

Floral structure and evolution in the Anacardiaceae

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WANNAN, B. S. & QUINN, C. J., 1991. **Floral structure and evolution in the Anacardiaceae.** Carpel morphology and anatomy is investigated in 17 genera and carpelode morphology in 12 genera. There is an evolutionary sequence in the family from poorly differentiated, nearly apocarpous gynoecia towards syncarpous gynoecia with clearly defined stigmata, styles and ovaries. There has also been marked reduction culminating in pseudomonomy. The carpelodes of the male flowers appear more conservative, and provide evidence of affinities between genera with quite different fertile gynoecia. The characters have been polarized using Burseraceae as a sister group. Data from these sources, as well as from pericarp anatomy, wood anatomy and biflavonoid content indicate that the long standing intrafamilial classification into five tribes is artificial, and that the two small satellite families, Blepharocaryaceae and Julianiaceae should be included in the family. A large monophyletic group is recognized comprised of essentially four of the existing tribes (Anacardiæ, Dobineæ, Semecarpeae, Rhoëae), as well as the two satellite families. This group incorporates two subgroups of more closely allied genera. The remaining genera (mostly Spondiadeae) are very diverse, and for the present are placed in an artificial group characterised by a set of plesiomorphs. Relationships within this group must be resolved before a satisfactory taxonomy of the family can be achieved.

ADDITIONAL KEY WORDS:—Blepharocaryaceae – carpel – carpelode – gynoecia – Julianiaceae – systematics – taxonomy.

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INTRODUCTION

The Anacardiaceae is a well recognized family placed in the Sapindales/Rutales (Bentham & Hooker, 1862; Cronquist, 1981; Dahlgren,

1980; Takhtajan, 1980, 1987). Cronquist placed it with the Julianiaceae and Bursaceae, the only families in the Sapindales (*sensu* Cronquist, 1981) in which occur biflavonyls (Wannan *et al.*, 1985, 1988) and vertical intercellular secretory canals in the primary and secondary phloem. Since Lindley (1830) described the Anacardiaceae, there has been a number of infrafamilial classifications proposed (Bentham & Hooker, 1862; Engler, 1876, 1883, 1892; Marchand, 1869, 1874), all relying upon flora characters, especially the number of locules in the ovary and the manner of ovule insertion. The most widely used (Engler, 1883, 1892), divided the family into five tribes (Anacardiëae, Rhoëae, Semecarpeae, Spondiadeae, Dobineëae), principally using carpel and locule number at anthesis and in the fruit, styler morphology, ovule insertion and leaf morphology. Although widely accepted for nearly a hundred years (Ding Hou, 1978; Linchevskii, 1949; Ming Tien-lu, 1980; Tardieu-Blot, 1962), there are obvious difficulties with the classification: tribes are circumscribed on different sets of characters, and there is conflict between tribal and generic circumscriptions. As a result, there is a number of related genera (*Dobinea*, *Campylopetalum*, *Orthopterygium*, *Amphipterygium*, *Blepharocarya*) which authors have found difficult to integrate.

Most recently Takhtajan (1987) has divided the family into five subfamilies, namely: Anacardioideae, Dobineoideae, Spondioideae, Julianioideae and Pistacioideae. The first two represent existing tribes raised to subfamily rank. The Spondioideae contains the existing tribes Spondiadeae, Semecarpeae and Rhoëae (including *Blepharocarya*). The Pistacioideae represents a reinstatement of the Pistaciaceae Caruel (1879), albeit at a lower level; it contains only *Pistacia*, which has previously been referred to the Rhoëae. The Julianioideae contains the two genera *Amphipterygium* and *Orthopterygium*. He provides neither a critical appraisal of the tribal and subfamilial circumscriptions nor a major reassessment of the affinities within the family.

Although morphological and anatomical characters of the flower have always been used for infrafamilial divisions of the Anacardiaceae, there have been few critical studies in the family. Eichler (1878) provided a comparative account of 17 genera, which he divided into five groups based on *Spondias*, *Schinus*, *Rhus*, *Anacardium* and *Pistacia*, largely using carpel number, staminal number and presence/absence of perianth. This contribution is one of the most informative to date. Baillon (1878) gave a description of the floral morphology and anatomy of many genera now assigned to the Anacardiaceae, although he largely reiterated many of Eichler's ideas. As well, there have been detailed studies of a few species, mostly of the readily available tropical Anacardiëae (*Anacardium*, *Mangifera*) and Spondiadeae (*Spondias*, *Lannea*), or temperate Rhoëae (*Rhus*, *Cotinus*, *Pistacia*, *Schinus*). Little is known of the floral morphology and anatomy of the Semecarpeae and Dobineëae. Thus, although Engler's classification is largely derived from floral characters, there is no detailed background to support his assertions.

The female flowers of *Campylopetalum* and *Dobinea* (Dobineëae) are described as lacking any indication of perianth; as well, the pedicel of this naked pistil is adnate to the large subtending bract. These structural novelties have been considered sufficient justification to create a new family (Podoaceae: Dahlgren, 1980; Hutchinson, 1969; Willis, 1973), though many authors continue to treat them as part of the Anacardiaceae (Cronquist, 1981; Forman, 1954; Radlkofer,

1890; Scholz, 1964; Takhtajan, 1987). Certainly, these specializations are not found elsewhere in the Anacardiaceae, although some Rhoëae have reduced perianths (*Haplorhus*, *Pistacia*, *Scassellatia*). Engler (1892) believed the Dobineëae was most closely related to the Rhoëae, even though its unicarpellary ovary and simple leaves are suggestive of the Anacardiëae. He stated that differences in the petals, anthers and stigma precluded a close relationship with the Anacardiëae, but failed to elaborate them.

Julianiaceae (*Orthopterygium*, *Amphipterygium*) are distinguished from Anacardiaceae largely by the involucre enclosing the female flowers and the apparent lack of perianth. However, there has yet to be a critical appraisal of either of these anatomical peculiarities. The involucre encloses the ultimate unit of the female inflorescence. Fritsch (1908) described it as containing four collateral flowers with discernible spaces between them, the two inner flowers being the only ones to produce fruit; these observations agree with figures in Hemsely (1908). Although not commenting on the absence of perianth, Fritsch noted that the bases of the flowers are completely embedded in the tissue of the involucre.

Blepharocarya has also been placed in a separate family (Blepharocaryaceae; Airy Shaw, 1965) on the basis of its opposite pinnate leaves and specialized female inflorescence. Its inflorescence structure, pollen, stem anatomy and biflavonoids, however, indicate that it is a natural member of the family (Wannon *et al.*, 1985, 1987), although its pinnate leaves and apparently unicarpellary ovary exclude it from all current tribes.

The infrafamilial systematics of the Anacardiaceae have relied mainly on locule and carpel number, number of staminal whorls and ovule insertion. The number of staminal whorls varies greatly in the family, being constant only in the two smallest tribes: Semecarpeae with one and Dobineëae with two. Spondiadeae mostly possess two whorls but there are up to four in *Pouparia* (Perrier de la Bathie, 1946), and up to six in *Sclerocarya* (Van der Veken, 1960). *Operculicarya* is reported to have a single whorl (Perrier de la Bathie, 1944, 1946), but is poorly documented and of uncertain affinity. Rhoëae have usually one or two whorls, though *Sorindeia* has up to four whorls (Van der Veken, 1960). The largest variation is shown in the Anacardiëae, where the number of stamens ranges from indefinite in species of *Gluta*, to a single whorl in *Bouea*, *Fegimanra* and *Swintonia*. The number of whorls varies within and between genera as well as between the tribes of the family, and does not distinguish any of the tribes as presently circumscribed.

Ovule insertion has been used in all attempts at family subdivision; the character refers to the position in the locule where the funicle joins the ovary wall, and the orientation of the ovule. The ovule in the Anacardiaceae is described as apotropous (Cronquist, 1981) with the funicle attached to the top (apical) or to the base of the locule (basal). In addition to these two states, there is an intermediate state that Engler (1883, 1892) referred to as a lateral funicle. This character is constant in Dobineëae (basal) and Spondiadeae (apical), but varies in Anacardiëae, Semecarpeae, and Rhoëae (Engler, 1883, 1892). The Julianiaceae have a basal funicle and *Blepharocarya* is reported either basal (Airy Shaw, 1965; Radlkofer, 1879) or lateral (Wannan *et al.*, 1987). Thus, although widely scored across the family, the different states of this character occur in almost every tribe.

The determination of carpel number in this family is complicated by abortion in the ovary, especially in Spondiadeae, Rhoëae and Semecarpeae. The number of locules has often been stated to be different from the number of carpels, the latter apparently being inferred from the number of stigmas or styles at anthesis. This kind of deduction is supported by developmental and organographic studies (Marchand, 1869; Payer, 1857; Takeda *et al.*, 1979). The number of carpels in the ovary varies across the tribes, being constant only in Dobineëae (unicarpellary) and Semecarpeae (tricarpellary). Anacardiëae are unicarpellate except for the apocarpous genera, *Androtium* and *Buchanania*, which have five carpels, of which only one is fertile. The gynoecia of Spondiadeae have been described (Engler, 1883) as usually isomerous with the corolla and calyx, the number varying from three to five; between one and five eventually produce seed. However, *Pleiogynium* has been recorded as having from five to 12 seed-bearing carpels. *Sclerocarya*, though generally isomerous, sometimes possesses only two or three carpels, whilst *Solenocarpus* has been described with only a single carpel. Rhoëae, though described as having from one to five carpels, seem mostly to possess a unilocular ovary with three styles or stigmata (Engler, 1883). *Faguetia* have five stigmata, while *Campnosperma*, *Pentaspadon* and *Pseudoprotorhus* have only a single style; all these genera again have unilocular fruit. Julianiaceae possess a tripartite style and unilocular ovary (Hemsley, 1908; Willis, 1973), and thus would seem to conform to the most common pattern in the Rhoëae. *Blepharocarya* has a single style and stigma and is unilocular (Airy Shaw, 1965); Engler (1897) placed it next to *Lithraea* in the Rhoëae despite the absence of the three stigmata that are nearly universal in this tribe.

This study includes an investigation of carpel anatomy and morphology in the family, not only in some of those genera that appear to be anomalous, but also in some that appear typical of the tribes to which they are assigned.

The number and structure of carpelodes in the male flower has not been used in any of the family subdivisions; a preliminary survey has suggested, however, that it is taxonomically useful. The character can only be scored where there are unisexual flowers, but this excludes only seven genera. These structures have been seldom noted, and then often poorly described. It appears that Spondiadeae often possess four or five carpelodes and Rhoëae either three or none at all. In the other three tribes there are no data, the carpelodes being described as absent or rudimentary. An investigation has been made of this character across the family.

METHODS

Details of voucher specimens are given in the Appendix. Most material was fixed in FAA, but some was obtained from herbarium specimens and reconstituted before study.

Prior to embedding some material was softened and cleared using either lactic acid or sodium hypochlorite. Paraffin embedded material was sectioned serially on a steel knife at 10–50 μm and stained in either safranin-fast green or basic fuchsin-orange G, and made permanent according to the methods of Sass (1958). Material embedded in LR White (soft grade) was sectioned on a glass knife at 1–10 μm and stained with toluidine blue (pH 4.4). Drawings were obtained using a Leitz Orthoplan microscope and Leitz drawing apparatus.

Whole flowers were prepared for scanning electron microscopy by critical point drying, mounted on stubs using double sided adhesive tape, and sputter-coated; micrographs were obtained mostly using backscattered electrons.

RESULTS

Carpel structure and morphology

Spondiadeae

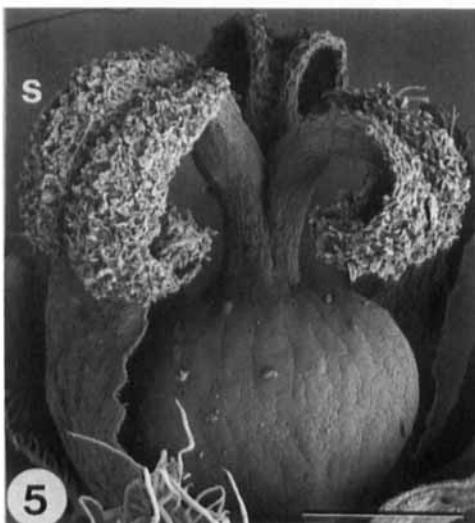
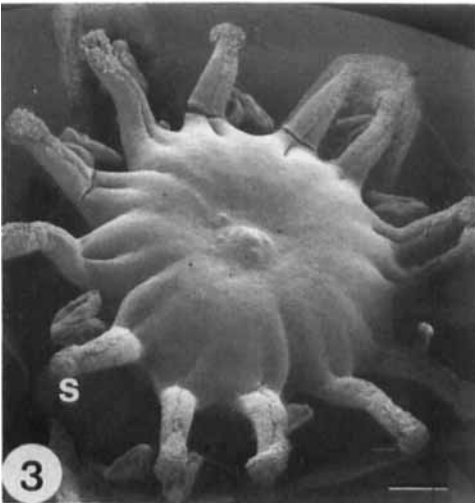
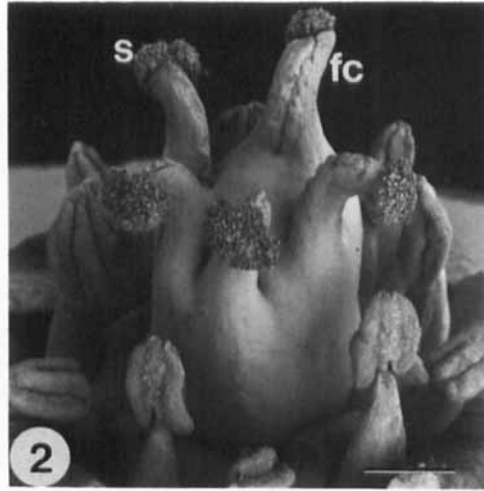
Dracontomelon. The flowers are bisexual with ten functional stamens. The carpels are isomerous with, and opposite, the petals (antipetalous). In this material (Fig. 7D), the syncarpous ovary contained four locules, all with ovules (ov). The carpels are connate from the base to above the top of the locules, although on the outside there is an obvious furrow (f) between each of the carpels, even in their lower parts (Fig. 1, 7D). The styles cohere just below their stigmata (Figs 7B, 21J, 26), but are free lower down (Fig. 7C); the broad styler bases are continuous with the top of the ovaries. Each style has transmitting tissue for its full length (Fig. 21J, 26). The stigma (s) is a small region adjacent to the transmitting tissue at the top of each style (Fig. 1, 7A). In their upper parts each style has a dorsal bundle, accompanied by a resin canal, and two smaller ventral vascular bundles (Fig. 7B). Lower down, in the free region, one or both ventral bundles (v) disappear (Figs 7C, 21J), but reappear in the region of the locule, eventually becoming grouped in the axile position (Fig. 7D).

Harpephyllum. The flowers are unisexual, the stamens in the female flowers having well formed but sterile anthers. The ovary is syncarpous, antipetalous and usually pentamerous (Fig. 2). There are no external furrows between the carpels in the ovary. The styles are free and always have a dorsal vascular bundle, but the occurrence of the ventral bundles is variable (Fig. 7E, F). Each style contains transmitting tissue and has a capitate stigma (s). Usually there is one fertile carpel (fc) and four small vestigial locules (vl), without ovules, indicating the position of the other carpels (Figs 7G, 22). Studies on mature fruits indicate that occasionally two carpels are fertile. Below the level of the fertile locule the ovary contains five dorsal bundles (df and ds), one from each carpel (Fig. 7H).

Pleiogynium. The flowers are unisexual; stamens are present in the female flowers but their anthers, although well formed, are sterile. In this material the syncarpous ovary contained either 13 (Fig. 3) or 11 locules, all of which had ovules (ov) and thus appeared to be fertile (Fig. 7J). There are no external furrows between the carpels in the ovary. The styles are free and have a dorsal vascular bundle associated with a resin canal (Fig. 7I). Each style also contains transmitting tissue and bears a capitate stigma (s). Ventral vascular bundles become evident in the region of the locules, in the axile position; also appearing at this level are many small resin canals, without vascular tissue, near the dorsal bundles (Fig. 7J).

Rhoëae

Rhus. Stamens are present in the female flowers, but the anthers do not contain viable pollen. The ovary is unilocular with a single style terminating in three short branches (Fig. 4), each with a capitate stigma (s). Vascular bundles were



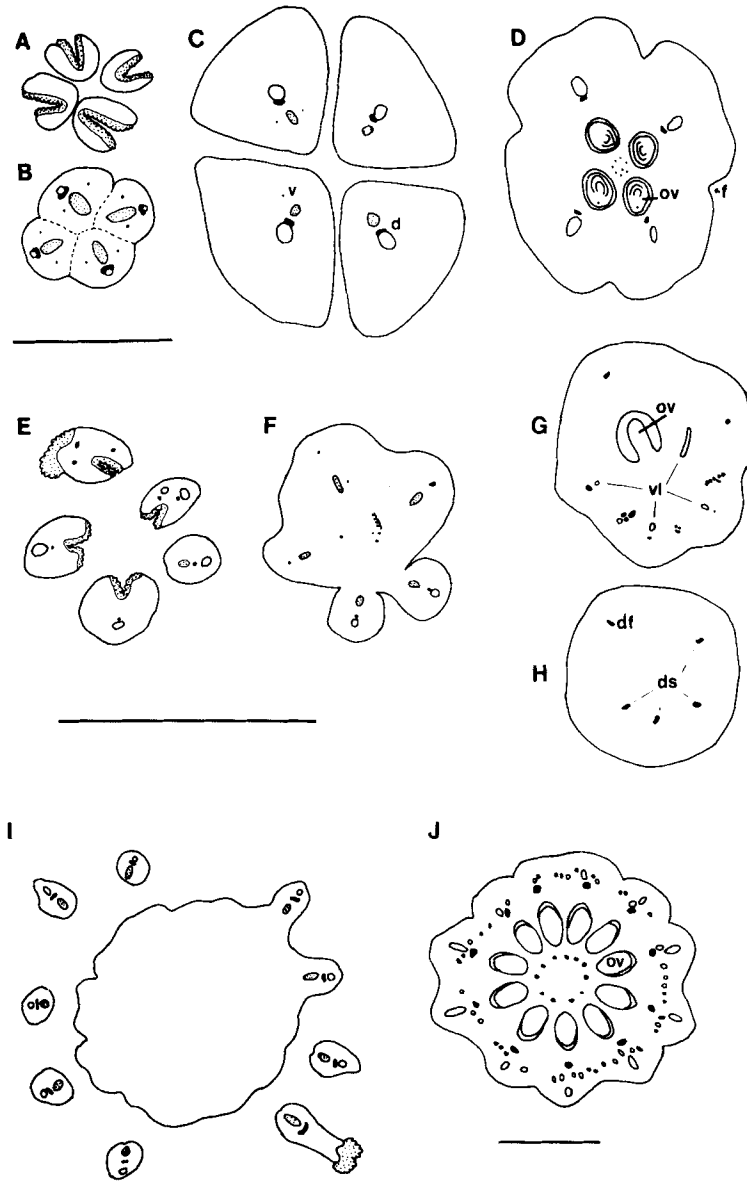


Figure 7. Transverse sections of fertile gynoecia. A–D. *Dracontomelon lenticulatum*, Pullen 1178. Top scale. A. Stylar apices. B. Upper, fused region of styles; the line of suture between the carpels is a thin region of smaller cells (broken line). C. Lower, free region of styles. D. Ovary, showing complete fusion of carpels. E–H. Unisexual female flower of *Harpephyllum caffrum*, UNSW 14701. Middle scale. E. Stylar apices. F. Top of ovary. G. ovary, at level of locules. H. Ovary, below level of locules. I–J. Unisexual flower of *Pleio gynium timoriense*, UNSW 20355. Bottom scale. I. Top of ovary. J. Ovary, at level of locules. d, dorsal vascular bundle; df, dorsal vascular bundle of fertile carpel; ds, dorsal vascular bundles of sterile carpels; f, furrow between carpels in ovary; fc, fertile carpel; ov, ovule; vf, ventral vascular bundle of fertile carpel; vl, vestigial locules; v, ventral vascular bundle; ○, resin canal; ●, vascular tissue sectioned transversely; ▨, vascular tissue sectioned obliquely; stippled areas, stigmatic or transmitting tissue. Scale bars = 1 mm.

Figures 1–6. Scanning electron micrographs of fertile gynoecia. Fig. 1. *Dracontomelon lenticulatum*, bisexual flower, Pullen 1178. Fig. 2. *Harpephyllum caffrum*, female flower, UNSW 14701. Fig. 3. *Pleio gynium timoriense*, female flower, UNSW 20355. Fig. 4. *Rhus succedanea*, female flower, UNSW 11535. Fig. 5. *Pistacia chinensis*, female flower, UNSW 12893. Fig. 6. *Schinus azeira*, UNSW 5080. f, furrow between the carpels in the ovary; fc, fertile carpel; s, stigma. Scale bars = 0.5 mm.

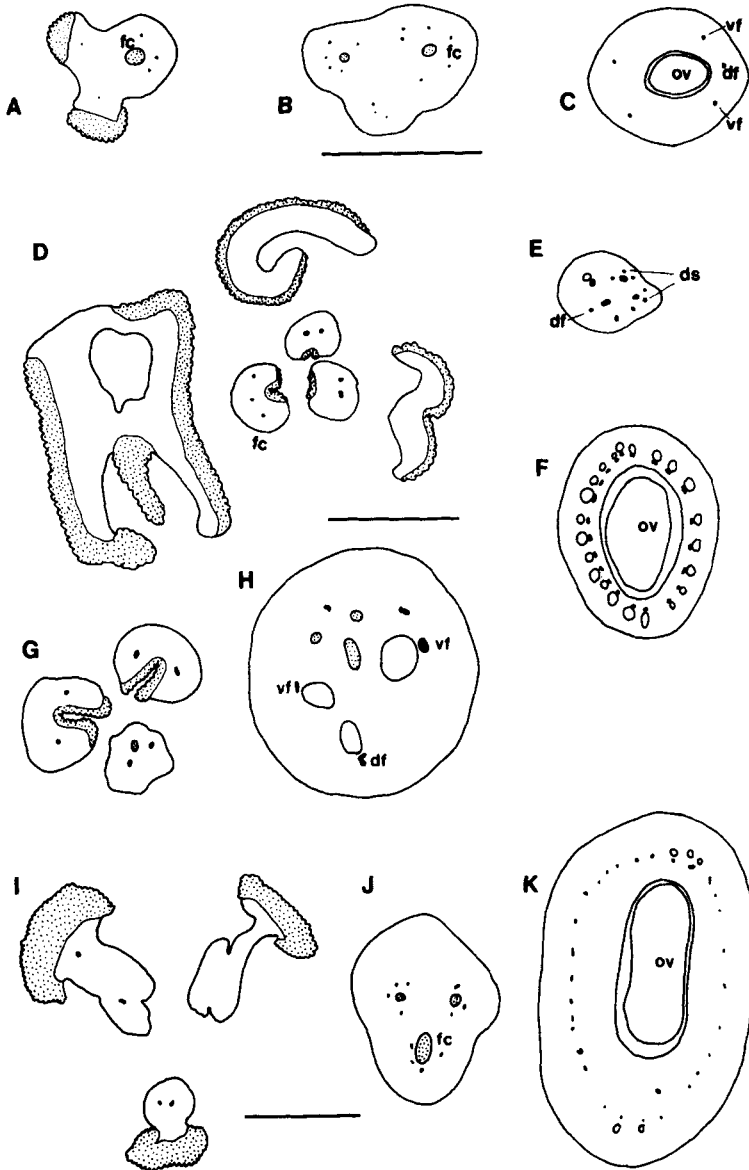


Figure 8. Transverse sections of fertile gynoecia. A–C. *Rhus succedanea*, UNSW 11535. Top scale. A. Upper part of style. B. Lower part of style. C. Ovary, showing the three vascular bundles of the fertile carpel and one each from the two sterile carpels. D–F. *Pistacia chinensis*, UNSW 12893. Middle scale. D. Upper branches of style and reflexed spatulate stigmata. E. Lower part of the style. F. Ovary; styler bundles are indistinguishable among a large number of accessory bundles. G & H. *Schinus areira*, UNSW 5080. Middle scale. G. Upper branches of style. H. Lower part of style. I–K. *Rhodospaera rhodanthema*, UNSW 5160. Bottom scale. I. Upper branches of style. J. Lower part of style. K. Ovary, showing large number of accessory bundles. Symbols as in Figure 7. Scale bars = 0.5 mm.

traced from all three stigmata down the style into the top of the ovary (Fig. 8A–C); one branch (fc) contains a dorsal (df) and two ventral (vf) bundles, the others only a single (? dorsal) bundle. Some flowers have transmitting tissue associated only with the first of these branches (Fig. 8A), whilst in others it was

present in all three and could be traced almost to the top of the locule. Thus the gynoecium is tricarpeal, but with two of the carpels lacking locules, and the apparently single style is really the result of the fusion of three elements.

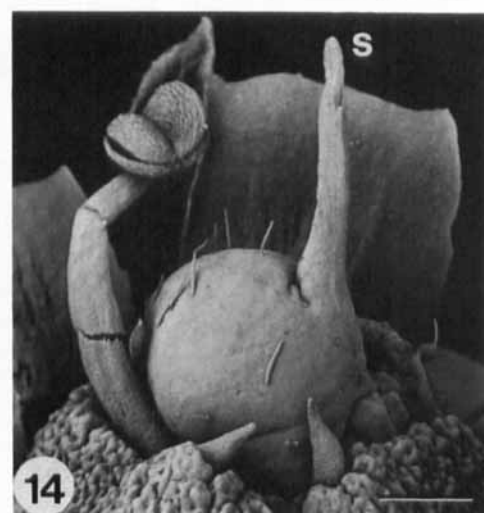
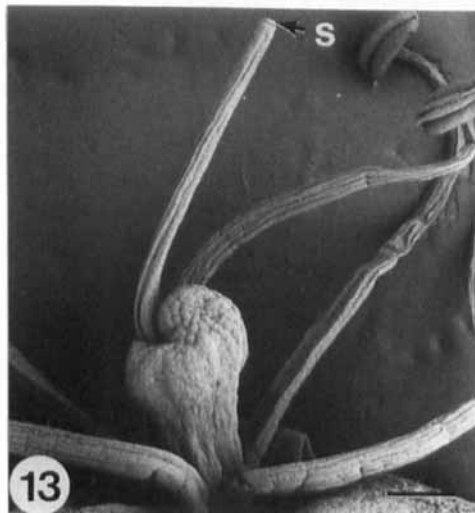
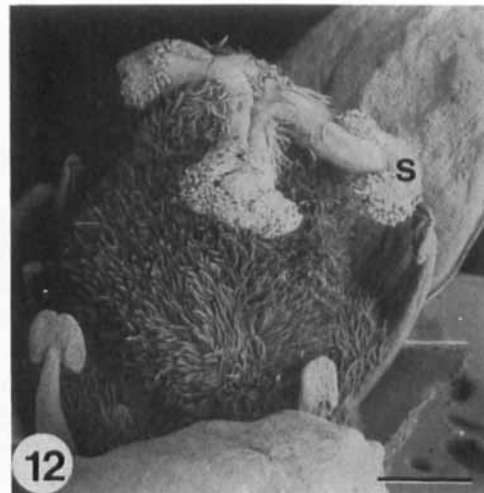
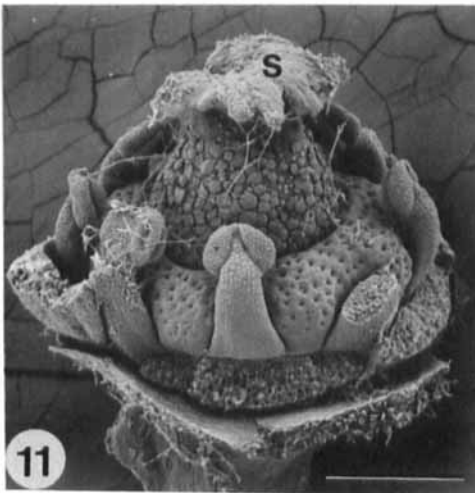
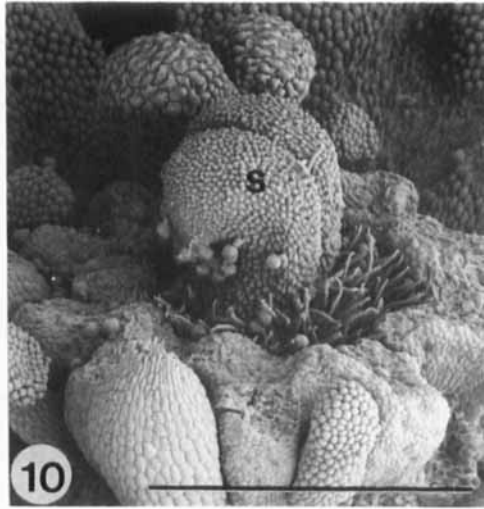
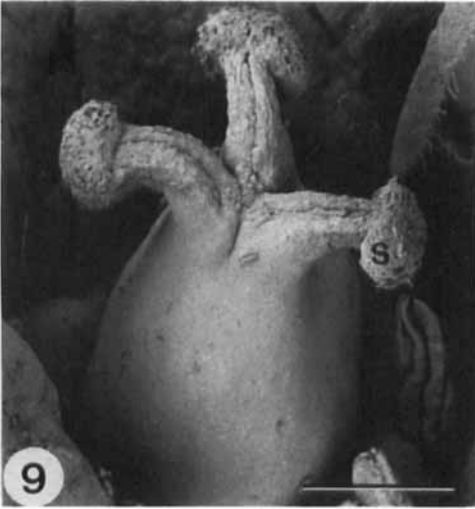
Pistacia. The female flowers have no trace of stamens; the ovary is unilocular with three styles, each with a spatulate stigma (s in Fig. 5). Vascular bundles were traced from all three stigmata down into the ovary (Fig. 8D–F); one branch (fc) contains a dorsal and two ventral bundles, the others have only two (? ventral) bundles. Transmitting tissue occurs in all three styles, disappearing at about the level of the locule. Thus the gynoecium is tricarpeal, but with two of the carpels lacking locules, and represented only by their styles. The wall of the locule is vascularized by many accessory bundles so that the styler bundles are not recognizable (Fig. 8F).

Schinus. The female flowers have apparently normal stamens, but the anthers contain no pollen and do not dehisce (Fig. 6). The ovary is unilocular with three styles (Fig. 6), each bearing a capitate stigma (s). Vascular tissue was traced from all three stigmata down into the top of the ovary; initially all the styles have two (? ventral) bundles (Fig. 8G), but lower down one of them gains a dorsal bundle (df in Fig. 8H). The styles all possess transmitting tissue, which fuses just above the locule. Thus the gynoecium is tricarpeal, but with two of the carpels represented only by their styles. At the level of the locule it is possible to discern the vascular bundles from each style.

Rhodospaera. The female flowers have stamens whose anthers are well formed but sterile. There are three styles that are connate just above the unilocular ovary (Fig. 9); each is terminated by a conspicuously capitate stigma (s). Vascular tissue was traced from the stigmatic regions of all styles down to the top of the ovary (Figs 8I–K, 23); the fertile style (fc) contains a dorsal and two ventral bundles whilst the sterile styles have only two vascular bundles. Lower down there are up to four vascular bundles per style. Transmitting tissue was present in all three styles and was traced down to the locule. Thus the gynoecium is tricarpeal, but with two of the carpels represented only by their styles. The wall of the locule contains many accessory bundles so that it is not possible to recognize the styler bundles (Fig. 8K).

Pentaspadon. The female flowers possess two types of stamens: one whorl of staminodes with short filaments and obviously aborted anthers, and a second whorl with normal morphology and containing some pollen, but which have never been observed to dehisce in our material. The ovary is unilocular and bears a single prominent recurved style (Fig. 10) containing a single channel of transmitting tissue and two (? ventral) vascular bundles (Figs 15A, B, 24), all of which are traceable down to the locule, where the former ceases and the latter are joined by accessory bundles (Fig. 15C). Thus, the gynoecium is unicarpeal with no indication of any other carpels.

Camptosperma. The flowers have stamens devoid of pollen. The ovary is unilocular (Fig. 15G), with a rather unusual stigma (s) that is irregularly lobed (Fig. 11). At the ventral position of the disc-shaped stigma there is an obvious suture (su) which further down the style gives way to transmitting tissue (Fig. 15E). Some of the stigmatic lobes contain vascular tissue (Fig. 15D), often just a single xylem element. Although the ovary is unilocular and there is only a single region of transmitting tissue, there are usually five vascular bundles in the style (Fig. 15F). These may represent more than one carpel.



Semecarpaeae

The female flowers of *Semecarpus* possess stamens with well formed anthers that are devoid of pollen. The ovary is unilocular with three styles (Fig. 12) that are connate just above the ovary and terminate in capitate stigmata (s). Each style has a dorsal and two ventral bundles (Fig. 15H–J), as well as a channel of transmitting tissue, although the latter fuses into a single strand just above the locule (Fig. 15I). The vascular bundles from each style are traceable to this same level, below which they become indistinguishable from the rest of the vasculature in the ovary wall (Fig. 15J). Thus the gynoecium is tricarpellary, but with two of the carpels lacking locules and represented only by their styles.

Anacardiäae

Gluta. The flowers are bisexual with five functional stamens and a single antisepalous carpel (Fig. 13). The style is gynobasic, joining the ovary on the ventral side, and the stigma is a small region of papillose tissue lying on the ventral side at the stylar apex (Fig. 15K). The style contains a single channel of transmitting tissue as well as a dorsal (d) and two ventral (v) bundles, all of which can be traced to the top of the locule (Figs 15L, M, 25). From there the dorsal trace continues across the top of the ovary and down the dorsal side. At the locule level the ovary wall contains many accessory bundles (Fig. 15N).

Mangifera. The flowers are bisexual containing a single antisepalous carpel with a lateral (gynobasic) style that joins the ovary on the ventral side (Figs 14, 21K, 27). There is a single fertile stamen opposite the carpel (i.e. at the dorsal end of the carpel) and nine other stamens reduced to staminodes. At the apex of the style is the stigma, a small region of papillose tissue on the ventral side. The style contains a single channel of transmitting tissue as well as a dorsal (d) and two ventral (v) bundles, all of which can be traced to the top of the locule (Figs 20A–C, 21K, 27). From there the dorsal trace continues across the top of the ovary and down the dorsal side. Further down, where the ovule (ov) becomes visible, the ovary wall contains accessory vascular bundles (Fig. 20D).

Buchanania. The bisexual flowers of *Buchanania* have two whorls of functional stamens and an almost apocarpous gynoecium of four to six antipetalous carpels, of which one is fertile (fc in Fig. 16). The style of the fertile carpel lacks a stigma (Fig. 16), and transmitting and vascular tissue (Fig. 20E, F); the last extends to just above the locule. The sterile carpels have no locules, but bear stigmata (s) at their apices (Fig. 16). The transmitting tissue and vascular bundles of the sterile carpels can be traced down into the base of the flower (Fig. 20E–H); the sterile carpels fuse first with the nectariferous disc (Fig. 20G), and then with the ventral surface of the fertile carpel, just above the base of its locule. A little lower, the dorsal surface of the fertile carpel fuses with the disc (Fig. 20H). Hence the sterile carpels appear to operate as styles.

Bouea. The flowers with fertile gynoecia are bisexual (Fig. 17), with a single antisepalous carpel bearing a capitate stigma (s) and a single whorl of fertile

Figures 9–14. Scanning electron micrographs of fertile gynoecia. Fig. 9. *Rhodospaera rhodanthema*, female flower, UNSW 5160. Fig. 10. *Pentaspadon molleyi*, female flower, Pullen 7406. Fig. 11. *Campnosperma brevipetiolatum*, female flower, Hoogland & Craven 10635. Fig. 12. *Semecarpus australiensis*, female flower, Gray 3248. Fig. 13. *Gluta renghas*, bisexual flower, Ding Hou 781. Fig. 14. *Mangifera indica*, bisexual flower, UNSW 3178. s, stigma. Scale bars = 0.5 mm.

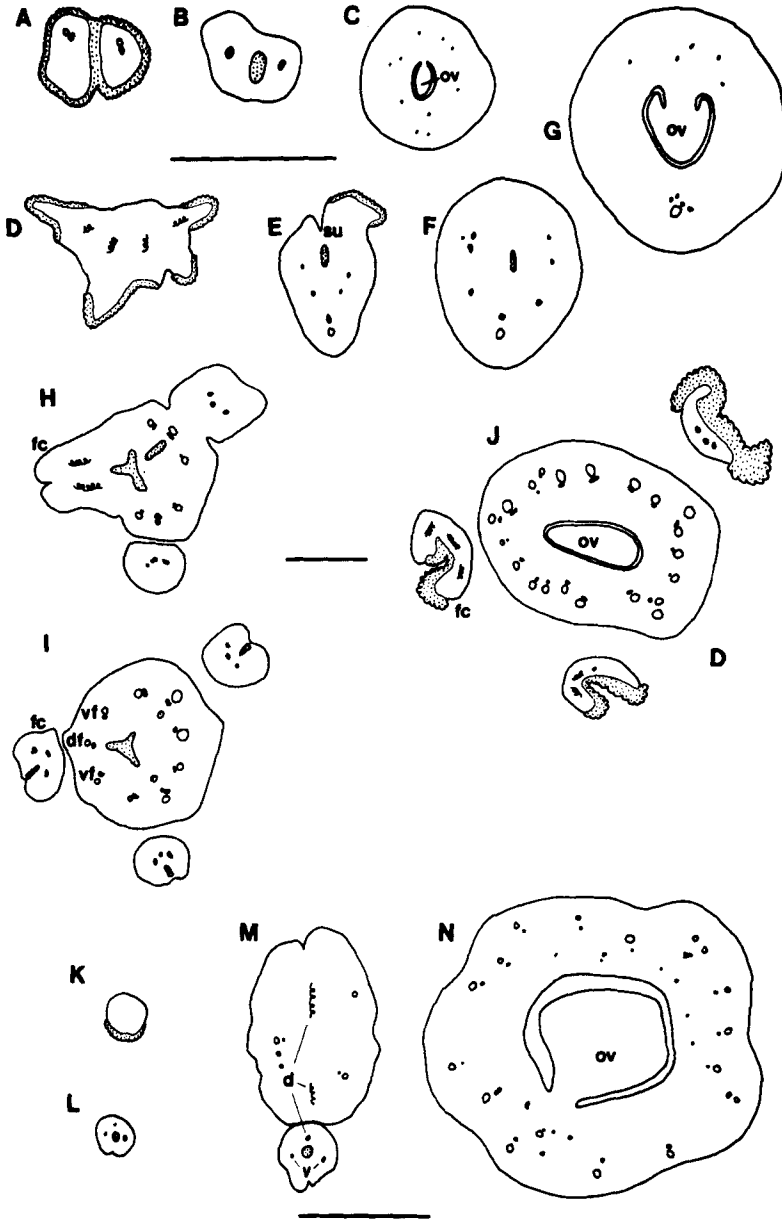
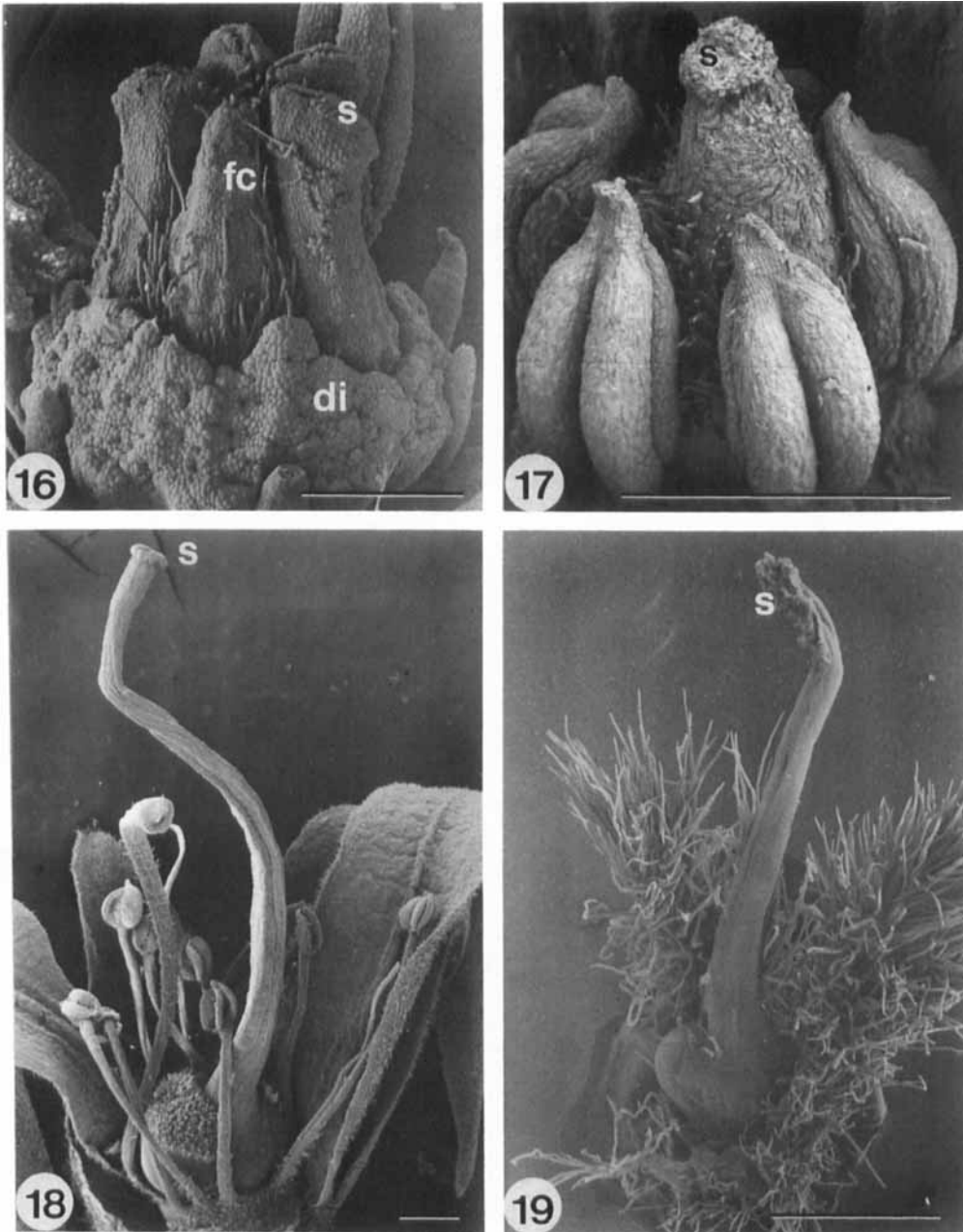


Figure 15. Transverse sections of fertile gynoecia. A–C. *Pentaspadon motleyi*, Pullen 7406. Top scale. A. Stigmatic region. B. Lower part of style. C. Ovary at level of locule. D–G. *Campnosperma brevipetiolatum*, Hoogland & Craven 10635. Top scale. D. Upper part of stigma. E. Lower part of stigma. F. Lower part of style. G. Locule. H–J. *Semecarpus australiensis*, bud in which styles are strongly recurved. Gray 3248. Middle scale. H. Lower parts of styles, showing fused basal region in the middle and recurved upper parts around the edge. I. Ovary and surrounding distal regions of recurved styles. J. Locule and surrounding stigmata, where stylar bundles are indistinguishable among a large number of accessory bundles. K–N. *Gluta renghas*, Ding Hou 781. Bottom scale. K. Stigma. L. Upper part of style. M. Lower part of style and top of ovary. Note continuous vascular bundle (d) crossing top of ovary and ascending the lateral style. N. Lower part of ovary. su, suture; other symbols as in Fig. 7. Scale bars = 0.5 mm.



Figures 16–19. Scanning electron micrographs of fertile gynoecia. Fig. 16. *Buchanania arborescens*, bisexual flower UNSW 16750. Fig. 17. *Bouea macrophylla*, bisexual flower Jacobs s.n. Fig. 18. *Anacardium occidentale*, bisexual flower, Zanoni 26418. Fig. 19. *Blepharocarya depauperata*, unisexual flower, UNSW 10201. di, nectariferous disc; fc, fertile carpel; s, stigma. Scale bars = 0.5 mm.

stamens. In its upper parts the style contains a dorsal and two ventral bundles (Fig. 20I); closer to the ovary a single zone of transmitting tissue is also apparent. At the level of the ovule (ov) the ovary wall contains accessory bundles.

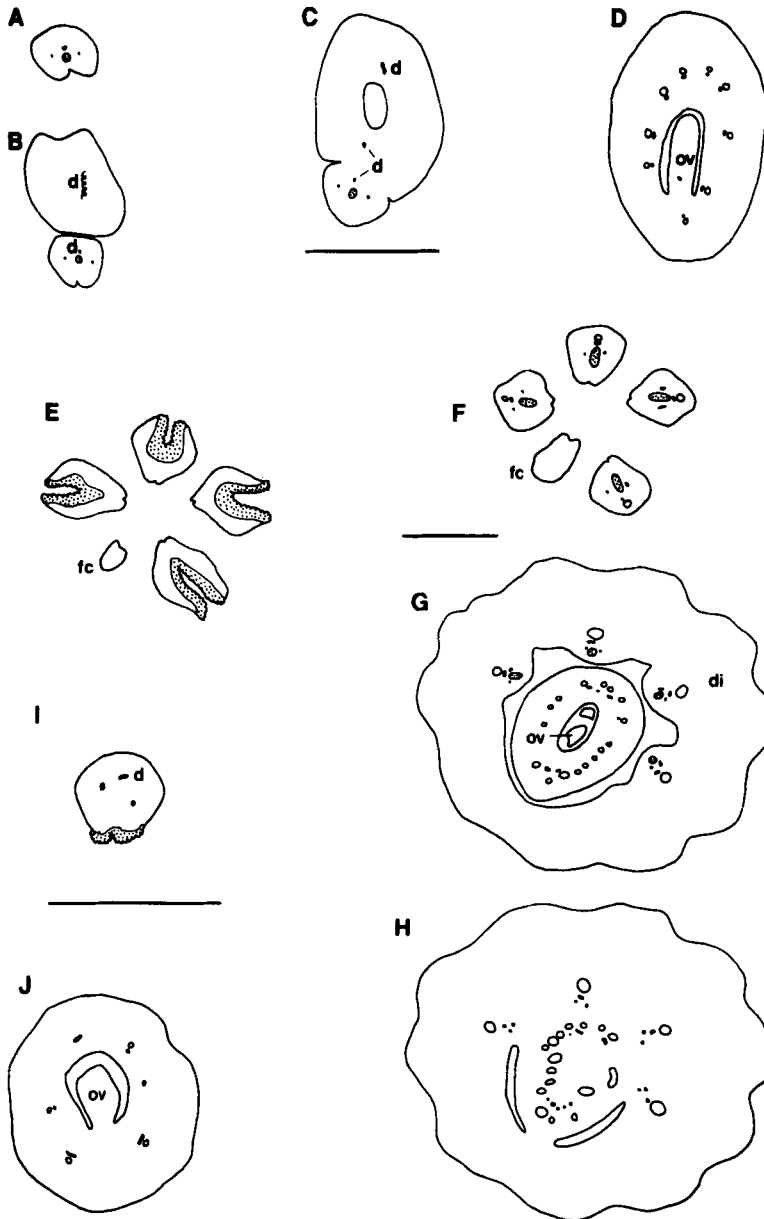


Figure 20. Transverse sections of fertile gynoecia. A–D. *Mangifera indica*, UNSW 3178. Top scale. A. Upper part of style. B. Lower part of style and top ovary. Note continuous vascular bundle (d) crossing top of ovary and ascending the lateral style. C. Upper part of ovary, showing fusion of style with ventral surface of the ovary. D. Lower part of ovary. E–H. *Buchanania arborescens*, UNSW 9042. Middle scale. E. Styler apices. F. Upper parts of styles. G. Lower part of locule, with bases of the four sterile carpels embedded in nectariferous disc (di). H. Base of fertile carpel below locule; note fusion between dorsal surface of fertile carpel and disc (di). I–J. *Bouea macrophylla*, Jacobs s.n. Bottom scale. I. Upper part of style. J. Ovary at level of locule. Symbols as in Fig. 7. Scale bars = 0.5 mm.

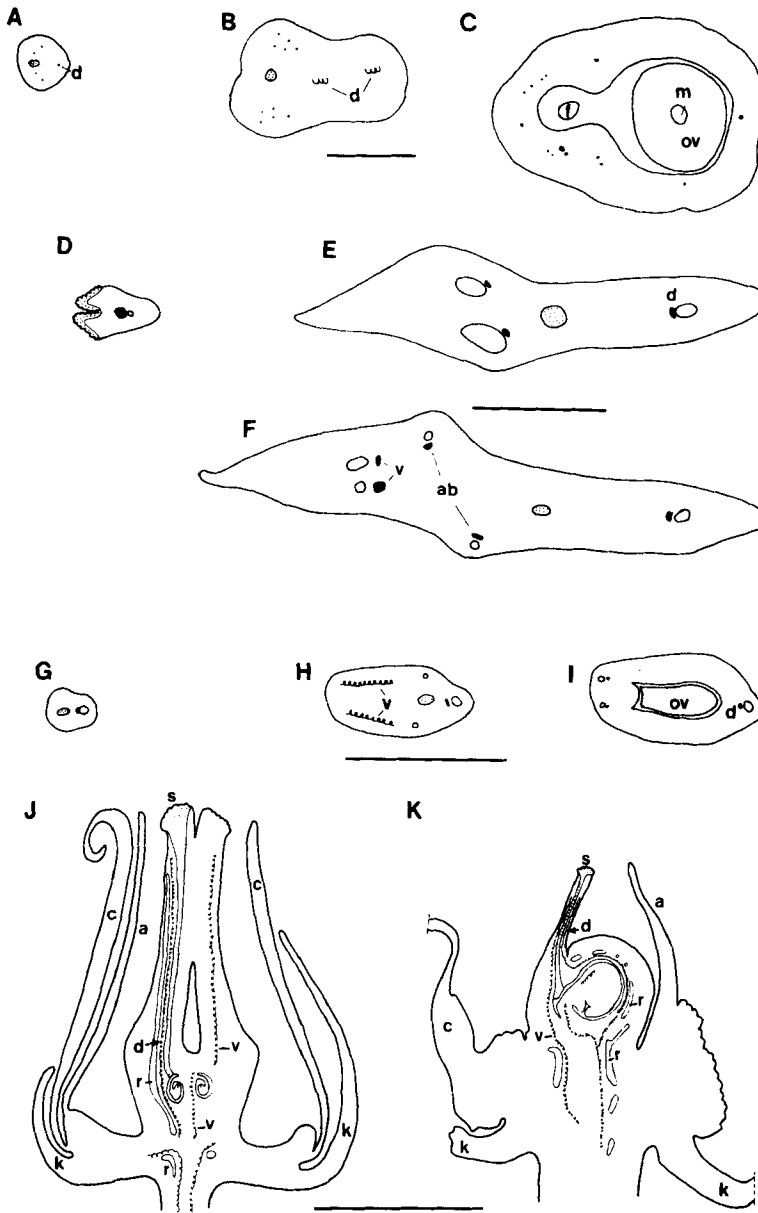
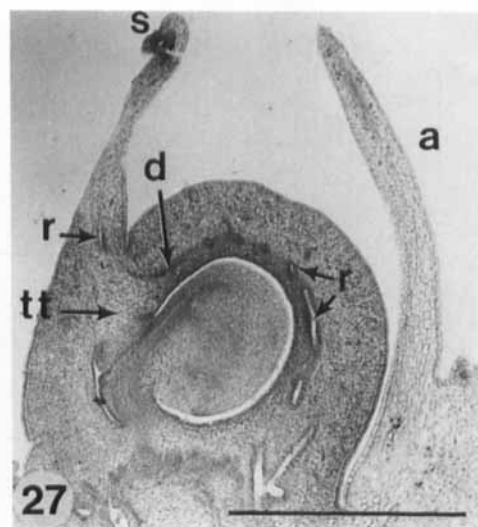
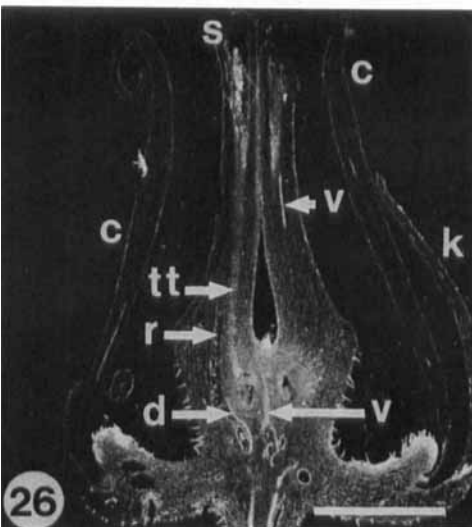
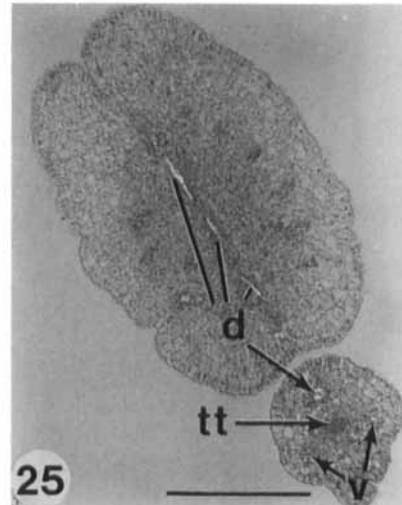
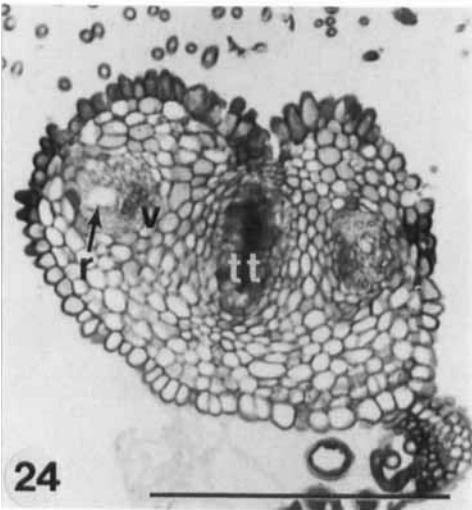
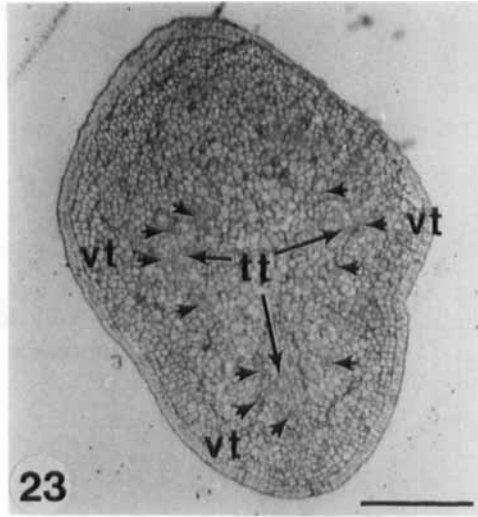
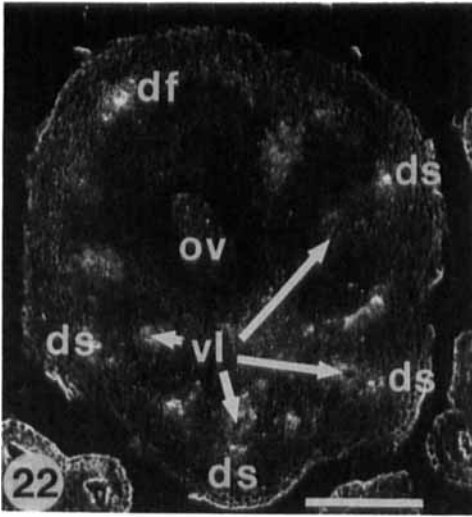


Figure 21. A-I. Transverse sections of fertile gynoecia. Scale bars = 0.5 mm. A-C. *Anacardium occidentale*, Zanon 26418. Top scale. A. Upper part of style. B. Base of style and top of ovary. Note continuous vascular bundle (d) crossing top of ovary. C. Middle of locule. D-F. *Dobinea delavayi*, De Ding 60-015. Middle scale. D. Upper part of style. E. Lower part of style. F. Top of ovary, just above locule. G-I. *Blepharocarya depauperata*, UNSW 10201. Bottom scale. G. Upper part of style. H. Base of style and top of ovary. Note continuous vascular bundles (v) crossing top of ovary. I. Locule. J, K. Longitudinal sections of fertile gynoecia. Scale bar = 1 mm. J. *Dracontomelon lenticulatum*, Pullen 1178. K. *Mangifera indica*, UNSW 3178. a, stamen; ab, accessory vascular bundle; c, corolla; f, funicle; k, calyx; m, micropyle; r, resin canal; s, stigma; other symbols as in Fig. 7.



Anacardium. The flowers that have fertile gynoecia are bisexual (Fig. 18), with a unilocular, antisepalous ovary. There is a single fertile and nine non-functional stamens in the same arrangement as in *Mangifera*. The single lateral style is attached to the ventral surface of the ovary and bears a punctiform stigma (s). The style contains a channel of transmitting tissue, one vascular bundle (d) in the dorsal position and several in the ventral position. In the upper part of the style there are usually four ventral bundles (Fig. 21A), but this increases to about ten where the style joins the ovary (Fig. 21B). From there the dorsal trace (d) runs across the top of the ovary and down the dorsal side. Below this level the vasculature of the ovary wall increases (Fig. 21C).

Dobineëae

The flowers of *Dobinea* are unisexual with the female having a unilocular ovary and a simple style (Hooker, 1876). Although no female flowers were available from this tribe, a study was made of the persistent style on young fruits of *Dobinea*. The upper portion of the style contains a dorsal bundle and a single zone of transmitting tissue (Fig. 21D); also at this level are stigmatic papillae on the ventral surface of the style. Somewhat lower, two ventral vascular bundles are apparent (Fig. 21E). In the ovary wall there is a pair of accessory bundles which fuse with the ventral bundles of the style just above the level of the locule.

Genus with uncertain affinities: Blepharocarya

The flowers are unisexual, with no sign of stamens in the female (Fig. 19). There is a single antisepalous carpel which has a lateral style that is attached to its dorsal surface. The stigma (s) is a papillose area of tissue on the ventral side of the stylar apex (Fig. 19). In the upper parts of the style there is a single zone of transmitting tissue and a dorsal vascular bundle (Fig. 21G); further down two ventral bundles are added. After the style fuses with the ovary, the ventral bundles (v) cross the top of the ovary to the ventral side (Fig. 21H). All three bundles are present in the ovary wall at the level of the locule (Fig. 21I).

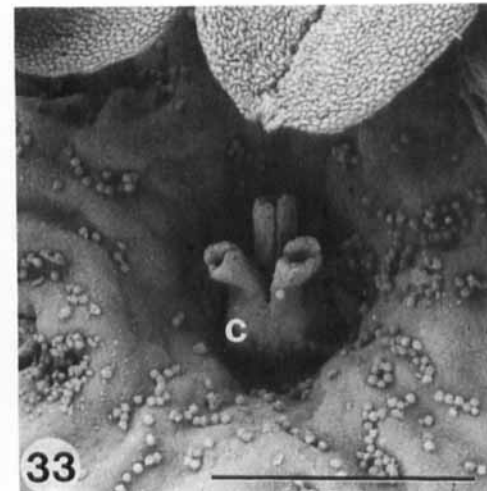
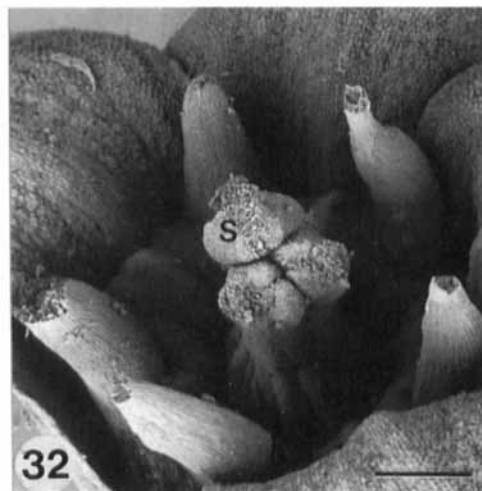
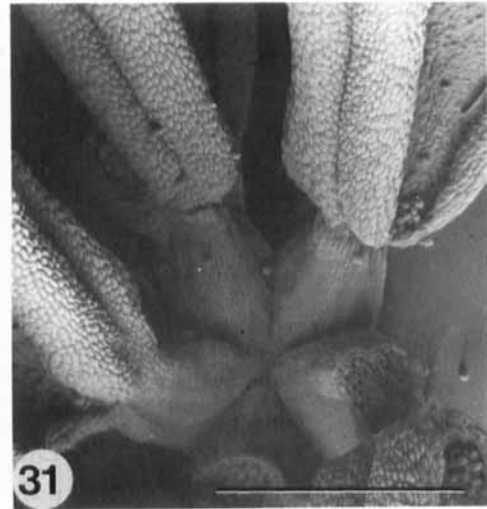
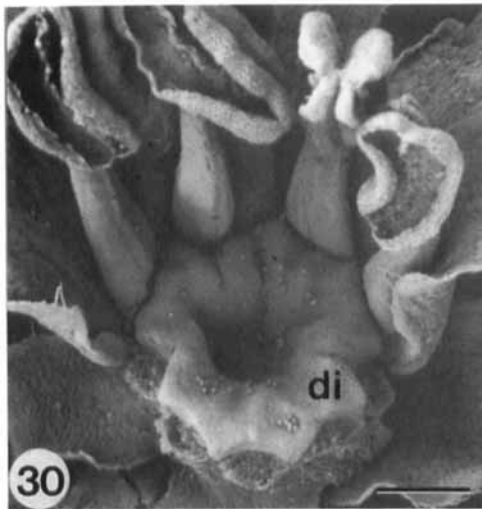
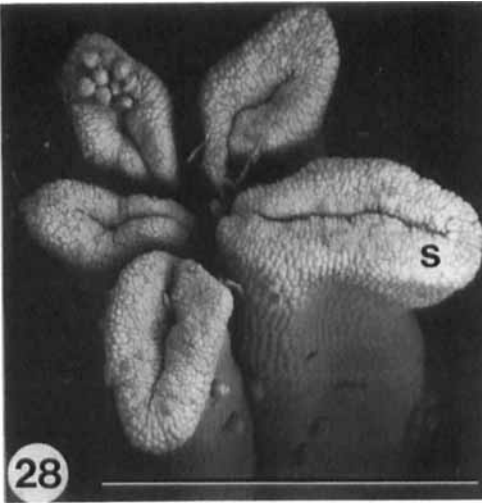
Carpellode structure and morphology

Spondiadeae

Harpephyllum. The male flower has four or five antipetalous carpelodes with vascular bundles frequently present in the dorsal and sometimes also in the ventral position (Fig. 34A). Each carpellode has a style with a vestigial stigmatic region (s), to which pollen grains are often attached (Fig. 28). Lower down (Fig. 34B), the styles fuse and there is a small canal (c), which in the most developed carpellode joins a locule containing a vestigial ovule (Fig. 24C).

Pleiogynium. There are five antipetalous carpelodes visible as small projections (c) in the centre of the nectariferous disc (Fig. 29). In their upper parts each

Figures 22–27. Light micrographs of fertile gynoecia. Figs 22–25. Transverse sections. Scales = 0.2 mm. Fig. 22. *Harpephyllum caffrum*, UNSW 14701, at locule level. Fig. 23. *Rhodospaera rhodanthema*, UNSW 5160, lower part of style. Fig. 24. *Pentaspadon motleyi*, Pullen 7406, lower part of style. Fig. 25. *Gluta renghas*, Ding Hou 781, lower part of style and top of ovary. Figs 26, 27. Longitudinal sections. Scales = 1 mm. Fig. 26. *Dracontomelon lenticulatum*, Pullen 1178. Fig. 27. *Mangifera indica*, UNSW 3178. a, stamen; c, corolla; k, calyx; r, resin canal; s, stigma; tt, transmitting tissue; vt, vascular tissue; other labels as in Fig. 7.



Figures 28–33. Scanning electron micrographs of male flowers. Fig. 28. *Harpephyllum cafrum*, UNSW 5162. Fig. 29. *Pleio gynium timoriense*, UNSW 3105. Fig. 30. *Rhodosphaera rhodanthema*, UNSW 3179. Fig. 31. *Pistacia chinensis*, UNSW 20388A. Fig. 32. *Rhus succedanea*, UNSW 11534. Fig. 33. *Schinus areira*, UNSW 14801. c, carpelloid; di, nectariferous disc; s, vestigial stigma. Scale bars = 0.5 mm.

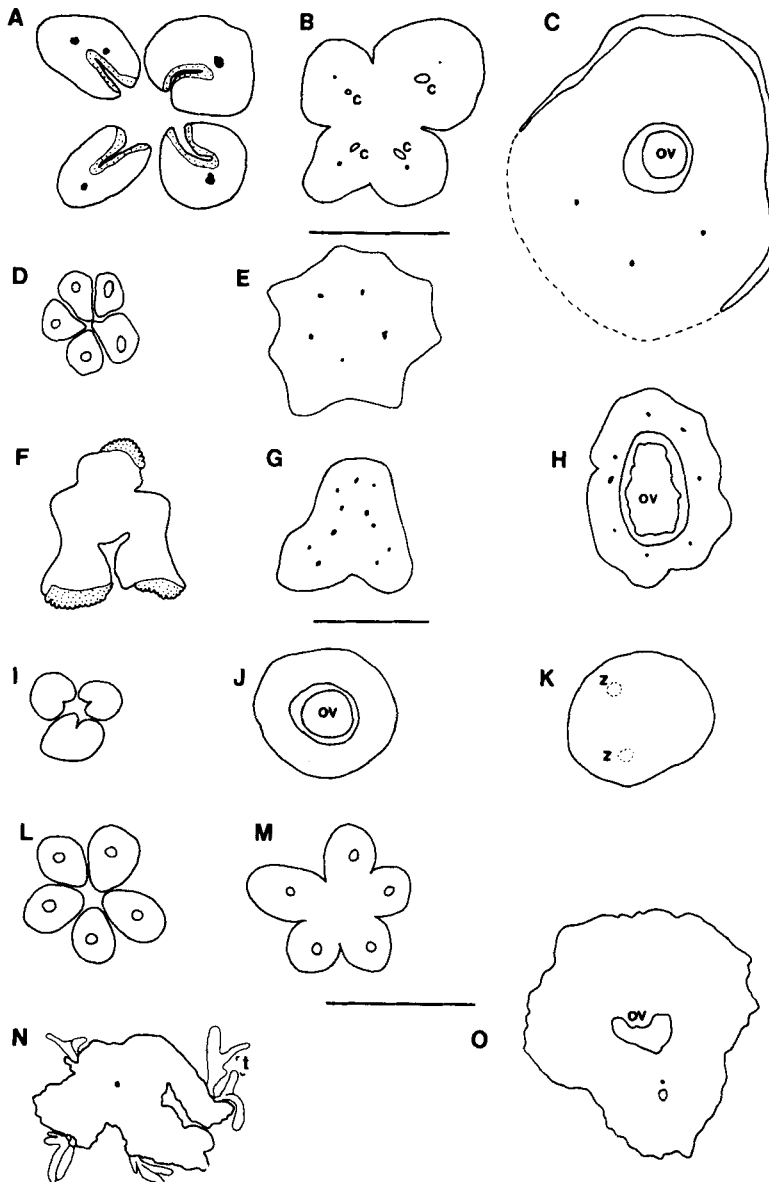
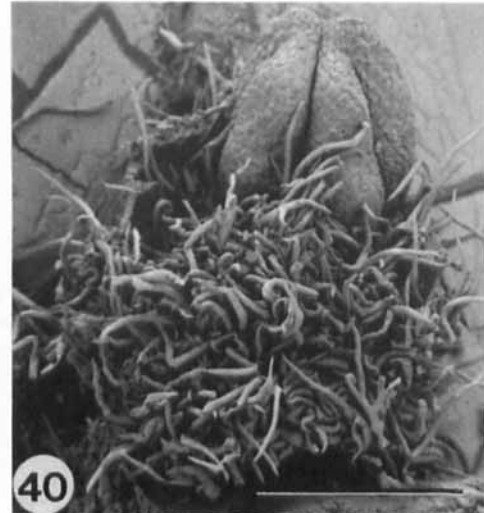
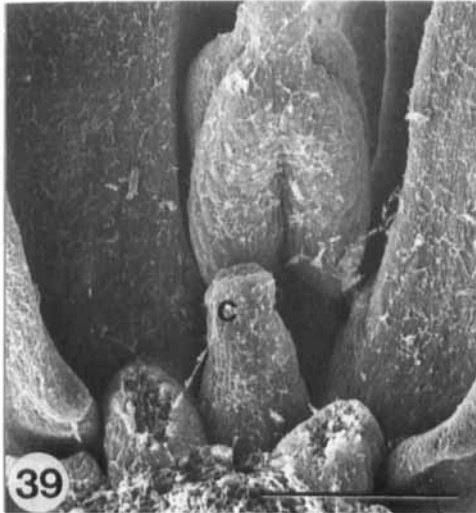
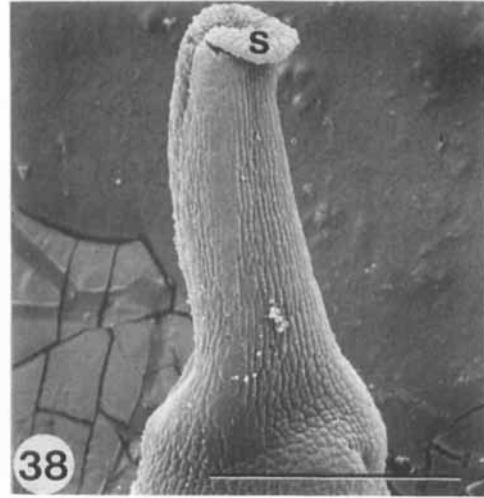
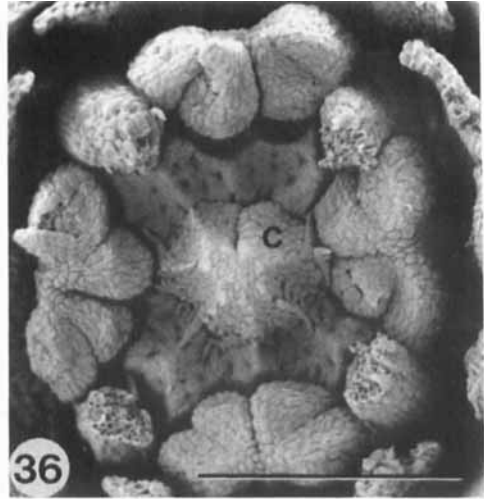
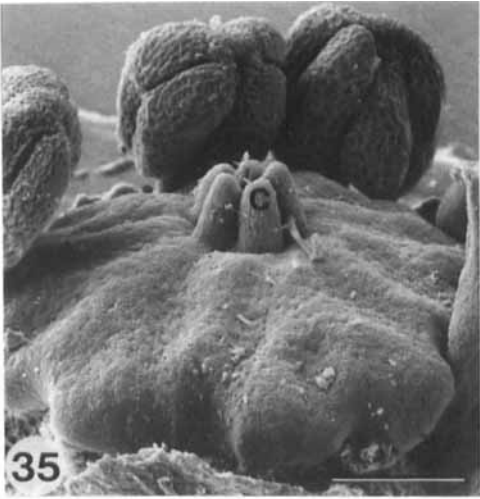


Figure 34. Transverse sections of carpelodes. A–C. *Harpephyllum cafrum*, UNSW 3177. Top scale. A. Upper parts of carpelodes. B. Lower parts of carpelodes, showing canals (c) in positions occupied by transmitting tissue in female flower. C. Base of carpelodes, showing a locule with a vestigial ovule (ov). The broken line indicates region of fusion between base of carpelodes and receptacle. D–E. *Pleio gynium timoriense*, UNSW 3105. Top scale. D. Upper parts of carpelodes. E. Lower parts of carpelodes that are embedded in disc. F–H. *Rhus succedanea*, UNSW 11534. Middle scale. F. Fused upper stylar parts of carpelodes. G. Fused lower stylar parts of carpelodes. H. Locule, with vestigial ovule. I–K. *Schinus areira*, UNSW 14801. Middle scale. I. Upper parts of carpelodes. J. Lower parts of carpelodes, showing a locule with vestigial ovule. K. Base of carpelodes just below locule. Note two small specialized zones of tissue (z). L–M. *Pentaspadon molleyi*, Pullen 6566. Bottom scale. L. Upper parts of carpelodes. M. Lower parts of carpelodes, just above disc. N–O. *Campnosperma coriaceum*, Ding Hou 780. Bottom scale. N. Upper part of carpelode, including trichomes (t). O. Lower part of carpelode, showing a locule with very small vestigial ovule (ov). ○, resin canal; ●, vascular tissue; stippled areas, vestigial stigmatic or transmitting tissue. Scale bars = 0.25 mm.



contains a resin canal but no vascular tissue (Fig. 34D); lower down in the receptacle there is one vascular bundle per carpelode that continues into the pedicel (Fig. 34E). There is no evidence of either locules or transmitting tissue.

Rhoëae

Rhodosphaera and *Pistacia*. Neither of these genera has any carpelodes in its male flowers (Figs 30, 31).

Rhus. The carpelodes closely resemble the gynoecium in the female flower except that they are smaller, having three stylar branches and vestigial stigmata (s in Fig. 32). In the stylar region there is a number of vascular bundles but no transmitting tissue (Fig. 34F, G). The locule contains a sterile ovule (ov), and both this and the ovary wall have an irregular cellular arrangement (Fig. 34H).

Schinus. Again there is a close resemblance with the gynoecium in the female flower, the three carpelodes being represented by three stylar branches (Figs 33, 34I), and a vestigial, unilocular ovary containing an abortive ovule (Fig. 34J). The carpelodes contain no vascular tissue, but under the locule there are two small specialized zones of tissue (z) which may be the vestiges of the locules from the other two carpelodes (Fig. 34K).

Pentaspadon. There are five antipetalous carpelodes visible as protrusions (c) from the centre of the disc (Fig. 35). Each contains a resin canal but no vascular tissue; in their upper parts they are free (Fig. 34L), but they become fused lower down (Fig. 34M). There are five vascular bundles in the centre of the disc, in line with the carpelodes, that terminate at the level at which the stamens fuse with the disc.

Camposperma. The vestigial gynoecium is a small cone-shaped piece of tissue (c) with an apparent suture down one side (Figs 34N, 36). It contains a vestigial locule with a small remnant of an aborted ovule (ov), and a single xylem vessel and resin canal in what appears to be the dorsal position (Fig. 34O). This structure seems to represent a vestigial antipetalous carpel.

Semecarpeae

In *Semecarpus* there is no external trace of any carpelodes (Fig. 37, 41A), although there is a small depression (de) covered by trichomes in the centre of the nectariferous disc (di), underneath which there are small amounts of vascular tissue which may be the vestiges of the vascular supply to the gynoecium.

Anacardiëae

Anacardium. The vestigial gynoecium is quite well developed with a stigma (s), style and ovary visible (Fig. 38). The upper parts are solid tissue devoid of vascular bundles. The rudimentary ovary has a locule with a vestigial ovule (ov) and a single xylem element in the dorsal position in the ovary wall (Fig. 41B). At

Figures 35–40. Scanning electron micrographs of male flowers. Fig. 35. *Pentaspadon molleyi*, Pullen 6566. Fig. 36. *Camposperma coriaceum*, FD 45239. Fig. 37. *Semecarpus australiensis*, Hyland 11166. Fig. 38. *Anacardium occidentale*, Zanon 26418. Fig. 39. *Bouea macrophylla*, Jacobs s.n. Fig. 40. *Blepharocarya involucrigera*, UNSW 12500, the carpelode obscured by trichomes. c, carpelode; di, nectariferous disc; s, vestigial stigma. Scale bars = 0.25 mm.

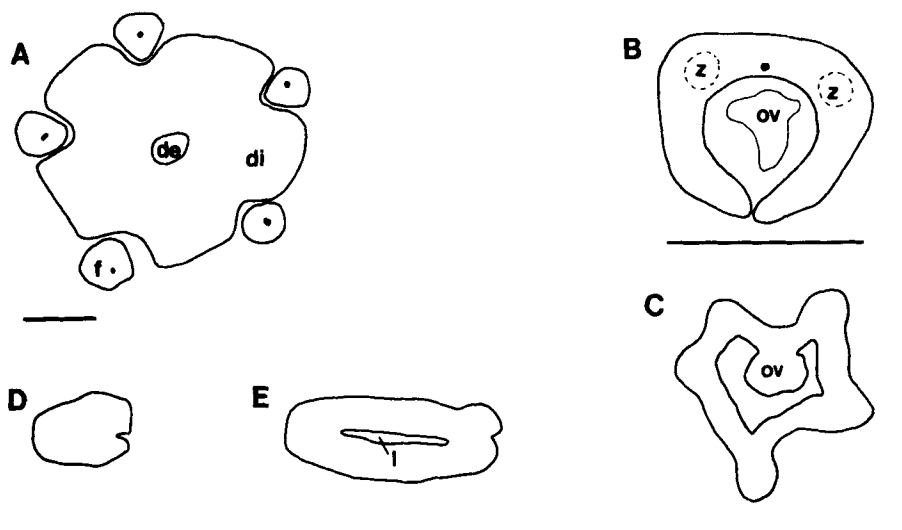


Figure 41. Transverse sections of carpelodes. A. *Semecarpus australiensis*, Hyland 11166. Top of nectariferous disc (di), showing small depression (de) in centre. Top left scale. B. *Anacardium occidentale*, Zanoni 26418. Lower part of carpellode, showing a locule with vestigial ovule (ov) and two small specialized zones of tissue (z). Top right scale. C. *Bouea macrophylla*, Jacobs s.n. Lower part of carpellode, showing a locule with vestigial ovule (ov). Bottom right scale. D–E. *Blepharocarya involucrigera*, UNSW 12500. Bottom left scale. D. Upper part of carpellode. E. Lower part of carpellode, showing empty locule (l). f, staminal filament; ●, vascular tissue. Scale bars = 0.25 mm.

this level, also, are two small circular zones of specialized tissue (z) in the ovary wall which remain visible to the base of the locule. These are poorly defined from the surrounding tissue and lack any vascular tissue; they may represent the vestiges of two other carpelodes.

Bouea. The vestigial gynoeceum is composed of a single carpellode (c) that contains neither vascular bundles nor resin canals (Figs 39, 41C). In the base there is a small locule with a vestigial ovule (ov).

Genus with uncertain affinities: Blepharocarya

In this species there is a single carpellode which is obscured by trichomes (Fig. 40); it is totally devoid of vascular tissue even down to the level at which the stamens fuse with the disc. In its upper parts it is a solid block of tissue which bears an apparent suture (Figure 41D); lower down it contains an empty locule (Fig. 41E).

DISCUSSION

Carpel structure and morphology

In most of the styles sectioned it has been possible to recognize a single dorsal and two ventral bundles. Occasionally less than three vascular bundles could be distinguished in the styles of abortive carpels, and only rarely were there more, as in *Rhus* and *Rhodosphaera*, which sometimes had up to five bundles in the fertile stylar element. However, three stylar bundles are present in genera from all

tribes, as well as in *Blepharocarya*, indicating that it is a basic and widespread feature of the family.

Spondiadeae

The number of carpels in the ovary varies from twice the number of petals (up to 13) in *Pleiogynium* to one in *Solenocarpus*; they are, however, often equal in number to the petals (Ding Hou, 1978; Engler, 1883, Tardieu-Blot, 1962). In *Harpephyllum* and *Dracontomelon* the carpels are positioned opposite the petals (antipetalous); this feature has previously been noted by Baillon (1878) and Eichler (1878), each of whom used it to define a group of genera in their treatments, using *Spondias* as type-genus. Baillon included *Poupartia*, *Sclerocarya*, *Buchanania* and *Spondias*, whilst Eichler include the last two only. This character is also present in *Antrocaryon* (Van der Veken, 1960), *Koordersiodendron* (Boerlage, 1901), *Lannea* (Ding Hou, 1978; Van der Veken, 1960), *Pegia* (Ding Hou, 1978), *Poupartia* (Engler, 1883) and *Pseudospondias* (Van der Veken, 1960). *Solenocarpus* appears to be the only unilocular member of the tribe (Ding Hou, 1978; Engler, 1883), in this case the single carpel being antisepalous (Lauterbach, 1920).

Engler's (1883, 1892) circumscriptions of the Spondiadeae describe the fruit as "mostly 5-3-locular, rarely by abortion 2-1-locular". In this study it has been possible to verify the occurrence of abortion in the ovaries of *Harpephyllum* and *Dracontomelon*. In *Harpephyllum* some locules abort early in the flower's development, containing no sign of an ovule at anthesis and with no indication of aborted carpels in the fruit. In *Dracontomelon*, however, abortion occurs post-anthetically; all the locules are fully formed with ovules at anthesis, and aborted locules are evident in the fruit. Abortion in the ovary, at whatever stage, would seem to be a characteristic of many Spondiadeae, there being discrepancies between the number of carpels observed in the flower, and the number of seeds (i.e. fertile locules) in the fruit (Engler, 1883; Wannan & Quinn, 1990).

In the three genera studied, two basic types of styler morphology were apparent. In the syncarpous gynoecium of *Dracontomelon* the proximal styles form a central pillar in the middle of the flower; they are connate just below their apices but free lower down. The styler bases are poorly differentiated and are therefore difficult to distinguish from the top of the ovary, and there is a furrow extending to the base of the ovary between each of the carpels. The stigmata are small, relatively inconspicuous areas immediately adjacent to the transmitting tissue at the top of the style. Descriptions and illustrations indicate that this type of morphology is typical also of *Spondias* (Engler, 1883; Tardieu-Blot, 1962), *Allospodias* (Stapf, 1901; Tardieu-Blot, 1962) and *Solenocarpus* (Airy Shaw & Forman, 1967; Engler, 1883; Lauterbach, 1920).

The second type of styler morphology occurs in *Harpephyllum* and *Pleiogynium*, where the styles are free and are clearly differentiated from the ovary; they are quite separate, being located towards the outer margin of the ovary, and bear conspicuously capitate apical stigmata. There are no visible lines of fusion or demarcation between the carpels on the surface of the ovary. From descriptions and illustrations, this type of styler morphology also occurs in *Antrocaryon* (Van der Veken, 1960), *Choerospondias* (Tardieu-Blot, 1962), *Lannea* (Engler, 1883; Fernandes & Fernandes, 1966; Van der Veken, 1960), *Poupartia* (Engler, 1883), *Pseudospondias* (Fernandes R. & A., 1966; Van der Veken, 1960), *Sclerocarya*

(Fernandes R. & A., 1966) and *Tapirira* (Blackwell & Dodson, 1967; Engler, 1883). Previous accounts have incorrectly described the stigmata of *Harpephyllum* as sessile (Dyer, 1975; Fernandes R. & A., 1966, 1969; Coates Palgrave, 1983), a mistake due perhaps to the study of older flowers in which the styles had withered or fallen.

There are five genera in need of further investigation. In the protologue of *Koordersiodendron*, Engler (1898) described the styles as "recurved with the tips flattened and emarginate". Boerlage (1901: plate 8, figs 12–14) illustrates the styles as proximal with diverging apices, bearing stigmata at their tips. This does not conform with either the *Harpephyllum* or *Dracontomelon* type. The same seems true of *Cyrtocarpa*, which has been described and illustrated with a single style divided at the apex into between three and five stigmatic lobes (Engler, 1883: plate 8, fig. 39). There are contradictory accounts of the structure of the styles in *Pegia*. Engler (1883: plate 9, fig. 3) clearly shows them as separate and distal, a view supported by Tardieu-Blot (1962); Ding Hou (1978) described them as united. The stylar morphologies of *Haematostaphis* and *Operculicarya* have not been described or illustrated.

Rhoëae

Rhus, *Pistacia*, *Rhodosphaera*, *Schinus* and *Cotinus* (Payer, 1857) possess tricarpellary gynoecia that are unilocular by abortion; the fruit of these genera are, therefore, pseudomonomerous drupes. Organographic studies of *Rhus* (Marchand, 1869; Payer, 1857), *Cotinus* (Payer, 1857) and *Pistacia* (Marchand, 1869; Takeda *et al.*, 1979) have shown that the abortion of the locules in the two sterile carpels occurs quite early in the development of the flower. Two additional styles are all that remain of the aborted carpels. In this study, all three styles possessed apparently functional stigmata, as well as vascular bundles and transmitting tissue that extended down into the ovary, suggesting that all three styles may transmit pollen tubes to the fertile carpel.

The illustrations of *Pentaspadon* in Hooker (1860) and Engler (1883) closely resemble the micrographs in this study. The gynoecium of *Pentaspadon* is composed of a single carpel, with no signs of additional abortive carpels. Marchand's (1869) assertion that there are "2 or 3 stigmata, of which a single persists" is not borne out. In *Camptosperma* there is only a single zone of transmitting tissue in the style and the fruit is also single-seeded. The presence of five vascular bundles in the style that originate in the complex stigmatic region suggests that the gynoecium may be derived from a multicarpellary structure. This idea is supported by the presence of a vestigial locule between the tips of the horseshoe-shaped fertile locule in the fruit; this vestigial locule contains no ovule but is bounded by a well differentiated endocarp (Wannan & Quinn, 1990). On the basis of carpel number, *Pentaspadon* (1), *Camptosperma* (1) and *Pseudoprotorhus* (2; Perrier de la Bathie, 1944) are atypical of the tribe in that they lack any clear indication of a tricarpellary ovary. *Faguetia* also differs from the tribal pattern, in having from two to five carpels (Engler, 1883; Perrier de la Bathie, 1946).

Within the tricarpellary, unilocular genera of the Rhoëae there is considerable variation in the degree of stylar fusion. At one extreme, *Schinus* has three styles that are connate only at the base; at the other, *Mauria* and *Sorindeia* have a 'single' style crowned by a trilobed stigma (Engler, 1883). The latter condition

occurs in *Rhus succedanea*, except that in this case the style is very shortly trilobed with three separate stigmata. Anatomically, the single style is clearly the result of fusion. The rest of the tricarpellary, unilocular genera of the Rhoëae have a styler morphology which is intermediate between that of *Schinus* and *Mauria*. Whilst generic descriptions and illustrations, most notably those of Engler (1883), record apical styles in many genera of the Rhoëae, some have lateral styles. In *Micronychia* (Oliver, 1881; Perrier de la Bathie, 1946) and *Loxopterygium* (Engler, 1883) the styles are situated on the dorsal side of the ovary, while in *Cotinus* (Engler, 1883) they are on the ventral side; it is unfortunately not clear to which side of the ovary the lateral styles of *Loxostylis*, *Schinopsis* and *Smodingium* are joined.

Most genera of the tribe have capitate stigmata, although this structure is obviously less pronounced where the styles are very short or are fused for most of their length. The exceptions are *Campnosperma* with a lobed discoid stigma, *Pentaspadon* with a single recurved stigma, and *Pseudoprotorhus* (Perrier de la Bathie, 1944) and some species of *Pistacia* which have spatulate or dorsiventrally flattened stigmata.

Semecarpeae

The tricarpellary gynoecium of *Semecarpus* is unilocular with three basally connate styles and capitate stigmata, in many respects similar to the condition in *Schinus*. The same is true of *Holigarna* (Baillon, 1878; Engler, 1883). *Melanochyla*, with a single style and three capitellate stigmata (Ding Hou, 1978), resembles other genera in the Rhoëae. Although Engler (1883, 1892) used the presence of a tricarpellary unilocular ovary to define this tribe, its presence in *Drimycarpus* and *Nothopegia* is yet to be verified; both are recorded as having a single style with either a single capitate or trilobed stigma (Bentham & Hooker, 1862; Engler, 1883).

Anacardiëae

In this tribe there are two groups on carpel number and styler morphology. *Buchanania* and *Androtium* (Ding Hou, 1978) have gynoecia of four to six antipetalous carpels, of which only one has a locule. Although always previously described as apocarpous, Jessup (1985) has stated that the carpels in *Buchanania* are connate at the base and that "*Buchanania* and probably also *Androtium* exhibit an extreme form of partial syncarpy already observed in *Dracontomelon* and *Koordersiodendron*". The ovaries of *Dracontomelon* and *Koordersiodendron* (Boerlage, 1901), however, are clearly syncarpous with only the styles being partly free, but in *Buchanania* the carpels are free almost to their bases. The single fertile carpel of *Buchanania*, and probably also *Androtium* (Stapf, 1905), has neither stigma nor transmitting tissue; the stigmata and styles of the sterile carpels appear to function as gynobasic styles, as suggested by Jessup (1985).

Although *Buchanania* and *Dracontomelon* differ in their degree of syncarpy, there are important similarities in their styler morphology. In both, the styles are continuous with the top of the ovary and, by reason of their close proximity, form a column in the centre of the flower. Their stigmata are small relatively unspecialized areas, adjacent to the transmitting tissue, at the top of the style. The terminal regions of the style are, however, somewhat broader in *Buchanania*.

The remaining genera have a gynoecium with a single style and locule: *Gluta*,

Mangifera, *Anacardium*, *Fegimanra*, *Swintonia* and *Bouea*. *Gluta*, *Mangifera* and *Bouea* possess a single antisepalous carpel; *Bouea* has an apical style and capitate stigma whilst *Mangifera* and *Gluta* have lateral (gynobasic) styles that join the ventral margin of the ovary and rather obscure stigmatic regions close to the top of the style. *Anacardium* also has a lateral style which joins the unilocular, antisepalous ovary on the ventral side; in *A. occidentale* the stigma is punctiforme, though in other species it is capitate (Mitchell & Mori, 1987). Although there is only a single zone of transmitting tissue, there are considerably more vascular bundles in the style than in *Bouea*, *Mangifera* and *Gluta*. The occurrence of extra vascular bundles in the upper part of the style perhaps suggests that it consists of more than one carpel. It may be a reduced tricarpellary pistil, as suggested by Copeland (1961), but the presence of a single zone of transmitting tissue and single stigma does not support this idea. The floral morphology of the genus *Fegimanra* appears similar to *Anacardium*, including the growth of an expanded floral axis in the fruit (Aubreville, 1950).

Preliminary studies on the remaining genus, *Swintonia*, indicate that it has a single antistepalous carpel with an apical style and capitate stigma which allies it with *Bouea*, *Gluta* and *Mangifera*.

Dobineëae

The gynoecium of *Dobinea* is unicarpellary with a long apical style containing three vascular bundles and a zone of transmitting tissue in its upper parts. The presence of accessory vascular bundles just above the level of the locule may indicate the presence of abortive carpels, or it may be due to extra vascularization which occurs in post-anthetic ovaries. Interestingly, the existence of extra-carpellary remnants is suggested by Forman (1954) in *Campylopetalum*, where there is a small knob at the base of the style which he interpreted as the rudiment of another styler branch. Further anatomical studies may resolve this problem.

Dobinea is described as having stigmatic tissue at the apex and on the inside of the style (Hooker, 1876), which perhaps represents a derivative of the smaller ventrally situated type of stigmata seen in *Gluta* and *Mangifera*; the stigma in *Campylopetalum* has not yet been described. This tribe, though largely defined by the absence of a perianth in the female flower, has a carpel morphology and structure similar to that of the Anacardiëae.

Genus with uncertain affinities: Blepharocarya

With a single antisepalous carpel and a lateral style, the gynoecium of *Blepharocarya* seems, initially, similar to those of *Mangifera* and *Gluta*. However, as noted by Radlkofer (1879) and confirmed in this study, the lateral style of *Blepharocarya* joins the ovary on the dorsal side. *Micronychia* (Oliver, 1881) and *Loxopterygium* (Engler, 1883), both in the Rhoëae, are the only other genera in the Anacardiaceae that can be confirmed as having dorsally located, lateral styles. *Loxostylis* (Engler, 1883), *Schinopsis* (Ragonese & Castigliani, 1947) and *Smodingium* (Engler, 1883), in the Rhoëae, are described and illustrated with lateral styles, but with no indication as to which side they are joined. Although described as capitate (Airy Shaw, 1965), the stigma of at least *B. depauperata* is similar to *Gluta*, being a papillose region on the ventral side of the style at its

apex. The gynoecium of *Blepharocarya* has characters of both the Rhoëae and Anacardiëae, but conforms with neither as presently circumscribed.

General discussion of carpel structure and morphology

Female flowers in this family range from bisexual (e.g. *Dracontomelon*, *Mangifera*) to clearly unisexual with no sign of stamens (e.g. *Pistacia*). The flowers of a number of genera studied had stamens with seemingly fertile anthers which upon sectioning were found to contain either obviously aborted pollen or no pollen at all: *Harpephyllum*, *Pleiogynium*, *Rhus*, *Schinus*, *Pentaspadon*, *Camptosperma*, *Semecarpus*. Of these genera, the occurrence of well formed staminodes has been previously noted in more recent descriptions of *Harpephyllum* (Coates Palgrave, 1983; Fernandes & Fernandes, 1966; Phillips, 1951; Von Teichman & Van Wyk, 1988), *Pleiogynium* (Ding Hou, 1978), *Rhus* (Copeland & Doyel, 1940; McNair, 1921), *Schinus* (Copeland, 1959), *Camptosperma* (Ding Hou, 1978) and *Semecarpus* (Backer & Bakhuizen, 1965; Ding Hou, 1978), although earlier descriptions had recorded the flowers as polygamous. However, in *Pentaspadon* the female flowers have been mostly described as bisexual with a whorl of functional stamens and a whorl of staminodes (Backer & Bakhuizen, 1965; Baillon, 1878; Ding Hou, 1978; Engler, 1883, 1892; Hooker, 1860; Jacobs, 1961; Marchand, 1869; Ridley, 1922). Our observations reveal that, while the antipetalous stamens are obviously reduced, the apparently normal antisepalous stamens contain little or no pollen and do not dehisce; indeed they have always been illustrated as undehisced. It seems likely that this condition may well also be present in the female flowers of other genera previously described as polygamous. Only *Bouea* was found to be polygamous, with male and bisexual flowers.

There is considerable variation in both carpel and locule number across the family. The number of fertile locules in the fruit is most frequently one; only in the Spondiadeae are there genera which regularly produce more than one fertile locule in the fruit. The number of carpels is the more useful character since abortion of locules, either before or after anthesis, is widespread, particularly in the Spondiadeae, Rhoëae and Semecarpeae. Owing to the nearly constant occurrence of a single dorsal and two ventral bundles in the styles throughout the family, it has been possible to detect traces of aborted carpels in many unilocular gynoecia.

In the Spondiadeae there are usually five carpels which are opposite, and therefore equal in number to, the petals. Elsewhere, there are five antipetalous carpels in *Buchanania* and *Androtium* (Anacardiëae), and three in *Comocladia* (Rhoëae). Antisepalous carpels occur only in genera with unicarpellary gynoecia. Tricarpellary gynoecia seem to be characteristic of the Rhoëae, with *Faguetia*, *Pentaspadon*, *Camptosperma* and *Pseudoprotorhus* being atypical in this regard. Like the Rhoëae, the Semecarpeae and the Julianiaceae (Hemsley, 1908; Willis, 1973) appear to be characterized by tricarpellary gynoecia. Genera from the Anacardiëae (excluding *Buchanania* and *Androtium*), the Dobineëae and *Blepharocarya* possess a unilocular ovary with a single style. Whilst *Bouea*, *Gluta*, *Mangifera* and *Blepharocarya* are unicarpellary, there are suggestions of aborted carpels in *Anacardium* (Anacardiëae) and the Dobineëae (Forman, 1954).

There is a wide variety of stylar morphologies in the family. *Dracontomelon*, *Spondias*, *Allospodias*, *Buchanania*, *Androtium* and probably *Solenocarpus* possess styles that are poorly differentiated from the top of the ovary, and stigmata that

are relatively unspecialized regions adjacent to the transmitting tissue at the apex of the style. In many other genera of the Spondiadeae, as well as Rhoëae and Semecarpeae the styles are clearly differentiated from the top of the ovary and have conspicuously capitate, or rarely spathulate stigmata. In the Rhoëae and the Semecarpeae the styler bases are closer together or sometimes fused. All genera in the Dobineëae and Anacardiëae (excluding *Buchanania* and *Androtium*) have a single style. *Mangifera*, *Gluta*, *Anacardium* and probably *Fegimanra* are characterized by a gynobasic style on the ventral side of the ovary. Gynobasic or lateral styles also occur in the Rhoëae, but there can be on either the dorsal or ventral side. Thus the presence of a dorsally attached lateral style in *Blepharocarya* links it with those genera in the Rhoëae with dorsal styles rather than with any in the Anacardiëae.

Capitate stigmata are distributed widely in the family, being present in the Spondiadeae, Semecarpeae, Rhoëae and the Anacardiëae. In the Anacardiëae, capitate stigmata are limited to *Swintonia*, *Bouea* and some species of *Anacardium*. In *Gluta*, *Blepharocarya*, *Mangifera* and the other species of *Anacardium*, the stigma is located ventrally at the top of the style; a similar stigmatic region occurs also in the Dobineëae, but in this case it extends downwards nearly to the top of the ovary. Spathulate or dorsiventrally flattened stigmata are uncommon, being limited to the Rhoëae (*Pistacia* and *Pseudoprotorhus*) and Julianiaceae (*Orthopterygium* and *Amphipterygium*).

All the tribes, apart from the Dobineëae, show variability in characters derived from the gynoecium. The Anacardiëae appear fairly uniform, except for *Buchanania* and *Androtium*, whose gynoecia are more like those of the Spondiadeae. The Rhoëae, Semecarpeae and Julianiaceae have similar gynoecia, the latter resembling *Pistacia*. *Camposperma*, *Pentaspadon*, *Pseudoprotorhus*, *Solenocarpus* and *Blepharocarya* have gynoecia which are atypical of the present tribes.

Carpellode structure and morphology

In male flowers investigated from the Spondiadeae (*Harpephyllum* & *Pleiogynium*), the carpelodes are antipetalous; this is also the case in *Lannea* (Baillon, 1878) and *Pseudospondias* (Fernandes & Fernandes, 1966). There are apparently no carpelodes in *Haemantostaphis* (Engler, 1883) and *Choerospondias* (Chandra, 1978); contradictory reports exist for *Poupartia* (Engler, 1883; Perrier de la Bathie, 1946) and *Sclerocarya* (Fernandes & Fernandes, 1966, 1969; Keay, 1958; Van der Veken, 1960). This character has not been scored in *Operculicarya*, *Allospondias* and *Spondias*.

In the Rhoëae, there are three carpelodes in *Rhus*, *Schinus*, *Euroschinus* (Bentham, 1863), *Loxopterygium* (Barkley, 1962) and *Pseudosmodingium* (Barkley & Reed, 1940); they are absent from *Rhodospaera*, *Pistacia*, and *Loxostylis* (Baillon, 1878). Therefore, *Pentaspadon*, with five, and *Camposperma*, with one, are atypical of the tribe.

The reported absence of carpelodes in *Semecarpus* (Ding Hou, 1978) is supported by this study. Elsewhere in the Semecarpeae they are recorded as absent from *Holigarna* (Engler, 1883), but there are contradictory reports for *Drimycarpus*, *Melanochyla* and *Nothopegia* (Ding Hou, 1978; Engler, 1883). A

single carpellode occurs in both *Anacardium* and *Blepharocarya*, though it is somewhat more developed in the former.

In general, the carpelloses of the Spondiadeae are larger and more developed than in other tribes. The proximal styles and elongated vestigial stigmata of the carpelloses in *Harpephyllum* bear little resemblance to the distal styles and capitate stigmata of the female flowers, being more like the upper parts of the sterile carpels in *Buchanania*. When carpelloses occur in the family, they are frequently equal in number to the carpels in the female flower. However, notable exceptions are *Pleiogynium*, which has two whorls of carpels in the female flower but only a single whorl in the male flower, and *Pentaspadon*, which is unicarpellary in the female flower but has five carpelloses in the male. In both cases, the state in the male flower is more generalized for the family, while that in the female flowers is derived. Hence, the male flowers appear to be more conservative in this character. The occurrence of five carpelloses in *Pentaspadon* suggests that the affinities of this genus lie with the Spondiadeae rather than with the Rhoëae.

Other data sources

The inclusion of the Julianiaceae within the Anacardiaceae, in close relationship to the Rhoëae, is suggested by evidence from fruit anatomy (Wannan & Quinn, 1990), wood anatomy (Bailey, 1940; Heimsch, 1942; Kramer, 1939; Kryn, 1953; Moseley, 1973; Record, 1949; Stern, 1952; Youngs, 1955), phloem anatomy (Fritsch, 1908), ovule anatomy (Copeland & Doyel, 1940), flavonoids (Young, 1976), biflavonoids (Wannan & Quinn, 1988), serology (Petersen & Fairbrothers, 1983) and a critical evaluation of the descriptions of carpel morphology of Hemsley (1908) and Willis (1973). Recent work on pollen, biflavonoids, inflorescence structure and bark anatomy (Wannan *et al.*, 1985, 1987) has shown that *Blepharocarya* also belongs in the Anacardiaceae.

While there is little correlation between characters of reproductive morphology and anatomy and the existing tribes, there are marked discontinuities apparent in the family. Wannan & Quinn (1990) recognized two distinct types of pericarp structure: the *Anacardium*-type, which characterizes Dobineëae, Semecarpeae, most Rhoëae (excluding *Camposperma* & *Pentaspadon*) and Anacardiëae (excluding *Buchanania* & *Androtium*), *Blepharocarya*, *Amphipterygium* and *Orthopterygium* (Group A in Table 1), and the *Spondias*-type, which characterizes Spondiadeae as well as *Buchanania*, *Androtium*, *Pentaspadon* and *Camposperma* (Group B in Table 1).

The inclusion of *Blepharocarya* in Group A is supported by data on distribution of wood parenchyma, which Dadswell and Ingle (1948) used to group it with genera of the Rhoëae. However, the gynoecium of *Blepharocarya* has features of both the Rhoëae and the Anacardiëae (excluding *Buchanania* & *Androtium*). A close link with the Anacardiëae seems unlikely, as *Blepharocarya* has septate wood fibres, only paratracheal wood parenchyma (Dadswell & Ingle, 1948; Kryn, 1953), and pinnate leaves, all of which are atypical of the tribe. Hence, despite its unicarpellary gynoecium, the closest affinities of *Blepharocarya* are with the Rhoëae. There is some evidence to suggest that *Amphipterygium* and *Orthopterygium* are related to *Pistacia*: all have a single perianth whorl, though this is apparently

TABLE 1. Tentative arrangement of genera in the Anacardiaceae

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- Group A.** Fruit with an endocarp that is composed of discrete and regularly arranged layers of cells. Carpels usually three or less; fruits unilocular; agathisflavone often present in leaves and/or fruits.
- Subgroup A1.** Gynoecium unicarpellary; endocarp with reduced number of layers. Leaves simple. Wood with bands of apotracheal parenchyma but without septate fibres: *Bouea*, *Gluta*, *Mangifera*, *Swintonia*.
Allied genera: *Semecarpus*, *Drinycarpus*, *Melanochyla*, *Nothopogia*, *Holigarna*.
- Subgroup A2.** Gynoecium mostly tricarpellary; endocarp usually with 4 distinct layers, mostly sclerenchymatous. Leaves mostly pinnate. Wood with septate fibres but without bands of apotracheal parenchyma.
Flowers protected by perianth: *Actinocheita*, *Anacardium*, *Astronium*, *Bonetiella*, *Cardenasiodendron*, *Comocladia*, *Cotinus*, *Euroschinus*, *Fegimanra*, *Haplorhus*, *Heeria*, *Lawrophyllus*, *Lithraea*, *Loxopterygium*, *Loxostylis*, *Mauria*, *Metopium*, *Micronychia*, *Mosquitoxylum*, *Ochoterena*, *Ozoroa*, *Pachycormus*, *Parishia*, *Pistacia*, *Protorhus*, *Pseudosmodingium*, *Rhodospaera*, *Rhus*, *Scasellatia*, *Schinopsis*, *Schinus*, *Smodingium*, *Sorindeia*, *Thyrsodium*, *Trichoscypha*.
Perianth absent; flowers clustered within an involucre. *Amphipterygium*, *Orthopterygium*.
Flowers with a gynoecium that is protected by neither perianth nor involucre: *Campylopetalum*, *Dobinea*.
Allied genus: *Blepharocarya*.
- Group B.** Fruit with a thick endocarp usually composed of heavily lignified and irregularly oriented sclereids, the only discrete cell layer being that bounding the locule; fruits often multilocular; agathisflavone absent from leaves and fruits.
- Subgroup B1.** Gynoecium in the female flowers of five carpels (or more) with clearly defined styles and capitate stigmata: *Antrocaryon*, *Choerospondias*, *Harpephyllum*, *Lansea*, *Pleiogynium*, *Poupartia*, *Pseudospondias*, *Sclerocarya*, *Tapirira*.
- Subgroup B2.** Gynoecium in the female flowers of one to five carpels with neither clearly defined styles nor capitate stigmata: *Allospodias*, *Androtium*, *Buchanania*, *Camposperma*, *Dracontomelon*, *Pentaspadon*, *Solenocarpus*, *Spondias*.
Genera of group B unassigned to a sub-group: *Cyrtocarpa*, *Haematostaphis*, *Koordersiodendron*, *Operculicarya*, *Pegia*.
Genera unassigned to a group: *Faguetia*, *Pseudoprotorhus*.
-

lacking in the female flowers of the last, and there are some species of *Pistacia* with pollen and stylar morphologies similar to those of *Amphipterygium* and *Orthopterygium* (Erdtman, 1952; Hemsely, 1908).

In Group A there are a number of smaller groups of genera that appear more closely related. *Dobinea* and *Campylopetalum* are distinguished from the remainder by their extended ventral stigmata (Baillon, 1878; Forman, 1954), *Dobinea*-type pollen (Erdtman, 1952, 1954), a chromosome number of $n = 7$ (Forman, 1954; Goldblatt, 1981) and a gynoecium that is enclosed by neither perianth nor involucre; these character states occur nowhere else in the family.

A second sub-group of genera is distinguished by simple leaves, absence of septate wood fibres and a cupuliform receptacle around the gynoecium in the female flower. This set of states defines a group corresponding to the tribe Semecarpeae, although in *Nothopogia* the ovary appears quite free of the receptacle (i.e. superior). The anatomy of the expanded receptacle, and its homology in each genus, is yet to be investigated; the only material examined here was from a species of *Semecarpus* that does not have an expanded receptacle. Thus, the apparent affinities between these five genera have yet to be confirmed.

A third sub-group (*Bouea*, *Gluta*, *Mangifera*, *Swintonia*) is distinguished by simple leaves, a derived form of the *Anacardium*-type pericarp, absence of septate

wood fibres, tangential bands of apotracheal wood parenchyma and a unicarpellary ovary. This group corresponds to the Anacardiæae with the exclusion of *Anacardium*, *Fegimanra*, *Buchanania* and *Androtium*.

The remaining genera of Group A constitute a heterogeneous assemblage with variable leaf and carpel morphology, and wood anatomy.

The inclusion of *Buchanania* and *Androtium* with Group B is supported by the presence, in all three, of poorly differentiated carpels. *Buchanania* is also linked with Group B on the absence of apotracheal bands of wood parenchyma that characterize the Anacardiæae (Dadswell & Ingle, 1948). It is also atypical of the Anacardiæae in the presence of septate wood fibres (Heimsch, 1942; Kryn, 1953), mucilage in the epidermal cells of the leaves and the presence of phloem fibres in the stem, as well as the feeble development of cortical parenchyma (Goris, 1910). Finally, all genera of the Anacardiæae have ovules with basally attached funicles and, where recorded, inferior micropyles; the funicle of *Buchanania*, however, although basally attached, has a superior micropyle.

The inclusion of *Pentaspadon* in Group B is supported by the presence of five carpelodes in the male flower, a number that is atypical of the Rhoëae.

Within Group B, there is a close-knit group of genera (Table 2, sub-group B1) with syncarpous ovaries of up to five antipetalous carpels, clearly defined separate styles and capitate stigmata: *Antrocaryon*, *Harpephyllum*, *Lannea*, *Poupartia*, *Pseudospondias*, *Sclerocarya* from Africa, as well as *Choerospondias* from Asia and *Tapirira* from Mexico. *Pleiogynium* has twice the number of carpels that is typical of this group, but displays the styler and stigmatic features, and the male flowers possess five carpelodes; hence, it must be seen to have close affinities with this sub-group. The remainder of Group B appear to constitute a fairly heterogeneous assemblage varying in carpel number and anatomy, leaf morphology and pericarp anatomy (Wannan & Quinn, 1990). *Buchanania* appears most isolated, as it is the only genus in which the ovule has a basally attached funicle. Although *Solenocarpus* has been submerged in *Spondias* (Airy Shaw & Forman, 1967), their distinct pericarp anatomies and constant difference in carpel number suggest that they should be recognized as separate genera (Wannan & Quinn, 1990). *Operculicarya* was described as a member of the Spondiadeae with close affinities to *Sclerocarya* (Perrier de la Bathie, 1944). There is still little known of its gynoecium, the number of carpels being inferred from the styler scars on the fruit. Its inclusion in Group B is tentative, especially since it is the only member with a single whorl of stamens.

Evolution of characters within the family

The Burseraceae, being the only remaining family of the Sapindales (Cronquist, 1981) also possessing biflavonyls and vertical intercellular secretory canals in the primary and secondary phloem (v.s.), is selected as sister group.

Leaf morphology

Since pinnate leaves are the most widely expressed character state, occurring in 46 genera of the Anacardiaceae, all 16 genera of the sister group (Burseraceae), and in all other families of the Sapindales (Cronquist, 1981), they are the plesiomorphic condition in the family. Bipinnate leaves, which occur in one species of *Spondias*, and simple leaves, which occur in 34 genera, are derived

conditions. There is a transformation series in several distantly related genera (e.g. *Solenocarpus* and *Schinus*) from pinnate to simple leaves through intermediate species with trifoliolate and unifoliolate leaves. This suggests that reduction in the number of leaflets has occurred a number of times, and is thus not necessarily an indication of affinity. Lam (1932) and Engler (1892) considered that the pseudostipules (i.e. the 1–2 pairs of subulate laccinae on the petiole) of *Holigarna* represent leaflets of a compound leaf; perhaps the petiolar auricles of *Campnosperma* are also the remnants of a pinnate leaf.

Ovule insertion

The most widespread condition in the family is an apically attached funicle bearing an ovule which has a superior micropyle. Since the sister group also has apically attached funicles and superior micropyles, although the ovules are epitropous (Cronquist, 1981), this condition is considered plesiomorphic. The most derived condition is a basally attached funicle bearing an ovule which has an inferior micropyle; this character state is restricted to Group A. Evolution appears to have been first towards an ovule with a laterally (e.g. *Laurophyllum*) or basally (e.g. *Loxostylis*) attached funicle and a superior micropyle; reorientation of the micropyle (e.g. *Metopium*) seems to have occurred later as there are no ovules with apically attached funicles and inferior micropyles.

Carpel morphology and structure

The most widespread condition in the Sapindales is five antipetalous carpels, and the same condition is also common in the Burseraceae. This condition is therefore considered plesiomorphic. Reduction in the number of carpels would appear to have occurred a number of times. In Group B there has been reduction to a single carpel with little or no evidence of remaining carpellary remnants (e.g. *Pentaspadon*, *Solenocarpus*, *Campnosperma*), whereas in Group A there has been reduction to three carpels (e.g. *Rhus*), and to a single carpel (e.g. *Mangifera*, *Anacardium*, *Blepharocarya*). In those genera with tricarpellary gynoecia, there is evidence of further reduction, only one carpel being fertile with the others represented by styles. Two whorls of carpels is an apomorph occurring only in *Pleiogynium*.

Syncarpous gynoecia occur in all multicarpellary genera of the Anacardiaceae except *Buchanania*, where near apocarpy is associated with plesiomorphy in endocarp structure, carpel number and stylar morphology. This, together with the scattered occurrence of apocarpous gynoecia throughout the Rutales, suggests that, as in many other angiosperm families, syncarpy is the derived state.

Carpels in which the stigma, style and ovary are not clearly differentiated occur in *Androtium*, *Buchanania*, *Dracontomelon*, *Allospodias*, *Spondias* and *Solenocarpus*. This type of undifferentiated carpel occurs widely in the Burseraceae and therefore is considered plesiomorphic. In addition, all these genera possess a *Spondias*-type pericarp, pinnate leaves, apically attached funicles and mostly have five carpels, all of which are plesiomorphs. The most widespread apomorph (e.g. *Harpephyllum*, *Schinus*) is a well-differentiated carpel in which the style is clearly defined from the top of the ovary, and bears a capitate stigma. The fused styles of the Rhoëae and Semecarpeae are a further development. It is concluded that the single styles of the Anacardiëae, the Dobineëae and *Blepharocarya* are derived, by

reduction, from the condition that is common in the Rhoëae. Lateral styles, either dorsally or ventrally attached, appear to be separate specializations derived from the widespread apically attached condition. Dorsally attached styles are restricted to the Rhoëae (*Micronychia*, *Loxopterygium*) and *Blepharocarya*, whilst ventrally attached styles occur in both the Anacardiëae (*Gluta*, *Mangifera*) and the Rhoëae (*Cotinus*).

Taxonomic conclusions

The derived *Anacardium*-type endocarp defines a large group (Group A) comprising essentially four tribes *sensu* Engler (1883) (Anacardiëae, Dobineëae, Semecarpeae, Rhoëae), as well as the five genera which have often been placed in separate families (*Blepharocarya*, *Orthopterygium*, *Amphipterygium*, *Dobinea*, *Campylopetalum*). This group appears to be supported by two other apomorphs, an initial reduction to a tricarpeal gynoecium and the ability to synthesize agathisflavone (Wannan *et al.*, 1985; Wannan & Quinn, 1988). Further reduction to a unicarpeal state with a ventrally attached style, along with apotracheal bands of wood parenchyma, simple leaves and the loss of septate wood fibres defines a subgroup (A1) incorporating *Bouea*, *Gluta*, *Mangifera* and *Swintonia*. All four genera also possess a derived form of the *Anacardium*-type endocarp. Most of the remaining genera (subgroup A2) retain clear evidence of the tricarpeal nature of the ovary, pinnate leaves (in at least some species) and an unmodified *Anacardium*-type endocarp anatomy. It should be noted that *Pistacia*, which Takhtajan (1987) separated into a monogeneric subfamily, fits well within this subgroup. *Dobinea* and *Campylopetalum* are distinguished from the remaining A2 genera by the absence of perianth or involucre around the flowers, as well as a number of other autapomorphs cited above.

The *Semecarpus* sub-group also falls within Group A. It is linked to the A1 genera by the absence of septate fibres, but is distinguished by an autapomorph, viz., its cupuliform receptacle. *Blepharocarya* possesses most of the features of the A2 genera, but is distinguished by what appears to be a separate line of reduction to the unicarpeal condition in which the style is in the dorsal position (also seen in some A2 genera: e.g. *Loxopterygium*).

Group B, which is essentially the tribe Spondiadeae (with the addition of *Buchanania*, *Campnosperma* and *Pentaspadon*), is very diverse, being an artificial grouping on the plesiomorphic *Spondias*-type endocarp. There is one sub-group (B1) of largely African genera having syncarpous ovaries, clearly defined styles and capitate stigmata. These states are also present in group A (best seen in the tricarpeal A2 genera), and so this assemblage is at present defined only by the absence of the apomorphs in endocarp structure, carpel number and biflavones defining group A.

Of sub-group B2, *Campnosperma*, *Solenocarpus* and *Pentaspadon* are unicarpeal. The first genus is distinguished by its simple leaves, unusual discoid stigma, and some evidence of additional carpels in the female flower, but only a single carpelode in the male. *Buchanania* (and apparently *Androtium* also) has five virtually apocarpous carpels, but is distinguished by a specialized gynobasic stylar arrangement to the single fertile locule, basally attached ovules and simple leaves.

Further investigation of other data sources is required to obtain evidence of

the affinities of group B genera. While no formal taxonomic arrangement can be constructed until this has been done, it is clear from the pattern of affinities demonstrated among group A genera that the present taxonomy of the Anacardiaceae does not adequately reflect the distribution of states of the reproductive, vegetative and secondary product characters so far examined. Neither the five subfamilies proposed by Takhtajan (1988), nor the five tribes of Engler (1883) are supported by the distribution of apomorphs in the characters that have been systematically investigated. The membership of the informal groups recognized in this study is set out in Table 1. Group A, as well as subgroup A1, are each defined by several synapomorphs, and could be recognized at either the subfamilial or tribal level. There is still insufficient information about several genera to place them in this preliminary system.

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REFERENCES

- AIRY SHAW, H. K., 1965. Diagnoses of new families, new names, etc. for the seventh edition of Willis' Dictionary. *Kew Bulletin*, 18: 254–255.
- AIRY SHAW, H. K. & FORMAN, L. L., 1967. The genus *Spondias* L. (Anacardiaceae) in tropical Asia. *Kew Bulletin*, 21: 1–19.
- AUBREVILLE, A., 1950. Anacardiaceae. In *Flore Forestière Soudano-Guinéenne*: 392–415. Paris: Société d'Éditions Géographiques, Maritimes et Coloniales.
- BACKER, C. A. & BAKHUIZEN VAN DEN BRINK, R. C., 1965. Anacardiaceae. In *Flora of Java*, 2: 146–154. The Netherlands: N.V.P. Noordhoff-Groningen.
- BAILEY, I. W., 1940. In H. F. Copeland & B. E. Doyel. *Some of the Structures of Toxicodendron diversiloba*. *American Journal of Botany*, 27: 932–939.
- BAILLON, H., 1876. Traité du développement de la fleur et du fruit—Anacardiées. *Adansonia*, 11: 158–163.
- BAILLON, H., 1878. *The Natural History Of Plants*, 5. Translated M.M. Hartog. London: L. Reeve & Co.
- BARKLEY, F. A., 1962. Anacardiaceae: Rhoideae: *Loxopterygium*. *Lloydia*, 25: 109–122.
- BARKLEY, F. A. & REED, M. A., 1940. *Pseudosmodingium* & *Mosquitoxylum*. *American Midland Naturalist*, 24: 666–679.
- BENTHAM, G., 1863. Anacardiaceae. In *Flora Australia*, 1: 488–492. London: L. Reeve & Co.
- BENTHAM, G. & HOOKER, J. D., 1862. Anacardiaceae. In *Genera Plantarum*, 1: 415–428. London: Reeve & Company.
- BLACKWELL, W. H. & DODSON, C. H., 1967. Flora of Panama, Part 6. *Annals of the Missouri Botanical Garden*, 54: 351–379.
- BOERLAGE, J. G., 1901. *Icones Bogorienses*, 1: 55–58. Leiden: E. J. Brill.
- CHANDRA, D., 1978. *Choerospondias auriculata* (Anacardiaceae)—A new species from India. *Journal of the Bombay Natural History Society*, 75: 457–460.
- COATES PALGRAVE, K. C., 1983. *Trees of Southern Africa*, 2nd edn. Cape Town: C. Struik Publishers.
- COPELAND, H. F., 1959. The reproductive structures of *Schinus molle* (Anacardiaceae). *Madroño*, 15: 14–25.
- COPELAND, H. F., 1961. Observations on the reproductive structures of *Anacardium occidentale*. *Phytomorphology*, 11: 315–325.
- COPELAND, H. F. & DOYEL, B. E., 1940. Some features of the structure of *Toxicodendron diversiloba*. *American Journal of Botany*, 27: 932–939.
- CRONQUIST, A., 1981. *An Integrated System of Classification of Flowering Plants*. New York: Columbia University Press.

- DADSWELL, H. E. & INGLE, H. D., 1948. The anatomy of timbers of the southwest Pacific area: I. Anacardiaceae. *Australian Journal of Scientific Research, Series B1*, 4: 391-415.
- DAHLGREN, R. M. T., 1980. A revised system of classification of the angiosperms. *Botanical Journal of the Linnean Society*, 80: 91-124.
- DING HOU, 1978. Anacardiaceae. In C. G. G. J. van Steenis (Ed.), *Flora Malesiana, series I*, 8: 395-548. Netherlands: Sijthoff and Noordhoff.
- DYER, R. A., 1975. *The Genera of Southern African Flowering Plants*, 1: 326-330. Pretoria: Department of Agricultural Technical Services.
- EICHLER, A. W., 1878. *Blüthendiagramme construirt und erläutert*, 2: 332-337. Leipzig.
- ENGLER, A., 1876. Anacardiaceae. In C. F. P. Martius (Ed.), *Flora Brasiliensis*, 12: 367-418. Munich.
- ENGLER, A., 1883. Anacardiaceae. In A. P. & A. C. De Candolle (Eds), *Monographie Phanerogamarum*, 4: 171-546. Paris: G. Masson.
- ENGLER, A., 1892. Anacardiaceae. In A. Engler & K. Prantl (Eds), *Die Natürlichen Pflanzenfamilien*, III (5): 138-178. Leipzig: Engelmann.
- ENGLER, A. 1897. Nachträge zum II-IV. In A. Engler & K. Prantl (Eds), *Die Natürlichen Pflanzenfamilien*: 214. Leipzig: Engelmann.
- ENGLER, A., 1898. *Koordsiodendron, Mededeelingen uit's Lands Plantentuin*, 19: 410-411.
- ERDTMAN, G., 1952. *Pollen Morphology and Plant Taxonomy*. Waltham: Chronica Botanica Company.
- ERDTMAN, G., 1954. In L. L. Forman. A new genus from Thailand. *Kew Bulletin*, 6: 555-564.
- FERNANDES, R. B. & FERNANDES, A. C. S., 1966. 59: Anacardiaceae. In A. W. Exell, A. Fernandes & H. Wild (Eds), *Flora Zambesiaca*, 2: 550-615. London: Crown Agents for Overseas Governments and Administrations.
- FERNANDES, R. B. & FERNANDES, A. C. S., 1969. 54: Anacardiaceae. In A. Fernandes (Ed.), *Flora de Moçambique*: 1-60. Lisboa: Centro de Botanica.
- FORMAN, L. L., 1954. A new genus from Thailand. *Kew Bulletin*, 6: 555-564.
- FRITSCH, F. E., 1908. The anatomy of the Julianiaceae considered from the systematic point of view. *Transactions of the Linnean Society of London*, 7: 129-151.
- GOLDBLATT, P. (Ed.), 1981. *Index to Plant Chromosome Numbers. 1975-1978*. Missouri: Missouri Botanical Gardens.
- GORIS, M. A., 1910. Contribution à l'étude des Anacardiées de la tribu des Mangiférées. *Annales des Sciences Naturelles (Botanique)*, Series 9, 11: 1-29.
- HEIMSCH, C. Jr., 1942. Comparative anatomy of the secondary xylem in the Gruinales and Terebinthales of Wettstein with reference to taxonomic grouping. *Lilloa*, 8: 83-198.
- HEMSLEY, W. B., 1908. On the Julianiaceae: a new natural order of plants. *Philosophical Transactions of the Royal Society London, Botany*, 199: 169-197.
- HOOKER, J. D., 1860. Illustrations of the floras of the Malayan archipelago and of tropical Africa. *Transactions of the Linnean Society*, 23: 155-172.
- HOOKER, J. D., 1876. *The Flora of British India*, 1 & 2. London: L. Reeve & Co.
- HUTCHINSON, J., 1969. *Evolution and Phylogeny of Flowering Plants*. London: Academic Press.
- JACOBS, M., 1961. Three new reductions in the Anacardiaceae. *Acta Botanica Neerlandica*, 10: 105-106.
- JESSUP, L. W., 1985. Anacardiaceae. In *Flora of Australia*, 25: 170-187. Canberra: Australian Government Publishing Service.
- KEAY, R. W. J., 1958. Anacardiaceae. In *Flora of West Tropical Africa*, 2nd edn., 1: 726-739.
- KRAMER, P. R., 1939. The woods of *Billia*, *Cassia*, *Hemorea* and *Juliania*. *Tropical Woods*, 58: 1-5.
- KRYN, J. M., 1953. *The anatomy of the wood of the Anacardiaceae and its bearing on the phylogeny and relationships of the family*. Unpublished Ph.D. thesis of the University of Michigan.
- LAM, H. J., 1932. Beiträge zur morphologie der Burseraceae, insbesondere der Canarieae. *Annales du Jardin botanique de Buitenzorg*, 42: 97-226.
- LAUTERBACH, C. A., 1920. Beiträge zur Flora von Papuasien—7. Die Anacardiaceae Papuasien. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 56: 273-400.
- LINCZEWSKI, I. A., 1949. Anacardiaceae. In V. L. Komarov (Ed.), *Flora of U.S.S.R.*, 14: 518-539. Leningrad: Academy of Sciences, U.S.S.R.
- LINDLEY, J., 1830. *An Introduction to the Natural System of Botany*. London: Longman, Rees, Orme, Brown and Green.
- MARCHAND, N. L., 1869. *Révision du groupe des Anacardiées*. Paris: J. B. Bailliere & Sons.
- MARCHAND, N. L., 1874. Anacardiaceae. In E. Warming (Ed.), *Symbolae ad floram Brasiliae centralis cognoscendam*, 15: 57-64. Copenhagen: Havniae.
- McNAIR, J. B., 1921. The morphology and anatomy of *Rhus diversiloba*. *American Journal of Botany*, 8: 179-191.
- MING, T.-L., 1980. The geographic distribution and floristic character of Chinese Anacardiaceae. *Acta Botanica Yunnanica*, 2: 390-401.
- MITCHELL, J. D. & MORI, S. A., 1987. The cashew and its relatives (*Anacardium*: Anacardiaceae). *Memoirs of the New York Botanical Garden*, 42: 1-76.
- MOSELEY, M. F., 1973. Vegetative anatomy and morphology of Amentiferae. *Brittonia*, 25: 356-370.
- MUSTARD, M. J. & LYNCH, S. J., 1946. Flower-bud formation and development in *Mangifera indica*. *Botanical Gazette*, 108: 136-140.

- OLIVER, D., 1881. *Micronychia*. In J. D. Hooker (Ed.), *Icones Plantarum*, 14: 27, t. 1337. London: Longman, Rees, Orme, Brown, Green.
- PAYER, J. B., 1857. *Traité d'organogénie comparée de la fleur*. Paris: V. Masson.
- PERRIER DE LA BATHIE, H., 1944. Révision des Anacardiacees de Madagascar et des Comores. *Mémoires du Muséum National d'Histoire Naturelle*, 18: 243–270.
- PERRIER DE LA BATHIE, H., 1946. Anacardiaceae. In Humbert (Ed.), *Flore de Madagascar*: 1–85.
- PETERSON, F. P. & FAIRBROTHERS, D. E., 1983. A serotaxonomic appraisal of *Amphipterygium* and *Leitneria*—two Amentiferous taxa of Rutiflorae (Rosidae). *Systematic Botany*, 8: 134–148.
- PHILLIPS, E. P., 1951. *The Genera of South African Flowering Plants*. 2nd ed. *Botanical Survey Memoir*, 25: 470–474. Pretoria: Government Printer.
- RADLKOFER, L., 1879. Ueber *Cupania* und damit verwandte Pflanzen. *Sitzungsberichte der königlich bayerischen Akademie der Wissenschaften, math.-phys. Cl.*, 1879: 457–678.
- RADLKOFER, L., 1890. Ueber die Gliederung der Familie der Sapindaceen. *Sitzungsberichte der königlich bayerischen Akademie der Wissenschaften*, 20: 105–379.
- RAGONESE, A. E. & CASTIGLIONI, J. A., 1947. Nueva especie del genero *Schinopsis* y area geografica de las especies Argentinas. *Revista de Investigaciones Agricolas*, 1: 93–100.
- RECORD, S. J., 1949. In P. C. Standley & J. A. Steyermark, 1949. Flora of Guatemala. *Fieldiana: Botany*, 24: 175–195.
- RIDLEY, H. N., 1922. *Flora of the Malay Peninsula*, 1: 517–543. London: L. Reeve & Co.
- SASS, J. E., 1958. *Botanical Microtechnique*, 3rd edn., Ames: Iowa State University Press.
- SCHOLZ, H., 1964. 28: Reihe Sapindales. In H. Melchior (Ed.), *A. Engler's Syllabus der Pflanzenfamilien*, 12th edn, 2: 277–288. Berlin: Gebrüder Borntraeger.
- STAPP, O., 1901. *Allospandias*. In W. T. Thiselton-Dyer (Ed.), *Icones Plantarum*, 27: t. 2667.
- STAPP, O., 1905. *Androtum astylum*. In W. T. Thiselton-Dyer (Ed.), *Icones Plantarum*, 28: t. 2763.
- STERN, W. L., 1952. The comparative anatomy of the xylem and the phylogeny of the Julianiaceae. *American Journal of Botany*, 39: 220–229.
- TAKEDA, F., CRANE, J. C. & LIN, J., 1979. Pistillate flower bud anatomy in Pistachio. *Journal of the American Society of Horticultural Science*, 104: 229–232.
- TAKHTAJAN, A., 1980. Outline of the classification of flowering plants (Magnoliophyta). *Botanical Review*, 46: 226–267.
- TAKHTAJAN, A., 1987. *Systema Magnoliophytorum*. Leningrad: Izdatel'stvo Nauka.
- TARDIEU-BLOT, M., 1962. Anacardiaceae. In A. Aubreville (Ed.), *Flora du Cambodge du Laos et du Vietnam*, 2: 67–200. Paris: Muséum National d'Histoire Naturelle.
- VAN DER VEKEN, P., 1960. Anacardiaceae. In *Flore du Congo Belge et du Ruanda-Urundi*, 9: 5–108. Bruxelles: I.N.E.A.C.
- VON TEICHMAN, I. & VAN WYCK, A. E., 1988. The ontogeny and structure of the pericarp and seed-coat of *Harpephyllum caffrum* Bernh. ex Krauss (Anacardiaceae). *Botanical Journal of the Linnean Society*, 98: 159–176.
- WANNAN, B. S. & QUINN, C. J., 1988. Biflavonoids in the Julianiaceae. *Phytochemistry*, 27: 3161–3162.
- WANNAN, B. S. & QUINN, C. J., 1990. Pericarp structure and generic affinities in the Anacardiaceae. *Botanical Journal of the Linnean Society* 102: 225–252.
- WANNAN, B. S., WATERHOUSE, J. T., GADEK, P. A. & QUINN, C. J., 1985. Biflavonyls and the affinities of *Blepharocarya*. *Biochemical Systematics and Ecology*, 13: 105–108.
- WANNAN, B. S., WATERHOUSE, J. T. & QUINN, C. J., 1987. A taxonomic reassessment of *Blepharocarya* F. Muell. *Botanical Journal of the Linnean Society*, 95: 61–72.
- WILLIS, J. C., 1973. *A Dictionary of Flowering Plants and Ferns*, 8th edn. Revised by H. K. Airy Shaw. Cambridge: Cambridge University Press.
- YOUNG, D. A., 1976. Flavonoid chemistry and the phylogenetic relationships of the Julianiaceae. *Systematic Botany*, 1: 149–162.
- YOUNGS, R. L., 1955. The xylem anatomy of *Orthopterygium* (Julaniaceae). *Tropical Woods*, 101: 29–43.

APPENDIX

Locations of the voucher specimens not held at UNSW are given by herbarium acronym. *Anacardium occidentale* L., *Zanoni* 26418; *Bouea macrophylla* Griff., *Jacobs s.n.* (CANB); *Blepharocarya depauperata* Specht, UNSW 10201; *B. involucrigera* F. Muell., UNSW 12500; *Buchanania arborescens* (Bl.) Bl., UNSW 9042, 16750; *Campnosperma brevipetiolatum* Volkens, *Hoogland & Craven* 10635 (CANB); *C. coriaceum* (Jack) Hall. f. ex Steen., FD 45239, *Ding Hou* 780 (L); *Dobinea delavayi* (Baill.) Engl., *De Ding* 60-015; *Dracontomelon lenticulatum* Wilkinson, *Pullen* 1178 (CANB); *Gluta renghas* L., *Ding Hou* 781 (L); *Harpephyllum*

caffrum Bernh. ex Krauss, UNSW 3177, 5162, 14701; *Mangifera indica* L., UNSW 3178; *Pentaspadon motleyi* Hook. f., Pullen 6566, 7406 (CANB); *Pistacia chinensis* Bunge, UNSW 12893, 20388A; *Pleiogynium timoriense* (DC.) Leenh., UNSW 3105, 20355; *Rhodosphaera rhodanthema* Engl., UNSW 3179, 5160; *Rhus succedanea* L., UNSW 11534 & 11535; *Schinus areira* L., UNSW 5080, 14801; *Semecarpus australiensis* Engl., Gray 3248 (QRS), Hyland 11166.