



## Cuticle morphology of Australasian Sapindaceae

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Sapindaceae is one of the most important plant families in the warmer and, particularly, drier Australasian rainforests, but there are also representatives in more arid regions. The leaf cuticles of a representative selection of Australasian species of Sapindaceae are illustrated with transmitted light and scanning electron microscopy. The family exhibits a diverse range of characters, with no one feature being diagnostic. Four basic stomatal types can be recognized, but these grade between each other. Trichomes, glands and papillae are often present. A brief description of the epidermis of all genera in Australasia is given, and character combinations are discussed which may allow the identification of these in the fossil record. A rich cuticular fossil record in the early Miocene of New Zealand includes *Alectryon* and members of the tribe Cupanieae. © 2010 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2010, **164**, 264–292.

ADDITIONAL KEYWORDS: epidermis – Miocene – plant fossils.

### INTRODUCTION

Sapindaceae (Sapindales; APG III, 2009) is a common component of Australasian rainforests. Members of this family are most prominent in drier rainforests, but also extend to wetter ones, and some species are found in arid regions. The family has a diverse range of foliage and cuticular morphology. It is also receiving attention from molecular and morphological workers who are analysing the phylogeny of the family and elucidating the biogeography (e.g. Turner, 1996; Edwards & Gadek, 2001a). These factors make Sapindaceae an ideal subject for study in the fossil record. The last two decades have seen a large increase in attention given to the plant macrofossil record of Australasia. Mostly, this has involved the study of organically preserved leaves or fragments of leaf. In this type of preservation, the leaf cuticle is preserved and thus the characters of the leaf epidermis are available for taxonomy. The number of angiosperm families that can be identified with some confidence in Australasia on the basis of their cuticle remains low. They include Lauraceae (Hill, 1986), Myrtaceae (Lange, 1980; Christophel & Lys, 1986),

Cunoniaceae (Barnes & Hill, 1999) Ericaceae (Jordan & Hill, 1996), Proteaceae (Lange, 1978; Carpenter, 1994) and Nothofagaceae (Hill & Read, 1991). Clearly, there remain many families, even those which were likely to have been common, which have not yet had their cuticle adequately documented. During the course of research on dispersed fossil cuticles (i.e. small fragments obtained by sieving fossiliferous sediment) from various Tertiary localities in Australia and New Zealand, I came across some types of cuticle which were strikingly papillate. Browsing through preparations of cuticle from extant plants, I found that a papillate cuticle was present in several families, but the most similar appearance to some of the fossils seemed to be with Sapindaceae. A concerted attempt was therefore made to collect Australasian species of Sapindaceae in the hope that their study might lead to the identification of the fossils. *Dodonaea* Miller is the largest genus of Sapindaceae in Australia, with 61 species (West, 1984), but is largely restricted to relatively dry vegetation and is least likely to be encountered in the overwhelmingly rainforest-dominated Tertiary fossil record. West (1984) monographed the genus and included illustrations and a discussion of the cuticle. Therefore, no attempt was made to sample *Dodonaea* widely. For the other genera of Sapindaceae, the cuticle database

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used for this study includes almost all extant species from Australasia. The aim of this article is to document the cuticular morphology of the Australasian species of Sapindaceae and to derive criteria which may identify the Sapindaceae cuticle in the fossil record. Features of the cuticle may allow the identification of fossils to extant genera, or to groups of extant genera, or even suggest extinct genera and their affinities. At the same time, the data from this study may corroborate relationships within a large plant family which is only now beginning to be understood. The study of Australasian Sapindaceae is a first step in a larger project, which can be extended to extra-Australasian Sapindaceae, and then to the families allied with, or those which, in some classifications, are placed within Sapindaceae (e.g. Harrington *et al.*, 2005; APG III, 2009).

## MATERIAL AND METHODS

The tribal-level taxonomy follows Engler & Prantl (1895), Radlkofer (1895, 1933) and Muller & Leenhouts (1976). The taxonomy of Australian Sapindaceae used here follows Reynolds (1981, 1982, 1987), Reynolds & West (1985) and Adema & van der Ham (1993) with a number of more recent changes. *Heterodendron* Desf. is now regarded as a synonym of *Alectryon* Gaertn. (for further discussion of this, see Reynolds, 1987; Edwards & Gadek, 2001b), and *Jagera dasyantha* (Radlk.) Reynolds has been placed in *Cnesmocarpon* Adema (see Adema & van der Ham, 1993). Four more recently described species are *Cupaniopsis papillosa* P.I.Forst. (Forster, 2006a), *Jagera madida* P.I. Forst. (Forster, 2006b), *Mischarytera megaphylla* P.I.Forst. (Forster, 2006c) and *Synima reynoldsiae* P.I.Forst. (Forster, 2006d). Reynolds & West (1985) recognized 29 genera of Sapindaceae native to Australia with *c.* 190 species. In this article, the genera follow the order according to these authors (with additional genera included). There are two further species in New Zealand (Allan, 1961): *Alectryon excelsus* Gaertn. (sometimes regarded as two species, including *A. grandis* Cheeseman) and *Dodonaea viscosa* Jacq.

Samples of all non-*Dodonaea* Australasian Sapindaceae were obtained, with the exception of *Allophylus ternatus* (J.R.Forst.) Radlk., *Arytera linoosquamulata* H.Turner, *Dimocarpus leichhardtii* (Benth.) S.T.Reynolds (presumed extinct), *Guioa chrysantha* Radlk. and *Rhysotoechia florentula* S.T.Reynolds.

Cuticle preparation followed a standard process. A small fragment (about 0.5–1.0 cm<sup>2</sup>) of leaf material was removed from a herbarium specimen and placed in 10% aqueous chromium trioxide for several days. This destroyed all noncuticular material. The remain-

ing cuticle was then washed and stained. Initially, safranin was used, and then latterly crystal violet was found to give a better result. Adaxial and abaxial cuticular surfaces were mounted in glycerine jelly on microscope slides for transmitted light microscopy (TLM). For scanning electron microscopy (SEM), surfaces were placed on a stub and coated in platinum. All specimens were studied under TLM but, for economic reasons, only selected specimens were further studied using SEM. A mixture of light microscope and electron microscope images is given. All specimens in this study are housed in the Queensland Herbarium (AQ), Toowong. Prefixes are as follows: AQ, Queensland Herbarium, Brisbane; CANB, Australian National Herbarium, Canberra; DNA, Northern Territory Herbarium, Darwin; NSW, National Herbarium New South Wales, Sydney; OTA, Botany Department Herbarium, University of Otago, Dunedin; UNSW, John T. Waterhouse Herbarium, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney. Where catalogue numbers were not available, the collector's field number follows the institutional prefix. Material on scanning electron microscope stubs is prefixed with 'S'.

## TERMINOLOGY

### STOMATAL DISTRIBUTION

'Hypostomatic' is used for stomata which are located essentially on one leaf surface only. 'Partially amphistomatic' refers to a condition in which stomata are concentrated on one surface, but, in addition, there is a narrow but dense zone of stomata on either side of the midrib on the other surface. The author has not seen this condition outside of Sapindaceae. It is present in at least *Atalaya* Blume, *Alectryon*, *Arytera* Blume, *Mischarytera* and *Toechima* Radlk. 'Amphistomatic' is used for stomata which are widely distributed over both leaf surfaces. This is found in *Diplopeltis* Endl., *Distichostemon* F.Muell. and some *Dodonaea*.

### STOMATAL COMPLEX TYPES

There are several publications dealing with the terminology of stomatal complexes, one of the most widely used being that of Dilcher (1974) and one of the most recent being Carpenter (2005). One of the main issues that has arisen is the necessity of distinguishing between a purely structural terminology of mature complexes and a purely ontogenetic one. The problem with herbarium and fossil material is not having the luxury of closely following ontogenetic development. Stomatal complexes which fall into the same structural type may have had completely different ontogenetic histories. Even so, in some mature or

fossil specimens, there is some evidence of ontogeny reflected in the relative cell size, thicknesses of the cell walls and shape. To ignore it would be perverse, but no terms seem to exist to apply to these 'hybrid' structural-ontogenetic observations. The terminology used here incorporates Payne (1970, 1978), Hewson (1988) and Timonin (1995) with some modifications. With such a large group, the basic philosophy has been to group, rather than recognize, every permutation of stomatal design which exists, even within an individual. 'Contact cell' is applied to any epidermal cell in contact with a guard cell, whereas 'subsidiary cell' is a contact cell distinguished from ordinary epidermal cells by shape, differential staining in TLM (something which seems temperamental to me) or internal texture in SEM. Among Australasian Sapindaceae, four types of stomatal complex are recognized here, but it must be emphasized that these typically intergrade with one another.

1. *Actinocytic* (Fig. 1): Wilkinson (1979: 99) used this term for 'stomata surrounded by subsidiary cells that are somewhat radially elongated'. Their example illustration indicates that 'somewhat radially' can be applied fairly loosely, in fact to virtually isodiametric cells. In this sense, actinocytic stomatal complexes are found in many Sapindaceae genera. However, two species have subsidiary cells attached via a distinctly short margin and are radially elongate: *Lepiderema pulchella* Radlk. and *Sarcotoechia protracta* Radlk.

2. *Cyclocytic* (Figs 2, 3): Contact cells isodiametric to shortly rectangular and small (on the order of one-half to one-third of the length of a guard cell) (Wilkinson, 1979). There are often around six or seven cells in direct contact with the guard cells and these often appear to have been cut off by a tangential division of a progenitor. Under TLM, the radial walls of subsidiary cells in these complexes often end at an indistinct guard cell margin, or project slightly over the guard cell margin. This is the result of the subsidiary cell projecting under the guard cells. Therefore, the original dimensions of the rather small and adpressed subsidiary cells were actually larger than those reflected in the cuticle. Cyclocytic stomates are present in *Atalaya*, *Alectryon*, *Castanospora* F.Muell., *Cupaniopsis* Radlk., *Dimocarpus* Lour., *Elattostachys* (Blume) Radlk., *Guioa* Cav., *Jagera* Blume and *Mischocarpus* Blume.

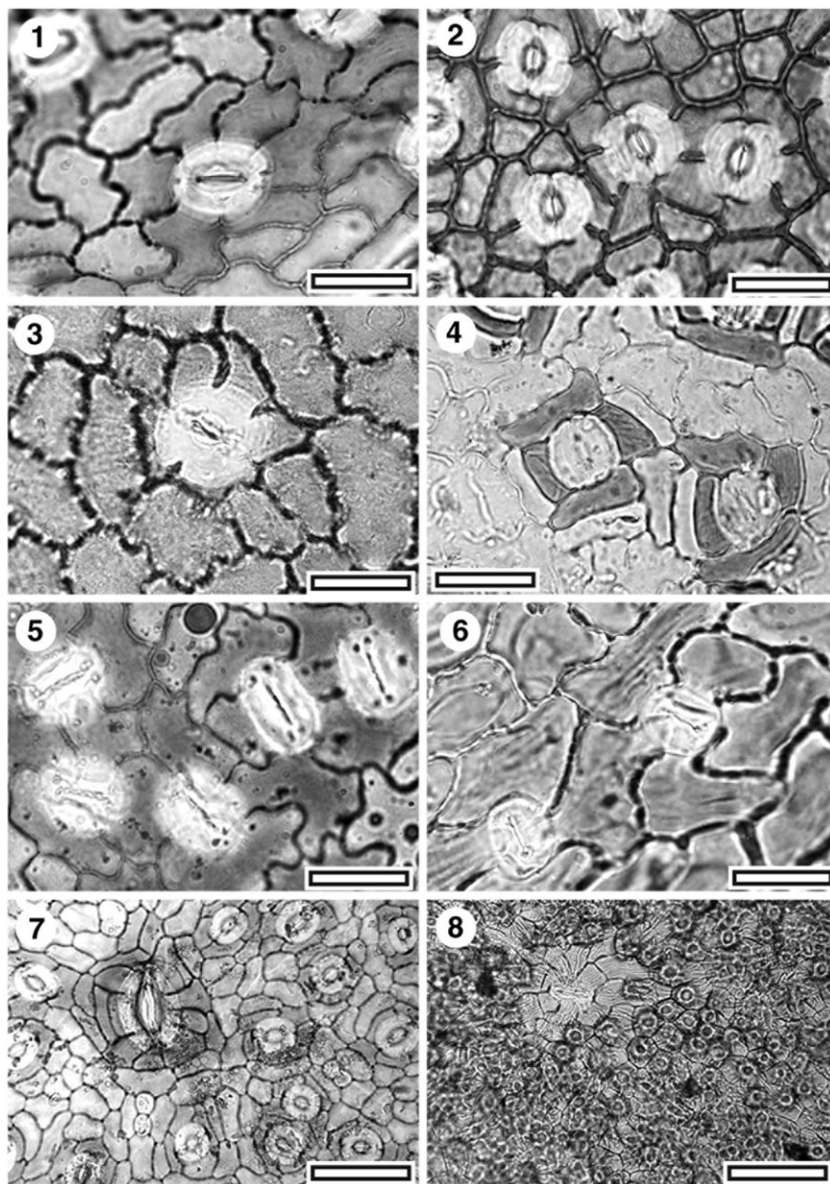
3. *Tangencytic* (Fig. 4): 'Tangencytic' is an ontogenetic term introduced by Timonin (1995) that does not seem to have any good, pre-existing structural equivalent. There are typically four subsidiary cells, and all can be seen to have divided tangentially from a progenitor. 'Laterocytic' may apply in some

instances, but the use of this term seems outside what the original authors had in mind ('stomata flanked by 3 or more subsidiary cells all bordering on the lateral sides of the guard cell pair; anticlinal walls separating adjacent subsidiary cells radiating from the guard cell pair'; Hartog, Tholen & Bass, 1978). It should be noted that this differs from Baranova's (1983) laterocytic type, in which the polar cells are unspecialized epidermal cells. 'Laterocytic' does not convey the elongate shape of the tangencytic contact cells, and would specifically exclude those complexes in which the polar cells divide tangentially. Stomatal complexes may be irregularly tangencytic, with no clear orientation, or orthogonally tangencytic, where there are two lateral subsidiary cells parallel to the stomatal axis and two polar cells at right angles to the axis. This latter form typifies *Harpullia* Roxb., although examples are scattered across other genera.

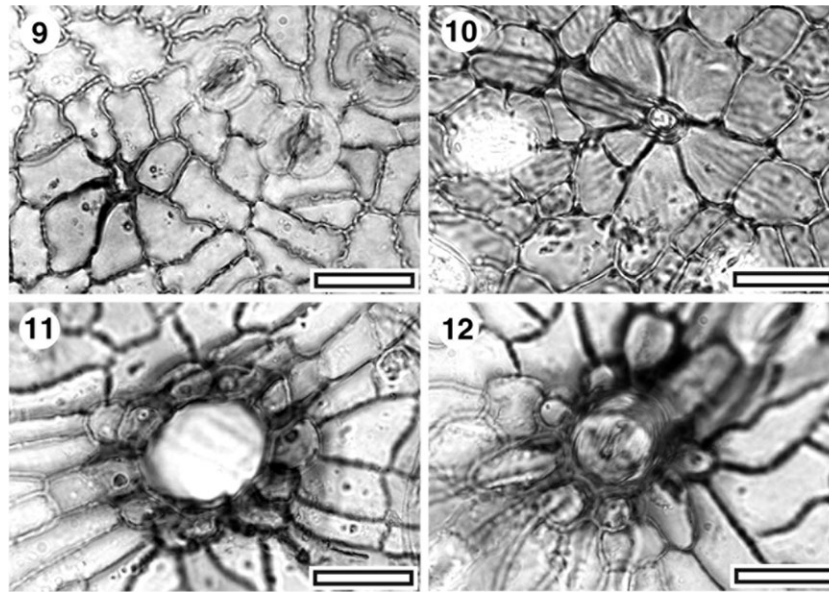
4. *Anisocytic*: 'Anisocytic' has long referred to an arrangement of three subsidiary cells, one smaller than the others (Payne, 1970). Ontogenetically, they are clearly derived from a heliocytic process (Timonin, 1995) and the three cells are often of three distinct sizes. However, in leaves which have typical anisocytic stomatal complexes, there are also many with four subsidiary cells, which have clearly formed as part of the same process (although not illustrated by Timonin, 1995). As there is no structural term which specifically applies to both three and four subsidiary cell types, and which recognizes their relationship, in this work, 'anisocytic' will be used for both. In Australasian Sapindaceae, anisocytic complexes are characteristic of, and restricted to, *Distichostemon* and *Dodonaea*.

*Networked stomatal complexes* (Figs 5, 6): Stomatal complexes that commonly share contact or subsidiary cells with neighbouring stomatal complexes are those that I have previously termed 'networked' (Pole, 1998). Although it is probably possible to find isolated instances of shared contact cells in almost any leaf, in some taxa it is clearly a distinctive feature. In Australasian Sapindaceae, networking is a distinctive feature of some *Cupaniopsis*, *Diploglottis* Hook.f., *Guioa*, *Lepiderema* Radlk., *Sarcopteryx*, *Sarcotoechia* and *Toechima*.

*Giant stomatal complexes* (Figs 6, 7): These are stomatal complexes that are distinctly larger than the other stomatal complexes. They tend to have many more subsidiary cells associated with them (i.e. they are cyclocytic), perhaps arranged in more than one distinct ring, are often located over veins and, if the surface is densely papillate, the giant stomatal complexes are often the only ones not obscured by the



**Figures 1–8.** Stomatal complexes. Fig. 1. *Diploglottis bernieana*, transmitted light microscopy (TLM) view of stomatal complex with subsidiary cells attached by a short dimension (AQ229865; scale bar, 20  $\mu\text{m}$ ). Fig. 2. *Synima macrophylla*, TLM view of stomatal complexes linked by networking. Note radial walls abut guard cell outlines and sometimes intersect them (AQ606565; scale bar, 20  $\mu\text{m}$ ). Fig. 3. *Arytera dictyoneura*, TLM view of stomatal complex. Note radial walls of subsidiary cells intersect guard cell outline (AQ572388; scale bar, 20  $\mu\text{m}$ ). Fig. 4. *Harpullia arborea*, TLM view of orthogonally tangencytic stomatal complexes. Note tangentially placed polar and lateral subsidiary cells (AQ589371; scale bar, 20  $\mu\text{m}$ ). Fig. 5. *Guioa sarcopterifruta*, TLM view of stomatal complexes linked by networking (AQ546237; scale bar, 20  $\mu\text{m}$ ). Fig. 6. *Sarcotoechia cuneata*, TLM view of stomatal complexes linked by networking (AQ657240; scale bar, 20  $\mu\text{m}$ ). Fig. 7. *Ganophyllum falcatum*, TLM view showing typical giant stomatal complex with repeated division of subsidiary cells (AQ561438; scale bar, 50  $\mu\text{m}$ ). Fig. 8. *Alectryon coriaceus*, TLM view of giant stomatal complex, recognized by being unobscured by papillae, but not significantly larger than the normal ones obscured by papillae (AQ572070; scale bar, 50  $\mu\text{m}$ ).



**Figures 9–12.** Simple trichomes. Fig. 9. *Sarcotoechia serrata*, transmitted light microscopy (TLM) view of a simple trichome base (lower left) with radially elongate basal cells and thickened radial walls (AQ555392; scale bar, 20  $\mu\text{m}$ ). Fig. 10. *Tristiropsis canarioides*, TLM view of a simple persistent trichome with radially elongate basal cells (AQ519622; scale bar, 20  $\mu\text{m}$ ). Fig. 11. *Diploglottis australis*, TLM view of large trichome base with many small basal cells (AQ011903; scale bar, 20  $\mu\text{m}$ ). Fig. 12. *Diploglottis bernieana*, TLM view of large trichome base with many small basal cells, and persistent trichome (AQ229865; scale bar, 20  $\mu\text{m}$ ).

papillae. They are found in *Alectryon*, *Arytera*, *Atalaya*, *Cupaniopsis*, *Dimocarpus*, *Elattostachys*, *Guioa*, *Lepiderema*, *Mischocarpus*, *Rhysotoechia* and *Toechima*.

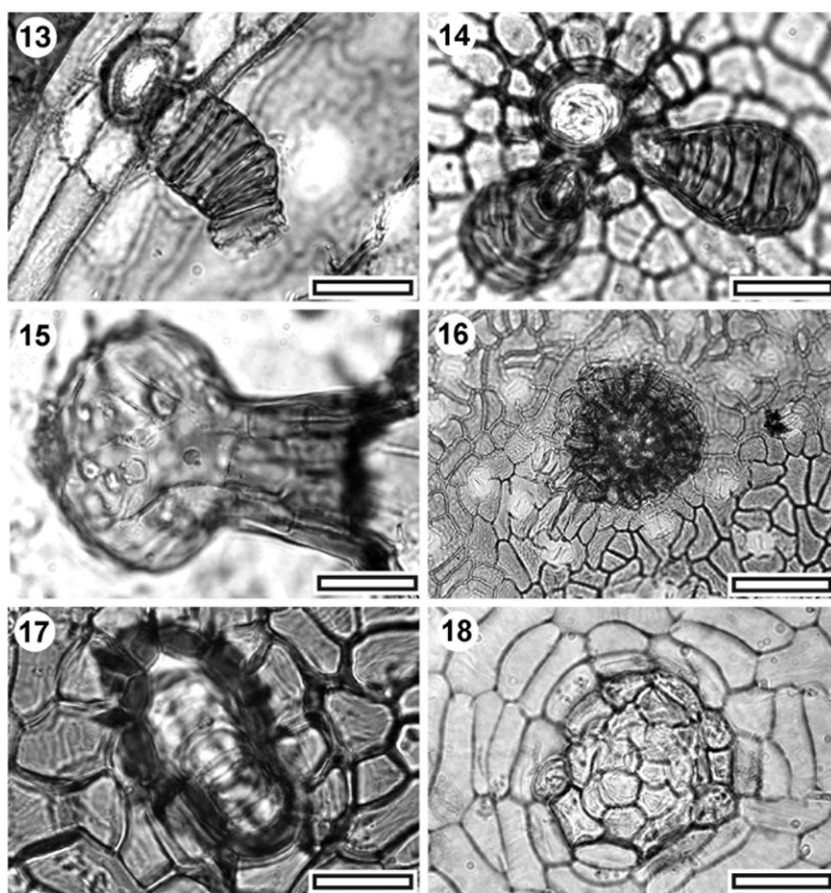
#### PAPILLAE AND ORNAMENTATION

When papillae are present, they consist of a single raised boss per cell. They may be flanged (with flanges continuing from one papilla to the next, forming a network) or smooth. Coverage by papillae varies from almost complete, in which all but giant stomatal complexes are hidden from view, to scattered, in which low papillae are found just in the area around stomatal complexes. Papillae are found in *Alectryon*, *Atalaya*, *Castanospora*, *Cupaniopsis*, *Dimocarpus*, *Diploglottis*, *Guioa*, *Jagera*, *Mischocarpus* and *Sarcopteryx*.

#### TRICHOMES AND GLANDS

The epidermal surface of Sapindaceae may be glabrous or present a range of trichome types. These may be dense or sparse, or limited to the traces of trichome bases, the trichomes themselves having detached earlier in ontogeny. They may be scattered across the epidermis or restricted to positions above major veins. Trichome types may be classified as:

1. Nonglandular trichomes.
  - i. Simple trichomes: these tend to fall into two types: small simple trichomes of relatively small diameter which are either not associated with distinct base cells (Fig. 9) or are associated with distinctly radial, but not strongly thickened, base cells (Fig. 10), or large simple trichomes: these have a relatively broad diameter and are associated with a distinct rim of many (sometimes up to 12) thickened base cells (*sensu* Stace, 1965), which are often strongly thickened (Figs 11, 12). Both types are found in a wide variety of genera.
  - ii. Stellate trichomes: these are restricted to *Cossinia* Comm. ex Lam., *Dimocarpus* and *Harpullia*.
2. Glandular trichomes.
  - i. Chain trichomes: these are formed of a chain of short cells, and a final long cell (although this is often missing) (Fig. 13). They are equivalent to van Welzen's (1989) type 'm' ('many stalk cells and a small glandular top cell'). They are found in *Cupaniopsis*, *Diploglottis* and *Mischocarpus*.
  - ii. Balloon trichomes: these have a short, uniseriate stalk and expand into a compound, glandular head (Fig. 14). They are equivalent to van Welzen's (1989) type l ('few stalk cells and



**Figures 13–18.** Glandular trichomes. Fig. 13. *Diploglottis macrantha*, transmitted light microscopy (TLM) view of a chain trichome (AQ484797; scale bar, 20  $\mu$ m). Fig. 14. *Lepisanthes rubignosa*, TLM view of two balloon trichomes on either side of a simple trichome base (AQ031154; scale bar, 20  $\mu$ m). Fig. 15. *Diplopeltis petiolaris*, TLM view of a stalked multicellular gland (AQ593099; scale bar, 20  $\mu$ m). Fig. 16. *Cupaniopsis fleckeri*, TLM view of sessile compound gland (AQ620445; scale bar, 50  $\mu$ m). Fig. 17. *Atalaya calcicola*, TLM view of sessile compound gland (AQ398909; scale bar, 20  $\mu$ m). Fig. 18. *Ganophyllum falcatum*, TLM view of sessile compound gland (AQ561438; scale bar, 20  $\mu$ m).

a large glandular top cell'). They are present in *Allophyllus*, *Jagera* and *Lepisanthes*.

3. Stalked multicellular glands. These have a multicellular stalk which expands out into a mushroom-like head (Fig. 15). They are restricted to *Diplopeltis*.
4. Sessile multicellular glands. These are found in *Atalaya calcicola* S.T.Reynolds, *Dodonaea* spp. and *Ganophyllum* Blume (Figs 17, 18).

#### EPIDERMAL CELL ANTICLINAL WALLS

Typically, the anticlinal walls of 'normal' epidermal cells are straight to slightly curved, or wavy. In the author's broader experience, these states may have an at least partial environmental basis and are not distinguished here. Highly sinuous cell walls appear to be taxonomically stable. They are a feature of *Arytera*, *Lepiderema*, *Lepidopetalum* Blume and *Sar-*

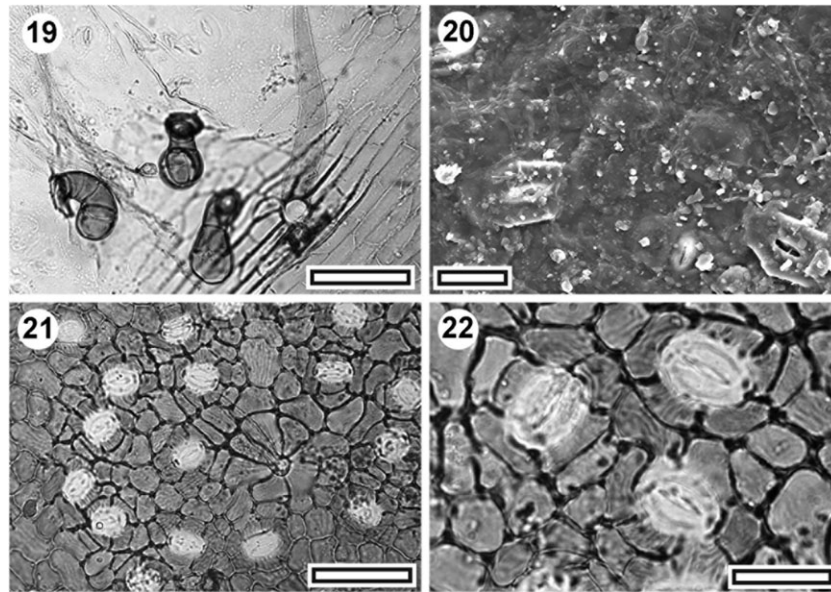
*copteryx*, and are present in some species of *Harpullia*, *Mischocarpus* and *Sarcotoechia*.

#### SYNOPSIS OF GENERAL EPIDERMAL FEATURES OF GENERA OF SAPINDACEAE

##### 1. *ALLOPHYLUS* L. (Figs 19, 20)

*Observed specimens:* *Allophylus cobbe* (L.) Blume, UNSW11343, *Ap. ternatus* (J.R.Forst.) Radlk.

The leaves are hypostomatic. The stoma are 13–23  $\mu$ m long, but the cuticle is very thin and the walls of the epidermal and stomatal complex cells are too indistinct to be clear of their structure. The abaxial surface is characterized by many balloon trichomes and fewer persistent simple trichomes (associated with veins). Both kinds of trichome are also present on the adaxial surface, but with a much lower density.



**Figures 19–22.** *Allophylus* and *Tristiropsis*. Fig. 19. *Allophylus cobbe*, transmitted light microscopy (TLM) view of balloon and simple trichomes. Stomatal complexes are almost invisible (UNSW 11343; scale bar, 50  $\mu\text{m}$ ). Fig. 20. *Allophylus cobbe*, scanning electron microscopy (SEM) view of outer surface showing two stomatal complexes (AQ650003, S-1303; scale bar, 20  $\mu\text{m}$ ). Fig. 21. *Tristiropsis canarioides*, TLM view of stomatal complexes and trichome base (AQ519622; scale bar, 50  $\mu\text{m}$ ). Fig. 22. *Tristiropsis canarioides*, TLM view of stomatal complexes (AQ519622; scale bar, 20  $\mu\text{m}$ ).

## 2. *TRISTIROPSIS* RADLK. (Figs 21, 22)

*Observed specimens:* *Tristiropsis canarioides* Boerl. ex Valeton in J.G. Boerlage, AQ519622.

The leaves are hypostomatic. The stoma are 18–23  $\mu\text{m}$  long and the stomatal complexes are irregular to orthogonally tangencytic, and have typically four subsidiary cells with periclinal walls staining darker than normal epidermal cells, and distinctive tangential polar cells. Epidermal cell anticlinal walls are relatively thick. Both the adaxial and abaxial surfaces are ornamented by subdued striae, and are glabrous, or sometimes with a few, deciduous trichome bases, but without prominently thickened base cells.

## 3. *ATALAYA* BLUME (Figs 23–28)

*Observed specimens:* *Atalaya angustifolia* S.T.Reynolds, CANB240195, AQ674214; *At. australiana* Leenh., CANB221586, AQ632218; *At. calcicola* S.T.Reynolds, CANB302727, AQ398909; *At. collina* S.T.Reynolds, AQ440574; *At. hemiglauca* (F. Muell.) F.Muell. ex Benth., AQ594469; *At. multiflora* Benth., CANB379725, AQ636196, AQ393006; *At. oligoclada* S.T.Reynolds AQ113191; *At. rigida* S.T.Reynolds, CANB356987, AQ636198; *At. salicifolia* (A. DC.) Blume, CANB436876, AQ636245, AQ398615; *At. sericopetala* S.T.Reynolds, AQ622849; *At. variifolia*

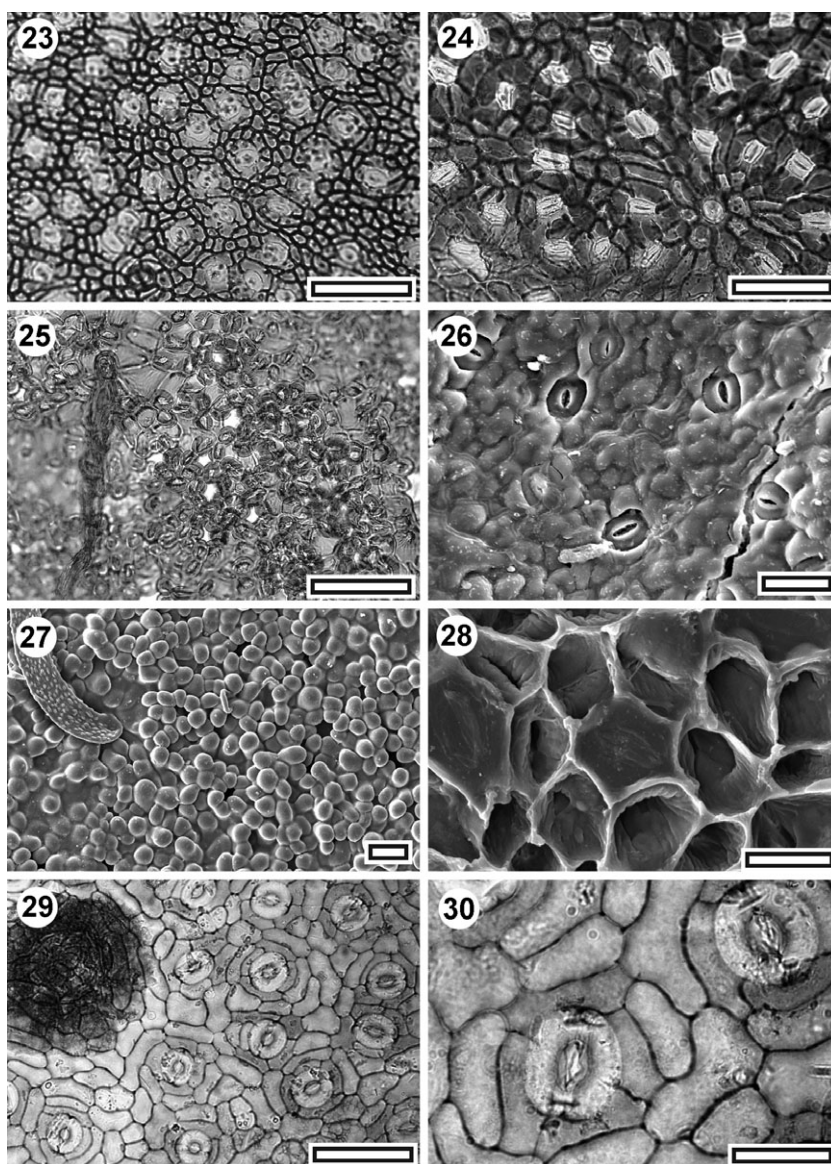
(F.Muell.) F.Muell. ex Benth., CANB27555, AQ375224.

The genus is typically hypostomatic, although stomatal complexes may also be scattered over the adaxial surface (*At. salicifolia*, *At. variifolia*) or crowded along the midvein on the adaxial surface (*At. hemiglauca*). The stoma are 13–30  $\mu\text{m}$  long and the stomatal complexes are actinocytic to cyclocytic or irregularly tangencytic. *Atalaya australiana*, *At. salicifolia*, *At. multiflora* and *At. rigida* form a group having a similar cuticle with dense stomatal complexes and distinctly small and thick-walled epidermal and subsidiary cells (typically smaller than the stomatal complexes). *Atalaya hemiglauca* and *At. variifolia* are distinct in having smooth papillae on the subsidiary cells. *Atalaya calcicola* has distinctive laminar glands. Most species are glabrous, although some have sparse, persistent simple trichomes (persistent in *At. calcicola*, *At. oligoclada* and *At. variifolia*) or the bases of deciduous trichomes (*At. multiflora*), and typically they are restricted to the veins.

## 4. *GANOPHYLLUM* BLUME (Figs 29, 30)

*Observed specimens:* *Ganophyllum falcatum* Blume, CANB248123, AQ561438.

The leaves are hypostomatic. The stoma are 18–28  $\mu\text{m}$  long and the stomatal complexes are



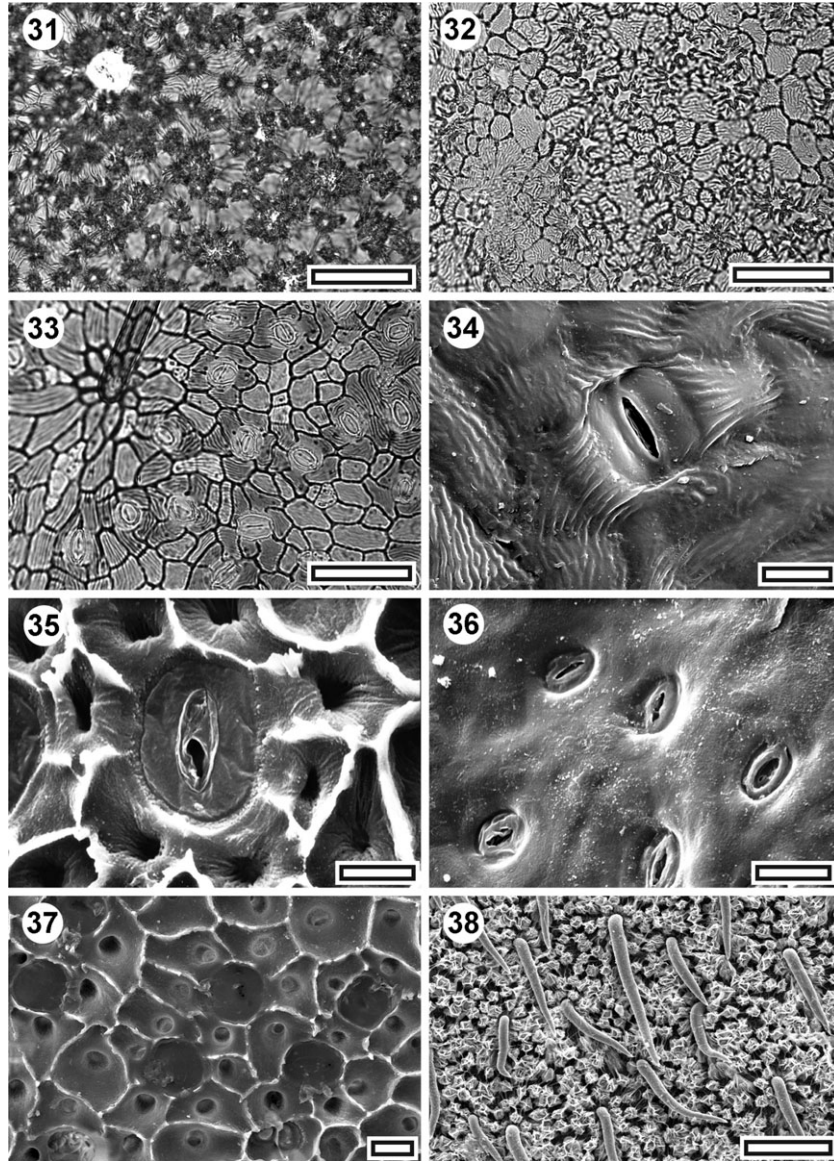
**Figures 23–30.** *Atalaya* and *Ganophyllum*. Fig. 23. *Atalaya collina*, transmitted light microscopy (TLM) view of stomatal complexes (AQ636193; scale bar, 50  $\mu$ m). Fig. 24. *Atalaya oligoclada*, TLM view of stomatal complexes and trichome base (AQ113191; scale bar, 50  $\mu$ m). Fig. 25. *Atalaya variifolia*, TLM view of stomatal complexes, obscured by papillae, and persistent trichome (AQ001021; scale bar, 50  $\mu$ m). Fig. 26. *Atalaya collina*, scanning electron microscopy (SEM) view of outer surface showing stomatal complexes surrounded by epidermal cells that have domed up as papillae (AQ502612, S-1305; scale bar, 20  $\mu$ m). Fig. 27. *Atalaya variifolia*, SEM view of outer surface showing discrete, smooth papillae which obscure the stomatal complexes. A persistent trichome is at left (AQ375224, S-1306; scale bar, 20  $\mu$ m). Fig. 28. *Atalaya variifolia*, SEM view of inner surface showing two stomata surrounded by papillate subsidiary cells (AQ001021, S-1591; scale bar, 10  $\mu$ m). Fig. 29. *Ganophyllum falcatum*, TLM view of stomatal complexes. Note compound gland at upper left and occasional tangentially paired subsidiary cells (AQ561438; scale bar, 50  $\mu$ m). Fig. 30. *Ganophyllum falcatum*, TLM view of stomatal complexes (AQ561438; scale bar, 20  $\mu$ m).

irregularly tangencytic and distinct in that the tangential divisions are curved. Epidermal cell anticlinal walls and outer surfaces are smooth. The surface is glabrous, except for large cyclic compound glandular structures on both the adaxial and abaxial surfaces.

##### 5. *ALECTRYON* GAERTN. (Figs 31–38)

*Observed specimens:* *Alectryon connatus* (F.Muell.) Radlk., AQ472228, AQ473545, AQ376182; *A. coriaceus* (Benth.) Radlk., NSW 256393, AQ572070, AQ072855;

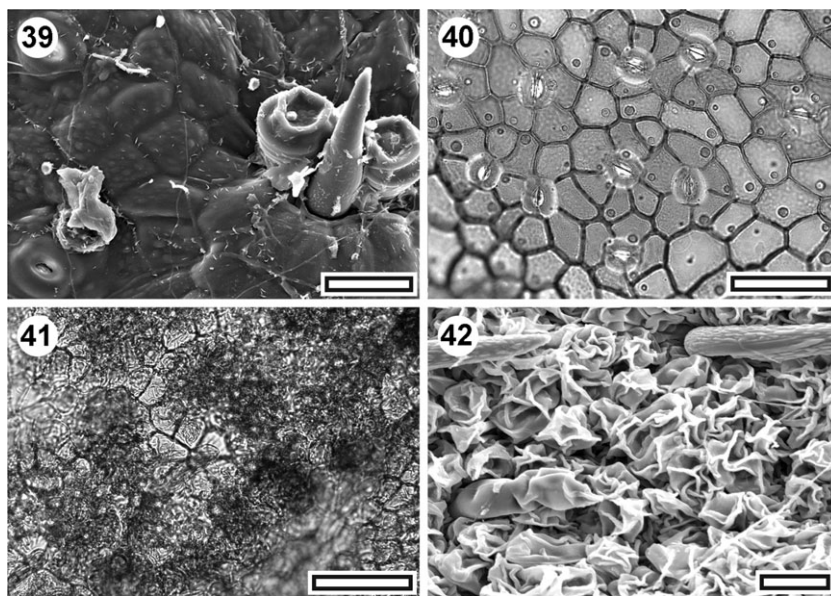




**Figures 31–38.** *Alectryon*. Fig. 31. *Alectryon coriaceus*, transmitted light microscopy (TLM) view showing papillae which obscure the normal stomatal complexes, and an unobscured giant stomatal complex at upper left (AQ013793; scale bar, 50  $\mu$ m). Fig. 32. *Alectryon subcinereus*, TLM view of stomatal complexes surrounded by overarching papillae (AQ568329; scale bar, 50  $\mu$ m). Fig. 33. *Alectryon ramiflorus*, TLM view of stomatal complexes and persistent trichome (AQ659306; scale bar, 50  $\mu$ m). Fig. 34. *Alectryon diversifolius*, scanning electron microscopy (SEM) view of outer surface of a single stomatal complex (AQ483165, S-1295; scale bar, 50  $\mu$ m). Fig. 35. *Alectryon forsythii*, SEM view of inner surface of a single stomatal complex (J.R.H. 265, S-1349,  $\times$  2400). Fig. 36. *Alectryon unilobatus*, SEM view of outer surface showing stomatal complexes in an otherwise smooth surface (AQ441329, S-1347; scale bar, 10  $\mu$ m). Fig. 37. *Alectryon coriaceus*, SEM view of inner surface showing stomata surrounded by papillate contact cells (AQ013793, S-1590; scale bar, 10  $\mu$ m). Fig. 38. *Alectryon semicinereus*, SEM view of outer surface showing flanged papillae which obscure the stomatal complexes, and persistent trichomes (AQ650842, S-1299; scale bar, 100  $\mu$ m).

*A. diversifolius* (F.Muell.) S.T.Reynolds, AQ568421, AQ483165, AQ587294; *A. excelsus* Gaertn., OTA04670; *A. forsythii* (Maiden & Betcke) Radlk., J.R.H. 265, AQ477952; *A. kimberleyanus* S.T.Reynolds, AQ460276; *A. oleifolius* (Desf.) S.T.Reynolds, NSW168272,

AQ430593, AQ573032; *A. pubescens* S.T.Reynolds, NSW 221389, AQ366882; *A. ramiflorus* S.T.Reynolds, AQ659306; *A. repandodentatus* Radlk., AQ033683, AQ033683; *A. reticulatus* S.T.Reynolds, AQ441329; *A. semicinereus* (F.Muell.) Radlk., AQ650842; *A. subci-*



**Figures 39–42.** *Lepisanthes* and *Castanospora*. Fig. 39. *Lepisanthes rubiginosa*, scanning electron microscopy (SEM) view of outer surface showing persistent simple trichome flanked by a pair of balloon trichomes (AQ031150, S-1330; scale bar, 20  $\mu$ m). Fig. 40. *Lepisanthes senegalensis*, transmitted light microscopy (TLM) view of stomatal complexes. Note high degree of networking (AQ480175; scale bar, 20  $\mu$ m). Fig. 41. *Castanospora alphandi*, TLM view showing patches of papillae which obscure the stomatal complexes, and persistent trichomes (AQ656946; scale bar, 50  $\mu$ m). Fig. 42. *Castanospora alphandi*, SEM view of outer surface showing flanged papillae which obscure the stomatal complexes, and persistent trichomes (AQ656946, S-1308; scale bar, 20  $\mu$ m).

*nereus* (A.Gray) Radlk., AQ568329; *A. subdentatus* (F.Muell. ex Benth.) Radlk., AQ030211, AQ531927; *A. tomentosus* (F.Muell.) Radlk., AQ456896; *A. tropicus* S.T.Reynolds, AQ032040; *A. unilobatus* S.T.Reynolds, AQ441329.

The leaves are typically hypostomatic, although sometimes there are scattered stomatal complexes on the adaxial surface (e.g. *A. tropicus*) or in a dense zone along the adaxial midrib (*A. diversifolius*). The stomata are 13–23  $\mu$ m long, and stomatal complexes are typically actinocytic or sometimes cyclocytic (*A. diversifolius*). Simple trichomes may be present and persistent or deciduous or absent. The adaxial surface is typically ornamented with striations and may be papillate, or simply smooth (*A. unilobatus*). *Alectryon connatus*, *A. coriaceus*, *A. forsythii*, *A. kimberleyanus*, *A. semicinereus* and *A. subdentatus* form a similar group with a dense covering of flanged papillae over the abaxial surface. Despite the epidermal similarity, this is not a natural group as its members are spread over two of the clades recognized by Edwards & Gadek (2001a, b) and are not restricted to any particular habitats.

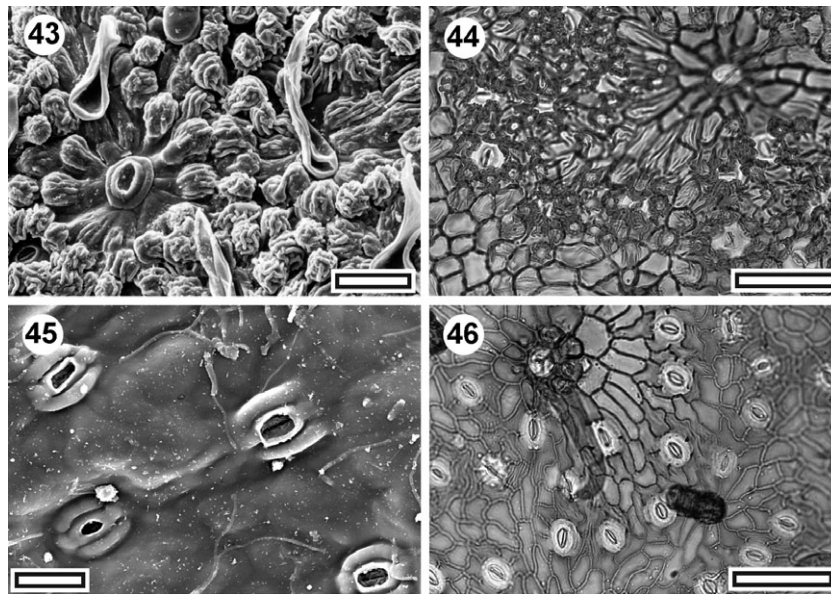
Other *Alectryon* spp. have more restricted papillae. In *A. pubescens*, *A. subcinereus* and *A. tomentosus*, the papillae are found only on the subsidiary cells, whereas, in *A. pubescens* and *A. tropicus*, the

guard cells are sunken below overarching subsidiary cells, and there are rough outgrowths on the subsidiary cells which could be considered as incipient papillae (these structures may extend to nearby epidermal cells). *Alectryon oleifolius* has a dense covering of persistent simple trichomes on both surfaces, obscuring all stomatal detail. The New Zealand species, *A. excelsus*, does not have papillae or persistent trichomes. It has small stomata and distinct subsidiary cells with an ornamentation of low ridging, and is most similar to Australian *A. diversifolius*.

#### 6. *LEPISANTHES* BLUME (Figs 39, 40)

*Observed specimens:* *Lepisanthes rubiginosa* (Roxb.) Leenh., CANB267745, AQ031150, AQ031154; *L. senegalensis* (Poir.) Leenh., AQ731246.

The leaves are hypostomatic, stomata 18–23  $\mu$ m long, and the stomatal complexes are actinocytic. The epidermal cells have distinctly straight-walled anticlinal walls, whereas the periclinal walls bulge outwards, but the surface is unornamented. *Lepisanthes rubiginosa* has a unique combination of having its simple trichomes flanked by two, or sometimes one or three, balloon glands (illustrated by Adema, 1991, fig. 12d, e). These occur on both the adaxial and



**Figures 43–46.** *Diploglottis*. Fig. 43. *Diploglottis bracteata*, scanning electron microscopy (SEM) view of outer surface showing flanged papillae which obscure normal stomatal complexes, whereas a giant stomatal complex remains visible at lower right. Persistent trichomes are also visible (B. Gray 1873, S-1336,  $\times 600$ ). Fig. 44. *Diploglottis bracteata*, transmitted light microscopy (TLM) view of stomatal complexes surrounded by papillae, and trichome base (AQ512759; scale bar, 50  $\mu\text{m}$ ). Fig. 45. *Diploglottis campbellii*, SEM view of outer surface showing stomatal complexes with discontinuous peristomatal rims in an otherwise smooth surface (AQ012512, S-1317; scale bar, 20  $\mu\text{m}$ ). Fig. 46. *Diploglottis diphylostegia*, TLM view of stomatal complexes, persistent trichome at upper left and chained trichome at lower right (AQ 0011960; scale bar, 50  $\mu\text{m}$ ).

abaxial surfaces. In *L. senegalensis*, the balloon and simple trichomes are independent, and the stomatal complexes are distinct, with stomatal complexes smaller than epidermal cells and subsidiary cell flanges projecting over the guard cell outline.

#### 7. *CASTANOSPORA* F.MUELL. (Figs 40–42)

*Observed specimens:* *Castanospora alphanthii* (F.Muell.) F.Muell., AQ656946.

The leaves are hypostomatic, the stomata are 14–17  $\mu\text{m}$  long and the stomatal complexes are cyclocytic. The entire surface is papillate (obscuring the stomatal complexes), with persistent simple trichomes, whereas the adaxial surface is glabrous and not papillate.

#### 8. *DIPLOGLOTTIS* HOOK.F. (Figs 43–46)

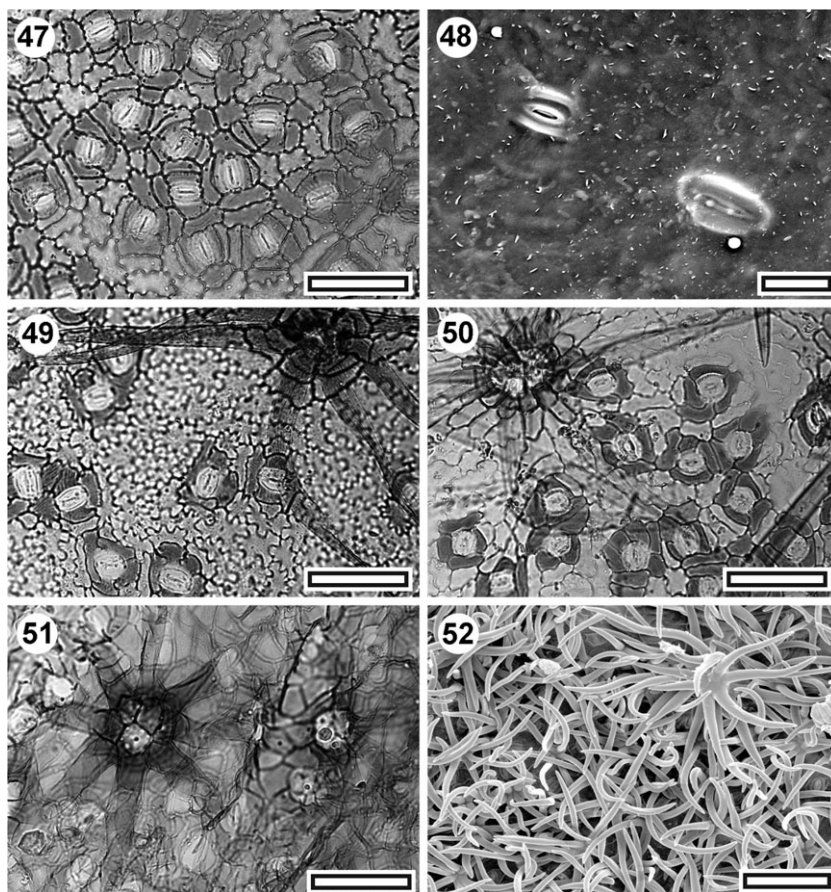
*Observed specimens:* *Diploglottis australis* (G.Don.) Radlk., AQ011903; *D. bernieana* S.T.Reynolds, AQ229865; *D. bracteata* Leenh., B. Gray 1873, AQ512759; *D. campbellii* E.Cheel., NSW11423, AQ012512; *D. diphylostegia* (F.Muell.) F.M. Bailey, AQ0011960; *D. harpullioides* S.T.Reynolds, CANB310651, AQ376242; *D. macrantha* L.S.Smith ex

S.T.Reynolds, AQ393009, AQ484797; *D. obovata* S.T.Reynolds, AQ629722; *D. pedleyi* S.T.Reynolds, NSW862893, AQ581440; *D. smithii* S.T.Reynolds, CANB31289, AQ484796.

The leaves are hypostomatic. The stomata are 13–28  $\mu\text{m}$  long and the stomatal complexes range from actinocytic (*D. harpullioides*, *D. pedleyi*) to irregularly tangencytic (*D. campbellii*). *Diploglottis campbellii* has a distinct peristomatal rim. *Diploglottis australis*, *D. bernieana*, *D. diphylostegia*, *D. macrantha* and *D. obovata* form a group with similar stomatal complexes which are frequently networked, with chained trichomes and large bases of deciduous trichomes with a prominent ring of foot cells. *Diploglottis smithii* is similar, but without the large trichomes, and small, smooth papillae were noted on one specimen (AQ487796), but not on another (AQ484796). *Diploglottis bracteata* is characterized by flanged papillae on just the subsidiary cells, whereas *D. harpullioides* and *D. campbellii* are essentially glabrous.

#### 9. *HARPULLIA* ROXB. (Figs 47–50)

*Observed specimens:* *Harpullia alata* F.Muell., AQ223003, AQ740633; *H. arborea* (Blanco) Radlk.,



**Figures 47–52.** *Harpullia* and *Cossinia*. Fig. 47. *Harpullia leichhardtii*, transmitted light microscopy (TLM) view of stomatal complexes (AQ462698; scale bar, 50  $\mu$ m). Fig. 48. *Harpullia alata*, scanning electron microscopy (SEM) view of outer surface showing subdued stomatal complexes in an otherwise smooth surface (AQ740633, S-1326; scale bar, 20  $\mu$ m). Fig. 49. *Harpullia pendula*, TLM view of stomatal complexes and persistent stellate trichome at upper right (AQ504130; scale bar, 50  $\mu$ m). Fig. 50. *Harpullia arborea*, TLM view of stomatal complexes and persistent stellate trichome at upper left (AQ589371; scale bar, 50  $\mu$ m). Fig. 51. *Cossinia australiana*, TLM view of stomatal complexes below stellate trichomes (AQ679155; scale bar, 50  $\mu$ m). Fig. 52. *Cossinia australiana*, SEM view of outer surface showing dense stellate trichomes (AQ679155, S-1310; scale bar, 100  $\mu$ m).

CANB392899, AQ589371; *H. frutescens* Bailey in Meston, AQ630514; *H. hillii* F.Muell., AQ512026; *H. leichhardtii* F.Muell. ex Benth., AQ481850; *H. pendula* Planchon ex F.Muell., AQ504130, AQ395936; *H. ramiflora* Radlk., CANB153795, AQ507139; *H. rhyticarpa* C.White & Francis, AQ349550, AQ420129.

The leaves are hypostomatic. The stomata are 13–23  $\mu$ m long and the stomatal complexes of all species are typically orthogonally tangencytic. Most species possess some sessile stellate trichomes in addition to simple trichomes, although some species (e.g. *H. leichhardtii*) are glabrous. The anticlinal walls of epidermal cells are relatively straight walled to markedly sinuous. See Buijsen (1995) and Buijsen, van Welzen & van der Ham (2003) for further comments on the leaf anatomy.

#### 10. *COSSINIA* COMMERSON EX. LAM. (Figs 51, 52)

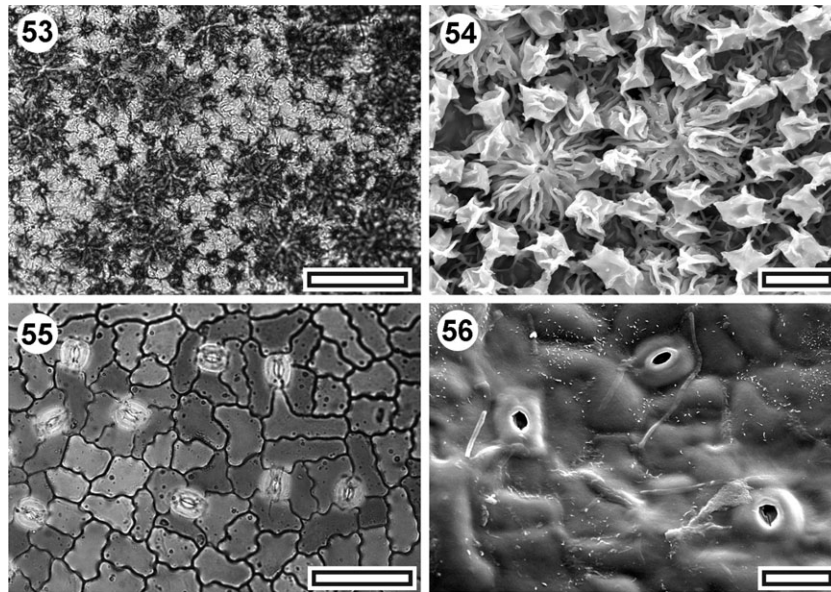
*Observed specimens:* *Cossinia australiana* S.T.Reynolds, AQ657136, AQ679155.

The leaves are hypostomatic with a dense mat of stellate trichomes on the abaxial surface (which obscure stomatal details under TLM). The stomata are 19–25  $\mu$ m long, and the stomatal complexes are cyclocytic. There is a glabrous adaxial surface with a striated ornamentation. Epidermal cell walls are smooth and curved.

#### 11. *DIMOCARPUS* LOUR. (Figs 53, 54)

*Observed specimens:* *Dimocarpus australianus* Leenh., CANB284114, AQ485230, AQ569261.

The leaves are hypostomatic, stomata 15–20  $\mu$ m long and the stomatal complexes are cyclocytic. The



**Figures 53–56.** *Dimocarpus* and *Dictyoneura*. Fig. 53. *Dimocarpus australianus*, transmitted light microscopy (TLM) view of patches of papillae which obscure stomatal complexes (AQ485230; scale bar, 50  $\mu$ m). Fig. 54. *Dimocarpus australianus*, scanning electron microscopy (SEM) view of outer surface showing flanged papillae and two stomatal complexes which are obscured by papillae projecting laterally over them (AQ485230, S-1314; scale bar, 20  $\mu$ m). Fig. 55. *Dictyoneura obtusa*, TLM view of stomatal complexes with clearly staining subsidiary cells (AQ503017; scale bar, 50  $\mu$ m). Fig. 56. *Dictyoneura obtusa*, SEM view of outer surface showing three stomatal complexes on a smooth surface (AQ503017, S-1313; scale bar, 20  $\mu$ m).

abaxial surface is entirely papillate (obscuring all but the giant stomatal complexes), but sparse stellate trichomes are present.

## 12. *DICTYONEURA* BLUME (Figs 55, 56)

*Observed specimens:* *Dictyoneura obtusa* Radlk., AQ503017.

The leaves are essentially hypostomatic, but have scattered stomatal complexes on the adaxial surface. The stomata are 13–18  $\mu$ m long, and the stomatal complexes are actinocytic, and sometimes networked. The subsidiary cells stain darkly, and normal epidermal cells have wavy and buttressed anticlinal walls with smooth outer periclinal wall surfaces. Simple persistent and deciduous trichomes are very sparse.

## 13. *GUIOA* CAV. (Figs 57–62)

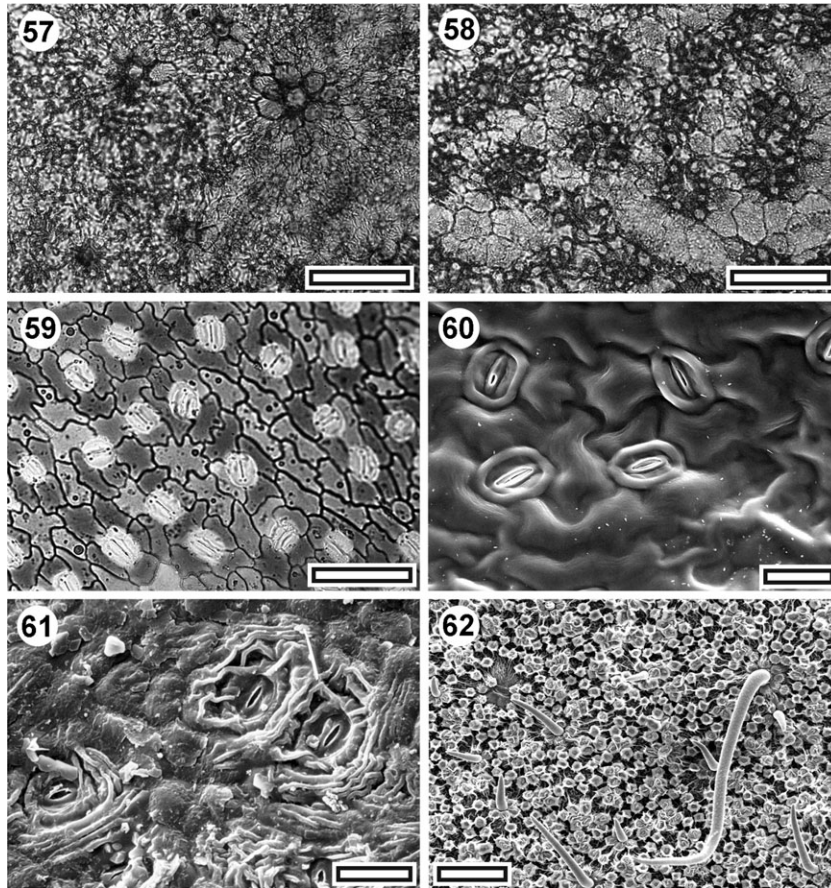
*Observed specimens:* *Guioa acutifolia* Radlk., NSW-B. Gray 377; AQ512782, AQ032333; *Gu. comesperma* Radlk. AQ033908; *Gu. coriacea* (Radlk.) Radlk., AQ257607; *Gu. lasioneura* Radlk., AQ475278, AQ032358; *Gu. montana* C.T.White, NSW-Isotype Flora of QLD 1286, AQ538127; *Gu. sarcopterifruca*

Welzen, AQ546237; *Gu. semiglauca* (F.Muell.) Radlk., NSW236071, AQ600414.

van Welzen (1989) monographed *Guioa* and illustrated its epidermal features. The leaves are hypostomatic, stomata 13–25  $\mu$ m long and stomatal complexes are actinocytic–cyclocytic. The guard cells are simply impressed into a thin cuticle, without distinct enclosing walls. Trichomes, when present, are simple and persistent. *Guioa lasioneura*, *Gu. montana* and *Gu. semiglauca* form a group in which the abaxial surface is entirely papillate, whereas *Gu. acutifolia* and *Gu. comesperma* have papillae only on the subsidiary cells (and those of the latter are very reduced), *Gu. coriacea* and *Gu. sarcopterifruca* are nonpapillate, but the periclinal walls bulge outwards and they both have prominent peristomatal rims. *Guioa coriacea* has an ornamentation of irregular ridges.

## 14. *LEPIDEREMA* RADLK. (Figs 63–66)

*Observed specimens:* *Lepiderema hirsuta* S.T.Reynolds, AQ485030; *Ld. ixiocarpa* S.T.Reynolds, NSW-B. Hyland 5016, AQ602210; *Ld. largiflorens* S.T.Reynolds, NSW-P.H. Weston 934, AQ011566; *Ld. pulchella* Radlk., NSW89228, AQ488825; *Ld. punctulata*



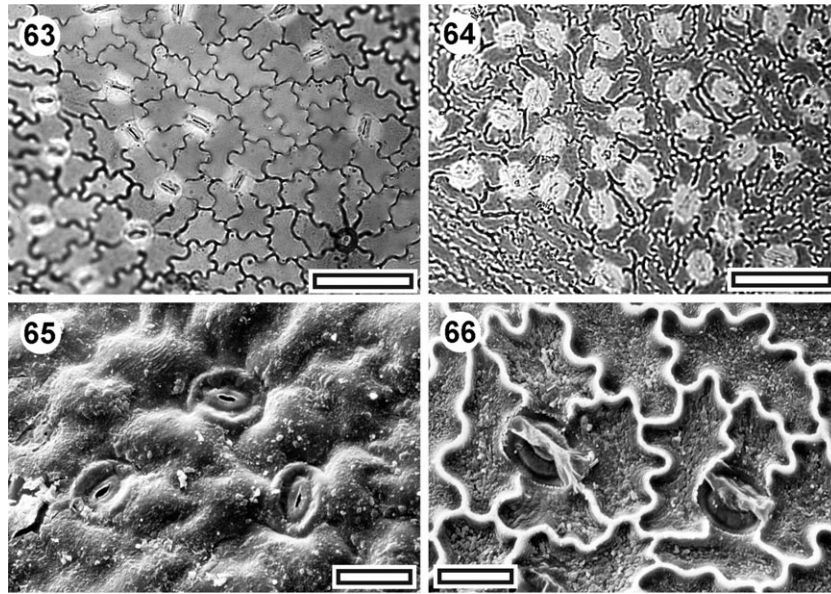
**Figures 57–62.** *Guioia*. Fig. 57. *Guioia lasioneura*, transmitted light microscopy (TLM) view showing papillae which obscure the stomatal complexes. Note also the trichome bases (AQ032358; scale bar, 50  $\mu$ m). Fig. 58. *Guioia acutifolia*, TLM view showing papillae which obscure the stomatal complexes (AQ512782; scale bar, 50  $\mu$ m). Fig. 59. *Guioia sarcopterifruca*, TLM view of stomatal complexes with clearly staining subsidiary cells (AQ546237; scale bar, 50  $\mu$ m). Fig. 60. *Guioia sarcopterifruca*, scanning electron microscopy (SEM) view of outer surface showing rimmed stomatal complexes in an otherwise subdued outer surface (AQ546237, S-1325; scale bar, 20  $\mu$ m). Fig. 61. *Guioia coriacea*, SEM view of outer surface showing three stomatal complexes (with peristomatal rims) partially obscured by striae (NSW 168626, S-1348; scale bar, 10  $\mu$ m). Fig. 62. *Guioia lasioneura*, SEM view of outer surface showing flanged papillae which obscure the stomatal complexes, and persistent trichomes (AQ475278, S-1323; scale bar, 100  $\mu$ m).

(F.Muell.) Radlk., CANB399996, AQ621565; *Ld. sericolignis* (Bailey) Radlk., NSW200357, AQ485848.

The leaves are hypostomatic. The stoma are 13–23  $\mu$ m long and the stomatal complexes are actinocytic and typically networked, especially in *Ld. punctulata*, and in *Ld. ixiocarpa* they are surrounded by a peristomatal rim. *Lepiderema* is characterized by tightly sinuous epidermal cells on both abaxial and adaxial surfaces, and in *Ld. pulchella* and *Ld. punctulata* the adaxial epidermal cells are also buttressed. The outer surfaces of the epidermal cells are smooth. With the exception of *Ld. pulchella* (glabrous), all species have the bases of deciduous trichomes.

#### 15. *CUPANIOPSIS* RADLK. (Figs 67–70)

*Observed specimens:* *Cupaniopsis anacardioides* (A.Rich.) Radlk., AQ393007; *Cu. baileyana* Radlk., AQ396232; *Cu. cooperorum* P.I.Forst., AQ605728; *Cu. dallachyi* S.T. Reynolds, AQ631990; *Cu. diploglottoides* Adema, AQ396122; *Cu. flagelliformis* S.T.Reynolds, AQ653184; *Cu. fleckeri* S.T.Reynolds, AQ620445; *Cu. foveolata* (F.Muell.) Radlk., AQ604837, AQ632498; *Cu. newmanii* S.T.Reynolds, A.G. Floyd 1821, AQ398302; *Cu. papillosa* P.I.Forst. AQ557409; *Cu. parvifolia* (Bailey) L.Johnson, AQ570826, AQ621477; *Cu. serrata* (F.Muell.) Radlk.,



**Figures 63–66.** *Lepiderema*. Fig. 63. *Lepiderema largiflorens*, transmitted light microscopy (TLM) view of stomatal complexes and trichome base. Note subsidiary cells are clearly stained and often link stomatal complexes: networking (P.H. Weston 934; scale bar, 50  $\mu$ m). Fig. 64. *Lepiderema punctulata*, TLM view of stomatal complexes which are often networked (AQ621565; scale bar, 50  $\mu$ m). Fig. 65. *Lepiderema ixiocarpa*, scanning electron microscopy (SEM) view of outer surface showing stomatal complexes surrounded by rims and an otherwise smooth surface (B. Hyland 5016, S-1335; scale bar, 10  $\mu$ m). Fig. 66. *Lepiderema ixiocarpa*, SEM view of inner surface showing two stomatal complexes (B. Hyland 5016, S-1335; scale bar, 10  $\mu$ m).

AQ439006, AQ439085; *Cu. shirleyana* (F.M.Bailey) Radlk., AQ436426, AQ527791; *Cu. simulata* S.T.Reynolds, AQ459891; *Cu. tomentella* (F.Muell. ex Benth.) S.T.Reynolds, AQ431207, AQ348827; *Cu. wadsworthii* (F.Muell.) Radlk., NSW225556, AQ633318, AQ543635.

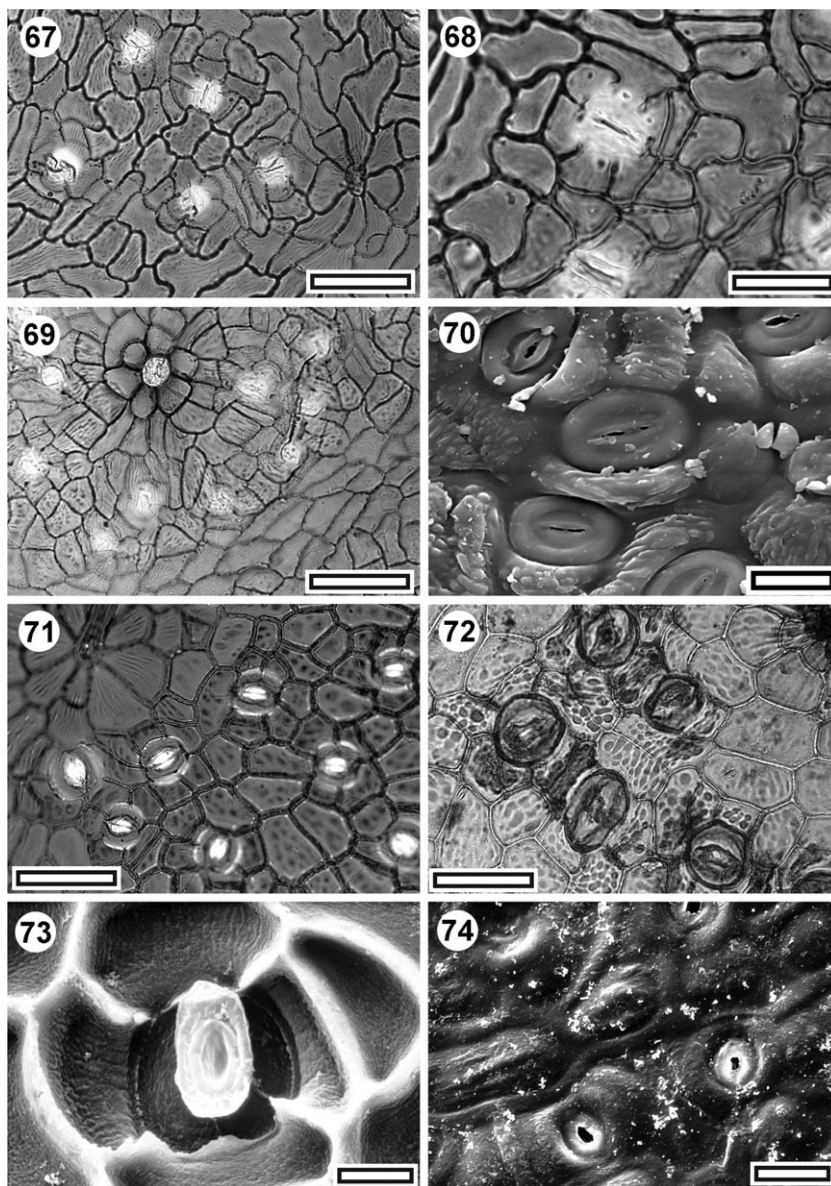
Adema (1991) monographed *Cupaniopsis* and illustrated a range of epidermal features. The leaves are typically hypostomatic, although, in some species (*Cu. anacardioides*, *Cu. parvifolia*, *Cu. fleckeri*, *Cu. shirleyana* and *Cu. wadsworthii*), stomatal complexes are scattered over the upper surface. The stomata are 13–23  $\mu$ m long and the stomatal complexes range from actinocytic to irregularly tangencytic (*Cu. parvifolia* with lighter subsidiary cells) to cyclocytic (*Cu. dallachyi*, *Cu. shirleyana*). A few have tangential walls in lateral contact cells making them appear brachyparacytic. They are sometimes networked (*Cu. dallachyi*, *Cu. fleckeri*). Stomatal complexes have surficial, thin-walled guard cells, simply impressed into the cuticle, without distinct enclosing walls, and surrounded by epidermal cells which have flanges which protrude slightly over the borders of the guard cells (the guard cells are slightly embedded below the contact epidermal cells). Trichomes, if present at all, are deciduous or

simple persistent, and typically sparse. *Cupaniopsis diploglottoides* is distinct in having relatively large-diameter trichome bases with many foot cells and some rare chained trichomes. Epidermal cells are typically ornamented by striations, either strong enough to obscure the stomatal outline in TLM view (*Cu. newmanii*), or very faint (e.g. *Cu. anacardioides*), and they may be on both leaf surfaces (*Cu. serrata*) or, more typically, restricted to one leaf surface. *Cupaniopsis baileyana* is the only Australasian species with papillae, although they are localized. *Cupaniopsis anacardioides*, *Cu. fleckeri*, *Cu. foveolata* and *Cu. parvifolia* form a rather similar group with small stomatal complexes and irregularly sized subsidiary cells.

#### 16. *RHYSOTOECHIA* RADLK. (Figs 71–74)

*Observed specimens:* *Rhysotoechia bifoliolata* Radlk., NSW-J.B. Williams J14, AQ621310; *R. flavescens* Radlk., NSW-B. Hyland 8650, AQ031862; *R. mortoni-ana* (F.Muell.) Radlk., NSW247550 (type); NSW 166307, AQ509433; *R. robertsonii* (F.Muell.) Radlk., NSW-A.K. Irvine 1726, AQ512773.

The leaves are hypostomatic. The stomata are 15–45  $\mu$ m long and the stomatal complexes are typi-

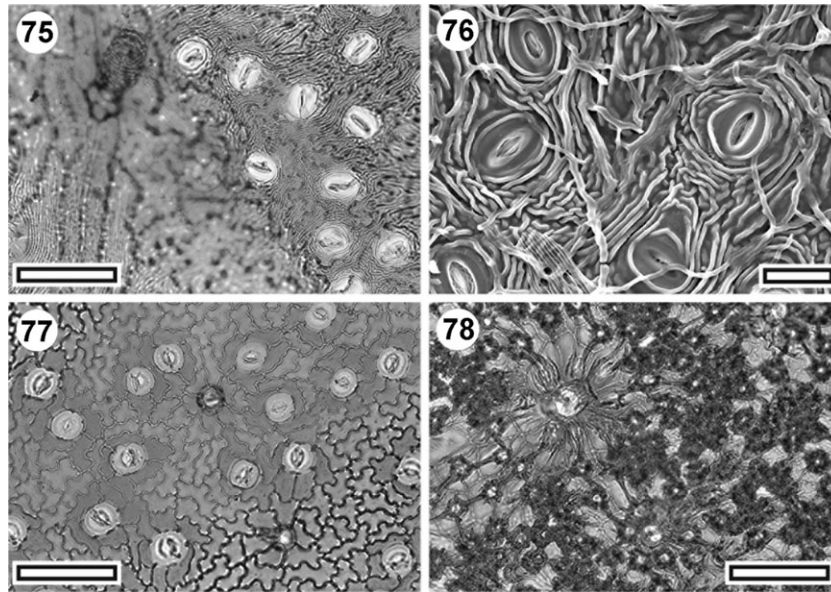


**Figures 67–74.** *Cupaniopsis* and *Rhysotoechia*. Fig. 67. *Cupaniopsis folveolata*, transmitted light microscopy (TLM) view of stomatal complexes and trichome base (AQ632498; scale bar, 50  $\mu$ m). Fig. 68. *Cupaniopsis anacardioides*, TLM view of stomatal complexes (AQ380045; scale bar, 20  $\mu$ m). Fig. 69. *Cupaniopsis serrata*, TLM view of stomatal complexes and trichome base upper left (AQ439085; scale bar, 50  $\mu$ m). Fig. 70. *Cupaniopsis anacardioides*, scanning electron microscopy (SEM) view of outer surface showing stomatal complexes surrounded by raised epidermal cells with short striae on them (AQ719827, S-1311; scale bar, 20  $\mu$ m). Fig. 71. *Rhysotoechia bifoliolata*, TLM view of stomatal complexes, and persistent trichome at top left (AQ504166; scale bar, 50  $\mu$ m). Fig. 72. *Rhysotoechia mertoniana*, TLM view of stomatal complexes (AQ509433; scale bar, 50  $\mu$ m). Fig. 73. *Rhysotoechia flavescens*, SEM view of inner surface of a single stomatal complex (B. Hyland 8650, S-1346,  $\times$  2400). Fig. 74. *Rhysotoechia flavescens*, SEM view of outer surface showing stomatal complexes in an otherwise smooth surface (B. Hyland 8650, S-1346; scale bar, 10  $\mu$ m).

cally actinocytic, but some have had tangential wall formation in lateral contact cells, making the complex appear brachyparacytic. The guard cells are thin-walled and simply impressed into the cuticle,

without distinct enclosing walls. All species are either glabrous or have sparse bases of deciduous trichomes. The leaf surface is either smooth or with faint ridging.





**Figures 75–78.** *Jagera* and *Cnesmocarpon*. Fig. 75. *Jagera javanica*, transmitted light microscopy (TLM) view of stomatal complexes and, at upper left, a balloon trichome. Note prominent striae (AQ256453; scale bar, 50  $\mu$ m). Fig. 76. *Jagera javanica*, scanning electron microscopy SEM view of outer surface showing prominent striae, some of which pass over the stomatal complexes (AQ515675, S-1327; scale bar, 20  $\mu$ m). Fig. 77. *Jagera pseudorhus*, TLM view of stomatal complexes and bases of trichomes (AQ485909; scale bar, 50  $\mu$ m). Fig. 78. *Cnesmocarpon dasyantha*, TLM showing clusters of papillae which obscure the stomatal complexes and, at upper left, a trichome base (AQ519900; scale bar, 50  $\mu$ m).

#### 17. *JAGERA* BLUME (Figs 75–77)

*Observed specimens:* *Jagera javanica* (Blume) Blume ex Kalkman, CANB63200, AQ515675, AQ510089; *J. madida* P.I.Forst., AQ510094; *J. pseudorhus* (A.Rich.) Radlk., AQ603276.

The leaves are hypostomatic. The stomata are 18–23  $\mu$ m long and the stomatal complexes are cyclocytic to actinocytic and have irregularly shaped subsidiary cells. These and other surrounding epidermal cells have striae that tend to ‘swirl’ around the stomatal complexes, but radiate from hair bases and some stomatal complexes. The striae are stronger in *J. javanica* and tend to obscure the stomatal complex outline in TLM view, and, in SEM view, they may be seen to occasionally cross the outer stomatal ledges. Epidermal cells which are distal to the stomatal groups are not striated. Persistent simple trichomes and balloon glands are present, more abundantly so in *J. pseudorhus*. The adaxial surface is striate and simple trichomes are present.

#### 18. *CNESMOCARPON* ADEMA (Fig. 78)

*Observed specimens:* *Cnesmocarpon dasyantha* (Radlk.) Adema, AQ512879.

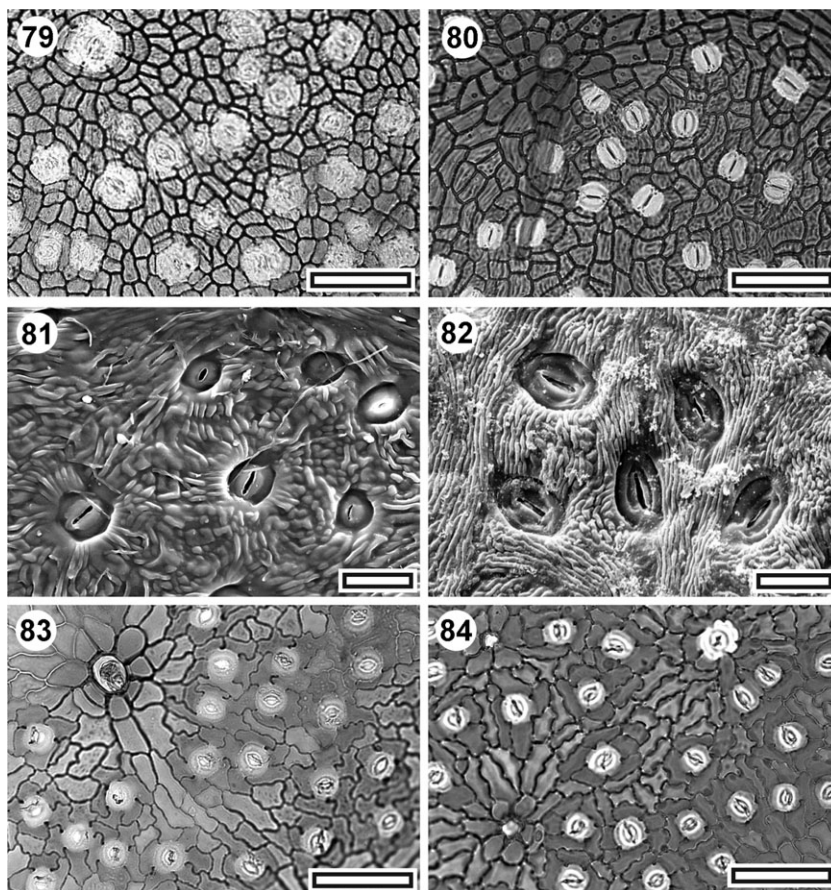
The leaves are hypostomatic, stomata 18–20  $\mu$ m long and the stomatal complexes cyclocytic. The

abaxial surface is covered in flanged papillae (a character which distinguishes *Cnesmocarpon* from *Jagera* Adema (Adema & van der Ham, 1993), except for the regions over major veins (which have the bases of deciduous trichomes). The adaxial surface has neither papillae nor trichome bases, and the epidermal cells are slightly buttressed and with fine surficial striae.

#### 19. *ELATTOSTACHYS* (BLUME) RADLK. (Figs 79–82)

*Observed specimens:* *Elattostachys megalantha* S.T.Reynolds, NSW-B. Hyland 3166 RFK (isotype); *E. microcarpa* S.T.Reynolds, AQ531569; *E. nervosa* (F.Muell.) Radlk., AQ510656; *E. xylocarpa* (A.Cunn. ex F.Muell.) Radlk., NSW-J. Pickard & D.F. Blaxell 243, AQ345514, AQ431212.

The leaves are typically unevenly amphistomatic, with some stomatal complexes on the adaxial surface. The stomata are 13–25  $\mu$ m long and the stomatal complexes are typically cyclocytic (*E. nervosa* has a well-defined ring of isodiametric darker subsidiary cells clearly cut off from mother cells). Sometimes the contact cells are clearly the result of tangential cut-offs from a mother cell, but they do not have the elongate shape more typical of this stomatal type. *Elattostachys microcarpa*, *E. nervosa* and *E. megalantha* have an ornamentation of fine ridges all over



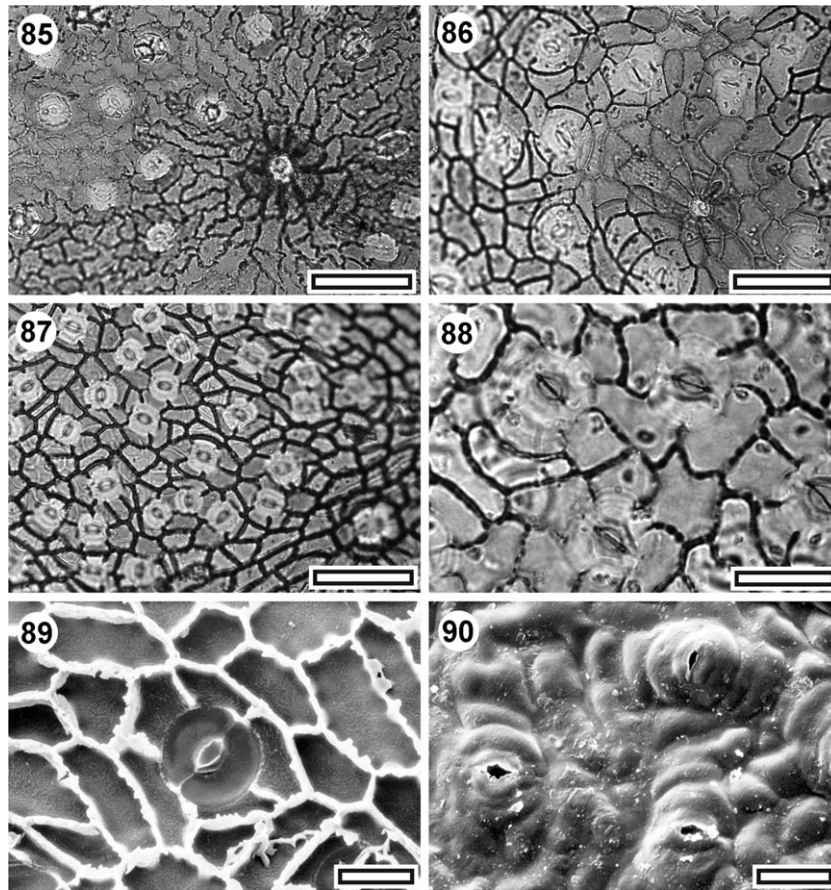
**Figures 79–84.** *Elattostachys* and *Sarcopteryx*. Fig. 79. *Elattostachys nervosa*, transmitted light microscopy (TLM) view of stomatal complexes. Note giant stomatal complex at upper left (AQ510656; scale bar, 50  $\mu$ m). Fig. 80. *Elattostachys xylocarpa*, TLM view of stomatal complexes and persistent trichome at upper left (J. Pickard & D.F. Blaxell 243; scale bar, 50  $\mu$ m). Fig. 81. *Elattostachys nervosa*, scanning electron microscopy (SEM) view of outer surface showing stomatal complexes depressed within a shortly striated surface (AQ510656, S-1320; scale bar, 20  $\mu$ m). Fig. 82. *Elattostachys megalantha*, SEM view of outer surface showing stomatal complexes depressed within a finely striated surface (B. Hyland 3166 RFK Isotype, S-1343; scale bar, 10  $\mu$ m). Fig. 83. *Sarcopteryx martyana*, TLM view of stomatal complexes and trichome base. Note subsidiary cells are clearly stained and are sometimes shared between complexes: networking (AQ330731; scale bar, 50  $\mu$ m). Fig. 84. *Sarcopteryx reticulata*, TLM view of stomatal complexes and trichome base (AQ790075; scale bar, 50  $\mu$ m).

the epidermal cells and a very thin cuticle over guard cells, and the rest are generally smooth. Species are glabrous or almost so, with scattered glandular trichomes.

#### 20. *SARCOPTERYX* RADLK. (Figs 83, 84)

*Observed specimens:* *Sarcopteryx acuminata* S.T.Reynolds, CANB186377, AQ389437; *S. martyana* (F.Muell.) Radlk., CANB302704, AQ506768; *S. montana* S.T.Reynolds, AQ485836; *S. reticulata* S.T.Reynolds, AQ668282, AQ790075; *S. stipata* (F.Muell.) Radlk., AQ335693, AQ600134.

The leaves are hypostomatic. The stomata are 13–20  $\mu$ m long and the stomatal complexes are actinocytic and sometimes networked. The guard cell pair is distinctly circular and is placed above the subsidiary cells. With the exception of *S. martyana*, which has distinctive surficial structures (either compound glands or simple trichomes with extensive foot cell development), the trichomes are simple, typically deciduous or sometimes persistent (*S. montana*, *S. stipata*). Adaxial epidermal cells are typically sinuous, buttressed, or both, and they may be glabrous or with the bases of deciduous trichomes. The outer surface is smooth.



**Figures 85–90.** *Toechima* and *Synima*. Fig. 85. *Toechima dasyrrhache*, transmitted light microscopy (TLM) view of stomatal complexes and trichome base (AQ477950; scale bar, 50  $\mu$ m). Fig. 86. *Toechima tenax*, TLM view of stomatal complexes and trichome base (AQ265395; scale bar, 50  $\mu$ m). Fig. 87. *Synima macrophylla*, TLM view of stomatal complexes. Note giant stomatal complex at bottom left (AQ606565; scale bar, 50  $\mu$ m). Fig. 88. *Synima cordieri*, TLM view of stomatal complexes (AQ606566; scale bar, 20  $\mu$ m). Fig. 89. *Synima macrophylla*, scanning electron microscopy (SEM) view of inner surface of single stomatal complex. Note radial walls of contact cells abutting stomatal outline, which is not walled, but simply depressed (P.H. Weston 809, S-1334; scale bar, 10  $\mu$ m). Fig. 90. *Synima macrophylla*, SEM view of outer surface showing stomatal complexes in a generally smooth surface (P.H. Weston 809, S-1334; scale bar, 10  $\mu$ m).

## 21. *TOECHIMA* RADLK. (Figs 85, 86)

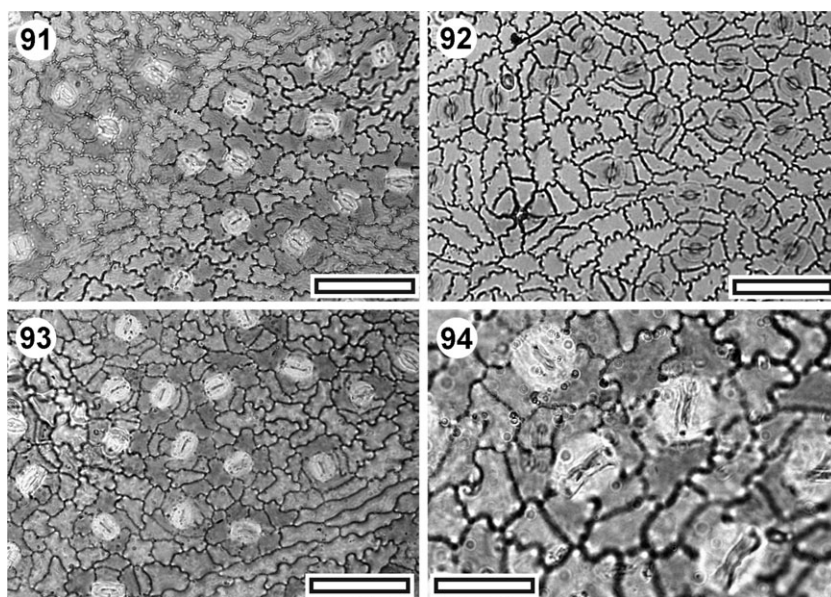
*Observed specimens:* *Toechima daemelianum* (F.Muell.) Radlk., NSW-B. Hyland 2547 RFK; *To. dasyrrhache* Radlk., NSW132369, AQ477950; *To. erythrocarpum* (F.Muell.) Radlk., NSW233922; *To. monticola* S.T.Reynolds, AQ073973; *To. pterocarpum* S.T.Reynolds, NSW-G & N Sankowsky 289 (isoparatype); *To. tenax* (Cunn. ex Benth.) Radlk., AQ265395.

The leaves are mostly hypostomatic, but, in *To. Tenax*, stomatal complexes are abundant along the midvein on the adaxial surface, and scattered away from it, whereas, in *To. Monticola*, there are rare stomatal complexes scattered over the adaxial surface. The stomata are 10–25  $\mu$ m long, and stomatal complexes are typically networked or acti-

nocytic, with frequently one, sometimes two, lateral contact cells (*To. tenax* and *To. dasyrrhache*). Stomatal complexes are simple and, in the larger complexes, the anticlinal walls of subsidiary cells project over the stomatal outline. In *To. erythrocarpum* and *To. Pterocarpum*, the guard cell pair is smaller than the typical epidermal cells. Species may be glabrous (*To. pterocarpum*) or with persistent simple trichomes, or with multicellular glandular trichomes (*To. daemelianum*). The outer surface of the epidermal cells is smooth.

## 22. *SYNIMA* RADLK. (Figs 87–90)

*Observed specimens:* *Synima cordierorum* (F.Muell.) Radlk., AQ606566; *Sy. macrophylla* S.T.Reynolds, AQ606565; *Sy. reynoldsiae* P.I.Forst. AQ485891.



**Figures 91–94.** *Sarcotoechia* and *Lepidopetalum*. Fig. 91. *Sarcotoechia lanceolata*, transmitted light microscopy (TLM) view of stomatal complexes (AQ602143; scale bar, 50  $\mu$ m). Fig. 92. *Sarcotoechia serrata*, TLM view of stomatal complexes and trichome base (AQ555392; scale bar, 50  $\mu$ m). Fig. 93. *Lepidopetalum subdichotomum*, TLM view of stomatal complexes (AQ031481; scale bar, 50  $\mu$ m). Fig. 94. *Lepidopetalum subdichotomum*, TLM view of stomatal complexes (AQ031481; scale bar, 20  $\mu$ m).

The leaves are hypostomatic and the stomata are 15–20  $\mu$ m long. Both species are similar in having stomatal complexes with irregular development of tangential subsidiary cells, anticlinal walls which project over the stomatal outline, and also sparse simple trichomes as well as balloon trichomes. The outer surface of the epidermal cells is smooth.

### 23. *SARCOTOECHIA* RADLK. (Figs 91, 92)

*Observed specimens:* *Sarcotoechia cuneata* Radlk., AQ550520, AQ657240; *St. heterophylla* S.T.Reynolds, CANB399984, AQ451344; *St. lanceolata* (C.White) S.T.Reynolds, AQ602143, UNSW 13421; *St. protracta* Radlk., AQ602371; *St. serrata* S.T.Reynolds, AQ0010264, AQ555392; *St. villosa* S.T.Reynolds, AQ468949.

The leaves are hypostomatic, stomata 13–20  $\mu$ m long and the stomatal complexes are often distinctly actinocytic (*St. cuneata*, *St. lanceolata*, *St. protracta*) and are occasionally to frequently networked. *Sarcotoechia villosa* has guard cell pairs which are elliptic, with a poorly defined outer margin and no T-pieces, and are positioned above the subsidiary cells. Epidermal cells have straight to slightly wavy anticlinal walls. *Sarcotoechia protracta* has similar guard cells, but sinuous epidermal cells. *Sarcotoechia heterophylla* is distinct in that the guard cell pair has a well-defined outer rim and bars. Giant stomatal complexes are frequent, and trichome bases, with strong

flanges and a regular ring of foot cells, are common. Projecting walls of anticlinal subsidiary cells often seem to stop a little short of the guard cell margin. Adaxial epidermal cells are typically buttressed (except in *St. heterophylla*), with smooth outer surfaces, and either glabrous or with simple, deciduous and sometimes persistent trichomes.

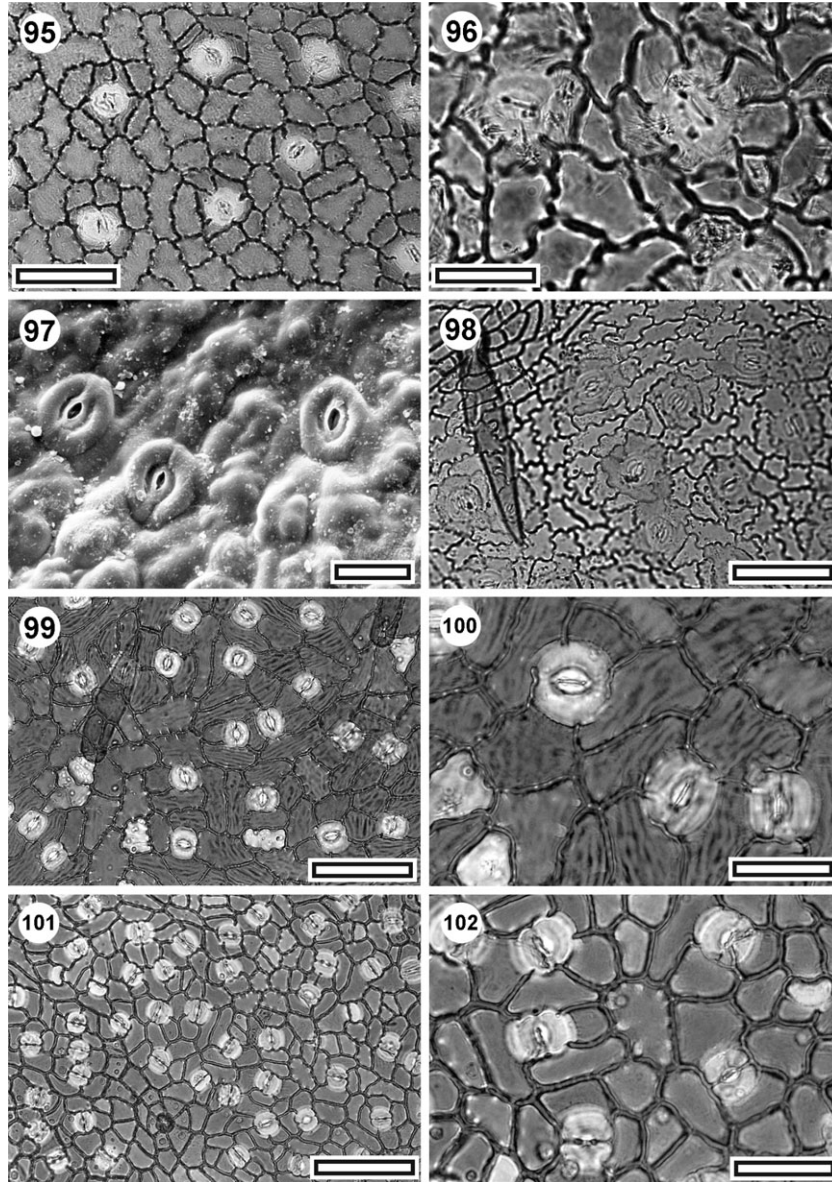
### 24. *LEPIDOPETALUM* BLUME (Figs 93, 94)

*Observed specimens:* *Lepidopetalum fructoglabrum* Welzen, CANB90045.

The leaves are hypostomatic, stomata 13–18  $\mu$ m long and the stomatal complexes are irregularly tangencytic. The guard cells are simply impressed into a thin overlying cuticle, without distinct enclosing walls. Giant stomatal complexes are present over veins. The epidermal cells are highly sinuous, with smooth outer surfaces, and bases of deciduous trichomes are rare.

### 25. *ARYTERA* BLUME (Figs 95–98)

*Observed specimens:* *Arytera bifoliolata* S.T.Reynolds, AQ348645; *Ar. dictyoneura* S.T.Reynolds, AQ407836, AQ572388; *Ar. distylis* (F.Muell. ex Benth.) Radlk., NSW-S. Clark, J. Pickard, R. Coveny 1576, AQ441669; *Ar. divaricata* F.Muell., S. King 402, AQ606272, AQ620955; *Ar. foveolata* F.Muell., NSW-K.A. Williams 83070, AQ641667; *Ar. microphylla*



**Figures 95–102.** *Arytera* and *Mischarytera*. Fig. 95. *Arytera dictyoneura*, transmitted light microscopy (TLM) view of stomatal complexes. Note sinuous and slightly buttressed epidermal cell walls (AQ572388; scale bar, 50  $\mu\text{m}$ ). Fig. 96. *Arytera divaricata*, TLM view of stomatal complexes (AQ620955; scale bar, 20  $\mu\text{m}$ ). Fig. 97. *Arytera divaricata*, scanning electron microscopy (SEM) view of outer surface showing stomatal complexes with raised outer stomatal ledges in a slightly bumpy surface (S. King 402, S-1333; scale bar, 10  $\mu\text{m}$ ). Fig. 98. *Arytera pauciflora*, TLM view of stomatal complexes and persistent trichome at upper left (AQ343905; scale bar, 50  $\mu\text{m}$ ). Fig. 99. *Mischarytera lautereriana*, TLM view of stomatal complexes and persistent trichomes. Note striate surface (B. Gray 1697; scale bar, 50  $\mu\text{m}$ ). Fig. 100. *Mischarytera lautereriana*, TLM view of stomatal complexes (B. Gray 1697; scale bar, 20  $\mu\text{m}$ ). Fig. 101. *Mischarytera macrobotrys*, TLM view of stomatal complexes and trichome base (AQ605813; scale bar, 50  $\mu\text{m}$ ). Fig. 102. *Mischarytera macrobotrys*, TLM view of stomatal complexes. Note buttressing of epidermal cells (AQ605813; scale bar, 20  $\mu\text{m}$ ).

(Benth.) Radlk., NSW225997, AQ039352; *Ar. pauciflora* S.T.Reynolds AQ343905; *Ar. pseudofoveolata* H.Turner, AQ584660.

The morphology of all species is similar. The leaves are typically hypostomatic, but there may be many

stomatal complexes along the midvein on the adaxial surface (*Ar. distylis*), or scattered over the adaxial surface but concentrated near large veins (*Ar. foveolata*). The stoma are 13–25  $\mu\text{m}$  long and the stomatal complexes are irregularly tangencytic and may be

networked. The abaxial and abaxial epidermal cells are often sinuous, buttressed or both. The outer surfaces are smooth and glabrous or with rare persistent simple trichomes, tending to be restricted to the midvein on the abaxial surface.

#### 26. MISCHARYTERA (Figs 99–102)

*Observed specimens:* *Mischarytera lautereriana* (F.M.Bailey) H. Turner, NSW-B.Grey 1697; *M. macrobotrys* (Merr. & L.M.Perry) H.Turner, AQ605813; *M. megaphylla* P.I.Forst. AQ174075.

*Mischarytera macrobotrys* is hypostomatic and *M. lautereriana* has, in addition to those on the abaxial surface, stomatal complexes scattered along the midvein on the adaxial surface. The stomata are 9–11 µm long. Both species are similar in having highly networked stomatal complexes, relatively small, actinocytic stomatal complexes and subsidiary cell flanges which abruptly abut against, sometimes across, and sometimes deflect to run partly along the guard cell outline. *Mischarytera macrobotrys* and *m. megaphylla* have strongly buttressed adaxial epidermal cells, *M. lautereriana* less so. In contrast, only a few of the epidermal cells on the abaxial surface of *M. macrobotrys* are buttressed. These tend to be those once-removed from stomatal complexes and may therefore be ‘true’ epidermal cells (not subsidiary cells). Most epidermal/subsidiary cells on the abaxial surface of *M. lautereriana* are buttressed. *Mischarytera lautereriana* has a striated abaxial surface and scattered, persistent simple trichomes, whereas *M. macrobotrys* and *m. megaphylla* are unornamented and has scattered trichome bases.

#### 27. MISCHOCARPUS BLUME (Figs 103–106)

*Observed specimens:* *Mischocarpus albescens* S.T. Reynolds, AQ326247; *Mc. anodontus* (F.Muell.) Radlk., AQ457675; *Mc. australis* S.T.Reynolds, AQ454680, AQ396382; *Mc. exangulatus* (F.Muell.) Radlk., NSW96891, AQ509432; *Mc. grandissimus* Radlk., AQ485846; *Mc. lachnocarpus* (F.Muell.) Radlk., CANB293158, AQ603130, AQ601779; *Mc. macrocarpus* S.T.Reynolds, AQ005204; *Mc. pyriformis* (F.Muell.) Radlk., NSW Bauerler 1023, AQ658291; *Mc. stipitatus* S.T.Reynolds, AQ389174.

The leaves are hypostomatic. The stomata are 13–23 µm long and the stomatal complexes vary from cyclocytic to actinocytic and irregularly tangencytic. All species, with the exception of *Mc. exangulatus* (glabrous) and *Mc. pyriformis* (with unusual trichome or glandular bases), have chained glandular trichomes. Of these, *Mc. australis*, *Mc. anodontus* (where the glandular trichomes are often in pairs) and *Mc. grandissimus* only have chained glandular

trichomes, and the remaining species also have scattered bases of deciduous trichomes. In one specimen of *Mc. lachnocarpus* (AQ601779) the simple trichomes are dense, whereas, in another specimen (AQ603130), the density of trichome bases was much lower, and if the trichome body was still present, appeared degraded. *Mischocarpus albescens* is highly distinct in having discrete, smooth papillae projecting from all epidermal cells on the abaxial surface. On the adaxial surface, the epidermal cells are typically sinuous or wavy and buttressed with smooth outer surfaces (the exceptions being *Mc. australis*, *Mc. albescens* and *Mc. grandissimus*, which have relatively straight-walled and unbuttressed cells, but a striated ornamentation), and they are not papillate.

#### 28. DIPLOPELTIS ENDL. (Figs 107–110)

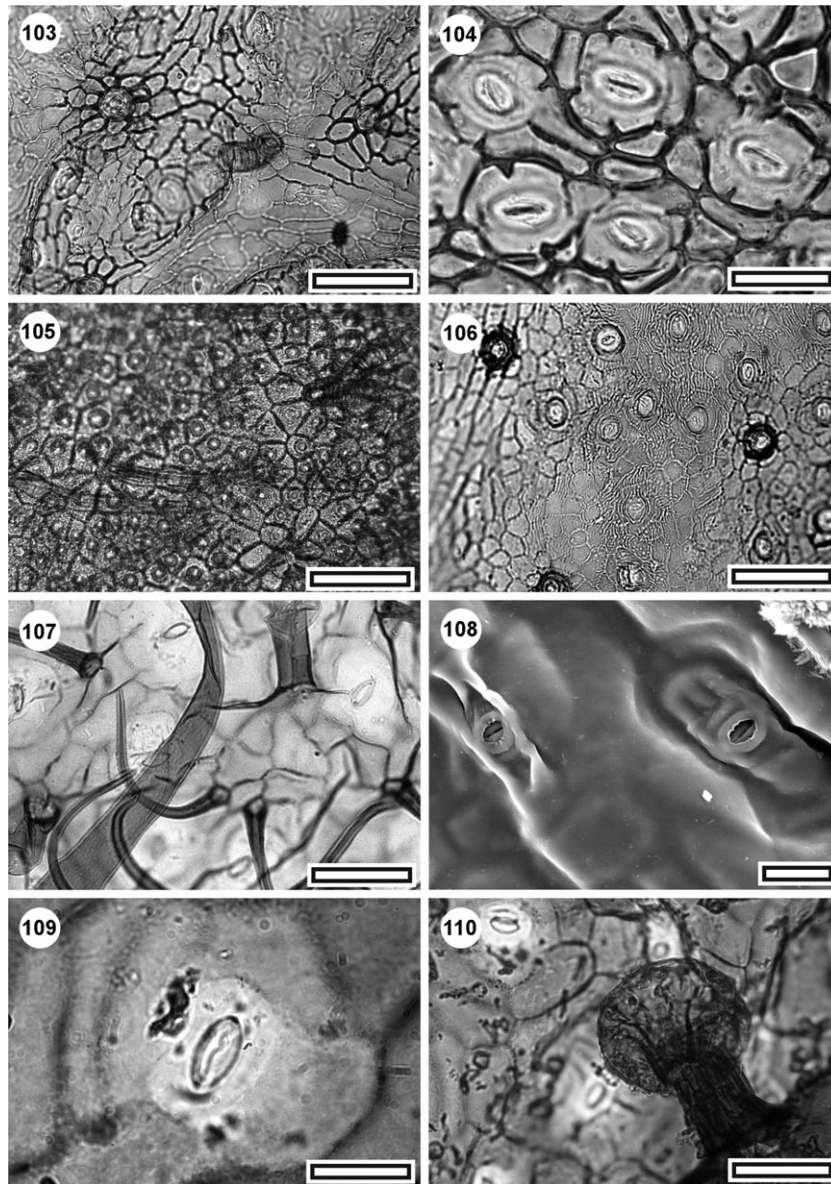
*Observed specimens:* *Diplopeltis eriocarpa* (Benth.) Hemsley, CANB297566, AQ030712; *Dp. huegelii* Endl., CANB323274, AQ479323; *Dp. intermedia* A.S.George, CANB348619; *Dp. petiolaris* F.Muell. ex Benth., AQ593099; *Dp. stuartii* F.Muell., CANB129108, AQ030729.

The leaves are amphistomatic. The stomata are 20–35 µm long, but with guard cell outlines that are typically faint, whereas the anticlinal walls of epidermal cells vary from well defined to absent. Stomatal complexes in *Dp. stuartii* are tangentially divided actinocytic, typically with four subsidiary cells (often with distinct lateral and polar cells). *Diplopeltis stuartii* has stalked multicellular glands and is glabrous, *Dp. huegelii* has thick simple, falcate trichomes of a range of sizes and no stalked multicellular glands, and *Dp. petiolaris* has stalked multicellular glands and simple, recurved trichomes. The surface of *Dp. eriocarpa* is obscured by a dense covering of small, simple, recurved trichomes and a scattering of larger multicellular ones. The surface of the epidermal cells is smooth.

#### 29. DISTICHOSTEMON F.MUELL. (Figs 111–114)

*Observed specimens:* *Distichostemon arnhemicus* S.T.Reynolds, DNA6297, AQ339831, AQ598283; *Ds. barklyanus* S.T.Reynolds, DNA6874, AQ489399; *Ds. dodecandrus* Domin., CANB369651, AQ512067; *Ds. filamentosus* S.Moore, CANB333948, AQ030931; *Ds. hispidulus* (Endl.) Baillon, J.T. Waterhouse 4107, AQ518286; *Ds. malvaceus* Domin., CANB199574, AQ546189.

The leaves are amphistomatic, the stomata are 20–35 µm long and all species have anisocytic stomatal complexes of three or four subsidiary cells. All species have large persistent trichomes surrounded by a ring of large basal cells. Epidermal cell walls and outer surfaces are smooth.

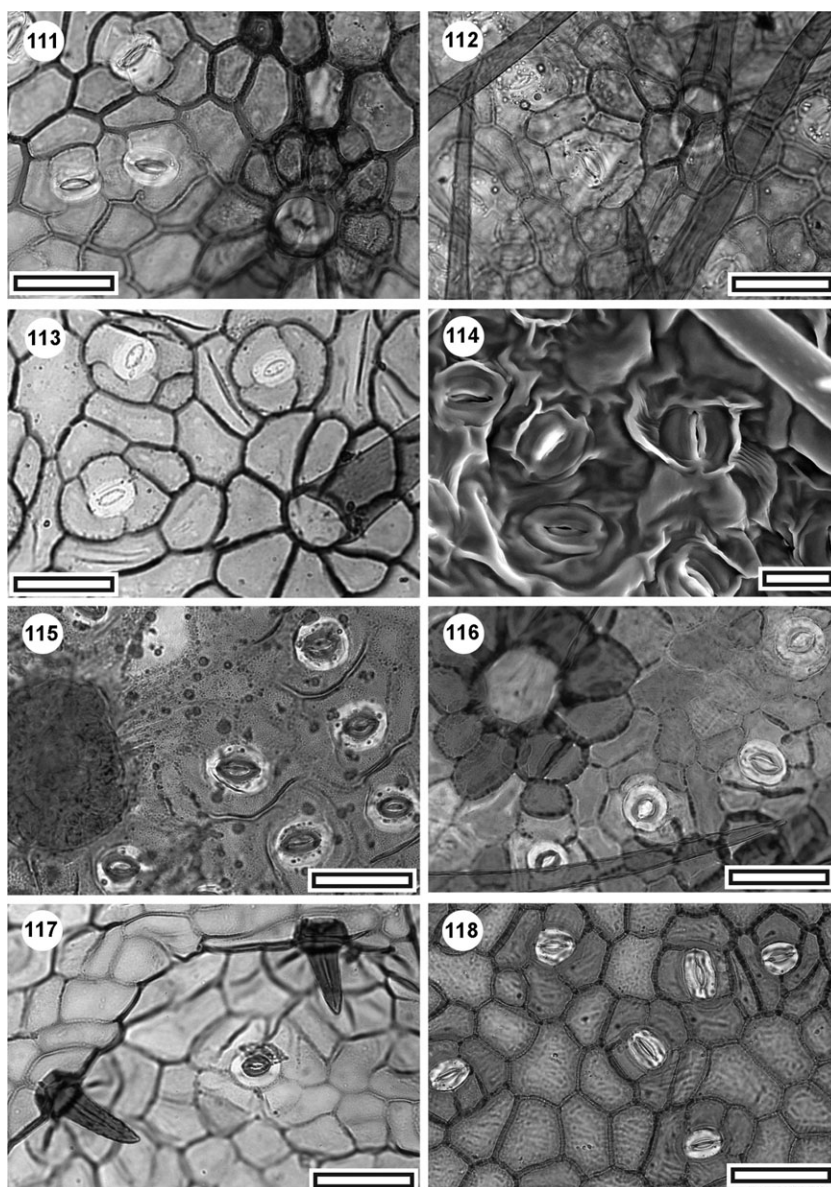


**Figures 103–110.** *Mischochloa* and *Diplopeltis*. Fig. 103. *Mischochloa lachnocarpus*, transmitted light microscopy (TLM) view of stomatal complexes, chained trichome in centre and simple trichome bases to left and right (AQ601779; scale bar, 50  $\mu$ m). Fig. 104. *Mischochloa stipitatus*, TLM view of stomatal complexes (AQ389174; scale bar, 20  $\mu$ m). Fig. 105. *Mischochloa albescens*, TLM view showing papillae which obscure stomatal complexes, and persistent trichomes (AQ326247; scale bar, 50  $\mu$ m). Fig. 106. *Mischochloa grandissimus*, TLM view of stomatal complexes and trichome bases (AQ485846; scale bar, 50  $\mu$ m). Fig. 107. *Diplopeltis intermedia*, TLM view of stomatal complexes and large, persistent falcate trichomes (CANB 348619; scale bar, 50  $\mu$ m). Fig. 108. *Diplopeltis stuartii*, scanning electron microscopy (SEM) view of outer surface showing two stomatal complexes sunken below the level of the epidermal cells (AQ030729, S-1318; scale bar, 20  $\mu$ m). Fig. 109. *Diplopeltis stuartii*, TLM view of stomatal complex (AQ030729; scale bar, 20  $\mu$ m). Fig. 110. *Diplopeltis stuartii*, TLM view showing compound glandular trichome (AQ030729; scale bar, 50  $\mu$ m).

30. *DODONAEA* MILLER (Figs 115–118)

Observed specimens: *Dodonaea baueri* Endl. AQ109113; *Do. biloba* J.G.West, AQ763395; *Do. coriacea* (Ewart & Davies) McGill, AQ378406; *Do. falcata*

J.G.West, AQ033192; *Do. humifusa* Miq., AQ382119; *Do. lanceolata* F.Muell., AQ762508; *Do. oxyptera* F.Muell., AQ765213; *Do. rhombifolia* N.A.Wakef., CANB 369373; *Do. triangularis* Lindl., AQ399711; *Do. viscosa* Jacq., OTA02105.



**Figures 111–118.** *Distichostemon* and *Dodonaea*. Fig. 111. *Distichostemon barklyanus*, transmitted light microscopy (TLM) view of stomatal complexes and persistent trichome at bottom left. Note prominent basal cells (AQ777400; scale bar, 50  $\mu$ m). Fig. 112. *Distichostemon arnhemicus*, TLM view of stomatal complexes and persistent trichome at upper right. Note prominent basal cells (AQ334834; scale bar, 50  $\mu$ m). Fig. 113. *Distichostemon filamentosus*, TLM view of stomatal complexes and persistent trichome at bottom left. Note prominent basal cells (AQ030931; scale bar, 50  $\mu$ m). Fig. 114. *Distichostemon arnhemicus*, scanning electron microscopy (SEM) view of outer surface showing stomatal complexes amongst an irregularly raised surface (AQ598283, S-1319; scale bar, 20  $\mu$ m). Fig. 115. *Dodonaea humifusa*, TLM view of stomatal complexes with compound gland to left (AQ382119; scale bar, 50  $\mu$ m). Fig. 116. *Dodonaea oxyptera*, TLM view of stomatal complexes and persistent trichome with prominent basal cells at upper left (AQ765213; scale bar, 50  $\mu$ m). Fig. 117. *Dodonaea baueri*, TLM view of stomatal complex and two small persistent trichomes (AQ109113; scale bar, 50  $\mu$ m). Fig. 118. *Dodonaea lanceolata*, TLM view of stomatal complexes (AQ762508; scale bar, 50  $\mu$ m).

Ten species of *Dodonaea* were prepared, and all except one were found to be characterized by distinctive sessile multicellular glands which appear to be unique to *Dodonaea*. West (1984) reported that

‘the viscous nature of most species is a common feature in the genus and is usually associated with the presence of sessile, flat glands’. She reported multicellular hairs from two species (*Do. humilis*



Endl. and *Do. glandulosa* J.G.West), and only a few species (four) lacked glands. Most species are either fully or unevenly amphistomatic, with *Do. viscosa* the only hypostomatic species noted. The stomata are 21–33 µm long, and all species observed had an anisocytic stomatal construction, or a four-celled derivation of it. Epidermal cell walls and outer surfaces are smooth. The leaves range from glabrous (e.g. *Do. lanceolata*) to hirsute, with many persistent simple trichomes (e.g. *Do. oxptera*) or widely spaced simple persistent trichomes (*Do. baueri*, *Do. biloba*).

## DISCUSSION

The subfamilial taxonomy of Sapindaceae *s.s.* was established by Radlkofer (1890, 1933). His system was tested with information on pollen morphology by Muller & Leenhouts (1976), but only recently has molecular phylogenetics begun to seriously test these relationships (e.g. Harrington *et al.*, 2005). Some comments can be added in the light of the current study on epidermal morphology.

Many of the genera have a distinct epidermal morphology (see summary in Table 1), but some generalizations can be offered here. Most leaves of Sapindaceae are essentially hypostomatic with stomata restricted to the abaxial surface, but some have a narrow zone of stomatal complexes on either side of the midrib on the adaxial surface, sometimes extending along larger lateral veins, and a few species are truly amphistomatic. Typically, the guard cells are randomly oriented, surficial or slightly above and partly overlapping the surrounding contact cells. When viewed in TLM, this means that the anticlinal walls of the contact cells remain of normal thickness right up to the margins of the guard cells, and then slightly project over the outline of the guard cells (this feature was noted by Dilcher, 1974, fig. 15). Genera in tribe Cupanieae Blume tend to have this feature in combination with simply impressed guard cells with a thin overlying cuticle and without distinct enclosing walls. In general, Sapindaceae have simple, thin, outer stomatal ledges (remaining almost clear in stained specimens), and without any ornamentation except for some fine striations in some species. In terms of Wilkinson's (1979) pragmatic distinction into small (< 15 µm), medium (15–38 µm) and large (> 38 µm), most stomatal complexes in Sapindaceae are small to medium (although mostly at the small end of the medium class). A typical size range is 13–18 µm, but the largest reach 45 µm. Subsidiary cells are sometimes clearly distinguished, staining more deeply than ordinary epidermal cells, or they may not be distinguishable. The contact cell number varies from three to four and often up to seven in

some species. Networking is common in some species and present in many others, and some species are typified by papillae.

Certain characters have not been noted in Australasian Sapindaceae, including a paracytic stomatal construction, glandular lid cells, multicellular hair bases, deeply sunken or aligned stomatal complexes, complex outer stomatal ledges and robust ornamentation (other than papillae).

A few genera of Sapindaceae share characters which help to support phylogenetic relationships. Stellate trichomes are found in *Cossinia* and *Harpullia*, which are moderately closely related in Dodonoideae (= Dyssapindaceae), but also in *Dimocarpus* which is in Sapindoideae (= Eusapindaceae). The anisocytic stomatal arrangement and large prominent trichome base cells of *Distichostemon* and *Dodonaea* support their close relationship. The presence of papillae is restricted to Eusapindaceae but, within this group, it is widely spread.

A distinctive stomatal shape is found across several genera, in which the outline is almost a small, rounded rectangle, and the outer stomatal ledge is thin and simple. This shape is found in, for example, *Cupaniopsis* (Fig. 68), *Guioa* (Fig. 59), *Harpullia* (Fig. 47), *Lepiderema* (Fig. 63), *Lepidopetalum* (Fig. 94) and *Tristiropsis* (Fig. 21), but it cuts across several tribal boundaries.

A key is offered (Appendix) to distinguish some genera and groups of genera. Some genera, particularly those in tribe Cupanieae, probably cannot be distinguished solely on epidermal features.

It might be expected that some of the morphological variation within Sapindaceae reflects the local environment. A climatic analysis of species of Sapindaceae is beyond the scope of this work, but clearly the more or less evenly amphistomatic species with thick or persistent trichomes are *Diplopeltis*, *Distichostemon* and *Dodonaea*, which are all found in relatively drier open forests or shrublands. However, *A. tropicus* is found in semideciduous vine forest. There appears to be no obvious relationship between papillae and habitat, but clearly this requires detailed study. Most cuticles are reasonably robust, but the most delicate cuticle from the point of view of processing was that of *H. alata*, a rainforest species.

Of related interest to stomatal morphology is the determination of the stomatal density, and the more meaningful stomatal index (SI), parameters which are related to climate and atmospheric composition (e.g. Salisbury, 1927; Woodward, 1987; Beerling, 1999; Royer, 2003). Some species of Sapindaceae would make ideal candidates for study as their stomatal and epidermal cell outlines are clearly visible. However, SI is regarded as species specific, and well beyond the scope of this study. As examples taken from single

**Table 1.** Summary of some important character distributions at the generic level

	Stomatal distribution	Stomatal construction	Epidermal surface	Trichomes	Connectivity	Peristomatal rim	Epidermal cell walls
1. <i>Allophylus</i>	0	?	0	3	0	0	0
2. <i>Tristiropsis</i>	0	1	3	0, 1	0	0	0
3. <i>Atalaya</i>	0, 1	1, 2, 3	0, 1	0, 1, 4	0	0	0
4. <i>Ganophyllum</i>	0	1	0	0	0	0	0
5. <i>Alectryon</i>	0, 1	2, 3	0, 1, 2	0, 1, 4	0	0	0
6. <i>Lepisanthes</i>	0	3	0	3	0	0	0
7. <i>Castanospora</i>	0	2	1	4	0	0	0
8. <i>Diploglottis</i>	0	1, 3	0, 1	1, 7	1	0, 1	0
9. <i>Harpullia</i>	0	1	0	0, 2, 4	0	0	0, 1
10. <i>Cossinia</i>	0	2	3	2	0	0	0
11. <i>Dimocarpus</i>	0	2	1	2	0	0	0
12. <i>Dictyonera</i>	1	3	0	1, 4	0	0	0
13. <i>Guioa</i>	0	2, 3	0, 1, 2	0, 1	0	0, 1	0
14. <i>Lepiderma</i>	0	3	0	0, 1	1	0, 1	1
15. <i>Cupaniopsis</i>	0, 1	1, 2, 3	0, 1, 2, 3	0, 1, 4, 7	1	0	0
16. <i>Rhysofoechia</i>	0	3	0, 3	0, 1	0	0	0
17. <i>Jagera</i>	0	2, 3	2	3, 4	0	0	0
18. <i>Cnesmocarpon</i>	0	2	1	4	0	0	0
19. <i>Elattostachys</i>	1	2	0, 3	0, 6	0	0	0
20. <i>Sarcopteryx</i>	0	3	0, 1	0, 1	1	0	1
21. <i>Toechima</i>	0, 1	3	0	0, 4, 5	1	0	0
22. <i>Synima</i>	0	1	0	3, 4	0	0	0
23. <i>Sarcotoechia</i>	0	3	0	0, 1, 4	1	0	0, 1
24. <i>Lepidopetalum</i>	0	1	0	1	0	0	1
25. <i>Arytera</i>	0, 1	1	0	0, 4	0	0	1
26. <i>Mischarytera</i>	0, 1	3	0, 2	1, 4	1	0	0
27. <i>Mischocarpus</i>	0	1, 2, 3	0, 1, 2	1, 4, 7	0	0	0, 1
28. <i>Diplopeltis</i>	2	3	0	0, 4, 5	0	0	0
29. <i>Distichostemon</i>	2	0	0	4	0	0	0
30. <i>Dodonaea</i>	0, 2	0	0	0, 4	0	0	0

**Stomatal distribution** (0, hypostomatic; 1, partially amphistomatic; 2, amphistomatic).

**Stomatal construction** (0, anisocytic; 1, tangencytic; 2, cyclocytic; 3, actinocytic).

**Epidermal surface** (0, smooth; 1, papillae present; 2, prominent ridges on surface; 3, subdued ridges or striations on surface).

**Trichomes** (0, glabrous; 1, deciduous; 2, stellate; 3, balloon; 4, persistent simple; 5, multicellular; 6, glandular; 7, chained).

**Connectivity** (0, not networked; 1, networked).

**Peristomatal rim** (0, absent; 1, present).

**Epidermal cell anticlinal walls** (0, straight, curved or wavy; 1, distinctly sinuous).

locations on a leaf (several locations are needed for meaningful results), *M. macrobotrys* shown in Figure 101 has an SI value of about 0.19 ( $n = 290$ ) and *At. collina* shown in Figure 23 has an SI value of about 0.07 ( $n = 216$ ), giving an idea of the variation involved.

There is a wealth of fossil epidermal morphology becoming apparent in the Cenozoic of New Zealand. At present, something like 160 angiosperm cuticle morphologies can be distinguished in the early Miocene alone, and most are clearly not in the extant New Zealand flora. Some have clear affinities with the recent flora of Australia and New Caledonia, and it might be expected that some of the extant genera of Sapindaceae are among them. Pole (1996) identified one leaf with cuticle (CUT-Z-012) as Sapindaceae, although did not compare it with any particular genus. The present study suggests that, on the basis of the papillae, cyclocytic stomatal construction and the distinctive flattened and continuous ring of the guard cell cuticle (compare Pole, 1996: fig. 9G with Fig. 37 in the current work), it is *Alectryon*. Pole (2008) identified a further five cuticle parataxa as belonging to Sapindaceae, with three most closely resembling *Cupaniopsis*, and the other two with more general affinities to *Diploglottis*, *Rhysotoechia* and *Mischocarpus*, all in tribe Cupanieae.

### CONCLUSIONS

This study has reviewed the epidermal morphology of Australasian Sapindaceae, highlighting characters which make some species distinct, and attempting to find some generalities at the genus level. Some genera are distinct on the basis of epidermal features, but others, particularly those in tribe Cupanieae, tend to group together and cannot be distinguished on epidermal morphology alone. As the cuticle morphology of extant taxa becomes better known, and the fossil cuticle continues to be investigated, the evolution and biogeography of the Sapindaceae will gain a firmer temporal basis.

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## APPENDIX

## KEY TO DISTINGUISHING AUSTRALASIAN SAPINDACEAE GENERA USING EPIDERMAL CHARACTERS

1. Leaves essentially amphistomatic.....2
1. Leaves essentially hypostomatic, partially amphistomatic, or unknown (i.e. when dealing with fossil fragments) .....4
2. Stalked multicellular trichomes and falcate trichomes present, actinocytic.....*Diplopeltis*
2. Stalked multicellular trichomes absent, anisocytic.....3
3. Large simple trichomes with distinct ring of basal cells.....*Distichostemon*
3. Sessile multicellular glands present.....*Dodonaea*
4. Stomatal complexes very indistinct (cuticle very thin), balloon trichome present.....*Allophylus*
4. Stomatal complexes anisocytic.....*Distichostemon, Dodonaea*
4. Stomatal complexes cyclocytic.....5
4. Stomatal complexes tangencytic.....9
4. Stomatal complexes actinocytic.....11
5. Papillae present.....6
5. Papillae absent.....8
6. Papillae located only on subsidiary cells.....*Guioa*
6. Papillae located on epidermal and subsidiary cells.....7
7. Stellate trichomes present.....*Dimocarpus*
7. Stellate trichomes absent.....*Alectryon* (tribe Nephelieae), *Castanospora* (tribe Melicocceae) and *Cupaniopsis, Cnesmocarpon, Guioa, Mischocarpus* (tribe Cupanieae)
8. Stomatal complexes frequently networked.....*Cupaniopsis*
8. Stomatal complexes not networked.....*Atalaya, Ellatostachys, Guioa, Jagera, Mischocarpus* (all tribe Cupanieae) and *Alectryon* (tribe Nephelieae)
9. Stomatal complexes with distinctive curving tangential walls.....*Ganophyllum*
9. Stomatal complexes with more or less straight tangential walls.....10
10. Stomatal complexes often distinctly orthogonally tangencytic.....*Harpullia*
10. Stomatal complexes irregularly tangencytic.....*Arytera, Atalaya, Cupaniopsis, Diploglottis, Lepidopetalum, Mischocarpus, Synima*, (all tribe Cupanieae) and *Tristiropsis* (tribe Melicocceae)
11. Presence of distinctive combination of a simple trichome flanked by 2–3 balloon trichomes.....*Lepisanthes*
11. No distinctive combination of simple and balloon trichomes.....12
12. Epidermal cells markedly sinuous.....*Lepiderema*
12. Epidermal cells not markedly sinuous.....13
13. Stalked multicellular trichomes and/or falcate trichomes present.....*Diplopeltis*
13. Stalked multicellular trichomes and/or falcate trichomes absent.....*Atalaya, Cupaniopsis, Diploglottis, Guioa, Jagera, Lepiderema, Mischocarpus, Rhysotoechia, Sarcopteryx, Sarcotoechia, Toechima* (all tribe Cupanieae) and *Alectryon* (tribe Nephelieae).