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## HOMEOSIS IN THE FLOWERS OF THE ZINGIBERALES<sup>1</sup>

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Homeosis has played an important role in the evolution of the flowers of the Zingiberales, especially those of the Ginger Group. In the Zingiberaceae, two members of the outer androecial whorl are replaced by a lip, and two members of the inner androecial whorl are replaced by petaloid staminodes. Most of the androecium of the Costaceae has also been replaced by petaloid structures, and the single fertile stamen is often attached to an enlarged petaloid "filament." The Cannaceae and Marantaceae have one-half of one fertile anther and three to four variously modified staminodes. In contrast, homeosis has played a minor role in floral evolution of the Banana Group. Only in the Heliconiaceae has a stamen been replaced by a staminode. In none of the families of the Zingiberales do the staminodes assume the total "form or character" of any perianth members. Because of this, it is reasonable to extend the definition of homeosis to include replacement by an organ like, but not identical to, some other part of the plant.

Research on homeosis in plants has focused primarily on homeotic phenomena at the species level or below (Leavitt, 1909; Poethig, 1985; Sattler, 1988; Hill and Lord, 1989). Consequently, there are few documented examples of the role of homeosis in the evolution of higher taxa. The role of homeosis in the macroevolution of an order will be demonstrated in this contribution, with reference to the flowers of the Zingiberales. I also review the definition of homeosis in light of the data presented here and follow Sattler (1988) in arguing for a broad definition for use in describing homeotic phenomena in plants.

### MATERIALS AND METHODS

The material used in this study was collected over a period of 10 years in Costa Rica; at Fairchild Tropical Garden, Miami, Florida; Lyon Arboretum, Oahu, Hawaii; Waimea Arboretum, Oahu, Hawaii; and from the Duke University Greenhouses, Durham, North Carolina. Observations were made either in the field or on material fixed in formalin-acetic acid-alcohol (Berlyn and Miksche, 1976). The sources of the species pictured in this paper are given in Table 1. The morphological interpretations of the flowers of the Zingiberales are based on studies of flower development in the order (Kirchoff 1983a, b, 1988a, b, unpublished data), and on data extracted from the literature.

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### RESULTS AND DISCUSSION

The Zingiberales are a monophyletic order of monocotyledons of uncertain affinities (Tomlinson, 1962; Cronquist, 1978; Dahlgren, Clifford, and Yeo, 1985; Kress, 1990). Simpson (1989) suggests a relationship with the orders Haemodiales and Pontederiales based on pollen wall development. The eight families of the order are united by several synapomorphies (Dahlgren and Clifford, 1982; Dahlgren and Rasmussen, 1983; Dahlgren, Clifford, and Yeo, 1985; Kress, 1990): number of stamens five or less (the occurrence of six stamens in some species of the Musaceae and Strelitziaceae are interpreted as autapomorphies of these species); sepal nectaries present in the flowers; leaves supervolute in bud; petiole containing air canals; pollen exine reduced or absent; pollen grains without distinct apertures; stigma surface wet; silica bodies present; sieve tube plastids with starch grains. Based on overall similarity, the order may be divided into two informal groups. The first, the Banana Group, consists of the Musaceae (bananas), Strelitziaceae (birds-of-paradise), and the two monogeneric families Heliconiaceae (*Heliconia*) and Lowiaceae (*Orchidantha*). The second, the Ginger Group, consists of the remaining four families: Zingiberaceae (gingers), Costaceae, Marantaceae (prayer plant family), and Cannaceae.

The flowers of the Banana Group are less specialized than are those of the Ginger Group (Eichler, 1875; Lane, 1955; Dahlgren, Clifford, and Yeo, 1985). They consist of six perianth members differentiated into a calyx and a corolla, five or six stamens, and a trilocular inferior ovary (Figs. 1C, F, 3-8). The perianth members may be variously "fused" to each other in the

TABLE 1. *Species pictured*

Species	Collector/voucher	Deposited	Accession no. <sup>a</sup>
<i>Ravenala madagascariensis</i> J. F. Gmel.	—	—	W 73S32
<i>Heliconia indica</i> Lam.	Kirchoff 87-109	BISH	W 79P1202
<i>Kaempferia</i> sp.	—	—	W 83P316
<i>Canna indica</i> L.	Kress 76-541	DUKE	Duke unaccessioned
<i>Costus scaber</i> Ruiz et Pavon	Kirchoff 84-6	FTG	FTG P.609
<i>Marantochloa purpurea</i> (Ridl.) M. Redh.	Kress 78-894	DUKE	Duke unaccessioned

<sup>a</sup> W: Waimea Arboretum, Oahu, HI; FTG: Fairchild Tropical Garden, Miami, FL; Duke: Duke University greenhouses, Durham, NC.

different families. The androecium of the Banana Group families closely resembles that of an idealized monocotyledon: six stamens arranged in two whorls (Fig. 1F). However, most genera lack one stamen from the inner whorl. In *Heliconia* the inner whorl consists of three stamens, while the outer whorl has two stamens and one staminode.

Homeosis has played only a minor role in the floral evolution of the Banana Group. The flowers of the Strelitziaceae (Figs. 1F, 3), Lowiaceae, and Musaceae do not show homeosis. In the Heliconiaceae, a stamen of the outer whorl has been replaced by a dorsiventral, bifacial staminode (Figs. 1C, 2B, 4, arrow). Kress (1984) and Andersson (1985) provide illustrations of staminode shape across the genus. This staminode shares some properties more normally associated with the perianth than with the androecium (Fig. 2). Most notably, it is reduced in length and expanded in width to produce an organ that is slightly longer than broad. It also has a more

elaborate vascular system than is normally found in a stamen (Fig. 2B). Its nonpetal-like characteristics include its small size, its thickness, and of course, its position.

The flowers of the Ginger Group are highly modified compared to a "typical" monocotyledon flower (Eichler, 1875, 1884; Kirchoff, 1983b, 1988a; Kunze, 1984; Dahlgren, Clifford, and Yeo, 1985). The perianth is differentiated into two whorls of three members each. The sepals are either united into a synsepalous calyx (Fig. 1A, B; Zingiberaceae, Costaceae), or are free above the ovary (Fig. 1D, E; Cannaceae, Marantaceae). The petals are united with all other floral organs, including the androecium and style, into a floral tube of varying extent and complexity. The androecium is highly modified in this group. The number of stamens that produce pollen is reduced to one (Fig. 1A, B; Zingiberaceae, Costaceae) or one-half (Fig. 1D, E; Cannaceae, Marantaceae). This fertile stamen (or half stamen) is always the same member

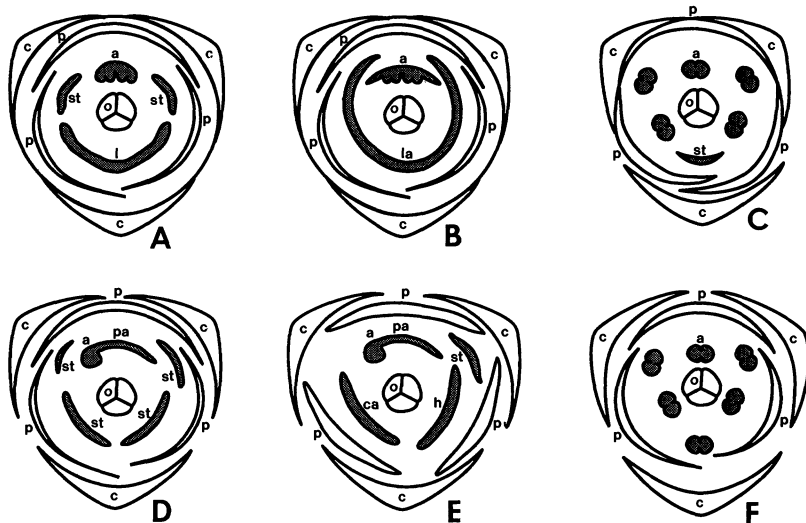


Fig. 1. Floral diagrams of six families of the Zingiberales, with androecial members shaded. A, Zingiberaceae; B, Costaceae; C, Heliconiaceae; D, Cannaceae; E, Marantaceae; F, *Ravenala* (Strelitziaceae). The other members of the Strelitziaceae have five stamens. *Figure abbreviations*: a, androecial member (stamen); c, sepal (calyx); ca, callose staminode; f, petaloid filament; h, hooded staminode; l, lip; la, labellum; o, trilocular inferior ovary; p, petal; pa, petaloid appendage; st, staminode.

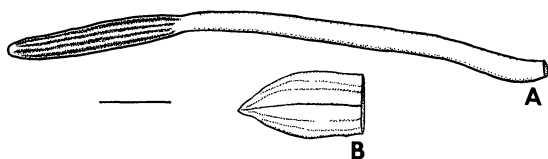


Fig. 2. Androecial members of *Heliconia indica* Lam. (Heliconiaceae). A, Stamen; B, staminode showing the major vascular strands. Bar = 5 mm.

of the inner androecial whorl. The other androecial members are transformed into petaloid structures, which have various forms and degrees of "fusion." The ovary is inferior and mono-, bi- or trilocular.

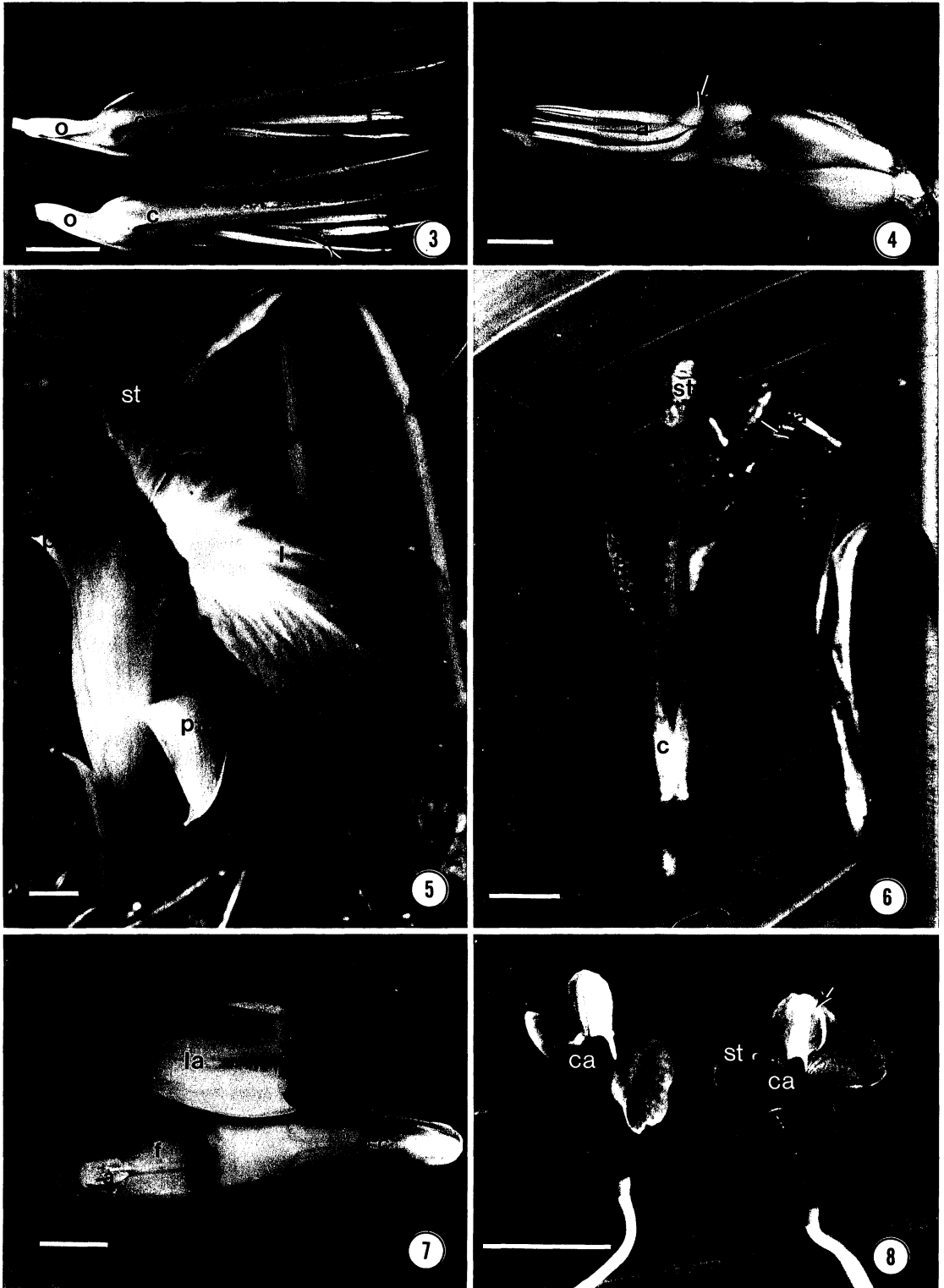
Homeosis has played an important role in the floral evolution of the Ginger Group. In the Zingiberaceae, two members of the inner androecial whorl are replaced by a lip, which may be two-lobed (Figs. 1A, 5). The outer androecial whorl is represented by two staminodes, which are either petaloid and "fused" to the lip (subfamily *Zingibereae*), petaloid and free from the lip (subfamily *Globbeae*, most *Hedychieae*) (Figs. 1A, 5), or small, nonpetaloid, and present only at the base of the lip (subfamily *Alpineae*, some *Hedychieae*) (Holtum, 1950; Smith, 1981). Most of the androecium of the Costaceae has also been replaced by petaloid structures (Kirchoff, 1988b). There is a single fertile stamen that is often attached to an enlarged petaloid "filament," and a large labellum (Figs. 1B, 7). The size and texture of the labellum varies across the family from relatively small and callose (e.g., some *Costus* spp., Maas, 1972) (Fig. 7) to large and delicate (e.g., *Dimerocostus*; Maas, 1972). The androecia of the Cannaceae and Marantaceae are constructed along very similar lines (Fig. 1D, E). Both consist of one-half of one fertile anther and three to four staminodes (Figs. 6, 8). The other half of the fertile anther is replaced by a petaloid appendage that is attached to the fertile locules (Fig. 6, arrow). In the Cannaceae, the size of the petaloid appendage is quite uniform. It is usually only several times larger than the fertile locules. In the Marantaceae, the petaloid appendage ranges in size from almost nonexistent to many times larger than the fertile locules (Fig. 8, arrow). The staminodes proper are relatively unmodified in the Cannaceae (Fig. 6) and resemble petals more so than in the Marantaceae. The staminodes function in the attraction of pollinators in both families. In addition, certain of the staminodes of the Marantaceae are variously modified to function in pollen placement on the insect (Kennedy, 1978; Kirchoff, 1983a). The greatest modifications occur in the callose and hooded staminodes. Kunze (1984) describes the structure

and vascularization of these staminodes in selected genera, and Kennedy (1978) describes their function in pollination for some members of the genus *Calathea*.

The above examples show the relevance of a study of homeosis to the evolution of at least one major group of plants. In both the Banana and Ginger Groups, members of the androecial whorls have been replaced by structures that resemble petals. Despite the resemblance between the staminodes and petals, we should not lose sight of the fact that these organs are not exactly like petals. The staminodes are often much larger, thinner or thicker, and more brightly colored than the petals, with a correspondingly more elaborate vascular system. In the proceeding paragraphs homeosis has been used in a broad sense, without definition. What relevance do these observations have to the definition of homeosis?

The term homeosis was proposed by Bateson (1894) and defined as "the assumption by one member of a meristic series, of the form or characters proper to other members of the series." If we accept this definition in a strict sense, we must exclude the replacement of stamen by staminodes in the Zingiberales from homeosis. The staminodes do not assume the total "form or characters" of any perianth members. They merely resemble the perianth in some respects, being considerably different in others. That this problem is not unique to the Zingiberales is shown by Hill and Lord's (1989) work on the *Arabidopsis* mutant, *pistillata*. Hill and Lord (1989) found that the sepal-like organs that replace petals are not exact equivalents of sepals, either in structure or development. The sepal-like organs merely resembled sepals in some respects. Many more examples of replacement by an organ similar, but not identical to, a serially homologous organ could be cited (see Sattler, 1988). Bateson (1894) indicated that phenomena such as these should be included in homeosis in the same paragraph in which he defines the term: "The case of the modifications of the antenna of an insect into a foot, of the eye of a crustacean into an antenna, of a *petal* into a *stamen*, and the like, are examples of the same kind" (emphasis added).

The examples presented above argue that exact replacement of one organ with another is unlikely in plants. Rather, the new organ is merely "like" some other organ. The relationship is one of semiquantitative homology, in the sense of Sattler (1966). With this in mind, it is reasonable to extend the definition of homeosis to include replacement by an organ like, but not identical to, some other organ. Schwartz's (1971) definition of homeosis comes close to



Figs. 3-8. Flowers of the Zingiberales. 3. *Ravenala madagascariensis*, Strelitziaceae. Bar = 4 cm. 4. *Heliconia indica*, Heliconiaceae. The sepals and petals have been removed above the floral tube; arrow indicates staminode. Bar = 1 cm. 5. *Kaempferia* sp., Zingiberaceae. Bar = 1 cm. 6. *Canna indica*, Cannaceae. The flower on the right has been split longitudinally; arrow indicates petaloid appendage. Bar = 1 cm. 7. *Costus scaber*, Costaceae. The style is clasped between the locules of the anther with the stigma borne above the anther. The petals have been removed. Bar = 1 cm. 8. *Marantochloa purpurea*, Marantaceae; arrow indicates petaloid appendage (anther hidden). Bar = 1 cm.

this ideal: "A variation in plants in which one organ takes on the characteristics of another." Here, the phrase "takes on the characteristics of another" should be understood not in an all or none sense, but in the sense that some of the characteristics normally associated with one organ have been "transferred" to another organ. Holmes (1979; as discussed in Sattler, 1988) makes this distinction more explicit: homeosis is "the assumption by one part of likeness to another part."

The only clarification I would like to add to this definition is that to be considered homeosis in the classic sense, the part being transferred must be present elsewhere on the same plant. For example, the modification of a stipule to resemble a foliage leaf (Sattler, 1988) is an example of homeosis because characteristics have been transferred from one organ to another on the same plant. A counter example is the presence of staminodial nectaries in the Lauraceae (Walters and Keil, 1977, Fig. 11.2 C, D; Tomlinson, 1980, Figs. 62–65). Since extrafloral nectaries are unknown in the Lauraceae (Elias, 1983) they cannot have been transferred to the stamens from elsewhere on the plant. Thus, the staminodial nectaries of the Lauraceae should not be considered an example of homeosis. With this clarification, I support a broad definition of homeosis such as that proposed by Holmes (1979) and championed by Sattler (1988).

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