Paleophysiographic and paleoenvironmental histories in northern Latin America—Possible impact on modes of speciation

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Although land surfaces between central and southern Mexico and northern South America are presently continuous, the area encompasses three zones that have had different physiographic and environmental histories. In central and southern Mexico highlands were present in the Late Cretaceous, and significant physiographic relief and habitat diversity have existed since the Late Tertiary. Continuous land connections existed to the north throughout the Cenozoic, and to the south after about 3.5 Ma, and these connections provided source areas for the immigration and emigration of temperate and tropical elements, as well as introductions throughout the Cenozoic by long-distance dispersal. The region experienced the global climatic cooling of the Late Cenozoic, which was augmented by coastal upwelling with closure of the Panama land bridge. In contrast, central America has never had the extensive high elevations or habitat diversity of central to southern Mexico; the region consisted of islands and peninsulas for most of the Cenozoic with limited access to source areas both to the north and south until about 3.5 Ma; and the impact of Late Cenozoic climatic change was muted, in part, because of the lower latitude, low physiographic relief, and the insular environment. The Amazon Basin of northern South America has had low physiographic relief throughout the Cenozoic, but it is surrounded by the northern Andes that had attained substantial relief and habitat diversity by the Miocene. Biotas in the Amazon Basin experienced some effects of Late Cenozoic climatic change, and these were augmented by fluctuations in the water table resulting from sea-level changes caused by the expansion and contraction of polar glaciers. The effect was the periodic fragmentation of the lowland biota, accompanied by expansion of drier-habitat communities during intervals of cool glacial climates and lowered water tables. This was followed by periods of warmer temperatures, higher water tables, coalescence of rain forest communities, and restriction of drier-habitat species to the bordering uplands they occupy at present. The pace of these changes produced a dynamism that was not experienced, at least to the same degree, by communities to the north. These differences in physiographic and climatic histories likely had an effect on the nature of speciation mechanisms operating in the three regions through a reordering of the components of the speciation process. Some residue of this reordering may still reside in large speciose genera distributed through northern Latin America in the form of morphological (leaf epidermal cell size, pollen aperture number, pollen sterility) and cytological (polyploidy) characters. If so, recognition of the separate histories may be useful in explaining features in modern taxa that are correlated with geography.

Key-words—Tertiary, Palynology, Paleoenvironments, Speciation, Northern Latin America.

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सारांश

उत्तरी लेटिन अमेरिका में पुराआकृतिकीय एवं पुरावातावरणीय इतिहास–जातिघटन पर सम्भाव्य प्रभाव

एलॅन ग्राह्म

यद्यपि केन्द्रीय एवं दक्षिणी मेक्सिको तथा उत्तरी दक्षिण अमेरिका के मध्य अविरल भूमि है, इस क्षेत्र में तीन विभिन्न भूआकृतिकीय एवं पुरावातावरणीय इतिहास वाले तीन मंडल हैं। केन्द्रीय एवं दक्षिणी मेक्सिको में अनंतिम क्रीटेशी कल्प में उच्च भूमि विद्यमान थी तथा अनंतिम तृतीयक काल से अभी तक विशेष भूआकृतिक संरचना एवं विभिन्नता विद्यमान है। सम्पूर्ण नूतनजीवी कल्प में सतत भूमि संयोजन के कारण शीतोष्ण एवं उष्णकटिबन्धीय अवयवों का प्रवासन तथा अन्तर्वेशन सम्भव हुआ है। उत्तरी दक्षिण अमेरिका की अमेजन द्रोणी पूरे नूतनजीवी कल्प में निम्न भूमि के रूप में थी, परन्तु यह उत्तरी ऐंडीज से घिरी हुई

है जिसमें कि मध्यनूतन कल्प तक कुछ सुधार हुआ है। ध्रुवीय ग्लेशियरों के संकुचन एवं प्रसार के कारण समुद्री जल के उतार एवं चढ़ाव का प्रभाव अमेजन द्रोणी के वनस्पतिजात पर पड़ा है। इस प्रकार विभिन्न प्रकार की वनस्पति का प्रवासन और अन्तर्वेशन सम्भव हुआ। इन्हीं कारकों के अविरल प्रभाव के कारण इन तीनों क्षेत्रों में जातिघटन प्रक्रिया पर महत्वपूर्ण प्रभाव पड़ा है।

THE results of paleobotanical investigations are being used in an increasing variety of studies on past environments and biotic history. The information is a key component of ground-truth evidence used to evaluate the accuracy of large-scale climate models (hindcasting), and is a source of characters for reconstructing phylogenies. Under certain circumstances, paleobotanical data also may be useful in better understanding the interaction of past physical events and speciation. This is especially true for areas that are presently part of a contiguous physiographic setting, but which have had separate environmental histories.

In the area of central and southern Mexico the Veracruz Basin has been receiving sediments eroded from the Sierra Madre Oriental since the Late Cretaceous/Paleocene (Helu *et al.*, 1977). Highlands have been in existence in the Transvolcanic Belt since the Early Tertiary, where there was major uplift in the Late Miocene, Pliocene, and Pleistocene (de Cserna, 1989; Demant, 1978; Nixon, 1982; Thorpe, 1977; Ferrusquía-Villafranca, 1993). At the confluency of the eastern Transvolcanic Belt with the southern terminus of the Sierra Madre Oriental east and southeast of Mexico City, these highlands include the Pico de Orizaba (5650 m), Popocatepetl (5450 m), and Ixaccihuatl (5280 m). Throughout the Tertiary a variety of habitats were available, and continuous land surfaces extended to the north that allowed the interchange of tropical, warm-temperate, and higher-altitude temperate elements.

Climatic conditions in southeastern Mexico are reflected in the composition of the Paraje Solo plant microfossil flora of south-coastal Veracruz (Graham, 1976). The flora is preserved in lignites and clays that are partly contemporaneous with the Agueguexquite Formation which contains calcareous nannofossils and planktic foraminifera. These place the Paraje Solo Formation in the mid-N20 nannofossil zone and provide an age estimate of 3.3 Ma (Middle Pliocene). As will be seen later, this date is important because it is just after final closure of the Isthmus of Panama at about 3.5 Ma. The area presently supports a coastal mangrove community of *Rhizophora mangle* (manglar) that is bordered immediately inland by the lowland tropical rain forest (selva alta perenifolia). The Paraje Solo lignites and clays accumulated in this zone. The dominant genera of the modern rain forest in southeastern Veracruz include *Bernoulia, Brosimum, Calophyllum, Dialium, Ficus, Inga, Lonchocarpus, Nectandra, Pouteria,* and *Pseudolmedia*. Woods (bosques) and forests (selvas) occupy inland and upland sites, and include a number of deciduous trees and shrubs of shorter stature in progressivley drier habitats (e.g., *Pinus-Quercus* forest; bosque de pino y encino). At an elevation between 1000-2000 m there is a temperate forest of *Quercus* and *Liquidambar* (bosque caducifolia) with a number of genera disjunct from the deciduous forest of the eastern United States (*Acer, Alnus, Carpinus, Celtis, Cornus, Fagus, Ilex, Juglans, Platanus, Populus, Ulmus,* and others). At higher elevations there are other species of *Pinus* mixed with *Abies* (bosque de oyamel), and an alpine tundra (paramo) grows above timberline (Gómez-Pompa, 1973).

The fossil flora contains abundant pollen of *Rhizophora,* but a salient feature of the assemblage is the absence or poor representation of rain forest taxa. Pollen of none of the above-mentioned genera characteristic of the rain forest was recovered. The lignites were being deposited at the contact between the mangroves and the adjacent inland vegetation,

which suggests that the rain forest was not prominent. In addition, pollen of upland communities such as the *Quercus-Liquidambar* forest, the *Pinus-Quercus* forest, and even the high-altitude *Pinus-Abies* forest was present in the lowland basin of deposition. Also, unfragmented pollen of *Picea* was recovered. *Picea* presently grows in the mountains of northern Mexico 1000 km distant from southeastern Veracruz. The inference is that cooler climates associated with early stages of northern hemisphere glaciations were affecting the biota, probably through more frequent and intense 'nortes' that occasionally reach this latitude today (17° N). Another factor was the upwelling of cold bottom waters that reduced temperatures along the coast. Upwelling intensifies with increased flow of ocean currents, and this occurred with the progressive closure of the Isthmus of Panama which was completed about 3.5 Ma. The Cenozoic plant communities of southeastern Mexico grew in a setting of significant physiographic relief, continuous land connections to the north, and they were affected by the climatic changes of the Late Tertiary and Quaternary.

The physical setting and climatic history of central America was quite different from that of central and southern Mexico. The landscape consisted of islands and peninsulas with no continuous land surfaces either to the north or to the south until about 3.5 Ma. Several plant microfossil assemblages of Late Tertiary age are known from the region, including the Miocene Uscari flora of Costa Rica (Graham, 1987), and the Miocene Culebra (Graham, 1988a), Cucaracha (Graham, 1988b), and La Boca (Graham, 1989a) and the Mio-Pliocene Gatun flora of Panama (Graham, 1991a, b, c). The fossil floras indicate that the islands and peninsulas were low-lying, with maximum elevations of about 1400 m in the Miocene and increasing to about 1700 m in the Mio-Pliocene (Graham, 1989b). The present highest elevations are represented by a few scattered peaks in Costa Rica (Cerro Chirripo, 3820 m; Volcan Irazu, 3432 m) and Panama (Volcan Baru, 3475 m). The fossil floras also reveal a tropical vegetation similar to that of present low-lying regions, and which experienced little impact from the Late Cenozoic cooling. Changes in the vegetation were due mostly to volcanism and uplift associated with plate movement. By the Pliocene there were a few upland temperate habitats as shown by the first appearance of *Quercus* in the Gatun flora, and at that time there began a differentiation of the biota into wet northern (Atlantic) and drier southern (Pacific) zones.

In the Amazon Basin of northern South America physiographic relief is low, and there is no evidence for highlands anytime during the Cenozoic. However, the area is bordered by the northern Andes, which attained significant relief in the Miocene, and other upland areas which support a variety of vegetation types, including the drier caatingas and cerrado grasslands- savanna. The vast extent of land surfaces provided interior continental climates that were affected to some extent by the Late Cenozoic cooling. It is estimated that the lowland rain forest experienced a mean annual temperature lower by 4°-5° C during the coolest periods of the Quaternary (Liu & Colinvaux, 1985). Equally important were fluctuations in water table associated with sea-level changes resulting from the polar glaciations. When it was earlier thought that there were only four major glacial advances and retreats during the Quaternary, the pace of these changes was assumed to be a leisurely 1,75,000 yrs for each glacial and interglacial interval. It is now recognized that there were 18-20 cycles, with the glacial intervals representing 90 per cent of Quaternary time. Although the nature and role of Quaternary refugia in the Amazon Basin is unsettled, it is evident that the biotas were subjected to greater direct and indirect effects of climatic changes than those of central America and central and southern Mexico.

There were other differences in environmental histories between the three regions. Volcanism and fragmentation of the landscape was most active in central America due to subduction of the Pacific plate beneath the Caribbean plate and the movements of the South American and North American plates. This type of habitat disturbance was less in central and southern Mexico, and still less in northern South America. The impact of the establishment of complete land connections between North and South America on the biotas was also likely different. The numbers and diversity of organisms moving from South America caused increased competition and

extinction in central America, but probably had less impact progressively to the north. The result of immigration from central America into South America must have been comparatively minor.

Collectively, the geological and paleobotanical data indicate that the region presently encompassed between central Mexico and northern South America includes three paleophysiographic provinces that have had distinct physical and climatic histories. It may be speculated that these differences may have had an influence on the relative importance or ordering of the various components of the speciation process (Grant, 1981). If so, some evidence of these differences may still be evident in morphological and cytological features that are geographically correlated among species of genera distributed across the provinces.

The generation of novel genotypes (catastrophic selection) increases with habitat disturbance, and disturbance was most intense in proto-Central America. Hybridization enhances variation within populations, but to constitute speciation the breeding behavior of the progeny must be stabilized through reproductive isolation. This is most likely to occur in settings that are frequently disturbed. These conditions especially characterize the history of central America, and were less prevalent in central and southern Mexico, and least characteristic of the Amazon Basin. Plants that have arisen through hybridization frequently have large stomatal and other epidermal cells, increased sterility, and a high percentage of abortive pollen.

Polyploidy results in increased genetic heterozygosity, and regions providing a diversity of habitats offer greater opportunities for the establishment of polyploids than those with more uniform topography and edaphic conditions. Habitat diversity has been greater in central and southern Mexico throughout the Cenozoic than in the paleoprovinces to the south. Polyploidy is often evident by an increase in pollen pore number. The numerous isolated peaks of the Sierra Madre Oriental and the Transvolcanic Belt also provided sites for establishment of geographically isolated populations through founder effect mechanisms (Mayr, 1954, 1963).

Allopatric speciation via vicariance occurs when the range of a species is subdivided by a change in the physical environment. After the breeding systems have been stabilized through geographic/reproductive isolation, sympatry and hybridization may occur with subsequent changes in the environment that bring the isolates back into contact. This mechanism operated on a far greater scale in Amazonia than in areas to the north, and may be a factor in the high species diversity evident in the lowland tropical rain forest.

The expression of differences in history in the form of geographically correlated morphological and cytological characters may be preserved among populations of wide-ranging genera with multiple centers of diversity (*Cuphea,* ~260 species; *Salvia,* ~300; *Senecio,* ~1250; *Vernonia,* ~500), or in more ancient woody perennials such as *Ilex, Mryica, Quercus, Salix,* all of which are presently distributed across the three provinces. Efficient speciation mechanisms are necessary for the perpetuation of a lineage through time, but it does not follow that the mechanisms must be the same in all groups (White, 1977, p. 14), or the same throughout the entire range of a widespread taxon. Differences in the ranking of the components of the early speciation process, if detectable, would likely be blurred by subsequent physical, climatic, and reproductive events. Nonetheless, if during the course of taxonomic studies genotypic or phenotypic characters are found that show correlation with geography, it is worthwhile to know that northern Latin America includes three regions that have had distinct histories.

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