

## Origin of High-Elevation *Dendrochilum* Species (Orchidaceae) Endemic to Mount Kinabalu, Sabah, Malaysia

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**ABSTRACT.** Mount Kinabalu, (Sabah, Malaysia) is the youngest (ca. 1.5 million yrs old) and highest (4,095 m) mountain between the Himalayas and Irian Jaya, Indonesia. Because of this combination of youth and isolation, considerable mystery surrounds the origins of its high elevation endemics. We chose a group of high-elevation species from *Dendrochilum* subgen. *Platyclinis* sect. *Eurybrachium* to begin an investigation of the origin(s) of endemism on Mount Kinabalu. We tested biogeographic hypotheses that the Kinabalu endemics arose from ancestors in: 1) the high mountains of Sumatra, 2) the high mountains of Mindanao, Philippines, and 3) lower elevations on Mount Kinabalu or elsewhere in Borneo. Using phylogenetic patterns predicted by the three competing hypotheses, we evaluated which had the highest support in a likelihood framework. Based on analyses of ITS 1 and ITS 2 sequence variation in *Dendrochilum*, we rejected hypotheses that the Kinabalu high-elevation endemics arose from ancestors in other high mountains of southeast Asia (Sumatra or the Philippines), and tentatively accepted their origin from lower elevation ancestors in Borneo. The origin of high-elevation endemics from lower elevation Bornean ancestors appears to be a general mode of evolution for many species on Mount Kinabalu.

Mount Kinabalu, a granitic batholith in northern Borneo, (Sabah, Malaysia) has attracted the attention of botanists since 1894 because of its diverse flora with remote geographic relationships. Early researchers, like Stapf (1894), were fascinated to find representatives of plant genera such as *Ranunculus* (Ranunculaceae) and *Potentilla* (Rosaceae), common in temperate regions of Europe, on the top of this tropical southeast Asian mountain. Floristic affinities with regions as disparate as the Himalayas and Australia-Antarctica further enhance the mystery surrounding the origins of endemic plant species occurring on Mount Kinabalu today. A consideration of the geographic and geologic setting of Mount Kinabalu highlights the dilemma that the flora of the mountain poses to phytogeographers.

Mount Kinabalu (4,095 m) towers above the surrounding terrain reaching a height approximately 1,500 m above any other peak on Borneo. The nearest mountains over 2,900 m in elevation are otherwise found on Java, Sulawesi, Sumatra, and Mindanao (Smith 1980, 1986). This geographical isolation makes Mount Kinabalu a virtual high-elevation "island" surrounded not only by true seas (South China and Sulu) but also by "seas" of lower montane and lowland forest, which serve to isolate it from comparable habitat by at least 900 km (Fig. 1).

Mount Kinabalu is a geologically young mountain formed by the intrusion and uplift of the gra-

nitic batholith that comprises its core (Collenette 1964; Roe 1964; Jacobson 1970; Choi 1996). Although intrusion of the core is suggested to have begun within the last nine million years, uplift to its current height is thought to have occurred only within the last 1.5 million years. This recent formation makes Mount Kinabalu the youngest mountain within Southeast Asia higher than 3,000 m (Fitch 1964; Jacobson 1970; Hamilton 1979). Further, the highest elevation habitats now available for colonization were covered by an ice cap during the Pleistocene (Koopmans and Stauffer 1967; Wood and Lamb 1994).

**Botanical Setting.** Although formal treatments are not completed, it is estimated that Mount Kinabalu possesses a flora of approximately 5,000–6,000 vascular plant species (J. H. Beaman, pers. comm.) with a high level of endemism, particularly at high elevations. For example, there is a 10:1 ratio of endemic:non-endemic orchid species found on Mount Kinabalu at elevations above 2,700 m (Wood et al. 1993). Because Mount Kinabalu is the most recently formed high mountain in southeast Asia, high elevation endemic species are assumed to be newly evolved there (Beaman and Beaman 1990).

A framework for analyzing Mount Kinabalu plant geographic distributions established by van Steenis (1964) and Stapf (1894) was based on the assumption that certain endemic species are centric,

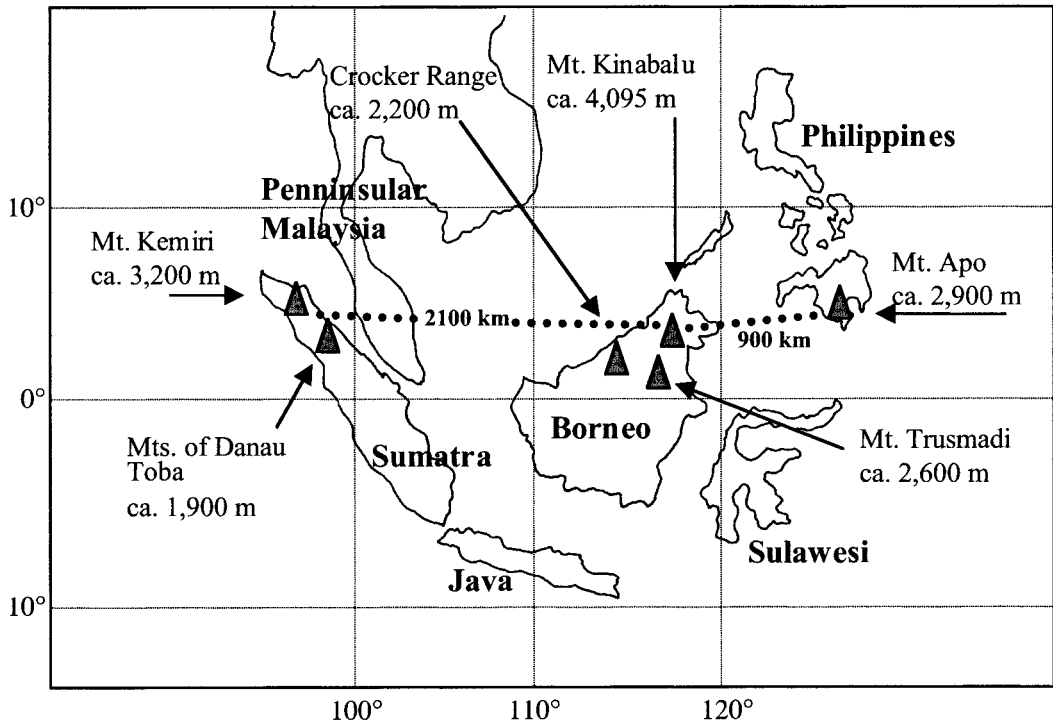


FIG. 1. Map of Southeast Asia showing Mount Kinabalu; the youngest and highest mountain in the region. Some of the nearest high mountains are found in the Philippines and Sumatra. Approximate altitude of each mountain or range is given in meters above sea level. Approximate distances between Mount Kinabalu and other high mountains are given in kilometers (Adapted from van Steenis 1964).

having evolved in situ, while others are eccentric in origin, having "migrated from remote centres of development" (van Steenis 1964 p. 8). In spite of the wide separation of other high mountains from Mount Kinabalu, van Steenis (1964) suggested that it has intimate montane floristic relations with Sumatra and various islands of the Philippines. In addition to floristic donations from outside areas, van Steenis thought that a considerable portion of the endemic montane flora may have been derived in situ. He hypothesized that many species were derived from pre-existing Bornean montane species or from lower elevation congeners (van Steenis 1964). Below, we investigate these biogeographic hypotheses using a small group of high elevation *Dendrochilum* (Orchidaceae) species.

The genus *Dendrochilum* is particularly diverse on Mount Kinabalu, where 34 species may be found growing as epiphytes, lithophytes, and terrestrials at elevations ranging from ca. 600–3,700 m (Wood et al. 1993). While no comprehensive monograph for *Dendrochilum* has been produced, a recent ge-

neric subdivision by Pedersen et al. (1997) resulted in the definition of four subgenera and 13 sections. Subgenera *Acoridium* and *Pseudoacorioidium* are almost completely comprised of Philippine species while subgenus *Dendrochilum* is restricted to Malaysia and Indonesia (with the exception of one widespread species). The remaining and largest subgenus, *Platyclinis*, is comprised of species distributed throughout the Philippines, Indonesia, and Malaysia. Its highest level of diversity is in Borneo where 77 out of 193 species are found. The Bornean center of diversity of subgenus *Platyclinis*, measured in terms of species numbers, is Mount Kinabalu where 32 species occur, all belonging to sections *Platyclinis*, *Cruciformia*, and *Eurybrachium*. Although placed in the same subgenus, floral morphology differs substantially between these sections. Illustrated in Fig. 2 are representative column, stelia (column arms), and labellum morphologies of representative members of subgenus *Platyclinis* sections *Eurybrachium*, *Platyclinis*, *Cruciformia*, and *Mammosa*. The primary distinguishing

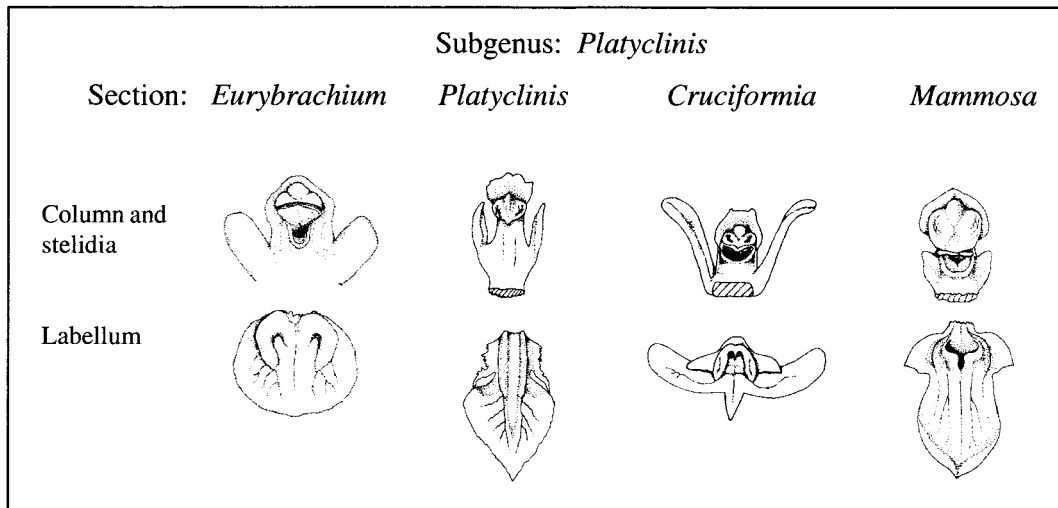


FIG. 2. Comparison of column and labellum morphologies for *Dendrochilum* subgen. *Platyclinis* sect. *Eurybrachium*, *Platyclinis*, *Cruciformia*, and *Mammosa* (Pedersen et al. 1997). Major differences between the sections include the number and shape of labellum lobes, if present, and the shape and position of column arms (stelidia).

features of these sections include the number and shape of labellum lobes (if present) and relative shape, length, and position of stelidia.

The biogeographic study described below focused on members of *Dendrochilum* subgen. *Platyclinis* section *Eurybrachium* for two reasons. First, *Eurybrachium* species are particularly interesting because all 10 species found on Mount Kinabalu are endemic and mostly found at high elevations (Wood et al. 1993; Pedersen et al. 1997). Second, a small group of the Kinabalu members of section *Eurybrachium* appear to be closely related because most of them share a suite of unique covarying characters (e.g., a short broad column with basal, broad, rounded stelidia and a labellum that is unlobed, and usually as broad as long; Fig. 2). Carr (1935) originally circumscribed an informal group based on this covarying suite of morphological features that was restricted to eight Bornean species. More recently, Pedersen et al. (1997), described section *Eurybrachium*, which included Carr's (1935) informal group, in addition to 62 other morphologically diverse species. While 11 out of 15 Bornean species of section *Eurybrachium* share these characters, others placed within this section have lateral labellum lobes, with elongate stelidia (reminiscent of section *Platyclinis*) indicating that the entire section may not be monophyletic.

This suite of floral morphological features (short, broad stelidia and unlobed labellum) is found in

few *Eurybrachium* taxa outside of Borneo but some species from the Philippines, Sumatra, and lower elevation areas in Borneo appear relatively similar as shown in Fig. 3. Because the taxa of Fig. 3 all have rather short broad stelidia and an unlobed labellum, we hypothesized that the Kinabalu high elevation endemics could share a most recent common ancestor with species in any of these three areas (as suggested by van Steenis [1964] for Kinabalu endemics in general). Our goal in this paper is to discern whether the Kinabalu *Dendrochilum* endemics arose from ancestors in: 1) the high mountains of Sumatra, 2) the high mountains of Mindanao, Philippines, and 3) lower elevations on Mount Kinabalu or elsewhere in Borneo. Below we investigate these biogeographic hypotheses in a molecular phylogenetic framework using sequence variation from the internal transcribed spacer regions (ITS 1 and ITS 2) of the nuclear rDNA loci.

#### MATERIALS AND METHODS

**Species Sampling.** In total, 27 *Dendrochilum* taxa were sampled from Borneo, the Philippines, and Sumatra (Table 1). These taxa belong to the three main sections of subgenus *Platyclinis* as circumscribed by Pedersen et al. (1997). In addition, one member of the closely related genus, *Pholidota*, was used as an outgroup for phylogenetic estimates. In this paper, we focused on the origins of a small

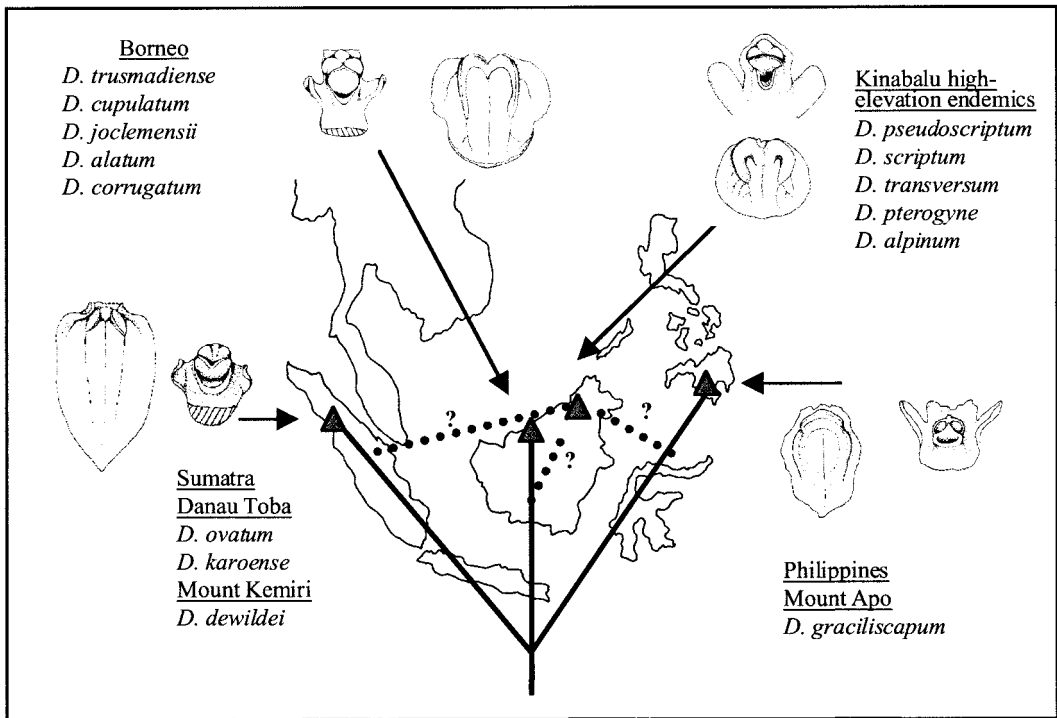


FIG. 3. Hypothesized relationships of Kinabalu high elevation endemic *Dendrochilum* species to species found elsewhere in Borneo, Sumatra, and the Philippines. The species listed in this figure have a shared covarying suite of morphological features including an unlobed labellum and short, broad, basal steldia. The hypothesized relationships (represented by dotted lines) will be evaluated in a phylogenetic context below.

group of Kinabalu high elevation endemics that Carr (1935) suggested were closely related. This includes *D. scriptum*, *D. transversum*, *D. pterogyne*, *D. pseudoscriptum*, and *D. alpinum*. Although other Kinabalu high elevation endemics have been referred to Pedersen et al.'s (1997) section *Eurybrachium* (specifically *D. stachyodes* and *D. acuíferum*), we restricted our tests to this subset of five taxa due to their overwhelming morphological similarity that suggests they may be monophyletic. For our tests of a Philippine or a Sumatran origin, we sampled *D. graciliscapum* from Mount Apo, Philippines, *D. ovatum*, and *D. karoense* from the mountains of Sumatra surrounding Danau Toba, and *D. dewildei* from Mount Kemiri, Sumatra. These Philippine and Sumatran taxa were hypothesized to be close relatives of the Kinabalu endemics because: 1) they have a relatively similar floral and vegetative morphology (Fig. 3), 2) they are all placed in section *Eurybrachium* by Pedersen et al. (1997), and 3) they grow in similar habitats. To investigate the hypothesis of a Bornean origin, we sampled three Bornean species

from section *Eurybrachium* that are endemic to lower elevations on Mount Kinabalu, *D. alatum*, *D. corrugatum*, and *D. joclemensii*. Two additional putative Bornean relatives *D. trusmadiense* and *D. cupulatum*, were sampled from Mount Trus Madi and the Crocker Range respectively.

**Total DNA Extraction.** Total cellular DNA was extracted primarily from field collected fresh leaf material of single individuals in the phytochemistry laboratory at Kinabalu Park, Sabah, Malaysia following the protocol of Doyle and Doyle (1987). When liquid nitrogen was not available for pulverizing leaf tissue we either froze the tissue in a  $-20^{\circ}$  freezer before grinding or simply ground the leaf tissue in hot 2xCTAB. Leaves were cut into small pieces before grinding in order to enhance the break-up of the highly sclerified tissue of certain species. In some cases, DNA was obtained from silica gel-dried material according to the protocol of Chase and Hills (1991).

**Molecular Methods.** The Polymerase Chain Reaction (PCR) was performed using standard con-

TABLE 1. Species sampled from Borneo, Sumatra, and the Philippines listed by taxonomic section (Pedersen et al. 1997) followed by voucher number and GenBank accession numbers for DNA sequences of ITS 1 and ITS 2. All specimens are deposited at Sabah Parks Herbarium, Sabah Parks, Sabah, Malaysia. *Dendrochilum muluense* was cultivated in the Mountain Garden on Sinsuron Road, Sabah, Malaysia. *Dendrochilum glumaceum* and *D. cobbianum* are cultivated at the University of Texas, Austin. *Dendrochilum dewindtianum* (-M) and *D. pseudoscriptum* had identical ITS sequences to *D. dewindtianum* (-H) and *D. scriptum* respectively.

	Voucher	ITS 1	ITS 2
<b>Borneo:</b>			
<i>Dendrochilum</i> subgenus <i>Platyclinis</i> section <i>Eurybrachium</i>			
<i>D. alatum</i> Ames	TJB 137	AF076708	AF076746
<i>D. alpinum</i> Carr	TJB 142	AF076697	AF076735
<i>D. corrugatum</i> (Ridl.) J. J. Sm.	TJB 11	AF076696	AF076734
<i>D. cupulatum</i> J. J. Wood	TJB 228	AF076707	AF076745
<i>D. joclemensii</i> Ames	TJB 261	AF076710	AF076748
<i>D. pseudoscriptum</i> T. J. Barkman & J. J. Wood	TJB 16	AF315840	AF315842
<i>D. pterogyne</i> Carr	TJB 2	AF076698	AF076736
<i>D. scriptum</i> Carr	TJB 9	AF076695	AF076733
<i>D. transversum</i> Carr	TJB 95	AF076694	AF076732
<i>D. trusmadiense</i> J. J. Wood	TJB 154	AF076700	AF076738
<i>Dendrochilum</i> subgenus <i>Platyclinis</i> section <i>Cruciformia</i>			
<i>D. exasperatum</i> Ames	TJB 212	AF076713	AF076751
<i>D. gibbsae</i> Rolfe in Gibbs	TJB 51	AF076720	AF076758
<i>D. grandiflorum</i> (Ridl.) J. J. Sm.	TJB 10	AF076702	AF076740
<i>D. haslamii</i> Ames	TJB 17	AF076704	AF076742
<i>Dendrochilum</i> subgenus <i>Platyclinis</i> section <i>Platyclinis</i>			
<i>D. dewindtianum</i> (-H) W. W. Sm.	TJB 1	AF076706	AF076744
<i>D. dewindtianum</i> (-M) W. W. Sm.	TJB 267	AF315841	AF315843
<i>D. kamborangense</i> Ames	TJB 64	AF076705	AF076743
<i>D. muluense</i> J. J. Wood	TJB 349	AF076703	AF076741
<i>D. tenompokense</i> Carr	TJB 262	AF076715	AF076753
<b>SUMATRA:</b>			
<i>Dendrochilum</i> subgenus <i>Platyclinis</i> section <i>Eurybrachium</i>			
<i>D. dewildei</i> J. J. Wood & J. B. Comber	TJB 324	AF076721	AF076759
<i>D. karoense</i> J. J. Wood	TJB 326	AF076726	AF076764
<i>D. oxatum</i> J. J. Sm.	TJB 325	AF076727	AF076765
<b>PHILIPPINES:</b>			
<i>Dendrochilum</i> subgenus <i>Platyclinis</i> section <i>Eurybrachium</i>			
<i>D. graciliscapum</i> (Ames) Pfitz.	TJB 329	AF076719	AF076757
<i>Dendrochilum</i> subgenus <i>Platyclinis</i> section <i>Platyclinis</i>			
<i>D. glumaceum</i> Lindl.	TJB 350	AF076712	AF076750
<i>D. cobbianum</i> Rchb.f.	TJB 348	AF076716	AF076754
<i>D. arachnites</i> Rchb.f.	TJB 330	AF076725	AF076763
<b>Outgroup</b>			
<i>Pholidota clemensii</i> Ames	TJB 45	AF076730	AF076768

ditions to amplify the entire nrDNA ITS region using primers P1A (Barkman 1998) and P4 (Baldwin et al. 1995). PCR protocols and cycling conditions are available from the authors upon request.

Manual sequencing followed dideoxy chain ter-

mination reaction procedures using the Sequenase protocol (U.S. Biochemical). This protocol was modified to incorporate the snap-chill method of Winship (1989). Both strands of ITS 1 and 2 were sequenced using the two PCR primers in conjunction

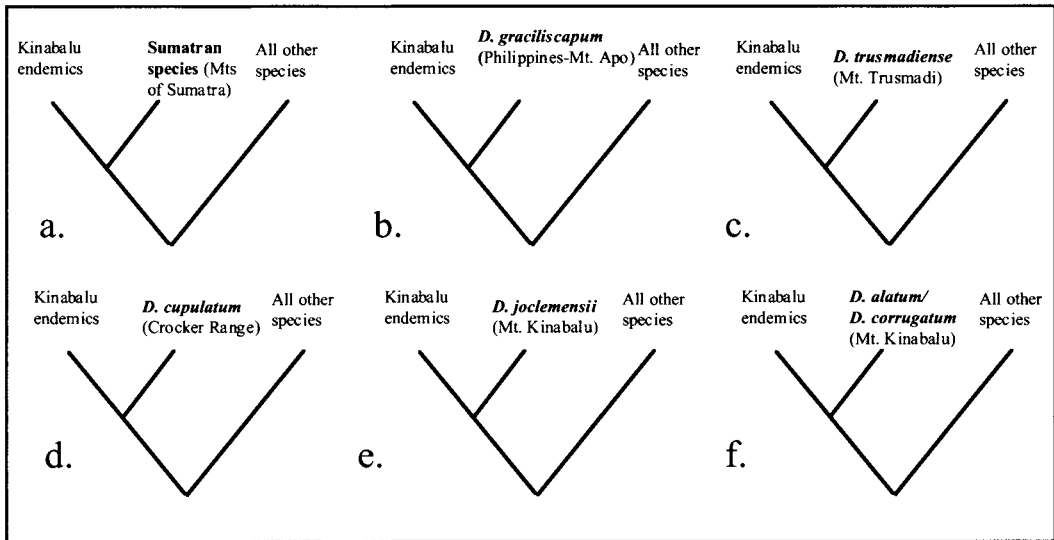


FIG. 4. Constraint trees used to test hypotheses of a Sumatran (a), Philippine (b), and Bornean origin (c-f) for Kinabalu high elevation *Dendrochilum* endemics.

with P2 and P3 (Baldwin et al. 1995). Although we amplified the intervening 5.8S region it was not sequenced.

**Phylogenetic Analyses.** Sequences were aligned by eye and analyzed by maximum likelihood using PAUP\*4.0d64 (Swofford 1997). Gaps were treated as missing data for phylogenetic analyses. The aligned sequences used for all analyses are available from <http://www.biosci.utexas.edu/IB/people/simpson/Dmatrix.doc>. Missing data were coded as "?" and comprised only 0.002% of the total data matrix. For the results presented below, the F81 model of nucleotide substitution was used (Felsenstein 1981). Alternative nucleotide substitution models (HKY) and methods (neighbor joining and maximum parsimony) were used but the results were similar in all cases and did not affect the conclusions reached (data not shown). Heuristic searches were performed with 10 random addition sequences and TBR swapping. Bootstrapping (Felsenstein 1985) was performed using 500 pseudoreplicated data sets with the same model used in the original search.

**Biogeographic Hypothesis Testing.** Several constraint topologies (Fig. 4) were used to represent the biogeographic hypotheses to be evaluated. To investigate whether the Kinabalu *Dendrochilum* endemics arose from high elevation ancestors outside of Borneo, we hypothesized that they share an ancestor with species now found on Mount Kemiri

(Leuser) and Danau Toba in Sumatra (Fig. 4a) or Mount Apo in the Philippines (Fig. 4b). To investigate whether the Kinabalu endemics evolved in situ, we hypothesized that they arose from lower elevation ancestors either on Mount Kinabalu or elsewhere in Borneo. Figures 4c, d, e, and f show the expected branching patterns if the Kinabalu endemics arose in situ using species from lower elevations in Borneo.

The support scores of constraint topologies representing the Bornean, Philippine, and Sumatran origin hypotheses were compared to a topology estimated in an unconstrained search using the Kishino-Hasegawa test (Kishino and Hasegawa 1989). The Kishino-Hasegawa (K-H) test as implemented in PAUP\*4.0d64 uses the mean and variance of maximum likelihood support score differences between the competing trees to assess significance. In this study we performed multiple tests on the same data and therefore used sequential Bonferroni corrections to avoid inflated type I error without sacrificing power (Rice 1989, 1990).

**Inference of Ancestral Elevational Range.** In order to infer the elevational range of ancestors on the optimally estimated topology, a continuous-valued character representing the mean elevation at which each extant taxon is distributed was defined using MacClade 3.07 (Maddison and Maddison 1997). Ancestral states were then reconstructed by

minimizing the sum of squared changes on the rooted topology.

## RESULTS

Unconstrained maximum likelihood analyses of the 28 ITS 1 and ITS 2 sequences resulted in a single tree with a score  $\ln L = -1947.13902$  (Fig. 5). Although the molecular systematics of *Dendrochilum* is the topic of a separate paper (Barkman and Simpson, in prep) a few interesting results will be mentioned here. The monophyly of species placed in sections *Platyclinis*, *Eurybrachium*, or *Cruciformia* was not supported in these analyses (Fig. 5). Instead, it appears that geography may be a better predictor of relationships than the floral or vegetative morphology used to delimit the three sections (Fig. 5). Although the three sections were not monophyletic, several previously proposed relationships were supported. Most notably, the results supported the monophyly of a group of species identified by Carr (1935) as closely related (*D. alpinum*, *D. pterogyne*, *D. scriptum*, *D. transversum*, and *D. pseudoscriptum* [not known to Carr]). It is not clear if two other species, *D. alatum* and *D. corrugatum*, are allied to this lineage based on these data alone. *Dendrochilum gibbsae*, *D. haslamii*, and *D. exasperatum* appear closely related in all our analyses as suggested by Ames (1920) and Carr (1935). Another species placed within this section by Pedersen et al. (1997), *D. grandiflorum* does not appear to be closely related to this group, however. The widespread *D. dewindtianum* appears to be closely related to *D. tenompokense* supporting the earlier suggestion of Carr (1935).

Three constraint analyses produced tree estimates that were not significantly worse than the unconstrained analysis as shown in Table 2. In fact, the constraint topology that forced the two mid-elevation Bornean species, *D. corrugatum* + *D. alatum*, to be sister to the high elevation endemics (Fig. 4f) had the same level of support as the unconstrained topology. The constraint trees forcing either of the mid-elevation Bornean species, *D. cupulatum* (Fig. 4d) or *D. trusmadiense* (Fig. 4c), to be sister to the Kinabalu high elevation endemics had poorer support (but not significant at  $P < 0.05$ ) than the unconstrained tree estimate. In contrast, there is little evidence supporting close relationships between the Kinabalu endemics and species found in either Philippines or Sumatra. In addition, there is no support for a close relationship of the Bornean species, *D. joclemensii*, with the high-ele-

vation endemics in spite of a relatively similar floral morphology.

## DISCUSSION

**High Elevation Colonization.** We infer that the Kinabalu high elevation endemic *Dendrochilum* species (referable to Carr's informal group) are centric, having evolved in situ (on or near Mount Kinabalu), and belong to a single lineage. The data suggest that species occurring at lower elevations on Mount Kinabalu, Mount Trus Madi or the Crocker Range are the closest relatives of the high elevation endemics. However, a lack of resolution of branching relationships prohibits certain identification of the closest relatives. Morphological evidence suggests that *D. alatum* and *D. corrugatum* are the closest relatives (Carr 1935). If indeed these lower elevation species are the sister taxa to the endemics, then it would seem that the high elevation taxa arose on Mount Kinabalu. Alternatively, if *D. trusmadiense* or *D. cupulatum* are the closest relatives of the endemics, then their origin was also in situ. *Dendrochilum trusmadiense* is endemic to Mount Trus Madi (ca. 2,600 m) and *D. cupulatum* is found largely in the Crocker Range. Both of these mountains are older than Mount Kinabalu and geographically close to it. Mount Trus Madi is only 60 km away from Mount Kinabalu and the Crocker Range is largely contiguous with Mount Kinabalu, although ridges above 2,000 m are at least 20 km distant. While we conclude that the endemics arose on or near Kinabalu, we make no assumption about dispersal or vicariance because the geographic distribution of the ancestor is unknown.

A local origin of the Mount Kinabalu high elevation endemics is compatible with van Steenis' notion (1964) that many montane endemics have arisen from widespread lower elevation progenitors distributed there. There is some genetic support for this pattern of endemic origin for other organisms on Mount Kinabalu. In *Leptospermum* (Myrtaceae), allozyme partitioning suggested that a lower elevation ancestor gave rise to a high-elevation endemic (Lee and Lowry 1980). Studies of morphology suggested a similar pattern within *Dacrycarpus* (Podocarpaceae) by de Laubenfels (1988) as well as in *Calanthe* (Orchidaceae; Chan and Barkman 1997). Furthermore, Holloway (1996) has described many "duplexes" or high-elevation species with lower elevation sister species in several genera of butterflies and moths. Although based on morphological evidence alone, it seems likely that the elevational spe-

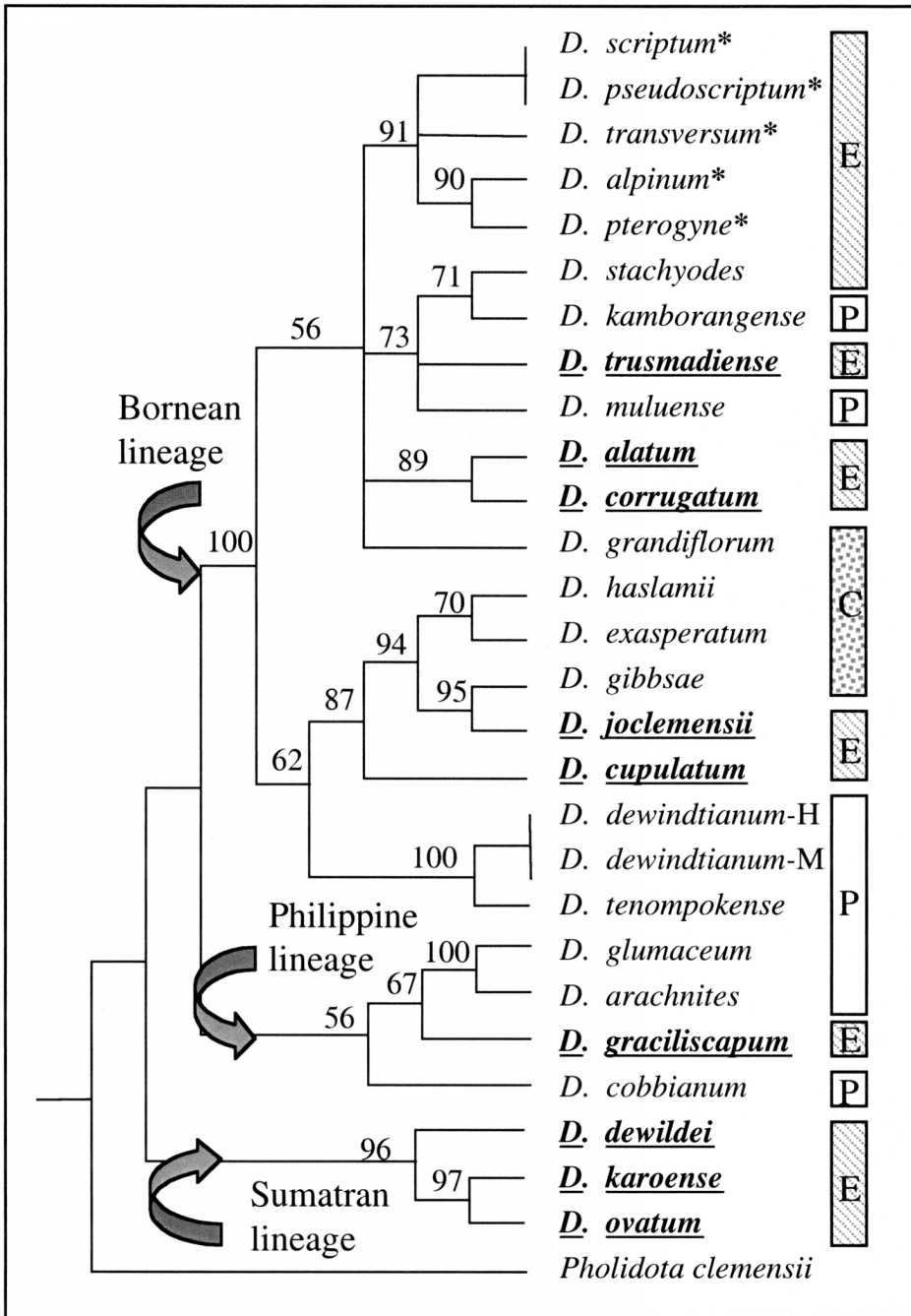


FIG. 5. Single tree found in an unconstrained heuristic search (-ln(L) = 1947.139). High elevation Mount Kinabalu *Dendrochilum* endemics considered in this study are marked by asterisks. Species underlined in bold were used in constraint analyses designed to determine if the Kinabalu high elevation endemics have origins in Borneo, Sumatra, or the Philippines. Sections *Eurybrachium* (E), *Platyclinis* (P), and *Cruciformia* (C) (Pedersen et al. 1997) are labeled in boxes next to each lineage. Bornean, Philippine, and Sumatran lineages are labeled.



TABLE 2. Kishino-Hasegawa test results for 6 hypotheses concerning biogeographic origin of Kinabalu high-elevation endemics. Tree names correspond to topologies illustrated in Figs. 4 & 5. Trees constrained to make *D. alatum*/*D. corrugatum*, *D. trusmadiense* or *D. cupulatum* monophyletic with high-elevation endemics are the only hypotheses not rejected at sequential Bonferroni-corrected  $P < 0.05$  level. Support scores ( $-\ln L$ ) are listed for each topology. The difference between the  $-\ln L$  (diff  $-\ln L$ ) of the best supported tree and each constraint tree is followed by the standard deviation (s.d.) of each difference. \* marks probabilities of T-values (T) that were significant at sequential Bonferroni-corrected  $P < 0.05$ .

Figure	Trees	Distribution	$-\ln L$	diff $-\ln L$	s.d.	T	P
5	Unconstrained	—	1947.1	—	—	—	—
4a	Sumatra	Sumatran	2003.1	55.9	14.2	3.9	0.0001*
4e	<i>D. joclemensii</i>	Bornean	2000.4	53.2	15.2	3.5	0.0005*
4b	<i>D. graciliscapum</i>	Philippine	1992.2	45.0	14.7	3.1	0.0023*
4d	<i>D. cupulatum</i>	Bornean	1971.9	24.8	11.8	2.1	0.0359
4c	<i>D. trusmadiense</i>	Bornean	1959.0	11.9	8.1	1.5	0.1437
4f	<i>D. alatum/corrugatum</i>	Bornean	1947.1	0.0	0.0	0.0	1.0000

ciation model is applicable to these groups of flying insects as well.

Elevational or gradient speciation may be a general process occurring within *Dendrochilum* in Borneo whereby high elevation species have arisen from lower elevation ancestors. Figure 6 shows the elevational distribution of species sampled in this study and a reconstruction of the elevational distributions of their ancestors inferred from the optimal tree illustrated in Fig. 5 using MacClade 3.07 (Maddison and Maddison 1997). *Dendrochilum stachyodes*, *D. haslamii*, *D. dewindtianum*, and the lineage including *D. pterogyne*, *D. alpinum*, *D. scriptum*, *D. pseudoscriptum*, and *D. transversum* are all distributed at high elevations and are inferred to have independently arisen from ancestors distributed at lower elevations ranging from ca. 2,000–2,900 m (Fig. 6). Although the closest relative of the *D. pterogyne*-*D. transversum* lineage is ambiguous, the inference of the ancestral state is unaffected by any possible resolution of the polytomy shown in Fig. 6. Although not explicitly examined in this paper, the origins of the Mount Kinabalu high elevation endemics *D. stachyodes* and *D. grandiflorum* are also inferred to be from lower elevation Bornean ancestors (Fig. 6).

A possible mechanism for the elevational diversification within *Dendrochilum* endemic to Mount Kinabalu would rely on lower elevation ancestors being able to colonize the novel habitat formed by the uplift of the mountain within the last 1.5 million yrs. A consideration of the present-day ecological conditions that vary with elevation on Mount Kinabalu indicates that in colonizing high elevation habitats, lower elevation species would have to cope with differences in pollinators, water availability, light, nutrients, and temperature. Kitayama (1992)

has documented the linear decrease in temperature that occurs along an increasing elevational gradient on Mount Kinabalu. Lower temperature may have a direct effect upon the physiology of species at high-elevations but also an indirect effect through its influence on microbial decomposition rates and therefore nutrient availability. Water availability also changes with elevation on Mount Kinabalu but not in a linear manner (Kitayama 1992, 1995). At higher elevations, water stress conditions significantly affect the plants there causing death in extreme cases (cf. Lowry et al. 1973; Kitayama 1996; Kudo and Kitayama 1999; Kitayama et al. 1999). We are currently investigating various morphological features that covary with elevation in a phylogenetic context in order to infer which changes might represent adaptations to the high-elevation habitat.

In spite of gross morphological and ecological similarity, molecular data indicate that the high-elevation *Dendrochilum* taxa found in the Philippines and Sumatra are not closely related to the high elevation endemic species found on Mount Kinabalu (Table 2). Therefore, we reject hypotheses that the Kinabalu endemic species share most recent common ancestors with species from the high mountains of Sumatra or the Philippines. Although we found no close relationship of the Kinabalu endemics with species found on more distant mountains, several areas (Java and Sulawesi) were not sampled. It is unlikely that any close relatives to the Mount Kinabalu endemics occur in Java or Sulawesi because our morphological surveys of all of the species of section *Eurybrachium* suggested that the most likely relatives were in the areas we sampled—either Mindanao or northern Sumatra. However, as with any hypothesis, we only tentatively

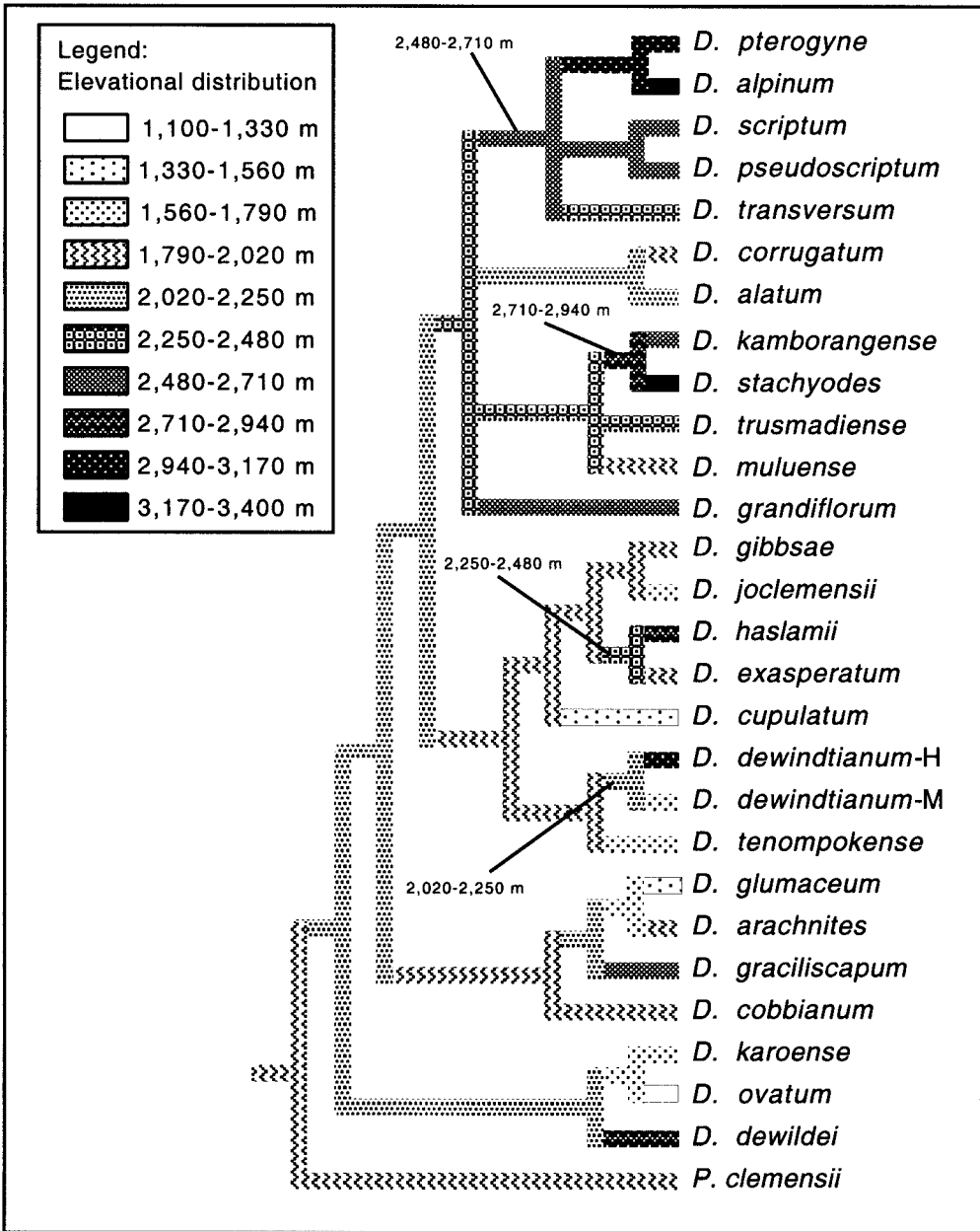


FIG. 6. Inference of the elevational distribution of the ancestors of sampled *Dendrochilum* species. Four independent origins of high-elevation species from mid elevation ancestors distributed between 2,000–2,900 m are inferred (marked by arrows).

accept the lower elevation Bornean origin for the Mount Kinabalu high elevation endemics. Further scrutiny will be possible once more data are available from additional species of the genus.

The geographic distributions of members of sec-

tion *Eurybrachium* are interesting because none of the species are shared between Sumatra and Borneo or the Philippines. Furthermore, a high percentage of the genus is endemic to each area (94%, 91%, and 83% on the Philippines, Borneo, and Su-

matra respectively). Pedersen (1997) suggested that the high level of endemism in *Dendrochilum* was due to the formation of many species during or after the Pleistocene and that endemism is simply an artifact of insufficient time for these recent species to expand their ranges. Our results are consistent with Pedersen's theory (1997). However, more species from throughout the range of *Dendrochilum* should be investigated to determine if any montane endemics have distant geographic origins.

We have provided evidence that suggests an in situ origin for the Kinabalu high elevation endemic *Dendrochilum* species. Hopefully more taxa will be studied to determine if this centric model of origin (sensu van Steenis 1964) is generalizable to other genera found on the mountain. While other Mount Kinabalu high elevation endemic species (e.g. *Ranunculus lowii* and *Potentilla borneensis*) undoubtedly have more distant (non-Bornean) origins, this possibility remains to be investigated. These alternative, long standing biogeographic hypotheses should continue to be evaluated in a phylogenetic context in order to improve our understanding of the origins of the endemic flora of Mount Kinabalu.

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