CHAPTER 9

GENERAL DISCUSSION

This study is a step closer to the goal of publishing a definitive "Flora" for southern Africa. The present multidisciplinary study of *Lachnaea* has contributed to an improved understanding of the diversity of the group. Of the 29 species and eight varieties recognised by Van Wyk (1993), 24 species are upheld, three have been reduced to synonymy, all the varieties have been reduced to synonymy and 12 new species and two subspecies have been newly described. Two of the 12 new species have already been validly published (Beyers & Van Wyk 1998a & 1998b). The circumscription of the genus *Lachnaea* has been extended to include all the species of *Cryptadenia*. Of the five *Cryptadenia* species recognised by Van Wyk (1993) four have been transferred to *Lachnaea* and one has been reduced to synonymy. *Lachnaea*, now comprising 40 species and two subspecies, is endemic to the Cape Floristic Region. The species occur almost exclusively in fynbos vegetation on oligotrophic soils derived from the orthoquartzites of the Cape Supergroup. A few species, however, occur on shale or limestone. Most of the *Lachnaea* species can be regarded as montane taxa. The concentration of species is in the 3319 (Worcester) grid, with the number of species per unit area decreasing from this centre of diversity.

The previous full revision of *Lachnaea* was exclusively based on macromorphological characters derived from herbarium specimens (Wright 1915). In the present multidisciplinary study, extensive fieldwork was undertaken to study the live plants and populations, which resulted in a far better understanding of the genus. For the first time attention has been given to the regeneration strategy of the species. Although the regeneration strategy varies infraspecificaly in some species, it is of considerable taxonomic significance.

Phyllotaxis and indumentum of the leaf margins were found to be of taxonomic significance. Other leaf characters, for example, their orientation and shape (in outline and in cross section), were useful but where the range of a character is infraspecifically wide, it becomes less relevant.

In *Lachnaea* the leaf shape varies from linear to orbicular. There are leaf types very similar to those of unrelated groups as illustrated in Dahlgren's (1971) Figures 1–4 of *Cliffortia* (Rosaceae) and *Aspalathus* (Fabaceae) and those in the *Relhania* (Asteraceae) revision by Bremer (1976). These convergent similarities are not restricted only to leaf shape. In three *Relhania* species for example the leaves have several parallel ribs (Bremer 1976) as in *L. striata* and *L. ruscifolia*. Fibre bundles running along the leaf margins, as in *L. aurea* and *L. striata*, were also found in many of the *Relhania* species (Bremer 1976). The similarities discussed above are yet more examples of convergent evolution in leaves of especially the flora of the Cape Floristic Region (Went 1971).

The following leaf anatomical characters are taxonomically impotrant: the occurrence of stomata on both sides of the leaves or only adaxially as well as the position of the stomata in relation to the adjacent epidermal cells; presence of prominent extraxylary fibre caps associated with the mid and lateral bundles, expressed externally by the ribbed leaves and schlerenchymatous fibres running parallel to the leaf margins in the mesophyll; crystals of diosmin, occurring as sphaerocrystalline to somewhat dendritic masses, have for the first time been recorded in the leaves of *Lachnaea*.

Inflorescence morphology in *Lachnaea* is taxonomically significant. Species can be arranged into three main groups, namely, those with terminal, solitary flowers, those with capitula and those with umbels. Three groups within the umbellate group, namely those with ebracteate umbels, pseudobracteate and bracteate umbels are also recognised. Although the pseudobracteate and bracteate umbels are diagnostic features, it is sometimes difficult, when working with herbarium material, to distinguish between them. For that reason in compiling the key to the species the pseudobracteate and bracteate umbels were not used to delimit groups of species. The indumentum and to a lesser degree the shape of the involucral bracts and bract-like leaves were also taxonomically useful.

As with past treatments of *Lachnaea*, floral morphology has proved to be of considerable taxonomic importance. Floral characters that for the first time have been used to delimit species are:

- presence or absence of the pedicel;
- whether the pedicel elongates in the fruiting stage;
- whether the pedicel elongates abaxially beyond the point of attachment of the flower or not;
- whether the upper portion of the hypanthium is basally invaginated;
- the position of the stamen insertion.
- whether the antipetalous stamens are exserted or enclosed or only their anthers are fully or partially exserted;
- presence or absence of filament ridges on the hypanthium;
- presence or absence of broad connective tissue abaxially on the anther;
- position of scale insertion on the hypanthium; whether they are exserted or enclosed and whether they are basally or abaxially attached to the hypanthium wall;
- the shape of the trichomes on the hypanthium.

Palynology proved taxonomically unimportant in the delimitation of the genera in the subtribe Gnidiinae and in the delimitation of the species within *Lachnaea*. Similarly, the chromosome number is taxonomically insignificant at the generic and specific levels.

In the present study the large number of traditional macro- and micro-morphological characters held promise of elucidating possible phylogenetic trends in the group. Unfortunately, many of the characters either vary to a large degree within taxa or are constant in all the taxa. In the present cladistic analysis polymorphic characters were excluded since HENNIG86 (Farris 1988) cannot distinguish between polymorphic and unknown or missing characters. However, polymorphic characters can contain significant phylogenetic information (Thiele 1993; Wiens 1995). The data set, including polymorphic characters, should in future be analysed using PAUP (Swofford 1993), which can accommodate such characters, to compare the outcome with the present cladograms. The incorporation of molecular data is desirable and would, most likely, improve our understanding of the phylogeny of the genus. Available evidence nevertheless strongly supports the monophyletic status of the group. Since this present study is the first to attempt a cladistic analysis of *Lachnaea*, there is clearly room for considerable speciation of the genus. Goldblatt (1978) suggests that the origin and relationships of the Thymelaeae should be investigated as the Thymelaeaceae has undergone particularly extensive radiation in southern Africa. Of the 179 species represented in southern Africa, no less than 170 are endemic to the region.

CHAPTER 10

CONCLUSIONS

- The genus *Lachnaea* is monophyletic and easily distinguished from other genera of the Thymelaeaceae in southern Africa by the eight floral scales, which are inserted on the upper portion of the hypanthium below the insertion of the two stamen whorls.

- The circumscription of *Lachnaea* has been extended to include the genus *Cryptadenia* (previously with five species).

- Currently *Lachnaea* comprises 40 species and two subspecies. No sections are upheld; the resolution of such species groups is not clear. A key to the species is provided, as well as an illustration and distribution map of each species.

- The conservation status of each species was evaluated and the IUCN Red List Categories (Walter & Gillett 1998) were assigned as follows: 18 species—Vulnerable, 18 species—Lower Risk Least Concern, two species—Lower Risk Near Threatened, one species—Extinct and one species—Data Deficient.

- *Lachnaea* is endemic to the Cape Floristic Region (CFR) as defined by Goldblatt (1978).

- Members of *Lachnaea* occur almost exclusively in fynbos vegetation on oligotrophic soils derived from the orthoquartzites of the Cape Supergroup. A few species occur on shale or limestone.

- The centre of diversity for *Lachnaea* species is in the quarter degree, 3319 AD and the one degree 3319 (Worcester) grids with the number of species per unit area decreasing from this area.

- *Lachnaea* demonstrates a high percentage of regional endemism with 55% of the species endemic to the Northwestern, Southwestern, Karoo Mountain and Langeberg Centres of the CFR. Although species of *Lachnaea* also occur in the Bredasdorp-Riversdale and Southeastern Centres, none of the species are endemic there.

- Macromorphologically, the following characters proved to be of particular taxonomic significance:
  - regeneration strategy (reseeder vs. resprouter);
  - leaf characters, for example phyllotaxis, indumentum of leaf margins, absence or presence of parallel ribs on abaxial leaf surface;
  - type of inflorescence;
  - floral characters:
    - pedicel—present or absent, point of attachment of flower, whether elongating in fruiting stage;
    - hypanthium—shape, indumentum and trichome shape;
    - sepals—zygomorphy, colour and indumentum;
    - androecium—position of insertion and whether exserted or enclosed; anther with or without broad connective tissue abaxially;
    - scales—position of insertion on hypanthium, whether exserted or enclosed, whether basally or abaxially attached to hypanthium wall, shape and indumentum;
    - stigma—shape and length of papillae.

- Taxonomically the most useful leaf anatomical characters include:
  - whether the leaves are amphi- or epistomatic;
  - stomata sunken or on same level as adjacent epidermal cells;
  - presence of prominent extraxylary fibres capping mid and lateral vascular bundles;
  - presence of extraxylary fibres not associated with the vascular bundles running parallel to the leaf margins in the mesophyll;
  - presence of diosmin crystals.

- Anatomical adaptations in the leaves of *Lachnaea* probably enable the plants to withstand the long, dry summers of the mediterranean or semi-mediterranean climate of the CFR.

- Palynology is unimportant in the delimitation of the genera in the subtribe Gnidiinae and in the delimitation of the species in *Lachnaea*. All these groups are characterised by pollen grains which are spheroid in shape, pantoporate, with a *Croton*-pattern. The surface structure of the triangular supratectal subunits revealed a continuum of variation.

- Chromosome number is taxonomically insignificant at the generic and specific level. All the members of the genus investigated have 2n = 18.

- Both anatomical and morphological characters were used in a cladistic analysis. Two analyses, one with *Struthiola leptantha* as the outgroup (Analysis A) and another with multiple taxa as the outgroup (Analysis B) were done. The cladistic analysis showed that the sections *Sphaeroclinium*, *Conoclinium* and *Microclinium*, established by Meisner (1840) are paraphyletic and are therefore not upheld. Analyses A and B produced conflicting results with regard to the hypothetical evolutionary pathway of certain characters. The hypothesis of relationships within *Lachnaea* presented here should be seen as a starting point and by no means the final word.

- Allopatric speciation appears to have been the most important speciation mechanism in *Lachnaea*. Additional variables along which diversification may have taken place are altitudinal difference, allochrony and regeneration strategy of species after fire.

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SUMMARY

A TAXONOMIC REVISION OF *LACHNAEA* L. (THYMELAEACEAE)

by

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PHILOSOPHIAE DOCTOR
April 2000

The main objective of this study was to provide a taxonomic revision of the genus *Lachnaea*, which is endemic to the Cape Floristic Region. Members of the group occur almost exclusively in fynbos vegetation. In this revision a brief taxonomic history of the genus is given. Taxonomic decisions are based mainly on comparative morphology, distribution and ecology. More than 2500 herbarium specimens from 16 herbaria were studied. This was supplemented with extensive fieldwork.

Leaf-anatomical and palynological studies of all the species were conducted. Chromosome counts for 18 species are presented. Leaf-anatomy proved to be a valuable additional source of evidence for the delimitation of the species. Palynology and chromosome number were taxonomically insignificant at infrageneric levels.

The phytogeographical study showed that the highest number of species occur in the 3319 (Worcester) grid, with the highest diversity of species in the Hex River Mountains (3319 AD), followed by the Groot Winterhoek Mountains (3319 AA). Species richness of the genus declines to the north, south, east and west of the above centres of diversity. *Lachnaea* demonstrates a high percentage of regional endemism with 55% of the species endemic to one of four of the Centres of the Cape Floristic Region.

Circumscription of *Lachnaea* is extended to include the genus *Cryptadenia*. Sections in *Lachnaea* are not upheld. Forty species and two subspecies are now recognised. Four species and all varieties are reduced to synonymy, 12 species and two subspecies are newly described and one new name is proposed. One neotype and 16 lectotypes were selected.

The taxonomic treatment provides keys to the species and to the subspecies. Each species is described in detail and accompanied by a list of specimens examined. Diagnostic features and relationships, distribution, ecology, conservation status and, where applicable, infraspecific variation are discussed for each species. Line drawings and a distribution map are provided for each species.

The dominant process in speciation in *Lachnaea*, as far as can be assessed, appears to be allopatric speciation. Additional variables along which diversification may have taken place are altitudinal difference, allochrony and regeneration strategy of species after fire.

A hypothetical phylogeny of *Lachnaea* using cladistic methodology is presented. Two analyses were made, one with a single species as the outgroup and another with multiple taxa as the outgroup. The results of the analyses show that *Lachnaea* is monophyletic and that the sections are paraphyletic. The two analyses produced mixed resolution regarding the solitary-flowered species and gave conflicting results with regard to the evolutionary pathway of certain characters.

OPSOMMING

'N TAKSONOMIESE HERSIENING VAN *LACHNAEA* L. (THYMELAEACEAE)

deur
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Die hoofdoelwit van hierdie ondersoek was die daarstelling van 'n taksonomiese hersiening van die genus *Lachnaea*. Verteenwoordigers van die genus is endemies tot die Kaapse Floristiese Gebied en kom hoofsaaklik in fynbos plantegroei voor. In hierdie hersiening word 'n kort oorsig van die geskiedenis van die genus gegee. Taksonomiese besluite is hoofsaaklik op 'n vergelykende ondersoek van die morfologie, verspreiding en ekologie gebasseer. Meer as 2500 herbarium eksemplare van 16 herbaria is bestudeer en deur uitgebreide veldwerk aangevul.

'n Ondersoek van die blaar-anatomie en stuifmeelmorfologie van al die spesies is onderneem. Chromosoomgetalle van 18 spesies word verskaf. Blaaranatomie het geblyk 'n waardevolle bykomende bron van inligting te wees vir die omgrensing van die spesies. Stuimeelmorfologie en die chromosoomgetal is daarteenoor taksonomies onbelangrik bevind op infrageneriese vlak.

Die fitogeografiese ondersoek het getoon dat die grootste aantal spesies in die 3319 (Worcester) ruit voorkom en dat die hoogste diversiteit gesetel is in die Hexrivierberge (3319AD) gevolg deur die Groot Winterhoekberge (3319AA). Die hoë spesiediversiteit neem af na die noorde, suide, ooste en weste vanaf bogenoemde sentrums van diversiteit.

Lachnaea toon 'n hoë persentasie van streeksendemisme met 55% van die spesies endemies aan een van vier van die substreke van die Kaapse Floristiese Gebied.

Die omskrywing van *Lachnaea* is verbreed om die genus *Cryptadenia* in te sluit. Seksies in *Lachnaea* word verwerp. Veertig spesies en twee subspesies word tans erken. Vier spesies en al die varieteite is gereduseer tot sinonieme, 12 spesies en twee subspesies is nuut beskryf en een nuwe naam word voorgestel. Een neotipe en 16 lektotipes is gekies.

In die taksonomiese behandeling word sleutels tot die spesies en subspesies verskaf. Elke spesie word in besonderhede beskryf en is vergesel van 'n lys van eksemplare wat ondersoek is. Diagnostiese eienskappe en verwantskappe, verspreiding, ekologie, bewaringstatus en waar toepaslik die variasie binne 'n spesie, word bespreek. Lyntekeninge en 'n verspreidingskaart word vir elke spesie veskaf.

So ver vasgestel kon word, blyk allopatrie die dominante proses in die spesiasie van *Lachnaea* te wees. Addisionele veranderlikes soos verskille bo seevlak, bloeityd en regenerasie strategie van spesies na vuur kon ook bygedra het tot die diversifikasie van dié spesies.

Die filogenie-hipotese van *Lachnaea* gebasseer op kladistiese metodologie word voorgestel. Twee ontledings is gedoen, een met 'n enkele spesie as die buitegroep en een met veelvoudige taksa as die buitegroep. Die resultate van die ontledings toon dat *Lachnaea* monofileties is en dat die seksies parafileties is. Die twee ontledings het verskillende patrone getoon betreffende die spesies met terminale, enkelstandige blomme en teenstrydige resultate met verwysing na die evolusionêre ontwikkeling van sekere eienskappe.

CURRICULUM VITAE

Josephine Bertha Pauline Beyers (nèe Minnaar) was born on 18 April 1944 in Bloemfontein. She attended the Clarendon Girls High School, East London, where she matriculated in 1961. In 1962 she enrolled at the University of Stellenbosch, and in 1964 was awarded a B.Sc. degree with Botany and Zoology as majors. In 1965 she was appointed as Technical Assistant in the Botany Department of the University of the Orange Free State and at the end of that year she married and left to raise a family. Between 1966 and 1987 she held temporary teaching posts in Biology, Science and Mathematics, attained a B.Sc. (Hons.) *cum laude* from the University of Stellenbosch in 1979, worked as a bookkeeper for a firm of attorneys for eight years and was co-director and manager of a ladies boutique.

In 1987 Jo was appointed to the staff of the Stellenbosch Herbarium, one of the regional herbaria of the Botanical Research Institute, later the National Botanical Institute. She obtained her M.Sc. degree *cum laude* from the University of Stellenbosch in 1992. She currently holds the post of Assistant Curator: Collections at the Compton Herbarium, Kirstenbosch, where she is engaged in systematic research, information services and curatorial activities. She has concentrated on collecting plant specimens of the Cape Flora and is the author or co-author of seven scientific publications.

List of publications

1. BEYERS, J.B.P. 1997. New combinations in *Lachnaea*. *Bothalia* 27: 45.
2. BEYERS, J.B.P. & MARAIS, E.M. 1998. Palynological studies of the Thymelaeaceae of the Cape Flora. *Grana* 37: 193–202.
3. BEYERS, J.B.P. & VAN DER WALT, J.J.A. 1994. Inflorescence morphology of *Lachnaea* and *Cryptadenia* (Thymelaeaceae). *Bothalia* 24: 195–202.
4. BEYERS, J.B.P. & VAN DER WALT, J.J.A. 1995. The generic delimitation of *Lachnaea* and *Cryptadenia* (Thymelaeaceae). *Bothalia* 25: 65–85.

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7. CAFFERTY, S. & BEYERS, J.B.P. 1999. (1398) Proposal to reject the name *Lachnaea conglomerata* (Rhamnaceae). *Taxon* 48: 171–172.

APPENDICES

APPENDIX 1

NEW COMBINATIONS IN *LACHNAEA*[*]

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[*] Published in *Bothalia* 27: 45 (1997).

THYMELAEACEAE

NEW COMBINATIONS IN *LACHNAEA*

The genus *Cryptadenia* Meisn. comprising five species, was established by Meisner in 1840 and based on Drège's collections (Meisner 1840). In De Candolle's *Prodromus* the same five species were recognized by Meisner (1857). Wright (1915) in his treatment of the genus recognized four of these species, reduced one to synonymy and described a new species. Beyers & Van der Walt (1995) concluded that *Cryptadenia* and *Lachnaea* L. are congeneric and that *Cryptadenia* should be included within *Lachnaea*. In accepting these findings, the necessary nomen- clatural changes are made to the five species which are currently recognized (Van Wyk 1993) following Wright's treatment of the genus.

Lachnaea filicaulis *(Meisn.) Beyers* comb. nov.

Cryptadenia filicaulis Meisn.: 407 (1840); Meisn.: 574 (1857); C.H.Wright: 17 (1915).

Lachnaea grandiflora *(L.f.) Baill.*: 109, t. 77 (1880).

Passerina grandiflora L.f.: 226 (1782). *Cryptadenia grandiflora* (L.f.) Meisn.: 405 (1840); Meisn.: 573 (1857); C.H.Wright: 16 (1915).

Cryptadenia breviflora Meisn.: 406 (1840); Meisn.: 573 (1857); C.H.Wright: 17 (1915). Type: *Ecklon 360* (?holo, K!; NBG!, iso.).

Lachnaea laxa *(C.H.Wright) Beyers* comb. nov.

Cryptadenia laxa C.H.Wright: 17 (1915).

Lachnaea uniflora *(L.) Beyers* comb. nov.

Passerina uniflora L.: 560 (1753). *Cryptadenia uniflora* (L.) Meisn.: 406 (1840); Meisn.: 573 (1857); C.H.Wright: 16 (1915).

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MS. received: 1996-08-28.

APPENDIX 2

PALYNOLOGICAL STUDIES OF THE THYMELAEACEAE OF THE CAPE FLORA.[*]

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[*] Published in *Grana* 37: 193–202 (1998).

Grana 37: 193–202, 1998

Palynological studies of the Thymelaeaceae of the Cape Flora

JOSEPHINE B. P. BEYERS and ELIZABETH M. MARAIS

Beyers, J. B. P. & Marais, E. M. 1998. Palynological studies of the Thymelaeaceae of the Cape Flora. – Grana 37: 193–202. ISSN 0017-3134.

The pollen of the four genera of the Thymelaeaceae occurring in the Cape Floristic Region was studied with the LM, SEM and TEM. All four genera have spherical, pantoporate pollen grains and in *Gnidia*, *Lachnaea* and *Struthiola* the grains have a typical *Croton*-pattern similar to that of the majority of genera in the Thymelaeaceae. The exine of these three genera comprises triangular, supratectal subunits attached to a reticulum or semitectum, which is connected with short columellae to the nexine. In *Passerina* the supratectal subunits are lacking. Instead, the reticulum is ornamented with sparsely distributed spinules and can be described as supra-microechinate. Polymorphism with regard to pollen size was found in some specimens of three of the *Lachnaea* species, but since it was not consistent for all the specimens of the three species concerned, the phenomenon of polymorphism is ascribed to temporary ecological conditions. The structure of the tectum of *Gnidia*, *Lachnaea* and *Struthiola* is very similar and reveals a continuum of variation so that the palynology seems not to be of any taxonomic value within the three genera. The pollen morphology revealed a closer relationship between *Gnidia*, *Lachnaea* and *Struthiola*, which show a *Croton*-pattern, whereas *Passerina*, with the subunits lacking, confirms the present idea of placing it in a separate subtribe.

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The Thymelaeaceae is a medium-sized family comprising 53 genera and 750 species occurring in both temperate and tropical regions (Mabberley 1997). In the Cape Floristic Region four genera occur (Bond & Goldblatt 1984) of which *Lachnaea* L. s.l. (including *Cryptadenia* Meisn.) with 34 species, is endemic to the region (Beyers & Van der Walt 1995). *Gnidia* L. with about 150 species is mainly an African genus (Dyer 1975) with approximately one third of the species (47 species) in the Cape Floristic Region (Bond & Goldblatt 1984). Both *Struthiola* L., with about 40 species, and *Passerina* L. with about 17 species (Bredenkamp & Van Wyk 1996) occur mainly in the Cape Floristic Region. *Passerina* is a Cape Fynbos genus with one species extending to Zimbabwe (Thoday 1924, Dyer 1975) in the northern extensions of the Fynbos biome along the eastern mountains of southern Africa (Bredenkamp & Van Wyk 1996).

Wright (1915) maintained *Arthrosolen* C.A. Mey., *Gnidia* and *Lasiosiphon* Fresen. as separate genera. Domke (1934) regarded *Arthrosolen* as a synonym of *Lasiosiphon* and thus recognised *Gnidia* and *Lasiosiphon* as separate genera. Peterson's concept of *Gnidia* included both *Arthrosolen* and *Lasiosiphon* (Peterson 1959), and this concept is still being upheld by Van Wyk (1993). *Gnidia*, *Lachnaea*, *Passerina* and *Struthiola* belong to the subfamily Thymelaeoideae, with *Gnidia*, *Lachnaea* and *Struthiola*, with anthers introrse, belonging to the subtribe Gnidiinae and *Passerina*, with anthers extrorse, to the monogeneric subtribe Passerininae (Domke 1934).

Thoday (1924) described *Passerina* as readily distinguishable from the above mentioned genera by its ericoid leaves and small wind-pollinated flowers with exerted stamens, dust-like pollen and penicillate stigma. Hutchinson (1969) emphasised the wind-pollination by stating that the South African members of the Thymelaeaceae are the most advanced members of the family, and that *Passerina* has become so much evolved and reduced as to have reverted to wind-pollination. None of them gave any reason or confirmation to the assumption that *Passerina* species have wind-pollinated flowers. Bredenkamp & Van Wyk (1996) regarded the distribution of *Passerina* in areas in the Fynbos biome where persistent winds prevail throughout the year, the flowering time shortly after the rainy season when wind velocities are high, and the exerted stamens and extrorse anthers of the flowers as adaptations to anemophily. They also stated that insects could be secondary pollen vectors of *Passerina*. According to Bredenkamp & Van Wyk (1996) characteristics of the pollen grains which enhance the possibility of wind-pollination are the size of the pollen grains and the smoother exine sculpture.

In evaluating the generic delimitation of *Lachnaea* and *Cryptadenia*, differences and similarities in the pollen morphology of these two genera were studied (Beyers & Van der Walt 1995). To understand the value of the differences and similarities within the pollen grains of these two endemic genera of the Cape Flora, we compared them to *Gnidia*, *Struthiola* and *Passerina*, genera of the same family, also

Table I. *Pollen morphology of studied species of Thymelaeaceae (LM, SEM, and TEM*[1]*) and chromosome numbers.*

Diameter of pollen grains: mean with range followed in parentheses; sculpturing of supratectal subunits: smooth (sm); striate (str); striate with horisontal intercostal striations (str/retic); striate-granular (str/gran); granular-striate (gran/str); granular (gran); wart-like spinules[2], indicated after number of spinules; base-sides: emarginate = EM, straight = ST.

				Sculpturing of supratectal subunits								
Taxon	Specimen	Herb	Diameter (µm)	sm	str	str/ retic	str/ gran	gran/ str	gran	no. of spinules	basesides	Chromosome no. (2n)
Lachnaea												
L. alpina Meisn.	Forsyth 508	NBG	36 (30–38)				X			1 & 4	EM	
	Oliver 9299	NBG	40 (35–46)					X		1 & 4	ST	18
L. aurea Meisn.	Beyers 135	NBG	47 (39–51)			X				1	EM	
	Oliver 10550	NBG	54 (49–57)			X				1	EM	
L. axillaris Meisn.	Spreeth 160	NBG	27 (24–30)						X	4	ST	
	Steyn 331	NBG	22 (20–23)		X					1	ST	
	Thomas NBG 84653	NBG	25 (22–27)		X					1	ST	
L. burchellii Meisn.	Oliver 9241	NBG	34 (30–41)			X				1	EM	
	Oliver 9251	NBG	34 (27–38)			X				1	EM	
L. buxifolia Lam.	Beyers 118	NBG	52 (49–55)		X					4	ST	
	Beyers 122	NBG	47 (43–53)		X					4	ST	18
	Compton 21088	NBG	52 (43–58)		X					1	ST	
	Oliver 3791	NBG	51 (43–57)			X				1	EM	
	Taylor 8648	NBG	49 (47–59)		X					1	EM	
L. capitata (L.) Crantz	Beyers 128	NBG	29 (23–33)						X	1 & 4	ST	
	Oliver 10519	NBG	32 (30–35)					X		1 & 4	ST	18
	Rourke 729	NBG	37 (35–41)					X		4	ST	
L. densiflora Meisn.	Beyers 115	NBG	27 (23–31)						X	4	ST	
	Beyers 117	NBG	32 (29–35)		X					1	ST	
	Beyers 145	NBG	29 (23–45)					X		4	ST	18
	Beyers 154	NBG	29 (26–33)			X				4	EM	
	Beyers 244	NBG	29 (27–35)			X				1	EM	
L. diosmoides Meisn.	Beyers 181	NBG	29 (23–33)					X		4	ST	18
	Van Niekerk 53	NBG	30 (27–33)					X		4	ST	
L. elsiae Beyers ined.	Oliver 9689	NBG	27 (22–30)		X					1	EM	
	Stokoe 4504	BOL	26 (24–27)		X					1	±EM	
	Taylor 11775	NBG	26 (22–38)				X			4	±EM	
L. ericoides Meisn.	Beyers 172	NBG										18
	McDonald 1842	NBG	28 (25–31)		X					1	EM	
	Zeyher 3776	SAM	27 (23–31)			X				1	EM	
L. eriocephala L.	Beyers 54[1]	NBG	50 (39–57)			X				1	EM	18
	Beyers 238	NBG	42 (40–46)			X				4	ST	
	Rugge s.n.	NBG	42 (40–46)			X				1	ST	18
	Spreeth 141	NBG	45 (39–55)			X				1	EM	
	Stokoe SAM 65580	NBG	43 (37–48)			X				1	ST	
L. filamentosa (L.f.) Thunb.	Beyers 110	NBG	45 (39–55)		X					1 & 4	EM	
	Beyers 245	NBG	40 (35–46)		X					4	EM	
	Taylor 10675	NBG	43 (37–56)		X					4	ST/EM	
	Taylor 10770	NBG	50 (47–56)		X					1	ST/EM	
L. filamentosa. ssp. nov.	Forsyth 89	NBG	45 (37–56)			X				1	EM	
	Hansford 47	NBG	49 (43–65)			X				1	EM	
	Spreeth 144	NBG	55 (49–67)			X				1	EM	
L. filicaulis (Meisn.) Beyers	Esterhuysen 34370	NBG	33 (29–39)						X	1	ST	
	McDonald 1989	NBG	32 (24–40)					X	X	1 & 4	ST	18
L. funicaulis Schinz	Hugo 2332	NBG	24 (22–27)			X				1	ST	
L. globulifera Meisn. ssp. *globulifera*	Beyers 240	NBG	33 (30–38)			X				1 & 4	EM	
	Beyers 253	NBG	36 (32–41)			X				1	EM	
	Esterhuysen 18911	NBG	33 (30–38)			X				4	EM	
L. globulifera Meisn. ssp. *incana* Beyers ined.	Beyers 246	NBG	37 (30–49)				X			4	ST	
	Brown 575	NBG	33 (30–35)			X				1	EM	18
L. cf. *globulifera*	Esterhuysen 11102	BOL	29 (24–40)		X					1	ST	
L. glomerata Fourc.	Beyers 192	NBG	38 (32–40)		X	X				1 & 4	ST	18
	Vlok 2378	NBG	31 (27–35)		X	X				1 & 4	ST	18
L. gracilis Meisn.	Bean & Trinder Smith 2689	NBG	29 (27–32)					X		1	ST	
	Bean & Viviers 2613	NBG	29 (24–32)					X		1	ST	
	Beyers 126	NBG	29 (27–32)				X			1	ST	
	Beyers 219	NBG	28 (24–30)				X			1	ST	
	Oliver 10415	NBG	29 (27–32)						X	4	ST	
	Oliver 10416	NBG	33 (30–35)						X	4	ST	18
L. grandiflora (L.f.)	Beyers 129	NBG	56 (47–64)		X					4	ST	

Table I. (*Continued*)

Taxon	Specimen	Herb	Diameter (μm)	Sculpturing of supratectal subunits: sm	str	str/ retic	str/ gran	gran/ str	gran	no. of spinules	basesides	Chromosome no. (2n)
Baillon	Beyers 151	NBG	48 (45–58)		X			X		1 & 4	ST	
	Beyers 241[1]	NBG	48 (35–51)				X			1	EM	
	Beyers 242	NBG	47 (32–59)					X		4[2]	EM	
L. greytonensis Beyers ined.	Beyers 209	NBG	26 (19–40)			X	X	X		1 & 4	EM/ST	
	Stokoe 8031	BOL	24 (18–26)									
L. laniflora (C.H. Wright) Bond	Forsyth 507	NBG	33 (27–35)			X				1	EM	18
	Oliver 10679	NBG	31 (24–35)		X					4	ST	
L. cf. *laniflora*	Hanekom 667	NBG	32 (27–35)				X			4	ST	
L. laxa (C.H. Wright) Beyers	Bolus 7875	BOL	40 (33–43)		X					1	EM	
L. leipoldtii Beyers ined.	Taylor 10871	NBG	27 (22–30)				X	X		1 & 4	ST	
L. macrantha Meisn.	Esterhuysen 17723	BOL	39 (35–43)			X				1	ST	
	Forsyth 527	NBG	36 (33–41)		X					4	±ST	
	Oliver 8029	NBG	41 (38–43)			X				1	EM	
	Oliver, I. 3	NBG	42 (32–46)				X			4	ST	18
L. marlothii Schltr.	Kotze 124	NBG	26 (22–30)			X				1	EM	
L. montana Beyers ined. ssp. *montana*	Beyers 141	NBG	41 (38–46)			X				4	ST	18
	Esterhuysen 29730	BOL	37 (35–40)			X				4	ST	
	Krige s.n. STEU 10539	NBG	48 (43–54)			X				4	ST	
L. montana Beyers ined. ssp. *pedicellata* Beyers ined.	Compton 18719	NBG	33 (27–38)			X				1	EM	
	Oliver 9282	NBG	34 (30–40)				X			4	ST	
L. naviculifolia Compton	Andrag 105	NBG	53 (46–60)			X				4	ST	
	Forsyth 525	NBG	47 (38–51)			X				1	EM	
	Oliver 9038	NBG	49 (41–55)			X				1	EM	
L. nervosa (Thunb.) Meisn.	Beyers 215	NBG	43 (27–49)				X			1	ST	
	De Kock 152	NBG	35 (31–39)		X					4	ST	
	Esterhuysen 19230	BOL	37 (16–49)			X				1	EM	
	Esterhuysen 36180	BOL	36 (26–48)									
	Hansford, M 3	NBG	29 (12–40)									
	Oliver 9259	NBG	37 (30–48)			X				1	EM/ST	18
	Stokoe SAM 64621	PRE	50 (49–54)		X	X				1 & 4	EM/ST	
L. oliverorum Beyers ined.	Oliver 10478	NBG	42 (27–51)			X	X			1 & 4	EM/ST	
	Williams 1195	NBG	30 (24–34)									
L. pendula Beyers ined.	Esterhuysen 29780	BOL	22 (19–24)				X			4	ST	
L. penicillata Meisn.	Beyers 173	NBG	29 (23–39)		X					4	ST	
	McDonald 1631	NBG	26 (22–32)		X					4	ST	
	Oliver & Fellingh 9145	NBG	28 (19–35)		X					4	ST	
L. pudens Beyers	Beyers 161	NBG	26 (24–30)				X			1	EM	
	Beyers 210	NBG	28 (24–32)				X			1	EM	
L. pusilla Beyers ined.	Beyers 243	NBG	27 (28–30)						X	4[2]	ST	
L. ruscifolia Compton	Vlok 2084	NBG	35 (31–39)		X						ST	
L. sociorum Beyers	McDonald 2059	NBG	40 (35–46)			X				1	EM	
	Oliver 10524	NBG	39 (32–46)				X	X		1 & 4	ST/EM	
	Beyers 176	NBG	41 (35–49)				X			4	ST	18
L. striata (Lam.) Meisn.	Bolus 9087	BOL	29 (22–33)		X					4	ST	
	Compton 4412	BOL	33 (30–35)			X				1	EM	
	Esterhuysen 21152	BOL	30 (27–43)			X				1	ST	
L. uniflora (L.) Crantz	Beyers 136	NBG	54 (47–62)		X					1 & 4	ST/EM	18
	Boucher 4570	NBG	41 (38–43)					X		4	ST	
	Compton 9508	NBG	48 (43–57)				X			1 & 4	ST	
	Haynes 447	NBG	52 (49–55)		X					1	ST	
L. villosa Beyers ined.	Beyers 125	NBG	25 (20–27)				X			1	±EM	
	Du Toit s.n.	NBG	24 (19–27)						X	4[2]	ST	18
	Oliver 9808	NBG										18
	Oliver 10400	NBG	24 (22–27)					X		4	ST	
Gnidia												
G. deserticola Gilg (=*Lasiosiphon deserticola* (Gilg) C.H. Wright)	Taylor 11326	NBG	33 (29–38)					X		1	ST	
G. laxa (L.f.) Gilg (=*Anthrosolen laxa* (L.f.) C.A. Mey.)	Hector 2	STEU	32 (30–37)							1	ST/±EM	
G. oppositifolia L.	Beyers 199	NBG	36 (33–37)	X						1	ST	
	Kruger 314	NBG		X						1	ST	
G. penicillata Licht. ex Mey.	Beyers 147	NBG	33 (30–35)				X			2–4	ST	14
G. pinifolia L.	Beyers 198	NBG	32 (30–37)					X		2–4	ST	
	Boucher 438[1]	NBG	34 (27–38)					X		2–4	ST	

Table I. (*Continued*)

				Sculpturing of supratectal subunits								
Taxon	Specimen	Herb	Diameter (µm)	sm	str	str/ retic	str/ gran	gran/ str	gran	no. of spinules	basesides	Chromosome no. (2n)
G. squarrosa (L.) Druce	Koekemoer 528	PRE	49 (44–56)					X		1	ST	
	Koekemoer 565	PRE	36 (30–41)					X		1	ST	
	Pool 36	NBG	40 (32–46)					X		1	ST	
G. versiculosa Eckl. & Zeyh. ex Meisn. (=*Anthrosolen ornatus* Meisn.)	Beyers 133	NBG	39 (27–51)					X		1	ST	
Struthiola												
S. argentea Lehm.	Boucher 2492	NBG	34 (30–37)					X		4		
S. ciliata (L.) Lam.	Beyers 211	NBG	23 (22–24)					X		4		
	Koekemoer 587	NBG	30 (22–33)					X		4		
S. martiana Meisn.	Boucher 1810	NBG	38 (33–40)					X		1		
S. macowanii C.H. Wright	Dahlstrand 2517a	NBG	23 (19–25)					X		1		
S. myrsinites Lam.	Beyers 200^1	NBG	27 (22–32)					X		4		
	Bos 274	NBG	27 (22–30)					X		4		
S. striata Lam.	Willemse 620	NBG	24 (19–30)					X		4		
Passerina												
P. filiformis L.	Thompson 801	NBG	38 (33–44)									
P. paleacea Wickstr.	Taylor 8166	NBG	37 (33–44)									
P. rigida Wickstr.	Marsh 1327	NBG	40 (37–41)									
P. vulgaris Thoday	Beyers 143	NBG	34 (30–37)									
	Beyers 144^1	NBG	34 (30–38)									

represented in the Cape Flora. The inclusion of the genus *Gnidia* was important because the latest taxonomic treatment of *Gnidia* includes genera which were previously treated separately, thus representing a similar situation as found in *Lachnaea* s.l. Special emphasis has been placed on the species of *Lachnaea* to assess the taxonomic value of the pollen morphology in the taxonomic treatment of *Lachnaea* s.l.

MATERIALS AND METHODS

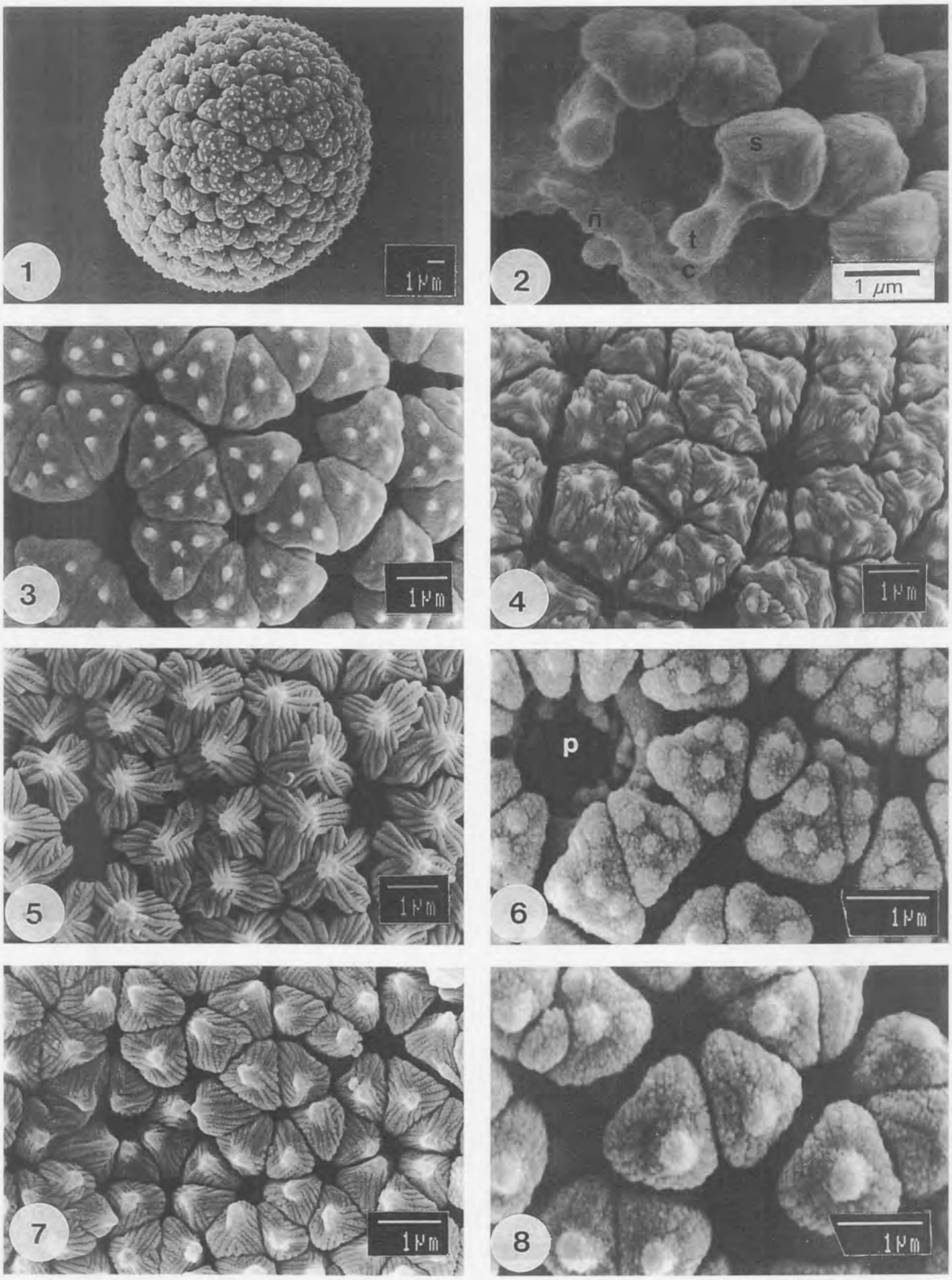
Pollen was taken from herbarium specimens and from material collected in the wild (Table I). For both light microscopy (LM) and scanning electron microscopy (SEM), pollen was acetolyzed according to Erdtman (1960). At least 20 pollen grains of each taxon were measured. Transverse sections of *ca.* 15 µm thick were made with the aid of a freeze-microtome to study the structure of the pollen wall. The terminology used to describe the pollen morphology is that of Punt et al. (1994). *Gnidia* species, selected for this study, included species from the different genera previously distinguished by Wright (1915), but now incorporated in *Gnidia* (Peterson 1959; Table I).

For transmission electron microscopy (TEM) flowers from herbarium specimens (Table I) were embedded in 1% agar (Tiedt 1985) to facilitate the handling of small specimens. Small pieces of agar containing pollen grains were fixed in 2% glutaraldehyde buffered in 0.1 M Na-phoshate (pH 7.4) and 1% tannic acid (Rodewald & Karnovsky 1974). After rinsing in the same buffer, postfixation in OsO_4 and dehydration in acetone followed. Specimens were embedded in spurr (Spurr 1969) and sectioned on a Sovall ultramicrotome. Ultra-thin sections (*ca.* 80 nm) were stained with 4% uranyl acetate (Gabriel 1982), followed by 2% lead citrate (Reynolds 1963).

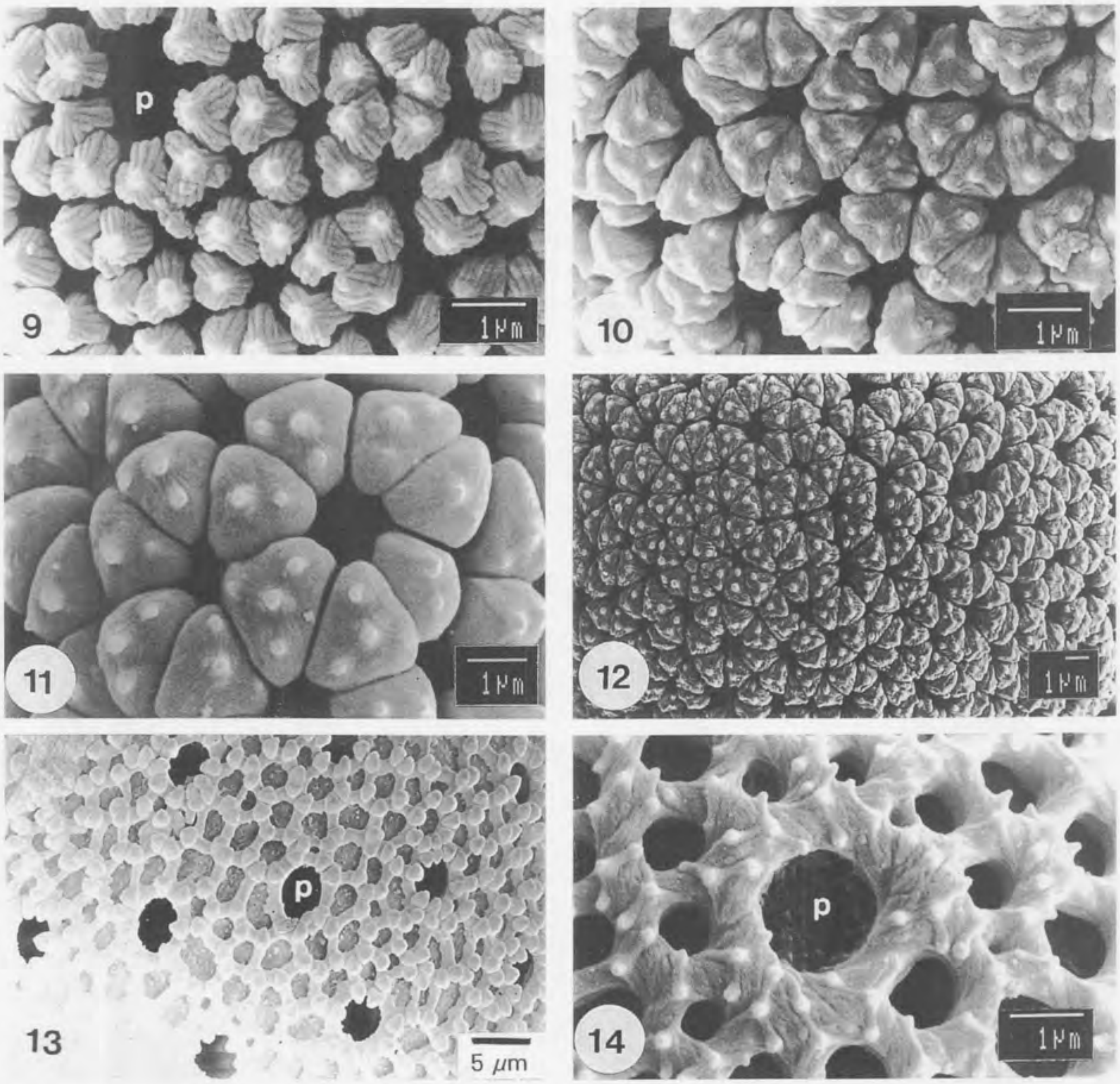
RESULTS

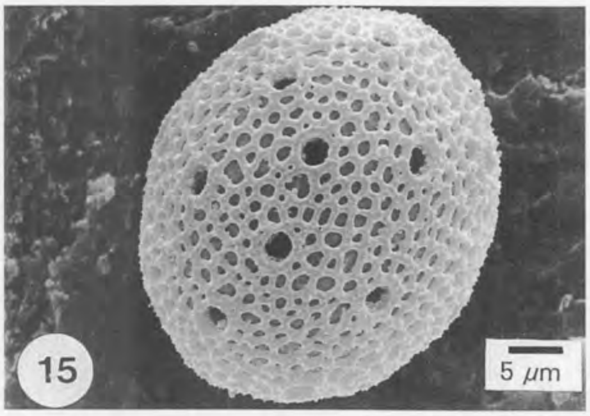
The pollen of the Thymelaeaceae is remarkably uniform: spheroidal in shape, pantoporate, with a *Croton*-pattern or a derivative thereof (Nowicke et al. 1985). The *Croton*-pattern (named by Erdtman 1966) comprises triangular supratectal elements attached to a reticulum (semitectum: Punt et al. 1994) having short or irregular columellae (Nowicke 1994). The triangular supratectal elements or subunits can be psilate, striate, furrowed or ridged, or pitted. The subunits can be closely spaced or arrayed in more open configurations (Nowicke 1994).

Gnidia, Lachnaea and *Struthiola* have monads (Fig. 1) with the structure of the triangular supratectal subunits revealing a similar continuum of variation as described and illustrated for several genera of the Thymelaeaceae by Nowicke et al. (1985) and Nowicke (1994), for *Wikstroemia* Endl. by Mayer (1991) and for seven southern African genera of the Thymelaeaceae by Bredenkamp & Van Wyk (1996). The subunits are tetrahedral with a single central spinule (Fig. 2) or it can be flattened but then having four spinules (Fig. 3). The majority of species of *Lachnaea* reveal a striation on the subunit (Fig. 4). Usually, when the basesides of these subunits are emarginate, horizontal intercostal striations also occur (Fig. 5). These intercostal striations are mostly associated with a single central spinule (Fig. 5). A small number of species of *Lachnaea* shows a granular pattern on the subunit (Fig. 6) and these subunits are usually associated with four spinules, or instead of the spinules, wart-like structures or verrucae (Fig. 6). A continuum of variation was found between the striate and granular surfaces (Figs. 7, 8) as well as the number of spinules on the subunits. Variation was not only found amongst species but often within a species or even a specimen (Figs. 9, 10). The subunits in the pollen of *Gnidia* (Fig. 11) and *Struthiola* (Fig. 3) are smooth to granular-striate. The number of spinules also varies between one and four in these two genera. The subunits in all three genera are usually closely spaced giving the sculpture a dense configuration so that in



Figs. 1–8. SEM micrographs of pollen grains of the Thymelaeaceae. (1) Pollen grain of *Struthiola ciliata* (Beyers 211). (2) Freeze microtome section of the pollen grain wall of *Lachnaea uniflora* (Haynes 477). 3–8. Parts of the pollen grain wall showing the variation of the supratectal subunits. (3) *Struthiola myrsinitis* (Beyers 200). (4) *Lachnaea nervosa* (Stokoe 64621). (5) *L. eriocephala* (Rugge s.n.). (6) *L. gracilis* (Oliver 10416). (7) *L. funicaulis* (Hugo 2332). (8) *L. gracilis* (Bean & Vivier 2613). (*c*) columella, (*n*) nexine, (*p*) pore, (*s*) supratectal subunits, (*t*) tectum, (*arrowhead*) intercostal striation. Scale bars = 1 µm.





Figs. 9–15. SEM micrographs of pollen grains of the Thymelaeaceae. 9–11 Portions of the pollen grain wall showing the variation of the supratectal subunits. (9–10) Lachnaea greytonenis (Beyers 209). (11) *Gnidia pinifolia* (Boucher 438). 12–13 Portions of the pollen grain wall to show pores. (12) *L. sociorum* (Beyers 176). (13) *L. grandiflorum* (Beyers 151). 14–15 Pollen grain wall of (14) *Passerina vulgaris* (Beyers 144). (15) *P. filiformis* (Thompson 801). (*p*) pore. Scale bars – 1 μm (9–12 & 14), 5 μm (13 & 15).

the majority of species of *Gnidia, Lachnaea* and *Struthiola* the pores are almost indistinct (Fig. 12). In a few species, however, pores are clearly distinguishable and included in a brochus (Fig. 13) as in *Daphne* (Faegri & Iversen 1989).

The exine of the pollen wall of *Passerina* consists of a reticulum, similar to that of *Gnidia, Lachnaea* and *Struthiola* and the different genera of the Thymelaeaceae as illustrated by Nowicke et al. (1985), but it lacks the prominent supratectal subunits. Bredenkamp & Van Wyk (1996) regarded the supratectal subunits as completely fused to form a secondary reticulum, and the basal reticulum is no more discernible but apparently lost through reduction or by fusion with the new reticulum. SEM and TEM studies in this project did not give a clear image as to whether the supratectal units are reduced to spinules or whether there is a fusion of two layers. The SEM micrographs of *Passerina* pollen grains reveal a diagonal striation with sparsely distributed spinules, which could be described as supra-microechinate (Fig. 14). However, the tectum appears much smoother than that of *Gnidia, Lachnaea* and *Struthiola.* Without the presence of supratectal subunits the pores in *Passerina* pollen grains are distinct and each clearly situated within a brochus (Fig. 15).

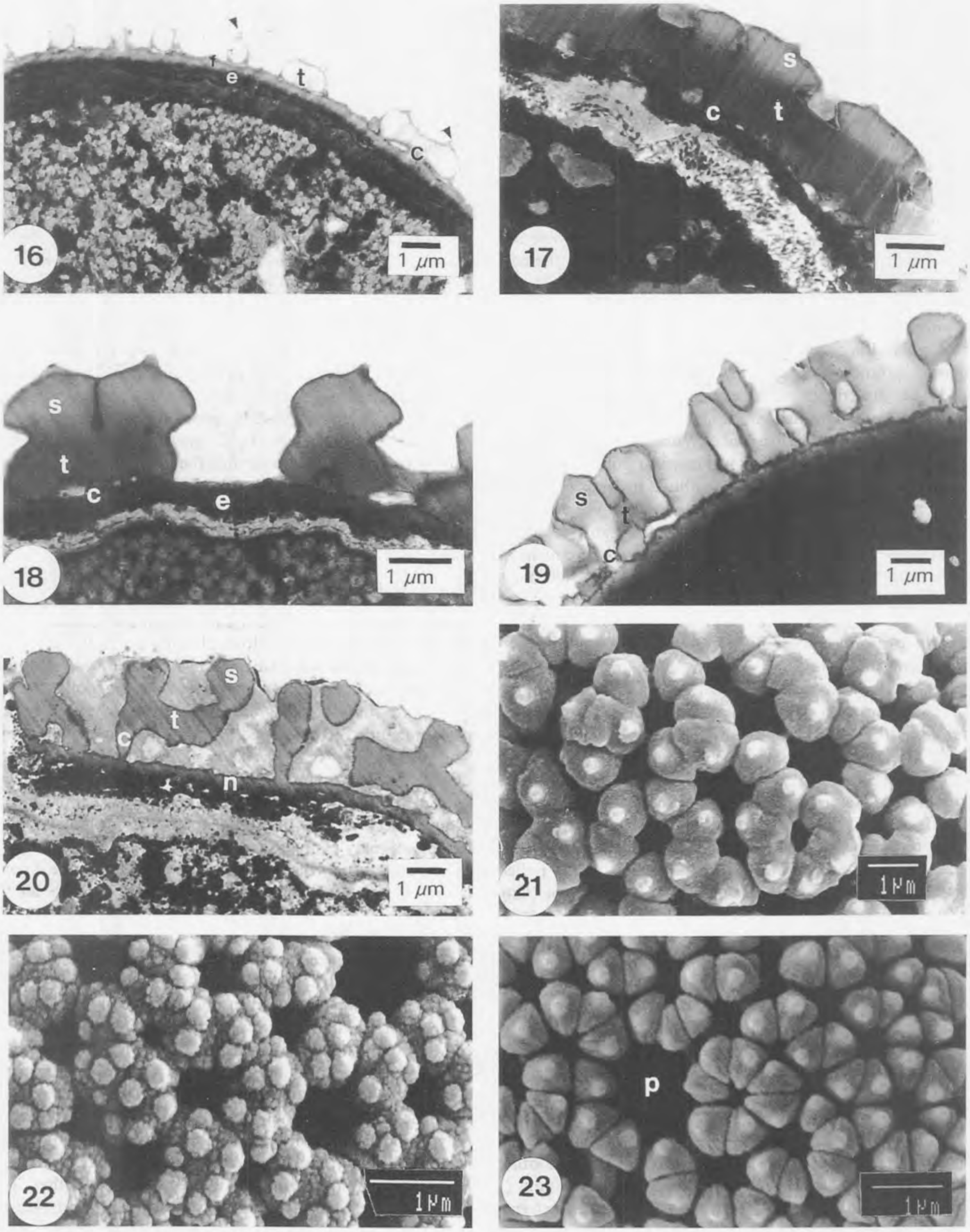
The pollen size of all species investigated ranged from 19–67 µm (Table I). The pollen size for the eight specimens of *Struthiola* ranged from 19–40 µm; for the 11 specimens of *Gnidia* it varied from 27–56 µm; and for the five specimens of *Passerina* from 33–44 µm. The pollen size of all the *Lachnaea* species studied ranged from 19–67 µm. The variation in size formed a gradient from small to medium-sized grains and from medium-sized to large grains. In three species, viz. *L. nervosa*, *L. greytonensis* and *L. oliverorum* the pollen size varied greatly within a specimen, with the smallest grains less than half or almost half the size of the largest grains. In *Lachnaea* the stamens are arranged in two whorls. In these three species the filaments of the inner stamens are shorter than filaments of the outer stamens or the inner whorl is inserted deeper down in the hypanthium and being less exposed. The first pollen specimens studied of these three species showed only small and large grains. Since pollen polymorphism was already described in *Wikstroemia* (Ong & Rao 1973) and because of the differences in the stamen whorls in *Lachnaea*, polymorphism with regard to pollen size was considered for these three species. More samples of the same collections were examined and the anthers of the different whorls were sampled separately. This revealed a continuum of pollen size, ranging from very small to large in each species and this continuum also occurred in both whorls of each species. Eventually seven collections from different localities of *L. nervosa* were sampled. Only three collections (Esterhuysen 19230, BOL, Esterhuysen 36180, BOL and Hansford M 3, NBG) showed the extreme sizes of small to large pollen grains. Subsequent sampling of other collections of *L. greytonensis* (Stokoe 8031, BOL) and *L. oliverorum* (Williams 1195, NBG) did not reveal the extreme sizes of small to large pollen grains as was found initially in the specimens studied of these two species. No tests on the viability of the pollen grains were performed. Variation in pollen size in most plant species is often correlated with the ploidy of the species (Ong & Rao 1973). Unfortunately only the chromosome number ($2n = 18$) of *L. nervosa* (Oliver 9258, NBG) is known and not that of the specimens showing the polymorphism with regard to size. So far no polyploidy is known in *Lachnaea.* All known chromosome numbers for *Lachnaea* species are $2n = 18$ (Table I).

Studies with the transmission electron microscope (TEM) also show the triangular supratectal subunits attached to a reticulum in *Lachnaea*, *Gnidia* and *Struthiola.* In *Passerina* only short spinules are attached to the reticulum (Fig. 16). The tectum is supported by columellae underlaid with a footlayer and endexine. The tectum is about three times of the thickness of the nexine in *S. myrsinites* (Fig. 17); slightly thicker to twice the thickness of the nexine in *G. pinifolia* (Fig. 18), *P. vulgaris* (Fig. 16), *L. grandiflora* (Fig. 20), or more or less the same thickness than the nexine in *L. eriocephala* (Fig. 19). The columellae are well developed in *L. eriocephala* (Fig. 19) and *L. grandiflora* (Fig. 20), but reduced and very short in *S. myrsinites* (Fig. 17), *G. pinifolia* (Fig. 18) and *P. vulgaris* (Fig. 16). The nexine in *S. myrsinites* and *G. pinifolia* comprises a prominent endexine and an extremely thin footlayer. In *L. grandiflora*, *L. eriocephala* and *P. vulgaris* the footlayer has the same thickness or is up to twice the thickness of the endexine. The prominent footlayer in *Passerina* is in agreement with the results of Bredenkamp & Van Wyk (1996).

DISCUSSION AND CONCLUSION

The diameter for the pollen grains of all the species studied lies between 19–67 µm. Although only a small number of specimens of *Struthiola*, *Gnidia* and *Passerina* was measured, it seems that *Struthiola* has the smallest pollen grains (19–40 µm in diameter) and *Gnidia* and *Passerina* have predominantly medium-sized grains (27–56 µm in diameter). The pollen size of *Lachnaea* varies from 19–67 µm in diameter, which represents the whole spectrum of the species studied. Within this range species of *Lachnaea* could not be grouped according to the size of the pollen grains. Although polyploidy may express itself directly in pollen size (Muller 1979), this is not the case in *Lachnaea*, since the known chromosome numbers of 18 *Lachnaea* species are all the same ($2n = 18$; Table I), with no polyploidy known. Pollen size in *Lachnaea* could rather be correlated to flower size (Muller 1979) since small flowers have small pollen grains and larger flowers have larger grains (Table II).

Concerning the variation in pollen size within *L. nervosa*, *L. greytonensis* and *L. oliverorum*, Pozhidaev (1993) pointed out that in most palynological investigations deviated pollen forms are regarded as abnormal and thus left unregistered and that published data do not reveal the true occurrence of these deviations. Mathew & Valsaladevi (1989) described polymorphism of pollen grains as a phenomenon of two or more pollen morphoforms occurring in the same species, or occasionally in a single plant or even the same anther. This polymorphism occurs naturally or due to various factors such as ecological conditions. Mathew & Valsaladevi (1989) and Pozhidaev (1993) also pointed out that deviated pollen forms were found in very different and distant angiosperm groups. As the variation in pollen size in the three *Lachnaea* species was not consistent within a species the phenomenon could be due to temporary ecological conditions or other



Figs. 16–23. TEM and SEM micrographs of pollen grains of the Thymelaeaceae. 16–20. TEM micrographs of thin sections of the pollen grain wall of selected species. (16) *Passerina vulgaris* (Beyers 144). (17) *Struthiola myrsinitis* (Beyers 200). (18) *Gnidia pinifolia* (Boucher 438). (19) *Lachnaea eriocephala* (Beyers 54). (20) *L. grandiflorum* (Beyers 241). 21–23. SEM micrographs to show portions of the pollen grain wall. (21) *G. deserticola* (Taylor 11326). (22) *L. pusilla* (Beyers 243). (23) *L. leipoldtii* (Taylor 10871). (*c*) columella, (*e*) endexine, (*f*) footlayer, (*n*) nexine, (*p*) pore, (*s*) supratectal subunits, (*t*) tectum, (*arrowhead*) spinules. Scale bars – 1 μm.

Table II. *Pollen of Lachnaea species.*

Size of pollen and flower arranged according to pollen size.

Species	Pollen size (μm)	Flower size (mm)
L. pendula	22.0 (19–24)	2.4–3.9
L. funicaulis	24.0 (22–27)	3.7–5.1
L. villosa	24.3 (19–27)	3.2–4.7
L. axillaris	24.6 (20–30)	3.0–4.8
L. greytonensis	25.0 (18–40)	3.2–5.5
L. marlothii	26.0 (22–30)	3.8–5.6
L. elsiae	26.3 (22–38)	2.2–4.2
L. leipoldtii	27.0 (22–30)	4.3–5.6
L. pusilla	27.0 (28–30)	4.0–5.7
L. pudens	27.0 (24–32)	5.0–8.4
L. ericoides	27.5 (23–31)	3.2–4.6
L. penicillata	27.6 (19–39)	3.6–5.3
L. cf. *globulifera*	29.0 (24–40)	3.9–4.1
L. densiflora	29.2 (23–45)	3.4–7.4
L. diosmoides	29.5 (23–33)	3.4–5.8
L. gracilis	29.5 (24–35)	3.9–8.0
L. striata	30.6 (22–43)	4.8–9.5
L. laniflora	32.0 (24–35)	3.9–8.2
L. cf. *laniflora*	32.0 (27–35)	5.3–5.8
L. filicaulis	32.5 (24–40)	4.3–7.5
L. capitata	32.6 (23–41)	3.7–7.4
L. montana ssp. *pedicellata*	33.5 (27–40)	5.1–8.2
L. burchellii	34.0 (27–41)	4.3–9.2
L. globulifera ssp. *globulifera*	34.0 (30–41)	3.7–7.0
L. glomerata	34.5 (27–40)	2.9–4.9
L. globulifera ssp. *incana*	35.0 (30–49)	5.8–8.3
L. ruscifolia	35.0 (31–39)	9.0–10.0
L. oliverorum	36.0 (24–51)	7.1–9.5
L. nervosa	38.1 (12–54)	5.8–18.0
L. alpina	38.0 (30–46)	7.2–12.2
L. macrantha	39.5 (32–46)	14.9–26.9
L. sociorum	40.0 (32–49)	4.2–7.5
L. laxa	40.0 (33–43)	6.2–16.5
L. montana ssp. *montana*	43.5 (35–54)	10.5–24.8
L. eriocephala	44.4 (37–57)	12.0–25.3
L. filamentosa	44.5 (35–56)	12.8–31.2
L. uniflora	49.0 (38–62)	12.0–20.0
L. filamentosa ssp. nov.	49.6 (37–67)	26.5–37.5
L. naviculifolia	49.6 (38–60)	11.0–21.0
L. grandiflora	49.7 (32–64)	11.8–28.5
L. buxifolia	50.2 (43–59)	18.5–29.0
L. aurea	50.5 (39–57)	13.1–23.3

factors, but could not be regarded as being well established within the species.

The triangular supratectal subunits in *Gnidia*, *Lachnaea* and *Struthiola* reveal a variation between one and four spinules per subunit. This variation was found not only within a species as seen in *Lachnaea* where several specimens per species were studied (Table I), but also within a specimen as in *L. greytonensis* (Figs. 9, 10). The surface structure of the supratectal subunits and the spinules varied from smooth (*G. deserticola*: Fig. 21) through striate (Figs. 4, 5) to granular (Figs. 6–8). This character seemed almost to be consistent within a specimen (Table I), but where several specimens per species were studied transitional forms degrade the taxonomic value of this character.

No correlation could be made between the inflorescence types or the flower morphology in *Lachnaea* and the structure of the supratectal subunits. As in the size of the pollen grains, the sculpture of the tectum revealed a continuum of variation. Although species could not be grouped according to the pollen morphology, the pollen morphology can assist in some cases in the delimitation of species with similar inflorescence and floral structures. For example in two closely related species, viz. *L. pusilla* (Fig. 22) and *L. leipoldtii* (Fig. 23), the sculpture of the supratectal subunits can be used as one of the distinguishing characters. In the former species the supratectal subunits are granular with wart-like spinules whereas in the latter the subunits are striate-granular with one or four spinules.

The ultra-structure of the pollen wall reveals a closer relationship between *Gnidia* and *Struthiola* because both have very thin footlayers and reduced columellae. *Passerina* shares the reduced columellae with *Gnidia* and *Struthiola*, but the presence of a more prominent footlayer with *Lachnaea*. According to Nowicke et al. (1985) the well-developed columellae of *Lachnaea* show a resemblance to those of *Thymelaea arvensis* Lam., *Linodendron cubanum* (A. Rich.) Urb. and *Daphne mezereum* L.

The differences in the pollen morphology of *Gnidia* species, previously included in the genera *Arthrosolen* and *Lasiosiphon*, are insignificant and made no contribution to the subdivision of *Gnidia*. Similar to this is the insignificance of the variations in the structure of the tectum in *Gnidia*, *Struthiola* and *Lachnaea*. This wider spectrum in the palynology of the Cape Flora genera of the Thymelaeaceae convinced us that the palynology is not an important tool to apply in the delimitation of the different genera of the subtribe Gnidiinae and did not contribute anything in the decision to include *Cryptadenia* into *Lachnaea*. Neither did pollen morphology contribute much to the delimitation of species in *Lachnaea* or to the grouping of species within the genus. This conclusion corresponds with the results of Heads (1990) for *Kelleria* and *Drapetes* and for the Hawaiian species of *Wickstroemia* (Mayer 1991).

The sculpture of the tectum reveals a closer relationship between *Struthiola*, *Gnidia* and *Lachnaea* whereas *Passerina*, with the subunits lacking, stands apart. The closer relationship between *Gnidia*, *Lachnaea* and *Struthiola* supports the placement of these genera in the same subtribe, whereas the distinctly different pollen morphology of *Passerina* supports the classification by Domke (1934), where *Passerina* is placed in a separate subtribe or the newly instated tribe Passerineae (Domke) Bredenkamp & Van Wyk by Bredenkamp & Van Wyk (1996).

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APPENDIX 3

INFLORESCENCE MORPHOLOGY OF *LACHNAEA* AND *CRYPTADENIA* (THYMELAEACEAE).*

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Inflorescence morphology of *Lachnaea* and *Cryptadenia* (Thymelaeaceae)

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Keywords: *Cryptadenia*, inflorescence morphology, *Lachnaea*, Thymelaeaceae

ABSTRACT

The current delimitation of *Lachnaea* L. and *Cryptadenia* Meisn. is based on the inflorescence morphology. In *Lachnaea* both indeterminate and determinate inflorescences occur, whereas in *Cryptadenia* only determinate inflorescences are present. The indeterminate inflorescences in *Lachnaea* are capitate or umbellate. The determinate inflorescences in both genera comprise a solitary, terminal flower. It is concluded that the two genera cannot be distinguished on inflorescence structure.

UITTREKSEL

Lachnaea en *Cryptadenia* word tans op grond van hul bloeiwyses onderskei. Beide onbepaalde en bepaalde bloeiwyses kom by *Lachnaea* voor, terwyl by *Cryptadenia* net bepaalde bloeiwyses voorkom. Die onbepaalde bloeiwyses by *Lachnaea* is hofies of skerms. Die bepaalde bloeiwyses by beide genera bestaan uit 'n enkel, terminale blom. Die gevolgtrekking word gemaak dat dié twee genera nie op grond van die struktuur van die bloeiwyses onderskei kan word nie.

INTRODUCTION

The Thymelaeaceae, which is regarded as a medium-sized family comprising 50 genera and 720 species, occurs in both temperate and tropical regions (Mabberley 1990). Most genera belong to the subfamily Thymelaeoideae including the genus *Lachnaea* L. and the genus *Cryptadenia* Meisn. Both these genera are endemic in the Cape Province.

In the classification systems of the Thymelaeaceae by Endlicher (1847, sec. Domke 1934), Meisner (1857), Bentham & Hooker (1880), Gilg (1894) and Domke (1934), *Lachnaea* and *Cryptadenia* have always been placed next to each other, reflecting their close affinity. Only one previous worker, Baillon (1880), did not regard *Cryptadenia* as a separate genus but as a section of *Lachnaea*. In the last taxonomic treatment of the two genera, Wright (1915) followed the classification of Bentham & Hooker (1880).

The floral morphology of *Lachnaea* and its closest related genus, *Cryptadenia*, is similar. The flowers are bisexual, tetramerous, apetalous, with eight floral scales inserted on the hypanthium below the insertion of the eight stamens, which are arranged in two whorls of four each. To distinguish between these two genera Wright (1915) used the inflorescence structure. In *Lachnaea* he regarded the flowers to be terminal, capitate or rarely solitary, whereas in *Cryptadenia* he described them as axillary, solitary and bibracteolate. A study of the descriptions of the different taxa of both genera revealed that *L. axillaris* Meisn., *L. micrantha* Schltr. and *L. ruscifolia* Compton have flowers which are axillary and solitary, whereas the flowers of *L. penicillata* Meisn., according to Wright (1915), are terminal and solitary. If one should apply the criterion used by Wright (1915), the former three species should rather be placed in *Cryptadenia*. Thus, the criterion used by Wright does not hold.

A preliminary examination of herbarium specimens of the Western Cape herbaria has brought to light numerous misidentifications and *incertae*, illustrating the poor state of our knowledge of *Lachnaea* and *Cryptadenia*. The confusion which presently exists regarding the delimitation of *Lachnaea* and *Cryptadenia* can be partly ascribed to the inconsistencies in Wright's interpretation of the inflorescence morphology of these two genera (Wright 1915). As the inflorescence has been considered to be of great taxonomic importance in the past, the study of the inflorescence morphology was undertaken with the view to improving our understanding of these two genera.

Meisner (1840) instituted three sections, *Sphaeroclinium* Meisn., *Conoclinium* Meisn. and *Microclinium* Meisn., within *Lachnaea*, based on the inflorescence morphology. In his later publication of 1857 he followed the same classification. In the section *Sphaeroclinium* he included those taxa having a terminal, dense, many-flowered capitulum, which was either involucrate or evolucrate, the sessile flowers being arranged on a moderately thick, globose receptacle. Meisner (1840, 1857) included *L. buxifolia* Lam. and *L. filamentosa* (Thunb.) Meisn. in this section. In the section *Conoclinium* he regarded the inflorescence as a terminal or subterminal, few- to many-flowered, evolucrate capitulum. Here the moderately thick receptacle was at first hemispherical to conical but by later elongating, became subcylindrical. From the regular arrangement of the flower scars on the receptacle, he regarded the inflorescence as a spike and not a capitulum. In this section he included *L. capitata* (L.) Meisn. and *L. densiflora* Meisn. In the section *Microclinium* he included those taxa having flowers in sessile, terminal, subcapitate or subsolitary inflorescences, or those rarely having axillary, solitary flowers, namely *L. axillaris*, *L. diosmoides* Meisn., *L. ericoides* Meisn. and *L. penicillata* Meisn. Meisner (1840)

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regarded the flowers of *Cryptadenia* as terminal, solitary or geminate, or occasionally as axillary and solitary, but in his later publication of 1857 he described the flowers as being terminal and subsolitary.

Gilg (1894) regarded the inflorescences in *Lachnaea* as usually being terminal, many-flowered heads, but occasionally, when consisting of two flowers, as mostly axillary. In *Cryptadenia* he regarded the flowers as solitary, axillary, with two bracteoles.

Domke (1934) described the inflorescences in *Lachnaea* as being usually terminal heads, which are basally enclosed by an involucre, or congested heads without an involucre. No mention was made of the solitary-flowered inflorescence in his generic description of the genus. In *Cryptadenia* he regarded the flowers as being solitary or few, either terminal or axillary with two bracteoles.

Dyer (1975) followed Wright (1915) and also used the inflorescence structure to distinguish between *Lachnaea* and *Cryptadenia.* According to Dyer (1975) the flowers in *Lachnaea* are arranged either in terminal, bracteate or ebracteate heads or a congested spike, or are rarely solitary, whereas in *Cryptadenia* the flowers are axillary and solitary.

In the most recent publication on the inflorescence morphology of the Thymelaeaceae, Weberling & Herkommer (1989) regarded the inflorescences in *Lachnaea* as being capitate or spicate, or having solitary, axillary flowers borne on a proliferating spike as in *L. axillaris.* In *Cryptadenia* they considered the flowers as being solitary and terminal.

From the above literature survey there seems to be consensus with regard to the terminal, many-flowered heads but not with regard to the position of the single-flowered inflorescences in *Lachnaea.* Similarly in *Cryptadenia* different views are expressed with regard to the position of the inflorescence and the number of flowers in an inflorescence.

The aim of the present investigation was to determine whether the inflorescence morphology could be used to delimit the two genera.

MATERIALS AND METHODS

Material used in this study comprised herbarium specimens and plants collected in the wild, with the exception of *L. nervosa* Meisn. of which fresh material was unobtainable. Eighteen taxa were selected, 14 from *Lachnaea* and four from *Cryptadenia*. The aim in selecting the taxa was to have as broad a representation as possible of all the taxa in the two genera. The criteria used for selecting the taxa were: 1, taxa representative of the three sections instituted by Meisner (1840), taking in account the variation in each section; and 2, taxa with solitary flowers.

Four of the five species of *Cryptadenia* currently recognized were studied. *Cryptadenia breviflora* Meisn. was excluded as it is an intermediate taxon between *Cryptadenia grandiflora* (L.f.) Meisn. and *Cryptadenia uniflora* Meisn. Levyns (1950) considered *C. breviflora* as a hybrid between the two species.

The 18 species studied were: *Lachnaea aurea* Eckl. & Zeyh., *L. axillaris*, *L. burchellii* Meisn., *L. buxifolia*, *L. capitata*, *L. densiflora*, *L. diosmoides*, *L. ericoides*, *L. eriocephala* L., *L. filamentosa*, *L. funicaulis* Schinz, *L. nervosa*, *L. penicillata*, *L. ruscifolia*, *Cryptadenia filicaulis* Meisn., *C. grandiflora*, *C. laxa* Wright and *C. uniflora* (nomenclature according to Arnold & De Wet 1993).

RESULTS

Inflorescence structure within *Lachnaea*

Both major types of inflorescences, as recognized by Radford *et al.* (1974) and Cronquist (1988), namely indeterminate and determinate, occur in *Lachnaea.*

Indeterminate inflorescences

Within the indeterminate inflorescences the capitulum and the umbel are represented.

1. Species with capitula

L. buxifolia, *L. capitata*, *L. densiflora* and *L. filamentosa* have terminal, multi-flowered, ebracteate capitula. These capitula are borne singly at the ends of branches on sericeous peduncles, which vary in length from 3–10 mm. The sessile flowers are arranged on a moderately thick, convex receptacle, which elongates during the flowering period, becoming narrowly conical or conical. Different stages of flower development are present within a capitulum. The fruiting stage may be present basally while buds are still developing distally. An accurate number of flowers in an inflorescence is therefore not easily determined. The number of mature flowers, at a given time, varies from ± 50 in *L. buxifolia*, 20–50 in *L. filamentosa*, ± 12 in *L. densiflora* and only 1–3 in *L. capitata.*

After flowering, vegetative growth is resumed by lateral branches developing in the axils of the upper leaves immediately beneath the capitulum. These will eventually terminate in new capitula in the following flowering period. However, some of these lateral shoots, as in *L. densiflora*, may terminate in capitula within the same flowering period. Lateral branches may also develop from the axils of the leaves below the distal leaf on the main flowering branches. These branches will, in the following flowering period, be terminated by capitula (Figure 1).

2. Species with umbels

Two types of indeterminate umbels, namely bracteate umbels as in *L. eriocephala* and ebracteate umbels as in *L. diosmoides*, are recognized. The pedicels remain in the old inflorescences for some time after the upper portion of the flowers and the fruits have been shed. The number of pedicels present indicates the number of flowers in each inflorescence.

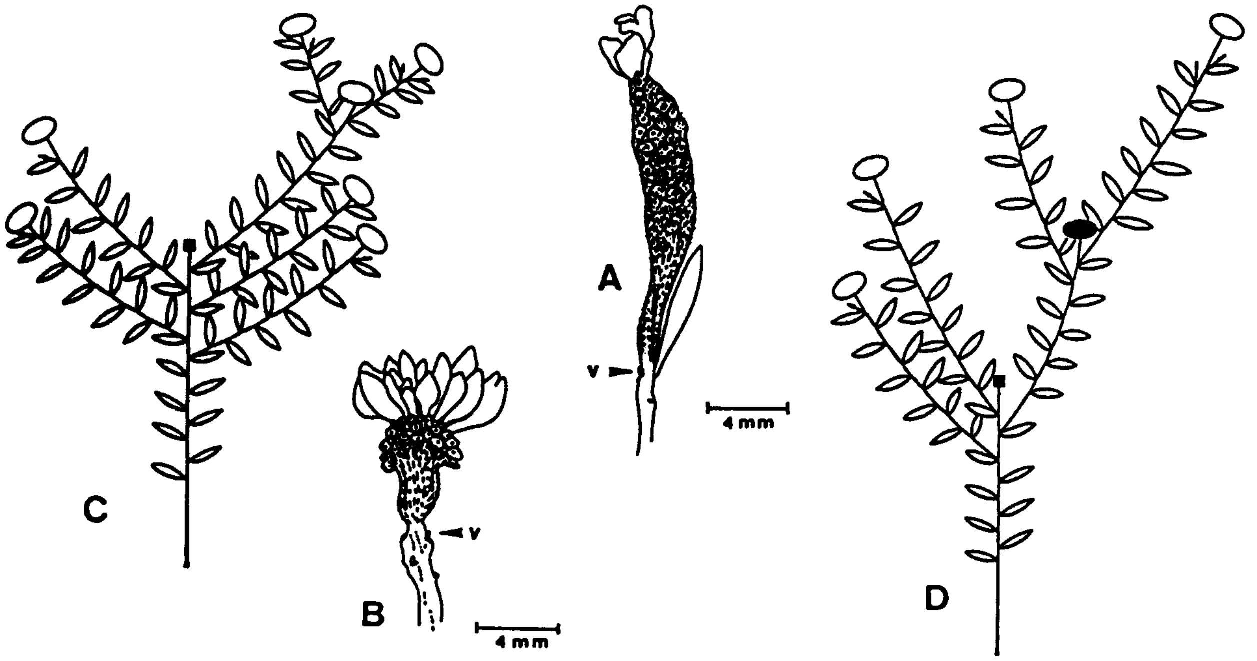

FIGURE 1.—Capitate inflorescences of *Lachnaea* species. A, capitulum of *L. capitata*, *Beyers 128*, illustrating elongated receptacle after lower flowers have been shed; B, capitulum of *L. buxifolia*, *Beyers 122*, with flowers partly removed. Diagrammatic illustration of branching pattern of flowering branches: C, *L. densiflora*; D, *L. filamentosa*: ■, remains of previous year's inflorescence; ○, flowering capitulum; ●, capitulum with fruits only; v, bud of new vegetative shoot.

2.1. Species with sessile bracteate umbels

Sessile, bracteate umbels occur in *L. aurea*, *L. eriocephala* and *L. penicillata*. In *L. eriocephala* (Figure 2) the inflorescence is comprised of about 40 shortly pedicellate flowers, which are surrounded by a bracteate involucrum consisting of four large bracts, in two whorls of two. These bracts follow on the stem after the linear-elliptic to lanceolate leaves. Similarly in *L. aurea* the ± 50-flowered umbel is surrounded by 8–10 bracts which are spirally arranged. From the axils of the foliage leaves immediately below the bracteate umbels, vegetative growth is resumed by lateral branches in both species. These lateral branches will eventually terminate in bracteate umbels in the following flowering period. Lateral branching is not only restricted to the axil of the distal leaf when the leaves are alternately arranged as in *L. aurea*, or to the distal pair of leaves, when opposite as in *L. eriocephala*, but may originate from the axils of the other upper foliage leaves. These lateral branches are also terminated by bracteate umbels in the following flowering period. In both cases the lateral branches may elongate considerably.

In *L. penicillata* (Figure 3) the inflorescence is also a terminal bracteate umbel. The umbel, usually eight-flowered, is surrounded by four bracts, in two whorls of two each. Only the distal portion of a single mature flower is visible at a time. Wright (1915) inadvertently regarded the flowers as being 'terminal, solitary, sessile'. The elongated pedicels and buds enclosed by the bracts were ignored by him. Lateral branching arises from the axils of either the first or second pair of foliage leaves immediately below the inflorescence. These lateral branches may elongate considerably or may be reduced to comprising only one or two pairs of foliage leaves before being ter-

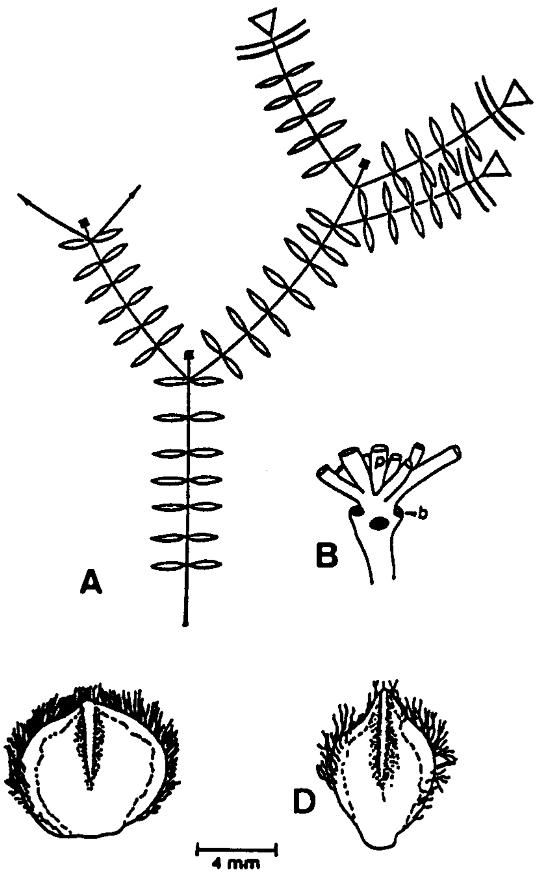

FIGURE 2.—*L. eriocephala*, *Beyers 54*. A, diagrammatic illustration of branching pattern of flowering branches; B, bracteate umbel with flowers and bracts removed; C, abaxial view of one of inner pair of bracts; D, abaxial view of one of outer pair of bracts; ■ remains of previous year's inflorescence; V, umbel; b, scar of removed bract; p, pedicel.

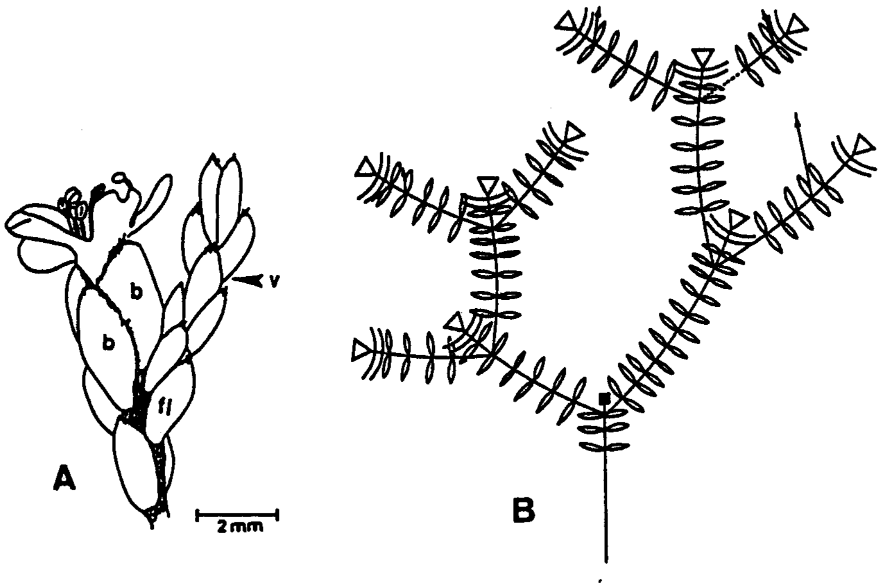

FIGURE 3.—*L. penicillata*, *Oliver & Fellingham 9145*. A, flowering branch with a terminal bracteate umbel; B, diagrammatic illustration of branching pattern of flowering branches; ■, remains of previous year's inflorescence; ∇, umbel; b, bract; fl, foliage leaf; v, new vegetative shoot.

minated by an inflorescence. Up to three generations of flowering branches may develop in one flowering period. Vegetative growth is resumed by lateral branches developing from the axils of the upper foliage leaves of the last flowering generation.

2.2. Species with sessile ebracteate umbels

In *L. diosmoides*, *L. ericoides*, *L. funicaulis* and *L. nervosa* the flowers are borne in sessile, ebracteate umbels at the tips of the branches. No bracts surround the inflorescence as new vegetative growth arises from the axils of the leaves immediately beneath the umbel (Figure 4). The number of flowers per umbel varies among the different species and also within each species. In *L. diosmoides* and *L. funicaulis* 6–20 flowers are present, whereas in *L. nervosa* the number varies from 4–14 and in *L. ericoides* from 2–8. As a result of the different developmental stages of the flowers present in each umbel, only a few mature flowers are present at a time. Lateral branching is resumed from the axil of the upper leaves below the inflorescences but is not restricted only to the most distal leaves immediately behind the inflorescence. In *L. nervosa* (Figure 4) short, lateral branches also arise in the axils of the leaves lower down on the main flowering branch, which in the same flowering period are terminated by inflorescences. Consequently the main flowering

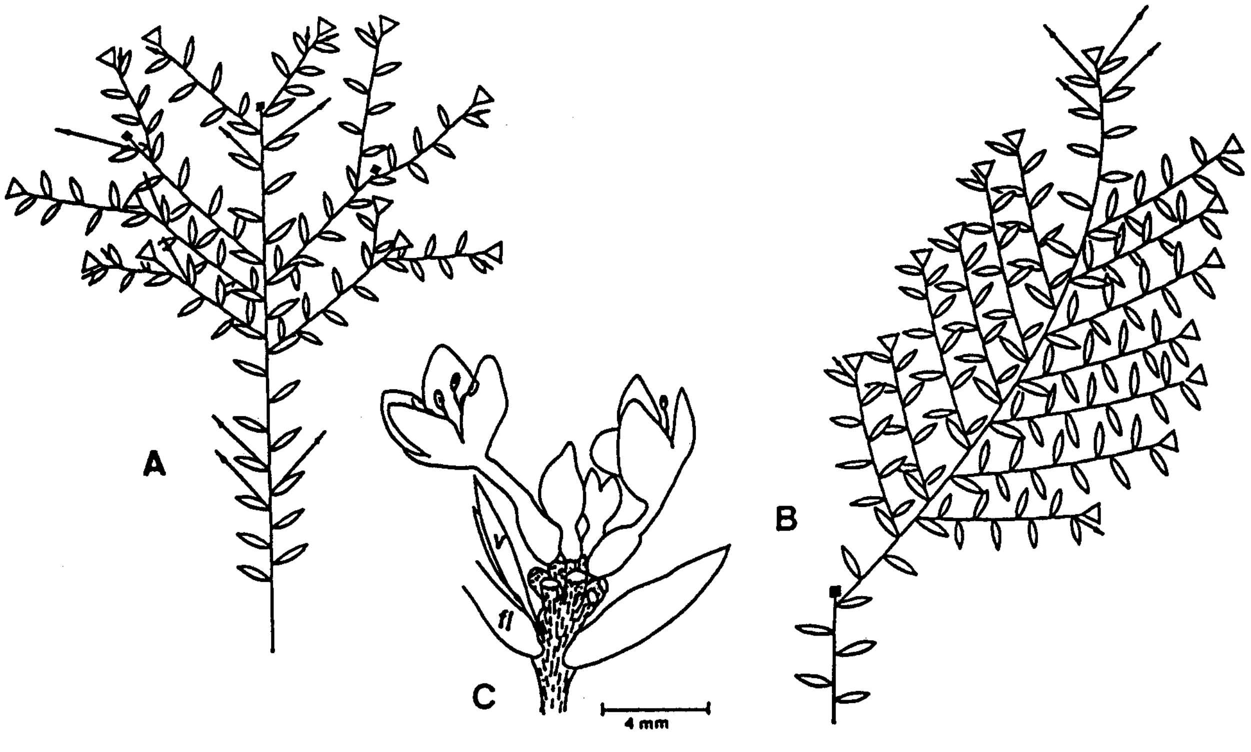

FIGURE 4.—Diagrammatic illustration of branching pattern of flowering branches: A, *L. ericoides*; B, *L. nervosa*. C, terminal ebracteate umbel in *L. nervosa*, *De Kock 152*, illustrating new vegetative shoot (v) in the axil of the distal foliage leaf (fl). ■, remains of previous year's inflorescence; ∇, umbel.

branch has the appearance of a racemose inflorescence. Similarly in *L. diosmoides* lateral vegetative shoots arising in the axils of the leaves immediately below the inflorescence, may be terminated by inflorescences in the same flowering period. Here they may overtop the umbel on the main flowering branch, forming a dense cluster of umbels, and at the same time reduced lateral shoots may develop lower down in the axils of the foliage leaves of the same main branch with a racemose appearance, as in *L. nervosa*.

In *L. ericoides* (Figure 4) a first and second generation of flowering shoots may occur. These shoots, as in the previous taxa, develop from the axils of the leaves immediately below the inflorescence. Below the most distal leaf on the main flowering shoot, further lateral shoots may develop which may terminate in inflorescences in the same flowering period or in the next flowering period. These flowering shoots are, unlike those in *L. diosmoides*, restricted to the upper leaves on the main flowering branch. Vegetative shoots may also develop lower down on the main flowering branches of the previous flowering period which again will be terminated by inflorescences in the following flowering period.

In *L. funicaulis* a pair of bract-like foliage leaves occurs at the base of the umbels. These umbels appear bracteate and resemble those of *L. penicillata*, but, unlike *L. penicillata*, lateral vegetative growth develops in the axils of the bract-like foliage leaves. These lateral vegetative shoots will terminate in ebracteate umbels in the following flowering period. Reduced lateral shoots also develop in the axils of the upper leaves, behind the bract-like foliage leaves on the main flowering branch, which may terminate in ebracteate umbels within the same flowering period, forming a cluster of inflorescences towards the end of the main flowering branch.

In *L. burchellii* (Figure 5), contrary to the interpretation of Meisner (1840, 1857) and Wright (1925) who regarded the inflorescences to be bracteate, the inflorescences are terminal, sessile, ebracteate umbels. The umbels consist of up to ten flowers, with 1 or 2 mature flowers at a time. Vegetative growth is resumed from the axils of the leaves immediately below the umbels. On some specimens the inflorescences appear to be bracteate. These 'bracteate' umbels are in fact reduced lateral branches, each terminated by an ebracteate umbel. The leaves on these branches differ in size and shape from the foliage leaves on the rest of the plant. In the axil of the most distal leaf

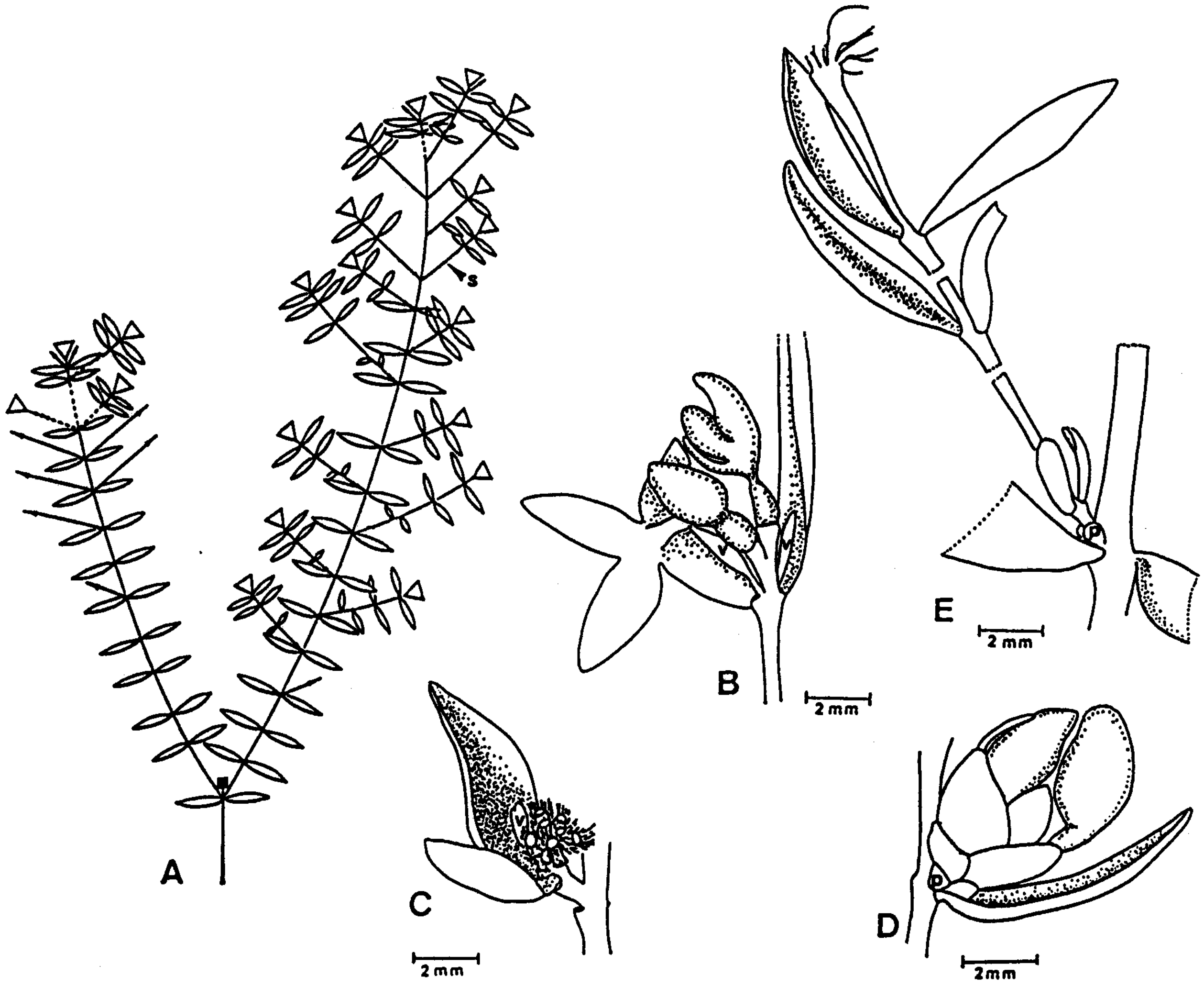

FIGURE 5.—*L. burchellii*. A, diagrammatic illustration of branching pattern of flowering branches; B, terminal ebracteate umbel, *Spreeth 155*; C, short lateral flowering shoot illustrating new vegetative shoot (v) in axil of bract-like leaf, *Spreeth 155*; D, short lateral flowering shoot, *Oliver 9251*; E, elongated lateral flowering shoot showing similar small prophylls (p) basally; s, scar of caducous bract-like leaves; ∇, umbel.

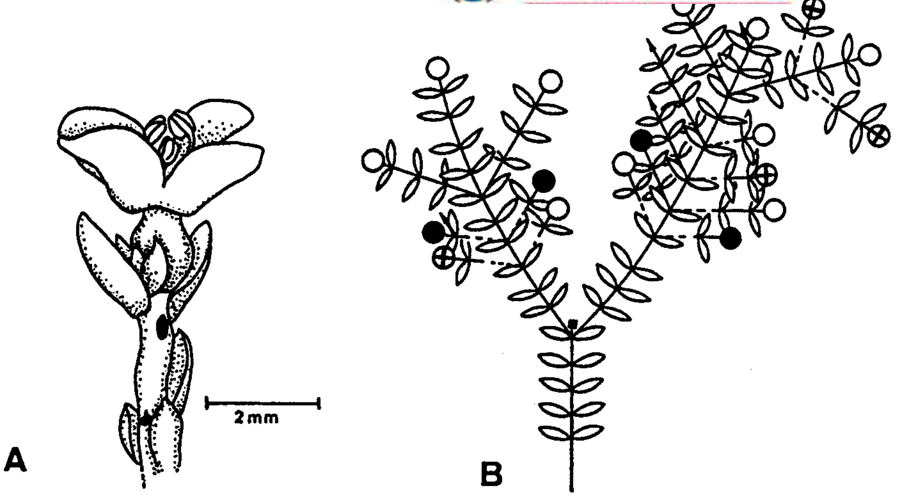

FIGURE 6.—*L. axillaris*. A, flowering shoot illustrating new vegetative shoot in axil of distal leaf, *Morley 174*; B, diagrammatic illustration of branching pattern of flowering branches; ■, scar of flower of previous year; ⊕, flower bud; ○, open flower; ●, fruit.

on one of these reduced flowering branches, a well-developed bud of the new vegetative shoot was observed. The lower two pairs of leaves on some of the elongated lateral flowering branches, resemble those modified foliage leaves of the reduced flowering branches. These leaves are often caducous. Vegetative growth is resumed by lateral branches developing from the axils of the upper leaves immediately below the umbel and may also originate from the leaf axils lower down on the main flowering branch. These lateral branches will terminate in umbels in the following flowering period. Flowering branches may develop at random on the main flowering branch, as in *L. nervosa*. These flowering branches arise from the axils of the leaves behind the most distal leaf pair during the same flowering period. The main flowering branch thus has the appearance of a racemose inflorescence.

Determinate inflorescences

Meisner (1840) described the flowers of *L. axillaris* as being axillary, opposite or scattered, always solitary, with two intra-axillary bracteoles. In his later publication (1857) he referred to the flowers as being subsolitary, axillary or rarely terminal. Wright (1915) regarded the flowers as being axillary and solitary. According to Weberling & Herkommer (1989) the flowers of *L. axillaris* are solitary, axillary with two transverse bracteoles.

The flowers of *L. axillaris* were found to be solitary and terminal. A well-developed bud of the new vegetative shoot occurs in the axil of one of the leaves of the pair of foliage leaves immediately below the flower (Figure 6). Lateral branches, each terminated by a solitary flower, develop at random on the main flowering branches within the same flowering period. These flowering branches arise from the axils of the foliage leaves below the leaf pair immediately behind the terminal flower. These lateral flowering branches vary in length and may even be reduced to having one pair of opposite leaves. Consequently the main flowering branch may have the appearance of a racemose or spicate inflorescence (Figure 6). Previous authors inadvertently regarded these leaves immediately behind the solitary flower as transverse bracteoles. It was found that the new vegetative growth originates in the axils of these leaves and terminates in flowers in the following flowering period. This growth is not always visible on herbarium material as specimens are usually collected when they are in full flower.

The flowers of *L. ruscifolia* were regarded by Compton (1953) as being 'solitary, axillary, sessile'. On studying fresh material in the fruiting stage, well-developed vegetative buds were found in the axils of the bracteoles (Figure 7). These bracteoles are in fact bracteose foliage leaves similar to those found on the short lateral flowering shoots in *L. burchellii*. In *L. ruscifolia* the flowers are therefore solitary and terminal on much reduced, lateral, flowering shoots which develop at random in the axils of the foliage leaves on the main flowering branches giving them a spicate appearance (Figure 7). Occasionally the lateral flowering shoot may consist of an additional pair of foliage leaves between the bracteose leaves (prophylls) and the flower (Figure 7). No terminal flower was observed on the main branches probably due to the abortion of the apical meristem. From the axil of the leaf behind the aborted meristem new vegetative growth may resume or a reduced flowering shoot may develop (Figure 7). Two scarious prophylls which resemble the bracteose leaves on the lateral flowering shoot, occur at the base of the developing lateral vegetative shoot (Figure 7).

Thus, in both *L. axillaris* and *L. ruscifolia* the inflorescences are determinate, consisting of solitary, terminal flowers.

Inflorescence structure within *Cryptadenia*

The inflorescences in *Crytadenia* are all cymose. In all the taxa well-developed buds of the new proliferating shoot develop in the axils of the upper leaf pair immediately behind the flower (Figure 8). These vegetative shoots usually terminate in flowers in the following flowering period, except in *C. filicaulis* and *C. grandiflora* where they may terminate in flowers in the same flowering period. Lateral branches may also arise at random from the axils of the leaves beneath the distal pair below the terminal flower on the main flowering branch. These branches vary in length and may even be reduced to only the terminal flower and a pair of foliage leaves as in *C. filicaulis* (Figure 8). Consequently the main flowering branch, as in *L. axillaris*, has the appearance of a racemose or spicate inflorescence. Lateral branches, each terminating in a solitary flower in the following flowering period, may also develop from the axils of the leaves lower down on the main flowering branches (Figure 8).

DISCUSSION

In the genus *Lachnaea* the flowers are arranged in terminal, indeterminate, capitate or umbellate inflorescences, or they are solitary and terminal. In *Cryptadenia* the flowers are solitary and terminal. Determinate inflorescences occur in both *Lachnaea* and *Cryptadenia*, whereas indeterminate inflorescences occur only in *Lachnaea*. Table 1.

In both genera the differentiation of a long shoot/short shoot system can be observed. In some taxa within *Lachnaea* and *Cryptadenia* this system is more conspicuous than in others. In both genera new vegetative growth arises from the axils of the foliage leaves immediately below the inflorescences, and this may terminate in an inflorescence within the same flowering period. Thus two generations of flowering branches may occur together on a plant (Figures 4 & 8).

Weberling & Herkommer (1989) regarded the terminal, single-flowered inflorescence found in *Cryptadenia* as a monotelic inflorescence. The inflorescence in *L. axillaris* and *L. ruscifolia* can therefore be regarded as monotelic. The polytelic inflorescence on the other hand would, according to their terminology, include the capitulum and umbel in *Lachnaea*. According to Weberling (1983) the polytelic type of inflorescence has probably been derived repeatedly from the monotelic type during the evolution of angiosperms by the reduction of the terminal flower and specialization of the paracladia of the monotelic system. The distal elements are reduced to single lateral flowers or lateral cymes, which constitute elements of an apical system composed of lateral flowers. Therefore the floral axis, instead of terminating in a single flower, terminates in a multi-flowered polytelic inflorescence.

According to Weberling & Herkommer (1989) *Gonystylus* Teijsm. & Binn. and *Amyxa* van Tiegh. of the Gonystyloideae which is regarded as a relatively primitive group, have monotelic synflorescences (synflorescence according to Weberling 1983). Within the Thymelaeoideae, the Gnidioideae and probably the Aquilarioideae, certain taxa were also found to have monotelic synflorescences. They came to the conclusion that, considering the other more or less primitive characters and the different taxonomic evaluation of those combinations, it was impossible to draw any taxonomic conclusions exclusively from the existence of the monotelic synflorescences within those taxa.

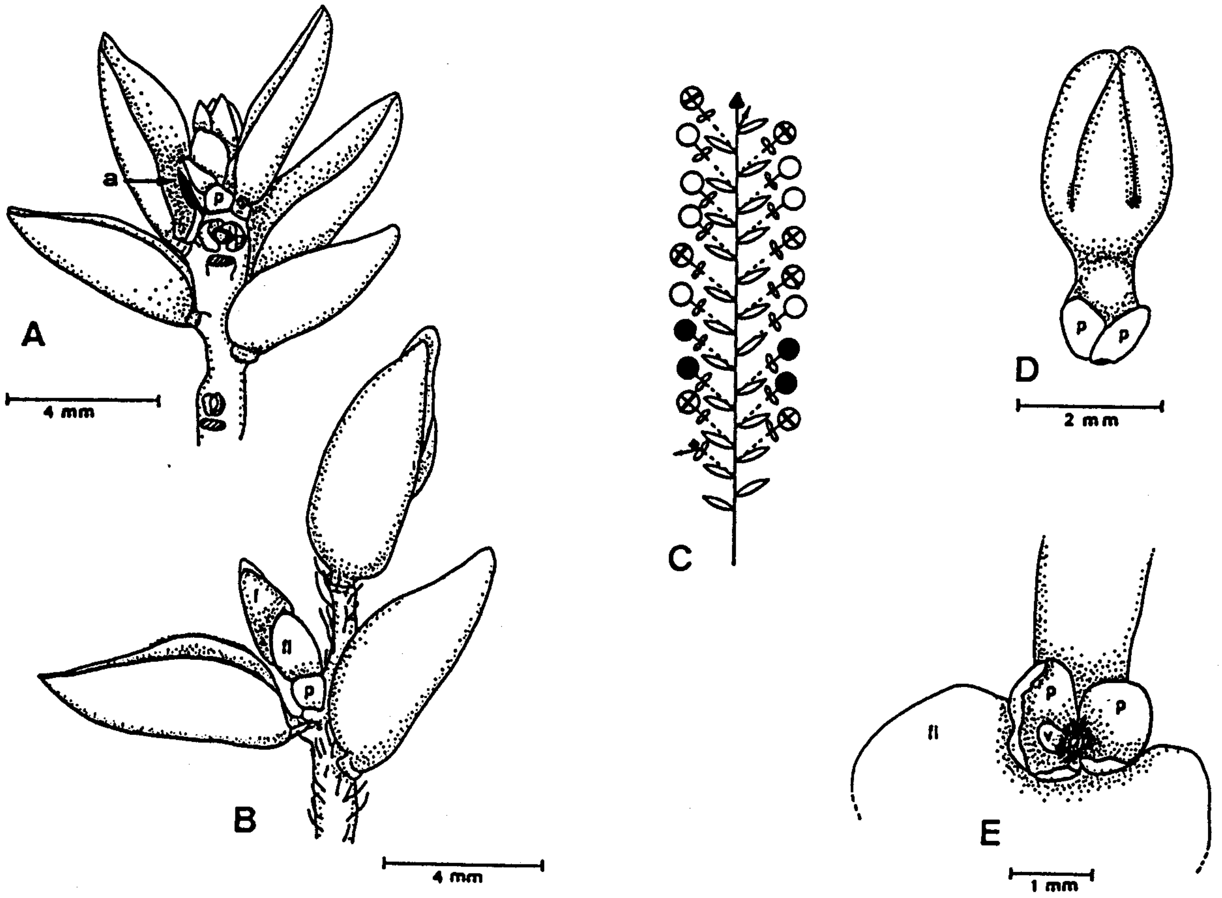

FIGURE 7.—*L. ruscifolia*. A, branch illustrating aborted apical meristem (a) being displaced by new lateral shoot developing from axil of distal foliage leaf, *Marshall 39*; B, main branch with short lateral flowering shoot, *Vlok 166*; C, diagrammatic illustration of branching pattern of flowering branches; D, flower bud with two bracteose leaves (p), *Vlok 166*; E, vegetative shoot (v) arising from axil of one of bracteose leaves; f, flower; fl, foliage leaf; ▲, aborted apical meristem; ⊕, flower bud; ○, open flower; ●, fruit; ■, scar of flower of a previous year.

TABLE 1.—Inflorescence characters of *Cryptadenia* and *Lachnaea*

Species	Indeterminate inflorescences				Determinate inflorescences with solitary flower
	Capitulum	Umbel	No. bracts	No. flowers	
Cryptadenia					
filicaulis					x
grandiflora					x
laxa					x
uniflora					x
Lachnaea					
aurea		x	8–10	± 50	
axillaris					x
burchellii		x	0	±10	
buxifolia	x		0	± 50 (mature)	
capitata	x		0	1–3 (mature)	
densiflora	x		0	± 12 (mature)	
diosmoides		x	0	6–20	
ericoides		x	0	2–8	
eriocephala		x	4	± 40	
filamentosa	x		0	20–50 (mature)	
funicaulis		x	0	6–20	
nervosa		x	0	4–14	
penicillata		x	4	± 8	
ruscifolia					x

Weberling & Herkommer (1989) regarded the ramification type of the polytelic synflorescences in the Thymelaeaceae to be thyrsic. Within many genera, according to them, these synflorescences have been reduced to racemes, spikes or umbels and in some taxa, as in *Lachnaea*, the umbel-like aggregation of flowers is combined with the formation of an involucrum.

From the above one could conclude that within *Lachnaea* the terminal, solitary flower is the primitive state and that the bracteate umbel is the advanced state.

CONCLUSION

The inflorescence morphology revealed determinate and indeterminate inflorescences in *Lachnaea* and only determinate inflorescences in *Cryptadenia*. In both genera the determinate inflorescence comprises a solitary, terminal flower. No distinct differences with regard to the inflorescence morphology could be found between these two genera. Therefore the inflorescence structure can not, as in the past, be used to distinguish between the two genera.

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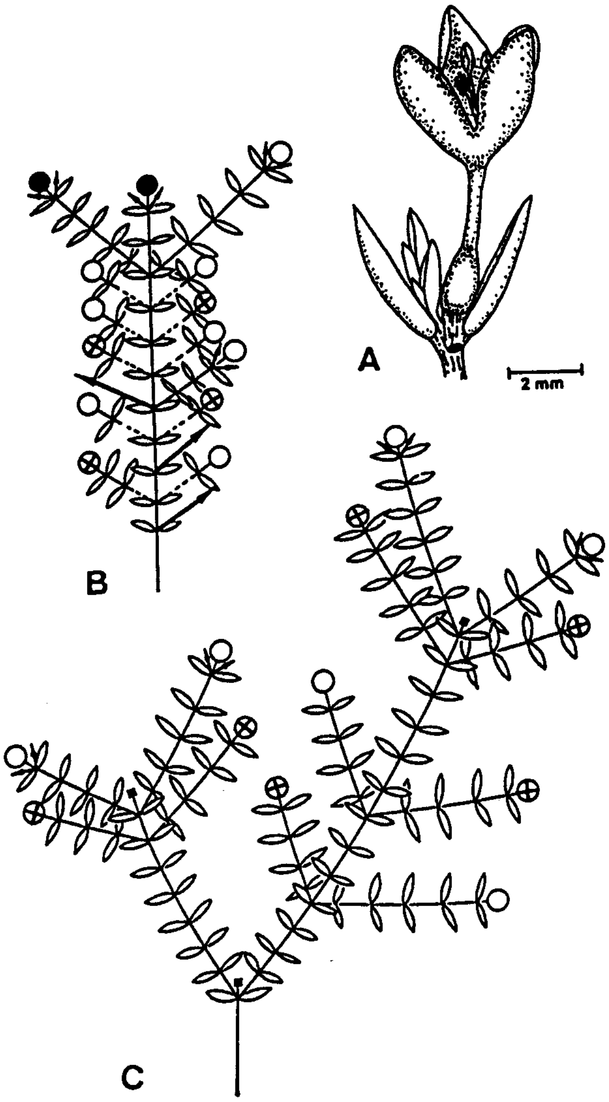

FIGURE 8.—Inflorescence structure and branching patterns of *Cryptadenia* species. A, flowering shoot in *C. laxa*, *Bodkin sub Guthrie 3585*. Diagrammatic illustration of branching pattern of flowering branches: B, *C. filicaulis*; C, *C. uniflora*; ⊕, flower bud; ○, open flower; ●, fruit; ■, scar of flower of a previous year.

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APPENDIX 4

THE GENERIC DELIMITATION OF *LACHNAEA* AND *CRYPTADENIA* (THYMELAEACEAE).*

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The generic delimitation of *Lachnaea* and *Cryptadenia* (Thymelaeaceae)

J.B.P. BEYERS* and J.J.A. VAN DER WALT**

Keywords: *Cryptadenia*, generic delimitation, *Lachnaea*, Thymelaeaceae

ABSTRACT

The current generic delimitation of *Lachnaea* L. and *Cryptadenia* Meisn. was investigated. A multidisciplinary approach was followed. This included a study of the habit, phyllotaxis, morphology and anatomy of the leaves and flowers, pollen morphology and karyology.

No major differences were found between the two genera. The range of variation of certain diagnostic characters of these genera is such that the genera merge into each other. It was concluded that the two genera are congeneric and the inclusion of *Cryptadenia* within *Lachnaea* is proposed.

UITTREKSEL

Die huidige generiese afbakening van *Lachnaea* L. en *Cryptadenia* Meisn. is ondersoek. 'n Multidissiplinêre benadering is gevolg. Die groeiwyse, blaarstand, morfologie en anatomie van die loofblare en blomme, stuifmeelmorfologie en kariologie is bestudeer.

Geen noemenswaardige verskille tussen die twee genera is gevind nie. Die variasiegradiënt van sekere diagnostiese kenmerke van hierdie genera is van so 'n aard dat die twee genera oorvleuel. Die insluiting van *Cryptadenia* binne die omskrywing van die generiese grense van *Lachnaea* word voorgestel.

CONTENTS

INTRODUCTION

The genera *Lachnaea* L. and *Cryptadenia* Meisn. belong to the family Thymelaeaceae. Their close affinity is reflected by their placement in the different classification systems of the Thymelaeaceae (Endlicher 1847, sec. Domke 1934; Meisner 1857; Bentham & Hooker 1880; Gilg 1894 and Domke 1934). Only Baillon (1880) did not recognize *Cryptadenia* as a separate genus but treated it as a section of *Lachnaea*. He found that the flowers of *Lachnaea* varied from regular to irregular and that intermediate forms made it impossible to split the genus.

The genus *Lachnaea*, based on two species, was established by Linnaeus in 1753. In subsequent publications, such as Lamarck (1792, 1804), Salisbury (1808) and Sims (1813, 1814), new species were described, but only in 1840 was a detailed taxonomic account of the genus published by Meisner based on Drège's collections. Three sections were established, namely *Sphaeroclinium* Meisn., *Conoclinium* Meisn. and *Microclinium* Meisn., based on the inflorescence structure. Thirteen species and six infraspecific taxa were recognized (Meisner 1840). Meisner's earlier contribution on *Lachnaea*, with some alterations, was published in De Candolle's *Prodromus* in

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which 18 species and 17 infraspecific taxa were recognized (Meisner 1857). The most recent taxonomic treatment of the genus was that of Wright (1915) in *Flora capensis*. In this treatment no mention was made of the sections established by Meisner. Wright (1915) recognized 19 species and eight infraspecific taxa, and referred to one imperfectly known species. In the Addenda to the same volume, a further two species and two infraspecific taxa were added (Wright 1925). Since then four new species have been described, namely three by Compton (1934a & b, 1953) and one by Fourcade (1934). When Thoday (1924) published the revision of the genus *Passerina*, he noted that the type of *Passerina laniflora* C.H. Wright was not a *Passerina* species but indeed a species of *Lachnaea*. Bond (1982) proposed the new combination, *Lachnaea laniflora* (C.H. Wright) Bond. *L. marlothii* Schltr. (Schlechter 1896) and *L. gracilis* Meisn. (Meisner 1840) were both overlooked by Wright. At present 29 species and eight infraspecific taxa are recognized (Van Wyk 1993).

The genus *Cryptadenia*, comprising five species, was established by Meisner in 1840 and was also based on Drège's collections (Meisner 1840). According to Meisner (1840) the main characters by which *Cryptadenia* can be distinguished from the closely related genus *Lachnaea*, are the glands which are positioned much lower down in the hypanthium just above the ovary, and by the conspicuous filaments which are adnate to the hypanthium. In De Candolle's *Prodromus* the same five species were recognized by Meisner (1857). The most recent taxonomic treatment of *Cryptadenia* was that of Wright (1915) in *Flora capensis*, in which four of the species in Meisner's treatment were recognised, whereas one was reduced to synonymy. A new species was also described. The criterion used by Wright (1915) to delimit the two genera was the position of the flowers: 'Flowers axillary, solitary' in *Cryptadenia* opposed to 'Flowers terminal, capitate, rarely solitary' in *Lachnaea*. At present *Cryptadenia* is considered to comprise five species (Van Wyk 1993).

Both *Lachnaea* and *Cryptadenia* are endemic to the Cape Province. *Lachnaea* is found mainly at high altitudes from Clanwilliam in the north to the Cape Peninsula in the south and eastwards along the coastal areas as far as Uitenhage. Further inland it occurs on the mountain ranges from Ceres through Worcester to Ladismith (Bond & Goldblatt 1984). The centre of diversity is in the southwestern area. *Cryptadenia* occurs on sandy flats and lower mountain slopes from Piketberg in the west to the Cape Peninsula, and along the coastal areas to Bredasdorp and inland to Ceres (Bond & Goldblatt 1984).

Lachnaea and its closest related genus, *Cryptadenia*, are both characterized by the absence of petals and by a hypanthium having scales below the insertion of the stamens. Beyers & Van der Walt (1994), contrary to Wright (1915), found that the two genera could not be distinguished on the inflorescence structure. With the large number of herbarium specimens now available, compared to the small range of material on which earlier studies were based, a sound delimitation of the two genera is possible. The aim of the present investigation was to compare the two genera using a multidisciplinary approach, with the view to establishing whether they are congeneric or not. Besides the morphological study accompanied by field work, anatomical, palynological and karyological investigations were undertaken to assess the taxonomic value of the evidence derived from these sources.

MATERIALS AND METHODS

Eighteen taxa were selected, 14 from *Lachnaea* and four from *Cryptadenia*. The aim in selecting the taxa was to have as broad a representation as possible of all the taxa in the two genera. The criteria used for selecting the *Lachnaea* taxa were as follows: a, taxa representative of the three sections instituted by Meisner (1840), taking into account the variation in each section; b, all taxa with solitary flowers; c, the position of the scales in the floral tube; d, the stigma types; e, the degree of asymmetry of the calyx lobes.

Wright's revision of *Lachnaea* and *Cryptadenia* in *Flora capensis* (1915 and 1925) was followed. Type specimens and quoted specimens were examined to verify the species concepts for the taxa used in this study. Infraspecific variation has been included in each taxon studied and has not been treated individually.

Four of the five species of *Cryptadenia* currently recognized were studied. *Cryptadenia breviflora* Meisn. was excluded as it is an intermediate taxon between *Cryptadenia grandiflora* (L. f.) Meisn. and *Cryptadenia uniflora* Meisn., which Levyns (1950) considered to be a hybrid between these two species.

The following species were studied: *Lachnaea aurea* Eckl. & Zeyh., *L. axillaris* Meisn., *L. burchellii* Meisn., *L. buxifolia* Lam., *L. capitata* (L.) Meisn., *L. densiflora* Meisn., *L. diosmoides* Meisn., *L. ericoides* Meisn., *L. eriocephala* L., *L. filamentosa* (Thunb.) Meisn., *L. nervosa* Meisn., *L. penicillata* Meisn., *L. ruscifolia* Compton, *Cryptadenia filicaulis* Meisn., *C. grandiflora*, *C. laxa* C.H. Wright and *C. uniflora* (author citations according to Van Wyk 1993).

For the anatomical study of the foliage leaves, both material preserved in FAA and herbarium material was used. The herbarium material was soaked in 50% ethanol for 24 hours, thereafter treated as preserved material. The preserved material was dehydrated and embedded in wax according to the tertiary butyl method (Johansen 1940). Transverse sections 12 µm thick were made through the middle of the leaf blade with the aid of a rotary microtome and stained with Alcian Green Safranin (AGS) (Joel 1983). Scanning electron micrographs of the leaf surfaces were obtained by mounting portions from the same region of the leaf blade of herbarium material on stubs which were coated with gold and studied with a Joel JSM-35 scanning electron microscope. Epidermal cell patterns of the leaf blade were studied under a light microscope after the adaxial and abaxial epidermal layers were peeled off and mounted in water.

The anatomical study of the flowers was done on material preserved in FAA. The preserved material was dehydrated and embedded in wax according to the tertiary butyl method (Johansen 1940). For the anatomy, transverse

TABLE 1.—Voucher specimens of *Lachnaea* species for the leaf anatomy, floral anatomy, pollen morphology and karyology

Species	Voucher specimens	Leaf anatomy	Floral anatomy	Pollen morph.	Karyology
aurea	*Beyers 135* (STE)	×		×	
axillaris	*Beyers 127, 180* (STE)	×	×		
	Beyers 197 (STE)		×		
	Schlechter 7702 (BOL)	×			
	Steyn 331 (NBG)			×	
burchellii	*Oliver 9241* (STE)	×		×	
	Oliver 9251 (STE)	×			
buxifolia	*Beyers 118* (STE)		×	×	
	Beyers 122 (STE)	×		×	
	Taylor 8648 (STE)			×	
capitata	*Beyers 128* (STE)		×	×	
	Beyers 138 (STE)	×			
	Hugo 231 (STE)			×	
densiflora	*Beyers 115* (STE)	×		×	
	Beyers 117 (STE)			×	
	Beyers 145 (STE)	×		×	×
	Beyers 171 (STE)	×			
	Beyers 177 (STE)	×			
diosmoides	*Beyers 181* (STE)	×	×	×	×
	Spreeth 158 (STE)	×			
	Van Niekerk 53 (BOL)			×	
ericoides	*Beyers 172* (STE)	×			×
	McDonald 1842 (STE)			×	
	Zeyher 3776 (SAM)			×	
eriocephala	*Beyers 54* (STE)	×	×	×	×
	Spreeth 141 (STE)			×	
filamentosa	*Beyers 110* (STE)	×		×	
	Taylor 10770 (STE)			×	
funicaulis	*Beyers 125* (STE)	×		×	
	Du Toit s.n. (STE)				×
nervosa	*De Kock 152* (STE)	×		×	
penicillata	*Beyers 173* (STE)	×		×	
	McDonald 16321 (STE)			×	
	Oliver & Fellingham 9145 (STE)			×	
ruscifolia	*Beyers 193* (STE)	×			
	Goldblatt & Manning 8870 (STE)	×			
	Vlok 2084 (STE)	×	×	×	

sections were used almost exclusively and longitudinal sections were resorted to only to verify the points of attachment of the floral structures. Serial sections were cut 12 µm in thickness. AGS staining (Joel 1983) as well as Crystal Violet and Erythrosin staining (Jackson 1926) were used. The AGS staining technique was found to give better results.

Pollen was taken from herbarium specimens and from material collected in the wild. For both light microscopy (LM) and scanning electron microscopy (SEM), pollen was acetolyzed according to Erdtman (1960). Acetolyzed samples were prepared for both SEM and LM according to the method of Marais (1990). At least 20 pollen grains of each taxon were measured. Transverse sections ± 15 µm thick were made with the aid of a freeze-microtome to study the structure of the pollen wall of two taxa in each genus. The terminology used to describe the pollen morphology is that of Walker & Doyle (1975).

For chromosome studies inflorescences were fixed in Carnoy's fixative in the field. After 24 hours, the fixative was replaced with 85% ethanol for 15 minutes and then finally replaced with 70% ethanol. Flower buds were stained in Snow's fluid (1963). The anthers were removed and squashed in 45% acetic acid.

Voucher specimens for the anatomy of leaves and flowers and for pollen morphology and karyology are given in Tables 1 and 2.

RESULTS

Habit

In *Lachnaea* the species are sparsely to densely branched, erect shrubs or erect to sprawling shrublets 0.15–2.00 m high. There is considerable variation in appearance and size among, and sometimes within species. The *Cryptadenia* species are erect or sprawling, moderately to densely branched shrublets 0.12–0.80 m high. In both genera the species are either basally single-stemmed, multi-stemmed, or single-stemmed and multi-stemmed within a single species. The branches are leafy, usually with an adpressed pubescence, later becoming naked and glabrous, and usually marked with the leaf scars of the fallen leaves.

Morphology of foliage leaves

In *Lachnaea* the leaves are alternate or decussate, but in *L. burchellii* they are opposite or subopposite and in *L. diosmoides* they are alternate to subopposite. The leaves are adpressed, ascending, patent or occasionally reflexed, and imbricate to scattered. The leaves in *Cryptadenia* are decussate, adpressed, ascending or sub-patent, and imbricate or scattered. In both genera the orientation and position of the leaves on the axis may vary inter- and intraspecifically.

TABLE 2.—Voucher specimens of *Cryptadenia* species for the leaf anatomy, floral anatomy, pollen morphology and karyology

Species	Voucher specimens	Leaf anatomy	Floral anatomy	Pollen morph.	Karyology
filicaulis	*Boucher 5071* (STE)	×	×		
	Esterhuysen 34370 (BOL)			×	
	McDonald 1989 (STE)				×
	Oliver 9803 (STE)	×	×		
grandiflora	*Beyers 129, 151* (STE)	×		×	
	Beyers 196 (STE)		×		
laxa	*Bolus 7875* (BOL)	×		×	
	I. Oliver 4 (STE)	×	×		
uniflora	*Beyers 136* (STE)	×	×	×	×
	Haynes 447 (STE)			×	

The leaves in both genera are always entire and usually sessile except in *L. ruscifolia* where they may be subpetiolate. The shape of the leaves in *Lachnaea* can be linear-elliptic to elliptic, oblanceolate, obovate or ovate (Figures 1, 2). Again, the variability is not only among the species but may be within a particular species (Figure 2). The leaves range in size from 2–34 × 0.6–9.0 mm. Within some species, as in *L. filamentosa* (Figure 2), the variation in leaf size may be considerable, namely from 5–34 × 1.8–12.0 mm. In *Cryptadenia* the shape of the leaves can be lanceolate, narrowly elliptic, narrowly ovate or obovate. In *C. uniflora* the leaves are always narrowly elliptic but in *C. grandiflora* they are narrowly elliptic, narrowly obovate, obovate or oblanceolate. As in *Lachnaea* the shape and size of the leaves vary inter- and intraspecifically (Figure 3). The range in leaf size is 2.9–12.8 × 0.6–3.2 mm. The leaves in both genera are coriaceous but in *L. densiflora* they are occasionally semi-succulent.

In *Lachnaea* the abaxial side of the leaves may be flat, obtusely convex to convex, or faintly keeled or keeled in the distal half. Adaxially they may be flat, obtusely concave or concave. Both surfaces of the leaves are usually smooth. However, the abaxial surface in *L. ruscifolia* and *L. nervosa* has several longitudinal ribs, whereas in *L. diosmoides* there is only a single midrib. The abaxial surface is usually green and shiny, whereas the adaxial surface is usually pale green, dull and white-punctulate but in some species the leaves are concolorous. The concolorous leaves are usually green but in *L. buxifolia*, and sometimes in *L. filamentosa*, they are glaucous. In *Cryptadenia* the abaxial side of the leaves is convex, faintly

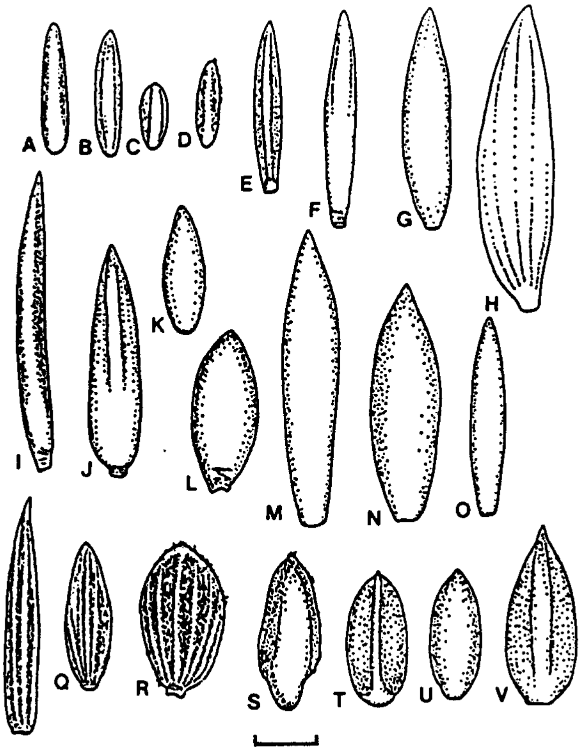

FIGURE 1.—*Lachnaea*. Variation of leaf shape and size, abaxial view. A, *L. eriocephala*, *Beyers 54*; B & C, *L. ericoides*, *Beyers 172*; D, *L. funicaulis*, *Beyers 125*; E, *L. diosmoides*, *Beyers 181*; F, *L. capitata*, *Beyers 128*. G & H, *L. burchellii*: G, *Oliver 9251*; H, *Spreeth 155*. I–L, *L. densiflora*: I & J, *Oliver 9129*; K, *Taylor 12023*; L, *Beyers 171*. M–O, *L. aurea*, *Beyers 135*; P & Q, *L. nervosa*, *De Kock 152*; R, *L. ruscifolia*, *Beyers 193*; S, *L. penicillata*, *Beyers 173*. T–V, *L. axillaris*: T, *McDonald 1395*; U & V, *Beyers 197*. Scale bars: A–R, 3 mm; S–V, 1 mm.

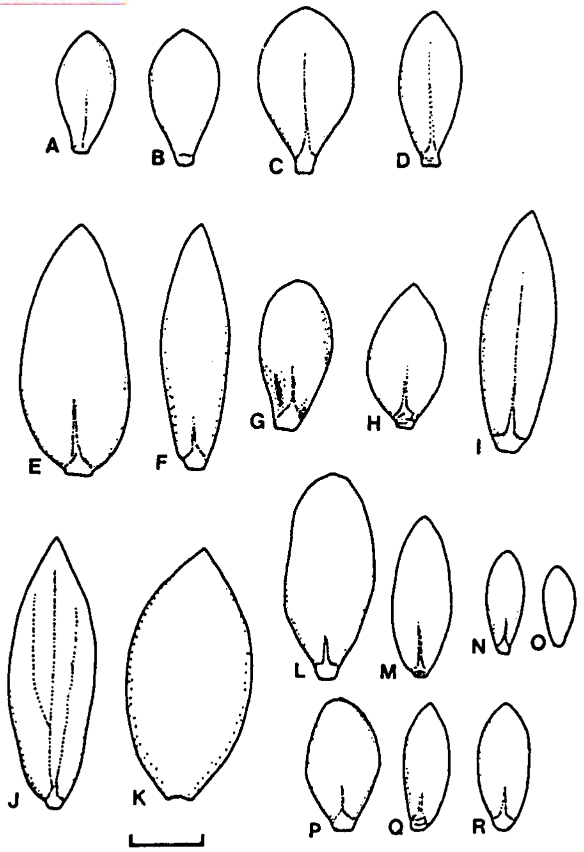

FIGURE 2.—*Lachnaea buxifolia* and *L. filamentosa*. Variation in leaf shape and size, abaxial view. A–I, *L. buxifolia*: A–C, *McDonald 1683*; D, *Marais s.n.*; E–G, *Beyers 118*; H & I, *Beyers 122*. J–R, *L. filamentosa*: J & K, *Low 1246*; L & M, *Beyers 109*; N & O, *Beyers 118*; P–R, *Taylor 12001*. Scale bar: 6 mm.

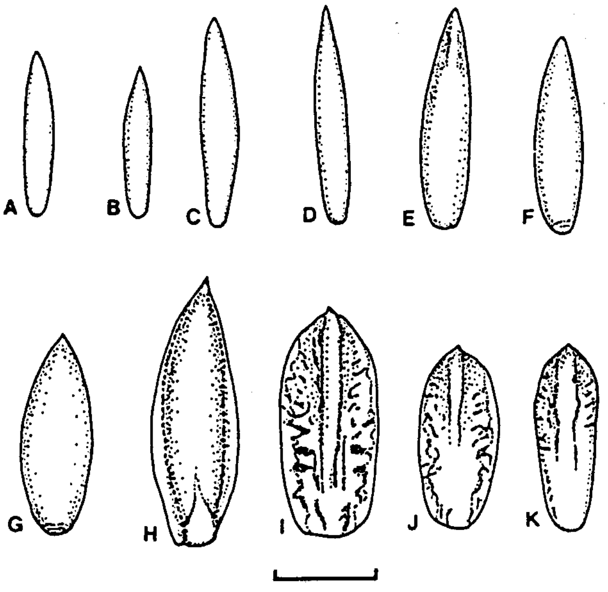

FIGURE 3.—*Cryptadenia*. Variation in leaf shape and size, abaxial view. A–C, *C. filicaulis*: A, *McDonald 1988*; B & C, *Oliver 9803*. D, *C. uniflora*, *Beyers 136*; E & F, *C. laxa*, *I. Oliver 4*. G–K, *C. grandiflora*: G, *Beyers 136*; H, *Vlok 2179*; I–K, *Beyers 129*. Scale bar: 3 mm.

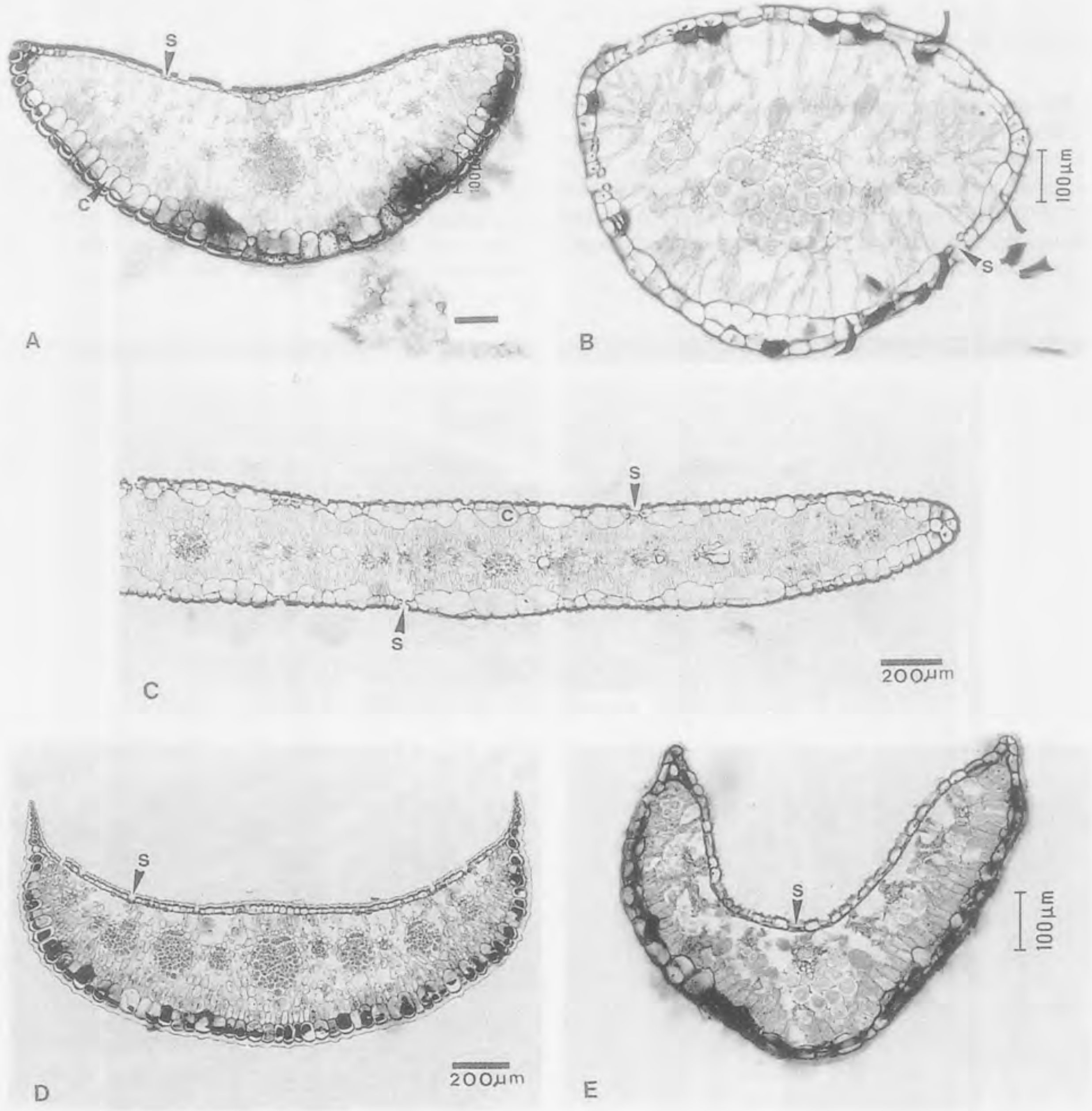

FIGURE 4.—*Lachnaea* and *Cryptadenia*. Leaf transections, adaxial face above. A, *L. eriocephala, Beyers 54*; B, *L. densiflora, Beyers 115*; C, *L. buxifolia, Beyers 122*; D, *C. grandiflora, Beyers 151*; E, *C. laxa, I.Oliver 4*. c, large cells of inner layer of biseriate epidermis; s, stoma. Scale bars: A, B, E, 100 µm; C, D, 200 µm.

keeled or keeled, smooth or transversely rugulose towards the margins with a shiny, green surface, whereas adaxially they are concave with a smooth, dull, pale green, white-punctulate surface.

In *Lachnaea* the leaves are glabrous or pubescent at the margins but the marginal pubescence is often deciduous, whereas in *Cryptadenia* the leaves are always glabrous.

Anatomy of foliage leaves

In transverse sections the leaves of most *Lachnaea* species and all *Cryptadenia* species appear concave adaxially and convex abaxially (Figure 4A, D, E), but in *L. densiflora* both surfaces are flat or the adaxial one may be slightly convex (Figure 4B); in *L. buxifolia* (Figure 4C) and *L. filamentosa* both surfaces are flat.

Cuticle

In *Lachnaea* the cuticle is well developed and of even thickness on both sides, or thicker on the abaxial side, whereas in *Cryptadenia* the well-developed cuticle is always thicker abaxially. Under the SEM the adaxial and abaxial cuticles of the *Lachnaea* species are unsculptured (Figure 5A, D), undulate (Figure 5B, E) or minutely papillate (Figure 5C, F). In *Cryptadenia* the cuticle is usually minutely papillate adaxially, as in *C. grandiflora* (Figure 6A), but in *C. filicaulis* it is unsculptured (Figure 6B). The relief of the abaxial cuticle is either minutely papillate (Figure 6C) or undulate (Figure 6D). In *C. grandiflora*, however, both types of cuticular sculpturing occur abaxially.

Waxes in the form of small flakes occur commonly on the adaxial leaf surfaces of *Cryptadenia* species and most *Lachnaea* species (Figure 7A, C). In both genera, when waxes are present on the abaxial surface, they are sparse and flakelike (Figure 7B, D). Cutter (1978) is of the opinion that it is this wax deposit that gives the 'bloom' to glaucous leaves.

Trichomes, when present, are non-glandular and uniseriate in both genera.

Epidermis

In both genera the adaxial epidermis is composed of small cells with thin anticlinal and inner tangential walls and slightly thicker outer tangential cell walls. In *L. eriocephala* the outer tangential cell walls are the thickest (Figure 4A). In *Lachnaea* and *Cryptadenia* the adaxial epidermis is uniseriate as in *L. eriocephala* (Figure 4A)

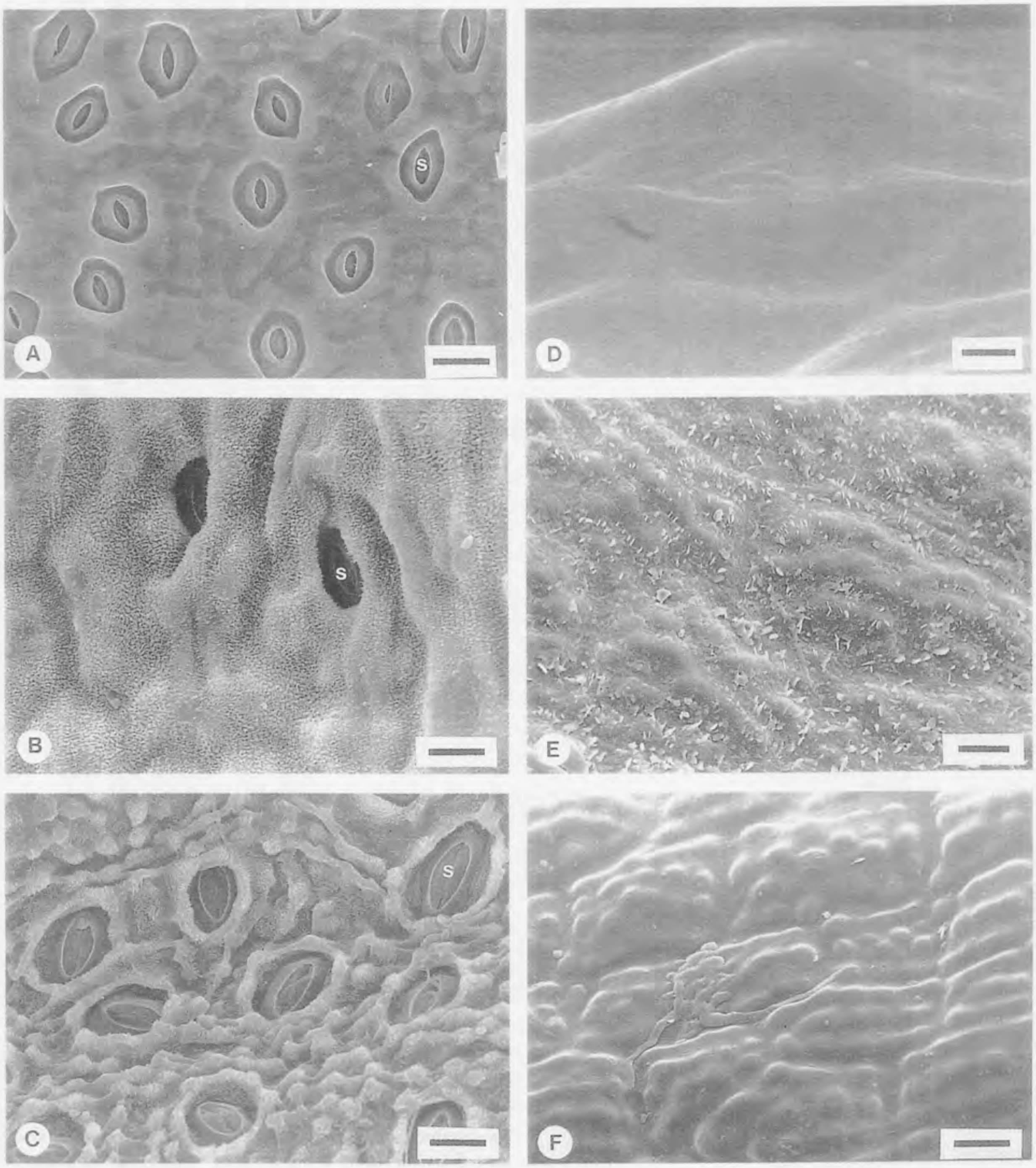

FIGURE 5.—*Lachnaea*. SEM micrographs of cuticular relief of leaf. A–C, adaxial surface: A, *L. funicaulis*, *Beyers 125*, smooth; B, *L. buxifolia*, *Beyers 122*, undulate; C, *L. ericoides*, *Beyers 172*, minutely papillate. D–F, abaxial surface: D, *L. ericoides*, *Beyers 172*, smooth; E, *L. diosmoides*, *Beyers 181*, undulate; F, *L. funicaulis*, *Beyers 125*, minutely papillate. s, stoma. Scale bars: A–F, 20 µm.

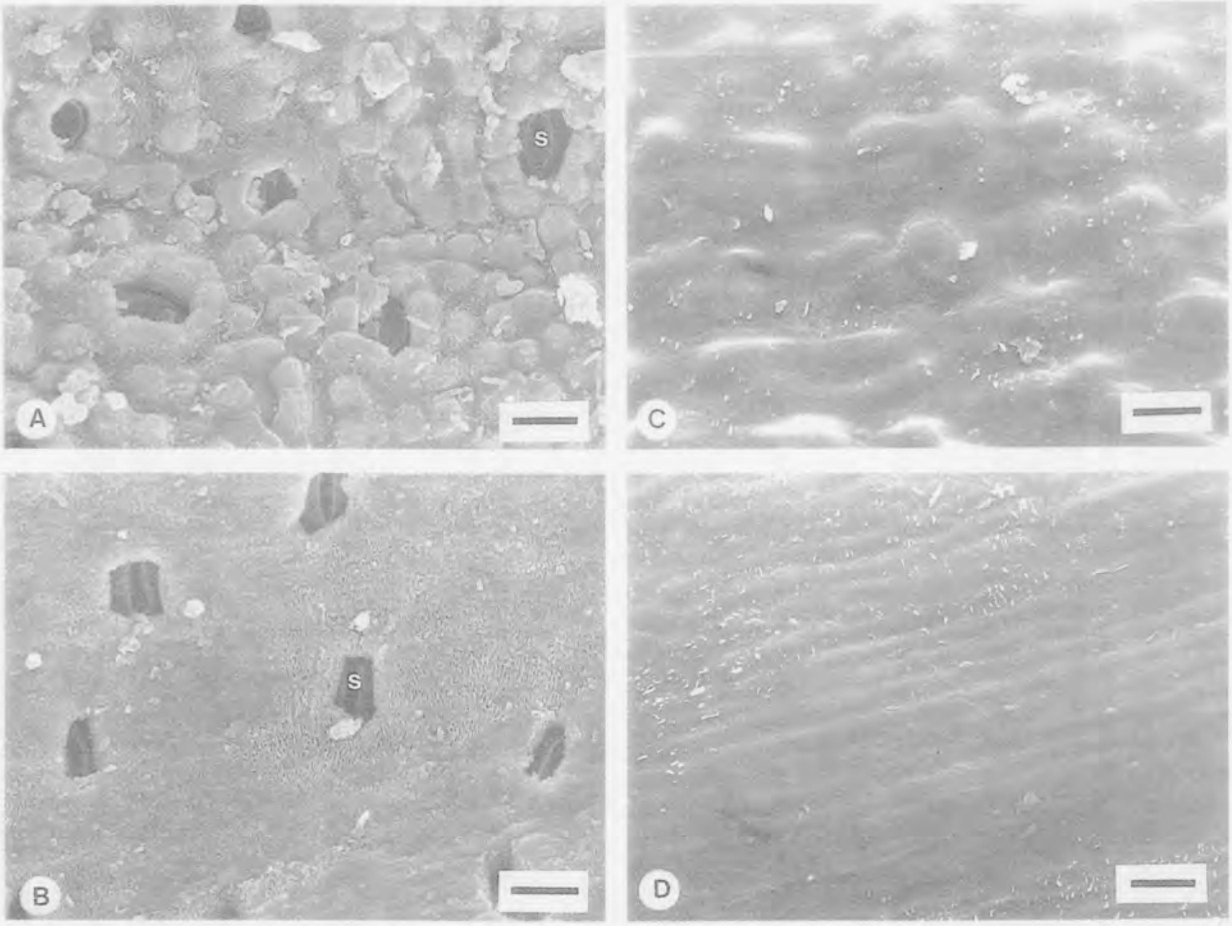

FIGURE 6.—*Cryptadenia*. SEM micrographs of cuticular relief of leaf. A, B, adaxial surface: A, *C. grandiflora*, *Beyers 129*, minutely papillate; B, *C. filicaulis*, *Boucher 5071*, smooth. C, D, abaxial surface: C, *C. grandiflora*, *Beyers 129*, minutely papillate; D, *C. filicaulis*, *Boucher 5071*, undulate. s, stoma. Scale bars: A–D, 20 µm.

and *C. grandiflora* (Figure 8D, E), incompletely uniseriate (occasional cells with periclinal walls) as in *L. ericoides* (Figure 8A) and *C. uniflora* (Figure 8C), incompletely biseriate (occasional cells without periclinal walls) as in *L. densiflora* (Figure 4B) and *C. laxa* (Figure 4E) or biseriate as in *L. buxifolia* (Figure 4C). The abaxial epidermis is usually biseriate in both genera. However, in *L. axillaris* and *L. ericoides* (Figure 8A) it is incompletely biseriate and in *C. grandiflora* it may be uniseriate (Figure 8D) or incompletely biseriate (Figure 8E).

When the epidermis is biseriate, the cells of the inner layer are usually larger than those of the outer layer. The epidermis contains mucilage, except in *C. grandiflora* where it was not always observed. The mucilage may be present in the cells of the inner and outer epidermal layers, or in the cells of the inner layer only.

Tannin occurs in the epidermis of *L. axillaris*, *L. burchellii*, *L. diosmoides*, *L. ericoides*, *L. funicaulis*, *L. penicillata*, *C. grandiflora* and *C. uniflora*.

Druse crystals were observed in the epidermis of *L. buxifolia*, *L. filamentosa* and *L. ruscifolia*, and sometimes in the adaxial epidermis of *C. grandiflora*.

Stomata

The stomata in both genera are anomocytic and sunken except in *L. funicaulis* and *L. penicillata* where they are on the same level as the outer walls of the surrounding epidermal cells. In *Lachnaea* the leaves are epistomatic or amphistomatic but in *Cryptadenia* they are only epistomatic. When the leaves are amphistomatic, there are usually more stomata adaxially.

Mesophyll

In both genera the cells of the mesophyll are chlorenchymatous and palisade-like (elongated perpendicular to the axis) with the exception of *C. grandiflora* where they are either palisade-like (Figure 8E) or short and more or less round (Figure 8D). As a result of the size of the intercellular spaces, the leaves can be classified as dorsiventral or isobilateral. When dorsiventral, the smaller intercellular spaces occur abaxially and the larger ones adaxially as in *L. axillaris*, *L. diosmoides* (Figure 8B), *L. ericoides*, *L. eriocephala*, *L. funicaulis*, *L. nervosa*, *L. penicillata*, *C. filicaulis*, *C. laxa* and *C. uniflora* (Figure 8C). The isobilateral arrangement occurs in *L. aurea*, *L. burchellii*, *L. buxifolia*, *L. capitata*, *L. densiflora* (Figure 4B), *L. filamentosa* and *L. ruscifolia*. In *C. grandiflora* however, a dorsiventral or an almost isobilateral arrangement is found.

Tannin occurs in the parenchymatous cells surrounding the median vascular bundle in *L. penicillata* and sometimes in the mesophyll in *C. grandiflora*.

Druse crystals are present in the mesophyll of *L. aurea, L. axillaris, L. burchellii, L. buxifolia, L. capitata, L. densiflora, L. filamentosa, L. nervosa* and the four *Cryptadenia* species, and in the vascular tissue of *L. filamentosa*.

Venation and vascular bundles

The venation in both genera is reticulate and the vascular bundles are collateral. As Metcalfe & Chalk (1950) stated, no internal phloem occurs in the midrib.

In both genera, extraxylary fibres occur abaxially in association with the vascular bundles. A prominent median fibre strand (Figure 8) is present in all the species except in *L. buxifolia* and *L. filamentosa*. In addition to the prominent median fibre strand, equally prominent fibre strands occur in association with the larger lateral vascular bundles in *L. nervosa, L. ruscifolia* and *C. grandiflora* (Figure 8E). In *L. ruscifolia* the median and larger lateral strands extend to the abaxial epidermis.

Extraxylary fibres not associated with the vascular bundles, occur along the lateral margins immediately below the epidermis in *L. aurea* (Figure 8F).

Morphology of flower and fruit

Pedicel/floral articulation

The flowers in *Lachnaea* are either sessile or shortly pedicellate with pedicels up to 2.5 mm long. In *Cryptadenia* the flowers are always sessile. In *L. eriocephala, L. funicaulis* and *L. penicillata* the sericeous to villous pedicels elongate in the fruiting stage and remain on the plant long after the fruit has been shed. These hairy pedicels are responsible for the woolly appearance of the old inflorescences. The flowers of *Lachnaea* and *Cryptadenia* are at their bases surrounded by a ring of trichomes, which occurs at the floral articulation of the sessile flowers or on the pedicels.

Hypanthium

In *Lachnaea* the basal portion of the hypanthium is ellipsoid to widely ellipsoid, ovoid to widely ovoid, or obovoid, whereas the portion above the plane of circumscision is funnel-shaped, cylindrical, obconical, cup-shaped or cup-shaped with a sigmoid curve at the base (Figure 9). In *Cryptadenia* the basal portion of the hypan-

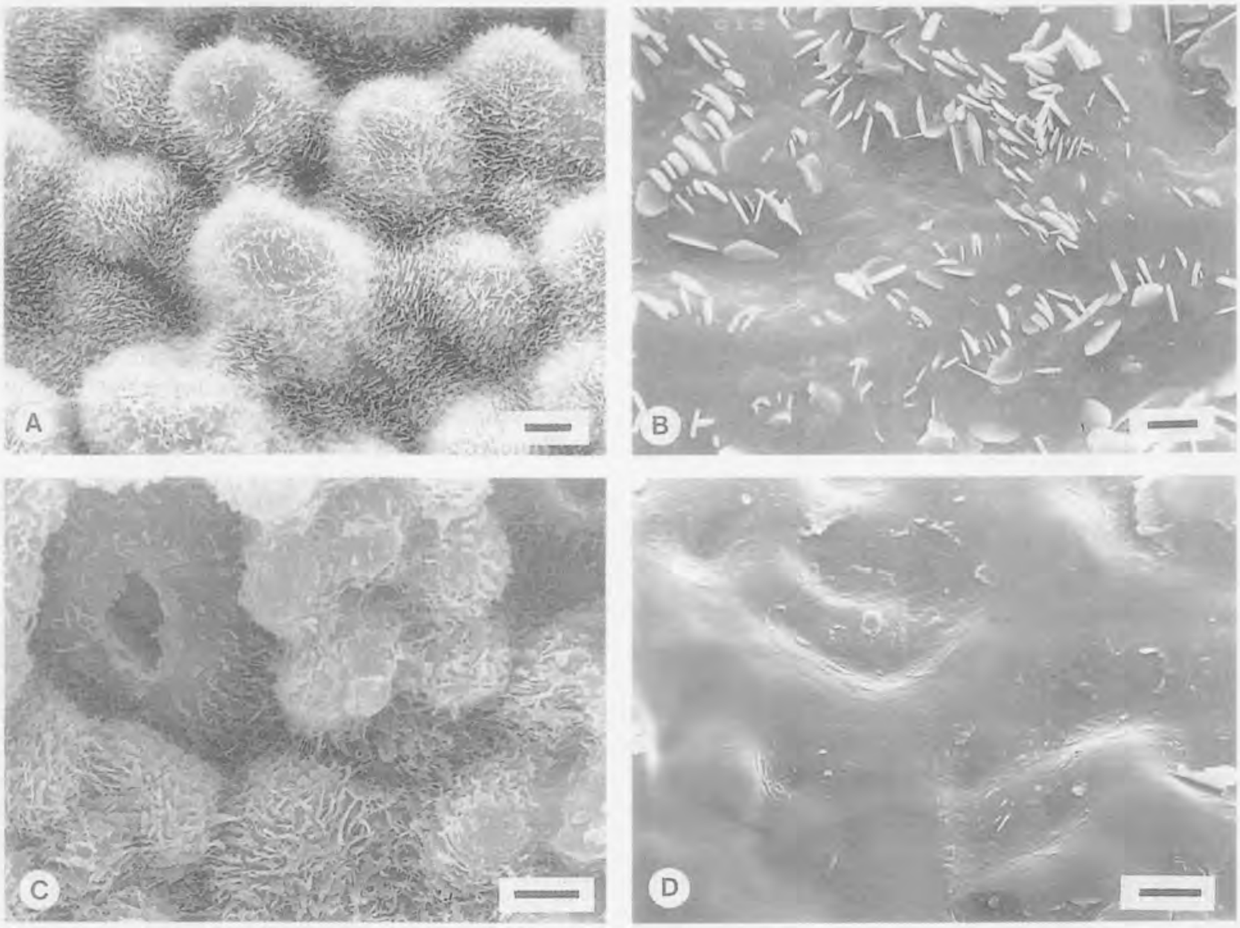

FIGURE 7.—*Lachnaea* and *Cryptadenia*. SEM micrographs of flaky surface wax on leaf. A, B, *L. aurea*, *Beyers 135*: A, adaxial surface; B, abaxial surface. C, D, *C. laxa*, *Bolus 7875*: C, adaxial surface; D, abaxial surface. Scale bars: A–D, 5 µm.

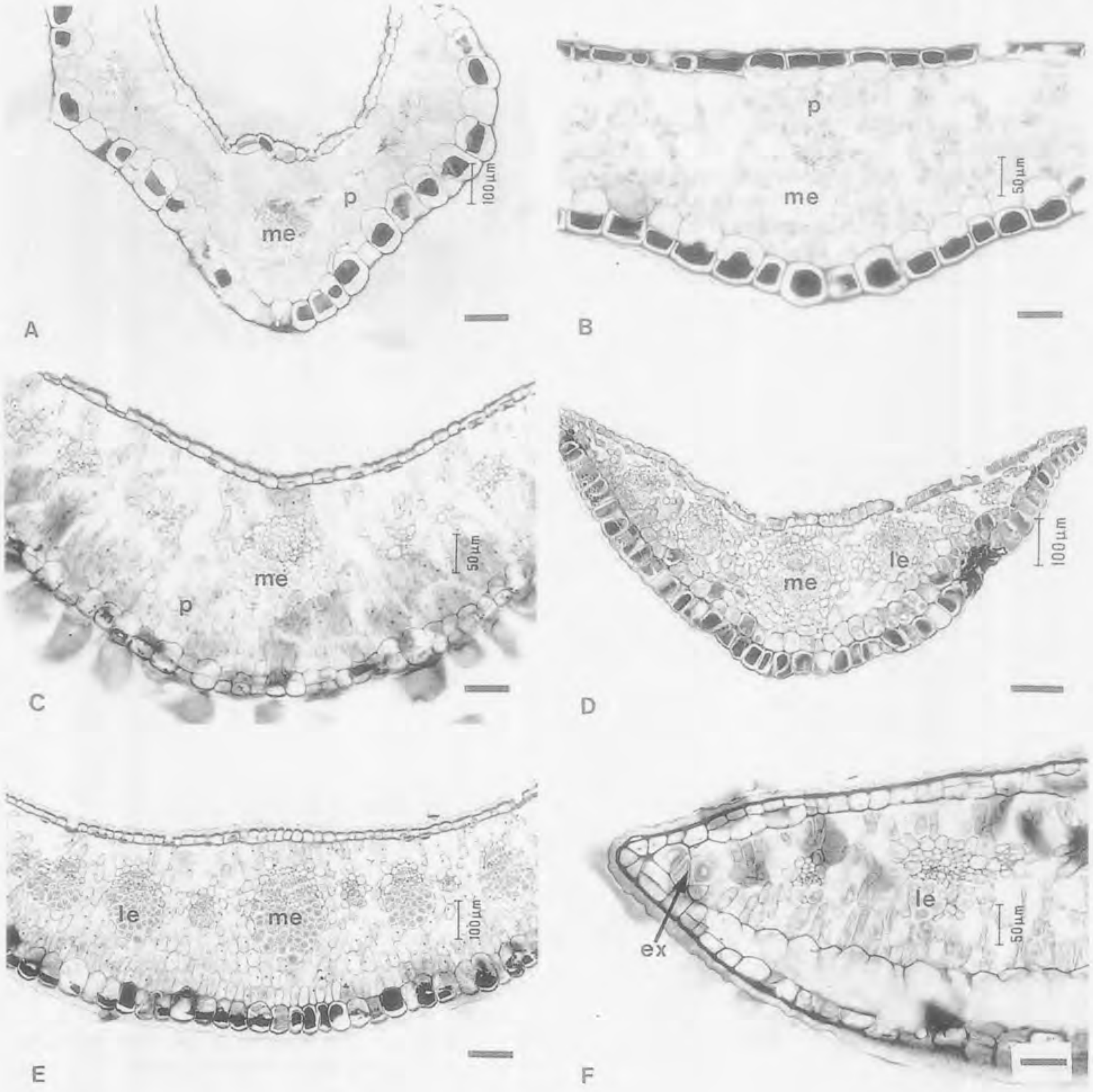

FIGURE 8.—*Lachnaea* and *Cryptadenia*. Leaf transections, adaxial face above. A–E, median vascular bundle: A, *L. ericoides*, *Beyers 172*; B, *L. diosmoides*, *Beyers 181*; C, *C. uniflora*, *Beyers 136*; D, *C. grandiflora*, *Beyers 129*; E, *C. grandiflora*, *Beyers 151*. F, leaf margin of *L. aurea*, *Beyers 54*, showing extraxylary fibres (ex) along lateral margin. p, palisade-like chlorenchyma; me, median extraxylary fibre strand; le, lateral extraxylary fibre strand. Scale bars: A, D, E, 100 µm; B, C, F, 50 µm.

thium is ovoid or ellipsoid, whereas the upper portion above the plane of circumscision is funnel-shaped or cup-shaped (Figure 9). The position of the plane of circumscision, expressed as a percentage of the length of the base to the total length of the hypanthium, varies from 20–80% in both genera. The upper portion of the hypanthium abscises soon after seedset at the plane of circumscision. The length of the hypanthium ranges from 1.5–17.5 mm in *Lachnaea* and from 2.2–11.0 mm in *Cryptadenia*.

The outer surface of the base of the hypanthium is pubescent or glabrous in *Lachnaea* and pubescent in *Cryptadenia*, whereas the inner surface is usually glabrous in both genera, except in *L. buxifolia* and *C. uniflora* where it is pubescent. The outer and inner surfaces of the upper portion of the hypanthium in both genera are usually pubescent, but in *L. axillaris* the outer surface is glabrous.

In both genera the shape of the trichomes and type of pubescence on the outer surface of the hypanthium often changes around the plane of circumscision. In *L. burchellii* the trichomes on the basal portion are clavate, whereas those on the upper portion are longer and acicular (Figure 10). In *C. laxa* the trichomes of the basal portion are obtuse, whereas those of the upper portion are acicular. The pubescence on the outer surface of the hypanthium is denser in the vicinity of the scales in both *Lachnaea* and *Cryptadenia*. The upper portion of the hypanthium and the calyx are concolorous.

Calyx

The calyx in both genera comprises four sepals which are fused to the rim of the hypanthium. In *Lachnaea* the sepals vary from being almost equal to distinctly unequal, but with a gradual transition from one form to the other (Figure 11). In the distinctly zygomorphic forms the anterior lobe is usually the longest. The sepals are narrowly to widely elliptic, ovate to widely ovate, or obovate to widely obovate. The size of the anterior sepal ranges from 1.3–22.0 × 0.8–7.5 mm, that of the two lateral sepals from 1.3–7.5 × 0.6–4.5 mm, and that of the posterior sepal from 1.2–5.5 × 0.7–3.5 mm. Because the flowers of *L. axillaris* and *L. ruscifolia* are solitary, the outer sepals represent the posterior and anterior sepals and the two inner sepals represent the two lateral sepals. The abaxial surface of the sepals is pubescent, except in *L. axillaris* where it is glabrous. The adaxial surface of the sepals is usually pubescent, but in *L. aurea* and *L. nervosa* it is glabrous and in *L. axillaris* and *L. funicaulis* it is partly glabrous and partly pubescent. The calyx is white, cream, pink, pale blue, white or cream tinged with pink or blue, or yellow.

The sepals in *Cryptadenia* are almost equal (Figure 12), narrowly to widely elliptic, ovate or orbicular, varying in size from 1.6–10.7 × 1.2–5.8 mm with the apices acute, rounded or obtuse. The abaxial surface is pubescent whereas the adaxial surface is either glabrous or pubescent. The calyx is white, cream, white tinged with pink, pink or mauve-pink.

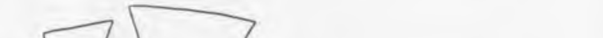

FIGURE 9.—*Lachnaea* and *Cryptadenia*. Hypanthia, showing plane of circumscision, lower dotted line; and scales, upper dashed line. A, *C. uniflora, Beyers 136*; B, *C. grandiflora, Beyers 129*; C, *L. densiflora, Oliver 9129*; D, *L. capitata, Beyers 138*; E, *C. filicaulis, Thompson 3789*; F, *L. axillaris, Bolus 8596*; G, *L. ericoides, Beyers 172*; H, *L. burchellii, Oliver 9241*; I, *L. funicaulis, Beyers 125*; J, *L. penicillata, Beyers 173*; K, *L. ruscifolia, Vlok 2084*; L, *C. laxa, Bolus 7875*; M, *L. nervosa, De Kock* 152; N, *L. diosmoides, Compton 7580*; O, *L. aurea, Beyers 135*; P, *L. filamentosa, Beyers 110*; Q, *L. buxifolia, Beyers 118*; R, *L. eriocephala, Beyers 54*. Scale bar: 2 mm.

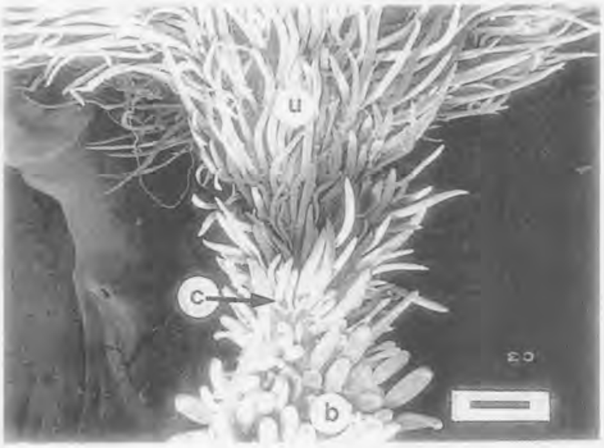

FIGURE 10.—*Lachnaea burchellii, Oliver 9241*. SEM micrograph of trichome structure on outer surface of hypanthium around circumscision zone. b, basal portion of hypanthium; c, plane of circumscision; u, upper portion of hypanthium. Scale bar: 200 µm.

The aestivation of the sepals is decussate-imbricate in *Lachnaea* and *Cryptadenia*.

Petals

Petals are absent in all taxa.

Androecium

Eight stamens in two whorls of four are present in all taxa. In *Lachnaea* the outer whorl, the antisepalous stamens, are episepalous, inserted on the basal portion of the sepals, or they are inserted on the rim of the hypanthium (Figure 11). The stamens of the inner whorl, the antipetalous stamens, are inserted on or very close to the rim of the hypanthium or a third of the way down the throat of the upper portion of the hypanthium as in *L. capitata* (Figure 11F).

In *Cryptadenia* the outer whorl, the antisepalous stamens, are episepalous, fused to the basal portion of the sepals as in *C. grandiflora* and *C. laxa*, or inserted in the upper throat of the hypanthium as in *C. uniflora* and *C. filicaulis* (Figure 12). The inner whorl, the antipetalous stamens, are inserted at the rim of the hypanthium in *C. laxa*, a quarter of the way down in the upper portion of the hypanthium in *C. uniflora* and a third of the way down in *C. filicaulis* and *C. grandiflora* (Figure 12). The stamens are fully exserted in *Lachnaea* (Figure 11). In *Cryptadenia* the antisepalous stamens of all the taxa and the antipetalous stamens of *C. laxa* are exserted. In the other *Cryptadenia* species only the anthers of the antipetalous stamens are exserted or semi-exserted (Figure 12).

The anthers are basifixed and introrse. In *Lachnaea* they are either spherical or oblate-spherical, whereas in *Cryptadenia* they are ellipsoid or ovoid.

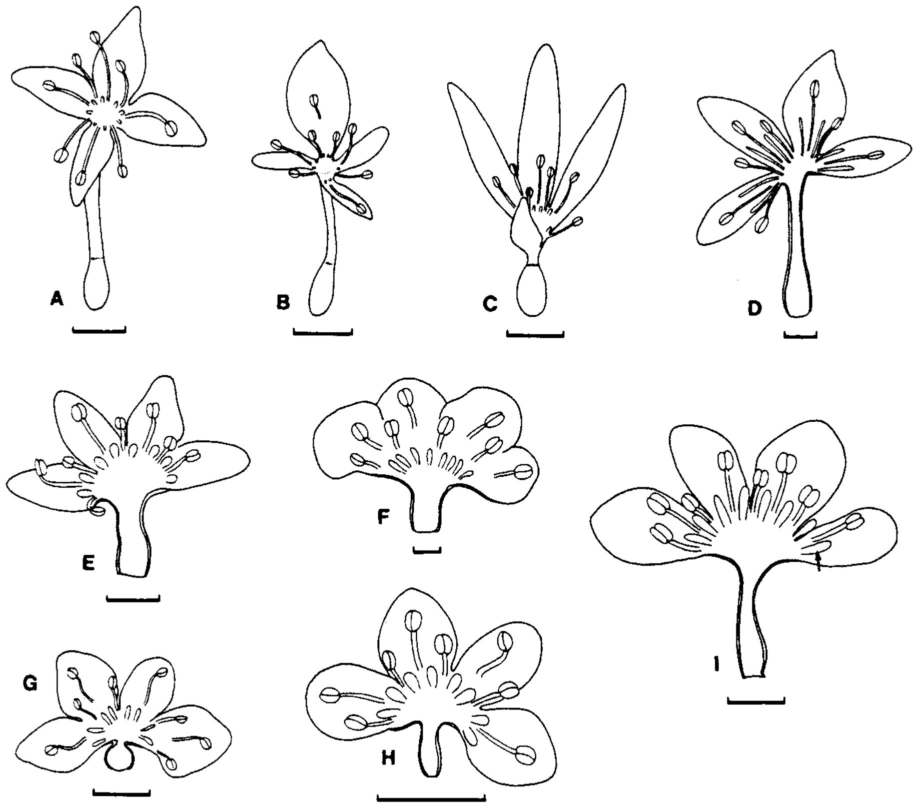

FIGURE 11.—*Lachnaea.* Flowers. A, *L. buxifolia, Beyers 122*; B, *L. filamentosa, Kruger 977*; C, *L. aurea, Gillett 4343*; D, *L. nervosa, De Kock 152*; E, *L. funicaulis, Marsh 758*; F, *L. capitata, Beyers 138*; G, *L. densiflora, Boucher 1767*; H, *L. ericoides, McDonald 2027*; I, *L. penicillata, Oliver & Fellingham 9145*. D–I: flowers split longitudinally with gynoecia removed; floral scales (arrow in I) shown in each flower below stamens. Scale bars: A–C, 4 mm; D–I, 2 mm.

Scales

Eight scales are inserted on the upper portion of the hypanthium below the attachment of the antipetalous stamens and alternating with the stamens. The position of the scales varies in different species of both genera. In most *Lachnaea* species the scales are inserted at the mouth of the hypanthium but in some species they are inserted two thirds or halfway down the upper portion of the hypanthium (Figure 11). In *Cryptadenia* they are inserted either at the mouth of the hypanthium or from midway to three quarters of the way down the upper portion of the hypanthium (Figure 12).

The shape of the scales varies in the different taxa. They can be linear, clavate, subrotund, capitate, ovoid or obovoid in *Lachnaea*, whereas in *Cryptadenia* they are subrotund, narrowly oblong, oblong or ellipsoid. In both genera the scales are either translucent-white or yellow. They are usually glabrous, except in *L. buxifolia* where they have long stiff trichomes at their apices. In all the *Lachnaea* species and in *C. laxa* the scales are basally attached to the hypanthium. In *C. filicaulis* the scales are basally and partly abaxially attached to the hypanthium, and in *C. grandiflora* and *C. uniflora* they are abaxially attached to the hypanthium.

Disc

A disc is absent in both genera.

Gynoecium

In *Lachnaea* the ovary is sessile, oblong, narrowly ellipsoid, ellipsoid, ovoid or obovoid, 0.5–4.4 × 0.2–2.5 mm, completely glabrous or glabrous with a tuft of hairs at the apex. In *L. filamentosa* the ovary is usually glabrous with a tuft of hairs at the apex but occasionally it may also be adpressed hairy and tufted at the apex.

In *Cryptadenia* the ovary is sessile, ellipsoid, 0.7–1.8 × 0.4–0.7 mm, usually glabrous, but in *C. filicaulis* it is

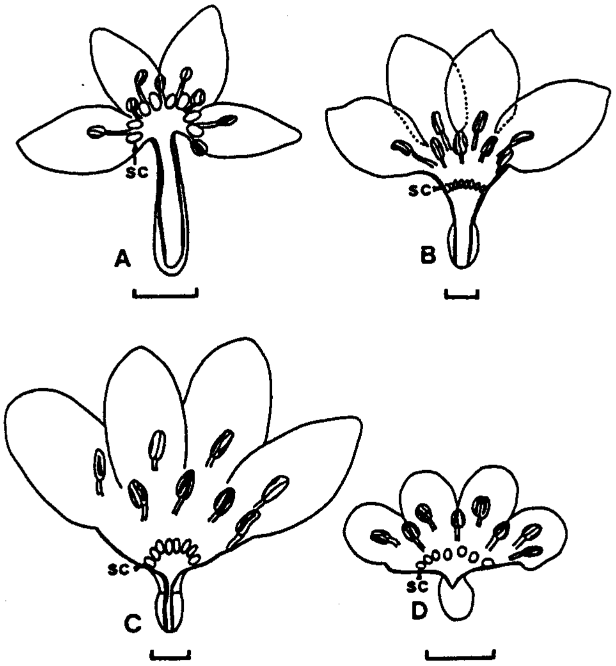

FIGURE 12.—*Cryptadenia.* Flowers split longitudinally with gynoecia removed. A, *C. laxa, I. Oliver 4*; B, *C. uniflora, Beyers 197*; C, *C. grandiflora, Beyers 151*; D, *C. filicaulis, Thompson 3789*. sc, scale. Scale bars: A–D, 2 mm.

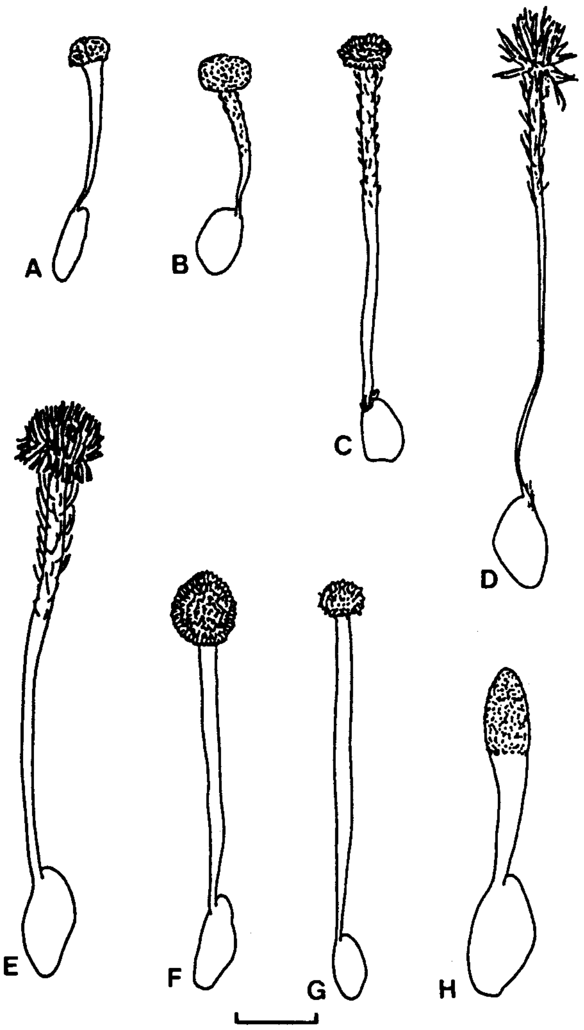

FIGURE 13.—*Lachnaea* and *Cryptadenia*. Gynoecia. A, *L. funicaulis, Marsh 758*; B, *L. ericoides, Beyers 172*; C, *L. ruscifolia, Goldblatt & Manning 8870*; D, *L. nervosa, De Kock 152*; E, *C. laxa, I. Oliver 4*; F, *C. uniflora, Beyers 197*; G, *C. grandiflora, Leighton BOL21142*; H, *C. filicaulis, Thompson 3789*. Scale bars: A–E, H, 1 mm; F, G, 2 mm.

either glabrous or pubescent towards the apex on the side where the style is inserted.

In both genera the ovary is unilocular, with a solitary anatropous ovule laterally attached near the top of the ovary; the style is laterally attached, linear or linear-obconical. The style is either completely glabrous or pubescent in the distal third to two thirds, or completely pubescent in *Lachnaea*, whereas in *Cryptadenia* it is usually glabrous but in *C. laxa* the distal half is pubescent.

The stigma in *Lachnaea* is either brushlike or capitate and papillate, or capitate and elongate-papillate (Figure 13). In *Cryptadenia* it is either conical or capitate and elongate-papillate, or brushlike (Figure 13).

Fruit

The fruit in both genera is an achene which is enclosed in the persistent base of the hypanthium. The pericarp is dry and thin, whereas the seed coat is thick and crustaceous.

Vascular anatomy of the flower

The basic vascular pattern is the same in both genera. The eight traces supplying the calyx, depart from the vascular tissue of the pedicel or the floral axis, where they are arranged in a continuous cylinder (Figure 14A) or in a ring of bundles (Figure 15A) in *Lachnaea* and in a continuous cylinder in *Cryptadenia* (Figure 16A). The eight sepal traces extend upwards in the hypanthium. The lateral bundles of the sepals arise commissurally after the departure of the antipetalous stamen traces (Figure 17A, C, G, H, I) or at the same point of departure of the antipetalous stamen traces (Figure 17B, D, E, F, J) at various levels on the hypanthium. The vascular supply of the sepals consists of a midrib bundle and two lateral bundles.

The stamens are single-trace organs. The antipetalous stamen traces are fused to the commissural sepal traces, and the antisepalous stamen traces to the sepal midrib traces at their point of origin from the stele. The stamen traces separate from the sepal traces in two whorls at different levels in the hypanthium. The antipetalous stamen traces diverge from the commissural sepal bundles before

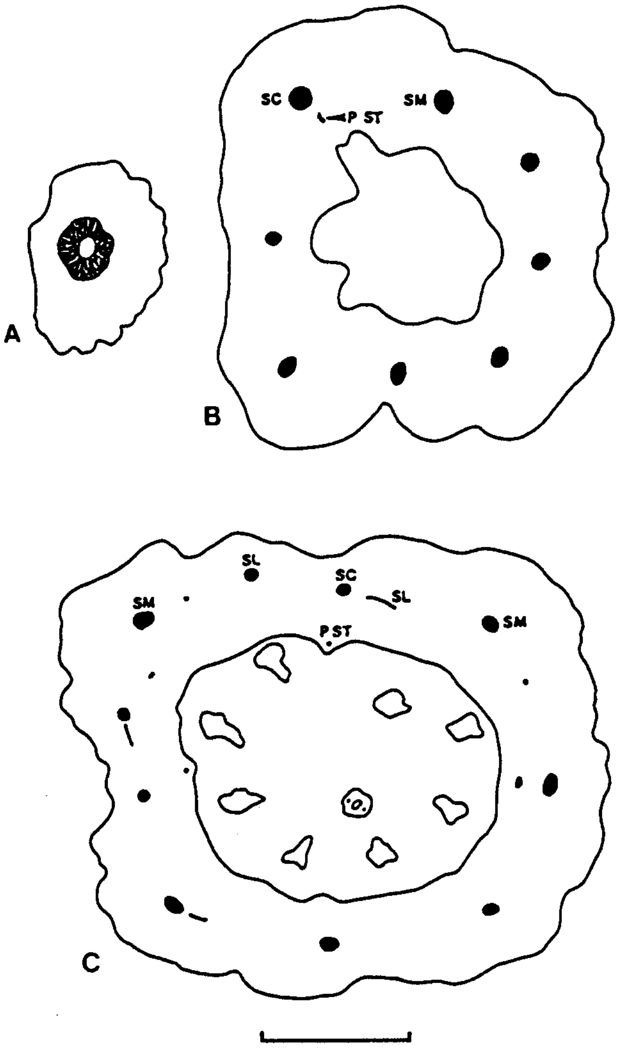

FIGURE 14.—*Lachnaea capitata, Beyers 128*. Floral anatomy. A, transection through floral axis. B, C, transections of flower: B, vasculature of hypanthium, separation of antipetalous stamen trace (P ST) from commissural sepal bundle (SC); C, splitting of commissural sepal bundles into sepal lateral bundles (SL). SM, sepal midrib bundle. Scale bar: 500 µm.

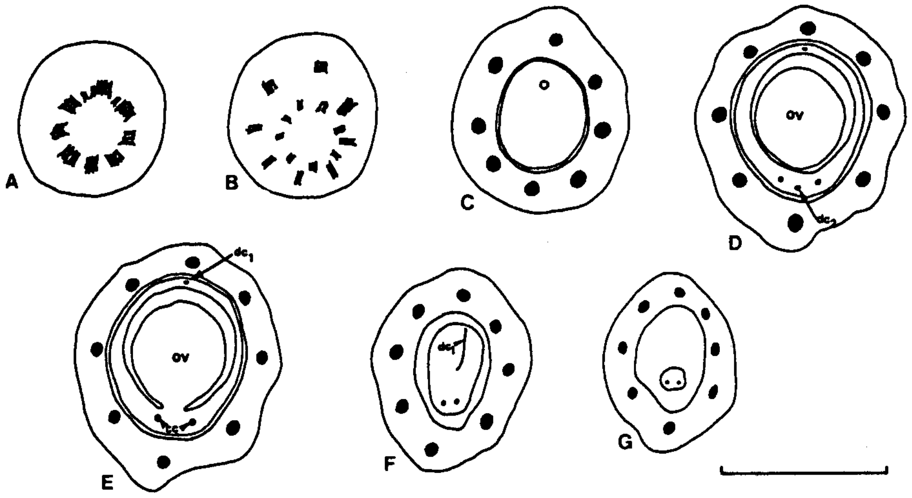

FIGURE 15.—*Lachnaea diosmoides*, *Beyers 151*. Transections of flower. A, pedicel showing ring of vascular bundles; B, base of hypanthium showing departure of whorl of eight bundles; C, hypanthium at base of ovary; D, lower portion of ovary; E, middle of ovary; F, top of ovary; G, base of style. o, ovary; ov, ovule; dc$_1$, dorsal carpellary of fertile carpel; cc, commissural carpellary; dc$_2$, dorsal carpellary of sterile carpel. Scale bar: 500 µm.

the antisepalous stamen traces diverge from the sepal midrib bundles (Figure 14). The antisepalous stamen traces leave the sepal midrib bundles at or just below the rim of the hypanthium, except in *C. filicaulis* (Figure 17H) where they depart a quarter of the way down the upper portion of the hypanthium. The antipetalous stamen traces leave the commissural sepal bundles at various levels on the upper portion of the hypanthium. In *L. buxifolia* (Figure 17F), *L. diosmoides* (Figure 17B), *L. eriocephala* (Figure 17D), *L. ruscifolia* (Figure 17E) and *C. laxa* (Figure 17J) these stamen traces depart near the rim of the tube, in *L. axillaris* (Figure 17C), *C. filicaulis* (Figure 17H), *C. grandiflora* (Figure 17I) and *C. uniflora* (Figure 17G) they depart midway and in *L. capitata* (Figure 17A) they depart three quarters of the way down the tube. The stamens become free from the hypanthium a short distance above the divergence of their traces as in *L. buxifolia* (Figure 17F) and *C. filicaulis* (Figure 17H), or are adnate to the hypanthium for some distance before becoming free as in *L. capitata* (Figure 17A) and *C. uniflora* (Figure 17G). In *L. buxifolia* (Figure 17F), *L. diosmoides* (Figure 17B), *L. eriocephala* (Figure 17D), *C. grandiflora* (Figure 17I) and *C. laxa* (Figure 17J) the antisepalous stamens are adnate to the basal portion of the sepals. In *Cryptadenia*, with the exception of *C. laxa*, the hypanthium, above the insertion of the scales, is further augmented by small median sepal bundles whose stelar extensions have been aborted (Figures 17G, H, I; 18A). Branches of these median sepal bundles may anastomose with the midrib bundles and the commissural sepal bundles. A rich vascular plexus exists in the hypanthium of *C. laxa* at the level of insertion of the scales (Figure 17J).

The eight scales arise as emergences from the adaxial wall of the hypanthium (Figure 19) at different levels on the upper portion of the hypanthium. They emerge a short distance below the divergence of the antipetalous stamen traces from the commissural sepal bundles, as in *L. capitata* (Figure 17A) and in *C. grandiflora* (Figure 17I), or just above the divergence of the antipetalous stamen traces and the lateral sepal traces from the commissural sepal bundles, as in *L. buxifolia* (Figure 17F) and in *C. laxa* (Figure 17J). No vascular tissue is present in or at the base of the scales, even in those taxa in which the scales are inserted in close juxtaposition to the sepal lateral bundles and the sepal midrib bundles. In *Lachnaea* the scales are usually non-glandular (Figure 20A) but in *L. axillaris* (Figure 20B) they are composed of compact thin-walled cells rich in cytoplasm with large nuclei, thus appearing glandular (Esau 1965). Similarly in *Cryptadenia* the scales are either non-glandular or appear glandular. No secretion was observed from the scales in either genus.

The ovary is bicarpellate. In *Lachnaea* the dorsal carpellary bundle of the fertile carpel is always present, whereas the dorsal carpellary bundle of the sterile carpel is present in *L. capitata* and *L. diosmoides* (Figure 15), but absent in *L. eriocephala* (Figure 21) and *L. axillaris*. In *Cryptadenia* the dorsal carpellary bundle of the fertile carpel is usually present, but absent in *C. filicaulis* (Figure 16) whereas the dorsal carpellary bundle of the sterile carpel is always present (Figure 16).

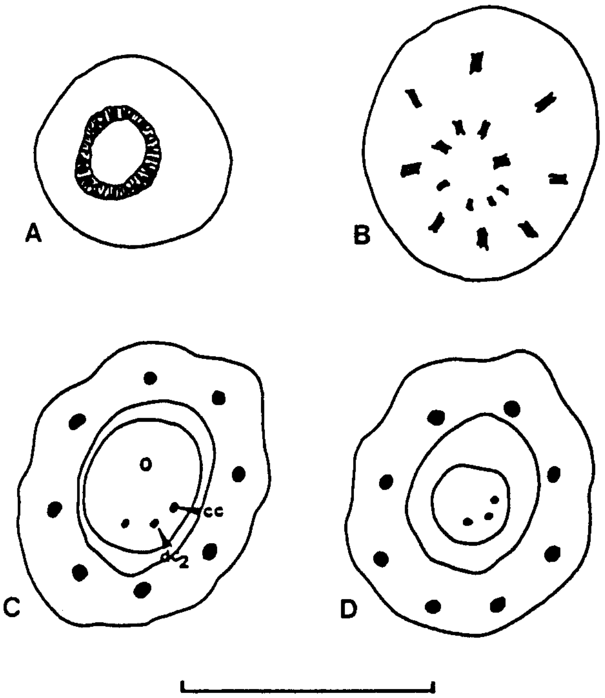

FIGURE 16.—*Cryptadenia filicaulis*, *Oliver 9803*. A, transection through floral axis. B–D, transections of flower: B, base of flower showing departure of whorl of eight bundles; C, lower portion of ovary showing abortion of dorsal carpellary of fertile carpel; D, base of style showing commissural carpellaries and dorsal carpellary of sterile carpel entering style. cc, commissural carpellary; dc$_2$, dorsal carpellary of sterile carpel. Scale bar: 500 µm.

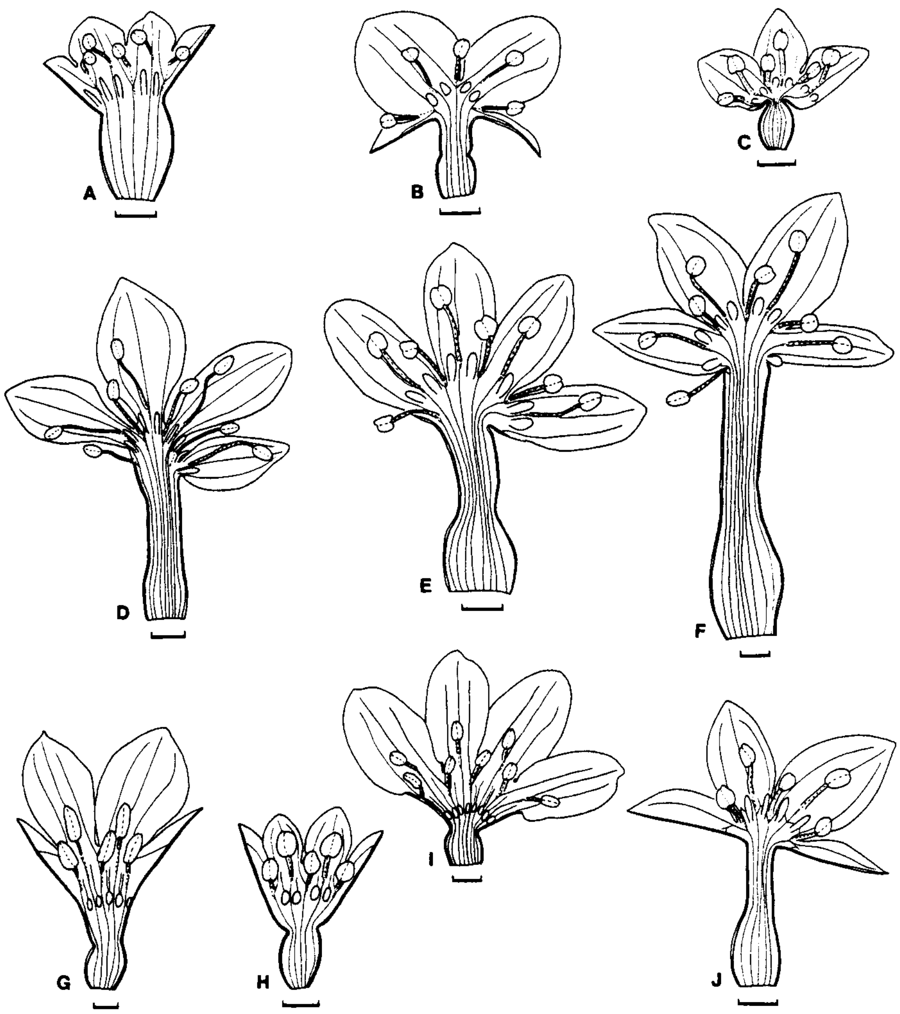

FIGURE 17.—*Lachnaea* and *Cryptadenia*. Vasculature of hypanthium, stamens and sepals. A, *L. capitata*, *Beyers 128*; B, *L. diosmoides*, *Beyers 151*; C, *L. axillaris*, *Beyers 197*; D, *L. eriocephala*, *Beyers 54*; E, *L. ruscifolia*, *Vlok 2084*; F, *L. buxifolia*, *Beyers 118*; G, *C. uniflora*, *Beyers 136*; H, *C. filicaulis*, *Oliver 9803*; I, *C. grandiflora*, *Beyers 196*; J, *C. laxa*, *I. Oliver 4*. Scale bar: 1 mm.

The commissural carpellary bundles (Heinig 1951) are closely associated with the dorsal bundle of the sterile carpel (Figures 15, 16), or when the latter is absent they are in the associated position (Figure 21).

The vasculature of the style is variable. It may consist of: the commissural carpellary bundles as in *L. diosmoides* (Figure 15), *L. axillaris* and *L. capitata*; the two ventral bundles of the sterile carpel arising from the split commissural carpellary bundles as in *L. eriocephala* (Figure 21); the dorsal bundle of the fertile carpel, the dorsal bundle of the sterile carpel and the commissural carpellary bundles as in *C. grandiflora*; the dorsal bundle of the sterile carpel and the commissural carpellary bundle as in *C. filicaulis* (Figure 16) and *C. uniflora*; or the dorsal bundle of the fertile carpel and the dorsal bundle of the sterile carpel as in *C. laxa*.

Pollen morphology

Pollen grains of the *Lachnaea* and *Cryptadenia* species examined, have the same basic morphology. The grains are monads, globose and polyforate (Figure 22) with a diameter of 22–52 µm in *Lachnaea* and 40–50 µm in *Cryptadenia* (Table 3).

The pollen is tectate and supra-ornate (Figure 22). Erdtman (1971) describes the sculpture pattern as crotonoid. The sexine is thicker than the nexine. The sexine is attached to the nexine by means of columellae, which unite into a tectum above. The tectum is reticulate with supratectal triangular projections. These supratectal structures are trihedral to shallowly trihedral with the basal sides straight as in *L. buxifolia* (Figure 23A), *L. ruscifolia* (Figure 23B) and *C. uniflora* (Figure 23E) or emarginate as in *L. aurea* (Figure 23C), *L. eriocephala* (Figure 23D) and *C. laxa* (Figure 23F). A vestigial spinule occurs at

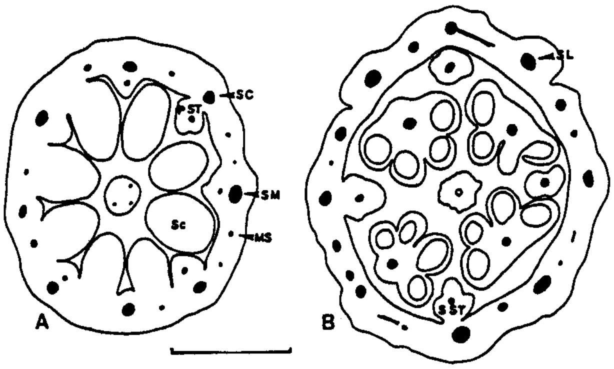

FIGURE 18.—*Cryptadenia filicaulis*, *Oliver 9803*. Transection of hypanthium of flower. A, at level where scales (Sc) separate from hypanthium; B, where antisepalous stamens (S ST) separate from tube. P ST, antipetalous stamens; SM, sepal midrib bundle; SC, commissural sepal bundle; SL, sepal lateral bundle; MS, median sepal bundle. Scale bar: 500 µm.

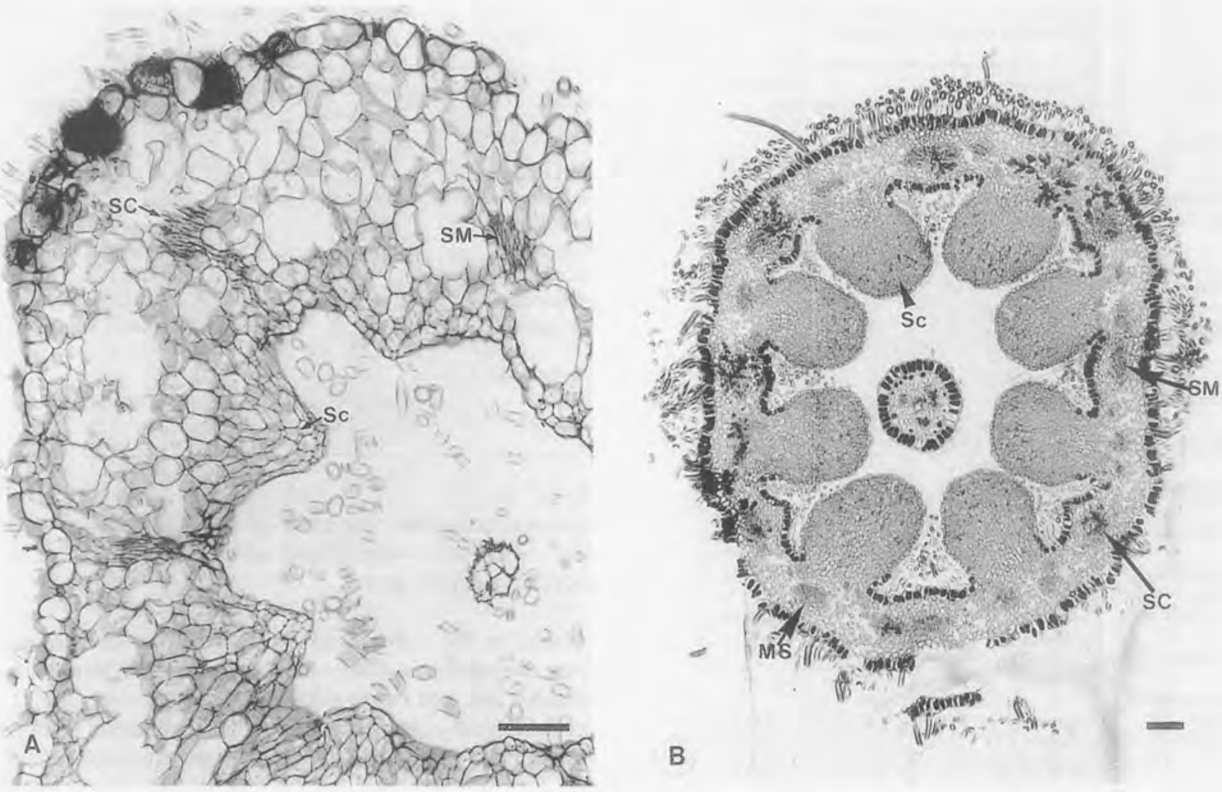

FIGURE 19.—*Lachnaea* and *Cryptadenia*. Floral anatomy of hypanthia. Vasculature and scales (Sc) arising from adaxial wall. A, *L. capitata*, *Beyers 128*; B, *C. grandiflora*, *Beyers 196*. SM, sepal midrib bundle; SC, commissural sepal bundle; Sc, scale; MS, median sepal bundle. Scale bars: A, B, 100 µm.

the base of each of the three main ridges in some *Lachnaea* species (Figure 23A, B) but was absent in all the *Cryptadenia* species (Table 4). The surface of the lateral sides of the supratectal trihedral projections is striate in all the species (Figure 23).

Karyology

The haploid chromosome number of n = 9 was observed in six species of *Lachnaea* and in two species of *Cryptadenia* (Table 5). The meiotic chromosome behaviour was normal.

DISCUSSION

Habit, phyllotaxis and foliage

The habit, phyllotaxis and macromorphological characters of the foliage leaves are rather variable among the

FIGURE 20.—*Lachnaea*. Longitudinal section of scale. A, *L. capitata*, *Beyers 128*; B, *L. axillaris*, *Beyers 127*. Sc, scale. Scale bars: A, B, 50 µm.

TABLE 3.—Size range of pollen grains (mean followed by range in parentheses) in *Lachnaea* and *Cryptadenia*

Taxon	Collector	Diameter (µm)
Lachnaea		
aurea	*Beyers 135*	47 (39–51)
axillaris	*Steyn 331*	22 (20–23)
burchellii	*Oliver 9241*	29 (23–37)
buxifolia	*Beyers 122*	47 (43–53)
	Beyers 118	52 (49–55)
	Taylor 8648	49 (47–59)
capitata	*Hugo 231*	26 (23–29)
	Beyers 128	29 (23–33)
densiflora	*Beyers 145*	29 (23–45)
	Beyers 117	32 (29–35)
	Beyers 115	27 (23–31)
diosmoides	*Beyers 181*	29 (23–33)
	Van Niekerk 53	30 (27–33)
ericoides	*McDonald 1842*	28 (25–31)
	Zeyher 3776	27 (23–31)
eriocephala	*Beyers 54*	50 (39–57)
	Spreeth 141	45 (39–55)
filamentosa	*Beyers 110*	45 (39–55)
	Taylor 10770	50 (47–56)
funicaulis	*Beyers 125*	25 (20–27)
nervosa	*De Kock 152*	35 (31–39)
penicillata	*Oliver & Fellingham 9145*	28 (19–35)
	Beyers 173	29 (23–39)
ruscifolia	*Vlok 2084*	35 (31–39)
Cryptadenia		
filicaulis	*Esterhuysen 34370*	33 (29–39)
grandiflora	*Beyers 151*	48 (45–58)
	Beyers 129	56 (47–64)
laxa	*Bolus 7875*	40 (33–43)
uniflora	*Haynes 477*	52 (49–55)
	Beyers 136	54 (47–62)

TABLE 5.—Chromosome numbers of *Lachnaea* and *Cryptadenia* species studied

Taxon	Haploid chromosome number	Voucher specimen
Lachnaea		
buxifolia	9	*Beyers 122*
densiflora	9	*Beyers 145*
diosmoides	9	*Beyers 181*
ericoides	9	*Beyers 172*
eriocephala	9	*Beyers 54*
funicaulis	9	*Du Toit s.n.*
Cryptadenia		
filicaulis	9	*McDonald 1989*
uniflora	9	*Beyers 136*

species and sometimes even within individual species of *Lachnaea* and *Cryptadenia*. The variation range within *Cryptadenia* is smaller than in *Lachnaea* but one must take into account that *Cryptadenia* is a much smaller group of species. With regard to the habit, phyllotaxis and macromorphological characters of the foliage leaves no major differences were found which could be used to demarcate the two genera.

Based on the anatomy of the leaves, two leaf groups can be distinguished within *Lachnaea*: 1, those which are amphistomatic and either isobilateral or almost centric; 2, those which are epistomatic and either isobilateral or dorsiventral. The leaves of *Cryptadenia* are epistomatic and either almost isobilateral or dorsiventral. The anatomy of the latter resembles that of the second group in *Lachnaea*. Similar cuticular patterns, namely unsculptured, minutely papillate or undulate, occur in both genera. These characters confirm the close relationship between *Cryptadenia* and *Lachnaea*.

TABLE 4.—Comparison of sculpturing of supratectal projections of tectate pollen in *Lachnaea* and *Cryptadenia*

Taxon	Base sides		Vestigial spinules at base of main ridges
	± straight	emarginate	
Lachnaea			
aurea	–	+	–
axillaris	+	–	–
burchellii	+	–	+
buxifolia	+	–	+
capitata	+	–	+
densiflora	+	–	+
diosmoides	+	–	+
ericoides	–	+	–
eriocephala	–	+	–
filamentosa	–	+	+
funicaulis	–	+	–
nervosa	+	–	+
penicillata	+	–	+
ruscifolia	+	–	+
Cryptadenia			
filicaulis	+	–	–
grandiflora	+	–	–
laxa	–	+	–
uniflora	+	–	–

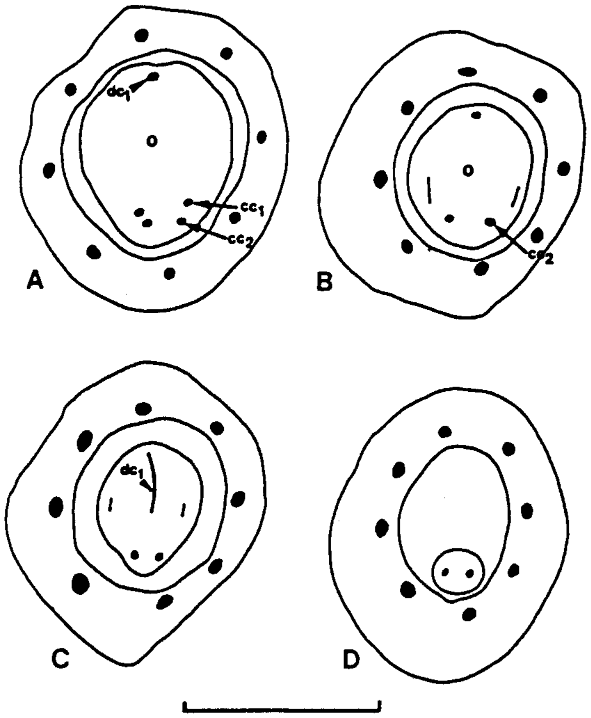

FIGURE 21.—*Lachnaea eriocephala, Beyers 54*. Transections of flower: A, base of ovary; B, upper portion of ovary; C, top of ovary; D, base of style. o, ovary; dc$_1$, dorsal carpellary of fertile carpel; cc$_1$, commissural carpellary of fertile carpel; cc$_2$, commissural carpellary of sterile carpel. Scale bar: 500 µm.

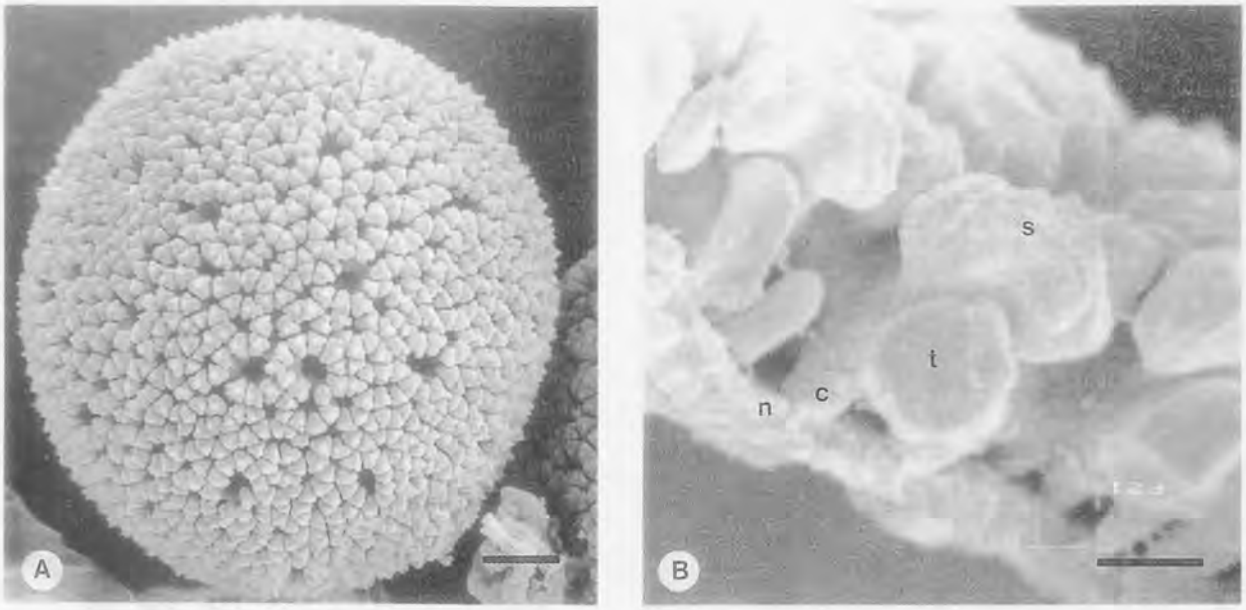

FIGURE 22.—*Lachnaea* and *Cryptadenia*. SEM micrographs of pollen morphology. A, *L. aurea*, *Beyers 135*, pollen grain; B, *L. buxifolia*, *Beyers 122*, transection of pollen grain wall. n, nexine; c, columella; t, tectum; s, supratectal structure. Scale bars: A, 5 µm; B, 1 µm.

Morphology of flower and fruit

Pedicel/floral articulation

The study of the floral morphology revealed the strong similarity between *Lachnaea* and *Cryptadenia*. Sessile flowers are found in both genera. The ring of trichomes at the base of the flower, occurring at the floral articulation, corresponds to that found by Heads (1990) in *Kelleria* Endl. This structure, according to Heads (1990) is reminiscent of the calycular pappus of many members of the Asteraceae and the peltate hairs of Elaeagnaceae, and could be regarded either as a compressed pubescent 'pedicel' or as the 'calyx' of a sessile flower. The pedicels of pedicellate flowers of *Lachnaea* species are always pubescent. The trichomes at the floral articulation do not differ from those on the pedicel and it is therefore more acceptable to regard the ring of trichomes at the base of the sessile flowers as a compressed pubescent 'pedicel'.

Hypanthium

The nature of the hypanthium of the flower of the Thymelaeaceae has been interpreted as being appendicular (foliar) and representing a calyx tube by Meisner (1857), Wright (1915), Peterson (1959) and Dyer (1975), or as being receptacular by Eichler (1878), Baillon (1880), Gilg (1894), Wettstein (1935), Rendle (1938) and Bunninger (1972). According to Lawrence (1951) the hypanthium is more commonly and inaccurately termed the calyx tube or floral tube. Heads (1990), Heinig (1951) and Saunders (1939) regard the floral tube of the Thymelaeaceae as a hypanthium. The vascular anatomy undertaken in this study has shown that the floral tube in both genera can be regarded as a hypanthium.

The position of the plane of circumscision expressed as a percentage of the total length of the hypanthium varies in both genera between 20% and 80%. The shape, length and pubescence of the hypanthium of *Cryptadenia* falls well within the variation range found in *Lachnaea*.

Calyx

The sepals in *Lachnaea* vary from being almost equal to distinctly unequal. The transition from one form to the other is gradual. The sepals of *Cryptadenia* are almost equal which was one of the reasons why Baillon (1880) incorporated *Cryptadenia* as a section in *Lachnaea*.

The aestivation of the sepals is the same in both genera and a basic floral vascular pattern is common to both genera.

Androecium

Eight stamens in two whorls of four each are present in both genera. The position of insertion on the floral tube shows a varying degree of adnation within both *Lachnaea* and *Cryptadenia*. The stamens are always exserted in *Lachnaea*, but in *Cryptadenia* they are either exserted or only the antisepalous stamens are fully exserted.

Scales

In the different genera of the Thymelaeaceae organs comparable to the scales in *Lachnaea* and *Cryptadenia* have been interpreted by various authors as petaloid glands, scales, mere outgrowths of the perigynium, aborted stamens, squamellae which should be regarded either as new structures of uncertain origin or as modified parts of the androecium, stipules or petals which might be reduced or greatly modified in form (Heinig 1951).

In *Lachnaea* various views regarding the nature of these scales have been expressed, namely that they should be regarded as staminodes, scales, glandular or scale-like receptacular effigurations, or petaloid scales homologous

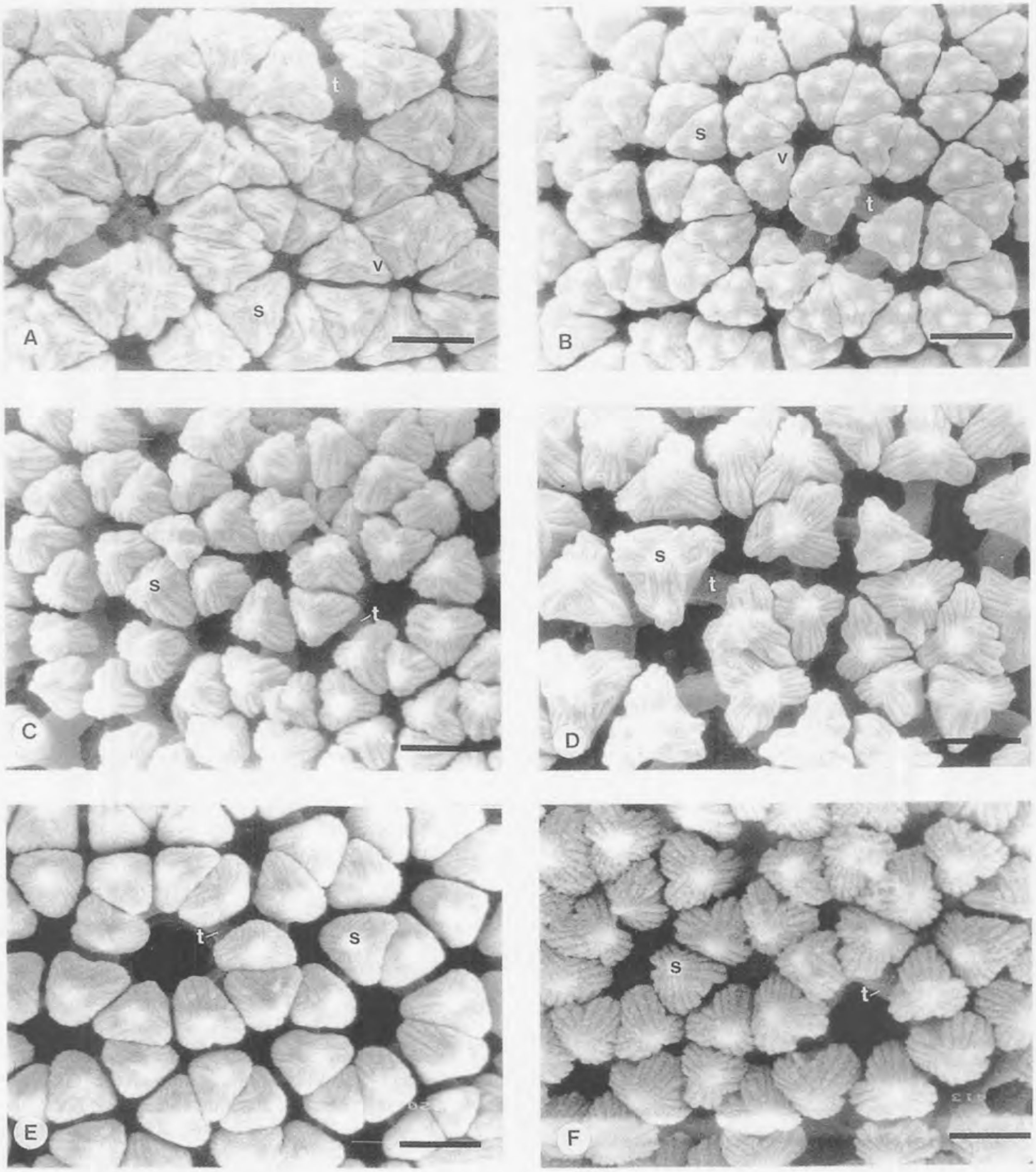

FIGURE 23.—*Lachnaea* and *Cryptadenia*. SEM micrographs of pollen grains. A, *L. buxifolia*, *Beyers 122*; B, *L. ruscifolia*, *Vlok 2084*; C, *L. aurea*, *Beyers 135*; D, *L. eriocephala*, *Beyers 54*; E, *C. uniflora*, *Haynes 477*; F, *C. laxa*, *Bolus 7875*. s, supratectal structure; t, tectum; v, vestigial spinule. Scale bars: A–F, 2 µm.

to petals. In those species of *Lachnaea* where these structures are narrowly straplike or filiform, Domke (1934) regarded them to be in their original form and for that reason Meisner (1840), according to Domke (1934), mistakenly considered them to be staminodes. These structures, in their original position according to Domke (1934), are inserted at the base of the calyx lobes and slightly higher than the insertion of the antipetalous stamens but through zygomorphy these structures have positioned themselves in a single whorl at the same height as, or sometimes below, the filament insertion. This situation is not met in other genera such as *Gnidia* and *Struthiola*, where the petal-like structures are inserted above the insertion of the filaments at the mouth of the tube. From the vascular anatomy of the flowers one would rather believe the converse, namely that the scales were orginally positioned below the antipetalous stamen whorl and through zygomorphy have been slightly displaced to above the antisepalous stamen insertion, as in *L. filamentosa*. Heinig (1951) considered these structures to be stipules of the calyx lobes and found no reason to consider them to be vertical extensions of the disc as Gilg (1894) did. Taxonomists have not been eager to accept the interpretation of the petaloid scales as stipules on the grounds that stipulate sepals would not occur in a group in which the foliage leaves are exstipulate. Heinig (1951) supported her interpretation on the grounds that the absence of stipules on the foliage leaves and the presence of stipular appendages in the floral organs should be considered another aspect of the progressive reduction from a more primitive state. Heads (1990) rejects Heinig's interpretation of the petaloid scales being stipules on the grounds that she used the concepts of 'leaf' and 'stipule' of Eames & MacDaniels (1948) which were in turn derived from Van Tieghem's (1871 in Heads 1990) morphology which he regards as being fundamentally flawed. Heads (1990) refers to the comparable organs in *Kelleria* as gland scales.

In *Cryptadenia*, as in *Lachnaea*, different views regarding the scales have been expressed. They have been referred to as glands, scales, glandular or scale-like receptacular effigurations, or petaloid scales. Although Domke (1934) referred to them as 'glands', he regarded them as petaloid scales homologous to those of *Lachnaea*. According to Domke (1934) the 'effigurations' in *L. axillaris*, *L. diosmoides* and *L. ericoides*, because of their position and shape, lead directly to those in *Cryptadenia* where these structures are nearly completely attached abaxially to the hypanthium.

Because of their position and anatomy, we regard these structures in both *Lachnaea* and *Cryptadenia*, as scales which are mere emergences of the adaxial wall of the hypanthium.

The position of the scales in both genera is usually below the insertion of the antipetalous stamens. In the more zygomorphic forms in *Lachnaea* and in one species of *Cryptadenia*, where they are in close juxtaposition to the stamens, they emerge between the insertion of the antipetalous and antisepalous stamens. The position of the scales in the upper portion of the hypanthium is variable in both genera. Those of *Lachnaea* are inserted at the mouth of the hypanthium to midway down the upper portion of the hypanthium, whereas those in *Cryptadenia* are inserted at the mouth of the hypanthium to three quarters of the way down the upper portion of the hypanthium. On the grounds of the position of the scales, a generic character used by Meisner (1840, 1857), no cutoff point can be made to separate the two genera as the displacement of the scales is gradual. In both genera the scales may be non-glandular or glandular. Another generic character which Domke (1934) used, was the attachment of the scales to the hypanthium. According to him the scales in *Lachnaea* are basally attached, whereas those in *Cryptadenia* are abaxially attached. In *L. axillaris* the cup-shaped and sigmoid basal part of the upper portion of the hypanthium gives the impression that the scales are basally attached. If however, the sigmoid curve is removed by extending the hypanthium upwards, the scales would in fact be abaxially attached and would correspond to the situation in the flower of *C. filicaulis*.

Gynoecium

The ovary in both genera is sessile, pseudomonomerous (consisting of one expanded or fertile carpel and one contracted or sterile carpel) and unilocular with a solitary anatropous ovule laterally attached near the top of the ovary. The style is always laterally attached to the ovary. The stigma is either brush-like or capitate in both genera but may also be conical in *Cryptadenia*.

Zygomorphy is expressed in both genera through the lateral placement of the style and the single locule.

Fruit

In both genera the fruit is an achene which is enclosed within the persistent base of the hypanthium. According to Domke (1934) the achene is, without exception, characteristic of the Thymelaeoideae and thus at the generic level the fruit is not of taxonomic importance.

Pollen morphology

The pollen grains of *Lachnaea* and *Cryptadenia* have the same basic morphology. Based on the sculpture of the supratectal structures two pollen grain types can be distinguished within *Lachnaea*, namely those with vestigial spinules at the base of the three main ridges and those without spinules. In *Cryptadenia* the supratectal structures are devoid of spinules at the base of the three main ridges and are thus similar to the latter pollen grain type of *Lachnaea*. Furthermore, in both genera, the lateral sides of the trihedral structures are striate and the basal sides are either straight or emarginate. The pollen grain size, following Radford *et al.* (1974), is medium to large in *Cryptadenia* and small to large in *Lachnaea*. This feature, therefore, also overlaps in the two genera.

Karyology

In most Thymelaeaceae the haploid chromosome number (n = 9) and the somatic chromosome number (2n = 18) have been observed (Nevling & Woodbury 1966 in Ornduff 1968. The following references are given in Moore 1973: Sharma & Sarkar 1967, 1968, Bjorkquist *et al.* 1969, Delay 1969, Gupta & Gillett 1969, Majovsky *et al.* 1970. Bhat *et al.* in Löve 1974. In Moore 1977: Kuzmanov 1973, Loeve & Kjellqvist 1974, Majovsky *et al.* 1974. Heads 1990). Polyploidy has been recorded in *Daphne* (Heads 1990), *Daphnopsis* (Nevling & Woodbury 1966 in Ornduff 1968), *Edgeworthia* Meisn. (Heads 1990), *Pimelea* Banks & Sol. (Heads 1990), and *Wikstroemia* Endl. (Gupta & Gillett 1969 in Moore 1973; Heads 1990).

The chromosome number of *Lasiosiphon eriocephalus* Decne., according to Subramanyan & Kamble in Löve 1967, is n = 8. The genus *Lasiosiphon* Fresen. was incorporated in the genus *Gnidia* for southern Africa (Dyer 1975). Although the above species is not indigenous to South Africa, it was the only chromosome number previously available for a genus of the Thymelaeaceae represented in South Africa.

The chromosome counts of n = 9 here reported for the species of both *Lachnaea* and *Cryptadenia*, are the first records for these two genera. The basic chromosome number of x = 9 was recorded for most genera of the

TABLE 6.—Comparison of characters in *Lachnaea* and *Cryptadenia*

Character	*Lachnaea*	*Cryptadenia*
Habit	shrubs or shrublets multi- or single-stemmed at base, 0.15–2.0 m tall	shrublets multi- or single-stemmed at base, 0.12–0.8 m tall
Phyllotaxis	alternate or decussate	decussate
Flower	hermaphrodite, tetramerous	hermaphrodite, tetramerous
Hypanthium	circumscissile	circumscissile
Position of circumscision zone above base of hypanthium	⅕–⅘	⅕–⅘
Basal portion of hypanthium	ellipsoid, widely ellipsoid, ovoid, widely ovoid or obovoid	ovoid or ellipsoid
Upper portion of hypanthium	funnel-shaped, cylindrical, obconical, cup-shaped or cup-shaped with a sigmoid curve	funnel-shaped or cup-shaped
Stamens	4 + 4, exserted	4 + 4, exserted or semi-exserted
Stamen insertion	epipetalous to third of the way down upper portion of hypanthium	epipetalous to three quarters of the way down upper portion of hypanthium
Floral scales	8, non-glandular or glandular	8, non-glandular or glandular
Scale insertion	mouth of hypanthium to midway down upper portion of hypanthium	mouth of hypanthium to three quarters of the way down upper portion of hypanthium
Style	lateral	lateral
Stigma	brush-like or capitate	brush-like, capitate or conical
Fruit	dry, enclosed in persistent base of hypanthium	dry, enclosed in persistent base of hypanthium
Leaf anatomy	epistomatic, isobilateral or dorsiventral; or amphistomatic, isobilateral or almost centric	epistomatic, almost isobilateral or dorsiventral
Pollen grains	monads, globose, polyforate, 22–52 µm in diameter, tectate and supraornate	monads, globose, polyforate, 40–50 µm in diameter, tectate and supraornate
Sculpture of supratectal structures	vestigial spinules present or absent, lateral sides of trihedral structures striate	vestigial spinules absent, lateral sides of trihedral structures striate
Chromosome number	n = 9	n = 9

Thymelaeaceae and can therefore not be used to demarcate genera.

CONCLUSIONS

The Thymelaeaceae is a family in which it is difficult to find sound characters for generic delimitation. According to Peterson (1959), only a few characters can be used and they are of superficial significance. While revising the thymelaeaceous genera of the African continent, Peterson (1959) experienced difficulties with the classification. According to him these difficulties were not so much connected to the species concept but rather to the delimitation of genera which showed morphologically continuous characters which merged them into each other.

According to Baillon (1880), the only other worker who has discussed generic characters in the Thymelaeaceae, the following characters are generally of generic value:

- the number of floral parts,
- the point of insertion of the stamens and the dimension of their filaments which render them exserted or enclosed,
- presence or absence of the scales in the throat of the hypanthium,
- presence or absence of a disc at the base of the gynoecium,
- whether the base of the hypanthium is shed or persists growing around the ripe fruit, and
- the arrangement of the inflorescence.

In evaluating the results obtained from the present multidisciplinary study, consideration was given to those characters which Baillon (1880) advocated as being of value at generic level as well as those used by Heads (1990) to illustrate the major differences between *Kelleria* Endl. and *Drapetes* Lam. The results of this multidisciplinary approach, as summarized in Table 6, illustrate the great similarity between *Lachnaea* and *Cryptadenia*. These also show that several characters within *Lachnaea* exhibit a variation range which includes the variation in *Cryptadenia*, and that in a few other characters the variation range is extended in *Cryptadenia*. No distinguishing characters of generic value were found to support the present demarcation of *Lachnaea* and *Cryptadenia*. Furthermore Beyers & Van der Walt (1994) concluded that the inflorescence morphology revealed no distinct differences between *Lachnaea* and *Cryptadenia*.

With the view of establishing natural genera, and on the basis of the findings of this multidisciplinary study, we support the viewpoint of Baillon (1880) that *Cryptadenia* should be included within *Lachnaea*. A detailed taxonomic treatment of *Lachnaea sensu lato* should now be undertaken.

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APPENDIX 5

A NEW SPECIES OF *LACHNAEA* (THYMELAEACEAE) FROM THE WESTERN CAPE.*

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A new species of *Lachnaea* (Thymelaeaceae) from the Western Cape

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Lachnaea pudens Beyers, a new, one-flowered shrublet from the Western Cape is described. Descriptions and illustrations of the macromorphology, leaf anatomy, and pollen, as well as a distribution map, are provided. The new species resembles *L. axillaris* Meisn. in floral shape, but differs in that the flowers are dark red and sericeous on the outside, whereas those of *L. axillaris* are cream to dark pink and glabrous.

Keywords: Anatomy, *Lachnaea*, new species, palynology, taxonomy, Thymelaeaceae.

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Introduction

Lachnaea L., with about 34 species, is endemic to the Cape Floral Region as defined by Bond and Goldblatt (1984). The species are found mainly on mountain ranges, often at high altitudes and the centre of diversity of the genus lies in the southwestern area.

The most recent taxonomic revision of *Lachnaea* is that of Wright (1915). In the course of a new revision of the genus, which is currently in progress, this new species was identified. The generic position of the new species was in doubt until recently, and specimens were filed in herbaria under *Lachnaea* or doubtfully under *Cryptadenia*. However, the delimitation of these two genera has recently been resolved (Beyers & Van der Walt 1995).

Material and Methods

Transverse sections of wax-embedded leaves were cut with a rotary microtome and stained with alcian green safranin (Joel 1983). Leaf surfaces were studied by mounting portions of the leaf blade obtained from herbarium material on stubs which were coated with gold and studied with a Joel scanning electron microscope (SEM). For both light microscopy (LM) and SEM, pollen was acetolised according to Erdtman (1960). At least 20 pollen grains of each sample were measured.

Sprecies treatment

Lachnaea pudens Beyers, sp. nov. distincta propter ramos florescentes declinatos floribus solitariis atrorubentibus; *L. axillaris* affinis sed floribus externe sericeis, non glabris, atrorubentibus, non albidis ad atroroseis.

TYPUS.—Western Cape: Riviersonderend Mountains, Jonaskop, upper north slopes, 3319 DC, *Beyers 161* (NBG, holotypus; BOL, K, NY, PRE, isotypi).

Erect to decumbent, much branched shrub to 0.6 m tall, multistemmed at base. *Branches* flexuous, intertwined, moderately thick, ridged below leaf bases, tomentose or tomentose-sericeous, leafy, becoming glabrescent and naked with prominent leaf scars; flowering branches declinate. *Leaves* decussate, ascending incurved, imbricate, distal two pairs of leaves inclined, erect or slightly recurved, subverticillate, sessile, 3.8–5.7 × 1.0–1.3 mm, elliptic, subfleshy, glabrous, adaxially flat to obtusely concave, smooth, dull, ± white-punctulate, abaxially convex, keeled, glossy, smooth, sometimes with a reddish brown tinge, apex apiculate, base obtuse. *Inflorescence* terminal, one-flowered, but appearing to be axillary when much-reduced, lateral branches comprise only one pair of leaves and a solitary flower. *Flowers* sessile, subactinomorphic, dark red. *Hypanthium* 3.0–4.5 mm long, circumscissile four-fifths from base, upper portion widely cup-shaped with a basal invagination, basal portion pyriform, sericeous outside, upper portion glabrous within but villous above circumscission zone in vicinity of scales, basal portion glabrescent within. *Sepals* 4, patent, subequal, 2.0–3.9 × 2.6–3.6 mm, widely ovate or widely depressed ovate, acute or obtuse, abaxially sericeous, adaxially glabrous. *Petals* absent. *Stamens* 4 + 4, exserted, outer, antisepalous whorl adnate to upper portion of hypanthium and becoming free just above base of sepals, inner antipetalous whorl adnate to upper hypanthium and becoming free two-thirds up hypanthium; filaments filiform, 0.3–0.5 mm long; anthers 0.5–0.6 mm long, depressed-spheroid, abaxially with broad connective tissue. *Scales* 8, inserted midway on upper portion of hypanthium below antepetalous stamens, 0.3–0.4 mm long, subrotund, glabrous. *Ovary* 1.0–1.3 mm long, ovoid, glabrous. *Style* 2.2–2.6 mm long, linear-obconical, glabrous. *Stigma* penicillate (Figure 1).

Leaf anatomy (vouchers: *Beyers 161 & 210*)

Blade dorsiventral, epistomatic, glabrous, more or less triangular in transverse section (Figure 2). *Cuticle* well developed, equally thick ad- and abaxially; surface papillate adaxially, smooth or weakly papillate abaxially, both surfaces with flaky wax deposits, particularly adaxially (Figure 3). *Epidermis* uniseriate, epidermal cells usually square to periclinally elongated, slightly larger abaxially, outer tangential walls thicker than inner tangential walls (before gelatinization), inner tangential cell walls abaxially wholly gelatinized with abundant mucilaginous deposits, adaxially partly gelatinized, mainly towards lateral blade margins; stomata on same level as adjacent epidermal cells. *Mesophyll* differentiated into palisade and spongy parenchyma; palisade abaxial, uniseriate; spongy parenchyma adaxial, cells palisade-like, loosely arranged with fairly large intercellular spaces. *Vascular bundles* comprising a large mid-bundle and very small lateral ones; mid-bundle capped abaxially by a prominent bundle of large extraxylary fibres, bundle sheath present, uniseriate, parenchymatous, incomplete, interrupted by extraxylary fibre cap; lateral bundles without fibre caps and with poorly developed parenchymatous bundle sheath. *Crystals* of diosmin (potasium hydroxide test: Jackson & Snowdon 1990) present in epidermis and mesophyll, occurring as shaerocrystalline to somewhat dendritic masses, pale yellow. *Tanniniferous* deposits absent.

Palynology (vouchers: *Beyers 161 & 210)*

Pollen grains shed as monads, spheroidal, pantoporate, 26–28 μm in diameter. Tectum reticulate with tetrahedral supra-tectal subunits (crotonoid pattern *sensu* Erdtman 1966); supra-tectal subunits triangular in surface view, with a single central spinule, lateral sides ±

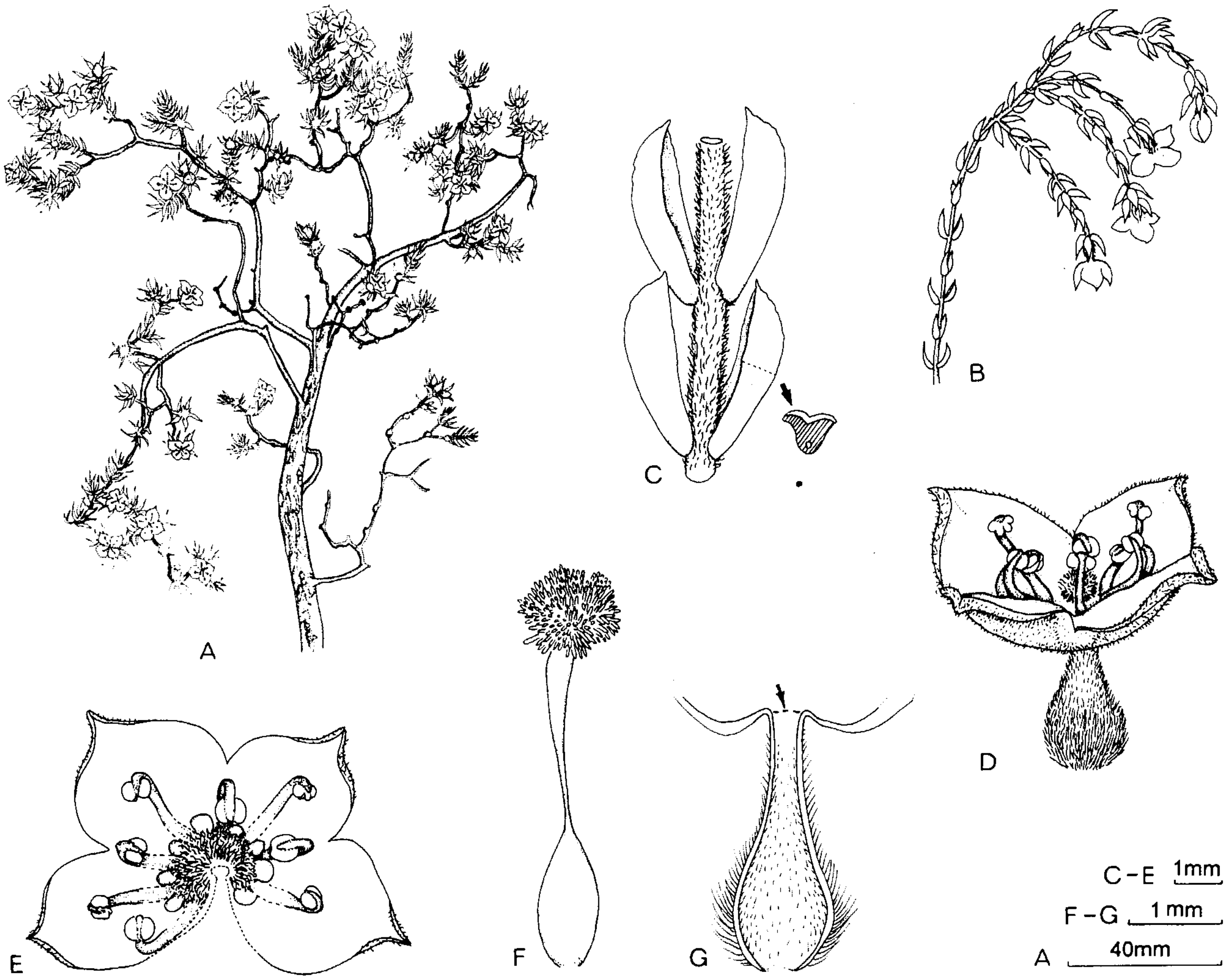

Figure 1 *Lachnaea pudens* (drawn from the type collection, *Beyers 161*). **A**, portion of plant. **B**, flowering branch (life size). **C**, branch with leaves and cross section of a leaf (close-up). **D**, flower. **E**, upper portion of a flower above the circumscission zone. **F**, gynoecium. **G**, portion of the hypanthium with the gynoecium removed (in half section), illustrating the basal invagination of the upper portion of the hypanthium just above the circumscission zone (arrowed).

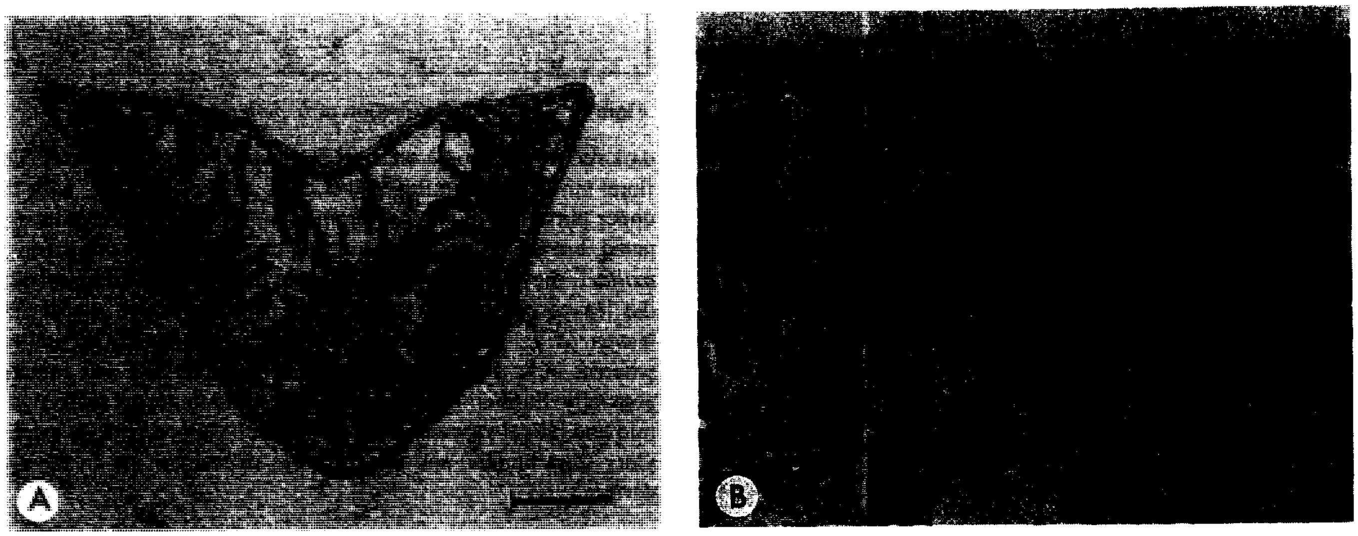

Figure 2 *Lachnaea pudens*, leaf anatomy, transverse sections (*Beyers 210*). **A**, leaf lamina; note triangular outline, lack of tanniniferous deposits and abaxial epidermal cells with inner tangential cell walls wholly gelatinized. **B**, Portion of lamina showing abaxial epidermal cells with gelatinized (mucilaginous) inner tangential walls (m), and sphaerocrystalline masses of diosmine crystals in epidermal and palisade cells (arrowed). Scale bars: **A** = 200 µm; B = 50 µm.

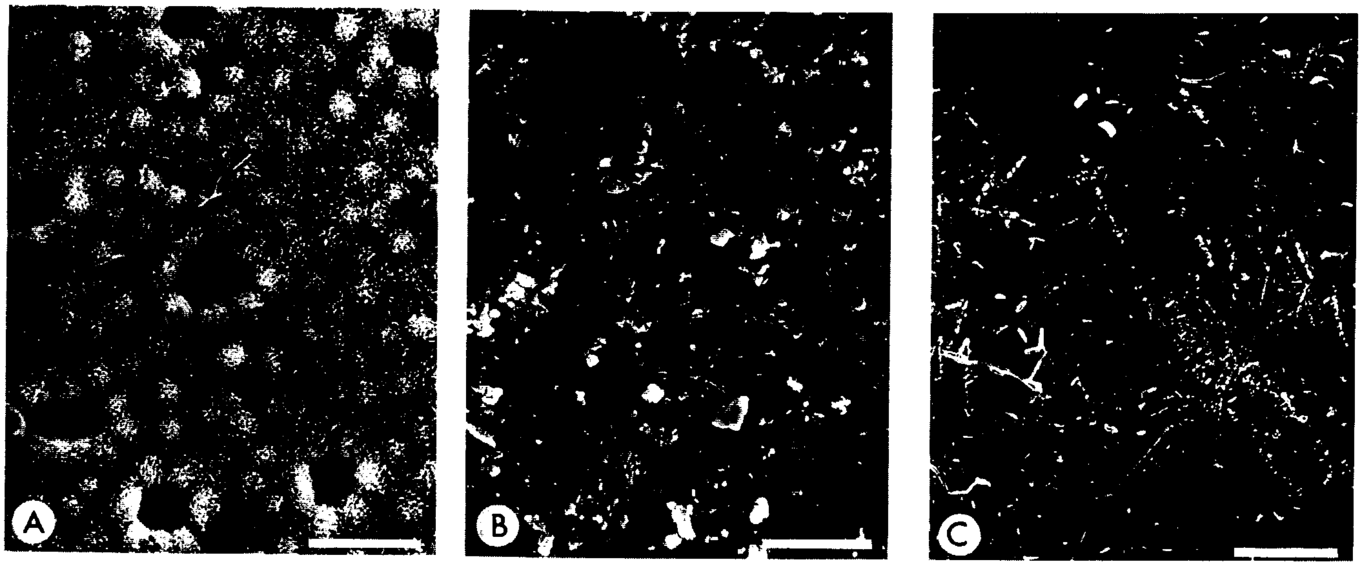

Figure 3 *L. pudens*. SEM micrographs of leaf surfaces illustrating the cuticular relief (A & C, *Beyers 161*; B, *Beyers 210)*. **A**, adaxial cuticle papillate with flake-like wax deposit. **B**, abaxial cuticle shallowly papillate with a sparse flake-like wax deposit. **C**, abaxial cuticle unsculptured with a sparse flake-like wax deposit. Scale bar on A–C = 2 µm.

emarginate, surface around spinule granular-striate, with muri (ridges) often cross linked (Figure 4).

Distribution and ecology

This species occurs on the mountain slopes of Jonaskop near Villiersdorp and on the Riviersonderend Mountains above Greyton and Genadendal, at altitudes between 330–1530 m, growing in sandy, stony soils overlying sandstones of the Table Mountain Group of the Cape Supergroup (Figure 5). Flowering has been recorded in February, May, August and October to December.

Etymology

The specific epithet, *pudens*, meaning shy, bashful or modest, refers to the flowers which are borne on short branches facing downwards; only when the main flowering branches are lifted upwards do the dark red-coloured flowers become noticeable.

Diagnostic characters and relationships

Lachnaea pudens is easily distinguished by the terminal, solitary, dark red flowers borne on short branches facing downwards. The floral structure is similar to that of *L. axillaris* Meisn., with the upper portion of the hypanthium cup-shaped and basely invaginated, but the flowers are sericeous on the outside whereas in *L. axillaris* they are glabrous and cream to dark pink. Anatomically the leaves of the two species differ. In transverse section the leaves of *L. pudens* are more or less triangular in outline, whereas in *L. axillaris* they are flattened adaxially and concave abaxially. Furthermore, in *L. axillaris* the stomata are sunken, the mid and lateral vascular bundles are each capped with an extraxylary fibre bundle, and tanniniferous deposits occur in the epidermis.

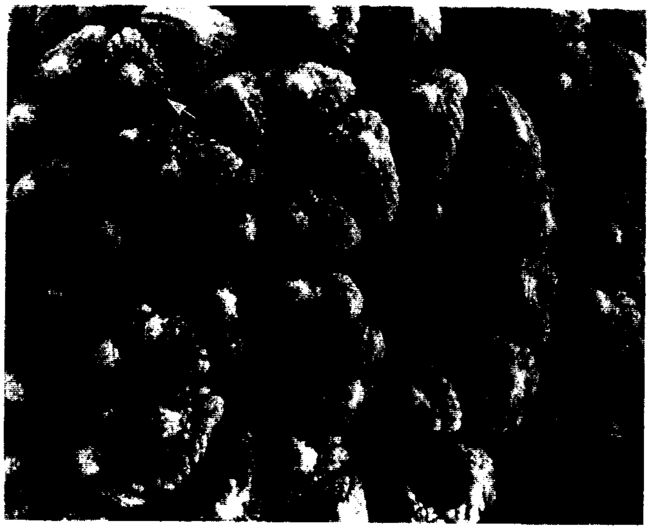

Figure 4 *L. pudens* (*Beyers 161*). SEM micrograph of a pollen grain illustrating the crotonoid tectum. Cross-links between muri (ridges) indicated by an arrow.

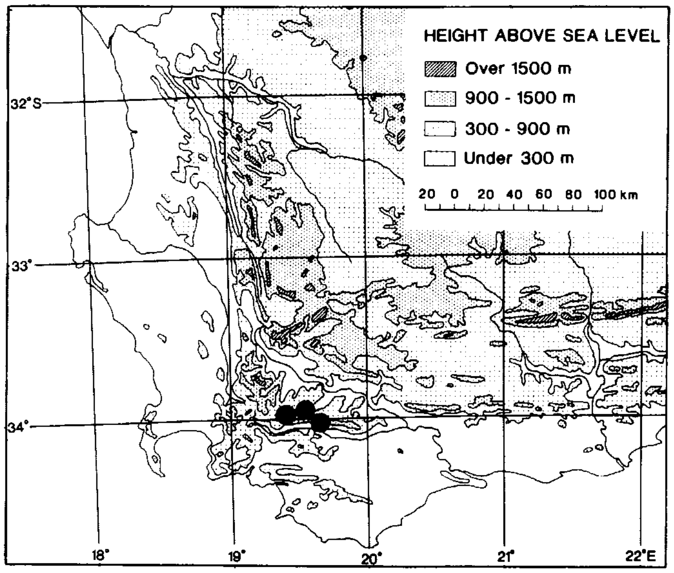

Figure 5 Known distribution of *L. pudens*.

Specimens examined

Western Cape

—**3319** (Worcester): Villiersdorp, Paulsgat area above Kleinfontein, NE slopes SW of Vetkop, 680 m, (–CD), 4–10–1997, *Oliver 10730* (K, PRE, NBG); Riviersonderend Mountains, lower N slopes on

APPENDIX 6

A NEW SPECIES OF *LACHNAEA* ENDEMIC TO THE SOUTHEASTERN MOUNTAINS OF THE WESTERN CAPE.*

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* Published in *Bothalia* 28: 49–53 (1998).

THYMELAEACEAE

A NEW SPECIES OF *LACHNAEA* ENDEMIC TO THE SOUTHEASTERN MOUNTAINS OF THE WESTERN CAPE

Lachnaea sociorum *Beyers*, sp. nov., structura inflorescentiae florisque *L. ericoidis* similis, sed sepalis tomentosis, stigmate penicellato, foliis lanceolatis ad anguste ellipticis, abaxiale leviter 3-costatis, apice acuto, glabris.

TYPE.—Western Cape, 3321 (Ladismith): Langeberg, Bergfontein, S-facing midslopes of Koksposberg, 379 m, (–DC), 18-01-1991, *McDonald 2059* (NBG, holo.; BOL, K, NY, PRE, iso.).

Erect, compact, moderately branched shrub up to 0.6 m tall, multistemmed at base, resprouting after fire. *Branches* erect, slender, ridged below leaf bases, covered with long, straight, adpressed hairs admixed with crooked ones, densely leafy, becoming naked with prominent leaf scars. *Leaves* alternate, ascending or occasionally inclined to patent, with apex curled inward, imbricate, sessile, lanceolate to narrowly elliptic or occasionally elliptic to obovate, 3.6–6.0 × 0.9–2.4 mm, coriaceous, green, those below inflorescence sometimes tinged maroon, glabrous, adaxially concave, smooth, dull, ± white-punctate, abaxially convex, faintly 3-ribbed or subkeeled towards apex, glossy, subpapillate, apex acute, base cuneate. *Inflorescence* a terminal, sessile, ebracteate, 6–14-flowered umbel with up to 9 open flowers at a time, on main flowering branches. *Flowers* subactinomorphic, white, skunk-scented. *Pedicel* 0.3–0.7 mm long, sericeous. *Hypanthium* 2.5–3.7 mm long, circumscissile, three-fifths to three-quarters from base, upper portion funnel-shaped, tomentose outside, adpressed hirsute within, basal portion oblong, glabrous, rarely tomentose outside, glabrous within. *Sepals* 4, patent, subequal, widely ovate or subrotund, 1.7–3.0 × 1.7–3.2 mm, apex rounded or obtuse, adaxially and abaxially tomentose. *Petals* absent. *Stamens* 4 + 4, exserted, outer, antisepalous whorl inserted at base of sepals, 0.7–1.5 mm long, inner, antipetalous whorl inserted at rim of hypanthium, 0.5–1.2 mm long (inner stamens the shortest or equal to the shortest of outer stamens); anthers widely ellipsoid, 0.4–0.6 mm long, abaxially without broad connective tissue. *Scales* 8, exserted, inserted at mouth of hypanthium immediately below antipetalous stamens, obovoid or subglobose, 0.3–0.5 mm long, glabrous, translucent-white when fresh. *Ovary* ellipsoid or obovoid, 0.9–1.4 mm long, glabrous. *Style* linear-obconical, 2.0–2.9 mm long, with straight, adpressed or incurled hairs in upper half to two-thirds. *Stigma* penicillate. *Chromosome number*: 2n = 18 (*Beyers 176*). Figure 8.

Leaf anatomy

Blade dorsiventral, epistomatic, glabrous, in transverse section slightly concave to more or less plane adaxially, convex abaxially (Figure 9). Cuticle well developed, thicker abaxially, surfaces papillate, with flaky wax deposits, particularly adaxially (Figure 10). *Epidermis* uniseriate, adaxial epidermal cells much smaller than abaxial ones, usually periclinally elongated; abaxial epidermal cells square to radially elongated, with outer tangential walls thicker than inner tangential walls (before gelatinisation), inner tangential cell walls of some cells gelatinised; adaxial epidermal cells incompletely and weakly gelatinised; stomata sunk below adjacent epidermal cells. *Mesophyll* differentiated into palisade and spongy parenchyma; palisade abaxial, 1- or 2-seriate; spongy parenchyma adaxial, cells palisade-like, loosely arranged with fairly large intercellular spaces. *Vascular bundles* comprising a large midbundle, flanked by 2 smaller lateral bundles on either side, with small intermediate bundles in between these two types; each bundle capped abaxially by large extraxylary fibres which are particularly well developed in the mid- and lateral bundles; bundle sheath present, uniseriate, parenchymatous, incomplete, interrupted by extraxylary fibre cap. *Crystals* of diosmin (potassium hydroxide test: Jackson & Snowdon 1990) present in adaxial epidermis and mesophyll, occurring as shaerocrystalline to somewhat dendritic masses, pale yellow; crystals and tanniniferous deposits mutually exclusive. Tanniniferous deposits present in all abaxial, and in some adaxial epidermal cells.

Vouchers: *Beyers 176; McDonald 2059.*

Pollen morphology

Pollen grains shed as monads, spheroidal, pantoporate, 39–41 µm diam. Tectum reticulate with triangular supratectal subunits, (crotonoid pattern *sensu* Erdtman 1966); supratectal subunits triangular in surface view, with either a single central spinule or with usually four spinules, lateral sides of subunits straight or emarginate, surface around spinules striate to granular-striate, with muri (ridges) cross-linked in subunits with lateral sides emarginate. Figure 11.

Vouchers: *Beyers 176; Oliver 10524.*

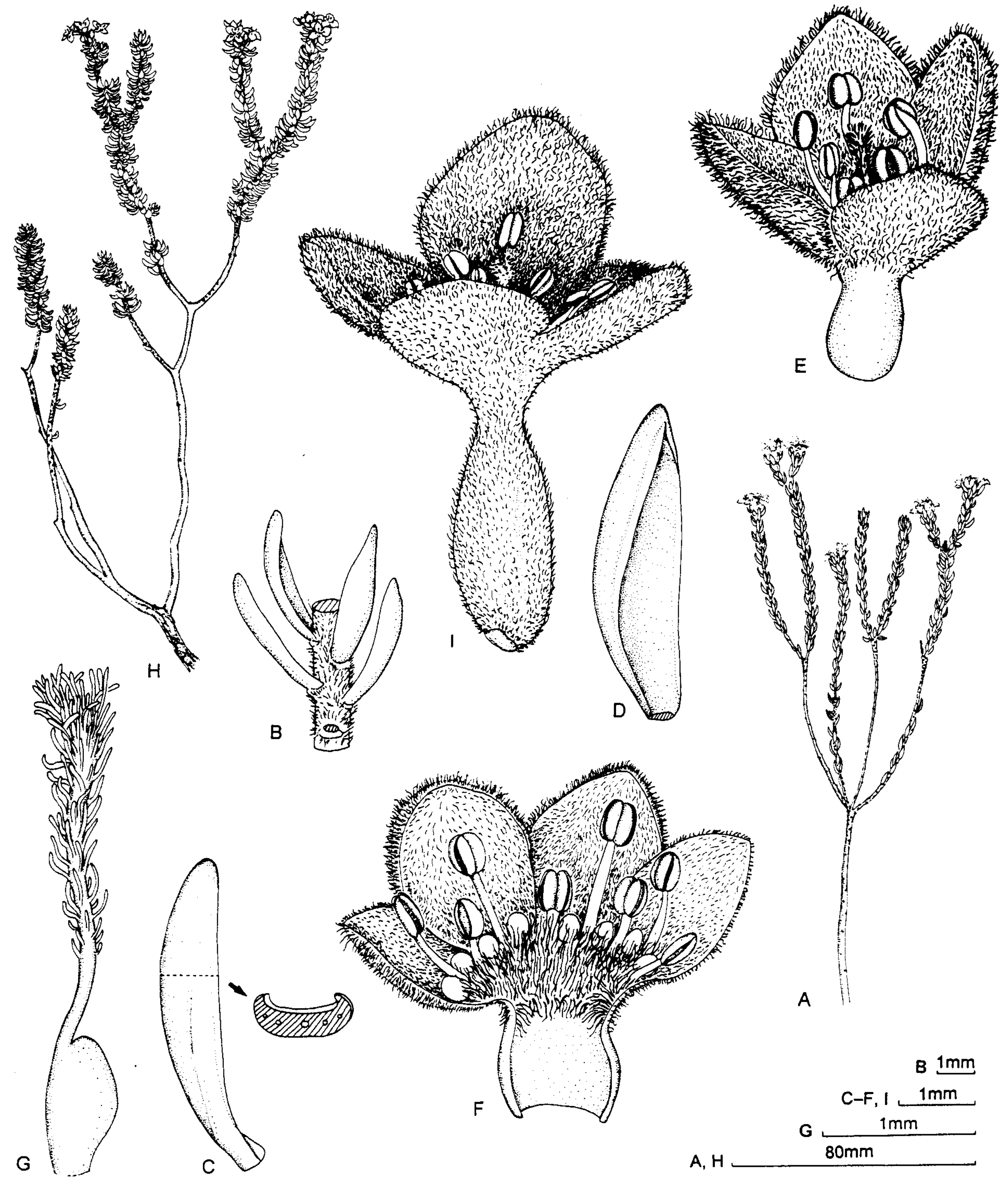

FIGURE 8.—*Lachnaea sociorum*. A, portion of plant; B, branchlet (enlarged); C, leaf (abaxial view and cross section); D, leaf (lateral view); E, flower; F, flower split longitudinally with gynoecium removed; G, gynoecium; H, portion of plant; I, flower; atypical pubescent form. A–G, *McDonald 2059*; H, I, *Beyers 176*.

Distribution, ecology and variation

Recorded from the eastern end of the Langeberg Mountains, from Perdeberg in the west eastwards to Gavelsbos and the southern slopes of the Attakwa Mountains below Perdekop. Plants occur in stony soil on the southern and northern slopes, at altitudes between 300 and 1 100 m (Figure 12). Flowering recorded from August to January.

The population on the northern side of the Langeberg at Tygerberg, west of Huisrivier, is very localised and reasonably old. These plants are single-stemmed at the base, branching close to the ground and are open at the crown

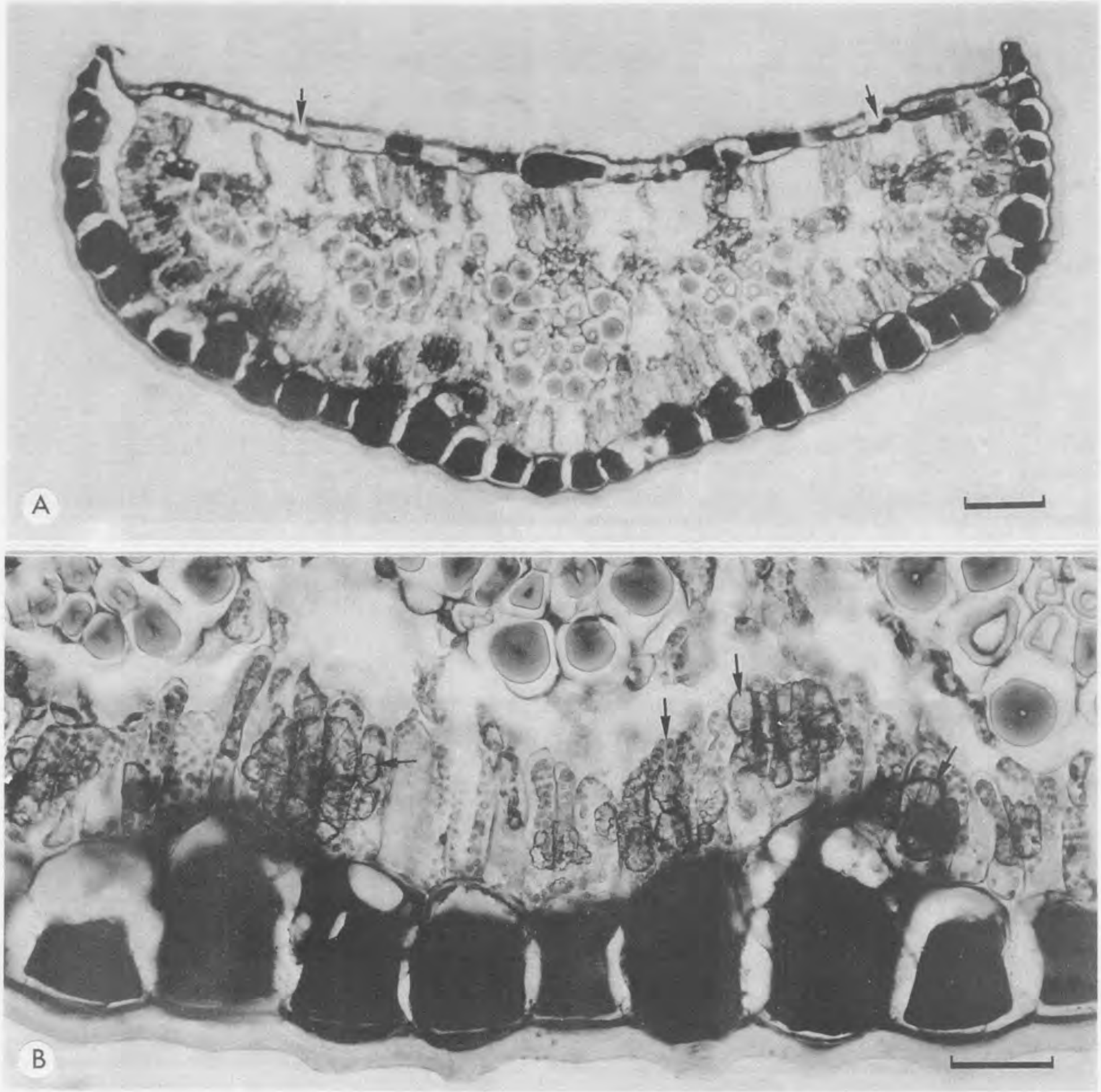

FIGURE 9.—*Lachnaea sociorum, McDonald 2059*, leaf anatomy, transverse sections. A, leaf lamina, note outline of shape, tanniniferous epidermal cells (particularly abaxially), sunken stomata (arrowed) and vascular bundles with prominent caps of extraxylary fibres; B, portion of lamina showing tanniniferous abaxial epidermal cells, adjacent palisade layer and extraxylary fibres, note masses of diosmin crystals (arrowed) in palisade cells. Scale bars: A, 100 µm; B, 50 µm .

with decumbent branches. Whether they would resprout after a fire remains to be seen. Two collections were made from this area, viz. *Beyers 176* and *McDonald 1780*. In all the material collected by McDonald, the basal portion of the hypanthium is glabrous as in all collections from other localities. However, in the material collected by Beyers the basal portion of the hypanthium on the outside is tomentose like the rest of the flower. This variation in hairiness needs further investigation before it can perhaps be formally expressed taxonomically.

Etymology

The specific epithet, *sociorum*, is derived from the Latin *socius*, meaning associate or colleague. This species is dedicated to colleagues Ted Oliver and Dave McDonald, who on field trips always scouted for fresh *Lachnaea* material for the first author.

Diagnostic characters and relationships

Lachnaea sociorum is closely related to *L. ericoides* Meisn. Both have a similar inflorescence and floral structure. In both species the lower portion of the hypanthium is glabrous (except for the one collection of *L. sociorum, Beyers 176*, where it is tomentose). In *L. sociorum* the leaves are usually lanceolate to narrowly elliptic, abaxially faintly 3-ribbed, with an acute, glabrous apex, the sepals adaxially tomentose and the stigma penicillate. In *L. ericoides*, on the other hand, the leaves are narrowly

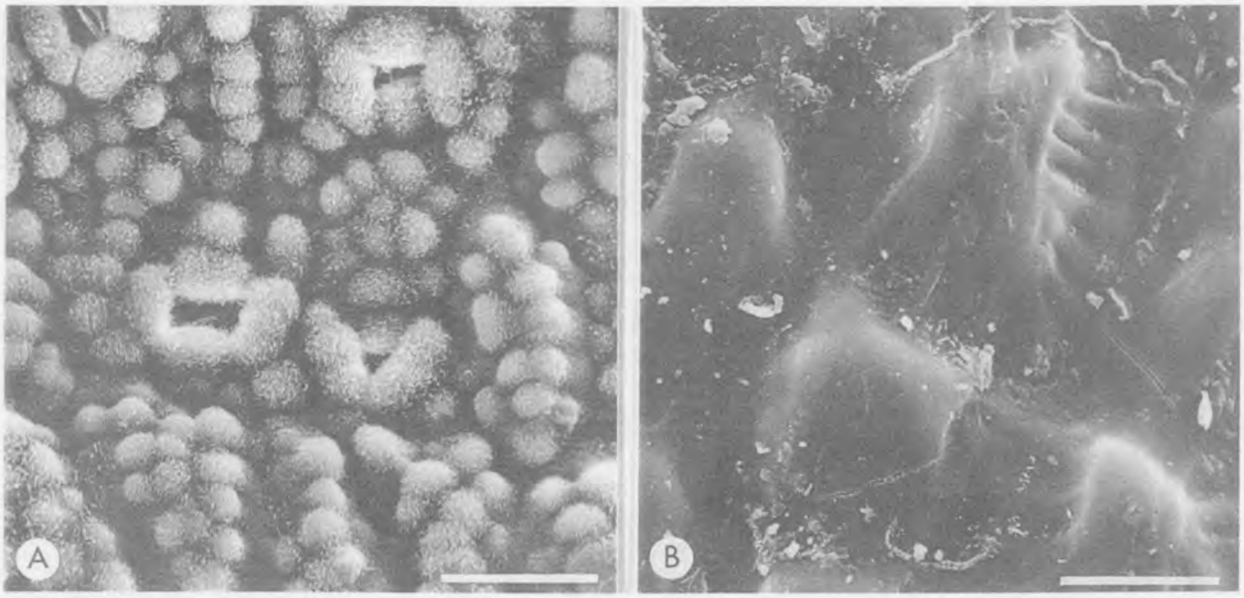

FIGURE 10.—*Lachnaea sociorum, McDonald 2059.* SEM micrographs of leaf surfaces illustrating papillate cuticular relief: A, adaxial surface with dense flake-like wax deposit; B, abaxial surface with sparse flake-like wax deposit. Scale bar: 2 µm .

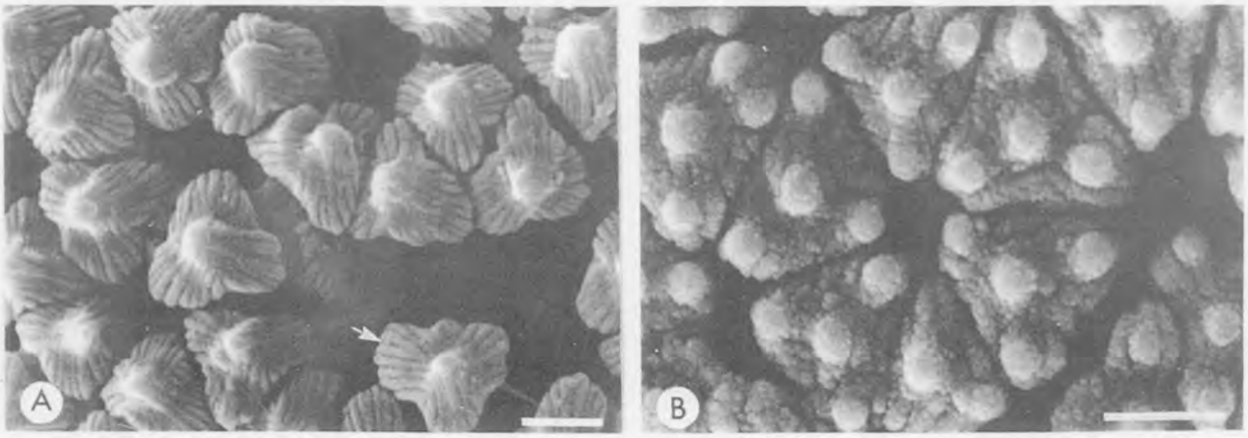

FIGURE 11.—*Lachnaea sociorum.* SEM micrographs of acetolized pollen grains illustrating crotonoid tectum. A, supratectal subunits with single spinule, sides emarginate and with surface striate, note cross-links between muri (ridges), indicated by an arrow, *McDonald 2059*; B, supratectal subunits, each with usually four spinules, sides straight and surface granular-striate, *Oliver 10524* . Scale bar: 1 µm .

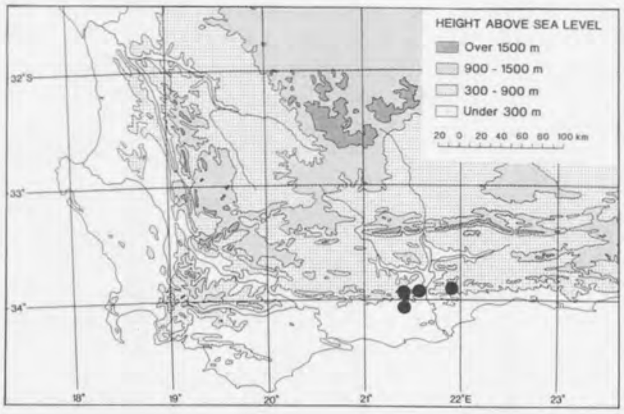

FIGURE 12.—Known distribution of *L. sociorum*.

elliptic to obovate, abaxially keeled, with a rounded, tufted apex, the sepals adaxially sericeous-tomentose and the stigma capitate with elongated papillae. The leaf anatomy of these two species is very similar except that in transverse section the leaves of *L. ericoides* are deeply concave adaxially and the extraxylary fibre strands capping the lateral vascular bundles are not as prominent as in *L. sociorum* (Beyers & Van der Walt 1995: fig. 8a).

Specimens examined

WESTERN CAPE.—3321 (Ladismith): Langeberg, Paardeberg, 1 100 m, (–CD), 11-08-1977, *Haynes 1401* (NBG); E of Garcia's Pass on northern side of Langeberg, Tygerberg, west of Huisrivier, 300 m, (–DC), 15-12-1989, *Beyers 176* (BOL, K, NBG, NY, PRE, Z), 17-12-1988, *McDonald 1780* (BOL, NBG, PRE); Langeberg, Bergfontein area, lower slopes of Koksposberg, 425 m, (–DC), 30-10-1990, *McDonald 1963* (PRE, NBG); Langeberg, Bergfontein, S-facing mid-slopes of Koksposberg, 379 m, (–DC), 18-01-1991, *McDonald 2059* (BOL, K, NBG, NY, PRE); Riversdale Dist., Langeberg, W of Witelsberg, upper Witelsrivierkloof, 610 m, (–DC), 01-09-1994, *Oliver 10524* (BOL, NBG, PRE); Langeberg, lower SW slopes of Witelsberg, N of Koksposberg, 488 m, (–DC), 01-09-1994, *Oliver 10536* (BOL, K, NBG, PRE, Z); Mossel Bay Road to Perdekop before forest plantation, 600 m, (–DD), 17-10-1978, *Bond 1578* (NBG). 3421 (Riversdale): Riversdale, Farm Gavelsbos, mountain slope, SW aspect, stony soil, 307 m, (–AB), 08-09-1984, *Bohnen 8479* (NBG, PRE). Grid ref. unknown: Riversdale Flower Show, 01-09-1994, *comm. Oliver* (NBG); Riversdale Div., Langeberg, 01-10-1923, *Muir 2824* (BOL), *Muir 3053* (PRE).

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