FLORAL ONTOGENY, PATTERN FORMATION, AND EVOLUTION IN Hibbertia and Adrastaea (Dilleniaceae)1

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Floral development was compared with scanning electron microscopy in 12 Australian species of Hibbertia representing most of its morphological variation, and in the related Adrastaea (Dilleniaceae). Calyx and corolla arise in quincuncial helices in radially symmetrical species, while the petals initiate unidirectionally from one side in zygomorphic species. Stamen number (3–200+) proliferaes by centrifugal addition of individual primordia or by innovations of common primordia and ring meristems. Common primordia arise in single-stamen positions alternately with petals, and each produces one to several stamens centrifugally that remain attached to a shared base and form a stamen fascicle. A ring meristem in Adrastaea initiates a whorl of five stamens, alternate with the first stamens but outside their whorl. In radially symmetrical species of Hibbertia, a first ring of stamens is supplemented centrifugally by additional stamens on a meristem ring. The first stamens in zygomorphic species of Hibbertia initiate as a terminal ridge on the floral apex, with subsequent stamens added centrifugally on one side and two carpels initiated on the opposite side. The carpels arise as a simultaneous ring in radially symmetrical flowers, or as a simultaneous pair in zygomorphic species. Staminodial presence is viewed as of minor significance. Four pollinator syndromes are proposed for Hibbertia, related to differing floral architecture.

Key words: Adrastaea; androecium; centrifugal; Dilleniaceae; flower; Hibbertia; stamen fascicles; zygomorphy.

Hibbertia (Dilleniaceae) includes over 150 species of lianas, shrubs, and small trees distributed through Australasia, Madagascar, Malesia, and Fiji (Mabberley, 1990). The temperate Mediterranean coast of southern Australia (south of the Tropic of Capricorn) and montane sites on the island of New Caledonia are centers of diversity for Hibbertia (Stebbins and Hoogland, 1976). Stebbins and Hoogland (1976) noted that the genus is remarkable for the striking interspecific diversity in floral symmetry (radial vs. dorsiventral or zygomorphic), in stamen number (3–200+ per flower), and carpel number (1–10 per flower). Wilson (1965) showed that highly varied floral vasculature reflects differences in floral symmetry in the genus. Stamens are singly produced and free in some species, in fascicles or tufts in others, or forming a ring, more or less fused at base in yet others. The order of organ initiation may be entirely centripetal or may include centrifugal elements.

The gynoecium shows variation in that styles are erect in some species, prostrate and projecting laterally in others. Carpels may be free or fused basally to some degree among different species (Dickison, 1968). The species also vary greatly in habit, wood structure, leaf morphology and anatomy, inflorescence type, chromosome number, and karyology (Dickison, 1969, 1970a; Stebbins and Hoogland, 1976; Rury and Dickison, 1977; Dickison, Rury, and Stebbins, 1978; and Ehrendorfer, 1987).

Our aim is to compare floral development among diverse representatives of the genus Hibbertia (Dilleniaceae) to elucidate the basis for the floral diversity that abounds in the genus. Adrastaea salicifolia also will be included, since this segregate genus differs primarily in the fusion of the outer five stamens. It had previously been considered a Hibbertia, monotypic in its own section Adrastaea (Stebbins and Hoogland, 1976). The developmental bases will be sought for the following floral features that vary among taxa: symmetry (radial or zygomorphic); staminodia present or not; stamens in fascicles or not; stamen fusion; and carpel number. Although diversity also occurs in type of anther dehiscence (lateral slits or terminal pores), ovule number per carpel, and stigma type, consideration of these features will be deferred until a later paper. The variable floral features of species of Hibbertia and Adrastaea are associated with presumed contrasting pollinator behavior that has been investigated by Bernhardt (1984, 1986). Comparing floral development of Hibbertia species and of the satellite genus Adrastaea salicifolia (Syn.: Hibbertia salicifolia) allows us to add four overlapping pieces of information to the knowledge of Hibbertia sensu lato as a model system.

First, an ontogenetic approach identifies the developmental bases for distinct floral features that vary among species, including symmetry, presence of staminodia, occurrence of staminal fascicles, ring meristems, stamen connation, and carpel number. Second, these developmental differences can then be re-

1 Manuscript received 26 October 1999; revision accepted 15 February 2000.

The authors thank Anna Bass for technical assistance; Alison Schroeer for drawings; Frank Maglione for computer expertise; Robert Coveny, Andrew Douglas, and Peter Weston for collections of flower buds and herbarium vouchers in Australia; the staff of the University of California Arboretum at Santa Cruz (Brett Hall, Manager), the Royal Botanic Gardens (Sydney and Mount Annan), and the rangers of Royal National Park (New South Wales) for access to live specimens; Former Director T. C. Chambers and Former Director of Research Dr. B. Briggs of the Royal Botanic Garden, Sydney, for supporting the expansion and completion of this project; and the EM facility and the Department of Botany, Louisiana State University, Baton Rouge, Louisiana 70803, the Department of Biological Sciences (Ecology, Evolution, and Marine Biology) and the Department of Geology, University of California, Santa Barbara, California, 93106, for access to scanning electron microscopes. S. T. acknowledges partial support by National Science Foundation grant DEB-9420158 (DEB-9596281), and Boyd Professorship funds provided by Louisiana State University. P. B gratefully acknowledges fieldwork and travel funds provided by the National Geographic Society in Washington, D.C. (1991), Royal Botanic Garden Trust Fund (1990–1992, 1994) and a St. Louis University Travel Award (1998).

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lated to functional aspects of floral morphology such as pollination biology (Bernhardt, 1984, 1986, 1996; Keighery, 1991). Third, floral development in *Hibbertia* and *Adrastaea* can be compared with that of other dilleniaceous genera. Finally, an assessment of comparative floral development in *Hibbertia* provides an opportunity to test the hierarchical-significance hypothesis of Tucker (1984, 1997), developed from work on legume flowers, in a markedly different plant family—the Dilleniaceae.

This project on *Hibbertia* was first planned in 1992, when a research proposal on comparative floral development of *Hibbertia* was submitted to the National Science Foundation by the senior author. It was not funded, nor was a sister proposal on pollination biology of *Hibbertia* by the second author. Due to recent interest in the project from another laboratory, the work on floral development has now been revived and updated for publication.

**MATERIALS AND METHODS**

**Materials**—Most plant collections were made by the second author in Australia, and by the first author in Santa Barbara, California and at the Arboretum of University of California, Santa Cruz, California. The buds were preserved in FAA (formalin-acetic acid-50% ethyl alcohol) and later transferred to 70% ethyl alcohol for storage. Vouchers are either in S. T.’s private herbarium, for material collected in California, or at the Royal Botanic Gardens, Sydney (RBG), Australia, and at Missouri Botanical Garden (MO), for plants collected by P. B. in Australia. Collections with accession numbers made in Australian botanic gardens were not vouchedered. Table 1 gives the provenance of the species included in this work.

**Selection of species for study** —Two bases were used for selection of species: first, representatives of each of the currently accepted subgeneric categories, and second, representatives showing a diversity of evolutionary trends among species. *Hibbertia* was examined with SEM and species showing radial symmetry, a complete circle of fertile stamens, short filaments emerging from a solitary cluster of 2–12 fertile stamens, poricidal anthers, no staminodia, and carpels no more than two.

*Other genera—Adrastaea salicifolia* has been segregated from *Hibbertia*, but is very close. The genera differ in that *Adrastaea* has two alternating whorls of stamens, and the filaments of the outer circle of stamens form a fused tube, while the stamens of *Hibbertia* are not fused to this extent. *Adrastaea* will be studied together with the species of *Hibbertia*, because of the possibility that developmental evidence may support uniting it with *Hibbertia*.

**Methods**—The buds were dissected in 95% ethanol and then dehydrated through an ethyl alcohol series, critical point dried with CO2 in a Tousimis “Samdry-780” drier, and mounted on aluminum stubs with carbon conductive adhesive tabs (T. Pella Co., Redding, California, USA). They were coated with gold-palladium in a Denton “Desk-1” sputter coater. Scanning electron microscopy utilized a Cambridge S-260 in the Electron Microscope Facility at Louisiana State University, Baton Rouge, Louisiana, and a JEOL JSM-6300V in the Geology Department at University of California, Santa Barbara, California.

**RESULTS**

**Floral structure in the genus Hibbertia** —Although our survey covers most of the variation in the genus, it is important to first discuss the complete range of floral structure. The radially symmetrical perianth is highly uniform throughout, consisting of two pentamers, alternating whorls of sepals and petals. The calyx shows some basal connation, while petals remain free and equal. Sepals are generally green (rarely purple, e.g., in *H. dentata*), and petals are different shades of yellow (rarely rusty orange, e.g., in *H. stellaris* Endl.) that lack UV patterns (Bernhardt, unpublished data on *H. stricta, H. fasciculata,* and *H. scandens*). The petals are ovobate and emarginate or notched distally in many species. In contrast to the rather uniform perianth in *Hibbertia* species, androecial and gynoecial characters show great variation.

Organ numbers within individual androecia are species specific, ranging from three to 200, with a centrifugal order of initiation in most taxa with more than five stamens. Some androecia combine fertile stamens and staminodia (relatively un-specialized structures with filaments but nonfunctional anthers). Stamens are produced either singly or in discrete fascicles. Some fascicles are elongated structures resembling miniature candelabras, while others resemble an arch “hand” of bananas. In flowers of the satellite genus *Adrastaea salicifolia*, the filaments of an outer whorl of stamens unite to form a conuate tube. Therefore, flowers of different *Hibbertia* species are either actinomorphic (radially symmetrical) or zygomorphic, depending mainly on variation in stamen arrangement (Stebbins and Hoogland, 1976).

The gynoecium consists of one to ten carpels per flower, with some ovaries showing minor connation (Dickison, 1968). Carpels number often is correlated with the presentation and symmetry of the androecium. Styles are held erect in some species, or project laterally in others (Bernhardt, 1996). Upon reviewing the genus, Stebbins wrote (1974, p. 184) “there is probably no other genus of angiosperms that exhibits such a high degree of variation in those floral characteristics that are regarded as “fundamental” and are usually associated with the separation of genera or of even higher categories.”

Androecium and gynoecium characters are so stable within species of *Hibbertia* that they have been given priority as taxonomic characters for almost 140 yr. Bentham and Mueller
(1863) organized the Australian species into four sections. While sectional names and characters have changed, to date they continue to be treated as natural subunits, identified on the bases of stamen/staminodium numbers, androecium symmetry, and, to a lesser extent, carpel number (see Stebbins and Hoogland, 1976). The majority of keys to species begin with couplets comparing the relative positions of stamens around the ovaries (Bentham and Mueller, 1863; Stanley and Ross, 1983; Wheeler, 1987; Harden and Everett, 1990).

**Phenology**—The majority of species of *Hibbertia* in temperate-Mediterranean regions of Australia flower from mid-winter to mid-summer (July to January in Australia). Individual plants in subtropical populations of *H. scandens* (Fig. 1a) may flower twice a year with peaks in September and March (T. Hawkeswood, personal observations). Each *Hibbertia* flower arises terminally on a vegetative branch (often on a short side branch without elongated internodes) or in a leaf axil. In contrast to cymose species of New Caledonia, the majority of Australian species bear solitary flowers, with each bud subtended by a vegetative leaf. Flower buds open in acropetal or subacropetal order along the stem. Flower presentation may be erect, horizontal, or nodding, depending on species habit (Bernhardt, 1984, 1986; Harden and Everett, 1990).

Flower life span is 3–7 d, with large flowers (e.g., *H. scandens*) lasting longer than small flowers (e.g., *H. fasciculata*). The androecium withers before the carpels, and the styles collapse before the petals abscise. The drying sepals close over the ripening ovaries in all species observed, a feature that is probably diagnostic for the family Dilleniaceae (see Gottsberger, 1977). In the majority of species, flower-bearing shoots collected for herbarium vouchers drop their petals within an hour of cutting. Retention of petals on cut branches appears limited to a few species bearing thick, leathery leaves (e.g., *H. dentata, H. scandens*).

In *Adrastaea salicifolia* (Fig. 5a), ovaries are covered by the stamens, and erect styles protrude from the center of two whorls of stamens in recently opened flowers. In most *Hibbertia* species, stamens arch inward at anthesis so that the ovaries are largely obscured by the stamens, particularly where the stamen number is high. Therefore, stigma exposure in radially symmetrical flowers depends on stamen number per flower and on the angle of stylar position. *Adrastaea salicifolia* and a few species of *Hibbertia* (e.g., *H. dentata*) bear longitudinally dehiscent anthers. Most *Hibbertia* species have anthers that are porose or poricidal (sensu Buchmann, 1983) with the dehiscence of sutures restricted to two expanding subapical slits. *Hibbertia* flowers are weakly fragrant with a characteristic honey and/or cow dung odor; a citrus-peel-like odor has been noted infrequently (e.g., *H. dentata*). Fragrance is best assessed using the scent-jar technique of Buchmann, Jones, and Colin (1978). Scent production is centered in anther sac interior, in pollenkitt, and on stigmas, based on neutral red tests (Bernhardt, 1984, 1986) on *H. dentata, H. diffusa, H. fasciculata, H. saligna, H. scandens,* and *H. stricta*. The flowers lack nectar glands or secretion (Bernhardt, unpublished data); pollen is the primary edible reward.

**Organography of selected species**—Each flower of the examined Australian species of *Hibbertia* arises terminally on a vegetative branch (often on a short branch without elongated internodes); the branch or stem may bear flowers in each leaf axil. Technically flowers are solitary (because each is subtended by a vegetative leaf), although a stem may bear several flowers. Inflorescences are found in some New Caledonian species and a few Australian species (Stebbins and Hoogland, 1976; Veillon, 1990), but no developmental series of these were available for this study. The petals of *Hibbertia* species are obovate and yellow to yellow-orange, with anthers slightly darker.

*Hibbertia scandens* (Willd.) Gilg (Figs. 1a–c, 6–20, 22)—*Hibbertia scandens* is a scrambling vine 2–5 m tall from Queensland, Northwest Territory, and New South Wales. Flowers are yellow to gold, solitary and terminal on otherwise vegetative branches. They are sessile or short-stalked. Floral symmetry is radial, and calyx, corolla, and gynoecium are pentameros (Fig. 1a, c). Sepals are 8–12 cm long, silky-hairy abaxially; petals are 2–3 cm long and membranous; stamens are numerous (150–200) with occasional staminodia (2–6 per flower), and carpels are 3–8 and glabrous (Elliot and Jones, 1990).

**Organogeny of Hibbertia scandens**—The five sepals are initiated successively in a 2/5 quincuncial spiral (Fig. 6), the outer sepals largest and partially enclosing the rest during initiation (Fig. 7) and in bud (Fig. 1b). The five petals are initiated nearly simultaneously and alternate to the sepals (Fig. 8) around a flat floral apex. Because petal primordial size diminishes inward along a 2/5 spiral (Figs. 9–11), their initiation may be successive, although no petal stages were seen with less than all five petals present. The ontogenetic spiral is continuous and in the same direction from sepals through petals (Figs. 1c, 9).

Prior to stamen initiation, the floral apex is circular and slightly raised peripherally around a flat to depressed center (Fig. 10). Eight to 13 stamen primordia are initiated in a whorl (Figs. 12, 13), although not simultaneously. Additional stamen primordia are next initiated in centrifugal direction on a ring meristem, outside and alternate to stamens of the first whorl (at arrowheads, Fig. 14). The ring meristem can be seen in Figs. 14 and 15, centrifugal to the already initiated stamen primordia. Up to seven rows of stamen primordia are initiated in centrifugal order (Figs. 16–19). In polar view, the androecium has a roughly pentagonal outline (Fig. 20), with indented areas in front of each petal base.

Five carpels are initiated in a circle (at arrowheads, Fig. 15) inside the original whorl of stamens, concurrently with the centrifugally initiated stamens. The carpel primordia heighten, develop adaxial clefts (Fig. 17), and become tapered terminally (Fig. 18). At anthesis the stamen anthers are lanceolate, basifixd, tetrasporangiate, and poricidal (Fig. 22). The stigmas at anthesis (Fig. 22) are narrow and truncate.

*Hibbertia grossulariifolia* (Salisb.) Salisb. (Fig. 21)—*Hibbertia grossulariifolia* is a prostrate shrub from Western Australia. The flowers are ~15 mm in diameter with radial symmetry, solitary on peduncles 20–30 mm long. The five sepals are 5–6 mm long, ovate and acuminate; the five petals are 5–8 mm long, light yellow, obovate and shallowly indented. Stamens are ~100, and staminodia are also present. There are 8–15 hairy free carpels (Elliot and Jones, 1990). Organogenetic stages of this species were not available to us, but Payer (1857) described and illustrated some stages in its development. Five stamens are initiated on mounds that alternate with
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the petals. Additional stamens form centrifugally on each of the five mounds until ~100 have been initiated, when the original five groups can no longer be distinguished. Five carpel primordia are initiated concurrently with, and alternate to, the first five stamen primordia and above them on the floral apex. A second whorl of approximately five carpels then is initiated acropetally from the first carpel whorl. A large flower bud with numerous stamens and eight carpels is shown in Fig. 21 (perianth removed).

_Hibbertia perfoliata_ Endl. (Figs. 23–37)—_Hibbertia perfoliata_ is a weakly ascending (to 0.5 m) or prostrate shrub from
Western Australia. The flowers are solitary and axillary, 15–28 mm in diameter, on peduncles 10–65 mm long. The ovate sepals are 7–10 mm long, glabrous, acuminate, and reflexed, and the five petals are ~7–15 mm long. The flower resembles that of *H. scandens* except that the total stamen number is less than half that of *H. scandens*. The 60–80 free stamens have anthers that are elliptic, oblong, or obovate, and dehisce by longitudinal slits. There are numerous staminodia outside the stamens. The three to five carpels are glabrous (Marchant et al., 1987).

Fig. 5. *Adrastaea salicifolia*. (a) Flower at anthesis, with two alternating whorls of stamens. ×2. (b, c) Androecium and gynoecium at anthesis, polar and side views. (d) Androecium in bud, with only the antepetalous stamens visible. (e) Floral diagram.

Figs. 6–22. Floral organogenesis in *Hibbertia scandens* (Figs. 6–20, 22) and *H. grossulariifolia* (Fig. 21) (SEM). Some or all sepals have been removed in Figs. 6, 8–22; some or all petals were removed in Figs. 16–22. Bars = 100 µm in Figs. 6–18; = 200 µm in Figs. 19–21; = 1 mm in Fig. 22. Figs. 6–20, 22. *H. scandens.* 6. Four of five sepal primordia, numbered consecutively, have been initiated in helical succession. One at base has been removed. 7. Undissected flower with four of five sepal primordia. A leaf base scar encircles the bud. 8. Five petal primordia (one labeled) have been initiated nearly simultaneously. 9. Low-magnification polar view of flower, sepals removed but scars numbered consecutively, showing that petals (numbers 6, 7 are the first two of five) have been initiated on same ontogenetic spiral as sepals. 10, 11. Oblique and polar views of flower with five petals still graded in size according to order of their helical initiation. 12. Initiation of approximately eight stamens (four at arrowheads) in a ring (oblique view). 13. Polar view of flower with five petal primordia and 12 stamen primordia in a ring. 14. Oblique view of floral apex with additional stamen primordia (at arrowheads) forming slightly outside the original ring. 15. Centrifugal initiation of stamen primordia outside the first ring, and initiation of five carpel primordia at center (at arrowheads; oblique view). 16, 17. Side and polar views showing centrifugally initiating outermost stamen primordia. 18. Longitudinal section of flower showing carpel primordia developing adaxial clefts, apical residuum at center, and stamen primordia, the innermost (the oldest) being the largest. 19, 20. Side and polar views of flower, perianth removed, with full complement of stamen primordia. The carpels are shorter than the adjacent stamens. 21. *H. grossulariifolia* (polar view) shows eight carpels and numerous stamens. 22. Side view of flower bud of *H. scandens* approaching anthesis, with some stamens removed. The three carpels shown are free, with ovaries, styles, and truncate stigmas differentiated. The stamens have differentiated filaments and elongate anthers, longest toward the center.
**Organogeny of Hibbertia perfoliata**—The five sepal primordia are initiated in 2/5 helical succession (Fig. 23) on a low-convex floral apex. The sepal primordia enlarge in their order of succession, so that the order remains obvious at least in early stages (Figs. 24, 25). The five petal primordia are initiated essentially simultaneously (Figs. 25, 26, at arrowheads). They remain small while successive organs are initiated.

Stamen initiation is preceded by an increase in apical diameter (compare Figs. 27 and 28). The first stamen primordia are initiated successively, beginning with a few high on the apical flanks (at arrowheads, Fig. 27). More stamens are initiated until there is a ring or whorl of ~12 (Fig. 28) around the floral apex. These stamen primordia at first show little regular alignment with respect to the petal primordia. Subsequent stamen primordia are initiated in gaps among the primordia of the original ring (compare numbers of primordia in the innermost ring in Figs. 30 and 33), and centrifugally (Figs. 29 at arrowheads, 30), outside the first ring. In Fig. 31, it becomes evident that there are five antesepalous “triplets” or clusters of stamen primordia; one triplet is bracketed. Each triplet consists of a cluster of organs initiated in a predictable sequence: a single one high on the apical flank, then a pair centrifugally, one on either side of the first. Each triplet is here augmented by another single primordium on the same radius as the first, then another pair centrifugally. Additional primordia continue to be initiated centrifugally (Figs. 31–34), which obscure the original five tripods. In this species, there are no common primordial mounds preceding triplet initiation. Eventually there are ~65 stamens present, four to five deep radially (Fig. 37). Anthers are differentiating in Fig. 37, with the innermost stamens becoming differentiated first, the others in their order of initiation. The “triplet” aspect will be more prominent and persistent in the next species, *H. huegelli*.

The floral meristem of *Hibbertia perfoliata* inside the original ring of stamen primordia is flat to very low convex (Figs. 28, 29). The five carpel primordia are initiated simultaneously on the apex (Figs. 30–32, at arrowheads), utilizing most of the remaining apical meristem and leaving a small residuum at center. The carpel primordia are at first small distinct mounds (Figs. 32–34). They heighten and show an incipient cleft (Figs. 35, 36) at ~70 μm in height. No older stages of carpels were available for study.

**Hibbertia huegelli** (Endl.) F. Mueller (Figs. 2a, b, 38–52)—*Hibbertia huegelli* is a low shrub, sometimes semiprostrate to 0.5 m high, of Western Australia (Marchant et al., 1987). Flowers are terminal on axillary branches, solitary or paired. Each flower (Fig. 2a) is 20–35 mm in diameter, subtended by leaves and brown scabrous bracts. The five sepals are ovate to elliptic, 10–17 mm long, the inner wider than the outer, with acuminate ciliate tips. The petals are obovate, indented, and 15–20 mm long. The 25–35 stamens are arranged in five fascicles of four to eight stamens each (Fig. 2a, b). The stamens in each fascicle are connate (Marchant et al., 1987), with occasionally one free. Anthers dehisce by longitudinal slits. The five carpels are glabrous.

**Organogeny of Hibbertia huegelli**—The five sepals are initiated successively in a 2/5 spiral (Figs. 38, 39). Next, five petals are initiated simultaneously or in very close succession (Figs. 39, 40). In Fig. 40, two of the petal primordia are slightly larger (at 2 o’clock and 7 o’clock), indicating a 2/5 spiral order of initiation. The petals are equidistant. They enlarge, broaden, and overlap, the outer two being larger than the rest during development (Fig. 51).

The post-petal floral apex is low convex and starts to expand in diameter (compare Figs. 41 and 42). Five broad common primordia are initiated in antesepalous positions (Fig. 42). Stamen initiation begins on the common primordia in a helical succession with the first two (of five) stamens (Fig. 42 at arrowheads). Each of the five stamen primordia becomes the center of further stamen initiation, in centrifugal order, to form a fascicle. Two stamen primordia form on either side of and below each of the first five stamens (Figs. 43–45). A fourth stamen primordium may next be initiated directly below and outside each of the first five (Fig. 44, at arrowhead). In Fig. 47, a fascicle of four stamen primordia is bracketed. Another pair of stamen primordia then may form below that (Fig. 49). Each of the antesisepalous stamen clusters now contains three to seven stamens, depending on the number initiated beyond the first three in each cluster or fascicle. During initiation, the largest stamen primordia are toward the center of the flower, while successively smaller ones are toward the outside. By midstage, all of the stamens are equal in height (Fig. 49) except for the first five, which remain taller than the rest. Figure 50 shows an exceptional flower that has three large stamens at center (rather than the usual five), resembling the arrangement in *H. racemosa*, to be described next. As each cluster of stamens differentiates in *H. huegelli*, the stamens develop basifixied anthers that are attached to a common basal stalk (Fig. 52), forming a fascicle of stamens. At anthesis, the filaments elongate, becoming aggregated in fascicles. The trunk of the fascicle is at first short (Fig. 52) but elongates somewhat by anthesis (not shown). The five fascicles are recognizable at anthesis (Fig. 2a).

Just before carpel initiation, the floral apex flattens and is pentagonal (Fig. 46). The five carpels are initiated simultaneously (Figs. 47, 48) on the edges of the flat apex, alternate to the five stamen fascicles. The carpels remain free and are shorter than the surrounding stamens during development. The carpel clefts form adaxially (Fig. 51).

**Hibbertia racemosa** (Endl.) Gilg (Figs. 53, 54)—*Hibbertia racemosa* is a small erect shrub (to 0.4 m high) of Western Australia, with flowers on slender peduncles 1–3 cm long, in leaf axils. Flowers are radially symmetrical and have sepals 0.5–0.6 cm long, with the outer ones narrower than the inner; petals 0.5–0.7 cm long, obovate; stamens 10–12, joined in three bundles of three or four; one or two stamens free; infre-
of approximately ten stamen primordia. 29. Floral apex has enlarged, and additional stamen primordia (at arrowheads) are being initiated centrifugally around the first ring. 30–32. Flowers showing initiation of five carpel primordia (at arrowheads) at center, in polar and oblique views. In Fig. 31, five anteseptalous centers of stamen initiation are first evident, each a set called a “triplet” (one is indicated by a bracket; see text). The triplets are also seen in side view in Fig. 32 (one between brackets). 33, 34. Polar and oblique views of flower with heightened carpel primordia (some at arrowheads). The initiation of numerous additional stamen primordia centrifugally has obscured the limits of the original five triplets. 35, 36. Oblique and polar views of flower with adaxial clefts beginning in each carpel primordium. Petals are laminar and some have an apical notch. 37. Older floral bud in which anthers have differentiated in most stamens, the oldest toward the center. The carpels are short and obscured below the stamens at center.
quent staminodia; and three glabrous carpels (Elliot and Jones, 1990). *Hibbertia racemosa* resembles *H. saligna* (Fig. 3a) in having stamen fascicles and relatively few stamens.

**Organogeny in *Hibbertia racemosa***—Developmentally, *Hibbertia racemosa* differs from *H. huegelii* in that only three stamen primordia are initiated in the first whorl. Developing around these three are three common primordia that initiate most of the stamen primordia, although there are five common primordia in all. The three most productive common primordia are antepetalous, with a truncate outer periphery. Each of these three common primordia produces four or five stamens (Figs. 53, 54), the innermost first (at arrowheads), followed by a pair, one on either side of the first. The fourth stamen primordium of each common primordium is on the same radius as the first and centrifugal to it; a fifth may be added (Fig. 54, at arrow). Each of the two less active common primordia initiates one to three stamens (arrows, Fig. 53). The flower becomes asymmetrical at initiation of the first three stamen primordia and the three carpel primordia, which together form an asymmetrical pattern (Fig. 53). Although nearly zygomorphic, positions of the two weaker common primordia disrupt that configuration so that the flower is asymmetric. In no way is this a transition between actinomorphic and zygomorphic flowers.

Only three carpels are initiated in *H. racemosa*, a number correlated with the three most prolific stamen fascicles, even though there were five common primordia. The three carpels are not symmetrically arranged (Fig. 53) when seen at a young stage.

*Hibbertia saligna* R. Br. ex DC. (Figs. 3a, b, 55)—*Hibbertia saligna* is a small shrub to 2 m high and 1.5 m wide, native to New South Wales. The radially symmetrical flowers (Fig. 3a, b) are 30–40 mm in diameter, sessile above a cluster of bracts. The five sepals are 12–16 mm long, thick, and imbricate, trending from outer acute to inner blunt-tipped. The five membranous obovate, imbricate petals are 15–20 mm long, bright yellow, obovate and with only a shallow notch (Fig. 3a). There are 20–30 stamens evenly distributed in three clusters around the three glabrous carpels at center (Fig. 3a, b; Elliot and Jones, 1990). Rarely, staminodia may be present in the fascicles that are only weakly developed.

**Organogeny of *Hibbertia saligna***—Initiation of organs in *Hibbertia saligna* is similar to that of *H. huegelii*, including radial symmetry and stamen-fascicle formation, except that the first whorl of stamens includes three rather than five members. Carpel number also is fewer: three, vs. five in *H. huegelii*. Two of the five stamen fascicles in *H. saligna* are only weakly developed, as in *H. racemosa*. Three stamens are initiated symmetrically in the first whorl (Fig. 53) compared to five in *H. huegelii*, and three asymmetrically in *H. racemosa*. The three early stamen primordia are equidistant and in antepetalous sites (at arrowheads, Fig. 55). Each serves as a locus for centrifugal initiation of three additional stamens: a pair below and to either side of the first (Fig. 55), and then a single primordium directly below the first stamen. The flower of *H. saligna* in Fig. 55 is radially symmetrical, although the number of stamens per common primordium differs somewhat. The 12 stamens in these three fascicles are augmented in some flowers by two to four additional single stamens that are not in fascicles. *Hibbertia saligna* demonstrates a modification toward reduction in stamen number by limitation of the number and development of fascicles.

*Hibbertia fasciculata* R. Br. ex DC. (not illustrated)—Although only large buds and open flowers were available to us, *Hibbertia fasciculata* is a species of interest because it varies from three stamens per flower in New South Wales populations to seven to nine stamens in Victoria populations. In the former material, three stamens alternate with the three carpels in a radially symmetrical flower. However, the base of each stamen is attached to a broad flat platform, similar to that supporting two or more stamens from a common primordium in species such as *H. huegelii*. This feature will be discussed later.

*Hibbertia banksii* Benth. (Figs. 56–67)—*Hibbertia banksii* is a small shrub to 2 m high from Queensland, having one-sided terminal leafy branches of flowers, and brown tomentose flower buds. The flowers have zygomorphic symmetry, five sepals 0.6–0.8 cm long, rusty-hairy abaxially; five yellow petals 1.3–1.8 cm long, obovate, notched, margins often crinkled; and 20–30 stamens plus 12–20 staminodia, clustered on one side of the two hairy carpels (Elliot and Jones, 1990).

**Organogeny of *Hibbertia banksii***—The five sepals are initiated in helical 2/5 quintessential succession (Fig. 56). Zygomorphic symmetry begins with initiation of three adjacent petal primordia in close succession on one side of the flower Figs. 38–55. Floral organogenesis in *Hibbertia huegelii* (Figs. 38–52), *H. racemosa* (Figs. 53, 54), and *H. saligna* (Fig. 55) (SEM). Some or all sepal have been removed in all, and some or all petals in Figs. 49, 50, 52–54. Bars = 100 μm in Figs. 38–49, 51, 55; = 200 μm in Figs. 50, 52–54. Figs. 38–52. *H. huegelii*. 38. All five sepal primordia have been initiated in helical succession. 39. At least one petal primordium (at arrowhead) has been initiated. 40, 41. Four of the five petal primordia have been initiated and appear to be in helical order based on relative sizes (polar and oblique views). 42. Polar view of floral apex enlarging after petal initiation. At least two stamen primordia (arrowheads) on common primordia are visible in antepetalous positions. Cracks are artifactual. 43. Oblique view showing two of the five stamen-initiating common primordia (two triplets in brackets). 44. Floral apex is becoming flat-topped, and at least one of the triplets of stamens has a fourth primordium added centrifugally (at arrowhead). 45, 46. Initiation of the five carpel primordia at arrowheads (side and polar views). 47, 48. The carpel primordia have enlarged outward but have not heightened. Each stamen fascicle has four primordia (one in brackets in Fig. 47). 49. Polar view after five oldest stamen primordia (at arrowhead) have heightened, obscuring the carpel primordia at center. The cluster of smaller stamen primordium centrifugal to each of the five larger stamen primordia will form a fascicle. 50. An atypical flower at the same stage as Fig. 49, but with only three fascicles of stamen primordia (the three large stamens are at arrowheads), and three carpel primordia. 51. Oblique view of flower with laminar petals beginning to overlap one another. The carpel clefts are visible at center. 52. Side view of flower, perianth removed, to show the differentiating anthers and filaments. The fascicles can be identified by two or more anthers emerging from a shared base (at arrowheads). Figs. 53, 54, *H. racemosa*, 53, 54. Polar and oblique views of androecium around three carpel primordia. Three larger stamen primordia (at arrowheads) have initiated first in antepetalous positions. Each of the three has been the nucleus of a common primordium that formed 4–5 stamen primordia. At the two remaining antepetalous positions (at arrows), a single stamen primordium has been initiated. 55. *H. saligna*. A radially symmetrical flower in polar view, with three carpels, showing the first three stamen primordia (at arrowheads), each the beginning of a fascicle of 3–5 stamens.
Figs. 56–70. Floral organogenesis in Hibbertia banksii (Figs. 56–67) and H. hypericoides (Figs. 68–70) (SEM). Some or all sepal scars have been removed in all except Fig. 56, and some or all petals removed in Figs. 59–70. Bars = 50 μm in Figs. 56, 59; = 100 μm in Figs. 57, 58, 60–63; = 300 μm in Figs. 64, 65, 68–70; = 1 mm in Figs. 66, 67. Figs. 56–67. H. banksii. 56. Initiation of first three sepal primordia. 57, 58. Floral buds (polar and oblique views) in which first three petals initiated on the adaxial side. 59. Flower with five petals removed, the three largest toward the upper (adaxial) side. Five stamen primordia have initiated as a row across the middle of the floral apex. 60. Flower in which the first row of stamen primordia has been augmented by a second row of three stamen primordia, parallel to the first and on the adaxial flank. 61. Flower in which two carpel primordia (at arrowheads) are initiating on the adaxial side. 62, 63. Polar and oblique views of flower in which the carpel primordia (at arrowheads) each have a curved tip, the incipient style. Five or six carpels are initiated successively in each of the two carpel primordia. 64. Flower with petals removed, the two carpels are basally connate (at arrowheads). 65. plus 12–20 staminodia initiated last, along the periphery of the adaxial side. The center staminodia are initiated first in each row, the end staminodia last in each row. The total stamen number is approximately 23–30 (Figs. 64, 65). 66. 12–20 staminodia initiated first along the periphery of the adaxial side (at arrowheads). The style forms early (Figs. 62, 63), becoming reflexed and folded distally. Clefts become visible after the styles slits (Figs. 81, 82). 67. Additional stamen primordia are initiated: two or three adaxially (Figs. 77, 78) and two laterally (Fig. 78) on either end of the original row of three. Depending on the number formed after the first three, the total stamen number is 5–8 in a single fascicle. 68, 69. Flower in which two carpel primordia (at arrowheads) are initiating on the abaxial side. 69. The two pistils have densely hairy ovaries, slender styles, and narrowly punctiform stigmas (Figs. 66, 67).

Hibbertia hypericoides (DC.) Benth. (Figs. 68–70)—Hibbertia hypericoides is a small spreading shrub to 1 m high from Western Australia, with flowers solitary in leaf axils (Elliot and Jones, 1990). Flowers are deep golden yellow and zygomorphic. The five sepals are 0.5–0.6 cm long and densely covered with stellate hairs; the five petals are 0.7–1.2 cm long, cuneate, and deeply notched. The ten to 15 fertile stamens are in a single fascicle (Figs. 68, 69) on one side of the flower. Staminodia are ~15 in number, spathulate, and positioned around the bases of the two trichome-covered carpels (Figs. 69, 70). Organogenesis in this species is very similar to that of H. banksii, so is not shown. An exceptional feature of H. hypericoides is the unusual morphology of its staminodia (Figs. 69, 70).

Hibbertia empetrifolia (DC.) Hoogl. (Figs. 4a, b, 71–78)—Hibbertia empetrifolia is either a small shrub to 2 m tall and to 3 m wide, or a scrambling vine with wiry stems, native to Victoria, Tasmania, and New South Wales (Elliot and Jones, 1990). The flowers (Fig. 4a, b) are ~10 mm in diameter on peduncles 5–15 mm long. The five sepals are 3–4 mm long, in an imbricate whorl; petals are 4–5 mm long, bright yellow, and notched (Fig. 4a, b). There are four to 12 stamens in a fascicle on one side of the two carpels (Fig. 4a, b) and no staminodia.

Organogeny of Hibbertia empetrifolia—The five sepals are initiated successively along a 2/5 quincuncial spiral (Figs. 71–73) around a somewhat depressed floral apex. Five petal primordia are initiated successively (Figs. 74, 75). The order is unidirectional, with the three largest adjacent to one another, on the adaxial side of the flower. Prior to stamen initiation, the floral apex becomes increasingly convex, with an incipient ridge between adaxial and abaxial sides (Fig. 75). Stamen initiation begins with three stamen primordia in a row across the middle of the floral apex (Fig. 76). Additional stamen primordia are initiated: two or three adaxially (Figs. 77, 78) and two laterally (Fig. 78) on either end of the original row of three. Depending on the number formed after the first three, the total stamen number is 5–8 in a single fascicle. The stamen anthers are tetrasporangiate, basifixed, with filaments attached to a common broad base as a single fascicle (Figs. 79, 80). The anthers dehisce by lateral slits (Figs. 81, 82).

The two carpel primordia are initiated on the abaxial side of the floral apex (at arrowheads, Figs. 76, 77). The carpels become arcuate in polar view, and their clefts face each other (Fig. 78). The two carpels are basally connate (Fig. 81), and each has a fused adaxial suture extending its full length (Figs. 81–83). The ovaries become covered by stiff trichomes; the styles are twisted, and the stigmas are punctiform (Figs. 82, 83).

Adrastaea salicifolia DC. (Figs. 5a–e, 84–96)—Adrastaea salicifolia is monotypic; it resembles a Hibbertia closely in its five-merous calyx and corolla, each with imbricate aestivation (Fig. 5a–e). The androecium differs from any Hibbertia, however, in that the outer whorl of five stamens is antepetalous and the inner whorl of five is antepetalous (Fig. 5a, c–e). There are two free carpels (Harden and Everett, 1990).

Organogeny of Adrastaea salicifolia—The floral apex is low convex before sepal initiation. Five sepals are initiated successively in a 2/5 helix (Fig. 84). Initiations are high on the flanks, so that the remaining apex is nearly flat; the peduncle...
six parallel rows of stamen primordia can be seen, and more are being initiated centrifugally. 64. Abaxial side view, with the two carpels connate basally and beginning differentiation of styles. Trichomes are beginning to form on the ovaries. 65. Adaxial side view showing centrifugal order among stamen rows. The smallest stamen primordia (at arrowheads) would have become staminodia. 66, 67. Carpel-side (abaxial) and stamen-side (adaxial) views, respectively, of flower during organ differentiation. Fertile stamens have elongate anthers, and staminodia (at arrowheads) are short and linear without anthers. Carpels are densely trichome-covered. Figs. 68–70. H. hypericoides. 68. The single fascicle of stamens, each with an anther and filament. 69. Abaxial side view shows two glabrous carpels with erect styles. The 11 stamens (two others removed) are parts of a single fascicle attached on the adaxial side. A cluster of staminodia is at the base of the two carpels. 70. Carpels at anthesis, with glabrous styles and ovaries covered by short trichomes. The staminodia (at arrowheads) have a papillate epidermis.
Figs. 71–83. Floral organogenesis in *Hibbertia empetrifolia* (SEM). Some or all sepals have been removed in all, and some or all petals removed in Figs. 76–83. Bars = 100 μm in Figs. 71–78; = 200 μm in Figs. 79–83. 71. First three sepal primordia have been initiated in helical order (one removed). 72, 73. Oblique and polar views in which the last three of five sepal primordia have been initiated in helical order (two outer ones removed). 74. First four petal primordia (one damaged) have been initiated, the three larger toward one side (adaxial) of the flower. 75. Five petal primordia, the three larger initiated first but successively. The two most recently initiated petal primordia are at arrowheads. A ridge is forming across the floral apex. 76, 77. Polar and oblique views of flower in which three stamen primordia have initiated in a row across the apical summit. In the first row, an additional primordium has initiated at either end. Two additional stamen primordia (at arrows) are initiating in a second row on the adaxial side. Two carpel primordia are initiating abaxially (at arrowheads). 78. Polar view of flower in which the carpels have each developed an indentation that will become the cleft. The seven stamen primordia in two rows have enlarged. 79. Polar view of flower after differentiation of tetrasporangiate anthers, and carpels with ovaries and styles. 80. Adaxial side view of stamen fascicle after formation of anthers and filaments. 81, 82. Abaxial views at two stages of differentiation. The carpels are connate basally, and the cleft is visible the length of the styles. The carpels are at first sparsely hairy (Fig. 81), then become more densely so (Fig. 82). 83. One carpel from large bud. The ovary has long stiff trichomes, the style is twisted, and the stigma is punctiform.
Figs. 84–96. Floral organogenesis in *Adrastaea salicifolia* (SEM). Some or all sepals have been removed in all except Fig. 84, and some or all petals removed in Figs. 92–96. Bars = 100 μm in Figs. 84–92; = 200 μm in Figs. 93–95; = 1 mm in Fig. 96. 84. Five sepal primordia (numbered consecutively) have been initiated in helical succession. 85. Petal initiation (at arrowheads) is nearly simultaneous, but with some primordia slightly larger, indicating a helical order. 86, 87. The post-petal floral apex has enlarged in diameter. Stamen primordia (at arrowheads) are being initiated in antepetalous positions (oblique and side views). 88. Initiation of a whorl of five antepetalous stamen primordia (indicated by asterisks) and two carpel primordia (at arrowheads: polar view). 89. The five stamen primordia (asterisks) have enlarged, leaving a ring meristem (at arrowheads) between petals and stamens. There is insect damage in the carpel area at center. 90, 91. Initiation of five antepetalous stamen primordia (at arrowheads) on the ring meristem (oblique views, with insect damage in the carpel area). 92, 93. Side and polar views of flower with petals now laminar (perianth removed except for two petals). Both antepetalous (asterisks) and antepetalous (A) stamen primordia also appear laminar. Antepetalous stamens are basally connate (at arrowheads). 94, 95. Polar and side views of large bud with differentiated anthers, emarginate apically. The antepetalous stamens (A) show basal connation. Extra stamens are present (at arrows) outside the antepetalous whorl in Fig. 94. The two styles are erect and exerted at center. 96. Part of an open flower with two carpels, one intact and one cut away to show a single ovule. Two antepetalous stamens with dehiscing anthers are beginning to reflex.
is formed at this time. Five petal primordia are initiated nearly simultaneously (Fig. 85) but in a 2/5 helix, judging from slight differences in petal sizes (Figs. 85, 88). Sepals, petals, and stamens are on the same phylloclastic spiral (Fig. 88). After petal initiation, the floral apex is a low-convex mound (Figs. 86, 87). Five stamens are initiated (at arrowheads, Figs. 86, 87) in antepetalous sites. These first five stamen primordia are indicated by asterisks in Figs. 88–91 during completion of organogeny. The two carpels are initiated next (at arrowheads, Fig. 88) around the floral apex. One is on the same radius as the earliest initiated petal, while the other is opposite a sepal. The floral apex then expands as a narrow ring meristem (at arrowheads, Fig. 89) between the petals and stamens. An outer whorl of five antepetalous stamen primordia is next initiated on the ring meristem (Figs. 90, 91), centrifugally from the first whorl of stamens. The facts that the stamens of the outer whorl form last and are antepetalous (and the flower obdiplostemonous) are highly unusual and provide support for generic segregation of the taxon. Centrifugal order of initiation prevails in the androecium and contributes to the obdiplostemonous condition. The outer five stamen primordia (A, Figs. 92–95) are laminal, emarginate at their tips, and confluent basally (Figs. 92, 93, at arrowheads). Occasionally, one or two extra stamen primordia are initiated outside the outer five (at arrows, Fig. 94).

As the flowers open, the stamen filaments lengthen and the anthers of the outer stamens are reflexed so that they are held horizontally, parallel with the petals (Figs. 5a, c, 96). The five inner-whorl stamens are less strongly reflexed (Fig. 5a, c). The anthers dehisce by longitudinal slits on their adaxial side. The two pistils become acuminate with punctiform stigmas and full-length adaxial sutures (Fig. 96); each usually has a single ovule (Fig. 96).

**DISCUSSION**

*Floral symmetry*—Developmental distinctions strongly support two major suprageneric entities in *Hibbertia* (including *Adrastaea*): a radial or actinomorphic group and a zygomorphic group. Phylogenetic analysis based on molecular evidence also supports recognition of two major groups, aligned with floral symmetry (Horn and Manos, 1999). Sections *Hibbertia* and *Candollea* are included in the first group with radial symmetry. The two sections are distinguished by presence of staminodia in *Hibbertia* and by presence of stamen fascicles in *Candollea*. Innovations in the radially symmetrical group provide various means of achieving polystamony; by meristem rings and increased floral-apical size among members of section *Hibbertia*, by common primordia in section *Candollea*, and by a late-forming meristem ring without apical size increase in *Adrastaea*. Staminodial development is activated at a later stage when floral organs differentiate; some of the last-initiated stamen primordia around the periphery may fail to develop anthers. The distinction between presence and absence of staminodia is hence a mere superficial distinction that does not affect later stages of development.

The group of taxa with zygomorphic symmetry includes species in sections *Hemistemma* and *Pleurandra*. The flower is actinomorphic during sepal initiation, then becomes zygomorphic with unidirectional petal initiation. Stamen primordia are initiated as a linear row across the summit of the floral apex, which may be augmented by additional rows on either side. Two carpel primordia are initiated laterally on one side. This order of organ initiation, with stamens terminal on the floral apex and carpels lateral, is highly unusual, and has not previously been reported for any angiosperm. The two sections are distinguished by presence of staminodia in *Hemistemma*, vs. their absence in *Pleurandra*. This distinction in presence/absence of staminodia is of minor significance, depending on events during organ differentiation.

Despite the marked morphological differences in symmetry, Stebbins and Hoogland (1976) upheld the unity of the genus *Hibbertia*, based on presumed intermediates in floral structure between the two types of symmetry. Baillon (1871) also reported what he considered intermediates in symmetry in *Hibbertia*. In one example (Stebbins and Hoogland, 1976), *Hibbertia hermannifolia* DC. has two carpels with stigmas both curved downward and stamens somewhat unequally placed around the carpels. The bending of the styles (radiating outward in actinomorphic flowers, or parallel in zygomorphic ones) is a late event in floral development, occurring as the flower bud opens. Late developmental events such as this stylar inflexion tend to be potentially more labile than early organogenetic events (Tucker, 1984, 1997). One of the “intermediates” noted by Baillon is *H. angustifolia* (R. Br. ex DC.) Benth., in which there are two carpels at center and six fascicles: two of fertile stamens, both on one side but separated by a fascicle of staminodia. Two other staminodial fascicles stand on the side opposite the fertile clusters of stamens. It would be desirable to examine organogenesis of stamens in these putatively intermediate species.

We found examples that might be thought to show intermediate symmetry in *H. saligna*, which has three antepetalous fascicles of stamens and two single stamens in the other two antepetalous positions. Thus the flower has zygomorphic symmetry, but only in a subtle sense not easily recognized at anthesis when the stamens become rather evenly distributed around the periphery. Zygomorphic symmetry in this species results from a different developmental mechanism (failure of common primordia to proliferate equally) from that in the *Hemistemma*/*Pleurandra* group (stamen initiation in apical rows, followed by lateral carpel initiation). Zygomorphy has arisen at least twice in evolution of the genus, based on our small sample. The two zygomorphic states are alternate states and not homologous since they arise by quite different mechanisms. An example of asymmetry was found in *H. racemosa*, which shows reduced activity in two of the five common stamen primordia.

*Centrifugal order of initiation*—Species of *Hibbertia* having only three or five stamens per flower show acropetal order of initiation for all organs. But the great majority of species of *Hibbertia* (including those studied here) with more than five stamens per flower show centrifugal order of stamen initiation. Payer (1857) remarked on centrifugal order of stamen initiation in several families, but the character has received little other attention. Corner (1946) reported centrifugal stamen order in 14 dicotyledonous families, with particular attention to *Wormia* and *Tetracera* in Dilleniaceae and *Bixa* in Bixaceae. Sattler (1972) described widespread examples among plant families of centrifugal order of initiation of particular floral organs, but indicated that no flower has entirely centrifugal order. In flowers of *Lythrum*, three types of organs are initiated centrifugally (Cheung and Sattler, 1967; Sattler, 1972). Stamens are the organs that most commonly are initiated centrifugally, often in flowers having numerous stamens. Examples

**Fascicled stamens vs. free stamens**—In sections Pleurandra and Candollea of *Hibbertia*, stamens are produced in clusters called fascicles. The filaments are fused basally, with three to ten anthers on one fascicle. Wilson (1965) investigated many species of *Hibbertia* having fascicles, and Sporne (1958) found that each fascicle is generally supplied by a shared vascular trace. Tucker (1972) explored the strong correlation between fascicled stamens, common stamen traces, and centrifugal initiation among angiosperm taxa. Several other plant families have one or more stamens with fascicled stamens: Actinidiaceae (Brown, 1935; Wilson, 1937, 1965, 1974; Aizoeaceae (Payer, 1857; Kawanoo, 1965); Bombaceae (Wilson, 1937); Clusiaceae (Leins and Erbar, 1991); Flacourtiaceae; subfamily Merobonoideae of Guttiferae (Kawanoo, 1965); Hydrangeaceae (Hufford, 1998); Hypericaceae (Corner, 1946; Hirmier, 1918; Sporne, 1958); Loasaceae (Hufford, 1990); Malvaceae (Wilson, 1937; van Heel, 1966, 1984); Paeoniaceae (Schöffel, 1932; Hiepko, 1965; Leins and Erbar, 1991, 1994); Sterculiaceae (Payer, 1857); Theaceae (Erbar, 1986; Tsou, 1998), and Tiliaceae (Payer, 1857).

Developmentally, each stamen fascicle develops from a single common primordium. In *Hibbertia* (and other families: e.g., Hufford [1990, 1998]—Loasaceae and Hydrangeaceae) the first stamen primordium is median and on the innermost side of the common primordium. Subsequent organs form centrifugally beginning with a pair, one on either side of the first. This set of three stamens from the common primordium is termed a “triplet” by Hufford (1998). Stamen organogeny may cease after the first triplet on the common primordium, or it may continue by adding pairs and single primordia alternately outward.

The stamen-forming common primordia in *Hibbertia* species are antepetalous, standing in the sites of individual stamens in many other dicot flowers. For this reason, the stamen fascicle has been interpreted occasionally as equivalent to a single highly branched stamen that has been telescoped at its base (Wilson, 1937). Stebbins and Hoogland (1976) suggested that the fascicle (rather than individual stamens) in *Hibbertia* is “the fundamental unit of the androecium.” However, developmental evidence shows that the stamens of each fascicle are initiated individually and become “fused” basally by intercalary elongation below the filament bases.

**Ring meristem**—Stamen proliferation by activity of a ring meristem (“Ringwall” in some European literature), interpolated between whorls of petals and carpels, is an innovation recognized in some species of *Hibbertia* (*H. scandens*), *Adrastaea salicifolia*, and other genera of Dilleniaceae that have been studied developmentally (Corner, 1946; Endress, 1997). Such ring meristems have evolved in many other plant families, for example, Bixaceae (*Bixa*—Corner, 1946; Ronse Decraene, 1989), Cactaceae (Leins and Schiwatalla, 1986), Capparidaceae (*Capparis*—Leins and Metzenauer, 1979), Cochlospermaceae (*Cochlospermum*—Corner, 1946; Keating, 1972; Ronse Decraene, 1989), Hypericaceae (*Hypericum*—Leins, 1964a, b), Lecythidaceae (*Couroupita*—Leins, 1972), Lythraceae (*Lagerstroemia*—Mayr, 1969), Malvaceae (Payer, 1857; Sattler, 1973), Punicaceae (*Punica*—Mayr, 1969; Leins, 1988), and Theaceae (*Stewartia*—Erbar, 1986, 1988; Camellioideae—Tsou, 1998). A more extensive compilation is given by Ronse Decraene and Smets (1992). Most taxa with a ring meristem are polystemonous, but a few legumes having a ring meristem produce only ten stamens (Tucker, 1990, 2000).

**Homology among floral organs**—Burger (1996) recently challenged the convention that stamens are homologous to other floral organs. One basis was the supposed cylindrical shape of stamen primordia during early stages, compared to a “laminar” shape in petal primordia. But during development (before microsporangia become evident), primordia of stamens often appear broad tangentially. Examples can be seen in *Cas sia* and *Chamaecrista* (Tucker, 1996a, b), *Ceratonia* (Tucker, 1992), and *Gleditsia* (Tucker, 1991), among many examples available. In the current work, the stamen primordia of the outermost whorl in *Adrastaea salicifolia* are broadly laminar (see Figs. 92–95). Another misconception by Burger about floral development is that the cylindrical stamen filament is derived directly from the cylindrical stamen primordium. However, in most taxa, the anther is the first part of the stamen to form from the primordium, as a sessile structure. The filament is formed late in development, in many cases appearing very short until a late stage.

The strongest evidence for homology of stamens with other floral organs is ontogenetic, namely that perianth members and stamens all are initiated alike in most flowers, as lateral appendages on the flanks of the floral apical meristem. Histological details of initiation are basically alike. Small differences in depth of the initiatory periclinal cell divisions have been available. In the current work, the stamen primordia of the outermost whorl in *Adrastaea salicifolia* are broadly laminar (see Figs. 92–95). Another misconception by Burger about floral development is that the cylindrical stamen filament is derived directly from the cylindrical stamen primordium. However, in most taxa, the anther is the first part of the stamen to form from the primordium, as a sessile structure. The filament is formed late in development, in many cases appearing very short until a late stage.

**Floral vasculature as it relates to centrifugality**—Literature on this subject is reviewed here because of the fact that previous work on vasculature showed the need for ontogenetic study to explain some of the anomalies. Stebbins and Hoogland (1976) pointed out the need for developmental studies in *Hibbertia*, because of the high level of androecial diversity. Anatomical structure of stamens (Dickison, 1970b) and carpels (Dickison, 1968) has been examined for the family. Carpel anatomy is rather uniform among species (Dickison, 1968). Wilson (1965, 1974) demonstrated in detail the remarkable range of stamen structure and vasculature at anthesis among 58 species representing the major sections of *Hibbertia* and other genera of the family. Ozenda (1949) and Sastri (1958) also reported on the floral vascular system of several dilleniaceous taxa. Sporne (1958) illustrated the unusual stamen trunk bundles in diverse families, including *Hibbertia scandens* in Dilleniaceae. He asserted that occurrence of these
highly branched vascular trunk bundles is correlated with centrifugal direction of initiation. The numerous stamen traces are basally connected to a few trunk bundles, because in a centrifugal system there is no remaining undifferentiated procumbent tissue in the receptacle, within which additional stamen traces could differentiate downward from the newly initiated primordia. Tucker (1972) explored this hypothesis of correlation between fasciated stamen clusters and internal trunk bundles from a developmental point of view.

Previous work on floral structure and ontogeny of *Hibbertia*—Baillon (1871) described the floral morphology of the major taxa. Floral development has been reported for two species of *Hibbertia, H. scandens* (Sattler, 1973), and *H. grossulariifolia* (Payer, 1857). *Hibbertia scandens* has a pentameric calyx and corolla, 150–200 stamens produced centrifugally, and five carpels. Order of initiation is helical in the calyx and helical to simultaneous in the corolla. The first five stamens arise alternately to the petals, after which additional stamen primordia arise outside the first five in a centrifugal direction. The five carpels are initiated last, in helical succession at the center of the androecium. Sattler was uncertain whether common primordia were present preceding initiation of stamens (they were not found in the present study) and about the exact order of stamen initiation among the numerous stamens after the first five, except for their centrifugal direction.

The description of floral ontogeny in *H. grossulariifolia* (Payer, 1857) differs from that just described, in that Payer reported simultaneous petal initiation, then five common primordia on which several stamen primordia are initiated in basipetal (centrifugal) order, and two whorls of five carpels each. Structure and function of the common primordia described by Payer resemble those in *H. huegelii* and *H. racemosa*, examined here.

Evolutionary trends in Australian species of *Hibbertia*—The major trends are from radial symmetry to zygomorphy, toward either increase or decrease in stamen number and carpel number, and toward basal fusion among stamen filaments. Two additional trends in the New Caledonian species, toward heteranthry and aggregation of solitary flowers into inflorescences, were not studied because of a lack of material. One may ask whether the observed evolutionary trends in *Hibbertia* confirm the hierarchical-significance hypothesis that one of us (Tucker, 1984, 1997) has proposed? This hypothesis proposes that early events in a developmental cascade tend to be stable and canalized, while late events are more prone to evolutionary lability. The stable, early-expressed character states often characterize suprageneric levels of hierarchy (here sections), while the late-expressed character states typically distinguish lower levels of hierarchy such as species. Any change in early events has a profound effect on development of subsequently produced organs, while a change in late events has relatively little effect on other organs. Many examples in legumes support the hypothesis (Tucker, 1997), and it is important to test it in other plant families with differing floral structure as well.

In *Hibbertia* the shift from radial to zygomorphic floral symmetry is determined early, directly after sepal initiation, which is uniform throughout the genus. Subsequent developmental pathways of stamen and carpel organogenesis differ markedly in the two groups. In radially symmetrical flowers, petals are initiated helically and stamen primordia are initiated in a circle all round the floral apex, followed by initiation of a circle of carpel primordia acropetally and by additional stamen primordia basipetally. In zygomorphic species, petals are initiated unidirectionally, and the first stamen primordia are initiated in a linear row across the summit of the floral apex, followed by additional stamens to one side centrifugally and initiation of two carpel primordia on the opposite side. The fact that symmetry is determined early in *Hibbertia* suggests that it is a stable feature in each group, not likely to be labile or to show transitions. The division between radially symmetrical and zygomorphic taxa is a sharp one in which it is difficult to imagine a flower combining these two markedly different pathways. A putative transition, down-turned styles (typical of the zygomorphic taxa) in the otherwise radially symmetrical flower of *H. hermannifolia*, was thought to be transitional by Stebbins and Hoogland (1976). This species certainly merits developmental study if and when material can be obtained. However, the inclination of the styles is a feature that is expressed late in development as the flower bud opens and may result from differing genetic controls from those that govern floral symmetry.

Evolutionary changes in stamen number in the genus *Hibbertia* have mostly tended toward increase, via at least four developmental shifts: increase in number within a “whorl,” addition of more primordia basipetally (centrifugally), or by the innovations of either a ring meristem or common primordium. By “whorl” we mean here a circle of stamen primordia initiated at approximately the same level on the flanks of the floral apex. The stamen positions later become somewhat reoriented, so that whorls are not evident at anthesis. The flowers with few stamens result where there is a single “whorl” with relatively few primordia, or where common primordia are present but show limited proliferation.

High stamen numbers may result first where the stamen number increases over time within each “whorl” or by additional initiations centrifugally (as in *H. perfoliata* and *H. scandens*), enabled by marked increase in apical meristem surface during stamen initiation. Additional stamen primordia are four to five rows deep radially in *H. perfoliata* and up to seven rows deep in *H. scandens*. The difference developmentally is the amount of available meristematic surface for new initiations (which is probably a function of meristem duration over time), and also whether the initiatory activity is evenly distributed. In the ring meristem in *H. scandens*, initiations occur uniformly around the periphery, while in *H. perfoliata*, initiatory activity is concentrated in five areas, the common primordium. The ring meristem in *Adrastaea salicifolia* has a very limited duration, producing only five stamen primordia. All of these modes of stamen-number increase occur early (during organogeny) and hence tend to be stable as patterns of development.

Stamen number increases in many species of *Hibbertia* by the innovation of common primordia. Five meristematic mounds form on the flanks of the floral apex, alternately with petals. On each mound (or common primordium) a succession of stamen primordia is formed. The total number depends on whether three or five common primordia are active, and the duration of primordial initiation activity in each. This innovation can produce a 20–35-staminate flower in *H. huegelii* or a 100-stamen flower in *H. grossulariifolia* (latter based on Payer, 1857).

The two differing populations of *H. fasciculata* may be an example of stamen-number evolution in progress. The Victoria
populations have seven to nine stamens in three fascicles per flower. The New South Wales populations have three-stamineate flowers in which each stamen has a broad base resembling that derived from a common primordium. Further developmental studies are planned for this species. Common primordia are the most versatile innovation in evolution of the *Hibbertia* androecium.

While the mode of stamen-number increase is stable among *Hibbertia* species, the actual number may be labile. The genus abounds in species that differ in number of stamens, and number can increase simply by extending the time of meristematic activity of the floral apex. As centrifugally initiated stamen primordia are the last organs to initiate, increasing their number does not affect subsequent organogeny.

Carpel number also has undergone evolution in *Hibbertia*, although the range (1–10) is narrower than for stamens and is closely related to floral symmetry and stable evolutionarily. Radially symmetrical flowers have three, five, or rarely up to ten carpels, depending on the species, while zygomorphic taxa generally have two. (In New Caledonia, all *Hibbertia* species have radially symmetrical flowers, and two carpels per flower.)

The carpels are initiated simultaneously in each flower. In *H. grossulariifolia* with up to ten carpels, they appear to initiate in two whorls in acropetal succession (based on Payer, 1857; no developmental material was available to us).

The innovation of fusion among stamens is most evident in *Adrastaea salicifolia*, a segregate genus sometimes placed in *Hibbertia*. The outer five stamens, which result from a ring meristem, remain basally connate during their enlargement. The filaments also are connate in stamen fascicles resulting from common primordia. Fusion thus is another character that results from events early in ontogeny, and one that is stable and resistant to change. No fusion occurs among stamens that are initiated directly on the floral apex.

Key characteristics of *Hibbertia* flowers that are first expressed late in ontogeny and that are relatively labile include staminodial occurrence and the type of anther dehiscence. Staminoidea (defined here as sterile organs in stamen positions) are said to occur commonly in sections *Hibbertia* (with radial flowers) and *Hemistemma* (with zygomorphic flowers). However, one of us (P. B.) with considerable field experience observing *Hibbertia* flowers reports often finding occasional staminoida even in species reported to lack them (e.g., *H. racemosa, H. saligna*). Developmentally, staminodia are usually in the last-initiated stamen sites; for example, a few may be found around the periphery of the androecium in *H. scandens*. Staminoidea may be initiated after the majority of stamen primordia in the flower have undergone microsporogenesis and gametogenesis. Staminal nodal presence, although it has been used as a sectional distinction in *Hibbertia*, is probably more variable and labile than has been realized, and has questionable significance evolutionarily.

Another relatively labile key character is the type of stamen anther dehiscence, which can be either lateral (a full-length slit) or porose/poricidal (a subterminal pore or slit). Our SEM (scanning electron microscopy) examinations of anther dehiscence in *Hibbertia* (Tucker, unpublished data) show a lateral suture line in anthers of all species; none have the bordered pores seen in some other plant families (e.g., the legume *Cha maecrista nictitans* in Tucker, 1996a, 1997). Dehiscence may occur uniformly throughout the length of the suture, or it may begin distally and proceed proximally until the entire slit is open. In poricidal anthers the initially distal dehiscence does not progress far down the anther. We found a developmental continuum over time in some species (*H. dentata*), beginning as poricidal and becoming full-length lateral dehiscence. The dehiscence process is obviously a late event in flower development, occurring usually as the flower opens or shortly thereafter. The anatomical particulars of the anther dehiscence process in *Hibbertia* have not been studied, but should prove worth investigating. The lack of sharp distinctions between the types of anther dehiscence suggests that the character may be too unstable to characterize sections.

Summarizing, floral symmetry, number and position of sepals and petals, mode of stamen and carpel initiation, position of organs, and centrifugal stamen organogeny are significant features in evolution in the genus *Hibbertia*. They are determined early in ontogeny and tend to be stable. But stamen number is highly variable among species in the genus, resulting from several alternative developmental pathways. Centrifugal order of stamen initiation and the developmental innovations of the ring meristem and common primordia have contributed to high levels of speciation.

**Evolutionary relationships among sections of *Hibbertia*—** In Baillon's day (1871), the genus *Hibbertia* included taxa with flowers having indefinite numbers of stamens and free carpels, while *Candollea* included taxa with definite numbers of stamens, often in fascicles. The two are currently combined under *Hibbertia* sensu lato. Strong dissimilarities such as those in floral symmetry have generally not been considered sufficient to separate the genus; supposed "intermediates" between actinomorphic and zygomorphic symmetry (Baillon, 1871; Stebbins and Hoogland, 1976) have been used as evidence to maintain the genus. Our developmental evidence supports a separation of two entities that differ in floral symmetry, because the zygomorphic species of sections *Hemistemma* and *Pleurandra* have markedly different floral organogeny from those with radially organized flowers. The latter group includes species with free stamens (section *Hibbertia*) and those with stamen fascicles (section *Candollea*). Recently, Horn and Manos (1999) have reported two major clades in the genus, based on molecular evidence that is correlated strongly with floral symmetry.

**Does *Adrastaea* deserve generic status?**—*Adrastaea salicifolia* has some unique developmental features: a ring meristem that produces only five stamens, the obdiplostemonous arrangement of the outer stamens, and strongly reflexed anthers of the outer stamens. But it shares most other aspects of the floral developmental pathway with radially symmetrical Australian *Hibbertias*: solitary floral position, pentameres alternating whorls in calyx and corolla, helical order of initiation of the sepals and petals, the whorled arrangement of the first stamens and the carpels, and centrifugal order among additional stamens. Androecium development differs widely in *Hibbertia* and could easily include the features found in *Adrastaea*. The developmental pathway of the radially symmetrical species of *Hibbertia* is much more similar to that of *Adrastaea* than it is to zygomorphic species of *Hibbertia*. On developmental evidence, *Adrastaea* appears undeserving of separate generic status.

**Pollination in *Hibbertia*—** Variation in the diversity of pollen vectors and their activity depends primarily on four interrelated morphological characters: (1) whether anther dehis-
cence is longitudinal or poricidal; (2) whether the androecium forms at least one complete whorl of fertile stamens; (3) whether there are 40 stamens or more per flower; and (4) whether the gynoecium contains fewer than three carpels and the styles are straight and erect or curved and laterally extended at anthesis. The androecium is at least as important in controlling pollinator activity (Bernhardt, 1996) as the perianth, which receives much more notice from pollination investigators. In *Hibbertia*, androecial characters control pollinator activity (Bernhardt, 1996), just as perianth characters control the movement of pollinators in flowers with zygomorphic or tubular corollas.

*Hibbertia* species are pollinated primarily by female pollen-collecting bees (Apidae s. l., Colletidae, and Halictidae) and pollen-eating flies in the family Syrphidae (Bernhardt, 1996, unpublished data). Bees are far more significant pollinators of *Hibbertia* species than beetles (Keighery, 1975; Armstrong, 1979). While the same bee taxon pollinates several *Hibbertia* species, androecium morphology predetermines different sites for pollen deposition on the bee’s body. Different bees also forage differently, based on variation in mouthparts, vestiture, and physical size. Accordingly, four pollinator syndromes have been detected by the second author among species of *Hibbertia*; all are represented among the species studied here.

Pollination of the larger-flowered radially symmetrical species of *Hibbertia* such as *H. scandens*, with up to 200 stamens that conceal the ovaries, poricidal anther dehiscence, and erect, ascending styles, is effected by thoracic vibration by large bees 7–22 mm long (Halictidae and large-bodied anthophorine bees in the Apidae). The bees circle the center of the flower, clasp ing groups of stamens at different points and vibrating them to release the pollen (Buchmann, 1983; Bernhardt, 1996; Endress, 1997).

In the *H. fasciculata* pollination syndrome (Bernhardt, 1986), flowers have radial symmetry, a single whorl of 8–12 stamens that conceal the three ovaries with bent styles outside the anther tuft, and poricidal anthers. Bees 7 mm long or larger (Anthophoridae, Colletidae, and Halictidae) clasp the whole tuft of fertile anthers, apply thoracic vibration, and spin around the androecium, collecting pollen while the stigmas contact the underside of the pollen-storing abdomen. This syndrome is represented by *H. huegeli*ii, *H. racemosa*, *H. saligna*, and *H. cuneiformis* among species in our study.

Species of *Hibbertia* with longitudinally dehiscent anthers, radial symmetry, two or more whorls of over 100 stamens that conceal the three ovaries, and erect styles (e.g., *H. dentata*; see Bernhardt, 1996) are pollinated primarily by small-bodied bees (4–7 mm) and by large syrphids. The insects crawl over the protruding stigmas as they forage directly on the exposed, extruded pollen. This pollination syndrome prevails in *H. dentata* and *H. grossulariifolia* among the species studied here.

In zygomorphic flowers of *Hibbertia* in sections Hemistemma and Pleurandra (e.g., *H. stricta*—Bernhardt, 1984), stamens are aggregated on one side of the flower, and the styles of the two carpels curve upward with stigmas parallel on either side of the bundle of stamens. *Hibbertia banksii*, *H. empetrifolia*, and *H. hypericoides* in our study represent this syndrome. Bees 7–22 mm long hang longitudinally or inverted from the flower while clutching the anthers and apply thoracic vibration to extract the pollen. The stigmas of the two up-curving styles contact the bee’s abdomen.

With the exception of *Trigoma* and introduced *Apis* (both in Apidae sensu stricto) bearing true corbiculae, and some col letids (*Hylaeus*) that collect pollen by swallowing and regurgitating grains, all native Australian bees carry deposits of pollen on scopal hairs on their hind legs and at the base of the abdomen. Pollen grains are packed in scopae without using nectar as a pollen mortar. The way in which a bee’s hindlegs or hairy abdomen transfer loosely collected pollen from a po rose anther to a stigma depends ultimately on stamen number in the flower, androecial architecture, and the angle of the styles. The significance of organographic distinctions among *Hibbertia* species remains enigmatic until they are interpreted in the light of function at anthesis. We are still only beginning to understand floral function in *Hibbertia*. Insect behavior in species of *Hibbertia* will be explored in more detail in a second paper.

**Developmental comparison with other Dilleniaceae—**
Systematic treatments of Dilleniaceae include those by Gilg and Werdermann (1925), Hutchinson (1964), and Hoogland (1952, for *Dillenia*). The family Dilleniaceae was viewed as relatively primitive, a southern-hemisphere equivalent to Magnoliidae (Cronquist, 1981) on the basis of many of the same characteristics as Magnoliidae: scalariform vessels; perfect, hypogynous actinomorphic flowers; numerous stamens; essentially apocarpous gynoecium with conuplicate carpels not completely sealed; ovules bitegmic and crassinucellar. However, taxa of Dilleniaceae differ from Magnoliidae in the centrifugal direction of organ initiation in the androecium. The significance of this organogenetic distinction between Dilleniaceae and Magnoliidae and Rosidae has been judged highly significant by Sattler (1972), Tucker (1972), and Cronquist (1981).

Taxa of Dilleniaceae also differ chemically; they have elagic acid, proanthocyanins, and raphide crystals (none of which are found in Magnoliidae), and they lack alkaloids and ethereal oils that are present in Magnoliidae (Kubitski, 1968; Cronquist, 1981; Gurni and Kubitski, 1981).

Dilleniaceae currently are considered to have little relationship to Magnoliidae and, instead, are allied to Rosidae, based on a large-scale cladistic analysis by Chase et al. (1993). It is the sister group in this analysis to an assemblage of Caryophyllidae. No detailed cladistic analysis within Dilleniaceae has been done, although Horn and Manos (1999) are working on a much-needed molecular analysis.

Radial floral symmetry occurs in all genera in the family; zygomorphy occurs only in *Hibbertia* pro parte. Some species of *Dillenia* have as many as 700 stamens per flower; the flowers are much larger than even the largest in *Hibbertia*. Heteranthery is found in some species of *Dillenia* (with short feeder stamens and long pollination stamens as well as staminodia), and in some New Caledonian species of *Hibbertia* (with both lanceolate and falcate anthers). Organogeny is similar between *Dillenia* species described by Endress (1997) and *Hibbertia scandens*, with its ~200 stamens per flower, helical acropetal initiation of five sepals and five petals, then a ring of eight stamen primordia, and lastly a ring of seven or eight carpel primordia. After the first stamen whorl, other stamens are initiated in a centrifugal direction on a ring meristem. The outermost stamen primordia become staminodia, as in *Hibbertia banksii*. Poricidal anthers and punctiform stigmas in *Dillenia* also resemble those of species of *Hibbertia*. *Dillenia* differs from most species of *Hibbertia* in heteranthery, in more numerous carpels and styles (usually eight vs. two to five in most species of *Hibbertia*), and in its syncarpous ovary. *Hibbertia* is essentially apocarpous, although Dickson (1968)
mentioned some basal coevolution of ovaries. Styles in *Dillenia* are broad and flat and are disposed in a flat rosette over the top of the reflexed anthers of the androecium (Endress, 1997); neither of these characters are found in *Hibbertia*. While *Hibbertia* has staminodia as well as fertile stamens, all the latter are alike in any one Australian species, unlike the heteranthery among functional stamens in *Dillenia* (Endress, 1997).

Centrifugal order of stamen initiation and frequent occurrence of staminodia toward the outside of the androecium as the last-initiated primordia appear to be common developmental features among taxa of Dilleniaceae that have been studied (Endress, 1997). A ring meristem producing stamens occurs in all genera but is not universal in *Hibbertia*, in which other mechanisms for stamen-number increase also have arisen during evolution. Summarizing, *Hibbertia* includes most of the character states responsible for familial diversity among other dilleniaceous genera that have been investigated developmentally.

**LITERATURE CITED**


