OBLIGATE TWIG EPIPHYTISM IN THE ONCIDIINAE AND OTHER NEOTROPICAL ORCHIDS

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ABSTRACT. Orchid twig epiphytes are diminutive plants that occur on the smallest axes of their hosts. In the neotropics, many of these species are not restricted to twigs and exhibit vegetative features indistinguishable from related taxa that occur on the larger axes, but a small subset of neotropical twig epiphytes have a series of traits unusual in the Orchidaceae. These features probably not only adapt them for the harsh and ephemeral conditions present on the outermost twigs in the canopy but also appear to be responsible for restricting them to these sites. These characteristics include shortened life cycles, psygmoid or leafless habits, seeds with testa extensions, and modified root velamen cells. Although each of these features exists in other orchid groups, they characterize a distinct subset of twig epiphytes, here termed obligate twig epiphytes, in reference to their restricted distribution on a host. Obligate twig epiphytes are a distinct evolutionary phenomenon in the Orchidaceae and are most abundant and diverse outside the center of familial diversity in the Andes of northwestern South America.

The branching system of a canopy tree in tropical forests is the layer most exposed to direct radiation and to temporary desiccation. These environmental conditions are reflected in a vascular epiphyte flora that often is succulent or at least water absorbing and storing in some of their organs. This flora includes epiphytic Apocynaceae, Bromeliaceae, Cactaceae, Crassulaceae, Ericaceae, Melastomataceae, Orchidaceae, and Polypodiaceae, among others (Madison, 1977; Kress, 1986). The unevenness of water availability is probably compensated for by more favorable light conditions. These factors produce two inverse continua, which together create a series of microenvironments that partition the canopy into at least three zones. Each of these zones contains a characteristic subset of the bryophyte (Pócs, 1982) and orchid floras. The latter flora has not been well documented, and its occurrence in the harshest zone is the subject of this report.

These three epiphytic zones are not static, but rather demonstrate a form of succession similar to that of terrestrial sites (Dudgeon, 1923). Vascular epiphytes are most abundant on the larger axes, which are more stable in terms of water fluctuation and longevity. This zone is by far the most important in terms of total surface area and species diversity (Johansson, 1975; Catling et al., 1986).

Smaller axes, divided into high and low light areas, comprise the other two zones. Branches in these categories are one to two years old and 2.5 cm or less in diameter (commonly referred to as "twigs"). These zones are occupied principally by the nonvascular flora (Pócs, 1982). The low light zone is composed of the smaller axes of lianas and shrubs that occur in the lower level of the forest. In the New World, orchid subtribes, such as the Ornithocephalinae and Pleurothallidinae, have specialized in this low light zone composed of twigs. Species from these groups are missing from survey lists when this low light/high humidity zone is absent (Catling et al., 1986). Under the more uniform moisture conditions of cloud and rain forests, these species occur ubiquitously (Chase, pers. obs.).

The high light zone occurs in the outermost portions of the canopy and has, in addition to the highest light, the greatest fluctuation in water availability. On the outermost twigs are found a number of vascular epiphytes restricted to the Orchidaceae in the palaeotropics (subtribes Angraecinae and Sarcanthinae; E. A. Christenson, pers. comm.) and the Bromeliaceae and Orchidaceae in the neotropics (subtribes Angraecinae and Oncidiinae). In contrast to the taxa that occur in the low light zone, these species are restricted to this zone (Catling et al., 1986) and are here termed obligate twig epiphytes. This term is used to distinguish them from those species that occur in the low light zone and which may, under the relaxed water conditions of perpetually wet forests, move onto the twigs in the outer zone as well. The neotropical orchids restricted to the outermost axes of the canopy are the focus of this paper.

CHARACTERISTICS OF NEOTROPICAL, OBLIGATE TWIG EPIPHYTES

Ephemerality

Short life histories are correlated with existence on smaller axes. Dodson and Dressler (1972), Chase (1986a), and Benzing (1987) have
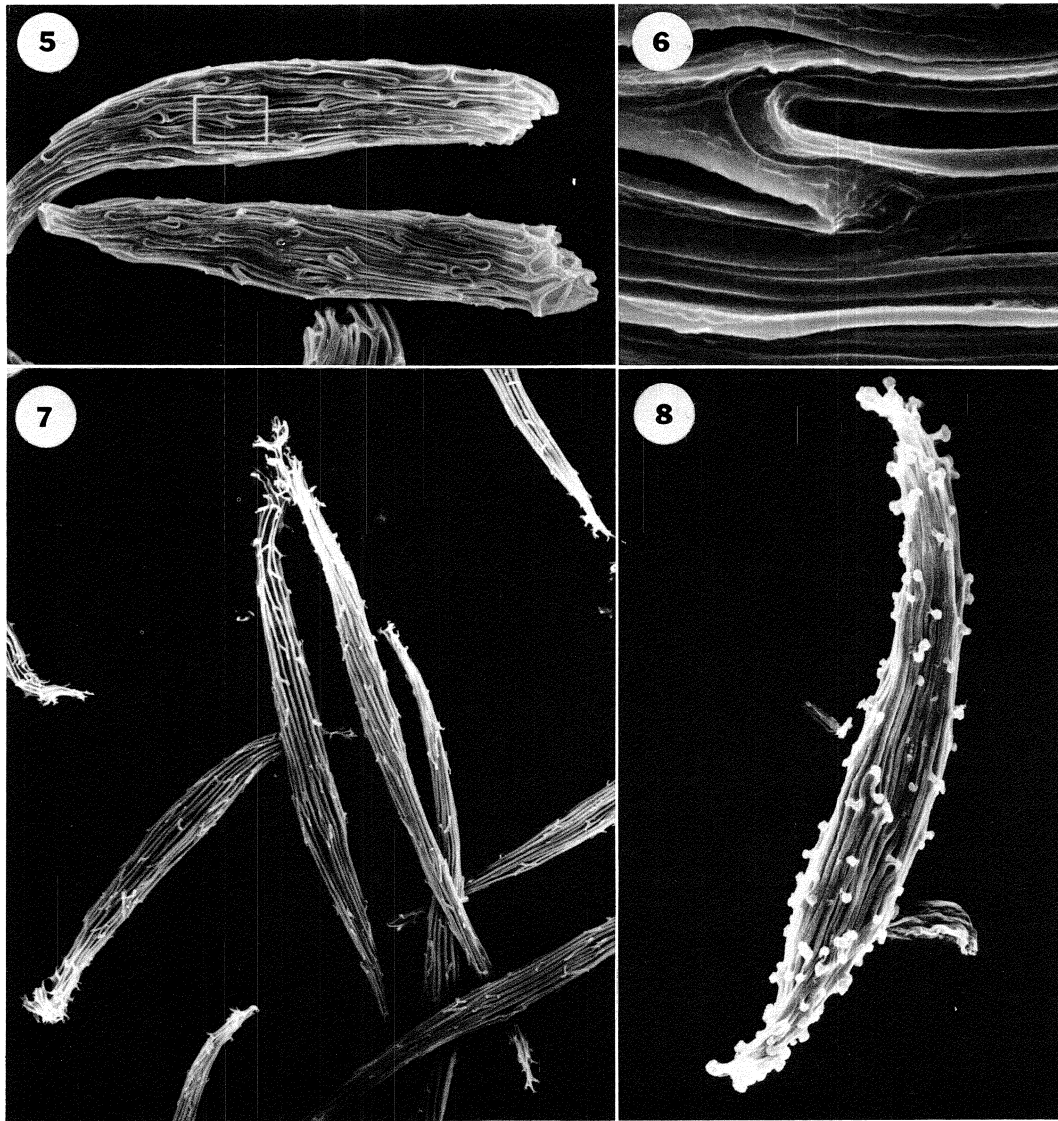
FIGURES 5–8.   Scanning electron micrographs of seeds in the Onciidinae. 5. Seeds of *Oncidium gardneri* (Oncidiinae), typical of seeds of species not confined to the outermost canopy (200×). 6. Details of testa cells from enlarged rectangle in FIGURE 5 (2,000×). The raised anticlinal walls are the most prominent feature of these seeds; the smooth, upper periclinal walls are barely visible. 7. Seeds of obligate twig epiphyte, *Psygmorchis pusilla* (Oncidiinae), with hooked extensions (100×). 8. Seeds of obligate twig epiphyte, *O. variegatum,* with knobbed extensions (180×).

Habit

An association exists between psygmoid form (fan-shaped with laterally flattened, unifacial leaves) and small size. Only rarely does this habit occur in plants larger than 10 cm; an example of such is *Maxillaria valenzuelana* (A. Richard) Nash. Many small-statured plants are not psyg- moid, but nearly all psygmoid plants are small. All oncidioid obligate twig epiphytes have psyg-moid seedlings (FIGURE 1); the smallest retain this habit and become paedomorphic adults (FIGURE 2), while the rest begin to produce pseu-dobulbs and conduplicate leaves (FIGURE 3; the standard habit for the Oncidiinae) as they reach maturity at the end of the first season (Chase,
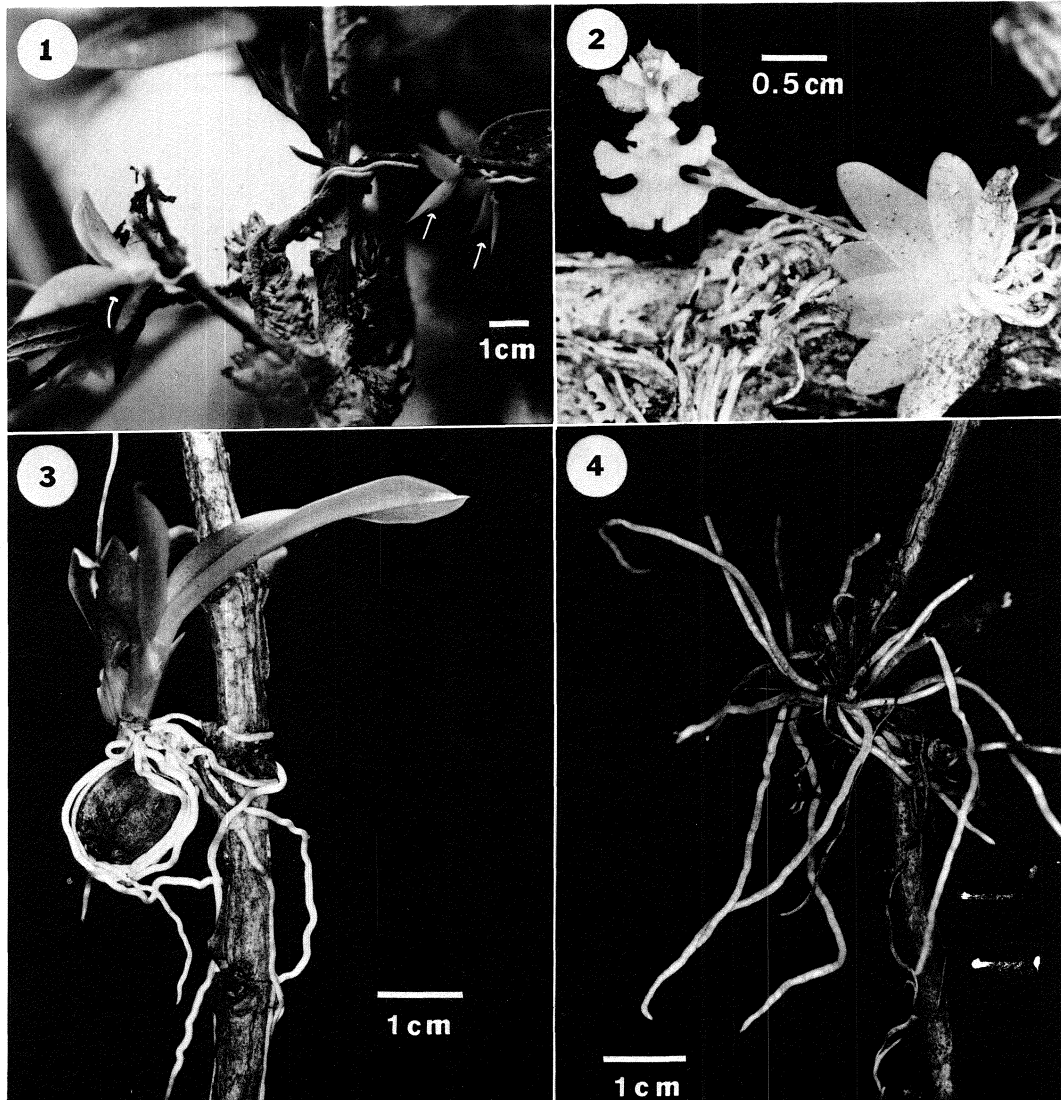
FIGURES 1–4.　Habits of neotropical obligate twig epiphytes. 1. Three psygmoid seedlings (arrows) of *Leochilus labiatus* on *Calliandra*. The seedling on the left is approximately five months old and is beginning the transition to the standard adult habit in the Oncidiinae: conduplicate leaves and pseudobulbs (as in FIGURE 3). 2. One-year-old psygmoid adult of *Psygmorchis pumilio* (Oncidiinae). 3. Two-year-old adult of *L. labiatus* that germinated on and trapped with its roots a coffee bean. 4. Two-year-old leafless adult of *Harrisiella porrecta* (Angraecinae) on *Crataegus*.

cited in *Leochilus* Knowles & Westcott and *Psygmorchis* Dodson & Dressler a rapid development uncharacteristic of epiphytes in general. A continuum of strategies exists even within congeneric species in the Oncidiinae from nearly annual duration in *L. labiatus* (Swartz) Kuntze to long-lived life histories more typical of the bulk of oncidioid species in *L. carinatus* (Knowles & Westcott) Lindley (Chase, 1986a). Even though most oncidioid obligate twig species can persist for several years, nearly all of them mature within the first season of growth. Such rapidity is totally uncharacteristic of bromeliads inhabiting similar depauperate sites. These plants exhibit much slower development and often require five or more years to begin reproducing (Benzing, 1978). Neotropical angraecoid species also develop quickly (Catling et al., 1986; Chase, pers. obs.), i.e., plants may flower on branches less than a year old.
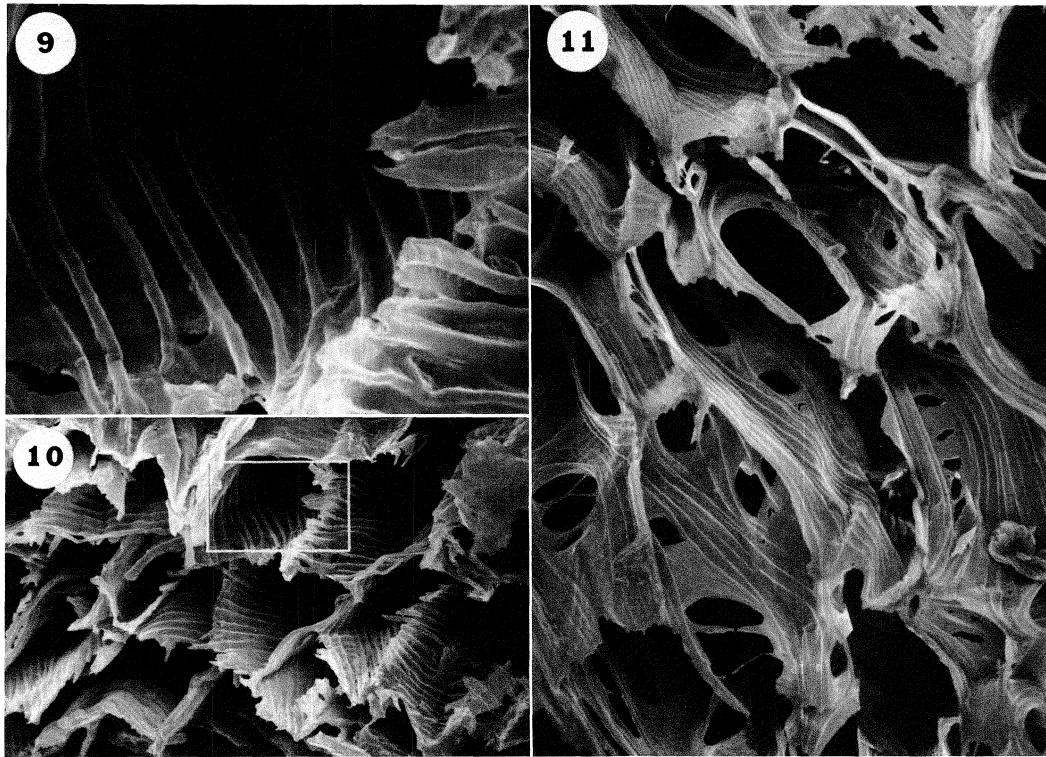
FIGURES 9–11.   Scanning electron micrographs of root velamen in *Leochilus* and *Oncidium* (Oncidiinae). 9. Detail of regular secondary thickenings in a velamen cell of *L. scriptus* (enlarged rectangle in FIGURE 10; 5,000×). 10. Tangential section through the velamen of *L. scriptus*; outer surface is at the top (1,000×). 11. Tangential section through the velamen of *O. stenotis* (500×); outer surface is at the top. Note larger size and highly irregular secondary thickenings.

1986a, 1986b). Obligate twig epiphytes in the Angraecinae mainly exhibit the other neotropical habit type: leaflessness (FIGURE 4). A few, such as *Campylocentrum micranthum* (Lindley) Rolfe, have a more typical habit for their subtribe, but most are leafless. Like the psygmoid habit, however, not all leafless species are obligate twig epiphytes. Instead of occurring on twigs, some leafless species, such as *Polyradicion lindenii* (Lindley) Garay, grow on naked trunks in deep shade (Luer, 1972; Benzing, 1987).

Seed Morphology

Seeds of the more highly evolved vandoid orchids are typically 90–125 μm wide by 300–500 μm long with unsculptured periclinal and anticlinal walls (FIGURES 5, 6; Chase & Pippen, 1988). The seeds of twig dwelling species are uniformly much longer, 650–950 μm, while maintaining the same width as those that occur on larger axes. Another prominent difference is the presence of hooked (FIGURE 7) or knobbed (FIGURE 8) extensions of the testa, especially on the ends of the seeds (Chase & Pippen, 1988).

Velamen Anatomy

A preliminary analysis of root anatomy (Chase, 1986a) demonstrated a different type of root velamen anatomy in the oncidioid obligate twig species. Species inhabiting larger axes have larger, more or less equidimensional velamen cells with uneven secondary thickenings (FIGURES 9, 10), whereas obligate twig species have smaller velamen cells much longer for their width with evenly spaced secondary thickenings (FIGURE 11). This difference is not totally consistent; *Psygmorchis* has the former type of velamen cells. Thus far, the elongate form has been associated with only oncidioid, obligate twig epiphytes. A more extensive survey is needed to investigate velamen anatomy in the Oncidiinae and other subtribes in which obligate twig epiphytes occur.

TABLE 1. Distribution and center of diversity (*) of the genera of larger axes orchids in the Oncidiinae.

	Caribbean/ Mexico	Central America	Non-Andean South America	Andes of NW South America
Ada		X		X*
Amparoa	X	X*		
Aspasia		X	X	X*
Brachtia				X*
Brassia	X	X	X	X*
Caucaea				X*
Cischweinfia		X		X*
Cochlioda				X*
Cuitlauzina	X*			
Dignathe	X*			
Gomesa			X*	
Helcia				X*
Lemboglossum	X*	X		X
Mesoglossum	X*			
Mesospinidium		X		X*
Miltonia			X*	
Miltoniopsis		X	X	X*
Neodryas				X*
Neoescobaria				X*
Odontoglossum				X*
Oliveriana				X*
Oncidium	X	X	X	X*
Osmoglossum	X	X*		
Otoglossum		X	X	X*
Palumbina		X*		
Psychopsis†	X	X	X	X
Rodrigueziella			X*	
Rhyncostele	X*			
Rossioglossum	X*	X		
Rusbyella				X*
Sigmatostalix	X	X	X	X*
Solenidium			X	X*
Symphyglossum				X*
Systeloglossum		X*		X
Ticoglossum		X*		
Trichocentrum	X	X	X	X*
Trichopilia		X	X	X*
Totals	15, 6*	19, 5*	28, 3*	25, 22*

† Widespread genus without an apparent center of diversity.

TABLE 2. Distribution and center of diversity (*) of the genera of obligate twig species in the Oncidiinae.

	Caribbean/ Mexico	Central America	Non-Andean South America	Andes of NW South America
Antillanorchis	X*			
Capanemia			X*	
Comparettia	X	X	X	X*
Cypholoron				X*
Diadenium			X*	X
Erycina	X*			
Goniochilus		X*		
Hirtzia			X*	
Hybochilus		X*		
Ionopsis†	X	X	X	X
Konanzia				X*
Leochilus	X	X*	X	X
Macroclinium	X	X	X*	X
Macradenia	X*	X	X	X
Neokoehleria				X*
Notylia	X	X	X*	X
Oncidium (Variegata group)	X*			
Papperitzia	X*			
Plectrophora			X*	X
Polyotidium			X*	
Pterostemma			X*	
Psygmorchis	X	X	X*	X
Quekettia			X*	
Rodriguezia	X	X	X*	X
Rodrigueziopsis			X*	
Sanderella			X*	
Saundersia			X*	
Scelochilus		X	X	X*
Suarezia			X*	
Trizeuxis†	X	X	X	X
Warmingia			X*	
Totals‡	18, 5*	12, 3*	27, 12*	16, 5*

† Widespread genus without an apparent center of diversity.

‡ Significantly different in overall distribution (χ^2 = 4.81; 0.05 < P < 0.20) and centers of diversity (χ^2 = 57.09; $P \ll 0.01$) than totals for genera in TABLE 1.

ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

While the list of differences between obligate twig orchids and their relatives on the larger axes is not extensive, the variable features are significant in terms of the adaptive radiation of orchids into epiphytic habitats (e.g., root velamen and seed morphology) or the ephemeral and harsh habitat in which obligate twig epiphytes exist (i.e., rapid life histories and psygmoid/leafless habits).

Also evident is the fact that no single one of the characteristics described above can serve independently to identify a species as an obligate twig epiphyte. In parallel with the occurrence of nearly all "epiphytic" features in nonorchidaceous, terrestrial taxa (Benzing, 1986, 1987), each of these features occurs in species that grow on larger axes. These traits also appear to have evolved independently a number of times in the Orchidaceae. For example, the psygmoid habit occurs in species of *Bolusiella* Schlechter (Aerangidinae), *Maxillaria* Ruiz & Pavón (Maxillariinae), *Oberonia* Lindley (Malaxideae), and *Ornithocephalus* Hooker (Ornithocephalinae), none of which are obligate twig epiphytes although they all are diminutive plants.

The most consistent morphological characteristic identifying a species as an obligate twig epiphyte is elongate seeds with testa extensions. No obligate twig epiphyte has yet been found to lack this type of seed, including palaeotropical species (E. A. Christenson, pers. comm.; Chase & Pippen, unpubl.). The extensions on the seeds of twig epiphytes appear to be modifications for clinging to the smoother axes of twigs. However, at the sizes of most orchid seeds the forces of surface attraction are probably far more important in this regard than any specific surface feature. The hooked seed morphology increases the surface area of the seeds substantially (in addition to their increased length relative to species of the larger axes) and permits a more rapid uptake of water that is available for shorter periods on twigs than on larger and less exposed axes. The presence of hooked seeds in species that inhabit larger but naked axes (e.g., *Polyradicion lindenii*) supports the water-uptake hypothesis. The differences in seed structure may also affect their aerodynamics (J. D. Ackerman, pers. comm.).

The shortened life histories of obligate twig epiphytes clearly are a necessary specialization for the ephemeral nature of their habitat. Twigs are either shed or become larger axes, in which case they are no longer suitable substrates for obligate twig epiphytes. Likewise their unusual habits could easily be seen as modifications for the extreme conditions of exposure at the tips of the canopy. The psygmoid and leafless habits are perhaps more efficient ways for small plants to deal with water/surface area relations than are standard habits, which have more elongate growths with bifacial, dorsiventrally flattened plicate or conduplicate leaves (Chase, 1986a). Such hypotheses are difficult to test except by correlation.

While some of the features described above may be responsible for permitting germination and establishment on small branches, other factors are responsible for restricting them to these sites. Catling and co-workers (1986) identified a phenomenon among obligate twig epiphytes that is perhaps illuminating with regard to the factor(s) responsible for their absence from other sites. In a grapefruit orchard which they surveyed, trees were of only three age classes: 13-, 20-, and 30-year-olds. Branches of less than 2.5 cm in diameter on 13- and 20-year-old trees were heavily populated by obligate twig orchids (species from both the Angraecinae and Oncidiinae) but became less suitable sites on 30-year-old trees. These species declined without replacement by other orchids. The surveyors noted a well developed nonvascular flora that was absent from these same sized branches on smaller trees. The appearance of bryophytes and lichens was a result of an increase in humidity associated with closing of the canopy in these older trees. Under natural conditions in undisturbed primary forest, twig species are present only on the uppermost branches of the canopy, and they are not numerous even there (Chase, 1986a). The younger grapefruit trees were an ideal habitat: high light and low humidity. As the trees grew, their crowns began to interdigitate, and more humidity caused the decline of the twig species. Benzing (1981) found that twig-adapted *Tillandsia* seedlings experienced higher mortality with long periods of moistness. A similar process could account for the restriction of obligate twig species to axes that do not experience prolonged, moist periods.

Another unusual aspect of the genera of obligate twig epiphytes in the Oncidiinae is their geographical distribution and centers of diversity. Neotropical orchids are most diverse in the Andes of northwest South America (Dressler, 1981), and most of these genera have their center of diversity in that same region. This is true of the oncidioid genera that inhabit the larger axes as well (TABLE 1). A secondary center of diversity occurs in the mountains of Costa Rica and western Panama in Central America (TABLE 1). Oncidioid obligate twig epiphytes are significantly more diverse ($x^2 = 4.81$; $0.05 < P < 0.20$) away from these centers of family and subtribal diversity (TABLE 2), and most of these genera have their center of diversity outside the Andes ($x^2 = 57.09$; $P \ll 0.01$). If present distributions and centers of diversity are indicative of origin and habitats conducive to speciational activity, then obligate twig epiphytism has had a different evolutionary history than the major lines of neotropical Orchidaceae. Obligate twig epiphytes are particularly depauperate in the Andes where other lineages are most diverse.

CONCLUSION

One purpose of this report is to suggest that precision be used in categorizing twig epiphytes. Obligate twig epiphytes are restricted to the outermost axes and exhibit several modifications for the extreme conditions encountered there (although the exact functions of these modifications have not been demonstrated). This definition differentiates between obligate twig epiphytes and other small, vascular epiphytes that can occupy twigs in the outermost canopy under more humid conditions. The most definitive aspect of other classes of epiphytes that may occasionally inhabit twigs is that they are not restricted to the sites, and, when they do occur on the smaller branches, they are ubiquitous and have the same life histories and morphological features as their relatives confined to the larger axes.

The second purpose of this report is to focus attention on obligate twig epiphytes as subjects for further research. They have a series of morphological and physiological traits that serve to distinguish them from other epiphytes. If the adaptive value of these features can be understood, insights may be provided on the adaptive value of the features of taxa inhabiting other epiphytic sites. Obligate twig epiphytes are an enigma: they exist under one of the harshest and most depauperate sets of environmental conditions known among vascular plants, yet they have incredibly rapid life histories. This pattern alone makes them worthy of attention because it marks them as an extreme example of morphological and physiological modification.

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