Utility of Ontogenetic and Conventional Characters in Determining Phylogenetic Relationships of Saururaceae and Piperaceae (Piperales)

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ABSTRACT. Morphological and developmental evidence is utilized in a phylogenetic analysis of Piperales. Best resolution of trees was obtained by combining ontogenetic data with conventional morphological data. Floral ontogeny provides a means to determine homology among character states as well as to provide additional characters not observable in mature flowers. Both Lundberg and outgroup rooting were performed using a hypothetical ancestor defined by general ontogenetic states in the former and by five taxa presumably related to the ingroup in the latter. Polarization of character states via ontogenetic generality principles is congruent with outgroup polarization. Saururaceae and Piperaceae are each monophyletic. Saururaceae are supported by three synapomorphies, with Saururus as the basal taxon. The other three saururaceous genera (Anemopsis, Houttuynia, Gymnotheca) share the derived character states of syncarpy, stamen-carpel adnation, and an inferior or half-inferior ovary. Piperaceae are supported by seven synapomorphies with Zippelia as the basal taxon. Six other synapomorphies unite the remaining Piperaceae suggesting that Macropiper and Pothomorpha are specialized offshoots of the morphologically variable Piper. Numerous autapomorphies support Peperomia as a distinct and specialized offshoot within Piperaceae. Within the sister clades Saururaceae and Piperaceae, there are parallel reduction trends in floral organ number and in the sequence of floral organ initiation.

This paper summarizes the morphological, anatomical, and developmental studies in our laboratory on the small relict family Saururaceae in the past 15 yr. These studies have been essentially completed, although not all observations have yet been published. Similar developmental studies have been made on representative Piperaceae, hypothesized as the sister group. Phylogenetic analyses of Saururaceae and Piperaceae, using cladistics, are presented. The small size of the family Saururaceae (four genera, six species), the marked differences among the taxa, a large data base and the availability of a commonly accepted sister family, Piperaceae, make Saururaceae well-suited to such analyses.

An additional stimulus to our phylogenetic analyses of Piperales was a publication on the flower structure of Zippelia (Omori 1982), which strongly resembles Saururus and which has been variously placed in either Saururaceae or Piperaceae. We have developmental studies of Zippelia under way. It was felt that cladistic analysis might clarify the position of Zippelia within one or the other family, or as a connecting link.

Floral organogenesis and development have been compared for all four saururaceous genera: Saururus (Tucker 1975, 1976, 1979), Houttuynia (Tucker 1981), Anemopsis (Tucker 1985), and Gymnotheca (Liang and Tucker 1989). Floral vasculature of all taxa of Saururaceae was reported by Liang and Tucker (1990). Floral developmental studies of representative Piperaceae include those on Peperomia (Tucker 1980) and Piper (Tucker 1982a, 1982b). In addition, we have some unpublished data on other piperaceous genera: Zippelia, Pothomorpha, and Macropiper. New data on development of the vascular system in flowers of saururaceous and piperaceous taxa have been obtained and incorporated, particularly on flowers of Gymnotheca, Zippelia, and certain other related taxa (Liang and Tucker 1990).

The aim of this paper, besides summarizing our work on Saururaceae and Piperaceae, is to show the advantages of using floral ontogenetic evidence, in combination with conventional
morphological characters, in phylogenetic analysis. The use of ontogenetic data is somewhat controversial (see Fink 1982; Guarrant 1988; Roth 1984, 1988 for reviews) and has rarely been utilized for vascular plants. It can be used as a method of determining homologies and as a method to determine primitive states based on von Baer’s principle of generality (Nelson 1978; Weston 1988). Ontogenetic sequences form transformation series of character states that have the potential to be ordered and polarized using Nelsonian theory (see Mabee 1989; Nelson 1978; Nelson and Platnick 1981; Weston 1988). The argument rests on the assumption that most changes in ontogeny occur as terminal additions, losses, or substitutions. Relative modifications from a general structure represent derived states (Nelson 1985; Weston 1988). Ontogeny also reveals rare, non-terminal additions.

There have been several challenges to the use of ontogeny in phylogenetic analyses. Mabee (1989) claims that ontogenetic evidence can be useful in establishing order and homology of character states but not polarity. Mishler (1986) also suggests that polarity of character transformations cannot rely on ontogeny alone, because cases of paedomorphosis might occur and could be misleading. Mishler (1986) claims an independent phylogeny should be established based on outgroup comparison (where possible), avoiding “a priori notions about ontogenetic patterns.”

Flowers lend themselves to evolutionary studies in three ways. First, plant development is relatively simple compared to that of animals; second, all developmental stages of flowers are easily accessible; and third, flowers have modular and determinate, repetitive ontogenies (Kaplan 1984; Tomlinson 1984). Early ontogenetic stages, which often have a simpler and more straightforward organization than the mature stages, can elucidate complex floral organization and homologies. Developmental information is usually not evident from mature flowers. Tucker (1984a) hypothesized that early developmental features of a flower tend to be taxonomically conserved. Developmental divergence tends to be more common late in development below the generic level. This suggests that the relatively conservative nature of early developmental processes can be used to determine the modifications that have given rise to, or are prevalent among, related taxa. Thus, the more ancestral (or generalized) states tend to be conserved at early stages in ontogeny. Therefore, developmental modifications of floral characters that could have played a role in the evolution of taxa can be easily identified.

METHODS

Phylogenetic Analysis. Parsimony analysis using PAUP (version 3.0 q, Swoford 1991) was performed with a Macintosh computer on all data sets. Separate analyses of the data with justifications are described below. In all analyses, the genera tested included all four genera of Saururaceae, plus five genera of Piperaceae (Fig. 1). Outgroup taxa were also included in select analyses described below (Fig. 1J–M). In all cladistic analyses, the Branch and Bound search option and Accelerated Transformation (ACCTRAN) and Delayed Transformation (DELTRAN) optimizations were used.

Representation of Taxa within Piperaceae. Five genera of Piperaceae are included in the analysis (Fig. 1E–G). We have minimal developmental data for Piperaceae except for selected species of Piper (in sects. Ottonia and Enckea; Callejas 1986; Tucker 1982b), Peperomia (Tucker 1980), and the single species of Zippelia (Liang, in manuscript; Omori 1982), considered a possible intermediate between Piperaceae and Saururaceae. Pothomorphe and Micropiper are usually considered to be discrete segregate genera related to Piper. There are several other segregate genera of Piper that are not included in our study because of a lack of developmental material and information (i.e., Artanthe, Heckeria, Chavica, Nemanthanthera, Verhuellia, and others, as reviewed in Tucker 1982b). All of these, including Macropiper, Pothomorphe, and Zippelia, were considered subgenera of Piper in a preliminary cladistic analysis of the entire family (Callejas 1986) using Saururaceae as the outgroup. The family Piperaceae undoubtedly deserves a thorough phylogenetic analysis including all taxa. Until the genera Piper and Peperomia, each with approximately 1000 species, are more comprehensively collected and studied, such an analysis is not possible.

Outgroups. It is essential to use outgroups to the order Piperales in order to polarize the non-ontogenetic characters of both Saururaceae and Piperaceae (Maddison et al. 1984; Watrous
Fig. 1. Floral diagrams of ingroup and outgroup taxa excluding Magnolia. Numbers represent order of initiation of individual floral organs. Bars between floral organs in separate whorls represent fusion between different floral whorls (adnation). Bars between similar floral organs represent common primordial origin of stamens and/or connate organs. It should be noted that the order of organ initiation in Anemopsis differs from that reported in Tucker (1985).
and Wheeler 1981). There are no obvious close sister-groups to Piperales although many suggestions have been made. We have selected as outgroups five taxa that represent different combinations of generalized character states: *Cabomba* (Cabombaceae), *Chloranthus* (Chloranthaceae), *Lactoris* (Lactoridaceae), *Magnolia* (Magnoliaceae), and *Saruma* (Aristolochiaceae) (Fig. 1J–M). We also use a hypothetical, generalized ancestor in some analyses. The rationale for using each of these outgroups follows.

*Chloranthus* was selected as a representative of Chloranthaceae, a family of taxa lacking a perianth, a feature absent in all Piperales (Swamy 1953). Although Endress (1987) viewed the chloranthaceous genera *Sarcandra* and *Ascarina* as the more primitive members of Chloranthaceae, *Chloranthus* has bisexual flowers (like *Sarcandra* and the majority of Piperales), and we had more complete data for *Chloranthus* than for *Sarcandra*.

Chloranthaceae were previously included in Piperales (Baillon 1874; Melchior 1964; Payer 1857). Endress (1987), after a thorough morphological and ontogenetic study of members of Chloranthaceae, asserts that this family is closest to Trimeniaceae and Amborellaceae in Laurales, and possibly is a link between Laurales and Piperales. Donoghue and Doyle (1989a), on the basis of phylogenetic analysis of many angiosperm families, concur, suggesting that Piperales are not closely related to Chloranthaceae. Dahlgren and Bremer (1985) also distance Chloranthaceae from Piperales, indicating that the former have affinities to Myristicaceae and Degeneriaceae.

*Magnolia* is used as one outgroup representing primitive woody angiosperms with generalized flower structure, although it is probably not a close relative of Piperales. Much is known about floral ontogeny of several of its species (Erbar and Leins 1981, 1983) and their floral vasculature (Skipworth and Philipson 1966).

One of us has previously indicated doubt that Saururaceae and Piperales are closely related to the woody magnoliid line, based on a number of piperallean features (Tucker 1975, 1976). The difference in symmetry (radial in Magnoliidae and dorsiventral in Piperales) is a significant discontinuity, as is the presence of a perianth in magnoliids and complete absence in Piperales.

It has been suggested that the apetalous condition and the symmetry shift are autapomorphies that would not rule out close relationships between groups having different states of these characters. However, there are differing views on whether apetaly is always derived; some suggest that there could have been an early line of angiosperms that never had a perianth (Dahlgren 1983; Friis and Crepet 1987). The shift to dorsiventral symmetry admittedly is a derived condition, but it is a state that changes the states of many other characters especially in development. For example, differences occur in the order of initiation on the floral apex, shape of the floral apex, sites of organs, and number of parts. A shift in symmetry, in other words, is associated with an assemblage of accompanying changes.

Many systematists have presumed derivation of Piperales from Magnoliales: Bessey (1915), Cronquist (1957, 1981), Hallier (1912), Hutchinson (1964), Takhtajan (1969). Cronquist (1968) suggested derivation of Piperales from Laurales via Chloranthaceae. Putative supporting evidence for an association with Magnoliales rests primarily on characteristics of the flower in *Saururus* (Saururaceae), usually judged as the most primitive taxon in the order. *Saururus* shares with magnolialian taxa the following features: apocarpy, open stigma and style, long-decurrent stigma, monocolpate pollen, oil cells (West 1969), and scalariform vessels. Presumed helical arrangement of parts in the flower has been refuted for *Saururus* (Tucker 1975, 1976). Oil cells were shown by West (1969) to be heterogeneous in origin and contents, and hence lend only minimal support to close relationships among woody magnoliids. The open stigma and style are found not only in Magnoliidae but are also widely distributed among members of Rosales, Contortae, and Helobiae (Baum 1948), suggesting that this character also is weak evidence for a direct line relationship between Magnoliales and Piperales. Historically, the open carpel state is considered plesiomorphic and hence not informative in terms of cladistics. On the other hand, developmentally, the open carpel can be viewed as a result of a heterochronic shift in relative timing of ovule initiation and carpel closure.

In two recent papers, Donoghue and Doyle (1989a, 1989b) describe a monophyletic herba-

ceous clade of angiosperms, the "paleoherbs," which includes Piperales as well as Nym-
phaeales, Aristolochiales, Monocots (Liliopsida) and others. The paleoherbs are thought to represent a line coordinate with woody Magnoliidae, Laurales, and Hamamelidales. Several recent phylogenetic analyses that include paleoherbs suggest that they are not a monophyletic assemblage (Hamby 1990; Hamby and Zimmer 1990; Taylor and Hickey 1992). Although these papers show a lack of congruence in the positions of the paleoherbs among the angiosperms, they are similar in that the paleoherbs, at best, represent a disjunct grade that evolved early in angiosperm history.

We use three outgroup taxa from the “paleoherbs” of Donoghue and Doyle: Cabomba (Cabombaceae), Lactoris (Lactoridaceae), and Saruma (Aristolochiaceae). The outstanding characters shared by “paleoherbs” and the ingroup taxa include primarily herbaceous habit (exceptions in Piper pro parte, Lactoridaceae and Aristolochiaceae pro parte). Paleoherbs differ from Piperales in having two perianth cycles (exception in Lactoris with only one), radial symmetry, and a trimerous perianth and androecium. Other characters of Piperales, such as tetracytic stomata, perisperm, and distichous phyllotaxis, link them with some but not all paleoherbs. Based on this evidence the relationship between paleoherbs and Piperales needs re-examination. The “paleoherbs” are useful here as outgroups in order to polarize some of the character states in the ingroups. Lactoris, another “paleoherb,” is also used here as a sister group because of evidence (Carlquist 1990) that its wood is strikingly similar to that of the woody members of Piperaeaceae. Carlquist (1990) suggests that Lactoris should be included in Piperales on the grounds of wood anatomy as well as some floral characters.

**Cladistic Analyses.** Several cladistic analyses were performed independently, using various polarizations and character treatments as described below.

**Preliminary Analysis.** The first analysis provided a phylogenetic framework independent of ontogenetic patterns as suggested by Mishler (1986). Considering the diversity of mature floral forms in Piperales (especially Saururaceae; Fig. 1), this analysis was used to determine polarity, synapomorphies and homologies, as well as apparently homoplastic character states of the various mature floral characters. Twenty-eight vegetative and mature floral characters were determined, based on the literature and on personal observations of plant structures. The outgroups were used to root the tree(s). Twenty-two characters were based on mature floral structures. The floral characters used included total stamen number, lateral stamen number, median sagittal stamen number, stamen positions relative to carpels, carpel number, median sagittal carpel number (see Fig. 1) and characters 6–9, 11, 12, 17–19, 22–25, 27–35 described below. Ontogenetic analysis of the floral characters for each taxon were compared and new states, new characters, or elimination of certain characters resulted.

**Ontogenetic Analysis.** The analysis is based on accumulated evidence of floral ontogeny among Piperales using anatomical techniques and scanning electron microscopy (SEM). In establishing characters for a cladistic analysis, floral features at different levels of organization and development were analyzed. The ontogenetic pattern of all sets of floral organs was studied and the qualitative events were coded. Although this method entails a risk of artificially multiplying the weight of correlated characters, it also enables a more detailed and resolved analysis of the various patterns and processes that result in the morphological diversity of flowers within the order. Therefore, our ontogenetic analysis started with an analysis of all organs in a floral series or whorl as well as the ontogenetic events associated with the floral organs and their interaction with the structure of the flower as a whole (i.e., symmetry).

A primary assumption of ontogenetic character analysis used in this study is that similar mature structures or patterns between taxa that arise via separate or different developmental means do not necessarily have similar states. For example, to clarify this point, we do not suggest that stamens between two taxa cannot be homologous. Rather, different processes (initiation, position at initiation, and specific locations of meristematic activity) represent independent suites of character states (see characters 9, 10, 15, 20, 21, and 23). In this case, the structures, in and of themselves, are homologous, whereas the various processes that give rise to the patterns of the structures represent different states. Therefore, if different taxa have differing developmental processes in-
volved in structurally homologous organs, the
processes represent potentially parallel develop-
mental convergences.

From the ontogenetic data, two types of char-
acters were determined. First, *ephemeral develop-
mental characters* are defined here as characters
that are present at various stages in the flower's
ontogeny and not determinable at maturity (i.e.,
characters 13–15, 20, 21, 26 scored ** below).
The second type of characters, termed *persistent
developmental characters*, are characters based
on a developmental difference that is evident
in the mature flower, where contrasting develop-
mental states can be polarized via ontogenetic
comparisons (9, 10–12, 17, 19, 23, 25, 27,
28, 31, 32 scored * below). In both character
assessments, polarity is based on Nelson's bio-
genetic law (1978) as well as Tucker's (1984a)
hypothesis that floral characteristics distingui-
shing genera or supra-generic taxa arise rela-
tively early as compared to floral characters
that distinguish species, which arise later in the
flower's ontogeny.

A cladistic analysis of characters derived from
the ontogenetic analysis was performed, both
with and without the outgroups, to determine
the distribution of the various states.

**Cumulative Analyses.** The third analysis
uses characters from the preliminary and on-
togenetic analyses in four different phyloge-
etic treatments (described below). Floral char-
acters from the preliminary analysis (i.e., mature
states), if found to have a different suite of char-
acters or states established through ontogenetic
analysis, were excluded from this analysis. There
are two reasons for these exclusions. First, in
certain cases, the coding of the mature and on-
togenetic characters could artificially weight
those floral characters. Second, in other cases,
the mature states were not homologous relative
to the ontogenetic states. In this case new states
were polarized based on ontogenetic compari-
sions. Excluded mature floral characters includ-
ed total stamen number, lateral stamen number,
median sagittal stamen number, stamen posi-
tions relative to carpels, carpel number and me-
dian sagittal carpel number (Fig. 3A). Four sepa-
rate phylogenetic treatments were performed
using the combined characters. In the first three
analyses, all characters were coded as unor-
dered. This was done to obtain total trees as
suggested by Mabee (1989). Following the anal-
yses, character state changes for each branch in
all trees were identified. Using ontogenetic evi-
dence of transformations between states and
the likelihood of the aforementioned state
changes on the trees, one character was deter-
mined to be irreversible (carpel fusion, char-
acter 25) and is discussed below.

First—the combined data set with all taxa was
rooted using outgroup comparison.

Second—Lundberg rooting (1972) using a hy-
pothetical ancestor derived from the ontoge-
etic characters was utilized. The outgroup taxa
were not included. In this analysis, the polarity
of characters that could not be established via
ontogenetic analysis were scored as unknown
in the ancestor (?)

Third—and similar to the second treatment,
Lundberg rooting was used after establishing a
hypothetical ancestor. The characters that lacked
an ontogenetic polarizing criterion in the hy-
pothetical ancestor in the second treatment were
scored via outgroup consensus. Character states
were scored uniquely only when all outgroups
agreed. Variable states between outgroup taxa
were scored as uncertain.

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**Figure 2.** Strict consensus of eight most-parsimoni-
ous trees obtained from 28 non-ontogenetically de-
duced characters in the preliminary analysis. Saurura-
ceae and Piperaceae are each monophyletic although
there is little resolution of the genera in each family.
Fig. 3. Two cladistic networks of the ingroup taxa comparing the results of an analysis of mature floral characters (3A) with analysis of developmentally derived floral characters (3B). Piperaceous taxa underlined; saururaceous taxa in plain text. A. Seven character network of ingroup taxa. The characters used are based on mature floral morphologies (total stamen number, lateral stamen number, median sagittal stamen number, stamen positions relative to carpels, carpel number, lateral carpel number, and median sagittal carpel number). Five characters and states are graphically represented suggesting trends towards reduction and/or amplification. B. Ten character network of ingroup taxa. Characters used are derived from ontogenetic analysis of floral characters (2, 8, 15, 16, 18, 27, 29; see text). The families seem to separate based on the ontogenetic characters and suggest two trends of reduction, one among Piperaceae and the other among Saururaceae.

Fourth—using the previous three treatments, three ingroup topologies were found, all of which had *Saururus* changing positions within Piperales and Saururaceae (discussed in results). Using developmental evidence of the ontogenetic character state changes, we coded character 25 (carpel fusion) as irreversible (see "Characters Used in Cladistic Analysis" below). With the character thus coded, the previous treatment was rerun.

**Characters Used in Cladistic Analysis.** We include this section in the body of the paper because it explains and supports the interpretations of certain ontogenetic characters and the polarization of individual states as urged by Stevens (1991). We agree with Stevens (1991) that "explicit justification for the delimitation of character states should be included in phylogenetic analyses" and, we add, particularly when ontogenetic techniques are used to delimit characters and polarize and/or order states (see below ** = ephemeral developmental characters; * = persistent developmental characters; Table 1). In our analyses we left all multistate characters unordered.

1. Stem Vascular Cylinder. The taxa of Saururaceae all have a single cylinder of vascular bundles in the stem (Metcalfe and Chalk 1950)
|   | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 |
| Chloranthus | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | ? | ? | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 3 | 2 | 1 | 3 | 0 | 0 | 0 |
| Magnolia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Lactoris | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cabomba | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 |
| Saruma | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | ? | ? | 1 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 1 | 0 | 0 |
| Anemopsis | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| Houttuynia | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gymnotheca | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | ? | 0 |
| Saururus | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Zippelia | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Piper | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 4 | 2 | 1 | 2 | 1 | 1 |
| Peperomia | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 2 | 1 | 1 |
| Pothomorphæ | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | ? | 1 | 1 | 1 | 0 | 1 | 4 | 2 | 1 | 2 | 0 | 0 | 0 |
| Macropiper | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | ? | 1 | 1 | 1 | 0 | 2 | 4 | 2 | 1 | 2 | 0 | 0 | 1 |
in common with most primary dicotyledonous stems (Esau 1965), including outgroups Cabomba (Moseley et al. 1984), and Magnolia (Metcalfe and Chalk 1950). A double cylinder of vascular bundles characterizes Piperaceae (Metcalfe and Chalk 1950). This feature, uncommon among dicotyledons, involves leaf traces remaining in transit for two or more internodes (Hoffstadt 1916; Rousseau 1927), and is probably an apomorphy. Polarization in analyses using Lundberg rooting is based on outgroup comparison.

0—single cylinder of primary vascular bundles
1—double cylinder of primary vascular bundles

2. Woodiness. Magnolia and Lactoris represent outgroup taxa that produce woody growth via a vascular cambium. Piper and Macropiper are the only two ingroup taxa that also exhibit this type of growth.

0—woody
1—herbaceous

3. Perforation Plate Type in Vessel Members. Scalariform perforation plates are considered to be a more primitive state than simple perforation plates in vessel members of angiosperms (Bailey 1953), based on correlation studies that may be considered a form of outgroup comparison. Vessels are lacking altogether in Cabomba.

0—scalariform perforation plate
1—simple perforation plate

4. Leaf Venation. The venation patterns within the ingroup vary among taxa.

0—pinnate venation
1—palmate venation (cordate base with three or more main veins)

5. Stipules. The presence or absence of stipules varies among the taxa examined. Multiple origins of stipules among angiosperms have been argued from recent cladistic analyses (Carlquist 1990; Donoghue and Doyle 1989a). Although evidence on the developmental processes involved in stipule ontogeny is lacking in the taxa examined, we assume homology of states for the taxa concerned (Hennig’s auxiliary principle, 1966, p. 122).

0—stipules free
1—adnate stipules
2—stipules absent

6. Inflorescence Position. The sympodial architecture of Piperaceae, Saururaceae and Saruma is an unusual one among plant families. A corollary of sympodial architecture is the fact that most inflorescences are terminal on the axis. Macropiper and Pothomorph are the only taxa studied here in which there are axillary, lateral inflorescences. Magnolia has solitary terminal flowers; Cabomba has solitary axillary flowers (Moseley et al. 1984; Raciborski 1894); both taxa are scored as “?”.

0—axillary position of inflorescences
1—terminal sympodial position of inflorescences

7. Number of Flowers or Inflorescences at a Position. Inflorescences are solitary at a position in most Saururaceae and Piperaceae except in Macropiper, Pothomorph, and some Peperomia species, where they are clustered at a node. There are solitary flowers in all of the outgroups. Developmentally, a morphocline for this character could proceed either to increase or decrease flower number and inflorescence number; hence we left it unordered.

0—solitary flower at a site
1—solitary inflorescence at a site
2—clustered inflorescences at a site

8. Peloria. A peloria, an atypically radially symmetrical flower, may be present at the tip of an inflorescence in Anemopsis (Tucker 1985) and Houttuynia (Liang and Tucker 1990; Rohweder and Treu-Koene 1971). Of all piperalian taxa examined thus far, these are the only two taxa with a peloria. None of the outgroups has a peloria; thus its presence is considered a derived state.

0—no peloria present
1—peloria present

9. *Presence of Pedicel/Peduncle*. The shift from a sessile to a pedicellate or pedunculate condition or the reverse is a relatively simple one involving intercalary elongation (or its suppression) at the base of the flower above the bract primordium base. During ontogeny the sessile condition is always present first, and can either persist or be modified by development of a pedicel or peduncle. The pedicellate con-
dion is considered derived based on outgroup comparisons and ontogenetic criteria.

0—sessile
1—pedicellate or pedunculate

10. *Flower-bract Stalk*. The presence of a "flower-bract" stalk as in Saururus (Tucker 1975, 1976) and Gymnotheca (Liang and Tucker 1989) is different from a pedicel in that intercalary elongation occurs below the fused base of the flower and the bract. Pedicels develop via intercalary elongation between the bract and flower as described above (character 9). The end result is a stalk that supports both the flower and the bract. We do not consider the pedicel and flower-bract stalk homologous because the position of intercalary elongation differs. Early developmental evidence suggests *Saururna* has a flower-bract stalk. We polarized this character based on ontogenetic evidence, the sessile condition being unspecialized and the more general morphology. Conversely we consider the development and presence of a floral-bract stalk to be a derived state.

0—no floral-bract stalk present
1—floral-bract stalk present

11. *Floral Bract Shape*. The bracts subtending individual flowers vary in shape. Bracts are characteristically lanceolate or linear in Saururaceae, versus peltate or shield-shaped in many Piperaceae, with a diversity of elaborate variations. Peltate bract shape is not encountered in Saururaceae or the outgroups except in *Cabomba* in which development of the peltate bract is ontogenetically different from the peltate form found in Piperaceae. In the ontogeny of *Piper* and *Peperomia* species, the lanceolate form precedes the peltate form (Tucker 1980, 1982a, 1982b), so ontogenetically the peltate form is derived from the ovate or linear state. Ontogenetic polarization is congruent with outgroup polarization.

0—ovate bracts
1—linear to lanceolate bracts
2—peltate bracts

12. *Showy Inflorescence Bracts*. In three saururaceous taxa, the inflorescence bears 4–8 showy white bracts at the base. One or two foliaceous bracts are commonly present basally in other taxa of both Saururaceae and Piperaceae, but these are small, green, and in some cases ephemeral. Ontogenetic evidence proves homology between the small, green bract state and the showy condition because showy and non-showy bracts are similar during early development. Additional differentiative events are added on at the end of development (continued growth, and development of the white color). Outgroup comparison also supports lack of showy bracts as a plesiomorphy, since they are absent in the outgroups. This character is polarized developmentally; ontogeny clarified the relationship among the states.

0—lacking inflorescence bracts
1—only small green bracts present basally
2—basal bracts showy

13. **Initiation of Bract-flower as a Single Primordium**. The usual pattern of initiation of a floral apical meristem is similar to that of vegetative buds. In the spicate or racemose inflorescences of Saururaceae and Piperaceae, each flower is axillary and is subtended by a bract, a modified leaflike organ. In the overwhelming majority of racemes and spikes, the bract precedes its subtended floral bud in time of initiation, as most leaves precede their axillary buds. However, in some saururaceous inflorescences, each bract and associated flower are initiated simultaneously as a common structure (Tucker 1975, 1981). Subsequently, this common primordium bifurcates into a bract primordium and a floral apex; thereby this state represents a developmental modification. The character states are polarized based on outgroup comparison.

0—discrete bract and flower initiation
1—common primordial initiation of bract and flower

14. **Floral Symmetry**. Flowers of most angiosperm taxa that are viewed as primitive have radially symmetrical flowers, as in *Drimys*, *Magnolia* and the other outgroup genera (Fig. 1J–M). In contrast, dorsiventral symmetry (called bilateral in earlier papers) prevails in flowers of Piperaceae (Tucker 1980, 1982a, 1982b) and Saururaceae (Liang and Tucker 1989, 1990; Tucker 1975, 1976, 1981, 1985). Radial symmetry was hypothesized to be more primitive than dorsiventral or zygomorphic by Bessey (1897, 1915) and Hallier (1912); this view has not been challenged successfully. Ontogeny supports this
hypothesis, on several lines of evidence. First, radial symmetry characterizes most vegetative shoots, from which floral shoots have arisen evolutionarily, so the most primitive flowers should share this feature (see Tucker 1961). In many plants (e.g., Magnolia, but not Piperales) there is a direct transition from the vegetative state to a terminal flower by conversion of the apical meristem to a flower meristem. Another line of evidence is the common conversion of floral apices from radial (in early floral organogenesis) to dorsiventral or zygomorphic symmetry (in later stages) (Payer 1857; Sattler 1973; Tucker 1984a). This character is composed of two states that were polarized ontogenetically as well as through outgroup analysis.

0—radial symmetry
1—dorsiventral or zygomorphic symmetry

15. **Organogeny**. Bessey’s dicta (1915) proposed that helical arrangement of floral organs typifies the most primitive angiosperms. The arrangement predominates for all organs in Magnoliaceae (Erbar and Leins 1981; Tucker 1961). Derived conditions include whorled or paired initiation. This is supported by outgroup analysis for the groups concerned, and by comparative ontogenetic evidence (Tucker 1984a). Erbar and Leins (1981, 1983) and Erbar (1988) showed that helical initiation is prevalent in Magnoliaceae but also that there is a shift from whorled perianth initiation to helical stamen initiation in Magnolia denudata Desr. They concluded that both states can occur in primitive taxa. Tucker (1961) showed a developmental transformation series from helical to whorled arrangement of carpels. In Michelia figo Spreng. (Magnoliaceae), carpels are initiated helically but later become aggregated in whorls by differential elongation of internodes. Another piece of evidence that helical organogenesis is the generalized state, and whorled the derived state, is in Ranunculaceae. Flowers of Ranunculus (Payer 1857; Sattler 1973; Tepfer 1953) and most other Ranunculaceae (Clematis, Garidella, Nigella, Thalictrum, etc. in Payer 1857) are helically initiated; the exceptions in the family show whorled initiation of floral organs as in Aquilegia (Tepfer 1953).

0—helical organogeny
1—whorled organogeny
2—paired or decussate organogeny

16. **Lateral Vein Branching**. In most Piperales, the leaves are palmate (except Anemopsis and Piper pro parte). The lateral vein branching patterns differ between taxa. In most Saururaceae, the lateral veins are equally dichotomizing as opposed to other taxa where the branching patterns of the lateral veins do not dichotomize equally.

0—lateral veins lacking
1—equal dichotomous branching of lateral veins
2—branching of lateral veins not dichotomous
3—radiating lateral veins

17. *Ovary Type*. Bessey (1915) and Hallier (1912) proposed that hypogyny is the more general condition in flowers, and epigyny and perigyny are the more derived states. This polarization is upheld by both outgroup comparison and ontogeny. Developmentally, hypogyny is the earlier condition in Houttuynia (Tucker 1981), Anemopsis (Tucker 1985), and Gynnotheca (Liang and Tucker 1989) followed by transition to perigyny in the former and epigyny in the latter two. A similar ontogenetic transition from hypogyny to epigyny occurs in Downingia (Kaplan 1967). Some six monocots and nine dicots also have been shown to undergo this shift (Hannah 1916).

0—hypogynous
1—perigynous
2—epigynous

18. **Flower Vasculature**. Most flowers, like most vegetative shoots, have a vascular cylinder at the base composed of several bundles (Eames 1961; Tepfer 1953). In some small, reduced flowers, including those of Piperales that have been investigated, a single bundle supplies each flower at its base (Murty 1959b; Quibell 1941; Tucker 1979). The latter condition is probably an apomorphy, based on outgroup comparison.

0—each flower is vascularized by a cylinder of several vascular bundles
1—each flower is supplied by a single vascular bundle

19. Perianth. No vestige of a perianth (either tepals, sepals or petals) is present in any Saururaceae or Piperales that have been investigated developmentally. Four outgroup taxa have a perianth: tepals (undifferentiated or-
gans) in Magnolia, and sepal plus petal whorls in Saruma and Cabomba. The presence of petals in Saruma is highly unusual (but putatively primitive) for its family Aristolochiaceae (Wagner 1907). Chloranthus lacks a perianth; Hedyos- mum has been said to have a perianth, but this is a matter of interpretation.

0—no perianth
1—one type of perianth organ present
2—two types of perianth organs present

20. **Separate Stamen Initiation vs. Common-primordial Origin**. Stamen primordia are initiated separately as individual structures in most flowers, including those of the outgroup taxa: Magnolia (Erbar and Leins 1981), Lactoris and Saruma (Tucker and Douglas, in manuscript), Cabomba (Douglas and Tucker, in manuscript) and Piperaceae (Tucker 1980, 1982b). Origin of a pair of stamens from a common primordium is unusual, but occurs in certain Saururaceae (Liang and Tucker 1990; Tucker 1985), and is considered here as a derived trait. The origin of such a phenomenon is still being researched. These pairs may not appear fused in any way at maturity. Polarization is supported by outgroup analysis.

0—separate stamen initiation
1—common primordial origin of stamens

21. **Initiation of Median Sagittal Adaxial Stamens**. Almost all Piperales have a median sagittal adaxial stamen (exceptions in Peperomia with only two stamens). The timing of initiation varies among all genera (Fig. 1). In Lactoris and Saruma, three stamens in each of the two or three series are initiated simultaneously (pers. obs.). However, the median sagittal adaxial stamen (second whorl) is initiated following the initiation of the series of lateral stamens in the first whorl. Cabomba lacks stamens in the median sagittal plane (Fig. 1K). Based on outgroup comparison of this ontogenetic character, the initiation of the median sagittal adaxial stamen after the initiation of other stamens is considered a general or primitive state. This persistent ontogenetic character is polarized using the outgroups.

0—lateral stamens precede the initiation of the median sagittal adaxial stamen
1—median sagittal adaxial stamen initiation precedes lateral stamen initiation

22. Anther Dehiscence. The stamens of taxa in Saururaceae are relatively simple, composed of distinct filaments and anthers, with an un-bifurcated, longitudinally extended stomium between the pollen sacs of the thecae (Endress and Hufford 1989). The position of the stomium and its length vary among taxa. Zippelia differs from all investigated taxa in that the stomium is present from the proximal (basal) portion of the anther to approximately half-way up the anther. Anthers of other piperaceous taxa can dehisce along the full length of the anther (also across the top) or can have predominantly distal dehiscence. Using outgroup comparison, deviations from the complete longitudinal dehiscence patterns are the derived states.

0—stomium along entire length of anther
1—stomium predominantly in proximal position
2—stomium predominantly in distal position

23. *Stamen Fusion*. At anthesis, stamens may be free or fused; if the latter, they are connate, and/or adnate to the carpels in Gymnotheca, Anemopsis, and Houttuynia. Ontogenetic evidence (Liang and Tucker 1989, 1990; Tucker 1981, 1984a, 1984b, 1985) has shown that stamen primordia arise in a free condition and may either remain free or later undergo fusion via intercalary growth below the level of stamen attachment, depending on the taxon.

0—stamens free
1—stamens connate

24. Stamen Traces Discrete or Fused with Carpel Trace. In many plant families or genera, a trend towards increasing fusion has been postulated between vascular bundles supplying adjacent organs (traces), in the more derived taxa (Eames 1961). Evidence concerning the vascular system of flowers of Magnolia (Skipworth and Philip- son 1966) shows no connection between stamen traces and those of the carpels, at the level of trace divergence. This lack of vascular connection is in contrast to the vasculature of most flowers, in which stamen and carpellar traces frequently diverge from the common vascular bundles in the receptacle (Tucker 1964, 1966). Among Saururaceae, one finds conditions where stamen traces are separate from carpel traces, and others where they fuse completely or half-way with the dorsal carpellary trace (Liang and
Tucker 1990). The stamen and carpel traces fuse at the base in Chloranthus (Endress 1987). Based on outgroup comparison, we infer that the character state of fusion between the traces is the derived state.

0—stamen traces distinct from dorsal carpellary trace
1—stamen traces fused in part or completely with dorsal carpellary trace

25. *Carpel Fusion*. Free carpels are viewed as the generalized condition on the basis of the outgroup comparison with Magnolia, Cabomba, and Lactoris, which are apocarpous (Canright 1960; Erbar and Leins 1981; Ozenda 1948), and on the basis of ontogeny. Most carpel primordia in primitive flowers are free at initiation (apocarpous) even if later they become fused (syncarpous) (Baum 1948). The gynoecia of Piperales, exclusive of Saururus (apocarpous) and Peperomia (presumably unicarpellate), are multicarpellate and syncarpous. Reversals are not known in which syncarp precedes apocarp (Eyre 1975). This character was coded as irreversible in a final treatment.

0—apocarpous
1—syncarpous

26. **Median Sagittal Carpels**. An observable trend in ontogeny is reduction of carpel number among the ingroup taxa. In Saruma, there are two carpels in the median sagittal position. Cabomba and Lactoris have a single carpel in the abaxial portion of the median sagittal plane and lack a carpel in the adaxial portion (Fig. 1K–M). Magnolia carpels are not aligned on particular radii (therefore it was scored "?"). Using the outgroup criterion, the loss of the carpel in the abaxial median sagittal position is considered to be a derived trait.

0—adaxial and abaxial carpels present in median sagittal plane
1—one carpel (adaxial) in median sagittal plane
2—one carpel (abaxial) in median sagittal plane

27. Styles and Stigmas. Number of styles and stigmas is the same as the carpel number in apocarpous gynoecia as a rule. In compound ovaries in Piperaceae, however, style and stigma numbers can differ from carpel number (Tucker 1982b). In many taxa, the stigma is sessile and might include structures that are not homologous to single-carpel stigmas. Outgroup comparison suggests that the reductions are derived.

0—style and stigma numbers are equal to carpel number
1—style and stigma numbers are less than carpel number

28. *Style Presence*. The development of the style in Saururaceae results from zonal growth above the ovary and below the differentiating stigmatic region (Tucker 1976, 1981, 1985; Liang and Tucker 1989). The virtually sessile stigmas in taxa of Piperaceae do not have a similar developmental process. Magnolia also has relatively unspecialized sessile stigmatic regions. Based on outgroup comparison using Magnolia the sessile condition is considered plesiomorphic. The development of a differentiated style can be argued as a derived process that deviates from a general groundplan.

0—sessile stigma (no zonal growth)
1—style present (zonal growth between ovary and stigma)

29. *Stigma Shape*. The shape of the stigma and its position vary among taxa. Papillate regions along the stigmatic stylar carpel margins predominate in Magnoliaceae, Saruma, Lactoris and Saururaceae. The stigma in piperaceous taxa may resemble the stylar cleft of Saururaceae (Zippelia and some Piper species) or may be capitate or lobed (Peperomia, Pothomorphae, Macropiper and most Piper species). Based on outgroup comparison, relatively unspecialized stigmatic regions seem plesiomorphic. Ontogenetically, the differentiation of stigmatic regions is a relatively late event in gynoecium development. Therefore, ontogeny supports outgroup polarization of the character state transformations.

0—stigmatic stylar cleft
1—capitate or tufted stigma
2—divided stigma

30. Ovule Number per Carpel. Reduction in ovule number per carpel is generally considered to be a derived state (Canright 1960; Smith 1926) on the basis of outgroup comparison. We use ovule number rather than seed number because seed number does not always correspond to number of ovules initiated, because of abor-
tion. This character is logically correlated with ovule position (33) although not strictly correlated.

0—three or more ovules per carpel
1—two ovules per carpel
2—one basal ovule per carpel
3—one apical ovule per carpel
4—less than one ovule per carpel, in a syncarpous ovary

31. Carpellary Vascular Bundle Supply. Two ventral bundles per carpel are present in Magnolia (Canright 1960; Skipworth and Philipson 1966) and Cabomba (Moseley et al. 1984; Padmanabhan and Ramji 1966; Ramji and Padmanabhan 1965). Evidence on carpel vasculature in Saururaceae (Liang and Tucker 1990; Tucker 1976) showed that the ventral bundles from adjacent carpels fuse to form one placental bundle in three saururaceous taxa; in Piperaeae (Eckardt 1937; Murty 1959a; Schmitz 1872) there is a single ovular bundle per carpel. Based on outgroup comparison, two ventral bundles per carpel is the plesiomorphic condition.

0—two ventral bundles per carpel
1—ventral bundles from adjacent carpels converge to form one placental bundle at higher levels
2—presence of a single ventral bundle

32. *Ovule Orientation*. Ovules may be oriented in different positions on their funiculi: anatropous, orthotropous, or hemitropous for example. Although opinions differ on this point, the anatropous condition is most usually considered to be the archaic type in angiosperms based on association with other primitive character states (Bocquet and Bersier 1960; Bouman 1984; Eames 1961; Takhtajan 1969). Donoghue and Doyle (1989a) concluded that the anatropous state is primitive based on cladistic analysis in which character states were not polarized a priori because of mixed conditions in the outgroups. Taylor (1991) asserted that the orthotropous state is primitive, based on the ontogenetic argument that all taxa studied go through an orthotropous phase. Therefore, Nelson’s ontogenetic criteria (Nelson 1978; Weston 1988) could be used to argue for the opposite polarity of the states.

0—anatropous
1—orthotropous

33. Placentation. Polarization of the character states is based on outgroup and ontogenetic comparison. Magnolia and the outgroups have submarginal placentation. Parietal placentation is more derived, since it is associated with or dependent upon fusion among carpels. Basal and pendulous placentation are considered derived by reduction (Eames 1961). Taylor (1991) used ontogeny as well as character association to polarize this character. Although his results indicated basal, orthotropous ovules are the generalized condition in angiosperms, our analyses suggest that these conditions are derived in Piperaeae.

0—submarginal
1—parietal
2—basal
3—pendulous

34. Type of Embryo Sac. The monosporic condition (Polygonum type) is considered primitive by Eames (1961) and Takhtajan (1969); it occurs in Saururaceae, Chloranthaceae, Magnolia, and all Piperaeae except Peperomia and Piper. The tetrasporic “Fritillaria type” embryo sac occurs in Piper and Peperomia. All except Peperomia are 8-nucleate in the species compared. The 16-nucleate embryo sac is a derived state found only in Peperomia of the assemblage under consideration, an autapomorphy that is, therefore, not cladistically useful. Outgroup comparison is used to determine polarity.

0—monosporic (Polygonum type)
1—tetrasporic (Fritillaria type)

35. Perisperm. Perisperm is storage tissue of nucellar origin in the seed (Esau 1963), and is rather infrequent and sporadically distributed taxonomically. It occurs in all Piperaeae and Saururaceae that have been investigated, but not in Magnolia, Lactoris, or Saruma. The character is polarized with the outgroup.

0—no perisperm
1—perisperm present

Some characters are not useful because they occur in only one taxon (autapomorphies): e.g., 16-nucleate embryo sac, non-aperturate pollen grain, and unitegmic ovules only in Peperomia, the condition of the bract adnate to the carpel only in Anemopsis, and unisexuality in Macro-piper and several species of Piper. Other characters are significant but not useful because they
are ubiquitous in the ingroup taxa concerned here (although not restricted to them): e.g., monosulcate or monocolpate pollen, dry stigma, crassinucellate ovule, cellular endosperm, oil cells, multilacunar nodes, and xylem characteristics. Some are useful, however, as synapomorphies for Piperales.

**RESULTS**

**Mature Floral Morphologies.** The preliminary analysis of 28 characters that includes the mature floral characters, but does not include the ontogenetically determined characters, resulted in eight most-parsimonious trees of 80 steps (strict consensus in Fig. 2). Piperales and Piperaceae each form a monophyletic group. *Zippelia* appears as the basal taxon of Piperaceae. The other piperaceous taxa formed a tetrachotomy. Saururaceous taxa remain unresolved in the strict consensus (Fig. 2).

Character states were traced on the above cladogram and the number of steps and consistency indices for each character were determined. The mature floral characters of total stamen number, lateral stamen number, median sagittal stamen number, stamen positions relative to carpels, carpel number, median sagittal carpel number and the type of gynoecium (character 17) had very low consistency indices (c.i. < 0.40; r.c. < 0.17).

Cladistic analysis of the seven mature floral characters, using the ingroup taxa only and taken from the preliminary analysis above, scrambles the two families, suggesting that trends in reduction of numbers of floral organs are parallel or convergent among the two families. This is demonstrated in the seven-character network (Fig. 3A). The poor resolution of the network using seven mature floral characters could also be due to the small number of characters used, fewer than the number of taxa. When additional characters such as vascular characters are used in the analysis (Fig. 2), monophyly of both families seems resolved. The number of steps of each character and the homoplasy ratios are high suggesting multiple origins of the mature floral characters between and among both families.

**Floral Ontogenies.** Virtually all (6 of 7) of the characters from the mature floral analysis (Fig. 3A) were abandoned and/or re-coded for various states (see characters 25 and 26) via developmental comparisons. Ten characters, established from the ontogenetic analyses (10, 13–15, 17, 20, 21, 25, 26, 28), were subsequently used in a cladistic analysis. This unrooted analysis was performed to test for apparent trends in reduction, parallelisms and convergences in the flowers of the different taxa.

A cladistic analysis of the 10 floral ontogenetic characters resulted in a separation of the families as seen in the network in Figure 3B. Our analyses indicate that there are at least two trends of reduction occurring in each of the two families. One trend was identified as a change or reduction of stamen number. This was determined by comparing the timing of initiation of the stamens, including a relationship with the 'common primordial' origin inherent in most of the Saururaceae. The second trend seems to involve the timing and position of carpel initiation and the relatively precocious zonal growth between the carpels resulting in the syncarpous/hypogynous state in Piperaceae and the syncarpous/epigynous or perigynous state in Saururaceae (except *Saururus*). Other floral characters supporting the separation of the families in this network include zonal growth beneath the stigma and above the placenta, stigma shape, and ovule numbers (over three per carpel) in Saururaceae.

**Cumulative Analyses.** First Treatment (Outgroup Polarization). Figure 4 shows the result of a phylogenetic analysis that included the ontogenetic characters (Fig. 3B) and all other characters, but excluded the mature floral characters (Fig. 3A). All characters were unordered and polarized with the outgroups. This analysis resulted in two most parsimonious trees (Fig. 4A–B; 83 steps, c.i. = 0.64, r.c. = 0.48, r.i. = 0.74). Piperales appear to be monophyletic supported by nine synapomorphies (5, 6, 9, 11, 12, 15, 18, 26, 35). *Zippelia* is supported as the basal member of Piperaceae with eight synapomorphies for the family in Figure 4A and six synapomorphies in Figure 4B. The difference in the topologies of the two trees is seen in Figure 4A and 4B. Saururaceae are not monophyletic in Figure 4A, and *Saururus* is the basal member of Piperales. Saururaceae are monophyletic in Figure 4B, supported by four synapomorphies (10, 16, 21, 28), with *Saururus* appearing as the most basal taxon of the family. The other three genera of Saururaceae are united by seven synapomorphies (12, 17, 20, 23, 25, 31, 33).

It should be noted that in many cases the
outgroup taxa demonstrated relatively different specialized developmental events, specific to each, that are probably indicative of the divergences between the groups used [e.g., perianth parts, stamen features as in Endress (1992) and merosity as in Fig. 1]. Although a single topology was found for the outgroups considered here, it is perhaps a function of the outgroups specified. Any outgroup configuration, in our results, should be viewed simply as an unrooted network; the position of the root could be at any of several places among the taxa sampled here or other angiosperm taxa not sampled here.

Second Treatment. Developmental Polarization. We performed a cladistic analysis on the ingroup alone, based on developmentally polarized characters, in view of the lack of similar developmental events of certain character states between the outgroup and ingroup. We reason that the developmental characters inherent in the ingroup are not applicable to developmental trends in the outgroup taxa in many cases. We use Nelson’s (1978) direct test of ontogeny as a polarizing test using a definition of ancestral states based on previous ontogenetically determined general states (e.g., apocarpy vs. syncarpy).

In this treatment, a hypothetical ontogenetic ancestor was established using the ontogenetic characters. Character polarity that was not determined ontogenetically was scored as uncertain in the ancestor. Lundberg rooting of the ingroup with the hypothetical ancestor resulted in a reduction of informative characters from 35 to 27. The analysis produced three most par-
systematic botany

Anemopsis

Houttuynia

Gymnotheca

Saururus

Zippelia

Piper

Peperomia

Pothomorphe

Macro piper

epigyny/perigyny

syncarp

flowerbract stalk

init. of med. sag. carpel

syncarpy epigyny

epipacry hypogyny

REVERSAL

Fig. 5. One of the most parsimonious trees obtained from the Lundberg rooted analyses (second and third treatments, see text). Two hypothetical ancestors were determined, one using ontogenetic information and the other combining ontogenetic generalized states with outgroup consensus of non-ontogenetic characters. Saururaceae and Pipera-ceae are each monophyletic. Saururus and Gymnotheca form a clade within Saururaceae suggesting a reversal from fused carpels to free carpels (syncarp to apocarp) and a reversal from an inferior ovary to a superior ovary. Characters relevant to discussion in text are indicated.

Pipera ceae. There were no characters supporting the inclusion of Zippelia as a saururaceous taxon.

Saururaceae are monophyletic in two trees supported by three synapomorphic characters (10, 21, 28; Figs. 4B, 5). Saururaceous taxa, excluding Saururus, are supported as a monophyletic group with three synapomorphic characters (25, 31, 33), with Anemopsis appearing more closely related to Houttuynia than to Gymnotheca.

Third Treatment (Combination Polarization). The third treatment used a hypothetical ancestor and Lundberg rooting. The hypothetical ancestor’s ontogenetic character states were scored in the same way as above. Characters that were scored as unknown in the previous treatment were coded with outgroup scores if unique. Variable states in the outgroup taxa were scored as uncertain. Two most parsimonious trees were found (46 steps, c.i. = 0.76, r.c. = 0.60, r.i. = 0.78) that had topologies identical to the trees illustrated in Figures 4B and 5. Saururaceae and Pipera-ceae each appear to be monophyletic in this analysis. Differences in the topologies are found in Saururaceae. Saururus and Gymnotheca form a clade in one tree (Fig. 5) and Saururus is the basal taxon of the remaining saururaceous genera in the other (Fig. 4B).

Fourth Treatment (Character 25 Irreversible). In the fourth treatment, character 25 was coded as irreversible. The previous treatment was executed with this change. In all cases, the number of steps increased by at least one. A single most parsimonious topology of the ingroup taxa was found (Fig. 6). In this case, Saururaceae are monophyletic with Saururus as the basal member of the family. Interestingly, this topology was found in each of the previous three treatments (see Fig. 4B). It should be noted that apocarpy is presumably derived in Peperomia via reduction and hence was coded as “?” because of a lack of similarity to the fusion processes present in multicarpellate taxa (see Discussion).

Discussion

Floral Ontogenies and Phylogenetics. Our analyses indicate that a higher resolution of character evolution and phylogenetic hypo-

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Fig. 6. The single most parsimonious tree obtained via Lundberg rooting of the hypothetical ancestor derived from ontogenetically general states and outgroup consensus for all other characters (fourth treatment in text). Character 25, fusion of carpels, is coded as irreversible based on developmental evidence. Certain character state changes are traced that support particular clades as discussed in the text.
eses can be attained by including ontogenetic analyses. Ontogenetic analysis is undoubtedly a valuable technique in clarifying whether character states are homologous (see below). Ontogenetic evidence can also establish characters not observable in the mature forms (e.g., sequences of organ initiation, timing of zonal growth), enabling one to identify discrete characters, as well as to identify differing or similar developmental processes that give rise to similar mature floral morphologies. The value of ontogeny is best demonstrated by comparing the analysis excluding the ontogenetic characters (Fig. 2) with the analysis of ontogenetic characters solely (Fig. 3B). In the cladistic analysis excluding ontogenetic characters (Fig. 2), there is lack of resolution between the taxa of Saururaceae and the piperaceous taxa *Pothomorphae, Piper, Macrosperma* and *Peperomia*. There is better resolution of the terminal taxa in the cladistic analysis of ontogenetic characters (Fig. 3B) although the result still is not congruent with the analyses using all characters. By combining the ontogenetically established characters with the other characters (excluding the mature floral characters from Fig. 3A) there appears to be greater resolution of the taxa (Figs. 4–6). The combined data set suggests a certain degree of character congruence, as well as enhanced resolution of phylogenetic relationships.

Understanding the developmental events associated with the mature floral morphologies is invaluable in defining homologous characters, character states, and polarity or transformational information of each character. Ontogenetic evidence has proven invaluable in assessing putatively homologous structures, an essential principle of phylogenetic theory (Hennig 1966; Kaplan 1984; Mabee 1989; Stevens 1991; Tomlinson 1984; Weston 1988).

The value of ontogenetic analyses as a method of assessing homologous character states and parallelisms of the mature floral organs and forms is illustrated by comparing the analysis of characters in the mature floral morphologies (Fig. 3A) to the floral characters produced after an ontogenetic analysis (Fig. 3B). The mature floral characters (e.g., stamen numbers, stamen positions) appear convergent between the two families, resulting in an increased number of steps and homoplasies when trees are constructed with the mature characters and the rest of the data set excluding the ontogenetically established characters (Fig. 2). One valuable feature of ontogenetic data in phylogenetic analyses is to show whether apparent homoplasies should be treated *a priori* as the same character “state.” The present study allows us to examine homoplasies from this point of view.

One example of an apparent homoplasy is the similar groundplan of flowers of *Saururus* and *Gymnotheca* in Saururaceae and of *Zippelia* in Piperaceae (Fig. 1A, B, E). Numbers of stamens and carpels are identical in the three, and positions of these organs appear identical in flowers at anthesis. However, ontogenetic evidence indicates that the developmental pathways that produce these flowers differ qualitatively (e.g., in whether stamens arise paired from common primordia or solitary), as well as quantitatively (e.g., organ number, and in relative timing of initiation among the organs). Although the groundplan is similar in the three genera mentioned, the order differs among them. Compare, for example, the locations of the first stamen(s) produced, labeled “1” in each floral diagram. *Saururus* produces a pair in the sagittal plane, *Gymnotheca* produces only one in the same plane, and *Zippelia* produces a pair of first stamens in lateral positions. Hence the similarities (homology) of stamen organ structure and position number mask the fact, revealed through ontogenetic evidence, that these conditions are achieved through heterochronically differing pathways.

The tetracarpellate gynoeicum is a homoplasy at one level; at another level, differing sequences of carpel initiation reveal that the tetracarpellate conditions differ and have arisen by heterochronically dissimilar events. Carpel timing differs since carpels are initiated in different sequences. The two sagittal paired carpels (of four) are initiated first and simultaneously in *Saururus*, but last and successively in the other two genera.

Similarly, the reduction in carpel number among the other saururaceous and piperaceous taxa is probably a parallel feature developmentally based on tree topologies (Figs. 4–6). Early developmental features of the gynoeicum in the two lines of Piperales appear to be similar in reduction of carpel number via loss of the abaxial carpel. A reduction series can be visualized for numbers and positions of carpels (and stamens). An *a posteriori* character analysis (Don-
oghue and Cantino 1984; Mickevich 1982), of carpel and stamen numbers suggests two parallel reduction series, one from *Saururus* in Saururaceae, and the other from *Zippelia* in Piperaeae. Both show reduction in number of stamens and carpels. The saururaceous line leads to synapomorphies such as fusion among organs, showy bracts, elongate styles, and fused stamen vascular traces, while the piperaceous line has synapomorphies such as unisexuality, reduced stomium extent in anthers, and reduced ovule numbers. The pattern of carpel reduction is consistently a loss of the abaxial median sagittal carpel, which is initiated last in virtually all taxa studied (*Peperomia*, presumably having only one carpel, cannot be categorized). A developmental theory concerning the order of loss of organs (Rensch 1959) hypothesized that the last parts (organs) initiated, the most distal, are generally the ones that are lost first in evolution. Rensch’s hypothesis was based on the loss of the distal-most parts of insect wings, and was supported by studies of the loss of wrist bones in salamanders (Hanken 1986). Tucker (1988) similarly hypothesized that the floral organs that tend to be lost are those that are initiated last in a whorl (series), or the entire whorl that is initiated last (e.g., the inner stamen whorl of legumes). Although complete loss of floral organs from development (with no vestiges) is difficult to assess by using *a posteriori* character analysis in a phylogenetic context, we conclude that there is a general reduction in stamen number and carpel number among piperalian taxa.

We found that other stages of carpel development differed between Saururaceae and Piperaeae which, taken together, support the status of the two families as monophyletic sister taxa. Saururaceous taxa have meristematic activity between the stigma and the distal portion of the ovary, producing a style. Piperaceous taxa lack meristematic activity in this location, and therefore do not develop an elongate stylar region. They also differ in size of placenta, number of ovules initiated per carpel, and in the fusions and zonal growth that produce the perigynous and epigynous states.

**Phylogenetic Analyses. Saururaceae.** Three most parsimonious trees (Figs. 4–5) were obtained from the first three treatments using all of the characters including those determined ontogenetically. Although there is strong support for the Piperales as a monophyletic order (Fig. 4A, B), there does not appear to be a great deal of support for monophyly of Saururaceae. Three hypotheses of relationships among genera in Saururaceae emerged from the three analyses: one with *Saururus* basal to the remaining Piperales (Fig. 4A) using treatments one and two, one with *Saururus* and Gymnotheca forming a clade within a monophyletic Saururaceae (Fig. 5) using treatments two and three, and one with *Saururus* basal to the other saururaceous taxa (Fig. 4B) using all three treatments.

The poor support for the monophyletic status of Saururaceae in our analyses appears to be due largely to the lack of derived character states in *Saururus* that unite the remaining saururaceous taxa (characters 12, 17, 20, 23, 31). Even though *Saururus* shares the common floral-bract primordia character state (character 13), a similar initiation of the median sagittal adaxial stamen character state (character 21) with *Gymnotheca*, and the flower-bract stalk character state (character 10) with *Houttuynia*, these taxa are separated from *Saururus* by taxa without these states so they lose their value as synapomorphies. *Saururus* is clearly much more primitive or generalized than the other three genera in the family. Considering these states as well as the presence of a style (character 28) and leaf venation pattern (character 16) shared with almost all other Saururaceae and the fact that *Saururus* shares no synapomorphies with Piperaeae, as well as the results from the fifth treatment (Fig. 6), we maintain that Saururaceae are monophyletic.

In a logical attempt to resolve the relationships among the saururaceous taxa, character state changes were traced on trees using both ACCTRAN and DELTRAN options separately. In all cases, data were obtained from the third treatment described above. In the topology where *Saururus* and *Gymnotheca* form a dichotomy in Saururaceae (Fig. 5), the clade is supported by two synapomorphies, the presence of a flower-bract stalk and initiation of the median sagittal carpels. It should be noted that in this tree, fusion of the carpels (syncarp) and an inferior ovary are two of several synapomorphies for the Piperales and Saururaceae respectively (Fig. 5). In the Gymnotheca/Saururus clade, the apocarpous condition in *Saururus* as well as the superior ovary, free stamen initiation, and lack of fusion of the ventral carpel bundles would all be considered reversals from their
alternate states, and the common primordium of bract and flower would be a parallelism (Fig. 5). There has never been a report of flowers with multiple carpels in a syncarpous state evolving to an apocarpous state. In our opinion, this is a highly improbable evolutionary event. It should be noted that the reduction of carpel number to a single carpel as in Peperomia (as seen from our results) is a completely different process that results in apocarpy, probably a reduction process that has undoubtedly occurred in several angiosperm lineages. From this conclusion, it seems logical to exclude the topology in Figure 5 from being a robust hypothesis.

In an attempt to test for the unlikely event of a reversal from a multicarpellate, syncarpous gynoecium to a multicarpellate, apocarpous gynoecium using parsimony analysis, we ran a fourth treatment coding character 25 (carpel fusion) as irreversible. This resulted in one most parsimonious tree (53 steps, c.i. = 0.78, r.c. = 0.60, r.i. = 0.78, Fig. 6) only one step greater than that found in the third treatment. Saururaceae are monophyletic with Saururus appearing as the most basal genus of the family (Fig. 6).

Considering that we used Nelson's (1985) "general to specific" criteria, our ontogenetic analysis could have been biased by rooting the Piperales with Saururus. However, when the outgroup criterion was restricted to characters lacking an ontogenetic component (Fig. 2), Saururaceae similarly appeared to be a monophyletic assemblage.

Piperaceae. Many synapomorphies support Piperaceae s. str. as a monophyletic family (Figs. 4–6). The genus Piper is highly heteromorphic and probably should be divided into segregate genera, although the database is weak for most taxa. Callejas (1986) presented a cladogram for the Piperaceae, with the caveat that it is very preliminary. In his tree, he compared 25 subgenera of Piper s. str., including entities that we have treated as genera: Zippelia, Macropiper, and Pothomorphe. He concluded that it is best to treat all as subgenera until more information is available on interrelationships. In his tree, Macropiper is the sister group to Piper s. str. on one branch of a trichotomy, a second branch bears Zippelia, and the third includes Pothomorphe, Ottorina, and Enckea (the latter two are subgenera of Piper s.l.). Peperomia is well separated, as are Saururaceae, which Callejas used as the outgroup. The monophyletic status of Peperomia would be strengthened in our study by addition of several autapomorphies that we excluded (16-nucleate embryo sac, unitegmic ovule, solitary carpel, unusually small size of pollen, non-apericarpy pollen, and monothecal bisporangiate stamens).

From our analysis of Piperaceae, Zippelia represents the most basal taxon. This poorly known genus (Circaeocarpus is a synonym) has been viewed as an intermediate between Saururaceae and Piperaceae; it has been placed in each family at various times (Wu and Wang 1957, 1958).

Its floral organization (Fig. 1A) closely resembles that of Saururus (Fig. 1A) except for a syncarpous ovary, a single basal ovule, and a different order of stamen initiation. Omori (1982) concluded that the floral morphology and vascular anatomy of Zippelia are closer to those of Saururus chinensis Hort. ex Loud. than to any Piperaceae. Zippelia, as the sister group to the rest of the Piperaceae clade, is the closest piperaceous taxon to Saururus in our analysis in terms of number of intervening nodes on the cladogram, but has more derived states uniting it with Piperaceae rather than with Saururus or the rest of Saururaceae. Zippelia appears to represent a morphologically transitional genus between Saururaceae and Piperaceae, although indisputably belonging to the latter.

Some early botanists (Baillon 1874; Rousseau 1927) included Saururus and Houttuynia in Piperaceae. However, most other systematists, past and present, maintain Saururaceae as a separate family (Cronquist 1957, 1968; Dahlgren 1983; Eichler 1878; Melchior 1964; Metcalfe and Chalk 1950; Payer 1857; Takhtajan 1954, 1969). On the basis of primitive characteristics of Saururus, Saururaceae as a whole have been viewed as considerably more primitive than Piperaceae. Our analyses suggest Saururus represents the most primitive extant member of Piperales, and the other saururaceous taxa and piperaceous taxa represent separate evolutionary lineages within Piperales from an ancestor that was more like Saururus than any other genus.

Two other recent papers examine phylogenetic relationships of Saururaceae and Piperaceae, together with numerous other angiosperm families. Dahlgren and Bremer's analysis (1985) uses 61 characters and shows two of many trees obtained. Saururaceae and Piperaceae are sister taxa. Piperaceae are well supported (stelo
type, placentation type, syncarpy). Synapomorphies for Saururaceae include radicle duration, length ratio of root hair cell/epidermal cell, and stelar type in one tree, but no synapomorphies in the other tree. However, no source for the root data used by these authors could be found, particularly for individual genera in our analysis. Also, in our analysis, the stelar type in Saururaceae (single cylinder of bundles in stem) is plesiomorphic, while Dahlgren and Bremer consider it an apomorphy, based on the dubious premise (based on Burger’s 1977 hypothesis) that dicotyledons are descended from monocotyledons. The complex vascular system with more than one cylinder is a specialization, in our view, since the outer cycle constitutes leaf traces. Dahlgren and Bremer show strong support for the Saururaceae–Piperaceae clade, and adequate support for Piperaceae alone (four characters) but none for Saururaceae alone in one tree (their fig. 3); in another tree (their fig. 2), three characters provide support for Saururaceae, and two other characters provide support for Piperaceae.

The analysis by Donoghue and Doyle (1989a), using 54 characters, is similar in showing robust support (nine characters) for the Saururaceae–Piperaceae clade, but only weak support for the families individually. Piperaceae is supported by two synapomorphies (ovule number, lack of fruit dehiscence) while Saururaceae has only one (pollen aperture sculpturing), and that indicated as doubtful by the authors (Bornstein 1989; Walker 1976).

Molecular sequence analysis (Hamby 1990; Hamby and Zimmer 1990) using the 18s ribosomal RNA of many basal angiosperms including Saururus, Piper, and Peperomia shows very strong support for monophyly of Piperales although there is little resolution of the genera in the two families.

**Positions of Floral Organs.** The four genera of Saururaceae show an interesting interplay of states for certain characters: a) organ position, b) organ number, c) organ loss, and d) organ initiation. The four genera and six species undoubtedly form a natural group; they are considered relicts of a once larger and more diverse family on the basis of present geographic isolation. Floral structure in the four genera differs qualitatively in many major respects (Fig. 1A–D). Saururus has the most general and probably most primitive character states: six stamens, four carpels, apocarpy, minimal basal connation of carpels, no adnation of stamens to the carpels (Fig. 1A). Its two species [S. cernus L. and S. chinensis (Louis.) Baill.] also have individually wide ranges of distribution, on different continents (North America and Asia, respectively). Saururus has a basic haploid chromosome number of 11, and lacks polyploidy or other chromosomal specializations.

Gymnotheca (two species in southeast China; Fig. 1B) shows adnation and connation of floral organs, stamens initiating in pairs from common primordia; the latter stand in positions similar to the stamens in Saururus. It shows aneuploidy and has a basic haploid number of nine.

Anemopsis (North American southwest and Mexico; Fig. 1C) has showy, white, basal involucral bracts, adnation and connation of floral organs, stamens initiating in pairs from common primordia but in positions different from those in Saururus and Gymnotheca, loss of the abaxial carpel, aneuploidy (n = 11), and polyploidy (up to n = 44).

Houttuynia (Asian; Fig. 1D) has showy, white, basal involucral bracts, reduction of stamen number to three (in the positions of the common primordia in Anemopsis, by loss of paired initiation or loss of common primordia?), adnation and connation of floral organs and a haploid chromosome number of 12.

Two of the genera, Saururus and Gymnotheca, have two extant species each, although the species differ rather little from one another. Saururus cernus and S. chinensis, although on different continents, differ primarily in that S. chinensis has elongate pedicels, slight adnation of stamens to carpel bases, short styles (Raju 1961), and a slightly different vascular supply (in the relative level of departure of the ventral carpellary bundles; Liang and Tucker 1990; Murty 1959b; Omori 1982). These differences are small, and in no way do they dispute monophyly for the genus.

The two species of Gymnotheca also are very similar. They intergrade to some extent, although *G. involucrata* P’ei has showy white basal involucral bracts (rather like *Anemopsis* and *Houttuynia*) that are lacking in *G. chinensis* Decaisne Minor differences between them include degree of stigma recurvation, slight difference in ovule number, slight difference in length of flower-bract stalk, and number of bundles in...
the bract lamina. The genus is undoubtedly monophyletic, based on the minor nature of differences (all quantitative) between the two species. In our analysis, Anemopsis and Houttuynia are very closely related while Gymnotheca is the taxon nearest to the latter two.

Evolution in Saururaceae has involved heterochrony, losses, common primordia, fusion of organs, and order of initiation in both stamens and carpels. The order of stamen initiation differs heterochronically and is genus-specific in Saururaceae (Fig. 1A–D). The first stamen initiated is the median adaxial in Gymnotheca; subsequent order of initiation is uniformly adaxial to abaxial. In Saururus, the two median stamens appear to be initiated simultaneously, followed by an abaxial to adaxial order of initiation of the remaining four stamens (Fig. 1A). In Anemopsis and Houttuynia, the first stamens are the two laterals (common primordia in Anemopsis). Next to initiate in Houttuynia is the solitary median adaxial stamen (there are only three stamens). In Anemopsis, initiation of the adaxial stamen pair follows, and lastly the abaxial stamen pair. Stamen sites in Houttuynia correspond to sites of common primordia in Anemopsis. The four genera share certain features, such as simultaneous initiation of mirror-image pairs of lateral stamens, but the differences in order among the four genera are consistent and pronounced.

The gynoeicum consists of either four carpels (Saururus and Gymnotheca), or three (Anemopsis and Houttuynia). The order of carpel initiation is unique in each of the four genera (Fig. 1A–D). In Saururus, the sagittal pair is initiated first, and the lateral pair last. In Gymnotheca, the lateral pair is first, the sagittal pair successive and last. Of the two genera with tricarpellate gynoecia, Anemopsis has simultaneous carpel initiation, while in Houttuynia the lateral pair is initiated first, followed by the median adaxial carpel.

**Symmetry in Saururaceae.** The flowers of all four saururaceous genera show dorsiventral (zygomorphic) symmetry, in which the upper or adaxial half of the flower differs from the lower or abaxial half. Cursory examination of flowers at anthesis suggests radial symmetry (Eichler 1878; Melchior 1964), and sections of older buds and flowers also have led to this conclusion (Murty 1959a; Raju 1961). However, the course of organogeny (demonstrated with SEM) clearly shows dorsiventral organization during initiation (Tucker 1975, 1976, et seq.). In some other taxa, dorsiventrality arises during initiation and persists to anthesis, as in many papilionoid legumes (Tucker 1984b).

**Trimery.** The condition of trimery undoubtedly is an ancient condition; Dahlgren (1983) suggested that trimery may have predated separation of monocotyledons from dicotyledons. Of the four outgroups used here, three are trimeros (Fig. 1J–L) and one, Magnolia, includes at least one species, *M. denudata*, with a trimeros perianth (Erbar and Leins 1981).

Piperales have incorrectly been called trimeros based on erroneous early conclusions using sectioned mature flowers. Dorsiventral symmetry has been established through ontogenetic studies of the four genera of Saururaceae, and in representatives of the major genera of Piperaceae (Tucker 1975, et seq.). Stamen numbers per flower have been reported to include 2, 3, 4, 6 or 7 in various species of *Piper* depending on the taxon (Tucker 1982b). The idea of trimery for Piperales should be reevaluated. The possibility exists that the ancestor to Piperales was trimeros. From our analysis and the lack of a well accepted sister group to Piperales, we cannot make a conclusion as to trimery being primitive to Piperales. Donoghue and Doyle’s paleoherbs are united by several characters including trimery and radial organization, neither of which apply to Piperales. Since apparent trimery results from equalization and realignments during floral development, this trimery results from convergent pathways. Organs in other trimeros flowers like *Scilla violacea* Hutch. (Sattler 1973), *Lactoris* and *Saruma* (unpubl. data), and *Asarum* (Leins and Erbar 1985) have been shown to arise as simultaneous whors, or as helices.

**Apetalia.** There is no anatomical or developmental evidence that taxa of Saururaceae or Piperaceae have ever had petals or sepals. We used outgroups having one or both whors or none. Our analysis supports the contention that loss of a perianth (petals and/or sepals) preceded evolution of Piperales as a group, so that its taxa are unlikely to undergo reversal of this character state. Recently several authors have considered the possibility that an apetalous line was present among early angiosperms (Dahl-

Obviously, the current treatment emphasizes internal relationships among Piperales, and does not include all possible outgroups that would be needed to accurately convey relationships of the Piperales to outgroups. Our analyses limit outgroup taxa to those that were appropriate and available for floral developmental study. Hence relationships among the outgroups included should be viewed as subject to change, if all possible related groups were to be added.

In other primitive magnoliid angiosperm groups, there are some taxa having a perianth, others lacking it (Endress 1987). In Chloranthaceae, Hedyosmum has three lobes on the carpel which have been interpreted as tepals (Endress 1987), so that absence of a perianth in other taxa would constitute a loss and be considered derived. Within Chloranthaceae, “the perianth can easily disappear, since its integration in the floral organization is weak” (Endress 1987). This is in contrast to a specialized family such as Asteraceae, in which organs may be suppressed but rudiments may remain (Harris et al. 1991). The consequences of loss versus suppression of floral organs are discussed in Tucker (1988).

Specializations. In a family such as Saururaceae with many derived character states, several are highly unusual. Common primordia (a specialization) can occur at two stages of development: 1) the bract-flower primordium occurs in Saururus and Houttuynia, and 2) the stamen-pair primordium occurs in Houttuynia and Gymnotheca. Common primordia were thought rare when the condition was found in Saururus (Tucker 1975); they had, however, been reported in several taxa of Primulales (Sattler 1962). Some additional reports of common primordia have appeared for Areaceae (Uhl 1988), Loasaceae (Hufford 1988), Vitaceae (Gerrath and Posluszy 1988), and Zingiberaceae (Kirchoff 1988). Some other early but undocumented reports are mentioned in Tucker (1981).

Another specialization in Saururaceae is the presence of showy inflorescence bracts, which occur in three of the four genera (Anemopsis, Houttuynia, Gymnotheca) and probably arose only once. The character state of showy bracts may be considered to be reversible, based on the fact that the two species of Gymnotheca (although very similar otherwise) differ in the character, and also by the occurrence of occasional intermediates in field populations (pers. obs.). Fusion of carpels, another specialization, is shown by the tree topology (Fig. 6) to have occurred twice, independently in the piperaeous and saururaceous lines. This fusion is one of several convergent features shared by the two families that blur morphological distinctions between them.

Conclusions

Ontogenetic evidence has enhanced the present phylogenetic analysis by increasing the number, clarity, and diversity of characters and character states. Also, ontogenetic evidence has been used here to polarize character states, since the states are shown in many cases, by direct observations, to be developmentally successive. We have shown that both outgroup and ontogenetic polarization result in the same tree, which vindicates the latter as a legitimate method of polarization. Ontogenetic analysis also helps to resolve homologous characters when the ontogenetic processes associated with the mature morphologies are compared. This results in a lower number of homoplastic characters and a more logically sound phylogeny. The developmental data are particularly useful in this case because the genera are developmentally distinctive on the basis of qualitative characteristics; discovery of relevant useful developmental data may be less practicable where genera are not as distinct developmentally or where differences are quantitative or heterochronic only.

Ontogenetic analysis provides new light on the relationships within Piperales. Piperaceae and Saururaceae appear to represent distinct but related monophyletic evolutionary lines when floral, inflorescence, and vascular characters are cladistically tested. We demonstrate that many of the mature floral morphologies that appear similar within the order are due to convergences, based on evidence from ontogenetic analysis and from the fact that similar-appearing floral morphs appear at different points in the tree based on non-ontogenetic characters.

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**LITERATURE CITED**


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The Rupert Barneby Award

The New York Botanical Garden is pleased to announce that Mr. David Clarke, of the University of Illinois, Urbana is the recipient of the 1992 Rupert Barneby Award. Mr. Clarke will use the award to complete a taxonomic treatment of Acacia series Gummiferae of the Caribbean, both as part of his graduate thesis and as a contribution to the Flora of the Greater Antilles.

The New York Botanical Garden also invites applications for the 1993 Rupert Barneby Award. The award of $1000.00 is to assist researchers planning to come to the New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought, and how the collection at NYBG will benefit their research. Travel to NYBG should be planned between January 1, 1994 and January 31, 1995. The letter should be addressed to Dr. Enrique Forero, Director, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126 USA, and received no later than December 3, 1993. Announcement of the recipient will be made by December 17. Anyone interested in making a contribution to THE RUPERT BARNEY FUND IN LEGUME SYSTEMATICS, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Forero.