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Late Cenozoic uplift and paleogeography of the Colombian Andes: constraints on the development of high-andean biota

Salomon B. Kroonenberg, Jos G.M. Bakker & A. Marian van der Wiel
Department of Soil Science and Geology, Agricultural University, P.O. Box 37, 6700 AA Wageningen, The Netherlands

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Abstract

An analysis of published and newly obtained data on the timing of uplift in the Colombian Andes shows that some areas were already uplifted above the (present) forest line as early as 16 Ma ago. Elsewhere early uplift data (Oligocene- Mid-Miocene) have only been obtained from elevations below 3000 m. Most other areas above 3000 m reached their present altitude only after 6-4 Ma ago by more recent uplift or by the formation of stratovolcanoes on dissected planation surfaces. Accretion of the Panamanian isthmus between 7-3 Ma may have been contemporaneous with the latter, most vigorous Plio-Pleistocene uplift phase in the northernmost Colombian Andes but cannot be related to the earlier phases in the whole Andean chain. The accretion enabled immigration of holarctic species into the Andes. There is no reason to suppose a topographic interruption in the Andean Chain at the Huancabamba deflection during the Tertiary, and hence immigration of australantarctic species depended only on the presence of suitable high-Andean climatic conditions along the whole of the Andean chain.

Introduction

High-andean (> 3000 m) biota in the Colombian Andes, especially the open tundra-like, páramo vegetation above the forest line, have been analysed in detail by numerous studies of the ECOANDES group headed by Prof. Van der Hammen (Van der Hammen & González 1960, Van der Hammen et al. 1973, Van der Hammen 1974, Cleef 1981, Van der Hammen et al. 1983, Van der Hammen & Ruiz 1984, Van der Hammen & Cleef 1986). This biome represents a unique equatorial mountain environment, which only occurs in the higher parts of Costa Rica, Colombia and Ecuador. Van der Hammen & Cleef (1986), following Cleef (1979), distinguished and defined seven geographical floral elements on the base of 259 genera of vascular plants in the páramo region.

– Páramo elements	7.3%
– Other neotropical elements	33.8%
– Austral-antarctic element	9.2%
– Holarctic element	11.0%
– Wide temperate element	19.6%
– Wide tropical element	10.4%
– Cosmopolitan element	7.7%
– Unknown affinity element	
– (probably wide temperate element)	1.0%

The in situ evolution or migration of these elements into the Colombian Andes is closely related to geological development. In situ development of endemic páramo genera requires adaptation of preexisting (neotropical?) genera to temperate equatorial conditions: Late Tertiary to Quaternary uplift of the Andean mountain chain plays an important role, together with simultaneous lowering of the forest line as a result of climatic deterioration. Immigration of Holarctic species is probably related to the closing of the Panamanian isthmus in the Late Tertiary. Immigration of Austral-antarctic species requires consideration of the topographic continuity of the Andean range from the Late Tertiary onward, as well as a certain climatic continuity along the Andean chain.

A fourth factor of importance emerges when the distribution of páramo species is considered: most of them are situated on high-mountain 'islands' separated from each other by lower areas with different vegetation types. The similarity from one páramo island to another requires a former continuity, which is probably related to Pleistocene climatic changes (Van der Hammen et al. 1973, Van der Hammen 1974, Van der Hammen & Cleef 1986).

In this paper we will review the available geological and geomorphological data to establish a tentative chronological framework for the development of high andean biota. The in situ evolutionary process itself is not dealt with here, this has been extensively discussed by Van der Hammen & Cleef (1986).

Present tectonic setting of the Colombian Andes

The Colombian Andes are situated at the junction of four major lithospheric plates, the South American, Caribbean, Nazca and Cocos plates (Fig. 1). The Nazca plate moves eastwards from the East Pacific Rise and is obliquely underthrusted below the South American plate at a rate of 6 cm/year (Meissner et al. 1976), causing recent seismicity and volcanism in the Central and Southern part of the Colombian Andes and the Ecuadorian Andes. Some authors consider the entire Colombian and Ecuadorian Andes as a separate block, which is severed from the South American plate by major strike-slip faults along the front of the Eastern Cordillera (Pennington 1981, Mann & Burke 1984). A major subdivision of the Colombian Andes according to the angle of subduction of the Nazca plate is given by Pennington (1981, cf. also Hall & Wood 1985). The Bucaramanga segment of the Nazca plate is subducted at a low angle of only 20–22°, due to the collision with the Panamanian block or subduction of an aseismic ridge. This led to considerable eastward migration of the deformation belt and hence broadening of the Andean chain as a whole. It also explains the absence of volcanism in this part of the Andes. Along the Cauca segment further south, oceanic crust without resisters in the bottom topography is subducted along an angle of 35° leading to extensive volcanism in the Central Cordillera and a much narrower deformation belt. The Ecuador segment still further south has a similar dip (Pennington 1981).

Meanwhile, the Caribbean plate is moving eastwards, squeezed between the convergent North American and South American plates (Sykes et al. 1982). At the same time the Caribbean Plate is subducted southeastwards below the northwestern corner of the South American plate at a rate of 3.7 cm/year (Sykes et al. 1982). The Cocos plate is subducted northeastwards below the eastwards moving Caribbean Plate at the Pacific coast of Panamá and Costa Rica.

As a result of these movements and associated complicated stress field, considerable crustal shortening takes place in the Colombian Andes in an intricate mosaic of tectonic blocks, each with its own uplift history (Fig. 1). It is beyond the scope of this paper to reconstruct the details of the tectonic history. There are many excellent reviews of the tectonic history of the whole of the Colombian Andes (e.g. Irving 1971, 1975, Zeil 1979, Pennington 1981, Etayo Serna et al. 1983 and the papers in Bonini et al. 1984). We will focus on the uplift chronology from the Early Tertiary onwards, when the present trident-shaped orogenic belt of the Western, Central and Eastern Cordillera had already been formed, but the accretion of the Panamanian Block and the main uplift of the whole mountain chain had not yet taken place.

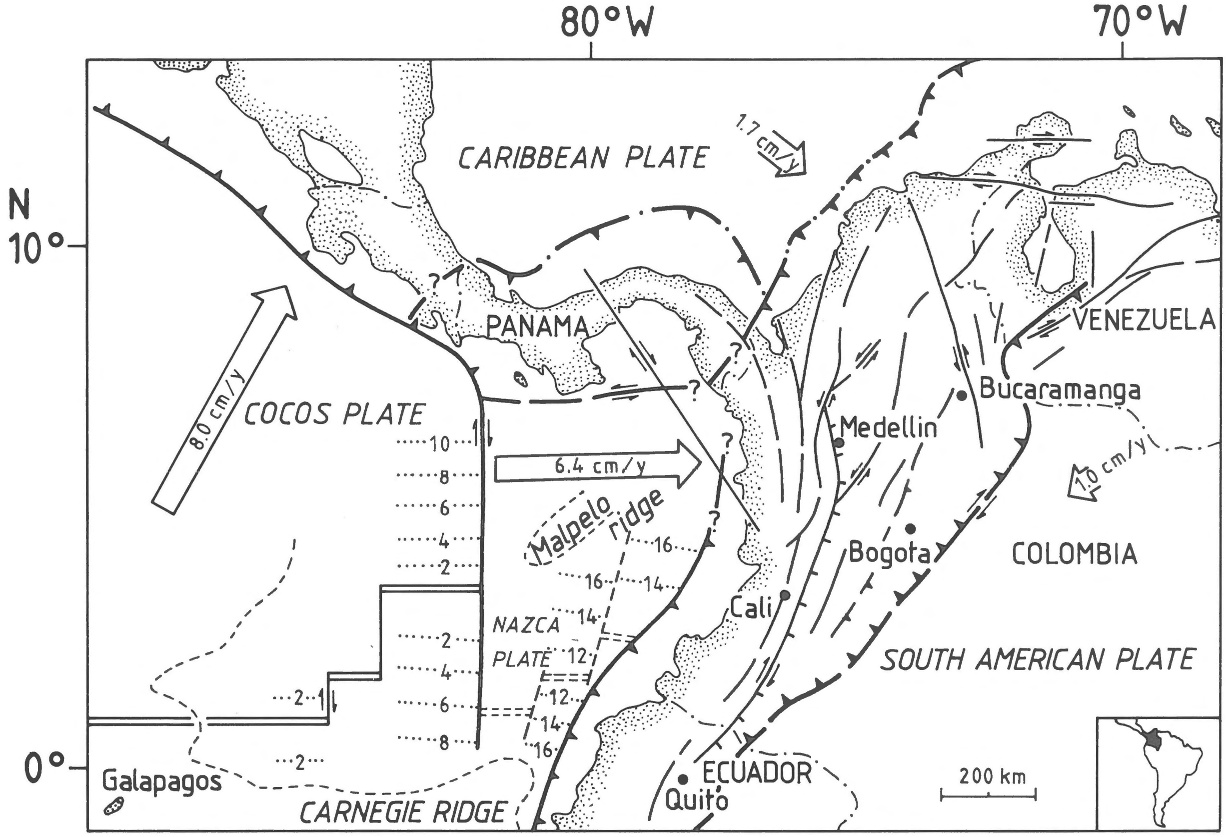

Fig. 1. Plate-tectonic situation of the Colombian Andes.

Late Tertiary and Quaternary uplift of the Colombian Andes

Late orogenic uplift in the Andes was recognized already very early (Berry 1917, Steinmann 1922). The Cenozoic Andean diastrophical cycle, as it was called by Oppenheim (1941) was subdivided in an often cited paper by Van der Hammen (1961) into Eocene Pre-Andean phases, Oligocene Proto-Andean phases and Miocene-Pliocene Eu-Andine phases. This subdivision was based on a rigorous analysis of the stratigraphy of the main Cenozoic basins of the Colombian Andes. Although since then an enormous volume of data has been gathered, much of Van der Hammen's analysis still holds.

In this paper it will be attempted to review the uplift chronology in a complementary way by assembling the data that have been obtained from the mountain massifs themselves. Spectacular new results on uplift chronology have been obtained by fission-track dating of the thermal and erosion history of crystalline massifs, as explained by Wagner et al. (1977) for the Alps. This method has been applied by Kohn et al. (1984) and Shagam et al. (1984) for parts of the Venezuelan and northernmost Colombian Andes, and Van der Wiel & Andriessen (in prep.) in the Southern Colombian Andes. In addition geomorphic evidence of uplift, such as dissected and tilted planation surfaces will be considered.

There are only two areas in Colombia where uplift alone led to the formation of relief elements above the present snow line (now at 4800 m). These are the Sierra Nevada de Santa Marta (5800 m) and the Sierra Nevada del Cocuy (5500 m) (Fig. 2). It is a striking fact that these highest reliefs are also adjacent to the deepest basins in the Andes (see

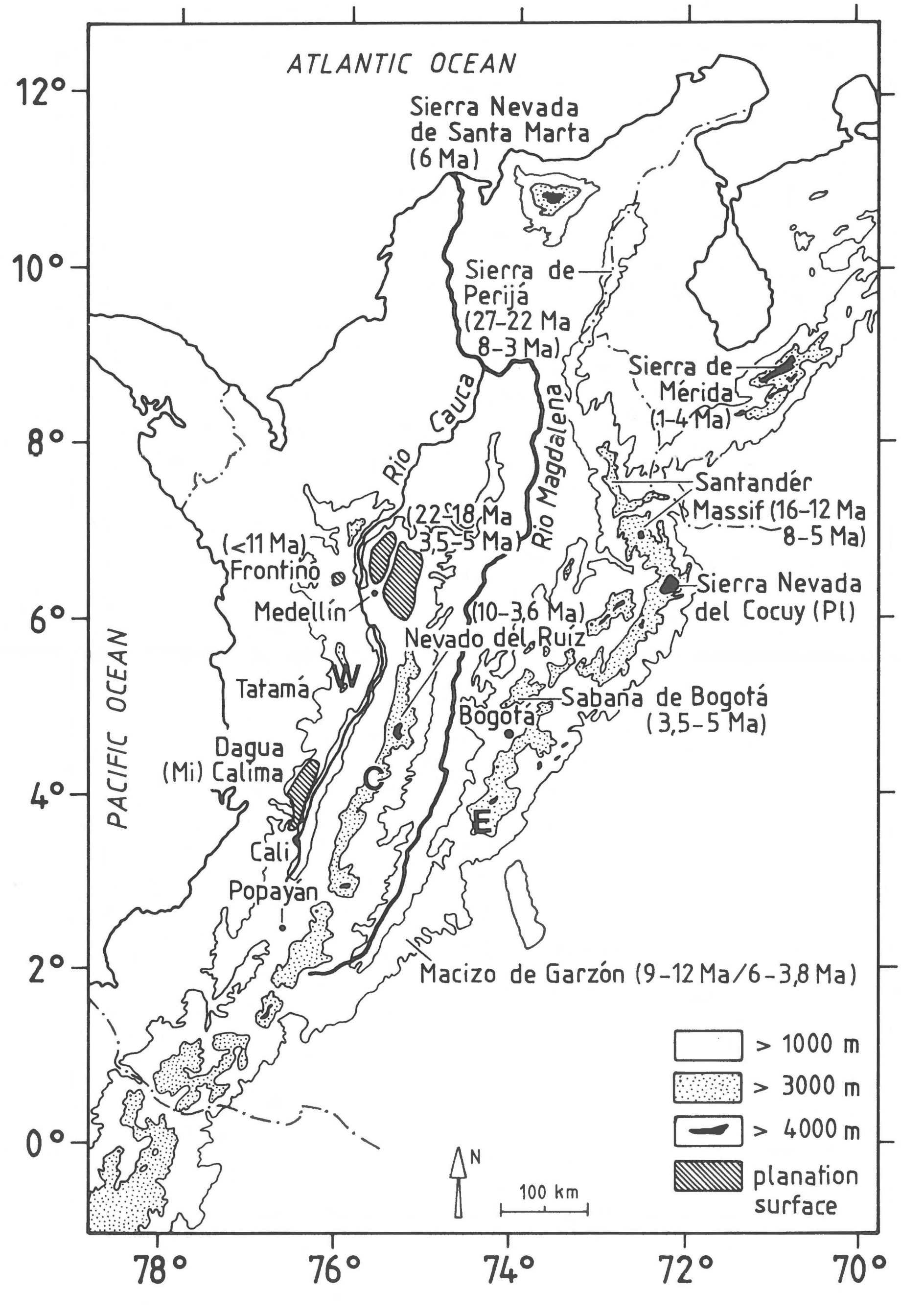

Fig. 2. Compilation of existing uplift data for the Colombian Andes. E, C, W: Eastern, Central and Western Cordillera. Ages between brackets are explained in the text. (Mi) = Miocene, (Pl) = Pliocene.

below). Both areas belong to the low-angle subduction zone of the Bucaramanga segment. The areas further south in the Cauca segment of the Nazca plate that project above 4800 m are Quaternary stratovolcanoes the base of which is usually situated between 3000 and 3500 m (Nevado del Ruiz area, Nevado del Huila area). Areas which have been subject to Pleistocene glaciation are much more widespread; they comprise almost all terrain above 3000 m above sea level. We will now review what is known about uplift in different parts of the Colombian Andes and adjacent areas.

Sierra Nevada de Santa Marta, Sierra de Perijá, and Mérida Andes

The Sierra Nevada de Santa Marta, the highest peak of Colombia (5800 m) consists mainly of basement rocks and is bordered by two major fault systems, the right-lateral Oca fault in the N and the left-lateral Santa Marta-Bucaramanga fault to the west. Towards the SE it is separated from the NE-SW striking Sierra de Perijá by the Cesar valley. The Maracaibo basin further southeast is bounded by the Sierra de Perijá and the Andes de Mérida in Venezuela. These ranges and basins form part of the thrust zone associated with southeastwards subduction of the Caribbean plate below the South American plate. Fission-track data about uplift chronology and rate of the latter two ranges have been published by Shagam et al. (1984) and Kohn et al. (1984). They show that uplift already started in Cretaceous-Paleocene times, but accelerated during the Tertiary to culminate in the Plio-Pleistocene (?). Early mild uplift is evidenced in the low Sierra de Perijá. However, the strongest and most recent uplift was evidenced in the Sierra de Mérida (5006 m), with calculated rates of about 0.8 mm/year between 5 and 2 Ma ago, and possibly faster thereafter. Kohn (1980, cited by Kellogg 1984) gives a 6 Ma uplift age for the uplift age of the Sierra Nevada de Santa Marta itself, without further details. In view of its tectonic position between the thrust front and the other two ranges its uplift rates must be at least in the same order of magnitude as those of the Sierra de Mérida. Their data seem to indicate that the areas with highest elevation (especially above 3000 m) are also the ones that have been uplifted most recently (< 6 Ma for the Mérida Andes).

Taking into account the height of the Sierra Nevada de Santa Marta and the Sierra de Mérida, and the depth of the adjacent Maracaibo and Lower Magdalena basins (6000 m), the structural relief developed as a result of these orogenic movements is in the order of 12 km (Kellogg & Bonini 1982).

Sierra Nevada del Cocuy and Santander Massif

A second region for which some uplift data are available is the Santander and adjacent Cocuy Massif, where the deflection of the Cordillera Oriental from a NE to a NW orientation occurs (Fig. 2). The Cocuy massif which consists mainly of folder Cretaceous and Tertiary sedimentary rocks, reaches a height of 5493 m, while the adjacent oil-producing Arauca basin in the Llanos Orientales to the east is at least 6000 m deep – again a structural relief of some 12 km. A detailed stratigraphical analysis by Fabre (1983a, b) shows that the sedimentation basin of the Cocuy was still continuous with the adjacent Arauca basin up to the Oligocene. Strong folding occurred in the Miocene and uplift took place mainly in the Pliocene and Quaternary.

Shagam et al. (1984) studied zircon and apatite fission-track chronology in the Santander Massif west of the Cocuy, but their data did not allow for the construction of a single uplift curve. The oldest apatite fission track age above 3000 m in the Santander Massif, and, for that matter, from the Colombian Andes, is 16.0 ± 2.5 (Páramo Rico, 3680 m). Earlier ages invariably refer to samples from low elevations. Taking into account other geological data, the most probable interpretation is a minor initial uplift at a slow rate during a relatively lengthy time span, followed by progressively stronger uplift at faster rates through shorter time spans (Shagam et al. 1984). The implication of these data is that uplift in the Santander massif had already taken place while the Cocuy basin was still in its final stage of subsidence.

The Sabana de Bogotá area

The Sabana de Bogotá is a large synclinal basin in the Eastern Cordillera at 2600 m surrounded by reliefs ranging up to 4000 m consisting mainly of folded Cretaceous and Tertiary sedimentary rocks

(Fig. 2). Van der Hammen et al. (1973) showed that the Tilatá Formation, consisting of Pliocene sediments which unconformably overlie folded Oligocene and older sediments at the border of the High Plain of Bogotá, contains macrorests (*Humiria* fruits) which indicate that this formation cannot have been deposited at altitudes higher than 500 m above sea level. At present these sediments occur at 2700 m above sea level. Ash layers included in this formation were dated at 4–5 Ma, suggesting that uplift has taken place after that date (Van der Hammen et al. 1973). In a palynological study of a deep core from the centre of the same high plain Hooghiemstra (1984, 1989) did not yet record pre-uplift lowland species in the deepest part of his section approximately dated at 3.5 Ma. This leaves only the time span between 3.5 and 4–5 Ma for the main uplift of this area. Fabre (1983a) suggests that the Tilatá formation has only been deposited in synclinal valleys between already uplifted anticlinal ridges, thus enlarging the time span in which uplift could have taken place. Helmens & Kuhry (1986) suppose that the ages cited by Hooghiemstra (1984) are too high. At present new cores from deeper parts of the Sabana depression are being obtained, so that more detailed data about the uplift history will be available before long (Hooghiemstra, in prep.).

The Garzón Massif, Eastern Cordillera

The Garzón Massif (3600 m) in the southern part of the Eastern Cordillera (Fig. 2) is a Precambrian crystalline massif overlain by Paleozoic through Quaternary sedimentary rocks and intruded by Jurassic granitoid plutons. The sedimentary rocks have been folded as a result of the uplift of the Eastern Cordillera, and are overlain unconformably by Plio-Pleistocene syn- and postorogenic sediments (Kroonenberg et al. 1981, Kroonenberg & Diederix, 1982). Remnants of an uplifted erosion surface are visible in some places (Khobzi & Usselmann 1974, Ruiz 1977, 1981, Soeters 1981b).

The adjacent Upper Magdalena Valley is filled with molasse deposits derived from both the Central and Eastern Cordilleras which unconformably overlie older Cretaceous rocks. Many Upper Tertiary and Quaternary sedimentary rocks are volcaniclastic, and some pyroclastic flows are intercalated (Wellman 1970, Howe 1974). Paleocurrent analyses by these authors and Van der Wiel & Van den Bergh (in prep) confirm the earlier hypothesis by Van Houten & Travis (1968) that the Eastern Cordillera did not exist as a major topographic barrier at least until the end of the deposition of the Honda Formation some 12 Ma ago, enabling the major rivers emerging from the Central Cordillera to connect directly with the Amazon basin. For the uppermost folded volcaniclastic Gigante Formation Van Houten (1986) published an 8.3 Ma age, for the oldest post-orogenic terrace deposits he gives an age of 3.8 Ma.

New data, including a detailed K-Ar and fission-track dated stratigraphy of the Gigante Formation and a fission-track uplift history of the crystalline part of the Garzón Massif indicate a major uplift phase around 9–12 Ma (Van der Wiel 1989, Van der Wiel & Andriessen, in prep.).

In a conterminous tectonic basin further southwest in the Eastern Cordillera at least 1200 m of sediment were deposited during the last 4.5 Ma (Bakker 1990).

Central Cordillera

The Central Cordillera consists in its highest parts essentially of Paleozoic low-grade metamorphic rocks intruded by plutonic rocks of Permian to Tertiary age, overlain by Late Tertiary to Quaternary volcanic rocks. The contact between volcanic cover and the subjacent basement is commonly situated about 3000 m above sea level.

Near the Nevado del Ruíz area (Fig. 2), strongly dissected undated pre-uplift volcanics of the Manizales Formation are overlain at 3300 and 3700 m by lavas dated by K-Ar at 3.6 ± 0.36 and 2.7 ± 0.19 Ma, respectively (Flórez 1986). Other data of early volcanism in this area have been published by Thouret et al. (1985). These authors assume an age of 3–4 Ma for the Manizales Formation. The contact between the Manizales Formation and the underlying deeply weathered crystalline basement is situated around 2000 m; both are now dissected by canyons over 1 km deep (Flórez 1986). Jaramillo (1978) reports an 10.5 ± 1 Ma apatite fission-track age and a 62.4 ± 3.6 Ma zircon fission-track age of a single sample from the Manizales Pluton (crystalline basement) at Fresno (1500 m). Uplift in this area, therefore, must have taken place between about 10 and 4 Ma ago.

From the northernmost, non-volcanic part of the Central Cordillera near Medellín (Fig. 2) extensive remnants of at least three uplifted planation surfaces have been recognized by Page & James (1981), the Pre-Cordillera Central Erosion surface (Pre-S-1) over 3000 m, the Cordillera Central Erosion Surface (S-1) around 3000–2500 m and the Río Negro surface (S-II) around 2200 m. Dissection around Medellín amounts to over 600 m. The tilted S-1 surface is found to underlie the Miocene Honda Formation both here and further south (Soeters 1981a). By combining limited palaeomagnetic evidence on terrace deposits and dissection depth of major rivers Page & James (1981) calculated ages 22–18 Ma for the development of the S-1 surface, which accords well with the 14–16 Ma age found for volcaniclastic components in the Honda Formation elsewhere (Setoguchi & Rosemberger 1985). The Río Negro surface is probably older than 3 M or even older than 5.3 Ma. According to Soeters (1981a), the volcaniclastic Mesa Group truncates this erosion surface. The Mesa Group was dated palynologically in the Pliocene (Dueñas & Castro 1981) and Thouret et al. (1985) obtained 4.3 ± 0.4 and 3.5 ± 0.4 Ma K-Ar ages from it. The Río Negro surface was truncated therefore around 4 Ma. The Mesa Group itself was estimated by Dueñas & Castro (1981) to have been uplifted at least 460 m since the Pliocene in the area adjacent to the Magdalena valley.

Overall denudation rates around 0.01–0.02 mm/a have been calculated by Page & James (1981) assuming rates being constant in time. However, there is considerable uncertainty in the interpretation of the palaeomagnetic data of Page & James (1981), extrapolations in time are far stretched, the assumption of constant denudation rates is probably not correct, and the importance of lithology on the altitude of planation surface (Kroonenberg & Melitz 1983) has not been taken into account. More quantitative data are needed to corroborate their findings.

Western Cordillera

Extensive remnants of uplifted peneplains occur in the Dagua-Calima area west of Cali in the central part of the Western Cordillera (Fig. 2, Padilla 1981). Contrary to the Central and Eastern Cordillera, the Western Cordillera consists essentially of oceanic crust not older than 120 Ma (Aspden & McCourt 1986). The Dagua-Calima area is underlain mainly by Upper Cretaceous basic volcanic rocks of the Diabase Group, with intercalated sediments and intruded by equally Upper Cretaceous gabbroic and granitoid rocks (Aspden & McCourt 1986). The western Cordillera was accreted to the South American Plate also in the Upper Cretaceous. Uplift has been in the order of 2000 m here, and is reflected according to Padilla (1981) in Middle Miocene hiatuses in the adjacent sedimentary basins.

The Páramo de Frontino in the Western Cordillera, situated at about 4000 m is underlain by an 11 Ma dioritic stock (Zuluaga & Mattsson 1981). Taking the time into account needed for unroofing the stock, uplift here is probably much younger than Middle Miocene. There are several other massifs reaching to levels around 4000 m in the Western Cordillera, including the Cerro Tatamá (Van der Hammen et al. in prep.), all of which show evidence of Pleistocene glaciation.

Repeated leveling along transects in the Western Cordillera indicate actual vertical movements in the order of magnitude of 0.5–1 mm/y (Lüschen 1983).

The closing of the Panamanian isthmus

The Panamanian isthmus and adjacent parts of southern Costa Rica show the characteristics of an island arc, which was still largely submerged up to Upper Miocene time. It started to form already in the Eocene by subduction at the western border of the Caribbean Plate (Weyl 1980, Sykes et al. 1982). The different models that exist for the development of the Caribbean Plate (Pindell & Dewey 1982, Sykes et al. 1982, Kellogg & Bonini 1982, Burke et al. 1984, Mann & Burke 1984) all concur in that at that time this island arc was situated at least 1400 km west from its present position. This is based on the inferred rate of eastward motion of the Caribbean plate as measured along the Cayman Trench and on other data (Sykes et al. 1982). As a result of the continuous eastward movement of the Caribbean Plate, the island arc approached the South American mainland in the Neogene. At the end of the Miocene, around 7 Ma ago, the island arc had become so close to Colombia that the sea shoaled (Wadge & Burke 1983). This is reflected in several stratigraphic unconformities in some Neogene basins, according to Mann & Burke (1984). Between 7 Ma and 3 Ma the southern part of the island are collided with the South American Mainland (Sykes et al. 1982). It is understood that the Serranía de Baudó, actually the fourth and westernmost Cordillera of the Colombian Andes along the Pacific coast, is the southernmost extension of this island arc.

The date of accretion is of importance, as the formation of a land bridge enabled Holarctic biota to invade South America, and viceversa. There is ample evidence that this accretion was completed around 3 Ma (Mann & Burke 1984). Keigwin (1978) shows from the distribution of planktonic foraminifera in cores from both the Pacific and the Caribbean Sea that complete closure of the isthmus must have taken place between 3.6 and 3.1 Ma. Carbon and oxygen isotope characteristics of benthic foraminifera on either side of the isthmus start to diverge 6 Ma ago and modern circulation patterns developed by 3 Ma ago (Keigwin 1982). This is in harmony with data on the migration of fauna (Marshall et al. 1979) and flora (Hooghiemstra 1984). Hooghiemstra dated the arrival of the Holarctic genus *Alnus* in the High Plain of Bogotá at 2.6 Ma, and of *Quercus*, a much more slowly migrating genus, around 1 Ma, by means of palynological studies of a deep well. Helmens & Kuhry (1986) speculate that these data may be much too high, however.

The southern connection

Van der Hammen (1952) already noted that the paleocurrents in the Upper Tertiary sands in the Apaporis river in the Amazon basin ran counter to the present one. This has been fully corroborated by later studies by Hoorn (1988, in prep.). Such observations, as well as the study of large scale lineaments led several authors working in the Amazon area to propose a direct connection between the Pacific Ocean and the Amazon basin in the Tertiary, at the site of the deflection of the Andes near the Gulf of Guayaquil in Ecuador (Beurlen 1970). The notion that the Amazon debouched westwards into the Pacific until the Late-Tertiary uplift of the Andes is widespread. Almeida (1975) even calls the Tertiary fluvial sediments in the Brazilian Amazone area Sanozama Formation, which is Amazonas spelled backwards. If such a breach had existed, it could have hampered immigration of austral-antarctic species into the Colombian Andes.

Other authors, however, consider the western Amazon basin as a Tertiary fluvial molasse basin which was partially inundated at some time, but not necessarily connected with the sea (see reviews by Fernandes et al. 1977, Khobzi et al. 1980, Räsänen et al. 1987). Recent data on the Ecuadorian Andes indicate that there is little support for a breach in the Andean mountain belt; the Pacific coastal basin was already separated from the Oriente (Amazonian) basin in the Cretaceous by a proto-Andean barrier and there is a general continuity of N-S structures in the Sierra of Ecuador (Baldock 1982). The deflection of the Andes is probably a much older feature, determined by the geometry of the cratonic hinterland, as evidenced by the parallellism of Andean and Precambrian mobile belts (Litherland et al. 1985).

The combined evidence suggests that the general westerly paleocurrents of Late Tertiary fluvial sediments in the western Amazone basin reflect drainage towards subandean molasse troughs, not towards the Pacific. Therefore, there is no reason to suppose that immigration of biota from southern latitudes was impeded by topographic discontinuities in the Andes.

Of course, the immigration of cold-climate species requires the presence of high areas in the Central and Southern Andes as well. Also there, uplift seems to have accelerated towards the end of the Tertiary (Central Andes: Myers 1976, Allmendinger 1986; Southern Andes: Nelson 1982) roughly contemporaneously with orogenic events in the Colombian Andes.

Discussion

Differential uplift of all three Cordilleras and concomitant subsidence or at least stability in the surrounding tectonic basins occurred in a period ranging from at least the Oligocene up to the present. Early uplift data (>16 Ma) have been acquired mainly from low elevations, however. The first evidence of uplift above 3000 m is found around 16 Ma in the Santander Massif. This coincides with the oldest dates obtained for the initiation of Cenozoic volcanism in the Andes (Honda Formation). The Venezuelan Andes, the Central Cordillera, the Western Cordillera and the other parts of the Eastern Cordillera, remained far below this datum, however. In the interval between 12 Ma (Central Cordillera) and 4 Ma (Central Cordillera, Sabana de Bogotá) large parts of the Eastern and Central Cordillera, and probably also the Western Cordillera were uplifted, rarely exceeding 3000 m, however. Remnants of Miocene planation surfaces became deeply dissected and partly overlain by stratovolcanoes in the highest part of the Central Cordillera and by volcaniclastic molasse deposits in the Magdalena Basin. Páramo vegetation in the Central Cordillera could develop mainly as a result of the formation of these high volcanic structures after 4 Ma.

The most vigorous uplift that gave rise to the formation of the highest reliefs in the Sierra de Mérida, the Sierra Nevada de Santa Marta and the Sierra Nevada del Cocuy was probably also the most recent one (younger than 6 Ma). Uplift up to the actual páramo zone above 3000 m, therefore, has been taking place during a considerable time interval from the Middle Miocene to the present. This suggests that high-Andean biota could not develop everywhere at the same time. It would be interesting to investigate whether there exist substantial differences in evolutionary stage between early uplifted areas such as the Santander Massif and late uplifted areas such as the Sierra Nevada de Santa Marta, especially as the former developed already before the immigration of holarctic species by the closing of the isthmus (7-3 Ma, see above). Whether early development of páramo vegetation in the Santander Massif indeed occurred, however, does not depend only on its uplift date but of course also on the position of the forest line 16 Ma ago. According to Mann & Burke (1984) closing of the Panamanian isthmus in the Miocene-Pliocene led to uplift of the three cordilleras of Colombia (Irving 1975, Pindell & Dewey 1982) as well as of the Mérida Andes and the Sierra de Perijá (Kellogg & Bonini 1982). Though the accretion indeed took place in a period of general uplift in the Colombian Andes, uplift is not restricted to the area affected by the collision with the Panamanian block. The accretion of the Panamanian block at most can be held responsible for the last and most vigorous uplift spasm in the Sierras Nevadas de Santa Marta and Cocuy and Sierra de Mérida, because these are all located in the northernmost part of the Andes where the impact was probably greatest. This is obviously related to the low angle of subduction of the Bucaramanga segment of the Nazca plate. But the main Mid-Miocene to present uplift phase is a much more general feature along the whole Andean chain, and cannot easily be attributed to local collisional events or subduction of 'resisters' such as the Panamanian block or, as in Ecuador, the Carnegie ridge. Uplift also took place in the Mio-Pliocene in southern Costa Rica and Panamá (Weyl 1980), although the island arc did not at all impinge upon continental crust in that area. Crustal uplift in orogenic zone is a phenomenon in itself. The Eu-Andine Orogeny as coined by Van der Hammen (1961) therefore must be considered a phenomenon on its own.

There is no reason to suppose that immigration of austral-antarctic species was hindered at any time by a breach in the Andes at the Gulf of Guayaquil in Ecuador. Assuming that uplift in the Central and Southern Andes equally took place less than about 10 Ma ago, the spread of cold-climate vegetation from the south if also relative recent.

Conclusions

Uplift in the Colombian Andes started already around 25 Ma ago, but only isolated areas were uplifted to over 3000 m until the Late Miocene. A more general uplift phase up to 3000–3500 m occurred around 9–12 Ma in the Central and Eastern, and possibly also in the Western Cordillera. The most recent uplift phase around 4–6 Ma which thrust up the Santa Marta, Cocuy and Mérida Massifs affected only the northern non-volcanic part of the Colombian Andes characterized by low-angle subduction, and coincides both geographically and in time with the accretion of the Panamanian Isthmus to the continent.

Adaptation of lowland biota to higher altitudes must have started well before the immigration of holarctic species, therefore. Immigration of austral-antarctic species can have taken place continuously, but its character may have changed with time as uplift at more southern latitudes kept pace with the rise of the Colombian Cordilleras.

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