DIVERSITY AND BIOGEOGRAPHY OF NEOTROPICAL VASCULAR EPIPHYTES[1]

ALWYN H. GENTRY AND C. H. DODSON[2]

In his classic work Schimper (1888), emphasizing the taxonomic diversity of epiphytes, listed 33 families and 232 genera of epiphytes. Until very recently, subsequent authors have generally accepted Schimper's figures (Richards, 1957; Johansson, 1974). However, epiphytism (here used in a broad sense to include hemiepiphytes, see Kress, 1986) was recently reported to exist in 65 different vascular plant families (56 families excluding ferns), 38 of these with epiphytes in the Neotropics (Madison, 1977). Our own data (Appendix 1) and additional records compiled by Kress (1986) now record 83 vascular plant families with epiphytic species.[3] At least 876 genera include at least one epiphytic species and there are perhaps 29,000 epiphytic species, ca. 10% of all vascular plants (Table 1). Thus at first sight epiphytism seems a very widespread and successful life-style, which very many unrelated taxa have evolved.

However, a closer examination suggests that even though there are both many species and higher taxa of epiphytes, few of the higher taxa account for most of the species. Burger (1985), for example, emphasized that relatively few lineages have been able to enter the epiphytic niche, presumably because of the complex suite of adaptations needed. Thus even though it is true that the evolution of an epiphytic habit has been a relatively common feature of vascular plant evolution, it is equally true that very few of the taxa that have evolved an epiphytic habit have radiated successfully to produce other epiphytic species (Table 2). In most of the epiphyte-containing families, epiphytism is a rather insignificant anomaly. Indeed, eliminating a mere 85 such "oddball" species from the roster of the world's epiphytes removes 31 families from the epiphytic ranks. Only 32 seed plant families have as many as five or more epiphytic species, 26 of these with epiphytes in the Neotropics. It is on the 42 families (Table 3) that contain epiphytes in the Neotropics that this paper will focus.

Even though this analysis of epiphyte diversity and distribution is largely focused on the Neotropics, a few comparisons with the Paleotropics are instructive. There are actually slightly more families with epiphytes in the Paleotropics (43) than in the Neotropics (42), with all of the paleotropical epiphytic families having epiphytic representatives in Australasia but only 15 in Africa and Madagascar. If only the 32 seed plant families with five or more epiphytic species are considered, there are also roughly equal representations of epiphyte-containing families in the Neotropics (26) and Australasia (25) but only about half as many in Africa (14).

At the species level the story is very different. There are many more epiphytes in the Neotropics, at least half again as many as in Australasia and six times as many as in Africa. Although similar numbers of genera and families evolved epiphytism in the different regions, subsequent speciation as epiphytes was dramatically greater in the Neotropics. A major objective of this paper, then, will be to try to explain why there is so much epiphyte diversity in the Neotropics.

EPIPHYTE FAMILIES

One approach to an overview of neotropical epiphyte diversity is a taxonomic one. Table 3 summarizes the neotropical epiphytic seed plant flora by family. Of the 42 families represented by at least one habitually epiphytic species in the Neotropics, the Orchidaceae are by far the most important with ten times as many epiphytic neo-

TABLE 1. Taxonomic distribution of vascular epiphytes (modified from Madison, 1977 and Kress, 1986).

	Families with Epiphytes	Genera with Epiphytes	Species of Epiphytes
Pteridophytes	13	92	2,593
Gymnosperms	2	2	4
Monocots			
Without orchids		80	2,657
Orchids (fide Madison)		500	20,000
Orchids (compiled from Dressler, 1981)		460	15,000
Orchids (fide Kress, 1986)		440	13,951
Total (fide Kress, 1986)	17	520	16,608
Total (our estimate)	17	540	22,657[1]
Dicots	51	262	4,251
Total	83	896	29,505

[1] Includes Madison's orchid figure (see text).

tropical species as runners-up Araceae and Bromeliaceae. All three of these most speciose neotropical epiphyte families are monocots. One other monocot family, Cyclanthaceae, also has a significant number of epiphytes. Commelinaceae, Rapateaceae, and Philesiaceae, although with few species, have an exclusively epiphytic genus (respectively, *Cochliostemon, Epidryos, Luzuriaga,* and (in our experience) *Philesia*). As summarized by Madison (1977), the rest of the epiphytic monocot flora of the Neotropics consists of single species of *Burmannia* and *Yucca* and a few Central American species of *Smilacina.*

Since orchids are so overwhelmingly the most diverse group of epiphytes (about 70% of their species are epiphytic), estimates of orchid diversity are critical to an evaluation of epiphyte diversity. Unfortunately, orchids are amazingly poorly known taxonomically (compare the ca. 12 orchid taxonomists with the ca. 200 systematists specializing in the similar-sized Compositae). Estimates of the number of orchid species range from 12,000 ("some authors" fide Dressler, 1981) or 17,000 (Airy Shaw, 1973) to 30,000 (Madison, 1977) or 35,000 ("some authors" fide Dressler, 1981). In the best available review Dressler (1981) counted almost 20,000 species

and suggested 20,000–25,000 as the best estimate of orchid species numbers. Since 70% of the total number of orchid species should approximate the number of species of epiphytic orchid, there should be between ca. 12,000 (from Airy Shaw's estimate) and ca. 20,000 (from Madison's estimate). Unfortunately, the 8,000 species "slop" between these two estimates is as great as the total number of epiphytes in all other families combined! Madison (1977) used the higher figure for his calculations, whereas Dressler (1981) generally opted for more conservative estimates of orchid species numbers. We have mostly taken the higher values since we know of many cases where Dressler's figures for species numbers are significant underestimates but none where he has overestimated. For example, Dressler suggested that there are 830 species in subtribe Epidendrineae, whereas in Ecuador alone there are 500 species in the single genus *Epidendrum* and we think 1,200 species would be a better subtribal estimate.

Moreover, new orchid species are being discovered at an astonishing rate, especially in the northern Andean region, again suggesting that Dressler's estimates of species numbers will have to be adjusted dramatically upward. For example, about 2,315 orchid species are now known from Ecuador, ca. 700 of these described only in the last 15 years. Nevertheless, more than 1,500 additional Ecuadorian orchid "morphospecies" have not been identified with any published name. Even if the 300 unaccounted for names should all prove applicable to the unidentified specimens at hand, it is inevitable that most of the unidentified taxa will prove undescribed and the list of orchids for Ecuador alone will increase to well over 3,000 species.

The neotropical epiphytic dicot flora is more diverse in families but much less diverse in species than the monocots. Twenty-nine dicot families have at least one habitually epiphytic species in the Neotropics. The largest of these are Piperaceae (ca. 500 spp.), Gesneriaceae (483 spp.), Melastomataceae (227 spp.), Ericaceae (ca. 300 spp.), Cactaceae (133 spp.), Guttiferae (ca. 90 spp.), and Marcgraviaceae (87 spp.). In addition there are perhaps 110 neotropical species of Moraceae stranglers in the genera *Ficus* and *Coussapoa*. The only other dicot families with more than 20 epiphytic species in the Neotropics are Araliaceae, Bignoniaceae, Compositae, Rubiaceae, and Solanaceae (Table 3).

In addition, Bombacaceae, though with few

TABLE 2. Largest epiphyte families (in part from Madison, 1977).

Family	No. Genera with Epiphytes	No. Epiphytic Species	Total No. Species	Percent Epiphytes
Orchidaceae	460	20,000	30,000	67
		(−13,951[1])	(−19,128[1])	(73)
Bromeliaceae[1]	26	1,144	2,500	46
Araceae	15	1,100[2]	2,500+[2]	42
Polypodiaceae[1]	53	1,023	1,100	93
Piperaceae	2	710	3,000	24
Melastomataceae	33	ca. 647[3]	4,770[3]	14
Gesneriaceae	28	598[4]	3,000[4]	20
Moraceae (incl. stranglers)	3	521	1,400	37
Ericaceae	28	478[5]	4,000	23
Hymenophyllaceae[1]	2	400	600	67
Aspleniaceae[1]	1	400	675	59
Dryopteridaceae[1]	10	292	1,920	15
Rubiaceae	21	217	6,000	4
Lycopodiaceae[1]	1	200	400	50
Davalliaceae[1]	8	139	150	10
Asclepiadaceae	6	135	2,000	7
Cactaceae	25	133	2,000	7
Cyclanthaceae	7	125[6]	205	61
Vittariaceae[1]	9	112	112	100
Guttiferae	6	92	1,000	9
Marcgraviaceae	7	89[7]	117	76
Araliaceae	5	73	700	10

[1] Kress, 1986.
[2] Croat, pers. comm.
[3] Renner, 1986 and pers. comm.
[4] Wiehler, 1983.
[5] Luteyn, pers. comm.
[6] Hammel, pers. comm.
[7] Bedell, pers. comm.

species, has an epiphytic genus (*Spirotheca*). The other 16 epiphytic neotropical dicot families are represented by only occasional epiphytic species of predominantly terrestrial genera.

In addition to these angiosperm families, there are two gymnosperm families with single epiphytic neotropical species in generally terrestrial genera and at least 838 epiphytic fern species belonging to 32 different genera, a common epiphytic *Psilotum,* and some epiphytic species of *Lycopodium.*

REPRODUCTIVE BIOLOGY

A number of salient characteristics that may be critical to success as epiphytes are shared by many different neotropical epiphytic taxa. Madison (1977) nicely summarized many of the features of epiphyte reproductive biology and this discussion is largely based on his. From the viewpoint of dispersal biology, there are three main types of epiphyte propagule. The great majority of epiphyte genera and species have tiny dustlike wind-dispersed sporochores, often with highly sculptured epidermis, to aid in air flotation. Such seeds, representing an extreme in r-selection and a high risk gamble on chance establishment, are found in the two most successful epiphyte groups, orchids and ferns, as well as in such taxa as *Begonia* (although at least one African epiphytic species has a fleshy fruit, pers. obs.), *Utricularia,* Rapateaceae, and perhaps capsular melastomes, although seeds of capsular melastomes may be 1 mm long and are not strictly comparable (Renner, pers. comm.). In closed-canopy tropical forests such seeds are virtually unique to epiphytes. While tiny sporochore seeds are found in some tropical weedy herbs, they are unknown among tropical forest lianas (except mostly hemiepiphytic *Adelobotrys*) and trees (excluding tree ferns), although the pterochore seeds of genera like *Chimarrhis* may not be any larger.

TABLE 3.   Epiphytic neotropical seed plant families (in part from Madison, 1977).

Family	Number of Neotropical Epiphytic Species	Neotropical Genera with Epiphytes	Distribution of Epiphytes
Gnetaceae	1	*Gnetum*	also epiphytic in Malaysia
Zamiaceae	1	*Zamia*	Costa Rica, Panama; only in Neotropics
Agavaceae	1	*Yucca*	Mexico; only in Neotropics
Araceae	1,034	*Anthurium, Caladiopsis, Monstera, Rhodospatha, Philodendron, Stenospermation, Syngonium*	also epiphytic in Africa and Asia
Bromeliaceae	1,144 (fide Kress, 1986)	18 genera entirely or predominantly epiphytic; 5 others with some epiphytes	only in Neotropics
Burmanniaceae	1	*Burmannia*	also epiphytic in New Guinea
Commelinaceae	3	*Cochliostemon, Campelia*	only epiphytic in Neotropics
Cyclanthaceae	125	*Asplundia, Dicranopygium, Evodianthus, Ludovia, Sphaeradenia, Stelestylis, Thoracocarpus*	only in Neotropics
Dioscoreaceae	1	*Dioscorea*	Ecuador
Liliaceae	4	*Smilacina*	also epiphytic in Australia, Pacific, and Madagascar
Orchidaceae	11,000 (fide Madison)	ca. 80 genera entirely or predominantly epiphytic	also epiphytic in Africa and Australasia
Philesiaceae	3	*Luzuriaga, Philesia*	also epiphytic in New Zealand
Rapateaceae	6	*Epidryos, Stegolepis*	only in Neotropics
Apocynaceae	1	*Mandevilla*	Costa Rica
Alzateaceae	1	*Alzatea*	Costa Rica-Colombia
Araliaceae	45	*Schefflera, Oreopanax*	also epiphytic in Africa and Australasia
Asclepiadaceae	2	*Cynanchum*	mostly epiphytic in Malaysia
Begoniaceae	25	*Begonia*	also epiphytic in Africa and Asia
Bignoniaceae	29	*Schlegelia, Gibsoniothamnus*	only in Neotropics
Bombacaceae	4	*Spirotheca*	only in Neotropics; mostly Andean
Burseraceae	1	*Bursera*	Costa Rica
Cactaceae	133	25 genera entirely or predominantly epiphytic	*Rhipsalis* also epiphytic in Africa and Ceylon
Campanulaceae	7	*Burmeistera*	neotropical; mostly Andean
Compositae	ca. 30	*Mikania, Nelsoniothamnus, Neomirandea, Pseudogynoxys, Senecio (Pentacalia), Sinclairia, Tuberostylis*	Central America and Andean; *Senecio* also epiphytic in New Zealand and Madagascar
Crassulaceae	2	*Echeverria*	also few epiphytic in Himalayas and Madagascar
Ericaceae	ca. 300	18 genera entirely or predominantly epiphytic; several with epiphytic species	also epiphytic in Australasia
Gentianaceae	1	*Voyria*	South America
Gesneriaceae	483	12 genera entirely or predominantly epiphytic; 4 other	also epiphytic in Africa and Australasia

TABLE 3. Continued.

Family	Number of Neotropical Epiphytic Species	Neotropical Genera with Epiphytes	Distribution of Epiphytes
		genera with some epiphytic species	
Griseliniaceae	3	*Griselinia*	Chile and Brazil; also epiphytic in New Zealand
Guttiferae	ca. 90	*Clusia, Clusiella, Havetiopsis, Oedematopus, Quapoya, Renggeria*	only epiphytic in Neotropics
Lentibulariaceae	12	*Utricularia*	also 2 epiphytic in Africa and Australasia
Marcgraviaceae	89	all 7 genera entirely or predominantly epiphytic or hemiepiphytic	only in Neotropics
Melastomataceae	227	7 genera entirely or largely epiphytic; 5 others with some epiphytic species	also epiphytic in Africa and Asia
Moraceae	111	*Coussapoa, Ficus* subg. *Urostigma,* and 1 *Pourouma*	*Ficus* stranglers also in Africa and Australasia
Myrsinaceae	ca. 12	*Cybianthus, Grammadenia, Myrsine (Rapanea)*	also epiphytic in Africa and Asia
Onagraceae	3	*Fuchsia*	only epiphytic in Neotropics
Piperaceae	ca. 500	*Peperomia, Piper*	also epiphytic in Africa and Asia
Rubiaceae	ca. 57	*Balmea, Coprosma, Cosmibuena, Hillia, Malanea, Manettia, Psychotria, Ravnia, Relbunium, Schradera*	also epiphytic in Australasia
Sapotaceae	1	*Bumelia*	Costa Rica
Saxifragaceae	ca. 3	*Hydrangea, Phyllonoma*	only in Neotropics
Solanaceae	ca. 30	*Juanulloa, Lycianthes, Markea* (+ segregates), *Solanum*	also epiphytic in Malaysia (*Solanum, Lycianthes*)
Urticaceae	ca. 15	*Pilea*	also epiphytic in Indo-Malaysia

The second most prevalent dispersal mode among epiphytes is via birds. Most bird-dispersed epiphytes have indehiscent berry fruits but a few, including *Drymonia* and *Clusia,* have dehiscent capsules with arillate seeds. In either case the seeds tend to be smaller and more numerous than in related nonepiphytic taxa (Madison, 1977). In some families there is a marked change in dispersal mode accompanying the shift to epiphytism. In Bignoniaceae all epiphytic species (with two probably bat-dispersed exceptions) are bird-dispersed but only one nonepiphytic species (*Synapsis ilicifolia*) is (see Gentry, 1983). In Melastomataceae 85% of the epiphytic species have berry fruits as compared with 60% of the nonepiphytic species (Renner, 1986).

The third major diaspore dispersal syndrome in epiphytes is wind-dispersal via winged or plumed seeds (pterochory and pogonochory, respectively). Interestingly, plumed seeds as compared with winged seeds greatly predominate among epiphytes, whereas the opposite holds true for trees and lianas, at least in mature forest species. Some of the important epiphyte taxa with pogonochore diaspores are Bromeliaceae subfamily Tillandsioideae, Asclepiadaceae, Gesneriaceae, and Rubiaceae. In Rubiaceae some epiphytic genera have small winged seeds while others have true pogonochores; the difference between these dispersal modes tends to break down in such groups, with some species having such narrow reduced wings that these effectively approximate large hairs.

Finally there are a few epiphyte taxa with such

miscellaneous dispersal syndromes as bat-dispersal (some strangler figs), exozoochory via sticky diaspores (some *Peperomia*), and the not readily classifiable "sloppy corn-on-the-cob" ingestion of some cyclanth fruits by *Callicebus* and other primates (Terborgh, pers. comm.).

In general, epiphyte seeds are smaller and more numerous than those of nonepiphytic relatives. For example, Renner (1986 and pers. comm.) noted that in Melastomataceae mostly epiphytic *Blakea* and *Topobea* have ca. 1,000 seeds per fruit compared with a few dozen seeds per fruit in typical nonepiphytic genera such as *Miconia* and *Clidemia*. Madison (1977) estimated that seeds of epiphytic *Anthurium* are typically ca. 2 mm long as compared with 4–8 mm long in terrestrial *Anthurium* species. There are also exceptions to this pattern. For example, Rockwood (1985) pointed out that in Gesneriaceae epiphytic species actually have significantly larger seeds than do shrubs and herbs. According to Rockwood's (1985) analysis, epiphyte seed size tends to be bimodal; those groups with dust-seeds or other wind-dispersed seeds have the smallest seeds of any habit type while taxa not dispersed by wind have seeds averaging larger than those of herbs, vines, and shrubs, similar to lianas, and only smaller than trees. Nevertheless, since the great majority of epiphytes are wind-dispersed, the epiphyte habit class as a whole is generally characterized by the smallest seeds of any habit class. A dispersal strategy emphasizing many small seeds and chance establishment is typical of the r-selection syndrome often found in weedy species. Epiphytes would seem to be most unusual in being r-selected components of mature forest ecosystems.

POLLINATION

Madison (1977) emphasized animal-pollination as a characteristic trait shared by all angiosperm epiphytes. While true, this is hardly remarkable in a tropical context since, with virtually no exceptions (*Myriocarpon* (pers. obs.), *Trophis* (Bawa et al., 1985), and just possibly *Sorocea* and a few *Chamaedorea* species (fide Bawa et al., 1985)), all lowland tropical forest angiosperms are animal-pollinated. Nevertheless, epiphytes as a whole surely have a more pronounced trend toward highly specific and specialized pollination systems than do nonepiphytes, if for no other reason than that so many epiphytes are orchids. In addition to the well known orchid pollination specializations (e.g., Dodson, 1967; van der Pijl & Dodson, 1966; Williams, this symposium), many aroids have similar Euglossine-attracting scent systems. Five of the largest neotropical orchid genera have specific bee pollinators attracted by specific scents and *Anthurium* is the largest nonorchid genus in the Neotropics. While *Pleurothallis,* the largest neotropical epiphyte genus, does not participate in the presumably speciation-promoting Euglossine-pollination syndrome, it is pollinated by the large and diverse fly genus *Bradesia* (CD, pers. obs.) and similar coevolutionary patterns may be involved; among other small-flowered and inconspicuous but highly diverse orchid genera, *Stelis* and *Lepanthes* are probably pollinated by *Drosophila* and similar flies, and *Telipogon* is pollinated by pseudocopulation with tachinid flies, another very large and diversified insect taxon.

Unique to the Neotropics, hummingbird-pollination is also much more prevalent among epiphytes (and terrestrial herbs) than in trees or free-climbing lianas. Epiphytic taxa among which hummingbird-pollination is prevalent include Ericaceae, Bromeliaceae, Gesneriaceae (especially *Columnea*), Marcgraviaceae (*Norantea,* sensu lato), Rubiaceae (*Ravnia, Manettia*), and Cactaceae (e.g., *Schlumbergera*). The correlation between hummingbird-pollination and epiphytism is well shown by Bignoniaceae. Of the two epiphytic genera of Bignoniaceae, one (*Gibsoniothamnus*) is entirely hummingbird-pollinated and the other (*Schlegelia*) also has several hummingbird-pollinated species; hummingbird-pollination is rare elsewhere in the family. Other specialized pollination systems shown by epiphytes include hawkmoth-pollination in Cactaceae (e.g., *Epiphyllum*) and Rubiaceae (e.g., *Cosmibuena, Hillia,* perhaps *Schradera*), bat-pollination in *Marcgravia* (though most species may be autogamous, Bedell, pers. comm.), and rat-pollination in *Blakea chlorantha* (Lumer, 1980). Perhaps more striking than the diversity of highly specialized pollination systems among neotropical epiphytes is their lack of the small, inconspicuous, generalist-pollinated flowers that characterize the great majority of trees in the wet forests where epiphytes are prevalent. The only epiphytic taxa characterized by such flowers are Araliaceae, Moraceae, Piperaceae, Myrsinaceae, and Urticaceae, the latter two only marginally epiphytic. If hummingbirds, well known as specialist pollinators (Stiles, 1981), are taken as an

example, this pattern may be clearly seen at the community level: in lowland tropical forests hummingbird-pollination is almost exclusively confined to herbs and epiphytes.

Another relevant aspect of epiphyte pollination biology is that such phenomena as self-compatibility and autogamy are apparently much more prevalent than typical in tropical lowland taxa. For example seven of seven species of *Blakea, Topobaea,* and *Adelobotrys* tested at Monteverde, Costa Rica were self-compatible (Lumer, 1980; Renner, 1986) vs. 34 of 43 tested terrestrial melastome species in the Manaus area (Renner, 1984). In Marcgraviaceae this is carried to an extreme with all species tested being autogamously pollinated in bud despite the elaborate floral adaptations (Bedell, pers. comm.).

In summary, epiphyte reproductive biology appears to be a unique mix of r-selection and specialization. Unlike other components of mature forest communities, epiphytes share many reputedly r-selected traits with weedy herbs, especially in their dispersal ecology. Yet at the same time most epiphytes have highly specialized pollination systems, strong niche specificity, and many other traits more characteristic of k-selected mature forest species.

DISTRIBUTIONAL PATTERNS

To this point, we may conclude that, although an epiphytic habit has arisen many times during the course of plant evolution, very few higher taxa have been more than marginally successful at speciation and adaptive radiation as epiphytes. However, the few taxa that have successfully radiated as epiphytes have done so very prolifically. Even though remarkably similar numbers of plant families have achieved epiphytism in the Neotropics and Paleotropics, the process of epiphyte speciation would seem to have been much accelerated in the former, to judge from the very many more neotropical species of epiphytes.

We would now like to examine some trends in epiphyte distribution that may help to understand not only neotropical epiphyte biogeography but also some of the continental differences in epiphyte occurrence.

MOISTURE

One of the most striking distributional patterns shown by epiphytes is a tremendous decrease in both numbers of species and individuals in drier habitats. Although this pattern seems obvious, it is by no means well-documented. Indeed Walter (1985: 57) claimed that epiphytes, contrary to such other habit groups as lianas, are found in dry as well as wet tropical forests. At the other extreme, Schimper (1903) suggested that in areas with marked dry seasons epiphytes are either completely wanting or rare and that presence of epiphytes outside the rain forest is always a sign that the dry season is not long or is accompanied by copious dew. Data for 1,000 m^2 samples of western Ecuadorian dry forest (Capeira, 804 mm per year) and moist forest (Jauneche, 1,855 mm) quantify the extent of this difference (Gentry & Dodson, 1987; Table 4, Fig. 1). If our results are indicative, most plants in a wet forest are epiphytes. At Río Palenque such a sample included 4,517 epiphytic plants representing 63% of all individuals sampled. At Capeira a mere ten epiphytic plants were included in a similar sample of dry forest, representing 0.2% of the sampled individuals. The moist forest Jauneche site was intermediate with 116 epiphytes constituting 4% of the individual plants sampled. The difference in epiphyte density between wet and dry forest is almost 500 fold.

Moreover the decrease of epiphyte density in dry forest contrasts greatly with the situation for other habit groups. The number of herbs more than doubles from our moist and wet forest samples to our dry one. Contrary to Walter's assertion (1985: 57), lianas double from wet to dry forest; they are much commoner yet in our moist forest sample, the latter presumably atypical since Jauneche happens to be the most liana-rich site in the Neotropics (of 45 similar samples). Shrub density also increases somewhat from wet to dry forest; unlike lianas, shrubs are only about half as abundant in the intermediate moist forest as in dry and wet forest. In contrast, the number of individual trees ≥10 cm DBH, and thus the apparent density of the forest, changed little (52, 64, and 69 trees ≥10 cm DBH in wet, moist, and dry forest, respectively).

Epiphytes are also important contributors to the species richness of neotropical wet forests. Indeed there are 35 epiphyte species in our 0.1 ha. wet forest sample, accounting for over a third of the sampled species. This compares with only 13 epiphytes (8% of the species) in the comparable moist forest sample and three (2% of the species) in the dry forest one (Fig. 2).

The importance of the epiphytic contribution to species diversity is equally apparent when en-

TABLE 4. Number of species and individuals of different habit types in 1,000 m^2 samples of three forests in western Ecuador. Río Palenque is wet forest, Jauneche is moist forest, Capeira is dry forest (from Gentry & Dodson, 1987).

Habit Group	Río Palenque				Jauneche				Capeira			
	No. Spp.	%	No. Ind.	%	No. Spp.	%	No. Ind.	%	No. Spp.	%	No. Ind.	%
Herbs (incl. palmettos)	50	14	1,220	17	18	11	944	34	50	29	2,854	53
Shrubs	39	11	531	7	16	10	279	10	13	8	742	14
Epiphytes (incl. hemi-epiphytes)	127	35	4,517	63	13	8	116	4	3	2	10	.2
Climbers (incl. lianas; excl. hemiepiphytes)	36	10	117	2	58	34	484	17	58	34	895	16
Lianas ≥2.5 cm (excl. herbaceous + hemi-epiphyt.)	12	3	28	.4	43	25	124	4	19	11	58	1
Total tree spp. (incl. juven.)	114	31	653[1]	9	64	38	960	34	48	28	927	17
Trees <2.5 cm DBH (= saplings + seedlings)	87	24	559[1]	8	48	28	672	24	38	22	750	14
Trees ≤10 cm, ≥2.5 cm	86	24	217	3	35	21	245	9	32	18	108	2
Trees ≥10 cm DBH	32	9	52	1	30	18	64	2	29	17	69	1
Total herbs (epiphytes + herbs—woody epiphytes)	162		5,525		31		1,060		53		2,864	
Shrub layer (shrubs + saplings)	126		1,090		65		948		51		1,492	
Underlayers (< ca. 3 m) (herbs + shrubs + saplings)	176		2,310		83		1,892		101		4,346	
Total	365		7,210[1]		169		2,783		173		5,428	

[1] Excluding dense patch of 123 *Quararibea asterolepis* seedlings.

tire florulas are compared (Table 5, Fig. 3). Almost one fourth of all the Río Palenque plant species are epiphytes (Dodson & Gentry, 1978). Similarly, in another lowland wet forest at La Selva, Costa Rica, 25% of the species are epiphytes (Hammel, pers. comm.). Even in moist forest sites like Barro Colorado Island, Panama (Croat, 1978) and Jauneche, Ecuador (Dodson et al., 1985), epiphytes constitute 12–16% of the total flora. Only in dry forests are epiphytes relatively insignificant, accounting for 2–4% of the species of Capeira (Dodson & Gentry, 1987) and Santa Rosa National Park, Costa Rica (Janzen & Liesner, 1980).

We conclude, contrary to Walter (1985), that epiphytes decrease more drastically in drier areas than does any other habit group, but contrary to Schimper's (1903: 198) emphasis, a few vascular epiphytes are characteristically present in even the driest neotropical forests (e.g., Capeira with 804 mm of annual precipitation).

Familial makeup of the epiphytic flora also

changes with precipitation (Table 6). Many more families have epiphytic representatives in wet forests than in drier ones (Fig. 4), and many epiphytic taxa are confined entirely to wetter forests. In the Neotropics the same families tend to be represented by epiphytes under similar climatic conditions. In the driest forests, the only epiphytes are orchids and bromeliads, perhaps the two most specialized epiphytic families. Ferns, peperomias, and Cactaceae join orchids and bromeliads in slightly moister conditions. The next epiphytic families to appear with increasing humidity are aroids, Moraceae (stranglers), and Gesneriaceae, joining representatives of all the dry forest families, each of whose number of epiphytic species is maintained or increased. The two local florula sites with over 2,500 mm of precipitation, Barro Colorado Island (Croat, 1978) and Río Palenque (Dodson & Gentry, 1978), have remarkably similar epiphytic floras. The same seven epiphytic families are most species rich at both sites, in roughly the same
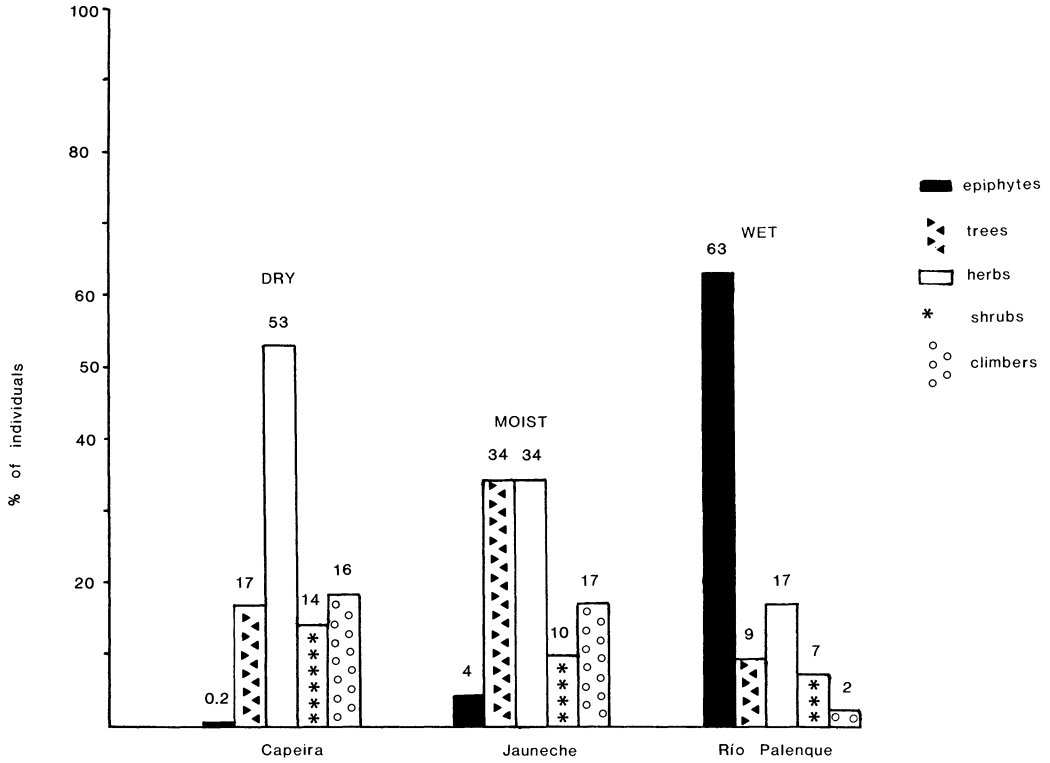
FIGURE 1. Percent of individual plants belonging to different habit groups in 1,000 m² samples of three western Ecuadorian forests.
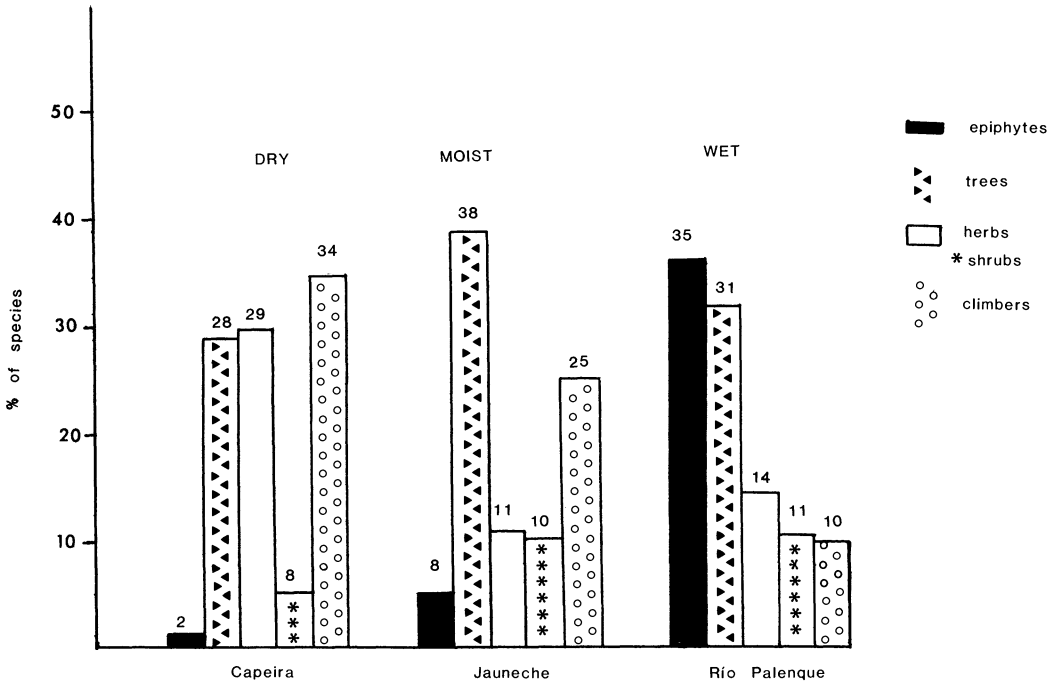

FIGURE 2. Percent of species belonging to different habit groups in 1,000 m² samples of three western Ecuadorian forests.
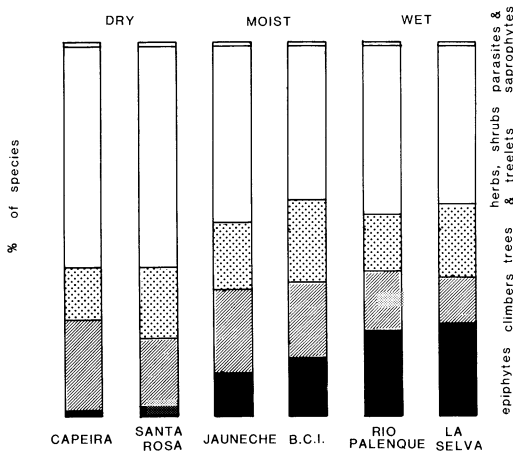
FIGURE 3. Percent of species in local florulas belonging to different habit groups.

order, just as they are in Hammel's unpublished La Selva, Costa Rica, species list. Remarkably, there are 81 epiphytic species of orchids at Río Palenque and 82 at Barro Colorado Island (BCI), 35 epiphytic aroids at Río Palenque vs. 30 at BCI, 18 species of epiphytic Bromeliaceae, and 14 species of epiphytic or strangler Moraceae at both sites. Only epiphytic ferns and fern allies are noticeably better represented at BCI than at Río Palenque and only epiphytic Gesneriaceae and Cyclanthaceae show the reverse pattern. Both sites have three epiphytic cacti and one epiphytic melastome plus one or two epiphytic Araliaceae, Solanaceae, and begonias. Only Rubiaceae and Saxifragaceae have epiphytic members at BCI but not Río Palenque; only Urticaceae, Polemoniaceae, Bignoniaceae, and Ericaceae have

epiphytic representatives in the Río Palenque flora but not the Barro Colorado one.

Again, the same epiphyte families predominate at other wet sites in western Ecuador (Table 7). The exact same seven most species rich families at BCI, La Selva, and Río Palenque are the most species rich at Centinela, again in roughly the same order. Even at Tenafuerste (alt. 1,000 m) the five families richest in epiphytes are exactly the same ones that are most species rich at the other Ecuadorian wet forest sites.

At the extreme wet end of the precipitation gradient there are other, as yet unquantified, changes in the epiphytic flora. In the wetter part of Chocó (precipitation > 8,000 mm) berry-fruited epiphytes like Melastomataceae, Araceae, Marcgraviaceae, and Ericaceae, along with arillate-seeded Guttiferae, appear to predominate to a much greater degree than at Río Palenque, while ferns (Sota, 1972) and dust-seeded orchids are more poorly represented. Possibly this change is related to the inability of dust-seeds to establish themselves in the face of such superabundant rainfall.

There is also a noticeable habit change in the epiphytic flora of the wettest sites. Most of the predominant Chocó epiphytic families are actually hemiepiphytic, many of them woody as well. In the same sites with abundant hemiepiphytes, free-climbing lianas become noticeably less prevalent. While the average of climbers ≥ 2.5 cm in diameter for 0.1 ha. samples at two pluvial forest sites in the Colombian Chocó was exactly the same (68) as that for a series of 20 similar samples from neotropical lowland moist and wet forests, half the sampled pluvial forest climbers were hemiepiphytic vs. an average of

TABLE 5. Habit compositions of complete local florulas. Capeira, Ecuador and Santa Rosa National Park, Costa Rica, are dry forest; Jauneche, Ecuador and Barro Colorado Island, Panama, are moist forest; Río Palenque, Ecuador, is wet forest.

Habit Category	Capeira		Santa Rosa		Jauneche		Barro Colorado		Río Palenque	
	No.	%	No.	%	No.	%	No.	%	No.	%
Trees ≥ 10 cm DBH	69	15	141	21	112	18	290	22	165	16
Small trees + large shrubs	28	6	64	10	60	10	151	11	99	9
Herbs + subshrubs	242	52	317	48	224	37	389	30	376	36
Epiphytes (including stranglers)	9	2	24	4	72	12	216	16	238	23
Parasites and saprophytes	4	1	6	1	4	1	12	1	6	1
Lianas	46	10	52	8	81	13	149	11	87	8
Small vines	66	14	63	9	55	9	109	8	84	8
Total species	464		667		608		1,316		1,055	

TABLE 6.   Familial composition of epiphyte floras in lowland forests with different precipitations.

Family	La Selva, Costa Rica[1] 4,000 mm	Río Palenque, Ecuador[2] 2,980 mm	Barro Colorado, Panama[3] 2,750 mm	Jauneche, Ecuador[4] 1,855 mm	Santa Rosa, Costa Rica[5] 1,550 mm	Capeira, Ecuador[6] 804 mm	Makokou, Gabon[7] 1,755 mm
Orchidaceae	109	81	82	33	8	5	21
Araceae	76	35	30	10	—	—	10
Ferns and allies	59	28	43	5	7	—	26
Piperaceae	12	19	10	4	1	1	—
Bromeliaceae	29	18	18	6	3	2	—
Moraceae	13	14	14	9	2	—	7+
Gesneriaceae	16	12	4	2	—	—	—
Cyclanthaceae	11	8	1	—	—	—	—
Marcgraviaceae	8	5	2	—	—	—	—
Guttiferae	11	4	2	—	—	—	—
Cactaceae	6	3	3	3	3	1	1
Ericaceae	2	3	—	—	—	—	—
Araliaceae	2	2	1	—	—	—	1
Bignoniaceae	3	2	—	—	—	—	—
Melastomataceae	2	1	1	—	—	—	—
Polemoniaceae	—	1	—	—	—	—	—
Solanaceae	1	1	2	—	—	—	—
Urticaceae	1	1	—	—	—	—	—
Begoniaceae	2	1	1	—	—	—	—
Rubiaceae	4	—	1	—	—	—	—
Saxifragaceae	—	—	1	—	—	—	—
Commelinaceae	1	—	—	—	—	—	—
Total epiphytes	368	238	216	72	24	9	66+
Percent of flora	24	23	16	12	4	2	6+
No. families with epiphytes	20	18	17	8	6	4	6

[1] B. Hammel, pers. comm.
[2] Dodson & Gentry, 1978.
[3] Croat, 1978.
[4] Dodson et al., 1985.
[5] Janzen & Liesner, 1980.
[6] Dodson & Gentry, 1987.
[7] Hladik & Gentry, in prep.; Florence & Hladik, 1980 and cited references.

2.7 hemiepiphytic climbers sampled at the moist and wet sites (Gentry, 1986). In a sense, hemiepiphytic climbers seem somehow to replace free-climbing lianas in the wettest lowland forests and also in middle elevation cloud forests.

ALTITUDINAL

The epiphytic flora also changes in both diversity and composition on an altitudinal gradient. The general tendency is for epiphytes to be better represented in intermediate elevation cloud forests. In the Andes the peak in epiphyte diversity appears to be between 1,000 m and 2,000 m, but it lies somewhat lower in Costa Rica and Panama. Few data are available, but a comparison of incomplete data sets for several

Ecuadorian sites (Table 7) documents this trend for the lower part of the gradient. The sites for which relevant data are available are Centinela (600 m) and Tenafuerste (1,000 m), both on the western slopes of the Central Ecuadorian Andes, and Mera (1,000 m) on the eastern slope. Of the well-documented sites, Centinela has the most species of epiphytes, 337, or 35% of the flora. This compares with 238 epiphyte species accounting for 23% of the flora at nearby Río Palenque (alt. 200 m). The data for the two 1,000 m sites are less complete, with many species remaining to be discovered. Tenafuerste, with much less cloud forest effect than Centinela or Mera, has the poorest epiphyte representation, only 31% of the flora. The extreme is pluvial Mera where few collections have been made as yet. Three

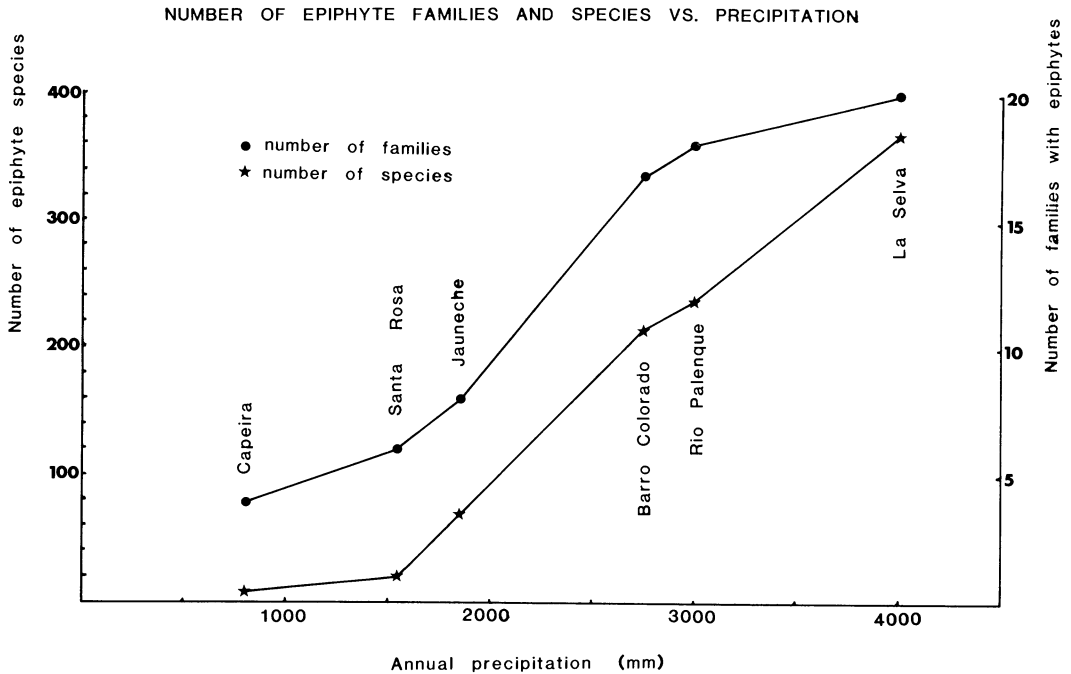NUMBER OF EPIPHYTE FAMILIES AND SPECIES VS. PRECIPITATION

FIGURE 4.   Increase in numbers of epiphyte species and families in local florulas as a function of precipitation.

hundred twenty-two orchid species are already known and we expect that there may be as many as 200 additional epiphytes as well.

In contrast, Peru's Huascarán National Park, 3,500–5,000 m in altitude, has only seven epiphytic species, constituting a mere 1% of the park's flora (Smith, pers. comm.).

The differences between Mera and Tenafuerste point out that altitudinal and moisture effects on epiphytes are complexly interrelated. Similarly Gilmartin (1973) showed that the 17 species of Bromeliaceae that occur on both sides of the Ecuadorian Andes occur at lower altitudes on the moister eastern slopes.

Density of epiphytes, although also greatest at intermediate altitudes, does not closely parallel diversity; although unquantified, we feel that epiphyte density in the Andes tends to be greatest around 2,000–2,500 m, again occurring at somewhat lower elevations in Costa Rica and Panama. Due to the high densities, epiphytes are often most conspicuous at these relatively high altitudes, even though relatively few species may be present. In middle elevation cloud forests, epiphytes may make up as much as 30% of the foliar biomass and 45% of the foliar mineral capital of a forest (Nadkarni, 1984).

Contrary to what happens along the moisture

gradient, familial composition of the epiphyte flora changes very little along an altitudinal gradient, or at least on that part of it for which we have data. The same families are important in roughly the same order. The seven families with the most epiphyte species at Centinela (600 m) are the same seven that have the most species at Río Palenque (200 m). The five families with the most species at Tenafuerste (1,000 m) are the same five that have the most species at Río Palenque and Centinela. The most noteworthy difference between these sites is the absence of Moraceae stranglers at Tenafuerste; Gesneriaceae are also conspicuously less diverse at the 1,000 m Tenafuerste site but Ericaceae are more diverse (nine species vs. three at Río Palenque). Melastomataceae is another family that has notably more epiphyte diversity at intermediate altitudes (four spp. at Centinela and two at Tenafuerste but only one at Río Palenque; see also Renner, 1986). A few families (e.g., Bignoniaceae) disappear from the middle elevation epiphyte flora and most other families have decreasing numbers of epiphytes at higher elevations.

Our only high altitude data set is for Huascarán National Park, Peru (Smith, pers. comm.), where the seven epiphyte species, all restricted to the lower part of the park between 3,500 and

4,000 m, belong to four families. The four families with epiphytes—Piperaceae, Bromeliaceae, Orchidaceae, and ferns—are all in the top five epiphytic families in the wet Ecuadorian sites. Of the usually prevalent epiphyte families, only Araceae is lacking. Perhaps more interesting, the epiphyte families at Huascarán are exactly the same ones that are represented at Santa Rosa, Costa Rica, except that Cactaceae is missing. Apparently at environmental extremes, either altitudinal or precipitational, only these same families that are otherwise most successful as epiphytes are able to survive.

The very interesting but controversial suggestion has been made that in the tropics diversity is generally greatest at middle elevations along an altitudinal gradient. This has been shown for leaf litter herps (Scott, 1976), insects (Janzen, 1973; Janzen et al., 1976), and suggested for plants. Greater equability is a likely controlling factor for this putative "mid-elevation bulge" in species diversity. However, data for 0.1 ha. samples of plants ≥2.5 cm DBH suggest that plant species diversity decreases more or less uniformly from the most diverse lowland wet forest sites to the least diverse high altitude ones (Gentry, 1982a, 1987c). If a mid-altitude bulge in plant species richness really does occur, it must be due largely to epiphytes. Unfortunately our data sets from middle and upper elevation forests are too incomplete to be definitive. Indeed one of us (CD) thinks that because of the increase in epiphytes there are more plant species at middle elevations than in lowland tropical forest while one of us (AG) thinks that the decrease in species numbers of such other habit groups as lianas and trees with altitude outweighs the increased number of epiphytes. In either case the role of epiphytes in the plant community is presumably greatest in middle elevation forests.

SOIL FERTILITY

To our knowledge no attempt to relate epiphyte diversity to soil fertility has been made previously. Indeed one might suppose that since epiphytes are intrinsically "insulated" from direct dependence on soil nutrients they would be relatively unaffected by changes in soil fertility. For example, Janzen (1974a) discussed the symbiotic relationships between several epiphytes and ants in low-diversity poor soil "kerangas" habitats in Borneo, with the implication that epiphytes are unusually well represented in such

TABLE 7. Familial composition of epiphyte floras in wet forests at different altitudes in Ecuador.

Family	Río Palenque 200 m	Centinela 600 m	Tenafuerste 1,000 m
Orchidaceae	81	133	68
Araceae	35	52	26
Ferns	28	38	28
Piperaceae	19	19	11
Bromeliaceae	18	23	18
Moraceae	14	10	—
Gesneriaceae	12	16	8
Cyclanthaceae	8	5	3
Marcgraviaceae	5	3	2
Guttiferae	4	9	3
Cactaceae	3	2	1
Ericaceae	3	9	9
Araliaceae	2	4	—
Bignoniaceae	2	2	—
Melastomataceae	1	4	2
Polemoniaceae	1	1	—
Solanaceae	1	2	1
Urticaceae	1	1	1
Acanthaceae	—	1	—
Rubiaceae	—	1	—
Total	238	337	181
Percent of flora	23	35	31

habitats. Whitmore (1984) also emphasized the frequency of epiphytes in these forests.

It is increasingly well-documented that major changes in the diversity and floristic composition of other components of tropical plant communities are associated with changes in soil fertility (e.g., Ashton, 1976, 1977, 1978; Huston, 1979, 1980; Gentry, 1987b; Gentry & Emmons, 1987). For example, there are generally fewer tree, liana, and terrestrial herb species in neotropical forests on poorer soils (Gentry, 1981; Gentry & Emmons, 1987). We have few data with which to relate epiphyte community composition to soil fertility. One of us (AG) has compiled species lists for a series of sites on different substrates in the Iquitos, Peru, area which share a similar rainfall and climatic regime. Of these, the site with the poorest soil (Mishana, on almost pure white sand) has the fewest epiphytes (31 epiphyte species plus a few "indets." in a relatively intensively inventoried area vs. 38 identified and many unidentified at less intensively studied better-soil Yanamono), suggesting that epiphyte diversity varies with soil fertility as does the diversity of other habit groups. However, to date the sam-

pling of epiphytes at these sites has been much less intensive than at our Ecuadorian local florula sites and is probably too haphazard and incomplete to make these data very meaningful.

Data are also available for understory composition and levels of flowering and fruiting for a broad array of neotropical (and paleotropical) sites (Gentry & Emmons, 1987). If the data for epiphytes are extracted from that data set, a very strong reduction in numbers of fertile species of understory epiphytes on poorer soils is apparent, paralleling the overall trend of decreased numbers of flowering and fruiting understory species on the same gradient. Our data for habit composition of the understory suggest that epiphytes, like terrestrial herbs, are especially sensitive to loss of soil fertility: as soil fertility decreases, terrestrial herbs, epiphytes, understory shrubs, and lianas disappear from the understory in that sequence, leaving virtually only tree saplings and seedlings in the most severely stressed forests (Gentry & Emmons, 1987).

Anecdotal evidence also indicates that epiphytes are much less diverse and abundant on poor soils. We have observed many fewer epiphytes in poor soil parts of Central Amazonian Brazil, southern Venezuela, and elsewhere in the Guiana shield area than in parts of the Neotropics with richer soils. Large-scale biogeographical analysis also indicates that epiphytic taxa are poorly represented in these areas compared with richer soil areas nearer the Andes and in Central America (Gentry, 1982b). In a somewhat different context, Janzen (1977) has suggested that the paucity of epiphytes in dipterocarp forests results from the generally nutrient-poor Southeast Asian soils. Among the evidence for this hypothesis cited by Janzen (1977) is the observation that trees cultivated in Malesia along roads, where dust stirred up by passing vehicles increases the nutrients available to epiphytes in an otherwise unusually poor-soil situation, have relatively large epiphyte loads compared with the native forests.

On balance it seems clear that the epiphytic plant community is very sensitive to soil fertility, with fewer epiphytes and fewer epiphytic species in forests on poorer soils. Indeed epiphyte diversity may be even more sensitive to change in soil fertility than is tree or liana diversity, a suggestion that would accord with the idea (Gentry & Emmons, 1987) that plants (presumably including epiphytes despite their lack of direct contact with the soil) that are barely able to eke out a marginal existence should be more susceptible to the effects of relatively slight decreases in environmental favorability.

LATITUDE

It is well known that the presence of vascular epiphytes is a characteristic of tropical forests as compared with temperate ones. We know of only four vascular epiphytes that occur north of Florida in the temperate United States—*Tillandsia usneoides, T. recurvata* (only in southernmost Arizona), *Epidendrum conopseum,* and *Polypodium polypodioides.* Even *Tillandsia usneoides,* the northernmost vascular epiphyte, does not reach the Mason-Dixon line. The only continental United States epiphyte species that is not widespread in the tropics is *Tillandsia simulata* Sm., endemic to Central Florida but sometimes lumped with *T. bartramii* Ell. (The Mexican range of *Epidendrum conopseum* is also somewhat limited.) Even in very wet areas that would be full of epiphytes in the tropics, only lower plants have adopted the epiphytic habit. In intermediate subtropical areas a gradient of increasing epiphytism at lower altitudes is evident. The decrease in vascular epiphytes with increasing latitude can be clearly seen in Florida where subtropical South Florida (latitude 25°N) has 46+ (= 2.8%) epiphytic species (Long & Lakela, 1971), Central Florida has 41 (= 1.9%) (Wunderlin, 1982), and Florida Caverns State Park in northern Florida (30°50'N latitude) has only two (= 0.4%), *Tillandsia usneoides* and *Polypodium polypodioides* (Mitchell, 1963).

Curiously, the decrease in vascular epiphytes with increasing latitude is not symmetrical on both sides of the equator. A number of epiphytic species and even a few endemic genera of epiphytes occur in south temperate forests. Endemic temperate South American epiphytic genera include the monotypic fern *Synammia,* the monotypic cactus *Pfeiffera,* three monotypic Gesneriaceae genera (*Asteranthera, Sarmienta,* and facultatively epiphytic *Mitraria*), and the Liliaceae (or Philesiaceae) *Luzuriaga* and *Philesia.* In the Australasian region, New Zealand is especially noteworthy for its autochthonous epiphytes including genera like the monotypic fern *Anarthropteris,* the liliaceous *Collospermum* (also reaching Fiji and Samoa), the only epiphytic species of families like Cunoniaceae (with two different genera having epiphytic members), and genera like *Microlaena* (Gramineae) and *Metrosideros* (Myrtaceae). There is even a largely epiphytic south temperate family shared by New

Zealand and Southern Argentina–Chile—Grise-liniaceae (sometimes included in Cornaceae). In the north the only noteworthy temperate epi-phytes are in the Himalayas where aberrant epi-phytic species of otherwise terrestrial genera like *Ilex, Tripogon, Euonymous, Sedum,* and *Tha-lictrum* occur. This latitudinal asymmetry was already noted by Schimper (1903), who pointed out that north temperate epiphytes are merely range extensions of widespread tropical species, whereas many unusual and distinctive epiphytic taxa occur in the South Temperate region.

At the community level the same trend is ap-parent. For example, Parque Nacional El Rey in Argentina, at 24°45′S latitude, has a species list (L. Malmierca, pers. comm.) of well over 500 vascular plants including 47 species of epiphytes: 20 ferns, four orchids, three species of *Rhipsalis* and *Peperomia,* and no fewer than 17 bromeliads including 14 tillandsias. In contrast, Florida Cav-erns State Park at 30°50′N latitude has only two epiphytes in its similar-sized flora of 485 native species (Mitchell, 1963). Even in rather dry south temperate vegetations vascular epiphytes can be extremely prevalent, a situation apparently with-out parallel in the North Temperate region. For example, in the Valley of Lerma near Salta, Ar-gentina (1,200 m, ca. 700 mm ppt.), there are at least 14 angiosperm epiphytes including at least ten *Tillandsia* species in a flora of over 750 species (Novara, 1984).

Farther south in the Valdivian region of Chile vascular epiphytes, mostly belonging to endemic genera, are conspicuous elements of local floras, ranging from six species (3% of the native flora) at relatively dry Parque Nacional Tolhuaca (38°15′S) (Ramírez, 1978) to 17 species (17% of the native flora) at very wet Fundo de San Martín (39°30′S) (Cárdenas, 1976; Riveros & Ramírez, 1978); even at 41°S there are 15 vascular epi-phyte species in Puyehue National Park (Muñoz, 1980). New Zealand forests have even more epi-phytes than the Chilean ones; even well south of 40°S, about 30 vascular epiphytes are typically included on local species lists (Dawson, 1980). However, at comparable latitudes in North America there are no vascular epiphytes.

Why there are more, and more distinctive, epi-phytes in south temperate than in north tem-perate forests is unclear but presumably relates to the relatively mesic, more or less oceanic cli-mates that prevail in the Southern Hemisphere. There are more epiphytes at 25°S (47 epiphytes constituting ca. 8.5% of the flora of Parque El Rey, L. Malmierca, pers. comm.) as compared with 25°N (46 epiphytes constituting ca. 2.8% of the South Florida flora, Long & Lakela, 1971). At least in South America, the prevalence of many species of the genus *Tillandsia* in southern forests (e.g., 14 at Parque El Rey), perhaps due purely to biohistorical reasons, is another important factor. A similar pattern occurs with lianas, which are better represented in New Zealand than in north temperate forests (Dawson, 1980).

CONTINENTAL TRENDS

There are several conspicuous differences be-tween the epiphytic floras of different continents. Obviously, predominantly extratropical conti-nents have few vascular epiphytes. However, there are also striking differences within the trop-ics between the Neotropics, tropical Africa, and tropical Australasia. The African epiphytic flora has been widely noted to be very impoverished compared with the other two regions, presum-ably reflecting a loss of mesic-adapted species during the dry periods associated with the Pleis-tocene glacial advances at higher latitudes (Rich-ards, 1973; Madison, 1977). According to Mad-ison there are only ca. 2,400 epiphytic species in Africa, less than a sixth as many as in the Neo-tropics and a quarter as many as in tropical Aus-tralasia. Even though several families and genera with epiphytes in Madagascar were omitted from Madison's (1977) epiphyte summary (see Ap-pendix), their inclusion does not appreciably in-crease the number of African epiphyte species.

Curiously, the depauperate nature of the Af-rican epiphytic flora is not obvious at the com-munity level. For example, the 59 epiphyte species at Makokou, Gabon, constitute 5% of the total Makokou flora (Table 8; compiled from Hladik & Gentry, in prep.; Florence & Hladik, 1980, and included references). While 5% of a moist forest flora might seem fewer epiphytes than would be expected in the Neotropics, Ma-kokou is quite dry, with only 1,785 mm of annual rainfall, and its 66 (6%) epiphytic species (in-cluding stranglers) are quite in line with the 72 (12%) epiphytic species at Jauneche and 24 (4%) at Santa Rosa (Table 9). Johansson (1974) stud-ied a relatively moist region in the Nimba moun-tains of northern Liberia and reported 153 vas-cular epiphyte species (excluding six filmy ferns and 23 "facultative" epiphytes) in his study area, up to 44 species in a single 750 m plot, and up to 22 species on a single tree. In even wetter areas

TABLE 8. Habit distributions of Makokou, Gabon plant species.

Habit	Ferns	Gymno-sperms	Monocots	Dicots	Total
Epiphytes	26	0	31	2	59
Parasites + saprophytes	0	0	3	6	9
Climbers	1	2	8	248	259
Trees	0	0	5	390	395
Herbs, shrubs, and treelets	42	0	125	251	418
Total species	69	2	172	897	1,140

like southwestern Cameroon epiphytes are almost as prevalent as in many similar areas of the Neotropics (AG, pers. obs.).

That tropical Australasia is also floristically impoverished with respect to the Neotropics has only recently been realized (Raven, 1976; Gentry, 1982b). Epiphytes account for much of the overall difference between the two regions with half again as many epiphytes in the Neotropics as in Australasia (15,500 vs. 10,200) according to Madison's (1977) figures. Moreover, at least in those lowland Asian forests we have visited, there also seem to be many fewer epiphytic individuals than in comparable neotropical forests. Richards's (1936) remark is typical: "One of the most striking features of the Sarawak rain forest, especially when compared with that of tropical South America, is the poverty of the epiphytic vegetation both in species and individuals." Madison suggested that the fewer tropical Asian epiphytes might stem simply from lack of the extensive cloud forest habitats of the Neotropics, but that would hardly explain the lower numbers of individuals in comparable lowland forests. Janzen (1974b, 1977) emphasized that many tropical Asian forests tend to have relatively nutrient-poor soils, and, if so, our suggestion of a positive correlation between epiphytes and soil fertility might help explain the relatively low epiphyte diversity and biomass in tropical Asia.

Another important continental level difference in epiphytes is taxonomic. Orchids and ferns are the predominant vascular epiphytes nearly everywhere, but the other elements of the epiphytic flora are often very different on different continents (Table 10). Johansson (1974) generalized that the African epiphytic flora is made up almost entirely of pteridophytes and orchids, whereas these groups are joined by bromeliads and Cactaceae as important epiphytic taxa in South America and by Asclepiadaceae and Rubiaceae in Southeast Asia. Although there are 18 seed plant families with epiphytic species only in Australasia and 15 with epiphytes only in the

TABLE 9. Representation of different habits in local florulas.

Habit	Capeira No.	%	Santa Rosa No.	%	Jau-neche No.	%	Barro Colo-rado No.	%	Río Pa-lenque No.	%	La Selva[1] No.	%	Makokou No.	%
Epiphyte (incl. stranglers)	8	2	19	3	72	12	216	16	238	23	368	25	66+	6+
Parasites + saprophytes	4	1	6	1	4	1	12	1	6	1	8	1	9	1
Climbers	112	24	115	18	136	22	258	20	171	16	182	12	259	23
Trees ≥10 cm DBH	69	15	142	21	112	19	290	22	165	16	310	21	389	34
Terrestrial herbs, shrubs, tree-lets	270	58	381	58	280	47	540	41	475	45	622	42	418	37
Total species	463		667		604		1,316		1,055		1,490		1,140	

[1] Data from B. Hammel (pers. comm.).

TABLE 10. Taxonomic distribution of epiphytic taxa in some lowland florulas.

Site	Ferns		Monocots			Dicots			Total	
	No. Spp.	%	No. Fam.	No. Spp.	%	No. Fam.	No. Spp.	%	No. Spp.	%
Neotropics										
Capeira, Ecu.	—	—	2	7	88	2	2	22	9	2
Santa Rosa, C.R.	7	29	2	11	46	3	6	25	24	4
Jaueche, Ecu.	5	7	3	49	68	4	18	25	72	12
Barro Colorado, Pan.	43	20	4	131	61	12	42	19	216	16
Río Palenque, Ecu.	28	12	4	142	60	14	69	29	238	23
La Selva, C.R.	59	16	5	226	61	15	83	23	368	25
Africa										
Makokou, Gabon	26	44	2	31	53	3	9+	3	66+	6+
Asia										
Flora of Java	200	24	3	520	63	11	109	13	829	—

Neotropics (in the case of Campanulaceae there are also 11 Hawaiian species), Africa has only one family uniquely epiphytic. That family, Costaceae, is a dubious segregate of Zingiberaceae, the latter with epiphytes in Asia. At least nine seed plant families have epiphytic species in both the Neotropics and Australasia (but not Africa), but not a single one has epiphytes in both the Neotropics and Africa-Madagascar but not Australasia. There are 14 families with epiphytic species in all three of the world's main tropical regions. In total there are 33 (or 34 if Costaceae is segregated) families with epiphytes on only one continent as compared with 23 with epiphytes on more than one continent: clearly most seed plant families have epiphytes on only a single continent.

Many of the "epiphytic" families included in the above analysis are actually terrestrial families with one or two aberrant species adapted to epiphytism. There are only 32 seed plant families with five or more epiphytic species. If the continental representations of these 32 families are compared, seven (Bromeliaceae, Cyclanthaceae, Rapateaceae, Bignoniaceae, Campanulaceae, Marcgraviaceae, and Guttiferae) have epiphytes only in the Neotropics; six (Myrtaceae, Nepenthaceae, Pittosporaceae, Loganiaceae, Balsaminaceae, and Zingiberaceae, sensu stricto) have epiphytes only in Australasia; 14 have epiphytes in all three tropical regions; and five (Asclepiadaceae, Ericaceae, Rubiaceae, Solanaceae, and Urticaceae) have epiphytes only in the Neotropics and Australasia.

Put another way, there are 42 neotropical seed plant families with epiphytes (Table 3) but epiphytism is minimal in 19 of these (one to four epiphytic species in the Neotropics). Of the families with at least five epiphytic species in the Neotropics, seven—Bromeliaceae, Cyclanthaceae, Rapateaceae, Campanulaceae (also in Hawaii), Bignoniaceae, Marcgraviaceae, Guttiferae—are epiphytic exclusively in the Neotropics, and another, Cactaceae, has only one epiphytic species widespread in the Paleotropics. Fourteen of the families with some neotropical epiphytic species have epiphytes in all three tropical regions—Araceae, Orchidaceae, Liliaceae, Araliaceae, Begoniaceae, Compositae, Crassulaceae, Gesneriaceae, Lentibulariaceae, Melastomataceae, Moraceae, Myrsinaceae, Piperaceae (plus, marginally, Cactaceae). In addition to exclusively south temperate Griseliniaceae and Philesiaceae, seven families—Gnetaceae, Burmanniaceae, Asclepiadaceae, Ericaceae, Rubiaceae, Solanaceae, Urticaceae—have epiphytes only in the Neotropics and Australasia.

The sharing of epiphytic taxa between Australasia and the Neotropics but not with Africa is a very different pattern from that normally found in angiosperms, where close floristic relationships between Africa and the Neotropics (reflecting a shared early angiosperm Gondwanan flora, Raven & Axelrod, 1974) or between Africa and tropical Asia (reflecting the relatively direct migration route provided by today's geography) are the general rule.

Even within the same family paleotropical and neotropical epiphytes are often not closely related. For example, the paleotropical epiphytic

Gesneriaceae belong to subfamily Cyrtandroideae while neotropical ones are mostly in the endemic subfamily Gesnerioideae (Wiehler, 1983). Madison (1977) noted that epiphytism has arisen independently in at least three different groups of aroids. Most epiphytic neotropical orchids belong to subtribes Pleurothallidinae, Maxillarinae, and Oncidinae, while most paleotropical ones belong to Dendrobiinae and Bulbophyllinae. The few epiphytic Central American species of *Cynanchum* are quite unrelated to the many paleotropical epiphytic species of Asclepiadaceae. Most epiphytic neotropical Ericaceae belong to subfamily Vaccinioideae, half the paleotropical ones to Rhododendroideae. Most epiphytic neotropical Rubiaceae belong to tribe Cinchoneae (subfamily Cinchonioideae), most paleotropical ones to Psychotrieae (subfamily Rubioideae).

Even when the same genus has epiphytic species in all three continental regions, these may not be closely related to each other. Altogether only 30 epiphyte-containing seed plant genera are found in more than one of the three main tropical regions, and only 14—*Liparis, Malaxis, Vanilla, Polystachya, Bulbophyllum, Schefflera, Begonia, Rhipsalis, Vaccinium, Utricularia, Ficus, Myrsine, Peperomia, Senecio*—are pantropical. Twelve of the genera that occur as epiphytes on more than one continent are large, diverse, terrestrial genera in which epiphytism has arisen occasionally. For example, there are at least two independent origins of epiphytism in *Utricularia* (P. Taylor, fide Madison, 1977). Genera like *Gnetum, Myrsine, Burmannia, Schefflera, Begonia, Senecio, Gaultheria, Vaccinium, Piper, Psychotria, Solanum,* and *Pilea* have independently derived and mostly quite unrelated epiphytic species in Old and New Worlds. There are five exclusively paleotropical genera with epiphytic species in Africa and Asia: predominantly epiphytic *Medinilla* (Melastomataceae) and the orchid genera *Acampe, Oberonia,* and *Taeniophyllum,* and occasionally epiphytic *Embelia* (Myrsinaceae). We are left with only *Schefflera, Rhipsalis, Ficus, Peperomia, Liparis, Malaxis, Vanilla, Polystachya,* and *Bulbophyllum* as genera in which epiphytism is widely prevalent on all three continents. Indeed the only genera in which epiphytism in both the New and Old Worlds seems to represent a true synapomorphy are three south temperate genera (*Luzuriaga, Griselinia,* and *Coprosma*), *Ficus, Rhipsalis,* probably *Peperomia,* and possibly *Schefflera.* The

clearest cases of a shared epiphytic ancestor are Cactaceae where long distance dispersal of one species of *Rhipsalis* is responsible for the pattern seen today (Barthlott, 1983), and the peculiar case of *Ficus* where the large successful pantropical subgenus (*Urostigma*) has specialized as stranglers. The five pantropical epiphytic orchid genera likely achieved their present distributions via long-distance dispersal of their dustlike seeds. Predominantly epiphytic *Peperomia* may have been originally epiphytic; it is probably ancient (cf. Burger, 1977) and in many aspects of its biology, in addition to its pantropical distribution, it is anomalous among epiphytes.

Schefflera is predominantly epiphytic in the Neotropics, predominantly terrestrial in the Paleotropics; according to Madison's (1977) estimate only 65 species are epiphytic. Many species grow both as epiphytes and terrestrials; epiphytism, though widespread, does not seem fundamentally intrinsic to *Schefflera* and may have arisen independently in all three regions and probably within a given region as well.

Ferns, notorious for the ease of long-distance dispersal of their dustlike diaspores, contrast with the angiosperms in having most large epiphytic genera preponderately pantropical. There are even exclusively epiphytic pantropical fern genera including *Pleopeltis, Platycerium, Ctenopteris, Xiphopteris, Psilotum, Vittaria,* and (almost) *Polypodium*; there is not a single exclusively epiphytic pantropical seed plant genus. Even in ferns the majority of the epiphytic genera are restricted to one geographical region. Only one epiphytic fern genus is disjunct between the Neotropics and Asia (*Ophioglossum,* a large genus with only two epiphytic species separately arisen on the two continents). Five epiphytic fern genera occur in both tropical Asia and Africa but not the Neotropics, three of them on Madagascar but not continental Africa; again this is a pattern without parallel in the seed plants.

We may conclude that, except for the ferns, strangler figs, *Peperomia, Rhipsalis,* and a few orchid genera, the epiphytic floras of the different tropical regions are independently derived, even in most cases where the same family or genus is involved in different regions.

While certain taxa are preadapted to an epiphytic lifestyle, evolution of an extensive array of epiphytic species in any given taxon depends largely on the peculiarities of that region's evolutionary milieu. Epiphytism has arisen very many times in very many groups. However, cer-

tain regions have given rise to many epiphytes; others have not. In this context, the partial explanation offered by Madison (1977) for the greater representation of epiphytes in the Neotropics—that historical accident in the distribution of families like Bromeliaceae, Cactaceae, Marcgraviaceae, and Cyclanthaceae has led to the neotropical predominance in epiphytic species—seems largely irrelevant. Indeed, as many families (and other supraspecific taxa) have evolved epiphytism in the Paleotropics as in the Neotropics; the difference is that in the Neotropics evolutionary experiments with an epiphytic life-style have subsequently led to much more profuse speciation. Madison (1977) also thought that one element in explaining the continental difference of epiphyte diversity is a paucity of paleotropical nonorchid monocot epiphytes. However, our analysis emphasizes that it is not the evolution of epiphytism itself in such taxa that is the critical factor, but rather that there has been little subsequent radiation. Why have epiphytic taxa of Zingiberaceae, Costaceae, Pandanaceae, or Liliaceae not evolved into paleotropical versions of Bromeliaceae or Cyclanthaceae? We will try to analyze why this should be so in the next section.

EVOLUTION OF EPIPHYTE SPECIES DIVERSITY

Why are epiphytes so much better represented in some habitats than in others within the Neotropics? Part of the answer to that question can be adduced from the diversity gradients discussed above. From the patterns documented above we can generalize that epiphytes are most diverse in wet, middle elevation, rich-soil, tropical American forests. With the exception of the somewhat tenuously established trend toward greater diversity at middle elevations, these are exactly the trends shown by angiosperms in general (Gentry, 1982a, 1982b, 1987c). In a previous paper, based on data extrapolated from a large array of published monographs of neotropical taxa, Gentry (1982b) concluded that plant families belonging to different habit groups have fundamentally different distributional patterns. Families composed mostly of canopy trees or lianas have their greatest diversity in Amazonia whereas families made up mostly of epiphytes, shrubs, or palmetto-type herbs are largely extra-Amazonian and are especially concentrated along the lower slopes of the northern Andes and to a lesser extent in southern Central America. For epiphytes this concentration of species diversity could have been predicted from the trends outlined above. But *why* are epiphytes (and some other plants) so much more diverse in these regions?

One reason that epiphytes are especially diverse in wet aseasonal forests is that they are able to achieve a much finer niche partitioning, and thus a higher alpha diversity, there. Western Ecuador provides a good example of how this phenomenon operates. In the evergreen Río Palenque wet forest nearly all of the epiphytes have a characteristic and usually very restricted habitat, occurring only in the understory, the middle story, or the canopy. Altogether 41 species of vascular epiphytes at Río Palenque are understory specialists: 19 species of Araceae, one of Begoniaceae, one of Bignoniaceae, five of Cyclanthaceae, eight of Piperaceae, one of Solanaceae, and six ferns. However, there is not a single understory-specialist epiphyte species in the highly seasonal semideciduous moist forest at Jauneche, only a few tens of kilometers away. The presence of 41 species of understory specialist epiphytes at Río Palenque accounts for much of the difference between its diverse epiphytic flora and the relatively depauperate one at Jauneche. Nonstrangling epiphytic trees like *Clusia,* another specialized habit not occupied by Jauneche epiphytes, account for another five species of the difference. Presumably the more constant environment at Río Palenque favors within-community microhabitat specialization by epiphytes. Thus classical ideas about the greater spatial heterogeneity of everwet tropical forests (e.g., Baker, 1970) are certainly applicable to epiphyte diversity patterns both within the tropics and on a latitudinal gradient.

To some extent niche fine-tuning in constant environments also occurs in nonepiphytes. A good example is provided by *Gasteranthus* at Centinela, Ecuador (see Gentry, 1987b). Six species occur together sympatrically. All are terrestrial herbs and five are strictly endemic. The nonendemic species, *G. oncogastris,* occurs on the lower slopes away from the 600 m ridge top. Another species, *G. crispus,* grows only in sandy creek beds of the north part of the ridge and is not strictly sympatric with the other four species. Of the four strictly sympatric species, one, *G. atratus,* has switched from hummingbird- to bee-pollination and has yellow flowers completely distinct from the orange flowers of the other

species. Two of the strictly sympatric species both have large flowers and grow in the deep shade along creek beds, but *G. macrocalyx* blooms in the wet season and *G. pubescens* in the dry season. The final species, *G. carinatus,* is morphologically differentiated by slightly smaller flowers and ecologically by growing only along the ridge top. In *Gasteranthus,* as in the Río Palenque epiphytic flora, very fine niche partitioning in a relatively constant climate seems an important key to maintenance of high species diversity. To the extent that such niche partitioning is related to equable montane cloud forest conditions, it might be expected to be relatively favored in the Neotropics.

A second explanation for the great epiphyte diversity in the Andean area focuses on β-diversity resulting from the greater microsite differentiation typical of mountainous regions. A test of this hypothesis might come from comparing epiphyte diversity in areas with high and low microsite differentiation. The two "nudos" where the eastern and western Andean cordilleras come together briefly at opposite ends of Ecuador provide such a test. The southern Nudo de Loja (or Sabanilla) marks the beginning of the Huancabamba biogeographic discontinuity (cf. Berry, 1982); the northern Nudo de Pasto, mostly across the border in Colombia, marks the point where the three Colombian cordilleras diverge. In both of these areas a tremendous variety of habitats spanning the gauntlet from very wet to very dry occur together in very close proximity due to the unusually broken terrain and very different orientations of adjacent slopes. *Telipogon* (Orchidaceae) provides a good example of how such microsite heterogeneity can multiply epiphyte species diversity. There are 37 *Telipogon* species in Ecuador and five more on the Colombian side of the Nudo de Pasto. There are 14 species on the Nudo de Loja and 16 species on the Nudo de Pasto, as compared with only 14 species in the entire intervening 600 km. More instructive, nine of the *Telipogon* species on Nudo de Loja and five on Nudo de Pasto are locally endemic, each found in a single valley or a single slope. In the much larger intervening area there are only nine endemic species, each restricted to a small area of a few hectares, in several cases representing unusual and restricted microhabitats similar to those around the Nudos. It seems clear that in *Telipogon* diversity is associated with local speciation and microgeographic specialization. Again, epiphytes are not the only

group to show such patterns, but they do seem especially prone to this kind of microgeographic speciation. Probably the association of accentuated microgeography with mountainous terrain, which is much more prevalent in the Neotropics, explains some of the intercontinental diversity differences.

A third, not necessarily mutually exclusive, potential explanation for high epiphyte diversity in the northern Andean and southern Central American cloud forests is the "evolutionary explosion" hypothesis advanced by Gentry (1982b) in an attempt to explain why there are so many more neotropical than paleotropical plant species. A relatively small number of genera of epiphytes, understory shrubs, and palmetto-type herbs have speciated profusely in the northern Andean region, in each case giving rise to very many locally endemic and often rather poorly differentiated species. Gentry (1982b: 587) interpreted the high local endemism (cf. Gentry, 1987b) and apparent "species swarms" in such large evolutionarily plastic genera as *Anthurium, Piper,* and *Cavendishia* as reflecting "shifting balance" founder effect phenomena (Wright, 1977; Templeton, 1980) with major genetic reorganizations or genetic transilience (Templeton, 1980) optimized by small and localized populations and by the need for constant recolonization in a habitat partitioned by mountains, local rainshadows, vertically shifting cyclically coalescing vegetational zones, and frequent landslides. If genetic founder effects associated with recolonization of the open areas resulting from landslides or unusually frequent tree falls in these geologically and ecologically dynamic regions are major determinants of speciation events, then much speciation in Andean-centered taxa could well be essentially sympatric and largely random. This model thus differs from the "microgeographic speciation" model in that speciation could take place at a much finer "sympatric" scale, e.g., as colonization of a specific landslide, with many of the resultant species ecologically indistinguishable from each other, rather than each adapted to a specific microsite. Since this scenario is largely dependent upon the extreme ecological dynamism imputed to be associated with tropical mountains it would be expected to be most applicable in the Andean region, by far the most extensive mountain system in the world's tropics.

We have indirect but highly suggestive evidence for speciation associated with genetic tran-

FIGURE 5.   *Stanhopea jenishiana* Reichb. f.

silience in founder populations in several genera of epiphytes. *Embrya rodigasiana* (Cogn.) Dodson provides a good example of a founder event. This species is distributed mostly in western Colombia, between 1,000 m and 1,500 m, ranging from west of Medellín to near Buenaventura. There is also a disjunct population in a small area of southern Ecuador near Panguí, at 1,500 m above Bomboiza and Gualaquiza; prior to recent widespread habitat destruction, the species was very common in the disjunct and geographically very limited Ecuadorian part of its range, where it was surely introduced by a long-distance dispersal founder event. *Masdevallia chontalensis* is a similar example. Well known and occurring in a well-known habitat, it ranges from Guatemala to Panama with a small disjunct population near Piñas in southern Ecuador. There are several similar cases of unsuccessful founder events by dust-seeded tropical epiphytes that have temporarily established disjunct populations in Florida, been duly recorded as members of the Florida flora, and then subsequently disappeared. An example is *Leochilus labiatus* which grew for a while near Fackahatchee.

The *Stanhopea jenishiana* complex, well characterized by a suite of distinctive morphological characters, provides an example of the next step in such a process. *Stanhopea jenishiana* Reichb. f. (Fig. 5) ranges from Cali to Popayán in the Cauca Valley of Colombia, with a disjunct population near Piñas in southern Ecuador. There are two other small geographically isolated populations of this complex in western Ecuador, each of them specifically distinct but clearly derived from *S. jenishiana* and each likely resulting from a single long-distance dispersal event—*Stanhopea frymirei* Dodson is endemic to a range of relatively moist hilltops near the coast in Manabí and Guayas provinces and *S. embreei* Dodson occurs only around 1,000 m in the Bolivar-Cañar border area (Fig. 6).

The herbaceous and shrubby taxa that show such patterns have relatively short generation times, providing conditions appropriate for rapid evolutionary diversification. Under either the microgeographic or founder effect hypothesis, epiphytes, as the major herbaceous component of wet tropical forests, might be expected to show unusually rapid "evolutionary explosion" type speciation. Relatively specific pollination systems constitute a second factor suggested by Gentry (1982b) as potentially promoting unusually rapid speciation in "Andean-centered" taxa, with shifts in specific pollinators accompanied by coevolutionary fine-tuning of precise plant-pollinator systems apparently a common evolutionary theme. Again epiphytes, often characterized by high pollinator specificity, should be prime candidates for rapid speciation.

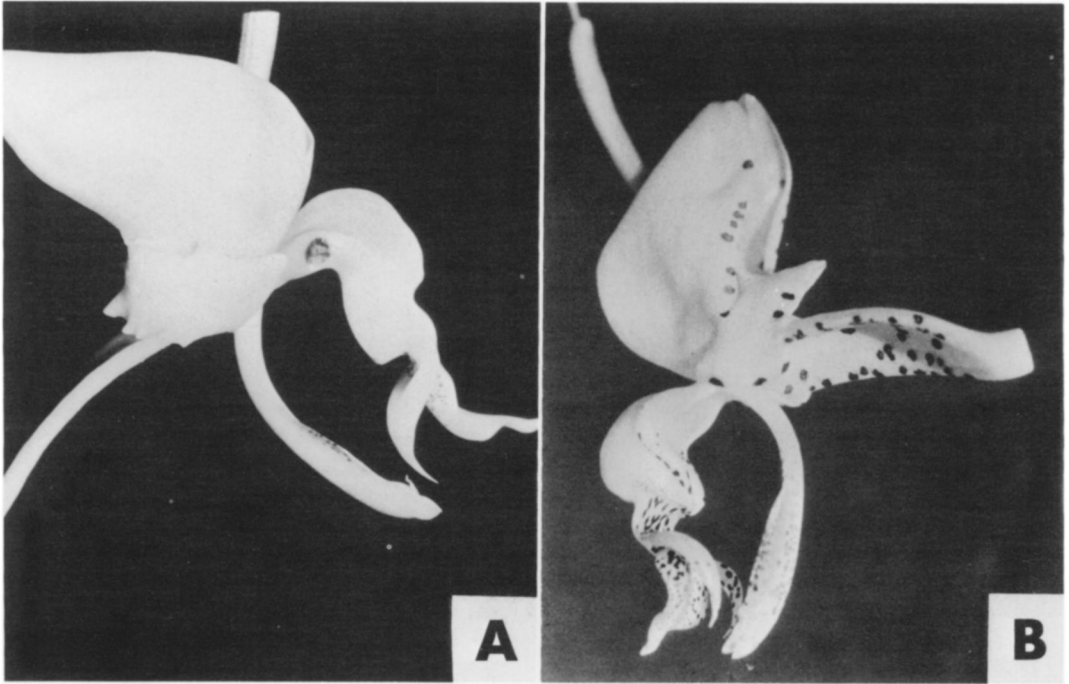The *Stanhopea jenishiana* complex (see above) is a good example of how founder events and

FIGURE 6. Two localized derivatives of *Stanhopea jenishiana.*—A. *S. embreei* Dodson.—B. *S. frymirei* Dodson.

shifts in pollination syndromes can combine to give rise to new species. The presumed ancestral species, *S. jenishiana,* has orange flowers and is pollinated by bees of the genus *Euglossa* while both of the locally endemic derivative species in central Ecuador have white (*E. embreei*) or straw-colored (*E. frymirei*) flowers and have switched to pollination by *Eulaema bomboides.* All three species have methyl cinnamate as the major scent attractant but each has a different set of scent-modifying compounds. *Eulaema bomboides,* a very effective pollinator that specializes on flow-ers producing methyl cinnamate, is endemic to central Ecuador. We interpret this situation as reflecting three different instances of long-dis-tance dispersal. In the southern Ecuador Piñas population, outside the range of *E. bomboides,* pollination by *Euglossa* was maintained and no speciation occurred. In the two isolated central Ecuadorian populations speciation to take ad-vantage of *Eulaema bomboides* as a pollinator occurred with essentially the same selection op-erating in these two different founder popula-tions. Different evolutionary solutions reflected by the two distinct derivative species resulted.

Scelochilus, another epiphytic genus of orchid, provides an even more intriguing indication of

how rapid speciation might be in such taxa. *Sce-lochilus* is a genus of 34 species found mostly epiphytic in guava trees; sparsely represented in natural vegetations, it was apparently ideally pre-adapted for the special conditions provided by guava plantations. Fifteen species of *Scelochilus* occur in Ecuador. In 1957 one of us (CD) made an intensive study of populations of *Scelochilus* in an extensive guava grove near the edge of wet forest at 1,000 m altitude at km. 94 of the old Guayaquil-Cuenca road in Ecuador. Two un-described species of *Scelochilus* were present, growing intermixed, both very common, and to-gether averaging about 30 flowering plants per host tree. Vegetatively the two species were in-distinguishable, but their flowers, though some-what variable in each species, were very distinc-tive with no overlap whatsoever between the two species. Indeed the original study, intended to focus on hybrid introgression, had to be aban-doned because the two taxa proved to be so con-sistently differentiated. These species were de-scribed as *S. frymirei* and *S. embreei* (Fig. 7). Fifteen years later, in 1982, a return visit was made to the same guava grove. In the intervening years most of the nearby forest had been cut and converted to pasture. As a result the habitat was

very different, with a much dryer aspect and the remaining guava trees rather old and decrepit. *Scelochilus* was much rarer but ca. 50 plants were located in the remaining guavas. Incredibly, neither *S. embreei* nor *S. frymirei* was present in 1982, but rather two *different* new species were found, later described as *S. gentryi* and *S. romansii*. As in 1957, both of these species, vegetatively indistinguishable, were clearly differentiated from each other by floral characters (Fig. 7). Both of the species present in 1982 are closely related to *S. frymirei*. We suspect that they may represent in situ speciation events, at least in the case of *S. romansii* (*S. gentryi* has also been found in several other localities in western Ecuador). If so, natural speciation in *Scelochilus* can occur in as little as 15 years!

An obvious alternative interpretation is that specific limits in *Scelochilus* are too finely drawn, with *S. gentryi* and *S. romansii* representing part of the intraspecific variability within polytypic *S. frymirei*. However, this possibility seems obviated by the fact that the two co-occurring *Scelochilus* species of 1982 pass the test of sympatry as biologically differentiated populations, even though they are more similar to each other than to their putative ancestor *S. frymirei*. We favor the interpretation that the kind of genetic reorganization that reflects speciation in *Scelochilus,* and presumably other orchids and even some nonorchid epiphytes, is so labile that it can be effected in incredibly short times. If this interpretation is correct, then it is no wonder that many epiphytic taxa have undergone what appears to be truly explosive speciation in the Neotropics. Obviously, it is also possible that *S. gentryi* and *S. romansii* immigrated to the guava grove in question sometime between 1957 and 1982 with *S. frymirei* and *S. embryi* coincidentally becoming locally extinct during the same time interval. But the mere fact that natural speciation in fifteen years seems an equally plausible explanation for these observations is surely significant.

Another line of reasoning also supports the idea that certain neotropical epiphytes have undergone explosive evolution. It is probably safe to assume that, as a general rule and despite many potential exceptions, genera with many species are those which have, on the average, undergone the most rapid speciation. Thus an examination of the largest epiphyte genera might indicate some of the trends, both geographic and ecological, that characterize successful epiphytism. Table 11 lists the 47 largest genera of vascular epiphytes worldwide (those with 90 or more epiphytic species) and provides the data for such an analysis. Again orchids are preeminent. Half (22) of the 47 largest epiphyte genera are orchids. While orchids might appear to be exceptional in their unusual genetic plasticity and highly specific pollination systems, they must unavoidably be regarded as the most successful practitioners of the art of being epiphytic. Biogeographical analysis of the large orchid genera is instructive. Three are pantropical, nine exclusively neotropical, and ten exclusively paleotropical. Even though the number of large neotropical and paleotropical orchid genera is the same, there is a dramatic difference in the number of species that they contain. The nine neotropical genera are far larger, accounting for 5,240 species (average 582 spp. per genus) vs. 2,626 species (average 263) for the ten paleotropical ones.

Ferns account for eight of the largest epiphyte genera. Not surprisingly, in view of their diaspore vagility, nearly all of the large epiphytic fern genera are pantropical, showing little evidence of unusually rapid differentiation or speciation in the Neotropics. Only one fern genus, *Pyrrhosia,* is restricted to the Paleotropics, none to the Neotropics.

The remaining 15 of the largest epiphytic genera are split evenly between dicots and monocots. The two largest dicot genera, *Peperomia* and *Ficus,* are pantropical, although the former, at least, is better represented in the Neotropics; the other largest epiphytic dicot genera are two neotropical gesneriads (*Drymonia* and *Columnea,* sensu lato), two ericads (*Rhododendron* and *Cavendishia*), one each epiphytic in Old and New Worlds, and two melastome genera (*Medinilla* and *Blakea*), restricted respectively to the Old and New Worlds (and extremely similar to each other as well as to another large neotropical genus *Topobea*). In general, there seems a reasonable numerical balance between Old and New World representation in the largest dicot epiphyte genera, except in Gesneriaceae. The situation is very different among the nonorchid monocot epiphytes. Six of the seven largest genera—*Anthurium, Tillandsia, Philodendron, Vriesia, Guzmania,* and *Aechmea*—are exclusively neotropical; only *Rhaphidophora* is paleotropical. Thus the very many species that have evolved among certain monocot epiphyte genera seem a peculiarity of the Neotropics.
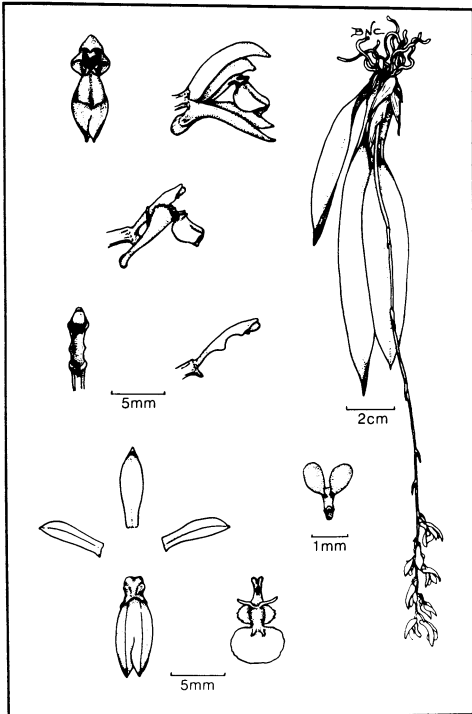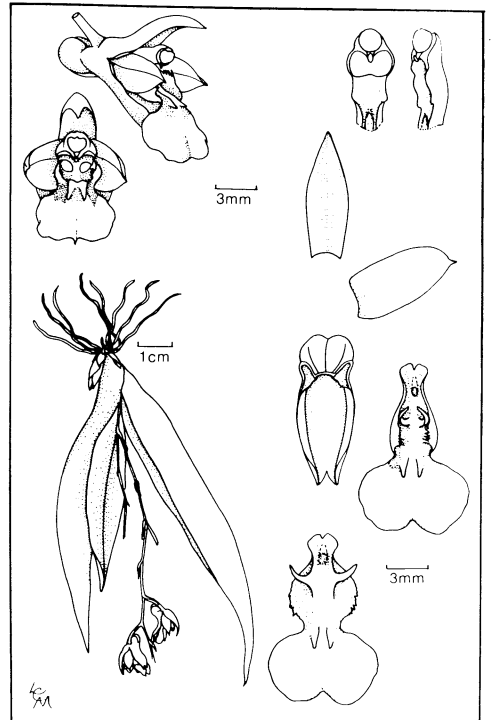
Why have epiphytes been especially suscep-
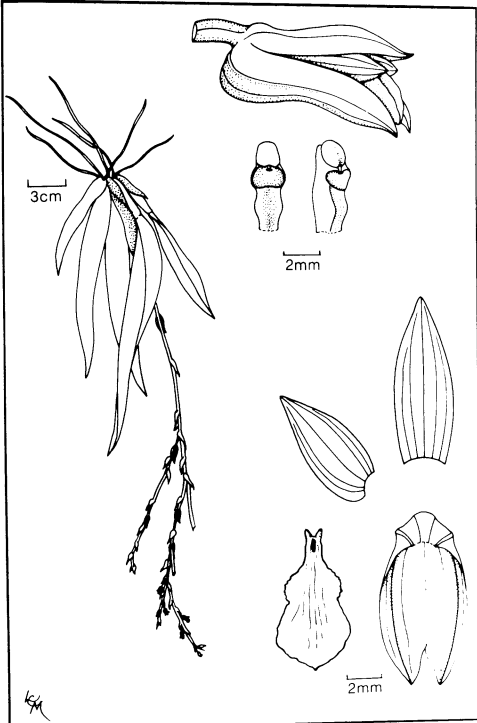
SCELOCHILUS EMBREEI Dodson
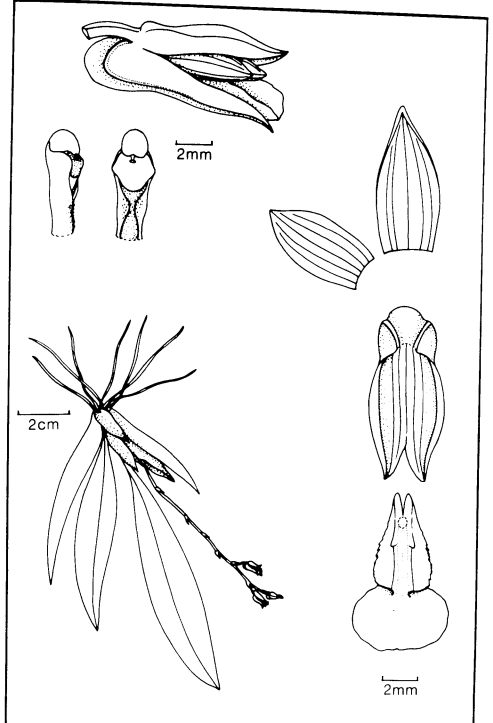
SCELOCHILUS FRYMIREI Dodson

SCELOCHILUS GENTRYI Dodson

SCELOCHILUS ROMANSII Dodson & Garay

tible to the rapid, even explosive, speciation that seems to have characterized a large element of the neotropical flora? At least in the case of orchids, unusually specific pollination systems have clearly played a major role in making possible very active speciation. Like the orchids, the non-orchid epiphyte families that have speciated the most profusely in the northern Andes and southern Central America—Gesneriaceae, Bromeliaceae, Ericaceae, and Araceae—all share, to a greater or lesser extent, relatively specialized pollinators and specific pollination systems as compared with the "average" tree, shrub, or free-climbing liana (e.g., prevalent hummingbird or euglossine pollination). On the other hand the epiphytic taxa that have speciated most profusely are characterized, as a group, by more generalized, higher risk dispersal strategies than typical of other mature forest habit groups. If speciation along the lower slopes of the Andes and in southern Central America typically derives from suboptimal genetic transilience related to multiply replicated founder events in a dynamic and kaleidoscopically changing habitat as Gentry (1982b) suggested, then epiphytes, characterized by their unique combination of r- and k-selected reproductive traits, might be uniquely equipped to react to this adaptive milieu. Like weeds, they have diaspores intrinsically adapted for quick colonization of newly available habitats. In epiphytes, like weeds, the primary need for such adaptation is presumably a response to the short-lived and unstable nature of their normal substrate, a reproductive strategy ideally preadapting epiphytes for rapid speciation in an environment in which the need to recolonize dynamically changing microhabits is unusually frequent. However, unlike weeds whose diversification is generally constrained by overly generalized pollination syndromes (frequently even with loss of sexual recombination), the rich array of specialized pollination systems that characterizes the successful epiphytic taxa would seem to preadapt them for rapid, pollinator-related evolutionary diversification. In this context, it is not likely to be an accident that the preeminently successful epiphytic family, Or-

chidaceae, is precisely that family that has both the most specific pollination systems and the tiniest, most r-selected diaspores of any angiosperm. Moreover, from the viewpoint of "accidental" speciation via founder effect phenomena, the unusual genetic similarity among the potential-colonizer orchid propagules that arrive together at a specific site—due to orchid seeds' unique sharing of fathers as well as mothers, thanks to their pollinia—might be expected to accentuate the potential for genetic drift in colonizing populations. Interestingly, the closest parallel to the postulated rapid speciation among Andean cloud forest epiphytes is found in herbaceous and palmetto taxa that most closely approximate the unique epiphyte combination of specific pollination systems and an r-selected high-risk dispersal mode.

CONCLUSION

Although many unrelated kinds of plants have evolved epiphytic habits, most of these represent isolated species or genera in otherwise terrestrial families. Only three nonfern families—Orchidaceae, Cyclanthaceae, Marcgraviaceae (and possibly also Bromeliaceae)—are predominantly epiphytic. Eighty percent of all vascular epiphytes are concentrated in only four families—Orchidaceae, Bromeliaceae, Polypodiaceae, and Araceae—and 89% in eight families. Very few families have been successful at undergoing extensive radiation as epiphytes. Indeed over two-thirds of all epiphyte species belong to the single family Orchidaceae, and to a large degree understanding epiphytic diversity is synonymous with understanding orchids.

Although notably few families have been very successful as epiphytes, these few taxa have made a tremendous contribution to the diversity of the world's flora. At least 10% of all vascular plant species are epiphytes and in some places epiphytes may constitute a third of all plant species in a local flora or 63% of the individual plants in a given sample area.

Epiphytes have speciated most profusely in the Neotropics, especially in northwest South Amer-

FIGURE 7. Postulated rapid speciation in *Scelochilus.* Top two species were described as new from 1957 collections from guava grove at km. 94 of Guayaquil-Cuenca road. In 1982 they had been replaced by bottom two species, both new and both closely related to *S. frymirei.* (Illustrations from Orchids of Ecuador, Icones Plantarum Tropicarum.)

TABLE 11.   Major epiphyte genera (in part after Madison, 1977; Dressler, 1981; Kress, 1986).

Genus	No. Epiphytic Spp.	Total No. Spp.	Distribution
Pleurothallis	1,520	1,600	Neotropical
Bulbophyllum	1,000	1,000	Pantropical
Dendrobium	900	900	Australasian
Epidendrum	720	800+	Neotropical
Peperomia	700	1,000	Pantropical
Anthurium[1]	600	850	Neotropical
Lepanthes	600	600	Neotropical
Stelis	540	600	Neotropical
Ficus	500	800	Pantropical
Maxillaria	570	600	Neotropical
Eria	500	550	Australasian
Oncidium	475	500	Neotropical
Asplenium	400	650	Pantropical
Tillandsia	400	450	Neotropical
Grammitis	400	400	Pantropical
Philodendron[1]	350	475	Neotropical
Masdevallia	400	400	Neotropical
Medinilla	300+	400+	Paleotropical
Liparis	300	350	Cosmopolitan
Oberonia	300	300	Paleotropical
Odontoglossum	285	300	Neotropical
Columnea (sensu lato)	262	265	Neotropical
Elaphoglossum	250	500	Pantropical
Hymenophyllum	250	300	Pantropical
Angraecum	206	206	Trop. Africa
Lycopodium	200	400	Cosmopolitan
Polystachya	200	210	Pantropical
Ctenopteris	200	200	Pantropical
Vriesia	200	260	Neotropical
Phreatia	190	190	Australasian
Trichomanes	150	300	Pantropical
Polypodium	140	150	Pantropical
Encyclia	130	130	Neotropical
Octomeria	130	130	Neotropical
Taeniophyllum	120	120	Paleotropical, esp. Afr.
Guzmania	120	140	Neotropical
Dendrochilum	120	120	Australasia
Aechmea	120	150	Neotropical
Rhododendron	112	850	Mostly Asian
Coelogyne	100	100	Trop. Asia
Drymonia	100	110	Neotropical
Pyrrosia	100	100	Paleotropical
Rhaphidophora	100	100	Paleotropical
Appendicula	100	100	Australasia
Blakea[2]	98	100	Neotropical
Thrixspermum	90	100	Australasia
Cavendishia[3]	90	100	Neotropical

[1] Croat, pers. comm.
[2] Renner, 1986 and pers. comm.
[3] Luteyn, pers. comm.

ica and southern Central America. The explosive speciation of relatively few epiphyte genera in this region has been responsible to a large extent for the excess floristic diversity of the Neotropics as compared with the Paleotropics.

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APPENDIX I. Changes in data base from epiphyte list in Madison (1977).

Additions

Lycopodiaceae
  Lycopodium (200/450)
Araceae (1,200 species, not 850)
  Anthurium (600/850)
  Philodendron (350/475)
Cyclanthaceae (125 species, not 31)
  Dicranopygium (few/44)
  Evodianthus (1/1)
  Stelestylis (4/4)
Dioscoreaceae
  Dioscorea (1/600) (Ecuador, pers. obs.)
Liliaceae
  Rhodocodon (1/8) (Madagascar, pers. obs.)
Philesiaceae
  Philesia (1/1) (Chile, pers. obs.)
  Luzuriaga (3/3) (Chile, pers. obs.)
Alzateaceae
  Alzatea (1/2)
Anacardiaceae
  Spondias (1/10) (SE Asia, fide Kress)
Apocynaceae
  Mandevilla (1/114) (*M. pittieri,* Costa Rica)
Begoniaceae
  Begonia (40/1,000)
Bignoniaceae
  Gibsoniothamnus (11/11)
  Schlegelia (18/18)
Bombacaceae
  Spirotheca (4/4)
Burseraceae
  Bursera (1/80) (*B. standleyana,* Costa Rica)
Compositae (ca. 30 epiphytic species, not 3)
  Liabum (*Sinclairia*) (2/90)
  Mikania (1/300)
  Neomirandea (20/24)
  Nelsoniothamnus (1/1)
  Pseudogynoxys (1/21)
  Senecio (*Pentacalia*) (5/1,500) (epiphytic in Neotropics, Madagascar, N.Z.)
  Tuberostylis (2/2)

Crassulaceae
  Kalanchoë epiphytic in Madagascar, pers. obs.
Marcgraviaceae (89 epiphytic species, not 94)
  Marcgraviastrum (10/15)
  Marcgravia (ca. 50–55/55)
  Norantea (1/2)
  Ruyschia (7/7)
  Sarcopera (4/10)
  Schwartzia (8/14)
  Souroubea (9/19)
Melastomataceae (567 epiphytic species, not 483)
  The paleotropical genera *Baekeria, Dalenia, Diccochaeta, Neodissochaeta, Omphalopus,* and *Plechiandra* each has at least one hemiepiphytic species fide Renner, 1986.
Myricaceae
  Myrica (1/35) (SE Asia, fide Kress, pers. comm.)
Sapotaceae
  Bumelia (1/60) (Costa Rica, fide Kress, pers. comm.)
Saxifragaceae
  Hydrangea (2/80) (epiphytic in Neotropics)
Solanaceae
  Lycianthes (also epiphytic in Neotropics)

Deletions

Apostasiaceae = Orchidaceae
Dulongiaceae = Saxifragaceae
Bromeliaceae—*Ananas*
Cyclanthaceae—*Carludovica*
Balsaminaceae—*Impatiens* not epiphytic in Neotropics
Bignoniaceae—*Radermachera*
Guttiferae—*Clusia* only occurs in Neotropics
Marcgraviaceae—*Caracasia*
Araliaceae—*Sciadophyllum* = *Schefflera*

Note: Additional occasional or sporadic epiphytes included by Kress (e.g., *Myrrhidendron donnellsmithii, Cyperus, Pseudoeverardia* (= *Everardia*), *Arenaria, Stellaria, Maranta, Pourouma*) are also excluded.