of this area (scale 1:25.000; Instituto Geográfico Militar, Bogotá, Colombia) indicate mountains of over 1000 meters elevation just east of the headwaters of the Rio Salaquí (Rio Montorodó) at the Panamanian border. When working in this area I have seen this fairly high range which connects the Serranía de los Saltos with the Pirre ridge. The Serranía de los Saltos averages 300 to 600 meters in elevation and can be traced south to the head of the Rio Napipí. This ridge is crossed by the upper Ríos Salaquí and Truandó in narrow rocky canyons with numerous impassable rapids. The divide between the ri-

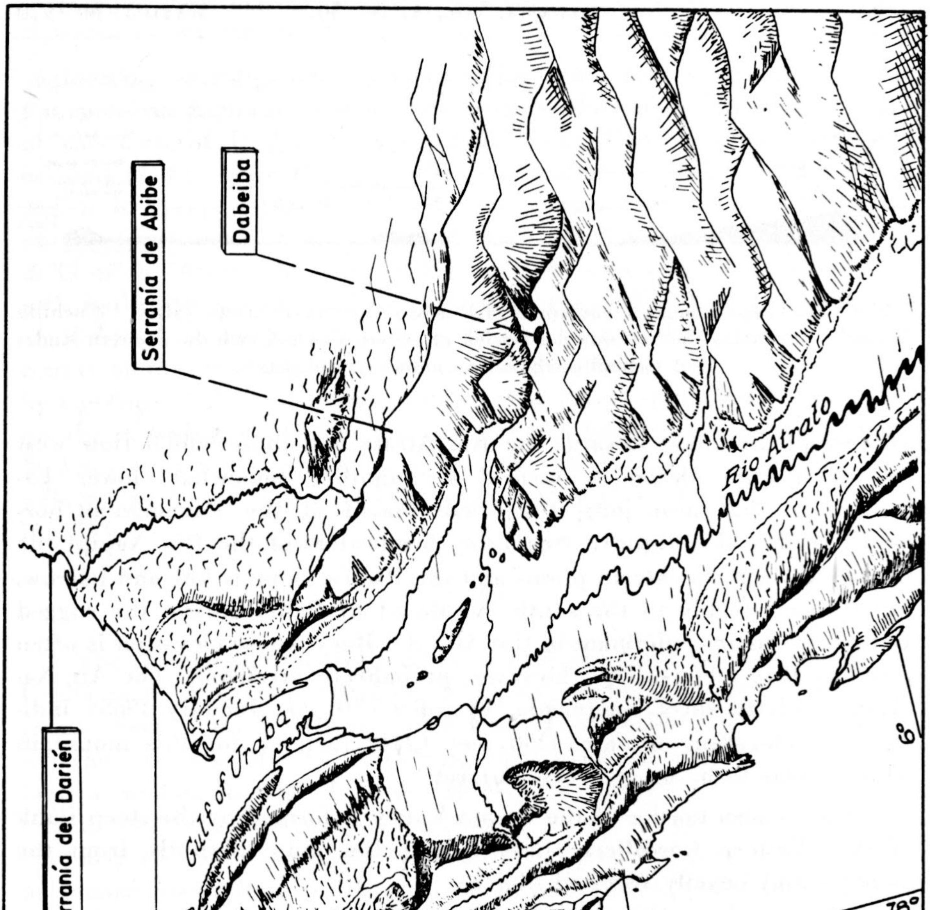

Fig. 3. Northwestern Colombia and adjoining parts of eastern Panamá. View over the region where Central America joins the South American continent.

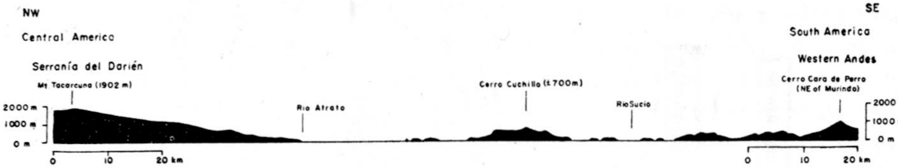

Fig. 4. The discontinuous mountain bridge across the lower Atrato valley ("Cuchillo bridge") connecting the Serranía del Darién of eastern Panamá with the Western Andes of Colombia (based on author's field data).

vers which flow east towards the Río Atrato and those which flow west to the Pacific Ocean is formed by another somewhat lower basalt range that also joins the Pirre massif at the Panamanian border (Alturas de Nique). Near the headwaters of the Río Napipí the divide between the Atrato plains and the Pacific slope is low and narrow, but it rises steeply to the south. Southeast of Bahía Solano the rugged Baudó mountains culminate in the Alto del Buey whose elevation is often given as 1810 meters. This, however, probably is erroneous. The Air Navigation Chart, sheet Guatemala - Ecuador (7th ed., January 1965) indicates an elevation of only 4400 feet (1342 meters) for this mountain which seems to be more nearly correct.

The eastern border of the Atrato Valley is formed by the steep flank of the Western Cordillera which often rises quite abruptly from the swampy and heavily forested plains.

The lowest part of the divide between the Atrato Valley and the Tuira Valley of easternmost Panamá is formed by low hills, 100 to 300 meters in elevation, along the international boundary. A similar divide between the Atrato and San Juan basins to the south is only 110 meters high. These low divides originated during a rather recent (Pleistocene) uplift, prior to which the three basins had communicated freely.

The first description of parts of the country around the Gulf of Urabá and along the Atrato Valley were given by Trautwine (1854), Michler (1861), Selfridge (1874), Wyse (1877) and Collins (1879) who explored the feasability of an inter-Ocean ship canal along the Atrato - San Juan, Atrato - Truandó, Atrato - Tuira and Atrato - Napipí route, respectively. Troll (1930 a, b), Hubach (1930), Vallejo (1928, 1930), Murphy (1936, 1939) and Ossa (1955) published more detailed information on the area. A second effort to study the possibility of a canal connecting the Gulf of Urabá and the Pacific Ocean along the Atrato-Truandó route led to the publication of a "Special report" in 1949. Topographic and engineering investigations in conjunction with the construction of the Panamerican highway system have been conducted in Darién and south of the Gulf of Urabá (Guardia 1957). The first regional geographic account of the entire Pacific lowlands of Colombia, including the Urabá region, was prepared by West (1957) who concentrated his main fieldwork on the Chocó area to the south of the Gulf. Vann (1959) studied the delta of the Atrato river in detail. The distribution of different types of soils in the lower Atrato Valley and around the Gulf of Urabá was mapped on the basis of air photographs by Goosen et al. (1962). Interesting accounts of the Sinú region to the east of the Urabá area were published by Gordon (1957) and Parsons (1952); the latter (1960) also commented on the rediscovery of the ruins of the old Spanish town Santa María la Antigua at the northern margin of the Atrato delta. It was from this village that Vasco Núñez de Balboa set out to discover the Pacific Ocean in 1513.

People

The construction of the road from Dabeiba to Turbo on the Gulf of Urabá some 20 years ago has favored forest clearing by settlers along its course. Several small villages at the crossings of major rivers were greatly enlarged, such as Mutatá, Chigorodó, Apartadó and Currulao. These villages as well as the port of Turbo experienced a surprising increase of activity in 1962 and 1963 when United Fruit Company has successfully concluded preliminary agricultural studies and promoted the establishment of banana plantations in this area. Turbo boomed into activity. Airplanes from Medellín and Montería called daily, prices of land rose steeply, and large tracts of forest on the level plains between Chigorodó and Turbo were cleared for plantations. Workers and new settlers moved in from the interior of Antioquia, clearing additional land along the rivers which drain the hill country east of the Turbo road. A first attempt by a German company to convert parts of the plains south of Turbo into banana plantations around 1910 was abandoned during the first World War.

The small town of Acandí and the fishing willage of Titumate are the only settlements on the western shore of the Gulf of Urabá. They remained essentially unaffected by the recent increase of activity across the Gulf. Communication with Turbo is maintained by boat service. Aerotaxi offers scheduled flights to Acandí and Unguía, west of the mouth of the Atrato river, during some months of the year.

Several villages have also sprung up along the banks of the lower Atrato river where less swampy portions are frequently covered with plantations of banana, rice, corn, etc. Sautatá is a former sugar cane plantation now devoted to cattle raising. It is located at the base of the Serranía del Darién where this range reaches the Río Atrato.

Indians inhabiting the more remote parts of the Urabá region belong to two racial groups: the Cuna indians migrated from eastern Panamá eastward to the Gulf of Urabá during the sixteenth century (West 1957) and inhabit today reservations granted by the Colombian government north of Turbo in the Río Caimán Nuevo - Viejo area and west of the Gulf along the Ríos Arquía, Tigre and Cutí. The Chocó indians (Emberá) live in isolated family groups along the upper reaches of many of the larger rivers to the south and southeast of the Gulf of Urabá, ranging into southern Darién and almost reaching the lower Río Cauca to the east (Reichel-Dolmatoff 1963).

Climate

The humid tropical climate of the Urabá region is characterized by a long rainy season from April to November (barely interrupted by a drier spell in June) and a dry season from December to March. The dry season results from the southward shift of the northern tradewind belt to include the lowlands of northern Colombia during the northern winter. A steady northeasterly wind blows in the Urabá region during the winter months south to about the Río Napipí. I also experienced occasional strong winds somewhat to the south of this river in the Río Uva Valley. Still farther south the influence of the northern tradewinds terminates. The rains fall without a break the year around, so that the climate of the central Chocó region near Quibdó is extremely humid (annual rainfall over 400 inches!, Table 1).

The tradewinds, in crossing the lower Atrato Valley in a southwesterly direction, cause a conspicuous south westward bulging of the isohyets (Figure 5). The winds are strongly felt on the Pacific coast around Juradó, where the coastal waters are smooth as a gentle lake during the months when the tradewinds blow off the land. The rather high rainfall recorded in Juradó during 1934/35 (Table 1) may not be representative for this area. The climate of eastern Panamá is very similar to that of the adjacent Urabá region, and is also characterized by a dry season from December to March.

Schmidt (1952) discussed the rainfall distribution in Colombia and included the Urabá region in the "tradewind area" of northern Colombia which is confirmed by the data given above. More recent summaries of rainfall data were published by West (1957) and Trewartha (1963). The great detail shown on the rainfall map by Trojer (1958) is based on relief interpretation, but is not backed by corresponding field data. The high rainfall area near Villa Arteaga southeast of the Gulf of Urabá

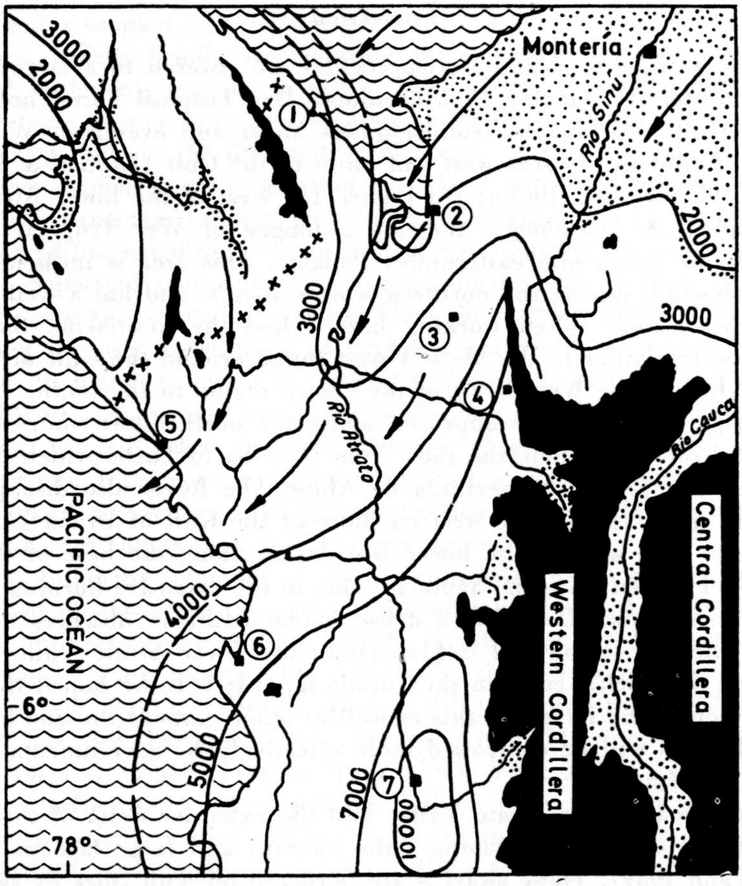

Fig. 5. Annual rainfall in the Urabá region (millimeters per year). Modified from Schmidt (1952) and West (1957). For numbered stations see Table 1; arrows indicate path of trade winds during the dry season; stippled areas are unforested; rainfall in the comparatively dry Andean mountain valleys is *not* mapped on this chart.

probably is connected with the very humid region along the western foot of the Western Andes to the south (Figure 5) rather than a small wet "island", as indicated by Trojer (1958) who located Villa Arteaga too far north on his map. The forest and climate grow increasingly more humid as one goes south from this village along the western slope of the mountains.

Discussions of the climate and rainfall distribution of the adjacent areas of Panamá are included in the articles by Portig (1965) and Hastenrath (1967 b) on Central America. Interesting weather observations over and around the Gulf of Urabá were published by Michler (1861; see also Murphy 1936: 112) and Brückner (1951).

Vegetation

The entire Urabá and Darién regions are covered to a large extent with "rainforest", ranging from deciduous Dry Tropical Forest northeast of the Gulf of Urabá to semideciduous Moist and evergreen Wet and Pluvial Forest in the area west and south of the Gulf (Espinal & Montenegro, 1963; Haffer, 1967 a: see Figure 1). West of the lower Atrato river Espinal & Montenegro indicate a tongue of Wet Tropical Forest that reaches north into easternmost Panamá. This area is influenced by the tradewinds during the northern winter months and has a well developed dry season. When working here I had the impression that the forests were similar to the Moist Forest found around the Gulf of Urabá rather than to the Wet Forest of the Chocó region to the south.

Large clearings have appeared along the northeastern shore of the Gulf of Urabá and along the road from Dabeiba to Turbo which follows the western base of the Serranía de Abibe; the forest also disappeared around the villages on the western shore of the Gulf of Urabá (Acandí, Titumate) and west of the lower Río Atrato along the base of the Serranía del Darién (Unguía, Sautatá). Due to the extensive burning of the forests in northern Colombia a dense smoke (calima) obscures the sky during the dry season and is blown into the lower Atrato Valley, even reaching the Pacific coast in the Juradó area. It is to be hoped that the destruction of the forests in this as well as other parts of the South American Tropics will be controlled more effectively by governmental agencies in the future.

The broad lower Atrato Valley and the extensive delta of this river are covered with grass swamps, palm swamps and large lagoons (West 1957, Vann 1959). These swamps are bordered on both sides by swampy forests which are flooded during the wet season. Mangrove swamps form the coast line of the head of the Gulf of Urabá from the mouth of the Río Atrato to Turbo on the eastern shore.

Paleogeographic and paleoclimatic history of the north-Andean region and southern Central America [1].

Extensive fieldwork has been carried out in the northern part of the Neotropical Region in recent decades and much new data has come to light which aids in our attempt at reconstructing the geological history of Colombia and southern Central America. Nevertheless, there are still unexplored areas of the more remote forest covered mountains and low-

[1] Published with permission of the Colombian Petroleum Company, Bogotá, Colombia.

lands and a number of problems remain to be resolved by future investigations. Before briefly summarizing the presently known facts a few general statements may be in order. Most of the deposits which record the geologic history were accumulated under water cover in sedimentary basins and show us the distribution of oceans and inland seas. However, no direct evidence of the location of a land mass is available in most cases. The existence, location and shape of the rising land areas can only be inferred but not directly be proven. It also happens too often that previously deposited sediments were eroded during later periods of uplift, thus erasing the geological record. These inherent difficulties in reconstructing the past distribution of land and sea should be borne in mind for our discussion below. It is especially difficult to estimate the amount of uplift of a given land mass and its absolute elevation above sea level. Another problem refers to the correlation of geologic strata of far distant regions. Incorrect correlation may lead to differences in the interpretation of the sequence of geologic events which differences may be only apparent rather than real and vice versa.

The following summary of present knowledge of the paleogeographic history of northwestern Colombia and southern Central America is based on the publications by Hubach (1930), Troll (1930), Schuchert (1935), Woodring & Thompson (1949), Gansser (1950), Nygren (1950), Woodring (1954), Belding (1955), Terry (1956), Hofstetter (1960), Bürgl (1961), van der Hammen (1961), Dengo (1962), Harrington (1962), Jacobs, Bürgl & Conley (1963), Weyl (1961, 1965, 1966), Lloyd (1963), Maldonado-Koerdell (1964), and Henningsen (1966 a, b). It was checked against the results of the author's fieldwork in Colombia, particularly in the northern and northwestern parts of the country from 1958 to 1967.

Our inquiry into the geologic past is confined to the Upper Cretaceous and Tertiary, as direct geologic information prior to that period is very scanty or missing in the area under discussion. The paleogeographic evolution of northwestern Colombia and southern Central America is illustrated on Figure 6.

UPPER CRETACEOUS

The broad geosyncline of the Colombian Andes developed during the Upper Jurassic and Lower Cretaceous as a rapidly sinking sedimentary basin between the large land mass of the Guiana Shield to the east and the more or less stable floor of the Pacific Ocean to the west. It probably also comprised southern Central America. An extremely thick sequence of submarine lava flows accumulated in the central and western parts of this geosynclinal basin (Western Andes of Colombia, eastern

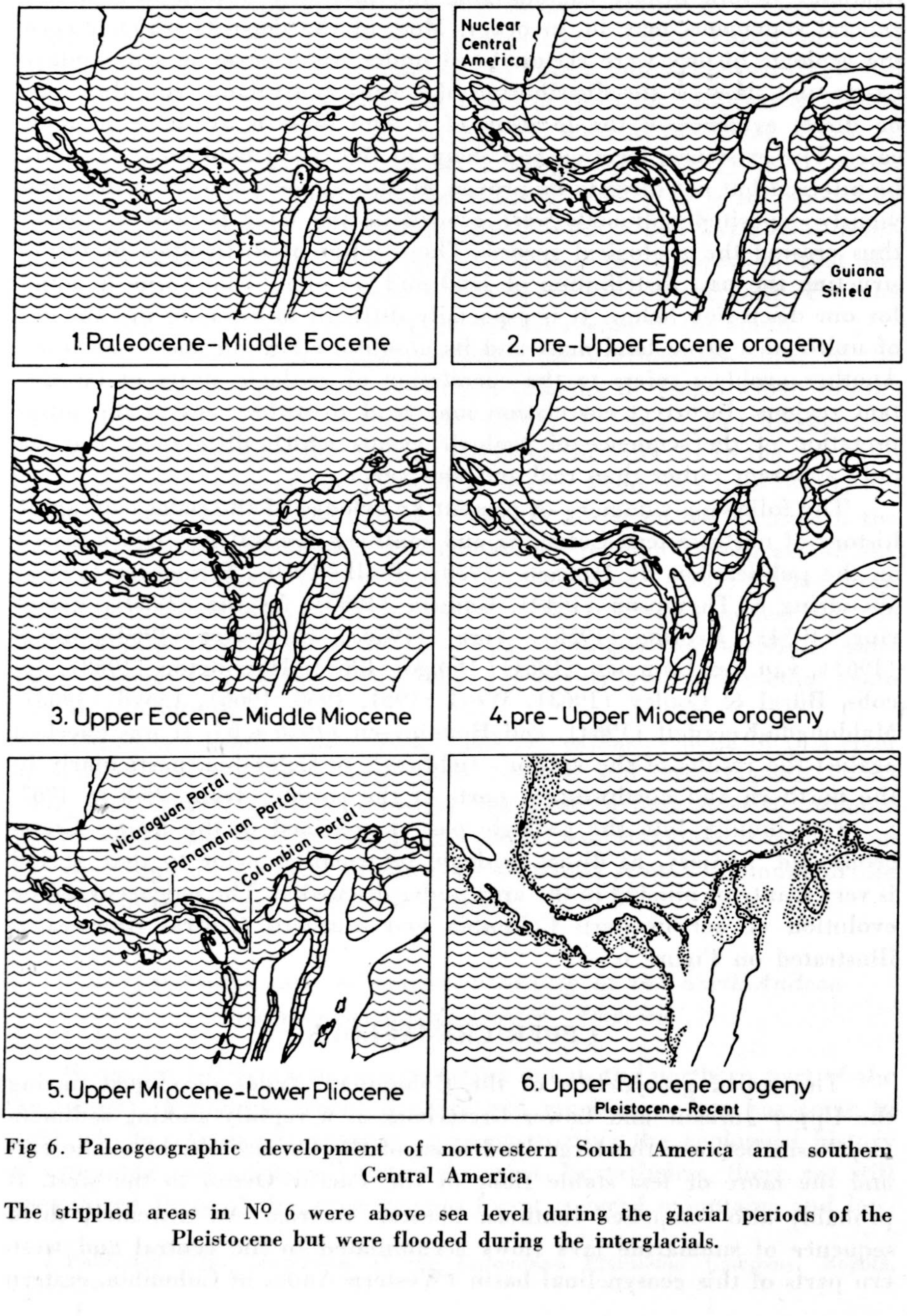

Fig 6. Paleogeographic development of nortwestern South America and southern Central America.

The stippled areas in Nº 6 were above sea level during the glacial periods of the Pleistocene but were flooded during the interglacials.

& central Panamá). Only thin intercalations of fossil bearing cherty sediments are found interbedded with these largely volcanic deposits. Non volcanic calcareous strata and shales are found towards the margins of the geosyncline, i.e. in the basin of the Eastern Andes of Colombia and in parts of present northern Central America south to Nicaragua and Costa Rica. Sections from a transitional facies in westernmost Panamá and southern Costa Rica have been described and paleontologically dated by Fisher & Pessagno (1965) and Henningsen (1966 a, b), respectively. It appears that the land areas of parts of present Guatemala-Nicaragua and South America (Guiana Shield) remained separated by a wide ocean covering most of southern Central America and Colombia during the Upper Cretaceous. Some scattered volcanic islands in the Pacific Ocean southwest of Costa Rica and in the Caribbean Sea, and others outlining parts of the Central Cordillera of the Colombian Andes may already have been above sea level.

TERTIARY

Paleocene-Middle Eocene: Northern Central America was uplifted during lowermost Tertiary time and remained connected with North America as a southern peninsula ever since [1]. Towards the opposite margin of the eugeosyncline parts of the Eastern Andes of Colombia emerged above sea level, and continued to rise gently as did the somewhat older Central Cordillera. Otherwise the Upper Cretaceous paleogeographic conditions probably did not change considerably during Paleocene and Lower Eocene time, although the geological record is admittedly scarce in western Colombia and in southern Central America. This is mainly due to intensive volcanic activity towards the end of the Middle Eocene which obscured the previous geologic history in large areas, particulary in Costa Rica, Panamá and western Colombia.

There is no field evidence for strong orogenic movements in our area during the Upper Cretaceuos-Paleocene or for the existence of a continuous landbridge connecting Central and South America during this time interval. Sedimentation continued uninterruptedly from late Cretaceous into the Paleocene and Eocene in westernmost Panamá (Fisher & Pessagno 1965). Various isolated fault blocks of Paleocene-Lower Eocene shales within the volcanic "basement complex" of Panamá (Terry 1956: 28) and nortwestern Colombia (Gansser 1950; Haffer unpubl.), partly intruded by the volcanics, indicate the continuation of marine sedimentation also in these areas from late Cretaceous into lowermost Tertiary

[1] This tectonism caused local transgressions of Upper Cretaceous formations in western Costa Rica (Dengo 1962) and the metamorphism of part of the section in Central Nicaragua (Figge 1966) at the southern margin of Nuclear Central America.

time. Henningsen & Weyl (1967: 38) report Paleocene or Eocene siliceous limestone from Pacific coastal Costa Rica near Quepos which was originally believed to belong to the Upper Cretaceous "Nicoya complex". Upper Cretaceous sediments possibly occur in the Serranía del Baudó interbedded in, or in fault contact with, the "basement" rocks. *The temporary existence of a continuous landbridge connecting Nuclear Central America and South America during the late Cretaceous or earliest Tertiary cannot be proven geologically on the basis of presently available field evidence* (which rather favors the interpretation of scattered islands in a wide ocean). A stratigraphic gap at the base of the Tertiary and a partial emergence of Costa Rica, Panamá and northwestern Colombia during Paleocene-Lower Eocene time was postulated by Nygren (1950), Lloyd (1963: "Panamá spur"), Weyl (1965, 1966) and Henningsen (1966 a, b). This interpretation, however, is strictly hypotetical! It has been based upon the assumption of an Upper Cretaceous age of the "basement complex" which is only known to be older than the transgressing Upper Eocene strata and may be largely of Lower to Middle Eocene age (see below).

pre-Upper Eocene orogeny: Tectonic movements at the end of the Middle Eocene have been of great paleogeographic importance over large parts of the north - Andean region, southern Central America, and the Antilles. In our area long submarine volcanic ridges were built up by thick basaltic and andesitic lava flows which often must have reached above sea level as chains of volcanic islands. These islands outlined the present configuration of Panamá and western Colombia for the first time: A long island arc followed the Colombian Pacific coast from Gorgona Island over the Baudó mountains northwestward into southeastern Panamá (Mt. Sapo, Mt. Pirre). The Serranía de San Blas - Darién (Mt. Tacarcuna) probably formed a long series of islands which may have been connected temporarily with the Western Andes of Colombia across the present lower Atrato Valley ("Cuchillo bridge"). The Serranía de Abibe southeast of the Gulf of Urabá also consists of basic igneous rocks which probably originated during this orogeny. Large ocean areas of central Panamá were affected by this extensive Eocene volcanic activity and blocks of older Cretaceous and Paleocene volcanics and sediments have been in part slightly metamorphosed, uplifted and included in the "basement complex". The Colombian Andes and the Caribbean Ranges of Venezuela (Mencher 1963) experienced a period of folding and uplift as evidenced by widespread transgressions of Upper Eocene strata. The intensity of the orogeny and volcanic activity probably decreased towards Costa Rica where it may have terminated in the area of the present Talamanca range.

The Lower Tertiary age of the extensive volcanic activity of western Colombia is indicated by "...titan augite dolerites and basalts, augite diabases and augite gabbros, intruding white algal limestones of Middle Eocene age, and complex Paleocene and Eocene siliceous shales, as well as green and reddish hornstones of the same age. Limestones and siliceous shales often form isolated blocks within the igneous mases. Similar occurrences were observed further to the North, between Cabo Corrientes and Panamá". (Gansser 1950: 235). Since the mountain ranges of the Coastal Cordillera of Colombia continue into Panamá, it seems probable that large portions of the basaltic extrusives composing the "basement complex" of Panamá and parts of Costa Rica are also Lower Tertiary rather than Upper Cretaceous in age [1].

Upper Eocene-Middle Miocene: Shallow seas dotted with islands covered the area of the Eocene volcanism in Panamá and western Colombia. The Upper Eocene calcareous sediments deposited unconformably on the basaltic "basement complex" in these areas initiate a relatively quiet period of sedimentation, comprising the Oligocene and Lower to Middle Miocene. During these periods many of the volcanic islands which had appeared in southern Central America and western Colombia foundered and were covered by the extensive Oligo-Miocene seas of the mid-American channel. Volcanic activity continued only in restricted areas of Panamá and off the Pacific coast of Costa Rica where Lloyd (1963) and Dengo (1962) assume the presence of a volcanic island arc which yielded the sediments for the Costa Rican-Panamanian trough.

pre-Upper Miocene orogeny: The next period of major folding and faulting occurred toward the end of the Middle Miocene or at the beginning of the Upper Miocene. All Andean cordilleras and the chains of islands of southern Central America and western Colombia were strongly uplifted by this tectonism as well as during the subsequent period of plutonic activity (granites and granodiorites of the Costa Rican Talamanca range, in western Panamá and parts of the Serranía del Darién [2], Cerro Cuchillo and in the Western Andes of Colombia). The northern extensions of the Eastern Andes, i.e. Serranía de Perijá and the Mérida Andes of west-

[1] An interesting cross section through the Coastal Cordillera of Colombia along the Río Napipí (latitude 6º 40' N), also worked by this author, was published in Böckh, Lees & Richardson (1929, p. 166, Plate 21) and reproduced by Gerth (1955, p. 132, with incorrect ages assigned to the various horizons). The older Tertiary horizons are folded and faulted in the foothills west of the Río Atrato. The oldest shales are slightly metamorphic and are intruded by the basaltic igneous rock. These shales may not be older than Paleocene to Lower Eocene.

[2] Terry (1956) gathered the scattered records of granitic intrusive rocks from these areas. This author has seen major outcrops of granodiorite just west of Unguia at the southeastern end of the Serranía del Darién. This occurrence may be connected underneath an alluvial cover with the granodioritic stock of the isolated Cerro Cuchillo which rises from the swamps south of the Gulf of Urabá (Hubach, 1930, Troll 1930).

ern Venezuela, as well as the Talamanca range of southern Central America were strongly uplifted. The Serranía del Darién was again temporarily connected with the Western Andes ("Cuchillo bridge"). There are geological reasons to assume that this connection lasted for only a short period after which the Cuchillo bridge was again submerged. Browsing mammals have reached central Panamá from North America during the early Middle Miocene (Whitmore & Stewart 1965), although a complete land connection with northern Central America is not known to have existed during this time interval. These authors assume the existence of a seaway in the Urabá region separating the San Blas area of eastern Panamá (Tacarcuna range) from the Colombian Andes throughout the Tertiary. The repeated uplift of the "Cuchillo bridge" south of the present Gulf of Urabá makes this interpretation highly unlikely.

The present orographic configuration of the area under discussion originated during this pre-Upper Miocene orogeny when, however, the mountains were still much lower and the present lowlands were still covered by shallow seas.

Upper Miocene-Middle Pliocene: The Nicaraguan, Panamanian and Colombian Portals (Figure 6) remained open during this period. Although the stratigraphy of the Upper Miocene-Pliocene deposits of the area under discussion is still very imperfectly known, it seems probable that the last connection of the Atlantic and Pacific Ocean existed through the Colombian Portal in the lower Atrato Valley. This water gap connected the Caribbean Sea of the Gulf of Urabá (including the eastwardly adjoining lowlands of northern Colombia) with the Pacific Chocó basin to the south. This basin communicated freely with the Tuira basin of eastern Panamá and with the Pacific Ocean through what is now the valley of the Río San Juan.

Upper Pliocene orogeny: The final tectonism took place during the Upper Pliocene when the folding and faulting also affected the sedimentary basins surrounding and separating the present mountain ranges, i.e. the Tuira basin, Atrato basin, Sinú basin, etc. Large parts of the present lowlands were raised above sea level during this time interval, and the final connection of North and South America along the isthmus of southern Central America was established. As a result of this orogeny the mountains of southern Central America and of the northern Andes were uplifted to about their present elevation around the turn Pliocene-Pleistocene (van der Hammen 1961 a).

QUATERNARY

The post-orogenic Uppermost Pliocene Tilatá Formation of the Sabana de Bogotá in the Eastern Andes of Colombia still contains seeds and pollen of a rich, purely tropical lowland flora (Hubach 1958, van der Hammen & González 1964, van der Hammen 1966). On the other hand, the overlying Pleistocene Sabana Formation yielded exclusively pollen of an upland flora under cool climate (van der Hammen & González 1964, van der Hammen 1966). This indicates that the main uplift of the Colombian Andes probably took place during the time interval uppermost Pliocene-lowermost Pleistocene. Still more recent vertical movements of the mountains are indicated by the tilting and faulting of Pleistocene gravel beds in these areas.

The highest peaks of the Talamance range in Costa Rica were glaciated only during the last glacial period which points to a recent uplift or this range. Large mountains plateau areas, presently at 1000 to 2000 meters elevation or more, are characterized by a very low relief and are deeply dissected at their margins by narrow river canyons. This low relief probably originated during a period of pronounced erosion after the Pliocene tectonism in Upper Pliocene time. The uplift to the present elevation occurred around the turn of the Pliocene-Pleistocene continuing to the present time. The rapid and very late uplift of the mountains in the area under discussion has been emphasized by various authors. The mountain ranges of central portion of the Andean system in Perú and Bolivia may have reached appreciable elevations already during the Upper Tertiary. Ahlfeld & Branisa (1960) believe that part of the Bolivian Andes had attained 1500 to 2000 meters elevation at the end of the Miocene. This assumption, however, needs to be confirmed by more conclusive evidence. The present elevation of the Andes in these areas was reached during the late Pliocene and Pleistocene periods of uplift (Machatschek 1944).

Environmental conditions in northern Colombia and southern Central America during the Pleistocene were influenced by sea level fluctuations and by alternating dry and humid climatic periods. During the glacial periods sea level was lowered by about 100 meters or more. On the other hand, sea level rose by about 30 to 50 meters above the present level during the interglacials, thus flooding the Maracaibo basin and great parts of the north Colombian plains and the lower Atrato Valley (Link 1927, Haffer 1967 a). Refrigeration of the climate during the glacial periods of the Pleistocene was not strong enough to permanently reduce the faunas and floras of the tropical lowlands. However, humid and dry climatic periods caused drastic contraction and expansion of forest and non-forest vegetation, respectively, in northern South and Central America. Similar, although less severe, climatic fluctuations continued during the post-Pleistocene up to the present time (Wilhelmy 1954, van der Hammen & Gonzalez 1960, van der Hammen 1961, Haffer 1967 a, b).

A clear understanding of the causes of these climatic changes and their correlation with the glacial and interglacial periods has not yet been reached (see discussion in Büdel 1949, 1951, 1963; Wilhelmy 1957, Maarleveld & van der Hammen 1959, Flohn 1963, Kessler 1963, Schwarzbach 1963: 189, Butzer 1964: 328 - 334, Galloway 1965, Flint 1963, Messerli 1966, Blüthgen 1966, Moreau 1966: 42 ff.). In general, lower average temperatures and correspondingly reduced evaporation must have increased the humidity in the tropical lowlands during the glacial periods. Increased humidity and slightly cooler winds would increase cloud cover, thus further reducting temperature and creating ecological conditions similar to those of the "Subtropical" life zone of the mountain slope. Possibly the equatorial rain belt was contracted during the dry-warm interglacials with the result that the northwardly adjoining tradewind belt expanded to the south and the humid forests were pushed southward on both sides of the Andes. A strengthened influence of the tradewinds in northern Colombia would increase the length of the winter dry season and would eventually prohibit the growth of heavy forests in large parts of these areas. The present connection between the Central American and northwest Colombian forests probably was interrupted in the Urabá region during several of these dry climatic periods (Haffer 1967 a). A southward shift and westward extension of the abnormally dry climatic zone along the northern coast of South America (Lahey 1958) during the interglacials also may have been in part responsible for the increased aridity of the climate and a corresponding reduction of forest growth in northern South and southern Central America. Probably only a few rather restricted forest refugia remained along the Caribbean slope of Central America (Honduras, Nicaragua, Costa Rica), on the Pacific slope of southwestern Costa Rica and adjacent Panamá (Chiriquí Refuge), in the central Chocó region of western Colombia (Chocó Refuge), at the northern base of the Western and Central Andes (Nechí Refuge), and at the eastern base of the Serranía de Perijá (Catatumbo Refuge). Additional isolated forests probably existed on the northern and northeastern slopes of the mountains of eastern Panamá, along the base of the mountains on both sides of the Colombian Magdalena Valley, and on the northern slope of the Sierra Nevada de Santa Marta near the Caribbean coast. These isolated forests to the west, north and east of the Andes were broadly connected in the north Colombian lowlands during humid climatic periods which probably coincided with the glacial periods (when sea level was lowered and the shallow Lake Maracaibo and the Gulf of Urabá had disappeared). It is to be hoped that future palynological studies of Pleistocene and post-Pleistocene sediments of the Urabá region and other parts of northern South to Central America will provide us with more detailed data on the climatic and vegetational history of these areas [1].

The effects of the Pleistocene refrigeration were more severe in the highlands of tropical mountains than in the surrounding lowlands, due to a possible increase of the temperature gradient in the lower latitudes (Mortensen 1957, Wilhelmy 1957). For this reason the climatic transition from the tropical lowlands to the cool mountain life zones probably was more abrupt. The Colombian Andes as well as the highest peaks of the Costa Rican Talamanca range were glaciated during the cold periods. The "Temperate" and "Subtropical" life zones were lowered considerably, thus attaining a much greater continuity along the mountain slopes than they have today. At the height of some of the glacial periods the lower limit of the "Temperate Zone" may have been located at about 1000 meters and that of the "Subtropical Zone" at about 500 to 600 meters above then sea level (Haffer 1967 a, e). A great number of animal species presently restricted to the foothills and lower slopes of the mountains ranged across the intervening lowlands where temperatures have been about 4º C lower than today (Wilhelmy 1957). Reduced evaporation and more continued cloud cover must have resulted in a substancial increase of the humidity of the tropical lowland forest habitat. Increased cloud cover would cause of itself a reduction in temperature, as well as increase in humidity.

The position of the Recent and Upper Pleistocene snow lines is lower in the Colombian Andes and in southern Central America than in the Mexican and Peruvian Andes to the north and south, respectively (Wilhelmy 1957, Hastenrath 1967 a). This is partly due to the increased humidity of southern Central America and Colombia as compared to the Peruvian Andes. The northward rise of the snow lines from Costa Rica toward México is contrary to the poleward decrease of temperature and is at least partly due to the heating effect of the Mexican mountain mass (Hastenrath 1963). A particulary low position of the "Subtropical" zone on the mountain slopes during the glacial periods and a strong increase of humidity and "coolness" of the lowlands should be expected in southern Central America and northern Colombia where no heating effect of large mountain masses dampened the climatic effect of the glacial periods in the lower elevations.

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[1] Results of recent field work in other parts of tropical South America support the view of alternation in cool-wet and warm-dry climatic phases during the late Pleistocene and early Recent, as indicated by carbon dating, pollen analysis, human artifacts, and geomorphology (Bigarella 1965, Martin 1964, Lanning 1965, Lanning & Patterson 1967, Wymstra & van der Hammen 1966, Hester 1966, van der Hammen 1967).

Faunal exchange through the Urabá region.

1. *Tertiary.*

The ancestors of the Tertiary South American mammal fauna probably reached the continent over a discontinuous island bridge toward the end of the Upper Cretaceous. Among these were early condylarths, edentates and marsupials (Simpson 1950, Hofstetter 1954, Thenius 1964). Unfortunately the late Cretaceous and lowermost Tertiary paleogeography of western Colombia and southern Central America is very imperfectly known. The existence of a complete land connection of North and South America over the present Central American isthmus and through the Urabá region during this time interval has not been proved geologically, and seems unlikely to this author. The early South American mammal immigrants probably are only a small fraction of a northern fauna. They may indeed have come "across a waterbarrier which blocked other mammals" (Darlington 1957: 364). The history of the freshwater fish fauna of Central America (Myers 1966) also supports the interpretation of a *discontinuous* island bridge between northern Central and South America during lowermost Tertiary time.

Numerous volcanic islands appeared within the wide mid-American chanel toward the end of the Middle Eocene and again toward the end of the Middle Miocene, providing twice a temporary discontinuous connection between northern Central America and the gently rising Andes of Colombia. The "Cuchillo bridge" of the Urabá region, connecting the Panamanian islands with the Tertiary Western Andes of Colombia, probably has been above sea level during these periods. The old and late "island hoppers" (Simpson 1950, 1965), including early rodents, primates, and procyonids, very probably reached South America over these island bridges. A rather intensive exchange of northern and southern Tertiary bird faunas probably took place during these time intervals (Mayr 1964 a, b). The periods of uplift were both followed by periods of subsidence when large portions of the land areas foundered and became again covered by the Oligo-Miocene and Lower Pliocene seas, respectively. The process of foundering was less pronounced in the Lower Pliocene than during the Oligocene. The Nicaraguan, Panamanian and Colombian Portals connecting the Atlantic and Pacific Oceans, remained open until Upper Pliocene time. The Colombian Portal probably was the last to be closed by the Cuchillo bridge south of the present Gulf of Urabá. A Lower Pliocene mammal fauna of Honduras is still exclusively of North American origin, indicating that most of the larger South American mammals were not yet able to advance across the Cuchillo bridge and the Isthmus of Panamá at that time (Olson & McGrew 1941).

2. *Quaternary.*

The exchange of the Middle and South American faunas during the generally warm Tertiary period was mainly influenced by the emergence and subsidence of low islands and partial land bridges in southern Central America and northwestern Colombia. On the other hand, faunal migrations in this region during the Quaternary were mainly determined by the following events: (1) The closing of the last watergap separating Central and South America in the Urabá region during the late Pliocene, thereby establishing a continuous landbridge which had never existed before. (2) The strong uplift of the South and Central American mountains which caused the expansion of dense tropical forests along the foothills on the windward side and an increased aridity of the lowlands on the leeward side. The mountains themselves formed new zoogeographic barriers which had not existed before. (3) The alternation of cold-wet and warm-dry climatic phases throughout the Quaternary. These climatic changes influenced the distribution of forest and non-forest vegetation and also determined the changing altitudinal position of the temperature life zones and their continuity or discontinuity along the slopes of the mountain ranges.

During the humid periods the Urabá region probably was covered with heavier forest than today. The Gulf had disappeared, thus providing a broad connection of the South and Middle American lowland forest faunas which intermingled extensively. A large number of species rectricted to the lower slopes of the mountains during the interglacials now ranged continuosly across the lowlands (Griscom 1932, Haffer 1967 e). The presently isolated small hills of the Cuchillo bridge were less eroded during the early Pleistocene and probably provided a more complete connection of the Western Andes of Colombia and the Serranía del Darién of eastern Panamá. The assumption of the former existence of high mountain bridges in central Panamá and south of the Gulf of Urabá (Chapman 1917) seems to be unnecessary.

During the interglacial arid climatic periods drier types of vegetation probably replaced the forests in the Urabá region which became restricted to comparatively small refuge areas in certain foothill regions of the mountains. The non forest faunas of Central and South America probably were broadly connected in the Urabá region [1]. However, the partial flooding of the north Colombian plains and of the Atrato Valley may have hindered the faunal exchange to a certain extent. The post-Pleistocene

[1] Eisenmann (1955) already pointed out that the gap in the range of bird species of semi-arid areas in southern Costa Rica and in Panamá was best explained by changes in climate which resulted in forests that extirpated a former connecting population.

dry phases were not accompanied by pronounced sea level fluctuations. However, we do not know whether thes latter periods have been arid enough to allow an unrestricted exchange of the non-forest faunas through Panamá and the Urabá region (Haffer 1967 d).

The forest fauna of the northern foothills of the Colombian Andes ranges northward through Central America today, mainly occupying the forested Caribbean slope. On the other hand, part of the fauna of the drier portions of the Caribbean lowlands of Colombia and Venezuela reoccurs in Pacific Panamá "crossing over" the forests of the Urabá region (Chapman 1917, Dunn 1940, Duellman 1966, Savage 1966). This "crossing over" of the two faunas might be explained historically on the basis of past climatic cycles which caused the repeated withdrawal and return of forest and non-forest vegetation, respectively, in the Urabá and Darién regions.

The above discussion indicates that the Pleistocene and post-Pleistocene differentiation of the Neotropical fauna at the species and subspecies level probably was mainly determined by alternating dry and humid climatic phases and the corresponding changes in the distribution of forest and non-forest vegetation and their respective faunas. Comparatively small animal populations were isolated in various refuge areas. Here they deviated from one another and from their parental population by selection and chance, eventually developing into new subspecies and species and re-expanding their ranges during later favorable climatic periods (Haffer 1967 a). This interpretation closely resembles the historic analysis of the Ethiopian and Holarctic faunas recently presented by Moreau (1966) and the Lattin (1967). In contrast to the northern continents and Africa details on the changing vegetation cover and the location of most refuge areas during each of the various climatic phases are not yet known in South America.

It seems possible that new species originated in many animal families during the Pleistocene, besides a great number of more weakly differentiated subspecies. A few zoogeographic notes on several groups, with reference to the Urabá region, are given in systematic order below:

Some of the speciation phenomena of the *butterfly* genus *Heliconius* and of the Central American *herpetofauna* described by Emsley (1965) and Savage (1966) might be explained by the Pleistocene climatic rather than the Tertiary paleogeographic history of the northern Neotropical region.

The *freshwater fish fauna* of the Atrato and Tuira rivers, the latter in easternmost Panamá, are extremely similar (Hildebrand 1938, Myers 1966). This is explained by the fact that the uplift of the hills separating the headwaters of these rivers along the Panamanian-Colombian boundary probably is a very recent geologic event.

Birds: The great majority of the ancestors of the bird species inhabiting the forested lowlands west of the Andes today, probably advanced into these regions after the final connection with the Amazonian lowlands was established at the end of the Tertiary and when dense forests developed around the rising mountain ranges. The differentiation of the trans-Andean populations was then related mainly to the Pleistocene and post-Pleistocene climatic history of northern South America and of Central America (Haffer 1967 a). Comparatively recent (Pleistocene) speciation in a number of bird families has been discussed by Mengel (1964), Selander (1965) and Moreau (1966 a, b: 9 - 12).

At the present time the Urabá region is the meeting place of various forest bird faunas (Haffer 1967 a, b). These faunas probably developed in different forest refugia during arid climatic phases and came into secondary contact after the return of sufficient forest growth in the Urabá region. The fact that a comparatively large number of allopatric, noninterbreeding species pairs and hybridizing semispecies and subspecies pairs occur in this region is considered evidence for former separation and later (secondary) contact of the populations concerned.

Mammals: Hershkovitz (1966: 746) concluded that a number of northern families of mammals must have reached South America prior to the closing of the last watergap because he felt that "there is slight likelihood that the species and genera of cricetines, canids, procyonids, mustelids, deer, and others could have become peculiary specialized for isolated niches in South America since the Pleistocene only" (1966: 746). The rate of speciation in these families under the constantly changing environmental conditions of the Pleistocene and post-Pleistocene indeed may have been high enough to account for the present differentiation. This is not known to have been the case, but should be kept in mind as a distinct possibility.

A similar situation as found in the bird fauna apparently is present in the mammal fauna of the Urabá region today. The distribution pattern of a number of superspecies indicates a secondary contact of semispecies or species pairs whose members probably met in this area after the return of sufficient forest growth in the recent geologic past. Baird's tapir *(Tapirus bairdi)* of Central America to western Colombia and the South American tapir *(T. terrestris)* come into contact in the valley of the upper Sinú river east of the Gulf of Urabá where specimens of both species have been collected at the same locality one year apart (Hershkovitz 1954). It would be interesting to find out the interrelationship of these two tapirs, whether both are actually sympatric in marginal parts of their ranges or whether they replace each other geographically in the Sinú region as a result of ecologic competition. Hershkovitz (1966: 743) believes that each species of South American tapir represents a separate invasion from the north, *Tapirus bairdi* being the last immigrant. However, the possibility exists that the three forms originated during the Pleistocene in the Neotropical region from only one Pliocene immigrant ancestor: *Tapirus pinchaque* on the rising Andes, *T. terrestris* in the lowlands east and *T. bairdi* west of the Andes. It probably will remain unknown whether the latter species was differentiated in the Chocó Refuge of western Colombia and then moved northward, or whether it originated from a South American immigrant in one of the forest refugia of Central America, later re-entering Colombia from the north. A similar situation is found in the monkey genus *Marikina* (Hershkovitz 1949).

Man: It has been suggested by Sauer (1944), Lothrop (1961), and Reichel-Dolmatoff (1965, see also Hester (1966), that the early American man followed the immigration route of the large browsing mammals, entering South America from the north during a late Pleistocene dry climatic period when the forest had largely disappeared from eastern Panamá and northern Colombia. This assumption is very reasonable in view of the paleoclimatic and zoogeographic evidence discussed above.

Plants: There has not been published any account on the historical phytogeography of the Chocó and Urabá regions which are still very imperfectly known botanically. For this reason no discussion of the above hypothesis of repeated disappearance and return of forest growth in the Urabá region from a botanical point of view is possible at the present time.

The flora of the Pacific lowlands of Colombia seems to be rich in endemic species as indicated by Steyermarck (1964: 117) "...there exists in this department of Colombia a great wealth of endemism and variety in the flora, which species have not been found in other parts of Colombia".

The existence of a continuous landbridge connecting Central and South Central American and Colombian mountains has been described by Penland (1941), Weber (1958), Troll (1959), Lauer (1959), Bader (1960), Knapp (1965), and Hueck (1966). However, none of these authors discusses the evolution of the disjunct distribution pattern of the numerous upland plant species in these areas and their dispersal across the gaps in the mountain ranges.

SUMMARY

The existence of a continuous landbridge connecting Central and South America during the uppermost Cretaceous and/or the lowermost Tertiary

cannot be proven on the basis of presently available field evidence. Scattered outcrops of Upper Cretaceous and Paleocene to Lower Eocene shales indicate the continuation of sedimentation in northwestern Colombia during these time intervals. The volcanic "basement complex" consists mostly of basaltic igneous rocks which intrude Middle Eocene shales and limestones. The pre-Upper Eocene orogeny and the strong pre-Upper Miocene orogeny led to the temporary uplift of the "Cuchillo bridge" which connected the Western Andes of Colombia with the Serranía del Darién of eastern Panamá. Both these orogenies were followed by periods of subsidence when parts of the previously uplifted areas foundered and were covered by the Oligo-Miocene and Upper Miocene-Pliocene seas, respectively. The main uplift of the northern Andes and of the mountains of southern Central America took place during the uppermost Pliocene and lowermost Pleistocene; vertical movements continued throughout the Pleistocene to the present day. The final connection of Central and South America was established during the Upper Pliocene.

The exchange of the Middle and South American faunas during the generally warm Tertiary period was mainly influenced by the emergence and subsidence of low islands and partial land bridges in southern Central America and northwestern Colombia. On the other hand, faunal migrations in these regions during the Quaternary were mainly determined by the following events: (1) The closing of the last water gap separating Central and South America in the Urabá region during the late Pliocene. (2) The strong uplift of the South and Central American mountains which caused the expansión of dense tropical forests along the foot hills on the windward side and the increased aridity of the lowlands on the leeward side. The mountains themselves formed new zoogeographic barriers which had not existed before. (3) The alternation of cold-wet and warm-dry climatic phases throughout the Quaternary. These climatic changes influenced the distribution of forest and non-forest vegetation and also determined the changing altitudinal position of the temperature life zones and their continuity or discontinuity along the slopes of the mountain ranges.

The Urabá region was a transit area for the faunas of the more open and drier vegetation during dry climatic periods of the past and is an important meeting place of various Central and South American forest faunas today.

TABLE 1. Annual precipitation in the Urabá region. Data from Goosen et al. 1962, West 1957 and the Instituto Geográfico Militar, "Agustín Codazzi", Bogotá Colombia.

Station	Year of observation	Annual precipitation in millimeters
1. Acandí	1941 - 1944	3280
2. Turbo	1938 - 39, 1952 - 54, 1959	2062
3. Chigorodó	1951 - 1954, 1960	3415
4. Villa Arteaga	1952 - 1957, 1959 - 1960	5420
5. Juradó	1934/35	4376,7
6. Ciudad Mutis	1945 - 1946, 1958 - 1960	4501
	1959	4142
	1964	4608
7. Quibdó	1932 - 1946, 1949 - 1952	10545

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