PHYLOGENY OF *HEDYCHIUM* AND RELATED GENERA (*ZINGIBERACEAE*) BASED ON ITS SEQUENCE DATA

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The phylogeny of *Hedychium* J. Koenig was estimated using sequence data of internal transcribed spacer regions 1 and 2 (ITS1, ITS2) and 5.8S nuclear ribosomal DNA. Sequences were determined for 29 taxa, one interspecific hybrid of *Hedychium* and one species in each of 16 other genera of *Zingiberaceae* representing tribes *Hedychieae*, *Globbeae*, *Zingibereae* and *Alpinieae*. Cladistic analysis of these data strongly supports the monophyly of *Hedychium*, but relationships to other genera are poorly supported. Within *Hedychium*, four major clades are moderately supported. These clades are also distinguishable on the basis of number of flowers per bract and distribution. *Stahlianthus*, *Curcuma*, and *Hitchenia* also form a strongly supported clade. Based on this limited sample, the currently defined tribes of *Zingiberoideae* are not monophyletic. The Asiatic genera form a monophyletic group within this broadly defined *Hedychieae*. The taxonomy and biogeography of *Hedychium* are reviewed.

Keywords. Biogeography, ginger, *Hedychium*, ITS, phylogeny, *Zingiberaceae*.

INTRODUCTION

Within the *Zingiberaceae* four tribes are currently accepted (Smith, 1981): *Globbeae* (bow-shaped filament with unilocular ovary with parietal placentation; four genera); *Zingibereae* (pointed anther crest surrounding the style and staminodal lobes adnate to the labellum; one genus, *Zingiber*); *Hedychieae* (plane of leaf distichy parallel to the rhizome, lateral staminodes petaloid and free from the lip except in *Siphonochilus* and *Curcumorpha,* ovary trilocular with axile placentation or unilocular with basal or free columnar placentation; 21 genera); and *Alpinieae* (distichy of leaves perpendicular to the rhizome, lateral staminodes reduced to teeth or swellings or absent, ovary trilocular with axile placentation; 22 genera). *Alpinieae* have no capacity to shed the stems or inflorescences by abscission. The other three tribes readily shed their stems and form a corky abscission layer on the rhizome in response to old age, photoperiod, soil temperature or drought. The position of *Hedychium* within tribe *Hedychieae* is uncertain.

The tribe *Alpinieae* is pantropical, ranging from New Guinea and Fiji in the East through Asia, Africa, and Central and South America (Wood, 1991; Wu, 1994). The other three tribes occur mainly in southern Asia with sparse representation in Oceania (with no truly indigenous species east of the Moluccas). The only exception is

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Siphonochilus which is endemic to Africa. All fossil *Zingiberaceae*, some of which date from the late Cretaceous, have been interpreted as having affinities with *Alpinieae* (Friedrich & Koch, 1970; Hickey & Peterson, 1978).

The tribe *Alpinieae* are all tetraploids with $2n=44$, 48, 96. *Globbeae* are diploids, tetraploid, hexaploids, and octaploids with basic numbers $x=8$, 10, 12. *Zingibereae* are all $2n=22$. *Hedychieae* are mostly diploid but with $x=9$, 10, 11, 12, 14, 17 (*Hedychium*, *Cautleya*), 21, 25 (Chen, 1987, 1989).

The taxonomy of the horticulturally important genus *Hedychium* has been controversial since the middle of the nineteenth century. At least 115 names have been published in the genus; we currently estimate that about 65 of these are biologically valid species. The species are concentrated in northeast India (24 spp.), Burma (11), and in China [in Yunnan province (18), Guangxi province (8), Guangdong and Hainan provinces (2)], northern Vietnam (10), Nepal (12), northern Thailand (14), peninsular Malaysia (7), southern India (4), Borneo (4), the Philippines (2), Java (3), and Moluccas (1).

The terrestrial species in the circum-himalayan region grow in cool, wet mountains up to 2400m, whereas the Malesian species are mostly epiphytes. Species delimitation has varied among authors; for example some divide *H. coronarium* into 9 species, and *H. coccineum* into 7 species (Roscoe, 1828; Turrill, 1914). All authors agree that the genus is monophyletic. It is characterized by long, linear or lanceolate lateral staminodes, persistent, coriaceous bracts, and a long, exserted stamen with a lower dorsifixed anther. The labellum is showy and usually emarginate or cleft into two lobes.

Wallich (1853) circumscribed the following subgeneric divisions: *Coronariae* (more or less tightly imbricate spikes); *Spicatae* (elongated spikes with distant, spreading bracts); *Siphonium* (one species, *H. scaposa*, a slightly crested anther and a stemless habit similar to the genus *Kaempferia* to which it has long since been transferred); and *Brachychilum* (*H. horsfieldii*, a cleistogamous plant almost lacking a labellum with two wide lateral staminodes, formerly a segregate but recently placed within *Hedychium* (Newman, 1990). Horaninow (1862) divided *Hedychium* into three groups: *Gandasulium* (stamen shorter than or equal to the length of the labellum), *Macrostemium* (stamen much longer than the labellum), and *Brachychilum* (one species, lacking a significant labellum). He also classified four Indonesian species as *incertae sedis*. Schumann (1904) redefined *Gandasulium* to include taxa with a dense, short and wide, ellipsoid, ovoid, rarely long cylindrical inflorescence; with bracts flat, densely imbricate, rarely arched; and with rachis always hidden. He defined his other subgenus, *Euosmianthus*, to include species with less dense, with longer than wide inflorescence; bracts never densely imbricate, commonly patent, or divergent, or distant from each other, clasping the flowers; and with rachis not hidden. He also maintained a separate genus for *Brachychilus*, comprising a Moluccan species and *H. horsfieldii*. It is the aim of this paper to examine the validity of these classification schemes in light of modern molecular phylogeny.

The first author is writing a monograph of *Hedychium*. Preliminary phenetic analysis of 15 species (Wood, 1996) using 11 inflorescence characters showed some support for grouping of the species into imbricate and tubular bracted groups. Later analysis (Wood, unpublished data) using 110 specimens of 67 species did not indicate well-supported clustering of the two bract types in factor analysis; however, discriminant analysis correctly scored bract types in 90% of the observations and five of the eleven misclassifications involved Malesian species. The only published molecular studies of *Zingiberaceae* use *rbcL* sequences (Clark *et al*., 1993; Kress, 1995). In these analyses *Costaceae* are unresolved among the other five families of Zingiberales and only the four tribes of the *Zingiberaceae* form a single clade. When morphological characters are added to the *rbcL* data the *Alpineae* becomes the outgroup to the other three tribes.

Wood (1991) hypothesized that the *Costaceae* and *Alpinieae* are the earliest groups in the *Zingiberaceae* and originated in Western Gondwanaland before the effective separation of South America and Africa, although fossil evidence from North America and Europe run counter to this hypothesis. These two groups were rafted on the Indian subcontinent from Africa to Asia. Sometime when the subcontinent was in the middle latitudes, when the paleoclimate was fairly dry, the progenitors of the other three tribes of the *Zingiberaceae* evolved in response to climate, and the ancestors of the African genus *Siphonochilus* dispersed to eastern Africa. Upon the collision of India with Asia, the uplift of the Himalayas provided many isolated and seasonally favorable habitats that prompted a massive radiation of genera of the *Hedychieae, Globbeae,* and *Zingibereae* in upland areas while the *Alpinieae* flourished in the lowland tropics of Asia and Oceania.

MATERIALS AND METHODS

Leaf samples of 29 species and cultivars of *Hedychium* plus representative species from 16 genera in the tribes *Hedychieae*, *Globbeae*, and *Zingibereae*, and one member of the tribe *Alpinieae* were obtained from material cultivated by the first author. The *Alpinia* was selected as the outgroup based on Kress (1995), fossil evidence, and the biogeographic evidence cited above. Also, one specimen that was thought to be an interspecific hybrid (Schilling, 1982) and a wide interspecific hybrid created by hand pollination were included in the analysis in order to evaluate our ability to detect natural interspecific hybrids. A list of taxa examined and voucher numbers is presented in Table 1. Vouchers are deposited in the University of Florida Herbarium (FLAS).

Fresh or dried tissue was ground and extracted by the modified CTAB method (Doyle & Doyle, 1990). The ITS1 and ITS2 regions along with the intervening 5.8S nrDNA region were amplified using PCR with primers 5 and 4 of Baldwin (1992). The amplified products were cleaned on Qiagen® columns according to manufacturer's instructions. Dye terminator cycle sequencing reactions were performed using Applied Biosystems reagents and protocols. AutoAssembler software (Applied Biosystems) was used to assemble the complementary strands and edit nucleotide

TABLE 1. Taxa sampled

Species	Group	Voucher
Hedychium acuminatum Ker Gawl.	*Hedychieae*	T. Wood 14
H. borneense R.M. Sm.	*Hedychieae*	T. Wood 18
H. bousigonianum Gagnep.	*Hedychieae*	T. Wood 11
H. carneum sensu Y.Y. Qian	*Hedychieae*	T. Wood 35
H. coccineum Ker Gawl.	*Hedychieae*	T. Wood 6
H. coronarium König	*Hedychieae*	T. Wood 15
H. cylindricum Ridl.	*Hedychieae*	T. Wood 13
H. densiflorum Wall.	*Hedychieae*	T. Wood 24
H. densiflorum 'Stephen'	*Hedychieae*	T. Wood 47
H. elwesii Baker	*Hedychieae*	T. Wood 10
H. ellipticum Ker Gawl.	*Hedychieae*	T. Wood 29
H. flavescens Roscoe	*Hedychieae*	T. Wood 37
H. gardnerianum Roscoe	*Hedychieae*	T. Wood 8
H. glabrum S.Q. Tong	*Hedychieae*	T. Wood 16
H. gracile Roxb.	*Hedychieae*	T. Wood 35
H. gracillimum A.S. Rao & Verma	*Hedychieae*	T. Wood 36
H. greenii W.W. Sm.	*Hedychieae*	T. Wood 26
H. hasseltii Blume	*Hedychieae*	T. Wood 23
H. horsfieldii Wall.	*Hedychieae*	T. Wood 2
H. longicornutum Baker	*Hedychieae*	T. Wood 9
H. muluense R.M. Sm.	*Hedychieae*	T. Wood 12
H. maximum Roscoe	*Hedychieae*	T. Wood 27
H. puerense Y.Y. Qian	*Hedychieae*	T. Wood 30
H. spicatum Ker Gawl.	*Hedychieae*	T. Wood 38
H. stenopetalum Lodd.	*Hedychieae*	T. Wood 28
H. tenuiflorum K. Schum.	*Hedychieae*	T. Wood 7
H. thyrsiforme Ker Gawl.	*Hedychieae*	T. Wood 25
H. urophyllum Lodd.	*Hedychieae*	T. Wood 40
H. yunnanense Gagnep.	*Hedychieae*	T. Wood 17
H. hasseltii × *gardnerianum*	*Hedychieae*	T. Wood 49
Alpinia intermedia Gagnep.	*Alpinieae*	T. Wood 1
Boesenbergia aurantiaca R.M. Sm.	*Hedychieae*	T. Wood 32
Cautleya robusta Baker	*Hedychieae*	T. Wood 51
Cornukaempferia aurantiflora J. Mood & K. Larsen	*Hedychieae*?	T. Wood 19
Curcuma petiolata Roxb.	*Hedychieae*	T. Wood 50
Gagnepainia godefroyi K. Schum.	*Globbeae*	T. Wood 21
Globba pendula Roxb.	*Globbeae*	T. Wood 31
Haniffia cyanescens Holttum	*Hedychieae*	T. Wood 38
Hitchenia glauca Wall.	*Hedychieae*	T. Wood 43
Kaempferia roscoeana Wall.	*Hedychieae*	T. Wood 20
Pommereschea lackneri Wittm.	*Hedychieae*	T. Wood 45
Roscoea humeana Balf. & W.W. Smith	*Hedychieae*	T. Wood 46
Rhynchanthus beesianus W.W. Smith	*Hedychieae*	T. Wood 32
Scaphochlamys biloba Holttum	*Hedychieae*	T. Wood 33
Siphonochilus kirkii B.L. Burtt	*Hedychieae*	T. Wood 41
Stahlianthus involucratus Craib	*Hedychieae*	T. Wood 44
Zingiber corallinum Hance	*Zingibereae*	T. Wood 34

sequences. Sequences were easily aligned manually. The sequences are deposited in GenBank (accessions AF202374-AF202420) and the aligned matrix is available from the first author. PAUP* 4.0 b2 (Swofford, 1999) was used for parsimony analysis. Initial analyses consisted of 1000 replicates of random taxon addition using SPR and MULTREES, saving only three trees per replicate. These trees were then swapped to completion, or until 10,000 trees were saved. The data set was then subjected to three rounds of successive weighting (reweighted on rescaled consistency index; 1000 replicates, saving 5 trees per replicate) to decrease the effects of highly homoplasious sites. Lledó *et al.* (1998) gave convincing reasons for using successive weighting. Successive weighting reduces the effects of highly homoplasious sites, and thus emphasises sites that are more consistent.

In addition to maximum parsimony analyses, we evaluated support of the clades by: 1, bootstrap analyses (Felsenstein, 1985) to obtain bootstrap support for nodes using both equally weighted and successively weighted trees with 1000 replicates of bootstrapping using SPR swapping, MULTREES on, holding 10 trees/replicate; 2, by use of Bremer support (Bremer, 1988, 1994) to obtain branch support for the equally weighted trees using the program Autodecay, version 4.0 (Eriksson, 1998) and PAUP* 4.0b2 (Swofford, 1999); and 3, by the reliability percentages obtained by the quartet puzzeling method of maximum likelihood (ML) (Strimmer and von Haeseler, 1996) as available in PAUP* 4.0b2. The ML parameters were the H-K-Y model, ti/tv = 2, with other parameters set to default. Bremer support trees and ML trees were drawn in the TREEVIEW program (Page, 1996).

RESULTS AND DISCUSSION

The aligned matrix is 733 base pairs (bp) long, and consists of the 3′ end of 18S (30bp), ITS1 (235bp), the 5.8S region (165bp), ITS2 (238bp), and 16bp of the 26S region. Twenty-four bases were excluded due to ambiguous alignment. Of the 709 included sites, 330 were variable and 169 parsimony informative.

The initial unweighted analyses yielded 10,000 + trees with a length of 726 (CI = 0.618, RI = 0.644). After three rounds of successive weighting (100 replicates, saving 5 trees per replicate), the final analysis produced 500 trees of length 315.56 (CI = 0.875, RI = 0.838). The Fitch length of the successively weighted trees (equal weights reapplied) was 728 (CI = 0.617, RI = 0.641), two steps longer than the shortest unweighted trees. The CI for unweighted trees with uninformative characters excluded was 0.485, and the CI for weighted trees with uninformative characters excluded was 0.690. Fig. 1 shows a randomly-chosen reweighted tree with branch lengths above the lines, bootstrap support values (if $\geqslant$70%) directly under lines, and decay values (given as d =) below the bootstrap values. Decay values are only given for major clades if $\geqslant$1.

The monophyly of *Hedychium* is highly supported (bootstrap = 100%). The tree in Fig. 1 shows four moderately supported clades within *Hedychium* and illustrates poor resolution within these clades due to low sequence divergence. The four clades

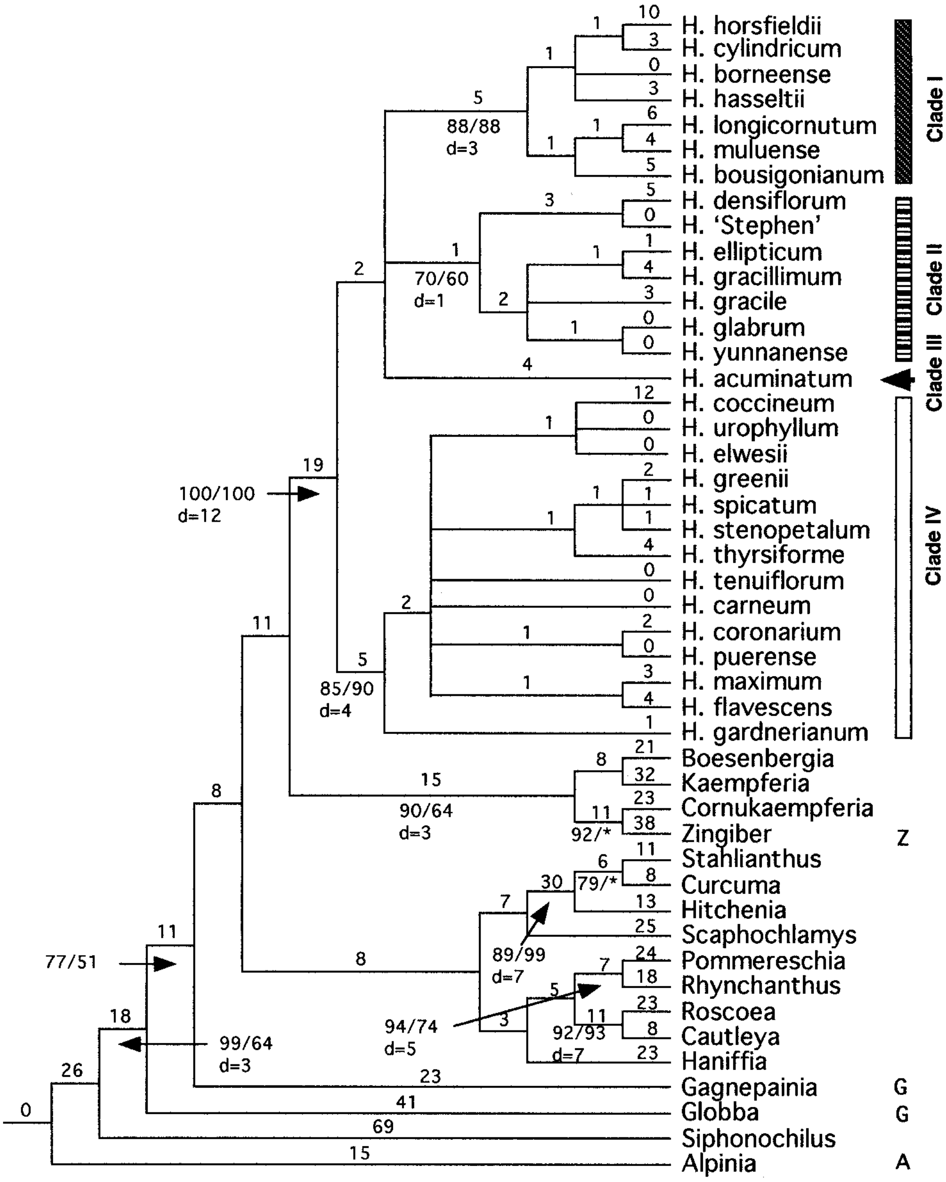

FIG. 1. One of 500 reweighted equally most parsimonious trees with branch lengths given above the lines and the bootstrap support values directly below the lines, with weighted bootstrap values followed by unweighted bootstrap values. Weighted boostrap values are not given for clades with values <70%. Decay values are below the bootstrap values and indicated by d = (value). Additional statistics are given in the text. Genera not in the *Hedychieae* are indicated by (Z, *Zingibereae*), (G, *Globbeae*), and (A, *Alpinieae*).

form an unresolved polytomy in the bootstrap analysis. Clade I plants occur only in southern Vietnam, the Malay Peninsula, and Oceania. They are short, generally epiphytes or calciphiles, with a short day or day neutral photoperiod, slender inflorescences, one or two flowers per bract (three in *H. bousigonianum*), and flowers much exserted from the bracts. Clade II is sister to Clade I in the successively weighted strict consensus tree, and these two clades have weak decay support ($d=1$). Clade III, represented here by only *H. acuminatum*, is sister to clades II and I in the strict consensus tree (not shown). Clade III and Clade II are high altitude Himalayan species that have only one flower per bract and a strict dormancy requirement. Clade IV species have a wider circum-himalayan distribution at lower altitudes than Clades II + III. A comparison of collection information from 23 herbarium specimens from Clade II and 43 specimens from Clade IV showed a mean altitude for Clade II of 1783m and 1260m for Clade IV. This difference is highly significant ($\alpha<0.0005$) using a students t-test. These tall plants do not normally go dormant in the winter and have three or more flowers per bract.

Because artificial interspecific hybrids of *Hedychium* are easily created (Wood, personal observation), natural hybridization is a potential source of taxonomic confusion in *Hedychium*. The ITS sequence of the artificial hybrid (*H. gardnerianum* × *hasseltii*) was intermediate between that of the two parents. The parents differed by 17 bases; at each of these positions, the hybrid sequence displayed polymorphic states, indicating ITS copies from each parent. These positions were scored using ambiguity codes. When the hybrid sequence was included in the PAUP analyses (not shown), the hybrid was sister (on a zero-length branch) to one or the other parent, depending upon the addition-sequence replicate. In contrast, *H. densiflorum* and the aberrant variety named ‘Stephen’ possess nearly identical sequences and are sister taxa in the analyses with high bootstrap support. The sequence of cultivar ‘Stephen’ revealed no ambiguous sites. The similarity of these two sequences does not support the hypothesis that ‘Stephen’ is a cultivar of recent hybrid origin (Schilling, 1982) and suggests that it is merely an aberrant form of *H. densiflorum*. These examples show that ITS sequences may reveal recent interspecific hybridization that might otherwise confound phylogenetic analyses. Because ITS regions are known to undergo rapid concerted evolution (Baldwin, 1992), species of ancient hybrid origin may be difficult to detect without additional lines of evidence.

On a higher taxonomic level, a clade consisting of *Cautleya, Pommereschea, Rhynchanthus,* and *Roscoea* is weakly supported (61% bootstrap), but not as the sister group to *Hedychium* as we had expected on the basis of morphology. The clade of *Pommereschea* and *Rhynchanthus* has a bootstrap support of 94% and a decay value of $d=5$, with both values indicating very strong support for this clade. This supports the idea that these two genera are in the tribe *Hedychieae* not the *Alpiniae* as Schumann indicated based on the lack of lateral staminodes. This classification has been supported by Smith (1980) and by Z.Y. Chen (personal communication). They both lack petaloid staminodes, making them quite different from *Hedychium*. *Roscoea* is sister to *Cautleya* with 92% bootstrap support and a decay value of d = 7. These are high altitude Himalayan taxa that bear single flowers in each bract. The flowers have oblong, petaloid lateral staminodes and a bifid labellum like *Hedychium*. The four genera together form a weakly supported clade.

Other related clades, while not reflecting on the phylogeny of *Hedychium*, do shed light on the evolution of the *Zingiberaceae*. A clade consisting of *Hitchenia*, *Curcuma*, and *Stahlianthus* has a high bootstrap support of 89% and very strong decay support of d = 7. The separation of *Hitchenia* from *Curcuma* on the basis of exserted flowers and non-versatile anthers has never seemed adequate, but *Stahlianthus* (single bell shaped bract) perhaps should be considered as a *Curcuma* with two adnate bracts.

The position of *Zingiber* makes the tribe *Hedychieae* polyphyletic. In spite of describing the genus *Cornukaempferia* as having an 'anther crest (that) shows a striking resemblance with the anther appendage characterizing *Zingiber*', Mood and Larsen (1997) placed it close to *Kaempferia* on the basis of vegetative habit. The ITS data indicate that *Cornukaempferia* is sister to *Zingiber* (92% bootstrap support) and might not be generically distinct. The placement of *Gagnepainia* and *Globba* make tribe *Globbeae* paraphyletic. It is notable that the Asian species of *Globbeae*, Zingibereae, and *Hedychieae* form a monophyletic group with a bootstrap support of 99% and decay support of d = 3. The fact that the African genus *Siphonochilus* appears as the sister group to the rest lends credence to the theory of an origin of these tribes on the Indian subcontinent 40–50 million years ago.

The results of the quartet puzzling analysis also provides strong support for the monophyly of *Hedychium*, which has a reliability percentage of 100. Within *Hedychium*, clade II has a reliability of 94%, clade IV 99%, and clade I 98%. The other clades with high puzzle support are *Boesenbergia* clade (83%), *Pommereschea*/*Rhynchanthus* (92%), *Stahlianthus*/*Curcuma*/*Hitchenia* (98%), *Curcuma*/*Hitchenia* (98%), and the large clade of Asian species (86%).

In conclusion, sequence data show that the genus *Hedychium* is monophyletic and includes the genus *Brachychilum*. We propose these clades which may be described later as subgenera: 1, Clade IV (three to five flowers per bract) and 2, Clade II (one flower per bract), both of which have a natural circum-himalayan distribution; and 3, Clade I (one or two flowers per bract) that occur only in the Malay Peninsula, Philippines, Borneo, Sumatra, Java, Sulawesi, and the Moluccas. The position of Clade III (*H. acuminatum*) is uncertain but probably includes *H. venustum* (not available for this study) on the basis of morphology. This molecular phylogeny runs counter to Schumann's classification because species in three of these clades occur in each of his subgenera. This analysis also emphasises that the most important factor in the evolution of this genus is geographic and ecological isolation. Because tribes *Globbeae* and *Zingibereae* make tribe *Hedychieae* paraphyletic we recommend that only tribe *Zingibereae* be retained. The position of the African genus *Siphonochilus* is uncertain and must be evaluated along with other genera in the tribe *Alpinieae* and *Costaceae*, preferably including African species, to determine its placement. This data set suggests that tribal concepts need to be re-evaluated in the *Zingiberaceae*. Expanded data sets, such as the conserved *matK*, need to be used before the existing taxonomy is radically altered. The sister group of *Hedychium* is uncertain based on this sample.

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