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Floral Morphology and Phylogeny of Vochysiaceae

by

Amy Litt

A dissertation submitted to the Graduate Faculty in Biology in partial
fulfillment of the requirements for the degree of Doctor of Philosophy,
The City University of New York

1999

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Abstract

FLORAL MORPHOLOGY AND PHYLOGENY OF VOCHYSIACEAE

by

Amy Litt

Advisors: Scott A. Mori, Ph. D. and Dennis W. Stevenson, Ph.D.

Traditionally Vochysiaceae have been divided into two tribes, Erismeae and Vochysieae. Vochysieae include five Neotropical genera, whereas Erismeae include one Neotropical genus (Erisma) and the only Paleotropical member of the family (Erismadelphus). Studies of floral structure indicated that the tribes were based on poorly understood characters, and that some of the genera were not well defined, therefore a phylogenetic analysis of Vochysiaceae was undertaken to clarify relationships within this family. Chapter one of this dissertation includes background information on Vochysiaceae and a brief taxonomic history. Chapter two covers floral development, in particular with reference to the structure of the gynoecium. Chapter three includes developmental and anatomical information regarding the position of the single fertile stamen. The final chapter presents the results of the phylogenetic analysis.

The work presented here shows that the single fertile stamen, described as being antesepalous or antepetalous in different genera, is fundamentally antepetalous throughout the family, although in one clade it is unique in being slightly offset. The results also clarify

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several elements of gynoecium structure among the genera, in particular the number of locules and the position of the ovary. Regarding the latter, the work presented here shows that although the position of the ovary does vary, it is always initiated in an inferior position, on a concave floral apex.

The results of the phylogenetic analysis bear out the hypotheses that the tribes and genera as currently recognized are not all monophyletic. The species form three clades, but the relative positions of these clades are unresolved. One clade consists of the Erismeae, with *Erismadelphus* as sister-group to *Erisma*. A second group comprises *Vochysia*, with the monotypic *Salvertia* nested within. The third group includes *Qualea*, with *Ruizterania* and *Callisthene* nested within. These latter two clades include the members of Vochysieae, thus these results do not support the monophyly of that tribe. They also indicate that *Salvertia*, *Ruizterania*, and *Callisthene* can not be recognized as distinct genera.

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To my mother, and
to my father.

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Table of Contents

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List of Tables

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List of Figures

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Chapter 1

Introduction

I. Brief description

The flowers of Vochysiaceae are easily recognized by their bilateral symmetry, spurred calyx, and single fertile stamen. Most also have fewer than five petals. The seven generally recognized genera are distinguished by ovary position (inferior or superior and surrounded by a short hypanthium) and petal number (five, three, one), and in some cases by details of floral, fruit, or vegetative structure. They are all woody and nearly all trees, often extremely tall, with opposite or whorled stipulate simple leaves. The genera range in number of species from Salvertia, with one, to Vochysia, with more than 100. The family is largely confined to tropical South America, with a few species extending into Central America and even into the Yucatán. The only genus found outside of the Neotropics is Erismadelphus (two species), from western Africa. Vochysiaceae are found in rain forest and savanna; some genera (Vochysia, Qualea) have species in both, whereas other genera are confined to either rain forest (Erisma, Erismadelphus) or savanna (Callisthene).

Vochysiaceae are a dominant element of the South American savanna vegetation, and some of the species of that habitat are being studied for their aluminum accumulating abilities (Felippe and Dale 1990); however, the family has attracted little attention. Species have not been successfully cultivated as ornamentals.

II. Uses

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Cronquist (1981) said of Vochysiaceae: "None of the species is of much economic importance or especially well known to botanists generally." Stafleu agreed, noting that "*Salvertia convallariodora* St. Hil. is of no use whatsoever, and the same is true of most species of *Vochysia*" (Stafleu 1948); he made similar statements regarding the other genera as well (Stafleu 1952, 1953, 1954). Some species are used locally for sundry purposes, but none is exploited on a commercial scale except to a small extent for their wood. Species of *Vochysia* and *Qualea* are used for timber or lumber (e.g. Stevenson and Stevenson 1925; Francis 1926; Stafleu 1948 and references therein, 1953; Hess et al. 1950; Chant 1978; Flores 1993), and have been important in reforestation schemes (e.g. Butterfield 1994). Wood of *Callisthene fasciculata* and other savanna species of Vochysiaceae is used for charcoal (Stafleu 1952 and B. Walter, pers. comm.).

There are few and rather varied documented local medicinal uses of Vochysiaceae. In parts of Brazil, leaf extracts of *Q. grandiflora* and *Q. multiflora* are used to treat diarrhea, and *Q. acuminata* is used to treat worms (Elisabetsky & Posey 1994). The bark and leaves of *V. ferruginea* are used by the Kubeo Indians of Colombia to wash sores, and various parts of *V. laxiflora* are employed by several Indian groups in Peru to treat asthma, painful urination, and sores (Schultes 1977). The leaves and bark of *V. lomatophylla* apparently were used by the Barasana Indians of Peru as a contraceptive (Altschul 1970; Schultes 1977, 1987), but this practice has been discontinued. In the cerrado of central Brazil, exudate of *Q. grandiflora* is used to cover and protect small cuts and scrapes (pers. obs.).

There are few other documented uses of Vochysiaceae species, and it is not clear how many of these practices are still followed. Saint-Hilaire (1820) reported that the bark of savanna species of *Qualea* was

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used by inhabitants of Minas Gerais to make a dye. In southeast Brazil the sap of V. tucanorum was fermented to make a kind of wine (Stafleu 1948), and the bark of V. columbiensis was used by the Kabuyarí Indians as the primary ingredient in a potent arrow poison (Schultes 1977, 1987). The oil of the seeds of several species of Erisma have been used for a variety of purposes including soap-making, livestock feed, margarine additive, and industrial uses (Pesce 1985). In the past the seeds of Erisma japura were pounded and fermented by indigenous people in Amazonian Venezuela and Colombia to make a nutritious, highly prized, and strong smelling "cheese" (Dufour and Zarucchi 1979; Berry and Aymard 1997). With the availability of packaged foods, however, this practice has apparently been all but abandoned (P. Berry pers. comm.).

III. Taxonomic history

The taxonomic history of Vochysiaceae begins in 1775 with the description by Aublet of Vochy guianensis. The name of the genus is derived from a common name and was latinized three separate times. "Vochya" was published in 1788 by Vandelli, "Vochisia" in 1789 by Jussieu (although this was actually written in 1774), and "Vochysia" by Poiret in 1808. This last spelling is listed as a conserved name (Reg. Int. Nom. Bot. art. 20, cited in Stafleu 1948), but in that listing is incorrectly attributed to Jussieu. As a result there was some disagreement as to whether the conserved name was intended to be Vochisia Juss. or Vochysia Poir., and both were used (refs. in Stafleu 1948). In his revision Stafleu (1948) noted, however, that most authors of species in that genus used Vochysia Poir., and he concluded that these were the intended orthography and attribution.

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Qualea was also described by Aublet in 1775, and Erisma by Rudge in 1805. Saint-Hilaire (1820) described the family Vochisiée and included both Vochisia (his spelling), Qualea, and Salvertia, which he also described in that publication. Martius (Martius and Zuccarini 1824) included Erisma in Vochysiaceae, and was the first to use this spelling for the family. In this publication Martius described Callisthene and Amphilochia, and included them in the family as well. In 1828 Candolle divided the genera within the family into two groups based on having a free (Vochysia, Qualea, Amphilochia, Callisthene, Salvertia) or adherent ovary (Erisma), and Dumortier (1829) recognized and named these groups as two tribes: Vochysieae (free ovary) and Erismaceae (adherent ovary)(= Erismeae).

The next major contribution to Vochysiaceae taxonomy was Warming's treatment for Flora Brasiliensis (1875). In this monograph he included Amphilochia as a series within Qualea. He therefore recognized five genera within the family: Vochysia, Salvertia, Qualea, Callisthene, and Erisma. Within Vochysia he recognized five series. Salvertia included only Salvertia convallariodora; the only other described species was S. thyrsiflora Pohl, which Warming judged to be a monstrosity. Qualea was subdivided into three series, one of which was Martius's genus Amphilochia. The other genera recognized by Warming, Callisthene and Erisma, were each subdivided into two sections.

Trigonia was described by Aublet in his Histoire des Plantes de la Guiane Française (1775). Martius (1835) recognized the family Trigoniaceae, but Bentham and Hooker (1867) and Baillon (1878) included Trigonia in Vochysiaceae. Warming monographed Trigoniaceae in Flora Brasiliensis (1875), and since that treatment most taxonomists (e.g. Peterson 1897; Bessey 1915; Benson 1959; Hutchinson 1969; Stebbins 1974; Cronquist 1981; Takhtajan 1997) have recognized that Trigonia

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does not belong in Vochysiaceae. As currently understood, Trigoniaceae includes *Trigonia* and two monotypic genera: *Trigoniastrum* Miq. from Malaysia and *Humbertiodendron* Leandri from Madagascar.

Euphronia was described in 1824 (Martius and Zuccarini 1824). *Lightia*, a synonym for *Euphronia*, was published by Schomburgk (1847), who included it in Vochysiaceae. Bentham and Hooker (1867) and Baillon (1878) also included *Lightia* in Vochysiaceae, with affinities to *Trigonia*. Warming (1875) included *Lightia* with *Trigonia* in his treatment of Trigoniaceae, and *Lightia*/*Euphronia* remained there until Lleras (1976, 1978) monographed Trigoniaceae for Flora Neotropica. He recognized the synonymy of *Lightia*, and transferred *Euphronia* to Vochysiaceae. Marcano-Berti (1989) erected the monotypic family Euphroniaceae to accommodate the genus. Litt and Chase (1999), using *rbc*L DNA sequence data, showed the affinities of *Euphronia* to be with Chrysobalanaceae, Dichapetalaceae, and Trigoniaceae, not with Vochysiaceae, and agreed with Marcano-Berti that is is best recognized as a separate family.

Two more genera were added to Vochysiaceae in this century. In 1913 Mildbraed published *Erismadelphus*; this genus from western Africa is the only member of the family not found in the Neotropics. Marcano-Berti (1969) created a new genus by segregating Stafleu's sect. *Trichanthera* of *Qualea* and publishing it as *Ruizterania*. Thus the family currently comprises two tribes and seven genera: Erismeae (*Erisma*, *Erismadelphus*), and Vochysieae (*Vochysia*, *Salvertia*, *Qualea*, *Callisthene*, *Ruizterania*).

Vochysiaceae were last monographed as a family by Stafleu (1948, 1952, 1953, 1954; Keay and Stafleu 1953), who recognized most of Warming's infrageneric subdivisions but changed the ranks of some and addded a few others. Since then *Callisthene* (Martins 1981) and *Erisma*

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(Kawasaki 1998) have been revised, and Ruizterania has been segregated from Qualea and monographed (Marcano-Berti 1969). No other major taxonomic work has been undertaken.

In Aublet's description of Vochy guianensis (1775) he referred the species to "Diandria, Monogynia" following the Sexual System of Linnaeus ("Diandria" referring apparently to a single filament with two anthers, see Stafleu 1948). Jussieu (1789) placed Vochisia in "Polypetalae germine superior" and Poiret (1808) felt the affinities were uncertain. Various authors subsequently suggested affinities with Clusiaceae (leaf venation), Combretaceae (convolute cotyledon), Onagraceae (perigyny/epygyny), Rosaceae (Chrysobalanaceae; zygomorphy), and Geraniaceae (spur)(e.g. Saint-Hilaire 1820; Candolle 1828; Meyer 1825; Payer 1857; Bentham and Hooker 1862). Clarke (1859), looking at floral structure, rejected a relationship with Onagraceae, Combretaceae and "the epigynous families." Other authors pointed out the differences in floral structure between Vochysiaceae and Clusiaceae and rejected that relationship (e.g. Saint-Hilaire 1820; Meyer 1825). Baillon (1878) described the relationship to Geraniaceae as one of analogy rather than affinity.

At the same time, many authors pointed to Polygalaceae as having close affinities with Vochysiaceae (e.g. Saint-Hilaire 1820; Meyer 1825; Lindley 1853; Baillon 1878). Since the turn of the century and the focus on "natural" systems of classification, the relationship of Vochysiaceae to Polygalaceae and in particular to Trigoniaceae in the order Polygalales has been undisputed (e.g. Bessey 1915; Benson 1959; Hutchinson 1969; Stebbins 1974; Cronquist 1981; Dahlgren 1980; Thorne 1992). Takhtajan (1997) differed only in placing five families generally included in Polygalales - among them Vochysiaceae and Trigoniaceae - in the order Vochysiales. In his system, Polygalaceae

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and two monotypic families (Xanthophyllaceae and Emblingiaceae) comprise Polygalales, a related order.

Polygalales (in the sense of Cronquist 1981) is a heterogeneous order of families with 5-merous, generally hypogynous, zygomorphic flowers. Several of the families are small and have confined or disjunct distributions (e.g. Xanthophyllaceae, one genus, Indomalaysia; Trigoniaceae, three genera, one each in S. America, Madagascar, Malaysia). Cronquist (1981) stated that "the mutual affinity of 5 of these families [including Vochysiaceae, Trigoniaceae, and Polygalaceae] has been widely accepted." However, an examination of his description of the order indicates that there are neither specific features, nor is there even a suite of overlapping features, that unite and distinguish the families in this order. He stated, for instance, that petals are "distinct... or connate at the base, or only some of them connate," that anthers dehisce by "longitudonal slits or by terminal or subterminal pores or short slits," and that a nectary-disk is "extrastaminal in Tremandra, otherwise intrastaminal or opposed to the stamens or wanting." Thus it is difficult to find a concrete basis in descriptions of morphology for concluding that these families are related. However, none of them have clear affinities to any other families, and thus there was no obvious alternative position.

Molecular data have proved particularly useful for generating hypotheses regarding relationships of families and genera such as those that have been included in Polygalales, that is, taxa that have no obvious affinities with any other group. Studies using rbcL, atpB, and rbcL with 18S rDNA and atpB (e.g. Chase et al. 1993; Chase and Albert 1998; Soltis et al. 1999; Savolainen et al. 1999; Soltis et al. submitted) have indicated that the affinities of Vochysiaceae lie not with the zygomorphic, oligostemonous taxa of Polygalales, but with the

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actinomorphic, polystemonous Myrtales. More in-depth analyses of relationships within Myrtales, using rbcL, matK, and ndhF (Conti et al. 1996; Conti et al. 1997; C. Quinn, P. Gadek, and P. Wilson, pers. comm.; K. Sytsma pers comm.) have indicated that Vochysiaceae are the sister-group of Myrtaceae, and the clade formed by these two families is most closely associated with Melastomataceae. Other families in Polygalales are scattered on the phylogenetic tree, and none are close to Vochysiaceae (Chase et al. 1993; Chase and Albert 1998; Soltis et al. 1999; Savolainen et al. 1999; Soltis et al. submitted).

Over 100 years ago affinities with myrtalean families had been suggested (see e.g. Candolle 1828 and discussions in Saint-Hilaire 1820 and Baillon 1878) largely on the basis of the perigyny/epigyny in Vochysiaceae and the common occurrence of these morphologies in Myrtales. Nonetheless as more evidence, particularly of floral structure, was taken into account, this position was rejected or at least neglected. As a result of the analyses with rbcL, this hypothesis has been re-examined. This process of reciprocal illumination has brought to light some shared features that had gone unnoticed or had been ignored, for instance Vochysiaceae have bicollateral bundles and vestured pits, a combination of characters nearly unknown outside Myrtales (Metcalfe and Chalk 1950; Quirk 1980). Ingle and Dadsworth (1953), considering only families with vestured pits, state that a particular combination of wood characters (vessels predominately in multiples, paratracheal, confluent parenchyma, heterogeneous rays, and scalariform vessel-ray pitting) is present only in Melastomataceae, Lythraceae, Myrtaceae, and Vochysiaceae. In addition, Tobe and Raven (1983) identified a suite of seven embryological features that characterize Myrtales; preliminary information and observations indicate that these are all present in

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Vochysiaceae (Boesewinkel and Venturelli 1987; Carmo-Oliveira pers. comm.; pers. obs.).

Nonetheless, reconciling the apparent dramatic difference in floral structure between Vochysiaceae and Myrtaceae is daunting for many taxonomists. One obvious similarity is the epigynous and perigynous floral structure in Vochysiaceae, but there are also obvious differences, including zygomorphy, the reduction in floral parts, and the absence of a nectary disk in Vochysiaceae flowers. Additional floral similarities may be sought at the levels of development, anatomy, and histology, but there is ample evidence from embryology and wood anatomy to support the hypothesis presented by the DNA data.

IV. Questions

This study was undertaken to gain a better understanding of floral structure and phylogenetic relationships within Vochysiaceae. Preliminary work indicated that there were several points of floral morphology that needed clarification. First was the position of the single fertile stamen: the observation that it varied among genera indicated that the presence of a single stamen in different genera might be the result of independent reduction events. Second was the structure of the gynoecium in the family; there were hints that in some genera the position and the number of locules had been misinterpreted. The position of the gynoecium became even more interesting with the hypothesis that Vochysiaceae are myrtalean, which indicated that they might have an epigynous ancestry. These issues are addressed in chapters two and three.

The segregation of Ruizterania by Marcano-Berti, the uncertain position of Euphronia, and the lack of clear boundaries between, for instance, Qualea and Callisthene, indicated that a phylogenetic

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analysis was in order. Such an analysis had been performed for the family by Kawasaki (1992), but she accepted generic boundaries as given. The current analysis, presented in chapter four, attempted to answer questions regarding generic boundaries and relationships using newly acquired and reinterpreted morphological information as well as DNA sequence data. The results of the analysis are also used to discuss hypotheses of character evolution within the family.

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Chapter 2

Floral development and morphology of Vochysiaceae I. The structure of the gynoecium.

Vochysiaceae, a small family of tropical trees, are known for their distinctive and beautiful flowers. The flowers are strongly zygomorphic, with a spurred calyx, a single fertile stamen, and most often a reduced number of petals (Fig. 1). The family is confined to the New World with the exception of one small west African genus (Erismadelphus). Until recently, Vochysiaceae were placed in Polygalales (Hutchinson 1969; Stebbins 1974; Dahlgren 1980; Cronquist 1981; Thorne 1992), a group of families that are characterized by unusual zygomorphic flowers. Phylogenetic analyses based on rbcL sequence data first indicated that this order is polyphyletic and that Vochysiaceae are most closely related to Myrtaceae (Chase et al. 1993; Conti et al. 1996; Conti et al. 1997; Chase and Albert 1998). This unexpected position is supported by additional molecular data sets (Soltis et al. 1999; Soltis et al. submitted; C. Quinn, P. Wilson and P. Gadek, pers. comm.; K. Sytsma pers. comm.), as well as by a suite of anatomical, embryological, and developmental characters (Conti et al. 1997).

Taxonomists have recognized seven or eight genera in Vochysiaceae (Table 1). Recent analyses indicate that Euphronia is more appropriately allied with Chrysobalanaceae (Litt & Chase 1999), and it will not be discussed here. The other seven genera are grouped into two tribes that differ in characters of the ovary and fruit (Dumortier

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1829; Stafleu 1952)(Table 1). According to published descriptions, Vochysieae (Vochysia, Salvertia, Qualea, Callisthene, and Ruizterania, a segregate of Qualea) have a superior trilocular ovary that develops into a loculicidal capsule, whereas Erismeae (Erisma and Erismadelphus) have an inferior unilocular ovary that matures into an indehiscent winged fruit.

Vochysiaceae flowers are unusual, but the placement of the family as sister-group to Myrtaceae raises even more questions about the morphology and evolution of these flowers. Whereas flowers of Myrtales are generally actinomorphic, and those of Myrtaceae in addition often have numerous stamens, those of Vochysiaceae are decidedly zygomorphic (or even asymmetrical) and have a single - frequently large - fertile stamen. Thus there is little obvious morphological common ground between the two families. However, the inclusion of Vochysiaceae in Myrtales casts the inferior ovary of Erismeae in a new light, as epigyny is characteristic of the order and of Myrtaceae, the putative sister-group. This indicates that the superior ovary of Vochysieae may be secondarily derived. Relatively few examples of such independent derivations of a superior ovary are documented (e.g. Eyde & Tseng 1969; Igersheim et al. 1994; Chase et al. 1995; Gustafsson & Albert in press; R. Kuzoff pers. comm.).

A review of the literature also raised an additional question about the gynoecium of Erismeae. Whereas the ovary of both genera (Erisma and Erismadelphus) has a single locule, Kopka and Weberling (1984) reported additional aborted locules in cross-sections of floral buds of Erismadelphus but not of Erisma. This indicated that the unilocular ovaries of the two genera might not be equivalent, and that the character might not be a synapomorphy of the Erismeae. Their study was limited, however, and included neither observations of development

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nor extensive sampling. Thus it seemed appropriate, in light of this information on the relationships and the floral structure of Vochysiaceae, to examine floral development, anatomy, and morphology in this family.

In this paper I report my observations of floral development and vascular anatomy in Vochysiaceae. In particular I attempted to determine: (1) whether there is evidence that more than one carpel is involved in the development of the gynoecium in *Erisma* and *Erismadelphus*, and (2) if there is anatomical or morphological evidence that the ovary of Vochysieae is not homologous with the superior ovaries of other taxa. The development and vasculature of the corolla and androecium are the topic of chapter three.

MATERIALS AND METHODS

I. Taxa

Floral buds of five genera were used (Table 2). Suitable material of *Salvertia* and *Ruizterania* was not available, however phylogenetic analyses based on morphological and molecular data indicate that *Salvertia* may not be taxonomically distinct from *Vochysia*, nor *Ruizterania* from *Qualea* (from which it was segregated; Marcano-Berti 1969)(chapter four). Furthermore, *Salvertia* and *Ruizterania* do not differ from *Vochysia* and *Qualea* respectively in features of the gynoecium. Thus I assume that in these two genera the development and the vasculature of the ovary do not differ significantly from what is observed in *Vochysia* and *Qualea*, respectively.

General descriptions of the flowers of the five genera included in the study follow. All have a complete whorl of five sepals, one of which (the fourth) bears a spur or enlarged sac at the base, and all have a single fertile stamen. The genera vary in features such as petal number and relative sepal size, as well as in the features that define the two tribes.

A. Vochysieae: The flowers of the genera in this tribe (*Vochysia*, *Salvertia*, *Qualea*, *Ruizterania*, *Callisthene*) are described as perigynous (St.-Hilaire 1820; Warming 1875; Baillon 1878; Stafleu 1948), the floral organs being inserted on a short hypanthium that surrounds the superior, trilocular ovary. Flowers of *Vochysia* (100+ species) almost always have 3 petals (Figs. 1, 2), although a very few species (none included in this study) have one or none. The fourth sepal is approximately four times the length of the others. The fertile stamen is on the line of symmetry, in front of the middle petal; two staminodes are nearly always present and are in front of the two lateral petals. The ovary contains two ovules in each of the three locules. Flowers of *Salvertia* (one species, not included in this study) differ in having five petals, and sepals that are nearly equal in size.

The remaining three genera of Vochysieae (*Qualea*, *Ruizterania*, *Callisthene*) each have one petal, although in some species of *Qualea* (50 species) there are in addition two minute rudimentary petals (Fig. 2). The fertile stamen is not directly in front of the petal but is slightly offset towards the fifth sepal, and these flowers are asymmetrical (Fig 2, 33). Two staminodes in antepetalous positions are present in some species of *Qualea* and *Ruizterania*. Each of the three locules of the ovary contains numerous ovules. *Ruizterania* (13 species, not included in this study) and *Callisthene* (8 species) differ from *Qualea* in features of anther ornamentation, and of fruit dehiscence and seed shape, respectively (Stafleu 1952, 1953; Marcano-Berti 1969; Martins 1981)(Table 1).

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B. Erismeae: The flowers of the two genera in this tribe are epigynous, although the ovary is free on the spurred side of the flower in Erismadelphus and some species of Erisma. The ovary is described as unilocular (Stafleu 1954; Kopka and Weberling 1984; Kawasaki 1998). Erisma (16 species) flowers have one petal, although there may also be up to four rudimentary petals (Fig. 2). The fertile stamen is in front of the petal (on the line of symmetry). Staminodes (most often two) are also common and antepetalous. The single locule of the gynoecium contains two ovules. Erismadelphus (2 species) differs in having five petals (Fig. 2) and only one ovule (Keay & Stafleu 1953). The spur in Erismadelphus is particularly broad and sac-like, so that the ovary is free for perhaps a third of its circumference (Fig. 41, 42).

II. Procedures

With the exception of the buds of Erismadelphus, all material was fixed in the field in FPA and stored in 70% ethanol. Material of Erismadelphus was obtained from herbarium specimens (Table 2), rehydrated in 10% Aerosol, fixed in FPA, and stored in 70% ethanol.

Material for scanning electron microscopy was dissected in 95% ethanol, dehydrated in an ethanol/acetone series, critical point dried, sputter coated with gold/palladium, and viewed at 5 kv with a JEOL 5410LV. Material for serial sectioning was dehydrated in an ethanol/toluene series, embedded in paraffin, and sectioned with a microtome at 10-15u. Buds that were particularly difficult to section were softened by exposing their tips in the paraffin block and soaking them for at least one week in 2:5 glycerin:ethanol (70%) with acetic acid added to 10% of the total volume. Material that was particularly rich in tannins was treated with Stockwell's bleach (Schmid 1977) before staining. All material was stained with Johannson's safranin

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and counterstained with chlorazol black E, fast green followed by orange G, or astra blue. All available species of *Qualea*, *Callisthene*, *Erisma*, and *Erismadelphus* were used (Table 2). Species of *Vochysia* were chosen to represent as many of Stafleu's taxonomic sections and subsections as possible given the available material. Drawings of selected sections were made using a camera lucida.

The available material of *Erismadelphus* was not suitable for scanning electron miscroscopy thus for this genus only serial sectioning data are available. SEM data are also available only for a very few stages of development of *Callisthene*. Relatively complete series of developmental and anatomical data were obtained for multiple species of *Qualea*, *Vochysia*, and *Erisma*.

RESULTS

Floral development and vasculature are described below for the taxa used in this study. Details of the development and vasculature of the corolla and androecium are presented in chapter three. Interpretations of the organization of Vochysiaceae flowers are complicated by the fusion and (where they are free) extensive overlap of the sepals, the reduction of the corolla and androecium, and, in *Qualea* and *Callisthene*, the slant of the receptacle. This last can be seen in longitudonal sections of buds, which show that the ovary and the base of the flower are lower (relative to an imaginary line drawn perpendicular to the pedicel) on the spurred side than on the opposite side (Fig. 45). Thus cross-sections taken near the base of the flower frequently contain oblique sections of the ovary. In dissections this tilt of the base of the flower and of the ovary complicates efforts to locate the horizontal plane and the center of the floral apex.

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The term "hypanthium" is used to refer to a free floral cup surrounding an ovary (a perigynous flower), and is also used by some authors to denote the outer layers of tissue surrounding the inferior ovary of an epigynous flower (e.g. Eames 1961). This latter usage leads to confusion, and implies homology of the outer tissue layers surrounding the inferior ovary to the free floral cup. This homology is commonly accepted among morphologists, but generally can not be proven, thus in this discussion I will restrict the use of the term to the floral cup of a perigynous flower.

I. Organogenesis

General aspects of floral development will be presented below, followed by descriptions of the development of the gynoecium.

A. Calyx. In all taxa the five sepals are initiated in a 2/5 spiral, clockwise or counterclockwise (Figs. 3, 4). The floral apex becomes noticeably concave with the initiation of the sepals and remains so throughout the remainder of floral development, although it may be relatively flat in some *Qualea* species (Fig. 9). The sepals broaden rapidly. Aestivation is quincuncial, although this pattern may become partly obscured as the extent of overlap of the sepals increases. In almost all Vochysiaceae the fourth sepal is overgrown by the fifth and completely surrounds the inner organs; in *Vochysia*, *Ruizterania*, and some species of *Callisthene*, it is also significantly longer than the other four sepals, which are subequal in size.

In most taxa the first two sepals are free to a greater extent than the other three, which is related to the fact that the spur, which is at the base of the fourth sepal, emerges between the first two (Fig. 2, 27, 28). There is disagreement in the literature as to the nature of the spur. Historically it has been described as an outgrowth of the

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fourth sepal (e.g. Candolle 1828; Warming 1875; Stafleu 1952; Cronquist 1981), whereas Kopka and Weberling (1984) interpreted it as an extension of the floral axis. Recent work has shown that the spur develops in a position that is ambiguous and can not be unequivocally designated receptacle as opposed to calyx (R. Carmo-Oliveira, pers. comm.). However in species of *Qualea* the first and second sepals, which flank the fourth, are inserted below the level at which the spur emerges. In some species these sepals enclose the spur until anthesis. Furthermore, the spur abscises with the calyx (pers. obs. and P. Oliveira, pers. comm.). These lines of evidence support the hypothesis that the spur is part of the calyx, not the floral axis.

The sepals of several species of *Qualea* and *Callisthene* were observed to have small triangular, claw-like structures at their tips which do not enlarge as the sepals grow and are thus inconspicuous at maturity (Fig 5). These structures, possibly glandular, were also observed at the tips of young leaves and bracts in these species (see also Martins 1981).

The sepals of the two species of *Callisthene* bore structures at the base of their adaxial surfaces that are reminiscent of colleters (see also Martins 1981)(Fig. 6). In *C. major* they are small and roughly triangular, whereas in *C. fasciculata* they are elongate, in some cases reaching the tip of the sepal. These flattened structures, also possibly glandular, were irregular in number and shape, and were also found between the petiole and the axis (Figs. 7, 8).

B. Corolla and androecium. Petals are initiated when the sepals (at least the first three) are already quite large and broadly overlapping (Fig. 9, 10). Stamen initiation occurs when the petal primordia are still relatively small. In most species the petals and stamen/staminodes arise on the vertical flank of the floral cup, and in

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early stages the organs, particularly in *Vochysia* and *Erisma* species, grow horizontally (Fig. 11) and perpendicular to the surface on which they insert. As the organs enlarge and the ovary begins to elongate, the petals and stamen/staminodes become more vertically oriented (Fig. 12). Vochysiaceae anthers are characterized in general by a relatively massive connective, and the style lies between the two thecae. In *Vochysia* the connective also forms a conspicuous, large-celled cap over the stigma (Fig. 13).

The position of the thecae on either side of the style is important in the secondary pollination presentation of *Vochysia* (Yeo 1993; Oliveira 1998). In all species observed so far, the anthers shed their pollen onto the style before anthesis. As the bud opens, the stamen abscises or is broken off at the base and falls out of the flower, leaving the exserted style (but not the stigma) covered with pollen.

It is common in the development of Vochysiaceae flowers for considerable packing and twisting to occur within the developing buds. It is not unusual for the style and/or the filament to be curved, for the anther to become bent at an angle relative to the filament, or for the single petal of *Erisma* and *Qualea* species to be highly crumpled in bud. The limbs of staminodes and lateral or rudimentary petals are generally displaced, presumably to maximize space-packing efficiency (Fig. 12). In open flowers of many species the style and filament are strongly twisted, variably in some species (e.g. *Ruizterania cassiquiarensis*) and predictably in others (e.g. *Qualea grandiflora*).

C. Gynoecium: In all taxa the gynoecium is first visible, after all other floral organs have been initiated, as a ring primordium on the floral apex (Figs. 14, 17). Early development is similar in all species, and differences among the taxa do not become apparent until

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near maturity when the difference in ovary position between Erismeae and Vochysieae becomes apparent.

1. Vochysia, Qualea, and Callisthene (Figs. 14-16) - The opening at the center of the ring primordium is roughly triangular (Fig. 14), and in most species observed it becomes distinctly three-lobed as development progresses (Fig. 15, 16). Eventually the opening closes to a three-pronged slit at the apex of the style.

2. Erisma (Figs. 17, 18) - A ring primordium is formed as well, but the opening in the center is oval or round (Fig. 17). As development proceeds, it narrows to a longitudonal slit (Fig. 18). In other features the development of the inferior ovary of Erisma is indistinguishable from that of the ovary of Vochysia, Qualea, and Callisthene.

II. Vasculature

The following descriptions are based on serial sections, presented here in acropetal sequence. General observations of floral vasculature and anatomy will be presented, followed by descriptions of the vasculature of the gynoecium.

In all species of Vochysiaceae the floral vasculature, which has the internal phloem characteristic of the vasculature of the vegetative structures of this family, is derived from a cylinder of vascular tissue in the pedicel. Medullary bundles were observed in Vochysia, Erisma, and Erismadelphus (Fig. 19); these anastomose with the vascular cylinder or in some cases contribute to the vasculature of the gynoecium. In the base of the flower the vascular cylinder separates entirely into or splits off discrete bundles that supply the floral organs (Fig. 20, 21, 28, 34). These bundles travel through the hypanthium (in Vochysieae) or the outer layer of the ovary/floral cup

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(in Erismeae) to enter the sepals. In Qualea, Callisthene, and Erisma, all of which have one petal, one bundle branches to supply the petal and the fertile stamen (Figs. 30-32, 37, 38). Rudimentary petals and staminodes, when present, were not observed to contain vascular tissue. In Vochysia and Erismadelphus, with two staminodes and three and five petals respectively, three or five of the "floral cup" bundles branch to supply the petals and stamen/staminodes (Figs. 23, 24, 42, 43).

Vochysiaceae flowers are characterized by several other features that were observed in serial sections; in general these structures have not been included in the figures. These include gum canals, found in the pedicel and often in the sepals (V. tucanorum, V. pumila, all Qualea species except Q. dichotoma, and E. bracteosum)(Fig. 19), and crystals, found in all organs (all species except possibly absent from Q. rosea, E. floribundum, and E. uncinatum). Simple intra-ovarian hairs were seen in Erismadelphus exsul and all species of Erisma, as well as in Qualea mori-boomii and Q. lineata. In all species, densely staining cells line the inner surface of the nectary spur and are also found in the outer tissue of the ovary; they are also seen in the outer cells of the sepals and other organs in some species. Additional densely staining cells surrounding the apparent stylar canal in all species were identified as transmitting tissue. An epidermal layer of large, non-staining cells was seen in the connective of all species (see Fig. 13).

A. Vochysieae gynoecium: In all species of Vochysieae the vascular cylinder of the pedicel produces branches that enter the hypanthium (or the sepals directly), and the remainder of the cylinder supplies the gynoecium (Figs. 20-22, 28, 29). In most cases the vascular tissue that enters the gynoecium forms three dorsal carpel bundles and three major lateral carpel bundles. These latter are

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located at the outer edge of each of the three septa and may be as large or larger than the dorsal bundles (Figs. 22, 23, 29, 30). There are arcs of numerous small bundles between these that form an anastomosing network that supplies the ovary wall. In most species the major lateral bundles divide, each producing a bundle that travels through the septum to lie at its inner margin (Figs. 22, 29). These ventral carpel bundles supply the ovules of the two adjacent carpels.

1. *Vochysia* (Figs. 19-25) - There was no significant variability observed in the species of *Vochysia*. In cross-section the ovary is three-lobed; the sulci mark the center of the locules, where the fruit will dehisce (Fig. 24). The ovary is slightly adherent to the floral cup at its base: the locules extend below the level at which the ovary becomes completely free from the surrounding tissue (Figs. 21, 22). Thus, the vasculature to the gynoecium becomes organized at the same level at which branches are being supplied to the floral cup. In *Vochysia*, the bundles at the inner end of each septum come together to form a ring in the center of the gynoecium (Fig. 23), which then separates into three bundles that lie one in front of each locule. These bundles supply the two ovules of each locule (Fig. 24). The three major lateral bundles and the three smaller dorsal bundles continue into the style (Fig. 25).

2. *Qualea* and *Callisthene* (Figs. 28-33) - In cross-section the ovaries of these genera are more-or-less circular and unlobed (Figs. 30, 31, 33). There is no evidence that the locules extend below the level at which the ovary is free from the surrounding floral cup, as in *Vochysia*. In both genera the base of the flower and the ovary are mildly to strongly slanted, with the side opposite the spur being higher (Fig. 26). The ovary becomes free on the spur side at a lower level, and thus the vasculature to the ovary also becomes separate from

that of the floral cup at a lower level on that side (Figs. 26, 27). Furthermore the slant of the ovary means that in most species the vascular cylinder can not continue straight up into the ovary but must curve towards the horizontal as the ovary emerges at an angle from the base of the flower (Fig. 26). Thus sections through the ovary often contain vascular tissue that appears to be branching horizontally but in fact is bending to enter the ovary (Fig. 27). The species described below differ in details such as the number of bundles in the style and the configuration of the ventral carpel bundles.

a. Q. parviflora, Q. dichotoma (Figs. 28-30) - There are no significant deviations from the pattern described for Vochysieae. In the ovary wall of Q. parviflora the dorsal carpel bundles are relatively inconspicuous as opposed to the larger major lateral carpel bundles (Fig. 30).

b. Q. lineata, Q. rosea, Q. mori-boomii (Fig. 31) - The origin of the ventral bundles is slightly different in these species in that numerous lateral bundles contribute to them. There is no conspicuously larger major lateral bundle at the outer edge of each septum, as in Vochysia or other Qualea species (Fig. 31). The style of Q. lineata contains a ring of discrete bundles. The three dorsal bundles are conspicuously the largest, with numerous small bundles between. In the style of Q. rosea, which is significantly twisted in the bud, there is a continuous six-pointed ring of vascular tissue. The style of Q. mori-boomii contains only three bundles, the dorsal bundles.

c. C. major - The available material of C. major was not adequate to determine the details of the vascular supply to the gynoecium, however the structure of the flower and the pattern of vasculature in this species is similar to that seen in Qualea.

d. C. fasciculata (Figs. 32-33) - The ovary of this species is

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more elongate and slender than that of other species of Vochysieae that were examined in this study. Although the base of the ovary is slanted, the vascular tissue does not have to curve appreciatively to enter the ovary as it does in *Qualea* species. After the dorsal and major lateral carpel bundles branch off from the vascular tissue in the base of the gynoecium, a triangular mass of vascular tissue remains in the center. This coalesces into a ring that appears to supply the numerous ovules of each of the three carpels (Figs. 32, 33). The major lateral bundles and the dorsal bundles continue into the style.

B. Erismeae gynoecium: In these epigynous flowers the vascular cylinder separates into discrete bundles that travel the length of the ovary and supply the three outer whorls of floral organs. These bundles also produce numerous small branches that form an anastomosing network surrounding the single locule of the ovary (Fig. 37, 41). There is no clearly identifiable dorsal carpel bundle, although in some cases a bundle can be interpreted as such.

1. *Erisma* (Figs. 34-40) - Examination of four species of this genus turned up no evidence of aborted carpels. The shape and orientation of the single locule and details of the vasculature varied among the species examined.

a. *E. bracteosum*, *E. floribundum* (Figs. 34-39) - In these species the spur is inserted at the top of the ovary (Figs. 36-38). The locule is oriented somewhat diagonally in the bud, although it is possibly more symmetrically oriented in *E. floribundum*. The placenta is more-or-less in front of the position of the fifth sepal, or between the second and fifth in *E. floribundum*. This position is either clockwise or counter-clockwise from the spur (used as a point of reference).

The vascular bundles on the adaxial side of the floral bud

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produce small branches that anastomose in the center with some of the medullary bundles. An arc of bundles is thus formed, which coalesces into one bundle that supplies the two ovules (Figs. 34-36). The bundles that form the network surrounding the locule anastomose into a ring of several bundles that enter the style and further anastomose to form three (sometimes four or five) bundles that surround the stylar canal (Figs. 38, 39). In *E. floribundum* the bundles are conspicuously off-center, and this is also variably the case in *E. bracteosum* (Fig. 39).

b. *E. uncinatum* and *E. japura* (Fig. 40) - In these species the spur is inserted at the base of the ovary, thus the ovary is free on that side of the flower (Fig. 40). The locule is symmetrical, lying on the midline of the bud with the placenta in front of the petal (between the third and fifth sepals)(Fig. 40). In *E. japura* the bundle that supplies the two ovules is formed from an arc of bundles in the same way as in *E. bracteosum* and *E. floribundum*. In *E. uncinatum*, one vascular bundle branches from the bundle that will eventually become the median bundle of the fifth sepal; this bundle supplies the two ovules. The small bundles surrounding the locule anastomose to form several bundles that enter the style, but the exact number of bundles in the style could not be determined accurately. One bundle is larger than the others, which form an arc surrounding the transmitting tissue.

2. *Erismadelphus* (Figs. 41-44) - One species, *Erismadelphus exsul*, was available for this study. Examination of serial sections revealed one aborted locule in two of the four specimens available (Figs. 41, 42); this was particularly clear in one specimen. The other two showed no signs of additional locules. The fertile locule is irregularly shaped, although it should be noted that these observations were made on rehydrated herbarium material. In contrast to what was

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seen in Erisma, in which the placenta is in front of the position of the fifth sepal or thereabouts, the placenta in Erismadelphus exsul is in-between the positions of sepals one and three (Figs. 42, 44). As with Erisma, this position may be either clockwise or counterclockwise from the spur.

As the cylinder separates into discrete bundles, one bundle remains separate and supplies the ovule (Fig. 41, 42). There are no bundles occupying the position of a ventral carpel bundle of the aborted carpel.

There is no bundle associated with the fertile locule that can be identified as a dorsal carpel bundle. However, there is a bundle that can be followed into the style in the position where one might look for the dorsal bundle of the aborted carpel. It should be noted, however, that the curve of the style makes tracing this bundle somewhat difficult (Figs. 42, 43). This appears to be the only vascular bundle in the style, although in some specimens this could not be determined.

DISCUSSION

This study was undertaken to provide information on the development and vasculature of the flowers of Vochysiaceae, as well as to answer two questions about the gynoecium: (1) is there evidence of more than one carpel in the gynoecium of Erismeae, and (2) is there evidence that the superior ovary of Vochysieae is secondarily derived? With regard to the first question, our results show that there is at least one additional carpel in Erismadelphus but not in Erisma. Regarding the second question, development and morphology do provide some confirmation that the superior ovary of Vochysieae is independently derived and not homologous with the superior ovaries of

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other angiosperms. These points are discussed below.

Ontogeny of the flowers of Vochysiaceae is basically similar, despite their morphological differences at maturity. The manner in which the organs of all whorls are initiated and the broad outlines of their development are fundamentally similar, whether the ovary is superior or inferior, trilocular or unilocular, or the corolla includes three petals or one. Vasculature is also similar among the genera, the biggest difference being that in the epigynous Erismeae there are no discrete dorsal or other regularly organized carpel-wall bundles as in Vochysieae. Rather there is a network of anastomosing bundles that surround the locule, and which form the bundle(s) that will enter the style (Figs. 37, 38, 42, 43)(as in Hufford 1989). At first glance it may appear that the vasculature of *Qualea* and of *Callisthene major* differs substantially from that of *C. fasciculata* and *Vochysia*, however the observed differences in fact reflect the slant of the ovary in the former species as well as the more slender shape of the ovary of *C. fasciculata*. If the tilt is taken into account it can be seen that in all species of Vochysieae the vascular cylinder of the pedicel enters the gynoecium more-or-less directly, after splitting off branches that will supply the other floral organs.

In a few cases the patterns observed follow established subgeneric taxonomic groupings, although a phylogenetic analysis that will evaluate the monophyly of these groups is in progress (chapter four). *Qualea rosea*, *Q. lineata*, and *Q. mori-boomii* all show similar patterns of vasculature, differing only in the number of bundles in the style. *Qualea mori-boomii* is a segregate of *Q. coerulea* (Marcano-Berti 1989); *Q. coerulea* was included with *Q. lineata* and *Q. rosea* by Stafleu (1953) in his series *Calophylloideae* (section *Qualea*, subgenus *Qualea*)(Table 2) and based on his taxonomy this is also where *Q. mori-*

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boomii would be placed. However, it should be noted that he placed fully 27 of his 59 species in this series (27 of 46 without the segregate genus Ruizterania). Furthermore, the buds and flowers of these three species are larger - considerably larger in the cases of Q. rosea and Q. lineata - than those of Q. parviflora and Q. dichotoma, and this size difference may produce differences in vasculature. Thus the observed similarities in vasculature may reflect evolutionary relationship or may reflect independently derived similarities in floral development or structure.

Stafleu (1954) recognized two sections in Erisma, each including half the species. Erisma japura and E. uncinatum both belong to section Rixa, and E. floribundum and E. bracteosum to section Erisma. The similarities and differences seen in locule and placenta orientation in these species thus conform to Stafleu's notions of relations within the genus. However, a cladistic analysis of the 16 species, based on 21 morphological features, did not show these sections to be monophyletic, and placed E. uncinatum and E. japura in different clades (Kawasaki 1992). Erisma bracteosum and E. floribundum are found in the same clade. Additional work on gynoecium structure in Erisma is needed to determine the pattern of character evolution within the genus and tribe Erismeae.

The data collected also highlight the similarities between Qualea and Callisthene, and accentuate the differences between these two genera and Vochysia, with which they have been allied in tribe Vochysieae. All three have a trilocular ovary, but it is partly epigynous in Vochysia and completely superior in the other two (Figs. 21, 22). Vochysia also does not have the strongly slanted receptacle seen in Qualea and Callisthene (Fig. 45). In fact it is not entirely clear there is a hypanthium in Qualea and Callisthene. If one changes

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the frame of reference and views the base of the ovary as horizontal, the putative hypanthium becomes a broad receptacle (Fig. 45).

I. Symmetry in Vochysiaceae

In all species, sepals are initiated in spiral sequence, either clockwise or counterclockwise (Fig. 3, 4). Subsequent organs are initiated with reference to the sepals, thus the single petal of *Qualea*, *Erisma*, and *Callisthene* is always between the third and fifth sepals (Fig. 2), opposite the spur, as is the center petal of *Vochysia*. The stamen in *Vochysia* and *Erisma* (and *Salvertia* and *Erismadelphus*) is located in front of this petal, on the line of symmetry. In *Qualea* and *Callisthene* (and *Ruizterania*) the stamen is displaced towards the fifth sepal, thus these flowers are asymmetrical (Fig. 2). Because the sepals are arranged in left-handed and right-handed spirals, the fifth sepal is either to the left or the right of the petal, and thus the stamen is also either to the left or the right of the petal. There has been speculation that these left-handed and right-handed morphologies may be significant for pollination, but both are found on the same plant and therefore can provide no special opportunity for cross-pollination. However, it should be noted that if there were not right- and left-handed flowers there would in fact be no pollination at all.

Flowers of *Erisma* and *Erismadelphus* are superficially bilaterally symmetrical, with the stamen on the midline, but in two of four species of *Erisma*, and in *Erismadelphus*, the single locule of the ovary is not symmetrically oriented (Figs. 36, 42). In *Erismadelphus*, and in *E. bracteosum* and *E. floribundum*, the placenta may be positioned to the left or the right of the spur, as with the stamen of *Qualea*. This again presumably reflects the spiral initiation of the sepals. Any structure that is off the line of symmetry will be found clockwise from

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the spur in some flowers and counterclockwise in others.

II. Gynoecium of Erismeae

A. Locule number - These results show that there is a structural difference between the functionally unilocular ovaries of the two genera of Erismeae. In *Erismadelphus*, there is at least one aborted carpel in the gynoecium (Figs. 41, 42), and the vasculature of the style derives from a bundle that is associated with the aborted carpel rather than with the fertile carpel (Fig. 42). Two aborted carpels were reported by Kopka and Weberling (1984). In the limited material available for this study one was seen, inconsistently. In contrast, aborted carpels were never seen in *Erisma*, and there is no evidence from vasculature to indicate that any might exist. Developmental data are not available for *Erismadelphus*, but development of the ovary of *Erisma* is consistent with the notion that the gynoecium consists of a single carpel. In all Vochysiaceae the gynoecium is initiated as a ring primordium; in Vochysieae the depression in the center of the ring, and subsequently the opening at the apex of the developing ovary, is triangular or three-parted. This is not the case in *Erisma*, in which the depression is oval and the opening is longitudonal. The presence of aborted carpels in *Erismadelphus* flowers makes this an important genus from which to obtain developmental data.

The only suggestion in *Erisma* of a multi-carpellate condition is the asymmetrical position of the locule and the placenta in *E. bracteosum* and *E. floribundum*. This position is similar to what one might expect if the carpel were one of several in the gynoecium. Nontheless it does not of itself provide direct evidence of other carpels. Phylogenetic analyses have not yet resolved relationships within Erismeae, but it is difficult to refrain from speculating that the different morphologies found within the family represent stages in a reduction series. The starting point would be a multicarpellate gynoecium such as that of Vochysieae, with Erismadelphus (aborted carpels) and species such as E. bracteosum and E. floribundum representing intermediate stages. Erisma uncinatum and E. japura, with a single, symmetrical locule, would represent the final stage.

B. Pseudomonomery - Ronse de Craene and Smets (1998) noted that in 95% of unicarpellate taxa the carpel is oriented toward the inflorescence axis; away from the axis is uncommon, and taxa in which the position is variable are rare. Clarke (1859) commented of Vochysiaceae that "one of the most remarkable characters in this family is that the carpel when single is posterior"; this description was based only on Erisma, as Erismadelphus had not yet been described (Mildbraed 1913). Clarke was following common usage in applying the term "posterior" to the spur-side of the flower in Vochysiaceae, although it is the second, and not the spurred fourth sepal, that is in front of the axis (Fig. 2). Based on this usage, Clarke's description is correct for E. uncinatum and E. japura; in these species the locule is oriented away from the spur (Fig. 40). However in E. floribundum and E. bracteosum the locule is oriented obliquely, more towards the axis (Fig. 36). Thus Erisma in fact is one of the rare taxa in which there is variability in the position of the locule.

Eckardt (1937) used Clarke's description, along with the fact that other Vochysiaceae were trilocular, to conclude (without seeing material himself) that the gynoecium of Erisma is pseudomonomerous. Eckardt used this term to describe a unicarpellate gynoecium that is derived by reduction from a syncarpous one, in contrast to a "true" unicarpellate gynoecium derived by reduction from an apocarpous one (e.g. Fabaceae). Pseudomonomery sensu Eckardt (also Eames 1961;

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Hufford 1989), therefore, refers to an evolutionary derivation, not a morphological condition, although he does present morphological evidence of the derivation for the taxa that he observed. Ronse de Craene and Smets (1998) defined it in morphological terms, as an ovary where several carpels are initiated but all abort except one. However their actual application of the term is variable because they incorporated information from the literature, in which usage is inconsistent.

Authors since Eckardt (1937) have followed his lead in describing the ovary of Erismeae, including Erismadelphus, as pseudomonomerous (e.g. Cronquist 1981; Takhtajan 1997). When describing floral structure, there are two problems with using the term in this historical sense. First, it is applied to gynoecia that differ in structure. For instance, there may be physical evidence of reduction in carpel number (as in in Erismadelphus), or there may be no such evidence (as in Erisma). When the same term is used to describe both, information is lost, and a reader might conclude that the ovaries are the same. Second, it is inappropriate to use assumed evolutionary derivation in describing characters. Current practices dictate that the pattern of character state changes be deduced from the results of an analysis. If one assumes the evolutionary history of a character state a priori, one will then be coding the character state for analysis using information that should be obtained from the results of the analysis. The analysis thus becomes circular.

It is also worth noting that this use of "pseudomonomerous" artificially isolates the unilocular condition. Using the same logic, one should describe the ovary of Vochysieae as "pseudotrimerous," because the inclusion of Vochysiaceae in Myrtales indicates that the trimerous ovary is derived by phylogenetic reduction from a pentamerous

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ovary. "Pseudotrimerous" is not used, although there seems no reason to distinguish reduction to one carpel from the reduction to two or three that is seen in other taxa.

I recommend restricting the use of the term "pseudomonomery" to the morphological condition described by Ronse de Craene and Smets (1998) and Weberling (1981), in which there is only one fertile locule in the mature ovary, but in which there is direct evidence that more than one carpel is initiated. This requires looking at the development and morphology of the ovary (as noted by Weberling, 1981, and Ronse de Craene and Smets, 1998), and can not be deduced on the basis of relationships. A term that describes the structure of a floral feature in terms of the feature's historical derivation carries a risk of being misunderstood, therefore I recommend that these terms be avoided. Furthermore, it does not seem necessary to have a term the purpose of which is to describe the evolutionary derivation of a character; this information can be gleaned from the results of a phylogenetic analysis.

Using this criterion, the gynoecium of _Erismadelphus_ is pseudomonomerous, whereas that of _Erisma_ is not. I suggest describing the gynoecium of _Erisma_ as monomerous rather than unicarpellate; because the ovary is never distinct from the surrounding floral tissue, a discrete carpel can not be identified. Nonetheless there is no evidence for more than one structure in the ovary, thus monomerous is an accurate description of what can be observed. There are eight species of _Erisma_ that were not examined in this study, thus the possibility exists that future work will show evidence in some species of more than one carpel. However, such a result can not be anticipated.

III. Ovary position in Vochysieae

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A. Structure - Serial sections of *Vochysia* buds show that in this genus the base of the gynoecium is not free from the surrounding tissue, that is, the ovary is not wholly superior. The locules of the three carpels can be seen in sections in which the ovary is still continuous with the surrounding tissue (Figs. 21, 22), thus mature flowers of *Vochysia* are epigynous to a small degree.

In contrast, the ovary of *Qualea* and *Callisthene* does not appear to be inferior to any degree. In sections of flowers of these genera the locules are not apparent until the ovary is completely free, and there is no clear-cut morphological evidence to distinguish the superior position of the ovary of *Qualea* and *Callisthene* from that of other taxa. However, the slanted base of these flowers and of the ovary, as well as the presence of the spur on one side, make it difficult to determine the exact position of the base of the ovary (Fig. 45). Likewise, it is difficult to identify what should be considered hypanthium as opposed to receptacle. Thus it is possible that the ovary can be interpreted as slightly adherent on one side.

Our results indicate that there are three distinct floral plans within Vochysiaceae: *Erisma* and *Erismadelphus* are epigynous; *Vochysia* is partly epigynous; and *Qualea*, *Callisthene*, and *Ruizterania* are perigynous. There are qualifications to all these basic descriptions: the ovary in flowers of *Erismadelphus*, *E. uncinatum* and *E. japura* is free on the spurred side of the flower; *Vochysia* flowers are perigynous above the insertion point of the hypanthium; and *Qualea*, *Callisthene*, and *Ruizterania* flowers can perhaps be considered hypogynous if they are tilted.

B. Development: the "epigynous groundplan" - In spite of these differences in the structure of the mature flowers, the early stages of development of the gynoecium are the same in all species of

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Vochysiaceae, and conform to an "epigynous groundplan" (Boke 1963, 1964; Kaplan 1967; Gustafsson & Albert in press; Kuzoff pers. comm.). The gynoecial primordium, in this case a ring primordium, arises on a concave floral apex; it is therefore initiated as an inferior ovary, beneath the level of the other floral organs. Subsequent differential growth results in the ultimately superior (or nearly superior) position of the ovary in Vochysieae. This is in contrast with the pattern seen in most species with superior ovaries, in which the floral apex is convex and therefore the ovary is initiated above the level of the other floral organs (Gustafsson and Albert in press). Thus developmental data indicate that the superior or nearly superior ovary of Vochysieae is not homologous with the superior ovary of other species.

There is then historical as well as developmental (and morphological in the case of Vochysia) evidence that the superior ovary of Vochysieae is not homologous with superior ovaries of other angiosperms. The term "pseudosuperior" has been suggested to designate superior ovaries that are secondarily derived from inferior ovaries, analagous with Eckardt's use of pseudomonomerous (R. Kuzoff, pers. comm.). Again, I would advise against this. As with pseudomonomery, incorporating phylogenetic information into a morphological term is inappropriate and leads to confusion. Furthermore, there is an important caveat concerning the interpretation of the developmental data. A concave floral apex is considered characteristic of epigynous flowers, but it is also seen in perigynous flowers. This may indicate a relationship between epigyny and perigyny, or it may indicate that we have overemphasized the significance of the correlation of a concave floral apex with epigyny. The conclusion that a concave floral apex predicts a floral structure that is epigynous or historically derived

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from epigyny can only be based on the results of phylogenetic analysis. In the case of the gynoecium of Vochysiaceae, early development and adult morphology are apparently decoupled by differential growth during development. The significance of the concave floral apex is thus unclear. Taking it to indicate a fundamental epygyny can once again lead to circular reasoning.

It is preferable to describe the position of the ovary in the flower as one character based strictly on morphological structure, and to describe developmental features as a separate character or set of characters. "Superior" is a descriptor of position and implies no developmental or phylogenetic information. Initiation of the gynoecium on a concave floral apex can be coded as a separate character, thereby increasing the amount of information in the analysis. Thus in Vochysiaceae all taxa share the same state for the development character (concave floral apex) but differ in the character of ovary position: in Erisma and Erismadelphus it is inferior, in Vochysia it is semi-inferior, and in Qualea and Callisthene it is superior. For information regarding character evolution, one should consult the results of phylogenetic analyses. In this case, the status of Vochysiaceae as a monophyletic family indicates that these different morphologies share a common evolutionary history. The inclusion of Vochysiaceae in Myrtales and the sister-group relationship with Myrtaceae indicate that they are all probably derived from a flower with an inferior, multilocular ovary.

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Table 1. Some features distinguishing the tribes and genera of Vochysiaceae, according to Dumortier (1829), Stafleu (1952), and Kawasaki (1998).

	ovary position	**locule number**	**fruit type**	**elongate 4th sepal**	**petal number**	**ovules/ locule**	**seeds/ locule**	**seed wing**
Vochysieae	superior	3	capsule					
Vochysia				present	3	2	1	unilateral
Salvertia				absent	5	2	1	unilateral
Qualea				absent	1	many	many	unilateral
Ruizterania				present	1	many	many	unilateral
Callisthene				present/ absent	1	many	few-many	circum- ferential
Erismeae	inferior	1	winged, indehiscent					
Erisma				absent	1	2	1	---
Erismadelphus				absent	5	1	1	---

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Table 2. Taxa used in this investigation to study organ initiation and/or vasculature.

		organo-genesis	**vascu-lature**	**voucher**
Vochysia				
Section *Ciliantha*				
Subsection *Ferrugineae*	*V. densiflora* Spruce ex Warm.		+	JRN 716 (INPA)
Subsection *Lutescentes*	*V. tucanorum* Mart.	+	+	Litt et al. 69 (NY)
Section *Vochysiella*				
Subsection *Calophylloideae*	*V. haenkeana* Mart.		+	Rizzo et al. 11395 (NY)
Subsection *Decorticantes*	*V. pumila* Pohl	+	+	Litt et al. 75 (NY)
	V. elliptica Mart.	+		Litt et al. 4 (NY)
Qualea				
Subgenus *Amphilochia*	*Q. dichotoma* (Mart.) Warm.		+	Gomez Klein 3279 (NY)
Subgenus *Qualea*				
Section *Costatifolium*	*Q. grandiflora* Mart.	+		unvouchered
		+		Litt et al. 54 (NY)
	Q. multiflora Mart.	+		Litt et al. 76 (NY)
	Q. parviflora Mart.		+	unvouchered
		+	+	Litt et al. 48 (NY)

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Section *Qualea*	*Q. lineata* Stafleu		+	Daly 6220 (NY)
	Q. mori-boomii Marc.-Berti	+	+	Mori et al. 24723 (NY)
	Q. rosea Aubl.		+	Mori et al. 24688 (NY)
Callisthene				
Section *Cataphyllantha*	*C. fasciculata* Mart.		+	Litt et al. 52 (NY)
Section *Callisthene*	*C. major* Mart.		+	unvouchered
Erisma	*E. bracteosum* Ducke	+	+	Litt et al. 64 (NY)
	E. floribundum Rudge	+	+	Mori et al. 24721 (NY)
	E. japura Spruce ex Warm.		+	Berry 6844 (NY)
	E. uncinatum Warm.		+	Mori et al. 24725 (NY)
Erismadelphus	*Erismadelphus exsul* Mildbr.		+	Jean-Louis 2031 (NY)

Fig. 1. *Vochysia venezuelana* Stafleu. Note zygomorphy, spurred sepal, single fertile stamen, and reduced number of petals (three). Drawn from photograph (Mori 22871).

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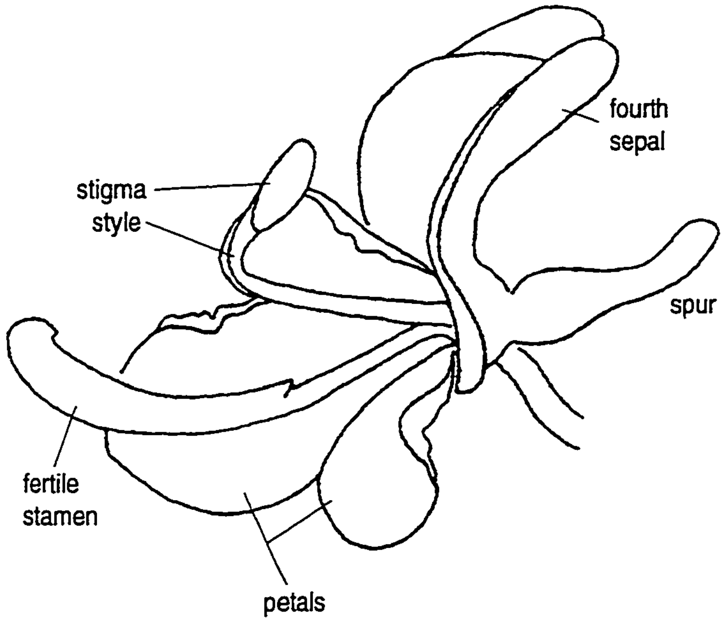

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Fig. 2. Floral diagrams of the seven genera of Vochysiaceae. Vochysieae (superior trilocular ovary) are on the left, Erismeae (inferior unilocular ovary) on the right. Top row genera have three or five petals, bottom row genera have one petal. *Callisthene* differs from *Qualea* and *Ruizterania* in never having rudimentary petals or staminodes, although some species of the other two genera also lack these structures. Symbols are as indicated in figure legend.

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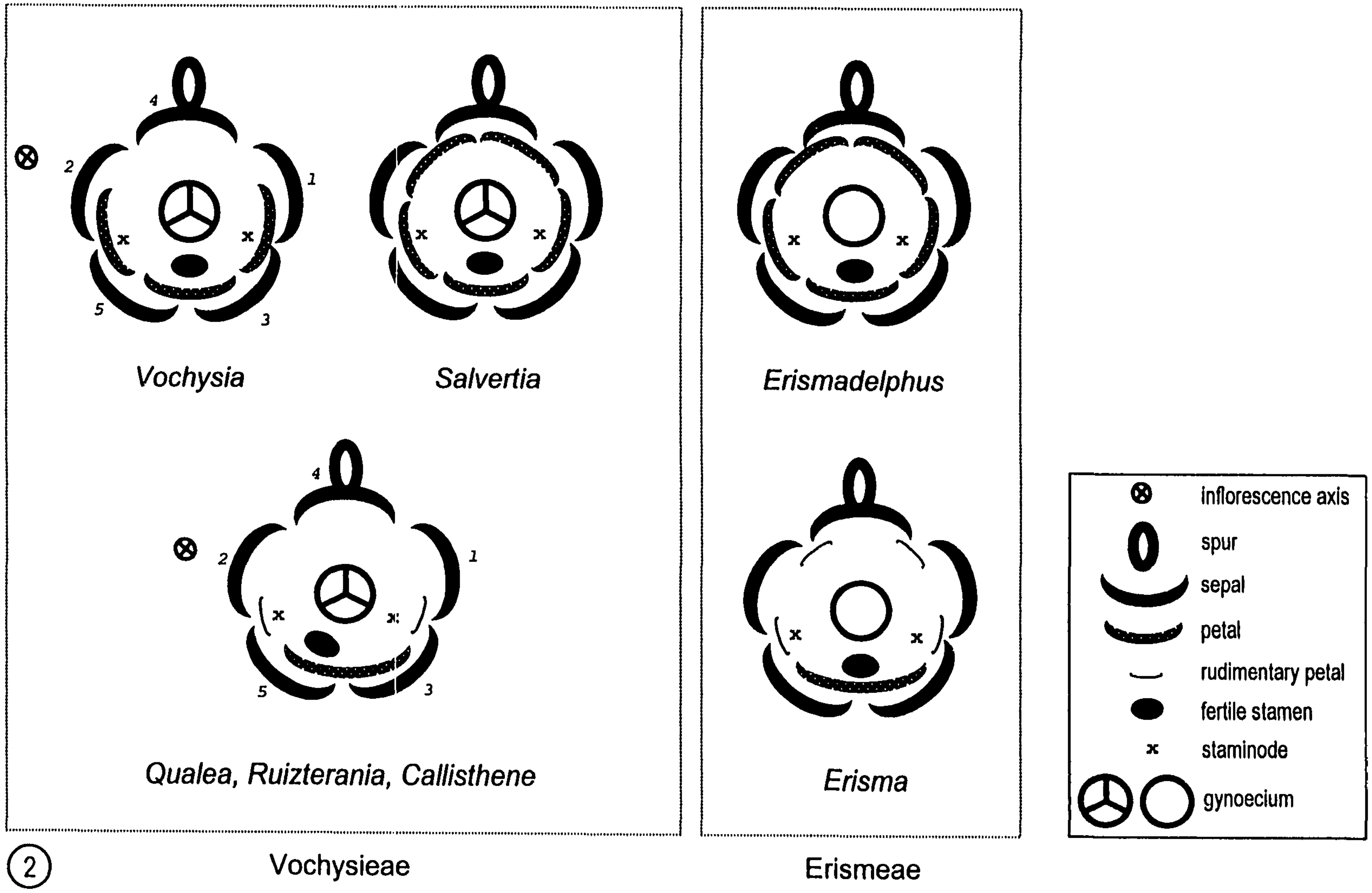

Figs. 3, 4. Sepal initiation in Qualea grandiflora (unvouchered). 3. Clockwise initiation. 4. Counter-clockwise initiation. s2-s5, sepals (some removed) in order of initiation. Scale bars = 100um

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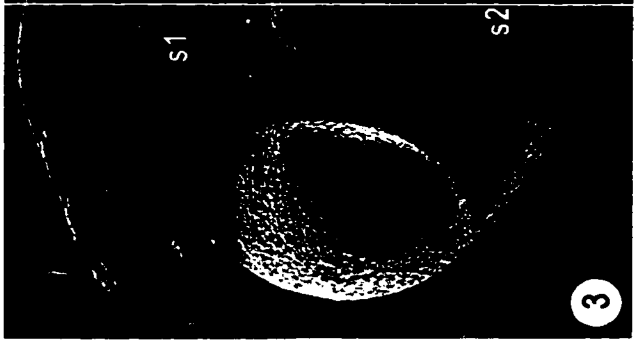
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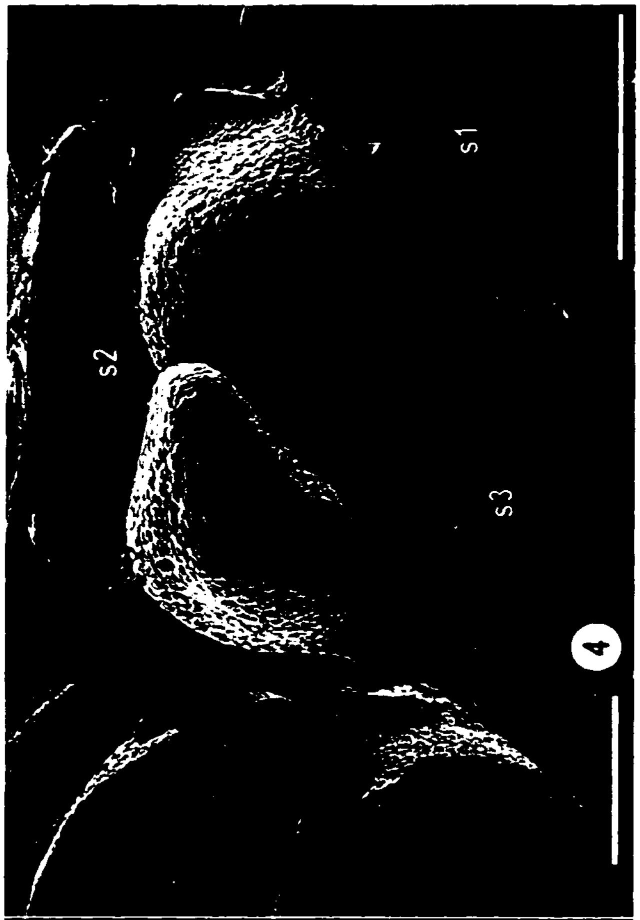
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Figs. 5-8. Appendages of unknown function. 5. *Qualea grandiflora* (unvouchered). Claw-shaped structure at tip of sepal. 6. *Callisthene major* (unvouchered). Structures at base of inner surface of sepal. 7. *C. fasciculata* (Litt et al. 52). Structures in-between petiole (removed) and stem, flanking bud (the latter with hairs). 8. *C. major* (unvouchered). Structures in between petiole (removed) and stem. Scale bars = 100um

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Figs. 9, 10. Petal initiation. 9. *Qualea grandiflora* (Litt et al. 54). Initiation of two petal primordia. Note extensive of growth of sepals and relatively flat floral apex. Only one primordium will continue to develop. 10. *Erisma bracteosum* (Vicentini 1111). Initiation of two petal primordia. Note slightly less extensive growth of sepals and considerably deeper concave floral apex than in Fig. 9. Three more primordia will be initiated but only one will develop to full size. Early petal growth is nearly horizontal over the concavity. p, petal primordium; s1-s5, sepals (removed) in order of initiation. Scale bars = 100um

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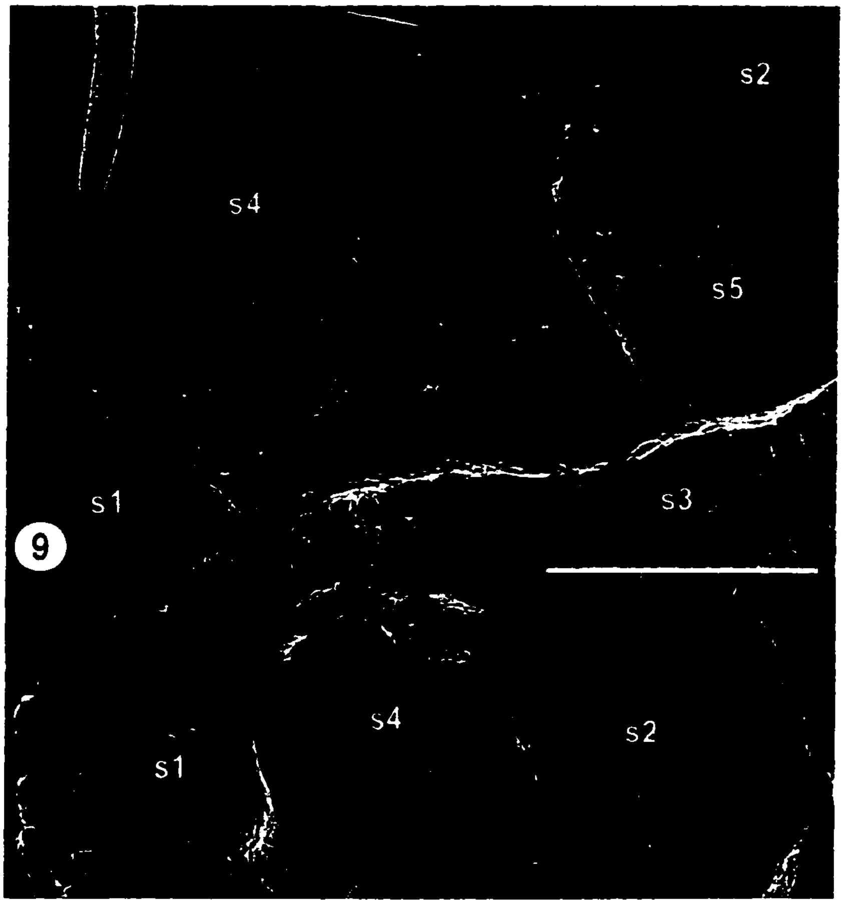

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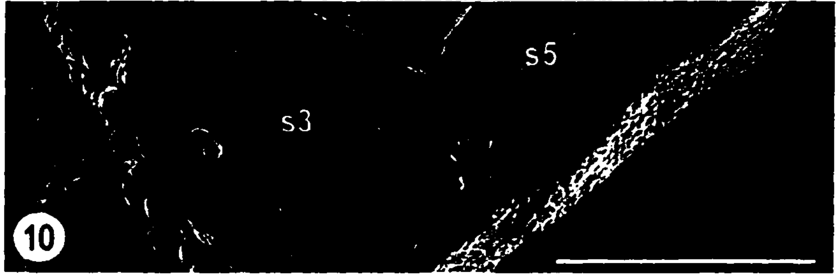

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Figs. 11-13. Development of the corolla and androecium in *Vochysia*. Figs. 11, 12, *Vochysia tucanorum* (Litt et al. 69); Fig. 13, *Vochysia* sp. (Litt et al. 21). 11. Horizontal early growth of petals perpendicular to floral cup. Stamen primordia are directly underneath petals. 12. Petals, fertile stamen, and staminodes enlarge, become vertically oriented, and their free portions shift to fill the available space within the floral cup. 13. Nearly mature bud. Note connective of anther forming cap over stigma. Petals are at base of fertile stamen. Staminodes are not visible. fs, fertile stamen; p, petal; s1-s5, sepals (removed) in order of initiation; sp, spur; st, staminode. Scale bars = 100um

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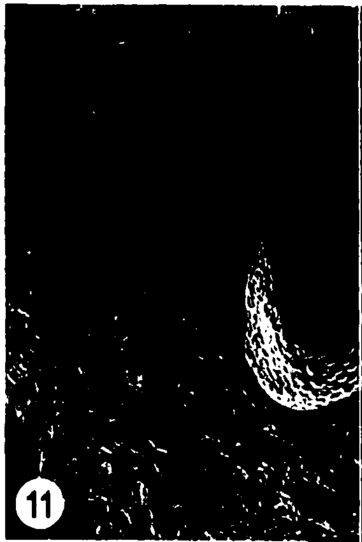
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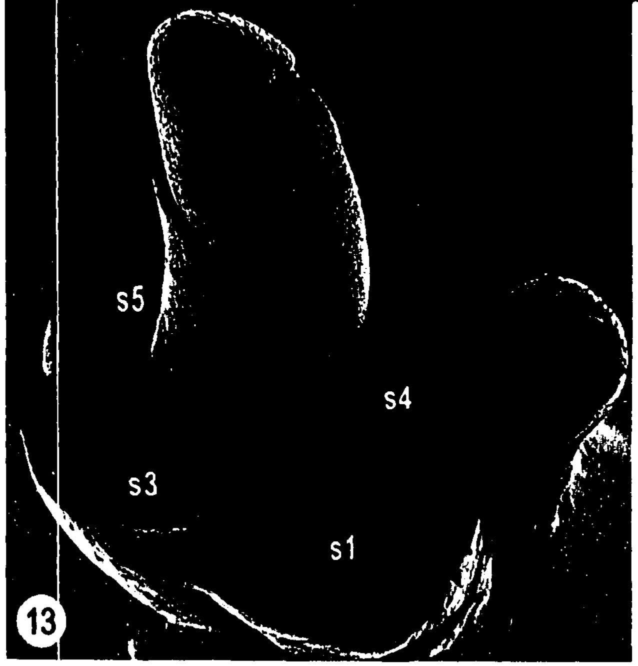
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Figs. 14-16. Gynoecium development in Vochysieae. 14. *Vochysia pumila* (Litt et al. 75). Gynoecium appears as a ring primordium with a triangular-shaped center. All other floral organs have been removed. 15. *V. tucanorum* (Litt et al. 69). Later development. Three-part nature of gynoecium is apparent. All other floral organs have been removed. 16. *Qualea parviflora* (Litt et al. 48). Three part opening at apex of gynoecium is visible under stamen and petal. Sepals have been removed. fs, fertile stamen; g, gynoecium; p, petal; s1-s5, sepals in order of initiation; st, staminode. Scale bars = 100um

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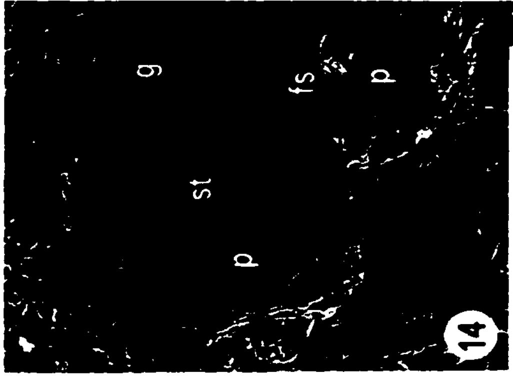
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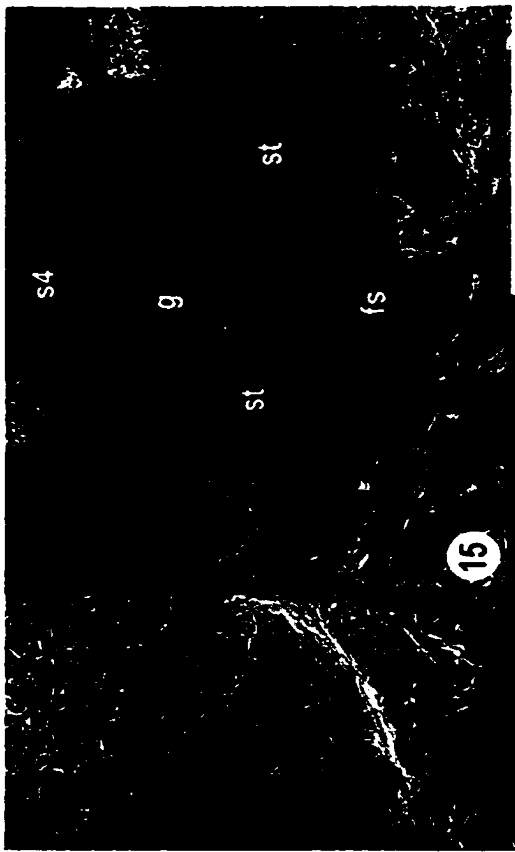
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Figs. 17-18. Gynoecium development in Erisma. All floral organs other than gynoecim have been removed. 17. E. floribundum (Mori et al. 21630). Gynoecium appears as a ring primordium with an oval-shaped center (thumb-print). Scale bar = 20um. 18. E. bracteosum (Vicentini 1111). Later development. Opening at apex of gynoecium is a longitudonal slit. Scale bar = 100um. as, accessory structure (unidentifiable as rudimentary petal or staminode); fs, fertile stamen; g, gynoecium; p, petal; rp, rudimentary petal; s4, fourth sepal; st, staminode.

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Figs. 19-25. Floral vasculature of Vochysia tucanorum (Litt et al. 69). 19. Pedicel. Note medullary bundles (mb), present in flowers only in the pedicel, and gum canals (gc), present in other sections but not drawn. 20. Vascular cylinder begins to separate into bundles that will supply the floral organs and the gynoecium. 21. One locule is visible, three segments of gynoecium vasculature are identifiable. 22. Three dorsal carpel and three major lateral bundles are recognizable. Two major lateral bundles have split to produce ventral carpel bundles; the third is doing so (asterisk). Ventral carpel bundles move through septa to center of gynoecium. 23, 24. Three ventral carpel bundles form a ring in the center, which then divides into three discrete ventral bundles, one per carpel, which supply the ovules. Note three-lobed shape of ovary. 25. Dorsal and major lateral bundles continue into style. Open circles represent vascular bundles. br, bract; dcb, dorsal carpel bundle; fs, fertile stamen; fst, fertile stamen trace; gc, gum canal; gv, gynoecium vasculature; lcb, lateral carpel bundle; loc, locule of gynoecium; mb, medullary bundle; mlb, major lateral bundle; ov, ovule; p, petal; pt, petal trace; se, sepal; sp, spur; st, staminode; stt, staminode trace; sty, style; vbr, ventral bundle ring; vc, vascular cylinder. Scale bar (Fig. 19) is the same for all figures.

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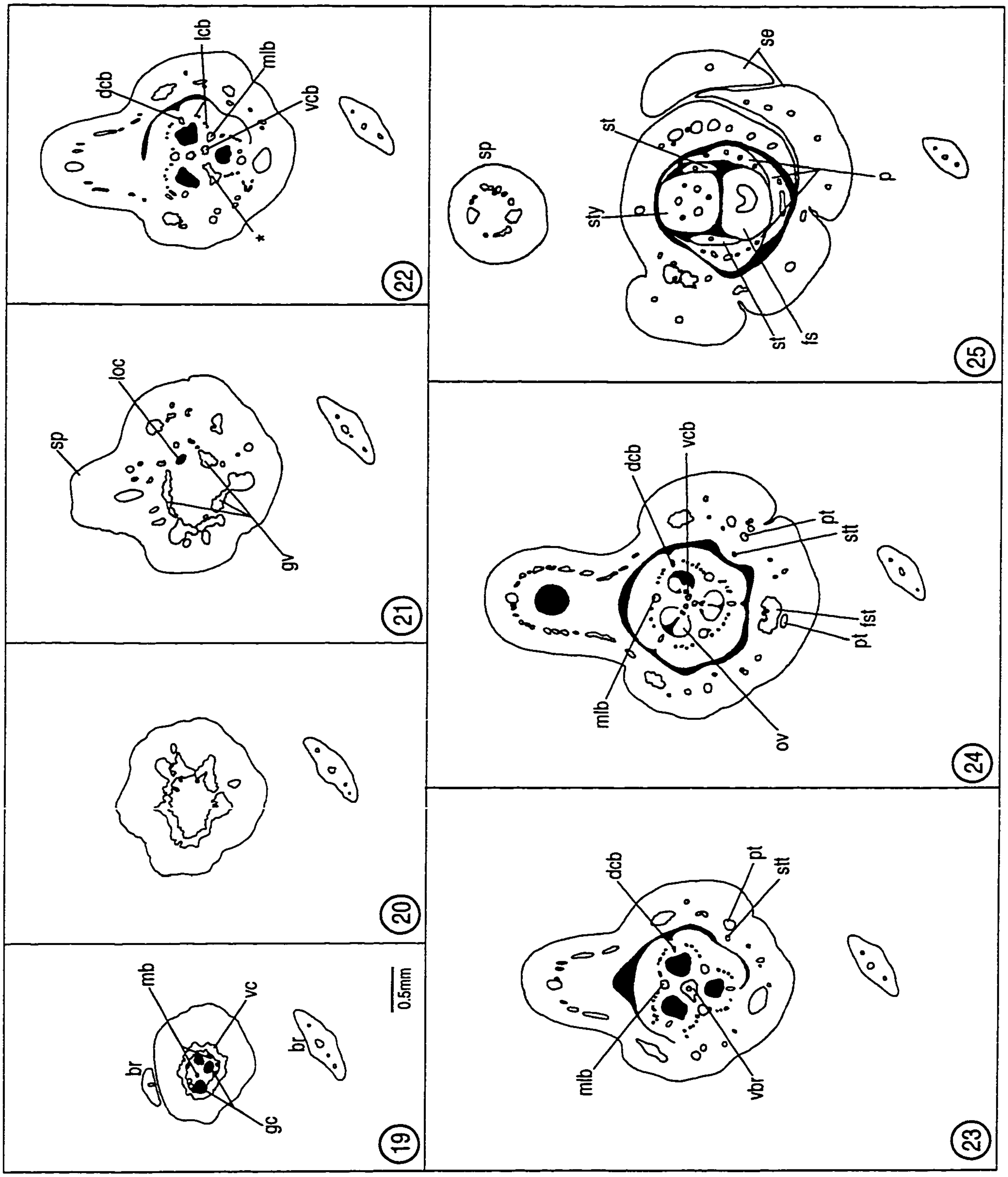

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Figs. 26, 27. Effect of slant of ovary of *Qualea* and *Callisthene*. *Qualea parviflora* (unvouchered). 26. Median longitudonal section. Base of ovary is higher on the side of the flower opposite the spur; ovary inserts on receptacle at an angle. Vascular supply from pedicel must bend to enter gynoecium (asterisk). 27. Cross-section through base of ovary. In serial sections the bend in the vasculature as it enters the gynoecium (asterisk) gives the appearance of the vasculature branching (sections include horizontal segments of bundles). Open circles represent vascular bundles. a, anther; fst, fertile stamen trace; g, gynoecium; gv, gynoecium vasculature; p, petal; pt, petal trace; se, sepal; set, sepal trace; sp, spur; vc, remnants of vascular cylinder.

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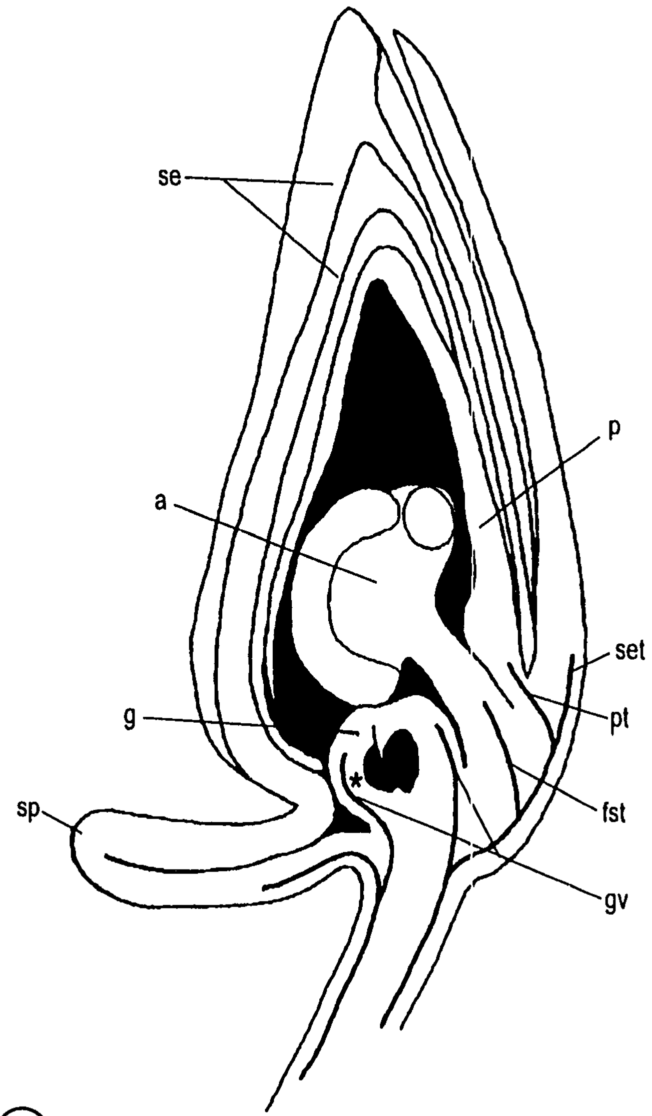

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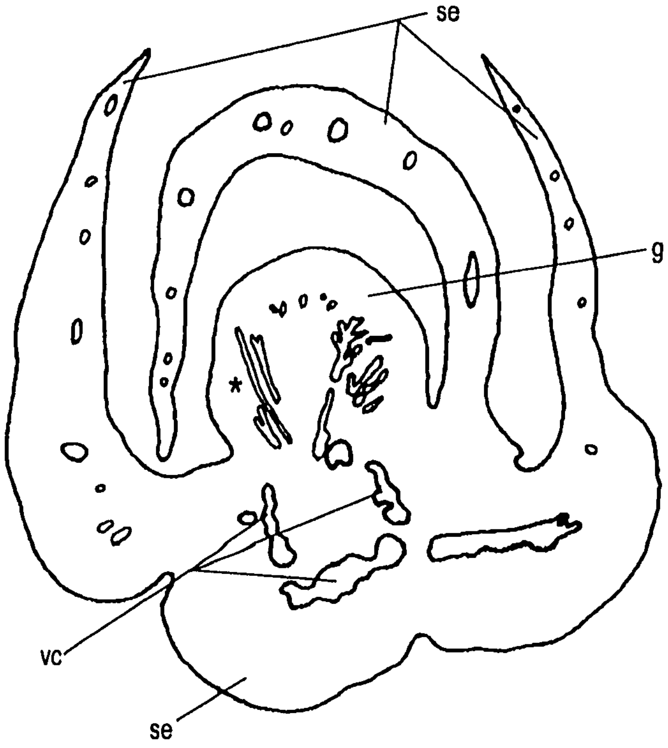

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Figs. 28-33. Floral vasculature of Qualea and Callisthene. 28-30. Qualea parviflora (unvouchered). 28. Vascular supply to gynoecium separates at a lower level on the spurred side of the flower in keeping with the slant of the base of the ovary. Labelled sepals are the first and second; note spur emerges between them. 29. Locules are not visible until the ovary is free from the surrounding tissue. Major lateral carpel bundles split to produce ventral bundles (asterisk). 30. Vasculature of the ovary. Ovary is unlobed. 31. Qualea mori-boomii (Mori et al. 24723). Note absence of large major lateral carpel bundles. Ventral carpel bundles are formed by coalescence of several small bundles from the carpel wall supply. Ovary is unlobed. 32-33. Callisthene fasciculata (Litt et al. 52). 32. Dorsal, lateral, and ventral carpel bundles all form concurrently out of mass of vascular tissue in base of gynoecium. 33. Ring of vascular tissue in center of gynoecium supplies ovules. Ovary is unlobed. Open circles represent vascular bundles. dcb, dorsal carpel bundle; fs, fertile stamen; fst, fertile stamen trace; gv, gynoecium vasculature; lcb, lateral carpel bundle; loc, locule of gynoecium; mlb, major lateral bundle; ov, ovule; p, petal; pt, petal trace; se, sepal; sp, spur; vc, remnants of vascular cylinder; vcb, ventral carpel bundles; vcbr, ring of vascular tissue that supplies ovules. Scale bar in Fig. 28 is the same for Figs. 29 and 30; scale bar in Fig. 32 is the same for Fig. 33.

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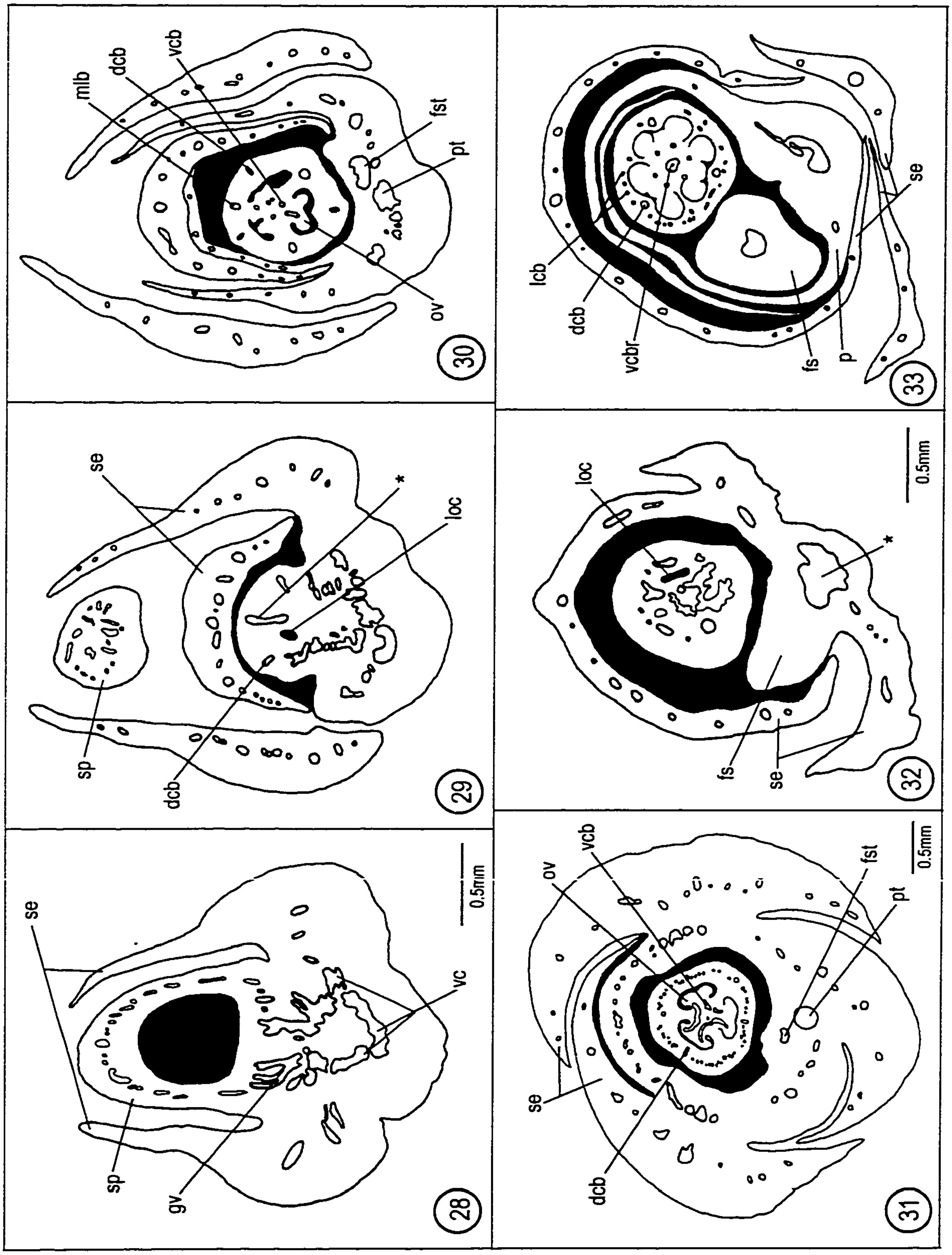

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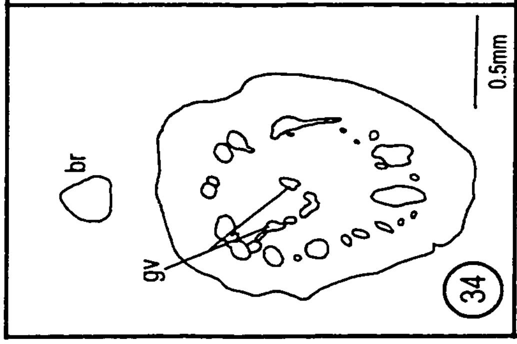
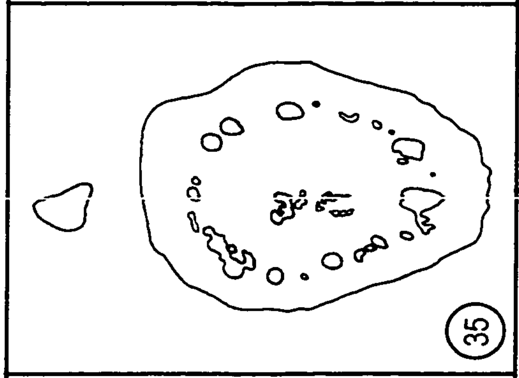
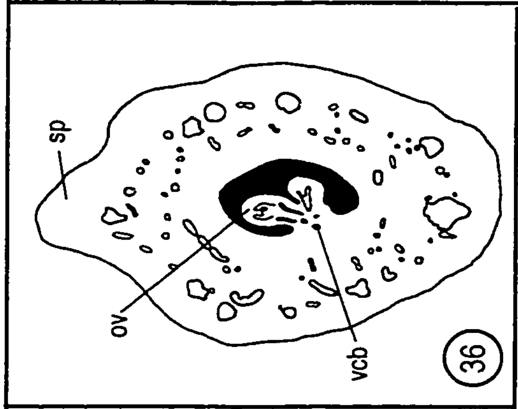
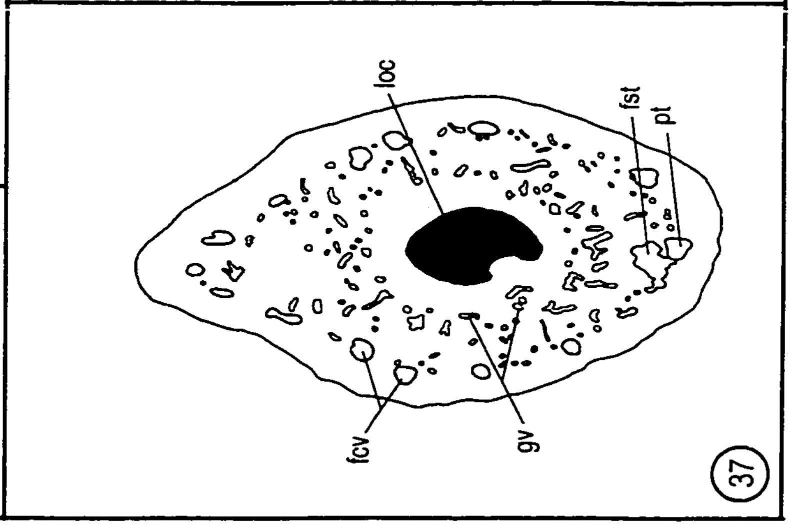
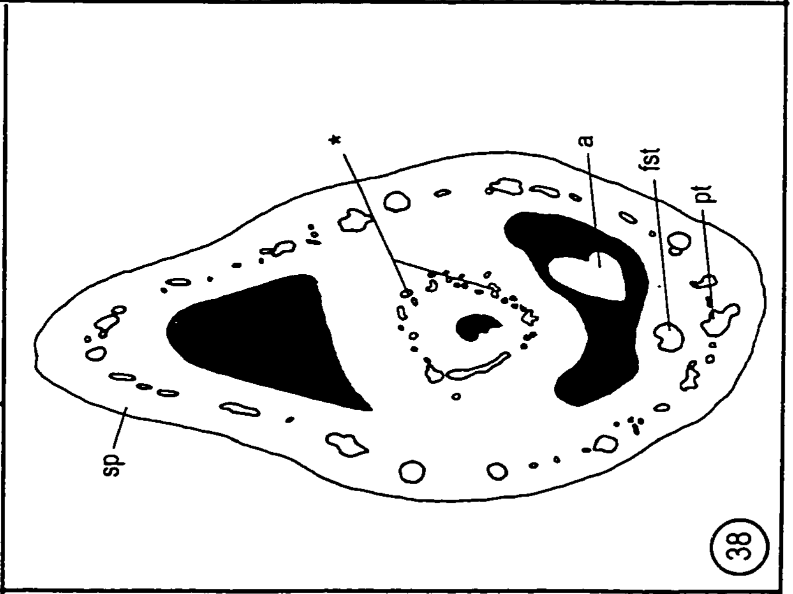
Figs. 34-39. Floral vasculature of Erisma bracteosum (Vicentini 1111). 34, 35. Several peripheral bundles supply branches to center that anastomose to form ventral carpel bundle. 36, 37. Note asymmetrical orientation of locule and placenta. Peripheral bundles all supply branches that form a network around locule. 38, 39. Vessels in network (asterisk) anastomose into a few vessels that enter the style and resolve themselves as 3-5 bundles. Note that spur does not emerge until the top of the ovary. Black regions with white dots are pollen sacs. Open circles represent vascular bundles. a, anther; br, bract; fs, fertile stamen; fcv, floral cup vasculature; fst, fertile stamen trace; gv, gynoecium vasculature; loc, locule of gynoecium; ov, ovule; p, petal; pt, petal trace; se, sepal; sp, spur. Scale bar (Fig. 34) is the same for all figures.











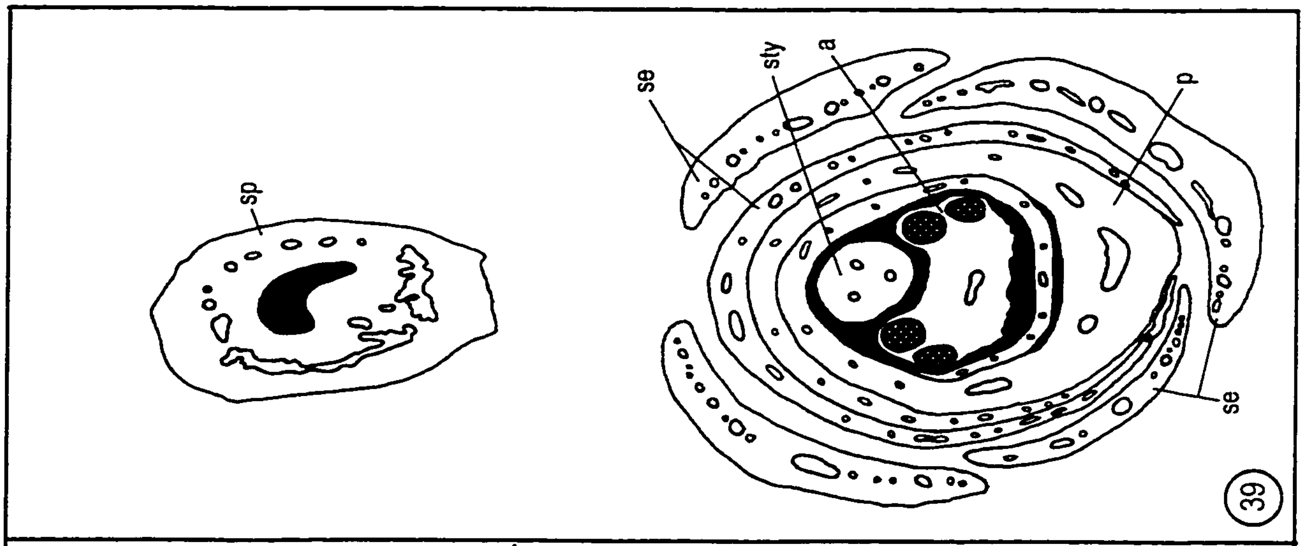


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Fig. 40. Floral vasculature of Erisma uncinatum (Mori et al. 24725). Note symmetrical position of locule and placenta, and position of spur at the level of the ovules. Open circles represent vascular bundles. asterisk, bundle that will divide to supply fertile stamen and petal; ov, ovule; sp, spur.

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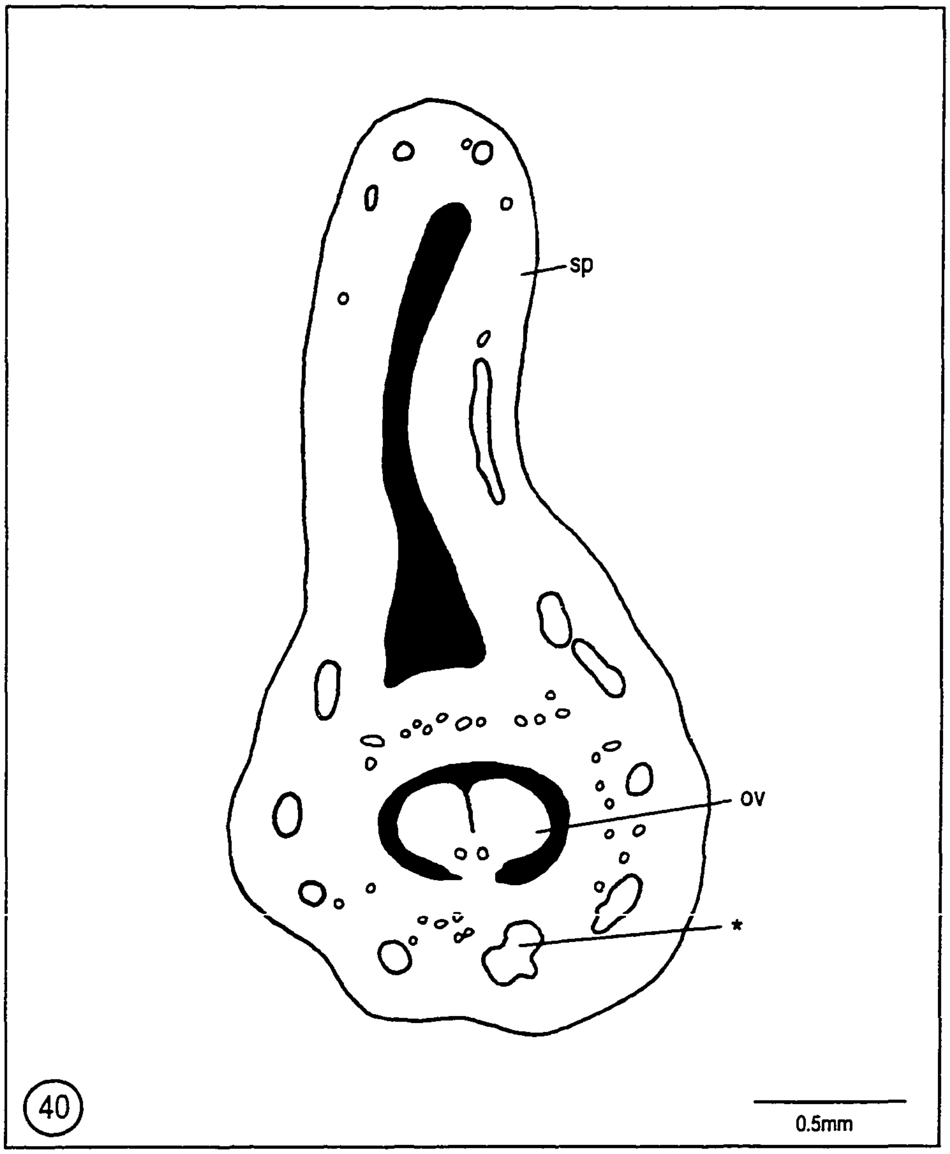

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Fig. 41-44. Floral vasculature of Erismadelphus exsul (Jean-Louis 2041). 41, 42. Note aborted locule and asymmetrical position of fertile locule. In Fig. 42 note bundle in position of dorsal carpel bundle of aborted locule (boxed double asterisk); this bundle enters the style. Single asterisk indicates bundle that will divide to supply fertile stamen and petal. 43. Vasculature anastomoses into bundles that enter the style but do not appear to go far. 44. Vasculature of all floral organs. The two thecae (black areas with white dots) and the filament of the anther are all separate in this section. Open circles represent vascular bundles. a, anther; aloc, aborted locule; f, filament of fertile stamen; fst, fertile stamen trace; ov, ovule; p, petal; pt, petal trace; se, sepal; sp, spur; st, staminode; stt, staminode trace; sty, style; vcb, ventral carpel bundle. Scale bar (Fig. 44) is the same for all figures.

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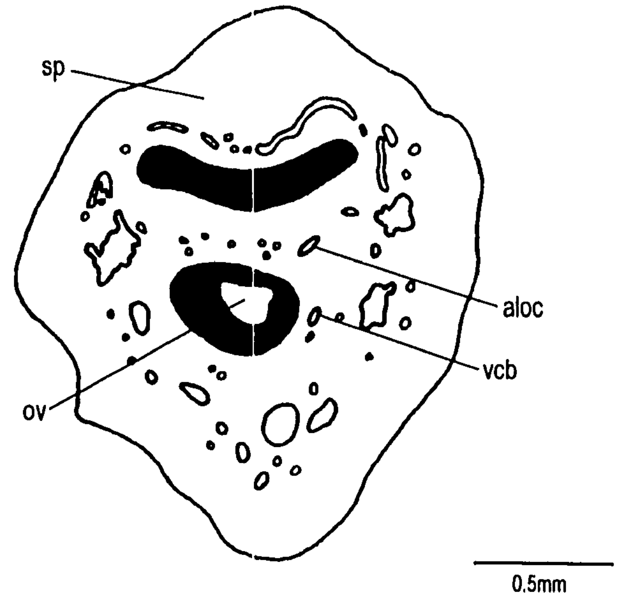

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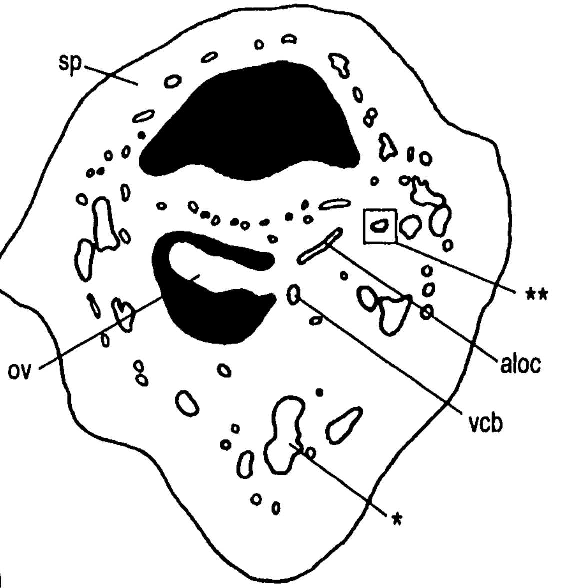

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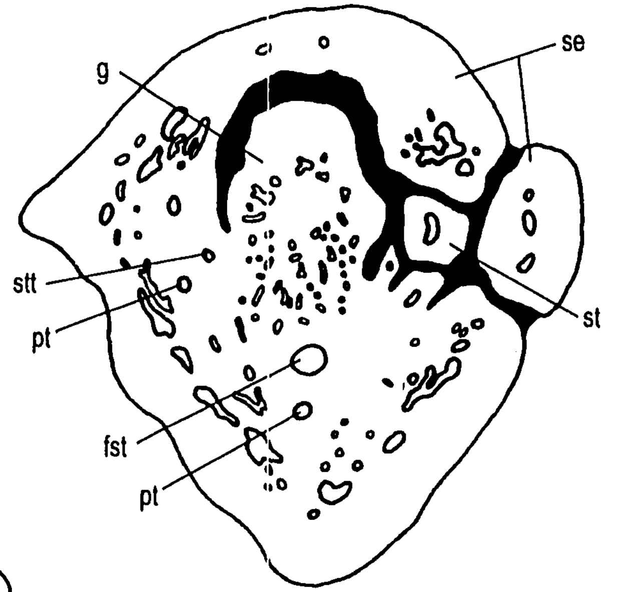

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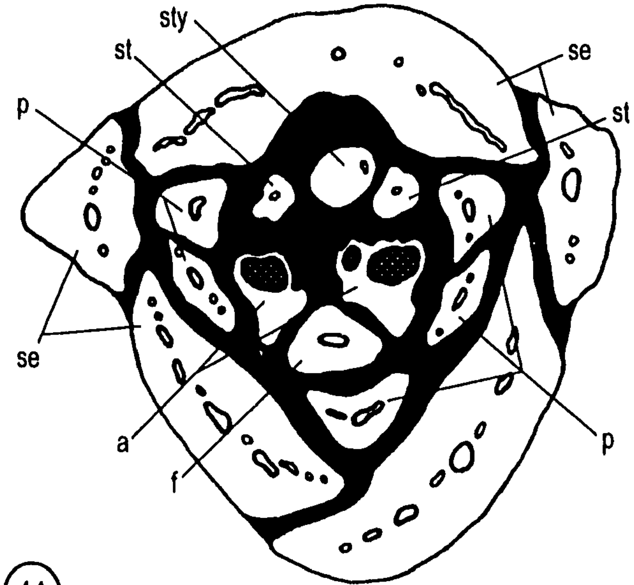

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Fig. 45. Effect of structure of base of flower. Median longitudonal sections. A, B. Qualea parviflora (unvouchered). A. Base of ovary is strongly slanted and the stamen and petal are inserted on a hypanthium (asterisk), or B. Base of ovary is flat, there is no hypanthium, but there is a broad receptacle (asterisk). B. Vochysia tucanorum (Litt et al. 69). Base of ovary is not significantly slanted. br, bract, fs, fertile stamen, g, gynoecium, ov, ovule; p, petal; se, sepal.

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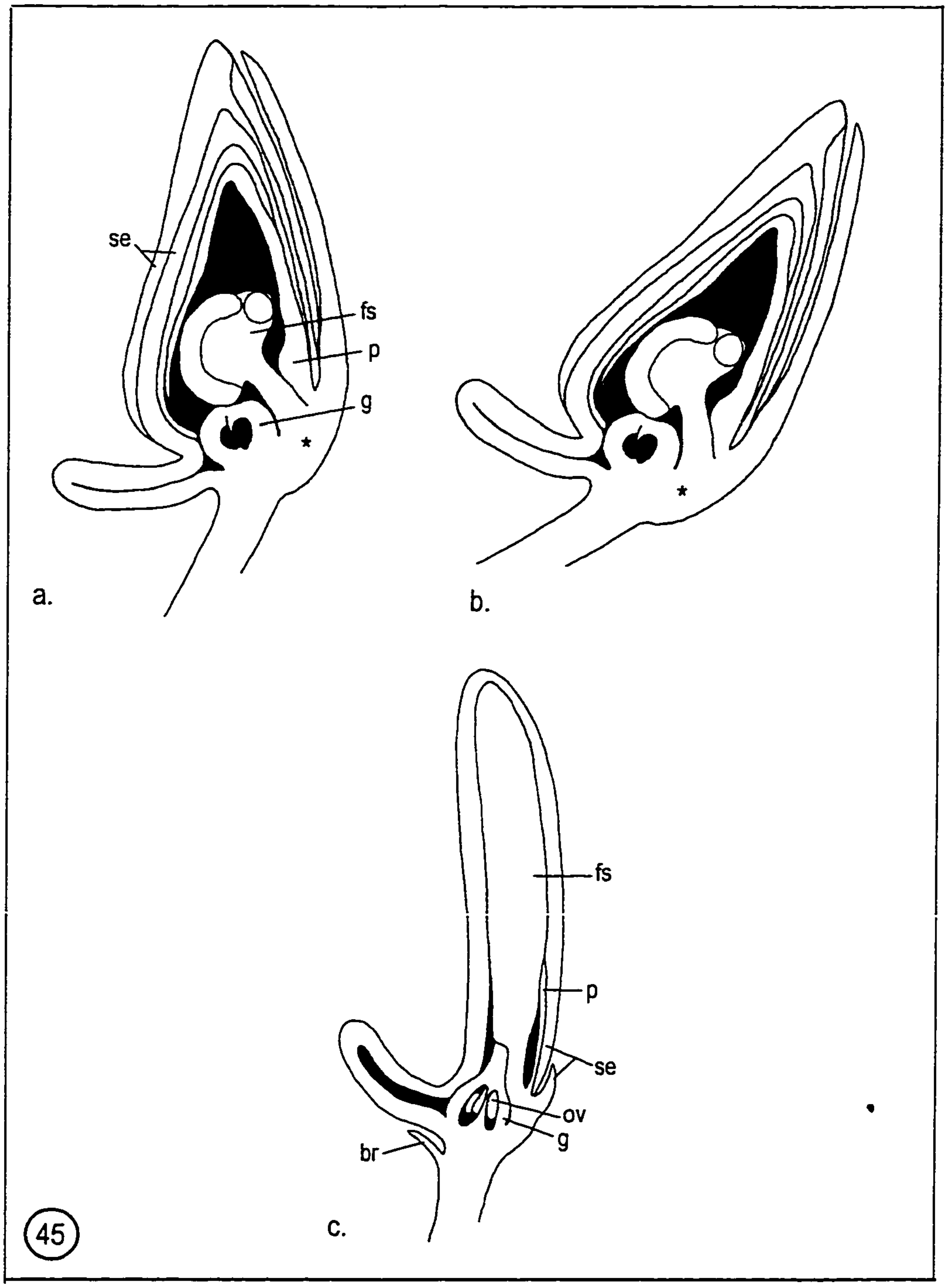

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Chapter 3

Floral development and morphology of Vochysiaceae II.

The position of the single fertile stamen.

Vochysiaceae, a largely neotropical family of rain forest and savanna trees with a single genus in western Africa, have distinctive flowers that can be recognized by their strong bilateral symmetry, spurred calyx, and single fertile stamen (Fig. 1). The family includes seven genera, divided into two tribes, Vochysieae and Erismeae, on the basis of ovary and fruit characters (Table 1)(Dumortier, 1829; Stafleu, 1952).

Vochysiaceae flowers are characterized by a reduction in the number of floral parts (Figs. 1, 46). All species have five sepals, with the base of the fourth drawn out into a spur. However, only three of the more-than-200 described species have a corolla of five full-sized petals; most species have three petals or only one. Tribe Vochysieae have a trilocular gynoecium; Erismeae are unilocular. In addition, all genera have only one fertile stamen.

Published descriptions of the flowers (Warming, 1875; Stafleu, 1948, 1952, 1953, 1954; Keay and Stafleu, 1953; Kawasaki, 1998) indicate that the position of the fertile stamen varies by genus and is correlated with petal number (Fig. 46). According to the observations of these workers, genera with more than one petal (Vochysia, Salvertia, Erismadelphus) have the stamen in front of a petal, whereas those with only one petal (Qualea, Ruizterania, Callisthene, Erisma) have the stamen in front of the fifth sepal. Staminodes, according to Stafleu (1952), are always antepetalous.

Stafleu's discussion of the androecium in Vochysiaceae implies that the variability in the position of the fertile stamen is the result of reduction from two complete whorls of stamens to a single stamen (Stafleu, 1952). In the case of antepetalous stamens an inner whorl stamen was retained, whereas in the case of antesepalous stamens an outer whorl stamen was retained. This explanation is unsatisfactory for two reasons. First, there is little supporting evidence. According to Stafleu, species with an antesepalous fertile stamen and antepetalous staminodes (species of Qualea, Ruizterania, and Erisma) are examples in which stamens from two whorls are present in one flower. However, the position of staminodes relative to perianth parts is often difficult to determine based on gross morphological examination, and even the identity of these organs as staminodes or reduced petals may be obscure. Moreover, neither of the proposed closest relatives of the family is useful as a point of reference for understanding floral organization. Trigoniaceae (Polygalales), historically considered the closest relatives on morphological grounds (St.-Hilaire 1820; Lindley 1853; Baillon 1878; Hutchinson, 1973; Dahlgren, 1980; Cronquist, 1981; Takhtajan, 1997), have a papilionaceous corolla and an androecium that consists of 5-8 (most often six) stamens with fused filaments, all inserted on the anterior side of the flower (Lleras, 1978). Myrtaceae (Myrtales), identified by molecular data as the sister-group (Chase et al., 1993; Conti et al. 1996; Conti et al., 1997; Chase and Albert 1998; Soltis et al. 1999; Soltis et al. submitted; C. Quinn, P. Gadek, and P. Wilson pers. comm.; K. Sytsma pers. comm.), have actinomorphic flowers generally with a proliferation of stamens.

The second and more significant concern that arises from Stafleu's discussion is that it implies that the single fertile stamen is not homologous across the family. Both stamen positions are found in each of the two tribes (Fig. 46), thus if both tribes are monophyletic Stafleu's explanation would require four different reduction events (Fig. 47). Defined as "one fertile stamen," this character would almost certainly be a synapomorphy for Vochysiaceae in any phylogenetic

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analysis. This simplistic character definition would, however, obscure the fact that in different genera the stamen was derived independently. Under these circumstances the single fertile stamen could not be considered one character shared by all the genera.

Alternative hypotheses to explain this character are (1) there is a developmental/genetic switch that toggles between antesepalous and antepetalous, and (2) all primordia are initiated in the same position, but in one-petaled taxa the stamen is displaced during development. We do not, at the moment, have the molecular tools to examine the first hypothesis. The second hypothesis is based on the conjecture that the primordium of the fertile stamen originates between the gynoecium and the petal. Space-packing requirements might then result in the displacement of the stamen to an antesepalous position (Fig. 48). The second hypothesis is the subject of this study.

Two observations provide further reason to examine stamen position. First, published descriptions are contradictory regarding the position of the fertile stamen in Erismadelphus. Keay and Stafleu (1953) described it as antepetalous, as in other multi-petaled taxa, whereas Kopka and Weberling (1984) reported it as antesepalous. Second, although the stamen of Erisma has consistently been described as antesepalous (Warming, 1875; Stafleu, 1954; Kopka and Weberling, 1984; Kawasaki, 1998), my own examination of mature buds and open flowers indicated otherwise.

This study was designed to determine where stamen primordia are initiated and how many are formed in one-petaled and multi-petaled taxa. This information is used (1) to clarify the position of the fertile stamen, particularly in Erisma and Erismadelphus, and (2) to determine the number of reduction events necessary to explain the distribution of fertile stamen positions in the family and thus to address the issue of floral homologies.

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MATERIALS AND METHODS

Floral structure in the genera of Vochysiaceae is described in chapter two.

Floral buds of five genera, from both tribes and with both stamen positions, were used in this study (Table 2). With the exception of those of Erismadelphus, all were fixed in the field in FPA and stored in 70% ethanol. Buds of Erismadelphus were obtained from herbarium material, rehydrated in 10% Aerosol, and stored in FPA. In the cases of Qualea, Callisthene, Erisma, and Erismadelphus, and for organogenesis in Vochysia, all species for which appropriate developmental stages were available were used. For serial sections of Vochysia, species were chosen from the available material to represent as many of Stafleu's three taxonomic sections and eight subsections as possible (Stafleu, 1948)(Table 2).

Appropriate material of Ruizterania and Salvertia was not available. A re-evaluation of generic limits in Vochysiaceae is underway at this point, and preliminary analyses of DNA sequence data and morphological features (chapter four) indicate that Ruizterania may be nested within Qualea, from which it was segregated by Marcano-Berti (1969). The data also indicate that the monotypic Salvertia may not be distinct from Vochysia. More important, these genera do not differ from Qualea and Vochysia, respectively, in any characters that affect the patterns investigated in this study. Thus I assume that my observations of floral development and vasculature in Qualea and Vochysia also apply to Ruizterania and Salvertia respectively.

Material for SEM work, undertaken to investigate organ initiation, was dissected and dehydrated in an ethanol/acetone series, critical point dried, and coated with gold/palladium. Images were produced with a JEOL 5410LV at 5 kvolts.

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Material for serial sectioning, undertaken to examine vasculature, was dehydrated in an ethanol/toluene series and embedded in paraffin. Relatively mature buds were used to ensure as much development of the vasculature as possible. Specimens that were difficult to section were exposed at the tip in their paraffin blocks and soaked for at least one week in 2:5 glycerin:ethanol (70%) with acetic acid added to 10% of the total volume. Microtome sections were made at 10-15um. Those that were particularly rich in tannins were treated for up to two hours with Stockwell's bleach (Schmid, 1977). All were stained with Johansen's safranin in 50% ethanol, and counterstained with either chlorazol black E or fast green followed by orange G. Illustrative sections were drawn using a camera lucida.

RESULTS

Only elements of development and vasculature related to the corolla and androecium will be presented here; development and vasculature of the other floral organs are described more fully in chapter two. In all Vochysiaceae the floral apex is concave, therefore floral organs in general develop underneath (equivalent to "in front of" or "adaxial to") the previously initiated organs. Descriptions of floral vasculature are based on serial sections, presented in acropetal sequence.

I. Vochysia

All species of Vochysia that were examined (Table 2) had three petals and two staminodes, the most common configuration in this genus (Stafleu, 1948). Suitable material was not available of species with one or no petals. No significant variability was found among the species of Vochysia used in this study.

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A. Organ initiation (V. tucanorum, V. pumila, V. elliptica)(Figs. 49-52) - SEM photos show that three petal primordia are initiated on the flanks of the developing floral cup. The first two primordia appear between the third and fifth and the first and third sepals. These are followed by the third petal primordium, which arises between the second and fifth sepals (Fig. 49). A stamen primordium is then initiated directly below (adaxial to) each of these (Figs. 50,51). The order of initiation could not be determined, but the central one, which becomes the fertile stamen, elongates rapidly, becoming noticeably larger than the three petals and two staminodes. The six organs (three petals and three stamens) are squeezed into the area defined by the floral cup, and although their bases are not affected, the distal portions shift to fill the space (Fig. 52). At this stage neither the style nor the filament has elongated; the style shows some growth prior to anthesis, but substantial elongation of both structures occurs at anthesis.

B. Vasculature (V. tucanorum, V. pumila, V. haenkeana, V. densiflora)(Figs. 53-57) - The pedicel contains a continuous ring of vascular tissue; there are also small medullary bundles that anastomose with the vascular cylinder (Fig. 53). The cylinder separates at the base of the flower into discrete bundles that enter the floral cup and the ovary. One of the former then branches to supply a trace to the fertile stamen (Figs. 54, 55). Higher in the floral cup a second branch goes to the middle petal and then divides to supply lateral traces to adjacent regions of sepals three and five (Fig. 56). The staminodes and lateral petals are supplied in similar fashion in pairs (one staminode and one petal) by the bundles that terminate as lateral traces of adjacent regions of sepals one and three and sepals two and five (Figs. 56, 57).

II. Erisma

The number of staminodes and rudimentary petals (herein referred to together as "accessory structures") was variable in the taxa used in this study. Furthermore, the specific identity of a structure as one or the other was often a matter of conjecture because their position is not clear relative to the fused sepals and the petal (Figs. 58, 63). No significant variability in the development or vasculature of the corolla and androecium was found among the species of Erisma used in this study (Table 2).

A. Organ initiation (E. bracteosum, E. floribundum)(Figs. 59-63) - Flowers of these species have at least four accessory structures, but may have up to six (four rudimentary petals and two staminodes). Five petal primordia are initiated, the first three between sepals one and three, two and five, and three and five. This last enlarges rapidly relative to the other two, and becomes the full-sized petal. Petal primordia four and five appear in the remaining positions, on either side of sepal four (Figs. 59, 60). During the course of development, some of the lateral petal primordia may abort and persist as irregularly shaped bumps on the flanks of the floral cup (Fig. 63).

Whereas five petal primordia are always initiated, this is not the case with stamen primordia. In some buds there may be five initiated, but it is more common to see three, directly in front of (under, or adaxial to) the petal primordia (between sepals three and five, one and three, and two and five). The stamen primordium that is directly in front of the full-sized petal develops into the fertile stamen. The stamen primordia of E. bracteosum appear to arise as downward elongations of the petal primoridia rather than as separate discrete mounds (Figs. 61, 62). In E. floribundum this was observed in the formation of the primordia of the staminodes but not the fertile stamen, which first appears as a discrete mound below the primordium of the major petal. Few specimens of E. floribundum were observed at this specific stage.

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At maturity, Erisma flowers always possess one fully developed petal and one fertile stamen, however the number of accessory organs varies. It seems the number of lateral stamen primordia that are initiated can vary, as can the number of petal primordia that abort. As a result, the identity of a structure at maturity can only be determined with certainty when there is both a staminode and a rudimentary petal (or aborted vestige) at one position (Fig. 63). These pairs occur most often at the positions directly adjacent to the petal/fertile stamen pair (between sepals one and three and sepals two and five)(Fig. 46). If there is only one accessory organ, as occurs frequently on either side of sepal four, it cannot be determined to which whorl it belongs. Nonetheless, it may be reasonable to assume that these are most often rudimentary petals, because petals are always initiated in these positions, whereas stamens are much less frequently so.

The petal may grow relatively large in the bud, wrapping around the stamen and gynoecium and becoming highly wrinkled and folded. The filament and style elongate to varying degrees at anthesis, and considerable twisting may occur in one or both; this twisting obscures the position of attachment of the stamen.

B. Vasculature (E. bracteosum, E. uncinatum, E. floribundum, E. japura)(Figs. 64-66) - Vasculature to the petal and fertile stamen is similar to that seen in Vochysia. Although some weakly developed vascular tissue was observed in the rudimentary petals and staminodes of some specimens, this vasculature was isolated and no connection was observed with the vascular bundles that supply the calyx (Figs. 64-66).

III. Erismadelphus

This genus is poorly known, and little material is available.

A. Organ initiation - Immature material was not available for studies of early development, but dissections of mature buds of Erismadelphus exsul show that the stamen is in front of a petal, as

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described by Keay and Stafleu (1953). Staminodes are antepetalous as well.

B. Vasculature (Erismadelphus exsul) - Vasculature is similar to that seen in Vochysia and Erisma. Each staminode is supplied by a branch of the bundle that also supplies the petal directly behind it, as in Vochysia.

IV. Qualea

The species of Qualea examined in this study vary in the number of staminodes and rudimentary petals they possess. As in Erisma, the specific identity of structures is often difficult to determine from mature material. The observed configuration of these structures in each species will be noted below in the descriptions of development and vasculature. Preliminary floral dissections showed that at maturity the fertile stamen is not directly in front of the petal (Fig. 67), as it is in Vochysia, Erisma, and Erismadelphus, and that the position of these two organs relative to each other varies slightly among species.

A. Organ initiation - Early development is not identical in the four species examined in this study.

1. Qualea parviflora, Q. grandiflora, Q. multiflora (Figs. 68-72) - The flowers of these species, which are probably closely related (Stafleu 1953; also see chapter four), have no staminodes or reduced petals. Stages in petal initiation were observed only in Q. grandiflora. SEM photos show that a petal primordium is initiated between sepals one and three and a second between sepals three and five (Fig. 68). The primordium between sepals three and five continues to develop, whereas the other disappears as the floral apex expands. Occasional flowers of several Qualea species are found with two petals, but the position of the second petal has not been documented.

Three stamen primordia are initiated (Fig. 69) in all three species, although the third primordium, which is much smaller, was not

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observed in all specimens. The position of the lateral primordia is difficult to determine conclusively because the sepals overlap extensively, the floral apex is irregular in shape, and there is only one petal primordium to use as a landmark (see legend for Fig. 69). The lateral primordia abort immediately and generally are not present at subsequent stages of development. Occasionally one will persist as a protrusion on the floral cup near the base of the ovary (Fig. 71).

The primordium that will develop into the fertile stamen arises in an ambiguous position (Figs. 69, 70). It is partly under (adaxial to) the petal primordium but not directly so as in Vochysia and Erisma (Figs. 50, 51, 61, 62). On the other hand, it is not directly in front of the fifth sepal, as reported in published floral descriptions (e.g. Warming, 1875; Stafleu, 1953). As the organs develop there is some shifting of position within the area enclosed by the sepals; it appears, however, to be the petal that is displaced. The edge of the petal behind the enlarging fertile stamen is relatively displaced backwards as the floral cup expands; the petal appears to pivot on its edge in front of the third sepal. The petal is tangential to the ovary or nearly so, facing the stamen broadside, and its position in the bud is asymmetrical (Figs. 72).

In mature buds the petal is highly wrinkled and folded, and in some species is large enough to wrap around the stamen and gynoecium twice. As in Vochysia and Erisma, substantial elongation of the filament and style does not occur until anthesis. At that time there may be considerable twisting of the filament, particularly at its base, and of the style.

2. Qualea mori-boomii (Figs. 73, 74) - The flowers of this species have one pair each of rudimentary petals and staminodes (Fig. 67). Three petal primordia are initiated in sequence between sepals one and three, three and five, and two and five respectively (Fig. 73). The middle primordium (between sepals three and five), which becomes the

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full-sized petal, enlarges more rapidly than the others. Three stamen primordia are initiated lower on the sides of the floral cup (Fig. 74). The two lateral primordia, which develop into staminodes, form directly under the lateral petal primordia (between sepals one and three and sepals two and five). The middle primordium, which develops into the fertile stamen, arises nearly directly under (in front of) the middle petal primordium and is only very slightly offset if at all. However, the angle of attachment of the two organs differs; a line drawn to bisect the petal primordium will not bisect the stamen (Fig. 74), and the petal already appears slightly askew relative center of the flower.

B. Vasculature - Vasculature to the petal and the fertile stamen is somewhat variable in the six species examined. In all cases, and as in the other genera, the vascular tissue in the pedicel forms a ring surrounding the pith. Medullary bundles were not seen in any of the species examined. As in the other genera described, branches from the vascular cylinder enter the floral cup, and the remaining vascular tissue of the cylinder supplies the gynoecium. In all cases the bundle supplying the petal also branches to supply small bundles that become lateral traces in sepal three on one side and sometimes sepal five on the other side. Only where noted below was the stamen bundle observed to branch before entering the stamen. The species differ in details of the origin of the stamen trace.

1. Qualea parviflora (Figs. 75-78) - No staminodes or reduced petals were observed in this species. As the vascular cylinder separates into bundles, one segment divides laterally into two bundles that will supply the stamen and the petal (Fig. 75). The bundle supplying the stamen appears to migrate slightly laterally through the floral cup to enter the stamen (Fig. 76, 77). The petal trace is also displaced slightly in the floral cup, in the direction opposite the displacement of the stamen bundle (Figs. 76, 77).

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2. *Qualea mori-boomii*, *Q. rosea* (Figs. 79-81) - One pair each of staminodes and reduced petals were reported by Stafleu (1953) for *Q. rosea* but only one pair of structures of indeterminate identity was observed. Marcano-Berti (1989) does not mention staminodes or rudimentary petals in his description of *Q. mori-boomii*; one pair of each was found in this study. As the vascular cylinder separates into discrete bundles, one large bundle, which will supply both the stamen and the petal, can be identified. Higher in the floral cup two bundles branch off from the adaxial side of this bundle (Fig. 79). These anastomose and the resulting bundle develops laterally in the floral cup for a short distance and enters the stamen (Fig. 80). The remaining large bundle becomes the petal midrib (Fig. 79). Staminodes/rudimentary petals were not visible in all specimens sectioned; where present they did not appear to have vascular tissue (Fig. 81). However, their points of attachment to the floral cup alternate with the median vascular bundles of the sepals. This supports the hypothesis of a position alternate with the sepals.

3. *Qualea lineata* - Both staminodes and rudimentary petals were observed in this species, although Stafleu (1953) reported only staminodes. The vasculature of this species is similar to that observed in the preceding two species, except that the large bundle that will supply both the petal and the fertile stamen comprises numerous extremely small bundles. Several of these bundles separate from the adaxial side of this group and anastomose into one bundle that enters the stamen. Vascular tissue was observed in neither the staminodes nor the reduced petals.

4. *Qualea dichotoma* (Figs. 82-84) - No staminodes or rudimentary petals were observed in this species. As the vascular cylinder separates in the floral cup, one segment divides laterally into three bundles (Fig. 82). The two flanking bundles anastomose, and the resulting bundle moves laterally to enter the stamen (Fig. 83). The

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remaining large bundle, which supplies the petal, moves in the floral cup to become oriented at an angle to the ovary (Fig. 84) as in the other species.

V. Callisthene

A. Organ initiation - Material at suitable stages for studies of organogenesis was not available. Examination of developing buds shows that the relationship of the petal and the stamen to each other and to the ovary and sepals is similar to what is seen in Qualea species.

B. Vasculature (C. major, C. fasciculata) - The pattern of vasculature to the petal and stamen in these two species is essentially identical to that seen in Q. mori-boomii and Q. rosea.

DISCUSSION

The results of this investigation do not support the hypothesis that in all genera of Vochysiaceae the fertile stamen is initiated in the same (antepetalous) position and that in one-petaled taxa the stamen is displaced as it develops. However, my observations also provide no evidence for antesepalous stamens in any genus, and thus offer no basis for Stafleu's hypothesis of reduction from two whorls. It can be seen from SEM studies that in species of Qualea the stamen does not arise directly in front of the petal (e.g. Fig. 69). However, the position at which the stamen does arise in these species is not antesepalous, but is slightly offset from antepetalous. The second half of my hypothesis is also contradicted: in no cases does it appear that the stamen is displaced. Rather, in species of Qualea and most likely Callisthene, it appears that the petal is displaced during development (Figs. 71, 72).

I. Fertile stamen position

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A. Erisma - In contradiction to published descriptions (Warming, 1875; Stafleu, 1954; Kopka and Weberling, 1984; Kawasaki, 1998), the fertile stamen of Erisma is antepetalous. Dissections of mature buds before elongation of the filament show that the stamen lies directly in front of the petal (Figs. 58, 63). At anthesis the filament twists at the base; superficially it may appear that the stamen is attached adjacent to the petal. However, if the stamen is removed, it can be seen that the scar marking the point of attachment is directly in front of the petal. Further evidence comes from observations of floral development in Erisma bracteosum, in which the petal primordium becomes elongated and forms the petal from the top portion and the fertile stamen from the bottom portion (Figs. 61, 62). Moreover, the pattern of vasculature to the stamen and petal is identical to that seen in the unequivocally antepetalous Vochysia (Figs. 54-56, 64-65).

B. Qualea and Callisthene - As in Erisma, the twist at the base of the filament of most species of Qualea and Callisthene can lead an observer to misjudge the position of the stamen and conclude that it is antesepalous (e.g. Warming, 1875; Stafleu, 1952, 1953). In fact the base of the stamen is not centered in front of the fifth sepal. Rather, it lies towards the edge of that sepal. The position at which the primordium is initiated also indicates that the stamen is not antesepalous (Fig. 69, 70, 74). Furthermore, the pattern of vasculature is fundamentally similar to that seen in Erisma, Vochysia, and Erismadelphus, in that the vascular supply to the stamen is continuous with the midrib of the petal (Figs. 75, 79, 82). This indicates that the stamen can be considered offset from antepetalous rather than antesepalous; in the latter case it would be more likely that the vasculature of the stamen would be continuous with the median bundle of the associated (fifth) sepal.

Stafleu (1953) said that staminodes in Vochysiaceae are always in front of petals, even in cases in which the fertile stamen is not. This

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study supports his observations. *Callisthene* has no staminodes, but in *Qualea* the erratic position is confined to the fertile stamen.

The species examined in this study differ in the exact position of the stamen. In the two species of *Callisthene* examined, as well as in *Q. mori-boomii*, *Q. rosea*, and *Q. lineata*, the stamen is little offset from antepetalous, whereas in *Q. parviflora*, *Q. multiflora*, and *Q. grandiflora* the offset is more substantial. This difference can be seen at the time of stamen initiation. In *Q. grandiflora*, *Q. parviflora*, and *Q. multiflora*, the stamen primordium is clearly not directly in front of the petal (Fig. 71), however the primordium of *Q. mori-boomii* is only slightly offset (Fig. 74). The greater degree of separation between the petal and stamen in *Q. parviflora* is also reflected in the vasculature. In this species the stamen and petal bundles separate laterally from a common supply, rather than radially into an inner and an outer bundle as in most of the other species (compare Figs. 75, 79, 83); they also separate farther down in the floral cup. However, in all cases anatomical data support the interpretation of the single fertile stamen as antepetalous.

II. Phylogenetic implications

The results of this study have clarified and simplified the distribution of the stamen position character in the family: *Vochysia*, *Salvertia*, *Erisma*, and *Erismadelphus* have the antepetalous position and only *Qualea*, its segregate *Ruizterania*, and *Callisthene* differ in having an offset stamen. Preliminary analyses of DNA sequences and morphology (chapter four) strongly indicate support these last three genera as a monophyletic group (hereinafter the "QRC" clade), thus the stamen position character can be explained by one reduction at the base of the family and one change of position within the family. Because only one reduction event is required, the single fertile stamen is homologous across Vochysiaceae, and this character is a synapomorphy for the

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family. The offset position is a synapomorphy of the QRC clade (Fig. 85).

The same preliminary phylogenetic studies have prompted a re-evaluation of some morphological features, and the resulting observations reinforce the notion that some characters shared by the genera of the Vochysieae, such as the unilateral wing of the seed, are only superficially similar (in Vochysia and Salvertia it is formed from compressed hairs; in the QRC group it is an extension of the testa). Other characters, such as the capsular fruit, are likely to be plesiomorphic, but further analysis is needed. The studies reported here have uncovered additional differences between the putatively monophyletic QRC group and the rest of the family: the former are the only genera lacking medullary bundles, and are of course the only genera with an offset fertile stamen and displaced petal. Thus the monophyly of the tribe Vochysieae is called into question; a phylogenetic analysis is presented in chapter four.

As noted, evidence from sister-group analysis is not helpful in understanding the evolutionary history of the androecium of Vochysiaceae. The condition of having only one fertile stamen is an autapomorphy of Vochysiaceae no matter which family, Trigoniaceae or Myrtaceae, is the sister-group. Nonetheless it is interesting to note that obhaplostemony, the condition of having a single whorl of antepetalous stamens, is found scattered throughout Myrtales (Dahlgren and Thorne, 1984; Ronse de Craene and Smets, 1995). This study has shown that the Vochysiaceae can be considered fundamentally obhaplostemenous, with the androecium of the QRC group being a derived variant of that condition. Among families in which the first or only whorl of stamens is antepetalous, there are several, including Myrtaceae and Onagraceae of Myrtales, in which common petal/stamen primordia have been observed (Ronse Decraene et al., 1993). In this study such primordia were observed in the two species of Erisma in which

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organogenesis was examined. However, in a broad examination of this feature, Ronse Decraene et al. (1993) concluded that there is little evidence that these common primordia are of systematic value.

III. Loss versus suppression

Tucker (1984, 1988, 1997) and Basile and Basile (1993) have addressed the significance of reduction of floral parts. Tucker (1988) drew a distinction between loss and suppression; loss can be seen as the endpoint on a continuum of degrees of suppression, but the effects of loss and suppression on floral development can be different (Tucker, 1988). When organs are suppressed, primordia are initiated, but at some stage they cease development. At maturity the flower may show little or no sign that the primordia ever existed; nonetheless, primordia can serve as placeholders in the development of remaining floral organs so that the spatial arrangement of the remaining organs is maintained. In contrast, when organs are truly lost, no primordia are initiated. Without a complete whorl of primordia to determine spacing, organs in that whorl or the next may arise in unexpected and sometimes unpredictable positions (Tucker, 1988; Ronse de Craene and Smets, 1995).

Tucker (1984, 1997) suggested that features of early floral development (organogeny) are more likely to be constant across broader taxonomic categories than features of middle or late development (organ growth and tissue differentiation, respectively). The latter are likely to vary among genera or species. Thus since true loss of organs is manifest early in floral development, one might expect it to be stable across genera or an entire family. Suppression, on the other hand, can occur at a wide variety of stages during development and is likely to be variable even within genera.

Within Vochysiaceae reduction in floral parts is a constant feature, but the numbers of those parts varies among and within genera and in some cases even within species or individuals. According to

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Tucker's hypothesis, this variability would implicate suppression as the important force in organ reduction. This prediction is only partially born out by this study.

A. Androecium - In the androecium of all three genera examined, two stamens are completely lost and two are suppressed to a greater or lesser extent. It must be noted, however, that descriptions of monotypic *Salvertia* and some species of *Vochysia* indicate that they may possess up to four staminodes (Stafleu, 1948), in which case no stamens have been completely lost. It is also possible that in some *Erisma* flowers four stamen primordia are initiated, but this was not conclusively seen in any specimens. In *Vochysia*, *Erisma*, and some species of *Qualea*, two of the three primordia that are initiated become staminodes (the third becomes the fertile stamen). In other species of *Qualea*, suppression of the two lateral stamen primordia occurs immediately, and there are no staminodes.

B. Corolla - *Salvertia* and *Erismadelphus* have a complete corolla of five petals; all other genera have fewer. All species of *Vochysia* examined in this study have three petals, and in all species three petal primordia were initiated. In *Vochysia*, therefore, two petals are lost (possibly more in species with one or no petals). *Qualea*, *Callisthene*, *Ruizterania*, and *Erisma* have one petal. In *Erisma* five primordia were always initiated (Figs. 60-62), and thus only suppression is involved in corolla reduction.

Species of *Qualea* show both loss and suppression of petals. In *Q. mori-boomii* three primordia are initiated, thus two petals are lost as in *Vochysia*. Development of the two lateral primordia is limited, and they form two thread-like rudiments (Figs. 67, 81). In *Q. grandiflora* only two primordia were observed (Fig. 68), thus an additional petal has been completely lost. One of the primordia disappears immediately as the floral apex expands; the other completes development. Thus although all *Qualea* species have one full-size petal, the two species on which

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clear observations could be made differ in the number initiated and therefore the number that can be considered lost. There is further variability in the timing of suppression of those that do not complete development.

Thus of the three genera examined in this study, Vochysia shows loss of two petals, Erisma shows suppression of four to varying degrees, and Qualea shows both loss and suppression. Because the number of fully developed petals varies from five to none within the family, differences in the pattern of loss and suppression might be expected among the genera. However the pattern observed is not consistent: both Qualea and Erisma have one petal at maturity, but Erisma has five initiated whereas Qualea has three (perhaps two in some cases). Furthermore, whereas Vochysia has three petals to the one of Qualea, both have three initiated (at least in some Qualea species).

Thus Vochysiaceae show both loss and suppression in both the corolla and the androecium, with less variability in the androecium. The variability among Qualea species in the number of petals initiated is not in complete accord with Tucker's hypothesis that events early in development are more likely to be constant within genera. However, floral development is flexible enough to provide examples contrary to any hypothesis. Furthermore it is possible that a third petal primordium exists too briefly in Q. grandiflora to have been observed in this study. In the androecium of Qualea and in the corolla and androecium of the other genera examined no variability was observed in the number of primordia initiated, as predicted by Tucker. There is, however, considerable variation among the genera.

Tucker (1988) and Ronse de Craene and Smets (1995) have noted that when loss occurs in the corolla whorl, the position of the stamens may become irregular. The complete loss in Qualea of two petals (in some cases possibly three) might then be implicated in the erratic position of the fertile stamen. However, staminodes of Qualea are antepetalous,

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and the stamen and staminodes of *Vochysia* are likewise unaffected by the loss of corolla parts. Furthermore, although the position of the fertile stamen in *Qualea* is unusual, it is reasonably predictable, being always more-or-less offset from directly in front of the single petal. Thus there are no observations that lead to an obvious and consistent developmental explanation for the offset position of the fertile stamen in *Qualea*. It does, however, provide a distinctive synapomorphy for the clade consisting of *Qualea*, *Ruizterania*, and *Callisthene*, in contrast to the strictly antepetalous position seen in the other genera of both tribes.

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Table 3. Some features distinguishing the tribes and genera of Vochysiaceae, as described by Dumortier (1829), Stafleu (1952), and Kawasaki (1998). † = QRC clade. circum. = circumferential; incl. phloem = included phloem; indehisc. = indehiscent; seed wing comp. = seed wing composition; unilat. = unilateral.

	ovary position	**fertile locule number**	**fruit type**	**incl. phloem**	**petal number**	**ovules/ locule**	**seed wing**	**seed wing comp.**
Vochysieae								
Vochysia	superior	3	capsule	-	3	2	unilat.	hairs
Salvertia	superior	3	capsule	-	5	2	unilat.	hairs
†*Qualea*	superior	3	capsule	-	1	many	unilat.	testa
†*Ruizterania*	superior	3	capsule	-	1	many	unilat.	testa
†*Callisthene*	superior	3	capsule	-	1	many	circum.	testa
Erismeae								
Erisma	inferior	1	winged, indehis.	+	1	2	---	---
Erismadelphus	inferior	1	winged, indehis.	+	5	1	---	---

Fig. 46. Floral diagrams of genera of Vochysiaceae according to descriptions in the literature (e.g. Warming 1875; Stafleu 1948, 1952, 1953, 1954; Kopka and Weberling 1984; Kawasaki 1998). Genera in top row have more than one petal and an antepetalous fertile stamen. Genera in bottom row have one petal and an antesepalous fertile stamen. Tribe Vochysieae comprises the four genera on the left, Erismeae the two on the right. Numbers of staminodes and rudimentary petals is variable in Qualea, Ruizterania, and Erisma. Symbols are as indicated in legend on figure.

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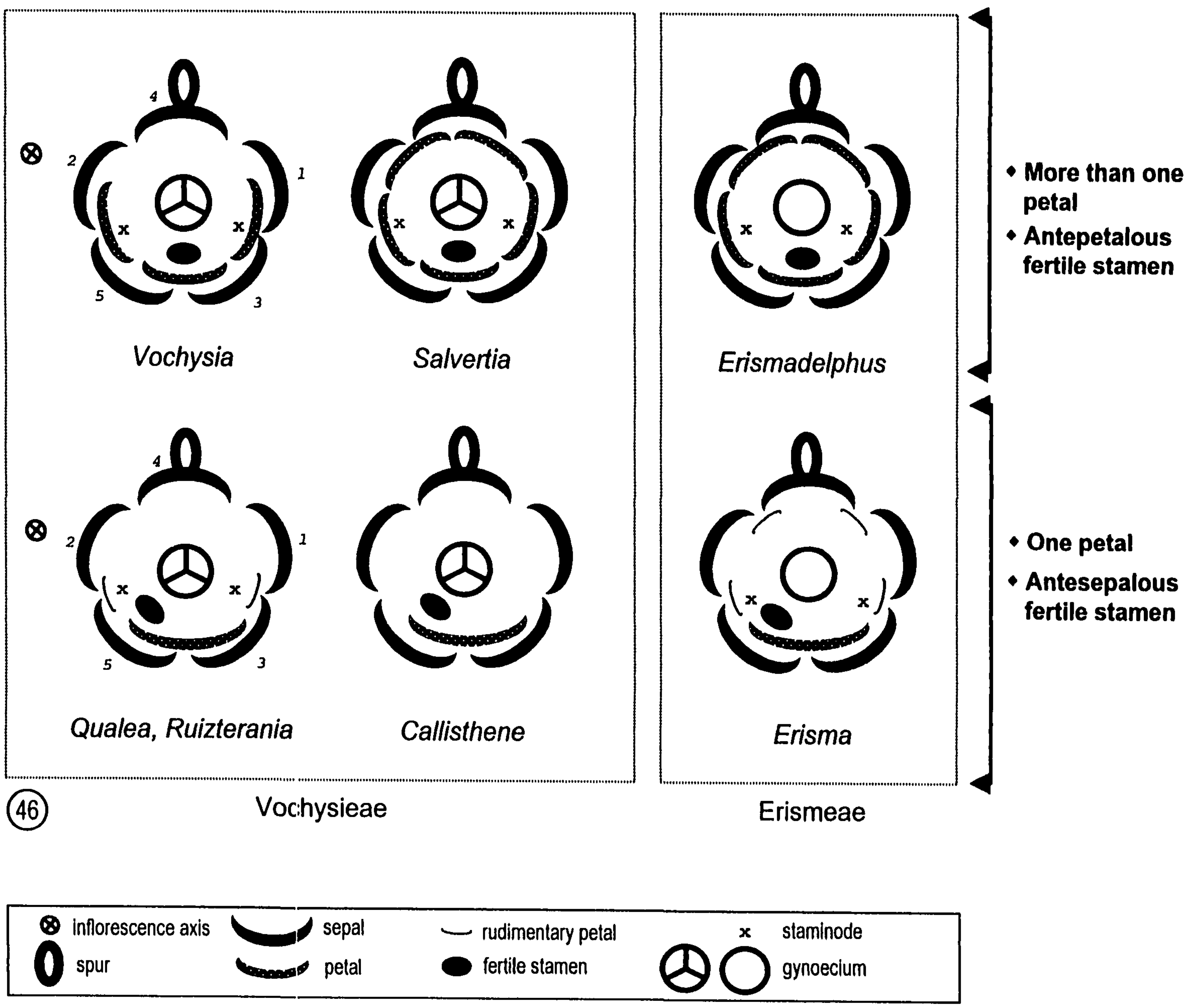

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Fig. 47. Diagram of traditionally accepted relationships among genera of Vochysiaceae, with the position of the fertile stamen indicated. Tribe Erismeae comprises the top two genera, Tribe Vochysieae the bottom five. Taxa indicated by a dotted line are described as having an antepetalous stamen, those with a double line an antesepalous stamen. Note that both morphologies are present in both tribes.

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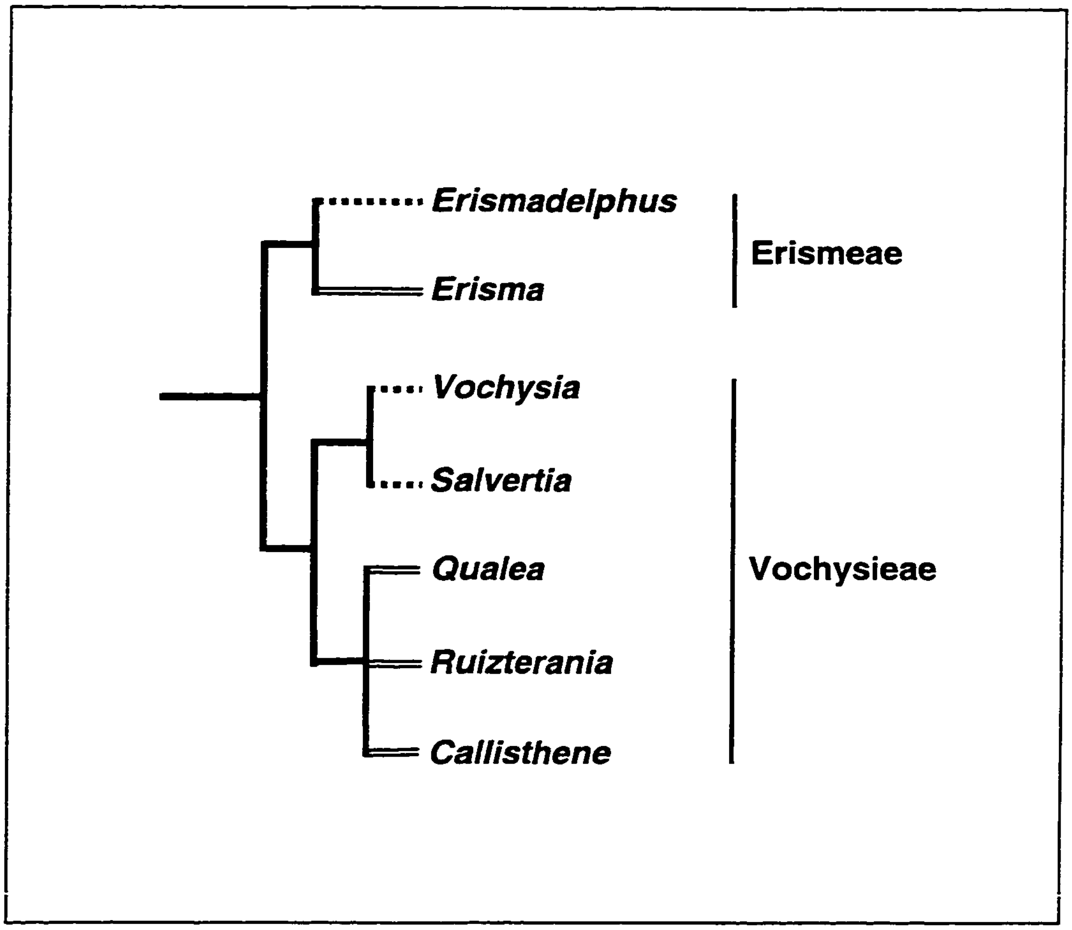

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Fig. 48. Illustration of possible mechanism of displacement of fertile stamen during development in single-petaled taxa such as _Qualea_. In the top diagram the stamen has been initiated in front of the petal. In the middle diagram these two organs have enlarged and the ovary has been initiated, creating space-packing problems and causing the stamen to be displaced. In the bottom diagram development is complete and the stamen has been displaced to a position in front of the fifth sepal. Dotted line bisects petal (and ovary); solid line bisects fifth sepal.

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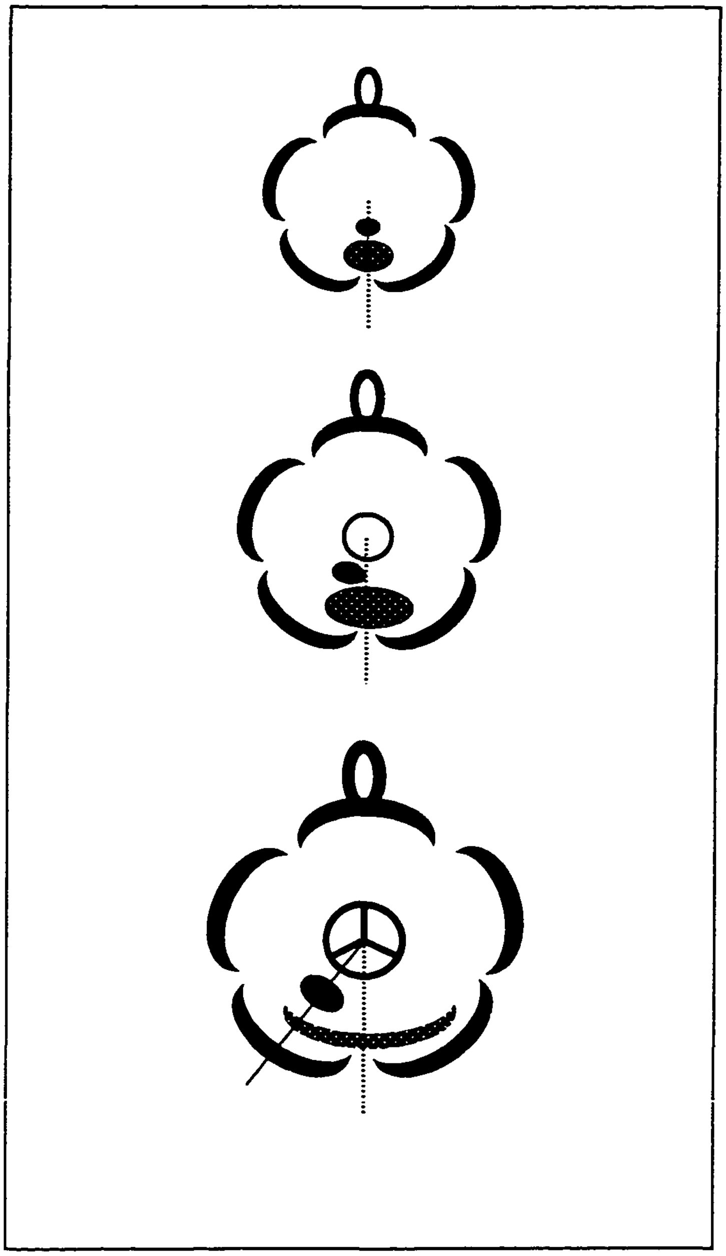

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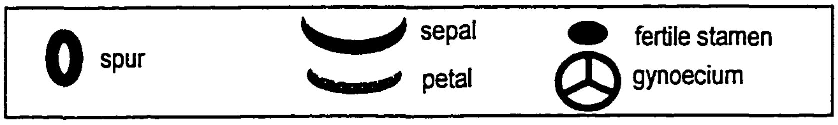

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Figs. 49-52. Floral development in Vochysia tucanorum (Litt et al. 69). Sepals have been removed. 49. Initiation of first two of three petal primordia on floral cup. 50. Initiation of two stamen primordia directly under petal primordia. 51. Later stage of development. Petal primordia removed. 52. Later stage of development. Fertile stamen is at center. Staminodes are attached directly under lateral petals but upper portions have been displaced to fill available space. fs, fertile stamen; p, petal, st, staminode. Figs. 49, 51, 52, Scale Bar = 100um; Fig. 50, Scale bar = 20um

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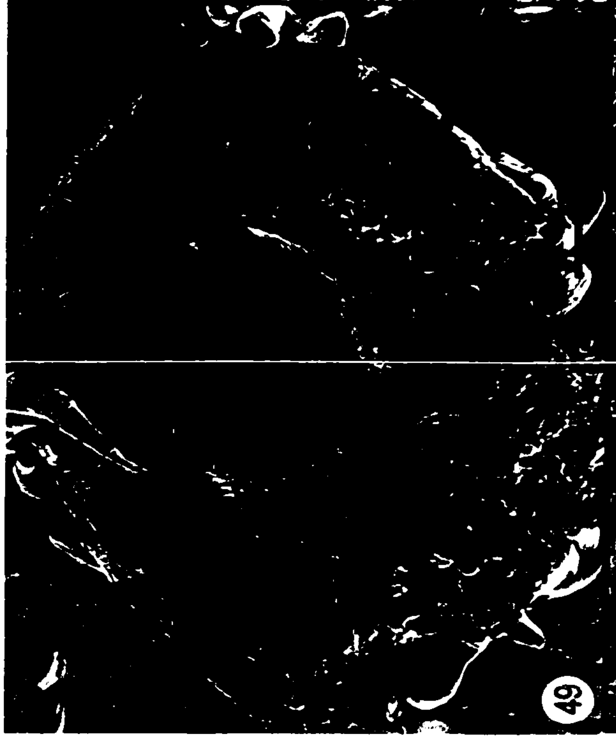

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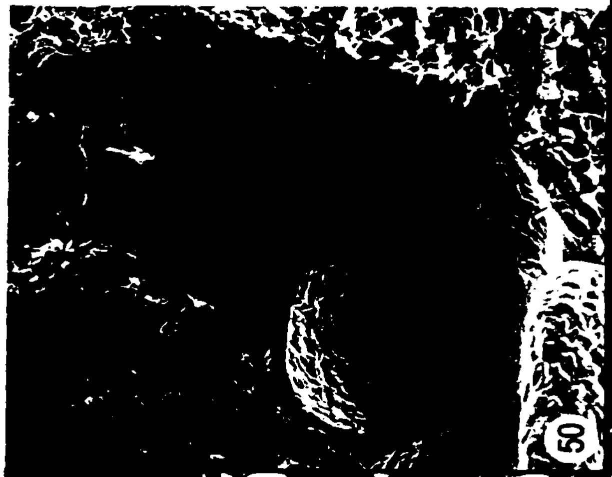

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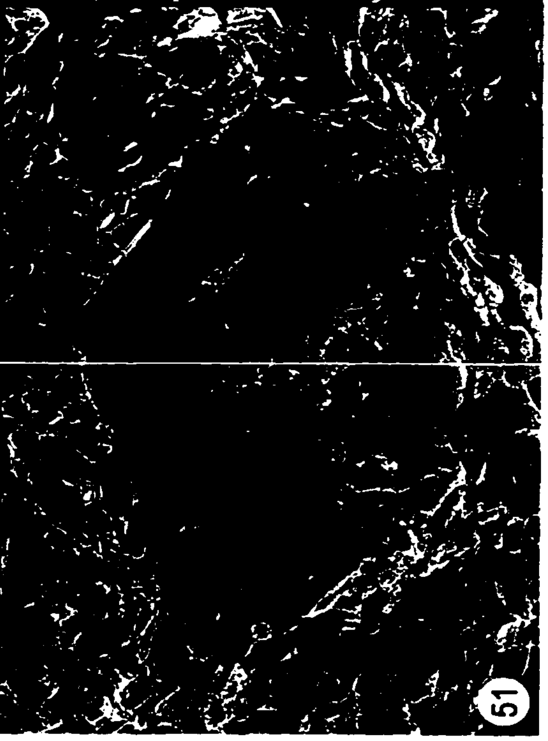

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Figs. 53-57. Floral vasculature of <u>Vochysia</u> <u>tucanorum</u> (Litt et al. 69). 53. Vascular cylinder in pedicel. Note medullary bundles (mb), gum canals (gc, not shown in subsequent sections). 54-56. Origin of stamen, staminode, and petal bundles. 54. Asterisk indicates bundle that will divide to supply fertile stamen and petal. 57. Section higher in bud showing position of stamen, staminodes, and petals. Open circles represent vascular bundles. br, bract; fs, fertile stamen; fst, fertile stamen trace; g, gynoecium; gc, gum canal; loc, locule of gynoecium; ov, ovule; p, petal; pt, petal trace; se, sepal; set; sepal trace; sp, spur; st, staminode; stt, staminode trace; sty, style; vc, vascular cylinder. Scalde bar (Fig. 53) is the same for all figures.

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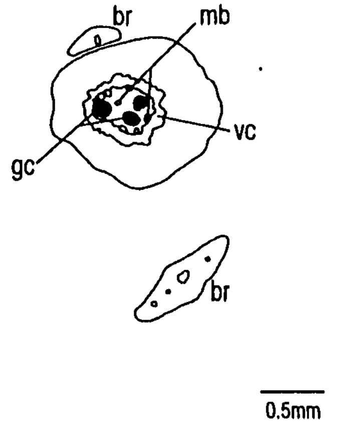
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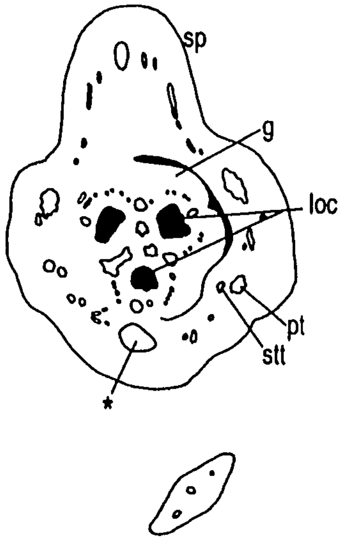
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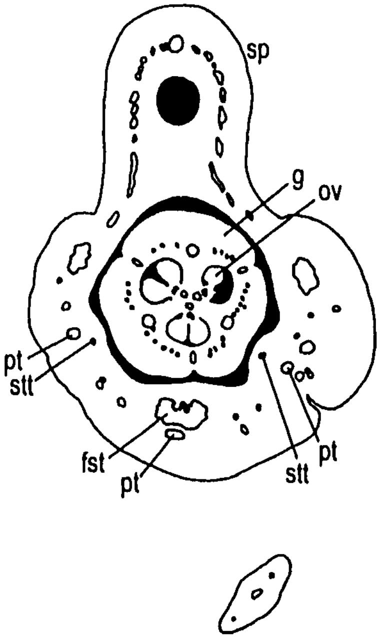
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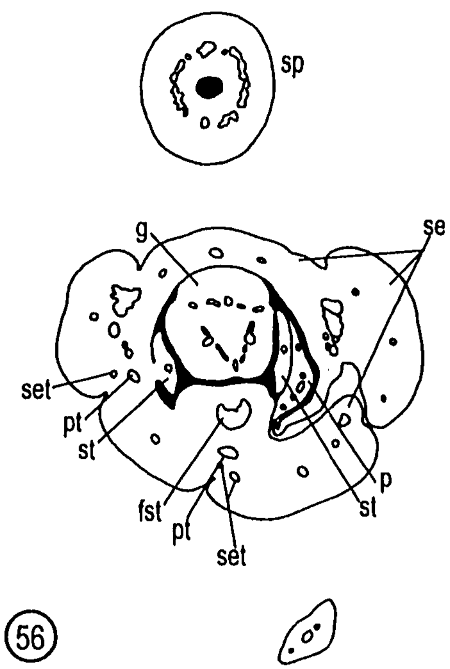
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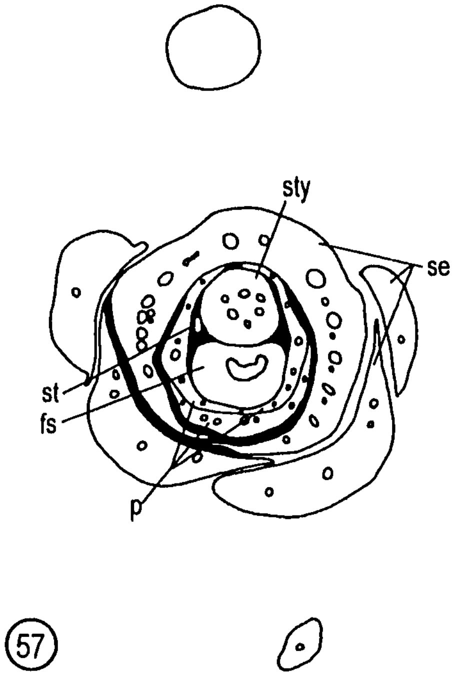
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Fig. 58. Cross-section of nearly mature bud of _Erisma_ _bracteosum_ (Vicentini 1111). Note fertile stamen is in front of petal. Also note ambiguous identity and position of accessory organs (asterisks). a, anther; f, filament; fs, fertile stamen; p, petal; se, sepal; sty, style.

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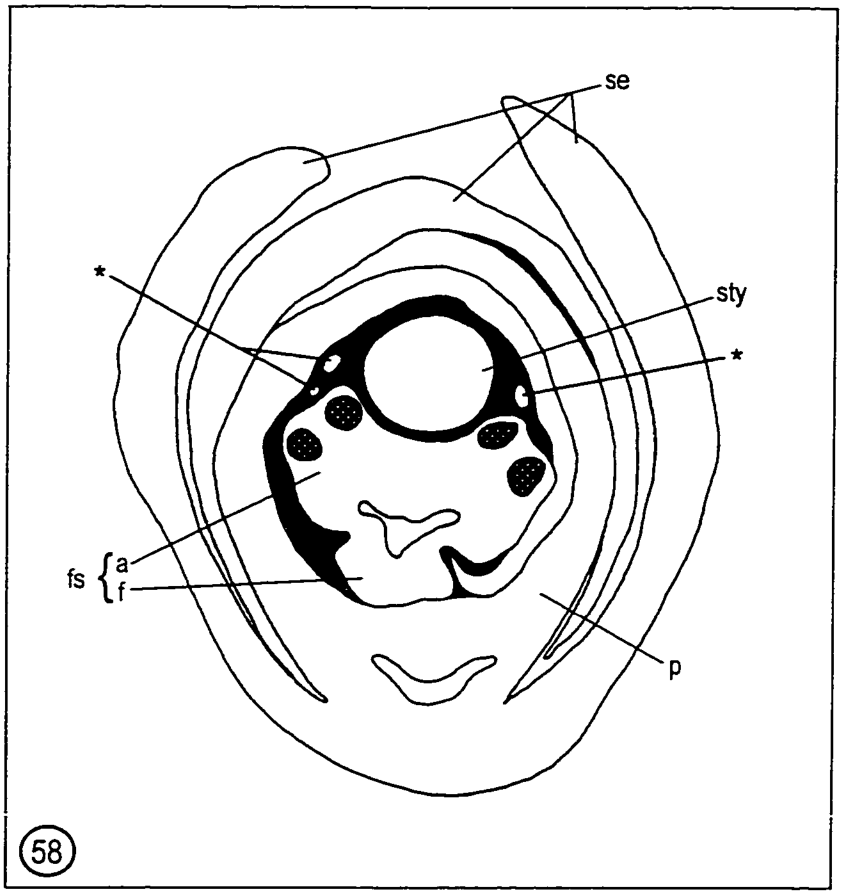

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Figs. 59-63. Floral development in Erisma bracteosum (Vicentini 1111) 59. Initiation of first three petal primordia. Fifth sepal has not been removed. 60. All five petal primordia. Fifth sepal has not been removed. 61. Initiation of fertile stamen and one staminode. The primordium of the center and one of the lateral petal primordia have been removed. Note continuity between petal and staminode primordia (asterisks). 62. "Common" stamen/petal primordia (asterisks). Center petal primordium has been removed. Two flanking primordia have elongated and can potentially form a rudimentary petal and a staminode. 63. Later stage of development. Petal has been removed; developing fertile stamen is directly in front of the scar. Adjacent and to the left is an aborted rudimentary petal with a staminode below it. The identity of the two other organs that have been removed is unclear. The one on the left is at a level even with the aborted petal and thus may be a member of the same whorl; the one on the right has a small bump of tissue above it that may be an aborted petal, thus it may be a staminode. as, accessory structure (see text); fs, fertile stamen; g, gynoecium; p, petal; rp, rudimentary petal; s2-s5, sepals (removed) in order of initiation; st, staminode. Scale bars = 100um except Fig. 60 (scale bar = 20um)

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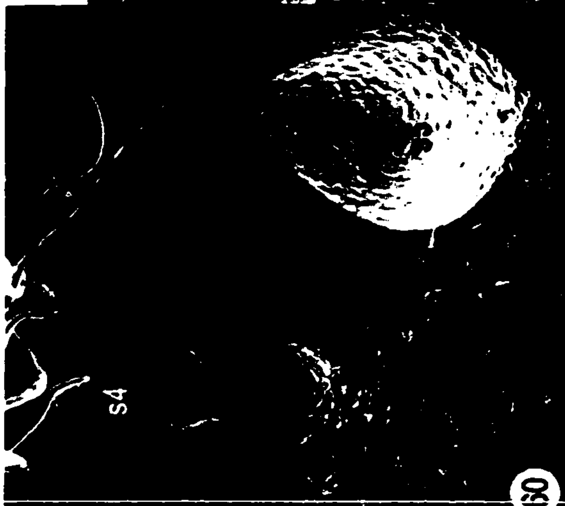

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Figs. 64-66. Floral vasculature of Erisma bracteosum (Vicentini 1111). 64. Origin of stamen bundle. 65. Origin of petal bundle from same bundle that produced stamen bundle. 66. Section higher up in bud showing relative positions of stamen and petal. Open circles represent vascular bundles. Black circles with white dots are pollen sacs. *, accessory structure; a, anther; f, filament; fs, fertile stamen; fst, fertile stamen trace; gv, gynoecium vasculature; loc, locule of gynoecium; p, petal; pt, petal trace; sp, spur; sty, style. Scale bar (Fig. 64) is the same for all figures.

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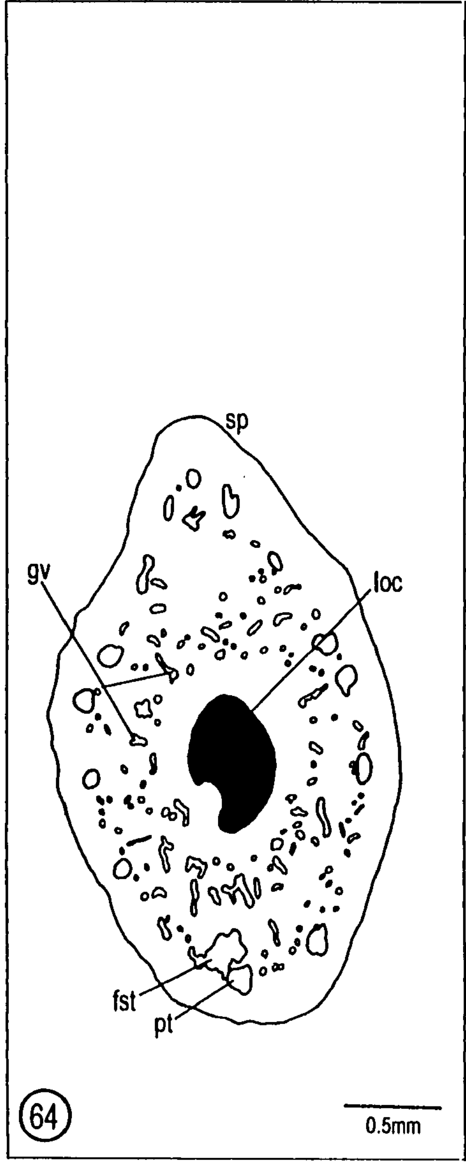

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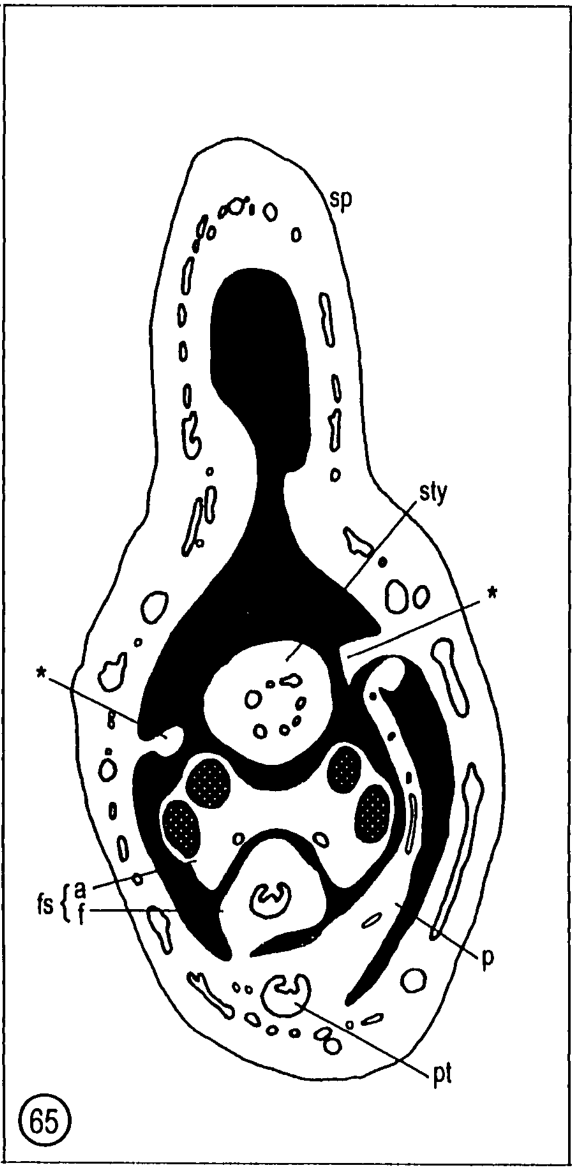

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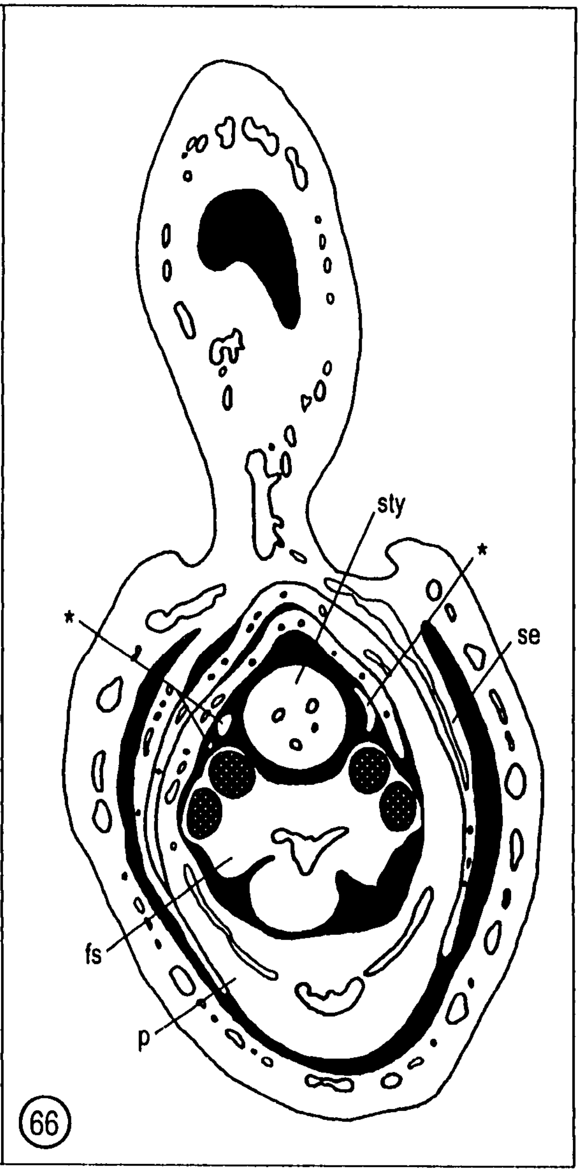

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Fig. 67. Cross-section of nearly mature bud of *Qualea mori-boomii* (Mori et al. 24723) taken near base of fertile stamen and petal. Note relative positions of stamen (represented by base of filament) and base of petal, and angle of petal relative to ovary. *, accessory structure; fs, fertile stamen; g, gynoecium; ov, ovule; p, petal; se, sepal.

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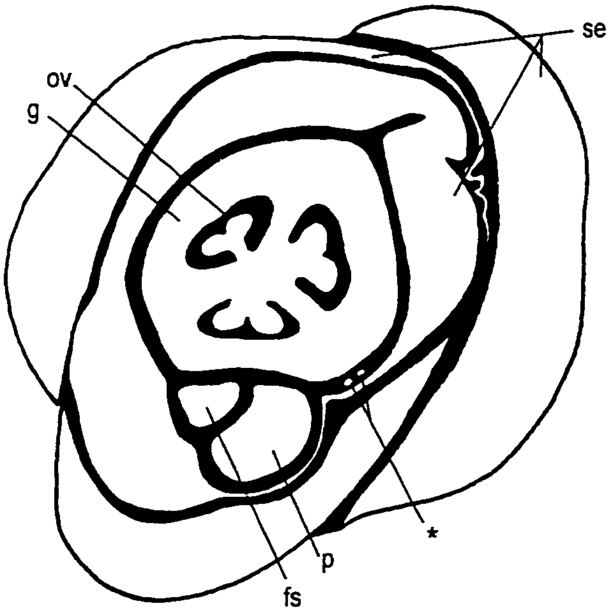

67

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Figs. 68-72. Floral development in Qualea grandiflora (Litt et al. 54) and Q. multiflora (Litt et al. 76). Fig. 70 is Q. multiflora; all others are Q. grandiflora. 68. Initiation of two petal primordia. 69. Initiation of two stamen primordia. Note that primordium in front of sepal 3 can be interpreted as being between sepals one (upper left) and three, between sepals three and four, in front of sepal one, or in front of the lateral edge of sepal three. 70. Position of fertile stamen primordium in Q. multiflora. 71. Later stage of development. Note bump (asterisk) next to ovary that appears to be aborted second stamen primordium. 72. Later stage of development. Note position of stamen and petal, and angle of petal relative to gynoecium. fs, fertile stamen; g, gynoecium; p, petal; s1-s5, sepals (removed) in order of initiation). Scale bars = 100um

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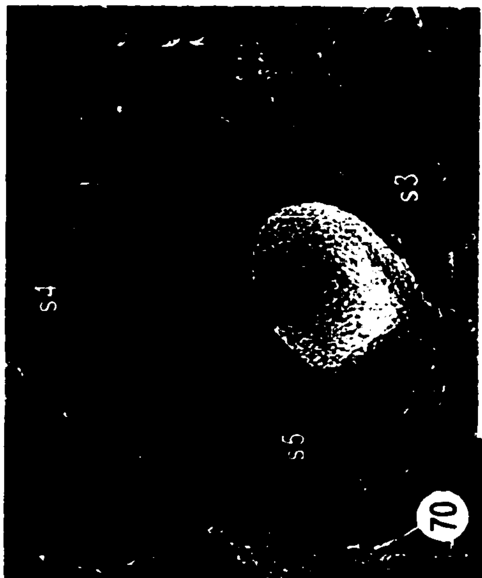
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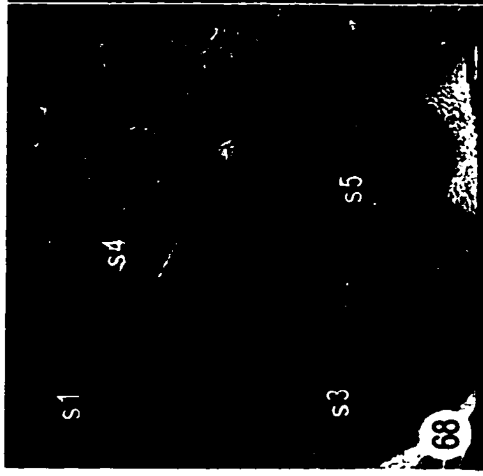
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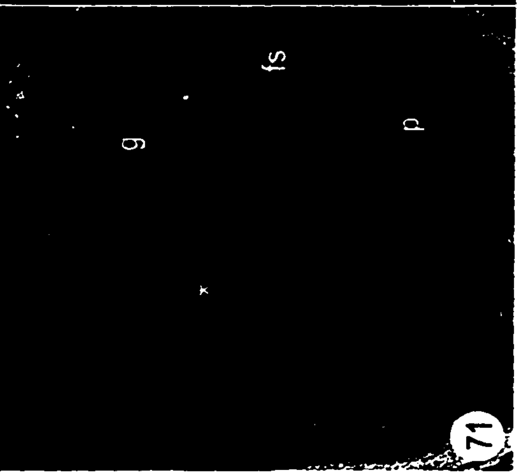
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Figs. 73-74. Floral development in Qualea mori-boomii (Mori et al. 24723). Sepals have been removed. 73. Initiation of three petal primordia. 74. Initiation of two stamen primordia (fertile stamen and one staminode). Petal primordia have been removed. Lines drawn across petal and fertile stamen primordia indicate slightly different orientation of these two organs. fs, fertile stamen; p, petal; st, staminode. Scale bars = 100um.

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Figs. 75-78. Floral vasculature of Qualea parviflora (unvouchered). 75. Bundles that will supply stamen and petal are beginning to separate laterally. 76. Vascular supply to stamen entering stamen, and petal bundle branching from bundles of sepal. Asterisk indicates base of filament. 77. Stamen bundle and petal midrib bundle. 78. Section higher in bud showing positions of stamen and petal. Black circles with white dots are pollen sacs. Open circles represent vascular bundles. a, anther; f, filament; fs, fertile stamen; fst, fertile stamen trace; g, gynoecium; p, petal; pt, petal trace; se, sepal; sp, spur; sty, style. Scale bar (Fig. 75) is the same for all figures.

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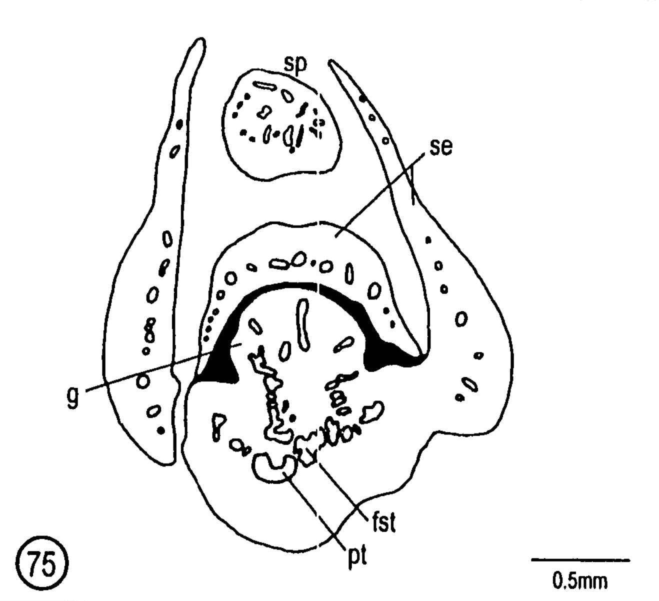

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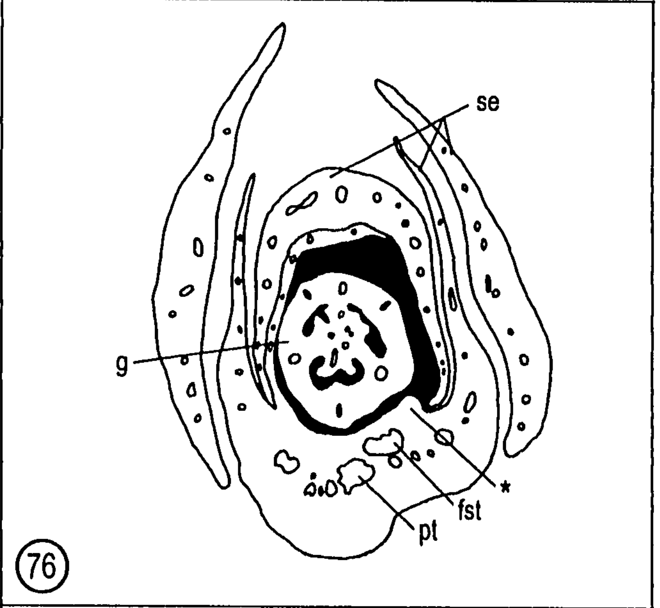

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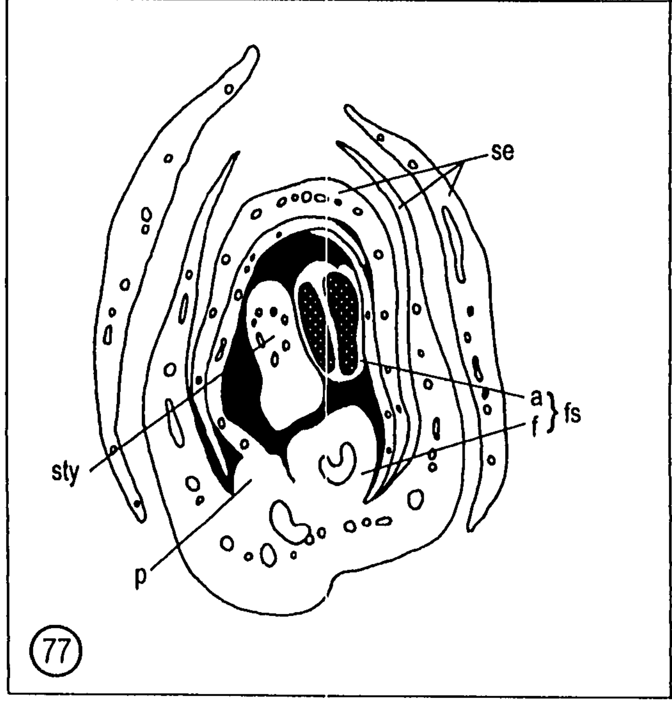

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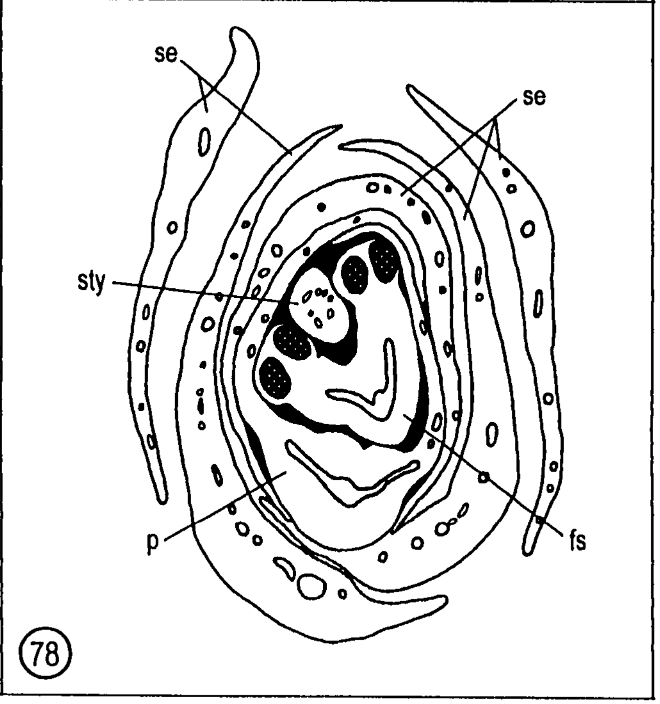

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Figs. 79-80. Floral vasculature of Qualea mori-boomii (Mori et al. 24723). 79. Two small bundles (asterisk) separate from bundle that will supply petal. 80. The two bundles fuse to form the stamen bundle; stamen bundle moves laterally and enters stamen. Open circles represent vascular bundles. f, base of filament; fst, fertile stamen trace; g, gynoecium; loc, locule of gynoecium; ov, ovule; pt, petal trace; se, sepal. Scale bar (Fig. 79) is the same for both figures.

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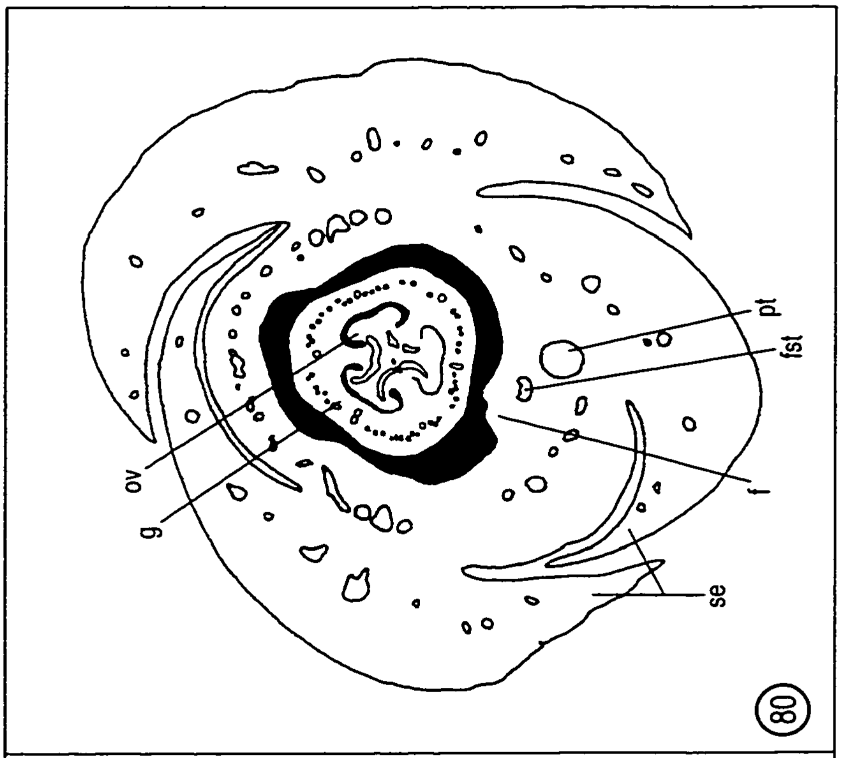

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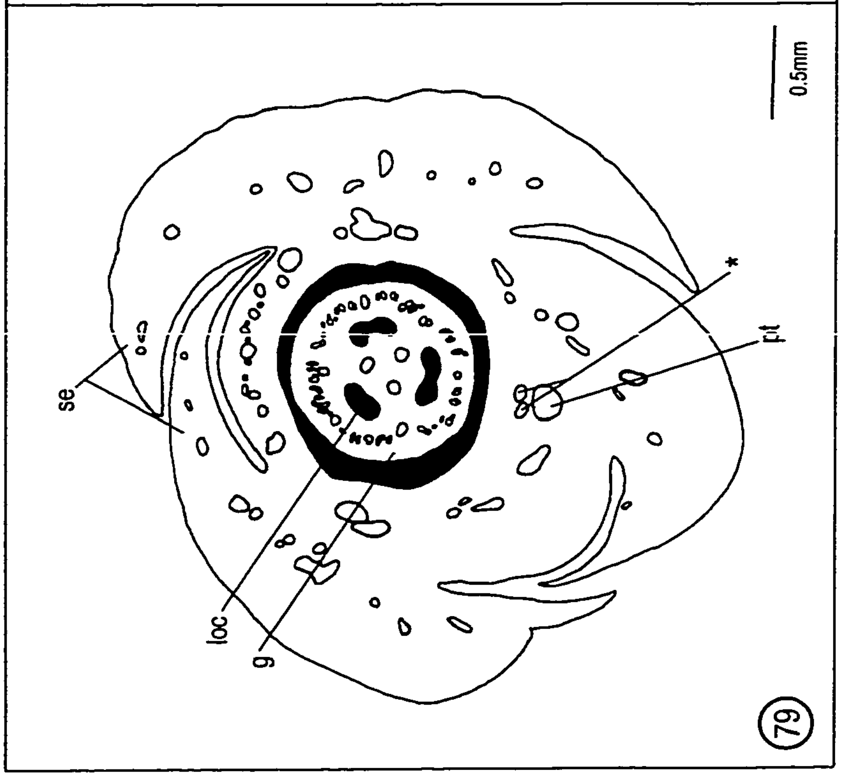

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81. Floral vasculature of Qualea mori-boomii (Mori et al. 24723). Section higher in bud than Figs. 79, 80. Note lack of vasculature in accessory organs (asterisk), as well as their ambiguous identity and position. Open circles represent vascular bundles. fs, fertile stamen; g, gynoecium; ov, ovule; p, petal; se, sepal; sp, spur.

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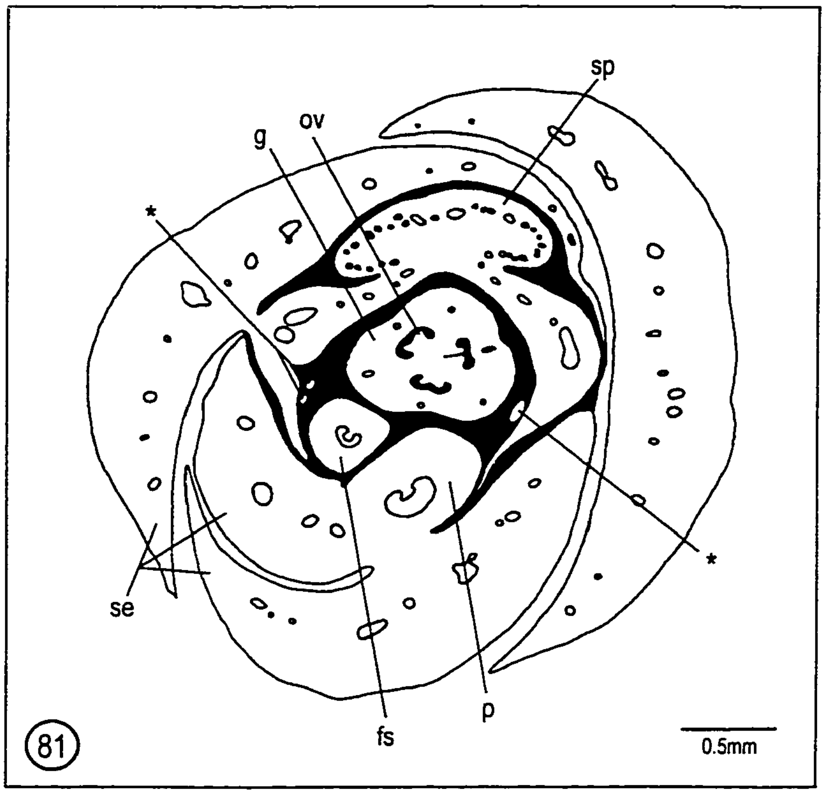

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Figs. 82-84. Floral vasculature of _Qualea_ _dichotoma_ (Gomez Klein 3279). Sepals 1,2, and 4 have not been drawn in Figs. 83 and 84. 82. Single bundle dividing into three large bundles. Single asterisk indicates portion that will supply the petal, double asterisk the two segments that will anastamose and supply the fertile stamen. 83. Outer two bundles (double asterisk) anastomose to form the stamen bundle. Single asterisk indicates bundle that will supply petal. 84. Petal midrib bundle. Note angle of petal relative to ovary. fs, fertile stamen; g, gynoecium; ov, ovule; p, petal; se, sepal. Scale bar (Fig. 82) is the same for all figures.

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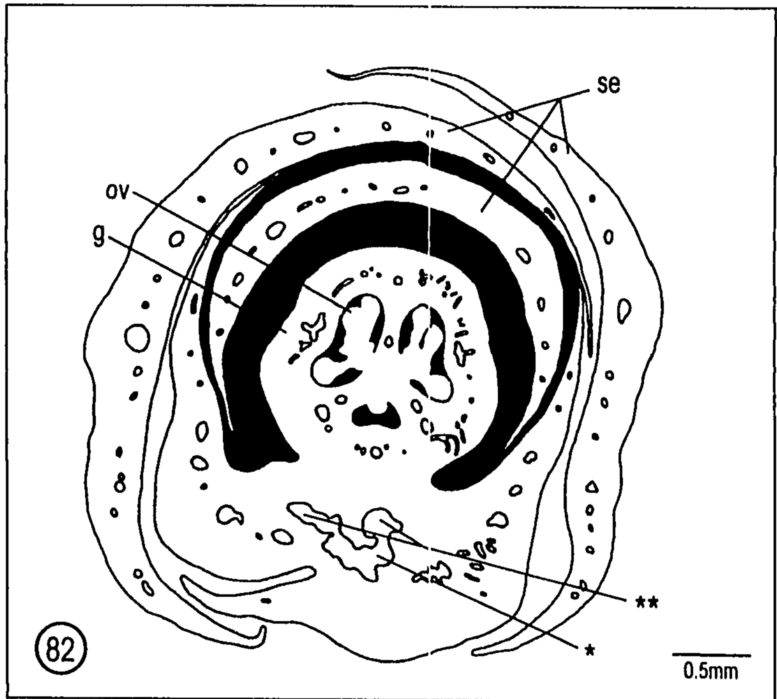

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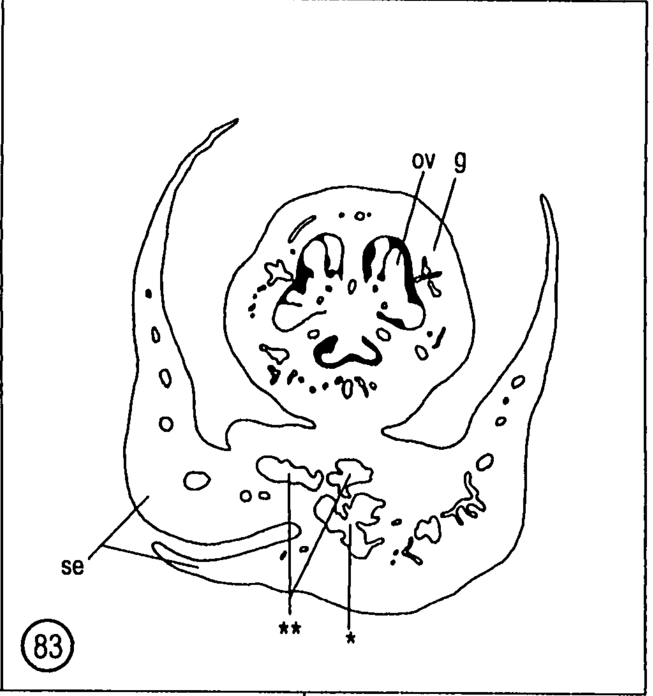

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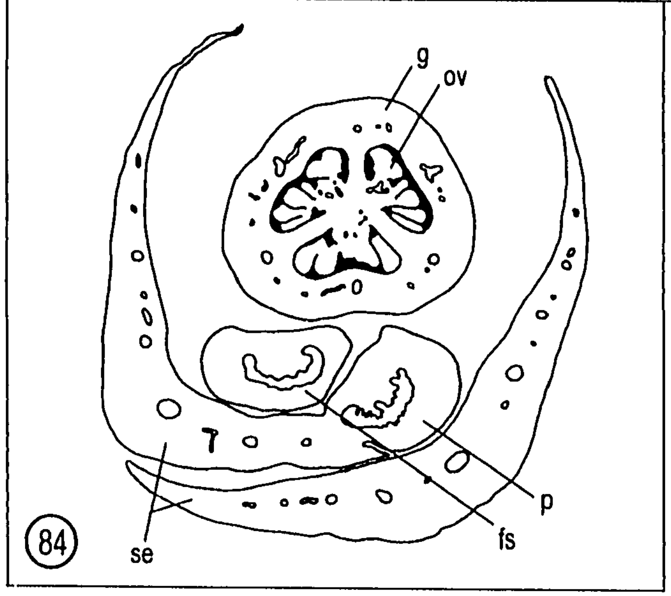

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Fig. 85. Diagram of traditionally accepted relationships among genera of Vochysiaceae, and the position of their fertile stamen as understood as a result of this study. Only the clade comprising _Qualea_, _Callisthene_, and _Ruizterania_ (striped branches) has a stamen in a position other than antepetalous, and it is an offset position that appears to be derived from antepetalous. The offset position is a synapomorphy for this group.

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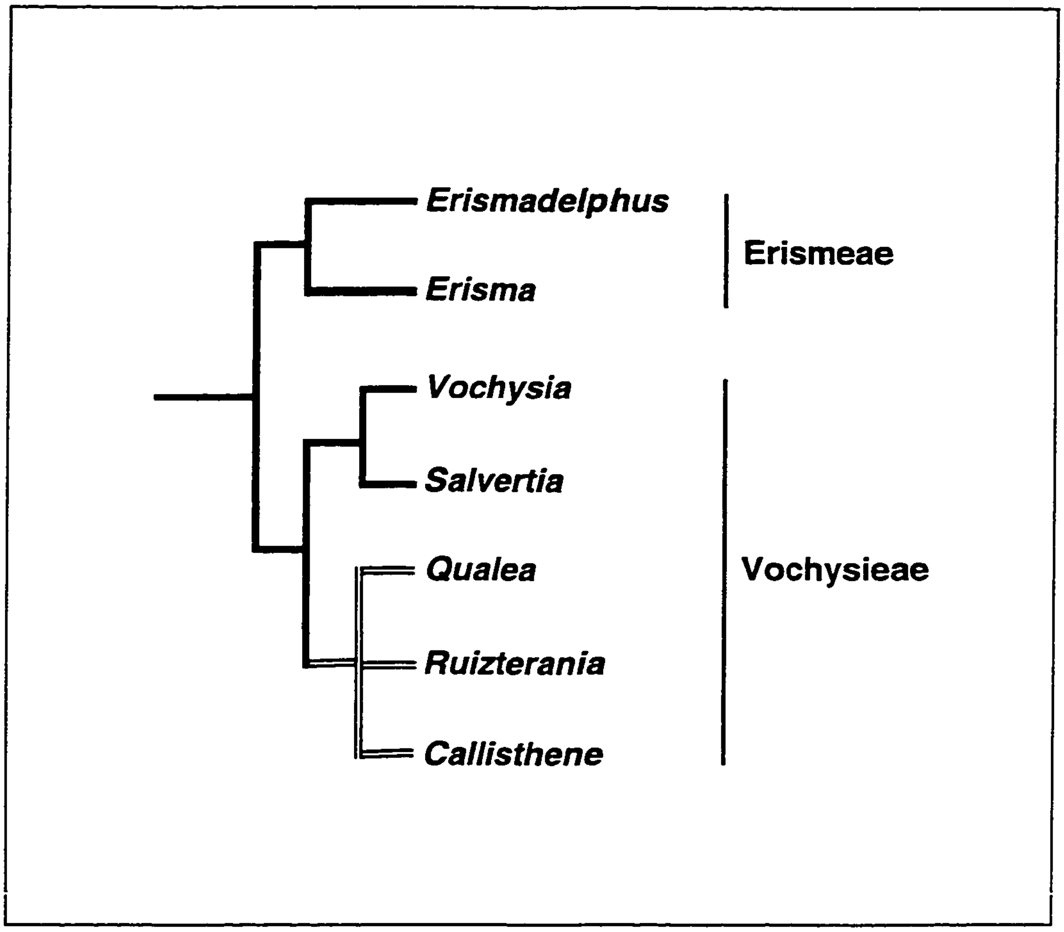

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═ offset fertile stamen

▬ antepetalous fertile stamen

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Chapter 4

Phylogeny and character evolution in Vochysiaceae

Vochysiaceae, a largely neotropical family found in savannas and rain forest, are known for their beautiful and highly distinctive flowers (Fig. 1). These are easily identified by their strong bilateral symmetry, spurred sepal, and single fertile stamen. Most also have a reduced number of petals. The family comprises seven genera (excluding *Euphronia* Mart. & Zucc.; Litt and Chase 1999) and upwards of 200 species (Stafleu 1948, 1952, 1953, 1954; Keay and Stafleu 1953; Marcano-Berti 1969; Martins 1981; Kawasaki 1998), all woody and mostly trees. Although treatments of the family often describe them as "trees, shrubs, and lianas" (e.g. Chant 1978; Cronquist 1981; Takhtajan 1997), there are no described species that are climbers or twiners, or true shrubs. There are a few savanna species of *Vochysia* Poir. that present the appearance of being herbacous (e.g. *V. pumila* Pohl in this study), but these in fact have underground xylopodia that survive the frequent fires of the habitat. All other species are small to large trees.

Six of the seven genera of Vochysiaceae, and nearly all the species, are found in the New World tropics. *Erismadelphus* Mildbr., the lone paleotropical genus, grows in the lowland rain forest of western Africa (Keay and Stafleu 1953). The range of the family in the Neotropics extends from southern Brazil up into the Yucatan, and from the Andes to the Atlantic; they are most diverse in Brazil (Stafleu 1948, 1952, 1953, 1954). The majority of species are confined to the lowland rain forest, and a few species are found in gallery forests.

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However, Vochysiaceae are a dominant and characteristic element of the dry savanna, particularly the Brazilian cerrado; Qualea grandiflora Mart. has been documented as the single species most commonly found in the savannas of northern and central South America (Ratter and Dargie 1992; Oliveira 1998).

The genera of Vochysiaceae have been divided into two tribes (Vochysieae Dumort. and Erismeae Dumort.) based on characters of the ovary and fruit (Dumortier 1829; Stafleu 1952)(Table 1). A careful reading of the literature, as well as field, herbarium, and laboratory observations of Vochysiaceae flowers, led me to realize that some of the features that have been used to relate the genera and to distinguish the tribes have been inaccurately described. Other characters that vary among the genera within the tribes, particularly Vochysieae, have been overlooked. In combination, these characters cast doubt on the integrity of the tribe Vochysieae as well as on the circumscription of some of the genera. Thus a phylogenetic analysis of the currently recognized genera of Vochysiaceae was in order.

The features of Vochysiaceae have also been scrutinized in the past few years in the wake of the results of phylogenetic analyses using DNA sequence data. Until recently, the unusual structure of Vochysiaceae flowers led systematists to include the family in the order Polygalales (Bessey 1915; Hutchinson 1969; Stebbins 1974; Dahlgren 1980; Cronquist 1981; Thorne 1992), with other families that are also characterized by distinctive zygomorphic flowers. Their closest relatives have been considered to be Trigoniaceae; Trigonia Aubl. was even included in Vochysiaceae by some authors (e.g. Bentham and Hooker 1862; Baillon 1878). However, an examination of the floral and vegetative structure makes it clear that similarities are superficial (for instance both have spurred flowers, but in Trigonia it

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is a petal that is spurred, as opposed to a sepal in Vochysiaceae) or common among flowering plants (for instance capsular fruit).

The presumed close relationship between Vochysiaceae and Trigoniaceae remained essentially unchallenged, in spite of the lack of specific apomorphic characters supporting it, until large-scale cladistic analyses - made possible by the use of DNA sequence data - were performed. The first such analysis (Chase et al. 1993), using *rbc*L, placed *Qualea* Aubl. in an alliance with myrtalean taxa. Reanalyses of the same data set (Chase and Albert 1998), and analyses combining *rbc*L with 18S and with 18S and *atp*B confirm this position (Soltis et al. 1999; Savolainen et al. 1999; Soltis et al. submitted). Analysis with 18S alone placed *Qualea* in Malpighiales (in the sense of APG 1998) but the taxa used in that analysis included few Myrtales and only one - unusual - Myrtaceae (*Heteropyxis* Y. B. Harv.)(Soltis et al. 1999), thus this was not a robust test of relationships. A more detailed analysis using *rbc*L to determine relationships among families of Myrtales and their relatives placed Vochysiaceae as sister-group to Myrtaceae sensu stricto (Conti et al. 1996; Conti et al. 1997); in this analysis *Heteropyxis* and *Psiloxylon* Thou. ex Tul., two genera that have been either included in Myrtaceae or elevated each to familial rank, fell outside Vochysiaceae (Fig. 86a). Subsequent analyses, using *mat*K (C. Quinn, P. Gadek, and P. Wilson, pers. comm.), *ndh*F (K. Sytsma, pers. comm.), and *rbc*L with a different selection of taxa (AL unpub. data), have all placed Vochysiaceae as sister-group to a Myrtaceae that includes *Heteropyxis* and *Psiloxylon* (Fig. 86b).

Whereas the suggested affinities of Vochysiaceae - with zygomorphic, single-stamened flowers - with Myrtaceae - with actinomorphic, multi-stamened flowers - were unpredicted and unexpected, an analysis of features other than those of the mature

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flower has revealed a variety of characters that appear to support this relationship. Among these are the possession of vestured pits and bicollateral vascular bundles (Metcalfe and Chalk 1950; Quirk 1980), antepetalous stamens, an epigynous developmental groundplan, and a suite of embryological features considered characteristic of Myrtales (Tobe and Raven 1983, Conti et al. 1997). In addition many species of Vochysiaceae have peeling bark on their twigs, opposite leaves, and leaf venation similar to that of Myrtaceae species.

The inclusion of Vochysiaceae in Myrtales, and the sister-group relationship with Myrtaceae, requires that we reevaluate hypotheses of character evolution within Vochysiaceae. Most obviously, it casts doubt on the assumption that the inferior ovary of Erismeae is the derived condition, as epigyny is characteristic of Myrtaceae and Myrtales. It had been assumed that the apparently superior ovary of Vochysieae was ancestral (Stafleu 1952; Kawasaki 1998), based on the relationship with other families in Polygalales and probably on the widespread acceptance of a superior ovary as being primitive among angiosperms. Thus the inclusion of Vochysiaceae in Myrtales provides additional reason to undertake a phylogenetic analysis of the family, to determine patterns of character transformation as well as to generate hypotheses of relationships.

A cladistic analysis of the relationships of the seven genera of Vochysiaceae was performed by Kawasaki (1992), using Trigoniaceae (coded as a single terminal) as outgroup (Fig. 87). Her data matrix included 27 characters of morphology and anatomy, culled largely from the literature. She did not attempt to examine generic concepts within the family, but the results of her analysis support the recognition of the tribes Vochysieae and Erismeae. However our current information indicates that it is more appropriate to use Myrtaceae as outgroup, and

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that several characters that she used were misinterpreted in the literature and as a result coded incorrectly. Thus, her analysis requires updating in the light of new information and new sources of data.

Here I report the results of a phylogenetic analysis of Vochysiaceae using both DNA sequence data and non-molecular data. The results of the analyses were used to address the following general questions:

1. Are the currently recognized tribes, genera, subgenera, and sections monophyletic?
2. What are the relationships of the taxa within Vochysiaceae?
3. What are the patterns of character transformation within Vochysiaceae, particularly with regard to floral features?

MATERIALS AND METHODS

I. Taxa

The following descriptions of the seven currently recognized genera of Vochysiaceae focus on characters that have been reinterpreted and/or are used in this analysis.

A. Vochysieae

The tribe Vochysieae are easily subdivided into two groups, although these have no taxonomic ranking. One group includes _Vochysia_ and _Salvertia_ A. St.-Hil. (hereinafter referred to as VS), multi-petaled taxa with one seed per locule (Table 1, Fig. 2). The other group comprises _Qualea_, _Callisthene_ Mart., and _Ruizterania_ Marc.-Berti (QRC), taxa with one petal and many seeds per locule. In the cladistic analysis performed by Kawasaki (1992) these latter formed a

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monophyletic group, but *Vochysia* and *Salvertia* were successive sister groups to that clade (Fig. 87). These two groups of genera have been united in one tribe on the basis of their superior trilocular ovary that becomes a loculicidal capsule, and winged seeds (Dumortier 1829; Stafleu 1952; Kawasaki 1998)(Table 1). However, there are differences between VS and QRC in all of these characters except locule number, and these differences may mean that the characters are not homologous. The ovary of *Vochysia* and *Salvertia* is partly inferior whereas that of QRC is wholly superior. The seed wing in *Vochysia* and *Salvertia* is composed of compressed hairs, whereas that of *Qualea*, *Ruizterania*, and *Callisthene* is formed from an extension of the testa (Boesewinkel and Venturelli 1987). Differences in fruit dehiscence are explained below. These characters, as well as others that highlight the divergence between the two groups, are discussed more specifically below. Homology of these characters is explored later in this chapter.

1. *Vochysia* and *Salvertia*. The largest genus, *Vochysia* (100+ species, Stafleu 1948), and the smallest, *Salvertia* (1 species), have long been recognized as similar to each other (e.g. Warming 1875; Baillon 1878; Stafleu 1948). *Vochysia* is found throughout the range of the family, in rain forest, gallery forest, and savanna. It shows the greatest variability in vegetative structure, with species ranging from tall rain forest trees to small suffrutescent savanna dwellers. Many of the savanna species share a suite of characteristics that are considered adaptations to this dry, fire-mediated environment and are found in species of other families as well: ample mucilage production, thick dry leaves, soft porous wood, peeling and/or corky bark, and contorted stems. Gallery forest and rain forest species generally do not exhibit these characteristics, although individual features (e.g. peeling bark) may be present in some species. Forest species are

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generally tall to very tall trees.

The flowers of *Vochysia* are remarkably stereotyped (Figs. 1, 2). They are all yellow, including generally all floral organs, although in some species the calyx is covered with brown, reddish-brown, or beige hairs. The fourth sepal is elongated, being characteristically at least three-times the length of the other sepals; the buds are relatively long and slender. A hypanthium, on which the outer floral organs are inserted, surrounds the gynoecium. Nearly all species have three oblong-obovate petals, although a few have one (e.g. *V. apopetala* Ule, *V. pinkusii* A. C. Smith) or none (e.g. *V. pacifica* Cuatrec., *V. eximia* Ducke). The fertile stamen is in front of the middle petal, and there are generally two staminodes, one in front of each of the lateral petals. The anther, like those of other Vochysiaceae, has a broad connective, which in *Vochysia* forms a cap that covers the stigma prior to anthesis. The thecae open and shed their pollen onto the style before the flower opens, and the stamen falls out of the flower at anthesis (Yeo 1993; Oliveira 1998). The gynoecium is adherent to the hypanthium at the base, and each of the three locules contains two ovules (only one of which forms a seed). In cross-section the ovary is three-lobed (Fig. 55). The fruit is an oblong loculicidal capsule, generally triangular or three-pronged in cross-section. Each locule contains one seed with a unilateral wing composed of densely matted hairs. At dehiscence the relatively thin pericarp folds back at each locule to expose the seeds.

Stafleu (1948) recognized three sections within the genus (Table 4): sect. *Vochysiella* Stafleu, with a pilose ovary and exfoliating bark; sect. *Ciliantha* Stafleu, with a glabrous ovary; and sect. *Pachyantha* Stafleu, with a suite of unusual features including no petals and subcoriaceous calyx lobes. Section *Pachyantha* includes only

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three species, sect. Vochysiella 20, and sect. Ciliantha 74 - the bulk of the genus. The latter two sections were further subdivided by Stafleu into subsections based on venation, pubescence, and additional features (Table 4).

When not in flower, Salvertia (1 species, S. convallariodora A. St.-Hil.), a common resident of South American savannas, can easily be mistaken for a species of Vochysia. A small-to-medium tree, it has the lightweight wood, thick corky bark, copious gum, and contorted growth form characteristic of cerrado vegetation. The fruits and seeds of Salvertia are identical to those of Vochysia. However, the flowers are conspicuously different: those of Salvertia have sepals of nearly equal size (although the bud is still elongate), and a corolla of five white petals (Fig. 2). In spite of the striking difference between five white and three yellow petals, the flowers are similar. The shape of the petals is similar, and the structure of the gynoecium identical, except that in Salvertia the stigma is large and lateral. The fertile stamen remains in the flower, and the connective is not extended into a cap, although according to the literature Salvertia has the same secondary pollen presentation mechanism seen in Vochysia (Oliveira 1998). Whereas Vochysia species are thought to be mainly bee pollinated, Salvertia has been shown to be hawkmoth pollinated (Oliveira 1996). Stafleu (1948) considered Salvertia, the only five-petaled member of the tribe Vochysieae, to possess the "simplest," or least derived, flower in the family.

2. Qualea, Callisthene, and Ruizterania. These three genera do not show the range of growth forms seen in Vochysia - they are all trees. However there is much greater diversity in the shape, color, and size of the flowers. Many of the savanna species share the same distinctive suite of vegetative features seen in Salvertia and some

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savanna Vochysia species. The leaves of some species of Qualea and Callisthene are deciduous. Species of all three genera have extrafloral nectaries associated with stipules at the base of the leaf. They are round and generally flat or crateriform, and additional pairs may be found along the young internodes and on the inflorescence rachis. Stafleu (1953) separated these glands into four groups based on whether they are formed from the base of the stipules, completely replace the stipules, or are found in the axils of the stipules. However, examination of herbarium specimens indicates that these categories are not clear cut and can be difficult to identify in mature material, thus developmental and anatomical studies are needed to clarify the structure of these organs. Work on cerrado species has indicated that these extrafloral nectaries may be important in attracting protective ants (Oliveira et al. 1987; Costa et al. 1992). Some species in these genera also may have small claw-shaped structures at the tips of young leaves and sepals. These structures, possibly glandular, are also considerably more prominent in the newly formed organs and are generally inconspicuous at maturity. Additional work is needed to determine their distribution among the species in this group. These three genera are also the only ones observed to lack medullary bundles in the pedicel.

A fruit with an exocarp that fractures irregularly and falls off at the time of dehiscence has been considered characteristic of Callisthene (Stafleu 1952; Martins 1981; Kawasaki 1998), however there are species of both Qualea and Ruizterania as well with this feature. One of the most conspicuous features of the flowers of these three genera is that the base of the flower is oblique, the spurred side being lower than the side on which the stamen and petal are inserted (Fig. 45). The flowers are described as perigynous (St.-Hilaire 1820;

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Warming 1875; Baillon 1878; Stafleu 1952, 1953; Cronquist 1981; Kawasaki 1998), although the slant makes this open to interpretation; it is unclear exactly what should be considered hypanthium and what should be considered receptacle (Fig. 45).

Qualea (55 species) has a wide distribution, but unlike Vochysia it does not extend north beyond eastern Panama (Stafleu 1953). Whereas the fourth sepal of Qualea flowers is generally somewhat longer than the other sepals, it is not greatly elongate as in Vochysia. Buds are generally broad at the base and taper to a point at the apex. In some species the fourth sepal is petaloid on the inner surface. The spur may be free or enclosed by the outer two sepals prior to anthesis (in other genera it is free). In the eight species of subgenus Amphilochia (Mart.) Stafleu the spur is sac-like, and thus these species have been described as "spurless" (Stafleu 1953). However the sac has been shown to be histologically identical to the spur (R. Carmo-Oliveria, pers. comm.), and because there is considerable variability in spur shape and size (and it is quite sac-like in Erismadelphus) there is no reason not to consider this structure a spur.

Qualea species have one petal (Fig. 2), although some species also variably have two minute rudimentary petals (Stafleu 1953 and pers. obs.). The petal is clawed and generally round or obcordate and varies in size. It is often white or blue/purple and frequently has brightly colored markings. The fertile stamen is in an asymmetrical and unusual position, between the petal and the fifth sepal (Fig. 2). The anther is variable in shape, in various species being oblong, triangular, or semi-circular and recurved, and the connective sometimes emarginate or extended beyond the thecae (Stafleu 1953). Two staminodes are present in some species, and these are antepetalous (or would be if there were lateral petals). The trilocular ovary appears

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to be wholly superior, although it is possible it is adherent to a slight degree on the side opposite the spur (Fig. 45). In cross-section it is more-or-less circular and unlobed (Fig. 79). Each locule contains numerous ovules on a relatively large placenta. The fruit is a thick-walled woody loculicidal capsule. At dehiscence the three segments of the fruit pull away from the central column, remaining attached to each other only at the base. The column persists in some species. Each locule produces many seeds, which have a unilateral oblong wing that is an extension of the seed coat (Boesewinkel and Venturelli 1987).

Stafleu (1953) recognized two subgenera in Qualea - the "spurless" subgenus Amphilochia and subgenus Qualea (Table 4). Amphilochia was originally described as a genus by Martius (1824) but Warming (1875) included it as series in Qualea, and Stafleu (1953) followed suit although with the rank of subgenus. Stafleu divided subgenus Qualea into four sections, one of which (sect. Trichanthera Stafleu) is distinguished by a "Vochysia-type" bud (with an elongate fourth sepal) and by a distinctive fringed anther. Marcano-Berti (1969) elevated this section to generic status, as Ruizterania (13 species). In other features Ruizterania conforms to the description of Qualea (Stafleu 1953)(Fig. 2), although the inflorescences are often small axillary cymes (cincinni) as opposed to the thyrses (racemes of cymes) characteristic of the rest of the family. The range of Ruizterania is similar to that of Qualea, although the former does not extend as far to the north and west.

Callisthene (8 species) is found in the savannas of Brazil but generally in more mesophytic environments with calcareous soils, and sometimes in gallery forests (Stafleu 1952; Martins 1981). Most species of Callisthene have slender twigs that bear small, distichous

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opposite leaves that give the impression of compound leaves. The leaves are deciduous, and are thin and soft ("subdiaphanous to subchartaceous," Stafleu 1952) in contrast to the thick coriaceous leaves typical of the rest of the family. Callisthene inflorescences are often axillary cymes, and the fourth sepal is petaloid. Staminodes and rudimentary petals have not been described in any species of Callisthene, prompting Stafleu (1952) to conclude that it is the most advanced of the genera of Vochysieae. The fruit has relatively few seeds, with a circumferential rather than unilateral wing. In other features it conforms to the description of Qualea (Fig. 2).

In the two species of Callisthene examined, small possibly glandular structures were seen at the base of the adaxial surface of the sepals. These structures are reminiscent of colleters, and are either small and deltoid (C. major Mart.) or very long and thin (C. fasciculata Mart.). Similar structures were seen between the petiole and axillary bud in C. major (see also Martins 1981).

Two sections have been recognized in Callisthene (Table 4): sect. Cataphyllantha Stafleu, comprising only the species C. fasciculata; and sect. Callisthene, with the remaining species. Callisthene fasciculata is distinctive by its significantly larger leaves and flowers, elongate "Vochysia-type" bud and fruit that splits into six segments.

B. Erismeae

All 18 species of Erismeae are found in lowland rain forest (Keay and Stafleu 1953; Stafleu 1954; Kawasaki 1998). The tribe is sometimes described as having stellate hairs (Cronquist 1981; Kawasaki 1998) but this is true only of Erisma Rudge. The two genera of this tribe possess an inferior unilocular ovary that forms a winged fruit with a single seed. However the gynoecium of Erismadelphus is

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pseudomonomerous; two or three locules are initiated but only one matures, as evidenced by the presence of aborted locules in sectioned floral buds. Aborted locules were not seen in *Erisma* (chapter two; Kopka and Weberling 1984). The wings of the fruit are the sepals, which continue to grow as the fruit matures.

1. *Erisma* (16 species)(Fig. 2) is mainly confined to Amazonia, with one species (*E. blancoa* Marc.-Berti) extending into eastern Panama, and one recently described species (*E. arietinum* Kawasaki) endemic to the Atlantic Coastal Forest of Brazil (Kawasaki 1998). Species of *Erisma* are among the tallest trees in the neotropical rain forest (Spruce 1908). The buds are similar in shape to those of *Qualea*. The sepals are subequal in size, and the fourth (spurred) is petaloid on the inner surface and deciduous. Flowers have one petal that varies in shape and size, and is generally white, yellow, or blue/purple, often with contrasting markings. Up to four tiny rudimentary petals are commonly present. The fertile stamen of *Erisma* has been described as being off the line of symmetry, as in *Qualea* (Warming 1875; Stafleu 1954; Kopka and Weberling 1984; Kawasaki 1998) but this is not the case. The fertile stamen is in front of the petal, and staminodes, which are commonly present, are also in antepetalous positions (Fig. 2, and see chapter 3). The gynoecium is unilocular and contains two ovules. The fruit is four-winged, because the fourth sepal is deciduous, and it contains one seed. The fruits of *E. calcaratum* (Link) Warm., a species native to Amazonia, are wingless and have a corky pericarp that allows them to be dispersed by water.

2. *Erismadelphus* (2 species)(Fig. 2), found in the lowland rain forest of West Africa, differs most obviously from *Erisma* in having five petals, which are more-or-less elliptical and white. In the two described species the spur is two-lobed and saccate, and the sepals are

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equal in size. The stamen is antepetalous, as are the two staminodes. These have tiny structures at their apices that are similar in external appearance to the anther but contain no pollen. The gynoecium has three locules initiated, but only one is fertile and contains one ovule. All five sepals are persistent and thus the fruit is five-winged. A third species, as yet undescribed, has been collected recently (Cheek 8814) in which two of the sepals are relatively quite small and the other three are petaloid and white, giving the flower the appearance of having eight petals.

C. Outgroup

Five species of Myrtales were used as outgroup, including one species of Tibouchina Aubl. (Melastomataceae), two "core" Myrtaceae (Backhousia Hook. & Harv. and Eugenia Mich. ex Linn.), and two Myrtaceae outliers (Heteropyxis and Psiloxylon). In the analysis of Conti et al. (1997) these latter two genera were sister-group to a monophyletic clade comprising Vochysiaceae + Myrtaceae; in other analyses they have been sister-group to the rest of Myrtaceae, with Vochysiaceae as sister-group to that assemblage (Fig. 86).

II. Data

A. DNA sequence analysis

The species included in this study are listed in Appendix 1 along with voucher information. Cerrado species are disproportionately represented, because Vochysiaceae are common and easily collected in that environment. Rain forest species are less frequently encountered and more difficult to collect, and it was not possible to obtain material from individual desired species. Representatives were obtained of all of Stafleu's major taxonomic divisions of all genera

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except those of Vochysia (Table 4). Attempts to extract DNA from herbarium material were not successful.

DNA was extracted from all species according to a modification of the protocol of Doyle and Doyle (1987). It was purified either on a 1.55 g/ml cesium chloride gradient or by using QIAquick PCR purification columns (QIAGEN). The single-copy plastid gene matK was used in this analysis. It is easily amplified and sequenced, and has been used successfully to study relationships within and between families (Soltis and Soltis 1998). It is approximately three times as variable as rbcL (Soltis and Soltis 1998 and refs. therein; P. Gadek and C. Quinn pers. comm.), but is nonetheless often not informative at the species level. The gene is approximately 1500 bp long, and often contains small insertions and deletions (indels, collectively). However, only 750 bp from the middle of the gene were used in this analysis, and no indels of significance were encountered in this region thus alignment was easily performed by eye.

Amplification reactions followed established recipes using standard amplification reagents. The reactions were carried out over 30 cycles, with an annealing temperature of 37ºC, which did not produce multiple bands or other evidence of the non-specific primer binding that might be expected at such a low temperature. Primers used were supplied by the laboratory of Dr. Christopher Quinn of the University of New South Wales. This laboratory also supplied the matK sequences for the five members of the outgroup. Although there is length variability in matK that makes it difficult to know exactly how far from the 5' end the primers anneal, these bind at approximately sites 150 and 1100. The 5' and 3' ends of matK were amplified and sequenced in only a few species; these data are not included in the analysis. PCR products were purified with GeneClean (BIO101) or QIAquick PCR

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purification columns (QIAGEN).

Both strands were sequenced, using the amplification primers and internal primers that were also supplied by the University of New South Wales. Cycle sequencing reactions were carried out according to standard automated sequencing protocols (ABI Prism), using Big Dye terminator reagents (ABI Prism). Sequences were collected by either an ABI 373 or 377, and the data were edited with Sequencher (Gene Codes Corporation). The data matrix is presented in Appendix 2.

B. Morphology data

A data matrix of 75 non-molecular characters was compiled for the same taxa used in the molecular analysis. The taxa are listed in Appendix 1, the characters and character states in Appendix 3, and the data matrix in Appendix 4. These characters are not all morphological, but for convenience these data will be referred to as the "morphology" data set in contrast to the molecular and combined data sets. The data were gathered from specimens in the herbarium of The New York Botanical Garden, information in the literature (Stafleu 1948, 1952, 1953, 1954; Keay and Stafleu 1953; Quirk 1980; Martins 1981; Kawasaki 1998; Boesewinkel and Venturelli 1987; Oliveira 1998), and field observations. Features like pollen morphology and ovule orientation are relatively invariant across the family and were not included. Other characters such as those of phytochemistry are known for only a few species. The family in general is considered to be characterized by chemicals loosely referred to as "gums and resins" but these terms are used imprecisely in the literature and it is not clear if there are true resins in the family. Mucilaginous compounds and traumatic intercellular canals are common but are not documented species by species. These phytochemical characters require further study and

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clarification.

Characters of the following categories were also omitted.

1. Inconsistently described. Characters such as color of pubescence are described using terminology that varies and is not always clearly defined or differentiated.

2. Too variable within species. Characters such as features of leaf shape were highly variable within individual species and could not reasonably be coded for analysis. Some features may be distinctive and diagnostic in one species but variable in others, such as the shape of the leaf base.

3. Autapomorphies. Some distinctive features are without phylogenetic utility in this context because of the specific set of taxa used. An example is the distichous leaf arrangement in Callisthene major, which is also found in other species in Callisthene sect. Callisthene. Because there were no other species from that section in this study, the character is an autapomorphy.

4. Inaccurately recorded. Some characters such as the number of buds in each cymose partial inflorescence are difficult to determine accurately, and the literature is not reliable.

Measurements were made of several features that are used to distinguish species of Vochysiaceae, such as petiole length or bud length and width. When possible, measurements were taken from 10 herbarium sheets, and from as many mature (based on size, shape, and texture) leaves/buds as possible on each sheet. A range of values was established for each species. Size categories were then set up on the basis of discontinuities in the ranges. In all cases these discontinuities were apparent, thus for instance for petiole length there are no examples of a species for which the range of lengths transgresses any of the established boundaries of <0.3mm, 3-10mm, 10-

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30mm, or >30mm. There are only three instances in which the range for a species extends across two categories: stipule length (character 14) in V. elliptica Mart., leaf length/width (character 15) in V. elliptica, and bud length/width (character 35) in V. tucanorum Mart.. These were coded as polymorphic. In establishing character classes one is suggesting homology, that is, we are saying that all petioles shorter than 0.3 mm are "more" homologous with each other than they are with other petioles. The analysis is somewhat circular in that we are including hypotheses of homology in our character coding, but this is always the case. However, parsimony analyses can evaluate these assumptions of homology, thus rather than omitting these continuous characters because the coding is somewhat arbitrary.

It is obvious that some measurement characters are not independent, for example, large buds will be both long and wide relative to small buds. Scoring both these characters separately would be redundant. However bud proportions may vary, and a large bud may be relatively narrow even though absolutely wide. Thus bud length was included, as a measure of size, and the ratio of length/width as a measure of shape.

Whereas characters that are obviously dependent were excluded, those that might simply be correlated were included. The fourth sepal and the attached spur are deciduous in Erisma but not Erismadelphus, and the fruit of the former has four wings whereas that of the latter has five. However, the wings are formed by the accrescent growth of the sepals, therefore if one sepal is deciduous it is obvious that the fruit formed from that flower can only have four wings. Thus these two features are the same, and only one (deciduous fourth sepal, character 41) was included. On the other hand, fruits of Qualea, Callisthene, and Ruizterania are characterized by a particular mode of dehiscence

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and are also all woody. There may be a single underlying factor responsible for both of these features, but because it is not apparent both were included (Appendix 3, characters 70, 72; Appendix 4).

Although the outgroup DNA sequences used herein are each derived from an individual species, the morphological features for the outgroup taxa are scored for the genus wherever possible. The taxa that are chosen as outgroup are integral in determining the patterns of character-state distribution, and as a result the choice will affect the outcome of the search for the most parsimonious trees. In an analysis such as this it is not feasible and it is beside the point to include all genera in the outgroup taxa much less all the species, and this would simply move the problem to a new level, as a new outgroup would have to be chosen. Selecting four genera of Myrtaceae and one of Melastomataceae is already restricting the possible states from among those present in the outgroup families. Scoring features such as habitat or size for a particular species, when such features vary within the genus, compounds this problem, thus these were scored as polymorphic. The characters and coding are presented in Appendices 3 and 4.

III. Analysis

Parsimony analyses were performed on each data set independently, and on the two sets combined, using NONA 1.6 (Goloboff 1993). Data matrices were edited and trees viewed in DADA (Nixon 1998a) and CLADOS (Nixon 1998b). All characters were coded as nonadditive and equally weighted in all analyses (one analysis was also performed with ovary position, character 58, coded as additive). Tree searches consisted of 1000 repetitions of heuristic searches on random taxon-addition sequences, with TBR branch swapping. Consistency index and retention

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index were determined for most-parsimonious trees as well as for individual characters, and the Mickevich-Farris Incongruence Length Difference (Mickevich and Farris 1981; Farris et al. 1995) was calculated to assess the degree of incongruence between the two data sets. Support for each clade was determined as the number of unambiguous (independent of optimization) synapomorphies present in all most-parsimonious trees, and by calculating bootstrap percentages (Felsenstein 1985) based on 1000 replicates and Bremer Support (Bremer 1988) through NONA. NONA calculates a "strict consensus" bootstrap (Davis et al. 1998), that is, for each replicate a clade is counted as present only if it is present in all most-parsimonious trees from that replicate. This implementation gives lower bootstrap values than the "frequency-within-replicates" bootstrap, in which for each replicate a clade is given a percentage score based on the number of most-parsimonious trees in which it is present. Thus the bootstrap percentages presented here can be seen as highly conservative. Bootstrap percentages were not computed for the analysis that included only morphology data.

For the morphology data matrix, the effect of highly homoplasious characters was investigated by deactivating all those with CI < 0.20, and then CI < 0.30, and performing the same analysis.

RESULTS

I. Morphology data analysis

Two most-parsimonious trees of 320 steps were found (CI=0.38; RI=0.65; Fig. 88a, b). Branch lengths (Fig. 88a) include only unambiguous synapomorphies for nodes that are present in both trees. The two trees differ only in the placement of _S. convallariodora_ and

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the relative positions of V. elliptica, V. pruinosa Pohl, and V. pumila Pohl. The analysis was repeated with ovary position (Character 58) coded as additive; there was no effect on the number of trees found or their toplogies. No other characters were considered to have states that were obviously likely to be ordered.

The trees show the family divided into two major clades, one comprising VS and Erismeae (Bremer Support=2), and the other comprising QRC (BS=5)(Fig. 88). Within the latter clade the two species of Ruizterania form a moderately well supported clade (BS=3), and the two species of Callisthene a well supported one (BS=5), but these are nested within the species of Qualea. No clades include only Qualea species.

The VS/Erismeae clade is subdivided into Erisma and Erismadelphus on the one hand (BS=2), and Vochysia and Salvertia on the other (BS=5)(Fig. 88). Erismadelphus is sister to the two species of Erisma, which have relatively strong Bremer Support as sister-species (BS=5). Within the Vochysia/Salvertia clade there are no groups with Bremer Support >3. Salvertia is nested well within Vochysia.

Elimination of all characters with CI <0.20 removed five characters (11, 16, 21, 22, 64), all dealing with pubescence or leaf venation. It was thought that perhaps these frequently changing characters were disproportionately adding conflict to the data and preventing resolution in some areas, although Wenzel and Siddall (1999) have shown using simulations that in most cladistic analyses noise (random data) will not obscure the phylogenetic signal present in the data. A highly resolved tree is not inherently more or less correct than an unresolved one, but it does allow one to generate and evaluate more hypotheses about character transformation within a clade. The search found 15 trees of 269 steps, with the same major clades as the

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complete data set but with less resolution within VS and QRC.

This analysis was repeated with the deactivation of all characters with CI <0.30. The 24 excluded characters include most of the pubescence, leaf venation, and continuous measurement characters. The analysis produced 32 trees of 153 steps, with no change in the relationships of the three major groups (*Qualea*/*Ruizterania*/*Callisthene*, *Erisma*/*Erismadelphus*, *Vochysia*/*Salvertia*). Whereas in the original analysis the lack of resolution in the *Qualea* and *Vochysia* clades was found mainly towards the tips of the tree, in the CI <0.30 analysis there were unresolved taxa throughout, and the clades are more pectinate.

A. Character support

Characters that support the clades present in both most-parsimonious trees are listed below. Character numbers are in parentheses; clade numbers are indicated on Fig. 88a. Character states are described in Appendix 3. Some characters could not be scored for the outgroup (e.g. spur length/width, character 38) or part of the ingroup (e.g. fruit dehiscence, character 70, or seed wing composition, character 75, for Erismeae). In some of these cases a character state is unambiguously synapomorphic for a particular clade in comparison with the other taxa and character states in the family, however it can not be polarized in that an ancestral state can not be determined. Characters of this type are listed as "additional characters." Although monophyly of Vochysiaceae was not being evaluated, the characters that support it in this analysis are presented. Taxa within a clade that show a character state other than that which is synapomorphic for the clade are noted. Support for clades within the outgroup is not discussed.

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1. Vochysiaceae: Compared to the outgroup, Vochysiaceae are characterized by being large trees (1) with stipules (12), a zygomorphic corolla (30), a spurred fourth sepal (37), and a single fertile stamen (50). With the exception of size and the possession of stipules, these are the classic features used to distinguish this family. Buds 10-15mm (34) also maps as an unambiguous synapomorphy at this node, but there is considerable variation within Vochysiaceae; the entire outgroup has buds <5mm whereas no Vochysiaceae do, thus a useful synapomorphy in this context would be buds >5mm. *E. floribundum* Rudge and *V. pumila* lack stipules, and *S. convallariodora* and *E. exsul* Mildbr. have an actinomorphic corolla. There are numerous changes in character 1 (size) within the ingroup.

2. *Qualea*/*Callisthene*/*Ruizterania* (BS=5): Synapomorphies of the QRC clade in this analysis include the presence of stipular extrafloral nectaries (27), an oblique receptacle (36), a round or obcordate petal (44), the fertile stamen in an offset, asymmetrical position (51), a superior, pubescent ovary (58, 59), and a relatively thick, woody pericarp (72). Additional characters that change considerably on the tree but map as synapomorphies include a sulcate midrib on the upper surface of the leaf(20), prominent venation on the upper surface of the leaf (22), and yellow or white petal markings (47). In *Q. dichotoma* (Mart.) Warm. the midrib is not sulcate nor is the venation prominent. The ovary in the *Callisthene* species is glabrous. *Qualea dichotoma* has red/magenta petal markings, and both *Q. multiflora* Mart. and *Q. paraensis* Ducke have both yellow and red/magenta markings (*C. major* may as well). Additional characters noted in this analysis that define the clade but could not be polarized because they are not present in the outgroup include stipules <1mm (14) and fruit dehiscence in which segments separate from central column (70).

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With the exception of the extrafloral nectaries and obcordate petal, none of these are characters that have traditionally been used to delimit this group. The fertile stamen was thought to be in the same position in Erisma (erroneously thought to be antesepalous in both Erisma and QRC), the ovary was thought to be completely superior in VS, and the oblique receptacle and woody fruit were not noted. Other characters, such as a single clawed petal and sepals subequal in size, have traditionally been used to characterize this group but are also found in Erismeae and therefore are not unambiguous synapomorphies in this analysis. The characters of venation, pubescence, and petal markings that are synapomorphies in this analysis have generally been considered diagnostic of species or species groups.

QRC1 (BS=1): This clade includes all species in the QRC clade except Q. paraensis. Only one character supports it: a pilose style base (64). The Callisthene species show a reversal to a glabrous style base. Qualea paraensis, the species excepted from this clade, is the only representative of Stafleu's sect. Qualea (subgenus Qualea)(Table 4) and is the only rain forest representative of the genus Qualea in this analysis. It is the most autapomorphic species in this clade, with seven character changes in contrast to the 1-5 in the other species (Fig. 88a).

Ruizterania (BS=3): This group, which has moderate Bremer Support, was segregated from Qualea and erected as a separate genus on the basis of three of the characters that set it apart in this analysis: the elongate fourth sepal (39) and the basifixed and barbate anther (54,55). In addition, the adult leaf that is glabrous underneath (17) and bud length/width ratio of 3-6 (35) distinguish these species in this analysis.

QRC2 (BS=1): This weakly supported clade includes the savanna and

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gallery forest species in the QRC group that were included in the study. *Savanna habitat (0) is the only synapomorphy.* Within this clade there are two sister-clades with weak Bremer Support. One comprises *Q. multiflora* and *Q. parviflora* Mart. (BS=1), the two members of Stafleu's sect. *Costatifolium* (Table 4) that were included in this analysis. In these results they are united by soft wood (2) and spur length/width ratio of 2-9 (38).

Q. dichotoma/*Callisthene* (BS=2): This is the other clade comprising the QRC2 clade. In these three species the lateral leaf veins are <60° to the midrib (21), the style is 10-20mm (63), and the exocarp fragments at maturity (71). This last synapomorphy is particularly noteworthy as the fragmenting exocarp has been seen as a distinguishing character of *Callisthene*.

Callisthene (BS=6): These two species, strongly supported as sister-species, are united by their deltoid stipules (13), relatively round leaves (leaf length/width <1.5)(15), axillary cymose inflorescences (29), petaloid fourth sepal (40), basifixed anther (54) with the connective extended beyond the thecae but not forming a cap (56), and circumferential, elliptically shaped seed wing (74). Prominent venation on the under surface of the leaf (23) and a glabrous ovary and style (59, 64) are also unambiguous synapomorphies in spite of the variability of these characters on the tree. *Callisthene* has been distinguished from *Qualea* by its seed wing shape, fragmenting exocarp, and persistent central column in the fruit (Stafleu 1952). In this analysis the fragmenting exocarp is a synapomorphy for a larger clade. Persistence of the central column was not included in this study because it has been observed in some *Qualea* species as well, and the information was insufficient to allow accurate scoring. It is possible that the column in *Callisthene* is a distinctly different shape

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from that in Qualea, but more observations are needed. Thus although the species of Callisthene are well separated from the Qualea species, it is not on the basis of the expected characters with the exception of the seed wing. Furthermore, Callisthene is nested within Qualea.

3. Erismeae/Vochysia/Salvertia (BS=2): The taxa in this clade, which includes the two remaining major groups of the family, are united in having two ovules and one seed per locule (62, 73). Petal length 7-15 mm (43) also maps as a synapomorphy at this node although this character changes numerous times within the clade.

a. Erisma/Erismadelphus (BS=2): This clade is the tribe Erismeae which, in light of their suite of unusual features, has surprisingly low Bremer Support. These taxa have included phloem within the secondary xylem (3), one fertile gynoecium locule (61), and the unusual indehiscent winged fruit (68, 69).

Erisma (BS=6): These two species are united by having stellate hairs (8), a fourth sepal that is petaloid on the inner surface and is deciduous (40, 41), a round or obcordate petal that is pubescent (44, 48), and only one locule in the gynoecium (60). Floral buds are 5-10mm (34). These species are unique in having up to four rudimentary petals (49), but this could not be optimized because this character is inapplicable in the outgroup and Erismadelphus.

b. Vochysia/Salvertia (BS=5): This clade includes all the species of Vochysia and the single species of Salvertia. Members have a basifixed anther (54) and a partly inferior ovary (58). In all species except S. convallariodora the fourth sepal is at least three times as long as others (39), there are three petals (42), and the anther connective is extended beyond the thecae to form a cap that covers the stigma in the bud (56). In S. convallariodora the sepals are equal in size, there are five petals, and the connective is not

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extended. Several characters are synapomorphies for this group but vary considerably at more distal nodes; these include deltoid stipules (13), dense inflorescence (28), and spur length/width ratio 2-8 (38). Additional characters that are distinctive for this clade but cannot be optimized are fruit segments that do not separate at dehiscence (70), and a seed wing composed of matted hairs (75).

Vochysia neyratii D. Normand/*V. densiflora* Spruce ex. Warm./*V. pyramidalis* Mart. (BS=2): These three species, found in rain forest or gallery forest, all have a pubescent juvenile leaf and petals (16, 48). Within this clade *V. densiflora* and *V. pyramidalis* are sister-taxa (BS=3). Both have partly lateral and lobed stigmas (66, 67). In addition the midrib is not sulcate on the upper leaf surface (20), and the lateral leaf veins are <60º to the midrib (21). These last two are highly variable characters. The three species in this clade are all members of Stafleu's sect. *Ciliantha*, subsect. *Ferrugineae* (Table 4) based on their glabrous ovary, pubescent petals, and ferrugineous-pilose young leaves, but only the latter two characters are synapomorphies at this node.

VS1 (BS=3): This clade includes species found in savanna and gallery forest. Synapomorphies at this node include medium-sized trees (1), whorled phyllotaxis (6), glabrous adult leaves (17), prominent venation on the upper leaf surface (22), and brochidodromous venation (25). However, none of these features is found in all species of the clade: *V. cinnamomea* Pohl, *V. rufa* Mart., *V. elliptica*, and *V. pruinosa* are all small trees and *V. pumila* is suffruticose; phyllotaxis in *V. pumila* is unclear (the leaves appear to be randomly scattered on the stem); adult leaves are pubescent underneath in *V. cinnamomea* and *V. rufa*; venation is not prominent on the upper leaf surface in the clade that consists of *V. elliptica*, *V. pumila*, and *V. pruinosa*; and the VS3

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clade that is nested within VS1 has irregularly anastomosing venation.

Within the VS1 clade there are two sister clades (Fig. 88). Vochysia haenkeana Mart. and V. tucanorum (BS=3) form one, characterized by subulate stipules (13) and slender spurs (spur length/width >8)(38). The juvenile stem is glabrous (9), and the midrib on the upper leaf surface is sulcate (20). These two species are found in gallery forests and savanna. They were not considered similar by Stafleu, who put them in different sections of the genus (Table 4).

The other clade (VS2) includes exclusively savanna species of Vochysia as well as Salvertia, but this is not a synapomorphy because of variability in the sister clade. VS2 (BS=1) is distinguished by styles >20mm (63) and by bud length >20mm (34) although in V. cinnamomea, V. rufa, V. pumila, and V. elliptica the bud is 15-20mm. V. thyrsoidea Pohl is sister to the rest of the clade; it has been included with V. tucanorum in sect. Ciliantha, subsect. Lutescentes (Table 4) by Stafleu based on its glabrous ovary and features such as deltoid stipules and non-exfoliating bark that are shown to be plesiomorphic in this analysis.

VS3 (BS=1): The taxa in this clade are united by exfoliating bark (4), irregularly anastomosing lateral leaf venation (25), and a pubescent ovary (59). They are all small-to-medium trees (except suffrutescent V. pumila) that exhibit distinctive savanna-adapted features. Aside from Salvertia, all species in this clade are placed by Stafleu in sect. Vochysiella (based on their pilose ovary and peeling bark), subsect. Decorticantes (Table 4), which is characterized by inconspicuous leaf venation, pubescent inflorescences, and a variety of details of floral proportions, none of which are synapomorphies at this node in this analysis.

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The VS3 clade includes three groups, the relative positions of which differ in the two most parsimonious topologies (Fig. 88). One of the three branches is *Salvertia convallariodora*, which is relatively autapomorphic in this clade with six changes as opposed to the 1-3 in most *Vochysia* species (five in *V. haenkeana*)(Fig. 88a). Four of the autapomorphic character states of *S. convallariodora* are reversals of synapomorphies for Vochysiaceae or the VS clade. Predictably, these include actinomorphic corolla (30), five petals (42), and equal-sized sepals (39).

The second of the three branches of the VS3 clade comprises *V. elliptica*, *V. pumila*, and *V. pruinosa* (BS=1) all of which have a glabrous juvenile stem (9) and glaucous leaves (18) as well as venation on the adaxial surface of the leaf that is not prominent. *Vochysia elliptica* and *V. pruinosa* are difficult to distinguish in the field and herbarium. The leaves of the latter are larger, but this feature is variable in a number of species and was not included in this analysis. Unambiguous autapomorphies for *V. elliptica* are venation visible on the bottom surface of the leaf (23) and style base pilose (64). Autapomorphies of *V. pruinosa* are pedicel <5mm (33) and bud length/width ratio >6 (35). With the possible exception of pilose style base, these are all features that can be variable within species. *Vochysia pumila* is easily distinguished by its suffrutescent habit (1), and absence of stipules (12), both autapomorphies in this analysis, and the seemingly random positions of the leaves on the stem (6, scored as unknown phyllotaxis in this analysis).

The remaining clade of VS3 includes *V. cinnamomea* and *V. rufa* (BS=3), which share pubescent juvenile leaves(16), adult leaves that are pubescent on the bottom surface (17), and bud length/width >6 (35). These two species are distinguished mainly by the color of the

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pubescence on the leaves and the inflorescences. However, Stafleu (1948) recognized two subspecies and two varieties within V. rufa, and a key character in differentiating these is color of pubescence. In this analysis V. cinnamomea has one autapomorphy, leaf length/width ratio >2.5 (15) and V. rufa has none (Fig. 88a).

II. Molecular data analysis

This search found 52 most-parsimonious trees of 356 steps each including all characters (CI=0.82, RI=0.85), and 239 steps including only phylogenetically informative characters (127 base sites)(CI=0.74). One of the 52 most parsimonious trees (arbitrarily chosen) is shown in Fig. 89 with branch lengths for nodes present in all 52 most-parsimonious trees. The strict consensus is shown in Fig. 90, with Bremer Support and bootstrap percentages indicated. The consensus shows three monophyletic groups within the family, but these groups are unresolved with respect to each other. Bremer Support, numbers of supporting synapomorphies, and bootstrap percentages are moderate- to-high for the three major clades (Figs. 89, 90), but within each clade there is little resolution, and support for many of the nodes that are present is negligible (Bremer Support=1 or 2, bootstrap <50%). The numerous zero-length branches in the most parsimonious trees indicate that the lack of resolution within these clades is due to a lack of informative characters rather than to character conflict within the data set.

Excluding the outgroup, the total number of informative and unambiguously optimized transitions (ts) and transversions (tv) is 31 and 25; there are an additional 39 and 47 autapomorphic transitions and transversions, some of which are homoplasies, within the ingroup. The distribution of these changes is not uniform: two species account for

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28 of those 86 autapomorphies, and five species (including those two) account for 52. Eighteen species account for the remaining 34, fewer than two autapomorphies per species (Fig. 89).

Whereas the analysis of the morphology data shows Erismeae and VS forming a monophyletic group (Fig. 88), this topology was not seen in any of the most parsimonious trees found in the molecular analysis. Four of the 52 trees place the QRC clade and VS clade together; the remaining 48 place the QRC and Erismeae clades together. Aside from the VS, QRC, and Erismeae clades, and the Callisthene, Erisma, and Q. multiflora/Q. parviflora species pairs (Figs. 88, 90), there are no monophyletic groups that are identical in the morphology and molecular consensus trees. The molecular consensus shows V. pruinosa and V. elliptica as sister-taxa, and that topology was also found in one but not the other most parsimonious morphology tree. There are also some areas of the molecular tree that are unresolved and therefore not in conflict with the more resolved morphology tree (e.g. unresolved placement of Q. paraensis in molecular tree vs. basal position in QRC clade in morphology tree).

A. Support

1. Vochysiaceae: Four transitions and eight transversions support Vochysiaceae as monophyletic (BS>10; bootstrap=99%) in all 52 most-parsimonious trees, an assumption that was not being evaluated in this analysis (Fig. 89). An additional 15 characters are synapomorphic for the family but could not be optimized. In most of these instances, one character state is found in Tibouchina, a second in the four myrtacean taxa, and a third in Vochysiaceae. This three-taxon statement with three character states does not allow determination of the plesiomorphic state, nonetheless the character state for

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Vochysiaceae is synapomorphic.

2. QRC: This clade (BS=5; bootstrap=99%) is supported as monophyletic by two transitions, three transversions, and one change that could not be polarized. In this analysis the two species of *Ruizterania* are not sister-taxa (Fig. 90). With essentially no support (BS=1; bootstrap<50%), *R. cassiquiarensis* (Spruce ex. Warm.) Marc.-Berti is sister to *Q. multiflora* and *Q. parviflora*; this relationship is present and supported by at least one base change in all of the most parsimonious trees, but there is in fact no one particular base change that supports it in every tree thus there is no unambiguous synapomorphy. The sister-taxon relationship between *Q. multiflora* and *Q. parviflora*, found also in the morphology analysis, is one of the more strongly supported clades in the molecular consensus (one ts, three tv; BS=4; bootstrap=93%).

In contrast to the strong support in the morphology analysis, the two species of *Callisthene* are weakly supported as sister-taxa by the molecular data (one ts; BS=2; bootstrap=50%). The two *Callisthene* species are relatively autapomorphic (eight changes in *C. fasciculata* and 14 in *C. major*). Because the QRC clade has a 5-way basal polytomy, this analysis does not explicitly include *Callisthene* in *Qualea* as the morphology analysis did.

3. Erismeae are supported as monophyletic by four transitions, one transversion, and one character that cannot be optimized (BS=4; bootstrap=80%). Although the number of supporting characters is similar to that for the QRC and VS clades, Bremer Support and bootstrap percentage are lower (Fig. 90). Within Erismeae the two species of *Erisma* have strong support as sister-taxa (10 ts, three tv; BS>10; bootstrap=100%). The branch to the two species of *Erisma* (13 steps) is similar in length to the *Erismadelphus* branch (14)(Fig. 89). Along

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with the *C. major* branch, these are the longest internodes/branches within the ingroup.

4. The VS clade is well supported as monophyletic (five ts, three tv; BS=7; bootstrap=100%) but no clade within this group has Bremer Support greater than 2, and branch lengths in general are short (1-3 steps); three species of *Vochysia* have no autapomorphies (Fig. 89). *Salvertia* is part of a basal polytomy in the consensus (Fig. 90). Within VS, one clade comprises *V. haenkeana*, *V. tucanorum*, and *V. thyrsoidea* (one ts, one tv; BS=1; bootstrap=85%). The first two species were also placed together in the morphology analysis (Fig. 88). Stafleu (1948) included *V. tucanorum* and *V. thyrsoidea* together in sect. *Ciliantha* (glabrous ovary), subsect. *Lutescentes* (Table 4); he did not consider *V. haenkeana* to be close (sect. *Vochysiella*, pilose ovary).

A second monophyletic group (two tv; BS=1; bootstrap<50%) within VS includes all the savanna species except *S. convallariodora* and *V. thyrsoidea*, but unexpectedly also includes *V. neyratii*. This rain forest species, which is relatively autapomorphic in this analysis (nine changes), is weakly supported as sister to *V. rufa* (one ts; BS=1; bootstrap<50%). In the morphology analysis *V. neyratii* groups with *V. pyramidalis* and *V. densiflora*, which are unresolved at the base of the VS clade in the consensus tree from this analysis.

Vochysia elliptica and *V. pruinosa* are sister-taxa within the *Vochysia* savanna clade (two ts, BS=2; bootstrap=84%). These species were found together in a clade with *V. pumila* in the morphology analysis, but as sister-taxa in only one of those two most-parsimonious trees (Fig. 88b). In the molecular consensus *V. pumila* is unresolved at the base of the savanna clade.

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III. Combined-data analysis

The Mickevich-Farris Incongruity Length Difference for the two data matrices is 0.0244. This measure indicates the additional amount of homoplasy that is generated when the two matrices are combined, thus giving an indication of the amount of incongruence in the data sets. The value obtained does not indicate significant incongruity between the data matrices, a result that is not wholly unexpected given the lack of resolution in the molecular data. The combined-data matrix comprises 750 molecular characters (127 informative) and 75 non-molecular characters. The search found only two most-parsimonious trees (all characters: 688 steps, CI=0.60, RI=0.72; informative characters only: 573 steps, CI=0.52)(Fig. 91). Not surprisingly the same three major clades are recovered in this analysis (QRC, VS, Erismeae); the two trees differ from each other only in the position of the Erismeae clade with respect to the other two major clades. In one tree (Fig. 91b) Erismeae is sister-group to the VS clade, as was found in the morphological analysis. The other tree (Fig. 91a) places Erismeae with the QRC clade, as was found in 48 of the 52 molecular trees. In neither most-parsimonious tree is there support for a monophyletic tribe Vochysieae. Within each of the three major clades there is no conflict between the two most parsimonious trees.

A. Tree topology comparisons

The topology of the combined-data trees agrees closely with that of the morphology trees, disagreeing only in the position of V. thyrsoidea and Q. dichotoma. One of the two most-parsimonious morphology trees is identical to one of the two most-parsimonious combined-data trees with the exception of the positions of these two species (Figs. 88a, 91b). This congruence is predictable: the

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molecular data by-and-large were unable to resolve relationships among the species whereas the morphology analysis achieved nearly complete resolution. The disagreement between the two morphology topologies is resolved by molecular data in the combined-data analysis.

In addition to finding the same three major clades (VS, QRC, Erismeae), all three analyses agree on Erismadelphus as sister-taxon to the two species of Erisma, and on the affinities of the two species of Callisthene and of Q. multiflora and Q. parviflora (Figs. 88, 90, 91).

1. QRC clade. Aside from Callisthene and Q. multiflora/Q. parviflora, the only resolution within this clade in the molecular analysis is the position of R. cassiquiarensis as sister-taxon to those two Qualea species, a placement that is weakly supported and is in conflict with the morphology and combined-data topologies. The morphology and combined-data analyses agree on the sister-taxon relationship of the Ruizterania species and on their position as sister-group to a clade that includes all other QRC species except Q. paraensis. Both the morphology and combined-data analyses place this species as sister to all other species in the QRC clade (Figs. 88, 91). As noted, they disagree on the placement of Q. dichotoma.

2. VS clade: As in the morphology and molecular data analyses, support for individual clades within this group is low in the combined-data analysis. There is close agreement between the combined-data and the morphology topologies regarding structure within the VS clade (Figs. 88, 91). They disagree only on the placement of V. thyrsoidea: in the morphology trees this species is sister to the VS3 clade, whereas in the combined-data trees it is sister to V. haenkeana and V. tucanorum. This latter position is compatible with the topology of the molecular tree. The position of Salvertia, and the relationships among V. elliptica, V. pruinosa, and V. pumila in the combined-data trees are

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identical with the topology of one of the two most-parsimonious morphology trees (Fig. 88a, 91b).

Because the configurations of the morphology and combined-data trees are similar, the conflict in the VS clade between the topologies of the molecular consensus and of the combined-data trees is similar to that between the molecular consensus and the morphology trees as discussed under the results of the molecular analysis. The position of *V. neyratii* differs in the molecular consensus and the combined-data trees (Figs. 90, 91), and *S. convallariodora*, *V. pyramidalis*, and *V. densiflora* are unresolved in the molecular consensus tree. Both analyses recover a clade comprising *V. haenkeana*, *V. tucanorum*, and *V. thyrsoidea*, as well as one that includes both *V. elliptica* and *V. pruinosa*.

B. Support

Bremer Support, bootstrap percentages, and the molecular and morphological characters that support each node in both of the most-parsimonious trees from the combined-data analysis are described below (Fig. 91). Character numbers for morphology data (Appendix 3) are given in parentheses. Where clade membership is the same as in the morphology trees, only differences in supporting morphology characters are noted. Where clade membership is the same as in the molecular tree, differences in molecular support are indicated in parentheses as more (+) or fewer (-) transitions or transversions.

1. Vochysiaceae (BS>10; bootstrap=100%): The same six characters that support this assemblage in the morphology analysis are also unequivocal synapomorphies here. Six transitions (+2), eight transversions, and 16 synapomorphic base changes that could not be polarized support this node.

2. QRC clade (BS=10; bootstrap=97%): Eight of the ten synapomorphies from the morphology analysis also support this clade in the combined-data analysis, but round/obcordate petal (44) and pubescent ovary (59) no longer do. In addition, it is supported by five transitions (+3) and two transversions (-1).

QRC1/combined (BS=1; bootstrap<50): As in the morphology analysis, one morphological character supports this clade: pilose style base (64) (although not pilose in Callisthene). One transition also supports this group, which was not present in the molecular consensus.

Ruizterania (BS=2; bootstrap=56%): This species pair, which has weak bootstrap and Bremer Support, shares the same five characters that distinguish it in the morphological analysis; there is no support in the molecular data. This is consistent with the results of the molecular analysis, which did not put these two species together.

QRC2/combined (BS=1; bootstrap<50%): This clade, which has practically no support, includes the same taxa as in the morphology analysis but in a slightly different configuration (Fig. 88, 91). Savanna habitat (0), as in the morphology analysis, is the only supporting character. Apparently there are no contradicting characters in the data.

Q. multiflora/Q. parviflora/Callisthene (BS=1; bootstrap<50): This clade is not present in the morphological or molecular analyses. It is supported by the presence of an appendage on the leaf tip (26), as well as by one transition and one transversion.

Q. multiflora/Q. parviflora (BS=6; bootstrap=82%): This pair is found in both the morphology and molecular consensus topologies and is reasonably well supported in this analysis. The relationship between these two members of Stafleu's sect. Costatifolium is supported by the same two morphological characters, and by 2 transitions (+1) and 4

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transversions (+1).

Callisthene (BS=9; bootstrap=99%): Eight of the ten morphology characters that support this node in the morphological consensus tree are also synapomorphies in the combined-data analysis. The anther connective extended beyond the thecae (56) and prominent venation on the underside of the leaf (23) do not map to this clade in the combined-data consensus tree. One transition and two transversions (+2) also support this topology. This species-pair has strong Bremer Support and a high bootstrap percentage, presumably from the large number of morphology synapomorphies since molecular support is unimpressive.

3. Erismeae (BS=7; bootstrap=95%): The same four characters support the monophyly of Erismeae as in the morphological analysis. Five transitions (+1), one transversion (-1), and three changes that cannot be optimized support this clade.

Erisma (BS>10; bootstrap=100%): Six of the seven characters that support this species pair in the morphology analysis are also synapomorphies in the combined-data analysis, but as with the QRC clade, round/obcordate petal is no longer an unambiguous synapomorphy because of the conflict in the positions of the three major clades. Nine transitions (-1) and three transversions support this relationship.

4. VS clade (BS=10; bootstrap=100%): Only four of the eight characters that support this clade in the morphology analysis also support it in this combined-data analysis. A dense inflorescence (28), basifixed anther (54) with the connective extended beyond the thecae (56), and a partly inferior ovary (58) still map to this node, but deltoid stipules (13), spur length/width ration 2-8 (38), elongated fourth sepal (39), and three petals (42) no longer do. Fruit segments

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that do not separate at dehiscence (70) and a seed wing composed of compressed hairs (75) are still synapomorphies that can not be optimized. Four transitions (-1) and two transversions (-1) also support this clade. In spite of the reduction in character support, Bremer Support and bootstrap percentage are still very strong.

V. neyratii/V. densiflora/V. pyramidalis (BS=3; bootstrap=68%): In addition to the two characters that support this clade in the morphology analysis, pubescent stamen (53) and leaf length/width >2.5 (15) are also synapomorphies. No molecular characters support this clade, which includes members of Stafleu's sect. Ciliantha subsect. Ferruginea (Table 4). The species pair V. densiflora/V. pyramidalis (BS=1) is defined by the same four morphological characters as in the morphology analysis, and by no molecular characters (in keeping with the unresolved positions of these two species in the molecular consensus).

VS1/combined (BS=3; bootstrap=52%): Four of the characters supporting this clade are the same as in the morphology analysis, however brochidodromous venation (25) is no longer a synapomorphy at this node. Instead, savanna habitat (0) and revolute leaf margin (19) are. No molecular characters support this clade, which was not found in the molecular analysis.

V. thyrsoidea/V. haenkeana/V. tucanorum (BS=1; bootstrap<50%): This three-taxon assemblage is not found in the morphology trees but was recovered as a trichotomy in the molecular analysis. It is supported by visible venation on the lower surface of the leaf (23), although this is in fact not the case in V. tucanorum, as well as by one transition and two transversions (+1). V. tucanorum and V. thyrsoidea are included by Stafleu in sect. Ciliantha subsect. Lutescentes (Table 4), however in this analysis, as in the

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morphological analysis, V. haenkeana and V. tucanorum are supported as sister taxa (BS=4; bootstrap=59%). The same four features that relate this pair in the morphology analysis are synapomorphies in this analysis, along with leaf length/width >2.5 (15), and pubescent stamen (53). There is no molecular support for this clade.

VS2/combined (BS=2; bootstrap<50%): This clade has the same membership as the VS3 clade of the morphology analysis. Exfoliating bark (4) and irregularly anastomosing venation (25) still support this clade, however pubescent ovary (59) does not. Lateral sigma (66) is a synapomorphy as well, atlhough in V. pumila the stigma is terminal and in V. elliptica it is partly lateral. No molecular characters support this clade.

VS3/combined (BS=3; bootstrap=52%): This clade is found in one of the morphology most-parsimonious trees, and in the molecular consensus with the addition of V. neyratii. They are small trees (1) (although V. pumila is suffrutescent); venation on the underside of the leaf is not visible (23) (except in V. elliptica), and there is less than one vein per cm on the leaves (24). Three transversions support this assemblage. These five savanna species all belong to Stafleu's sect. Vochysiella subsect. Decorticantes (Table 4).

V. cinnamomea/V. rufa (BS=2; bootstrap=72%): This species pair, present in the morphology trees but not the molecular, is defined by the same three characters that support it in the morphology analysis as well as by inflorescences of medium density (28), and by no molecular characters.

V. pumila/V. elliptica/V. pruinosa (BS=1; bootstrap=51%): The same three characters that support this clade in the morphological analysis also support it here. There are no molecular characters supporting this clade, which is not present in the molecular consensus.

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V. elliptica and V. pruinosa (BS=1) are sister-taxa in the molecular analysis and in one of the morphology most-parsimonious trees; here they are are supported as sister taxa by a midrib that is not sulcate on the upper leaf surface (20), and by two transitions.

DISCUSSION

The molecular data are not sufficiently variable to resolve the relationships within Vochysiaceae other than to separate the three major clades and to define a few clades within each. This is consistent with the results of other studies using matK, which has only in some cases been able to resolve relationships among species (Soltis and Soltis 1998 and refs. therein). In contrast, the morphology data almost completely resolved the relationships among the species. This is not surprising, because the matrix includes numerous characters that have been used by Stafleu and other taxonomists (e.g. Stafleu 1948, 1952, 1953, 1954; Marcano-Berti 1969; Martins 1981; Kawasaki 1998) to define subgeneric categories. These consist in this analysis mainly of characters of pubescence (e.g. characters 9,16), leaf venation (characters 20-25), and continuously varying quantitative features (e.g. characters 33-35). Most of these contribute at least seven steps on the most parsimonious morphology and combined-data trees, and many contribute more than 10 (Appendix 3). Omission of these characters from the analysis produced considerably less highly resolved trees. Thus it is predictable that the analysis of the combined data sets would produce a consensus tree similar in details to that found in the analysis of the morphological data, since only the morphology data were informative at that level. The molecular data were able, however, to add resolution to the area in which the morphology data were

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insufficient, the relative positions of the taxa in VS3 and VS2/combined (Figs. 88, 91).

I. Branch lengths and support

Among branches within the ingroup in the combined-data trees, numbers of molecular apomorphies range from zero to 14 (Fig. 92), but in fact most branches within the three clades show nine or fewer base changes and only three are longer: Erismadelphus (14), C. major (14), and the branch to the two Erisma species (12). Regarding the morphological characters, numbers of changes range from eight (QRC, Callisthene) to zero (V. rufa). Thus with the exception of a few molecularly apomorphic branches, the range within the ingroup of changes per branch is the same (0-8/9) for both molecular and morphological characters.

In all three analyses the three major clades (QRC, VS, Erismeae) are supported by multiple morphological and/or molecular synapomorphies. Molecular support for the clades is similar (4-5 transitions, 1-2 transversions) but QRC has twice as many morphological synapomorphies as the other two clades (Figs. 88, 92). Bootstrap percentages are high for all three; Bremer Support for Erismeae is somewhat lower (BS=7) than for the other two clades (BS=10) but all things considered all three clades are strongly supported.

Within the three clades, branches are longest within Erismeae. Erismadelphus is the most autapomorphic taxon in the ingroup (19 autapomorphies)(Fig. 91). This may reflect the fact that the analysis includes data from only one species of Erismadelphus, thus the branch to the species includes the length of the branch to the genus. The numbers of autapomorphies of the two Erisma species are in line with the numbers in the rest of the family (five and six including all

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characters for E. floribundum and E. uncinatum respectively), however the branch leading to this species pair from the node with Erismadelphus is 18 steps long. Only three species are included in this analysis, whereas there is greater representation in the other two clades, however Erismeae only includes 18 described species, as opposed to the over 65 and over 100 of QRC and VS respectively.

Within the QRC clade numbers of morphological and molecular synapomorphies vary (Fig. 92) among the clades present. Molecular support ranges from zero to six synapomorphies, considerably fewer than the 12 that support Erisma. Morphological clade support within QRC ranges from one to eight characters. Including all characters, the shortest branches are those that lead to QRC1/combined, QRC2/combined and the Q. multiflora/Q. parviflora/Callisthene clade. These branches, which form the "backbone" of the QRC clade, also have weak Bremer Support (BS=1 or 2) and low bootstrap percentages (<50%), therefore the relative positions of the five major branches are based on flimsy support (Fig. 91). The only two well supported nodes within the clades are Callisthene and Q. multiflora/Q. parviflora.

Within the VS clade there is also weak support for many of the clades. Morphological clade support ranges from one to six characters, in keeping with what is seen in most of QRC (Fig. 92). Molecular support for many clades is weak or absent: seven clades have no molecular synapomorphies, as perhaps predicted by the lack of character support and resolution in the molecular analysis. Numbers of molecular autapomorphies are mostly zero to four, but V. neyratii has nine in the combined-data analysis. The unexpected position of V. neyratii among the savanna species as sister-taxon to V. rufa in the molecular analysis (Fig. 89, 90) draws attention to this relatively disparate branch length in comparison to the few molecular changes on most other

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branches in this clade. In the molecular analysis *V. neyratii* shares only one apomorphy with *V. rufa* compared to the nine autapomorphies of the former (and one of the latter). The autapomorphic nature of the *V. neyratii* sequence indicates that it should be reexamined, but the most appropriate way to evaluate the hypotheses generated by these analyses regarding the position of *V. neyratii* is by the addition of more characters and in particular of more taxa.

Within the VS clade four clades have Bremer Support>2 (BS=3 or 4): VS1/combined and VS3/combined (bootstrap=52% for both), *V. neyratii*/*V. densiflora*/*V. pyramidalis* (bootstrap=68%), and *V. haenkeana*/*V. tucanorum* (bootstrap=59%)(Fig. 91). Of these four clades, only the VS3/combined clade has molecular data supporting it; the others are supported by 4-6 morphology synapomorphies (Fig. 92). It is a common observation that *Vochysia* species are quite similar to each other, and it is not a surprise to discover that they are close molecularly as well as morphologically. This may reflect imprecise circumscription of species (for instance among the savanna species) or recent divergence, but in any event indicates that further study is in order.

II. Monophyly of tribes

The recovery of the same three major clades in all three analyses (Figs. 88, 89, 91) is not unexpected, because the similarities between the genera in each group have been recognized for over 100 years (e.g. Warming 1875; Baillon 1878; Stafleu 1952). The analyses are unanimous in supporting a monophyletic tribe Erismeae, but provide no support for a monophyletic tribe Vochysieae. A clade corresponding to the latter tribe is found in four of the 52 most-parsimonious trees generated from the molecular data set. It is not found at all in the trees generated

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by the morphological or the combined data sets (Figs. 88, 91).

It is perhaps paradoxical that the morphology data do not support the monophyly of Vochysieae; this tribe was, after all, described on the basis of morphological similarities among the genera (Dumortier 1829; Stafleu 1952). Vochysieae have been distinguished by their superior trilocular ovary (58, 61), dehiscent fruit (68), and winged seeds, in contrast to the inferior unilocular ovary and indehiscent fruit of the Erismeae. However, serial sections confirm that the ovary of QRC is superior, but show that the ovary of Vochysia and Salvertia is partly inferior. Locule number (61) cannot be optimized because of variability in the outgroup in this analysis. Dehiscent fruit is plesiomorphic (68) in this analysis, and furthermore, the fruits dehisce in different fashions in the two clades thus the homology of this character is murky in any event. The seed wings, while similar in shape (74), are entirely different in composition (75)(Boesewinkel and Venturelli 1987). Thus none of the features that have been used to unite QRC and VS in tribe Vochysieae is both shared and derived in this analysis.

The literature contains additional examples of misinterpreted features that have been used to unite QRC and VS. For instance, Kawasaki's key to the tribes describes Vochysieae as having three or more seeds, and Erismeae as having one seed (Kawasaki 1998). However, this does not take into account the number of locules in the gynoecium. In fact, Erismeae and Vochysia/Salvertia all have one seed per locule (for a total of one and three seeds per fruit, respectively), whereas QRC species generally have many seeds per locule. Since the total number of seeds depends on the number of locules, these two characters overlap. However, locule number (61) and seeds per locule (73) are not obviously dependent and provide more information because in combination

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they also indicate the total number of seeds. Regarding these two characters, QRC and VS both have three locules; this character could not be optimized in this analysis but may be plesiomorphic (it is a common state in Myrtaceae), and is also present in Erismadelphus (although only one locule is fertile). VS and Erismeae both have one seed per locule. Thus locule number and seeds per locule do not explicitly support the tribe Vochysieae.

Studies of floral morphology have also brought to light features of QRC that set it apart from VS and the rest of the family. These include the oblique receptacle (although this is ambiguous in Erismeae), the absence of medullary bundles in the pedicel, and the offset position of the fertile stamen. QRC species are also distinctive in having extrafloral nectaries on the stem, and in some species claw-shaped appendages on the leaf and sepal tips. In previous works the superior trilocular ovary and dehiscent fruit were emphasized in relating QRC and VS; in light of the results of this study and our better understanding of these characters, there appears to be no basis for combining QRC and VS into a single tribe.

In direct contradiction to the concept of a tribe Vochysieae, the combined data set indicates that there is some - albeit conflicting - support for a sister-group relationship of Erismeae with either QRC or VS. The first configuration (QRC/Erismeae), seen in one of the two most-parsimonious trees (Fig. 91a) as well as in 48 of the 52 molecular trees, is supported in that combined-data topology by two molecular characters, as well as by possession of clawed petals (45). Characters such as sepals that are subequal in size (39) and single petals (42) are also absent from the outgroup and VS, and are shared by essentially all taxa in QRC and Erismeae except Erismadelphus. The position of this African genus as sister to the species of Erisma (Fig. 91) means

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these characters cannot be unambiguously optimized as synapomorphies of a QRC/Erismeae clade. The other most parsimonious tree places Erismeae with VS (as in the morphology trees)(Figs. 88, 91b); this is supported by two ovules per locule (62) and one seed per locule (73), but by no molecular characters. The VS/Erismeae affiliation is also supported by petals 7-15 mm (43)(as in the morphology analysis), even though this feature is highly variable on the tree (12 steps, CI=0.25, RI=0.25).

III. Taxonomy

A. QRC clade

The results of the combined-data analysis show *Ruizterania* (Stafleu's sect. *Trichanthera*) and *Callisthene* nested within *Qualea* (Fig. 91). Whereas there are synapomorphies that distinguish *Ruizterania* and *Callisthene*, there are no characters that define *Qualea* to their exclusion. Thus this analysis indicates that *Ruizterania* and *Callisthene* cannot be maintained as separate genera. This is not unpredicted, as all three genera share and overlap in apomorphic characters. For instance species of all three have stipular extrafloral nectaries (27) and crumbling exocarps (71), both *Ruizterania* and *Callisthene* have elongate fourth sepals (39) and cymose inflorescences (29), and species of both *Qualea* and *Callisthene* lack staminodes (57), which are found in nearly all other species in the family.

The analysis includes only one species from Stafleu's spurless subgenus *Amphilochia* (*Q. dichotoma*)(Appendix 1, Table 4), thus the monophyly of that group (8 spp) was not evaluated. However, *Q. dichotoma* is nested among the other species and thus renders subgenus *Qualea* paraphyletic (Fig. 91). There is also only one representative of subgenus *Qualea* sect. *Qualea* (*Q. paraensis*) thus the status of that section cannot be assessed. Qualea paraensis has only one molecular autapomorphy but is morphologically divergent from the rest of the QRC clade, with eight morphological autapomorphies. Its position as sister to the rest of the clade must be evaluated by the inclusion of other species from sect. Qualea, particularly because the sister-clade has only one molecular and one morphological synapomorphy (pilose style base, character 64) (Fig. 92).

This study includes two species from Stafleu's subgenus Qualea, sect. Costatifolium, Q. multiflora and Q. parviflora. These two savanna species are small-to-medium trees with soft wood, corky bark, and contorted branches, and their fruits are similar, thus when not in flower they present similar appearances and have been considered closely related (Stafleu 1953). Nonetheless in this morphological data set they differ in 10 characters, and their position as sister-taxa in the morphology analysis has only weak support (Fig. 88). Molecular support is, however, stronger, and the combined-data analysis places them together with eight supporting synapomorphies and Bremer Support = 6 (Fig. 91).

The results of the combined-data analyses indicate that QRC should be recognized as one genus. However, it should be noted that in the combined-data topologies the clade comprises five branches, and each branch represents a different described genus, subgenus, or section (Table 4, Fig. 91) of Stafleu (1953). If this topology withstands the inclusion of additional species, the separation of this group into five genera would warrant consideration. However, the eight synapomorphies of floral, fruit, and vegetative morphology, as well as the relatively strong molecular support (7 synapomorphies) for the QRC clade and the weak support for individual clades within (0-3 synapomorphies except for Q. multiflora/Q. parviflora), argue strongly

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in favor of combining these taxa into one genus.

B. VS clade

In the combined-data analyses *Salvertia* is nested within *Vochysia*, as sister-group to a clade comprising the five members of Stafleu's sect. *Vochysiella* subsect. *Decorticantes* (Table 4, Fig. 91). *Salvertia* is morphologically autapomorphic (e.g. equal-sized sepals and five white petals), however it is not especially divergent molecularly. It has three molecular autapomorphies, which is in line with the 0-4 of most of the *Vochysia* species. This analysis indicates that *Salvertia* is in fact a hawkmoth-pollinated species of *Vochysia* (which are generally bee pollinated), with a suite of floral characteristics that are presumably related to this difference in pollinator.

The combined-data analysis supports the monophyly of Stafleu's sect. *Vochysiella* subsect. *Decorticantes* (Table 4, Fig. 91), the savanna clade, and indicates that *Salvertia* might be included in this group. These are all drought-adapted species, and it can be suggested that their morphological similarities are convergent. However, the molecular data alone also place the five subsect. *Decorticantes* species together, although with the unexpected addition of *V. neyratii* (Table 4, Fig. 90). The combined-data analysis also supports the monophyly of Stafleu's sect. *Ciliantha* subsect. *Ferrugineae* (*V. pyramidalis*, *V. densiflora*, and *V. neyratii*), a group characterized by abundant rust-brown pubescence. The data include two members of sect. *Ciliantha* subsect. *Lutescentes* (*V. thyrsoidea* and *V. tucanorum*), which form a clade with the one representative of Stafleu's sect. *Vochysiella* subsect. *Calophylloidea* (*V. haenkeana*)(Fig. 91) but do not themselves comprise a monophyletic group. There are no representatives of the other four subsections of sect. *Ciliantha*, and in general branch

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lengths and support values are low for most clades within VS, thus conclusions about infrageneric structure in *Vochysia* are premature.

As noted, *Vochysia* species are quite similar to each other. Stafleu's monograph was based on herbarium specimens, and several species were described from only one or two collections. Examination of pressed material as well as field observations indicate that the boundaries of some species are ill-defined. Examples of similar species in this analysis include *V. rufa* and *V. cinnamomea*, which seem to differ significantly only in pubescence color, and *V. elliptica* and *V. pruinosa*, which are mainly distinguished by leaf size. Other characters that distinguish them vary substantially within individual species. Further study of these and related species is needed to determine the range of variability within and the boundaries between the species of *Vochysia*.

C. Erismeae

This is the only clade in which more than one traditional genus can be recognized. Only three species are included in this analysis thus it is possible that with additional species of *Erismadelphus* or *Erisma* the distinction between the genera will be obscured. However, the branches to *Erisma* and *Erismadelphus* are the longest in the ingroup (Fig. 91, 92), that is, there is significant difference, in terms of both molecular and morphological characters, between *Erisma* and *Erismadelphus*. Furthermore, preliminary analysis with two additional species of *Erisma* maintains the position of *Erismadelphus* as sister-taxon to *Erisma*. It is perhaps not a coincidence that the only group within Vochysiaceae that can be divided into two traditional genera is the group that is found on two continents.

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IV. Character evolution

A. Optimization issues

One of the purposes of an outgroup is to provide a means of determining the plesiomorphic state of characters in the ingroup. However, the specific choice of taxa - outgroup and ingroup - may have an unexpected influence on the optimization of some characters. In this case the outgroup taxa are mainly small-medium trees and shrubs, and the character state "large trees" is optimized in the combined-data analysis as a synapomorphy for Vochysiaceae. Although this is certainly a possible scenario, in fact Myrtaceae are varied and include many species that are large trees, and the particular choice of taxa may have produced a synapomorphy for Vochysiaceae that accurately reflects this set of data but not the characters of the family as a whole. Within the ingroup, white/yellow petal markings being a synapomorphy for QRC falls into this category; this feature varies extensively among species and addition of taxa might well eliminate it as a synapomorphy of the clade. Nonetheless all analyses are constrained by the specific selection of taxa and characters and thus these issues are built into all phylogenetic studies.

The conflict between the two combined-data trees in the positions of the three major clades means that some characters cannot be unambiguously optimized and thus the homology of the character states cannot be assessed. For example, the phylogenetic derivations of the two types of seed wings (75), fruit dehiscence (70), petal number (42), and stipule shape (13) cannot be optimized because of the conflict between the two trees and, in some cases, because they are inapplicable in the outgroup. This holds true also for molecular characters, which in some cases can be seen to be unique to a clade but nonetheless can not be polarized.

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B. Character analysis

The inclusion of Vochysiaceae in Myrtales, and the sister-group relationship with Myrtaceae, indicate that previous interpretations of ovary position in Vochysiaceae may be incorrect. In this analysis inferior ovary (58) is plesiomorphic, with superior and partly inferior both being derived states (Fig. 93). Common wisdom is that an inferior ovary is derived from a superior one, but other examples of a secondarily derived superior ovary have been documented (Eyde and Tseng 1969; Igersheim et al. 1994; Chase et al. 1995; Gustafsson and Albert in press, R. Kuzoff pers. comm). In Vochysiaceae, as in other cases of secondarily derived superior ovaries, there is evidence that the superior position is not homologous with that of other taxa. One clue is that the ovary of Vochysia is not entirely superior, but is adnate at the base to the hypanthium. In addition, all Vochysiaceae show a mode of floral development that is associated with epigynous flowers, in which the floral apex is concave and the ovary is initiated in an inferior position (Kaplan 1967; Gustafsson and Albert in press). Differential growth is responsible for the ultimately superior (or mostly superior) position of the ovary. Thus there is developmental as well as phylogenetic evidence that the superior ovary is derived in this family.

Erismeae have generally been considered advanced within Vochysiaceae. Whereas the ovary position is plesiomorphic, other features of Erismeae are derived in this analysis, for instance, the accrescent sepals (69) and the single fertile locule (61). Still others are ambiguous: two ovules per locule (62) and one seed per locule (73) are shared by Erismeae with Vochysia and are derived relative to the outgroup, but whether they are synapomorphies for VS

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and Erismeae or are independently acquired in the two clades cannot be determined (Fig. 94).

The QRC clade is characterized by a number of morphological characters that have not been previously noted, at least five of which are unambiguous and uncontradicted synapomorphies in this analysis: the offset stamen position (51), oblique receptacle (36), completely superior ovary (58), woody pericarp (72), and extrafloral nectaries (27) are all unique to this clade.

Within Qualea, it has been suggested that the so-called spurless condition of subgenus Amphilochia is primitive, however the position of Q. dichotoma nested within the group indicates that it is derived (Fig. 91). Stafleu (1952) considered Callisthene to be the most specialized member of Vochysieae, due to its apparent lack of staminodes and rudimentary petals; its position in the combined-data consensus tree supports it being derived within QRC even while disallowing its recognition as a separate genus. Short branch lengths and slim taxon sampling within QRC require, however, that caution be used in framing conclusions.

Salvertia has been seen as the basal and least derived member of Vochysieae based on its five petals and equal sized sepals (Stafleu 1948). Its position within Vochysia in the combined-data analysis contradicts this, as well the correlated hypothesis that hawkmoth pollination is ancestral in the family (Oliveira 1996, 1998). In fact, if a five-petaled species is to be considered a candidate for the ancestral type, it would have to be Erismadelphus, which is at least in a position in the combined-data topologies that does not contradict that hypothesis (Fig. 91). Whether five petals is plesiomorphic in the family or is a reversal in Erismadelphus cannot be resolved, but even in the former case, there is one reversal within the family, from three

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to five petals in Salvertia.

It is not possible to make general statements regarding the homology of the character states defined for quantitative, continuously varying characters. As an example, leaf length/width ratio (character #15) has three character states and is nine steps long in the combined-data analysis. Whereas some of the steps are autapomorphies, in other cases they are synapomorphies (e.g. C. major and C. fasciculata, V. haenkeanum and V. tucanorum)(Fig. 91). Some changes cannot be optimized because there is too much variability within a clade. Similarly, pedicel length (31) is a synapomorphy for Erismeae but changes an additional nine times on the tree. This is in keeping with the observation that some of these features are constant and diagnostic in certain species or groups of species but vary extensively within other species and groups (e.g. leaf shape and size are relatively constant in V. pyramidalis but variable in V. elliptica and V. tucanorum), and adds to the argument that species, particularly in Vochysia, need to be reexamined and clearly defined.

The results of the combined-data analysis indicate that there may be patterns of habitat evolution in QRC and VS (Fig. 95). The plesiomorphic state in the family is rain forest, but there are missing data in the outgroup, and the taxa chosen to represent Myrtaceae and Melastomataceae, members of which are found in all habitats, may have influenced this optimization. The topologies of the two combined-data trees indicate that the pattern of habitat distribution in QRC and VS is slightly different. In QRC, the savanna species are monophyletic (Fig. 95) and nested within the paraphyletic rain forest species. Callisthene are found as well in gallery forest and mesophytic habitats; their distribution is apparently dependent on calcareous soils. It is perhaps not the most intuitively obvious hypothesis, but

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this analysis indicates that *Qualea* went from rain forest to savanna to gallery forest/moist woodlands. More species from this clade, particularly rain forest taxa, are needed to evaluate this hypothesis.

The VS group is divided into two clades in the combined-data analysis, one comprising two rain forest and one gallery forest species, and the other comprising all savanna and two savanna/gallery forest species (Fig. 95). There is no mixing of savanna and rain forest species in any clade as in QRC, and neither group is monophyletic. The plesiomorphic state in this clade is also rain forest, and the position of the gallery forest species in their respective clades indicates that this habitat is derived in both cases. However, support for most individual clades within *Vochysia* is weak and thus so is the basis for these hypotheses.

C. Biogeography

Whereas much interest has been expressed in the amphi-Atlantic distribution of Vochysiaceae, in fact phylogenetic analysis is not very enlightening regarding the biogeographic history of the family. *Erismadelphus* is sister to *Erisma*, a placement confirmed by preliminary analysis with additional species of *Erisma*. However, it cannot be determined whether the current distribution of the genera arose as a result of dispersal or vicariance - although the ranges of the two genera certainly make vicariance an attractive hypothesis. Virtually any scenario can be supported by the results of this analysis, or any phylogeny of this family. The best that can be said is that the number of molecular and morphological differences between the two genera suggests that the divergence occurred some time ago.

V. Conclusions

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On the basis of this analysis I would recommend that *Ruizterania* and *Callisthene* be included in *Qualea*, and that *Salvertia* be included in *Vochysia*. *Erismadelphus* and *Erisma* are recognizable as separate genera, although this must be confirmed with the addition of more species from both genera. The family would thus comprise four genera. The tribe Erismeae can still be maintained, however Vochysieae can not, thus we either abandon Erismeae as a tribe or erect two new tribes, each of which includes only one genus - but considerably more species - than Erismeae. As this work is still in progress, and information from more species is required to confirm the hypotheses generated, no formal taxonomic revision is being proposed at this time. However, in anticipation of such revision, a summary description of the three groups and four genera follows. These descriptions include as many characters as are currently understood, but clearly not all are useful for identification purposes as some require access to a microtome and microscope. Characters that vary only within a group, and do not serve to identify one group in comparison with the others, are not included. Thus for instance the barbate anthers of *Ruizterania*, the fragmenting pericarp of *Callisthene* and some *Qualea* species, and unwinged corky fruit of *Erisma* *calcaratum* are not included.

1. Medullary bundles present in pedicel, extrafloral nectaries absent, receptacle not strongly oblique, petal(s) clawed, fertile stamen antepetalous, anther connective not extended into a cap over the stigma in the bud, staminodes two, ovary inferior, fertile locule one, sepals accrescent forming wings of fruit, fruit indehiscent, seed one. (Erismeae)

a. Hairs stellate and simple, fourth sepal deciduous and wings of fruit four, petal one, color varied, obcordate or round, rudimentary

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petals up to four, gynoecium of only one locule, ovules two. Neotropical. Erisma.

b. Hairs simple, fourth sepal persistent and wings of fruit five, petals five, white, elliptic, gynoecium with up to two aborted locules, ovule one. Paleotropical. Erismadelphus.

2. Medullary bundles present in pedicel, extrafloral nectaries absent, receptacle not strongly oblique, fourth sepal at least three times as long as others (or equal), petals three (or five), not clawed, yellow (or white), obovate/elliptical, fertile stamen antepetalous, anther connective extended and forming a cap over the stigma in the bud, staminodes two, ovary partly inferior, trilocular, sulcate in cross-section, ovules two per locule, fruit a loculicidal capsule, thin-walled, pericarp folding back at dehiscence, seed one per locule, winged, wing of compressed hairs. Vochysia (including Salvertia).

3. Medullary bundles absent in pedicel, extrafloral nectaries present, receptacle strongly oblique, sepals subequal (or fourth sepal at least three times the length of the others), petal one, color varied, clawed, obcordate or round, sometimes two rudimentary petals, fertile stamen offset, anther connective may be extended but not forming a cap over the stigma in the bud, sometimes two staminodes, ovary superior, trilocular, round in cross-section, ovules many per locule, fruit a loculicidal capsule, thick walled and woody, splitting into three segments at dehiscence, seeds many per locule, winged, wing an extension of the testa. Qualea (including Ruizterania and Callisthene).

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Table 4. The subgeneric classifications of Stafleu (1948, 1952, 1953). Numbers of species are in parentheses; species used in this study are listed in each category. Erismadelphus and Salvertia do not have subgeneric categories. Erisma was divided into two sections by Stafleu (1954) but Kawasaki (1998) does not recognize these. There are only two species of Erisma in this analysis and thus no hypotheses regarding the sections can be evaluated.

Vochysia

- Section Vochysiella (20)
    - Subsect. Calophylloidea (10)
        - V. heankeana
    - Subsect. Decorticantes
        - V. rufa, V. cinnamomea, V. elliptica, V. pumila, V. pruinosa
- Section Ciliantha (74)
    - Subsect. Micranthae (11)
    - Subsect. Lutescentes (23)
        - V. tucanorum, V. thyrsoidea
    - Subsect. Discolores (3)
    - Subsect. Chrysophyllae (1)
    - Subsect. Megalanthae (5)
    - Subsect. Ferrugineae (31)
        - V. pyramidalis, V. neyratii, V. densiflora
- Section Pachyantha (3)

Qualea

- Subgenus Amphilochia (8)
    - Q. dichotoma

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- Subgenus Qualea (50)
  - Section Qualea (26)
    - *Q. paraensis*
  - Section Costatifolium (7)
    - *Q. parviflora*, *Q. multiflora*
  - Section Trichanthera (16) = Ruizterania
    - *R. albiflora*, *R. cassiquiarensis*
  - Section Polytrias (1)

Callisthene

- Section Cataphyllantha (1)
  - *C. fasciculata*
- Section Callisthene (7)
  - *C. major*

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Fig. 86. Comparison of the phylogenetic position of Vochysiaceae relative to Myrtaceae and *Heteropyxis* and *Psiloxylon* in some recent analyses. 86a. The results of Conti et al. (1996), based on *rbcL* (redrawn). According to this result Vochysiaceae would have to be included in Myrtaceae if the latter family were defined to include *Heteropyxis* and *Psiloxylon*. 86b. Results obtained more commonly with a variety of genes (see text).

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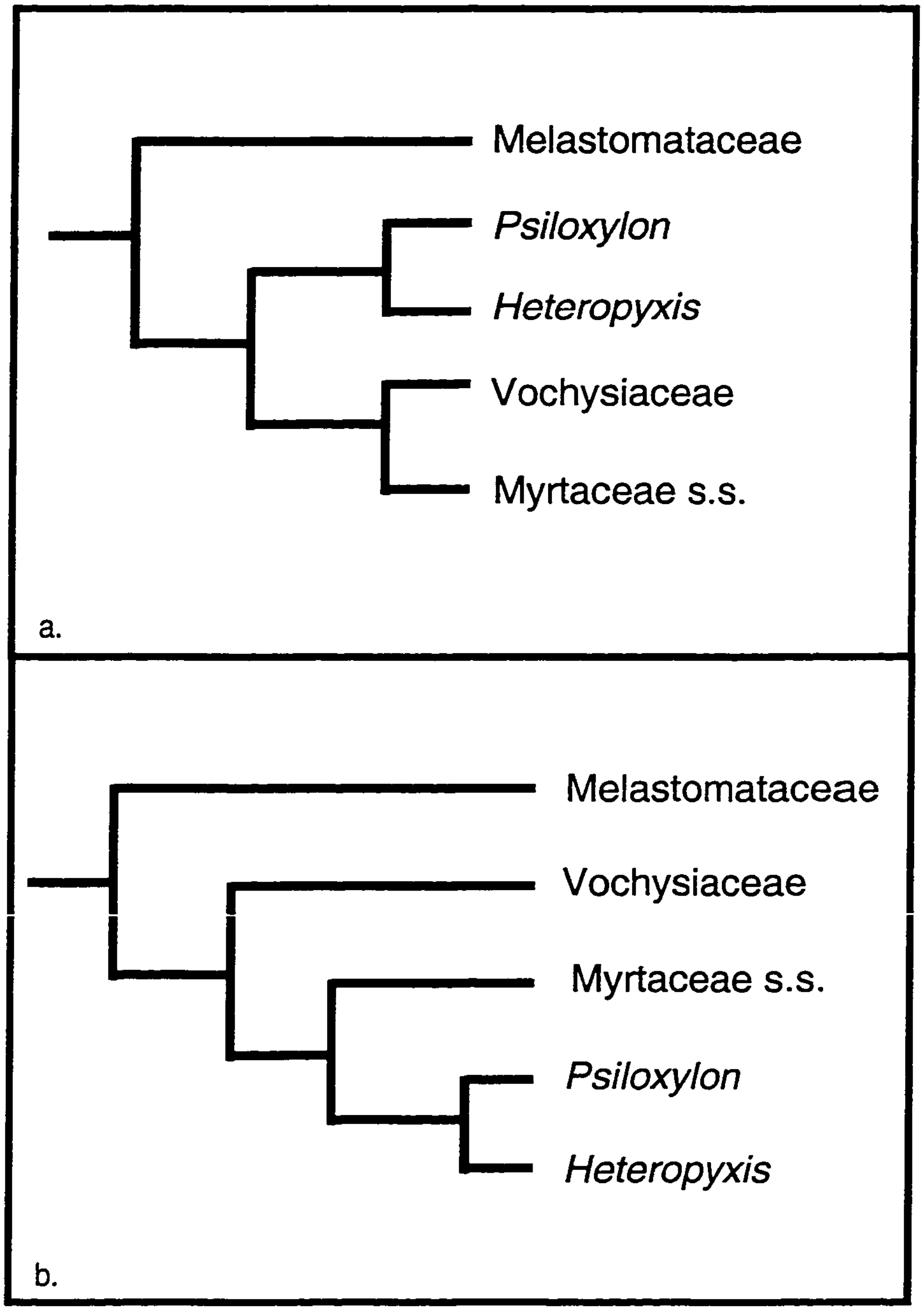

(86)

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Fig. 87. Single most parsimonious tree from cladistic analysis of Kawasaki 1992 (redrawn).

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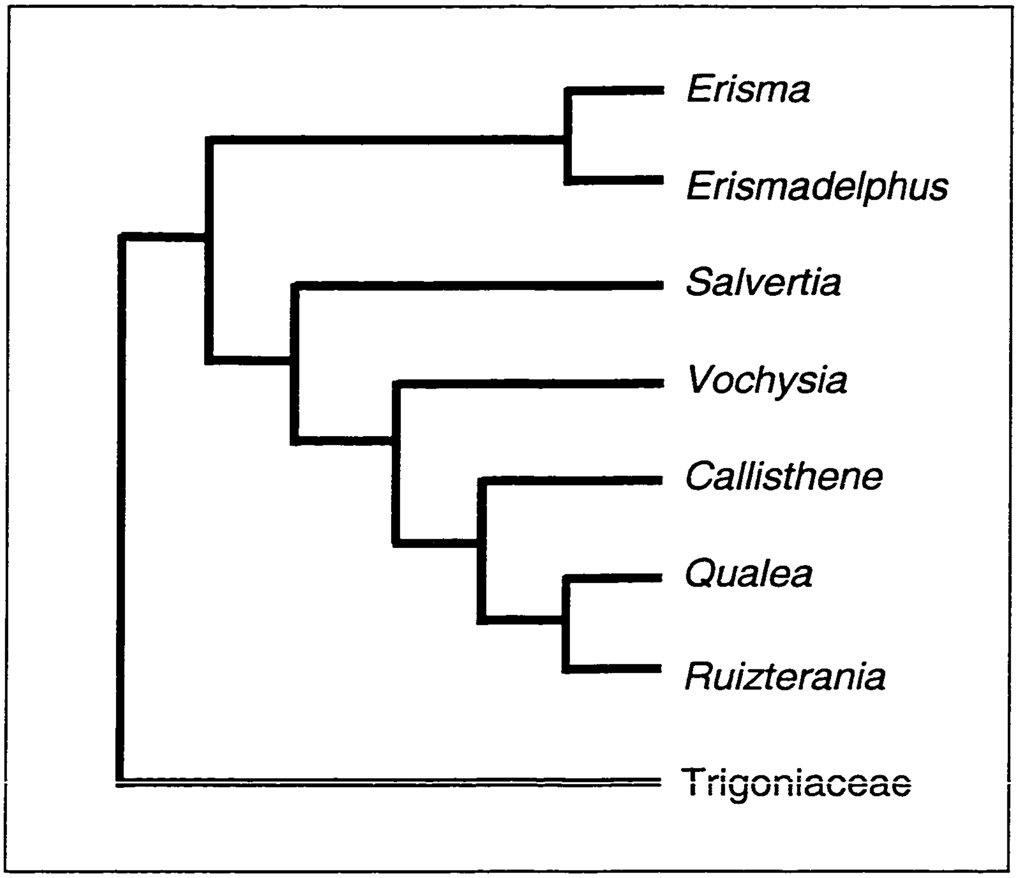

(87)

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Fig. 88. Two most parsimonious topologies based on the morphology data matrix. 320 steps, CI=0.38, RI=0.65. 88a. Branch lengths, listed above the branches, are based on changes found in both topologies for nodes present in both trees. Branch lengths are not listed for nodes that are not present in both topologies. Clade designations ("QRC1" etc.) are as in text for morphology data analysis. 88b. Bremer Support is indicated below branches.

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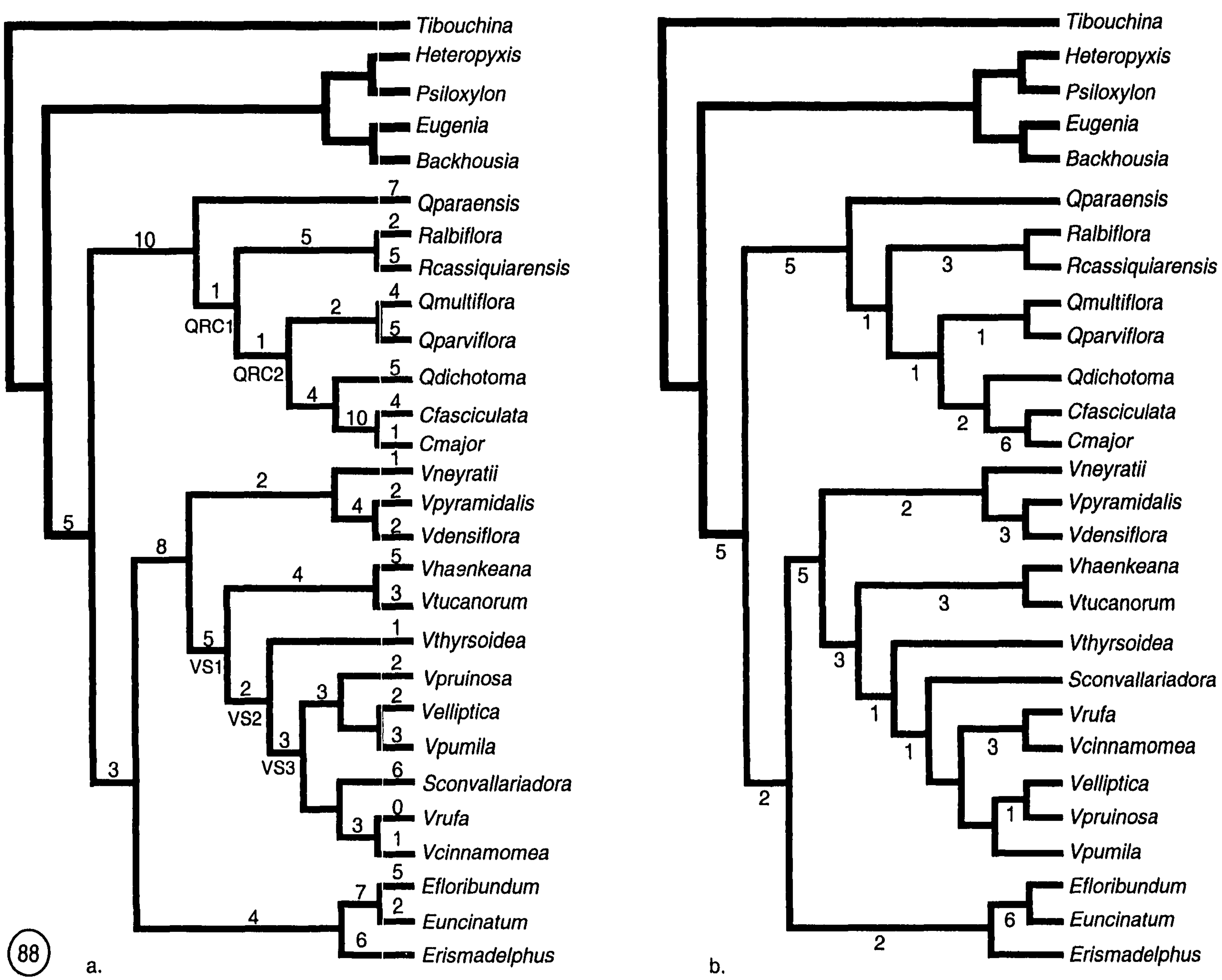

Fig. 89. One of 52 most parsimonious trees from analysis of matK data. All characters: 356 steps, CI=0.82, RI=0.85. Informative characters only: 239 steps, CI=0.74, RI=0.85. Branch lengths, indicated above branches, are based on changes found in all 52 most parsimonious trees for nodes present in all trees, and are listed only for nodes present in all 52 trees. Where two numbers are given (e.g. "12 + 15") the second is the number of characters that are unambiguously synapomorphic but that cannot be polarized due to variability in the outgroup.

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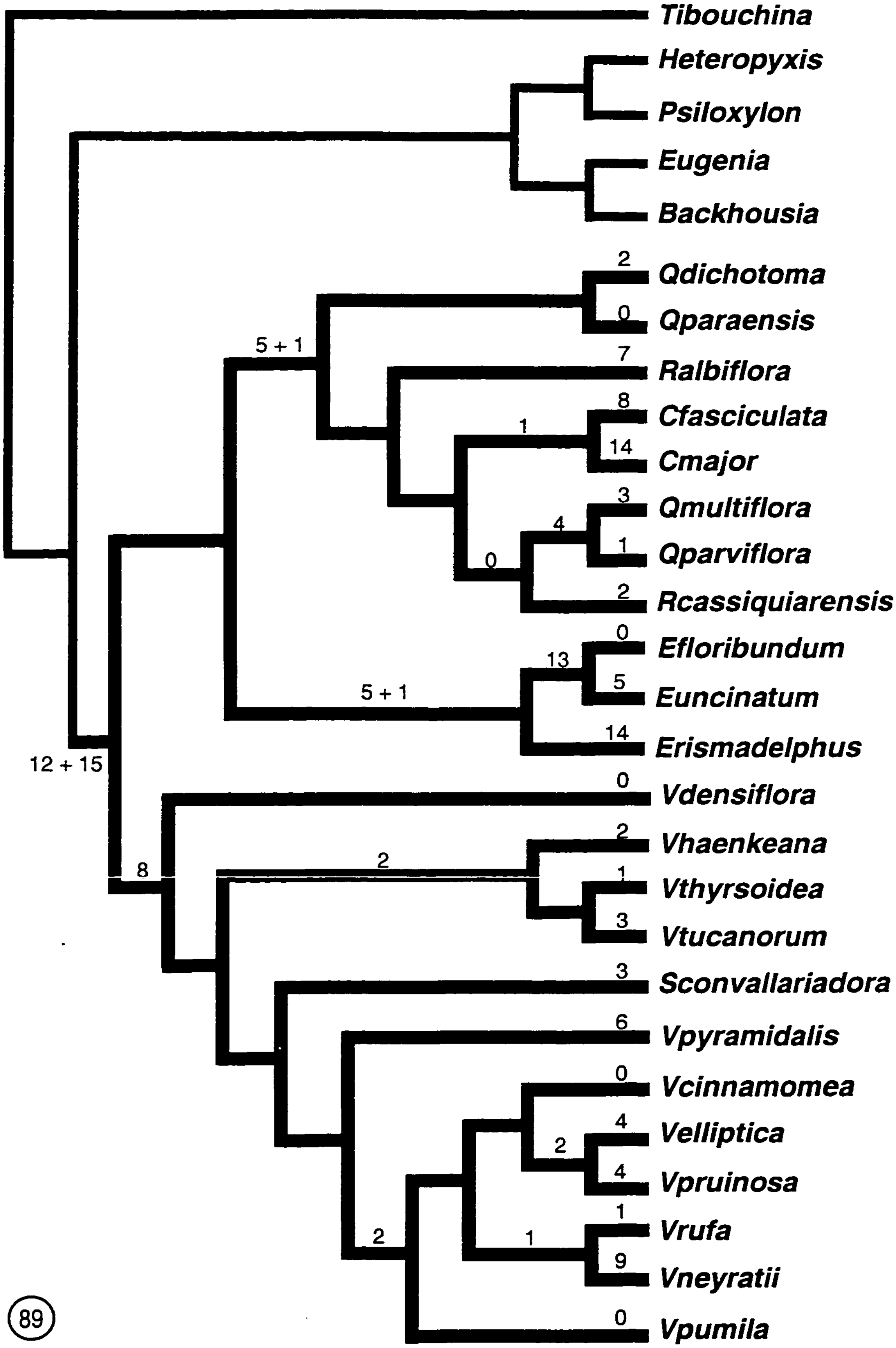

(89)

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Fig. 90. Strict consensus of 52 most parsimonious trees from analysis of *matK* data. Bootstrap percentages >50% are indicated above branches, Bremer Support below.

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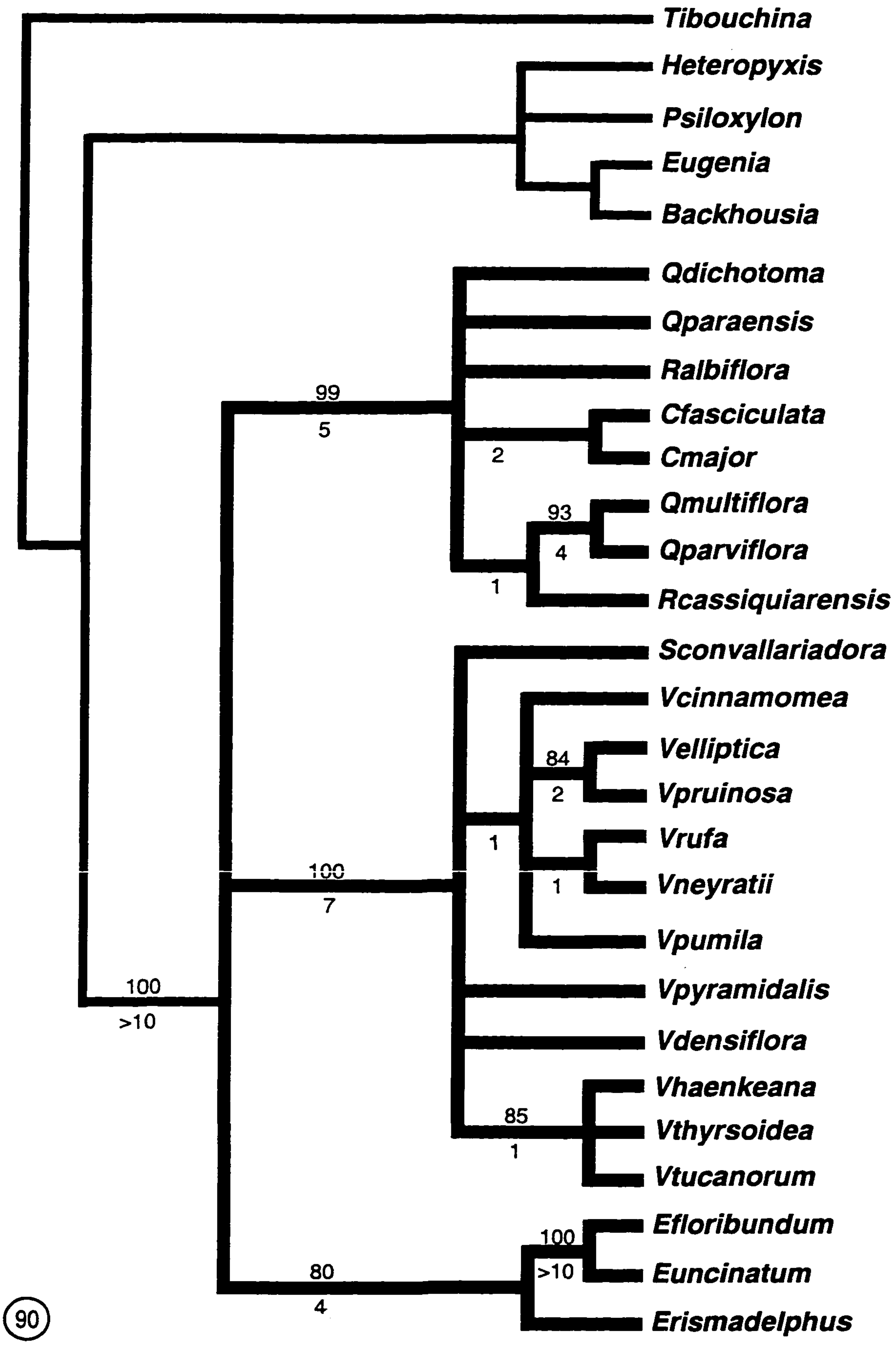

(90)

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Fig. 91. Two most parsimonious trees from analysis of the combined data sets. All characters: 688 steps, CI=0.60, RI=0.72. Informative characters only: 573 steps, CI=0.520, RI=0.72. 91a. Branch lengths, indicated above the branches, are based on changes found in both topologies for nodes present in both trees. Clade designations ("QRC1/comb." etc.) are as in text for combined-data analysis. 92b. Bootstrap percentages >50% are indicated above branches, Bremer Support below.

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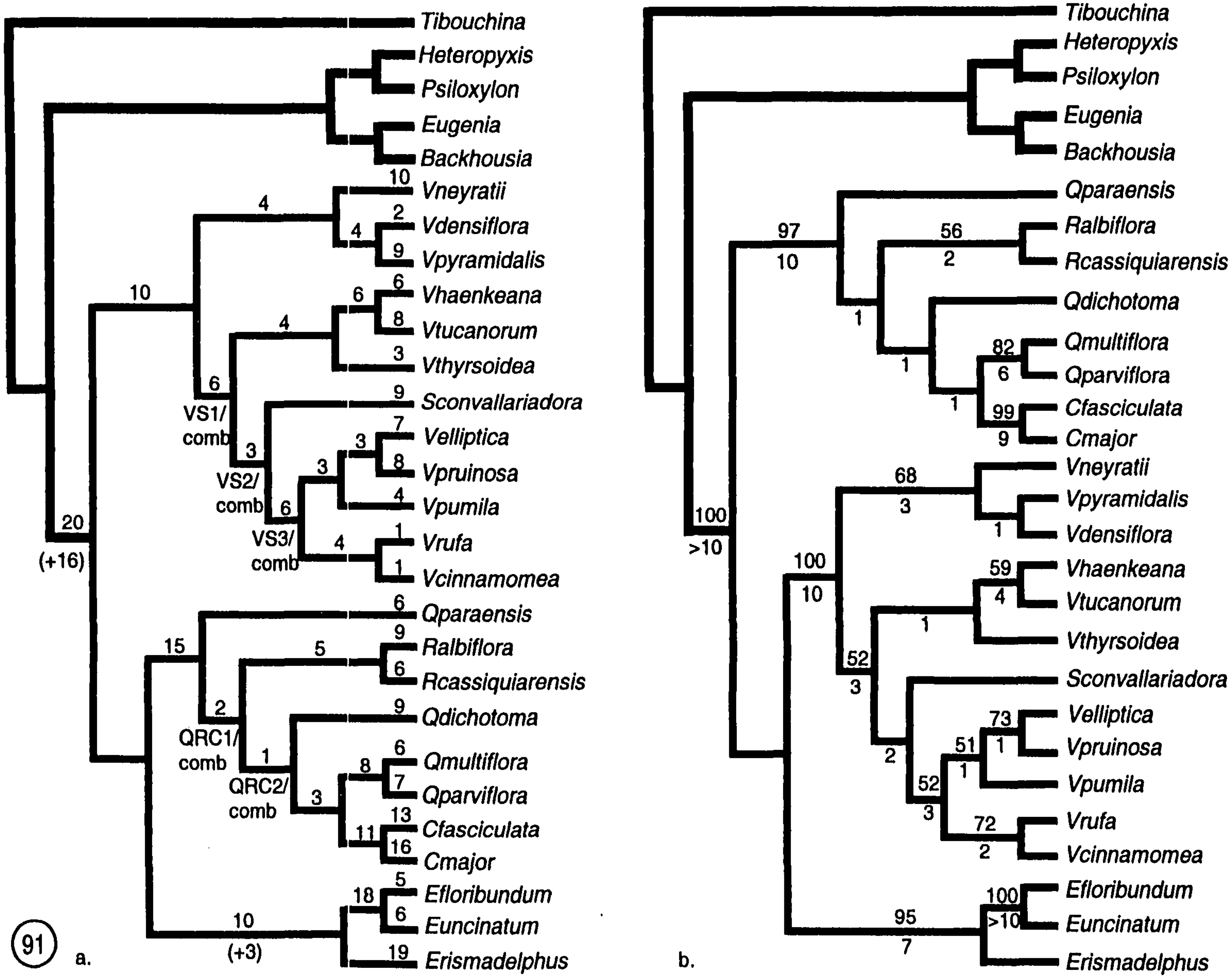

Fig. 92. One of two most parsimonious trees from analysis of combined data sets. Numbers above branches indicate unambiguous morphological/molecular changes based on both topologies. Where an additional number is given in parentheses, that number is the number of molecular changes that are unambiguously synapomorphic but that cannot be polarized due to variability in the outgroup.

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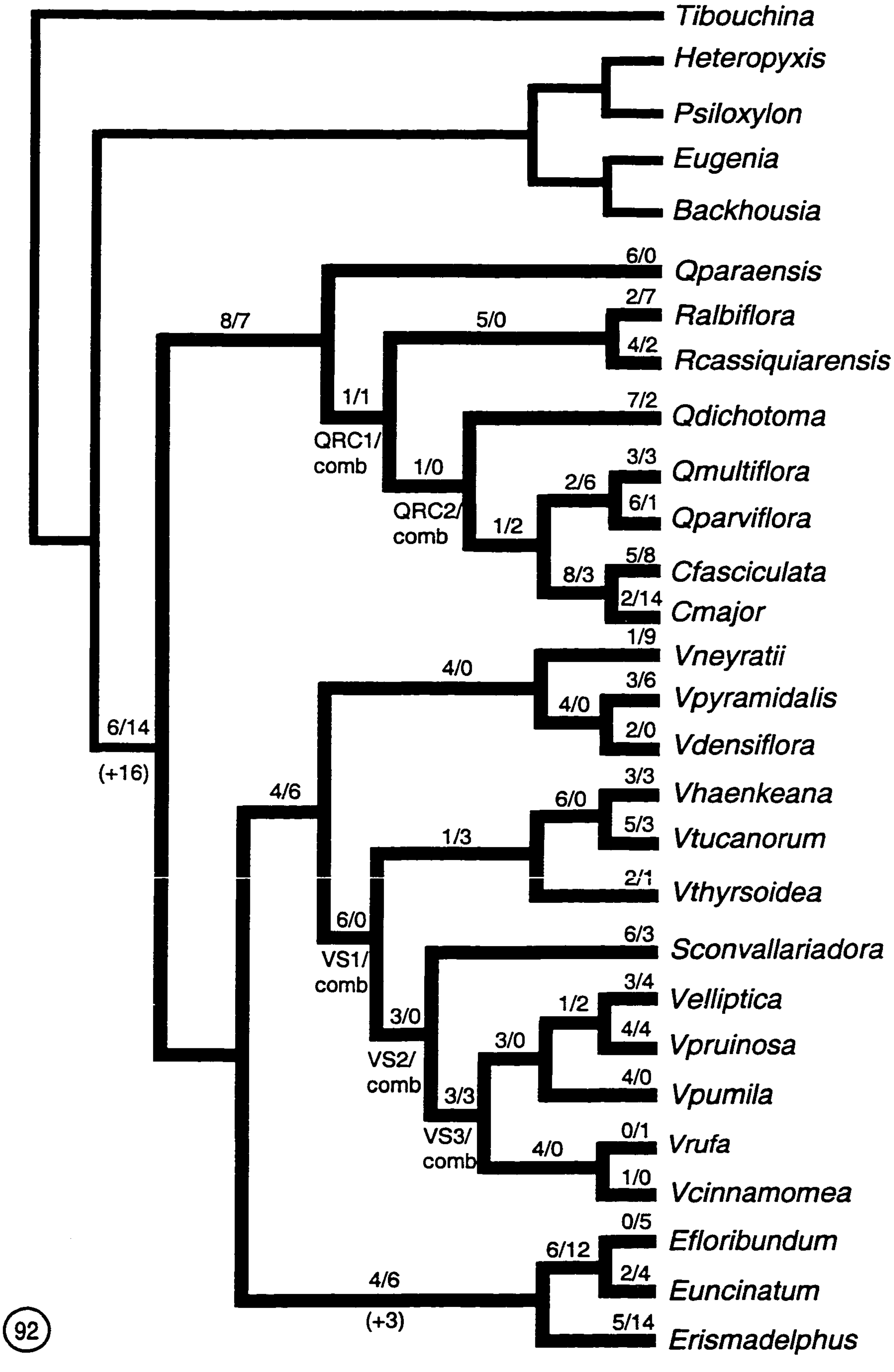

(92)

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Fig. 93. Optimization of ovary position character (character 58) on one most parsimonious tree from analysis of combined data sets. Dark gray = inferior ovary (plesiomorphic); light gray = superior ovary (apomorphic); black = partly inferior ovary (apomorphic).

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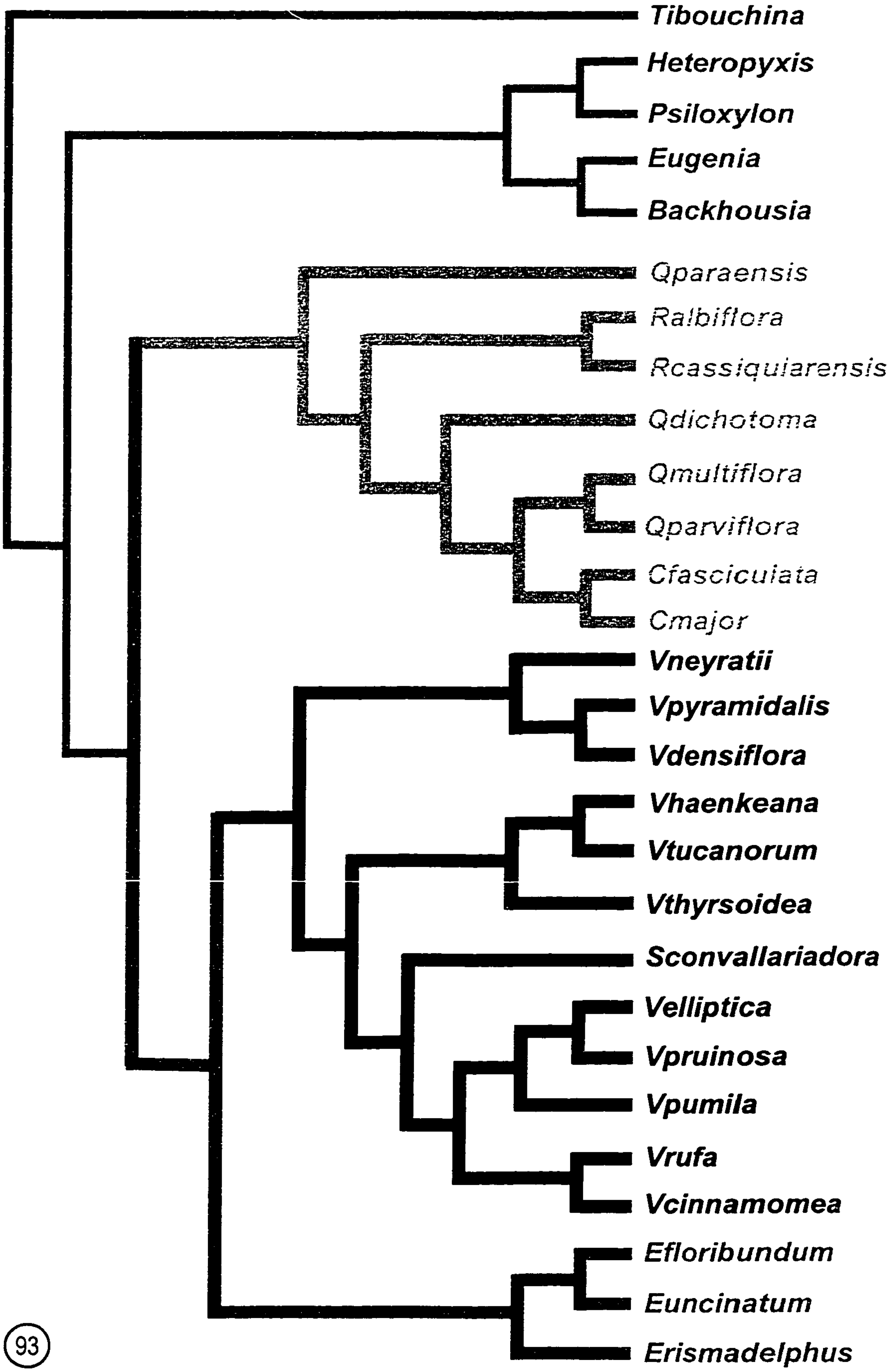

(93)

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Fig. 94. Optimization of character 73, number of seeds per locule, on one most parsimonious tree from combined-data analysis. Dark gray = many; black = one; diagonal stripes = uncertain. The character can be transformed two ways: one change at the base of Vochysiaceae and a reversal in the QRC clade, or two independent changes at the base of the Erismeae and the VS clade.

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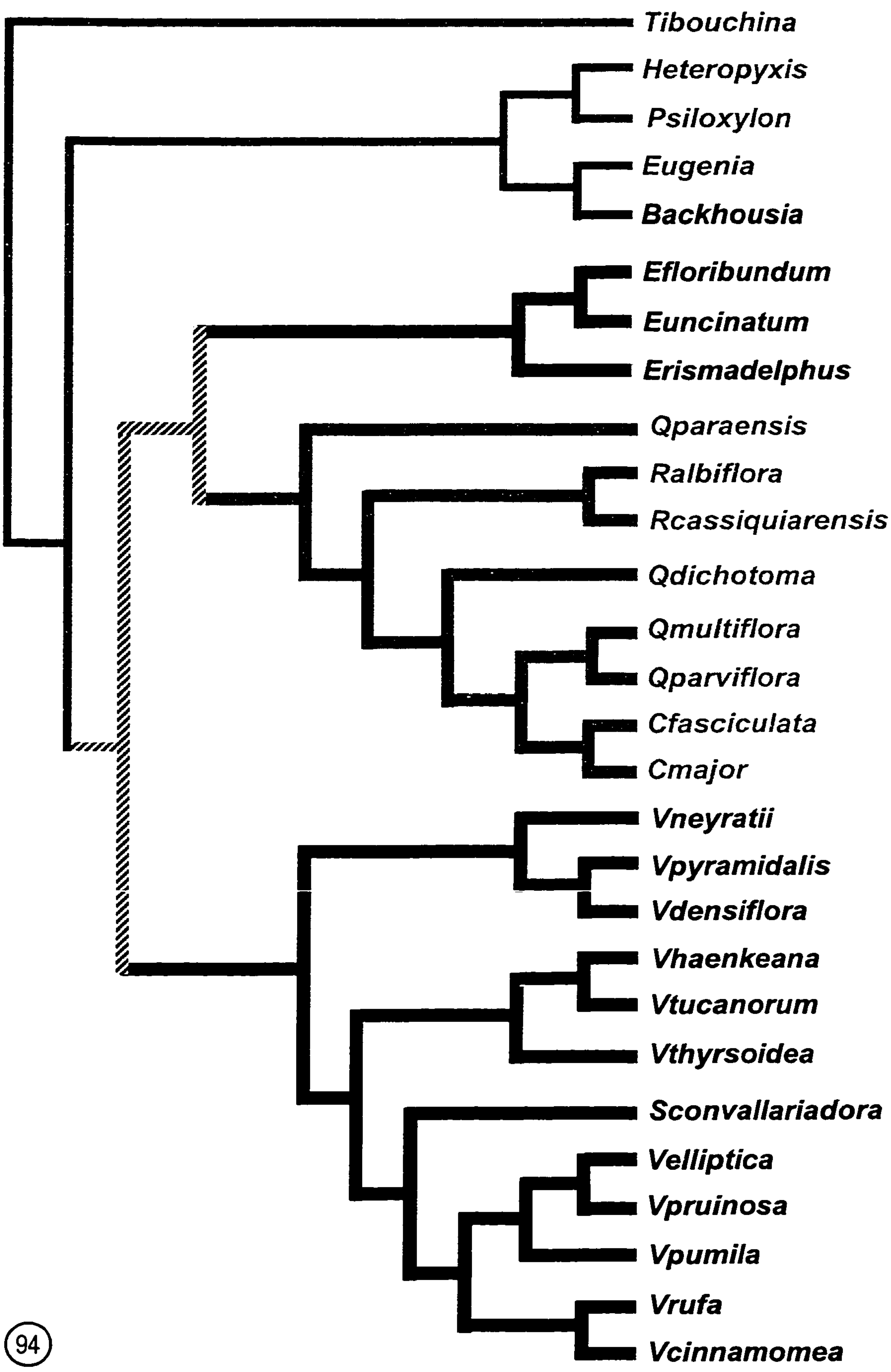

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Fig. 95. Optimization of habitat character (character 0) on one most parsimonious tree from combined-data analysis (optimization is the same in both trees). Light gray = rain forest; dark gray = gallery forest; black = savanna; black diagonal stripes = savanna/gallery forest; gray diagonal stripes = missing data or all states possible. In both the QRC and VS clades there is a single origin of the savanna habitat, and gallery forest is derived relative to both savanna and rain forest rather than being transitional. However, missing data in the outgroup makes the optimization suspect, as only two of the five taxa are scored for this character. Furthermore sparse taxon sampling in the ingroup makes conclusions tenuous.

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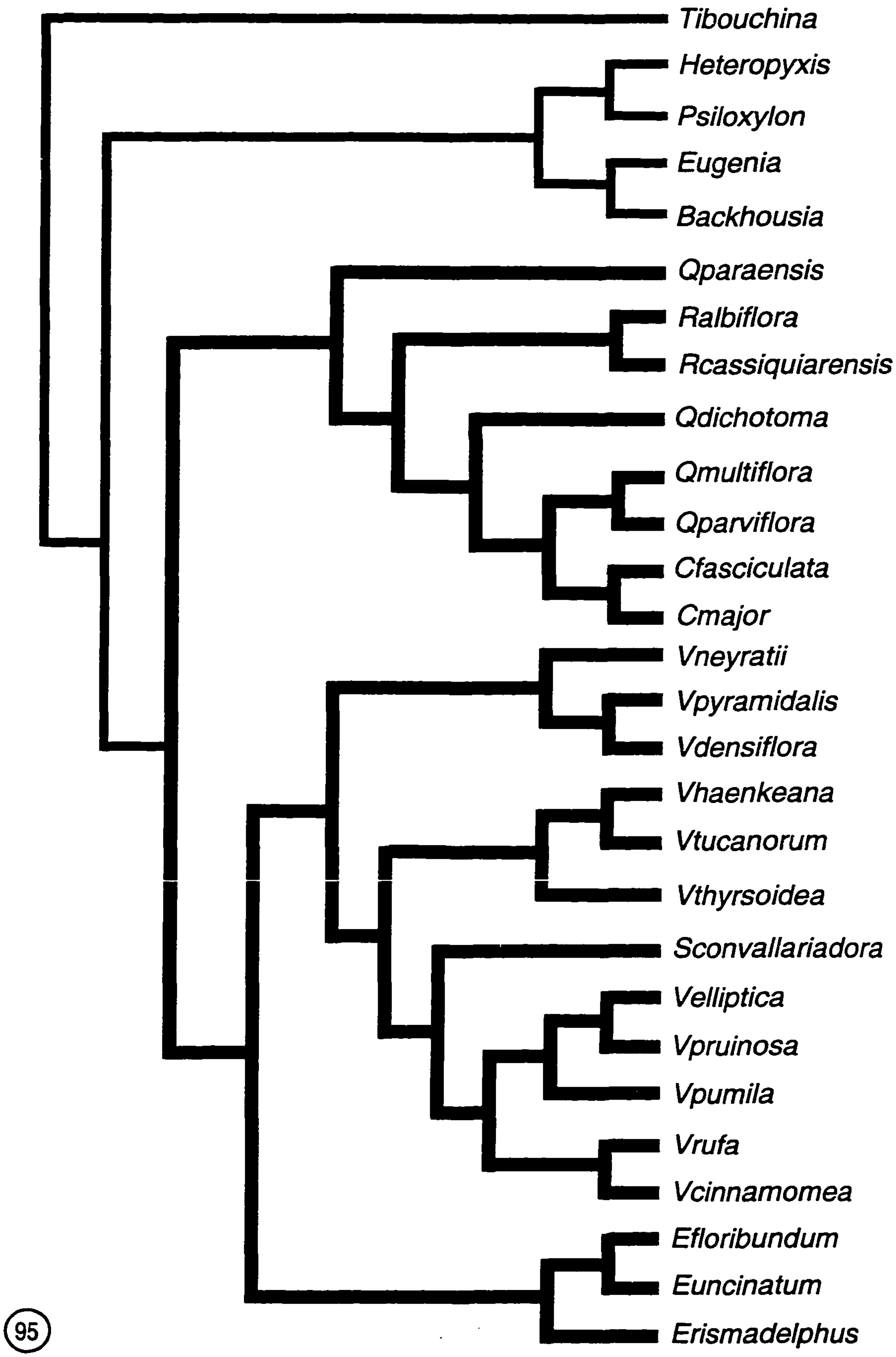

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Appendix 1. Voucher information for material used for DNA extraction and sequencing as described in text.

Outgroup:

Melastomataceae:

Tibouchina Aubl. - UNSW 22623 (UNSW)

Myrtaceae:

Backhousia myrtifolia Hook & Harv. - UNSW 22391 (UNSW)

Eugenia Mich. ex Linn. - PGW 1335 (NSW)

Heteropyxis natalensis Y. B Harv. - unvouchered (RBG 13823)

Psiloxylon mauritanium Thou. ex Benth. - Briggs 7233 (NSW)

Vochysiaceae:

Vochysia

V. cinnamomea Pohl - Litt et al. 41 (NY)

V. densiflora Spr. ex Warm. - JRN 716 (INPA)

V. elliptica Mart. - Litt et al. 22 (NY)

V. haenkeana Mart. - Rizzo et al. 11395 (NY)

V. neyratii D. Normand - Mori et al. 22964 (NY)

V. pruinosa Pohl - Litt et al. 2 (NY)

V. pumila Pohl - Litt et al. 75 (NY)

V. pyramidalis Mart. - Litt et al. 49 (NY)

V. rufa Mart. - Litt et al. 14 (NY)

V. thyrsoidea Pohl - Litt et al. 61 (NY)

V. tucanorum Mart. - Litt et al. 32 (NY)

Salvertia

S. convallariodora St.-Hil. - Litt et al. 15 (NY)

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Qualea

Q. dichotoma (Mart.) Warm. - Litt et al. 45 (NY)

Q. multiflora Mart. - Litt et al. 12 (NY)

Q. paraensis Ducke - Litt et al. 63 (NY)

Q. parviflora Mart. - Litt et al. 27 (NY)

Callisthene

C. fasciculata Mart. - Litt et al. 55 (NY)

C. major Mart. - Litt et al. 34 (NY)

Ruizterania

R. albiflora (Warm.) Marc.-Berti - Rib. 1498 (INPA)

R. cassiquiarensis (Spruce ex Warm.) Marc.-Berti - Vicentini 1120 (INPA)

Erisma

E. floribundum Rudge - Mori et al. 22847 (NY)

E. uncinatum Warm. - Mori et al. 21585 (NY)

Erismadelphus

Erismadelphus exsul Mildbr. - unvouchered

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Appendix 2. Molecular data matrix. Data are from chloroplast gene matK (see text).

	0 5 10 15 20 25 30 35 40 45 50
Tibouchina	223?12000?3232223?032010012003?302331003003323000?1233
Heteropyxis	323312000032102233032010020003130233300300332320001233
Psiloxylon	32331200003210223303201002000313023330030033232000 1$33
Eugenia	333112000012102233033010030003130233100300332320001233
Backhousia	323112000032302233032210030003130233100300332320001233
Cfasciculata	323312000032202233030010030003330233331300332320001233
Cmajor	?23312000032202233032010230003330233331300332320001223
Efloribundum	?23312000032302233032010030003330233331300332320001233
Erismadelphus	323312000032302233032110030003330233331300332320001233
Euncinatum	323312000032302233032010030003330233331300332320001233
Qdichotoma	323312000032302233032010030003330233331300332320001233
Qmultiflora	3233120010322?2233032010030013330233331300332310001233
Qparaensis	??????????????22330320?0030003330233331300332320001233
Qparviflora	??????????????22330320?0030003330233331300332310001233
Ralbiflora	????????????????3303201003000333023333130033232000 1233
Rcassiquiarensis	??????????????2233032010030003330233331300332320001233
Sconvallariodora	?23312000032302233032010030003330233331300332320001233
Vcinnamomea	323312000032302233032010030003330233331300332320001233
Vdensiflora	323312000032302233032010030003330233331300332320001233
Velliptica	?23312000032302233032010030003330233331300332320001231
Vhaenkeana	323312000032302233032010030003330233331300332320001233
Vpruinosa	?233121?0032302233032010030003330233331300332320101231
Vpumila	323312000032302233032010030003330233331300332320001233

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Vpyramidalis        323312000032302233032010030003330233331300332320001233
Vrufa               323312000032302233032010030003330233331300332320001233
Vthyrsoidea         323312000032302233032010030003330233331300332320001233
Vtucanorum          323312000032302233032010030003330233331300332320001233
Vneyratii           323312000032302233032010330003330233331300332320001233


                    54   59   64   69   74   79   84   89   94   99   104
                    |    |    |    |    |    |    |    |    |    |    |
Tibouchina          300330331201323031001020031123320330333220301320331 30
Heteropyxis         300330131200323031001020031133321333333102130032033130
Psiloxylon          300330131200323031001020031133321333333102130032033130
Eugenia             100330131200323031001020031133320333333102110032033130
Backhousia          300330131200323031001020031133320333333122130032033130
Cfasciculata        300330331200302231001000031133310330333122130032033130
Cmajor              300330331200302231001000031133320330333122130032033130
Efloribundum        300330331200322231001000031133310330333102130032033130
Erismadelphus       300330331200320231001000031133310330333322130032033130
Euncinatum          300330331200322231001000031133310330333102130032033130
Qdichotoma          300330331200302231001000031133310330333122130032033130
Qmultiflora         300330331100302231001000031133310330333122130032033130
Qparaensis          300330331200302231001000031133310330333122130032033130
Qparviflora         300330331100302231001000031133310330333122130032033130
Ralbiflora          300330331200302231001000031133310330333122130032033130
Rcassiquiarensis    300330331200302231001000031133310330333122130032033130
Sconvallariodora    300330331200322231001000031133310332333122130032033130
Vcinnamomea         300330331200322231001000031133310332333122130032033130
Vdensiflora         300330331200322231001000031133310332333122130032033130
Velliptica          300330331200322231001000031133310332333122130032033130
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Vhaenkeana         300330331200322231001000031133310332333122130032033130
Vpruinosa          300330331200322231001000031133310332333122130032033130
Vpumila            300330331200322231001000031133310332333122130032033130
Vpyramidalis       300330331200322231001000031133310332333122130032033130
Vrufa              300330331200322231001000031133310332333122130032033130
Vthyrsoidea        300330331200322231001000031133310332333122130032033130
Vtucanorum         300330331200322231001000031133310332333122130032033130
Vneyratii          300330331200322231001000031133310332333122130032033130
```

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                   108  113  118  123  128  133  138  143  148  153  158
                   |    |    |    |    |    |    |    |    |    |    |
Tibouchina         201000030223312332003010010020033323033101020331303132
Heteropyxis        211000030103333333221010010020033323033131000330313102
Psiloxylon         211000030103333333221010010020033323033131000330313102
Eugenia            311000031103333312221010010020033323033131000333313102
Backhousia         3110000310033333332221010010020033323033131000330313102
Cfasciculata       23100003110333 3?22221010010020033323033131000330303112
Cmajor             2310000311033333?22213010010020033323033131000330303112
Efloribundum       231000031103323322221010010020033323033131000330303112
Erismadelphus      011000031103333322221010010020033323033131000330303112
Euncinatum         231000031103323322221010010020033323033131000330303112
Qdichotoma         23100003110333**22221010010020033323033131000330303112
Qmultiflora        231000031103332322221010010021033323033131000330303112
Qparaensis         231000031103333322221010010020033323033131000330303112
Qparviflora        231000031103332222221010010021033323033131000330303112
Ralbiflora         231000031103333322221010010020033323033131000330303112
Rcassiquiarensis   231000031103333322221010010021033323033131000330303112
Sconvallariodora   231000031103333333220010010020033323033131000330303112
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Vcinnamomea      2310000311033333333221010010020033323033131000330303112

Vdensiflora      2310000311033333333221010010020033323033131000330303112

Velliptica       2310000311033333333221010010020033323033131000330303112

Vhaenkeana       2310000311033333333221010010020033333033131000330303112

Vpruinosa        2310000311033333333221010010020033323033131000330303112

Vpumila          2310000311033333333221010010020033323033131000330303112

Vpyramidalis     2310000311033333333221010010020033323033131000330303112

Vrufa            2310000311033333333221010010020033323033131000330303112

Vthyrsoidea      2110000311033333333223010010020033323033131000330303112

Vtucanorum       2310000311033333333223010010020033323033131000330303112

Vneyratii        2310000311033333333221010010020033333033131000330303112



                 162  167  172  177  182  187  192  197  202  207  212

                 |    |    |    |    |    |    |    |    |    |    |

Tibouchina       022103332102310122322200033110333313333120????????33113

Heteropyxis      0222033321023103323222000331103333111301203302303133113

Psiloxylon       0223033321023103323222000331103333111301203302303133113

Eugenia          0222033321023103323222000331103333111301203302303133113

Backhousia       0222033321023003323222000331203333111301303302303133333

Cfasciculata     0222033321021113303220003311033331113212033021011333 13

Cmajor           0222033321021103303220003311033333111321203302101133313

Efloribundum     0222033321023103323222000331103333111301201302103133313

Erismadelphus    0022033321023103323222000331103333111301003302121133313

Euncinatum       0222033321023103323222000331103333111301201302103133133

Qdichotoma       022203332102110333$32200033110333311113212033021011 33$13

Qmultiflora      0222033321021103303220003311033333111321203302101133313

Qparaensis       0222033321021103323220003311033333111321203302101133313

Qparviflora      0222033321021103303220003311033333111321203302101133313
```

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```
Ralbiflora        022203332102110330322000331103333111321203303101133313
Rcassiquiarensis  022203332102110330322000331103333111321203302101133313
Sconvallariodora  022203332102310332322000331103333111301203302103133313
Vcinnamomea       022203332102310332322000331103333111301203302103133313
Vdensiflora       022203332102310332322000331103333111301203302103133313
Velliptica        022203332102310332322000331103333111301203302103133$13
Vhaenkeana        022203332102310332322000331103333111301203302103133313
Vpruinosa         022203332102310332322000331103333111301203302103133313
Vpumila           022203332102310332322000331103333111301203302103133313
Vpyramidalis      022203312102310332322000331103333111301203302103133$13
Vrufa             022203332102310332322000331103333111301203302103133313
Vthyrsoidea       022203332102310332322000331103333111301203302103133313
Vtucanorum        022203332102310332322000331103333111301203302103133313
Vneyratii         022203332102310332322000331103331113101203302103133313


                  216  221  226  231  236  241  246  251  256  261  266
                  |    |    |    |    |    |    |    |    |    |    |
Tibouchina        23????????????????????????????????????????????????????
Heteropyxis       3020031331310333012231001031331322003133333?2021200303
Psiloxylon        302003133131033301223100103133132200313333332021200303
Eugenia           302003133131033301223100103133132200313333332021200313
Backhousia        3020031331310333032231001031331322003133333??021200303
Cfasciculata      3020031331310333032231001231333322023133333320$1200313
Cmajor            3020031331310333032231001031333332023133333320$1200313
Efloribundum      3020031331310333032231001031332222023133333320$1200333
Erismadelphus     302003133131033303223100303133322202313333332001200313
Euncinatum        302003133131033303223100103133222202313333332001200333
Qdichotoma        3020031331310333032231001031333322023133333320$1200313
```

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Qmultiflora        302003133131033303223100103133332202313333032001200313

Qparaensis         30200313313103330322310010313333$2202313333332 0$1200313

Qparviflora        3020031331310333032231001031333322023133333320$1200313

Ralbiflora         302003133131033303223100103133332202313333332001200313

Rcassiquiarensis   3020031331310333032231001031333332023133333320$1200313

Sconvallariodora   3020031331110333032231001031333022023133333320$1200313

Vcinnamomea        302003133111033303223100203133302202313333332001200313

Vdensiflora        302003133111033303223100103133302202313333332001200313

Velliptica         302001133111033303223100203133302202313333332011200313

Vhaenkeana         302003133111033303223100203133302202313333332001200313

Vpruinosa          3020031331110333032231002031333022023133333320$1200313

Vpumila            302003133111033303223100203133302202313333332001200313

Vpyramidalis       302003133111033303223100203133302202313333332001200313

Vrufa              3020031331110333032231002031333022023133333320$1200313

Vthyrsoidea        302003133111033303223100103133302202313333332001200313

Vtucanorum         3020031331110333032231001031333002023133333320$1200313

Vneyratii          302003133111033303223100203133302202313333332221200313



                   270  275  280  285  290  295  300  305  310  315  320

                   |    |    |    |    |    |    |    |    |    |    |

Tibouchina         ?????????3????????????????????????????????????????????

Heteropyxis        033313032300000302001033332320002313333332030033033331

Psiloxylon         033313032300000302001033332320002313333332030032033331

Eugenia            033313032300000302001033332110002313313332030032033331

Backhousia         0333130323000003020010333?2310002313313332030032033331

Cfasciculata       033313032300000302001033332310002303333332030032013331

Cmajor             033313032300030302001033332310003303333332030032013331

Efloribundum       333313032300000302001033332310000303333332030032013311
```

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```
Erismadelphus      033313032300000302001033332310002303333332030032013331
Euncinatum         333313032300000302001033332312000303333332030032013311
Qdichotoma         033313032300000302001033332310002303333332030032013331
Qmultiflora        033313032300000302001033332310002303333332030032013331
Qparaensis         033313032300000302001033332310002303333332030032013331
Qparviflora        033313032300000302001033332310002303333332030032013331
Ralbiflora         033313032300000302001033332311002303333332030032013331
Rcassiquiarensis   033313032300000302001033332310002303333332030032013331
Sconvallariodora   033313032300000302001033332310002303333332030032013331
Vcinnamomea        033313032300000302001033332310002303333332030032013331
Vdensiflora        033313032300000302001033332310002303333332030032013331
Velliptica         033313032300000302001031332310002303333332030032013331
Vhaenkeana         033313032300000302001033332310002303333332030032013331
Vpruinosa          033313032300000302001033332310002303333332030030013331
Vpumila            033313032300000302001033332310002303333332030032013331
Vpyramidalis       033313032300000302001033332310002303333332030032013331
Vrufa              033313032300000302001033332312002303333332030032013331
Vthyrsoidea        033313032300000302001033332310002303333332030032013331
Vtucanorum         033313032300000302001033332310002303333332030032013331
Vneyratii          033313032300000302001033332312002303333332030032013331
```

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                   324  329  334  339  344  349  354  359  364  369  374
                   |    |    |    |    |    |    |    |    |    |    |
Tibouchina         ??????????????????????????????????????????????????????
Heteropyxis        022210311303223333310002031133330321033032330203031002
Psiloxylon         022010311303223313310002031133330321033032330203031002
Eugenia            023210311303223313310002031133310321033032330003031002
Backhousia         023210311303223313310002031133310321033032330203031002
```

Cfasciculata	220010313303221333310022031133310321033032331203031002
Cmajor	220010313303223313310022031133310321033032331203031002
Efloribundum	222010333303223313310022031133310321033032331203031002
Erismadelphus	222010313303223313310022031133310321033032331203031002
Euncinatum	222010333303223313310022031133310321033032331203031002
Qdichotoma	220010313303223313310022031133310321033032331203031002
Qmultiflora	220010313303223313310022031133310321033032331203031002
Qparaensis	220010313303223313310022031133310321033032331203031002
Qparviflora	220010313303223313310022031133310321033032331203031002
Ralbiflora	220010313303223313310022031133310321033032331203031002
Rcassiquiarensis	220010313303223313310022031133310321033032331203031002
Sconvallariodora	220010313303223313310022031133310321033032331203031002
Vcinnamomea	220010313303223313310022031133310321033032331203031002
Vdensiflora	220010313303223313310022031133310321033032331203031002
Velliptica	220010313303223313310022031133310321033032331203031002
Vhaenkeana	220010313303223313310022031133310321033032331203031002
Vpruinosa	220010313303223313310022031133310321033032331203031002
Vpumila	220010313303223313310022031133310321033032331203031002
Vpyramidalis	220010313303223313310022031133310321033032331203031002
Vrufa	220010313303223313310022031133310321033032331203031002
Vthyrsoidea	220010313303223313310022031133310321033032331203031002
Vtucanorum	220010313303223313310022031133310321033032331203031002
Vneyratii	220010313303223313310022031133310321033032331203031002

378 383 388 393 398 403 408 413 418 423 428

| | | | | | | | | | | |

Tibouchina	?????????????????????????????????????211-0011003211103
Heteropyxis	2000031003313221331000020301221313313203100300032200?3

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Psiloxylon	2000031003313221331000020301211313313203100300032200 03
Eugenia	20000310033132211310000203012 1?3133?3103200300032200 03
Backhousia	20000310033?3221031000020301211313333203200300032200 03
Cfasciculata	20000311033130313310000203012113133132032002000322 0003
Cmajor	200003110331303133100002030121131331320320020003220003
Efloribundum	200003110331303133100002030121113333320300020003220003
Erismadelphus	200003110331323133300002230121331331320320020003220003
Euncinatum	200003110331303133100002030121113333320300020003220203
Qdichotoma	200003110331303133100002030121131331320320020003220003
Qmultiflora	200003110331303133100002030121131331320320020003220003
Qparaensis	200003110331303133100002030121131331320320020003220003
Qparviflora	200003110331303133100002030121131331320320020003220003
Ralbiflora	200003110331303133100002030121131331320320020003220003
Rcassiquiarensis	200003110331303133100002030121131331320320020003220003
Sconvallariodora	200003110331323133100002030121103331320320020003220003
Vcinnamomea	200003010331323133100002030121103331320320020003220003
Vdensiflora	200003110331323133100002030121103331320320020003220003
Velliptica	200003010331323133100002030121103331320320020003220203
Vhaenkeana	200003010331323133100002030121103331320320020003220003
Vpruinosa	200003010331323133100002030121103331320320020203220003
Vpumila	200003010331323133100002030121103331320320020003220003
Vpyramidalis	200003110331323133100002030121103331320320020003220003
Vrufa	200003010331323133100002030101103331320320020003220003
Vthyrsoidea	200003110331323133100002030121103331320320020003220003
Vtucanorum	200003110331323133100002030121103331320320020003220003
Vneyratii	200003010331323133100002030121103331320320020003220203
	432 437 442 447 452 457 462 467 472 477 482

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```
                  |    |    |    |    |    |    |    |    |    |    |
Tibouchina        03303333?331033303203220021023131332013333322233031333
Heteropyxis       0330113322300 33?03203210023033131332013333322213031233
Psiloxylon        033011332330033303203210023033131332013333322213031233
Eugenia           033011332330033303203210033033130332013333302233031233
Backhousia        033011332330033303203210023033131332013333322213031233
Cfasciculata      033011332330033303203210023033132332013333302233031233
Cmajor            033011332330033303203210023033132332013333302233031233
Efloribundum      033011332330033303203210023033131332013333302233031233
Erismadelphus     033011332330033303203210023033131332013333302233031233
Euncinatum        033011332330033303203210023033131332013333302233031233
Qdichotoma        033011332330033303203210023033131332013333302233031233
Qmultiflora       033011332330033303203210023033131332013333302233031233
Qparaensis        033011332330033303203210023033131332013333302233031233
Qparviflora       03301133233003330320321002303313133201 33?3302233031233
Ralbiflora        0330113323300333 03?03210023033131332013333302233031233
Rcassiquiarensis  033011332330033303303210023033131332013333302233031233
Sconvallariodora  033011332330033303203210023033131332013333302233031233
Vcinnamomea       033011332330033303203210023033131332013333302233031233
Vdensiflora       033011332330033303203210023033131332013333302233031233
Velliptica        033011332330033303203210023033131332013333302233031233
Vhaenkeana        033011332330033303203210023033131332013333302233031233
Vpruinosa         033011332330033303203210023033131332013333302233031233
Vpumila           033011332330033303203210023033131332013333302233031233
Vpyramidalis      033011332330023303203210023033131332013333302233031233
Vrufa             033011332330033303203210023033131332013333302233031233
Vthyrsoidea       033011332330033303203210023033131332013333302233031233
Vtucanorum        033011332330033303203210023033131332013333302233031233
Vneyratii         033011332330033303203210023033131332013333302233031233
```

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	486 491 496 501 506 511 516 521 526 531 536
	| | | | | | | | | | |
Tibouchina	1002023013003101331331023223012202310003223020000033103
Heteropyxis	10021232120130003313310232230122023100032130200001?103
Psiloxylon	100212321?013000331331023223012?0231000321302000033103
Eugenia	10021232120130003??31102322301 2?0231000321302000033103
Backhousia	100211321$013000?3133102322301200231000321302000033303
Cfasciculata	100212321001300033133102322301220231000321302000033103
Cmajor	100212321001300033133102312321220231000323302000033103
Efloribundum	100212321221300033133102122321220231000321302000033103
Erismadelphus	100212321221300033133102122321220231000321302000033113
Euncinatum	100212321221300033133102122301220231000321302000033103
Qdichotoma	100212321201300033133102322321220231000321302000033103
Qmultiflora	100212321001300033133102122301220231000321302000033103
Qparaensis	100212321201300033133102322321220231000321302000033103
Qparviflora	1002?2321001300033133102122321220231000321302000033103
Ralbiflora	100222321201303033133102322301220231000321302000033303
Rcassiquiarensis	100212321201300033133102322321220231000321302000033103
Sconvallariodora	100212321201300033133102322301220231000321302000033103
Vcinnamomea	100212321201300033133102322301220231000321302000033103
Vdensiflora	100212321201300033133102322301220231000321302000033103
Velliptica	100232321201300033133102322301220231000321302000033103
Vhaenkeana	100212321201300033133102322301220231000321302000033103
Vpruinosa	100232321201300033133102322301220231000321302000033103
Vpumila	100212321201300033133102322301220231000321302000033103
Vpyramidalis	100212321201300033133102322301220231000321302000033103
Vrufa	100212321201300033133102322301220231000321302000033103

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Vthyrsoidea      10021232120130003313310232230122023100032130200003310 3
Vtucanorum       100212321201300033133102322321220231000321302000033103
Vneyratii        100212321201300033133102322301220231000321302000033103


                 540  545  550  555  560  565  570  575  580  585  590
                 |    |    |    |    |    |    |    |    |    |    |
Tibouchina       3313013120300321303211000213120001012023301013302311 00
Heteropyxis      331300302030032130320020023312000100302331100330331131
Psiloxylon       3313?0300030032130320030023312000100302331100330331131
Eugenia          331300300030032130322?200233120201 0???33112033033113 1
Backhousia       3?0300300030032110320020023312 0????302331100330331121
Cfasciculata     031300302031032130320020023312020100302331130330331131
Cmajor           031300302031032130320020123312010100302331130330331131
Efloribundum     031300302031032130320020023332020100302331130330331100
Erismadelphus    031300302031032130320020023332020100102331130330331110
Euncinatum       031300302031032130320020023332020100102331130330331100
Qdichotoma       0313003$2031032130320020023312020100302331130330331131
Qmultiflora      031300322031032130320020023312020100302331130330331131
Qparaensis       0313003$2031032130320020023312020100302331130330331131
Qparviflora      031300322031032130320020023312020100302331130330331131
Ralbiflora       031300302031032130320020023312020100302331130330331131
Rcassiquiarensis 0313003$2031032130320020023312020100302331130330331131
Sconvallariodora 031300302031032130320020023312020100302331130330331131
Vcinnamomea      031300302031032130320020023312020100302331130330331131
Vdensiflora      031300302031032130320020023312020100302331130330331131
Velliptica       031300302031032130320020023312020100302331130330331131
Vhaenkeana       031300302031032130320020023312020100302331130330331131
Vpruinosa        031300302031032130320020023312020100302331130330331131
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Vpumila           031300302031032130320020023312020100302331130330331131
Vpyramidalis      031300302031032130320020023312020100302331130330331131
Vrufa             031300302031032130320020023312020100302331130330331131
Vthyrsoidea       031300302031032130320020023312020100302331130330331131
Vtucanorum        031300302031032130320020023312020100302331130330331131
Vneyratii         031300302031032130320020023312020100302331130330331131


                  594  599  604  609  614  619  624  629  634  639  644
                  |    |    |    |    |    |    |    |    |    |    |
Tibouchina        32033203310332313000212000333323001110330220103112?332
Heteropyxis       320332203103323130002120033333230010103322221031110330
Psiloxylon        320332203103323130002120033333230010103302221031110330
Eugenia           320332203103323130002120033333230012103302221031110330
Backhousia        32033220310332313000212003333?2300101033022210311?0330
Cfasciculata      020332203103003130002100003333230012103302201031110330
Cmajor            320332303103303130002100003333230012103302201031110330
Efloribundum      320332203103323130002100003333230012103302201031110330
Erismadelphus     320332203103323130002100003333230012103302201031110330
Euncinatum        320332203103323130002100003333230012103302201031110330
Qdichotoma        320332203103303130002100003333230032103302201031110330
Qmultiflora       320332203103303130002100003333230032103302201031110330
Qparaensis        320332203103303130002100003333230032103302201031110330
Qparviflora       320332203103303130002100003333230032103302201031110330
Ralbiflora        320232203103303130002100003333233012103302201031110330
Rcassiquiarensis  320332203103303130002100003333230032103302201031110330
Sconvallariodora  320332303103313130002100003333230012103302201011110330
Vcinnamomea       320332203103323130002100003333230012103302201011110330
Vdensiflora       320332203103323130002100003333230012103302201011110330
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Velliptica         320332203103323130002100003333230012103302201011110330
Vhaenkeana         320332203103323130002100003333230012103302201011110330
Vpruinosa          320332203103323130002100003333230012103302201011110330
Vpumila            320332203103323130002100003333230012103302201011110330
Vpyramidalis       320332203103023130002100003333230012103302201011110030
Vrufa              320332203103323130002100003333230012103302201011110330
Vthyrsoidea        320332203103323130002100003333230012103302201011110330
Vtucanorum         320332203103323130002100003333230012103302201011110330
Vneyratii          320332203103023130002100003333230012103302201011110330


                   648  653  658  663  668  673  678  683  688  693  698
                   |    |    |    |    |    |    |    |    |    |    |
Tibouchina         230021122113222132033103132033132030330312011003331331
Heteropyxis        230001120111222132033103102033132030330312011233333321
Psiloxylon         230001120111222132033103102033132030330312011233333321
Eugenia            230001120111222132033103102033112030330312011233333321
Backhousia         2300011201112?313203?10311203313203033031001123333332 1
Cfasciculata       230001120111222132033103122033232030330312011233333321
Cmajor             230001120111222132033103122033222030330312011233333321
Efloribundum       230001122111222132033103122033232030330312011233333321
Erismadelphus      230001122111222132033103122033232031330312011233333321
Euncinatum         230001122111222132033103122033232030330312011233333321
Qdichotoma         230001120111222132033103122033232030320312011233333331
Qmultiflora        230001120111222132033103122033232030320312011233333321
Qparaensis         230001120111222132033103122033232030320312011233333321
Qparviflora        230001120111222132033103122033232030320312011233333321
Ralbiflora         230001120111222132033103122033232030320312011233333321
Rcassiquiarensis 230001120111222132033103122033232030320312011233333321
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Sconvallariodora 2300011201112221320331031220332320303303120112333333321
Vcinnamomea      2300011201112221320331031220332320303303120122333333321
Vdensiflora      230001120111222132033103122033232030330312011?33333321
Velliptica       2300011201112221320331031220332320303303120122333333321
Vhaenkeana       2300011201112221320333031220332320303303120211333333331
Vpruinosa        2300011201112221320331031220332320303303120122333333321
Vpumila          2300011201112221320331031220332320303303120122333333321
Vpyramidalis     2300011201112221320331031220332320300303120112333333321
Vrufa            2300011201112221320331031220332320303303120122333333321
Vthyrsoidea      2300011201112221320333031220332320303303120211333333331
Vtucanorum       2300011201112221320333031220332320303303120113333333331
Vneyratii        2300011201112221320331031220332320303303120122333333321


                 702  707  712  717  722  727  732  737
                 |    |    |    |    |    |    |    |
Tibouchina       230303211200031333131033031010232203 1
Heteropyxis      2303032102000313331310330310102322031
Psiloxylon       2303032102000313331310330310102322031
Eugenia          2303032102000313331310330310102322031
Backhousia       2303032102000313331310330310302322031
Cfasciculata     2303032102000313333310330300302322031
Cmajor           2303032102000313333310330310302322031
Efloribundum     2303032102000313333310330310102122031
Erismadelphus    2303032102000313333310330310102122031
Euncinatum       2303032102000313333310330310102122031
Qdichotoma       2303032102000313333310330310302322031
Qmultiflora      2303032102000313333310330310302322031
Qparaensis       2303032102000313333310330310302322031
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Qparviflora	2303032102000313333310330310302322031
Ralbiflora	2303032102000313333310330310302322031
Rcassiquiarensis	2303032102000313333310330310302322031
Sconvallariodora	2303032102000313333310330330102322031
Vcinnamomea	2303032102000313333310330330102322031
Vdensiflora	2303032102000313333310330330102322031
Velliptica	2303032102000313333310330330102322031
Vhaenkeana	2303032102000313333310330330102322031
Vpruinosa	2303032102000313333310330330102322031
Vpumila	2303032102000313333310330330102322031
Vpyramidalis	2303032102000313323310330330102322031
Vrufa	2303032102000313333310330330102322031
Vthyrsoidea	2303032102000313333310330330102322031
Vtucanorum	2303032102000313333310330330102322031
Vneyratii	2303032102000313323310330330102322031

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Appendix 3. Characters and states used in morphology and combined-data analyses. Taxa that are polymorphic for a given character are listed at the end of that character, with their character states indicated. The number of steps, CI, and RI are for the morphology data analysis; values are similar or identical for the combined-data analysis.

0. Habitat: savanna (0); gallery forest (1); rain forest (2). "Savanna" refers specifically to the seasonally dry, fire-mediated habitats, to the exclusion of the gallery forests that may cut through these. Some species, however, may be found in both. *V. tucanorum*, *C. major*, *C. fasciculata* 0,1. Steps= 4; CI=0.50; RI=0.80.

1. Size: small tree (0); medium tree (1); large tree (2); subterranean xylopodium (3). *Eugenia*, *R. albiflora*, *R. cassiquiarensis* 1,2; *Q. dichotoma*, *Q. multiflora*, *V. tucanorum* 0,1. Steps= 10; CI=0.30; RI=0.41.

2. Wood: not soft (0); soft (1). This is a feature found in some savanna species; large branches are easily pulled off by hand and are extremely lightweight. Steps= 3; CI=0.33; RI=0.50.

3. Included phloem: absent (0); present (1). This refers not to the bicollateral vascular bundles found throughout Vochysiaceae and Myrtales ("internal phloem"), but to small bits of phloem found within the secondary xylem. Steps= 1; CI=1.00; RI=1.00.

4. Bark exfoliating: yes (0); no (1). In species descriptions this is also referred to as "cortex exfoliating" but this is an incorrect use of the term cortex. The bark of these species peels or flakes off.

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This has been suggested as a character shared by Vochysiaceae and Myrtaceae (e.g. K. Sytsma pers. comm.) however it should be noted that in Vochysiaceae the exfoliation is generally restricted to the bark of the twigs, whereas in Myrtaceae it is most commonly associated with the trunk. Steps= 3; CI=0.33; RI=0.80.

5. Oil glands: absent (0); present (1). Steps= 2; CI=0.50; RI=0.50.

6. Phyllotaxis: opposite (0); whorled (1); alternate (2). *E. floribundum*, *E. uncinatum*, *Q. multiflora*, *Q. parviflora* 0,1. Steps= 2; CI=1.00; RI=1.00.

7. Leaf spacing on stem: uniform (0); clustered at branch tips (1); irregular (2). Steps= 3; CI=0.66; RI=0.66.

8. Stellate hairs: no (0); yes (1). Thought to be a synapomorphy of Erismeae, these are found only in *Erisma*. "Biramous" hairs have been reported from *Vochysia* species but were not seen in this study. Steps= 1; CI=1.00; RI=1.00.

9. Juvenile stem: pubescent (0); glabrous (1). *C. major*, *Q. multiflora*, *Q. parviflora* 0,1. Steps= 5; CI=0.20; RI=0.50.

10. Petiole length: <3mm (0); 3-10mm (1); 10-30mm (2); >30mm (3). Steps= 14; CI=0.20 RI=0.0.

11. Petiole: pubescent (0); glabrous (1). *C. major*, *Q. dichotoma*, *Q. multiflora*, *Q. parviflora* 0,1. Steps= 6; CI=0.16; RI=0.54.

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12. Stipules: present (0); absent (1). Stipules are commonly deciduous in Vochysiaceae and thus may be overlooked. Steps= 3; CI=0.33; RI=0.66.

13. Stipule shape: deltoid (0); subulate (1); ovate (2). Steps= 4; CI=0.50; RI=0.66.

14. Stipule length: <1mm (0); 1-2mm (1); >2mm (2). V. elliptica 0,1. Steps= 8; CI=0.25; RI=0.14.

15. Leaf length/width: <1.5 (0); 1.5-2.5 (1); >2.5 (2). V. elliptica 0,1. Steps= 9; CI=0.22; RI=0.36.

16. Juvenile leaf: pubescent (0); glabrous (1). C. major, Q. multiflora, Q. parviflora 0,1. Steps= 7; CI=0.14; RI=0.40.

17. Adult leaf abaxial surface: pubescent (0); glabrous (1). C. major, Q. multiflora, Q. parviflora 0,1. Steps= 5; CI=0.20; RI=0.60.

18. Leaf glaucous: no (0); yes (1). Steps= 1; CI=1.00; RI=1.00. Q. dichotoma 0,1.

19. Leaf margin: flat (0); revolute (1). "Revolute" also includes conditions described as "subrevolute" as the distinction is vague and there is considerable variability. Steps= 3; CI=0.33; RI=0.75.

20. Midrib sulcate on adaxial surface: yes (0); partly (1); no (2). In many species the midrib is sulcate only towards the leaf apex. As it is not clear if this condition is derived from/homologous to sulcate

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or not-sulcate, or both, it was decided to leave it as a separate state. Steps= 7; CI=0.28; RI=0.61.

21. Venation angle: < or =60º (0); >60º (1). Measured relative to the midrib. Steps= 7; CI=0.14; RI=0.33.

22. Venation on adaxial surface: not prominent (0); prominent (1). Steps= 7; CI=0.14; RI=0.53.

23. Venation on abaxial surface: prominent (0); visible (1); not visible (2). On the abaxial side of leaves of some species the surface becomes so thick the venation is completely obscured. This is seldom the case on the adaxial surface, thus "not visible" was included as a state only for the abaxial surface. Steps= 9; CI=0.22; RI=0.41.

24. Number veins/cm: <1 (0); 1-10 (1); 10-20 (2); >20 (3). Steps= 9; CI=0.33; RI=0.14.

25. Major lateral veins at leaf margin: eucamptodromous (0); brochidodromous (1); undulate marginal vein (2); marginal vein (3); irregular anastomosing (4). States 0, 1, and 3 follow the terminology of Hickey (1973), but two additional possible fates of the major veins were seen in Vochysiaceae. In some species the major lateral veins connect via a typical marginal collecting vein, which is very close to the margin and parallels it (state 3). In others the collecting vein is a few millimeters in from the margin and undulates irregularly, nonetheless it is distinct (state 2). In still others the major lateral veins simply branch repeatedly and these branches anastomose in no obvious pattern (state 4). *C. fasciculata*, *E. uncinatum* 0,1. Steps=

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11; CI=0.36; RI=0.58.

26. Leaf tip: no appendage (0); appendage (1). In some species of Qualea and Callisthene (all cerrado or gallery forest species) a small, possibly glandular, claw-shaped structure was seen at the tip of young leaves and sepals. It is completely inconspicuous at maturity, thus it is possible it is present and as yet unnoticed in other species. Steps= 2; CI=0.50; RI=0.66.

27. Extra-floral nectaries: none (0); stipular (1). These are found on the stems associated with (or replacing) the stipules and in some cases in pairs of diminishing size along the young stem. They may also be found on the inflorescence rachis, and are not visible on mature stems. Steps= 1; CI=1.00; RI=1.00.

28. Inflorescence density: dense (0); medium (1); lax (2). Steps= 8; CI=0.25; RI=0.50.

29. Inflorescence: axillary or terminal raceme (0); axillary cyme (1). The typical Vochysiaceae inflorescence is a terminal or axillary thyrse, a branched raceme with cymose partial inflorescences (cincinni). A few taxa have inflorescences that are axillary cincinni. It should be noted that other interpretations of these cymose inflorescences are possible (for instance they can be seen as partial inflorescences, as in the typical Vochysiaceae thyrse, with the entire inflorescence being the branch) but these were rejected as confusing. In any event the character would have the same distribution. R. albiflora 0,1. Steps= 1; CI=1.00; RI=1.00.

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30. Corolla symmetry: actinomorphic (0); zygomorphic (1). This could also be called "corolla complete" vs "corolla reduced" as the zygomorphy is due to the reduction in the number of petals. Salvertia and Erismadelphus have nearly actinomorphic corollas and have been scored that way, although the petals do not actually insert evenly around the flower (they are displaced on the spur side). Steps= 3; CI=0.33; RI=0.66.

31. Flowers: bisexual (0); unisexual (1). Steps= 1; CI=1.00; RI=1.00.

32. Nectary disc: absent (0); present (1). Steps= 1; CI=1.00; RI=1.00.

33. Pedicel length: <5mm (0); 5-10mm (1); >10mm (2). Steps= 10; CI=0.20; RI=0.27.

34. Bud length: <5mm (0); 5-10mm (1); 10-15mm (2); 15-20mm (3); >20mm (4). Steps= 13; CI=0.30; RI=0.47.

35. Bud length/width: <2.5 (0); 3-6 (1); >6 (2). V. tucanorum 1,2. Steps= 7; CI=0.28; RI=0.64.

36. Receptacle: not oblique (0); oblique (1). Steps= 1; CI=1.00; RI=1.00.

37. Spur on fourth sepal: absent (0); present (1). Steps= 1; CI=1.00; RI=1.00.

38. Spur length/width: <2 (0); 2-8 (1); >8 (2). Steps= 8; CI=0.25; RI=0.44.

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39. Relative length of sepals: equal (0); subequal (1); fourth sepal >3 times as long as others(2). Steps= 6; CI=0.33; RI=0.66.

40. Fourth sepal petaloid: yes (0); inner surface (1); no (2). Steps= 3; CI=0.66; RI=0.66.

41. Fourth sepal (only) deciduous: no (0); yes (1). Steps= 1; CI=1.00; RI=1.00.

42. Petal number: 5 (0); 3 (1); 1 (2). Steps= 4; CI=0.50; RI=0.86.

43. Petal length: <7mm (0); 7-15mm (1); 15-30mm (2); >30mm (3). Steps= 11; CI=0.27; RI=0.33.

44. Petal shape: round/obcordate (0); oblong/ovate/rhomboid (1). Steps= 2; CI=0.50; RI=0.88.

45. Petal: clawed (0); not clawed (1). Steps= 2; CI=0.50; RI=0.90.

46. Petal color: yellow (0); white (1); blue/violet/purple (2). Steps= 7; CI=0.28; RI=0.58.

47. Petal markings: none (0); magenta/red (1); yellow/white (2). Q. paraensis and Q. multiflora petals have markings that are yellow and magenta; they are coded 1,2. Steps= 2; CI=1.00; RI=1.00.

48. Petal: glabrous (0); pubescent (1). Petals are generally pubescent only at the clawed insertion, and/or on the abaxial surface. Steps= 6;

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CI=0.16; RI=0.37.

49. Rudimentary petals: absent (0); 2 (1); up to four (2). These are inconspicuous in the open flower, generally minute and threadlike. Steps= 3; CI=0.66; RI=0.50.

50. Fertile stamen number: 1 (0); 5 (1); 10 (2); numerous (3). Steps= 3; CI=1.00; RI=1.00.

51. Stamen position: antepetalous, or if more than one whorl, alternating antepetalous and antesepalous (0); offset (1). State 1 describes the stamen position in Qualea, Callisthene, and Ruizterania, which is in-between antepetalous and antesepalous. Steps= 1; CI= 1.00; RI=1.00.

52. Stamen inflexed in bud: no (0); yes (1). Steps= 2; CI=0.50; RI=0.50.

53. Stamen: glabrous (0); pubescent (1). Steps= 4; CI=0.25; RI=0.50.

54. Anther attachment: basifixed (0); dorsifixed (1). Steps= 3; CI=0.33; RI=0.88.

55. Anther barbate: no (0); yes (1). This refers to a linear fringe of hairs on the side of the anther where dehiscence occurs. Steps= 1; CI=1.00; RI=1.00.

56. Connective extended beyond thecae: not extended (0); extended (1); extended into cap over stigma (2). Steps= 5; CI=0.40; RI=0.76.

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57. Staminodes: absent (0); present (1). Steps= 3; CI=0.33; RI=0.80.

58. Ovary position: superior (0); partly inferior (1); inferior (2). A superior ovary has been thought to be characteristic of both Vochysia and Qualea (and their relatives) however the gynoecium of Vochysia is slightly inferior. Steps= 3; CI=0.66; RI=0.92.

59. Ovary: glabrous (0); pubescent (1). Steps= 4; CI=0.25; RI=0.57.

60. Total locule number: 5 (0); 3(-4) (1); 2 (2); 1 (3). Steps= 4; CI=0.75; RI=0.50.

61. Fertile locule number: 5 (0); 3(-4) (1); 2 (2); 1 (3). Steps= 4; CI=0.75; RI=0.66.

62. Ovules/locule: 1 (0); 2 (1); >2 (2). Callisthene is described as having "few" and Qualea as having "many" but in the absence of numbers it was deemed best to combine these. Steps= 2; CI=1.00; RI=1.00.

63. Style length: <2mm (0); 2-10mm (1); 10-20mm (2); >20mm (3). Steps= 8; CI=0.37; RI=0.66.

64. Style base: not pilose (0); pilose (1). Steps= 6; CI=0.16; RI=0.37.

65. Sunken style: absent (0); present (1). Steps= 1; CI=1.00; RI=1.00.

66. Stigma: terminal (0); partly lateral (1); lateral (2). Steps= 7;

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CI=0.28; RI=0.37.

67. Stigma lobes: absent (0); present (1). Steps= 4; CI=0.25; RI=0.25.

68. Fruit type (dry): dehiscent (0); indehiscent (1). "Dry" was specified to avoid assuminging homology between the berry of Eugenia and the winged fruits of Erisma and Erismadelphus, which are all indehiscent. Steps= 2; CI=0.50; RI=0.66.

69. Sepals: not accrescent (0); accrescent (1). In Erisma and Erismadelphus the sepals continue to grow and form the wings of the fruit. Steps= 1; CI=1.00; RI=1.00.

70. Fruit segments separate from column at dehiscence: yes (0); no (1). In Qualea, Ruizterania, and Callisthene the capsular fruit dehisces by the three segments pulling away from a central column and remaining attached only at the base. In some Qualea species the column falls out; in others it persists, as it generally does in Callisthene. In Vochysia and Salvertia the fruit dehisces by the pericarp reflexing back at each carpel midrib and thereby exposing the seed in the locule. Steps= 1; CI=1.00; RI=1.00.

71. Exocarp fragments: no (0); yes (1). In Callisthene and some species of Qualea and Ruizterania (although none of the latter included in this study) the outer layer of the fruit crumbles and falls off at maturity. Steps= 1; CI=1.00; RI=1.00.

72. Pericarp: not stony (0); stony (1). In Qualea and its relatives the fruit wall becomes hard and woody, and sometimes quite thick.

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Steps= 1; CI=1.00; RI=1.00.

73. Seeds/locule: 1 (0); >1 (1). Steps= 2; CI=0.50; RI=0.90.

74. Seed wing shape: oblong (0); elliptical (1); attenuate (2); crescentic (3). Steps= 3; CI=1.00; RI=1.00.

75. Wing formation: testa (0); matted hairs (1). Steps= 1; CI=1.00; RI=1.00.

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Appendix 4. Matrix of 75 non-molecular characters used in analysis. -, character inapplicable; ?, character state unknown or inapplicable; *, polymorphic, all character states included; $, polymorphic, subset of available states included. Characters, character states, and polymorphisms listed in Appendix 3 Species names and voucher information are listed in Appendix 1.

```
                0    5    10   15   20   25   30   35   40   45   50   55   60   65   70   75
                |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
Tibouchina      *000000000001--000001100130020000010000-02002??2000201010002-2221100000-001--
Heteropyxis     ?000012000211--111001101000000001110000-020001110001000100000112001000 0-00120
Psiloxylon      ?100?0200?111--1?10011111300100110 0?00-0200??1?0?02000?0?00-0020?1?1-0-001--
Eugenia         2$00010001111--111001011110010001100 00-02000111000301010002-22210000-0-00130
Backhousia      2000010001111--2110111012100100011000 0-02000111000301010002-1120000010-000--
Cfasciculata    $1001000001000000000000100$11-110012111220022000100010000100011220000000011110
Cmajor          $10010000*2*0000**000010121?-110001011010021001100010000100011220000000011110
Efloribundum    220110$010111--2000011001200201000110111112100001200001 0012-3312000011--00--
Erismadelphus   2201100001210211110010001000200000200100200110100-000010012-1300001111--00--
Euncinatum      220110$01010011110000000 1$002010001101011121002012000010012-3312100011--00--
Qdichotoma      0$001000001*021100*020010001001000101101202100111001011000011122100000011100
Qmultiflora     0$1010$00*1*0221**0001001211001001201111202200 1$000100101001112110000000 1100
Qparaensis      22000000 0?000201100001111301201001301101102300 1$010101101101111210010000?1100
Qparviflora     001010$00*1*0202**00011122112010021011112022002210010010000111211000000 01100
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Ralbiflora	2$00100000100?01010001111301-*1001211102202200121101000101011121100000001100
Rcassiquiarensis	2$00100001000?0111000111330120100141110220230012000100010001112310000000?1100
Sconvallariodora	0110001100000021110110101400200002410110200211100-0000000111111300200010 0001
Vcinnamomea	0010001100100002000111 1-04001010013201022012110000000000211111130020001 00001
Vdensiflora	2200100000200012000020001300001002320102201?1100100001002110111100110010 0001
Velliptica	00000010010100$$111121010400001001310112201111000000000021111113101000100001
Vhaenkeana	1100101001310112110101111100101001110122201011000000010021111112100000100001
Vpruinosa	0000001001010001111121021400001000420112201211000000000021111113002000100001
Vpumila	03-000?201111--2111111020400001001310112201111000000000021111113000000100001
Vpyramidalis	11001000001000220000200-1000001000220112201111001000010021101111001100100001
Vrufa	0010001100200001000111120400101001320122201111000000000021111113002000100001
Vthyrsoidea	0100101100210011010111111000010024101122012110000000000211011130010001 00001
Vtucanorum	$$001010011101021100001211000010012$01222011110010000100211011110001001 00001
Vneyratii	2200100000200002000011001200001002220112201?1100100001002110111?000000100001

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