Between Cancer and Capricorn: Phylogeny, evolution and ecology of the primarily tropical Zingiberales

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The Zingiberales are a group of primarily tropical monocots that includes eight families, ca. 96 genera, and about 2,000 species. Phylogenetic results based on sequence data and morphology show that the four "banana-families" (Musaceae, Lowiaceae, Strelitziaceae, and Heliconiaceae) share the plesiomorphic state of five or six fertile stamens and comprise a basal paraphyletic assemblage. The four "ginger-families," with the synapomorphy of a single fertile anther and four or five highly modified staminodia, form a terminal clade of two lineages with the Zingiberaceae + Costaceae and Cannaceae + Marantaceae as sister groups. The Zingiberales are found on all major continents with tropical climates. While Marantaceae, Zingiberaceae, and Costaceae are pantropically distributed, Musaceae is found only in Southeast Asia and Africa, Strelitziaceae only in Africa and the Americas, and Heliconiaceae only in the Americas and Melanesia. The two families most restricted in distribution, Lowiaceae and Cannaceae, are found only in Southeast Asia or the Americas, respectively. The historical biogeography of the family was reconstructed using dispersal-vicariance analysis in combination with dating of nodes based on evidence from the fossil record and local molecular clocks using *atpB* sequence data. The common ancestor of the Zingiberales is estimated to have originated 158 Ma with six of the eight families established by the end of the Cretaceous. Dispersal-vicariance analyses suggest that the ancestral Zingiberales were distributed in tropical Gondwanaland encompassing the present day Americas, Africa, and Southeast Asia with subsequent dispersals between Africa and the Americas. The current distribution of the Zingiberales is a product of numerous secondary and tertiary dispersal events between the major tropical regions of the world. The phylogenetic diversification and biogeographic dispersal of the Zingiberales was in part driven by the evolutionary radiation and diversification of their associated animal pollinators, which include bats, birds, non-flying mammals, and insects. Six of the eight families of the Zingiberales contain taxa specialized for pollination by vertebrates, which appears to be the plesiomorphic state in the order. Of these six families two are exclusively vertebrate-pollinated (Strelitziaceae, Heliconiaceae). Pollination by insects also occurs in six families with one (Marantaceae) or possibly two (Lowiaceae) families predominantly specialized for insect visitors. Current models of the genetic regulation of floral development coupled with phylogenetic data and ecological observations provide new insights into the evolutionary pathways that have resulted in the wonderful diversity of this widespread order of tropical angiosperms.

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Introduction

The Zingiberales (sensu Dahlgren *et al.* 1985), a distinctive clade within the "commelinoid" monocotyledons, have always been recognized as a monophyletic or "natural" group of plants and are often classified at a high taxonomic rank (*e.g.*, subclass, superorder or order; Cronquist 1981; Dahlgren *et al.* 1985; Kress 1990a; Judd *et al.* 1999). Earlier classifications used the name Scitamineae (at the rank of family or order) for these plants and often placed the taxa of the Costaceae in the Zingiberaceae and combined the genera of the Lowiaceae, Strelitziaceae, Heliconiaceae, and Musaceae into a single family (*e.g.*, Bentham & Hooker 1883; Petersen 1888; Schumann 1900, 1902, 1904; Loesener 1930, Winkler 1930; for summary see Kress 1990a). The Angiosperm Phylogeny Group accepts the Zingiberales as one of the ten primary orders in the monocotyledons (APG II 2003). Although less than 4% of extant monocot species are contained within this clade, the unique features of its members, including chemical, anatomical, and macromorphological features (Kress 1990a, 1995), make it an easily recognizable order. The usually large petiolate leaves with a central midrib and transverse venation, and the colourful, bracteate inflorescences while not entirely unique among the monocotyledons serve to identify members of the order in the field.

The pantropical Zingiberales include eight families, 96 currently recognized genera (although some generic boundaries are still in dispute), and about 2,000 species. The families can be separated into two morphological groups based on the number of fertile, pollen bearing stamens. Four families (Musaceae, Strelitziaceae, Lowiaceae, and Heliconiaceae) possess five fertile stamens (in two genera six). These families generally have large banana-like leaves and are hence referred to as the "banana-families." In the past these taxa were often combined into the single family Musaceae and the relationship among the component genera was uncertain. The remaining four families, collectively called the "ginger-families," either have one fertile stamen with two anther sacs (Zingiberaceae and Costaceae) or one stamen with only one anther sac (Cannaceae and Marantaceae). The remaining sterile stamens are modified into elaborate staminodia that play an important role in the floral biology of the plants. In *Canna*, even the sterile half of the single fertile stamen is petaloid.

In this paper we will first review the taxonomic diversity, geographic distribution, and habitat specializations of the taxa in the Zingiberales, then discuss their date and place of origins, and conclude with an analysis of the diversification of the pollination systems in the order.

Taxonomic Diversity and Geographic Distribution

The paraphyletic group of the banana-families exhibit considerably lower taxonomic diversity than the ginger-families. The Musaceae includes three genera with 42 species currently distributed in tropical Asia and Africa (Liu *et al.* 2002b), although fossil evidence indicates that members of this family were in North America and possibly Europe in the Tertiary (Manchester & Kress 1993). The three allopatric genera of the Strelitziaceae are distributed in Madagascar (*Ravenala*: one species), southern Africa (*Strelitzia*: three species), and the Amazon Basin (*Phenakospermum*: one species) while its sister family Lowiaceae with the single genus *Orchidantha* (15 species) is restricted to Southeast Asia. The largest family of the banana group, the Heliconiaceae, is made up of a single genus *Heliconia* with about 200 species found primarily in the neotropics, but with six species in the Pacific region from Samoa to Sulawesi

(Kress 1990b; Berry & Kress 1991; Kress *et al.* 1999).

Three of the ginger-families (Zingiberaceae, Costaceae, and Marantaceae) have members found in tropical regions around the world. The fourth family, Cannaceae, comprised of eleven species all within the single genus *Canna*, is native to the New World tropics although one species, *C. indica*, is commonly cultivated in most tropical areas. The two largest families of the order are the Zingiberaceae with over 53 genera and about 1000 species and the Marantaceae that contains over 30 genera and about 500 species. Currently four genera and ca. 150 species are recognized in the Costaceae. Imminent revisions in generic concepts in all of the ginger-families (except the Cannaceae) may radically change the number of taxa recognized in each (see below under "Phylogenetic Relationships").

Habitat Diversity

The Zingiberales are found predominantly in the wet tropics of Asia, Africa, and the Americas with a few taxa (species of *Roscoea*, *Cautleya*, *Alpinia*, *Canna*, and *Thalia*) reaching into the subtropics and even temperate regions. It would be difficult to find a tropical wet lowland or middle elevation forest in which at least several members of the order are not prominent components of the understory flora. Whereas Heliconiaceae, Marantaceae, and Costaceae predominate in the neotropics, Zingiberaceae is most prevalent in Southeast Asian wet understory habitats. In these regions, Zingiberales are mostly small to medium-sized herbs, in some cases acquiring a vine-like habit. A few species of herbaceous Zingiberaceae (*e.g.*, *Alpinia boia*) and *Heliconia* (*e.g.*, *H. titanium*, *H. gigantia*) can attain shoot heights surpassing ten meters, but only *Ravenala madagascariensis* (Strelitziaceae), an endemic of the island of Madagascar, can be considered a component of the canopy. Commonly referred to as the

Madagascar traveler's palm, *Ravenala* has thick, palm-like trunks that push the fan-shaped crown of leaves into the top layers of the forest. In addition to primary forest understory habitats, other Zingiberales prefer more bright sunlit areas and occupy either light gaps in forests or forest margins and open secondary growth along rivers and streams.

Some members of the Zingiberaceae, especially in the subfamily Zingiberoideae, are adapted to the monsoonal climates of Southeast Asia (Kress *et al.* 2002; Wood *et al.* 2000). These plants have evolved the capacity to go into dormancy during the dry season when almost no rain falls for a period of four to six months. During this time all above ground parts are shed and the plants "overwinter" as thick, fleshy underground rhizomes that in some species possess starch-filled roots or tubers. Either just prior to or at the earliest sign of the wet season, individuals will break dormancy usually with reproductive shoots and complete their life cycle during the intense rainy months before the next dry period begins. Some taxa in the Marantaceae, Costaceae, and Musaceae have also evolved this dormancy capability and are found in the same habitats with the Zingiberaceae. Although these plants can withstand significant periods of extremely dry conditions, no Zingiberales are naturally found in true desert habitats.

In contrast to Zingiberales that are able to withstand an extended dry period, several species are considered to be true aquatics. Some Zingiberaceae (*e.g.*, *Alpinia aquatica*), Marantaceae (*Schumannianthus*, *Thalia* spp.), Heliconiaceae (*Heliconia marginata*), and Cannaceae (*Canna glauca* and *C. flaccida*) are always found growing along river margins, ponds, and swampy areas with their rhizomes rooted underwater for a significant period of the year.

Fig. 1. The single most parsimonious tree resulting from a combined analysis of molecular and morphological data sets. Branch lengths are given above the line; bootstrap values (if ≥50%) and decay indices are provided below the line (from Kress *et al.* 2001).

Fig. 2. "Rhizogram" indicating the basic phylogenetic relationships among the eight families of the Zingiberales (modified from Kress 1990a).

Phylogenetic Relationships

Ordinal Level

The most recent investigation of the phylogenetic relationships among the eight families of the Zingiberales (Kress *et al.* 2001) included both parsimony and maximum likelihood analyses of four character sets: 1) morphological features; 2) chloroplast *rbcL* gene sequence data; 3) chloroplast *atpB* gene sequence data; and 4) nuclear 18S rDNA gene sequence data. The closely related Commelinaceae + Philydraceae + Haemodoraceae + Pontederiaceae + Hanguanaceae as well as seven more distantly related monocots and palaeoherbs were used as outgroups. Only slightly different estimates of evolutionary relationships resulted from the analysis of each character set. The morphological data yielded a single fully resolved most par-
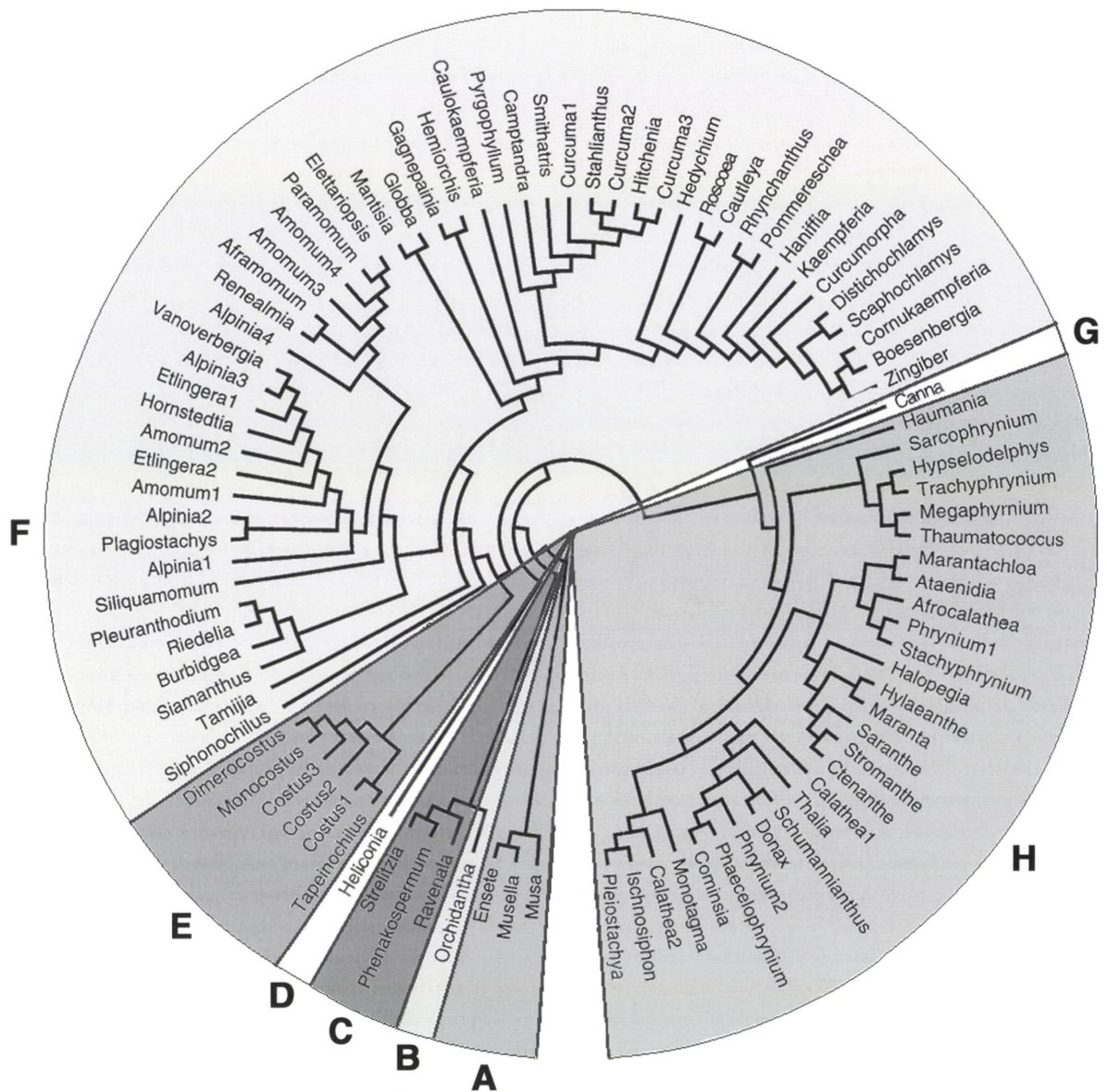
Fig. 3. An informal supertree of representative genera of the Zingiberales derived from source trees based on molecular and morphological analyses of individual families (see references in text). This topology represents one of multiple equally parsimonious trees. A. Musaceae; B. Lowiaceae; C. Strelitziaceae; D. Heliconiaceae; E. Costaceae; F. Zingiberaceae; G. Cannaceae; H. Marantaceae.

simonious tree, but none of the molecular data sets alone completely resolved interfamilial relationships. The analyses of the combined molecular data set provided more resolution than individual genes and the addition of the morphological data resulted in a well-supported estimate of phylogenetic relationships (Fig. 1, 2). The four banana-families form a

paraphyletic assemblage of lineages with the Musaceae the most basal, Strelitziaceae and Lowiaceae sister families, and the Heliconiaceae sister to the remaining four ginger-families. The derived monophyletic group of the four ginger-families are arranged with the Zingiberaceae sister to the Costaceae and the Marantaceae sister to the Cannaceae. Based on evidence from branch lengths in the parsimony analyses of sequence data and from the fossil record Kress *et al.* (2001) suggested that the Zingiberales originated in the Early Cretaceous and underwent a rapid radiation in the mid-Cretaceous by which time most extant family lineages had diverged.

Family and Generic Level

Recently a number of investigations on phylogenetic relationships within the various families of the Zingiberales using molecular sequence data have been completed and/or published (Musaceae: Liu, Kress & Li unpubl.; Lowiaceae: Pedersen 2003; Zingiberaceae: Kress *et al.* 2002; Costaceae: Specht *et al.* 2001; Marantaceae: Andersson & Chase 2001; Prince & Kress unpubl.; Cannaceae: Prince & Kress unpubl.). In most of these family-level analyses previous classifications were shown to be incongruent with the new molecular results (Zingiberaceae: Kress *et al.* 2002; Marantaceae: Andersson & Chase 2001; Prince & Kress unpubl.) and many large and complex genera were demonstrated to be para- or polyphyletic (*Costus*: Specht *et al.* 2001; *Alpinia, Amomum, Curcuma*: Kress *et al.* 2002; *Calathea, Phrynium*: Prince & Kress unpubl.). Several analyses at the generic level have succeeded in clarifying to varying degrees the patterns of evolutionary relationships among species (*e.g.*, *Roscoea*: Ngamriabsakul *et al.* 2000; *Globba*: Williams *et al.* 2004), but others have been limited in breadth of taxon sampling and/or have not shown significant resolution between species. (*Hedychium*: Wood *et al.* 2000; *Alpinia*:

Rangsiruji *et al.* 2000a, b; *Aframomum*: Harris *et al.* 2000; *Amomum*: Xia *et al.* 2004; *Orchidantha*: Pedersen 2003). Because of the difficulties with sequence alignments across families no single analysis has been attempted that combines all available sequence data for the order. However, an informal "supertree" (Bininda-Emonds *et al.* 2002), which was derived by directly combining the individual source trees for each family, provides an approximate and reasonable picture of overall relationships at the generic level in the Zingiberales (Fig. 3).

Time and Place of Evolutionary Divergence

Despite the absence of fossilized pollen of this order due to its very reduced exine (Kress *et al.* 1978), the fossil leaf, seed, and fruit record (Boyd 1992; Manchester & Kress 1993; Rodriguez-de la Rosa & Cevallos-Ferriz 1994) provide good evidence for the occurrence of both the basal family Musaceae and the derived family Zingiberaceae in the Santonian of the Cretaceous over 80 million years ago (Ma). Kress *et al.* (2001) demonstrated in their phylogenetic analyses using sequence data that short branch lengths connect families and long branch lengths are found in the stems lineages of the families. They suggested that these bimodal branch lengths coupled with the fossil evidence indicate a rapid diversification of the major family lineages of the Zingiberales in the Mid- to Late Cretaceous with most of the within-family diversification following in the Tertiary.

Local clock methods (Yoder & Yang 2000) have been used to more accurately estimate the ages of divergence for the eight lineages of the Zingiberales, using *atp*B sequence data for determining branch lengths and the *Ensete oregonense* fossil seed as the calibration point for converting relative rates to absolute ages (Specht 2004). While other fossils are known for the Zingiberales, many are based on leaf

Table 1: Results from the Local Clock and DIVA analyses for the Zingiberales data set.

Node	Date of divergence	Ancestral distribution*
Outgroup ancestral split	158.28 +/- 18.7	AF AM ML
Musaceae – remaining	96.56 +/- 8.74	AM SE
Lowiaceae+Strelitziaceae – remaining	96.56 +/- 8.7	AM, AF AM, AF AM SE
Lowiaceae – Strelitziaceae	49.1 +/- 8.7	AF AM SE
Heliconiaceae – ginger group	96.36 +/- 8.7	AM
Ginger group	88.48 +/- 8.4	AM
Costaceae – Zingiberaceae	83.03 +/- 11	AF AM ML SE
Marantaceae – Cannaceae	80.08 +/-8.4	AM, AF AM
Musaceae		SE
Musa	47.45 +/- 8.69	SE
Musella-Ensete	43.0 +/- 8.69	SE
Lowiaceae (_Orchidantha_) diversification	2.91 +/- 1.5	SE
Strelitziaceae		AF AM
Ravenala	25.26 +/- 6.6	AF
Strelitzia-Phenakospermum	25.0 +/- 6	AF AM
Heliconiaceae crown diversification	4.7 +/- 3.4	AM ML
Neotropical _Heliconia_	1.80 +/- 1.8	AM
Costaceae crown diversification	23.23 +/- 5.7	AM ML
Neotropical _Costus_	23.2 +/- 5.7	AM
Dimerocostus-Monocostus	2.53 +/- 2.5	AM
Zingiberaceae crown diversification	65.0 +/- 15.9	AF SE
Globba	41.5 +/- 11.5	SE
Hedychium-Zingiber	34.6 +/- 10.6	SE
Cannaceae (_Canna_) crown diversification	31.88 +/- 7.4	AF AM, AM
Marantaceae crown diversification	56.73 +/- 7.7	AF AM SE
Maranta-Marantochloa	55.7 +/- 7.7	AF AM SE ML

*Ancestral Distributions reconstructed with multiple options separated by commas. Distributions not separated by commas indicate presence in more than one area, as optimized by DIVA. AF = Africa, SE = South East Asia, ML = Melanesia, AM = Tropical Americas.

characters that have been shown to yield uncertainty in taxonomic identification (Manchester & Kress 1993; Rodriguez-de la Rosa & Cevallos-Ferriz 1994). As a check for accuracy of calibration one additional reliable fossil, the Late Cretaceous/Early Tertiary _Zingiberopsis_, was used. Ancestral distributions were then determined by DIVA optimization (Ronquist 1996) of four general distribution areas (Africa, Southeast Asia, Melanesia, and the Americas) using a composite Zingiberales phylogeny representing all currently recognized
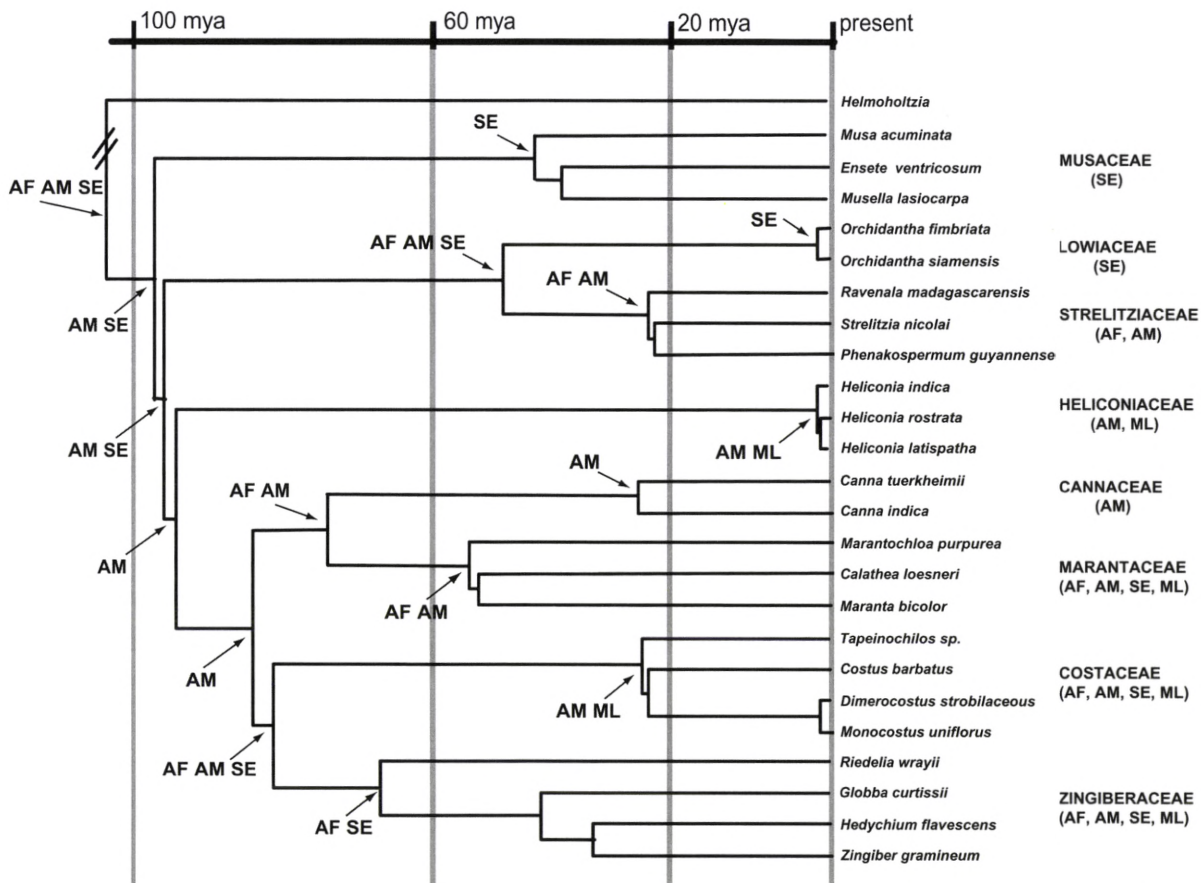
Fig. 4. Chronogeogram of the Zingiberales based on Figure 1 resulting from the Local Clock and DIVA analyses indicating the time of diversification and ancestral areas of the major nodes. Geographic areas given below family names are current distributions. AF = Africa, SE = South East Asia, ML = Melanesia, AM = Tropical Americas.

clades (Fig. 4) and a hypothetical outgroup coded as present in all four areas. These tandem methods enabled the diversification of the order to be analyzed in both a spatial and temporal context.

The results indicate that the Zingiberales originated in the Jurassic, 158 Ma, with an ancestral distribution in the Americas, Africa, and Southeast Asia (*i.e.*, tropical Gondwanaland). If this date is correct, it suggests that this specialized group of plants had an early origin in angiosperm history with a broad tropical distribution. However, it is known that the reliabil-

ity of dating nodes decreases as the distance increases from the calibrated node, in this case the 43 Ma divergence within the Musaceae. Dating the divergence between the ingroup and the outgroup is also problematic in this type of analysis so this ancient date should be considered tentative at this point.

The three main lineages of the banana-families originated about 97 Ma in the early Cretaceous although the split between the Lowiaceae and the Strelitziaceae did not occur until 49 Ma in the middle Eocene (Fig. 4; Table 1). The ginger-families began to diversity 88

Ma with the Costaceae diverging from the Zingiberaceae and Marantaceae from the Cannaceae 83 and 80 Ma, respectively. Therefore by the end of the Cretaceous six of the eight currently recognized families had become independent lineages with the final two families (Strelitziaceae and Lowiaceae) diverging in the early Tertiary.

Within-family diversification represented by extant taxa in some cases did not occur until much later (Fig. 4; Table 1). In the banana-families taxa began to diverge in Musaceae at 47 Ma, in the Strelitziaceae at 25 Ma, in the Heliconiaceae at about 5 Ma, and in the Lowiaceae at only 3 Ma. Unlike the first three families in which taxon sampling was broad, in the Lowiaceae the two sampled species of *Orchidantha* are closely related (Pedersen 2003) therefore most likely underestimating the age of species diversification in this family. In the ginger-families within-family lineages began to diverge in the Late Cretaceous and Teritary at 65 Ma in the Zingiberaceae, 57 Ma in the Marantaceae, 32 Ma in the Cannaceae, and 23 Ma in the Costaceae. Clearly rates of evolutionary divergence are significantly heterogeneous in this order. Low taxon sampling in the molecular analyses as well as undetected extinction may influence these results.

The DIVA reconstruction called for 34 dispersals with no constraints on optimization. A variety of most parsimonious solutions resulted and the one represented here (Fig. 4; Table 1) illustrates the combination of areas best supported for the nodes where more than one alternative is optimal. The common ancestor of the Zingiberales appears to have had a pantropical distribution in a possible Gondwanan configuration, but current distributions of the families with wide geographic ranges can best be understood as a combination of restricted ancestral areas with secondary or even tertiary dispersals to new tropical habitats, for example, secondary dispersal to the

neotropics in the Zingiberaceae, to Southeast Asia in the Marantaceae, and to Africa and Southeast Asia in the Costaceae. Investigations currently in progress, which employ an expanded molecular data set with additional taxa to reconstruct distributions using DIVA and calculate divergence times using local clock methods, may produce further insights into the place and time of these taxonomic radiations (Kress & Specht 2005).

Diversification of Floral Biology and Pollination Systems

The wide variation in the basic structural organization of the flower among the eight families of the Zingiberales (Fig. 5) indicates that a significant diversity may exist in the floral biology and pollination systems as well. The evolutionary transformation of the five to six fertile, pollen-producing stamens in the banana-families into diverse petal-like organs in the four ginger-families provides the morphological potential for the evolution of various types of pollination mechanisms. Investigations to date have proven this suggestion to be true (Fig. 6). The variety of pollination systems is first briefly summarized below and then an analysis is presented of their evolutionary origin and diversification in the order.

Vertebrates

All of the major groups of known vertebrate pollinators have been shown to be important floral visitors of various taxa in the Zingiberales. Both megachiropteran and microchiropteran nectar-feeding bats pollinate flowers of species in several families of the order, especially in the banana-families. In Asia some of the earliest accounts of pollination by bats documented the relationship between nectar feeding fruit bats and the genus *Musa* and possibly *Ensete* (van der Pijl 1936; Nur 1976; Itino *et al.* 1991). Pollination of South Pacific species of
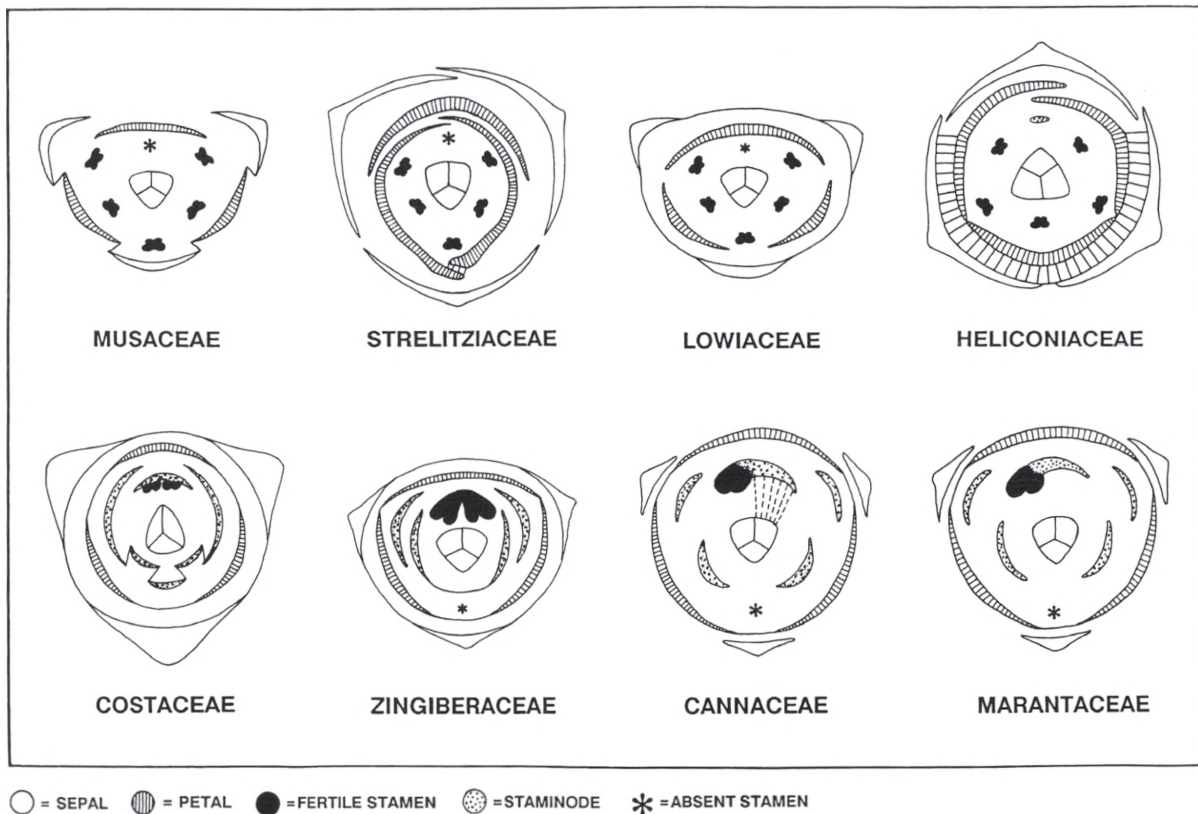
| ○ = SEPAL | ⦀ = PETAL | ● =FERTILE STAMEN | ⊛ =STAMINODE | ✳ =ABSENT STAMEN |

Fig. 5. Floral diagrams representing the eight families of the Zingiberales with perianth whorls, fertile stamens, staminodia, and carpels (not drawn to scale; taken from Kress 1990a).

the genus *Heliconia* by other megachiropteran bats has also been shown (Kress 1985a). In the Neotropics, the Amazonian monotypic *Phenakospermum* of the Strelitziaceae is dependent on microchiropteran bats in the family Phyllostomidae for successful pollination (Fig. 6; Kress & Stone 1993). Although actual field observations are still lacking, floral characteristics such as perianth size and shape, odor, and phenology also suggest that some members of the Zingiberaceae (*e.g.*, species of *Alpinia* in the Pacific islands) and Cannaceae (*e.g.*, *Canna liliiflora* of Bolivia and Peru) may be primarily bat-pollinated (Kress unpubl.).

Pollination by non-flying mammals has been demonstrated for some members of the Musaceae and the Strelitziaceae. In Madagascar, the endemic *Ravenala madagascariensis* is pollinated by lemurs, especially the Black and White Ruffed Lemur (*Varecia variagata*), which extract large amounts of nectar from the explosive flowers and in so doing transfer pollen between anthers and stigma (Fig. 6; Kress *et al.* 1994). In addition it has been documented that tree shrews (species of *Tupaia*) often visit the flowers of wild species of *Ensete* and *Musa* in Asia (Nur 1976; Itino *et al.* 1991) although their effectiveness as pollinators has not been adequately documented. Floral characteristics and preliminary observations suggest that tree shrews also visit flowers of at least one species of the genus *Orchidantha* (*O. fimbri-*
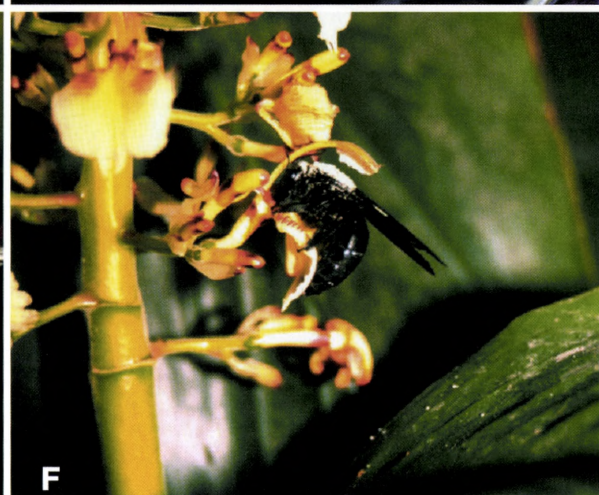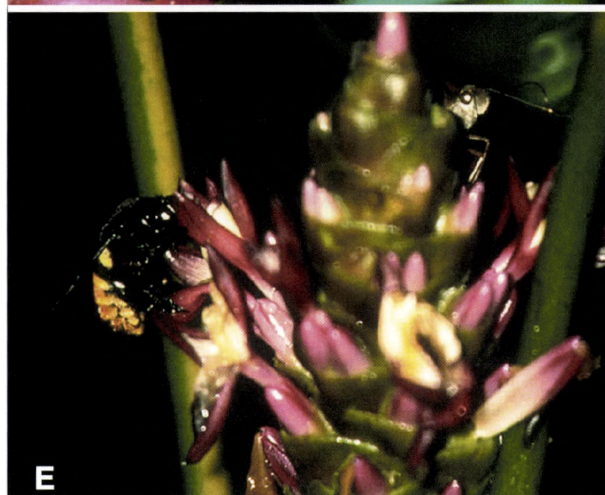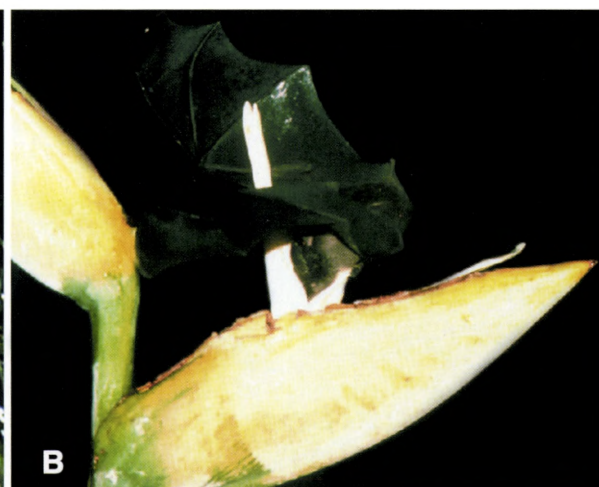
ata; Lowiaceae) in the lowland wet forests of Malaysia (Kress unpubl.), but as in the Musaceae data on actual pollination are absent. These flowers lack nectaries, but attract floral visitors by the specialized medial petal, called the labellum, which is expanded into a fleshy structure that produces a sweet, sugary substance and serves as the attractant and reward for these non-flying, crepuscular mammals (see below for observations of insect pollination in the Lowiaceae).

Birds are the most diverse group of vertebrate pollinators for members of at least seven of the eight families of the Zingiberales. Sunbirds (Nectarinidae) pollinate flowers of species of *Strelitzia* in South Africa (Frost & Frost 1981) and many species of the genus *Musa* in Asia that have erect, brightly colored inflorescences (Itino *et al.* 1991; Kato 1996; Liu *et al.* 2002b). In Borneo sunbird and spider-hunter pollination has been reported for a number of wet forest understory genera of the Zingiberaceae, including *Amomum*, *Etlingera*, *Hornstedtia*, and *Plagiostachys* (Classen 1987; Kato *et al.* 1993; Kato 1996; Sakai *et al.* 1999) and possibly *Siamanthus* as suggested by Larsen and Mood (1998). The wattled honeyeater of Samoa and Fiji (Melaphagidae: *Fulihao carunculata*) are the primary pollinators of the two native species of *Heliconia* in these Pacific Islands (Pedersen & Kress 1999). Honeyeaters have been documented as pollinators of the genus *Hornstedtia* in tropical Australia (Ippolito & Armstrong 1993) and may play a role in the pollination of the poorly known genus *Tapeinochilos* in the Costaceae (Gideon 1996).

Hummingbirds (Trochilidae) have evolved the most intricate relationships as pollinators in several families of the Zingiberales, primarily the Heliconiaceae, Costaceae, Zingiberaceae, and Cannaceae. In the genus *Heliconia* ample documentation has been provided on the ecology and evolution of the features of both the hummingbirds and the plants that link them in a highly coevolved relationship (*e.g.*, Stiles 1975; Linhart 1973; Kress 1985b; Feinsinger 1983; Kress & Beach 1994; Temeles *et al.* 2000; Temeles & Kress 2003). Flower length and curvature, position of anthers, phenological patterns, and nectar amount and composition are all closely associated with hummingbird bill size and shape as well as the pollinator's energetic requirements. Of all the pollination systems in the Zingiberales, the relationship between heliconias and their hummingbird floral visitors is the most thoroughly studied and represents an often cited example of coevolution and adaptation. Further fieldwork is needed to investigate the role that hummingbirds play as pollinators of neotropical members of the Zingiberaceae (*e.g.*, *Renealmia*; Stiles 1975; Maas 1977; Kress & Beach 1994), Costaceae (Stiles 1975; Maas 1977; Sytsma & Pippen 1985; Kress & Beach 1994), Cannaceae (Kress & Beach 1994), and even a few Marantaceae (Kennedy 2000).

Insects

Many different groups of insects play important roles as pollen vectors in six of the eight families of the Zingiberales; the Strelitziaceae and Heliconiaceae are exclusively vertebrate-pollinated. Only recently have beetles been conclusively demonstrated to pollinate the

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← **Fig. 6**. The diversity of pollinators in some representative members of the Zingiberales. A. The Black and White Ruffed Lemur (*Varecia variegata*) visiting the flowers of *Ravenala madagascariensis* (Strelitziaceae). B. *Phyllostomus hastatus* pollinating the flowers of *Phenakospermum guyannense* (Strelitziaceae). C. The Crowned Woodnymph Hummingbird (*Thalurania furcata*) taking nectar from the flowers of *Heliconia imbricata* (Heliconiaceae). D. A Dung Beetle entering the flower of *Orchidantha inouei* (Lowiaceae). E. A euglossine bee hovering at an inflorescence of *Calathea latifolia* (Marantaceae). F. A carpenter bee visiting the flowers of *Alpinia* (Zingiberaceae). Photo in D. provided by S. Sakai; all other photos by W.J. Kress.

flowers of species of the genus *Orchidantha* in the Lowiaceae. These flowers have no nectaries and deceive their pollinators by producing a foul, dung-like odour and thereby attracting dung beetles to the flowers (Fig. 6; Sakai & Inoue 1999). It has been suggested that in other species of the genus the white labellum mimics a fungus that also deceives specialized beetles, which normally lay their eggs in fungi, to visit the flowers (Pedersen 2003). Another species, *O. chinensis*, also produces foul odors, but these flowers attract small dung flies, rather than beetles, which mate in the flowers and appear to facilitate pollination in the process (Kress unpubl.). Fly pollination has not been reported in other Zingiberales.

Floral visitation by lepidoptera (butterflies and moths) has not been adequately documented in this order of plants. In some genera in the Zingiberaceae, such as *Hedychium*, *Hitchenia*, and *Curcuma*, flowers possess long floral tubes, open in the evenings, and may produce a strong, sweet fragrance, which are all characteristics suggesting pollination by long-tongued hawkmoths (Mood & Larsen 2001; Kress unpubl.). Schumann (1904) citing earlier studies suggested that both hawkmoths and butterflies pollinate various species of *Hedychium*, but these observations are suspect being made on naturalized plants outside their native distributions. In the Costaceae, butterflies of the genus *Eurybia* have been observed visiting the flowers in at least one species in South America, *Costus scaber* (Specht & Hanner pers. comm.). Further investigations of pollination by lepidopterans are therefore warranted in the Zingiberaceae, Costaceae, and maybe some Marantaceae (*e.g.*, *Cominsia*; Kennedy 2000).

Bees are by far the most common insect pollinators at the species-level in the Zingiberales and probably are responsible for pollination in the majority of genera in the order. Bee pollination is only present in one genus of the banana-families, *Musella* in the Musaceae where it is clearly secondarily derived from vertebrate-pollinated ancestors (Liu *et al.* 2002a). Pollination by a number of families of bees is found in all four of the ginger-families and probably occurs pantropically, although it is surprisingly poorly documented, especially in Africa. Early accounts provided evidence for bee pollination of *Roscoea* (Lynch 1882) and *Costus*, *Canna*, and *Heliconia* (Heide 1927) although the latter observations were made on non-native, cultivated plants in gardens. In Southeast Asia, pollination by both small halictid and medium-sized anthophorid (*Amegilla*) bees has been demonstrated (Kato *et al.* 1993; Kato 1996; Sakai *et al.* 1999) in a number of genera of the Zingiberaceae (*Alpinia*, *Amomum*, *Boesenbergia*, *Elettaria*, *Elettariopsis*, *Globba*, *Plagiostachys*, *Zingiber*), Costaceae (*Costus*), and Marantaceae (*Phacelophrynium*, *Stachyphrynium*). In the neotropics pollination by bees is especially common in species of *Costus* (Costaceae; Schemske 1981; Sytsma & Pippen 1985), *Renealmia* (Zingiberaceae; Maas 1977; Kress & Beach 1994) and at least a few species of *Canna* (Cannaceae; Kress & Beach 1994). Members of the Marantaceae possess very specialized and highly complex flowers with explosive secondary pollen presentation and are pollinated primarily by euglossine bees in the American tropics (Fig. 6) with *Amegilla* and halictid bees predominant in the Old World tropics (Kennedy 1978, 2000). Two staminodia, which are petaloid in the flowers of the other three ginger-families, have evolved into a trigger-like mechanism in the flowers of the Marantaceae that allows only a single effective pollinator visit to a flower and may promote out-crossing in these plants (Kennedy 1978).

One of the most unusual floral mechanisms found in the Zingiberales has evolved in species of *Alpinia* and *Amomum* (Zingiberaceae) pollinated by large bees (*e.g.*, *Xylocopa*; Fig. 6). Species that exhibit this mechanism,

called flexistyly (Li *et al.* 2001, 2002), have two specific floral phenotypes in a population: cataflexistyle individuals possess flowers with stigmas that are held erect at anthesis and turn downward in the late morning after anther dehiscence is complete, whereas stigmas of anaflexistyle individuals that are turned downward and receptive at flower opening become reflexed backwards out of the way of the dehiscing anther of the same flower in the late morning. This mechanism promotes pollen movement between individuals of the two floral types in the population and has apparently evolved to ensure outcrossing. The great floral diversity in the family Zingiberaceae suggests that many interesting mating systems and floral phenomena, such as flexistyly, are yet to be discovered in these plants.
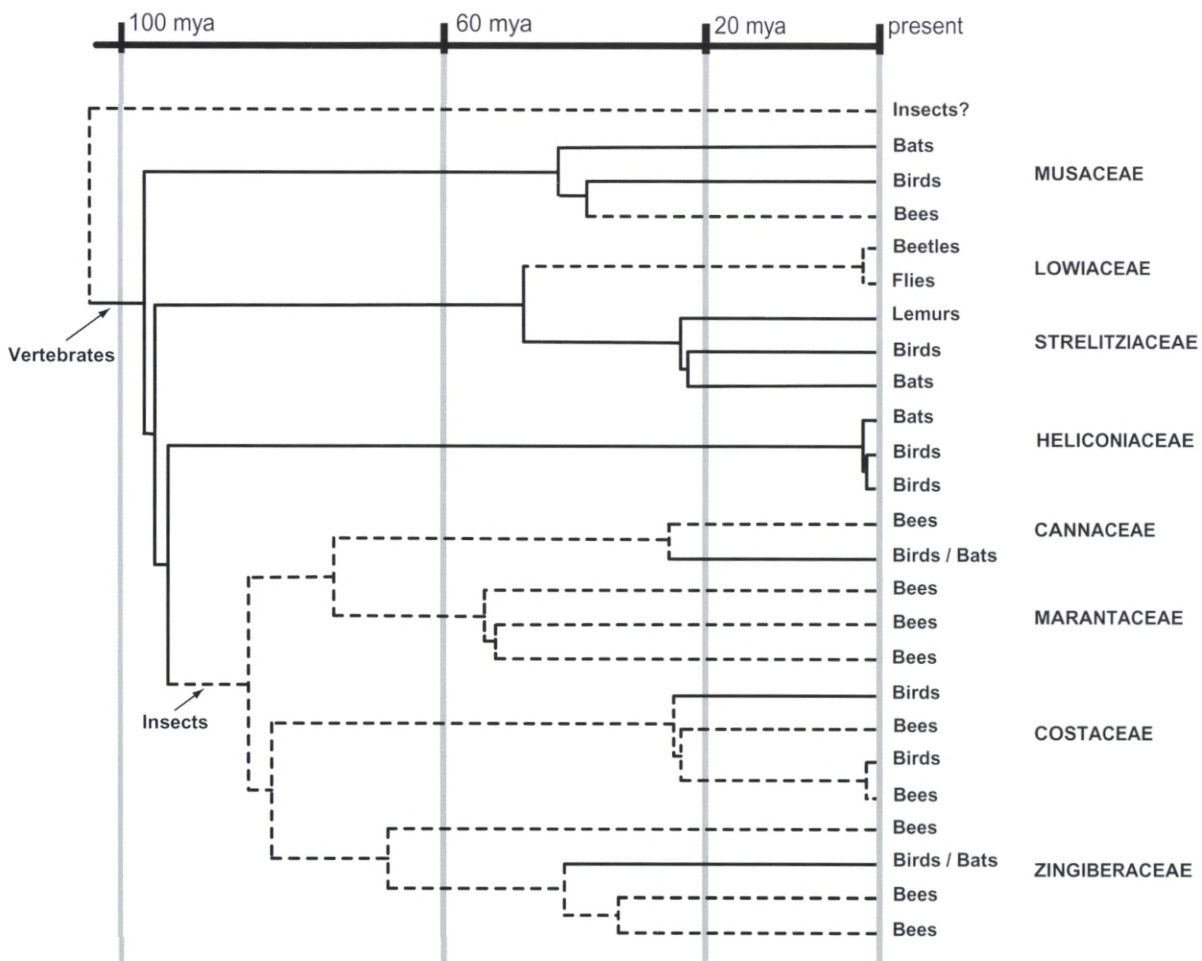

Fig. 7. Chronogram of the Zingiberales as in Figure 4 with major pollinators indicated for each clade. Terminal taxa have been replaced with pollinator types known to be found in each family. Incidental or unsubstantiated reports of pollinators are not included here, but are discussed in the text. Solid lines indicate vertebrate pollination; broken lines indicate insect pollination.

General patterns of origin and diversification of pollination systems

By mapping the types of pollinators onto the phylogenetic tree of the Zingiberales a broad picture of the evolutionary origins and transitions between the different pollinator types emerges (Fig. 7). Based on the prevalence of vertebrate pollinators (bats, birds, and non-flying mammals) in the three basal banana-families lineages (Musaceae, Strelitziaceae + Lowiaceae, and Heliconiaceae), the parsimony criterion suggests that the Late Jurassic and Early Cretaceous common ancestor of the order was also pollinated by some early vertebrate taxon. It is difficult to envision which vertebrates may have been pollinators at that time because most vertebrate groups that serve as extant pollinators evolved much later in the Tertiary (Sibley & Ahlquist 1990; Nowak 1991; Bleiweiss 1998). Possible candidates include the early mammalian multituberculates or even small dinosaurs. Although this conclusion is not unreasonable, little additional evidence exists to support it. An alternative hypothesis involving a slightly less parsimonious reconstruction is that the flowers of the common ancestor of the Zingiberales were pollinated by large insects and that vertebrate pollination has been independently derived in the three basal lineages of the banana-families as the vertebrate lineages themselves diversified (see below).

If vertebrate pollination represents the plesiomorphic state in the Zingiberales, then pollination by insects appears to be the derived condition in the specialized ginger families as well as in the genera *Musella* (Musaceae) and *Orchidantha* (Lowiaceae), and some derived species of *Canna* (Fig. 7). This evolutionary pattern, in which the ancestral taxa are pollinated by vertebrates and the derived taxa by insects, contradicts the generally accepted notion that insect pollination systems have usually given rise to more specialized bat- and bird-

pollinated taxa (*e.g.*, Faegri & van der Pijl 1979). In some families and genera in the order this latter pattern is indeed the case. For example, in three of the families where most taxa are pollinated by insects, bird-pollinated taxa (Zingiberaceae: *Etlingera, Hornstedtia, Amomum*; Costaceae: *Costus* sect. *Ornithophilus, Tapeinochilos*; and Marantaceae: *Calathea timothei*) and bat-pollinated taxa (*e.g.*, Zingiberaceae: a few species of *Alpinia*) appear to have evolved independently from insect-pollinated taxa. Recent studies indicate that shifts in rates of speciation may co-occur with these shifts in pollination systems (Specht in press). More fine-grained phylogenies will help to sort out these evolutionary patterns at the generic and species levels.

By utilizing both the branching pattern within the ordinal phylogeny derived from the molecular and morphological data and the temporal pattern as revealed by the molecular clock analysis, the time of origin and diversification of particular pollination systems in the Zingiberales also can be estimated (Fig. 7). The three major lineages containing taxa primarily pollinated by vertebrates appear to have undergone relatively long periods of stasis from their origin at about 96 Ma until the Mid-Tertiary (Musaceae: 49 million year stasis period; Strelitziaceae-Lowiaceae: 48 Myr stasis period) and even the Quarternary (Heliconiaceae: 92 Myr stasis period). Although extinction cannot be ignored, these long periods of stasis can be compared to the much shorter time periods from origin to early diversification in the crown lineages in the insect-pollinated ginger-families. For example, the crown lineage of the Zingiberaceae-Costaceae clade diversified after five million years, the Cannaceae-Marantaceae clade after eight million years, the family Zingiberaceae after 18 million years, and the family Marantaceae after 23 million years. Within the primarily insect-pollinated ginger-families the Costaceae and Can-

naceae, both with bird-pollinated as well as insect-pollinated taxa had relatively long periods of stasis before major episodes of divergence occurred, *e.g.*, 60 my and 72 my, respectively. In other words, pollination by vertebrates either has not given rise to the same rate of diversification as seen in insect-pollinated lineages, or vertebrate-pollinated taxa have gone extinct much faster.

Another interpretation of the temporal analysis of pollination systems is the corroboration of the evolutionary origin of various taxa of pollinating animals and the time of origin of their ecological interactions with members of the Zingiberales. For example, although several lineages giving rise to bat-pollinated taxa extend back into the Cretaceous (Musaceae, Strelitziaceae-Lowiaceae, and Heliconiaceae) the within family diversification occurred at about the same time as the earliest fossil records of both the phyllostomid (Miocene) and pteropid (Oligocene) bats about 20 and 40 Ma, respectively (Fig. 7; Nowak 1991). These ages correspond to the origin at 25 Ma of the phyllostomid-pollinated taxon *Phenakospermum* and the 47 Ma origin of the pteropid-pollinated taxa *Musa* and *Ensete*. It is estimated that hummingbirds diverged from their common ancestor with the swifts 58.5 Ma, followed by within-family diversification beginning about 18 Ma (Bleiweiss 1998). This timing of the hummingbird radiation roughly coincides with the diversification of hummingbird-pollinated taxa in the Zingiberales, such as *Heliconia*, *Canna*, and some Costaceae, all of which took place less than 32 Ma. Because of the limited taxon sampling in the analyses, these results are only suggestive of the temporal patterns of diversification. However, they illustrate a potentially powerful analytic tool for understanding the origin and diversification of plant-pollinator interactions in a quantifiable temporal context. Current investigations using additional gene sequences and taxa (Kress & Specht unpubl.) may provide a more detailed understanding of the temporal origin of these plant-pollinator interactions.

Conclusion

The brief summary presented above provides an overview of the morphological, taxonomic, and habitat diversity as well as the extent of pollinator diversity found in the tropical Zingiberales, both past and present. Investigations are now focusing on the genetic control of floral development in these plants in order to obtain a more complete picture of the evolutionary origin of plant-pollinator interactions. The "floral organ identity" genes, or ABC genes, in angiosperms have been proposed as the control agents for determining floral primordia (Coen & Meyerowitz 1991; Theissen 2001). Current studies in progress to identify these genes and their transcriptional products in a selected number of taxa in the Zingiberales (Rehse *et al.* 2003) may provide answers to the developmental origin of the highly modified floral structures in these plants, especially the evolutionary transformation of the fertile stamens in the banana-families to the petal-like staminodia in the ginger-families. Unlike the experimentally-induced mutant floral types in the model organism *Arabidopsis* that has been the focus of much of the work on the ABC genes, the ancient origin of fixed floral mutants in the Zingiberales provides a natural experiment to understand the evolutionary patterns of floral development. By combining molecular studies of floral development with results from phylogenetic analyses and ecological investigations, such as are now being carried out for the tropical Zingiberales, a more robust and vibrant model of evolutionary diversification will be realized. The results on the Zingiberales when coupled with similar

studies of other taxa will potentially provide new insights into the evolution of flowering plants.

Acknowledgments

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