



**Angiosperm Ovules and Carpels:  
Their Characters and Polarities,  
Distribution in Basal Clades,  
and Structural Evolution**

David Winship Taylor

(Received 30 June 1990)

**Abstract**

Angiosperm ovules and carpels have numerous characters and character states, not all of which have been utilized in phylogenetic analyses. A character analysis of these two organs is performed, including description of characters and states, and character polarization to identify the ancestral states. In addition, the distributions of these states are examined in the Magnoliidae and putatively basal orders of Hamamelidae, Caryophyllidae, Dilleniidae, Rosidae, Alismatidae (sensu Cronquist 1981), and Liliiflorae (sensu Dahlgren et al. 1985). These support two hypotheses: the ancestral ovules were orthotropous, bitegmic and crassinucellar, based on current terminology; and ancestral carpels had ascidate morphology and one or two ovules. Separate structural hypotheses for the evolution of ovules and of carpels are interpreted and indicate that anatropous ovules and plicate (conduplicate) carpels are derived. Finally, these analyses suggest that since the dicots Chloranthaceae, Saururaceae, Piperaceae and Amborellaceae and the monocots

Dioscoreales (e.g., Stemonaceae and Smilacaceae) have all the suggested ancestral states, they may be most similar to the morphology of the ancestral angiosperm.

**Key Words**

Angiosperms, ancestral morphology, carpel, ovule, structural evolution.

**Introduction**

Morphological features of ovules and carpels have had a long history of use for understanding the relationships of angiosperms. These applications have been from the level of intrafamilial relationships (e.g., Moeliono 1970; Tobe and Raven 1986, 1987) to the level of angiosperm origin and superfamilial relationships (e.g., Leinfellner 1950; Bailey and Swamy 1951; Philipson 1974, 1977; Dahlgren 1980; Dahlgren et al. 1981). These studies show the potential usefulness of these organs for phylogenetic analyses. This usefulness arises from their generally conservative nature and their numerous characters and character states. In addition, it is possible to polarize the ovule characters with outgroup comparison to identify the ancestral states (e.g., Stebbins 1974).

Yet the characters of ovules and carpels are currently underutilized in phylogenetic studies. The current terminology for ovules appears to conceal characters (Bouman 1984) that may be of phylogenetic and evolutionary





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**Introduction**

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Yet the characters of ovules and carpels are currently underutilized in phylogenetic studies. The current terminology for ovules appears to conceal characters (Bouman 1984) that may be of phylogenetic and evolutionary

significance. In contrast, the terminology for carpels is quite small. This both obscures differences in general carpel types as well as makes detailed comparisons between taxa difficult.

This study presents a character analysis of ovules and carpels. Such an analysis not only provides lists of useful characters for phylogenetic analysis, it also suggests hypotheses for structural homologies and ancestral characters states (Neff 1986, Bryant 1989). It is realized that this is only an initial list, as new characters will continue to be proposed. In addition, the characters are polarized by outgroup comparison, developmental transformation series, and association between characters from different organs as appropriate. Finally, the distribution of these character states is documented in the families at the base of the angiosperm phylogeny (Magnoliidae and basal orders of Hamamelidae, Caryophyllidae, Dilleniidae, Rosidae, Alismatidae [sensu Cronquist 1981], and Liliiflorae [sensu Dahlgren et al. 1985]).

These data and analyses are used to suggest two groups of hypotheses. The first hypotheses concern the structure of the ancestral ovules and carpels of angiosperms (based on the polarizations), whereas the second group deals with the structural evolution of ovules and carpels (based on the polarizations, and structural and developmental transformation series). Lastly, I speculate how these data affect our understanding of the hypothetical ancestral angiosperm and the most basally placed monocot.

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## Materials and Methods

A total of 77 families of angiosperms were examined in this study. These were chosen to represent and document the diversity of the major basal clades of angiosperms. Sixty-seven of these families were from dicot taxonomic groups circumscribed by Cronquist (1981), and include all the families of the Magnoliidae; the basal two orders of the Hamamelidae (Trochodendrales and

Hamamelidales); the basal two orders of the Caryophyllidae (Polygonales and Plumbaginales) with the addition of the putatively ancestral Phytolaccaceae, Molluginaceae and Caryophyllaceae of the Caryophyllales; the basal order of the Dilleniidae (Dilleniales), and the members of the basal order of the Rosidae (Rosales) which had crassinucellar ovules. Two potentially ancestral groups of monocots were also examined. The first is the ancestral order of Alismatidae (Alismatales), sensu Cronquist (1981), and the second group is the basal order Dioscoreales as defined by Dahlgren et al. (1985).

In addition, I examined a number of fossil and extant taxa that are thought to be the sister-group or otherwise cladistically close to angiosperms, based on the recent analyses by Crane (1985, 1988) and Doyle and Donoghue (1986, 1987). These taxa included Bennettitales, *Caytonia*, corystosperms, glossopterids, Gnetales and *Pentoxylon*.

Data compiled for the angiosperm families are found in the Appendices. General data, compiled from Cronquist (1981) and Davis (1966) are presented for each family. Under each family are entries for representative genera, using information available from the literature. Ovule characters were usually collected from medial sections taken at the embryo sac stage, in order to avoid variation (e.g., additional curvature) introduced during subsequent development of the seed. Carpel characters were obtained from both longitudinal and transverse sections of young carpels, when available.

The genera listed under each family document the extent of the variation of each character. In some cases, several genera in a family had identical suites of character states, and these states are represented by one genus in the Appendices. In addition, I attempted to secure data for both the ovules and carpels for the same genus.

To describe the ovules and carpels, additional characters and states were created when appropriate. Characters with quantitative measurements, such as ovule angle, were divided into character states

based on the natural breaks found in the data. No doubt further work will subdivide and more stringently define some of the characters and states used, especially those which are shown to have had multiple evolutionary origins. Additional characters are likely to be added, particularly those relating to developmental morphology.

Polarization was determined by: outgroup comparison (Watrous and Wheeler 1981); developmental transformation series (Nelson 1978; Crisci and Stuessy 1980; Kraus 1988); and association of character states from different organs (Crisci and Stuessy 1980). Detailed outgroup comparison, even in ovules where structural homologies to the outgroups exist, is difficult due to the variability in the outgroups and because the exact relationships of the outgroups to the angiosperms is not certain (Crane 1988).

Because of this variation in states, the outgroup ovule states for the angiosperm clade were determined by four methods and topologies. The first two were analyzed using the method of Maddison et al. (1984) for resolved cladograms. The first cladogram used was that of Crane (1985, fig. 22). It has Gnetales as the sister-group to angiosperms and a clade composed of Bennettitales and *Pentoxylon* as the next outgroup. This clade is followed sequentially, towards the base, by corystosperms, *Caytonia* and glossopterids. The second cladogram, from Doyle and Donoghue (1986), has the angiosperm sister-group composed of a clade with three taxa. These include Gnetales and *Pentoxylon* as terminal sister-groups and with Bennettitales as a sister-group to those; this clade is followed sequentially, towards the base, by *Caytonia* and glossopterids.

The last two methods were considered since the relationships of the outgroups are uncertain (Crane 1988). One method considered common as ancestral (from the six taxa in the cladogram of Crane 1985), which may be considered a legitimate method when relationships are unresolved (but see discussion in Maddison et al. 1984). The last method was that of de Queiroz (1987). This is essentially a modification of the outgroup

substitution method of Cantino (1982, Donoghue and Cantino 1984), and was developed for determining outgroup states when the outgroup relationships are unresolved. In this case it was based on the consensus cladogram of Crane (1988) which shows a polychotomy between Gnetales, Bennettitales, *Pentoxylon*, *Caytonia* and glossopterids.

Statistical tests for association between characters (Sporne 1977) are based on a Chi squared 2 by 2 and 2 by C contingency tests (Snedecor and Cochran 1967). In these comparisons only one monocot group (Dioscoreales) was used. The matrix of presence and absence of the states from the two characters was filled at the family level. Thus a family might have combinations of states not found in any single extant taxon. In addition, if the family had more than one character state, the occurrence was recorded in more than one place in the matrix.

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## Results

Ovules and carpels each have unique suites of characters that are treated in separate parts below. Each part is subdivided into three other categories: characters and states; character polarization; and distribution of ancestral states in basal angiosperms. The characters and states are discussed first, and this section is supplemented by tables defining the characters and states, and figures showing many of the states. Next is a discussion of character state polarity based on the methods discussed above. In the final section, the distributions of the states in the classification of Cronquist (1981) and the phylogeny of Donoghue and Doyle (1989) are examined.

## Ovules

Although the terminology dealing with ovules is extensive (see summaries of Maheshwari 1950; Bocquet and Bersier 1960), it has been noted that considerable morphological variability is included within single descriptive

**Table 1**

Definitions of ovule characters and states. Many of these states are illustrated in Figure 1.

**Ovule Morphology**

1. Relative position of the chalaza to the micropyle: 0 **opposite**, at the opposite or nearly opposite end from the micropyle end (e.g., Fig. 1A); 1 lateral, **distal**, laterally, midway to distally between the two ends of the ovule (e.g., Fig. 1G); 2 lateral, **proximal**, laterally, midway to beside the micropyle (e.g., Fig. 1D).
2. The angle between a line along the funiculus through the chalaza and a line from the micropyle through the embryo sac: 0 **orthoangle**, 0 to 5° (e.g., Fig. 1B); 1 **semiangle**, 6 to 89°; 2 **hemiangle**, 90 to 159° (e.g., Fig. 1A); 3 **ana-angle**, 160 to 200° (e.g., Fig. 1C); 4 **circumangle**, coiled greater than 200° (e.g., Fig. 1I).
3. Complete symmetry of all portions of ovule with a section through funiculus and embryo sac: 0 **symmetrical**, all portions symmetrical (e.g., Fig. 1B); 1 **asymmetrical**, some portions asymmetrical (e.g., Fig. 1C).
4. Levels of symmetry of section through funiculus and embryo sac: 0 **outer** symmetry, 2 or more integuments, nucellus and embryo sac symmetrical in size, shape and general orientation (e.g., Fig. 1B); 1 **inner** symmetry, only one integument, nucellus and embryo sac symmetrical in size, shape and general orientation (e.g., Fig. 1C); 2 **nucellar** symmetry, nucellus and embryo sac symmetrical in shape (e.g., Fig. 1F); 3 **sac** symmetry, embryo sac symmetrical in shape; 4 **lacking** symmetry, not symmetrical (e.g., Fig. 1E).
5. Relative position of attachment of nucellus to micropyle end: 0 **opposite**, at the opposite or nearly opposite end from the micropyle (e.g., Fig. 1A); 1 lateral, **distal**, extending to side of embryo sac near distal end; 2 lateral, **proximal**, extending to side of embryo sac near proximal (micropyle) end (e.g., Fig. 1D).

**Ovule Integument Morphology**

6. Continuity between the integument and funiculus: 0 **apo**, outermost integument equally free abaxially and adaxially, has no continuity with the funiculus (e.g., Fig. 1A); 1 **semi**, outermost integument unequally free with abaxial (outer) portion adjacent to the funiculus having 5 to 50% continuity with the funiculus; 2 **hemi**, outermost integument unequally free with abaxial (outer) portion adjacent to the funiculus having partial continuity which is greater than 50% with the funiculus (e.g., Fig. 1C); 3 **syn**, outermost integument unequally free with abaxial (outer) portion beside the funiculus having complete continuity with the funiculus, outer integument missing beside the funiculus (e.g., Fig. 1H).
7. Integument number: 0 **bitegmic**, nucellus surrounded by two integuments and the outer in-

tegument may be free or have continuity with the funiculus (e.g., Fig. 1A); 1 **unitegmic**, nucellus surrounded by one integument and the integument may be free or have continuity with the funiculus; 2 **ategmic**, nucellus not surrounded by any integuments, naked; 3 **multitegmic**, nucellus surrounded by three or more integuments and the outermost integument may be free or have continuity with the funiculus.

8. Integuments forming micropyle: 0 **inner**, only by inner, which may project past outer (e.g., Fig. 1A); 1 **both**, both form similar-sized pore (e.g., Fig. 1C); 2 **both zigzag**, both form similar-sized pore but the hole through the outer is displaced from the hole formed by the inner integument (e.g., Fig. 1D); 3 **outer**, only by outer, inner of shorter length.

**Nucellus Morphology**

9. Division of archesporial cell and layers above embryo sac: 0 **multiparietal**, division of the archesporial cell to produce a parietal cell that divides to form at least two layers; 1 **uniparietal**, division of the archesporial cell to produce a parietal cell that may form up to one layer, 2 **none**, no parietal cell.
10. Division of the nucellar epidermis to form layers above the embryo sac: 0 **multiepidermal**, division of the epidermis to produce more than one layer, forming a nucellar cap; 1 **uniepidermal**, division of the epidermis to produce only one layer, forming a nucellar cap; 2 **none**, no division of the epidermis.

terms (Bocquet 1959; Bocquet and Bersier 1960; Davis 1966; Bouman 1984). The following list of characters attempts to document the extensive variation in ovule morphology, particularly that masked by current terminology. In the future additional characters will undoubtedly be proposed, including a suite based on developmental traits (e.g., Bouman 1984).

**Characters and States** The characters and their states are summarized in Table 1. The characters can be assigned to one of the following suites of characters: general ovule morphology (characters 1–5), integument morphology (characters 6–8) and nucellar morphology (characters 9, 10).

General ovule morphology includes five characters that show: the position of the attachment of the chalaza and nucellus relative to the micropyle; the angle of the ovule relative to the funiculus; and the symmetry of the ovule and parts (Table 1). Character 1 shows the position of the chalaza attachment relative to the micropyle. This can vary from opposite (Fig. 1A), lateral, distal (Fig. 1G) to lateral, proximal (Fig. 1D). Character 2 records the angle between a line from the funiculus through the chalaza and a line from the micropyle through the embryo sac. The states are divided by the natural breaks recorded in ovule angles, and include orthoangle (Fig. 1B), semiangle, hemiangle (Fig. 1A), ana-angle (Fig. 1C) or circumangle (Fig. 1I).

Character 3 indicates the symmetry of the entire ovule and the states are symmetrical (Fig. 1B) or asymmetrical (Fig. 1C). The next character, 4, records the general symmetry of the various layers of the ovule and the states are outer symmetry (Fig. 1B), inner symmetry (Fig. 1C), nucellar symmetry (Fig. 1F), sac symmetry or lacking symmetry (Fig. 1E). Finally, character 5 indicates the position of the nucellar connection to the ovule relative to the micropyle. The states are opposite (Fig. 1A); lateral, distal; or lateral, proximal (Fig. 1D).

Thus an ovule considered in conventional terms to have campylotropous morphology (Fig. 1D, F) would have the chalaza attached proximal, have an ana-angle, and would have been asymmetrical overall with at least the embryo sac symmetrical. Yet the two could vary in the internal symmetry (sac or nucellar) and the nucellar attachment site (proximal or opposite).

There are three characters describing variation in integument morphology: continuity (a term of preference over fusion, Sattler 1978) between the integument and funiculus (character 6), integument number (character 7) and integumentary composition of the micropyle (character 8). The states of character 6 are given as prefixes to be attached to the term for integument number (character 7) and include: the states with the

outermost integument *apo*, totally free (Fig. 1A); *semi*, mostly free; *hemi*, mostly continuous (Fig. 1C); or *syn*, missing alongside the micropyle (Fig. 1H).

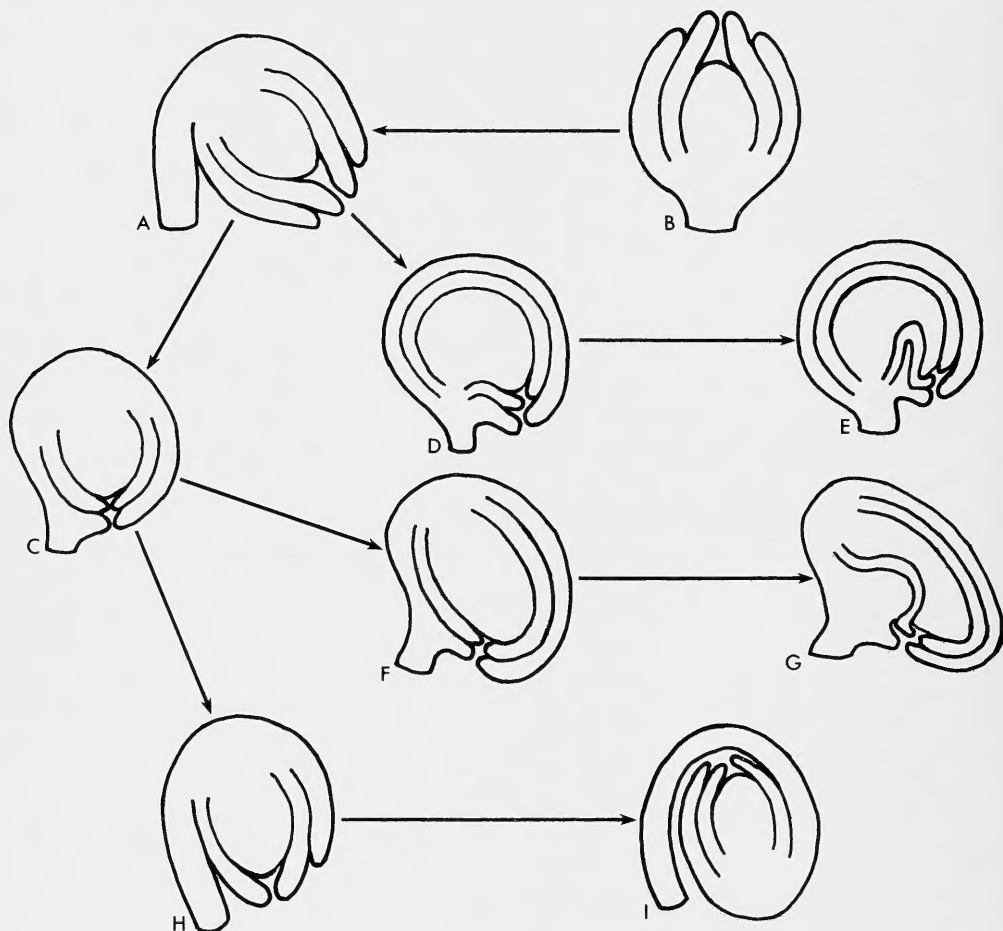
The integument number includes the commonly used bitegmic (Fig. 1A), unitegmic, ategmic or multitegmic states. Lastly, the micropyle may be formed by the inner integument (Fig. 1A), both integuments (Fig. 1C), both integuments arranged in a zigzag (Fig. 1D) and the outer integuments.

Thus an ovule considered to have anatropous morphology (Fig. 1C, H) with the existing terminology could have hemibitegmic morphology and a micropyle formed from both integuments (Fig. 1C) or synbitegmic morphology and a micropyle formed from the inner integument (Figure 1D).

The last two characters deal with nucellar morphology which indicate whether the archesporial cell divides and the number of cell layers it produces (character 9), and division and extent of cell layers derived from the nucellar epidermis (character 10). These distinctions have been discussed by Davis (1966). The states for the archesporial cell are multiparietal, uniparietal and none; and those for the nucellar epidermis are multiepidermal, uniepidermal and none.

**Character Polarization** The ovule character states were polarized with outgroup comparison (Watrous and Wheeler 1981). The distribution of character states was examined for the six outgroups (Table 2) determined by Crane (1985) and/or Doyle and Donoghue (1986, 1987). Most of these taxa have also previously been suggested to be the specific sister-group to angiosperms (see Stebbins 1974; Retallack and Dilcher 1981; Crane 1985; Doyle and Donoghue 1986).

For defining the morphology of the outgroups, I have accepted the recent interpretations that: Bennettitales and *Pentoxylon* are bitegmic (Crane 1985), there is a lack of fusion between the outer integument and funiculus in corytosperms (G. J. Retallack, personal communications 1988); and the outer envelopes of Gnetales ovules

**Fig. 1**

Diagrammatic representations of basic ovule types showing their evolutionary relationships based on the proposed ancestral character states and developmental transformation series. (See text for further discussion.) The ovule in B is considered ancestral. The specific character states (based on characters 1–8 and their codes in Table 1) for each ovule are A) 02000000; B) 00000000; C) 23110201; D) 23132002; E) 13142102; F) 23120201; G) 24140202; H) 23110300; I) 24110300. (D–G redrawn from Bocquet and Bersier 1960).

and outer integuments of angiosperms are not homologous (Crane 1985). In addition, a hypothetical bitegmic ovule, which would be considered homologous to angiosperms, was created for *Caytonia* (Doyle and Donoghue 1986), glossopterids (Retallack and Dilcher 1981) and Gnetales. These are coded under the respective taxa as “hypothetical” (Table 2).

The polarization is complicated because there is some variability in states between these taxa, and the relationships of the outgroups to angiosperms are equivocal. Two recent cladistic analyses (Crane 1985, Doyle and Donoghue 1986) did not produce the same topology (Crane 1988) and the topology of trees with the same length or several steps longer suggest that any of these outgroup

**Table 2**

Distribution of ovule states in fossil and extant outgroups. ? = no data. Abbreviations for each character: character 1, attachment of chazala: *opp* = opposite, *prox* = proximal; character 2, angle: *ana* = ana-angle, *hemi* = hemiangle, *ortho* = orthoangle, *semi* = semiangle; character 3, complete symmetry: *asym* = asymmetrical, *sym* = symmetrical; character 4, levels of symmetry: *inner* = inner symmetry, *outer* = outer symmetry; character 5, attachment of nucellus: *opp* = opposite; characters 6,7, continuity of integument and funiculus, and integument number: *apobi* = apobitegmic, *apouni* = apounitegmic, *synbi* = synbitegmic; character 8, micropyle: *both* = both, *inner* = inner; character 9, division of archesporial cell: *multi* or *mult* = multiparietal; character 10, division of nucellar epidermis: *multi* = multiepidermal, *none* = none.

TAXON	GENERAL OVULE MORPHOLOGY					INTEGUMENT MORPHOLOGY		NUCELLAR MORPHOLOGY		REF.
	1	2	3	4	5	6, 7	8	9	10	
Bennettitales	opp	ortho-semi	sym	outer	opp	apobi	inner	multi	?multi	1, 2
<i>Caytonia</i>	opp	ortho	sym	inner	opp	apouni	inner	?	?	3
—hypothetical	prox	ana	asym	inner	opp	synbi	both	?	?	
corystosperms	opp	hemi	sym	outer	opp	apobi	inner	?	?	4, 5
glossopterids	opp	ortho	sym	inner	opp	apouni	inner	multi	?none	6
—hypothetical	opp	ortho	sym	outer	opp	apobi	both	multi	?none	
Gnetales	opp	ortho	sym	inner	opp	apouni	inner	multi	multi	7
—hypothetical	opp	ortho	sym	outer	opp	apobi	inner	multi	multi	
<i>Pentoxylon</i>	opp	ortho-semi	sym	outer	opp	apobi	inner	?multi	?	1

1. Crane 1985; 2. Crepet 1974; 3. Doyle and Donoghue 1986; 4. Thomas 1933; 5. Retallack, personal communication, 1988; 6. Gould and Delevoryas 1977; 7. Takaso and Bouman 1986.

taxa could be the sister-group. Because of this variability I determined the ancestral state for the internode below the angiosperms using the four methods described in the Materials and Methods section above. In all four of these polarizations I also separately examined the empirical codings and hypothetical codings (Table 3).

For most characters, these four polarizations produced the same results (Table 3). Characters 1–3, 5, 6 and 9 are all polarized the same, suggesting the ancestral ovule had the following character states: chalaza opposite the micropyle; an orthoangle (less than 5°; total symmetry (based on a section through the funiculus and embryo sac); the nucellus attached opposite the micropyle; the outermost integument equally free; and a multiparietal nucellar morphology (Fig. 1B). If one uses current terminology only orthotropous (Fig. 1B) ovules have such a morphology.

Character 4 refers to the symmetry of the various layers of the ovule. Empirical coding is either outer or inner symmetry, and hypothetical coding denotes outer symmetry. This equivocal polarization is an artifact

because unitegmic ovules cannot have outer symmetry.

The plesiomorphic state of character 7 is either unitegmic or bitegmic (empirical coding) or bitegmic alone (hypothetical coding). Until recently (Les 1988), no one has seriously suggested that the unitegmic condition was ancestral (e.g., Bocquet and Bersier 1960; Cronquist 1968, 1988; Takhtajan 1969, 1980). This is based both on the distribution of the state in the angiosperms (ingroup commonality) and the developmental transformation series that shows that the unitegmic state arose independently in several lineages (Maheshwari 1950; Bouman 1984). Due to these different justifications, I consider the bitegmic state as ancestral. Therefore the ancestral state for character 4 is outer and for character 7 is bitegmic.

In character 8, the condition where the inner integument forms the micropyle is ancestral in all the polarizations except the topology of Doyle and Donoghue (1986) and the topology of Crane (1988) with the hypothetical coding. Since only the inner integument can form the micropyle in unitegmic ovules and the inner integument

**Table 3**

The ancestral carpel states based on four methods and topologies (see Materials and Methods section) using the documented empirical (*e*) and hypothetical (*h*) states. (See text for further discussion.) *A* Based on the topology of Crane (1985). *B* Based on the topology of Doyle and Donoghue (1986). *C* Based on the taxa in Crane (1985). *D* Based on the topology of Crane (1988). ? = equivocal polarization between two states; I = insufficient data for method.

		CHARACTERS									
		1	2	3	4	5	6	7	8	9	10
<i>A</i>	<i>e</i>	0	0	0	?	0	0	?	0	0	0
	<i>h</i>	0	0	0	0	0	0	0	0	0	0
<i>B</i>	<i>e</i>	0	0	0	?	0	0	?	0	0	0
	<i>h</i>	0	0	0	0	0	0	0	?	0	0
<i>C</i>	<i>e</i>	0	0	0	?	0	0	?	0	0	0
	<i>h</i>	0	0	0	0	0	0	0	0	0	0
<i>D</i>	<i>e</i>	0	0	0	?	0	0	?	0	I	I
	<i>h</i>	0	0	0	0	0	0	?	I	I	I

forms the micropyle in all known bitegmic outgroups (Bennettiales, corystosperms and *Pentoxylon*), this state will be accepted as ancestral.

Lastly, there is little data on the division of the nucellar epidermis (character 10). Examination of bennettitalean ovules (Crepet 1974) and data from the literature on Gnetales (e.g., Takaso and Bouman 1986) suggest that there is a division to form at least one layer and thus is ancestral.

**Discussion of Polarization.** Authors have previously used other data to polarize angiosperm states. Presently the literature is in conflict about which type, anatropous or orthotropous, is ancestral for angiosperms. In general, angiosperm phylogenists (e.g., Cronquist 1968, 1988; Takhtajan 1969, 1980; Crane 1985; Doyle and Donoghue 1986) have concluded that anatropous is ancestral, based in its occurrence in putatively ancestral angiosperm taxa (Magnoliales) and its common distribution in all angiosperms (Davis 1966). This conflicts with the common view of ovule morphologists (e.g., see reviews in Takhtajan 1980 and Bor 1978) who believe that the orthotropous ovule is ancestral based on development.

A dissenting morphological view is that of Bor (1978) who points out that the angle of the anatropous ovules is not due to the bending followed by fusion of an orthotropous ovule. The angle of an anatropous ovule is initiated by the formation of the integuments on one side of the ovule primordium. Actually, there are three related processes: change in the placement of the chalaza from an opposite position to proximal position with the concurrent formation of a raphe; an increase of the continuation between the funiculus and the outermost integument; and an increase of the angle to approximately 180°. The question is whether or not there are similarities in the developmental programs of the two ovule types which show transformations from one type to the other.

Similar developmental transformation series can be found in ovules of Chloranthaceae (Vijayaraghavan 1964), Molluginaceae (Narayana and Lodha 1963) and Potamogetonaceae (Takaso and Bouman 1984). They all have initiation of the ovule terminally on the ovule primordium yet the ovules in the latter two families become curved, at different stages of development. The ovules at the embryo sac stage of development in Potamogetonaceae have a semiangle and are apobitegmic, whereas the ovules in Molluginaceae have an ana-angle and are hemibitegmic. Thus the three ovules share the same early developmental transformation stages, but the latter two have additional stages to those found in Chloranthaceae.

Based on these data, orthotropous type ovules, as found in Chloranthaceae, are ancestral if no neoteny or other shifts in developmental timing have occurred. It also appears that ovules with distal chalazas and semi- to hemicontinuation are more similar to orthotropous ovules than those with proximal attachment and syncontinuation.

Further evidence is found in species of the families Barclayaceae, Lardizabalaceae and Platanaceae. In these families, the ovules in a single carpel have angles ranging from ortho to semi, and at least in Platanaceae the attachment is opposite to distal (personal

observation). Thus developmental data is compatible with the polarizations from outgroup comparison.

In conclusion, an ovule with opposite relative position of the chalaza, orthoangle, total and outer symmetry of ovule, an opposite relative position of the nucellar attachment, apobitegmic integuments, inner integument micropyle and multiparietal nucellus (Fig. 1B) is ancestral for angiosperms. These states are found in some bitegmic ovules of Bennettitales and *Pentoxylon*.

### Character States in Basal

**Angiosperms** The distributions of ovule character states are shown by representative genera for each family (Appendix 1). Many of the major clades of basal angiosperms have families with the ancestral states mentioned above. In Magnoliidae, six families from four orders (Amborellaceae, Chloranthaceae, Saururaceae, Piperaceae, Barclayaceae and Lardizabalaceae) have the ancestral states. These states are also found in two families of basal Hamamelidae (Platanaceae, Hamamelidaceae). Ancestral states are found in the order Polygonales Caryophyllidae (Polygonaceae) and nearly all of these states are found in Crassulaceae (Rosidae). Although none of the taxa in Dilleniales (Dilleniidae) have the ancestral states, some members of the closely related Flacourtiaceae (Hickey and Wolfe 1975) have them. Lastly, two families (Stemonaceae and Smilacaceae) from the basal monocots examined have taxa with the ancestral state.

The distribution suggests that ancestral character states are found in most clades but are rarely common. If the distributions of these states are plotted on the cladogram of Donoghue and Doyle (1989) a similar result is obtained with the ancestral states found scattered in a number of clades. Both these distributions suggest that either the polarization is fundamentally incorrect or that the most common character states (basically anatropous morphology) are homoplasous and have evolved multiple times.

### Carpels

Unlike the relatively well-defined characters for ovules, only general morphological types of carpel have been defined (see Leinfellner 1950; Bailey and Swamy 1951; Weberling 1981; van Heel 1981). Some problems arise because even the definition of the carpel itself is in dispute (Sattler 1974; Sattler and Perlin 1982). In some configurations carpels have ovules attached to a gynoeical appendage (Sattler 1974), while in others they are attached in a cauline or axillary position (e.g., Moeliono 1970; Sattler and Lacroix 1988). In this study a carpel is considered as a gynoeical "appendage which encloses ovule(s)" (Sattler and Perlin 1982) which may have the ovules attached to the appendage, or in a cauline or axillary position to it. The list of characters documents some of the variation that exists in carpel morphology. Again, it is likely that developmental characters will be important for future descriptions (van Heel 1981, 1983, 1984).

**Characters and States** The characters that describe carpels can be divided into two suites (Table 4; Fig. 2): general carpel morphology and anatomy; and ovule placement. The former includes a character for carpel morphology (character 11) and one for anatomy (character 12).

The character for carpel morphology (character 11) uses terms that are in general usage, but I define them in a topological manner so that they can usually be identified without developmental data. The terms refer to the actual developmental closure of the carpel and not to a hypothetical evolutionary suture. It should be noted that developmental data are a preferable adjunct since redifferentiation of epidermal cells in the carpel has been well documented (e.g., Siegel and Verbeke 1989).

There are six character states for carpel morphology. The first is ascidate, in which the ovules are attached proximal to the closure (Fig. 2A-C, I-L). The second is ascoplicate, in which some ovules are attached proximal and some adjacent to the closure (Fig. 2F, G). The

**Table 4**

Definition of carpel characters and states. Most states illustrated in Figure 2.

**General Carpel Morphology and Anatomy**

11. Carpel morphology: 0 **ascidate**, placenta of the ovule(s) attached proximal to the closure of the carpel either on the gynoeceal appendage, axillary or terminally (e.g., Fig. 2A); 1 **ascoplicate**, placentae of some of the ovules are proximal to the closure of the carpel and some are adjacent to the closure of the carpel (e.g., Fig. 2F); 2 **plicate A**, placentae of the ovule(s) attached adjacent to the closure of the carpel and on the gynoeceal appendage, but the base below the attachment of the ovules is ascidate (Fig. 4G); 3 **plicate B**, placentae of the ovule(s) attached adjacent to the closure of the carpel and on the gynoeceal appendage and closure reaches base of carpel (Fig. 2H); 4 ascidate, **notched**, as in ascidate, but in which the outer portion of the carpel has a notch in the admedial (ventral) surface that does not penetrate the locule at the level of the attachment of the ovules (e.g., Fig. 2E); 5 ascidate, **split**, as in ascidate, but in which the proximal part of the placenta is split and the two parts thereby formed are contiguous with the base and margins of the closure. (Thus the placenta could be considered proximal to the closure or marginal at the base of the closure; e.g., Fig. 2D.)
12. Vasculature to the ovule(s): 0 **one trace**, one (usually ventral) trace in the base of the carpel, from which the ovular trace(s) originate. (The one trace state includes the situation in which the trace branches and each branch extends to an ovule.); 1 **two trace**, two (usually ventral) traces in the base of the carpel from which the ovular traces originate; 2 **multiple trace**, more than two traces in the base of the carpel from which the ovular traces originate; 3 **residual trace**, the remains of the receptacular stele goes directly to a single ovule.

**Ovule Attachment**

13. Position of attachment of the placentae in the carpel: 0 **basal**, at or near the base of the locule or near the attachment of the carpel to the receptacle (e.g., Fig. 2C); 1 **apical**, at or near the apex of the locule (e.g., Fig. 2A); 2 lateral, **marginally**, along the lateral margins or sub-margins of the closure of the carpel (e.g., Fig. 2H); 3 lateral, **admedially**, not along the closure, but towards the central axis of the flower or inflorescence (e.g., Fig. 2B); 4 lateral, **exmedially**, not along the closure, but opposite closure or away from the central axis of the flower or inflorescence (e.g., Fig. 2I); 5 lateral, **radial**, not along the margin, but along the radial walls (e.g., Fig. 2J); 6 **chaotic**, arranged in an apparently random manner in the carpel (Fig. 2K).
14. Ovular orientation with respect to the plane of

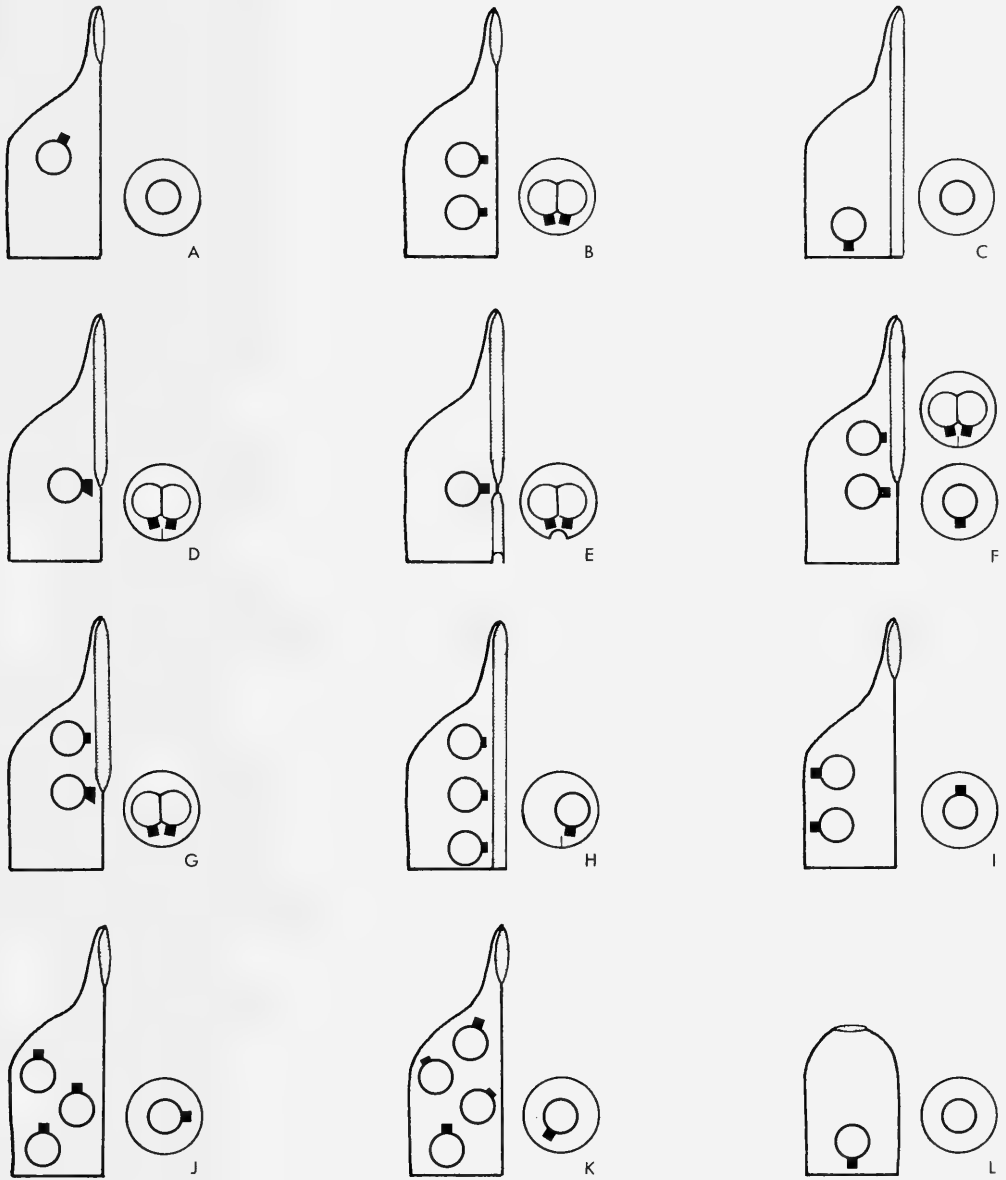
symmetry of the carpel. The plane of symmetry is a radial plane originating from the central axis of the flower or inflorescence that evenly bisects the carpel, usually along the closure of the carpel or the pollen-tube conducting tissue. If the carpel is terminal, the plane is the one that evenly bisects the carpel and dissects the lateral closure of the carpel: 0 **planar**, ovule attached in the plane (Fig. 2A); 1 **nonplanar**, ovule not attached in the plane (Fig. 2B); 2 **planeless**, this occurs when the carpel is terminal, has no lateral closure and is radially symmetrical so no single plane is possible (Fig. 2L).

15. Number and arrangement of ovules: 0 **single**, ovule one (e.g., Fig. 2A); 1 **double, alternate**, ovules two, at different levels; 2 **double, opposite**, ovules two, paired at the same level (e.g., Fig. 2D); 3 **few, alternate**, ovule 3 to 6, at different levels (e.g., Fig. 2H); 4 **few, opposite**, ovules 3 to 6, pairs of ovules at the same level (e.g., Fig. 2B); 5 **few, clustered**, ovules 3 to 6, ovules at the same level; 6 **many, alternate**, ovules more than 6, at different levels (e.g., Fig. 2K); 7 **many, opposite**, ovules more than 6, pairs of ovules at the same level; 8 **many, clustered**, ovules more than 6, ovules at the same level.

next two are plicate or conduplicate: plicate A has the ovules attached adjacent to the closure, but the base of the carpel below the closure is ascidate or cup-shaped (Fig. 4G); plicate B has a form similar to plicate A, but the closure extends to the base of the carpel (Fig. 2H).

The last two states are special cases of ascidate: ascidate, notched and ascidate, split. In the first the ovules are attached proximal to the closure yet having a notch on the admedial surface which does not penetrate the locule at the level of ovule attachment (Fig. 2E). In ascidate, split, the proximal part of the placenta is split and the two parts formed are contiguous with the base of the closure (Fig. 2D).

The character for vasculature to the ovule(s) has four states and refers to the number of traces at the carpel base. The trace states may be one, two, multiple or residual. In this last state, the remains of a receptacular stele extend into a single ovule.



**Fig. 2**  
 Diagrammatic representations of basic carpel types showing most of the morphological, ovule attachment, ovule orientation, and ovule number and arrangement character states. The shading shows the closure, the portion of the carpel that closes during ontogeny. The diagrammatic cross-sections of the carpels are oriented so that the right side of the longitudinal section is down. Specific character states (based on characters 11, 13–15 and their codes in Table 4) are A) 0100; B) 0314; C) 0000; D) 5312; E) 4312; F) 13(lower) 2(upper) 0(lower) 2(upper)4; G) 13(lower) 2(upper)14; H) 3213; I) 0401; J) 0516; K) 0616; L) 0020.

The second suite of characters includes: the position of ovule attachment in the carpel (character 13); the orientation of the ovule in respect to the plane of carpel symmetry (character 14); and the number and arrangement of the ovules to each other (character 15). The character states for position of attachment including three previously described states (e.g., Cronquist 1988): basal (Fig. 2C), apical (Fig. 2A), and lateral, marginal, which is along the closure (Fig. 2H). Additional states include lateral, admedial which is not along the closure but towards the central axis of the flower (Fig. 2B); lateral, exmedial which is away from the central axis of the flower (Fig. 2I); lateral, radial which is along the radial walls (Fig. 2J) and chaotic which is in an apparently random manner in the carpel (Fig. 2A).

The states for the character of ovule orientation in respect to plane of symmetry are as follows: planar, in the plane (Fig. 2A); nonplanar, out of the plane (Fig. 2B); and planeless, for carpels with a terminal ovule and radial symmetry (Fig. 2L).

The last character, number and arrangement of ovules, has nine states. These states are: single, double and alternate; double and opposite; few and alternate; few and opposite; few and clustered; many and alternate; many and opposite; and many and clustered. These states are based on numbers enclosing natural modes in the taxa studied.

Based on this character suite, an ascidate carpel may have the ovules attached: apically and planar (Fig. 2A); lateral; admedially and nonplanar (Fig. 2B); radially and nonplanar (Fig. 2J) or basally and aplanar (Figure 2L). Plicate carpels are usually marginal and nonplanar (Fig. 2H). Ascoplicate carpels have a mixture of a number of states, with the lower ovule(s) admedial and planar (Fig. 2F) or admedial and nonplanar (Fig. 2G); and the upper ovule(s) marginal.

**Character Polarization** Polarization to identify the ancestral carpel states is difficult due to the uncertain homologies between angiosperm carpels and reproductive organs

of related taxa. Thus it is not possible to use outgroup comparison, as knowledge of such structural homologies is needed. As a result, several secondary and less reliable methods were used to polarize the carpel characters. The potential problems with character association (e.g., Stebbins 1974; Crisci and Stuessy 1980) and developmental transformation series (e.g., Kraus 1988) are realized and the results should not be considered as robust as those from the ovule analysis.

In the sections below, I discuss the polarity of carpel characters based on: 1) association of characters and 2) developmental morphology and transformation series. In the first analysis, the frequency of six polarized ovule characters were examined to see if they were correlated with carpel characters. These characters include: position of funicular attachment; angle of ovule to funiculus; symmetry of the entire ovule; position of nucellar attachment; degree of continuation of the outermost integument; and division of the archesporial cell to form a parietal cell. The ovule characters were chosen because they were unequivocally polarized with outgroup comparison (see above).

The mode of micropyle formation was not included in the comparison since it did not appear to be independent from other characters. First, all unitegmic ovules must necessarily have this state. In addition, there is a significant correlation between both apo and syncontinuation to inner integument (Table 5). The correlation to syncontinuation occurs since the micropyle cannot be formed by the outer integument, because a portion of the outer integument is missing along the funiculus. A few synbitemgmic ovules are exceptions and have the micropyle formed by both integuments and the funiculus (e.g., Magnoliaceae).

Two carpel characters were chosen: general carpel morphology and number of ovules in each carpel. These were chosen because they contrast the two major hypotheses of the carpel composition: that the carpel is composed of a sterile gynoeceal appendage and a fertile meristematic region

usually in the axillary or cauline position (an ascidate carpel usually with one or two ovules; e.g., Moeliono 1970) or is a megasporophyll, basically a fertile leaf with a conduplicate or peltate structure (a plicate carpel usually with few or many ovules). The conduplicate carpel is considered to be similar to a folded vegetative leaf, without an adaxial meristem, whereas the peltate carpel is similar to a peltate leaf having an adaxial meristem (or cross-zone). To examine these hypotheses, the frequencies of the ascoplicate, plicate A and plicate B carpel character states were combined and contrasted with the combined ascidate states. In addition, the frequencies of the families with "few" and "many" ovules states were combined to contrast with the combined "single" and "double" states.

The initial comparison between the ancestral ovule states and the carpel states (Table 6) shows that in most comparisons a higher percentage of ancestral ovule states are found in ascidate carpels and carpels with low numbers of ovules than are found in ascoplicate or plicate carpels and carpels with few or many ovules. Only two states, opposite attachment of the nucellus and existence of a parietal cell, were found more often in the carpels with more than two ovules though only by a few percent. These observations suggest that ascidate carpels with one or two ovules may be ancestral.

The levels of significance of these correlations were examined (Table 6). Ten of the correlations between ascidate and one or two ovules were positively, though not significantly, correlated with ovule state. Only two (opposite attachment of nucellus and existence of parietal cell) were negatively correlated (Table 6), though these had the smallest Chi squared values. This suite of generally positive correlations to the ancestral ovule states again suggests that the ancestral states may have been ascidate and had one or two ovules.

In addition, several highly significant ingroup correlations were found. Ascidate morphology was significantly correlated to carpels with one or two ovules, whereas ascoplicate and plicate morphology were

**Table 5**

Statistical analysis of the correlation within ovules for the families in Appendix 1 excluding Alismatales. Comparison between continuation and micropyle type in bitegmic ovules.

	APOBITEGMIC	HEMIBITEGMIC	SYNBITEGMIC
Inner	10 (62%)	16 (47%)	25 (78%)
Both	6 (38%)	18 (53%)	7 (23%)
	0.01 > p > 0.005		

significantly correlated to those with greater than two ovules (Table 7A). These data provide evidence that the ascidate carpels with one or two ovules are real entities, and the data in the Appendices show that ascidate carpels with high numbers of ovules are rare.

The frequency of combinations of basic carpel states within families was also examined (Table 7B). Each family was examined to see what type of carpel morphology was found and whether there was only one type, referred to as *alone* or were several types (in combination). The highly significant results show that the families with ascidate carpels are most likely to have only ascidate morphology. In contrast, families with ascoplicate carpels are almost always found in combination with either ascidate or plicate morphology. Lastly, plicate carpels are found alone in only half the families with this carpel type, whereas in other families they are associated with other morphologies. These results are again consistent with the notion that the ascidate morphology is ancestral.

Another potentially useful method of polarizing characters is the use of developmental transformation series based on developmental morphology (Nelson 1978; Crisci and Stuessy 1980; Kraus 1988), though there are obvious limitations to this method. The fundamental questions are: do carpels with different morphologies share developmental stages and are developmental transformation series found between types?

Fortunately, the growing number of studies of carpel development provides a preliminary understanding of the developmental stages of

**Table 6**

Statistical analysis of the correlation between polarized ancestral ovule characters and select carpel characters (morphology and ovule number) for the families in Appendix 1 and 2 excluding Alismatales. *A* Position of attachment of funiculus. *B* Angle of ovule to funiculus. *C* Symmetry of the entire ovule. *D* Position of attachment of nucellus. *E* Continuation of outermost integument. *F* Formation and division of parietal cell.

<i>A</i>	opposite	other		opposite	other
ascidate	10 (71%)	49 (58%)	1 or 2 ovules	9 (56%)	48 (44%)
nonascidate	4 (29%)	36 (42%)	>2 ovules	7 (44%)	62 (56%)
	0.50 > p > 0.25			0.50 > p > 0.25	
<i>B</i>	orthoangle	other		orthoangle	other
ascidate	10 (67%)	49 (58%)	1 or 2 ovules	9 (53%)	48 (44%)
nonascidate	5 (33%)	35 (42%)	>2 ovules	8 (47%)	61 (56%)
	0.75 > p > 0.50			0.50 > p > 0.25	
<i>C</i>	symmetrical	other		symmetrical	other
ascidate	10 (63%)	49 (59%)	1 or 2 ovules	9 (56%)	48 (44%)
nonascidate	6 (37%)	34 (41%)	>2 ovules	7 (44%)	62 (56%)
	0.75 > p > 0.50			0.50 > p > 0.25	
<i>D</i>	opposite	other		opposite	other
ascidate	54 (61%)	5 (50%)	1 or 2 ovules	50 (45%)	7 (47%)
nonascidate	35 (39%)	5 (50%)	>2 ovules	61 (55%)	8 (53%)
	0.75 > p > 0.50			p > 0.90	
<i>E</i>	apo	other		apo	other
ascidate	14 (70%)	45 (57%)	1 or 2 ovules	14 (61%)	43 (42%)
nonascidate	6 (30%)	34 (43%)	>2 ovules	9 (39%)	60 (58%)
	0.50 > p > 0.25			0.25 > p > 0.10	
<i>F</i>	parietal	no parietal		parietal	no parietal
ascidate	48 (58%)	4 (40%)	1 or 2 ovules	49 (43%)	5 (42%)
nonascidate	35 (42%)	6 (60%)	>2 ovules	64 (57%)	7 (58%)
	0.50 > p > 0.25			p > 0.90	

the various carpel types (e.g., van Heel 1981, 1983, 1984; Endress 1972; Erbar 1983; Tucker 1959, 1981; Tucker and Gifford 1966). Some carpels have a U-shaped primordium with a meristematic area that produces the ovules either within or between the tips of the primordium (Fig. 3Aa). The mature carpels that

develop have an ascidate morphology (e.g., Fig. 3Ab) with basal to apical attachment. (The latter placentation occurs when the carpels are laterally attached to an elongate receptacle.)

The second, and apparently most common type of primordium, has the shape of a

**Table 7**

Statistical analysis of the correlation within carpels for the families in Appendix 1 and 2 excluding Alismatales. *A* A selected pair of carpel characters (morphology and number of ovules). *B* Between carpel morphology and whether they are found alone or in combination within families.

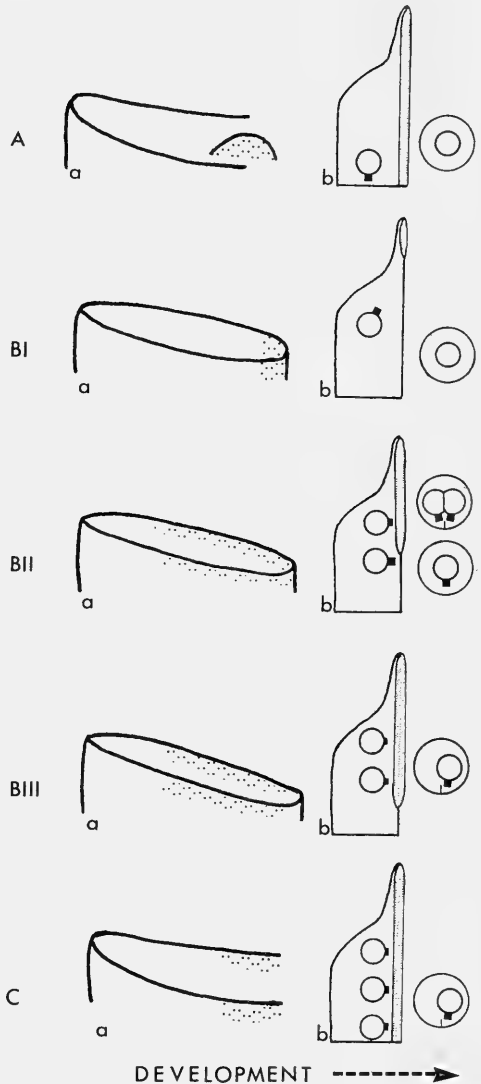
<i>A</i>	ascidate	ascoplicate	plicate
1 or 2 ovules	49 (77%)	4 (27%)	6 (21%)
>2 ovules	15 (23%)	11 (73%)	23 (79%)
		p < 0.005	
<i>B</i>	ascidate	ascoplicate	plicate
Alone	40 (74%)	1 (8%)	14 (54%)
In combination	14 (26%)	12 (92%)	12 (46%)
		p < 0.005	

circular or elliptical cup (Fig. 3Bl, II, III) and variable placement of the placental regions. Some have the meristematic area that produces the ovules confined to the admedial end that is toward the floral apex (Fig. 3Bl a). Others have the meristematic area both at the admedial end and along portions of the rim of the cup (Fig. 3BlI a). Finally, the remainder apparently have the meristematic area only along the rim (Fig. 3BlII a).

The mature carpels developing from the first type, with the meristematic area only at the end (Fig. 3Bl a), are similar to those seen in Figure 3Bl b. Primordia with the fertile areas on the admedial end and the rim (Fig. 3BlI a) produce carpels of two types. One type has a distal closure and a period of intercalary growth producing a mature carpel with an ascidate morphology similar to Figure 2J and K; in addition, some of the ovules would have an admedial placement. The other type has an ascoplicate morphology (Fig. 3BlI b; Fig. 2G). Finally, primordia with the fertile area restricted to the rim (Fig. 3BlII a) mostly produce carpels with a plicate A type morphology (e.g., Fig. 3BlII b). If there is a distal closure and intercalary growth, they may have an ascidate morphology similar to Figure 2I, J, K, but the ovules will not be admedially placed.

The final type has a U-shaped primordium with the fertile region along the margins of the closure (Fig. 3Ca). The mature carpel would have a plicate B type morphology (Fig. 3Cb). It is actually unclear whether this type exists as many plicate carpels have a cross-zone (e.g., van Heel 1981; Erbar 1983; Tucker and Gifford 1966). Such a cross-zone may be reduced to a few cells (Tucker and Gifford 1966) and may not be recognizable. Plicate B carpels are apparently found in Canellaceae, Saururaceae, Ranunculaceae, Lardizabalaceae, Paeoniaceae, and Trilliaceae.

**Carpel Transformations.** In all these types, the greatest development of the carpel primordium occurs on the portion distal to the center of the apical meristem (except, perhaps, *Cercidiphyllum*, but see van Heel 1987). In later development the separate



**Fig. 3**

Comparison of the types of carpel primordia (a) and representative mature morphologies (b). In the former (a) the shading shows the region of the primordium from which the ovules develop, whereas in the latter (b), it shows the closure, the portion of the carpel that closes during ontogeny. The diagrammatic cross-sections of the carpels are oriented so that the right side of the longitudinal section is down. Based on developmental transformation series, Type A has evolved into Type B and ultimately to Type C. (See text for further discussion.)

meristem or the cup fully develops. The few studies that have compared development of these types suggest that they also all share a separate meristematic origin of the gynoeceal appendage and the ovules (e.g., Hagerup 1934, 1936, 1938). Thus Type A is the simplest as seen in *Illicium* (Robertson and Tucker 1979). Type B1 is an elaboration of Type A with the connation of the gynoeceal and ovule meristems (see Leins 1972 and Sattler 1974, 1978 for the developmental basis of connation and adnation between floral parts) which results in a gynoeceum such as that in Chloranthaceae (as figured by Endress 1987).

Type BII has the same developmental steps as B1 with the additional stage of extension of the ovule meristem along the closure as can be seen in a number of genera in Ranunculaceae (van Heel 1981). Type BIII is developmentally identical to BII (e.g., Swamy 1949), except for the inability to produce ovules medially, though the cross-zone still exists.

Finally, Type C appears to be the total integration of the two meristems with the inhibition of the medial portion of the cross-zone, though it is impossible to tell from the current data whether its cell division completely ceases or whether a few cells are produced (e.g., Tucker 1981). The similarity of the Types A and B and the proposed developmental transformation series would support the hypothesis that ascidate carpels are ancestral.

If this is correct, one might expect to find phylogenetic examples of this developmental transformation series. Ideally, they should exhibit a basic transformation (Fig. 3) from the Type A developmental pattern to the Type C pattern (Hagerup 1934, 1936, 1938, though I disagree with the comparisons to gymnosperms). Unfortunately, independent analyses of the relationships of the taxa are tentative and only potential phylogenetic evidence for portions of this transition series exists, based on the variability of certain families.

For example, van Heel's (1981) work on Ranunculaceae shows examples of the B1 type, which produces a mature ascidate

morphology, as well as carpels of the BII type, which produces an ascoplicate morphology. In addition, some of the taxa have carpels of the BIII type with a mature plicate A morphology.

Study of *Drimys winteri* shows that the mature carpel is ascoplicate with two rows of ovules (Tucker 1959). The primordium is the BII type, but the origin of the submarginal region that makes the fertile portion of the rim may be from the subapical initial (which forms the gynoeceal appendage) and the adaxial initials or both. The primordium can be considered transitional between type BII and type BIII because the ovules originate from the submarginal region and the portion of the submarginal region produced on the admedial side of the carpel may originate from the adaxial initials. Also of interest is the observation that the plicate A carpel of *Drimys lanceolata* has poorly defined meristematic regions along the rim and in a very restricted portion of the admedial side (Tucker and Gifford 1966). This could be considered to be an example of how the transition between Type BIII and Type C would occur.

Finally, the fertile region of the Type C primordium has been suggested to have originated from a distal (adaxial) meristem (Hagerup 1938). *Acer* has a syncarpous, bicarpellate ovary with parietal placentation. The carpels have plicate B morphology and Type C development. Hagerup (1938) has suggested, based on detailed ontogenetic work, that the placentae originate from a portion of the floral meristem adaxial to, or more terminal than, the gynoeceal appendage. If this were indeed so, and even Hagerup considers it equivocal, it would indicate that carpels with Type C development have two separate meristems, one for the gynoeceal appendage and one for the placentae. These meristems would be directly homologous to those found in other developmental types.

**Discussion of Polarization.** The preliminary evidence suggests that ascidate carpels with one or two ovules are ancestral. This contrasts to the current hypotheses that indicate that plicate carpels with many, marginally-placed ovules are basic. In either case, the adaxial (admedially placed)

placental meristem of a carpel with a sterile gynoecial appendage is structurally homologous with the adaxial (admedially placed) cross-zone of a plicate carpel, and with the adaxial (admedially placed) meristem that produces the marginal placentae of a conduplicate carpel.

This understanding of the developmental morphology does away with the concept of "congenital fusion" and replaces it with the concept that the formation of many ascidate and conduplicate carpels is due to the integration of the two meristematic areas. This concept of integration of meristems (see Sattler 1974, 1978) has been already documented for other floral organs (e.g., Leins 1972, Sattler 1974, 1978).

Although there appear to be examples of the developmental transformation between carpel primordia types, the direction of the series can be disputed. Is Type A or Type C ancestral? The distribution of the types in the ancestral angiosperms is informative. Type C primordium has only been found in a few taxa thus far; Type A and Type B1 are found throughout the basal angiosperms. In addition, ascidate carpels are more commonly found alone in families as opposed to the ascoplicate and plicate morphologies (Table 7). These distributions are at least suggestive that A or B1 is ancestral. Both Type A and Type B1 produce mature carpels with ascidate morphology and usually low numbers of ovules. Based on these observations, a carpel having ascidate morphology and one or two ovules can be considered ancestral and all ascoplicate and plicate carpels derived. This hypothesized polarity is suggestive but should be corroborated with further work.

### Character States in Basal

**Angiosperms** The distributional data on the carpel states are compiled in Appendix 2. The ancestral states of ascidate morphology and single or double ovules are common in Magnoliidae, Caryophyllidae, Rosidae and Dioscoreales. These states are also found somewhat less commonly in Hamamelidae, Dilleniaceae and Alismatales.

These data show that the proposed

ancestral carpel states are commonly found in every basal clade. Thus the common carpel character states (ascidate morphology, lateral attachment and nonplanar orientation, and one or two ovules in an alternate arrangement which is similar to Fig. 2D) also included the polarized ancestral states. When the distribution of states is examined on the tree of Donoghue and Doyle (1989), it also appears that the trees are more parsimonious when the ancestral states are considered to be ascidate morphology and one or two ovules.

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### General Discussion

Outgroup comparison, with which data from developmental transformation series is compatible, suggests that the ovule of ancestral angiosperm had certain characteristics. This hypothesized ovule had: the funiculus and nucellus attached opposite the micropyle; an orthoangle; symmetry throughout all layers of the ovule; no fusion between the funiculus and the adjacent integument; a micropyle formed from the inner integument only; division of the archesporial cell; and probably two integuments. Based on conventional terms, such an ovule would be considered orthotropous, bitegmic and crassinucellar.

A structural hypothesis of ovule evolution is possible based on the polarization of characters, the developmental transformation series, and distribution of ovule types in families (Fig. 1). This hypothesis suggests that the ancestral ovule (Fig. 1B) gave rise to ovules that only differed in angle (semi- or hemiangles) and attachment of the chalaza (opposite or distal; Fig. 1A). From this type evolved two later types of ovules: those with proximal funicular attachment, an ana-angle, inner symmetry and hemicontinuation (anatropous, the most common type in the basal angiosperms; Fig. 1C) as well as those with proximal funicular attachment, an ana-angle, sac symmetry and hemicontinuation (orthocampylotropous morphology; Fig. 1D). From the former (Fig. 1C) arose the ovules

with syncontinuation (anatropous; Fig. 1H), and nucellar symmetry (anacampylotropous; Fig. 1F). These ovules with synbitegmic integuments and anatropous morphology (Fig. 1H) produce the ovules with circinangle (circinatanatropous; Fig. 1I). Orthocampylotropous (Fig. 1D) and anacampylotropous (Fig. 1F) give rise to their respective amphitropous morphologies (Fig. 1E, G).

Several ovule characters are not shown in Figure 1. The polarized states of characters 7, 9, and 10 suggest that all ovules with abitegmic integuments are derived from ovules with the bitegmic state, and all ovules that lack a parietal cell, with or without division of the nucellar epidermis (pseudocrassinucellar and tenuinucellar nucelli), are derived from ovules with the crassinucellar state.

The above is a structural hypothesis, in which the steps may have occurred in parallel in different clades. The distributions of the ancestral and derived states (Appendix 1) strongly suggest that anatropous (and other suggested derived types) ovules are homoplasous. It was found in the survey of basal angiosperms (Appendix 1) that ovules considered anatropous are quite variable. Thus "anatropous" ovules vary in their angle, symmetry, and continuation of the funiculus and outermost integument. This variability would support the hypothesis that they originated multiple times. One hypothesis for the multiple origins of "anatropous" ovules is that the micropyle can be directed away from the pollen tube transmission tissue.

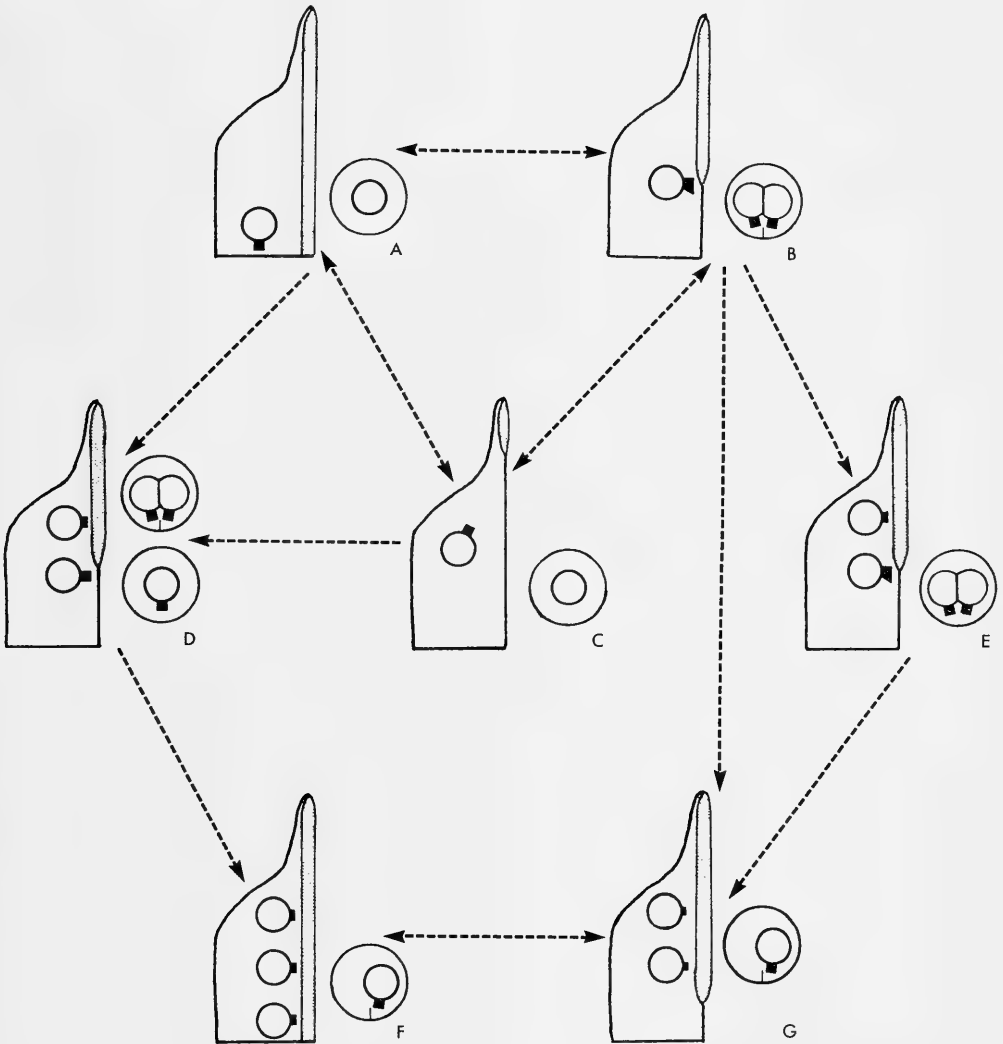
Work on ovule development could further test this hypothesis. The hypothesis suggests that the curvature and late initiation of the outermost integument along the funiculus are derived. Comparative study of the genetics and expression of the developmental programs, perhaps by sampling the proteins expressed during ovule development, and developmental morphology of ovules with no curvature (e.g., orthotropous) with those which have a higher angle (e.g., anatropous) from the same family could test the hypothesis. In addition, phylogenetic analysis of clades with variable states could show whether the

structural hypothesis is corroborated in specific cases by the phylogenetic relationships.

The polarizations of the carpel states are less robust than those of the ovules. Yet the polarizations consistently suggest that the ascidate morphology and one or two ovules per carpel are the ancestral states. The developmental data suggest a transformation series between the ascidate to plicate state. Based on these data the following evolutionary structural relationships between general carpel types are suggested (Fig. 4).

The ancestral carpel with its ascidate morphology may have had the ovule basally (Fig. 4A), laterally (Fig. 4B) or apically (Fig. 4C) attached, and the orientation either planar with one ovule or nonplanar with two, opposite ovules. According to this model, carpels having ascoplicate morphology with both lateral, marginal attachment, and lateral admedial arrangement (of a single ovule in planar orientation; Fig. 4D) originated from carpels with the ascidate morphology and basal or apical ovule attachment (Fig. 4A, C). The position of the marginal ovules may have been either alternate or opposite. If the medial ovule and cross-zone in this carpel type was lost, the resulting carpel has a plicate B morphology (Fig. 4F). Two forms may have evolved from the ascidate carpel with lateral ovules (Fig. 4B), one having ascidate morphology and few or many ovules (Fig. 4E), and the other having plicate morphology, but an ascidate base (Fig. 4G). Again, attachment of the ovules may have been opposite or alternate. The plicate types (Fig. 4F, G) may have also originated from each other. All other carpel types (e.g., those in Fig. 2) are considered derived from one of the above types.

The distributions of the ancestral and derived states (Appendix 2) suggest that ascoplicate and plicate ovules may have evolved multiple times. The placement of the ovules and the morphology of the carpel base is quite variable in carpels having the ascoplicate morphology. Similar variation is found in carpels with plicate morphology, especially the marginal to submarginal

**Fig. 4**

Evolutionary relationships of the basic carpel types based on the proposed ancestral character states and developmental transformation series. (See text for further discussion.) The shading shows the closure, the portion of the carpel that closes during ontogeny. The diagrammatic cross-sections of the carpels are oriented so that the right side of the longitudinal section is down. The types found in A, B, and C are equally ancestral, whereas the remaining are considered derived.

placement of ovules along the margins of the closure (e.g., Bailey and Swamy 1951; Puri 1952, 1961; Canright 1960; Eames 1961). This hypothesis suggests that this variability is due to multiple origins of ascoplicate and plicate carpels.

The correlation of these two carpel types with high ovule numbers may suggest an evolutionary explanation for their multiple origins and frequency. In this survey, carpels with ascidate morphology rarely have high ovule numbers. The study of additional

characters, such as exact placement of the ovules along the closure, also may clearly show that the derived carpels are not structurally similar and may have evolved due to selection for high seed number.

Further tests of the hypothesis are possible with experimental morphogenetic analysis. Based on the polarized characters and the developmental morphology of the primordia, a transition series of carpel types have been suggested (Fig. 3A–C). The most divergent types are carpels with ascidate morphology and basal ovule attachment (Type A development) and with plicate B morphology and lateral, marginal ovule attachment (Type C development). Carpels possessing ascidate and basal states have placentae that originate from a separate meristem, distal to the meristem forming the gynoecial appendage. This morphology must be homologous with a carpel having plicate and lateral, marginal states in which the placenta may originate from the marginal area of the gynoecial appendage. Hagerup (1938) has already suggested that the placental regions in both morphologies originate from a distal (abaxial) meristem. This suggestion would indicate that the gynoecial appendage of a carpel showing plicate morphology is a composite structure produced by the integration of two meristems.

Such a structural homology between the two carpel types is testable by following cell lineages in the gynoecial appendage and the region producing the placentae to see whether they have separate origins. Tracking of cell lineages is possible with clonal analysis as described by Poethig (1987). If the cell lineages for the placentae are found to have a separate origin from the gynoecial appendage (particularly in carpels with plicate morphology), this hypothesis would be supported.

Importantly, results supporting this hypothesis would cast serious doubts on the concept that the angiosperm carpel is a megasporophyll with laminar ovules. The new concept would suggest that the ovule carpel complex is best interpreted as a short shoot with the gynoecial appendage equivalent to a bract or bracteole, and the ovule being the

apical portion of an axillary bud or terminal apex. Thus an angiosperm carpel and ovule system would potentially be homologous with the bract-bracteole-terminal ovule system found in the outgroups such as *Cruciferales* and *Gnetophytes*. Further work on the origin and development of the gynoecial and placental tissue will be necessary before complete understanding of the origin and evolution of the angiosperm carpel can be achieved.

Another test would be a phylogenetic analysis of the genera in families that show a number of primordial and mature carpel morphologies (e.g., *Ranunculaceae*). If the phylogeny showed congruence with the suggested structural transformation, the hypothesis would be corroborated.

The results of the above analysis and hypotheses of ovule and carpel structural evolution have interesting implications for basal angiosperm evolution. Currently, there is growing equivocal evidence (Walker and Walker 1984; Friis et al. 1986; Hamby and Zimmer 1990) that families with diminutive flowers may be closest to the ancestral angiosperm groundplan (Taylor 1988; Hickey and Taylor 1989; Taylor and Hickey 1990). The ovule and carpel data support these suggestions by indicating that only the piperalean families and *Amborella* have the ancestral states of both organs. In addition, there continues to be debate as to which group is ancestral in the monocots: *Alismatales* (Cronquist 1981) or *Dioscoreales* (Dahlgren et al. 1985). These data suggest that only members of *Dioscoreales* have the complete collection of ancestral ovule and carpel states.

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## Appendix 1

Ovule character states at the embryo-sac stage for a select number of basal angiosperm families. Data for families from Cronquist (1981) and Davis (1966) with number under character 10 on family line referring to the number of archesporial cells that are produced. Character states in parentheses for characters 9 and 10 refer to survey of Davis (1966) on the entire family if states not represented by the genera examined. — = lack of data; ( ) = rare state for the taxon; and ? = probable but uncertain state.

**Abbreviation for each character:** **character 1**, attachment of chazala: *dist* = distal, *opp* = opposite, *prox* = proximal; **character 2**, angle: *ana* = angle, *circ* = circumangle, *hemi* = hemiangle, *ortho* = orthoangle, *semi* = semiangle; **character 3**, complete symmetry: *asym* = asymmetrical, *sym* = symmetrical; **character 4**, levels of symmetry: *inner* = inner symmetry, *lack* = lacking symmetry, *nucel* = nucellar symmetry, *outer* = outer symmetry, *sac* = sac symmetry; **character 5**, attachment of nucellus: *dist* = distal, *opp* = opposite, *prox* = proximal; **character 6, 7**, continuity of integument and funiculus, and integument number: *apobi* = apobitegmic, *apouni* = apounitegmic, *biteg* = bitegmic, *hemibi* = hemibitegmic, *hemiumi* = hemiumitegmic, *obtur* = obturator, *semibi* = semibitegmic, *semiumi* = semiumitegmic, *synbi* = synbitegmic, *triteg* = tritegmic, *uniteg* = unitegmic; **character 8**, micropyle: *both* = both, *both z* = both zigzag, *inner* = inner; **character 9**, division of archesporial cell: *crass* = crassinucellar, *mixed* = mixed types, *multi* = multiparietal, *none* = none, *pcras* or *pcr* = pseudocrassinucellar, *tenu* = tenuinucellar, *uni* = uniparietal; **character 10**, division of nucellar epidermis: *m* = many layers, *multi* = multipidermal, *none* = none, *uni* = uniepidermal.

GENUS	GENERAL OVULE MORPHOLOGY										INTEGUMENT MORPHOLOGY				NUCELLAR MORPHOLOGY				REF
	1	2	3	4	5	6,7	8	9	10	1	2	3	4	5	6	7	8	9	
<b>Winteraceae</b>	anatropous										biteg	inner	crass (multi)	1					
<i>Drimys</i>	prox	ana	asym	inner	opp						synbi	inner	multi	uni					1
<i>Pseudowintera</i>	prox	ana	asym	inner	opp						synbi	inner	multi	uni					2
<b>Degeneriaceae</b>	anatropous										biteg	inner	crass	1					
<i>Degeneria</i>	prox	ana	asym	inner	opp						synbi	inner	multi	none					3
<b>Himantandraceae</b>	anatropous													(1)					
<i>Galbullimima</i>	prox	ana	asym	inner	opp						synbi (obtur)	inner	multi	none					4
<b>Eupomatiaceae</b>	anatropous										biteg	—	crass	—					
<i>Eupomatia</i>	prox	ana	asym	inner	opp						synbi	inner	multi	—					5
<b>Austrobaileyaaceae</b>	anatropous										biteg	inner	crass	1					
<i>Austrobaileya</i>	prox	ana	asym	inner	opp						synbi	both	multi	uni					6
<b>Magnoliaceae</b>	anatropous										biteg	inner	crass	1, m					
<i>Liriodendron</i>	prox	ana	asym	inner	opp						synbi (obtur)	both z	multi	none					7
<b>Magnolia</b>	prox	ana	asym	inner	opp						synbi	both z	multi	none					8
<b>Lactoridaceae</b>	anatropous										biteg	—	crass	—					
<i>Lactoris</i>	prox	ana	asym	inner	opp						synbi	inner	multi	uni					9

Continued on next page

## Appendix 1

Continued

GENUS	GENERAL OVULE MORPHOLOGY					INTEGUMENT MORPHOLOGY			NUCELLAR MORPHOLOGY		REF
	1	2	3	4	5	6,7	8	9	10		
<b>Annonaceae</b>	anatropous, campylotropous					biteg (triteg)	inner	crass	1		
<i>Annona</i>	prox	ana	asym	inner	opp	synbi	inner	—	—	10	
<i>Asimina</i>	—	—	asym	sac	—	—	—	multi	none	11	
<i>Cananga</i>	prox	ana	asym	inner	opp	synbi	inner	—	—	12	
<b>Myristicaceae</b>	± anatropous					biteg	—	crass	1		
<i>Myristica</i>	prox	ana	asym	inner	opp	hemibi	inner	multi	none	13	
<b>Canellaceae</b>	hemianatropous					biteg	both z	crass			
<i>Warburgia</i>	dist	hemi	asym	nucel	opp	semibi	both z	multi	none	3	
<b>Amborellaceae</b>	anatropous					biteg	—	crass			
<i>Amborella</i>	opp	ortho	sym	outer	opp	apobi	inner	—	—	14	
<b>Trimeniaceae</b>	anatropous					biteg	both z	crass	m		
<i>Trimenia</i>	prox	ana	asym	inner	opp	synbi	inner	?mult	?none	15	
<b>Monimiaceae</b>	anatropous					biteg	inner	crass	1, m		
						uniteg					
Monimioidaeae											
<i>Hedyocarya</i>	prox	ana	asym	inner	opp	synbi	inner	—	—	16	
<i>Wilkiea</i>	prox	ana	asym	inner	opp	synbi	inner	—	—	16	
Siparunioideae											
<i>Siparunia</i>	prox	hemi	asym	nucel	opp	hemiluni	inner	multi	multi	17, 18	
Hortonioidaeae											
<i>Hortonia</i>	prox	ana	asym	inner	opp	synbi	inner	multi	none	27	
Atherospermoideae											
<i>Doryphora</i>	prox	hemi	asym	inner	opp	synbi	inner	multi	uni	18	
<b>Gomortegaceae</b>	anatropous					—	—	—	—		
Calycanthaceae	anatropous					biteg	inner	pcrass	m		
<i>Calycanthus</i>	prox	ana?	asym	inner	opp	hemibi	both	none	multi	19	
<i>Chimonanthus</i>	prox	ana?	asym	inner	opp	hemibi	both	—	multi	18	
<b>Idiospermeaceae</b>	anatropous					biteg	—	—	—		
<b>Lauraceae</b>	anatropous					biteg	inner	crass	1, m		
							both	multi	none		
<i>Cassytha</i>	prox	circ	asym	inner	opp	synbi	both z	multi	none	20	

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GENUS	GENERAL OVULE MORPHOLOGY					INTEGUMENT MORPHOLOGY			NUCELLAR MORPHOLOGY		REF
	1	2	3	4	5	6,7	8	9	10		
<i>Cinnamomum</i>	prox	circ	asym	inner	opp	sympi	both z	multi	multi	18	
<i>Laurus</i>	prox	circ	asym	inner	opp	sympi	both z	multi	multi	18	
<b>Hernandiaceae</b>	anatropous					biteg	—	crass			
<i>Gyrocarpus</i>	prox	ana	asym	inner	opp	hermibi ?obtur	both z	—	—	21	
<b>Chloranthaceae</b>	orthotropous					biteg	inner	crass	1		
<i>Ascarina</i>	opp	ortho	sym	outer	opp	apobi	both	multi	none	22	
<i>Chloranthus</i>	opp	ortho	sym	outer	opp	apobi	inner	multi	none	22	
<i>Hedyosmum</i>	opp	ortho	sym	outer	opp	apobi	inner	multi	none	22	
<i>Sarcandra</i>	opp	ortho	sym	outer	opp	apobi	both	multi	none	22	
<b>Saururaceae</b>	orthotropous, hemitropous					biteg	both	crass	1		
<i>Anemopsis</i>	opp	ortho	sym	outer	opp	apobi	both	tenu	none	23	
<i>Houttuynia</i>	opp	ortho	sym	outer	opp	apobi	both	multi	none	24	
<i>Saururus</i>	opp	ortho	sym	outer	opp	apobi	both	multi	none	25	
<b>Piperaceae</b>	orthotropous					biteg	inner	crass	none		
<i>Heckeria</i>	opp	ortho	sym	outer	opp	apobi	both	multi	none	26	
<i>Peperomia</i>	opp	ortho	sym	inner	opp	apouni	inner	multi	none	26	
<i>Piper</i>	opp	ortho	sym	outer	opp	apobi	inner	multi	none	26	
<b>Aristolochiaceae</b>	anatropous (circinanatropous)					biteg	both	crass	1 (m)		
<i>Aristolochia</i>	prox	ana	asym	inner	opp	hermibi	inner	mixed	none	28	
<i>Asarum</i>	prox	ana	asym	inner	opp	sympi	inner	multi	none	29	
		hermi		(nucl)		hermibi	both	multi	(uni)		

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GENUS	GENERAL OVULE MORPHOLOGY					INTEGUMENT MORPHOLOGY			NUCELLAR MORPHOLOGY			REF
	1	2	3	4	5	6,7	8	9	10			
<b>Illiciaceae</b>	anatropous					biteg	—	crass	m			
<i>Illicium</i>	prox	ana	asym	inner	opp	hemibi	both	multi	none	30		
<b>Schisandraceae</b>	campylotropous	to anatropous				biteg	both	crass	m			
<i>Schisandra</i>	prox	ana	asym	sac	opp	hemibi	both	multi	none	31		
<b>Nelumbonaceae</b>	anatropous					biteg	inner	crass	(uni)			
<i>Nelumbo</i>	prox	ana	asym	inner	opp	synbi	inner	multi	1	32		
<b>Nymphaeaceae</b>	anatropous					biteg	inner	crass	multi	36		
<i>Nymphaea</i>	prox	ana	asym	inner	opp	hemibi	both	(multi)	(multi)	33		
<i>Nuphar</i>	prox	ana	asym	inner	opp	synbi	inner	multi	none	34		
<b>Barclayaceae</b>	orthotropous					biteg	—	crass	1			
<i>Barclaya</i>	opp	ortho	sym	outer	opp	apobi	?inner	multi	none	35		
<b>Cabombaceae</b>	anatropous					biteg	inner	crass	1			
<i>Brasenia</i>	prox	ana	asym	inner	opp	synbi	inner	uni	none	36		
<i>Cabomba</i>	prox	ana	asym	inner	opp	synbi	inner	multi	multi	37,81		
<b>Ceratophyllaceae</b>	orthotropous					uniteg	inner	crass	1			
<i>Ceratophyllum</i>	opp	ortho	sym	inner	opp	apouni	inner	multi	none	11		
<b>Ranunculaceae</b>	hemianatropous					biteg	—	crass	1 (m)	38		
<i>Anemone</i>	anatropous					uniteg		pcrass	(multi)	39		
	prox	ana	sym	inner	opp	apouni	inner	—	—			
		circ	asym	nucel		semiuni						
<i>Aquilegia</i>	prox	ana	asym	inner	opp	hemibi	both z	—	—	40		
<i>Delphinium</i>	prox	ana	asym	inner	opp	synbi	inner	—	—	40		
<i>Ranunculus</i>	dist	hemi	asym	nucel	opp	hemiumi	inner	none	multi	39		
<i>Thalictrum</i>	prox	circ	asym	inner	opp	synbi	inner	uni	(?uni)	41		
<b>Circaeasteraceae</b>	orthotropous					uniteg	—	tenu	1			
<i>Circaeaster</i>	opp	ortho	sym	inner	opp	apouni	inner	none	none	42		

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GENUS	GENERAL OVULE MORPHOLOGY			INTEGUMENT MORPHOLOGY			NUCLEAR MORPHOLOGY			REF
	1	2	3	4	5	6,7	8	9	10	
<b>Berberidaceae</b>	hemianatropous, anatropous									
<i>Achlys</i>	prox	hemi	asym	inner	opp	sybi	both z	crass	m	40
<i>Berberis</i>	prox	ana	asym	inner	opp	hemibi	both z	(multi)	(multi)	40
<i>Epimeedium</i>	prox	hemi	asym	inner	opp	hemibi	both z	(none)	(multi)	11
<i>Nandina</i>	prox	ana	asym	inner	opp	hemibi	both z	—	—	40
<i>Podophyllum</i>	prox	hemi	asym	inner	opp	hemibi	both z	—	—	40
<i>Ranzania</i>	prox	hemi	asym	inner	opp	hemibi	both z	—	—	40
<b>Sargentodoxaceae</b>	hemianatropous to almost anatropous									
<i>Sargentodoxa</i>	dist	hemi	asym	inner	opp	semibi	inner	—	—	43
<b>Lardizabalaceae</b>	orthotropous, campylotropous									
<i>Akebia</i>	opp	ortho	sym	outer	opp	apobi	?inner	crass	1	44
<b>Decaisnea</b>	prox	semi	asym	inner	opp	hemibi	inner	multi	none	45
<b>Menispermaceae</b>	hemitropous to amphitropous									
<i>Cocculus</i>	dist	hemi	asym	sac	dist	uniteg	inner	multi	multi	46
<i>Menispermum</i>	dist	semi	asym	inner	opp	apobi	inner	—	—	47
<i>Tinospora</i>	dist	hemi	asym	sac	dist	semiuni	inner	multi	multi	49
<b>Coriariaceae</b>	anatropous									
<i>Coriaria</i>	prox	circ	asym	inner	opp	biteg	—	crass	1	47
<b>Sabiaceae</b>	hemianatropous									
<i>Meliosma</i>	dist	semi	asym	nucel	opp	uniteg	—	crass	1	47
<i>Sabia</i>	dist	semi	asym	nucel	opp	semiuni	inner	multi	(multi)	47
<b>Papaveraceae</b>	campylotropous, amphitropous									
<i>Eschscholzia</i>	prox	ana	asym	inner	opp	biteg	—	crass	m (1)	50
<i>Sanguinaria</i>	prox	ana	asym	inner	opp	hemibi	both z	multi	multi	51
<b>Fumariaceae</b>	anatropous, campylotropous									
<i>Fumaria</i>	dist	hemi	asym	lack	dist	biteg	—	crass	1 (m)	52

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GENUS	GENERAL OVULE MORPHOLOGY			INTEGUMENT MORPHOLOGY			NUCELLAR MORPHOLOGY			REF
	1	2	3	4	5	6,7	8	9	10	
<b>Tetractraceae</b>										
<i>Tetracentron</i>	anatropous	hemi	asym	inner	opp	biteg	—	crass	—	53
<b>Trochodendraceae</b>										
<i>Trochodendron</i>	anatropous	ana	asym	inner	opp	biteg	inner	crass	—	53
<b>Cercidiphyllaceae</b>										
<i>Cercidiphyllum</i>	anatropous	ana	asym	inner	opp	biteg	both	crass	1	54
<b>Eupteleaceae</b>										
<i>Euptelea</i>	anatropous	ana	asym	inner	opp	biteg	both	crass	1	55
<b>Platanaceae</b>										
<i>Platanus</i>	prox	hemi	asym	inner	opp	biteg	both	crass	1	56
	orthotropous to slight	ortho	sym	outer	opp	biteg	—	crass	1	
	dist	semi	asym	inner	opp	apobi	both	multi	none	
<b>Hamamelidaceae</b>										
	anatropous, orthotropous					biteg	both z	crass	1	
<i>Altingia</i>	opp	ortho	sym	outer	opp	apobi	inner	—	—	57
<i>Distylium</i>	prox	ana	asym	inner	opp	hemi	both	—	—	58
<i>Hamamelis</i>	prox	ana	asym	sac	dist	hemi	both z	multi	none	59
<i>Liquidambar</i>	prox	?semi	asym	?inner	?opp	?synbi	—	—	—	60
<b>Myrothamnaceae</b>										
<i>Myrothamnus</i>	anatropous	ana	asym	inner	opp	biteg	—	crass	1	61
<b>Phytolaccaceae</b>										
<i>Myrothamnus</i>	prox	ana	asym	inner	opp	synbi	both z	multi	none	62
<i>Didymothea</i>	campylotropous	hemi	asym	sac	dist	biteg	—	crass	1	63
<i>Gisekia</i>	dist	ana	asym	sac	prox	semibi	inner	—	—	64
<i>Hillieria</i>	prox	ana	asym	sac	prox	semibi	inner	multi	—	64
<i>Phytolacca</i>	prox	ana	asym	sac	prox	hemi	inner	—	—	64
<b>Molluginaceae</b>										
<i>Phytolacca</i>	dist	ana	asym	sac	dist	semibi	inner	—	—	64
<i>Limnium</i>	campylotropous (to almost anatropous)	ana	asym	sac	dist	biteg	inner	crass	1 (m)	65
<i>Mollugo</i>	dist	ana	asym	sac	dist	semibi	inner	multi	none	66
						hemi	inner	multi	multi	
<i>Orygia</i>	dist	ana	asym	sac	dist	hemi	inner	multi	uni	67
<b>Caryophyllaceae</b>										
	hemianatropous to campylotropous					biteg	—	crass	m	
								(uni)	(none)	
								(multi)	(multi)	

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GENUS	GENERAL OVULE MORPHOLOGY					INTEGUMENT MORPHOLOGY			NUCELLAR MORPHOLOGY		REF
	1	2	3	4	5	6,7	8	9	10		
<i>Scleranthus</i>	prox	semi	asym	none	prox	semibi	inner	—	—	68	
<i>Telephium</i>	dist	hemi	asym	sac	dist	semibi	inner	—	—	68	
<i>Uebelinia</i>	dist	circ	asym	sac	dist	semibi	inner	—	—	69	
<b>Polygonaceae</b>	orthotropous (anatotropous)					biteg	inner	crass (multi) (uni)	m (uni) (none)		
<i>Brunnichia</i>	opp	ana	sym	outer	opp	apobi	inner	—	—	70	
<i>Rheum</i>	opp	ortho	sym	outer	opp	apobi	inner	—	—	70	
<b>Plumbaginaceae</b>	anatropous					biteg	—	crass	1 (m)		
<i>Plumbago</i>	prox	circ	asym	inner	opp	synbi	inner	multi	none	71	
<i>Vogelia</i>	prox	circ	asym	inner	opp	synbi	inner	multi	none	72	
<b>Dilleniaceae</b>	atropous, anatropous, amphitropous, hemianatotropous					biteg	—	crass	1 (m)		
<i>Acrotrema</i>	prox	ana	asym	sac	dist	?hemibi	both z	multi	multi	73	
<i>Dillenia</i>	prox	ana	asym	sac	dist	hemibi	both z	multi	none	74	
<i>Hibbertia</i>	prox	hemi	asym	sac	opp	hemibi	inner	multi	uni	75	
	?dist	ana	asym	sac	opp	hemibi	both z	multi	none	75	
<i>Wormia</i>	dist	ana	asym	sac	dist	synbi	both z	multi	none	76	
<b>Paeoniaceae</b>	anatropous					biteg	—	crass	1	74	
<i>Paeonia</i>	prox	hemi	asym	inner	opp	hemibi	both z	multi	multi	77	
<b>Brunelliaceae</b>	anatropous					biteg	—	crass	multi		
<b>Connaraceae</b>	orthotropous, hemianatotropous, anatropous					biteg	both	crass	m	78	
<i>Conarus</i>	dist	semi	asym	inner	opp	semibi	both	multi	none	78	
<i>Fourcopsis</i>	dist	semi	asym	nucel	opp	apobi	both	multi	none	78	
<b>Eucryphiaceae</b>	anatropous					biteg	—	—	—		
<b>Cunoniaceae</b>	hemianatotropous, campylotropous, anatropous					biteg	both z	crass (multi)	m (multi)		
<i>Aphanopetalum</i>	prox	ana	asym	nucel	opp	hemibi	both z	multi	none	78	
<i>Ceratopetalum</i>	dist	hemi	asym	inner	opp	semibi	inner	multi	none	78	
<i>Schizomeria</i>	dist	hemi	asym	inner	opp	semibi	both z	multi	none	78	
<b>Davidsoniaceae</b>	anatropous					biteg	—	—	—		
<b>Dialypetalanthaceae</b>	anatropous					biteg	—	—	—		

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GENUS	GENERAL OVULE MORPHOLOGY			INTEGUMENT MORPHOLOGY			NUCELLAR MORPHOLOGY			REF
	1	2	3	4	5	6,7	8	9	10	
<b>Greviaceae</b>	anatropous	ana	asym	inner	opp	biteg	—	crass	1	47
<i>Greyia</i>	prox					synbi	both z	multi		
<b>Crassulaceae</b>	anatropous	anatropous				biteg	both (inner)	crass	1	
<i>Crassula</i>	opp	semi	sym	outer	opp	apobi	both	uni	none	79
<i>Sedum</i>	prox	ana	asym	inner	opp	hemibi	both	?uni	?	79
<b>Cephalotaceae</b>		circ		nucel		semiuni	inner			
<b>Saxifragaceae</b>	anatropous	anatropous				biteg	—	crass		
						biteg	—	crass	1 (m)	
						uniteg	—	tenu		
<i>Parnassia</i>	prox	ana	asym	inner	opp	synbi	both z	none	none	80
<i>Saxifraga</i>	prox	ana	asym	inner	opp	synbi	both z	multi	uni	80
<i>Tiarella</i>	prox	ana	asym	inner	opp	hemibi	both	none	uni	81
<b>Rosaceae</b>	hemianatropous,	anatropous,	asym,	campylotropous		biteg	inner	crass	m	
						uniteg	both			
<i>Amelanchier</i>	prox	hemi	asym	inner	opp	hemibi	inner	multi	multi	82
<i>Amygdalus</i>	dist	semi	asym	inner	opp	apobi	inner	?none	?	82
<i>Crataegus</i>	prox	hemi	asym	inner	opp	hemibi	inner	multi	multi	82
<i>Fragaria</i>	dist	semi	asym	nucel	opp	semiuni	inner	multi	multi	82
<i>Spiraea</i>	prox	ana	asym	inner	opp	hemibi	inner	multi	multi	82
		hemi		nucel		synbi				
						hemiumi				
<b>Neuradaceae</b>	anatropous					biteg	—	crass		
<b>Crossosomataceae</b>	campylotropous,	amphitropous				biteg	—	crass		
<i>Crossosoma</i>	prox	ana	asym	?sac	opp	hemibi	both z	—	—	78
<b>Surianaceae</b>	anatropous					biteg	—	crass	m	
<i>Suriana</i>	prox	ana	asym	?lack	—	?hemibi	—	multi	multi	11, 83
<b>Butomaceae</b>	anatropous					biteg	inner	pcras	1	
<i>Butomus</i>	prox	ana	asym	inner	opp	synbi	inner	none	uni	84

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GENUS	GENERAL OVULE MORPHOLOGY			INTEGUMENT MORPHOLOGY			NUCLEAR MORPHOLOGY			REF
	1	2	3	4	5	6,7	8	9	10	
<b>Limnocharitaceae</b>										
<i>Limnocharis</i>	campylotropous, anatropous prox ana	ana	asym	inner	opp	biteg sympi (obtur))	— inner	pcras none	1 (m) uni	85
<b>Alismataceae</b>										
<i>Alisma</i>	anatropous, amphitropous prox ana	ana	asym	inner	opp	biteg sympi (obtur)	inner inner	pcras none	1 uni	39
<b>Trichopodaceae</b>										
<i>Trichopus</i>	anatropous prox ana	ana	asym	inner	opp	biteg sympi (obtur)	— both z	tenu none	1 none	86
<b>Dioscoreaceae</b>										
<i>Dioscorea</i>	anatropous prox ana	ana	asym	inner	opp	biteg hermbi	both both	crass multi	1 none	87
<b>Taccaceae</b>										
<i>Schizocapsa</i>	campylotropous, anatropous prox circ	ana	asym	inner	opp	biteg sympi	inner	crass uni	1 none	88
<i>Tacca</i>	prox ana	ana	asym	inner	opp	sympi	inner	uni	none	89
<b>Stemonaceae</b>										
<i>Croomia</i>	orthotropous, anatropous prox semi	ortho	asym	?inner	opp	biteg hermbi	inner	crass	1	86
<i>Stemona</i>	opp prox	ana	sym	—	—	apobi	inner	—	—	86
<b>Trilliaceae</b>										
<i>Medeola</i>	anatropous prox ana	ana	asym	inner	opp	biteg	inner	uni	none	92
<i>Paris</i>	prox hemi	hemi	asym	inner	opp	hermbi	—	crass	1 (m)	90
<i>Scoliopus</i>	prox hemi	hemi	asym	inner	opp	hermbi sympi (obtur)	inner	uni	multi	90
<i>Trillium</i>	prox ana	ana	asym	inner	opp	hermbi	inner	uni	multi	90
<b>Smilacaceae</b>										
<i>Smilax</i>	orthotropous, hemianatropous, campylotropous opp ortho	ortho	sym	outer	opp	biteg apobi	— —	(multi) crass	(none) —	57

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GENUS	GENERAL OVULE MORPHOLOGY			INTEGUMENT MORPHOLOGY			NUCLEAR MORPHOLOGY			
	1	2	3	4	5	6,7	8	9	10	REF
<b>Petermanniaceae</b>										
<i>Petermannia</i>	prox	ana	asym	inner	opp	biteg synbi	inner	?mult	?multi	91
<b>References.</b>										
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**Appendix 2**

Carpel character states for a select number of basal angiosperm families. The number of ovules in the family row is from Cronquist (1981). — = lack of data, ( ) indicates that the state is rarely found in the taxon, and ? indicates that state is probable but not certain. Abbreviation for characters: **character 11**, morphology; **character 12**, number of traces: *m* = multiple trace; *r* = residual trace; **character 13**, position of placentae: *lat. admedial* = lateral, admedially; *lat. admedial/marginal* = lateral, admedially placed proximally and lateral, marginally placed distally; *lat. exmedial* = lateral, exmedially; *lat. marginal* = lateral, marginally; *lat. radial* = lateral, radially; **character 14**, orientation; **character 15**, number and arrangement: *alt.* = alternate; *opp.* = opposite.

FAMILY (GENUS)	CARPEL MORPHOLOGY		POSITION OF PLACENTAE	ORIENTATION	NUMBER AND ARRANGEMENT	REF.
	11	12	13	14	15	
<b>Winteraceae</b>					1 to many	
<i>Drimys</i>	ascoplicate	2	lat. admedial/ marginal	nonplanar	many, opp.	1
<i>Pseudowintera</i>	plicate A ascoplicate	2	lat. marginal lat. admedial to apical	nonplanar	many, opp.	
<b>Degeneriaceae</b>					many	
<i>Degeneria</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	2
<b>Himantandraceae</b>					1 (2)	
<i>Galbulimima</i>	ascidate (plicate A)	2 (1) 2)	lat. admedial (lat. marginal)	nonplanar (double, alt.)	single	3
<b>Eupomatiaceae</b>					2 to ca. 11	
<i>Eupomatia</i>	ascidate	2	lat. admedial	nonplanar	2 to 3, alt.	4
<b>Austrobaileyaaceae</b>					8 to 14	
<i>Austrobaileya</i>	ascidate	2	lat. admedial	nonplanar	many, alt.	5
<b>Magnoliaceae</b>					2 to 6 (many)	
<i>Liriodendron</i>	ascidate	1	lat. admedial	nonplanar	single to dou- ble, opp.	6
<i>Magnolia</i>	ascidate split	1	lat. admedial	nonplanar	double, opp.	7
<b>Lactoridaceae</b>					4 to 8	
<i>Lactoris</i>	plicate —	2	lat. marginal	nonplanar	few-many, alt.	8
<b>Annonaceae</b>					1 to many	
<i>Cananga</i>	plicate —	2	lat. marginal	nonplanar	many, alt.	9
<i>Polyalthia</i>	ascidate	—	basal	planar	single	10
<b>Myristicaceae</b>					1	
<i>Myristica</i>	ascidate	<i>m</i>	basal	planar	single	11
<b>Canellaceae</b>					2 to many	
<i>Warburgia</i>	plicate B	2	lat. marginal	nonplanar	many —	12
<b>Amborellaceae</b>					1	
<i>Amborella</i>	ascidate	1	lat. admedial	planar	single	13
<b>Trimeniaceae</b>					1	
<i>Trimenia</i>	ascidate	1	apical	planar	single	14
<b>Monimiaceae</b>					1	
Monimioideae						
<i>Hedycarya</i>	ascidate	1	apical	planar	single	15
<i>Wilkiea</i>	ascidate	1	apical	planar	single	16
Siparunioideae						
<i>Siparunia</i>	ascidate	1	basal	planar	single	17
Hortonioidaeae						
<i>Hortonia</i>	ascidate	1	apical (lat. admedial)	planar (nonplanar)	single (double, alt.)	18
Atherospermoideae						
<i>Laurelia</i>	ascidate	1	basal to lat. admedial	planar	single	19

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## Appendix 2

Continued

FAMILY (GENUS)	CARPEL MORPHOLOGY		POSITION OF PLACENTAE	ORIENTATION	NUMBER AND ARRANGEMENT	REF.
	11	12	13	14	15	
<b>Gomortegaceae</b>					1	
<i>Gomortega</i>	?ascidate	—	apical	?planar	single	20
<b>Calycanthaceae</b>					1 (2)	
<i>Calycanthus</i>	plicate —	2	lat. marginal	nonplanar	double, alt. (one aborts)	21
<b>Idiospermaceae</b>					1 (2)	
<i>Idiospermum</i>	ascidate	2	lat. admedial	nonplanar	single, dou- ble, alt.	22
<b>Lauraceae</b>					1	
<i>Cassytha</i>	ascidate	1	apical	planar	single	23
<i>Cinnamomum</i>	ascidate	1	apical	planar	single	24
<i>Laurus</i>	ascidate	1	apical	planar	single	24
<b>Hernandiaceae</b>					1	
<i>Gyrocarpus</i>	ascidate	1	apical	planar	single	24
<b>Chloranthaceae</b>					1	
<i>Ascarina</i>	ascidate	1	apical	planar	single	25
<i>Chloranthus</i>	ascidate	1	apical	planar	single	25
<i>Hedyosmum</i>	ascidate	1	apical	planar	single	25
<i>Sarcandra</i>	ascidate	1	apical	planar	single	25
<b>Saururaceae</b>					(1) 2 to 10	
<i>Anemopsis</i>	plicate B	2	lat. marginal	nonplanar	few to many, alt.	26
<i>Houttuynia</i>	plicate B	2	lat. marginal	nonplanar	many, alt.	27
<i>Saururus</i>	ascidate to split	2	lat. admedial	nonplanar	double, alt., opp.	28, 56
<b>Piperaceae</b>					1	
<i>Heckeria</i>	ascidate	—	basal	aplanar	single	29
<i>Peperomia</i>	ascidate	1	basal	aplanar to planar	single	30
<i>Piper</i>	ascidate	—	basal	aplanar	single	31
<b>Aristolochiaceae</b>					many	
<i>Aristolochia</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	32
<i>Asarum</i>	ascidate	2	lat. admedial	nonplanar	few to many, alt.	33
	ascoplicate	2	lat. admedial/ marginal	nonplanar	many, opp	89
<b>Illiciaceae</b>					1	
<i>Illicium</i>	ascidate	1	basal	planar	single	34
<b>Schisandraceae</b>					2 to 5 (to 11)	
<i>Schisandra</i>	?ascidate	—	basal to lat. admedial	nonplanar	double, ?alt.	35
<b>Nelumbonaceae</b>					1 (2)	
<i>Nelumbo</i>	ascidate	m	apical	planar	single	36
<b>Nymphaeaceae</b>					many	
<i>Nymphaea</i>	ascidate (ascopli- cate) both dorsal and ventral	m	lat. radial	nonplanar	many, alt.	37
<i>Nuphar</i>	ascidate both dorsal and ventral	m	lat. radial to chaotic	nonplanar	many, alt.	38
<b>Barclayaceae</b>					many	

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## Appendix 2

Continued

FAMILY (GENUS)	CARPEL MORPHOLOGY		POSITION OF PLACENTAE	ORIENTATION	NUMBER AND ARRANGEMENT	REF.
	11	12	13	14	15	
<i>Barclaya</i>	ascoplicate both dorsal and ventral	m	lat. radial	nonplanar	many, alt.	39
<b>Cabombaceae</b>					(1) 2 to 3	
<i>Brasenia</i>	ascidate both dorsal and ventral	m	lat. exmedial	nonplanar to planar	single to few, alt.	40
<i>Cabomba</i>	ascidate both dorsal and ventral	m	chaotic	nonplanar	few, alt.	37
<b>Ceratophyllaceae</b>					1	
<i>Ceratophyllum</i>	ascidate	—	apical to lat. exmedial	?planar	single	41
<b>Ranunculaceae</b>					1 to many	
<i>Anemone</i>	ascoplicate	1	lat. admedial/ marginal	planar/non- planar	single/few, opp.	42
<i>Aquilegia</i>	ascoplicate	2	lat. admedial/ marginal	nonplanar	?many, alt.	43
<i>Delphinium</i>	plicate B	2	lat. marginal	nonplanar	?few, opp.	42
<i>Ranunculus</i>	ascidate	1	basal to lat. admedial	planar	single	42
<i>Thalictrum</i>	ascidate	1	lat. admedial	planar	single to dou- ble, opp.	44
<b>Circaeasteraceae</b>					1 to 2	
<i>Circaeaster</i>	ascidate	1	apical to lat. admedial	?planar- nonplanar	single to dou- ble, opp.	45
<b>Berberidaceae</b>					1, 2 to many	
<i>Achlys</i>	ascidate	1	basal to lat. admedial	planar	single	46
<i>Berberis</i>	ascidate	2	basal	nonplanar	double, opp.	46
<i>Caulophyllum</i>	ascidate	2	basal	nonplanar	double, opp.	46
<i>Epimedium</i>	ascoplicate	2	lat. admedial/ marginal	nonplanar	many, alt.	46
<i>Nandina</i>	ascidate	2	lat. admedial	nonplanar	single	47
<b>Sargentodoxaceae</b>					1	
<i>Sargentodoxa</i>	ascidate	—	apical to lat. admedial	?planar	single	48
<b>Lardizabalaceae</b>					(few) many	
<i>Akebia</i>	plicate B both dorsal and ventral	m	chaotic	nonplanar	many, alt.	49
<i>Decaisnea</i>	plicate	—	lat. marginal	nonplanar	many, alt.	50 <sup>*</sup>
<b>Menispermaceae</b>					2	
<i>Cocculus</i>	ascidate split	—	lat. admedial	nonplanar	double, alt. (1 aborts)	51
<i>Menispermum</i>	ascidate split	—	lat. admedial	nonplanar	double, opp.	52
<i>Tinospora</i>	?ascidate	—	lat. admedial	nonplanar	double, ?opp. (1 aborts)	53
<b>Coriariaceae</b>					1	
<i>Coriaria</i>	ascidate	1	apical to lat. admedial	planar	single	54
<b>Sabiaceae</b>					1 to 2	
<i>Meliosma</i>	ascidate	—	lat. admedial	nonplanar	double, opp.	55

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## Appendix 2

Continued

FAMILY (GENUS)	CARPEL MORPHOLOGY		POSITION OF PLACENTAE	ORIENTATION	NUMBER AND ARRANGEMENT	REF.
	11	12	13	14	15	
<b>Papaveraceae</b>					(1) many	
<i>Eschscholtzia</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	57
<i>Sanguinaria</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	57
<b>Fumariaceae</b>					2 to many	
<i>Corydalis</i>	plicate B	2	lat. marginal	nonplanar	2, alt.	58
<i>Fumaria</i>	plicate —	2	lat. marginal	nonplanar	single	58
<b>Tetracentraceae</b>					5 to 6	
<i>Tetracentron</i>	plicate A	2	lat. marginal	nonplanar	few, alt.	59
<b>Trochodendraceae</b>					many	
<i>Trochodendron</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	59
<b>Cercidiphyllaceae</b>					many	
<i>Cercidiphyllum</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	59
<b>Eupteleaceae</b>					1 to 3 (4)	
<i>Euptelea</i>	ascidate	1, 2	apical	nonplanar	single to few, clustered	59
<b>Platanaceae</b>					1 (2)	
<i>Platanus</i>	ascidate	2	apical-lat. ad- medial	nonplanar	single to dou- ble, opp.	60
<b>Hamamelidaceae</b>					2 to several	
<i>Altingia</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	61
<i>Distylium</i>	ascidate split	2	lat. admedial	nonplanar	single	62
<i>Hamamelis</i>	plicate A	2	lat. marginal	nonplanar	single (2)	63
<i>Liquidambar</i>	ascoplicate	—	basal to lat. admedial/ marg.	nonplanar	many, alt.	61
<b>Myrothamnaceae</b>					many, alt.	
<i>Myrothamnus</i>	ascidate (ascoplicate)	2	lat. admedial (lat. admedi- al/marginal)	nonplanar	many few, alt.	64
<b>Phytolaccaceae</b>					1	
<i>Didymotheca</i>	ascidate	?1	lat. admedial	planar	single	111
<i>Gisekia</i>	ascidate	—	basal	planar	single	65
<i>Hillieria</i>	ascidate	r	basal	planar	single	66
<i>Phytolacca</i>	ascidate	1	basal to lat. admedial	planar	single	66
<b>Molluginaceae</b>					1 to many	
<i>Mollugo</i>	ascoplicate	2	lat. admedial/ marginal	nonplanar	many, alt.	67
<i>Limeum</i>	ascidate	—	basal	?planar	single	112
<b>Caryophyllaceae</b>					1 to many	
<i>Melandrium</i>	ascidate	m	lat. admedial	nonplanar	few, opp.	68
<i>Scleranthus</i>	ascidate	1, ?r	lat. admedial to basal	?aplanar	single	69
<i>Telephium</i>	ascidate	2	lat. admedial	nonplanar	many, opp.	69
<i>Uebelinia</i>	ascidate	r	lat. admedial	?aplanar	single	70
<b>Polygonaceae</b>					1	
<i>Brunnichia</i>	ascidate	r	basal	—	single	71
<i>Rheum</i>	ascidate	r	basal	aplanar	single	71
<b>Plumbaginaceae</b>					1	
<i>Plumbago</i>	ascidate	r	basal	—	single	72
<i>Vogelia</i>	ascidate	—	basal	—	single	73
<b>Dilleniaceae</b>					1 to many	

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## Appendix 2

Continued

FAMILY (GENUS)	CARPEL MORPHOLOGY		POSITION OF PLACENTAE	ORIENTATION	NUMBER AND ARRANGEMENT	REF.
	11	12	13	14	15	
<i>Acrotrema</i>	ascoplicate split	2	lat. admedial/ marginal	nonplanar	double to many, alt.	74, 75
<i>Didesmandra</i>	ascidate	r	basal	planar	single	74, 75
<i>Dillenia</i>	ascoplicate (two pairs)	m	lat. admedial/ marginal	nonplanar	few to many, alt.	74, 75
<i>Hibbertia</i>	ascidate split	2	lat. admedial	nonplanar	double, opp.	75, 76
	ascoplicate	2	lat. admedial/ marginal	nonplanar	alt.	77, 93
<i>Pachynema</i>	plicate A	2	lat. marginal	nonplanar	many, alt.	77
<b>Paeoniaceae</b>	ascidate split	2	lat. admedial	nonplanar	double, opp.	75, 76
<i>Paeonia</i>	plicate B	—	lat. marginal	nonplanar	several to many few to many, alt.	78
<b>Brunelliaceae</b>					2	
<i>Brunellia</i>	ascidate (notched)	2	basal-lat. ad- medial	nonplanar	double, opp.	79
<b>Connaraceae</b>					2	
<i>Connarus</i>	ascidate (to split) notched	2	lat. admedial	nonplanar	double (1), opp.	80
<i>Roreopsis</i>	ascidate split	—	lat. admedial	nonplanar	double, opp.	80
<b>Eucryphiaceae</b>					several to many	
<i>Eucryphia</i>	ascidate	2	lat. admedial	nonplanar	few to many, alt.	81
<b>Cunoniaceae</b>					(1), 2 to many	
<i>Aphanopetalum</i>	ascidate	1	apical-lat. ad- medial	planar	single	113
<i>Ceratopetalum</i>	ascidate	—	lat. admedial	nonplanar	few, opp.	82
<i>Cunonia</i>	ascoplicate	—	lat. admedial/ marginal	nonplanar	many, opp.	82
<i>Schizomeria</i>	ascidate split	—	lat. admedial	nonplanar	double to few, opp.	113
<b>Davidsoniaceae</b>					5 to 7	
<i>Davidsonia</i>	ascidate	2	lat. admedial	nonplanar	few to many, clustered	113
<b>Dialypetalanthaceae</b>					many	
<i>Dialypetalanthus</i>	ascidate	—	lat. admedial	nonplanar	many, —	84
<b>Greyiaceae</b>					many	
<i>Greyia</i>	?ascidate	—	lat. admedial	nonplanar	many, alt.	55
<b>Crassulaceae</b>					(1) few	
<i>Bulliarda</i>	plicate —	—	lat. marginal	nonplanar	many, opp.	52
<i>Kalanchoe</i>	ascoplicate	2	lat. admedial/ marginal	nonplanar	many, alt.	85
<i>Sedum</i>	ascoplicate	—	lat. admedial/ marginal	nonplanar	many, alt.	52
<b>Cephalotaceae</b>					1 (2)	
<i>Cephalotus</i>	ascidate	—	basal	planar	single	86
<b>Saxifragaceae</b>					(1) several	

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**Appendix 2**

Continued

FAMILY (GENUS)	CARPEL MORPHOLOGY		POSITION OF PLACENTAE	ORIENTATION	NUMBER AND ARRANGEMENT	REF.
	11	12	13	14	15	
<i>Parnassia</i>	ascoplicate	—	lat. admedial/ marginal	nonplanar	many, alt.	87
<i>Penthorum</i>	ascidate split	—	apical	nonplanar	many, clustered	88
<i>Peltiphyllum</i>	plicate A	—	lat. marginal	nonplanar	many, alt.	89
<i>Tiarella</i>	plicate —	—	lat. marginal	nonplanar	many, alt.	90
<b>Rosaceae</b>					1, 2 to many	
<i>Amelanchier</i>	ascidate split	2	lat. admedial	nonplanar	double opp.	91
<i>Crataegus</i>	ascidate (split)	2	basal to lat. admedial	nonplanar	double, opp.	92
<i>Fragaria</i>	plicate A	—	lat. marginal	nonplanar	1 (2), alt.	93
<i>Spiraea</i>	ascoplicate split	2	lat. admedial/ marginal	nonplanar	few, opp.	94
<b>Neuradaceae</b>					1	
<b>Crossosomataceae</b>					(1), 2 to many	
<i>Crossosoma</i>	?plicate —	—	lat. marginal	nonplanar	many, —	95
<b>Surianaceae</b>					2 (to 5)	
<i>Suriana</i>	ascidate split	1	basal to lat. admedial	nonplanar	double, opp.	96
<b>Butomaceae</b>					many	
<i>Butomus</i>	plicate A dor- sal and ventral	2 m	lat. radial	nonplanar	many, alt.	97
<b>Limnocharitaceae</b>					many	
<i>Hydrocleys</i>	ascoplicate	2	lat. radial	nonplanar	many, alt.	97
<i>Limnocharis</i>	ascidate	m	lat. radial	nonplanar	many, alt.	97
<b>Alismataceae</b>					1 (several)	
<i>Alisma</i>	ascidate	1	basal	planar	single	97
<b>Trichopodaceae</b>					1, 2	
<i>Trichopus</i>	ascidate	?2	lat. admedial	planar	single, dou- ble, opp.	98
<b>Dioscoreaceae</b>					2 to many	
<i>Dioscorea</i>	?ascidate	—	lat. admedial	nonplanar	double (1), —	99
<i>Stemomeris</i>	ascidate	?2	lat. admedial	nonplanar	many, opp.	100
<b>Taccaceae</b>					many	
<i>Schizocapsa</i>	plicate B	—	lat. marginal	nonplanar	many, clustered	101
<i>Tacca</i>	plicate B	—	lat. marginal	nonplanar	many, alt.	102
<b>Stemonaceae</b>					2 (many)	
<i>Croomia</i>	ascidate	1	apical	nonplanar	few, opp.	103
<i>Stemona</i>	ascidate	m	basal	nonplanar	few, cluster	104
<b>Trilliaceae</b>					—	
<i>Medeola</i>	plicate B	2	lat. marginal	nonplanar	few to many, opp.	105
<i>Paris</i>	ascidate	—	lat. admedial	nonplanar	many, —	106
<i>Scoliopus</i>	ascidate split	—	lat. admedial	nonplanar	double, opp.	107
<i>Trillium</i>	ascidate	—	lat. admedial		many, alt.	108
	ascoplicate	—	lat. admedial/ marginal			
<b>Smilacaceae</b>					1, 2	
<i>Rhipogonum</i>	ascidate	—	lat. admedial	?planar	single	109

Continued on next page

## Appendix 2

Continued

FAMILY (GENUS)	CARPEL MORPHOLOGY		POSITION OF PLACENTAE		ORIENTATION		NUMBER AND ARRANGEMENT		REF.
	11	12	13	14	15	16	17		
<i>Smilax</i>	ascidate	—	apical	?planar-non-planar	single-double, ?opp.			110	
<b>Petermanniaceae</b>									
<i>Petermannia</i>	plicate-	—	lat. marginal	nonplanar	many	many, —		98	

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