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Origins of Neotropical Leafy Hepaticae

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Abstract. The neotropical hepatic flora, predominantly constituted by members of the Jungermanniales and Metzgeriales, includes a disproportionate number of genera which are endemic (over 38) and a number which evidently originated here but have shown slight and in a geological sense, modern dispersal by solitary species. Endemism is confined almost to the Jungermanniales; it is to a large degree of a unique sort: confined to highly apomorphic derivatives, often extremely reduced, sometimes confervoid or thalloid (aside from 'normal' sexual branches). These endemics are derivatives of basically cool-Gondwanalandic suborders, chiefly Lepidoziineae and Cephaloziineae which, in the Antipodes today include a wide range of plesiomorphic taxa. The highest proportion of endemic genera, often stenotypic (1-3 species each) occurs in the upper montane zone: from upper Andean forest to páramo, to the edge of permanent snow and ice; a smaller number occurs at upper elevations of the Guyana Shield, but more occur in the riverine systems that dissect this shield. The taxa found there (i.e., *Zoopsidella*, *Pteropsiella*, *Schusterolejeunea*, *Cephalantholejeunea*) are among the most apomorphic of all hepatics.

The amount of endemism is shown to be higher than in any comparable region of the globe. It is assumed that this is owing to: (a) isolation, exceeding 40 m.y. and probably exceeding 60 m.y.; (b) continuous tectonic activity, preserving the 'raw' and 'pioneer' habitats which are necessary for the survival of 'fugitive', 'shuttle' and other types of pioneer taxa; (c) the antiquity of the Guyana Shield and its riverine system; (d) creation of striking ecological gradients, many biotic islands; (e) fluctuation in extent and degree of isolation of these 'islands', leading to (f) rapid evolution due to genetic drift and perhaps enhanced selection pressures. It is concluded that part of the complexity of the flora is due to preservation of some elements on the old Guyana Shield but most is due to relatively rapid evolution during Tertiary times. A final contributing element has been the fact that movement of the South American plate has been primarily from east to west, so that the relevant land area has not been rafted into regions with very different climatic parameters: the degree of extinction seen in, e.g., India and Australia is not evident here. It is concluded that the amount of endemism seen, and its extreme kinds, 'need' in excess of the 40-60 m.y. time span which seems available. In particular, the large number of high elevation endemics, some (such as *Ruizanthus*) very isolated, cannot be satisfactorily explained by assuming their evolution in the few million years available since alpine regions were created by the rise of the Andes. It is almost necessary to conclude that limited 'pre-Andes' must have existed and that the ancestors of the isolated taxa seen today in alpine loci in Colombia and Venezuela originated elsewhere. The other side of the outlined scenario is that with the near-total isolation of tropical America until the Andes were elevated, and until the Pliocene connection to North America arose, one would expect to see few and scattered intruders from cool-Gondwanalandic areas and from Laurasia. The modern flora reflects exactly this.

I. Introduction

Attempts at a discussion of the origins of the neotropical hepatic flora run into a host of problems which are only partially — and imperfectly — soluble today. Some, but not all, of the limitations are briefly discussed in Part II of this paper. In essence, the asymmetry of the available data base limits its use.

Although the poor taxonomic knowledge of neotropical hepatics is a serious limiting factor, this is counterbalanced by accumulation, since the 1960's, of a large pool of data dealing with tectonic events in the area. The asymmetry between a defective understanding of the pertinent taxonomy and the modern, highly suggestive data available from tectonics is briefly outlined in Part II. In this essay I largely limit myself to Jungermanniales, and specifically to the more stenotypic groups whose taxonomy is reasonably well known. Admittedly, this may appreciably distort the conclusions arrived at, yet trying to derive phytogeographical generalizations based on demonstrably defective taxonomy (as in Fulford, 1951) leads one to predictably fallacious conclusions.

II. Taxonomic vs. Tectonic Data Bases

Taxonomic Perimeters and their Validity

Since Spruce (1884-85), essentially single-handedly founded neotropical hepaticology, the field has had a discouraging history. After the excellent start made by Spruce, the 'nadir' was reached with Stephani (1898-1924) who practiced the 'geographical' species concept to the point of absurdity; he redescribed the same taxon, often repeatedly, sometimes in 3-4 or more 'wrong' genera. One result is that we have been submerged in a plethora of ill-founded species, especially in Lejeuneaceae and Jubulaceae, lost in incorrect genera and/or families.

Unfortunately, there has been little worthwhile revisionary work on neotropical hepatics. Isolated exceptions are more limiting than helpful: thus even though Castle (1937-69) revised the cumbersome genus *Radula* on a world-wide basis including numerous neotropical taxa his work has proved routine, when not downright bad. At the level of floristics, Herzog between 1923 and 1960 published numerous papers on neotropical bryophytes, describing scores of new species. He, however, spread his net too far: thus he never caught the nuances of generic concepts, especially in the complex Lejeuneaceae, with the consequence that a high proportion of the 'new' taxa he described are synonyms and/or described in the wrong genus. An end result has been a limited pattern of activity which falls into two categories: (a) coincidental revisions of neotropical taxa when entire genera are revised; (b) taxonomy best characterized as 'hit and run': describe the seemingly obviously new genera and species, and 'forget' the rest. I myself have been guilty of the latter: thus some 10 new genera and 40 new species are described from Venezuela in Schuster (1978, 1978a), the most readily recognizable elements among several thousand collections made, the bulk of which (especially in genera like *Lejeunea*, *Frullania*, and *Plagiochila*) remain undetermined, or are given provisional names.

This sad litany of limitations could be amplified but I have made my point. Verdoorn (1950) had made it earlier, noting that perhaps only about 25% of 'exotic' (chiefly neotropical) taxa can be 'named easily' and another 25% be named 'approximately' while fully half 'cannot be named by any responsible, modern worker.' This appalling situation has been eased only marginally in the nearly forty years which have elapsed.

In one sense the problem has worsened: we have learned in the last third of the

century that we really do not know enough about neotropical hepatics, in the modern sense, to name even 50% of our material. For this reason I have felt compelled to base my conclusions on a very limited data base, almost exclusively on recently revised genera which, in virtually all cases, are small (with an average of under 10 species). Recognition of our very imperfect knowledge of neotropical hepatics comes from basically two sources: (1) Intensive study of supposedly stenotypic and well-known 'textbook' hepatics like *Pellia endiviifolia* and *Marchantia polymorpha* has shown that they are indeed highly 'complex' species groups; the former may include at least three taxonomically distinct entities, only one of which (*P. megaspora* Schust.) has yet been described and intensively studied (Schuster, 1981, Newton, 1981, Krzakowa, 1981, Mendelak, 1981). *Marchantia polymorpha* includes evidently three well-defined species (Schuster, 1988), separable anatomically, geographically, and ecologically. Even the ubiquitous *Conocephalum conicum* apparently includes a series of cryptic taxa which may possibly represent distinct species. (2) Cytological study of in excess of 120 Colombian Jungermanniales, in October-December, 1988, has shown that in genera like *Taxilejeunea* and *Cheilolejeunea* there is a whole ensemble of species that may be difficult, if not impossible, to separate from dead gametophytes, i.e. herbarium specimens, but which have drastically different oil-body criteria and are, without doubt, good and repeatedly recognizable species. In short, herbarium-based phytogeography will likely lead to only partially valid conclusions.

Extrapolating from data of this type leads us to assume that neotropical hepatics are very poorly understood. There has been a recent, admirable attempt at consolidating the numerous ill-founded species but the nagging suspicion remains that, a century from now, when our knowledge of

neotropical hepatics will approach our comprehension of European and North American taxa, rescucitation of synonymized taxa will become necessary. A fully satisfactory analysis of the origins of the neotropical liverworts is thus not yet feasible; only part of the needed data is even marginally reliable.

Of countless examples which could be cited, three suffice. (1) A suite of antipodal species which had been placed (by, i.a., Spruce and Stephani) into the largely holarctic genus *Cephalozia* were shown (Schuster, 1965, 1969) to belong to Geocalycaceae (*Xenocephalozia* Schust.), Lepidoziaceae (*Pseudocephalozia* Schust., *Zoopsidella* Schust., *Bonneria* Fulf. & Tayl., s. lat.) as well as Cephaloziaceae (*Metahygrobiella* Schust.). (2) Neotropical species here assigned to the single genus *Zoopsidella* Schust. were described by Fulford (1968) under *Zoopsis* and *Regredicaulis*, and placed in 2 separate families. (3) Neotropical species I regard as belonging in the single genus *Paracromastigum* Fulf. & Tayl. are placed by Fulford (1966) in part in two genera, *Paracromastigum* s. str. and *Bonneria* Fulf. & Tayl., in the Lepidoziaceae; yet in Fulford (1968) species assigned to the former are placed in a separate family, the Paracromastigaceae, and assigned in part to a third genus, *Leucosarmentum* Fulf. Thus any phytogeographic conclusions based on the Fulford papers would lead to vastly differing conclusions from those drawn from more 'conservative' genus and family concepts.

I do not wish to belabor such instances but we need to note that these examples are drawn from stenotypic groups where taxonomic problems are resolvable today. There is no sense whatsoever in trying to use large, polytypic groups (e.g., *Lejeunea* s. lat., with perhaps 11-12 subgenera; *Plagiochila* with perhaps 150-175 neotropical taxa and perhaps 600 taxa

world-wide) in any attempt at deciphering the origin or origins of the neotropical hepatic flora. Drawing distribution maps and, especially, trying to derive far-reaching conclusions from such an unreliable data base are exercises in futility. Some perspective on these limitations is available from consideration of one fact: there are fewer workers dealing with the estimated 250+ genera and perhaps 2500+ species of neotropical Hepaticae than there are those, today, concerning themselves with the single genus *Sphagnum*!

Pertinent Tectonic History

A cardinal principle implicitly adopted by the biogeographer is that the length and degree of isolation condition the evolutionary process: if a flora is physically isolated, especially if associated with the isolation are physical and/or climatic changes which act as stimuli on the selection process, that flora undergoes progressive differentiation from the "undifferentiated" parent flora. This effect of isolation is admittedly more strongly expressed when population sizes are small (the Sewall-Wright Drift, or genetic drift) rather than large. We must almost assume, however, that the area today comprising tropical America has never been biologically a unitary area, but consisted of a large number of biological islands.

Based on modern tectonics, a number of working assumptions, all relevant to such an appraisal, seem germane. They, in essence, inform us as to when a flora was isolated, and from where it may have derived. Working assumptions (oversimplified because of spatial constraints) are as follows; tentative conclusions follow:

(1) Prior to ca. 90 m.y. BP South America was joined with Africa; prior to this time there was an Afro-American undifferentiated Gondwanaland-derived flora that characterized the area.

(2) Until ca. 60 m.y. BP the South American Plate was united, tenuously at least, with the Antarctic Plate specifically with West Antarctica, which then presumably was much more extensive (a broad and rather shallow sea to the west of West Antarctica is assumed by some geologists to have been above water much as the Bering Land Bridge; the current submersed condition is assumed to be due to isostatic pressure derived from the extant ice sheet). This broad land bridge began to disappear with Oligocene spread of the Antarctic ice sheet. Early in the Tertiary westward movement of South America resulted in the Scotia Arc — formerly constituting a bridge between South America and Antarctica — being progressively 'stretched' so that former almost vertical and complete connections were broken. Thus until early Tertiary times migration from South America across Antarctica remained feasible.

(3) Aside from tenuous and at least intermittently broken connections, South America was isolated from the North American Plate until some time in the Pliocene. The existence of connecting island 'filters,' or 'archipelagic filters,' remains somewhat conjectural — although vertebrate zoologists such as Simpson insist on them. The two principal contending modern theories dealing with creation of such archipelagic filters have been dealt with by Buck (this symposium). In any event, as succeeding pages show, for hepatics, transgression of Laurasian types into tropical America has been very limited and may not have occurred until late in the Tertiary, coincident with elevation of the Andes, and creation of cool, moist niches.

(4) If South America and Africa were joined, prior to 90 m.y. BP, then this considerable land mass had to drain in part toward the West. The Amazonian Basin represents what is left of a formerly

extensive and complete E-W sea way. At least as regards Hepaticae, this served presumably as a very effective barrier to N-S or S-N migration of all but lowland taxa.

(5) With opening of the South Atlantic and westward drift of the South American Plate, the leading edge of the western margin of that plate came into collision with the Pacific Plate. With subduction of the latter, the western edge of the South American Plate was progressively elevated. Only well after initiation of this elevation was the former sea way blocked in the west.

(6) The relatively late creation of the Andes and their precursor served, simultaneously, to (a) bridge the former gap between southern and northern sectors; (b) create a wide range of new environments; (c) continuously make available for ecesis pioneer sites — the kinds of sites most hepatics revel in. As the following pages suggest, the degree of endemism in the hepatic flora suggests the 'need' for a pre-Cordilleran epoch.

(7) For a considerable period, thus, the principal if not only contact between South America and other land masses appears to have been to the south — with Antarctica and, through it, to Australia. A rough guess — which will form the operating basis for what follows — is that by 80 m.y. BP a gap existed between South America and Africa; from then until ca. 60 m.y. BP the only biogeographically relevant land connection appears to have been to the south, and this appears to have been operative until the start of the Tertiary.

Thus, until the requisite movement west of the South American Plate and concomitant subduction of the adjacent sectors of the Pacific and Nazca plates, a sea way existed that cut across South America, E-W — much like the Cretaceous embayment that cut North America, N-S.

This E-W sea way must have been a significant barrier to N-S migration of all but lowland taxa with suitably efficient modes of dispersal. This barrier seems as real to me as that to the east (the opening South Atlantic), west (the Pacific) and north (the remnant of the Tethys Sea separating North and South America). Essentially, the bulk of the area constituting today's tropical America existed in isolation — and the hepatic flora reflects this degree of isolation.

(8) The broad picture I am trying to paint is one of a region strikingly isolated until firm links with North America were forged in the Pliocene.

Central to this region is the ancient Guyana Shield, embracing areas from tropical lowlands to cloud forest summits — the nucleus of an area that was biotically rather isolated from at least 80 m.y. BP until perhaps 3-5 m.y. BP. Only, perhaps, New Zealand was equally, if not more strongly, isolated for an equal length of time. The degrees of endemism among Hepaticae, chiefly at the generic level, which characterize both regions, I think reflect comparable levels of isolation. The east-west nature of the water barrier, in effect, separated the evolving South American hepatic flora into a southern component, with persistently very strong Gondwanalandic links (and clear similarities to the flora of similar latitudes in Australasia) and into a northern flora which, as we shall see, evolved a high degree of individuality. The time of evolution of such a northern, tropical element in the northern portions of South America can be deduced with a fair degree of precision today, thanks to the physical geologist.

(9) I have drawn an overly simple picture, above, because the isolated northern sector of the South American Plate was in abrasive contact with not only the Pacific Plate but with two other smaller plates, the

Antillean and the Nazca Plates. The influence of the biota of the land areas of these plates on the South American one — the amount of reciprocal exchange — remains highly uncertain. In part, as the example of *Phycolepidozia*, cited later, shows, because our inventory of the biota remains very fragmentary. If the 'contribution' of these plates to the Hepaticae of the South American plate is uncertain, however, the contact points have been very important in resulting in complex mountain orogeny — a pattern of land elevation that profoundly influenced the flora of the Northern Andes.

III. Some General Effects of the Tectonic Events Outlined

In an essay on the 'Phytogeography of the Bryophyta' (Schuster, 1983, pp. 463-626) I had the temerity to include, almost as an after-thought, a few pages (pp. 616-20) dealing with 'Tectonics and Diversity: Some Speculations.' What I had to say then I said 'with considerable trepidation'; my reservations remain almost as strong today — yet, then as now, the subject matter is 'fascinating and the correlation seems... compelling.'

I found that there was a considerable correlation between tectonic instability (and its consequences, e.g., mountain building, erosion, valley cutting, climate alteration, the creation of a very rapid climatic zonation coincident with creation of high mountains) and (a) richness and diversity of the hepatic flora and (b) preservation of at least some generalized, if not archaic, types. This is true not only of the specific area here under discussion, but it seemed to be true along the entire 'Ring of Fire' peripheral to the Pacific. Thus, from the range of *Takakia* (cf. maps, figs. 27, 50 in Schuster, 1983) it is obvious the extant dispersal, from the Himalaya to British Columbia, accurately mirrors the distribution of plate interactions — running from contact points of the Indian-Eurasian

Plates to that of the North American-Juan de Fuca-Pacific Plates. The only three hepatic genera endemic to North America, all phylogenetically isolated organisms, are *Schofieldia*, *Geothallus* and *Gyrothyra* — the last the only member of an isolated family; these genera occur strictly along a western fringe of the continent where Pacific, North American and Juan de Fuca Plates are in contact (cf. map, fig. 6, in Schuster, 1983).

Diversity and richness of the hepatic flora — a phenomenon that may have dual causes (preservation + evolution) — thus appears to accurately reflect the extent to which tectonic instability has occurred in the past. Indeed, I suspect there is a rather good quantitative correlation. Thus all of eastern North America virtually lacks endemic Hepaticae and there are no genera or families endemic to it. Endemic genera of mosses in eastern North America also are lacking (the few described, known only from sterile gametophytes, remain suspect). This may reflect the effects of stability. It is often assumed 'old' areas are centers of both endemism and diversity, but the perhaps paradoxical fact is that the reverse is the case. Thus the rapid and continuing elevation of the Andes is correlated with a rich and diverse flora, including endemic hepatic genera; the old Appalachian ranges, which have been eroding for about 400 m.y. are notable chiefly for the lack of significant levels of endemism. I am not proposing that geologically old and stable areas are wholly devoid of endemic types, but as — is noted later — even in tropical South America the oldest area, the Guyana Shield, seems relatively poorer in endemic genera than the tectonically unstable areas going from Venezuela and Colombia south all the way to southern Chile. The answer to the paradox appears to reside — and this is my chief point — not in preservation of isolated taxa in stable areas, but in preserving and, indeed, continuously creating the pioneer loci to which many of the

'fugitive' and 'shuttle' species seem to be confined.

A number of factors appear to be involved in the dual combination of enhancement and preservation of diversity, briefly:

(a) Creation of climatic diversity. In tropical America one goes, in short distances, from hot and humid tropical climates to permanent snow and ice — as near Merida, Venezuela, or Santa Marta, Colombia. One can also go from hyperhumid areas with high precipitation levels all year long (east slope of the Peruvian and Bolivian Andes) to areas where rain hardly ever falls (west slopes of these areas). Thus temperature and precipitation gradients can be very steep. The degree of climatic diversity along a single gradient (e.g., the western slopes of the Cordillera de Merida, above Merida, Venezuela) going from over 4200 meters (permanent snow and ice) to 2000 meters (humid, tropical rain forest) is roughly the same as going from Greenland to the Antilles. As is obvious, the 'steepness' of the gradient is a factor in also producing almost unbreachable climatic barriers.

(b) With recent elevation of the Andes — and simultaneous preservation of the old Guyana Shield — we have the best of all possible worlds as regards (1) 'stimulation' of diversity and (2) preservation of diversity. The two phenomena are difficult to separate at times. But, for example, the presence of isolated generic types, apparently found nowhere else except on the Guyana Shield, such as *Haesselia*, *Trabacellula*, *Odontoseris*, suggests that preservation, as distinct from creation, of new types is a very different phenomenon. On the following pages some attempt will be made to separate these phenomena.

(c) There has also been creation of a diversity of rock types — aside from the old rocks of the Guyana Highlands and their periphery we see the exposure in the

Andes of immense layers of a wide range of sedimentary rocks. Any one who takes the train from Lima to Huancayo — one of the great experiences of the world — can hardly fail to be impressed by the tortured and folded layers of sediments exposed, e.g., near La Oroya, between 3000–4000 meters — sediments which were once ocean bottom.

(d) With very complex folding patterns, northern portions of South America have a very complex series of mountains. Thus we see three Cordilleras in Colombia, as well as isolated high massifs like that of Santa Marta; we see rather strongly isolated mountain ranges in Venezuela, the Cordillera near Merida being quite isolated from the high, though somewhat lower, mountains of the Colombian-Venezuelan border, near Cucuta and San Cristobal. This complexity reflects complicated tectonic interactions between four plates: the South American, Pacific, Nazca, and Caribbean Plates.

(e) Rapid and recent elevation of these mountains has occurred — and is occurring — during a time of climatic instability. Not only were steep climatic gradients created, but superimposed were the well-documented cooling episode of the Oligocene and rapid climatic fluctuations in the Pleistocene. It is beyond the scope of this paper to document this history in detail. Relevant is recognition of the fact that existing alpine areas — paramo and areas above permanent snow and ice — expanded during each pleistocene maximum (migration from one paramo system to the next was then facilitated); during interglacials the páramo and alpine areas became progressively more restricted to progressively more isolated higher elevations and the floras of each system were isolated. It is tempting to speculate that each such biotic island, limited in extent, exhibited all the preconditions necessary for rapid genetic drift. The well-documented history of many

angiosperms (e.g., endemism in *Espeletia*) serves as a model.

The occurrence of endemic species of chiefly tropical groups such as Lejeuneaceae at high elevations on such alpine islands may also reflect these complex phenomena. Thus in the Sierra Nevada de Merida an isolated species of the tropical genus *Dicranolejeunea* was found, frozen solid, at 4100 meters and higher; in and just below the Paramo de Tama occur 'dwarf' species of *Cheilolejeunea* (*C. erostrata* Schust., *C. invaginata* Schust.) and *Ceratolejeunea* (*C. andicola* Schust.)—the last unique in being soil-inhabiting—at ca. 2500-3200 meters. Such endemism appears to reflect the 'island phenomenon.'

(f) Finally, one must recognize the relevance of the fact that the majority of hepatics are plants of unstable environments—many occur on exposed rock faces or on soil where other vegetation either cannot or has not yet invaded. A high and significant proportion is limited to pioneer or near-pioneer loci, ranging from living leaves to twigs and unstable banks. There is a growing literature on the 'opportunistic' or 'fugitive' nature of many taxa, with the life strategies characterized as those of 'fugitives,' 'colonists,' and 'shuttle species' (During, 1979; Longton & Schuster, 1983). With the complex and rapid mountain orogeny outlined above, there is essentially continuous creation of 'new' or 'raw' sites or r-selecting environments. [I have, with my friend Lewis Anderson, often made invidious remarks about 'roadside collections.' Yet, in its defense, a considerable range of taxa are found there precisely because of rather recent disturbance. Thus, for example, in New Zealand, *Haplomitrium gibbsiae* (Steph.) Schust. occurs principally on unstable, moist roadside banks; in Australia the ancient *H. intermedium* Berrie was seen only on ledges at the edge of a road.] With increase in elevation, cascading streams, hyperhumid streamside environments, and

similar diverse and 'favorable' loci are created which can be exploited by delicate, mesophytic 'pioneer' plants like the Jungermanniales, Metzgeriales, and Monocleales.

From the foregoing, thus, I think it is fair to conclude that the dual (and I think nearly inextricable) phenomena of preservation and enhancement of biotic diversity has, at least in the case of the Hepaticae, had very complex and closely interdigitated causes.

In essence, both opportunity (due to long isolation) and stimulus (due in part to selection pressures induced by rather rapid climatic changes, in turn induced by (a) mountain building and (b) late Tertiary and Pleistocene climatic changes) have operated jointly. The bulk of the Hepaticae that lend such a unique aspect to the hepatic flora of tropical America have had a long time, in isolation, to evolve into the strange and unique patterns that impress the student, even with superficial examination.

I do not mean to imply that this is the entire story. Endemic elements which evolved in situ have been 'enhanced' by two other chief sources: (a) taxa belonging to the basically cool-temperate Gondwana flora, found from southernmost South America into Australasia; (b) taxa of the cool to cold zones of the Holarctic. As a consequence, the origins of the present flora seem to be derived from three disparate sources.

An examination of these three primary sources suggests that the flora of tropical Latin America has had a complex origin: thus, as the title of this essay suggests, the flora has had origins—not a single origin. However, the cool-Gondwana-derived intruders, and those of the cool to cold sectors of Laurasia, are both relatively recent immigrants, reflecting the relatively recent geological origin of the Andes and volcanic mountains of Central America.

Probably most of the immigration from these two sources has been in the last 2-10 m.y., and some probably much more recently. Proliferation of montane areas in otherwise tropical and subtropical zones has surely facilitated intrusion of taxa like *Blepharostoma trichophyllum* and *Anthelia juratzkana*.

Cyclonic tracks and wind patterns in general, however, mitigate against any amount of migration from north to south. It is much more likely that such elements in the flora of the Appalachians and westernmost Europe such as *Anomylia cuneifolia* and *Plagiochila exigua* (*P. tridenticulata*) are derived from Latin American sources, and were carried north and northwest by cyclonic disturbances, rather than the reverse.

IV. Major Elements in the Hepatic Flora

As noted, three elements constitute the bulk of the leafy hepatics in tropical America: (1) endemic taxa, often with only remote relationships to the floras of other regions; (2) elements derived by migration from the cool Gondwana flora; (3) elements driven by migration from the cool to cold-adapted flora of Laurasia. From the prior discussion of tectonics it is evident that the factors (lofty mountains, moisture-trapping clouds) which made ecesis of these last two elements feasible are geologically rather recent events: the rather small number of taxa constituting the second and third elements (and their brief treatment) reflect these time constraints.

A very few taxa do not fit comfortably into these three categories; these are cited under (4) Disharmonic elements. A brief discussion of the Afro-American 'connection' (5) concludes this analysis.

1. Endemic (Autochthonous) Taxa

A series of genera (in some cases,

subgenera) are endemic to the Neotropics, s. str. (here taken as the area including the Amazonian Basin, northward). I assume that this ensemble of groups differentiated from an "undifferentiated" and relatively generalized flora that existed, probably by the Early or Mid-Cretaceous, when — by extrapolation — groups like the Lepidoziaceae, Calypogeiaceae, and Balantiopsidaceae had begun to differentiate. At that time Africa + South America remained joined, and the western edge of the megacontinent fringed on Panthalassa, the ancestor of today's Pacific. The eastern edges of South America and western edges of today's Africa were part of an interior, continental land mass and must have had relatively inimical climates: at least seasonally arid and probably of quite a continental character. If one examines contemporary reconstructions (e.g., that of Dietz & Holden, 1970; cf. Schuster, 1976, p. 58, fig. 2) it is evident that only northernmost sectors (the Guyana Highlands) and westernmost sectors of present-day South America had an oceanic location and, reasonably, could have been expected to enjoy an oceanic climate in appropriate latitudes, with appropriate prevailing winds. If one maps current distributions of isolated endemic elements present today in South America, all but an insignificant number still exist along this oceanic fringe, extending from the present-day Guyanas to Chile. Such a reconstruction, also, makes evident the fact that drainage of the western sector of this megacontinent must have been westward. By the start of the Tertiary, South America was clearly isolated, except for persistent tenuous connections via its 'tail' to Antarctica (cf. fig. 3 in Schuster, 1976). If we consider this figure, one very relevant detail stands out: the physical isolation, by the start of the Tertiary, of South America, was more nearly total than that of any other comparable land mass. It seems reasonable to assume that on this isolated land area a highly unique and specialized flora should have evolved.

In Schuster (1982, pp. 19-20) some 40-odd genera/subgenera are listed as endemic to this area; the more outstanding are as follows; where modern distribution maps exist, these are cited in square brackets, [].

(1) *Zoopsidella* Schust. Including at least 7 neotropical taxa in 2 (perhaps 3) subgenera: *Z. antillana* (Steph.) Schust., *Z. cynosurandra* (Spr. ex Steph.) Schust., *Z. integrifolia* (Spr.) Schust., *Z. macella* (Spr.) Schust., *Z. richardsiana* Schust. (of Guyana), *Z. dichotoma* Schust. (Colombia) and, probably *Z. serra* (Spr.) Schust. An eighth taxon, much less derivative morphologically, is the Australasian *Z. ceratophylla* (Spr.) Schust. In this genus there is a well-entrenched tendency for leaf lobes to be reduced to papillae.

The allied genus *Zoopsis* occurs from Australasia to the Philippines and southernmost Japan. No taxa of either genus occur in the cool parts of South America.

(2) *Pteropsiella* Spr. Including 2 taxa, both of the Amazonian and Orinoco drainages: *P. frondiformis* Spr. and *P. metzgeriaeformis* Schust. A well-known and unique endemic, with secondarily 'thallose' vegetative gametophytes. Leaves are also reduced to ephemeral papillae.

(3) *Protocephalozia* (Spr.) Schiffn., a monotype with only *P. ephemeroideis* (Spr.) Schiffn. This nearly unique taxon has a confervoid gametophyte, with uniseriate branched filaments that give rise to leafy sexual branches.

(4) *Phycolepidozia* Schust., also monotypic, with only *P. exigua* Schust., also an algal-appearing taxon with polyseriate axes and leaves reduced to slime papillae. Known only from Dominica.

(5) *Monodactyloopsis* (Schust.) Schust., bitypic, with only *M. minima* (Schust.) Schust. and *M. monodactylus* (Spr.) Schust., a genus of highly reduced taxa with leaves of only 2-5(6) cells. Although similar to *Arachniopsis* in some respects, the type species, with a 12+4-seriate seta differs from all preceding genera in seta anatomy: 8+4-seriate seta (*Zoopsidella*, *Pteropsiella*, *Protocephalozia*; all Lepidoziaceae) or a 4+4-seriate one (*Phycolepidozia*, *Phycolepidoziaceae*). The prevalent axial anatomy (4 cortical + 1 medullary cell rows) may recur in reduced taxa of *Arachniopsis* e.g., *A. confervoides* Schust. (compare Schuster, 1988, figs. 1:6 and 2:10).

The five genera, all strictly endemic to tropical Latin America (aside from one primitive species of *Zoopsidella*, found in Australasia), represent some of the most apomorphic types that exist in the Suborder Lepidoziineae — a suborder which is highly polytypic in cooler sectors of former Gondwanaland. The suborder almost surely is of Gondwanalandic derivation, and I assume ancestral types were widespread there prior to the breakup of Gondwanaland. The above ensemble presents a unique constellation of features: all show massive reduction or loss of leaves, with photosynthesis largely a function of a thallus (*Pteropsiella*) or of a vastly expanded, hyalodermous axis, or of persistent protonemal filaments. All also show varying degrees (or loss) of a gametophytic axis and reduction or loss of leaves or lobes. All but *Protocephalozia* show elaboration of papilliform leaf lobe apices (or, *Phycolepidozia*, *Pteropsiella*, reduction of leaves to papillae). Although the Lepidoziineae are subcosmopolitan, only in tropical America has there been such experimentation with paedomorphosis and neoteny in the Lepidoziineae. The same phenomenon is exhibited by two endemic species of *Radula*:

(6) *Radula yanoella* Schust. (cf. Schuster, 1984, fig. 11, p. 799) of the Serra Curicuriari, Brazil and (7) *R. aguirrei* Schust. (cf. Schuster, 1990) of Colombia; both are epiphylls, of the subg. *Metaradula* Schust., with highly reduced axes, very limited development of gemmiparous leafy axes, which develop from an extensive, lobed and furcate monostromatic thallus. Neither develops gametangia.

These examples of gametophytic reduction — simplification when not loss of the axis and reliance on algal-appearing structures (filaments or thalli) as the main photosynthetic apparatus — exist again only in the basically Australasian genus *Zoopsis* and the monotypic genus of Lejeuneaceae, *Metzgeriopsis* Goebel. The latter is widespread in and near tropical parts of Australasia (New Caledonia-New Guinea, into Fiji; westward to Indonesia). Both genera seem to be Gondwanalandic in origin, as are — as already noted — the Lepidoziaceae. There is thus a qualitative difference between these taxa and those found in Laurasia. Why is somewhat of a mystery: it is difficult and perhaps foolish to assume that there is something in the history, or climates, of Gondwanaland that 'stimulated' such parallel selection paths. Goebel (1893) and Schiffner (1893) long ago dealt at length with such groups in which we see persistence of 'Jugend' manifestations which reproduce sexually (taxa 1-5, above) or asexually (6-7).

Not only do we see a nearly unique pattern of evolving unrelated 'reduced' genera of Lepidoziaceae and allied Phycolepidoziaceae (genera 1-5, above) but there has been evolution of a series of other mono- or stenotypic genera endemic in tropical America, including the following:

(8) *Micropterygium* Lindenb., with ca. 18 species, found from the Antilles to Brazil and southward to Colombia. The center of diversity appears to be the Guyana

Highlands.

(9) *Mytilopsis* Spr., with only *M. albifrons* Spr., known from Jamaica and Venezuela to Peru and recently found on the Serra Curicuriari, near the Rio Negro, Brazil, an outlier of the Guyana Shield.

These two genera constitute the very isolated subfamily Micropterygioideae, possibly a very highly derived end-group evolved from a stock identical with that of the almost exclusively cool-Gondwanalandic Lembidioideae (the latter is monographed by Schuster & Engel, 1987; cf. map, fig. 1) Again there is a suggestive — if tenuous — connection to elements of the old cool-Gondwana flora.

Several other endemic genera (and species) show more diffuse and controversial phylogeographical "moorings," i.e.:

(10) *Anomoclada* Spr., with only *A. portoricensis* (Hampe & Gottsche) Vána in Gradstein, Bryologist 92: 344, 1989. A highly specialized derivative of *Odontoschisma*, a genus with a peculiar range: 2-3 Laurasian species, and a wide array of poorly known antipodal and tropical taxa.

(11) *Cephaloziopsis* (Spr.) Schiffn., a very derivative genus of 2-3 spp., possibly evolved from *Cephaloziella*-like antecedents. The 1 or 2 neotropical taxa are monographed in Schuster (1972a); they had been treated as '*Cladopodiella intertextata* (G.) Fulf.' in Fulford (1968) but the 4+4-seriate seta, and all other criteria prohibit any association with *Cladopodiella* (Cephaloziaceae).

An additional species, possibly belonging to an autonomous subgenus, *Metacephalozia*, is known from the Ryukyu Islands (Inoue & Schuster, 1974).

(12) *Alobiellopsis* Schust. (cf. Schuster, 1965, 1969b), a genus perhaps loosely allied to the next, consists of two neotropical

species [*A. acrosyphus* (Spr.) Schust. and *A. dominicensis* (Spr.) Fulf.], a South African species [*A. heteromorphus* (Lehm.) Schust.; cf. Schuster, 1969b and Schuster & Engel, 1987] and one from Japan [*A. parvifolius* (Steph.) Schust.]

(13) *Alobiella* (Spr.) Schiffn; cf. Schuster (1969b), Fulford (1968), with only 2 neotropical species, *A. husnotii* (G.) Schiffn. of the Antilles to Trinidad and *A. campanensis* Steph. of montane areas of Peru and Venezuela. Although this genus is assigned to the 'Family Alobiellaceae' by Fulford, the genus is allied to the former, and is placed in Schuster (1969b) in the subfam. Alobielloideae within the Cephaloziaceae.

(14) *Iwatsukia* Kitagawa (cf. Schuster, 1968; Fulford, 1968, as *Cladomastigum*). Including 4 species, one (*I. exigua* Kitagawa) in Borneo, one [*I. jishibae* (Steph.) Kitagawa] from east Asia, Nepal, islands of the Indian Ocean and Central America, 2 from Venezuela, from the Guyana Shield [*I. bifida* (Fulf.) Schust. and *I. spinosa* (Fulf.) Schust., **comb. nov.** (Basionym: *Cladomastigum spinosum* Fulford, Mem. N.Y. Bot. Garden 23:840, 1972)].

Iwatsukia was regarded as a member of the Lophoziaceae (by Grolle), Lepidoziaceae (by Kitagawa) and, as *Cladomastigum* Fulf., placed into its own family by Fulford (1968). I regarded it as a member of the Cephaloziaceae subfam. Alobielloideae Schust. (Schuster, 1969b). The diversity of opinions reflects the isolation of the genus. The two purely neotropical taxa are rather isolated from the other two species and probably should be regarded as forming an autonomous subgenus, *Iwatsukia* subg. *Cladomastigum* (Fulf.) Schust.

The three genera of Alobielloideae fail to fit 'comfortably' into any phytogeographic 'mold': only *Alobiella* is strictly endemic

to the Neotropics. Five of the seven species in the other two genera (*Alobiellopsis*, *Iwatsukia*) occur in the Neotropics. The subfamily perhaps originated in our area, but has undergone secondary long-distance dispersal to the area of the Indian Ocean, Borneo, the Himalaya, and southern Japan. Noteworthy is the absence of the group from any portion of the cool sectors of Gondwanaland. The two Guyana Shield endemics perhaps deserve segregation as an autonomous subgenus, *Cladomastigum*; they surely do not warrant a distinct 'family' Cladomastigaceae.

(15) *Trabacellula* Fulf. (cf. Fulford, 1968), monotypic, with *T. tumidula* Fulf., endemic to the Guyana Highlands.

(16) *Fuscocephaloziopsis* Fulf. (cf. Fulford, 1968) with 2 taxa, *F. biloba* (Herz.) Fulf. and *F. pulvinata* (Steph.) Fulf. Considered to represent only a subgenus of *Cephalozia*, i.e., *Macrocephaloziopsis* Schust. (Schuster, 1979, p. 688). Whatever its status, this small group, like genera (12-14) and (17), clearly belongs in the Cephaloziaceae, although Fulford ascribes them to a new family, Trabacellulaceae. Both taxa inhabit an area from the Antilles into Colombia.

(17) *Haesselia* Grolle & Gradst. (cf. Grolle & Gradstein, 1988), monotypic, with only *H. roraimensis* Grolle & Gradst. of the Guyana Highlands. As Grolle and Gradstein note, these 3 genera (15-17) are clearly allied members of the Cephaloziaceae and they fit into the subfam. Trabacelluloideae (Fulf.) Schust., teste Grolle & Gradstein — a derivative of the more generalized Cephaloziaceae. Again, each of the 3 genera is small (1-2 species) and each is quite apomorphic, contrasted to such plesiomorphic genera as *Pleurocladula* Grolle and *Metahygrobiella* Schust.

(18) *Odontoseris* Fulf., monotypic, with *O. chimantana* Fulf. (Fulford, 1968). This

poorly known monotype — known only from the Guyana Highlands — lacks reproductive organs. The partly 3-4-lobed leaves and underleaves with rhizoids restricted to their bases suggest it may be allied to *Pseudocephalozia* Schust. (cf. Schuster & Engel, 1987) of the Lepidoziaceae but — Fulford assigns it to a family Regredicaulaceae.

Genera 1-18 form a suggestive whole: they all belong to two allied suborders of Jungermanniales, the Lepidoziineae and Cephaloziineae. In my opinion, aside from the isolated *Phycolepidozia* and *Cephaloziopsis* (Phycolepidoziaceae and Cephaloziellaceae, respectively), the rest belong to Lepidoziaceae (1-3, 5, 8-9, 18) or Cephaloziaceae (10, 12-17). All of these are basically phylogenetically outlying elements in their respective families; all appear to show Gondwanalandic moorings. All are 'modern' taxa, often highly specialized in one or more respects.

Several other taxa can be cited that fail to neatly fall into the preceding pigeon holes:

(19) *Stephaniella* Jack. The genus has perhaps no more than 6 species, found in treeless páramo regions, from Mexico to Bolivia. One species (*S. paraphyllina*) recurs in the Drakensberg area of South Africa: I have collected it, with Shaun Russell, at over 10,000 feet near the Sani Pass Rd., on both sides of the Lesotho-South Africa border.

Stephaniella is a very isolated genus, placed (Schuster, 1984b, p. 67) into a monogeneric subfamily of Gymnomitriaceae, to other genera of which it is only marginally related. The genus surely originated on the summits of the forerunners of the present-day Cordilleras and has diversified there. The isolated disjunction of one species to the Drakensberg is surely relatively recent; since *Stephaniella* reproduces only via spores and is limited to treeless montane

areas, spore dispersal via strong westerly winds is easily conceivable.

Like many of the genera, 1-18 cited above, *Stephaniella* is a 'peculiar' genus: it is unique in the Hepaticae in having echlorophyllose leaves shielding chlorophyllose paraphyllia that form a carpet on the antical stem surface. The evolution of such a strikingly isolated genus, restricted to the intensely illuminated páramo regions, raises very troubling questions: if the Cordillera are so young, how can one account for the evolution of such an isolated entity in such a limited time period?

(20) *Ruizanthus* Schust. (Schuster, 1978, p. 240). This isolated genus of Balantiopsidaceae may be the most plesiomorphic element in the Balantiopsidineae, a suborder which is wholly Gondwanalandic, aside from a few *Isotachis* taxa, and of *Balantiopsis*, that have succeeded in (probably geologically recent times) migrating as far north as southernmost Japan and the Philippines, respectively. *Ruizanthus*, with 2 Andean species (*R. venezuelana* Schust. occurs northward to Costa Rica; *R. lopezii* Schust. seems entirely Andean in range), appears to be allied only to the genus *Austroscyphus* Schust., whose 4 species occur from New Zealand and Tasmania to New Caledonia, with one outlier in Indonesia (Schuster, 1985a).

It is possible that these two genera, constituting the subfamily Ruizanthoideae (Schuster, 1984), are the remnants of the ancestral complex from which other Balantiopsidineae, all apomorphic in the spirally coiled capsule valves, evolved. The joint ranges of *Ruizanthus* + *Austroscyphus* parallel that of *Hymenophyllum* + *Monoclea*, subsequently discussed as disharmonic elements.

(21) *Gymnocoleopsis* (Schust.) Schust. (*Gymnocolea* subg. *Gymnocoleopsis*

Schust.). The sole species fitting here, *G. multiflora* (Steph.) Schust., is an isolated element in the Lophozioideae, found from Bolivia to Colombia and Venezuela; it is apparently confined to the paramo-andine forest ecotone, where it may grow under *Polylepis*. I know of no direct ally. It is apomorphic in the reduced sporophyte seta, formed of two cell rings.

(22) *Pseudocephaloziella* Schust. Again an isolated monotype of the Lophozioideae, without close affinity to anything else in the group. The single species (*P. epiphytica* Schust.) is a tiny plant epiphytic on twigs at the paramo margin at 3140 meters, in Venezuela. It is very plesiomorphic in being almost isophyllous in both vegetative regions and within gynoecia — a feature not again seen in Lophozioideae (Schuster, 1978).

(23) *Lophonardia* Schust. Like the two preceding genera, a plant of the páramo margin, found at 4150 meters under *Polylepis* in Venezuela. The plant, known only sterile, resembles a *Marsupella* (Gymnomitriaceae) but has the terminal branching often seen in the Lophozioideae. Its correct disposition remains to be established.

(24) *Chiloscyphus* subg. *Fragilifolia* (Schust.) Engel & Schust. This monotypic subgenus, found at ca. 3600 meters on twigs in the shrub zone of the paramo, contains a single species, *C. fragmentissima* (Schust.) Engel & Schust. The species is unique in the entire family Geocalycaceae in having freely caducous leaves; perhaps an autonomous genus is at hand.

(25) *Rhodoplagiochila* Schust. Monotypic, with only *R. rosea* Schust., known only in cold forests at 3700-3750 meters in Venezuela. The only member of the Plagiochiloideae I have seen with reddish, anthocyanin-type pigments. Inoue, who is monographing South

American Plagiochilaceae, would even exclude the genus from that family; I have no idea as to where else it could be placed.

(26) *Marsupella* subg. *Nanomarsupella* Schust. Again, a monotypic group with only *M. xenophylla* Schust. This dwarf species, from 4160 meters in the paramo of Venezuela, is isolated from *Marsupella* by the tumid, Pigafettoa-like thick-walled papilliform cells and the massive system of subterranean axes. Considered (Schuster, 1978, p. 249) to 'possibly' belong to 'n independent genus.'

(27) *Acrobolbus* subg. *Xenopsis* Schust. [Map, Schuster, 1979, fig. 17]. Again a monotype, with only *A. laceratus* Schust., from 3140 meters in the Páramo de Tama in Venezuela. Regarded as 'so isolated from' other taxa of *Acrobolbus* 'that separate generic status may become unavoidable...' (Schuster, 1978, p. 249).

Genera (and subgenera) 19-27 are all montane elements, either from high Andean forests of the *Polylepis* zone or from the paramo itself. As repeatedly noted, they form isolated and 'strange' types, without obvious contact points to other genera or subgenera. Endemism at this level is believed to have been 'stimulated' by intense selection pressure as new high-altitude habitats, unsaturated biotically, were repeatedly created. They chiefly occur in the *Espeletia* zone; their proliferation is exactly analogous to that of the numerous taxa of *Espeletia*.

An analysis of these 27 generic types, and of others (e.g., the monotypic montane-Andean elements *Platycaulis* Schust. and *Leptoscyphopsis* Schust., both known only from Venezuela; Schuster, 1978), suggests that one can differentiate, with admitted difficulties, between taxa which seem basically to have evolved as montane elements in the Andes (*Chaetocolea* Spr., *Lophonardia* Schust., *Gymnocoleopsis* Schust., *Rhodoplagiochila* Schust.,

Pseudocephaloziella Schust., *Platycaulis* Schust., *Leptoscyphopsis* Schust.) and perhaps 'older' elements which occur on or near the ancient sandstone mountains of the Guyana Shield (*Trabacellula* Fulf., *Iwatzukia* subg. *Cladomastigum* (Fulf.) Schust., *Mytilopsis* Spr., *Haesselia* Grolle & Gradst., *Odontoseries* Fulf., *Fuscocephaloziopsis* Fulf.).

In addition, 'outlier' species of Laurasian genera exist whose taxonomic isolation is such that they fail to fit well into their respective genera. Thus the large, polytypic Laurasian genus *Scapania* Dumort. has a single common species in the Neotropics, *S. portoricensis* Hampe & Gott., isolated from all others in, e.g., the stellate gemmae; it has been assigned to a monotypic subgenus *Macroscapania* (Schuster, 1974). Within the similarly polytypic Laurasian genus *Nardia* there is an isolated element formed by *N. succulenta* (Rich. ex Lehm.) Spr. montane-neotropical (Gradstein & Hekking, 1979) in range. Such isolated, usually monotypic outlier species of basically circum-Laurasian groups cannot be regarded as 'recent' immigrants from Laurasia. I would assume they are 'old' immigrants, arriving as 'settlers' on unsaturated, newly created montane summits. The problem with such a scenario is that I question the adequacy of the time available (if current dogma as to the 'youth' of the Andes is accepted) to account for the degree of taxonomic isolation seen.

A third group of genera, all members of the very specialized family Lejeuneaceae, form isolated, usually monotypic elements in the family. These are all rheophytes, or grow on rocks or branches in the spray zone. I assume these elements all evolved at relatively mid-elevations peripheral to the Guyana Shield and/or eastern Andean slopes.

They include:

(28) *Myriocolea* Spr., with its solitary species known only from Peru.

(29) *Schusterolejeunea* Grolle (*Cladocolea* Schust.) with a single species in the Amazonian drainage.

These two monotypic genera constitute the isolated, highly apomorphic subfamily Myriocoleoideae Schust. (cf. Schuster, 1963).

(30) *Cephalantholejeunea* Schust., with only *C. temnanthoides* Schust.

(31) *Potamolejeunea* (Spr.) Evs., with 2-3 species of northern South America.

(32) *Myriocoleopsis* Schiffn., with one species known only from Brazil.

Of these five genera, the first four show highly reduced sexual branches and (28-30) are highly apomorphic in all having evolved very complex, sympodial systems of sexual branches, with male and female gametangial branches forming closely integrated bisexual complexes in *Cephalantholejeunea* and *Myriocolea*.

These five endemic genera of Lejeuneaceae are exceedingly isolated elements. An additional suite of genera/subgenera of Lejeuneaceae, endemic to tropical America, include, i.a. (33-47) *Taxilejeunea* subg. *Macrolejeunea* (Spr.) Schust., *Neurolejeunea* (Spr.) Schiffn., *Dicranolejeunea* (Spr.) Schiffn., s. str., *Amphilejeunea* Schust., *Cystolejeunea* Evs., *Cyrtolejeunea* Evs., *Dactylolejeunea* Schust., *Amblyolejeunea* Jovet-Ast, *Leirolejeunea* Evs., *Trachylejeunea* (Spr.) Schiffn. (at least subg. *Trachylejeunea*), *Cyclolejeunea* Evs., *Symbiezidium* subg. *Symbiezidium* Trevis., *Stictolejeunea* (Spr.) Schiffn. [the allied genus ***Leptostictolejeunea* (Schust.) Schust., gen. nov.** Basionym: *Stictolejeunea* subg. *Leptostictolejeunea* Schust., *Phytologia* 56:70, 1984, has a wider range], *Verdoornianthus* Gradst., and

Lindigianthus Kruijt & Gradst.

The suite of endemic subgenera/genera (28-47) of Lejeuneaceae listed above is even more impressive when we consider that: (a) in all of Europe, North America and Africa there fails to exist a single endemic genus of the family; (b) the very often highly apomorphic nature of these genera. Some of these derived ecological and morphological specializations have already been noted for genera 28-31. The remainder, in many cases, also show very apomorphic features, i.e.: very reduced and innovation-free sexual branches (*Taxilejeunea* subg. *Macrolejeunea*), reduced sexual branches bearing minute sterile innovations (*Stictolejeunea*), asexual reproduction via discoid gemmae (*Cyclolejeunea*), longly stipitate calyptrae and perianths (*Amphilejeunea*), maximally dorsiventrally flattened perianths (*Lindigianthus*), or ocellate leaves (*Neurolejeunea*, *Stictolejeunea*, *Cyclolejeunea*, etc.).

A suite of other genera, mostly also highly derived, seem to have found their origin in tropical America (at least their center of variability is there) but show limited, and I think recent, dispersal to Africa. Included are, i.e., (48) *Odontolejeunea* (Spr.) Schiffn., with three species, one *O. lunulata* (Web.) Schiffn. highly polymorphous (and probably encompassing a species complex). All three taxa are centered in tropical America, but *O. lunulata* has, surely secondarily, extended its range to Africa and Madagascar. Included here, also, is the (49) *Omphalanthus*-*Aureolejeunea* complex, with *Omphalanthus* Lindenb. & Nees (probably 6 neotropical species; one species, *O. roccatii* (Gola) Schust., in tropical Africa) and *Aureolejeunea* [probably 5 species; one, *A. decurrens* (Steph.) Schust. in Indomalaya, may be misplaced]. The taxonomy of this complex remains to be clarified, but it is clear that the center of diversity is in tropical America

and the sole taxon in Africa may be the result of relatively recent dispersal. (50) *Bryopteris* (Nees) Lindenb., with 7 or fewer species, has 6 reported for tropical America [1-2 appear to recur in Madagascar, but the records are a century or more old; the report of one species (*B. trinitensis*) from the Himalaya (Stotler & Crandall-Stotler, 1974) is based on an error].

The point of the preceding lines is to reinforce the impression gained from an examination of the other genera (1-27) previously briefly discussed. Pervasive is the repeated presence of a very wide range of clearly apomorphic features which lend the endemic elements of the flora such a very unusual and distinctive aspect. This impression is strongly reinforced when we contrast the comparably, if not equally, rich floras of cold sectors of South America and of Australasia (cf. section V).

What are we to conclude from perusal of this list of some 50 genera or generic complexes? Numerically, only, this listing is impressive. In Schuster (1982) there is a map (fig. 1) which gives indices of endemism, at the genus and family levels; at that time some 39 genera and 50 subgenera were found to be endemic to tropical America. We now know that ca. 47 genera are endemic to this area (vs. 3 for North America, 1 for Europe, 2 for Africa, 11 for eastern Asia, 28 for [temperate] Australasia + New Caledonia. If we include genera that appear to be neotropical in origin, with very limited secondary dispersal subsequently (e.g., genera 48-50; others could be cited), the extraordinary richness and diversity of the neotropical hepatic flora becomes evident.

Much of this essay, however, is devoted to not documenting numbers; rather the nature of the endemics is a recurrent theme to which I have returned at intervals above. This can best be summarized by an overall, encompassing generalization: the

neotropical hepatic flora has shown explosive diversification in the case of a number of families (Lepidoziaceae, Cephaloziaceae, Lejeuneaceae) and the generic types which have evolved in the Neotropics are among the most apomorphic known in these groups. It would take many pages to adequately document, for each of the genera cited, this assertion; in each case the evidence may be different. A single example illustrates the problem: the cool Gondwanalandic *Tuyamaelloideae* were until recently known only from southern South America into Australasia (one species 'crossed' Wallace's Line; cf. map 12 in Schuster, 1969), aside from the east Asiatic-Indomalayan *Tuyamaella* Hatt. More recently a genus *Haplolejeunea* Grolle was described from the Afro-American tropics; the two included species are apomorphic vis-a-vis all other *Tuyamaelloideae* in being ocellate — a highly derivative feature whose significance is unknown. The hepatic flora of the Neotropics, which I have stated to have acquired its basic features due to its evolution in long isolation, can thus perhaps be best compared to the mammal fauna of Australia: both, associated with similarly impressive periods of total isolation, have developed 'peculiar' biotas — for probably many of the same reasons. As with the case of the mammals of Australia, the distinctive qualities of the neotropical Hepaticae, as repeatedly emphasized, are in part due not only to what is present, but to what is lacking. This is briefly examined in section V.

Part of the striking nature of the hepatic flora also resides in the fact that, for reasons already examined, there has been intrusion of only a limited number of disharmonic elements, almost all from Laurasia or from cooler parts of Gondwanaland. These are briefly examined next.

2. Laurasian Elements

A very finite number of species have been able to cross from appropriate montane loci in North America southward, some of them leaving isolated populations on, e.g., the volcanoes of central Mexico, the volcanic mountains of Costa Rica, and perhaps elsewhere. The timing of this 'crossing' is debatable; some taxa, such as *Anthelia juratzkana* and *Cephalozia pleniceps* (for this last see Schuster, 1986), and perhaps *Blepharostoma trichophyllum* may have made the migration as early as the Oligocene; the first species has reached Fuegia (Schuster, 1966; cf. map, fig. 1, in Schuster, 1983a) and occurs in intermediate stations (Bolivia, Venezuela, Mexico); the second occurs in Magallanes — but so far is unknown in intermediate sites between boreal North America and Magallanes (Schuster, 1986); the third occurs from Peru (Schuster, 1966), Venezuela and Costa Rica (Schuster, 1985), Colombia (Gradstein & Hekking, 1979) and Mexico (Schuster; unpublished) and probably at high elevations in between. Thus *Jamesoniella autumnalis*, previously reported only from Laurasian loci, occurs at the Paramo de Tama, in Venezuela, near the Colombian border (Schuster, 1978, p. 245); *Nowellia curvifolia*, previously reported only from Laurasian loci, recurs in Venezuela (Schuster, 1983, cf. map, fig. 63) and Colombia (Winkler, 1976). A plant allied to *Lophozia incisa* (Schrad.) Dumort., described as subsp. *austrigena* Schust. (Schuster, 1978, p. 242) is reported as 'new' to Latin America. It also occurs in Colombia (Gradstein & Hekking, 1979). Finally, *Anastrophyllum minutum*, circumholarctic in range and found far northward into the Arctic (Schuster & Damsholt, 1974; Schuster, 1969a), has been found at single stations in Mexico and Venezuela (cf. map, fig. 65, in Schuster, 1983).

The 'intrusion' of these cool- to cold-adapted Laurasian elements seems clearly related to both tectonic factors (the recent rise of the Northern Andes, and of volcanic peaks

in Central America) and the reproductive biology of the taxa involved. The cases of *Anthelia juratzkana* and *Anastrophyllum minutum* are discussed in detail in Schuster (1983a); these taxa exhibit differing adaptations that enhance dispersibility. The *Anthelia* is paroecious and copiously produces bisexual spores; the *Anastrophyllum* copiously produces gemmae (and in cold areas, often spores as well). Of the other taxa cited, the *Cephalozia*, *Blepharostoma*, *Nowellia* and *Lophozia* all produce gemmae; only the *Jamesoniella* is both unisexual and lacks asexual modes of producing diaspores.

The relative rarity, both in numbers of taxa and in the frequency of populations, of these taxa in our area deserves some emphasis. I collected both the *Anthelia* and the *Anastrophyllum* a single time in the Sierra Nevada de Merida; the *Jamesoniella* was collected a single time, a little later, in the Páramo de Tama; the *Nowellia* I recall collecting a single time. An additional, paradoxical case may be cited: *Marsupella revoluta*, with a highly disjunct range (low arctic-alpine in Europe, Japan and Taiwan, Borneo, the Himalaya, Mt. Wilhelm in New Guinea, Greenland, Baffin I., Alberta; cf. Schuster, 1974) occurs in the Sierra Nevada de Merida in Venezuela (collected there by Josef Poelt). This taxon lacks any capacity to reproduce asexually and has never been found to produce sporophytes in the Western Hemisphere. Only the *Blepharostoma* appears to be relatively frequent in both Venezuela (Schuster, 1985) and Colombia (Gradstein & Hekking, 1979) southward to Peru (Schuster, 1966). Plants similar to the circumboreal *Cephalozia bicuspidata* occur in Colombia (Fulford, 1968) and Venezuela (Schuster, 1978a; as *C. venezuelana* Schust.) — their taxonomic status needs careful investigation. [Early reports (Kunth, 1822) of *Cephalozia connivens*, another circumboreal taxon, from Colombia, are surely due to some error.] *Chiloscyphus cuspidatus* (Nees)

Engel & Schust. [= *Lophocolea cuspidata* (Nees) Limpr.] is also reported from a single station in Venezuela (Schuster, 1978, p. 246); this is the 'typical' autoecious plant, sensu Schuster (1974 and earlier authors).

There are a few other reports of Laurasian taxa from northern South America, e.g., *Jungermannia sphaerocarpa*, *J. hyalina*, *Lepidozia reptans*, *Metzgeria conjugata* (cf. Fulford, 1966; Gradstein & Hekking, 1979); the bases for these reports should be verified from adequate, fertile materials. (*)

3. Gondwanalandic Elements

The taxa found in tropical America which have Gondwanalandic roots are of two kinds: (a) those which represent probably relatively recent immigration and appear identical at the species level with those found in southernmost South America; and (b) presumably relatively early immigrants, which have evolved into — sometimes strikingly — distinct endemic species.

The first group is represented, i.e. by:

(1) *Pseudocephalozia quadriloba* (Steph.) Schust. [maps in Schuster, 1979, fig. 9 and Schuster & Engel, 1974], found in Venezuela (Schuster &

 (*) Note by the editors: additional data on this subject are provided by Gradstein & Vana 1987: On the occurrence of Laurasian Liverworts in the Tropics. Mem. N.Y. Bot. Garden 45: 388-425. Engel, 1974), Colombia (Gradstein & Hekking, 1979), northward to Volcan Poas, Costa Rica (Schuster & Engel, 1974). The bulk of the taxa are in southernmost South America and Australasia.

(2) *Hygrolembidium andinum* (Herz.) Schust. (cf. Schuster & Engel, 1987), found in central Chile (type) and in Venezuela at 3850 meters. The Venezuelan population appears to diverge

appreciably from the Chilean one. [The map, fig.2, in Schuster, 1982, shows the then-known range. The Venezuelan station was found later.]

Pseudocephalozia Schust. and *Hygrolembidium* Schust. are typically subantarctic genera of the isolated subfamily Lembidioideae [cf. the map cited above]; the former occurs south to Tasmania and southern New Zealand and to Fuegia; the latter, to the Prince Edward Islands, Fuegia, the Antarctic and Campbell Island, and to Kerguelen. *P. quadriloba* occurs at 3200-4100 meters in Colombia, *H. andinum* at 3850 meters in Venezuela. Both taxa appear to have been able to make their northward migration only after (a) Oligocene cooling and, perhaps, as late as Pleistocene glaciation; (b) elevation of the Andes to nearly their present height. Both are limited largely to 'unstable' environments, or difficult loci (e.g., late snow areas).

(3) *Triandrophyllum subtrifidum* (H. f. & T.) Fulf. & Hatch. This species, s. lat., is widespread in cool- or cold-Gondwanalandic areas from Tasmania and New Zealand to southern South America; it extends northward to Colombia, where it is predominantly a paramo species.

The second group is represented by endemic species whose 'moorings' are clearly with cool-Gondwanalandic groups. Included are, i.e.:

(4) *Temnoma chaetophylla* Schust. (of Venezuela); all other taxa are Gondwanalandic, with only *T. setigerum* (Lindenb.) Schust. secondarily expanded northward to the Philippines and Hawaii.

(5) *Telaranea (Neolepidozia) rectangularis* Schust. (of Venezuela). The only neotropical member of subg. *Neolepidozia*; the other 3 taxa [*T. (N.) capilligera* (Schwaegr.) Schust., *T. (N.) seriatitexta* (Steph.) Schust., *T. (N.)*

oligophylla (L. & L.) Schust.] occur in southernmost Chile to South Georgia and Fuegia.

(6) *Lophozia (Protolophozia) verruculosa* Schust., a paramo species found at 3130-3140 meters in Venezuela. Allied to *L. crispata* Schust. of Fuegia and Magallanes.

(7) *Marsupidium latifolium* Schust., known only from 3100 meters in the Páramo de Tama, Venezuela (Schuster, 1978, p. 249); perhaps allied to *M. urvilleanum* (Mont.) Mitt. and *M. renifolium* (Haessel & Solari) Schust., both of southernmost South America. The genus, s. str. (as distinct from *Tylimanthus*), is exclusively cool-Gondwanalandic, aside from *M. knightii* Mitt., which penetrates into New Guinea and across Wallace's Line. A second species, *M. gradsteinii* Grolle has just been reported as an endemic in Guyana (Grolle, 1989).

(8) *Paracromastigum granatensis* (G.) Schust. [*Bonneria granatensis* (G.) Fulf. & Tayl.; probably including as synonyms, *Leucosarmentum portoricense* Fulf. and *L. bifidum* (Steph.) Fulf.]. The genus, s. lat., to include *Bonneria*, is widespread and polytypic in the area from New Zealand to southernmost South America, with perhaps 5-6 species. [*P. pachyrrhizum* (Nees) Fulf. extends north to southern Brazil].

The above list could be supplemented to a modest extent. Our taxonomic understanding of many groups, however, prohibits a more meaningful analysis.

Within group (b) above, are also several groups which may have been cool Gondwanalandic in origin, dispersed relatively early into our area, and there underwent diversification, sometimes explosive diversification. Included here are, i.e.:

(9) *Adelanthus* Mitt. (s. lat.) [Map, in

Schuster, 1979, fig. 11]. The greatest diversity is in the area from Australasia to southern South America (three subgenera represented), with a second center in elevated areas of tropical South America. [Two taxa have shown presumably recent, secondary dispersal to Macaronesia and hyperoceanic westernmost Europe; two to Africa + Madagascar.] The tropical American taxa are, in part, highly apomorphic (e.g., *A. aureomarginatus* Schust. of Venezuela and Colombia — a species with highly specialized, pigmented, swollen and pluridentate leaf margins).

(10) *Syzygiella* Spr. [Map, in Schuster, 1969, fig. 22]. Of the 19 (perhaps 20) species, 13 occur in our area; one (*S. pseudoconnexa*) occurs only in cool-Gondwanalandic parts of South America. This species is by far the most plesiomorphic and represents a distinct, monotypic subgenus (or allied genus). Presumably secondary dispersal has occurred from cool-Gondwanalandic areas to tropical America, where explosive diversification has taken place, with limited dispersal to Indomalaya, to Sri Lanka and Taiwan (3 species) and montane eastern Africa (1 species). The cited map abundantly illustrates the massive explosive evolution of this highly derivative genus (all species are unusual in having opposed leaves).

4. Disharmonic Elements

A few genera cited above (*Alobiellopsis*, *Cephaloziopsis*, *Iwatsukia*) have the majority of taxa in tropical America, but outlier species occur in the area from the Ryukyu Islands to southern Japan, and, in part, to Borneo and the Himalaya. Since allied genera (*Alobiella*, *Cylindrocolea*) are either endemic to or widespread and diverse in tropical America, it seems likely the East Asiatic outliers represent secondary centers. I have cited the fact that a considerable array of taxa is characteristic of the area of the 'Ring of

Fire.' Both *Alobiellopsis* and *Cephaloziopsis* occur chiefly as pioneer elements on moist rock faces and are frequent in volcanic areas (the latter is a 'weedy' element in parts of the Cordillera Central in Colombia, and in the volcanic mountains of Dominica; the former has a similar ecology).

Wholly different in nature is the distribution of two mesophytic elements which occur widespread in Australasia, then recur in tropical America; *Monoclea* and *Hymenophytum*. Evans (1925) reported *Hymenophytum flabellatum* (Labill.) Dumort. from a wide area of Australasia, eastward to Fiji, Juan Fernandez, and then Huafe Island, Chile, the Andes of Bogota, Colombia. If the ancient and isolated genus *Monoclea* contains only one species, as I believe, that species, *M. forsteri* Hook., occurs disjunctly in New Zealand and from Chile northward to Mexico and Cuba. It is conceivably possible that these two monotypic genera — both representing wholly isolated families (and the Monocleales represent an isolated Order) — are among the last modern survivors of elements of the ancient, undifferentiated Gondwana flora that existed prior to the breakup of Gondwanaland. As such, they may only seem to be disharmonic in nature.

5. Afro-American Connections

In addition to a series of either sibling or identical species, linking tropical Africa (and Madagascar) and tropical America (for which see Gradstein, Pócs & Vana, 1983), there are a few older, more intriguing connections. Where identical species occur on both sides of the South Atlantic [e.g., *Telaranea nematodes* (G. ex Aust.) Howe, *Lejeunea autoica* Schust., *Rectolejeunea brittoniae* Evs., *Caudalejeunea lehmanniana* (G.) Evs.] or where sibling species occur [e.g., *Cylindrocolea rhizantha* (Mont.) Schust. and *C. atroviridis* (Sim) Schust.; cf. Schuster, 1980, p. 27], I would assume

that the disjunction reflects long-distance dispersal after the South Atlantic began to open, with — at best — limited subsequent speciation.

There are several instances of older and/or more isolated elements, whose Afro-American dispersal may reflect a relict status today, with presumably a former less discontinuous range when Africa and South America were still joined.

Among such cases are the following: (1) *Haplolejeunea* Grolle, an isolated element, presumably with two species only, one from Madagascar to West Africa, the other [*H. cucullata* (Steph.) Grolle] in tropical America from Brazil to Guyana and Surinam (Gradstein & Hekking, 1989). The genus is the only tropical element of the rather plesiomorphic subfam. Tuyamaelloideae — a subfamily (as noted earlier) basically dispersed over cool Gondwanalandic areas, with only one species of *Siphonolejeunea* “crossing” Wallace’s Line.

(2) *Symbiezidium* Trevis., an isolated genus belonging in its own ‘genus complex’ (Schuster, 1963), with perhaps only two well-defined neotropical taxa in subg. *Symbiezidium* and a more plesiomorphic species in Madagascar, constituting subg. *Eosymbiezidium* (Gradstein & van Beek, 1985).

That such putatively ancient, perhaps pre-rift connections between Africa and South America are very few is a notable fact; the bulk of obvious connections are clearly recent and often formed by relatively ‘weedy’ taxa, e.g., *Lejeunea caespitosa* Lindenb., *Cheilolejeunea rigidula* (Mont.) Schust., *Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) Evs., and *L. uncioloba* (Lindenb.) Evs. Only the last two taxa are sufficiently plesiomorphic that the extant range could be argued to reflect pre-rift continuous distribution patterns.

The absence of any considerable suite of taxa linking these two regions has several causes: (a) the length of isolation — approximately 80-90 m.y.; (b) the, in large part, more continental and seasonally arid climate of much of tropical- subtropical sectors of Africa vs. the very extensive regions with copious and non-seasonally limited precipitation in tropical America; (c) the more complex and continuous history of mountain building in tropical America, with its combination of creation + continuance of suitable niches for a large diversity of taxa. The high African mountains — basically all volcanic and recent in origin — offer a limited suite of suitable environments. There one finds invasion, to a large extent, of Laurasian elements (e.g., *Tritomaria*, *Scapania spp.*) or other elements lacking in tropical America (e.g., *Chandonanthus*). Thus a comparison of the floras of the two regions illuminates the quantitative and qualitative differences in their hepatic floras, rather than suggests any obvious connections.

The limited Afro-American connections also suggest that much of the pertinent evolution has occurred subsequent to the opening of the South Atlantic. The basic time frame involved — at least 80 m.y., perhaps as many as 90 m.y. — is about the same as is involved in the case of the isolation of New Zealand. In Schuster (1979) there are speculations as to rates of speciation and genus formation, based on an evaluation of tectonic data + morphological (hence taxonomic) differences; it is concluded that 80 m.y. has been adequate, in the case of groups where internal evidence suggests limited or no dispersibility, for evolution of distinct genera or genus-pairs. The data from cool sectors of Gondwanaland and those from the Neotropics are thus quite congruent.

V. The Absence of Certain Families and Suborders: its Significance

One of the more tenuous — if not profitless

— exercises of the biogeographer is speculating why specific elements are lacking in the biota of a particular region. However, the absence of a diversity of such elements may, collectively, be very significant and one can hardly avoid considering the topic. I am reminded of Sherlock Holmes's famous dog that did not bark in the night; as much fuel for speculation can be obtained from purely negative data. Thus the diversity which almost overwhelms the student of hepatics in tropical America, when analyzed closely, is seen to be of a peculiar and strikingly limited nature: in essence, several obvious, or less than obvious, attributes are noted:

- (1) Entire families and even suborders of Jungermanniales are absent.
- (2) The groups present are, by and large, relatively modern or even highly derivative groups, with in many cases the more generalized, or plesiomorphic, groups present in cooler parts of former Gondwanaland.
- (3) Exceptions to these generalizations occur chiefly as a consequence of geologically recent events.

For example, the rather generalized and relatively stenotypic Blepharostomataceae (Pseudolepicoleaceae) are richly diversified in southern South America and Australasia — yet in tropical America they are represented by only three elements: (a) a highly derived endemic genus, *Chaetocolea* Spr., whose sole species, *C. palmata* Spr. occurs from Ecuador to Colombia and barely into Venezuela (Schuster, 1985); (b) a reduced, derivative species of the cool-Gondwanalandic genus *Temnoma* Mitt., *T. chaetophyllum* Schust., belonging to an isolated subgenus; (c) *Blepharostoma trichophyllum*, clearly a recent immigrant from the Northern Hemisphere. All three taxa are montane; the last two have been previously

discussed.

If we leave aside the limited disharmonic elements, and those clearly derived from cool-Gondwanalandic and cool-Laurasian loci, the remaining elements in the hepatic flora form a highly distinctive whole. They exhibit reproductive patterns and a general 'life style' which is distinctive. Some examples: (1) Unlike in groups which proliferated in Laurasian regions (e.g., Scapaniaceae, Lophoziaceae), asexual reproduction via gemmae is a rare phenomenon — found principally in *Anastrophyllum stellatum* Schust., and a few *Cephaloziella* and *Cephalozia* species, if we exclude recent Laurasian derivatives (e.g., *Nowellia curvifolia*, *Lophozia incisa*, *Blepharostoma trichophyllum*, *Anastrophyllum minutum*, *Cephalozia bicuspidata*). Indeed, a very disproportionate percentage of the taxa which reproduce via gemmae are evidently rather recent invaders — mostly in montane and/or alpine environments. (2) Asexual reproduction, if it occurs at all, is often by caducous or fragmenting leaves (many spp. of *Plagiochila*, also *Acrobolbus laceratus* Schust. and *A. caducifolius* Schust. & Agu.) and such asexual reproduction is typical even of some families in which it is otherwise not known to occur [thus in Geocalycaceae, gemmae are known in *Geocalyx*, *Harpanthus* and *Chiloscyphus* subg. *Lophocolea*, in Laurasian taxa; in *C. (Caducifolia) fragmentissimus* (Schust.) Engel & Schust., of the northern Andes, asexual reproduction is via caducous leaves; caducous leaves are otherwise unknown in the family]. Alternatively, discoid gemmae are a common mode of asexual reproduction (*Radula* spp., nearly all of the many Cololejeuneoideae, *Caudalejeunea*, *Cyclolejeunea*). (3) As noted earlier, experiments with neoteny, in its broad sense, are frequent. In addition to the examples cited earlier is the notable one of *Plagiochila moniliformis* Schust., a tiny species, which is apparently wholly

sterile; it is the only one of this enormous genus which freely reproduces by cutting off rows of thick-walled, 1-celled gemmae from teeth of leaves (Schuster, 1978); this species reproduces asexually when of a size and configuration that corresponds to that seen in juveniles of more 'normal' *Plagiochila* species. Similar asexual reproduction, basically by fragmentation from teeth of the leaves, also occurs in *Chaetocolea* Spr.

My point is that not only are entire groups lacking (or represented by a single taxon) but there is a shift in reproductive biology from what we consider 'normal' in Northern Hemisphere taxa. Again, this points up the distinctiveness of the neotropical hepatic flora.

Since the most obvious physical connections of tropical America have been with the temperate to cool areas to the south, a comparison between these two areas may prove profitable. If we analyze the nature of the cold-Gondwanalandic taxa present in southernmost South America, it becomes evident that the qualitative differences between the tropical belt and the cold-Gondwanalandic belt are profound. Lacking in our area are many genera, e.g., *Isophyllaria* Hodgs., *Pseudolepicolea* Fulf. & Tayl., *Archeophylla* Schust., *Archeochaete* Schust. and *Herzogiaria* Fulf. of the Blepharostomataceae; *Grollea* Schust. of the Grolleaceae; *Vetaforma* Fulf. & Tayl. of the Vetaformaceae; *Acrolophozia* Schust. and *Herzogobryum* Grolle of Gymnomitriaceae; *Blepharidophyllum* Angstr., *Clandarium* (Grolle) Schust., and *Krunodiplophyllum* Grolle, of Blepharidophyllaceae; *Austrolophozia* Schust. of Acrobolbaceae; *Pleurocladopsis* Schust., *Paraschistochila* Schust., *Schistochila* Dumort. and *Pachyschistochila* (Schust.) Schust. & Engel, all genera of Schistochilaceae; *Ptilidium* Nees of Ptilidiaceae; *Lepidolaena* Dumort., *Gackstroemia*

Trevis. and *Lepidogyna* Schust. of Lepidolaenaceae; *Treubia* Goeb. of the Treubiaceae; *Phyllothallia* Hodgs. of Phyllothalliaceae. These are all typical elements in the cold-Gondwanalandic regions to the south. Such an analysis is relevant because it emphasizes the uniqueness of the tropical American flora and its separateness from that of the regions to the south. It strongly suggests that the E-W barrier between the two areas had a profound effect. If we further analyze the taxa cited above we see that they basically consist of unisexual taxa (exceptions: isolated species of *Acrolophozia*, *Herzogobryum* and *Gackstroemia*) which nearly always lack asexual propagula (exceptions: *Acrolophozia*, *Austrolophozia* and *Treubia*, all of which bear gemmae). These taxa thus share, in general, reproductive 'strategies' that promote outbreeding and that prevent successful migration.

It would be incorrect to conclude that the drastically differing hepatic floras reflect only or principally differences in available environments. The cold, wet niches found in many páramo areas exhibit most or nearly all of the environmental parameters found on the cold, foggy and rainy coast of Chile. Indeed, one unique genus, *Eopleurozia* Schust., has the same species [*E. paradoxa* (Jack) Schust.] present at high elevations in Colombia and at sea level in southernmost Chile! The lack of more than isolated taxa with such a dispersal strongly supports the thesis that the barriers (climatic: the E-W sea way) that separate these two areas have been profound. We must, indeed, conclude that only the handful of taxa cited on previous pages has been able to migrate from cool- or cold-Gondwanalandic areas to tropical America.

It is exactly the absence of a wide range of cool-Gondwanalandic taxa that returns us again to the basic questions to which I have tried to address myself: what are the

origins of the neotropical hepatic flora and, implicitly, when did this flora originate? The available tectonic data limit us to a certain time frame; with extrapolation from fossil data we can — precariously, because of the fragmentary nature of the evidence — also deduce a time frame. As repeatedly emphasized, opening of the South Atlantic, disruption of the Scotia Arc and peripheral areas, and lack of significant connections northward until the Pliocene suggest isolation in the vicinity of 80-90 m.y. The E-W sea way cutting South America into southern and northern sectors, isolated the northern sector during a period when the connections of the southern sector to Antarctica (and through it to Australasia) were still functional. Recent fossil data suggest that until some time in the Cretaceous the types of Jungermanniiidae present were very different from modern types (cf. Krassilov & Schuster, 1984; Schuster & Janssens, 1989), while by Eocene-Oligocene times relatively modern types already existed (Miller, 1984; Grolle, various papers on amber hepatics); see next section. If these data have any relevance at all, they suggest that some time between 90 m.y. BP and early Tertiary times, the tropical American flora attained roughly its present form; it attained its dimensions, qualitative and quantitative, in isolation. I suspect — but cannot prove — that many of the peculiar endemic types were established some time after the mid-Cretaceous initiation of the rift now separating America from Africa, and prior to the late Tertiary 'creation' of the Cordilleran mountain systems. The explosive diversification in modern groups (chiefly Lejeuneaceae, also *Plagiochila*, *Radula*, and *Frullania*) is a Tertiary phenomenon.

Much of the previous discussion of absence of specific elements, or their presence as isolated, disharmonic taxa, has centered on the rich and diversified flora of the uplands. If, by contrast, we

study the composition of the Lowland Rain Forest, the absence of many elements becomes even more overwhelming. Intensive study of two lowland areas: the Rio Negro and tributaries like the Rio Curicuriari and Rio Marie, in Brazil, reveal almost an identical pattern of what is present vs. what is lacking as study of the Pacific Lowland Rain Forest on Isla Gorgona, Colombia. In both areas the very large bulk of species is formed by very few families: Lejeuneaceae, Radulaceae, Jubulaceae, Plagiochilaceae, Metzgeriaceae, Aneuraceae and a few specialized members of the Lepidoziaceae. Lacking, or virtually lacking, in such lowland forests are at least 50 families of hepatics found in the non-tropical parts of southern South America (i.e., Lepidolaenaceae, Grolleaceae, Schistochilaceae, Gymnomitriaceae, Lophoziaaceae, Blepharostomataceae, except for Trichocolea, Lepicoleaceae, Vetaformaceae, Scapaniaceae, Blepharidophyllaceae, Acrobolbaceae, Cephaloziaceae, Ptilidiaceae, Pleuroziaceae).

Thus, even though initially the student is overwhelmed by the richness of the flora, analysis reveals that it is really a very limited flora, characterized by explosive diversification of a very few families, supplemented chiefly in upland areas by geologically recent immigrants.

VI. Some Conclusions: Origin vs. Origins

Any analysis of the origin — or origins — of the neotropical hepatic flora must concern itself with the problem of the kinds and degrees of endemism seen in that area.

The preceding analysis suggests that two kinds of endemism are relevant: (a) a large number of the poorly known taxa of the essentially circumtropical Lejeuneaceae (whose taxonomy remains so impenetrable

that attempts at a phytogeographic evaluation seem almost senseless) and Plagiochilaceae, and of the genera *Frullania* (no modern monograph exists) and *Radula* (the revision by Castle needs revision) — all of which seem to have evolved countless modern endemic species; (b) a complex neotropical flora which involves a great deal of qualitatively highly 'peculiar' endemism. These endemics include a large array of taxa which have little or no affinity to those of other areas and which give the impression of having evolved over long time periods in isolation.

The extant geological data suggest that the pertinent northern sector of Latin America showed a more nearly total physical isolation from other land areas than any other comparable land mass during virtually the whole Tertiary. A minimum of 40-50 m.y. of physical isolation is assumed. If the still fragmentary data dealing with leafy fossil hepatics are evaluated, it may be concluded that from Oligocene time on we find species of even modern Lejeuneaceae that are strikingly similar to modern taxa — and similar species of 'modern,' mostly apomorphic genera like *Cephaloziella*, *Radula*, *Frullania* and *Bazzania* occur; moss fossils from early Tertiary times on are also very similar to modern taxa. Yet fossil Jungermanniales from the Cretaceous fail to fit into any modern families (Krassilov & Schuster, 1984) and some Cretaceous Jungermanniales are so isolated they are referred to their own suborder (e.g., *Diettertia*; cf. Schuster & Janssens, 1989). These data, still woefully fragmentary, collectively suggest that the leafy Hepaticae and Metzgeriales of tropical America (a) acquired their unique spectrum only in Tertiary times; or (b) the African component of the presumably common Afro-American flora died out — in part owing to the cycles of aridity to which most of Africa was subject. Although not susceptible to proof, it is reasonable to

suggest that a combination of these two factors obtains. In any event, if we compare the amount of endemism seen in South America, and that of formerly adjoining or recently adjoined land masses (Africa, Antarctica, North America), the paucity of endemics in the latter three regions stands out — that of Antarctica being due to Tertiary climatic extinction.

More illuminating is an analysis of the qualitative nature of the endemism evident in the area encompassing the Guyana Shield, the Andes and outlying mountains, and the peripheral lowlands of the Amazonian-Rio Negro basins, and the Antilles. If we compare both the quantitative and qualitative nature of the endemism to that of southern South America, North America, Africa the distinctiveness of the tropical American flora clearly emerges. In Schuster (1983, fig. 42) a numerical analysis is attempted. Tropical America has at least 39 endemic hepatic genera (40, including the recently described *Haesselia*), 50 endemic subgenera, and 2 endemic families. Using admittedly subjective evaluations, one can regard only 2 of the endemic genera as relatively primitive; both families are, on balance, very apomorphic (the Phycolepidoziaceae are among the most specialized of all hepatics).

All of North America, by contrast, has only 3 endemic genera and no endemic families. Southern South America shows many fewer (18) endemic genera (21 subgenera) but has 2 endemic families (both primitive). Eight of the genera can be regarded as relatively primitive. The entire African flora has, at most, 2 endemic genera (*Cephalojonesia* Grolle is monotypic; the other, *Sprucella* Steph., with 2 species, is a weak segregate; *Anomalolejeunea* has been reduced to a subgenus of *Cheilolejeunea*, cf. Schuster, 1980). Both endemic genera are quite apomorphic and the area has no endemic families.

With regard to endemism, there is, indeed, only one comparable region: Australasia, with 28 endemic genera (29, including *Austroscyphus*) and 7 endemic families; of these some 10 genera are primitive, as are two of the 7 endemic families. Both the degree and time of isolation of New Zealand and New Caledonia (of the general 'rise' that rifted off from the rest of Australasia) are comparable to the isolation of tropical America: the former has been isolated for over 60 — perhaps ca. 80 m.y. — the latter may have begun to be isolated by 90 m.y. BP. Until the Pliocene contact with North America and until the Andes were elevated, tropical South America appears to have been just as isolated as Australia-New Caledonia. Of the two regions, tropical America clearly is quantitatively richer in endemics, but Australasia is far richer in generalized types.

The ultimate conclusion, then is that the exceptionally diverse hepatic flora of tropical America has largely evolved in isolation; its origin is to be sought in the gradual modification, starting in the Cretaceous and continuing during all of the Tertiary, of a relatively non-differentiated, widespread, pre-Oligocene Gondwanalandic flora.

It is thus surely correct to speak of the origin of the present-day tropical American hepatic flora as a singular event brought about by gradual differentiation coincident to isolation. No hepatic flora exhibits a similar degree of evolution of highly apomorphic types — often involving maximal reduction and simplification, sometimes involving aspects of neoteny. Intrusion of heterogeneous elements from Laurasia has been very limited; intrusion of cool Gondwanalandic types has been almost as limited; and what once must have been close floristic contacts with the African flora are now reduced to a dwindled, insignificant number. Modern, successful groups (e.g., many Lejeuneaceae, *Radula*, *Frullania*, *Plagiochila*) which are subcosmopolitan, lend a superficial sameness to most tropical floras. When these are excluded, what is left is unique and cannot be duplicated in other hepatic floras.

The preceding analysis leaves many questions for the future. Some will become susceptible to analysis only after the taxonomy of many groups has been further refined. Modern molecular/genetic

