

FOSSIL FLOWERS AND FRUITS OF THE ACTINIDIACEAE FROM THE CAMPANIAN (LATE CRETACEOUS) OF GEORGIA¹

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A new genus and species of Actinidiaceae (*Parasaurauia allonensis* gen. et sp. nov.) are established for fossil flowers and fruits from the early Campanian (Late Cretaceous) Buffalo Creek Member of the Gaillard Formation in central Georgia, USA. The fossil flowers, which are exquisitely preserved as charcoal, have five imbricate, quincuncially arranged sepals and petals. The androecium consists of ten stamens with anthers that are deeply sagittate proximally. The gynoecium is tricarpellate, syncarpous, and has three free styles that emerge from an apical depression in the ovary. The fruit is trilobular and contains numerous ovules on intruded axile placentae. The structure of mature fruits is unknown. Comparisons with extant taxa clearly demonstrate that the affinities of *Parasaurauia allonensis* are with the Ericales, and particularly with the Actinidiaceae, which have been placed among the Ericales in recent cladistic analyses. Because *Parasaurauia allonensis* is not identical to any one genus of Actinidiaceae, or other member of the Ericales, phylogenetic relationships of the fossil were evaluated through a cladistic analysis using morphological and anatomical characters. Results of this analysis place *Parasaurauia allonensis* within the Actinidiaceae as sister to the extant genera *Saurauia* and *Actinidia*. *Parasaurauia allonensis* differs from extant *Saurauia* only in having ten rather than numerous stamens.

Key words: Actinidiaceae; Campanian; fossils; Georgia; Late Cretaceous; *Parasaurauia allonensis*.

The application of bulk sieving techniques to unconsolidated sediments of Cretaceous age has led to the recovery of abundant, well-preserved, charcoaled, or lignitized fossil flowers, fruits, and seeds from many localities in Europe and North America (e.g., Crane, Friis, and Pedersen, 1995; Crane and Herendeen, in press). These discoveries have greatly increased knowledge of early angiosperm diversity and have clarified substantially the systematic relationships of Cretaceous angiosperms. Currently available data demonstrate that numerous angiosperm families and higher taxa had already differentiated during the Late Cretaceous (Crane, Friis, and Pedersen, 1995; Crane and Herendeen, in press). One such group that is now known to have undergone significant diversification during the Late Cretaceous is the order Ericales (Friis, 1985b; Nixon and Crepet, 1993).

The Ericales comprise a diverse group of angiosperm families, which is characterized by anthers that invert during ontogeny, the presence of ellagic acid, an apical depression in the ovary, and multicellular trichomes on the leaves (Anderberg, 1992; Judd and Kron, 1993). In addition to the "core" ericalean families (Clethraceae, Cyrillaceae, Empetraceae, Epacridaceae, Ericaceae, Monotropaceae, and Pyrolaceae) Takhtajan (1969) also included the Actinidiaceae in the Ericales and several re-

cent studies have supported this treatment. Cladistic analyses of both morphological and molecular data place the Actinidiaceae as a basal member of the Ericales (Anderberg, 1992, 1993; Hufford, 1992; Judd and Kron, 1993; Kron and Chase, 1993). Although Cronquist (1981) placed the Actinidiaceae in the Theales based on its unspecialized, nonericalean features, he also recognized that the family might be better assigned to the Ericales based on evolutionary grounds (Cronquist, 1981, pp. 326, 461–462). In this paper we describe fossil flowers and fruits from a Campanian fossil flora in central Georgia that exhibit synapomorphies of the Ericales and Actinidiaceae, and provide further evidence of the presence of diverse Ericales in the Late Cretaceous.

MATERIALS AND METHODS

The material examined in this study is from an early Campanian locality in Crawford County, Georgia, ≈ 9.5 km southeast of Roberta. The fossil material was isolated from a carbonaceous clay lens that is exposed on the south face of the south pit of the Atlanta Sand and Supply Company in Gaillard, Georgia (Knoxville Quadrangle, 32°37'47"N latitude, 83°59'10"W longitude; Herendeen, Crane, and Drinnan, 1995). These sediments have been assigned to the Buffalo Creek Member of the Gaillard Formation, which is thought to be of early Campanian age based on palynological data (Christopher, 1979; Huddleston and Hetrick, 1991). Mesofossils isolated from these sediments are preserved as charcoaled or lignitized material, and include flowers, fruits, seeds, dispersed stamens, conifer shoots, wood, and coprolites containing plant material. Angiosperms dominate the Allon flora and include taxa such as Fagaceae (Herendeen, Crane, and Drinnan, 1995), Hamamelidaceae (Magallon-Puebla, Herendeen, and Endress, in press), Juglandales, Saxifragales, Lauraceae, and at least two monocots (Crane and Herendeen, in press).

Samples of clay from the Allon locality were allowed to dry and then dissolved in water and washed through sieves (500- μ m and 125- μ m mesh). A detergent dissolved in water was used to disperse the remain-

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ing clay and the organic residue was cleaned with 10% HCl followed by concentrated HF for several days. The material was then washed with 10% HCl and rinsed with water (changed daily) for several days. The material was air dried and then sorted and examined using a binocular stereomicroscope. Specimens of flowers and fruits were mounted on stubs, coated with gold, and examined with an Amray 1810 scanning electron microscope (SEM). After photographic documentation, selected specimens were dissected, recoated, and rephotographed with the SEM. Modern material for detailed comparison (*Clematoclethra*, *Actinidia*, *Saurauia*, *Clethra*, *Rhododendron*, and *Erica*) was obtained from the Field Museum herbarium (F). The data matrix of Anderberg (1992) was also verified using specimens from the Field Museum herbarium. The fossil specimens are deposited in the paleobotanical collections of the Department of Geology, The Field Museum (PP).

SYSTEMATICS

Order Ericales
Family Actinidiaceae

Parasaurauia Keller, Herendeen et Crane, gen. nov.

Type species—*Parasaurauia allonensis* Keller, Herendeen et Crane, sp. nov.

Generic diagnosis—Flowers actinomorphic, calyx composed of five imbricate sepals with multicellular trichomes on the abaxial surface, corolla composed of five imbricate petals. Both sepals and petals are quincuncially arranged. Androecium of ten stamens with basifixed, deeply sagittate anthers (pollen unknown). Gynoecium trilocarpellate, with a syncarpous, superior ovary and three free styles emerging from an apical depression. Ovary trilobular with intruded axile placentae bearing numerous ovules. Mature fruit structure is unknown.

Parasaurauia allonensis Keller, Herendeen et Crane, sp. nov.

Figures—1-22

Specific diagnosis—As for the genus with the following additions: flowers 0.7–1.2 mm long, 0.6–0.8 mm wide; anthers markedly sagittate, free basal lobes comprise one-half of the anther length, anther apex slightly emarginate. Stamens that alternate with the petals are approximately twice as large as stamens that are opposite the petals, at least early in development.

Holotype—PP44612 (Figs. 3, 6, 9–17)

Additional specimens—Four flowers: PP44591, PP44609, PP44610, PP44611; Two fruits: PP44476, PP44650.

Type locality—Allon quarry of the Atlanta Sand and Supply Company, near Gaillard, central Georgia, USA (Knoxville Quadrangle, 32°37'47"N latitude, 83°59'10"W longitude) (Herendeen, Crane, and Drinnan, 1995).

Stratigraphic position—Buffalo Creek Member, Gaillard Formation

Age—early Campanian (Late Cretaceous)

Description and remarks—Flowers are hypogynous, actinomorphic, and apparently bisexual. The five imbricate sepals are ≈ 0.7 – 1.2 mm long and ≈ 0.5 – 0.8 mm wide at the base with multicellular trichomes on the abaxial surface. Trichomes range from 10 μm in length in the middle of the sepals to 200 μm at the margins (Figs. 1, 2, 4, 5, 8). The trichomes are composed of five to seven cells in cross-section (Fig. 2). The five imbricate petals are ≈ 0.9 mm long and ≈ 0.6 mm wide at the base and have a smooth surface (Figs. 3, 6, 7). Aestivation of calyx and corolla is imbricate and quincuncial (Figs. 1–8).

The androecium consists of ten stamens with tetrasporangiate, dithecal anthers (Figs. 9–15). The five antepalous stamens have larger anthers than the five stamens opposed to the petals (Figs. 10, 11). However, because this observation is based on a single flower with immature anthers, this size difference may not have persisted to anthesis. Anthers of the larger stamens are ≈ 0.6 mm long, 0.2 mm wide, and the filaments are slender and ≈ 0.2 mm long. Anthers of the smaller stamens are ≈ 0.3 mm long, 0.15 mm wide and the filaments are ≈ 0.1 mm long. Anthers are basifixed and deeply sagittate for half their length below the point at which the filament is attached (Figs. 12–14). The apex of the anthers is slightly emarginate. Pollen was not found in any of the flowers (common in charcoaled flowers in which the anthers have not yet dehisced).

The gynoecium is trilocarpellate, syncarpous, with a trilobular ovary and three free styles that emerge from an apical depression (Figs. 16, 17). The styles are ≈ 0.25 mm long, 90 μm \times 50 μm in cross section, and have a longitudinal groove on the adaxial surface (Fig. 17). The trilobular ovary has numerous ovules borne on axile intruded placentae (Figs. 18, 19). The ovules are ≈ 70 μm \times 55 μm and have a reticulate surface (Fig. 20).

Details of mature fruit structure are unknown, but one specimen shows an apical depression from which the styles have abscised (Figs. 18, 19). The same specimen also contains what appear to be ovules and has an abraded outer surface (Fig. 18). The other specimen is incomplete but shows a papillate surface and some evidence of a fleshy fruit wall. The floral organization of *Parasaurauia allonensis* is summarized in the floral diagram (Fig. 31).

Association of flowers and fruits—The species is represented by five flowers and two fruits. Flowers and fruits are described here as dispersed parts of the same species of plant for the following reasons: (1) the fruits and the ovary in the two flowers in which the gynoecium can be observed all have three locules and an apical depression from which the styles emerge (Figs. 16–19); (2) a five-parted calyx is present on both flower and fruit (Figs. 8, 19); (3) the base of the sepal attached to the fossil fruit (Fig. 21) is identical to the base of sepals removed from a flower (Fig. 22) in bearing multicellular trichomes on the abaxial surface. At the base of sepals in larger (more developed?) flowers, multicellular trichomes are sparse (Fig. 5), as is the case with the sepal removed from the immature fruiting specimen (Figs. 18, 19, 21).

DISCUSSION

Comparison of *Parasaurauia* with extant Ericales—*Parasaurauia allonensis* exhibits several characters that are indicative of a relationship to the Ericales, and particularly the Actinidiaceae (Table 1). The following characters of *Parasaurauia* are likely synapomorphies of Ericales: deeply sagittate and probably inverting anthers (Figs. 9–15), syncarpous ovary with styles inserted in an apical depression (Figs. 16–19), and multicellular trichomes on the sepals (Figs. 1, 2, 4, 5, 8, 21, 22). Other aspects of the morphology of *Parasaurauia allonensis* are also consistent with a relationship to the Ericales, including the loculicidal capsule, axile placentation (Figs. 18, 19), syncarpous gynoecium (Fig. 16), and pentamerous floral architecture (Figs. 3, 6). A relatively basal position of *Parasaurauia allonensis* within this order, specifically close to or within the Actinidiaceae, is indicated by free as opposed to connate petals, an open rather than urceolate corolla morphology (Figs. 3, 6, 7), anthers lacking spurs and awns, a superior rather than inferior ovary, and free (Figs. 16, 17) rather than united styles that form a hollow, fluted column. In addition, the ten stamens of *Parasaurauia allonensis* may reflect the plesiomorphic condition of the androecium in the subclass Dilleniidae. Recent studies in the Dilleniidae, and for the eudicots as a whole (Drinnan, Crane, and Hoot, 1994) suggest that at this level of angiosperm evolution the presence of more numerous stamens is a derived feature. Based on these comparisons we conclude that the fossil flowers show significant similarities to flowers of Actinidiaceae, Clethraceae, Cyrillaceae (*Purdiaea*), and Sarraceniaceae (*Heliamphora*).

In general appearance the fossil flowers are most similar to the family Actinidiaceae. The morphology and anatomy of the family has been studied by Li (1952), Vijayaraghvan (1965), Hunter (1966), Soejarto (1969), Dickison (1972), and Schmid (1978a, b). Extant Actinidiaceae include three genera, *Clematoclethra*, *Actinidia*, and *Saurauia* (Dickison, 1972; Cronquist, 1981). Of these, *Parasaurauia allonensis* is most closely comparable to *Saurauia*, differing only in the number of stamens (ten in the fossil vs. 15 to numerous in *Saurauia*) and perhaps the apparent alternation of large and small stamens in the fossil (but see above). Like *Parasaurauia allonensis*, *Saurauia* also has free styles with an adaxial longitudinal groove, simple stigmas (Figs. 17, 25), and 3–5 carpels. *Actinidia* has numerous stamens, three to more frequently up to 30 carpels, and free styles with capitulate stigmas. Although flowers of *Clematoclethra* are similar to *Parasaurauia* in having ten stamens (see Appendix 1, character 19), *Clematoclethra* differs from *Parasaurauia* in having four or five carpels with a single style that is hollow and internally fluted. Thus, although *Parasaurauia allonensis* is most comparable to the Actinidiaceae, and *Saurauia* in particular, it is not identical to the flowers of any extant genus in the Actinidiaceae or any other ericalean family. Flowers of *Parasaurauia*

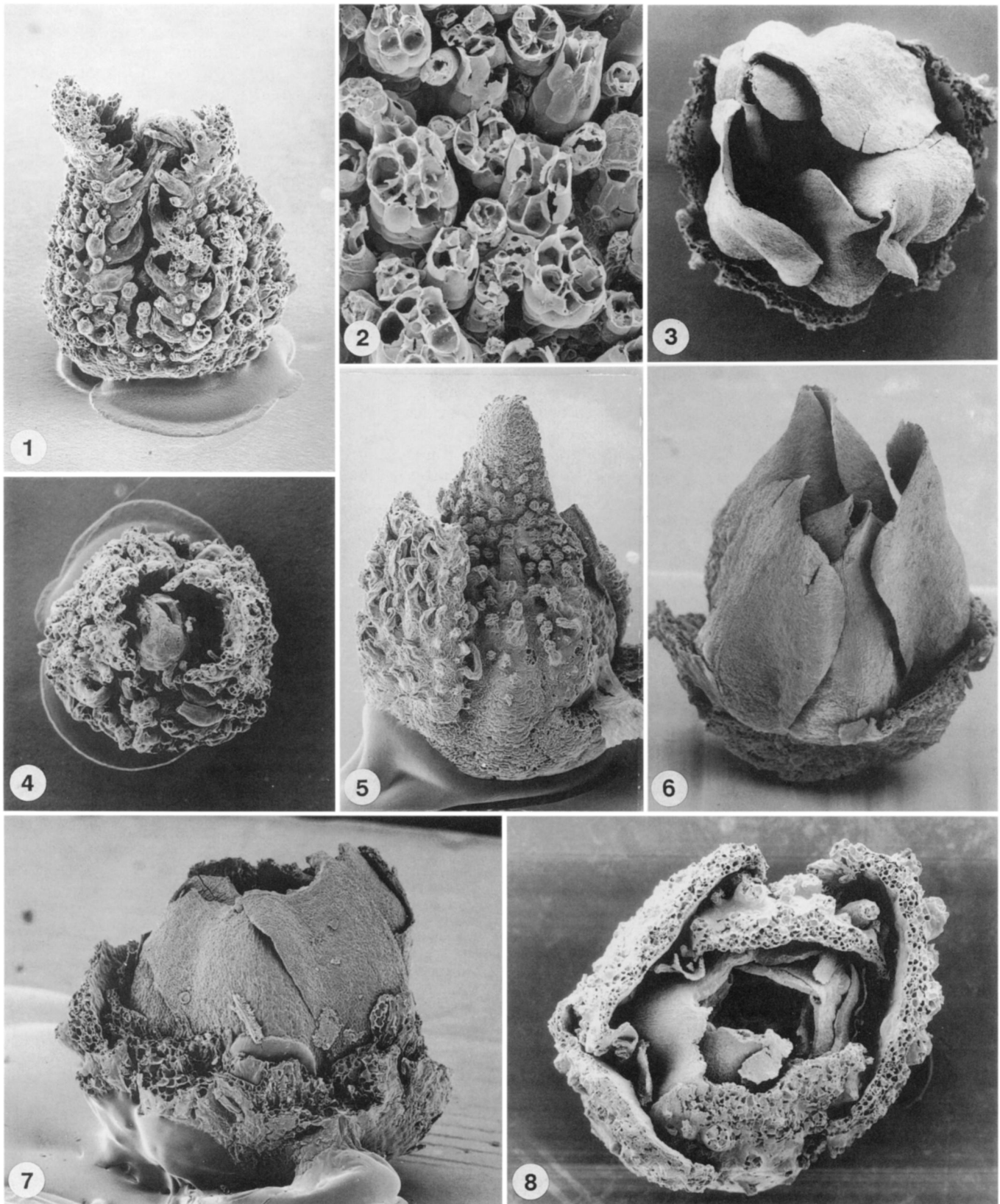
are similar to Clethraceae and Diapensiaceae in being consistently tricarpetate, and are like most members of the Ericales in bearing ten stamens. However, *Parasaurauia* differs most conspicuously from Clethraceae and Diapensiaceae and other Ericales by its free styles.

Phylogenetic analysis of the relationships of *Parasaurauia*—Because *Parasaurauia allonensis* shares some features with *Actinidia* and *Saurauia*, and others with *Clematoclethra*, Sarraceniaceae, Clethraceae, and other Ericales, we used a cladistic analysis to evaluate the phylogenetic relationships of the fossil material. Phylogenetic relationships within the order Ericales have been addressed, either directly or indirectly, in several recent studies (Anderberg, 1992, 1993; Hufford, 1992; Judd and Kron, 1993; Kron and Chase, 1993). Results of these studies are largely in agreement on the composition of the ericalean clade, which includes the Ericaceae, Pyrolaceae, Monotropaceae, Epacridaceae, Empetraceae, Clethraceae, Cyrillaceae, Actinidiaceae, and sometimes the Sarraceniaceae and Roridulaceae. For interpreting the phylogenetic relationships of *Parasaurauia* the studies of Anderberg (1992, 1993) and Judd and Kron (1993) are particularly relevant because they address the circumscription of the Ericales and Ericaceae, respectively.

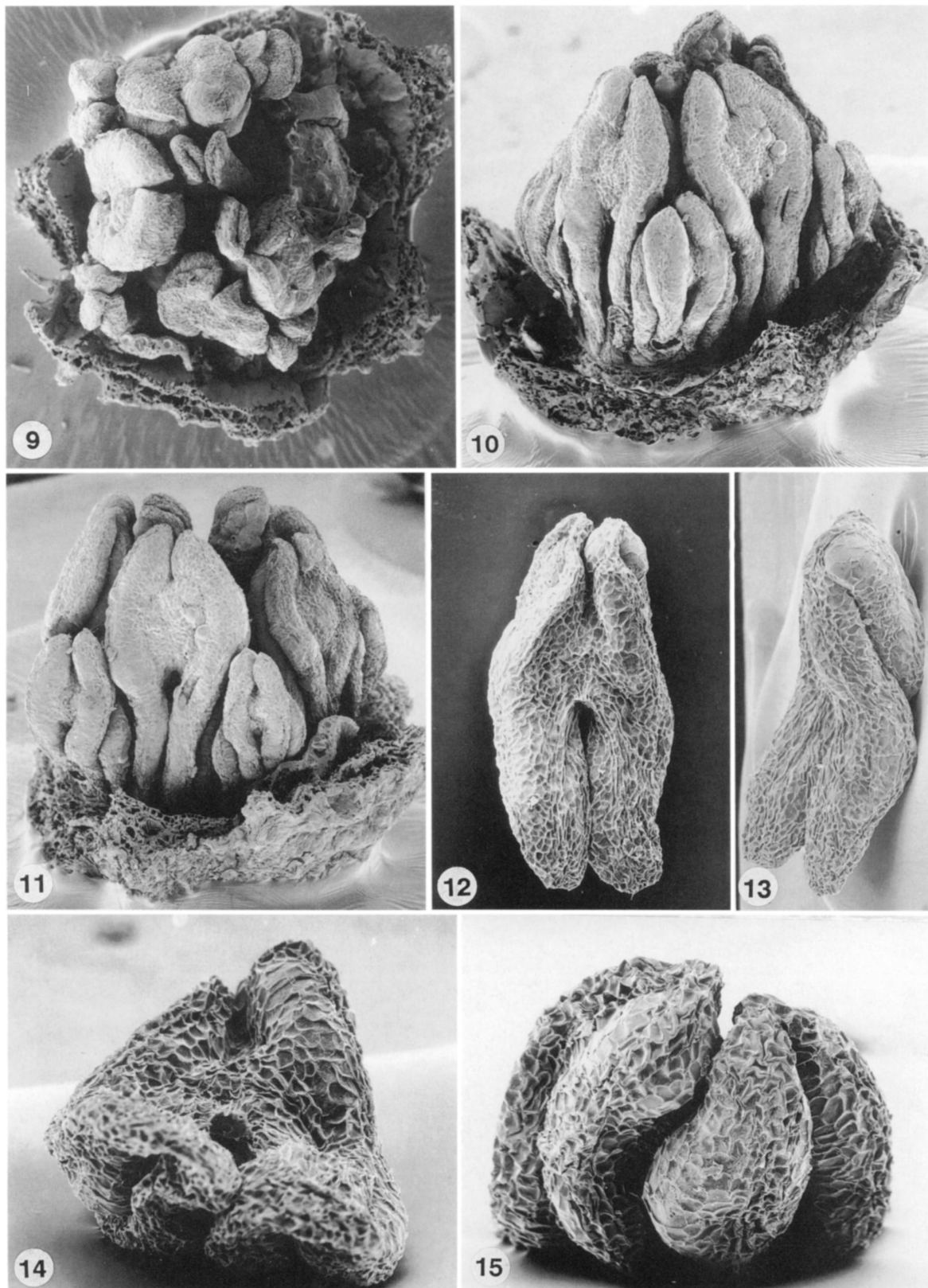
In conducting our analysis of the phylogenetic relationships of *Parasaurauia* we have used the study of Anderberg (1992) because it encompasses the broadest scope of potentially ericalean taxa in an analysis largely based on morphological characters, many of which can be observed in the fossil. The 1992 cladistic analysis of Anderberg was a ground-breaking effort to circumscribe the Ericales and investigate patterns of character evolution within the order. While the Anderberg (1992) study provided an excellent starting point for our analysis, we found it desirable to make several modifications to the characters, taxa, and data matrix as published by Anderberg (1992). In addition to Magnoliaceae we have added *Tetracentron* and Hamamelidaceae as outgroups to represent more effectively basal eudicots (Drinnan, Crane, and Hoot, 1994). We also divided two heterogeneous families to form more homogeneous taxa for purposes of our analysis. We represent Actinidiaceae by *Actinidia-Saurauia* and *Clematoclethra*, and Cyrillaceae by *Cyrilla-Cliftonia* and *Purdiaea*. Characters, as we have defined them, are listed in Appendix 1 and differences in interpretation from Anderberg (1992) are specified. Instances where we have scored taxa differently from Anderberg (1992) are indicated in the data table (Table 2) by underlined entries. Where our interpretations follow those of Anderberg we have not repeated Anderberg's discussion of individual characters. The reader is referred to Anderberg (1992) for details.

In an effort to reduce potential ambiguity in our analysis we have examined numerous herbarium specimens and literature sources to fill in some of the unknown/polymorphic entries (scored as ?) in the Anderberg data

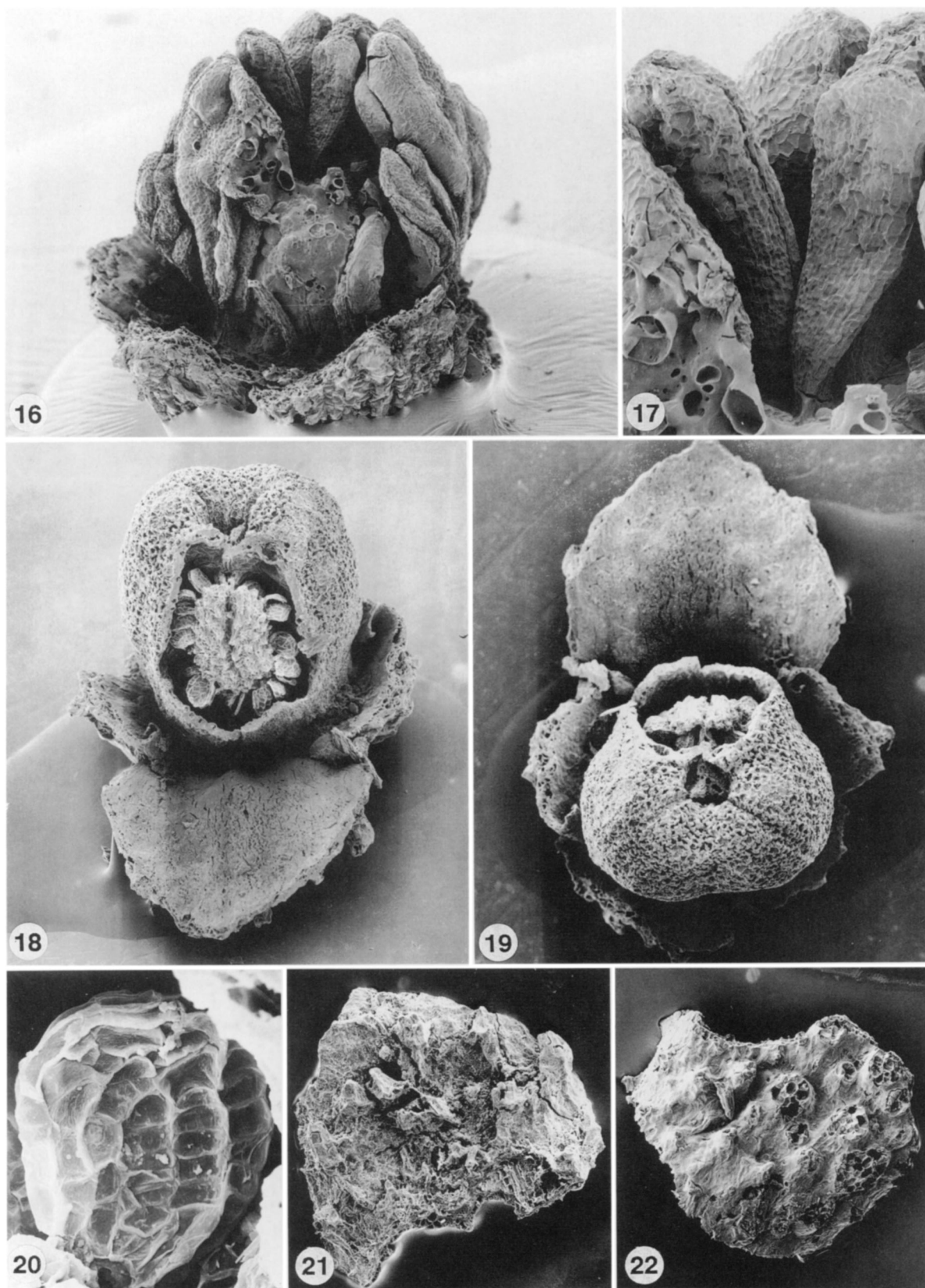
Figs. 1–8. *Parasaurauia allonensis* gen. et sp. nov., flower buds, $\times 75$ (except as noted). 1. Immature flower bud showing two exterior sepals with multicellular trichomes, PP44609. 2. Detail of sepal showing multicellular trichomes, PP44609, $\times 300$. 3. Apical view of flower bud without



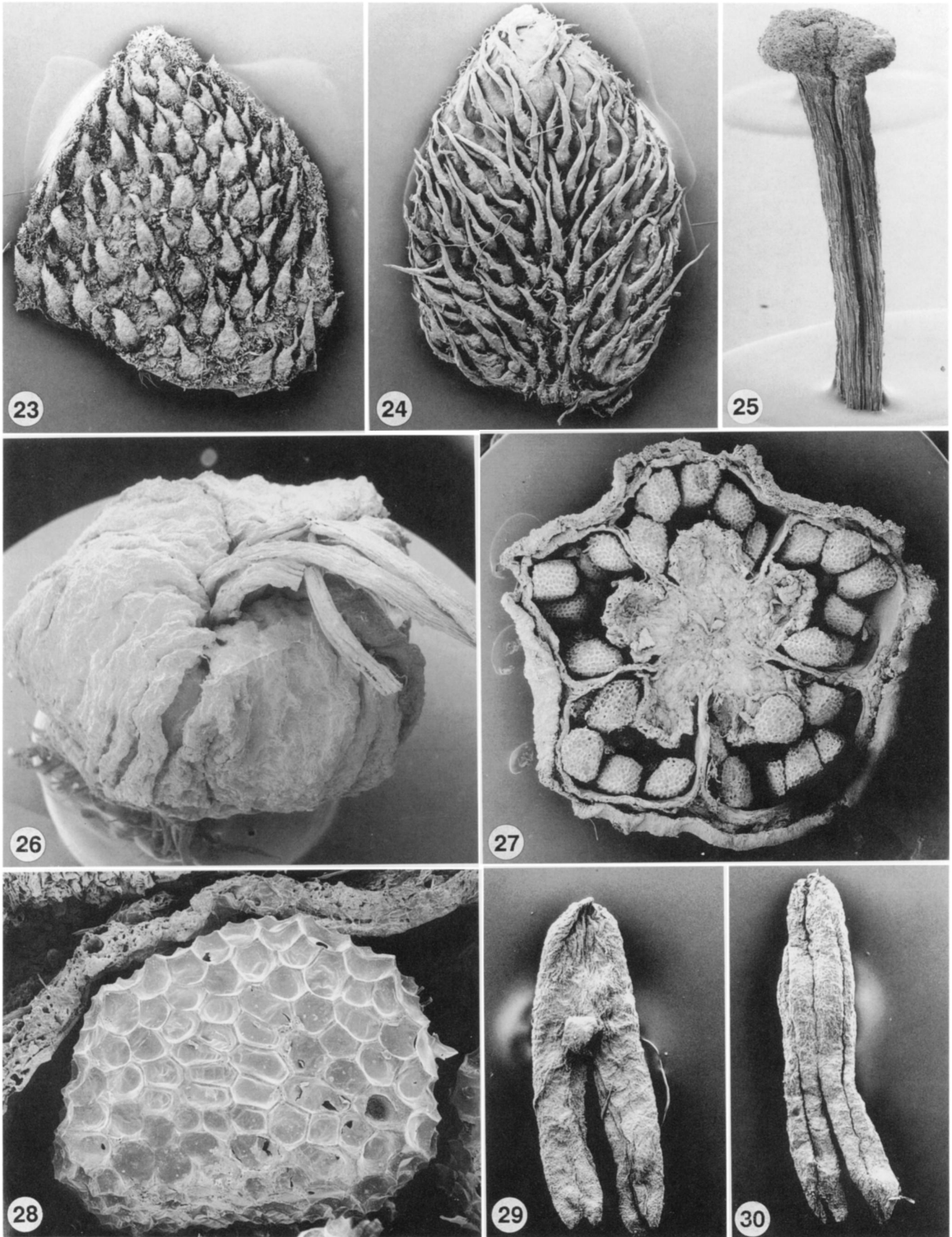
sepals, showing petals, PP44612, holotype. **4.** Apical view of flower bud (same as Fig. 1) showing sepals with multicellular trichomes, PP44609. **5.** Mature flower showing sepals with multicellular trichomes, PP44591. **6.** Lateral view of flower bud (same as Fig. 3) without sepals, showing petals, PP44612, holotype. **7.** Lateral view of flower bud with sepals removed to show petals, PP44610. **8.** Flower bud (same as Fig. 7) without apices of sepals, showing parts of petals, PP44610.



Figs. 9–15. *Parasaurauia allonensis* gen. et sp. nov., androecium, PP44612, holotype. **9.** Apical view of androecium showing alternating arrangement of large and small stamens, $\times 100$. **10–11.** Lateral views of androecium showing deeply sagittate anthers and alternating arrangement of stamens, $\times 100$. **12.** Adaxial side of anther removed in dissection showing basal attachment site for filament and deeply sagittate anther base, $\times 200$. **13.** Lateral view of anther removed from flower in Fig. 9 to illustrate arrangement of locules, $\times 200$. **14.** Basal view of anther removed from flower in Fig. 9 to illustrate basal attachment of filament, $\times 400$. **15.** Basal view of anther removed from flower in Fig. 9 to illustrate arrangement of locules, $\times 400$.



Figs. 16–22. *Parasaurauia allonensis* gen. et sp. nov., gynoecium. 16. Lateral view of gynoecium, PP44612, holotype, $\times 100$. 17. Detail of gynoecium showing styles with adaxial groove emerging from an apical depression in the ovary, PP44612, holotype, $\times 250$. 18. Lateral view of immature fruit showing reticulate ovules/seeds, axile placentation, apical depression from which styles abscised and a sepal, PP44476, $\times 75$. 19. Apical view of immature fruit showing axile placentation, apical depression from which styles abscised and a sepal, PP44476, $\times 75$. 20. Reticulate ovule/seed from fruit in Figs. 18 and 19, PP44476, $\times 750$. 21. Abaxial surface of sepal removed from fruit in Figs. 18 and 19, PP44476, $\times 75$. 22. Abaxial surface of sepal removed from flower bud in Fig. 8, PP44610, $\times 75$.



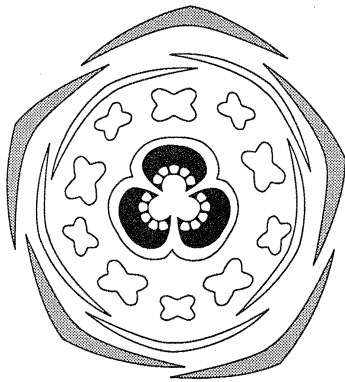


Fig. 31. Schematic diagram of flower of *Parasaurauia allonensis* showing five sepals and petals, quincuncially arranged, alternating arrangement of five small and five large stamens, and three carpels with numerous ovules in a trilobular ovary.

matrix. In the process we have checked as many characters as possible for all taxa in the analysis. Particular attention was paid to key characters for the ericid group (e.g., stamen number and insertion, anther inversion and dehiscence, style structure, endosperm haustoria). Four additional characters are included in our analysis (50. Anther base, 51. Insertion of style, 52. Pollen aperture, 53. Seed coat). We also excluded two characters included by Anderberg (1992). Among the characters with a substantial number of missing values, character 35 (embryogeny, six states, unordered; Anderberg, 1992; Appendix 1), which has 15 missing values (28%), seems to be particularly problematic because it allows various subclades to assume different positions on the cladograms with considerable loss of resolution in the consensus cladogram. Although this character may be informative when it is known in more taxa, we have excluded it in the present analysis. Character 40 (seco-iridoids, three states, ordered; Anderberg, 1992) was excluded for different reasons. Although there are few unknown entries for this character in the data set, Anderberg (1992) acknowledges that records are rather sparse for this chemical character. It is unclear, therefore, that all of the taxa that are scored as lacking these chemicals have actually been surveyed. In addition, iridoids, which are a class of compounds, are also represented in the data by character 39 (carboxylic iridoids). All taxa scored present for character 40 are also scored present for character 39. For these reasons the presence of seco-iridoids is not included in our analysis. Although excluded from our study, characters 35 and 40 are maintained in the data table presented here so that character numbers are directly comparable to Anderberg (1992).

Phylogenetic analyses were conducted using *Hennig86* (Options- mhennig* and bb*; Farris, 1988) and *PAUP* (Options- heuristic search using TBR branch swapping,

MULPARS enabled, random stepwise addition with 10 replicates; Swofford, 1993) and cladograms were printed using *Clados* (Nixon, 1992). Analyses were conducted with and without the inclusion of the fossil taxon *Parasaurauia*. Identical results were obtained with *Hennig86* and *PAUP*. The analyses including and excluding *Parasaurauia* yielded identical results: six minimum length trees of 183 steps (CI = 0.32, RI = 0.71). These six trees differ only in the relationships among three families in each of two clades: Ericaceae-Monotropaceae-Pyrolaceae and Valerianaceae-Caprifoliaceae-Dipsacaceae, which is shown in the strict consensus tree (Fig. 32).

Results of the analysis presented here are very similar to those obtained in other recent studies (Anderberg, 1992, 1993; Hufford, 1992; Judd and Kron, 1993; Kron and Chase, 1993; Olmstead et al., 1993). The Actinidiaceae are consistently placed with a "core" ericalean clade composed of Ericaceae, Pyrolaceae, Monotropaceae, Epacridaceae, Empetraceae, Clethraceae, and Cyrillaceae, and sometimes Sarraceniaceae and Roridulaceae, and this is maintained in all of the available morphological and molecular phylogenetic studies of the Ericales (Anderberg, 1992, 1993; Judd and Kron, 1993; Kron and Chase, 1993). However, while largely comparable with the results of Anderberg (1992), the results obtained here differ in the placement of several taxa: Grubbiaceae is not placed in the ericalean clade in our study, and Diapensiaceae and Roridulaceae are placed in a more basal position in the ericalean clade in our analysis. Sarraceniaceae is placed in the ericalean clade in our study rather than a basal position in the tree near Theaceae in Anderberg (1992). In the studies of Anderberg (1993), Judd and Kron (1993), Kron and Chase (1993), and Olmstead et al. (1993) the Ericaceae were represented by multiple taxa and their results place the Epacridaceae, Empetraceae, Pyrolaceae, and Monotropaceae (morphological study only, not included in the *rbcL* studies) within the Ericaceae sensu lato. One novel result from our analyses is that *Cyrilla-Cliftonia* and *Purdiaea* (Cyrillaceae) are widely separated in the minimum length cladograms. Although seeds lacking a seed coat (character 53) is a potential synapomorphy for the family, differences between *Purdiaea* and *Cyrilla-Cliftonia* in style structure, anther morphology, and anther inversion are largely responsible for the results obtained here.

In all six minimum length trees obtained when *Parasaurauia* is included in the analysis, the fossil taxon is placed within the Actinidiaceae as sister to *Actinidia* and *Saurauia*, with *Clematoclethra* the basal genus in the family. In this configuration, contrary to the interpretation of Anderberg (1992), the free styles of *Parasaurauia*, *Actinidia*, and *Saurauia* are interpreted as a synapomorphy that unites these genera and is most parsimoniously interpreted as a reversal rather than a retained plesiomorphy in this group. In our analysis flowers of the eri-

Figs. 23–30. Extant Actinidiaceae. **23.** Sepal of *Saurauia stapfiana* showing multicellular trichomes, $\times 15$. **24.** Sepal of *Saurauia scabra* showing multicellular trichomes, $\times 15$. **25.** One style of *Saurauia bullosa* showing adaxial longitudinal groove, $\times 35$. **26.** Fruit of *Saurauia brachybotryus*, showing styles emerging from an apical depression, $\times 15$. **27.** Fruit of *Saurauia brachybotryus*, transverse section showing reticulate seeds and axile placentation, $\times 10$. **28.** Seed of *Saurauia brachybotryus* showing reticulate seed coat, $\times 70$. **29.** Adaxial surface of anther of *Saurauia scabra* showing deep sagittation and basal filament attachment, $\times 20$. **30.** Abaxial surface of anther of *Saurauia scabra* showing locule arrangement, $\times 20$.

TABLE 1. Comparison of floral characters of *Parasaurauia allonensis* with extant taxa.

Taxon	Stamen number	Anther shape	Anther orientation	Anther dehiscence	Style structure	Ovary apex	Petals	Carpel number
<i>Parasaurauia allonensis</i>	10	sagittate	inverted?	short terminal slits or pores?	free	apical depression	free	3
<i>Saurauia</i> (Actinidiaceae)	numerous	sagittate	inverted	short terminal slits or pores	free	apical depression	free	3-5
<i>Actinida</i> (Actinidiaceae)	numerous	sagittate	inverted	short terminal slits or pores	free	apical depression	free	3-30 or more
<i>Clematoclethra</i> (Actinidiaceae)	10	sagittate	inverted	short terminal slits or pores	united, hollow, fluted	apical depression	free	4-5
Clethraceae	10 (12)	sagittate	inverted	terminal pores	united, hollow, fluted	apical depression	free	3
Ericaceae	10 (-20)	sagittate	inverted	terminal pores	united, hollow, fluted	apical depression	mostly united	(2)-5-(10)
Pyrolaceae	8-10	sagittate	inverted	terminal pores	united, hollow, fluted	apical depression	free	5
Monotropaceae	6-12	sagittate	inverted	terminal pores	united, hollow, fluted	apical depression	free or united	(4)-5-(6)
Empetraceae	2-4	not sagittate	inverted	longitudinal slits	united, hollow, fluted	apical depression	free	2-9
Epacridaceae	4-5	not sagittate	inverted	longitudinal slits	united, hollow, fluted	apical depression	united	1-4
Diapensiaceae	5	not sagittate	inverted? (inflexed 90°)	longitudinal slits	united, hollow, fluted	apical depression	free or united	3
<i>Purdiaea</i> (Cyrillaceae)	10-14	sagittate	inverted	terminal pores	united, hollow, fluted	apical depression	free	(3-4) 5
<i>Cyrella</i> and <i>Cliffonia</i> (Cyrillaceae)	5-7 10-14	not sagittate	not inverted	longitudinal slits	united, solid	apical depression	free	<i>Cyrella</i> 2-3 <i>Cliffonia</i> 3-5
Roridulaceae	5	not sagittate	inverted	pores	united, solid	apex acute	free	2-3
Sarraceniaceae	10-numerous	sagittate	inverted	terminal pores	united, solid	apical depression	free	3-5
Theaceae	numerous	not sagittate	not inverted	longitudinal slits	united, solid	apex acute	free	(2)-3-5-(10)

TABLE 2. Data table used in the phylogenetic analysis.^a

Taxa	Characters					
	123456789	1 0123456789	2 0123456789	3 0123456789	4 0123456789	5 0123
Magnoliaceae	000000000	000000000	000000000	000000000	000000000	0000
<i>Tetracentron</i>	000-00000	0001--0002	000000000	00000??100	0000000?00	0010
Hamamelidaceae	000001000	0001000001	0000000001	00001?0001	?0?0000?00	0010
Theaceae	000000100	000100000 <u>3</u>	0000000000	<u>2</u> 001112000	0010000010	0020
Roridaceae	000000000	0001000002	0011001000	<u>2</u> 011010001	00?????000?	0020
<i>Actinidia/Saurauia</i>	000000 <u>1</u> 00	010000000 <u>3</u>	00110?0000	<u>0</u> 01101 <u>0</u> 001	0010000000	1120
<i>Clematoclethra</i>	000000 <u>1</u> 00	010000000 <u>1</u>	00110?0000	<u>1</u> 01101 <u>0</u> 001	0010000000	1120
<i>Parasaurauia</i>	?????????	?????00001	00110?????	0?1?????0?	???????????	1120
Grubbiaceae	000000010	00000?0101	00000??0?1	<u>2</u> 1110?0000	00?0?000?	0020
<i>Purdiea</i>	000000100	0001000001	0011000000	11110?000?	001??00000	1121
<i>Cyrrilla/Cliftonia</i>	000000100	0001000001	0000000000	<u>2</u> 1110?000?	001??00000	0121
Clethraceae	000000100	0001000001	0011000000	1111020001	0000000000	1120
Ericaceae	000?0?000	0001?00?01	00110011?0	1111010011	00?1110100	1120
Epacridaceae	000 <u>1</u> 0?100	000110000 <u>2</u>	10100011?0	1111030001	0001000000	0120
Empetraceae	000 <u>1</u> 00100	0001000002	0010021100	1111010000	0011000100	0120
Monotropaceae	000-00100	0001?00001	001 <u>1</u> 001000	1111030111	000?11000?	1120
Pyrolaceae	000?00100	0001000001	0011001100	1111030111	0001100000	1120
Diapensiaceae	000000100	0001100001	?010000000	1011010000	0010000100	0120
Sarraceniaceae	000000?00	000100000 <u>3</u>	00 <u>1</u> 1000000	<u>2</u> 011030001	1000000000	1120
Garryaceae	000001010	0000??0102	0000010000	0010110001	0000000011	0020
Alangiaceae	010000000	000001010?	0000000000	<u>2</u> 010??0001	0000000001	0020
Cornaceae	000001010	1000010102	000000?000	<u>2</u> 0100?0001	10?100001?	0020
Loasaceae	0001001?0	101011010?	00000??0?0	<u>2</u> 111010001	1000000001	0020
Hydrangeaceae	000001010	11000?0101	000000?0?0	?0110??001	1000100000	0020
Sambucaceae	000 <u>1</u> 00010	0000100102	0000000010	<u>2</u> 0110?1001	101100000?	0020
Adoxaceae	000100010	0000100102	0000010010	<u>0</u> 011021001	100000000?	0020
Fouquieriaceae	000100100	0000100001	000000?000	<u>2</u> 001020001	0010000000	0020
Polemoniaceae	0001001?0	0000120002	100001000?	<u>2</u> 011150000	000000000?	0020
Araliaceae	001?00000	0000010102	000000001?	001?1?0000	000000201?	0020
Apiaceae	001100000	0100010102	0000000011	0011110000	0000002011	0020
Pittosporaceae	001100000	0000100002	000000?01?	<u>2</u> 011??0000	0000002000	0020
Oleaceae	000111110	01001?0002	1000000001	<u>2</u> 0110?0001	1001000001	0020
Gentianaceae	100100?11	0100120002	1000000??1	<u>2</u> 011110001	1001000001	0020
Apocynaceae	100110111	0000120002	100000???1	<u>2</u> 011130001	200100000?	0020
Rubiaceae	000110?11	0100120102	10000000?1	<u>2</u> 011110001	200110000?	0020
Valerianaceae	000100010	0000101112	1000010010	<u>2</u> 011020001	1000000001	0020
Caprifoliaceae	000001010	0000101112	100001001?	<u>2</u> 011020001	100000000?	0020
Dipsacaceae	000100010	0000101112	1000010011	<u>2</u> 011040001	1000000001	0020
Boraginaceae	000101100	1110100002	10000000?1	<u>2</u> 011??0000	0100000001	0020
Hydrophyllaceae	000100100	1010100002	100000?001	<u>2</u> 011110000	0000000001	0020
Convolvulaceae	110100100	0100120002	100000?0?1	<u>2</u> 011130000	0000000001	0020
Buddlejaceae	000100110	0000100002	10000??001	<u>2</u> 111000001	0000000001	0020
Bignoniaceae	100100110	010?101002	1100010001	<u>2</u> 111000001	0001000001	0020
Plantaginaceae	0001001?0	0001100002	100000?0?1	<u>2</u> 111000001	0001000001	0020
Lamiaceae	000100110	0100101002	1100000001	<u>2</u> 111000001	0001000001	0020
Verbenaceae	000100110	1110101002	1100000001	<u>2</u> 111000001	0001000001	0020
Menyanthaceae	000100000	0000100002	1000000011	<u>2</u> 011020001	1100000001	0020
Goodeniaceae	000100100	000?111102	1000100001	<u>2</u> 011010001	1101000001	0020
Calyceraceae	000100100	0000110102	1000100001	<u>2</u> 0110?0001	1100000001	0020
Stylidiaceae	000100?00	000?101102	00000000?1	<u>2</u> 111010001	010000000?	0020
Lobeliaceae	010100100	0101111102	10001000?1	<u>2</u> 111010000	0101001001	0020
Campanulaceae	010100100	1110111102	100010000?	<u>2</u> 111010000	0100001001	0020
Asteraceae	011101000	0101111102	1000110011	<u>2</u> 011020000	010100100?	0020

^a Unordered multistate characters: 15 19 25 30 35 36 46; excluded characters: 35 and 40.

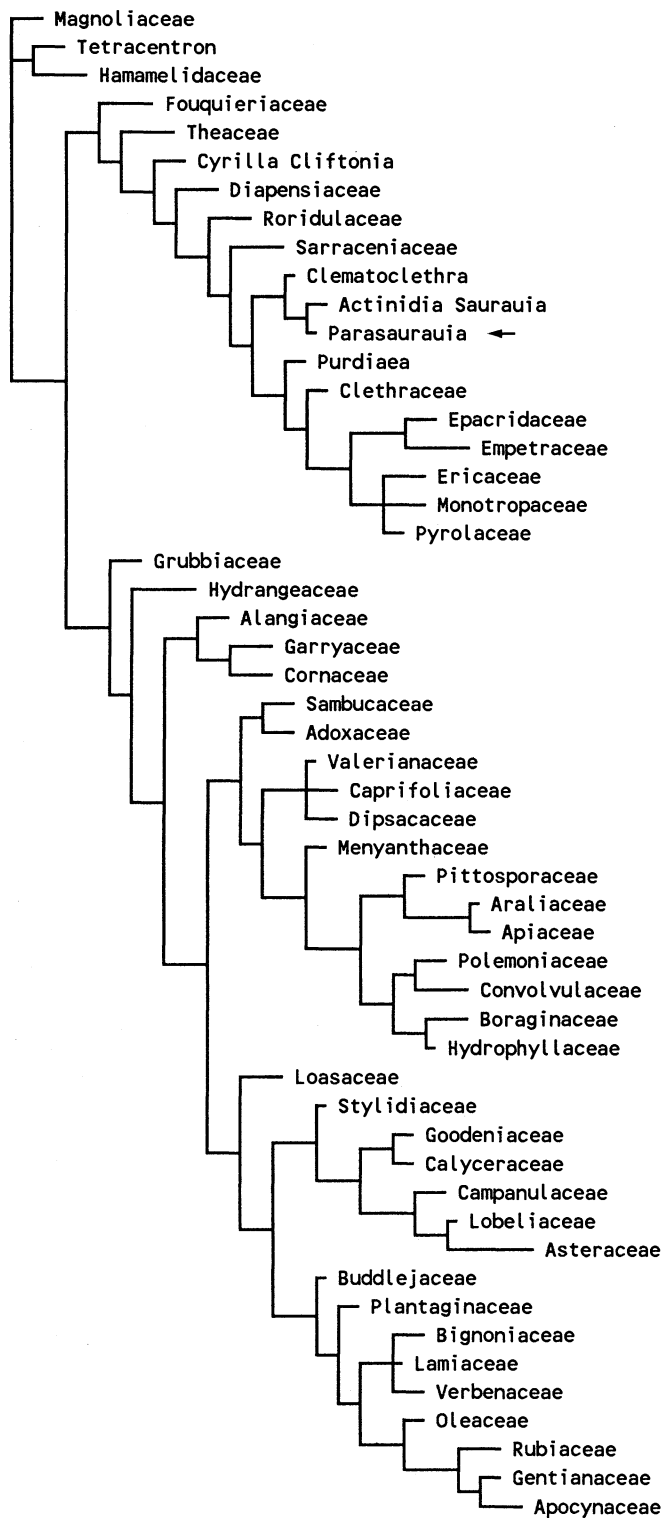


Fig. 32. Strict consensus tree calculated from six minimum length trees. The fossil taxon *Parasaurauia* is indicated by an arrow.

calean clade are primitively diplostemonous (including *Clematoclethra*) and the haplostemonous and polystemonous conditions are interpreted as apomorphies. Within the Actinidiaceae the presence of numerous stamens is a synapomorphy uniting *Actinidia* and *Saurauia*. This in-

terpretation is thus contrary to the suggestion of Anderberg (1992) that polystemonous flowers are plesiomorphic in the Ericales.

Fossil record of the Ericales—Recent studies have dramatically expanded the fossil record of the Ericales and have unequivocally documented the presence of the group during the Late Cretaceous. The earliest record of the Ericales based on reproductive material is *Paleoenkianthus sayrevillensis*, which is known from fossil flowers and fruits from the Turonian (Late Cretaceous, $\approx 90 \times 10^6$ yr ago) of New Jersey (Nixon and Crepet, 1993). Nixon and Crepet (1993) interpreted *Paleoenkianthus* as most comparable to basal Ericaceae (probably near *Enkianthus*) but not identical to any extant genus. Fossil flowers called *Actinocalyx bohrii* have been described from the Åsen locality in southern Sweden, which is thought to be of Santonian/Campanian age (Friis, 1985b). *Actinocalyx* was interpreted to be most similar to the Diapensiaceae and is probably very close in age to *Parasaurauia*. Fruits and seeds resembling those of extant *Leucothoe* have been described from the Maastrichtian of Europe (Knobloch and Mai, 1986). The Ericales have an extensive fossil record during the Tertiary (e.g., Collinson and Crane, 1978; Friis, 1985a). In Actinidiaceae, seeds similar to those of *Saurauia* are known from the Late Cretaceous (Maastrichtian) and Tertiary in Europe (Knobloch and Mai, 1986; Collinson, Boulter, and Holmes, 1993), and seeds of *Actinidia* have been described from the Middle Eocene of Oregon (Manchester, 1994) and the Middle Miocene of Denmark (Friis, 1985a). There is no currently recognized fossil record of pollen of Actinidiaceae (Collinson, Boulter, and Holmes, 1993).

The occurrence of *Parasaurauia* in the early Campanian provides evidence of additional ericalean diversity in the Late Cretaceous. This fossil representative of the Actinidiaceae, when viewed together with the other Late Cretaceous ericalean taxa and the hypothesized phylogenetic relationships among the Ericales and related families (e.g., Anderberg, 1992, 1993; Hufford, 1992; Judd and Kron, 1993; Kron and Chase, 1993), implies that among the diversity of Late Cretaceous eudicots (Crane and Lidgard, 1989) the ericad clade must have undergone considerable differentiation by the Turonian–early Campanian.

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APPENDIX 1. Characters used in the phylogenetic analysis.^a

1. Intraxylary phloem: absent (0); present (1).
2. Laticiferous ducts: absent (0); present (1).
3. Secretory canals: absent (0); present (1).
4. Vessel perforations: scalariform perforation plates predominate (0); simple perforation plates predominate (1). This character, as defined by Anderberg (1992), is based on generalizations in Metcalfe and Chalk (1950), Dahlgren (1980), and Cronquist (1981). The present scoring does not reflect the variability that occurs in some of the families included in this study. In future analyses this character should be critically reevaluated. Note also that because simple perforation plates have clearly evolved independently numerous times among angiosperm families, and also have evidently reversed to the scalariform condition in some groups, the utility of this character at higher systematic levels is questionable (P. S. Herendeen, unpublished data).
5. Vestured pits: absent (0); present (1).
6. Fibers with spiral thickenings: absent (0); present (1).
7. Nodes: multilacunar to trilacunar (0); unilacunar (1).
8. Leaf arrangement: alternate (0); opposite (1).
9. Colleters: absent (0); present (1).
10. Calcified or silicified hairs: absent (0); present (1).
11. Raphides or acicular crystals: absent (0); present (1).
12. Cystoliths: absent (0); present (1).
13. Inflorescence structure: cymose (0); racemose (1).
14. Corolla: choripetalous (0); sympetalous (1).
15. Aestivation: imbricate (0); valvate or induplicate (1); contorted (2). Unordered.
16. Floral symmetry: not zygomorphic (0); zygomorphic (1).
17. Ovary position: ovary superior (0); ovary inferior (1).
18. Floral tube nectaries: unicellular "Dipsacalean" nectary absent (0); unicellular "Dipsacalean" nectary present (1).
19. Stamen number: numerous, spirally arranged stamens (0); diplostemonous/obdiplostemonous (1); haplostemonous (2); numerous cyclically arranged stamens (3). Unordered. This character has been redefined from Anderberg (1992), in which state 0 represented both numerous spiral stamens and numerous cyclic stamens (our state 3). These states are not a priori homologous and we have scored them separately. *Clematoclethra* has been cited in the literature as having ten to numerous stamens (e.g., Dickison, 1972), but this is almost certainly incorrect. Tang and Xiang (1989) recognize a single species of *Clematoclethra* and it is characterized by the presence of only ten stamens (see also Airy Shaw, 1936; confirmed by P. S. Herendeen, personal observation).
20. Stamen insertion: free from petals (0); adnate to petals (1).
21. Stamen length: of more or less equal length (0); stamens didynamous (1).
22. Anther orientation: anthers not inverted (0); anthers inverted (1). We differ from Anderberg (1992) in how several taxa are scored for this character. Sarraceniaceae is scored as having inverted anthers based on the genus *Heliamphora*, in which this character has been observed (P. S. Herendeen, personal observation). Although the anthers of Grubbiaceae are said to be inverted by Cronquist (1981), they are a very different morphology from other Ericales and in fact Cronquist notes they are not comparable to stamens of any other member of the Ericales. In Grubbiaceae the anther sacs are abaxially directed and there is no evidence of anther inversion (P. S. Herendeen, personal observation). Although Cronquist (1981) indicates that there is no evidence of anther inversion in Cyrillaceae, the anthers of *Purdiaea* are clearly inverted at maturity. However, the anthers of *Cyrilla* and *Cliftonia* do not appear to invert (Anderberg, 1993; P. S. Herendeen, personal observation).
23. Anther aperture: dehiscence longitudinal, not by terminal pores or restricted terminal slits (0); dehiscence by terminal pores or restricted terminal slits (1). Many ericalean taxa have anthers that are said to be poricidally dehiscent, and because the anthers are inverted the terminal pores are morphologically basal, not distal. However, it should be noted that there is variation among the taxa in the degree to which the pore is developed, and in some taxa the aperture is better characterized as a restricted terminal slit. It may be preferable to redefine this as a three-state character, but there is sufficient variation within genera and families to make this impractical within the context of the present study. Sarraceniaceae is scored as having poricidal dehiscence based on its occurrence in *Heliamphora* (P. S. Herendeen, personal observation).
24. Pollen presentation apparatus: staminal tube with pushing style absent (0); staminal tube with pushing style present (1).
25. Tapetum: glandular (0); amoeboid (1); *Empetrum* type (2). Unordered.
26. Endothecium: endothecium with fibrous thickenings (0); endothecium without fibrous thickenings (1).
27. Pollen tetrads: pollen not dispersed in tetrads (0); pollen dispersed in tetrads (1).
28. Pollen nuclei: pollen binucleate when released (0); pollen trinucleate when released (1).
29. Carpel number: fruit with three or more carpels (0); fruit of two carpels (1).
30. Style structure: styles free (0); styles united with a hollow central canal that is fluted in alignment with the locules (1); styles united, solid, no central canal (2). Unordered. This character has been reinterpreted from Anderberg (1992), in which only two states were recognized (solid vs. united and hollow) and the morphological difference between free styles and styles that are united into a solid structure was ignored. Because it is plausible that the united, hollow style represents either an intermediate evolutionary step between free styles and styles that are united into a solid structure, or an independent origin of united styles, we have rescored all taxa for this character.
31. Endosperm haustoria: terminal endosperm haustoria absent (0); terminal haustoria present (1). As Anderberg (1992) notes, the literature regarding this character is somewhat confused. Some references clearly distinguish among terminal haustoria, chalazal haustoria, and micropylar haustoria. We base our scoring on Dahlgren (1989, 1991) and note that there are several corrections to Anderberg (1992) (absent in Actinidiaceae, Boraginaceae, and Hydrophyllaceae). Anderberg (1992) scored Actinidiaceae as unknown because of contradictions in the earlier literature, but it seems clear from Dahlgren (1989, 1991) that terminal haustoria (i.e., present at both micropyle and chalaza) are absent. Likewise, Boraginaceae have micropylar haustoria only, and Fouquieriaceae and Hydrophyllaceae have chalazal haustoria only (Cronquist, 1981; Dahlgren, 1989, 1991).
32. Ovule integument: ovules bitegmic (0); ovules unitegmic (1).
33. Ovule nucellus: ovule crassinucellate (0); ovules tenuinucellate (1).
34. Endosperm development: endosperm cellular (0); endosperm nuclear (1).
35. Embryogeny: onagrad type (0); solanad type (1); asterad type (2); caryophyllad type (3); piperad type (4); chenopodiad type (5). Unordered. This character is problematic because numerous taxa are scored as unknown, and because six character states are recognized. Anderberg (1992) implies a degree of structure for this character based on ontogenetic patterns, but this is not reflected in the unordered treatment of the character. It may be worthwhile exploring different treatments of the character, but its value will remain limited until more taxa can be examined. For these reasons this character is excluded from our analysis.
36. Embryo sac: polygonum type (0); *Adoxa* type (1); *Allium* type (2). Unordered.

APPENDIX 1. Continued.

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37. Embryo development at maturity: embryo differentiated (0); embryo undifferentiated (1). Anderberg (1992) scored Ericaceae as having an undifferentiated embryo. However, according to Cronquist (1981) the embryo is small but differentiated. We have therefore scored Ericaceae accordingly.
 38. Seed with an appendage at each end: seeds not appendiculate (0); seeds appendiculate (1). We score Ericaceae unknown (?) for this character because appendages are present in only some genera of the family.
 39. Iridoids: carboxylic iridoids absent (0); carboxylic iridoids present (1).
 40. Seco-iridoids: seco-loganin absent (0); seco-loganin present (1); indole alkaloids of tryptophan type present (2). Ordered (see Anderberg, 1992 for discussion). We exclude this character from the analysis for the reasons outlined in the text.
 41. Inulin: absent (0); present (1).
 42. Ellagic acid: absent (0); present (1).
 43. Ursolic acid: absent (0); present (1).
 44. Arbutin: absent (0); present (1).
 45. Andromedotoxins: absent (0); present (1).
 46. Polyacetylenes: absent (0); polyacetylenes other than falcarinone present (1); polyacetylene falcarinone present (2). Unordered.
 47. Gossypetin: absent (0); present (1).
 48. Petroselenic acid: absent (0); present (1).
 49. Proanthocyanins: present (0); absent (1).

New characters added for this analysis:

50. Anther base: morphological base of anther not sagittate (0); morphological base of anther markedly sagittate beyond insertion of filament (1). Because this character occurs in some of the taxa with inverted anthers, the sagittate base may appear to be in a distal position, but it is morphologically basal.
51. Insertion of style at ovary/fruit apex: style not inserted in a depression at the ovary/fruit apex (0); style inserted in an apical depression (1).
52. Pollen aperture: monosulcate (0); tricolpate (1); tricolporate or tricolporate-derived (2). Ordered.
53. Seed coat: present (0); seed coat lacking (1).

^a Characters 1–49 are from Anderberg (1992). Differences in interpretation and character treatment are explained for the relevant characters. See Anderberg (1992) for detailed character discussion, which is not repeated here. Two of the eight multistate characters are treated as ordered (chars. 40 and 52). One of these is excluded in our analyses (char. 40).