

PLACING THE MEXICAN CLOUD FORESTS IN A GLOBAL CONTEXT: A TRACK ANALYSIS BASED ON VASCULAR PLANT GENERA

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ABSTRACT.- The geographic distribution of 18 genera of vascular plants with different life histories and dispersal syndromes distributed in the Mexican cloud forests was analysed, applying a panbiogeographic approach and contrasted with dispersalists viewpoints. Seas and straits in eastern Asia and the Pacific basin were used to identify major patterns of distribution. Three generalised tracks and seven nodes are suggested based on this analysis. The generalised tracks coincide with others recognised in previous studies, and nodes with centres of diversification for other plant and animal taxa.

KEY-WORDS.- Cloud forests, Vascular plants, Panbiogeography, Track analysis, Mexico

RESUME.- La distribution géographique en forêt mexicaine caducifoliée humide de montagne de 18 genres de plantes vasculaires ayant des cycles vitaux et des modes de dispersion différents, a été analysée en s'appuyant plutôt sur une approche panbiogéographique que sur une vision chorologique. Les principaux modèles de répartition ont été définis de la même manière que ceux établis sur la géographie des mers et détroits du sud-est asiatique et du Pacifique. Cette analyse a conduit à proposer trois tracés généraux et sept nœuds. Les tracés généraux coïncident avec ceux reconnus par des études antérieures : de même, les nœuds correspondent à des centres de distribution déjà proposés pour d'autres groupes végétaux et animaux.

MOTS-CLES.- Forêt caducifoliée humide de montagne, Plantes vasculaires, Panbiogéographie, Track analysis, Mexique

INTRODUCTION

From a dispersalist viewpoint and due to its position intermediate between the Nearctic and Neotropical biogeographic regions, it has been considered that great part of the Mexican biota arrived by successive migrations of elements originated in other parts of the world, principally from the northern and southern areas of the American continent (RZEDOWSKI, 1978; HALFTER, 1987; GONZÁLEZ-MEDRANO, 1996). This proposal has been well-documented in the Mexican cloud forests, and several authors (PUIG, 1976; RZEDOWSKI, 1978; among others) have suggested that this community is basically composed by floristic elements of three types: (1) temperate, particularly represented by the canopy trees, of Nearctic origin; (2) tropical, mainly represented by herbs, epiphytes, and shrubs, of Neotropical affinities; and (3) endemic, relatively unimportant if considered at the generic level, but very significant at a species level (LUNA *et al.*, 1999). The biotic relationship between certain areas of the Old and the New World was recognised since long ago. In the case of vascular plants, this relationship is so strong that many of the genera and species are the same, or at least are closely related.

The floristic richness of the Mexican cloud forest, joined to its particular distribution in small isolated islands in form of an archipelago, in which each of the patches has a particular biotic composition (LUNA *et al.*, 1999; LUNA *et al.*, 2001b)

makes it extremely interesting from a biogeographic point of view. This vegetation type harbours taxa common to eastern and western North America, eastern Asia, and Central and South America (MATUJDA, 1953; SHARP, 1953, 1966; DRESSLER, 1954; MARTIN & HARRELL, 1957; SHARP & IWATSUKI, 1965), that constitutes with the endemic element a whimsical mosaic of species (LUNA *et al.*, 2001a). TAKHTAJAN (1981) sustained that south-east Asia (Assam, upper Burma, Yunnan, Thailand, Laos, Vietnam, Malasia, Melanesia, and adjoining parts of north-east India) was the centre of origin of angiosperms, based principally in the extremely rich flora in primitive groups, *i.e.* Magnoliaceae, Lauraceae, Annonaceae, and Chloranthaceae, among others, taxa that are very well represented in the Mexican cloud forests. Paleobotanic evidence confirmed that many of these taxa, mainly the woody ones, had a broad distribution range in the past (*e.g.* *Ulmus*, *Liquidambar*, *Magnolia*, and *Nyssa*), principally in North America and eastern Asia. WOOD (1972) suggested that many of these areas can currently be considered mesic refugia for many of the surviving descendants of formerly more widespread taxa.

Panbiogeography constitute a different historical biogeographic approach proposed originally by CROIZAT (1958), which offers the possibility to recognise a complex area, provide information about where, when, and how animal and plant distributions evolve, and identify relict fragments that can show the pre-existence of a broadly distributed ancestral biota (CRAW, 1988; MORRONE & CRISCI, 1995; CRAW *et al.*, 1999).

Our objective is to review the distributional patterns of 18 genera of vascular plants, considered by some authors as characteristic of this vegetation type in Mexico (*i.e.* RZEDOWSKI, 1969, 1996), based on track analysis, and to contrast these results with previous dispersalist viewpoints.

MATERIAL AND METHODS

A list of genera of the Mexican cloud forests was selected, considering primarily the following criteria (*sensu* ALCANTARA *et al.*, 2001, in part): (a) principally woody taxa; (b) to be well-represented in the current Mexican cloud forest patches; (c) they must be important as dominant or co-dominant in Mexican cloud forests, or at least important on its composition; (d) genera with complete taxonomic and distributional information. Based on these four criteria, we chose the next genera: *Carya* (Juglandaceae), *Chiranthodendron* (Sterculiaceae), *Clethra* (Clethraceae), *Clusia* (Clusiaceae), *Cyathea* (Cyatheaceae), *Drimys* (Winteraceae), *Fagus* (Fagaceae), *Fuchsia* (Onagraceae), *Illicium* (Illiciaceae), *Liquidambar* (Hamamelidaceae), *Magnolia* (Magnoliaceae), *Meliosma* (Sabiaceae), *Nyssa* (Nyssaceae), *Oreomunnea* (Juglandaceae), *Sloanea* (Elaeocarpaceae), *Syrax* (Styracaceae), *Symplocos* (Symplocaceae), and *Weinmannia* (Cunoniaceae).

Distributional data of these genera were obtained from monographic and revisional studies of URBAN (1895), SMITH (1943a, 1943b), WILLIAMS (1963a, 1965b, 1965c), SLEUMER (1967a, 1967b), BEUSEKOM (1971), MURRAY (1972), STONE (1972), GOOD (1974), NOOTEBOOM (1975), SOSA (1976, 1978), BERRY (1980), D'ARCY (1980), GENTRY (1980), BARCENA (1981), BALGOOY & COODE (1993), WEN & STUESSY (1993), VAZQUEZ (1994), STAHL (1995), DURAN (1997), BRADFORD (1998), and LI *et al.* (1999). These taxa have different life histories and seed (spore in the case of pteridophytes) dispersal syndromes (Table I).

The panbiogeographic method (CROIZAT, 1958, 1964) followed herein consists in plotting the localities of distribution of the different taxa on maps and connecting their distribution areas or localities with lines called individual tracks, in accordance to their minimal geographical proximity. The individual tracks are then oriented by a baseline,

that is a geological feature such as ocean basin crossed by the track. Individual tracks of different organisms are then superimposed and if they coincide, the resulting summary lines are considered generalised tracks. A generalised track indicates the pre-existence of an ancestral biota, that subsequently become fragmented by tectonic and/or climatic changes (MORRONE & CRISCI, 1995; CRAW *et al.*, 1999). Convergence or intersection of two or more generalised tracks let us recognise a node, which is a complex and composite geological area (CRAW, 1982) and may represent a centre of biodiversity or "hot spot" (GREHAN, 1993).

RESULTS AND DISCUSSION

Distributional analysis of 18 genera of Mexican cloud forests showed that two of them have restricted distributions, and thus were not included in the analysis. These genera and the areas in which they occur are: *Chiranthodendron* (southern Mexico and Guatemala) and *Oreomunnea* (southern Mexico, Guatemala, El Salvador, and Costa Rica), allowing to identify this zone as an area of endemism (Figs. 1 and 2). Other taxa that support this area of endemism are *Ceratozamia*, *Cobaea*, *Gibasis*, *Lopezia*, *Loxolobos*, and *Prinosciadium* of vascular plants (MAYORGA *et al.*, 1998), *Eickworthia* of Apoidea (Hymenoptera) (MCGINLEY, 1999), and *Helthis*, *Hilipinus*, and *Pseudanthonus* of Curculionidae (Coleoptera), the latter also inhabiting Guadalupe island (MORRONE *pers. com.*). Individual tracks of the remaining genera are shown in figures 3 to 18. The individual tracks of *Cyathea* and *Clusia* (Figs. 13 and 15) are partially overlapped between them and with the tracks of other genera in the Neotropics.

Three generalised tracks were found (Fig. 19); all of them cross the Pacific basin, but the first one is located in the north, the second in its middle part, and the third in its southern portion. The generalised tracks, the genera that support them, and the areas involved are as follows:

1. Northern Pacific generalised track. This generalised track includes almost all the Northern Hemisphere, connecting central Europe, the Mediterranean, southeastern Asia (China, Burma, Vietnam), Japan, eastern North America, southeastern Mexico, and northern Central America. This track includes the individual tracks of *Carya* (Fig. 7), *Fagus* (Fig. 10), *Illicium* (Fig. 8), *Liquidambar* (Fig. 11), *Magnolia* (Fig. 6), *Nyssa* (Fig. 5), and *Syrax* (Fig. 4).

In previous works similar individual tracks (or parts of these tracks) to the Northern Pacific generalised track have been found, *i.e.* *Cupressus*, *Taxus*, *Pseudotsuga*, *Torreya* (CONTRERAS-MEDINA *et al.*, 1999), and *Stewartia* (LUNA & CONTRERAS-MEDINA, 2000).

The discontinuity in plant range among temperate North America and eastern Asia recorded in this work in this first generalised track has been recognised since the past centuries (*e.g.* GRAY, 1859; HEMSLEY, 1879-1888). TAKHTAJAN (1981) with a dispersalist point of view suggested that temperate and subtropical elements reached North America very early by way of the North Pacific across the Bering-Aleutian areas. This fact has been revised by LI (1952), GRAHAM (1972), WOOD (1972), GOOD (1974), and XIANG *et al.* (1998), among others. ZHENG YI (1983) mentions about 120 genera of vascular plants with this disjunct range, many of them are woody and in some places co-dominant and/or characteristic in the Mexican cloud forests *i.e.* *Mahonia*, *Gordonia*, *Hamamelis*, *Toxicodendron*, *Cornus*, *Leucothoe*, *Osmanthus*, *Symphoricarpos*, and *Schizandra*. RZEDOWSKI (1978) cited the following genera with the same distributional pattern: *Deutzia*, *Distylum*, *Mitrostemon*, and *Staphylea*. Many explanations have been proposed to explain this biogeographical pattern, *e.g.* GOOD (1974) proposed that many of these genera could be survivors of an ancient flora now

extinct in Europe and western Asia, and regarded them as "circumboreal" in distribution. Instead, ZHENG YI (1983) assumed that these genera might be relicts of a warm temperate-subtropical montane flora derived from a Tertiary paleotropical flora, that was present on the mountains of the Old World in the early Tertiary or late Cretaceous. More recently, XIANG *et al.* (1998) argued that many eastern Asia taxa are sister groups of the North American ones, based on phylogenetic analysis using DNA data sets; for him this disjunction represents the fragmentation of a once continuous mixed mesophytic forest, involving two major vicariant events: an initial split between Eurasia and North America, followed by the biotic isolation of biotas between eastern and western North America.

This distributional pattern has great biogeographic significance in Mexican cloud forest evolution. The fact that areas distantly located as eastern Asia and North America (including south-eastern Mexico) have similar floristic composition (with genera represented in both areas as *Carya*, *Fagus*, *Illicium*, *Liquidambar Magnolia*, and *Nyssa* among others) can be explained if we consider both zones constitute composite areas, as the panbiogeographic method suggests. These two areas were previously recognised as nodes by GREHAN (1993) and LUNA & CONTRERAS-MEDINA (2000).

2. Middle Pacific generalised track. Located across the middle Pacific, this track connects eastern Asia and Indonesia with Mesoamerica, including the Greater Antilles. In northern South America a bifurcation is present, with one branch leading to eastern South America and another to western South America. It consists of the individual tracks of *Clethra* (Fig. 9), *Meliosma* (Fig. 12), and *Symplocos* (Fig. 15).

LUNA & CONTRERAS-MEDINA (2000) found a similar generalised track to the Middle Pacific track based in genera of Theaceae (*Ternstroemia* and *Cleyera*). This remarkable disjunction pattern, comprising tropical Asia and tropical America was formerly discussed by RZEDOWSKI (1978) among others. ZHENG YI (1983) listed 37 genera of plants common to these very distant regions and supports that they could represent an early disjunction; many of them are important elements in Mexican cloud forests, e.g. *Gaultheria*, *Gordonia*, *Hedyosmum*, *Litsea*, *Microtropis*, *Persea*, *Phoebe*, *Saurauia*, and *Turpinia*. ZHENG YI (1983) explains the presence of these elements as descendants of a vegetation type that seems to have predominated in the subtropical mountains of the Northern Hemisphere in the Late Cretaceous-Early Tertiary. In the case of *Meliosma* and *Symplocos*, BEUSEKOM (1971) and NOOTEBOOM (1975) suggested that the close similarity between the distribution ranges of both taxa, fossil and recent, lead to the thing that they belonged to a mixed mesophytic Northern Hemisphere forest type prevalent in Eurasia and North America in the Tertiary, which was later broken in the Glacial Epoch, and that the current distribution of several species of these genera represent remnants of this once widespread vegetation type. They supposed that this forest existed under warm temperate conditions and was floristically diverse, with members of different vascular plant families such as Aceraceae, Betulaceae, Ericaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Rhamnaceae, Rosaceae, Salicaceae, and Ulmaceae. BEUSEKOM (1971) proposed that several species of *Meliosma* originated in Asia and expanded its range via Beringia to North America, and that this migration took place in the Late Tertiary. Notwithstanding, when he tried to explain the relevance of Central America as a minor and old centre of diversification of this taxa and other members of Sabiaceae (*i.e.* the endemic genus *Ophiocaryon*, which is certainly closely related to *Meliosma*) sustained that the presence in tropical America of a closely related genus cannot be explained by migrations via Beringia, which took place recently (early Tertiary); it was more plausible to think that these sabiaceous lineage has a more ancient origin.

As BEUSEKOM (1971) argued, this transpacific disjunction suggested a former and direct contact between southeastern Asia and Central America, which became later broken; this fact agrees with the statements of CROIZAT (1958), who suggested that Central America is today only a remnant of a geographical and biological world that in

the past was much more extensive. Southern Mexico and northern Central America have been considered as an exceptional complex geological area and place where are found elements of different origin (CROIZAT, 1958; LUNA & CONTRERAS-MEDINA, 2000); our track analysis supports the hybrid character of the biota that inhabits this area.

3. Southern Pacific generalised track. It runs in the south Pacific connecting south-east Asia, Malaysia, Indonesia, and western South America. In this last region a bifurcation is present, with one branch leading to eastern South America and another to Central America and southeastern Mexico. It consists of the individual tracks of *Drimys* (Fig. 3), *Fuchsia* (Fig. 18), *Sloanea* (Fig. 17), and *Weinmannia* (Fig. 16).

TANGNEY (1989), MORRONE (1996) and CONTRERAS-MEDINA *et al.* (1999) also found partially overlapping individual tracks with the Southern Pacific generalised track found in this work, the first with mosses (*Eucampitodon*, *Hyphodendron* sect. *Hyphodendron*, *Macromitrium longirostre*, and *Macromitrium microstomum*), the second with Coleoptera (Rhinohydnichini, Mecomacerini, Belini, Agnesiotidina, Pachyurina, and Caridae), and the last with gymnosperms (*Araucaria*, *Lepidothamnium*, *Podocarpus*, *Prumnopitys*, and *Retrophyllum*). There are also other genera with similar distribution patterns that support this track e.g. *Acaena* and *Piper*, among others (GOOD, 1974).

RAVEN (1972) claimed that many plant and animal taxa present disjunct ranges in the Southern Hemisphere, and that this fact is related to the geographic position of Australia and South America at the end of the Eocene, time in which both were directly connected with the Antarctica, and that these three land masses were occupied by a cool temperate forest composed by gymnosperms and evergreen angiosperms, as well as many groups of non vascular plants and invertebrates that at the present time have disjunct distributions.

TAKHTAJAN (1981) argued that South America have had, at least, two links with southeast Asia: one through Africa and another via the Antarctic land bridge. This author suggested that these connections can explain the disjunct amphi-transpacific distributions of many families and genera of flowering plants (Winteraceae, *Nothofagus* of Fagaceae, Lardizabalaceae), possibly due to a fairly large and widespread archipelago during the Cretaceous period, that permit the dispersal of temperate and subtropical elements from south-east Asia to America, via the Andes and Chile, ideas that have been supported by other authors as VAN STEENIS (1962, 1963), and AXELROD (1960).

NODES

Convergence or intersection of these three generalised tracks allowed the recognition of seven nodes (Fig. 19), located in southeastern Asia, New Guinea, southeastern United States, Mesoamerica (southeastern Mexico and Central America), the Caribbean, Indonesia, and eastern South America. The southeastern United States node is recognised by the overlap of Northern and Middle Pacific generalised tracks. The eastern South America and New Guinea nodes are recognised by the intersection of Middle and Southern generalised tracks. The coincidence between the three generalised tracks support four nodes in southeastern Asia, Indonesia, Caribbean, and Mesoamerica. In the Mesoamerican node inhabits most of the genera, and includes the endemic genera *Chiranthodendron* and *Oreomunnea*.

CONCLUSIONS

Our analysis shows that many of the relevant genera of vascular plants inhabiting the Mexican cloud forests have a transpacific distribution, many of them are represented in both sides of the Pacific ocean by closely related groups or vicariant species. Many of the facts involved in these work were already observed and analysed by other authors (TAKHTAJAN, 1981; AXELROD, 1960; VAN STEENIS, 1962, 1963, among others), with a dispersalist point of view. The main difference between this approach and panbiogeography are the way in which these taxa got their current distributional pattern: in the dispersalist one it depends mainly on their life history features and dispersal capabilities, and in the panbiogeographic one in the continental drift, tectonic movement or climatic change.

Contrasting our results with the dispersalist approach, we noted that the different modes of dispersal and life histories of these taxa are not relevant to determine and explain their current distribution; possibly these features only have relevance in their local distribution.

The results obtained here and in previous works support that these regions represent complex areas, and thus do not seem to constitute natural areas, facts that can explain their high biodiversity; many of them constitute areas of endemism for other groups of organisms (CONTRERAS-MEDINA *et al.*, 2001). Some of these areas correspond with "hotspots" (MYERS *et al.*, 2000) and with Pleistocene refugia proposed in the world (HAFFER, 1982).

From the perspective of conservation biology, panbiogeographic nodes should be considered as priority areas, because they harbour elements from different biotic origin (CRAW, 1982; MORRONE & CRISCI, 1992; GREHAN, 1993; MORRONE & ESPINOSA, 1998; MORRONE, 1999). Many of the nodes found in this work coincide with "hot spots" proposed for the world (MYERS *et al.*, 2000), that comprise different overlapping biotas. In this work we recognise seven nodes from the intersection of two or more generalised tracks; two of them coincide with the Mesoamerican-Caribbean and Altai gates proposed by CROIZAT (1958). Some nodes are congruent with the results obtained by LUNA & CONTRERAS-MEDINA (2000) with Theaceae; the Northeastern Australia, New Caledonia and Japan nodes, have been previously suggested by CONTRERAS-MEDINA *et al.* (1999) with gymnosperms.

Mexican cloud forest holds a high number of endemic taxa (*e.g.* *Carya palmeri*, *Ceratozamia mexicana*, *Dalbergia palo-escrito*, *Diospyros riojae*, *Juglans mollis*, and *Litsea glaucescens*, among others), as well as species with highly restricted distribution patterns (*e.g.* *Fagus grandifolia* var. *mexicana*, *Illicium floridanum*, *Nyssa sylvatica*, and *Schizandra glabra*). Many of the fragments of this vegetation type may be considered as priority conservation areas, because they include taxa from different ancestral biotas, and for their high species richness, endemism, and habitat fragility.

Track analysis methods help us to integrate efficiently distributional data, which could be alternative to other methods as vicariance biogeography, phylogenetic indices, or complementarity. Also, from a conservation perspective, track methods measure the distinctiveness among biotas, overweighting those areas with representatives of different ancestral biotas (LUNA *et al.*, 2000).

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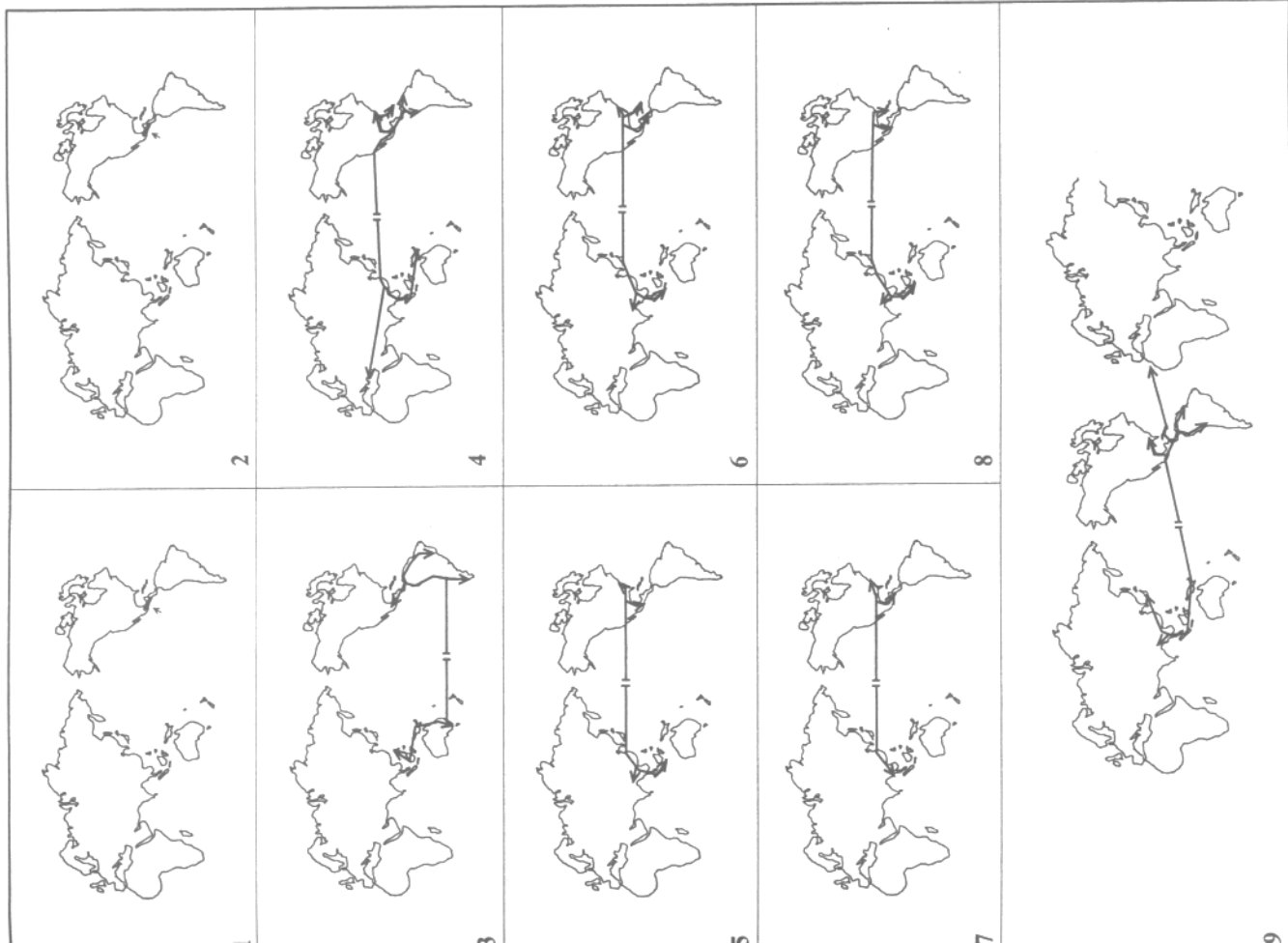
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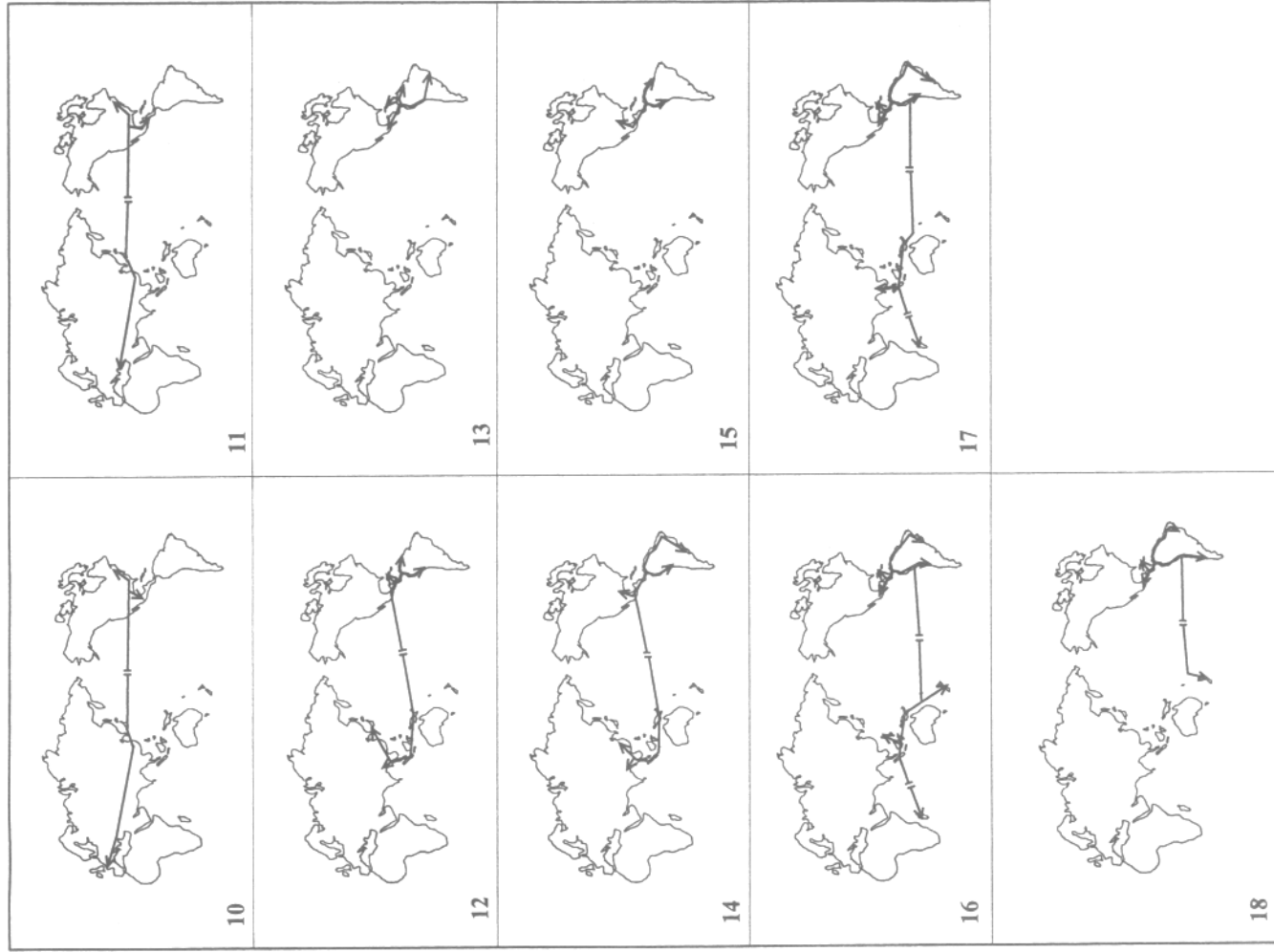
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Table 1. Seed (or spore) dispersal syndromes.

Family	Genera	Most common seed or spore dispersal syndrome
Clethraceae	<i>Clethra</i>	wind
Clusiaceae	<i>Clusia</i>	birds
Cunoniaceae	<i>Weinmannia</i>	wind
Cyatheaceae	<i>Cyathea</i>	wind
Elaeocarpaceae	<i>Sloanea</i>	birds
Fagaceae	<i>Fagus</i>	arboreal and terrestrial mammals
Hamamelidaceae	<i>Liquidambar</i>	wind
Illiciaceae	<i>Illicium</i>	beetles?
Juglandaceae	<i>Carya</i>	squirrels
Juglandaceae	<i>Oreomunnea</i>	wind
Magnoliaceae	<i>Magnolia</i>	birds
Nyssaceae	<i>Nyssa</i>	birds and small mammals, water and gravity
Onagraceae	<i>Fuchsia</i>	birds
Sabiaceae	<i>Meliosma</i>	arboreal mammals
Sterculiaceae	<i>Chiranthodendron</i>	perching birds (passerines)
Styracaceae	<i>Styrax</i>	birds
Symplocaceae	<i>Symplocos</i>	birds
Winteraceae	<i>Drimys</i>	birds



Figs. 1-9. Individual tracks of vascular plants of Mexican cloud forests: 1. *Chiranthodendron*; 2. *Oreomunnea*; 3. *Drimys*; 4. *Syrax*; 5. *Nyssa*; 6. *Magnolia*; 7. *Carya*; 8. *Illicium*; 9. *Clethra*.



Figs. 10-18. Individual tracks of genera of vascular plants of Mexican cloud forests: 10. *Fagus*; 11. *Liquidambar*; 12. *Meliosma*; 13. *Cyathea*; 14. *Symplocos*; 15. *Clusia*; 16. *Weinmannia*; 17. *Sloanea*; 18. *Fuchsia*.

GEOGRAPHIC DISTRIBUTION OF LIZARDS OF THE GENUS *TEIUS* (SQUAMATA: TEIIDAE) IN SOUTHERN SOUTH AMERICA

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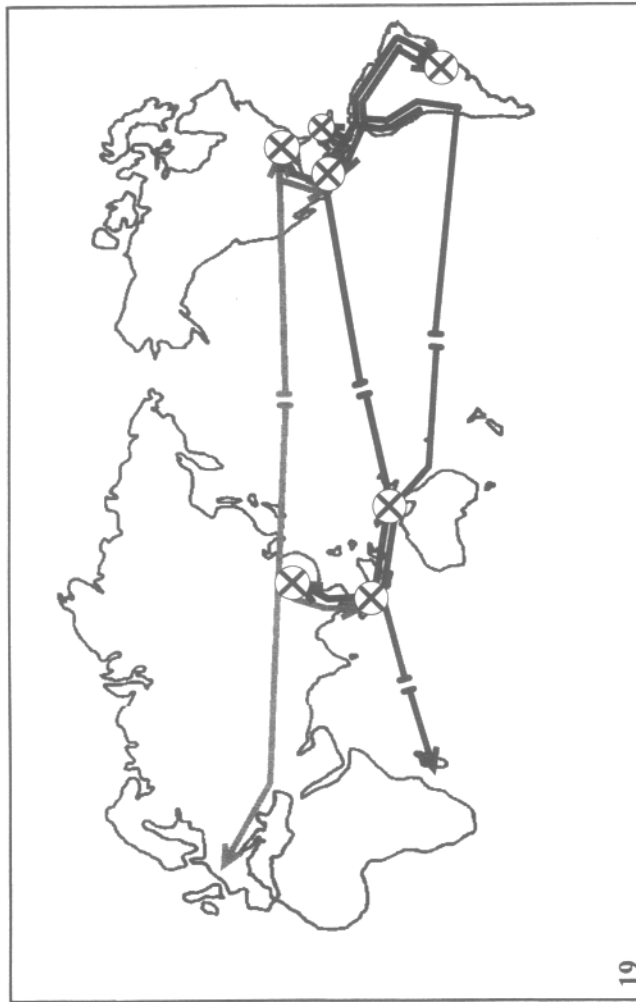
ABSTRACT.- Geographic distribution of *Teius suquiensis*, *T. teyou* and *T. oculatus* in Argentina, Bolivia, Brazil, Uruguay, and Paraguay is presented and discussed with special emphasis in Argentinean populations. Known sympatry and syntopy zones in central Argentina are discussed.

KEY WORDS.- *Teius*, Geographic distribution, South America, Parthenogenesis

RESUME.- Les répartitions géographiques de *Teius suquiensis*, *T. teyou* et *T. oculatus*, sont présentées et discutées pour l'Argentine, le Brésil, l'Uruguay et le Paraguay, avec une attention particulière pour les populations argentines. Les zones connues de sympatrie et de syntopie en Argentine centrale sont discutées.

MOTS-CLES.- *Teius*, Répartition géographique, Amérique du Sud, Parthénogenèse

Fig. 19. Generalised tracks found and recognised nodes obtained from the distribution analysis.



INTRODUCTION

Lizards of the genus *Teius* are widely distributed in lowland areas of southern South America, east of the Andes, and comprise at least three species of medium-sized lizards (350 mm total length in *T. teyou*, the largest species). This genus is characterized by the presence of only four digits in the hind legs and, as other teiid lizards have slender bodies, a large tail, and bright coloration. *Teius suquiensis* was described in 1991 as a parthenogenetic species distributed only in the central part of Argentina, and is the more austral parthenogenetic lizard in South America (AVILA & MARTORI, 1991); *T. teyou* and *T. oculatus* are bisexual species with an extended geographic range; all species are diurnal, oviparous, and insectivorous.

Although all species are common, and with high population densities, only in the last two decades have biological and ecological information been published (GUDYNAS 1979; GUDYNAS *et al.*, 1981; TRIVI DE MANDRI & CHANI, 1985; ACOSTA & MARTORI, 1990; MARTORI & ACOSTA, 1990; ACOSTA *et al.*, 1991; AVILA *et al.*, 1992; ALVAREZ *et al.*, 1992; MARTORI & ACOSTA, 1994; D'AGOSTINI *et al.*, 1997; BLANCO & ACOSTA, 1998; CRUZ *et al.*, 1999; MARTORI & AUN, 1993; SOUZA BUJES, 1998, 1999), but species limits and an appropriate knowledge of geographic range of each species was obscure and uncertain due to taxonomic and nomenclatural confusion between *T. teyou* and *T. oculatus* (CEI, 1980, 1986, 1993; CEI & LESCURE, 1985). After CEI and LESCURE's (1985) work, when the nomenclatural confusion between both bisexual species was solved, only CEI (1986, 1993) provided additional information about the geographic distribution of each species, but with several mistakes. Successive works add additional and more precise information for some small geographic areas or political regions (YANOSKY *et al.*, 1993; AVILA, 1995; MARTORI & AUN, 1995; TIRANTI & AVILA, 1997; ACOSTA & MURUA, 1998; AVILA *et al.*, 1998; GUERRERO *et al.*, 1998;