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SYSTEMATICS OPTION
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Questioning the *Cunonia* in *C. capensis*.

ABSTRACT

All members of *Cunonia*, excluding *C. capensis*, occur on the island of New Caledonia. Dickison has repeatedly noted (1973, 1975, 1980, and 1984,) that evolutionary patterns may have led to incorrect systematic conclusions among many cunoniaceous genera, which are likely to generate incorrect systematic conclusions. For this reason, a study into the morphological characters defining *C. capensis* was undertaken. Although the possibility that the disjunct biogeographical pattern of *C. capensis* might be explained on the basis of taxonomic error was appealing, it was not conclusively supported from this investigation. Instead it was found that of the six characters supposed to distinguish *Cunonia* from *Weinmannia*, three agreed with the present position of *C. capensis* with *Cunonia*, whilst the other three placed *C. capensis* with *Weinmannia*. This study also served to highlight the need for further investigation and identification of characters which separate *Cunonia* and *Weinmannia* at the species level.

INTRODUCTION

The Cunoniaceae is a woody, dicotyledonous family almost exclusively confined to the Southern Hemisphere (Dickison, 1980a). Of the twenty four genera currently recognised in this family, *Weinmannia* is very widespread, and accounts for almost half of the total 360 species (Dickison, 1980a). All the rest are more or less narrowly endemic, with much of the distribution concentrated in New Guinea and Australasia (Good, 1974) (Figure 1).

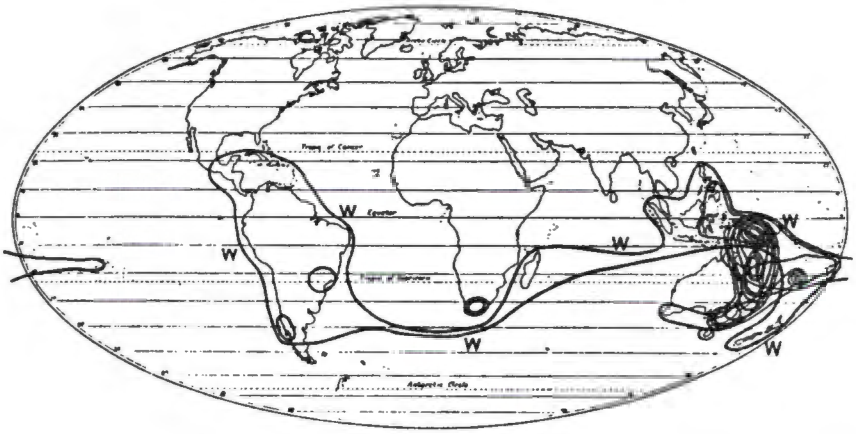


Figure 1: The distribution of the genera of the family Cunoniaceae. (*Weinmannia* represented by the letter W). (From Good, 1974)

The Cronquist (1968) classification system places this family between the Eucryphiaceae and Davidsoniaceae, in a large and rather heterogenous order Rosales (Dickison, 1980a). Studies of angiosperm phylogeny using protein sequences (Martin and Dowd, 1991) also placed Cunoniaceae with Rosaceae and Saxifragaceae, whilst rbcL data from Chase *et al.*, (1991) places Cunoniaceae amongst the basal groups of the "higher" rosids. Clearly, as was noted by Dickison (1980a), modern systems of angiosperm classification place Cunoniaceae in a key evolutionary position from which many other groups may be derived.

Members of Cunoniaceae are morphologically diverse, and considerable difference of opinion still exists regarding both generic, intra- and interfamilial relationships (Dickison, 1980a). Dickison (1984) notes however, that "parallel and reticulate evolution have often produced superficially similar morphologies among cunoniaceous genera, whilst the previously available morphological and anatomical data have often led to inaccurate systematic conclusions" (1984:149). The possibility that faulty systematic interpretation might account for the disjunct distribution pattern observed for *C. capensis*, (where 16 species occur on the island of New Caledonia, and one species, *C. capensis* L., in South Africa (Dickison, 1980a)), led to this investigation into the affinities of *C. capensis* with other taxa in the Cunoniaceae. A study of the characters defining *C. capensis* was undertaken, with the goal being to derive a set of nested monophyletic taxa which test its association with Cunonia.

MATERIALS AND METHODS

In order to ascertain the status of *C. capensis*, this species was examined relative to the remainder of its genus. Autapomorphies identifying this group were emphasised, along with those characters isolating *Cunonia* from other genera, notably the most closely related genus (according to Hufford and Dickison, 1992), *Weinmannia*.

Building on the character matrix produced by Hufford and Dickison, (1992), which described the Cunoniaceae at generic level, an independent set of characters for *C. capensis* was generated. This data was obtained from literature or, where the characters were undescribed, from research. Fresh plant material was collected from Table Mountain and preserved in FAA, with characters associated with leaf anatomy, petiole and ovular vasculature, as well as fruit capsule morphology requiring further investigation.

The discovery of a complete matrix produced by Hideux and Ferguson (1976), describing the pollen characters for the Saxifrigaceae sensu lato, allowed for the extraction of relevant Cunoniaceae data from their work. This, with slight modification, was added to the matrix of Hufford and Dickison, (although no novel pollen characters were studied).

LEAF ANATOMY

Leaf clearing, following the NaOH method of Foster (1966), was unsuccessful. Instead, these tannin-filled coriaceous leaves were soaked in 80% alcohol for two weeks, causing the venation patterns to colour red. This highlighted the major venation patterns, allowing for their photography using incident light on a stereo microscope.

The leaves were soaked in 5% NaOH for 18 hours, bleached, and placed in a saturated solution of chloral hydrate in order to investigate areolation patterns. Portions of leaf material were then examined on a compound microscope using both light and dark field illumination.

Both veinlet sheathing and medullary vascularisation of the petiole were investigated from material sectioned at *ca* 20 μm on a sledge microtome. The sections were stained in a combined Safranin and Alcian stain (Tolivia and Tolivia 1987), transferred through a dehydration series, mounted in DPX, and examined with brightfield optics on a compound microscope.

FRUIT CAPSULE MORPHOLOGY

Mature fruits were collected later in the season, and examined under a stereo microscope, prior to their photography with a macro lens.

OVULAR VASCULARISATION

Ovaries were dissected from the flowers, transferred through a dehydration series (18 hours in two baths of 70%, 80%, 95%, 100% ethanol, N-propanol, and N-butanol), and set into wax blocks. Serial sections were cut from these blocks at 10µm thickness, using a Leitz Wetzlar rotary microtome. Finally these sections were stained with safranin and fast green (Johansen, 1940), mounted in DPX on slides, and examined under a compound microscope using brightfield optics.

CHARACTERS

The characters collected from the above methods were fitted into a complete data set for *C. capensis,* congruent with the character matrix produced by Hufford and Dickison (1992). The entire matrix of Hufford and Dickison (1992) could then be reanalysed, with *C. capensis* isolated from the rest of its genus.

Following the addition of twenty characters extracted from pollen studies on the Saxifragaceae sensu lato, (as described by Hideux and Ferguson, 1976), a total of sixty-three characters, (appendix 1, state assignments for taxa in table 1,) were defined for use in the analysis. The synthetic outgroup constructed by Hufford and Dickison (1992) to polarise character states in the parsimony analysis was maintained for the modified matrix, however no outgroup character-states were available from the pollen data.

DATA ANALYSIS

Cladistic analyses were performed using both Hennig86 (Farris, 1988) and PAUP (version 3.0, Swofford 1989). Most parsimonious cladograms were sought using Fitsch parsimony. Initially all multistate characters were treated as unordered, (to provide the least biased approach possible for state evolution,) however final analysis involved the ordering of several pollen characters (marked with an asterisk in Appendix 1). For comparability with the analysis by Hufford and Dickison (1992), a simple addition sequence, using the tree bisection-reconnection (TBR) branch swapping option during initial heuristic search procedures was used. Strict consensus cladograms were formed when multiple trees were identified, however the final tree was derived from the successive weighting option (where only one tree was found). The bootstrap option was run in order to ascertain support for the various nodes, whilst MacClade, (version 2.97+, Maddison and Maddison, 1989) was used in conjunction with PAUP to explore character state evolution and the ramifications of alternative topologies.

RESULTS

OBSERVATIONS OF *C. capensis*

Leaf anatomy

The venation of *C. capensis* is pinnate, with a single midvein following a straight, unbranched course. The secondary venation type is semicraspedodromous, i.e. the secondaries branch just within the margin, one of the branches terminating at the margin, the other joining the superadjacent secondary (Figure 2). The tertiary veins show a random-reticulate pattern anastomosing with other tertiary or secondary veins, and the marginal ultimate venation is incomplete.

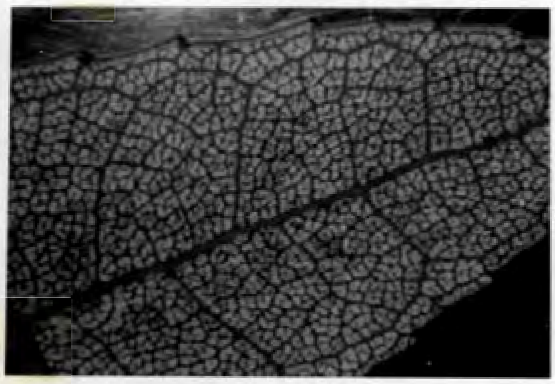


Figure 2: Venation patterns of *C. capensis* (0.8X).

Areoles, the smallest areas of leaf tissue surrounded by veins, are incomplete. One or more sides of the mesh is thus not bounded by a vein, giving rise to anomalously large meshes of highly irregular shape (Figure 3). Also, irregularly-shaped parenchymatous bundle sheaths were found in association with the veinlets of *C. capensis* (Figure 4).

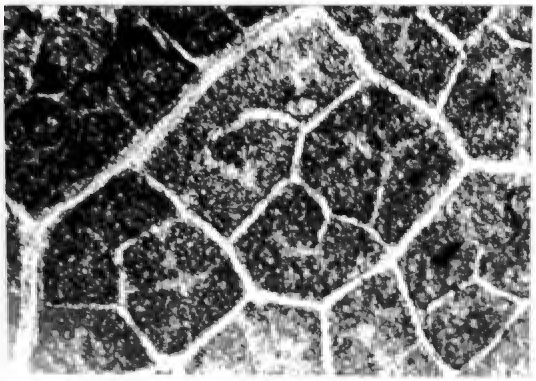


Figure 3: Areolation in *C. capensis* (5X).

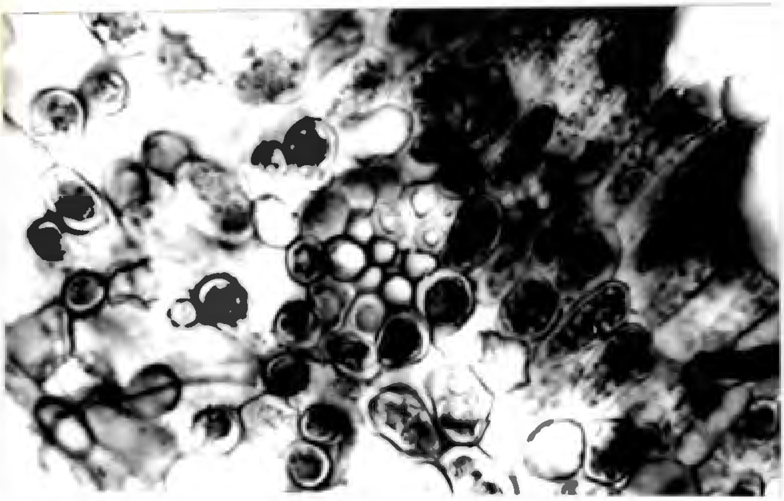


Figure 4: Transverse section of lamina showing bundle sheath cells around veinlets of *C. capensis* (400X)

The major vasculation of the petiole is in the form of a nearly complete, adaxially flattened, medullated cylinder (Figure 5). Rib bundles with an amphicribal organisation are present, and the vascular cylinder is surrounded by a prominent ring of perivascular fibres.

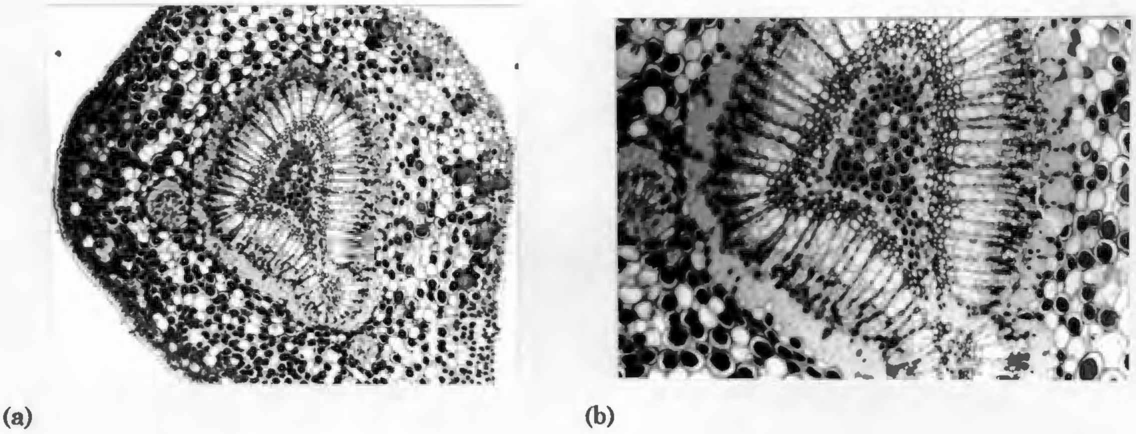


Figure 5: Medullary vasculature in petiole (a) 100X; and (b) 200X.

Reproductive structures

A half-flower and floral diagram, presented in figure 6, shows floral arrangement of *C. capensis*. Floral development is described in figure 7, whilst the mature flower structure is shown in figure 8, and a half-section of the ovary in figure 9. Ovular vasculature in carpels of *C. capensis* begin as a single, independent strand at the base of the locule. After traversing the septum in a position midway between the two pairs of united ventral bundles, and upon entering into the placenta, the ovular trace bifurcates (Figure 10a). Thereafter it remains separate (Figure 10b).

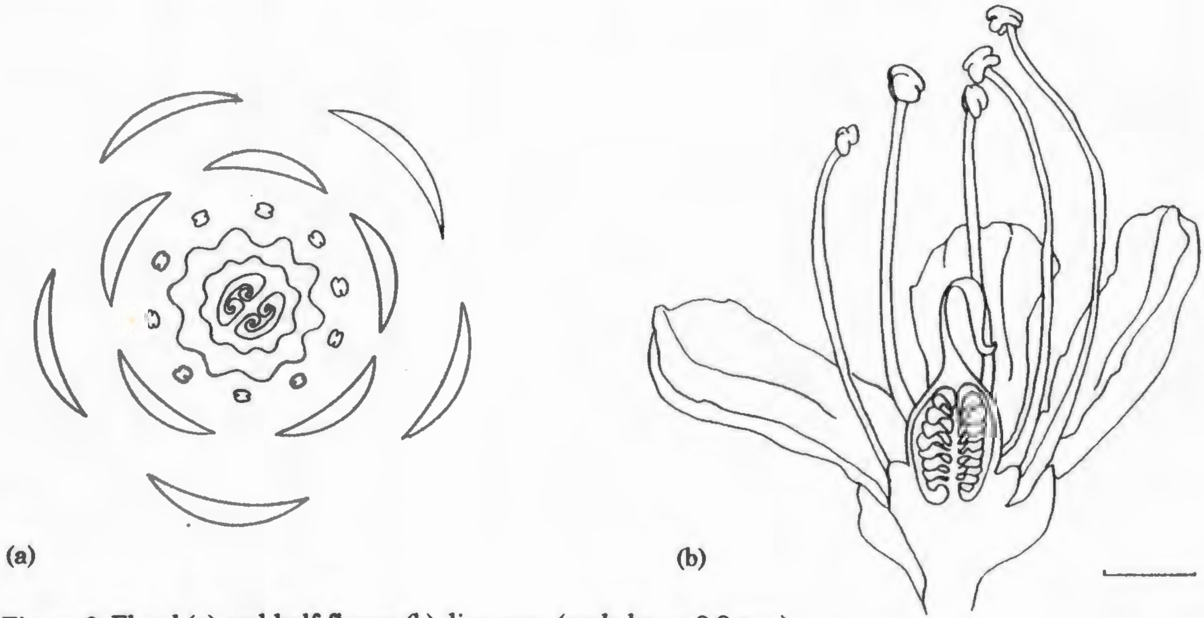


Figure 6: Floral (a) and half-flower (b) diagrams (scale bar = 0.8 mm).

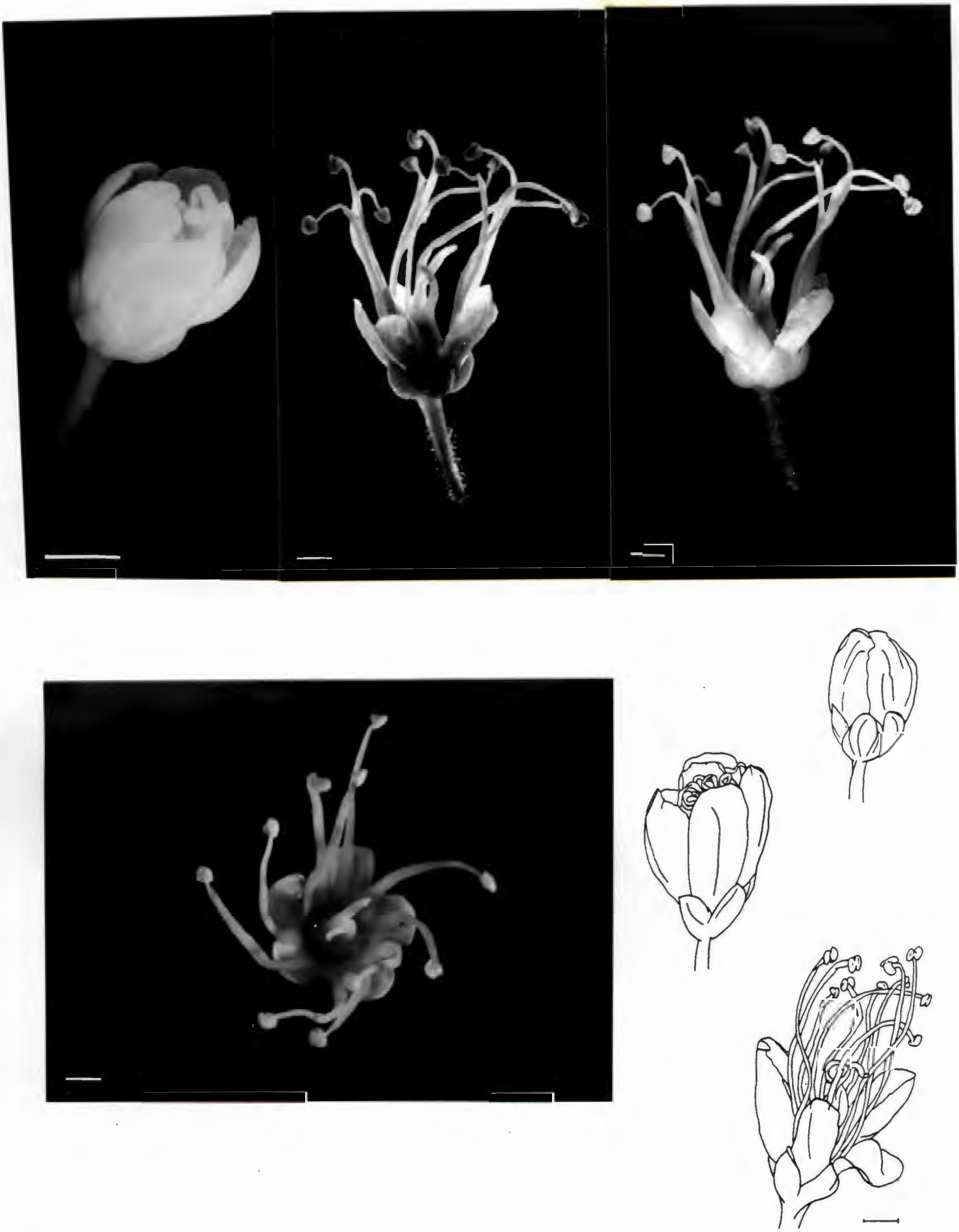


Figure 7. Floral development from bud to mature flower (scale bar = 0.75mm).

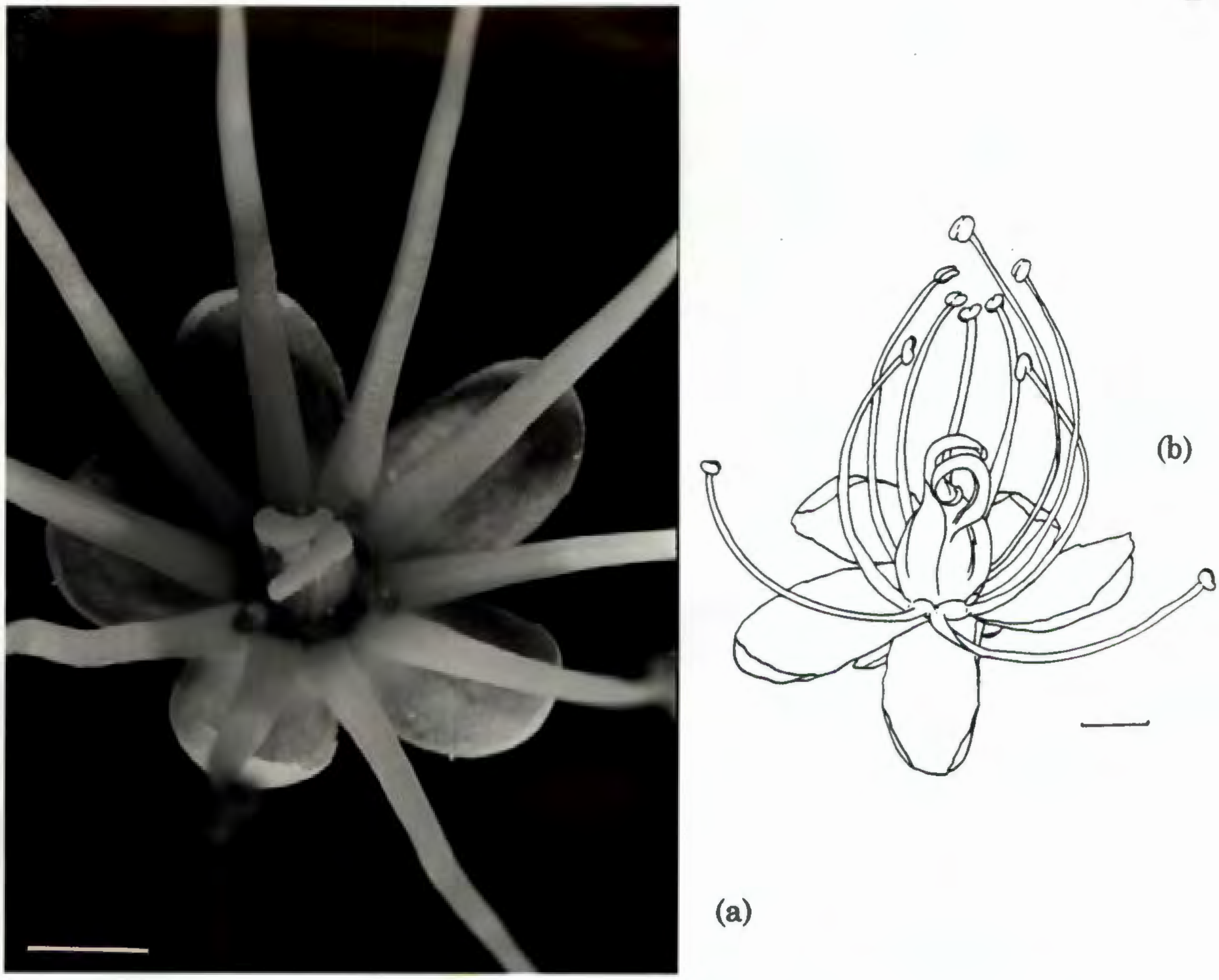


Figure 8: Mature flower top (a) and side (b) view (with front anthers drawn away in side view). Scale bar = 1.5mm

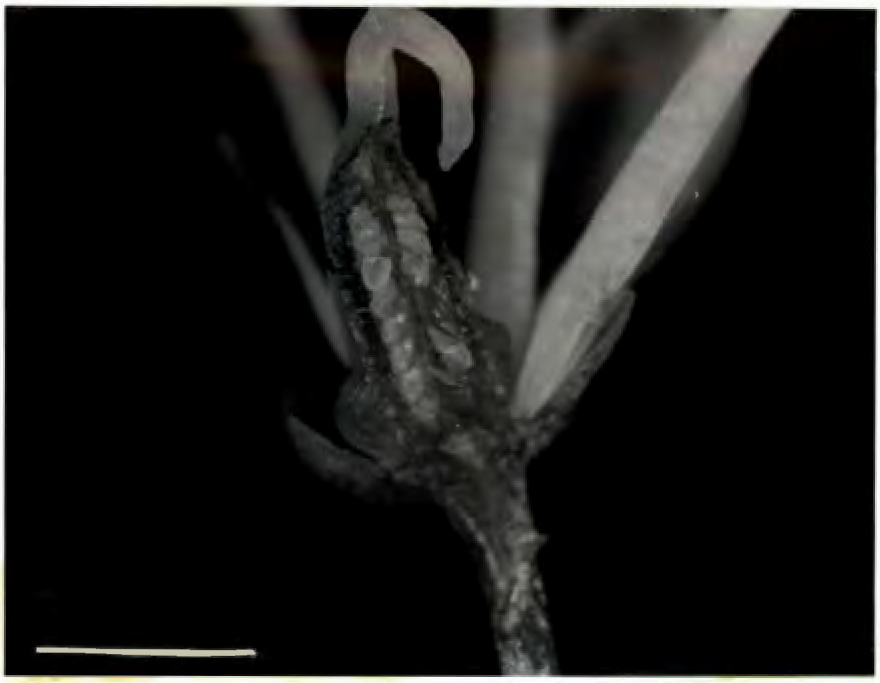


Figure 9: Half-section of ovary (1cm=1mm)

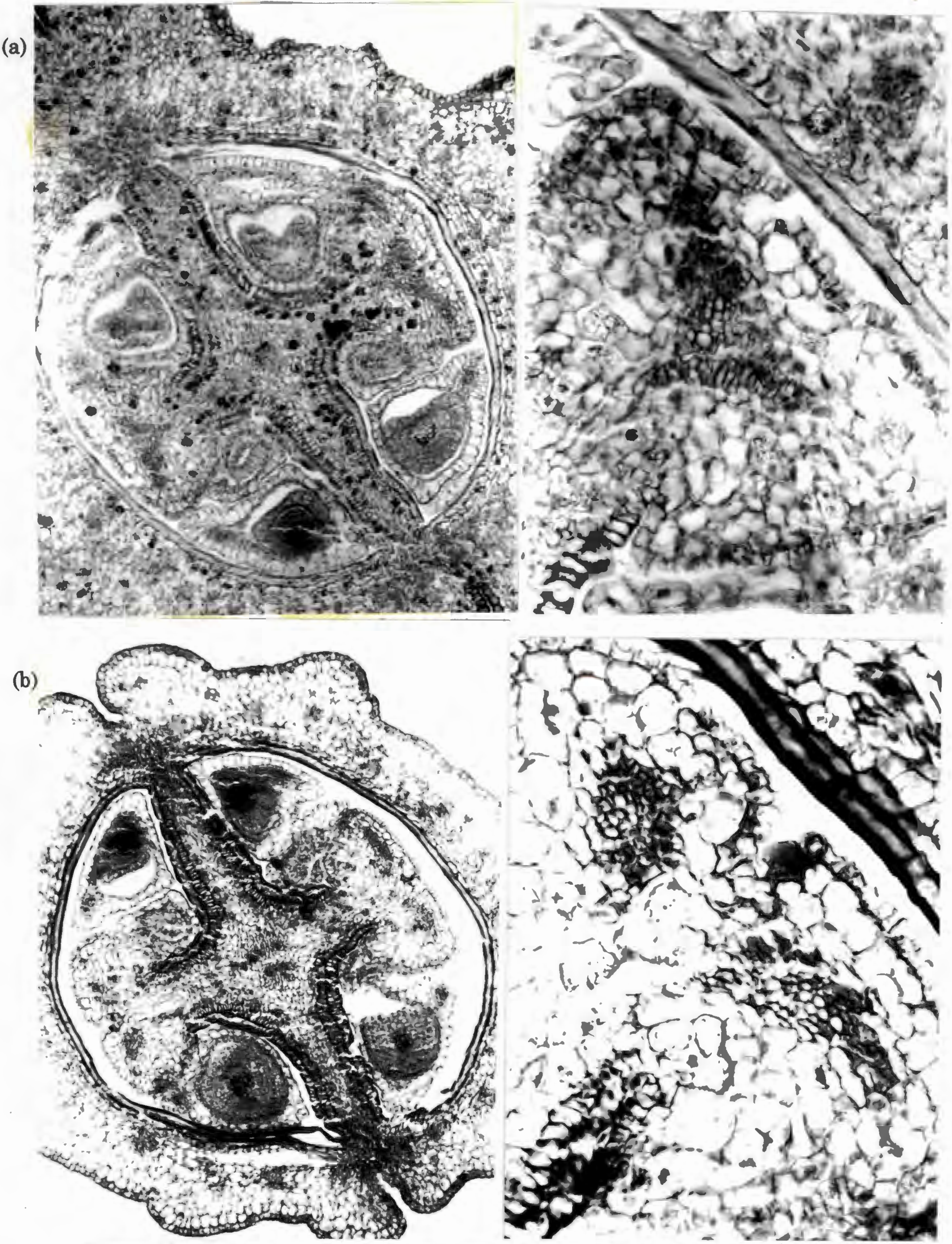


Figure 10: Ovular vascularisation at level of placentation (a), and midway through the gynoecium (b) (200X and 400X respectively for both a and b).

In contrast with the fruit capsules of other genera, those of *Cunonia* dehisce by means of acropetal separation of the carples from the persistent central column of tissue (figure 11). Being angular and winged, the seeds are then wind dispersed.

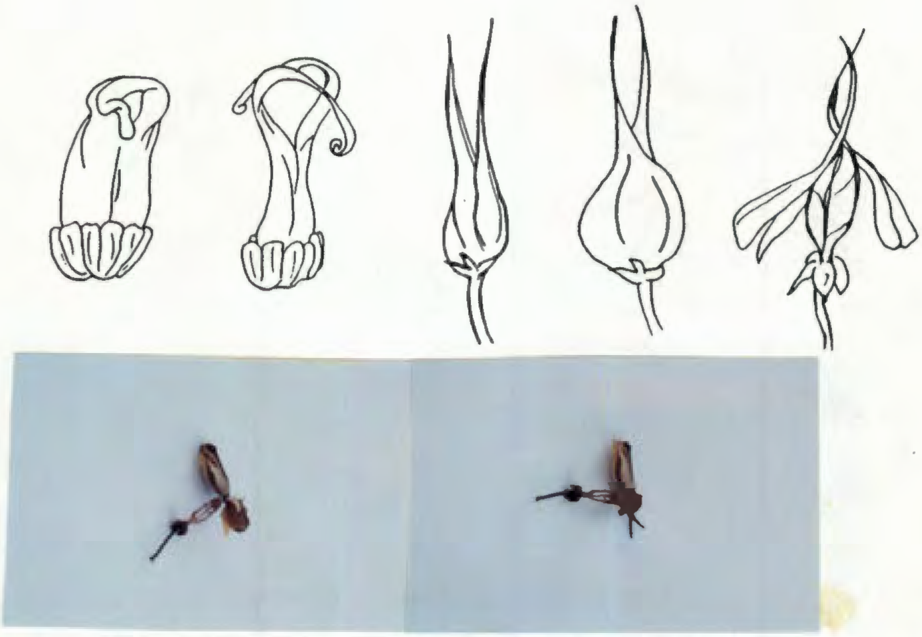


Figure 11: Development of fruit capsule (1cm=1mm); and mature fruit capsule photographed below (1.5X life-size).

ANALYSES

Analysis of Hufford and Dickison's original 44 character matrix on Hennig86 found 708 trees with a shortest length of 163 steps. The strict consensus was highly unresolved, collapsing all but seven of the nodes defined in the original analysis (Figure 12a). This may be attributable to the lack of specificity concerning variability between specific character states within a taxon. Re-analysis of Hufford and Dickison's matrix using PAUP produced a strict consensus tree identical to that presented in their paper (1992) (Figure 12b). Although the same number of shortest trees (i.e. 47) were recovered, the tree length was forty-three steps longer than was reported by Hufford and Dickison (1992).

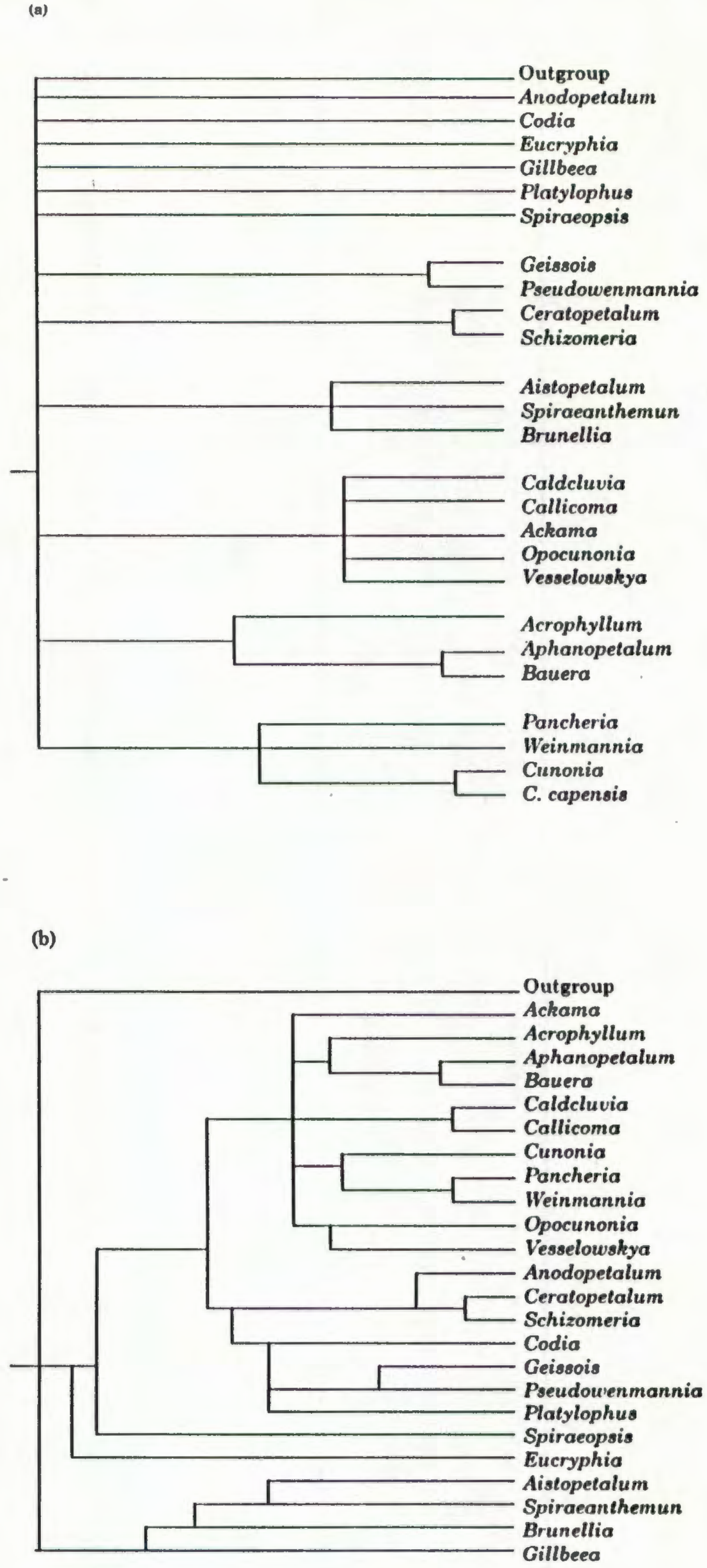


Figure 12: Strict consensus cladograms based on original matrix from Hufford and Dickison (1992) derived from Hennig86 (a) and PAUP (b).

Unrooted tree topologies based on the pollen characters described by Hideux and Ferguson, (1976) are presented in figure 13. Analysis of the data considering all multistate characters to be unordered resulted in the identification of four shortest trees, the strict consensus producing the highly resolved topology shown in figure 13(a). Re-analysis of this data, constraining several characters into an ordered sequence, produced the topology shown in figure 13(b). Fifteen trees were found in this search, and the clade containing *C. capensis* was broken down, causing *C. capensis* to be sister to, and nested within, the *Cunonia* clade.

The last set of analyses were based the matrix generated from the combined data sets of Hufford and Dickison (1992), and Hideux and Ferguson (1976) (modified, with ordered characters). Sixteen trees with a tree length of 313 steps were found. The strict consensus produced the cladogram presented in figure 14, showing weak resolution, but maintaining *C. capensis* sister to the *Cunonia* group.

The final tree topology, upon which the remainder of this paper is based, was derived from a successive weighting search of the modified, combined matrix (Figure 15). Only a single tree, in which *C. capensis* was again placed sister to the *Cunonia* group, was found. This was the most highly resolved tree recovered, having a tree-length of 308 steps, a Ci 0.55, and Ri 0.59. Support for the various nodes, as obtained from a bootstrap analysis, are printed on figure 15 (where the nodes without annotation scored less than 2.00).

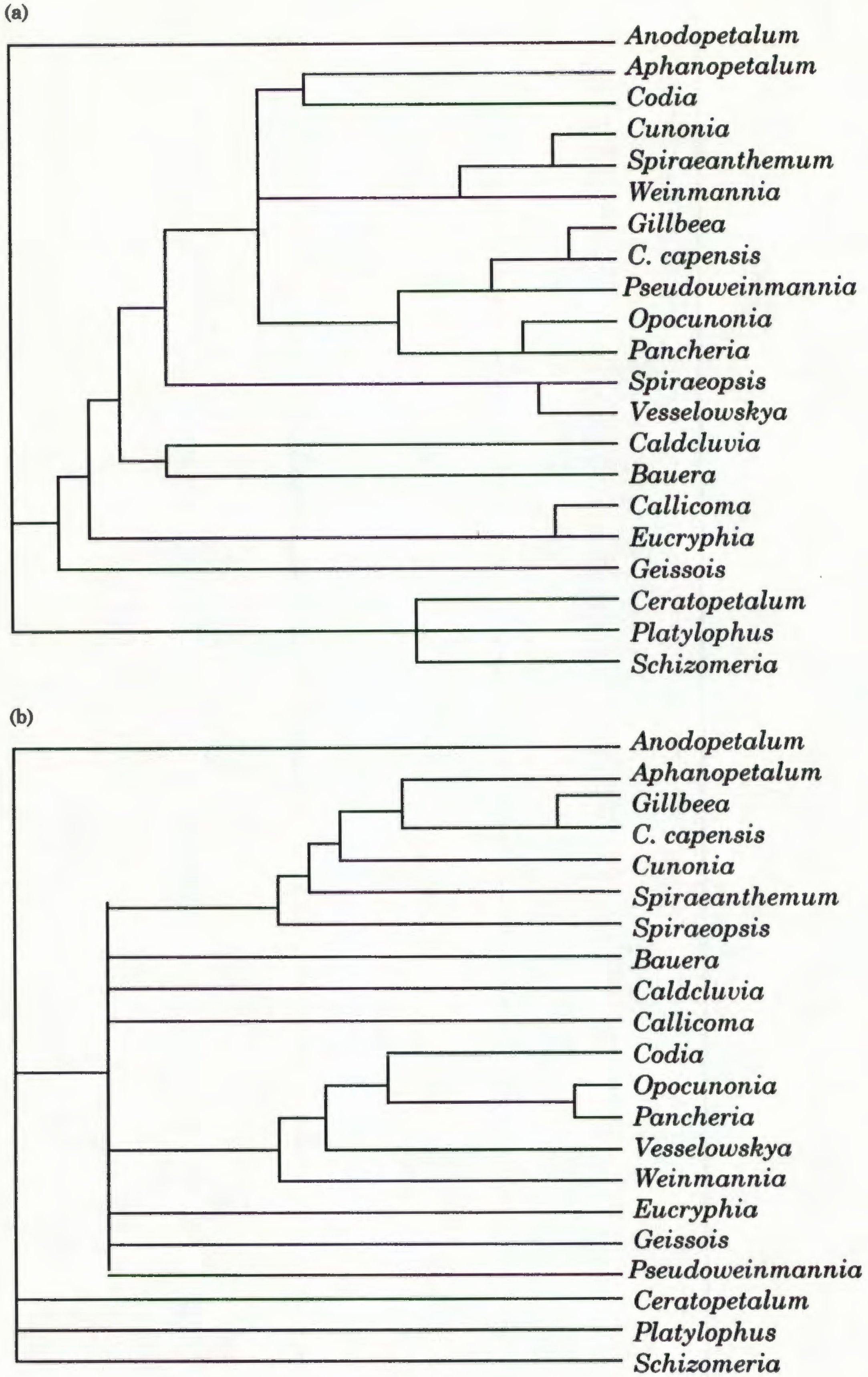


Figure 13: Strict consensus topologies from data matrix presented by Hideux and Ferguson (1976) based on unordered (a), and several ordered (b), pollen characters.

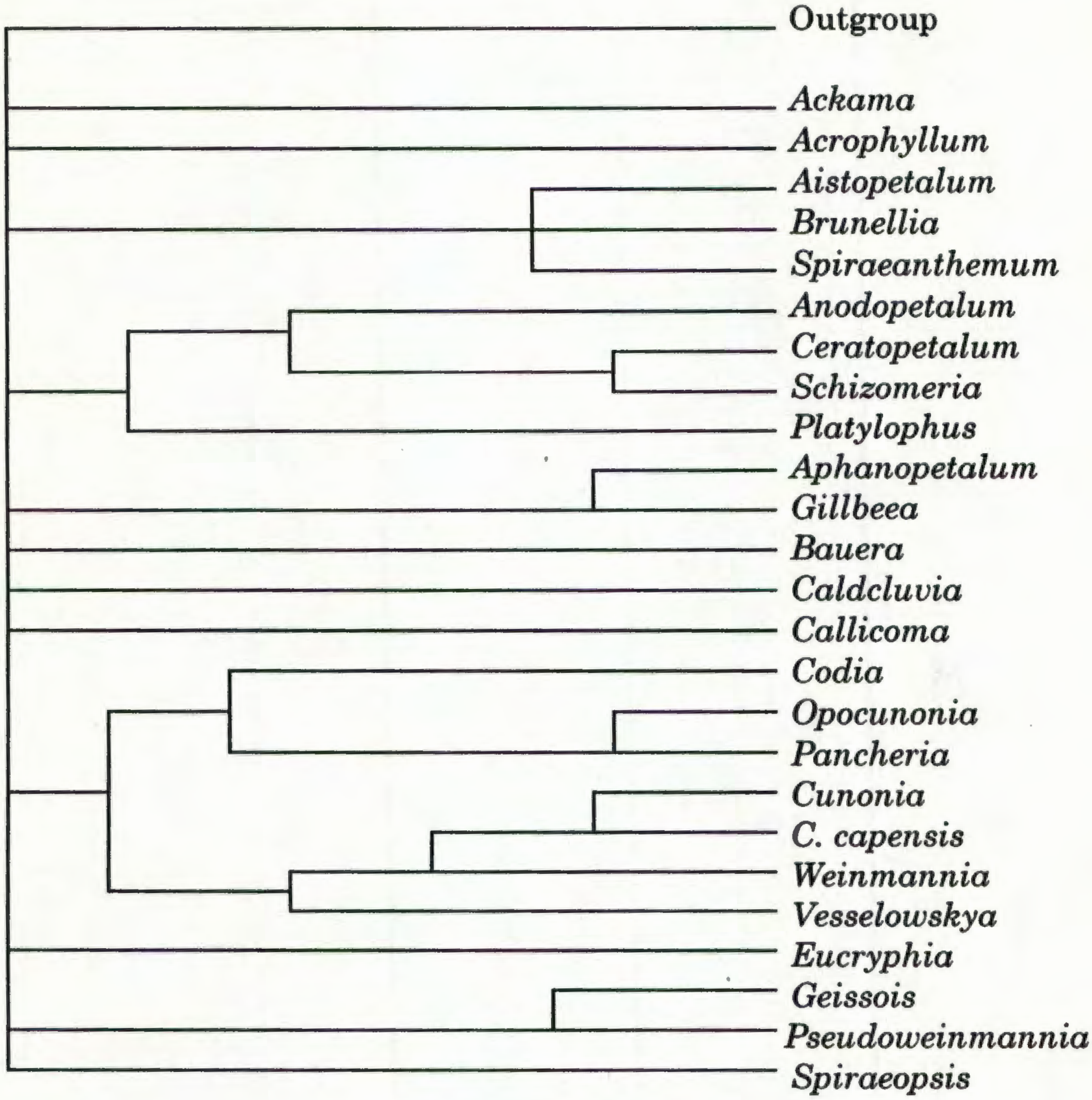


Figure 14: Strict consensus cladogram produced from (modified, ordered,) combined matrices.

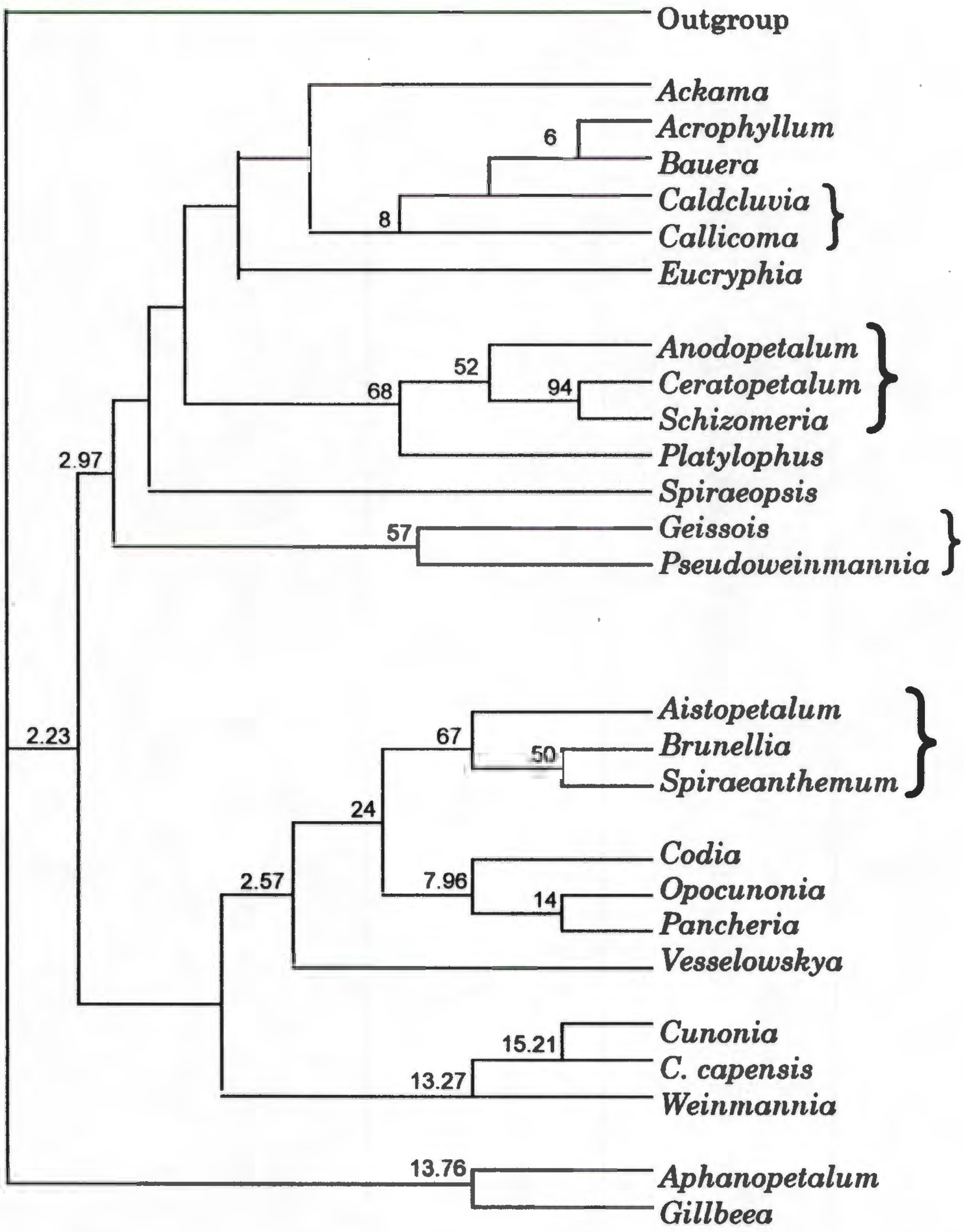


Figure 15: Successive weighting search based on combined, modified matrix (brackets indicate clades recovered as from Hufford and Dickison, 1992; numbers indicate support as derived from bootstrap analysis).

DISCUSSION

The cladogram derived from the successive weighting search has produced a number of distinct monophyletic groups, several of which remain as identified by Hufford and Dickison, 1992. Groups which have remained unchanged (from Hufford and Dickison's 1992 cladogram,) despite the addition of pollen characters and the isolation of *C. capensis* as an independent taxon, are bracketed in figure 15.

The results from the combined data sets show *Cunonia* to be the sister group of *C. capensis*, supporting either the placement of *C. capensis* in the correct genus, or it's similarity with the remaining members of *Cunonia*. The *Cunonia-C. capensis* clade is then positioned as the sister group of *Weinmannia*. This entire clade is constructed basal to two monophyletic clades (*Aistopetalum*, *Brunellia*, *Spiraeanthemum*; and *Codia*, *Opocunonia*, *Pancheria*), as well as *Vesselowskya* (Figure 15). This clade of three monophyletic groups, plus *Vesselowskya* differs from that found by Hufford and Dickison (1992) (Figure 12b). Hufford and Dickison (1992) suggested that *Weinmannia* was most closely affiliated with *Pancheria*, with *Cunonia* sister to the *Pancheria-Weinmannia* clade, this set then sister to *Vesselowskya*. Interestingly however, Hufford and Dickison do note that *Cunonia*, *Vesselowskya*, *Weinmannia*, and *Pancheria*, "may represent assemblages and/or segregates of a single monophyletic group," and that the "inclusion of paraphyletic groups in the analysis might have led to lack of resolution in this part of (their) cladogram" (1992:193).

C. capensis appears to have a correct taxonomic position when one excludes palynological structures from the investigation. Indeed, of the twenty pollen characters added to Hufford and Dickison's (1992) data set, eleven of them support the isolation of *C. capensis* from *Cunonia*.

Before considering the (primarily palynological) data supporting isolation of *C. capensis* from its genus, we will consider those characters which support the present taxonomic position of *C. capensis*.

Support for *C. capensis* in *Cunonia*

Although this successive weighting cladogram appears to depict a high level of resolution, it should be noted that no autapomorphic characters exist for neither the *Cunonia* - *C. capensis* group, nor the *Cunonia* - *C. capensis*-*Weinmannia* clade. Leaf areolation, medullary vasculature, ovular trace patterns, tectum differentiation, and sculptural elements, are the only characters supporting the *Cunonia*-*C. capensis* structure. Hufford and Dickison (1992), did propose acropetal fruit dehiscence as a tentative autapomorphy for *Cunonia*, however, due to the variability of fruit structure and dehiscence below genus level, this was not established in this investigation, (where fruit dehiscence was broadly described in terms of ventrally dehiscent, dry indehiscent, and fleshy indihiscent states). Clearly the capsule of *C. capensis* does undergo acropetal dehiscence, thus if this character is assumed to be autapomorphic, it does support the present taxonomic status of *C. capensis*.

Leaf areolation

Leaf areolation pattern is the most significant character supporting the *Cunonia* - *C. capensis* clade, with both *Cunonia* and *C. capensis* having an incomplete pattern, as opposed to the more common imperfect structure found for the majority of Cunoniaceae. Only three other genera (*Aistopetalum*, *Anodopetalum*, and *Aphanopetalum*) share this incomplete pattern with *Cunonia* and *C. capensis*.

As a character state of imperfect versus incomplete patterns, this character appears informative and rigorous. Unfortunately, upon closer investigation, differentiation between these two states becomes rather ambiguous. The appearance and characteristics of the areoles are based on a classification system concerning the architectural features of dicotyledonous leaves according to Hickey, 1973. 'Imperfect' areole development includes "meshes of irregular shape, more or less variable in size" (1973:32), whilst 'incompletely closed meshes' are those for which "one or more sides of the mesh are not bounded by a vein, giving rise to anomalously large meshes of highly irregular shape" (1973:32). The point at which anomalously large, highly irregular meshes, (incomplete areolation,) can be discerned from more or less variable, irregularly shaped meshes, (imperfect areolation), is subjective.

The following two characters illustrate the point noted by Dickison, (1975,) that "very few characters are uniformly found in all species", therefore many characters are "unable to provide immediate clues towards elucidating the relationships of cunoniaceous genera" (1975:275). For both medullary vasculature of the petiole, as well as ovary vasculature, the variability of these characters within genera weakens their value as informative characters.

Medullary vasculature

Within Cunoniaceae, major vasculation of the petiole is predominantly in the form of a nearly complete, usually adaxially flattened, medullated cylinder (Dickison, 1975). Only *Aistopetalum*, *Spiraeanthemum*, and *C. capensis* have a bundle-shaped arrangement of vascular tissue (within the cylinder structure). This would therefore seem an ideal character to define whether *C. capensis* is congruent with *Cunonia*. Unfortunately this is not possible, since shape of medullary vasculature is variable amongst several species of *Cunonia* (figure 16), resulting in the state of *C. capensis* being uninformative.

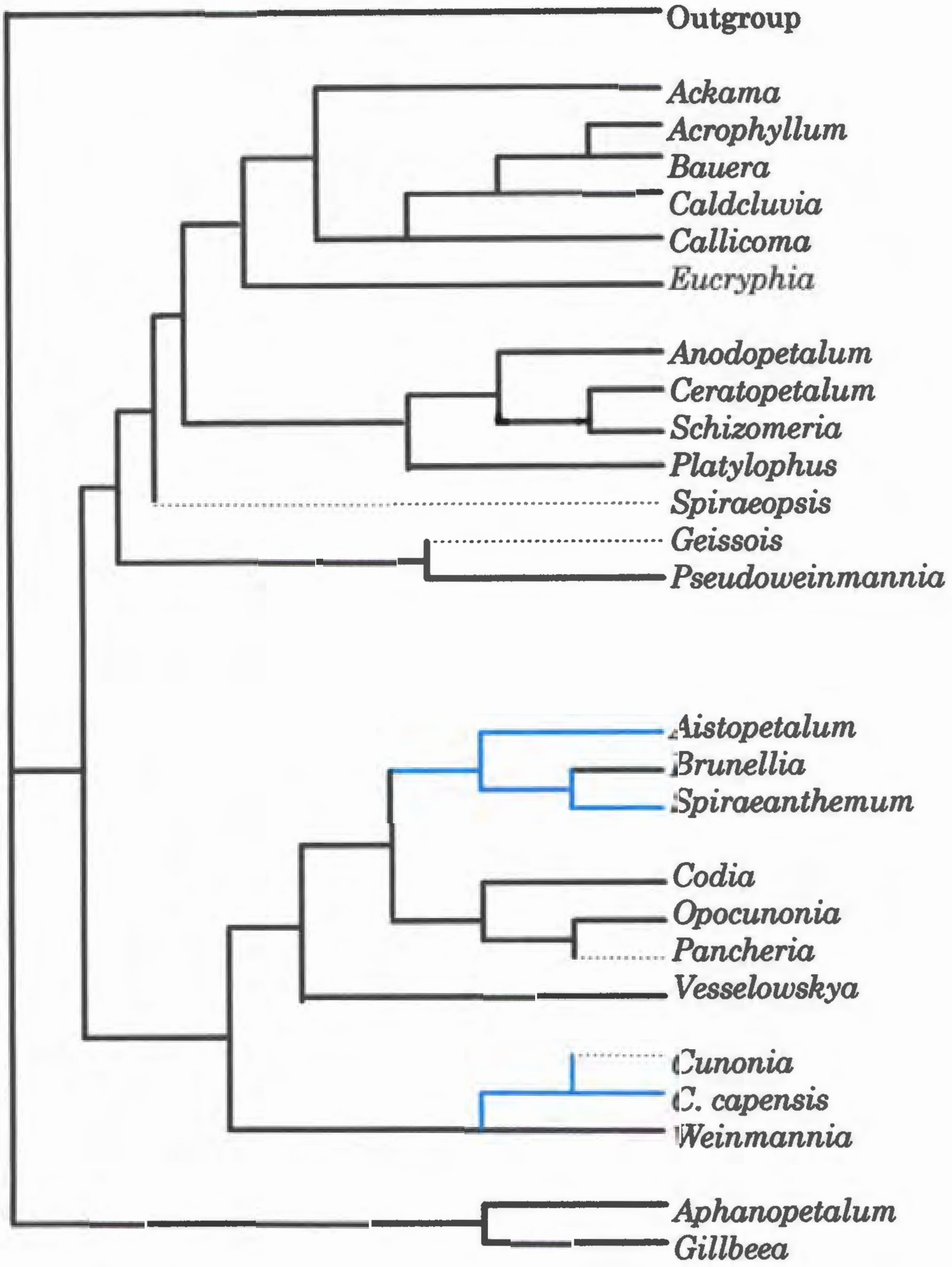


Figure 16: Cladogram showing distribution of medullary vasculature arrangement (black=medullary vasculature not bundle-shaped; blue=medullary vasculature bundle-shaped; dotted=variable state).

Ovary vascualture

The third character supporting *C. capensis* also results from this character being variable within *Cunonia* (figure 17). Carpels of Cunoniaceae are vascularised by a dorsal and two ventral bundles. The two pairs of ventral bundles supplying adjacent carpels are fused for *C. capensis*, *Cunonia*, and *Weinmannia* until, above the level of placentation, the united ventral strands separate, and enter the styles of adjacent carpels.

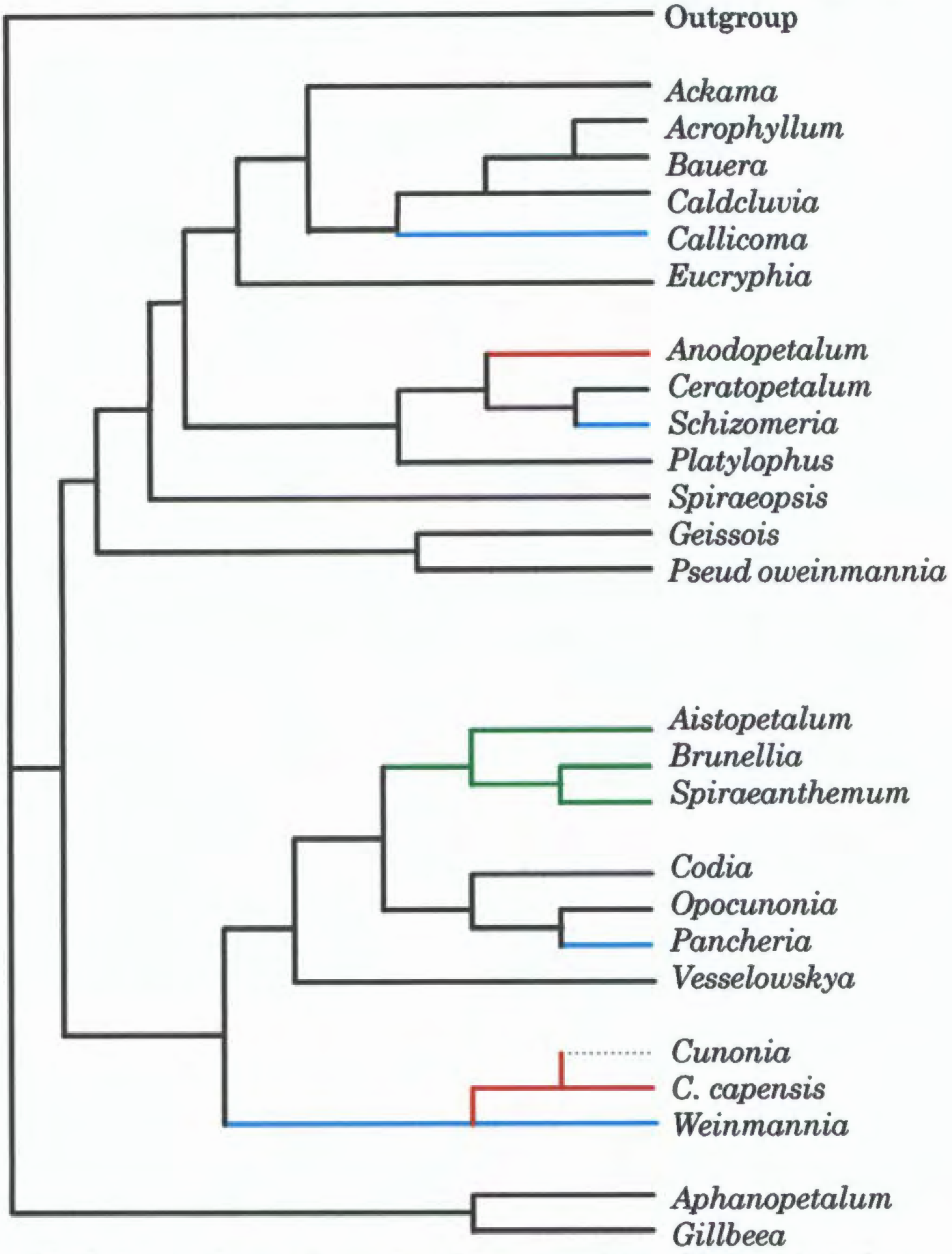


Figure 17: Cladogram showing distribution of ovary vasculature (black=originate from ventral bundles and remain separate; blue=originate from ventral bundles and anastomose; red=originate at base of locule; green=ovular traces separate from ventrals; dotted=variable character).

Ovary vasculature in *C. capensis* begins as a single, independent strand at the base of the locule. After traversing the septum in a position midway between the two pairs of united ventral bundles, the ovular trace bifurcates, prior to entering the placenta. For other members of *Cunonia*, such as *C. purpurea*, ovular vasculature also arises at the base of the carpel, but consists of several weak traces to each placenta, whilst remaining genera have ovules that are vascularised by veins which branch from the ventral carpellary bundles at the level of placentation (Dickison, 1975). This character clearly isolates the *Cunonia* group from *Weinmannia*, since the two ovular traces in each carpel of *Weinmannia*, (and *Pancheria, Schizomeria,* and *Callicoma,*) unite immediately after diverging from the ventral, and do not separate until they have entered the placenta.

The last two characters identified between the nodes separating *Weinmannia* from *C. capensis* and *Cunonia* arise from the pollen data set, and suggest the presence of *C. capensis* as an intermediate between these two genera. *C. capensis* might be considered an intermediate in that it has rugulate-reticulate sculptural elements, and a partially-complete tectum, whereas *Weinmannia* has reticulate sculptural elements and a partially perforate tectum, and *Cunonia* completely perforate sculptural elements, and a complete tectum (figure 18) (Hideux and Ferguson, 1976).

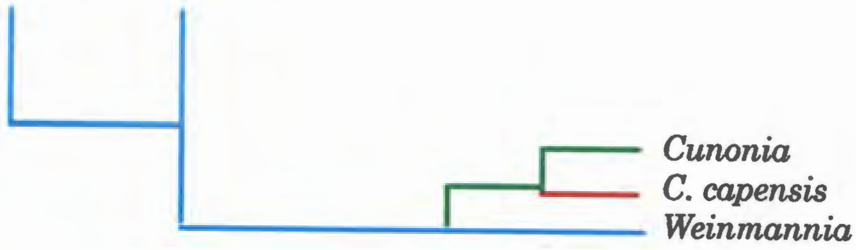


Figure 18: Extract from cladogram showing pollen character states (blue=partially perforate tectum with reticulate sculptural elements; green=complete tectum with perforate sculptural elements; red= partially-complete tectum and rugulate-reticulate sculptural elements).

Support for isolation of *C. capensis* from *Cunonia*

The only characters supporting the separation of *C. capensis* from *Cunonia* are those derived from the pollen data set. The differences between the pollen of these two groups is extreme, causing them to be completely separated from each other during analyses of the pollen data sets (figure13a and b).

When the pollen characters are mapped onto the tree, it is clear that, aside from isolating *C. capensis*, and supporting the two clades plus *Vesselowskya* sister to the *C. capensis, Cunonia,* and *Weinmannia* group, the pollen data is complementary to those characters described by Hufford and Dickison (1992). It is surprising that Hufford and Dickison (1992) did not consider including the vast number of pollen characters generated by Hideux and Ferguson (1976) into their data set. Instead of incorporating the work by Hideux and Ferguson (1976), Hufford and Dickison (1992) only coded pollen as a single character, tricolporate versus syncolpate. Not only is this a simplification of reality, but it is inaccurate. Hideux and Ferguson (1976) note that apertural association involves colpate, colporate, and modified colporate states.

Hufford and Dickison (1992) provide only brief mention of the hypothesis suggested by Hideux and Ferguson (1976) that *Pancheria* might well be more similar to *Vesselowskya,* and *Cunonia* more closely related to *Weinmannia,* as has been reflected in my results. Since the addition of pollen characters has an enormous effect in terms of resolving distinct monophyletic groups, (specifically in the *C. capensis- Cunonia- Weinmannia* and associated regions,) and since Dickison, in all his papers regarding Cunoniaceae, failed to extract available material concerning palynological relationships within the Cunoniaceae, these potentially informative characters, and their distribution as determined from my successive-weighting cladogram, will be discussed below.

Discussion of Pollen Characters

All cunoniaceous genera have isopolar pollen grains, i.e. the proximal and distal faces look alike. Pollen within the Cunoniaceae have second and third order radial symmetry, this character supporting two monophyletic groups (Figure 19). All Cunoniaceae genera contain single pollen grains (Hideux and Ferguson, 1976) (i.e. grains which, when mature, do not remain united with other pollen grains), and are thus referred to as monads (Erdtmann, 1992).

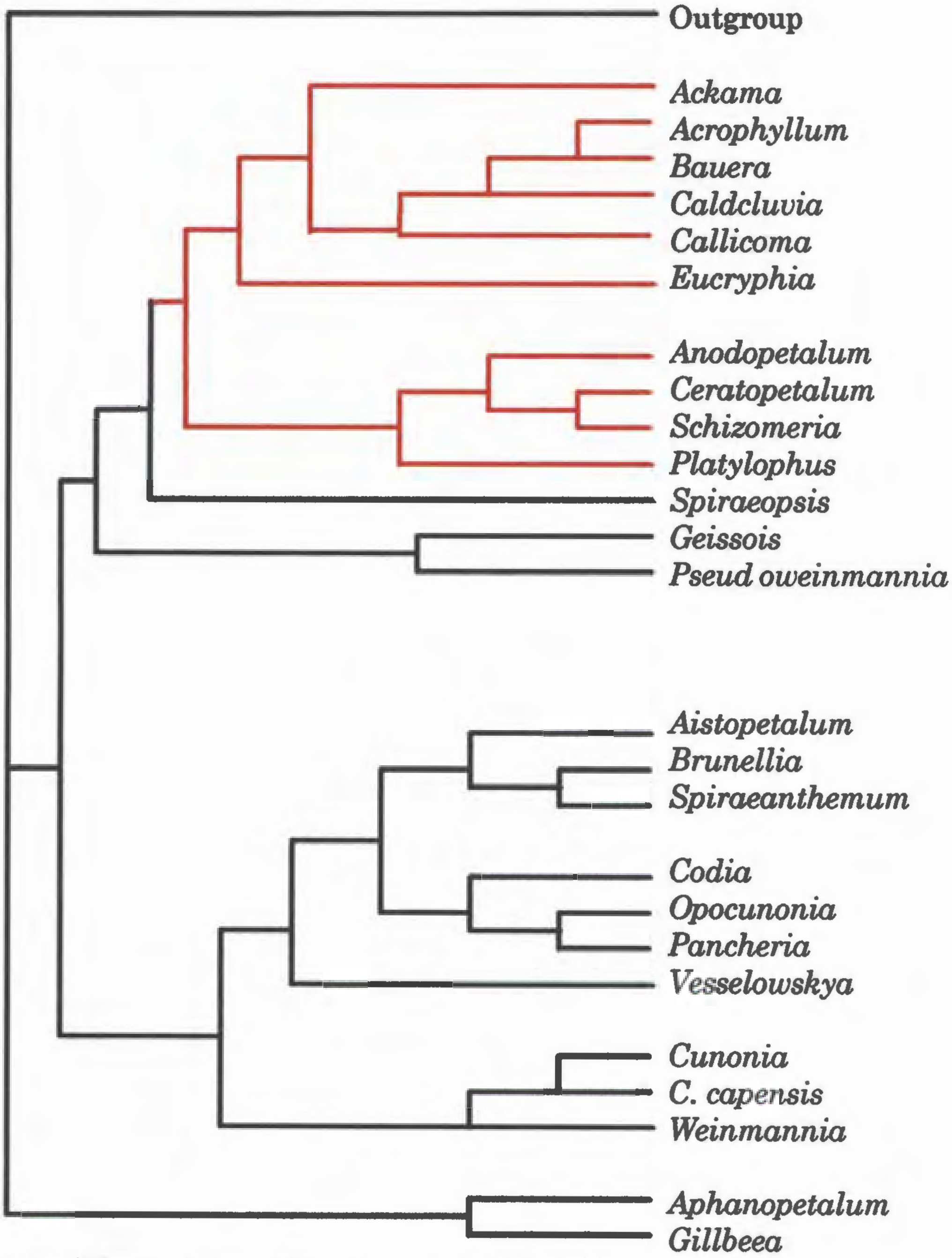


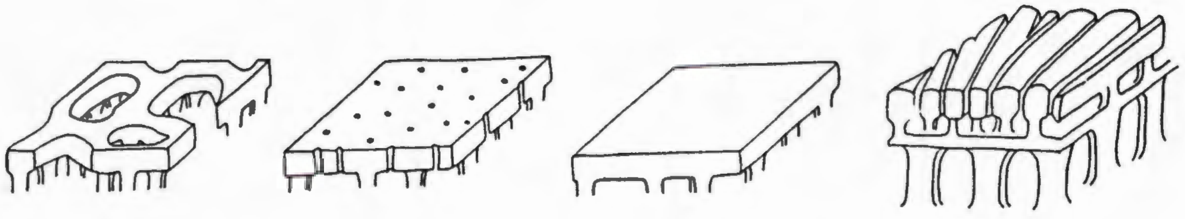
Figure 19: Cladogram depicting second (red) and third (black) order radial symmetry.

In regular, radially symmetrical pollen grains with several planes of symmetry, the equator runs round the surface of the pollen grain midway between the poles. For the majority of members in this family, the pollen grains are roughly spherical, with both the equatorial diameter, and the polar axis ranging between 10 and 15 μm. Similarly all Cunoniaceae genera, except *Codia*, have an exine thickness which does not exceed 1 μm (for *Codia* it ranges between 1-2 μm) (Hideux and Ferguson, 1976).

Tectum

The tectum, or outer layer of the sexine, may be closed (complete), incomplete (open or partially closed) or comprise of an intermediate between these two (figure 20). A partial tectum is a very common tectum type for this family. Partial tectum types include perforate, (characterised by densely distributed small circular lumina,) perforate-partial, perforate-complete, and partial-continuous tectum types

The primary criterion for the recognition of this tectum type is the ratio of muri and lumina width, although it is also recognised through the visibility of columellae in oblique view through the lumina (Hideux and Ferguson, 1976). Only *Aphanopetalum* has a complete tectum, whilst only *C. capensis*, has a "partial-complete" tectum. A partial-complete tectum is considered a transitional type between partial, densely reticulate, and complete tectum types (Hideux and Ferguson, 1976).

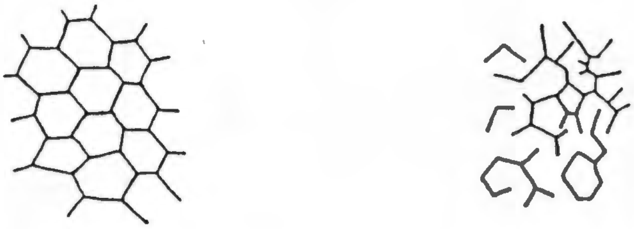


(a) Partial (b) Perforate (c) complete (d) complete heterogenous

Figure 20: Tectum types in Cunoniaceae (Hideux and Ferguson, 1976).

For most of the family the tectum is a homogenous set or layer, without structure. *C. capensis*, *Platylophus* and four other genera are the only exceptions, having a heterogenous tectum divided into subunits (Hideux and Ferguson, 1976). In contrast, the nexine-2 is predominantly heterogenous for Cunoniaceae, with thickening in relation to the ectoapertural foldings (Hideux and Ferguson, 1976).

A reticulate arrangement of the sculptural elements which constitute the tectum is the most common pattern (figure 21a). *C. capensis*, *Gillbeea*, and the monophyletic group containing *Anodopetalum, Ceratopetalum, Schizomeria*, and *Platylophus,* all show a rugulate-reticulate arrangement however, (figure 21b), whilst the remainder of the *Cunonia* genus, *Ackama, Aphanopetalum*, *Opocunonia* and *Pancheria* lack sculptural elements (figure 22) (Hideux and Ferguson, 1976).



(a) Reticulate (b) Rugulate reticulate

Figure 21: Disposition of sculptural elements (Hideux and Ferguson, 1976)

For the most part, lumina are of equal proportions, (lumina length equaling width,) such as for, amongst others, *Weinmannia, Vesselowskya, Pancheria*, and *Cunonia* (excluding *C. capensis).* For a few members of this family, lumina length:width ratios may range from equaling 1, to being greater than one, whilst *C. capensis* is unique as the only member of this family with the lumina always being longer than they are wide (Hideux and Ferguson, 1976).

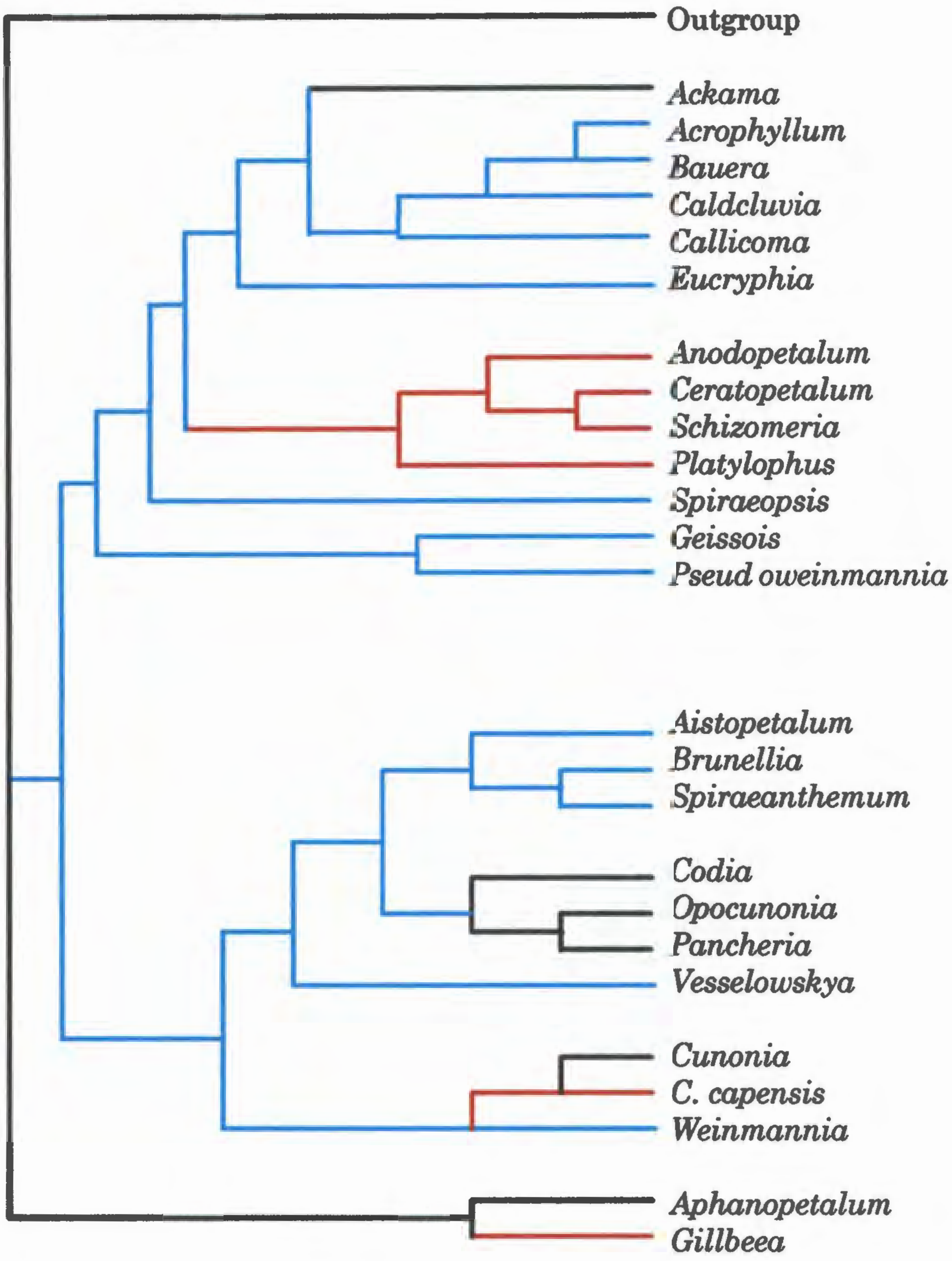


Figure 22: Distribution of sculptural element disposition (blue=reticulate; red=rugulate-reticulate; black=lack elements)

Lumina shape ranges from lumina absence, through large lumina with plan (or convex) sides, to acute (or obtuse) angled lumina. An intermediary form between large convex-sided obtuse angled and plan-sided acute angled lumina are dominant for this family (highlighted in blue on figure 23). *C. capensis, Vesselowskya, Bauera* and *Gillbeea* have large plan-acute lumina, whilst the rest of *Cunonia*, along with *Pancheria, Opocunonia* and *Spiraeopsis*, have perforations and linear reduced lumina (Hideux and Ferguson, 1976).

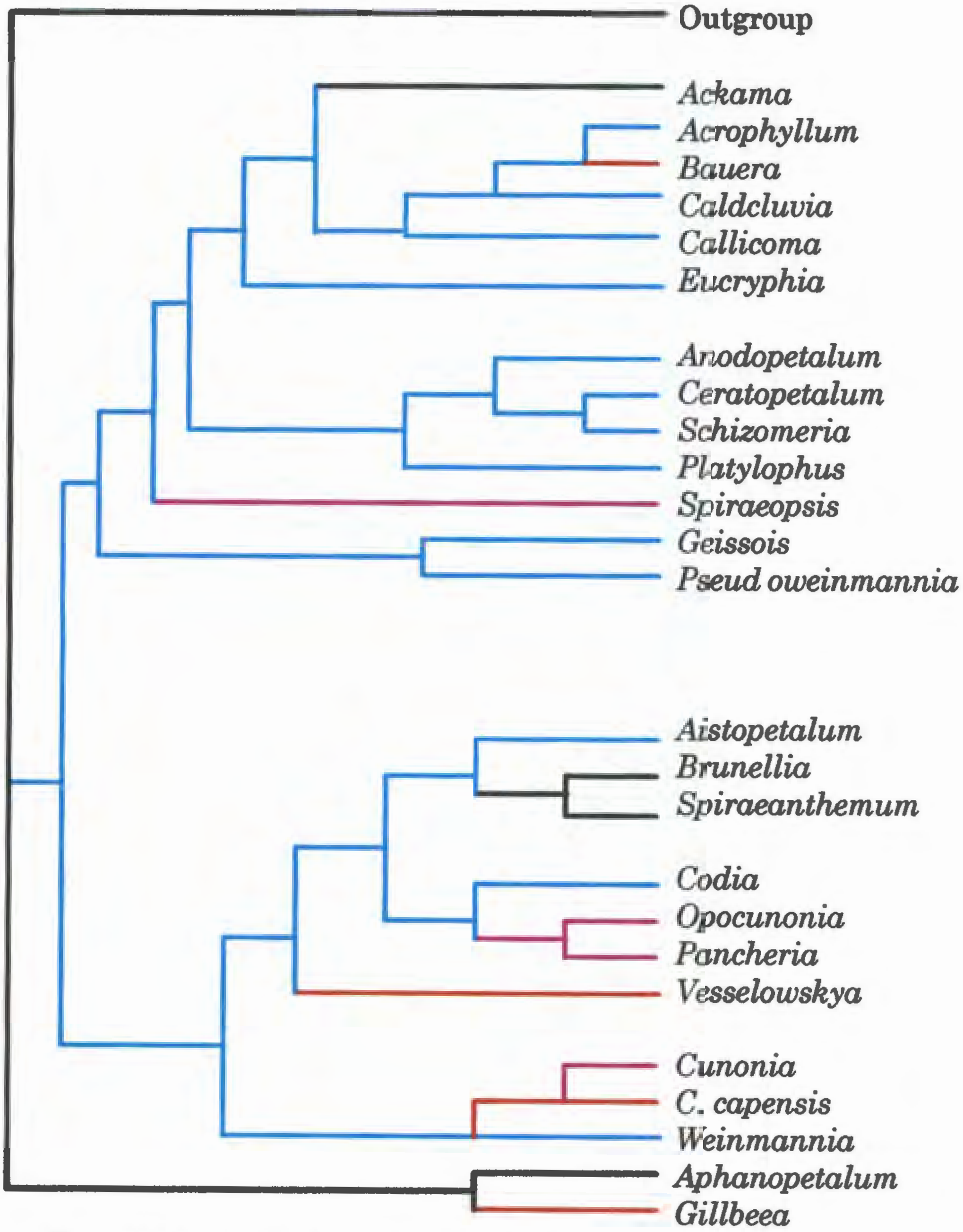


Figure 23: Distribution of lumina shape (Red=large lumina; blue=intermediate; purple=perforated; black=lack lumina)

Lateral meridional thinning of the exine is usually absent in the Cunoniaceae (including for *C. capensis,* highlighted blue in figure 24,) although a short, H-shaped endoaperture does appear to have been derived for the clades nested within the *Cunonia- C. capensis- Weinmannia* group (highlighted red in figure 24). An intermediary form of exine thinning, without the creation of a distinct apertural shape, only occurs for the *Weinmannia* and remaining *Cunonia* genera (shown in green on figure 24).

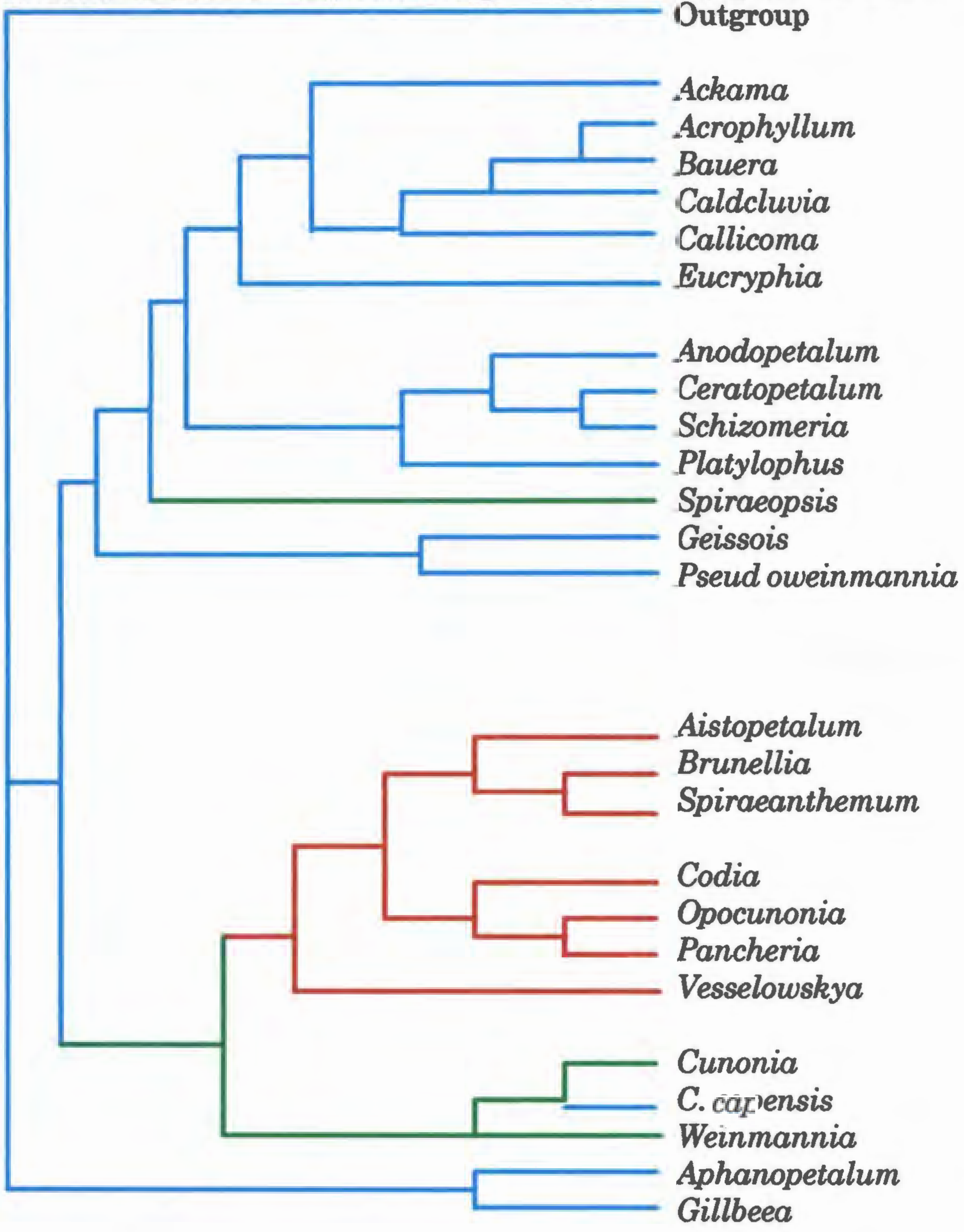


Figure 24: Distribution of meridional thinning of endexine (blue=absent; green=barely distinct; red=H-shaped)

Apertures:

Apertures are any weak, preformed part of the general surface of a pollen grain which may be engaged, directly or indirectly, in forming an opening for the normal exit of material in connection with the germination of a pollen grain or spore (Erdtman, 1992). In this discussion, the terminology of the apertures will be following that of Hideux and Ferguson, (1976) where ectoapertures (ECA) are modifications of the ectexine (sexine, according to Erdtman, 1992); and endoapertures (EPA), are modifications of the endexine (nexine-2, according to Erdtman 1992).

The optical equatorial view, based on light microscopy, shows that all members of Cunoniaceae (excluding *Bauera, Gillbeea, Aphanopetalum, Aistopetalum* and *Cunonia*, but including *C. capensis,*) possess an obtuse apertural angle, with a convex interapertural zone (figure 25a). *Bauera* has an obtuse angled aperture, but a lobate interapertural zone; whilst the remaining genera have a subtriangular equatorial view (Hideux and Ferguson, 1976).

Figure 25: Aperture characteristics: equatorial view (a), and meridional view (b), showing planes of symmetry (Erdtman, 1992)

Another quasi-geographical term, meridional, implies an orientation in a pole-to-pole direction, at right angles to the equator (Erdtman, 1992). The optical meridional view, as observed through light microscopy, shows wide variation from circular or subcircular (for *Cunonia* excluding *C. capensis,* highlighted in green on figure 26) through oval (for *C. capensis* L. and others depicted in black on figure 26), to rectangular or subhexagonal in shape (for *Bauera* only).

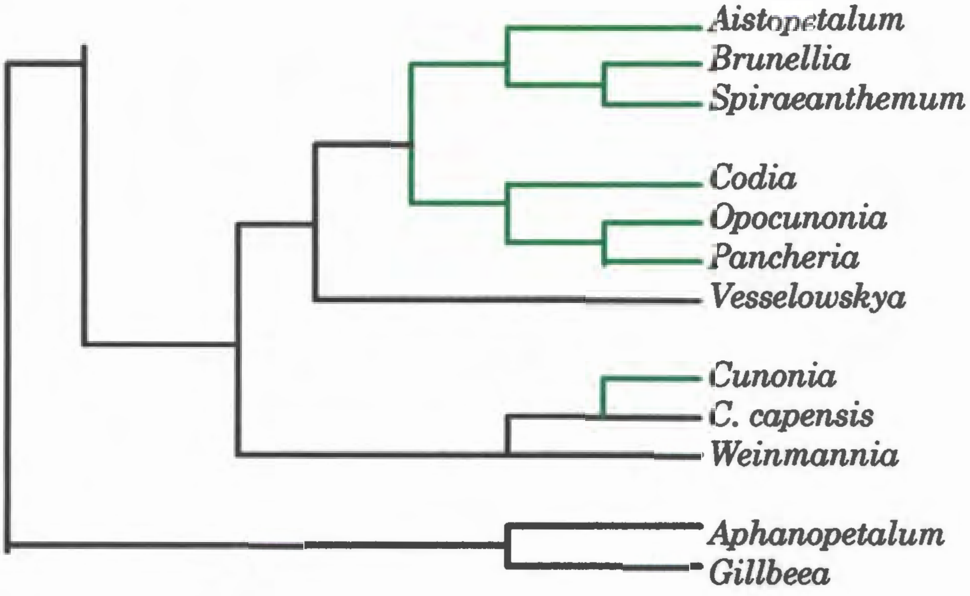


Figure 26: Extract from successive weighting cladogram, circular or subcircular optical meridional view highlighted in green, oval view in black.

All members of the Cunoniaceae have ectoapertures with long meridional furrows, although in *Bauera* and *Gillbeea* these occur more as "belt-like" meridional furrows (Hideux and Ferguson, 1976). *C. capensis* is the only member of its family to have colpate pollen (unbranched, furrow-like apertures which are at least twice as long as they are broad (figure 27a). Scanning electron microscopy study reveals a narrow, discrete ECA, but the presence of an ENA is uncertain. According to Hideux and Ferguson (1976), the absence, or the presence of a very discrete ENA is significant. In their study of the entire Saxifrigaceae sense lato, they conclude that the pollen of *C. capensis* "appears especially interesting", with this type having the possibility of representing a fundamental pollen type in the evolutionary origin of apertural structures (Hideux and Ferguson, 1976).

The remainder of the family have colporate pollen grains (figure 27b). Colporate grains being those which are compound, consisting of an outer, or marginal, colpal (furrow-like) part, and an inner, or central, often not very distinctly delimited oral structure (Erdtman, 1992).

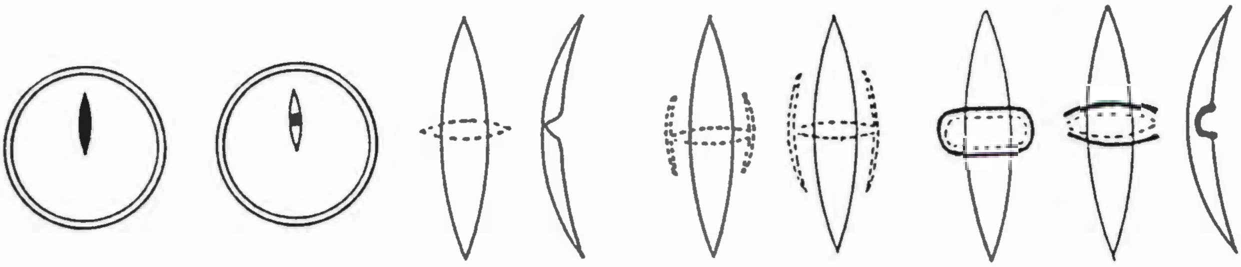

(a) colpate (b) colporate (c) simple (d) simple-complex (e) complex

Figure 27: Apertures found in Cunoniaceae (Hideux and Ferguson, 1976)

Various types of endoapertures, along with intermediate forms, can be distinguished (figure 28). Modification of the endexine into a distinctly interrupted region is referred to as "simple ENA" (figure 27c), and occurs in the larger number of genera in Cunoniaceae, excluding *Cunonia*, but including *C. capensis* (shaded blue in figure 28) . Complex endoapertures (figure 27e) are only found nested within the *C. capensis- Cunonia-Weinmannia* clade (shaded red,) whilst *Cunonia, Weinmannia, Acrophyllum,* and *Bauera* appear to be a transitional form (shaded green), with simple-complex endoapertures (figure 27d) (Hideux and Ferguson, 1976).

Whilst many of the pollen characters support the separation of *C. capensis* from *Cunonia*, a number of them do not support the *Weinmannia -C. capensis-* and *Cunonia* monophyly at all. In the three pollen tectum character distributions plotted, (figures 22-24), not only is *C. capensis* distinct to *Cunonia*, but for two of the characters, three different states are distributed across the *Weinmannia -C. capensis-* and *Cunonia* clade. This re-occurs for the apertural characteristics plotted in figures 26 and 28. Ultimately the lack of support for *C. capensis- Cunonia - Weinmannia* monophyly based on pollen characters is weak, thereby forcing one to consider the possibility that, like Hufford and Dickison (1992), inclusion of paraphyletic groups might well exist in this analysis.

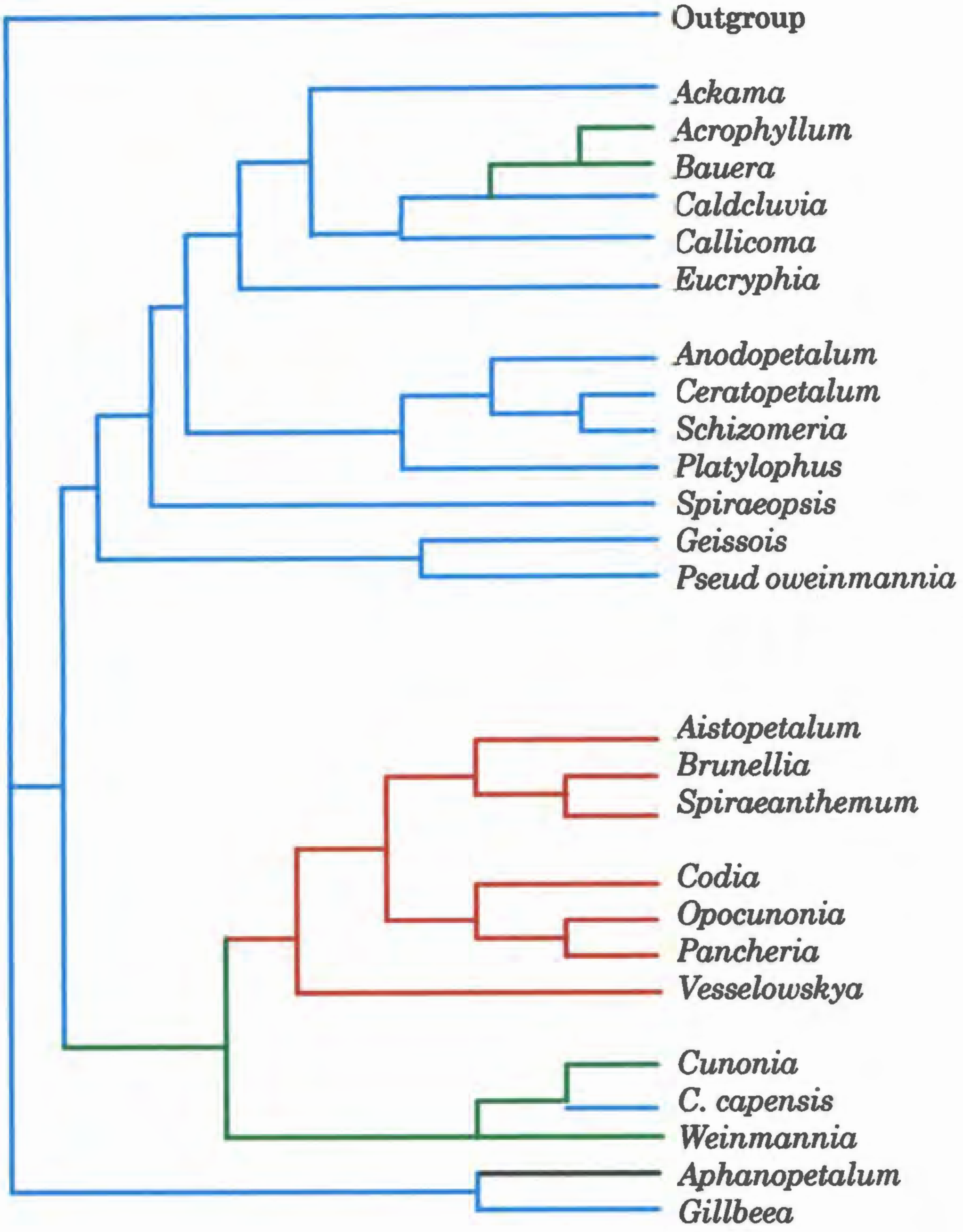


Figure 28: Extraction from successive weighting cladogram with endoaperture character distributions (blue=simple; black=simple-diffuse apertures; green=simple-complex; red=complex endoapertures)

From this extended discussion concerning pollen characters, it should be evident that further investigation into this area needs to take place. The palynological structures described in this analysis provide some of the strongest consistency and retention indices for this cladogram, and appear to give strong support for the isolation of *C. capensis* from its genus.

General discussion of other characters

Whilst the pollen data is variable, the morphological data derived from Hufford and Dickison (1992) seems to strongly support the *C. capensis*, *Cunonia*, and *Weinmannia* group. The presence of foliar sclereids, a foliar hypodermis with mucilage cells, and anisocytic stomata, are common for all members of this clade (although both foliar hypodermis and stomatal structure are variable within the terminal of *Weinmannia*).

Although bootstrap values derived for the entire monophyletic group from *Aistopetalum* to *Weinmannia* are low, those values generated for several of the clades within this group are relatively high, and several characters to suggest monophyly for this group. These characters include foliar, reproductive, and palynological structures, which will be elaborated upon below.

Terminal idioblasts

Terminal idioblasts, specialised elements which terminate the leaf veinlets, are found in all members of this potentially monophyletic group, (shown in red on figure 29), although this character has been lost in *Opocunonia* and *Vesselowskya,* whilst *Caldcluvia* and *Ceratopetalum* appear to have acquired terminal idioblasts (Dickison, 1975).

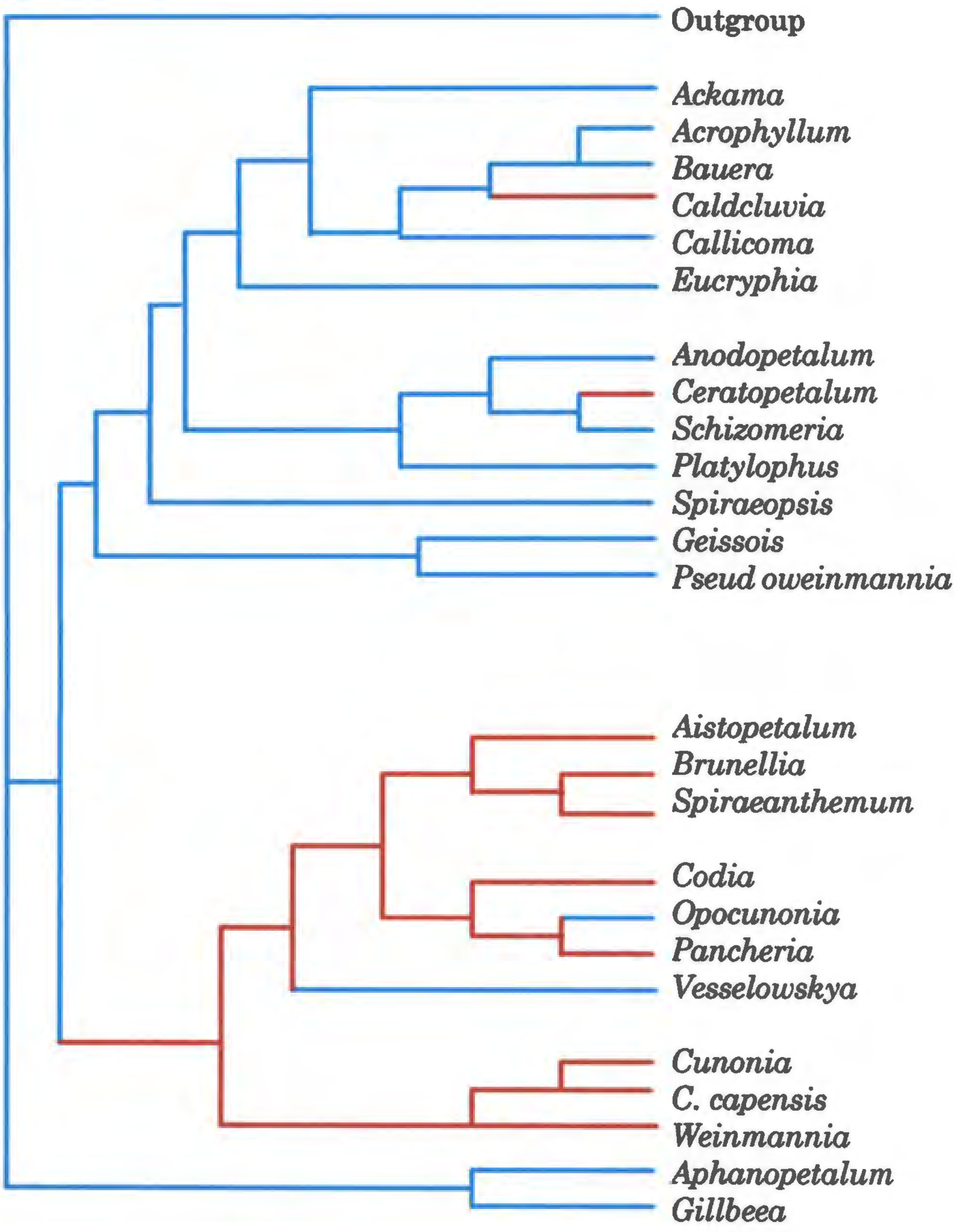


Figure 29: Character distribution of terminal idioblasts (Blue=absent; red=present)

This basal monophyletic group might also be characterised by the vessel distribution of solitary vessels, or in radial multiples up to nine (red shading figure 30), and a distribution whereby the vessels are found infrequently in pairs, or in radial orders up to three (blue shading figure 30). The presence of this third radial order in both the outgroup, *Aphanopetalum* , *Gillbeea*, and *Ackama* to *Callicoma* group weakens this distinction however.

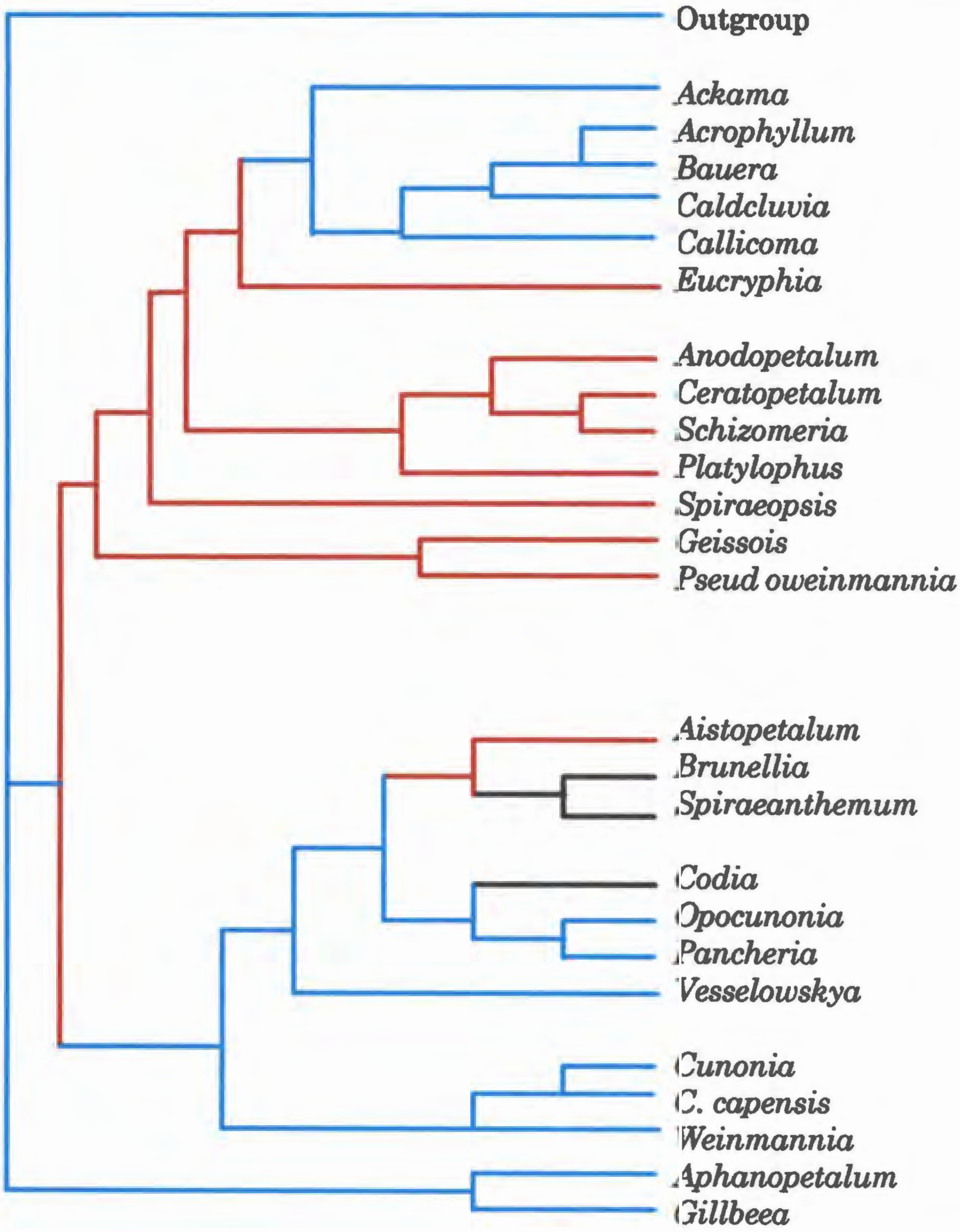


Figure 30: Vessel distribution (black=vessels solitary; blue= radial order of 3; red=radial order of 9)

The final character supporting this basal monophyly is that of calyx aestivation. For the majority of this family, aestivation is valvate, however for the *C. capensis*-*Cunonia* - *Weinmannia* clade, as well as for *Vesselowskya*, *Pancheria*, and *Eucryphia*, the calyx is imbricate during aestivation (highlighted red in figure 31). Hufford and Dickison (1992) suggest that *Cunonia* , *Vesselowskya*, *Weinmannia*, and *Pancheria*, may represent a single monophyletic group, with the autapomorphy of imbricate perianth aestivation, however they fail to describe where *Eucryphia* would then fit into this hypothesis. The polymorphic state occurring for this character in *Ceratopetalum* and *Codia* further defies this hypothesis.

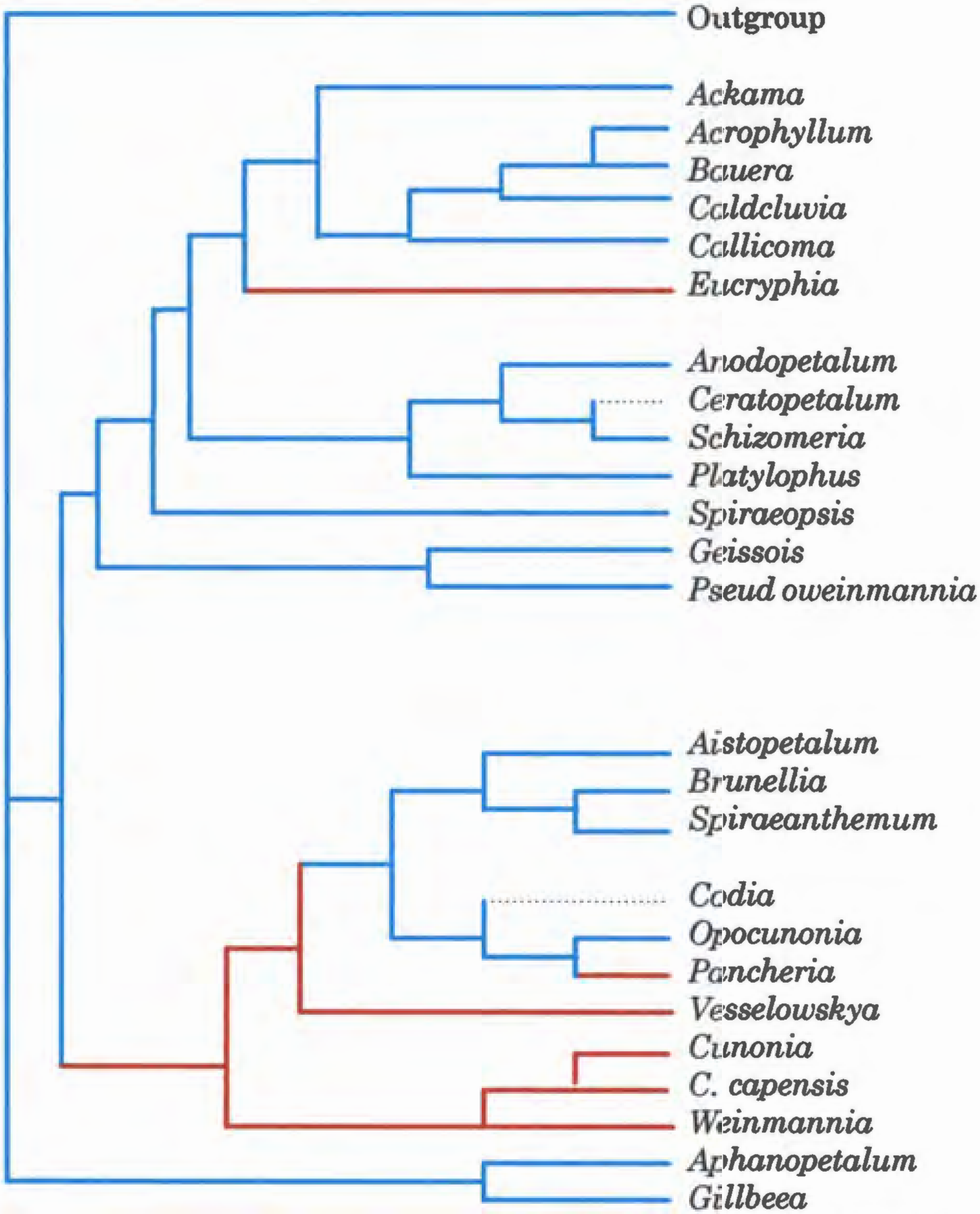


Figure 24: Calyx aestivation distribution (blue=valvate; red=imbricate; dotted=polymorphic)

CONCLUSION

It is unfortunate that no characters derived from investigation into wood anatomy (Dickison, 1980) were informative with respect to identifying the relationship of *C. capensis* within *Cunonia* and *Weinmannia,* all of whom share the same character states (Hufford and Dickison, 1992). Similarly the work by Bate-Smith (1977), was in agreement concerning the phenolic chemistry within these genera. Improved embryological knowledge (Davis, 1966), would also improve our understanding concerning relationships within the Cunoniaceae

This analysis has provided support for a number of monophyletic groups within Cunoniaceae, as were identified by Hufford and Dickison, (1992). Notable among these clades were the *Anodopetalum-Ceratopetalum-Schizomeria* group; the *Aistopetalum-Brunellia-Spiraeanthemum* clade; and the *Acrophyllum-Bauera-Caldcluvia-Callicoma* assemblage. Resolution concerning the placement of *C. capensis* within the *Weinmannia- Cunonia* clade remains unclear, with this analysis unable to provide support for *C. capensis* being more closely affiliated to either of these genera. Instead it shows limited support for placement into either genus.

Ultimately it is not surprising that the true evolutionary relationships between *C. capensis, Cunonia,* and *Weinmannia* are difficult to establish since, in reality, differentiation at the generic level between *Weinmannia* and *Cunonia* remains ambiguous. Indeed, the only apparent characters arguing against a merger of *Weinmannia* with *Cunonia* are those associated with seed morphology. Whilst the seeds of *Weinmannia* are always hirsute (covered by long, but not stiff hairs,) those of *Cunonia* (including *C. capensis,*) are uniformly winged. Since both these character states exist for *Caldcluvia* however, the strength of this distinction is weakened. The placement of *C. capensis* in its true taxonomic position might only proceed from lower level phylogenetic analyses, specifically investigation into those characters identifying the 160 species presently recognised in *Weinmannia*. Analysis at the species level is likely to be important in the identification of monophyletic groups in the *Cunonia* - (*C. capensis*) - *Weinmannia* - *Vesselowskya* - *Pancheria* - *Opocunonia* - and *Codia* assemblages.

Certainly the hypothesis suggesting *C. capensis* to be intermediate between *Weinmannia* and the remainder of the *Cunonia* genus remains appealing. In a biogeographic sense, *Weinmannia,* with its southern hemispheric distribution, excluding mainland Africa, but including Madagascar; and *Cunonia* occurring singularly in New Caledonia aside from *C. capensis,* still lends itself as a possible explanation for this disjunct phenomena.

ACKNOWLEDGMENTS

I would like to extend gratitude towards Peter Linder for his guidance and support throughout this project.

Table 1: Character states for Cunoniaceae

	123456789012345678901234567890123456789012345678901234567890123
Outgroup	?00 ?00?00?0??0 ??0?? ? ??00000 ?? ??0?? 0?0000?0? ???? ? ????? ???? ?? ????
Ackama	001010000002*001010101010000001010100001110 ???? ? ??? ?? ???? ??????
Acrophyllum	1?22100100021000001011000000001010100001100 ???? ? ???? ??? ???? ????
Aistopetalum	00101000002002101202200001?0000223010021?00101001312?10140313 ?1
Anodopetalum	0012100011010000020200300000001022100111?0000112111011114021310
Aphanopetalum	12120100000002000? ????*0100000021000001? ?0?10?0110101100111?022
Bauera	12120000000**200021111300001011020100101?0000023021012006031410
Brunellia	00**0100100220100202010001?0100103011001?00 ???? ? ??? ??? ???? ?????
Caldcluvia	001200000102121001010100000000101010000000000111111011005032310
Callicoma	001210001102120001010120*1?000101110000000000112111011015031301
Ceratopetalum	001*1011110110100202000*0*100110*0100021?0000112111011114021300
Codia	00121000110111100*00*100**00011*20100*1100211?10131211004132311
Cunonia	0010100111100*10*1010110100000102*10000000010?00121111012002211
Eucryphia	00101011012**1000202013010010000*001000000000112111011015031300
Geissois	0011000001012000*2022*100? ?1001010100000000?0112?11?11024031311
Gillbeea	00100000010010000102010*0010000*2001001110010101011011120022401
Opocunonia	00101000102111000101110*000000101010000010010110131?11003002211
Pancheria	00**100110011*10*1010120100000112100000000010?10131211003002211
Platylophus	001110000101100002020100001000112010001102001112111011114021300
Pseudoweinmannia	0011000000*110000212201001?1001010?00011100?0111111011025032311
Shizomeria	0012101110011*00020220010010001021100021?0000112111011114021300
Spiraeanthemum	00121001002010101000010001?01001030*0000000*0?101*1*110**031111
Spiraeopsis	00101000001*2001*2022100000000102011000000010110111011004032200
Vesselowskya	001010000002*000000101001001001020101000000101111131211015132411
Weinmannia	001*1001*1*11*100101011*100000102110000101010111121111014032311
C.capensis	001010011111001011010110100000102210000000010?11110000120020401

APPENDIX 1. Characters and character states defined for genera of Cunoniaceae.

(All multistate characters, (excluding those with a star, *) were treated as unordered in the parsimony analysis.) [Characters 1-43 from Hufford and Dickison 1992; characters 44-63 from Hideux and Ferguson 1976.]

PLANT HABIT AND STEM ATTRIBUTES

1. Plant habit: tree or shrub (0); subshrub or liana (1)
2. Nodal anatomy: trilacunar, 3 trace (0); unilacunar (1)

LEAF STRUCTURE AND ARRANGEMENT

3. Leaf arrangement: helical (0); decussate (1); whorled (2)
4. Leaf form: imparipinnate (0); digitate (1); unifoliate (2)
5. Stipule position: lateral from inception (0); interpetiolar (1)
6. Stipular size: large to moderate (0); diminutive (1)
7. Stipular secretory ribs: absent (0); present (1)
8. Foliar sclereids: absent (0); present (1)
9. Foliar hypodermis: absent (0); present (1)
10. Leaf epidermis or hypodermis with mucilage cells: absent (0); present (1)
11. Stomates: anomocytic (0); anisocytic (1); paracytic (2)
12. Secondary venation:brochidodromous(0);semicraspedodromous(1);craspedodromous (2)
13. Leaf areoles: incomplete (0); imperfect (1); well-developed (2)
14. Bundle sheath of veinlets: parenchymatous (0); sclerenchymatous (1); absent (2)
15. Terminal idioblasts near veinlet endings: absent (0); present (1)
16. Leaves with stellate trichomes: absent (0); present (1)
17. Medullary (bundle-shaped) vasculature in petiole: absent (0); present (1)

WOOD

18. Vessel perforations: exclusively scalariform, usually with more than 20 bars (0); exclusively scalariform or usually scalariform, usually with fewer than 20 bars (1); exclusively simple or usually simple with smaller vessels having 1-15 bars (2)
19. Mean vessel length: >700μm (0); <700μm (1)
20. Vessel distribution: solitary (0); predominately solitary (>70%), infrequently in pairs or in radial multiples of three (1); vessels often solitary (10-70%), others in radial multiples up to 9 (2)
21. Intervessel pitting: scalariform or scalariform opposite (0); opposite (1); opposite transitional to alternative or predominately alternate (2)
22. Tangential bands of axial parenchyma: present (0); absent (1)

REPRODUCTIVE STRUCTURES

23. Inflorescence: branched inflorescence with secondary and tertiary branches bearing flowers (including cymose and paniculate forms) (0); racemose or spicate (1); spherical heads (2); solitary flowers (3)
24. Inflorescence position: axillary (0); terminal (1)
25. Calyx aestivation: valvate (0); imbricate (1)
26. Petals: present (0); absent (1)
27. Petal form: entire (0); bifid (1)
28. Androecial merosity: 8-10 (0); numerous (1)
29. Carpel connation: over most or all of carpel (0); apocarpous or only basally united (1)

30. Appendage/ovary insertion: hypogyny or slight epigyny (less than 50% of ovary length) (0); extensive epigyny (1)
31. Carpel merosity: 3-5 (0); 2 (1)
32. Ovules per carpel: >2 (0); 2 (1); 1 (2)
33. Vasculature entering gynoecium: five traces (or four representing modified five trace) (0); three traces with unfused ventrals (1); three traces with fused ventrals (2)
34. Ovular traces: originate from ventral bundles and remain separate (0); originate from ventral bundles and anastomose(1); originate at base of locule (2); ovular traces separate from ventrals (3)
35. Gynoecial locules: separate (0); some confluence (1)
36. Stylar canal: present (0); absent (1)
37. Stigma position: terminal (0); decurrent (1)

FRUIT AND SEEDS

38. Pericarp structure: endocarp present (0); endocarp absent (1)
39. Fruit dehiscence: ventrally dehiscent (0); dry indehiscent (1); fleshy indehiscent (2)
40. Seed wings: present (0); absent (1)
41. seed surface: reticulate (); papillate (1)
42. Seed hairs: absent (0); present (1)
43. Seed coat fibrous layer: one or few discontinuous layers (0); many continuous layers (1); absent (2)

PALYNOLOGICAL STRUCTURES

44. Symmetry: radial order 2 (0); radial order 3 (1)
45. Thickness of exine (µm): 0-1(0); 1-2 (1)
46. Tectum height/tectum width ratio: <1 (0); 1 (1)
47. Optical equatorial view (from light microscopy observation): subtriangular (0); apertural angle obtuse, interapertural zone convex (1); apertural angle obtuse, interapertural zone lobate (2)
48. Optical meridional view (from light microscopy observations): circular or subcircular (0); oval (1); rectangular or subhexagonal (2)
49. Ectoaperture: meridional furrow syncolpate (0); long meridional furrow (1)
50. *Endoaperture: simple-diffuse (0); simple (1); simple-complex (2); complex (3)
51. Apertural mechanic: no influence on morphology (0); influence on morphology (1)
52. *Lateral meridional thinning of endexine: absent (0); small indistinct shape (1); short H-shaped endoaperture (2)
53. Endexine: homogenous (0); thickening related to the ectoapertural fold (1)
54. Apertural association: colpate (0); colporate (1); colporate with two pores by colpus (2)
55. Tectum homogeneity: homogeneity (0); heterogeneity (1)
56. *Margin: absent (0); diffuse (1); present (2)
57. *Tectum: partial-complete (0); complete (1); complete-perforate (2); perforate (3); perforate-partial (4); partial-continuous (5); partial-discontinuous (6)
58. Structure of tectum: non-structured (0); simple structure striate-rugulate (1)
59. Disposition of sculptural element which constitute the tectum: tectum complete (0); radiate-rugulate (1); rugulate-reticulate (2); reticulate (3)
60. Lumina length/lumina width: >1 (0); >1 or equals 1 (1); equals 1 (2)
61. *Lumina shape: no lumina (0); reduced lumina with perforations and linear regions (1); perforations (2); intermediary form of large lumina convex-obtuse (3); large lumina plan-acute (4)
62. *Polar axis (µm): <10 (0); 10-15 (1); 15-20 (2)
63. *Equatorial diameter (µm): <10 (0); 10-15 (1); 15-20 (2)

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