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# Floral anatomy of *Thomandersia* (Lamiales), with particular reference to the nature of the retinaculum and extranuptial nectaries

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Received July 2004; accepted for publication April 2005

*Thomandersia* is an isolated genus that is currently unplaced in Lamiales. In the past it has been classified in Acanthaceae or Pedaliaceae, on the basis of intuitive assessments of a limited number of morphological characters. Recent molecular sequenced-based phylogenies have suggested a relationship to Bignoniaceae, Schlegeliaceae or Verbenaceae. Here we present new observations of the floral anatomy of *Thomandersia*, with particular emphasis on the structure of the retinaculum, a character shared with Acanthaceae, and calyx nectaries, which may be shared with other families in Lamiales. The morphological and anatomical characters of *Thomandersia* are discussed in the context of recent phylogenetic hypotheses for Lamiales, with the aim of identifying potential primary and secondary homologies between *Thomandersia* and related families in Lamiales. We find that *Thomandersia* shares a range of characters with each of the families to which it might be sister-group, and that some of these primary homologies must therefore be homoplastic. In particular, if the topology based on molecular sequence data is correct, the retinacula of *Thomandersia* and Acanthaceae are homoplastic and represent an example of parallel morphological evolution. © 2005 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2005, 149, 469–482.

ADDITIONAL KEYWORDS: Acanthaceae – Africa – flowers – systematics – Thomandersiaceae.

## INTRODUCTION

*Thomandersia* Baill. consists of six species of trees and shrubs from western and central Africa (Baillon, 1891; De Wildemann & Durand, 1898–1902; De Wildemann, 1905, 1906; Heine, 1966). The genus is distinguished by its conspicuously swollen calyx nectaries, and fruits in which the seeds are supported by retinacula (Heine, 1963; Bouquet, 1969; Corner, 1976). *Thomandersia* belongs in the large asterid eudicot order Lamiales, although its precise placement within the order remains uncertain (Scotland & Vollesen, 2000). According to present estimates, Lamiales include c. 22 000 species, which represents approximately 12% of all eudicots (Stevens, 2001) and encompasses a wide range of morphological diversity.

Previous classifications of Lamiales have mostly focused on selected morphological characters and have assigned *Thomandersia* to different groups depending on the particular characters emphasized (e.g. Bentham, 1876; Bremekamp, 1942; Heine, 1966; Sreemadhaven, 1976). Most frequently, *Thomandersia* has been classified in Acanthaceae (e.g. Bentham, 1876; Baillon, 1891; Lindau, 1894, 1897; Burkill & Clarke, 1899; Thiselton-Dyer, 1906; Hutchinson & Dalziel, 1931; Heine, 1963, 1966), although its morphological similarities with this family are controversial (Bremekamp, 1942; Heine, 1966). Recent investigations suggest that *Thomandersia* is sufficiently distinct in morphological and molecular terms to merit family status as Thomandersiaceae (Sreemadhaven, 1976, 1977; Wortley, 2004).

Classification of *Thomandersia* in Acanthaceae was based on the presence of a retinaculum in all species of *Thomandersia*. The retinaculum is a lignified, hook-

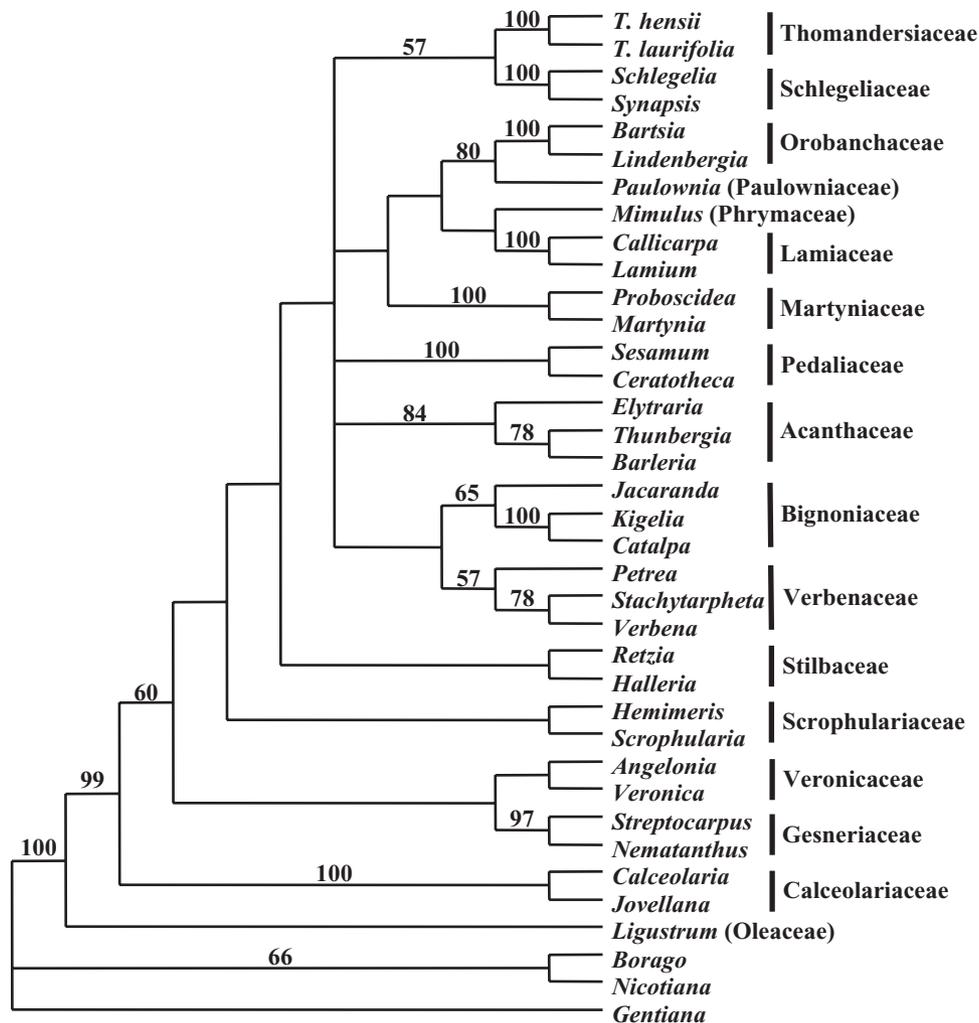
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like structure supporting the seed, which is thought to play a role in seed expulsion (Bremekamp, 1926; Corner, 1976; Witztum & Schulgasser, 1995). It is otherwise regarded as unique to Acanthoideae–Acanthaceae (Lindau, 1897; Leonard, 1951; Long, 1970; Judd *et al.*, 1999).

Other sources of evidence indicate that *Thomandersia* should be excluded from Acanthaceae. Lindau (1897) retained *Thomandersia* in Acanthaceae, but recognized it as anomalous in pollen morphology and in the presence of a staminode. Bremekamp (1942) transferred it to Pedaliaceae, largely on the basis of pollen morphology (Bremekamp, 1942; Raj, 1961) but also citing its small, scattered bracts, minute bracteoles and tardily dehiscent capsules (as opposed to the explosive capsules of Acanthaceae). He also

questioned whether *Thomandersia* had true retinacula, instead describing these structures as ‘excrescences of the placenta’.

Analyses of molecular and morphological data suggest that both Acanthaceae and Pedaliaceae are well-supported monophyletic groups to the exclusion of *Thomandersia* (Wortley, 2004). Molecular and morphological phylogenetic analyses data implicate variously Bignoniaceae, Verbenaceae and most frequently Schlegeliaceae as more likely sister-groups of *Thomandersia* (e.g. Fig. 1). Interestingly, in one recent study, Schlegeliaceae have also been linked with Acanthaceae (Bremer, Friis & Bremer, 2004). In light of this contradictory evidence it is important to re-examine in detail the morphological and anatomical characters of *Thomandersia* in the context of other Lamiales, to



**Figure 1.** Strict consensus of three most parsimonious trees generated by parsimony analysis of combined *ndhF* and *rbcL* gene sequences and morphological data for 37 exemplar taxa in Lamiales, showing bootstrap support values greater than 50%. From Wortley *et al.* (2005); family circumscriptions from Olmstead *et al.* (2001). Acanthaceae and Pedaliaceae are strongly supported families, Bignoniaceae and Verbenaceae less so; *Thomandersia* is tentatively linked to Schlegeliaceae.

assess their underlying homology. In particular, the structure of the retinaculum in *Thomandersia* and Acanthaceae requires thorough investigation. Other investigations of floral structure in Acanthaceae and other Lamiales have not focused on this aspect (e.g. Schönenberger & Endress, 1998; Schönenberger, 1999; Manktelow, 2000; Moylan, Rudall & Scotland, 2004). Here we present new observations of inflorescence morphology and floral anatomy of *Thomandersia*. Particular attention is paid to two distinctive characters of the genus, retinacula and calyx glands, and the results are discussed in the context of the morphology and anatomy of all candidates for the sister-group of *Thomandersia* in Lamiales.

## MATERIAL AND METHODS

### TAXON SAMPLING

Anatomical investigations were conducted on all species of *Thomandersia*, and representatives of possible relatives within Lamiales: Bignoniaceae, Pedaliaceae, Schlegeliaceae, Verbenaceae and a range of Acanthaceae, including those with retinacula (Acanthoideae) and without (represented by Thunbergioideae). The subfamily Acanthoideae comprises two tribes, Ruellieae and Acantheae. *Thomandersia* has previously been classified with members of Ruellieae

(Bentham, 1876; Lindau, 1897), but shares some morphological characters with Acantheae, such as colpate pollen and a lack of cystoliths (Scotland & Vollesen, 2000). Therefore, representatives of both Acantheae and Ruellieae were examined here.

The majority of observations for *Thomandersia* were made on material of *T. hensii* collected in the Central African Republic. Material of other Lamiales was obtained from living collections at the Royal Botanic Gardens, Kew (HK) and elsewhere. Observations were made on dried collections and spirit material from the herbaria of BM, BR, FHO, K, MO, P and WAG (Table 1).

### METHODS

Fresh plant material was fixed in formalin acetic acid alcohol (FAA) and stored in 70% aqueous ethanol. Dried material was softened in boiling water and taken through an aqueous ethanol series to 70% aqueous ethanol.

For light microscope observations, material was embedded in Paraplast using standard methods, and sectioned using a Reichert Jung 2040 rotary microtome. Sections (6–12.5 µm thickness) were stained in safranin and Alcian blue, and mounted in DPX (distyrene, the plasticizer tricresyl phosphate, and xylene).

**Table 1.** Specimens examined

Species and authority	Voucher/collection	Herbarium	Source country
<i>Asystasia calycina</i> Benth.	AW2	FHO	HK
<i>Ballochia rotundifolia</i> Balf.f.	AW3	FHO	HK
<i>Petrea volubilis</i> L.	K spirit collection #16936	K	–
<i>Pseuderanthemum tunicatum</i> (Afzel.) Milne-Redh.	AW1	FHO	HK
<i>Ruellia tuberosa</i> L.	AW4	FHO	HK
<i>Schlegelia violacea</i> Griseb.	AW7	FHO	HK
<i>Thomandersia anachoreta</i> Heine	<i>Aké Assi</i> s.n. (1964)	MO	Côte d'Ivoire
	<i>Baldwin, Jr.</i> 11264	K	Liberia
	<i>Geerling &amp; Bokdam</i> 2436	K	Côte d'Ivoire
<i>Thomandersia butayei</i> De Wild.	<i>Gillard</i> 235	BR	Democratic Republic of Congo (DRC)
	<i>McPherson</i> 16790	MO	Gabon
<i>Thomandersia congolana</i>	<i>Breteler</i> 6942	BR	Gabon
De Wild. & T.Durand	<i>Claessens</i> s.n. (1921)	BR	DRC
<i>Thomandersia hensii</i>	<i>Harris</i> s.n. (2000)	–	Central African Republic
De Wild. & T.Durand	<i>Onochie</i> 9314	BM	Cameroon
	<i>Sapin</i> s.n. (1912)	BR	DRC
	<i>Vanderyst</i> 2964	BR	DRC
<i>Thomandersia laurentii</i> De Wild.	<i>Robyns</i> 4279	BR	DRC
<i>Thomandersia laurifolia</i>	<i>Bos</i> 6080	K	Cameroon
(T.Anderson ex Benth.) Baill.	<i>de Wilde</i> 9400	WAG	Gabon
	<i>Talbot</i> 381	BM	Nigeria
	<i>Wieringa</i> 3883	WAG	Gabon
<i>Thunbergia grandiflora</i> Roxb.	AW6	FHO	HK

Photomicrographs were taken using a Leica DMLB microscope fitted with a Leica MPS60 camera and a Leitz Dialux 20EB microscope fitted with a Fuji S1 digital camera.

For scanning electron microscope (SEM) examination, fixed flower material was dehydrated in absolute ethanol, then critical-point-dried using a Balzer CPD 030, mounted onto SEM stubs on double-sided Sello-tape, coated with gold using an Emscope SC 500 sputter coater, and examined using a Hitachi S-4700 dual detector field-emission microscope, at an accelerating voltage of 2 kV and 10  $\mu$ A, taking a 50 : 50 mix of signals from the upper and lower detectors.

## OBSERVATIONS

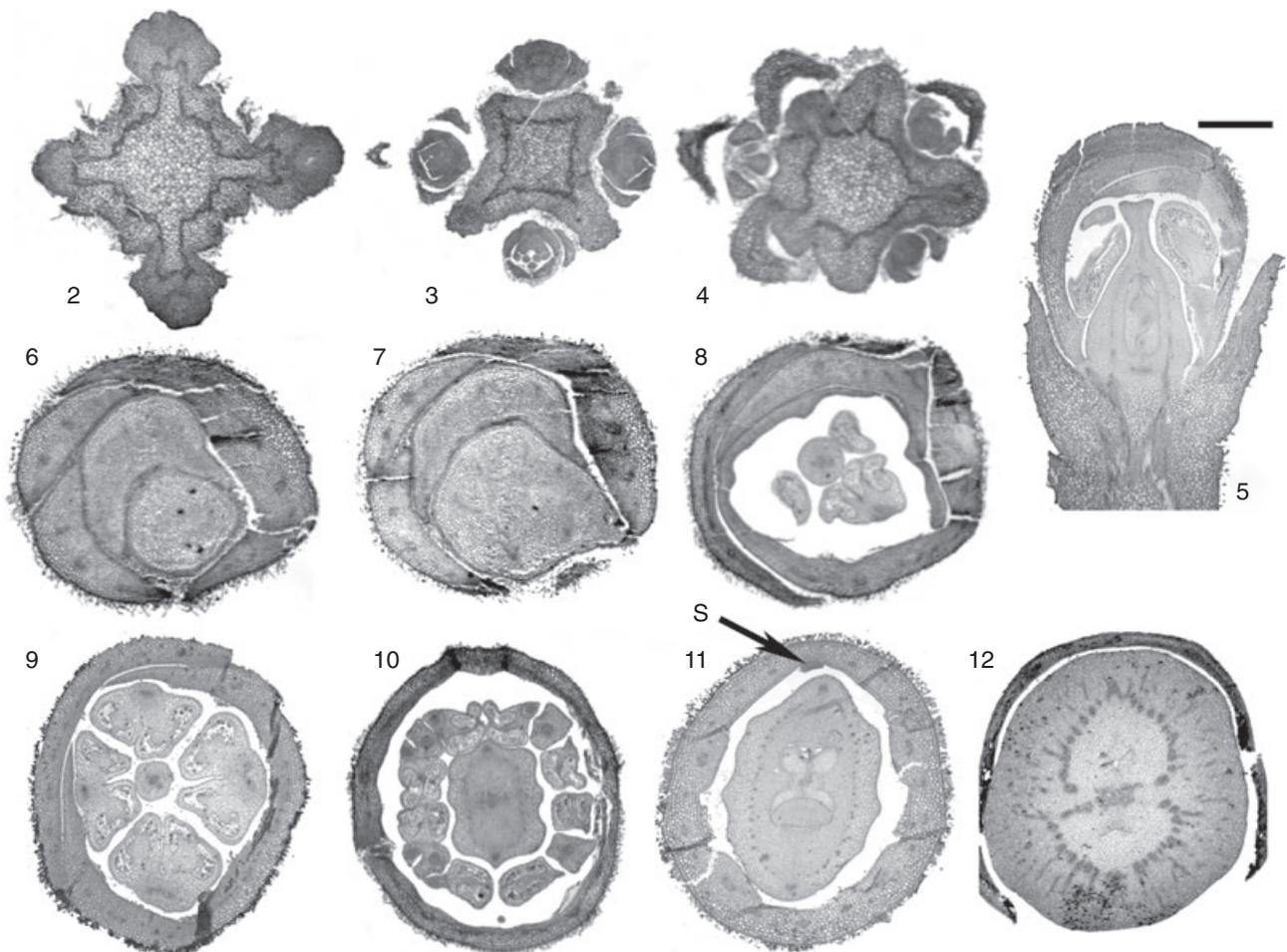
### INFLORESCENCE MORPHOLOGY

*Thomandersia* inflorescences are terminal, subterminal or axillary, indeterminate and superficially race-

mose, with sessile or pedicellate flowers. Each flower is preceded by two bracteoles and subtended by a small abaxial bract.

### FLORAL ANATOMY (FIGS 2–12)

The inflorescence axis of *Thomandersia* contains a single ring of vascular traces, from which a subsidiary ring branches into each flower (Fig. 2). The flowers are arranged irregularly or, more commonly, in whorls of three or four. Each floral vascular trace diverges from the main axis above the floral bract. In the pedicel, four separate traces diverge from the floral ring: two lateral traces supply the bracteoles and two traces the extranuptial nectary. The next whorl of bracts, flowers and their vascular traces diverge from the main axis at an angle of 90° to those of the previous whorl (Fig. 3). Toward the tip of the inflorescence, the bracts and bracteoles become increasingly prominent



**Figures 2–12.** *Thomandersia hensii*, inflorescence and floral anatomy. 2–4. Serial transverse sections (proximal to distal) through inflorescence axis. 5. Longitudinal section of flower along abaxial–adaxial axis. 6–12. Serial transverse sections (distal to proximal) through bud. *Abbreviation:* s, staminode. Scale bar = 0.5 mm.

relative to the size of the floral buds (Fig. 4); accessory floral buds are present in bract axils.

The calyx of all *Thomandersia* species is thick, leathery and approximately campanulate, with five more or less equal lobes. It is accrescent in fruit and, as it matures, the epidermis becomes red-staining, suggesting lignification.

The corolla is zygomorphic, pentamerous and bilabiate. It is adaxially swollen (gibbous) at the base. The upper labium consists of two fused petals and the lower one three. The corolla is supplied by a ring of 15 vascular traces, three to each lobe, in addition to those leading to the androecium. Aestivation does not conform to a recognized pattern at any stage of maturity; the position of the petals relative to one another varies along their length. Thus, aestivation does not correspond entirely to either the cochlear (one lobe wholly outside, one wholly inside, three half-overlapped) or the quincuncial (two lobes wholly outside, two wholly inside, one half-overlapped) patterns (Weberling, 1992; Scotland, Endress & Lawrence, 1994). In bud, the large abaxial corolla lobe entirely surrounds the two lateral lobes and overlaps the adaxial lobes (Figs 6–8). In sections just proximal to the corolla tip (Fig. 6), the abaxial lobe is wholly outside, the two lateral lobes wholly overlapped, one adaxial lobe wholly outside and the other half-overlapped. At this point aestivation corresponds to a quincuncial pattern. More proximally (Figs 7, 8), the two adaxial lobes of the upper labium are fused together and the abaxial lobes are fused with the two lateral lobes in turn. These form the lower labium, which lies inside the upper labium at this level. At the base of the flower (Figs 10–12), the two labia are united in a single tube.

*Thomandersia* has five androecial members which alternate with the corolla lobes at their bases. There are four didynamous fertile stamens (Fig. 9) and a single adaxial staminode (Fig. 11). All five androecial members are fused to the corolla tube for part of their length. The stamens each contain a single vascular bundle. The staminode is minute (Fig. 11), and lacks vascular tissue in the free part. The anthers are bithecate.

The gynoecium of *Thomandersia* is superior (Fig. 5). The pistil is bicarpellary and syncarpous. There are two rings of vascular bundles, meeting in the central (ventral) septum, each supplying one side of the dorsal ovary wall (Fig. 12). The ovary wall is thick, extremely so in *T. hensii*. The dorsal vascular bundles of both carpels pass into the style. The ovary wall of *Thomandersia* is distinctively thick and well vascularized, and ripens into a woody pericarp with a red-staining epidermis.

The style is solid with two vascular traces and a central core of loosely packed transmitting tissue which extends to the interior surface of the carpels.

In *Thomandersia* the base of the gynoecium is surrounded by a dark-staining nectary region, which is well supplied with phloem-rich vasculature originating from the dorsal carpellary traces (Fig. 12).

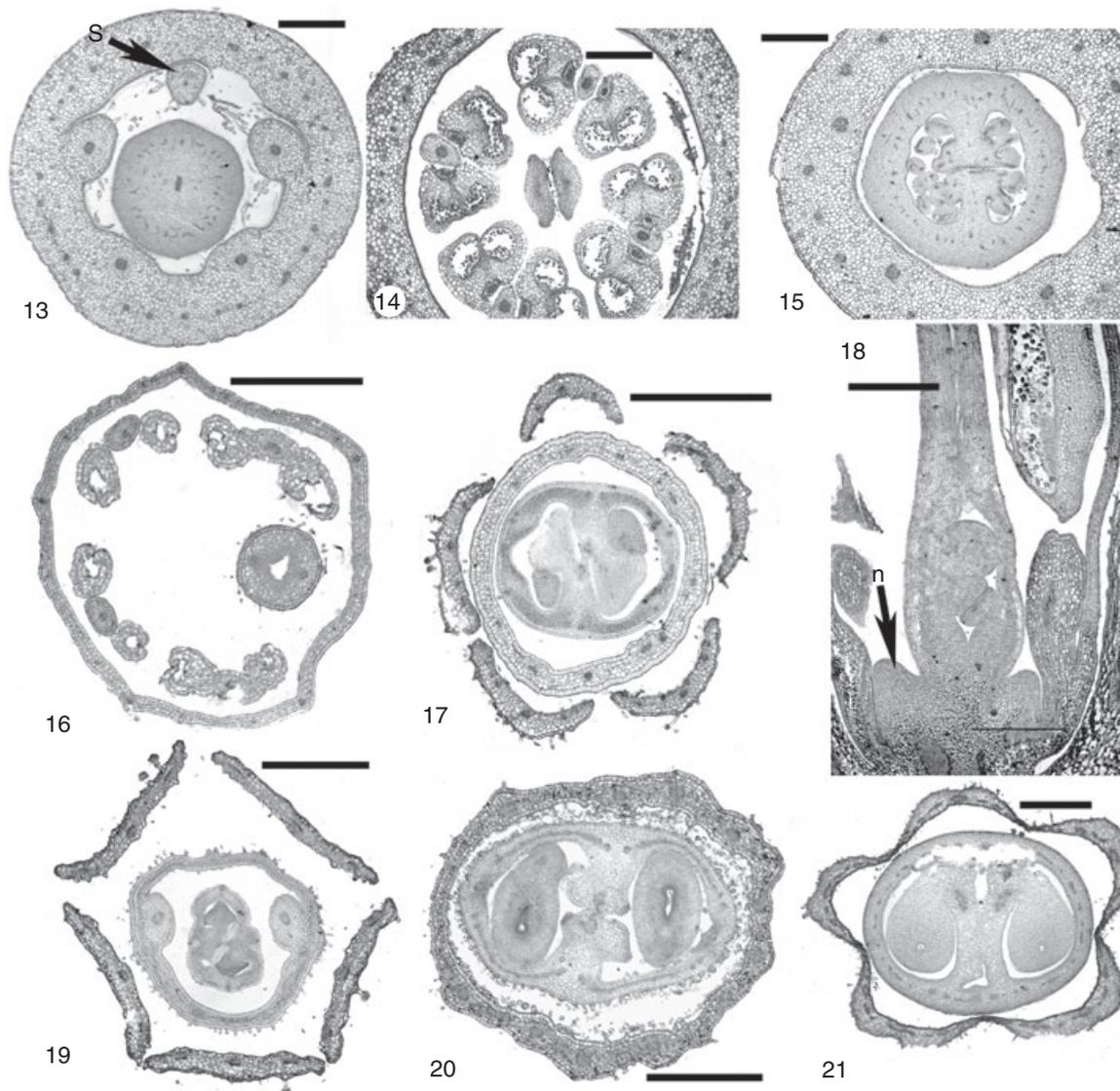
#### OVULE, OVARY AND SEED

One to three ovules are borne, one above the other, in each locule of the ovary (Fig. 22). Ovules are usually attached at alternate sides and held in opposing directions (Fig. 24). Placentation is axile and the placentas are enlarged and crescent-shaped in transverse section, spreading inside the ovary wall in the spaces between the ovules (Fig. 23). The funicles are very short and broad and the demarcation between funicle and placenta is indistinct; tissues between the two are continuous. The ovules are approximately hemianatropous. In ovules of *Thomandersia* the nucellus is orientated at right-angles to the funicle and the embryo sac held horizontally at all stages, from young buds to anthesis (Figs 23, 24). At the chalazal end, the nucellus forms a distinct hypostase of suberized cells, in which the ventral vascular supply of the carpel terminates. The ovules have a single integument.

After fertilization, the gynoecium of *Thomandersia* matures into a woody, bilocular capsule, which dehisces loculicidally (but not explosively, as in *Acanthaceae*), each valve containing 1–3 seeds (Fig. 27A). The seeds are roughly spherical with a large hilum (approximately 2 mm long) left by the broad funicular attachment. As previously observed (Sreemadhaven, 1976), there is no endosperm present in mature seeds.

#### RETINACULA (FIGS 25, 26, 28–32)

In the capsule of all *Thomandersia* species there is a hook-shaped retinaculum basally surrounding each seed. The retinaculum develops rapidly, between the placenta and ovule, late in the development of the carpel. It remains attached to the capsule after dehiscence. Retinacula are absent from flower buds, and are only found associated with seeds that develop to maturity (frequently one or more are aborted), although the placentas of abortive ovules develop normally. This indicates that the retinaculum develops from the funicle, a structure that is associated with the seed rather than the placenta. Transverse sections through a retinaculum (Figs 25, 26) show that it diverges from the funicle distally to the hilum (where a complex vascular bundle passes into the seed, which may be identified by the large cells of the testa); this confirms that it is unlikely to be a placental tissue. Towards its tip (Fig. 26) the retinaculum contains no vascular bundles and consists of uniform parenchyma cells. As the fruit matures, the retinaculum differentiates into two layers: a blue-staining outer layer and a red-staining one adjacent to



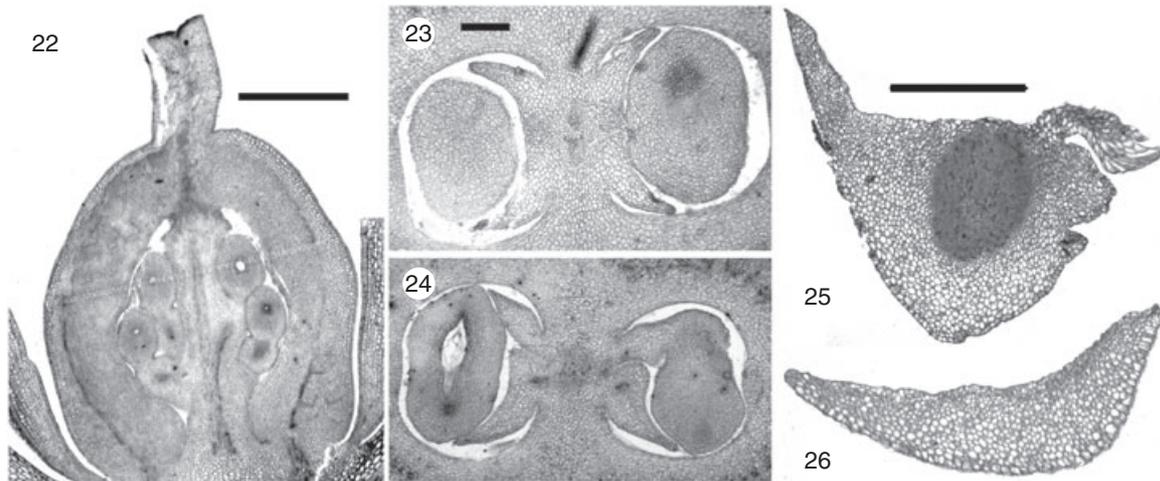
**Figures 13–21.** Sections of flowers of Lamiales (all transverse, except (18), longitudinal, across adaxial–abaxial axis). 13–15. *Schlegelia violacea* Griseb. (Schlegeliaceae). 16. *Ruellia tuberosa* L. (Acanthaceae). 17. *Pseuderanthemum tunicatum* (Afzel.) Milne-Redh. (Acanthaceae). 18. *Thunbergia grandiflora* Roxb. (Acanthaceae). 19. *Ballochia rotundifolia* Balf.f. (Acanthaceae). 20. *Asystasia calycina* Benth. (Acanthaceae). 21. *Petrea volubilis* L. (Verbenaceae). Abbreviations: n, nectary; s, staminode. Scale bars = 0.5 mm.

the seed, suggesting cell-wall lignification. In mature capsules, the retinaculum is approximately 5 mm long and 1.5 mm wide, narrowing to 1 mm at the tip.

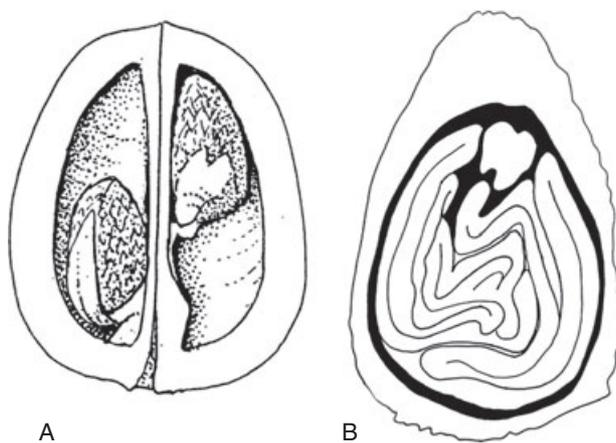
#### EXTRANUPTIAL NECTARY (FIGS 34–37)

In all species of *Thomandersia* the base of the calyx bears 1–2 conspicuous swellings, particularly obvious in bud, 1–2 mm in diameter and depth, between the two abaxial lobes. This tissue is richly vascularized, supplied by a branch of the main vascular ring in the pedicel, and contains a multicellular, sometimes

multipartite gland, approximately 1 mm long (Figs 34, 35). In *T. hensii*, *T. butayei*, *T. congolana*, *T. laurentii* and *T. laurifolia* there is always a single swelling, although in some specimens of *T. hensii* it has been found to contain two distinct glands with separate vascular supplies (Fig. 36), and in *T. congolana* two ostioles are sometimes observed (D. Champluvier, pers. comm.). In *T. anachoreta* there are always two swellings, each containing a gland; each gland has a separate ostiole. In *T. hensii* the opening is a narrow channel; in *T. anachoreta* it is broader and cup-shaped. The glands are composed of clearly



**Figures 22–26.** *Thomandersia hensii*. 22. Longitudinal section of gynoecium, cut across adaxial–abaxial axis. 23, 24. Transverse sections of carpels in bud (23) and flower just prior to anthesis (24). 25, 26. Serial transverse sections of young retinaculum from base to tip. Scale bars: in 22 = 0.5 mm, in 23 (for 23 and 24) = 100  $\mu$ m, in 25 (for 25 and 26) = 0.5 mm.



**Figure 27.** *Thomandersia hensii*, drawings of fruit and seed. A. Capsule, single valve just after dehiscence, showing seeds and retinacula (drawing by R. Wise). B. Longitudinal section of seed.

defined cell layers. A central cavity is bounded by a cuticle and surrounded by dark-staining, columnar epithelial cells, which are probably secretory. The secretory cells are surrounded by a single layer of large, colourless cells, possibly a barrier layer as in other extranuptial nectaries (Schnepf, 1969; Subramanian & Inamdar, 1989). Surrounding this is a region of smaller, dark-staining cells containing starch grains, around which the vascular trace passes.

## DISCUSSION

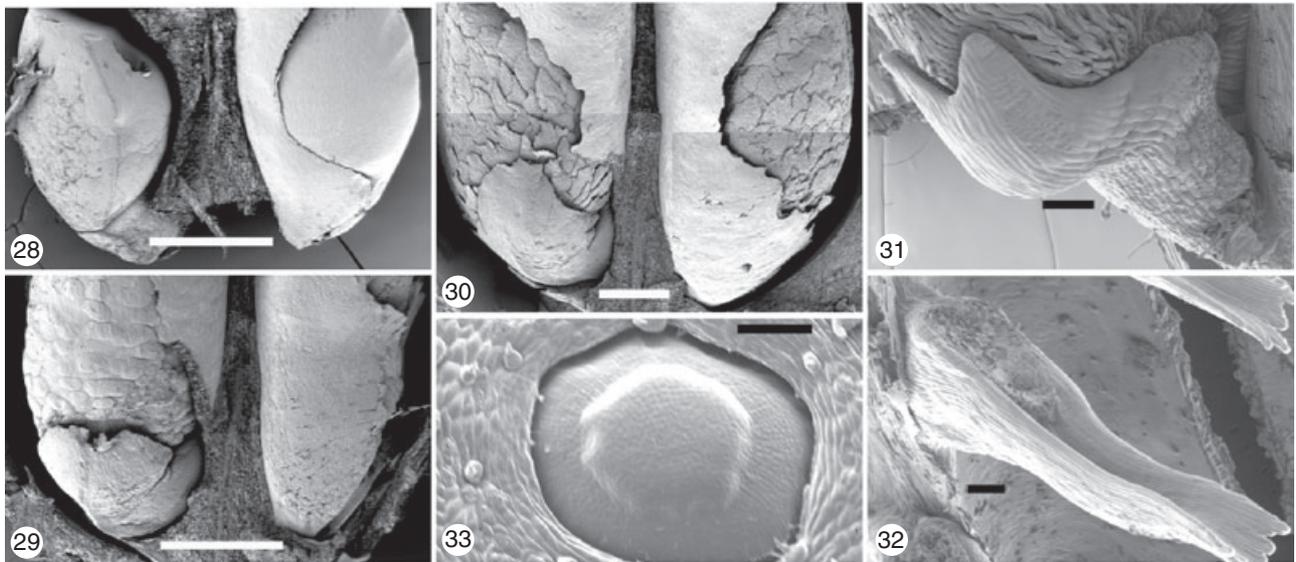
In common with many other eudicots, Lamiales are characterized by the possession of pentamerous flow-

ers, a single syncarpous style, anatropous ovules and cellular endosperm formation. Additional characters that unite the order (but may be reversed in more derived groups) include a distinct, synsepalous calyx and sympetalous corolla, dorsifixed anthers, gynoecium surrounded by a vascularized disc nectary, unitegmic ovules with a hypostase, and both micropylar and chalazal endosperm haustoria (Yamazaki, 1974; Cantino, 1982; Wagenitz, 1992; Judd, Sanders & Donoghue, 1994; Stevens, 2001). In this context, the characters described for *Thomandersia* can each be interpreted in three ways: (1) as plesiomorphies of Lamiales, (2) as autapomorphies of *Thomandersia* or (3) as primary homologies shared with potential sister-groups. They are discussed here in comparison with potential sister-groups.

## INFLORESCENCE MORPHOLOGY AND FLORAL ANATOMY

The floral arrangement of *Thomandersia* indicates that its inflorescence should be interpreted as a reduced indeterminate thyrses (Weberling, 1992). Its calyx shows characteristics of various Lamiales, including *Schlegelia*, some Verbenaceae and some Bignoniaceae. *Schlegelia*, in particular, has a thickened, leathery and richly vascularized calyx with an epidermis that stains red.

A gibbous corolla base is a relatively uncommon character that is also displayed by some Bignoniaceae (e.g. *Eccremocarpus*) and Pedaliaceae (e.g. *Sesamothamnus*). Corolla aestivation in *Thomandersia* does not exactly parallel that of any Acanthaceae (Scotland *et al.*, 1994), but this aspect is poorly known in most other Lamiales.



**Figures 28–33.** Scanning electron micrographs showing retinacula (28–32) and calyx gland (33). 28–30. *Thomandersia hensii*, developing ovary (placenta removed from left carpel in each case, viewed perpendicular to adaxial–abaxial axis). 31. *Ruellia tuberosa* (Acanthaceae), emergence of retinaculum from funicle. 32. *Pseuderanthemum tunicatum* (Acanthaceae), retinaculum, with seed removed. 33. *Schlegelia violacea* (Schlegeliaceae), calyx surface showing gland. Scale bars: in 28 = 500  $\mu$ m, in 29, 30 = 1 mm, in 31–33 = 100  $\mu$ m.

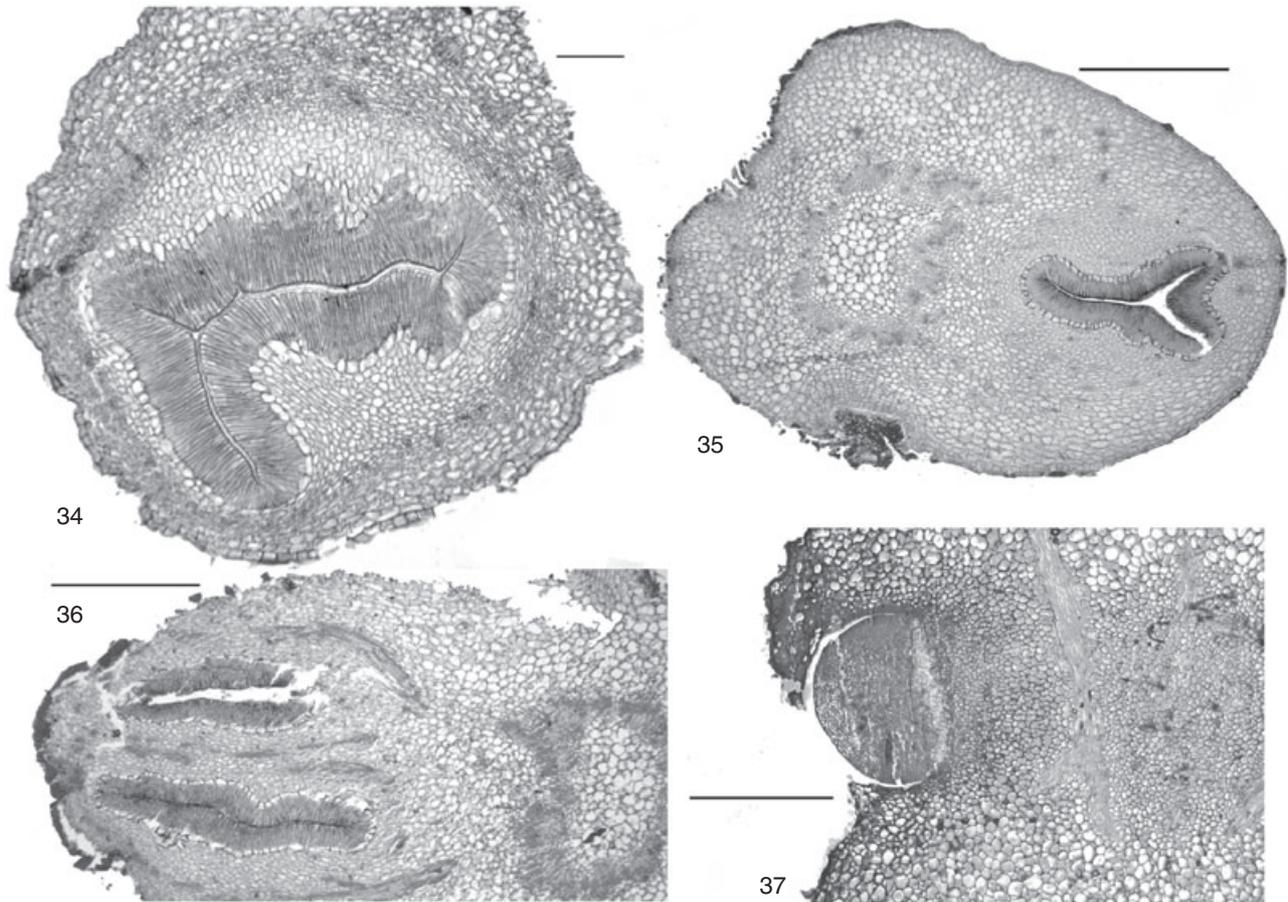
The didynamous androecial arrangement present in *Thomandersia*, with four fertile stamens in unequal-sized pairs, is common in other Lamiales, including Acanthaceae, Bignoniaceae, Pedaliaceae, Schlegeliaceae and Verbenaceae (Figs 13–21). As in *Thomandersia*, the staminode of *Petrea* (Verbenaceae) lacks vascular tissue, whereas staminodes of *Schlegelia* (Fig. 13) and *Eccremocarpus* are vascularized. By contrast, staminodes are entirely absent from flowers of many Acanthaceae (Endress, 2001), although they are present at least in Thunbergioideae (Schönenberger & Endress, 1998). In *T. hensii*, the staminode is flanked by a row of hairs on either side.

The pistil of *Thomandersia* is typical of many Lamiales. In Acanthaceae the gynoecium is also bilocular, and (sometimes only proximally) syncarpous, but contains only a single ring of discrete vascular bundles. In Bignoniaceae the gynoecium may be bilocular or secondarily unilocular, but in species where it is bilocular it contains vascular bundles in the septum (i.e. there are two rings of vascular bundles in the gynoecium, as in *Thomandersia*). In Verbenaceae the ovary is usually bilocular, syncarpous and subdivided by a false septum into four locules. Sometimes (e.g. in *Petrea*) the ovary is bilocular (probably secondarily: the aborted locule can be seen in transverse section as a small cavity; Fig. 21). In Pedaliaceae the ovary may also be 2–4-locular. In Schlegeliaceae the gynoecium is bilocular and syncarpous (Fig. 15), with each locule surrounded by a ring of vascular traces. The thickened ovary wall

is similar to that of Schlegeliaceae and Verbenaceae (Rueda, 1994). In *Schlegelia* the ovary wall is thickened and richly vascularized (Fig. 15).

A solid style is the commonest condition in Lamiales. In Acanthaceae the style may either be solid, e.g. in *Pseuderanthemum*, or hollow, usually where carpel fusion is incomplete, as in *Thunbergia* and *Ruellia*. In Verbenaceae the style may also be proximally hollow. In Schlegeliaceae the style has a central core of loosely packed transmitting cells continuous with the septum. In *Thomandersia*, by contrast, transmitting tissue extends from the interior margin of the locules.

Gynoecial nectaries similar to those of *Thomandersia* (i.e. a proliferation of gynoecial tissues supplied by the main carpellary vascular traces) are found in several other Lamiales, including Pedaliaceae, Verbenaceae and Schlegeliaceae. Indeed Gentry (1980) distinguished Schlegeliaceae from other Bignoniaceae (in which they were formerly classified) primarily on the basis of this character. In most Bignoniaceae and Pedaliaceae, the floral nectary takes the form of an annular disc, distinct from the gynoecium, supplied by its own ring of vascular traces. In Acanthaceae not all species have a floral nectary; in species where there is a nectary it is also distinct from the pistil and separately vascularized (e.g. *Thunbergia*; Fig. 18). Floral nectaries are widespread in dicotyledons and usually considered plesiomorphic in Lamiales (e.g. Lu, 1990). Therefore, their absence from many Acanthaceae, like the absence of staminodes and vascular bundles in the



**Figures 34–37.** Calyx glands. 34–36. *Thomandersia hensii*. 37. *Schlegelia violacea*. Scale bars = 0.5 mm.

septum of the gynoecium in this family, may be indicative of its highly derived position (Carlquist & Zona, 1988; Endress, 2001). Acanthaceae, together with Lamiaceae, Orobanchaceae, *Mimulus* and *Paulownia*, is sometimes suggested to form a group nested within the rest of Lamiales including *Thomandersia* (Endress, 2001; Bremer *et al.*, 2002).

The 1–3 ovules per locule in *Thomandersia* are hemianatropous like those of some Bignoniaceae; most other Lamiales have anatropous ovules. Ovule number in *Thomandersia* was considered by previous authors to be constant at two per locule (e.g. Bremekamp, 1942; Heine, 1966). In Acanthaceae there may be two (e.g. *Thunbergia*; Fig. 18) to multiple (e.g. *Ruellia*) ovules per carpel. In other Lamiales, ovules are usually multiple. A single integument is common to all Lamiales.

Fully syncarpous, bilocular ovaries are usually characterized by axile placentation, as in *Thomandersia*. In Acanthaceae, placentation is predominantly axile but distally parietal where the carpels are not fully fused (e.g. in *Pseuderanthemum*). In some Bignoni-

aceae, such as *Eccremocarpus*, there are two bilobed, parietal placentas. The distinctively expanded, crescent-shaped placentas of *Thomandersia* may be a unique feature of the genus, although there is also a placental swelling above the ovules in *Petrea volubilis* (Verbenaceae), and in *Schlegelia violacea* (Schlegeliaceae) the placenta is also expanded, spreading inside the carpels beyond the point at which it is fused to the septum (Fig. 15).

The spherical seeds of *Thomandersia* differ from those of most Bignoniaceae, which are usually winged, and Acanthaceae, which are usually flattened discs, although *Thunbergia* has spherical seeds with a large hilum. Endosperm is also lacking from mature seeds of Bignoniaceae, most Verbenaceae and all subfamilies of Acanthaceae except Nelsonioideae, but present in seeds of Schlegeliaceae and Pedaliaceae (Stevens, 2001). The cotyledons are distinctively folded (Fig. 27B); the only other families of Lamiales in which folded cotyledons have been reported are Phrymaceae and Acanthaceae (Schwarzbach & McDade, 2002).

## RETINACULUM

A retinaculum is associated with seeds of both *Thomandersia* and subfamily Acanthoideae (Acanthaceae), but is absent from the basal branches of Acanthaceae: Mendoncioideae, Nelsonioideae and Thunbergioideae (Bremekamp, 1965; Long, 1970).

There are three possibilities for the origin of the retinaculum in Lamiales: it may be (1) a true secondary homology of a *Thomandersia*–Acanthoideae clade, (2) a primary homology but not secondary homology derived from a common ancestral state (De Pinna, 1991) or (3) the result of convergent evolution from a different precursor state in the two taxa. Primary homology may be tested according to the criterion of similarity (Rieppel & Kearney, 2002), based upon detailed structural investigation; secondary homology is tested by congruence with the distribution of other characters on a phylogeny (Patterson, 1982; De Pinna, 1991). To determine whether retinacula are potentially homologous, or merely analogous, as proposed by Bremekamp (1942), their similarity in structure, development and position must be assessed. Topographical position is examined relative to associated structures, in this case the placenta, ovule and funicle. In *Thomandersia* the retinaculum develops, after fertilization, from the funicle (Fig. 29) and lies between the placenta and ovule. In Acanthaceae it also emerges at the distal end of the funicle, rather than the placenta (Fig. 31). In both cases the retinaculum remains attached to the fruit following dehiscence and seed expulsion. In these respects the retinacula of *Thomandersia* and Acanthaceae are topographically correspondent funicular outgrowths.

Retinacula of *Thomandersia* and Acanthaceae differ in shape and size: those of *Thomandersia* are broad and flat, whereas in Acanthaceae they are narrower and U-shaped in cross-section. However, these differences could be attributed to constraints imposed by the shape of the adjacent developing seed. In *Thomandersia* the retinaculum is constrained to lie flat between the surface of the spheroid seed and the carpel wall, whereas in Acanthaceae the seeds are usually disc-shaped and the retinaculum, lying along one edge of the seed, is forced into the shape of a channel. The retinacula of *Thomandersia*, up to 5 mm long and 1.5 mm wide, are larger than those of many Acanthaceae, but there is a broad size range across Acanthaceae as a whole, from rudimentary in *Nelsonia* and *Elytraria* to 3 mm long in *Trichanthera* (Mohan Ram & Masand, 1963; Rosales, 1997).

The retinacula of *Thomandersia* and Acanthaceae are histologically similar, comprising a mass of small parenchyma cells with no vascular tissue. There is an epidermal layer of larger, red-staining cells which may indicate lignification associated with the stiffening of

the structure. However, in Acanthaceae (at least in *Ruellia*) the uniseriate red-stained layer extends around the entire perimeter of the retinaculum, whereas in *Thomandersia* it is multiseriate and confined to the inner epidermis.

Retinacula develop late in the maturation of *Thomandersia* fruits, once the associated ovule has been fertilized. It is possible that Bremekamp (1942) was misled by the enlarged placentas of *Thomandersia* when he stated that the retinacula were placental structures developing early in the ontogeny of the gynoecium. In Acanthoideae, retinacula also develop after fertilization, although again this observation is often hampered by other structures adjacent to the developing ovule, usually considered to be obturators or strophioles. Most pertinent to this study, the retinacula themselves do not emerge until a much later stage of maturity.

The function of the retinacula of Acanthaceae is presumed to be related to the expulsion of the seed (Bremekamp, 1926; Corner, 1976; Witztum & Schulgasser, 1995). In *Thomandersia* its role seems to be more to retain the seed within the capsule even after dehiscence, perhaps resulting in an increased likelihood that the seeds will be dispersed by herbivorous animals eating the capsules.

Based on their similarity in relative position (topographic correspondence), detailed structure and ontogeny, the retinacula of *Thomandersia* and Acanthaceae are primary homologues. They differ in function, and in shape and size, but this can plausibly be attributed to mechanical constraints on development imposed by adjacent structures. In relative position, both are outgrowths of the funicle. In composition and anatomy the two outgrowths are also more or less similar. In development, both retinacula emerge after the ovules are fertilized. Previous authors have described the appearance of the retinaculum in Acanthaceae only in association with post-fertilization ovules, just as observed here for *Thomandersia* (Mohan Ram, 1960, 1962; Phatak & Ambegaokar, 1961). However, retinacula are probably not secondary homologues between *Thomandersia* and Acanthaceae. Homoplasy can be demonstrated by incongruence with other morphological or molecular characters (Patterson, 1982; Brower & Schawaroch, 1996). Molecular phylogenetic analyses of Lamiales and other floral characters imply that *Thomandersia* may not be a member of Acanthaceae (Fig. 1). If this is a correct representation of relationships, the presence of retinaculum is a convergent, homoplastic character.

## EXTRANUPTIAL NECTARY

A conspicuous character, possibly unique to *Thomandersia*, is the single or paired ‘extranuptial’

nectary at the base of the calyx (Figs 34–36). These have been observed to attract ants and may therefore possibly play a role in protection against herbivory. The histological organization of these nectaries is common to a wide range of plant secretory glands (Fahn, 1988). Multicellular, multilayered extrafloral and extranuptial nectaries are widespread in Lamiales, and members of a number of families display nectary-like structures potentially similar to those of *Thomandersia*. However, the nectaries of *Thomandersia* are exceptional in terms of both the size of the gland itself and the conspicuous swelling in which it is contained.

Bremekamp (1942) hypothesized that the nectaries of *Thomandersia* are homologous to nectaries in the axils of the bracteoles of Pedaliaceae, which are derived from a much-reduced axillary bud (Singh, 1960; Monod, 1986). This hypothesis is supported by the facts that the nectaries of *Thomandersia* are found at the base of the flowers in a compound raceme, and (in *T. anachoreta*) occur in pairs between paired bracteoles. Examination of a number of inflorescences in *Thomandersia* demonstrates the presence of a variety of nectaries and buds in the axils of the bracts of individual flowers, particularly towards the tip of the indeterminate inflorescence. By contrast, in *Thomandersia* the nectaries are present at the base of the calyx rather than at the base of the pedicel, and are adjacent to the bracteoles rather than in their axils. Furthermore, there are no derivatives of floral whorls in the anatomy of the glands of *Thomandersia*, as in Pedaliaceae, which would indicate a floral origin (Singh, 1960; Monod, 1986). Instead, the extranuptial nectaries of *Thomandersia* consist of distinct layers of specialized secretory cells, with vascular traces passing around the associated secretory tissues but not feeding directly into the gland.

Among other Lamiales, conspicuous extrafloral nectaries are most common in Bignoniaceae, on various parts of the plant including the abaxial exterior of the calyx (Seibert, 1948; Fahn, 1979; Thomas & Dave, 1992). In most cases these calyx glands are multiple, small (less than 100 µm in diameter), possess a single large barrier cell, are not vascularized and are flush with the epidermis rather than in a tissue swelling. In species of *Campsis* and *Tecomaria* the abaxial calyx nectaries have a cellular structure very similar to those of *Thomandersia* and are supplied by vascular bundles beneath (Elias & Gelband, 1976; Subramanian & Inamdar, 1989). However, these nectaries reach a maximum of 0.3 mm in diameter (vs. 2 mm in *Thomandersia*) and are found in aggregations of c. 28 nectaries per flower (Subramanian & Inamdar, 1989). Seibert (1948) described 'exceptionally large' calyx nectaries in *Callichlamys*, but examination of herbarium specimens reveals these to reach a maximum size of 0.5 mm, and the nectaries are again multiple rather

than solitary. None of the nectaries described in Bignoniaceae is embedded in the calyx with a channel to the surface; rather, they are broad, cup-shaped structures open to the epidermis. However, these features may be relatively plastic; even in *Thomandersia* the extent of channelling varies between *T. hensii* and *T. anachoreta*, so similarity may be better determined by the underlying cellular structure. In summary, species of Bignoniaceae and *Thomandersia* bear extranuptial nectaries in similar topographic positions, sometimes with a similar anatomical structure, although in Bignoniaceae they are smaller, multiple, with a broad opening and lack a surrounding swelling.

*Schlegelia* also displays multiple large, multicellular glands on the abaxial side of the calyx (Figs 33, 37), which have not been described in previous treatments (e.g. Burger & Barringer, 2000). The glands are larger (c. 0.5 mm in diameter) than in Bignoniaceae but smaller than those of *Thomandersia*. They are found in groups on the abaxial surface of the calyx, sunken in the epidermis but not in a noticeable swelling. Their cellular organization (Fig. 37) is somewhat similar to that of *Thomandersia*, comprising columnar, apparently secretory cells, opening to the epidermis, surrounded by a single layer of large, colourless barrier cells, themselves surrounded by a region of small, dark-staining cells with crystals that are visible under phase contrast microscopy. A vascular supply surrounds this layer of cells. The opening of the gland to the epidermis is broader than the narrow channel seen in *T. hensii* and the gland itself rises to the opening rather than invaginating around a central channel.

Using the three criteria of similarity outlined above, similarity of position is fulfilled for the nectaries of *Thomandersia*, Schlegeliaceae and some Bignoniaceae, as all are found on the calyx, although in Bignoniaceae they are also common elsewhere. The nectaries of Bignoniaceae and Schlegeliaceae differ in relative size, number and shape from those of *Thomandersia*, but are structurally very similar. This implies that the criteria of similar detailed structure and ontogeny are also fulfilled. The extranuptial nectaries of *Thomandersia* might therefore be primary homologues of those in *Schlegelia* and some Bignoniaceae such as *Campsis* (Elias & Gelband, 1976), although their large size may be autapomorphic for *Thomandersia*. The secondary homology of the character cannot, however, be determined without testing it against a rigorous phylogenetic hypothesis.

#### SYSTEMATIC IMPLICATIONS FOR *THOMANDERSIA* IN LAMIALES

In the majority of earlier treatments of *Thomandersia*, retinacula were strongly weighted as a unique character linking *Thomandersia* to Acanthaceae (e.g.

Bentham, 1876; Baillon, 1891; Lindau, 1897; Heine, 1966). Our investigations suggest that retinacula are homoplastic, and reveal a variety of additional characters that could link *Thomandersia* with other families in Lamiales.

Acanthaceae are probably a highly derived family, distinguished by flowers preceded by large bracts and bracteoles, a persistent calyx, staminode often absent, asymmetric anthers, a bilobed, non-papillate stigma, axile placentation with 2–10 ovules in two rows in each locule, endosperm absent (except in Nelsonioideae), flat seeds, explosively dehiscent, and retinacula. Inclusion of *Thomandersia* in Acanthaceae is contradicted by its lack of many of the diagnostic features of this family, such as large bracts and bracteoles, the lack of a staminode, and explosively dehiscent capsules. *Thomandersia* does share with Acanthaceae a persistent calyx and lack of endosperm (both characters also shared with other putative sister-groups) as well as folded cotyledons and retinacula. However, *Thomandersia* also shares characters with each of the other families of Lamiales investigated.

Bremekamp (1942) suggested a relationship between *Thomandersia* and Pedaliaceae on the grounds of similar pollen morphology and the shared presence of axillary nectaries. Because our study indicates that the axillary nectaries are not homologous, this hypothesis now appears unlikely, although it requires further testing; *Thomandersia* does share with Pedaliaceae a gibbous corolla and vascularized nectary continuous with the gynoeceum.

Of the families most frequently and strongly associated with *Thomandersia* in molecular analyses (Wortley, 2004; Wortley *et al.*, 2005), Bignoniaceae shares with *Thomandersia* a thick, red-staining calyx, apparently open in bud, calyx extranuptial nectaries, a typically gibbous corolla tube, vascularized nectary continuous with the gynoeceum, two rings of vascular bundles in the gynoeceum, hemianatropous ovules and non-endospermic seeds (Gentry, 1974, 1980, 1992, 1997; Armstrong, 1985; Manning, 2000). With Schlegeliaceae, *Thomandersia* shares a red-staining calyx, calycine extranuptial nectaries, vascularized floral nectary continuous with the gynoeceum, two rings of vascular bundles in the ovary wall and septum, and a thick, woody pericarp. With Verbenaceae, *Thomandersia* shares a red-staining, persistent calyx, a staminode lacking vascular bundles, vascularized nectary continuous with the gynoeceum, very thick ovary wall and woody pericarp, and non-endospermic seeds (Cantino, 1982; Sanders, 2001).

## CONCLUSIONS

The majority of floral and inflorescence features of *Thomandersia* can be interpreted as plesiomorphic

for Lamiales, such as racemose inflorescences with bracts and bracteoles, a pentamerous, sympetalous, calyx and corolla, four didynamous stamens and a superior, eusyncarpous, bicarpellary pistil. Unique and potentially diagnostic characters of *Thomandersia* include the structure and size of the calyx nectary, form of the expanded placentas, corolla aestivation pattern, cylindrical stigma and spherical, scaly seeds.

Several floral characters are potential shared derived characters (primary homologies *sensu* De Pinna, 1991) of *Thomandersia* and other families in Lamiales, including all three families to which phylogenetic analyses have suggested a possible relationship. However, most of these characters are shared with more than one family and/or are polymorphic within families, suggesting that they are homoplastic and/or widely distributed in Lamiales. It is therefore not surprising that previous classifications of *Thomandersia*, based on one or a few morphological characters, are contradictory and do not reflect evolutionary relationships (Bremekamp, 1942; Heine, 1966; Sreemadhaven, 1976). The extranuptial nectary of *Thomandersia* may be a primary homologue of structures in Bignoniaceae or Schlegeliaceae, while the retinaculum is a primary homologue of that of Acanthaceae. This distribution of characters makes it inevitable that some primary homologies will be found to be homoplastic. Rigorous phylogenetic analyses are urgently needed to produce a well-resolved, robust phylogeny for Lamiales, in order to determine which morphological characters are secondary homologies and which are homoplasies, and thereby to evaluate character evolution in the order. Neither morphological nor molecular sequence-based analyses have hitherto conclusively determined the sister-group of *Thomandersia* (Wortley *et al.*, 2005), but they indicate that it is an isolated family, not closely related to Acanthaceae. The distinctive retinaculum that primarily led to its classification in Acanthaceae is therefore likely to be of independent origin, an example of parallel morphological evolution.

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