GONDWANAN VICARIANCE OR DISPERSAL IN THE TROPICS? THE BIOGEOGRAPHIC HISTORY OF THE TROPICAL MONOCOT FAMILY COSTACEAE (ZINGIBERALES)

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ABSTRACT

Costaceae are a pantropical family, distinguished from other families within the order Zingiberales by their spiral phyllotaxy and showy labellum comprised of five fused staminodes. While the majority of Costaceae species are found in the neotropics, the pantropical distribution of the family as a whole could be due to a number of historical biogeographic scenarios, including continental-drift mediated vicariance and long-distance dispersal events. Here, the hypothesis of an ancient Gondwanan distribution followed by vicariance via continental drift as the leading cause of the current pantropical distribution of Costaceae is tested, using molecular dating of cladogenic events combined with phylogeny-based biogeographic analyses. Dispersal-Vicariance Analysis (DIVA) is used to determine ancestral distributions based upon the modern distribution of extant taxa in a phylogenetic context. Diversification ages within Costaceae are estimated using chloroplast DNA data (*trn*L–F and *trn*K) analyzed with a local clock procedure. In the absence of fossil evidence, the divergence time between Costaceae and Zingiberaceae, as estimated in an ordinal analysis of Zingiberales, is used as the calibration point for converting relative to absolute ages. The results of the temporal analysis based on extant taxa indicate that the initial diversification within Costaceae occurred approximately 65 million years ago, long after the final break up of the Gondwanan supercontinent. Considering this minimum age of diversification, potential scenarios for the current biogeographic patterns found in Costaceae are presented in a temporal and spatial context. The evolution of specialized floral forms associated with specific pollinators is also discussed within the biogeographic framework.

Key words: Costaceae, diversification rates, Gondwana, local clocks, molecular clock, pantropical, Zingiberaceae.

INTRODUCTION

Pantropical distributions of plants and animals that are lacking intrinsic mechanisms for long-distance dispersal are often considered to indicate historic Gondwanan distributions, with the break-up of the supercontinent leading to vicariance-mediated diversification within lineages (Baum et al. 1998; Hurr et al. 1999; Bargelloni et al. 2000; Trewick 2000). While it has been suggested that the pantropical Costaceae exhibit a Gondwanan distribution pattern, this assumption has never been tested by cladistic or historical biogeographic methods. Recent studies of the monocotyledonous orders and families therein (Bremer 2000, 2002; Vinnersten and Bremer 2001) show that the origin of the major monocotyledonous lineages date back only to the early Cretaceous, approximately 100 million years ago (mya). This is about the time of the separation of major portions of Gondwana, notably the final separation of Africa from South America around 110–90 mya (Metcalf 2002; Sanmartín and Ronquist 2004) and thus vicariance via continental drift could have provided a mechanism for diversification within the major monocot lineages. Based on recent work dating the origin of and major diversification events within the monocot order Zingiberales (Kress and Specht 2006), it is quite possible that Zingiberales date back to 110 mya, making it possible that late Cretaceous continental drift played

a major role in the diversification of basal lineages of the order.

One of the four "Ginger families," Costaceae form part of the crown group of Zingiberales. The four families in this crown clade taken together have a modern pantropical distribution, however the ancestral distribution of the ginger families clade is optimized as neotropical (Kress and Specht 2006). Modern Costaceae are pantropically distributed with their center of species diversity located in South and Central America (ca. 95 neotropical species, ca. 15 African, ca. 23 Southeast Asian). According to previous analyses (Kress and Specht 2006), the common ancestor of Costaceae and its sister family, Zingiberaceae, was distributed in Africa, America, Melanesia and Southeast Asia. This geographic area is considered consistent with an historic Gondwanan distribution pattern.

Costaceae have small (2–4 mm long) arilate seeds contained in a thin-walled capsulate fruit that can be dry and dehiscent or fleshy and indehiscent, in the latter case the seeds being released with the decaying of the fruit wall. Little is known about seed dispersal, although ants and birds are thought to be involved in some species (Maas 1972; Schemske 1983), with the potential for bird dispersal of seeds effectively increasing the changes of long distance colonization events across terrestrial barriers and open water. Floating capsules could potentially be involved in dispersal across long distances in water, although the longevity of the seeds under such circumstances has not been tested.

Previous work at the ordinal level (Kress and Specht

2006) shows Costaceae diverged from Zingiberaceae approximately 105 mya. At this time, Gondwana was still largely intact. It is possible, then, based on biogeographic and temporal analyses, that the break-up of Gondwana influenced speciation within the Costaceae lineage during the mid-late Cretaceous, and long-distance dispersal and colonization events would not be required to explain the current wide distribution in modern-day wet tropical forests. Taxon sampling within the family is not sufficient in the ordinal-level study to date major cladogenic events, thus the role of continental vicariance or long-distance dispersal in speciation and diversification within Costaceae cannot be determined.

The following is a presentation of a more detailed investigation into the rates and dates of diversification within the Costaceae lineage, with special emphasis on the historical biogeography of the clade. Utilizing a chloroplast DNA-derived molecular phylogeny for a broad sampling of taxa representing the full taxonomic and biogeographic diversity of the family, the historical patterns of biogeography and dates of diversification are analyzed to test the Gondwanan-origin and dispersal/vicariance scenario that could best explain the events leading to the current pantropical distribution of the group. Biogeographic scenarios for species radiations within the family are also discussed, and associations with specific pollinators as a potential factor in the increased species diversity in the neotropics is addressed.

MATERIALS AND METHODS

Phylogenetic Reconstruction

A data matrix was constructed with chloroplast DNA sequence data (*trn*L–F and *trn*K, including the full *mat*K coding region) for 36 ingroup taxa (out of ca. 125 total Costaceae) and 1 outgroup taxon (*Siphonochilus* J. M. Wood & Franks, Zingiberaceae) [Table 1]. Ingroup taxa represented all major monophyletic lineages within Costaceae (Specht in press) and were chosen to reflect the full geographic distribution of the family, with multiple samples within each area so as to enable dating of nodes that are common to unique geographic regions (see Table 1). The complete chloroplast DNA data set yielded a total of 4066 unambiguously aligned characters (811 informative) for 37 taxa with no missing data except for gapped regions treated as missing data. Parsimony analysis was performed using PAUP* vers. 4.0b10 (Swofford 2003) as a heuristic search with tree bisection reconnection (TBR) branch swapping, characters unordered, and stepwise addition for matrix building with 100 replicates and one tree held at each step. Insertions/deletions (indels) were coded as unique characters (21 total) and included in the parsimony analysis for topology building, but both coded indels and gapped regions were excluded in the branch length estimates for the subsequent maximum likelihood analysis.

Model Selection and Branch-Length Estimation

Modeltest vers. 3.0 (Posada and Crandall 1998) was used in combination with PAUP* vers. 4.0b10 to compare likelihood models and select the simplest model for estimating branch lengths that is not significantly different from the best-fitting model, using the Akaike Information Criterion (AIC) and likelihood ratio tests (LRT) with the default alpha level of significance (0.01). The use of simpler models decreases the error of estimated parameters, including branch length estimations critical for molecular dating analyses (Swofford and Olsen 1990). A parsimony-derived starting tree was used to select the model and estimate parameters (search = heuristic, addition sequence = random, number of replicates = 100, branch swapping = TBR). A full heuristic maximum likelihood search was performed with PAUP* vers. 4.0b10 using the appropriate model with base frequencies and gamma shape parameter estimated from the data, 10 random addition sequence replicates retaining all minimal trees and TBR branch swapping. Analyses were performed with and without the ''enforce molecular clock'' option selected and a LRT was performed using the log likelihood scores from these searches in order to test for adherence to a global molecular clock.

Divergence Time Estimation

A pairwise relative rates test was used to investigate rate heterogeneity among and between taxa, implemented in Hy-Phy vers. 0.95 beta (Kosakovsky-Pond and Muse 1998–2003): model = F81, local option and all parameters constrained, outgroup = *Siphonochilus decorus* (Druten) Lock. This pairwise test examines rate constancy between the outgroup taxon (*Siphonochilus*) and two ingroup taxa simultaneously, testing for divergence from the expected pairwise rates under the null assumption of a molecular clock. The output provides information on statistical similarity of rates for each combination of taxa. For each pairwise comparison, taxa were grouped into bins that showed no statistically-significant dissimilarity from the expected substitutions per branch, as indicated by the absence of an asterisk (*) in the Hy-Phy output table. Taxa for which significantly dissimilar pairwise rates from the expected (as indicated with *, **, or *** as indications of statistically dissimilar rates at $P = 0.05$, 0.01 and 0.001, respectively) are noted and are grouped with taxa with similar pairwise relative rates based on multiple independent pairwise comparisons. Each bin was analyzed by investigating the individual branch lengths leading to the terminal taxa included in the bin, and an individual rate class corresponding to each bin was assigned to the appropriate branch or branches determined to be the cause of the rate heterogeneity based on visual inspection of branch lengths on the unconstrained chloroplast DNA phylogram (Jordan et al. 2003).

As with the Zingiberales data (Kress and Specht 2006), the local molecular clock method (Yoder and Yang 2000; Yang and Yoder 2003) was used to analyze the molecular data and estimate node ages for the chloroplast DNA data (*trn*L–F and *trn*K sequence data for 37 ingroup taxa plus one outgroup taxon). The local clock option of PAML vers. 3.14 (Yang 1997, 2003) was executed with four rate classes (0–3) assigned to designated branches on the tree. Using the Combined Analysis option in PAML (clock = 3), the chloroplast sequence data was divided into four data partitions: 1st, 2nd, and 3rd codon positions within the *mat*K coding region of the *trn*K gene region (partitions 1–3), and non-coding for the chloroplast intron and intergenic spacer regions
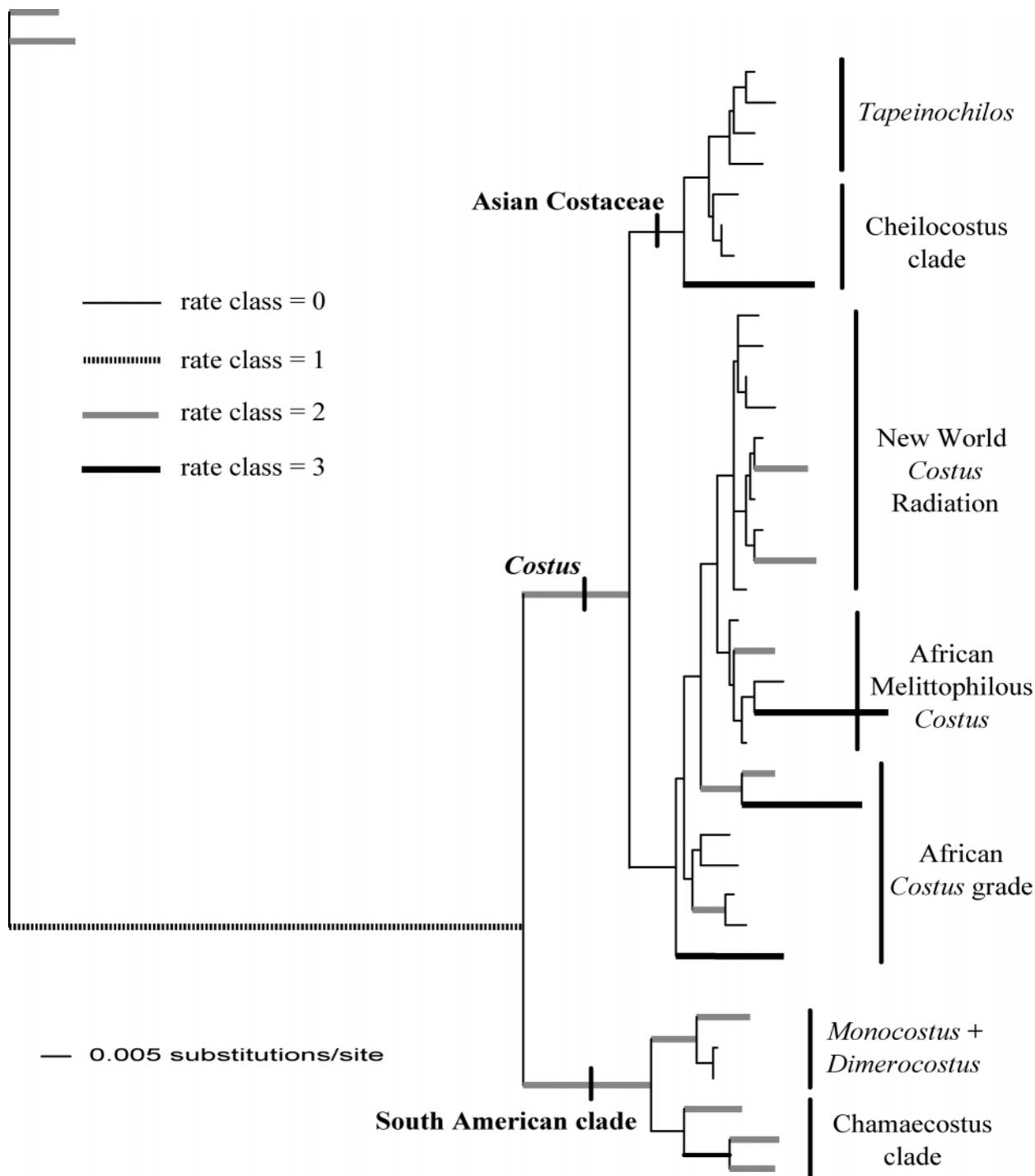
Fig. 1.—Phylogram of Costaceae based on analysis of chloroplast DNA data. Branch lengths estimated from combined maximum likelihood analysis of 37 *trn*L–F and 37 *trn*K (including *mat*K) sequences under the F81uf model of evolution (Felsenstein 1981). Similarly colored branches indicate single rate classes as assigned for PAML local molecular clock analysis. Rate classes were based on the results of multiple pairwise relative rates tests (implemented in Hy-Phy [Kosakovsky-Pond and Muse 1998–2003]).

(partition 4). Different alpha and kappa values were obtained for each data partition, thus accommodating heterogeneity in the combined data set. The *baseml* program of PAML was run with the following options: model = 2 (F81), Mgene = 4 (different rate ratio and frequency parameters for different partitions with proportional branch lengths), estimate kappa, estimate alpha, Malpha = 1 (different gamma distribution

for different parameters), ncatG = 5 (number of categories), clock = 3 (Combined Analysis), method = 0 (simultaneous). Option G was specified in the sequence file, which, in combination with the Mgene option, accounts for heterogeneity in the data. Standard errors were obtained as part of the algorithm.

At least one calibration point is required to convert rela-

Table 1.   Voucher and distribution information for species used in analysis. Living vouchers were sampled when herbarium vouchers were not available. Living collection localities are Harold L. Lyon Arboretum (L), New York Botanical Garden greenhouses (NY), Smithsonian greenhouses (NMNH), unless otherwise identified.

Species	Herbarium voucher no.	Living collection no.	GenBank accession numbers: trnL–F, trnK	Biogeographic distribution	Revised taxonomic affinity
Costus afer Ker Gawl.	Specht 02-312 (NY)	L. 87.0185	AY994588, AY994653	AY994653	African melittophilous Costus
Costus allenii Maas		NY 347/95A	AY994587, AY994652	Panama and NW South America	NW Costus radiation
Costus amazonicus (Loes.) J. F. Macbr.	Specht 02-327 (NY)	L. 95.0667	AY994586, AY994651	Central South America (Brazil, Peru, Ecuador)	NW Costus radiation
Costus claviger R. Benoit	Nagata 2361 (HLA, E)	L 80.0705	AY994584, AY994649	Northern South America	NW Costus radiation
Costus curcumoides Maas		X95-0116-29 (Brussels)	AY994601, AY994668	French Guiana	Chamaecostus
Costus cuspidatus (Mart. & Nees) Maas	Kress 94-3681 (US)	NMNH 94-676	AY994582, AY994647	Southeastern Brazil	Chamaecostus
Costus deistelii K. Schum.		61-5174 (Brussels)	AY994599, AY994666	West Africa	African melittophilous Costus
Costus dinklagei K. Schum.	Mass 3549 (U)	L 92.0048	AY994596, AY994663	Africa	African melittophilous Costus
Costus dubius (Afzel.) K. Schum.	Kress 94-3664 (US)	NMNH 94-668	AY994581, AY994646	Africa	African melittophilous Costus
Costus erythrocoryne K. Schum.	Specht 02-326 (NY)	L 93.0128	AY994579, AY994644	Eastern Peru	NW Costus radiation
Costus fissiligulatus Gagnep.	Maas 3500 (U)		AY994600, AY994667	Africa	African Costus grade
Costus gabonensis J. Koechlin	Specht 02-339 (NY)	Alan Carle	AY994593, AY994660	West Africa	African Costus grade–C. gabonensis clade
Costus globosus Blume	Mood 1713	JM 1713	AY994592, AY994659	Indo-Malaysia	Cheilocostus
Costus guanaiensis Rusby var. tarmicus (Loes.) Maas	KMN 2811 (HLA, U)	L 80.0707	AY994577, AY994642	Central to South America (Andean)	NW Costus radiation
Costus lacerus Gagnep.	Kress 00-6777 (US)	NMNH 99-144	AY994578, AY994643	Indo-Malaysia	Cheilocostus
Costus lanceolatus Peterson	Maas 9153 (U)		AY994598, AY994665	Colombia and Amazonian Brazil	Chamaecostus
Costus lateriflorus Baker	Kress 00-6599 (US)	NMNH 98-224	AY994574, AY994639	West Africa	African Costus grade–epiphytic clade
Costus letestui Pellegr.	Specht 02-331 (NY)	L 99.0468 JM 97p023	AY994573, AY994638	West Africa	African Costus grade–epiphytic clade
Costus lucanusianus J. Braun & K. Schum.	Specht 02-321 (NY)	L 87.0286	AY994594, AY994661	West and central Africa	African melittophilous Costus
Costus montanus Maas	Kay s. n.		AY994569, AY994634	Costa Rica	NW Costus radiation
Costus phaeotrichus Loes.	Specht 02-323 (NY)	L 95.0440	AY994561, AY994626	West Africa	African Costus grade–C. gabonensis clade
Costus pictus D. Don (ex Lind.)	Kress 94-3691 (US)	NMNH 94-685	AY994566, AY994631	Central America	NW Costus radiation
Costus pulverulentus Presl.	Kress 94-3680 (US)	NMNH 94-667	AY994563, AY994628	Central America and NW South America	NW Costus radiation
Costus speciosus (J. Konig) Sm. (1)	Kress 94-5298 (US)	NMNH 94-684	AY994557, AY994622	Indo-Malaysia	Cheilocostus
Costus speciosus (J. Konig) Sm. (2)	Specht s. n. (alcohol)	L 92.0166	AY994544, AY994609	Indo-Malaysia	Cheilocostus
Costus spectabilis (Fenzl) K. Schum.		NMNH 96-284	AY994556, AY994621	Africa	African Costus grade
Costus stenophyllus Standl. & L. O. Williams	Specht 02-313 (NY)	L 75.0439	AY994560, AY994625	Costa Rica	NW Costus radiation
Costus talbotii Ridl.	Specht 02-334 (NY)	L 2000.0270	AY994554, AY994619	Africa	African Costus grade–epiphytic clade

Table 1.   Continued.

Species	Herbarium voucher no.	Living collection no.	GenBank accession numbers: *trn*L–F; *trn*K	Biogeographic distribution	Revised taxonomic affinity
Costus varzearum Maas	*Specht 01-277 (NY)*		AY994551, AY994616	Amazonian South America	NW *Costus* radiation
Costus villosissimus Jacq.	*Nagata 632 (HLA)*	L 67.0478	AY994550, AY994615	Central America to NW South America	NW *Costus* radiation
Costus woodsonii Maas	*Specht 01-264 (NY)*		AY994549, AY994614	Central America	NW *Costus* radiation
Dimerocostus argenteus (R. & P.) Maas	*Specht 99 229 (NY)*		AY994548, AY994613	Bolivia	*Dimerocostus*
Dimerocostus strobilaceus O. Kuntze subsp. *gutierrezii* Maas	*Specht 98-182 (NY)*		AY994547, AY994612	Central America to South America, Andean	*Dimerocostus*
Monocostus uniflorus (Poepp. ex O. G. Pet.) Maas	*Specht 01-278 (NY)*		AY994546, AY994611	Central Peru	*Monocostus*
Siphonochilus kirkii (Hook. f.) B. L. Burtt	*Kress 94-3692 (US)*	NMNH 89-058	AY994538, AY994603	Africa	Zingiberaceae
Tapeinochilos ananasse (Hassk.) K. Schum.		NY Conservatory	AY994545, AY994610	New Guinea	*Tapeinochilos*
Tapeinochilos dahlii K. Schum.		NMNH 90-012	AY994541, AY994606	New Guinea	*Tapeinochilos*
Tapeinochilos pubescens Ridl.	*Nishimoto 025 (HLA)*	L 93.0038	AY994543, AY994608	New Guinea	*Tapeinochilos*
Tapeinochilos queenslandiae (F. M. Bailey) K. Schum.	*Hay 7052 (NSW)*	911894 RBG, Sydney	AY994542, AY994607	New Guinea	*Tapeinochilos*

tive ages to absolute dates of diversification. Although many fossil taxa have been found in Zingiberales lineage, no fossils have been assigned to Costaceae. The calibration point used in this analysis is a secondary calibration age, taken from the parallel local clocks analysis of Zingiberales (Kress and Specht 2005, 2006). Based on the Zingiberales results, there are two potential dates that can be used for calibration: the age of the node connecting Costaceae and Zingiberaceae (i.e., the date of divergence, 105 mya) and the age associated with the initiation of cladogenesis within Costaceae (i.e., date of diversification, 52 mya). However, the 52 mya date is the result of a divergence estimate using only four exemplar taxa in the crown group Costaceae. This age does not take into consideration the divergence dates of the basal-most members of the family, nor does it consider any potential extinction events that would indicate an earlier date of diversification. For these reasons, the age estimation for diversification of Costaceae was calibrated with the Costaceae–Zingiberaceae divergence age of 105 ± 4 mya, using 101 mya and 109 mya in separate analyses in order to bracket the calibration age according to standard error calculations from Kress and Specht (2006).

Biogeographic Analysis (DIVA)

The topology obtained from the chloroplast data set was analyzed with DIVA vers. 1.1 (Ronquist 1996), with geographic areas scored as presence or absence characters for each of the 37 taxa. The areas of distribution used for the DIVA analysis were: tropical Americas (divided into Central America [CAM] and South America [AM]), Africa (AF), Southeast Asia (SE), and Melanesia (ML, New Guinea and northern Australia). These areas were chosen as representatives of the major geographic areas of endemism for Costaceae and because defined taxonomic divisions (species and clades) do not typically span more than one of these areas. Coding of wide distributions can complicate reconstruction of the basal nodes, leading to reconstructions that consist of all possible combinations without providing resolution necessary to determine past biogeographic patterns (Sanmartín and Ronquist 2002). The outgroup was coded as present in Africa based on the current distribution of basal-most extant Zingiberaceae. The number of areas allowed at each node (maxareas) was restricted to two, three, and four in independent analyses in order to look for optimal solutions that restricted the number of optimal basal node distributions reconstructed without significantly increasing the number of required dispersal events (i.e., compromising parsimony as defined by DIVA algorithm: Ronquist 1996).

RESULTS

Phylogenetic Analysis

The resulting topology (Fig. 1) was fully resolved and is identical to the phylogenetic results of a combined molecular and morphological analysis for Costaceae (Specht, in press), with the exclusion of the two Paracostus-clade taxa, *Costus paradoxus* K. Schum. and *C. englerianus* K. Schum., of the Asian Costaceae clade. Genera *Monocostus* K. Schum., *Dimerocostus* O. Kuntze, and *Tapeinochilos* Miq. were recovered as monophyletic while the genus *Costus* L. was found
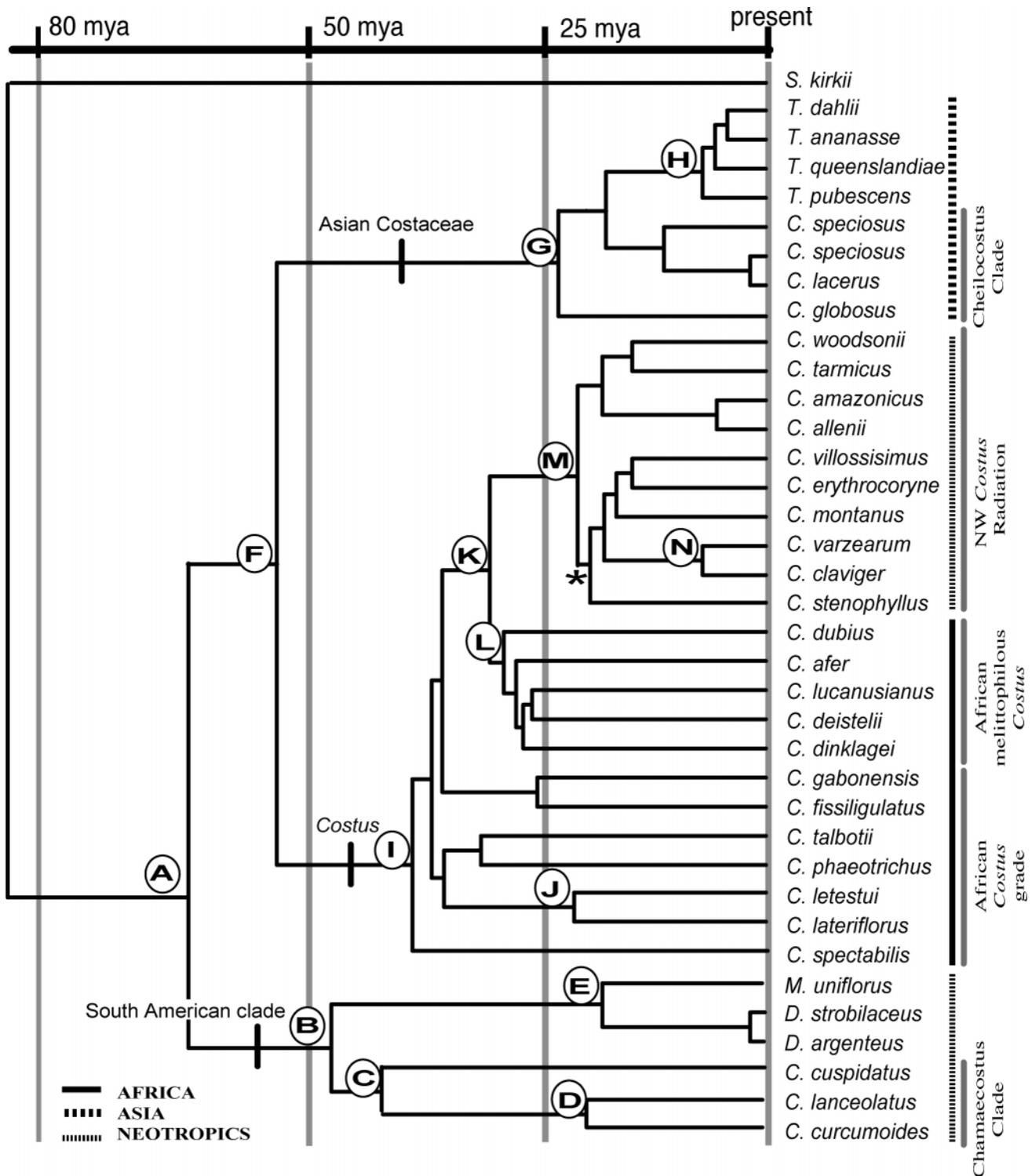
Fig. 2.—Chronogram of Costaceae based on local clock analysis of chloroplast DNA data with calibration point set as the split between Costaceae and Zingiberaceae (105 mya) based on Kress and Specht (2006). Nodes are arranged according to the age estimates obtained using a local clock method for determining ages of diversification. Mya = million years ago. Lettered nodes are referred to in text and Table 2. Node marked with * corresponds to the appearance of the derived hummingbird pollination morphology in New World *Costus*. Generic abbreviations are: *C. = Costus, M. = Monocostus, D. = Dimerocostus, T. = Tapeinochilos*.

Table 2. Results from Local Clock and DIVA analyses for major nodes and subclades of the Costaceae phylogeny based on maximum likelihood analysis of plastid DNA sequence data.

Node description	Node[a]	Date of divergence (mya)	Ancestral distribution[b]
Zingiberaceae—Costaceae		**105**	AF AM
South American clade—remaining	A	65.6 ± 7.73	AM AF SE
South American clade diversification (stem)	B	48.92 ± 6.88	AM
Chamaecostus clade diversification (stem)	C	43.93 ± 6.69	AM
Chamaecostus clade speciation (crown)	D	21.91 ± 4.66	AM
Monocostus—Dimerocostus	E	20.88 ± 4.99	AM
Dimerocostus speciation		0 ± 0.15	AM
Costus—Asian Costaceae	F	56.76 ± 6.34	AF SE
Diversification of Asian taxa (stem)	G	24.25 ± 4.48	SE
Cheilocostus clade—*Tapeinochilos*		19.01 ± 3.88	SE ML
Cheilocostus clade diversification		14.88 ± 4.11	SE
C. speciosus—C. globosus		4.74 ± 3.13	SE
Tapeinochilos radiation (stem)	H	10.76 ± 2.94	ML
Basal African diversification (stem)	I	40.75 ± 4.04	AF
C. lateriflorus lineage		39.97 ± 3.9	AF
C. gabonensis lineage		39.03 ± 3.82	AF
C. letestui—C. lateriflorus speciation (crown)	J	23.15 ± 5.94	AF
African melittophilous *Costus*—New World *Costus* radiation	K	33.66 ± 3.46	AF AM
African melittophilous *Costus* diversification (stem)	L	33.25 ± 3.65	AF
African melittophilous group speciation (*C. afer—C. dubius*; crown)		28.8 ± 3.91	AF
New World *Costus* radiation diversification (stem)	M	21.71 ± 2.91	AM
NW—*Costus* radiation speciation (crown)	N	14.67 ± 3.77	AM

[a] Node letter corresponds to Fig. 2.

[b] DIVA optimizations shown with maximum areas per node limited to three (maxareas = 3). AF = Africa, SE = Southeast Asia, ML = Melanesia, AM = South America. No nodes optimized as Central America (CA) although this area was included as a terminal distribution in the analysis. **Bold** = date set as calibration point. "—" indicates split of lineage between taxa on each side of em dash.

to be polyphyletic and is divided into three major clades: *Costus,* the Chamaecostus clade, and the Cheilocostus clade. The Chamaecostus and Cheilocostus clades correspond to lineages recovered with more complete taxon sampling of Costaceae (Specht in press) and are pending taxonomic recognition as genera (Specht and Stevenson in press). In that the topology obtained from this analysis reflected that of the larger and more completely sampled combined analysis, the chloroplast DNA phylogeny was used for the subsequent DIVA analysis and for estimating maximum likelihood branch lengths for the molecular clock analysis without need for topological constraints.

Estimating Branch Lengths and Assigning Rate Classes

A global likelihood ratio test indicated that the data fail to adhere to a global molecular clock ($P = 0.0001$; −12711.193 with clock enforced, −12574.969 without clock enforced). A local clock analysis was thus used to estimate ages of diversification in Costaceae. The F81uf + I + G model was determined to be the least parameter-rich model to fit the data (I = 0.2726, G = 0.8927). The topology from the maximum likelihood analysis is shown in Fig. 1, along with corresponding branch length estimates. Pairwise relative rates tests implemented in Hy-Phy indicate that the branches are optimally divided into four rate classes (0–3) as shown (Fig. 1). These rate classes are assigned to the branches as indicated for the local clocks analysis.

Biogeographic Analysis (DIVA)

DIVA analysis indicates potential ancestral distributions for key nodes in the Costaceae phylogeny (Table 2). The results shown in Table 2 and discussed throughout the remainder of this paper are those obtained when the maximum number of area optimizations for each node was constrained to three (maxareas = 3), the condition which gave the most parsimonious solution (15 dispersal events) with the least number of optimal reconstructions for the basal-most node thereby minimizing the effect of wide distributions coded at the terminals.

Age Estimation

The resulting chronogram from the PAML local molecular clock analysis with the 105 mya calibration date is shown in Fig. 2. Exact node ages with standard error as determined by the local clocks algorithm in PAML are given in Table 2. With the exception of two pairs of terminal branches (the *C. speciosus–C. globosus* speciation event and *Dimerocostus* speciation), the use of 101 my and 109 my as calibration points did not increase the standard error beyond that around the 105 my age; therefore only the results of the analysis using 105 mya as the fixed calibration point are discussed further.

The first major cladogenic event discernable with extant taxa (Fig. 2: node A) dates back to the late Cretaceous ca. 65 mya. DIVA places the ancestral distribution in South America and Africa. The two clades resulting from the initial

lineage split are a ''South American clade'' including the
Chamaecostus clade and *Dimerocostus + Monocostus,* and
a large clade containing the remaining species of Costaceae.
The South American clade (Fig. 2: node B) began to diver-
sify around 49 mya with the separation of the *Monocostus
+ Dimerocostus* clade from the Chamaecostus clade. The
ancestral distribution of this clade is optimized as neotropi-
cal. The Chamaecostus lineage (Fig. 2: node C) began to
diversify shortly thereafter (44 mya) while the *Dimerocostus*
and *Monocostus* lineages did not diverge from one another
until much later (node E: 20.88 mya). Speciation within the
Chamaecostus clade (Fig. 2: node D) is estimated as having
occurred as early as 21.9 mya. This conclusion can be made
based on results of larger analyses showing that *C. lanceo-
latus* Petersen and *C. curcumoides* Maas are indeed sister
taxa (Specht, in press). The ancestral distributions for all
lineages within the Chamaecostus clade are South American,
with all extant taxa having current ranges within South
America.

Following the split-off of the South American lineage, the
remaining Costaceae (Fig. 2: node F) existed in Southeast
Asia and Africa and subsequently divided into two major
lineages around 57 mya. Of these lineages, a DIVA-opti-
mized vicariance event led to one lineage occupying South-
east Asia (Fig. 2: node G) and a second lineage colonizing
Africa (Fig. 2: node I). The Southeast Asian lineage began
to successfully diversify around 24 mya. At 11 mya (Fig. 2:
node H) a dispersal event to Papua New Guinea (Melanesia)
leads to a Melanesian ancestral distribution optimized for the
monophyletic *Tapeinochilos* Miq. The Africa clade (Fig. 2:
node I) begins to successfully diversify around 40.7 mya
with a DIVA-optimized distribution in Africa only. This lin-
eage remains in Africa and undergoes speciation in small
numbers (see Fig. 2: node J) forming a basal paraphyly with-
in the *Costus* clade until sometime around 33.7 mya, when
a split (node K) occurs between an African clade (African
melittophilous *Costus*; see Fig. 2: node L) and a New World
clade (New World *Costus* radiation; Fig. 2: node M). The
ancestor of this Africa-New World split has a distribution in
Africa alone, requiring a dispersal event at this time to South
America. All migration to Northern South America (e.g.,
Fig. 2: node N) and Central America occurs at the tips within
the New World *Costus* radiation clade (no nodes are opti-
mized with Central America as the ancestral distribution; see
Table 2) and is considered to comprise multiple dispersal
events and potential sympatric speciation events within var-
ious Central and South American populations. A more com-
plete sampling of this clade is required to further investigate
the details of neotropical migrations.

DISCUSSION

Recent uses of molecular clocks in combination with cur-
rent phylogenetic hypotheses have enabled researchers to ad-
dress temporal questions using genetic divergence (Sander-
son 1997; Bremer 2000, 2002; Yang and Yoder 2000, 2003;
Thorne and Kishino 2002; Yoder and Yang 2004). Phylo-
genetic dating using molecular sequence data requires at
least one reference node to be fixed in order to calibrate the
clock, converting the relative ages based on estimated branch
lengths to absolute ages of lineage divergence and species

diversification. The clock is often calibrated using fossil taxa
or biogeographic events with known ages that can be as-
signed to a given node in the phylogeny. For Costaceae, no
fossils have been identified. The date used for calibrating the
molecular clock is thus inferred from the analysis of Zingi-
berales (Kress and Specht in press), using the divergence
date between Zingiberaceae and Costaceae (105 mya) as the
calibration date for converting relative to absolute rates.

The local clock method used in this analysis incorporates
models that account for heterogeneity in different data par-
titions (Yang 2003; Yang and Yoder 2003), enabling the use
of multiple gene partitions in a combined evidence analysis.
When using single genes for determining rates or branch
lengths, the confounding nature of rate and time are not ac-
counted for, i.e., there is no way to distinguish between a
high rate of sequence change over a short period of time and
a low rate of divergence over a long period of time. Because
the divergence times reflect the lineage divergences of
unique organisms, they are shared for each gene region an-
alyzed despite the inherent variation in evolutionary rates of
the individual genes. Thus, the confounding problem of rate
vs. time is potentially overcome by using multiple gene loci
in a combined analysis that accounts for rate heterogeneity
in the partitions, and the common parameter (i.e., divergence
time) emerges from the combined data.

On Dating Costaceae

The use of 105 mya as the date for calibration of the
Costaceae chronogram is based on two criteria. First, the
dating of Zingiberales by Kress and Specht (2006) used
*rbc*L, *atp*B, and 18S data, all of which are slowly evolving
genes that do not fully resolve the Costaceae data set at the
species level. The lack of sequence diversity between the
four Costaceae exemplars used in Zingiberales can result in
an underestimation of divergence times within the family.
While the data set used for the Zingiberales analysis is ap-
propriate for examining ages of diversifications among the
major family lineages, within individual families it is more
appropriate to use a molecular system that provides suffi-
cient informative characters upon which to base a relative
rates test and branch length estimation.

The use of the divergence time between Costaceae and
Zingiberaceae (105 mya) as the calibration point allows the
internal nodes of Costaceae to be dated based on branch
lengths estimated the chloroplast DNA clock. Thus the ages
of diversification within the family are estimated from the
branch lengths of a more thorough sampling of Costaceae
(37 rather than 4 taxa) and a molecular data set with suffi-
cient character variation to resolve the appropriate species-
level relationships within the family (as per Specht et al.
2001; Specht in press). Furthermore, the 105 mya date is
closer topologically to the dates of calibration for the Zin-
giberales analysis (43 mya *Ensete oregonensis* S. Manches-
ter & W. J. Kress fossil: Manchester and Kress 1993). It has
been shown that closer proximity to the calibrated node
yields greater fidelity of the age estimation results, therefore
the 105 mya divergence date will be more accurate than the
52 mya diversification date (Yang et al. 1995; Yoder and
Yang 2000; K. Bremer pers. comm.)

Costaceae Diversification in Space and Time

The ancestral distribution of Costaceae–Zingiberaceae is optimized by DIVA as Africa, Southeast Asia and South America. The first divergence within Costaceae (Fig. 2: node A) led to a division between a South American and an African + Southeast Asian lineage, dating to 65 mya with a distribution identical to that of the ancestral population (AF, SE, AM). A second divergence separating an African and Southeast Asian ancestral population (Fig. 2: node F) occurred about 52 mya. The Asian clade appears to have diversified in SE Asia (Fig. 2: node G) starting around 23 mya. A dispersal to New Guinea approximately 11 mya (Fig. 2: node H) resulted in the *Tapeinochilos* lineage radiation. Meanwhile, the African lineage spread throughout the moist forest habitat of tropical Africa (Fig. 2: node I), forming several distinct clades each with only a few surviving taxa (Fig. 2: African *Costus* grade). About 34 mya however, a split occurs between an African lineage and a neotropical lineage (Fig. 2: node K). The African lineage continued to diversify in Africa (Fig. 2: node L), forming what is today a clade of bee-pollinated taxa with approximately twelve species (Fig. 2: African melittophilous *Costus*). Part of this lineage, potentially a single taxon, is likely to have dispersed to the neotropics from Africa. The resulting lineage (see Fig. 2: node M and ''New World *Costus* radiation'' clade) comprises the majority of neotropical species currently found throughout Central and South America.

Most of the species in the New World had evolved by the time of the Andean uplift (10 mya), thus major geographic changes in the region do not seem to be largely involved in speciation events within the neotropics. Within the New World *Costus* radiation, Central American and Caribbean species are sister to South American taxa (data not shown), indicating short distance dispersal to these areas from a core distribution along the base of the Andes and the Amazon and Orinoco basins. A more detailed investigation of this group, requiring rapidly evolving genetic markers to distinguish between species and populations, will yield more specific results about the patterns of speciation in this group and how they correlate with the historical geography of South and Central America and the Caribbean.

Are Costaceae a Gondwanan Family?

The current distribution of Costaceae is pantropical, a distribution often associated with Gondwana as the result of vicariance during the continental break-up. However, the dates of major early Costaceae cladogenesis (starting at 65 mya) do not suggest that the major lineages of Costaceae were formed coincidentally with the breakup of the supercontinent. This suggests that long distance inter-continental dispersal is more likely to have played a role in the formation of the major Costaceae lineages, with subsequent secondary dispersals along with localized speciation events leading to the levels of diversification we see today.

According to modern theories of geological activity and continental drift, the Gondwanan supercontinent began to separate around 180–150 mya (Hallam 1994; Scotese et al. 1988). At this time Africa and South America remained together forming a unified western portion of Gondwanaland, but were separated from the Eastern landmass that included Australia, Antarctica, Madagascar and India. Subsequent rotation of continental plates provided a land bridge connection between South America and Australia via Antarctica that remained until the Tertiary, approximately 65 mya (Hallam 1994). South America eventually became isolated from Australia at the end of the Eocene (55–35 mya) following the deterioration of connections across Antarctica. Africa and South America geologically split from one another around 110–90 mya (Sanmartín and Ronquist 2004), however recent studies show that biotic exchange of flora and fauna was prolific until at least 80 mya due to the proximity of the continents and the shallowness and low salinity of the separating body of water (Lundberg 1993). The 105 mya separation between Zingiberaceae and Costaceae occurred during a time when exchange between the South American and African continents was likely. It is possible then that the early ancestors of Costaceae may have been present across the Western portion of Gondwana. The final break-up of Africa and South America could have led to the vicariance of lineages within Costaceae eventually leading to the separation and independent diversification of the South American and African lineages within the family, although the data with extant taxa alone indicate that divergence between these two lineages (Fig. 2: node A) does not initiate until 65 mya, long after the continents had separated. This could be an effect of unsampled (extinct) taxa that may have diverged earlier than 65 mya.

A potential scenario for the early cladogenesis of Costaceae (Fig. 2: node A) would be that the ancestral Costaceae lineage separated from the Zingiberaceae lineage in western Gondwana (AM and AF). A portion of the African lineage would then have given rise to the Asian population, potentially via the collision of India with Southeast Asia, provided that a population of Costaceae had dispersed to the continent of India as it rafted north and collided with Southeast Asia approximately 40 mya. A Laurasian migration via a North Atlantic land bridge during the late Eocene (Tiffney 1985), a route recently discussed for the migration of various lineages of tropical plants with modern pantropical distribution (Davis et al. 2002) and for Zingiberales (Kress and Specht 2006), could also explain the dispersal of an African clade to Southeast Asia. Fossil zingiberalean taxa present in North America during the Cretaceous and the Eocene (Friis 1988; Manchester and Kress 1993) lend credence to a scenario involving a northern migration.

During the late Eocene (up to 40 mya), periodic inundation of the Malaysian and Indonesian islands due to increased sea levels would have resulted in a lack of continuity in the Asian lineages and could have promoted isolation and extinction of local populations inhabiting small islands. This changing landscape makes it difficult to determine which direction Asian Costaceae migrated; however it does appear to explain the presence of highly localized taxa and morphologically variable species complexes (e.g., *Costus globosus*) as well as the relatively recent diversification date (22 mya; Fig. 2: node G) for the Asian taxa relative to the diversification of the sister African clade (40 mya; Fig. 2: node I).

The genus Costus.—The *Costus* clade (including New World *Costus* radiation, the African melittophilous *Costus,* and the

African *Costus* grade: Fig. 1, 2) is by far the largest lineage in the family with a total of approximately 85 species distributed in Africa and the neotropics. The stem age of the *Costus* lineage is around 56 million years old (Fig. 2: node F) with the divergence of the African *Costus* lineage and the Asian lineage. *Costus* began to diversify around 40.7 mya (Fig. 2: node I) but continued to occupy Africa for about 23 million years without any successful long distance dispersal events leading to extant populations. Around 33.7 mya, however, a new floral form developed in Africa that was morphologically adapted to specialized pollination by bees (Fig. 2: node L). Based on extant taxa, this melittophilous (bee pollinated) clade speciated more rapidly than did previous African lineages; between 33 and 27 mya, in a span of 6 million years, 8 species were formed in this clade, effectively doubling the number of taxa in Africa. The absolute diversification rate for this clade calculated in the absence of extinction is 0.06 speciation events per million years, in comparison with clades within the African grade calculated as having absolute rates of speciation of 0.01 to 0.03 (Specht 2005). An early member of this bee-pollinated clade is likely to have dispersed to tropical America, initiating the New World *Costus* radiation (Fig. 2: node M).

New World Costaceae and pollination.—During the mid-Tertiary (50–25 mya), the Costaceae flora of the New World consisted of a single South American clade that began to diversify around 49 mya (Fig. 2: node B). This clade currently comprises approximately 12 species all maintaining a plesiomorphic generalist-pollinated floral form, including *Monocostus* (1 sp.), *Dimerocostus* (3 spp.), and the Chamaecostus clade (8 spp.). A dispersal event from Africa around 34 mya (Fig. 2: node K) led to the establishment of New World *Costus* radiation lineage, which began to diversify approximately 22 mya (Fig. 2: node M). The New World *Costus* radiation taxa all have flowers that are specialized for either bird or bee pollination (Specht 2005, in press).

Historically, then, taxa from the African-dispersed clade quickly outnumbered the generalist-pollinated lineage already established in the neotropics: species radiation within the New World *Costus* clade began around 22 mya (21.71 ± 2 mya) with both bird and bee-pollinated floral forms being represented by 20 mya (Fig 2: *) while the basal South American clade remained relatively species-poor, based on the analysis of extant taxa. The current higher species diversity of the New World *Costus* radiation clade (ca. 68 species) relative to that of the basal South American clade (12 species) may be due in part to the close association of the New World *Costus* radiation clade with specific pollinators, and the relative ecological success of this strategy for survival, dispersal, and diversification. Species-level diversification occurred rapidly in the New World *Costus* radiation clade.

The Asian Costaceae: Tapeinochilos *and Cheilocostus-clade lineages.*—The date of the origin (19 mya) and diversification (11 mya; Fig. 2: node H) of the *Tapeinochilos* lineage corresponds well with the known geology and geography of the New Guinea region. The emergence of the island of New Guinea occurred around 25 mya in the late Oligocene–early Miocene, with the current tropical habitat developing around 15 mya (Whitmore 1987; Metcalf 2002). Major speciation

has been recorded for the flora of New Guinea during the Miocene as a result of the rapidly changing landscape of the island, and the quaternary has been important to subsequent speciation and diversification of lineages (Whitmore 1987). Upon its emergence, New Guinea quickly developed a diversity of tropical lowland and fragmented montane rainforest habitats as volcanic eruptions and subducting plate activity to the north quickly built a series of mountain ranges in the northern coastal area. *Tapeinochilos,* with its current center of diversity in Papua New Guinea, is likely to have evolved on this island. The increasing habitat diversity and resulting geologic barriers to gene flow may have played a role in the radiation of the *Tapeinochilos* lineage following its arrival in New Guinea.

The current distribution of *Tapeinochilos* throughout Papuasia (the biogeographic unit extending from New Guinea to the Solomon Islands and including the Bismarck Archipelago) is likely the result of inter-island dispersal from New Guinea to the surrounding archipelagos. The fruit of *Tapeinochilos* is an indehiscent capsule with a thin wall that becomes slightly swollen and fleshy when ripe (Gideon 1996). The fruit remains attached to the inflorescence stalk, supported by the subtending bract, until either the inflorescence disintegrates or the seeds are removed by animal dispersal agents (i.e., birds, small mammals) that are attracted to the seeds by the small but fleshy aril. The arillate seeds have a hard testa that is likely to survive ingestion, thus bird dispersal is a likely scenario for explaining the diversity of *Tapeinochilos* on the various island chains of Melanesia. Reports of bird dispersal for Costaceae include seeds of *Costus allenii, C. laevis* Ruiz & Pav. and *C. guanaiensis* Rusby in Panama (Schemske 1983). In addition, birds have been reported as effective seed dispersers of other Zingiberales taxa in New Guinea (Lamothe 1979; Beehler 1983) and Australia (Stocker and Irvine 1983; Barker and Vestjens 1989). While ant dispersal is also reported for Zingiberales (Horvitz and Beattie 1980; Horvitz and Schemske 1986), the indehiscent capsule of *Tapeinochilos* makes the seeds inaccessible to ants. Floating dispersal is another option, and could be possible based on the indehiscent capsule. The tolerance of *Tapeinochilos* fruits and seeds to periods of immersion in salt water has not been investigated.

Borneo has most recently been interpreted as an early Cretaceous island arc that was thrust on to the Asian margin in the mid-Cretaceous (McElhinny et al. 1974; Mitchell 1993; Metcalf 2002), and thus not rifted from Gondwana as a continental fragment as previously thought. Species currently found in Borneo are *Costus paradoxus* of the Paracostus clade (not included in this analysis), and *C. globosus* and *C. speciosus* of the Cheilocostus clade, all of which form part of the Asian Costaceae clade. Based on the geological and temporal context, population of Borneo by *C. globosus* and *C. speciosus* would have occurred via dispersal, likely from populations in India or southern Indochina where *Costus speciosus* is currently found in conjunction with *C. globosus* and *C. lacerus* Gagnep. The *C. globosus* complex extends from mainland Southeast Asia (China and Thailand) through the Malay Peninsula to Java and Borneo and across Sarawak to New Guinea. The diversity of this complex could have resulted from the movement (short-distance dispersal) of taxa across Malaysia from tropical India or Africa, and the

clear morphological and ecological diversity inherent in this group could have played a role in the evolution of the *Tapeinochilos* lineage. *Costus sopuensis* P. J. M. & H. Maas, known only from two collections from Celebes (Sulawesi, Palu) but presumed to be part of the Cheilocostus clade, may provide additional evidence of patterns of range expansion and diversification of the Southeast Asian lineages. Efforts to obtain sequence data from this taxon will help to determine its role in the biogeography of Asian Costaceae.

CONCLUSION

Modern pantropical patterns of species distribution within lineages tends to be interpreted as resulting from the historic fragmentation of the ancient landmass of Gondwanaland, regardless of whether or not the lineage predates the late Cretaceous breakup of the southern supercontinent. This analysis shows that while several lineages of Zingiberales, including the common ancestor of the Zingiberaceae–Costaceae lineages, were likely occupying the tropical areas of Gondwana prior to its breakup, the vicariance of Gondwana was not likely to have played a large role in the major diversification of modern Costaceae. While the earliest lineages may have been influenced by the fragmentation of Africa and South America, the current pantropical distribution of the family is better explained by a series of more recent local vicariance and dispersal events. It is possible that early Zingiberales had a more northern distribution, and that the current southern distribution is a result of the migration of tropical habitat from geographic areas that are now located in the Northern Hemisphere to its current equatorial position across northern South America, Africa and Southeast Asia. In this event, Costaceae as a lineage would have benefited from Asian island dynamics to spread to New Guinea and develop the *Tapeinochilos* lineage, and to spread into Africa. Dispersal to America across the spreading Atlantic Basin, first from a formerly tropical southern Europe (Chamaecostus clade) and second from tropical Africa (New World *Costus* radiation), would then explain the two dispersal events to the New World. These types of hypotheses can be further tested with additional information about biogeographic patterns that show similar patterns of migration over time.

LITERATURE CITED

BARGELLONI, L., S. MARCATO, L. ZANE, AND T. PATARNELLO. 2000. Mitochondrial phylogeny of Notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Syst. Biol.* **49**: 114–129.

BARKER, R. D., AND W. J. M. VESTJENS. 1989. The food of Australian birds. CSIRO Publishing, Collingwood, Victoria, Australia. 557 p.

BAUM, D. A., R. L. SMALL, AND J. F. WENDEL. 1998. Biogeography and floral evolution of Baobabs (*Adansonia,* Bombacaceae) as inferred from multiple data sets. *Syst. Biol.* **47**: 181–207.

BEEHLER, B. 1983. Frugivory and polygamy in Birds of Paradise. *The Auk* **100**: 1–2.

BREMER, K. 2000. Early Cretaceous lineages of monocot flowering plants. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 4704–4711.

———. 2002. Gondwanan evolution of the grass alliance of families (Poales). *Evolution* **56**: 1374–1387.

DAVIS, C. C., C. D. BELL, S. MATHEWS, AND M. J. DONOGHUE. 2002. Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. *Proc. Natl. Acad. Sci. U.S.A.* **99**: 6833–6837.

FELSENSTEIN, J. 1981. Evolutionary trees from DNA sequence: a maximum likelihood approach. *J. Molec. Evol.* **17**: 368–376.

FRIIS, E. M. 1988. *Spirematospermum chandlerae* sp. nov., an extinct species of Zingiberaceae from the North American Cretaceous. *Tertiary Research* **9**: 7–12.

GIDEON, O. G. 1996. Systematics and evolution of the genus *Tapeinochilos* Miq. (Costaceae–Zingiberales). James Cook University, Queensland, Australia. 532 p.

HALLAM, A. 1994. An outline of phanerozoic biogeography. Oxford University Press, Oxford, UK. 254 p.

HORVITZ, C. C., AND A. J. BEATTIE. 1980. Ant dispersal of *Calathea* (Marantaceae) seeds by carnivorous Ponerines (Formicidae) in a tropical rain forest. *Amer. J. Bot.* **67**: 321–326.

———, AND D. W. SCHEMSKE. 1986. Seed dispersal of a Neotropical myrmecochore: variation in removal rates and dispersal distance. *Biotropica* **18**: 319–323.

HURR, K. A., P. J. LOCKHART, P. B. HEENAN, AND D. PENNY. 1999. Evidence for the recent dispersal of *Sophora* (Leguminosae) around the Southern Oceans: molecular data. *J. Biogeogr.* **26**: 565–577.

JORDAN, S., C. SIMON, AND D. POLHEMUS. 2003. Molecular systematics and adaptive radiation of Hawaii's endemic Damselfly genus *Megalagrion* (Odonata: Coenagrionidae). *Syst. Biol.* **52**: 89–109.

KOSAKOVSKY-POND, S., AND S. MUSE. 1998–2003. HY-PHY: hypothesis testing using phylogenies, 0.99ß for Mac OSX (Carbon). *www.hyphy.org* (Mar 2005).

KRESS, W. J., AND C. D. SPECHT. 2005. Between Cancer and Capricorn: phylogeny, evolution, and ecology of the tropical Zingiberales, pp. 459–478. *In* I. Friis and H. Balslev [eds.], Proceedings of a symposium on plant diversity and complexity patterns—local, regional and global dimensions. Biologiske Skrifter, The Royal Danish Academy of Sciences and Letters, Copenhagen, Denmark.

———, AND ———. 2006. The evolutionary and biogeographic origin and diversification of the tropical monocot order Zingiberales, pp. xx–xx. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution, 2 vols. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

LAMOTHE, L. 1979. Diet of some birds in *Araucaria* and *Pinus* forests in Papua New Guinea. *Emu* **79**: 36–37.

LUNDBERG, J. G. 1993. African-South American freshwater fish clades and continental drift: problems with a paradigm, pp. 156–199. *In* P. Goldblatt [ed.], Biology relationships between Africa

and South America. Yale University Press, New Haven, New York, USA.

MAAS, P. J. M. 1972. Costoideae (Zingiberaceae). *Fl. Neotrop. Monogr.* **8**: 1–140.

MANCHESTER, S. R., AND W. J. KRESS. 1993. Fossil bananas (Musaceae): *Ensete oregonense* sp. nov. from the Eocene of western North America and its phytogeographic significance. *Amer. J. Bot.* **80**: 1264–1272.

MCELHINNY, M. W., N. S. HAILE, AND A. R. CRAWFORD. 1974. Palaeomagnetic evidence shows Malay Peninsula was not part of Gondwanaland. *Nature* **252**: 641–645.

METCALF, I. 2002. Permian tectonic framework and palaeogeography of SE Asia. *Journal of Asian Earth Sciences* **20**: 551–566.

MITCHELL, A. H. G. 1993. Cretaceous–Cenozoic tectonic events in the western Myanmar (Burma)-Assam region. *Journal of the Geological Society, London* **150**: 1089–1102.

POSADA, D., AND K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817–818.

RONQUIST, F. 1996. Dispersal-Vicariance analysis (DIVA vers. 1.1). Computer program and manual available by anonymous FTP from Uppsala University (*ftp.uu.se* or *ftp.systbot.uu.se*). *http://www.ebc.uu.se/systzoo/research/diva/manual/dmanual.html* (Mar 2005).

SANDERSON, M. J. 1997. A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molec. Biol. Evol.* **14**: 1218–1232.

SANMARTÍN, I., AND F. RONQUIST. 2002. New solutions to old problems: widespread taxa, redundant distributions and missing areas in event-based biogeography. *Animal Biodiversity and Conservation* **25**: 75–93.

————, AND ————. 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Syst. Biol.* **53**: 216–243.

SCHEMSKE, D. W. 1983. Breeding system and habitat effects of fitness components in three neotropical *Costus* (Zingiberaceae). *Evolution* **37**: 523–539.

SCOTESE, C. R., L. M. GAHAGAN, AND R. L. LARSEN. 1988. Plate tectonic reconstructions of the Cretaceous and Cenozoic ocean basins. *Tectono-physics* **155**: 27–48.

SPECHT, C. D. 2005. Phylogenetics, floral evolution and rapid radiation in the tropical monocot family Costaceae (Zingiberales), pp. 29–60. *In* A. K. Sharma and A. Sharma [eds.], Plant genome: biodiversity and evolution. Science Publishers, Inc., Enfield, New Hampshire, USA.

————. In press. Systematics and evolution of the tropical monocot family Costaceae (Zingiberales): a multiple data set approach. *Syst. Bot.*

————, W. J. KRESS, D. W. STEVENSON, AND R. DESALLE. 2001. A molecular phylogeny of Costaceae (Zingiberales). *Molec. Phylogen. Evol.* **21**: 333–345.

————, AND D. W. STEVENSON. In press. A new generic taxonomy for the monocot family Costaceae (Zingiberales). *Taxon.*

STOCKER, G. C., AND A. K. IRVINE. 1983. Seed dispersal by cassowaries (*Casuarius casuarius*) in North Queensland's rainforests. *Biotropica* **15**: 170–176.

SWOFFORD, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods), vers. 4.0ß 10. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

————, AND G. J. OLSEN. 1990. Phylogeny reconstruction, pp. 411–500. *In* D. M. Hillis and C. Moritz [eds.], Molecular systematics. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

THORNE, J. L., AND H. KISHINO. 2002. Divergence time and evolutionary rate estimation with multilocus data. *Syst. Biol.* **51**: 689–702.

TIFFNEY, B. H. 1985. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *J. Arnold Arbor.* **66**: 243–273.

TREWICK, S. A. 2000. Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *J. Biogeogr.* **27**: 1189–1200.

VINNERSTEN, A., AND K. BREMER. 2001. Age and biogeography of major clades in Liliales. *Amer. J. Bot.* **88**: 1695–1703.

WHITMORE, T. C. (editor). 1987. Biogeographical evolution of the Malay archipelago. Clarendon Press, New York, USA. 165 p.

YANG, Z. 1997. PAML: a program package for phylogenetic analysis by maximum likelihood. *CABIOS* **13**: 555–556.

————. 2003. PAML: a program package for phylogenetic analysis by maximum likelihood. vers. 3.14ß. *http://abacus.gene.ucl.ac.uk/software/paml.html* (Mar 2005).

————, N. GOLDMAN, AND A. FRIDAY. 1995. Maximum likelihood trees from DNA sequences: a peculiar statistical estimation problem. *Syst. Biol.* **44**: 384–399.

————, AND A. D. YODER. 2003. Comparison of likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. *Syst. Biol.* **52**: 705–715.

YODER, A. D., AND Z. YANG. 2000. Estimation of primate speciation dates using local molecular clocks. *Molec. Biol. Evol.* **17**: 1081–1090.

————, AND ————. 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Molec. Ecol.* **13**: 757–773.