

A new phylogeny-based generic classification of Costaceae (Zingiberales)

Chelsea D. Specht^{1,2} & Dennis Wm. Stevenson¹

¹ New York Botanical Garden, Bronx, New York 10458, U.S.A.

² Current address: University of California, Department of Plant and Microbial Biology, Berkeley, California 94720, U.S.A. cdspecht@nature.berkeley.edu (author for correspondence)

Recent cladistic analysis of multiple molecular data from chloroplast and nuclear genomes as well as morphological data have indicated that a reclassification of the family Costaceae is necessary in order to appropriately reflect phylogenetic relationships. The previously described genera *Tapeinochilos*, *Monocostus*, and *Dimerocostus* are all upheld in the new classification. *Monocostus* and *Dimerocostus* are found to be sister taxa. The large pantropical genus *Costus* is found to be polyphyletic and is thus divided into four genera, three of which are new (*Cheilocostus*, *Chamaecostus*, *Paracostus*). *Costus* has now a more concise generic concept including morphological synapomorphies previously absent due to the polymorphic nature of the prior non-monophyletic assemblage. Of the three new genera, one (*Paracostus*) was previously recognized as a subgenus of *Costus*. *Cheilocostus* comprises several Asian taxa and is sister to *Tapeinochilos*, whereas *Chamaecostus* comprises entirely neotropical taxa and is sister to a neotropical *Monocostus* + *Dimerocostus* clade. A reevaluation of the traditional taxonomy indicates that floral characters and pollination syndromes commonly used to identify groups exhibit homoplasy when analyzed in a cladistic framework and are thus unreliable as taxonomic indicators.

KEYWORDS: Costaceae, *Costus*, Zingiberales, classification, phylogenetic taxonomy.

INTRODUCTION

Costaceae is one of the most easily recognizable groups within the Zingiberales, distinguished from other families within the order by well-developed and sometimes branched aerial shoots that have a characteristic monostichous (one-sided) spiral phyllotaxy (e.g., Kirchoff & Rutishauser, 1990). Its close relationship with Zingiberaceae is evidenced by its former placement as a subfamily within the larger Zingiberaceae family. The placement of Costaceae within Zingiberaceae was largely based on broad similarities of inflorescence and floral characters. Tomlinson (1962) suggested that, although these types of characters may indicate common ancestry, they are not sufficient to overcome the morphological and anatomical differences that warrant independent familial rank of the two lineages which had been proposed by Nakai (1941).

Costaceae sensu Tomlinson (1962) consisted of four genera: *Costus*, *Monocostus*, *Dimerocostus* and *Tapeinochilos*. *Costus*, which contains the majority of the species and maintains the greatest morphological diversity, is pantropical with its greatest diversity centered in the neotropics (c. 40 spp.); 25 species occur in tropical Africa and about five species in southeastern Asia. A separate genus, *Cadalvena*, was recognized when Costoideae was part of Zingiberaceae (Scitaminae) (Fenzl, 1865) and was maintained in some subsequent treatments of the

family (e.g., Thiselton-Dyer, 1898), but in later treatments was reduced to subgeneric status within *Costus* (Schumann, 1904). Floristic treatments that included species of *Cadalvena* either did not distinguish subgenera (Koechlin, 1964, 1965; Hepper, 1968) or treated *Costus* and *Cadalvena* as subgenera within *Costus* (Maas, 1972, 1977). Maas (1972) described several new species from South America which he included in *C.* subgenus *Cadalvena*. No new species from Africa have been added to *Cadalvena* since Schumann (1904) and, in fact, many of the species included in Schumann's treatment have been subsequently synonymized with the generic type, *Costus spectabilis*.

In addition to *Cadalvena*, Schumann (1904) recognized four other subgenera in *Costus* in his treatment of global Zingiberaceae (including the Costoideae): *Eucostus* (= *C.* subg. *Costus* according to the current International Code of Botanical Nomenclature, ICBN, Greuter & al., 2000), *Metacostus*, *Epicostus* and *Paracostus*. These same subgenera were maintained by Loesener (1930). In Maas' treatments of neotropical Costaceae (1972, 1977), a formal division between the two subgenera that are found in South America (*Costus*, *Cadalvena*) was maintained. In addition, subgenus *Costus* was divided into two separate sections: *Costus* sect. *Ornithophilus* and *Costus* sect. *Costus*. These sections were based upon characters of the labellum and reflected two distinct floral forms associated with polli-

nation syndromes. Taxa placed in *Costus* sect. *Ornithophilus* all have a tubular labellum adapted to bird pollination (Fig. 1.5), whereas those in *Costus* sect. *Costus* have a broad labellum with a distinct exposed limb that appears to be adapted to pollination by bees. While all neotropical *Costus* species can be placed rather easily into one of the two sections based on floral and inflorescence characteristics, African and Asian *Costus* do not share this distinction of forms. Subsequent to Schumann (1904) and Loesener (1930), the division of African and Asian *Costus* into various subgenera has not been maintained, with the exception of *Costus spectabilis* as subgen. *Cadalvena* (Lock, 1985).

In contrast to the large pantropical *Costus*, the remaining genera of Costaceae (*Monocostus*, *Dimerocostus* and *Tapeinochilos*) are restricted in distribution. *Dimerocostus* and *Monocostus* are both restricted to the neotropics, the former extending from Honduras in the north to central Bolivia in the south and the latter known only from the Rio Huallaga region of central Peru. *Monocostus* is the only taxon to have a solitary flower in the axils of the leaves rather than a highly structured inflorescence of spirally arranged bracts subtending single or paired flowers. Although differing in overall plant morphology, *Monocostus* and *Dimerocostus* share a floral morphology that is at least superficially similar to that of *Cadalvena*. *Tapeinochilos* is restricted to the paleotropics where it is found primarily in New Guinea with a few species extending into the surrounding Indonesian islands and south to Queensland, Australia. Although most closely resembling the *Costus* sect. *Ornithophilus* in floral form, the floral and inflorescence morphology of *Tapeinochilos* is distinct from that of other Costaceae.

Few species of *Costus* have distributions falling within the range of *Tapeinochilos*, and those that do have a floral form of the type found in *Cadalvena*, *Monocostus* and *Dimerocostus*. These Asian *Costus* species share with *Tapeinochilos* the tendency to undergo vegetative branching, and both possess woody inflorescence bracts in contrast to the herbaceous and chartaceous bracts of the African and neotropical taxa. The bracts are often red, but can be dark brown or even black in color. Despite these similarities, no specific or formal affiliation between Asian species of *Costus* and *Tapeinochilos* had been proposed.

Recent phylogenetic analyses of the family Costaceae (Specht & al., 2001; Specht, 2006) show that *Tapeinochilos*, *Monocostus* and *Dimerocostus* are all monophyletic lineages, whereas *Costus* is polyphyletic and requires a revised taxonomic circumscription. In order to reconcile taxonomy with the phylogenetic hypothesis, three new genera are segregated from *Costus*: *Paracostus*, *Cheilocostus* and *Chamaecostus*. *Costus* is maintained as a much smaller genus with a more restrict-

ed floral and geographic diversity. *Tapeinochilos*, *Monocostus*, and *Dimerocostus* are also maintained because the morphological distinction with which they were originally described corresponds to their monophyly. A new generic classification of the family is presented and species lists are given for each of the newly described genera. Several lineages within *Costus* having unique associations with pollinators are recognized.

MATERIALS AND METHODS

The most recent interfamilial classification for Costaceae is provided by a combined molecular and morphological cladistic analysis that includes a representative sampling of Costaceae taxa (Specht & al., 2001; Specht, 2006). A summary of the current evolutionary hypothesis for Costaceae based on the recent phylogenetic analysis is shown in Figure 1. This phylogenetic hypothesis forms the basis for the revised taxonomic classification system.

The formal generic classification is presented as governed by the current *ICBN*. In addition, a list of synapomorphies is provided for each of the newly described genera and follows the discussion of the individual group.

There was no major discrepancy between the molecular and morphological analyses, thus the topology obtained from the combined analysis was selected for the new classification system. Morphological distinctiveness was also considered in the definition of new genera, as was adherence to previously recognized natural lineages. Major clades with strong support (as determined by Bremer support, jackknife) and clear morphological synapomorphies are named. Within *Costus*, several clades are given informal recognition as having unique morphological characteristics but are not designated formally due to the resulting basal paraphyly.

TAXONOMIC TREATMENT

Costaceae Nakai in J. Jap. Bot. 17: 203. 1941, basionym: trib. *Costeae* Meisn., Pl. Vasc. Gen.: Tab. Diagn.: 389, Comm.: 291. 17–20 Aug 1842. – Type: *Costus* L., 1753.

Small to large non-aromatic perennial rhizomatous herbs, terrestrial or less commonly epiphytic. Stems erect from rhizome, spirally contorted, formed at the base by bladeless sheaths, leafy higher up, most often unbranched but always branching in some taxa. When branched, secondary branches breaking through the leaf sheath. Leaves spirally arranged on stem, phyllotaxis monostichous, base of blade attached to sheath by short

petiole, lamina narrowly to broadly elliptic, acuminate at the apex, obovate to cuneate at the base, rolled in bud. Sheath tubular with prominent ligule formed at the base of the petiole. Inflorescence open or dense, globose or ellipsoid, terminal on leafy stems or on separate leafless shoots, or flowers solitary in leaf axils (*Monocostus*). Bracts imbricate in a series of parastichies, usually broad and overlapping at the base, each subtending 1–2 flowers; linear nectariferous callus below tip in some taxa. Bracteoles smaller, laterally flattened, boat-shaped (folded) or tubular at the base. Flowers epigynous, perfect, zygomorphic. Calyx tubular, more or less deeply 2–3-lobed, lobes acute and sometimes pungent (*Cheilocostus*), sometimes unequal with the anterior broader than the other two. Corolla 3-lobed, lobes basally fused, imbricate in bud, overlapping at maturity. Labellum large, as long as or much longer than the corolla, obovate, thin, margin often crisped, sometimes lobed (3–5), brightly colored. Stamen with broad petaloid filament that curves forward and closes the entrance to the tube of the flower, tip upturned; 2 bisporangiate thecae attached below apex, slightly raised from surface, dehiscing introrsely by longitudinal slits, holding style between thecae. Basal part of stamen and labellum united into a papillate tube. Stigma bilobed with a two-pronged or rounded dorsal appendage. Ovary trilocular or bilocular, inferior, placentation axile; ovules many, organized in 2 rows, anatropous, crassinucellar; septal nectaries erect or sunken at base of floral tube in apex of ovary. Fruit a capsule, 3-angled and trilocular or flattened and bilocular, dry or fleshy, dehiscent loculicidally or indehiscent and irregularly breaking when old. Seeds numerous, angular or ellipsoid, dark brown or black with white or yellow, fleshy, cushion-like aril; embryo straight; endosperm poorly developed; perisperm abundant with copious starch in simple grains.

Costaceae, predominantly Neotropical in species diversity, is sister to the mainly Old World family Zingiberaceae. Molecular and morphological data analyzed in a phylogenetic framework suggest a single origin of Costaceae (Kress, 1990, 1995; Kress & al., 2001; Specht & al., 2001; Specht, 2006), supporting earlier investigations that suggested the separation of Costaceae and Zingiberaceae. Nakai (1941) cited the non-aromatic vegetative body, spirally arranged leaves, and anther appendages to separate the Costaceae from the Zingiberaceae. Anatomically, the monophyly of Costaceae and its separation from Zingiberaceae is supported by multicellular, uniseriate, unbranched hairs with the base never sunken as found in the Zingiberaceae (Tomlinson, 1956, 1962). In addition, the hypodermis is always well developed with one or more layers below each surface in contrast to the Zingiberaceae, which either lacks a hypodermis or has only a single hypodermal layer below each

surface. The leaf axis in Costaceae has one poorly developed system of air canals that are situated adaxially and often absent at certain levels, whereas the petiole of Zingiberaceae has a well-developed abaxial arc of air canals. The silica bodies of Costaceae are found in all examined species to be stellate or druse-like in shape, whereas the silica bodies found in the Zingiberaceae are frequently (but not universally) present and are spherical in shape. In *Costus*, the silica bodies never occur in the epidermis but rather are adjacent to the vascular bundles whether in the lamina, in which they are least common, or in the petiole, sheath, stem or rhizome (Tomlinson, 1956). Finally, the Costaceae completely lack oil cells, which are abundant in all parts of the Zingiberaceae. These characters indicate the uniqueness of the Costaceae lineage and provide morphological and anatomical synapomorphies for the family. Additionally, the well-developed, sometimes-branched aerial stem, the distinctive monostichous spiral phyllotaxy, and the fusion of five staminodes into a labellum (Kirchoff, 1988) versus three staminodes in Zingiberaceae, form the suite of synapomorphies most commonly cited as defining Costaceae.

Key to the Genera of Costaceae:

- 1. Flower solitary in the axils of leaves 1. *Monocostus*
- 1. Flowers arranged in a terminal strobilaceous spike or head 2
- 2. Ovary bilocular, ovules occur only below the stylar canal 3
- 2. Ovary trilocular 4
- 3. Plants without vegetative branching; labellum large, showy and delicate; bracteoles present; bracts green, herbaceous, not reflexed, sometimes appendaged never spiny; Neotropical 2. *Dimerocostus*
- 3. Plants with vegetative branching; labellum small, inconspicuous and rigid or fleshy; bracteoles rarely present; bracts typically red or red-brown, coriaceous, reflexed and often spiny at the apex; Papuasia and NE Australia 6. *Tapeinochilos*
- 4. Plants >1.5 m in height; bracts coriaceous to woody; stigma bilamellate with dorsal 2-lobed appendage 5
- 4. Plants <1.5 m in height; bracts chartaceous to herbaceous; stigma cup-shaped or bilamellate 6
- 5. Labellum open, showy; white, red or yellow with no lateral markings; bracts woody, spiny at the apex (or dilacerating into fibers, *C. lacerus*), red or brown; leaf-bearing shoots with axillary branching; SE Asia and Malesia 4. *Cheilocostus*
- 5. Labellum tubular, red, orange, yellow or white (if white then with exposed yellow central lobe and red lateral-lobe markings); bracts coriaceous, green, red, yellow or orange, never spiny; leaf-bearing shoots

- without axillary branching; Central and South America and Africa 5. *Costus*
6. Plants prostrate; leaves few or solitary; inflorescence few-flowered; bracts inconspicuous; West Africa/Borneo 7. *Paracostus*
6. Plants erect, occasionally acaulescent; leaves many, often terminating in a rosette; inflorescence many-flowered; bracts conspicuous, green or yellow . . . 7
7. Stigma cup-shaped; labellum yellow, orange or red; Neotropical 3. *Chamaecostus*
7. Stigma bilamellate; labellum purple, pink, yellow or white; Africa 5. *Costus* (African grade)

1928 – Type: *Mulfordia boliviana* Rusby

Plants large, rhizomatous unbranched perennial herbs, greater than 3 m in height. Stem very stout and somewhat spiral, comprised of leafless sheaths. Leaves spiral with ligulate sheaths, often congested near the tip of the elongate stem, oblong-oblongate, narrowly acuminate at the apex, cuneate to rounded at the base. Ligule very short or absent. Inflorescence cylindrical, spirally contorted, scarcely cone-like as in *Costus*. Bracts green to yellow-green, coriaceous, often sheathing, ovate, sometimes with deltate foliaceous appendage, much shorter than flowers. Bractole tubular, bicarinate. Calyx large, tubular, 3-parted with unequal lobes, often exceeding bracts. Corolla 3-lobed, white or light yellow. Labellum large and showy, white or yellow, if white then often with yellow spot at center. Stamen petaloid, tip reflexed, anthers attached at center. Pollen grains large, dicolpate or mixed colpate-porate. Stigma cup-shaped. Ovary bilocular, ovules biseriate. Fruit a capsule, tardily dehiscent or non-dehiscent, only slightly fleshy. Seeds glossy black, with small cushion-like white aril. Floral parts with red-brown punctations.

Dimerocostus is found in Central and South America from Nicaragua in the north to northern Bolivia in the south, mostly following the eastern slope of the Andes. The genus is currently comprised of two species.

Dimerocostus strobilaceus Kuntze, Rev. Gen. Pl. 2: 687. 1891.

a. *Dimerocostus strobilaceus* subsp. *strobilaceus*
Type: PANAMA, Monckhill, Kuntze 1873 (holotype, NY!).

= *Dimerocostus uniflorus* (Poepp. ex Petersen) K. Schum., in Engler, Pflanzenreich IV, 46: 427. f. 50A. 1904.

= *Dimerocostus elongatus* Huber, Bol. Mus. Goeld. 4: 545. 1906 – Syntypes: PERU, Loreto: Quebrada de Canchahuaya, Huber 1384 (MG!), Pampa del Sacramento, Huber 1461 (n.v.).

b. *Dimerocostus strobilaceus* subsp. *gutierrezii* (Kuntze) Maas, Fl. Neotrop. Monogr. 8: 23. 1972. ≡ *Dimerocostus gutierrezii* Kuntze, Rev. Gen. 3: 301. 1893 – Type: BOLIVIA, Santa Cruz: Puerto Gutiérrez, San Ignacio, Río Yapacaní, Kuntze s.n. (holotype, NY!).

= *Costus rurrenabaqueanus* Rusby, Bull. New York Bot. Gard. 7: 219. 1927 – Type: BOLIVIA, Beni: Rurrenabaque, Cardenas 1882 (holotype, NY!).

= *Dimerocostus tessmannii* Loes., Notizbl. Bot. Gart. Berlin-Dahlem 10: 715. 1929 – Type: PERU, Loreto: Parinari, Río Marañon, Tessmann 3751 (F!, GH!, MO!, NY!, U!, US!).

CIRCUMSCRIPTION OF GENERA IN COSTACEAE

1. **Monocostus** K. Schum., in Engler, Pflanzenreich IV, 46: 427. 1904 – Type: *Monocostus uniflorus* (Poepp. ex Petersen) Maas

Plants small herbs with non-rhizomatous, ribbed roots. Leaves small, glabrous except for ciliate margins, margins red. Stems erect from root system, spirally contorted, formed by sheathing leaf bases, unbranched. Ligule short to absent. Bracteole tubular. Flowers solitary in the axils of the leaves, shortly pedicellate. Calyx long, herbaceous, glabrous. Corolla light yellow, shorter than labellum. Labellum yellow, large, obovate. Stamen petaloid with reflexed tip, covering tube formed by the labellum, anther attached in the middle. Stigma cup-shaped. Ovary bilocular, ovules uniseriate. Fruit capsule elongate, bilocular, longitudinally dehiscent. Seeds glossy black; aril reduced, white. Stem, calyx, and center of labellum red-brown punctate.

Monocostus is a monotypic genus with the sole species, *M. uniflorus*, found only in San Martín, Peru, at an elevation of 500 m near the town of Tarapoto.

Monocostus uniflorus (Poepp. ex Petersen) Maas, Rev. Palaeobot. Palynol. 7: 37. Fig. 9. 1968. ≡ *Costus uniflorus* Poepp. ex Petersen, in Martius, Fl. Bras. 3, 3: 58. 1890 – Type: PERU, San Martín: Río Huallaga, Chazuta, Klug 4156 (neotype, GH!, designated by Maas, 1972, p. 18; isoneotypes, BM!, F!, K!, NY!, S!, U!, US!).

= *Monocostus ulei* K. Schum., in Engler, Pflanzenreich IV, 46: 428, 429. f. 51. 1904 – Type: PERU, San Martín: Río Mayo, vicinity of Tarapoto, Ule 6333 (lectotype, MG!, designated by Maas, 1972. p. 18.).

2. **Dimerocostus** Kuntze, Rev. Gen. Pl. 2: 687. 1891. Type: *Dimerocostus strobilaceus* O. Kuntze
= *Mulfordia* Rusby, Bull. Torrey Bot. Club 55: 165.

photographs of type; holotype destroyed at B).

= *Dimerocostus williamsii* J. F. Macbr., Field Mus. Nat. Hist. Bot. Ser. 11: 50. 1931 – Type: PERU, Loreto: Urimaguas, Fortaleza, *Williams 4291* (holotype, F!).

c. *Dimerocostus strobilaceus* subsp. *appendiculatus* Maas, Fl. Neotrop. Monogr. 8: 25. 1972 – Type: PERU, Loreto: Hacienda Indiana near mouth of Río Napo, *Asplund 14727* (holotype, S!).

Dimerocostus argenteus (Ruiz & Pav.) Maas, Rev. Palaeobotan. Palynol. 7: 37. f. 13. 1968. ≡ *Costus argenteus* Ruiz & Pav., Fl. Peruv. [Ruiz & Pavon] 1: 3. t. 4. 1798 – Type: PERU, Huánuco, near Chinchao and Cuchero, *Ruiz & Pavon s.n.* (holotype, MA!; isotypes, BM!, F!, FI, G!)

= *Costus mooreanus* Rusby, Bull. New York Bot. Gard. 4: 454. 1907 – Type: BOLIVIA, Cochabamba, *Bang 2058* (holotype, NY!; isotype, US!).

= *Mulfordia boliviana* Rusby, Bull. Torrey Bot. Club 55: 166, f. 1–6. 1928. ≡ *Dimerocostus bolivianus* (Rusby) Loes., Notizbl. Bot. Gart. Berlin-Dahlem 10: 716. 1929 – Type: BOLIVIA, Beni: Rurrenabaque, *Cardenas 1165A* (holotype, NY!).

= *Dimerocostus bicolor* J. F. Macbr., Publ. Field Columbian Mus., Bot. Ser. 8: 114. 1930 – Type: PERU, Huánuco: Hacienda Vilcabamba, Río Chinchao, *Macbride 5001* (holotype, F!; isotype, G!).

3. *Chamaecostus* C. Specht & D. W. Stev., gen. nov. – Type: *Chamaecostus subsessilis* (Nees & Mart.) C. Specht & D. W. Stev. Etymology: chamae (χαμαι) = low to the ground, creeping (Greek).

Plantae parvae aliquando acaulescentes vel caulis humilis provisae. Folia plerumque rosettam formantes. Inflorescentia multiflora. Bracteae herbaceae vel coriaceae. Bracteolae naviculiformes. Labellum magnum apertum speciosum, luteum vel aurantiacum ad albidum. Ovarium triloculare.

Low or diminutive plants, occasionally acaulescent rosettes, never exceeding 1 m in height with stems less than 1 cm in diameter. Leaves elliptical, acuminate to long-acuminate at the apex. Inflorescence often capitate, not tightly compressed. Bracts chartaceous to herbaceous, green or green-yellow often with deltate appendages. Bracteole membranous, tubular, bicarinate adaxially. Calyx membranous, cylindrical, toothed at apex. Corolla tube exerted from the calyx; lobes large, membranous, lanceolate. Labellum large, forming a long narrow tube that opens broadly to ovate at the apex, greatly ex-

ceeding petals and bracts in length. Corolla and labellum usually of the same color, yellow or orange to white (but vibrant red in *C. lanceolatus*). Stamen petaloid; tip reflexed, triangular, covering the opening to the nectary chamber. Pollen grains large to very large according to Maas (1972). Ovary trilocular. Stigma cup-shaped. Fruit capsule membranaceous, tardily dehiscent. Floral parts red-brown punctate.

The genus *Chamaecostus* comprises eight species with a distribution restricted to South America, from the Guyana Shield to the Amazonian lowlands of Bolivia and Brazil at the western edge of the Brazilian shield. The plants are small in stature, which initially prompted their separation from the remaining neotropical members of the genus *Costus* into the subgenus *Cadalvena*. In addition, they have an open labellum that is more character-

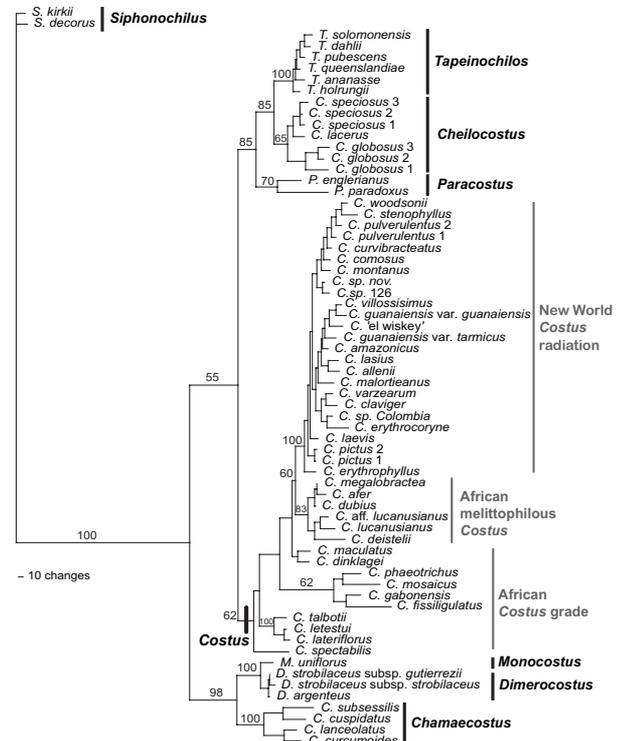


Fig. 1. The phylogenetic hypothesis for Costaceae from nuclear and chloroplast sequence data plus morphology (Specht & al., 2001; Specht, 2006). Genera in bold, including new genera. *Paracostus* and *Cheilocostus* include complete or almost complete taxonomic sampling of currently described species, while *Chamaecostus* is represented by 4 of 8 total species. Complete species lists are provided in the descriptions. *Tapeinochilos* is represented in the figure by six of the described 18 species, while *Monocostus* (monotypic) and *Dimerocostus* (2–3 species) are fully represented based on currently described taxa. Within *Costus*, three groups are informally recognized: a monophyletic New World *Costus* radiation clade, a monophyletic African melittophilous *Costus* clade, and a basal African *Costus* grade.

istic of *Monocostus* and *Dimerocostus* in the New World, as well as several species of African and Asian *Costus*.

The genus *Cadalvena* as described by Fenzl (1865) encompasses many of the characters that are used to distinguish the new genus *Chamaecostus*. However, *Cadalvena* was circumscribed to include African taxa, most notably *Cadalvena spectabilis* (= *Costus spectabilis*), the type of the genus. This species is not included in the current circumscription because it is a member of *Costus* (Fig. 1), and thus the *Cadalvena* name is inapplicable. *Cadalvena* was recognized as a genus by Thiselton-Dyer (1898) in his monograph for the Flora of Tropical Africa, where two species were recognized as described by Fenzl (1865) and one new species (*C. pistiaefolia*) was described. *Cadalvena* was later sunk to subgeneric status by Schumann (1904). This subgeneric status of *Cadalvena* was maintained by Loesener (1930) and became the standard circumscription for the placement of newly defined species and the organization of local floras and monographs. In the current study, the African species once placed in *Cadalvena* are not part of the *Chamaecostus* clade (Fig. 1) and thus will remain in the genus *Costus*. *Costus* s.s. does not retain any subgenera.

Thus, the early definition of *Cadalvena* as a separate genus from *Costus* appears to have been correct in theory, if not in circumscription. It is notable that Maas maintained *Cadalvena* as a subgenus and placed several of the later discovered South American taxa in the subgenus, all of which are transferred to the new genus *Chamaecostus*. Schumann's and later Maas' concept of *Cadalvena* is essentially correct.

Synapomorphies for identification of *Chamaecostus* include small stature (<1 m), cup-shaped stigma (shared with *Monocostus* and *Dimerocostus*), open labellum (shared with *Monocostus*, *Dimerocostus*, and *Cheilocostus* but those either not small in stature (*Cheilocostus* and *Dimerocostus*) or with solitary flowers (*Monocostus*), ovary and tube of labellum red-brown punctate (shared with *Monocostus*).

Chamaecostus subsessilis (Nees & Mart.) C. Specht & D. W. Stev., **comb. nov.** ≡ *Globba subsessilis* Nees & Mart., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11: 29. 1823. ≡ *Costus subsessilis* (Nees & Mart.) Maas, Acta Bot. Neerl. 24: 469. 1976 – Type: BRAZIL, Bahia: “ad viam Felisbertiam,” 1817, *Wied-Neuwied s.n.* (holotype, BR!).
= *Costus warmingii* Petersen, in Martius, Fl. Bras. 3, 3: 57. 1890 – Type: BRAZIL, Minas Gerais: Lagôa Santa, *Warming 502* (holotype, C!).

Chamaecostus cuspidatus (Nees & Mart.) C. Specht & D. W. Stev., **comb. nov.** ≡ *Globba cuspidata* Nees & Mart., Nova Acta Phys.-Med. Acad. Caes. Leop.-

Carol. Nat. Cur. 11: 28. 1823. ≡ *Costus cuspidatus* (Nees & Mart.) Maas, Acta Bot. Neerl. 24: 469. 1976 – Type: BRAZIL, Bahia: “ad ripas fluminis Ilhéos, circa viam Felisbertiam,” 1817, *Wied-Neuwied s.n.* (holotype, BR!).

= *Costus igneus* N. E. Brown, Ill. Hort. 31: 25. pl. 511. 1884 – Type: Hort. Kew, January 1884 (holotype, K!).

Chamaecostus curcumoides (Maas) C. Specht & D. W. Stev., **comb. nov.** ≡ *Costus curcumoides* Maas, Fl. Neotrop. Monogr. 8: 34. 1972 – Type: FRENCH GUIANA, Río Approuague: Crique Anis near Mapaou, *Oldeman B-553* (holotype, P!; isotype, P!).

Chamaecostus fusiliformis (Maas) C. Specht & D. W. Stev., **comb. nov.** ≡ *Costus fusiliformis* Maas, Fl. Neotrop. Monogr. 8: 37. 1972 – Type: BRAZIL, Pará: Rio Tapajós, Varadouro de Periquito near Pimental, *Kuhlmann 1916* (holotype, U!; isotype, RB!).

Chamaecostus fragilis (Maas) C. Specht & D. W. Stev., **comb. nov.** ≡ *Costus fragilis* Maas, Fl. Neotrop. Monogr. 8: 37. 1972 – Type: BRAZIL, Amazonas-Pará: Rio Tapajós, Cachoeira da Montanha, *Ducke 14127* (holotype, RB!; photograph, U!).

Chamaecostus lanceolatus (Petersen) C. Specht & D. W. Stev., **comb. nov.** ≡ *Costus lanceolatus* Petersen, in Martius, Fl. Bras. 3, 3: 56. 1890 – Type: FRENCH GUIANA: *L.C. Richard s.n.* (holotype, P!).

a. *Chamaecostus lanceolatus* subsp. *lanceolatus*
= *Costus phlociflorus* Rusby, Bull. Torrey Bot. Club 29: 694. 1902 – Type: BRAZIL, Amazonas: Rio Madeira, near falls, *Rusby 2229* (holotype, NY!; isotypes, F!, GH!, US!).

b. *Chamaecostus lanceolatus* subsp. *pulchriflorus* (Ducke) C. Specht & D. W. Stev., **comb. nov.** ≡ *Costus pulchriflorus* Ducke, Arch. Jard. Bot. Rio Janeiro. 3: 22. t. 2 a–c. 1922. ≡ *Costus lanceolatus* subsp. *pulchriflorus* (Ducke) Maas, Fl. Neotrop. Monogr. 8: 41. 1972 – Type: BRAZIL, Pará: Rio Tocantins, Alcobaca, *Ducke 15649* (lectotype, G, designated by Maas, 1972; isolectotypes, P!, RB!, US!).

Chamaecostus congestiflorus (Rich. ex L. F. Gagnep.) C. Specht & D. W. Stev., **comb. nov.** ≡ *Costus congestiflorus* Rich. ex L. F. Gagnep., Bull. Soc. Bot. France ser. 4, 2: 97. 1902 – Type: FRENCH GUIANA: locality unknown, *Poiteau s.n.* (holotype, K!).

4. *Cheilocostus* C. Specht, **gen. nov.** – Type: *Cheilocostus speciosus* (J. Koenig) C. Specht. Etymology: cheilo = lip (Greek) for the large labellum; close evolutionary relationship with *Tapeinochilos*.

Plantae magnae. Caules ramosae. Bracteae lignae, pungentae, rubrae vel rubiginosae ad brunneae. Labellum magnum, apertum, speciosum sine staminodiis lateralibus. Ovarium triloculare.

Plants tall, >1.5 m, branching at higher nodes with secondary branching, branches breaking through leaf-sheaths. Leaves seasonally deciduous, attached to sheath by short petiole which is articulated at the junction. Vegetative parts almost entirely glabrous with pubescence restricted to the underside of leaves. Inflorescence an elongate spike, terminal either emerging directly from the rhizome on a leafless stem or terminating a vegetative shoot. Bracts chartaceous (to woody), red or brown, unappendaged. Bracteole chartaceous, tubular, adaxially bicarinate. Calyx 3-lobed, lobes of equal size, pungent at each apex with a single hardened point, often greatly exceeding bracts in length, cylindrical. Corolla tube exerted from the calyx; lobes large, membranous, lanceolate. Labellum large, obovate, thin, forming a long narrow tube that opens broadly to ovate at the apex, greatly exceeding petals and bracts in length, never lobed; colored white, yellow to orange and sometimes red (*C. globosus*). Stamen petaloid; tip reflexed, triangular, covering the opening of the floral tube. Nectaries in two hollows connected to a gland in apex of ovary. Ovary trilocular; ovules many, in two rows. Stigma modified cup-shaped with small rounded dorsal appendage. Fruit capsule 3-angled, lateral angles smaller and spreading, loculicidal, dehiscent via 3 slits, not splitting to the apex, dry. Seeds angular, usually with a small white fleshy aril, all those in one locule adhering together by their arils upon dehiscence; embryo straight in copious endosperm.

The distribution of *Cheilocostus* is restricted to South East Asia, Malaysia and New Guinea. All taxa placed in the genus *Cheilocostus* were originally placed in *Costus* subg. “*Eucostrus*” (i.e., subg. *Costus*) by Schumann (1904). Based on Schumann’s definition, *C.* subg. *Costus* was the largest division of the genus *Costus* and included all structurally “large” plants (>1.5 m), independent of differences in inflorescence architecture or floral morphology within this group. The type subgenus included all large plants that occurred in the Neotropics as well as Africa and Southeast Asia. The Asian taxa placed in *C.* subg. *Costus* (here moved to *Cheilocostus*) were the only taxa with an open labellum which characterizes his subgenera *Cadalvena*, *Epicostus*, *Metacostus* and *Paracostus*. Several African taxa with the open floral form were also placed in *C.* subg. *Costus* due to their

large stature (e.g., *Costus dewevrei*, *C. fissiligulatus*, *C. phyllocephalus*, *C. deistellii*, and *C. ligularis*). These are not closely related to the Asian *Cheilocostus* clade but rather form a paraphyletic grade leading to the core *Costus* clade, which contains ornithophilus and melitotophilus floral forms with a closed labellum.

Cheilocostus lacerus is found to be closely related to *Cheilocostus speciosus*, with which it forms a strongly supported clade based on both morphological and molecular evidence (Fig. 1). Although closely aligned with *Cheilocostus speciosus* based on overall morphological similarity, *C. lacerus* is easily distinguished from *C. speciosus* by its densely imbricate bracts that form a rotund inflorescence and delacerate into fibers at the tips upon maturation of the inflorescence.

Cheilocostus sopuensis is only known from a single collection but is distinguished from the other taxa by its extremely long, lanceolate inflorescence with densely imbricate bracts and short calyces that do not extend beyond the bracts and are thus hidden within the inflorescence. *Cheilocostus sopuensis*, *C. lacerus*, and *C. speciosus* all have red bracts and calyces, whereas *C. globosus* (or species within this complex) have brown bracts and calyces.

Synapomorphies for the identification of *Cheilocostus* are pungent bracts either red or brown in color (as in *Tapeinochilos*) but combined with the open-labellum floral form; vegetative axillary branching (as in *Tapeinochilos*) with trilocular ovaries (*Tapeinochilos* has bilocular ovaries); seasonally deciduous; fruit a woody capsule that splits open on one side to expose black, angular seeds.

Cheilocostus speciosus (J. Koenig) C. Specht, **comb. nov.** ≡ *Costus speciosus* (J. Koenig) Sm., Trans. Linn. Soc. 1: 249. 1791. ≡ *Banksea speciosa* J. Koenig, in Retzius, Observ. 3: 75. 1784 – Type: EAST INDIES: *J. König s.n.* (C).

= *C. lamingtonii* F. M. Bailey, Queensland Agric. J. 3: 160. 1898 – Type: PAPUA NEW GUINEA, N. Division: Mambare river, May 1898, *Lord Lamington’s Party s.n.* (BRI!).

= *Costus formosanus* Nakai, J. Jap. Bot. 17: 199. 1941. ≡ *Costus speciosus* var. *formosanus* (Nakai) S. S. Ying, Quart. J. Chinese Forest. 21: 117. 1988 – Type: CHINA: Taiwan, Takao, Heitô (Akô-)Trail, opposite Datetu, *T. Sôma s.n.* (P!).

Cheilocostus speciosus has a long series of synonyms (see Maas, 1972) primarily due to its distribution throughout the tropics as a horticultural plant of interest. Plants growing in cultivation often escape into primary forest or disturbed habitats and become part of the local flora and named in local monographs. In addition, *C. speciosus* appears to be a highly variable taxon, and

many of the variations were ascribed to new species prior to Schumann's monograph (1899).

Cheilocostus lacerus (L. F. Gagnepain) C. Specht, **comb. nov.** ≡ *Costus lacerus* L. F. Gagnepain, Bull. Soc. Bot. France 4, ser. 3, 50: 261. 1903 – Type: INDIA, Ladak, 5000 ft, 30 July 1884, *unknown collector s.n.* (P!).

Cheilocostus globosus (Blume) C. Specht, **comb. nov.** ≡ *Costus globosus* Blume, Enum. Pl. Javae 62. 1828 – Type: Introduced from Java to hort. Leiden, *Blume s.n.* (L).

Cheilocostus globosus as currently circumscribed is probably a complex of species that need further monographic work. Species in this complex are (as cited in Maas, 1979) *Costus acanthocephalus* K. Schum. (Sumatra), *C. chrysocephalus* K. Schum. (New Guinea), *C. clemensae* Ridley (Philippines), *C. dhanivatii* K. Larsen (Thailand), *C. globosus* Blume (Java), *C. kingii* Baker [= *C. globosus* var. *kingii* (Baker) Holtt., Malaysia], *C. microcephalus* K. Schum. (Borneo), *C. oligophyllus* K. Schum. (Malaysia), *C. ridleyi* K. Schum. [= *C. globosus* var. *ridleyi* (K. Schum.) Holttum, Malaysia and Thailand], *C. sulfurous* K. Schum. (Sulawesi), *C. tonkinensis* L. F. Gagnep. (Tonkin), *C. velutinus* Ridley [= *C. globosus* var. *velutinus* (Ridley) Holtt., Malaysia]. The complex is characterized by an inflorescence on a separate leafless shoot and by woody bracts which are spiny at the apex. The major variations occur in labellum shape and structure as well as coloration of the petals and the labellum. However, the species have been distinguished primarily upon differences in pubescence of vegetative structures and bract characters. The variability in floral characters does not appear to coincide with variability of vegetative characters, making clear species distinctions difficult. For example, Ridley distinguished four separate species of *Costus* in the Malay Peninsula, whereas Holttum (1950) indicated that all these species were actually variants of a single species *C. globosus*. Clearly, further assessment of the situation requires a monographic revision of the *globosus* complex.

Cheilocostus sopuensis (P. J. M. & H. Maas) C. Specht, **comb. nov.** ≡ *Costus sopuensis* P. J. M. & H. Maas, Notes Roy. Bot. Gard. Edinburgh 41: 325. 1983 – Type: SULAWESI, Sopu valley c. 80 km SSE of Palu, 20 May 1979, *van Balgooy & al.* 3424 (holotype, L!).

5. *Costus* L. in Sp. PL. 1: 2. 1753 – Type: *Costus arabicus* L.
= *Banksia* J. Koenig, in Retzius, Observ. 3: 75. 1784 (not *Banksia* J. R. Forst. & G. Forst., 1775, nor

Banksia L. f., 1782, nom. cons.) ≡ *Hellenia* Retz., Observ. 6: 18. 1791 ≡ *Tsiana* J. F. Gmel., Syst. Nat. 2: 1, 9. 1791 ≡ *Planera* Giseke, Praelect. 205. 1792 (not of Gmelin, 1791) – Type: *B. speciosa* J. Koenig (≡ *Hellenia grandiflora*).

= *Jacuanga* T. Lestib., Ann. Sci. Nat. Bot. ser. 2, 15: 329, 341. 1841 – Type: *Costus pisonis* Lindl.
= *Cadalvena* Fenzl, Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 51: 139. 1865 – Type: *Cadalvena spectabilis*.

Rhizomatous perennial herbs of moderate to large habit, 2–5 m, stems unbranched. Stems erect from rhizome, covered near base with leafless sheaths, leafy higher up. Leaves spirally arranged with closed, ligulate sheaths. Ligule typically large and pronounced. Inflorescence terminal on leafy stem or on special leafless shoots directly from the rhizome, spiciform, cone-like, with conspicuous persistent imbricated bracts. Bracts coriaceous, narrowly to broadly ovate, often terminating in a foliaceous appendage. Calyx more or less equal lobed, rarely exceeding the bracts; stamen 1, petaloid. Labellum equaling or surpassing the corolla. Ovary inferior, trilocular, containing numerous ovules in rows of 2. Fruit fleshy, globose, tardily dehiscent or indehiscent in which case seeds are released by the decaying of the fruit wall. Seeds black, elliptical, with large white lacinate aril.

An exhaustive species list will not be given in this treatment considering that all *Costus* species not included in the proposed new genera will remain in the genus *Costus*. Based on the current phylogenetic results, several strongly supported monophyletic lineages of *Costus* are resolved such as the clade of Neotropical taxa (the *Costus* radiation clade) and the African melittophilous clade, however recognition of these clades would result in a basal grade of African taxa excluded from subgeneric recognition. For this reason, those taxa not explicitly mentioned in this treatment are considered to remain part of the genus *Costus*, which as currently described contains no official subgenera or sections.

The genus *Costus* is by far the largest genus in the family Costaceae and has the broadest circumscription, including most of the morphological diversity in the family. As circumscribed, its distribution is restricted to the tropical moist forests of Africa and America with species diversity centered in the neotropics.

As noted above, Schumann (1899) divided the large genus into five subgenera, with *C.* subg. *Costus* (“*Eucostus*”) being the largest and comprising the majority of the species included in the genus *Costus*. Schumann's type subgenus is not, however, completely congruent with *Costus*, as recognized here, as Schumann (1904) included all Asian taxa currently placed in *Cheilocostus*

and several taxa now included in *Chamaecostus*. Schumann also distinguished subgenera *Epicostus* and *Metacostus*, which for the most part include those taxa found, in the present study, in the basal grade (see Fig. 1). There is no support for the monophyly of these subgenera and the characters used to define them are found to be either plesiomorphic (open labellum, small stature) or are found in more than one lineage within the grade (epiphytic habit, Fig. 1).

Maas (1977) divided the neotropical species of *Costus* subgenus *Costus* into two sections, *Costus* and *Ornithophilus*, with sect. *Costus* being bee-pollinated and sect. *Ornithophilus* being hummingbird-pollinated. The first section he characterized as “having a labellum with a short, rather broad tube, and a distinct, exposed limb; its color varies from white to yellow, but the lateral lobes are often striped with red to purple.” The bracts of this group are typically green. The second section is comprised of species with “a small, tubular labellum of yellow, orange, or reddish colour: the bracts are of the same colour, or rarely green.” The results reported here show that these two sections do not actually form monophyletic groups, but rather that ornithophily and melittophily are homoplasious when viewed as individual characters. However, all New World taxa with these two floral forms comprise a strongly supported clade that is sister to a clade of African melittophilous taxa. This clade is informally referred to as the “*Costus* radiation clade” and will not be formally named here due to the paraphyly of the remaining *Costus* species (Fig. 1).

Further studies including a detailed monograph of the African species may yield better resolution within *Costus* and allow for taxonomic definition of significant infrageneric lineages. Further division of the genus *Costus* into subgenera awaits investigations involving revisionary work on African species.

6. *Tapeinochilos* Miq., Ann. Mus. Bot. Lugduno-Batavi 4: 101. t. 4. 1869. (nom. et orth. cons.) – Type: *Tapeinochilos pungens* (Teijs. & Binn.) Miq. ≡ *Costus pungens* Teijs. & Binn. = *T. ananassae* (Hassk.) K. Schum.

Plants medium to large rhizomatous herbs; rhizomes thick and fleshy, aerial shoots cane-like, up to 6 m tall, straight or slightly twisted, branching with spirally arranged branches emerging from upper nodes. Primary branches often emerge just below an inflorescence if inflorescence terminates a leafy stem. Leaves arranged spirally with closed sheaths; petioles very short, terminal leaves sessile; leaf blades obovate or elliptic; adaxial surface glabrous, abaxial surface glabrous or pubescent. Inflorescence a strobilaceous spike, terminating a leafy stem or on a separate leafless shoot arising directly from

the rhizome. Bracts coriaceous, woody, or sometimes herbaceous, each subtending a single flower, arranged into 13 straight or slightly curved orthostichies. Bracteoles mostly absent. Flowers sessile. Calyx tubular at base, 3-lobed, lobes unequal with anterior lobe smaller than the two posterior lobes. Corolla fused at the base, 3-lobed, posterior lobe broader and longer than other two, imbricate in bud. Stamen 1, petaloid. Labellum 5-lobed, ovate or oblong, inconspicuous. Ovary bilocular. Septal nectaries present in upper part of ovary. Stigma bilamellate. Fruit a capsule, slightly fleshy, indehiscent or tardily dehiscent along slits. Seeds black, arillate.

Sixteen species are currently recognized for *Tapeinochilos* (Gideon, 1996), all of which form a monophyletic group within the family Costaceae. The current study does not require any changes to be made to the accepted generic circumscription. The species are listed in Gideon (1996) and will not be repeated here.

The range of the *Tapeinochilos* extends from Sulu Islands of the Moluccas Archipelago through New Guinea, to Vanatu in the east and tropical Australia (Northern Queensland) in the south. The center of diversity of *Tapeinochilos* is in New Guinea, with over 80% of the species found there.

The status of *Tapeinochilos* as a separate genus within Costaceae has been recognized since the discovery and naming of the genus and the recognition of its close association with *Costus*. In the past, *Tapeinochilos* was proposed to be related to an ornithophilus group of new world *Costus*, based primarily on the closed labellum and the appearance of the bracts (Maas, 1977). The present study resolves *Tapeinochilos* as monophyletic and sister to *Cheilocostus*, forming a South East Asian with *Paracostus* (Fig. 1). Morphological synapomorphies supporting this sister relationship include woody, recurvate bracts often with a pungent or sharply-pointed apex, primary and secondary branching of vegetative stems, and the uniformly glabrous upper leaf surface, the lower leaf surface being either glabrous or puberulous. Although the flowers differ substantially between *Tapeinochilos* and *Cheilocostus*, the vegetative and inflorescence characters provide support for this evolutionary affiliation. *Tapeinochilos* thus appears to have evolved from a single common ancestor shared with *Cheilocostus*, most likely located in South East Asia and probably maintaining the plesiomorphic open labellum floral form found in *Cheilocostus*. A good candidate is a *C. globosus*-like ancestor. In several populations of *C. globosus*, the flowers are red and have a reduced labellum, potentially indicating a transitional state between the open floral form of *Cheilocostus* and the closed ornithophilus form of *Tapeinochilos*.

Following the separation of these two lineages, *Tapeinochilos* underwent a rapid but localized radiation

on the island of New Guinea. The *Cheilocostus* lineage seems to have undergone diversification at a much slower rate while maintaining (or possibly obtaining) a wider geographic distribution. The diversity within the *Cheilocostus globosus* complex, however, attests to the ability of the *Cheilocostus* lineage to diversify and potentially speciate. The comparatively rapid speciation within *Tapeinochilos* is particularly interesting in light of the current variability noted in the closely related *C. globosus* complex. As with the New World radiation, this rapid speciation in Asia may be related to the novel form of the flower enabling utilization of a novel resource for pollination by sunbirds.

7. *Paracostus* C. Specht, gen. nov. – Type: *Paracostus englerianus* (K. Schum.) C. Specht

Herbae humiles, scandentes. Folia pauca vel solitaria. Inflorescentia pauciflora, conica. Bracteae herbaceae acutae, virides vel atropurpureae. Labellum apertum speciosum album puncto centrali luteo. Ovarium triloculare.

Prostrate rhizomatous herbs or ascending as a climbing herb, 10–50cm in height with one or a few leaves each of which potentially subtends an axillary inflorescence. Rhizomes long, creeping. Leaves 1–4 per stem, fleshy, attached to sheath by short petiole. Vegetative parts entirely glabrous. Ligule short. Inflorescence an abbreviated spike emerging directly from the axis of a solitary leaf, few-flowered. Bracts membranaceous, green, unappendaged. Bracteole chartaceous, tubular. Calyx 3-lobed, lobes of equal size. Corolla tube exerted from the calyx; lobes membranous, narrow, lanceolate. Labellum large, obovate, thin, forming a long narrow tube that opens broadly to ovate at the apex, greatly exceeding petals and bracts in length, never lobed; white, sometimes with a yellow spot at the center directly opposite the fertile stamen. Stamen petaloid; tip reflexed, triangular, covering the opening of the floral tube. Ovary trilocular. Stigma cup-shaped without appendage. Fruit globose, capsular. Seeds angled with a membranaceous aril.

Paracostus was first defined by Schumann (1899) as one of his five subgenera of *Costus* and contained two species, *C. paradoxus* and *C. englerianus*. Maas (1979) recognized the subgenus in his description of *Costus paradoxus*.

The present results confirm that the two species are sister taxa and form a separate clade sister to the *Cheilocostus* plus *Tapeinochilos* lineage of South East Asia (Fig. 1). The *Paracostus* clade is elevated here to generic level, as it is not part of the genus *Costus* and is not nested in any other lineage.

Costus englerianus has always been described as having a terminal inflorescence with a single leaf. A recent study (C. Specht, unpubl.) shows that the inflorescence emerges from the axis of the leaf and appears terminal due to secondary displacement along with lack of continued apical growth of the shoot meristem. The axillary inflorescence together with together with the prostrate habit, unifoliate stems, and the few-flowered (<3 flowers) axillary inflorescence are a synapomorphies of *Paracostus*.

***Paracostus englerianus* (K. Schum.) C. Specht, comb. nov.** ≡ *Costus englerianus* K. Schum., Bot. Jahrb. Syst. 15: 419, t. 13. 1881 – Type: CAMEROUN: west of Barombi-ba-mbu, *Preuss n. 461* (B!). = *Costus unifolius* N.E. Br., Gard. Chron. ser. 3, 12: 696. 1892 – Type: cultivated at Kew, *N. E. Brown s.n.* (K).

***Paracostus paradoxus* (K. Schum.) C. Specht, comb. nov.** ≡ *Costus paradoxus* K. Schum., Bot. Jahrb. Syst. 27: 345. 1899 – Type: MALAYSIA, Sarawak: prov. Redjang, Bellaga, *Beccari, Pi. Born. 3791* (FI!).

ACKNOWLEDGEMENTS

The authors thank Michael Nee for nomenclatural advice and suggestions (especially for brainstorming the chamae- prefix), Dan Nicolson for his critical review of the manuscript and generous tutoring in Latin, S. Robbert Gradstein and John McNeill for providing helpful suggestions and editing, and Axel Poulsen and John Mood for supplying material of undescribed and described Asian Costaceae now included in *Cheilocostus*. This research was supported by NSF Doctoral Dissertation Improvement grant DEB-0206501, a J.S. Karling Graduate Student Research Award from the Botanical Society of America, the Graduate Studies Program at the New York Botanical Garden, New York University's Graduate School of Arts and Science and Department of Biology, a Fulbright Research Fellowship to CDS, and the Lewis B. and Dorothy Cullman Program in Molecular Systematic Studies.

LITERATURE CITED

- Fenzl, E. 1865. Scitaminae. *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1.* 51: 139.
- Gideon, O. 1996. *Systematics and Evolution of the Genus Tapeinochilos* Miq. (Costaceae, Zingiberaceae). Ph.D thesis, James Cook Univ., Queensland.
- Greuter, W., McNeill, J., Barrie, F. R., Burdet, H. M., Demoulin, V., Filgueiras, T. S., Nicolson, D. H., Silva, P. C., Skog, J., Trehane, P., Turland, N. J. & Hawksworth, D. L. (eds.). 2000. *International Code of Botanical*

- Nomenclature (Saint Louis Code) Adopted by the Sixteenth International Botanical Congress, St. Louis, Missouri, July–August 1999.* Koeltz Scientific Books, Königstein. [*Regnum Veg.* 138.]
- Hepper, F. N.** 1968. Zingiberaceae. *Flora of West Tropical Africa*, ed. 2, 3: 69–79.
- Holttum, R. H.** 1950. The Zingiberaceae of the Malay Peninsula. *Gard. Bull. Singapore* 13: 240–245.
- Kirchoff, B. K.** 1988. Inflorescence and flower development in *Costus scaber* (Costaceae). *Canad. J. Bot.* 66: 339–345.
- Kirchoff, B. K. & Rutishauser, R.** 1990. The phyllotaxy of *Costus* (Costaceae). *Bot. Gaz.* 151: 88–105.
- Koechlin, J.** 1964. Scitaminales. *Flore du Gabon* 9: 62–88.
- Koechlin, J.** 1965. Scitaminales. *Flore du Cameroun* 4: 1–104.
- Kress, W. J.** 1990. The phylogeny and classification of the Zingiberales. *Ann. Missouri Bot. Gard.* 77: 698–721.
- Kress, W. J.** 1995. Phylogeny of the Zingiberanae: morphology and molecules. Pp. 443–460 in: Rudall, P., Cribb, P. J., Cutler, D. F. & Humphries, C. J. (eds.), *Monocotyledons: Systematics and Evolution*. Royal Botanic Gardens, Kew.
- Kress, W. J., Prince, L. M., Hahn, W. J. & Zimmer, E. A.** 2001. Unraveling the evolutionary radiation of the families of the Zingiberales using morphological and molecular evidence. *Syst. Biol.* 50: 926–944.
- Lock, J. M.** 1985. Zingiberaceae. Pp. 1–23 in: Polhill, R. M. (ed.), *Flora of Tropical East Africa*. A. A. Balkema, Boston.
- Loesener, T.** 1930. Zingiberaceae. Pp. 547–640 in: Prantl, E. A. (ed.), *Die Natürlichen Pflanzenfamilien* 15A. W. Engelmann, Leipzig.
- Maas, P. J. M.** 1972. Costoideae (Zingiberaceae). *Flora Neotropica Monographs* 8: 1–140.
- Maas, P. J. M.** 1977. *Renealmia* (Zingiberoideae) and Costoideae additions (Zingiberaceae). *Flora Neotropica Monographs* 18: 1–218.
- Maas, P. J. M.** 1979. Notes of Asiatic and Australian Costoideae (Zingiberaceae). *Blumea* 25: 543–549.
- Nakai, T.** 1941. *Notulae ad Plantae Asiae Orientalis*. Costaceae. *J. Jap. Bot.* 17: 197–203.
- Schumann, K.** 1899. Monographie der Zingiberaceae von Malaisien un Papuasien. *Bot. Jahrb. Syst.* 27: 259–350.
- Schumann, K.** 1904. Zingiberaceae. Pp. 1–458 in: Engler, A. (ed.), *Das Pflanzenreich IV*. W. Engelmann, Leipzig.
- Specht, C. D.** 2006. Systematics and evolution of the tropical monocot family Costaceae (Zingiberales): a multiple dataset approach. *Syst. Bot.* 31: 88–105.
- Specht, C. D., Kress, W. J., Stevenson, D. W. & DeSalle, R.** 2001. A molecular phylogeny of Costaceae (Zingiberales). *Molec. Phylog. Evol.* 21: 333–345.
- Thiselton-Dyer, T.** 1898. *Flora of Tropical Africa*. Lovell Reeve and Co., London.
- Tomlinson, P. B.** 1956. Studies in the systematic anatomy of the Zingiberaceae. *Bot. J. Linn. Soc.* 55: 547–592.
- Tomlinson, P. B.** 1962. Phylogeny of the Scitamineae—morphological and anatomical considerations. *Evolution* 16: 192–213.