Systematic studies in the tribe Ericeae (Ericaceae-Ericoideae)

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Insights

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'This genus [*Erica*] is remarkable for an unusual degree of variability in the form of almost all its organs. It is therefore one difficult of definition as to the species, and of the arrangement into satisfactory groups'.

Francis Guthrie & Harry Bolus (1905)

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'Hybridisation between these two genera [*Simocheilus* and *Blaeria*] raises the question whether the division of the South African minor Ericaceae into micro-genera has been carried too far. Almost the whole classification of these plants into genera and species has been carried out by European botanists on the evidence of an absurdly limited quantity of material and it is only after attempting to dissect old dried specimens in these genera that their patience can be realised.'

Terence M. Salter (1936)

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'I am more and more against voting a genus a good one merely because it has a few good characters, but to judge of its value really one must take a view of the allied ones. Where a large group is natural and well defined I do not like lopping off a few species here and there on account of some remarkable exceptional character, for it is that which carried to excess has produced the present lamentable chaos in our botanical system.'

Letter of George Bentham to Asa Gray, 1.2.1861
(Stevens 1998)

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Chapter 1

INTRODUCTION

Ericaceae, to which the heaths and heathers belong, is a large widespread family comprising some 125 genera with 3000–4000 species (Sleumer 1966, Luteyn 1980). It has been divided up into several subfamilies and tribes and has included several other families, depending on the classification system being followed.

The early treatments of genera were based on Linnaeus' Sexual System (Linnaeus 1753, 1754) in which 'Classes', sometimes unnatural groupings, occurred and no families were defined, although many ericaceous genera were grouped together. The family Ericaceae was first proposed by Jussieu in 1789.

Within the last five years the family has been investigated by several workers based on morphological, embryological, anatomical and molecular data which have thrown a whole new light on the relationships and classification within the order Ericales and the family itself. Anderberg (1993) and Judd & Kron (1993) assessed morphological characters while Kron & Chase (1993) and Kron (1997) looked at various molecular sets. These investigations have led the way to a better understanding of the relationships and grouping of the genera, but none proposed any formal systems. Kron's most recent analysis of molecular data, concentrating on the Rhododendroideae *sensu stricto*, but including some Ericoideae, clearly shows the need to rationalise this group within the family (Kron 1997).

Resulting from all this recent work, a group of ericologists (Kron & Crayn pers. comm.) is currently formulating a new classification for the whole family, which will then also include the former families Empetraceae and Epacridaceae. The Ericoideae will be considerably expanded to include the Rhododendroideae and the Empetraceae. At the tribal level within the Ericoideae *sensu lato*, the Ericeae will comprise just *Erica s. lat.* (following the results of my current research), *Calluna* and, surprisingly, *Daboecia*, which up until now has always been placed in the Rhododendroideae (Stevens 1971). *Cassiope* is postulated to be the sister group of this enlarged Ericoideae and is placed in a separate subfamily, the Cassiopoideae.

When I began this study I was dealing with the subfamily Ericoideae (sensu Stevens 1971). With the new circumscription of the subfamily, the study group remains virtually the same except for the inclusion of *Daboecia*, only with a change in rank to the tribe Ericeae. This group of some 25 genera has been recognized as distinct on account of the marcescent corolla, the whorled, typically sulcate, narrow (ericoid) leaves and a predominantly dehiscent capsule, which is loculicidal in dehiscence, the exception being the monotypic *Calluna*, which has a septifragal capsule and sagittate leaves. The monotypic *Daboecia* may easily be distinguished by its deciduous corolla, alternate leaves and septicidal capsule.

The Ericeae has a restricted north-south distribution from southern Africa to northern Europe. Modern floras and taxonomic treatments covering various regions of this distribution range included their representatives of the tribe, but with generic boundaries virtually unchanged, thus avoiding any problems relating to generic circumscription: Madagascar (Perrier de la Bâthie 1927, 1930,

1932) *Adumbratio Florae Aethiopicae* (Pichi-Sermolli & Heiniger 1953), *Flora of Tropical West Africa* (Ross 1963), *Flore du Cameroun* (Letouzey 1970), *Flora Europaea* (except for the sinking of the European *Pentapera*) (Webb *et al.* 1972), *Flora zambesiaca* (Ross 1983), *Flore des Mascareignes* (Friedmann 1981), *Genera of South African Flowering Plants* (Oliver 1975) and a preliminary paper towards the account for the Flora of Tropical East Africa which has, regrettably, never been completed (Ross 1957).

The first genera in the Ericoideae were recognized by Linnaeus in 1754—*Erica* with 23 species from Europe and the Cape and *Blaeria* with a single species from the Cape. With the number of stamens being very important in his Sexual System, the four-stamened condition in *Blaeria ericoides* was clearly important to Linnaeus and did not fit the constantly 8-stamened condition of all the species of *Erica* that were available to him. Thus *Erica* was placed in the Octandria Monogynia and *Blaeria* in the Tetrandria Monogynia.

The increase in the number of species resulting from collecting in the Cape in the 1760's and 70's did not affect generic concepts as all 8-stamened species were placed under *Erica* and 4-stamened species under *Blaeria* without any apparent examination of the ovary complement as evidenced by the describing of *B. articulata* L. which has a 1-locular 1-ovulate ovary ($\mathbf{G}^1/_1$) and *B. purpurea* Bergius with a 2-locular 1-ovulate ovary ($\mathbf{G}^2/_1$), *Erica plumosa* Thunb. with a 2-locular 1-ovulate ovary ($\mathbf{G}^2/_1$) but with four stamens, *Erica albida* Thunb. with a 1-locule 1-ovulate ovary ($\mathbf{G}^1/_1$) but with four stamens, and others (see Bergius 1767; Linnaeus 1767 & 1771; Linn. fil. 1782; Thunberg 1802). Thunberg in fact published a revision of *Erica* (1785) including 91 species with a mixture of eight and four stamens, and later a revision of *Blaeria* (1802) containing 15 species (all 4-stamened), both works based largely on his own collections.

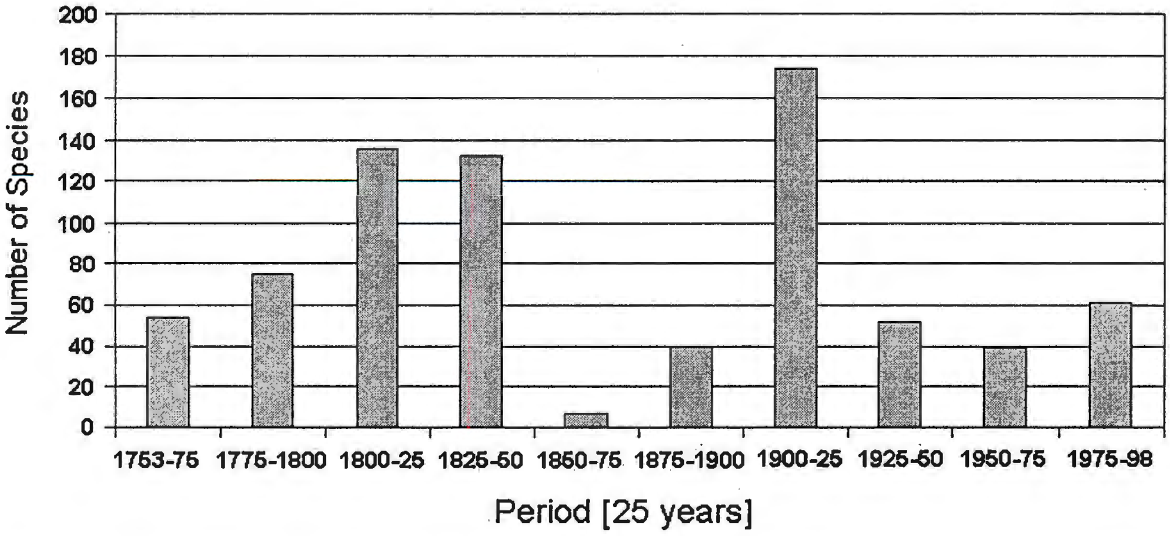

FIGURE 1.—Numbers of species of Ericeae described over the last 250 years in 25-year blocks.

With the further rapid expansion of collections in the late 1700's, it is not surprising that the number of described species increased dramatically as well (Aiton 1789 & 1810; Lamarck & Poiret 1789; Salisbury 1796, 1802; Willdenow 1799) (Fig. 1). The remarkable popularity of Cape heaths in horticultural circles stimulated the increase in collecting and from 1794 to 1830 Andrews figured several hundred species and horticultural varieties or hybrids. Surprisingly all his taxa were of 'true' ericas with eight stamens. At the same time Wendland at Herrenhausen in Germany, published extensively, although not quite to the same extent as Andrews. However Wendland differed in including several Minors[1] which he placed in the genus *Blaeria*.

A major step in the revision of the Ericoideae came with the publication of Salisbury's treatment of *Erica* in 1802 in which he listed 247 species. He apparently did not recognise *Blaeria* since he included several species earlier described in *Blaeria* with new names in *Erica*, and made no mention of *Blaeria* in his introduction. He defined *Erica* as having 'corolla persistent, anthers 4–10, fruit membranous, 4–8-loculed, valves 4–8 dehiscing with septa together with the valves (i.e. loculicidal); seeds 10–100 in each locule, shed'. He was thus the first worker to look at ovule numbers in the tribe.

More significant in this work was Salisbury's recognition of other genera. In his introduction he recognised *Erica vulgaris* L. as a distinct monotypic genus, *Calluna*, for which he used the distinctive septicidal capsule and sessile leaves as distinguishing features. However, according to the current Code of Botanical Nomenclature (Greuter *et al.* 1994), this was illegitimate. since Linnaeus, according to the protologue, had based his genus *Erica* mainly on either the European *Erica vulgaris* or the Cape *Erica gnaphaloides*, a fact not completely covered in the conserving of the name *Erica* with the lectotype species as *Erica cinerea* L. (Jarvis & McClintock 1990, Nicholson 1992, Jarvis pers. com.).

Salisbury also mentioned in his introduction another new genus, *Salaxis*, based on a large stigma, irregular calyx, and a trilocular, trispermous, drupaceous fruit. He mentioned four species as belonging to this genus, but did not name any of them. This was the first recognition of the presence of an indehiscent fruit in the Ericoideae and also the distinctive, and unusual nature of the calyx of many heaths. Willdenow (1809) took up Salisbury's name for several of his new Mascarene species that possessed an irregular calyx, but unfortunately ignored the fact that they had capsular fruits (see below).

The next significant addition to the Ericoideae was the description of the genus *Sympieza* by Roemer and Schultes (1818) using a manuscript name of Lichtenstein who had collected in the Cape in 1803/4. They recognized the distinctive bilobed calyx and corolla of their single species, *Sympieza capitellata*, which had in fact been described clearly by Salisbury (1802) as *Erica labialis*.

In 1829 Decaisne, working on the collections of a French expedition, recognized and described the distinctive genus *Scyphogyne* based on his *S. inconspicua*—not knowing that it was a well-known species described several times by previous workers under *Blaeria* (*Blaeria muscosa* Aiton) as well as *Erica* (both *E. albida* Thunb. and *E. albens* Thunb.).

Shortly afterwards in 1831 Reichenbach in Vienna decided that the unusual European species, *Erica spiculifolia* Salisb. was sufficiently different from *Erica* to warrant generic recognition. He thus described *Bruckenthalia* based only on the 4-fid calyx, i.e. partially fused and not free. He made no

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[1] In the Ericeae the overwhelming size of the genus *Erica* as compared with the rest of the genera, has prompted me to coin the name 'Minor' genera or just 'Minors' when referring to the small Cape genera.

mention of the absence of bracteoles, which was so important for subsequent workers. Little did he realise the significance of his statement 'calyx 4-fid' (see later under Characters, Char. 10).

In the same year Lehmann (1831) published a list of names in a seed-list from the Hortus Hamburgensis and among the ericads was the new monotypic genus, *Nabea*, but with no diagnosis. This was later validated by Klotzsch (1834) who noted the unusual calyx, much longer than the corolla, and also the winged seeds.

In 1832 Bartling catalogued Ericeae collected by Ecklon. Most were species of *Erica*, but he took up *Sympieza* of Roemer and Schultes. He placed the rest of the species, some of which were new, within the genus *Blaeria* without using any suprageneric system. One of his new species, *Erica tristis*, was not noted as having an irregular calyx (see Salisbury above) and his *Blaeria gracilis* could arguably have been placed in *Sympieza* because it has a bilobed corolla and four stamens. Bartling provided a subgeneric division within *Erica* based mainly on corolla shape; he recognized ten named, but unranked, groups within the 145 species covered by him.

The following year saw the first publication of Klotzsch from Berlin (1833). He, like Bartling, was cataloguing recent collections, this time mainly those of Mund and Maire, and dedicated his work to his superior, von Chamisso. He listed *Sympieza* and expanded the generic circumscription by including Bartling's *Erica gracilis* (see above). He expanded *Blaeria* and defined it by its **A4 G**$^{4}/_{2-6}$ formula, but included species with 1 or 2 locules and only 1 ovule per locule. He must not have examined ovaries very carefully, but assumed that 4-stamened species must have had G4 like *Blaeria*. He described the genus as having a dehiscent, loculicidal, 4-valved capsule. He validated Lehmann's *Nabea* and in a full description highlighted the fact that it had a calyx five times longer than the corolla and rotund compressed winged seeds, both of which were unique characters in the group at the time. He also included Salisbury's *Calluna* in his treatment.

Klotzsch continued his work on Ericoideae and in 1834 described the monotypic genus *Thoracosperma* based on **A**4 but with the important additional characteristics of 'berry juiceless, 2-seeded, arils (?) 2 stony fairly thick, ovoid, honeycombed empty [thus infertile] filling all the berry'. He took up Salisbury's genus *Salaxis* with its unequal calyx and drupe adding 'drupe (?) juiceless, stony (?) honey-combed, 3–4-locular'. In this genus he placed two new species, *Salaxis hexandra* and *S. octandra*. From his descriptions one can see that he had noted the interesting fruit details, but that he was confused by the structures which are in fact very different (see Characters, Chars. 32–34). Under *S. hexandra* he noted 'drupe globose epicarp membranous, stone 3–4-loculed fairly thick, locules disjunct'. This is, in fact, a berry with the so-called stone being the closely appressed testa of the 3–4 seeds.

Klotzsch also described *Philippia* to accommodate the Mascarene species, which Willdenow (1809) had noted possessed an irregular calyx and therefore had described them under *Salaxis*. However, Klotzsch realised they were different in having a 4-locular, 4-valved, loculicidal, dehiscent capsule. He also added several new Madagascan and Cape species.

The first major assessment of suprageneric taxa within the whole family (order sensu Don) appeared in the same year (D. Don 1834). David Don provided a framework for the major treatise on gardening and botany by his older brother (G. Don 1834). He divided Ericaceae into several tribes, one of which was Ericeae. The tribe Ericeae was then divided into two subtribes, Andromedeae, which included *Daboecia*, characterised by a deciduous corolla and the Ericeae Normales, the true heaths, characterized by a persistent corolla. Within the latter group he listed 22 genera most of which were just subdivisions of the large genus *Erica* that were based on differences incorolla shape. Only three were non '*Erica'* genera, namely *Sympieza*, *Salaxis* and his newly described *Eremia*, a monotypic genus based on *Erica totta* Thunb. characterized by **K**4 **C**4 **A**8 with cells of the 'capsule' 3-seeded. The fruit of *Sympieza* was not mentioned and that of *Salaxis* just repeated the description of Salisbury.

In two further papers dealing with the *Erica spp.* of the recent collectors who had sent material to German herbaria (Bergius, Lichtenstein, Mund & Maire, Hesse) and the already published species of other workers, Klotzsch (1833 & 1834) divided the genus up into three 'tribes', which were then divided into series.

Then, following closely on each other came two very important works on the heaths, the *Ericearum Genera et Species* by Klotzsch (1838) and the treatment of the Ericoids by Bentham (1839) in de Candolle's Prodromus.

TABLE 1.—Classification used by Klotzsch (1838)

GENERA ET SPECIES ERICEARUM (Genera & species of Ericeae with no rank)

Tribe 1: SYMPHYSANDRAE—anthers laterally connate

a) Stamens 8	*Salaxis*, *Philippia**, *Lagenocarpus**
b) Stamens 6	*Coccosperma**
c) Stamens 4	*Blepharophyllum**

Tribe 2: ADELOPHOSTEMONES—anthers free; filaments monadelphous

Bruckenthalia

Tribe 3: ELEUTHEROSTEMONES—anthers free; filaments distinct

a) Stamens 8	*Erica*, *Calluna*, *Nabea**, *Eremia*, *Eleutherostemon**
b) Stamens 6	*Hexastemon**
c) Stamens 4	*Blaeria*, *Ericinella**, *Thamnium**, *Comacephalus**, *Grisebachia**, *Acrostemon**, *Thoracosperma**, *Sympieza*, *Pachycalyx**, *Plagiostemon**, *Octogonia**, *Coilostigma**, *Thamnus**, *Simocheilus**, *Finckea**, *Anomalanthus**, *Codonanthemum*, *Syndesmanthus**, *Macrolinum**, *Omphalocaryon**
d) Stamens 3	*Tristemon**

(*=Klotzschian genera)

Klotzsch dealt with most of the known Ericoideae (excluding *Erica*) in a suprageneric and generic classification system (Table 1). This work was prompted by the many collections which had arrived in Berlin from the three German collectors, Drège, Ecklon and Zeyher. He dealt with 76 species and placed them in 33 genera of which only seven were from previous authors and three of his own from previous papers. He divided the genera into three 'tribes'. This terminology is confusing since in his earlier works he had used 'tribes' for the subgeneric groupings within the genus *Erica*. There was accepted standard for the terms used for suprageneric taxa both in rank and nomenclature. Klotzsch based his tribes on whether the anthers and filaments were fused or not, totally ignoring any ovary characters, and then keyed the respective genera into informal groupings based only on the stamen numbers.

In this paper Klotzsch described 23 new genera, one of which, *Omphalocaryon*, was in fact the previously described *Scyphogyne* of Decaisne, which he had overlooked. Of these genera nine were monotypic and 10 had only two species. Later in the same year he published an addendum to this work and added two further monotypic genera, the 5-merous European *Pentapera*, and the Cape *Microtrema* with **A6** $\mathbf{G}^{1}/_{1}$. This meant that 22 of the 35 genera recognized by Klotzsch had only one or two species each. He reduced all the segregates of *Erica* described by D. & G. Don to synonymy. He split up his previously described genus *Philippia* into two genera, *Philippia s.s.* itself with only two Cape species and *Eleutherostemon* with two Madagascan species. The other five Madagascan-Mascarene species of *Philippia* were ignored in this work. The two genera thus fell into different 'tribes' in his system because they differed in the single distinguishing character, free versus fused stamens.

Under the generic descriptions Klotzsch mentioned the ovary complement and fruit details in the cases where he had material; for 13 genera the fruit was unknown. He did not cite these details carefully as he referred to the ovary mostly as *n*-locular and *n*-ovulate, only sometimes clearly stating the number of ovules as 'per locule'. The fruit was mostly described rather vaguely as a capsule even though it is now known that the fruits are indehiscent in these species. In some cases he specifically noted that they were 'capsule *n*-valved, loculicidal'. In two cases he specifically noted dehiscence: 'capsule loculicidal, 2-locular, 2-valved, locules 1-seed' for *Acrostemon*, and 'capsule septicidal' for *Grisebachia*—both of which have indehiscent fruits. In four genera he specifically mentions an indehiscent fruit, either a drupe or a nut. His treatment of *Salaxis* is surprising, seeing that he had previously been rather observant with regard to the fruit. He referred to all the *Salaxis* species as having a capsule, thus ignoring one of Salisbury's diagnostic characters for the genus. However he removed one species, *S. hexandra*, and placed it in his new genus *Coccosperma* (as *C. forbesianum*) because of its six stamens and described the fruit as a 'drupe, 3–4-locular', and referred to the ovary as $\mathbf{G}^{3-4}/_{1}$. He was thus not able to assess the subtle differences between the fruits in these Minor genera, but did point the way towards understanding the variation of this important character.

Then came the second major, and most comprehensive, treatment of the Ericaceae by Bentham which covered all the known species at the time (Bentham 1839). He was working at the same time as Klotzsch and, perhaps surprisingly, on the same material, as he cites many specimens either seen in Berlin or received on loan, and he used quite a number of Klotzsch's manuscript names. Bentham divided his tribe Ericeae (Ericoideae *sensu* Stevens) into two subtribes, based just on the number of ovules per locule—Euericeae with locules many-ovuled and the Salaxideae with locules 1-ovuled (Table 2). Little did he know it, but this also placed all the genera with dehiscent capsules in the first subtribe and all the indehiscent-fruited genera in the Salaxideae. The genus *Erica* was listed with 429 species, certainly a dramatic increase over previous treatments of the genus (Fig. 1).

TABLE 2.—Classification used by Bentham (1839).

Tribe: ERICEAE

Subtribe: EUERICEAE—ovary 4- rarely 5- or 8-locular; locules many ovuled
Erica, *Pentapera*, *Calluna*, *Macnabia* [=Nabea], *Philippia*, *Ericinella*, *Blaeria*, *Bruckenthalia*

Subtribe: SALAXIDEAE—ovary 1–4-locular; locules 1-ovulate
Salaxis, *Eremia*, *Acrostemon*, *Sympieza*, *Grisebachia*, *Simocheilus*, *Syndesmanthus*, *Coilostigma*, *Codonostigma*, *Scyphogyne*, *Lagenocarpus*.

Bentham was conservative in his treatment of genera as he maintained only 19 genera as opposed to Klotzsch's 35, but was perhaps more liberal with his species concepts having 114 species as against Klotzsch's 78 (in both cases excluding *Erica*), although he attributed a number of new species to Klotzsch as a result of using Klotzsch's names on the Berlin sheets. His concepts of the genera were far more rational than those of Klotzsch and reveal a better, although far from perfect, understanding of the relationships of the species. He reduced many of Klotzsch's genera to sections and described no genera of his own. Like Klotzsch he also based the genera on numbers of parts in each whorl. His use and interpretation of fruit characters was also rather inadequate as he referred to many of the fruits as capsules, whether dehiscent of indehiscent, and in some cases recorded both types in a single genus. He also overlooked Salisbury's precise description of a drupaceous fruit in *Salaxis*. He perpetuated Klotzsch's erroneous statement that some genera had septicidally dehiscent fruits.

Bentham worked for only a very short time on Ericaceae under contract to Alphonse de Candolle since he did not publish anything prior to that work or subsequently other than a contribution to the Genera Plantarum (see below). Klotzsch, on the other hand, worked extensively on the family, which was not limited to the heaths, as evidenced by the range of his publications from 1829 to as late as 1851.

One interesting aspect of Bentham's work was his treatment of the genus *Eremia*, in which he included Salisbury's *Erica tubercularis* because he estimated it to possess a single ovule per locule ($\mathbf{G}^{1}/_{1}$). This species was transferred back to *Erica* by Guthrie and Bolus (1905) who noted it had a $\mathbf{G}^{4}/_{2}$ ovary. The type and only collection has fruits only, and a dehiscent capsule is clearly visible but with no indication of ovule number. Thus without taking cognisance of the fruits, it was not possible to assess its true relationship, and it landed up artificially in *Eremia*, solely on the grounds of the estimated ovule number. Another aspect was his inclusion of *Coccosperma* in synonymy under *Salaxis*; neither he nor Klotzsch noted the bi-ovulate locules in *Coccosperma*.

Harvey (1868) in his Genera of South African Plants went further than Bentham in reducing the number of genera within Salaxideae where he maintained only six. This was taken up by Bentham and Hooker in their *Genera Plantarum* (Hooker 1876), with *Syndesmanthus* reduced to synonymy under *Simocheilus*, *Lagenocarpus* under *Salaxis*, *Acrostemon* under *Grisebachia*, and *Coilostigma* and *Codonostigma* under *Scyphogyne*. The suprageneric division of Euericeae and Salaxideae remained the same as Bentham's earlier work (1839). Durand (1888) on the other hand kept just one major grouping, the tribe Ericeae, but with the same reduced set of genera.

Drude provided the next major work on the family in Engler's *Syllabus des Pflanzenfamilien* (1897) in which he established the currently accepted nomenclature of the groups within the family. Within the subfamily Ericoideae he maintained the same suprageneric groupings as Bentham, the tribe Ericeae and the tribe Salaxideae. He did not, however, follow completely the generic delimitation in the *Genera plantarum*; he reduced *Grisebachia* to synonymy under *Eremia* but resurrected Klotzsch's *Codonanthemum*, thus still having six genera in Salaxideae. There were no changes in the Ericeae.

With numerous additional collections being made in the 1890's by Bolus, Galpin, Marloth and Schlechter (Fig.1), the next major work to cover the Cape taxa provided numerous changes to the previous revisions. This was the treatment of the family by Guthrie and Bolus (1905) covering just *Erica*, and by Brown (1905-6), covering the rest of the genera, for Volume 4 of *Flora Capensis*.

Guthrie and Bolus recognized some 467 species of *Erica*, which now included the former monotypic genus *Nabea* [*Macnabia* of Bentham], and these were divided up among five subgenera and 41 sections. They provided a key to the subgenera based solely on corolla shape, size and relation to the calyx; their sections were listed in a synopsis with diagnostic characters. This was the first treatment of the genus by workers who had an intimate knowledge of the plants in the wild. This is reflected in their careful assessment of the large amount of variation they encountered.

The remaining genera were treated by Brown who unfortunately had only a small amount of herbarium material on which to work, in some cases just one collection per species, but overall much more than was available to either Klotzsch or Bentham. He did not employ any suprageneric system perhaps because his treatment was part of a regional flora and not a world monograph, and he recognized 22 genera as indicated below (*=monotypic):

Pre 1838 genera—*Blaeria*, *Salaxis*, *Sympieza*, *Scyphogyne*, *Eremia*, *Philippia*, *Ericinella* and *Thoracosperma*.

Klotzsch's 1838 genera—*Coilostigma*, *Hexastemon**, *Grisebachia*, *Thamnus**, *Acrostemon*, *Simocheilus*, *Syndesmanthus*, *Anomalanthus*, *Coccosperma* and *Lagenocarpus*.

Own genera—*Platycalyx**, *Eremiopsis**, *Aniserica** and *Lepterica**.

Klotzsch's genera reduced to synonymy—*Blepharophyllum**, *Comacephalus**, *Codonanthemum*, *Codonostigma*, *Eleutherostemon*, *Finckea*, *Macrolinum*, *Octogonia*, *Omphalocaryon*, *Pachycalyx*, *Plagiostemon*, *Thamnium** and *Tristemon*.

This was clearly a compromise between Klotzsch's liberalism and Bentham's conservatism with respect to the previously described genera. Once again the characters deemed useful for generic delimitation were the numbers of parts per whorl in the ovary and stamens, followed by calyx and corolla numbers, and then calyx and stamen fusion. However, he did introduce an additional delimiting character, namely the number of bracts [strictly bract and two bracteoles], although he did not understand the situation fully in that he noted that there are no 'bracts' when the calyx was unequal.

Brown's groupings of genera in his key appear to be purely artificial, merely facilitating their identification. The genera were placed in a totally different order in the taxonomic treatment and nowhere did Brown give any indication of relationships perhaps evident in the order of his placing of the genera. The grouping of all genera with an unequal or irregular calyx would suggest that he regarded them as forming a related entity, as the capsular genera were grouped at the beginning. However he placed *Coilostigma*, which possesses an unequal or irregular calyx, next to the regular calyxed *Thoracosperma*, and in fact this is confirmed by the findings presented below. He also placed the *Simocheilus-Syndesmanthus-Sympieza* group together. It would thus appear that the arrangement of genera was intentional and may reflect relationships as he saw them.

Details of the fruit and its structure, when available, were mentioned only in the descriptions of the genera. The family description records the fruit as 'a loculicidal or septicidal capsule, rarely baccate or drupaceous'. Presumably the 'septicidal' refers only to the fruit in the European *Calluna*; no such term is used for any of the South African genera, thus putting to rest the error first noted by Klotzsch and perpetuated by many later workers. Brown clearly investigated the fruits of what little fruiting material he had at his disposal. The capsular fruits present in *Blaeria*, *Philippia* and *Ericinella* were easily viewed and recorded as such. He managed to report the type and structure of the fruit in 11 of the remaining genera, yet for many he said just 'indehiscent, apparently indehiscent or indehiscent?', but with no mention whether the indehisent fruit was baccate or drupaceous. In only one case was he incorrect, i.e., the statement that *Acrostemon* has loculicidal fruits. Presumably due to the lack of availability of a complete dataset, he was unable to use fruiting characters for generic delimitation (see fruits for more detailed discussion) perhaps because many of the species included in his treatment were represented by only one or two specimens.

All told, in Brown's treatment the number of species in the Minor genera had increased to 157, with only 20 of these being capsular species. The former figure is a considerable increase from Klotzsch's 78 species and Bentham's 114 species.

Following Brown's work, several additional genera were subsequently described. Alm and Fries provided generic revisions of *Blaeria* (1924) and *Philippia* (1927) both of which had had a considerable number of species added to them through collections from tropical Africa and Madagascar in the late 1800s and early 1900s. They did not alter the generic limits in the former, but for the latter described the segregate genus *Mitrastylus*, based on two species from Madagascar with an unusual stellate stigma. They were the first workers to assess correctly the situation regarding the unequal calyx as being derived from a fully recaulescent bract in *Philippia*, but continued to regard the bracteoles as absent (see later). They accepted Bentham's reduction of Klotzsch's *Eleutherostemon* to synonymy under *Philippia*.

Perrier de la Bâthie (1927) working at the same time as Alm and Fries, but only on the Madagascan species of *Philippia*, clearly showed that there was sufficient variation in the form of the stigma to warrant the return of *Mitrastylus* to synonymy under *Philippia* (Perrier de la Bâthie 1930).

Phillips (1926) retained *in toto* Brown's generic delimitation in *Flora Capensis*. However, in 1944 he decided on a radical reassessment of the genera for the revised edition of his *Genera of Southern African Flowering Plants* (Phillips 1951). He noted that there was considerable polymorphism in floral form in *Erica*, whereas the Minors 'agree more among themselves in general appearance'; he considered the number of ovules to be more important in generic delimitation than the number of locules. He proceeded to retain only seven genera, including *Erica*, to accommodate all South African species of heaths (Table 3). He commented that his selection 'conforms to the grouping given in the Key to the genera in the 'Flora Capensis'. It is the separation of the genera within the groups, which the writer does not think justified.'

TABLE 3.—Genera recognized by Phillips (1944 & 1951) with genera reduced to synonymy.

Erica
Blaeria (*Philippia, Ericinella, Thamnus, Coccosperma*)
Eremia (*Platycalyx, Hexastemon, Arachnocalyx, Grisebachia, Acrostemon, Simocheilus, Thoracosperma, Aniserica*)
Sympieza
Scyphogyne (*Syndesmanthus, Anomalanthus, Eremiopsis, Lepterica*)
Salaxis (*Coilostigma*)
Lagenocarpus

This was an extremely radical step, which he justified on the degree of variation he encountered in many of the characters and on the importance that he placed on the single character, ovule number. Phillips pointed to the problem of generic delimitation in the Ericoideae, which clearly required some sort of rationalisation of the number of genera. But saying that there were too many genera, he proceeded to reduce them into anomalous entities based solely on the number of parts in the ovary. The system he produced is totally artificial, and there are no statements of relationship or of common ancestry of the species, or any overall assessment of their characters. He therefore remained bound to the concepts of some of his predecessors who also based genera totally on "formulae".

Ross (1957) criticized Phillips for his wider view of generic boundaries, but mainly with respect to *Philippia*. He still retained the Ericeae and Salaxideae, a division based on the number of ovules per locule. He thus placed *Coccosperma* close to *Philippia* in his key to the Ericeae (as did Phillips), rather than to *Salaxis*, although the latter did not occur in his area. Ross incorrectly keyed out *Bruckenthalia* with *Philippia* and *Coccosperma* on the grounds of the supposedly shared characters of no bracts [bracteoles] and an unequal calyx, both of which are in fact incorrect (see later for bracteoles); *Bruckenthalia* does not have an unequal calyx like the other two genera.

Marloth (1932) established an additional tribe within the subfamily, Lagenocarpeae, to accommodate *Lagenocarpus* of Klotzsch (=*Nagelocarpus* Bullock) with its ovary half-inferior to the corolla but not to the calyx. This character was noted by Brown as being unique in the family and Levyns later confirmed it through anatomical sectioning (Levyns 1956).

In the Cape region further expansion of herbarium collections resulted in the description of three monotypic genera, *Eremiella* (Compton 1934), based on its 3-merous flowers, *Arachnocalyx* (Compton 1953), based on several floral characters, including subbasally attached ovules, and *Stokoeanthus* (Oliver 1976b), based on a wind-pollinated species with a $\mathbf{G}^2/_{3-6}$ ovary producing an indehiscent fruit. These three species did not fit easily into the delimitation of genera accepted at the time. Compton did not mention the distinctive erect ovules in *Arachnocalyx*, despite illustrating them as such, and looked only for alliances based on meristicity, namely with *Hexastemon* and *Grisebachia*. He overlooked the close relationship between his *Arachnocalyx cereris* and *Acrostemon viscidus* N.E.Br., an anomalous species in that genus. These two species were then placed in *Acrostemon* (Oliver 1975), but later removed to the original *Arachnocalyx* (Oliver 1984) because both have a single erect, basally attached ovule in each locule.

The non-Cape floras, which appeared in the 20th century, dealt with small numbers of species and genera. The African floras maintained the status quo with regard to generic delimitation: *Flora of the Cape Peninsula* (Salter 1950) did not change any concepts of Brown (1906); *Flora of West Tropical Africa* retained *Erica*, *Philippia* and *Blaeria* (Ross 1963); *Flore de Cameroun* did likewise (Letouzey 1970); *Flore des Mascareignes* (Friedmann 1981) retained *Philippia*; *Flora zambesiaca* (Ross 1983) kept *Erica*, *Philippia*, *Blaeria* and *Ericinella*; *Flora Europaea* (Webb *et al* 1972) retained *Erica*, *Calluna*, and *Bruckenthalia*, but reduced Klotzsch's *Pentapera* to synonymy under *Erica* even with the addition of another 5-merous species, and likewise for the *Flora of Turkey* (Stevens 1978).

Nordhagen (1937/38) published the results of an in-depth investigation of the monotypic genus *Calluna* that at the time was included in Ericeae (following Drude, 1889). He introduced for the first time (Nordhagen 1938) the concept of a phylogenetic system for Ericoideae pointing to advanced and ancestral characters. His conclusion was that *Calluna* was sufficiently distinct to be recognized as a separate tribe, but still within the subfamily, but unfortunately he did not legitimize it. He maintained Ericeae and Salaxideae. In Ericeae he included all the genera recognized by Drude with the addition of Alm and Fries' *Mitrastylus* which had already been reduced to synonymy by Perrier de la Bâthie (1930). The genera of Salaxideae were not listed, but he retained the erroneous concept that some members of this group had septicidal fruits. One important aspect he raised was the reporting by Salter (1936) of putative hybrids between *Blaeria ericoides* (=*Erica ericoides*) and *Simocheilus depressus* (=*Erica glabella*). Nordhagen pointed out that these species belonged to two different tribes based on ovary complements.

Schultze-Motel (1964) in Engler's Syllabus maintained Drude's concepts of Ericoideae, keeping Ericeae with 10 unlisted genera and Salaxideae with 6 unlisted genera, based again on the number of ovules.

Watson (1967) performed a phenetic analysis of the Ericaceae and Epacridaceae and analyzed numerous characters using numerical methods as a first step in the infrafamilial taxonomic groupings of genera. His resultant system displayed a hierarchy, but he glossed over the nomenclature. His Subfamily 1 (Ericoids) included Tribe 1, containing *Calluna* and *Cassiope*, and Tribe 2 containing the rest of the genera, the Salaxids not being distinguished. In an earlier paper (Watson 1964) he suggested on anatomical grounds that *Cassiope*, hitherto always included in Arbutoideae, was very similar to *Calluna* and should therefore be placed in Ericoideae (near *Calluna*). Hagerup (1953) had earlier stated that all Ericaceae with ericoid leaves should be placed in the same group after studying the various narrow-leaved types in the family.

Stevens' landmark treatment of the whole family (Stevens 1971), unfortunately largely ignored Ericoideae apart from a detailed assessment of the placing of the enigmatic genus *Calluna*. He retained the tribal classification of Bentham for the Ericoideae, but included a new monotypic tribe, Calluneae, that had been proposed, but not validated, by Nordhagen (see above). He noted that Ericeae and Salaxideae were not as well-marked entities as Calluneae yet through lack of data could not decide on their fate. He continued like others before him to include the Klotzschian statement that some genera had septicidal capsules. Stevens (1970) rejected Watson's placement of *Cassiope* in the subfamily and postulated that similarities were due to convergent evolution and not close relationship, which has been substantiated in the recent cladistic analyses of the family (Anderberg 1993, Judd & Kron 1993, Kron 1997).

In a treatment of Ericaceae for Dyer's Genera of Southern African Flowering Plants (Oliver 1975), I maintained most of the generic concepts of Brown for want of a better, 'natural' system and listed 23 genera (excluding *Vaccinium*). The only differences were in the circumscription of *Acrostemon*, into which I placed Klotzsch's *Hexastemon* and Compton's *Arachnocalyx*, and of *Eremia*, into which I sunk Brown's monotypic *Eremiopsis*). However, it was mentioned in the footnote to the treatment (Oliver 1975: 429) that I was engaged on a revision of the family which 'may result in a reduction in the number of recognized minor genera'.

With the overwhelming preponderance of species and genera of Ericeae occurring in southern Africa it was obvious that any re-evaluation of the tribe required a revision of the genera for the Flora of Southern Africa. Thus began in the early 1970's my studies in this remarkable subfamily with its unique species richness, variation in floral morphology and diversity of pollination systems.

Several genera were initially investigated, revised and subsequently published—*Eremia* and *Eremiella* (Oliver 1976a), *Grisebachia* (Oliver 1980), *Coilostigma* (Oliver 1987b). This situation was caused by the necessity to publish work without waiting until the revision of the entire tribe had been completed. These revisions were rather unsatisfactory because, in my own mind, I was not completely satisfied with the generic delimitations. Further revisions were not published due to the increasing evidence of polyphyly in many of the genera and the breakdown in generic boundaries (Oliver 1991).

When this study began I was faced with a subfamily comprising some 850 species of which 77% occurred in the genus *Erica* and the remaining 23% were scattered among 26 minor genera. The delimitation of these genera in the Ericeae was based mostly on the number of parts per whorl with some additional characters added when necessary (Table 4). These genera were obviously artificial entities and were based on a small number of characters. Their recognition facilitated a pigeon-holing system. allowing one to deal easily with the large number of species. New species were therefore added to established genera based almost exclusively on the generic formula with almost total disregard for either overall similarity or genealogical relationships that should result from a knowledge of the whole subfamily—hence the reasons for this thesis.

The main characters used by previous workers were:

1) bract: this is always present and its position was taken into account—from axial (a) on the main branch or axis of the inflorescence through partially recaulescent (r) in various positions along the pedicel to fully recaulescent (R) and forming the abaxial lobe of the calyx.
2) bracteoles: the presence or absence of these organs was used (see Characters, Char. 9 regarding apparent absence in the fully recaulescent stage).
3) calyx: most genera have 4 sepals, but this number is 3 in some species of *Philippia* and *Syndesmanthus,* and in some flowers in some species of *Scyphogyne* and 2 and 3 in *Sympieza*. The situation regarding the fully recaulescent bract and bracteoles was not understood and therefore not correctly recorded. The sepals are free, as in *Acrostemon*, to almost completely fused and accrescent, as in *Anomalanthus*.
4) corolla: the number of lobes is mostly 4, but 3 in *Eremiella* and in some species of *Scyphogyne* and *Syndesmanthus* and only 2 in *Sympieza* and *Aniserica*.
5) stamens: the number varies from 8 to 4 with 3 in some species of *Syndesmanthus* and *Scyphogyne*; the stamens are mostly free, but can be fused to varying degrees in the *Salaxis* group of genera (not reflected in Table 4).
6) ovary: the number of locules is mostly 4 or 2, but only 1 in *Syndesmanthus*, *Anomalanthus*, *Eremiopsis* and *Scyphogynel*, and with some species of *Erica* having as many as 8.
7) ovules: these vary from as many as 180 per locule in some species of *Erica*, and 4 or down to 1 per locule in most of the Minor genera.

Permutations and combinations of the above characters were used to assign species to genera. Additional characters, like the ovary being half-inferior to the corolla (*Nagelocarpus*), ovules basal and erect (*Arachnocalyx*), the stamens free or fused (the *Philippia/Salaxis* group), the calyx accrescent (*Anomalanthus*) and the placenta free central (*Thamnus*), were also used. However, a species might possess the generic 'formula', yet not bear any resemblance to the other species in the genus. Some new species provided new variations on these formulae and were described as genera.

TABLE 4.—Generic formulae for the Ericoideae-Ericeae with known variations included.

Genus	Bract	Bracteoles	Calyx	Corolla	Stamens	Locules	Ovules	Fruit	Add
Erica	a–r–R	2[–0]	4[5]	4[5]	(4–6)8[10]	4(5–8)	[2]3–∞	#	
Bruckenthalia	a	0	4	4	8	4	∞	#	
Blaeria	r	r2	4	4	8	[3]4	∞	#	
Philippia	R	0	(3)4	(3)4	6–8	(3)4	∞	#	
Ericinella	R	0	4	4	4	3,4	∞	#	
Thamnus	r	2	4	4	4	1	4	θ	x1
Stokoeanthus	r	2	4	4	4	2	[2]3(4–6)	θ	
Platycalyx	r	2	4	4	[4](5)6–8	2[3]	1	θ	
Grisebachia	r	2	4	4	4	2	1	∅	
Eremia	r	2	4	4	8	2,4	1	∅	
Eremiopsis	r	2	4	4	8	1	1	∅	
Eremiella	r	2	4	3	6	3	1	∅	
Sympieza	a–r	0	2–4	2	4	2	1	∅	
Aniserica	r	0	4	2	4	2	1	∅	
Thoracosperma	a–r	2	4	4	4	(2)4	1	∅	
Acrostemon	a–r	2	4	4	4	(1)2(3,4)	1	∅	
Hexastemon	r	2	4	4	6	2	1	∅	
Arachnocalyx	r	2	4	4	4–8	2	1	θ	x2
Simocheilus	a–r	2–0	4	4	4	2–4	1[2]	∅	x3
Syndesmanthus	a–r	[2]–0	4,3	4,3	4,3	1	1	∅	
Anomalanthus	r	2	4	4	4	1	1	∅	x4
Salaxis	R	0	4	4	(4)6–8[9]	[1]2–4	1[2]	∅	
Coccosperma	R	0	4	4	4–8	1,2[3]	(1)2[3]	∅	
Lepterica	R	0	4	4	8	1	1	∅	
Scyphogyne	R	0	4,3	4,3	4,3	1[2]	1	∅	
Coilostigma	r–R	0	4	4	4	2(3)4	1	∅	
Nagelocarpus	R	0	4	4	4	2	2	∅	x5
Calluna	?a	?6–64	4	4	8	4	∞	#	x6
Daboecia	a	0	4	4	8	4	∞	#	x7

(a=axial, on the main axis; r=partially recaulescent; R=fully recaulescent; ( )=occasional occurrence; [ ]=rare occurrence; # =dehiscent; θ =partially dehiscent; ∅ =indehiscent; x1=free central placenta; x2=basal erect ovules; x3 =some species with accrescent fruits; x4 =accrescent fruits; x5 =half-inferior ovary; x6 =sessile, sagittate leaves and septifragal dehiscence; x7 =deciduous corolla, alternate leaves and septicidal dehiscence). Note: with those genera possessing a totally recaulescent bract (R), the figures for bracteoles and calyx reflect the parts recorded prior to this study and not the true situation [see later under Characters, Chars 7–10).

The genus *Eremia*, for example, is extremely heterogeneous. *Eremia totta* (*Erica totta*) has a formula **A**8 **G**$^{4}/_{1}$, while *Eremia recurvata* (=*Erica recurvifolia*), *Eremia peltata* (*Erica cetrata*) and *Eremia brevifolia* (*Erica velatiflora*) all have **A**8 **G**$^{2}/_{1}$, yet bear little resemblance to each other (and are probably not to be closely related). The recently discovered *Erica vlokii* would have had to be placed in the genus *Eremia* based purely on its floral formula **A**8 **G**$^{4}/_{1}$, yet it is not similar to the other species, but is phenetically very similar to the sympatric, dehiscent-fruited *Erica umbelliflora*.

Likewise, when new species were discovered that did not have any of the existing combinations, there was a problem and monotypic genera had to be described, such as *Eremiella* (*E. outeniquae*), *Arachnocalyx* (*A. cereris*) and *Stokoeanthus* (*S. chionophilus*). Some new, undescribed species fall into this category: *Erica karwyderi* looks like a species of *Simocheilus*, but has 8 stamens; *Erica jonasiana* with its **A**8 and asymmetrical **G**$^{1}/_{1}$ does not fit the formulation of any genus nor was it similar to any of the known Minors; *Erica perplexa* has the formula of the genus *Salaxis* with a fully recaulescent bract, but it has a totally different fruit and seed type and a dense willowy habit with plumose hairs on the branches. All these species would have caused generic boundaries to be radically redefined if forced into existing genera, or would have had to be described as monotypic genera, but both options I was hesitant to take.

Reference to herbarium collections in southern Africa and recent collections made in the field and requiring identification, immediately pointed to the problem of satisfactorily placing species in genera. This situation is epitomized by the problems with *Philippia* Klotzsch (Oliver 1988), when a single specimen could be identified to two species in two different genera depending on which flowers were examined. As my investigations into the delimitation of genera proceeded, it appeared that the three capsular genera that were panAfrican in their distribution, *Philippia*, *Blaeria* L. and *Ericinella* Klotzsch, were polyphyletic entities, and had multiple relationships with *Erica* (Oliver 1989). These genera were therefore included in synonymy under *Erica*: *Philippia* (Oliver 1987c, 1988, 1992, 1993a, Dorr & Oliver 1999a & b), *Blaeria* (Oliver 1993b & c), *Ericinella* (Oliver 1994). It was also recommended that the monotypic European genus, *Bruckenthalia*, return to its original identity, *Erica spiculifolia* Salisb. (Oliver 1989, 1996). In the present work the concept of *Erica* includes all the species having a loculicidal capsule.

During the taxonomic revision of the remaining 83 species not belonging to *Erica* as just defined, it appears that 15 species (9 individual species and 3 groups of 2 species each) were not closely allied to any other species of Minor genera or grouping thereof, but rather to various species within the genus *Erica*. It was clear that generic boundaries were weak and that the genera were very artificial, being based on a small number of characters; many genera could not be maintained.

The objectives of the current study, therefore, are primarily to assess generic delimitation in the tribe Ericeae. Can monophyletic (generic) groups be found within the tribe using cladistic (parsimony) analysis of morphological data? The main results of my work are a provisional hypothesis of the phylogenetic relationships in Ericeae, and a taxonomic revision of the 'Minor' genera.

Chapter 2

MATERIAL AND METHODS

This study follows the standard methods for taxonomic revisions. Literature was consulted in the libraries at BM, BOL, K, NBG and PRE (abbreviations according to Holmgren *et al.*1990). All the material of Ericeae in BM, BOL, K, NBG (STE)*, SAM, P, PRE, TCD, and of only Minor genera in B, E, G, GB, GOET, GRA, LD, LINN, MEL (in part), MO, S, UPS, W, Z, were consulted and recorded in a database. Curators of these herbaria are thanked for facilities and some for the loan of certain type specimens and problematic collections to NBG (STE). In all some 4230 collections comprising 8468 specimens were studied.

Morphological work was carried out on dried herbarium material. In Ericeae material is easily rehydrated by boiling very lightly for a few minutes in water with the addition of a drop of commercial dishwashing liquid added to reduce surface tension and help with penetration. Such material can then be successfully dissected and examined under water and the characters drawn and recorded without recourse to the preparation of whole mounts (see below). Only in cases of very well pressed and flattened old material is a perfectly resuscitated flower not produced. Examination of the pericarp was carried out on fresh and/or rehydrated material using hand-cut sections and dissections.

Most species were also studied in the wild from as many different populations as possible to ascertain the variability within the species and to fill in gaps in the herbarium collections. Fresh material was in most cases brought back to the herbarium for the examination of large numbers of flowers to save having to rehydrate dried material. Four species, *E. miniscula* [*Lepterica tenuis*], *E. eglandulosa* [*Scyphogyne eglandulosa*], *E. pulchelliflora* [*Syndesmanthus pulchellus*] and *E. kammanassieae* sp. nov., have not yet been located in the wild and for the first two I had to rely on the type collections made over 150 years ago.

Because most species have small flowers (in the range from 1.5 mm long to as little as 0.7 mm) having mostly microscopic features, the characters of some to most collections (depending on the amount of variability) were recorded on cards using a camera lucida on a Wild M5 stereomicroscope. This improved considerably comparison of specimens and characters and obviated the need for repeated examination under the microscope.

The anatomical investigation involved mapping the general distribution and relative sizes of tissues of the leaves in all the Minors and included some 190 species of *Erica* (25% of the genus) to assess the status of characters within that genus. For this investigation either fresh material or herbarium material was used and easily sectioned by hand under the 25x magnification of the stereomicroscope. The dry, very small, almost cylindrical leaves of the Ericeae with their relatively thick cuticle/epidermis were easily cut using a single blade from a twin-bladed razor. These sections, approximately 25µm thick, were mounted, unstained, in a drop of water with dishwashing liquid added. Herbarium material slightly boiled in water usually showed distortions of the cells and

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* NBG & STE were amalgamated in 1996; all holotypes previously housed in STE are cited as NBG(STE).

therefore rehydrating was not used. The sections were observed under a Zeiss and a Vickers light microscope and the distribution of tissues, which were readily distinguishable, were recorded by camera lucida drawings together with measurements of the epidermal cells. Thinner sections caused the delicate internal tissues to tear especially because of the frequent presence of crystals. Thicker sections (±50µm) were found to help in understanding the proportions and relationships of the various tissues.

A preliminary survey of 57 species using standard embedding and staining techniques was undertaken at my suggestion by A.D. Spreeth, University of Stellenbosch, but is as yet unpublished. He has kindly made his permanent slides available to me. Comparison of the results of the two techniques indicated that hand-cut sections were very good for the purpose of the present work and that they showed no distortions, which were often unavoidably present in the embedded sections. In addition, crystaline inclusions, of calcium oxalatae, where known, were not lost in the thicker, untreated, hand-cut sections.

Fruits and seeds were studied from material gathered in the field either on the plants for the current season's crop, or in the detritus under the shrublets for the previous season's fruits (the latter for the indehiscent fruited species). When not available in the field, fruits and seeds from herbarium material were used, when these were present.

Examination of the pericarp was carried out on fresh and/or rehydrated material using hand-cut sections or dissections.

In the dehiscent fruited species dry seeds were examined and drawn using a Wild M5 stereomicroscope and compared with seeds mounted on aluminium stubs with double-sided adhesive tape, gold-coated and then viewed and photographed using an ISI SX 25 scanning electron microscope with no special preparation being necessary. Some of these photographs were published in an earlier survey (Oliver 1991).

In species with indehiscent fruits, only seeds with a thick, hard testa could be dissected out of their fruit with relative ease. These were examined under the SEM in the same manner as above, again with no special preparation being needed. Seeds with a thin to ultrathin testa could not be cleanly separated from the pericarp and in these cases the testa, or small portions thereof, was mounted in water on a slide and examined under a Vickers light microscope using transmitted light and without any staining or preparation. Testa samples of all SEM-examined seeds were also investigated under the light microscope to record cell details, especially for the pits that are not visible under the SEM. Among the Minors fruits were not available for *E. pulchelliflora* and *E. niveniana*, and for *E. miniscula* the few fruits available contained no fertile seeds.

Fresh or dried pollen samples were examined under a Vickers light microscope solely for recording the pollen type of every species (tetrad or monad); no preparation was necessary. A preliminary examination of pollen under the SEM (Oliver 1980; Oliver 1991) using non-acetolysed pollen showed some differences in sculpturing, but an extensive investigation of the Ericeae to provide any meaningful characters could not be undertaken due to the large number of species and time constraints. Pollen material was, however, given to R. Davis of the University of Stellenbosch for SEM investigation (Davis 1997). His investigation covered 71 species of Ericeae consisting of

28 species of Minors, 42 species of *Erica* and the single species of *Daboecia* using acetolysed material. He concluded that groups based on exine sculpturing cannot be used to distinguish genera or the Minors from *Erica*.

The states of many characters within the family are not well documented. Several revisions were consulted, but the most useful data were provided in Sleumer's treatment of the family in *Flora malesiana* (Sleumer 1966), Stevens' review of the family (Stevens 1971) and in the excellent work on the superior-ovaried genera of South America, southern North America and the Antilles in the *Flora Neotropica* (Luteyn *et al.* 1995).

For the cladistic analysis the parsimony programmes Hennig86 (Farris 1988) and PAUP 3.1.1 (Swofford 1993) were used. Further details are discussed under the chapters covering analysis and phylogeny.

For ease of reference to the details of floral parts in the general main text, in the keys, and in the line drawings of the species (Chapter 6.5), I have used a formula that I adopted earlier (Oliver 1991) based on traditional floral formulae, viz. **L**=leaves per whorl; **Br**=bract; **br**=bracteoles; **K**=calyx; **C**=corolla; **A**=androecium; and **G**=ovary with the first figure representing the number of locules, the second the number of ovules per locule, thus $\mathbf{G}^2/_1$ is a 2-locular ovary with 1 ovule per locule. In the case of the bract and bracteoles additional symbols have been used to refer to the condition of recaulescence—a=axial, r=partially recaulescent, and R=fully recaulescent. This is similar to the formula adopted by Abbott (1936), but never taken up by other ericologists.

Chapter 3

PHYLOGENETIC ANALYSIS

3.1 STUDY GROUP

The tribe Ericeae as recently proposed for recircumscription by Kron (1997) and Kron, Judd, Stevens, Crayn, Gadek & Quinn (pers. comm.) was used as the study group in the cladistic analysis (Table 5).

TABLE 5.—Outline of new classification of Ericaceae proposed by Kron et al.

ERICACEAE

- **Enkianthoideae** (*Enkianthus* only)
- **Pyroloideae**
  - Pyroleae
  - Monotropeae
  - Pterosporeae
- **Arbutoideae**
- **Cassiopoideae** (*Cassiope* only)
- **Ericoideae**
  - Ericeae (*Erica s.l.*, *Calluna*, *Daboecia*)
  - Ledothamneae (*Ledothamnus*, *Bryanthus*)
  - Phyllodoceae (*Kalmia* s.l., *Elliotia s.l.*, *Kalmiopsis*, *Rhodothamnus*, *Epigaea*, *Phyllodoce*)
  - Empetreae (*Corema*, *Ceratiola*, *Empetrum*)
  - Rhodoreae (*Rhododendron s.l.*, *Therorhodion*, *Menziezia*, *Diplarche*, "*Bejaria*"?)
- **Harrimanelloideae** (*Harrimanella* only)
- **Epacridoideae**
  - Prionoteae (*Prionotes*, *Lebetanthus*)
  - Archerieae (*Archeria* only)
  - Oligarrhenieae (*Oligarrhena*, *Needhamiella*)
  - Cosmelieae (*Cosmelia*, *Andersonia*, *Sprengelia*)
  - Richeae (*Richea*, *Dracophyllum*, *Sphenotoma*)
  - Epacrideae (*Epacris* s.l., *Woolsia*, *Lysinema*)
  - Styphelieae (remaining fleshy fruited genera)
- **Vaccinioideae**
  - Lyonieae (*Lyonia*, *Pieris s.l.*, *Craibiodendron*, *Agarista s.l.*)
  - Gaultherieae (*Gaultheria s.l.*, *Diplycosia*, *Tepuia*, *Chamaedaphne*, *Leucothoe*, *Eubotrys*)
  - Vaccinieae (inferior-ovaried genera)

The monophyly of the Ericeae was corroborated by parsimony analysis of *rbc*L (Kron & Chase 1993), *matK* (Kron 1997), and morphological data (Anderberg 1993). Anderberg used the synapomorphies of the presence of anther spurs and a persistent corolla, both parallelisms, the latter shared with Empetreae.

The genus *Daboecia* has been variously placed in recent analyses, some being far removed from Ericeae, e.g. Stevens (1971), Judd & Kron (1993), Kron & King (1996). Anderberg (1993) has the genus placed next to the Ericeae and Kron (1997) within the 'ericoid' clade. However, Kron & Crayn (pers. comm.) are proposing in their a new circumscription of the family to place *Daboecia* within the newly defined tribe Ericeae as sister to *Calluna* and *Erica*.

The study group therefore comprises *Daboecia* and *Calluna*, the 83 species belonging to the Minors which are revised in the current study, and a selection of species representing *Erica s.l.*—10 species of *Erica s.str.*, three species formerly in *Philippia*, 5 species formerly in *Blaeria*, one species formerly in *Ericinella* and the former monotypic *Bruckenthalia*. It was decided to ignore current generic affiliations for the Minors and to treat them as individual species referred to only by their specific epithet.

3.2 OUTGROUP

One of the important steps in cladistic methodology is the establishing of hypotheses on the transformation of characters by determining the polarity of the character states. Only two criteria are generally used in establishing this polarity—outgroup comparison and ontogenetic studies (Linder 1988).

Linder (1988) noted that ontogenetic data have generally not been very useful in botanical studies. This type of data has clearly been useful and well documented in animal studies (Kluge 1985). Unfortunately no such data are available for Ericeae at present apart from the in-depth embryological work of Palser & Murty (1967) which unfortunately did not include any of the Minors.

Outgroup comparison was considered to be the most acceptable criterion (Stevens 1980) and has been described in detail by Watrous & Wheeler (1981) and Maddison et al. (1984) and has become standard practice in most recent cladistic analyses.

Within Ericeae the studies cited above under Study Group give convincing arguments for *Daboecia* and Calluna as the sister group of the rest of the tribe. Both are monotypic genera with only minor known infraspecific variability, which, if major, would otherwise compromise character states within the ingroup. *Calluna* is, however, very variable in the numerous aberrations that have been taken up in horticulture and is problematic due to difficulties with primary homology statements (see under Characters regarding inflorescence, bract and bracteoles). It was at first excluded as part of the outgroup and then later included to find arguably better resolved trees.

Ideally additional taxa should be included in the outgroup to overcome possible errors in distinguishing convergences from real shared ancestral states (see 3.6 Character Evolution). However, many recent cladistic studies have relied on single outgroups or even used a single hypothetical ancestor. No further outgroups could be considered in this study since the data available from any taxa within the former Rhododendroideae are currently unavailable for primary homology assessment in many characters and would have to be scored as unknown or inapplicable. Kron (1997) found the 'phyllodocoid' clade to be sister to the 'ericoid' clade and closer than the 'rhododendroid' or ' empetroid' clades. Thus any selection of taxa in the phyllodocoids could not be considered either due to the lack of data. In future studies it would be useful to include some of these taxa, such as *Bejaria*, *Loiseleuria* and *Kalmia*.

Nixon & Carpenter (1993) suggest that polarity values derived from initial outgroup comparisons are not necessary and they support simultaneous analysis with rooting of the cladogram providing the polarities. They contend that maximum parsimony will deal with the problems of polarity and "primitiveness" if the user provides the root—"polarity need not be decided before analysis". The analyses work on global parsimony of the data set with the root being provided by the user. With different roots the cladograms can alter and therefore the interpretation of character polarity is carried out after the analysis using the cladograms.

3.3 CHARACTER ASSESSMENT

On completion of the taxonomic revision of the 83 species belonging to the Minor genera of the tribe Ericeae, the morphological character set of the whole tribe was examined to provide an empirical basis for a reassessment of the generic classification of the Ericeae and to find characters that would be useful for reorganizing monophyletic groups and for postulating a possible phylogeny. In addition to the species of Minors, the 670 species of *Erica* from southern Africa were examined as well as a selection of the 22 species in Europe, the ca. 60 species occurring in tropical Africa, Madagascar and the Mascarenes, and the two monotypic European genera, *Daboecia* and *Calluna*.

Only morphological data was used in this study due to the virtual absence of data on other aspects of the species such as chromosomes, chemical constituents, and DNA. Only 26 species have had their chromosomes counted (Oliver 1991), 24 included in chemical investigations of the whole family (Harborne & Williams 1973) and 17 in various DNA analyses (Kron 1997, Mitchell & Kron pers. comm.)

Once a study group has been selected and an outgroup identified the next step in phylogenetic studies is the assessment and selection of the characters using criteria of similarity or 'homology' (Stevens 1991). Much has been written in recent years about this very important process (Pimentel & Riggens 1987, Chappill 1989, Kluge 1989, Stevens 1991, Thiele 1993, Pleijel 1995, Hawkins *et al.* 1997, Rae 1998, to cite only a few.). In the words of Hawkins *et al.* (1997) "the assessment of primary homology remains a contentious, subjective, and yet ultimately crucial and influential, step in any cladistic analysis."

Neff (1986) argues that characters have a large theoretical component and are essentially complex low-level hypotheses. Thus the primary homology assessment in an analysis implies the erection of initial hypotheses concerning the homology of the characters.

Stevens (1991) provides an overview and critique of character assessment and is of the opinion that "all analyses, phylogenetic or otherwise, are constrained by the initial circumscription of character states". He notes that this step in cladistic analyses had received the least amount of attention by researchers and advocates "explicit justification for the delimitation of character states....as a matter of course in all phylogenetic studies."

This leads to several aspects of primary homology assessment, which have recently received considerable attention—the use of quantitative data that are often regarded as exhibiting continuous variation, and the independence of characters. The former has received the most comment with authors arguing for their use, or at least limited use (Thiele & Ladiges 1988, Chappill

1989, Thiele 1993, Heenan 1998, Rae 1998) and others against their use (Pimentel & Riggens 1987, Stevens 1991, Cranston & Humphries 1988, Crisp & Weston 1987, Gift & Stevens 1997).

Stevens' (1991) often-quoted survey of character assessment stresses the fact that many qualitative characters used in cladistic analyses are in fact "based on a quantitative phenomological base". He states that it has been asserted that the requirement for sharp gaps between character states is a methodological requirement of cladistics, that many characters are quantitative and do not show such gaps, and that characters having an obvious continuous quantitative basis show a higher incidence of homoplasy, which may distort the analysis.

Gift & Stevens (1997) showed that one set of measurements allowed the generation of a whole series of character matrices among a group of individuals who were asked to delimit character states as an experiment. They therefore strongly advocated that continuously varying characters should not be used in phylogenetic systematics without proper justification.

Stevens (1991) noted that several statistical approaches (Almeida & Bisby 1984, Archie 1985) are available for use in partitioning continuous quantitative characters if these characters had to be used in an analysis. Complete measurement data from the taxonomic revision were not retained in this study and therefore could not be used for these methods; delimitation of states in such cases was based on my assessment of the ranges of variation and likely discontinuities.

Within the Ericeae there are problems in delimiting a complete set of discrete characters since many characters are quantitative and continuously varying (see analysis at end of this section). There are surprisingly few purely qualitative characters available in a large group such as the Ericeae. Indeed the comment of Chappill (1989) "in many plant groups, relationship at low taxonomic levels cannot be resolved without resort to at least a few [quantitative] characters", At this stage in the study of the Ericeae I am forced to include 31 quantitative characters in the analysis. Wherever possible the delimitation of states of these is based on boundaries that I estimate to be reasonably discrete.

The matter of character independence in cladistics has been mentioned in several papers. Kluge (1989) pointed to this being an important concept in phylogenetic inference, stating that the assumption of independence is critical in phylogenetic analyses, but noted that independence of characters does not mean that characters will not be correlated. Hawkins *et al.* (1997) suggested that the term 'independence' is often confused with notions of functional complexes of characters that have to evolve in concert. Wilkinson (1995) argued that if characters are not independent then "the evidential significance of the underlying variation may be overweighted".

In the Ericeae this concept was kept in mind when I was assessing floral characters that appear to have developed 'in concert'. The bract, when fully recaulescent, will always be accompanied by fully recaulescent bracteoles, but the opposite is not necessarily true. In *Daboecia* and *Bruckenthalia* the bract is always on the main axis, not even partially recaulescent, but the bracteoles are fully recaulescent. Similarly all species with a fully recaulescent bract and bracteoles always lack nectaries and have a large stigma but not all species without nectaries and a large stigma have a fully recaulescent bract and bracteoles (e.g. *Erica brownii* [*Syndesmanthus breviflorus*] and *E. erina* [*Syndesmanthus erinus*]).

Another feature that has been addressed by workers recently is the selection of coding methods, namely binary versus multistate characters. Pimentel & Riggens (1987) evaluated different aspects of coding procedures and concluded that characters should be coded as multistate variables rather than being split up as presence/absence binary characters. This was also supported by Hauser & Presch (1991) and Meier (1994). However, Pleijel (1995) argues that absence/presence binary states represent a similar and more straightforward approach, but goes on to suggest that the "whole issue of character coding deserves further evaluation".

In the selection of binary, nominal variable characters, Pimentel & Riggens (1987) argue that absence must not be excluded from cladistic data, it is only valid when it is considered as a loss, i.e., it can never be the plesiomorphic state. Platnick *et al.* (1991) drew attention to the fact that "absence" may be of three logically different kinds: unknown data; inapplicable data; polymorphism. In multistate characters the latter presents problems with some computer programmes, but they point out that the later versions of PAUP (Swofford 1993) apparently solve this problem (see data matrices in Tables 8 & 9). This is very important in regard to Ericeae since several species are polymorphic for certain multistate characters, exhibiting several, but not all, of the states. Recording these as variable for all of states of the character would provide erroneous data for the analysis and may well result in erroneous hypotheses of relationships.

Stevens (1991) argues that not recognising variation at all, i.e., scoring variable taxa as missing data, implies that there is no connection between taxa in which a character state is sometimes present and those in which it is always present and adds "there may be some sort of developmental potential..... It may be best to treat variation as polymorphism". I strongly support this procedure.

Forty-nine characters covering floral and vegetative morphology as well as the general anatomy of the leaf, all derived from the taxonomic studies, were recorded for the species (see Table 6). These characters were carefully assessed within the Minor genera and within *Erica*, *Calluna* and *Daboecia* for their possible usefulness in the phylogenetic analyses.

The following discussion assesses these characters and the delimitation of their states with respect to the genus *Erica* and the Minor genera as a group and also in the rest of the family, when applicable/available. I comment on their value for inclusion in this analysis. For a general review of characters within the tribe [subfamily Ericoideae *s.str.*] see Oliver (1991).

HABIT

The plants of Ericeae are woody perennials usually forming shrubs in the range 0.2–1.5 m tall. Some species, particularly those in tropical Africa and southern Europe, can form veritable trees up to 15 m tall (Miehe & Miehe 1993, 1994), and in Madeira even to 20 m. Among the 760 Cape species a treelike habit is rare (*Erica caffra*), but there is a reduction in height to those species that form prostrate spreading plants. The latter types may be associated with seepage zones (e.g. *Erica amicorum*, *E. oligantha*, *E. oxycoccifolia* among many), with limestone coastal flats (see here *Erica radicans* and *E. vernicosa*) or with higher drier altitudes in the inland areas, particularly the Ceres and Clanwilliam Districts (e.g. *Erica senilis*, *E. eriophorus*, *E. tegetiformis* *E. involucrata*, *E. pudens*, and *E. eremioides* (see species 51)). Occasionally individuals of otherwise prostrate species form erect shrubs when supported by other vegetation. The Minors are basically small shrublets 200–500 mm tall with only a few growing over 2 m (see *Erica urceolata* [*Scyphogyne urceolata*] and *E. uberiflora* [*Simocheilus multiflorus*]).

Most Ericeae are single-stemmed reseeders that regenerate from seeds after a fire. A preliminary survey of the Cape species (Ojeda 1998) records only 28 species, i.e., 6.4% as multi-stemmed resprouters with, in some cases, considerable underground lignotubers. The resprouting species are scattered throughout the sections as currently recognized in *Erica*. In some cases both traits may occur in the same species or at least species complex, e.g. *Erica coccinea*, *E. plukenetii*, *E. calycina*, *E. imbricata*, which are being investigated separately (Oliver in prep.). Within the Minors only three species are resprouters, *Erica cetrata* [*Eremia peltata*], *E. burchelliana* [*Coilostigma glabrum*] and *E. bolusanthus* [*Thoracosperma nanum*], which are not at all phenetically similar.

No clear-cut character states for habit and growth form could be found.

BRANCHES

Apart from features that are reflected in the habit, there are several characters which pertain to the surface of the branches that have been useful in species delimitation, namely indumentum types and infrafoliar ridges. The latter are very useful when distinct, but are often quite indistinct, especially in older branches.

Bark types have never been investigated in the Ericeae and could be of possible use as evidenced in my brief investigation of several Ethiopian samples (Miehe & Miehe 1994: 94–96) (corky bark versus stringy bark pealing off in strips). This may be useful in the treelike species in tropical Africa, but is unlikely to have any value in the small shrubby South African species.

Branch hairs (Char. 1): The presence and type of hairs on the young branches are useful characters in the delimitation of species in the Ericeae. Most species have hairs of some sort; totally glabrous being rare. The hair types vary considerably from simple unicellular or multicellular, uniseriate hairs to multicellular multiseriate hairs, to multicellular, multiseriate hairs with various types of basal, lateral or terminal branches, the plumose hair type (Fig. 2). The hairs may be very short and/or very long and either soft or stiff, straight or recurved. All hair types may be gland-tipped with glandular and eglandular hairs of the same or different type sometimes admixed on the same branch. Very often there are some glands in the youngest stages but these are soon lost. Also branches may have just short simple unicellular uniseriate hairs in the young stages but later develop stout multiseriate hairs which may be plumose. The plumose hairs vary considerably in morphology depending on the position of the side branches, so much so that it is very difficult to categorise them into discrete states. I have thus retained in this analysis only the single category of 'plumose' to cover all these forms which are mostly easily separable from the 'simple' unicellular to multicellular, unbranched hairs. In many cases both forms are present in the same species.

The character has been included in the analysis with the states taken as—no hairs present [0], only simple hairs present [1], plumose hairs present (sometimes exclusively) with simple hairs often also present [2] (Table 6).

ERICA: all types of ericead hairs occur in the genus in various combinations, often on the same branch.

MINORS: all types occur, but usually not mixed in the same species.

CALLUNA: only fine short simple hairs occur.

DABOECIA: has very short unicellular hairs mixed with much longer uniseriate multicellular hairs, all being eglandular.

FAMILY: from the literature it is not possible to assess whether the plumose ericead hair types occur outside the group. The distinctive lepidote hairs found in *Rhododendron* do not occur in any members of the Ericeae (see Seithe 1960 & 1980 for a detailed investigation).

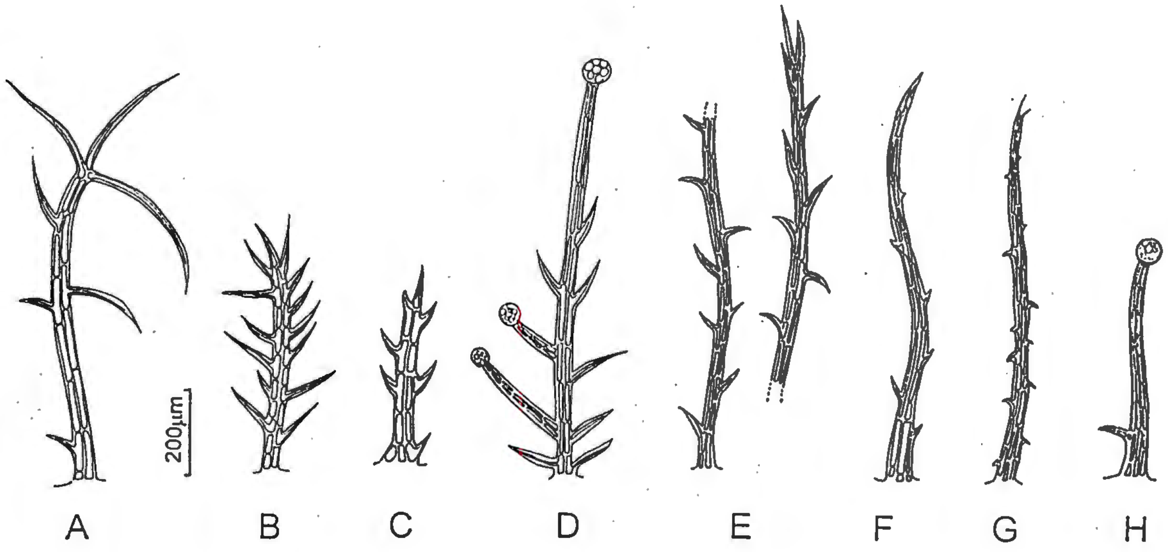

FIGURE 2.—Examples of some plumose hairs in Ericeae. A, *Erica stokoeanthus*; B, *E. perplexa* & *E. jacksoniana*; C, D & H, *E. rigidula*; E & F, *E. plumosa*; G, *E. totta*.

LEAVES

Narrow, needlelike leaves with a sulcate abaxial surface, the so-called 'ericoid' leaf, are characteristic of Ericeae. Both Hagerup (1953) and Stevens (1971) have investigated this condition. Similar leaves occur in other members of the family: *Ledothamnus* and *Tepuia* in South America (Luteyn 1995), *Empetrum* in South America and the northern Hemisphere (Anderberg 1994), *Daboecia* in Europe and *Rhododendron* (*R. ericoides*) in Indonesia (Sleumer 1966). These are postulated to be the result of parallel evolution (Stevens 1971; Watson *et al.* 1967), but, in part, possibly indicative of relationship, being possibly ancestral in Ericoideae s.l. with reversals to broad, flat leaves.

Variations in the shape of the leaves resulting from the degree of recurvature of the margins within Ericeae occurs only in *Erica*. Here the leaf may be completely flat and orbicular (e.g. *Erica marifolia*, *E. oxycoccifolia*, *E. amicorum*), being related to the wetness of the habitat and occurs in species inhabiting seeps or moist, south-facing, cliff-faces. There may even be infraspecific variation within a species depending on the habitat (*Erica hispidula*). In my opinion the shape and sulcus has very little taxonomic value except at the species level since species from a number of different sections in the genus *Erica* possess this feature.

Other morphological characteristics of the leaf are size, indumentum type and aspect, all equally shared throughout the subfamily. Long leaves (25–33 mm) occur only in the long-tubed species in Sections *Evanthe* and *Pleurocallis* and the *E. inflata* alliance in Section *Ceramus*. The rest of the hundreds of species with small- to medium-sized flowers have leaves in the range 5–10 mm. I have noticed that size can vary on a single plant depending on the position of the leaf in the growth cycle or whether or not it is on a coppice shoot.

The indumentum is mostly made up of simple hairs, either unicellular or uniseriate and short or long. Totally glabrous leaves are uncommon, but in some species both hairy and glabrous forms may occur even within the same population (e.g. *E. anguliger*). Additional types of hairs occur—gland-tipped and plumose, but these latter types are highly variable. In young leaves there are often some glands which soon disappear or these may persist into the mature stages; similarly with the plumose types. In some cases the hairs vary within a species and are used for subspecific delimitation (see *Erica plumosa*, *E. venustiflora*). The delimitation of indumentum types into discrete states is very difficult.

The aspect of the leaves, which varies from appressed and imbricate to squarrose-recurved, is very striking, especially in those species that have only erect, appressed leaves (e.g. *Calluna vulgaris* and *Erica juniperoides*), for squarrose-spreading leaves (e.g. *Erica bauera E. aristata, E. retorta*; and *E. recurvifolia* (see Plate 48) and *E. eremioides* subsp. *eglandula*). However, the intermediate condition of semispreading leaves is very common and leaves may vary from erect to fully spreading within a single plant, the younger leaves being erect but becoming variously spreading even to squarrose-recurved with age. The delimitation of discrete states is easy with the extreme cases but there is so much intergrading in the intervening states that the character cannot be used in a cladistic analysis.

The genus *Calluna* is unusual in the tribe because its leaves are sessile and auriculate; apomorphies that are not included in this study. All other Ericeae have petiolate (from very short to long) and non-auriculate leaves. Only a single Cape species, *Erica virginalis*, has sessile leaves, but these are not auriculate. *Calluna*-type leaves also occur in the genus *Cassiope*, which led Hagerup (1953) to place the latter within the Ericoideae *sensu stricto*. Stevens (1971) pointed out that this placement was incorrect postulating that the similarity was due to convergent evolution. The recent studies on *matK* sequences clearly substantiates this view, with *Cassiope s. str.* being basal to the whole ericoid/rhododendroid clade (Kron 1997).

The leaf of *Daboecia* does not have the same appearance as the typical 'ericoid' leaf. It lacks a distinct disjunction between the lamina and petiole and has a distinctive subapical glandular excrescence on the abaxial surface, a structure not found in other Ericeae.

The only characters involving the leaves that could be selected for analysis were in their arrangement and the meristic features of the whorls.

Leaf Whorls & arrangement (Chars 2 & 3): The whorled arrangement of the leaves is another leaf feature characteristic of the Ericeae. The states seem to be reasonably fixed within the species and have been useful for species delimitation. It was noted in the revision of the species that the number of leaves per whorl seemed to be correlated with what appeared to groups of allied species. The character thus was retained for the analysis (see Table 6).

The states of these characters are—alternate [0], and whorled [1]; 4-nate whorls [0], 3-nate whorls [1], and 2-nate whorls, i.e opposite [2].

ERICA: the leaves are 3-nate in most species but with ±160 species (23%) being 4-nate. Several of the long-tubed species in the Cape have the leaves up to 6-nate or sometimes scattered. Sometimes some species or particular plants may have slightly scattered leaves (not strictly arranged in whorls). Species in the *E. corifolia* complex have 2-nate or opposite leaves as do a few other species.

MINORS: most species have 3-nate leaves with only 10 species (12%) having 4-nate leaves. Only *E. globiceps* and *E. eriocephala* possess both states, sometimes on the same plant in the latter.

CALLUNA: leaves are always opposite (2-nate).

DABOECIA: leaves are alternate and spirally arranged, never whorled.

FAMILY: whorled leaves are rare, but occur in a few unrelated groups (Stevens 1971), most notably in *Ledothamnus* (see above). Most leaves are alternate and spirally arranged (scattered or pseudoverticillate).

INFLORESCENCE

Inflorescences are all terminal at the ends of first to fourth order branches. Most inflorescences are non-innovating, being determinate in growth with the apical meristem aborting after the flowering period. Some inflorescences that occur on first order branches can be indeterminate with a prolongation of the branch taking place from the apex of the inflorescence, usually after flowering. In all inflorescences the flowers are always borne laterally on the branch (but see discussion below for *Calluna*).

Lateral branches can be reduced to very short shoots no more than a millimetre long with a few whorls of highly reduced bracteose leaves or just the pair of prophylls (Fig 5.7). A single subterminal flower is all that is left of the inflorescence and as such appears axilliary on the main branch. Such few-flowered inflorescences may be aggregated along a main branch in a spike-like arrangement to form a synflorescence, which appears to be a simple raceme. Careful examination is required to assess the presence of synflorescences, and these have been misunderstood by numerous authors (Guthrie & Bolus 1905, Temple 1975). Synflorescences occur in the current subgeneric classification of *Erica* in the sections *Pleurocallis* with long-tubed flowers, *Chlorocodon* with small, mostly wind-pollinated flowers and *Gypsocallis* with small insect-pollinated flowers bearing exserted stamens. Synflorescences are found only in *Erica benthamiana* (=*Aniserica gracilis*) and *E. williamsiorum* sp. nov. among the Minors.

Temple (1975) investigated and categorised growth patterns and the positions of the inflorescences in the family using the architectural models proposed by Hallé and Oldemans (1970). She had difficulty in both interpreting the patterns as well as categorising them, and particularly when later confronted with numerous species of Ericeae in the Cape (Temple pers. comm.).

The monotypic *Calluna* is distinctive among Ericeae. It is recorded as having a raceme borne terminally on the main branches, the 'axillary' flowers each having a multibracteolate pedicel. In *Flora Europaea* it is recorded as having 'narrow racemes which are sometimes grouped into panicles' (Webb 1972). The situation regarding the numerous opposite bracteoles in *Calluna vulgaris* is unfortunately complicated by the leaf arrangement on vegetative branches also being opposite. The number of 'bracteoles' varies from the usual 4–12 (i.e. 2–6 whorls), up to as many as 64 (32 whorls) in forma *multibracteolata* (Beijerinck 1940: 21). These 'bracteoles' are opposite and decussate and are mostly indistinguishable from the vegetative leaves and, if no flower is formed (as sometimes happens), must then be referred to as leaves. Only the last whorl or two show signs of becoming petaloid (as also occurs in the leaves of some *Erica* species). However, an anomaly does occasionally occur in *Calluna* when lateral, either floral or vegetative, buds develop in the axils of the upper whorls of 'bracteoles'. When the buds are floral there is the repetition of the green bracteoles/leaves below the flower. This was noted by Nordhagen (1936), and also seen in material I have cultivated from seedlings appearing in imported Irish peat and in cultivated plants I have studied in Ireland. This feature would strongly suggest that the pedicel and 'bracteoles' are in fact a lateral vegetative branch with a terminal flower. There is no aborted apical bud present as in the rest of Ericeae. The elongate, supposedly simple, racemose inflorescence with its axillary, multibracteolate flowers can sometimes be altered by having a few lateral branchlets with two or three flowers occurring halfway up the 'raceme'. Beijerinck (1940) notes the occasional plant in which the terminal bud (normally vegetative) of a 'racemose inflorescence' may be a single flower.

Stevens (1971) commented that a similar multibracteolate pedicel in *Gaultheria* "seems to be the end-point of a reduction series whose starting point was a racemose inflorescence", but does not go as far as calling the flowers terminal in a 1-flowered inflorescence. Middleton (1991) noted that many species of *Gaultheria* have solitary flowers and quoted Airy-Shaw (1940), Sleumer (1957) and Stevens (1969) as arguing that solitary flowers were formed from racemes in which all but one of the flowers have been suppressed. However, his figures of multiflowered inflorescence types all show a terminal flower, and therefore are cymose and not racemose[3]. He went on to state that solitary-flowered species can have either bibracteolate or multibracteolate pedicels. In the latter case he also postulates that the multibracteolate pedicel is presumably composed of the bracteoles, bracts and perules of its racemose progenitor.

Nordhagen (1936) said the flowers are terminal in *Calluna* and uses the term 'zwischenblatter' (intermediate leaves) for the so-called bracteoles. I would agree with Nordhagen and postulate that

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[3] Middleton acknowledged the error in his figures during mutual discussions on Ericaceae taxonomy.

the inflorescence in *Calluna* is a single flower borne terminally on a short leafy lateral branchlet, which, as stated above, is the endpoint of a lateral many-flowered inflorescence. These lateral branchlets are then clustered along the main branches into spike-like synflorescences. In the rest of Ericeae the flowers are always borne laterally and subapically on a main or lateral branchlet—never terminally. Therefore the problem of homology of the leaflike organs referred to by Middleton (1991) is also relevant in Ericeae with respect to *Calluna*.

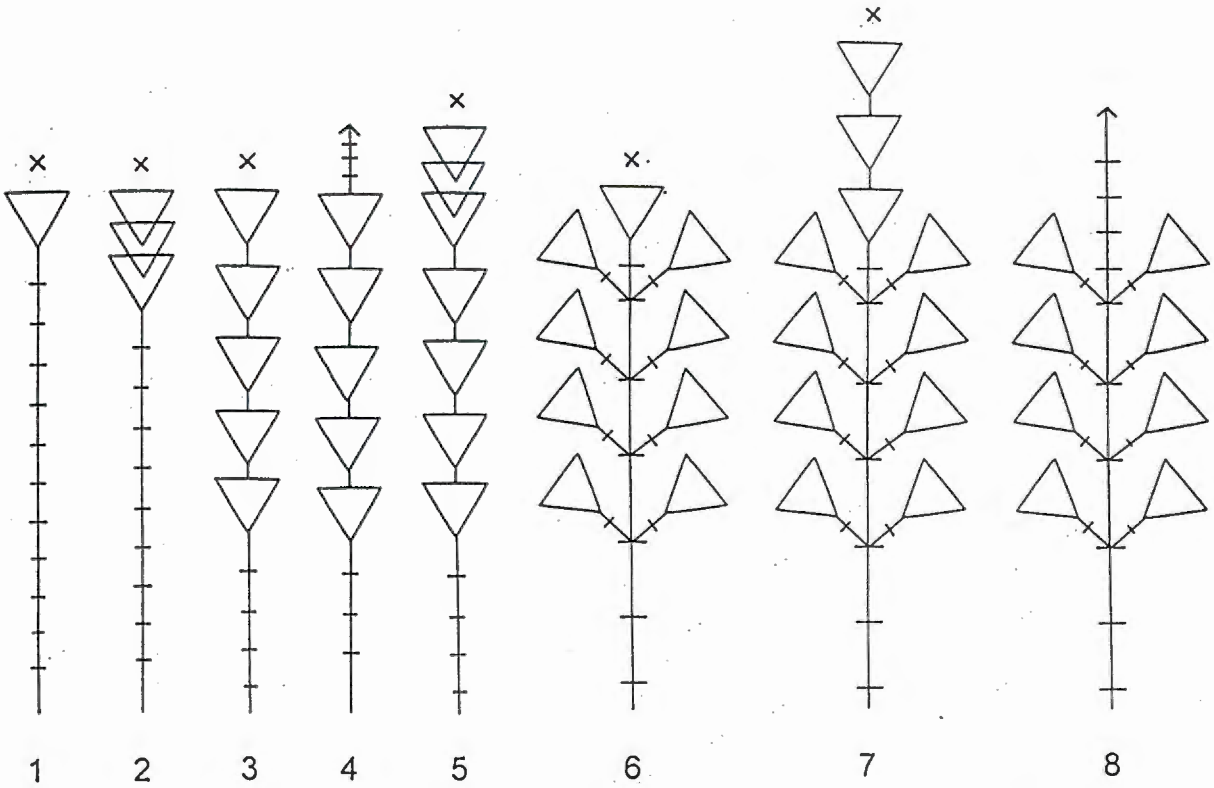

FIGURE 3.—Inflorescences: diagrammatic representation of various types and their structure; 1, terminal single unit; 2, terminal umbel with no internodes; 3 & 4, terminal raceme with internodes (4 continuing vegetative in growth); 5, terminal umbel with racemose basal portion; 6, single unit terminating main branch with lateral units terminating very short lateral branchlets all in a congested synflorescence; 7, same as 6, but with raceme terminating main branch; 8, same as 6, but with main branch continuing vegetative growth. ∇ represents a single inflorescence unit of one whorl of flowers (3-nate or 4-nate); a cross line represents a node with a whorl of leaves (here showing only two for clarity); x=an aborted apical bud; ↑=a growth point continuing vegetative growth.

The following three characters relating to the inflorescence were found to be divisible into discrete states and considered to be of potential use in the analysis (see Table 6).

Inflorescence position (Char. 4): inflorescences may occur: terminally on most or all lateral branches (2nd to nth order), but not on the primary or 1st order branches, which thus remain vegetative [0], sometimes on lateral branchlets as well as the primary branches [1], and mainly or only on the primary branches [2]. In most cases the apex of the inflorescence is non-innovating and growth resumes from buds just below the inflorescence. The character states chosen are relatively constant within the species.

ERICA: all states occur, the most common appearing to be inflorescences on secondary lateral branches with few species having them only on the primary branches.

MINORS: most species (69%) have inflorescences on primary and secondary branches; 20% have them only on secondary branches: 11% have them only on primary branches.

CALLUNA: The situation in *Calluna* is postulated as not homologous with the rest of the Ericeae (see above) and is therefore coded as inapplicable.

DABOECIA: the inflorescence is a simple non-innovating raceme that is terminal on the primary branches.

FAMILY: the inflorescence situation in the family is highly polymorphic and often poorly recorded and is therefore difficult to assess.

Inflorescence type (Char. 5): In those inflorescences consisting of more than one unit of flowers, several types can be recognized based on the presence or absence of internodes between the units. There can sometimes be two types within a single inflorescence—a racemose basal portion with distinct internodes and an umbel-like upper portion with no visible internodes (e.g. *Erica glabella* [*Simocheilus purpureus*] and *E. eriocephala* [*Acrostemon hirsutus*]). Most species with the multi-unit inflorescence have just the umbel-like arrangement (e.g. *Erica labialis* [*Sympieza labialis*]). No variation in this arrangement has been found and the states are found to be discrete (Fig. 3).

The states of this character are—raceme [0], raceme with a terminal umbel [1], an umbel [2], and a single unit or whorl of flowers which may be reduced to a single flower [3].

ERICA: all types occur. The innovating racemose inflorescence is rather rare with good examples occurring in *Erica massonii* and *E. fascicularis*.

MINORS: all types occur but only *Erica innovans* [=*Syndesmanthus pumilus*] has an innovating racemose inflorescence.

CALLUNA: see above for discussion. The character is coded as unknown.

DABOECIA: despite the non-whorled arrangement, the genus has been coded as having a raceme similar to that in the rest of the Ericeae. The raceme is non-innovating.

FAMILY: from the poor recording of inflorescence types in the literature it was not possible to assess this character accurately.

Units or whorls per inflorescence (Char. 6): An inflorescence in the Ericeae consists of whorls of flowers clearly corresponding to the arrangement in the leaves. The number of whorls or units can vary from one up to 15. When there is only a single unit, the number of flowers may be reduced to only one, i.e. an inflorescence consisting of one laterally borne flower near the apex of a vegetative branchlet (Fig. 5.7). The states are—more than 3 units [0], 2 but occasionally only 1 unit [1], 1 unit [2], and less than 1 unit [3].

ERICA: the usual arrangement is 1 or 2 units. Some species and species groups, e.g. sections *Pleurocallis*, *Hermes* and *Chlorocodon*, have less than one complete unit, with only a single flower forming the inflorescence. These inflorescences are often on extremely reduced branchlets (some as short as 0.5 mm long) and are aggregated into spike-like synflorescences. Some species have considerably more units, and may have a long, racemose inflorescence, e.g. *E. glandulifera* with up to 15 units and an inflorescence 200 mm long, or a very condensed head-like raceme, e.g. *E. bruniifolia* with up to 12 units and an axis only 10 mm long.

MINORS: mostly 1 or 2 units, but in some genera like *Syndesmanthus*, *Sympieza* and *Simocheilus*, there can be up to 9 units in a condensed raceme. There is never reduction to less than one complete unit as in *Erica*.

CALLUNA: because the inflorescence type was postulated not to be comparable with any inflorescence elsewhere in other Ericeae, this character has been recorded as unknown.

DABOECIA: this genus has an inflorescence consisting of many flowers alternating up the axis so the flowers are not strictly arranged in units, but it is recorded here as having the equivalent of more than 3 units.

FAMILY: this character does not apply in the rest of the family because only Ericeae have a whorled arrangement of the leaves and flowers. The inflorescences in *Rhododendron* are sometimes described as a 'condensed umbelliform raceme' (Sleumer 1966), a similar looking type, but at this stage, all one has to go on is similarity.

BRACT

The bract subtending an individual flower is always present in Ericeae, and nearly always present in the rest of the family (Stevens 1971). The bract has been used much in the delimitation of genera and species in the tribe.

Two characters relating to the bract have easily delimited states—the position and form.

Bract position (Char. 7): the position of the bract relative to the calyx is very critical in Ericeae and has caused problems for numerous workers in the past. It can be axial and inserted on the branch or peduncle (the main axis) or recaulescent on the pedicel to varying degrees (see Table 6). According to Weberling (1989) flowering branches can be modified by what is termed 'metatopy', i.e. displacement and fusion of organs. One of these modifications is recaulescence in which the axillary bud [flower in this case] is shifted onto the subtending leaf [bract], the insertion of which is displaced on the branch for a smaller or greater distance above its original position after stretching of the common basal zone of the organs. In practice this means that the bract is no longer inserted on the main axis (the branch or the peduncle) but on the pedicel of the flower it is subtending (Weberling 1989 Fig. 116.1). The position of the recaulescent bract on the pedicel can vary from basal to apical, where it then can be appressed to the calyx; this condition I term 'partial' recaulescence (Oliver 1988 Fig 2). In Ericeae there is often progressive recaulescence with the lower flowers of an inflorescence having the bract in the basal position (or even axial), the upper flowers having progressively greater degrees of recaulescence with the uppermost having the bract apical and appressed to the calyx (Oliver 1988 Fig. 3, left).

In some taxa the partially recaulescent bract in the apical position can suppress the development of the abaxial sepal and take over its position (and its function of protection for the base of the corolla). This condition I term 'full recaulescence. The bract can be slightly to considerably larger than the rest of the calyx (Oliver 1988 Figs 4 & 5) thus forming the so-called unequal calyx as first pointed out by Salisbury in 1802 when he described the genus *Salaxis*.

Alm & Fries (1927) examined this phenomenon in respect to the situation in *Philippia*. They stated that the bract 'ist bis dicht unter dem Kelch hinaufgerückt und ist mit dem vorderen Kelchblatte verschmolzen' and 'denkbaar aber sehr unwahrscheinlich ist, dass vordere Kelchblatt vollständig reduziert worden ist'. Their floral diagram (Alm & Fries 1927 Fig. 3c) shows the bract and calyx lobe fused together. This is actually not the case, since I have observed in several species, mainly *Erica peltata* and *E. burchelliana* [*Coilostigma glabrum*], very reduced remnants of the suppressed calyx lobe adaxial to (but quite free from) the appressed bract (Oliver 1988: Fig. 5,4). Also in cases where the bract is in the midposition in a species that normally has a fully recaulescent bract, there may be no abaxial sepal present (Oliver 1988 Fig. 5,5). The bract obviously suppresses the growth of the sepal and replaces it. Therefore in the modified diagram (Fig. 6.3) the abaxial sepal is not shown.

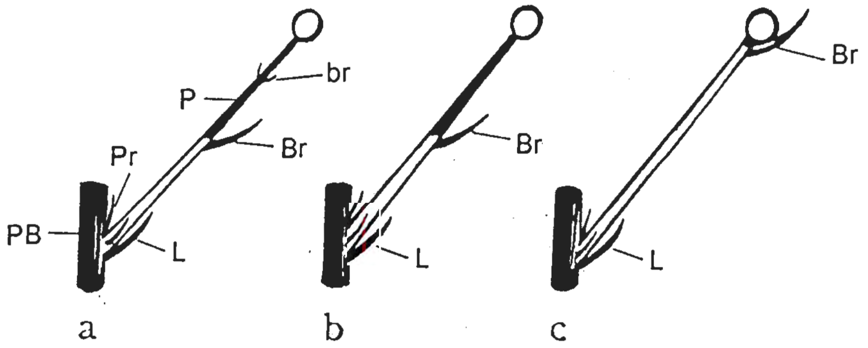

FIGURE 4.—Recaulescence of the bract and bracteole as depicted by Alm & Fries (1927). PB=primary branch; L=leaf; Pr=lateral branch prophylls; P=pedicel; Br=bract; br=bracteoles.

The earlier figure of Alm & Fries (1927 Fig. 2 a–c reproduced here as Fig. 4) shows clearly the partial to full recaulescence of the bract, but is unfortunately very confusing due to some additional 'organs' illustrated by them at the base of each pedicel. They have illustrated the bract as recaulescent on the pedicel (Fig. 4.a, Br), but also with one on the main axis subtending the lateral flower (Fig. 4.a, L) and with 'bracteoles' as well (Fig. 4.a, br). It would appear that they have confused a single flower arising from a bract/leaf on the main axis (see Fig. 5.1) with a one-flowered inflorescence borne subterminally on a very reduced lateral short shoot bearing very reduced bracteose prophylls and leaves (see Fig. 5.7), a situation which often occurs in *Erica* (see above under Char. 3). They have illustrated elements of both situations in all three of their drawings

(Fig. 4.a,b,c). However their drawing of a fully recaulescent bract (Fig. 4.c) cannot be reconciled with the above explanation because a 1-flowered inflorescence with fully recaulescent bract is rare, most are 3-flowered or more. The 1-flowered condition occurs when two flowers of a normal, 3-flowered inflorescence have aborted, but there is still a terminal, aborted growth-point to the axis of the inflorescence, therefore the inflorescence is not strictly 1-flowered.

The situation regarding the position of the bract is complicated by the two bracteoles when assessing the characters and states to be recorded for certain taxa (see below).

The states of this character are—axial on the branch [0], partially recaulescent up the pedicel [1], and fully recaulescent forming the abaxial segment/lobe of the calyx [2].

ERICA: Most species have a partially recaulescent bract in various positions on the pedicel (basal, middle or proximal positions to the calyx, r**Br**). Some have the bract as a typical leaf situated on the main axis or branch (axial, a**Br**) while others, previously placed in *Philippia* (Oliver 1987c, 1988) and *Ericinella* (Oliver 1994), have a fully recaulescent bract (R**Br**).

MINORS: The bract can be anywhere from axial to fully recaulescent depending on the species or species group and on the position of the flower in the inflorescence. Most of the wind-pollinated species have the bract fully recaulescent, the exceptions being *Erica brownii* [*Syndesmanthus breviflora*] and *E. erina* [*Syndesmanthus erinus*].

CALLUNA: because of the problems noted above under inflorescences (Char. 3), the exact nature and position of the bract in this genus is not known and has therefore been recorded as such.

DABOECIA: the bract is always axial on the main axis of the florescence.

FAMILY: the bract appears to be always axial in the rest of the family, never recaulescent.

Bract type (Char. 8): The size and texture of the bract is important in Ericeae. It can be foliaceous and indistinguishable from a leaf or, through reduction in size and change in texture, can be scarious and petaloid or bracteose. The apical, sulcate, leaflike portion of the bract may become considerably reduced or disappear completely. In some cases the bract, bracteoles and calyx may enlarge and become petaloid. The states are—leaflike to bracteose and mostly narrow [0], and petaloid, being scarious and broad [1].

ERICA: there is much variation in the size and form of the bract from totally leaflike to minute and bracteose to very enlarged and petaloid.

MINORS: there is not much variation among these species with most having small bracteose bracts. Only *E. eckloniana* [*Sympieza ecklonii*] has a large, fully leaflike bract, and *E. plumosa* [=*Grisebachia plumosa*] and *E. velatiflora* [=*Eremia breviflora*] have an enlarged petaloid bract.

CALLUNA: see above, the character was therefore coded as unknown

DABOECIA: the bract is always leaflike.

FAMILY: it is assumed from the rather vague references to the organ in the literature that the bract is mostly small and reduced, not enlarged and leaflike or petaloid.

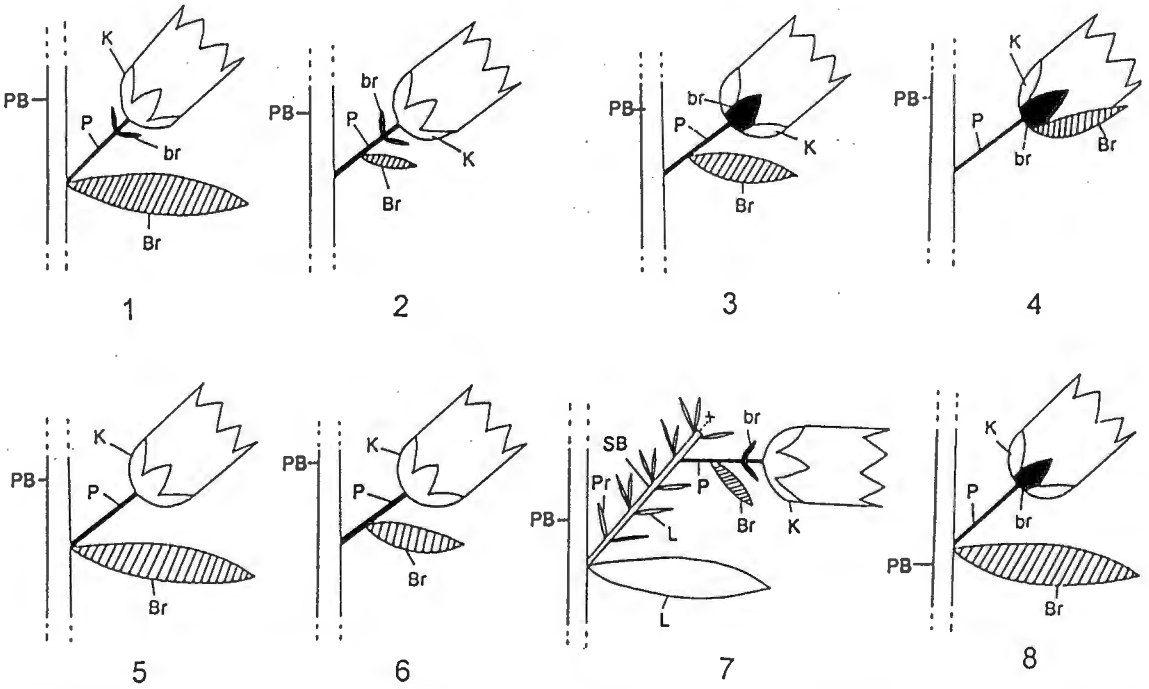

FIGURE 5.—Diagrammatic representation of the various positions of the bract and bracteoles in relation to the calyx in Ericeae. PB=Primary branch, SB=Secondary branch, L-leaf, P=Pedicel, Pr=Prophylls, Br=Bract, br=bracteoles, K=calyx, x=aborted apical growth. 1) a**Br1 br2 K4**; 2) r**Br1** **br** 2 **K4**; 3) r**Br1** R**br2** **K2**; 4) R**Br1** R**br2** **K1**; 5) a**Br1** **br0** **K4**; 6) R**Br1** **br0** **K4**; 7) a 1-flowered inflorescence on a short lateral branchlet; 8) a**Br1** R**br2** **K2**.

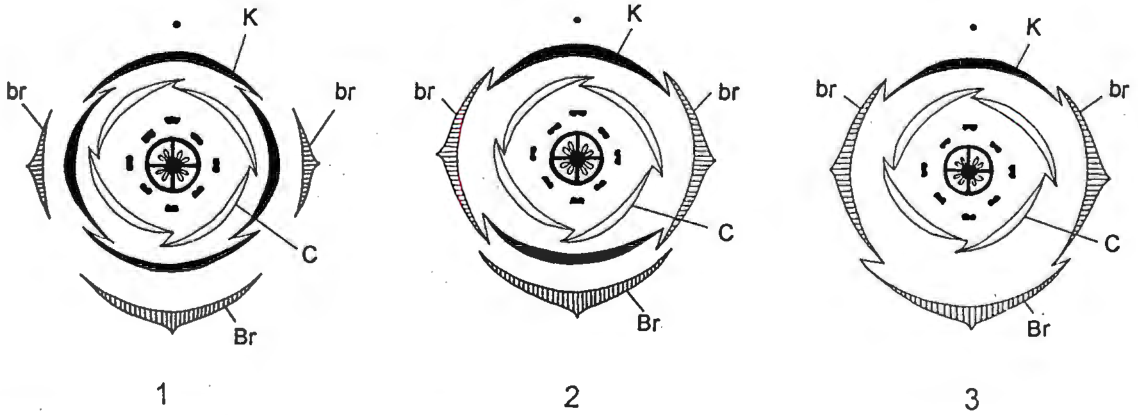

FIGURE 6.—Floral diagrams illustrating the position of the bract, bracteoles and sepals in partial and full recaulescence; 1, all whorls complete with partially recaulescent bract and two free bracteoles (r**Br1** **br2** **K**4); 2, bract partially recaulescent and bracteoles now fully recaulescent and replacing the adjacent sepal (r**Br1** R**br2** **K**2); 3, fully recaulescent situation for both bract and bracteoels (R**Br1** R**br2** **K**1). Note the change in aestivation in 2 & 3 thus showing that the lateral 'sepals' are the bracteoles. Modified from Alm & Fries (1927, Fig. 3).

BRACTEOLES

The Ericeae have two bracteoles associated with the pedicel. These may be absent in some genera. Stevens (1971) notes that some genera have a multibracteolate pedicel, e.g. *Cassiope*, some *Gaultheria spp.*, some Epacridaceae and *Calluna*. I believe that the situation in *Calluna* could be construed as whorls of normal vegetative leaves and not bracteoles (see above). The form of the bracteoles in the Ericeae generally mirrors that of the bract and is therefore of no additional value in the analyses.

As in the case of the bract the position of the bracteoles is useful in species delimitation and is the only one included in the data set.

Bracteole presence & position (Char. 9):

In most Ericeae there are two bracteoles on the pedicel of each flower in various positions from basal to apical and appressed to the calyx (Table 6). In some cases the bracteoles are absent in all flowers, or they may be present and highly reduced in the lowest flowers of an inflorescence and absent in the upper flowers. In other cases the bracteoles may appear to be absent, as has been recorded in the literature for genera such as *Philippia*, *Ericinella*, *Salaxis*, *Coccosperma*, *Scyphogyne*, *Nagelocarpus* and *Coilostigma*, all with the unequal calyx or fully recaulescent bract (see above). The exception is for *Bruckenthalia*, which has the bract always on the axis, and never recaulescent and bracteoles recorded as absent (Webb 1972) (Fig. 5.8).

When investigating the status of the calyx in *Philippia* certain anomalous situations were noted in *Erica peltata* [=*Philippia pallida*] with its large imbricate petaloid sepals (Oliver 1988). Hundreds of fresh flowers were carefully dissected and analyzed. In those cases where the intermediate ericoid-philippioid calyx occurred, some flowers were noted as having only one bracteole, either left or right in position, some with a single bract with no apparent bracteoles but four 'calyx' lobes, and some with a bract and only three 'calyx' lobes.

Normal calyx aestivation in the Ericeae is clearly visible in South African species with large petaloid sepals and consists of two outer, median segments (the ad- and abaxial sepals) and two inner segments (the lateral or transverse sepals). This has been previously recorded and illustrated via floral diagrams for several European species (Drude 1897, Nordhagen 1937, Schultze-Motel 1964) (Fig. 6.1). In the situation where only one bracteole is present in *Erica peltata* it was noted in the present work that the aestivation of the calyx lobe on the other side of the flower was different from the standard pattern. This led to the examination of the aestivation in numerous bud stages where it was discovered that the aestivation of the apparent lateral calyx lobes/segments changes when the bracteole is 'apparently absent'.

When only one bracteole is present, the lateral sepal adjacent to it is an inner sepal whereas the one on the opposite side where the other bracteole has apparently disappeared is now an outer sepal (Fig. 6.2). This led to the postulation that the 'sepals' in the outer whorl are in fact fully recaulescent bracteoles. The bracteoles have not disappeared, but rather the sepals adjacent to them, leading to the situation in an unequal calyx which consists of a fully recaulescent bract as the abaxial segment/lobe, two bracteoles as the lateral segments/lobes and only one remaining sepal in the adaxial position (Figs 5 & 6).

The reduction has been clearly observed in *E. burchelliana* [*Coilostigma glabrum*] and the tropical *E. rossii* [*Philippia excelsa*] to go even further in some flowers in which the adaxial sepal is also absent (R**B**r Rbr2 **K**0), a remarkable situation in which the 'apparent calyx' has no sepals present.

This also led to a close examination of the situation in *Bruckenthalia* in live material which was cultivated at Kirstenbosch for the purpose and in pickled material from Germany (K. Kramer pers. comm. *ex hort.*). The genus has always been recorded as having bracteoles absent (Nordhagen 1937, Webb 1972, Stevens 1978). The examination is complicated by the fact that the calyx is fused for half its length with non-imbricate lobes in mature flowers. However, in young buds the aestivation is clearly discernible and has the following pattern: two outer lobes are lateral and two inner lobes are ad- and abaxial, the same aestivation as in taxa with an unequal calyx and fully recaulescent bracteoles. The bracteoles are slightly larger than the ad- and abaxial sepals, which difference could have caused Alm and Fries (1927: 6) to note in their key "Blutenstiel ohne Bracteen. Kelch zygomorph (bei *Bruckenthalia* und einegen *Philippia* arten nur weinig)" and repeated by Ross (1957). Therefore *Bruckenthalia* also has two fully recaulescent bracteoles and only two sepals forming the calyx (Figs 5.8 & 6.2).

A similar situation to *Bruckenthalia* occurs in the rare Drakensberg species, *E. alticola*, in which the bract is likewise nearly always leaflike and situated on the main axis. The bracteoles are fully recaulescent, although sometimes borne just below the flower. In this case the sepals, which should have been situated adaxially to them, are clearly absent. The lateral 'calyx' lobes (the fully recaulescent bracteoles) are as long as or longer than the corolla and clearly longer than the ab- and adaxial sepals.

It has always been believed that *Daboecia* lacks bracteoles. Ascertaining the aestivation in the calyx in herbarium material was extremely difficult to undertake because of the very early separation of the sepals in the buds. Fortunately I was sent fresh material from Spain (Ojeda pers. comm.) and this provided very young buds which could be dissected easily. From this it was clear that the aestivation of the calyx mirrored that in *Bruckenthalia*—the calyx consisting of the ad- and abaxial sepals and two lateral, fully recaulescent bracteoles.

The form of the bracteoles in the Ericeae generally follows that of the bract and is therefore of no additional value in the analyses.

The states of the character are—present in various positions on the pedicel [0], fully recaulescent and incorporated into the calyx as the lateral segments/lobes [1], and absent [2].

ERICA: bracteoles are always present. Some are fully recaulescent, mainly due to the inclusion of *Philippia* and *Ericinella*.

MINORS: In 28% of the species the bracteoles are fully recaulescent and in 16% the bracteoles are totally absent, not fully recaulescent. Some species have the bracteoles present in the lowest flowers in a florescence, but becoming reduced in size up the axis and finally totally absent in the uppermost flowers (not fully recaulescent). *Bruckenthalia* has the bracteoles fully recaulescent and the bract on the main axis (Fig. 5.8).

CALLUNA: recorded as unknown due to the problems mentioned earlier.

DABOECIA: the bracteoles are recorded here as being present and fully recaulescent (Fig. 5.8).

FAMILY: in the rest of the family the bracteoles, when present, appear to be small and bracteose. There is no record of fully recaulescent bracteoles.

CALYX

The calyx has been much used in the taxonomy of the Ericeae—the meristic state, size, colour, shape, texture and indumentum all being used, however, many of these characters are variable and rather difficult to define precisely. The following six characters have been selected as they are considered to be discrete or at least reasonably so—sepal numbers, their fusion, type, size in fruiting stage, the presence of sessile glands, and the presence and size of the sulcus.

Sepal Numbers (Char. 10): See the discussion above under bracteoles regarding numbers of segments/lobes.

The number of calyx segments/lobes making up the calyx is complicated by the fully recaulescent bract and bracteoles in some species. When all three of the latter are incorporated, then only one sepal remains (Figs 5.4 & 6.3). When only the bracteoles are incorporated, then two sepals remain (Figs 5.3, 5.8 & 6.2). This feature has been totally misunderstood and incorrectly recorded in all earlier treatments of the tribe (see Table 4).

The states are—4 sepals [0], 3 sepals [1], 2 sepals [2], and 1 sepal [3].

ERICA: the overwhelming majority of species have a 4-merous calyx with the two species, *Erica sicula* and *E. bocquetii* [formerly the genus *Pentapera*] being mostly 5-merous. Some species formerly in *Philippia* and *Ericinella* are 3-merous, but with the bract and bracteoles incorporated into the calyx there appear to be no sepals at all.

MINORS: these species have calyces that range from 2–4-merous. Sometimes the numbers can vary within a single inflorescence, e.g., *E. labialis* [*Sympieza labialis*] with the lowest whorl of flowers 2-merous and the uppermost whorl 4-merous, but with its closest allies always 2-merous.

CALLUNA: has a 4-merous calyx.

DABOECIA: has a 4-merous calyx, but with the bracteoles being fully recaulescent, is coded as having only 2 sepals.

FAMILY: the predominant type appears to be 5-merous.

Calyx Fusion (Char. 11):

The states are—sepals free [0], and sepals fused for varying degrees [1].

ERICA: most species have free sepals, but some have them slightly fused at the base and some for about half their length, e.g. §*Gamochlamys* and those species formerly in *Philippia*, *Blaeria* and *Ericinella* (Table 6).

MINORS: most species have fused sepals with some being fused for more than three-quarters of their length. Only eight species have free sepals.

CALLUNA: the sepals are free.

DABOECIA: the sepals are very slightly joined at the base, recorded here as free.

FAMILY: fusion of the sepals is not determinable from the literature, but would appear to be partly fused in many species, at least those with superior ovaries.

Calyx type (Char. 12): variation in texture (from leaflike to expanded and petaloid) is similar to that in the bract and bracteoles. There appears to be a correlation in this variation between bract, bracteoles and calyx in a number of species, but this is not absolute.

The states are—leaflike to bracteose, mostly narrow [0], and petaloid, scarious and broad [1].

ERICA: there is most variation in this genus, in length as well as in texture. Several hundred species have petaloid sepals of which some may be as long as or slightly longer than the corolla, the extreme being in *Erica nabea* and *E. insignis* in which the calyx is coloured and up to 15 times the length of the corolla (Oliver 1991: 180).

MINORS: most species have rather scarious or thickish sepals, which may be coloured and broad in width. The latter condition is difficult to categorise in those species with fused sepals. Only a few species have leaf-like, narrow sepals.

CALLUNA: the sepals are very large, broadened and petaloid as in some species of *Erica*. The texture, however, is rather straw-like and unlike any that I have seen in the rest of the Ericeae.

DABOECIA: the sepals are thin and dark red, but are not scarious.

FAMILY: the situation in the rest of the family is difficult to assess, but sepals are mostly relatively small, thick and almost fleshy. No species have large petaloid calyces.

Calyx size in fruiting stage (Char. 13): the enlarging of the calyx, accrescence, in the fruiting stage is rare within the Ericeae (Table 6).

The states are—not enlarging in fruiting stage [0], and enlarging in the fruiting stage [1].

ERICA: no species has an accrescent calyx, but there are a few in which the calyx becomes hardened in the fruiting stage. This is most evident in the anomalous *Erica jacksoniana*. In *E. sessiliflora* the calyx hardens and protects the fruits, sometimes past the following flowering season, the only case of serotiny in the subfamily.

MINORS: an accrescent calyx is present in only five species (see *Erica inaequalis* [*Simocheilus puberulus*], *E. phaeocarpa* [*S. quadrisulcus*] *E. anguliger* [*Anomalanthus spp.*], *E. kammanassieae* sp. nov. & *E. inflaticalyx* sp. nov.). In the case of *E. anguliger* the fruiting calyx is polymorphic in size and shape and this was used for species delimitation in the former *Anomalanthus*, but is now regarded as variable and therefore only a single species with infraspecific variation in this character has been recognised (see Taxonomic Treatment).

CALLUNA: the calyx is not accrescent.

DABOECIA: the calyx is not accrescent.

FAMILY: accrescent calyces occur in some species of *Gaultheria* and *Vaccinium* (Stevens 1971, Luteyn 1995, Middleton & Wilcock 1990, Middleton 1991).

Calyx glands (Char. 14): this character refers to the large, conspicuous, sessile glands on the margins of the sepals or on the inner adaxial surface (Table 6). In both cases the viscid matter secreted by these glands in the bud stage produces a viscid corolla (this is not the case with gland-tipped hairs that may be found on the calyx).

The states are—sessile glands not present [0], sessile glands marginal [1], and sessile glands on adaxial surface [2].

ERICA: these glands are characteristic of certain groups, particularly the long-tubed species in the *E. versicolor* complex and some formerly in §*Pachysa*.

MINORS: these glands occur in a group of species that are postulated to be closely related.

CALLUNA: glands are absent.

DABOECIA: glands are absent.

FAMILY: this character may be unknown in the rest of the family, although prominent glands occur on the calyx margins of some Malesian species of *Vaccinium* (Sleumer 1966).

Calyx sulcus (Char. 15): this is a character very much restricted to Ericeae. The sulcus, reflecting the channel of the ericoid leaf, can be very long or confined to the very apex of the sepal, or even absent. The division of the states at the 30% length of the sepal is judged to be a reasonably discrete boundary (Table 6).

The states are—sulcus more than 50% the length of the sepal [0], less than 30% the length [1], and sulcus absent [2].

ERICA: the sulcus is nearly always present but is <30% the length of the sepal in most species. A few have a very reduced sulcus, but only one species, *Erica microdonta* [*Ericinella microdonta*], lacks a sulcus. The sulcus can be very narrow resembling the upper part of a leaf or broad and open with only slightly recurved margins. In some species it is very prominent due to raised lateral ridges (e.g. *Erica plukenetii* var. *bicarinata*).

MINORS: most species have sulcate sepals also <30% in length of the whole sepal. A few species have very long sulci (see *Erica recurvifolia* [*Eremia recurvata*], *E. pilosiflora* [*Acrostemon eriocephala*], *E. vallis-fluminis* sp. nov.). Some have no sulcus (see *Erica innovans* [*Syndesmanthus pumilus*], *E. erina* [*S. erinus*], *E. eckloniana* [*Sympieza ecklonii*]) and two species have just a pulvinus as a remnant of the sulcus (see *E. brownii* [*Syndesmanthus breviflorus*], *E. boucheri* sp. nov.).

CALLUNA: there is no sulcus present.

DABOECIA: the sulcus is small and very broad as indicated by the slightly recurved margins towards the apex of the sepal.

FAMILY: in those few species with ericoid leaves, the sepals are not sulcate (*Ledothamnus* - Luteyn 1995: 109, t.1; *Tepuia* - Luteyn 1995: 353, t.2).

COROLLA

The number of corolla lobes has always been an important character in the classification of the Ericeae at generic level, while at the specific level using shape, size and texture are important. In fact much of the subgeneric classification in *Erica* is based on corolla characters (see Rebelo *et al.* 1985 for shape types). However the shape and form of the corolla is too variable and difficult to categorize for cladistic analyses. Two characters have been selected: number of corolla lobes and the condition of the surface.

Corolla lobe numbers (Char. 16):

The states of this character are—lobes 4 [0], lobes 3 [1], and lobes 2 [2].

ERICA: the figures agree with those for the calyx (see above) with 4-merous being the predominant state.

MINORS: as with the calyx, these have the widest range, being 2–4-merous. The meristicity of the corolla is not always the same as that of the calyx or stamens, as it is elsewhere in the Ericeae.

CALLUNA: 4-merous.

DABOECIA: 4-merous.

FAMILY: the predominant type is 5-merous.

Corolla surface (Char. 17): the corolla indumentum in Ericeae is very variable, with similar types occurring throughout the subfamily. The three states chosen are—glabrous and smooth [0], verrucose/colliculate* [1], and hairy (whether simple or glandular) [2]. There is a reasonably clear distinction between the three states (Table 6). There are no differences overall between *Erica* and the Minors with all states being present. However, the types of indumentum present on the corolla could have some significance in groups of species. Some species of the Minors vary, being glabrous or puberulous both between and within populations (see *Erica zeyheriana*).

CALLUNA: the corolla is glabrous and smooth.

DABOECIA: the corolla is shortly hairy with some hairs being gland-tipped.

FAMILY: the character cannot be assessed.

STAMENS

The stamens are another important organ in the Ericeae. They have provided numerous characters for delimiting species, and they have been much used in generic delimitation. Seven characters have been selected here for the data set—numbers, position, fusion of filaments, filament type, filament surface, anther connation, and anther appendages.

Stamen numbers (Char. 18): the numbers vary in Ericeae from 10 to 3. The states selected are based on the predominant numbers occurring in *Erica* in which over 90% of the species invariably have 8 stamens and the predominant number of 4 in the Minors. Species having variable numbers of stamens range between 5, 6 and 7; odd flowers may have 8 stamens, but species have been coded for the predominant number.

The states are—8 stamens [0], 7, 6 or 5 stamens [1], 4 stamens [2], and 3 stamens [3].

ERICA: there are predominantly 8 stamens, some species having 7, 6, 5 and 4. The occurrence of the lower numbers has been increased with the recent inclusion of *Philippia*, *Blaeria* and *Ericinella*. *Erica sicula* and *E. bocquetii* both have 10 stamens.

MINORS: these species have a wider range of variation in numbers from 8 to as few as 3, but there is usually a constant number for each species. In *E. subcapitata* [*Coccosperma hexandrum*] there can sometimes be as many as 10 stamens in an otherwise 4-merous flower.

CALLUNA: there are always 8 stamens.

DABOECIA: there are 8 stamens.

FAMILY: the number of stamens in the family is mostly twice the number of petals, thus mostly 10 stamens in the predominantly 5-merous flowers, rarely only 5 stamens.

Stamen position at anthesis (Char. 19): the position of the stamens varies considerably from

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*colliculate=slightly bumpy, with the cells protruding slightly—not smooth.

those species in which the stamens are totally included, the anthers being held just above the ovary in the bottom of the flower, to those in which they are very far exserted. The position is clearly correlated with how the flower is pollinated. The two states selected are—included or with the anthers at most just showing at the mouth of the corolla (manifest) [0], versus exserted, with the whole anther being outside of the corolla [1]. There is no change in the position of the stamens from just before anthesis right through to fruit maturity.

ERICA: the full range of stamen positions occurs.

MINORS: most positions occur.

CALLUNA: the stamens are always included.

DABOECIA: the stamens are always included.

FAMILY: most stamen positions occur and are similarly correlated with the pollination syndrome (Sleumer 1966, Luteyn 1995).

Filaments: the filaments in Ericeae vary considerably in shape (linear to oblong, sometimes dilated at the base), degree of fusion (free or fused into a staminal tube) and indumentum (smooth and glabrous, or papillate, or strigose or villous). The shape is difficult to assess accurately due to the ratio of length to width varying depending on the actual length, curvature and fusion of the filament and this character has thus been left out of the current analyses. The dilated base is distinctive in some species of *Erica* and in a number of genera in other parts of the family, but does not occur in any of the Minors and can therefore not be used in these analyses.

Three characters relating to the filaments were considered to be of value in these analyses—the degree of fusion, the flexion and the indumentum.

Filament fusion (Char. 20): the degree of fusion of the filaments is divided into two states—free or very slightly joined at the base [0] versus variously fused from about 25% to fully fused [1]. The cut-off point of 25% was considered fairly discrete.

ERICA: most species have free filaments with some being slightly joined at the base. Some species (some of those previously in *Philippia*) have fully fused filaments.

MINORS: the wind-pollinated species of the Salaxid type have the filaments free to fused, even in the same species or inflorescence; whereas the insect-pollinated species have free stamens.

CALLUNA: the stamens are all free.

DABOECIA: the stamens are all free.

FAMILY: fused filaments are extremely uncommon in the rest of the family (see *Satyria)*.

Filament type (Char. 21): Stevens (1971) points to this character being of value within the family as a whole. There is, however, a problem in assessing discrete states for encoding as the degree of flexion of the filament cannot be easly quantified. The states have been selected as—straight [0] or variously flexed/geniculate below the anther [1].

ERICA: there is a wide range of types within the genus from straight to very markedly geniculate below the anther. There can be an apical bend which is coupled to dorsal attachment to the anther; this has been regarded as straight if no other bending below the anther is present. There is one remarkable species, *E. lanuginosa*, in which the filaments are of two different lengths because of the filament curvature of alternate stamens, but with anthers held at the same level.

MINORS: all the wind-pollinated species except for *E. perplexa* sp. nov. and *E. stokoeanthus* [=*Stokoeanthus chionophilus*] have straight filaments. The rest of the species have straight or slightly curved filaments with the curve occurring apically.

CALLUNA: the filaments are geniculate below the anther.

DABOECIA: the filaments are straight.

FAMILY: most taxa in the family have straight or slightly geniculate filaments; *Lyonia* has geniculate filaments (Judd 1995).

Filament surface (Char. 22): the indumentum of the filaments, when present, usually comprises long simple hairs all over the surface or confined to the upper region. There are also some species in which the apical portion is papillate. The three states of this character are—glabrous [0], papillate [1], and hairy [2].

ERICA: all types occur, but the vast majority are glabrous.

MINORS: all types occur, but only a few species have papillate filaments and only three species have hairy filaments, the hairiest being *E. jonasiana* (see Plate 56).

CALLUNA: the filaments are glabrous and smooth.

DABOECIA: the filaments are sparsely pilose.

FAMILY: hairy filaments are a feature of many genera in the other subfamilies.

Anthers: the anthers of Ericaceae are another distinctive character of the family with their developmental inversion, dehiscence by pores or slits and often two apical or basal appendages. The shape of the anthers is characteristic of many of the genera in the family. In Ericeae the shape of the anthers is very distinctive, but too complicated to categorise for cladistic analysis. Subterminal pores are characteristic of Ericeae excluding *Daboecia* which differs in having elongated slits and an open thin-textured apex similar to those in the other subfamilies; both characters unlike the rest of the Ericeae. Three characters relating to the anthers have been selected—anther connation, appendages and pore size.

Anther connation (Char. 23): this character needs close investigation together with the filaments. All species of Ericeae have the anthers connate into a ring around the style just below the stigma complex until the time of anthesis. Connation is by the lateral pores, and sometimes along the lateral edges of the thecae. At anthesis the thecae separate at the pore, either independently in wind-pollinated species or assisted by an animal pollinator. However, some species remain connate by the thecae after anthesis. Therefore anthers should be examined only after anthesis has clearly occurred. In this context Ross (1957: 736) commented that many species of *Philippia* and all those of *Coccosperma* had fused (connate) anthers. Connation of the anther may or may not be coupled with that of the filaments (Char. 18).

The states of this character are—free [0], and connate [1].

ERICA: most of the species have free anthers. Connate anthers are present only in a few species formerly in *Philippia* and in the showy, large, tubular-flowered *E. embothriifolia*.

MINORS: most species have free anthers, the exceptions being some of the wind-pollinated species with fully recaulescent bract and bracteoles (unequal calyx).

CALLUNA: the anthers are free.

DABOECIA: the anthers are free.

FAMILY: no species have anthers fused after anthesis.

Anther spurs (Char. 24): anther appendages are a striking characteristic of the family, but vary much in position and are also polymorphic in size and shape. The appendages on the anthers in Ericeae have been variously named as awns, spurs or crests. To maintain uniformity within the family it has been decided to name the appendages of Ericeae as spurs (Stevens pers. comm.). These are dorsal appendages arising from the point of attachment of the filament to the back of the anther as opposed to awns, which are terminal on the anther.

The states of this character are—spurs absent, i.e. anthers muticous [0], and spurs present [1].

ERICA: most species have spurs. These are usually small, but they may be broad and very conspicuous. About 200 species (30%) lack them (muticous). Spurs are usually very important characters in the classification of the genus due to their great diversity of shape, size, texture, colour and position (see Oliver 1991).

MINORS: most species have spurs, and only 26 species (30%) lack them. Unlike *Erica*, the spurs in the Minors are not of great taxonomic value due to their small size, invariat shape and lack of ornamentation. There is infraspecific variation in the presence of spurs and there may be lack of spurs even in the same flower or even anther (one side with a spur the other lacking a spur).

CALLUNA: the anthers are broadly spurred.

DABOECIA: the anthers are spurless.

FAMILY: most species lack spurs (or awns), many species in Vaccinieae have spurs.

POLLEN

Pollen characters have been used by many workers to assist with the delimitation of supraspecific taxa as well as in cladistic analyses. It was felt that this could have been the case in the Ericeae, hence the project undertaken by Davis (1997).

The pollen in Ericeae is either trizonocolpate or trizonocolporate tetrads or monads and is not accompanied by viscin threads. There is considerable range in size from very small monads of only 17.4μm equatorial axis in *Erica recurvifolia* [*Eremia recurvata*] to 82 μm in the tetrads of *Erica massonii*.

The investigation of pollen by Davis (1997) found that exine sculpturing alone could be used to group species phenetically; size variation was too great within the 63 species and the limited number of samples that he investigated. Exine sculpturing varied from smooth to verrucate to rugulate with numerous microgranules present. Davis found that the same types of sculpturing were present in both tetrads and monads, and that the boundaries between the types were not sharp since there was much intergradation. This was reflected in his tentative grouping of Ericeae into eight basic groups. He found that in *Erica* there was the whole spectrum of sculpture types, i.e., from psilate to completely granulate. Some groups he recognized consisted of both *Erica* species and Minors, some *Erica* alone but none with just Minors.

A preliminary investigation in *Grisebachia* (Oliver 1980) and of scattered samples in other genera (Oliver 1991) and that of Davis (1997), which included only 18 of the 83 species of Minors, led me to exclude pollen characters other than the basic pollen type from this analysis.

The two states of this character are—pollen in tetrads [0], and pollen in monads [1].

Pollen type (Char. 26):

ERICA: pollen is shed mostly in tetrads, monads occurring in only 32 species. These latter species are scattered throughout the sections of the genus currently recognized, sometimes one species in a section having monad pollen and the rest, tetrads. In the 21 species of *Erica* in Europe only *Erica terminalis* and *E. spiculifolia* [=*Bruckenthalia spiculifolia*] have pollen in monads.

MINORS: 30 species have pollen in tetrads and 57 species have pollen in monads. Monads are found in insect-pollinated species and tetrads in wind-pollinated species; there are a few exceptions in both cases, e.g. the wind-pollinated *E. zeyheriana* [=*Coilostigma zeyherianum*] and *E. burchelliana* [=*C. glabrum*] both have monads.

CALLUNA: the pollen is in tetrads which are irregularly tetrahedral, a feature not encountered in the rest of the tribe.

DABOECIA: the pollen is in tetrads.

FAMILY: pollen occurs in tetrads with very few exceptions according to Stevens (1971), but tetrads are present in many of the recently included Epacridoideae.

GYNOECIUM

Much emphasis has hitherto been placed on the ovary complement in the delimitation of the genera, but, surprisingly, excluding any reference to the situation in *Erica* itself. The current study emphasizes the importance of the number of ovules, the nature of the placenta, and the position of the ovules, as important characters for taxonomic delimitation. Eight characters relating to the gynoecium have been selected for the analysis on the grounds of reasonable discreteness of their states.

Locule number (Char. 27): this character is problematic in that very careful examination of young ovaries is needed to record the correct number since the septum can be very thin and delicate. In more mature ovaries these septa can be obscured by the abnormal development of unfertilized ovules and therefore it is quite possible to record incorrect numbers. This also applies to the number of ovules (Char. 30).

The states for this character are—4 locules [0], 3 locules [1], 2 locules [2], and 1 locule [3].

ERICA: most species have 4 locules with several species formerly in *Philippia* and *Ericinella* having 3 locules. Some of the tubular-flowered species have 6–8 locules. *E. jacksoniana* is anomalous in having a single locule (not previously recorded as such).

MINORS: there is a range from 4–3–2–1 locules, which can be variable within the same species, e.g. *E. glabella*, *E. dispar* and *E. bolusanthus* with 4–1 and *E. radicans* and *E. eriocephala* with 4–2.

CALLUNA: always 4 locules.

DABOECIA: always 4 locules.

FAMILY: the number varies from 5–10 locules with Epacridoideae having a reduction series down to 1 locule as occurs in Ericaeae.

Ovary apex (Char. 28): this character is divided into two states—emarginate [0] and obtuse/acute [1], which are not absolutely discrete. The states are sometimes difficult to assess, particularly in some Minors with a flattened apex to the ovary.

ERICA: the most frequent type is emarginate with some tending towards obtuse. There are no distinctly acute forms.

MINORS: most species have obtuse to acute ovaries, the few that have emarginate ovaries are the anomalous species with no clear affinities.

CALLUNA: the ovary has an obtuse apex.

DABOECIA: the ovary is distinctly acute. Judd & Kron (1993) incorrectly encoded the state as emarginate in this genus.

FAMILY: emarginate ovaries appear to be the predominant form (Anderberg 1993) except in *Rhododendron* (Sleumer 1966).

Nectaries (Char. 29): nectaries, in the form of a dark coloured, lobed, nectariferous disk around the base of the ovary, are frequent in the Ericeae and are clearly connected to the pollination syndrome. The states of this character are—present [0], and absent [1].

ERICA: most species possess small to large nectaries with the largest occurring in the bird-pollinated tubular-flowered species in which significant amounts of nectar are produced. The wind-pollinated species have lost their nectaries.

MINORS: there is a clear distinction between those that have nectaries (insect-pollinated) and those that lack nectaries (wind-pollinated).

CALLUNA: nectaries are present.

DABOECIA: nectaries are present.

FAMILY: the literature would suggest that most species have nectaries and are animal-pollinated, with wind-pollination and lack of nectaries apparently being confined to Ericeae and the small empetroid group.

Ovule numbers per locule (Char. 30): this character, like the ovary locule number (Char. 27), requires careful examination to record the correct numbers. The states are—3 or more ovules [0], 2 ovules [1], and 1 ovule [2].

ERICA: the genus was always recorded as just 'ovules numerous' but this study has shown that there is a wide range of numbers from as many as 200 ovules per locule down to a single ovule per locule. Approximately 225 species have 1–10 ovules with most species having 10–60 ovules per locule. The high numbers up to 200 occur in the large tubular-flowered species, e.g. *E. macowanii* and *E. cameronii*. *E. jacksoniana* is anomalous in having 6–9 ovules in a 1-locular ovary ($G^1/_{6–9}$), almost the same as the situation in the Minor genus *Thamnus* with $\mathbf{G}^1/_4$.

MINORS: most have 1 ovule per locule, which led to the tribal classification of Salaxideae (Bentham 1839, Drude 1889). However some of these species vary with sometimes 2 or even 3 ovules (*E. glabella* [*Simocheilus purpureus*], *E. radicans* [*Acrostemon schlechteri*], *E. atromontana* sp. nov., *E. vallis-fluminis* sp. nov.), and *E. stokoeanthus* [*Stokoeanthus chionophilus*] with 3, occasionally 4 to 6 and raely 2 ovules. Some of the wind-pollinated species (those formerly in *Coccosperma*) have 2 ovules per locule.

CALLUNA: there are 6–8, occasionally 10, ovules per locule (Beijerinck 1940).

DABOECIA: there are ±50 ovules per locule.

FAMILY: the number appears to be mostly 'numerous' ovules, but is very poorly recorded. In the Epacrids there is a reduction series from many down to one ovule per locule.

Ovule arrangement (Char. 31): this character is rather difficult to divide into discrete states particularly when numerous ovules are present in a locule as in *Erica*. However, in the few species that have been included in the cladistic analysis there has been no problem with categorization.

The states of this character are—pendulous [0], variously spreading [1], and erect [2].

ERICA: most species have spreading to pendulous ovules. Only 32 species have been recorded with erect ovules and these are found in groups of related species, the largest group being the 15 species in the *E. corifolia* complex.

MINORS: most are pendulous with only *E. arachnocalyx* [*Arachnocalyx/Acrostemon viscidus*] and *E. cereris* [*Arachnocalyx cereris*] having erect ovules (Plates 54, 55).

CALLUNA: the ovules are spreading to pendulous.

DABOECIA: the ovules are pendulous (Beijerinck 1940).

FAMILY: this character is very poorly recorded in the family and is presumed to be mostly pendulous.

Placenta position (Char. 32): this character has been categorized into three states, which may sometimes not be discrete—more or less the full length of the columella, i.e. a complete placenta that is central and often takes up the full length of the columella [0], one in the upper half representing the apical placenta [1], and one in the lower half of the columella representing the basal placenta [2].

ERICA: most of the species have the placenta in the upper half of the locule with some having the complete placenta. No species has the placenta distinctly in the lower half. Some species have an apical flap-like placenta with the ovules arranged around the margin and adaxial surface, but these species are scattered throughout the genus. None of them is included in this analysis.

MINORS: all the species have the apical placenta in the upper half with only two species in the basal half (see above Char. 31). No flap-like placenta occurs.

CALLUNA: the placenta is situated in the upper half and is large and flap-like (Beijerinck 1940) and confirmed in my own collections.

DABOECIA: the placenta is situated in the upper $^2/_3$ of the columella with a slight flap at the lower end; it is coded as complete.

FAMILY: only from the few drawings and figures available in the literature can one assess this character in the rest of the family. There are examples of apical and basal positions (Kron & Judd, 1997), but the complete placenta seems to be commonest.

Style (Char. 33): see discussion below under stigma for definitions. The states selected are—style longer than ovary [0], and style shorter than ovary [1].

ERICA: most species have a long thin cylindrical style, which is longer than the ovary. Some of the wind-pollinated species (ex *Philippia*) have very short styles.

MINORS: the insect-pollinated species have a long thin style whereas many of the wind-pollinated species with an unequal calyx have a much-reduced style or sometimes none.

CALLUNA: the style is longer than the ovary.

DABOECIA: the style is much longer than the ovary.

FAMILY: most taxa have long styles, although style length seems to depend on the shape of the flowers. Despite no wind-pollination in the rest of the family, reduction in length has occurred.

Stigma (Char. 34): This character is problematic due to the terminology particularly with regard to this organ in the wind-pollinated species. Strictly speaking the 'stigma' is the set of four short lobes being the terminal portions of the carpels at the end of the style (i.e., in a 4-carpellary ovary). This number reduces with the reduction in carpel numbers. These stigmatic lobes are always present and clearly visible in the fresh state, although very reduced and sunken in a glutinous mass in the so-called capitate stigma, or much enlarged, e.g. *E. gnaphaloides* and species formerly in the genus *Mitrastylus* Alm & Fries from Madagascar.

The terminology becomes complicated by the expansion of the apical portion of the style around the stigmatic lobes into a structure that has always been referred to as the stigma (*auct. mult.*), i.e., the capitate, cyathiform, peltate or funnel-shaped stigma (see Plates 65–84). In some species from Madagascar (Alm & Fries 1927, Perrier de la Bâthie 1930, Dorr & Oliver 1999a) this expanded portion may be reflexed and form a collarette around the apex of the style with the conspicuous stigmatic lobes spreading from the apex. In the wind-pollinated species with a philippioid calyx, this style/stigma complex is considerably enlarged and funnel-shaped taking up the whole mouth of the corolla or more with the minute stigmatic lobes or ridges just visible at the base of the funnel.

Here I have chosen to retain the term stigma for the entire enlarged apical portion of the style, and the style is then mostly a simple cylindrical structure. The receptive area, when clearly visible, is referred to as the stigmatic lobes. The states for the characters are therefore—simple and truncate, i.e. not expanded [0], capitate [1], and peltate or cyathiform [2].

ERICA: most species have a small, slightly capitate or cyathiform stigma with the stigmatic lobes not clearly visible. There is a tendency for wind-pollinated species to have an expanded stigma as occurs in those formerly in *Philippia*.

MINORS: the insect-pollinated species have a simple truncate stigma with no distinct lobes (at least in dried herbarium material, and only just visible at high magnifications in fresh material). The wind-pollinated species on the other hand have an enlarged cyathiform, peltate or funnel-shaped stigma with a small or hardly visible central stigmatic lobe(s) or ridge(s). In some species the stigma is very large compared to the flower.

CALLUNA: the slightly enlarged 4-lobed stigma (Linnaeus 1753) is encoded as capitate.

DABOECIA: the stigma is simple truncate.

FAMILY: the stigma appears to be mostly simple to slightly capitate. The only example of a large expanded stigma occurs in the Empetreae.

FRUIT

This has been the most neglected character in the tribe partly due, I presume, to the lack of fresh material. Resuscitated herbarium material is not always easy to interpret. This study has shown the great importance of this character for the delimitation of species.

Dehiscence type and capsule type (Char. 35 & 36): the types of dehiscence are complex and need precise definition within the context of the tribe and certainly the rest of the family for future overall phylogenetic studies, but will be a major undertaking seeing that there is very little data available at present.

Dehiscent fruits in the Ericeae are loculicidal capsules except in *Calluna* and *Daboecia* (see below). They can be of several types:-

1. fully and actively dehiscent when the valves move independently of the developed seeds inside, i.e. they depend on hydrochastic movements due to the flexing of the fibres of the endocarp. In this case the mature seeds, when loosened, are easily shed from the fully opened capsule.
2. partially dehiscent when the fruit splits along the suture lines but:-
   2.1 partially and actively dehiscent when the drying out of the valves cause the splitting which is not complete and the mature seeds are not able to exit from the capsule—this occurs in the former monotypic genera *E. thamnoides* [*Thamnus multiflorus*] and *E. serrata* [*Nagelocarpus serratus*] and also in *E. jacksoniana*.
   2.2 partially and passively dehiscent when the valves do not open independently but are forced apart due to the tight fit of the expanding seed which is, however, not shed from the fruit. These all have a thin papery pericarp with no fibrous endocarp. This type occurs in *E. platycalyx* [*Platycalyx pumila*], *E. jonasiana* sp. nov. and sometimes in *E. plumosa* [*Grisebachia plumosa*]. In *E. arachnocalyx* and *E. cereris* [both formerly *Arachnocalyx*] the remarkable situation occurs where the enlarging seed, which is basally attached, elongates beyond the passively opened valves to twice the length of the fruit. It may be shed, but remains within the corolla due to its size and the very small orifice to the corolla, which is blocked by the stamens.
3. indehiscent when no splitting takes place at any stage. Sometimes the dehiscence zone or suture is clearly visible as a white line down the carpel. These fruits are shed with the whole flower and have to disintegrate on the ground beneath the plants.

All the above fruit types are clearly loculicidal or derived from a loculicidal condition. No indications of dehiscence at the septum were noted other than that in *Calluna* and *Daboecia*. Sometimes the two halves of a 2-locular indehiscent fruit can be easily prized apart with needles and this could perhaps be mistaken for being septicidal.

Within *Erica* there is a wide range of types in respect of the size and position of the septa and this feature helps in species delimitation. Septa may be totally restricted to the central columella with only a vestige on the valve or vice versa, and this parallels the situation in *Calluna* where the septum remains on the columella and in *Daboecia* where it remains on the valves, the endocarp lining each locule splitting apart along the dehiscence line. I have thus coded both genera as having septicidal dehiscence.

The character states diagnosed for fruit characters are—dehiscent [0], partially dehiscent [1], and indehiscent fruit [2]; and within the dehiscence type, septicidal [0], and loculicidal [1].

ERICA: all species have actively and fully dehiscent capsules except for *E. jacksoniana* (see above).

MINORS: most species have indehiscent fruits, either drupaceous or baccate in both cases having a dry mesocarp, with a few mentioned above having partially dehiscent fruits, either actively or passively so. Some of the indehiscent fruits are in fact accessory fruits in which the delicate fruit is surrounded by a thick, much enlarged, accrescent calyx (see Char. 14). There is no fusion between the fruit and the accrescent calyx, the dried shrivelled corolla remaining between the two.

CALLUNA: the capsule is septicidally [septifragally] dehiscent.

DABOECIA: the capsule is septicidally dehiscent.

FAMILY: all types occur within the rest of the family from loculicidal to septicidal capsules to drupes to berries and capsules surrounded by an accrescent calyx. The epacrids appear to have the same series of dehiscence types. Details are very poorly recorded, if at all, in the rest of the family.

Pericarp (Char. 37): The nature and the structure of the pericarp in the dry state varies considerably in Ericeae from a thick, hard and woody structure to ultrathin and papery. The exocarp (epicarp) is always thin and involved only in the external ornamentation of the fruit. The mesocarp, and especially the endocarp, are the important layers in of the fruit. The mesocarp is composed of few to several layers of large thin-walled parenchyma cells, which are rarely sclerified. They sometimes contain red pigments which give colour to the fresh fruit. In some species, e.g. *Erica bolusanthus* [*Thoracosperma nanum*], the cells elongate considerably in a radial direction.

In dehiscent capsules the endocarp is the well-developed layer with a clear reduction series from very thick to thin and delicate. The mesocarp is usually thinnish, but forms the thicker juicy layer when slightly immature, drying out thin and insignificant. In indehiscent fruits careful examination is needed in order to ascertain the nature of the various layers, in particular, whether the endocarp or testa is the hard sclerified layer. If present, there are three types:-

1. baccate: the pericarp is originally fleshy and juicy but thin, and there is no thickened endocarp. The mature fruit becomes dry and leathery, a dry berry (or berry-like).
2. drupaceous: the mesocarp is originally soft, thin and juicy, there is a thick and sclerified endocarp of two layers; the testa is thin. The mature fruit is dry and leathery.
3. nutlike: the pericarp is very thin and papery with no thickening of the mesocarp or endocarp; the latter is sometimes not visible; the testa is usually very thin. The pericarp can be semitransparent. This type is always associated with the 1-locular 1-ovulate ovary ($\mathbf{G}^1/_1$).

Very often numerous crystals appear in the mesocarp especially in the inner layers and between the mesocarp and the endocarp. According to Scurfield *et al.* (1973), who used infra-red spectroscopy to investigate them, crystals are composed mostly of calcium oxalate or sometimes calcium carbonate. They are often contaminated with other impurities which might influence the form of the crystals.

The mesocarp was not included in the analysis because of difficulties in defining it.

The states of this character are—hard and more or less thick [0], thin and papery [1], and ultrathin [2].

Endocarp (Char. 38): the endocarp can be very thick and white with numerous well sclerified elongate fibre-like cells, which are arranged in two, opposing, layers in both dehiscent and indehiscent fruits, to very thin, unsclerified cells that are transparent and hardly visible in indehiscent fruits. This character is rather difficult to categorise into discrete states particularly in the different capsule types found in *Erica* from the very hard and woody types, e.g. *Erica plukenetii* (where the two cwll layers of the endocarp are 300μm thick) through leathery/horny to thin, brittle and subcartilagineous. Three states have been arbitrarily delimited—thick and well sclerified, mostly >50μm thick [0], thin and only slightly sclerified in the range 10–50 μm thick [1], and ultrathin and transparent, often with no cells visible, <2 μm [2].

No detailed microscopic studies of the endocarp were undertaken; this would be a major project in itself—scope for a thorough investigation in the future.

ERICA: the endocarp is mostly thick and sclerified (bony) varying to thin, leathery and/or cartilagineous, the latter in the range 3–7μm thick. This is associated with the dehiscent nature of the fruit with the endocarp sclereids presumably being involved in the actual process of dehiscence. However, in *E. jacksoniana*, alone in *Erica s. str.*, the endocarp is very thin and papery and this fruit is indehiscent.

MINORS: the endocarp is thick and well sclerified in the drupaceous fruits (60–80μm), but can be thin to ultrathin in the baccate and nutlike fruits.

CALLUNA: the endocarp is thin and sclerified, 12–18μm (Beijerinck, 1940; and my collections).

DABOECIA: the endocarp is thin and sclerified, 40–50μm, in my collections.

FAMILY: the capsular fruits have relatively thick endocarps as do the drupes; presumably baccate fruits have thin endocarps.

SEEDS

Like the fruits, the seeds have never been investigated in Ericeae in any detail. They provide many useful characters for species delimitation particularly within *Erica* s.str.. Peltrisot (1904) looked at the development of the seed in a selection of species from the whole family. In Ericeae he included *Daboecia*, *Calluna*, *Bruckenthalia* [=*Erica spiculifolia*] and six European species of *Erica*.

The seeds are more or less equal in size, those of the few-seeded Minors being no smaller than the many-seeded, large-ovaried species of *Erica*. The shapes are difficult to categorise and will need detailed future investigations to see if they can be used in phylogenetic studies. Some species have winged seeds, which are reminiscent of those of *Rhododendron*. A few have been noted with elaiosome-like apical appendages, never before recorded in the family. The colour of the seeds varies from yellow to golden brown to dark brown and almost black within *Erica*, but in the Minors it is uniformly yellowish brown (when the testa is sclerified), otherwise completely colourless (when the testa is ultrathin). Any use of the colour would be highly subjective.

Five characters relating to the testa were found to be distinguishable—thickness, sculpturing of the surface, shape of the cells, form of the anticlinal walls of the cells and the presence and size of the pits.

variable character like the endocarp and is rather similar in quality. The thickness has been coded into the following arbitrarily defined three states—thick to thin but well sclerified with both periclinal and anticlinal walls being sclerified (range 3–7μm) [0], thin and very slightly sclerified, the sclerification occurring only in the anticlinal walls (± 1μm) [1], ultrathin and transparent with no sclerification (± 0.2–0.5μm) [2].

The sculpturing of the surface depends on the position of the outer periclinal wall when the testa matures and dries out (Fig. 8). Four states have been selected—alveolate [0], smooth [1]. verrucose [2], and spiky [3].

A detailed microscopic investigation of testas would undoubtedly provide further data that would, I believe, substantiate the states that have been selected.

ERICA: the thick testa with indented (alveolate) cells seems to be the commonest type, the thinner outer periclinal wall of each cell being the one collapsing inwards with the inner periclinal wall and anticlinal walls being thick and sclerified (Fig. 8.3–5). Some species have outer cell walls that do not collapse inwards and are absolutely smooth and shiny, e.g. the *E. imbricata/calycina/coccinea* complex (Fig. 8.2). Other species have the cells with the outer periclinal wall protruding outwards into large conelike projections rather reminiscent of a hedge-hog (Fig. 8.1). The species with this latter character occur in groups which appear at present to be quite unrelated (see Oliver 1991).

MINORS: most of the seeds have a smooth testa. It is very thin in the indehiscent fruited species, indeed the testa in some species is completely transparent and very difficult to detect. The smooth testa is caused by the lack of development of the anticlinal walls. Other species have a thick testa, which is slightly to markedly indented in both dehiscent and indehiscent-fruited species.

CALLUNA: the seeds are alveolate and thick-walled, particularly the inner periclinal wall of 15μm thickness (Beijerinck 1940).

DABOECIA: the seeds are thick-walled with large outward projecting processes.

FAMILY: most of the genera appear to have thick-walled testas with slightly to deeply indented cells (Peltrisot 1904). The most remarkable type is that in *Daboecia*, actually identical to the 'hedgehog' type in *Erica* although noted by Stevens (1971) as being unique in the family. An anatomical investigation of fruits and seeds of selected *Vaccinium* species was undertaken by Brisson (1978) after an earlier report on the use of the SEM in seed studies (Brisson & Peterson 1976). Similar studies should be undertaken on a far wider basis in the family.

Testa cell shape (Char. 41): following the survey by Peltrisot (1904) and my survey in this study, this character has been divided into two states which can overlap somewhat, the separation being rather subjective at more or less equilateral to slightly elongate [0], versus very noticeably long/elongate (at least twice as long as broad) [1] (Fig. 7).

ERICA: most species have elongate cells with only a few having equilateral hexagonal cells or subrounded cells.

MINORS: most species have elongate cells with some of the thick-walled species having equilateral hexagonal cells, e.g. *E. zeyheriana* [*Coilostigma zeyherianum*].

CALLUNA: the cells are equilateral to slightly elongate.

DABOECIA: the cells are more or less equilateral.

FAMILY: elongate cells seem to be rare in the family according to Anderberg's listing (Anderberg 1993), but this depends on his circumscription of the states short and long. Peltrisot (1904) shows most species with elongate cells according to my circumscription. They are extremely long in some members of the Rhododendroideae, particularly those that have very long, thin seeds. Hedegaard (1980) shows a variation in cell shape from equal to very elongate occurring in *Rhododendron*.

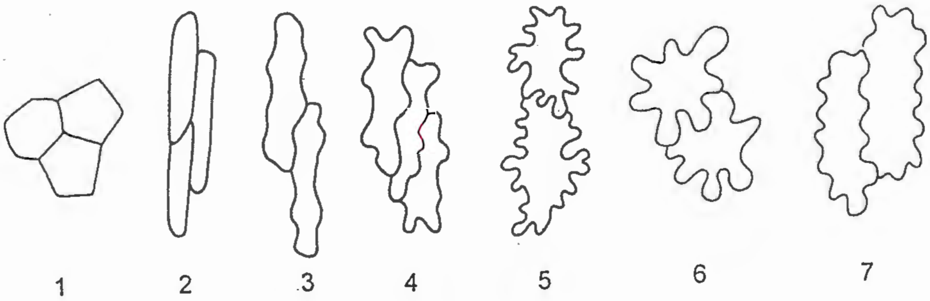

FIGURE 7.—Testa cells, outlines of different types in abaxial view. 1–4, straight to slightly undulate; 5–7, jigsawed; 1 & 6, length <2x width; 2–5 & 7, length >2x width.

Testa cell, form of anticlinal walls (Char. 42): the form of the anticlinal walls of the testa cells has been mentioned and illustrated only by Peltrisot (1904), but could, I think, be rather important in the family. The walls can be straight to curved to undulate to much convoluted (here termed jigsawed). The situation is complicated by the species with a very thick testa which appears to be straight-walled on the outer periclinal edges but on the inner periclinal edges clearly jigsawed. In these cases I have taken the form of the inner edges as the standard for the species There is a problem with assigning discrete states to this character and I have used the forms as illustrated in Fig. 7. There is obviously some variation in the character and the boundaries between undulate and the two extremes have had to be assigned on a subjective basis. The states are—jigsawed or convolute [0], undulate [1], and straight [2].

ERICA: the commonest type is the jigsawed cell wall, indeed, Peltrisot (1904) shows this type only in *Erica* and *Bruckenthalia* [=*Erica spiculifolia*]. There are few species with straight walls among the many that have been investigated thus far.

MINORS: the commonest type is likewise the jigsawed type.

CALLUNA: Peltrisot (1904) and Beijerinck (1940) show the anticlinal walls as being straight, and this has been confirmed in my own collections.

DABOECIA: Peltrisot (1904) shows the testa as slightly undulate and this has been confirmed in my own collections from Ireland and Spain.

FAMILY: most of the species illustrated by Peltrisot are of the jigsawed type, indicating that is the common one in the family, however Stevens (1971, fig.3) illustrates only straight-walled examples. Peltrisot shows the rhododendroid seeds having elongate straight-walled testas.

Testa pits (Char. 43): these are the pits on the inner periclinal wall and sometimes anticlinal walls of the testa cells (Fig. 8). Both Peltrisot (1904) and Stevens (1971) illustrate the pits and Dorr (1995) mentions them in some members of the Pyroloideae. These pits vary in size and shape and may also be absent. Again categorisation is rather subjective for the pits, when present, and the character is divided into three states—pits absent [0], pits equal and rounded (small to large) [1] and those that are elongate and look as though they are simple pits that have coalesced [2].

ERICA: most species have finely pitted walls. Very few species have no pits, e.g. *E. utriculosa* and some species formerly in *Philippia* and *Blaeria*.

MINORS: Pits vary from minute to very large and coalescing. 40% of the species have no pits present and these are associated with very thin testas.

CALLUNA: surprisingly has no pits present. The large 'bodies' shown by Peltrisot (1904) are in fact ribs on the collapsed outer periclinal wall which Beijerinck (1940) mentions but does not illustrate.

DABOECIA: numerous small pits are present.

FAMILY: from Peltrisot (1904) it would appear that pits are present in the rest of the family, but this character has not been discussed by any other workers.

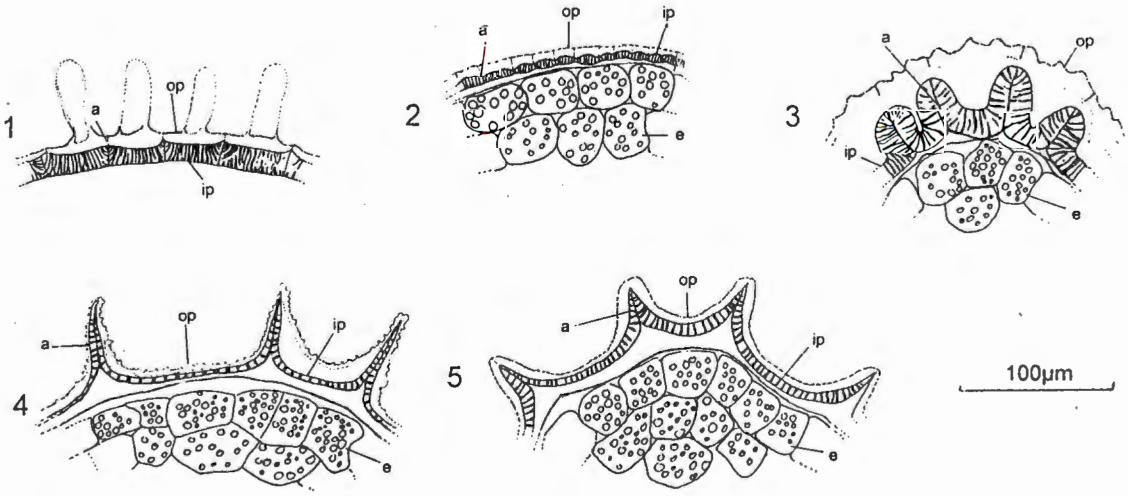

FIGURE 8.—Testa cells in cross-section. 1, *Daboecia* (no endosperm on slide); 2, *Erica karooica*; 3, *Erica versicolor*; 4, *Erica taxifolia*; 5, *Erica curviflora*; (all drawn from micropreparations). op=outer periclinal wall; ip=inner periclinal wall; a=anticlinal wall; e=endosperm cells

LEAF ANATOMY

Little has been published on the anatomy of the leaves in the tribe Ericeae, the most extensive study being that of Lavier-George (1936) for the 34 Madagascan species of *Philippia* (now *Erica*, Dorr & Oliver in press). A short paper gave the results of an investigation of the few British species of *Erica* (Smith 1930). Hagerup (1953) surveyed the leaves in the whole family and included several species of European Ericeae. An unpublished preliminary investigation was recently undertaken on material of 81 Cape species provided to D.A. Spreeth of University of Stellenbosch. He recorded 16 anatomical characters that have formed the basis of the current assessment of the group.

Lavier-George (1936) found several characters in the leaves to use to draw up a key to the species occurring on Madagascar. I regard most of these of use only at specific level and not at higher levels for generic or subgeneric grouping.

Leaf anatomy was used to make groups of species in *Rhododendron* (Hayes *et al.* 1951), but these groups were found to contradict the current taxonomic system based on the lepidote/elepidote scales. Leaf anatomy was, however, found useful at sectional level as a supplementary character.

The following set of six characters and their states was chosen following an assessment of Spreeth's permanent slides and an investigation of all 83 species of Minors and an additional 180 species of *Erica* from hand-cut sections of fresh or rehydrated leaves (Fig. 9).

Cuticlar zone (Char. 44): the actual boundary between the cuticle and the outer periclinal wall of the epidermal cell is not always clearly defined, even in permanent sections. I have therefore taken the whole zone including the cuticle and outer periclinal wall of the epidermal cells and termed that the cuticular zone for convenience (Fig. 9–cu). Beijerinck (1940, fig 32) clearly regards the major part of that zone as cell wall. The two character states have been selected subjectively. The state 'thin' covers zones mostly <10µm in thickness [0] and the state 'thick' covers those zones mostly >15µm [1]. For standardisation the cuticular zone was assessed mainly along the primary adaxial surface of the leaf. However there are variations with the secondary abaxial surface (the part outside the sulcus) sometimes having a thicker cuticular zone. This occurs when the leaves are erect and appressed (the secondary measurement is then used). The true abaxial surface within the sulcus (the primary abaxial surface) usually has a much thinner cuticular zone. In some instances the cuticular zone is thicker than the epidermis itself (Fig. 9.7) (up to three times in *Erica greyii*).

ERICA: the cuticular zone is thick in 56% of the species sampled and thin in 44%.

MINORS: the species are divided almost equally, with slightly more than half having a thick cuticular zone. Eight species are variable.

CALLUNA: the situation in the genus is complicated by the leaves being appressed to the branch. The primary adaxial cuticular zone is very thin whereas the secondary abaxial zone is thicker, being exposed to the elements. Beijerinck's figure shows the latter cuticular zone in

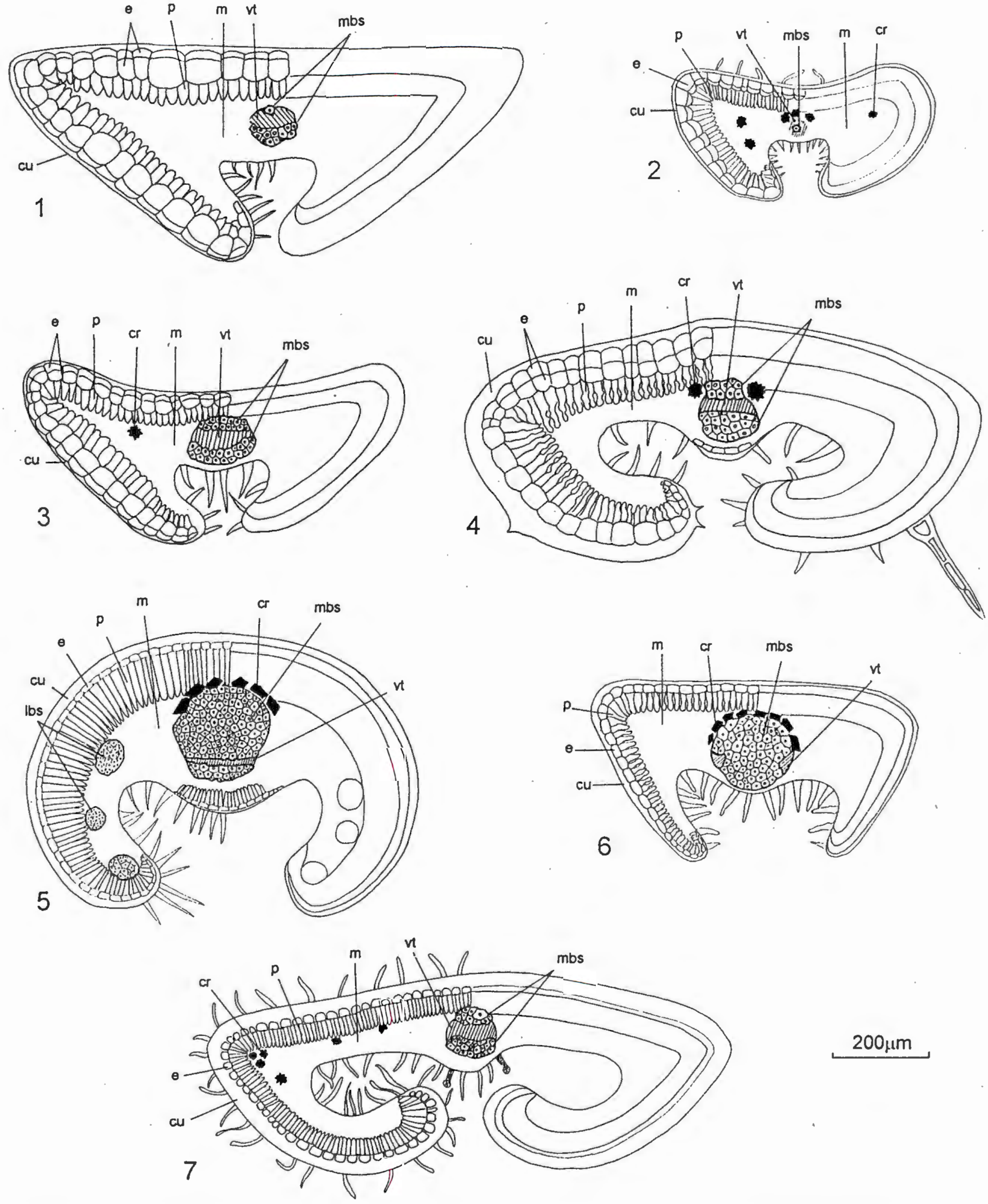

FIGURE 9.—Leaf anatomy. Diagrammatic cross-sections of the leaves of seven species of Ericeae showing the characters discussed in the text. 1, *Erica axillaris*; 2, *E. miniscula; 3, E. thamnoides*; 4, *E. articulata*; 5, *E. paucifolius*; 6, *E. rigidula*; 7, *E. plumosa*. mbs=middle bundle sclereids, lbs=lateral bundle sclereids, vt=vascular tissue, m=mesophyll, e=epidermis, p=palisade, cu=cuticular zone, cr=crystals.

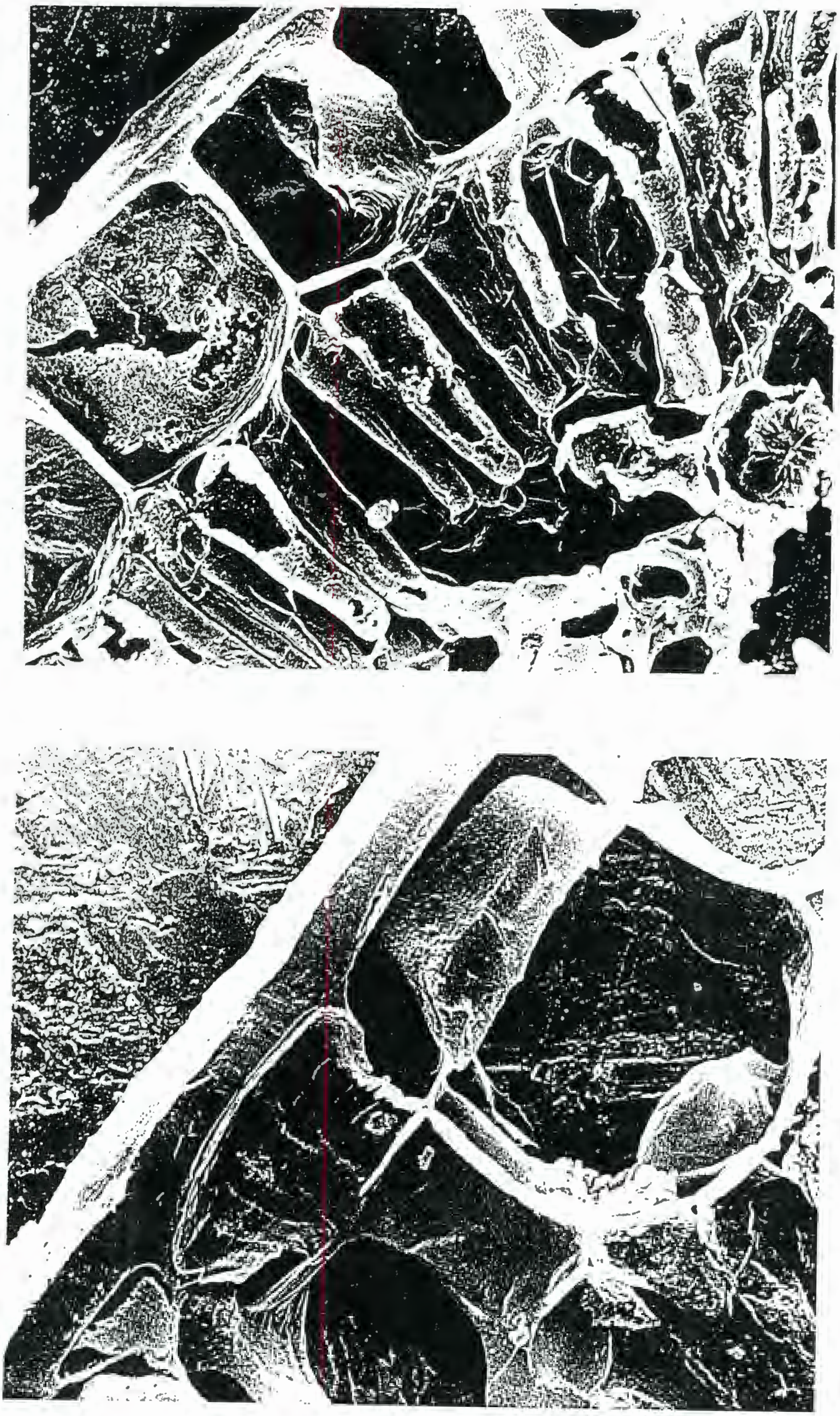

FIGURE 10.— SEM photomicrographs of cross-sections of epidermal cells of the leaf: upper photograph with single epidermal cells (*Erica baccans*), lower with 'double' cells showing the mucilaginous cross-wall (*E. uberiflora* [=*Simocheilus multiflorus*). (Photographs by D.A. Spreeth).

situation occurs in *Erica dianthifolia* which is, however, not included in this data set.

DABOECIA: the zone is thick, being >15µm in thickness.

FAMILY: this character is not possible to assess in the family since it is not recorded in the literature. Stevens (1971) shows a drawing of the leaf in *Bejaria mathewsii* from which it is deduced that the cuticle is 18–25µm thick.

Epidermis type (Char. 45): the terminology is rather confusing due to the various interpretations of the divisions that are visible in the epidermis. Stevens (1971) notes "it is not known if these periclinal walls are real walls, or parts of a single, layered, mucilaginous cell wall, or even if every compartment contains a nucleus". He records the several-walled type as a 'mucilaginous epidermis'. His drawing of the epidermis in the European *Erica sicula* [*Pentapera*] shows the crosswalls all originating from the outer corners of the epidermal cells. This can occur in African species, but there are also those species in which a straight wall occurs across the middle of a cell (Fig 9.1–4 & also Fig.10, Spreeth pers. comm.). Beijerinck (1940) regards the epidermis as single with a layer of mucilage appearing in the lamellae of the inner periclinal wall thus splitting the cell wall into two. Solereder (1908) refers to the gelatinization of the inner epidermal walls, with several internal cellulose lamellae observable, and Haberlandt (1965) refers to thickened mucilaginous inner walls of the epidermal cells with *Erica carnea* as an example. Napp-Zinn (1973) in his survey of leaf anatomy confirms these views and quotes several Ericaceae examples including *Erica caffra* and the work of Beijerinck above. In my recording of this character I have used the term 'multiple' for those species in which the epidermis has one or more visible 'crosswalls'. Future detailed ontogenetic studies should be undertaken to establish the true nature of these walls. Not all cells in the epidermis may exhibit the multiple epidermis, the second state is better phrased as 'some or most epidermal cells multiple-walled'.

The states of the character are—single [0], and 'multiple' [1].

ERICA: 75% of the species investigated have a multiple-walled epidermis, mostly with a single crosswall, but sometimes with two or three.

MINORS: 75% of the species have a multiple-walled epidermis, with only the occasional cell exhibiting three crosswalls.

CALLUNA: Beijerinck records multiple-walled epidermal cells but only in the revolute portion of the leaf, i.e. the secondary abaxial epidermis. The primary adaxial epidermis is single-walled (see discussions above). This is confirmed by my observations.

DABOECIA: the samples I collected in Ireland and Spain exhibit a simple single-walled epidermis.

FAMILY: this character is recorded by Stevens (1971) who lists a multiple mucilaginous epidermis occurring in several genera, mostly in the Rhododendroideae *s.str.*, some of which seem to have narrow ericoid leaves (see Char. 1 discussion).

Epidermis size (Char. 46): the states delimited here come from a comparison of the height of the epidermal cells relative to the height of the palisade—epidermis shorter than the palisade [0], equal in length [1], and longer than the palisade [2] (Fig. 9–e, p). There may be slight variation within a leaf in which case the ratio of the majority of cells is then taken as that for the species.

ERICA: in 56% of the species the epidermis is smaller than the palisade, in 30% equal to the palisade and in only 14% longer than the palisade.

MINORS: 45% smaller, 28% equal, only 7% longer than palisade with 20% variable species tending to be equal to smaller or to longer.

CALLUNA: the epidermis is shorter than the palisade cells (see also Beijerinck, 1940).

DABOECIA: the epidermis is very much shorter than the palisade cells.

FAMILY: this character is not recorded in the rest of the family.

Epidermis cell shape (Char. 47): the shapes are categorized as three main types based on the relationships of the periclinal and anticlinal dimensions in cross-section—oblate being broader than long [0], equal [1], and elongate longer than broad [2] (Fig. 10). The epidermal cells are regarded in this context as single cells. The state 'oblate' has an average dimension of 25µm long x 35µm wide; the state 'elongate' is the opposite with an average of 53µm long x 36µm wide.

ERICA: the distribution of states is more or less equal in the sample of species investigated with slightly fewer species having elongate cells.

MINORS: as in *Erica*. The extremes in the oblate state are 27 x 60µm in *Erica glabella* [*Simocheilus purpureus*] down to 15 x 30µm in *E. rigidula* [*Scyphogyne rigidula*] and in the elongate state from 60 x 50µm in *E. labialis* [*Sympieza labialis*] down to 40 x 25µm in *E. artemisioides* [*Scyphogyne micrantha*].

CALLUNA: the cells are more or less as wide as tall (see also Beijerinck, 1940).

DABOECIA: the epidermal cells are oblate in shape.

FAMILY: this character is not recorded in the rest of the family.

Sheath sclereids (Char. 48): these are the sclereids associated with the midrib vascular bundle. The number and distribution of these sclereids varies considerably (Fig. 9). The main pattern is with more sclereids abaxially than adaxially with the phloem/xylem tissue placed in-between. When there are numerous sclereids the vascular tissues are split into two zones placed laterally in the midrib. The absence of bundle sclereids is a rarity in the ericeads. Stevens (1971) noted the lateral sclereid bundles in the petiole and recorded this as being almost diagnostic for the ericeads, excluding *Calluna* (which has no petiole), but also appearing in the very ericoid-like *Daboecia* and *Ledothamnus* in the Rhododendroideae *s.str.*

Powell *et al.* (1996) state that there is no contact between the fibre sheath and the abaxial epidermal cells in the ericeads which feature has been found important in the epacrids. This is not the case as the current survey has shown numerous species with the sclereids adjacent to the epidermal cells on the abaxial surface. Others have palisade layers and sometimes mesophyll tissue between the sclereids and the epidermis.

The states of this character are— 0–20 sclereids [0], 20–60 sclereids [1], and more than 60 sclereids [2].

ERICA: 65% of the species investigated had 20–60 sclereids per bundle with 25% having fewer and only 10% more. So far seven species have been noted with no sclereids associated with the midrib.

MINORS: 52% of the species have on average between 20 and 60 sclereids with 30% having more and only 18% less than 20 sclereids. Only three species lack any bundle sclereids (*Erica melanomontana* [*Scyphogyne orientalis*], *E. miniscula* [*Lepterica tenuis*] and *E. binaria* sp. nov.) (Fig. 9.2).

CALLUNA: I have found the sclereids are mostly less than 20 and this is confirmed by examining Beijerinck's figures.

DABOECIA: there are fewer than 20 sclereids around the midrib-vein.

FAMILY: these do occur but mostly in the subfamily Vaccinioideae (Stevens 1971).

Lateral sclereids (Char. 49): lateral veins rarely occur in the leaves of ericeads, but when they do, they are usually dominated by sclereids with very little or no vascular tissue being present (Fig. 9: 5). They would appear to be more supporting than conducting structures. Lavier-George (1936) illustrates several Madagascan species with lateral veins.

The two states selected are—sclereids present [0], sclereids absent [1].

ERICA: most species have no lateral veins or sclereids. Those so far recorded with laterals are the *Erica imbricata* and *E. calycina* complexes and the Madagascan species (ex *Philippia*). In the former complex some species, surprisingly, have more sclereids in the furthest lateral bundle than in the sheath around the midrib (e.g. *Erica lasciva*, *E. accommodata*).

MINORS: most species have no lateral sclereids, but there are eight species with laterals, some of them being very markedly present, e.g. *Erica totta* [*Eremia totta*] and *E. paucifolia* [*Syndesmanthus paucifolius*].

CALLUNA: Beijerinck (1940) shows a few, very small lateral bundles.

DABOECIA: small lateral bundles of sclereids/vascular tissue are present.

FAMILY: with broad flat leaves being the dominant leaf form in the family, numerous lateral veins occur; these often have associated sclereids (see Char. 44).

TABLE 6.— Characters and character states used in the cladistic analysis of the Ericeae (no particular polarities are implied).

Branches

1. **indumentum:** simple [0]; variously plumose [1]; absent [2]

Leaves

2. **arrangement:** alternate [0]; whorled [1]
3. **number per whorl:** 4n [0]; 3n [1]; 2n [2]

Inflorescence

4. **position:** mainly or only 2nd branches [0]; equally 2nd and 1ry branches [1]; mainly or only 1ry branches [2]
5. **type:** raceme [0]; raceme plus a terminal umbel [1]; umbel [2]; single unit or less [3]
6. **number of units:** >3 [0]; 2, occ. 1 [1]; 1 [2]; <1 [3]

Bract

7. **position:** axial [0]; partially recaulescent [1]; fully recaulescent [2]
8. **type:** leaflike to bracteose, mostly narrow [0]; petaloid, scarious and broad [1]

Bracteoles

9. **presence & position:** on pedicel [0]; fully recaulescent [1]; absent [2]

Calyx

10. **sepal numbers:** 4 [0]; 3 [1]; 2 [2]; 1 [3]
11. **sepal fusion:** free [0]; fused [1]
12. **type:** leaflike to bracteose, mostly narrow [0]; petaloid, scarious and broad [1]
13. **calyx size in fruiting stage:** not enlarging [0]; enlarging [1]
14. **sessile glands:** absent [0]; marginal [1]; adaxial [2]
15. **sulcus:** ≥50% [0]; ≤30% [1]; absent [2]

Corolla

16. **lobe numbers:** 4 [0]; 3 [1]; 2 [2]
17. **surface:** smooth and glabrous [0]; verrucose/colliculate and glabrous [1]; hairy [2]

Stamens

18. **numbers:** 8 [0]; 7,6,5 [1]; 4 [2]; 3 [3]
19. **position at anthesis:** included/manifest [0]; fully exserted [1]
20. **filament fusion:** free &/or just basal [0]; ± 50% [1]; full [2]

21. **filament type:** straight [0]; geniculate below anther [1]
22. **filament surface:** glabrous [0]; papillate [1]; hairy [2]
23. **anther connation:** anthers free [0]; anthers connate [1]
24. **anthers:** muticous [0]; spurred [1]
25. **anther, pore size:** >50% [0]; 50–25% [1]; <20% [2]

Pollen

26. **Pollen type:** tetrads [0]; monads [1]

Gynoecium

27. **locule number:** 4 [0]; 3 [1]; 2 [2]; 1 [3]
28. **ovary, apex:** emarginate [0]; obtuse to acute [1]
29. **nectaries:** present [0]; absent [1]
30. **ovules per locule:** ≥3 [0]; 2 [1]; 1 [2]
31. **ovule arrangement:** pendulous [0]; variously spreading [1]; erect [2]
32. **placenta position:** ± full-length [0]; upper-half [1]; lower-half [2]
33. **style:** longer than ovary [0]; shorter than ovary [1]
34. **stigma type:** simple [0]; capitate [1]; peltate or cyathiform [2]

Fruit

35. **type:** dehiscent [0]; partially dehiscent [1]; indehiscent [2]
36. **dehiscence type:** septicidal [0]; loculicidal [1]
37. **pericarp(dry):** hard, ± thick [0]; thin, papery [1]; ultrathin [2]
38. **endocarp:** thick & sclerified [0]; thin, slightly sclerified [1]; ultrathin, not sclerified [2]

Testa

39. **thickness:** thick & sclerified [0]; thin, slightly sclerified [1]; ultrathin, not sclerified [2]
40. **sculpturing:** alveolate [0]; smooth [1]; verrucose [2]; spiky [3]
41. **cell shape:** equal to longish, <2X width [0]; long, >2X width [1]
42. **anticlinal cell walls:** jigsaw/convolute [0]; undulate [1]; straight [2]
43. **pits:** none [0]; small to medium holes [1]; large & slit-like [2]

Leaf

44. **cuticular zone:** thin [0]; thick [1]
45. **epidermis:** single [0]; multiple [1]
46. **depth of epidermis vs. palisade:** <palisade [0]; =palisade [1]; >palisade [2]
47. **epidermis cell shape:** oblate [0]; equal [1]; elongate [2]
48. **midvein sheath sclereids:** 0-20 [0]; 20-60 [1]; >60 [2]
49. **lateral sclereids:** present [0]; absent [1]

TABLE 7.—Summary of character types used in the data set.

31 multistate, (7 as 4 state, 25 as 3 state and 5 with the state 'absent')
18 binary or nominal variable (2 as present/absent)
19 qualitative
30 quantitative
3 inapplicable codings (leaf whorls for *Daboecia*; dehiscence type for all indehiscent-fruited Minors)
2 unknown (lack of fruiting material)
1 unknown (*Calluna* in inflorescence, bract and bracteole homology assessment)

TABLE 8.—Dataset 1, character matrix for use by PAUP; variable characters recorded with the states present placed in square brackets [ ].

```
                 0        1         2         3         4
                 1        0         0         0         0
------------------------------------------------------------------------
Daboecia         00-00000120100102000000000010000000000003011100000
Calluna          012?????00100200000100100000000101000000020010100
glabella         0101[01]0[01]0[02]01000100210000011210201002-2221100[01]1[01] [01]11
piquetbergensis  010100[01]00010001002100000[01]11010201002-1221101110[01]11
dregei           010100[01]0201000100210000011210201002-1221100110111
dispar           010110[01]0[02]0100010021000001 1[012]10201002-111110110[01] [01]10
albertyniae      01110000201000100210000011210201002-2221100110011
radicans         01012110[02]01001000210000[01]11[012]10201002-111110[01]110011
interrupta       0101[12]010001002100210000111210201001-01111011[01]0010
articulata       010000[01]0201000[12]00210000011310201002-2221100110111
erina            01100000201001200210000021311201022-2221110100001
malmesburiensis  011000[01]0201000100210000011310201002-22211[01]0[01]10011
globiceps        010000[01]0211000[12]10310000011310201002-2221100110[01]11
pulchelliflora   011000[01]0201000100210000011310201002-22211001[01] [01]111
venustiflora     01[01]00000[02]11000110310000011310201012-2221100000001
innovans         21100000211000210310010011310201002-2221100[01]1[01] [01]11
brownii          01000000211000210310000011311201022-2221100110111
labialis         011000002[012]1000[12]20210000011200201002-222111[01]011[12]01
ecklonii         01110000221000220210000011200201002-1211120011001
macrocalyx       0111[03] [01]00201000120210000011210201002-1221110011001
williamsiorum    011100[01]0221000120210000011210201002-??????010001
eriocephala      01[01]110[01]000100010021000001 1[012]10201002-00[12]11[12]0110[01]10
paucifolia       01112[01]10001000101210010001310201002-1221[01]00100020
pilosiflora      01112[01]10001000001210120011[23]10201002-1221100000020
niveniana        01112[01]10001001101210000011310201002-??????100010
xeranthemif      01112110000002100110000001210201002-122110101[12]111
viscosissima     01112[01]10001002100210000 0[01]1310201002-121110[12]100020
vernicosa        01112110001002000200100 0[01]1200201002-1111101100020
agglutinans      011121100010020002100000013102010[01]2-111110[12]100020
glabra           0102[23]110001010100210000110210201002-222110011[01]110
anguliger        0112[23]1100010101002100001113102010[02]2-11111[01]2010121
phaeocarpa       0112[23]210001010101210100111210201002-2221110112221
kammanassieae    011121100010111012 10[01]00011311201022-011110001[01]111
inflaticalyx     0112[23]110001011101210000111210201012-1211110112121
bolusanthus      0111[23]1100010001012100000 11[012]01201022-0021100110111
montishominis    0111[23]110001000100210100111310201012-1111100110111
atromontana      0111[23]1100010001002100001112102010[12]2-01[12]11100000[12]1
uberiflora       0110[123] [012] [01]0001000100210000111210201002-12211[01] [01]01[12] [12]11
angulosa         0111[23]110001000100210000111211201022-1221[01] [01]001[12]111
rosacea          0111[13] [01]1000[01]000100210000111010201002-00110[12]1012201
vallisflumin     01113210001000102200100111210201002-00211000[01] [01] [01] [12]1
puberuliflora    0111[23]110001000102200100 0[01]1011201022-00111011100[12]1
quadrifida       1112[13] [01]100010001002 10[01]00111010201012-1100021012201
zeyheriana       0111[13] [01]2013100010[02]210[01]00021211201022-1100021011201
burchelliana     01112120131000100210[01]00021011201022-1100021012201
totta            11122111000100100000000010000201012-0221110100020
curvistyla       01112110001100102000100011310201002-1221[01]20100021
recurvifolia     01112110001000002000100121210201002-11211101[01]0021
velatiflora      01113211000000102000000001211201012-1211110011211
plumosa          11112[01]1[012]001[012]00102200110011200201012-01[12]11011[01]0011
caprina          01112010001[012]00100200100111210201002-12211[01]0000001
eremioides       01113210001100102200100111210201012-12211[01]21100[12]1
lateriflora      01123210001000102200100111310201012-12111001[01]0010
cetrata          01113211001100100000000001210201022-12110[01]111[01]201
bokkeveldia      01112110001100100000100111210201002-12211[01] [012]012201
cereris          01112[01]10000000002[01]0000010020022200111111101100011
arachnocalyx     01112[01]10000000002[012]00000[01] [01]020022201111111101100011
platycalyx       0111211000100010 0[012]100000102102010011121011101[01]110
thamnoides       11112110001002100210000111310001001100000[02]101[01]111
outeniquae       01113210000000112100000010100201012-0011021011211
karwyderi        01113210001000100010000021210201002-121111101[12]211
```

jonasiana	0111211000000001002100200[01]1311201011111111[01]1110[01]11
vlokii	01113210000[012]00100010000111010201002-002111101[12]201
stokoeanthus	111221100000000100200100110210001022-121[01]111010101
perplexa	11123220131000100000100010111201122-12011[012]1011[12]01
axillaris	0112322013100010[02]00[012]001010[012]11201122-0011101011201
boucheri	0111[23] [12]20131000200200000000311201022-0111101111111
serrata	0112212013100010[02]00200[01]010211101121-01111[01]1[01]11211
bredasiana	01113220131000100102001000211201022-0121110011101
binaria	01113220131000100000000010211201122-0021100[01]11101
terniflora	0111[23] [12]2013100010010[012]000010211201[01]22-00211[12]1111111
subcapitata	01122120131001100[01]02001010301101122-02000[12]1011201
rugata	0111322013100010000200[01]010211101122-01101[01]10111[01]1
parviporandra	1111322013100010[02]10[012]000020311101122-00010[12]1111201
areolata	01113220131000100[12]02000010311101122-0200001[01]11101
remota	0112322013100010010[012]001010211201122-1210001011[12]01
artemisioides	01123220131000100100001010311201122-0200[01]01011[12]01
calcicola	0111[23] [12]20131000100202000010311201022-12100011112[012]0
urceolata	0112[23] [12]201310001[01]2300000010311201022-121110101[12] [01]11
muscosa	0112212013100010[02]200000010311201122-12[12]1101[01]1[12]011
phacelanthera	01120120131000100200001010311201122-1221101011110
eglandulosa	01123220131000102200000020311201[01]22-??????111011
melanomontana	01113220131000100[12]0[01]001010311201122-1211101110101
miniscula	01113220131000100001001020311201122-??????011101
rigidula	1111[23] [12]201310001[01]0202000000[23]11201022-00211[12]0[01] [01]0021
Eericoides	0101201000000000121000011101000100010000101011111
Ebarbigeroides	0100201000000100021000000001000100010010011010001
Eioniana	01012010001001000200000010010[01]0100010000101011101
Erussakiana	0100201000000100021000011100010100010000101001101
Elongimontana	01123210001000002210000110000[01]010201000010101[12] [01]11
Ecorifolia	21101000000100101000100100000002000010000001000001
Efloccifera	111232100001001000000[02]011001000100010001121011101
Ejacksoniana	1112321000110010000000011031100102111211001011[12]01
Eumbelliflora	0111321[01]000100100000000[01]100000011001000002111112[01]
Epeltata	111232[12] [012] [01] [023] [01]100100000100[01]1000100102010000111011101
Emacrotrema	0111321100110010000[01]00000001100102010010001111101
Eeriophoros	01022[01]1000000000201000001000002000010000011100[01]21
Echonantha	21123310001000100010000011000201000100????010101
Edeliciosa	11123210001000000001000011000000000010000021011101
Enudiflora	0112321000100010[01]010000111010001000100000[01]1111111
Ealtiphila	01123220131000102000100010011[01]0112010000021100021
Enotholeeana	0112322013100110000200100001110102010002021100021
Eexleeana	01123220131100100002001000001001020100020211[01] [01] [01]21
Eamatolensis	11112120131000201210[01]0011011[01]00102010000001010101
Bruckspic	0100000012100010000000000101100102010000101011111

3.4 CLADISTIC ANALYSES

Two data sets with different coding of polymorphic characters were produced for the cladistic analyses which were run using the maximum parsimony programs, PAUP 3.1.1 (Swofford 1993) and Hennig86 (Farris 1988). The use of PAUP was found necessary in order to cope with the size of the data set and the occurrence of partially variable multistate characters in a number of the taxa (Tables 7 & 9).

TABLE 9.—Polymorphic characters present in the data set—the number of binary and multistate characters per species with the number of species in which they occur.

Characters (polymorphic)	Species
Binary	41
1 multistate character	29
2 multistate characters	30
3 multistate characters	10
4 multistate characters	4
5 multistate characters	1
6 multistate characters	1

There are 170 instances (3.3% of the data set) of multistate characters in which 73 species possess several, but not all, of the states. PAUP is capable of distinguishing polymorphic characters that have been encoded as partially variable (Platnick 1989; Swofford 1993), *i.e.*, those states which are actually present. When the 'uncertainty' interpretation of polymorphism is used in PAUP the program will choose a state that allows minimization of the tree length. In Hennig86 this situation is recognized only as unknown data and as such all states are included in the analysis even though one of two may not occur. This aspect is very important here since there are so many variable taxa. In my opinion there is justification for regarding a hypothetical Species A having two states 0,1 of a 3-state character as being different from Species B with only state 2 and likely to show a link with Species C that has only the state 0. Encoding Species A as totally polymorphic (0,1,2) for the character would eliminate information which may have a bearing on phylogenetic relationships.

Nixon & Davis (1991), however, show that scoring polymorphisms as missing values can be misleading and should be avoided. They believe that some taxa could in fact be polyphyletic if they contain polymorphisms, and they advocate splitting such taxa into invariable subunits. However, in the Minors polymorphism can be found on the same plant or even the same inflorescence—in stamen and ovary mery, presence or absence of bracteoles and anther appendages. Weins (1995) undertook an analysis of characters over a range of data sets and found that polymorphic characters can contain significant phylogenetic information but that they can also contain more homoplasy than fixed characters and thus add to the length of trees.

The data set in Table 8 indicates those characters that are coded as polymorphic with the states enclosed within brackets. This form of the data set was used for the analysis using PAUP. A second form of the data set replaced the characters in brackets, whether fully or partially polymorphic, as an asterisk for use in the Hennig86 analyses. In these cases the species are regarded as having all the states for a polymorphic character. This problem could perhaps be partially overcome by encoding only one of the states, namely the most frequently occurring, and ignoring the less frequent states, for the species concerned, but was not done in this study.

With the matrix of 105 taxa and 49 characters the full data set could not be run satisfactorily using Hennig86 because of memory overflow at a maximum of only 611 trees using the heuristic search based on the branch breaker option. Hennig86 is constrained by the 640k RAM limit of the DOS environment (Farris pers. comm.). Another problem was encountered when it was found that Hennig86 would not accept multi-taxon outgroups using the full data set but did so for small samples. A series of simple tests using just the <hennig> option was run with an increasing number of taxa added to the data set and with *Daboecia* and *Calluna* designated as the outgroup. When the number of taxa exceeded 90 *Calluna* was rejected from the outgroup and placed in the ingroup. This was very surprising seeing that the <outgroup> command subsequently listed the genus as being in the outgroup.

As a result of this situation PAUP was used for analyzing the full data set and Hennig86 was used for the analysis of the smaller groups such as the one with fully recaulescent bract and bracteoles (**RBr-Rbr**) syndrome that was found in the output from PAUP. Hennig86 was used due to my familiarity with the DOS and Windows95 environments whereas PAUP required a Macintosh operating environment, which was not available until very recently.

A trial analysis was run for me on the full data set using the latest version of Parsimony Jackknife (Farris pers. comm.).

All analyses were run with the characters encoded as unordered thus avoiding any assumptions on character transformations.

3.4.1 ANALYSES 1

PAUP 3.1.1 provides two methods for searching for optimal trees, exact methods and heuristic methods. Exact methods guarantee to find the optimal trees but require prohibitive amounts of computer time for large sized data sets. They are not used for data sets with more than 10 or 11 taxa (Hendy & Penny 1989, Swofford 1993). On the other hand heuristic methods do not guarantee finding all the shortest trees but run much faster and are the only feasible methods for large data sets like the current one with 105 taxa of Ericeae. There are numerous protocols within the heuristic methods in PAUP. The branch & bound protocol works only for small data sets less than 20 taxa (Swofford 1993).

Running PAUP on the full data set, the following protocols were employed: 500 random entries were analyzed in the step-wise addition algorithm to produce an initial set of trees. These were then subjected to search using the most frequently used option, namely tree bisection-reconnection (TBR) with MULPARS off thus saving only one tree on each pass.

This procedure found two minimal length trees of 582 steps. These were then rerun with TBR on and MULPARS on to explore how many equally long trees were associated with these initial two trees. The search was terminated at 15700 trees with a length of L=581, consistency index of ci=0.151, and retention index of ri= 0.656. A strict consensus tree of this search was calculated as advocated by Anderberg & Tehler (1990). This tree, shown in Fig. 11, is poorly resolved and with 10 polytomies, with a major basal polytomy representing all of the Minors plus eight of the *Erica* species, the three species formerly in *Philippia*, the five species formerly in *Blaeria* and the single species formerly in *Ericinella*.

The above 15 700 trees were then used to calculate the appropriate weightings, based on the RI (not RC as used by Hennig86) to find characters that support the lower nodes on the tree (Table 11). With these weightings the above protocol was repeated and the search located 3906 trees of length=582, ci=0.151 and ri=0.849. The strict consensus tree of these numerous trees is a much more resolved tree (Fig.12), but still with seven polytomies present, though mainly at the higher levels.

The basic topologies of the two consensus trees are somewhat similar, but there are several changes in the placement of several taxa that are problematic in the consensus tree derived from the weighted analysis.

TABLE 10.—Characters and their weights derived from the weighted analysis by PAUP.

Char	Weight	Char	Weight	Char	Weight	Char	Weight	Char	Weight
1	0.111	11	0.470	21	0.277	31	0.333	41	0.640
2	1.000	12	0.538	22	0.000	32	0.250	42	0.457
3	0.600	13	0.750	23	0.444	33	0.800	43	0.714
4	0.511	14	0.214	24	0.600	34	0.711	44	0.586
5	0.758	15	0.421	25	0.260	35	0.740	45	0.550
6	0.740	16	0.857	26	0.795	36	1.000	46	0.744
7	0.857	17	0.400	27	0.677	37	0.716	47	0.625
8	0.790	18	0.634	28	0.315	38	0.773	48	0.666
9	0.950	19	0.860	29	0.810	39	0.745	49	0.562
10	0.935	20	0.500	30	0.769	40	0.777		

The main portion of the consensus tree contains in one clade all the Minors (60 species) that do not have the **RBr-Rbr** condition, and this clade is based on a mainly few-ovuled, indehiscent fruit and pollen in monads. A survey of the distribution of characters on the cladogram using the program CLADOS (Nixon 1993) shows that most branches are based on homoplastic synapomorphies, those with low consistency index values in Table 11. Some smaller clades at the tips of this main clade appear to be reasonably distinct and supportable, but others are totally inexplicable or, surprisingly, contain one or two species that are totally dissimilar phenetically.

In the strict consensus tree from the first, unweighted, PAUP analysis (Fig. 11) several, apparently strong, clades are apparent (see below):-

- In the basal polytomy clades A, B, C and D are all supported by homoplasies—A by the always secondary inflorescence and exserted stamens, B by an umbel-like inflorescence and four exserted anthers, C by muticous anthers, no nectaries and an enlarged stigma, D by the indehiscent fruit, monadinous pollen and single ovules. However, all these characters have subsequent reversals or parallelisms elsewhere on the cladogram.
- Clade C1 is defined by fully recaulescent bracteoles and therefore reduced calyx number. This character is only partially present in '*peltata*' which was shown to possess the *Erica/Philippia* overlap (Oliver 1988). *Bruckenthalia* is anomalous in having fully recaulescent bracteoles, but is the only taxon in the clade with the bract always placed on the rachis of the inflorescence (a**Br**). This character occurs again in the terminal clade J2. The subsequent clades (C2 and C3) share the character of fully recaulescent bract (R**Br**) with C2 having dehiscent fruits and C3 indehiscent fruits. Both of these characters are homoplastic (showing parallelisms).
- Clade D is a major clade supported by three homoplastic characters, namely indehiscent fruits, pollen in monads and single ovules. Indehiscent fruits and single ovules are convergences with clade C3, monads with clades A and B, but also with reversals higher up in the terminal taxa '*glabra*', '*totta*', '*cereris*' and '*arachnocalyx*' and in several of the higher taxa which revert back to two of more ovules.
- Clade E is consistent with my view of the possible relationships between the two taxa (see later under Discussion), but excludes the anomalous taxon '*perplexa*' in clade C3.
- Clade F consists of three taxa which I postulate being closely allied, but is supported by three homoplastic synapomorphies—four exserted anthers and similar thick sclerified testa, all of which occur as parallelisms in other clades elsewhere in the cladogram.
- Clade G contains four species with accrescent calyces but excludes the similar '*kammanassieae*', which is placed higher up in Clade I.
- Clade H contains an anomalous assemblage of species, many of which were formerly in the genera *Eremia* and *Grisebachia* (see discussion later regarding '*recurvifolia*'). They all have eight included stamens with geniculate filaments (as in many *Erica* species).
- Clade I contains an anomalous assemblage of species having a thin endocarp and slightly sclerified testa, features shared with several taxa in Clade C3. Most distinct in this clade is the subclade with '*cereris*' and '*arachnocalyx*', the only Minors with an erect, basal ovule in each locule (a feature also present in some species of *Erica*).
- Clade J contains the rest of the Minors, the species having more than three units per inflorescence and muticous anthers, although the latter character has reversals in a few terminal taxa.
- Clade J1 is defined by the presence of lateral sclereid bundles in the leaves, which is a reversal from the outgroup taxon *Daboecia*.
- Clade J2 is defined by the inflorescence being a raceme with an axial bract on the rachis (see Clade C1 above), most species lacking bracteoles and with a thin pericarp. Several of these

characters are homoplastic, the axial bract occurring in many *Erica* species (including *E. corifolia* in this data set) and in *Bruckenthalia* in Clade C1. The bracteoles in '*piquetbergensis*' and sometimes in '*glabella*' are reversals,

- Clade J3 is supported by the only non-homoplastic synapomorphy in the cladogram and indeed in the Ericeae, namely a 2-lobed corolla, which is the defining character for the genus *Sympieza*.

In the second PAUP consensus tree derived from the weighted analysis (Fig.12) there is far more resolution with fewer polytomies. The major basal polytomy of the first tree is now resolved into two major clades A & B.

Clade A is supported by three characters associated with wind pollination—lack of nectaries and anther appendages and with an enlarged stigma. Within the clade there is a weak reversal in a single species, '*amatolensis*', which is both wind- and insect-pollinated with small nectaries and a small but expanded stigma. However, both characters are independently present in seven species scattered in Clade C.

Clade C consisting of the majority of Minors is, as in the unweighted tree (Clade D), poorly supported by three characters. However, because of the inclusion of different species at the base of this group (see Fig. 12: 3 & 4), the characters are different—leaf-like calyx segments, exserted stamens and monadinous pollen grains. All these characters are homoplastic with reversals higher up the clade and parallelsims in Clade A.

Clade B is well supported by the **RBr-Rbr** calyx syndrome and is perhaps the most clear-cut clade in the tree (with no homoplasy). However, there are problems with the placement of some of the taxa (see below, note 2).

Clade D is supported by the inflorescence having more than three units and a leaf epidermis with oblate cells, both of which are homoplastic characters with reversals and convergences. It contains two subclades and shows more resolution than in the unweighted tree (Fig 11 Clade J2). However, it also includes some species of *Grisebachia* which were quite differently placed in the unweighted tree (Fig 11 Clade H).

Clade E is supported by three characters—a thin sclerified endocarp and testa and a thick leaf cuticle. As with the other clades mentioned above, these characters also have reversals and parallelisms.

Only two clades in the weighted tree are supported by unique non-homoplastic synapomorphies—Clade B (see above) and the small terminal group of four *Sympieza* species at Clade F with their 2-lobed corolla. The latter group was more prominently placed in the terminal polytomy of the unweighted tree (Fig. 11, Clade C2) (see above).

However, there is a problem with the placements of certain taxa that are quite different from those in the unweighted tree. These are undoubtedly due to the emphasis of certain characters by the weighting process. These changes are:-

- 1– '*jacksoniana*' is removed from its relationship with '*stokoeanthus*' (5), which in turn is now linked with '*bokkeveldia*', a most unlikely relationship that is quite unacceptable to me.

- 2– the two species of *Coilostigma*, '*zeyheriana*' and '*burchelliana*', are now regarded as part of the major clade characterised by the totally recaulescent bract and bracteoles, **RBr-Rbr,** due to the weighting of this feature, whereas in the unweighted cladogram they come out with '*quadrifida*' which does not possess this feature (see Discussion later).
- 3 & 4– the four *Erica* species (*nudiflora*, *chonantha*, *deliciosa* & *eriophoros*) are now separated from the five *Erica* species at the base of the cladogram, but still contain '*thamnoides*' (the monotypic *Thamnus*) embedded within them (4).
- 6– this is now a totally anomalous and inexplicable clade of species that are unlikely to be at all closely related. Their positions and relationships are not resolved in the unweighted tree.
- 7 & 8– '*anguliger*' is now parted from the group of species with an accrescent calyx (7).
- 9– '*recurvifolia*', an anomalous species in the Minors (see discussion below), is placed with the two closely related species, '*cereris*' and '*arachnocalyx*', in a clade with '*plumosa*' (*Grisebachia*) and '*vernicosa*' (*Acrostemon*), whereas in the unweighted tree it was included in the clade containing *Eremia* and the other species of *Grisebachia* (Fig 11 Clade H) (but see under Discussion below).
- 10– the position of the two species '*cereris*' and '*arachnocalyx*' is as unresolved in this tree as it is in the unweighted tree (see Discussion below).
- 11– '*totta*' and '*curvistyla*' are placed with the *Syndesmanthus/Acrostemon* clade based on several reversals and are quite unlike any of the other species phenetically.

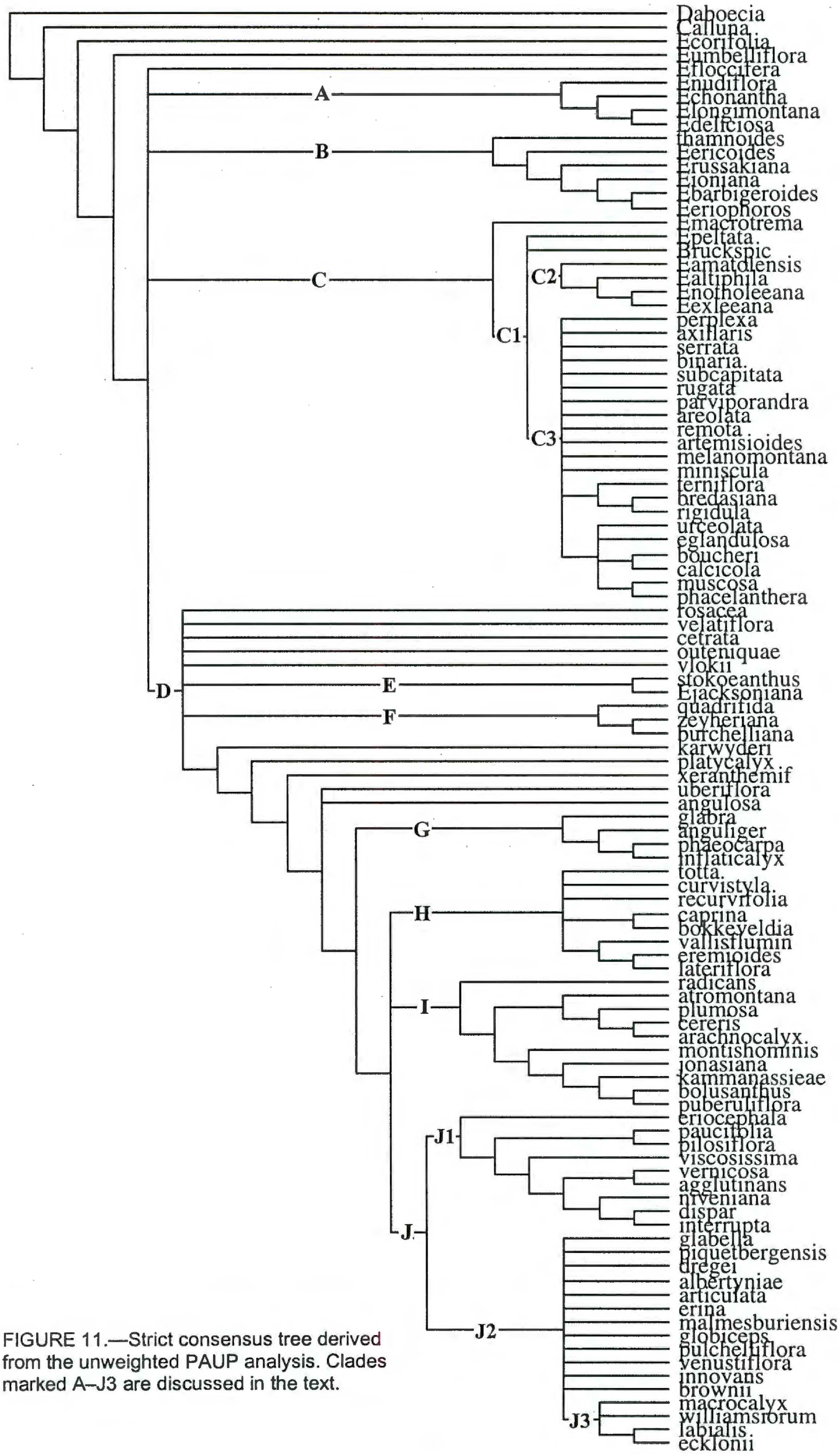

FIGURE 11.—Strict consensus tree derived from the unweighted PAUP analysis. Clades marked A–J3 are discussed in the text.

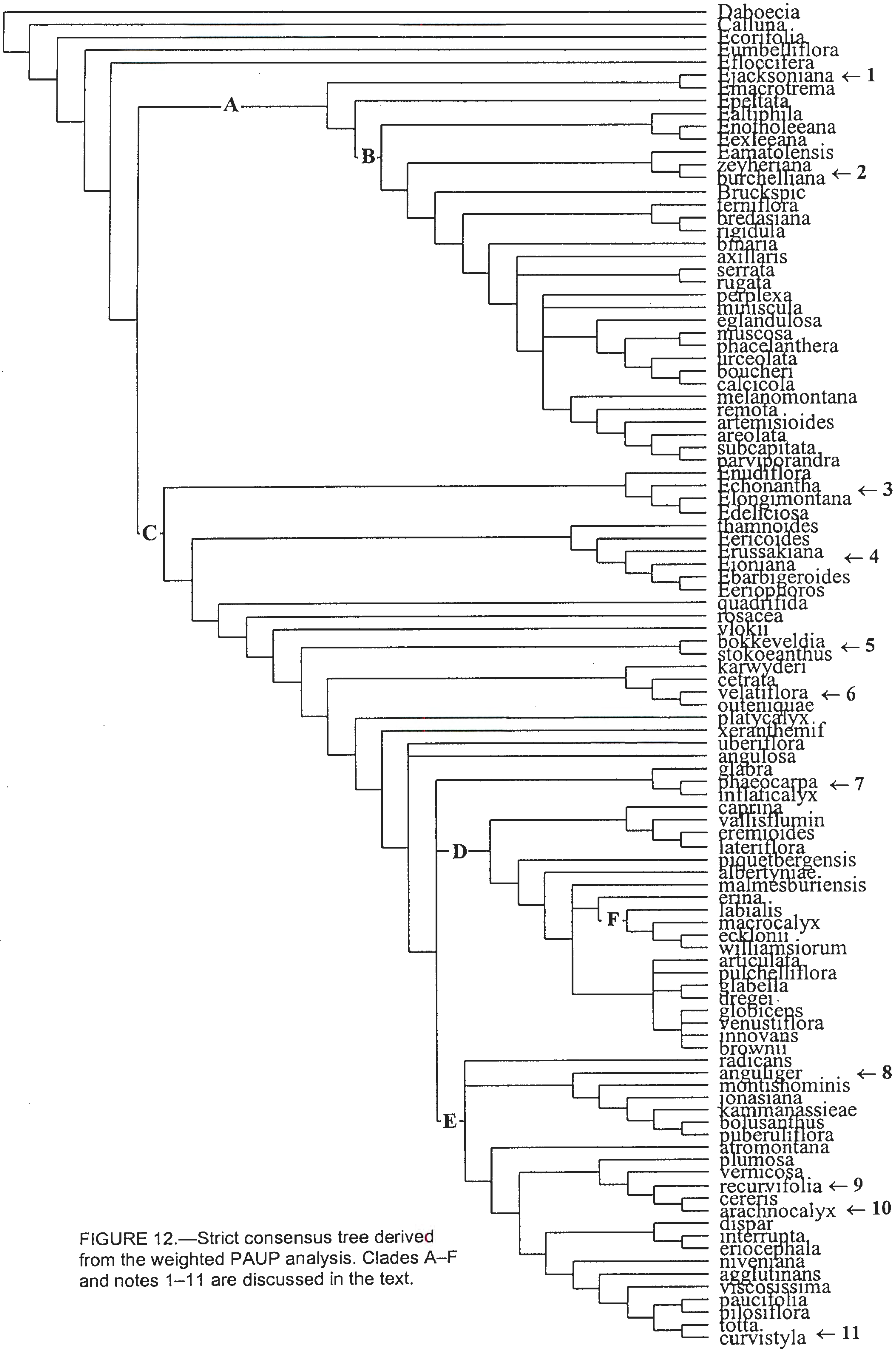

FIGURE 12.—Strict consensus tree derived from the weighted PAUP analysis. Clades A–F and notes 1–11 are discussed in the text.

3.4.2 ANALYSES 2

The analysis of the full data set using Hennig86 was unable to place *Calluna* in the outgroup despite the <outgroup> and <reroot> commands being applied. This is because of the anomaly of the 90 taxa boundary for multi-taxon outgroups. This analysis terminated at only 611 trees because of the memory constraints within the program. The strict consensus tree obtained was of length=623, ci=13 and ri=67 and is shown in Fig 13. The placement of *Calluna* deep within the *Erica* clade is perhaps because of the problem of homology assessment with regard to the inflorescence, bract and bracteoles (see Chapter 3.3, Chars 4–9); the characters were coded as unknown in the data-matrix. This step would perhaps explain the anomalies in the Hennig86 analysis, since the program would test for all the states present in the Ericeae.

A further analysis was run in which *Calluna* was excluded from the data set. This search was terminated at 617 trees of length=623, ci=13 and ri=67. The strict consensus tree contained two major basal polytomies and several minor ones among the terminal taxa. However in this case the position of several taxa was completely changed on the tree as occurred in the weighted tree using PAUP (Fig 12).

To overcome the problem with the multi-taxon outgroup a further analysis was run in which most species of *Erica* were excluded, thus reducing the data set down to 90 taxa. This allowed for *Calluna* to be placed in the outgroup with *Daboecia*. The search was limited to 714 trees of length=466, ci=18 and ri=64. The resultant strict consensus tree produced even larger major polytomies (Fig 14). This tree is poorly resolved but contains several terminal clades which agree with those produced by PAUP. The important aspects of this consensus tree are the separation of the former *Coilostigma* species from the rest of the species with fully recaulescent bract and bracteoles, the placement of the *Philippia* group deep within the R**Br**-R**br** clade, with the placement of '*stokoeanthus*', *Erica jacksoniana* and '*perplexa*' as basal to this major clade, and the monophyly of the '*Sympieza*' clade.

The Parsimony Jackknife program overcomes the memory constraints of DOS, can handle very large data sets and is much faster than any other program (Farris pers. com.). Three sets of 1000 replicates each were run with 36%, 15% & 5% of the characters deleted per jackknife replicate. The resultant consensus trees were highly unresolved with a major basal polytomy. The only tree showing some resolution was the tree based on the 5% deletion, which produced a basal separation of '*eriophoros*' and '*barbigeroides*' followed by a major polytomy of 66 taxa and 9 major terminal clades. The terminal portion of this polytomy is shown in Fig 15. Farris (pers. com.) noted on seeing the results that a significant increase in data would be required in order to produce better resolution for this number of taxa. Three of the clades with high support values are evident, '*zeyheriana*' & '*burchelliana*' at 98, '*cereris*' & '*arachnocalyx*' at 100, the *Philippia* group at 98 and the *Sympieza* group at 99. These are also present in the strict consensus trees produced by PAUP.

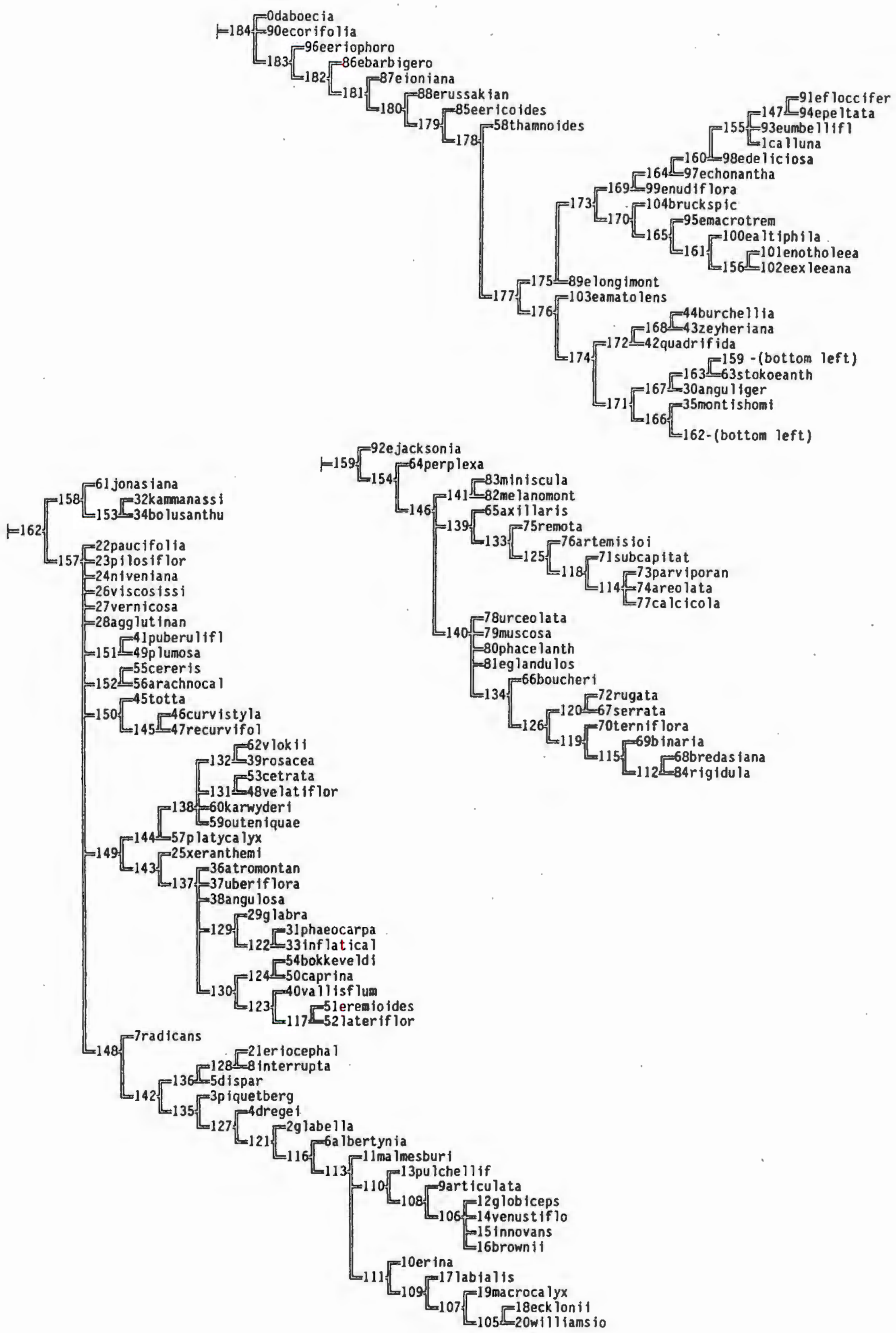

FIGURE 13.—Strict consensus tree derived from the Hennig86 analysis of the full data set of 104 taxa with *Daboecia* as the sole outgroup.

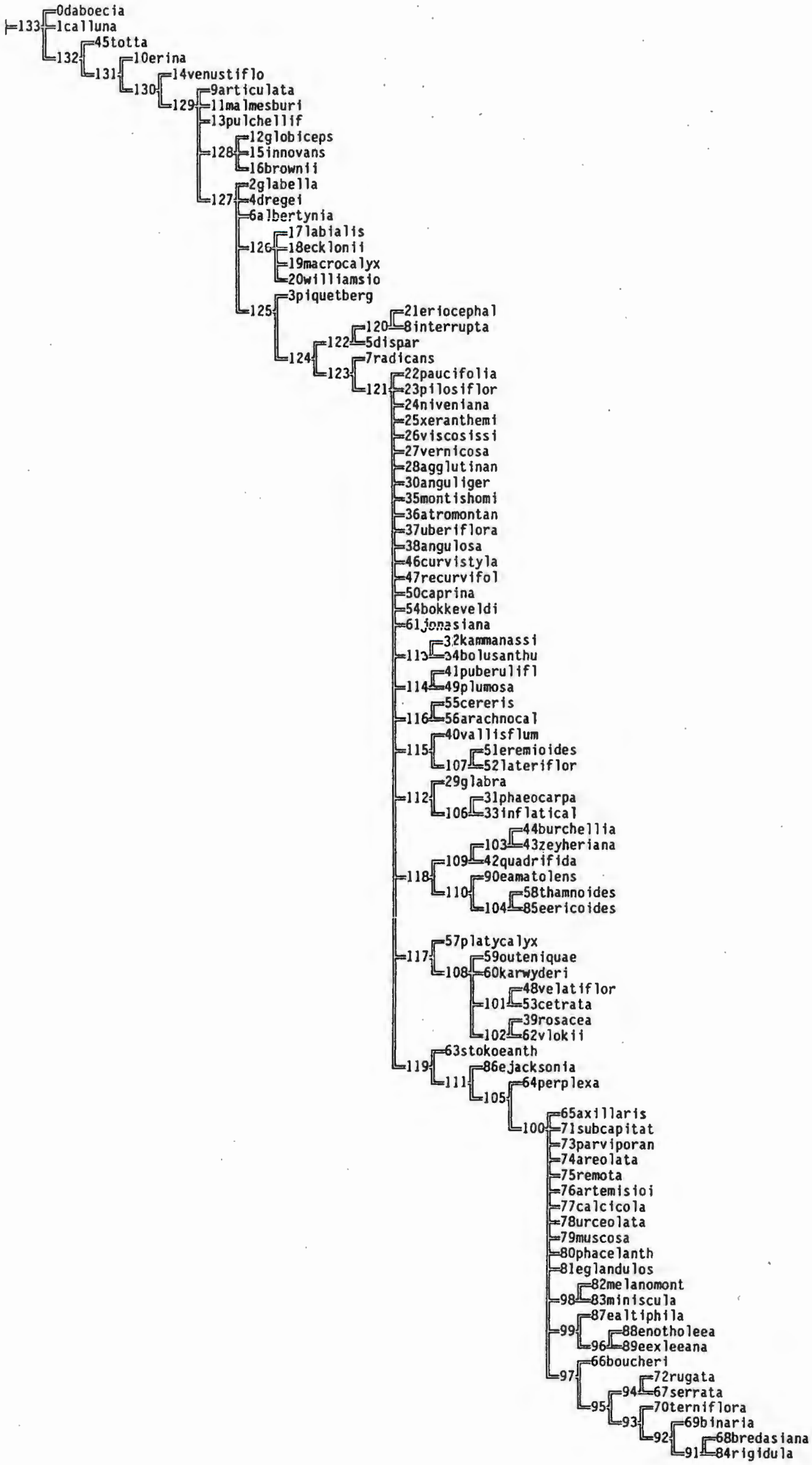

FIGURE 14.—Strict consensus tree derived from the Hennig86 analysis of the data set of 90 taxa with *Daboecia* and *Calluna* as the outgroup.

```
├─Ejacksoniana
├─Eumbelliflora
├─Epeltata
├─Emacrotrema
├─Echonantha
├─Edeliciosa
├─Enudiflora
├─Eamatolensis
├─Bruckspic
├68┬─Kammanassieae
│  └─Bolusanthus
├76┬─Bredasiana
│  └─Rigidula
├98┬─Zeyheriana
│  └─Burchelliana
├55┬─Phaeocarpa
│  └─Inflaticalyx
├100┬─Cereris
│   └─Arachnocalyx
├76┬─Dispar
│  └59┬─Interrupta
│     └─Eriocephala
├98┬─Ealtiphila
│  └100┬─Enotholeeana
│      └─Eexleeana
├70┬─Vallisflumin
│  └51┬─Eremioides
│     └─Lateriflora
└52┬─Glabella
   ├─Piquetbergensi
   ├─Dregei
   ├─Albertyniae
   ├─Articulata
   ├─Erina
   ├─Malmesburiensi
   ├─Pulchelliflora
   ├54┬─Globiceps
   │  ├─Venustiflora
   │  ├─Innovans
   │  └─Brownii
   └99┬─Macrocalyx
      ├─Williamsiorum
      └56┬─Labialis
         └─Ecklonii
```

FIGURE 15.—Output tree from the Parsimony Jackknife analysis showing only the terminal part of the major basal polytomy.

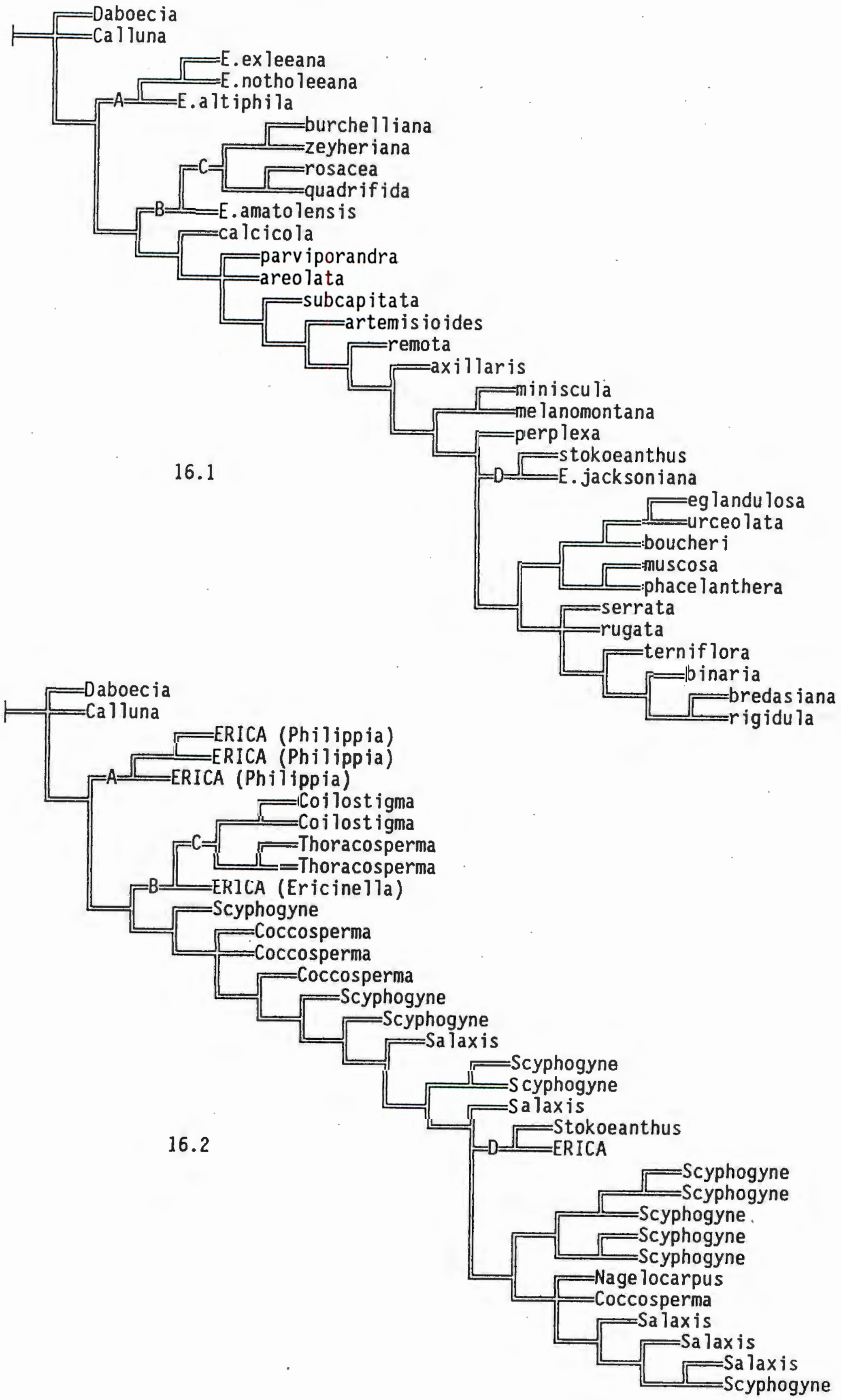

FIGURE 16.—Strict consensus tree derived from the Hennig86 analysis of the RBr-Rbr group of species and four additional species; 16.1 with specific epithets; 16.2 with generic names.

Meaningful analyses using Hennig86 were only possible with smaller samples of species extracted from the data set (Table 8). The implicit enumeration (ie*) option for examining smaller selections of taxa, even as low as 15, could not be employed due to time/memory constraints, analyses running interminably with no output. This is no doubt due to the high level of homoplasy in the study group. In contrast the heuristic searches using the options of multiple hennig <mh*> followed by the branch & bound algorithm <bb*> were found to work very quickly.

All initial runs using the above options produced multiple, equally parsimonious cladograms. In order to locate fewer, more resolved, trees the successive weighting procedure (xs w option) was applied (Farris 1969, Carpenter 1988). This calculates weights from the best fits to the most parsimonious trees using a rescaled consistency index. The weighting procedure is repeated on successively produced trees until the trees no longer change (Farris 1988).

Strict consensus trees were calculated using the 'nelsen' option since no single tree resulted from any of the analyses using the xs w option.

The group selected for the analyses using Hennig86 was the R**Br**-R**br** group identified by PAUP as being monophyletic (Fig. 11, Clade C1, Fig 12, Clade A) and Hennig86 (Fig. 13, Clade 154; Fig. 14, Clade 105) and clearly requiring additional resolution; the European *Bruckenthalia* was excluded from both because this species has the bract placed on the rachis (a**Br**). *Daboecia* and *Calluna* were retained as the outgroup. Also included in the analyses were several taxa, which, due to their phenetic similarities, are postulated to have possible alliances with some species within the R**Br**-R**br** group. This I postulated could help to resolve what I perceived to be problems in the group. The first set of species included was *Erica jacksoniana* (*Erica* s.str.), the monotypic *Stokoeanthus* [*E. stokoeanthus*], and an unusual undescribed species, '*perplexa*'. The second set consisted of the two species of *Coilostigma*, ['*burchelliana*' & '*zeyheriana*'] and two species of *Thoracosperma* ['*rosacea*' and '*quadrifida*']. This first set was not linked in either of the PAUP analyses but was placed basally to the R**Br**-R**br** clade in Hennig86 analyses.

The search found 6 trees of length=297 ci=51 and ri=71 after four successive weightings. The strict consensus tree is shown in Fig. 16.1. Here the three taxa formerly included in the genus *Philippia* (Oliver 1989) are separated off basally (Clade A) as the sister group to the rest of the taxa based on a single-layered epidermis and numerous sclereids in the vascular sheath of the midrib. Both of these synapomorphies are homoplastic with parallelisms appearing in '*rigidula*' at the bottom of Fig. 16.1, which is phenetically extremely similar to '*exleeana*' but differs mainly in the indehiscent fruit. Clade A is also supported by dehiscent fruits, but this feature appears again in '*amatolensis*', and by lateral secondary inflorescences, which appear again in several of the higher taxa as parallelisms.

Clade B is supported by a non-homoplastic synapomorphy of pollen in monads and Clade C by exserted anthers. Thus the '*zeyheriana/burchelliana*' group (*Coilostigma*) are placed in this analysis with '*quadrifida*' and '*rosacea*', but the latter fails to group with the others in all the other analyses. All four species are phenetically similar. In '*rosacea*' a single specimen (*Acocks 13708*) from the Hankey area in the Eastern Cape Province surprisingly showed several flowers that had the R**Br**-R**br** condition and therefore basically of the *Coilostigma* type, but which were not included in the current data set. In '*quadrifida*' there is a tendency towards wind pollination with a reduction in nectaries, slight enlargement of the stigma and sometimes loss of colour in the corolla—all characters present in the two species '*zeyheriana*' and '*burchelliana*'. The latter two species and '*quadrifida*' have dry berries with a very thin endocarp and thick testas whereas '*rosacea*' has a drupe with a hard thick endocarp and thin testa. The last species, '*rosacea'*, also differs from the rest of the species in this clade by having characters associated with insect pollination, namely nectaries and a simple truncate style.

The topology of the rest of this tree is well resolved apart from the single polytomy, no doubt caused by the relationships of '*perplexa*', '*stokoeanthus*' and '*jacksoniana*'. These species were better resolved in the larger Hennig86 analysis (Fig. 13, Clades 163, 159 & 154; Fig. 14, Clades 119, 11 & 105). Their placement confirms their close relationship especially with Clade D, which is present only in the unweighted PAUP analysis (Fig. 11 Clade E), (see Discussion later).

The placing of the two species '*melanomontana*' and '*miniscula'* together confirms their placing in the earlier Hennig86 analyses but not in the PAUP weighted analysis. In the PAUP unweighted analysis their position was unresolved in a large polytomy (Fig. 11 Clade C3).

The cladogram has numerous homoplasies supporting clades with, in some cases (e.g. stamen number), multiple reversals and forward changes involving a loss–gain–loss–gain series. The complex situation regarding relationships in this group of species is clearly shown in Fig 16.2 where generic names replace the specific epithets on the cladogram.

3.5 DISCUSSION

The consistency index has been a much-used method of estimating how well all of the character evidence in a given study fits a hypothesis of taxonomic relationships (Kluge & Farris 1969). The higher the consistency index the better the hypothesis of relationship is said to fit the evidence in the data set. Thus the most parsimonious hypothesis of relationships has the highest consistency index (Kluge 1989).

With the low values of the consistency indexes appearing in the analyses of the Ericeae, especially the ci=0.15 from the second PAUP analysis and ci=0.13 from Hennig86, there appears to be a high level of homoplasy in the Ericeae which fact does not offer much assistance in developing hypotheses on groups within the tribe (Tables 11 & 12).

Sanderson & Donoghue (1989) analyzed levels of homoplasy in a wide range of different cladistic studies of animal, plant, morphological and molecular data. This was prompted by numerous assertions in the literature about high levels of homoplasy and addressed the hypothesized relationship between homoplasy and the number of taxa, the number or characters and the taxonomic rank.

Their results indicate that as the number of taxa included in the analysis increases so the consistency index decreases. They also found that larger numbers of characters do not appear to be correlated with low ci values. Despite the failure of parsimony algorithms to identify the shortest trees in large data sets (and therefore possibly inflating the homoplasy value), they predict that the observed relationship between ci and the number of taxa would still hold when the sample of,

TABLE 11.—Character statistics for the unweighted PAUP analysis

Character	Minimum Steps	Tree Steps	Maximum Steps	CI	HI	RI	RC
1	2	10	11	0.200	0.800	0.111	0.022
2	1	1	1	1.000	0.000	0/0	0/0
3	2	9	17	0.222	0.778	0.533	0.119
4	2	24	45	0.083	0.917	0.488	0.041
5	3	18	65	0.167	0.833	0.758	0.126
6	3	18	57	0.167	0.833	0.722	0.120
7	4	11	53	0.364	0.636	0.857	0.312
8	1	10	44	0.100	0.900	0.791	0.079
9	2	4	42	0.500	0.500	0.950	0.475
10	3	6	34	0.500	0.500	0.903	0.452
11	1	10	18	0.100	0.900	0.471	0.047
12	1	8	14	0.125	0.875	0.462	0.058
13	1	2	5	0.500	0.500	0.750	0.375
14	2	13	16	0.154	0.846	0.214	0.033
15	2	13	21	0.154	0.846	0.421	0.065
16	2	3	9	0.667	0.333	0.857	0.571
17	2	17	27	0.118	0.882	0.400	0.047
18	3	19	44	0.158	0.842	0.610	0.096
19	1	8	51	0.125	0.875	0.860	0.108
20	2	6	10	0.333	0.667	0.500	0.167
21	1	14	19	0.071	0.929	0.278	0.020
22	2	5	5	0.400	0.600	0.000	0.000
23	1	6	10	0.167	0.833	0.444	0.074
24	1	14	31	0.071	0.929	0.567	0.040
25	2	20	25	0.100	0.900	0.217	0.022
26	1	10	45	0.100	0.900	0.795	0.080
27	3	22	62	0.136	0.864	0.678	0.092
28	1	14	20	0.071	0.929	0.316	0.023
29	1	8	38	0.125	0.875	0.811	0.101
30	2	8	28	0.250	0.750	0.769	0.192
31	1	3	4	0.333	0.667	0.333	0.111
32	2	5	6	0.400	0.600	0.250	0.100
33	1	4	16	0.250	0.750	0.800	0.200
34	2	17	54	0.118	0.882	0.712	0.084
35	2	9	29	0.222	0.778	0.741	0.165
36	1	1	2	1.000	0.000	1.000	1.000
37	2	18	55	0.111	0.889	0.698	0.078
38	2	16	55	0.125	0.875	0.736	0.092
39	2	17	61	0.118	0.882	0.746	0.088
40	3	10	30	0.300	0.700	0.741	0.222
41	1	12	26	0.083	0.917	0.560	0.047
42	2	23	37	0.087	0.913	0.400	0.035
43	2	12	37	0.167	0.833	0.714	0.119
44	1	21	47	0.048	0.952	0.565	0.027
45	1	11	21	0.091	0.909	0.500	0.045
46	2	15	49	0.133	0.867	0.723	0.096
47	2	22	50	0.091	0.909	0.583	0.053
48	2	22	56	0.091	0.909	0.630	0.057
49	1	8	17	0.125	0.875	0.562	0.070

phylogenetic studies is increased.

Sanderson & Donoghue provide a useful graph of ci versus the number of taxa and a formula which can be used to assess the degree of homoplasy in an analysis thus overcoming tendencies to overemphasize homoplasy. Unfortunately they state that their regression graph cannot be extended above about 60 taxa. They comment “the conclusion that homoplasy is extreme should not be based on the absolute value of ci, but on a significant deviation from the regression line”.

In the Ericeae analyses the ci calculated using their formula is –3.758 which is way below their lowest figure of –1.4 and the lowest point of their regression line at –1.3 for 70 taxa. The global ci of 0.15 derived from the unweighted PAUP analysis is very low but may be affected by a few very low values and the range of values for the individual characters. The distribution of ci values for each character is given in Table 11 with a summary of the highest values in Table 12. Despite what Sanderson & Donoghue say about the taxon limit, the above figure would indicate a high level of homoplasy in the tribe.

TABLE 12.—Characters with high consistency indexes (ci) in the range 0.25–0.66; the rest having low indexes in the range 0.04–0.22.

Character	CI
Bract recaulescence	0.36
Bracteole recaulescence	0.50
Calyx mery	0.50
Calyx accrescence	0.50
Corolla mery	0.66
Filament fusion	0.33
Filament indumentum	0.40
Ovule mery	0.25
Ovule position	0.33
Placenta position	0.40
Style length	0.25
Testa type	0.30

In the later Hennig86 analyses the number of taxa is reduced to 26 which falls well within the limits of the parameters of the analysis of Sanderson & Donoghue (1989). The ci derived from their formula comes to –0.18 which is rather far from the regression line for the number of taxa (–0.60). The actual ci of 0.51 lies well within the range of scattered points in their scatter-diagram, but is rather on the low side.

The most distinct division in the cladogram derived from the unweighted PAUP analysis is at Clade D (Fig. 11) which is part of the major basal polytomy and contains 62 species of the Minors. It is supported by indehiscent fruits, pollen in monads and a single ovule per locule. The remaining 22 species of Minors come out in one of the other clades in the polytomy (Clade C) and all possess the total recaulescence syndrome, **RBr-Rbr**. Unfortunately the three synapomorphies for Clade D are all homoplastic—indehiscent fruits and single ovules occurring in the other Minors (Clade C3); monads occurring in Clades A & B (non Minors); monads reverting to tetrads and indehiscent to dehiscent (or at least partially dehiscent) and ovules single to two and even six in several higher clades. This major clade is thus poorly supported.

The core set of Minors possessing the **RBr-Rbr** syndrome are reasonably well grouped together in all analyses with the exception of the two species of *Coilostigma*, '*zeyheriana*' and '*burchelliana*', which are either placed with the main group or well separated from them. The separation is supported by all the Hennig86 analyses and by the PAUP unweighted analysis. Only the weighted analysis of PAUP places them all together (Fig. 12, Clade B) and this can be ascribed to the excess weighting of the characters associated with this syndrome where Chars 9 & 10 in Table 11 have the highest weights of the analysis at 0.950 and 0.935 respectively.

The position of the three **RBr-Rbr** species formerly in *Philippia* relative to the rest of the Minors with this syndrome, varies in the analyses. Both PAUP analyses place them sister to the Minors in an unresolved polytomy. In the full Hennig86 analysis (Fig. 13) they are placed far from these Minors in a clade with the dehiscent fruited *Erica* species and *Bruckenthalia*. In the shortened data set of 90 taxa (Fig. 14, Clade 99) the philippias are nested within the Minors. This would require the hypothesis of a reversal from indehiscent and few-ovuled fruit back to the plesiomorphic dehiscent, multi-ovuled capsule, which seems highly unlikely. The position of the philippias basal to the Minors requires only forward steps in the evolution of the indehiscent fruits from the ancestral state—a more feasible hypothesis.

Bruckenthalia [*Erica spiculifolia*] appears nested with the **RBr-Rbr** clade in the PAUP unweighted analysis but with a mixture of capsular species in the full Hennig86 analysis (Fig. 13, Clade 170). In the PAUP weighted analysis it is placed between the *Philippia* and *Coilostigma* species and the rest of the **RBr-Rbr** Minors. This taxon does not possess a fully recaulescent bract (**RBr**) but does have fully recaulescent bracteoles (**Rbr**), the bract being on the main axis of the inflorescence (a**Br**). It is also not wind-pollinated according to the note on visitation by bees in Flora Europea (Webb *et al.* 1972). Its basal position would then require a hypothesis of reversal from **RBr** back to a**Br**. The species is clearly not related to the African **RBr-Rbr** group and I would postulate that the total recaulescence of the bracteoles is derived from the r**Br** condition present in all 21 European species of *Erica*—and represents convergent evolution.

The matter of wind-pollination adaptations, *i.e.*, lack of nectaries and enlargement of the stigma, has clearly held the **RBr-Rbr** group together but is not restricted to this group. These adaptations are also present in a number of scattered species that appear in the other major clade of Minors, species such as '*erina*', '*brownii*', '*cetrata*', '*velatiflora*', '*angulosa*' and '*stokoeanthus*'. This would lead to a hypothesis of multiple convergent evolution of wind pollination in these species. In my experience this hypothesis seems highly feasible since I know of several cases within *Erica s.str.* in which there is an evolutionary progression towards wind-pollination in totally unrelated groups of species, e.g. The *Erica imbricata-placentiflora-lasciva* complex and the single species, *Erica cristiflora*.

A problem in the PAUP analyses is the placing of '*perplexa*' with respect to several other species that are phenetically very similar, but do not appear to be cladistically closely related according to their positions in the cladograms resulting from the PAUP analyses (Figs 11 & 12). One of the species is the Minor, *Stokoeanthus chionophilus* (=*Erica stokoeanthus*). This is, however, resolved in the first two Hennig86 analyses with numerous taxa (Figs 13 & 14).

The species '*perplexa*' and '*stokoeanthus*' are both wind-pollinated species as evidenced by their shedding of pollen in the wild when disturbed coupled with their reduction in floral colour and increase in the size of their stigmas. The former was described by myself as a monotypic genus because of the formula having an unusual combination of **A4** $\mathbf{G}^{2}/_{2-6}$. The latter, an unusual new species, with its R**Br**-R**br** calyx syndrome should be placed in the genus *Salaxis* because of the floral formula—**A**8 $\mathbf{G}^{(2)3[-4]}/_{1}$. However it bears no resemblance to the other species in that genus. Both species occur in the mountains around the Elgin Basin, but in very restricted areas.

When dealing with the species of Ericaceae of the Elgin Basin I was struck by the similarity between *Erica jacksoniana*, *Stokoeanthus* and the new species in their growth form and vegetative characters. A detailed investigation of *E. jacksoniana* revealed an anomalous situation regarding the ovary which, according to the protologue (Baker 1969), had not been investigated but presumably just accepted as being the typical $\mathbf{G}^{4}/_{\infty}$ condition of *Erica*. The ovary has no crosswalls and thus consists of a single locule with six to nine ovules, $\mathbf{G}^{1}/_{6-9}$. This was confirmed in both herbarium and fresh material. Fruits were obtained and found to be unique for a species of *Erica*. The fruits, which have a thin papery pericarp, either did not dehisce or they split open only partially without shedding the mature seeds. The fruits remain on the plant for at least six months after the flowering period until the flowers are shed onto the ground, at which stage they are protected by the hardened calyx and basal part of the corolla.

A comparison of all the characters shows that the three species have a number of characters in common such as the willowy habit, plumose hairs on the branches (Fig. 2A & B), 3-nate leaves with terminal tuft of hairs, similar mostly indehiscent, papery fruits and seeds with shiny brown smooth testa. They could be postulated to have a closer cladistic relationship than is shown on the cladograms (Figs 11, 12). Thus the analyses on the R**Br**-R**br** group including these two additional species were run. The resultant consensus trees clearly show that the three species come out in close proximity on all trees, adding some weight to the postulated alliance mentioned above.

This case clearly shows a situation in which three species would have had to be treated as belonging to three separate genera under the old generic dispensation and therefore would have had their cladistic relationships completely obscured.

Several other cases of possible *a priori* species relationships came to light in the current taxonomic studies and need to be discussed in the light of the above statement: 1) *Erica recurvifolia* [*Eremia recurvata*]; 2) *Erica cetrata* [*Eremia peltata*]; 3) the *Arachnocalyx* group; and 4) *Erica vlokii* sp. nov.

Case 1). *Eremia recurvata* [=*Erica recurvifolia*]. The genus *Eremia* originally contained the single species *E. totta* with **A**8 and $\mathbf{G}^{4}/_{1}$. This circumscription was variously altered by subsequent authors to include a selection of species with $\mathbf{G}^{2}/_{1}$ but was restricted in *Flora Capensis* (Brown 1905/6) to just *Eremia totta*, this species and *Eremia brevifolia* (see below under *Erica velatiflora*), the latter two with $G^2/_1$. These three species bore no phenetic resemblance nor postulated relationship to one another other than that they were clearly members of the Ericeae. Within the expanded *Eremia* (Compton 1935 and Oliver 1976), only *Eremia curvistyla* showed some similarities to *Eremia recurvata* in the habit and the recurved leaves, but had petaloid sepals and a $G^1/_1$ ovary.

Eremia curvistyla is common in the Cold Bokkeveld and Cedarberg. In an examination of the species of *Erica* from the same area, a resemblance was seen to *Erica cederbergensis* and to a lesser extent to *E. aspalathoides*. They all possess similar looking flowers with leaflike hairy bract, bracteoles and sepals, similar recurved leaves, similar light brown to yellowish brown anthers and a partially erect to sprawling habit. Peculiar to *Eremia recurvata* are the delicate indehiscent fruit from a $G^2/_1$ ovary, the broadened filaments and pollen in monads; the two *Erica* species have dehiscent capsules with a $G^4/_{10-20}$ ovary.

In the PAUP analyses '*recurvifolia*' comes out in two different areas on the cladogram with two totally different sets of species (Fig. 11, Clade H; Fig. 12, Note 9) (see discussions above).

Case 2). *Eremia peltata* [=*Erica cetrata*] and *Eremia calycina* [=*Erica bokkeveldia*] are two species that were placed by Compton in *Eremia* based solely on the floral formula. Both species are probably closely related, but with the former being wind-pollinated and the latter insect-pollinated. They bear no obvious close phenetic similarities to the other species of *Eremia*. However, in the investigation of the species of *Erica* from the same areas in the Cold Bokkeveld a remarkable similarity was noted between *Eremia peltata* and *Erica macrotrema* var. *glabripedicellata* with its large slightly fused petaloid calyx, very similar anthers and wind-pollination syndrome (loss of nectaries and enlarged cyathiform stigma). Both species are resprouters, which is a rare occurrence in Cape Ericeae (Ojeda 1998). The latter species, however, has the dehiscent capsule formed from a $G^4/_6$ ovary, and pollen occurring in tetrads.

In the cladograms '*cetrata*' is placed basally in the large unresolved polytomy (Fig 11) and with an anomalous group of species (Fig. 12, Note 6; Fig.13, Clade 131).

Case 3). *Arachnocalyx* group: *Arachnocalyx cereris* [=*Erica cereris*] and *Arachnocalyx viscidus* [=*Erica arachnocalyx*]. Compton erected the monotypic genus *Arachnocalyx* based solely on the floral formula, but failed to see the relationship with the anomalous *Acrostemon viscidus* which I later transferred to *Arachnocalyx* (Oliver 1984). Both species were very similar with the unique character, at least for Minors, of basally attached, erect ovules. Both species have a variable number of stamens **A**4–8, pollen occurring in tetrads and a passively, sometimes only partially, dehiscent capsule from a $G^2/_1$ ovary. These ovary characters set them apart from all other Minors.

In the genus *Erica* there is a very rare species, *Erica greyi* Bolus, which is known only from the type collected in the 1860's from Ceres and a collection by Schlechter in 1896 from Kleinvlei in the Cold Bokkeveld. This species is very similar to *A. viscidus* in habit, has similar flowers with the same glands on the corolla lobes, approximate large glandular-hairy leaflike bract and bracteoles and sepals, similar anthers with small appendages but with hairy filaments. The hairy, emarginate ovary of $G^4/_{2(3)}$ has the ovules mostly in a one up and one down arrangement. Unfortunately no fruiting material of this very rare species is available for comparisons.

Several other species in the Cold Bokkeveld have similar habits and hairy flowers and have the ovary locules containing 3–6 ovules which are erect, e.g. *Erica senilis* with 6, *E. eriophoros* with 3(4) and *E. tegetiformis* with 6. On morphological similarities there is, in my opinion, a strong possibility that these two species of Minors are closely related to the above-mentioned *Erica* species and could therefore have a close phylogenetic link with them.

In the PAUP and Hennig86 cladograms these two species are well supported by two synapomorphies but are variously placed within the indehiscent fruited clade of Minors and as a result never come out near '*eriophoros*', which was included in the data set to allow for this possibility.

Case 4). *Erica vlokii* sp. nov. This new species was brought to my attention as a new species of *Eremia* based on the floral formula of **A**8 **G**$^{2}/_{1}$, but was quite unlike any other species in the genus and, coming from the eastern Little Karoo, was very far removed from the rest of the species in the Ceres area. It was also unlike any other Minor in the region.

Having looked at the genus *Erica* for other alliances I was struck by the similarity between the new species and *Erica umbelliflora* Benth., which also comes from the eastern mountains of the Little Karoo. The *Erica* species had most characters very similar to those of the new species—the petaloid bract, bracteoles and sepals, the dense retrorse hairs on the stems, and the same anthers. In the field the two species were found growing side-by-side near Meiringspoort. With the same habit they could be distinguished at first glance only by the pink flowers of the *Erica* and white flowers of the new species. The main difference lay in the ovary, **G**$^{4}/_{1}$ producing an indehiscent fruit with very thick endocarp and thin testa in the new species, and **G**$^{4}/_{4}$, with laterally arranged and appressed ovules producing a dehiscent capsule in *E. umbelliflora*.

As with the above three cases, it is postulated that *E. vlokii* is a recently derived indehiscent-fruited vicariad of a species of *Erica*, in this case *E. umbelliflora*, and not immediately related to any species of Minor.

In the PAUP cladograms '*vlokii*' is placed basally among the indehiscent-fruited Minors, again on the grounds of fruit and ovary characters, and not with the dehiscent-fruited '*umbelliflora*'. which was included in the data set for this specific reason.

The cladistic analyses using PAUP provided two consensus trees. The unweighted data in the first consensus tree fails to retrieve any meaningful pattern of phylogenetic relationships and the tree derived from successive weighting employed in the second analysis provides a more resolved tree, but results in the apparent misplacing of both individual species and species groups. The placing of these latter taxa is both surprising and difficult to justify. Even though the unweighted tree is less resolved it does provide more groupings, for many but not all of which one can suggest reasonable hypotheses of relationship.

A preliminary investigation of the value of data from atpß-rbcL spacers and ITS data for elucidating relationships within Ericeae is in progress (Mitchell & Kron, pers. comm.). They have looked at 17 species of Ericeae including six South African Minors, six South African and two

European species of *Erica*, and the monotypic European *Bruckenthalia*, *Calluna* and *Daboecia* using *Cassiope* as the outgroup. First results show all South African species forming a monophyletic group within *Erica*, with *Erica* species and the Minors mixed. *Bruckenthalia* is nested within *Erica*, and *Calluna* is the sister group to the rest of the Ericeae. It is hoped that many more taxa can be investigated to assist in the problems encountered with the morphological data.

3.6 CHARACTER EVOLUTION

With the cladograms containing so much homoplasy it is difficult to develop with any certainty a hypothesis on the evolution of many of the characters. With such a large percentage (63%) of multiple state characters in the data sets it was imperative to treat all of them as unordered to avoid any *a priori* assumptions of evolutionary trends.

There are, however, some clear indications of direction particularly with respect to the development of characters supporting the R**Br**-R**br** clade. Full recaulescence of the bract (and bracteoles), a character unique in the family and confined to the Ericeae, is clearly an evolutionary advancement on the plesiomorphic partially recaulescent condition. The analyses show that this character has arisen twice in the tribe, in the main R**Br**-R**br** group (Fig. 11, Clade C1) and in the two species of *Coilostigma*, '*zeyheriana*' and '*burchelliana*', (Fig. 11, Clade F). In '*peltata*' and in '*rosacea*' individual flowers may possess the R**Br**-R**br** condition.

This hypothesis of independent evolution is corroborated by the occurrence of total recaulescence as a feature diagnostic of the widespread *Philippia*. This was shown to be polyphyletic (Oliver 1988), with the R**Br**-R**br** syndrome evolving independently over a wide geographical range in Africa.

Coupled with the total recaulescence is the development of the wind-pollination syndrome and its associated characters—loss of nectaries, loss of attractive corolla colours and considerable increase in size of the style-stigma complex. Convergent evolution of this series of characters has occurred in several lines (see above under Discussion).

Throughout the Minors the change in character states in the various clades strongly suggests a reduction series in the mery of many of the characters—loss of bracteoles in the *Simocheilus/Syndesmanthus* group; reduction of calyx parts from the plesiomorphic four to two in the *Sympieza* group, four to three in the *Syndesmanthus* group, four to three in the *Scyphogyne* group; reduction in stamen number in many of the groups; reduction in the number of locules from four to one in many groups; and reduction in number of ovules from many to a single ovule. These reduction series occur in many groups, the latter two characters, however, not always evolving in concert. Similarly there are clear indications of a reduction from many-seeded, dehiscent fruits to few-seeded, indehiscent fruits. Again there appear to be numerous homoplasies including reversals, in all these characters; examples being the reversal from indehiscent to dehiscent fruits in *cereris* and *arachnocalyx*, the increase in ovule number from one to two in many taxa in clade D even up to six in *stokoeanthus*.

From my experience of the whole Ericeae I would postulate that character evolution has in many cases been driven by the evolution of pollination syndromes, namely from general insects to specialized insects (long tongued flies), to sunbirds, to wind. The first two cases occur in a number of groups of species within *Erica* s.str., but not within the Minors, whereas the proportion of wind-pollinated species in the Minors is much higher than in *Erica*. In *Erica* these syndromes have clearly evolved within several single-species complexes.

With *Daboecia* being monotypic its position as the sole outgroup to a large and highly diverse ingroup presents problems in relation to the polarity of characters. As an example I refer to one character in particular, the testa type. *Daboecia* has what Stevens (1971) regarded as a unique feature in the family—extended finger-like testa cells. This in itself would create problems within the ingroup in the current study in which this testa-type does not occur, whereas the common alveolate type is widespread here and in the rest of the family. However, I have recorded identical testa cells in about 23 species of Cape *Erica* not included in this study—20 falling into one section and the three others scattered among different sections. This would require the assumption of reversals in character evolution to explain these occurrences. The inclusion of *Calluna* to increase the size of the outgroup is problematic because of primary homology statements concerning six characters in the inflorescence, bract and bracteoles already discussed under character assessment (Chars 4–9).

Character evolution within the Ericeae is an intricate and variable web of processes that cannot easily be understood and explained with the current set of data and methods of analysis. Clearly there is room for considerable improvement in searching for new characters and assessing the situation from different analytical angles. The adoption of a wider outgroup including some members of the phyllodocoid clade or even rhododendroid clade (sensu Kron 1997) could possibly help to resolve the problems in future analyses. The difficulty with that approach at present is the lack of comparable data sets for the outgroups.

Chapter 4

PHYTOGEOGRAPHY

The tribe Ericeae is widespread but with a distribution confined to a north/south range covering Africa and Europe (Oliver 1989, 1991). *Erica* itself covers the whole range of the tribe from the Cape of Good Hope to Norwegian Lapland. Three of the genera are confined to the northern hemisphere—the monotypic *Calluna*, *Daboecia* and *Bruckenthalia* [=*Erica spiculifolia*]. The remainder of the tribe is African in distribution with the capsular species belonging to *Erica* [including *Philippia*, *Blaeria* and *Ericinella*] being pan-African and spreading into Madagascar and the Mascarenes. The main concentration of species of this genus is in the Cape Floristic Region of southern Africa where 95% of the species occur with a 93% level of endemism (Oliver 1994).

The 83 species of Minors, all with the indehiscent or partially dehiscent fruits, that are treated in this study are confined to the area between Cape Town and Port Elizabeth, the main area of the Cape Floristic Region (Goldblatt 1978, Taylor 1978, Oliver *et al.* 1983) (Fig. 17). As with most typical Cape taxa—*Erica s.str.*, Proteaceae, Restionaceae, Diosmeae (Rutaceae), two of the endemic families, Bruniaceae and Penaeaceae, *Muraltia* (Polygalaceae) and *Aspalathus* (Fabaceae) (Oliver *et al.* 1983), the pattern of species richness in the Minors follows the same L-shape centred on the Kogelberg/Grabouw area and radiating westwards to the Cape Peninsula and northwards along the main mountain ranges towards the Cedarberg and eastwards along the coastal and inland mountain ranges to Port Elizabeth with a reduction in numbers in both directions. The main mountain ranges are composed of quartzitic sandstone of the Table Mountain and Witteberg Groups and are areas with considerably higher rainfall than the surrounding flats.

The highest figures for the Minors of 16–18 species per grid cell occurs in the Kogelberg to Hermanus area where some 200 species of *Erica* with dehiscent capsules occur in the same grid cells. Several of the species are rather widespread, e.g. *E. anguliger*, *E. muscosa* and *E. rosacea*, but most are rather restricted to particular areas. The polymorphic species, *E. rigidula*, is unusual in being widespread in the western part of the Cape from Bredasdorp in the south to the Kamiesberg in Namaqualand, the only Minor to reach that area (five capsular *Erica* spp. have also been recorded there). *E. rigidula* is a typical wind-pollinated species with small, colourless flowers having an enlarged stigma, and no nectaries coupled with **RBr-Rbr** and therefore is evolutionarily quite advanced.

One area of particular interest is the Agulhas plain (in the region of 36°S 20°E) where several grid cells with scores of 12 and 13 species are recorded. Proportionally this figure is much higher in the Minors than in *Erica* s.str. This region consists of low sandstone hills and sandy plains with a coastal fringe of calcareous hills and ridges, and is recorded as being of recent origin with much of it having been submerged under the sea during Quarternary times (Hendey 1983). The Minors occurring on these plains mostly have highly derived formulae—**br0 K3 C3 A3** $\mathbf{G}^{1}/_{1}$, and therefore likely the most recently evolved.

Most of the Minors are associated with the quartzitic substrate of the Table Mountain group and inland Witteberg group of the Cape Supergroup. They grow either on stony/rocky slopes or sandy

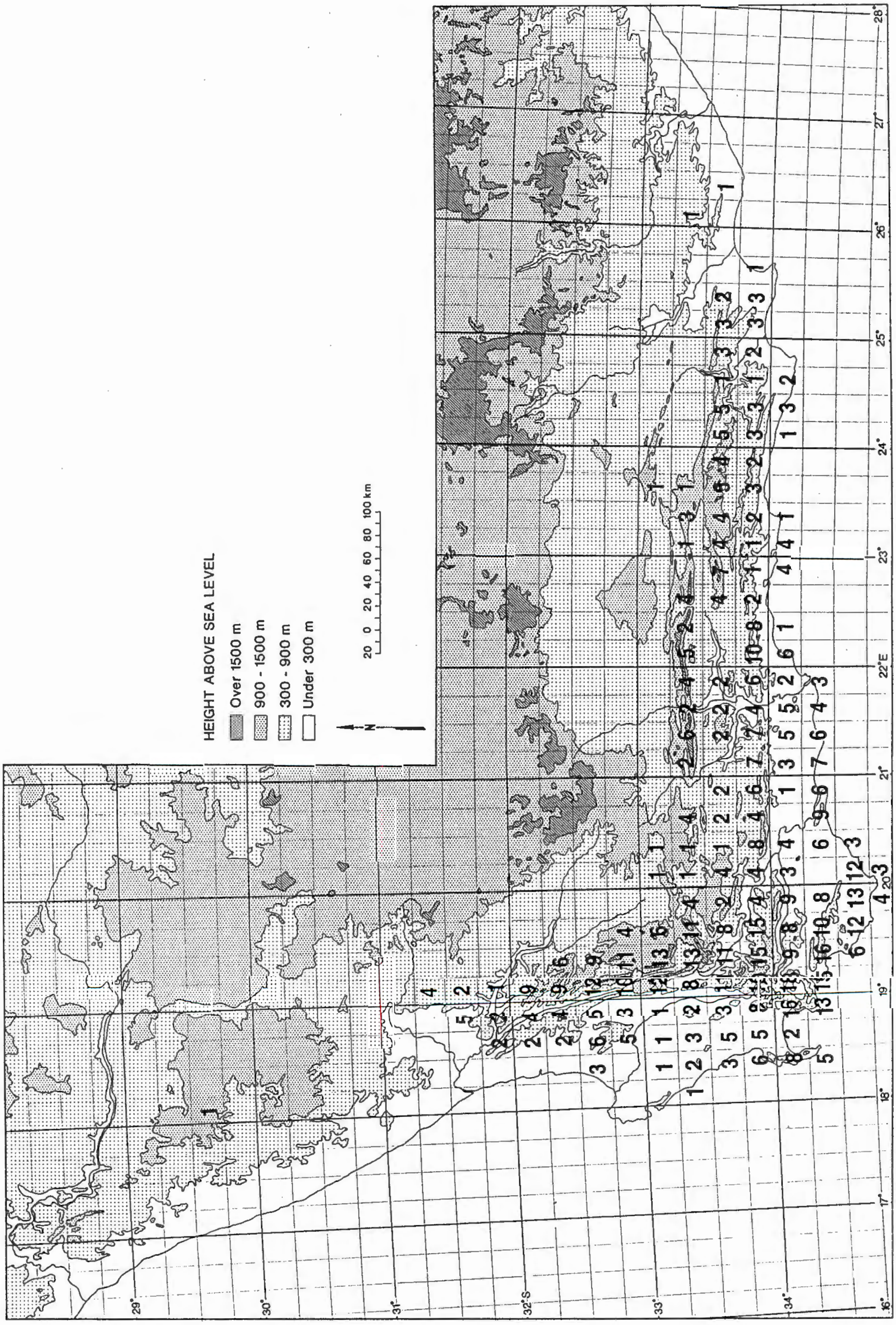

FIGURE 17.—Distribution of the species of Minor genera of the Ericeae in the Cape Floristic Region showing the number of species recorded per ¼ x ¼ degree block (ca.14 x 17km).

places on the mountains or open plains. None is known to occur exclusively on shales of the Malmesbury Supergroup or Bokkeveld Series in the Cape Supergroup, but they may perhaps be associated with the shalebands occurring in the sandstone, and which are now overlain by sandstone talus. Only 17 species are confined to the high altitude summits of peaks and ridges in the mountain ranges, and only three (*Erica urceolata, E. benthamiana* and *E. melanomontana*) are associated with cool, moist, upper south-facing slopes. Some of the Minors (*Erica calcicola* and *E. radicans*) on the southern coastal plains are associated with calcareous deposits. The vegetation is Macchia in the mountains and Coastal Macchia on the coastal plains according the Acocks' veld types (Acocks 1953) or the more modern classification of Mountain Fynbos (Wet, Mesic or Dry) and Lowland Fynbos (Sand Plain Lowland, Elim Lowland and Limestone Lowland) (Moll et al. 1984). On the west coast the single species, *Erica plumosa*, occurs wherever Sand Plain Lowland Fynbos is located. The 14 species on the southern coastal plains occur in the Sand Plain Lowland Fynbos associated with acid sands or in the Limestone Lowland Fynbos on calcareous outcrops or sands. A single species, *Erica brownii*, is associated with the laterite soils of the Elim Lowland Fynbos on the Agulhas plains; it is wind-pollinated.

The Minor, *Erica muscosa*, is one of the most common Ericeae in the Cape Floral Region, in places being dominant over whole mountain slopes, It is wind-pollinated with very small flowers that are not easily seen with the naked eye. The species is almost, apart from a single population on a peak in the Cape Peninsula, as dominant as the most common capsular *Erica*, *E. hispidula*, which is also wind-pollinated but has no total recaulescence of bract and bracteoles except for a single population on a peak in the Cape Peninsula. *E. labialis* is the only showy (pink-flowered) Minor that is abundant over large areas of mountain slopes in the Hermanus to Hottentots-Holland region—it is pollinated by bees.

A statistical analysis of the distributions was performed using an unweighted pair group average (UPGMA) method with Sorenson's coefficient of similarity to assess areas of speciation and find floristic zones (Kovach 1998). The resultant dendrogram is shown in Fig. 18. From this dendrogram five clear groupings of species are discernable and these have been plotted on the map in Fig. 19:–

1) a northwestern group occurring from the Niewoudtville escarpment down through the Cedarberg and Cold Bokkeveld to the plains and hills west of the main mountain ranges with a single species extending as far north as the Kamiesberg in Namaqualand;
2) a central southwestern group on the high mountains extending from the Ceres-/Tulbagh/Worcester area southwards to Kogelberg, Caledon and Hermanus;
3) a Peninsula group linking up with the western Bredasdorp-Agulhas plain;
4) a southern mixed group with minor groupings from the Bredasdorp flats, the southern coastal flats, the Langeberg, and the Little Karoo Mtns and Swartberg;
5) an eastern group occurring on the Outeniqua-Tzitzikama-Kammanassie-Kouga Mountains eastwards to the Vanstadens Mountains and Port Elizabeth flats with a few eastern outliers of a single species (*E. zeyheriana*) in the Albany District.

Another analysis, but using percentage similarity, gave almost the same results as above.

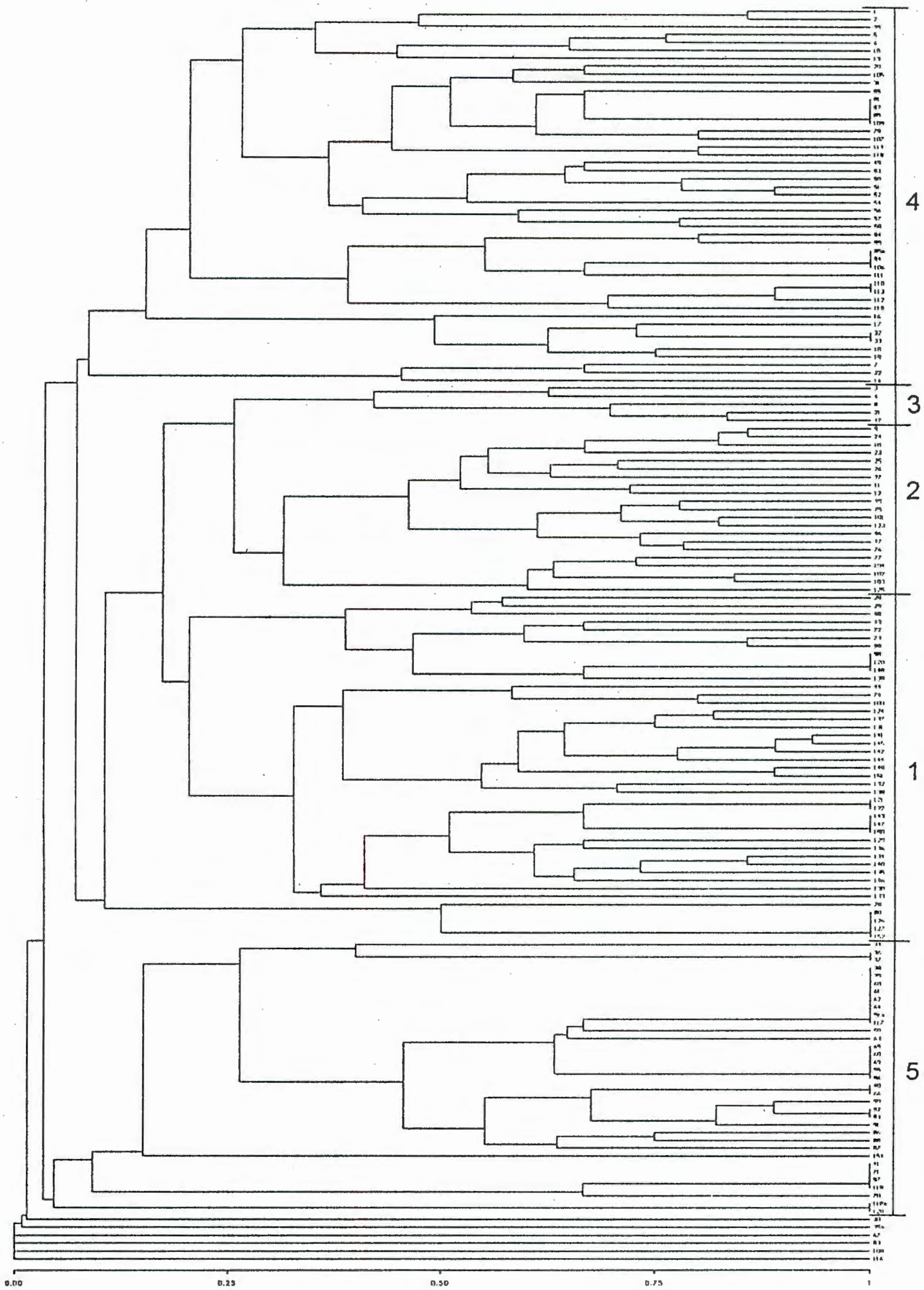

FIGURE 18.—UPGMA cluster analysis of the species distributions with the major phytogeographical groups highlighted and numbered as in the text (very small numbers at ends of branches refer to quarter-degree grid locks).

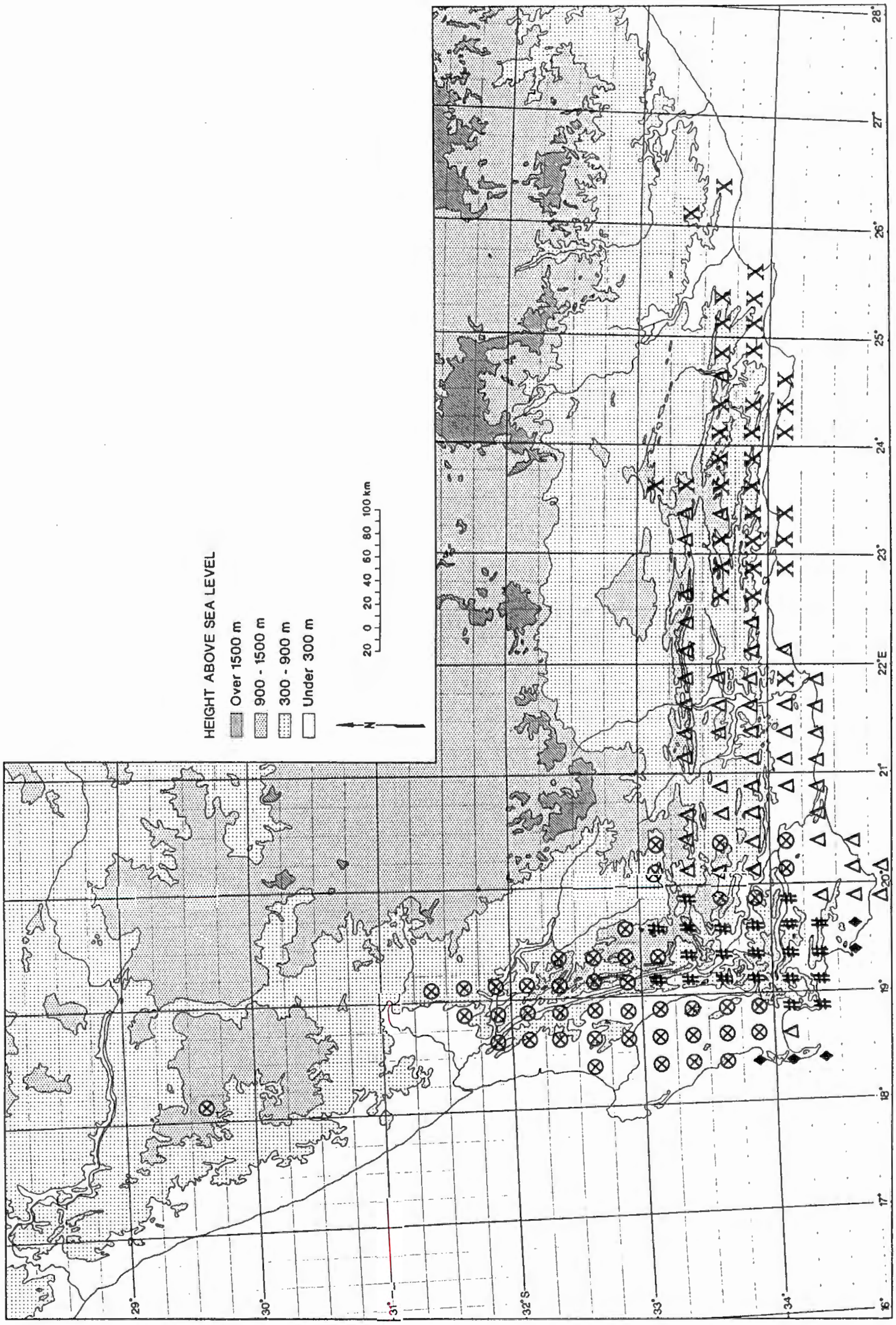

FIGURE 19.—Map of the Cape Floristic Region showing the major phytogeographical groups of species of the Minor genera identified by UPGMA cluster analysis; ⊗=northwestern group 1; #=central southwestern group 2; ♦=Peninsula group 3; Δ=southern group 4; X=eastern group 5 (group numbers as in the text).

These groups coincide to a major degree with the phytogeographical centres that were defined following a computer analysis of the distribution data of 1810 species in the Cape Floral Region (Oliver *et al.* 1983), which included, among others, all Ericaceae in the region. In that analysis the northern group was split into a montane and a western plains group, mainly because there were more species in the sample, and the southern group that we adopted was a very broad one encompassing the southern, central and eastern mountains. In the Minors the eastern group of species comes out clearly but there is a mixed array of patterns in the group 4 above with a slight indication of discrete groups in the Langeberg.

Two significant links in this analysis are those between the Agulhas plain in the Bredasdorp District and the Cape Flats and Cape Peninsula to the west. Rourke (1972) found almost the same link in *Leucospermum* (Proteaceae), which he hypothesized could be explained by coastline regression in the Middle Pleistocene, thus providing a lowland link, now inundated, between the two areas.

A biogeographical study (Morrone & Crisci 1995; Kurzweil *et al.* 1991) was not possible due to the lack of any resolved and well-supported phylogeny of *Erica s. lat.* However, a discussion of the distribution of the tribe in relation to morphological characters in it provides some interesting pointers to evolution of the tribe.

The 21 species of *Erica* in Europe are morphologically rather uniform, and show little variation in the floral formula. *Erica spiculifolia* (*Bruckenthalia*) is the only species with full recaulescence of the bracteoles (as is the case with *Daboecia*). Two species formerly in the genus *Pentapera* have retained or perhaps reverted to the ancestral pentamery of the subfamily. *Calluna vulgaris*, the most widespread and common species, shows no important morphological variations other than the numerous chance aberrations selected for horticultural purposes (Beijerinck 1940).

In tropical Africa several lines of evolution have occurred and are widely distributed. Firstly there is a reduction from **A**8 to **A**4 in the species formerly in *Blaeria* and *Ericinella* and, together with corolla mery, in several species of *Philippia.* Taxa with these reduced characters are spread from West to East Africa and down to the Cape. Species with total recaulescence of the bract and bracteoles occur across the continent—indeed more species, all those formerly in *Philippia* and *Ericinella*, have this condition than not. The 46 species in Madagascar, formerly in *Philippia* (Dorr & Oliver 1999 in press), all have **RBr-Rbr** and are wind-pollinated but with only a few having reduction in number of parts of the flower. All the species in Europe, tropical Africa and Madagascar have a dehiscent, multi-ovulate capsule.

The main group of Minors containing the more derived species are all restricted to the Cape Floral Region with only two species having a few localities just outside of this region, *E. rigidula* extending into the Kamiesberg of Namaqualand and *E. zeyheriana* extending to Alexandria in the east (Fig. 20). In this region an evolutionary 'explosion" has resulted in the large number of species of Ericeae (±740) with 83 of them evolving through a reduction series in mery of all floral parts, total recaulescence of the bract and bracteole, or a loss of bracteoles, and from dehiscent to partially dehiscent to indehiscent fruits. Total recaulescence here is postulated to have occurred independently from that in the rest of Africa as hypothesized in the polyphyletic origins of the former genus *Philippia* (Oliver 1988). Similarly the reduction in mery in the Cape is postulated to have occurred independently from that in tropical Africa (see Character Evolution above). Significantly, most reduction in mery has occurred in species found on the Agulhas Plain which is a geologically recent habitat (Hendey 1983).

FIGURE 20.—Strict concensus tree derived from the unweighted PAUP analysis with generic names in place of the species epithets (each separate occurrence of a genus numbered, • for a single occurrence, ?? for a single species of unknown genus).

Chapter 5

CONCLUSIONS

The delimitation of the species of the Minor genera of the Ericeae was made more difficult because of the great variability within certain groups. In most cases a conservative approach to species delimitation has been adopted, with several complexes being reduced to a single species—the *Grisebachia ciliaris/plumosa* complex from 13 to one species [*Erica plumosa*]; the genus *Anomalanthus* from 12 to one species [*Erica anguliger*]; the *Simocheilus glabellus* complex from seven to one species [*Erica glabella*]. Despite this variability and reduction, other collections constitute new species, most of them very distinct and some of them rather isolated in their postulated alliances. Thus the overall number of species in the Minors has been reduced from 123 to 83 including the 15 new species. These are listed in the taxonomic treatment together with keys to the species and line drawings of each species.

With the problems of species delimitation came the problems of assigning the species to their proper genera. Several of the new species lacked the characters of any current genera, and they did not show even phenetic similarities to any known species among the Minors. This was also true of several of the described species that were placed in apparent 'dustbin' genera such as *Eremia*. There were also cases where species bridged the boundaries between genera (e.g. *E. glabella*, *E. radicans* and *E. bolusanthus*).

The cladistic analysis was undertaken to assess the currently accepted genera and to find any well supported monophyletic groups. The first stage in the process was the selection of characters and delimitation of character states. This proved problematic due to the amount of variability in and between the 83 species and to the requirement of using discretely delimited states. Eventually 49 characters were selected for the analyses.

The cladograms that resulted from the several analyses run had consistency indexes with very low values compared to those published by Sanderson & Donoghue (1989). This clearly confirmed the very high level of homoplasy in the morphological data set representing the Minors.

A monophyletic group of species (Fig. 12, Clade A) diagnosed by the synapomorphies of totally recaulescent bract and bracteoles is apparent in the strict consensus tree derived from the weighted PAUP analysis. However, the unweighted PAUP analysis and smaller analyses run with a selection of species using Hennig86 suggested that this group was not completely stable, with three species (the two species of *Coilostigma* and '*perplexa*') being more closely allied to species outside of the clade that did not have the totally recaulescent condition.

There are other large monophyletic clades supported by unique synapomorphies. The only clades supported by non-homoplastic synapomorphies were those at a higher level of the *Sympieza* group of four species, based on the 2-lobed corolla, and the *Arachnocalyx* group of two species with basal erect ovules. Both of these groups are nested within a large set of other poorly defined clades. The species of *Erica* came out in several separate clades, one of which contained the monotypic genus *Thamnus* ('*thamnoides*') nested within it. All these other clades are supported only by homoplastic synapomorphies, i.e., parallelisms and/or reversals.

The only character separating the Minors from *Erica* s.str. would be the dehiscence of the fruit—dehiscent in *Erica* and indehiscent in the Minors. Partial/incomplete, passive dehiscence occurs in a few unrelated Minors and in the anomalous *Erica jacksoniana*. However in the cladistic analysis the bulk of the Minors is divided into two major clades, one of which contains the dehiscent-fruited *Erica* species. Dehiscence is therefore a homoplastic character in the Ericeae.

Phylogenetic relationships within Ericeae are not resolved in these analyses. Many trees are poorly resolved, and where there is greater resolution of relationships, when genera are plotted onto the consensus tree obtained from the unweighted PAUP analysis (Fig. 22) and Hennig86 analysis (Fig. 16.2) for the smaller data set, there is no clear pattern, with even small genera being para- or polyphyletic. Character analysis has shown several postulated lines of evolution in the reduction of mery and the phyletic fusion of these parts (recaulescence). However, these characters are not uniquely grouped nor confined to individual clades but rather randomly scattered throughout the whole cladogram including the clade with the totally recaulescent bract. The main problem in the cladogram revolves around the anomalous group defined by an indehiscent or partially dehiscent fruit—the bulk of the species of the Minor genera.

From the poorly resolved results of the cladistic analysis I would postulate that:-

1. the Minor genera are groups of species, some large, some consisting of only a single species, that have evolved from different points within the genus *Erica s. str.* and likely at different geological times;
2. the major evolution of characters, and therefore taxa, within the Ericeae in the Cape Region has occurred in a very restricted area compared to the extensive range of the whole tribe.
3. The monophyly of only two small genera, *Sympieza* and *Arachnocalyx*, is supported, but these are embedded within a heterogeneous assemblage of other species;
4. several of the Minor genera are polyphyletic in origin;
5. *Erica* itself is a paraphyletic genus.
6. There are no strongly supported groups of species that can be accorded generic rank.
7. there is therefore no justification for retaining any of the Minor genera.

Consequently all 23 Minor genera of Ericeae are reduced to synonymy under *Erica*, thus leaving the tribe with the megagenus *Erica*, with its 860 species, and the monotypic *Daboecia* and *Calluna*.

This will allow future research on the phylogenetic relationships and evolution within Ericeae using additional morphological data and also molecular data to proceed unhindered by the problems of having to cope with an ever-changing nomenclature.

The provisional nomenclatural changes necessitated, are given in the following taxonomic treatment of the 83 species of *Erica* that used to be placed in the Minors.

Chapter 6
TAXONOMIC TREATMENT

6.1 Introductory remarks

The proposed reduction of all the Minor genera of the tribe Ericeae, other than the monotypic European genera, *Daboecia* and *Calluna*, to synonymy under *Erica* is presented in this treatment. The 83 species recognized in the revision of the genera are included.

The phylogeny of the Ericeae is unfortunately still in an unresolved state with no clear indications of any natural groups of species. With the reduction of the capsular genera, *Philippia*, *Blaeria* and *Ericinella*, to synonymy under *Erica* in earlier papers (Oliver 1988, 1993, 1994) the Minors were held together, but as an unnatural group, based on the possession of an indehiscent or partially dehiscent fruit and mostly two or one ovule per locule. The taxonomic treatment below includes all these species. I have included the single species, *Erica jacksoniana*, because of its indehiscent fruit, which is anomalous for *Erica* s.str.

The species have been informally grouped according to my perceptions of their alliances. These groups will be corroborated or changed when additional data becomes available in the future, especially from DNA analyses.

The proposed names used here should be regarded as preliminary. The full taxonomic treatment formalizing the nomenclature is being prepared for publication in Contributions from the Bolus Herbarium that will be published in 1999. Full descriptions, and discussions, distribution maps, and full references to the taxonomic literature are to be found there and are omitted below. The basic nomenclature and line drawings of all species have been included to serve as a reference for the main text.

6.2 New circumscription of genus *Erica*

Erica L.

Erica L., Species plantarum 1: 352 (1753) nom. conserv. *et auct. mult.*; Salisb.: 323 (1802); Benth.: 613 (1839); Drude: 58 (1889); Guthrie & Bolus: 4 (1905); E.Phillips: 459 (1926); Alm & Fries: 1 (1927); T.M.Salter: 625 (1950); E.Phillips: 559 (1951); Pic.Serm. & Heiniger: 11 (1953); Dulfer: 25 (1965); D.A.Webb & Rix: 5 (1972); E.G.H.Oliv.: 431 (1975); R.Ross: 163 (1983).

Blaeria L., Sp. pl. 1: 112 (1753); Klotzsch: 656 (1833) & 221 (1838); Benth.: 697 (1839); N.E.Br.: 319 (1905); Alm & Fries: 231 (1924); E.Phillips: 460 (1926); T.M.Salter: 658 (1950); E.Phillips p.p.: 560 (1951); Pic.Serm. & Heinger: 36 (1953); Letouzey: 191 (1971); E.G.H.Oliv.: 432 (1975); R.Ross: 170 (1983).

Salaxis Salisb. in Trans. Linn. Soc. London 6: 317 (1802); Benth. p.p.: 711 (1839); N.E.Br.: 401 (1906); E.Phillips: 464 (1926); T.M.Salter: 661 (1950); E.Phillips p.p.: 561 (1951); E.G.H.Oliv.: 438 (1975).

Sympieza Licht. ex Roem. & Schult., Syst. Veg. 3: 171 (1818); Benth. p.p.: 705 (1839); N.E.Br.: 392 (1906); E.Phillips: 463 (1926); T.M.Salter: 659 (1950); E.Phillips: 560 (1951); E.G.H.Oliv.: 436 (1975).

Scyphogyne Decaisne, Voyage de la Coquille, Atlas t.54 (1829); Benth.: 709 (1839); N.E.Br.: 406 (1906); E.Phillips: 464 (1926); T.M.Salter: 662 (1950); E.Phillips p.p.: 561 (1951); E.G.H.Oliv.: 437 (1975).

Bruckenthalia Rchb., Fl. Germ. Excurs.: 413 (1831); Benth.: 694 (1839); Webb: 8 (1971).

Eremia D.Don in Edin. New Phil. J. 17: 156 (1834); Benth.: 699 (1839); N.E.Br.: 332 (1905); E.Phillips: 460 (1926); E.Phillips p.p.: 560 (1951); E.G.H.Oliv.: 433 (1975); E.G.H.Oliv.: 31 (1976.

Philippia Klotzsch in Linnaea 9: 354 (1834) ("1835"); Benth.: 695 (1839); N.E.Br.: 315 (1905); E.Phillips: 460 (1926); Alm & Fries: 9 (1927); T.M.Salter: 657 (1950); Pic.Serm. & Heiniger: 29 (1953); Letouzey: 200 (1971); E.G.H.Oliv.: 432 (1975); Friedmann: 6 (1981); Ross: 174 (1983).

Thamnus Klotzsch in Linnaea 9: 350 (1834); N.E.Br.: 356 (1906); E.Phillips: 462 (1926); E.G.H.Oliv.: 437 (1975).

Acrostemon Klotzsch in Linnaea 12: 227 (1838); Benth.: 702 (1839); N.E.Br.: 350 (1906); E.Phillips: 461 (1926); E.G.H.Oliv.: 434 (1975).

Anomalanthus Klotzsch in Linnaea 12: 238 (1838); N.E.Br.: 384 (1906); E.Phillips: 463 (1926); E.G.H.Oliv.: 435 (1975).

Coccosperma Klotzsch in Linnaea 12: 215 (1838); N.E.Br.: 398 (1906); E.Phillips: 464 (1926); T.M.Salter: 661 (1950); E.G.H.Oliv.: 438 (1975).

Coilostigma Klotzsch, Linnaea 12: 234 (1838); Benth.: 708 (1839); N.E.Br.: 327 (1905); E.Phillips: 464 (1926); E.G.H.Oliv.: 437 (1975); E.G.H.Oliv.: 166 (1987).

Ericinella Klotzsch in Linnaea 12: 222 (1838); Benth. p.p.: 697 (1839); N.E.Br.: 318 (1905); E.Phillips: 460 (1926); Alm & Fries: 45 (1927); E.G.H.Oliv.: 432 (1975); Ross: 173 (1983).

Grisebachia Klotzsch in Linnaea 12: 225 (1838); Benth.: 700 (1839); N.E.Br.: 337 (1906); E.Phillips: 461 (1926); E.G.H.Oliv.: 433 (1975); E.G.H.Oliv.: 69 (1980).

Hexastemon Klotzsch in Linnaea 12: 220 (1838); N.E.Br.: 336 (1905); E.Phillips: 461 (1926).

Simocheilus Klotzsch in Linnaea 12: 236 (1838); Benth. p.p.: 702 (1839); N.E.Br.: 357 (1906); E.Phillips: 462 (1926); T.M.Salter: 658 (1950); E.G.H.Oliv.: 434 (1975).

Syndesmanthus Klotzsch in Linnaea 12: 240 (1838); Benth.: 706 (1839); N.E.Br.: 371 (1906); E.Phillips: 463 (1926); T.M.Salter: 659 (1950); E.G.H.Oliv.: 435 (1975).

Thoracosperma Klotzsch in Linnaea 9: 350 (1838); N.E.Br.: 328 (1905); E.Phillips: 462 (1926); E.G.H.Oliv.: 436 (1975).

Lepterica Benth. in DC. Prodr. 7: 710 (1839); N.E.Br.: 397 (1906); E.Phillips: 464 (1926); E.G.H.Oliv.: 437 (1975).

Eremiopsis N.E.Br. in Fl. Cap. 4: 390 (1906); E.Phillips: 462 (1926); E.G.H.Oliv.: 434 (1975).

Platycalyx N.E.Br. in Fl. Cap. 4: 335 (1905); E.Phillips: 461 (1926); E.G.H.Oliv.: 433 (1975).

Aniserica N.E.Br. in Fl. Cap. 4: 391 (1906); E.Phillips: 463 (1926); T.M.Salter: 660 (1950); E.G.H.Oliv.: 436 (1975).

Arachnocalyx Compton in J. S. Afr. Bot. 9: 143 (1934): E.G.H.Oliv.

Eremiella Compton in J. S. Afr. Bot. 19: 119 (1953); E.G.H.Oliv.: 434 (1975); E.G.H.Oliv.: 45 (1976).

Nagelocarpus Bullock in Kew Bull. 1953: 533 (1954); E.G.H.Oliv.: 438 (1975). *Lagenocarpus* Klotzsch: 214 (1838); Benth.: 710 (1839); N.E.Br.: 416 (1906); E.Phillips: 465 (1926); E.Phillips: 561 (1951).

Stokoeanthus E.G.H.Oliv. in Bothalia 12: 49 (1976).

Type species: *Erica cinerea* L. (lectotype selected by Jarvis & McClintock 1990).

Prostrate shrublets, erect shrubs or trees up to 15[–30] m tall. *Leaves* 3- or 4-nate (6-nate) in whorls, rarely opposite or spirally arranged, mostly linear-oblong to ovate, trigonous, with revolute margins almost touching on underside (i.e., ericoid), less commonly broad, flat and open-backed but then less than 10 X 5 mm, sometimes very reduced and scale-like or enlarged coloured and sepaloid below the florescences. *Flowers* always axillary, in 1–12 whorls variously arranged in elongate racemose to umbellate florescences, either at ends of most leafy lateral branches or very reduced lateral branchlets or only the main branches, sometimes forming dense synflorescences; pedicel present (very reduced) [non-existent]; *bract* always present, on the main axis or partially recaulescent to fully recaulescent forming the abaxial lobe/segment of calyx; *bracteoles* [0,1]2, (fully recaulescent as the lateral lobes/segments of calyx). *Calyx* hypogynous, [0](1–)4[5]-partite or -lobed, small and leaf-like or large and showy [longer than corolla], sometimes enlarging and thickening considerably in fruiting stage. *Corolla* persistent, hypogynous, half fused to ovary in 1 species, (2–)4[5]-lobed, tubular, ampullaceous, urceolate, globose, ovoid, campanulate, cyathiform, obconic or funnel-shaped, small to large and brightly coloured, dull coloured in most wind-pollinated species. *Stamens* (3–)8[–10], free or completely fused, included or exserted; *anthers* dorsifixed or basifixed, with or without simple or elaborate dorsal appendages, thecae partly united (free), with small subterminal pores or pores sometimes as long as thecae; *pollen* shed as tetrads (monads). *Ovary* superior, lower half fused to corolla in 1 species, (1–)4[–8,]-locular, with 1–180 ovules per locule, sessile or stalked, nectaries usually prominent around base, absent in wind-pollinated species; *style* filiform to cylindrical [none], exserted or included; *stigma/style* complex simple-truncate, capitate, peltate, cyathiform or funnel-shaped and considerably enlarged in wind-pollinated species, [distinctly 4-lobed]. *Fruit* mostly a dehiscent loculicidal capsule (dry berry or drupe), pericarp hard and woody to very thin and papery; *seeds* with thick testa, mostly alveolate, some smooth or papillate, in indehiscent fruits the testa thick to very thin, transparent or almost non-existent; pits in inner periclinal and anticlinal walls present or absent. 2n = 24[36].

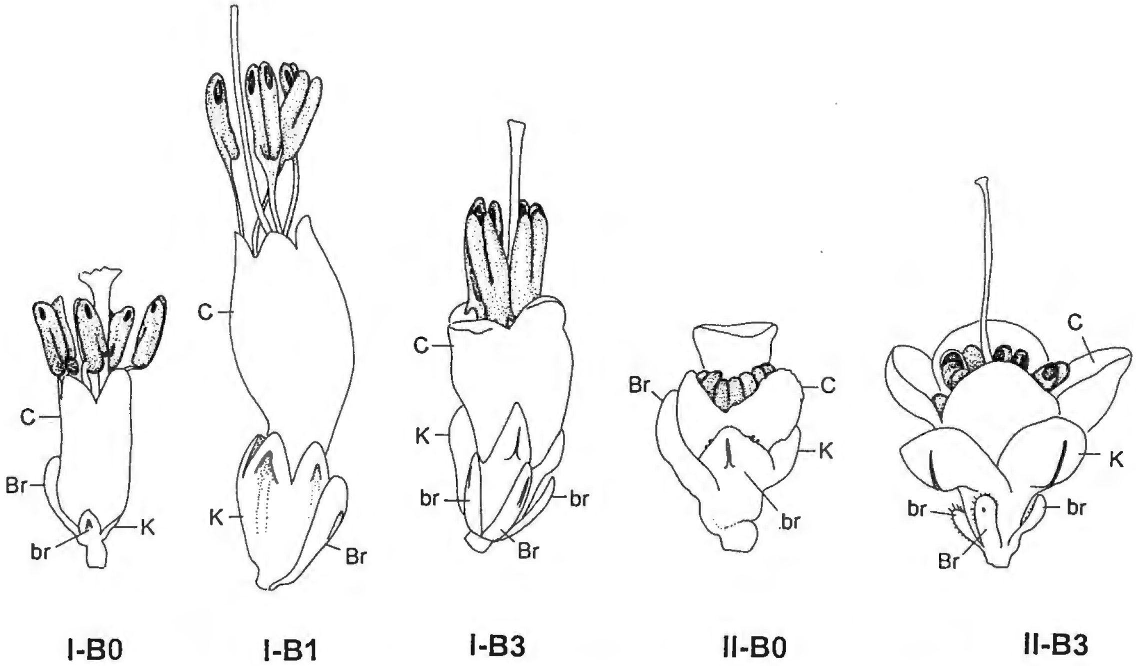

FIGURE 21.—Examples of the types of flowers used in the groups and subgroups of the keys to the species; annotations as in the text.

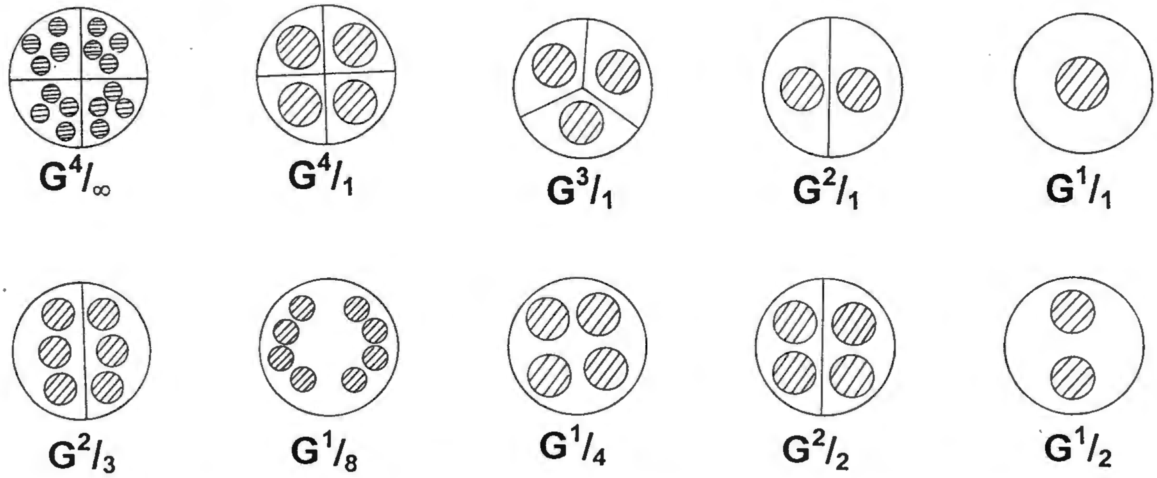

FIGURE 22.—Examples of diagrammatic cross-sections of the ovary showing the locule and ovule setup in the Ericeae with the ovules hatched; first example with black ovules is a general *Erica* producing a dehiscent capsule; unique cases are the $\mathbf{G}^2/_3$ in *Erica stokoeanthus*, $\mathbf{G}^1/_8$ in *E. jacksoniana* and $\mathbf{G}^1/_4$ in *E. thamnoides*.

6.3 Keys to the species

The following keys require the use of a dissecting microscope when the ovary complement is a key character and because most flowers are very small (only 0.7 to 2.0 mm long), otherwise the use of a good x10 hand lens is absolutely essential.

The terminology used for the floral parts and their numbers is given in an abbreviated formula-like form to reduce the number of words in the keys:- **B**=bract & bracteoles (not distinguishing between the two); **K**=calyx; **C**=corolla; **A**=anthers; **G**=ovary (gynoecium) with the upper numbers being the locules and the lower number being the ovules, eg. $G^{4-1}/_1$ is a 4- to 1-locular ovary with 1 ovule in each locule. In the case of the bract and bracteoles the number '0' is given when there are no separate and distinct bract and bracteoles visible on the flower stalk, these having become part of the unequal calyx. Characters enclosed in round brackets (.) occur occasionally, those in square brackets [.] occur rarely (see generic description).

Figure 21 shows examples of the groups used in the general sections of the keys, but in this case the bract and bracteoles are distinguished by the abbreviations Br=bract and br=bracteole.

Figure 22 shows examples of the distribution of loculi and ovules in the ovary in the Ericeae to help with their use in the keys.

Numbers after the species names in the keys is the same as that in the nomenclatural section (**6.5**) and in the plates with the line drawings in the Appendix.

Key to the Groups and Subgroups

1 Anthers well exserted in mature flowers .... **Group I**
Bract & bracteoles apparently absent; calyx unequal .... **Subgroup I - B0**
Bract 1; bracteoles absent; calyx equal .... **Subgroup I - B1**
Bract 1 & bracteoles 2, all clearly distinct from calyx .... **Subgroup I - B3**
1′ Anthers included, or in the mouth, in mature flowers .... **Group II**
Bract & bracteoles apparently absent; calyx unequal .... **Subgroup II - B0**
Bract 1 & bracteoles 2, all clearly distinct from calyx .... **Subgroup II - B3**

GROUP I (Anthers well exserted in mature flowers)

I - B0

1 $G^4/_1$($^3/_1$); flowers dark pink {Langeberg, Riversdale} .... ***E. burchelliana*** (33)
1′ $G^2/_1$($^3/_1$); flowers dull creamish green & papery {Humansdorp to Port Elizabeth, coastal flats} .... ***E. zeyheriana*** (47)

I - B1

1 C2 2

2 Lowest bracts like a large leaf; inflorescence spikelike, simple 3

3 K2 in all flowers; bract always leaflike; flowers white; $G^{2}/_{1}$ {Hermanus} ... ***E. ecklonii*** (19)

3′ Basal flowers of inflorescence with K2, then K3, and K4 at apex; bract becoming very small at apex of inflorescence; flowers pink [white] {Peninsula to Bredasdorp} .... ***E. labialis*** (18)

2′ Lowest bract basal ± $^{1}/_{2}$ or smaller than a leaf; inflorescence of many small heads forming a compound spikelike head 4

4 K2[4] with a distinct sulcus on lobes; flowers deep pink {Hermanus/Stanford Mtns} .... ***E. williamsiorum*** (21)

4′ K4, sulcus none, but a small indentation on lobes; flowers dull white (pale pink) {widespread, but not Hermanus/Stanford Mtns} .... ***E. benthamiana*** (20)

1′ C3 or 4 5

5 C3; $G^{1}/_{1}$ 6

6 Anthers with long apical hairs {Pearly Beach} .... ***E. innovans*** (11)

6′ Anthers without any hairs 7

7 Stigma peltate; no nectaries {Bredasdorp} .... ***E. brownii*** (12)

7′ Stigma simple-truncate; nectaries present 8

8 Leaves 4-nate; calyx with 3 acute vertical angles; A3, $G^{1}/_{1}$ {Bredasdorp/Caledon/Riviersonderend Mtns} .... ***E. globiceps*** (8)

8′ Leaves 3-nate [4-nate]; calyx with rounded vertical angles; $G^{1}/_{1}$ {Bredasdorp} .... ***E. venustiflora*** (10)

5′ C4; $G^{1-4}/_{1}$ 10

10 $G^{1}/_{1}$ 11

11 Stigma peltate; no nectaries; ridge on calyx tube running down lobes {Stanford} .... ***E. erina*** (15)

11′ Stigma simple truncate; distinct nectaries always present 12

12 Ridges running down calyx lobes, groove alternating with them {Cape Peninsula to George} .... ***E. articulata*** (14)

12′ Main ridges alternating with calyx lobes, main vein often thickened in groove down calyx lobes 13

13 Leaves 4-nate; groove opposite down calyx lobes, pale coloured; calyx ridges acute-angled {Bredasdorp/Caledon/Riviersonderend Mtns} .... ***E. globiceps*** (8)

13′ Leaves 3-nate 14

14 Main vein thickened, forming a ridge down calyx lobes {Malmesbury/Darling} .... ***E. malmesburiensis*** (13)

14′ Main vein not thickened, in groove down calyx lobes {Napier Mtns} .... ***E. pulchelliflora*** (9)

10′ $G^{2-4}/_{1}$ 15

15 Anthers with long apical hairs; K with adaxial sticky glands {Pearly Beach area} .... ***E. interrupta*** (7)

15′ Anthers without long apical hairs 16

16 Calyx lobes $^{1}/_{2}$ to $^{2}/_{3}$ of calyx length 17

17 Stigma peltate {Riversdale Langeberg} .... ***E. burchelliana*** (33)

17′ Stigma simple-truncate {Hermanus to Gourtiz, coastal} .... ***E. radicans*** (6)

16′ Calyx lobes $^1/_4$–$^1/_3$ of calyx length **18**

18 Leaves 3nate only {Bredasdorp to Potberg} .... ***E. albertyniae*** (5)

18′ Leaves mostly 4nate, occasionally 3nate on same plant **19**

19 Angles of calyx alternating with lobes, rather acute, grooves
down the lobes, white-transparent, midrib thickened only in basal
half {Hermanus/Stanford} .... ***E. globiceps*** subsp. ***consors*** (8)

19′ Angles of calyx alternating with lobes, rounded, grooves down the lobes,
not light coloured, midrib thickened from sulcus to the base **20**

20 **B1**; calyx and leaves densely hairy all over; fruit with thickened
columella (central axis) {Piketberg, flats only} .... ***E. dregei*** (3)

20′ **B1**(–3) on same spike; leaves & calyx if hairy then not densely so;
columella not thickened in fruit {Peninsula to Potberg} .... ***E. glabella*** (1)

I - B3

1 **A3** (**K3 C3** $G^1/_1$) {Bredasdorp} .... ***E. venustiflora*** (10)

1′ **A4–6** **2**

2 **A6–8** **50**

50 Corolla hairy {Ceres} .... ***E. cereris*** (55)

50′ Corolla glabrous **51**

51 $G^4/_1$ {Herold to Meiring's Poort} .... ***E. vlokii*** (59)

51′ $G^2/_1(^3/_1)$ **52**

52 Calyx glabrous, much shorter than the large pink corolla;
ovary stalked {Riversdale/Albertinia coastal region} .... ***E. platycalyx*** (58)

52′ Calyx hairy, $^1/_3$–$^3/_4$ as long as corolla **53**

53 Calyx edged with long woolly hairs, lobes ± free {Caledon} .... ***E. xeranthemifolia*** (29)

53′ Calyx with very short hairs, lobes very short {Bot River/Elgin} .... **E. karwyderi** (57)

2′ **A4** **3**

3 $G^1/_4$; calyx & corolla sticky {George to Uitenhage} .... ***E. thamnoides*** (30)

3′ $G^{4-1}/_1$ or $^2/_2$ **4**

4 $G^4/_1$ **5**

5 Ovary without nectaries; stigma mostly peltate; ovary & fruit with
lateral longitudinal slit {Kouga to Vanstadens} .... ***E. bolusanthus*** (38)

5′ Ovary with distinct nectaries; stigma simple-truncate **6**

6 Ovary with fine hairs **7**

7 Leaves 2–3 times longer than flowers; fruit with soft papery pericarp;
seeds with hard thick testa {Langeberg South side} .... ***E. quadrifida*** (32)

7′ Leaves as long as or just longer than flowers; fruit with hard pericarp;
seeds with thin soft testa {Little Karoo Mtns} .... ***E. rosacea*** (31)

6′ Ovary glabrous **8**

8 Calyx lobes almost free **9**

9 Calyx glabrous; fruit with very hard pericarp; $G^{4}/_{1}[^{2}/_{1}]$ .... ***E. rosacea*** (31)

9′ Calyx very hairy; fruit with thin papery pericarp; $G^{4-2}/_{1}$ {Hangklip to Tulbagh} .... ***E. eriocephala*** (27)

8′ Calyx lobed ¼–½ 10

10 Plants prostrate, rooting at nodes; calyx lobed $^{1}/_{2}$ way with 8 longitudinal ridges; bracteoles when present very small {coastal, Hermanus to Albertinia} .... ***E. radicans*** (6)

10′ Plants erect; calyx lobed $^{1}/_{4}$, the longitudinal ridges down the lobes **11**

11 Calyx lobes broader than long {Riversdale/Albertinia flats} .... ***E. dispar*** (4)

11′ Calyx lobes longer than broad **12**

12 All flowers on spikelet with **B3**; fruit with thickened columella; {Piketberg Mtn only} .... ***E. piquetbergensis*** (2)

12′ Basal flowers of spikelet with **B3**, the upper with **B1**; fruit without thickened columella {Peninsula to Potberg} .... ***E. glabella*** (1)

4′ $G^{3-1}/_{1}$ or $^{2\text{ or }3}/_{2}$ **13**

13 $G^{3\text{ or }2}/_{1}$ **14**

14 Anthers with long apical and abaxial hairs; $G^{2\text{ or }3}/_{1}$ {Pearly Beach} .... ***E. interrupta*** (31)

14′ Anthers without long apical hairs **15**

15 Corolla very shiny and sticky; calyx covered adaxially with sessile sticky glands {de Hoop} .... ***E. vernicosa*** (24)

15′ Corolla not sticky; calyx without adaxial glands **16**

16 Calyx segments almost free **17**

17 Sepals and pedicel with long hairs; $G^{4-2}/_{1}$ {Hangklip to Worcester/Tulbagh} .... ***E. eriocephala*** (27)

17′ Sepals glabrous; pedicel with very short hairs; $G^{4}/_{1}(^{3}/_{1})$ .... ***E. rosacea*** (31)

16′ Calyx fused, lobes distinct **18**

18 Calyx lobes $^{1}/_{2}$ as long as calyx **19**

19 Ovary without nectaries; stigma often peltate; ovary with longitudinal lateral slits; $G^{2}/_{1}(^{3\text{ or }4}/_{1})$ {Kouga to Vanstadens} .... ***E. bolusanthus*** (38)

19′ Ovary with nectaries **20**

20 Bracteoles much smaller than bract or missing; $G^{4-1}/_{1}$ .... ***E. radicans*** (6)

20′ Bracteoles more or less as large as bract; $G^{2}/_{1}(^{3}/_{1})$ {Swartberg} .... ***E. atromontana*** (37)

18′ Calyx lobes $^{1}/_{4}$–$^{1}/_{5}$ as long as calyx **21**

21 Calyx lobes broader than long {Riversdale/Albertinia flats} .... ***E. dispar*** (4)

21′ Calyx lobes longer than or as long as broad **22**

22 Calyx with longitudinal groove alternating with lobes, no ridge down the lobes, enlarging in fruit; $G^{2}/_{1}[^{3}/_{1}]$ {Swartberg} .... ***E. phaeocarpa*** (41)

22′ Calyx with rounded angles alternating with the lobes, longitudinal ridges on main vein down the lobes, not enlarging in fruit {Peninsula to Potberg} .... ***E. glabella*** (1)

13′ $G^{2}/_{1}$, $^{3}/_{2-1}$, $^{2\text{ or }1}/_{1}$ **23**

23 $G^{2}/_{2}$ or $^{3}/_{2-1}$ **24**

24 Bracteoles much smaller than bract or missing .... ***E. glabella*** (1)

24′ Bracteoles about as large as bract {Swartberg} .... ***E. atromontana*** (37)

23′ $G^{2\text{ or }1}/_1$ **25**

25 $G^2/_1$ **26**

26 Anthers with long apical and abaxial hairs; bract mostly **B1**; $G^2/_1(^3/_1)$
{Pearly Beach} .... ***E. interrrupta*** (7)

26′ Anthers without long hairs **27**

27 Corolla very sticky; sepals covered abaxially with numerous sessile
glands; $G^2/_1(^3/_1)$ {De Hoop} .... ***E. vernicosa*** (24)

27′ Corolla not sticky; calyx without abaxial sessile glands **28**

28 Ovary without nectaries; stigma mostly peltate **29**

29 Calyx $^1/_2$– $^3/_4$ the length of corolla, angled down the lobes; ovary
without longitudinal grooves; stigma peltate; $G^2/_1$ {Kouga}..................... ***E. angulosa*** (17)

29′ Calyx less than $^1/_2$ the corolla length; ovary with longitudinal
groove; style sometimes simple-truncate; $G^2/_1(^{3\text{ or }4}/_1)$ .... ***E. bolusanthus*** (38)

28′ Ovary with distinct nectaries **30**

30 Corolla very hairy **31**

31 Filaments hairy; $G^1/_1(^2/_1)$ {Sir Lowry's Pass to Robertson} .... ***E. pilosiflora*** (28)

31′ Filaments not hairy; $G^2/_1$ {Ceres} .... ***E. arachnocalyx*** (54)

30′ Corolla glabrous **32**

32 Calyx lobes nearly free and covered with long hairs; $G^{4-2}/_1$ .... ***E. eriocephala*** (27)

32′ Calyx fused $^1/_2$ or more of its length **33**

33 Filament attached abaxially on anther; calyx enlarging in fruit with 4 or 8
longitudinal lobes (ridges); $G^2/_1$ {Worcester to Niewoudtville} .... ***E. glabra*** (40)

33′ Filament attached at base of anther **34**

34 Calyx with longitudinal slits or grooves alternating with lobes **35**

35 Calyx with narrow acute slits alternating with lobes, glabrous,
enlarging in fruit {Swartberg} .... ***E. phaeocarpa*** (41)

35′ Calyx with broad grooves, hairy to glabrous, not enlarging
in fruit {George to Van Stadens} .... ***E. uberiflora*** (16)

34′ Calyx without longitudinal slits or grooves alternating with lobes,
with or without grooves down lobes **36**

36 Calyx when young with distinct groove down lobes and the midrib
thickened within groove; angles alternating with lobes; leaves 4-nate [3-n] **37**

37 Calyx lobes broader than long; columella thickened in fruit; plants
mostly rounded erect; **B3** $G^2/_1(^{4-1}/_1)$ {Riversdale/Albertinia flats} .... ***E. dispar*** (4)

37′ Calyx lobes longer than or as long as broad **38**

38 Calyx lobed $^1/_3$–$^1/_4$ its length; plants erect; **B3–1** sometimes in a
single spikelet; $G^2/_1(^{4-1}/_1)$ .... ***E. glabella*** (1)

38′ Calyx lobed about $^1/_2$ its length; plants prostrate; **B3–1** .... ***E. radicans*** (6)

36′ Calyx when young not distinctly grooved; leaves 3-nate **39**

39 Corolla inflated above calyx, narrowed at mouth and slightly sticky;
calyx enlarging in fruiting stage, papery, not succulent
{Robinson Pass area} .... ***E. inflaticalyx*** (43)

39′ Corolla obconical, not sticky; calyx not enlarging in fruiting stage {Swartberg} .... ***E. atromontana*** (37)

25′ $G^1/_1$ **40**

40 Corolla very sticky; calyx very reduced, hidden by large bract and bracteoles and adaxially covered with sessile glands **41**

41 Inflorescence of 6 flowers in 2 whorls; leaves recurved; ovary glabrous {Bredasdorp/Napier} .... ***E. agglutinans*** (23)

41′ Inflorescence of 12 flowers in 4 whorls; leaves subspreading; ovary apically hairy {Riversdale/Albertinia flats} .... ***E. viscosissima*** (22)

40′ Corolla not very sticky **42**

42 Corolla very hairy; calyx lobes more or less free; $G^1/_1(^2/_1)$ {Sir Lowry's Pass to Roberton} .... ***E. pilosiflora*** (28)

42′ Corolla glabrous; calyx fused $^1/_3$ or more its length **43**

43 Ovary without nectaries; stigma subpeltate; calyx enlarging in fruiting stage; $G^1/_1$ {Kammanassie Mtns} .... ***E. kammanassieae*** (44)

43′ Ovary with distinct nectaries; stigma mostly simple-truncate **44**

44 Flowers breaking off readily at apex of pedicel above the bract & bracteoles; filaments nearly as broad as anthers {Kleinmond to Caledon} .... ***E. pauciflora*** (25)

44′ Flowers not breaking off at apex of pedicel **45**

45 Calyx with hairs equal its length, lobed $^1/_4$ its length; filaments nearly as broad as anthers {Houw Hoek to Villiersdorp} .... ***E. niveniana*** (26)

45′ Calyx hairs shorter than calyx lobes; filaments narrower than anthers **46**

46 Calyx not longitudinally ridged or grooved in mature flowers; leaves 3-nate **47**

47 Calyx lobed $^3/_4$ its length, $^2/_3$ as long as corolla; calyx not enlargiing in fruiting stage {Mannetjiesberg} .... ***E. montis-hominis*** (39)

47′ Calyx lobed $^1/_3$ its length, $^1/_2$–$^1/_4$ as long as corolla, enlarging in fruiting stage and becoming succulent and sometimes irregularly ridged {widespread Grabouw, Worcester to George} .... ***E.* anguliger** (42)

46′ Calyx grooved & ridged in flowering stage; leaves 4-nate [3-nate] **48**

48 Calyx lobes broader than long; columella enlarging in fruit; B3 $G^2/_1(^{4-1}/_1)$; {Riversdale coastal region} .... ***E. dispar*** (4)

48′ Calyx lobes longer than or as long as broad; B3–1 .... **49**

49 Calyx lobed ±$^1/_2$ its length with 8 longitudinal ridges; plants prostrate; $G^{4-1}/_1$ {Hermanus to Albertinia, coastal} .... ***E. radicans*** (6)

49′ Calyx lobed at most $^1/_3$ its length, midrib usually forming a ridge; plants erect; $G^2/_1$ [$^{4-1}/_1$, $^{3\text{ or }2}/_2$] .... ***E. glabella*** (1)

GROUP II (Anthers included to manifest)

II - B0 (unequal calyx; large peltate to cyathiform stigma)

[Note: for variable species which key out in several places, the full species formula is given and this includes that character present under the relevant part of the key]

1 A3 .... **2**

2 Branches, leaves & sepals with long plumose or glandular hairs;
corolla not contracted below the mouth; **A**[3]4 $\mathbf{G}^{1}/_{1}\ {}^{2}/_{1}\ [{}^{3}/_{1}]$
{widespread, Kamiesberg to Bredasdorp} .... ***E. rigidula*** (84)

2′ Branches, leaves & sepals with dense, simple hairs only; corolla contracted
below the mouth; **A3** $\mathbf{G}^{1}/_{1}$ {Peninsula to Cedarberg} .... ***E. urceolata*** (78)

1′ **A4–8** 3

3 **A4** 4

4 **G** any combination other than ${}^{1}/_{1}$ 5

5 Branches, leaves & sepals with long glandular &/or plumose hairs
A4 $\mathbf{G}^{1}/_{1}\ {}^{2}/_{1}\ [{}^{3}/_{1}]$ .... ***E. rigidula*** (84)

5′ Branches, leaves & sepals with simple hairs only 6

6 Filaments always free ; **A4** $\mathbf{G}^{1}/_{1}\ [{}^{2}/_{1}]$ {Ouhangsberg, Worcester} .... ***E. boucheri*** (73)

6′ Filaments fused; $\mathbf{G}^{1}/_{2}$; $({}^{2}/_{2}\ {}^{2}/_{1})\ [{}^{1}/_{1}\ {}^{1}/_{3}]$ **A6–4** .... ***E. areolata*** (69)

4′ $\mathbf{G}^{1}/_{1}$ 7

7 Anthers with longish apical hairs; distinct articulation present between style
& stigma; **A4,5** $\mathbf{G}^{1}/_{1}$ {Swartberg} .... ***E. melanomontana*** (82)

7′ Anthers with short or no apical hairs; no articulation between style
& stigma 8

8 Leaves & sepals with large apical sessile sticky gland 9

9 Anthers pear-shaped or semi-obtriangular with internal pore between thecae;
A4 $\mathbf{G}^{1}/_{1}$ {widespread, Peninsula to Vanrynsdorp to George} .... ***E. muscosa*** (79)

9′ Anthers rectangular, higher than wide, with no internal pore;
A4 $\mathbf{G}^{1}/_{1}$ .... ***E. phacelanthera*** (80)

8′ Leaves & sepals without large apical sessile sticky gland 10

10 Branches, leaves & sepals with long glandular or plumose hairs;
A4 $\mathbf{G}^{1}/_{1}\ {}^{2}/_{1}\ ({}^{3}/_{1})$ .... ***E. rigidula*** (84)

10′ Branches, leaves & sepals without long glandular or plumose hairs 11

11 Leaves & flowers shorter than 1mm long; anthers obtriangular;
A4 $\mathbf{G}^{1}/_{1}$ .... ***E. eglandulosa*** (81)

11′ Leaves & flowers longer than 1mm 12

12 Anthers obtriangular or pear-shaped, with internal pore between thecae;
A4 $\mathbf{G}^{1}/_{1}$ .... ***E. muscosa*** 79)

12′ Anthers rectangular, with no internal pore between thecae 13

13 Leaves incurved; branches with infrafoliar ridges; **A4** $\mathbf{G}^{1}/_{1}$ .... ***E. calcicola*** (71)

13′ Leaves not incurved; branches without infrafoliar ridges 14

14 Sepals edged with a few non-sticky glands or hairs; **A**(4)**–6** $\mathbf{G}^{1}/_{1}$
{Riviersonderend} .... ***E. remota*** (68)

14′ Sepals edged with longish hairs & very few glands; **A4** $\mathbf{G}^{1}/_{1}[{}^{2}/_{1}]$
{Ouhangsberg, Worcester} .... ***E. boucheri*** (73)

3′ **A6**(5)**–8** 15

15 **A6**(5) 16

16 $\mathbf{G}^{3,4}/_{1}$ **A6** .... ***E. bredasiana*** (74)

16′ $\mathbf{G}^{1,2}/_{1}$, or ${}^{1,2}/_{2}$ 17

17 $G^{2}/_{1}$ **18**

18 Anthers with pores $^{2}/_{3}$ length of theca, internal pore present between thecae
A6 $G^{2}/_{1}(^{3,4}/_{1})$ .... ***E. bredasiana*** (74)

18′ Anthers with pores $^{1}/_{3}$ length of theca; no internal pore present **19**

19 Calyx, ovary & style glabrous; corolla not fringed; **A8–6** $G^{2}/_{1}$ .... ***E. binaria*** (76)

19′ Calyx hairy at least at base; ovary apically hairy; style hairy at base
A5,6 $G^{2}/_{1}(^{2}/_{2})$ .... ***E. terniflora*** (75)

17′ G combinations other than $^{2}/_{1}$ **20**

20 $G^{2}/_{2}$ **21**

21 Anthers with a few longish basal hairs; corolla fringed; **A5,6** $G^{2}/_{1}(^{2}/_{2})$ .. ***E. terniflora*** (75)

21′ Anthers without longish basal hairs **22**

22 Ovary warty; **A8–6** $G^{1,2}/_{2}$ .... ***E. subcapitata*** (65)

22′ Ovary not warty; **A6(4)** $G^{1,2}/_{2}$ .... ***E. areolata*** (69)

20′ $G^{1}/_{1}$ or $^{1}/_{2}$ **23**

23 $G^{1}/_{2}$ **24**

24 Ovary warty; **A8–6** $G^{1,2}/_{2}$ .... ***E. subcapitata*** (65)

24′ Ovary not warty **25**

25 Anther pore small, about $^{1}/_{5}$ length of theca, anther snouted, internal
pore between thecae; **A6(5–8)** $G^{1}/_{2}$ .... ***E. parviporandra*** (67)

25′ Anther pore $^{1}/_{2}$–$^{1}/_{3}$ length of theca, anthers not snouted, no internal pore
present between thecae; **A4–6** $G^{1,2}/_{2}[^{1}/_{4}]$ .... ***E. areolata*** (69)

23′ $G^{1}/_{1}$ **26**

26 Style straight arising from centre of ovary apex; **A6–4** $G^{1}/_{1}$ .... ***E. remota*** (68)

26′ Style with S-bend, arising excentrically from upper part of ovary;
A6 $G^{1}/_{1}$ .... ***E. artemisioides*** (70)

15′ **A8(7)** **27**

27 Branches covered with numerous long plumose hairs;
A8(7) $G^{3}/_{1}(^{2}/_{1})[^{4}/_{1}]$ .... ***E. perplexa*** (64)

27′ Branches without long plumose hairs **28**

28 Ovary warty; **A8** $G^{1,2}/_{2}$ .... ***E. subcapitata*** (65)

28′ Ovary not warty **29**

29 Ovary with basal half fused to corolla; filaments fused to corolla;
A8 $G^{2}/_{2}$ .... ***E. serrata*** (77)

29′ Ovary & filaments free from corolla **30**

30 $G^{1}/_{1}$ **31**

31 Anthers with a few long apical hairs, pore only $^{1}/_{5}$ length of theca; style
apical, straight, with a distinct articulation; **A8** $G^{1}/_{1}$ .... ***E. miniscula*** (83)

31′ Anthers without long apical hairs, pore $^{1}/_{3}$ length of theca; style excentric,
with S-bend, without articulation zone; **A(4–)6(–8)** $G^{1}/_{1}$ .... ***E. artemisioides*** (70)

30′ G combinations other than $^{1}/_{1}$ **32**

32 $G^{1}/_{2}$; anthers snouted adaxially, pore $^{1}/_{5}$ length of theca;
A(5)6(–8) .... ***E. parviporandra*** (67)

32′ $G^{2-4}/_{1}$ **33**

33 Anther pore $^2/_3$ length of theca, internal pore present between thecae; **A6–8** **$G^{2-4}/_1$** .... ***E. bredasiana*** 74)

33′ Anther pore $^1/_3$ length of theca **34**

34 Anthers with long basal hairs; stigma glabrous; ovary glabrous; **A6–8** **$G^2/_1$** .... ***E. binaria*** (76)

34′ Anthers without basal hairs **35**

35 Ovary glabrous, rugose; stigma glabrous; **A8** **$G^2/_2(^2/_1)$** .... ***E. rugata*** (66)

35′ Ovary with longitudinal apical ridges, hairy or papillate to glabrous, basal region glabrous and unevenly wrinkled; stigma often hairy below; **A8(7)[6][–9]** **$G^{2-4}/_1$** .... ***E. axillaris*** (72)

II - B3

1 Leaves 4-nate **2**

2 **A8** **C4** **$G^2/_1$**; {Attaquaskloof, Robinson Pass} .... ***E. velatiflora*** (61)

2′ **A6** **C3** **$G^3/_1$** {Outeniqua Mtns & Formosa Peak} .... ***E. outeniquae*** (60)

1′ Leaves 3-nate **3**

3 **A8** **4**

4 **$G^1/_{6-9}$**; branches with dense plumose hairs; plants erect; flowers pink {Hottentots Holland Mtns} .... ***E. jacksoniana*** (63)

4′ **$G^1/_1$** or $^2/_1$–$^4/_1$; 1 ovule per locule **5**

5 **$G^1/_1$**; leaves recurved; style curved; ovary oblique; {Bains Kloof to Piketberg} .... ***E. curvistyla*** (47)

5′ **$G^2/_1$**–$^4/_1$ **6**

6 **$G^4/_1$** **7**

7 Branches with numerous plumose hairs; plants mostly prostrate & spreading; flowers white {Somerset West to Cederberg} .... ***E. totta*** (49)

7′ Branches without plumose hairs; plants erect, flowers pink {Meiring's Poort-Kammanassie Mtns-Herold} .... ***E. vlokii*** (59)

6′ **$G^2/_1$** **8**

8 Stigma peltate, well exserted; {southern Cold Bokkeveld to Bonteberg} .... ***E. cetrata*** (45)

8′ Stigma simple-truncate or capitate **9**

9 Leaves recurved; plants prostrate **10**

10 Sepals green with hairs longer than width of sepal; filaments widened in lower half; {Cold Bokkeveld, Cederberg} .... ***E. recurvifolia*** (48)

10′ Sepals white to pinkish with hairs shorter than width of sepal; filaments equal in width & narrow; species usually **$G^1/_1$** ($^2/_1$) {Bains Kloof to Piketberg} .... ***E. curvistyla*** (47)

9′ Leaves erect to sub-spreading **11**

11 Corolla glabrous; calyx glabrous; {Cold Bokkeveld} .... ***E. bokkeveldia*** (46)

11′ Corolla hairy; calyx with short hairs & very long sticky hairs admixed; ovules erect **12**

12 A4–6[8]; long hairs of sepals & leaves stout & gland-tipped; ovary glabrous apically or with a few short hairs; {Hex River Mtns} .... ***E. arachnocalyx*** (54)

12′ A(6–)8; long hairs of sepals & leaves soft & often without glands; ovary hairy apically; {Cold Bokkeveld} .... ***E. cereris*** (55)

3′ A4(6) **13**

13 Locules with more than 1 ovule, $G^2/_{3\text{–}6}$, branches with scattered forked hairs; {Hottentots Holland Mtns} .... ***E. stokoeanthus***(62)

13′ Locules with only 1 ovule, $G^1/_1\text{–}^4/_1$ **14**

14 $G^1/_1$ **15**

15 Filaments hairy; plants prostrate; leaves glabrous; {Villiersdorp-Jonaskop} .... ***E. jonasiana***(56)

15′ Filaments glabrous; plants erect; leaves hairy with short plumose marginal hairs {eastern Cold Bokkeveld} .... ***E. lateriflora***(50)

14′ $G^4/_1\text{–}^2/_1$ **16**

16 $G^4/_1$ **17**

17 Stigma simple-truncate; anthers spurred {Little Karoo region from Touwsrivier to Baviaanskloof} .... ***E. rosacea***(31)

17′ Stigma cyathiform to peltate; anthers muticous {Elim to Riversdale} .... ***E. puberuliflora*** (35)

16′ $G^2/_1$ **18**

18 Corolla glabrous **19**

19 Inflorescence with only 1 whorl of 3 flowers; each vegetative node bearing flowering branches; corolla usually hairy; {Jonaskop to Cederberg} .. ***E. eremioides*** (51)

19′ Inflorescence with 2–4 whorls of 6–12 flowers; flowering branches not at each node; {Cold & Warm Bokkeveld} .... ***E. caprina*** (53)

18′ Corolla hairy or partially so **20**

20 Filaments hairy; corolla constricted below lobes & hairy in lower parts {Swellendam to Niewoudtville & West Coast flats} .... ***E. plumosa*** (52)

20′ Filaments glabrous **21**

21 Calyx lobes fused ±$^1/_2$ the length of calyx .... ***E. eremioides*** (51)

21′ Calyx lobes nearly free **22**

22 Inflorescence with 2 or 3 whorls terminal on main branches only; plants covered with stiff sticky gland-tipped hairs {Cold Bokkeveld} .... ***E. arachnocalyx*** (54)

22′ Inflorescence with only 1 whorl at ends of main, secondary & tertiary branches forming dense spike-like inflorescences; plant not sticky; {Langeberg Riversdale} .... ***E. vallis-fluminis*** (36)

ALTERNATIVE KEY TO GROUP II

B0 - Bract & bracteoles apparently absent; calyx unequal with larger abaxial lobe; large peltate to cyathiform stigma

1 Branches with numerous long plumose hairs **2**

2 A8(7) $G^3/_1$ $(^2/_1)$ $[^4/_1]$ .... ***E. perplexa*** (64)

2′ **A4 $G^{1,2}/_1$ [$^3/_1$]** .... ***E. rigidula*** (84)

1′ Branches with short to long simple hairs, occasionally with a few long plumose hairs admixed 3

3 Sepal lobes edged with long, glandular or eglandular, simple or plumose hairs; **A4** .... ***E. rigidula*** (84)

3′ Sepal lobes not edged with long glandular or eglandular, simple or plumose hairs, hairs when present very short simple or occasionally substellate, glands when present subsessile or sessile 4

4 Corolla constricted above anthers & below lobes; anthers as wide as long; **A3 $G^1/_1$** .... ***E. urceolata*** (78)

4′ **A4–8** 5

5 Distinct disjunction present between style & stigma 6

6 **A8, $G^1/_1$** {Langeberg, Riversdale, very rare} .... ***E. miniscula*** (83)

6′ **A4(5) $G^1/_1$** {Swartberg} .... ***E. melanomontana*** (82)

5′ No disjunction present between style & stigma 7

7 Leaves & sepal lobes with a large sticky sessile apical gland 8

8 Anthers rectangular, higher than wide; **A4 $G^1/_1$** .... ***E. phacelanthera*** (80)

8′ Anthers pear-shaped to obtriangular; **A4 $G^1/_1$** .... ***E. muscosa*** (79)

7′ Leaves & sepal lobes without a large sticky sessile apical gland 9

9 Leaves & flowers less than 1mm long; leaves appressed; anthers pear-shaped; **A4 $G^1/_1$** .... ***E. eglandulosa*** (81)

9′ Leaves & flowers more than 1mm long 10

10 Basal half of ovary fused to corolla; filaments fused to corolla; **A8; $G^2/_2$** .... ***E. serrata*** (77)

10′ Ovary free from corolla 11

11 Style arising excentrically from apex of ovary and with distinct S-bend **A6(4,8) $G^1/_1$** .... ***E. artemesioides*** (70)

11′ Style arising from centre of apex of ovary, straight 12

12 Ovary with numerous warts; **A8(7,6) $G^{1,2}/_2$** .... ***E. subcapitata*** (65)

12′ Ovary without warts 13

13 Leaves incurved; branches with infrafoliar ridges; **A4 $G^1/_1$** .... ***E. calcicola*** (71)

13′ Leaves not incurved; branches without infrafoliar ridges 14

14 Anthers adaxially snouted, pore small $^1/_5$ or less length of theca; **A6(5) $G^1/_2$** .... ***E. parviporandra*** (67)

14′ Anthers adaxially flattened, pore $^1/_3$ length of theca 15

15 Anthers with long thin basal hairs 16

16 Ovary & calyx glabrous; **A8(6) $G^2/_1$** .... ***E. binaria*** (76)

16′ Ovary apically hairy; calyx at least basally hairy; **A6(5) $G^2/_1$** .... ***E. terniflora*** (75)

15′ Anthers without long thin basal hairs 17

17 **A4 $G^1/_1$**; ovary smooth .... ***E. boucheri*** (73)

17′ **A6–8** 18

18 **A6** 19

19 $\mathbf{G}^{2,3}/_{1}$; anther pore $^{2}/_{3}$ length of theca or larger .... ***E. bredasiana*** (74)

19′ $\mathbf{G}^{1}/_{1,2}$ or $^{2}/_{2}$; anther pore $^{1}/_{3}$ length of theca **20**

20 $\mathbf{G}^{1}/_{1}$; fruit with attenuate beaked apex .... ***E. remota*** (68)

20′ $\mathbf{G}^{1}/_{2}(^{2}/_{2})$; fruit with rounded obtuse apex .... ***E. areolata*** (69)

18′ **A**8(7) **21**

21 Anther pore $^{2}/_{3}$ length of theca or larger; style distinct, cylindrical;
A6–8 $\mathbf{G}^{3,2}/_{1}$ .... ***E. bredasiana*** (74)

21′ Anther pore $^{1}/_{3}$ length of theca; style very short & funnel-shaped **22**

22 Ovary rugose all over; fruit with leathery pericarp; $\mathbf{G}^{2}/_{2}(^{2}/_{1})$ .... ***E. rugata*** (66)

22′ Ovary apical region with longitudinal ridges, either hairy or papillate, basal region unevenly wrinkled & glabrous; fruit with hard pericarp;
$\mathbf{G}^{2}/_{1}(^{4,3}/_{1})$ .... ***E. axillaris*** (72)

6.4 List of species and their full synonymy

(Species numbers are the same as the plate numbers in the Appendix)

1. **Erica glabella** Thunb., Prodromus plantarum capensium: 73 (1794); Thunb.: 364 (1823). *Blaeria glabella* (Thunb.) Willd.: 631 (1798). *Octogonia glabella* (Thunb.) Klotzsch: 233 (1833). *Simocheilus glabellus* (Thunb.) Benth.: 704 (1839); N.E.Br.: 363 (1906). Type: *Thunberg s.n.* (UPS, holo.).

Key to the subspecies

Corolla minutely colliculate ....subsp. **glabella** (**a**)

Corolla smooth ....subsp. **laevis** (**b**)

(**a**) subsp. **glabella**

Blaeria purpurea P.J.Bergius: 34 (1767), non *Erica purpurea* Thunb. (1794) [=*Erica equisetifolia* Salisb.]. *Simocheilus purpureus* (P.J.Bergius) Druce: 648 (1916). Type: CBS, *Grubb s.n.* (SBT, holo.!).

Blaeria pusilla L.: 39 (1767), non *Erica pusilla* Thunb. (1794) [=*Erica nudiflora* L.]. Type: ? Sec. Benth.: 698 (1839).

Erica fasciculata Thunb.: 71 (1794); Thunb.: 357 (1823); *Blaeria fasciculata* (Thunb.) Willd.: 629 (1798); Thunb.: 7 (1802); Roem. & Schultes: 169 (1818); G.Don: 804 (1834). Type: *Thunberg s.n.* (UPS!).

Erica scabra Thunb.: 72 (1794); Thunb.: 357 (1823); *Blaeria scabra* (Thunb.) Willd.: 629 (1797) non *Blaeria scabra* Wendl.: t.31 (1808); Thunb.: 7 (1802); Roem. & Schultes: 169 (1818); G.Don: 804 (1834). Type: *Thunberg s.n.* (UPS!).

Erica embolifera Salisb.: 340 (1802), nom. illegit. Type: as for *Erica glabella* Thunb. above.

Erica exilis Salisb.: 340 (1802), nom. illegit. Type: as for *Erica scabra* Thunb. above.

Blaeria depressa Licht. ex Roem. & Schultes: 168 (1818). *Simocheilus depressus* (Licht. ex Roem. & Schultes) Benth.: 704 (1839); N.E.Br.: 364 (1906); T.M.Salter: 659 (1950). Type: *Lichtenstein s.n.* (B†, holo.).

Simocheilus depressus (Licht. ex Roem. & Schultes) Benth. var. *patens* N.E.Br.: 364 (1906). Type: without locality, *Sieber 156* (K!, holo.).

(**b**) subsp. **laevis** E.G.H.Oliv., subsp.nov.; subsp. typica corolla laevis non minute colliculata differt. Typus: Western Cape, 3419DA, Pompieskloof NW of Elim, 100 m, 19-03-1985, *Oliver 8712* (NBG!, holo.).

Octogonia hirta Klotzsch: 233 (1838), non *Erica hirta* Thunb. (1785). *Thoracosperma hirta* (Klotzsch) O.Kuntze: 391 (1891). *Simocheilus hirtus* (Klotzsch) E.G.H.Oliv.: 284 (1984). Types: in Babylons-Toorensberg, altit. III & IV, near farm 'Zwart & Marais', Caledon, *Ecklon & Zeyher s.n.* (B†; iso.?); in hills between Caledon and Babylon's Tower, altit. II, Caledon, [loc. 52], August, *Ecklon & Zeyher s.n.* (B†; E!, P!, S!, UPS!, Z!); ibid., as *280* (MO!, S!, W!). Lectotype (designated here): *Ecklon & Zeyher s.n.* [loc 52] (P).

Simocheilus hirsutus Benth.: 704 (1839); N.E.Br.: 365 (1906), nom. illegit. *Thoracosperma hirsuta* (Benth.) O.Kuntze: 390 (1891). Type as for *O. hirta* above. [Note: Bentham's name appears to be an error since he was referring to Klotzsch's *Octogonia hirta*].

Simocheilus submuticus Benth.: 704 (1839); N.E.Br.: 365 (1906). Type: sandy places, Swellendam, *Mundt et Maire s.n.* (K, holo.!;).

Simocheilus subrigidus N.E.Br.: 367 (1906). Type: Bredasdorp Div., by the Koude River near Elim, 700 ft, *Schlechter 9583* (K, holo.!; BM!, BOL!, G!, GRA!, MO!, NBG!, P!, PRE!, S!, W!).

Simocheilus acutangulus N.E.Br.: 367 (1906). Type: Bredasdorp Div., hills near Mier Kraal, 200 ft, *Schlechter 10523* (K, holo.!; BM!, BOL!, G!, MO!, P!, S!, W!, Z!).

Simocheilus globiferus N.E.Br.: 366 (1906). Type: Swellendam Div., mountains along the lower part of the Zondereinde River [Appelskraal], *Zeyher 3313* (K, holo.!; BOL!, PRE!, SAM!, W!).

Simocheilus patulus N.E.Br.: 366 (1906). Types: Caledon Div., Klein River, 1000 ft, *Schlechter 7605* (BM!, BOL!, K!); Caledon Div., hills near Papies Valley [Papiesvlei], 500 ft, *Schlechter 10434* (BM!, BOL!, E!, G!, GRA!, K!, M!, MO!, PRE!, S!, W!).

2. **Erica piquetbergensis** (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Simocheilus piquetbergensis* N.E.Br. in Flora capensis 4: 362 (1906). Type: Piquetberg Div.; Piquet Berg, 2200 ft., *Galpin 2661* (BOL, holo.!; -K!, fragm., BOL!>NBG).

3. **Erica dregei** E.G.H.Oliv., nom. nov.

Simocheilus oblongus Benth. in De Candolle, Prodromus 7: 705 (1839), non *Erica oblonga* Sincl.: 17 (1825), hybrid. ex hort. Type: in sandy hills, Bergvalley, *Drege 7796* (BM!, BOL!, K!, MO!, P!, S!, W!). Lectotype (designated here): *Drege 7796* (K!, herb Benth.).

4. **Erica dispar** (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Simocheilus dispar* N.E.Br. in Flora capensis 4: 362 (1906) . Type: Riversdale Div.; near Riversdale, *Rust 557* (BOL! holo., K!). [Note: Brown annotated the BOL sheet as the type specimen (Jan 15 1906), but this is only a capsule with some fragments (two almost leafless branchlets and loose leaves and flowers) from the specimen that used to be in B. The fragment in K ex B is even sparser and must have been kept by him after he had examined the full sheet on loan from B and which he probably also labelled as the type].

5. **Erica albertyniae** E.G.H.Oliv., sp. nov.—Frutex compactus ad 250 mm altus. Rami pubescentes pilis reflexis. Folia 3-nata erecta appressa non imbricata. Bractea non recaulescens; bracteolae nullae. Flores 4–6-verticillati. Calyx 4-lobatus. Corolla 4-lobata. Stamina 4 libera exserta; pollen in monadis. Ovarium 2-loculare; ovulum 1 in quoque loculo pendulum. Fructus indehiscens pericarpio tenuissimo, testa tenuissima.

Typus: Western Cape, 3420CA, Bredasdorp Dist., Eliaskraal SW of Bredasdorp, 10 m, 26-04-1986, *Oliver 8821* (NBG!, holo.; BM!, BOL!, E!, G!, K!, MO!, NY!, PRE!, S!).

6. **Erica radicans** (L. Guthrie) E.G.H.Oliv., comb. nov.

Basionym: *Thoracosperma radicans* L. Guthrie in Annals of Bolus Herbarium 3: 181 (1924). Type: Riversdale Div. [hills near Still Bay sec. SAM], alt. 100 ft, fl. April, *Muir 2405* (BOL, holo.!; SAM!).

Key to subspecies

Ovary mostly 4-locular, corolla-ovoid urceolate, lobes erect ....subsp. **radicans (a)**

Ovary mostly 2-locular, corolla campanulate, lobes spreading ....subsp. **schlechteri (b)**

(a) subsp. **radicans**

Thoracosperma muirii L. Guthrie: 180 (1924), non *Erica muirii* L.Bolus: 76 (1914) [=*Erica recta* H. Bol.]. Type: Riversdale Div., prostrate over exposed rocks on summit of hills at Kanca [Canca], fl. April, *Muir 848* (BOL, holo.!, PRE!).

(b) subsp. **schlechteri** (N.E.Br.) E.G.H.Oliv., stat. et comb. nov.

Basionym: *Acrostemon schlechteri* N.E.Br. in Flora capensis 4: 353 (1906), non *Erica schlechteri* H. Bol.: 325 (1894). Types: Bredasdorp Div., Rhenosterkop, 50 ft, *Schlechter 10576* (BM!, BOL!, G!, K!, Z!); Bredasdorp Div., Cape Agulhas, 250 ft, *Schlechter 10559* (BOL!, K!, NBG!, P!, PRE!, W!). Lectotype (here designated): *Schlechter 10576* (BOL).

7. **Erica interrupta** (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Thoracosperma interruptum* N.E.Br. in Flora capensis 4: 331 (1906). Types: without locality, *Bowie s.n.* (K!) & *Ward s.n.* (K!). Lectotype (designated here): *Bowie s.n.* (K!).

Thoracosperma viscidum L. Guthrie: 22 (1925). Type: probably Ceres Div., exact locality unknown, obtained at the Wild Flower Show, Cape Town, Oct. 1920, *Anon. in BOL 16779* (BOL, holo.!).

8. **Erica globiceps** (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Syndesmanthus globiceps* N.E.Br. in Flora capensis 4: 382 (1906). Types: Bredasdorp Div., hills near Elim, 300 ft, *Bolus 6766* (BOL!, K!); Bredasdorp Div., hills near Elim, 300 ft, *Bodkin sub Bolus 6769* (BM!, BOL!, K!, PRE!); Bredasdorp Div., mountains near Koude River, 1000 ft, *Schlechter 9613* (BM!, BOL!, G!, K!, MO!, P!, PRE!, S!, W!, Z!). Lectotype designated here: *Bodkin sub Bolus 6769* (BOL). [Note: all BOL syntypes were determined by Brown with pieces removed later for Kew by Bolus, the one from the lectotype in 1907, i.e. after the publication of Flora Cap.].

Key to the subspecies

Calyx & corolla 3-lobed ....subsp. **globiceps (a)**

Calyx & corolla mostly 4-lobed, rarely a few flowers 3-lobed

  Ovary 2-locular, corolla distinctly colliculate ....subsp. **consors (b)**

  Ovary 1-locular, corolla smooth ....subsp. **gracilis (c)**

(a) subsp. **globiceps**

Syndesmanthus sympiezoides N.E.Br.: 383 (1906). Type: Bredasdorp Div., Elim, 250 ft, *Schlechter 7704* (BM!, BOL!, G!, K!, P!, PRE!, W!, Z!).

Syndesmanthus zeyheri H.Bol.: 381 (1906). Types: Caledon Div., mountains of Klein River Kloof, *Zeyher 3315* (BOL!, E!, K!, M!, MO!, P!, PRE!, S!, SAM!, STE/NBG!, TCD!, UPS! W!, Z!); Caledon Div., hills between Caledon and Elim, 600 ft, *Bolus 8464* (BM!, BOL!, K!); Bredasdorp Div., hills near Bredasdorp, *Bolus 8465* (BM!, BOL!, K!, PRE!).

(b) subsp. **consors** (N.E.Br.) E.G.H.Oliv., stat. et comb. nov.

Basionym: *Simocheilus consors* N.E.Br. in Flora capensis 4: 367 (1906). Type: Caledon Div., Shaws Mountain, 1300 ft, *Galpin 3724* (K, holo.!; BOL!).

(c) subsp. **gracilis** (Benth.) E.G.H.Oliv., stat. et comb. nov.

Basionym: *Syndesmanthus scaber* Klotzsch var. *gracilis* Benth, in De Candolle, Prodromus 7: 707 (1839). *Syndesmanthus gracilis* (Benth.) N.E.Br.: 383 (1906). Type: Cape Colony [stony hill at Ganze Kraal on the Slang River on northern side of Zonderend River, Caledon Div. sec. McKay: 64 (1943)] *Burchell 7558* (K, holo.!; PRE! W!).

9. Erica pulchelliflora E.G.H.Oliv., nom. nov.

Syndesmanthus pulchellus N.E.Br. in Flora capensis 4: 384 (1906), non *Erica pulchella* Houtt.: 504 (1775). Type: Bredasdorp Div.; mountains of Elands Kloof, 1000 ft, *Schlechter 9744* (BM!, BOLx2!, G!, K!, MO!, NBG!, P!, PRE!, S!, W!, Z!). Lectotype, designated here: *Schlechter 9744* (BOL! hololecto.; isolecto. BM!, BOL!, G!, K!, MO!, NBG!, P!, PRE!, S!, W!, Z!). [Note: The Kew material is labelled "type" by Brown, as is one of the sheets in BOL.]

10. Erica venustiflora E.G.H.Oliv., nom. nov.

Syndesmanthus venustus N.E.Br. in Flora capensis 4: 381 (1906), non *Erica venusta* Salisb.: 297 (1796) [=*Erica ventricosa* Thunb.]. Type: Caledon or Bredasdorp Div., hills between Caledon and Elim, 400ft, *Bolus 8466* (K! holo.!; BOL!).

Key to the subspecies

Calyx long ciliate, lacking sessile glands ....subsp. **venustiflora (a)**

Calyx hairless, edged with distinct sessile red glands ....subsp. **glandulosa (b)**

(a) subsp. **venustiflora**

(b) subsp. **glandulosa** E.G.H.Oliv., subsp. nov.—foliis calycibusque glandibus distinctis atrorubris sessilibus in marginibus tectis.

Typus: Western Cape, 3420AD, Bredasdorp Dist., hills E of Vrede on Bredasdorp–Swellendam road, on saddle, 950 ft, 12-08-1973, *Williams 1843* (NBG!, holo.).

11. Erica innovans E.G.H.Oliv., nom. nov.

Syndesmanthus pumilus N.E.Br. in Flora capensis 4: 382 (1906), non *Erica pumila* Andr.: t.234 (1809). Type: Bredasdorp Div., Elim, *Schlechter 7651* (K! holo.; BM!, BOL!, G!, GO!, MO!, NBG!, P!, PRE!, S!, W!, Z!).

12. Erica brownii E.G.H.Oliv., nom. nov.

Syndesmanthus breviflorus N.E.Br. in Flora capensis 4: 381 (1906), non *Erica breviflora* Dulfer: 30 (1965). Type: Bredasdorp Div., hills near Elim, 200 ft, *Schlechter 9727* (BM!, BOL!, G!, K!, MO!, NBG!, P!, PRE!, S!, W!, Z!). Lectotype, designated here: *Schlechter 9727* (BOL!). [Note: both the BOL & K sheets of *Schlechter 9727* are labelled as type by Brown.]

13. Erica malmesburiensis E.G.H.Oliv., sp. nov.—Fructus densus ad 300 mm altus. Rami pubescentes pilis recurvatis. Folia 3-nata erecta. Flores 3-verticillati; bractea non recaulescens vel partim recaulescens; bracteolae nullae. Calyx 4-lobatus. Corolla 4-lobata. Stamina 4 libera exserta. Ovarium 1-loculare; ovulum 1 pendulum. Fructus indehiscens, pericarpio tenuissimo, testa tenuissma.

Typus: Western Cape, 3318BC, Malmesbury Dist, Preekstoel, sandy slopes, W aspect, 8-04-1976, *Esterhuysen 34239* (BOL!, holo.; NBG!, PRE!).

14. Erica articulata (L.) Thunb., Prodromus plantarum capensium: 71 (1794); Thunb.: 357 (1823). *Blaeria articulata* L.: 198 (1771); Lam.: 429 (1785); Lam.: 315, t.78 (1791); Willd.: 629 (1797); Thunb.: 7 (1802); Wendl.: 19, t.44 (1808); Poiret:: 640 (1811); Roem. & Schult.: 169 (1818); Klotzsch: 666 (1833); G.Don: 804 (1834). *Syndesmanthus articulatus* (L.) Klotzsch: 241 (1838); Benth.: 706 (1839); N.E.Br.: 379 (1906); T.M.Salter: 659 (1905). Type: herb. Linn. 141.2 (LINN!).

Erica paleacea Salisb.: 341 (1802), *nom. superfl.*, type as for *Blaeria articulata*.

Syndesmanthus articulatus var. *hirtus* Benth.: 706 (1839). Type: *non cit.*

Syndesmanthus fasciculatus Klotzsch: 240 (1838). *S. articulata* var. *fasciculata* (Klotzsch) N.E.Br.: 380 (1906), non *Erica fasciculata* Thunb.: 71 (1794) [=*E. glabella* Thunb.]. Type: Cape of Good Hope, *Drege s.n.* (B†; iso.?).

Syndesmanthus scaber Klotzsch: 241 (1838); Benth.: 706 (1839), non *Erica scabra* Thunb.: 72 (1794) [=*E. glabella* Thunb.]. Type: Cape of Good Hope, *Ecklon & Zeyher s.n.* (B†, holo.; S!).

Blaeria eriantha Willd. ex Steud.: 208 (1840). Type: unknown.

Syndesmanthus elimensis N.E.Br.: 378 (1906), non *Erica elimensis* L.Bolus: 157 (1918). Types: Bredasdorp Div., hills near Elim, 200–900 ft, *Bolus 8517* (BOL!, K!, NBG!, PRE!, Z!); Bredasdorp Div., hills near Elim, 200–900 ft., *Schlechter 7641* (BM!, BOL!, E!, G!, K!, MO!, P!, PRE!, S!, W!, Z!).

Syndesmanthus elimensis N.E.Br. var. *incertus* N.E.Br.: 379 (1906). Type: Paarl Div. mountains near French Hoek, *Schlechter 10281* (K, holo.!; BOL!, PRE!).

Syndesmanthus similis N.E.Br.: 380 (1906). Type: Swellendam Div., mountains near Swellendam, 800 ft, *Bolus 8098* (K, holo.!; BOL!, NBG!, PRE!).

15. Erica erina (Klotzsch ex Benth.) E.G.H.Oliv., comb. nov.

Basionym: *Codonostigma erinus* Klotzsch ex Benth. in De Candolle, Prodromus 7: 709 (1839). *Syndesmanthus erinus* (Klotzsch ex Benth.) N.E.Br.: 377 (1906). Type: in Klynrivier [Klein River] Mtns, *Ecklon & Zeyher s.n.* (B†, holo.; -BOL fragm.!, -K fragm.!) as *297* (MO!, S!). Lectotype here designated: *Ecklon & Zeyher s.n.* [det. Klotzsch] (K!).

Syndesmanthus erinus (Klotzsch ex Benth.) N.E.Br. var. *validus* N.E.Br.: 378 (1906). Types: Caledon Div., Papies Vlei, 700 ft, *Schlechter 10439* (BM!, BOL!, E!, G!, K!, MO!, P!, PRE!, S!, W!, Z!); Bredasdorp Div., mountains near Koude River, 500 ft, *Schlechter 9728* (BM!, BOL!, E!, G!, K!, MO!, P!, PRE!, S!, W!, Z!).

16. Erica uberiflora E.G.H.Oliv., nom. nov.

Blaeria multiflora Klotzsch in Linnea 8: 661 (1833), non *Erica multiflora* L.: 355 (1753), species europea. *Simocheilus multiflorus* (Klotzsch) Klotzsch: 236 (1838); N.E.Br.: 360 (1906). Type: Cape of Good Hope, *Mundt & Maire s.n.* (B†, holo.; K!, P!, W!). Lectotype (designated here): *Mundt & Maire s.n.* [det. Klotzsch] (P!).

Blaeria carnea Klotzsch: 661 (1833) non *Erica carnea* L. (1753) species europaea. *Simocheilus carneus* (Klotzsch) Klotzsch: 236 (1838); Benth.: 703 (1839); N.E.Br.: 360 (1906). Type: Prom. b. sp.[Cape of Good Hope], *Mundt & Maire s.n.* (B†, holo.; –K! frag., S!). [Note: the K specimen has two labels, one as just Mund the other written by Klotzsch as "Mund & Maire", (it has a sketch of the Berlin type); the S material is labelled as just "Mund" and may not be an isotype].

Simocheilus pubescens Klotzsch: 236 (1838), non *Erica pubescens* L.: 506 (1762). Type: at the Elandsrivier, altit. III–V., Uitenhage, March, *Ecklon & Zeyher s.n.* (B†, holo.; LD!).

Simocheilus multiflorus Klotzsch var. *atherstonei* N.E.Br.: 361 (1906). Types: Caledon Div., "Caledon, R.W.R.," in the Cape Herb., *Anon. s.n.* (SAM!); George Div., without precise locality, *Atherstone s.n.* (BOL! holo.).

17. Erica angulosa E.G.H.Oliv., nom. nov.

Acrostemon fourcadei L. Guthrie in Annals Bolus Herbarium 4: 22 (1925), non *Erica fourcadei* L.Bolus: 185 (1933). *Simocheilus fourcadei* (L.Guthrie) E.G.H.Oliv.: 284 (1984).

Type: Uniondale Div., summit of the pass between Avontuur and Uniondale, *Fourcade 2093a* (BOL, holo.!; K!, NBG!).

18. Erica labialis Salisb. in Transactions of Linnean Society 6: 340 (1802). *Sympieza labialis* (Salisb.) Druce: 649 (1917); T.M.Salter: 660 (1905). Type: Hottentots Holland, *Masson s.n.* (BM, holo.!).

Blaeria bracteata Wendl.: 3, t.37 (1810). Type: loc. cit. t.37.

Sympieza capitellata Licht. ex Roem. & Schultes: 171 (1818); Spreng.: 432 (1838); Bartl.: 651 (1832); Klotzsch: 655 (1833); Klotzsch: 229 (1838); Benth.: 706 (1839); N.E.Br.: 396 (1906). Type: *Lichtenstein s.n.* (B†, holo.; BOL!, K!).

Sympieza tenuiflora Benth.: 706 (1839); N.E.Br.: 397 (1906). Types: in Cape Colony, *Forbes s.n.* (BOL!, G-DC!,K!, S!), *Mundt s.n.* (BOL!, K!) & *Burchell 7801* (BOL!, K!, NBG!, P!, PRE!, W!).

Sympieza brachyphylla Benth.: 706 (1839); N.E.Br.: 395 (1906). Types: in Cape Colony, *Forbes s.n.* (G-DC!, K!, S!) & *Mundt s.n.* (BOL!, K!).

Erica capitella Thunb. ex Rach: 721 (1853). Type: *Thunberg s.n.* (UPS).

Sympieza articulata sensu N.E.Br.: 395 (1906), non *Erica articulata* (L.) Thunb.(1794).

Sympieza breviflora N.E.Br.: 393 (1906); T.M.Salter: 660 (1950). Type: Cape Div., Simons Berg, *Wolley Dod 315* (BM!, BOL!, K!).

Sympieza pallescens N.E.Br.: 394 (1906). Type: Caledon Div., Houw Hoek, 1500 ft, *Schlechter 7328* (K, holo.!; BM!, BOL!, MO!, P!, PRE!, S!, W!, Z!).

Sympieza vestita N.E.Br.: 394 (1906). Types: Bredasdorp Div., mountains between Fairfield and Elim, *Bolus 8515* (BOL!); hills near Elim, *Bolus 8516* (BOL!, K!, PRE!); Napier, *Schlechter 9654* (BM!, BOL!, G!, K!, MO!, NBG!, P!, PRE!, S!, W!, Z!).

Sympieza articulata var. *hians* N.E.Br.: 395 (1906). Types: Caledon Div., mountains near Houw Hoek, *Bolus 6962* (BOL!, K!, PRE!) & *Bolus sub Guthrie 3626* (BOL!).

Sympieza capitellata var. *angustata* N.E.Br.: 396 (1906). Type: Caledon Div., Zwart Berg near Caledon, 2500 ft, *Bodkin sub Bolus 6767* (BOL, holo.!; PRE).

Sympieza capitellata var. *crassistigma* N.E.Br.: 396 (1906). Type: Caledon Div., summit ridge Zandfontein, 1500 ft, *Galpin 3721* (K, holo.!; BOL!, PRE!).

19. Erica ecklonii E.G.H.Oliv., nom. nov.

Sympieza eckloniana Klotzsch in Linnaea 12: 229 (1838), non *Erica eckloniana* Tausch: 625 (1839) [=*Erica vestita* Thunb.]; N.E.Br.: 393 (1906). Type: in mtns "Klynriviersberge" [Klein River Mtns], altit. I–IV., Caledon., Aug., *Ecklon & Zeyher s.n.* (B, holo†; LD!, P!); as *284* (G!, MO!, S!, SAM! W!). Lectotype designated here: *Ecklon s.n.* [det. by Klotzsch] (K!). [Note: the K specimen labelled as collected by Ecklon only is selected because it would appear to be the most authentic original material seen by the author].

20. Erica benthamiana E.G.H.Oliv., nom. nov.

Basionym: *Blaeria gracilis* Bartl. in Linnaea 7: 650 (1832), non *Erica gracilis* Wendl. (1798). *Aniserica gracilis* (Bartl.) N.E.Br.: 391 (1906). *Sympieza gracilis* (Bartl.) E.G.H.Oliv.: 550 (1993). Type: Swellendam Mtns, Voormansbos, *Ludwig & Beil s.n.* (? holo.; BOL!, SAM!). Lectotype chosen here: *Ludwig & Beil s.n.* (SAM).

Sympieza kunthii Klotzsch: 656 (1833); Klotzsch: 230 (1838); Benth.: 705 (1839), *nom. superfl.*, type as for *Blaeria gracilis.*

Sympieza kunthii var. *brachyphylla* Benth.: 705 (1839). Type: *Burchell s.n.* (K, holo.!).

Sympieza kunthii var. *hispida* Benth.: 705 (1839). *Aniserica gracilis* var. *hispida* N.E.Br.: 391 (1906). Type: sine loc., *Drege s.n.* (K).

Aniserica macrocalyx T.M.Salter: 77 (1941) non *Erica macrocalyx* (Baker) Dorr & E.G.H.Oliv. (1999 in press); T.M.Salter: 660 (1950). Type: Cape Peninsula, Constantiaberg, at the base of damp ledges, facing south-west, at about 2300 ft, *Pillans 9518* (BOL, holo.!; BOL, MO).

21. Erica williamsiorum E.G.H.Oliv., sp. nov.—Frutex erectus ramosissimus ad 1 m altus. Rami pubescentes et hirsuti. Folia 3-nata sparse hispida. Flores 3-nati 2–4-verticillati racemosi, in synflorescentibus capitatis aggregati; bractea non recaulescens vel approximata; bracteolae nullae. Calyx 2-[4]-lobatus lobis sulcustis. Corolla 2-lobata tubulosa glabra. Stamina 4 libera exserta. Ovarium 2-loculare; ovulum 1 in quoque loculo. Fructus incognitus.

Typus: Western Cape, 3419AC, Hermanus, Vogelgat Reserve, upper S slopes, 1600 ft [488 m], 22-02-1985, *Oliver 8686* (NBG!, holo.; BOL!, K!, MO!, P!, PRE!, S!).

22. Erica viscosissima E.G.H.Oliv., nom. nov.

Simocheilus viscosus H. Bol. in Journal of Botany 1894: 290 (1894) non *Erica viscosa* Steud.: 311 (1840) [=*E. viscaria* L.?]. *Syndesmanthus viscosus* (H.Bol.) N.E.Br.: 374 (1906). Type: Cape Colony, South-western Region, in sandy places, Droogevlakte near Riversdale, alt. 400 ft, fl. Jan., *Schlechter 2142* (BOL, holo.!; BM!, G!, K!, MO!, NBG!, P!, PRE!, UPS!).

23. Erica agglutinans E.G.H.Oliv., nom. nov.

Syndesmanthus schlechteri N.E.Br. in Flora capensis 4: 374 (1906) non *Erica schlechteri* H. Bol.: 325 (1894). Type: Bredasdorp Div., Vogelvlei, 150 ft, *Schlechter 10481* (BOL! holo.; K!, NBG!, PRE!, SAM!).

24. Erica vernicosa E.G.H.Oliv., sp. nov.—Frutex tegetiformis. Rami prostrati in terra radicantes sparse pubescentes pilis recurvatis. Folia 3-nata effuso-reflexa. Flores 1- vel 2-verticillati; bractea partim recaulescens approximata; bracteolae 2 approximatae. Calyx 4-lobatus. Corolla 4-lobata viscido-vernicosa. Stamina 4 libera exserta. Ovarium 2(3)[4]-loculare; ovulum 1 in quoque loculo. Fructus indehiscens pericarpio parum crasso fragili, testa tenui.

Typus: Western Cape, 3420CB, Bredasdorp District, flats near Skipskop, 40 ft, 6-03-1964, *Oliver 1835* (NBG!, holo.; BM!, BOL!, G!, K!, MO!, NY!, PRE!, S!).

25. Erica paucifolia (J.C. Wendl.) E.G.H.Oliv., comb. nov.

Basionym: *Blaeria paucifolia* J.C. Wendl., Collectio plantarum 2: 17 t.43 (1808). *Syndesmanthus paucifolius* (Wendl.) Benth.: 707 (1839); N.E.Br.: 376 (1906). Type: Wendl. op. cit. t.43 [iconotype]. [Note: no authentic Wendland material of this species is present in GOET nor MEL where many Wendland specimens are known to be housed (Stafleu & Cowan, Tax Lit 1988)].

Key to the subspecies

Calyx tube 4-angled, no glands on calyx lobes adaxially, anther pore $^1/_2$ the length of theca

Calyx long hirsute all over ....subsp. **paucifolia (a)**

Calyx glabrous with puberulous patches on tube alternating with angles ....subsp. **ciliata (b)**

Calyx tube 8-angled, with large sessile glands around margin adaxially, anther pore $^4/_5$ the length of theca ....subsp. **squarrosa (c)**

(a) subsp. **paucifolia**

(b) subsp. **ciliata** (Klotzsch) E.G.H.Oliv., stat. et comb. nov.

Basionym: *Macrolinum ciliatum* Klotzsch in Linnea 12: 243 (1838). *Syndesmanthus ciliatus* (Klotzsch) Benth.: 707 (1839); N.E.Br.: 375 (1906). Types: in hills between Caledon and Babylon's Tower, altit. II, Caledon, Aug., [loc. 52.8], *Ecklon & Zeyher s.n.* (B†, E!, UPS!, Z!) as *290* (G!, MO!, S!, SAM!, W!); in Babylon's Tower Mtn, altit. III & IV, near farms Zwart & Marais, Caledon, Aug., *Ecklon & Zeyher s.n.* (B†, iso.?).

(c) subsp. **squarrosa** (Benth.) E.G.H.Oliv., stat. et comb. nov.

Basionym: *Syndesmanthus squarrosus* Benth. in De Candolle, Prodromus 7: 707 (1839), non *Erica squarrosa* Salisb.: 380 (1802); N.E.Br.: 375 (1906). Type: Cape Colony, *Thom s.n.* (K, holo.!; S!).

26. Erica niveniana E.G.H.Oliv., nom. nov.

Syndesmanthus nivenii N.E.Br. in Flora capensis 4: 377 (1906) non *Erica nivenia* Andr.: 76 (1805) nec *E. nivenii* Benth.: 635 (1839) [ambae =*Erica embothriifolia* Salisb.]. Type: Without locality, *Niven 95* (K, holo.!;).

27. Erica eriocephala Lam., Encyclopédie méthodique. Botanique 1: 489 (1785). Type: herb. Lamarck, *Anon. s.n.* (P-LA!).

Erica hirsuta Thunb.: 72 (1794); Salisb.: 339 (1802); Thunb.: 358 (1823). *Blaeria hirsuta* Thunb.: 8 (1802). *Acrostemon hirsutus* (Thunb.) Klotzsch: 228 (1838); Benth.: 702 (1839); N.E.Br.: 352 (1906). Type: without locality, *Thunberg s.n.* (UPS sheet 9328, holo!, MEL!).

Blaeria thunbergii G. Don: 805 (1834), nom. superfl. *Acrostemon thunbergii* Alm & Fries: 263 (1924). Type: as for *Erica hirsuta* Thunb.

Comocephalus incurvus Klotzsch: 224 (1838). *Acrostemon incurvus* Benth.: 702 (1839); Rach: 790 (1853); N.E.Br.: 352 (1906). Type: Cape of Good Hope, near 'Waterfall' not far from Tulbagh, in mountain valley, alt. II–V; in mtns 'Winterhoeksberg, Witsenberg & near Vogelvalley [Voelvlei]', (Prov. Worcester), Nov., *Ecklon & Zeyher s.n.* (B†, holo.; iso.?).

Acrostemon incanus Klotzsch: 228 (1838). Type: near 'Waterfall' not far from Tulbagh, in mountain valley, alt. II–V, (Prov. Worcester), Nov., *Ecklon & Zeyher s.n.* (B holo†; iso.?); as *271* (G!, LD!, MEL!, MO!, P!, S!, SAM!, W!).

Acrostemon equisetoides Klotzsch: 228 (1838). Type: collected with *A. incanus* (i.e. near Waterfall not far from Tulbagh, Nov.), *Ecklon & Zeyher s.n.* (B†, holo.; LD!, NBG!, P!, S!, UPS!, Z!); as *272* (G!, MEL!, MO!, S!, W!).

Acrostemon glandulosus Rach : 790 (1853); N.E.Br.: 353 (1906). *Erica hirsuta* Thunb.: 72 (1794), pro parte excl. no 9328 in herb. Thunb. Lectotype: Cape of Good Hope, *Thunberg s.n. no 9327* (UPS lecto.!), selected by Rach (1853).

Acrostemon stokoei L. Guthrie: 23 (1925). Type: Hottentots-Holland Mtns, *Stokoe in BOL 17523* (BOL, holo.!).

Acrostemon barkerae Compton: 122 (1963). Type: Worcester Div.: Scherpenheuwel, hillside, 29 Aug. 1951, *Barker 7523* (NBG!, holo.!: BOL!, K!).

28. Erica pilosiflora E.G.H.Oliv., nom. nov.

Finckea eriocephala Klotzsch in Linnaea 12: 238 (1838), non *Erica eriocephala* Lam.: 489 (1785). *Grisebachia eriocephala* (Klotzsch) Benth.: 702 (1839). *Acrostemon eriocephalus* (Klotzsch) N.E.Br.: 355 (1906). Type: Cape of Good Hope, *Drege s.n* (B†, holo.; iso.?); as *7804* (BM!, BOL!, E!, K!, MEL!, MO!, NBG!, OXF!, P!, PRE!, S!, TCD!, W!). Lectotype (designated here): *Drege 7804* (P!). [Note: Brown presumably saw the type in Berlin as he noted that he had seen the type of *F. bruniades* when comparing it and Klotzsch's *F. eriocephala*. However, he cited only the numbered collection, *Drege 7804*, which I am selecting as the lectotype (the Paris sheet is annotated in Drege's own hand). Klotzsch never gave any collection numbers to the material he cited in his works.]

Finckea bruniades Klotzsch: 238 (1839) non *Erica bruniades* L.: 354 (1753). *Grisebachia bruniades* Benth.: 702 (1839). Type: Cape of Good Hope, *Ecklon & Zeyher s.n.* (B†, holo.; iso.?). [Note: It is very surprising that there are no isotypes of *Ecklon & Zeyher s.n.* in any herbarium. I am thus following Bentham and Brown, who presumably both examined the type material in B, in placing this name here.]

29. Erica xeranthemifolia Salisb. in Transactions of Linnean Society 4: 339 (1802). *Blaeria xeranthemifolia* (Salisb.) G.Don: 805 (1834); Klotzsch: 246 (1838). *Acrostemon xeranthemifolius* (Salisb.) E.G.H.Oliv.: 268 (1984). Type: Hottentots Holland, sandy places, *Masson s.n.* (K, holo.!).

Hexastemon lanatus Klotzsch: 220 (1838); N.E.Br.: 336 (1905). *Eremia lanata* (Klotzsch) Benth.: 700 (1839). Types: in Babylon's Tower Mtn (altit. III–IV.) near farm of Zwart & Marais, Caledon, Aug., *Ecklon & Zeyher s.n.* (B†; iso.?); in hills between Caledon and Babylon's Tower (altit.II.), Caledon, Aug., *Ecklon & Zeyher s.n.* (B†; BOL!, E!, K!, LD!, M!, P!, UPS!, Z!); as *264* (G!, MEL!, MO!, S!, W!).

30. Erica thamnoides E.G.H.Oliv., nom. nov.

Thamnus multiflorus Klotzsch in Linnaea 12: 235 (1838), non *Erica multiflora* L.: 355 (1753) species europea. Type: in mtns 'Van Staadensriviersberge' [Van Stadens River], altit. III–IV. (Prov. Uitenhage.), May–Jul., [loc. 4.5, 4.7], *Ecklon & Zeyher s.n.* (B†, holo.; GRA!, M!, MO!, S!, W!), as *274* (MO!, S!, SAM!, W!), as [loc. 4.2], *275* (S!, SAM!). Lectotype (designated here): *Ecklon & Zeyher 274* (SAM).

Thoracosperma paniculatum sensu Klotzsch: 229 (1838) quoad specimen cit., non *Thoracosperma paniculatum* (Thunb.) Klotzsch: 350 (1834) [=*Erica quadrifida* Benth.].

Simocheilus obovatus Benth.: 703 (1839) nom. superfl., type as for *Thamnus multiflorus* Klotzsch.

31. Erica rosacea (L. Guthrie) E.G.H.Oliv., comb. nov.

Basionym: *Thoracosperma rosaceum* L. Guthrie in Annals of Bolus Herbarium 4: 21 (1925). Type: Riversdale Div., hills at Muiskraal, alt. 1500 ft, fl. Aug., *Muir 2697* (BOL, holo.!).

Key to the subspecies

Ovary puberulous ....subsp. **rosacea (a)**

Ovary glabrous ....subsp. **glabrata (b)**

(a) subsp. **rosacea**

Thoracosperma galpinii N.E.Br.: 330 (1905), non *Erica galpinii* T.M.Salter: 35 (1935). Type: Riversdale Div., Garcias Pass, 200 ft, *Galpin 3732* (BOL!, K!).

Thoracosperma bondiae Compton: 206 (1941). Type: Oudtshoorn Div., Roodeberg, 1000 m, 24 March 1940, *Bond 235* (NBG!, holo.!).

Thoracosperma fourcadei Compton: 134 (1943). Type: Humansdorp Div., between the old Kouga road from Zuur Anys and the first bridge to the east, 400 m, Aug. 1942, *Fourcade 5656* (NBG!, holo.!).

(b) subsp. **glabrata** E.G.H.Oliv., subsp. nov.; a subspecie typica ovario glabro non puberulo differt.

Typus: Western Cape, 3321AD, Ladismith, Klein Swartberg, Bloupunt above Besemfontein, 1460 m, 5-02-1992, *Oliver 10038* (NBG!, holo.; PRE!).

Thoracosperma marlothii N.E.Br. in Flora capensis 4: 330 (1905), non *Erica marlothii* H.Bol.: 237 (1894). Types: Central Region, between 4500 and 4900 ft; Worcester Div., Witteberg Range, near Matjesfontein, *Marloth 2955* (BOL!, K!); ibid., *Marloth 2956* (BOL!, K!); Prince Albert Div., Zwartberg Range, near Sevenweeks Poort, *Marloth 2976* (BOL!, K!, PRE!).

32. Erica quadrifida (Benth.) E.G.H.Oliv., comb. nov.

Basionym: *Simocheilus quadrifidus* Benth. in De Candolle, Prodromus 7: 703 (1839). Type: in Cape Colony, *Burchell 6126* (K, holo.!; -BOL!, fragm.). [Note: Mackay (1943: 60) gives the locality as 'at the drift, Witte Els Rivier {George to Great Brak}, 7-10-1814'].

Erica paniculata Thunb.: 72 (1794), non *Erica paniculata* L. (1762); Thunb.: 360 (1823). *Blaeria paniculata* (Thunb.) Thunb.: 10 (1802). *Thoracosperma paniculatum* (Thunb.) Klotzsch: 350 (1834); N.E.Br.: 329 (1905). Type: *Thunberg s.n.* (UPS, holo.!; MEL!).

33. Erica burchelliana E.G.H.Oliv., nom. nov.

Coilostigma glabrum Benth. in De Candolle, Prodromus 7: 708 (1839), non *Erica glabra* Thunb. (1794); N.E.Br.: 328 (1906); E.G.H.Oliv.: 168 (1987). Type: in Cape Colony, *Burchell 6875* (K, holo.!; -BOL, fragm.!). [Note: according to McKay (1943: 62) the collecting details are 'between Little Vet River & Garcia's Pass, 27-11-1814'.]

34. Erica zeyheriana (Klotzsch) E.G.H.Oliv., comb. nov.

Basionym: *Coilostigma zeyherianum* Klotzsch in Linnaea 12: 234 (1838); N.E.Br.: 328 (1906); E.G.H.Oliv.: 167 (1987).Type: in mtns "Van Stadensriviersberge", altit. III–IV, (Uitenhage), Jul., *Ecklon & Zeyher s.n.* (B†, holo.; BOL, lecto.!; E!, K!, LD!, MEL!, P!, S!, UPS!, W!, Z!); idem as *296* (G!, MO!, W!). Lectotype designated by Oliver (1987).

Coilostigma dregeanum Klotzsch: 235 (1838); N.E.Br.: 1127 (1909). Type: Cape of Good Hope, *Drege 7753* (B†, holo., -K fragm.!, -BOL, fragm.!); as *Drege s.n.* (G!, G-DC!).

Coilostigma tenuifolium Klotzsch: 234 (1838); N.E.Br.: 327 (1905). *Coilostigma zeyerhianum* var. *tenuifolium* (Klotzsch) E.G.H.Oliv.: 183 (1988). Types: on flats between "Krakakamma" [Kragakamma] and mtns "Vanstadensrivierberge", altit. II, *Ecklon & Zeyher s.n.*(B†; E!, S!); as *294* (S, lecto.!; G!, GOET!, LD!, M!, MEL!, MO!, W!, UPS!, Z!); in forest at "Olifantshoek" near river "Bosjemansrivier" [Bushmans River], altit. I, *Ecklon & Zeyher s.n.*(B†; BOL!). Lectotype designated by Oliver (1988).

35. Erica puberuliflora E.G.H.Oliv., nom. nov.

Thamnium puberulum Klotzsch in Linnaea 12: 223 (1838) non *Erica puberula* Bartl.: 644 (1834) [=*Erica parviflora* L.]. *Coilostigma puberulum* (Klotzsch) Benth.: 708 (1839). *Thoracosperma puberulum* (Klotzsch) N.E.Br.: 331 (1906). Types: in hills, altit. II, at Riviersonderend near farms Linde, Knoblauch, Ecksteen, *Ecklon & Zeyher s.n.* (B†; iso.?); in mtns Caltit. [?Caledon], altit. III & IV, Zwellendam, *Ecklon & Zeyher s.n.* (B†; iso.?). Lectotype (designated here): without locality, *Ecklon s.n.* det. by Klotzsch (K!; isolecto. P!). [Note: with the usual vague labelling of and mixup with Ecklon & Zeyher collections and duplicates distributed by Klotzsch from Berlin, it was decided to select the material seen and determined by Klotzsch to serve as the type even though it was not labelled as a joint 'Ecklon & Zeyher' collection].

36. **Erica vallis-fluminis** E.G.H.Oliv., sp. nov.—Fruticulus prostratus usque erectus. Rami pubescentes glandibus paucis. Folia 3-nata puberula glandibus paucis sessilibus marginibus. Flores 3-nati 1-verticillati terminales pedicello pubescenti; bractea partim recaulescens approximata; bracteolae 2. Calyx 4-lobatus lobis lanceolatis pubescentibus. Corolla 4-lobata anguste cyathiformis usque obconica pubescens rosea. Stamina 4 libera inclusa; antherae bipartitae thecis aculeatis calcaris parvis in apice filamenti; pollen in tetradis. Ovarium 2-loculare ovoideum usque ellipsoideum, complanatum, obtusum, pubescens nectariis; ovulum 1 in quoque loculo pendulum; stylus exsertus; stigma truncatum. Fructus ovoideus pericarpio perduro, seminibus ellipsoideis, testa pergracili, cellulis elongatis perundulatis.

Typus: Western Cape, 3321DC, Riversdale Dist., Langeberg at Bergfontein, lower slopes of Witels-Voorberg, 470 m, 30-10-1990, *McDonald 1967* (NBG!, holo.).

37. **Erica atromontana** E.G.H.Oliv., sp. nov.—Frutex subeffusus usque erectus ad 500 mm altus. Rami hirtelli pilis effusis usque recurvatis. Folia 3-nata suberecta. Flores 3-nati 1(2)-verticillati; bractea partim recaulescentes; bracteolae 2. Calyx 4-lobatus rigidus crassus sed non accrescens. Corolla 4-lobata ovoidea obtuso 4angulosa. Stamina 4 libera exserta calcarata; pollen in monadis. Ovarium 2-loculare; ovulum 1 per loculo; stigma minute capitatum usque cyathiforme. Fructus indehiscens pericarpio tenui fragili, testa tenui.

Typus: Swartberg Mtns, peak N of Tierberg, steep S-facing slope, 6400 ft, 5-11-1985, *Vlok 1265* (NBG!, holo.; BM!, K!).

38. **Erica bolusanthus** E.G.H.Oliv., nom. nov.

Thoracosperma nanum N.E.Br. in Flora capensis 4: 331 (1905), non *Erica nana* Salisb.: 355 (1802). Type: Uitenhage Div., Van Stadens River Mountains, *Bolus 1580* (BOL! holo.; K!, SAM!).

39. **Erica montis-hominis** E.G.H.Oliv. sp. nov.—Frutex effusus usque suberectus ad 250 mm altus. Rami pubescentes pilis effusis. Folia 3-nata. Flores 3-nati 1- vel 2-verticillati; bractea partim recaulescentes, approximatae; bracteolae 2. Calyx 4-lobatus villosus. Corolla 4-lobata obconica colliculata. Stamina 4 libera exserta calcaris; pollen in monadis. Ovarium 1-loculare parum asymmetricum acutum; ovulum 1 pendulum; stylus rectus; stigma capitellatum. Fructus indehiscens, pericarpio tenui, testa tenui.

Typus: Western Cape, 3322DB, Mannetjiesberg, E slopes, 5600 ft, 2-10-1971, *Oliver 3609* (NBG!, holo.; BM!, BOL!, K!, MO!, PRE!, S!).

40. **Erica inaequalis** (Klotsch) E.G.H.Oliv., comb. nov.

Basionym: *Pachycalyx inaequalis* Klotzsch: 231 (1838). Type: near Waterfall not far from Tulbagh, mountain valley, altit. II–V, (Prov. Worcester), Nov., *Ecklon & Zeyher s.n.* (B†, holo.; iso.?); as *281* (MO!, S!, W!). Lectotype, selected here: *Ecklon & Zeyher 281* (S!).

Erica glabra Thunb., Prodromus plantarum capensis 1: 69 (1794); Thunb.: 346 (1823), non *Erica glabra* Gilib. (1781) [=*Calluna vulgaris* (L.) D.Don]. *Blaeria glabra* (Thunb.) Thunb.:

10 (1802). *Pachycalyx glaber* (Thunb.) Klotzsch: 231 (1838); Rach: 791 (1853). *Simocheilus glaber* (Thunb.) Benth.: 705 (1839); N.E.Br.: 371 (1906). Type: without locality, *Thunberg s.n.* (UPS! holo.; K fragm.!).

Blaeria bicolor Klotzsch: 660 [606 in error] (1833), non *Erica bicolor* Thunb. (1785). *Plagiostemon bicolor* (Klotzsch) Klotzsch: 232 (1838). *Simocheilus bicolor* (Klotzsch) Benth.: 703 (1839); N.E.Br.: 369 (1906); T.M.Salter: 659 (1950). Type: Cape of Good Hope, *Mundt s.n.* (B†, holo.; S!). *Mundt & Maire s.n.* (B†, K!).

Pachycalyx hispidus Klotzsch: 231 (1838). *Simocheilus hispidus* (Klotzsch) Benth.: 705 (1839). Type: in mountains of Nieuwekloof, altit. II, October, *Drege s.n.* (B†, holo.; iso.?); as *7789* (BM!, E!, K!, P!, S!, W!).

Plagiostemon puberulus Klotzsch: 232 (1838). *Simocheilus puberulus* E.G.H.Oliv.: 284 (1984). *Simocheilus klotzschianus* Benth.: 703 (1839); N.E.Br.: 368 (1906), *nom. superfl.* Type: Cape, near Olifantsrivier and farm Brakfontein, Clanwilliam, *Ecklon & Zeyher s.n.* (B†, holo.; iso.?). [Note: see the collection cited under *albirameus* below.]

Pachycalyx pubescens Klotzsch: 230 (1838). Type: in Tulbaghskloof, Tulbagh valley in Winterhoeksberge, Witsenberg also near Waterfall and Vogelvalley etc., altit. II–V, (Prov. Worcester), January, *Ecklon & Zeyher s.n.* (B†, holo.; iso.? W!).

Simocheilus ecklonianus Benth.: 705 (1839). Type as for *Pachycalyx pubescens* above.

Simocheilus albirameus N.E.Br.: 370 (1906). Type: Clanwilliam Div., by the Oliphants River near Brakfontein, *Ecklon & Zeyher 282* (K, holo.!; BOL!, S!, W!).

Simocheilus klotzschianus var. *glabrifolia* N.E.Br.: 369 (1906). Types: Vanrhynsdorp Div.: Knagas (Konaquas) Berg, *Zeyher 1120* (K!, S!, SAM!); Clanwilliam Div.: Blauw Berg, 1500 ft, *Schlechter 8464* (in *Herb. Bolus*) (BOL!, GRA!, PRE!); Cederberg Range, *Shaw in Herb. Bolus 5667* (BOL!, K!); Piquetberg Div.; Piquetberg Range, *Schlechter 7908* (BM!, BOL!, GRA!, K!, MO!, PRE!, S!, W!, Z!).

41. Erica phaeocarpa (N.E.Br.) E.G.H.Oliv., nom. nov.

Simocheilus quadrisulcus N.E.Br. in Flora capensis 4: 368 (1906) non *E. quadrisulcata* L.Bolus: 172 (1923). Types: Prince Albert Div., mountains near Seven Weeks Poort, 5000 ft, *Marloth 2977* (BOL!, K!, PRE!); ?Div., Zwart Berg, *Atherstone 267* (BOL!, -K, fragm!). Lectotype (designated here): *Atherstone 267* (BOL). [Note: the specific epithet '*quadrisulcus*' is regarded as too similar to '*quadrisulcata*' (which is in current use), to warrant its retention in *Erica*. The *Atherstone* collection in BOL is chosen as the lectotype because it was labelled as "type" by Brown with a note requesting a piece for Kew. Both syntypes are very much in the fruiting stage. Change sanctioned by the Commitee on Spermatophyta 1998].

42. Erica anguliger (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Anomalanthus anguliger* N.E.Br. in Flora capensis 4: 389 (1906). Type: Riversdale Div., Garcias Pass, 1000ft, *Galpin 3731* (BOL! lecto.; K!, PRE!). [Note: one of the sheets in BOL and the sheet in K were annotated as "Type" by Brown; the BOL sheet (BOL 45279) is therefore designated here as the lectotype.]

Blaeria puberula Klotzsch: 661 (1833) non *Erica puberula* Bartl. (1832) [=*E. parviflora* L. var. *puberula* (Bartl.) H.Bol.]. *Codonanthemum puberulum* (Klotzsch) Klotzsch: 240 (1838); Benth.: 707 (1839). *Anomalanthus puberulus* (Klotzsch) N.E.Br.: 388 (1906). Type: Cape of Good Hope, *Mundt & Maire s.n.* (B† holo.; -BOL fragm!, K!).

Blaeria parviflorus Klotzsch 8: 665 (1833) non *Erica parviflora* L. (1762). *Codonanthemum parviflorum* (Klotzsch) Klotzsch: 240 (1838); Benth.: 708 (1839). *Anomalanthus parviflorus* (Klotzsch) N.E.Br.: 387 (1906). Type: Cape of Good Hope, *Mundt et Maire s.n.* (B†, holo.; iso.?).

Anomalanthus discolor Klotzsch: 239 (1838) non *Erica discolor* Andr.:t.20 (1796); N.E.Br.: 387 (1906). *Codonanthemum discolor* (Klotzsch) Benth.: 708 (1839). Type: in mtns altit.IV near farm of Gideon Joubert in Kannaland not far from Gouritsrivier, Nov., [loc. 95.11], *Ecklon & Zeyher s.n.* (B†; iso.?); as *292* (MO!).

Anomalanthus scoparius Klotzsch: 239 (1838) non *Erica scoparia* L. (1753); N.E.Br.: 388 (1906). Types: in Houhoek Mtns and near Knoflookskraal, altit. III & IV, Stellenbosch, Jul., *Ecklon & Zeyher s.n.* (B†; iso.?); at Genadendal, rocky places, altit. V, October [30-10-1828], *Drege s.n.* (B†; P!).

Anomalanthus collinus N.E.Br.: 386 (1906) non *Erica collina* Guth. & Bol. (1905). Type: Worcester Div.; Touws River, 2500 ft., *Marloth 2995* (BOL!, K!, L!, NBG!, PRE!).

Anomalanthus curviflorus N.E.Br.: 386 (1906) non *E. curviflora* L. (1753) Type: Caledon Div., Houw Hoek, *Zeyher 3174* (BOL!, K!, PRE!, SAM!).

Anomalanthus marlothii N.E.Br.: 386 (1906) non *Erica marlothii* H.Bol. (1894). Type: Worcester Div., hills near Touws River, 2500 ft, *Marloth 2996* (BOL!, K!, NBG!, PRE!).

Anomalanthus galpinii N.E.Br.: 387 (1906) non *Erica galpinii* T.M.Salter (1935). Type: Riversdale Div., north spur of Mozambique Kop, near Garcias Pass, 2000 ft, *Galpin 3730* (BOL!, K!).

Anomalanthus turbinatus N.E.Br.: 389 (1906) non *Erica turbinata* Andr. (1812) [=*Erica spumosa* L.]. Type: Bredasdorp Div., hills near Elim, 400 ft, *Bolus 8463* (BOL!, K!, PRE!).

Anomalanthus salteri Compton: 340 (1932) non *Erica salteri* L.Bolus (1929). Type: Villiersdorp, 12 July 1931, *T.M.Salter 1155* (BOL, holo.!; K!).

Anomalanthus leslei Compton: 47 (1934). Type: Ceres Show, Oct. 1932, *Compton 4156* (BOL, holo.!; BM).

43. Erica inflaticalyx E.G.H.Oliv., sp. nov.—Frutex erectus ad 600 mm altus. Rami puberuli et pilis glandulosis aliquotque plumosis. Folia 3-nata erecta vel recurvata. Bractea partim recaulescens. Calyx 4-lobatus in fructu multo amplificatus et cucullatus. Corolla 4-lobata obovoidea colliculata. Stamina 4 libera exserta. Ovarium 2-loculare; ovulum unum in quoque lovulo, pendulum. Fructus indehiscens pericarpio papyraceo, testa gracili.

Typus: Western Cape, 3321DD, Outeniqua Mtns, foothills of Elandsberg/Zebrakop above farm Perdebont, 700 m, 7 Sept 1996, *Y van Wijk 924* (NBG!, holo.; BM!, K!, MO!, NY!, PRE!).

44. Erica kammanassieae E.G.H.Oliv., sp. nov.—Frutex erectus ad 0.8 m altus. Rami puberuli pilis reflexis. Folia 3-nata erecta puberula. Flores 3-nati 2-verticillati; bractea partim recaulescens; bracteolae 2. Calyx 4-lobatus accrescens. Corolla 4-lobata obovoidea colliculata. Stamina 4 libera exserta; antherae muticae. Ovarium 1-loculare assymmetricum; ovulum 1; stylus lateralis; stigma peltatum. Fructus indehiscens pericarpio crasso, testa tenuissima.

Typus: Western Cape, 3322DB, Kammanassie Mtns, N slopes above Buffelsklip, plot 456, arid fynbos on N-facing slopes, 4100 ft, 4-08-1979, *Campbell 14561*, (NBG!, holo.)

45. Erica cetrata E.G.H.Oliv. nom. nov.

Eremia peltata Compton in Journal of South African Botany 1: 147 (1935), non *Erica peltata* Andr.: t.276 (1812); E.G.H.Oliv.: 36 (1976). Type: Ceres Wildflower Show, Oct. 1934, *Compton 4921* (BOL, holo.!).

46. Erica bokkeveldia E.G.H.Oliv., nom. nov.

Eremia calycina Compton in Journal of South African Botany 1: 146 (1935), non *Erica calycina* L.: 507 (1762); E.G.H.Oliv.: 38 (1976). Type: Cold Bokkeveld, Rosendal, *Compton 4939* (BOL, holo.!).

Eremia virgata Compton: 148 (1935), non *Erica virgata* Thunb.: 18 (1785) [=*Erica hispidula* L.]. Type: Ceres Wildflower Show, *Compton 4933* (BOL, holo.!).

47. Erica curvistyla (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Eremiopsis curvistyla* N.E.Br. in Flora capensis 4: 390 (1906); *Eremia curvistyla* (N.E.Br.) E.G.H.Oliv.: 39 (1976). Types: Worcester Div., *Niven s.n.* (K, lecto.!; BOL!, TCD!); without locality, *Herb Salisb. s.n.* (BOL!, K!); without locality, *Ward s.n.* (K!). Lectotype designated by Oliver (1976).

48. Erica recurvifolia E.G.H.Oliv., nom. nov.

Eremia recurvata Klotzsch in Linnaea 12: 498 (1838), non *Erica recurvata* Andr.: t.282 (1812); Benth.: 700 (1839); N.E.Br.: 333 (1905); E.G.H.Oliv.: 42 (1976). Type: Cedarbergen, *Drege s.n.* (B†, holo.; iso.?). Neotype: Cedarberg, near Ezelbank, *Drege 2965* (E, neo.!; BM!, BOL!, G!, G-DC!, K!, MO!, P!, PRE!, TCD!, W!), designated by Oliver (1976).

49. Erica totta Thunb., Dissertatio botanica de Erica: 18 (1785); Thunb.: 70 (1794); Thunb.: 348 (1823); Bartl.: 647 (1832). *Eremia totta* (Thunb.) D.Don: 156 (1834); Klotzsch: 218 (1838); Benth.: 699 (1839) p.p.; N.E.Br.: 332 (1905); E.G.H.Oliv.: 33 (1976). *Euremia totta* (Thunb.) Rach: 789 (1855). Type: Cape, *Thunberg (a) no. 9437* (UPS, holo.!).

Erica ferox Salisb.: 324 (1802), nom. superfl., type as for *E. totta*.

Erica pectinata Bartl.: 647 (1832). Type: Tulbagh Kloof, *Ludwig & Beil s.n.* (B†, holo.; GOET!).

Eremia bartlingiana Klotzsch: 218 (1838); Benth.: 699 (1839). *Euremia bartlingiana* Rach: 789 (1855). *Eremia totta* var. *bartlingiana* N.E.Br.: 333 (1905). Type: Du Toit's Kloof, *Drege s.n.* (B†, holo.; K!, P!).

50. Erica lateriflora E.G.H.Oliv., nom. nov.

Grisebachia secundiflora E.G.H.Oliv. in Bothalia 13: 91 (1980), non *Erica secundiflora* Tausch: 617 (1834) [=*Erica viscaria* L.]. Type: Cape, Ceres District, Swartruggens in the Cold Bokkeveld, *Oliver 6105* (NBG[STE] holo.!; BM!, BOL!, E!, G!, K!, MO!, NBG!, P!, PRE!, S!, W!).

51. Erica eremioides (MacOwan) E.G.H.Oliv., comb. nov.

Basionym: *Grisebachia eremioides* MacOwan in Journal of Linnean Society, London 25: 392 (1890); N.E.Br.: 349 (1906); Compton: 151 (1935). Types: Witsenberg and Houw Hoek, *Zeyher 1117* (BOL!, G!, K!, NBG!, SAM!, W!); near Tulbagh Waterfall, *MacOwan 2685* (SAM!); ibid., *MacOwan sub Herb. Norm. 564* (BM!, BOL!, G!, K!, P!, PRE!, SAM!, UPS!, W!). Lectotype, designated here: *MacOwan 2685* (SAM).

Key to subspecies

Leaves erect to spreading, straight or slightly curved; calyx lobes acute to obtuse
  Corolla tube glabrous or puberulous in lower $^2/_3$; calyx usually glabrous .... subsp. ***eremioides***
  Corolla tube pubescent all over; calyx pubescent .... subsp. ***pubescens***
Leaves markedly recurved; calyx lobes subquadrate, subtruncate .... subsp. ***eglandula***

(a) subsp. **eremioides**

Eremia parviflora Klotzsch: 498 (1838), non *Erica parviflora* L.: 506 (1762); N.E.Br.: 334 (1905). *Grisebachia parviflora* (Klotzsch) Druce: 625 (1917); E.G.H.Oliv.: 86 (1980). Type: hills between Puspas Valley and Kogmanskloof mountains [loc. 96], *Ecklon & Zeyher s.n.* (B†, holo.; iso.?). Neotype: flats between Witsenberg and Skurfdeberg, *Zeyher 1117* (K! neo.; BOL!, G!, NBG!, SAM!, W!), designated by Oliver (1980).

Erica shalliana Hort. Berol. ex Klotzsch: 498 (1838), nomen nudum.

Grisebachia eremioides MacOwan var. *pubicalyx* N.E.Br.: 349 (1906). Type: Tulbagh Div., mtns of Tulbagh Kloof, 1400 ft, *Bolus 5304* (BOL!, K!, PRE!, SAM!).

Grisebachia similis N.E.Br.: 350 (1906). Type: Cold Bokkeveld, *Schlechter 8896* (BM!, BOL!, E!, G!, K!, MO!, NBG!, P!, PRE!, S!, W!).

(b) subsp. **eglandula** (N.E.Br.) E.G.H.Oliv. comb. nov.

Basionym: *Grisebachia eremioides* MacOwan var. *eglandula* N.E.Br. in Flora capensis 4: 349 (1906). *Grisebachia parviflora* (Klotzsch) Druce subsp. *eglandula* (N.E.Br.) E.G.H.Oliv.: 88 (1976). Type: Cedarberg Range at Ezels Kop, *Schlechter 8818* (BM!, BOL!, G!, K!, NBG!, P!, PRE!, Z!); near Clanwilliam, *Leipoldt 135* (BOL!, lecto.). Lectotype designated by Oliver (1976). [Note: The lectotype was the only syntype annotated by Brown; it is unfortunately without locality].

(c) subsp. **pubescens** (E.G.H.Oliv.) E.G.H.Oliv., comb. nov.

Basionym: *Grisebachia parviflora* (Klotzsch) Druce subsp. *pubescens* E.G.H.Oliv. in Bothalia13: 89 (1976). Type: Cape, Ceres Dist.: Katbakkies in the Swartruggens (-DC), *Oliver 4310* (NBG [STE], holo.; BM, BOL, E, G, K, MO, NBG, PRE, S).

52. Erica plumosa Thunb., Prodromus plantarum capensium 1: 73 (1794); Salisb.: 339 (1802); Schultes: 364 (1823). *Blaeria plumosa* Thunb.: 9 (1802); Type: *Thunberg no. 9393* (UPS!).

Blaeria ciliaris L.f.: 122 (1782) non *Erica ciliaris* L. (species europea); Willd.: 631 (1798); Wendl.: 49 (1805); Ait.: 249 (1810); Roem. & Schultes: 170 (1818); Klotzsch: 658 (1833); G.Don: 805 (1834). Type: Herb. Linn. (LINN, holo.; K, fragm.!). *Grisebachia ciliaris* (L.f.) Klotzsch: 255 (1838), quoad nom. excl. spec. in herb. Willd. No. 2890.

Erica ciliciiflora Salisb.: 339 (1802). *Blaeria ciliciiflora* (Salisb.) G.Don: 805 (1834); *Grisebachia ciliciiflora* (Salisb.) Druce: 625 (1917); *Grisebachia ciliaris* subsp. *ciliciiflora* (Salisb.) E.G.H.Oliv.: 79 (1980). Type: Hottentots-Holland, *Masson s.n.* (BM!).

Blaeria incana Bartl.: 650 (1832); *Grisebachia incana* (Bartl.) Klotzsch: 225 (1838); Benth.: 701 (1839); N.E.Br.: 344 (1906); E.G.H.Oliv.: 81 (1980); Type: on flats below Tygerberg at Rietvallei, *Ecklon s.n.* (B†, holo.; P!, lecto). Lectotype designated by Oliver (1980).

Grisebachia hirta Klotzsch: 226 (1838); Benth.: 701 (1839); N.E.Br.: 345 (1906). *Grisebachia plumosa* subsp. *hirta* (Klotzsch) E.G.H.Oliv.: 74 (1980). Type: sand flats near Groenkloof, *Drège s.n.* (B†), distributed as *7795* (BM!, BOL!, E!, G!, G-DC!, HAM!, K!, MEL!, MO!, P! lecto., PRE!, W!), Lectotype designated by Oliver (1980).

Grisebachia hispida Klotzsch: 226 (1838); Benth.: 701 (1839); Rach: 790 (1855); N.E.Br.: 339 (1906). *Grisebachia plumosa* subsp. *hispida* (Klotzsch) E.G.H.Oliv.: 72 (1980). Type: near Olifantsrivier and farm Brakfontein, July, *Ecklon & Zeyher s.n.* (B†, holo.; iso.?), distributed as *267* (G! lecto., S!, W!); mountains at Winterhoek, Witsenberg and near Vogelvlei, *Ecklon & Zeyher s.n.* (B†; LD!, P!,). Lectotype designated by Oliver (1980).

Grisebachia involuta Klotzsch: 227 (1838); Benth.: 701 (1839); Drège: 72 (1843); N.E.Br.: 340. *Grisebachia ciliaris* subsp. *involuta* (Klotzsch) E.G.H.Oliv.: 79 (1980). Type: Boschkloof, *Drège s.n.* (B†, holo.; G!, G-DC!), distributed as *7801* (BOL!, K! lecto., P!, S!). Lectotype designated by Oliver (1980).

Grisebachia plumosa Klotzsch: 226 (1838) non *Erica plumosa* Thunb.; E.G.H.Oliv.: 69 (1980), Types: Doornhoogde on the Cape Flats, *Ecklon & Zeyher s.n.* (B†), distributed as *268* (G!, MO! lecto., S!, W!); Doornhoogde, *Drège s.n.* (B†). Lectotype designated by Oliver (1980).

Grisebachia velleriflora Klotzsch: 227 (1838); Benth.: 701 (1839); N.E.Br.: 341 (1906). Type: between Twenty-four Rivers and Olifants River, *Drège s.n.* (B†, holo.; P!).

Grisebachia zeyheriana Klotzsch: 227 (1838); N.E.Br.: 342 (1906). Type: near Olifantsrivier and Farm Brakfontein, *Ecklon & Zeyher s.n.* (B†), distributed as *269* (G!, K!, LU!, MEL!, MO!, P!, S!, SA!, W!).

Blaeria ptilota E.Mey. ex Benth.: 701 (1839). Type: *Drège s.n.* (B†, iso.?).

Grisebachia dregeana Benth.: 701 (1839); N.E.Br.: 342 (1906). Type: Cape Colony, *Drège 7803* (K!).

Grisebachia serrulata Benth.: 701 (1839). *Grisebachia plumosa* var. *serrulata* (Benth.) N.E.Br.: 346 (1906). Type: Giftberg, *Drège 7802* (BM!, K!, MO!, P!, W!)

Grisebachia thunbergii Rach: 789 (1853); N.E.Br.: 347 (1906). Type as for *Erica plumosa*.

Grisebachia pentheri Zahlbr.: 42 (1905); N.E.Br.: 1128 (1909). *Grisebachia plumosa* subsp. *pentheri* (Zahlbr.) E.G.H.Oliv.: 73 (1980). Type: Elandsfontein, Clanwilliam, Aug. 1894, *Penther 2925* (BM!, BOL!, NBG!, W!).

Grisebachia dregeana var. *vestita* Zahlbr.: 43 (1905). Type: Olifants River valley, *Penther 2917* (W!).

Grisebachia alba N.E.Br.: 344 (1906). Type: without locality, *Grey s.n.* (K!).

Grisebachia apiculata N.E.Br.: 341 (1906). Type: mountains near Piekenier's Kloof, *Schlechter 469* (BM!, BOL!, G!, K! holo., NBG!, P!, PRE!, S!, W!, Z!).

Grisebachia bolusii N.E.Br.: 340 (1906). *Grisebachia ciliaris* subsp. *bolusii* (N.E.Br.) E.G.H.Oliv.: 78 (1980). Type: mountains near Pakhuis Pass, *Bolus 8681* (BOL!, K!, NBG!, NH!, PRE!, Z!).

Grisebachia nivenii N.E.Br.: 343 (1906); E.G.H.Oliv.: 84 (1980). Types: Hottentots-Holland, ?*Niven 128* (BOL!, K!, lecto.); near Zondereinde River, *Gill s.n.* (K!); near Swellendam, *Mund 3* (K!, PRE!). Lectotype designated by Oliver (1980).

Grisebachia pilifolia N.E.Br.: 346 (1906), Type: near Clanwilliam, *Leipoldt 46* (BM!, BOL!, K!, PRE!, SAM!).

Grisebachia plumosa var. *scabra* N.E.Br.: 346 (1906). Type: without locality, *Thom s.n.* (BOL!).

Grisebachia rigida N.E.Br.: 343 (1906); E.G.H.Oliv.: 83 (1980). Types: near Brand Vley, *Schlechter 9926* (BM!, BOL!, Z!); mountains between French Hoek and Villiersdorp, *Bolus 5193* (BOL!, K! lecto, PRE!, Z!). Lectotype designated by Oliver (1980).

Grisebachia solivaga N.E.Br.: 347 (1906). Type: Zeekoe Vlei, Clanwilliam, *Schlechter 8480* (BM!, BOL!, E!, G!, K!, MO!, P!, PRE!, W!).

Grisebachia ciliaris subsp. *multiglandulosa* E.G.H.Oliv.: 80 (1980). Type: Cape, Olifants River valley above Toorgat on farm Grootfontein, *Oliver 3972* (NBG/STE, holo.!; K!, MO!, NBG!, PRE!).

Grisebachia plumosa subsp. *eciliata* E.G.H.Oliv.: 72 (1980). Type: Ordinansiekop, Gifberg, *Oliver 4951* (NBG/STE!, holo.; BOL!, K!, NBG!, MO!, PRE!, S!).

Grisebachia plumosa subsp *irrorata* E.G.H.Oliv.: 72 (1980). Type: Bokbaai, *Taylor 5011* (NBG/STE!, holo.; PRE!).

53. Erica caprina E.G.H. Oliv., nom. nov

Eremia calycina Compton in Journal South African Botany 1: 146 (1935), non *Erica calycina* L. (1762); E.G.H.Oliv.: 38 (1976). Type: Cold Bokkeveld, Rosendal, *Compton 4939* (BOL!).

Eremia virgata Compton: 148 (1935), non *Erica virgata* Thunb. (1785) [=*Erica hispidula* L.]. Type: Ceres Wildflower Show, Compton 4933 (1935).

54. Erica arachnocalyx E.G.H.Oliv., nom. nov.

Acrostemon viscidus N.E.Br. in Flora capensis 4: 355 (1906); *Arachnocalyx viscidus* (N.E.Br.) E.G.H.Oliv.: 268 (1984). Types: Ceres Flats, *Guthrie 2181* (BOL!, K!); Skurfdeberg Range near Elandsfontein, *Schlechter 10013* (BOL! lecto.; G!, K!, PRE!, S!, W!). Lectotype: *Schlechter 10013* (BOL), lectotype designated by Oliver (1984).

55. Erica cereris (Compton) E.G.H.Oliv., comb. nov.

Basionym: *Arachnocalyx cereris* Compton in Journal South African Botany 1: 144 (1935). Type: Ceres Div. without exact locality, Ceres Wild Flower Show, 2 October 1933, *Compton 4424* (BOL holo.!).

56. Erica jonasiana E.G.H.Oliv., sp. nov.—Fruticulus prostratus effusus. Rami pubescentes. Folia 3-nata apicaliter strigosa. Flores 3-nati 2-verticillati umbellati, bractea basale, bracteolae 2. Calyx 4-lobatus parum connatus, lobis lanceolatis sparse et breviter ciliatis. Corolla 4-lobata urceolata 8-angulosa rosea glabra colliculata. Stamina 4 libera manifesta, filamentis pilosis, antheris muticis, polline in tetradis. Ovarium 1-loculare, asymetricum ellipsoideum pubescens; ovulum 1, pendulum; stylus base flexus; stigma subcapitata. Fructus partim dehiscens.

Typus: Western Cape, 3319DC, Villiersdorp, Paulsgat area above Kleinfontein, gentle slopes SW of Vetkop, 2000 ft, 4-10-1996, *Oliver 10726* (NBG!, holo.; iso. BM!, BOL!, E!, G!, K!, MEL!, MO!, NBG!, NY!, P!, PRE!, S!, W!, Z!).

57. Erica karwyderi E.G.H.Oliv., sp. nov.—Fruticulus erectus. Rami puberuli. Folia 3-nata glabra. Flores 3-nati 1-verticillati inflorescentibus aggregatis, bractea parte recaulescens approximata, bracteolae 2. Calyx 4-lobatus quadrangularis cartilagineus pubescens. Corolla 4-lobata tubulosa 4-angulosa colliculata. Stamina 8 libera exserta, antherae muticae, pollen in monadis. Ovarium 2-loculare 2-lobatum glabrum, ovulum 1 pendulum in quoque loculo, stigma simplex. Fructus indehiscens.

Typus: Western Cape, 3419AC, Caledon Dist., Karwyderskraal, sandy E-facing slopes NW of farmsteads, 700 ft [210 m], 23-06-1989, *Oliver 9227* (NBG!, holo.; BM!, BOL!, E!, G!, K!, MEL!, MO!, NY!, P!, PRE!, S!).

58. Erica platycalyx E.G.H.Oliv., nom. nov.

Platycalyx pumila N.E.Br. in Flora capensis 4: 335 (1905), non *Erica pumila* Andr.: t.234/t.258 (1809). Type: Riversdale Div., near Riversdale, *Rust 543* (BOL, holo.!; -K, fragm.!, -PRE, fragm.!). [Note: The Rust specimen in BOL, which Brown annotated as the type, consists of a mounted branchlet, mounted flower and some loose flowers given to Bolus when he made a sketch of the full original collection in Berlin. Brown could well have seen the Berlin sheet as he saw sheets of other species known to have been sent sent on loan to Kew, so it is surprising he did not cite it. The K and PRE specimens are a few loose flowers from the BOL collection.]

59. Erica vlokii E.G.H.Oliv., sp. nov.—Fruticulus erectus. Rami canescentes pilis retrorsis. Folia 3-nata glabra. Flores 3-nati 1-verticillati; pedicellus pilis reflexis; bractea partim recaulescens approximata; bracteolae 2. Calyx 4-partitus, segmentis rhombicis usque ovatis membranaceis roseis. Corolla 4-lobata ellipsoidea glabra rosea. Stamina 8 libera manifesta; antherae muticae vel rare minute calcaratae; pollen in monadis. Ovarium 4-loculare oblatum subemarginatum; ovulum 1 in quoque loculo; stylus exsertus; stigma truncatum. Fructus indehiscens endocarpio indurato lignoso, testa pergracili.

Typus: Western Cape, 3322CD, Herold area, Camferskloof, lower E side, NE slopes, 640 m, 27-08-1989, *Oliver 9243* (NBG!, holo.; BM!, BOL!, E!, G!, K!, MO!, P!, PRE!, S!).

60. Erica outeniquae (Compton) E.G.H.Oliv., comb. nov.

Basionym: *Eremiella outeniquae* Compton in Journal of South African Botany 19: 120 (1953); E.G.H.Oliv.: 46 (1976). Type: Ruyterskop, Mossel Bay, *Compton 21818* (NBG!, holo.!; BOL!, K!, PRE!).

61. Erica velatiflora E.G.H.Oliv., nom. nov.

Eremia brevifolia Benth. in De Candolle, Prodromus 7: 700 (1839), non *Erica brevifolia* Soland. ex Salisb.: 338 (1802); N.E.Br.: 334 (1905); E.G.H.Oliv.: 43 (1976). Types: Cape, Attaquaskloof, George Div., *Masson [=Niven] 57* (K lecto.!; BOL!, MEL!); Cape, Attaquaskloof, George Div., *Niven 85* (BM!, G-DC!, K!); lectotype designated by Oliver (1976).

62. Erica stokoeanthus E.G.H.Oliv., nom. nov.

Stokoeanthus chionophilus E.G.H.Oliv. in Bothalia 12: 49 (1976), non *Erica chionophila* Guth. & Bolus: 181 (1905). Type: Cape, 3418 (Simonstown), Somerset Sneeukop, south-facing slopes on shale band south of main peak, 1480 m, (-BB), 8 Nov 1973, *Oliver 4790* (NBG[STE] holo.!; BM!, BOL!, C!, E!, G!, GRA!, K!, MEL!, MO!, NBG! NY, P!, PRE!, S!, W!, Z!).

63. Erica jacksoniana H.A.Baker in Journal of South African Botany 35: 28 (1969), non *Erica jacksonii* Paxton (1841), hybrida. Type: Caledon district, Hottentots-Holland Mountains, Eastern slopes of Moordenaarskop, c.3800 ft, 5.April 1967, *Jackson s.n.* (NBG!, holo.).

64. Erica perplexa E.G.H.Oliv. sp. nov.—Frutex erectus. Rami pilis longis plumosis. Folia 3-nata, pilis marginatis plumosis parvis. Flores 3-nati 1-verticillati, terminales; bractea bracteolaeque perfecte recaulescentes. Calyx inaequaliter 4-lobatus. Corolla 4-lobata, cyathiformis vel obovoidea, glabra. Stamina 8(7) inclusa; filamenta libera vel plus minusve conjuncta geniculata; antherae adherrentes, muticae; pollen in tetradis. Ovarium [1]2 vel 3[4]-loculare ovoideum colliculatum; ovulum 1 per loculo; stylus brevissimus; stigma cyathiforme–infundibuliforme inclusum vel manifestum. Fructus indehiscens, pericarpio tenui fragili seminibus atrobrunneis laevibus rostellatis. Typus: Western Cape, 3419AA, Grabouw area, Groenlandberge, SE of Mt. Lebanon, 2700 ft [824 m], 3-05-1985, *Oliver 8740* (NBG!, holo.; BM!, BOL!, E!, G!, K!, MEL!, MO!, NY!, P!, PRE!, S!, W!).

65. Erica subcapitata (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Coccosperma subcapitatum* N.E.Br. in Flora capensis 4: 400 (1906). Type: Cape Div., on the Steenberg Plateau, near Muizenberg, *Wolley Dod 2723* (K, holo.!; BOL!).

Salaxis hexandra Klotzsch: 352 (1834), non *Erica hexandra* (S.Moore) E.G.H.Oliv.: 666 (1992), species zambesiaca; Benth.: 711 (1839). *Coccosperma hexandrum* (Klotzsch) Druce: 615 (1916); T.M.Salter: 662 (1950). Type: Cape of Good Hope, *Forbes s.n.* ex Herb. Soc. Hort. Lond. (B [Herb. Kunth?]†, holo., -BOL fragm.!, -K fragm.!).

Coccosperma forbesianum Klotzsch: 215 (1938); N.E.Br.: 399 (1906), nom. superfl. Type as for *Salaxis hexandra* above.

66. Erica rugata E.G.H.Oliv., nom. nov.

Basionym: *Coccosperma rugosum* Klotzsch in Linnaea 12: 215 (1838) non *Erica rugosa* Andr.: t.236 (1809) [hybrid. ex hort.]; N.E.Br.: 400 (1906). *Salaxis rugosa* (Klotzsch) Benth.: 711 (1839). Type: without locality, from early collections "Zeyheri", *Zeyher s.n.* (B†, holo., -K, fragm.!, -BOL fragm. ex K!,). Lectotype (designated here): Cape, mtns around Kapstadt [Cape Town] [loc. 84], *Zeyher s.n.* [ex B det. Klotzsch] (K!).

67. Erica parviporandra E.G.H.Oliv., sp. nov.—Fruticulus erectus ad 1.5 m altus. Rami pubescentes usque hirsuti pilis simplicibis usque stellatis usque plumosis, interdum glandibus. Folia 3-nata erecta. Flores 3-nati 1-verticillati terminales; bractea bracteolaeque plene recaulescentes. Calyx impariter 4-lobatus late campanulatus usque cyathiformis, glaber usque puberulus, interdum in marginibus glandibus sessilibus. Corolla 4-lobata obvoidea usque late cyathiformis glaber usque puberula. Stamina (5)6 vel 7(8), inclusa usque manifesta; filamenta libera vel semiconjuncta, poris parvis longitudine $^1/_6$–$^1/_4$ thecae partes aequantibus; pollen in tetradis. Ovarium 1-loculare, late rhomboideo-ellipsoideum, 4-angulosum; ovula 2 in quoque loculo pendula; stylus brevissimus; stigma manifestum usque plus minusve exsertum. Fructus indehiscens endocarpio lignoso, testa crassa.

Typus: Western Cape, 3321CD, Riversdale Dist., Langeberg just NE of Garcia's Forest Station, (hairy form), 1626 ft [396 m], 13-12-1984, *Oliver 8626* (NBG!, holo.; BM!, BOL!, E!, G!, K!, MEL!, MO!, NY!, P!, PRE!, S!, W!, Z!).

68. Erica remota (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Scyphogyne remota* N.E.Br. in Flora capensis 4: 413 (1906). Type: Caledon Div., near the River Zondereinde, 7000 [700] ft, *Schlechter 9897*(K, holo.!; BM!, BOL!, G!, P!, PRE!, S!, W!).

69. Erica areolata (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Coccosperma areolatum* N.E.Br. in Flora capensis 4: 399 (1906). Types: Clanwilliam Div., Koude Berg, 4000 ft, *Schlechter 8757* (BM!, BOL!, G!, K!, MO!, PRE!, S!, W!, Z!); Clanwilliam Div., Koude Berg, 4000 ft, *Schlechter 8772* (BOL!, G!, K!, NBG!, P!, PRE!, S!, W!); Tulbagh Div., on the Witsen Berg, near Tulbagh, *Burchell 8710* (K!, PRE!). Lectotype (designated here): *Schlechter 8757* (K!). [Note: Brown based his species on three collections, but labelled the *Schlechter 8757* at Kew as the type. This is in fruit as is *Burchell 8710*, whereas *Schlechter 8772* is in full flower. This collection must therefore be selected as the lectotype.]

70. Erica artemisioides (E.Mey. ex Klotzsch) E.G.H.Oliv., comb. nov.

Basionym: *Salaxis artemisioides* E.Mey. ex Klotzsch in Linnaea 12: 212 (1838), [*Erica artemisioides* E. Mey. ms. in synon.]; Benth.: 711 (1839). *Salaxis octandra* Klotzsch var. *artemisioides* (E.Mey. ex Klotzsch) N.E.Br.: 404 (1906). Type: Dietrisklooft [Dutoitskloof], altit. IV., *Drege s.n* (B†, holo., -K fragm. ex B!; G-DC!, P!, SAM!). Lectotype (designated here): *Drege s.n.* (K, fragm ex B!).

Salaxis micrantha Benth.: 711 (1839). *Scyphogyne micrantha* (Benth.) N.E.Br.: 414 (1906). Type: Cape Colony, *Roxburgh s.n.* (K, holo.!; -BOL, fragm.!; S!).

71. Erica calcicola (E.G.H.Oliv.) E.G.H.Oliv., comb. nov.

Basionym: *Scyphogyne calcicola* E.G.H.Oliv. in South African Journal of Botany 13: 448 (1981). Type: Bredasdorp Div, limestone hills near Heidehof (Awila) just north of Pearly Beach, *Oliver 7604* (NBG[STE], holo.!; BM!, BOL!, K!, MO!, NY ex NBG!, PRE!, S!).

72. Erica axillaris Thunb., Dissertatio botanica de Erica: 16 (1785); Thunb.: 69 (1794); Thunb.: 345 (1823). *Salaxis axillaris* (Thunb.) G.Don: 828 (1834); Klotzsch: 211 (1938); Benth.: 711 (1839); Rach: 792 (1853); N.E.Br. 403 (1906). Type: without locality, *Thunberg s.n.* (UPS, holo.!, -K, fragm.!).

Salaxis hexandra Klotzsch: 352 (1834). Type: Cape of Good Hope, *Forbes s.n. in Herb Kunth* (B†, holo.; -K fragm.!, ?BOL fragm.).

Salaxis octandra Klotzsch: 353 (1834); Klotzsch: 212 (1838); Benth.: 711 (1839): N.E.Br.: 404 (1906). Type: Cape of Good Hope, *Mundt et Maire s.n.* (B†, holo.; LD!, iso.?).

Erica calyciflora Tausch: 617 (1834). Type: *Sieber 176.* (PR, -BOL, fragm.!)

Salaxis flexuosa Klotzsch: 213 (1838); T.M.Salter: 661 (1950). Type: in Tulbaghkloof in Winterhoeksberg, Witsenberg and near Vogelvalley, *Ecklon & Zeyher s.n.* (B†, holo.; iso.?).

Salaxis puberula Klotzsch: 212 (1838); N.E.Br.: 402 (1906); T.M.Salter: 661 (1950). Type: in mtns with *octandra*, Jun. & Jul., mtns at Palmiet River near Grietjestgat farm between Palmiet & Steenbrass Rivers, *Ecklon & Zeyher s.n.* (B†, holo.; K!, P!); as [loc. 56.6] *307* (G!, LD!, MO!, SAM!, W!); as *310* (S!).

Salaxis sieberi Benth.: 711 (1839); N.E.Br.: 404 (1906). Type: near Capetown, without collector [presumably Sieber] (K!). See *calyciflora* above..

Salaxis major N.E.Br.: 403 (1906); T.M.Salter: 661 (1950). Type: Cape Div., hills about Simons Bay, *Prior 3* (K, holo.!; BOL!, PRE!).

Salaxis flexuosa var. *cognata* N.E.Br.: 405 (1906). Types: Cape Div., foot of Muizen Berg, near Fish Hoek, 100 ft, *Bolus 4478* (BOL!, K!); mtns near Simons Town, 1700 ft. *Bolus 4684* (BOL!, SAM!); Caledon Div., Houw Hoek, 1500 ft, *Schlechter 7327* (BM!, BOL!, E!, G!, GRA!, K!, MO!, P!, PRE!, S!, SAM!, W!, Z!); Hermanus, *Guthrie 3420* (BOL!); Bredasdorp Div., near Elim, 150–800 ft, *Bolus 6771* (BOL!); ibid. *Schlechter 7643* (BOL!, E!, G!, GRA!, K!, MO!, P!, PRE!, Z!).

73. Erica boucheri E.G.H.Oliv., sp. nov.—Planta erecta ad 500 mm alta. Rami canopubescentes pilis reflexis. Folia 3-nata imbricata glabra. Flores 3-nati 1- vel 2-verticillati; bractea bracteolaeque plene recaulescentes. Calyx impariter 4-lobatus glaber. Corolla 4-lobata obovoidea usque obovoideo-urceolata glaber. Stamina 4 inclusa libera; filamenta lata; antherae muticae laeves poro magno, pollen in tetradis. Ovarium 1(2)-loculare ellipsoideum apicale sparse puberulum; ovulum 1 per loculo; stylus distinctus 0.5 mm longus. Fructus mesocarpo crasso lignoso, testa tenuissima.

Typus: Western Cape, 3319CD, Worcester Dist., Ouhangsberg, SE of Beacon 152, stony upper end of shale band, slopes facing E with short fynbos, 777 m, 15-04-1984, *Oliver 8442* (NBG!, holo.; BM!, BOL!, E!, G!, K!, MEL!, MO!, NY!, P!, PRE!, S!, Z!).

74. Erica bredasiana E.G.H.Oliv., nom. nov.

Salaxis pumila N.E.Br. in Flora capensis 4: 402 (1906), non *Erica pumila* Andr.: t.234/258 (1809). Type: Bredasdorp Div., Zeekoe Vley, 100 ft., *Schlechter 10540* (K, holo.!; BM!, BOL!, G!, MO!, NBG!, P!, PRE!, S!, W!, Z!).

75. Erica terniflora E.G.H.Oliv., nom. nov.

Salaxis triflora Compton in Transactions of Royal Society of South Africa 19: 303 (1931) non *Erica triflora* L.: 354 (1753). Types: Witteberg (Whl.) [=Whitehill] summit, 5000 ft, 21 May 1925, *Compton 2953* (BM!, BOL!); ibid., 23 May 1926, *Compton 2987* (BM!, BOL!); ibid., 23 May 1926, *Compton 2990* (BM!, BOL!); ibid., 23 May 1926, *Compton 2991* (BM!, BOL!); ibid., 4500 ft, 28 Oct 1926, *Compton 3188* (BM!, BOL!). Lectotype (designated here): *Compton 2987* (BOL).

76. Erica binaria E.G.H.Oliv., sp. nov.—Planta erecta. Rami pubescentes pilis expansis. Folia 3-nata erecta usque subeffusa. Flores 3-nati 1-verticillati; bractea bracteolaeque plene recaulescentes. Calyx impariter 4-lobatus glaber. Corolla 4-lobata obovoidea glabra. Stamina 8(6); filamenta libera vel base conjuncta; antherae muticae pilis basalibus; pollen in tetradis. Ovarium 2-loculare; ovulum 1 in quoque loculo, pendulum; stylus 0.2 mm longus. Fructus indehiscens drupaceus.

Typus: Western Cape, 3318DD, Stellenbosch Dist., Jonkershoek, summit of The Twins, just S of beacon, 1490 m, 29 March 1997, *Oliver 10783* (NBG!, holo.; BM!, BOL!, K!, MO!, NY!, PRE!, S!, W!).

77. Erica serrata Thunb., Prodromus plantarum capensis: 69 (1794); Thunb.: 346 (1823). *Blaeria serrata* (Thunb.) Thunb.: 6 (1802). *Nagelocarpus serratus* (Thunb.) Bullock: 533 (1954); Levyns: 147 (1956). Type: without locality, *Thunberg s.n.* (UPS, holo.!).

Lagenocarpus imbricatus Klotzsch: 214 (1838); Benth.: 710 (1839); N.E.Br.: 417 (1906). Types in rocky places (Gnadenthal) Oct., *Drege s.n.* (B†; K!); in mtns "Zwartberg, Babylons-Toorensberg, Klynriviersberge" (altit. II–IV.) (Gnadenthal, Caledon), *Ecklon & Zeyher s.n.* (B†; E!, G!, K!, LD!, M!, MO!, P!, PRE!, S!, SAM!, UPS!, W!); in mtns "Houhoeksberge" (altit. I–IV.) (Stellenbosch), July–Aug., *Ecklon & Zeyher s.n.* (B†; S!).

Salaxis ciliata Benth.: 711 (1839). *Lagenocarpus ciliata* (Benth.) N.E.Br.: 418 (1906). *Nagelocarpus ciliata* (Benth.) Bullock: 533 (1954). Type: in Cape Colony, *Burchell s.n.* (K, holo.!).

78. Erica urceolata (Klotzsch) E.G.H.Oliv., comb. nov.

Basionym: *Tristemon urceolatus* Klotzsch in Linnaea 12: 245 (1838). *Scyphogyne urceolata* (Klotzsch) Benth.: 709 (1839); N.E.Br.: 415 (1906); T.M.Salter: 662 (1950); E.G.H.Oliv.: 284 (1984). Types: Cape of Good Hope, in mtns near town "Cap" (Prov. Cap) [Cape Town], *Bergius s.n.* (B†, BOL!, K, lecto.!); ibid., *Ecklon & Zeyher s.n.* (B†; P!), as *298* (G!, LD!, MO!, S!, SAM!, W!). Lectotype: *Bergius s.n.* (K) [ex B determined by Klotzsch] designated by Oliver (1984).

Tristemon puberula Klotzsch: 245 (1838); Benth.: 709 (1839); N.E.Br.: 416 (1906). Type: in mtn "Zwartberg" and at hotspring near town "Caledon" and in hills in the vicinity, Jul. & Aug., *Ecklon & Zeyher s.n.* (B†; iso.?); as *Ecklon s.n.* ex B det. Klotzsch (K!).

Scyphogyne burchellii N.E.Br.: 416 (1906). Types: Matroosberg, 700ft, *Bolus in Herb Guthrie 3942* (BOL!); tops of mtns of Baviaanskloof near Caledon, *Burchell 7747* (K!, PRE!); ibid., *Schlechter 9874* (BOL!, BOL!, K!, MO!, PRE!).

Scyphogyne trimera N.E.Br.: 415 (1906). Types: without locality, *Sieber 175* (BOL!, G!, G-DC!, K!, M!, MO!, P!, PRE!, W!); Cape Div.; eastern slopes of Devils Mountain, 1500 ft, *Bolus 4496* (BM!, BOL!, K!, Z!).

79. Erica muscosa (Aiton) E.G.H.Oliv., comb. nov.

Basionym: *Blaeria muscosa* Aiton, Hortus Kewensis edn 1,1: 150 (1789); Willd.: 630 (1798); Aiton: 249 (1810); Roem. & Schult.: 169 (1818); Klotzsch: 665 (1833). *Omphalocaryon muscosum* (Aiton) Klotzsch: 243 (1838) [α *pubescens*]; Rach: 792 (1853). *Scyphogyne muscosa* (Aiton) Druce: 646 (1916): T.M.Salter: 662 (1950). Type: without locality, *Masson s.n.* (BM holo.!).

Erica albens Thunb.: 70 (1794), non L. (1771). Type: without locality, *Thunberg s.n.* (UPS).

Erica albida Thunb.: 347 (1823). *Blaeria albida* (Thunb.) Thunb.: 9 (1802). Type: without locality, *Thunberg s.n.* (UPS!).

Blaeria pusilla Wendl.: 13, t.79 (1819) non L: 39 (1767) (=*E. glabra* Thunb.). Type: l.c. t.79.

Scyphogyne inconspicua Decaisne: t.54 (1829); Benth.: 709 (1839); N.E.Br.: 709 (1906). Type: op. cit. t.54. (iconotype).

Omphalocaryon muscosum var. *glabrum* Klotzsch: 244 (1838). *Scyphogyne inconspicua* var. *glabriflora* N.E.Br.: 408 (1906). Types: Tafelberg, *Ecklon & Zeyher s.n.* (B†; P!); in mtns near city "Cap", *Ecklon & Zeyher s.n.* (B†; SAM!); near Doornhoogde on Cape flats, *Ecklon & Zeyher s.n.* (B†); in Klynriviersberg; in Zwartberg and at town Caledon and hills in vicinity, *Ecklon & Zeyher s.n.* (B†); in mtns at Palmietrivier near farm Grietjiesgat between Palmiet and Steenbrassensrivier (Stellenbosch), *Ecklon & Zeyher s.n.* (B†). east side of Tafelberg near Constantia, *Ecklon & Zeyher s.n.*(B†); as *298* (G!, LD!, MEL!, S!, W!).

Scyphogyne schlechteri N.E.Br.: 409 (1906). Type: Ceres Div., near Sand River in the Cold Bokkeveld, *Schlechter 10111* (K, holo.!; BM!, BOL!, G!, MO!, P!, PRE!, S!, W!).

Scyphogyne inconspicua Decaisne var. *ciliata* N.E.Br.: 408 (1906). *Erica albida* Thunb. p.p. quoad specimen β herb. Thunb. Type: *Herb Thunberg sheet β* (UPS).

Scyphogyne inconspicua Decaisne var. *pubescens* N.E.Br.: 408 (1906). Types: Clanwilliam Div.; Ezelsbank, *Schlechter 8828* (BM!, BOL!, G!, K!, MO!, P!, PRE!, S!, W!, Z!); Cape Div.; Kasteel Mountain, *Ecklon 296* (G!, K!, M!, MO!, W!); Caledon Div.; near Steenbrass River, *Guthrie 2725* (BOL!); Bredasdorp Div.; Elim, *Schlechter 7663* (BM!, BOL!, G!, K!, P!, PRE!, Z!); Riversdale Div.; lower part of the mountain at Garcia's Pass, *Burchell 6928* (K!, P!).

Scyphogyne inconspicua Decaisne var. *vestita* N.E.Br.: 408 (1906). Type: Ceres, near Ceres, *Bolus 8483* (BOL, K, PRE, Z).

80. Erica phacelanthera E.G.H.Oliv., nom. nov.

Omphalocaryon capitatum Klotzsch in Linnaea 12: 244 (1838) non *Erica capitata* L.: 355 (1753). *Scyphogyne capitata* (Klotzsch) Benth.: 710 (1839); N.E.Br.: 413 (1906). Types: mountains near Caledon and Genadendal, *Ecklon & Zeyher s.n.* (B†; C!, E!, MEL!, S!, UPS!, Z!); as *301* (BOL! SAM!); mountains between Hottentots-Holland and Caledon, *Ecklon & Zeyher s.n.* (B†; iso.?), as *301* (MO!, MEL!, S!); as *309* (G!, W!). Lectotype, designated here: Cape of Good Hope, *Ecklon s.n.*[ex B determined by Klotzsch] (K!).

Scyphogyne viscida N.E.Br.: 414 (1906), non *Erica viscida* Wendl.: 7 (1804) [=*E. longifolia* L.]. Type: Robertson Div., rocky hills near Montagu Bath, *Bolus 6721* (BOL holo.!; K!).

Scyphogyne brevifolia Benth.: 710 (1839), non *Erica brevifolia* Soland ex Salisb.: 338 (1802). *Scyphogyne capitata* (Klotzsch) Benth. var. *brevifolia* (Benth.) N.E.Br.: 413 (1906). Type: mtns near Genadendal, *Burchell 7621* (K holo.!; PRE!).

81. Erica eglandulosa (Klotzsch) E.G.H.Oliv., comb. nov.

Basionym: *Omphalocaryon glandulosum* Klotzsch in Linnaea 12: 244 (1838) sphalm. *O. eglandulosum*; *Scyphogyne eglandulosa* Benth.: 710 (1839); N.E.Br.: 412 (1906). Type: in Zwartberg and at hotsprings near Caledon, alt. III, IV and in hills in vicinity, alt. II, Aug. & Sept., [loc. 51.7], *Ecklon & Zeyher s.n.* (B†; C!, P!, S!); [loc. 51.7] as *302* (B†; G!, MEL!, MO!, S!, W!). Lectotype, designated here: *Ecklon & Zeyher 302* determined by Klotzsch as '*O. eglandulosum*' (S!). [Note: The epithet published in the protologue was 'glandulosum' but nowhere did Klotzsch describe what part of the plant was glandular. The species is totally eglandular. The lectotype specimen was determined by Klotzsch as 'eglandulosum' in his own hand; Bentham and Brown used this epithet. I am therefore likewise treating the original epithet as a typographical error and use 'eglandulosa' (Art. 73,1)].

Scyphogyne fasciculata Benth.: 709 (1839); N.E.Br.: 412 (1906). Type: Cape Colony [Genadendal, Baviaanskloof Mtn, 16 Feb. 1815 (McKay 1943: 65)], *Burchell 7716* (K holo.!).

82. Erica melanomontana E.G.H.Oliv., nom. nov.

Scyphogyne orientalis E.G.H.Oliv. in South African Journal of Botany 3: 282 (1984) non *Erica orientalis* Dyer: 449 (1932). Type: Prince Albert, Swartberg above Kliphuisvlei, 1800 m, Jan. 1975, *Oliver 5519* (STE/NBG!, holo.!; BM!, BOL!, K!, MO!, NY, PRE!, S!).

83. Erica miniscula E.G.H.Oliv., nom. nov.

Lagenocarpus tenuis Benth. in De Candolle, Prodromus 7: 710 (1839), non *Erica tenuis* Salisb.: 329 (1802). *Lepterica tenuis* (Benth.) N.E.Br.: 397 (1906). *Scyphogyne tenuis* (Benth.) E.G.H.Oliv.: 284 (1984). Types: Cape Colony, *Mundt s.n.* (K!); ibid., *Burchell 7034* (K, lecto.!; BOL!, P!, PRE!, S!, W!); ibid., *Burchell 7126* (BOL!, K!). Lectotype designated by Oliver (1984).

84. Erica rigidula (N.E.Br.) E.G.H.Oliv., comb. nov.

Basionym: *Scyphogyne rigidula* N.E.Br. in Flora capensis 4: 409 (1906). Type: Ceres, on Skurfdeberg Range near Elandsfontein, *Schlechter 10028* (K, holo.!; BM!, BOL!, E!, G!, MO!, P!, PRE!, W!, Z!).

Blepharophyllum divaricatum Klotzsch in Linnaea 12: 216 (1838) non *Erica divaricata* Sincl.: 8 (1825) [=*Erica tenuis* Salisb.]. *Scyphogyne divaricata* (Klotzsch) Benth.: 710 (1839); N.E.Br.: 410 (1906); E.G.H.Oliv.: 282 (1984). Types: Drakensteenberg, *Drege s.n.* (B†;

iso?); as *7750* (G-DC!, K!, P!, S!); Waterfall, Worcester, *Ecklon & Zeyher s.n.* (B†; iso?); as *303* (SAM!); Houw Hoek, *Ecklon & Zeyher s.n.* (B† holo.; K, lecto.!; C!, E!, LD!, MO!, P!, UPS!, W!, Z!). Lectotype designated by Oliver (1984).

Scyphogyne biconvexa N.E.Br.: 410 (1906). Type: Paarl, French Hoek, *Schlechter 9244* (BM!, BOL!, E!, G!, K!, MO!, P!, PRE!, S!, W!, Z!).

Scyphogyne glandulifera N.E.Br.: 401 (1906). Type: Ceres Div., Cold Bokkeveld, *Schlechter 8897* (BOL!; BM!, G!, K!, MO!, P!, PRE!, S!, W!, Z!).

Scyphogyne longistyla N.E.Br.: 411 (1906). Types: Caledon Div., Houw Hoek, 1500 ft, *Schlechter 7556* (BOL!, GRA!, MO!, PRE!, Z!); Bredasdorp Div., Elands Kloof, 1000 ft, *Schlechter 9748* (BOL!, GRA!, K!, MO!, PRE!, S!, Z!).

Scyphogyne rigidula N.E.Br. var. *breviciliata* N.E.Br.: 410 (1906). Types: Clanwilliam Div., Blue Berg, *Schlechter 8464* (BM!, G!, K!, MO!, P!, S!, W!, Z!); Tulbagh Div., Mitchells Pass, *Schlechter 8954* (BOL!, K!, PRE!).

Scyphogyne brownii Compton: 304 (1931). Types: Witteberg, Laingsburg, *Compton 2535* (BM!); ibid., *Compton 2538* (BM!, BOL!); ibid., *Compton 2989* (BM!, K!); ibid., *Compton 2995* (BM!); ibid., *Compton 3000* (BOL!); ibid., *Compton 3183* (BOL!).

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APPENDIX OF PLATES

Full-page line drawings of each of the 84 species included in the taxonomic treatment and referred to in the character assessment and cladistic analyses.

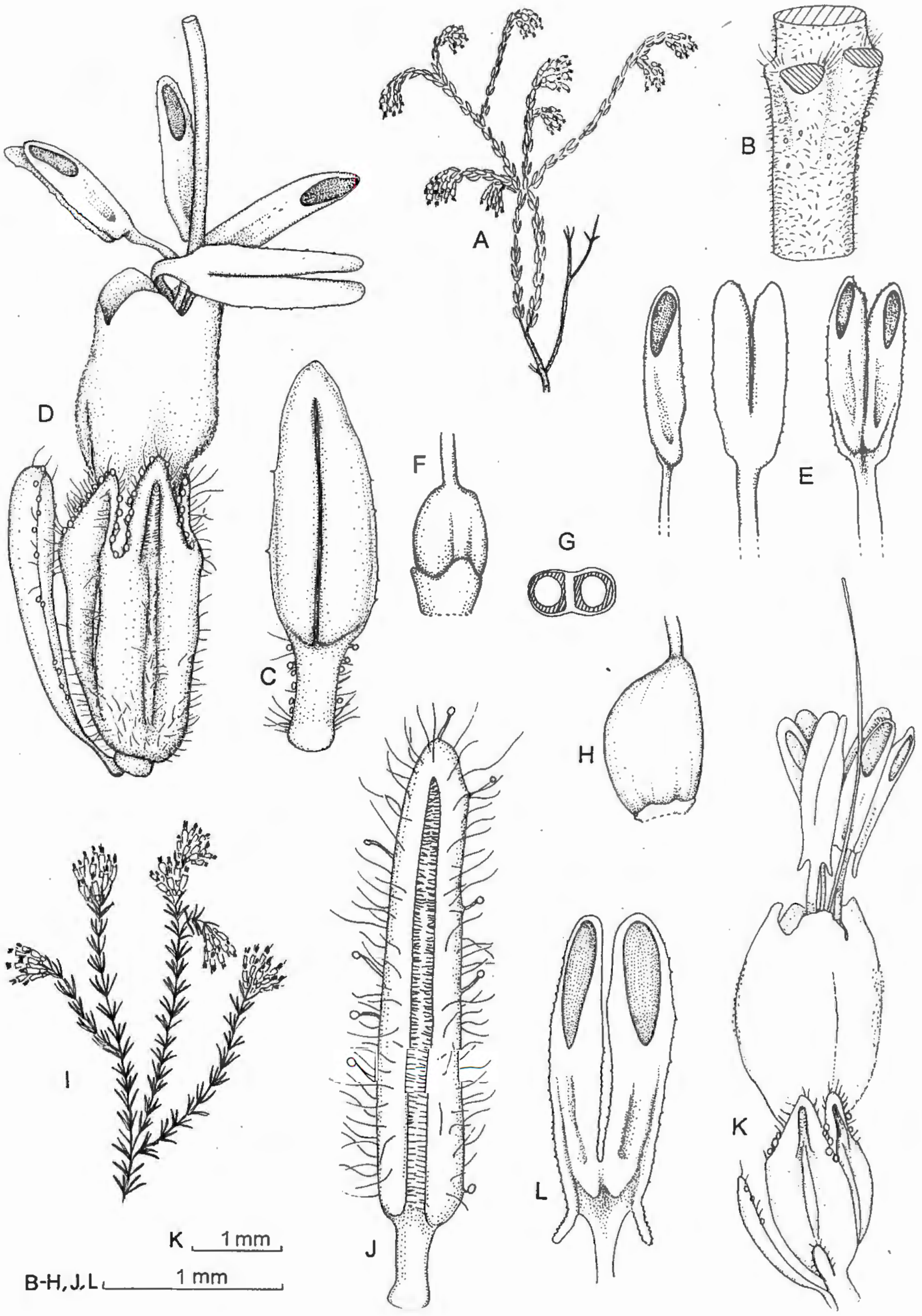

PLATE 1.—*Erica glabella*. Subsp. *glabella*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, back & front views; F, ovary; G, ovary T/S; all drawn from *Taylor 5717*: subsp. *laevis*. I, flowering branch, nat. size, drawn from *Strid 37228*; J, leaf; K, flower; L, anther, front view; all drawn from *Werdermann & Oberdieck 87*.

L4[3] a–rBr1 br0(2) K4 C4 A4 $G^{2}/_{1}\,({}^{1,3,4}/_{1\,(2,3)})$

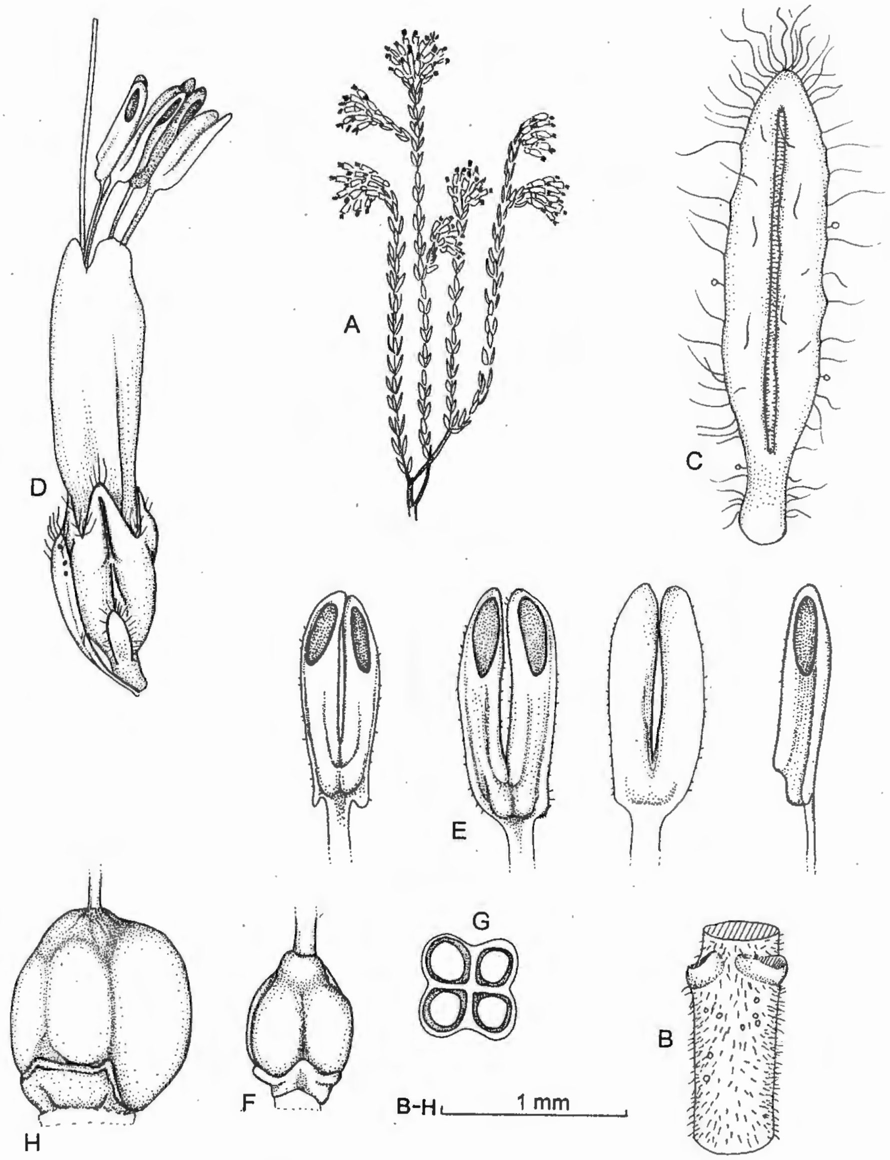

PLATE 2.—*Erica piquetbergensis*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, front back and side views showing spur variation; F, ovary; G, ovary T/S; H, fruit; A–G drawn from *Oliver 7873*, H from *Martin 871*.

L4 rBr1 br2 K4 C4 A4 $G^4/_1$

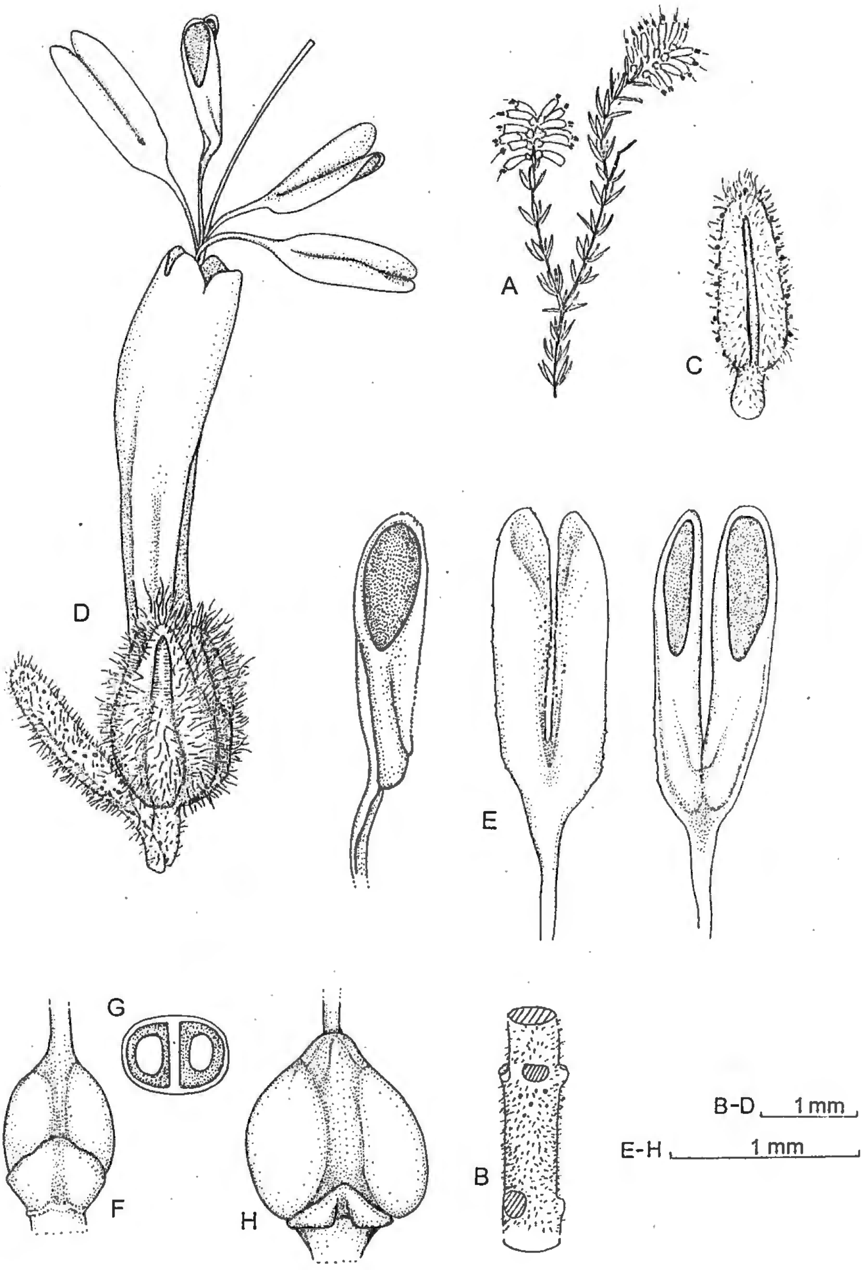

PLATE 3.—*Erica dregei*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, back & front views; F, ovary; G, ovary, T/S; H, fruit; all drawn from *Oliver 7687*. **L4 rBr1 br0 K4 C4 A4 G**$^{2}/_{1}$ [$^{3}/_{1}$].

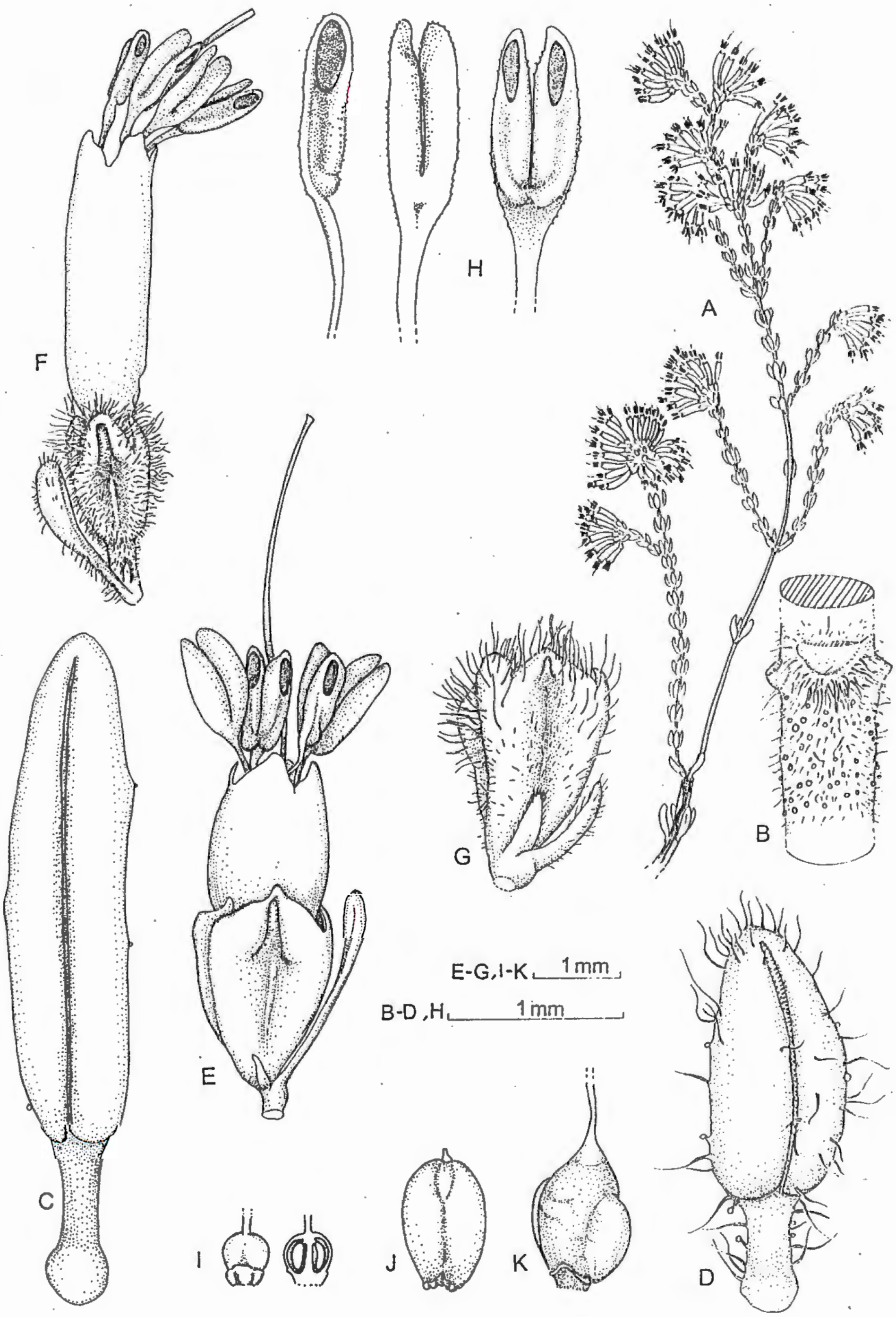

PLATE 4.—*Erica dispar*. A, flowering branch, nat. size; B, stem; C & D, leaf; E & F, flower; G, calyx; H, anther, side, back & front views; I, ovary; whole and L/S; J & K, fruits; A–C, E & H, drawn from *Acocks 22539*; D & F from *Compton 23526*, G & J from *Oliver 5991*, K from *McDonald 1398*.

L4 rBr1 br0(2) K4 C4 A4 $\mathbf{G}^2/_1$ ($^4/_1$ $^3/_1$ $^1/_1$).

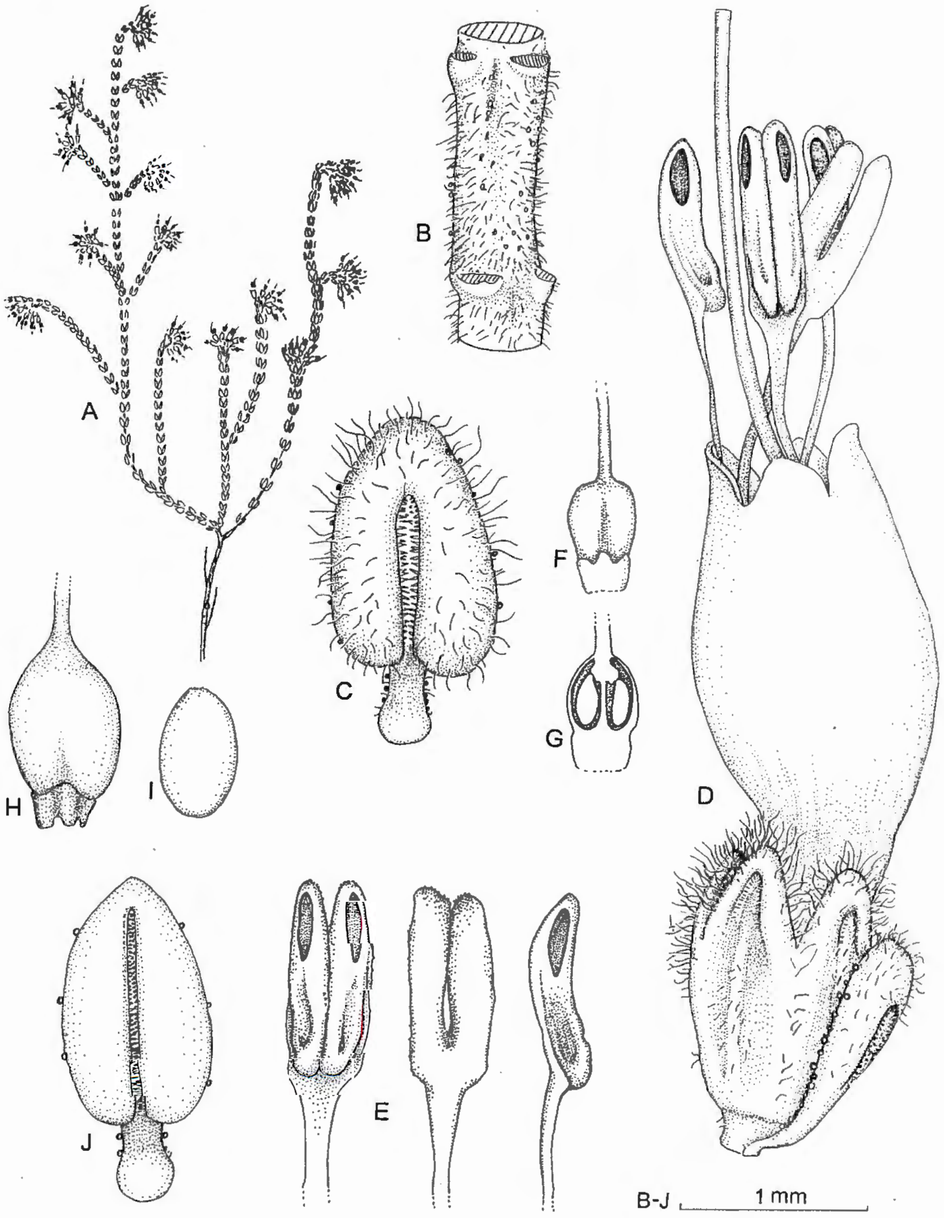

PLATE 5.—*Erica albertyniae*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, front, side & back views; bract; F, ovary; G, ovary L/S; H, ovary; I, seed; J, leaf; A–I drawn from *Burgers 1847*; J from *Oliver 8821*.

L3 aBr br0 K4 C4 $\mathbf{G}^2/_1$

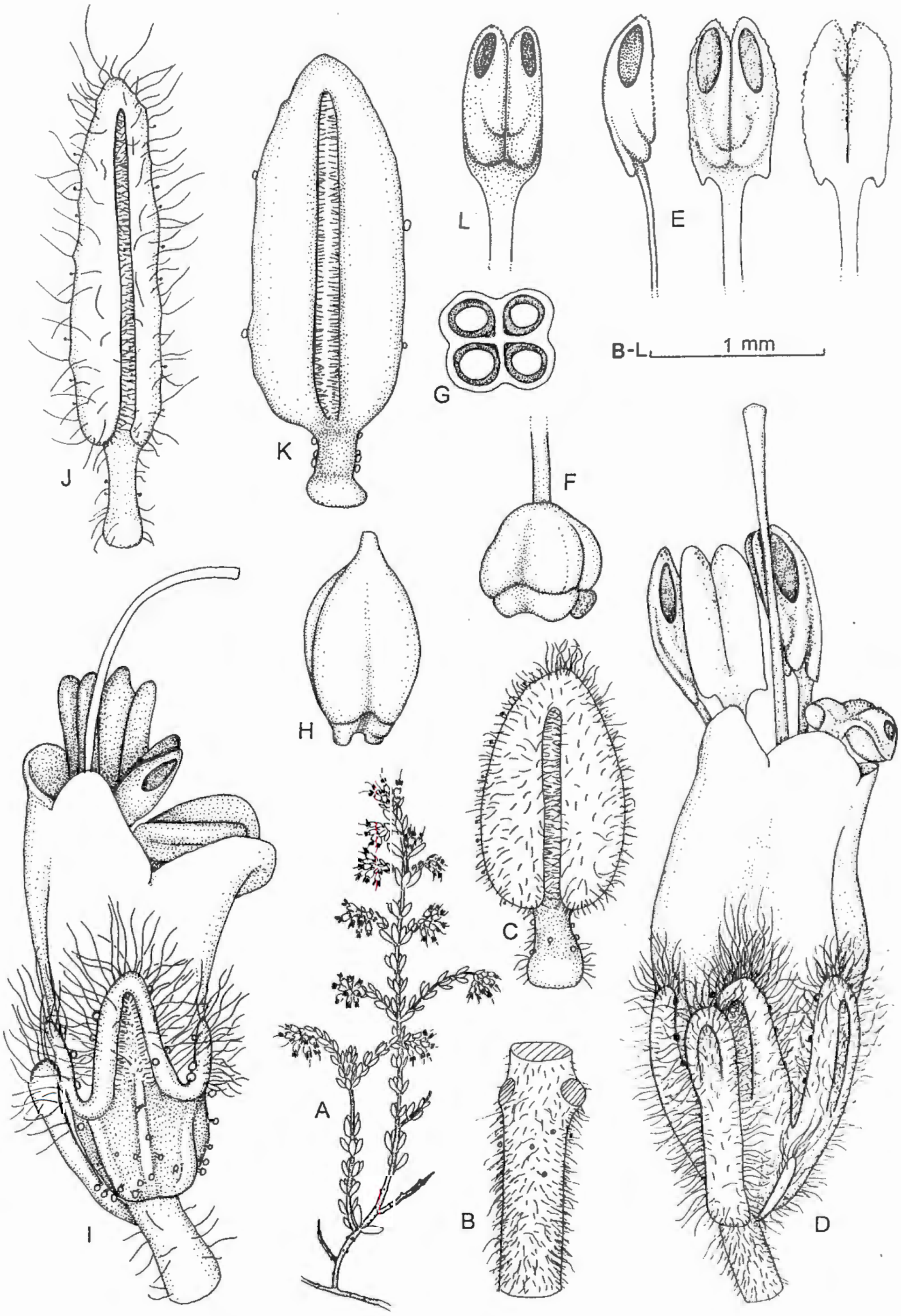

PLATE 6.—*Erica radicans* subsp. *radicans*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views; G, ovary, T/S; H, ovary; subsp. *schlechteri* I, flower; J, leaf; K, leaf; L, anther; B-G drawn from *Oliver 8805*, H from *Bohnen 3794*, I & J from Oliver 8738, L & K from *Williams 2479*. **L4[3] rBr1 br0,2 K4 C4 A4 G**$^4/_1\,^3/_1\,^2/_1\,(^2/_2)$

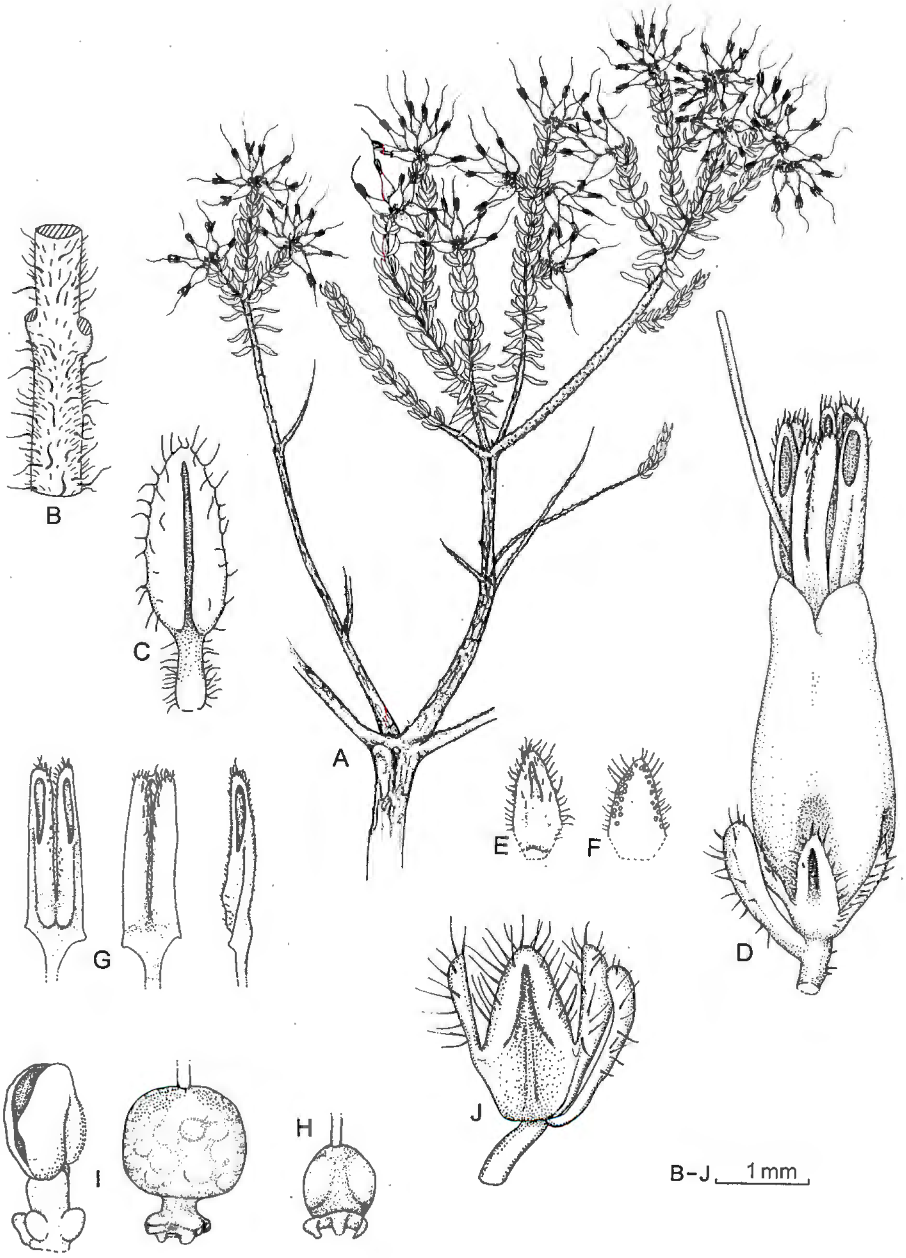

PLATE 7.—*Erica interrupta*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, sepal, abaxial view; F, sepal, adaxial view; G, anther, front, back & side views; H, ovary; I, fruit, left showing partial dehiscence; J, calyx; B–H, drawn from *Oliver 8755*, J, from *Fellingham 80*.

L4 rBr1 br0(2) K4 C4 A4 $G^2/_1(^3/_1)$.

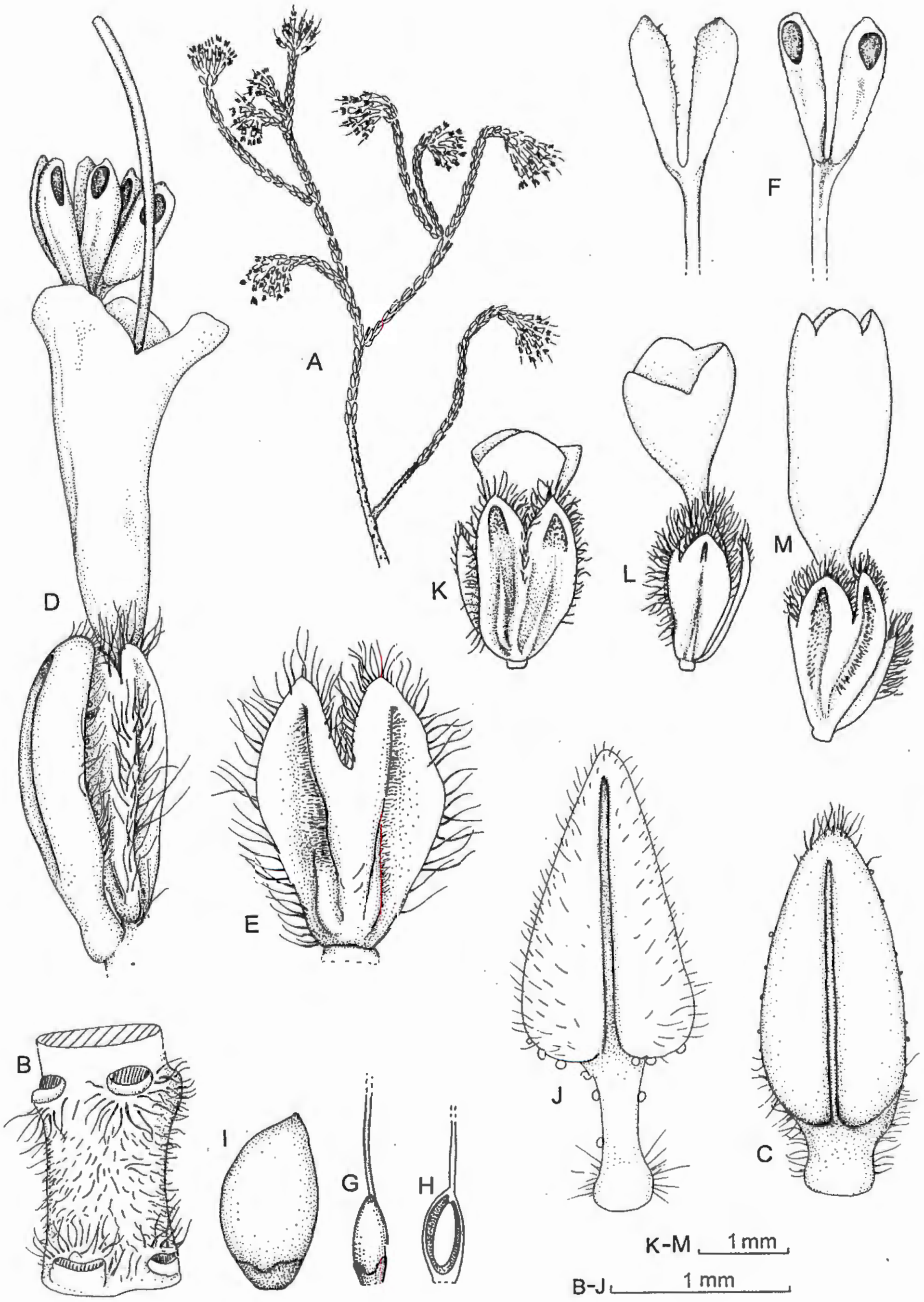

PLATE 8.—*Erica globiceps*. Subsp. *globiceps*: A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, calyx; adaxial side; F, anther, back & front views; G, ovary; H, ovary L/S; I, fruit; J, leaf; K–M, flower variation, without anthers; A–H drawn from *Albertyn 536*, J from *Oliver 8685*, K from *Oliver 7651b*, L from *Goldblatt 2615*, M (subsp. *consors*) from *Stokoe 6203*.

L4 a–rBr1 b r0 K3,4 C3,4 A3,4 $\mathbf{G}^{1}/_{1}\ {}^{2}/_{1}$

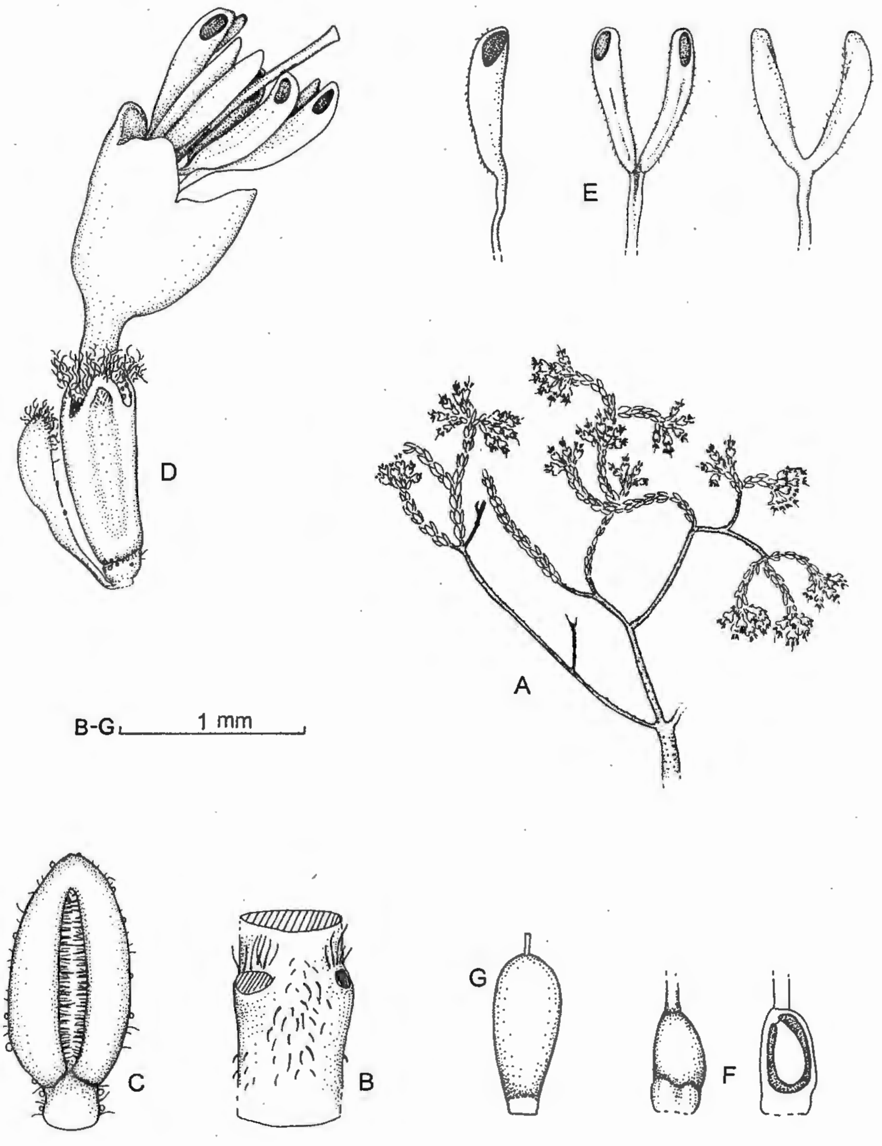

PLATE 9.—*Erica pulcheliflora*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views; F, ovary, whole & L/S; G, fruit; all drawn from the lectotype, *Schlechter 9744*. **L3** a–r**Br1** **br0** **K4** **C4** **A4** **G**$^{1}/_{1}$

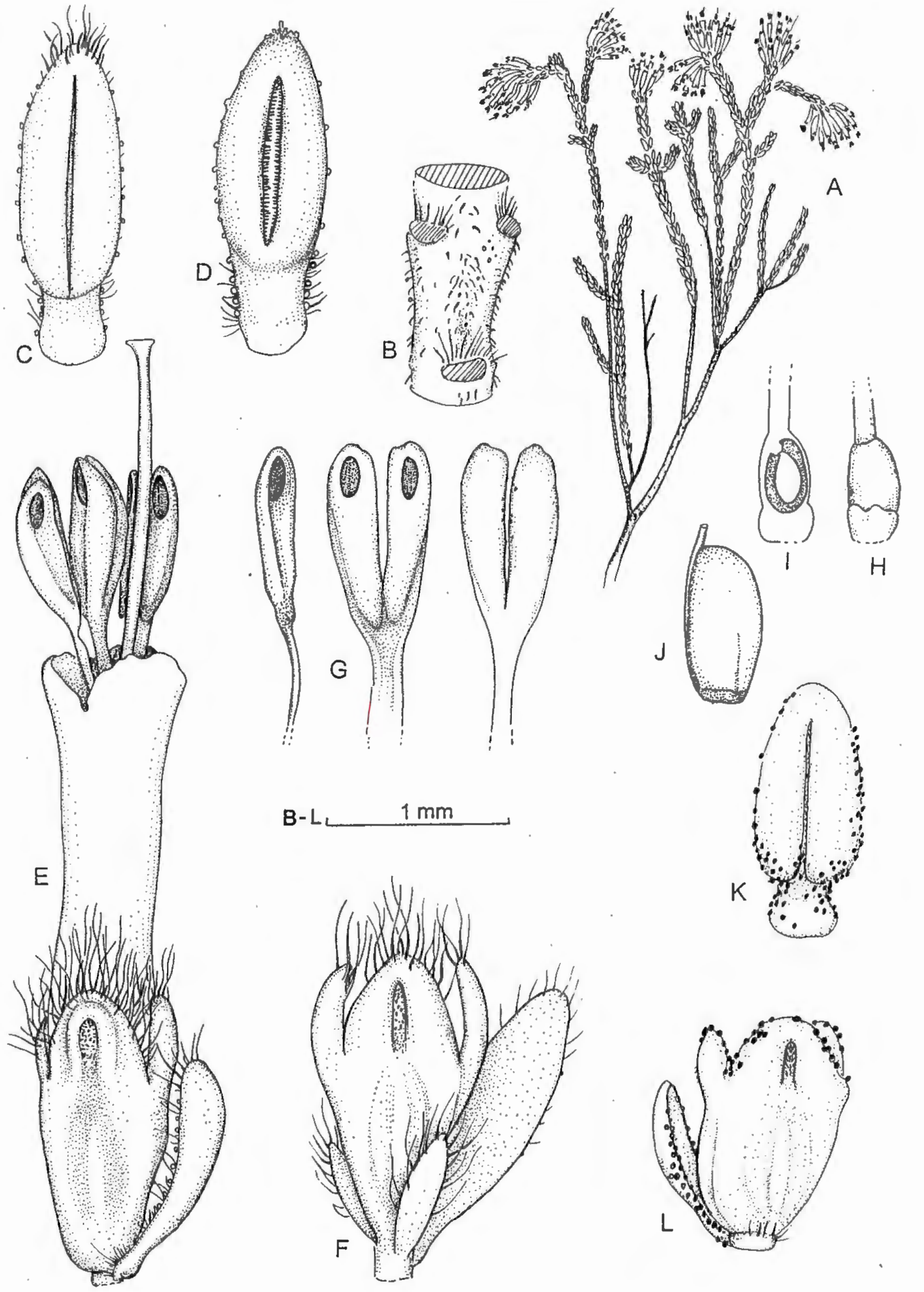

PLATE 10.—*Erica venustiflora*. Subsp. *venustiflora*; A, flowering branch, nat. size; B, stem; C, leaf; D, leaf; E, flower; F, bract, bracteoles & calyx; G, anther, side, front & back views; H, ovary; I, ovary L/S; J, fruit: subsp. *glandulosa*; K, leaf; L, bract & calyx; A–J drawn from *Compton 14766*, K & L from *Williams 1843*. **L**3[4] **rBr**1 **br**0[2] **K**3 **C**3 **A**3 **G**$^{1}/_{1}$

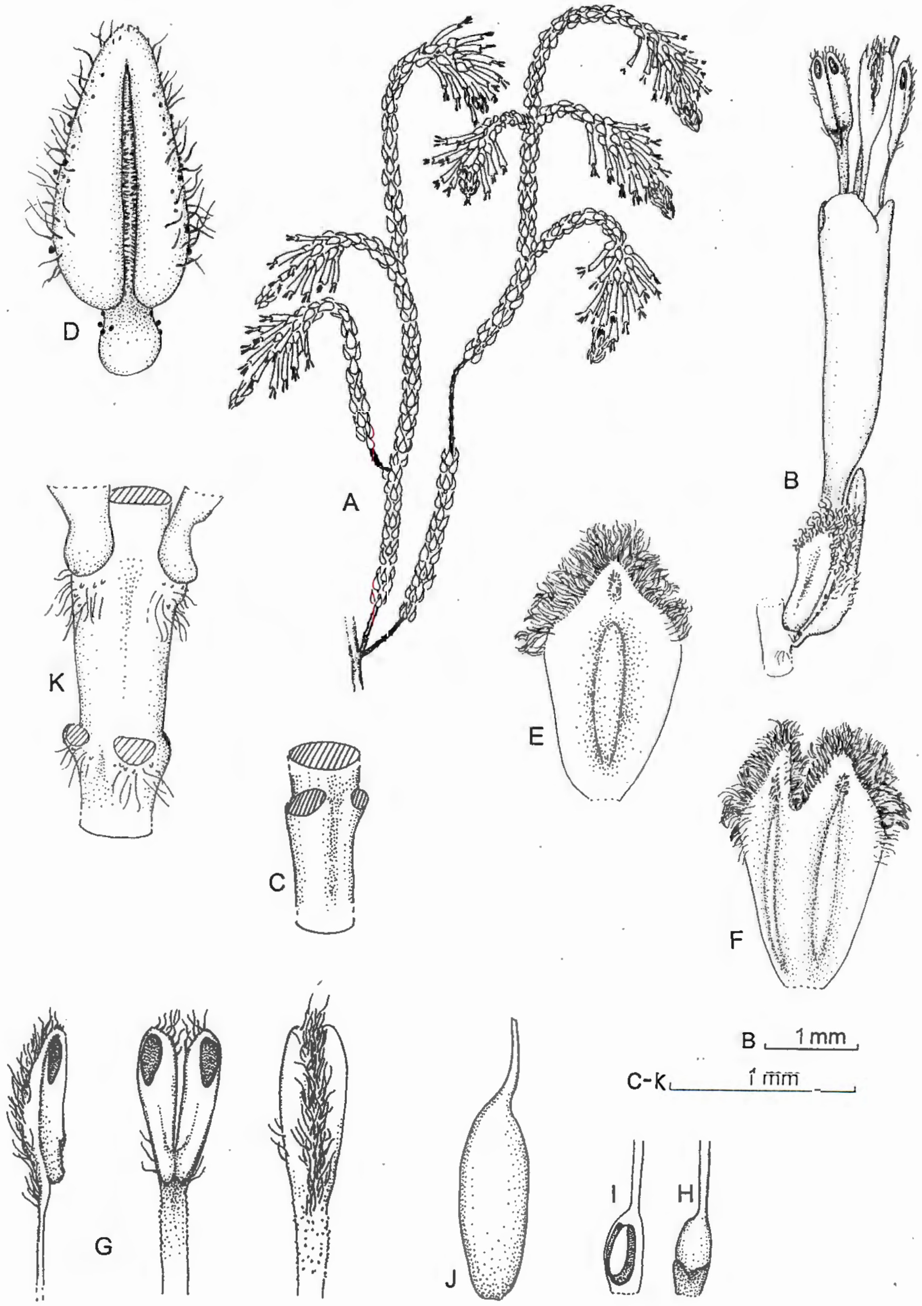

PLATE 11.—*Erica innovans*. A, flowering branch, nat. size; B, stem;C; leaf; D, flower; E, calyx, abaxial surface; F, calyx, adaxial surface; G, anther, side, front & back views; H, ovary; I, ovary L/S; J, fruit; A–H drawn from *Oliver 4269*, K from *Taylor 7432*. **L3 aBr1 br0 K3 C3 A3**(4) **G**$^1/_1$

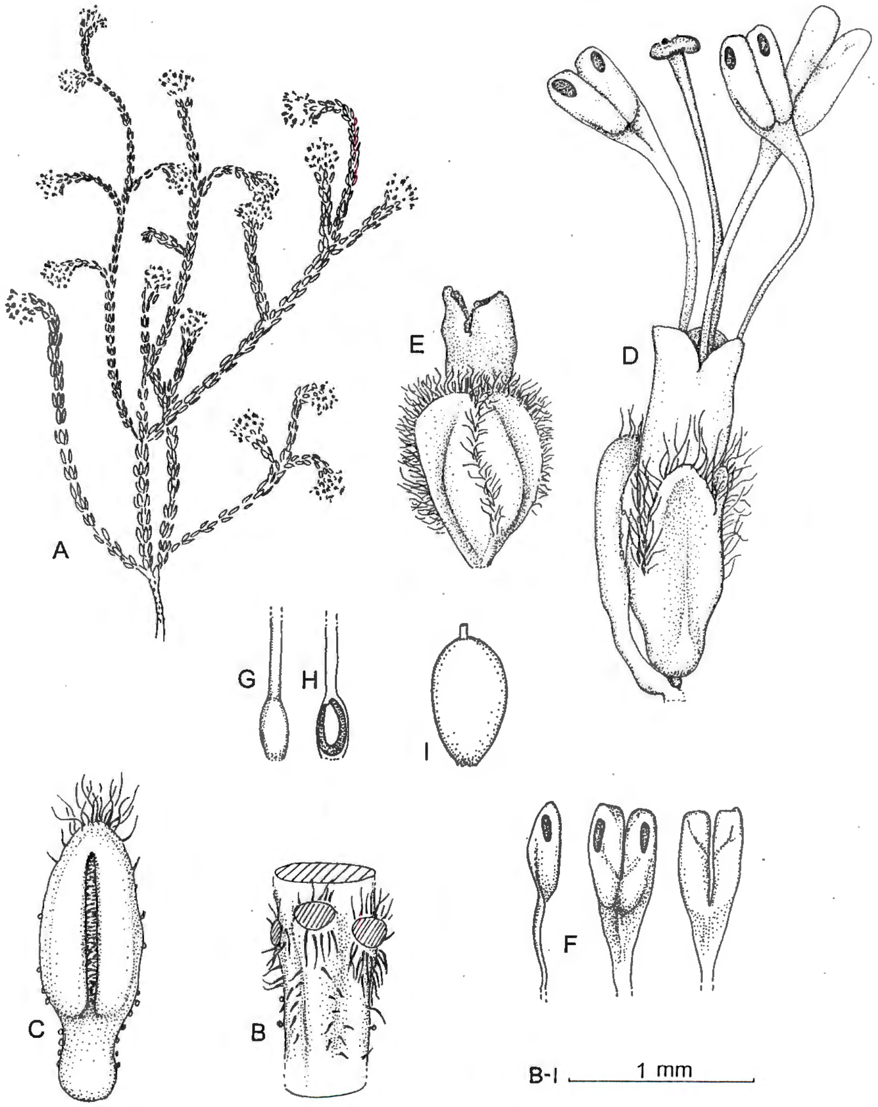

PLATE 12.—*Erica brownii.* A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, calyx, adaxial view; F, anther, side, front & back views; G, ovary (with no basal nectaries); H, ovary L/S; I, fruit; all drawn from *Oliver 4218.*

L4 aBr1 br0 K3 C3 A3 $\mathbf{G^{1}/_{1}}$

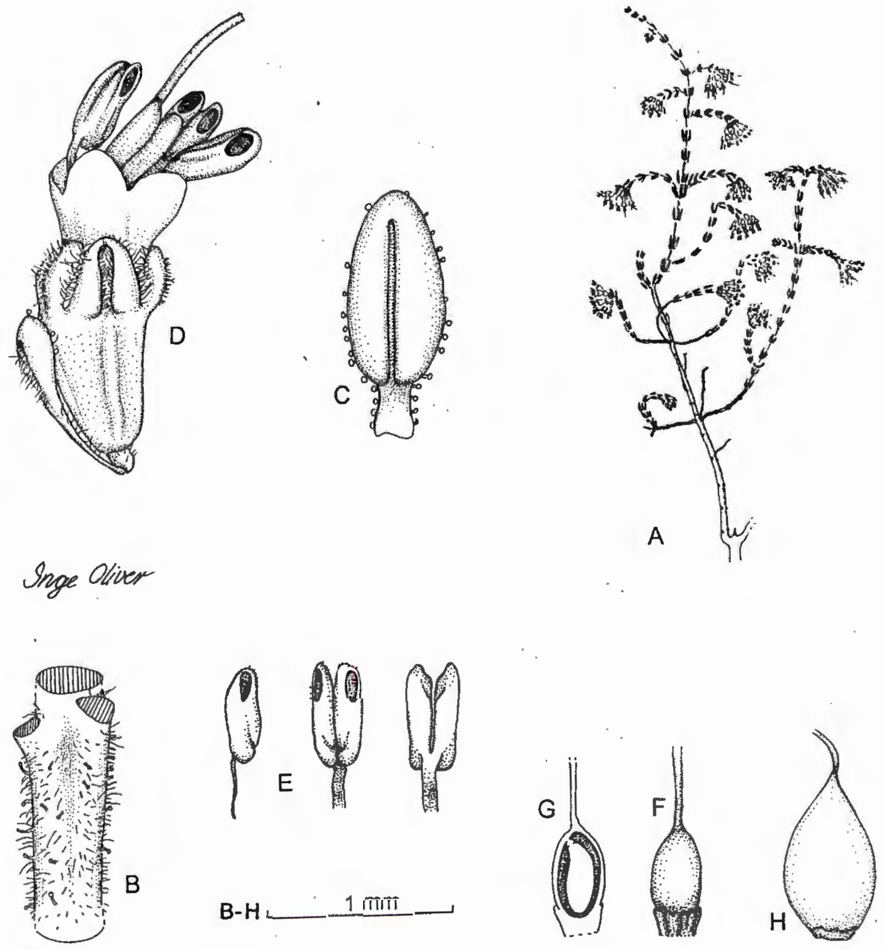

PLATE 13.—*Erica malmesburiensis*. A, flowering branch, nat.size; B, stem; C, leaf; D, flower; E, anther, side, front & back views; F, ovary; G, ovary, L/S; H, fruit; all drawn from *Esterhuysen 34239*. **L3 a–rBr1 br0 K4 C4 A4 G**$^1/_1$

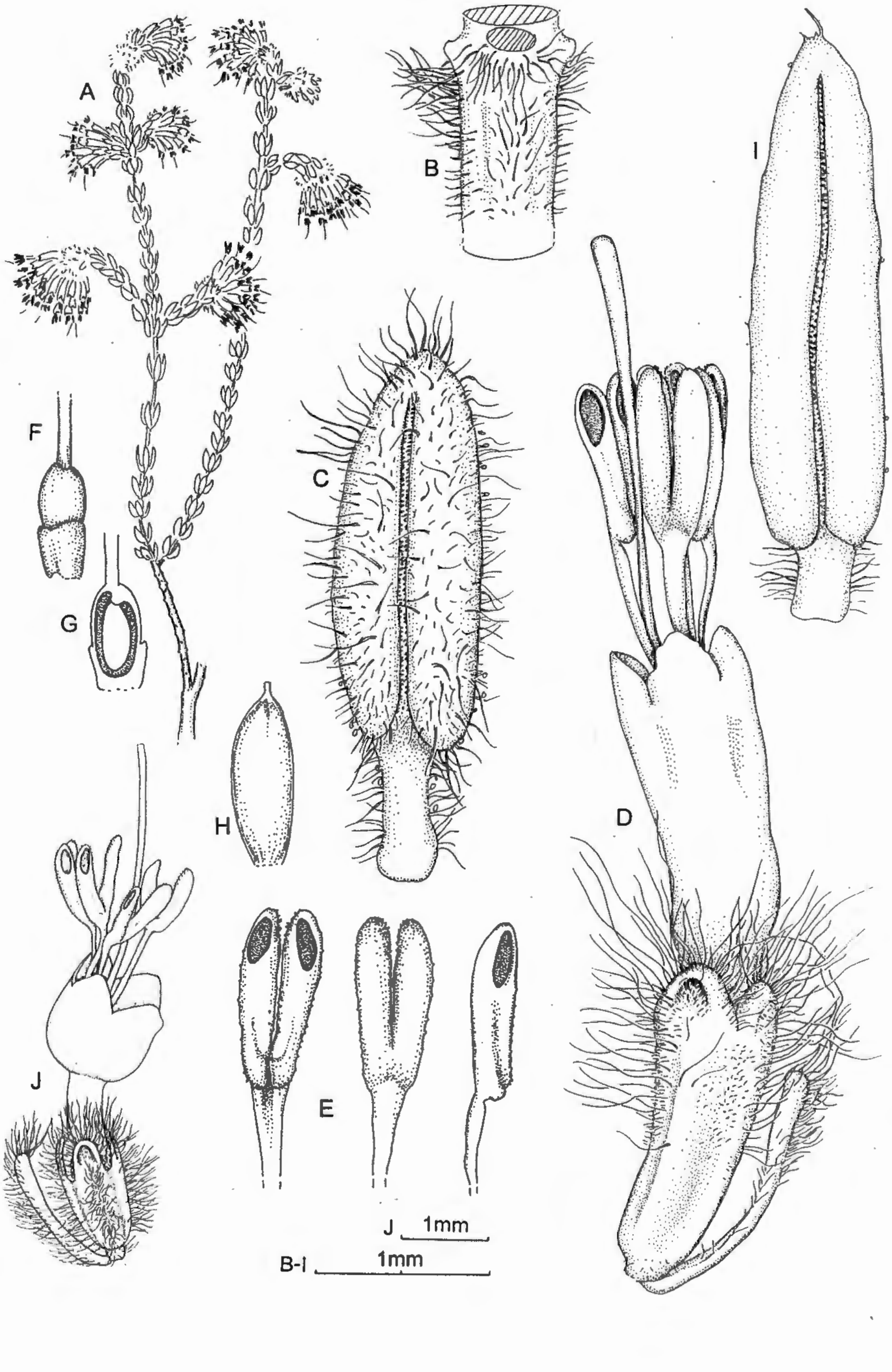

PLATE 14.—*Erica articulata*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower (note ridge opposite calyx lobes); E, anther, front, back & side views; F, ovary; G, ovary L/S; H, fruit; I, leaf; J, flower; A–G drawn from *Fellingham 844*, H from *Martin 4615*, I from *Taylor 7600*, J from *Oliver 8993*.

L4 a(r)Br1 br0 K4 C4 A4 $\mathbf{G}^{1}/_{1}$

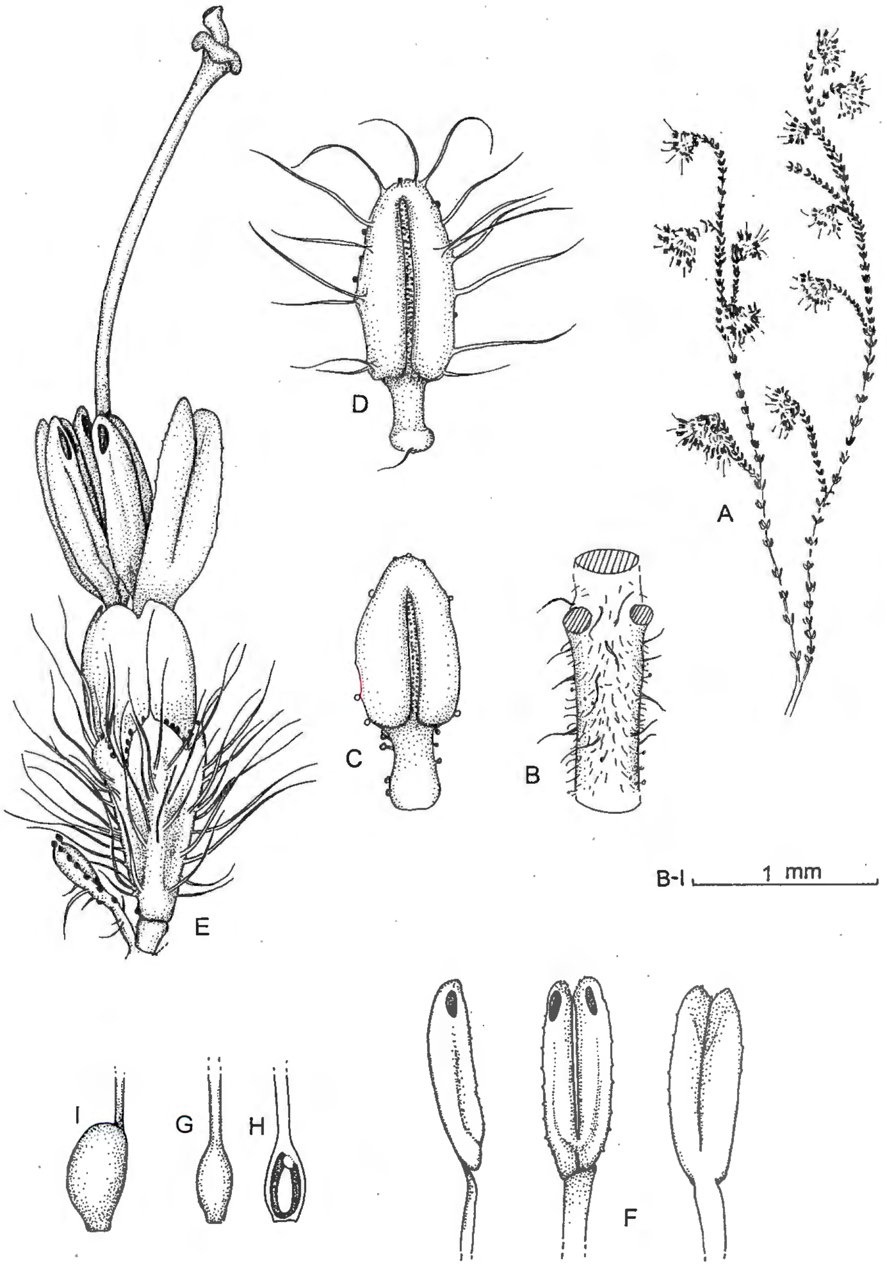

PLATE 15.—*Erica erina*. A, flowering branch, nat. size; B, stem; C, leaf; D, leaf; E, flower (note ridges opposite calyx lobes); F, anther, side, front & back views; G, ovary; H, ovary L/S; I, fruit; all drawn from *Oliver 8975*.

L3[4] aBr1 br0 K4 C4 A4 $G^1/_1$

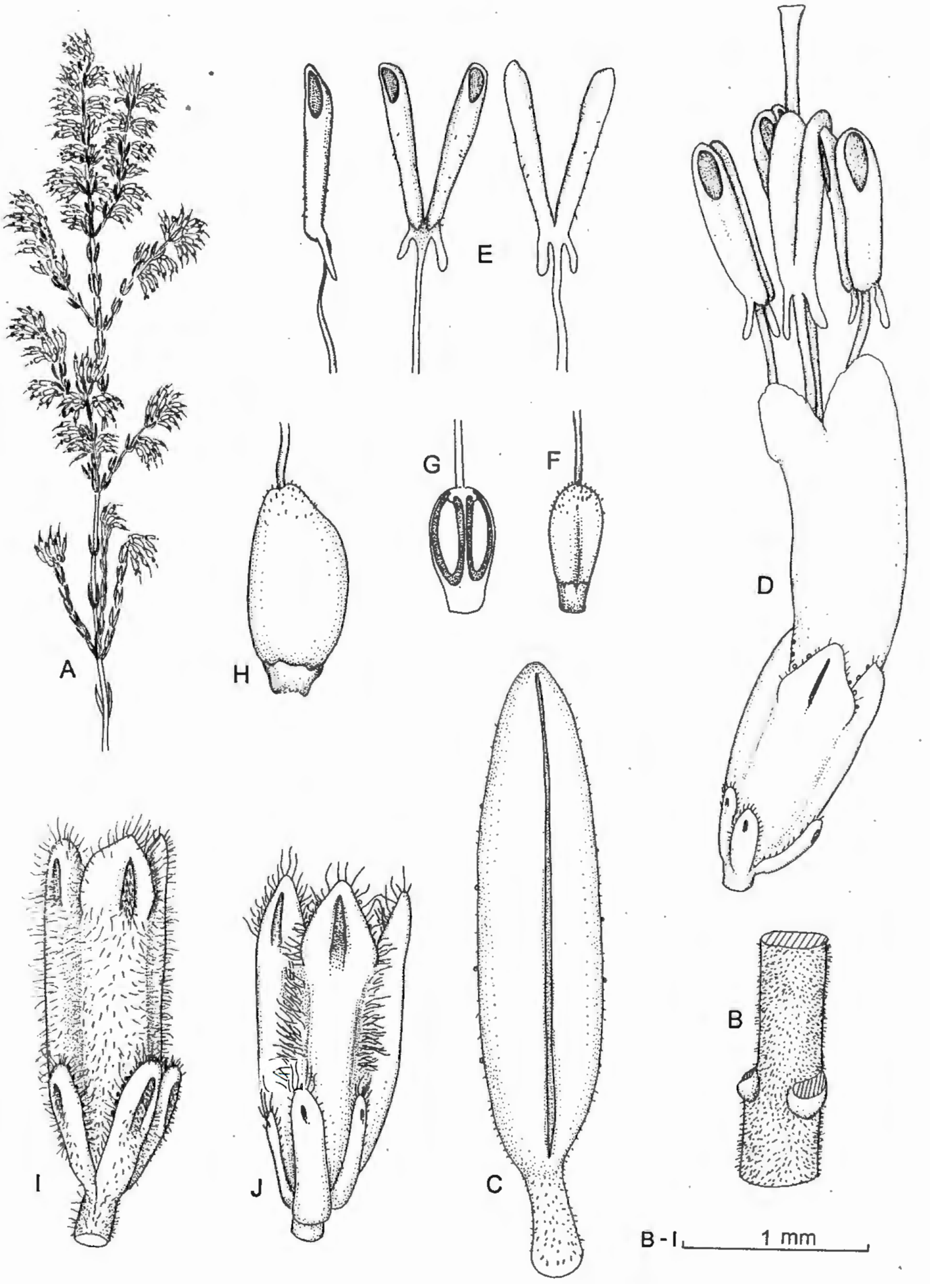

PLATE 16.—*Erica uberiflora*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views; F, ovary; G, ovary, L/S; H, fruit; B–G drawn from *Mund & Maire s.n.*; I from *Stokoe 7299*, J from *Viviers & Vlok 25*.

L3 a–r**Br1** br2 **K4** **C4** **A4** **G**$^{2}/_{1}$

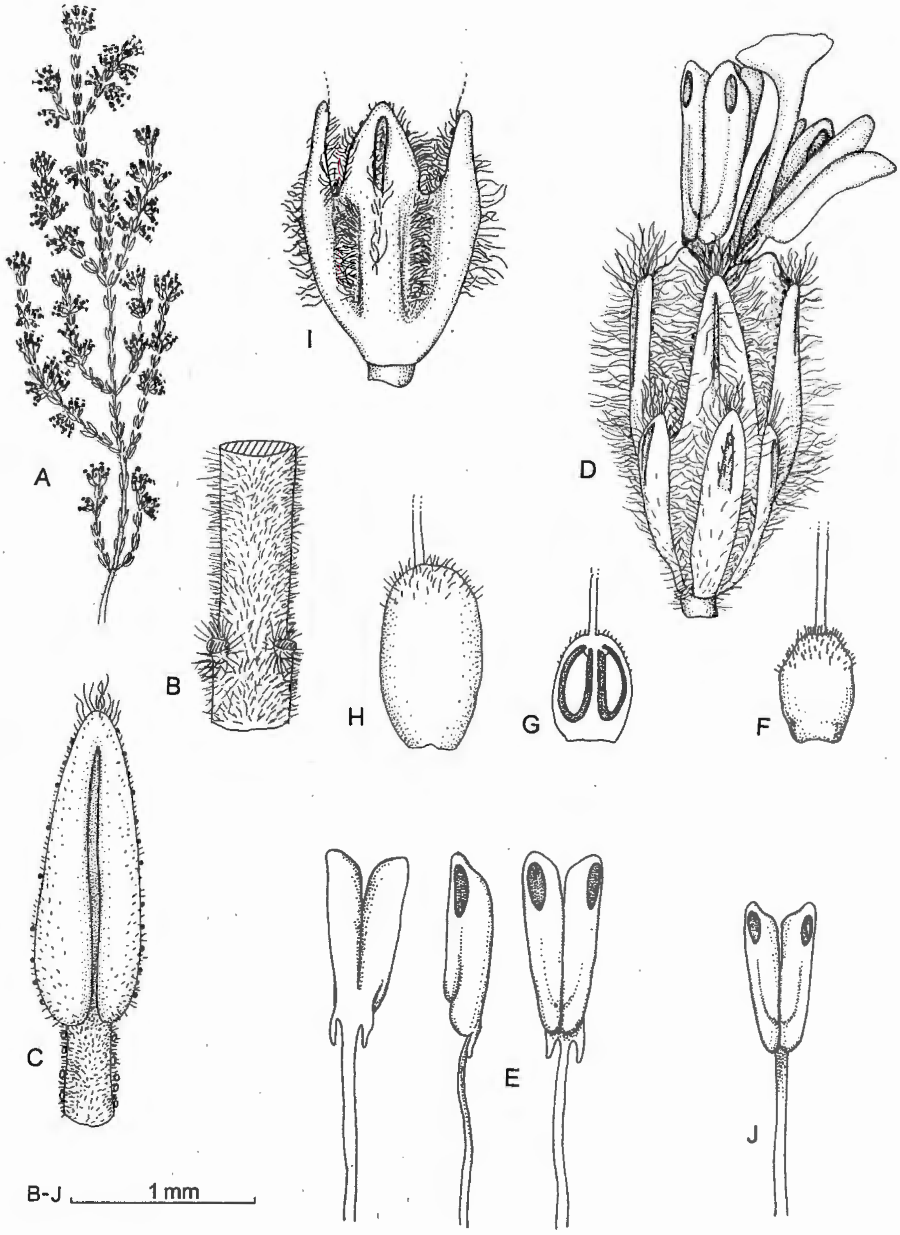

PLATE 17.—*Erica angulosa*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, back, side & front views; F, ovary; G, ovary L/S; H, ovary; I, calyx; J, muticous anther; A–G drawn from *Compton 23492,* H, from *Euston-Brown 101/11*, I & J from *Fourcade 29*. **L3 rBr1 br2 K4 C4 A4** $\mathbf{G^2/_1}$

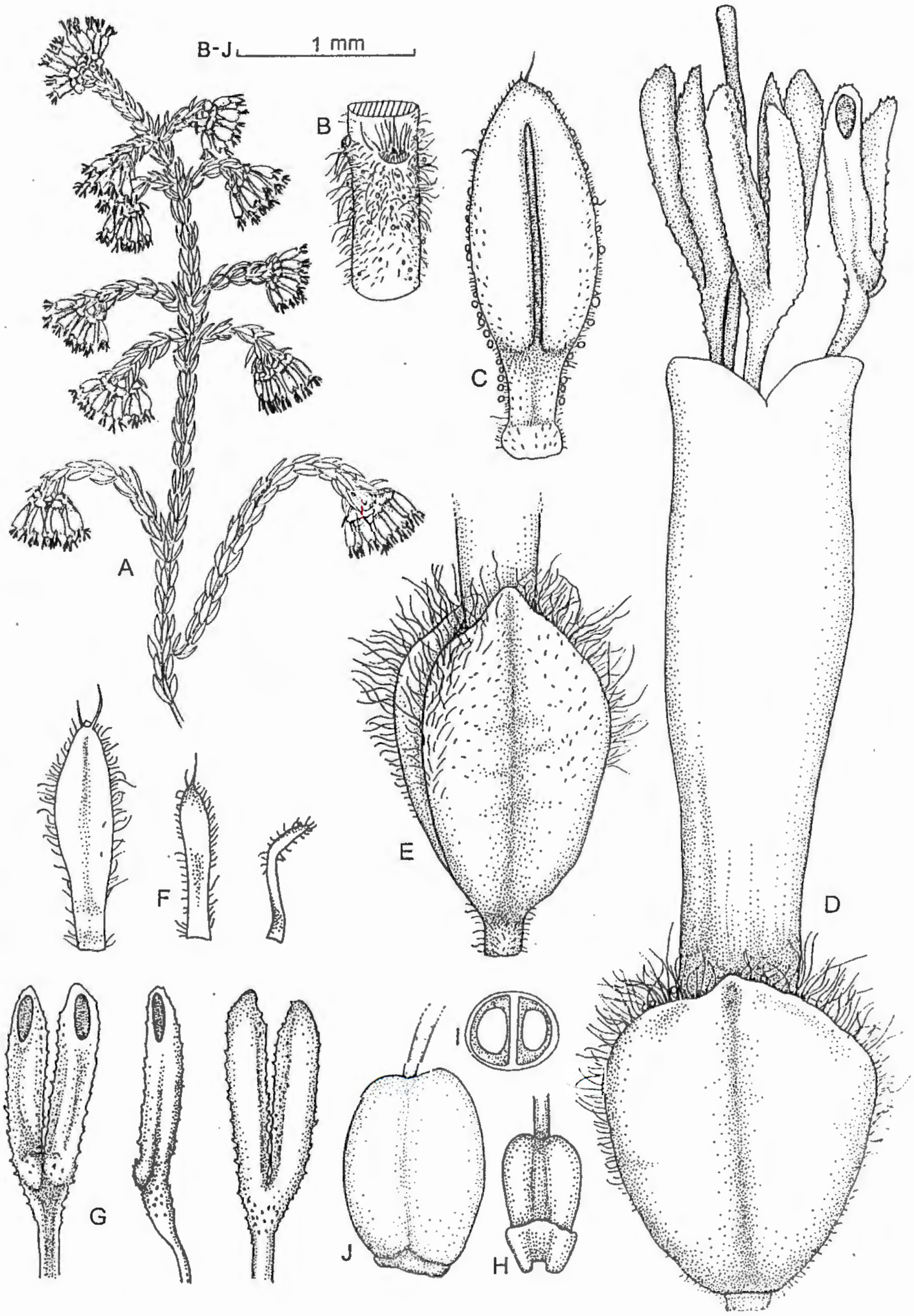

PLATE 18.—*Erica labialis*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower with 2-lobed calyx; E, 4-lobed calyx; F, bract variation in single inflorescence; G, anther, front, side & back views; H, ovary; I, ovary T/S; J, fruit; B–I drawn from *Oliver 3724*, J from *Oliver 8703*.

L3 aBr1 b0 K2–4 C2 A4 $G^{2}/_{1}$

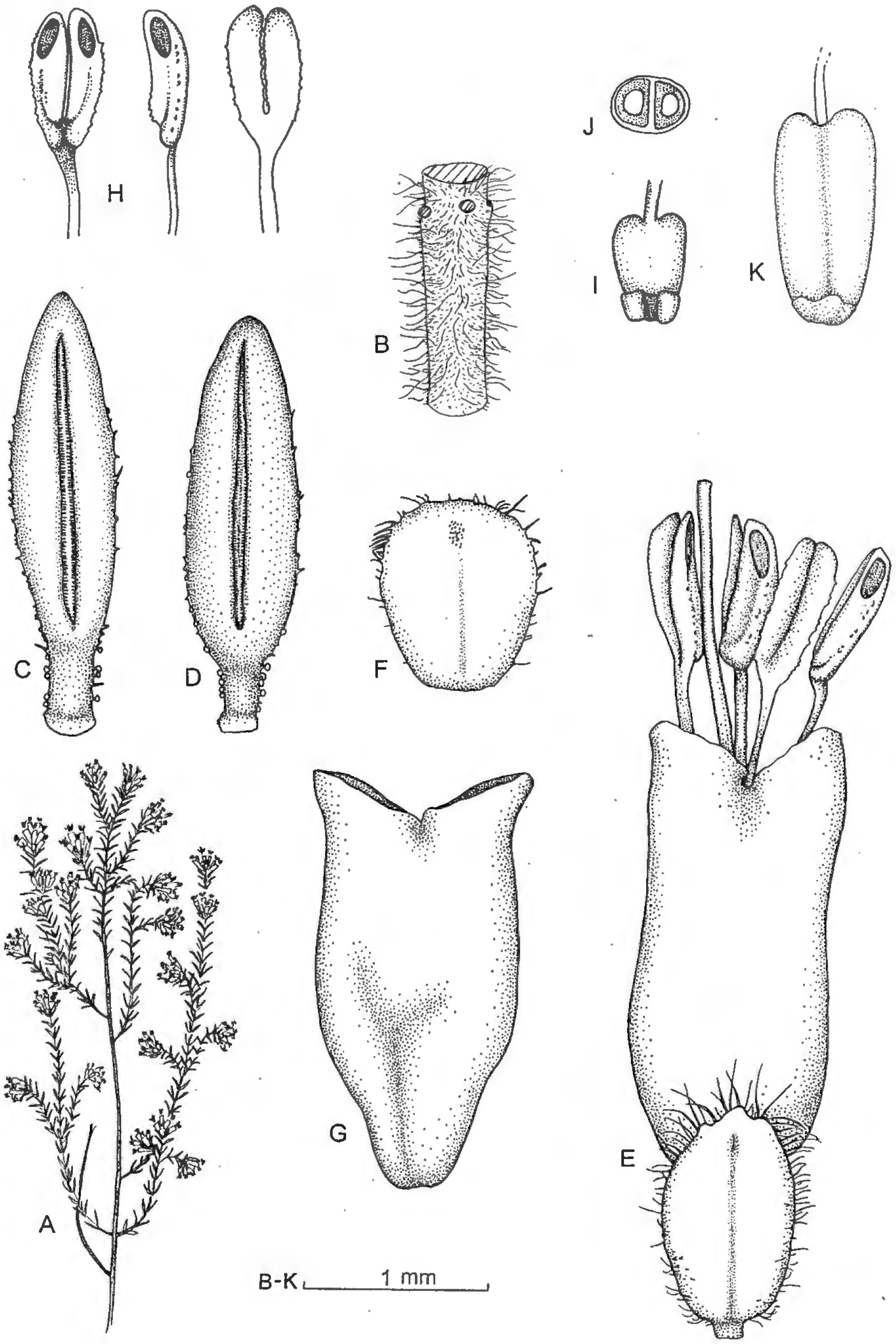

PLATE 19.—*Erica ecklonii*. A, flowering branch, nat. size; B, stem; C, leaf; D, bract; E, flower; F, 2-lobed calyx; G, corolla; H, anther, front, side & back views; I, ovary, J, ovary T/S; K, fruit; all drawn from *Oliver 8780*.

L3 aBr1 br0 K2 C2 A4 $G^2/_1$

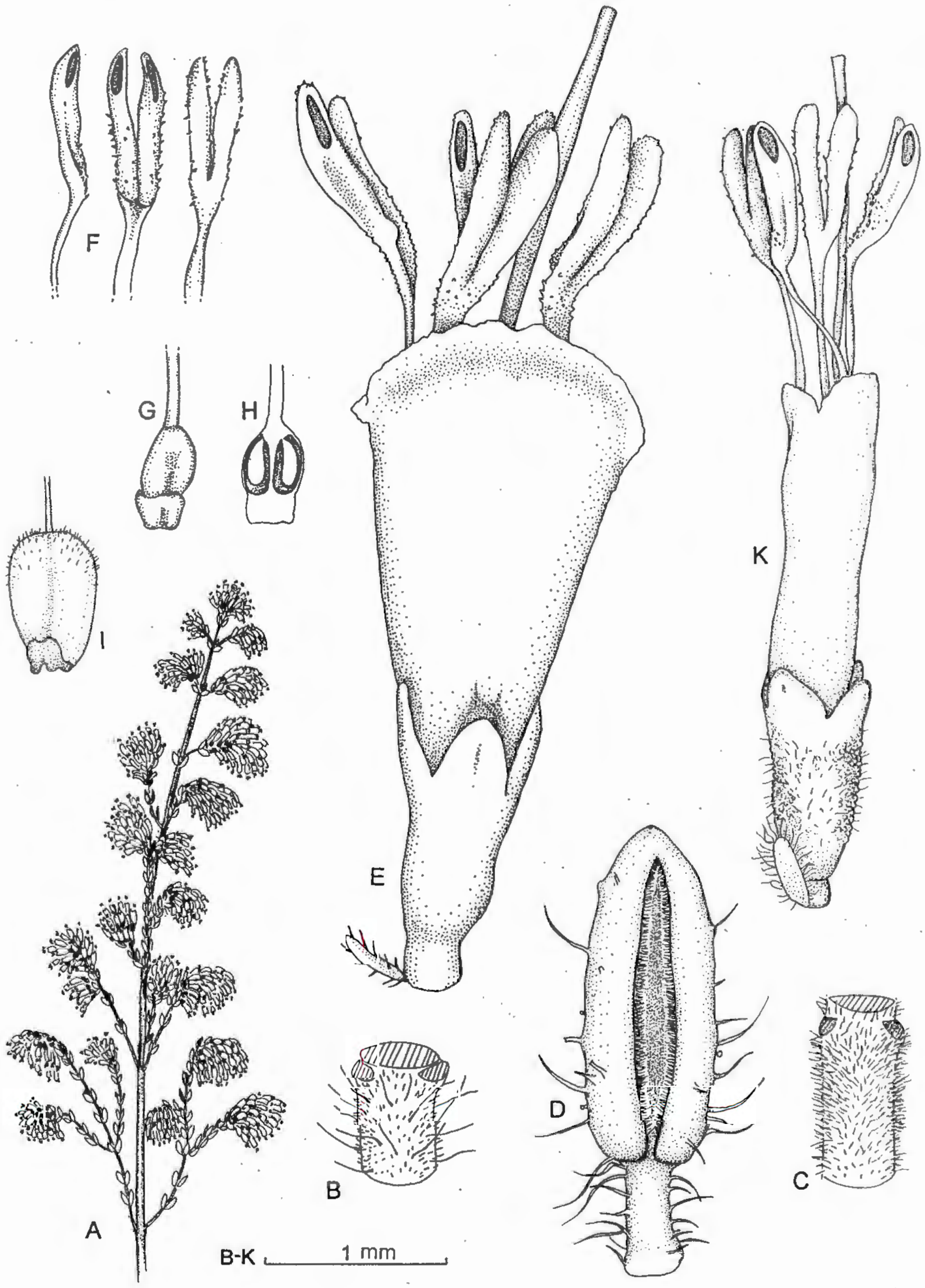

PLATE 20.—*Erica benthamiana*. A, flowering branch, nat.size; B & C, stem; D, leaf; E, flower, side view; F, anther, side, front & back views; G, ovary; H, ovary, L/S; I, fruit; K, flower, abaxial view; B–H drawn from *McDonald 1717*, K from *Oakes 7*.

L3 aBr1 br0 K4 C2 A4 $G^2/_1$

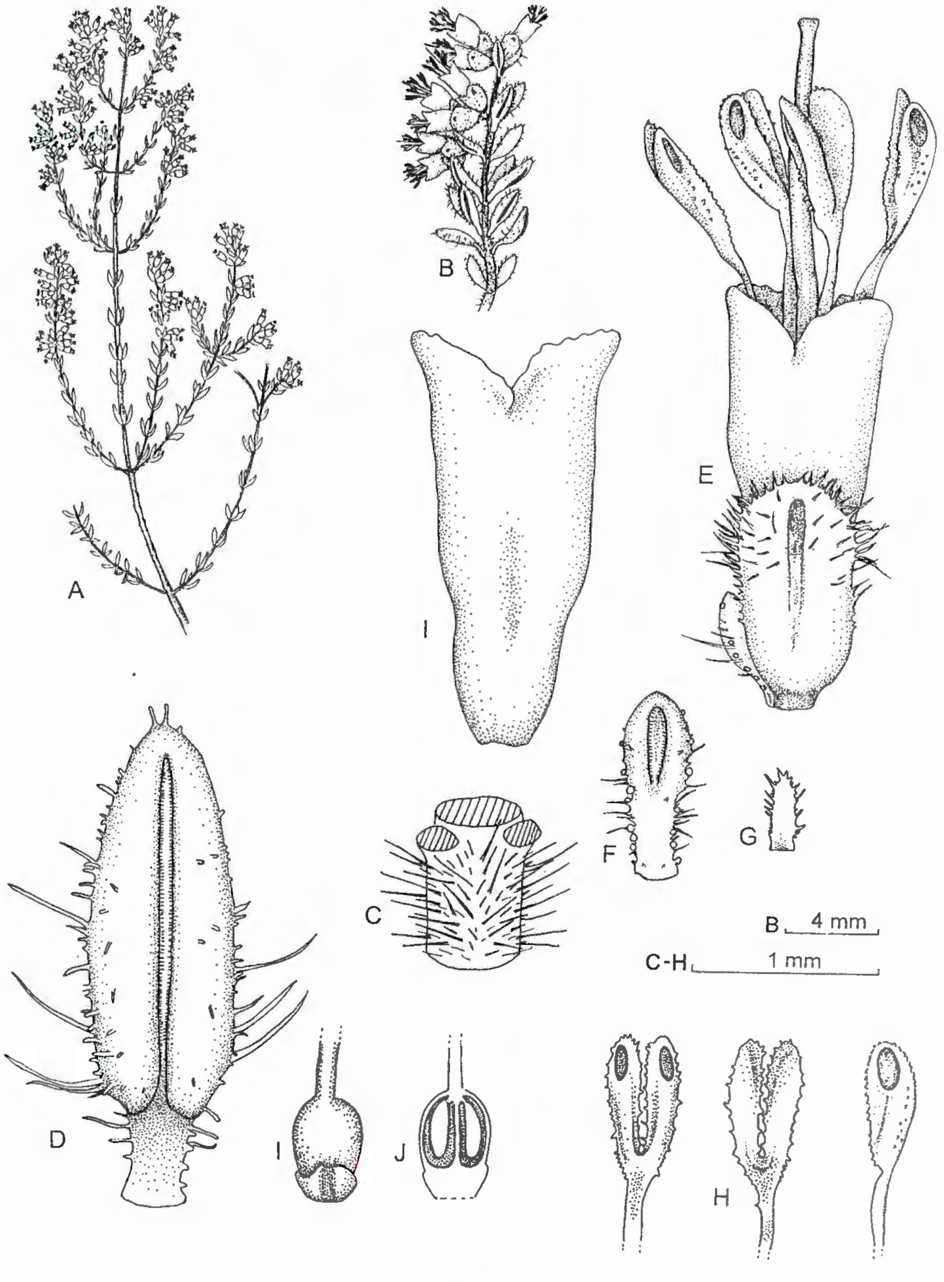

PLATE 21.—*Erica williamsiorum*. A, flowering branch, nat. size; B, flowering branchlet with three inflorescences; C, stem; D, leaf; E, flower; F & G, bract variation; H, anthers, front, back & side views; I, corolla; J, ovary, whole & L/S; all drawn from the type, *Oliver 8686*. **L3** a–**rBr1** **br0** **K2[4]** **C2** **A4** **G**$^2/_1$

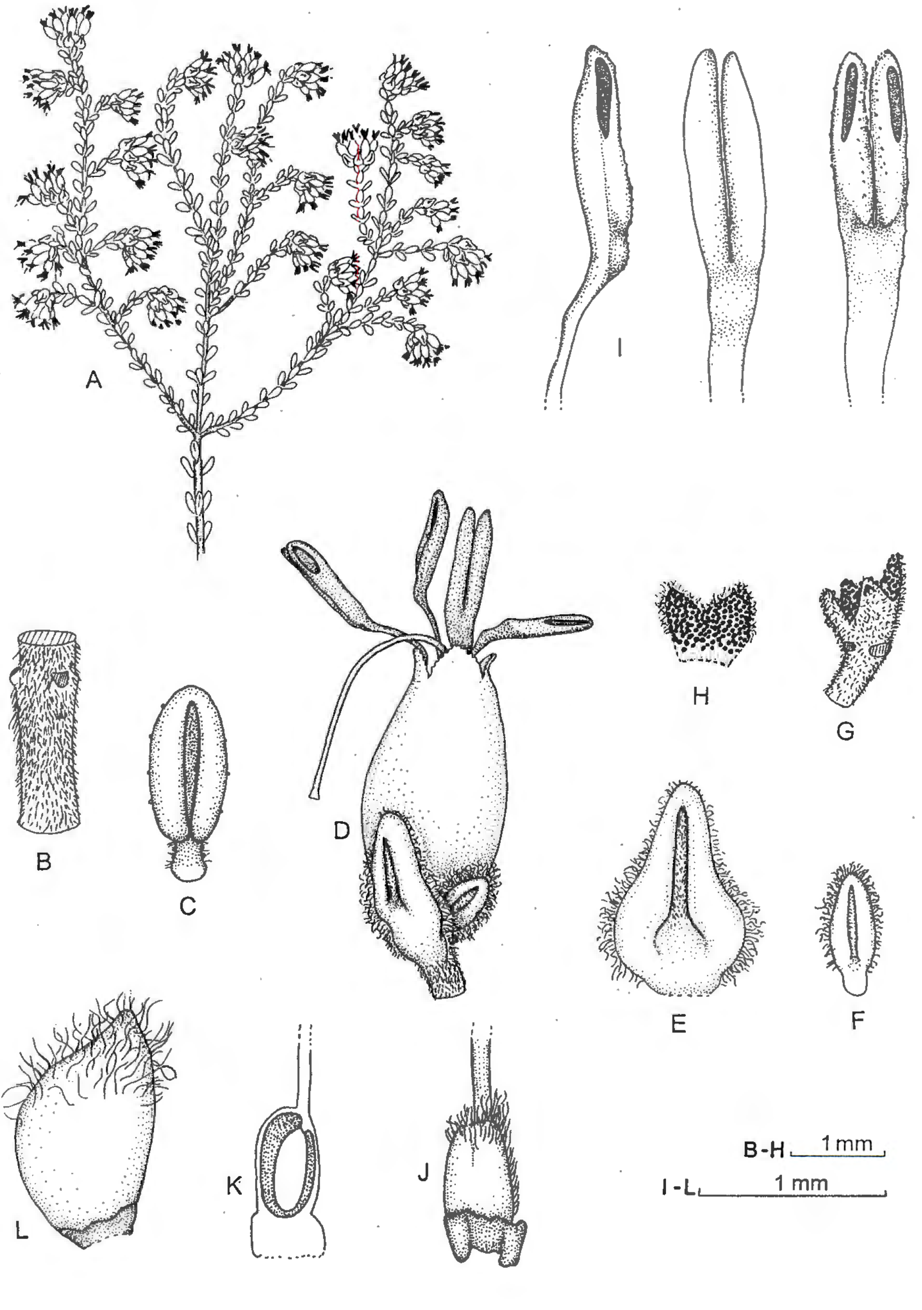

PLATE 22.—*Erica viscosissima*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, calyx; H, calyx, adaxial surface; I, anther, side, back & front views; J, ovary; K, ovary L/S; L, fruit; all drawn from *Oliver 5720*. **L3 rBr1 br2 K4 C4 A4 G**$^1/_1$

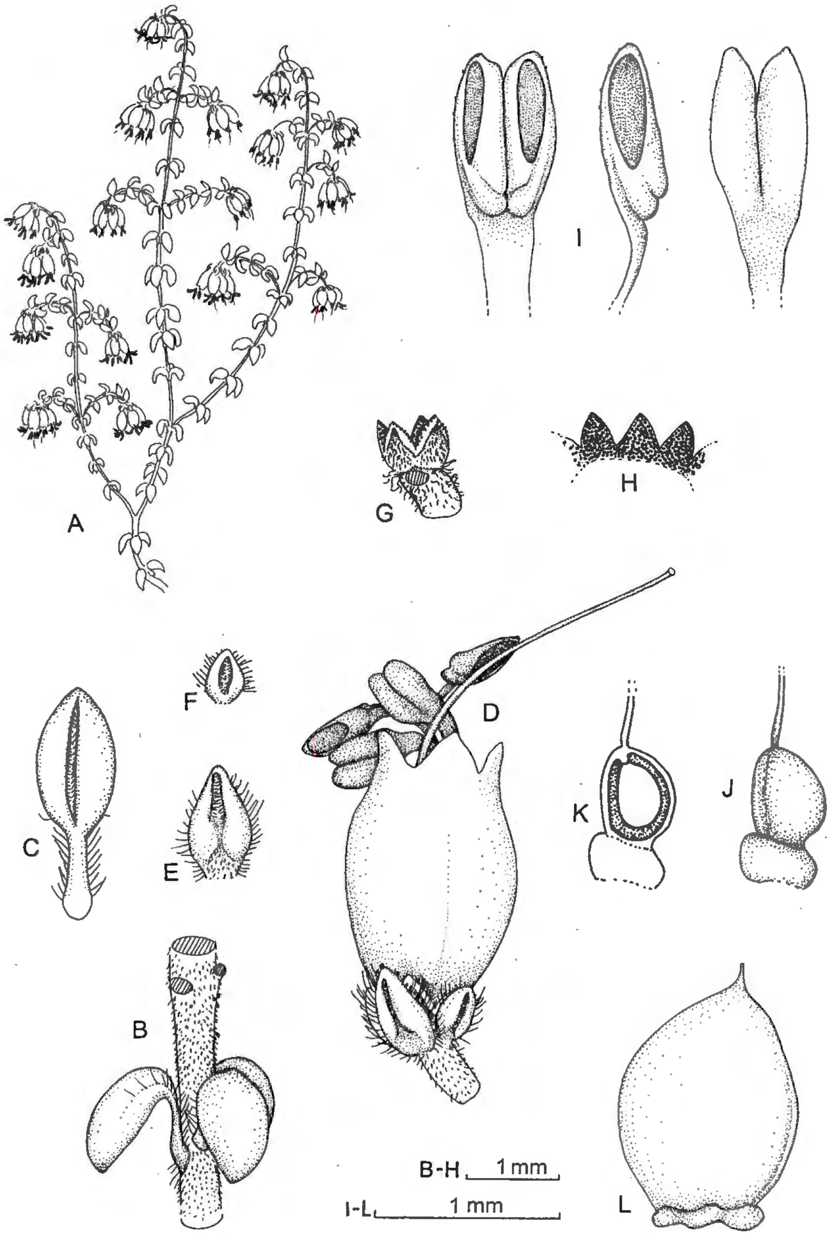

PLATE 23.—*Erica agglutinans*. A, flowering branch, nat. size; B, stem with whorl of leaves; C, leaf; D, flower; E, bract; F, bracteole; G, calyx; H, calyx, adaxial view showing sessile glands; I, anther, front, side & back views; J, ovary; K, ovary L/S. All drawn from *Oliver 4280.* **L3 rBr1 rbr2 K4 C4** $\mathbf{G}^1/_1$

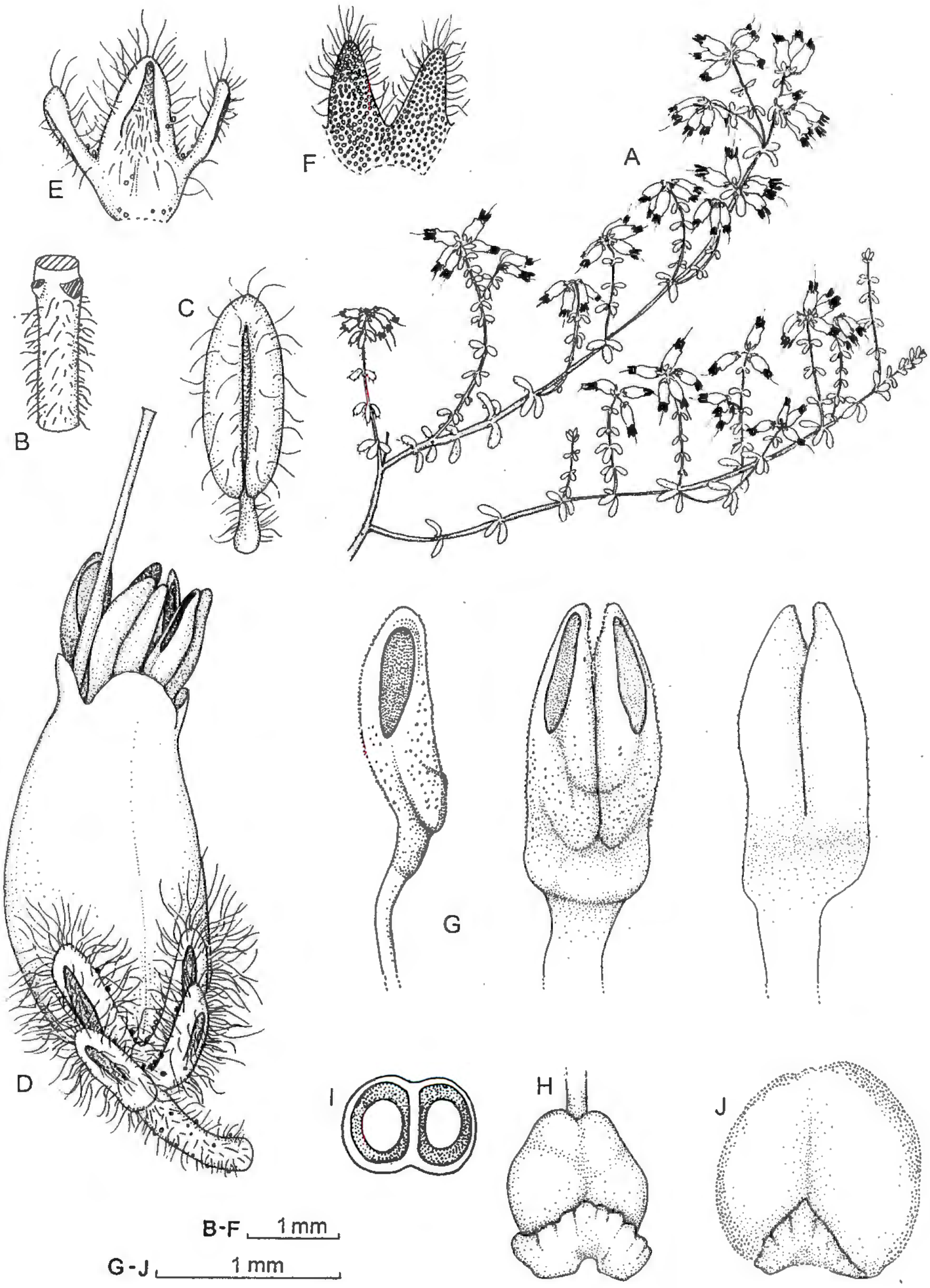

PLATE 24.—*Erica vernicosa.* A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, calyx; F, calyx, adaxial surface; G, anther, side, front & back views; H, ovary; I, ovary T/S; J, fruit; all drawn from the type, *Oliver 8587.*

L3 rBr1 br2 K4 C4 A4 $\mathbf{G}^{2}/_{1}$ ($^{3}/_{1}$) [$^{4}/_{1}$]

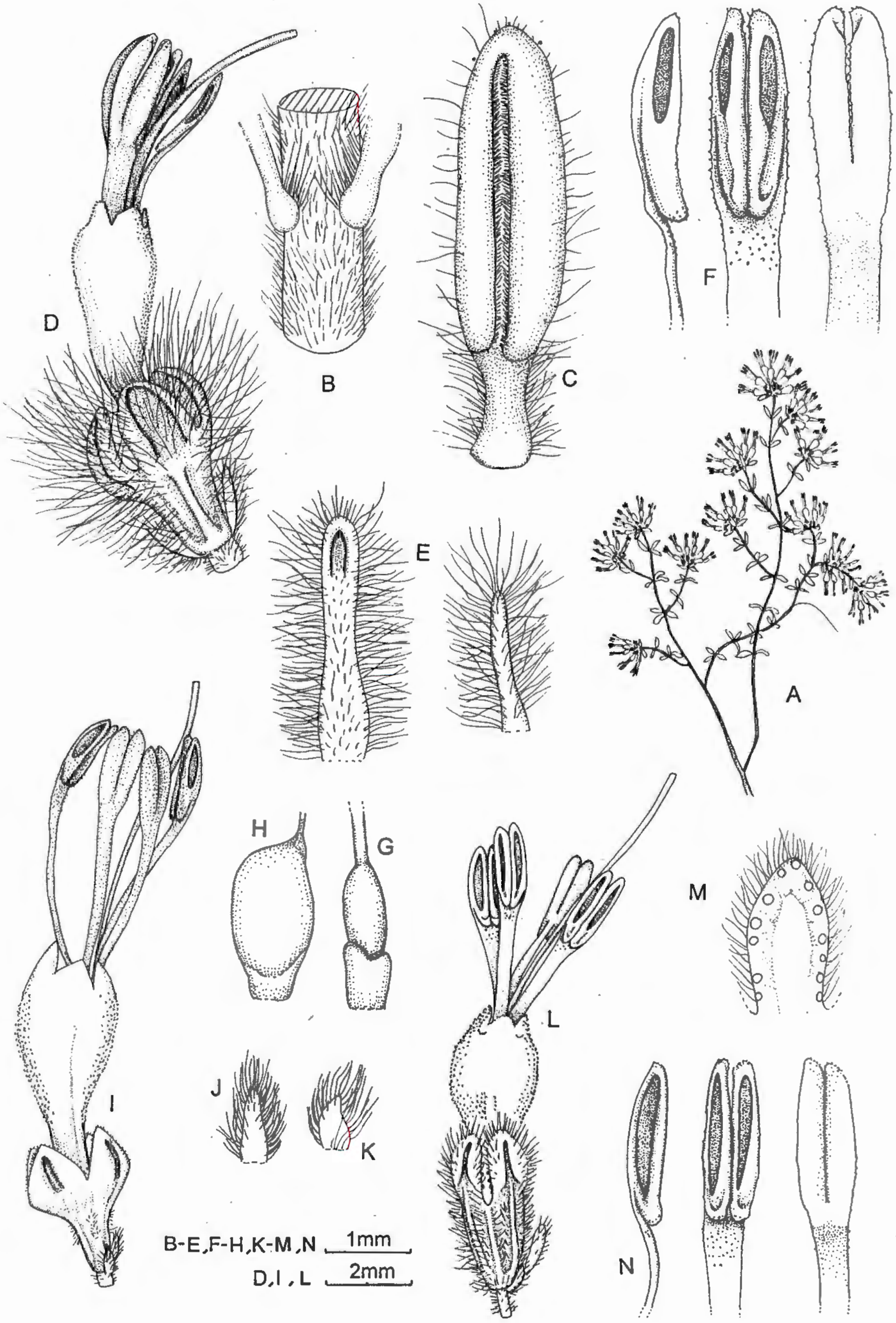

PLATE 25.—*Erica paucifolia*. Subsp. *paucifolia*: A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract (left) & bracteole (right); F, anther, side, front & back views; G, ovary; H, fruit; all drawn from *de Vos 203*: subsp. *ciliata*; I, flower; J, bract; K, bracteoles: subsp. *squarrosa*; L, flower; M, sepal, adaxial surface; N, anther side, front & back views; drawn from *Volk s.n.*

L3 rBr1 rbr2 K4 C4 A4 $G^1/_1$

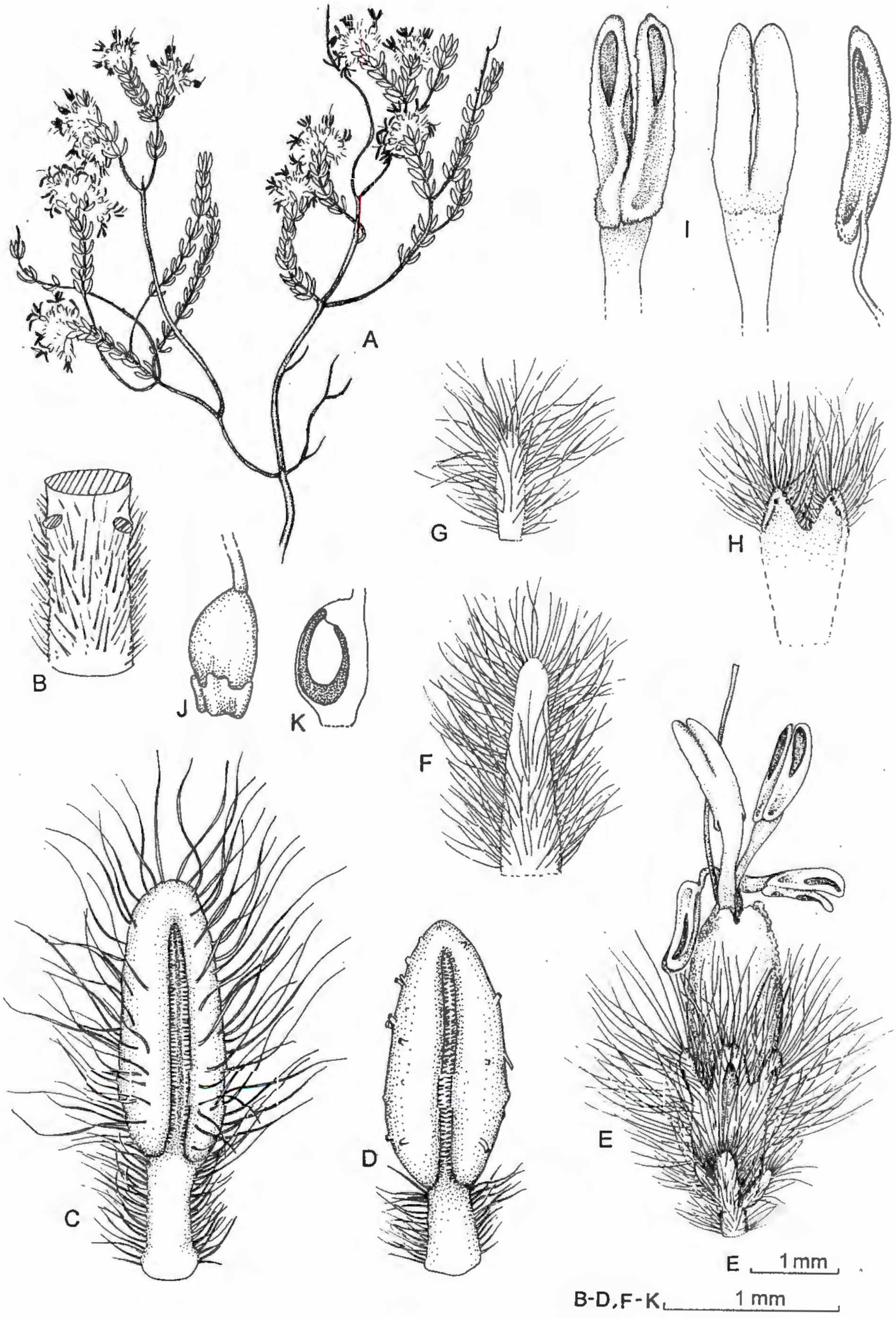

PLATE 26.—*Erica niveniana*. A, flowering branch, nat. size; B, stem; C, leaf, D, leaf; E, flower; F, bract; G, bracteole; H, calyx, adaxial surface; I, anther, front, back & side views; J, ovary; K, ovary L/S; all drawn from *Esterhuysen 34124*.

L3 rBr1 rbr2 K4 C4 A4 G$^{1}/_{1}$

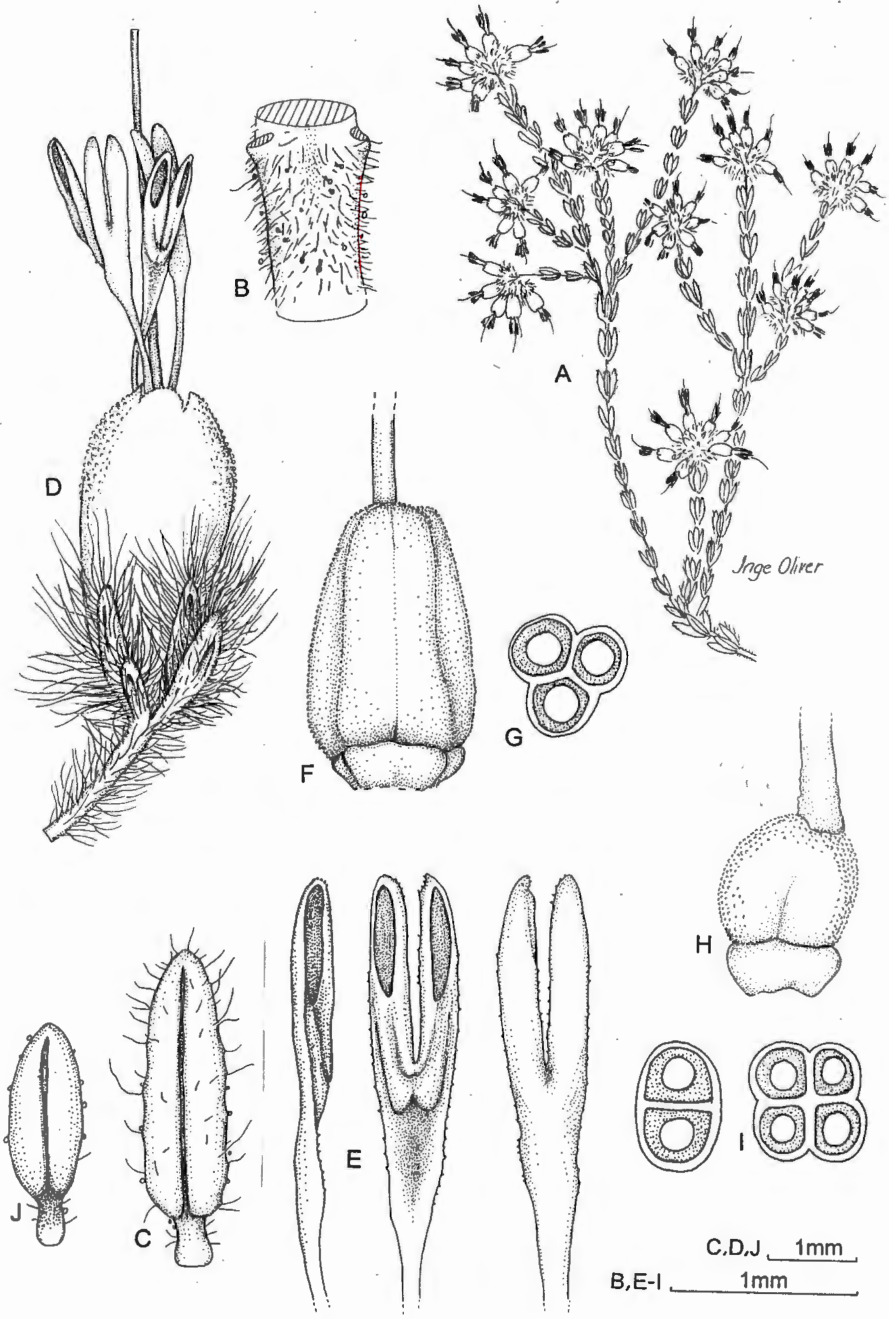

PLATE 27.—*Erica eriocephala*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views; F, ovary, 3-locular showing partial dehiscence line; G, ovary T/S; H, young ovary; I, ovary T/S; J, leaf; A–E drawn from *Oliver 8985*, F & G from *Oliver 10887a*, H from *Boucher 2520*.

L3,4 rBr1 br2 K4 C4 A4 G$^{2}/_{1}$ $^{3}/_{1}$ $^{4}/_{1}$

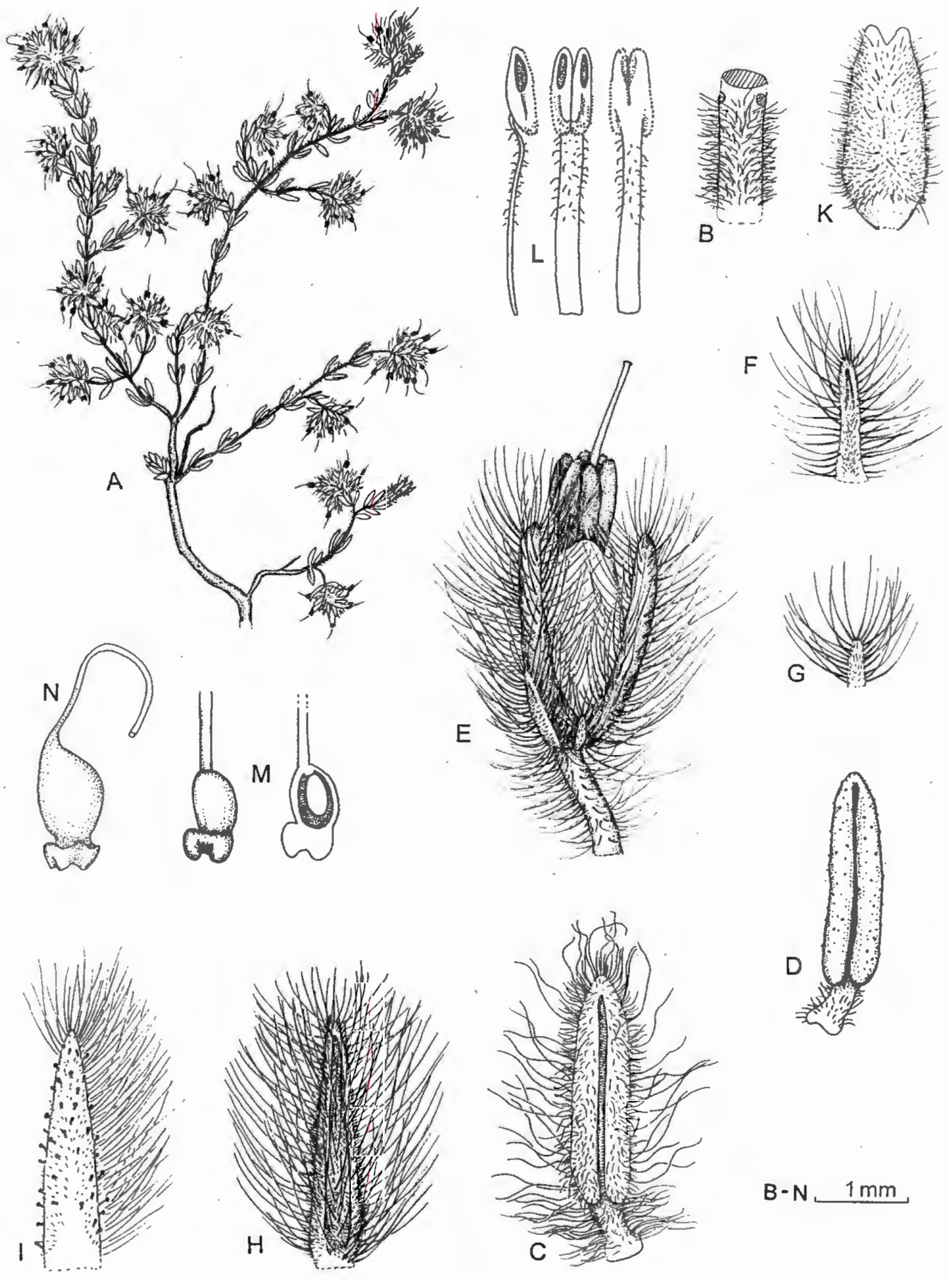

PLATE 28.—*Erica pilosiflora*. A, flowering branch, nat. size; B, stem; C & D, leaf; E, flower; F, bract; G, bracteole; H, sepal, abaxial surface; I, sepal, adaxial surface; K, corolla; L, anther, side, front & back views; M, ovary, whole & L/S; N, fruit; all drawn from *Oliver 1705*. **L3 rBr3 rbr2 K4 C4 A**4(6) **G**$^{1}/_{1}$ $(^{2}/_{1})$

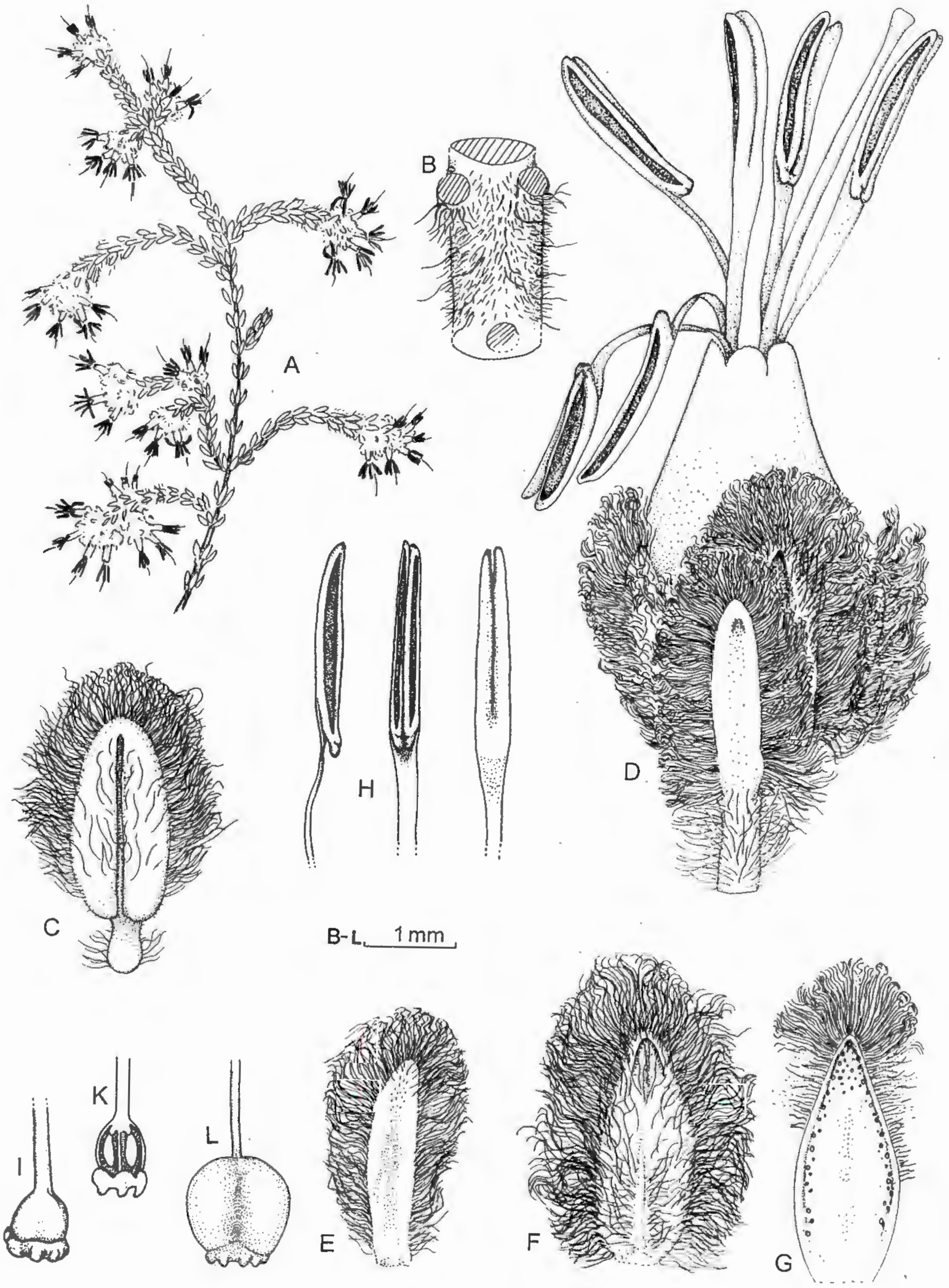

PLATE 29.—*Erica xeranthemifolia*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, sepal, abaxial surface; G, sepal, adaxial surface; H, anther, side, front & back views; I, ovary; K, ovary L/S; L, fruit; all drawn from *Oliver 3913*. L3 rBr1 br2 K4 C4 A6(7) $G^2/_1$

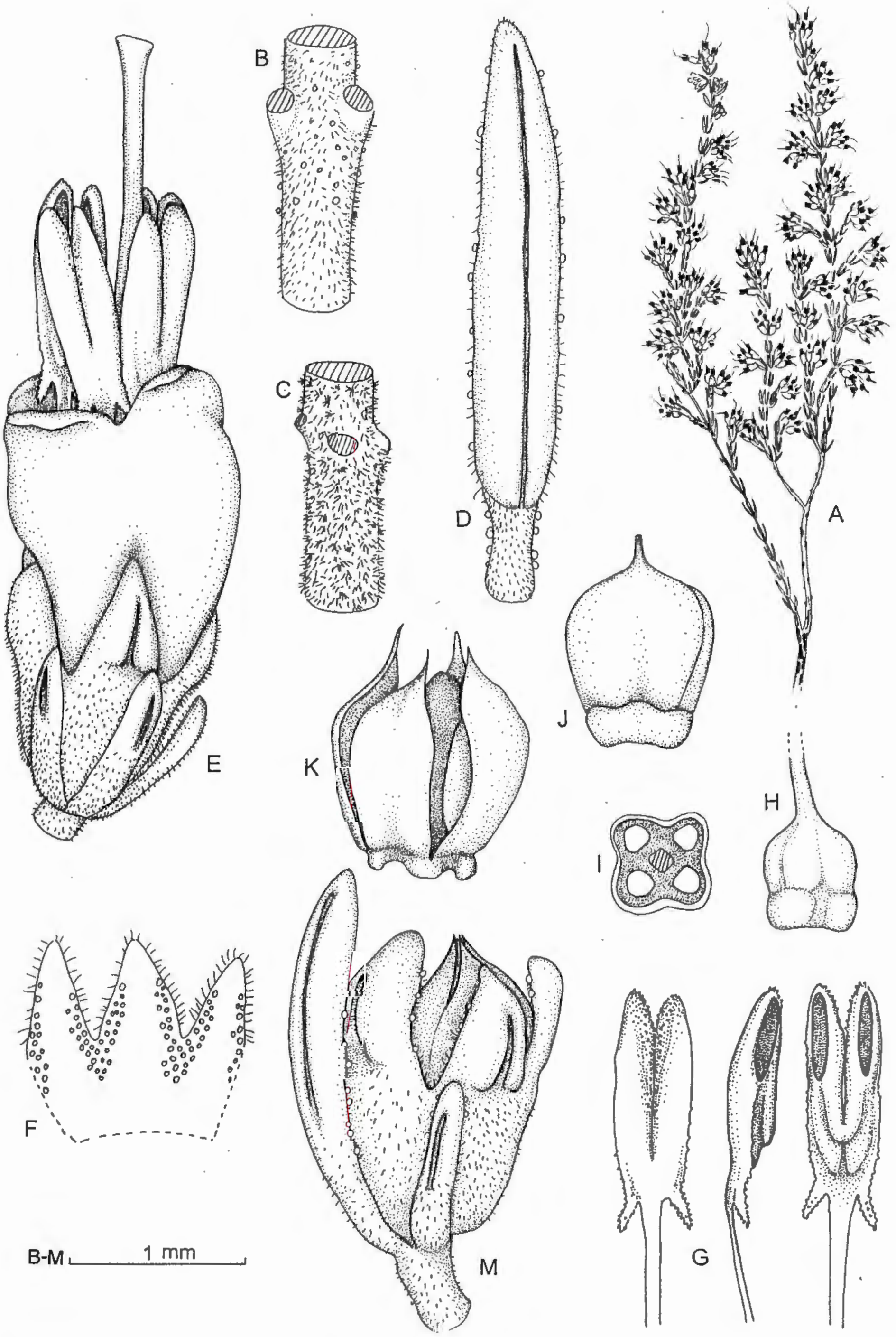

PLATE 30.—*Erica thamnoides*. A, flowering branch, nat. size; B & C, stem; D, leaf; E, flower; F, calyx, adaxial surface; G, anther, back, side & front views; H, ovary; I, ovary T/S; J, fruit, undehisced; K, fruit, partially dehiscent; M, fruiting flower with old corolla removed; A–I drawn from *Oliver 4440*, J–M from *Stirton 11605*. **L3 rBr1 br2 K4 C4 A4 G**$^{1}/_{4}$

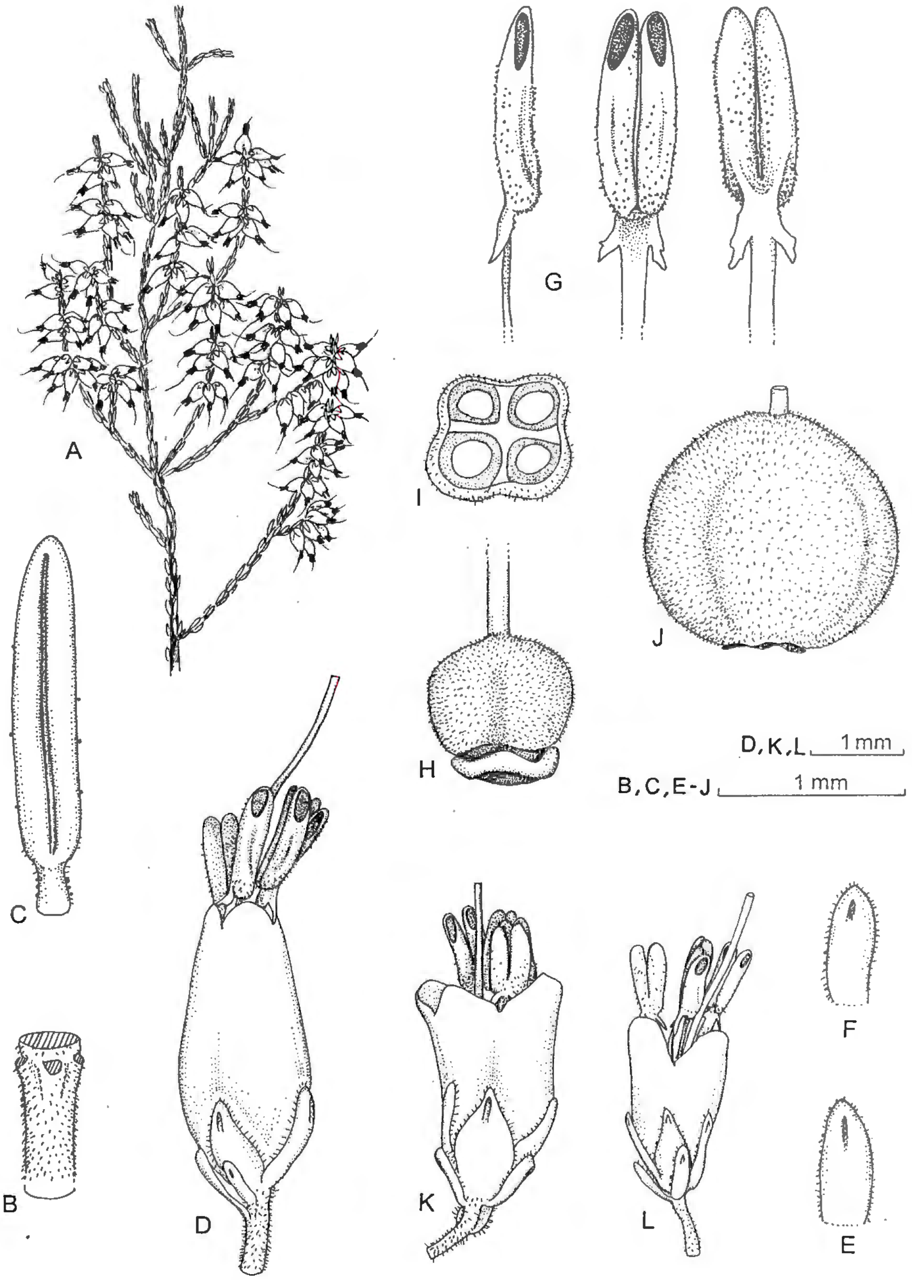

PLATE 31.—*Erica rosacea*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, anther, side, front & back views; H, ovary; I, ovary T/S; J, fruit; K, flower; L, flower; A–J drawn from *Oliver 5391*, K from *Oliver 3611*, from *Oliver 5608*. **L3 rBr br2 K4 C4 G**$^{4}/_{1}$

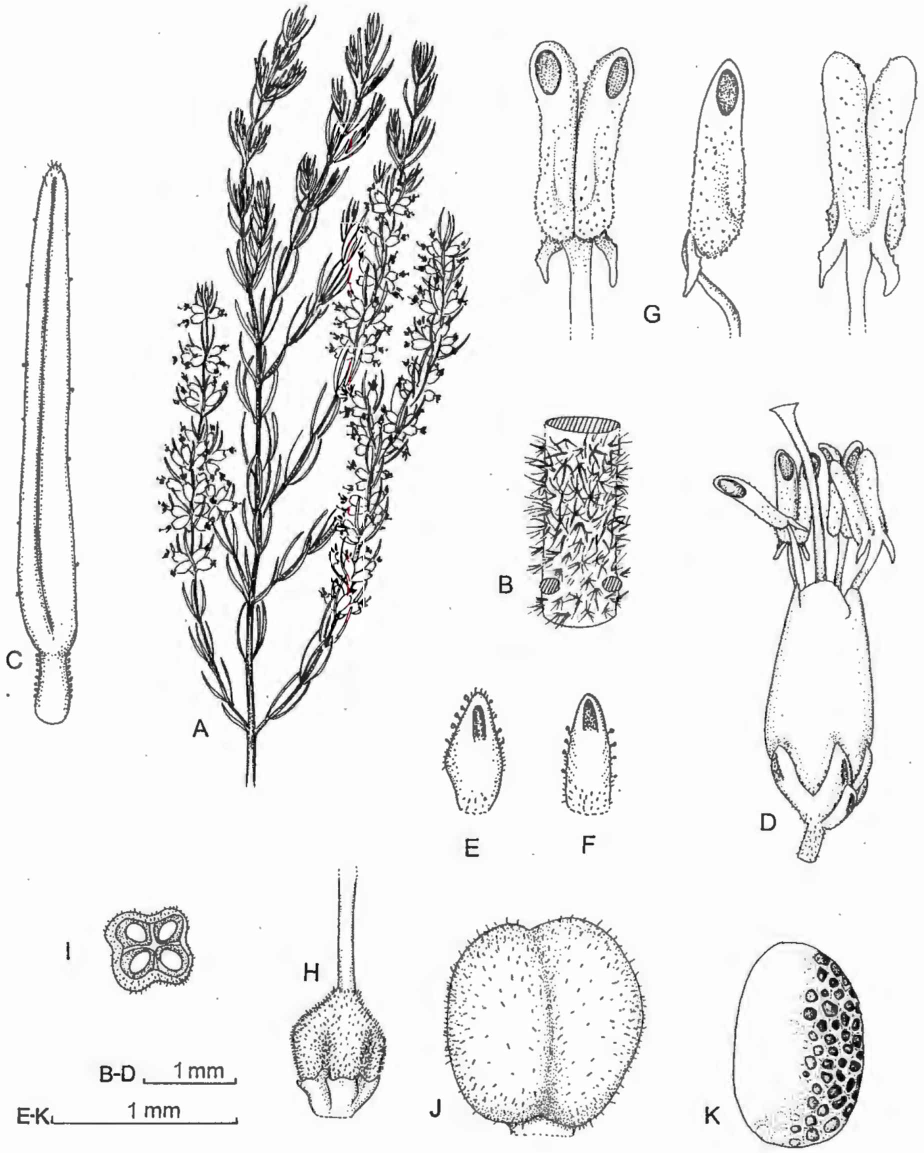

PLATE 32.—*Erica quadrifida*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, anther, front, side and back views; H, ovary; I, ovary T/S; J, fruit; K, seed; A–K drawn from *Oliver 4130*.

L3 rBr1 br2 K4 C4 A4 G$^{4}/_{1}$.

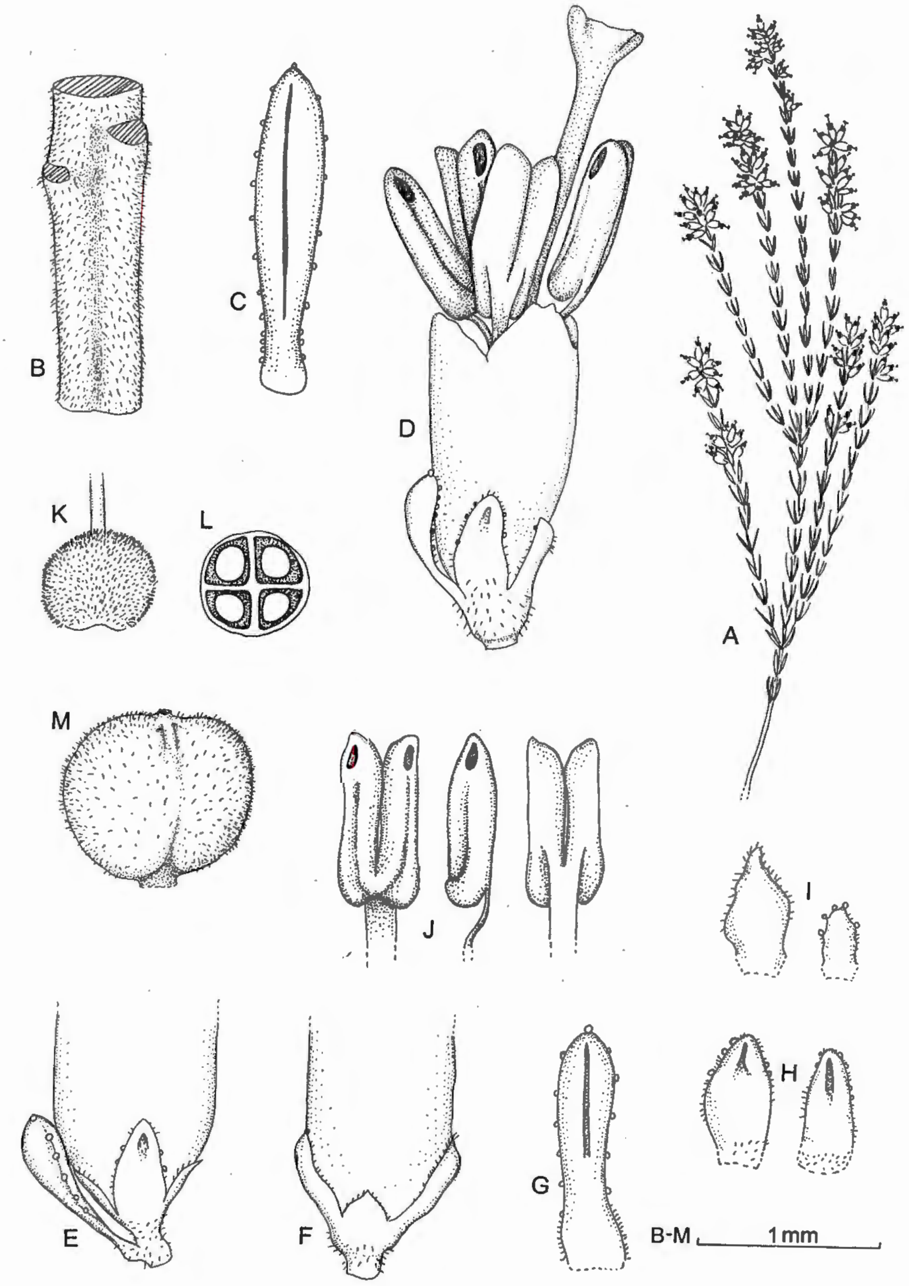

PLATE 33.—*Erica burchelliana*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, partially recaulescent bract, large fully recaulescent bracteole and two reduced sepals; F, two lateral fully recaulescent bracteoles and reduced adaxial sepal; G, partially recaulescent bract; H, fully recaulescent bract (left) and bracteole (right); I, sepals; J, anther, front, side & back views; K, ovary; L, ovary T/S; M, fruit; A–L drawn from *Oliver 8801*.

L3 (r)R**Br1** **Rbr2** **K1** **C4** **A4** $\mathbf{G}^4/_1\,(^3/_1)$.

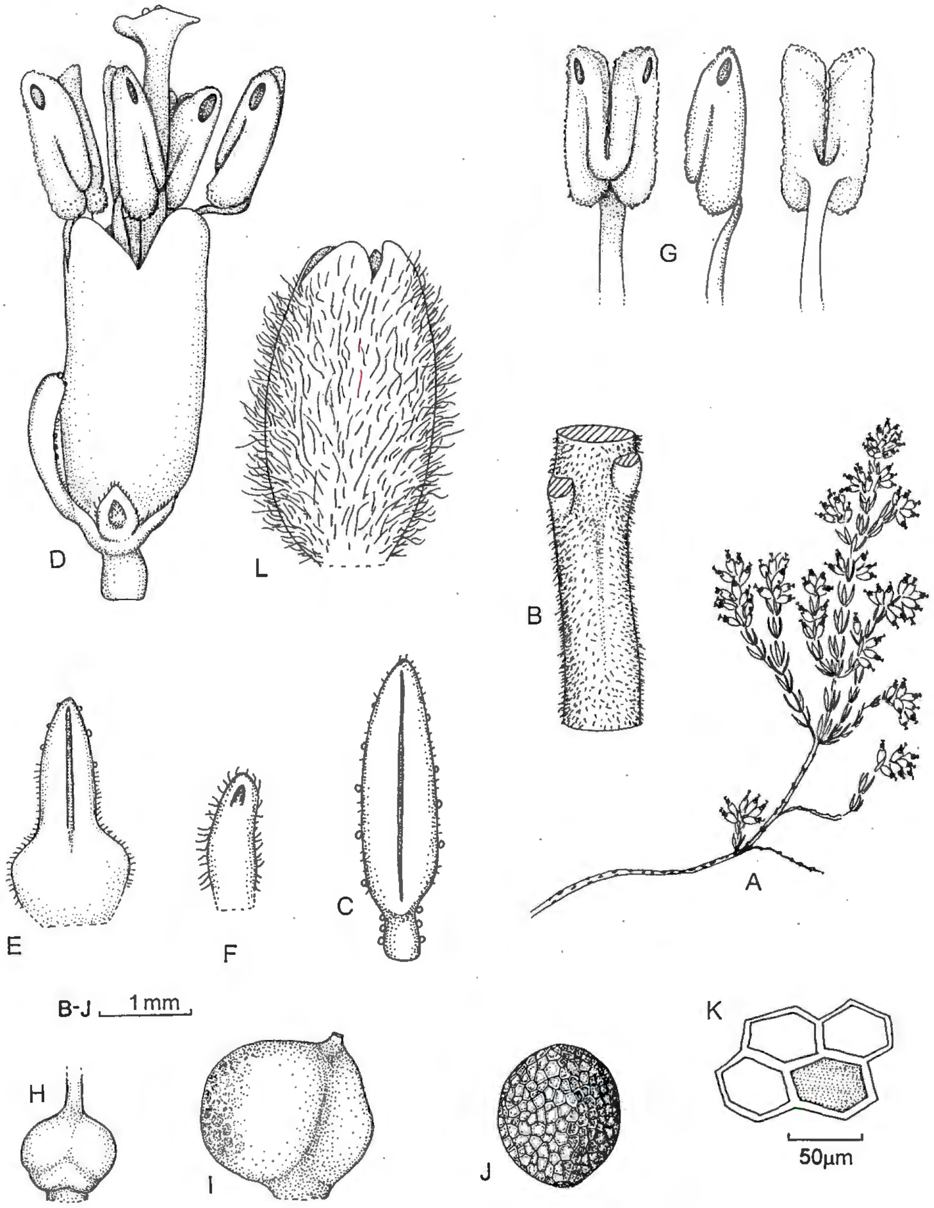

PLATE 34.—*Erica zeyheriana*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower, showing unequal calyx with fully recaulescent bract on left; E, bract; F, bracteole; G, anther, front, side & back views; H, ovary; I, fruit with one seed developed; J, seed; K, testa cells; A–H drawn from *Oliver 7949*.

L3 RBr1 Rbr2 K1 C4 A4 $G^{2}/_{1}$ ($^{3}/_{1}$).

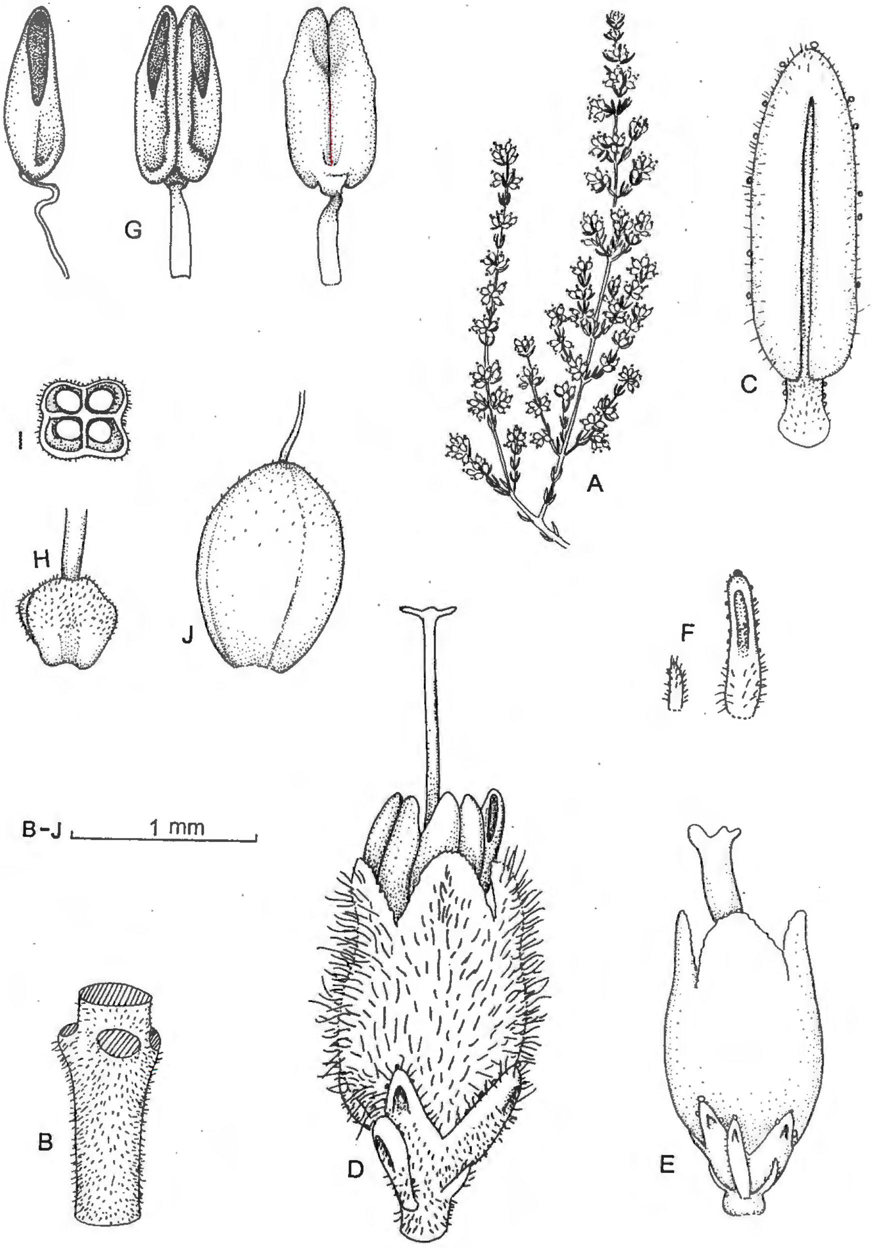

PLATE 35.—*Erica puberuliflora*. A, flowering branch, nat. size; B, stem; C, leaf; D, pubescent flower; E, glabrous flower; F, bracteole & bract; G, anther, side, front & back views; H, ovary; I, ovary T/S; J, fruit; A–D, F–J drawn from *Oliver 8560*, E, from *Fellingham 108*. **L**3 r**Br**1 **br**2 **K**4 **C**4 **A**4 **G**$^{4}/_{1}$.

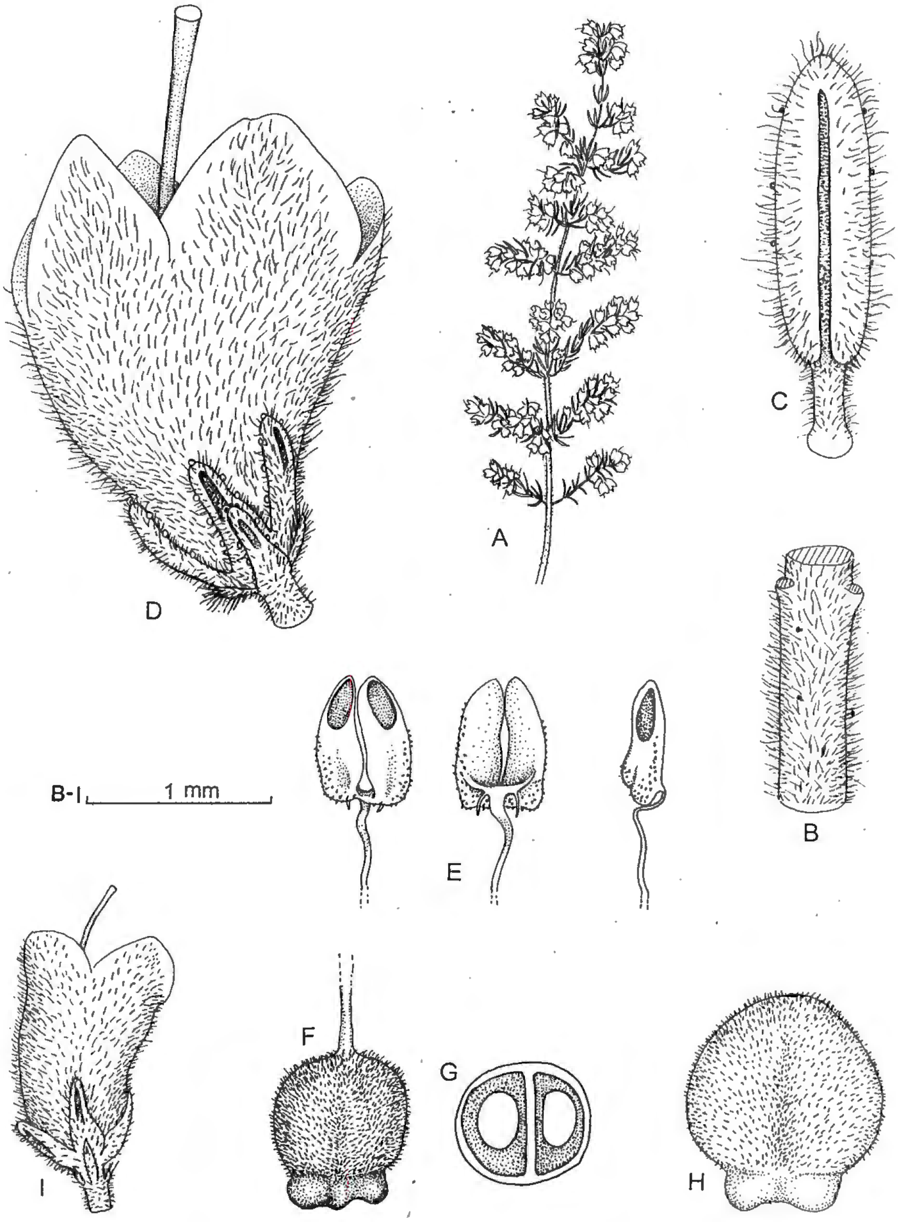

PLATE 36.—*Erica vallis-fluminis*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, front, back & side views; F, ovary; G, ovary T/S; H, fruit; A–H drawn from the type, *McDonald 1967*, I from *Oliver 10531*.

L3 rBr1 br2 K4 C4 A4 $G^{2}/_{1}$ [$^{2}/_{2}$].

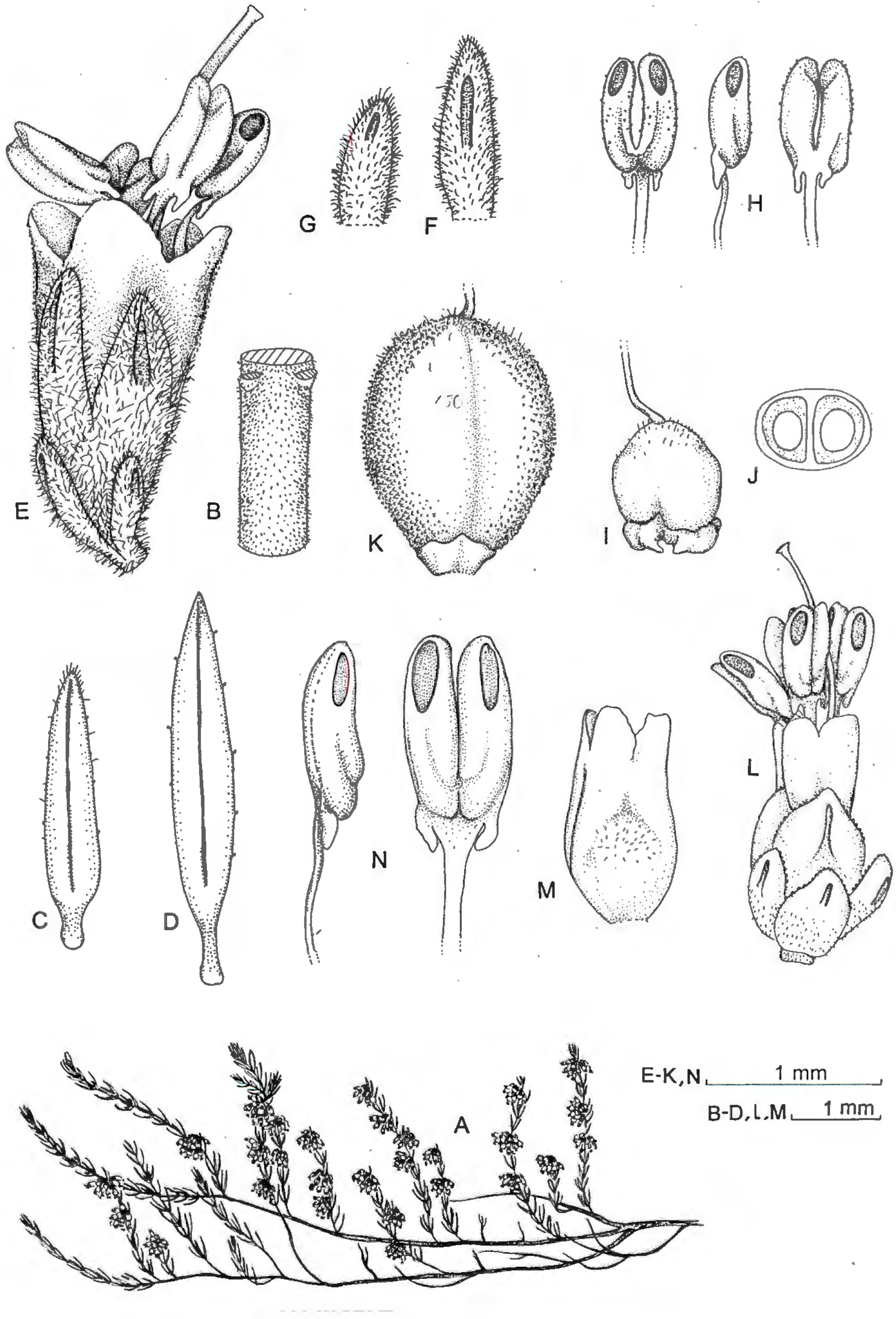

PLATE 37.—*Erica atromontana*. A, flowering branch, nat. size; B, stem; C, & D, leaf; E, flower; F, bract; G, bracteole; H, anther, front, side & back views; I, ovary; J, ovary, T/S; K, fruit; L, flower; M, corolla; N, anther side & front views; A–K drawn from *Vlok 1265*; L & N from *Oliver 10366*.

L3 rBr1 br2 K4 C4 A4 $\mathbf{G^2/_1[^2/_{1-2}]}$

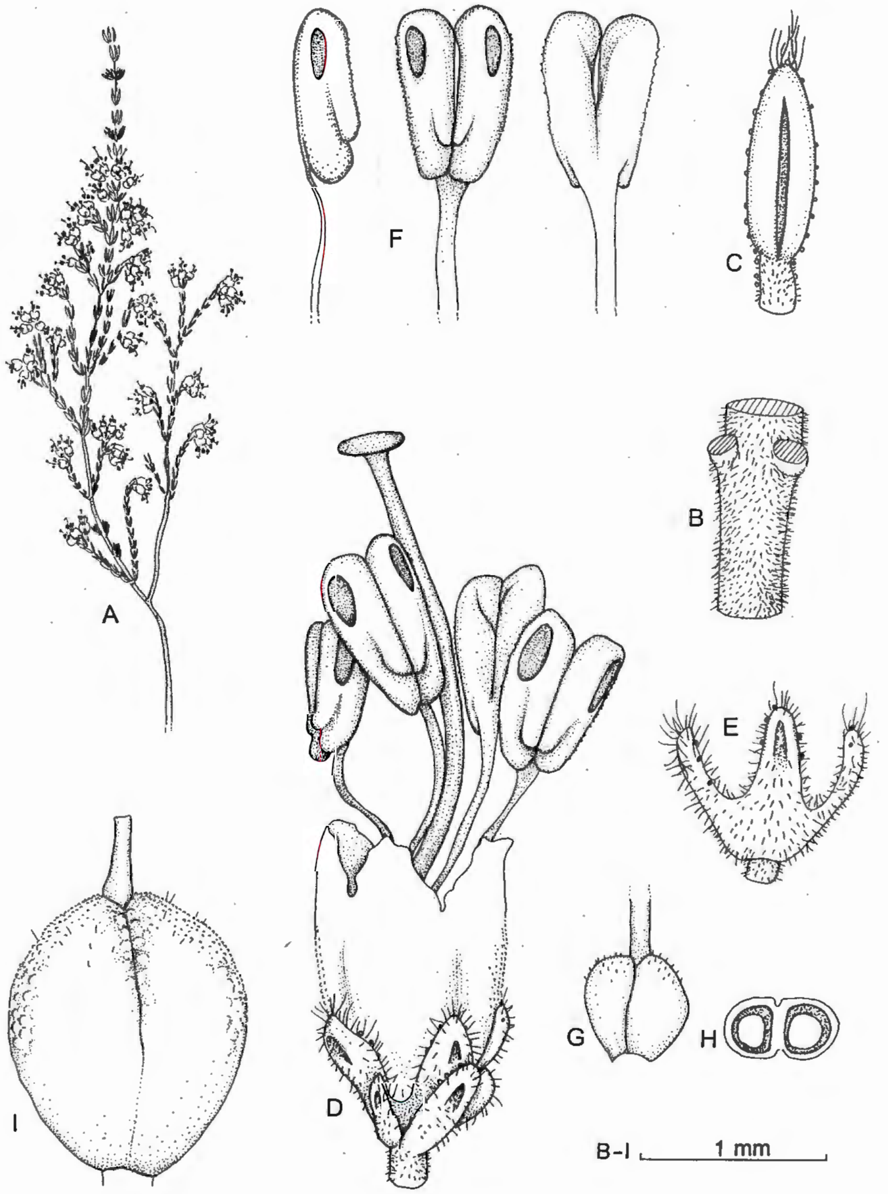

PLATE 38.—*Erica bolusanthus*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, calyx; F, anther, side, front & back views; G, ovary; H, ovary, T/S; I, fruit; A–H drawn from *Kruger 1639*, I from *Vlok 1199*.

L3 rBr1 br2 K4 C4 A4 $\mathbf{G}^{2}/_{1}\,(^{1}/_{1}\,^{3}/_{1}\,^{4}/_{1})$.

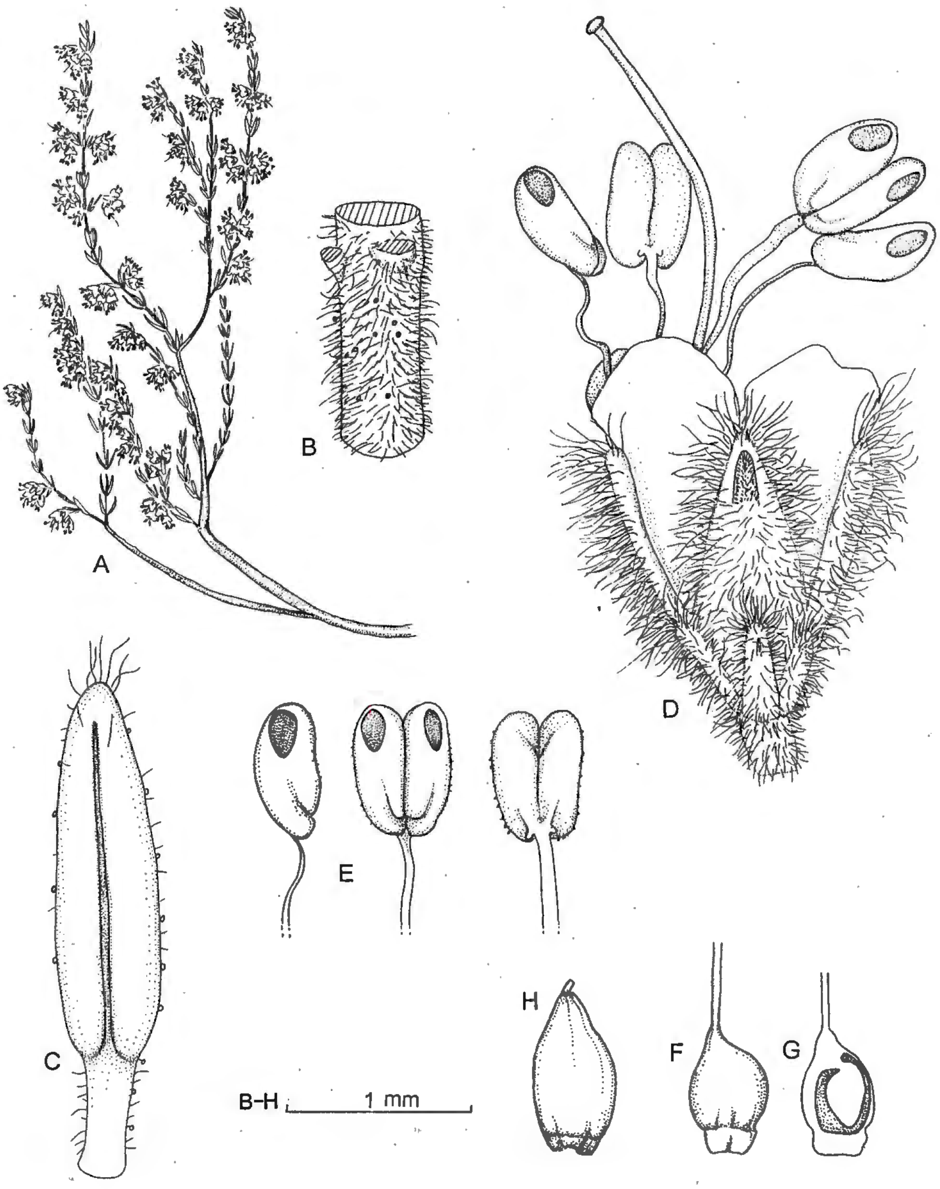

PLATE 39.—*Erica montis-hominis*. A, Flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views; F, ovary; G, ovary L/S; H, fruit; all drawn from the type, *Oliver 3609*. **L3 B1 rbr2 K4 C4 A4 G**$^{1}/_{1}$.

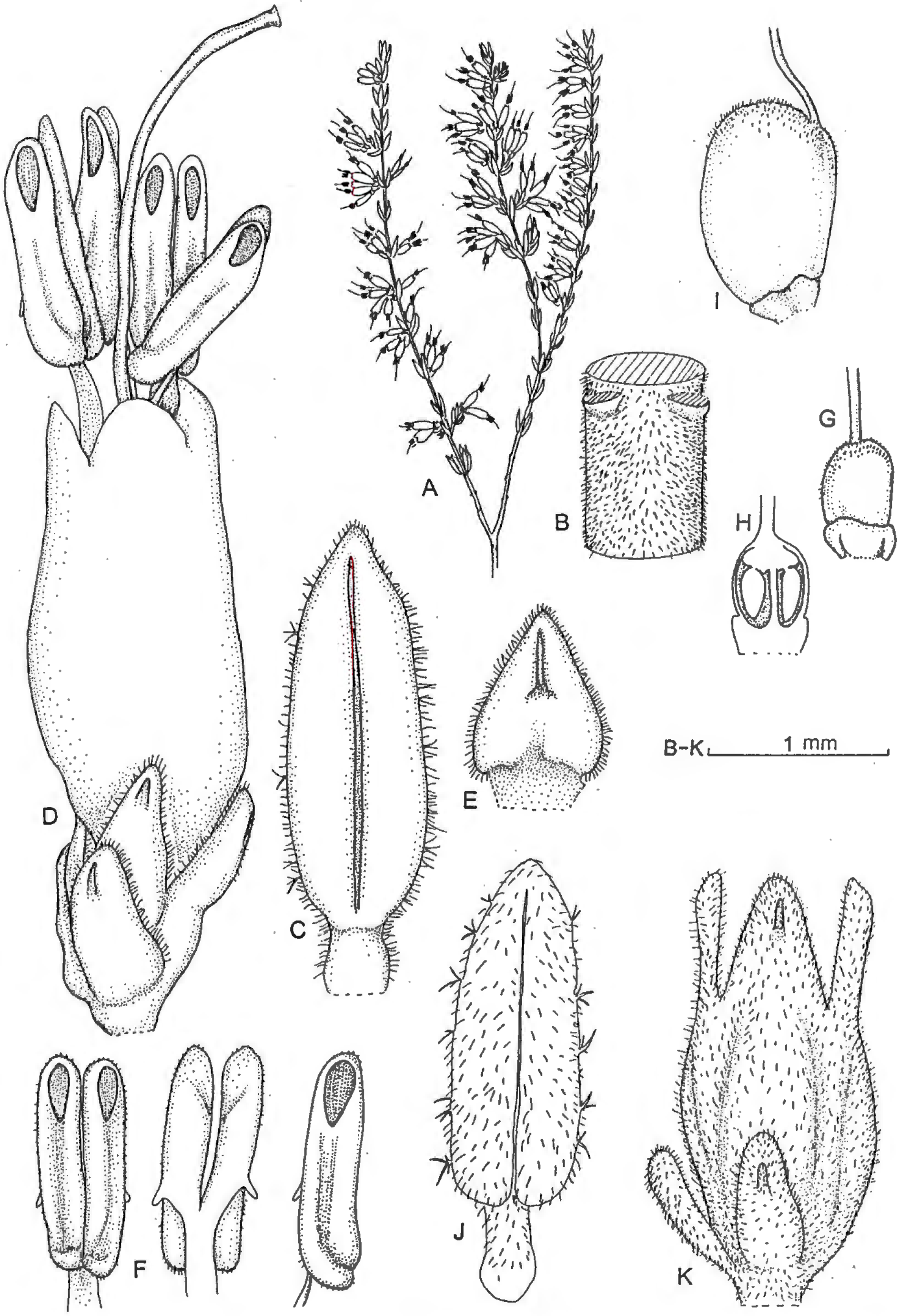

PLATE 40.—*Erica glabra*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, anther, front, back & side views; G, ovary; H, ovary L/S; I, fruit; J, leaf, K, fruiting calyx; B–H drawn from *Boucher 2876*, J & K from *Oliver 6087*. **L3 rBr1 br2 K4 C4 A4 G**$^{2}/_{1}$.

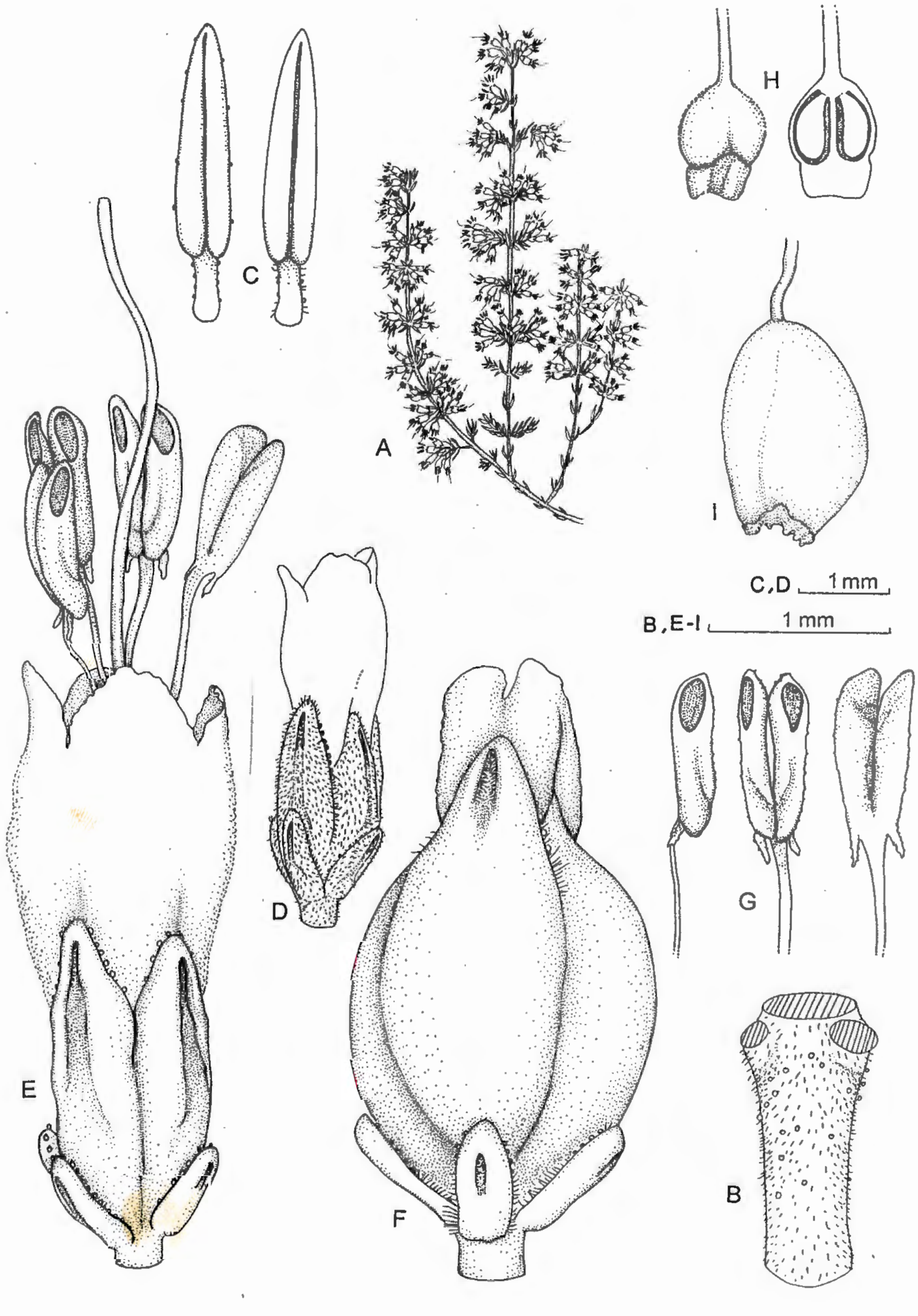

PLATE 41.—*Erica phaeocarpa*. A, flowering branch; B, stem; C, leaves; D, flower (without anthers); E, flower; F, fruiting calyx; G, anther, side, front & back views; H, ovary, whole & L/S; I, fruit; B, C, E, G, H drawn from *Rourke 435*, D, from *Oliver 10818*, F & I from *Oliver 9696*. **L3 rBr1 br2 K4 C4 A4** $\mathbf{G^{2}/_{1}[^{3}/_{1}]}$.

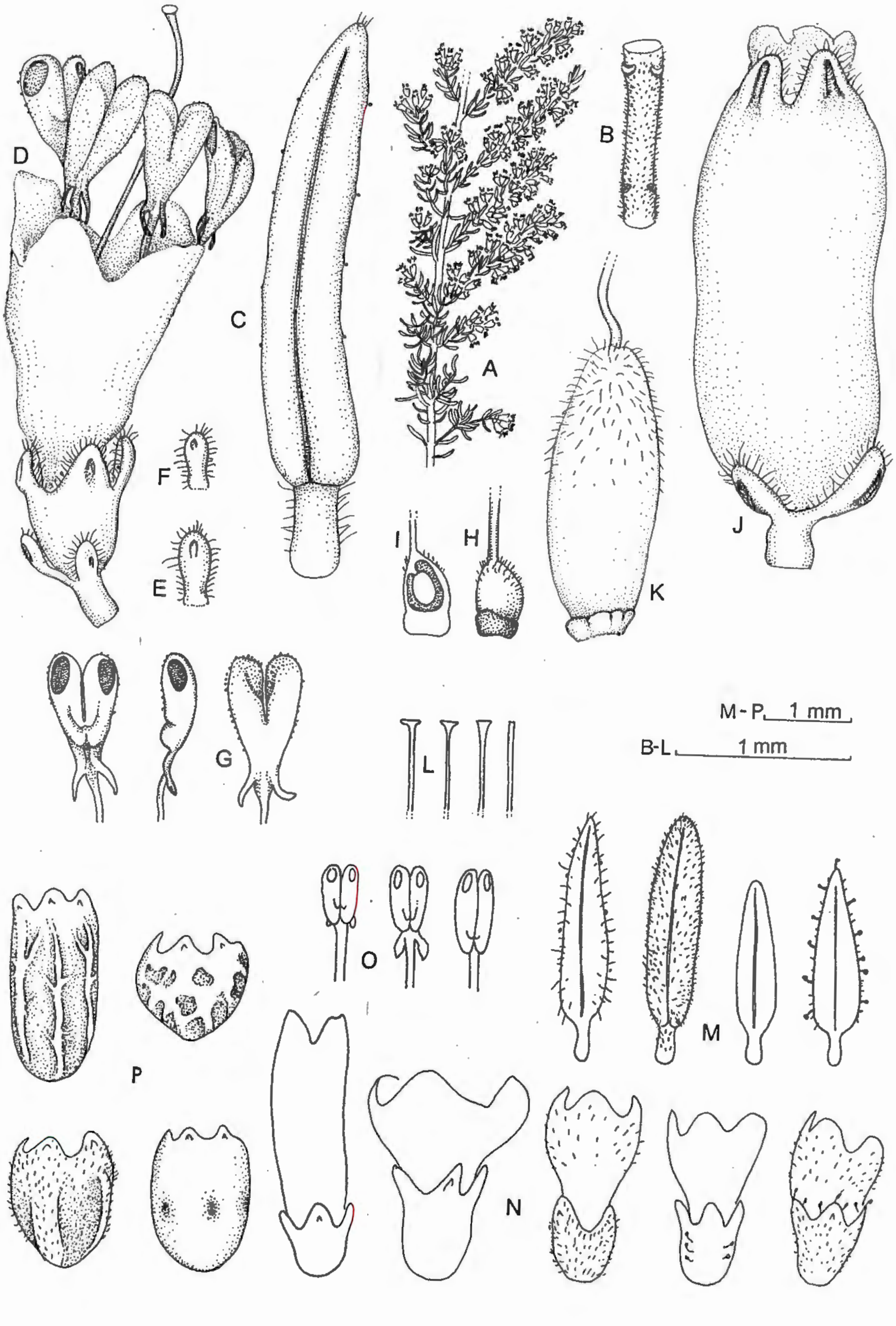

PLATE 42.—*Erica anguliger*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, anther, front, side & back views; H, ovary; I, ovary L/S; J, fruiting calyx; K, fruit; L, variations in stigma; M, variations in leaf (size and indumentum); N, variation in calyx and corolla types; O, variation in anther size and spurs; P, variation in types of fruiting calyces. A–I drawn from *Oliver 5921*; J & K from *Oliver s.n.* (Jonaskop); L–P from a range of collections.
L3 rBr br2 K4 C4 A4 $\mathbf{G}^{1}/_{1}$

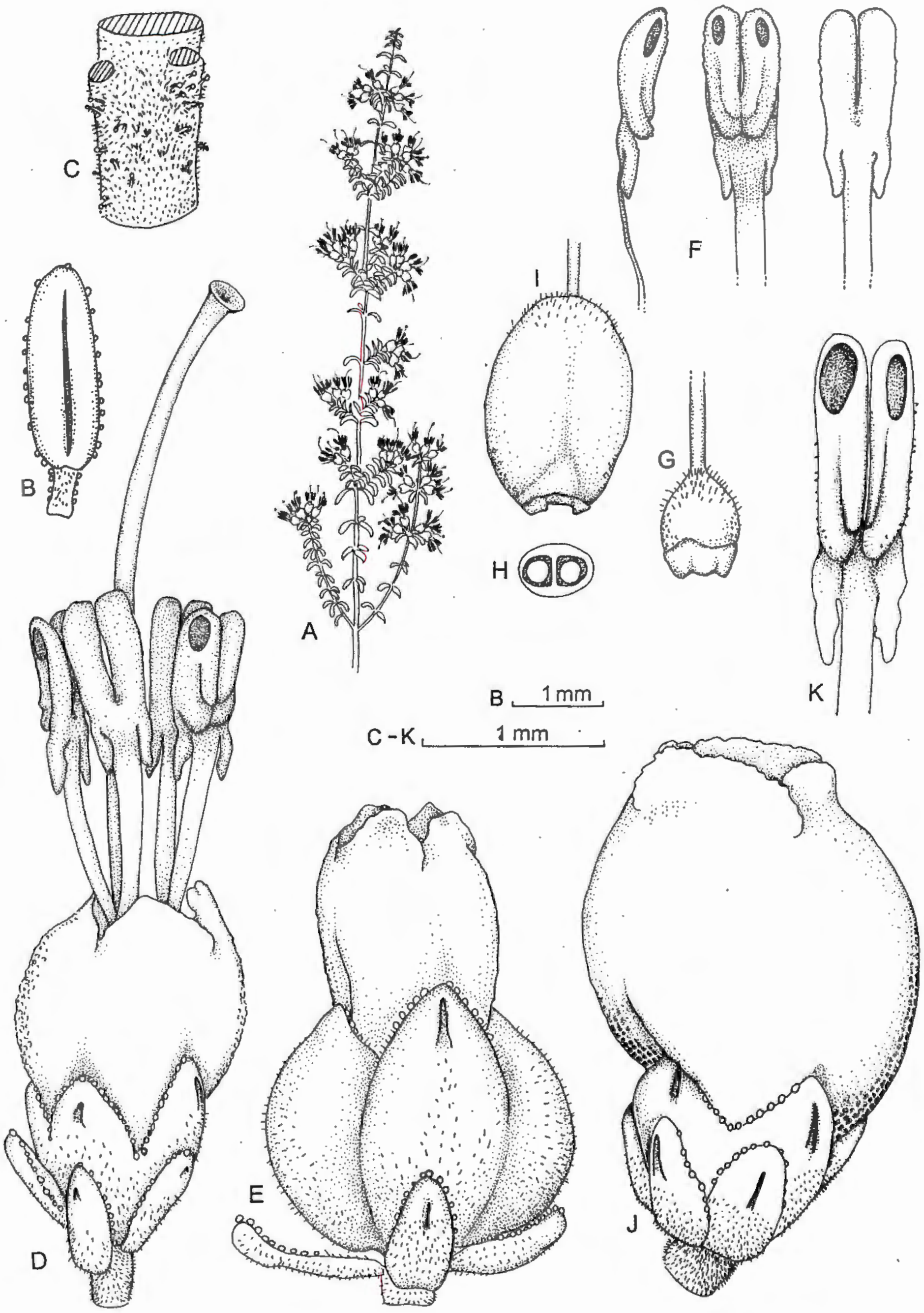

PLATE 43.—*Erica inflaticalyx*. A, flowering branch; B, leaf; C, stem; D, flower; E, fruiting flower; F, anther, side, front & back views; G, ovary; H, ovary, T/S; I, fruit; J, flower, without anthers; K, anther; A–I drawn from *Vlok 1511*, J & K from *van Wijk 924*. **L3 rBr1 br2 K4 C4 A4** $\mathbf{G^{2}/_{1}}$.

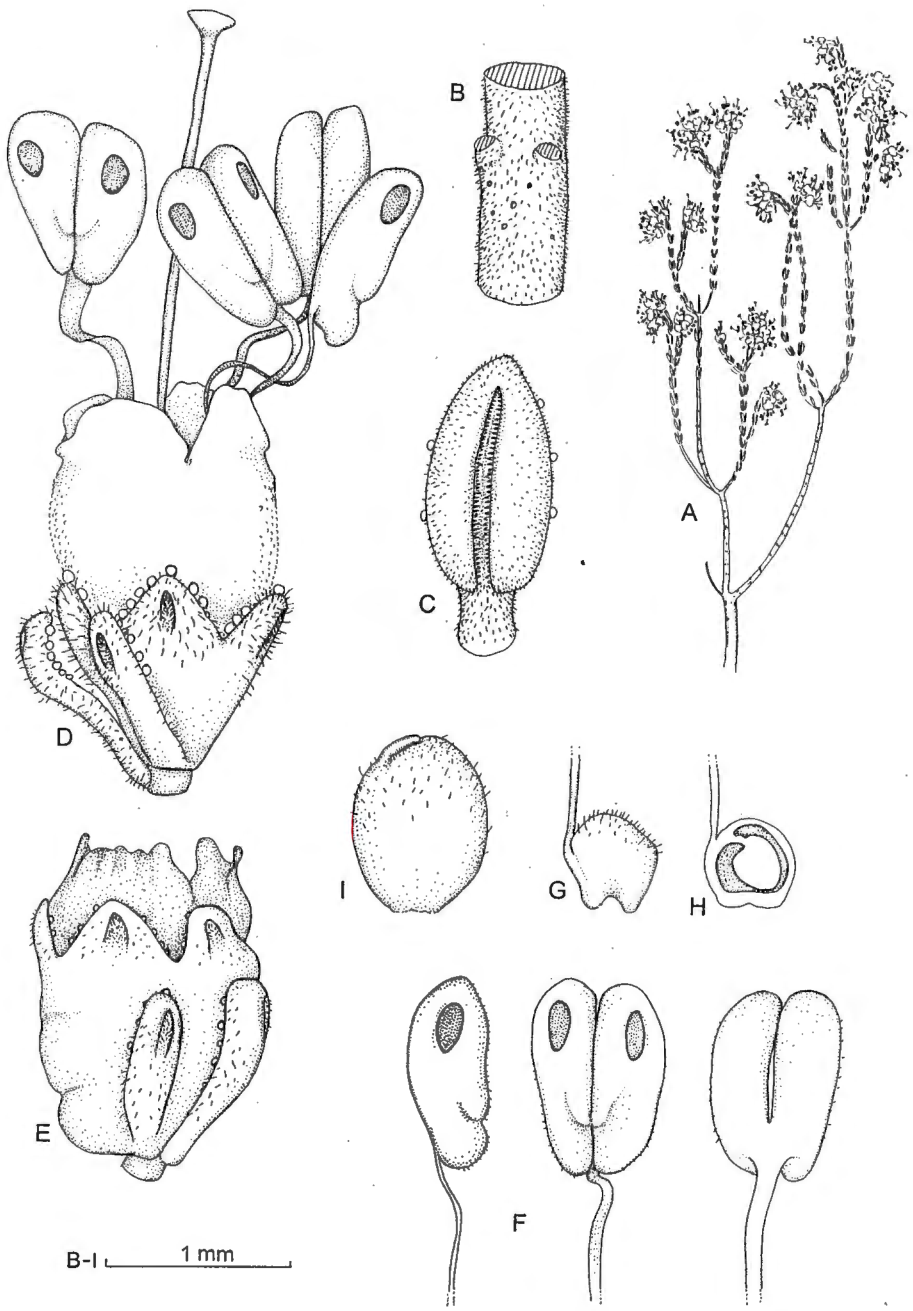

PLATE 44.—*Erica kammanassieae*. A, flowering branch; B, stem; C, leaf; D, flower; E, fruiting flower; F, anther, side, front & back views; G, ovary; H, ovary, L/S; I, fruit; all drawn from the type, *Campbell 14561*.

L3 rBr1 br2 K4 C4 A4 $\mathbf{G}^{1}/_{1}$.

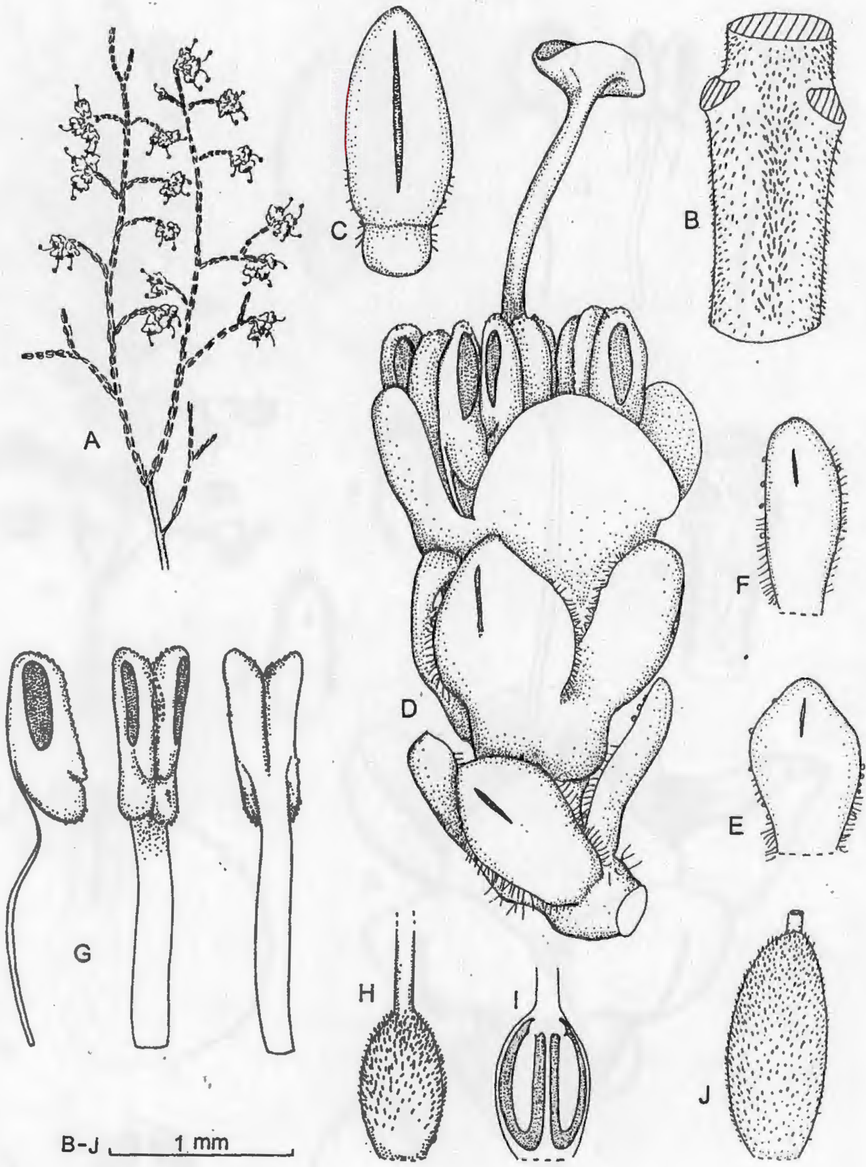

PLATE 45.—*Erica cetrata*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, anther, side, front & back views; H, ovary; I, ovary L/S; J, fruit; all drawn from *Oliver 9267*. **L3 rBr1 br2 K4 C4 A7,8 G**$^{2}/_{1}$

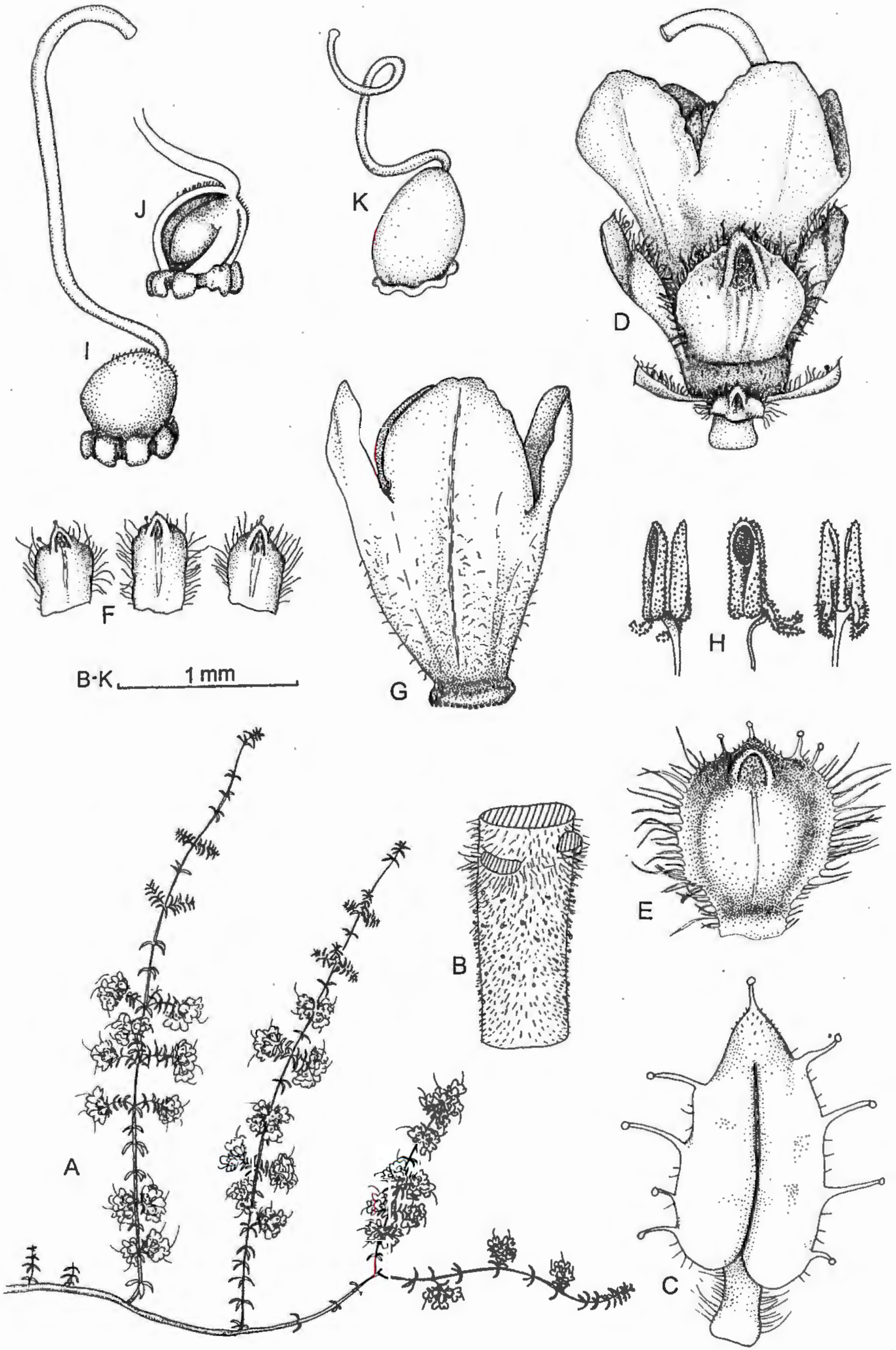

PLATE 47.—*Erica curvistyla*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, sepal; F, bract (centre) & 2 bracteoles; G, corolla; H, anther, front, side & back views; I, gynoecium; J, ovary L/S; K, fruit; B–D, F–H drawn from lectotype, *Niven s.n.*, E from *Hafstrom & Lindberg s.n.*, I & J from *Oliver 4072*.

L3 rBr1 br2 K4 C4 A8 G$^{1}/_{1}$ [$^{2}/_{1}$]

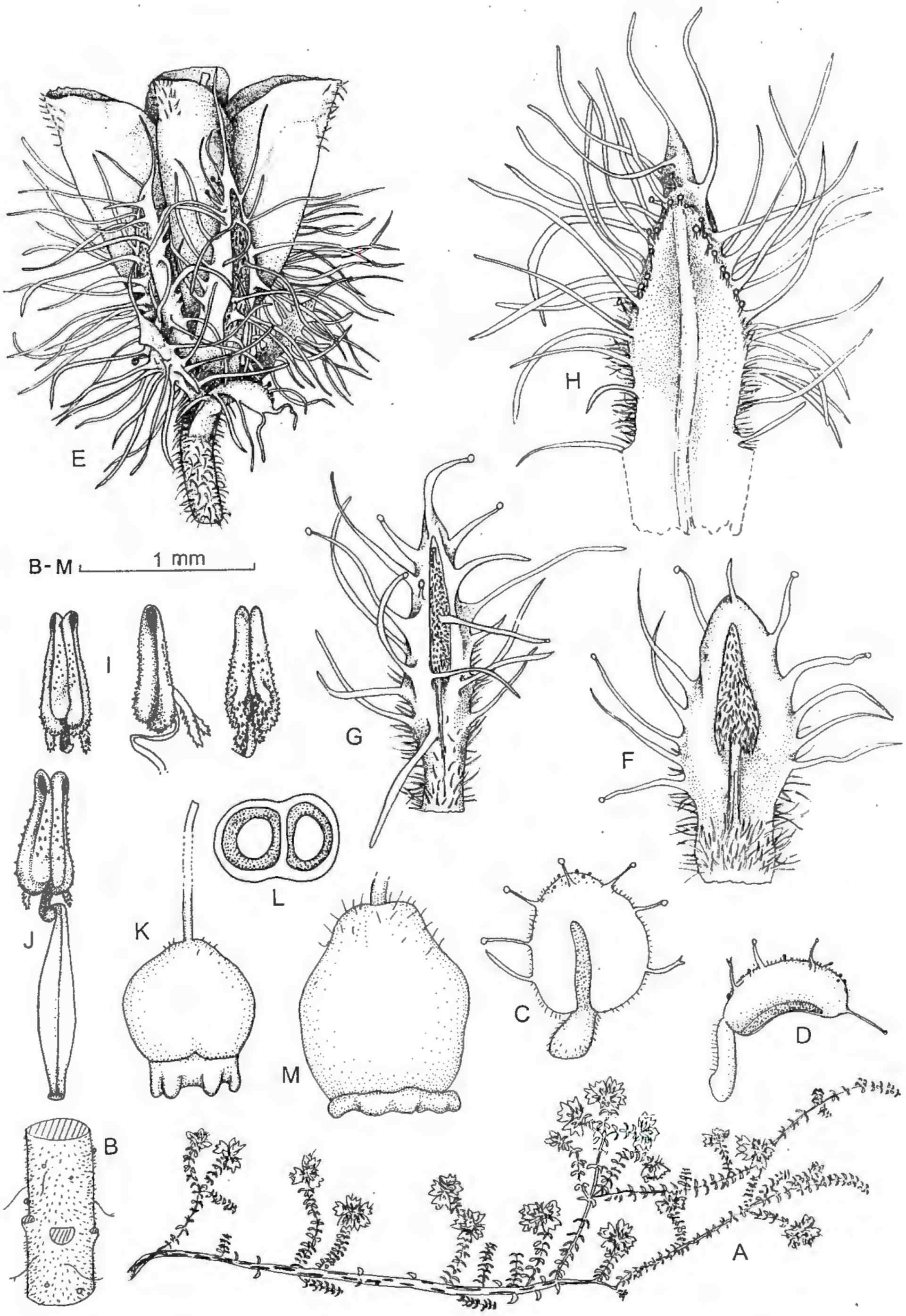

PLATE 48.—*Erica recurvifolia*. A, flowering branch, nat. size; B, stem; C, leaf; D, leaf seen laterally; E, flower; F, bract; G, bracteole; H, sepal, adaxial surface; I, anther, front, side & back views; J, stamen showing broadened filament; K, gynoecium; L, ovary T/S; M, fruit; B–L drawn from neotype, *Drege 2965*.

L3 rBr1 br2 K4 C4 A8 $\mathbf{G^{2}/_{1}}$

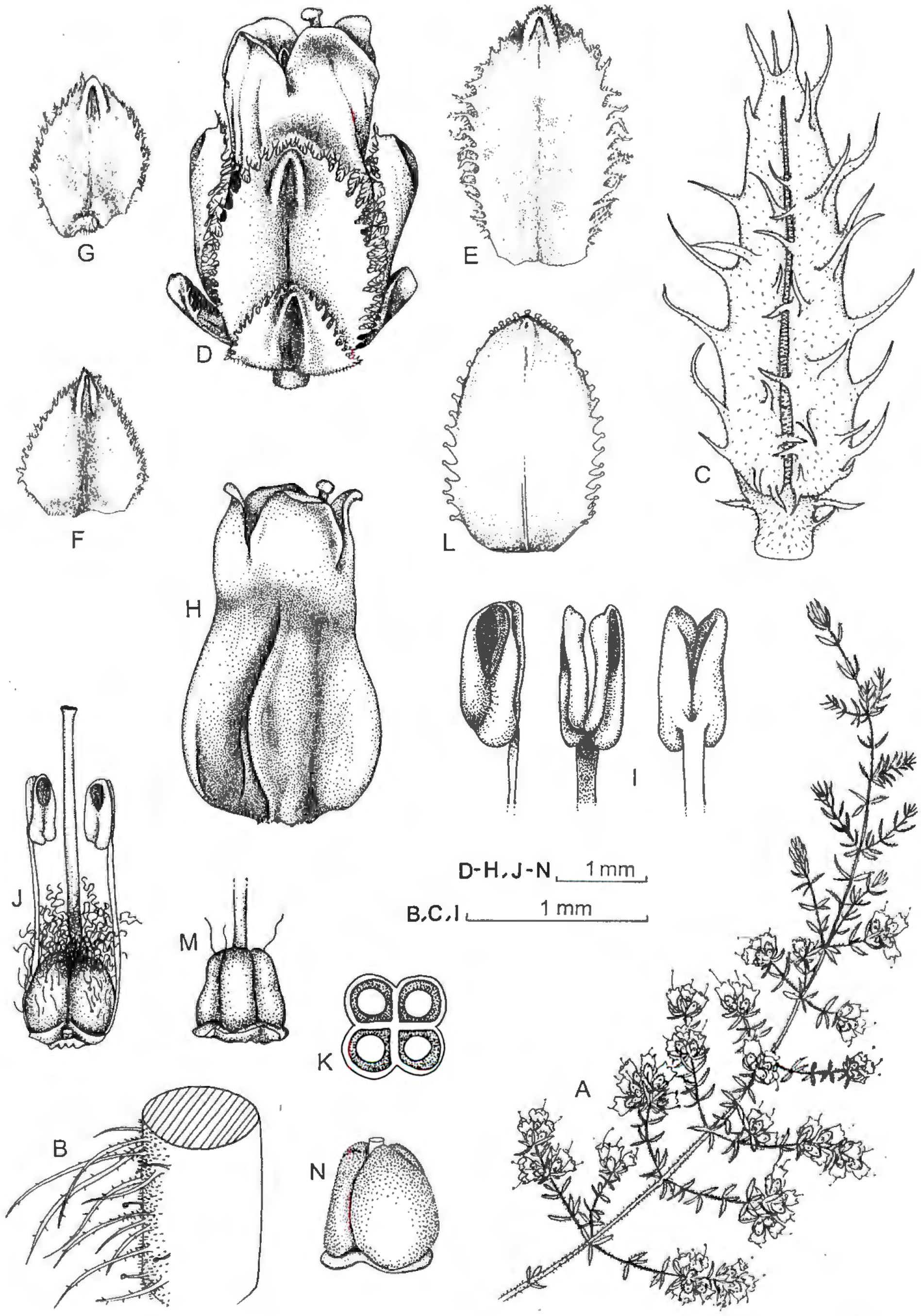

PLATE 49.—*Erica totta*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bract; G, bracteole; H, corolla; I, anther, side, front, back views; J, gynoecium & androecium; K, ovary T/S; L, sepal; M, ovary; N, fruit; B–K drawn from the type, *Thunberg 9437*; L, drawn from *Hutchinson 614*, M drawn from *Oliver 4061*, N drawn from *Oliver 11210*. **L3 rBr1 br2 K4 C4 A8** $\mathbf{G^4/_1}$

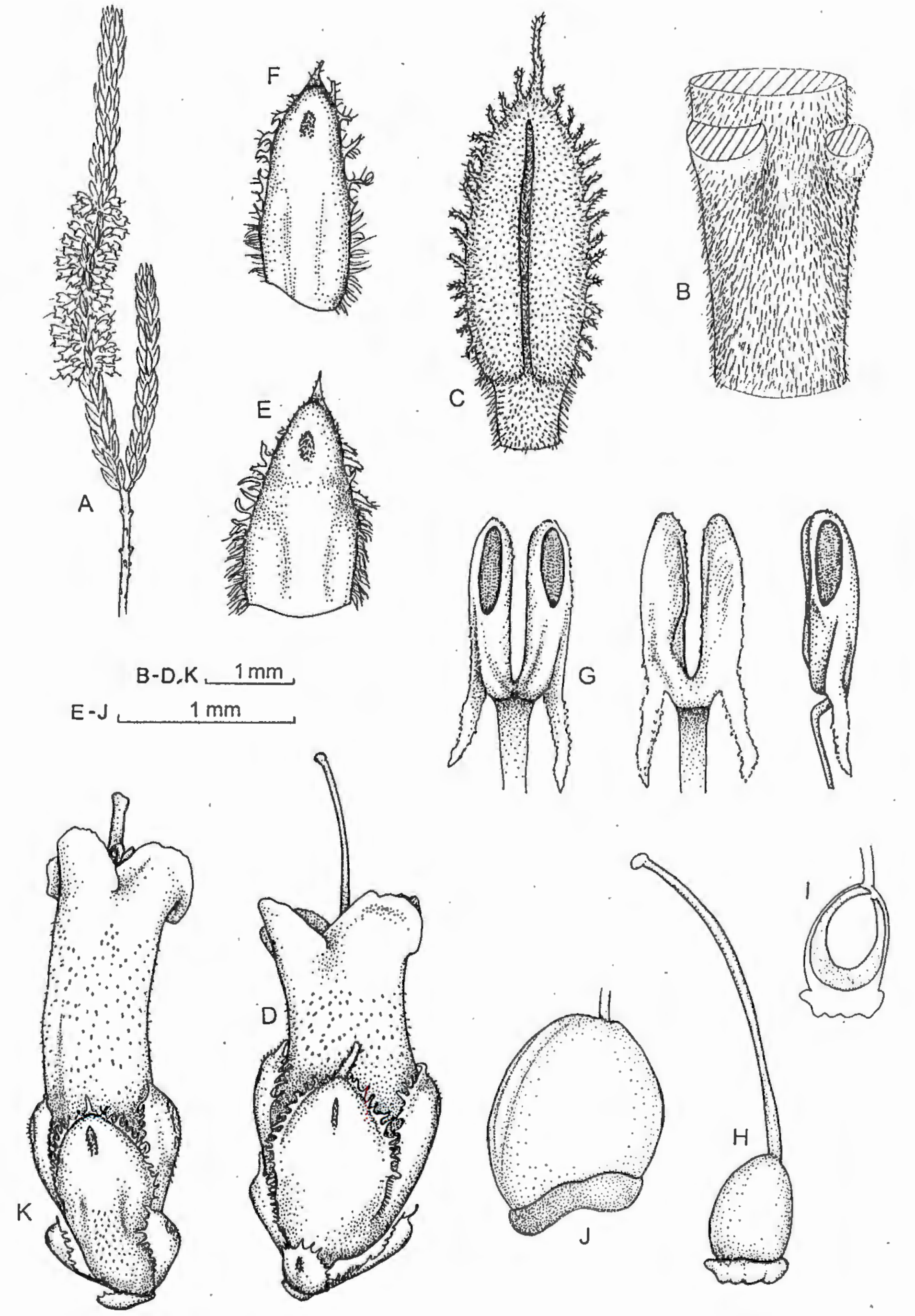

PLATE 50.—*Erica lateriflora*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, anther, front, back & side views; H, gynoecium; I, ovary L/S; J, fruit; K, flower; A–I drawn from the type, *Oliver 6105*, K drawn from *Oliver 5044*. **L**3 **rBr**1 **br**2 **K**4 **C**4 **A**4 **G**$^{1}/_{1}$

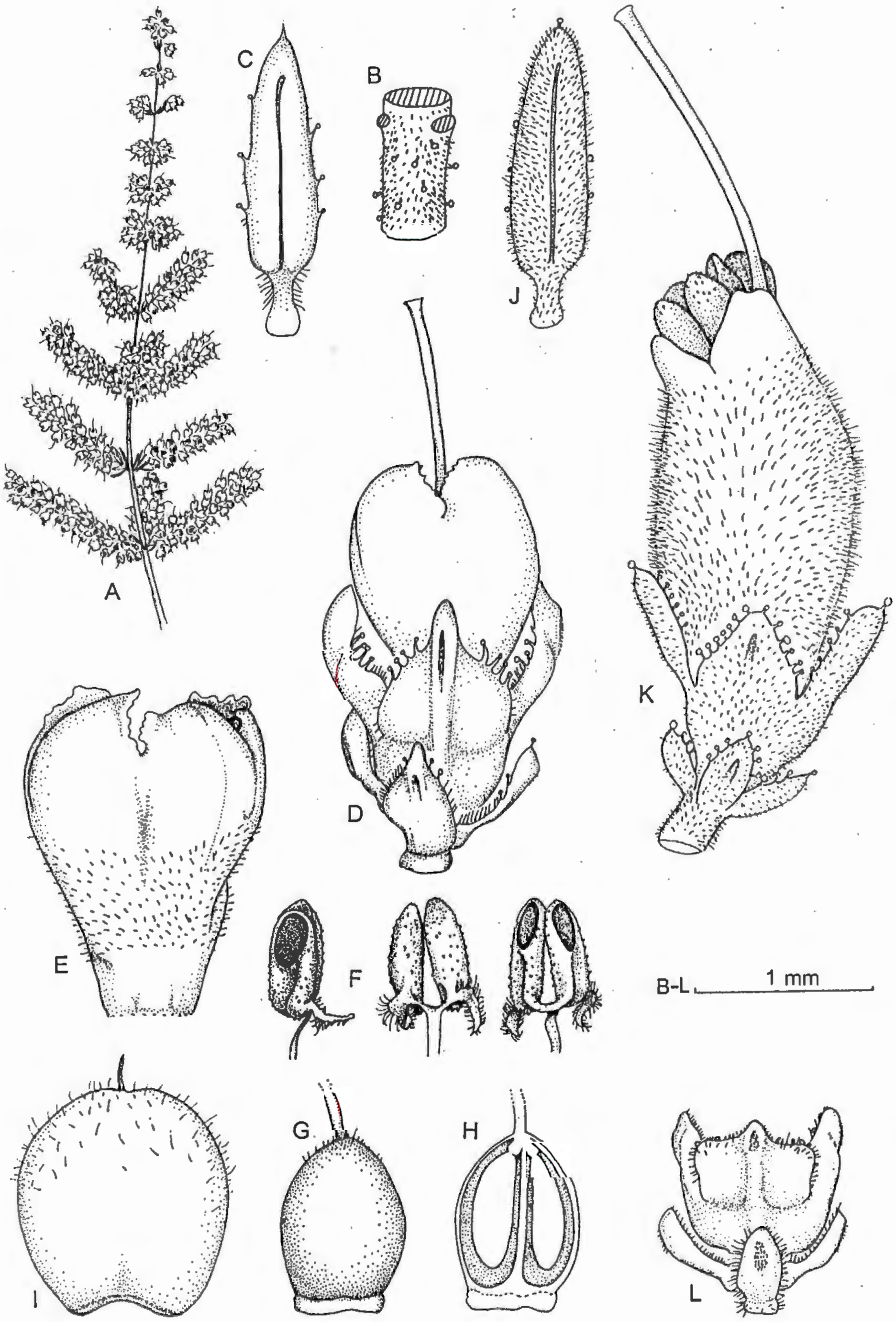

PLATE 51.—*Erica eremioides*. Subsp *eremioides*: A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, corolla; F, anther, side, back & front views; G, ovary; H, ovary L/S; I, fruit: subsp. *pubescens*: J, leaf; K, flower: subsp. *eglandula*: L, bract, bracteoles & calyx; A–H drawn from *Zeyher 1117*, I from *Oliver 6114*, J & K from *Oliver 4310*, L from *Esterhuysen 5924*.

L3 rBr1 br2 K4 C4 A4 $G^2/_1$

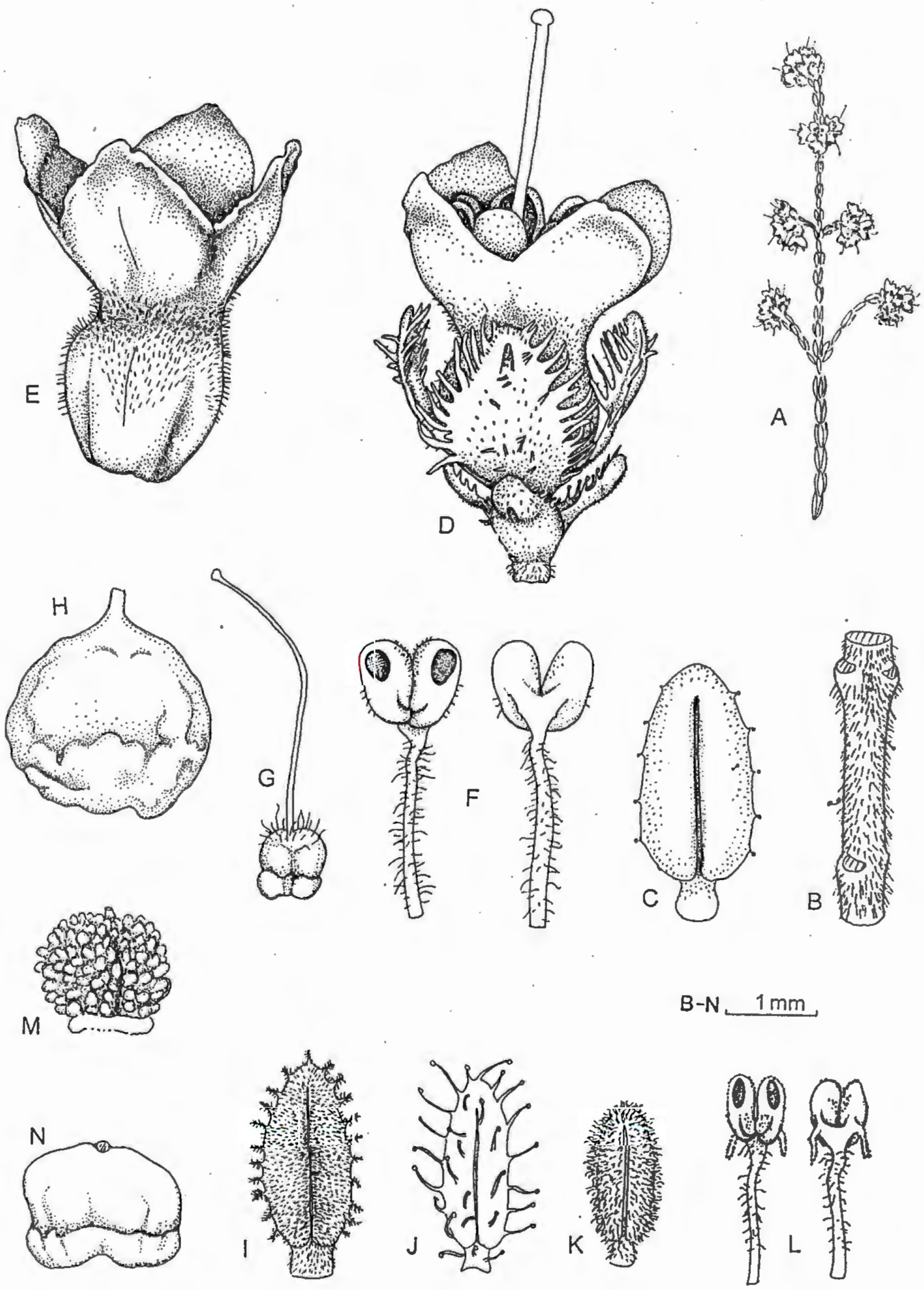

PLATE 52a.—*Erica plumosa*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, corolla; F, anther, front & back views; G, gynoecium; H, fruit; I, J & K, leaves with indumentum variation; L. anther, front & back views; M & N, fruits; A–H, drawn from *Oliver 3299*, I from *Oliver 3750*, J from *Oliver 3792*, K from *Oliver 3860*, L from *Oliver 3860*. **L**:3 **rBr1** **br2** **K4** **C4** **A4** **G**$^{2}/_{1}$

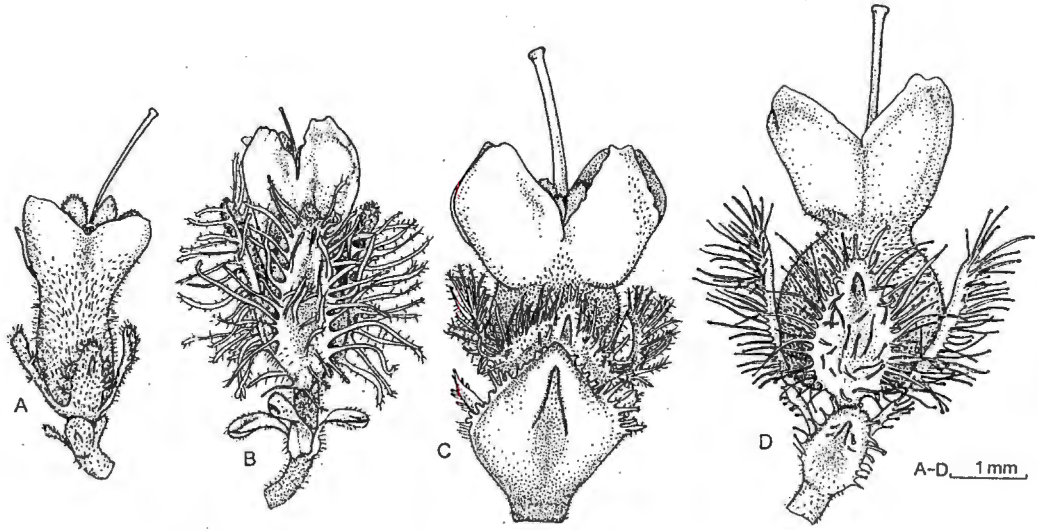

PLATE 52b.—*Erica plumosa*. Flowers showing variations. A, *Oliver 3750*; B, *Oliver 3860*; C, *Barker 10388*; D, *Oliver 3792*.

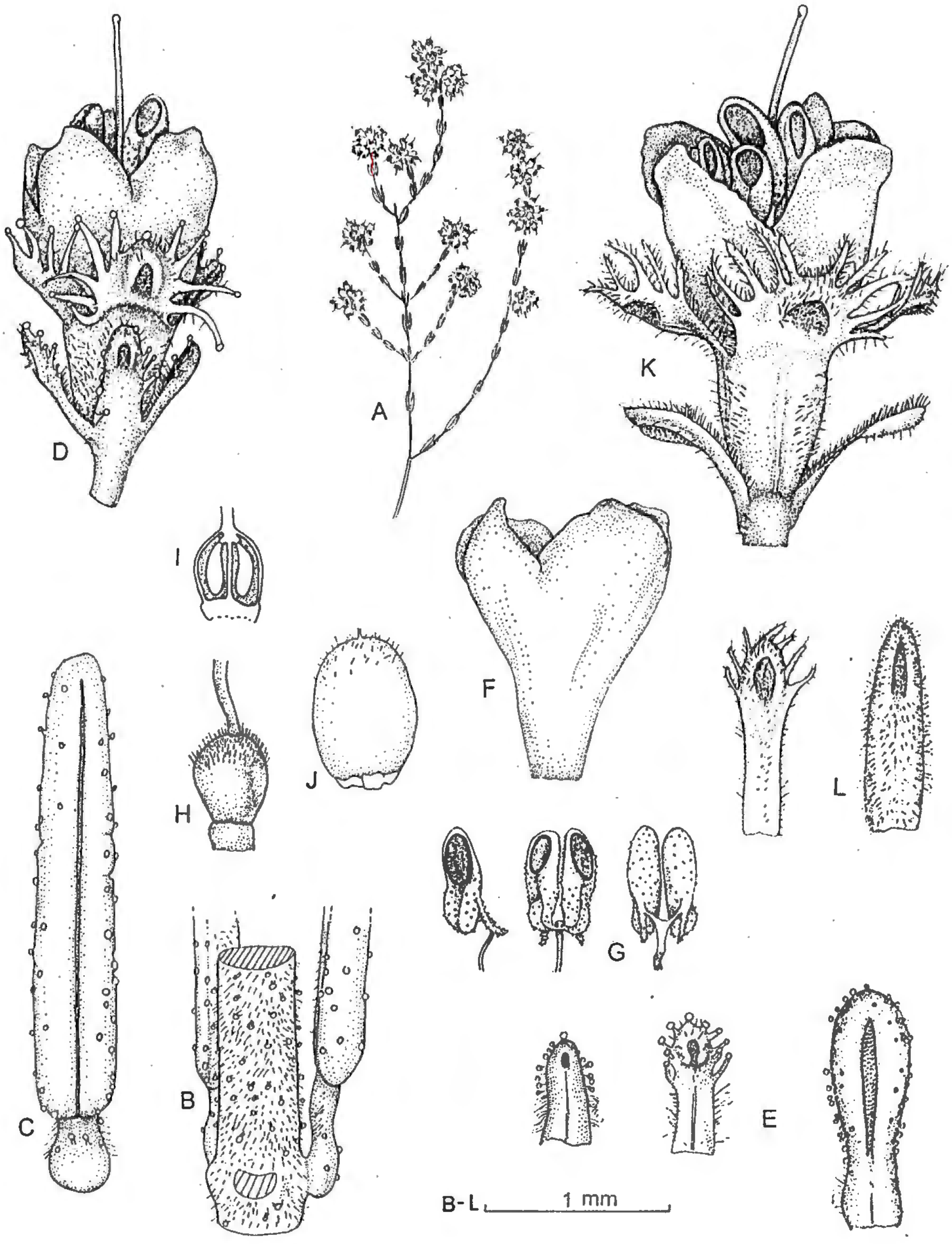

PLATE 53.—*Erica caprina*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract variation; F, corolla; G, anther, side, front & back views; H, ovary; I, ovary L/S; J, fruit; K, flower; L, bract variation; A–I drawn from the type, *Schlechter 10064*, J from *Cillié 47*, K & L from *Schlechter 10188*.

L3 rBr1 br2 K4 C4 A4 $G^{2}/_{1}$

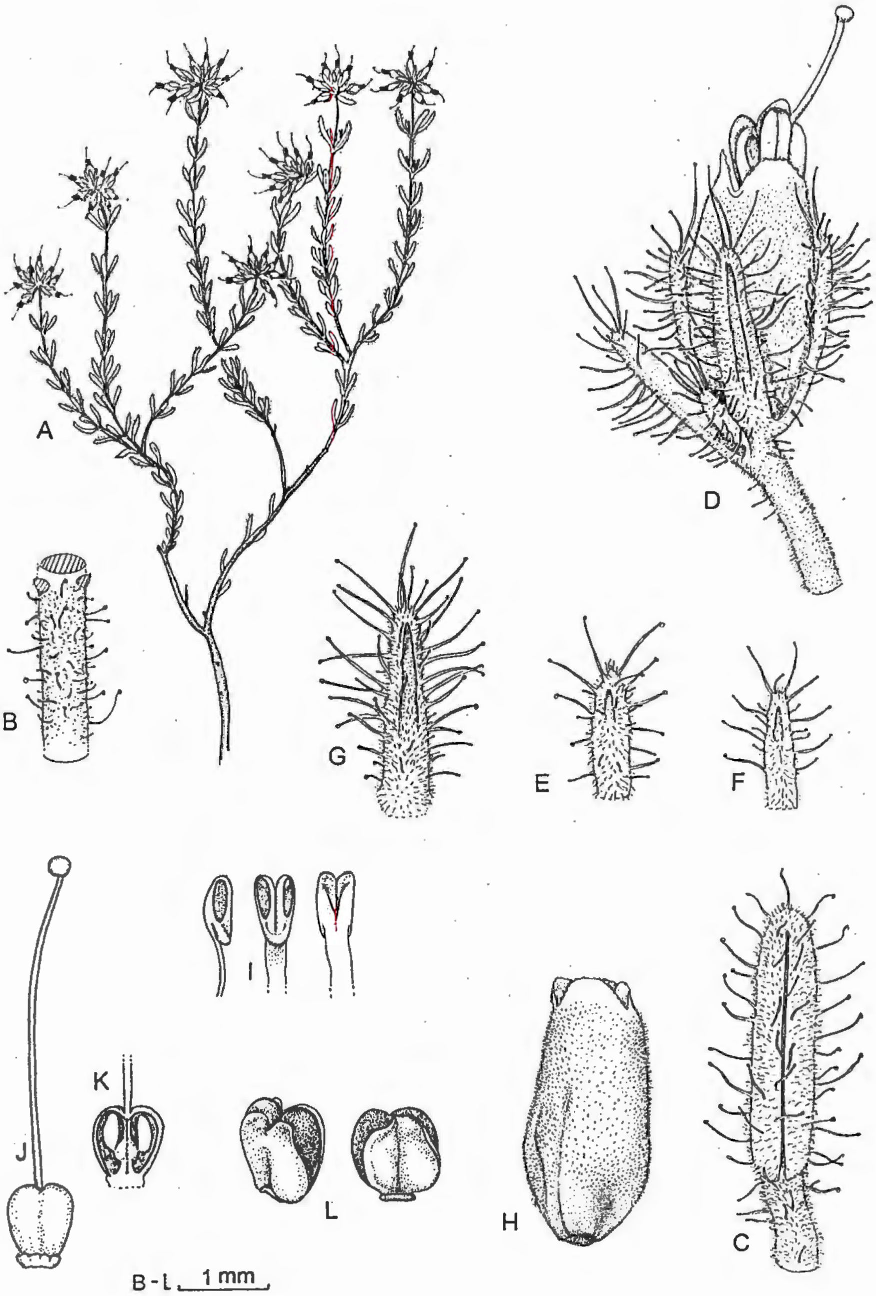

PLATE 54.—*Erica arachnocalyx*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, sepal; H, corolla; I, anther, side, front & back views;J, gynoecium; K, ovary L/S; L, fruits (passively dehiscent); all drawn from *Oliver 9266*. **L**3 **rBr**1 **rbr**2 **K**4 **C**4 **A**4–8 **G**$^2/_1$

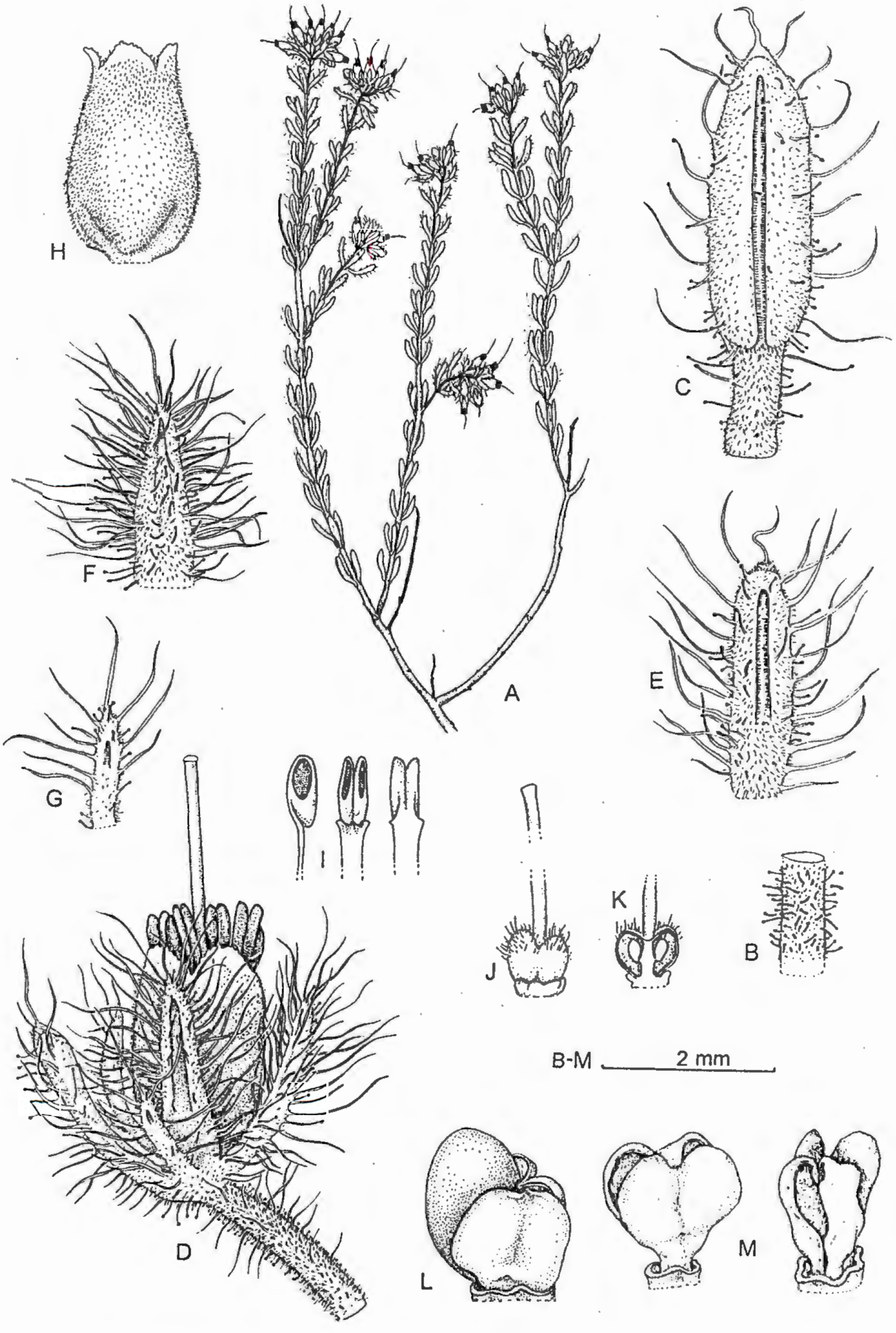

PLATE 55.—*Erica cereris*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, sepal; G, bracteole; H, corolla; I, anther, side, front & back views; J, gynoecium; K, ovary L/S; L, fruit with partially exserted basally attached seed; M, fruits; all drawn from *Oliver 5085*.

L3 rBr1 rbr2 K4 C4 A6–8 $G^{2}/_{1}$

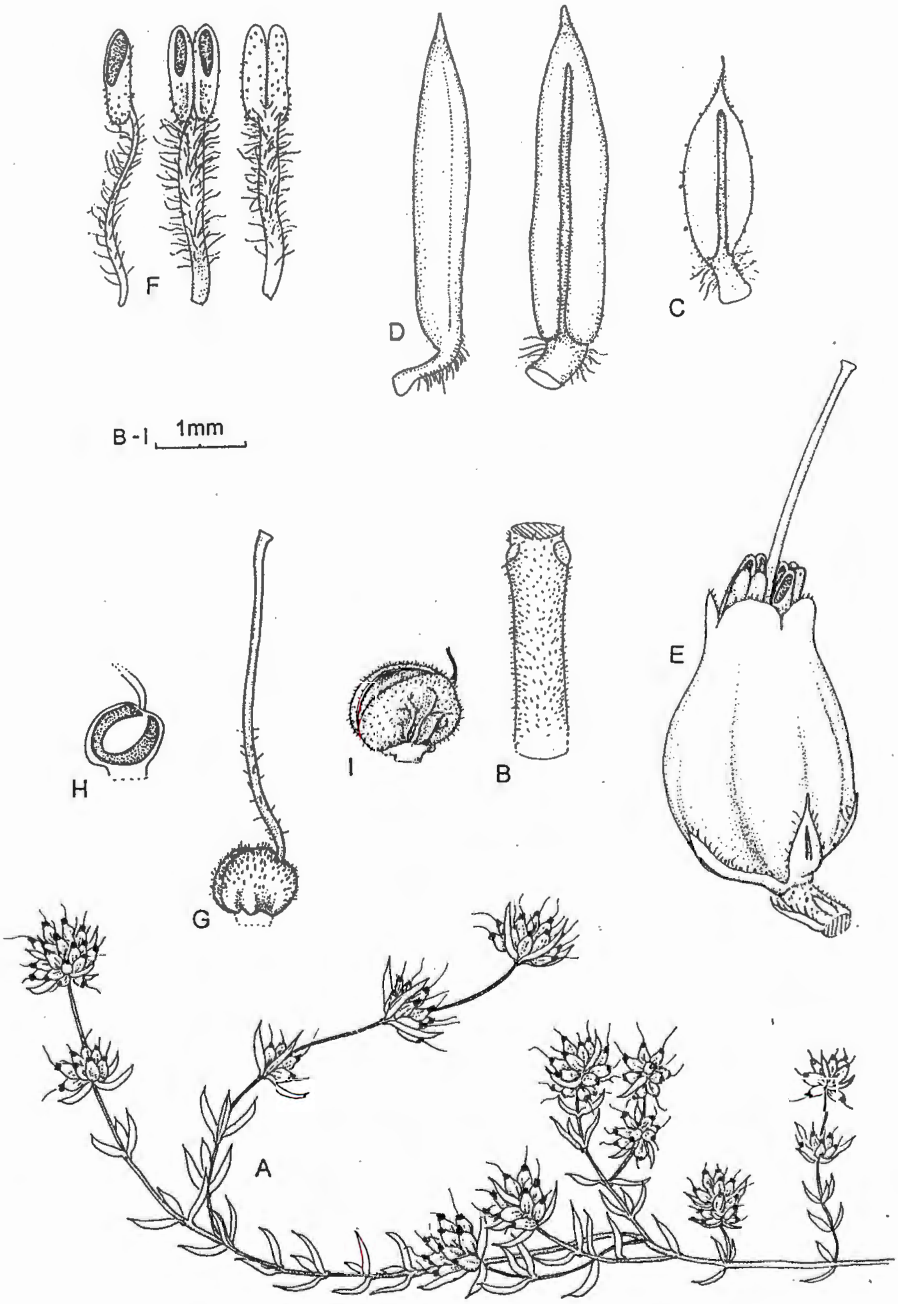

PLATE 56.—*Erica jonasiana*. A, flowering branch, nat. size; B, stem; C, young leaf; D, mature leaf, side and abaxial views; E, flower; F, stamen, side, front & back views; G, gynoecium; H, ovary L/S; I, partially dehiscent fruit; all drawn from *Esterhuysen 32703*. **L3 rBr1 rbr2 K4 C4 A4** $\mathbf{G}^{1}/_{1}$

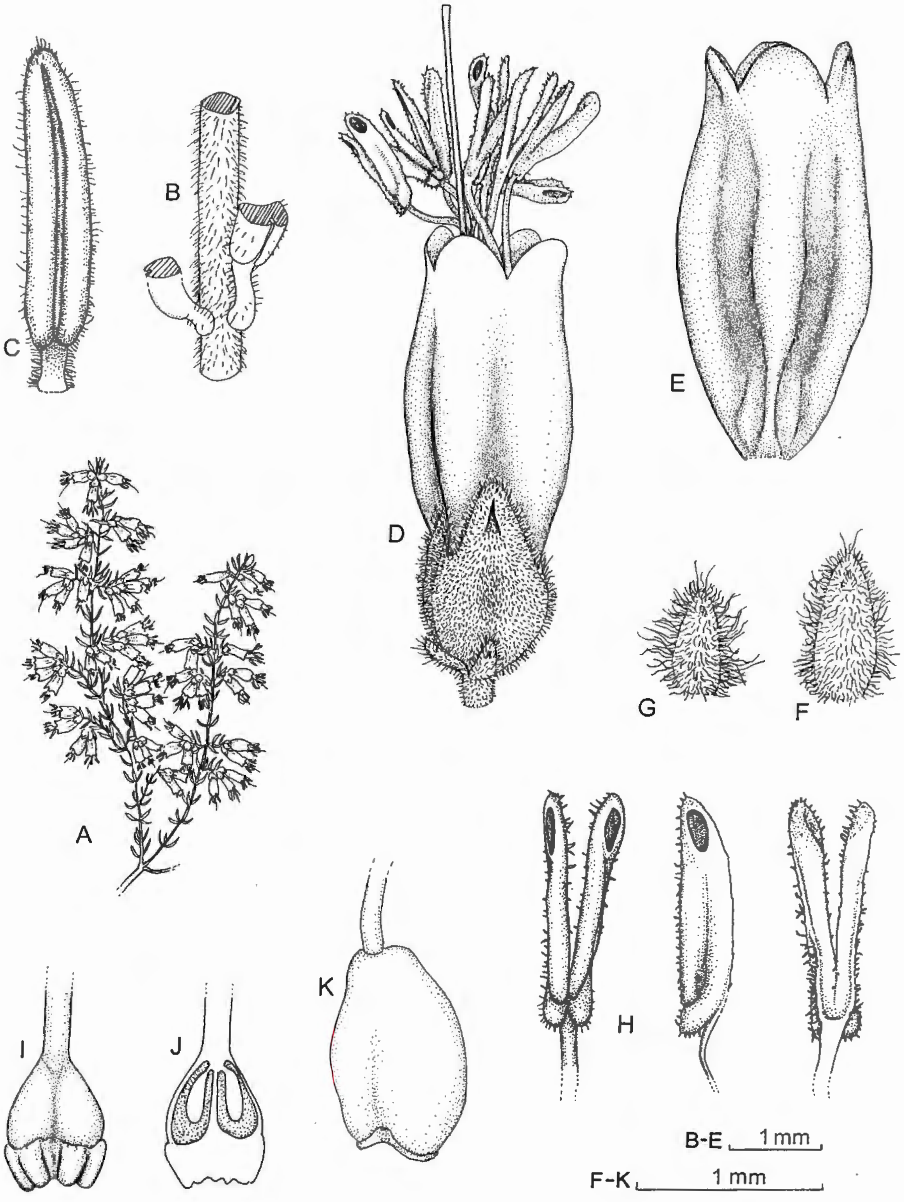

PLATE 57.—*Erica karwyderi*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, corolla; F, bract; G, bracteole; H, anther, front, side & back views; I, ovary; J, ovary L/S; K, fruit; all drawn from *Oliver 9227*.

L3 rBr1 rbr2 K4 C4 A8 $G^{2}/_{1}$

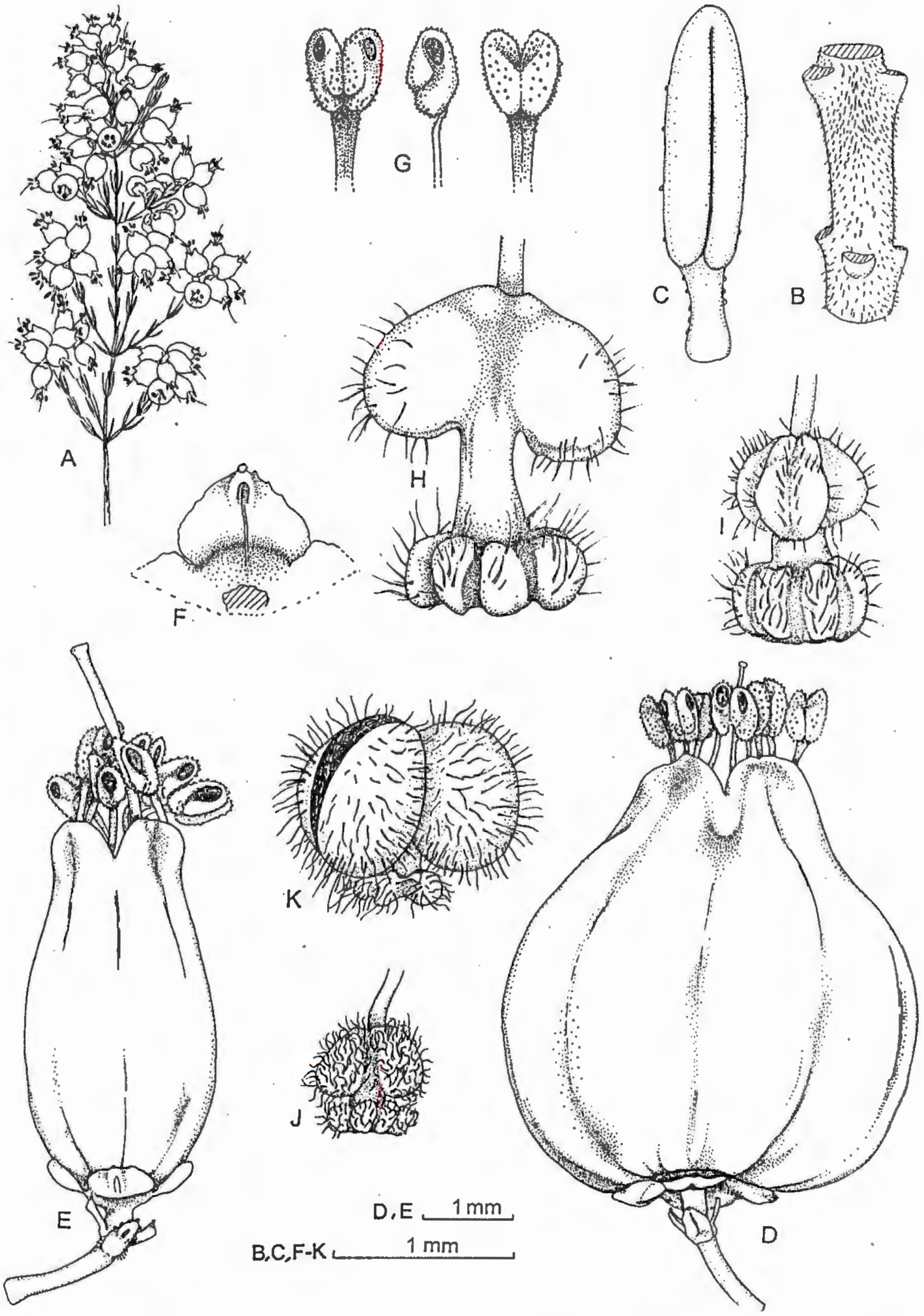

PLATE 58.—*Erica platycalyx*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, flower; F, calyx; G, anther, front, side & back views; H, gynoecium, 2-locular; I, gynoecium, 3-locular; J, ovary; K, fruit, partially dehiscent; A–D, G & J drawn from *Oliver 6005*, E, F & I from *Oliver 4638a*.

L3 rBr1 rbr2 K4 C4 A8–6(5)[4] **$G^{2}/_{1}$** $^{3}/_{1}$

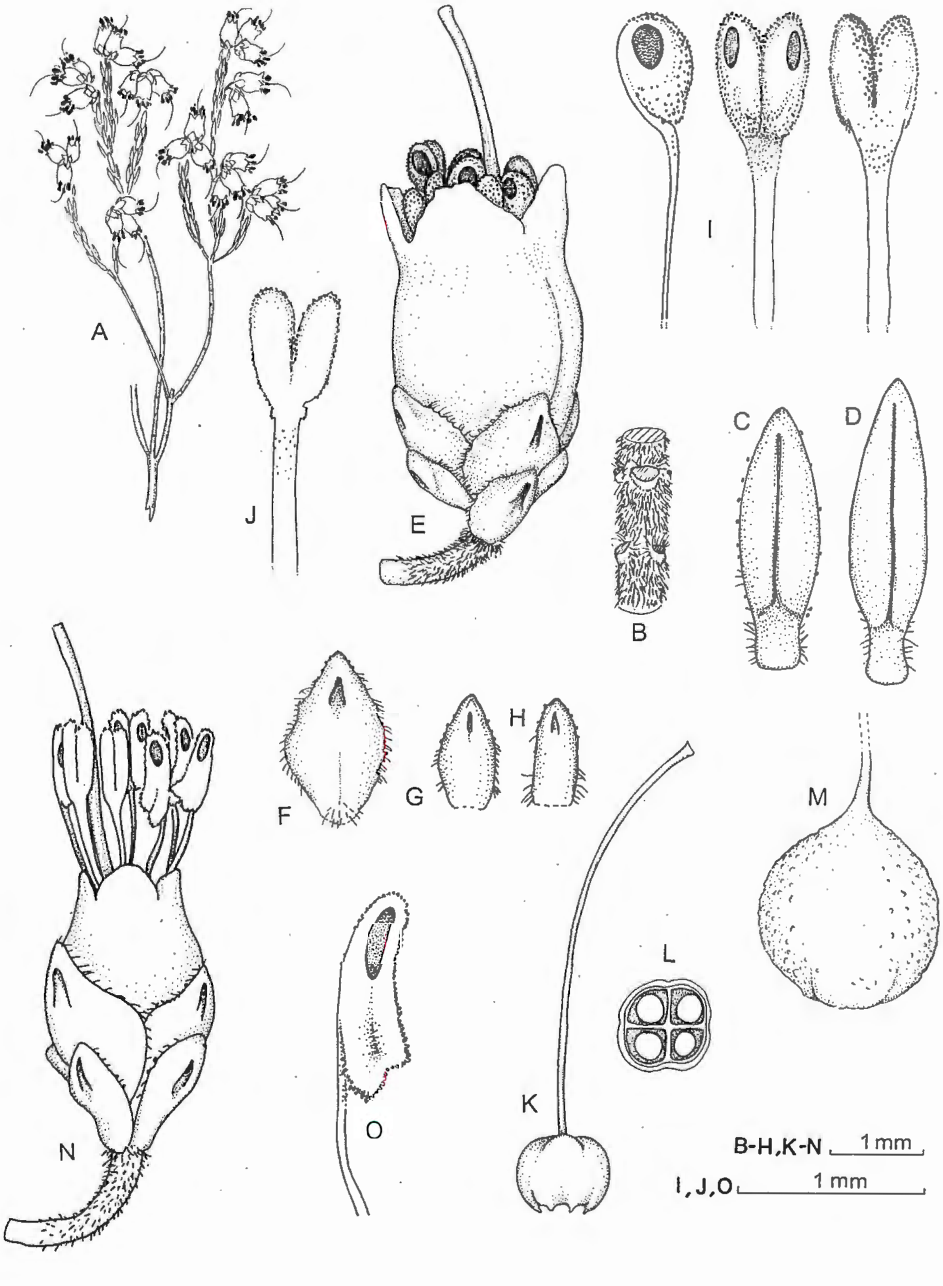

PLATE 59.—*Erica vlokii*. A, flowering branch, nat. size; B, stem; C & D, leaf; E, flower; F, sepal; G, bract; H, bracteole; I, anther, side, front & back views; J, anther, back view showing small decurrent spurs; K, gynoecium; L, ovary T/S; M, fruit; N, flower; A–L, drawn from *Oliver 9243*, N & O from *Vlok 2289*.

L3 rBr1 br2 K4 C4 A8 G$^{4}/_{1}$

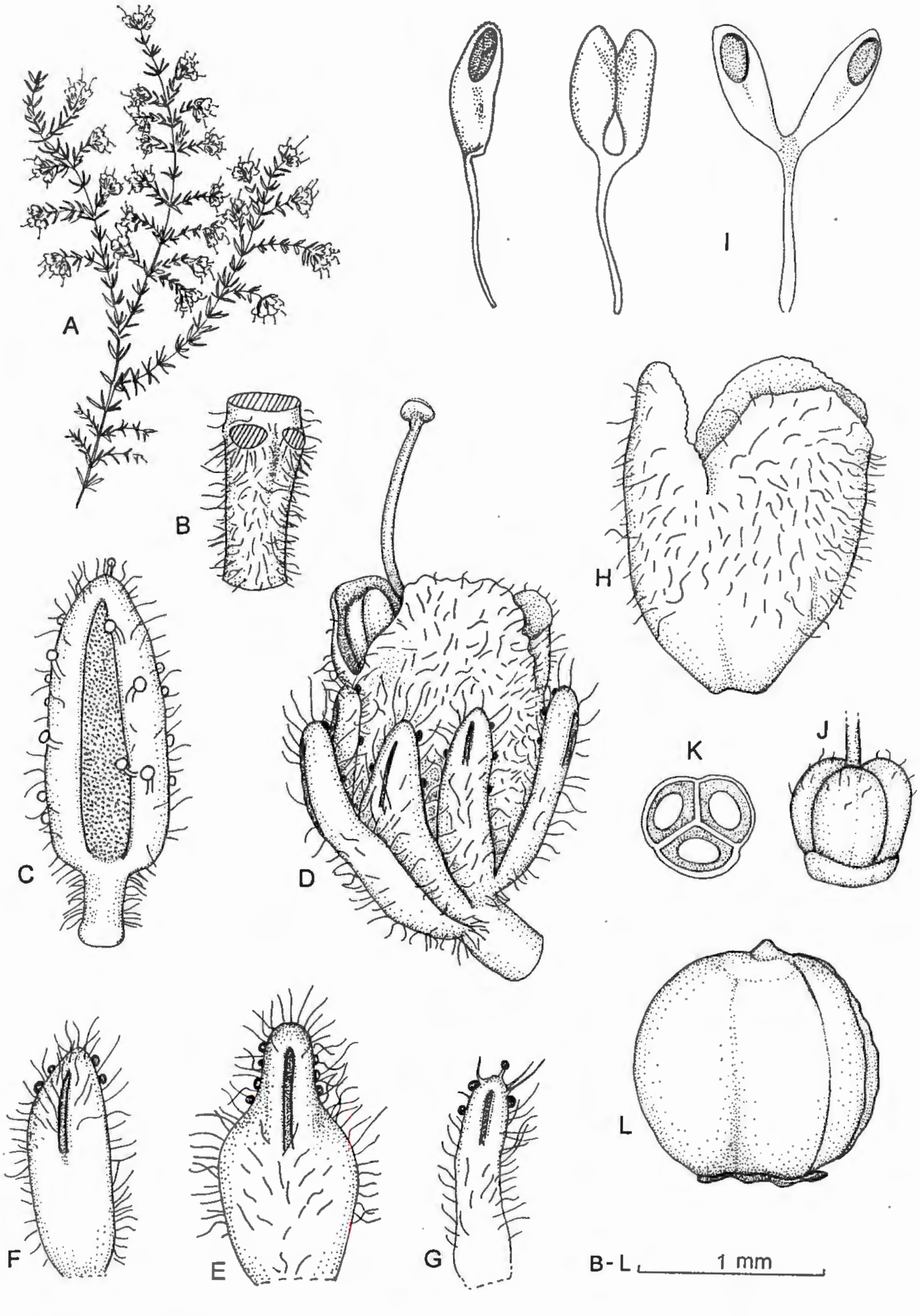

PLATE 60.—*Erica outeniquae*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, sepal; H, corolla; I, anther, side, back & front views; J, ovary; K, ovary T/S; L, fruit; all drawn from *Oliver 4115*.

L4 rBr1 rbr2 K4 C3 A6 G^3/$_1$

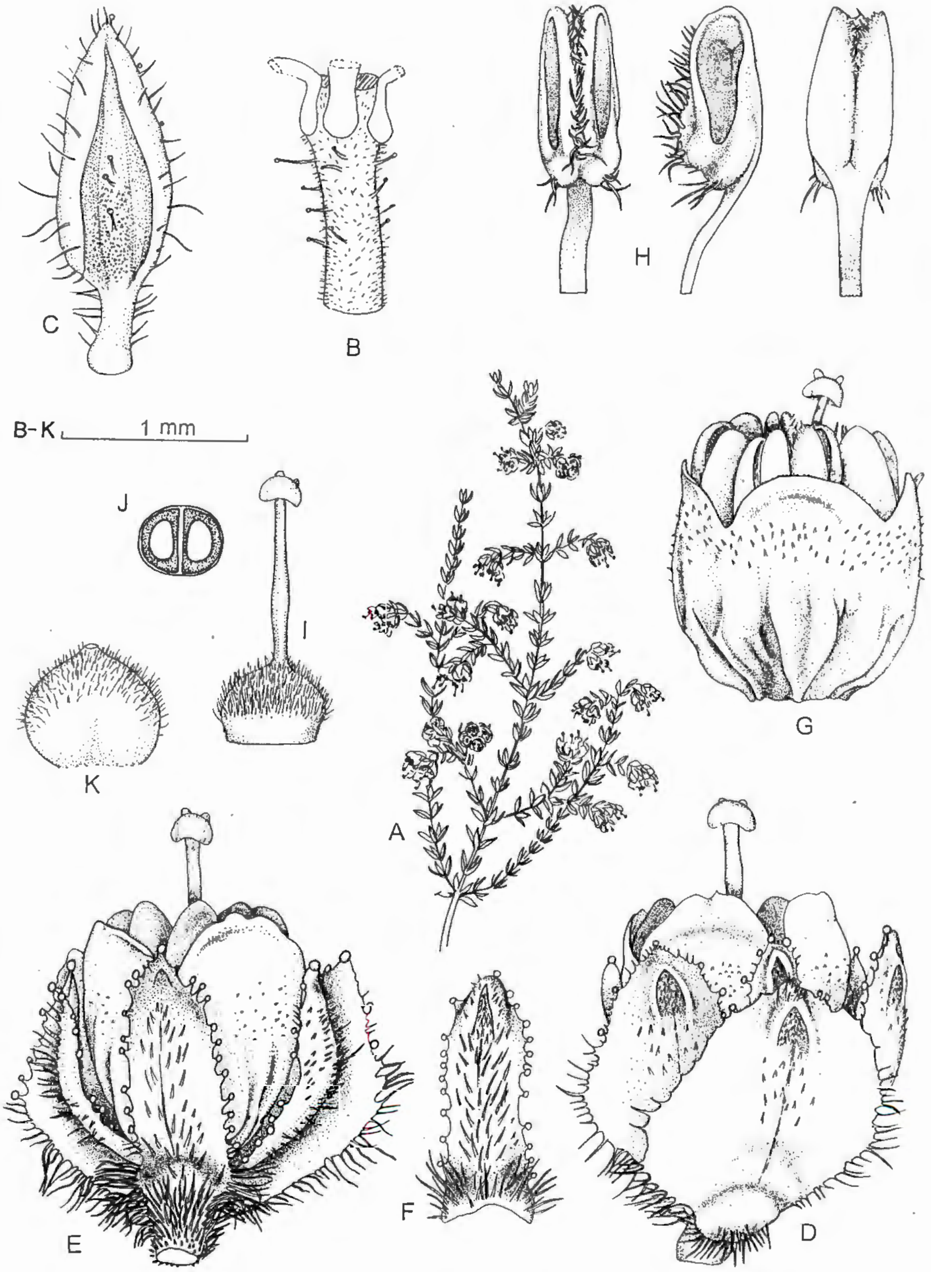

PLATE 61.—*Erica velatiflora*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower, aabaxial view; E, flower, abaxial view; F, sepal; G, corolla; H, anther, front, side & back views; I, gynoecium; J, ovary T/S; K, fruit; all drawn from Oliver 4128. **L4 rBr1 rbr2 K4 C4 A8 G**$^{2}/_{1}$

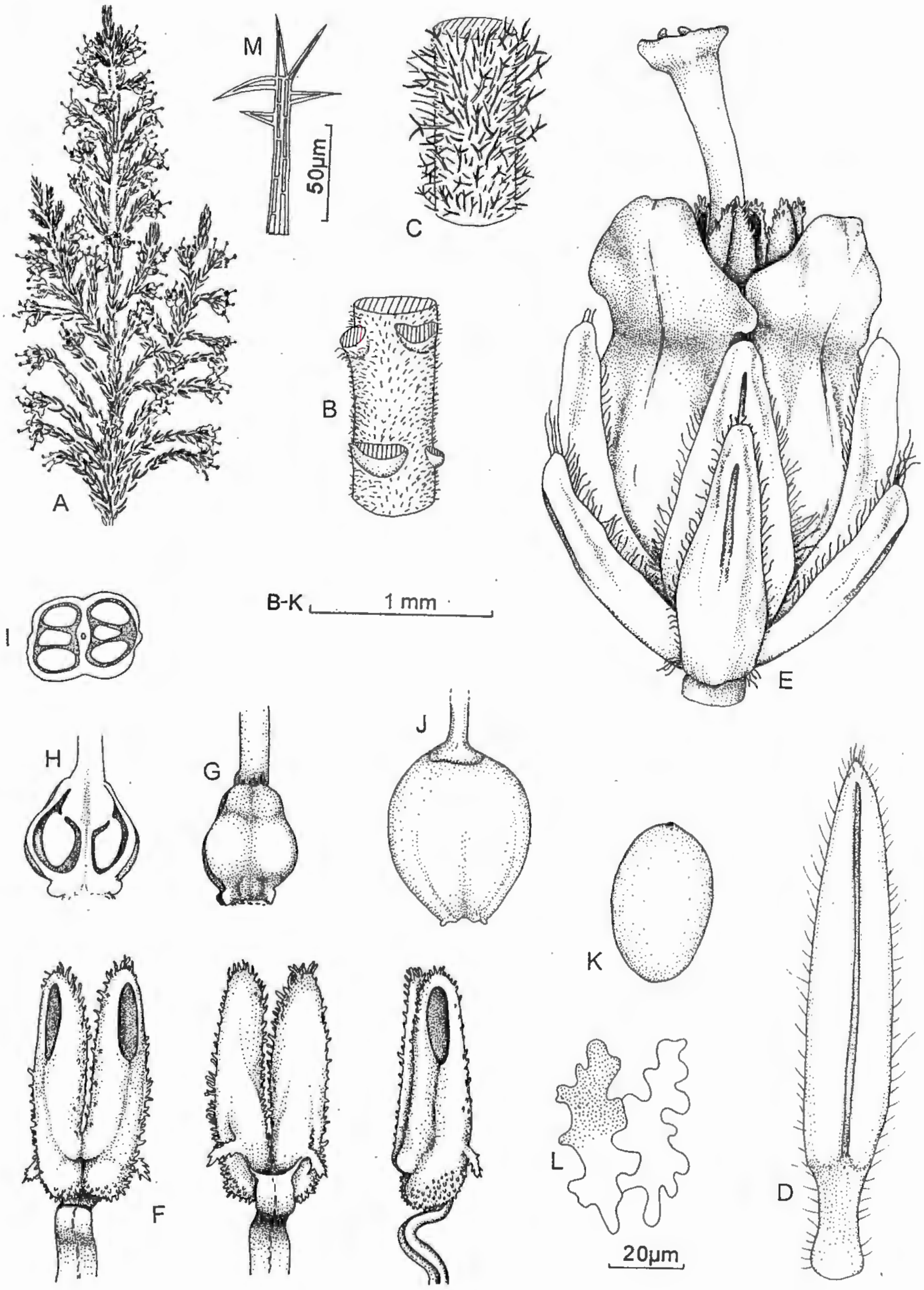

PLATE 62.—*Erica stokoeanthus*. A, flowering branch, nat. size; B, stem; C, older stem with plumose hairs; D, leaf; E, flower; F, anther, front, back & side views; G, ovary; H, ovary L/S; I, ovary T/S; J, fruit; K, seed; L, testa cells; M, plumose hair; all drawn from type, *Oliver 4790*.

L3 rBr1 rbr2 K4 C4 A4 G$^{2}/_{3}$ ($^{2}/_{2,4-6}$)

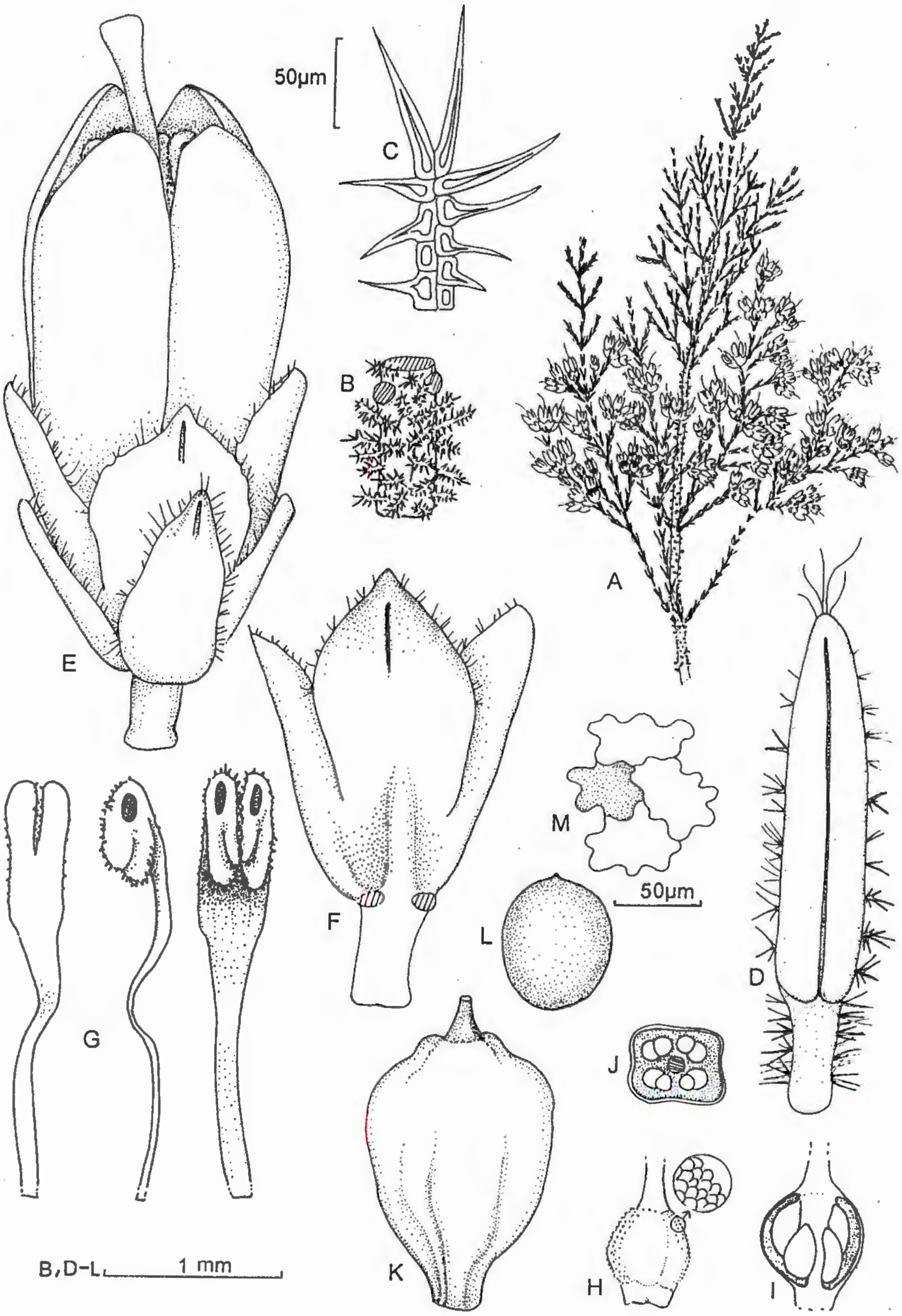

PLATE 63.—*Erica jacksoniana*. A, flowering branch, nat. size; B, stem; C, plumose hair; D, leaf; E, flower; F, calyx; G, anther, back, side & front views; H, ovary; I, ovary L/S; J, ovary T/S; K, fruit; L, seed; M, testa cells; A–J drawn from *Williams 1990*, K–M from *Oliver 10706*. **L**3 **rBr**1 **rbr**2 **K**4 **C**4 **A**8 **G**$^{1}/_{6\text{–}9}$

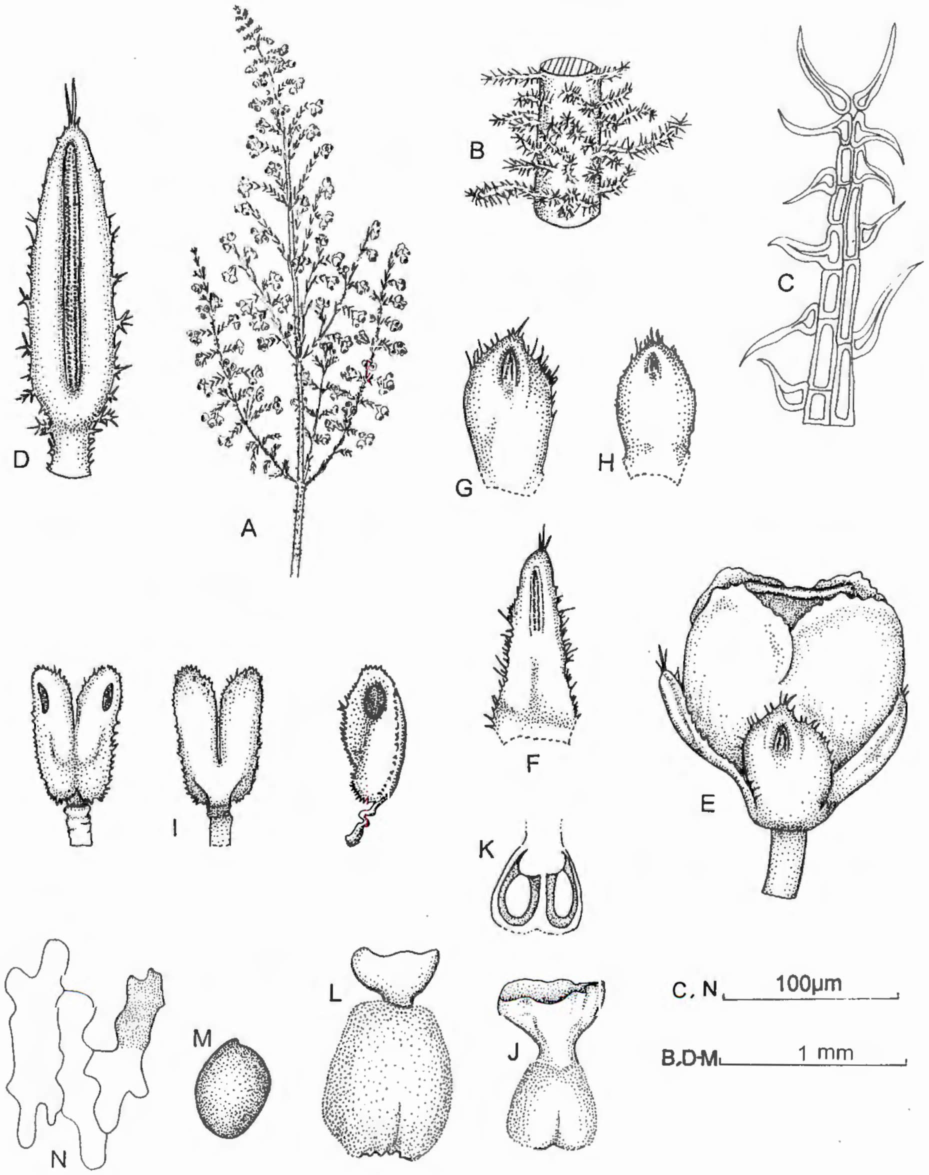

PLATE 64.—*Erica perplexa*. A, flowering branch, nat. size; B, stem; C, plumose hair; D, leaf; E, flower; F, bract; G, bracteole; H, sepal; I, anther, front, back & side views; J, gynoecium; K, ovary L/S; L, fruit; M, seed; N, testa cells; A–K drawn from the type, *Oliver 8464*, L–N from *Oliver 8762*.

L3 **RB**3 **K**1 **C**4 **A**8(7) $\mathbf{G}^{3}/_{1}\,({}^{2}/_{1})\,[{}^{4}/_{1}]$

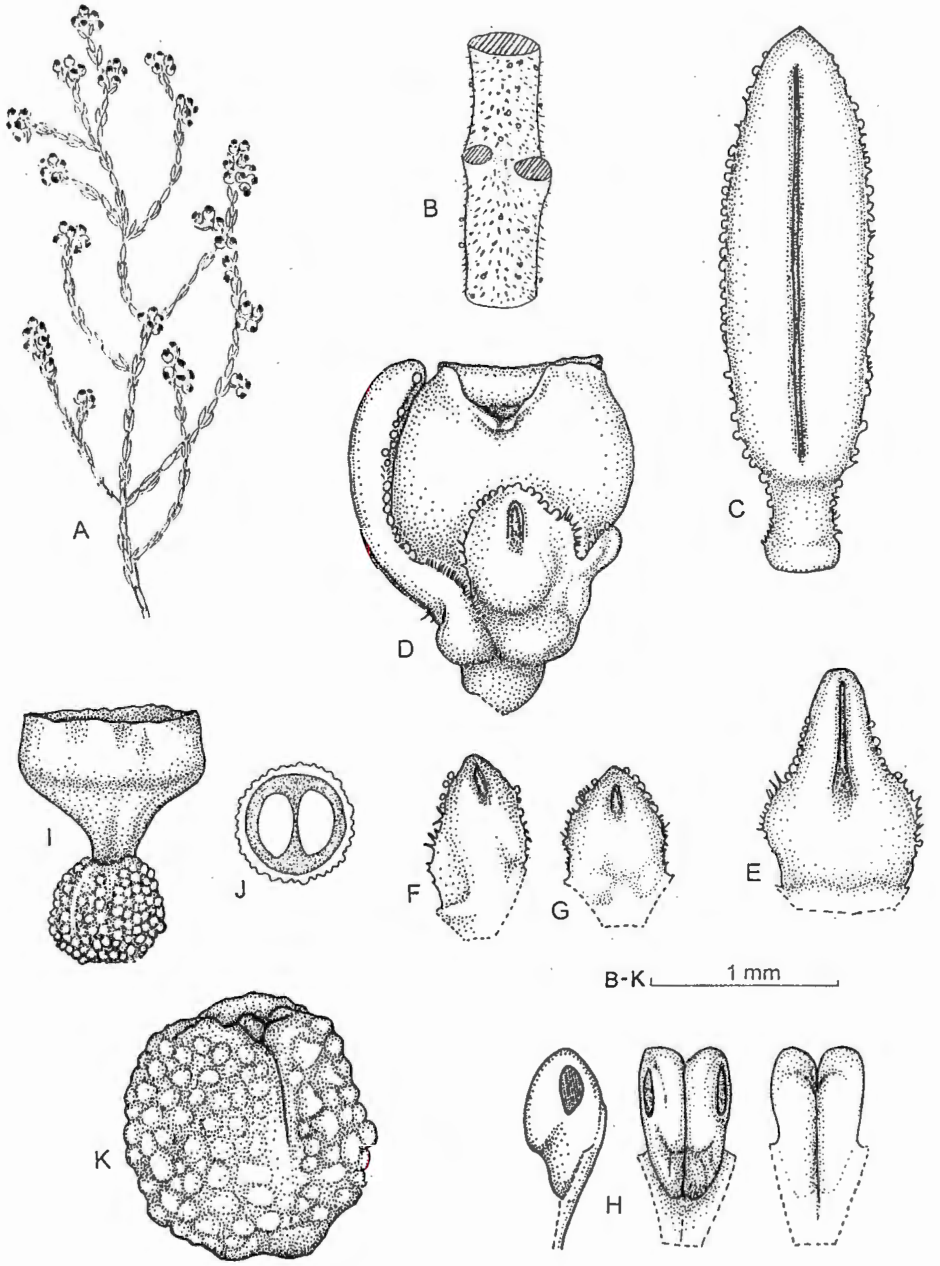

PLATE 65.—*Erica subcapitata*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, sepal; H, anther, side, front & back views; I, gynoecium; J, ovary T/S; K, fruit; A–J drawn from *Taylor 4979*, K from *Salter 2849*. **L**3 **RB**3 **K**1 **C**4 **A**8(7,6) **G**$^{1}/_{2}$ $^{2}/_{2}$

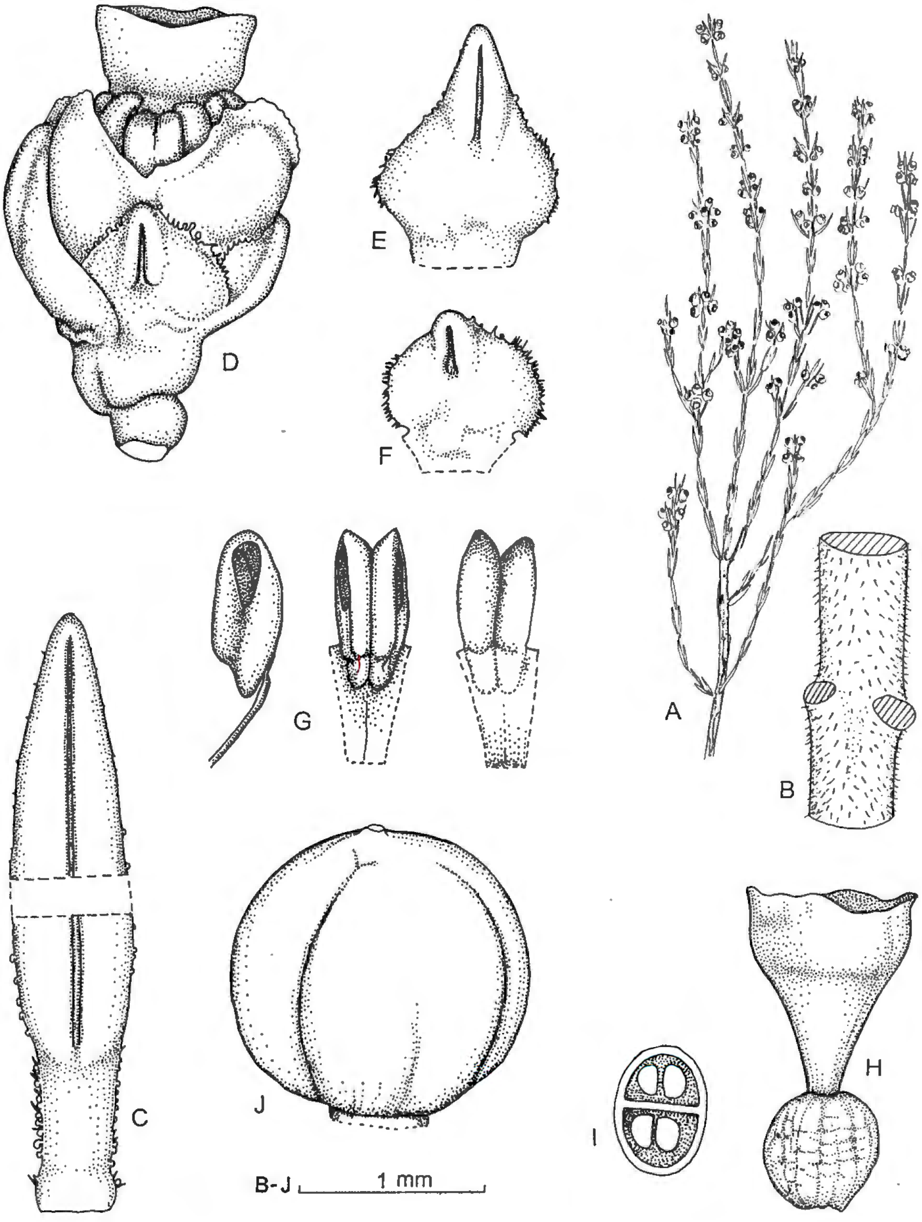

PLATE 66.—*Erica rugata*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, anther, side, front & back views; H, gynoecium; I, ovary T/S; J, fruit; all drawn from *Oliver 8420*.

L3 RB3 K1 C4 A8 $\mathbf{G}^{2}/_{2}\,(^{2}/_{1})$

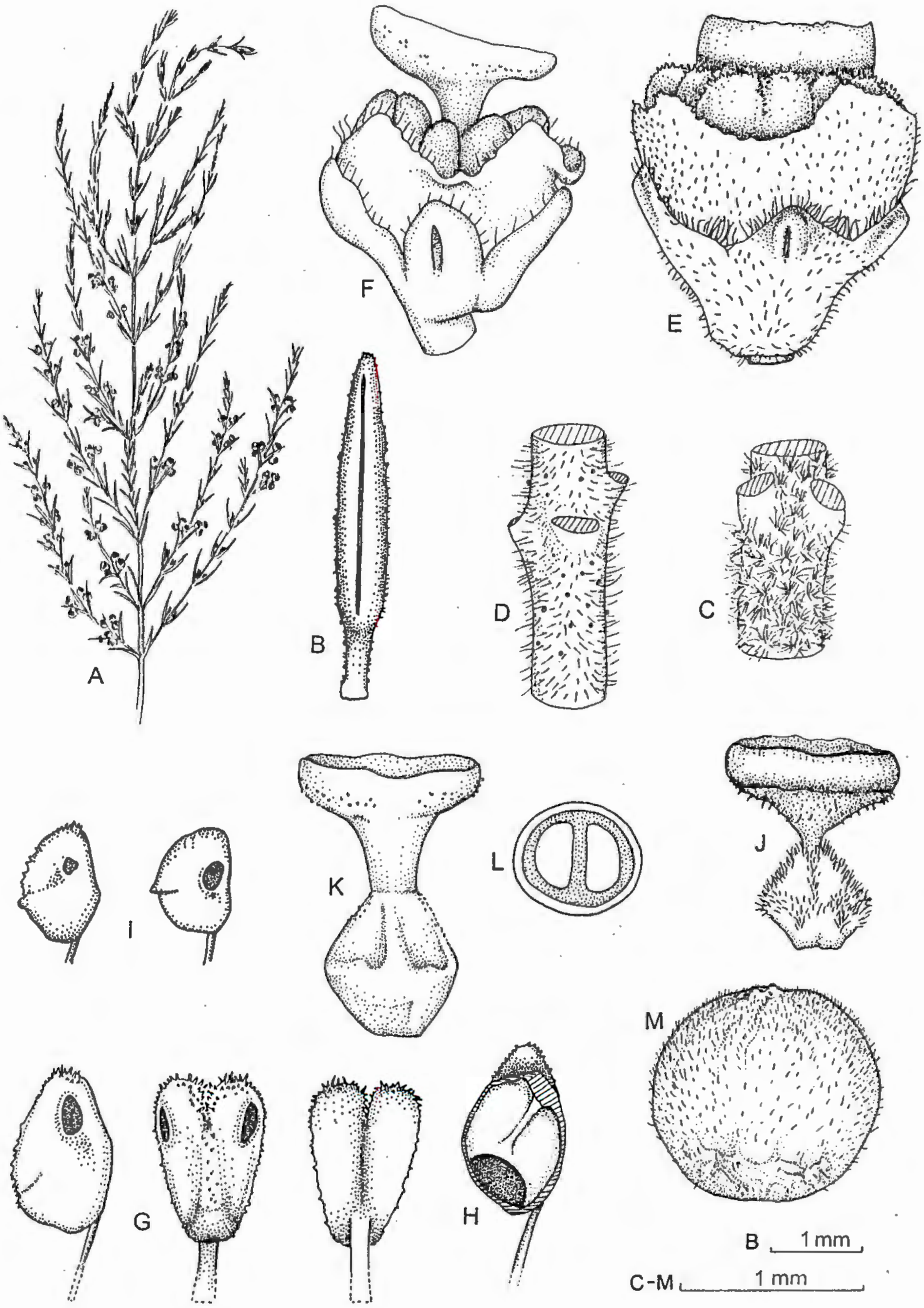

PLATE 67.—*Erica parviporandra*. A, flowering branch, nat. size; B, leaf; C & D, leaf; E, flower; F, flower; G, anther, side, front & back views; H, anther, cut open longitudinally to show internal hole between thecae; I, anther variation; J & K, gynoecium; L, T/S of gynoecium; M, fruit; A, B, D, E, G, H drawn from the type, *Oliver 8626*, C from *Oliver 8650*, F, I, K, L from *Marshall 62*.

L3 RB3 K1 C4 A6 G$^1/_2$

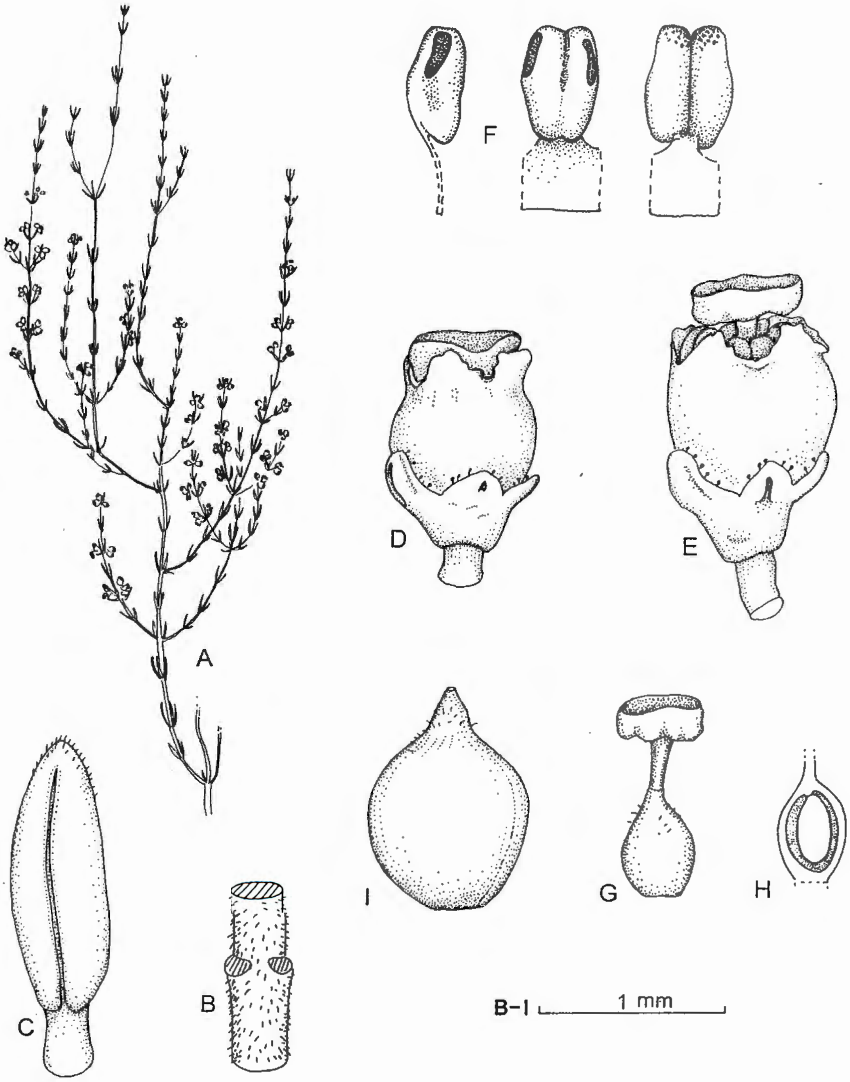

PLATE 68.—*Erica remota*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, flower in fruit; F, anther, side, front & back views; G, gynoecium; H, ovary L/S; I, fruit; all drawn from *Oliver 10386*. **L3 RB3 K1 C4 A**5,6(4) $\mathbf{G}^{1}/_{1}$

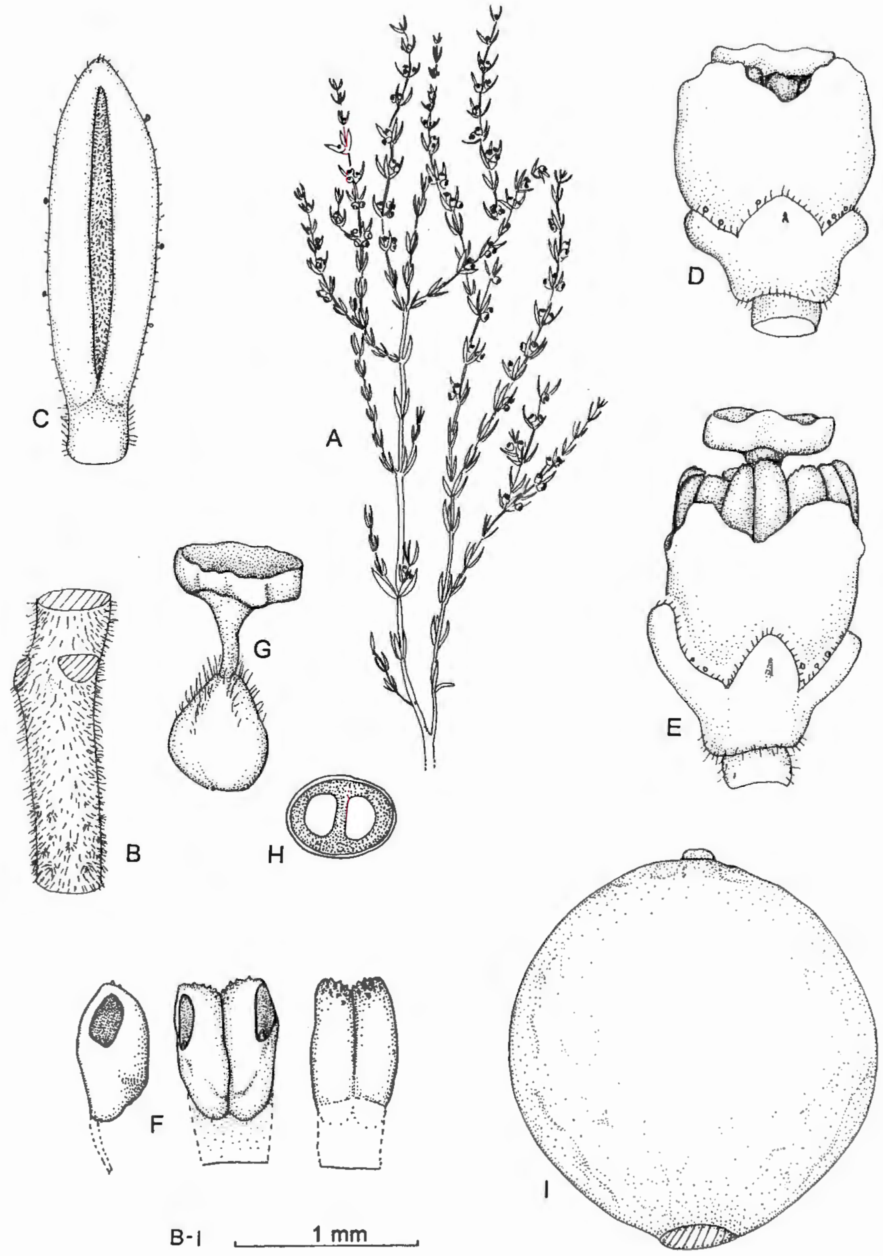

PLATE 69.—*Erica areolata*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, flower in young fruit; F, anther, side, front & back views; G, gynoecium; H, ovary T/S; I fruit; A–H drawn from *Oliver 9064*, I from *Oliver 6104*. **L3 RB3 K1 C4 A6** $\mathbf{G}^{1}/_{2}\,^{2}/_{2}\,^{2}/_{1}\,[^{1}/_{1}\,^{1}/_{3}]$

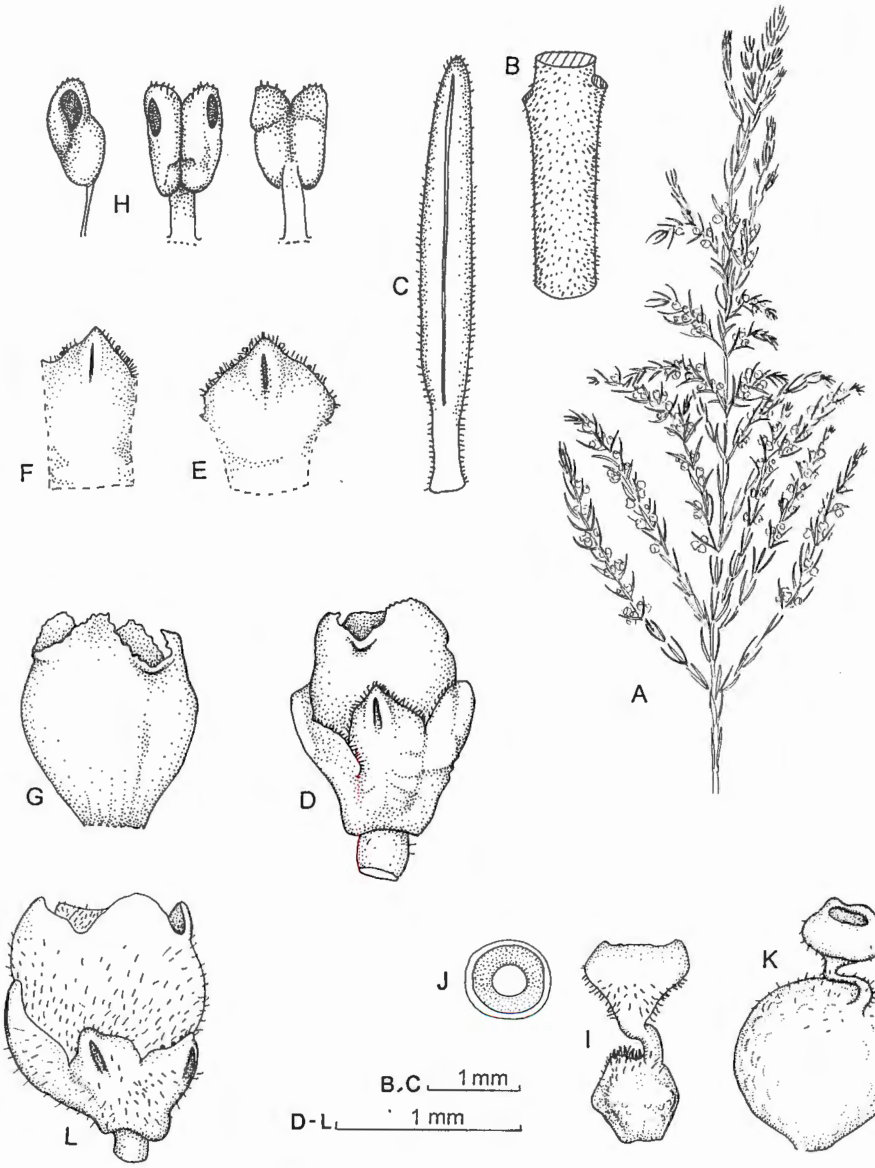

PLATE 70.—*Erica artemisioides*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, corolla; H, anther, side, front & back views; I, gynoecium; J, ovary T/S; K, fruit; L, flower; A–K drawn from *Taylor 10118*, L from *Roxburgh s.n.* **L3** **RB3** **K1** **C4** **A6**(4,5,7)[8] **G**$^1/_1$

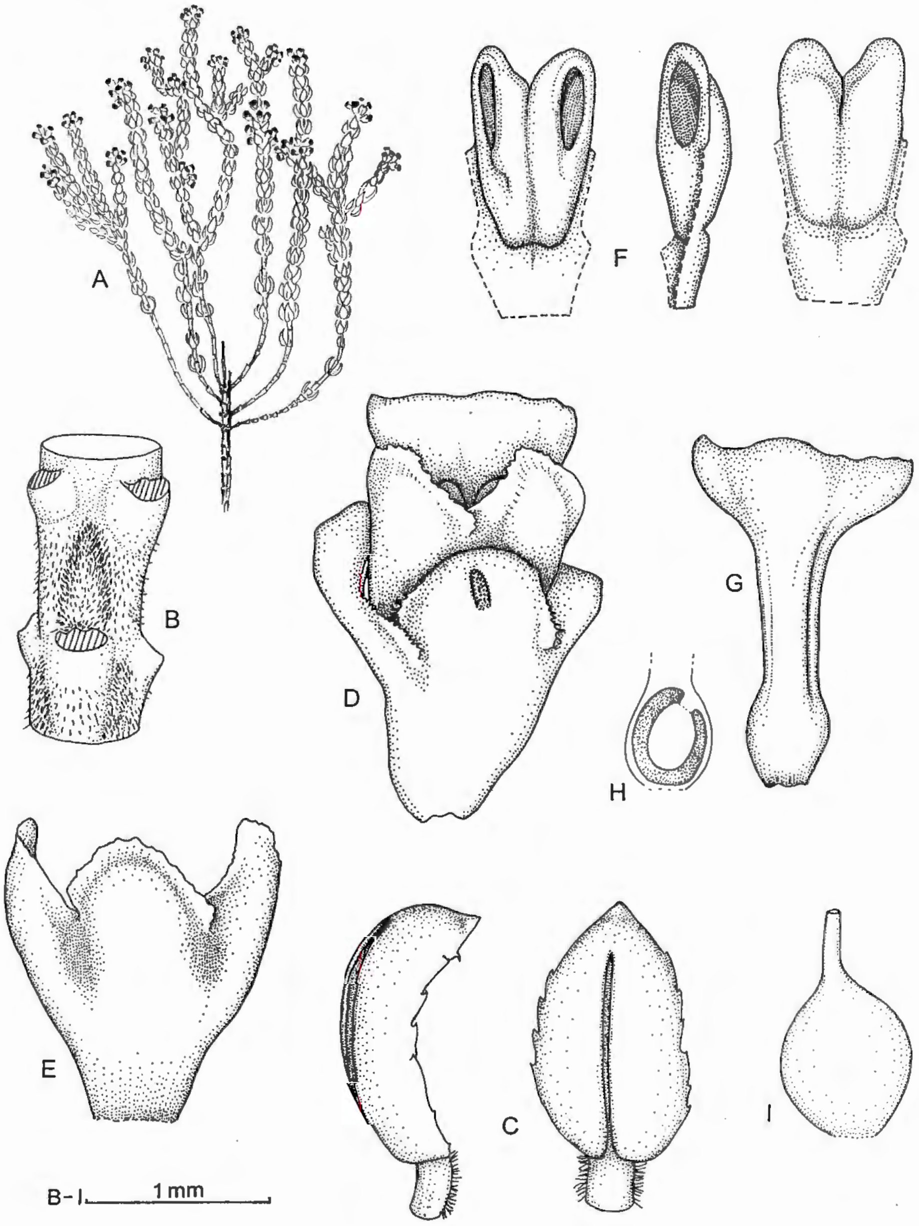

PLATE 71.—*Erica calcicola*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, corolla; F, anther, front, side & back views; G, gynoecium; H, ovary L/S; I, fruit; A–H drawn from the type, *Oliver 7604*, I from *Bohnen 5865*.

L3 RB3 K1 C4 A4 $\mathbf{G^{1}/_{1}}$

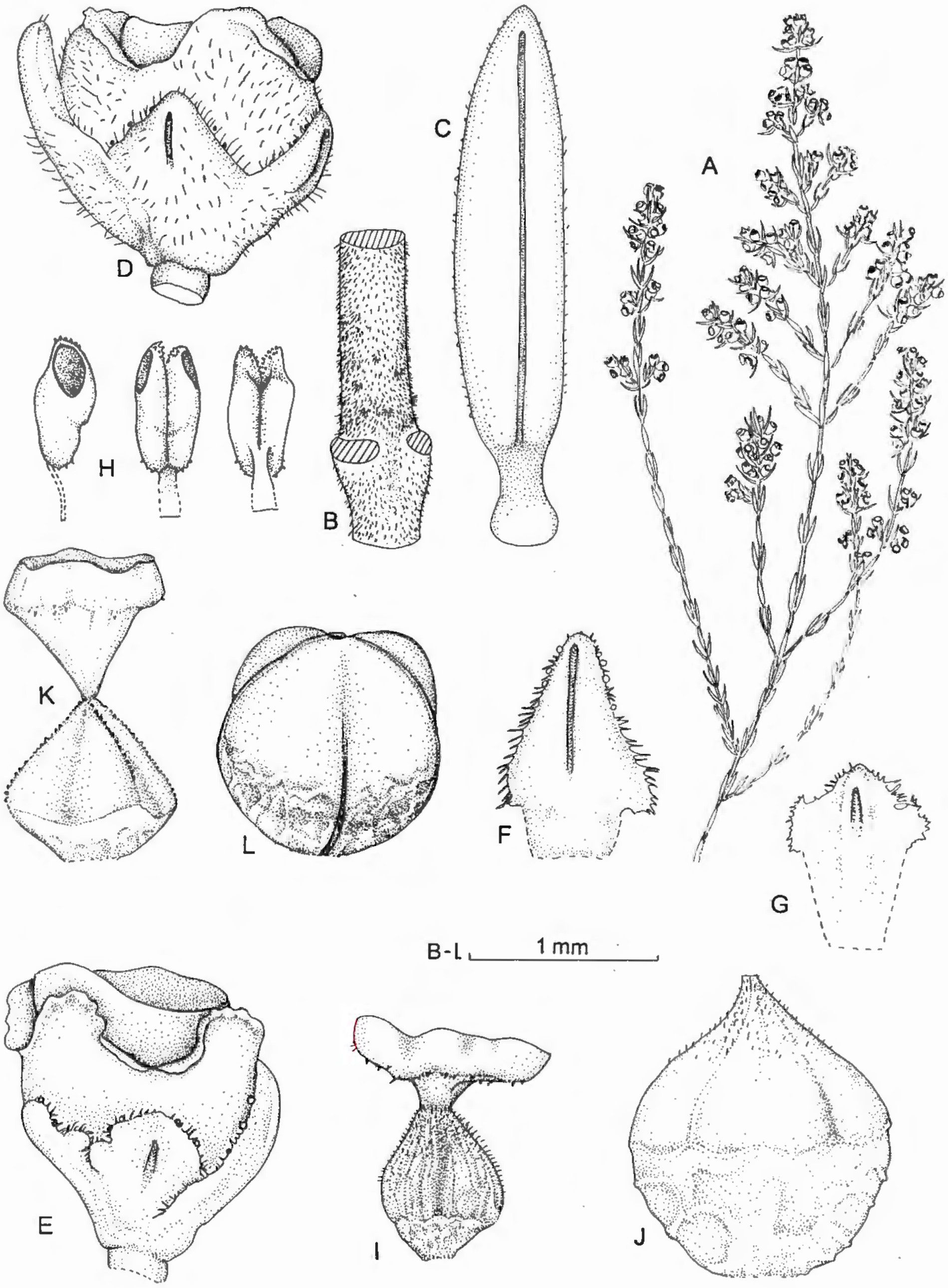

PLATE 72.—*Erica axillaris*. A, flowering branch, nat. size; B, stem; C, leaf; D & E, flower; F, bract; G, bracteole; H, anther, side, front & back views; I, gynoecium; J, fruit; K, gynoecium; L, fruit; A–D drawn from *Oliver 81*, E–J from *Oliver 4268*, K,L from *Haynes 127*. **L**3 **RB**3 **K**1 **C**4 **A**8(7) **G**$^2/_1$ ($^3/_1$) $^4/_1$

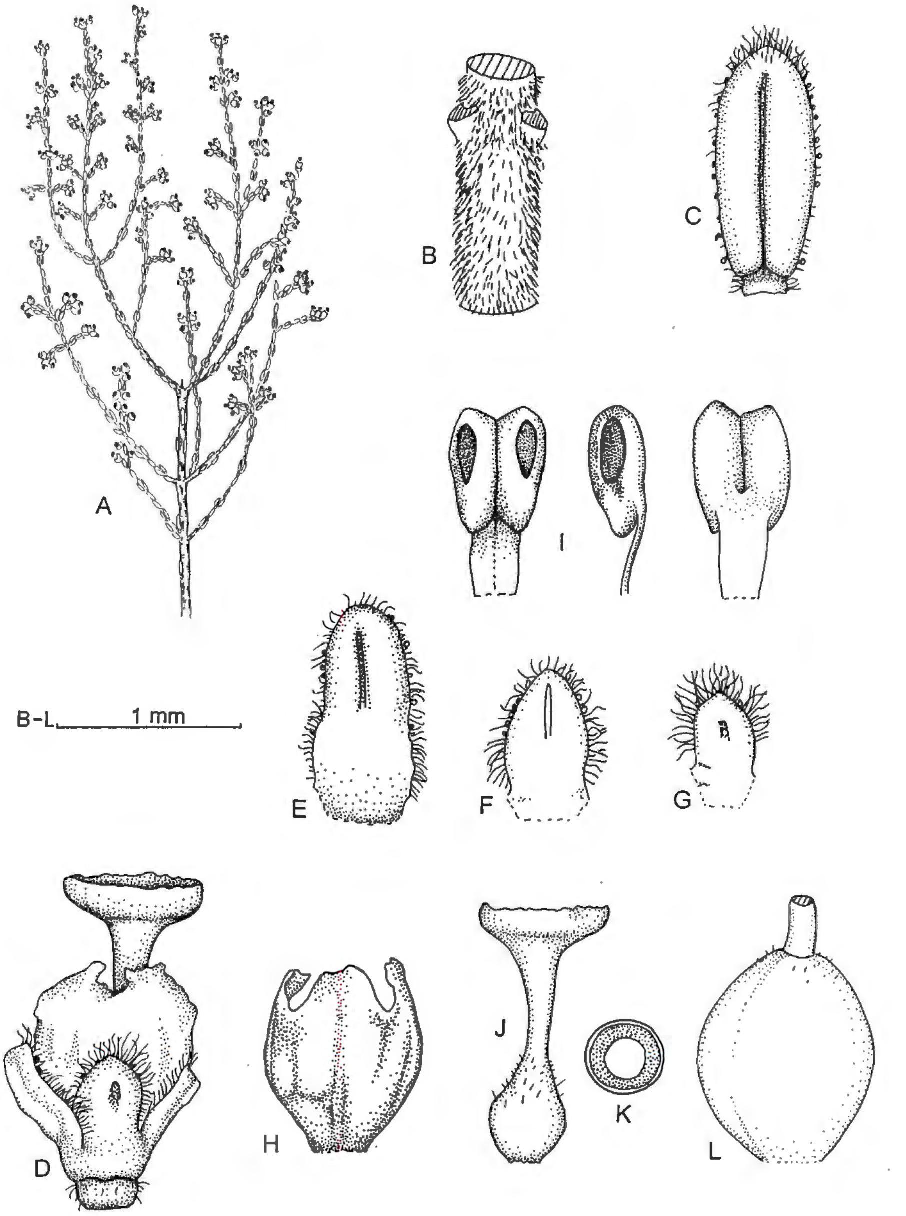

PLATE 73.—*Erica boucheri*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, bract; F, bracteole; G, sepal; H, corolla; I, anther, front, side & back views; J, gynoecium; K, ovary T/S; L, fruit; all drawn from the type, *Oliver 8442*.

L3 RB3 K1 C4 A4 G$^1/_1$ ($^2/_1$)

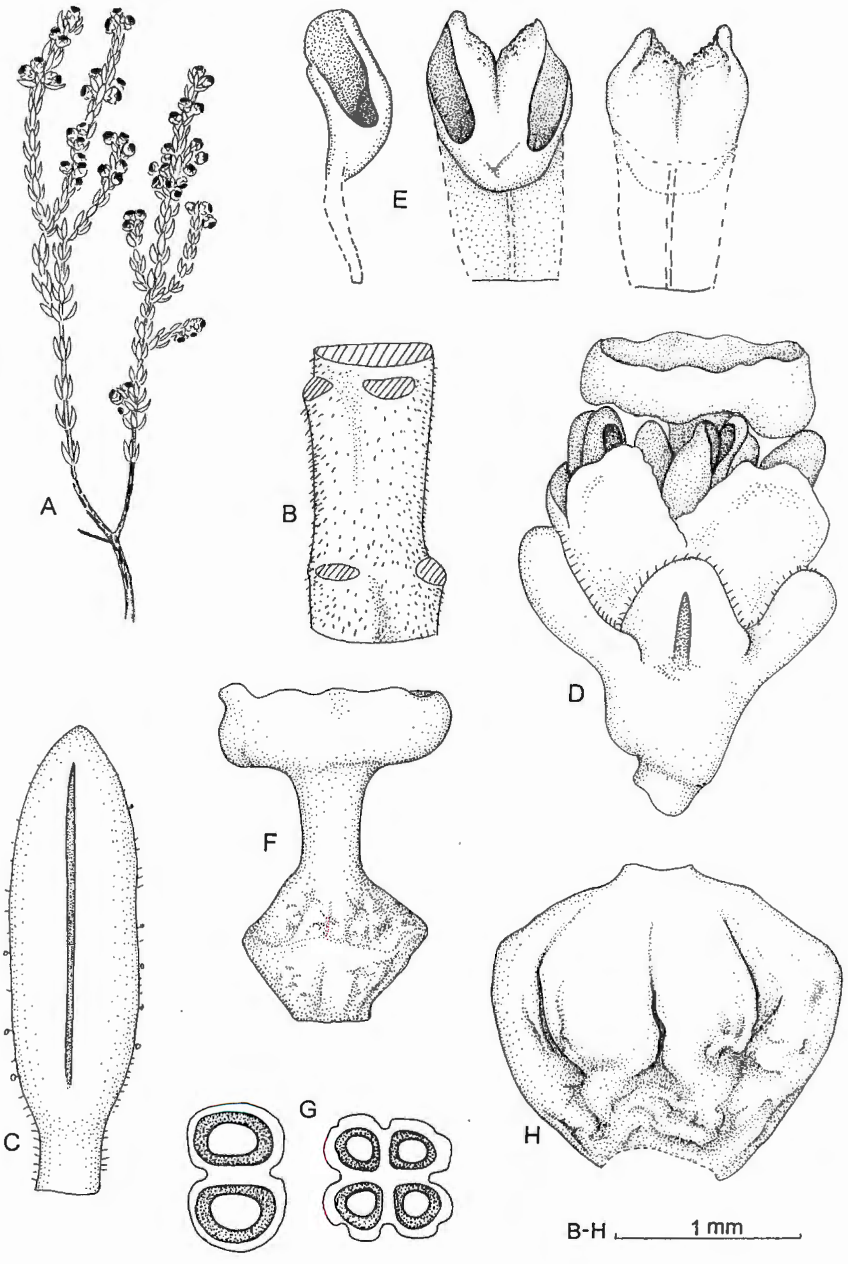

PLATE 74.—*Erica bredasiana*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views (side view showing internal hole); F, gynoecium; G, ovary T/S; H, fruit; all drawn from *Oliver 7653*.

L3 RB3 K1 C4 A6 G$^{2}/_{1}$ ($^{3}/_{1}$ $^{4}/_{1}$)

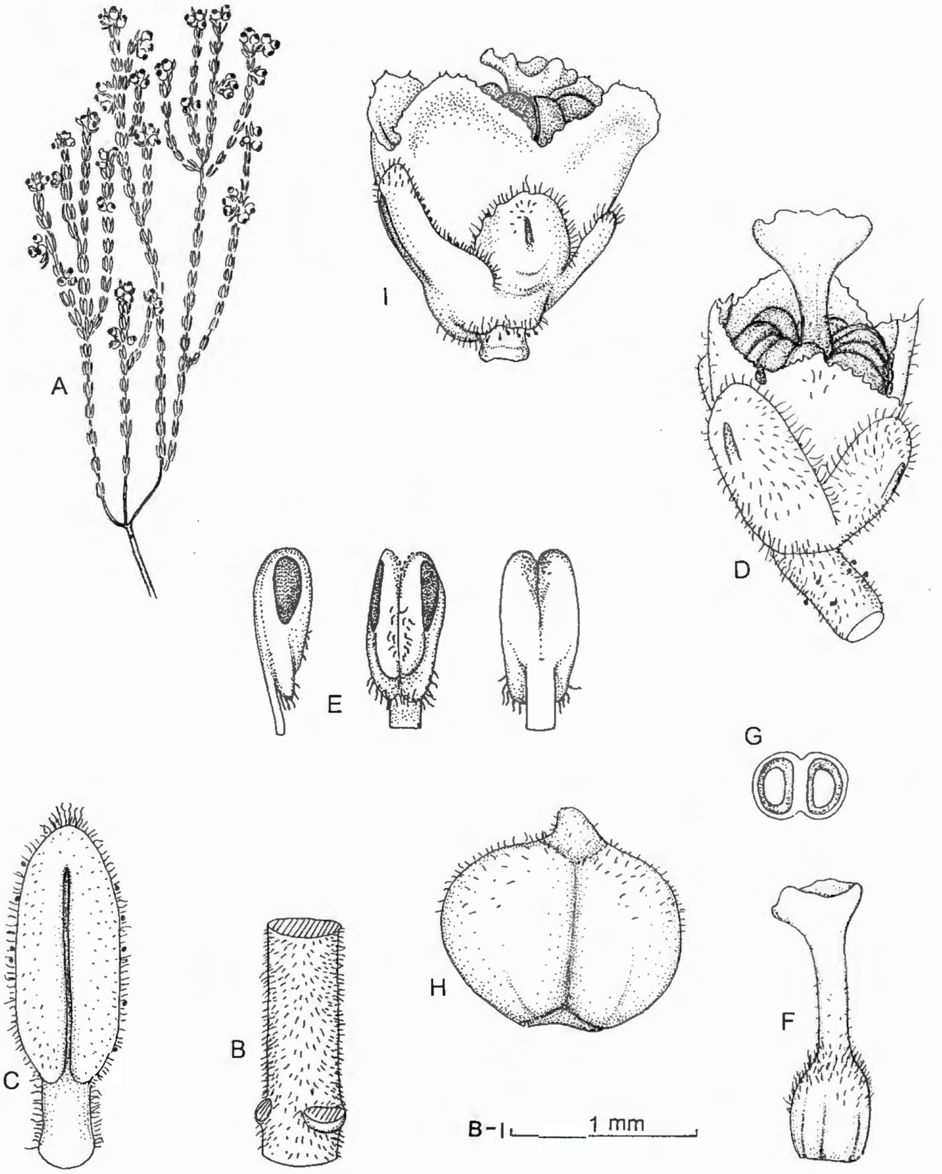

PLATE 75.—*Erica terniflora*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views F, gynoecium; G, ovary T/S; H, fruit; A–G drawn from *Stokoe 7668*, H, from *Esterhuysen 8100*, I from *Stokoe SAM55155*. **L**3 **RB**3 **K**1 **C**4 **A**6[5] **G**$^2/_1$ [$^2/_2$]

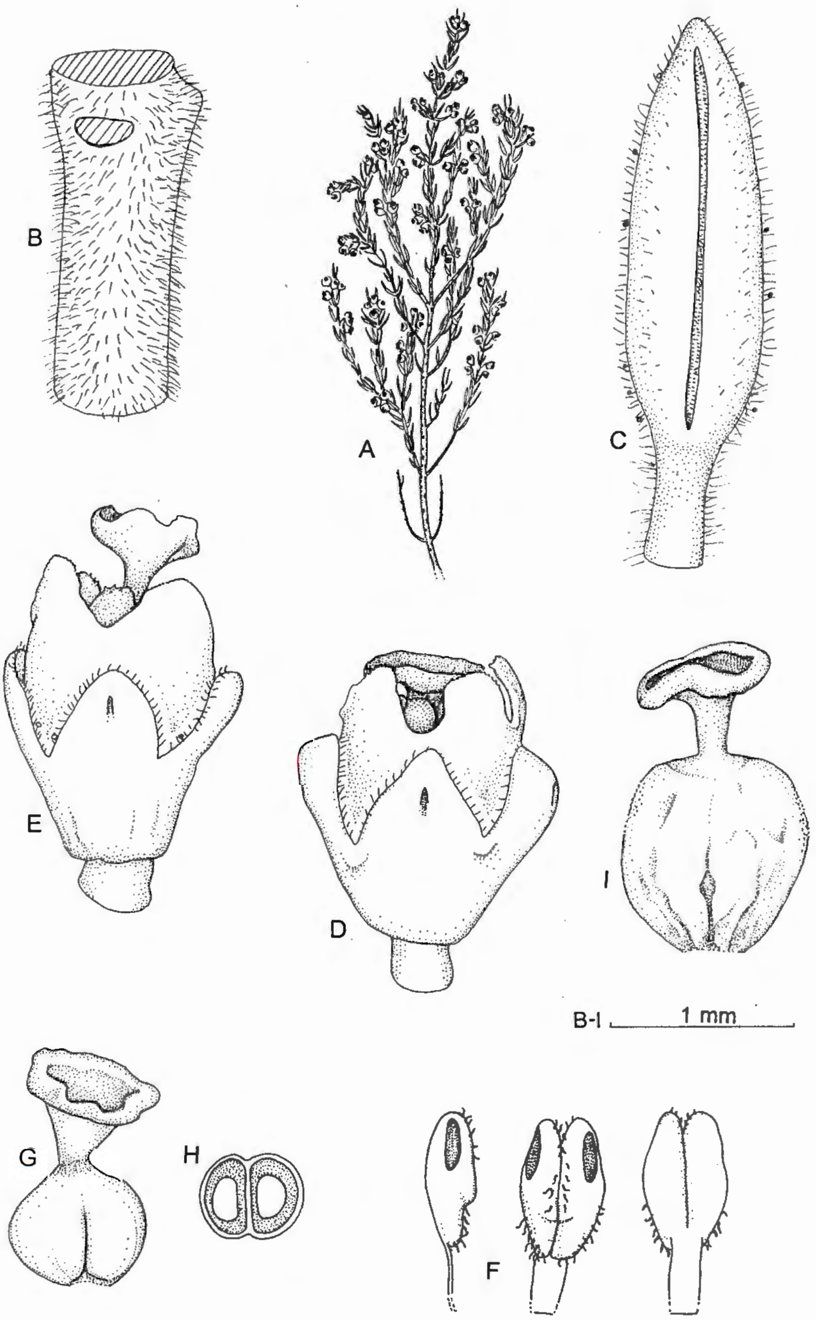

PLATE 76.—*Erica binaria*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, flower in fruit; F, anther, side, front, back views; G, gynoecium; H, ovary T/S; I, fruit; all drawn from the type, *Oliver 10783*.

L3 RB3 K1 C4 A8(7,6) **G**$^{2}/_{1}$

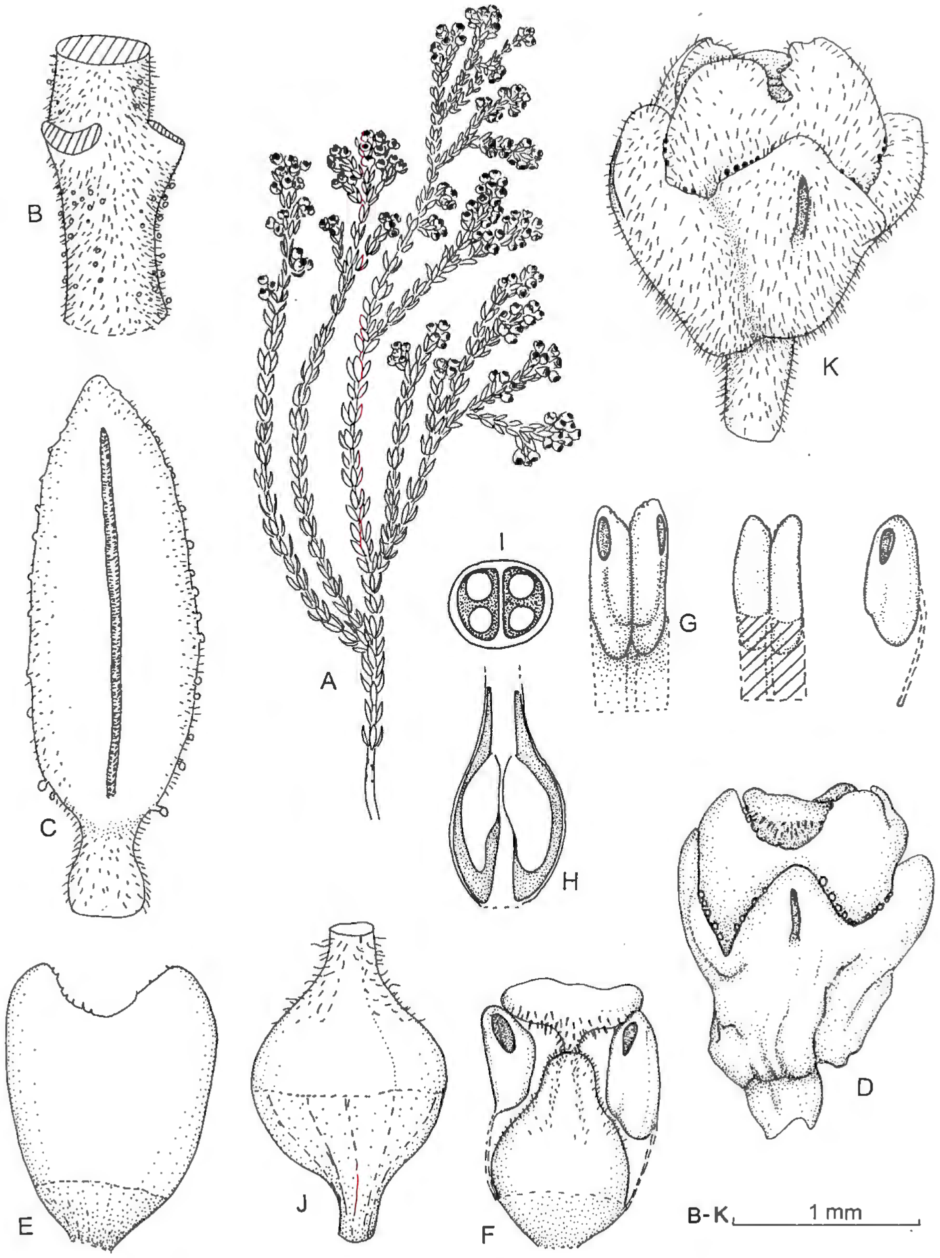

PLATE 77.—*Erica serrata*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, corolla showing zone of adnation; F, gynoecium & androecium showing zone of adnation; G, anther, front, back & side views; H, ovary L/S; I, ovary T/S; J, fruit; K, puberulous flower; A–I drawn from *Oliver 4246*, K from *Oliver 3424*. **L**3 **RB**3 **K**1 **C**4 **A**8 **G**$^{2}/_{2}$

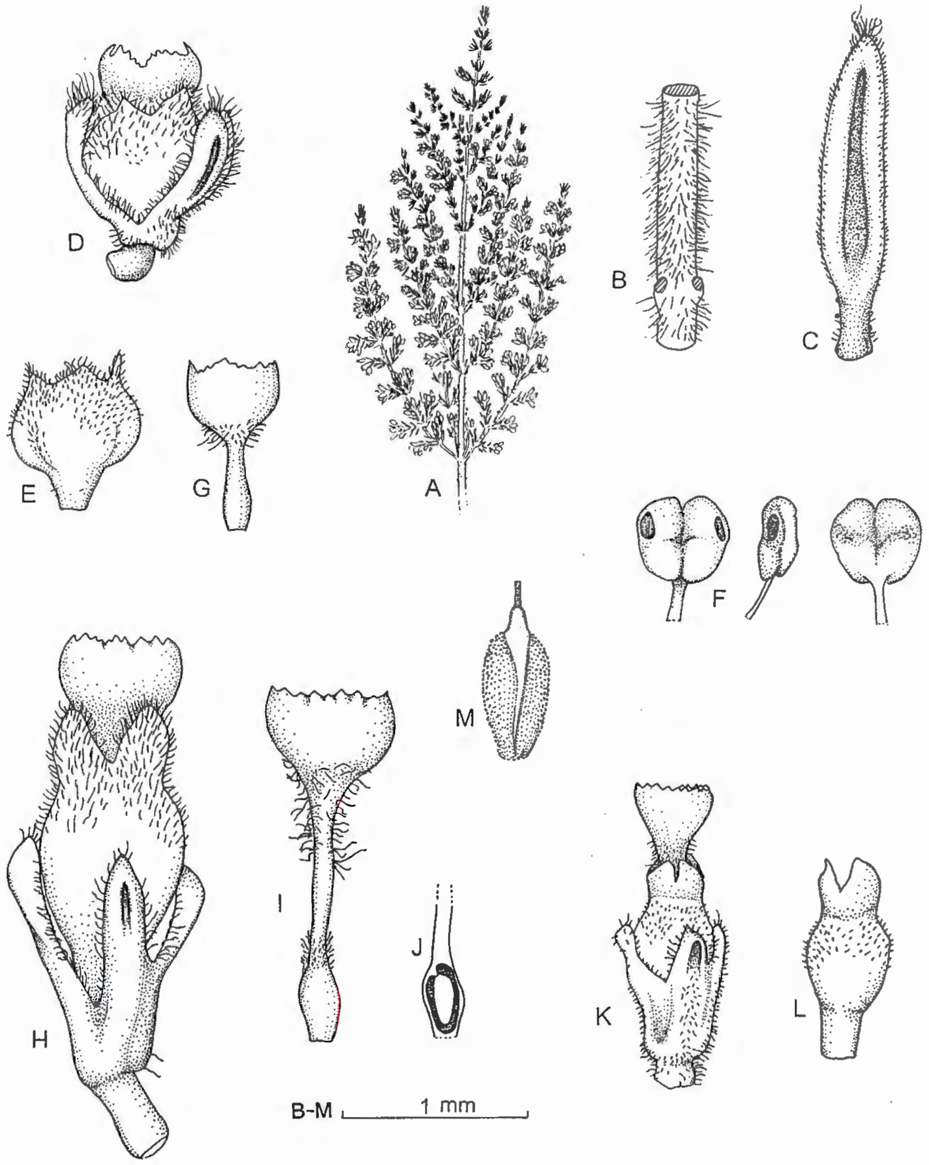

PLATE 78.—*Erica urceolata*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, corolla; F, anther, front, side & back views; G, gynoecium; H, flower; I, gynoecium; J, ovary L/S; K, flower, L, corolla; M, fruit; B–G drawn from *Oliver 8019*, H–J from type, *Bergius s.n.*, A, K, L from *Oliver 4254*.

L3 **RB**3 **K**1(0) **C**4(3) **A**3 **G**$^1/_1$

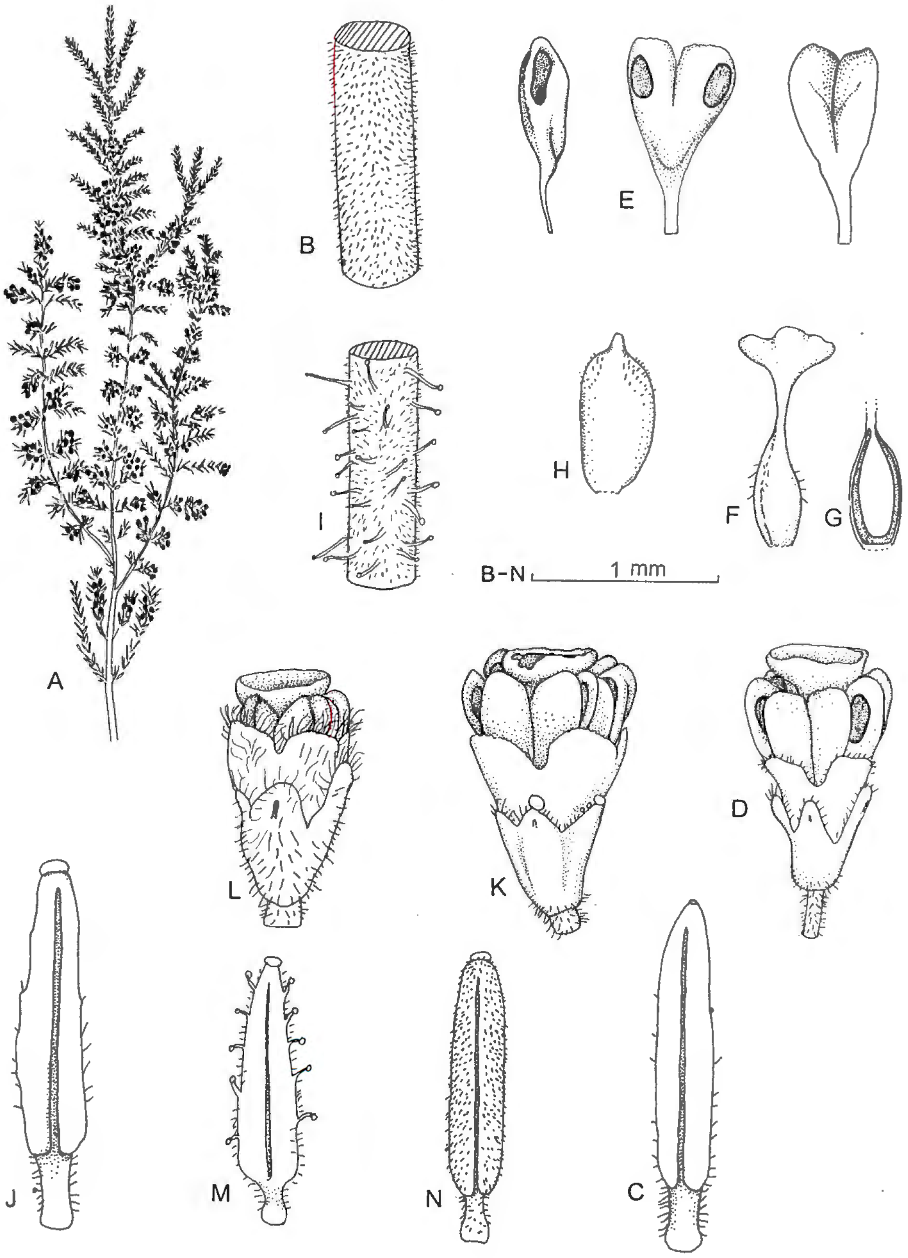

PLATE 79.—*Erica muscosa*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, anther, side, front & back views (side view showing internal hole); zF, gynoecium; G, ovary L/S; H, fruit; I, stem; J, leaf; K, flower; L, flower; M, leaf; N, leaf; A–G drawn from *Oliver 4099*, H,N from *Baker 578*, I–K from *Oliver 8007*, L from *Gillett 4383*, M from *Taylor 4527*. **L3 RB3 K1 C4 A4** $\mathbf{G}^1/_1$

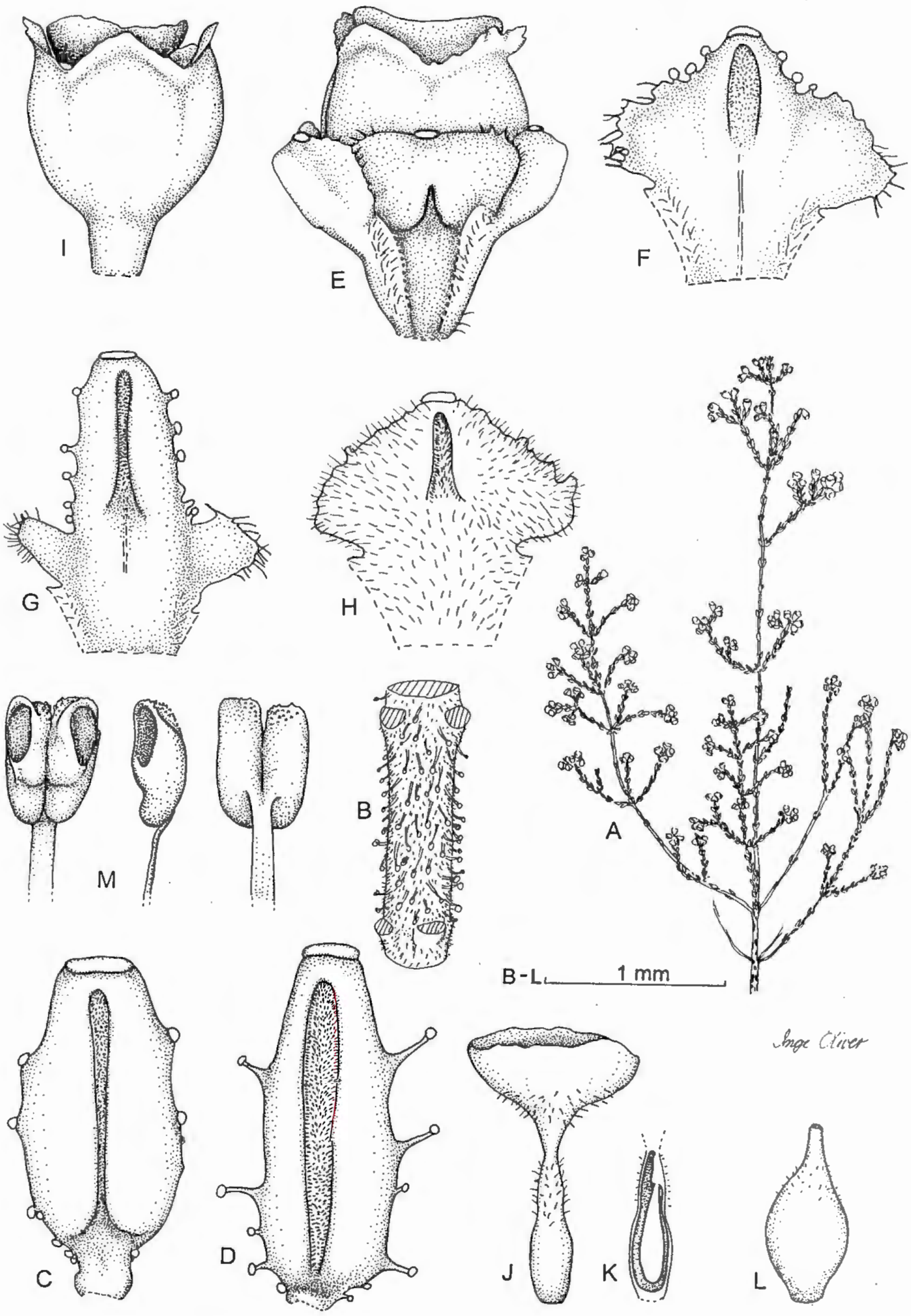

PLATE 80.—*Erica phacelanthera*. A, flowering branch, nat. size; B, stem; C & D, leaf; E, flower; F, G & H, bract variation; I, corolla; J, gynoecium; K, ovary L/S; L, fruit; M, anther, front, side & back views; A, B, E, I–M drawn from *Oliver 8987*, C from *Page s.n.*, D, H from *Esterhuysen 28231*, G, F from type, *Ecklon & Zeyher s.n.* **L**3 **RB**3 **K**1 **C**4 **A**4 **G**$^{1}/_{1}$

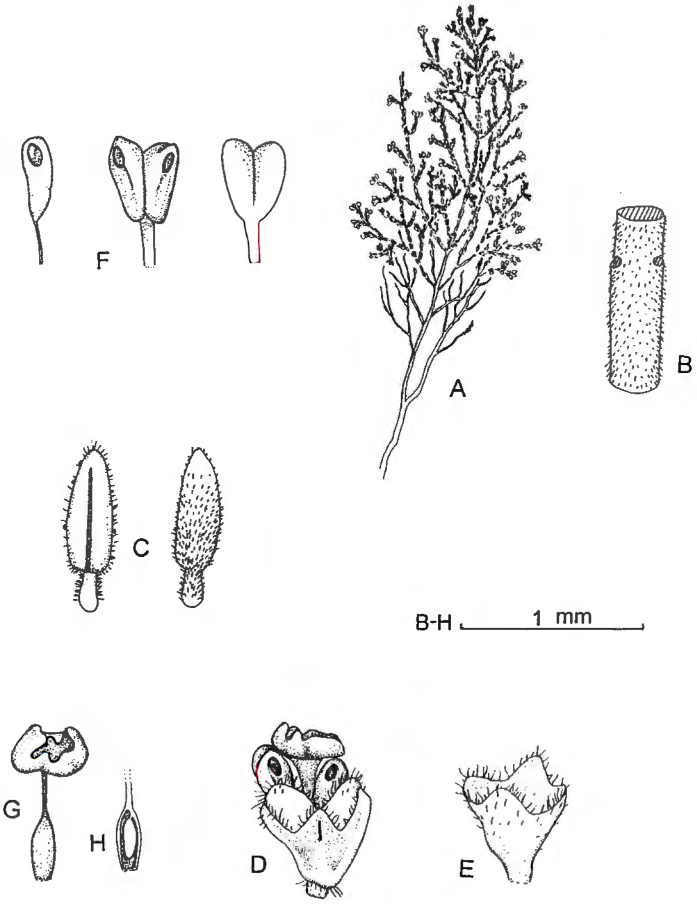

PLATE 81.—*Erica eglandulosa*. A, flowering branch, nat. size; B, stem; C, leaf, abaxial (left) & adaxial (right) views; D, flower; E, corolla; F, anther, side, front & back views; G, gynoecium; H, ovary L/S; all drawn from *Burchell 7716*.

L3 RB3 K1 C4 A4 $\mathbf{G}^{1}/_{1}$

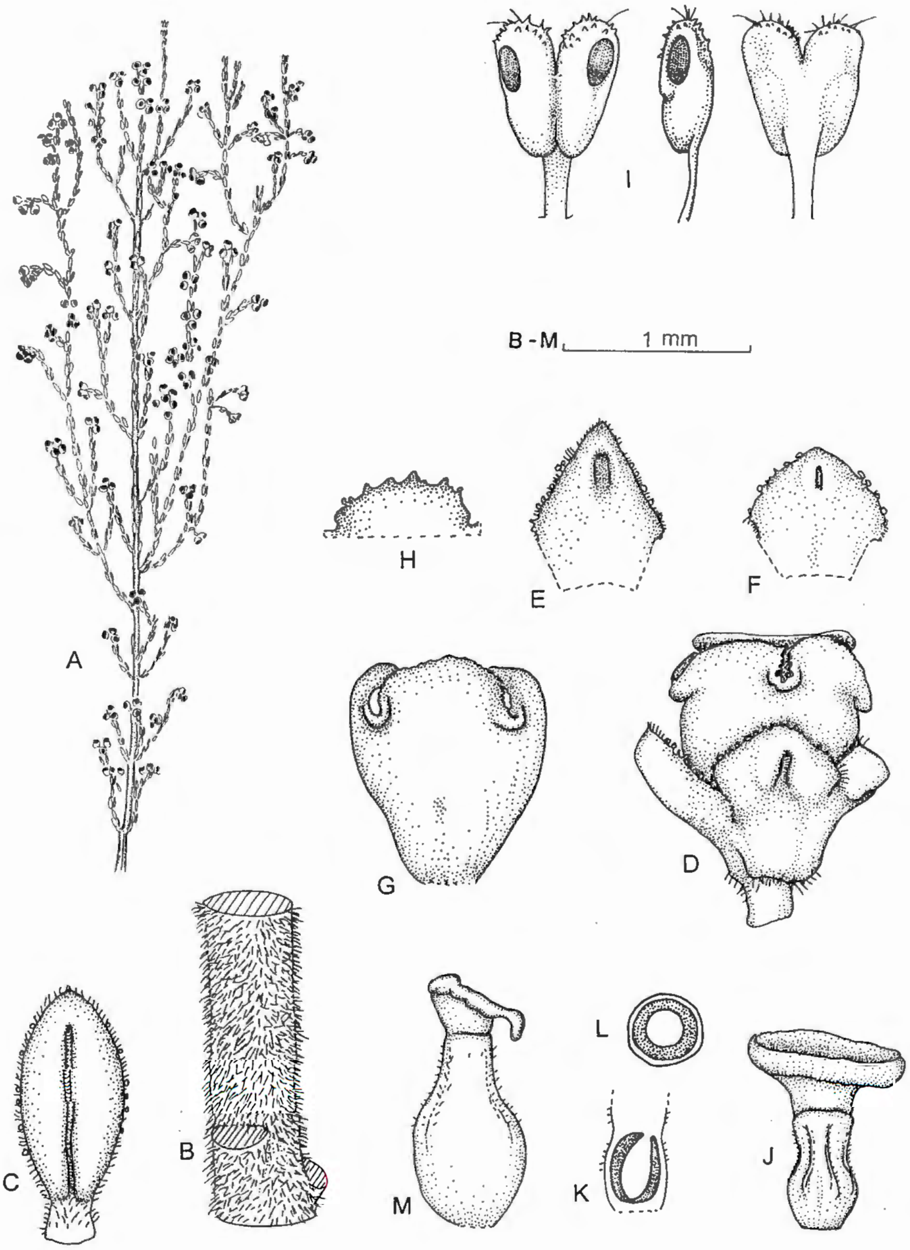

PLATE 82.—*Erica melanomontana*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E & F, bract; G, corolla; H, corolla lobe; I, anther, front, side & back views; J, gynoecium; K, ovary L/S; L, ovary T/S; M, fruit; all drawn from *Oliver 5519*. **L3** **RB3** **K1** **C4** **A4** **G**$^{1}/_{1}$

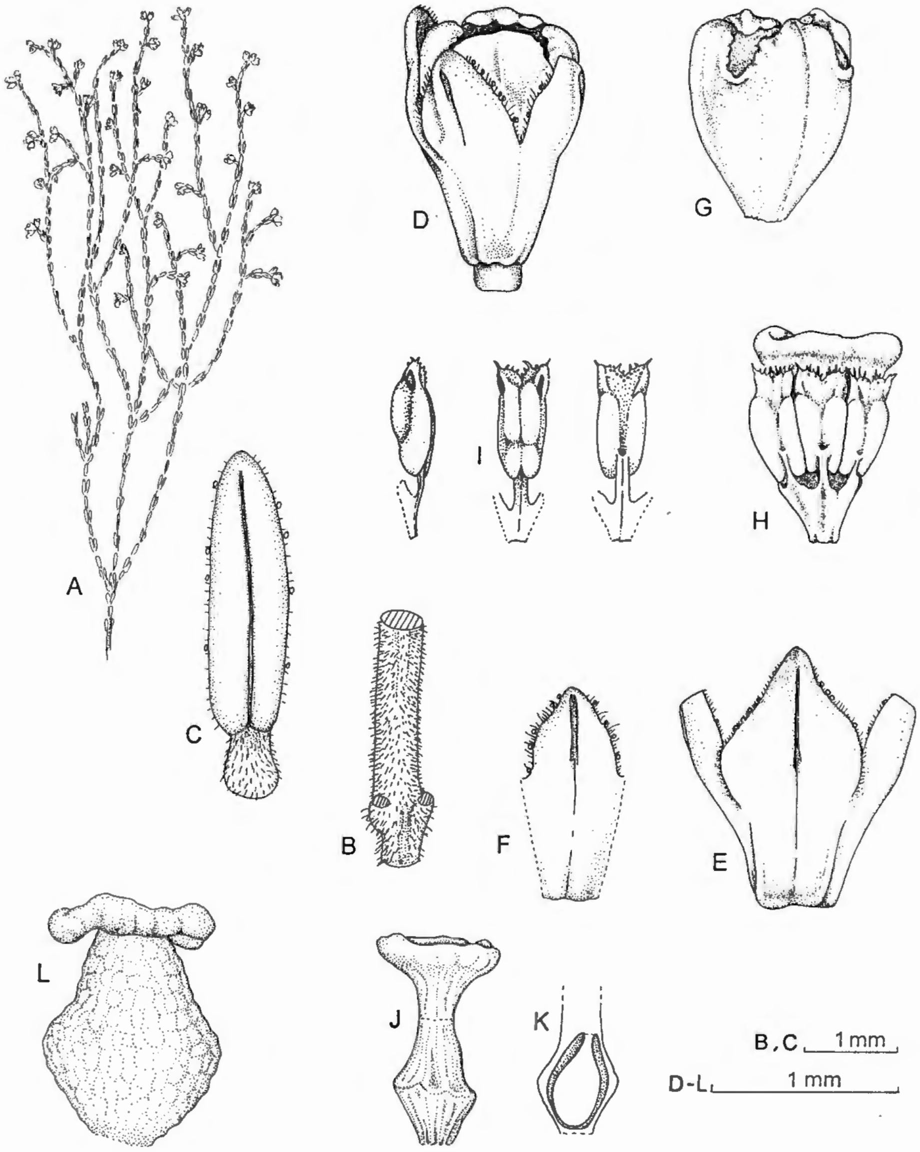

PLATE 83.—*Erica miniscula*. A, flowering branch, nat. size; B, stem; C, leaf; D, flower; E, calyx, abaxial view showing large fully recaulescent bract; F, bracteole; G, corolla; H, androecium; I, anther, side, front & back views; J, gynoecium; K, ovary L/S; L, fruit; all drawn from type, *Burchell 7034*.

L3 RB3 K1 C4 A8 $\mathbf{G}^1/_1$

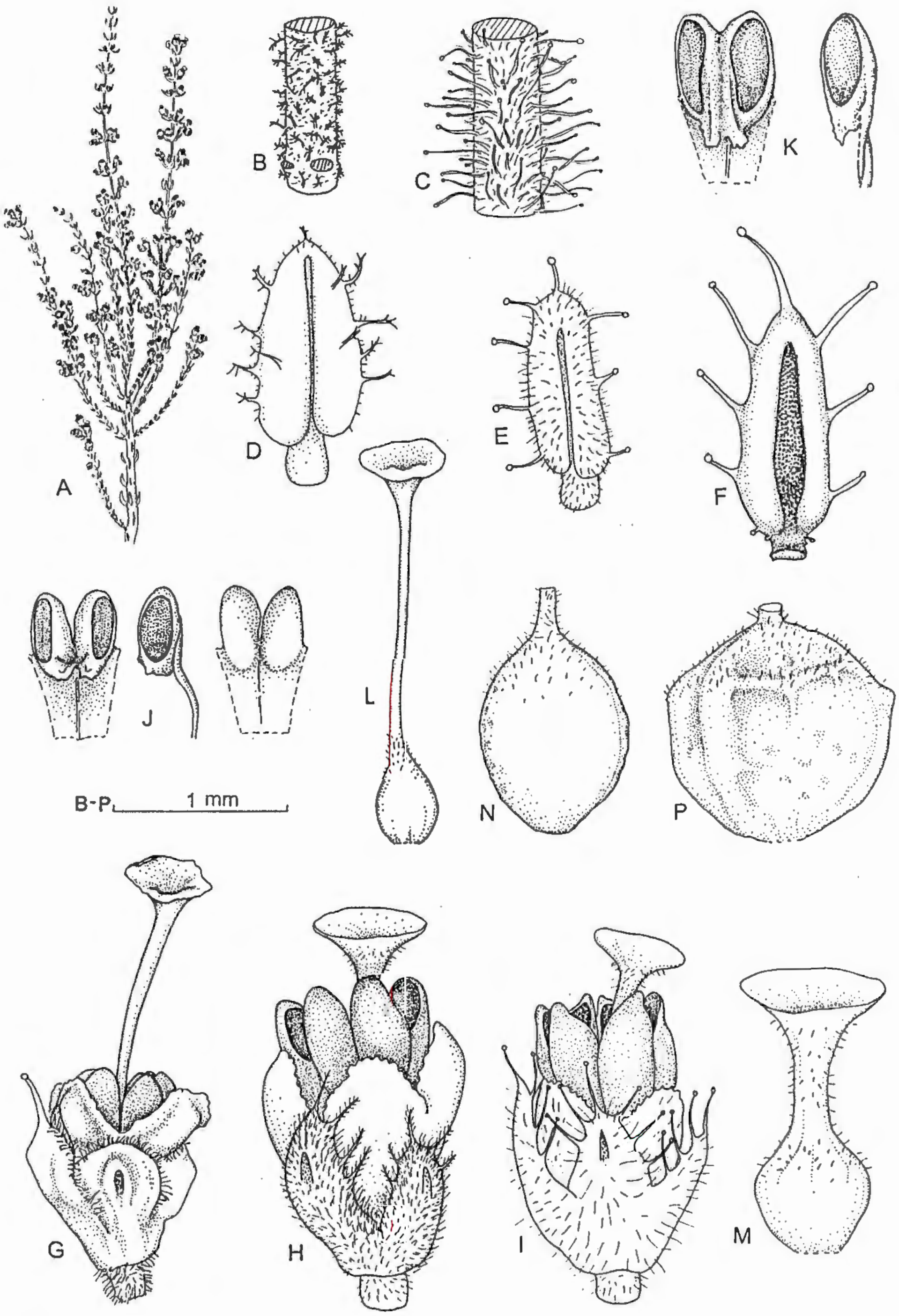

FIGURE 84.— *Erica rigidula*. A, flowering branch, nat. size; B, stem with glandular hairs; C, stem with plumose hairs; D, E & F, leaves with various indumenta; G, H & I, flowers showing variation; J, anther, front, side & back views (side view showing internal hole); K, anther, front & side views (lacking internal hole); L & M, gynoecium showing variation in style length; N & P, fruits; B–D drawn from *Oliver 5148*, A, C, E, H from *Pillans 8818*, G, J, L from *Schlechter 9748*, F, K from *Oliver 7986*, I, M from *Compton 3000*, P from *Stokoe SAM18397*, N from *Oliver 3939*. **L3 RB3 K1 C4 A4 G**$^{2}/_{1}$ $^{1}/_{1}$ [$^{3}/_{1}$]