TAXONOMIC STUDIES IN
EUPHRASIA L. (SCROPHULARIACEAE).
A REVISED INFRAGENERIC CLASSIFICATION,
AND A REVISION OF THE GENUS IN AUSTRALIA

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Abstract

The infrageneric classification of Euphrasia has been radically revised in the Australasian and Malesian regions. Fourteen sections are proposed. Two sections, Pauciflorae and Euphrasia (Semicakaratae auctt.), comprise two and four subsections, respectively. The sections Malesianae, Cuneatae, Phragmostomae, Pauciflorae and Lasiantherae, and the subsections Pauciflorae and Humifusae are new and the sections Striatae, Scabrae, Novaezeelandiae, and Anagoperae are given new status. The generic type E. officinalis L. is not a nomen ambiguum in the sense of the ICBN; it should be reinstated as the correct name for E. rostkoviana Hayne.

The classification of the genus in Australia has been completely restructured, with 42 taxa formally treated. Eighteen species are recognized, of which E. ramulosa, E. phragmostoma, E. semipicta, E. bowdeniae, E. lasianthera, E. eichleri, E. orthocheila and E. ciliolata are new and E. caudata, based on E. scabra var. caudata Willis, is given new status. Subspecies are proposed within four polymorphic species. E. gibbsiae has nine subspecies, of which four are new and four have changed status; E. collina, which has caused much confusion in the understanding of the genus in Australia, has 14 subspecies, four new and nine of changed status; E. crassiuscula has three subspecies, one new and one of changed status; and E. orthocheila has two subspecies, one new. In the highly variable species the degree and nature of distinction and amount of intergradation between subspecies is discussed, sometimes as a result of detailed field study. Clines and a limited amount of hybridism occur within species. Interspecific hybrids are rare.

In a chapter on morphology, the taxonomic and, where possible, biological significance of morphological attributes in Euphrasia is discussed. Important characters, e.g. the distinctive habit types in the perennial species, acropetal branch development in the New Zealand annuals, corolla coloration, and the high chromosome numbers of Australian species, have been previously poorly documented or unknown. A number of other characters are redefined to improve their usefulness in classification, while others are shown to be of reduced significance.

The origin and diversification of Euphrasia both on a world scale and within Australia are discussed. Cladistic analysis of the genus is difficult at this stage of our knowledge. However, through the postulation of primitive states of a few characters, several relict species are proposed which are remarkable in their scattered distribution in both hemispheres. From the character states present in the proposed relicts, six apparently monophyletic lineages are distinguished. Diversification of the genus seems to have been in at least two phases, one possibly in the early Tertiary or before, the other, from which most extant species are derived, since Neogene times. Apart from the recently derived, highly specialized Sect. Euphrasia, the genus shows no capacity for long-distance dispersal; much evidence points to the need for migration across suitable land. An association of at least two relict species with Nothofagus, which with Fagus has a distribution homologous to Euphrasia, is among the evidence presented for Euphrasia attaining its bihemispheric distribution by the early Tertiary. Deficiencies in the present fossil record allow latitude for this theory.
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I. INTRODUCTION

Many treatments of Euphrasia in Australia have referred to the inadequacies of our present knowledge of its taxonomy and to complex morphological variation involving possible hybridization. The status of a number of species recognized by Wettstein (1896) and Du Rietz (1948a,b), who respectively revised and surveyed the genus in Australia, has been questioned (e.g. Willis 1967), and there have been obvious difficulties in the application of names to taxa distinguished by writers of regional works (e.g. Burbidge & Gray 1970). This revision of the Australian species of Euphrasia is accordingly based on studies of a wide range of herbarium material supplemented by extensive field observations, with an emphasis on the interaction of sympatric taxa.

In order to clarify the relationships of the Australian taxa with those of neighbouring regions, much material was obtained from outside Australia, including many types from New Zealand, the Juan Fernandez Islands, Malesia and Taiwan. The revision of the infrageneric classification of the genus arose directly from the study of this material, together with the large amount of knowledge accumulated since Wettstein's (1896) revision, especially in the southern hemisphere and tropics.

The taxonomic and, where possible, adaptive significance of the many morphological attributes used in both the Australian and infrageneric revisions is discussed in a preliminary chapter.

Many have remarked on the completeness of the link, on the isolated mountain tops of Malesia, between the widespread temperate distributions of Euphrasia. The means by which the genus attained this distribution has been the subject of much speculation (e.g. Wettstein 1896; Du Rietz 1932b, 1948a; van Steenis 1962, 1971; Yeo 1968; Moore 1972; Raven & Axelrod 1972). In this paper an assessment of the origin and diversification of the genus on a world scale is made on the morphological evidence to hand in the light of current geological and palaeobotanical knowledge. The origins of the Australian taxa are dealt with in greater detail.

These investigations have been based on material (including types) from the following herbaria (abbreviations as designated in Lanjouw & Stafleu, 'Index Herbariorum', 1964): A, AD, ADW, AK, B, BM, BRI, CANB, CANTY, CBG, CHR, FI, G, GAUBA, GB, GH, HBG, HO, K, L, LY, MEL, MELU, NE, NSW, PERTH, PH, S, SYD, TAI, UPS, W, WU, the private herbarium of Mr Cliff Beauglehole of Portland, Victoria (cited as BEAUGLEHOLE), and the herbarium of the New South Wales National Parks and Wildlife Service at Waste Point near Jindabyne (cited as NSWNP). Unfortunately, as the specimens from FI and many of those from BM had to be returned before the classifications had been finalized, not all the sheets could be annotated. However, where it was not clear from previous annotations, type specimens were designated with their type status.

Many collections have been made in the course of the author's field studies. The main sheet of each is housed at AD. The many duplicate sheets have been distributed among herbaria, priority being given to CANB, MEL (mainland collections) and HO (Tasmanian) of the Australian herbaria, and of overseas herbaria, CGE with which the Euphrasia specialist Dr P.F. Yeo is associated, and W, where many types of overseas species and other specimens used in Wettstein's (1896) monograph are already housed. In this work the places of deposition of isotypes are cited, but for other personal collections only AD is cited. On the AD sheet is written the herbaria to which duplicates have been sent.

The work was initially produced in unpublished form in a doctoral thesis submitted to the University of Adelaide (Barker 1974). Many changes have been made subsequently. In particular, changes involving the name E. ramulosa, the status and
type of *E. bowdeniae* and the subspecies of *E. orthocheila*, and the types designated for *E. phragmostoma* and *E. ciliolata* should be noted. In addition a formal division of *E. caudata* into two subspecies has been decided against. Most annotations of relevant specimens seen will not have been modified. Study in the field or of fresh material in 1975 of a few New Guinea species, and field work in early 1979 covering the majority of New Zealand taxa have helped consolidate many ideas on the infrageneric taxonomy and evolution of the genus. A number of essential changes have been made. The remaining observations are left to future revisions of the genus in these countries.

**II. MORPHOLOGY: MEASUREMENT, TERMINOLOGY, DIAGNOSTIC IMPORTANCE AND BIOLOGICAL RELEVANCE**

The following is an enumeration of the attributes which have been described in the present and past taxonomic treatments of *Euphrasia*. Consideration is given to the nature and significance of the variability of characters and their diagnostic usefulness at the various levels of classification. Floral biology, which involves characters of several organs, is discussed separately.

**A. MEASUREMENT OF CHARACTERS**

Much of the taxonomic difficulty in *Euphrasia* stems from the closeness of the taxa, with the major differences often overlapping to a greater or lesser extent. It has therefore been considered advisable to adhere where practical to a policy of using quantitative terms to describe diagnostically useful characters in cases where the lack of precision, characteristic of many qualitative terms, might obscure the true variability of the characters. Even where precise mathematical definition has been given to some qualitative terms (e.g. the chart of simple symmetrical plane shapes: Stearn 1966), their actual usage is liable to be imprecise.

For each taxon the measurements of each character were usually taken from a sample of twenty to thirty specimens selected to cover the extremes of the geographical, ecological and altitudinal range of the taxon. In the more widespread taxa, many more measurements of the variable characters were made.

The range of variation in quantitative characters has been portrayed in the descriptions as follows. In presenting the measurements, the extremes of variation are usually placed in brackets at either end of the range. Most commonly, between these bracketed extremes is given the range of values covering the 80% of variation remaining after the 10% smallest and 10% largest values have been removed. If there are insufficient specimens to give an adequate sample only an average of the measurements taken is placed between the bracketed extremes. In a few obviously distinct taxa or where an organ is poorly collected only the overall range of variation has been given.

All measurements in centimetres (such as plant height) were taken to the nearest centimetre using a ruler. Small organs requiring millimetre measurements (such as corolla and leaf length and leaf tooth dimensions) were measured under a low-power microscope at 10x magnification with an ocular micrometer and were recorded to the nearest tenth of a millimetre. Measurements of less than one millimetre (such as awn length) were recorded to the nearest twentieth of a millimetre. Some other measurements are also given to the nearest half of an integer or decimal fraction, depending on the size of the organ involved, and particularly in cases of insufficient material.
B. Characters

1. Life-span

Both annual and perennial types of life-span are common in *Euphrasia* and their distinction is one of the major characters used in the infrageneric classification proposed in this work, and in the previous ones of Wettstein (1896) and Pugsley (1936).

The longevity of the perennial species has not been investigated, but it is considered that the sturdy Australian perennials may survive for several years. Generally, in populations of perennials first-year plants are much more scarce than plants of the previous year (detected by weather-worn old infructescences). *E. hookeri*, however, inhabiting a severe alpine environment, is one species which has the capacity to perennate but may rarely do so (q.v.: note 2).

2. Root system and semi-parasitism

The plant is a facultative semi-parasite with European species having the ability to parasitize a range of host species (Yeo 1964). Swellings or "haustoria", which are located on the finer rootlets, attach to the fine rootlets of the host. Evidence of these haustoria is present in most specimens which have been extracted from the soil with care, but fragments of the host roots still attached to the haustoria are less common.

I have observed haustoria in all Australian taxa. The presence of haustoria is widely documented for European species and has been described (Philipson 1959) for *E. cockayniana*, *E. zelandica* and *E. revoluta* of New Zealand. I have also seen haustoria in material (in AD) of *E. cuneata* (Sect. *Cuneatae*), all species of Sect. *Pauciflorae* and *E. integrifolia* (Sect. *Anagospermae*) in New Zealand, *E. papuana*, *E. mirabilis* and *E. lamii* (Subsect. *Pauciflorae*) of New Guinea, and the species of Taiwan (Sect. *Malesianae*: specimens ex TAI). Material from elsewhere in Malesia and South America was not inspected for haustoria.

Yeo (1964) reviewed experimental work in semi-parasitism on the northern hemisphere annuals. Since then Weber (e.g. 1976a,b,c, 1980) has published a continuing series of studies on the haustorial anatomy making comparisons with other genera of Subfam. Rhinanthoideae and Orobanchaceae, while Kuijt (1969) has reviewed physiological aspects of semi-parasitism, including theory that the sessile gland patches on underside of the leaves (see p. 25) produce a high transpirational pull on xylem contents of the host.

Simple slender roots may emerge from prostrate axes. This is probably a response to permanently moist conditions.

3. Habit

Within both the perennials and annuals of *Euphrasia* there is a variety of habit types. Differences in habit often appear to be associated with climate. Thus, similar habit types may be found in distantly related species under similar climatic conditions, while closely allied taxa, sometimes within a species or even variants in the one subspecies, may differ markedly in habit in association with corresponding climatic differences.

In this work the term *stem* has been used in the sense of Jackson (1928: "the main axis of a plant, leaf-bearing and flower-bearing as distinguished from the root-bearing axis"). The term stem seems to have been used more broadly by Wettstein (1896), Pugsley (1936) and Du Rietz (1948a,b), as well as the majority of flora writers, in describing the perennials and prostrate annuals. The first-year plants of several Australian species may have a single axis which is erect or ascending, is often profusely
branched, and produces an inflorescence. On the above definitions this would be the only true stem with any axes arising from this being branches. In subsequent years the stem may die back, often to the region of the upper branches. If the branching is confined to near ground level the plant has a “many-stemmed” appearance. These axes are, however, of a secondary (or greater) nature and should not by the above definitions be called stems. The presence of a single stem is clearer in those perennials which branch high above ground level. In these much of the stem persists throughout the life of the plant.

The term main axis(es) refers to the stem, or in perennials after their first year, the robust flowering branches. The term main inflorescence-bearing axis(es) derives from this.

Characters useful in defining habit are: the height of the plant or, to exclude variation caused by differences in the stage of development of the branches and inflorescence, the height of the main inflorescence-bearing axis to the base of the inflorescence; the position of the uppermost branches or young shoots on the main inflorescence-bearing axis (measured both by the number of nodes below the inflorescence, and by the proportion of main inflorescence-bearing axis between the inflorescence and the node bearing the uppermost shoot); the sequence of development and direction of the branches; and the number and length of the internodes on the main inflorescence-bearing axis relative to the length of the leaves.

a. Habit in the annuals

The habit type consisting of a single erect stem often branched at successive nodes is characteristic of almost all annual species of *Euphrasia*. In the Australian annuals the branches develop basipetally at consecutive nodes. Elsewhere, however, the order and consistency of branch development is not so strict. In the northern hemisphere species there is also a tendency for branches to develop basipetally but they are often, in the less robust plants, very few or even absent. In the New Zealand annuals of Sect. *Novaezeelandiae* branching is similarly rather sporadic and tends to be acropetal. The more ordered and consistent development of branching in the Australian species may be related to their apparent capacity for more vigorous growth, enabling stems to bear many internodes and flowers to be produced in large numbers.

Two species of Sect. *Anagospemae* of New Zealand, *E. disperma* and *E. integrifolia*, form loose mats with almost completely prostrate branches arising from a reduced stem (see Ashwin 1961). The remaining two species of the section, *E. repens* and *E. dyeri*, are intermediate in their habit between these species and Sect. *Novaezeelandiae*.

Until the present revision, habit in the annual species had only been studied in the extensive northern representatives of Sect. *Euphrasia*, in which the phenomenon of “seasonal (or pseudoseasonal) dimorphism” has been widely documented. Similar habit polymorphism occurs in other genera of the Trib. Rhinantheae e.g. *Melampyrum* and *Rhinanthus* (Soo & Webb 1972a,b). The two habit types of Sect. *Euphrasia* have been characterized as follows by Pugsley (1930).

*Aestival or early summer-flowering form*: Internodes very long. Flowers forming from generally the 4th stem node. Branching consequently limited.

*Autumnal or late summer-flowering form*. Internodes very short in lower parts, [?] longer above]. Flowering from the 5th-12th (or more) stem node. Branching copious.

Yeo (1964, p. 7) has made slight modifications of these categories.

The various habit types have been correlated with climatically based differences in the duration of the growing season. In *Euphrasia* the aestival form is found in alpine or
arctic regions with shorter growing seasons. It is also found in meadows which are frequently mown and where, accordingly, the time between germination and the production of seed is necessarily short. The autumnal or late summer-flowering forms occur in more lowland regions or lower latitudes with correspondingly longer annual periods of growth.

Pugsley (1930, 1936) defined a number of series in Sect. Euphrasia (his Sect. Semicalcaratae) partly on the basis of these habit differences. However, he and subsequent workers, such as Juzepcuk (1955), Sell & Yeo (1970) and Yeo (1972), have found the distinctions between the autumnal and aestival types in different complexes too variable to be useful in defining species. They have preferred to describe each taxon by its range of variation in the number of stem nodes, the length of the internodes and the relative abundance of branching.

Yeo (1964) has shown that in Sect. Euphrasia habit differences of this kind are retained when different forms are cultivated together, indicating that they are genetically determined. In addition, he observed precocious flowering (with a consequently reduced stem node number) in some plants of the normally later summer-flowering E. pseudokerneri during periods of unusually high temperatures: “this suggests that temperature is one of the main factors controlling flowering in Euphrasia, and that given sufficiently high temperatures E. pseudokerneri can be made to flower at about as low a node as the high mountain species”.

The length of the potential growing season as determined by the climate also appears to be a critical factor in determining the habit type of the Australian annuals (Sect. Scabrae, Sect. Lasiantherae). The longest potential growing season in the regions occupied by the annuals is likely to be in New South Wales, particularly in northern montane habitats where there is both summer and winter rain and winter snows are rare. The two annuals of this region, E. arguta and E. orthocheila, apparently in montane and/or lowland parts possess the tallest habit and the largest number of stem nodes of the Australian annuals (table 1).

Elsewhere in Australia the length of the potential growing season is shortened in one of two ways with an accompanying reduction in height and a number of stem nodes (table 1). In montane and lowland temperate Australia, in which E. scabra is widespread, snows are generally absent, but rainfall predominates in the winter months and the summers have irregular rain. The growing season is thus effectively shortened. The reduction in growing season for the remaining annuals which occupy alpine and subalpine zones is caused by the winter snows, with conditions ameliorating earlier with decreasing altitude at a given site, allowing for local differences such as in aspect. There is a progressive reduction in plant height and node number from the predominantly subalpine taxa, such as E. ciliolata and E. caudata through to the predominantly alpine E. alsa. E. eichleri, which occupies both alpine and subalpine localities, is intermediate between these types, while within E. caudata the dwarf variant occurs at a high subalpine site.

### Table 1. The climatic ranges and variation in selected characters of the Australian annuals of Euphrasia

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Height of stem base of inflorescence (cm)</th>
<th>No. of stem nodes</th>
<th>No. of flowers in stem nodes</th>
<th>No. of ovules in inflorescence</th>
<th>Length of seeds (mm)</th>
<th>Climatic zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. alsa</td>
<td>1.3-5.0(6.5)</td>
<td>(11)-3(4)</td>
<td>c.15-30</td>
<td>10-12(15)</td>
<td>1.8-2.5</td>
<td>+</td>
</tr>
<tr>
<td>E. eichleri</td>
<td>(2.5)-5.1(14)</td>
<td>(5)-6(12)</td>
<td>&gt;15</td>
<td>(20)-30(40)</td>
<td>1.5-2.0</td>
<td>+</td>
</tr>
<tr>
<td>E. caudata</td>
<td>(3.5)-6.7(11.0)</td>
<td>(5)-6(8)</td>
<td>(10)-18(26)</td>
<td>(20)-37(45)</td>
<td>(0.9)-1.2-1.5(1.9)</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>dwarf variant (7.3)-1-2(30)</td>
<td>(8)-1-4(17)</td>
<td>(12)-2(32)</td>
<td>(30)-62(10)</td>
<td>(1.0)-1.3-1.5(2.0)</td>
<td>(+) +</td>
</tr>
<tr>
<td></td>
<td>common variant (7.3)-1-2(30)</td>
<td>(8)-1-4(17)</td>
<td>(12)-2(32)</td>
<td>(30)-62(10)</td>
<td>(1.0)-1.3-1.5(2.0)</td>
<td>(+) +</td>
</tr>
<tr>
<td>E. ciliolata</td>
<td>(11)-18(23)</td>
<td>(10)-18(19)</td>
<td>(10)-16-26(36)</td>
<td>c.30-75</td>
<td>(0.9)-1.0-1.2(1.4)</td>
<td>+</td>
</tr>
<tr>
<td>E. scabra</td>
<td>(7.5)-11-25(45)</td>
<td>(6)-18(24)</td>
<td>(10)-14-32(54)</td>
<td>(37)-90(40)</td>
<td>(0.4)-0.5-0.8(1.0)</td>
<td>+</td>
</tr>
<tr>
<td>E. arguta</td>
<td>(12)-22(33)</td>
<td>(18)-24(30)</td>
<td>(30)-50-90</td>
<td>c.35-80</td>
<td>(0.4)-0.6-0.8(1.0)</td>
<td>+</td>
</tr>
<tr>
<td>E. orthocheila</td>
<td>(15)-17.5-37(50)</td>
<td>(10)-13(36)</td>
<td>(15)-25-40</td>
<td>(20)-45-100</td>
<td>(0.4)-0.5-0.8(0.9)</td>
<td>+</td>
</tr>
</tbody>
</table>
b. Habit in the perennials

Habit varies greatly in the perennial members of *Euphrasia*. Some habit types are important in distinguishing species or sections; others may show intraspecific polymorphism. As in the annuals, differences in habit type tend to be geographically restricted, but not all variants can be related to climate. The characters used to define the different habits are the portion of the main axis (axes) in which branches develop and the portion which remains simple, the direction of branching, whether the branching is at consecutive or occasional nodes, and the sequence of development of the branches. The various types are illustrated diagrammatically in figs 1 & 2 and are described as follows.

The "Malesianae" type (as in *E. philippinensis*).

This habit type is common to all species of Sect. *Malesianae*, *E. papuana* and *E. culminicola* (together with some specimens of *E. lamii*, which may be conspecific with the latter) of Sect. *Pauciflorae* Subsect. *Pauciflorae* and probably to some South American species. First-year plants are very scarce in collections, but may resemble those in the holotype of *E. merrillii* (Merrill 4720 NY: see Du Rietz 1932b f.5), in which there is apparently a single flower-bearing stem with lateral flower-bearing branches produced from the basal nodes of the plant; subsequently lateral branches probably develop at higher nodes. Most whole-plant material seen is clearly from subsequent years. Arising from their base such plants have several to many main inflorescence-bearing branches along which lateral branches occur sporadically in no fixed sequence. The lack of regular production of aerial branches may be related to the less robust nature of the main axes of these species and the lack of strict seasonal growth in their habitats in the high montane to alpine zones of tropical and subtropical mountains.

The "Cuneata" type (as in *E. cuneata*), fig. 28.

This habit type is restricted to Sect. *Cuneatae* of Australasia and Sect. *Atlanticae* of the Azores. Plants of this type have branches developing in a more or less strict basipetal sequence at consecutive axils from high on an erect inflorescence-bearing axis just below the inflorescence to ground level, just as in the annuals of the northern hemisphere and Australia. Two variations of this type can be distinguished on the abundance of branches developing from the main inflorescence-bearing axes, with the Azorean perennials tending to produce fewer lateral branches; there is a similar divergence in habit between the annuals of Australia and the northern hemisphere. The exact nature of first-year plants of this habit type is as yet unknown. In *E. ramulosa*, however, these plants may at least occasionally consist of a single erect or ascending stem in the first year; this dies back completely, producing several erect or ascending stem-like main axes from the perennating base in subsequent years. Alternatively there may be several main branches developing from the base in the first year, with die-back and subsequent development as in the previous case. Rooting may occur in the very proximal part of the axes. The species with this habit type occupy coastal scrub to subalpine habitats. It is proposed that the habit type is primitive in the genus (p. 53).

The "Paradoxa" type (as in *E. formosissima*).

This habit type is known only in *E. formosissima* (Sect. *Paradoxa*) of the Juan Fernandez Islands. Skottsberg (1921) referred to its unusual habit when he first described the species. The plant consists of a single erect stem with branches developing in consecutive axils and with the stem and lateral branches flowering simultaneously. The number of non-flowering nodes on the branches decreases from the base of the plant, where they have about four nodes, to below the inflorescence, where they lack nodes. The development of the branches is apparently acropetal. This is known in no other perennial of *Euphrasia*, and reflects a common ancestry with New Zealand annuals which also have acropetal development of branches. *E. formosissima* is the only
Fig. 1. Habit types in the perennials of *Euphrasia* (I): the "Malesianae", "Cuneata", "Paradoxae" and "Phragmostoma" types. (Where individual flowers are not shown, inflorescences are densely flowered and represented by their outline; branch remains of prior years are represented by thick lines, those of the current year by fine lines; nodes are shown as fine horizontal lines on the current year's branches.)
species with a means of perennation in which the stem and main branches (possibly after a dormant period) consistently continued to develop leaves and new shoots beyond the inflorescences. The species occurs in montane to alpine zones (Skottsberg 1921).

Fig. 2. Habit types in the perennials of Euphrasia (2): the "Striata", "Humifusa" and "Collina" types. (For explanation of diagrams see fig. 1.)
The "Phragnostoma" type (as in *E. phragnostoma*), fig. 29.

This habit type is confined to a single species in south-east Tasmania. First-year plants are as yet unknown and difficult to envisage. The main inflorescence-bearing axes seen have developed laterally from portions of an older axis from the previous year. These ascending main axes have each developed widely spaced groups of lateral branches, the distal group usually immediately or to 10 nodes below the terminal inflorescence, the next group several to many nodes below the distal one and earlier developed. Development of the branches in each group tends to be strongly basipetal, but occurs over only 2-3(4) consecutive nodes; occasionally, branching is limited to one node only. The more robust of the lateral branches also show development of two widely spaced groups of basipetally produced branches over 2-3 consecutive nodes, and the development of terminal inflorescences. The specimens seen show similar development in the stronger laterals of these branches. Young foliose lateral branches are erect, but the stout axes of previous years growth are procumbent.

The remains of the old axes which the main inflorescence-bearing axes had developed and the main axes themselves show die-back at the terminal growing points. Perennation of the plant is therefore usually by means of vegetative lateral branches. There is occasional reversion of the inflorescence rachis to a vegetative axis but it is not consistent as in the "Paradoxae" type. It is probable that *E. phragnostoma*, by its profuse branching, is one of the largest representatives of the genus. Whether there is any association between climate of the temperate coastal habitat and the initiation of the groups of branches or occasional vegetative growth of the axis after flowering seems worthy of study.

The "Striata" type (as in *E. striata*), figs 37-41, 43, 44, 46, 47, 66, 68, 75-80, 82-84, 87, 89, 100.

The majority of perennials in Australia, east Malesia, New Zealand and Australia have this type of habit, as may some of the South American species. Plants of this type have an erect or ascending stem terminated in the first year by an inflorescence. Vegetative buds are confined to ground level, and branches which are formed are also ascending, or prostrate in the proximal parts (sometimes rooting at the nodes) and distally erect. The habit found in *E. hookeri* (q.v.: note 2; figs 46, 47) is clearly a derivative of this type. Plants of this species are single-stemmed, sometimes with shoots forming at the base. The apparently rare plants over one year old have one to several simple, erect branches developed from ground level. The "Striata" type habit mainly occurs in the montane to alpine zones. For further discussion see p. 12.

The habit typical of *E. collina* ssp. muelleri (fig. 68) is somewhat different. The subspecies has been recorded throughout lowland and montane regions. Its habit resembles the "Striata" type in the confinement of the vegetative shoots to near ground level. Although an occasional branch or young shoot may sometimes develop in the lower half of the main branches above ground level, in many plants the great majority of branches arise from a perennating base composed of many densely clustered young shoots. This compact perennating base is not known elsewhere in the genus and may be a response to the prolonged hot dry periods which are characteristic of Australian conditions. The many young shoots may be dormant and develop only after periods of rain.

The "Humifusa" type (as in *E. humifusa*).

This is a habit type probably derived from either the "Malesianae" or the "Striata" type of habit. The axes are procumbent and root at the nodes, although van Royen (1972) has stated that the inflorescence-bearing axes may be erect in *E. callosa*. The nature of first-year plants and hence the stem is not known. The habit type is confined to and typical of Sect. *Pauciflorae* Subsect. *Humifusae* of alpine and subalpine grasslands (at least of New Guinea; van Royen 1972).
The "Collina" type (as in *E. collina* ssp. *collina*), figs 45, 63, 67, 70, 72-74.

In this habit type first year plants consist of a single erect stem, terminated by an inflorescence and developing branches above ground level in occasional axils with no fixed sequence. At the end of the first season the stem dies back to the upper branches and in the next season further branches develop from this region and below. There is never the perennation from the base of the plant that often occurs in the "Cuneata" type of habit. The "Collina" type of habit is restricted to the perennials of lowland and montane Australia.

The position of the uppermost branches or shoots on the stem relative to its height often differs significantly between taxa having the "Collina" type of branching, as illustrated in fig. 2. For example, the position of branching in the forms of *E. collina* ssp. *speciosa* and ssp. *paludosa* which have the "Collina" type of habit tends to be much lower than in ssp. *collina*. Within *E. collina* ssp. *tetragona*, which has consistently the "Collina" type of habit, there is a geographically based transition in the position of branching, from branching in the upper half of the stem or main branches to branching restricted more to the lower half of the plant (see *E. collina* ssp. *tetragona*: note 2; fig. 69).

The four habit types of the Australian perennials appear to be genetically determined, for they overlap in their climatic tolerances while generally retaining their integrity. There is no evidence of break-down of the localized "Cuneata" and "Phragmostoma" types, which are geographically sympatric with taxa of the "Collina" type.

Many cases of geographical sympatry of taxa with the widespread "Striata" and "Collina" habit types occur in lowland and montane south-eastern Australia, often with no evidence of intergradation. Some taxa, e.g. both ssp. *speciosa* and ssp. *paludosa* of *E. collina*, may have either the "Striata" or "Collina" type of habit. The specimens with the "Collina" type occur only north of Sydney in northern New South Wales.

In addition there are several cases of intergradation between taxa with a different habit type. Thus *E. collina* ssp. *collina* (of montane and lowland regions) with the "Collina" type of habit and ssp. *diemenica* (of alpine and subalpine regions) with the "Striata" type, intergrade in the upper limits of forest and woodland (see *E. collina*: Intraspecific Polymorphism). Similarly, the upper portion of an apparent intergradation between *E. gibbsiae* ssp. *comberi* of the alpine zone and of the "Striata" type of habit and ssp. *kingii* of wet lowland and montane moors with the "Collina" type, has been observed (see *E. gibbsiae*: Intraspecific Polymorphism).

The confinement of the vegetative buds to ground level in the "Striata" type is probably a result of the extreme cold experienced in their natural habitats, and the fact that the ground is somewhat warmer and less variable in temperature than the air or snow above. Plants with this habit are capable of existing at lower altitudes; *E. lasianthera* and *E. collina* ssp. *diemenica*, ssp. *paludosa*, ssp. *muelleri* and ssp. *speciosa* all occur in montane and lowland regions. In contrast, the "Collina" type of habit is absent from areas seasonally under snow. Vegetative shoots are developed above ground level with a resultant increase in height of the plants which may become even greater in successive years and assist the plant in the competition for light in the forests and dense shrubberies with which it is often associated.

4. Indumentum (excluding that on corolla, stamens and ovary which is discussed under each organ)

The distribution, composition, length and density of the indumentum on the axes,
leaves, rachis, bracts, pedicels and outer surface of the calyx are of major diagnostic importance at both the specific and infraspecific level throughout the genus. Hairs of both the glandular and eglandular types are common.

The length of the different types of hairs varies from organ to organ on a plant and also upon the one organ. For example, the glandular indumentum on the rachis and the axis is generally longer than that on the calyx and leaves, respectively, and the indumentum on the calyx shortens towards the base. Therefore, to compare taxa which differ in indumentum length, the length on each particular organ has been described. Rather than make exact measurements of many specimens, the lengths have generally been described in words covering particular ranges as follows: very short (to 0.05 mm), short (0.05-0.1 mm), moderately long (0.11-0.29 mm), long (0.3-0.45 mm), very long (c. 0.45 mm upwards). Where the indumentum length has been particularly important in distinguishing taxa an exact statement of the range of variation has been given for one or two organs, as with the glandular hairs on the outer surface of the calyx or on the axis or leaves of the lower parts of the plant.

The means by which density has been determined is less exact. If the hairs are almost touching or withing a few hairs’ breadth, they are described as dense.

a. Glandular hairs

The presence or absence of glandular hairs (more than 0.05 mm long when on the leaves, bracts and calyces) over all or some of the axis, leaves, rachis, bracts and calyces is of special diagnostic importance in almost every instance, as it is generally found to correlate with other character differences. The terms non-glandular and glandular have been used to describe these character states. These terms do not encompass the corolla, stamens and ovary, as the indumenta of these vary independently (see relevant sections).

The presence of tiny subsessile glandular hairs less than 0.05 mm long is of limited diagnostic use. It is likely that these hairs in the Australian species are identical to the very short ones found sporadically in Sect. Euphrasia of the northern hemisphere. Yeo (1972) attributed to these no taxonomic importance. They differ from the sessile glands which are stalkless and occur in indented patches on the underside of leaves and bracts and on the calyx (p. 25). Subsessile glands are common in all Australian taxa at the base of the clefts between the leaf and calyx teeth and along the narrow grooves which are on the upper sides of the leaves and bracts. Morphologically these hairs are similar to the longer diagnostically important glandular hairs; they differ only in the length and the number of cells of the stalk and in E. collina ssp. paludos a and its allied variants a complete transition can be observed. In the Australian Alps this typically non-glandular taxon (q.v.: note 2) has a sparse to dense cover of subsessile glandular hairs. The presence of a number of populations with glandular and non-glandular plants and the lack of correlation with other varying characters have meant that recognition of the plants with subsessile glands as a distinct taxon above the level of forma is not justified. However, in view of the lack of evidence of intergradation, two subspecies of E. orthocheila have been separated on the presence or absence of subsessile to short glandular indumentum.

b. Eglandular hairs

The eglandular hairs vary in rigidity and length. Length and density characters for weak eglandular hairs are described as outlined previously. However, in the case of plants which are covered on some or all parts by rigid eglandular hairs, another terminology, more descriptive of the nature and length of the indumentum, has been used. Scabrous has been used for such hairs over c. 0.1 mm long (they rarely attain more
than 0.2mm); these occur in *E. scabra* and to some extent in *E. collina* ssp. *muelleri*. *Scaberulous* describes a cover of shorter hairs or sharp excrescences (c. 0.02-0.1mm long), such as are characteristic of *E. ciliolata*, *E. ramulosa* and some individuals of *E. collina* ssp. *muelleri*.

In related taxa with non-glandular upper parts, the presence or absence of an eglandular indumentum on the external surface of the calyx and sometimes also on the bracts and upper leaves may be a character of diagnostic importance. The length and nature of the eglandular hairs may also be characteristic of taxa. Thus *E. crassiuscula* is remarkable, at least amongst the southern hemisphere species, in its indumentum which lines the calyces, bracts and leaves; it consists solely of long woolly eglandular hairs.

The eglandular hairs on the axis and rachis are rarely of taxonomic value. The indumentum usually becomes much sparser lower down the axis except when dense glandular hairs are present on the lower parts. In Australia eglandular hairs may surround the whole axis, e.g. in *E. scabra* and *E. orthocheila*, but more commonly they are confined to two rows or two pairs of lines decurrent from between the leaf bases. In New Guinea *E. humifusa* and *E. callosa* have been separated almost entirely on this character.

c. **Sessile glands** (see p. 25).

### 5. Leaves and bracts

*Bract* has been used for the leaf subtending the flowers of *Euphrasia*, following Wettstein (1896), Joergensen (1919: “Deckblatter”), Du Rietz (1932b; 1948a, b) and others. Others, including Pugsley (1930, 1936) and Sell & Yeo (1970) have used instead the term “floral leaf”.

*Blade* has been used in this work in the special sense of that part of leaf or bract excluding the teeth and, if present, the attenuate part of the base (fig. 3).

In an attempt to give a more precise statement of the shapes of the teeth of the calyces, bracts and leaves, the following method has been found useful (fig. 4). To describe the shape of the tooth overall, i.e. from base to apex, the terms obtuse, acuminate, acute, caudate, etc. have been used as defined in Stearn (1966) and Jackson (1928). This seems more descriptive and precise than methods entailing terms such as triangular. The very apex of the tooth is then described by the terms blunt and sharp (which it is realized are the respective English equivalents of obtuse and acute). Although the use of these characters has been avoided in the keys because the terms describing them could be misinterpreted, they are nevertheless often diagnostic.

Leaf and bract characters are of major importance in distinguishing taxa at all levels in *Euphrasia*. The major characters involved are the overall size and shape, the shape of the base, the number, length and region of distribution of the teeth, the size and shape of
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Fig. 4. Tooth apex terminology for the leaves, bracts and calyx of *Euphrasia*.
the apical tooth, the distribution and pattern of the sessile gland patches on the lower surface, and the indumentum, which has been described in the previous section.

The uppermost leaves and lowermost bracts are similar in all characters except sometimes those of indumentum. In the Australian species and probably elsewhere, there tends to be slight narrowing of the blade and broadening of the base (sometimes accompanied by an addition of an extra pair of teeth) from the lowermost bract down to two or three leaves below the inflorescence. Lower down the leaves gradually shorten and sometimes decrease in the number of teeth. Often correlated with these trends are transitions in the nature of the indumentum. From the lowest bracts to the last-formed ones there is a decrease in size and number of teeth.

To make consistent comparisons between taxa, the characteristics of the bracts and leaves have been described on the basis of a detailed analysis of the uppermost pair of leaves on the main inflorescence-bearing axis of the plant. The indumentum characters of the bracts and lower leaves are also often described by a comparison with the detailed description of indumentum of the uppermost leaves. A series of figures (figs 5-12) showing the size and shape of uppermost leaves on the main inflorescence-bearing axes of almost all Australian taxa is supplied. Where possible a sample from a population is displayed. If representative collections of a taxon were few, only one or two leaves were removed for display.

A number of very distinctive leaf and bract shapes are often of diagnostic importance at a sectional and subsectional level. They involve the size of the blade (defined above) relative to that of the whole leaf, and the shape of the base. Illustrations of extra-Australian types are found in Wettstein (1896: northern hemisphere including Japan and the Azores, New Zealand, South America), Du Rietz (1932b: Malesia), Ashwin (1961: New Zealand) and van Royen (1972: New Guinea). The most widespread, though only sporadic, type is the long attenuate leaf with a prominent blade; it characterizes the sections Cuneatae (fig. 5), Phragmostomae (figs 5, 30) and Paradoxae, some species of Sect. Pauciflorae (E. papuana), Sect. Malesianae and Sect. Euphrasia, and E. bella of Sect. Australes (fig. 6). A prominent blade with a short abruptly attenuate base is typical of Sect. Atlanticae and the remaining majority of species of Sect. Euphrasia and Sect. Malesianae. Du Rietz's (1948a) "subdigitate-toothed" and "digitate" leaf types are confined to the southern hemisphere. These have narrow attenuate leaves which comprise largely prominent teeth through the small size of the blade. Such types are characteristic of Sect. Trifidae, Sect. Anagosperrmae, mainly the New Zealand members of Sect. Pauciflorae and Sect. Striatae. Deeply trifid leaves are typical of the first two sections, but E. integrifolia (Sect. Anagosperrmae) has lost the lateral pair of teeth. Sect. Striatae (figs 5, 6) and the New Zealand members of Sect. Pauciflorae have a larger blade, and often more teeth. E. hookeri of Tasmania (figs 6, 31, 47) is remarkable for its many digitate teeth and (see below) their greatly recurved margins, which are the basis for retention as a monotypic series in Sect. Striatae. A curious leaf shape is typical of most New Guinea species (Sect. Pauciflorae); the leaf is dominated often for half its length by a hooded apex and the lateral teeth are all but lost.

Finally, the only non-attenuated leaf bases are found in Australia and characterize the sections Australes, Lasiantherae and Scabrae (figs 6-12). The leaf is composed mainly of blade through the cuneate, rounded or truncate base. Narrowly cuneate types outside Australia are extremes of variation in species with attenuate leaf bases.

The difference in the form of the cuneate to truncate leaf base among the Australian members of Euphrasia seems to be directly related to the nature of vascular system of the leaf at its very base. These non-attenuated types have 3-7 vascular strands arising from the base. Even taxa with narrower leaves, such as E. collina ssp. collina, may sometimes have 5 vascular strands arising from the base. In other Australian species, i.e.
Fig. 5. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of *Euphrasia* in Australia (1).

### Sect. *Cuneatae*

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### Sect. *Phragmostomae*

2. *E. phragmostoma*

- Bufton 7
- Bufton 8

### Sect. *Striatae*

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Fig. 6. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of *Euphrasia* in Australia (2).
Fig. 7. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of *Euphrasia* in Australia (3).

11a-b. *E. collina* ssp. *collina*-ssp. *diemenica*

Barker 1138  Barker 1146  Barker 1147

11b. *E. collina* ssp. *diemenica*

Barker 1141

Barker 1122

Barker 1079  Barker 1080

Barker 1078  Barker 1105

11d. *E. collina* ssp. *tetragona*

Barker 1450  Donner 186

Barker 1355

Barker 1374  Eichler 15384

11e. *E. collina* ssp. *trichocalycina*

Barker 1432  Barker 1438  Barker 1442

*Studies in Euphrasia*
Fig. 8. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of Euphrasia in Australia (4).

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Fig. 9. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of *Euphrasia* in Australia (5).

(Sect. Australes: *E. collina*, cont.)

111. *E. collina* ssp. *speciosa*

- Barker 1630
- Helms NSW10901
- Constable NSW48942

11m. *E. collina* ssp. *osbornii*

- Barker 854
- Barker 861
- Barker 862
- Barker 869
- Barker 1346
- Barker 1729
- Ising AD9622007
- Eichler 14452
- Hunt 3315
- Whibley 1278
- Whibley 4155

11n. *E. collina* ssp. *diversicolor*

- Barker 1684
- Barker 1704
- Barker 1703
- Barker 1702
- Barker 1701
- Barker 1677
- Barker 1663


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Fig. 10. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of *Euphrasia* in Australia (6).
(Sect. Australes: E. crassiuscula, cont.)

12b. *E. crassiuscula* ssp. glandulifera

![Image of leaves]

Barker 1596

12c. *E. crassiuscula* ssp. eglandulosa

![Image of leaves]

Barker 1572

Barker 1593

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![Image of leaves]

Barker 1498

14. *E. eichleri*

![Image of leaves]

Eichler 14825

15. *E. alsa*

![Image of leaves]

Barker 1696

Barker 1707

Sect. *Lasiantherae* x Sect. *Scabrae*

15 x 16. *E. alsa* x *E. caudata*

![Image of leaves]

Barker 1697

Fig. 11. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of *Euphrasia* in Australia (7).
### Sect. Scabrae

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<td></td>
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<td>Barker 1649</td>
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<tr>
<td><strong>17. E. scabra</strong></td>
<td>Ashby 4354</td>
<td></td>
<td>Mueller MEL41609</td>
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<tr>
<td><strong>18a. E. orthocheila ssp. orthocheila</strong></td>
<td>Beckler MEL41595</td>
<td>Crawford 19</td>
<td>Boorman NSW10878 Collie MEL41643</td>
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<tr>
<td><strong>18b. E. orthocheila ssp. peraspera</strong></td>
<td>Heron NSW10880</td>
<td>Wilcox MEL41718</td>
<td>Wilcox MEL41589</td>
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<tr>
<td><strong>19. E. arguta</strong></td>
<td>Woolls MEL41394</td>
<td>Crawford MEL41756</td>
<td>Musson MEL41397</td>
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<tr>
<td><strong>20. E. ciliolata</strong></td>
<td>Pullen 3792</td>
<td>Pulley 705</td>
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Fig. 12. Uppermost leaves, actual size dried, of main inflorescence-bearing axes in taxa of *Euphrasia* in Australia (8).
E. bella of Sect. Australises and commonly Sect. Striatae, there are only three main vascular strands arising from the base. In leaves with very shortly attenuate leaf bases abruptly expanded into the blade, the lateral pair of main strands may be branched a short distance from the base. In the long attenuate types the three strands may remain simple for their whole length or branch towards the base.

The adaptive significance to parasitism of the patches of sessile glands on the lower surface of the leaves and bracts has been alluded to on p. 5. The distribution and pattern of the patches are novel characters which have been found to be of diagnostic importance in some instances in Australia. An extended, more critical study elsewhere in the genus may show further examples of differences between taxa. The sessile glands (not be confused with the very shortly stalked subsessile glandular hairs: p. 13), occur on the lower surface in dense patches always in rows parallel to and just inside the margins; these rows are branched sporadically on their inner margin, the lateral extensions being short or very long, and are generally confined to the areas between the main veins of the leaf.

In E. hookeri (Sect. Striatae) the sessile gland patches on the lower leaf surface are hidden from view as a result of the extreme recurvature of the teeth margins (fig. 31K).

Whether the sessile glands occur towards the base of the leaf is related to the distribution of the teeth along the leaf. Except when the leaf teeth are very reduced (as they often are in the New Guinea species), sessile glands are always distributed along the margins from the apical tooth at least as far as the extent of the laterally toothed parts of the leaf. Thus if the leaf teeth reach the base of the leaf, as in the Australian cuneate to truncate-based leaves, so do the sessile glands. However, if the teeth are confined to the distal half of the leaf (e.g. in E. collina spp. collina), the sessile glands may extend along the margins well below the teeth and onto the lower half, but never to the base. In species with attenuate leaf bases the sessile gland patches hardly (if at all) extend onto the attenuated region.

The pattern of the sessile glands on the lower surface has been used in E. collina to distinguish ssp. diemenica, the sessile glands of which are almost entirely confined to the marginal rows except for very short lateral branches (fig. 48E), from other subspecies which have long lateral extensions of the marginal rows of glands (fig. 48D). Ssp. collina shows a transition in these same differences in pattern of the sessile glands. This appears correlated with a geographical cline in leaf shape, discussed on p. 179. Its south-eastern Tasmanian populations have a pattern of sessile gland patches and short leaf teeth similar to ssp. diemenica; the populations in the Grampians, however, approach ssp. paludosa in these characters. In Australia the sessile glands in the annuals and some densely glandular hairy perennials are apparently distributed over wider areas of the lower leaf surface than in the non-glandular hairy perennials.

Outside Australia the pattern of sessile glands on the leaves of Euphrasia is a character of potential taxonomic value. E. cuneata (Sect. Cuneatae), Sect. Phragmostomae and Sect. Paradoxae have very distinctive, reticulately patterned sessile gland patches. Yeo (1973) has indicated that Sect. Atlanticae is unique in the genus by the confinement of the sessile glands to the veins of the lower leaf surface as in related genera in Trib. Rhinantheae (p. 79).

6. Inflorescence

The arrangement and number of flowers is of importance in the infrageneric classification of Euphrasia. Throughout the genus the flowers develop acropetally along the axes. In most of the genus the flowers are arranged decussately in racemes. Both
flowers at one node usually develop simultaneously, but in certain conditions, such as where plants grow from the side of a dense shrub, development may be much earlier or possibly confined to the outward-facing side. Whenever plants of *Euphrasia* are completely prostrate (Sect. *Pauciflorae* Subsect. *Humifusae*, partly Sect. *Anagospermae*), flowers are distributed sporadically along the axes with usually one flower only at a node. However, the erect to ascending axes of Sect. *Malesianae* are terminated by racemes, which are sometimes interrupted by the absence of flowers from some nodes as well as sometimes having only one flower at a node.

In perennials transformation on the one axis from inflorescence to leaf-bearing and again to inflorescence occurs rarely in *E. gibbsiae* ssp. *kingii* (Sect. *Striatae*) and *E. phragmostorna* (Sect. *Phragmostomae*). Yeo (1964) has also seen this phenomenon in the annual *E. pseudokerneri* of Sect. *Euphrasia*, and has linked it with abnormal temperature fluctuations. In *E. formosissima* (Sect. *Paradoxae*), however, this apparently occurs regularly (Skottsberg 1921) as the means of perennation (p. 10).

The number of flowers has been used to separate Sect. *Pauciflorae* from Sect. *Striatae* and in Australia to distinguish species and subspecies. In the Australian annuals there is a correlation between the number of flowers in the main inflorescence and the climatic range of the species in parallel with other character trends (table 1). The number of flowers produced may be linked to some extent with the relative robustness of the species and hence the capacity to maintain the production of flowers. This is possibly applicable throughout the genus.

Pedicel length shortens acropetally in the inflorescence. Although not of major diagnostic importance in the genus in Australia, pedicel length is useful in separating *E. bella* and *E. bowdeniae* of Sect. *Australes*, and some New Zealand species.

Except in plants with very few flowers, the buds and bracts of the young inflorescence are generally crowded together at the tip of the axis in what has been termed in this work the *apical bud cluster*. In most of the genus this is broadly ellipsoid or ellipsoid-ovoid to spherical in shape. However, in the Australian species there is a wide variation in the number of flowers produced and there is some variation in the shape and degree of exsertion of the apical bud clusters from the uppermost flowers. Two types of bud cluster are discernible which have been given diagnostic importance in the past by Wettstein (1896), Curtis (1967) and Burbidge (Burbidge & Gray 1970); whether the differences have any genetic basis, however, is open to question. In the alpine species the apical bud clusters are short and broad and soon after flowering commences become hidden in the uppermost flowers of the inflorescence (e.g. figs 44, 66, 80) This inflorescence type has been termed "capituliformis" (Wettstein 1896; Du Rietz 1948a) or "capitata" (Wettstein 1896; Curtis 1967). In the lowland and subalpine members of *E. collina* the apical bud cluster in narrowly cylindrical or narrowly conical and remains extended above the upper corollas after the flowers at many nodes (sometimes over 20) have matured (e.g. figs 71, 73, 74). This inflorescence type has been termed "elongata" (Wettstein 1896), "spiciformis" (Du Rietz 1948b), and "conica[1]" (Wettstein 1896; Curtis 1967). In the past the character has been used particularly in separating the taxa now grouped under *E. collina*. It is considered that the variation may be an environmental response, particularly as the two types have never been observed to grow together. In addition, two subspecies have both character states. Ssp. *paludosa* is normally characterized by a narrowly subconical apical bud cluster, but in the highest parts of its range (e.g. on Mt Speculation, Victoria) it may have apical bud clusters of the other type. Ssp. *diemenica* typically has the short, broad type of cluster, soon hidden by the upper flowers. However, montane and even subalpine occurrences may have conical apical bud clusters. Because of this uncertainty about the genetic basis the variation, the initial shape and subsequent development of the apical bud cluster have been described in detail, but have not been used in the keys.
7. Calyx

The structure of the calyx is essentially the same throughout the genus. There is variation in size and the depth of the lateral and median clefts (the divisions between the teeth); these are of some diagnostic importance at the specific and infraspecific level. The shape of the apex of the teeth and the degree of recurvature of the margins tends to be associated with analogous characters in the uppermost leaves and bracts, although the recurvature in the calyx is not as marked as in the leaves. A special terminology, devised to describe the shape of the teeth, is discussed on p. 14.

The indumentum on the outer surface of the calyx is of major diagnostic importance. Its nature is closely related to that of the bracts, rachis, leaves and axis and is discussed under the general treatment of indumentum.

8. Corolla

The shape, size, colour and its distribution and indumentum are of diagnostic importance at various levels of classification.

a. Shape and size

The shape of the corolla is useful in separating only more distantly related sections and subsections for generally closely related infrageneric taxa are connected by a series of gradually changing forms of corolla.

The type of corolla characteristic of Sect. Euphrasia, as illustrated in Wettstein (1896, pl. 2), is the basic type which occurs throughout much of the range of distribution of Euphrasia (figs 30, 31, 37, 42-44, 47). Corollas of this type are two-lipped, with the tube directed obliquely away from the axis; the tube is cylindrical in the basal parts and distally expanded laterally and ventrally. The upper lip is hooded and more or less porrect with the lobes recurved sharply so that they are directed upwards and approximately lie in the same plane (i.e. they face forward). The lower lip spreads from its base away from the base of the upper lip; it is concave from above at its base.

In the southern hemisphere there are a number of corolla types divergent from this basic form. In Australia the corollas of Sect. Scabrae (figs 91, 95) are the most divergent. They are characterized by a porrect flat lower lip which lies against or hardly spreads from the upper lip (except in E. caudata in distal regions). The lower side is broadly grooved and flat or slightly convex from above. Except in E. caudata, the upper lobes are sharply reflexed, but are at a sharp angle to each other because they are more or less appressed against the side of the hood. The corollas of Sect. Lasiantherae (figs 17, 85, 87, 90), E. collina (figs 63, 66, 70, 71, 74, 77-80) and possibly E. bowdeniae and E. bella of Sect. Australes and E. caudata are intermediate between those found in the rest of Sect. Scabrae and the basic type. In these the upper corolla lobes are directed forward and lie in the same plane and the lower lip, although initially porrect, is spreading in the distal regions. The lower side is flat and sometimes broadly grooved. Sometimes, however, the lower lip and tube may be concave from above. Study of living material is required to verify these differences.

In the New Guinea perennials (Sect. Pauciflorae) and the New Zealand annuals of Sect. Anagosperrmae (fig. 18) the corolla tube is sometimes very long relative to the two lips. However, except in E. disperma of the latter section and possibly E. scutellaroides of Sect. Pauciflorae, plants with a relative tube length more typical of the genus occur in each of the species.

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The corolla of a number of New Zealand species shows some tendency to a more regular arrangement and equality in size of the lobes with the corolla rim facing upwards; this may relate to the low stature of plants and a likelihood of pollinators detecting the flowers from above, as is proposed for the Australian Mimulinae (Barker, in press).
Finally, Sect. *Trifidae* of South America diverges from the rest of the genus by the production of some remarkable corolla types. Some species, e.g. *E. antarctica* (Vallentin & Cotton 1921, pl. 45), differ very little from the basic corolla shape, although, by the arrangement and equal size of the upper and lower lobes, the corolla appears almost regular when viewed from the front (Wettstein 1896, pl. 6 f. 472,473). However, in *E. chrysantha* and *E. flavicans* the lower corolla lip is abruptly reflexed so that the corolla lobes are in the same plane, and *E. meiantha* (Wettstein 1896, pl. 6 f. 482) has a very long porrect hood and a minute lower lip reflexed from its base. Corollas in this section show the greatest divergence from the basic type and the greatest diversity.

A character sometimes important at all levels of classification is the shape of the corolla lobes. Sect. *Euphrasia*, Sect. *Atlanticae* (ex Wettstein 1896), Sect. *Malesianae* and Sect. *Pauciflora* Subsect. *Humifusae* of the northern hemisphere and tropics always have emarginate lobes. Throughout the remainder of the genus in the southern hemisphere, including Sect. *Pauciflora* Subsect. *Pauciflora* in New Guinea, the lobes vary from obtuse to emarginate, sometimes even within populations; occasionally, however, a species or subspecies may be characterized by consistently emarginate lobes.

In the Australian revision differences in shape and size of the corolla and its parts have been measured using a range of diagnostic parameters (fig. 13): the length along the upper side (i.e. excluding the lobes), the length of the tube from the base of the corolla to the point of insertion of the anterior filaments, the length of the hood (upper lip), the breadth of the hood (including and excluding the lobes), the length and breadth of the

![Fig. 13. Definition of the corolla parts of *Euphrasia* measured.](image-url)
lower lip and the depths of the clefts between the upper and lower lobes. All are of diagnostic value. Measurements were taken from the lowermost flowers of the main inflorescence, which had been fixed in the field in FAA and transferred to 70% ethanol, or taken from herbarium specimens and boiled in a weak detergent solution, or well-pressed and untreated. There seems to be little difference in corolla size in pressed as compared with fixed or boiled material.

b. Ground colour

The "ground colour" of the corolla (i.e. excluding striations and yellow nectar guides) is of limited diagnostic value, at least in Australia. It is useful, however, for separating the yellow-flowered species of Sect. Scabrae, Sect. Novaezeelandiaceae and apparently Sect. Trifidae from related species with corollas with a ground colour of white to purple or violet. In Sect. Euphrasia the presence of a yellow corolla is apparently not diagnostic at the species level (e.g. *E. minima* Jacq. ex DC.; Pugsley 1930, Yeo 1972). Ground colour in the Australian species, when not yellow, may vary from white to maroon, pink, violet or blue. A particular taxon may vary through all or part of this range, and may show different ranges of variation in different geographical regions. Elsewhere in the genus the ground colour is usually white, although sometimes lilac or purple corollas may occur. This is sometimes diagnostic at the species level in Sect. Euphrasia (Yeo 1972).

c. Coloration

Corolla coloration in *Euphrasia* has received little attention in past classifications in the genus. General reference to a basic type of coloration involving purple to violet-striped corollas with yellow blotches in the tube and at the base of the lower lip (e.g. fig. 31) have been made by Ashwin (1961), Yeo (1968) and van Royen (1972) for New Zealand species, the northern hemisphere annuals and New Guinea species, respectively. From my field observations of taxa in Australia, New Zealand and, to a limited extent, New Guinea, and from colour photographs, specimen annotations and well-preserved herbarium material of taxa elsewhere, it is clear that there is wide variation in the pattern and extent of both blotches and striations on the corolla, which is of potential diagnostic importance at a specific and infraspecific level.

In the following, reference to published illustrations is given, apart from Sect. Euphrasia, of which there are many sources, and usually Salmon (1967) and Mark & Adams (1973), which give a large cover of the New Zealand species. A photograph or painting is rarely sufficient to give all details of corolla coloration. For example, that of the rear of the lobes is rarely shown. It is vital that collectors record such characters in as much detail as practicable.

Geographically, the most widespread expression of the corolla striations is that usual in the northern hemisphere annuals, Sect. Lasiantherae and most species of Sect. Striatae of Australia (figs 17, 31, 37, 42, 44, 47, 85, 89, 90), Sect. Cuneatae of Australasia, in Sect. Paradoxeae (Skottsberg 1921, pl.20), *E. cheesemanii* of Sect. Novaezeelandiaceae, and *E. borneensis*, the sole known record for Sect. Malesiaceae (Stapf 1894). This consists of 3(5) purple or violet striations on each lobe, those of the upper lip extending from the hood; they are most prominent on the outer face of the upper lobes and the upper face of the lower lip.

In Sect. Striatae of Australia the limited extension of the striations onto the lower lip in *E. gibbsiae* ssp. pulvinestris (fig. 43) and *E. semipicta* is diagnostic. Some specimens of *E. semipicta* may completely lack striations.

Complete absence of striations is sometimes a sectional characteristic, as in Sect. Phragnostomatan, Sect. Australes and Sect. Scabrae of Australia (figs 63, 66, 70, 71, 74, 77-80, 95). In the New Guinea species (Sect. Pauciflorae) the fine purple striations on
the hood are replaced by a suffusion of purple throughout (personal observations in *E. mirabilis*, *E. humifusa* and *E. callosa*). The corolla of *E. papuana* also lacks prominent striations (Mr P. Kores, pers. comm. 1976).

In New Zealand, the three sections other than Sect. *Cuneatae* show divergence from the basic form of striations. *E. disperma* (Sect. *Anagospermae*) and *E. cheesemanii* (Sect. *Novaezeelandiae*) show the basic type. However, in many species the striations, if present at all, are prominent on the hood, rear surface of the upper lobes and the rear or lower surface of the lower lip, as strikingly portrayed by the 3 prominent striations on each corolla lobe in *E. townsonii* (pers. observ.). A number of New Zealand annuals, e.g. *E. zelandica*, *E. dyeri*, and possibly *E. repens*, often have a broad purple streak along the midline of the outside of the hood. *E. integrifolia* rarely has a finer streak along the edge of the hood on either side of the central streak (pers. observ.). In this species the lower lobes also have a single purple to indigo streak, on the rear or lower side only.

Sect. *Trifidae* of South America may also diverge from the basic form of corolla striation. *E. antarctica* has a single purple striation down the midline of the upper side of each of the lower lobes (Vallentin & Cotton 1921, pl. 45; Skottsberg 1913).

The other feature of the basic coloration type is the yellow blotches, which occur at the base of the lowest lip and in the tube at the base of each anterior filament. Such coloration occurs in all cases known to the author in the northern hemisphere annuals (Yeo 1968, 1972; Sell & Yeo 1970), in the New Zealand and New Guinea species, in Sect. *Paradoxa* of Juan Fernandez Islands (Skottsberg 1921, pl. 20), at least *E. antarctica* of Sect. *Trifidae* of South America (Vallentin & Cotton 1921, pl. 45), and Sect. *Phragmoostomae*, Sect. *Cuneatae* and Sect. *Striatae* (e.g. figs 31, 37) of Australia. There is variation in the size and shape of the blotch which may prove to be of some diagnostic importance. In particular, in some New Zealand perennials of Sect. *Pauciflorae*, e.g. *E. revoluta* and *E. townsonii*, the yellow blotches are continuous and extend well back towards the base of the tube. In *E. dyeri*, *E. integrifolia* and *E. disperma* of Sect. *Anagospermae* the tube is yellow throughout. In *E. disperma* occurs an apparently unique character of a yellow patch on the upper lobes bordering the dividing sinus. As remarkable is the ring of deep brown-purple at the base of the corolla tube of an undescribed taxon allied to *E. townsonii* in the Tasman Mts, New Zealand (pers. observ.).

The species of Sect. *Euphrasia* Subsect. *Alpicola* of Japan have the normal distribution of yellow blotches, but have a distinctive and possibly unique deep purple blotch on either side of the hood just above its base and also at the base of each anterior filament (Pugsley 1936; Yamakei Color Guide 1967, p. 40; Takeda 1959, pl. 65, n. 35, 36). Subsect. *Japonica* has the normal yellow blotch on the lower lip (Takeda 1959, pl. 65, n. 34).

In Sect. *Lasiantherae*, Sect. *Australis* and Sect. *Scabrae* of Australia, most taxa have the basic yellow markings. In the first section, *E. alsa* conforms in this way but *E. lasianthera* (fig. 85) lacks the yellow blotch behind the lower lip, but the small yellow blotches, one at the base of each anterior filament and distinctly demarcated and highlighted by the radiating striations, occupy a central position in the open-mouthed flower. The geographically and morphologically intermediate *E. eichleri* may be polymorphic in these features (p. 256). In Sect. *Australis*, *E. collina* is variable in the presence or absence of yellow blotches. The alpine subspecies, ssp. *diversicolor* (figs 77, 78), ssp. *lapidosa*, and ssp. *glacialis* (fig. 80), and the lowland ssp. *tetragona* (fig. 70) consistently have a yellow blotch on the lower lip and two others deep in the throat (sometimes the blotches are continuous). The yellow blotches are apparently completely lacking from ssp. *deflexifolia* and possibly ssp. *speciosa*. In a number of other subspecies the incidence of a yellow blotch behind the lower lip is varied. It is usually present in ssp. *collina*. Presence and absence vary on a geographical basis in ssp.
osbornii (p. 221) and on an ecotypic basis in ssp. diemenica (p. 185). In Sect. Scabre the nectar guide on the lower lip of at least *E. caudata* (figs 91, 95) and possibly *E. ciliolata* consists of a yellow to red streak down the middle of the lower lip, a character possibly unique in the genus.

d. Corolla indumentum

The distribution, length and density of the indumentum on the inner and outer surfaces of the corolla, and the composition of the indumentum on different parts of the corolla, in relation to whether or not both glandular and eglandular hairs are present, are variable and furnish characters of diagnostic importance at the level of species and below. The density and length of the glandular and eglandular hairs are described in the terms used for indumentum on the calyx, bracts, rachises, leaves and axes (see p. 13).

Consistencies seen in the corolla indumentum of the Australian species are: the dense eglandular indumentum on the outer surface of the hood extending to a greater or lesser extent onto the tube; the small or large patch of glandular hairs on the outer surface extending from the region about the lateral clefts towards the point of insertion of the anterior filaments; the dense patch of long eglandular hairs on the inner surface of the hood at the base of the sinus (or cleft) between the two upper lobes; and the glabrous nature of both the inner and outer surfaces of the very base of the tube.

The above regions of the corolla may vary in the incidence of other hair types not cited. In all other regions the indumentum is variable in its incidence and composition. Of particular diagnostic importance are: the presence or absence of an indumentum on the external surface of the lobes (for the lower lobes best seen in mature buds); the presence or absence of an indumentum on the inner surface of the tube; the presence or absence of hairs lining the margins of the lobes; and the presence or absence of hairs at the base of the lower lip.

The indumentum of the corollas of the extra-Australian members of the genus has not been investigated. Sell & Yeo (1970) mention that the inner surface of the throat is "papillose-hairy", presumably on the basis of their combined experience of Sect. Euphrasia of North America and Europe.

9. Androecium

In most species of *Euphrasia* the arrangement of the stamens is very constant. The stamens are didynamous. The anthers are fused along their narrowest sides in a U-shaped configuration, with the two posterior anthers quite free from each other, but connected with the two anterior anthers, which are themselves fused. The cluster of anthers is enclosed in the hooded upper lip and the anther awns project from the base of each cell into the mouth of the corolla. The rearmost pair of awns projects further into the mouth than the other awns as it is situated closer to the lower lip (being nearest the join of the two lips) and is longer than the other awns. Sect. Trifidae and *E. disperma* (Sect. Anagrospermae) are the only exceptions to this. In both, the anthers are free. In *E. disperma* (fig. 18) and some species of Sect. Trifidae the anthers occur at different levels and still lie against or under the hood. However, in other members of Sect. Trifidae the anthers are at the same level and are exserted from the corolla.

The length and indumentum of both the anterior and the posterior filaments, the length, breadth and indumentum of the anthers (excluding the awns), and the length and shape of the rearmost pair of anther awns have been described for all species (fig. 14). All except the indumentum of the filaments have been found to be of diagnostic importance, some more so than others.

Measurements of the stamens have been taken from the lowermost flowers of the main inflorescence. There is some decrease in size of the filaments and anthers in
successively formed flowers, but even when the anthers are much smaller than those in the lowermost flowers, the rearmost pair of anther awns apparently remains the same length (see p. 170).

![Fig. 14. Definition of the anther parts of *Euphrasia* measured. (a = anther length; b = anther breadth; c = awn length.)](image)

In the species with fused included anthers, the length of the two sets of filaments seems directly related to the length of the hood. These characters usefully distinguish related species in several cases.

The size of the anthers is also diagnostic at the specific and infraspecific level. The length of the anther is measured from the apex to the point where the awns arise (fig. 14), which is taken to be the point on the outward-facing surface of the anther where the colour abruptly changes from the light brown, orange or deep purple of the main body of the anther to the white or yellow of the awn (this is slightly higher than the actual point where the attenuation begins).

The anther awns of *Euphrasia* are with one exception alike in morphology. They are usually very narrow and sharp (figs 31, 48, 85, 91). However, the posterior awns of *E. phragnostoma* are remarkable, not only in their extreme length but also in the broadened and sometimes twisted or erosulate tip (fig. 30).

The length of the rearmost pair of anther awns has been found to be of diagnostic importance at the specific and infraspecific level throughout the genus in Australia. The length appears in some cases to be independent of the size of the corolla, measured, for example, by the length of the upper and lower lips. Thus, in similarly sized corollas in ssp. *paludosa*, ssp. *collina* and ssp. *diemenica* of *E. collina*, the length of the rearmost awns in the first is significantly shorter than in the other two subspecies. In other cases, however, such as in Sect. *Lasiantherae*, corolla size is correlated with awn length.

As pointed out by Du Rietz (1932b, 1948b), Bentham (1846) was incorrect in describing the anther awns of all southern members of the genus, except *E. cuneata*, as being equal. Du Rietz (1932b, p. 530), however, considered that “subequally mucronate” anthers were found in apparently all the South American species (Sect. *Trifidae*), all species now belonging to Sect. *Anagopramae*, *E. monroi* and *E. papuana* now in Sect. *Pauciflorae*, *E. striata* now in Sect. *Striatae*, and *E. merrillii* now in Sect. *Malesianae*. In no case, however, have I seen any taxon which consistently has equal anther awns. In some taxa the difference in length may be only slight, but it nevertheless exists. The possible loss of function of the longer rearmost anther awns in the taxa with free anthers, *E. disperma* and Sect. *Trifidae* is discussed on p. 46.
The indumentum of the anthers is of major diagnostic importance. Throughout most of the genus the anthers are completely glabrous but for dense hairs which line the slits of the inner surface (e.g. fig. 31). However, Sect. Australes, Sect. Lasiantherae (fig. 85) and Sect. Scabrae (fig. 91), which are confined to Australia, have a distinctive anther indumentum. Not only are the dehiscence slits lined by hairs which are probably longer and denser than anywhere else in the genus, but the anthers are almost always hairy on the outer surface. This indumentum on the outer surface is composed of straight or flexuose eglandular hairs identical to those occurring along the slits. It is usually very dense and long, but sometimes sparse and short, as occasionally in *E. collina* ssp. *glacialis* or on the anterior pair of anthers of the annuals. On rare occasions in some taxa, for example *E. scabra* and *E. collina* ssp. *lapidosa* and ssp. *diemenica*, the anthers may be completely glabrous on their outer surface.

In some New Zealand sections and those of the Juan Fernandez Islands and South America, there is a trend towards the complete loss of hairs from the anthers. Sect. Trifidae and *E. disperma* (Sect. Anagosomeae) have completely glabrous anthers. Although no anatomical studies have been made, it seems certain that the loss of fusion of the anthers is linked with the loss of the hairs lining the uppermost parts of the dehiscence slits (see Hartl 1972). Sect. Paradoxae, Sect. Novaezeelandiae and the other species of Sect. Anagosomeae link that part of the genus characterized by hairy anther slits with Sect. Trifidae with its completely glabrous anthers. *E. formosissima* (Sect. Paradoxae) has fused anthers which bear a few hairs within the slits. The anthers of Sect. Novaezeelandiae are also fused, but show a transition from the type with densely hairy slits (*E. cockayniana, E. cheesemanii*) to very sparsely hairy slits (*E. australis, E. zelandica*) as seen in Sect. Anagosomeae apart from *E. disperma*. This may relate to their reliance on a wide array of pollinators (p. 44).

10. Gynoecium

The few characters of the gynoecium which show variation in *Euphrasia* are the indumentum of the ovary, the ovule number, and the shape and size of the stigma. Although the shape of the capsule varies considerably, the shape of the ovary seems to show little variation.

The indumentum of the ovary is identical to that on the capsule and is discussed in the treatment of the latter.

The size of the stigma is of great importance at the sectional level as it is the one character which divides the northern members of the genus as a whole from all southern members. In the tropics it separates Sect. Malesianae from Sect. Pauciflorae. Care should be taken in measurements from flowers in which fertilization has taken place as the stigma soon shrivels. Although sometimes appearing capitate, the stigma is probably always bilobed with the lobing often obscure through its shortness or reduction of the upper lobe.

The number of ovules has been found to be of diagnostic importance at the level of species and below. In the Australian annuals there is an increase in ovule number as the climatic preferences of taxa change from alpine through subalpine to montane and lowland (table 1). The significance of this is discussed under the treatment of seeds.

The number of seeds rather than ovule number appears to have been used as a diagnostic character by previous workers in the genus (Wettstein 1896; Pugsley 1930, 1936). Du Rietz (1932b) found that *E. borneensis* differs from *E. philippinensis* and *E. merrillii* by its fewer ovules and seeds, but in discussing the relationships of the Philippines species with those of Taiwan, Japan and Norway, he compared seed numbers. This is probably because Takeda (1910), Nakai (1913) or Joergensen (1919) did not consider ovule number. The use of seed number as a diagnostic character is
questionable as the variation in it is not only determined by the number of ovules. Within the Australian species there is great variation in the proportion of ovules which develop into mature seed.

The number of ovules seems to be of particular diagnostic importance in the New Zealand annuals (Ashwin 1961: Sect. Novaezeelandiae and Sect. Anagosermae). There is apparently a progressive reduction in ovule number in these species as the habit becomes more procumbent and the corolla lengthens, with E. disperma with its single ovule per cell (see Simpson 1977), prostrate habit and extremely long corolla tube forming a possible endpoint of an evolutionary sequence (see p. 55). Counts of ovule number are too few, however, to be certain of this trend (Ashwin 1961). From a few samples of ovule number in each section it seems that the Australian species may have the highest numbers in the genus.

11. Capsules

The indumentum, size and shape of the capsule in lateral view are of diagnostic importance, usually at the level of species or below, but sometimes at the level of section or subsection.

Measurements have been made on the capsules at the lowest nodes of the main infructescence. Capsule size is often greatly reduced higher up the rachis. The last capsules formed are usually well below the last-formed flowers.

Apart from the remarkable bicornute capsules which occur in single species of Sect. Atlanticae (Pugsley 1936; Yeo 1973) and Sect. Anagosermae*, the capsule shape varies within rather narrow limits. The shape of the capsule is a product of the shape in lateral view, the median view apparently being consistently ovate to elliptic and usually caudate or acuminate. Capsule shape has been described excluding the base of the style which persists on the capsule summit.

Although there is not a great diversity of capsule shapes in the genus, apparently no section or subsection encompasses the whole range of variation. Broadly obovate or obcordate capsules occur throughout Sect. Pauciflorae Subsect. Humifusae, Sect. Novaezeelandiae and apparently Sect. Trifidae. The species of Sect. Anagosermae without the bicornute capsule are probably also of this type, although little fruiting material is available. Sect. Cuneatae, Sect. Malesianae and Sect. Pauciflorae (especially the New Guinea species) have some species with capsules of this type, and others (e.g. E. merrillii and E. lamii) which are oblong with obtuse to emarginate apices. Australian members of the genus and Sect. Paradoxaes of the Juan Fernandez Islands have oblong to ovate-elliptic capsules. In the latter the apex is obtuse to shallowly emarginate. However, the former shows a wide variation, some Australian taxa having oblong capsules with shallowly emarginate apices (fig. 31G), others narrowly ovate to ovate-caudate capsules with obtuse to acute apices (figs 48, 85). Most, however, fall between these extremes. Although capsules of only a few species in Sect. Euphrasia have been seen, it appears that the broadly obovate type of capsule is absent.

Du Rietz's (1932b, 1948b) notion of an "acuminate" type of capsule, which he considered to be restricted to and consistent throughout the Australian and South American species, is a misconception. With the constancy of the shape in median view, he could only have been referring to the lateral view. He apparently saw little or no fruiting material of the several Australian species with capsules broadly obtuse or emarginate in lateral view.

The distribution and density of the capsule indument is a useful character in Australia for the separation of species and infraspecific taxa. In Sect. Euphrasia it is one of the characters used to separate Subsect. Angustifoliae from Subsect. Ciliatae (Pugsley 1930, 1936; Sell & Yeo 1970; Yeo 1972).

* E. disperma (Sect. Anagosermae) is usually single-lobed through the development of only one ovule (Ashwin 1961; Simpson 1977).
12. Seeds

The nature of seed in relation to ability of *Euphrasia* species to disperse over long distance is discussed on p. 59.

Seed number and size are very useful diagnostically at the level of species and below in the Australian taxa. Seed number is less reliable diagnostically than the related character of ovule number (p. 33.) Sell & Yeo (1970) state that (in Sect. *Euphrasia*) "seed size tends to be proportional to capsule size and inversely proportional to the number of seeds in the capsule". This does not hold in the Australian species.

In the Australian annuals there is a clear correlation between the number of ovules, seed size and climatic range of each taxon (table 1). The fewest ovules and largest seed are found in alpine areas, while the highest ovule numbers and smallest seeds occur in the three lowland and montane species.

A similar relationship is found in the Australian perennials. In Sect. *Striatae*, *E. striata* of alpine and subalpine areas has larger seeds and fewer ovules and seeds than its close relative *E. semipicta* of lowland heath. In Sect. *Australes* seed in the alpine subspecies ssp. *diversicolor* and ssp. *glacialis* of *E. collina* similarly tends to be larger than that of the subspecies of montane and lowland regions. Ssp. *lapidosa* which inhabits fjeldmark of the highest alpine areas is one exception; its seed size is somewhat intermediate tending more to that of the lowland subspecies than its alpine herbfiel allies. Within ssp. *paludosa* (q.v.; note 2) there is an increase in seed size with increasing altitude. Although sampling of ovule and seed number is inadequate, the ovule and seed number in the three above subspecies of *E. collina* in the alpine region of the Snowy Mountains of New South Wales appears to be lower than that for lowland subspecies, such as ssp. *tetragona*, ssp. *osbornii*, ssp. *collina* and ssp. *paludosa*.

The several independent parallel trends of decreased ovule and seed number and increased seed size associated with the transition from lowland/montane to subalpine/alpine conditions in the Australian species may relate to several factors: the energy available to the plant for seed production (there is usually a parallel decrease in plant size and presumably photosynthetic area); the seed number required to maintain a viable population; and the nutrient reserves required in seed for germination and seedling development prior to attachment to a host in the different climatic conditions. The reversal in the trend, at least in seed size, in the fjeldmark perennial may be associated with lower water-holding capacity and nutrient availability of this community compared with the adjacent herbfiel (Costin et al. 1969) and their effect on optimum habit and organ size.

*E. disperma* of Sect. *Anagospertmae*, with its single ovule per locule and its usual development of only one locule with a large seed, shows some tendency to vivipary in the laboratory (Simpson 1977), for seed remains green up to germination and sometimes enlarges and germinates within the split capsule while it is still attached; other seeds germinate after release. Owing to an abundance of flowers, each plant produces many seeds. Simpson considers that the persistent moisture of the wet, poorly drained habitat in a mild humid climate provides ideal conditions for successful germination. Vivipary in this apparent annual would require the absence of a seasonal break between generations.

13. Chromosome number

With the exception of two counts, one diploid (*n* = 11) for *E. mirabilis* of New Guinea (Borgmann 1964: "E. rectiflora") and the other octoploid (*n* = 44) for *E. antarctica* from the Falkland Islands (D.M. Moore, fide Yeo 1968), studies of chromosome numbers in *Euphrasia* have been confined to Subsect. *Ciliatae* and
Subsect. *Angustifoliae* of Sect. *Euphrasia* in the northern hemisphere (e.g. Yeo 1954, 1970), both of which have diploid and tetraploid species. The current knowledge of chromosome numbers in Sect. *Euphrasia* is summarized in Yeo (1978b) and placed in abbreviated form in table 2.

Since *Euphrasia* shows greater morphological diversity in the southern hemisphere, material from Australian members of the genus has been investigated for chromosome numbers.

Table 2. Chromosome numbers in *Euphrasia*, a survey of the present knowledge, with the source of information in extra-Australian taxa and the voucher specimen (in AD) for Australian taxa.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Chromosome number</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sect. Euphrasia</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Subsect. Ciliatae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ser. Grandiflorae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. officinalis</em> L.</td>
<td>n=11</td>
<td>(Yeo 1972, 1978b)</td>
</tr>
<tr>
<td><em>E. rivularis</em> Pugsley</td>
<td>n=11</td>
<td>(Yeo 1954)</td>
</tr>
<tr>
<td><em>E. anglica</em> Pugsley</td>
<td>n=11</td>
<td>(Yeo 1954)</td>
</tr>
<tr>
<td><em>E. vigursii</em> Davey</td>
<td>n=11</td>
<td>(Yeo 1972)</td>
</tr>
<tr>
<td><em>E. hirtella</em> Reuter</td>
<td>n=11, c.11</td>
<td>(Yeo 1954, 1970)</td>
</tr>
<tr>
<td><em>E. picta</em> Wimmer</td>
<td>n=11</td>
<td>(Yeo 1978b)</td>
</tr>
<tr>
<td><em>E. marchesetii</em> Marchesetti</td>
<td>n=11</td>
<td>(Feoli &amp; Cusma, fide Yeo 1978b)</td>
</tr>
<tr>
<td>Ser. Alpinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. alpina</em> Lamk.</td>
<td>n=11</td>
<td>(Yeo 1970)</td>
</tr>
<tr>
<td>Five other series: 16 species</td>
<td>n=22</td>
<td>(Sell &amp; Yeo 1970; Yeo 1954, 1970, 1972, 1978b)</td>
</tr>
<tr>
<td><strong>Subsect. Angustifoliae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. cuspidata</em> Host</td>
<td>n=11</td>
<td>(Feoli &amp; Cusma, fide Yeo 1978b)</td>
</tr>
<tr>
<td><em>E. salisburgensis</em> Funk</td>
<td>n=22</td>
<td>(Yeo 1972)</td>
</tr>
<tr>
<td><strong>Sect. Pauciflorae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Subsect. Pauciflorae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. mirabilis</em></td>
<td>n=11</td>
<td>(Borgmann 1964)</td>
</tr>
<tr>
<td><strong>Sect. Striatae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. striata</em></td>
<td>n=c.20-30</td>
<td>Barker 1060</td>
</tr>
<tr>
<td><em>E. hookeri</em></td>
<td>n=c.26-30</td>
<td>Barker 1212</td>
</tr>
<tr>
<td><strong>Sect. Australes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. crassiuscula</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ssp. eglandulosa</td>
<td>n=c.27-30</td>
<td>Barker 1590</td>
</tr>
<tr>
<td>ssp. <em>E. crassiuscula</em></td>
<td>n=c.27-29</td>
<td>Barker 1593</td>
</tr>
<tr>
<td><em>E. collina</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ssp. paludososa</td>
<td>n=c.27-29</td>
<td>Barker 1489</td>
</tr>
<tr>
<td>ssp. <em>E. collina</em></td>
<td>n=c.50-60</td>
<td>Barker 1504</td>
</tr>
<tr>
<td>ssp. collina</td>
<td>n=c.28-30</td>
<td>Barker 1439, 1440</td>
</tr>
<tr>
<td>ssp. tetragona</td>
<td>n=c.30</td>
<td>Barker 1374</td>
</tr>
<tr>
<td>ssp. <em>E. crassiuscula</em></td>
<td>n=c.28-32</td>
<td>Barker 1438</td>
</tr>
<tr>
<td>ssp. diversicolor</td>
<td>n=c.50-60</td>
<td>Barker 1684 (tapetal cell mitosis)</td>
</tr>
<tr>
<td>ssp. <em>E. crassiuscula</em></td>
<td>n=c.27-30</td>
<td>Barker 1590</td>
</tr>
<tr>
<td><strong>Sect. Lasiantherae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. alsia</em></td>
<td>n=27</td>
<td>Barker 1696</td>
</tr>
<tr>
<td><em>E. lasianthera</em></td>
<td>n=c.38-40</td>
<td>Barker 1535</td>
</tr>
<tr>
<td>n=c.42-47</td>
<td></td>
<td>Barker 1536</td>
</tr>
<tr>
<td><strong>Sect. Scabrae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. caudata</em></td>
<td>n=27, 28, 27H-21, 25H+21</td>
<td>Barker 1649</td>
</tr>
<tr>
<td><strong>Sect. Trifidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. antarctica</em></td>
<td>n=44</td>
<td>(D.M. Moore, fide Yeo 1968)</td>
</tr>
</tbody>
</table>
a. Method

Bud material from plants in the field was used in the study. Young inflorescences were fixed immediately after collection in a mixture of 3 parts ethanol : 1 part acetic acid, transferred to 70% ethanol after approximately 24 hours, and stored, wherever possible, in ice until transfer to temperatures of below 0°C. Storage for periods of a week up to 18 months after collection showed no noticeable difference in chromosome definition.

In the fixed material it was found that pollen mother cell meiosis was confined to one or two consecutive bud pairs in each inflorescence. These buds were about 2mm long and usually 5-7 nodes above the youngest open flowers.

Difficulties, such as described by Yeo (1954) in Euphrasia and Heckard (1968) in the North American genus Castilleja (also of Trib. Rhinantheae), were experienced in obtaining preparations suitable for accurate determination of chromosome numbers. The chromosome exhibited poor differential staining against the cytoplasm, and overlapped in a high percentage of well-spread pollen mother cells at late prophase to anaphase of the first meiotic division, the best stages for study. Neither lactic-aceto-carmine nor lactic-propiono-carmine (see Dyer 1963; Cooperrider & Morrison 1967; Cooperrider & McCready 1970) were satisfactory in the present study.

The technique adopted was recommended by Dr B.A. Barlow (pers. comm. 1972). Standard anther squash techniques were employed using a light propiono-carmine stain of concentration of 1% carmine (or slightly less) in 45% propionic acid; no iron mordant or acid hydrolysis was found necessary. Meiotic figures were studied with the aid of phase-contrast illumination. This technique was not entirely satisfactory but was sufficient to give an indication of chromosome number.

b. Results

Despite the inaccuracy of the chromosome counts obtained for the Australian species of Euphrasia, the information is published to help resolve questions concerning the evolution of the genus and better define the more useful areas for future karyological study. The results obtained (table 2) cover representatives of all sections in Australia except Sect. Cuneatae and Sect. Phragmostomae, each with only a single Australian species.

Chromosome counts of the Australian species are sufficient to show that they differ in chromosome number from those known for the rest of the genus. Their numbers are rarely, if at all, a multiple of the generic base number, \( x = 11 \). They indicate that the species studied have had a complex history of karyotype evolution, and are unlikely to represent a primitive stock from which the rest of the genus evolved, as proposed for example by Yeo (1968) for the perennials. However, it should be noted that a number of key taxa, e.g. *E. bella* (Sect. Australes), Sect. Phragmostomae and Sect. Cuneatae, were not examined.

It is fairly certain that the haploid number of *E. alsa* is \( n = 27 \) (fig. 15). Its close relative *E. caudata* has \( n = 27 \) or 28 or both. In this species there is some evidence of abnormalities at least in the population Barker 1649, as within the one flower meiotic figures apparently exhibited 28 bivalents, others 27 bivalents and 2 univalents, another perhaps 25 bivalents and 2 trivalents (figs 15, 16).

The counts of the subspecies of *E. collina* (Sect. Australes) clearly show evidence of two levels of ploidy, with *E. collina* ssp. *paludosa* showing both. The lower ploidy level in *E. collina* approximates to the chromosome number estimates for *E. alsa* (Sect. Lasiantherae), *E. caudata* (Sect. Scabrae), *E. crassiuscula* ssp. *eglandulosa* (possibly a hybrid species from parent species in Sect. Australes and Sect. Striatae):
see below), and two species of Sect. *Striatae*, Sect. *Australes*, Sect. *Scabrae* and Sect. *Lasiantherae* apparently form a monophyletic assemblage (p. 55), and it is therefore likely that any differences in chromosome number masked by the variable estimates obtained in the present study are of an aneuploid nature, with secondary development of chromosome number differences within these sections being either polyploid (exemplified by the subspecies of *E. collina*) or even aneuploid (possibly indicated by the counts for Sect. *Lasiantherae*). The status of *E. crassiuscula*, with its position intermediate between Sect. *Striatae* and Sect. *Australes* (p. 64), in the evolutionary history of *Euphrasia* in Australia may well be resolved in a chromosome number survey of the Australian species.

Fig. 15. Sketches of meiotic chromosome configurations in pollen mother cells of *E. alsa* and *E. caudata* (not to scale). A, *E. alsa* (Barker 1696), diakinesis, n = 27; B, C, *E. caudata* (Barker 1649), diakinesis, n = 27/28; D, *E. caudata* (Barker 1649), part of cell at diakinesis.
Fig. 16. Sketches of meiotic chromosome configurations in pollen mother cells of *E. caudata* (Barker 1649) (not to scale). A, metaphase I - early anaphase I, n = 27/28; B, early anaphase I, n = 27II and 2I (arrowed); C, diakinesis, n = 25II + 7II (arrowed); D, early anaphase I, n = 28.
In conclusion, it has become obvious that the techniques used in the study of the chromosomes need to be improved and that future investigations in Euphrasia be extended to include species elsewhere in the southern hemisphere and tropics. Such a study would assist greatly in the clarification of evolution in the genus. Chromosome numbers of the New Zealand species must be especially important because of their possible intermediacy between the tropical members (with a single record of $n = 11$) and on the one hand the Australian species (with chromosome numbers apparently derived by a series of steps) and on the other the South American species (with their single record of an octoploid, $n = 44$). A survey of the chromosome numbers particularly of the perennial sections could also assist in assessing which of the present-day species are closest to the primitive stock from which Euphrasia and allies such as Odontites ($n = 10, 20$: Yeo 1972) and Bartsia ($n = 12, 24, 36$: Yeo 1972) are derived (p. 51).

14. Pollen sterility tests

The confusing taxonomy of Euphrasia in Australia has often been attributed to a possible high incidence of hybridization. A hybrid may often be detected simply by the incidence of a higher than normal proportion of sterile pollen.

The technique used for tests for pollen sterility is identical to that proposed by Owczarzak (1952). Only dried herbarium material was used. Pollen was taken from mature buds or young flowers prior to anthesis. The grains were mounted on a microscope slide in a medium of glycerol jelly containing phloxine, which stains the contents of the pollen, and methyl green, which stains the pollen wall. The slides upon which the counts are based are housed in AD, marked by the PS code given in the text. The estimates of the percentage of functionally appearing pollen have been listed in a duplicated table available on request from the author.

It is stressed that the technique does not measure pollen fertility. The estimate of the proportion of grains of “functional” appearance is only an approximation of this, as some of the grains may be incapable of fertilization. Furthermore, high pollen sterility need not be caused by hybridization. Abnormal environmental conditions and genetic aberrations in pure populations may also affect pollen development. However, if high pollen sterility occurs in plants which are intermediate between taxa which themselves produce mainly functional pollen, then this can be taken as good evidence that the intermediates are of hybrid origin. Finally, it is emphasized that hybrids may show no loss in pollen fertility.

C. FLORAL BIOLOGY

The flowers of Euphrasia are clearly adapted to cross-pollination by insects, as is shown by field observation of pollination in Europe (e.g. Yeo 1966) and Australia (see below).

There are two general flower types. One (type 1) is distinctly bilabiate, with a large lower lip, with anthers which are fused together and rigidly held to the upper side of the mouth under the hood and with, in most species, the stigma initially placed well in front of, and often below, the level of the anthers. The other (type 2) is sometimes erect and often with a long tube, and bilabiate but tending to be falsely actinomorphic by the lower lip being much shorter relative to the upper lip than in the first type and the upper and lower lobes being sharply reflexed and more or less equal. The stamens are free and appear to take up more room in the mouth and tube than in the first type. The stigma in most species is initially directed well above or in front of the anthers.
With few exceptions the process of flower development important to pollination is probably identical to that reviewed by Yeo (1966) for Sect. Euphrasia. Most species are apparently protogynous, with the stigma and anthers well separated at anthesis. Elongation of the corolla tube, which supports the stamens, finally brings the anthers into contact with the stigma. Thus the flowers seem primarily adapted to cross-pollination and, failing this, possibly self-fertilization, providing there are no self-compatibility barriers. This process apparently occurs in species with relatively tiny flowers such as *E. alsa* and *E. dyeri*. However, in the European species (Yeo 1966), whereas the larger-flowered species are essentially adapted to outcrossing, the smaller-flowered species are strongly adapted to self-pollination as the dehiscing anthers contact the stigma by the time the flower opens. Similarly, as the small flowers of *E. antarctica* (Sect. Trifidae) open, “the anthers stand exactly above the stigma, which is fully developed before the flower is opened. It is inevitable that pollen falls upon the stigma” (Skottsberg 1913, p. 51).

**Flower type 1 (e.g. fig. 17)**

This flower is characteristic of all species except those of South America and *E. disperma* of New Zealand. It is clearly adapted to pollination by bees for its morphology and coloration, usually of yellow blotches and often with purple striations, matches that characteristic of bee-pollinated flowers as described by Faegri & van der Pijl (1971), although other insects may occasionally act as pollinators (p. 44). In this flower type the structure of the anthers, which have rigid awns protruding into the corolla mouth and anther slits opening obliquely downwards, ensures that an insect entering a tube to gather nectar knocks pollen on to its upper parts.

Fig. 17. Native bee *Exoneura* (*Exoneura*) sp. visiting the prominently striated flowers of *E. lasianthera* (Sect. Lasiantherae), Macalister River headwaters, Eastern Highlands, Victoria (*Barker 1498*).
The awns of the posterior pair of anthers are presumably most involved in this process as they are longer than the other awns and nearer the tube. It is not known whether difference in length of the rearmost awns between taxa has any significance in pollination. The character is not always related to variation in size of the corolla mouth (p. 32). However, the remarkably long and often oddly shaped rearmost awns of *E. phragmostoma* (Sect. Phragmostoma: fig. 30) may relate either to some unusual pollinator or to the particularly large corolla mouth (fig. 30) or to both.

The Australian species of *Euphrasia* have this type of flower and all those seen in the field were found to be pollinated mainly by native bees. On all but two of the occasions on which they were seen visiting flowers of *Euphrasia*, one or two native bees were collected for identification. Bees were observed to enter the corolla tube, apparently to feed on nectar, and to crawl over the anthers to gather pollen. Their attraction for the flowers of *Euphrasia* was well-illustrated when a plastic bag containing three copiously flowering plants collected from a population of *E. collina* ssp. *osbornii* (Whibley 4155) was found to contain about twenty native bees hidden within the flowers. Bees have also been seen visiting flowers of *Euphrasia* in the northern hemisphere, but according to Yeo's (1966) observations their interest was mainly confined to gathering nectar rather than pollen.

The bees seen visited flower after flower in the populations of *Euphrasia*. In at least one location (Barker 1492: *E. collina* ssp. *paludosa*), if not all, the bees visited only *Euphrasia*; they ignored a *Ranunculus* species and two yellow composites, although they flew to these plants and hovered over them before returning to *Euphrasia*. At one site the same bee species may visit two species of *Euphrasia*, effecting hybridization. On the Central Plateau of Tasmania (Barker 994) where bees visited both *E. collina* ssp. *diemenica* and *E. striata*, which were flowering simultaneously and growing together, the two plant species hybridize (see p. 287). It is possible that bees (fig. 17) in the Mt Howitt region are responsible for hybridization between *E. lasianthera* and *E. collina* ssp. *paludosa*, which are sympatric and have overlapping flowering times (p. 288), for bees similar to those collected from the flowers of *E. lasianthera* (Barker 1498) were seen (but not collected) among the flowers of *E. collina* ssp. *paludosa* at localities several kilometres away (Barker 1492, 1495).

Dr T. Houston of the Western Australian Museum has kindly identified the bees collected (table 3). Seven different species of native bee from the three genera *Lasioglossum* (5 species), *Leioproctus* (1) and *Exoneura* (1) were collected at eight different sites, which encompassed lowland to alpine regions from Tasmania, the Australian Alps and South Australia. There were four cases of the same bee species being found in the flowers of *Euphrasia* at two separate sites in the same geographical region but often widely apart (table 3). Accordingly, despite the small number of collections made (a total of 35 bees), it would appear that out of 3,000 species of bee estimated to occur in Australia (Michener 1970), a significant proportion of these being polylectic (although there is little data on this: Dr T. Houston, pers. comm. 1977), only a limited number of taxa frequent the flowers of *Euphrasia*. Three of these twice-collected species were *Lasioglossum*, the other was the only species of *Leioproctus* collected.

The purple striations and yellow blotches on the corollas of many species with this flower type are considered to be nectar guides for the bee pollinators. Yeo (1968) considers that in *Euphrasia* the bee is guided to the nectar by the striations and the pollen by the yellow blotch on the lower lip onto which most pollen falls. However, it also seems likely that the yellow areas in the tube, which are often present when the yellow blotch on the lower lip is lacking, serve as a final guide to the nectary, for these blotches are well behind the anthers.
Some sections of *Euphrasia* in the southern hemisphere diverge by the complete lack of purple striations and common lack of yellow blotches on the lower lip. In Australia this is especially characteristic of Sect. *Australes*, Sect. *Scabrae* and Sect. *Phragmostomae*. From table 3, both of the genera of bee collected more than once, *Lasioglossum* and *Leioproctus*, apparently show no preferences for any one type of flower coloration. Thus *Lasioglossum* was found in striated and non-striated flowers and flowers with and without yellow blotches on the lower lip. Such non-specificity for coloration is shown within single species of both bee genera, and is supported by each of the few examples of interspecific hybridization in *Euphrasia* in Australia (table 4), in which corolla coloration and sometimes shape or size differ markedly.

The absence of purple striations and yellow blotches in Australian species of *Euphrasia* occurs in several unrelated groups. This is concordant with the fact (Dr T. Houston, pers. comm. 1973) that Australian native bees can recognize suitable flowers without such guides. For example the Myrtaceae, which provide the major source of nectar and pollen for these bees (Michener 1965, 1970), lack such stripes and blotches. The development in *Euphrasia* in Australia of special features of coloration, such as the wide variation in ground colour of the corollas of many species and the prominent pair of yellow blotches in the centre of the flower of *E. lasianthera* (Sect. *Lasiantherae*), and the diversity of floral shape can probably be linked to competition in the presence of a diverse Australian bee fauna and the wide diversity of floral shape and coloration in Australia’s bee-pollinated plants.
Table 4. Interspecific hybrids in *Euphrasia* in Australia with the floral characters of the parent species.

<table>
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<th>Parent Hybrids</th>
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<tr>
<td>E. alsa (open corolla, purple-striated, yellow-blotched)</td>
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<tr>
<td>× E. caudata (closed corolla, non-striated, reddish-blotched)</td>
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<tr>
<td>E. lasianthera (purple-striated, yellow-blotched)</td>
</tr>
<tr>
<td>× E. collina ssp. paludosa (non-striated, non-blotched)</td>
</tr>
<tr>
<td>E. striata (purple-striated, yellow-blotched)</td>
</tr>
<tr>
<td>× E. collina ssp. diemenica (non-striated, yellow-blotched)</td>
</tr>
<tr>
<td>E. orthocheila ssp. orthocheila (corolla closed, yellow)</td>
</tr>
<tr>
<td>×? E. collina ssp. paludosa (corolla ± open, white to lilac)</td>
</tr>
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</table>

There is a similar lack of prominence in striations and yellow patches in the corollas of the New Guinea and New Zealand species of *Euphrasia* (p. 29). I was able only to see *E. humifusa* and *E. mirabilis* in the field in New Guinea and found no pollinators visiting these species during my relatively short time studying them. The corolla lips of such species as *E. mirabilis* and *E. papuana*, however, are large relative to their small calyces, and the stigma initially projects in front of the anthers. Both attributes point to the species being cross-pollinated. It is noteworthy that the New Guinea bee fauna, which is very depauperate compared to the rest of the world, contains representatives of *Lasioglossum* and *Leioproctus* (Michener 1965).

In New Zealand the perennial Sect. *Pauciflorae* and the two annual species *E. zelandica* and *E. australis* (Sect. *Novaezeelandiae*) were seen to lack the prominent purple striations which characterize other New Zealand species, but to possess striking yellow coloration on the mouth and tube. Remarkably, prominent striations on the outside (rear) of the corolla lobes, out of view of the visiting insect, occur frequently in these species (p. 30). This may reflect the depauperate nature of the New Zealand bee fauna (Michener 1965, 1979), and the reliance of New Zealand plant groups with characteristic bee-pollinated flowers on a more generalized set of insect pollinators (Godley 1979; Wardle 1978). Furthermore, it seems clear that the absence of corolla striations on the front of the lobes is a derived condition for sometimes a vestige of pigmentation is apparent. There are no patterns in ultra-violet in the places where striations are lacking. The gradual loss of hairs on the anthers of a series of species in the New Zealand annuals culminating in the free completely glabrous anthers of *E. disperma* (p. 33), may also reflect a reduced dependence on bee pollination, to which the position, arrangement and structure of the anthers typical of Flower Type 1 are clearly adapted. Finally, it is noted that the New Zealand bee fauna includes *Lasioglossum* and *Leioproctus* (Michener 1965), species of which visit *Euphrasia* in Australia.

My collections of bees in Australia are confined to those visiting *E. collina* (Sect. *Australes*), *E. striata* (Sect. *Striatae*) and *E. lasianthera* (Sect. *Lasiantherae*), all perennials with similar corolla shape. A study of pollinators of Sect. *Scabraceae*, which consists of annuals with a more closed and elongated corolla mouth (p. 27), is desirable. Of further interest would be a comparison between *E. caudata* (Sect. *Scabraceae*), with a non-striated corolla of such a shape and with a long narrow blotch on the lower lip, and *E. alsa* (Sect. *Lasiantherae*), a closely related annual from the same geographical region, with a tiny striated corolla of the same shape as the perennials studied above. That such different corolla shapes at least sometimes attract the same pollinators is indicated by the hybridization between the two species (p. 290).

Whereas the native bees seem to be the most prevalent visitor to the flowers of *Euphrasia* in Australia, several other flying insects were seen visiting them. Among these were several species of butterfly. *Graphium macleayanus* was recognized visiting *E. crassiuscula ssp. crassiuscula*. It alternated between the flowers of *Euphrasia* and...
those of other plants. The variant of *E. collina* related to ssp. *diversicolor* on The Cobberas was also visited by a butterfly. A hover-fly (Syrphidae) was seen visiting flowers of *E. collina* ssp. *collina* (Barker 982). Butterflies and hover-flies have also been observed visiting the flowers of the same type in the northern hemisphere (Yeo 1966).

**Flower type 2 (e.g. fig. 18)**

It is uncertain whether the obvious differences between the two floral types reflect a general change in pollinator. This second type is found only in Sect. *Trifidae* of South America and the closely related *E. disperma* (Sect. *Anagospermae*) of New Zealand (fig. 18). *E. scutellarioides* (Sect. *Pauciflorae*) of New Guinea, a species bearing no close relationship with the above sections, has flowers of an intermediate type with a long-tubed corolla with much-reduced lips but retaining the fused anthers. It seems possible that these flowers are adapted to pollination by butterflies or moths (Yeo 1968). On morphology this seems very likely for the extremely long and narrowly tubed flowers of *E. disperma*. Yet in this species the indigo striations and yellow markings are very marked (p. 30) and seem to indicate bee pollination, although it would have to be a small and adventurous or very long-tongued bee if it gathered nectar. In some of the species of Sect. *Trifidae* the mouth of the flower opens downwards because of the long upper lip and the very short lower lip. These seem indicative of a type of flower pollinated by moths as described by Faegri & van der Pijl (1971). Only field studies of flowers of this type can show to what extent the different morphology has been paralleled by change in the nature of the pollinator, and whether such characters as the glabrous anthers have any significance in the pollination process. The lack of hairs along the anther slits in the former two sections may enable the pollen to be dispersed in larger masses. It seems unlikely that the anther awns would have much significance in these flowers, although they are long in some species.

Fig. 18. The flowers of *E. disperma* (Sect. *Anagospermae*) near Denniston, New Zealand (Barker 3716), showing the slender long erect corolla tube, striated lobes and free subexserted anthers.
Two of the anthers always possess one awn longer than the other six awns in the flower. These longer awns are the rearmost pair of awns in the bilabiate bee-pollinated flower from which this flower type has almost certainly evolved, but they have possibly lost any special functional significance.

III. THE ORIGIN AND DIVERSIFICATION OF EUPHRASIA

The means by which *Euphrasia* attained its distribution (fig. 19) in the temperate regions of both hemispheres with its greatest diversity in the southern hemisphere and a series of “connecting species” on the isolated mountain peaks of Malesia has been the subject of controversy. The genus has been considered either to be old and to have migrated by land from various places of origin to its widely scattered present day location, or to be young and to have spread by long-distance dispersal from its origins in the northern hemisphere through the young Malesian mountains into Australasia and South America.

After a brief survey of past proposals, this author presents evidence for his view of the age and means of dispersal of the genus, and then how the genus attained its present range and diversity both within Australia and on a world scale.

A. PAST HYPOTHESES

Perhaps the first attempt at explaining the remarkable bihemispheric distribution of *Euphrasia* was by J.D. Hooker (1859b), who was struck by the many European features of the Australian flora (p.xciv). He (p.xviii) proposed that partially submerged former mountain chains could have provided a means of dispersal between Japan and Australia, the existence of *Euphrasia* on “the lofty mountain Kini Balou in Borneo” (material probably cited in Stapf 1894) providing evidence of this.

Until the relatively recent wide acceptance of the reality and applicability of plate tectonics to biogeography, it has been believed that *Euphrasia* was an old Tertiary genus which had attained its world distribution by migration over land. Wettstein (1896) pointed to the lack of affinity between the North and South American populations, and proposed that the genus arose on a now submerged South Pacific land mass connecting Australasia, South America and Asia. Like Hooker, Du Rietz (1932b, 1948a) proposed that the genus was linked by more continuous bridges between Asia and Australia, and between Australia, New Zealand and South America, the Australasian representatives being morphologically intermediate between those of the northern hemisphere and South America.

More recently it has been suggested that *Euphrasia*, along with other advanced groups, attained its distribution by long-distance dispersal since the Neogene formation of subalpine and alpine outposts through the uplift of mountains surrounding the South Pacific and in Malesia and the Plio-Pleistocene glaciations (Raven & Axelrod 1972; Raven 1973). The genus belonged to the advanced sympetalous order Tubiflorae which is known in the fossil record largely from Neogene times when direct migration via Antarctica was impossible (Raven 1973). Wardle (1978) apparently also believed that *Euphrasia* could not have existed when Gondwanaland was whole, but disputed the need for genera such as *Euphrasia* being of Neogene age, commenting that a fragmented trans-Antarctic bridge would have been available for migration involving dispersal over ever-widening seas until the late Tertiary spread of the Antarctic ice sheet.

Van Steenis (1971), however, has continued to believe that the number of bihemispheric distribution patterns similar (homologous) to *Euphrasia*, including the *Nothofagus-Fagus* and Winteraceae-Magnoliaceae pairs, both of which are widely recognized to date back to the late Cretaceous, reflect a synchronous development of

The number of species in each section is shown, those largely comprising "microspecies", equivalent to subspecies in the Australian revision, are bracketed.

Fig. 19. The geographical distribution of the sections of Euphrasia, with the endemic Australian and New Zealand sections occurring within the blackened areas.

(Distribution of Sect. Euphrasia after Hulten 1976).
all such groups from the Cretaceous. In reaffirming these assertions (van Steenis 1979), he argued that the repeated use of long-distance dispersal for explaining discrepancies between widely disjunct ranges and current geophysical theory was fallacious, and suggested a late Cretaceous-Paleocene or older tectonic connection between the Asia and Australia plates to accommodate bihemispheric distributions with present-day links in Malesia.

There has been controversy over the site of origin of the genus. Wettstein (1896) and Hartl (1972) have both suggested that the genus has a common origin with its close relatives in Trib. Rhinantheae, in particular Bartrasia and Odontites. Wettstein believed it to have an origin on his South Pacific land mass, while van Steenis (1962) proposed that it originated in the south-west Pacific region for in New Guinea and New Zealand the genus showed its greatest morphological diversity, in marked contrast to the poorly differentiated species of the northern hemisphere.

The long-distance dispersalists (Raven & Axelrod 1972; Raven 1973) have proposed that a young Euphrasia had a northern origin, presumably on the grounds that this is where its present generic relatives occur. Du Rietz (1932b, 1948a), Hartl (1972) and Moore (1972) have not alluded to a centre of origin, but all believed that the southern hemisphere contained a number of old primitive or relictual types. Yeo (1968) also alluded to the primitiveness of the large-flowered Australian perennials. Compared with the diversity in Euphrasia in the southern hemisphere it has been widely recognized that the northern hemisphere annuals are a group showing great uniformity (Hartl 1972; van Steenis 1962) and of recent origin since the onset of the Plio-Pleistocene glacial periods (Yeo 1968, 1978a; Moore 1972; Hartl 1972; Karlsson 1974, 1976; Hulten 1976). Karlsson (1974) suggested that the complex ecotypic variation in these annuals in anthropogenic non-forest vegetation of temperate Europe may have developed in step with man’s influence. The arctic and warmer Mediterranean regions showed no comparable ecotypic variation. Before man modified the vegetation, Euphrasia may have existed there in isolated open habitats such as on cliffs and fens and in alpine regions. Sell & Yeo (1970), Karlsson (1976) and Hulten (1976) have pointed to the recent dispersal of some of these northern annuals, Karlsson suggesting that this capacity was confined to taxa which are adapted to man’s influence on the landscape.

B. PROBLEMS IN ESTABLISHING CLADISTIC RELATIONSHIPS OF THE SECTIONS AND SUBSECTIONS OF EUPHRASIA

The revision of the infrageneric classification of Euphrasia has produced a series of sections and subsections separable by about 25 characters of diagnostic importance (table 5), a few, e.g. chromosome number and corolla coloration, only potentially so because of poor data. The infrageneric taxa are separated entirely on phenetic grounds. Delimitation using only unique derived states, as required by the cladistic techniques of Hennig (1966), is not only impossible at this stage of our knowledge, but may also in theory remove from recognition distinctive species groupings such as Sect. Lasiantherae and Sect. Scabrae or, alternatively, dictate the division of Sect. Australes into two sections, as well as prevent the separation of E. hookeri from E. gibbsiae, since paraphyletic groups may be involved. However, the use of cladistics as the sole basis for production of classifications is questionable (e.g. McNeil 1978).

The phenogram (fig. 20) derived from the number of absolute character differences between each pair of sections and subsections shows a central group of poorly differentiated sections. In view of the possible occurrence of convergence and parallelism in several characters used to delimit the sections, for example in a number of leaf and habit characters and in the origin of annual duration, a number of the
Table 5. The character states for each section and subsection of *Euphrasia*. "+" indicates the possession of a character state, "-" its absence, and "?" its possible presence. States in italics are considered as primitive.

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**MAIN INFLORESCENCE-BEARING AXIS**

**Direction**

1. ± entirely prostrate
2. Initially prostrate, distally erect, simple above ground level
3. ± erect, branched well above ground level

**Incidence of branching**

1. Consecutive nodes
2. Sporadic nodes
3. Separated groups of nodes, consecutive in groups

**Order of branch development**

1. ± basipetal
2. No fixed order
3. ± acropetal

**UPPERMOST LEAVES**

**Depth of toothing**

1. Crenate
2. Serrate
3. (Pinnatifid)

**Number of pairs of teeth**

1. (0)(1)(2)
2. (1)2-6(more)
3. c. 6-many

**Base**

1. Attenuate, abruptly expanded into blade
2. Attenuate, gradually expanded into blade
3. Narrow-cuneate to truncate

**Distribution of teeth**

1. Distal 1/3 or less
2. Distal 1/2 or more

**Number of main veins produced from base**

1. (1)3 or 3
2. (3)5
3. 3-5 or more

Continued on page 50
### Table 5 (continued)

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<td>3. Racemes usually with 10-20 flowers</td>
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<td>4. Racemes usually with more than 20 flowers</td>
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<td>4. Bloch on lower lip</td>
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<td>8. Lobes (lower)</td>
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<td>9. Emarginate</td>
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<td>10. Acute or obtuse to truncate</td>
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<td>2. Free</td>
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<td>Area about connectives</td>
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<td>1. Glabrous</td>
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<tr>
<td>2. Hairy, at least on posterior anther pair</td>
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<td>1. Densely hairy</td>
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<td>2. One or two hairs</td>
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<td>1. All needle-like</td>
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<td>2. Rearmost pair flattened or with margins erosulate or twisted</td>
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<tr>
<td>STIGMA</td>
<td>1. 0.1-0.3mm long</td>
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<td>2. (0.2)0.3-0.5mm or more long</td>
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<td>CAPSULE</td>
<td>Lateral view (overall)</td>
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<td>1. Oblong order</td>
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<td>2. Broad-ovate order</td>
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Continued on page 51
and parallelism which are widespread in the family. However, it is difficult to define groupings. In a study of the Australian Mimulinae (Scrophulariaceae: Barker, in character states must be discerned (Hennig 1966). These define monophyletic evolutionary trends in characters is defined, i.e. primitive and derived states are determined, the direction of the lineages is questionable.

In considering the biogeography of any group, the formulation of evolutionary trees is of great use, and undoubtedly cladistic theory has conceptually many advantages here. However, to use cladistic techniques properly unique derived character states must be discerned (Hennig 1966). These define monophyletic groupings. In a study of the Australian Mimulinae (Scrophulariaceae: Barker, in press) sufficient unique states were available to offset the phenomena of convergence and parallelism which are widespread in the family. However, it is difficult to define such states in *Euphrasia*. Characters such as the hairy anther backs and sessile leaves of three Australian sections, and the glabrous free anthers and trifid leaves of the South American species and *E. disperma* of New Zealand are peculiar to these taxa within *Euphrasia*, but like their alternative states, are found elsewhere in the tribe and, indeed, other tribes of Scrophulariaceae. Such characters, nevertheless, usefully define closely allied groups of species, and provide a firm basis for consideration of infrageneric relationships.

Consideration of relationships with allied genera could help to define an archetype of the genus from which to erect a detailed scheme of diversification in the genus. This is not possible at this stage owing to problems of heterobathmy; apparently primitive attributes are spread over a number of genera in Trib. Rhinantheae, such that no one genus or group of genera can be designated as primitive within the tribe. Thus *Euphrasia* is closely allied to *Bartsia* and *Odontites*, and more distantly to *Parentucellia* and *Bellardia* in Trib. Rhinantheae (Hartl 1972). Whereas Hartl considers *Euphrasia* to be the most derived of these genera, Yeo (1968) suggests the corolla morphology of the genus is primitive in the tribe. Weber (1980) considers that this group of genera has a primitive haustorial anatomy; they lack the “wart haustoria” of the more advanced semiparasitic genera in the tribe. On the other hand, in considering the primitive traits of the tribe attention should be given to the genera...
Schwalbea of North America and Cymbaria (Pennell 1935) as well as Bungea, Monochasma and Phtheirospermum of central and east Asia. These genera have one or several traits considered by Pennell (1935) to be primitive in the Scrophulariaceae, namely a pair of bracteoles, a 5-partite calyx, and a septicidal capsule. It is noteworthy when considering possible derived character states in Euphrasia that the first three genera are perennials with basal branching and entire leaves, that at least Cymbaria and Bungea have glabrous, apparently free, but didynamous anthers, and that all apparently possess the porrect upper corolla lip which, apart from in Euphrasia, prevails in the tribe.

It is possible that critical morphological and anatomical studies may resolve a number of the problems of possible convergence within the genus and the tribe, and provide other characters, e.g. in the pattern and distribution of the sessile gland patches on the leaves, but only in wide family based studies are sufficient unique derived states likely to be defined. Such studies seem far off.

Primitive character states could arguably be defined as those which are the most frequent within the genus. Such a practice is dangerous as one (derived) part of a genus may diversify while the rest may remain stable or become extinct. Indeed, it is
proposed below that most of the extant taxa of *Euphrasia* have derived from a phase of diversification separate from the early radiation of the genus from which only a few, often very localized taxa survive. However, it has been possible to propose a series of relict species in *Euphrasia*, and on this basis a hypothetical set of primitive character states and in turn evolutionary lineages within the genus have been established.

**C. Relicts of an Early Phase of World Evolution**

Some attributes, which occur in several distantly related sections, seem hardly able to have been derived by convergence and therefore are likely to be primitive states. It follows that some of the characteristics of a possible archetype of *Euphrasia* are as follows. Undoubtedly it was a perennial. Its pattern of branching was basipetal in consecutive nodes of erect to ascending main branches. Its leaves had a large, shallowly toothed blade gradually attenuated (subpetiolate) at the base.

Very few of the species of *Euphrasia* existing today possess all or most of these proposed archetypal attributes. Those species that do tend to be morphologically isolated and geographically restricted, and are scattered through much of the range of the genus. These factors indicate that such species are likely to be relicts, as suggested for some of the species in the past (e.g. Skottsberg 1921; Du Rietz 1932b, 1948a).

Sect. *Cuneatae* comes closest to the proposed archetype, bearing all the character states, while the endemic Japanese subsections of Sect. *Atlanticae*, a few species of Sect. *Malesianae*, *E. papuana* of Sect. *Pauciflorae*, Sect. *Paradoxae*, *E. bella* of Sect. *Australies*, and Sect. *Phragmostomae* have all but one of the proposed primitive states. Among these Sect. *Cuneatae* (two very distinct species), Sect. *Phragmostomae* (monotypic), Sect. *Atlanticae* (two very distinct species), and Sect. *Paradoxae* (monotypic) comprise morphologically very isolated perennials. *E. bella* of Sect. *Australies* is phyletically connected by one or probably two other geographically isolated perennial species to the rest of the section, and it must be considered a relict, possibly along with the other two species (p. 62). The two Japanese subsections *Alpicolae* and *Japonicae* differ from the hypothetical archetype only in their annual duration, and it is likely that they are derived in more recent times directly from archetypal progenitors.

The world distribution of these proposed relicts is remarkable in the widely disjunct outposts of the Azores, Taiwan and Borneo in the northern hemisphere and northern and central montane New South Wales, Tasmania, New Zealand, southeast New Guinea (Mt Victoria), Ceram and the Juan Fernandez Islands in the southern hemisphere (fig. 21).

It seems, therefore, that the diversification in the genus was in at least two phases. The first produced an array of forms, some of the characters of which are likely to be retained in the proposed relicts. It is noteworthy that five of the evolutionary lineages proposed below (fig. 22) contain at least one relict species. The second phase involved the development of the present-day diversity of species with modification particularly to habit, leaf and floral characters.

**D. Major Evolutionary Lineages**

The proposed relict species were surveyed to determine the state of each character diagnostic at the sectional level which is the most common amongst them. For the purposes of producing a phyletic scheme, this state has been assumed to represent the primitive state for each character (table 5). Remarkably, Sect. *Cuneatae* possesses all such states and is accordingly close to the consequential archetype of the genus. For the very few characters (e.g. presence of corolla striations) which were shared equally amongst the relict groups, the state possessed by Sect. *Cuneatae* (i.e. striated corollas) was accordingly taken as primitive. In a few cases there are inadequate data (e.g. chromosome number) or Sect. *Cuneatae* had each state (e.g. of corolla lobe apex).
Fig. 21. Location of the proposed relict species of *Euphrasia*.
The world distribution of *Bartsia* (after Hartl 1969-72).
The degree of generic diversity in Trib. Rhinantheae (Scrophulariaceae) in various regions of the world, with total and endemic genera for each region shown respectively above and below the line (data modified from Wettstein 1891-95, 1897).
Using shared derived states six lineages have been produced (fig. 22), which on the above assumptions appear monophyletically defined. They conform with those generally obtained from a series of “Wagner Trees” using the methodology of Whiffin & Bierner (1972). Six sections (Striatae, Australae, Pauciflorae, Malesianae, Novaezeelandiae, Cuneatae) forming a central group in the genus on phenetic grounds (fig. 20) were used in turn as the taxon closest to an archetype of the genus in formulating the Wagner Trees. Such trees are not wholly cladistic, for they are derived through an assessment of relationships between the sections involving primitive as well as derived states.

Most of the lineages have throughout or in a substantial part one or more characters unique in the genus. Although Sect. Cuneatae and Sect. Phragnostomae represent an entirely relictual Australasian lineage, the latter section is unique in its groups of branches and remarkable pair of rearmost anther awns. The character linking the northern hemisphere sections, Malesianae, Atlanticae and Euphrasia, is the small stigma. The Australae-Lasiontherae-Scabrae lineage of Australia is characterized by hairy anther backs and the usually sessile leaves with 3-5 or more main veins. In a south-west Pacific lineage Sect. Paradoxa of the Juan Fernandez Islands shares with Sect. Novaezeelandiae and Sect. Anagoperae of New Zealand acropetal branch development and sparsely hairy anther slits, while E. disperma of Sect. Anagoperae shares with Sect. Trifidae of South America trifid leaves and free glabrous anthers (see below). In contrast, the two lineages comprising Sect. Striatae of Australia and Sect. Pauciflorae of New Zealand and New Guinea are defined by derived character states of habit, leaves and inflorescence which are shared with more than one other lineage. The geographical restriction of the six lineages to different parts of the world supports their naturalness.

Phyletic arrangements of these lineages, such as the one proposed in fig. 22, are debatable in some areas at this stage, but should be able to be tested by additional data, particularly chromosome numbers. In particular, morphological similarity between the sections of west Malesia (Sect. Malesianae) and east Malesia-New Zealand (Sect. Pauciflorae) presented under the proposed scheme (fig. 22) as reflecting close phyletic affinity, may be a product of convergence; the similar reduced habit with sporadic irregular branching could well have arisen in this way under similar ecological conditions in the high tropical mountains. The large leaf blade of Sect. Malesianae is evident in Sect. Pauciflorae only in E. papuana in New Guinea and in some New Zealand species. The other tropical species of Sect. Pauciflorae have a peculiar hooded leaf. Stigma size remains an important character, not only in dividing the genus into northern and southern hemisphere groups, but also possibly at a wider level in the tribe.

A second problem is the phyletic relationships of E. disperma (Sect. Anagoperae). A placement as a sister group of Sect. Trifidae by the shared attributes of trifid leaves and free glabrous anthers would not account for their apparently large difference in ovule number, with its possibly associated difference in capsule shape, and the absence of the prostrate habit and extremely long corolla tube of E. disperma within Sect. Trifidae. The adopted arrangement linking E. disperma phyletically with other New Zealand annuals assumes that trifid leaves and free glabrous anthers are convergent traits. As Du Rietz (1932a) and Ashwin (1961) have indicated, the species apparently represents an end-point in transitions involving these and other characters, i.e. involving leaf incision, anther slit indumentum, ovule number, corolla tube length and development of prostrate habit, this last character being shared with two other species.
Fig. 22. Six evolutionary lineages evident among the sections and subsections of *Euphrasia*, based on the assumption that the character states predominating amongst the proposed relict species are primitive, Sect. *Cuneatae* possessing all such primitive states. Derived attributes which are shared by the included taxa at each branch point, and distribution of each lineage are shown. Those sections which include proposed relics are in italics. One possible phyletic arrangement of the lineages is shown in the inset.
Sect. *Australes* presents a third problem. At this stage evidence points to this section comprising two paraplyletic groups within the lineage defined by the presence of hairy anther backs. Further work is needed to determine if the non-striated state of the corolla is a convergent trait, for the section as presently constituted seems natural phenetically.

The phyletic placement of Sect. *Striatae* provides a further problem, for it differs only in the number of flowers in the inflorescence and the number of veins at the leaf base from Sect. *Pauciflorae*, and yet its two character differences from Sect. *Australes* are transcended by a species in the Australian Alps (p. 64). Clearly there is still much comparative morphological and cytological work to be done within as well as outside the genus before a stable evolutionary arrangement of the lineages can be defined.

### E. TIMING OF DISPERSAL EVENTS ACROSS BARRIERS TO MIGRATION

This survey of the distribution patterns of the subspecies and species or natural groups of these taxa shows that two phases of dispersal of different chronology are involved. Sect. *Euphrasia* is excluded from this discussion because of its recently derived ready ability to disperse widely (p. 59).

If *Euphrasia* attained its present world distribution by long-distance dispersal during or since the late Tertiary, as proposed by Raven & Axelrod (1972), it must have crossed at least 13 ancient oceanic barriers (table 6). No taxon of species or subspecies rank crosses such a barrier today, although the sections *Malesianae*, *Pauciflorae* and *Cuneatae* do (fig. 19).

| Regions between which long-distance dispersal is required for *Euphrasia* to have attained its distribution in the last few million years (excluding Sect. *Euphrasia*). |
|---|---|---|
| Eurasia - Azores | North Borneo - Cream | Australia - New Zealand (probably 3 times) |
| Asia - Taiwan | Ceram - Celebes | New Zealand - Juan Fernandez Is. |
| Taiwan - North Philippines | Celebes - New Guinea | New Zealand - South America |
| North Philippines - North Borneo | New Guinea - Australia or New Zealand |

Within the continental boundaries, the distribution patterns in *Euphrasia* provide a substantially different picture. Such distributions encompass generally narrower barriers to migration, bridged by suitable vegetation in Plio-Pleistocene times (e.g. southern Australia: Costin 1959, Hope 1978; New Zealand: Grant-Taylor 1966, Wood 1966, Shaw & Steven 1966; bridging between Fuegia and the Falkland Islands from bathymetric contours). Table 7 sets out taxa which cross such barriers of substantial width. Within Australia a number of disjunctions, which are narrower or based on insufficient distribution data, have been omitted. Data for taxa outside Australia are limited by lack of revisional studies and lack of sufficient information on distribution. Table 8 shows vicarious groups in which the taxa are separated by barriers bridged periodically in Plio-Pleistocene times. It is limited to Australian examples for the above reasons, although it is likely that New Zealand has no more than one such vicarious pattern. This involves *E. drucei*, which being on the North Island is separated from most other species of Sect. *Pauciflorae* by Cook Strait; all other species on North or Stewart Islands also occur on South Island.

For the now well-documented Australian distribution patterns, out of 14 separate crossings of Plio-Pleistocene barriers, 9 are encompassed by a species or subspecies and 5 involve vicariance. Making a statistical comparison using the exact test for $2 \times 2$ contingency tables for small samples (Bailey 1959), the probability that patterns across
Table 7. Species and subspecies of *Euphrasia* which occur on either side of sea or other at present inhospitable regions in the South Pacific region.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Geographical barriers to present-day migration</th>
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<tr>
<td><strong>Australia</strong></td>
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<tr>
<td><em>E. collina</em> ssp. <em>tetragna</em></td>
<td>Bass Strait</td>
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<td></td>
<td>Nullarbor Plain</td>
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<td></td>
<td>Investigator Strait (Kangaroo Isl.)</td>
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<tr>
<td><em>E. collina</em> ssp. <em>osbornii</em></td>
<td>Investigator Strait (Kangaroo Isl.)</td>
</tr>
<tr>
<td><em>E. collina</em> ssp. <em>paludosa</em></td>
<td>Semi-arid Upper South-East, South Australia</td>
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<tr>
<td><em>E. collina</em> ssp. <em>collina</em></td>
<td>Bass Strait</td>
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<tr>
<td><em>E. scabra</em></td>
<td>Bass Strait</td>
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<tr>
<td></td>
<td>Nullarbor Plain</td>
</tr>
<tr>
<td></td>
<td>Semi-arid Upper South-East, South Australia</td>
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<tr>
<td><strong>New Zealand</strong></td>
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<tr>
<td><em>E. cuneata</em></td>
<td>Cook Strait</td>
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<tr>
<td></td>
<td>Region between Marlborough Sounds and Lake Ellesmere</td>
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<tr>
<td><em>E. laingii</em></td>
<td>Region between Marlborough Sounds and more southerly locations</td>
</tr>
<tr>
<td><em>E. revoluta</em></td>
<td>Cook Strait</td>
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<tr>
<td><em>E. zelandica</em></td>
<td>Cook Strait</td>
</tr>
<tr>
<td><em>E. dyeri</em></td>
<td>Foveaux Strait</td>
</tr>
<tr>
<td><em>E. repens</em></td>
<td>Foveaux Strait</td>
</tr>
<tr>
<td><strong>South America</strong></td>
<td></td>
</tr>
<tr>
<td><em>E. antarctica</em></td>
<td>Strait west of Falkland Islands.</td>
</tr>
</tbody>
</table>

Table 8. Species and section of *Euphrasia* with disjunct vicarious ranges on either side of at present inhospitable regions in Australia bridged by suitable vegetation in the Plio-Pleistocene.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Nature of disjunction</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. gibbsiae</em> ssp. <em>subglabrifolia</em></td>
<td>Subalpine taxon separated from rest of <em>E. gibbsiae</em> by Bass Strait and lowland-montane vegetation.</td>
</tr>
<tr>
<td><em>E. bella</em> - *E. sp. 'Tamworth' - <em>E. bowdeniae</em></td>
<td>Three closely related isolated montane species of northern and central New South Wales.</td>
</tr>
</tbody>
</table>

The ancient oceanic barriers reflect an identical set of conditions is extremely low (P = 0.0007). The New Zealand situation (not differing significantly from the Australian) would lower the P value even further. Since no taxon of species rank or below crosses the oceanic barriers, the lowness of the P value seems limited only by the number of oceanic barriers associated with the range of the genus.

The relatively large number of instances of specific or infraspecific taxa occurring on either side of the Plio-Pleistocene bridges can only be explained by overland migration, in view of the obvious rarity of successful long-distance dispersal across barriers, if it has occurred at all. It is clear that the spread of the genus across most, if not all, oceanic barriers has occurred at a much earlier time than the most recent intra-continental migrations.

**F. MEANS OF DISPERSAL**

It is possible to show that a plant group is capable of long-distance dispersal by the detection of propagules in transit and observation of establishment. However, it is impossible to prove a lack of such a capacity. One can only deal with probabilities based on the available data. It is important to remember that at least 13 independent instances of long-distance dispersal and successful establishment are required for the
Studies in *Euphrasia*

The following summary of various biological, morphological and chorological characteristics of *Euphrasia* shows no evidence for its present-day world distribution being attained by long-distance dispersal.

Notwithstanding this, one portion of *Euphrasia*, comprising the two subsections, *Angustifoliae* and *Ciliatae* of Sect. *Euphrasia*, widely distributed in temperate Eurasia and North America, is likely to have a capacity for long-distance dispersal. There are strong grounds for considering these groups to be exceptional in the genus. It is widely believed (e.g. Yeo 1968; Hartl 1972; Karlsson 1974, 1976; Hulten 1976) that these are a derived group of which many taxa have become adapted to grazing and mowing and other anthropogenic changes to the vegetation. Hulten (1976) has indicated that these taxa are easily spread, for example in hay, and has suggested that a number of the most northerly arctic occurrences may have been attained through the agency of man. Seed of some of these taxa has been found in excreta of horses, cattle and reindeer (Ridley 1930), which graze their pasture and meadow habitats. A number of taxa are adventive in parts of Europe (Karlsson 1974) and North America (Sell & Yeo 1970). It is, therefore, remarkable that Sect. *Euphrasia* has only rarely become naturalized outside its natural range. I know only of a localized New Zealand record of *E. nemorosa* (Sykes 1981). No taxon of any other section is known to have been recorded as adventive anywhere in the world. The specialized ecological characteristics of these subsections are derived features which cannot be taken as indicative of similar capabilities in the remaining members of the genus and their progenitors.

Seed morphology in *Euphrasia* shows no special adaptations for long-distance dispersal. Seeds are unlikely to be light enough to be dispersed by any but the most extreme winds. They are small but not minute and are, therefore, unable to be dispersed in a dust-like mass. Smith (1977) has reported a “splash-cup” method of short-distance dispersal in *E. mirabilis* of New Guinea, in which the hygroscopic capsule opens when wet and it is proposed that seed is splashed out by rain drops. It is difficult to see how this method of dispersal can significantly increase the chances of long-distance dispersal of this low-growing species, as proposed by Smith.

The seed surface is characteristically multi-sulcate and scalariform. There are no appendages or sticky substances which would facilitate dispersal externally by animals. Apart from Ridley's (1930) references to seed of Sect. *Euphrasia*, there is no evidence of animals, in particular birds, eating seed of *Euphrasia*, nor is there any apparent attraction for them to do so. Raven (1973) has suggested that seeds may have been dispersed between the lands of the southern hemisphere by mud caked on the feet of birds. The species of *Euphrasia* commonly occupy areas of grassland and low herbage, and some may associate with swamps or boggy sites, but unlike some widely distributed members of Scrophulariaceae, e.g. in *Mimulus*, *Peplidium* and *Glossostigma* (Barker, in press), few species, if any, grow in mud. The chances of such dispersal are therefore reduced considerably.

The species of *Euphrasia* are apparently all bisexual and cross-pollinated by insects, but probably able to be self-fertilized in the absence or cross-pollination. Breeding experiments showing this have been confined, however, to Sect. *Euphrasia* (p. 41). The plants are all able to parasitize roots of other plants, but this is not obligatory nor is there any specificity known in the choice of host. There is no known symbiotic relationship important in the establishment and maintenance of populations of the genus.

The high degree of endemism which characterizes the genus throughout its range points to an inability to disperse across even small disjunctions. The Australian taxa provide many examples, such as the local endemics *E. phragmostoma*, *E. semipicta*, *E. nemorosa* (Sykes 1981). No taxon of any other section is known to have been recorded as adventive anywhere in the world. The specialized ecological characteristics of these subsections are derived features which cannot be taken as indicative of similar capabilities in the remaining members of the genus and their progenitors.
E. bowdeniae and E. bella, and the three species of Sect. Lasiantherae which are separated from suitable habitats by distances of only 40-80km.

If any seed were transported by wind or birds over the long distances required, it may have little chance of forming an established population. Taxa of Euphrasia are strongly linked to their particular habitat, as exemplified by the strong ecotypic differentiation of the alpine and subalpine taxa of E. collina and E. gibbsiae in Australia. While Yeo (1964, 1966) has had considerable success cultivating European species of Sect. Euphrasia, reports of cultivation of Australian taxa are exceedingly rare despite their showiness, and the only record known to me (Malahide 1973) relates to transplantation. That no adventives are known from the genus apart from Sect. Euphrasia also attests to their strong ecotypic fixation. Moreover, from the general preponderance of old (pre-1900) herbarium specimens of montane and lowland taxa, no Australian taxon has flourished with the advent of European man, most if not all have diminished in range, and a number, both annual and perennial, may be extinct or threatened with extinction. It seems likely that successful germination and establishment after long-distance dispersal would require that the new habitat conforms with a narrow set of ecological conditions similar to the seed source.

It is concluded that apart from the recently derived, highly specialized species of two subsections of Sect. Euphrasia, the present-day members of the genus exhibit no evidence of a capacity for dispersal over the long distances required for Euphrasia to have attained its world distribution. In the absence of even one example, outside Sect. Euphrasia, of a species or subspecies presently encompassing one of the ancient wide oceanic barriers which species in the genus would need to have crossed in the past, it is concluded that the genus is far more likely to have migrated over land with plant associations to which it was closely adapted.

G. DIVERSIFICATION OF EUPHRASIA IN AUSTRALIA

The present-day Australian taxa have apparently been derived from three separate evolutionary lineages. The first lineage, involving two relictual sections, has shown no radiation in Australia, but the other two have diversified into a wide range of habitats, with the high polymorphy of two species in particular indicating that speciation is still going on today. In these last two lineages there is evidence for independent parallel evolution in a number of characters involving habit, ovule number and seed size commonly in association with a transition between montane/lowland and subalpine/alpine conditions. Speciation has apparently resulted primarily from geographical or ecological isolation. There is evidence for some speciation through hybridization between unrelated species, but this seems of secondary importance. The situation thus conforms to some extent with the picture presented by Karlsson (1976) for the European species. He refers to strong ecotypic differentiation in the indigenous Swedish species, parallelism in a range of characters, including some involved in the Australian situation, related to climatic and habitat factors, and a role for hybridization much more limited than proposed by Yeo (1978a, b).

Even more so than at the infrageneric level, the establishment of uncontroversial evolutionary trees on strict cladistic grounds at a level of species and subspecies seems impossible, owing not only to the almost complete absence of unique derived character states, but also to difficulties in defining primitive and derived states for almost all characters through their often quantitative nature and the clearly frequent possibilities of convergence or parallelism. The schemes are therefore by necessity a subjective assessment based on phenetic relationships.
Evolutionary line 1: Sect. Cuneatae - Sect. Phragmostomae (fig. 23).

This group comprises three relict species which are morphologically very distinct and widely disjunct (fig. 27). Of the two species of Sect. Cuneatae, E. cuneata is the more closely allied to E. phragmostoma (Sect. Phragmostomae). E. cuneata of New Zealand is polymorphic and has a wide ecological range, including Nothofagus forest and ranging from coastal to subalpine situations. It encompasses the different climatic ranges of the other two species, E. ramulosa extending from wet sclerophyll forest into subalpine grassland in northern New South Wales, and E. phragmostoma occupying coastal scrub in southern Tasmania.

Fig. 23. Evolutionary diversification of Euphrasia in Australia (1). Postulated evolution of the species of Sect. Cuneatae and Sect. Phragmostomae.

Evolutionary line 2: Sect. Striatae (fig. 24).

Sect. Striatae is represented today by five species, mostly occupying alpine and subalpine habitats on the summits of the many mountains of southern, central and western Tasmania. Two distinct lineages are evident while there may have been a third, now extinct. The presence of E. gibbsiae ssp. subglabrifolia on Mt Baw Baw of eastern Victoria attests to migration between the present mountain outposts via land across Bass Strait during the Plio-Pleistocene glacial periods.

The “E. gibbsiae line” appears to be undergoing active speciation in response to the shrinkage and expansion of the subalpine/alpine zones during the Plio-Pleistocene period. Subspecies such as ssp. wellingtonensis and ssp. pulvinestris, which are restricted to single massifs, may have evolved during the present interglacial period, while wider ranging subspecies such as ssp. comberi, ssp. gibbsiae and ssp. discolor may have evolved in earlier interglacial periods. The narrow ecological preferences and evidence for some development of barriers to interbreeding indicate that some subspecies have potential for wider morphological divergence. E. hookeri, with its remarkable hand-like leaves, may have evolved in this way from the progenitors of one group of present-day subspecies of E. gibbsiae. Its past placement (Wettstein 1896; Du Rietz 1932b, 1948a), with other “subdigitate”-leaved species of the section, close to Sect. Trifidae and Sect. Anagopormae is misconceived.

The “E. striata line” shows little evidence of active speciation. Of the three distinctive vicarious species, E. striata occurs on mountain tops in the subalpine zone, while the other two occur near sea level, with E. semipicta in coastal heath. Data are required on the morphology and ecology of the unnamed Southport species, but it is possible that E. semipicta is derived from hybridization with E. collina (p. 105).
Fig. 24. Evolutionary diversification of *Euphrasia* in Australia (2). Postulated evolution of the species and subspecies of Sect. *Striatae*, showing some derived states at the branch points. (* indicates a taxon possibly derived by hybridization with Sect. *Australes*; A is a possible alternative position for the origin of *E. gibbsiae* ssp. *wellingtonensis*; B' and B" are alternatives for the origin of *E. hookeri*.)

The former existence of a lineage of Sect. *Striatae* in the eastern highlands of Victoria is discussed on p. 64.


The taxonomic, morphological and ecological diversity of this natural group of sections is probably greater than any comparable group in the genus. It extends across temperate southern Australia, ranging from alpine fjaeldmark to semi-arid mallee communities, and from montane *Nothofagus* rainforest to coastal cliffs.

A relict of the early phase of diversification of the genus, *E. bella* of the perennial section *Australes*, is considered closest to the progenitors of the group. With two other morphologically distinct and geographically isolated species, *E. sp. 'Tamworth'* and *E. bowdeniae*, it forms a vicariant progression in montane eastern Australia (fig. 49). This lineage may itself be old. From their poor collection, the species are probably very rare, and with *E. bella* and *E. bowdeniae* being apparently confined to cliffs, they give the impression of struggling to survive under present conditions. The apparent paraphyletic relationship of this group of species with the rest of the section is indicated on p. 57.
Fig. 25. Evolutionary diversification of Euphrasia in Australia (3). Postulated evolution of the species and subspecies of Sect. Australes, showing some derived characters. (Figures 1 to 3 show the evolution of the species and subspecies of Sect. Australes, Sect. Striatae, and Sect. Seabrook.)
The bulk of the remaining taxa of Sect. *Australes* belong to the highly polymorphic *E. collina* which encompasses almost the whole ecological and geographical range of the genus in Australia. Morphological differences from the *E. bella* - *E. bowdeniae* lineage, may reflect its adaptation to seasonal conditions in sclerophyllous and alpine habitats and to pollinators possibly not available to its progenitors. A capacity for more vigorous growth in deeper soil and more open vegetation may have contributed to development of a more robust habit, and an increased seed production by each plant in response to seasonal drought or snow through a greater ovule number and the production of an abundance of flowers.

A number of lineages are evident in *E. collina*, which all centre on a group of subspecies occupying the sclerophyll forests of south-eastern Australia. It is proposed that the species arose in this habitat, possibly from a stock resembling ssp. *paludosa*. The present lineages appear to be derived from a series of episodes of migration in the Plio-Pleistocene glacial periods (using in some cases exposed land bridges into Tasmania and Kangaroo Island) and contraction in the interglacial periods as the forest and subsequently subalpine and alpine habitats spread and contracted. Disjunct and vicarious distributions in the present-day ranges of the subspecies (tables 7, 8) are evidence of this. At all stages new ecotypes would have been able to develop sympatrically, as seen today in the subspecies on Mt Kosciusko and in the local races of ssp. *diemenica*. In addition, during the migrational episodes, morphological divergence may have occurred on a geographical basis, as seen today in the geographical clines of ssp. *tetragona* and ssp. *collina*, which through extinction of intermediate forms in the contraction episodes, would enhance the creation of isolated variants. The isolated populations on mountains of eastern Victoria which, in a stepped morphological transition, connect the widespread ssp. *paludosa* and ssp. *speciosa* with ssp. *diversicolor* of the Mt Kosciusko region of southern New South Wales (p. 168), have arisen apparently in this way, as may have the vicarious species of Sect. *Lasiantherae* in the same region (see below).

The origins of the one remaining species of Sect. *Australes*, *E. crassiuscula* are problematical, for it possesses the characteristics of both Sect. *Striatae* and Sect. *Australes*. Two subspecies are variable in both characters separating the two sections. Ssp. *eglandulosa* more commonly possesses those of Sect. *Striatae* and in keeping with the climatic range of this section, occupies a higher altitudinal range, while ssp. *crassiuscula* more frequently has the character states of Sect. *Australes*, and, consistent with this, occupies a lower range.* The third subspecies, ssp. *glandulifera*, invariably has the character states of Sect. *Australes*. *E. crassiuscula* is restricted in eastern Victoria to the Bogong-Hotham mountain complex with an outlier on Mt Buffalo. It is proposed that the species evolved from the original sclerophyll forest stock of *E. collina* or from subalpine populations of ssp. *paludosa* with which it is parapatric, and that its characteristics of Sect. *Striatae* have been acquired through introgression, possibly from an extinct lineage, of which *E. gibbsiae* ssp. *subglabrifolia* of Mt Baw Baw may be the sole mainland remnant, and which extended along the higher parts of the eastern Victorian highlands in a former glacial period.

The three species of Sect. *Lasiantherae*, linked by their common attribute of striated corollas, form a vicarious evolutionary series in the Australian Alps (figs 26, 86) possibly derived from the progenitors of the ssp. *paludosa*-ssp. *speciosa*-ssp. *diversicolor* lineage of *E. collina*, to which the perennial *E. lasianthera* is the most closely related. The other two species, being annuals, are clearly derived. Because the

* Sect. *Striatae* occupies mainly alpine and subalpine environments, extending into lowland areas only in the extreme south of Tasmania where similar conditions occur. Sect. *Australes* also extends into subalpine and alpine habitats, but generally occupies lower (milder) altitudes when the two sections are sympatric.
differences between the species are very large in comparison to other allied species in *Euphrasia*, divergence may have occurred over a relatively long period.

The origins of Sect. *Scabrae*, a group of five robust annual species, are a little uncertain but it seems most likely that it was derived from the same stock from which particularly *E. eichleri* and *E. alsa* of Sect. *Lasiantherae* were derived (fig. 26). *E. caudata* (Sect. *Scabrae*) and *E. alsa* show strong similarities and occur sympatrically in the Australian Alps, with the former occupying montane and subalpine habitats, the latter alpine, rarely subalpine locations. *E. scabra* presumably spread during a glacial period across southern Australia, including south-west Western Australia and Tasmania. Relictual populations of its progenital links with *E. caudata* may still be evident in the Australian Alps (p. 276). The section has radiated in the northern and central New South Wales tablelands. A linking species may have occurred in the Blue Mountains (p. 284). Two lineages are apparent in this radiation, and it is likely that *E. orthocheila* ssp. *peraspera*, which shares derived characters of either line, has originated from hybridization between *E. orthocheila* ssp. *orthocheila* and *E. ciliolata*.

Fig. 26. Evolutionary diversification of *Euphrasia* in Australia (4). Postulated evolution of the species and subspecies of Sect. *Lasiantherae* and Sect. *Scabrae*, showing some derived states at the branch points.
H. Euphrasia—an old Tertiary genus?

The following facts are considered to lend support to Euphrasia existing in the early Tertiary or before.

1. The bihemispheric distribution of the genus is matched by a number of homologous distributions, including both primitive groups, e.g. Magnoliaceae-Winteraceae, Fagus-Nothofagus, Cunoniaceae-Dilleniaceae, and advanced groups, e.g. Veronica-Detzneria-Hebe-Parahebe-Chionohebe alliance of the Veroniceae (van Steenis 1971, 1979). The Nothofagus-Fagus generic pair is particularly remarkable for its close-matching range. Van Steenis (1971, 1979) concludes that these common patterns have arisen through an ancient synchronous development and migration across land.

2. As has been demonstrated, there is no evidence that the genus is capable of long-distance dispersal. Much evidence points to the need for migration across land.

3. Bartsia, the close generic relative of Euphrasia (Hartl 1972) has a somewhat complementary range; it occupies the mountains of tropical Africa (c. 8 species) and the northern and central Andes (c. 30 species) (fig. 21; Hedberg 1957; Hartl 1969-72). Diploid populations of B. alpina occupy the European Alps, with derived tetraploids and hexaploids occurring across formerly glaciated areas of the arctic regions. No species cross between the various continents. The two genera are the only members of Trib. Rhinantheae which extend into the tropics and the southern hemisphere (fig. 21). Just as with Euphrasia, the disjunct range of Bartsia appears difficult to explain by long-distance dispersal since the Pliocene.

4. The proposed relicts of the earliest phase of evolution of Euphrasia are widely scattered and often very restricted in their range (fig. 21).

5. At least two relicts show association with Nothofagus forest. E. cuneata of New Zealand is polymorphic and extends into other communities from sea level to subalpine tracts, while E. bella is known only in association with Nothofagus, but is poorly known. This link with Nothofagus is important in view of the late Cretaceous age of the genus (e.g. Muller 1970, 1981; van Steenis 1971; Raven 1979) and the similarity of the range of the Fagoideae and Euphrasia (see point 1).

6. At least some of the relicts occupy habitats which conform with conditions expected between the late Cretaceous and mid Tertiary. The early angiosperms are believed to have radiated into niches unoccupied by the dominant gymnosperms (Doyle & Hickey 1976; Doyle 1977). Doyle specifically mentions the forest floor, a habitat in which I found E. cuneata growing, with little other ground cover under Nothofagus mixed with other species near Wellington, New Zealand. E. bella, E. phragmostoma, E. cuneaia, E. grandiflora (Wettstein 1896) and E. formossissima (Skottsberg 1921) are all known from cliff-faces, with the first two possible confined there. Such a niche might well have been occupied by angiosperm shrubs and woody herbs in the late Cretaceous.

7. The relicts in Euphrasia possess leaves with a broad blade and poorly differentiated petiole, again characteristics of early angiosperms (Doyle 1977; Doyle & Hickey 1976). Euphrasia and other Scrophulariaceae have tricolpate and tricolporate types of pollen;
such generalized types were already known from the late Cretaceous (Muller 1970, 1981; Doyle 1977).

8. Other groups of Australasian Scrophulariaceae show widely disjunct ranges difficult to explain by recent dispersion either by long-distance dispersal or across-land migration. The Veronicaceae are similar to *Euphrasia* in their bihemispheric distribution (see point 1), and their southern representatives showing great diversity and including both primitive and derived attributes (Ehrendorfer 1971; Wardle 1978). The two other major extra-tropical groups, *Stemodia* and the Mimulinae, in particular the group of Australian-centred genera *Elacholoma*, *Peplidium*, *Microcarpaea* and *Glossostigma*, have disjunct trans-Pacific connections which may be as ancient (Barker, in press). To these groups can be added *Ourisia* and *Jovellana* which are the only representatives of their South American-centred tribes to extend from South America into Australasia and New Zealand, respectively. No wide-ranging species are involved, and their distributions may date back to when links across Gondwanaland existed. The ranges of *Gratiola* and *Limosella* remain of doubtful age as these groups need revision and they may include wide-ranging taxa which are associated with mud and are of indefinite evolutionary advancement within the genera.

For *Euphrasia* to have existed as far back as the late Cretaceous, not only must other representatives of the family have existed at that time, but so must have other advanced angiosperm families. A number of these families are cosmopolitan and, like Scrophulariaceae, should be considered in terms of infrafamilial taxa. Others, although small, nevertheless contain distribution patterns with wide disjunctions (e.g. *Bontia* in Myoporaceae, Mr R.J. Chinnock, pers. comm. 1980; *Josephinia* in Pedaliaceae).

The fossil record as yet contains no sufficiently authenticated Tertiary Scrophulariaceae, although (Muller 1981) there are unsubstantiated records from the Paleocene in England and Pliocene (*Hebe*) in New Zealand. The earliest identified pollen of the Scrophulariales is from the Eocene; most families date from the Miocene or more recently (Muller 1970, 1981). An advanced group such as the Compositae dates from the Oligocene. How can these groups be much older?

There is a sampling bias in the fossil pollen record. The chances of including plants which produce relatively little pollen at a given site are severely limited. Pollen production may be restricted by small population size, a limited seasonal production of flowers, and by efficient pollination mechanisms. All these attributes apply to most advanced angiosperms which are herbaceous and bee-pollinated.

Furthermore, the ecological range of a plant group significantly affects its chances of turning up in the fossil record (Martin 1978; Truswell & Harris, in press; Smith-White, in press). Plants such as bee-pollinated types, with a limited range of pollen dispersal, would have to have grown in or close to fossil-forming conditions, such as swamps, lakes or peat-forming sites, for pollen to be deposited in sufficient quantity there. The proposed relicts of *Euphrasia* rarely, if at all, grow in such sites, for below the tree-line their scattered populations may occur in Nothofagus forest which occurs on ridges or slopes, or they may grow on cliff-faces.

The poor coverage of the fossil record is demonstrated in several ways. It is deficient in transitional forms of pollen linking for example the elaborate and diverse types in the Acanthaceae to simpler more primitive types (Muller 1970). Furthermore, for a continent such as Australia, the total of about 50 taxonomic identifications for the Tertiary, some only to family (Martin 1978), indicates a very sparse knowledge of the flora of that period. The discrepancy between the macrofossil and pollen records at given sites also reflects this (Smith-White, in press). Finally, Truswell & Harris (in press) refer to the substantial amounts of fossil pollen belonging to generalized types

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which are able to be assigned to a number of modern families. The pollen of *Euphrasia* is of one such type (Mr W.K. Harris, pers. comm. 1979).

Michener (1979) proposes that bees existed in the latest Cretaceous, when predominantly bee-pollinated groups such as *Ilex* and *Myrtaceae* are first recorded as fossils. The earliest fossil bees, including the most advanced group, the long-tongued Apidae, are known from Eocene deposits in North America and Europe, and several widely disjunct ranges of distribution of bee genera are inexplicable on long-distance dispersal and the land connections available from that time. To accommodate these facts, Michener postulates that bees arose in the mid Cretaceous and became abundant in the late Cretaceous in the xeric interior of Gondwanaland, a view supported by Raven (1979).

A radiation of bees in the late Cretaceous must have been paralleled by a radiation of the plants they pollinated. In other words, advanced largely bee-pollinated groups such as the Scrophulariales and Compositae may well have attained their family and much of their generic make-up during that time. Michener (1979) suggests that the bees diversified in the xeric interior of Gondwanaland, in particular West Gondwanaland where (Raven 1979) the angiosperms are considered to have evolved. In such conditions there is little likelihood of gaining direct fossil evidence for either the bees or the flora. Accordingly, it is suggested that the bee-pollinated groups radiated in similar conditions in the late Cretaceous, but had only limited success invading valley forest or swampy sites until their explosive radiation in Neogene times, linked with newly formed alpine and subalpine sites and the large fluctuations of world climate which favoured diversification of such herbaceous groups.

I. Conclusion

It is accordingly proposed that the present day range and diversity of *Euphrasia* has been attained in two main phases.

Firstly, the genus evolved with other bee-pollinated groups, possibly under seasonally dry or xeric conditions in the late Cretaceous in Gondwanaland. At this time suitable migration routes were available into all continental regions, including the present northern and equatorial land masses, whether via Africa alone (Raven & Axelrod 1972; Raven 1979) or also via a subsequently severed link with south-east Asia (van Steenis 1979). Relictual forms, possibly closely allied to early *Euphrasia*, are scattered in the northern and southern temperate zones (fig. 21). A route via Africa would accommodate the occurrence of *Euphrasia* in the Azores and the allied genus *Bartsia* in the Andean and equatorial mountains of Africa (fig. 21), together with a division of *Euphrasia* into northern and southern hemisphere groups about "Wallacea" (p. 55). The similarity of the sessile gland patterns of the Azorean species and *Bartsia* (p. 79; Yeo 1973) provides confirmation of this. Until the Miocene, *Euphrasia* may have existed in temperate or subtropical conditions on the forest floor or in open sites such as cliff faces, habitats occupied by the proposed relicts today. Indeed, the semi-parasitic habit of Subfam. Rhinanthoideae of the Scrophulariaceae may have developed in response to seasonally dry conditions or to poor water retention by shallow soil in cliff face habitats. Flowers apparently pollinated by a more general group of insects (p. 44) or by Lepidoptera (p. 45), represented today in New Zealand and South America, possibly developed also at this time in habitats rarely frequented by bees. Michener (1979) proposes that the temperate forest which covered much of Gondwanaland was occupied then, as today, by few bees, New Zealand's depauperate bee fauna being explained by an almost complete forest cover at the time of its separation from Gondwanaland about 80 million years ago. However, Smith-White (in press) questions the reality of this broad Gondwanan forest cover as being an
The continued existence of apparently functionless striations on the rear of the corolla limbs of some New Zealand species of *Euphrasia* (p. 44) may point to a relatively recent demise of bees there.

The uplift of mountains and fall in world temperatures in the late Tertiary apparently heralded a second phase of evolution in *Euphrasia*. *Euphrasia* was one of the groups, already of predominantly herbaceous or shrub habit, which migrated into newly formed subalpine and alpine regions. During the climatic fluctuations of the Plio-Pleistocene period, the genus radiated into open communities through its capacity to form ecotypes. Many old forms of *Euphrasia* became extinct during this general phase of diversification in the angiosperms, for it has been proposed that only a few scattered relics remain.

In Australia, the newly diversifying sclerophyllous communities dominated by *Eucalyptus* which may have developed from late Pliocene times at the earliest (Truswell & Harris, in press) provided an opening for further radiation of *Euphrasia*, while in Europe the genus spread into man-made grassland and other communities which developed during the evolution of man's agricultural practices (Karlsson 1974, 1976; Hulten 1976).

The new habitats produced different demands on the morphology of the plant. In alpine conditions vegetative buds were limited to ground level, while pressure of grazing and mowing and/or shortness of growing seasons suppressed plant height and possibly the development of annuals. Reduction of the petioles may have given added strength to the leaf in exposed sites. To what extent floral form and coloration diversified from the late Tertiary in competition with the abundant herb and shrub floras for the available pollinators can only be speculated upon. The flower type restricted to Sect. *Trifidae* of South America and Sect. *Anagosermae* of New Zealand and that of Sect. *Scabrae* are not represented among the proposed relict species. However, if the first two sections are monophyletic (p. 55), it is likely that their flower type evolved during the early phase of generic diversification owing to their occurrence on either side of the south Pacific.

Today, in a region such as Australia where the vegetation has altered radically in the past two centuries, we see a third phase. *Euphrasia* was able to co-evolve with the relatively slow spread of man's influence in Europe during the Quaternary, but it has been incapable of coping with the rapid advent of European man in Australia and the associated pressures of clearing, ploughing and grazing. As a result many taxa are now rare and at risk. Some, indeed, may have become extinct.

**IV. A REVISED INFRAGENERIC CLASSIFICATION OF EUPHRASIA**

**A. PREVIOUS INFRAGENERIC CLASSIFICATIONS**

Although a number of botanists have discussed the infrageneric classification of *Euphrasia*, only Bentham (1846), Wettstein (1896), and Hartl (1972) have dealt with the classification on a world-wide basis. The two earlier workers are the only botanists to revise the entire genus. Except for changes in rank, the addition of two small morphologically and geographically isolated infrageneric taxa, and the segregation of two monotypic genera in New Zealand, which were soon reduced to synonymy, a basic framework of three large infrageneric taxa has been maintained since Bentham's time.

Bentham (1846) divided the genus into three categories of equal status, but with no clear indication of rank (see Sell & Yeo 1970). His S *Semicaratae*, characterized by "Antherae pilosae, mucronatae, duorum breviorum posticarum loculus alter longius calcaratus . . . Folia inferiorter crenata, floralia summa saepe acutius incisa vel dentata",
was confined to the northern hemisphere except for one species in New Zealand (E. cuneata). S Australes, distinguished by its “Antherae pilosae, omnes subaequaliter mucronatæ . . . Folia apice paucicrenata rarius fere a basi crenata”, was restricted to “Australasia” (which is probably Australia, as he cited only Australian species and localities). S Trifidae of South America, with one questionable record from the Himalayas, differed by its “Antheræ glabrae, aequaliter mucronatae . . . Folia sessilia cuneato-trifida vel tripartita”. Of the Himalayan plant resembling the South American species in habit and leaf shape, Bentham saw only one corolla and was doubtful of its placement even within the genus (he wrote “E. ? glandulosa”). The specimen was later placed by Bentham & J.D. Hooker (1876) in the related genus Phtheirospermum.

J.D. Hooker (1879) described a new species, E. disperma, from New Zealand which, together with E. repens, he placed in a new subgenus Anagosperrae. The subgenus, characterized by its 2-4-ovulate ovaries, solitary flowers, prostrate habit and remarkably long corolla tube, was possibly a distinct genus providing the capsules were found to be indehiscent. Two years later on the basis of meagre material containing a single flower, Armstrong (1881) described a new genus, Siphonidium, from New Zealand, closely related to Euphrasia but differing “in the long curved gibbous tube and bi-lobed stigma”. He did not mention Hooker’s subgenus even though the two descriptions are similar. Wettstein (1895), having seen fruiting material of what he considered to be E. disperma, elevated Hooker’s Subgen. Anagosperrae to a genus: “. . . . . . . . . . . differt ab Euphrasia tubo corollae elongato, labio corollae superiore non excavato, antheris patentibus et glaberrimis, imprimis vero loculis germinis uniovulatis et fructu bicorni bispermo. A Siphonidio Armst. differt tubo corollino recto, stigmate non bilobo, probabiliter etiam fructu et germine”.

At length the status of these genera was questioned. Certain that Anagosperrae and Siphonidium were identical, Cheeseman (1925) united them under the latter, earlier-published name. Then, in his detailed account of “The long-tubed New Zealand species of Euphrasia (= Siphonidium Armstr.)” Du Rietz (1932a) showed that: “there is such a gradual transition between Siphonidium and Euphrasia sens. strict., that it is not possible at our present stage of knowledge to retain Siphonidium as a separate genus . . . . it seems even doubtful whether Siphonidium should be retained as a subgenus or section”.

Wettstein (1896) saw much more material of the extra-European members of Euphrasia than Bentham, but like his fellow-European botanist, he knew nothing apart from a Bornean record in his addendum, of the Taiwanese and Malesian species. He saw material of most of the New Zealand species, whereas Bentham apparently saw only E. cuneata. His major classification of the genus was similar to Bentham’s using identical characters. He treated S Semicalcaratae (which included all the northern hemisphere occurrences in the genus) and S Australes (comprising all Australian and New Zealand species, including E. cuneata) as subsections of Sect. Eueuphrasia, Bentham’s S Trifidae excluding the Himalayan species, was treated as a section. Sect. Trifidae and Subsect. Australes were divided into annual and perennial groups which were not given formal taxonomic recognition. Wettstein also divided Subsect. Semicalcaratae into three unranked groups, § Parviflorae, § Grandiflorae and § Angustifoliae on the basis of differences in the time of elongation of the corolla tube relative to anthesis, the breadth of the leaves and the indumentum of the capsule. Subsequent European botanists (e.g. Joergensen 1919; Pugsley 1930, 1936; Sell & Yeo 1970; Yeo 1972) have considered the character of the elongation of the corolla tube to be of lesser, or even doubtful, diagnostic use.

The upgrading by Joergensen (1919) of Wettstein’s sections and subsections to subgenera and sections respectively has been followed in all subsequent works on the genus up to Hartl’s (1972) publication (see below). Joergensen’s recognition of two
subsections in Sect. *Eueuphrasia*, namely Subsect. *Angustifoliae* (equivalent to Wettstein's § *Angustifoliae*) and Subsect. *Ciliatae* (covering Wettstein's § *Parviflorae* and § *Grandiflorae*) on the same characters of leaf shape and capsule indumentum used by Wettstein, has been universally accepted. Joergensen refined the character of leaf shape by recognizing the apparently reliable differences between the two subsections in the proximity of the teeth along the margins. Since Joergensen's time Subsect. *Ciliatae* has been progressively divided into a number of series, especially by Pugsley (1930, 1936) and Sell & Yeo (1970). These series are distinguished by the combination of a number of often overlapping characters including habit, indumentum, leaf and bract shape, corolla size, and capsule size and shape.


In the same paper, Pugsley proposed two new sections. One Sect. *Atlanticae*, endemic to the Azores, was distinguished on the basis of its perennial life-span, rounded leaves and deeply emarginate capsules. Yeo (1972, 1973) has recently modified the diagnostic characters of this section, using its perennial life-span, more numerous leaf teeth, distinctive leaf indumentum and large flowers to distinguish it from the rest of the European and North American species. The distinctive capsule shape described by Pugsley for one species of the section was found not to occur in the other Azorean species.

Pugsley's other new section, Sect. *Paradoxae*, was based on a single species *E. formosissima* of the Juan Fernandez Islands west of South America. The section was characterized by a unique method of perennation and also by "entire (not emarginate) lobes of the lower lip of the corolla, . . . glabrate, unequally spurred anther-cells and . . . scarcely retuse, setulose-edged capsules". Skottsberg (1921), who described the species, and Wettstein (1921) had previously remarked on its isolated morphological characteristics and its apparent affinities to the Japanese and Australasian members of the genus.

There have been no major changes in the infrageneric classification of *Euphrasia* in the northern hemisphere since Pugsley's works. Sell & Yeo (1970) have correctly called the section containing the type species of the genus Sect. *Euphrasia* in place of Sect. *Semicalcaratae* (Benth.) Joerg. In addition they have revised Pugsley's classification of Subsect. *Ciliatae* at the level of series.

Although there has been little change in the formal classification of the genus in the southern hemisphere and Malesia since Wettstein's (1896) monograph, knowledge of the characters potentially useful in an infrageneric classification has been greatly increased by the work of Du Rietz (1932a,b; 1948a,b). Du Rietz never published his proposed paper (see Du Rietz 1932a, p.121) on the general subdivision of the genus. Considering the depth and breadth of his work he did little formal taxonomic work. He proposed on the basis of capsule shape two subsections, Subsect. *Australienses* and Subsect. *Novaezeelandiae* (Du Rietz 1948b), of (presumably) Sect. *Australes*, covering the Australian and New Zealand species respectively. He also divided the Australian species into four series, *Striatae, Collinae, Hookeriae* and *Scabrae*. For this he used characters of lifespan, habit and leaf shape (Du Rietz 1948a,b). In his critical discussions of the relationships between the species of *Euphrasia* in South America, the Juan Fernandez Islands, Australia, Tasmania, New Zealand, New Guinea, Borneo, the Philippines, Taiwan and Japan, Du Rietz discerned several characters to be useful in distinguishing groups of species. Among these were the pilosity and colour of the anthers, shape of the corolla lobes, leaf shape and habit. It is not clear
whether he recognized the importance of the free anthers characteristic of the South American species and *E. disperma* of New Zealand. His term “patent anthers” seems to refer more to the orientation of the cells of each anther in these species (see Du Rietz 1932a, p.118, especially in his comparison with f.1). In descriptions of the long-tubed species of *Euphrasia* in New Zealand (*E. disperma* sensu Ashwin 1961) he referred to the anthers as “non cohaerentes”. Du Rietz also questioned usage since Bentham’s time of the length of the rearmost pair of anther awns relative to the other awns to distinguish between the species of the southern and northern hemisphere, but he still considered that “subequally mucronate anthers” were characteristic of all the South American species, some New Zealand species and *E. striata* of Tasmania (Du Rietz 1932b, p.532).

Ashwin (1961) gave a synopsis of the main character differences in *Euphrasia* in New Zealand without proposing any formal infrageneric classification. She divided the perennial species into two main groups, one containing only *E. cuneata* and characterized by much-branched inflorescences and small bracts, the other with inflorescences simply racemose and with leaf-like bracts. This latter group, which contained the six remaining perennial species, was further divided on the indumentum of the calyx and the relative lengths of the calyx clefts. The annuals were divided into two main groups on leaf and habit characters, the species of the first group, *E. cockayniana*, *E. zelandica*, *E. australis*, and *E. cheesemanii*, having leaves of the “ovate order, crenate or toothed” and erect branches which never root, and those of the second group, *E. dyeri*, *E. repens*, *E. integrifolia* and *E. disperma* having mostly decumbent or prostrate branches, which sometimes root, and leaves either deeply divided or entire and of the lanceolate type. This second group was further split into three on the basis of the same characters of leaf and habit type.

In 1972 Hartl revised the higher classification of *Euphrasia* on a world-wide basis. Of significance is his treatment of all Joergensen’s (1919) and Pugsley’s (1936) taxa of the rank of subgenus or section at the one level of section. Thus his major classification of the genus was composed of five sections. He followed Pugsley’s division of Sect. *Semicalcareae* (Hartl’s Sect. *Euphrasia*) into four subsections without alteration of the somewhat obscure diagnostic characters of the Japanese subsections. Sect. *Australes* was expanded to include the Malesian and Taiwanese species, which had been previously unplaced in the infrageneric classification. He believed that both Sect. *Australes* and Sect. *Trifidae* could be subdivided into a number of subsections.

**B. THE REVISION**

1. **Introduction**

The proposed classification of *Euphrasia* represents a radical departure from the concepts in previous works, in which the genus has been divided into three major groups of varying rank, together with, from 1936, two peripheral sections. In the new classification, with the exception of Sect. *Pauciflorae* (2 subsections) and Sect. *Euphrasia* (the 4 subsections recognized by Pugsley being retained), the infrageneric groups recognized have been given equal status as sections (the many series in Subsect. *Ciliatae* have not been considered). Each section is separated by only one or two distinct characters from at least one other section. However, sometimes there is quite remarkable divergence of a transitional nature, away from the most closely linked species of related sections.

There are a number of differences in usage of characters from previous classifications, and several new diagnostic characters have been discerned. The characters are discussed in detail in the chapter dealing with morphology. The very obvious free anthers of the South American species and *E. disperma* of New Zealand have surprisingly never been used diagnostically before, except in the distinction of *E. disperma* from its related
species (Ashwin 1961). The presence or absence of corolla striations, the presence or absence of hairs on the back of the anthers, the number of main veins arising from the very base of the leaf, the distinctive corolla shape of Sect. *Australas* and especially Sect. *Scabrae*, and the size of the stigma are all characters which have previously not been used in the infrageneric classification of *Euphrasia*. Some of the characters, however, have been used to a small extent at the species level. Other characters have been refined in their definition. The distinction between "petiolate" and subsessile leaves used by Pugsley (1936) for *E. formosissima* and Ashwin (1961) for *E. cuneata* has not been considered an accurate statement of the differences. In this work the shape of the leaf base has been described adhering to a rigid terminology, and its diagnostic value is not in the areas used previously. The depth of the leaf toothing has been treated differently from the rather vague terminology used by Du Rietz (1948a,b) in which he separated "digitate" and "subdigitate" types from the rest of the genus. The "blade" (defined on p. 14) is either small (little of the area within the leaf outline) or large (much of the area within leaf outline).

Two characters used in the past to distinguish infrageneric taxa have been found to be of little use at that level. Contrary to observations of all previous workers on the infrageneric classification, the rearmost pair of anther awns has been found to be consistently longer than the other six awns in all the material seen (p. 32). Similarly, Du Rietz's opinion that the Australian and South American species have a unique "acuminate" capsule shape is a misconception (p. 34).

2. Revision

The extra-Australian species cited in the text are those recognized in the most recent regional treatments of the genus. These are Wettstein (1896) and Reiche (1911) for South America, Ashwin (1961) for New Zealand, van Royen (1972) for New Guinea, Du Rietz (1932b) and van Royen (1971) for Malesia, Ohwi (1933) and Li (1950, 1978) for Taiwan, Skottsberg (1921) for the Juan Fernandez Islands, and Yeo (1972, 1973) for the Azores. The many species in the remaining regions of the northern hemisphere have not been listed in this conspectus.

Where herbarium collections which are not types of a species have been seen, the species is designated by "!". If type material has been seen this is designated by "T".

Sections and subsections are ordered in a sequence which as far as possible places closest allies adjacent, commencing with the autonomous taxon.

**EUPHRASIA L.**


Annual or perennial terrestrial herbs or undershrubs; single main root branched laterally, the lateral rootlets often connected to the roots of other plants by haustorial swellings. Axes with indumentum consisting entirely or partly of eglandular hairs which are often in two bands or four lines decurrent from between leaf bases, sometimes all around, sometimes lacking in lower parts. Cotyledons entire, fleshy, glabrous. Leaves decussate, appressed to axis at base, usually then recurved, fleshy but usually brittle, rarely (*E. bowdeniae*) pliant when dry; abaxial surface usually with patches of sessile glands symmetrical about midrib, confined to marginal rows or extending over most of blade between veins, rarely (Sect. *Atlanticae*) with sessile glands confined to veins;
margins somewhat revolute, usually shallowly to deeply incised, rarely entire; main veins prominent on abaxial surface, submerged below adaxial surface and tipped by narrow grooves. Inflorescences simple, terminal, sometimes spike-like racemes, or consisting of solitary flowers. Bracts similar in morphology to leaves immediately below inflorescence, but often differing slightly in shape and indumentum. Calyx zygomorphic, campanulate or ± cylindrical, slightly recurved, 4-lobed, with median clefts equal to or longer than lateral clefts. Corolla bilabiate, with tube proximally cylindrical, distally expanded and then divided into hooded upper lip, which usually encloses the anthers and is terminated by two abruptly reflexed lobes, and a three-lobed lower lip; with at least outer surface and front of inner surface of hood pilose. Stamens 4, didynamous, the posterior pair inserted higher on the corolla tube than anterior pair; filaments straight or curved; anthers free, or fused to each other along margins into a U shape with the posterior pair free from each other, with each cell clavate, dehiscing introrse by longitudinal slit which is widest towards anther base and terminated in sharp awn, the rearmost pair of awns longer than the other six awns. Gynoecium: ovary 2-celled, slightly compressed laterally, with a nectary at base on abaxial side; style filiform, passing above or (sometimes when anthers free) between anthers, setose in upper half; stigma capitate, oblong or unequally bilobed; ovules 2-200. Capsule dehiscent loculicidally, with base of style persistent for short length; seeds 0-150, obliquely ± ellipsoid, longitudinally ribbed or (E. azorica) winged, scalariform between, whitish. Chromosome number: variable (see infrageneric taxa).

Typification

Euphrasia L. Linnaeus (1753) included under the protologue of Euphrasia the currently recognized genera Odontites (his E. odontites, E. linifolia and E. lutea) and Parentucellia (his E. latifolia). The remaining two species in the protologue, E. officinalis and E. tricuspidata, have been shown to fall closest to Linnaeus’s (1754) generic description of Euphrasia (Pennell 1930), which must be taken into account for typification (ICBN: Art. 13.4, Art. 41), and fall into the limits of the genus in the strict sense in which it has been generally treated since 1830 (Pugsley 1930).

The lectotypification of the genus began with Britton & Brown's (1913) selection of E. officinalis. Despite the arbitrary nature of their choice, Pennell (1930) argued that this was the logical decision taking Linnaeus’s (1754) generic description of Euphrasia into account. The selection also accords with Linnaeus's apparent generic concepts and methodology, for Stearn (1957) indicates that Linnaeus based his generic descriptions on the “best known and officinal plant”.

According to Pugsley (1930) material of the two Linnean species of Euphrasia s.str. is contained in the Linnean herbarium (LINN), “the sheet of the former [E. officinalis] showing three specimens, of which two are the glandular E. rostkoviana Hayne, and the third* an eglandular form that has been referred to E. nemorosa Pers. but is more probably the Scandinavian E. curta Fr. E. tricuspidata is represented by a single unmistakable example”. Sell & Yeo (1970) selected as lectotype of E. officinalis the element of the type which corresponds to E. rostkoviana.

Because of the difficult taxonomy of the northern hemisphere annuals (Sect. Euphrasia), E. officinalis has often been used in a very broad sense encompassing many described species accepted as distinct by others, and it is for this reason that the name has been rejected as a nomen ambiguum in recent times (Smejkal 1963; Sell & Yeo 1970; Yeo 1972, 1978b). On this basis also Smejkal (1963) rejected the species E. officinalis as the lectotype of Euphrasia in favour of E. tricuspidata, but the decision was reversed (without discussion) in favour of the initial choice E. officinalis by Sell

* Now considered to be E. stricta Wolff ex Lehm. (Yeo 1972).
& Yeo (1970), as lectotypified by them but with the name rejected in favour of *E. rostkoviana*. Article 69 of ICBN, however, places in serious question the rejection of the name *E. officinalis* as a *nomen ambiguum*, for it does not appear that the name has been used widely and persistently in a sense excluding its type, as is now required for rejection of a name under this article.

**Distribution** (fig. 19): *Euphrasia* is one of the few groups of rank higher than species with a centre of diversity in the temperate zone of both hemispheres and a connection through Malesia. *Euphrasia* is usually a microtherm (cold-inhabiting) genus spread widely in the northern temperate zone, with outposts in the Azores and North Africa. Its southern temperate distribution is in southern Australia, New Zealand and southern South America, including the Juan Fernandez and Falkland Islands. These zones of distribution in either hemisphere are connected by a relatively continuous series of localities on the highest mountains of Taiwan, the Philippines, Borneo, Celebes, Ceram and New Guinea.

The genus is divided in this revision into 14 sections. Twelve of these are well-defined homogeneous groups (*Sect. Pauciflorae* being subdivided into two subsections), and constitute all representatives of the genus between Taiwan and the Juan Fernandez Islands, as well as the distinctive species of the Azores. Together they comprise 59 species, although future revision adopting the species concepts of the present Australian revision, particularly in *Sect. Pauciflorae* and the Taiwanese species of *Sect. Malesianae*, may reduce this number to about 50.

Comparable numbers of subsections and species in the remaining two sections, *Sect. Euphrasia* and *Sect. Trifidae*, are difficult to estimate. While constituting natural groupings, they require revision at both the infrageneric and species level. There have been recent revisions at the species and series level in *Sect. Euphrasia* in parts of its wide range, for example for Europe (Yeo 1972, 1978b), North America (Sell & Yeo 1970), Russia (Juzepcuk 1955), China (Li 1953), Western Himalayas (Pennell 1943), and Japan (Kimura 1941, 1948; Ohwi 1965), but as the species concept has been very narrow and there are a number of widely distributed species (Sell & Yeo 1970; Hultén 1976), a revision encompassing the whole section seems desirable. This would also provide the basis for a review of the infrasectional taxonomy, in particular in relation to the segregation of the two Japanese endemic subsections (see Sect. *Euphrasia*: note). *Sect. Trifidae* has not been revised since Wettstein's (1896) monograph of the genus and Reiche's (1911) reappraisal of the Chilean representatives. The section shows diversity in duration (both annuals and perennials) and floral morphology (pp. 28, 45), characters of potential importance at the sectional or subsectional level.

### KEY TO THE SECTIONS AND SUBSECTIONS OF *EUPHRASIA*

1a. Anthers, at least posterior pair, hairy about connectives. Leaves usually truncate to cuneate at base, rarely (*E. bella*) attenuate, with (1)3-7 main veins arising from base.

2a. Corolla striated .................................................. IX. *Sect. Lasiantherae* (p. 85)

2b. Corolla lacking striations.

3a. Perennial. Branches on main inflorescence-bearing axis developing in no fixed sequence, not consistently in consecutive nodes if high above ground level. Upper corolla lobes ± coplanar, facing forward ................. VIII. *Sect. Australes* (p. 84)

3b. Annual. Branches on main inflorescence-bearing axis developing basipetally in consecutive nodes high above ground level from 1-few nodes below inflorescence. Upper corolla lobes usually angled sharply to each other, facing to side. .......................... X. *Sect. Scabrae* (p. 86)
1b. Anthers glabrous about connectives. Leaves attenuate at base, with (1)3(5) main veins arising from base.
4a. Anther slits glabrous or with 1 or 2 tiny hairs along margins.
5a. Perennial.
6a. Leaves shallowly lobed, with (3)4(5) pairs of teeth. Anthers fused, with slits very sparsely hairy. Corolla lobes obtuse. .... XII. Sect. Paradoxeae (p. 88)
6b. Leaves deeply divided with 1(2) pairs of teeth. Anthers free, with slits glabrous. Corolla lobes emarginate or shallowly so. .... XIV. Sect. Trifidae (p. 89)

5b. Annual.
7a. Leaves crenate to serrate. [Anthers fused.] .... XI. Sect. Novaezeelandiae (p. 87)
7b. Leaves pinnatifid, trifid or entire.
8a. Main inflorescences with more than 10 flowers. Anthers free. Plant erect, with uppermost leaves of main inflorescence-bearing axis with 1(2) pairs of teeth. .... XIV. Sect. Trifidae (p. 89)
8b. Main inflorescences with less than 10 flowers, or flowers sporadic along axes. Anthers fused or free. Plants either erect with uppermost leaves of main inflorescence-bearing axis with 1-3 pairs of teeth or prostrate with leaves entire or with 1 pair of teeth. .... XI. Sect. Anagospemae (p. 88)

4b. Anther slits distinctly hairy.
9a. Stigma (0.2)0.3-0.5mm long or longer. Corolla lobes emarginate to obtuse or acute.
10a. Annual .... XI. Sect. Novaezeelandiae (p. 87)
10b. Perennial.
12a. Rearmost pair of anther awns (1.5)2.5-3.2mm long, as long as or longer than anthers, sometimes needle-shaped and entire, sometimes distally flat and twisted or erosulate. [Branches or shoots on main inflorescence-bearing axes at widely spaced groups of nodes, developing within groups in basipetal sequence in consecutive nodes. Corolla lacking striations.] V. Sect. Phragmostomae (p. 81)
12b. Rearmost pair of anther awns to 0.8mm long, shorter than anthers, needle-shaped, entire.
13a. Plant tall. Branches or shoots on main inflorescence-bearing axis(es) developing in consecutive axils from 1-few nodes below inflorescence in basipetal sequence. [Corolla striated.] .... IV. Sect. Cuneatae (p. 80)
13b. Plant short or tall. Branches or shoots on main inflorescence-bearing axis(es) developing sporadically in axils, often only near ground level, and in no fixed sequence.
14a. Flowers in main inflorescence 2-8(12). Corolla striated or lacking striations. .... VI.A. Sect. Pauciflorae Subsect. Pauciflorae (p. 82)
14b. Flowers in main inflorescence (7)10-24(36). Corolla striated, at least partially. .... VII. Sect. Striatae (p. 83)

9b. Stigma 0.1-0.3mm long. Corolla lobes emarginate.
15a. Perennial.
16a. Uppermost leaves on main inflorescence-bearing axis(es) with (5)7-12 pairs of teeth. Corolla 13-17mm long along upper side. II. Sect. Atlanticae (p. 78)
16b. Uppermost leaves on main inflorescence-bearing axis(es) with 2-4 pairs of teeth. Corolla c. 6-10mm long along upper side. III. Sect. Malesianae (p. 79)
15b. Annual. [Uppermost leaves on main inflorescence-bearing axis with (1)2-6(7) pairs of teeth. Corolla c. 3-13.5mm long along upper side.] I. Sect. Euphrasia (p. 77)
I. Sect. Euphrasia


Annual. Main inflorescence-bearing axis single erect stem, developing branches ± basipetally in consecutive nodes from the node below the inflorescence. Uppermost leaves of main axis pinnatifid-serrate to crenate, with base attenuate, abruptly (Subsect. Ciliatae, ? Subsect. Japonicae p.p.) or gradually (Subsect. Angustifoliae, Subsect. Alpicolae) expanded into large blade, with (1) 2-6 (7) teeth along distal c. 2/3 - 7/8 of each margin; with 3 main veins arising from base of leaf, branched distally. Flowers 4-50 in (main) racemes. Corolla striated, with yellow blotch on lower lip, or (in Subsect. Alpicolae) with purple blotches behind upper lip and in tube, with lower side apparently concave from above, spreading from base of lower lip; lobes emarginate. Anthers fused, glabrous around connectives, hairy along slits; awns entire. Ovary with stigma capitate, 0.1-0.3mm long. Capsules in lateral view usually emarginate, sometimes obtuse or obliquely so. Chromosome number: n=11, 22.

Typification

S Semicalcaratae Benth. E. cuneata of New Zealand is excluded from consideration as a possible lectotype since it was omitted by Wettstein (1896) and all subsequent authors from infrageneric taxa based on S. Semicalcaratae. Similarly, E. grandiflora has not been considered in view of its segregation as a separate section since Pugsley’s (1936) work. E. officinalis is chosen as lectotype as it must almost certainly have been the most abundant of the remaining two species seen by Bentham. Under Bentham’s concept it covered a multitude of variants which are now considered to be distinct species.

Distribution: Sect. Euphrasia is widespread in the northern temperate and holarctic zones in North America, Eurasia as far south as the Himalayas, north-west Africa (Morocco) and Japan. Hulten (1976) gives a detailed account of the distribution of the section, including maps. Of particular biogeographical importance is the occurrence of the genus in North America and northern Eurasia in areas glaciated in the Pleistocene, with pre-glacial localities in the southern areas of Eurasia containing close relatives of the northern taxa. The taxonomy of this section is notoriously difficult. Its species are perhaps equivalent to geographical and ecological races and are often termed “microspecies” (Yeo 1967, 1978a,b; Sell & Yeo 1970; Hulten 1976; Karlsson 1974, 1976). The problem of classification is compounded by the phenomenon of “seasonal dimorphism” within species (p. 6).

Note: Pugsley (1936) divided Sect. Euphrasia into four subsections. From breeding and chromosomal studies (Yeo 1966, 1967, 1978b; Sell & Yeo 1970), the two subsections occurring in Europe, Subsect. Ciliatae and Subsect. Angustifoliae, represent natural groupings. Pugsley (1936) divided Subsect. Ciliatae, the largest of the two subsections, into a number of series. Sell & Yeo (1970) have found this useful, and have made a number
of modifications to Pugsley's classification including the description of several new series. Hartl (1972) retained Pugsley's four subsections of Sect. *Euphrasia* but has not clarified the status of the Japanese subsections. I have seen very few specimens of the Japanese species of these subsections, but a check of their descriptions by Ohwi (1965) shows some of Pugsley's diagnostic characters for the two subsections to break down, particularly the pilosity of the capsules and the calyx lobing. I am also doubtful of the diagnostic reality of the relative shape and depth of toothing of bracts and upper leaves. Nevertheless, there is clearly diagnostic potential at the infrageneric level in the peculiar purple blotching of the base of the corolla lip used by Pugsley (1936) in his diagnosis of Subsect. *Alpicolae*. The distinction of abruptly and gradually attenuated types of leaf base and the "glandular-fimbriate" corolla hood attributed by Pugsley to Subsect. *Alpicolae* may also prove useful diagnostically.

A. Subsect. *Ciliatae* Joerg. :
   
   In Europe 42 species (Yeo 1972, 1978), 15 (including possible introductions from Europe) in North America (Sell & Yeo 1970), and an undetermined number in Asia.

B. Subsect. *Angustifoliae* (Wettst.) Joerg. :
   
   In Europe 6 species (Yeo 1972, 1978) and one possibly introduced species in North America (Sell & Yeo 1970).

C. Subsect. *Japonicae* Pugsley :
   
   Undetermined number of species, endemic to Japan.

D. Subsect. *Alpicolae* Pugsley
   
   Undetermined number of species, endemic to high mountains of Japan.

II. Sect. *Atlanticae* Pugsley, J. Bot. (Lond.) 74 (1936) 284

Perennial, of "Cuneata" habit type; main inflorescence-bearing axes 1 to several, erect, developing branches basipetally in consecutive nodes from c. 1-2 nodes below the inflorescence. Uppermost leaves of main axes crenate to serrate, with base shortly attenuate, abruptly expanded into large blade, with (5)-7-12 teeth along greater part of each margin; with 3-5 main veins arising from base of leaf, branched distally. Flowers c. 15-20 or more in (?main) racemes. Corolla with presence of striations unknown, with yellow spots on the lower lip; lobes emarginate. Anthers fused, glabrous around the connectives, hairy along slits; awns entire. Ovary with stigma capitate, 0.2-0.25 mm long, Capsule in lateral view deeply emarginate (*E. grandiflora*) or acuminate to cuspidate (*E. azorica*). Chromosome number unknown.

Distribution: The section consists of two species which are endemic to the Azores of the Atlantic Ocean. They are apparently confined to the mountain regions (Yeo 1972) and geographically separated on two distinct groups of islands about 200km apart (Yeo 1973). *E. grandiflora* occurs on cliffs (Wettstein 1896) and on "shallow soils near lava flows" (Tutin 1953).
Notes

1. No material of this section has been seen. The description is compiled largely from information kindly provided by Dr P.F. Yeo (pers. comm. 1976) as well as from Wettstein (1896), Pugsley (1936) and Yeo (1972, 1973).

2. Yeo (1973) refers to the distinctive characters in Sect. Atlanticae of the type of leaf venation (a prominent reticulum of veins visible on the lower side of the leaf between the main veins) and leaf indumentum (sessile glands confined to veins on lower side, and eglandular hairs when present confined to the main veins and the spaces between the veins). He states that these characters are present nowhere else in Euphrasia, but occur in related genera of Trib. Rhinantheae. Unfortunately, little extra-Australian material was available to me when I learnt of these characters. Certainly such attributes are not present in any of the Australian species, E. cuneata of New Zealand, Sect. Novaezeelandiae, Sect. Pauciflorae and Taiwanese material of Sect. Malesianae. On the lower side of the leaves in all of the species studied, sessile glands occur between the veins, eglandular hairs may be spread generally over the leaves when they are present in profusion, and veins other than the main veins are not particularly, if at all, prominent.

3. Yeo (1973) draws attention to the unequally 5-6-winged seed, a character known only in E. azorica. As Yeo points out, with seed morphology unknown in E. grandiflora, it is not known whether this character may be diagnostic for Sect. Atlanticae. If, however, E. grandiflora has the typically many-ribbed seeds of the genus, then there would be strong grounds for separating E. azorica, also peculiar in its bicornute capsules, as a separate section or, at the least, a subsection of Sect. Atlanticae.

E. grandiflora Hochst.

E. azorica Watson

III. Sect. Malesianae Barker, sectio nova


Herbae perennes, Axes principales inflorescentigeri singularis usque multi, erecti ascendentesve, ramos inordinatos in nodis sporadicis continuisve usque 1-aliquot nodos infra inflorescentiam crescentes. Folia summa axis principalis crenata usque serrato-crenata, base breve attenuata, in laminam amplam abrupte expansa, (1)2-4 dentibus secus c. (1/5)2/5-4/5 partes distales cuiusque marginis; 3 venis principalibus ad basem folii. Flores 2-20 in racemis principalibus interdum interruptis. Corolla c. 6-10mm longa, striata in labio supero, labio infero e base de cucullo patenti; lobis emarginatis vel non profunde. Antherae coniunctae, circa connectivas glabrae, secus rimas pilosae; aristis integris. Ovarium stigma oblique capitata vel fere inaequaliter bilobata, 0.15-0.3mm longa. Capsulae in aspectu laterali obovatae vel late obovatae, apice obtuso vel non profunde ita, saepe oblique latere ita. Chromosomaturn numerus ignotus.

Holotypus: E. philippinensis Du Rietz

Perennial, of “Malesianae” habit type; main inflorescence-bearing axes one to many, ascending or erect, developing branches in no fixed sequence in occasional or consecutive nodes high above ground level, up to 1-few nodes below inflorescence. Uppermost leaves of main axes crenate to serrate-crenate, with base shortly attenuate, usually abruptly, rarely gradually expanded into large blade, with (1) 2-4 teeth along distal c. (1/5)2/5-4/5 of each margin; with 3 main veins arising from base of leaf. Flowers 2-20 in sometimes interrupted (main) racemes. Corolla striated (data on type of E. borneensis and from dried material of E. merrillii and E. philippinensis) on upper lip, with lower lip spreading from base away from hood; lobes emarginate but sometimes
(in *E. bilineata*, *E. nankotaizanensis*) very shallowly so. *Anthers* fused, glabrous about connectives, hairy along slits; awns entire. *Ovary* with stigma obliquely capitate or almost (unequally) bilobed, 0.15-0.3mm long. *Capsules* in lateral view obovate or broadly so, laterally compressed; apex in lateral view obtuse or shallowly emarginate, often obliquely or broadly so. *Chromosome number* unknown.

**Distribution:** Sect. *Malesianae* occurs in the highest parts of the mountains of Taiwan, the Philippines (Luzon), Borneo (Mt Kinabalu) and Ceram.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
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<tbody>
<tr>
<td><em>E. nankotaizanensis</em></td>
<td>Sect. <em>Malesianae</em></td>
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<tr>
<td><em>E. durietziana Ohwi</em></td>
<td><em>E. bilineata Ohwi</em></td>
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<tr>
<td><em>E. tarokoana Ohwi</em></td>
<td><em>E. transmorrisonensis</em></td>
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<tr>
<td><em>E. pumilio Ohwi</em></td>
<td><em>E. merrillii Du Rietz</em></td>
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<tr>
<td><em>E. exilis Ohwi</em></td>
<td><em>E. philippinensis Du Rietz</em></td>
</tr>
<tr>
<td><em>E. borneensis Stapf</em></td>
<td><em>E. ceramensis van Royen</em></td>
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<tr>
<td><em>E. masamuneana Ohwi</em></td>
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**IV. Sect. Cuneatae Barker, sectio nova**

**S Sect. Cuneatae Barker, sectio nova**


**S Semicalcaratae auct. non Benth.:** Benth. in DC., Prodr. 10 (1846) 552, p.p. (as to *E. cuneata*).


**Herbae perennes. Axis principalis inflorescentiger caulis erectus singularis vel aliquot rami erecti ascendentesve caulis similares, rami in nodis continuos de 1-aliquot infra inflorescentiam basipete crescentibus. Folia summa axis principalis crenata, base attenuata, in laminam gradatim expansa, (1)2(3) dentibus secus 1/4-1/2 partes distales cuiusque marginis; 3 venis principalibus ad basem folii. Flores c. 15-50 in racemis principalibus. Corolla striata, macula flava in tubo et (in *E. cuneata* solum) in labio infero, lato infero e base labii inferi de cucullo patenti; lobis vix usque profunde emarginatis. Antherae coniunctae, circa connectivas glabrae, secus rimas pilosae; aristis integris. Ovarium stigma obliquae usque oblongae usque inaequaliter bilobata, (0.2)0.3-0.6mm longa. Capsulae in aspectu laterali ovatae usque obovato-ellipticae, apice emarginato usque obtuso. Chromosomatum numerus ignotus.

**Holotypus:** *E. cuneata* Forst. f.

Perennial, of "Cuneata" habit type; main inflorescence-bearing axis single erect stem or several erect or ascending stem-like branches, with branches developing basipetally in consecutive nodes, from 1-few nodes below inflorescence. Uppermost leaves of main axis crenate, with base attenuate, gradually expanded into large blade, with (1)2(3) teeth along distal 1/4-1/2 of each margin; with 3 main veins arising from base of leaf. Flowers c. 15-50 in (main) racemes. *Corolla* striated, with yellow blotch and (in *E. cuneata* only) in tube at base of lower lip, lower side spreading from base of lower lip away from hood; lobes shallowly to deeply emarginate. *Anthers* fused, glabrous around connectives, hairy along slits; awns entire. *Ovary* with stigma obliquely oblong to unequally bilobed, (0.2) 0.3-0.6mm long. *Capsules* slightly compressed laterally, in lateral view ovate to obovate-elliptic; apex emarginate to obtuse. *Chromosome number* unknown.

**Distribution:** Sect. *Cuneatae* comprises two widely disjunct species, *E. cuneata* of lowland to subalpine regions of New Zealand (Ashwin 1961), and *E. ramulosa* of montane to subalpine regions of north-eastern New South Wales.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
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<tbody>
<tr>
<td><em>E. cuneata</em> Forst.: !, ? T</td>
<td><em>E. ramulosa</em> Barker !, T</td>
</tr>
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</table>
Studies in Euphrasia

V. Sect. Phragmostomae Barker, sectio nova

Perennial, of "Phragmostoma" habit type; main inflorescence-bearing axes inadequately known, probably several to many, initially prostrate, finally erect, with branches at widely-spaced groups of nodes developing within groups in basipetal sequence in consecutive nodes, the uppermost group 0-10(18) nodes below the inflorescence. Uppermost leaves of main axes serratate to serrate, with base attenuate, gradually expanded into large blade, with 1-2 teeth over distal 0.1-0.4 of either margin; with 3 main veins arising from base of leaf, branched distally. Flowers up to c. 15 in (main) racemes. Corolla lacking striations, with yellow blotch on lower lip and in tube, with lower side spreading from base of lower lip away from hood; lobes obtuse to deeply emarginate. Anthers fused, glabrous around connectives, densely hairy along slits; rearmost pair of awns towards apex flattened or twisted with erosulate margins. Ovary with stigma obliquely subcapitate, (0.3)0.4-0.5mm long. Capsule in lateral view obovate-elliptic, with apex obtuse. Chromosome number unknown.

Distribution: Sect. Phragmostomae is monotypic and confined to coastal cliffs in the south-east corner of Tasmania.

Note: The section is unique in the genus in both its habit and the size and shape of the rearmost anther awns. It is closest to Sect. Cuneatae of Australia and New Zealand by its basipetal development of minor branches on the main axes, large stigma, anthers with glabrous connectives but densely hairy slits, and leaves with a large blade gradually attenuated at the base. Sect. Cuneatae differs, however, in addition to the unique characters described above, by its striated corollas and many-flowered inflorescences.

E. phragmostoma Barker: !, T

VI. Sect. Pauciflorae Barker, sectio nova

Sect. Euphrasia: Wettst. in Engler & Prantl, Nat. Pflfam. IV3b (1893) 100, p.p. (probably as to one or two N. Zeal. species) "Eueuphrasia".


Perennials. Axes principales inflorescensugeri singularus usque multi, prostrati usque erecti, ramos inordinatos in nodis sporadicis crescentes. Folia summa axis principalis crenata usque crenato-serrata, base attenuata, in laminam parvum usque amplam abrupte gradatimve expansa, 1-2(3) dentibus secus c. 1⁄₁₃, partes distales crenatae margine, saepe dente apicali magno cucullatoque; 1-3(5) venibus principalibus ad basem folii. Flores 2-8(12) in racemis principalibus vel, in speciebus ramis prostratis, solitarii dispersi. Corolla striata vel non-striata; lobis emarginatis obtusis. Antherae coniunctae, circa connectivas glabrae, secus rimas pilosae; aristis integris. Ovarium stigma oblique capitate vel inequaliter bilobata (0.2)0.3-0.55mm longa.
longa. Capsulae in aspectu laterali obovatae vel ita late, obcordatae oblongaeve, apice obtuso vel emarginato, saepe ita late. Chromosomatum numerus: n = 11.

Holotypus: E. revoluta Hook.f.

Perennial, with habit variable. Uppermost leaves of main axes crenate to serrate-crenate, with base attenuate, abruptly or gradually expanded into blade, otherwise of variable shape; with 1-3(5) main veins arising from base. Flowers variable in number and arrangement. Corolla with variable coloration, with lower lip concave from above, spreading from base away from hood; lobes variable. Anthers fused, glabrous around connectives, hairy along slits; awns entire. Ovary with stigma obliquely capitate or unequally bilobed, (0.2)0.3-0.55mm long. Capsules variable. Chromosome number: n = 11 (known from only one species, E. mirabilis: Borgmann 1964). Variable characters: see under subsections.

Distribution: Sect. Pauciflorae, which consists of 16 species in two subsections, occurs in the mountains of three widely disjunct regions, New Zealand, New Guinea and the Celebes.

A. Subsect. Pauciflorae Barker, subsection nova

Subsectio nova Euphrasiae Sectionis Pauciflorae differt a Subsectione Humifusae floribus in racemis axibusque principalibus inflorescentigeris non prostratis.

Holotypus: E. revoluta Hook.f.

Habit of the “Malesianae” and “Striata” types; main inflorescence-bearing axes either several to many and ascending with simple erect parts, or single to few and erect with branches developing with no fixed sequence high above ground level in occasional nodes. Uppermost leaves of main axes with base attenuate, abruptly or gradually expanded into small to large blade, with 1-2(3) teeth on distal \( \frac{1}{3} \) of each margin, often (in most New Guinea species and ? sometimes E. revoluta) with apical tooth large and hooded and with small pair of lateral teeth; with 1 or 3 (in E. papuana rarely 5) main veins arising from base. Flowers 2-8(12) in (main) racemes. Corolla conspicuously striated, sometimes only on upper lip or on rear of lobes, or with striations absent, sometimes replaced by flush of colour, with yellow patches on lower lip and tube; lobes emarginate or obtuse. Ovary with stigma obliquely capitate or unequally bilobed, (0.25)0.3-0.55mm long. Capsules in lateral view obovate or broadly so, or obcordate to oblong; apex in lateral view obtuse or emarginate, often broadly so. Chromosome number: n = 11 (known from only one species, E. mirabilis: Borgmann 1964).

Distribution: Subsect. Pauciflorae occurs in the high montane to alpine zones of New Guinea (7 species) and New Zealand (6 species).

Note: The New Guinea and New Zealand members of this subsection form two divergent groups linked by E. papuana of New Guinea and E. revoluta of New Zealand. The New Guinea species have corollas lacking prominent striations, although data on this are incomplete (see p. 29), corolla lobes tending to be small relative to the length of the tube (measurements of the New Zealand species overlap, however), and leaves usually with only a single pair of teeth, often producing the ‘hooded’ leaf distinctive of these species. E. papuana differs by its non-hooded leaves with 1-2 pairs of teeth, a characteristic of the New Zealand representatives. The New Zealand species all have large-lobed corollas which tend to be striated and upward-directed, and, except for E. revoluta, have leaves with 1-2 pairs of teeth. E. revoluta vegetatively resembles E. mirabilis of New Guinea; its small leaves with a single pair of teeth are, however, not conspicuously hooded. Since there is no one pair of correlated characters
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New Guinea

E. mirabilis Pennell: !, T
E. scutellarioides Wernham: ??, T
E. spatulifolia Pennell: !, T

New Zealand

E. revoluta Hook.f.: !, T
E. drucei Ashwin: !

VII. Sect. Striatae (Du Rietz) Barker, stat. nov.

Subsect. Humifusae Barker, subsectio nova

Subsectio nova Euphrasiae Sectionis Pauciflorae differt a Subsectione Pauciflorae axibus principalibus inflorescentigeris prostratis floribusque sporadicis secus axes.

Holotypus: E. humifusa Pennell

Habit of the “Humifusa” type; main inflorescence-bearing axes several to many, prostrate and rooting at occasional nodes, developing branches along whole length in no fixed sequence, sporadically or in more or less consecutive nodes which are free of flowers. Uppermost leaves of main axes with base attenuate, abruptly or gradually expanded into small blade, with 1(2) teeth, often small, on distal $\frac{1}{2}$-$\frac{3}{4}$ of either side, with apical tooth often large and hood-like; with 1 or 3 main veins arising from base. Flowers sporadic in axils of leaves along axes, one at each node, developing acropetally. Corolla purple on upper lip, from dried material sometimes striated faintly on lower lip (E. callosa), possibly (in E. humifusa: van Royen 1972) lacking striations, with yellow blotch on lower lip (at least in E. callosa); lobes emarginate or shallowly so. Ovary with stigma capitulate or unequally bilobed, (0.2)-0.3-0.5 mm long. Capsules in lateral view broadly obovate, laterally compressed; apex in lateral view broadly obtuse to shallowly emarginate. Chromosome number unknown.

Distribution: The subsection comprises three species, two from the alpine and subalpine regions of New Guinea, and one from the summit of Mt Loemuet in the Celebes.

E. humifusa Pennell: !, T
E. callosa Pennell: !, T
E. celebica van Royen: T

V. Sect. Striatae (Du Rietz) Barker, stat. nov.


Perennial, of the “Striata” or “Collina” habit type; main inflorescence-bearing axes either several to many and ascending with simple erect distal parts, or single to few and erect with branches developing high above ground level in occasional nodes in no fixed sequence. Uppermost leaves of main axes crenate to serrate, with base gradually attenuate to cuneate, with blade small to large, toothed in distal $\frac{1}{4}$-$\frac{1}{2}$ of either side, in Ser. Striatae with 1-2(5) teeth along each margin, in Ser. Hookerae with (3)4-5(7) teeth...
along each margin; with 3-(sometimes in *E. gibbsiae*) 5 main veins arising from base. *Flowers* (7)10-24(36) in (main) racemes. *Corolla* conspicuously striated, sometimes only on lateral lobes or on tube, hood and base of lower lip but hardly extending onto lobes, with lower side concave from above, spreading from base or lower lip away from hood; *lobes* broadly obtuse to emarginate. *Ovary* with stigma obliquely capitate to oblong or unequally bilobed, 0.35-0.8mm long. *Capsules* in lateral view obovate to ovate-elliptic, sometimes broadly so; *apex* in lateral view emarginate to obtuse. *Chromosome number*: $n = c. 20-30$.

**Typification**

Ser. *Striatae* Du Rietz  Although no type was cited by Du Rietz (1948a), the selection is automatic as his series name was based upon the epithet of one of the species described in the protologue (ICBN, Art. 22).

**Distribution**: Sect. *Striatae* is restricted to Tasmania except for an outlier on the Baw Baw plateau of the eastern highlands of Victoria.

In a mountainous region further north in Victoria is a polymorphic species, *E. crassiuscula*, which varies in the characters distinguishing Sect. *Striatae* from Sect. *Australae* (p. 152).

Ser. *Striatae* Du Rietz  
*E. gibbsiae* Du Rietz: !, T  
*E. striata* R.Br.: !, T  
*E. semipicta* Barker: !, T

Ser. *Hookerae* Du Rietz  
*E. hookeri* Wettst.: !, T


Perennial, of the "Striata" or "Collina" habit types; *main inflorescence-bearing axes* either several to many and ascending with distal erect parts simple, or single to few and erect with branches developing high above ground level in occasional nodes in no fixed sequence. Uppermost *leaves* of main axes crenate to serrate-pinnatifid, with base gradually attenuate (*E. bella*) or cuneate to truncate (*E. collina*), with blade large, with (0)1-6(8) teeth along distal 1/6 to whole of each margin; with 3-7 *main veins* arising from base. *Flowers* (4)6-60(80) in (main) racemes. *Corolla* lacking striaations, with or without yellow spot on lower lip, with lower side (? always) flattened, sometimes forming a broad groove, with lower lip ± porrect proximally, spreading distally in region of lobes; *lobes* obtuse to deeply emarginate. *Anthers* fused, connectives almost always hairy, in a few subspecies of *E. collina* rarely glabrous, slits hairy; awns entire. *Ovary* with stigma obliquely oblong to capitate or unequally bilobed, 0.5-1.0mm long. *Capsules* in lateral view ovate to obovate, sometimes broadly so, or shortly caudate,
rarely linear; apex shallowly emarginate to acute or obtuse, rarely shortly broadly acuminate. **Chromosome number**: variable estimates (p. 36).

**Typification**

1. **S Australes** Benth. Except for *E. tetragona* R.Br. and *E. striata* R.Br., the descriptions of which are rearrangements of Brown's (1810) originals, any one of the other six species included by Bentham (1846) under **S Australes** would qualify equally as lectotype. In considering the characters used by Bentham to delimit **S Australes**, none of the species has the allegedly “subequally mucronate anthers” wrongly attributed to this group by Bentham (and other authors), while all bear hairs on the anthers to a greater or lesser extent. The final choice was based on the fact that Bentham saw much material of Brown’s “*E. alpina*”.

2. **Subsect. Australienses** Du Rietz  Any of the four species, *E. collina*, *E. gunnii*, *E. striata* and *E. gibbsiae*, described in great detail by Du Rietz (1948a,b) would have been suitable as lectotype. *E. collina* was chosen as it was a type of one of the two series *Collinae* and *Striatae* which encompass these four species. It also appears to have capsules corresponding to the “acuminate” type which was used by Du Rietz to distinguish the subsection from his Subsect. *Novaezeelandiae* (but see p. 34).

3. **Ser. Collinae** Du Rietz. Although no type was cited, *E. collina* is automatically holotype as the series name is based upon it (ICBN, Art. 22).

**Distribution:** The section is spread throughout temperate southern Australia (including Tasmania), the entire area of which is covered by one extremely polymorphic species, *E. collina*. Also included in the subsection are three species which are confined to small mountain regions; one of these, *E. crassiuscula*, intergrades with Sect. *Striatae* (see p. 152).

**Note:** This section, which appears so natural on phenetic grounds, may consist of two paraphyletic groups (pp. 57, 62). Confirmation by further study, particularly of chromosome numbers, is needed before the desirability of separating *E. bella*, *E. bowdeniae* and an unnamed close relative as a separate section can be considered.

*E. bella* Blake: !, T  *E. collina* R.Br.: !, T  *E. crassiuscula* Gandoger: !, T  *E. bowdeniae* Barker: !, T

**IX. Sect. Lasiantherae** Barker, sectio nova


Sect. *Trifidae* auct. non (Benth.) Wettst.: Wettst. in Engler & Prantl, Nat. Pflfam. IV3b (1893) 101, p.p. (as to Australian plants of *E. antarctica*).


Herbae annuae perennesse. Axes principalis inflorescentigeris vel (in herbis annuis) caulis singularis erectus ramis paucis in nodis continuis infra inflorescentiam basipete crescentibus, vel (in herbis perennibus) rami multi ascendentes, proxime prostrati et saepe ramosi, distale integri erectique. Folia summa axis principalis crenato-serrata usque pinnatifida, base anguste cuneata usque truncata, lamina magna, (1)2-4(7) dentibus secus 2/3-totas partes cuiusque marginis; 3-7 venis principalibus ad basem folii. Flores (14)15-26(30) in racemis. *Corolla* manifeste striata, sum vel sine macula flava in labio infero, labio infero ad basem plus
minusve porrecto, distale patenti; lobis plerumque emarginatis, interdum obtusis. Antherae conjunctae, circa connectivas et secus rimas pilosae; aristas integris. Ovarium stigma oblique capitata usque oblonga vel inaequaliter bilobata, 0.3-0.7mm longa. Capsulae in aspectu laterali ovatae usque obovatae, apice plerumque emarginato usque late obtuso, raro acuto. Chromosomatum numerus: n=27 et circa 38-47.

Holotypus: E. lasianthera Barker

Perennial of the "Striata" habit type, or annual; main inflorescence-bearing axes (in perennials) many ascending branches, initially prostrate and often branched, distally simple and erect, or (in annuals) a single erect stem with few branches developing basipetally in consecutive nodes below inflorescence. Uppermost leaves crenate-serrate to pinnatifid, with base narrowly cuneate to truncate, with large blade, with (1)2-4(7) teeth distributed over distal \(\frac{1}{2}\)-entire length of each margin; with 3-7 main veins arising from base. Flowers (14)15-26(30) in (main) racemes. Corolla prominently striated, with or without yellow blotch on lower lip, with lower side ± flat crosswise, with lower lip ± porrect near base, spreading distally; lobes usually emarginate, sometimes obtuse. Anthers fused, hairy about connectives and along slits; awns entire. Ovary with stigma obliquely capitate to oblong, or unequally bilobed, 0.3-0.7mm long. Capsules in lateral view ovate to obovate, slightly compressed laterally, apex in lateral view usually emarginate to broadly obtuse, rarely acute. Chromosome number: n=27 and c. 38-47.

Distribution: Sect. Lasiantherae is confined within montane to alpine zones of three disjunct mountain areas of south-east mainland Australia.

\(E. lasianthera\) Barker: !, T \(E. eichleri\) Barker: !, T \(E. alsa\) FvM.: !, T

X. Sect. Scabrae (Du Rietz) Barker, stat. nov.


Annuals. Main inflorescence-bearing axis: a single erect stem, with branches developing basipetally in consecutive nodes from 1-few nodes below inflorescence. Uppermost leaves of main axis crenate to deeply pinnatifid, with base narrowly cuneate to rounded, with blade prominent, with 0-3(5) teeth over distal \(\frac{1}{2}\)-entire length of each margin; with 3-7 main veins arising from base. Flowers (10)14-90 or more in racemes. Corolla lacking prominent striations, with (or ?without) yellow to red patch on lower lip or completely yellow, with lower side ± flat, broadly grooved, with lower lip porrect at least at base, distally in region of lobes sometimes spreading; lobes obtuse, sometimes shortly apiculate, to emarginate. Anthers fused, hairy about connectives, at least of posterior pair, and along slits; awns entire. Ovary with stigma obliquely oblong to capitate, or unequally bilobed, (0.2)0.35-1.1mm long. Capsules in lateral view oblong-ovate to obovate-elliptic, often obliquely so, sometimes broadly so, slightly compressed laterally; apex in lateral view emarginate to obtuse or acute, often obliquely so. Chromosome number: n=27 &/or 28 &/or 27I+2I &/or ? 25I+2III (\(E. caudata\)).
Although no type species was cited by Du Rietz (1948b), *E. scabra* must be considered the holotype since Du Rietz's series name was based upon the specific epithet (ICBN, Art. 22).

**Distribution:** Sect. *Scabrae* is confined to the temperate lowland to alpine regions of southern and eastern Australia, including Tasmania.

- *E. caudata* (Willis) Barker: !, T
- *E. orthocheila* Barker: !, T
- *E. ciliolata* Barker: !, T
- *E. arguta* R.Br.: !, T

**XI. Sect. Novaezeelandiae** (Du Rietz) Barker, stat. nov.


**Typification**


**Annual.** Main inflorescence-bearing axis a single erect stem, with branches developing apparently acropetally or in no fixed sequence in the few consecutive nodes available from 1-few nodes below inflorescence. Uppermost leaves of main axis crenate to crenate-serrate, with base attenuate, gradually or ± rapidly expanded into large blade, with 2-5 pairs of teeth distributed over distal 1/2-entire margin; with 3 main veins arising from base. Flowers 6-14 in (main) racemes. Corolla either conspicuously striated, with yellow patches or (in *E. cockayniana*) completely yellow, with lower lip spreading from base away from upper lip; lobes obtuse to acute or (in *E. cockayniana*) shallowly emarginate. Anthers fused, glabrous about connectives, very sparsely to densely hairy along slits; awns entire. Ovary with stigma obliquely capitate to linear, or unequally bilobed, 0.3-0.6mm long. Capsules in lateral view broadly obovate to shallowly obcordate, greatly compressed laterally; apex in lateral view broadly obtuse to emarginate. *Chromosome number unknown.*

E. cheesemani Wettst.: !, T
E. australis Petrie: !, T
E. cockayniana Petrie: !, T

**Distribution:** Sect. *Novaezeelandiae* is confined to the montane to alpine zones of the North and South Islands of New Zealand (ex Ashwin 1961).
Perennial, of the "Paradoxae" habit type; main inflorescence-bearing axis a single erect stem, with branches developing in all nodes apparently in an acropetal sequence, with growth continuing from some apices in later years. Uppermost leaves of main axis crenate, with base attenuate, abruptly to ± gradually expanded into large blade, with 3-5 teeth along distal \(\frac{1}{2}-\frac{3}{4}\) of each margin; with 3 main veins arising from base. Flowers c. 10-15 in (main) racemes. Corolla striated on upper and lower lip, with yellow blotches on lower lip and in tube, with lower side concave from above, spreading away from hood from base of lower lip; lobes obtuse. Anthers fused, glabrous around connectives, slightly hairy on slits; awns entire. Ovary with stigma obliquely capititate or oblong, c. 0.4mm long. Capsule in lateral view ? obovate or broadly so, laterally compressed; apex in lateral view shallowly emarginate. Chromosome number unknown.

**Distribution:** Sect. **Paradoxae** in monotypic and restricted to the Juan Fernandez Islands. It occurs in the higher parts of Masafuera, commonly in the alpine zone (Skottsberg 1921).

**Note:** Opinions as to the affinities of Sect. **Paradoxae** have been varied. Skottsberg (1921) pointed to the generally agreed remote relationship to the neighbouring South American species (herein Sect. Trifidae). Wettstein (1921) pointed to it being closest to both the New Zealand perennial *E. cuneata* (Sect. *Cuneatae*) and the Japanese annual *E. yabeana* Nakai (Sect. *Euphrasia* Subsect. *Alpicolae*). Du Rietz (1932b, 1948a), however, considered the section to be most closely allied to the Australasian species, in particular several New Zealand species. In my view (p. 55) *E. formosissima* is undoubtedly closest to Sect. *Novaezeelandiae*, a group of small New Zealand annuals with which it shares not only a unique acropetal pattern of branch development, but also sparsely hairy anther slits and shallowly toothed leaves.

*E. formosissima* Skottsb.: !, T.

### XIII. Sect. **Anagospertae** (Hook.f.) Barker, **stat. nov.**


**Annual. Main inflorescence-bearing axes** usually several branches, either initially prostrate and gradually ascending or completely prostrate, sometimes (*E. dyeri* p.p.) a single ± erect stem, with branches developing ± acropetally or sporadically, in occasional or consecutive axils. *Leaves* either entire and narrow-acuminate (*E. integri-folia*) or pinnatifid to pinnatifid-serrate, with base narrowly cuneate or gradually
attenuate, with only a small blade, with 1-3 teeth distributed over distal \( \frac{1}{2}-\frac{3}{4} \) of each margin; with 1-3 main veins arising from base. Flowers 2-6 in (main) racemes or (especially in prostrate plants) sporadic. Corolla with striation on the midline of hood and sometimes either side, sometimes with 1-5 striations on the lobes, with tube and lower side of mouth yellow, with lower lip spreading from base away from hood; lobes obtuse to truncate. Anthers fused or (E. disperma) free, glabrous around connectives, glabrous or with a few hairs along slits; awns entire. Ovary with stigma narrowly oblong, unequally bilobed, 0.35-0.8mm long. Capsules laterally compressed, broadly obovate to obcordate or bicornute in lateral view; apex in lateral view broadly obtuse to very deeply emarginate. Chromosome number unknown.

Distribution: The section, which contains four species, is endemic to the montane and wet coastal regions of the South Island of New Zealand.

Notes
1. The section, as here constituted, may be polyphyletic, with E. disperma possibly having a common origin with Sect. Trifidae, the rest sharing a common ancestry with Sect. Novaezeelandiae (p. 55). In addition, E. integrifolia, in my view, may be a perennial, in which case it would be misplaced with these species. It seems preferable to group these species together pending further study.

2. From J.D. Hooker’s description of Subgen. Anagosermae in 1879 to the present day there has been speculation whether the capsules of E. disperma and of its closest relatives, which are included in the section proposed herein, are indehiscent (see Du Rietz 1932a, Ashwin 1961). Simpson (1977) has shown that the capsules are truly dehiscent although there is a tendency to vivipary.

3. Wettstein (1895), in elevating J.D. Hooker’s Euphrasia Subgen. Anagosermae to generic level, incorrectly stated that Hooker had given it the status of section.

E. dyeri Wettst.: !, T
E. integrifolia Petrie: !, T
E. disperma Hook.f.: !, T
E. repens Hook.f.: !, T


Perennial, of the “Striata” and ? “Malesianae” habit types, or annual; main inflorescence-bearing axes either several to many and ascending, with branches developing in consecutive nodes up to several to many nodes below inflorescence, simple above, or single and erect with branches developing in no fixed sequence in consecutive nodes from 1-few nodes below inflorescence. Uppermost leaves of main axes deeply divided, with base attenuate to cuneate-attenuate, gradually expanded into small blade, with 1(2) pairs of teeth distributed over distal \( \frac{1}{2}-\frac{7}{8} \) of leaf; with 3 main veins arising from base of leaf. Flowers c. 10-30 in (main) racemes. Corolla striated with yellow area on lower lip or yellow throughout (Reiche 1911), with lower side apparently concave from above, with lower lip spreading from base away from hood; lobes emarginate, often shallowly so. Anthers free, glabrous around connective and along slits; awns entire. Ovary with stigma obliquely subcapitate, c. 0.3-0.5mm long. Capsules in lateral view broadly obovate, greatly compressed laterally; apex in lateral view broadly obtuse. Chromosome number: n=44 (known for a single species: D.M. Moore fide Yeo 1968).
Typification

Under Article 22 of the ICBN, *E. trifida*, which was described in the protologue (Bentham 1846), is automatically the type of *Trifidae* Benth.

**Distribution:** Sect. *Trifidae* is confined to the Andes mountains and their surroundings in the southern part of South America, with one species *E. antarctica* extending to the Falkland Islands to the east of Fuegia (Skottsberg 1913; Vallentin & Cotton 1921). Eighteen species are currently recognized, on the basis of the works dating from Wettstein’s (1896) monograph, but revision is needed at both the species level (Reiche 1911) and the infrageneric level (see p. 75).

There is controversy about the northern limit of the genus in South America. Wettstein (1896) shows it extending into Peru, but the northern half of this range is based upon the record of a single species *E. pubescens* described by Bentham (1846) and apparently only represented in herbaria (K, B, P: n.v.) by the type material which lacks a specific locality (Wettstein 1896; Edwin 1971). Thus with the Peruvian occurrence in question, Du Rietz (1940), Burbidge (1960), van Balgooy (1966), van Steenis (1971) and Hulten (1976) have shown the northern limits of the genus much further south at a latitude in the range 29-35° S. The last major work on the genus in South America was a revision of the Chilean species by Reiche (1911), who cited the northern limits at about 30-31° S. His northernmost locations in the Province of Coquimbo were of an annual which he called *E. antarctica*, a species widespread in the southern regions. Johnston (1929) described *E. adenotata* from about 180km further north at about 29° S; he believed that Reiche’s northern occurrences of *E. antarctica* were actually records of his new species. Descole & Borsini (1955) described a new annual species *E. piossekii*, which is undoubtedly a member of Sect. *Trifidae* from the description and illustration. Its location in Jujuy Province, Argentina extends the range of the genus much further north to about 24° S. Finally, to add to the controversy of a Peruvian occurrence of the genus, Ruiz & Pavon (1959) published posthumously (Stafleu 1967) seven new species of *Euphrasia* from Peru. Edwin (1971) considered that all but two of these species belonged not to *Euphrasia*, but to a related genus, probably *Bartsia*, which is prevalent in the northern Andes. In my view six of the species, including the two which Edwin considered to be of *Euphrasia*, seem to belong to *Bartsia* or at least to a genus not *Euphrasia*, on the basis of their serrat to crenate leaves, hairy anthers and entire corolla hoods (the first two characters are atypical of Sect. *Trifidae* and the last is a character separating the two genera). Contrary to Edwin I believe that *E. tripartita*, with its bilobed upper corolla lip and trifid leaves, belongs to *Euphrasia* Sect. *Trifidae*. Localities cited in the protologue were near Concepcion, Chile and at Cheuchin, Peru.

In view of the several cases documented above, there seems no doubt that Sect. *Trifidae* occurs well to the north of its currently accepted distributional range. It appears that north of latitude 33° S the genus may be represented by a series of annuals occurring in the Andes as far as Peru.

**Note:** The sectional description is based on material from NSW and MEL. The identity of the specimens was not checked.

**Perennials**

*E. andicola* Benth.  
*E. debilis* Wettst.  
*E. chrysanthi* Phil.  
*E. ephippii* Wettst.  
*E. flayicans* Phil.  
*E. intrica* Phil.  
*E. muscosa* Phil.

**Annuals**

*E. antarctica* Benth. (!, T)  
*E. meiantha* Clos  
*E. meliantha* Clos  
*E. philippii* Wettst.  
*E. adenosita* I.M. Johnston  
*E. piossekii* Desc. & Bors.  
*E. tripartita* Ruiz & Pavon
V. A TAXONOMIC REVISION OF EUPHRASIA IN AUSTRALIA

A. INTRODUCTION

The classification of Euphrasia in Australia has had to be completely restructured. Wettstein (1896), who published the last revision of the genus in Australia, recognized twelve species and proposed no formal infrageneric or infraspecific taxa. In the proposed classification, six of his twelve species are retained. Of the remainder five are reduced to subspecies and one is placed in synonymy.

Euphrasia in Australia consists of six sections with eighteen species, of which eight are newly described and one is an upgrading of status. Four species, in particular E. gibbsiae with nine subspecies and E. collina with 14 subspecies, are polymorphic. In all, 42 taxa at the subspecies or species level have been described, of which 18 are new. Fifteen new combinations and/or changes in status have been made, but three were validated by Curtis in 1978 (Stones & Curtis 1967-78). The difficulties in the taxonomy of Euphrasia in Australia encountered by previous taxonomists have been caused mainly by the complexities of E. collina, which encompasses a large proportion of the Australian populations of Euphrasia. E. collina as defined in this revision is more or less equivalent to Mueller’s (1865) “E. brownii”. All taxa have limited geographical and ecological ranges. Clines and a limited amount of hybridization occur within the species. Interspecific hybrids are rare.

B. TAXONOMIC HISTORY

The first Australian collections of Euphrasia were apparently made by Labillardière from southern Tasmania (see Nelson 1974; Apfelbaum 1977). He made at least three collections (verified in a note accompanying his handwritten description of the collection Labillardière 43 in FI) all of which he considered to be E. cuneata Forst.f. of New Zealand, the sole known representative of the genus in the southern hemisphere at that time, but which belong to three taxa, ssp. psilantherea and ssp. kingii of E. gibbsiae and E. collina ssp. collina.

It was Robert Brown who made the initial published contribution to the knowledge of Euphrasia in Australia. From perhaps no more than a dozen of his own collections, most of which are described exhaustively in his manuscript (Brown unpubl.), he described in his “Prodromus” (Brown 1810) eight species, all new, from localities throughout temperate Australia. Although not giving them any emphasis, he recognized the characters of duration and corolla coloration which have proved important in the proposed infrageneric revision. Subsequent works of Sprengel (1825) and Bartling (1845) were based largely on Brown’s work.

Although produced over 35 years after Brown’s published treatment of Euphrasia and based on additional collections, Bentham’s (1846) large monograph of Scrophulariaceae showed little modification of Brown’s concepts. He did not see Brown’s types and consequently applied Brown’s E. collina to the wrong taxon and erroneously erected a new species E. multicaulis. In addition he described four infraspecific taxa under Brown’s species. Two of these he later reduced to synonymy with other Brownian species (Bentham 1868). The third, E. paludosafi pedicularoides, was not referred to again; having seen no material, I cannot make any assessment of it. The fourth, E. scabra arguta, he later reinstated as a species (see below, also p. 284).

Subsequently, following explorations of montane to alpine areas of eastern temperate Australia, by Ferdinand Mueller, and Tasmania, by resident collectors such as Gunn and Archer sponsored by J.D. Hooker (see Burns & Skemp 1961), two distinctive new species were described, E. alsa by Mueller (1855, 1856) and E. cuspidata by J.D. Hooker (1857). Nevertheless, while large collections were accumulating
from throughout the range of the genus in Australia encompassing all but a few localized species (e.g. \textit{E. phragmostoma}, \textit{E. bella}, \textit{E. bowdeniae}) and the majority of infraspecific taxa, no other new taxa were recognized up to the end of the century. Publications utilized Brown's (1810) taxa and Bentham's (1846) taxonomy together with the two above additions. J.D. Hooker (1857, 1859a) agreed with Bentham that several species might be found to be forms of the one species. With his wide field experience of the genus, Mueller (1865) concurred and united five of Brown's species and that of Bentham into a single species \textit{E. brownii}. Despite an opinion to the contrary (van Royen 1972)*, the name \textit{E. brownii} is illegitimate as the author clearly and deliberately based the new name upon seven validly published species names, most of which are legitimate (ICBN, Art. 63).

\textit{E. striata} was considered by Mueller (1865) to be distinct from \textit{E. brownii} but he doubted its separation as a species. However, he had confused \textit{E. striata}, a distinctive Tasmanian alpine species which he had not then seen in the field (but later saw in 1869), with an undescribed taxon which he had collected in the alpine regions of the “Munyang Mountains” and which indeed falls into the \textit{E. brownii} complex, namely \textit{E. collina} ssp. \textit{glacialis}. Mueller erected a new variety \textit{psilantherea} of \textit{E. brownii}, and expressed some uncertainty as to the status of \textit{E. arguta}.

In his second account of \textit{Euphrasia} in Australia as part of “Flora Australiensis”, Bentham (1868) was able to refine his prior work. He recognized eight species. \textit{E. arguta} was reinstated as a species following its misapplication in his earlier work. He reduced four species to synonymy under \textit{E. collina}, a name which he considered more appropriate than Mueller's \textit{E. brownii} for the “collective species”. Bentham's \textit{E. collina} was thus narrower in circumscription than Mueller's \textit{E. brownii}. \textit{E. paludosa} was segregated as a variety of that species. However, Bentham agreed with Mueller that \textit{E. striata} was “not separated from \textit{E. collina} by any marked characters” and that Brown's \textit{E. speciosa} and \textit{E. alpina} may be further variants of the latter. He retained \textit{E. cuspidata} and \textit{E. alsa}, but considered the latter to be conspecific with the South American \textit{E. antarctica}.

Following this productive half century in the taxonomy of \textit{Euphrasia} in Australia came a period of almost a century in which Australian authors largely chose to follow the pre-existing concepts of the genus.

Mueller (1882, 1885-88, 1889) retained his viewpoint of the taxonomy of the genus and the usage of \textit{E. brownii} in his subsequent works on the Australian and Victorian flora, although he did follow Bentham in reducing \textit{E. alsa} to a synonym of \textit{E. antarctica}. Early Australian botanists tended to favour his concepts in the genus, e.g. in the works of Spicer (1878) on the Tasmanian flora, Tate (1890) on the South Australian flora, and Moore (1884), Moore & Betche (1893) and Dixon (1906) on the New South Wales flora.

Bentham's ideas concerning \textit{Euphrasia}, which differed from Mueller's only in his recognition of four closely related species under \textit{E. brownii}, were followed in the majority of other floristic works, such as those of Woolls (1891) on the plants of the Sydney region, Bailey (1883, 1890, 1901, 1913) on the Queensland flora, Gardner (1931) on Western Australian plants, Ewart (1931) and Galbraith (1955, 1967) on the Victorian flora, and Black (1926) and Robertson (1957) on the South Australian flora.

Rodway (1903) in his “Tasmanian Flora”, Ewart (1908) in his “Contributions to the Flora of Australia” series, and Maiden & Betche (1916) in their “Census of New South Wales Plants” went a stage further with Mueller's ideas by proposing as

* Dr P. van Royen (pers. comm. 1972) has since expressed some doubts as to the correctness of his conclusions concerning the legitimacy of \textit{E. brownii}.
varieties of *E. brownii* (Rodway, Maiden & Betche) or *E. collina* (Ewart), some or all of the four species and one variety which Bentham distinguished in the complex. Mueller at no stage proposed this idea as Maiden & Betche state, except with *E. striata*.

In a comprehensive and detailed monograph of *Euphrasia*, Wettstein (1896) described 12 species from Australia. The total lack of published reference to his treatise until 1965 in Australian works, other than by Du Rietz (1948a,b), is noteworthy, for the classification of the Australian species was dealt with in great detail and differed significantly from previous works. Even the hardly controversial reinstatement of *E. alsa* was not taken up to that time. Important German works in other genera, such as *Plantago*, *Epilobium* and *Blennodia*, were also not followed during this period (Dr Hj. Eichler, pers. comm. 1973). Nevertheless, the taxonomic difficulties with *Euphrasia*, which continued to recent times (e.g. Willis 1967; Burbidge & Gray 1970), may have led to distrust of this revision produced by an overseas botanist who lacked recourse to field studies. Wettstein's work was based entirely upon collections from European herbaria, but he failed to see those of the British Museum and Kew which housed most type specimens of the species described by Brown, Bentham and J.D. Hooker. As a result he misapplied the name *E. arguta* (see p. 284). *E. glacialis* and *E. muelleri* were described as new. No infraspecific taxa were recognized. Several species reduced by Bentham and Mueller and their followers under *E. collina* or *E. brownii* were reinstated. Substitute names were proposed for two species previously supplied with illegitimate names (later homonyms), the new name *E. hookeri* replacing *E. cuspidata* Hook.f. non Host (1831), and *E. diemenica* Spreng. replacing *E. alpina* R.Br. non Lamk. Mueller's *E. alsa* was resurrected, *E. antarctica* being shown to belong to a separate section of the genus. In fact, Wettstein used characters identical to those proposed by Bentham (1846) to separate the South American species as a distinct section but which he (Bentham 1868) had subsequently ignored in his union of *E. antarctica* and *E. alsa*. Wettstein informally divided the Australian and New Zealand species on duration.

Gandoger (1919) published seven new binomials in the "*E. brownii* complex" of Australia. Gandoger's study was taxonomically superficial. Indeed, he had previously written a Flora of Europe which was highly unconventional (Stafleu 1967, 1972; McGillivray 1973). There is no evidence that he saw any material other than the single specimens upon which he based the names. Whereas such a course of action is non-scientific, his names are validly published with short diagnoses (in key form) and with specimens adequately cited. Until very recently when Briggs (in McGillivray 1973) supplied probable affinities of Gandoger's species, workers in *Euphrasia* have rarely attempted to apply Gandoger's names because of the brevity of the descriptive information and the lack of opportunity to see the pertinent types (cf. Du Rietz 1948b).

Blake (1945) described and figured a distinctive new species *E. bella* from the mountains of southern Queensland.

As a continuation of his earlier papers on *Euphrasia* in the southern hemisphere and Malesia (Du Rietz 1932a,b), Du Rietz (1948a,b) published two papers primarily to clarify the classification of the Tasmanian species. He went further than this, however, and discussed in some detail the taxonomy of the Australian species as a whole and their affinities in the genus elsewhere. His work was based mainly on material from European herbaria, including the important collections of the British Museum and Kew. A few specimens were sent to him from the herbarium of the Botany Department, University of Adelaide (now housed in AD).

Throughout the work he mentioned possible distinct taxa which required further investigation. On such little material as he saw his predictions often proved remarkably good. Du Rietz described two new species, one of them, *E. gibbsiae*, with a number of
forms. Two of these forms he published formally, believing that, with further material and field studies, they might prove to be distinct species. He referred to several variants which he provisionally named as distinct species. While describing the second new species, E. gunnii, he rectified the misapplication of E. collina R.Br. by Bentham and subsequent authors. Like Wettstein he preferred to consider as distinct species the major variants in the "E. brownii complex". Du Rietz was the only person to provide a formal infrageneric classification of the Australian species, with which the one proposed in the current infrageneric revision in many respects agrees. Finally, in view of the high polymorphy in E. gibbsiae, Du Rietz concluded that "possibly hybridism plays an important role in the Tasmanian Euphrasia-population".

Eichler (1965), on the basis of the Australian studies by Wettstein and Du Rietz, considered that several species were involved in South Australia under E. collina as circumscribed by Black (1926) and Robertson (1957). Curtis (1967) recognized eight species in her 'Student's Flora of Tasmania'. Her concepts also followed Wettstein and Du Rietz. She described one new species, E. kingii, discussed the ecology and variability of the species, particularly of E. diemenica and E. gibbsiae, and noted Du Rietz's comments on the role of hybridism in this variability.

Willis (1967) published notes on Euphrasia in Australia, mainly on the taxa occurring in the Australian Alps. In acknowledging difficulty in taxonomic delimitation caused by intraspecific polymorphy and extensive hybridism, he preferred to use varietal rank in describing distinctive taxa, and questioned the status of several Tasmanian species recognized by Du Rietz. Under E. scabra he described a new alpine and subalpine variety caudata from the Australian Alps. This variety seemed to pass gradually into E. alsa, which he showed to be quite different from E. antarctica and which he reduced to a further variety of E. scabra. To Wettstein's E. glacialis of the Kosciusko and adjacent regions, he added the new variety eglandulosa, abundant in the higher central parts of the Victorian Alps, but with outliers as far away as the Brindabella Range, Australian Capital Territory. Burbidge & Gray (1970) could provide only a tentative treatment of Euphrasia in the Australian Capital Territory. Of the five taxa recognized, only two were attributed published names.

In extending his concepts in the 'Handbook to Plants in Victoria', Willis (1973) reiterated doubts of past authors concerning the separation at the species level of E. collina and E. speciosa, which had been reinstated by Wettstein (1896) and Du Rietz (1948b).

Six taxa were described and illustrated in Stones & Curtis's (1967-78) 'The Endemic Flora of Tasmania'. In the final part, following an exchange of correspondence, Curtis published lists including all taxa recognized by me as endemic to Tasmania. Most unpublished names and combinations were correctly cited as unpublished, but three (comb. & stat. nov.) were validated.

In conclusion, throughout the various taxonomic works dealing with Euphrasia in Australia, doubts have been frequently expressed as to the status of most species recognized to this time. Thus, species placed in separate infrageneric taxa by one worker (e.g. Du Rietz 1948a,b) have been considered distinguishable only at the infraspecific level in a later publication (e.g. Willis 1967). In addition much difficulty has been found in applying correct names to the taxa (e.g. Burbidge & Gray 1970), and consequently names have sometimes been wrongly applied. As Willis (1967) stated, these deficiencies have obviously arisen from a lack of detailed taxonomic study of Euphrasia throughout Australia based on extensive field experience. Indicative of the inadequacy of previous concepts of the genus is the fact that almost half of the taxa recognized in the proposed classification are new; the proportion would be increased even further if Gandoger's arbitrarily designated and never utilized new species were discounted.
C. TAXONOMIC PHILOSOPHY AND PRESENTATION

The aim of the work has been to produce a classification of the genus in Australia reflecting the natural situation, thus providing a relatively stable framework into which any future discoveries can be fitted. Field work was undertaken in two of the main centres of diversity in Australia, encompassing two months in late 1970-early 1971 in Tasmania, and a year later a brief visit to the Grampians and six weeks in the Australian Alps. It has not been possible to visit the third important region of northern and central eastern New South Wales.

In the course of the revision many problems have been encountered which, through paucity of material or need of field study, are unresolvable. In cases where distinct taxa are undoubtedly involved I have given them their postulated status and treated them informally as if species or subspecies, including distinguishing them in the keys. Already, early recognition of *E. bowdeniae*, *E. phragnostoma* and *E. semipicta* as distinct taxa on the basis of a few specimens has been supported by subsequent collections. It is suggested that in future ssp. *diemenica* (p. 185) and the ssp. *paludosa* -ssp. *speciosa*-ssp. *diversicolor* complex (p. 168) of *E. collina* may be usefully divided into varieties. Odd variants of more doubtful status and origin or apparently discordant localities are treated in notes under the appropriate taxon. Where such a variant might apply to several taxa, it is noted under the appropriate species or section to which they all belong.

**Determination of taxa and rank**

As far as possible in this work the basic unit for the natural delimitation of taxa has been the population. My collections have enabled characteristics of the population to be studied in the herbarium, for they are largely population samples made up of single specimens of each of the several to many plants collected. Variation in taxa of which I have little or no field experience, has been assessed on the basis of experience with other taxa.

In determining rank, a combination of the number of characters, the extent of overlap in their variation and the degree of intergradation with allied taxa has formed the primary basis. It became clear that there were two or possibly three main levels in the natural grouping of taxa near species level. A formal species-subspecies hierarchy (with possible potential extension to variety) was eventually decided upon. The view that in large complexes this leads to a system which is cumbersome to use (Yeo 1978b) is disputed, as in the proposed formal framework only a trinomial has to be used, identical to that widely accepted in species with few infraspecific taxa. Such a system gives the user not only the benefit of a natural system, but also the practical advantage of being able to avert the unavoidable difficulties of subspecific determination in a complex where the species name would amply suit his needs. Furthermore, it is believed that recognition of Australian subspecies as "microspecies", which has been done elsewhere in the genus (Sell & Yeo 1970; Yeo 1978b), would camouflage the well-defined species in Australia. From autecological, breeding and herbarium studies Karlsson (1974, 1976) believes that the Swedish taxa, traditionally recognized principally as species, can be more naturally treated under a species-subspecies system, although his conclusion suffers from coverage of only a portion of the range of the complexes involved. In his treatment of *Euphrasia* in central Europe, Hartl (1972) has also used a broader species concept in association with an infraspecific hierarchy incorporating subspecies, varieties, subvarieties and forms.

The species in this revision are distinct on a number of characters, some of which show little overlap. They show no evidence of complete clinal intergradation with their closest allies, although there is occasionally limited hybridization between species in
different sections (p. 287), often involving an increase in pollen sterility in the hybrids. Subspecies have been designated because of their substantially fewer character differences and/or greater degree of overlap of variation compared with the species. They often intergrade morphologically with their closest relatives on an ecotonal or geographical basis. In such cases tests of pollen sterility (p. 40) show that the intergrades may differ little in sterility from parent taxa.

Because of the long history of controversy about the rank of the taxa of _Euphrasia_ in Australia and elsewhere, it is essential to highlight the degree of distinction of taxa from their closest allies by demonstrating the amount of clinal intergradation between taxa, particularly using studies in the field (treated under the observations on the nature of polymorphism in relevant species and _E. collina_ ssp. _diemenica_), and by indicating all important diagnostic characters.

**Descriptions and keys**

In relation to the content of descriptions and keys, Yeo's (1978b) comments on his own experience with the genus are pertinent and echo my own views: "Bearing in mind the minor characters that have to be used to distinguish the species [his "microspecies": equivalent to subspecies here], it should be obvious that here is a group where it is especially important to hold fast to the principle that in classification as many characters as possible should be taken into account. There are many groups in which this principle can be ignored at the species level, since it is possible to separate absolutely the members of any pair of taxa by the use of one or two 'key characters'." He then refers to the breakdown of such weighted characters in the European species.

Detail in the keys is particularly important in this revision, as it provides a more complete summary of the differences between related taxa than is often found in discussion of relationships traditionally placed under each taxon. The keys provide a ready summary of the number and degree of overlap of characters used in assessing the rank at which taxa are separated.

In using keys in this complex group, all characters must be treated equally, and ideally the variation of several plants from a population should be determined. At any point in a key where character states overlap, the greater the number of diagnostically important characters there are, the more certain will be the identification. This also makes for more reliable identification of individual specimens. I can see no better way of providing a simple and as reliable Australia-wide key to taxa. Simplification should be possible, however, in regional accounts.

**Intergradation between taxa**

As already intimated, two types of intergradation between Australian taxa of _Euphrasia_ are apparent. The first involves intergradation of a primary nature between closely-related (apparently sister) taxa, e.g. ssp. _comberi_ and ssp. _kingii_ of _E. gibbsiae_, ssp. _collina_ and ssp. _diemenica_ of _E. collina_, and ssp. _diversicolor_ and ssp. _glacialis_ of _E. collina_. These intergrades occur on narrow to broad ecotones. As there is little or no evidence of increased pollen sterility in the intermediates, it is believed that these represent a stage in a process of vicarious or parapatric speciation, which seems to have been the principal method of diversification in Australia. The clines evident within taxa such as ssp. _collina_ and ssp. _tetragona_ of _E. collina_ are considered to represent incipient phases of this process, while the vicarious-parapatric pattern of distribution in Sect. _Lasiantherae_ and its closer allies in Sect. _Scabrae_, and vicarious pattern in the _E. bella-E. sp. 'Tamworth'-E. bowdeniae_ lineage are a logical endpoint of the process following isolation of parts of cines and subsequent divergence of the isolated populations.
The secondary type of intergradation involves hybridization or introgression of distantly related taxa. On the available data most examples evident today exhibit high pollen sterility and occur in disturbed sites rather than natural ecotones. An exception would be possible introgression in *E. gibbsiae* ssp. *pulvinestris* (p. 132). Furthermore, it is proposed that in the evolution of the genus a few taxa, namely *E. orthocheila* ssp. *peraspera*, *E. semipicta* and possibly *E. crassiuscula*, may have originated through hybridization or have been modified through introgression. All of these extant and historic cases involve parent taxa which are apparently not sister taxa (i.e. which are not derived directly by divergence from the same ancestral taxon). Most of the proposed parent taxa occupy different sections of the genus, but *E. orthocheila* ssp. *peraspera* and *E. collina* ssp. *paludosa* x ssp. *diversicolor* are exceptions.

The relative importance of hybridization in intergrade situations in Australian *Euphrasia* at first seems to contrast greatly with the substantial hybridization and introgression within the ecotypically differentiated microspecies of Europe (Yeo 1978b). However, the “hybrid swarms” of Yeo (1978b) occur in disturbed or intermediate habitats and are most frequent between closely related species growing nearby. Since in these instances intermediates are highly fertile, some of these may be analogues to the primary type of intergradation described above.

*Order of presentation of the taxa*

Taxa are ordered in a sequence which as far as possible places closest allies adjacent. Species begin with that postulated to be closest to the progenitors of the section or lineage. Subspecies begin with the autonymous taxon.

*Distribution and conservation status*

Many of the Australian taxa of *Euphrasia* are geographically and ecologically restricted. Some taxa are confined to rare localized habitats, e.g. in alpine habitats, *E. collina* ssp. *lapidosa* of fjeldmark, *E. collina* ssp. *glacialis* of moist communities with short herbage, and *E. gibbsiae* ssp. *pulvinestris* of blanket bog, and at lower elevation probably the cliff face home of *E. bella*, *E. bowdeniae* and *E. phragmostoma*. Other taxa, particularly of montane and lowland regions, occur in a range of often more widespread communities, but even some of these taxa, e.g. ssp. *tetragona* and ssp. *osbornii* of *E. collina*, are rare, if occasionally forming large local populations.

A number of taxa, i.e. *E. gibbsiae* ssp. *psilantherea*, *E. arguta*, *E. collina* ssp. *muelleri* and unnamed taxa such as an annual in the Blue Mountains, New South Wales (p. 284) and *E. sp. 'Tamworth', are known only from old specimens. The lack of collections may reflect extinction, but cases such as the recent discovery of *E. phragmostoma* after 80 years’ absence from collections, and single recent collections of each subspecies of *E. orthocheila*, previously not collected for decades, indicate that some of these taxa may still survive.

Conservation status of each taxon is provided using the formulae of Leigh, Briggs & Hartley (1981). The numerical rarity code relates to distributional range, 2 being very restricted, e.g. less than 100km, and 3 being for wider ranges of taxa with small local populations. The letter risk codes are: X, not collected in recent years, believed extinct; E, endangered, in risk of disappearing in 1-2 decades of continued present pressure; V, vulnerable, not endangered but at risk through depletion or if potential changes to land use threaten survival; R, rare but not endangered. The addition of a letter C indicates occurrence in a National Park or proclaimed reserve.
EUPHRASIA L.

For synonymy, description, typification and distribution, see p. 73.

KEY TO THE SECTIONS OF EUPHRASIA IN AUSTRALIA

1a. Anthers glabrous about connective. [Perennial.]
   2a. Rearmost pair of anther awns (1.5)2.5-3.2 mm long, as long as or longer than anthers, needle-shaped or sometimes distally twisted or dilated and eroseolate. Corolla lacking striations. [Branches or shoots on main inflorescence-bearing axes occurring at widely spaced groups of consecutive nodes.] .......... II. Sect. Phragmostomae (p. 102)
   2b. Rearmost pair of anther awns 0.2-0.8 mm long, shorter than anthers, needle-shaped, entire. Corolla partially to extensively striated.
   3a. Branches or shoots on main inflorescence-bearing axis(es) developing in basipetal sequence in consecutive axils from 1-few nodes below inflorescence. ........................................ I. Sect. Cuneatae (p. 98)
   3b. Branches or shoots on main inflorescence-bearing axis(es) developing in no fixed sequence, not consistently in consecutive nodes if high above ground level, often only near ground level. ........................................ III. Sect. Striatae (p. 105)

1b. Anthers of at least posterior pair hairy about connectives.
   4a. Corolla striated. ........................................ V. Sect. Lasiantherae (p. 247)
   4b. Corolla lacking striations.
   5a. Perennial. Branches or shoots on main inflorescence-bearing axis(es) developing in no fixed sequence, not consistently in consecutive nodes if high above ground level. Upper corolla lobes ± coplanar, facing forward. .......... IV. Sect. Australes (p. 147)
   5b. Annual. Branches or shoots on main inflorescence-bearing axis developing in basipetal sequence in consecutive nodes high above ground level from 1-few nodes below inflorescence. Upper corolla lobes facing to side or coplanar. ........................................ VI. Sect. Scabrae (p. 260)

I. Sect. Cuneatae Barker

For synonymy, Latin and English descriptions, typification and distribution, see p. 80.

One species, from north-eastern New South Wales, occurs in Australia (fig. 27).

1. Euphrasia ramulosa Barker, species nova
Species nova Sectionis Cuneatarum a E. cuneata differt axibus rhachidibusque saepe glandulosis, calyce scaberulo, lobis inferis corollae extra subglabris, capsula subglabra, et seminibus minoribus.

Perennial herb or undershrub, 25-50cm or more tall, with several or many ascending or erect foliaceous branches arising from ground level and terminated by inflorescence. Stem not seen; main inflorescence-bearing branches 19-30cm high to base of inflorescence, simple for (0)1-2(4) nodes below inflorescence, i.e. for 0.05-0.24 of height of inflorescence above ground level; upper 4-10 internodes as long as or longer than upper leaves, the longest internode 1.2-2.5 times length of upper leaves; branches developing basipetally in consecutive nodes, with all nodes, except the very upper ones, developing shoots; axes in upper parts with dense very short to short eglandular hairs all around or in two rows recurrent from between leaf bases, sometimes mixed all around with very sparse to moderately dense, very short to moderately long glandular hairs, lower down with sparser shorter eglandular indumentum in two rows apparently lacking glandular hairs, near base usually glabrous, sometimes (Williams ii.1963) bearing moderately dense, long glandular hairs. Cotyledons not seen. Leaves: uppermost stem leaves 5.4-9.2 x 2.3-5.4mm, obovate to spatulate,
sometimes narrowly so, crenately toothed, with sessile gland patches confined to distal 0.6-0.75 of lower surface, otherwise glabrous; base narrowly attenuate-cuneate to attenuate, often subpetiolate; teeth (1)2(3) along each margin, blunt, usually obtuse, sometimes acute, confined to distal 0.26-0.60 of leaf, with longest tooth 0.3-0.8mm long; apical tooth 1.2-1.5 x 1.1-2.3mm, bluntly broad-obtuse to acute; leaves lower down increasingly longer and more attenuate, glabrous or sometimes (Williams ii.1963) with sparse moderately long glandular hairs. Inflorescence racemes, ± dense in bud, sparse to moderately dense in flower and fruit, those of main axes with c. 30-50 or more flowers, with lowest 1-4 nodes bearing single flowers or only with undeveloped buds; pedicels at lowest node 1-3mm long, shorter higher up; rachis bearing moderately dense to dense, very short to moderately long glandular hairs, usually all around, sometimes in two rows with slightly sparser hairs between, often mixed all around with moderately dense to dense, very short to moderately long glandular hairs; apical bud cluster initially cylindrical to ovoid, sometimes narrowly so, c. 2-2.5cm long, hidden by or hardly emergent from corollas of uppermost flower pair after flowers at initial c. 10-15 or more nodes have reached anthesis. Bracts at lowermost node similar in size, shape and indumentum to uppermost leaves, toothed apparently at all nodes, shorter than or equal to calyx except rarely at lower 1-2 nodes. Calyx 4.2-6.5mm long, externally minutely scaberulous along ribs, densely so at base, sparsely to moderately densely so towards apex, internally glabrous; teeth blunt or sharp, acute to shortly narrow-acuminate; lateral clefts 0.6-1.3mm deep, shorter than median clefts, which are 1.3-3.5mm deep. Corolla 8.5-11mm long along upper side, white with purple striations and small yellow patches at base of anterior filaments (Sneddon 21; see also Williams xi.1960); tube 5.5-8mm long, with base narrow-cylindrical, distally near point of insertion of anterior filaments, at a point 4.5-6mm from base, expanded laterally and abaxially, glabrous at very base, otherwise externally covered by short to moderately long glandular hairs, dense on adaxial and lateral surfaces, sparse or absent on abaxial surface, with a few short glandular hairs behind lateral cleft, internally with
Fig. 28. Holotype of *E. ramulosa* Barker, *sp. nov.*

Fig. 29. Holotype of *E. phragmostoma* Barker, *sp. nov.*
dense, short to moderately long eglandular hairs all around; hood 2.5-4.2mm long, excluding lobes c. 3.5mm broad, including lobes c. 4.5-5mm broad, externally covered by dense short eglandular hairs, internally glabrous but for dense patch of long to very long eglandular hairs behind sinus; upper lobes emarginate to obtuse, glabrous with cleft between 1.2-2.2mm deep; lower lip 6.5-9.6 x 9-19mm, externally glabrous or with sparse to moderately dense, moderately long eglandular hairs at base, sometimes extending for a short distance onto lobes, which are otherwise glabrous; lower lobes usually shallowly to deeply emarginate, rarely truncate, with clefts between 3.3-4.7mm deep. Staminens with filaments sometimes glabrous, sometimes with eglandular hairs, either a few at base or dense over basal half, the anterior pair c. 4.5mm long, the posterior pair c. 2-2.5mm long; anthers 1.4-2.1 x 0.8-1.0mm, with area surrounding connectives glabrous, with slits lined sparsely to densely with moderately long to long eglandular hairs, with awns smooth and sharp, those of the rearmost pair 0.3-0.4(0.6)mm long, longer than other three pairs. Ovary in lateral view ovate-oblong to obovate-oblong, sometimes broadly so, laterally compressed, in median view narrowly ovate-caudate to linear, glabrous or with a few short setae at apex; apex in lateral view shallowly emarginate to truncate, sometimes obliquely so; ovules 20-35. Capsules (only 3 mature ones seen) c. 5-6mm long, in lateral view ovate to elliptic or oblong to obovate-elliptic, 1.8-3.4mm broad, laterally compressed, in median view linear or linear-elliptic to narrowly ovate-caudate, glabrous or with a few tiny setae at apex; apex in lateral view emarginate, sometimes obliquely so; seeds 8-22, ellipsoid to ovoid, often narrowly or obliquely so, (0.9)1.1-1.5(1.6) x 0.4-0.6mm. Chromosome number: unknown. Figs. 5, 28.

Distribution (fig. 27): E. ramulosa is endemic to the montane and possibly the subalpine zones of the Northern Tablelands region of New South Wales. Altitude, 900-1600m.

Ecology: In the Point Lookout-Ebor Falls area E. ramulosa occurs in wet or dry sclerophyll Eucalyptus forest or the margin of tall Eucalyptus woodland. Sparse data from other localities refer to rather moist or boggy habitats or an association with granite.

Flowering occurs approximately between November and May, but probably extends outside this range as the one November collection bears some capsules and the only May collection is in bud and flower.

Conservation status: 3R,C.

Notes: 1. E. ramulosa is most closely related to E. cuneata of New Zealand, which is distinguished by its densely setose capsules, lower corolla lobes externally hairy all over, the complete absence of glandular hairs from the rachis, externally glabrous calyx (except at base of median clefts) and larger seeds.

2. E. ramulosa shows variation in the incidence of glandular hairs on the rachis and the upper part of the axis. It is impossible to determine on the material available whether the variation between populations occurs constantly in this character (in which case taxonomic recognition would be warranted), or consistently within populations. Boorman NSW10931 contains material from apparently several plants which vary in the incidence of the glandular hairs on the rachis.

Specimens examined

II. Sect. Phragmostomae Barker

For synonymy, Latin and English descriptions, typification and distribution, see p. 81. Fig. 30.

Monotypic, confined to south-eastern Tasmania (fig. 27).

Fig. 30. Sect. Phragmostomae (E. phragmostoma). A, front view of flower; B, side view of flower; C, external view of anthers on one side of flower, with an anterior anther on left and posterior anther on right; D, abaxial view of uppermost leaf of main inflorescence-bearing axis (s = sessile gland patch). (A, B: Morris AD97842487, holotype; C, Bufton 8; D, Bufton 7).
Studies in Euphrasia

2. Euphrasia phragmostoma Barker, species nova


Species nova, Sectionis Phragmostomae sola, in generi unica et longitudine formaque singulari arista rum postremaunt et habitu ramis principalibus inflorescentigeris ramulos in gregibus dispersis nodorum product entibus notato.


Much-branched perennial herb or undershrub, to c. 50cm tall, with many ascending branches arising from procumbent stem or main branches of previous years. Stem possibly in first year erect or ascending, subsequently procumbent; main inflorescence-bearing branches to c. 60cm or more long, simple for 0-10(18) nodes below inflorescence; developing branches in axes of widely spaced groups of 1-3(4) nodes, within groups of more than 1 node usually developing basipetally at consecutive nodes with at least the initial pair of shoots ultimately bearing an inflorescence; upper 0-2(7) internodes as long as or longer than upper leaves, shorter lower down, and then often becoming longer again; axes with 2 rows of dense short eglanular hairs or covered by a dense mixture of moderately long to very long glandular hairs and short to moderately long eglanular hairs. Cotyledons not seen.

Leaves: uppermost leaves of main inflorescence-bearing branches (7)9-17 x 5-8(10)mm, spathulate, serrate-crenate to serrate, with sessile gland patches confined to distal 0.5-0.75 of undersurface, otherwise glabrous or bearing moderately long to long glandular hairs, sparse and confined to base or dense all over, mixed with short to moderately long eglanular hairs, moderately dense on upper side, sparse on lower side; base narrowly long-attenuate, subpetiolate; teeth 1-2 along each margin, confined to distal 0.1-0.4 of leaf, bluntly obtuse or acute, the longest tooth 0.2-1.2mm long; apical tooth bluntly broad-obtuse to shortly broad-acuminate, 1-3 x 3-6(8)mm; leaves lower down of similar size but sometimes for relatively shorter subpetiolate base, with similar indumentum; leaves on young shoots small, subpetiolate, with 1 tooth along each margin. Inflorescences racemes, moderately dense to dense in flower, with up to c. 15 flowers, sometimes reverting to a vegetative axis after flowering; pedicels at lowest node 1.3-3.5mm long, shorter higher up; rachis with indumentum similar to upper part of axis; apical bud cluster initially ± cylindrical or narrowly so, extended c. 0.2-2.5cm above the first pair of flowers, becoming hidden by corollas of uppermost flower pair after flowers at first c. 2-6 nodes have reached anthesis. Bracts: lowermost bracts similar in shape, size and indumentum to uppermost leaves, proximal ones progressively smaller, otherwise similar. Calyx 7-10mm long, externally glabrous or covered by sparse to dense, short eglanular hairs mixed with sparse to dense, short to long glandular hairs, internally bearing dense, short to moderately long glandular hairs, sometimes mixed with dense, short to moderately long eglanular hairs; teeth bluntly acute or obtuse; lateral clefts absent to 0.5-1.9mm deep, much shorter than median clefts, which are 3.2-5.0mm deep. Corolla cream-white, lacking prominent yellow patches or purple striations (W.M. Curtis pers. comm. 1976; also from colour slides sent by her), 14-24mm long along upper side; tube 7-12mm long, narrow-cylindrical in basal half, abaxially and somewhat laterally expanded below point of insertion of anterior filaments, externally covered all around by dense moderately long to very long downturned eglanular hairs, mixed with sparse moderately long to long glandular hairs on abaxial side and behind lateral cleft, internally covered all around by dense long downturned eglanular hairs; hood 6.5-10.5 x 6.5-8.2mm (including lobes), c. 4-5mm broad (excluding lobes), externally covered by dense long glandular hairs or eglanular hairs or a mixture of both, internally with dense long eglanular hairs between bases of filaments, with glandular hairs behind sinus, and sometimes with sparse to moderately dense, short to
moderately long glandular hairs above anthers, elsewhere glabrous; upper lobes obtuse to shallowly emarginate, covered behind by sparse to moderately dense, short to long glandular hairs extending onto margins, sometimes mixed with eglandular hairs, with cleft between 0.2-0.5mm deep; lower lip 7-12.5 x 9-17.5mm, concave from above, downturned from base apparently at more than right angles to upper side, lower side covered by sparse to moderately dense, moderately long to long glandular hairs extending to margins, sometimes mixed with eglandular hairs of a similar length, upper side glabrous; lower lobes obtuse to deeply emarginate, with clefts between 3-4.5mm deep. Stamens with filaments glabrous but for dense eglandular hairs at base of anterior pair, the anterior pair 6.5-9.5mm long, the posterior pair 3-5mm long; anthers 1.8-3.0 x 1.2-1.9mm, the posterior pair narrower than the anterior by the much narrowed and elongated rearmost cell, which is sometimes pilose on back near awn, with area about connectives glabrous, with slits densely lined by long to very long eglandular hairs, with rearmost pair of awns (demarcated by beginning of attenuation of anther cell, not by colour change from brownish to whitish) 1.5-2.5-3.2mm long, in distal part sometimes flattened with margins erosulate or twisted, with apex acute, with anterior awns 0.1-0.3mm long, smooth and sharp. Ovary in lateral view ovate-elliptic to elliptic, compressed laterally, in median view narrowly elliptic-acuminate to ovate-caudate, with sparse to dense, erect, short to long setae; ovules 60-75. Capsules 7-12mm long, in lateral view obovate-elliptic, 3-4mm broad, in median view narrowly elliptic-acuminate, covered at apex or on upper 1/4-1/3 by sparse to dense setae 0.1-0.3mm long; apex obtuse; seeds c. 20-30, obliquely ellipsoid to broadly obovoid, c. 0.9-1.4 x 0.3-0.9mm. Chromosome number: unknown. Figs. 5, 29, 30.

Typification: With the subsequent collection of a more suitable set of specimens, I have altered my choice of holotype for E. phragmostoma from the rather fragmentary collection (Bufton 8) designated in my unpublished thesis (Barker 1974).

Following discussion with Mr D.I. Morris about confusion over the dates and localities recorded for collections of E. phragmostoma made in 1974 and sent to AD, Dr A.E. Orchard (pers. comm. 1978) wrote, "Apparently the first collection was made by Mr & Mrs R.G. Williams at Dolomieu Pt on 10.xi.1974 (not 10.xii.1974). They showed the plant to [Morris], who went back to the same spot on 16.xi.1974. All of his material is the one collection, made on the same date, despite the varying descriptions of the locality . . . ."

Distribution (fig. 27): E. phragmostoma is known from three localities on the east coast of the Tasman Peninsula, south-east Tasmania, together with an old record from Marion Bay about 30km to the north. Altitude, 100m at Dolomieu Point, but the Marion Bay specimen (Bufton 8) comes from "a mountain top".

Ecology: Apart from the above old "mountain top" record, E. phragmostoma has been recorded at Dolomieu Point from the exposed upper edges and face of sheer, high coastal cliffs, scattered within a low scrub (Orchard 5042; Mr D.I. Morris per Dr Orchard, pers. comm. 1979).

From the condition of the available specimens, flowering probably occurs between late October and into January. Fruits occasionally begin developing in mid November and are profuse in the December material.

Conservation status: 2E.
Notes: 1. *Jarman & Kantvilas* 39 from Cape Hauy on the south side of Fortescue Bay differs from specimens from the northern side of the bay and elsewhere in the absence of glandular hairs on its axes, leaves, bracts and calyces, and by its calyces with lateral clefts varying from obliquely emarginate to completely absent. Studies of population variation in *E. phragnostoma* are needed to ascertain if two races exist.

2. I gratefully acknowledge the assistance of the recent collectors of *E. phragnostoma* and Dr W. M. Curtis who instigated their fruitful search for this species, previously represented in herbaria by two rather fragmentary old collections in MEL.

Specimens examined


III. Sect. *Striatae* (Du Rietz) Barker

For synonymy, description, typification and distribution, see p. 83. Fig. 31.

The section is endemic to Australia. Its four species are largely confined to Tasmania, but there is an outlying occurrence in the eastern highlands of Victoria (figs 32-36).

Notes: 1. *E. crassiuscula* has been included in Sect. *Australas* (q.v. note 2; p. 64), but because *E. crassiuscula* ssp. *eglandulosa* usually has conspicuously striated corollas and glabrous anther backs it has been treated in the key to species of Sect. *Striatae*.

These same anther and corolla differences also break down in *E. semipicta*. Its corollas are not as extensively striated as is usual in Sect. *Striatae*, and anther backs vary from glabrous to densely hairy, at least part of this range of variation occurring within populations. This species possibly originated from hybridization between a species of each section. Because of the presence of striations on the corollas, the common existence of plants with glabrous-backed anthers and the general resemblance in habit and leaf shape to taxa such as *E. gibbsiae* ssp. *kingii*, *E. semipicta* is placed in Sect. *Striatae*.

2. Three plants collected from Mt La Perouse in south-western Tasmania (fig. 36) apparently link *E. hookeri* with the other species of Sect. *Striatae* (F.A. Rodway s.n., xii.1899. NSW22280, p.p.). The plants resemble *E. hookeri* in size, their apparently single-stemmed habit with small imbricate leaves, their small corollas and their very short glandular indumentum confined mainly to the margins of the bracts and calyces. Only in their leaves, the margins of which are recurved but not coherent, do they differ from *E. hookeri*. From *E. striata* and *E. semipicta* they differ by their glandular inflorescence and habit, while from *E. gibbsiae* they differ in flower size and habit. These plants may represent an undescribed species or a hybrid between *E. hookeri* and another species of Sect. *Striatae*.
3. A fragmentary specimen from Tasmania (Scott s.n., s.dat. Without locality, MEL1790) almost certainly represents a new species or a monstrosity of unknown origin. It seems unlikely that it is of hybrid origin as it is different from all known Australian species. The plant is unique, its leaves having a very narrow attenuate base and a large bluntly broad acute to obtuse apical tooth extending well past a pair of short bluntly obtuse lateral teeth. Among the Australian species it approaches E. striata of Sect. Striatae in leaf shape (although the apical leaf tooth of E. striata is somewhat shorter relative to the lateral teeth). The leaves resemble most closely those of the New Guinea species of Sect. Pauciflorae. The glabrous anther backs ally it with both subsections, although the calyces, bracts and rachis are covered by a dense, long [0.3-0.4mm] glandular indumentum, a character unknown in the New Guinea species.

**Key to the species of Sect. Striatae**

1a. Leaf and bract teeth with margins recurved so greatly that they cohere along entire length, with sessile glands lacking on underside. (Ser. Hookerae Du Rietz) .............. 7. E. hookeri (p. 142)

1b. Leaf and bract teeth with margins recurved but clearly separated, with sessile gland patches apparent on underside. (Ser. Striatae Du Rietz).

2a. Calyces, bracts, and at least upper leaves lined by long woolly eglandular hairs. Inflorescences bearing c. 20-40 flowers; apical bud cluster conical, subacute. Sessile gland patches confined to distal \( \frac{1}{3} \) or more of lower surface of uppermost leaves, 12. E. crassiuscula (p. 236; also see Sect. Striatae: note 1)

2b. Calyces and bracts bearing short straight eglandular hairs on margins, leaf margins lacking them. Inflorescences bearing (6)10-20(26) flowers; apical bud cluster spherical to conical, broadly rounded. Sessile gland patches confined to distal \( \frac{1}{3}-\frac{1}{2}(\frac{2}{3}) \) of lower surface of uppermost leaves.

3a. Bracts, outer surfaces of calyces and often uppermost leaves, sometimes almost all leaves bearing glandular hairs. Corolla with hood (4.0)4.2-5.0(5.4)mm long; lower lip (6.8)7.8-10.8(11.2) x (13)14.5-17.5(20)mm. [Corolla partially to extensively striated. Stem reduced or conspicuous. Apices of capsules broadly acute to truncate to emarginate in lateral view. Ovules (38)52(71). Seeds (5)30(66), (0.8)1.1-2.0(2.2)mm long.] 3. E. gibbsiae (p. 111)

3b. Bracts, outer surfaces of calyces and leaves lacking glandular hairs; rarely with corolla bearing one or two tiny glandular hairs. Corolla with hood 2.3-4.2mm long; lower lip 5.8-8.0 x 9.6-15.5mm.

4a. Stem usually reduced; branches branched and rooting in prostrate regions, simple in erect parts. Apex of capsules emarginate to broadly obtuse in lateral view. Ovules 25-60. [Corolla on all three lower lobes prominently and ± equally red-purple striated. Hairs lining anther slits 0.05-0.15mm long. Seeds c. 7-33. (0.8)1.2-1.8(2.0)mm long.] 4. E. striata (p. 134)

4b. Stem conspicuous, bearing inflorescence in first year, then dying back to upper branches; branches arising from stem above ground level. Apex of capsules broadly acute to truncate in lateral view. Ovules 80-120.

5a. Corolla with cleft between upper lobes c. 0.5-0.6mm deep; lower lip c. 2.4 x 5.6mm. 5. E. sp. 'Southport' (p. 139)

5b. Corolla with cleft between upper lobes (1)1.5-2.5mm deep, lower lip (5.5)6-8(9) x (10)11-13(15)mm. [Corolla with lateral lobes red-purple-striated, lowest lobe finely blue-striated or striations lacking. Hairs lining anther slits 0.2-0.4mm long. Seeds c. 48-78, (0.5)0.7-0.9 (1.3)mm long.] 6. E. semipicta (p. 139)
E. gibbsiae

- **ssp. gibbsiae**
- **ssp. psilantherea**
- **ssp. wellingtonensis**
- **ssp. wellingtonensis**: doubtful locality

Fig. 32

50 miles
80 km

Fig. 33

Figs 32-33. Distribution of the species and subspecies of Sect. Striatae (I). 3000ft (910m) contour.
Fig. 34. Distribution of the species and subspecies of Sect. *Striatae* (2). 3000ft (910m) contour in Tasmania, 5000ft (1520m) contour in Victoria.
Fig. 35-36. Distribution of the species and subspecies of Sect. *Striatae* (3). 3000ft (910m) contour.


Perennial herb of variable habit with axes and rachises and, in part, leaves, bracts and calyces red-brown. Cotyledons not seen. Inflorescences but for lowestmost 0-1(3) nodes dense racemes, although buds often undeveloped at lowestmost nodes; stem inflorescence or, if stem reduced, branch inflorescences producing (10)14-24(36) flowers; rachis with variable indumentum; internodes hardly elongating after anthesis, such that, except sometimes at wider-spaced lower internodes, capsules usually extending past base of calyx above; pedicels of lowestmost flowers 1.0-2.5(4.0)mm long, shorter towards apex; apical bud cluster (excluding any buds at widely spaced lower nodes) usually ellipsoid to spherical, rarely acutely conical, initially c. 1-2.5cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after flowers at first 1-3(4) nodes have reached anthesis. Bracts similar to uppermost leaves, but with variable indumentum. Calyx (5.0)6.0-10.0(10.8)mm long, with indumentum on outer surface variable, with inner surface of teeth and distal half of tube with sparse to dense, usually short to moderately long, rarely long eglandular hairs, usually all over, sometimes confined to distal parts, mixed with very densely to moderately dense to dense, rarely sparse, usually short to moderately long, rarely long glandular hairs, usually all over, sometimes restricted to proximal parts; teeth sharply to bluntly acute; lateral clefts (1.7)2.2-4.0(5.0)mm deep, shorter than median clefts which are (2.4)3.3-6.0(6.5)mm deep. Corolla (9.8)11.6(13.0)mm long along upper side, white, lilac, deep lilac, purple or blue, with yellow to orange blotch behind lowest lobe and deep in tube at base of anterior filaments, with red-purple, purple or indigo striations confined almost entirely to tube and hood or with 3-5 striations extending well out onto each of some or all lobes; tube (5.3)7.0(8.5)mm long, narrowly cylindrical, abaxially and laterally broadened near point of insertion of anterior filaments which are (3.0)4.5(6.8)mm from base of corolla, externally glabrous at base, on distal, adaxial and lateral surfaces from at least base of anterior filaments covered by usually dense long, rarely moderately dense, moderately long eglandular hairs, glabrous below about base of anterior filaments, on abaxial surface glabrous further forward with widened part bearing moderately dense to dense, short eglandular or glandular hairs or mixture of both, with small dense patch of short glandular hairs about lateral cleft, internally glabrous at base, distally covered by moderately dense to dense, short to moderately long eglandular hairs about filaments and below, sometimes also between them, sometimes glabrous along midline of adaxial side; hood (4.0)4.2-5.0(5.4) x (3.8)4.0-5.0(5.5)mm (excluding lobes), (5.8)7.0-9.4(10.2)mm
broad (including lobes), externally covered by dense, moderately long to very long eglandular hairs, sometimes with sparse to dense, short glandular hairs on sides, internally usually glabrous but for dense long eglandular hairs sometimes mixed with sparse to dense, short glandular hairs in sinus region, sometimes with dense long eglandular hairs along midline above tube, rarely covered by sparse short glandular hairs denser along midline; upper lobes coplanar or almost so, obtuse to truncate, sometimes praemorsely so, to emarginate, glabrous on front surface and margins, on rear surface usually glabrous or with a few short to moderately long glandular hairs, sometimes mixed with eglandular hairs at base, sometimes covered by moderately dense, short to moderately long glandular hairs, sparser or absent distally, rarely with moderately dense, moderately long eglandular hairs in distal half, with cleft between (0.9)1.4-3.0(3.3) mm deep; lower lip (6.8)7.8-10.8(11.2) x (13.0)14.5-17.5(20.0) mm, concave from above, downturned from base such that more than perpendicular to upper side, externally usually covered by very sparse to dense, short to long eglandular hairs, often mixed with sparse to moderately dense, short to moderately long glandular hairs, rarely glabrous, internally and on margins glabrous except rarely for eglandular hairs lining margins; lower lobes broadly obtuse to truncate to emarginate, sometimes praemorse, with clefts between (3.3)3.8-6.0(6.4) mm deep.

Stamens with filaments glabrous, the anterior pair 4.5-5.7(6.2) mm long, the posterior pair (1.7)2.2-3.3(3.4) mm long; anthers (1.0)1.3-2.0(2.2) x (0.8)1.0-1.5(1.7) mm, with area about connectives usually glabrous, very rarely bearing a few moderately long flexuose eglandular hairs, with slits lined especially towards awns by dense, very short, long eglandular hairs, with rearmost pair of awns (0.25)0.3-0.5(0.6) mm long, longer than awns of other three pairs. Ovary in lateral view usually broadly oblong to broadly elliptic, sometimes ovate, rarely obovate-elliptic, often oblique, hardly compressed laterally, in median view ovate to elliptic-ovate, glabrous usually except for very sparse to dense, moderately long to very long setae, confined to upper 1/6-2/5 or very apex; apex in lateral view usually broadly obtuse to truncate, rarely broadly acute, often oblique; ovules (38)52(71). Capsules (6)6.5-10(11) mm long, in lateral view obovate to elliptic, (3)3.5-4.5(4.6) mm broad, laterally compressed, in median view narrowly ovate to elliptic, sometimes glabrous, sometimes bearing a few short to long setae at apex or moderately dense setae over upper 1/6-1/2, short to moderately long at apex, short lower down; apex in lateral view emarginate to truncate or broadly obtuse, often obliquely so; seeds (5)30(66), obovoid, oblong or ellipsoid, often obliquely so or flattened, (0.8)1.1-2.0(2.2) x (0.4)0.5-1.0(1.1) mm. Chromosome number: unknown.

Distribution (figs 32-34): E. gibbsiae is widespread in the alpine and subalpine areas of central, southern and western Tasmania and in the southern and western lowland areas of the island where rainfall is very high. The species extends into the eastern highlands of Victoria where it is known only from the subalpine areas of the Baw Baw plateau. Altitude, 0-1550 m or more.

The nine subspecies are more restricted in their geographical and altitudinal distributions. For details, see under treatment of distribution for each subspecies.

Ecology: E. gibbsiae occupies a wide spectrum of habitats, ranging from coastal heath and button-grass moorlands in lowland areas to alpine heath and blanket bog (cushion plant expanses) on the highest summits. Nine subspecies are strongly ecotypically defined. For details refer to ecological treatment under each subspecies.

The period of flowering of the montane species is limited to a definite period of two or three months, but the two lowland subspecies, ssp. psilantherea and ssp. kingii, may flower over a longer period. For details see under respective subspecies.
Conservation status: see subspecies.

Intraspecific polymorphism

E. gibbsiae is highly polymorphic. All nine subspecies, possibly apart from ssp. subglabrifolia, appear to have relatively continuous ranges of distribution, with any large discontinuities in range probably having arisen because the intervening ecologically suitable regions have been inadequately botanized to date.

The range of distribution of most subspecies coincides with that of at least one other subspecies. Observations of ecological preferences and the ability to retain morphological integrity have been made in some areas of overlap, and it has been found that character differences are usually, but not invariably retained.

1. Ssp. gibbsiae and ssp. pulvinestris. Ssp. gibbsiae and ssp. pulvinestris are ecotypically differentiated in the western portion of the Mt Field massif. Generally only ssp. pulvinestris occupies the extensive areas of blanket bog cushion plants in the summit regions, while ssp. gibbsiae occurs in the tall alpine heath, or low heath where clumps of Astelia sp. predominate. The collections Barker 1168-1169 come from the one area of overlap observed. Between pure cushion plants and open low heath occurs an ecotone consisting of cushion plants mixed with fine grass. In this ecotone plants of both subspecies were found growing side by side, but no morphological intermediates were observed. Apparently there is some barrier to interbreeding, since the two subspecies were flowering simultaneously.

2. Ssp. gibbsiae, ssp. comberi and ssp. aff. subglabrifolia. In the eastern portion of the Mt Field massif (fig. 34) a form closely related to ssp. subglabrifolia (q.v.: note: Barker 1187) occurs on the banks of shallow rivulets (c. 0.5m deep) running across a broad low subalpine heathland. Populations of ssp. gibbsiae (Barker 1184) and intergradations between ssp. gibbsiae and ssp. comberi (Barker 1189) occupy the surrounding ridges in snowgum woodland. No spatial overlap was observed and morphological distinctions of internode length and indumentum were retained. Flowering was apparently more or less simultaneous.

3. Ssp. gibbsiae, ssp. discolor and ssp. microdonta. Three subspecies of E. gibbsiae occur in the vicinity of Cradle Mtn. Ssp. gibbsiae (Barker 1205, 1216, 1218B) and ssp. discolor (Barker 1206, 1218A) both occupy the upper slopes of the mountain. There are no obvious differences in ecological preference except that ssp. gibbsiae may inhabit more sheltered areas in tall heath or among doleritic boulders. Near the very summit of Cradle Mtn the two subspecies were found growing either together or in close proximity. No morphological intermediates were observed, and since flowering occurred simultaneously, there must be some barrier to interbreeding. The third subspecies, ssp. microdonta, apparently grows in button-grass moorland in the broad valleys well below the habitats of the other two subspecies. E. gibbsiae has never been recorded from the intervening slopes of this relatively well-collected area. This spatial separation between ssp. microdonta and the other two subspecies, together with a difference in flowering period through altitudinal differences would give little opportunity for interbreeding.

4. Ssp. gibbsiae and ssp. comberi. Throughout the wide area of alpine heath above Clemes Tarn, along the track to Mt Field West (fig. 33) between the altitudes of 1250m and 1310m, plants of ssp. gibbsiae and ssp. comberi were found growing side by side (Barker 1173-1175). The specimens of both subspecies show their typical indumentum, and no intermediates were observed. Plants from each subspecies were
tested for pollen sterility. Both ssp. *gibbsiae* (PS141, 154-158) and ssp. *comberi* (PS143-145) showed almost entirely normal pollen. The plants in *Barker 1174(2)* with glandular hairs on the leaves well down the branches were similarly tested. Two fragments (PS151, 153) possibly from the same plant showed a high percentage of empty sterile pollen. The other four plants tested (PS142, 149, 152, 163, 164) showed normal pollen.

Two of the three other collections from the Mt Field massif contain a mixture of the two subspecies. Accordingly all are cited here rather than under the individual subspecies.

Because the distinction of the two subspecies is based on a single character difference, i.e. the distribution of glandular hairs on the vegetative parts, and as no range of intermediate types of indumentum distribution is apparent, it is impossible to determine from the above evidence whether the two subspecies interbreed or if there are strong barriers preventing this. Certainly there is amply opportunity for interbreeding as both taxa occur together over a wide area and flower simultaneously. If interbreeding does occur it is possible that the two indumentum types which separate ssp. *gibbsiae* and ssp. *comberi* are controlled by a simple dominant-recessive effect at a single gene locus, since there is no transitional range of indumentum types.

Specimens examined

**TASMANIA:** *Barker 1173 & 1173A*, 19.i.1971. Mt Field Nat. Park; along track to Mt Field West between c. 400 and 1200m W of Clemen's Tarn. AD.-*Barker 1174(1), 1174(2) & 1175*, 19.i.1971. Mt Field Nat. Park; c. 400m W of Clemen's Tarn on the track to Mt Field West. AD.-*Barker 1184*, 21.i.1971. Mt Field Nat. Park; on slopes of Mt Field East immediately above Windy Moor, c. 1/2km SW of summit. AD.-*Melville 2316, Willis, Curtis & Paton*, 12.xii.1952. Naturalist Peak. NSW (only ssp. *comberi*).-*Telford per Canning 2233*, 2.i.1969. Mt Field Nat. Park (Mt Field West). CBG.

5. Ssp. *comberi*-ssp. *kingii* intergrade. The two subspecies which are widespread in south-western Tasmania, ssp. *comberi* of alpine and subalpine areas and ssp. *kingii* of lowland areas, apparently intergrade along ecotones between their two habitats (fig. 33). Such an ecotone was observed in the Hartz Mountains National Park along the track to Mount Snowy (*Barker 1197, 1191, 1193, 1194*). The two subspecies can be distinguished on flower colour, with the corollas of ssp. *comberi* being consistently white and those of ssp. *kingii* varying from white to deep purple or blue, but a morphological study of these collections is impaired by the general lack of flowering material. They can also be distinguished by their distinct habits and the shape of the capsule apex (see ssp. *kingii*: note 1).

At its highest altitude ssp. *comberi* was found growing in "cushion plants, or amongst stems of prostrate woody plants in doleritic flat alpine moorland" (*Barker 1194*). The plants had the typical clusters of ascending branches arising from the reduced stem, or other branches at ground level and simple higher up. They also bore broad, emarginate to broadly obtuse capsules. In the lowest locality in snowgum woodland grew plants (*Barker 1197*) resembling ssp. *kingii* in their tendency towards erect branches (although no stem was apparent), the frequent occurrence of shoots and branches in the axils high above ground level, and the narrower broadly obtuse capsules. On the slopes connecting these two localities occurs alpine heath. Forms intermediate between the two subspecies occurred in this area in openings between shrubs, but it is unlikely that these intermediates were sterile hybrids as seed set appears normal. Rather, the intermediates appear to be part of a cline or hybrid swarm with fully fertile hybrids along an altitudinal and ecotonal gradient. It is probable that the intergrade continues to lower elevations in the area where pure populations of ssp. *kingii* may be found.
Similar intergrades may occur elsewhere in south-western Tasmania where the ranges of the two subspecies coincide. Six of the seven specimens* of Edwards AD97347079, apparently from such an intergrade on the Snowy Range, contained pollen almost entirely normal in appearance (PS159-161, 165-167). Thus, there is no evidence of any sterile hybrids from either seed or pollen set in intergrades between the two subspecies. Plants from Adamsons Peak (Kantvilas 9) have the short internodes of ssp. comberi but occasional ones branch in the upper parts. They may also come from such an intergradation.

The existence of intergradations between ssp. comberi and ssp. kingii must cast some doubt on the genetic basis of their few distinguishing characters. A study involving the raising of seedlings of one subspecies in the habitat of the other would help to determine whether they are solely environmental modifications.

Specimens intermediate between ssp. comberi and ssp. kingii

TASMANIA: Barker 1191, 23.i.1971. Hartz Mountains Nat. Park; c. 1km S of hut near car park at end road into Park, on the track to Mt Snowy, AD.—Barker 1193, 23.i.1971. Hartz Mountains Nat. Park; c. 11/2km from the hut near the car park at the end of the road into the Park; above the tarns on the Mt Snowy track. AD.—Barker 1197, 23.i.1971. Hartz Mountains Nat. Park; c. 100m from hut near the car park at the end of the road into the Park; beside the track to Mt Snowy. AD.—Edwards s.n., 27.xii.1970. Snowy Range. From L. Skinner to 1/2m below L. Skinner AD97347079.—Kantvilas 9, 10.xi.1979. Adamsons Peak (plateau). HO.

Key to the subspecies of E. gibbsiae

1a. Glandular hairs on inflorescence parts and over all vegetative parts excluding roots and old parts of axes and rarely also prostrate parts of axes. [Corolla white, with striations usually extending well out onto lobes, rarely confined to tube and hood.]

2a. Plant with single erect stem bearing branches above ground level...

2b. Plant with many branches arising from the base of the stem or prostrate parts of other branches.

3a. Glandular hairs on distal prostrate parts of axes (0.1)0.3-0.4(0.7)mm long. Uppermost leaves of inflorescence-bearing branches with (1)2(5) teeth along each margin, (4)6-9(11)mm broad. Inflorescence-bearing branches (3)5-9(12)cm high to base of inflorescence. Anthers (1.5)1.7-1.9(2.0)mm long. ........ a. ssp. gibbsiae (p. 116)

3b. Glandular hairs on distal prostrate parts of axes 0.05-0.2mm long. Uppermost leaves of inflorescence-bearing branches with 1-2 teeth along each margin, (2.5)4-6(7)mm broad. Inflorescence-bearing branches (1.5)3-6(10)cm high to base of inflorescence. Anthers (1.2)1.4-1.6(1.8)mm long. ........ c. ssp. wellingtoniensis (p. 120)

1b. Glandular hairs usually confined to inflorescence, sometimes extending onto upper vegetative parts, sparse or absent from uppermost parts of axis, lacking from axis lower down and from axes of shoots.

4a. Plant either with single erect stem, bearing shoots and branches from ground level to high in upper parts, or with one to several branches developing from base and similar to stem in branching well above ground level. [Corolla usually purple, lilac or blue, sometimes white, with striations extending well out onto lobes. Internodes below inflorescence usually longer than leaves, the longest internode (1)2(4) times length of upper leaves. Uppermost leaves of stem or main inflorescence-bearing branches with 1-2(3) teeth along each margin, the longest tooth 0.8-1.5mm long. Anthers (1.0)1.3-1.6(2.2)mm long.] ................. e. ssp. kingii (p. 124)

4b. Plant with many ascending branches arising from base of stem or prostrate parts of other branches.

* The single anomalous specimen with long glandular hairs occurring sparsely well down an inflorescence-bearing axis in Edwards A.D97347079 has a rather high pollen sterility count of 43% (PS162). It may be a hybrid between plants of the intergradation between ssp. comberi and ssp. kingii and an unknown parent (??ssp. gibbsiae) with glandular hairs occurring well down the axes.
5a. Corolla with striations usually confined to tube and hood and hardly extending onto lobes, sometimes extending well cut onto lateral lobes. [Corolla white. Upper 0-4(5) internodes of main inflorescence-bearing branches as long as or longer than upper leaves, the longest $(1/2)_{11/24}$ times length of upper leaves. Uppermost leaves of main inflorescence-bearing branches longer than broad, (34-79)mm broad, with 1-2(3) teeth along each margin, the longest tooth (1.2)1.4-2.3(3.0)mm long, with cuneate, often narrowly so, to attenuate base. Anthers (1.5)1.6-2.0(2.1)mm long.]. ssp. pulvinestris (p. 131)

5b. Corolla with striations usually extending from tube and hood well out onto lobes, sometimes with lowest lobe unstriated, rarely with only upper lobes striated.

6a. Upper (0)3-6 or more internodes of main inflorescence-bearing branches as long as or longer than upper leaves, the longest $(1/2)\sqrt[3]{14}$-3 or more times length of upper leaves.

7a. Uppermost leaves of main inflorescence-bearing branches with (1)2 teeth along each margin, the longest tooth 0.5-1.0mm long. [Corolla white. Anthers (1.4)1.5-1.7(2.0)mm long.]. f. ssp. microdonta (p. 126)

7b. Uppermost leaves of main inflorescence-bearing branches with 1-2 teeth along each margin, the longest tooth (0.7)1.2-2.1(2.6)mm long. [Corolla white. Anthers (1.4)1.5-1.9(2.0)mm long.]. g. ssp. subglabrifolia (p. 127)

6b. Uppermost 0(7) internodes of main inflorescence-bearing branches as long or longer than upper leaves, the longest $(1/2)\sqrt[3]{1/24}$ times length of upper leaves.

8a. Corolla white. Uppermost leaves of main inflorescence-bearing branches with (1)2-3(4) teeth along each margin, the longest tooth (0.5)1.5(2.0)mm long. Anthers (1.2)1.4-1.7(1.8)mm long. d. ssp. comberi (p. 122)

8b. Corolla white, lilac, deep lilac or purple. Uppermost leaves of main inflorescence-bearing branches with 1(2) teeth along each margin, the longest tooth (1.2)1.5-2.5(3.0)mm long. Anthers (1.6)1.7-2.0(2.1)mm long. h. ssp. discolor (p. 128)

3a. ssp. gibbsiae


E. gibbsiae Du Rietz f. comberi auct. non Du Rietz: Willis, Muelleria I (1967) 148, p.p. (as to Curtis MEL41527 from "K. Col on the track to Mt Field West").


Plant (5)7-11(14)cm tall in open areas, up to over 20cm high when sprawling in shrubs, with many long branches, proximally prostrate or (within shrub) scandent, distally erect, arising from reduced stem or prostrate or scandent parts of other branches. Main inflorescence-bearing branches: distal erect part (3)5-9(12)cm long to base of inflorescence; internodes between uppermost 0-3(5) nodes as long as or longer than upper leaves, the longest internode $(1/2)\sqrt[3]{1/24}$ times length of upper leaves, shorter than leaves lower down; axis bearing sparse to dense, moderately long to long eglandular hairs usually in two rows, sometimes in two pairs of lines decurrent from between leaf bases, mixed with usually long to very long, rarely short glandular hairs all around the axis and extending from the erect parts on to at least the young shoot and distal prostrate parts, where (0.1)0.3-0.4(0.7)mm long, absent from older proximal parts. Leaves: uppermost leaves of main inflorescence-bearing branches (6)7-11(13) x (4)6-9(11)mm, obovate to broadly ovate or spatulate in outline, covered by usually dense, sometimes moderately dense, usually moderately to very long, rarely short glandular hairs; base usually attenuate or narrowly cuneate to broadly cuneate, rarely rounded-cuneate; teeth (1)2(5) along each margin, the longest tooth (1.0)1.8(2.5)mm long; apical tooth bluntly or sharply, usually shortly acuminate, sometimes acute, rarely obtuse or broadly short-acuminate, (1.3)2.2(3.0) x (1.3)2.2(3.2)mm; lower leaves with similar indumentum. Inflorescences with rachis with indumentum similar to upper axis. Bracts with indumentum similar to uppermost leaves. Calyx with outer surface
covered on teeth and distal part of tube by dense, usually moderately long to long, rarely short glandular hairs, sparser on proximal part of tube. Corolla white, with yellow blotch behind lowest lobe and deep in throat, with usually indigo, sometimes purple striations usually extending well onto lobes, sometimes almost confined to tube and hood. **Stamens with anthers** (1.5)1.7-1.9(2.0)mm long. Figs 5, 31G, 37.

**Distribution** (fig. 32): Ssp. gibbsiae is at present known from several disjunct mountain areas of Tasmania, Frenchmans Cap, Mt Humboldt, the Denison Range, Mt Anne, the Mt Field massif and Cradle Mt. Future collections will probably show that the subspecies occurs in intervening high mountains. Altitude, 1030-1520m.

**Ecology:** Ssp. gibbsiae usually occupies the more protected sites above the tree-line. It is commonly found in dense alpine heath, often where it is interspersed with outcrops of dolerite rock. Plants either sprawl within shrubs or form large spectacular clumps in the openings between. They commonly grow in the clumps of *Astelia* sp. which are particularly abundant in open areas of heath (fig. 37). Ssp. gibbsiae has also been found in an ecotone between alpine heath and blanket bog on the summit of Mt Field West (fig. 37; Barker 1165, 1169). However, plants of the subspecies only rarely occur upon the blanket bogs (Barker 1165A). The subspecies is also known at lower altitudes from subalpine woodland (Barker 1189).

Flowering occurs between the beginning of January and early February at localities above the tree-line. At lower altitudes it may start at the beginning of December.

**Conservation status:** considered not at risk.

**Specimens examined**

Fig. 37. *E. gibbsiae* ssp. *gibbsiae*. A, population growing in open alpine heath and in ecotone into cushion plant expanses, near summit of Mt Field West, Tasmania (*Barker* 1165); B, plant growing in "pineapple grass" (*Astelia alpina*: *Barker* 1165), scale 5 cm; C, inflorescence showing white corollas with purple striations and yellow blotch on lower side of mouth, Rodway Range, Tasmania (*Barker* 1157), scale 1 cm.
3b. ssp. psilantherea (FvM.) Barker, comb. & stat. nov.


Plant c. 20-30cm or more high, with single erect stem bearing ascending branches above ground level. Stem to base of inflorescence c. 15-20cm high; internodes on stems or main branches longer than upper leaves between upper (3)5-10(15) nodes (i.e. sometimes for whole length), the longest node (1)2(3) times longer than upper leaves; axis in upper parts with two rows of moderately dense to dense, short eglandular hairs decurrent from between leaf bases, mixed with moderately dense to dense, moderately long to long glandular hairs all around, in lower parts with shorter eglandular indumentum, and sparse, often long glandular indumentum. Leaves: uppermost stem leaves c. 5-8 x c. 2.5-4.5mm, in outline elliptic to obovate, covered by moderately long to long glandular hairs, usually moderately dense to dense all over, sometimes dense on margins and towards base, sparser in middle and distally; base rounded-cuneate to cuneate; teeth (1)2 along each margin, the longest 0.5-1.3mm long; apical tooth bluntly or sharply, obtuse or acute, (1.2)1.8(2.1) x (1.2)1.6(2.5)mm; leaves lower down covered by a sparser shorter indumentum. Inflorescence with rachis covered by indumentum similar to upper axes. Bracts covered by short to moderately long glandular hairs, dense towards base, sparser towards apex. Calyx with external surface covered by short to moderately long glandular hairs, dense on teeth and distal part of tube, sparser or glabrous at base of tube. Corolla “white striated with dark lines” (Stuart 1745: MEL41688). Stamens with anthers 1.5-1.8mm long.

Typification: The two duplicates of Stuart 1745, each of which has been annotated “Euphrasia Brownii F.M. var. psilantherea” by Mueller, are considered candidates for lectotype since Mueller based his discussion more on these plants than the Mount Wellington collection. Both duplicates bear very similar annotations by both Stuart and Mueller and are in good condition apart from some breakages of axes. MEL41688 was chosen because it contained more flowering material.

It is somewhat doubtful whether the Mount Wellington collection cited above is the one referred to in the protologue. On the label bearing the locality annotations Mueller has identified the specimen, which contains a single plant allied to E. caudata (q.v.: note 2), as E. scabra. The annotation “This may possibly be a variety of E. scabra”, on a separate label with the specimen, indicates that Mueller was in doubt as to its exact identity. In the treatment containing the protologue, Mueller (1865) discusses exhaustively the differences between the yellow-flowered annual E. scabra, and the non-yellow-flowered perennial E. brownii, to which he ascribed his var. psilantherea. He must finally have placed greater emphasis on the apparently non-yellow flower colour of the Mt Wellington specimen than on its annual habit. Mueller’s account of the anther indumentum on a third label, “Antherae dorso imberbes secus rimas parum ciliatae”, gives further support to the possibility that it is the syntype as he has referred specifically to the glabrous anther backs of the specimen. The epithet “psilantherea” refers to the lack of indumentum from the anther
backs only, as on the South Port specimens Mueller also wrote “Antherae parum bar[b]atae” and “Antherae brevissime barbatae”. No other material that would qualify as the Mt Wellington syntype is known from MEL.

Distribution (fig. 32): The only specific locality recorded for ssp. psilantherea is that of the type “nr. South Port” in the extreme south of Tasmania. This locality is close to sea level. Labillardière’s collection probably also came from this general area since most of the collections of both his visits to Tasmania were made there (Stafleu 1966). However, he may have collected along the east coast of Tasmania (Dr E.C. Nelson, pers. comm. 1973).

Ecology: The ecological note of ssp. psilantherea given with Stuart’s (1745) collections indicates that it was very localized in boggy places frequently inundated in winter. As to flowering time Stuart has noted on the isolecotype that the collection, in full flower, was made in “Sept. 55 but in flower almost at all seasons”.

Conservation status: 2 ?X

Note: For further discussion of Labillardière’s collections of Euphrasia, see p. 125.

Specimens examined

TASMANIA: Labillardière s.n., s.dat. Van Diemen. G.—Milligan 16, s.dat. Without locality. AK(p.p.).—Stuart 1745, ix.1855. South Port. MEL41688 (lectotype); MEL41687.—Stuart s.n., s.dat. V.D.L. MEL 41465. LOCALITY EXTREMELY DOUBTFUL: Labillardière s.n., s.dat. N. Zealand. PH.

3c. ssp. wellingtonensis Barker, subspecies nova


Subspecies nova prope ssp. gibbsiae indumento glanduloso ab inflorescentia ad planum terrae extenso ramisque supra planum terrae simplicibus, sed differt indumento glandulosuo brevior praeipue versus basem, foliiis summis ramorum inflorescentigerorum dentibus minoribus, antherisque minoribus; inter subspecies indumento glandulosuo ad inflorescentiam et proxime infra eam limitato proxima ssp. comberi, sed differt non solum indumento latius patenti sed etiam foliiis summis ramorum inflorescentigerorum dentibus minoribus.


Plant (3.5)5-10(13)cm tall, with many usually ascending or ± erect branches arising from reduced stem or prostrate parts of other branches. Main inflorescence-bearing branches (1.5)3-6(10)cm high to base of inflorescence; internodes between uppermost (0)2-3(7) pairs of leaves as long as or longer than upper leaves, the longest (3/8)1-1/2(2) times length of upper leaves, lower down much shorter than leaves; axis with two pairs of lines of very short, sparse to moderately dense eglandular hairs, often almost absent, covered also by sparse to dense, very short to moderately dense glandular hairs, often almost absent, covered also by sparse to dense, very short to moderately dense glandular hairs, the glandular hairs extending from upper parts down to ground level, where 0.05-0.2mm long, on young shoots and often on prostrate parts of axes. Leaves: uppermost leaves of main inflorescence-bearing branches 5-9(11) x (2.5)4-6(7)mm, obovate or spathulate in outline, covered by sparse to dense, usually short to moderately long, rarely long glandular hairs; base usually attenuate or narrowly cuneate, rarely rounded-cuneate; teeth 1-2 along each margin, the longest (1.0)1.9(2.5)mm long; apical tooth sharply or bluntly acute or acuminate, (1.3)2.1(3.0) x (1.2)1.9(2.6)mm;
Fig. 38. Holotype of *E. gibbsiae* Du Rietz ssp. *wellingtonensis* Barker, *ssp. nov.* (scale 5cm).

Fig. 39. Holotype of *E. gibbsiae* Du Rietz ssp. *microdonta* Barker, *ssp. nov.* (scale 5cm).
leaves *lower down* with similar indumentum. *Inflorescences* with *rachis* similar to axis. *Bracts* with indumentum similar to uppermost leaves. *Calyx* with outer surface covered by dense, usually short to moderately long, rarely long glandular hairs, sometimes mixed with a few to moderately dense, short to moderately long eglandular hairs. *Corolla* white, with yellow blotch on lower side of mouth and deep in tube, with purple to indigo striations on tube and hood and extending well out onto lobes. *Stamens* with *anthers* (1.2)1.4-1.6(1.8)mm long. Figs 5, 38.

**Distribution** (fig. 32): Ssp. *wellingtonensis* is apparently confined to the summit plateau of Mt Wellington near Hobart. For a very doubtful record from Ben Lomond in north-east Tasmania (*Oldfield* W36919) see note. Altitude, c. 1200m.

**Ecology:** The subspecies occurs in alpine heath either in open areas between shrubs, and then often in cushion plants, or within the shrubs themselves.

It is the earliest flowering of the three species of *Euphrasia* which occur on the alpine summit plateau of Mt Wellington (see also Currey 1966, p.123). Flowering occurs from November (*Rupp* MEL41679) to early January, or perhaps later in some years.

**Conservation status:** 2V/R,C.

**Note:** While it is possible that ssp. *wellingtonensis* comes from Ben Lomond, an isolated massif in north-eastern Tasmania (fig. 32), the record is based on a single old collection, *Oldfield* W36919. It would constitute the sole known record of Sect. *Striatae* on this plateau. Ssp. *wellingtonensis* is otherwise only recorded from Mt Wellington well to the south, where Oldfield made a collection (W36922) of it. The possibility of a mix-up in annotation or labels arises.

**Specimens examined**


**3d. ssp. comberi** (Du Rietz) Barker, *stat. nov.*


**Plant, in open areas** (3.5)5-12(15)cm tall, with many ascending branches arising from reduced stem or prostrate parts of other branches, when growing in bushes reaching up to 25cm in height with many branches, proximally (within bush) scandent, simple and erect distally (outside perimeter of bush), arising from reduced stem or scandent parts of other branches. Main *inflorescence-bearing branches:* distal erect parts (2.5)3-10(12)cm long to base of inflorescence; *internodes* between uppermost 0(7) nodes as long as or longer than uppermost leaves, the longest internode
(l/4)1/5 - l(2) times length of upper leaves; axis in upper distal erect parts with two rows or two pairs of lines of dense, short to moderately long eglandular hairs decurrent from between each leaf base, sometimes also with very few to moderately dense, short to moderately long glandular hairs, in lower parts with shorter similar eglandular hairs but lacking glandular hairs; young shoots with axis bearing two rows of eglandular hairs but lacking glandular hairs. Leaves: uppermost leaves of main inflorescence-bearing branches (5)7-9(10) x (4)6-9(10)mm, usually broadly obovate or broadly spathulate to broadly elliptic in outline, sometimes obovate to spathulate, usually covered by sparse to dense, short to moderately long glandular hairs; base shortly attenuate or narrowly cuneate to rounded-cuneate; teeth (1)2-3(4) along each margin, the longest (0.8)1.5(2.0)mm long; apical tooth usually blunt, rarely sharp, usually broadly shortly acuminate, sometimes obtuse or shortly acuminate, (1.0)1.7(2.2) x (2.0)2.7(4.1)mm; leaves lower down glabrous or with sparser indumentum; lowermost leaves usually glabrous, sometimes with moderately dense, short to moderately long glandular hairs usually confined to apical tooth, rarely along margins. Inflorescences with rachis with indumentum similar to upper axis with somewhat denser glandular pilosity. Bracts usually covered by very sparse to dense, short to long glandular hairs on margins of apex and teeth, rarely glabrous. Calyx with external surface of teeth and distal part of tube covered by very sparse to dense, usually short to moderately long, rarely long glandular hairs, sparse or glabrous on base of tube. Corolla white, (?) with yellow blotches behind lowest lobe and deep in tube at point of insertion of anterior filaments), with 3-5 purple ("mauve": Edwards AD97121103) striations extending onto each lobe from hood and tube. Stamens with anthers (1.2)1.4-1.7(1.8)mm long. Fig. 5.

Typification: There is no specific type locality. A study of Comber's collection numbers either side of 1835 may give some indication of this.

Distribution (fig. 33): Ssp. comberi appears to be confined to the north-eastern or eastern parts of south-west Tasmania, where it is known only from a few of the many high mountain areas. At present populations are known from the Hartz Mountains, Federation Peak, the Snowy Range, Mt Anne and Mt Rufus, but they may also occur on the Mt Field massif (note 2). Altitude, 910-1220m; possibly higher as mountains in the region reach over 1400m.

Ecology: Ssp. comberi has been recorded mainly from alpine or subalpine heath (Barker 1194, Edwards AD97112103, AD97121099). It may grow within the prostrate branches of woody perennials or sprawl within the taller shrubs. It may also grow abundantly in areas of cushion plants in doleritic areas.

From the scanty material available flowering occurs at least in the period between early December and mid February.

Conservation status: considered not at risk.

Notes: 1. Ssp. comberi and ssp. kingii intergrade along an ecological gradient and it is uncertain whether the morphological differences between them are phenotypic or genotypic (see E. gibbsiae: Intraspecific Polymorphism; ssp. kingii: note 1).

2. Populations containing a mixture of ssp. comberi and ssp. gibbsiae occur on the Mt Field massif. These are discussed under E. gibbsiae (Intraspecific Polymorphism), where the specimens are cited separately.
3. The only notes on flower colour are by Orchard (5091) "white, purple striped" and Edwards (AD97121103), "white with mauve striations . . . varying in extent & intensity". From the dried specimens, however, the striations are not as restricted as in ssp. pulvinestris, but are prominent and extend at least on to the basal part of the lobes, and on many occasions stretch over almost their entire length.

Specimens examined


Plant (12)20-35(50)cm high, with single erect stem, bearing shoots and ± erect branches from ground level to high in upper parts, after flowering dying back to either upper branches which develop further, or ground level in which case 1-several ascending to ± erect stem-like branches develop from very base. Stem, or main inflorescence-bearing branches if no stem present, with internodes longer than uppermost leaves between uppermost (0)3 or more nodes, sometimes for whole length, the longest internode (1)2(4) times length of upper leaves, sometimes shorter than leaves lower down; axis bearing two rows of dense, short to moderately long eglandular hairs decurrent from between leaf bases. Leaves: uppermost leaves of stem, or of main inflorescence-bearing branches if upper part of stem absent, (5)6-8(10) x 3-7mm, obovate to elliptic in outline, usually glabrous, rarely covered in distal parts by sparse to dense, short glandular hairs; base usually cuneate, often narrowly so, sometimes narrowly attenuate; teeth 1-2(3) along each margin, the longest tooth 0.8-1.5mm long; apical tooth sharp or blunt, usually shortly acuminate, often broadly so, sometimes acute, (1.0)1.4(2.1) x (1.1)1.6(2.4)mm; leaves lower down glabrous. Inflorcescences with rachis with indumentum similar to axis, sometimes also with a few short glandular hairs. Bracts sometimes glabrous, sometimes covered by sparse to dense, short glandular hairs, denser in the apical half, the upper (younger) bracts sometimes with denser indumentum than lowermost ones. Calyx with external surface usually bearing short glandular hairs, sparse to dense towards apices and margins of teeth, absent or sparse on tube, and short eglandular hairs mainly confined to distal part of teeth, sometimes ± glabrous. Corolla usually purple, lilac or blue, sometimes white, with orange (Barker 992) (? to yellow) blotch behind lowest lobe, with deep red-purple striations on tube, extending well out onto lobes. Stamens with anthers (1.0)1.3-1.6 (2.2)mm long. Figs 5, 31 H, I.

Typification: The isotype lacks the locality "Port Davey" and has the extra annotation "peaty heath", but has been clearly labelled as an isotype of E. kingii by Curtis.

Distribution (fig. 33): Ssp. kingii is confined to low altitudes of the west, south-west and extreme south of Tasmania. Altitude, sea level to c. 400m.
Ecology: The subspecies is apparently common in button-grass (Gymnoschoenus sphaerocephalus) plains (equivalent to wet hummock sedgeland of Jackson 1965). More general specimen annotations referring to heath and swamp areas may also allude to this community.

The subspecies flowers from October or even earlier until March. A depauperate flowering specimen (Milligan 371) was collected on 24th May.

Conservation status: considered not at risk.

Notes: 1. Ssp. kingii is most clearly related to ssp. comberi and ssp. microdonta, which are distinguishable by the confinement of their branching to ground level or on the proximal ascending parts of the branches if growing in shrubs. Ssp. microdonta and ssp. comberi also apparently differ by their consistently white corolla colour. The shape of the mature capsule apex may also prove valuable diagnostically. The only specimens of ssp. kingii seen with fruiting material, Barker 992, M. Davis 1172, Carroll NSW 87057 and Hamilton HO (1 specimen), all bear capsules with apices broadly acute to obtuse in lateral view. Ssp. comberi has capsules with broad apices shallowly emarginate to truncate-obtuse in lateral view, and tending to be broader; they thus resemble the capsules of all other Tasmanian subspecies seen including ssp. psilantherea, which like ssp. kingii occurs in lowland areas.

Ssp. kingii and ssp. comberi intergrade along an ecological gradient and it is uncertain whether the above-mentioned morphological differences between them are environmental modifications or genetically based (see E. gibbsiae: Intraspecific Polymorphism).

Unless they have clearly come from such an ecotone, specimens tending to intermediacy have usually been placed under the subspecies to which they have closer affinities.

2. Specimens of ssp. kingii collected by Labillardière (GH, L908227161 p.p., NY p.p.) are discussed in relation to the French botanist’s collections on pp. 91, 120.

3. Some of Milligan’s collections of plants of E. gibbsiae ssp. kingii from the west coast of Tasmania (e.g. 766: l.viii.1846/x.1846. Heathy Plains M.Qr.Hr.) approach E. striata by their small flowers and very sparse glandular indumentum. A recent, more complete collection Gray 412 from the same region has all the characteristics of ssp. kingii apart from the paucity of glandular hairs. It seems that these collections represent a variant of ssp. kingii, with no actual links with E. striata (q.v.: note 3).

Specimens examined

3f. ssp. microdonta Barker, subspecies nova

Subspecies nova prope ssp. subglabrifolium et ssp. kingii internodiis longis ramorum floralium cauliferae indumentisque glandulosae ad et proxime infra inflorescentiam limitato, sed differt ab illa foliis summis ramorum floralium dentibus pleribus brevioribusque, ab hac ramis supra planum terrae simplicibus, corollis albis, foliisque summis ramorum floralium dentibus pleribus.


Plant (10)13-22(25)cm tall, with ascending branches arising from the reduced stems or lower ± prostrate parts of other branches. Main inflorescence-bearing branches (6)9-15(18)cm high to base of inflorescence; internodes between uppermost 4-8(10) nodes as long as or longer than upper leaves, the longest internode (1\(\frac{1}{4}\))2\(\frac{1}{4}\)(3\(\frac{1}{2}\)) times length of upper leaves; axis bearing two rows of moderately dense to dense, very short eglandular hairs decurrent from between leaf bases, in uppermost parts sometimes mixed with sparse to moderately dense, very short to moderately long glandular hairs confined to rows of eglandular hairs or also in areas between where sparser. Leaves: uppermost leaves of main inflorescence-bearing branches 5.5-10 x 3.5-6mm, obovate or spatulate in outline, sometimes glabrous, sometimes with sparse to dense, short glandular hairs confined to margins or all over, or with very short to short, sparse to dense eglandular hairs confined to margins of upper side, or all over, or with a mixture of both; base attenuate to narrowly cuneate; teeth (1)2-3 along each margin, the longest tooth 0.5-1.0mm long; apical tooth bluntly or sharply, shortly acuminate, usually broadly so, (0.9)1.3(1.8) x (1.3)2.1(2.5)mm; leaves lower down glabrous. Inflorescences with rachis with two rows of dense, very short eglandular hairs, sometimes mixed with sparse to moderately dense, sub sessile to short glandular hairs, mainly confined to rows of eglandular hairs. Bracts bearing short to moderately long glandular hairs, dense on margins, sparse to dense on upper and lower surfaces, sometimes, especially towards margins of upper side, with dense short eglandular hairs. Calyx with outer surface of teeth and distal part of tube covered by moderately dense to dense, short to moderately long glandular hairs, with base of tube having sparser indumentum or glabrous. Corolla white (Anderson 8), [from observation of dried specimens] with 3 dark ?purple striations extending well out onto each lobe from tube and hood; presence of yellow blotch unknown. Stamens with anthers (1.4)1.5-1.7(2.0)mm long. Figs 5, 39.

Distribution (fig. 33): Ssp. microdonta is known only from near Cradle Mountain, in the north-western mountains of Tasmania, and the King William Range in midwestern Tasmania. It may be found on intervening mountains which are poorly accessible. Altitude, 820-910m.

Ecology: The single record for ssp. microdonta is from button grass (Gymnoschoenus sphaerocephalus) moorland (Phillips 735) from the King William Range. The subspecies probably occurs in the same community around Dove Lake.

Flowering probably starts in late October (Phillips 87 was collected on 12th November and has some almost mature fruits) and continues well into December.

Conservation status: 2V/R,C.

Specimens examined

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3g. *Euphrasia* ssp. *subglabrifolia* (Du Rietz) Barker, stat. nov.


Plant (4)8-15(18)cm high, with many crowded branches, ascending, with short to very long proximal prostrate parts, arising from reduced stem or prostrate parts of other branches. Main inflorescence-bearing branches (3)5-12(14)cm high to base of inflorescence; internodes between upper (0)3-6(9) leaf pairs as long as or longer than upper leaves, the longest (78)11/4-21/4(4) times length of upper leaves, much shorter than leaves lower down; axis with moderately dense to dense, short to moderately long eglandular hairs in two rows or two pairs of lines decurrent from between leaf bases, sometimes in uppermost internodes mixed with sparse, short to moderately long glandular hairs all around axis. Leaves: uppermost leaves of main inflorescence-bearing branches (5)7-11(13) x (3)4-7(8)mm, obovate or spatulate to oblong-elliptic in outline, usually covered by sparse to dense, subsessile to moderately long glandular hairs, and then densest towards margins, especially distally, sometimes mixed with sparse to dense, usually short, rarely long eglandular hairs on upper surface, sometimes glabrous; base usually narrow-cuneate, sometimes long attenuate or cuneate; teeth 1-2 along each margin, the longest tooth (0.7)1.2-2.1(2.6)mm long; apical tooth sharply or bluntly acute or shortly acuminate, sometimes narrowly so, (1.3)2.0(3.0) x (1.1)1.8(3.0)mm; middle leaves with sparser indumentum or glabrous; lower leaves, at least those on prostrate parts, glabrous. Inflorescences with rachis bearing two rows of dense, very short to moderately long eglandular hairs decurrent from between bases of bracts, usually mixed with sparse to moderately dense, short to moderately long glandular hairs, denser within rows of eglandular hairs or similarly dense all around. Bracts with indumentum similar to but slightly denser than uppermost leaves, never glabrous. Calyx with outer surface bearing usually subsessile to short, sometimes moderately long glandular hairs, sparse to dense on margins and distal parts of teeth, sparser or absent towards base, sometimes with sparse to moderately dense, short eglandular hairs lining margins of teeth. Corolla white, with yellow blotch on lower lip behind lowest lobe extending to deep in tube about point of insertion of anterior filaments and sometimes behind two lateral lobes, with 3(4) striations on each lobe, purple to indigo on tube and hood, usually prominent and extending well out onto lobes, sometimes with lowest lobe unstriated, rarely with only upper lobes striated. Stamens with anthers (1.4)1.5-1.9(2.0)mm long. Figs 5, 31 A-F.

Typification: The GH specimen is almost certainly isotypic as its annotations are identical to those of both other type specimens as to data and handwriting. The difference in date is probably a copying error.

Distribution (fig. 34): Ssp. *subglabrifolia* occurs on the Baw Baw plateau in the southwest part of the eastern Victorian highlands. A population of similar plants is known in central Tasmania, but its derivation is obscure (see note). Altitude, 1300-1550m.

Ecology: Ssp. *subglabrifolia* is abundant in the extensive subalpine heathland which occurs in hollows between wooded ridges of the Baw Baw plateau. It is particularly common in sphagnum bogs and in damp areas near watercourses, sometimes within clumps of *Astelia* sp. The subspecies also occurs in openings in sparse snowgum (*Eucalyptus pauciflora*) woodland bordering the heathland.

Flowering occurs mainly between December and January, but possibly begins in November as plants collected in early December by Willis (MEL41532) bear flowers and fruits. The one February collection (Stone MEL415993) is in fruit.
Conservation status: 2V/R,C

Note: Barker 1187 is an unusual collection from near Mt Field East in central Tasmania (fig. 34). It came from an area of low subalpine heathland in a hollow between snowgum-covered ridges; plants occurred sporadically along the steep-sided banks of a series of narrow rivulets about 50cm deep. The specimens closely resemble ssp. subglabrifolia by their long upper internodes \([1\frac{3}{4}-2 \times \text{length of upper leaves}]\), the restriction of glandular hairs mainly to the inflorescence, and the 1-2 teeth along each margin of the uppermost leaves. They diverge slightly from the Victorian representatives in the sometimes broad apices of the uppermost leaves.

It is possible that the population has originated independently of ssp. subglabrifolia, perhaps by hybridization between ssp. gibbsiae (or forms intergrading into ssp. comberi) and E. striata, both of which occur in the area. Plants tested showed a low degree of pollen sterility (PS12,13,15,16).

Specimens examined


**Specimen with possible affinities to ssp. subglabrifolia**

**TASMANIA:** Barker 1187, 21.i.1971. Mt Field Nat. Park; Windy Moor, along track to Lake Fenton between c. 1/2 to 11/4km SW of Mt Field East summit. AD.

3h. ssp. discolor Barker, subspecies nova


Subspecies nova prope ssp. pulvinestrem et ssp. subglabrifoliam indumentum glandulosum ad et proxime infra inflorescentiam limitatum, ramis supra planum terrae simplicibus, et foliis similius ramorum floralium secus quamque marginem 1(2) dentibus, sed differt a duabus corollis albis, lilacinis, profunde lilacinis, purpureisve, etiam ab illa corollis extense striatis, ab hac internodiis brevioribus.

**Holotypus** (fig. 40): W. R. Barker 1218A, 28.i.1971. Cradle Mt.-Lake St. Clair National Park; Cradle Mt., on track to summit from Kitchen Hut, on east face between the first outcrop encountered on the climb and the summit, and on the summit itself. Altitude 5060 feet (1540m). AD97126159. Isotypi: B, CANB, CGE, GH, HO, K, MEL. W. See Typification.

**Plant** (4)4.5–10(13)cm tall, taller when in fruit, with many ascending branches arising from reduced stem or prostrate parts of other branches. *Main inflorescence-bearing branches* (1.5)3.5–8(11)cm high to base of inflorescence; *internodes* between upper 0(4) nodes as long as or longer than the upper leaves, the longest internode \((1\frac{4}{4})\) times length of upper leaves, shorter below; *axis* covered for all length by two rows or two pairs of lines of dense, short to moderately long eglandular hairs decent from between leaf bases, sometimes mixed in upper parts with short to long glandular hairs all around axis. *Leaves*: uppermost leaves of main inflorescence-
Fig. 40. Holotype of *E. gibbsiae* Du Rietz ssp. *discolor* Barker, ssp. nov. (scale 5cm).

Fig. 41. Holotype of *E. gibbsiae* Du Rietz ssp. *pulvinestris* Barker, ssp. nov. (scale 5cm).
bearing branches (6)7-10(13) x 4-7(9)mm, obovate in outline, usually glabrous, sometimes with very few, short to moderately long glandular hairs or sparse to dense patch of short eglandular hairs on margins of teeth and apex; base narrowly cuneate; teeth 1(2) along each margin, the longest tooth (1.2)1.5-2.5(3.0)mm long; apical tooth sharply or bluntly acute or acuminate, (1.8)2.6(3.2) x (1.6)2.2(3.4)mm; leaves lower down glabrous but for short eglandular hairs on tip of teeth. Inflorescences with rachis covered by two rows of sparse to dense, short to long eglandular hairs decurrent from between bases of bracts, sometimes with sparser eglandular hairs between or with sparse to moderately dense, short to moderately long glandular hairs all around or mixed with rows of eglandular hairs only. Bracts with upper surface usually covered by moderately dense to dense, short to moderately long eglandular hairs, mixed towards margins with sparse to dense, short to moderately long glandular hairs, rarely glabrous, with lower side usually bearing sparse to dense similar glandular hairs, sometimes glabrous. Calyx with external surface of teeth and distal part of tube covered by sparse to dense, short to moderately long, rarely long glandular hairs, mixed with sparse to moderately dense, short to moderately long eglandular hairs, base of tube with sparser indumentum, sometimes glabrous. Corolla white, lilac, deep lilac or purple, with yellow to yellow-orange patches at base of the anterior filaments and behind lowest lobe, with purple to deep purple, indigo or blue-indigo striations extending from tube and hood onto lobes. Stamens with anthers (1.6)1.7-2.0(2.1)mm long. Figs 6, 40, 42.

Typification: The majority of plants, if not all in the type collection, came from the extreme summit of Cradle Mountain. However, some may have come from the nearby outcrop, cited on the label, where plants of ssp. gibbsiae (segregated as Barker 1218B) occurred.

Distribution (fig. 34): Ssp. discolor is at present known with certainty from the region of the type locality Cradle Mountain in north-eastern Tasmania. Its range may extend

Fig. 42. E. gibbsiae ssp. discolor. Inflorescences showing purple-striated pink corollas with small pale yellow blotch on lower side of mouth, summit of Cradle Mountain, Tasmania (Barker 1218A, holotype), scale 1cm.

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well into the south-west depending on the true affinities of a number of specimens which appear closely related to it (see note). Altitude, 1200-1540m; allied south-west Tasmanian plants, 910-1220m.

**Ecology:** On the summit of Cradle Mountain ssp. *discolor* occupies flat exposed areas between dolerite boulders. One outlier (*Barker 1206*) was found on a steep slope near the base of the steep dolerite cap of the mountain in sparse soil in a rock crevice.

Some of the plants considered very closely related to ssp. *discolor* (see note) were also associated with rocks (*Olsen 39, Whaite 2257, 2262*). Divergent habitats are indicated by “in sphagnum bog on exposed dolerite plateau” (*Whaite 2267*), “sub-alpine herb community” (*Telford 2481*), and “straggling in dwarf shrubs” (*Gordon HO*).

Flowering of ssp. *discolor* in the Cradle Mountain area apparently occurs throughout January and well into February, and of its close relatives further south, between mid December and mid February.

**Conservation status:** 3V/R,C

**Note:** Although closely allied, ssp. *discolor* and ssp. *comberi* differ in the number of leaf teeth, anther size and flower colour. Differences have been gauged from a few large gatherings of each from widely separate localities, those of ssp. *discolor* from Cradle Mountain and ssp. *comberi* from various areas of south-western Tasmania. Fragmentary or small collections, made in parts of south-western and western Tasmania, have been placed under ssp. *discolor* for the present on the basis of their uppermost leaves of the inflorescence-bearing axes bearing 1-2 teeth along each margin. In addition, the flower colour in one specimen *Whaite 2262* has been recorded as “purplish”, which also links it with ssp. *discolor*. The true status of these specimens requires clarification.

**Specimens examined**

**TASMANIA:** Barker 1206, 28.i.1971. Cradle Mtn-Lake St Clair Nat. Park; just below W end of saddle between Little Horn and Weinforders Tower, on track along N side of Cradle Mtn; c. 100m E of plateau.

**Specimens with close affinities to ssp. discolor**


**3i. ssp. pulvinestris Barker, subspecies nova**


Subspecies nova prope ssp. *subgiabriifoliam* et ssp. *discolorum* indumento glanduloslo ad et proxime infra inflorescentiam limitatam, ramis supra planum terrae simplicibus, et foliis summis ramorum floralium secos
quemque marginem 1-2(3) dentibus. Differt a subspeciebus totis E. gibbsiae striis plerumque ad tubum cucullumque coronae limitatis, etiam a ssp. subglabrifoliam internodiis brevioribus et a ssp. discolori corollis albis.

Holotypus (fig. 41): W. R. Barker 1181, 19.i.1971. Tasmania, South-west. Mt Field Nat. Park; on top of K. Col, from the middle and east towards the Rodway Range. Altitude c. 4050 feet (1230m). AD97116046. Isotypi: CANB, CGE, HO, K, PERTH, W.

Plant (3.5)7-10(13) cm high, usually with a few to many densely crowded branches, proximally shortly prostrate or (in cushion plants) ± erect, distally (above ground level) erect, sometimes simple and erect. Main inflorescence-bearing branches (2.5) 4-7(9) cm high to base of inflorescence; internodes between upper 0-4(5) leaf pairs as long as or longer than upper leaves, the longest (1/2)1(2) times length of upper leaves, shorter than leaves lower down; axis with four lines of short to moderately long eglandular hairs decurrent from either side of each leaf base, with short glandular hairs often on internode above uppermost leaf pair, absent below. Leaves: uppermost leaves of main inflorescence-bearing branches (5)7-9(10) x (3)4-7(9) mm, spatulate to obovate in outline, usually glabrous but for a few eglandular hairs on extremities, sometimes with sparse to dense, short glandular hairs; base cuneate, often narrowly so, to attenuate; teeth 1-2(3) along each margin, the longest (1.2)1.4-2.5(3.0) mm long; apical tooth sharp or blunt, acute or acuminate, often narrowly so, (1.2)2.0(3.2) x (0.8) 1.3(2.0) mm; leaves lower down glabrous. Inflorescences with rachis with two rows of dioecious eglandular hairs, usually mixed with sparse to dense, short to moderately long eglandular hairs. Bracts glabrous but for eglandular hairs, or with short glandular hairs, usually sparse and confined to upper surface and distal margins, rarely dense all over, mixed with short eglandular hairs, usually confined to extremities, sometimes covering upper surface. Calyx with outer surface bearing short to moderately long eglandular hairs, dense on margins of teeth, sparse elsewhere, usually mixed with short to moderately long glandular hairs, sparse to dense on margins and distal part of teeth, absent to moderately dense at base of tube. Corolla white, with yellow blotch on lower lip behind lowest lobe to deep into tube about point of insertion of anterior filaments, with indigo striations usually confined to tube and hood and hardly extending onto lobes, sometimes extending well out onto lateral lobes. Stamens with anthers (1.5)1.6-2.0(2.1) mm long. Figs 6, 31J, 41, 43.

Distribution (fig. 34): Ssp. pulvinestris is known only from the western half of the Mt Field massif in central Tasmania, but it may occur on neighbouring high mountains in the same massif bearing similar cushion plant expanses. Whether it is confined entirely to this region must await a study of the nearby mountains of the south-west, which are relatively little known botanically. Altitude, 1200-1440 m.

Ecology: The subspecies is usually found growing in areas of pure blanket bog (fig. 43) which is a mixture of hard mat-forming species (McVean 1969; Curtis 1969), collectively known as cushion plants. One record from a different habitat is that of Barker 1178A, a single plant, typical of the subspecies, found growing on a steep slope in low alpine heath. It has also been found from an ecotone between the two habitats (Barker 1168; see E. gibbsiae: Intraspecific Polymorphism).

The subspecies is known to flower in January and February. However collections are too few to determine the limits of the flowering season.

Conservation status: 2V,C.

Note: The lack of prominence of the corolla striations in this subspecies (fig. 43B) is accompanied in some plants by the presence of a few flexuose eglandular hairs on the outer surface of the anthers near the connective. The possibility arises of introgression from populations of E. collina ssp. diemenica which occur at lower altitudes in the Mt Field massif.
Fig. 43. *E. gibbsiae* ssp. *pulvinestris* (Barker 1182), on K. Col, Mt Field National Park, Tasmania. A, plant growing in cushion plant expanse, scale 2cm; B, inflorescences showing white corollas with purple striations confined to mouth, with yellow blotch on lower side of mouth, scale 1cm.
Specimens examined

TASMANIA (MT FIELD NAT. PARK): Barker 1166, 19.i.1971. Immediately E of Mt Field West on plateau extending to Naturalist Peak. AD.—Barker 1167, 1168, 19.i.1971. C. 100m E of Mt Field West summit on plateau extending to Naturalist Peak. AD.—Barker 1170, 19.i.1971. From c. 200m E of Mt Field West summit over plateau for distance of c. 500m towards Naturalist Peak. AD.—Barker 1178A, c. 400m E of Clemes Tarn, on track from K. Col to Mt Field West. AD.—Barker 1181, 19.i.1971. On top of K. Col, from the middle E and W towards the Rodway Range. AD (holotype), CANB, CGE, HO, K, PERTH, W.

Barker 1182, 19.i.1971. C. 300m E of the middle of K. Col, on track to top of the Rodway Range, on east side of scree. AD.—Eichler 16750, 23.i.1960. Plains immediately below the summit of Mt Field West towards Naturalist's Peak. AD.—Elliott s.n., ii.1948. Summit Plateau, Mt Field West. HO.—Jackson s.n., 18.ii.1965. Mt Mawson summit plateau. MEL41530, HO.

4. Euphrasia striata R.Br., Prodr. (1810) 436


Perennial herb, (3)7-14(18)cm tall, with many crowded ascending branches arising from very short stem or prostrate parts of other branches, often rooting on prostrate parts. Stem reduced; main inflorescence-bearing branches (2)5-11(15)cm high to base of inflorescence, with distal erect parts simple; upper (1)3-5(7) internodes longer than leaves, the longest internode (1)2-3(5) times length of uppermost leaves, those lower down much shorter than leaves; axis purple-brown, bearing two rows of very short, dense eglandular hairs decurrent from between leaf bases, the rows sometimes divided by central glabrous band over all or part of internode. Cotyledons not seen. Leaves: uppermost leaves of main inflorescence-bearing branches (4.0)5.0-7.5(9.0) x (2.5) 3.0-6.0(8.0)mm, obovate, or broadly so in outline, purple-brown entirely or partly green and partly purple-brown, glabrous but for patches of sessile glands confined to distal half of lower surface; base long, narrowly attenuate, almost petiole-like; teeth 1-2(3) along each margin, sharp, usually acuminate or acute, rarely obtuse, confined to distal 1/4-1/2(3/5) of leaf, with longest tooth (0.9)1.0-2.0(2.3)mm long; apical tooth sharp, acuminate to acute or broadly so, (1.0)1.2-2.5(2.7) x 1.1-1.8(2.2)mm; lower leaves of similar dimensions; leaves on proximal parts of prostrate parts and on young shoots smaller. Inflorescences but for lowermost 0-1(2) nodes dense racemes bearing (7)10-16(22) flowers, with lowermost node often bearing only one flower; rachis as for axis; internodes not elongating after anthesis; pedicels of lowermost flowers (0.6)1.0-3.5 (4.0)mm long, shorter towards apex, i.e. (0.4)0.6-1.2(1.5)mm long, not elongating after anthesis; apical cluster (excluding buds at widely spaced lower nodes) spherical to broadly oblong-ellipsoid, initially (0.5)0.7-1.1(1.5)cm long, becoming hidden by
corollas of uppermost flower pair after opening of flowers at first (1)2-3(4) nodes. Bracts similar in shape and indumentum to uppermost leaves, but somewhat broader. Calyx (4.5)5.5-8.2(10.0)mm long, ribbed, externally glabrous but for a small dense patch of tiny glandular hairs at base of each cleft, rarely with one or two tiny glandular hairs elsewhere, internally with short glandular hairs, dense in apical half of teeth, sparser lower down, rarely extending onto tube, mixed with short glandular hairs, sparse to moderately dense in basal half of teeth, absent from tube and usually apical half of teeth, rarely sparse on the latter; teeth ± bluntly to sharply acute; lateral clefts 1.5-4.0mm deep, shorter than median clefts, which are 2.3-5.5mm deep. Corolla (7.8)8.5-10.5(12.5)mm long along upper side, white with yellow patches on lower side of mouth and deep in throat, with 3(4) red-purple striations extending well out onto each lobe, the striations ± equally distinct over all three lower lobes, sometimes simple, sometimes branched; tube (5.0)6.4(8.0)mm long, abaxially and somewhat laterally broadened at about point of insertion of anterior filaments, which are (3.5)5.2(7.3)mm from base of corolla, externally glabrous at base and on abaxial side, on distal adaxial and lateral surfaces covered by moderately dense to dense, short to moderately long eglandular hairs, with dense patch of short glandular hairs about lateral clefts, internally except for glabrous basal 1mm and behind lower lip, covered by dense very short to moderately long, downturned eglandular hairs extending to between bases of posterior filaments; hood (2.3)3.5(4.2)mm long, excluding lobes (2.5)3.0(3.5)mm broad, including lobes (6.0)7.7(10.5)mm broad, externally covered on midline and front by dense, short to moderately long eglandular hairs, sparse or absent from the sides, and sparse to dense, short glandular hairs on sides between sinus and lateral clefts, internally with very short to short glandular hairs, usually moderately dense to dense at sinus region or extending around margins, sometimes moderately dense over all hood, and dense, short to moderately long eglandular hairs at sinus; upper lobes almost in same plane, broadly obtuse, sometimes with short apiculation, to praemorse-truncate to shallowly emarginate, with cleft between (1.3)1.8(2.5)mm deep, with front surface and margins glabrous, with rear surface glabrous or bearing short to moderately long glandular hairs, sparse to dense and confined to base, or all over and dense at base, sparse distally; lower lip concave from above, downturned until almost parallel to upper side, (6.0)7.3(8.0) x (9.6)13.0(15.5)mm, externally bearing sparse to moderately dense, short glandular hairs, sometimes mixed with sparse to moderately dense, short glandular hairs about area between lowest or lateral lobes, with margins and inner surface glabrous; lower lobes broadly obtuse to praemorse-truncate to emarginate, with clefts between (2.7)3.4(4.3)mm deep. Stamens with filaments glabrous, the anterior pair (2.7)3.8(4.2)mm long, the posterior pair (1.1)1.9(2.4)mm long; anthers (1.1)1.4-1.9(2.2) x (0.6)0.9-1.2(1.3)mm, with connectives glabrous, with slits lined by short to very short glandular hairs, with rearmost pair of awns (0.2)0.3-0.4(0.5)mm long, usually longer than, occasionally ± equal to other three awn pairs. Ovary in lateral view oblong to broadly elliptic or broadly oblong-ovate, slightly compressed laterally, in median view usually narrowly ovate to ovate, sometimes elliptic, usually glabrous, sometimes with a few short setae at the apex, sometimes setae denser and extending ½ way down lines of dehiscence; apex in lateral view shallowly emarginate to truncate to obtuse, occasionally obliquely so; ovules (33)46(58). Capsules (few seen) c. 4.5-10.5mm long, slightly compressed laterally, in lateral view usually oblong-elliptic to elliptic or ovate-oblung, sometimes broadly so, c. 2.4-3.7mm broad, in median view ± ovate, usually glabrous, occasionally with apex covered by short to moderately long setae; seeds c. 7-33, usually ± ellipsoid to reniform, occasionally broadly so, (0.8)1.2-1.8(2.0) x 0.5-0.9mm. Chromosome number: n=c. 20-30 (Barker 1060). Figs 6, 44.
Fig. 44. *E. striata*: A, habitat and habit, near Clemes Tarn, Mt Field National Park, Tasmania (*Barker* 1176), scale 2cm; B, inflorescences showing white corollas with purple striations and with very faint yellow spot, on summit of Mt Wellington, Tasmania (*Barker* 1124), scale 1cm.
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Typification

1. *E. striata* R.Br. Du Rietz (1948a) designated the BM specimen as "holotypus", with the K specimen a "syntypus". The choice of lectotype thus follows the views of Du Rietz, as well as those expressed by Stearn (1960) in relation to Brown's types, namely that the lectotype be the most complete specimen in BM.

   The lectotype is mounted with a collection of *E. gibbsiae* ssp. wellingtonensis. Table Mountain is an old name for Mount Wellington, about 7km west of Hobart.

   The K isolecotype is mounted with two other collections of *E. striata* from Mt Wellington, including the lectotype of *E. alpina* var. *humilis* (see below).

   The exact date of collection of the type material was recorded in Brown's (unpubl.) manuscript. Otherwise the data in the manuscript and on the collection itself are more or less identical.

   It is clear that at some stage between the collection of the specimens initially named *E. striata* and the publication of that name in the 'Prodromus' (Brown 1810), Brown decided to call the species "E. picta". On the types in K and BM and in the manuscript, Brown has crossed out *E. striata* and substituted the other name, while the MEL type bears both names. The epithet "picta" has since been used for a European species of *Euphrasia*.

2. *E. alpina* R.Br. It is another annotated by Bentham with "Euphrasia alpina β humilis". In keeping with his later recognition of the synonymy of the variety with *E. striata* (Bentham 1868), Bentham subsequently re-determined the collection as that species.

   The date, 1844, stamped on Bentham's label on the lectotype is not the date of the collection.

   When Bentham (1846) initially described the taxon "E. alpina β humilis" he gave no indication of rank. However, the varietal rank of the taxon is clearly indicated in the subsequent works of Hooker (1857) and Bentham (1868).

   *Distribution* (fig. 35): *E. striata* is confined to higher parts of the Central Plateau of Tasmania and the crescent of mountains (to its west and south) bounded by Cradle Mountain in the north and Mt Wellington in the south. It is apparently absent from other mountain areas with subalpine zones in the south-west, extreme west and north-east of the island. Altitude, 1000-1370m.

   The reported occurrences of *E. striata* on the south-west coast of Tasmania (Curtis 1967; Stones & Curtis 1967-78) are probably based upon plants of *E. gibbsiae* ssp. *kingii*. Collections allegedly made by Milligan from such regions probably came from elsewhere (note 5).

   *Ecology*: *E. striata* is confined to the subalpine and alpine zones, where it usually occurs in open areas with grasses or low woody perennials (fig. 44), often protected by low to tall heath, or simply by the terrain. It rarely occupies dense tall heath or dense subalpine woodland, areas of cushion plants, or clumps of *Astelia alpina*. It appears to grow mainly on dolerite-based soils, although populations on the plateau immediately north of Cradle Mountain and nearby Mt Campbell (*Barker 1208, 1209, 1213, 1225*) are on apparently quartzitic soils.

   It seems that flowering begins in late December and rarely continues long after the end of February. There is one record of flowering in April (*Rodway 1411*). Fruits are increasingly apparent from early February, but rarely develop fully while the inflorescence is still in flower.

   *Conservation status*: considered not at risk.
Notes: 1. The collection Comber 2167 from Mt Sedgwick ("Sedgewick") at 610m in the western mountains of Tasmania is allied to E. striata, but differs by its long-toothed leaves and rather short internodes. In these characters the plants to some extent resemble E. hookeri but the leaves have fewer teeth, nor are the recurved margins joined on the underside. The small corolla size as well as the confinement of the tiny glandular hairs to the inner surface of the calyces clearly link the collection to E. striata and distinguish it from the other species of Sect. Striatae. There is no evidence that the specimens are hybrids; pollen from one young flower was almost entirely functional in appearance (PS 271).

2. All plants of the collection which Curtis (HO: 5.iii.1949) made from the Cradle Mountain plateau have upper internodes more or less equal in length to the upper leaves. Normally, in a random gathering from a population of E. striata most plants would bear longer upper internodes. In all other respects the plants agree with typical E. striata. Pollen from one of the plants was found to be almost entirely functional in appearance (PS 270), thus making a hybrid origin of the plants rather doubtful.

3. In the MacQuarie Harbour region of western Tasmania occur plants of E. gibbsiae ssp. kingii (q.v.: note 3) which by their unusually few glandular hairs may be confused with E. striata. They can be readily distinguished by the branching above ground level.

4. Occasional highly sterile hybrids between E. striata and E. collina ssp. diemenica are known in Tasmania from the Central Plateau and possibly also from Mt Wellington (see p. 287).

5. The collections placed by Milligan under 766 come from several localities and include E. striata, E. hookeri and E. gibbsiae ssp. kingii. Herbarium sheets inscribed with this number often bear mixtures of these species, but bear only the one locality label, which must accordingly be considered unreliable.

Collections of E. striata by Milligan (766: MEL41685, MEL41451 p.p., BM p.p.) are alleged to have come from Birch Inlet, MacQuarrie Harbour and questionably (see below) Kelly Basin, Port Davey. There are apparently no other herbarium collections of E. striata from south-west Tasmania. Accordingly, Milligan may have mixed his collections of E. striata from Mt Wellington (MEL41694) with collections of E. gibbsiae ssp. kingii from the above localities.

Additional confusion concerning the true source of Milligan's collections of E. striata arises from the annotation "Kelly's Basin, McQu. Harbour" on MEL41685. Kelly Basin is an inlet of Port Davey which is at the very south-west corner of Tasmania, about 85km south of MacQuarie Harbour. Milligan apparently collected at both localities.

Selected and cited specimens (c. 100 seen)

TASMANIA: Anon s.n., 20.i.1960. Projection Bluff. HO.—Barker 1011, 1016, 3.i.1971; 1124, 15.1.1971. Summit of Mt Wellington; moorland W of The Pinnacle. AD.—Barker 1040 (p.p.), 5.i.1971. C. 1km NE of the westernmost causeway, just S of dunes on the southern side of Lake Augusta. AD (p.p.).—Barker 1060, 1061, 7.i.1971. Lakes Highway at Doctors Creek, which is c. 4km S of Breona. AD.—Barker 1066, 1067, 1069, 7.i.1971. Beside Lakes Highway, c. 1'/2km N of Pine Lake, which is 5km N of Breona; near the northernmost snow fence near Pine Lake. AD.—Barker 1074, 19.i.1971. Mt Field Nat. Park; c. 400m W of Ski Village, on track to Tarn Shelf and Mt Field West. AD.—Barker 1176, 19.i.1971. Mt Field Nat. Park; Clemen Tarn area, from c. 100m NW of Tarn towards Mt Field West to c. 100m E towards K. Col. AD.—Barker 1183, 21.1.1971. Mt Field Nat. Park; summit of Mt Field East, and 100m SW of it. AD.—Barker 1186, 21.1.1971. Mt Field Nat. Park; Windy Moor, along track to Lake Fenton between c. 1/2 to 2km SW of Mt Field East summit. AD.—Barker 1213, 28.1.1971. On plateau on N side of Cradle Mtn, c. 100m along track to Waldheim from

Three collections from Southport, Tasmania (fig. 36) are intermediate between E. striata and E. semipicta. To the former they seem closer by the leaves with consistently one pair of teeth, to the latter by their erect stems branched above ground level. The corolla, of which the tube and base of the lobes are striated in at least the Curtis material, differs in shape from the other two species by the smaller upper lobes (the cleft between them is 0.5-0.6mm deep), a smaller lower lip (2.0-3.7 x c. 5-6mm) and a contrasting long tube (c. 6-7mm long). In addition the seeds in the Southport collections (0.9-1.4 mm long) cover the range of variation in both species, while the one count made of both ovule number (80) and seed number (43) falls in the lower part of the range of variation for E. semipicta.

It is unlikely that these plants are hybrids as pollen from a flower of each Stuart collection is almost entirely functional in appearance (PS168, 273). The specimens may represent an undescribed species with a distinctive corolla shape, the leaves of E. striata and the habit of E. semipicta, and seed size and ovule and seed numbers intermediate between the two species.

Perennial herb, (10)15-35(45)cm tall, with single erect stem, bearing axillary shoots and ascending to erect branches in lower aerial parts, apparently dying back to uppermost branches after first year. Stem bearing inflorescence in first year, (25)-27 (35)cm high to its base, bearing (15)25-60(80) pairs of leaves, usually branched with uppermost branches (5)10-25(33) nodes below inflorescence, rarely simple; internodes between uppermost (3)4-7(14) leaf pairs longer than leaves, the longest internode
Fig. 45. *Euphrasia* sp. 'Southport', Curtis HO (scale 5cm).

Fig. 46. Holotype of *E. semipicta* Barker, sp. nov. (scale 5cm).
(2)3-4(5) times length of uppermost leaves, in lower parts much shorter than leaves; axes purple-brown, bearing two rows of short dense eglandular hairs decurrent from between leaf bases, the rows sometimes divided by central glabrous band over part or all of internode. Cotyledons ± circular, entire, glabrous, caducous before stem flowers. Leaves: uppermost leaves of flowering stem (4)5-8(13)mm long, in outline obovate to obovate-oblong or broadly so, green, sometimes reddened in parts, glabrous but for patches of sessile glands confined to distal (1/3)1/2-2/3(3/4) of lower surface; base long attenuate; teeth (1)2(3) along each margin, usually sharply acute, sometimes bluntly obtuse, confined to distal (1/3)1/2(2/3) of leaf, with longest tooth (0.9) 1.2-1.8(2.6)mm long; apical tooth usually sharply acute to obtuse, sometimes bluntly obtuse, (1.0) 1.3-2.0(3.2) x 1.3-1.7(2.5)mm; leaves lower down and those on branches of similar shape but slightly smaller, much smaller on shoots. Inflorescences but for lowermost 0-1(5) nodes dense racemes, that of stem bearing (8)10-18(24) flowers, with lowermost node sometimes bearing one flower, those of branches bearing somewhat fewer flowers; rachis as for axes; internodes not elongating after anthesis; pedicels of lowermost flowers (0.5)0.7-2.7(5.5)mm long, shorter towards apex, i.e. 0.5-1.2(1.4)mm long, not elongating after anthesis; apical bud cluster excluding buds at widely-spaced lower nodes spherical to broadly rounded-conical, initially 0.6-1.5(2)cm long, becoming hidden by corollas of uppermost flower pair after opening of flowers at first (1)3(8) nodes. Bracts similar in shape and indumentum to uppermost leaves, but slightly broader. Calyx (5)6-7.5(8.5)mm long, 4-ribbed, externally glabrous except sometimes for a few tiny glandular hairs, internally with tube glabrous, with teeth covered by very short to short eglandular hairs, sparse to dense in upper 1/2-2/3, absent except on margins to sparser below, occasionally mixed with a few very short glandular hairs; teeth bluntly to sharply acute; lateral clefts (1.5)2-3(3.5)mm deep, shorter than median clefts, which are (2)3-4(5)mm deep. Corolla (7)8-10(11.5)mm long along upper side, white to “mauve” (Chinnock 2144) with faint or distinctive yellow patch on lower side of mouth, each lateral lobe lined by 3 red-purple striations varying in distance reached to lobe apex, the basal lobe bearing 3 fine indigo striations or unmarked, the upper lip unmarked but for indistinct striations sometimes on hood; tube (4)4.5-6(6.5)mm long, abaxially and laterally broadened at about point of insertion of anterior filaments, which are (2.5)3-4(5)mm from base of corolla, externally on distal adaxial and lateral surfaces and sometimes behind lateral lobes covered by dense, moderately long to long eglandular hairs, often with dense patch of glandular hairs behind lateral clefts towards base of anterior filaments, glabrous at base and on most of or entire abaxial surface, internally glabrous but for two rows of dense short eglandular hairs decurrent from bases of filaments on either side of midline of corolla, sometimes with sparse eglandular hairs between; hood 3-4(5)mm long, excluding lobes (2.5)3-4mm wide, including lobes (4)5.5(6.5)mm broad, externally covered by moderately long to long eglandular hairs, dense on midline and front, sparser or absent on sides, sometimes mixed with short glandular hairs, sparse to moderately dense on sides or at front, internally glabrous but for dense, short to long eglandular hairs in region of sinus; upper lobes in ± same plane, usually shallowly emarginate, sometimes obtuse, glabrous but for sparse to moderately dense, short glandular hairs occasionally at base of or all over rear surface, with cleft between (1)1.5-2.5mm deep; lower lip concave when viewed from above, down-turned from base, (5.5)6-8(9) x (10)11-13(15)mm externally glabrous or covered entirely or in part by sparse to dense, moderately long to long eglandular hairs, sometimes mixed with sparse short glandular hairs, internally glabrous; lower lobes usually emarginate to truncate, sometimes obtuse, with clefts between 3-5(6.5)mm deep. Stamens with filaments glabrous, the anterior pair (3)3.5-4.5(5.5)mm long, the posterior pair 1.5-2(3)mm long; anthers (1.4)1.5(1.7) x 0.7-1.0mm, with connectives usually glabrous, sometimes with a small patch of

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sparse to dense, moderately long to long flexuose eglandular hairs, denser on the rear pair of anthers, with slits lined by dense, moderately long to long, flexuose eglandular hairs, with rearmost pair of awns (0.25)0.3(0.4)mm long, longer than other three pairs. Ovary in lateral view oblong to elliptic or ovate-elliptic, slightly compressed laterally, in median view ovate, glabrous except often for a few, short to moderately long setae about apex; apex in lateral view usually obtuse, sometimes broadly or obliquely so or acute; ovules (79)93(110). Capsules (4)6-8(10)mm long, only slightly compressed laterally, in lateral view obovate to oblong or elliptic to ovate-elliptic, 2.2-3.0mm broad, in median view ± ovate or ovate-acuminate, glabrous except sometimes for sparse to dense, short setae at very apex; apex in lateral view truncate to broadly acute, often obliquely so; seeds c. 48-78, ± oblong-elliptic to almost reniform, often rather angular, (0.5)0.7-0.9(1.3) x (0.3)0.4(0.5)mm. Chromosome number: unknown. Figs 6, 46.

Distribution (fig. 36): E. semipicta is known from only a few localities in the western half of the Tasman Peninsula, south-eastern Tasmania. Altitude, c. 50m at West Arthur Head.

Ecology: E. semipicta occurs in heath often in near coastal situations, on sandstone (Hemsley K) or in deep sand (Barker 960-967).

The main flowering season is likely to be October to December or January. A few new fruits occur on plants collected in late October. A depauperate flowering branch occurs on a plant mainly finished fruiting on a specimen collected in early February.

Conservation status: 2V/R.

Notes: 1. The sectional placement of E. semipicta is discussed under Sect. Striatae: note 1.
2. I am grateful to Mr Arnold Himson of Buckland, Tasmania, for directing me to the populations of E. semipicta near West Arthur Head.

Specimens examined


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Perennial herb, (2)-5-12(15) cm tall, usually with simple erect stem, sometimes with 2(6) simple erect branches arising from very base of prominent (in first year plants) or reduced (in later year plants) stem. Stem, or branches, if no flowering stem present, (1.0)4.0-8.5(11.0) cm long to base of inflorescence; internodes much shorter than leaves at least in lower parts, often ± equal up to 1½(2) times length of upper leaves in region of upper (1)3(4) nodes below inflorescence; axes purple-brown, with two opposite rows of moderately dense, short to moderately long e glandular hairs decurrent from between bases of upper few pairs of leaves, glabrous or with very sparse e glandular hairs in lower parts. Cotyledons usually broadly ovate to elliptic-ovate, sometimes triangular, acute or obtuse, entire, (0.5)0.8-1.2 mm long, usually persistent, at least in first year plants, sometimes caducous before flowering. Leaves: uppermost leaves in outline elliptic to obovate to very broadly so, (5.0)6.5-10.5(11.7) x (4.2)5.5-10.0(11.5) mm, digitate, glabrous, lacking patches of sessile glands, green or partially reddened, with lamina obovate to broadly obovate; base narrowly cuneate; teeth (3)4-5(7) along each margin, confined to and constituting almost entire distal half of leaf, linear, acuminate, often ± hooked, of ± equal length except sometimes for small outermost teeth, (1.9)2.5-4.5(5.1) mm long, with margins recurved greatly on underside such that coherent for whole length; apical tooth identical to neighbouring teeth in shape, size and recurvature of margins, c. 0.6-0.9 mm broad; middle leaves similar to uppermost; lower leaves similar but smaller, fewer toothed, those at very base entire, subulate or with one tooth along each margin. Inflorescences dense racemes, that of stem producing (6)10-20(26) flowers, with lowest node occasionally bearing one flower, those of branches ± similar; rachis reddish-brown, covered by dense, moderately long e glandular hairs, sometimes mixed with sparse, short to moderately long glandular hairs; internodes hardly elongating after anthesis; pedicels of lowermost flowers (1.2)2.6(4.0) mm long, shorter higher up; apical bud cluster initially spherical to very broadly ellipsoid, 0.8-1.5 cm long, hidden by or hardly protruding from uppermost corollas after flowers at first 1-2 nodes have opened. Bracts similar to uppermost leaves in shape and morphology, but somewhat larger and often more toothed, glabrous on inner surface, with outer surface usually covered by sparse to moderately dense, short to moderately long e glandular hairs, mixed with short to moderately long glandular hairs mainly confined to margin of blade, rarely (Jarman HO) glabrous. Calyx (5.5)8.0(10.5) mm long, slightly 4-ribbed, externally with tube and lower part of teeth covered by moderately dense to dense, short to moderately long glandular hairs mixed with moderately dense to dense, short e glandular hairs, with upper part of teeth covered by dense short e glandular hairs, sometimes mixed with sparse short glandular hairs, internally with tube glabrous, with short glandular hairs, dense and mainly confined to lower part of teeth, with short e glandular hairs, dense and mainly confined to their upper half; teeth sharply acuminate, with margins in upper half recurved, coherent near apex; lateral clefts c. 2.0-5.0 mm deep, shorter than median clefts which are c. 3.3-7.0 mm deep. Corolla (7.0)8.5(9.5) mm long along upper side, usually white, sometimes pink-purple (Barker 1222), with yellow blotches, often continuous, on lower side of mouth and deep in throat, with red-purple striations c. 3 on each lobe, sometimes extending only short distance onto lobes; tube (4.8)5.7(6.7) mm long, laterally and abaxially broadened at about point of insertion of anterior filaments, which are (3.3)4.1(5.0) mm from base of corolla, externally glabrous but for most distal parts, on distal adaxial and lateral surfaces covered by dense moderately long e glandular hairs, with patch of dense short e glandular hairs about lateral clefts, on distal abaxial surface covered by sparse to moderately dense, short e glandular hairs, sometimes mixed with sparse to dense, short to moderately long e glandular hairs, internally sometimes glabrous, sometimes with two rows of sparse to dense, short to moderately long downturned e glandular hairs decurrent from bases of filaments, rarely with hairs also extending across midline between filament bases; hood (2.2)2.8(3.5) mm long, excluding lobes c. 2.8-3.2 mm broad, including lobes (4.0)5.0(5.8) mm broad, externally covered all over by dense, moderately
long to long eglandular hairs, with moderately dense short glandular hairs on sides, sometimes with a few glandular hairs at front, internally with dense long eglandular hairs in region of sinus, elsewhere usually glabrous, rarely with line of moderately long eglandular hairs down midline; upper lobes almost coplanar or at broad angle to each other, usually emarginate to praemorse to truncate-obtuse, rarely obtuse and shortly apiculate, with cleft between (1.2)1.6(2.0)mm deep, with front surface and margins glabrous, with rear surface glabrous or covered by sparse short glandular hairs, sometimes mixed with sparse short eglandular hairs; lower lip concave from above, downturned until almost parallel to upper side, (4.3)5.9(6.8) x (9.0)11.0(13.0)mm, externally bearing sparse to moderately dense, short glandular hairs, usually mixed with sparse to moderately dense, short to moderately long eglandular hairs, with margins and inner surface glabrous; lower lobes usually emarginate, sometimes truncate, with clefts between (3.0)3.6(4.3)mm deep. Stamens with filaments glabrous, the anterior pair (1.7)3.2(4.0)mm long, the posterior pair (0.9)1.4(1.7)mm long; anthers (1.1)1.3(1.5) x (0.7)0.9(1.2)mm, tending to separate after anthesis, with connectives glabrous, with slits lined by sparse to dense, short to long eglandular hairs, with rearmost pair of awns (0.15)0.2(0.3)mm long, longer than other three awn pairs. Ovary in lateral view oblong to oblong-elliptic, hardly compressed laterally, in median view ovate to broadly ovate, glabrous but for sparse to moderately dense, short to long setae in region of apex; apex in lateral view, usually emarginate to truncate to broadly obtuse, sometimes obliquely so; ovules c. 70-90. Capsules (7.8)9.2(11.0)mm long, only slightly compressed laterally, in lateral view ovate-elliptic to elliptic or oblong-elliptic, 3.5-4.5(5.5)mm broad, in median view ± ovate to elliptic, glabrous but for very few to moderately dense, usually short, rarely long setae at very apex; apex in lateral view obtuse to truncate-obtuse; seeds (60)72(84), usually oblong-ellipsoid to obliquely ellipsoid to ± reniform, often broadly so, (0.9)1.1-1.4(1.5) x (0.5)0.6-0.8(0.9)mm. Chromosome number: n = c. 26-30 (Barker 1212). Figs 6, 31K, 47.

Typification

E. cuspidata Hook.f. (≡ E. hookeri Wettst.) Wettstein (1896) stated that his E. hookeri and E. cuspidata Hook.f. were identical, the original name of the species having to be substituted because of the earlier homonym E. cuspidata Host (1831). Accordingly the two names must be considered as nomenclatural synonyms, with the typification of E. hookeri identical to and determined by that of E. cuspidata Hook.f. Oldfield’s collection (W), reputedly from Mt Wellington, therefore has no type status even though it was the only specimen of the species, other than the isolectotype of E. cuspidata in FI, seen by Wettstein and cited in his initial description of E. hookeri (Wettstein 1896).

Each syntype is typical of E. hookeri and comprises several plants. The Milligan collection was chosen as lectotype because of the presence of mature fruits as well as flowers. Archer’s collection has flowers but lacks fully-developed fruits. An additional advantage of this choice is the existence of several isolectotypes and the fact that one of these (in FI) was used by Wettstein (1896) in his description of E. hookeri.

Distribution (fig. 36): E. hookeri is known with certainty only from the mountains of north-west, west and south-west Tasmania. The species is notably absent from the more central and north-eastern mountain areas of the island. It is doubtfully recorded from Mt Wellington (see note 3) and the Central Plateau region (note 4). Altitude, c. 700-1300m. Ecology: E. hookeri mainly occurs in the dense hard mats of cushion plants. Plants are occasionally found in low prostrate compact woody shrubs bordering these areas. One plant in Barker 1227 was found growing in a clump of Astelia sp.

Flowering apparently occurs between December and late March. Mature fruits are found in collections made after mid-January.
Fig. 47. *E. hookeri*, from north side of Cradle Mountain, Tasmania (*Barker* 1207). A, habit, with cushion plant habitat in background, scale 2cm; B, inflorescence showing many-toothed leaves and bracts, and white corollas with purple striations and yellow blotch on lower side of mouth, scale 1cm.

**Conservation status:** 3V/ R, C

**Notes:** 1. The unique leaves of *E. hookeri* set it apart from the other species of Sect. *Striatae* (figs 6, 31K, 47). Of these species it most closely approaches *E. striata* and *E. semipicta* by its small corollas and leaves. Both species can be distinguished not only on leaf characters but also by the absence of glandular hairs from the calyces, bracts and rachises. In addition, *E. striata* differs by its many ascending branches and the absence of a flowering stem, while *E. semipicta* is clearly distinguished by the absence of purple striations from the upper and lowest lobes.

2. In the past *E. hookeri* has generally been considered an annual (*Hooker* 1857; *Bentham* 1868; *Rodway* 1903; *Du Rietz* 1948a,b; *Curtis* 1967; *Harris* 1970), despite the fact that its closest Australian relatives are perennials. *Wettstein* (1896) was not convinced that the species was an annual, since he mistakenly considered that the specimens seen by him were broken-off branches. They were actually whole plants comprising either a single
stem or a few branches. In his experience the annual species of *Euphrasia* always consisted of whole plants. In addition he referred to the perennial nature and similarity of appearance of the closest related species.

From my own field observations, *E. hookeri* is a perennial. Occasional plants (e.g. on the AD sheet of Barker 1207, 1212, 1214, and 1222) can be found bearing dead grey-white remains of branches, sometimes with parts of the inflorescence still attached. Similar remnants of inflorescence-bearing branches or stems are commonly found in all Australian perennial species, but not in the annual species. Thus it appears that plants of *E. hookeri* perennate at least occasionally. It is difficult to estimate the frequency of perennation, as it is possible that plants in such extreme habitats, snow-covered in winter, and comprising so few axes may rarely retain remnants of the branches or stem of prior years. In addition, although the majority of plants in the dried collections still bear the cotyledons, this does not necessarily signify that these plants were in their first year of growth. Cotyledons of the Australian perennial species of *Euphrasia* are found occasionally in the young seedlings of a few species (e.g. *E. semipicta*), while they often persist in the annual species. However, one plant in Barker 1207 bearing a dead stem with the remains of a pedicel in the upper part still has a pair of green fleshy cotyledons. Thus the protection provided by the hard compacted leaves of the “cushion plants” in which *E. hookeri* grows is apparently sufficient to allow the cotyledons to survive into the second year. It is concluded that *E. hookeri* is a perennial, although further study is required to determine how often the species survives for more than one year.

3. The Mt Wellington locality (fig. 36), attributed to a collection of *E. hookeri* by Oldfield (*W*) must be considered doubtful. The collection was originally mounted with plants of *E. striata* (see Wettstein 1896 p.269), which is common at that locality. However, no other collections of *E. hookeri* have ever been made from Mt Wellington, which is probably the most botanized alpine locality in Tasmania.

4. The locality “W[estern] Mts” on the Archer syntype is the old name for the Great Western Tiers, at the base of which Archer lived (Burns & Skemp 1961). Collections from the highest parts of these mountains are few and confined almost entirely to a few collectors of the early 1900s and before. However, as this locality would represent the sole record of *E. hookeri* from the Central Plateau region of Tasmania, it requires confirmation.

**Specimens examined**

IV. Sect. *Australes* (Benth.) Joerg.

For synonymy, description, typification and distribution, see p. 84. Fig. 48.

The section is endemic to Australia and consists of four species. One species (figs 50-55) is spread throughout the geographical and altitudinal range of the genus in Australia and is extremely polymorphic. The others are localized in mountain areas in eastern mainland Australia (figs. 49, 55: see also note 1).

**Notes:** 1. Although the four species of Sect. *Australes* are very closely related, it has been considered advisable to distinguish them at that rank as the three with restricted range are clearly distinct from the complex network of subspecies which together make up *E. collina*, and show no evidence of morphological intergradation with them. Indeed, it is possible that the two species and their unnamed ally restricted to the northern and central tablelands of New South Wales, *E. bella*, *E. sp. ‘Tamworth’* and *E. bowdeniae*, may constitute a separate paraphyletic group (p. 57).

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Fig. 49. Distribution of the species and subspecies of Sect. Ausrales (1). 3000ft (910m) contour.
Figs 50-51. Distribution of the species and subspecies of Sect. *Australes* (2). 1640ft (500m) contour.
Figs 52-53. Distribution of the species and subspecies of Sect. *Australes* (3). 1640ft (500m) contour.

E. collina
- ssp. trichocalycina
- ssp. 'tasmanica'
- ssp. gunnii
- ssp. diemenica-ssp. gunnii
- ssp. deflexifolia

E. collina
- ssp. paludosa
- ssp. paludosa-ssp. muelleri
- ssp. muelleri
- aff. ssp. muelleri
E. collina
ssp. nandewarensis
ssp. speciosa
ssp. aff. ssp. speciosa
ssp. osbornii

150 miles
240 km

S.A

Fig. 54. Distribution of the species and subspecies of Sect. Australes (4). 1640ft (500m) contour.
2. *E. crassiuscula* (q.v.: Intraspecific Polymorphism) varies in the characters of anther back indumentum and corolla coloration, which are the main attributes used to distinguish the two sections, Sect. *Australes* and Sect. *Striatae*, to which the species has closest affinities. Its evolutionary history is open to debate (p. 64). It has been included in Sect. *Australes* because it is closest related to the present-day species of that section.

*E. semipicta* of Tasman Peninsula, south-east Tasmania occasionally has hairy-backed anthers, but glabrous anther backs are common and the corolla is partially striated. Its sectional placement is discussed under Sect. *Striatae*: note 1.

**Key to the species of Sect. Australes**

1a. Calyx with a prominent beard of dense eglandular hairs 0.3-0.8mm long, rarely mixed with glandular hairs, the whole indumentum confined to the margins of the teeth, otherwise glabrous externally. ............... 12. *E. crassiuscula* (p. 236; also see Sect. *Australes*: note 2)
1b. Calyx lacking a prominent beard of dense long hairs confined to the margins of the teeth, [outer surface covered all over by glandular hairs, sometimes mixed with eglandular hairs, or covered all over by eglandular hairs, or glabrous but for usually sparse to moderately dense, rarely dense eglandular hairs 0.1-0.2mm long lining the margins, i.e. not beard-like].

2a. Inflorescences but for lower 0-3(5) nodes usually moderately dense to dense, rarely lax; with all nodes, but sometimes for the lowest 1(4), bearing 2 opposite flowers. Ovules (60)80-180(200). Leaves rigid and often brittle, ascending or deflexed, with base narrow cuneate to truncate. Main axes rigid, ascending or erect. ..... 11. E. collina (p. 159)

2b. Inflorescences lax; with lowest (0)1-5(7) nodes bearing single flowers. Ovules c. 20-60. Leaves either plant when dried, deflexed greatly, with base narrow cuneate, or ± rigid, somewhat deflexed, with base narrow attenuate and at least sometimes twisted. Main axes rather weak, procumbent, decument or ascending.

3a. Axis of inflorescence-bearing branches with glandular hairs usually present on younger parts well below inflorescence. Uppermost leaves of main inflorescence-bearing branches glandular hairy, at least on lower surface, 8.5-12.5 x 3.4-5.4 mm; base narrowly attenuate (subpetiolate); marginal teeth 2(3) along each margin, 0.6-1.4mm long; lowermost pedicels (3)4-8(9.2)mm long. Calyx 5-8mm long. Anthers 1.6-1.9mm long; rachis pair of awns 0.3-0.4mm long. ..... 8. E. bella (p. 153)

3b. Axis of inflorescence-bearing branches with glandular hairs lacking. Uppermost leaves of main inflorescence-bearing branches lacking glandular hairs, 4-7 x 1-3mm; base narrowly cuneate; marginal teeth 0.1-0.5mm long. Lowermost pedicels 1-4.5mm long. Calyx 3-6mm long. Anthers 1.3-1.7mm long; rachis pair of awns 0.05-0.2mm long.

4a. Axis of inflorescence-bearing branches with glandular hairs equally dense all around. Uppermost leaves of inflorescence-bearing branches with 2 teeth along each margin. ..... 9. E. sp. ‘Tamworth’ (p. 156)

4b. Axis of inflorescence-bearing branches with eglandular hairs in two rows, sometimes with sparser hairs between. Uppermost leaves of inflorescence-bearing branches with (0)1 teeth along each margin. ..... 10. E. bowdeniae (p. 156)

8. Euphrasia bella Blake, Qld Nat. 12 (1945) 88, pl. 5

Holotype (fig. 56): S. T. Blake 14652, 4.x.1942. Queensland. Moreton District: Mt. Merino, McPherson Range, near exposed edge of cliff, 3650ft. BR1001412; isotypes: MEL14403, GH.

Perennial herb, 9-30cm high, with many decumbent or ascending branches, arising from reduced stem or both prostrate and erect parts of other branches. Stem reduced; inflorescence-bearing branches with distal suberect parts 2-10cm long to base of inflorescence; internodes as long as or longer than upper leaves over the upper 0-4(7) nodes, the longest internode 1/2-13/4 times length of upper leaves, shorter lower down; axis covered all around by moderately dense short eglandular (?or decapitated glandular) hairs, usually also with very rare to moderately dense, long to very long glandular hairs well below inflorescence or on younger parts. Cotyledons not seen. Leaves usually opposite, sometimes alternate: uppermost leaves of inflorescence-bearing branches elliptic to obovate-spathulate in outline, 8.5-12.5 x 3.4-5.4 mm, shortly subpetiolate, serrate-crenate, with upper surface glabrous or bearing sparse, long to very long glandular hairs, lower surface covered by sparse to moderately dense, long to very long glandular hairs, with sessile gland patches extensive on margins and between veins, extending over distal 1/4 of leaf, with margins recurved, often shortly scaberulous; base narrowly attenuate; teeth 2(3) along each margin, bluntly or sharply acute or obtuse, distributed over distal 1/2, the longest 0.6-1.4mm long; apical tooth bluntly or sharply obtuse or broadly acute, 1.9-2.6 x 2.1-3.0mm, leaves lower down somewhat larger with a similar indumentum, sometimes with extra pair of teeth. Inflorescences lax racemes with (6)12-36 flowers, usually opposite with flowers at the lowermost (0)1-5(7) nodes single, sometimes alternate; pedicels long, the lowermost ones (3.0)4-8(9.2)mm long; rachis similar to upper parts of axis; internodes
Fig. 56. Holotype of *E. bella* Blake (scale 5cm).

Fig. 57. *Euphrasia* sp. 'Tamworth', Rupp MEL41404 (scale 5cm).
long, equaling the pedicel or pedicel and calyx combined; *apical bud cluster* loose, foliaceous, c. 1-2 cm long becoming hidden by or hardly emergent from uppermost corollas after flowers at first 1-9 nodes have reached anthesis. *Bracts* similar to uppermost leaves. *Calyx* 5-8 mm long, externally usually glabrous but for a very few short glandular hairs below median clefts sometimes covered in distal half by sparse to moderately dense, short to moderately long glandular hairs, internally glabrous but for short glandular hairs mainly confined to margins towards base of teeth; *teeth* bluntly or sharply obtuse; *lateral clefts* 0.8-2.5 mm deep, shorter than *median clefts*, which are 2.1-4.3 mm deep. *Corolla* 9-15 mm long along upper side, light mauve, light slightly lavender blue or deep blue, at least usually lighter behind lobes, with yellow blotch on lower lip (in all Blake specimens) apparently behind lowest lobe, with lower side apparently flattened, possibly grooved; *tube* 6-10 mm long, narrow cylindrical for 3.2-5.2 mm to base of anterior filaments, distally broadened laterally and somewhat medially, externally glabrous at base and on abaxial surface, distally covered by moderately dense to dense, short to long glandular hairs, mixed with sparse short glandular hairs which are sometimes confined to area behind lateral clefts, internally glabrous, short to long, setose glandular hairs all around tube at and below bases of filaments; *hood* 2.8-5.0 mm long, breadth uncertain, externally covered by moderately dense to dense, short to long glandular hairs, internally with dense long glandular hairs at front near sinus, and sparse short glandular hairs above and in front of anthers; *upper lobes* usually obtuse, sometimes very shallowly emarginate, with front surface glabrous, with rear surface covered by sparse to dense, short to long glandular hairs, sometimes mixed with sparse short glandular hairs, with margins lined sparsely to densely with short glandular hairs, with cleft between 1.7-3.7 mm deep; *lower lip* 5.0-10.2 x c. 10-18 mm, initially porrect, downturned from about base of lobes, externally covered by sparse to dense, short to long glandular hairs, sometimes mixed with sparse short glandular hairs, with margins lined sparsely to densely with short glandular hairs, internally glabrous; *lower lobes* usually obtuse or slightly truncate, sometimes shallowly emarginate, with cleft between 2.7-5.5 mm deep. *Stamens* with *filaments* glabrous, anterior pair 4.5-6.3 mm long, posterior pair 2.3-3.8 mm long; *anthers* 1.6-1.9 x 1.0-1.4 mm, with *connectives* of posterior pair surrounded by dense, long to very long glandular hairs, beard usually denser or more extensive than, rarely similar to, that of anterior pair, which are surrounded by sparse to dense, short to long glandular hairs, with *slits* lined by dense, very long glandular hairs; **rearmost pair of awns** 0.3-0.4 mm long, longer than other 3 pairs. *Ovary* (only two seen) ovate or elliptic in lateral view, laterally compressed, glabrous; *apex* obtuse or obliquely truncate in lateral view; *ovules* c. 60. *Capsules* (*Smith BRI144796*) 6.5-8.2 mm long, in lateral view ovate-elliptic to elliptic, sometimes obliquely so, 2.3-3.2 mm broad, slightly compressed laterally, glabrous; *apex* obliquely truncate in lateral view; *seeds* 14 (in the one capsule dissected), obliquely narrowly ellipsoid, 0.7-1.0 x 0.3-0.4 mm. *Chromosome number*: unknown. Figs 6, 56.

**Distribution** (fig. 49): *E. bella* is known from four or five plants (Blake sampled the same plant in different years), which occur on and near Mt Merino in the McPherson Range in Queensland close to the New South Wales border. The higher parts of this range are relatively inaccessible (Morcombe 1969), and it seems possible that the species is not confined to the one mountain. Altitude, 1000-1200 m.

**Ecology:** *E. bella* has been found on the edges of cliffs, apparently in exposed positions, in *Nothofagus* forest.

Flowering apparently occurs between late August and December. In the December collection (*Smith BRI144796*) capsules are predominant.
**Conservation status:** 2 ?E,C. The true extent of this species has yet to be determined.

**Note:** *E. bella*, *E. bowdeniae* and their geographical and morphological intermediate at Tamworth (see below) form a distinctive group in Sect. *Australes*. The differences between the species are detailed above in the key to species.

**Specimens examined**


**NEW SOUTH WALES:** *[Rupp] 2 or l, ix.1904. Tamworth. MEL41404.*

**Euphrasia sp. 'Tamworth'.** Fig. 57

A specimen from Tamworth, northern New South Wales (fig. 49), is allied to both *E. bowdeniae* of the Blue Mountains, about 250km to the south, and *E. bella* of the McPherson Range, about 350km to the north-east. It has their very weak habit, deflexed leaves and long-pedicellate flowers in weak sparse racemes which apparently lack flowers in the distal parts. By its narrow sessile leaves without glandular hairs it is more closely allied to *E. bowdeniae* than to *E. bella*, which is distinguished by its sub-petiolate leaves. It differs from *E. bowdeniae* in its uppermost leaves which possess two pairs of marginal teeth and by its densely hairy, ciliolate corolla lobes. It also characterized by the presence of young shoots well up the axis to a few nodes below the inflorescence, and by calyces which are glabrous but for the rare incidence of glandular hairs and very short eglandular hairs on the inner surface of the teeth. This specimen is likely to represent a distinct species, intermediate both geographically and morphologically between *E. bowdeniae* and *E. bella*.

**Specimens examined**

**NEW SOUTH WALES:** *Rupp 2 or l, ix.1904. Tamworth. MEL41404.*

**10. Euphrasia bowdeniae** Barker, *species nova*


**Species nova Sectionis *Australium* in foliis flexibilibus peculiaris, *E. bellae* affinis ovulis infra 60 inflorescentis laxis nodibus inferioribus saepe unifloribus, et ramis debilibus procumbentibus, sed differt pilis glandulosis ex ramulis foliisque carentibus, seriebus duobus pilorum eglandulosorum secus ramulos, foliis minoribus, anguste cuneatis dentibus paucioribus brevioribus, pedicellis brevioribus, calycibus, corollis, staminibusque plerumque minoribus, aristis postremis antherarum brevioribus, ovulis paucioribus, capsulis minoribus, et seminibus maioribus.

**Holotypus** (fig. 58): *R. Coveny 4776 & Miss Bowden, 18.xii.1972. National Pass, Wentworth Falls, N.S.W. Scattered on sandstone rock face with *Sprengelia, Dracophyllum.* Alt. c. 750m. NSW (s.n.). Isotypus: AD.

**Perennial herb,** 7-17cm high or higher (to 30cm from annotations on *Bowden NSW84075*), with many crowded ascending, decumbent or procumbent branches arising from very short stem or prostrate parts of other branches, or possibly (from position of vegetative buds on *Bowden NSW84075*) on erect parts of branches while flowering. **Stem** apparently reduced; inflorescence-bearing branches 4-19cm or more high to base of inflorescence, simple for 0-4(24) nodes below inflorescence, i.e. for much of height above ground level; upper 0-3(8) **internodes** as long as or longer than uppermost leaves, the longest 3/4-13/4 times length of upper leaves, shorter than leaves
Fig. 58. Holotype of *E. bowdeniae* Barker, sp. nov. (scale 5cm).

Fig. 59. Lectotype (middle and left-hand plant) and other syntype (the right-hand plant) of *E. collina* R.Br. (scale 10cm long).
lower down; axis in upper parts covered by two rows of moderately dense to dense, short stiff downturned eglandular hairs decurrent from between leaf bases, sometimes with sparse similar hairs between, in lower parts similar or somewhat sparser and shorter. Cotyledons not seen. Leaves usually opposite, rarely at a few nodes alternate; uppermost leaves of inflorescence-bearing branches elliptic to obovate-elliptic, sometimes narrowly so, 4.0-7.5 x 1.2-3.2mm, "lax" (Bowden NSW84075), plant when dried, deflexed, often greatly so, glabrous, with sessile gland patches in distal \( \frac{1}{2}-\frac{3}{4} \) length of leaf; base narrowly cuneate, sometimes obliquely so; teeth (0)1 along each margin, bluntly obtuse to acute, 0.1-0.5mm long; apical tooth bluntly acute or obtuse, 1.7-2.8 x 1.0-2.2mm; leaves lower down similar to uppermost leaves. Inflorescences racemes, sparse at least at base, with 4-10(20) flowers, the lowermost 1-5(11) nodes usually subtending a single flower only, the opposing bracts then sometimes displaced along rachis; pedicels at lowermost node 1.2-4.0mm long, shorter higher up; rachis usually similar to upper parts of axis, rarely covered all around by moderately dense to dense, short eglandular hairs; internodes long, in lowermost parts almost equalling length of pedicel and calyx combined; apical bud cluster somewhat loose, conical, c. 1cm long, becoming hidden by or hardly emergent from uppermost corollas after flowers at first 1-4 nodes have reached anthesis. Bracts similar to uppermost leaves. Calyx 3.3-60mm long, externally and internally glabrous, except sometimes for a few very short to short glandular hairs on margins of teeth; teeth bluntly to sharply obtuse to acute; lateral clefts 0.6-2.5mm deep; median clefts 1.5-3.5mm deep. Corolla 7.0-10.5mm long along upper side, mauve, purple or violet with deeper markings in throat, with yellow markings apparently lacking, with shape of lower side unknown; tube 5.5-8.0mm long, cylindrical for 2.2-4.5mm to base of anterior filaments, then broadened laterally and abaxially, externally glabrous on narrow part of tube, on broad part of tube covered by sparse to dense, short glandular hairs, sometimes mixed with sparse to dense, short to long eglandular hairs, internally with moderately dense to dense, short to moderately long eglandular hairs decurrent from bases of filaments, somewhat sparser or completely absent between; hood 1.5-2.8mm long, 4.0-4.5mm broad excluding lobes, 5.0-6.5mm broad including lobes, externally covered by sparse to dense, short glandular hairs, sometimes mixed with moderately dense to dense, short to long eglandular hairs confined to proximal parts or along midline, internally glabrous or with a few short eglandular hairs towards sinus; upper lobes ?± coplanar usually obtuse, sometimes somewhat praemorse or shallowly emarginate, with front surface and margins glabrous, with rear surface covered by sparse to moderately dense, short glandular hairs, with cleft between 1.7-3.5mm deep; lower lip 5.5-9.0 x 9.0-13.0mm, concave from above (Conabere & Garnet 1974, pl. 67 f.4), externally covered by sparse to moderately dense, short glandular hairs, internally glabrous; lower lobes usually obtuse, sometimes somewhat praemorse or shallowly emerginate, with clefts between 3.7-4.0mm long. Stamens with filaments glabrous, but sometimes for short eglandular hairs at base of anterior filaments, the anterior filaments 3.8-5.0mm long, the posterior 1.2-2.3mm long; anthers 1.1-1.7 x 0.9-1.3mm, with connectives and slits covered by dense, long to very long eglandular hairs; awns tiny, rearmost pair 0.05-0.2mm long, usually longer than, sometimes equal to those of other three pairs. Ovary in lateral view obovate-elliptic to narrowly ovate-elliptic, apparently laterally compressed, in lateral view narrow ovate, glabrous except sometimes for very few short setae at very apex; apex in lateral view obtuse to narrowly acuminate; ovules 19-40. Capsule 4-5.5mm long, in lateral view obovate-elliptic to ovate or broadly so, 2.2-8.0mm broad, laterally compressed, in median view ovate, acuminate, glabrous; apex broadly acute to truncate in lateral view; seeds 3-16, oblong-elliptic, 1.0-1.8 x 0.5-0.9mm. Figs 6, 58.

Distribution (fig. 49): E. bowdeniae is endemic to the higher parts of the Blue Mountains,
New South Wales, where it is currently known only from five localities. Dr B.G. Briggs (pers. comm. 1973) has stated that her "impression is certainly that... further searching in the particular habitat favoured by [E. bowdeniae] would also show up further localities in this same general region...". The sole altitudinal record is c. 750m, but from the available information it could range up to the top of the cliffs at c. 1000-1100m.

**Ecology:** The species has a very distinctive habitat on vertical sandstone cliffs in very shallow soil on rocky ledges or sometimes trailing over steep exposed rock.

Flowering material is known from September to mid December, with fruits from early December.

**Conservation status:** 2 ?E/V,C. In view of the highly restricted habitat of this species, it is imperative that its frequency be determined.

**Notes:** 1. The often procumbent habit, weak inflorescences, leaves and pedicels, few ovules and small capsules set *E. bowdeniae* well apart from *E. collina*. Differences from *E. bella* and the possible intermediate taxon from Tamworth are summarized in the key to species of Sect. *Australes*.

2. The species has been named after Miss I. Bowden of Wentworth Falls, New South Wales. On her copiously annotated collection *NSW84075*, she amply justified her belief that it was taxonomically distinct from *E. collina* ssp. *paludosa*, the common taxon in the area.

**Specimens examined**


*E. tetragona* R.Br., l.c. 436 [see ssp. *tetragona*].


*E. multicadis* Benth. in DC., Prodr. 10 (1846) 553 [see ssp. *collina*, ssp. *diemenica*, ssp. *tetragona*].


E. novae-cambricæ Gandoger, l.c. 218 [see ssp. deflexifolia].

E. trichocalycina Gandoger, l.c. 218 [see ssp. trichocalycina].

E. maidenii Gandoger, l.c. 218 [see ssp. glacialis].


E. collinoides Du Rietz, l.c. 352, pl. 3, 4 (nom. provis.) (see p. 163).


C. palticlosa Presl ex Wettst., Monogr.Gatt. Euphrasia (1896) 256 ("in sched.") pro syn. [see ssp. paludosa].

C. speciosa Presl ex Wettst., l.c. 259 ("in sched.") pro syn. [see ssp. speciosa].

Perennial herb or undershrub of variable habit. Cotyledons ovate-elliptic to elliptic, c. 6-12 x c. 6mm, entire, glabrous, present only in seedlings. Inflorescences racemes of varied nature. Calyx with variable length and indumentum; teeth blunt or sharp, usually acute, sometimes obtuse; lateral clefts (0.2)-3(4.5)mm deep, more shallow than median clefts which are (1.2)-2.5-4(6.5)mm deep. Corolla variable in size, colour and incidence of yellow blotches on lower lip and at point of insertion of anterior filaments, with lower side flattened or shallowly grooved; tube glabrous at base, distally with outer surface covered by short to long eglandular hairs, dense on the adaxial and lateral surface, sparse or absent on the abaxial surface, sometimes (in ssp. tetragona) completely lacking eglandular hairs, with sparse to dense patch of very short to short glandular hairs behind lateral cleft, with inner surface bearing moderately dense to dense, short to long glandular hairs, sparse all over or confined to area between filaments; hood excluding lobes 4-6 (6.5)mm broad, including lobes (5)5.5-9.5(12.5)mm broad, externally covered by dense, short to long hairs often mixed with short to moderately long glandular hairs on front and sides or all over, the indumentum usually all over hood, but in ssp. tetragona sometimes confined to midline or absent, internally usually with long to very long eglandular hairs in dense patch in sinus region, sometimes extending over distal half, often with sparse to dense, very short to short glandular hairs, confined to sinus region, or extending along sides or over hood, or all over; upper lobes coplanar or almost so, with cleft between (1.5)-2-4.5mm deep; lower lip ± flattened crosswise at base, initially porrect, distally spreading, (9)10-24(30)mm broad; lower lobes with clefts between 3.5-7.5(9)mm deep. Stamens with filaments glabrous, the anterior pair (2.8)4.5-7.5(9.2)mm long, the posterior pair (1.3)2.5-4.5(5.5)mm long; anthers variable
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in length, (0.9)1.2-1.7(2.0)mm broad, with area about connectives with variable indumentum, rarely glabrous, with slits lined by dense, moderately long to very long eglandular hairs, with rearmost pair of awns variable in length, longer than other three pairs. Ovary in lateral view ovate to elliptic or oblong, hardly compressed laterally; in median view ovate- to narrow ovate-caudate, glabrous or with sparse to dense, very short to moderately long setae confined to apex or distributed over distal ¾; apex in lateral view usually obtuse, sometimes acute or truncate-obtuse, rarely acuminate; capsules of variable shape and indumentum; seeds variable in number and size. Chromosome number: n = c. 27-32 (Barker 1374, 1438-1440, 1489) or c. 50-60 (Barker 1504, 1685).

Typification

1. E. collina R.Br. The type collection (fig. 59) consists of at least two elements, one of ssp. collina (equivalent to E. collina of previous usage, e.g. in Curtis 1967) and the other from the populations on the upper slopes of Mt Wellington which connect ssp. collina and ssp. diemenica (which is equivalent to E. diemenica in recent works). All three sheets (in BM, K, MEL) are in good condition except for the loss of some inflorescences. Material of the lectotype is in flower and fruit, while that of the other syntype is in bud and flower. The localities of Brown's collections are discussed later.

The choice of Brown 64 as lectotype is based on several grounds. By its oblong to narrowly oblong leaves with a single tooth on each margin the lectotype fits the protologue (Brown 1810: "... foliis lineari-cuneatis obtuse tridentatis glabris") better than the other syntype, which has broader leaves, often with two teeth on each margin. Of the two syntypes the lectotype is also the more divergent from Brown's E. alpina (now ssp. diemenica) which was described with E. collina in the protologue. The choice also preserves current application of the name in Tasmania (Curtis 1967). Finally, it avoids the taxonomic difficulties associated with a lectotype being an intergrade between two subspecies.

It should be noted that in the manuscript (Brown unpubl.) the name E. collina is ascribed to the collection intermediate between ssp. collina and ssp. diemenica (Barker 1974). Two provisional names, “E. alba” and “E. collina” were used in the manuscript. Brown's “E. alba” clearly corresponds to the lectotype of E. collina by the narrow trilobed leaves described in the manuscript. Thus, on several labels on the above types (including the two on the BM type) “E. alba” has been crossed out by Brown and replaced with “E. collina”.

On the other hand, in the manuscript, “E. collina” was described as intermediate between “E. alba” and “E. speciosa”, the name which Brown originally attributed to his E. alpina (see ssp. diemenica: Typification). From the leaf characters described in the manuscript there is no doubt that these correspond to the plants intermediate between ssp. collina and ssp. diemenica.

Brown's manuscript provides locality details more exact than those on the type specimens. The syntype upon which the manuscript “E. collina” was based is a collection made in July 1804 “In collibus prope Risdon” which is a suburb of Hobart on the River Derwent. It probably came from the upper slopes of Mt Wellington where similar specimens still flourish.

The lectotype, upon which the manuscript species “E. alba” was described is the collection numbered 64 made in February 1804 “In pratis sterilioribus prope Frederic Henry Bay”. There is some doubt, however, as to what Brown meant by this latter locality, since Flinders, who led the expedition upon which Brown was botanist, was
confused about its exact location*. If it is assumed that Brown's concept of Frederick Henry Bay was identical to that of Flinders at the time of his collection of "E. alba", then the collection must have come from either Marion Bay or the region including Storm Bay, Frederick Henry Bay and Norfolk Bay. Brown apparently confined most of his collecting activity to the mountains and lowland regions surrounding the mouth of the River Derwent (Stearn 1960). It, therefore, seems likely that the lectotype came from Storm Bay or Frederick Henry Bay of current concepts where Brown did most of his collecting.

2. For typification of other synonyms of *E. collina* see under relevant subspecies.

**Distribution** (figs 50-55). *E. collina* is the most common and widespread species of *Euphrasia* in Australia, being distributed throughout the temperate regions of the continent from sea level to the top of the highest summit, Mt Kosciusko at 2230m altitude. Its 14 subspecies and several other variants possibly warranting taxonomic recognition have much more limited ranges of distribution. Details are included under the respective treatments.

**Ecology:** The wide-ranging altitudinal and geographical distribution of *E. collina* is clearly the result of its ability to inhabit a correspondingly wide range of habitats. The various subspecies have more limited ecological preferences, their range of distribution often reflecting that of their habitats. Details are found in the notes on ecology under the treatments of the various subspecies.

Evidence of the strong ecological limits on the ranges of distribution of the subspecies of *E. collina* is seen when two or more occur in the same region. Such instances of sympathy are described under *E. collina*: Intraspecific Polymorphism. In addition to ecological differences between the subspecies, there are some subspecies which are wider in their ecological requirements than others. These tend to have associated, often apparently clinal variation which can sometimes be related to an environmental gradation between the habitats or regions occupied by the morphological extremes.

Flowering usually occurs in spring and summer. It varies with the climatic region. In lowland stations the main flowering season begins in August and continues until January or February, although in particular localities the duration is almost certainly less than this (see treatments of ecology under ssp. *trichocalycina* and ssp. *paludosa*). In alpine conditions flowering mainly occurs between December and March. For details see under the respective subspecies.

**Conservation status:** see subspecies.

**Notes:** 1. By their possession of a single erect stem some first year plants of ssp. *speciosa* and ssp. *paludosa* may be confused with the annuals of Sect. *Scabrae*. The perennials can easily be distinguished by the absence of branches from all but the lowest nodes. The annual species have branching in a more or less rigid basipetal sequence starting from a position one to a few nodes below the inflorescence and occurring in all lower nodes.

*In his "Observations of the Coasts of Van Diemen's Land", Flinders (1801: p.4) stated:-
"It does not seem to be well determined which is the Frederick Henry or Hendricks Bay of Tasmania. In the chart I affixe the name to the space which lies to the north of, and between Cape Frederick Henry and Cape Basaltes; and I have extended it to those large pieces of water, on each side of Green Head, calling them the upper bay."

From Flinders' detailed description (i.e.: p.3) of the south coast of Tasmania his Cape Frederick Henry corresponds to Cape Queen Elizabeth on Bruny Island, and Cape Basaltes to Cape Raoul on Tasman Peninsula. The region thus defined encompasses Storm Bay, Frederick Henry Bay and Norfolk Bay of Davies (1965: map 25). However, a different concept of the bay is shown in one of Flinders' charts (Flinders 1814: inset on pl. VI), published later than these observations but drawn earlier in 1798-9. It depicts "Fredk. Hendrik's Bay" on the east coast of Tasmania in what is currently known as Marion Bay.
2. A collection from Smith’s Lake, Bungwahl on the north coast of New South Wales (Rupp 2, i.1924. MEL41404) is unusual in its calyx indumentum which is a mixture of eglandular hairs, c. 0.05mm long, and similarly long glandular hairs. It is related to ssp. muelleri by these eglandular hairs on the calyx. However, it is also allied to ssp. trichocalycina by the presence of the glandular indumentum and its confinement to the calyx, its branching apparently well above ground level and its small upper leaves (on rather depauperate branches) with only one pair of teeth. Good collections are required from the Bungwahl area to establish the true affinities of this specimen.

3. A specimen (Weymouth s.n., 11.ix.1899. MEL41765) from Port Cygnet, southern Tasmania has hairy-backed anthers and corollas which do not appear to be striated. These are characteristics of Sect. Australes, but the specimen does not seem allied to any known species. The plant resembles Sect. Striatae in its very sharply acute, deeply toothed leaves, and is also unusual in that its leaves, bracts and flowers are in whorls of three. It cannot be determined whether the plant is a monstrosity, an extreme of E. collina, or a hybrid between E. collina and a species of Sect. Striatae. A pollen test (PS355) shows the pollen to be almost entirely functional in appearance.

4. The material in BM, which formed the basis of the taxon of uncertain status provisionally named “E. collinoides” by Du Rietz (1948b), had to be returned before my concepts of E. collina s.lat. had developed. It is likely that the specimens belong to the mainland Australian forms of E. collina ssp. collina (q.v.: note 2) which are characterized by longer leaf teeth than their Tasmanian counterparts.

Intraspecific polymorphism

It has been possible to formally divide this extremely polymorphic species into fourteen closely related subspecies. In addition, reference is made to a number of other variants, as yet inadequately known, which are possibly also distinct subspecies or may be recognizable in the future as varieties within a subspecies. Each subspecies has a distinctive geographical and ecological range.

The degree of variability within the subspecies varies greatly. In subspecies such as ssp. lapidosa and ssp. glacialis, which are very localized geographically because of their confinement to very restricted and specialized habitats, variation from population to population is slight. On the other hand, several subspecies which are widespread vary between populations apparently on geographical, ecotypic or climatic bases. Thus, a geographical pattern of divergence is evident in ssp. collina (q.v.: note 2), ssp. tetragona (q.v.: note 2), ssp. trichocalycina (q.v.: note), ssp. paludosa (q.v.: note 3), ssp. osbornii (q.v.: note 1) and ssp. diversicolor (q.v.: note 2); an ecotypic pattern in ssp. diemenica (q.v.: note 1), ssp. tetragona (q.v.: note 3) and ssp. diversicolor (q.v.: note 3); and a climatic pattern in ssp. paludosa (q.v.: note 2).

Field studies of sympatric interaction between taxa of E. collina have been confined largely to alpine and subalpine situations. There are many other instances of overlapping geographical range, mainly in montane and lowland south-eastern Australia, whose critical study would aid in the evolution of an optimum natural infraspecific classification of the species. These are detailed in Barker (1974).

The following studies provide an insight into the degree of distinction of the subspecies of E. collina and have formed an integral part in their recognition.

1. Interaction of ssp. lapidosa with ssp. glacialis and ssp. diversicolor. These subspecies occur in the alpine zone of the Kosciusko region of New South Wales, where each occupies distinct vegetation types. Ssp. lapidosa apparently remains morphologically
distinct from the other two subspecies with little evidence of overlap of populations. The first of the two localities seen was on the upper slopes of the Etheridge Range where populations of ssp. *diversicolor* (Barker 1704) occupied tall alpine herbfield near a population of ssp. *lapidosa* (Barker 1706) in stony fjældmark. Both subspecies occupy their typical habitat, although a small outlier (Barker 1705) of the fjældmark population was found in a small stony patch apparently divergent from pure "wind-swept" fjældmark by the presence of a diverse range of prostrate plants. Otherwise in the broad grassy stony ecotone between neither subspecies was seen to occur. No morphologically intermediate plants were observed.

The second population of ssp. *lapidosa* (Barker 1710) was found in a small area of a fjældmark-like community (see ssp. *lapidosa*: Ecology) on top of a platform jutting out from the valley floor into a channel cut out by a stream (fig. 60A). The locality is distinctive in that ssp. *lapidosa*, ssp. *glacialis* and ssp. *diversicolor* all occur within 1m of each other. The flat areas of sediment just above the level of the stream a little over 1m below the top of the platform are occupied by a short turf containing a profusion of plants of ssp. *glacialis* (Barker 1712). The steep sides of the platform are covered by tall alpine herbfield in which many plants of ssp. *diversicolor* occur (Barker 1711); these are part of the populations of the subspecies which abound in the extensive surrounding areas of tall alpine herbfield (Barker 1713). Unlike the situation at the first locality the boundary between the tall alpine herbfield and fjældmark-like vegetation is very sharp. No plants intermediate between ssp. *lapidosa* and either of the other subspecies were observed. In fact, on a smaller platform a few metres away which differs from the other by its almost complete absence of plants, two plants (Barker 1712A) in a somewhat depauperate condition, but otherwise typical of ssp. *glacialis*, were discovered near a single plant clearly of ssp. *lapidosa* (unfortunately mixed with the specimens from the other platform under Barker 1710). This indicates that the differences between these two subspecies are almost certainly genetically based.

On the basis of the above observations there must clearly be some barriers to interbreeding between ssp. *lapidosa*, and ssp. *diversicolor* and ssp. *glacialis*. One such barrier may be the much earlier flowering period of ssp. *lapidosa* relative to the other two subspecies; this was seen in both localities (see also Costin et al. 1979) and appears to be associated with the comparatively more ephemeral snow cover of fjældmark (Mr D.J. Wimbush, pers. comm. 1972). Genetic barriers to hybridization may also exist. In the first locality, where there was an almost absolute difference in flowering time between ssp. *lapidosa* and ssp. *diversicolor*, a broad ecotone between their respective habitats bore no plants of *Euphrasia*. In the second locality, where many plants of ssp. *lapidosa* still bore their last flowers while many of the plants of the other two subspecies were in full flower, such an ecotone is absent. There is no evidence of hybridization. Study of a locality with both an ecotonal situation and a sufficient overlap in flowering time would be useful in assessing the existence of genetic barriers to interbreeding between ssp. *lapidosa* and the other subspecies. However, it is difficult to conceive that the subspecies at the first locality studied had never overlapped significantly in flowering time.

2. Ssp. *diversicolor*-ssp. *glacialis*. The differences between ssp. *diversicolor* and ssp. *glacialis* of the Kosciusko region of southern New South Wales break down in ecotones between their respective habitats of tall alpine herbfield and the damp expanses of turf beside the streams. The graph (fig. 61) portrays the morphological intergradation between the two subspecies in a narrow ecotone between the habitats. In this particular locality (fig. 60B) both the populations of ssp. *glacialis* in the streamside turf (Barker 1685) and those of ssp. *diversicolor* in the tall alpine herbfield on the
two communities on the steep bank of a stream (Barker 1687, 1688).

broad valley floor (rear) bearing ssp. diversicolor (Barker 1711, 1713), the subspecies occurring within a few jutting into a channel cut out by a stream (Barker 1710), with a short turf bearing ssp. glacialis at stream level (Barker 1686) and ssp. glacialis in short turf at stream level (Barker 1685) intergrade along a narrow ecotone between the two communities on the steep bank of a stream (Barker 1687, 1688).

Fig. 60. Locations of sympatric interactions between subspecies of *E. collina*, in alpine regions surrounding Mt Kosciusko, New South Wales. A, valley location with stony fjaeldmark bearing ssp. *lapidosa* on a platform jutting into a channel cut out by a stream (Barker 1710), with a short turf bearing ssp. *glacialis* at stream level (Barker 1712: foreground and to left of platform), and with tall alpine herbfield on the sides of the platform and broad valley floor (rear) bearing ssp. *dversicolor* (Barker 1711, 1713), the subspecies occurring within a few metres of each other; B, location where ssp. *dversicolor* in tall alpine herbfield on the valley slopes (Barker 1684, 1686) and ssp. *glacialis* in short turf at stream level (Barker 1685) intergrade along a narrow ecotone between the two communities on the steep bank of a stream (Barker 1687, 1688).
surrounding slopes (Barker 1686) and higher up (Barker 1684) flower simultaneously. The intermediate plants on the steep sides of the channels cut out by the streams (Barker 1687, 1688) flower later, but with some overlap in flowering period with the populations of the two subspecies.

On much broader ecotones between the two habitats on the wide alpine valleys where the slope into the streams is very gradual, a transition from plants in full flower in tall alpine herbfield to plants mainly in bud in short turf was observed. Collections from such an area had to be divided somewhat artificially. The limits of the turf were reasonably clear and the specimens collected from there (Barker 1708) were found to be typical of ssp. glacialis. However the limits of the ecotope into the tall alpine herbfield were obscure and collections clearly from both were combined under Barker 1709. Between the tall alpine herbfield populations (Barker 1713) and streamside turf populations (Barker 1712) on the steep sides of the platform bearing ssp. lapidosa (mentioned on p. 164) occur some plants intermediate between ssp. glacialis and ssp. diversicolor and others clearly typical of the latter; all were collected under Barker 1711 as in the continuous intergradation it was again impossible to divide the specimens. Here also there were no clearcut difference in flowering time by which to divide the plants artificially. This variability in relative flowering times of the plants of the two subspecies and those on the connecting ecotope is apparently caused by the difference in the rate of thaw on areas with different slopes and exposures, with snow lying longer in spring on the steeper banks of the streams (Mr D.J. Wimbush, pers. comm. 1972).

The characters distinguishing the subspecies are clearly genetically based. For example plants of Barker 1711, including some definitely of ssp. diversicolor, and plants of ssp. glacialis (Barker 1712) were found next to each other in sphagnum. If the morphological distinctions between the subspecies are genetically based, strong selection pressure must be acting to maintain their morphological and ecotypic differences in the face of apparent facility of interbreeding between them.

An attempt has been made to determine the nature of the intergradation between ssp. diversicolor and ssp. glacialis by testing the degree of sterility of pollen from the anthers of all plants of the collections Barker 1685-1688 used in figure 61 (PS54-71, 337-354). In both the subspecies and the intergradation there are a small proportion of individuals with varying degrees of high pollen sterility. Higher sterility in the intermediates could indicate a hybrid swarm, but their range of sterility values is evidently no different from the two subspecies. There are similarly sporadic instances of plants with rather high degrees of pollen sterility (PS72-78) apparently unrelated to the morphological transition between the tall alpine herbfield and sphagnum populations of ssp. diversicolor in the Spencers Creek area (see ssp. diversicolor; note 3). Accordingly this incidence of abnormal levels of pollen sterility in populations of ssp. diversicolor, ssp. glacialis and their ecotonal intermediates may be caused by factors, such as adverse environmental influence and genetic or chromosomal irregularities, which may in this case be unrelated to hybridism between existing sympatric subspecies.

Specimens intermediate between ssp. diversicolor and ssp. glacialis


Fig. 61. Morphological intergradation between a population of E. collina ssp. diversicolor in tall alpine herbfield and a neighbouring population of ssp. glacialis in short streamside turf along an ecotope between the two communities, near the summit of Mt Kosciusko, New South Wales. (Each point represents a single individual).
### Explanation of symbols

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<thead>
<tr>
<th>Location of plant</th>
<th>Number of hairs on anther backs</th>
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<tr>
<td>![Short streamside turf](Barker 1685)</td>
<td>![Short streamside turf](Barker 1685)</td>
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<td>![Tall alpine herbfield](Barker 1684, 1686)</td>
<td>![Tall alpine herbfield](Barker 1684, 1686)</td>
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<td>![Ecotone](Barker 1687, 1688)</td>
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<tr>
<th>Number of teeth on uppermost leaves</th>
<th>Length of hairs on anther backs (mm)</th>
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<th>Corolla colour (from dried material)</th>
<th>Length of hairs on anther backs (mm)</th>
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<th>Length of anterior anthers (mm)</th>
<th>Indumentum on capsule apex</th>
</tr>
</thead>
<tbody>
<tr>
<td>![1.79](anterior anthers)</td>
<td>![1.79](anterior anthers)</td>
</tr>
<tr>
<td>![1.8-2.19](anterior anthers)</td>
<td>![1.8-2.19](anterior anthers)</td>
</tr>
<tr>
<td>![2.2-](anterior anthers)</td>
<td>![2.2-](anterior anthers)</td>
</tr>
</tbody>
</table>

| ![glabrous](indumentum)               | ![glabrous](indumentum)             |
| ![1/2 setae](indumentum)              | ![1/2 setae](indumentum)            |
| ![mod. densely to densely setose](indumentum) | ![mod. densely to densely setose](indumentum) |

<table>
<thead>
<tr>
<th>% pollen functional in appearance</th>
<th></th>
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<tbody>
<tr>
<td><img src="pollen" alt="90-100%" /></td>
<td><img src="pollen" alt="90-100%" /></td>
</tr>
<tr>
<td><img src="pollen" alt="70-89%" /></td>
<td><img src="pollen" alt="70-89%" /></td>
</tr>
<tr>
<td><img src="pollen" alt="50-69%" /></td>
<td><img src="pollen" alt="50-69%" /></td>
</tr>
<tr>
<td><img src="pollen" alt="30-49%" /></td>
<td><img src="pollen" alt="30-49%" /></td>
</tr>
<tr>
<td><img src="pollen" alt="0-29%" /></td>
<td><img src="pollen" alt="0-29%" /></td>
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</table>

FIG. 61
3. The ssp. *paludosa*-ssp. *speciosa*-ssp. *diversicolor* complex. These three subspecies are the clearly distinguishable, most extreme and most widespread variants of a complex of *E. collina* encompassing the majority of populations in the highlands of the south-east of Australia. Ssp. *glacialis* and ssp. *lapidosa* also occur in this region, but they are restricted to very localized habitats.

At this stage four variants, which cover the majority of records of the forms intermediate between ssp. *paludosa*, ssp. *speciosa* and ssp. *diversicolor*, can be recognized. Each has a different geographical (figs 54, 55) and ecological range and appears morphologically distinct in its own right (table 9). Two of these variants occur in the eastern highlands of Victoria, one in the Mt Wellington region, the other, of which population samples have not been studied, on the summit of Mt Howitt. The relationships of these glandular variants to ssp. *paludosa*, which in this region lacks the subsessile glands observed in other subalpine situations are discussed under ssp. *paludosa* (note 2). Another apparently restricted variant allied to ssp. *diversicolor* (q.v.: note) is found in the subalpine areas on The Cobberas in eastern Victoria. The fourth variant has a range of distribution similar to its close relative ssp. *speciosa*; it is confined to the montane and coastal areas of southern and central New South Wales. It is discussed under note 1 of that subspecies.

Ssp. *diversicolor* and its closely related variant from nearby Mt Cobberas are somewhat separated from the rest by the large seeds and large anthers and the consistent presence of a yellow blotch on the lower corolla lip. The other three variants and ssp. *paludosa* and ssp. *speciosa* form a series of very closely related races, each largely distinguished from its closest allies by difference in the frequency of character states in populations rather than absolute or substantially different ranges of variation in characters (table 9).

Only a few of the instances of sympatry between variants in the complex have been studied closely. Ssp. *paludosa* and the variant allied to ssp. *diversicolor* occur on The Cobberas in subalpine conditions as distinct populations with no intergradation. The important case of ssp. *paludosa* and typical ssp. *diversicolor* in the Snowy Mountains to the north is discussed in the next section. The possible types of interaction between ssp. *speciosa*, its allied variant and ssp. *paludosa* in lowland and montane New South Wales are dealt with under ssp. *speciosa* (note 1), while those between ssp. *paludosa* and its allied variants in the eastern highlands of Victoria are discussed in ssp. *paludosa* (note 2).

In this highly polymorphic complex with a number of ecogeographically defined variants, it is clear that maintenance of a taxonomic classification is highly desirable. The clearcut distinction particularly in anther and seed characters satisfactorily separates ssp. *diversicolor* and its neighbouring Cobberas variant. However, the proposed distinction of the remainder of the complex into two subspecies is a tentative solution pending essential study of population variability throughout the complex. Unless hybridization has a significant role, the most natural taxonomic system reflecting the low degree of distinction of the taxa may well involve the union of ssp. *paludosa* and ssp. *speciosa* into one subspecies with several varieties.

4. Sympatric interaction of ssp. *paludosa* and ssp. *diversicolor*. Although ssp. *paludosa* and ssp. *diversicolor* are geographically sympatric throughout the Snowy Mountains of southern New South Wales, they occupy different habitats and only rarely do the populations of the two come into close contact with each other. Ssp. *paludosa* extends only as high as the subalpine zone where it is particularly common. Ssp. *diversicolor* is most plentiful in the alpine regions, but extends into the subalpine zone where it is almost entirely confined to small populations on the surrounds of sphagnum bogs.

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</thead>
<tbody>
<tr>
<td>Glandular indumentum</td>
<td>always present</td>
<td>always present</td>
<td>absent, or frequent in many subalpine populations</td>
<td>some plants present, some lacking</td>
<td>always present</td>
<td>always present</td>
</tr>
<tr>
<td>Length on outer surface of calyx (mm)</td>
<td>0.1-0.2 (0.3) (0.05)</td>
<td>0.1-0.2 (0.3) (0.05)</td>
<td>0.02-0.05 (subsessile)</td>
<td>0.05-0.1</td>
<td>0.1 (0.15)</td>
<td>(0.05) 0.1-0.2 (0.4)</td>
</tr>
<tr>
<td>Extent on plant (if present)</td>
<td>usually all over, rarely absent on lower parts</td>
<td>usually in upper parts, often in lower parts</td>
<td>usually in upper parts, often in lower parts, sometimes only in lower parts</td>
<td>usually all over</td>
<td>always all over</td>
<td>usually all over, sometimes only in lower parts</td>
</tr>
<tr>
<td>Yellow blotch on mouth of corolla</td>
<td>present or absent, sometimes varying in populations</td>
<td>present or absent, sometimes varying in populations</td>
<td>present or absent, sometimes varying in populations</td>
<td>?</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Anthers (mm)</td>
<td>(1.3) 1.4-1.9 (2.2)</td>
<td>(1.3) 1.4-1.8 (2.6)</td>
<td>(1.3) 1.6-1.9 (2.1)</td>
<td>(1.2) 1.5-1.8 (2.2)</td>
<td>c. 1.5-1.8</td>
<td>(1.7) 1.8-2.2 (2.5)</td>
</tr>
<tr>
<td>Length of rearmost awns (mm)</td>
<td>(0.15) 0.2-0.3 (0.4)</td>
<td>(0.15) 0.2-0.3 (0.4)</td>
<td>(0.15) 0.2-0.3 (0.4)</td>
<td>0.2-0.4</td>
<td>c. 0.4(0.5)</td>
<td>0.3-0.5</td>
</tr>
<tr>
<td>Capsule setosity</td>
<td>always setose</td>
<td>sometimes setose, sometimes glabrous</td>
<td>sometimes setose, sometimes glabrous</td>
<td>sometimes setose, sometimes glabrous</td>
<td>?</td>
<td>always setose</td>
</tr>
<tr>
<td>Extent if present</td>
<td>distal $\frac{1}{2}$ - $\frac{3}{4}$</td>
<td>apex - distal $\frac{1}{2}$</td>
<td>apex only</td>
<td>apex - distal $\frac{1}{4}$</td>
<td>distal $\frac{1}{2}$</td>
<td>apex - distal $\frac{1}{4}$</td>
</tr>
<tr>
<td>Seed (mm)</td>
<td>0.4-0.9 (1.0)</td>
<td>c. 0.6-0.9</td>
<td>(0.50) 0.7-1.3 (1.5)</td>
<td>0.6-1.2</td>
<td>c. 0.7-1.0</td>
<td>(0.91) 1.2-1.7 (1.8)</td>
</tr>
</tbody>
</table>

In the subalpine zone no intergradation was observed in the several cases of contact between the two subspecies. The detection of plants of the two subspecies was greatly aided by the yellow blotch on the lower corolla lip being always absent from ssp. *paludosa* and consistently present, although rarely faint and detectable only in mature buds, in ssp. *diversicolor*, as well as by the usual earlier flowering of ssp. *paludosa*.

In the Toolong Range (Barker 1666, 1667, 1677), at Perisher Valley (Barker 1694, 1695), at Long Plain (Barker 1662, 1663) and at The Smiggin Holes above Pipers Creek (Barker 1690-1693) ssp. *paludosa* was widespread in grassy expanses in heath or tussock grassland, while ssp. *diversicolor* was restricted nearby to the margins of sphagnum bogs, creeks or moist hollows. In all these cases the populations of ssp. *paludosa* had almost completed flowering while those of ssp. *diversicolor* were still in flower. These differences in flowering time may be caused by the delayed spring growth of plants in moister areas (see also ssp. *diemenica*: note 1) relative to those on better-drained ground. Nevertheless, there must have been some overlap in flowering time. Clearly, whatever the extent to which phenological differences are involved, there must be some other means by which the genetic integrity of the two subspecies is retained when in such close proximity.

Subalpine populations of ssp. *paludosa* were seen to approach alpine populations of ssp. *diversicolor* in only two localities. At the Spencers Creek bridge on the Mt Kosciusko summit road ssp. *paludosa* occupies a region of low subalpine heath in the valley (Barker 1700), while ssp. *diversicolor* occurs on the slopes bearing a community allied to tall alpine herbfield (Barker 1703) or in sphagnum (Barker 1701) or its
surrounds (Barker 1702) on the edge of the water. The populations are apparently over 100m apart, except for an outlying plant of ssp. diversicolor (Barker 1699) with almost entirely functional pollen (PS335) which was found in herbfield close to the population of ssp. paludosa. No intergradation was observed.

On Mt Jagungal, however, a hybrid swarm occurs where ssp. paludosa approaches alpine stands of ssp. diversicolor. In the tall alpine herbfield on top of the southern spur of the mountain occurs typical ssp. diversicolor (Barker 1665, 1668 p.p.), glandular and with yellow-blotched corollas. On the slopes leading down from the summit and also on the upper slopes of the spur in what is either pure subalpine tussock grassland or an ecotone into the tall alpine herbfield occurs a large number of plants with (Barker 1667, 1671) and without (Barker 1666, 1670) yellow-blotched corollas. This was the only locality seen in the entire Snowy Mountains region where plants of the two corolla colorations grew side by side. Examination of these plants has shown that there is considerable variation in the characters distinguishing the two subspecies, namely the leaf shape, the length of the glandular indumentum (all plants resembling ssp. paludosa bear subsessile glands), the length of the lower corolla lip, the incidence of the yellow corolla blotch, the size of the anthers and the rearmost pair of awns, the shape and indumentum of the capsule, and the seed size. Thirty plants, some resembling either subspecies, others the intermediates, were selected for pollen sterility tests (PS305-334) and measurement of a selection of the above characters. The length of the rearmost anther awns was often taken from the final bud of an inflorescence, but it was found that in plants of each subspecies the range in size was still similar to that found in lower flowers when describing the subspecies. However, other characters distinguishing the two subspecies had to be measured from mature fruiting material or the lowest corollas of the inflorescence and these stages were not available in every plant.

The graph (fig. 62) clearly shows that the intergradation is a hybrid swarm between the two subspecies. This hybrid swarm gives an insight into the nature of the differences between the two subspecies. Firstly, since both subspecies retained their morphological distinctions where growing side by side in apparently the same conditions, it seems certain that the differences between them are genetically based. Furthermore, since this breakdown in morphological distinctions occurs apparently outside the typical habitats of either subspecies and because they are distinct ecotypes elsewhere, it appears that strong selection pressure related to habitat differences is acting on the genes determining the morphological differences between the two subspecies.

Specimens examined of ssp. paludosa x ssp. diversicolor
NEW SOUTH WALES (Kosciusko Nat. Park. SE end of Toolong Range): Barker 1666(p.p.), 1667, 22.i.1972. On top of the southern ridge of Mt Jagungal, c. 50m below and c. ½km S of summit. AD(p.p.).—Barker 1668(p.p.), 22.i.1972. As for Barker 1666, 1667, but c. 20m away. AD.—Barker 1670(p.p.), 1671, 22.i.1972. On top of southern ridge of Mt Jagungal, c. ½km S of summit. AD.—Barker 1672, 22.i.1972. On top of southern ridge of Mt Jagungal, c. 1½km S of summit. AD.

5. Ssp. collina-ssp. diemenica. On the upper slopes of Mt Wellington, Tasmania, along the summit road between The Springs at about 700m and the tree-line at about 1100m occur populations of plants belonging to ssp. collina or ssp. diemenica or a transition between them. Ssp. diemenica is predominantly an alpine inhabitant in the region but a population (Barker 1141), which is typical of ssp. diemenica by its calyx indumentum of subsessile glands, broad upper leaves on the main inflorescence-bearing axes (fig. 7) and decumbent branches simple above ground level, occurs in regenerating wet sclerophyll forest a little above The Springs. Ssp. collina in its typical
form does not seem to occur in the region; in the lower montane regions near Mt Wellington it is characterized by a non-glandular indumentum, narrow upper leaves on the main inflorescence-bearing axes (fig. 6: Barker 953, 955) and its stem and main inflorescence-bearing branches branched high above ground level. Populations intermediate between ssp. collina and ssp. diemenica in these characters occur in sclerophyll forest or woodland between The Springs and the tree-line (Barker 978, 1138, 1146, 1147, 1149). They resemble ssp. collina by their narrow uppermost leaves (fig. 7: Barker 1138, 1146, 1147) and a usually non-glandular indumentum, although

![Graph](https://via.placeholder.com/150)

Fig. 62. Variation in morphology and pollen sterility in a hybrid swarm between ssp. paludosa and ssp. diversicolor of E. collina, on the summit of Mt Jagungal, New South Wales. (Each point represents a single individual).
rarely (Barker 1149A) sparse glandular hairs may line the bracts and calyx teeth. These populations vary, however, in the extent of branching above ground level; often more or less decumbently branched plants, simple above ground level, are present.

It is not known whether plants in this area are truly part of an intergradation between the two subspecies, or whether the integrity of the two subspecies is maintained in the area, with the apparent breakdown in habit characteristics being caused by environmental factors or independent genetic variation. Pollen sterility tests on the intergrading populations (PS209-216, 336) and ssp. diemenica in both the alpine zone (PS217-225) and in the population (Barker 1141) much lower down the mountain (PS205-208) show little evidence for morphological intergradation caused by hybridization. Occasional individuals producing a high percentage of sterile pollen occur in both the pure populations of ssp. diemenica in the alpine zone and plants from the intermediate zone, but the majority of plants tested, including the narrow-leaved slightly glandular plant (Barker 1149A: PS336) mentioned above, show normal levels of pollen of functional appearance.

Specimens intermediate between ssp. collina and ssp. diemenica


6. Ssp. collina and ssp. trichocalycina. Both subspecies occur in the Grampians of western Victoria where they are respectively distinguished solely on their non-glandular and shortly glandular indumentum. Apart from the occasional presence of a yellow corolla blotch in ssp. collina alone, there are no other diagnostic characters. From samples and observations of nine populations of E. collina in the Grampians, the two subspecies are likely to be genetically independent and occupy distinct populations with similar ecological preferences (Barker 1974). There is no evidence of mixing of the two taxa in the many other collections of the species from the Grampians. However, further study is required of the morphological, genetic and ecological separation of the two subspecies throughout their common range to determine whether they are truly intersterile and identical in their ecological preferences.

7. Ssp. diemenica-ssp. gunnii. A specimen from the foot of the Great Western Tiers, northern Tasmania (Phillips s.n., 6.xii.1965. 5 miles from Poatina towards Miena. CBG015457) is intermediate between the two subspecies which occur in the region, namely ssp. diemenica of the alpine and subalpine zones and ssp. gunnii, which occupies the montane and lowland zones. The plant is allied to both subspecies by its complete cover of glandular hairs, which are 0.1-0.2mm long on the calyx and 0.3mm long on the axes at the base of the plant, its upper leaves with 0-1 teeth on each side and with the sessile glands confined to the margins, its shallowly emarginate lower corolla lobes, which are externally hairy all over, and its capsules with a densely setose
apex. It approaches ssp. *diemenica* and differs from ssp. *gunnii* by its many-flowered inflorescences (with c. 20-35 flowers), large flowers (over 14mm long) and large seeds (1.3-1.7mm) long; in contrast it resembles ssp. *gunnii* and diverges from ssp. *diemenica* by the narrowness of its leaves and the presence of shoots above ground level, but confined to the lower third of the main branches.

It is probable that rather than being a unique extreme of either of the two subspecies, this plant comes from an intergradation between nearby alpine and subalpine populations of ssp. *diemenica* and montane and lowland stands of ssp. *gunnii*.

8. Ssp. *paludosa*-ssp. *muelleri*. Two collections (Muir 2692, 3108) from open grassy areas in light sclerophyll forest or snowgum woodland near Mt Wellington in the eastern highlands of Victoria may come from an intergradation between ssp. *paludosa*, which is prevalent in the region, and ssp. *muelleri*, which has not been recorded in the area and is little-recorded in south-eastern Victoria. The specimens, which probably come from four plants in all, resemble both subspecies by the upper leaves with 2-3 teeth along the upper 1/2-3/4 of each margin, and obtuse to emarginate corolla lobes externally hairy all over. However, these plants diverge from the majority of members of both subspecies by the branching extending above ground level over the lower 1/3-1/2 of the main axes. The indumentum on the external surface of the calyx varies between the characteristics of both subspecies. That of one plant is almost absent and is therefore typical of ssp. *paludosa*, that of another two is densely scaberulous, typical of ssp. *muelleri*, while that of the fourth is very sparsely scaberulous. A study in the area is required to determine whether these collections are extreme variants of ssp. *paludosa* or are truly an intergradation between the two subspecies.

The three inflorescence-bearing branches which make up the collection Robertson NSW10938 from western Victoria point to a further example of intergradation between ssp. *paludosa* and ssp. *muelleri*. The branches have clearly come from the same population as they are almost identical in the stage of flowering, the shape of the apical bud cluster, and characters of the leaves in analogous positions on the branches, such as their size, extent and number of teeth and distribution of the sessile gland patches. Two of the branches resemble ssp. *paludosa* by their externally glabrous calyces, while the calyces of the third bear a dense, moderately long, weak eglandular indumentum. A search of the remaining large areas of natural vegetation in the Casterton-Wando Vale region may reveal populations which provide a basis for an understanding of the relationships of these subspecies. Neither, however, has been collected in the region for many years.

Specimens intermediate between ssp. *paludosa* and ssp. *muelleri*


**Key to the subspecies of E. collina**

1a. External surface of calyx glabrous (except for a small area below each cleft).

2a. Uppermost leaves of main inflorescence-bearing axes with 4-6 pairs of teeth. Base of plant glandular. [Branching from ground level; lower corolla lobes obtuse to truncate, externally pilose.]

2b. Uppermost leaves of main inflorescence-bearing axes with (0)1-3(6) pairs of teeth. Base of plant usually non-glandular, rarely (in ssp. *paludosa* and ssp. *diemenica*) glandular.

3a. Lowest node of main inflorescence with corollas 6.5-9(10)mm long along upper side, and capsules 4.5-7mm long. c. ssp. 'Northwest Tasmania' (p.189)

3b. Lowest node of main inflorescence with corollas (7.3)8.5-13.5mm long or longer along upper side, and capsules (6)7-9.5mm long or more.
Lower corolla lobes externally glabrous, [usually emarginate or deeply so, rarely shallowly emarginate, with lower lip (5.2)-6-10.5(13) mm long. Uppermost leaves of main axis with (0)-1-2(4) pairs of teeth confined to distal (0.15)-0.5(0.6) of leaf. Rearmost pair of anther awns (0.1)-0.2-0.5 mm long. Seeds (0.5)-0.6-0.9(1.0) mm long] 

Lower corolla lobes externally usually pilose all over or along midline, rarely pilose at base only (best seen in mature buds).

5a. Main inflorescence-bearing axes bearing branches or young shoots (sometimes very small) well above ground level, i.e. simple below inflorescence for (0.05)-0.1-0.5(0.8) of the height of the inflorescence above ground level.

6a. Uppermost leaves of main axes (1.5)-2.0-4.2(4.4) mm broad, with (0)-1(2) pairs of teeth confined to distal (0.15)-0.35(0.45) of leaf. Lower corolla lobes usually emarginate to truncate, rarely obtuse. Rearmost pair of anther awns (0.2)-0.3-0.5(0.6) mm long. 

6b. Uppermost leaves of main axes (2.4)-3.4-7.0(8.0) mm broad, with 1-3(6) pairs of teeth confined to distal (0.2)-3.0-6.5(0.85) of leaf. Lower corolla lobes usually obtuse or truncate, sometimes shallowly emarginate, rarely emarginate. Rearmost pair of anther awns (0.15)-0.2-0.3(0.4) mm long. 

5b. Main inflorescence-bearing branches or young shoots (sometimes very small) near ground level, i.e. simple below inflorescence for 0.8-1.0 of the height of the inflorescence above ground level.

7a. Uppermost leaves of main inflorescence-bearing axes with lateral extensions of the marginal rows of sessile glands on the lower surface usually short, rarely extended past the distal side of the base of the nearest proximal tooth (if one is present); teeth confined to distal (0.1)-0.2-0.45(0.55) of leaf; apical tooth (0.6)-0.8-1.8(2.5) mm long. Lower corolla lip (4.5)-5-12(14) mm long, with lobes usually emarginate or deeply so, sometimes shallowly emarginate, rarely truncate. Rearmost pair of anther awns (0.2)-0.3-0.5(0.6) mm long. 

7b. Uppermost leaves of main inflorescence-bearing axes with lateral extensions of the marginal rows of sessile glands on the lower surface usually long, often reaching past distal side of the base of the next proximal tooth (if one is present), rarely short; teeth confined to distal (0.2)-3.0-6.5(0.85) of leaf; apical tooth (1.1)-3.2-8.4(3.3) mm long. Lower corolla lip (4)-4.5-7 (8.5) mm long, with lobes usually obtuse or truncate, sometimes shallowly emarginate, rarely emarginate. Rearmost pair of anther awns (0.15)-0.2-0.3(0.4) mm long. 

lb. External surface of calyx hairy.

8a. Bracts and external surface of calyx covered by eglandular hairs. [Main inflorescence-bearing axes with shoots or branches usually forming near ground level, rarely higher up.]

8b. Bracts and external surface of calyx with glandular hairs, sometimes mixed with eglandular hairs.

9a. Main inflorescence-bearing axes bearing branches or shoots (which may be very short) high above ground level, i.e. simple below inflorescence for (0.05)-0.1-0.75 (0.85) of the height of the inflorescence above ground level. [Yellow blotch usually absent from lower corolla lip, rarely (in some populations of ssp. osbornii: q.v.: note 1) present.]

10a. Uppermost leaves of main inflorescence-bearing axis with (1)-3-6(8) pairs of teeth distributed over distal (0.35)-0.55-1.0 of leaf. Seeds 0.4-0.9(1.0) mm long. [Main inflorescences bearing (20)-24-56(60) flowers. Glandular hairs on calyx 0.1-0.25(0.3) mm long. Rearmost pair of anther awns (0.1)-0.2-0.4 mm long. Capsules with distal (1.9)-2(2.9) mm long and longest tooth (0.4)-0.9-1.7(2.9) mm long.]

m. ssp. osbornii (p. 218)
10b. Uppermost leaves of main inflorescence-bearing axes with (0)1-2(4) pairs of teeth distributed over distal (0.15)0.2-0.65(0.7) of leaf. Seeds (0.5)0.7-1.1 (1.5)mm long.

11a. Glandular hairs on calyx 0.05-0.1(0.2)mm long, those at base of plant, if present, up to 0.1mm long. Capsules glabrous or with few to moderately dense setae at apex.

12a. Main inflorescence with (14)20-40(48) flowers. Rearmost anther awns (0.1)0.2-0.4(0.5)mm long. Uppermost leaves of main inflorescence-bearing axis with apical tooth (1.2)1.7-3.0(3.4)mm long, with longest tooth 0.8-2.0(2.4)mm long. Glandular indumentum rarely at base of plant. e. ssp. trichocalycina (p. 196)

12b. Main inflorescences with fewer (c. 20) flowers. Rearmost anther awns c. 0.1-0.2mm long. Uppermost leaves of main inflorescence-bearing axis with apical tooth (0.8)1.0-1.9mm long, with longest tooth 0.5-1.0(1.2)mm long. Glandular indumentum often at base of plant. i. ssp. 'tasmanica' (p. 198)

11b. Glandular hairs on calyx 0.1-0.3mm long or longer, those at base of plant, if present, 0.1-0.2(0.3)mm long. Capsules usually with dense setae over distal (1/2)1/4-V8 or less, sometimes (ssp. gunnii) with few setae at apex or glabrous.

13a. Uppermost leaves of main inflorescence-bearing axis (1.9)2.1-3.2(4.2)mm broad, with 1(2) pairs of teeth. Main inflorescences with (10)12-24(28) flowers. Rearmost pair of anther awns (0.1)0.2-0.3mm long. g. ssp. gunnii (p. 199)

13b. Uppermost leaves of main inflorescence-bearing axes (2.5)2.9-6.0(7.4)mm broad, with 1-2(4) pairs of teeth. Main inflorescences with (16)18-40(46) flowers. Rearmost pair of anther awns (0.1)0.15(0.3)mm long. h. ssp. deflexifolia (p. 202)

9b. Main inflorescence-bearing axes bearing branches or shoots (which may be very short) near ground level, simple above or sometimes (in ssp. speciosa) branched some way up, i.e. simple below inflorescence for (0.5)0.7-1.0 of the height of the inflorescence above ground level.

14a. Glandular indumentum on external surface of calyx up to 0.1(0.15)mm.

15a. Glands on external surface of calyx sessile, up to 0.05mm long. i. ssp. paludosa (p. 204)

15b. Glands on external surface of calyx usually clearly stalked, 0.05-0.1(0.15)mm long.

16a. Uppermost leaves of main inflorescence-bearing axes with (0)1-2(4) pairs of teeth distributed over distal (0.1)0.2-0.45(0.55) of leaf. Lower corolla lobes usually emarginate or deeply so, sometimes shallowly emarginate, rarely truncate or praemorsely so. Seeds (0.9)1.1-1.9mm long. b. ssp. diemenica (p. 181)

16b. Uppermost leaves of main inflorescence-bearing axes with 2-4 (6) pairs of teeth distributed over distal (0.35)0.5-0.9(0.95) of leaf. Lower corolla lobes usually obtuse, sometimes truncate, rarely emarginate. Seeds 0.6-1.2mm long. [Mt Howitt-Mt Wellington region of Victoria.]. i. ssp. paludosa (variants) (p. 207)

14b. Glandular indumentum on external surface of calyx (0.05)0.1-0.2mm long or (in some taxa) longer.

17a. Uppermost leaves of main inflorescence-bearing axes with (0)1-2(4) pairs of teeth.

18a. Main inflorescences with (6)12-26(30) flowers. Main inflorescence-bearing axes (5.5)7-17(25)cm high to base of inflorescence; the longest internode (1.3)2.5-5(6) times the length of upper leaves. Uppermost leaves obovate or subspathulate to elliptic or oblong; lateral extensions of the marginal rows of sessile glands on lower surface usually short, rarely long and extended past the distal side of the base of the next proximal tooth (if one is present); apical tooth (0.6)0.8-1.8(2.5)mm long, (1.0)1.3-2.5(3.7)mm broad. Capsules usually sparsely to densely setose, rarely glabrous. b. ssp. diemenica (p. 181)
18b. Main inflorescences with c. 6-12 flowers. Main inflorescence-bearing axes (2.5)3.5-9.5(13) cm high to base of inflorescence; the longest internode (0.9)1.7-3(3.5) times the length of upper leaves. Uppermost leaves obovate to ovate, often broadly so; lateral extensions of the marginal rows of sessile glands on lower surface usually long, often extended past the distal side of the base of the next proximal tooth (if one is present), rarely short; apical tooth (0.9)1.2-2.5(3.5) mm long, (1.6)2.0-3.2(3.8) mm broad. Capsules subglabrous. .......... p. ssp. glacialis (p. 233)

17b. Uppermost leaves of main inflorescence-bearing axes with (1)2-4(8) pairs of teeth.

19a. The number of upper internodes on main inflorescence-bearing axes as long as or longer than upper leaves 0-3(4), the longest internode (0.3)0.5-1.8(2.1) times the length of upper leaves. [Glandular hairs on calyx (0.1)0.2-0.5 mm long. Yellow blotch always present on lower corolla lip. Rearmost pair of anther awns (0.25)0.3-0.5(0.6) mm long. Seeds (0.8)0.9-1.2(1.4) mm long.]. .......... o. ssp. lapidosa (p. 230)

19b. The number of upper internodes on main inflorescence-bearing axes as long as or longer than upper leaves (2)4-8(13), the longest internode (1.8)2.2-4.0 or more times the length of upper leaves.

20a. Seeds (0.9)1.1-1.7(1.9) mm long. Anthers (1.7)1.8-2.6(3.0) mm long, with rearmost pair of awns (0.25)0.3-0.5(0.6) mm long. Yellow blotch on lower corolla lip always present. .......... n. ssp. diversicolor (p. 223)

20b. Seeds 0.4-0.9(1.0) mm long. Anthers (1.3)1.4-1.9(2.2) mm long, with rearmost pair of awns (0.1)0.2-0.3(0.4) mm long. Yellow blotch on lower corolla lip ?absent. .......... l. ssp. speciosa (p. 215)

11a. ssp. collina


_E. multicaulis_ Benth.: Wettst., Monogr. Gatt. _Euphrasia_ (1896) 249, p.p. (as to Anderson _Fl_).


Erect perennial herb or undershrub (19)25-60(80) cm tall, with many ascending or erect branches arising from single erect stem, flowering in first year, subsequently dying back to upper branches. Stem or, after first year, main inflorescence-bearing branches (14)18-50(60) cm high to base of inflorescences, simple for 0-12(32) nodes below inflorescence, i.e. for (0)0.1-0.55(0.8) of height of inflorescence above ground level; upper (2)3-7(9) internodes as long as or longer than upper leaves, the longest internode (1.0)1.5-5.0(7.5) times the length of upper leaves; axes in upper parts bearing two rows or four lines of sparse to dense, very short to moderately long eglandular hairs decurrent from between leaf bases, sometimes with sparse eglandular hairs between, in lower parts usually sparser and shorter, sometimes glabrous. Leaves: uppermost leaves of stem or main inflorescence-bearing branches (4.5)5-12(16.5) x (1.5)2.0-4.2(4.4) mm, with sessile glands confined to distal (0.4)0.55-0.85(0.9) of under-surface, otherwise glabrous, but occasionally for a few eglandular hairs on margins near base, with blade ovate-elliptic to elliptic or oblong, often narrowly so; base rounded to narrowly cuneate; teeth (0)1(2) along each margin, confined to distal (0)0.15-0.35(0.45) of leaf, bluntly or sharply acute or obtuse, the longest tooth (0.2)0.5-2.1(2.3) mm long; apical tooth (0.6)1.1-3.5(4.0) x (0.6)0.9-2.0(2.3) mm, sharply or bluntly acute or obtuse; leaves lower down glabrous. Inflorescences racemes, lower 0-2(5) nodes sometimes widely-spaced, otherwise usually dense, rarely moderately dense in bud, usually moderately dense to dense, rarely lax in flower and fruit, those of stem or main branches with (16)20-44(48) flowers; pedicels at lowest node (0.3) 0.5-7.5(8.0) mm long, shorter higher up; rachis with indumentum similar to upper part of axis but denser and somewhat longer; internodes elongating prior to anthesis such that capsules reach well below or past node above; apical bud cluster (excluding lower widely-spaced nodes) usually narrow cylindrical to narrow conical-cylindrical, rarely ovoid, initially 1.2-4.0 cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after flowers at first 4-15 or more nodes have reached anthesis. Bracts glabrous, shorter than calyx, except sometimes for those at lower 3(4) nodes, sometimes all entire, sometimes all toothed, sometimes with proximal ones toothed and distal ones entire, those at lowest nodes similar in size and shape to uppermost leaves. Calyx (3.9)5.0-6.7(7.0) mm long, externally glabrous, internally with moderately dense to dense, very short to moderately long eglandular hairs on distal part of tube and lobes. Corolla (9.0)9.5-13.5(14.5) mm long along upper side, white, or pale or deep mauve, pink, purple, lilac, violet, lavender or blue but for either a white tube and mouth or white extremities, or coloured throughout, often with yellow blotch behind lowest lobe, sometimes with smaller blotch at base of each anterior filament, sometimes with blotch faint and apparent only in bud or lacking; tube (5.9)6-9.8(10.3) mm long; hood (2.9)3.2-4.2(5.0) mm long; upper lobes usually shallowly emarginate or truncate, rarely emarginate or obtuse, with rear surface bearing very short glandular hairs, usually moderately dense to dense all over, sometimes sparse or confined to base; lower lip (3.8)4.8-9.2(11.0) mm long; lower lobes usually emarginate to truncate, rarely obtuse, externally covered by very short to short glandular hairs, often mixed with short to moderately long eglandular hairs, the indumentum usually moderately dense to dense all over, rarely sparse or confined to proximal parts. Stamens with anthers (1.5)1.6-2.3(2.4) mm long, with connectives surrounded by usually moderately dense to dense, rarely sparse, long to very long eglandular hairs, sometimes with indumentum sparser on anterior connectives; rearmost pair of awns (0.2)0.3-0.5(0.6) mm long. Capsules (6)7.5(10.5) mm long, in lateral view ovate to...
Fig. 63. *E. collina* ssp. collina. A, two plants, near Hobart, Tasmania (*Barker* 953), scale 5cm; B, inflorescences showing white corollas sometimes flushed with lilac, lacking nectar guides, near Tunnack, Tasmania (*Barker* 980), scale 1cm.

ovovate, sometimes narrowly so or somewhat deflexed, 2.0-3.0(3.6)mm broad, in median view ovate to ovate- or elliptic-acuminate, sometimes narrowly so, glabrous or with few to moderately dense, very short to moderately long setae at very apex; apex in lateral view usually obtuse to truncate, sometimes acute, sometimes obliquely so; seeds (0)14-72(88), (0.7)0.8-1.2(1.3) x (0.25)0.3-0.5(0.7)mm, ellipsoid, oblong or ovoid, sometimes broadly or obliquely so. Figs 6, 59, 63, 64.

**Typification**


2. *E. walteri* Gandoger. The specimen upon which Gandoger (1919) based the name *E. walteri* consists of a mixture of ssp. *collina* and ssp. *muelleri*. The specimens of ssp. *collina*, by their glabrous calyces and leaves with 1(2) teeth along each margin, fit the protologue perfectly and have accordingly been chosen as lectotype.

Three pieces of evidence point to the Grampians being the source of the lectotype material and the probability that the NSW specimen is an isolectotype. Firstly, the leaves have a long, narrow, acute apex and teeth resembling plants from western Victoria (see note 2). Secondly, Walter apparently made only one collection of ssp. *collina* from the “Grampians”. The date “1902” on the type specimen does not refer to
the date of collection, but possibly the year in which the specimen was sent to Gandoger (see McGillivray 1973). Thirdly, one of the branches of the NSW collection has apparently been broken from a branch on the lectotype.

A similar procedure has been used to determine the type status of the isosyntype material. Walter's only collections of ssp. muelleri come from "Upper Yarra" and "Wimmera". Only the latter collections, by their broad leaves with two pairs of teeth, resemble the syntype. The labels on the three specimens without indication of the collector are written in a hand which differs in some respects from the samples of Walter's handwriting which I have seen. Their status as isosyntypes is, therefore, more doubtful.

**Distribution (fig. 50):** *E. collina* ssp. *collina* is widespread throughout lowland eastern Tasmania, in the southern lowland regions, the western highlands and (see note 1) possibly the south-western edge of the eastern highlands of Victoria, and in the south-east corners of South Australia and New South Wales. Altitude, near sea level to 750m.

**Ecology:** The subspecies inhabits sandy to clay soils, mainly in *Eucalyptus*-dominated sclerophyll forest or woodland with or without a well-developed shrub understorey. It is also found in heathland, particularly in coastal locations, and in swamps, which constitute the sole records from South Australia and neighbouring parts of Victoria.

Flowering begins in August and is completed by mid February, although there is one record of flowering material in April (*Staer NSW10948*). Capsules are formed from September onward.

**Conservation status:** considered not at risk.

**Notes:** 1. Ssp. *collina* and ssp. *paludosa* both occur in the western part of the eastern highlands of Victoria. Elsewhere in central and western Victoria, the two subspecies seem to occupy different areas of distribution, with ssp. *collina* mainly occurring in the western highlands and coastal regions, and ssp. *paludosa* being confined to the region of the basalt plains between Warrnambool and Port Phillip and to a possibly isolated occurrence in the region of Maryborough. However, many collections from outside the Grampians (fig. 50) are only tentatively placed in ssp. *collina* despite their uppermost leaves possessing a single pair of teeth typical of the subspecies. They contain only one or two plants and some could be uncommon variants from populations of ssp. *paludosa*.

2. Within ssp. *collina* there is a geographical variation in the shape of the uppermost leaves of the stem or main inflorescence-bearing branches. The graph (fig. 64) portrays the variation in the length of the apical and marginal teeth of the uppermost leaves in different geographical areas throughout the range of the subspecies. The leaf type with longer, more acute teeth (fig. 6: Barker 1439, 1443, 1446) occurs in populations in the Grampians and nearby mountain areas. "E. collinoides" of Du Rietz (1948b) probably belongs with these (see *E. collina*: note 4). Leaves tending to the other type from south-east Tasmania with shorter, blunter teeth (fig. 6: Barker 953, 955, 968) are found along the Victorian coast extending eastwards from Anglesea into southern New South Wales. However, the whole range of variation in leaf shape is found in collections from the western plains of Victoria from the coast to north of the Grampians and in specimens from the western highlands (excluding the Grampians) and southern and western margins of the eastern highlands. Although the extreme types are apparently scattered throughout this area, within those collections containing several plants there is little variation. This variation in leaf shape is correlated with differences in the pattern of the sessile gland patches on the leaf undersurface (p. 25).
Selected and cited specimens


AUSTRALIA. WITHOUT LOCALITY (10 seen)

Geographical regions
- Grampians, Victoria
- Inland western Victoria
- Edge of Victorian Alps
- Coastal Victoria and New South Wales
- South-eastern Tasmania

Fig. 64. Variation in the lengths of the apical and longest lateral teeth of the uppermost leaves of the main inflorescence-bearing axis in *E. collina* ssp. *collina* in different geographical regions throughout its range of distribution. (Each point represents a single individual).
**Specimens with affinities to ssp. collina (see note 1)**

VICTORIA (14 seen): Anon. s.n., s.dat. Forest Creek. MEL41385(p.p.). — Anon. 151, s.dat. Creswick Diggings.


— Musgrave s.n., s.dat. Wilsons Promontory. MEL41345. — Thorn 27, 1883. Lower Loddon. MEL.

— Tisdale 10, s.dat. Walhalla. MEL. — Wawra 534, s.dat. Dandenong. MEL.

— Wawra 534, s.dat. McIvor Ranges. W71487 (syntype of E. muelleri).


*E. diemenica* Spreng., Linn. Syst. Veg. (1825) 777 (substitute name for *E. alpina* R.Br. non Lamk.)


none at all, *pedicels* at lowest node (0.7)0.8-5.5(5.8)mm long, shorter higher up; *internodes* elongating prior to anthesis and sometimes continuing after; *rachis* as for upper part of axis but sometimes with sparse glandular hairs when lacking from axis; *apical bud cluster* narrow ovoid to spherical, initially c. 1-3.5cm long, hidden by or hardly emergent from corollas of uppermost flower pair after flowers at first 1-10 nodes have reached anthesis. *Bracts* at lowest nodes like uppermost leaves in size, shape and indumentum, although glandular hairs sometimes denser or present when absent from leaves, shorter than calyx, except rarely for those at lowest node, those at higher nodes shorter than uppermost leaves, those at lowest 1-10 or more nodes toothed, distal ones entire. *Calyx* (3.2)4.5-7.5(7.7)mm long, externally glabrous except for eglandular hairs decurrent from base of clefts or bearing very sparse to dense, very short to long glandular hairs sometimes mixed with short eglandular hairs, internally on teeth and distal part of tube covered by dense short to very long straight upturned eglandular hairs. *Corolla* (7.3)8.5-14.5(15.2)mm long along upper side, white or coloured palely to deeply in blue, violet, lilac, purple, mauve or pink, with colour sometimes confined to lobes and tube, with broad white area behind lower lobes, sometimes all over, with yellow area at point of insertion of each anterior filament, with a yellow blotch on lower lip behind lobes, sometimes present and distinct from or continuous with spots at base of filaments, sometimes absent; *tube* (4.5)6-9(10)mm long; *hood* (2.6)3-6(6.5)mm long; *upper lobes* usually emarginate or shallowly so, rarely entire, with rear surface glabrous or bearing sparse to moderately dense, short to very long eglandular hairs; *lower lobes* usually emarginate or deeply so, sometimes shallowly emarginate, rarely truncate or praemorsely so, externally covered by a moderately dense to dense indumentum of short to long eglandular hairs or glandular hairs or a mixture of both, sometimes all over, sometimes along middle of lobes. *Stamens* with *anthers* (1.2)1.4-2.0(2.2)mm long, with *connectives* usually surrounded by moderately dense to dense, almost long to very long, rarely short eglandular hairs, rarely glabrous; rearmost pair of *awns* (0.2)0.3-0.5(0.6)mm long. *Capsules* 6.8-10mm long, in lateral view ovate to elliptic or oblong, sometimes broadly so, 2.4-4.0mm broad, in median view narrow ovate-caudate or elliptic-acuminate, usually covered by very few to dense, short to long setae on apex only to on distal 1/2(2/3), rarely completely glabrous; *apex* in lateral view usually obtuse to truncate, sometimes acute or obliquely so; *seeds* (7)25(69), (0.9)1.1-1.9 x 0.4-0.8(0.9)mm, obliquely ovoid, oblong or ellipsoid, sometimes broadly so. Figs 7, 48E, 65.

**Typification:** *E. alpina*R.Br. and *E. diemenica* Spreng. are nomenclatural synonyms. Unaware of the existence of duplicate material, Du Rietz (1948b) designated the BM specimen as their holotype. Despite the poor quality of the BM specimen, the lectotypification follows the recommendation of Stearn (1960) that the lectotype be the most complete specimen in BM.

Brown gave two names to this species before deciding to call it *E. alpina* in publication (Brown 1810). On the lectotype and initially in his manuscript description (based on the collection "No. 63. In summitate Montis Tabularis versus fluvium Derwent. Feb:-Mar: 1804" which clearly corresponds to the lectotype label) he called the species "*E. speciosa*", a name which he finally used for a New South Wales species. In the manuscript he crossed out "speciosa" and replaced it with the epithet "grandiflora", a name which he apparently never used in publication.

The type collection clearly belongs with the much collected populations on the summit of Mt Wellington, called Table Mountain at the time of Brown's visit (Flinders 1814, pl.6).

**Distribution** (fig. 50): *E. collina* ssp. *diemenica* is endemic to Tasmania, where it is
restricted to the subalpine and alpine zones of the isolated north-east mountains, the
Central Plateau, the south-central mountain systems of Mt Field and Mt Wellington,
and the Cradle Mountain-Hampshire Hills region which forms the northernmost
extension of the Western Mountains. There is one collection from the mid-west of the
island from Mt King William (F.A. Rodway NSW22287) at the southern end of the
Western Mountains; another comes from Port Davey in the extreme south-west (Long
HO) which is somewhat atypical of the subspecies (note 3). Forms closely allied to
ssp. diemenica but diverging from it in some characters occur in north-east and north-
west lowland and montane Tasmania (note 2). Altitude, 850-1400m; the Port Davey
specimen may have come from nearer sea level.
Ecology: In the alpine zone ssp. *diemenica* occupies open to rather dense heathland in flat areas or within scree. In the subalpine zone, where it is most commonly recorded, it occurs in grassland, dense to open areas of heath (fig. 66) or *(Carolin 1222)* “margins of beech forest”. There is one record *(Barker 1141)* from wet sclerophyll forest “in burnt area among regenerating *Eucalyptus*”. The allied lowland to montane variant (note 2) has been recorded from grassy areas associated with *Eucalyptus* wet to dry sclerophyll forest *(Barker 923)* and wet soil at edge of a *Baumea* swamp *(Harwood 110)*.

Flowering occurs mainly between November and March, starting later at higher altitudes; there is one early October record *(Gunn 863 or 12207)*. Fruits begin forming in early December in some populations but appear to be mainly produced from January.

*Conservation status:* considered not at risk.
Notes: 1. Although ssp. diemenica forms a natural assemblage, it is polymorphic. Variation within the subspecies involves the characters of the presence or absence, distribution, length and density of the glandular indumentum on the calyces, bracts, rachises, leaves and axes, the size of the corollas, calyces and upper leaves and the extent and density of the setae on the capsules. It is considered inadvisable to produce a formal classification of the variants in the absence of field studies from a wider range of localities than those I have seen. However, for ease of future reference each of the distinctive variants discussed has been given informal varietal status and its own letter coding.

On the north-west edge of the Great Western Tiers near Lake MacKenzie two ecotypes were found growing side by side with no intermediates. One (var. A: Barker 1078), characterized by white corollas always with a yellow blotched lower lip and lacking glandular hairs from all parts bar the corolla, was found as a small population growing in a moist hollow on the open hill-side. The surrounding open grassy subalpine heath was occupied by an extensive population of plants (var. B: Barker 1079, 1080) apparently with somewhat smaller flowers with a sparse to dense, short glandular indumentum on the calyces, bracts, rachises and upper leaves and with white to lilac corollas varying in the incidence of the yellow blotch on the lower lip. The two populations were separable also by their different flowering times, the glandular plants of the heath having flowered much earlier. The probable retention of water in the hollow described above may prolong growth well into the summer and produce a delay in flowering time. It could also provide an environmental basis for the somewhat larger flower size in the population growing in the hollow. Although there was some spatial overlap of the two populations, the correlation between differences in indumentum and the stage of flowering was apparently without exception. A study of the pollen from plants of both populations showed some incidence of higher pollen sterility (PS196-204), but whether it is of taxonomic significance cannot be determined without further study.

Elsewhere in the Tasmanian highlands indumentum characters and flower and leaf size separate populations on a regional or local basis. Although treated separately in this account, differences in flower and leaf size may be produced by environmental differences; the larger-flowered large-leaved forms tend to occupy wetter or higher, more exposed situations. Such forms, discussed later, are found near Pine Lake near the summit of the Great Western Tiers in subalpine grassland (Barker 1068, 1070), in a marshy area of subalpine grassland on a hill overlooking Lake Augusta (Barker 1073), and on the alpine heath on the upper slopes and summit of Mt Wellington and the summit of Ben Lomond.

Among the small-flowered, small-leaved variants extensive populations of a form (var. C) with white corollas with yellow areas always in the throat but varying in their presence on the lower lip, and a short, sparse to dense glandular indumentum, at least on the upper parts, and sometimes extending onto the basal parts, abound on the alpine heath beside Lake Augusta on the Central Plateau (Barker 1020, 1023, 1041, 1042, 1045, 1047, 1049-1051, 1053). The Cradle Mountain-Hampshire Hills region is occupied by a form (var. D) lacking glandular hairs, except rarely at the base of the plant (Eichler 16567), and with usually white, sometimes lilac or purple corollas; the incidence of the yellow blotches is unknown. Another related variant (var. E) occurs beside the Lakes Highway west of Great Lake in grazed subalpine pasture (Barker 999, 1058). It is characterized by lilac corollas always with yellow blotches on the lower lip and deep in the throat, an absence of glandular hairs in the upper parts, but often a short glandular indumentum on the leaves and axes of the lower parts.

The only known instance of a breakdown of the character of the presence or
absence of glandular hairs on the upper parts of the inflorescence-bearing branches in the smaller-flowered, smaller-leaved forms of ssp. diemenica is found at Doctors Creek near Great Lake (Barker 1000-1003, 1062, 1064). In this population the yellow spot on the lower corolla lip was sometimes lacking. Unfortunately, the variation in indumentum could not be discerned in the field and collections were combined of plants occurring in the grassy, subalpine heath on the banks of the stream and those occupying the more open areas at stream level. It is therefore not known whether there was any association between ecology and indumentum variation. Pollen sterility tests (PS236-252) covering both indumentum types consist mostly of counts of low sterility. However in about a quarter of the counts only 50-80% of the pollen was functional in appearance, while one plant produced a very low proportion of such pollen (PS236). This relatively high incidence of sterility may reflect a hybrid situation.

The larger-flowered, larger-leaved forms of ssp. diemenica have complexities in indumentum similar to those found in the smaller forms. They seem always to have a yellow blotch on the lower lip which is often continuous with that in the throat and is rarely indistinct. On the Central Plateau occur populations of plants solely glandular in the upper parts (var. F: Barker 1073), while others contain only non-glandular plants (var. G: Barker 1068, 1070, 1078). However populations on Mt Wellington (var. H: Barker 1015, 1122, 1141) contain a small proportion of non-glandular plants as well as occasional individuals with only very few glandular hairs on the calyces, bracts or rachises. The majority of the plants bear a sparse to dense glandular indumentum. It is uncertain whether these non-glandular plants are extremes of variation of pure populations of ssp. diemenica on Mt Wellington or the product of an introgression of genes determining this character from the sympatric ssp. collina into populations of a purely glandular form of ssp. diemenica (see E. collina: Intraspecific Polymorphism).

In alpine heath on the summit of the Ben Lomond massif and Mt Barrow, which form part of an isolated mountain system in north-east Tasmania, occur populations (var. I: Barker 1095, 1097, 1098, 1105, 1107: fig. 65B, C), which are divergent from members of ssp. diemenica on the mountains of the centre, south and west of the island by their densely setose capsules, and by their longer glandular indumentum (c. 0.1-0.3(0.4)mm long on the calyx) usually confined to the upper parts, rarely also at the base of the plant or almost absent. Elsewhere in ssp. diemenica the capsules are often glabrous or sparsely setose at the apex, and the glandular hairs are short (0.05-0.1(0.2)mm long on the calyx) and similarly distributed.

On the edge of the Ben Lomond plateau in grassy areas sheltered by large shrubs and dolerite boulders (fig. 66) occurs a complex situation involving variation in indumentum and flower and leaf size. In the field the plants were separated into two collections, one of large-flowered plants just beginning to flower (Barker 1113: fig. 65A), the other of small-flowered individuals, many of which were bearing mature capsules (Barker 1112). The former collection resembles the populations from the plateau itself (Barker 1105) in size and the presence of a glandular indumentum of varying density in the upper parts, but differs by the shortness of the glandular hairs (c. 0.1mm on the calyx) and the presence of one plant with subglabrous capsules. The other collection (Barker 1112) contains a mixture of non-glandular and sparsely to densely shortly glandular plants with usually moderately densely to densely setose capsules; one plant has subglabrous capsules. They therefore tend to the variants of the mountains to the west. Pollen from the majority of plants was examined to determine the proportion of sterile pollen. The results are tabulated in table 10. Most sterility counts show a very high incidence of apparently functional pollen. Although few, the counts showing percentages of apparently functional pollen of below 80% are concentrated in a particular range of character combinations. It is possible that these
Table 10. Morphological variation in the two collections of *E. collina* ssp. *diemenica*, Barker 1112 and 1113, from a single population on the edge of the Ben Lomond plateau, Tasmania, with corresponding estimates of the percentage of pollen functional in appearance from a single flower, with only one estimate, as far as can be determined, coming from a single plant. The counts below 80% are in bold.

<table>
<thead>
<tr>
<th>Capsule indumentum</th>
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<th>Count Voucher slide</th>
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<th>Count Voucher slide</th>
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<tbody>
<tr>
<td>Densely setose</td>
<td>1112</td>
<td>1112</td>
<td>1113</td>
<td>1112</td>
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<tr>
<td></td>
<td>100% (PS187)</td>
<td>60% (PS278)</td>
<td>99% (PS191)</td>
<td>94% (PS185)</td>
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<tr>
<td></td>
<td>57% (PS188)</td>
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<td>95% (PS193)</td>
<td>95% (PS276)</td>
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<td>95% (PS190)</td>
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<td>99% (PS279)</td>
<td>45% (PS275)</td>
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<td>99% (PS282)</td>
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<td></td>
<td>97% (PS283)</td>
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<tr>
<td>Moderately densely setose or setose at very apex</td>
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<td>100% (PS194)</td>
<td>93% (PS183)</td>
<td>5% (PS189)</td>
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<td>98% (PS195)</td>
<td>5% (PS186)</td>
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<td>99% (PS277)</td>
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<td>63% (PS274)</td>
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<td>95% (PS281)</td>
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<td>93% (PS284)</td>
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<td>Subglabrous</td>
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<td>95% (PS285)</td>
<td>100% (PS182)</td>
<td>75% (PS184)</td>
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plants are partially sterile hybrids and that this locality is a point of overlap of two independent populations, one identical to those on the plateau itself (var. I: *Barker 1105*) comprising large glandular plants with densely setose capsules, the other, previously uncollected (except possibly for a single plant *Olsen 169*) consisting of smaller non-glandular variant with capsules probably subglabrous to moderately densely setose.

Ecological and cytogenetical studies of ssp. *diemenica* throughout its range of distribution may be required before it can be determined whether a classification involving the recognition of its main variants either as distinct subspecies or as infra-subspecific taxa is justifiable. Any attempt to formally classify these closely related variants should be based on the critical study of populations over a much wider range of localities than has been observed in this revision. In particular, evidence of clinal intergradation should be looked for and the interaction of sympatric variants closely studied.

2. The collections from lowland and montane north-eastern and north-western Tasmania (fig. 50) are closely allied to the alpine and subalpine populations of ssp. *diemenica*. The only seeds seen (*Morris HO, Phillips CBG015462*) were smaller (0.7-1.0mm long) than normal for the subspecies. These plants also diverge in the general narrowness of their uppermost leaves and large size of the apical leaf teeth which are 1.2-1.8 x (0.8)1.1-1.7mm. Although these still lie in the common range of variation of ssp. *diemenica*, populations in alpine and subalpine zones always appear to contain plants with much shorter apical teeth. Further collections are required to determine if these data truly reflect the range of variation in these characters in the populations throughout montane and lowland northern Tasmania. If these are representative then the collections probably belong to an undescribed subspecies or a variety of ssp. *diemenica*. 187
3. The specimen Long HO from Port Davey is the only collection of *E. collina* from the south-west of Tasmania. It seems closest to ssp. *diemenica* although there is insufficient material (three inflorescence-bearing branches probably from the one plant) to gauge the variation in the populations in the area. Possibly because of the rather depauperate condition of the material, it diverges to some extent from normal ranges of variation of ssp. *diemenica* by the obtuse lower corolla lobes and rather short rearmost pair of anther awns (0.25mm long). A study of populations of *E. collina* in south-west Tasmania is needed.

4. The locality “Western Mts” of Stuart 428, collected in 1849, undoubtedly refers not to the mountains of that name today on the west coast of Tasmania, but to what is now known as the Great Western Tiers, which form the northern face of the Central Plateau of Tasmania (see Burns & Skemp 1961). The locality “Great Western Mts” of *L. Rodway* HO, collected in 1908, presumably pertains to the same range.

5. Occasional highly sterile hybrids between *E. collina* ssp. *diemenica* and *E. striata* are known from the Central Plateau of Tasmania and possibly also from Mt Wellington (see p. 287).

**Selected and cited specimens (c. 110 seen)**


**Specimens with affinities to ssp. diemenica**

An apparently distinct subspecies of *E. collina* exists in sand dunes on the central north coast and the upper west coast of Tasmania (fig. 51). It seems clearly distinct from the other subspecies which lack glandular hairs (including ssp. *tetragona* which also occurs in dunes of the same general region) by its small oblong to broad oblong bracts and uppermost leaves (c. 5-7.5 x 2.2-4.5 mm) with 1-2(3) short lobes (c. 0.5-0.9 mm long) along each margin confined to the distal half, its small lowermost calyces (c. 3.7-5.5 mm long), its small corollas (c. 6.5-9 mm long, although the lowermost ones, which are absent, are possibly slightly longer) and its small capsules (c. 4.5-7 mm long). In addition the lower corolla lobes are shallowly emarginate to emarginate, and are glabrous or bear short dense eglandular hairs all over the external surface; the capsules are glabrous or with short setae confined to the apex or spread over the upper half, and the seeds are small (c. 0.7-0.8 mm long) and numerous. The plants from the west coast (*Barker 990, Jackson 293*) have branching in the aerial parts (fig. 67) but it is difficult to gauge the habit of the plants from which the three Stuart fragments were taken. Before formal recognition can be justified a study of the dune population of *E. collina* in Tasmania (at present only known from the dunes of the north-west) should be made to ascertain the degree of morphological variation within this apparently distinct taxon, to discover whether distinctions from ssp. *tetragona*, ssp. *diemenica*, ssp. *collina* and ssp. *paludosa* are maintained.

**Specimens examined**

**TASMANIA:** *Barker 990, 24.xi.1970. C. 1 km from the Arthur River holiday resort on the Marrawah Road.
AD.—*Jackson 293, i.1954. Corinna. Poo Dunes.
HO.—*Stuart 943, xi.1850. Nr Badger Head. MEL.—
Stuart 943, s.dat. Sand Hills on NW Coast. MEL.*

**1Id. ssp. tetragona** (R. Br.) *Barker, comb. & stat. nov.*


*E. multicaulis* Bentham in DC., Prodr. 10 (1846) 553; Hook.f., Fl. Tasm. 1 (1857) 297, p.p. (as to *Gunn 863, 200, and probably as to "South-western Australia?" occurrence? Wettst., Monogr. Gatt. Euphrasia (1896) 249, p.p. (as to some *Gunn* collections, n.v.). Lectotypus hic designatus: *Gunn 863/1837, 25.x.1836* (p.p.). Circular Head 25/10/36 Woolnorth. This very beautiful species is very common in the sandhills, &c. in the neighbourhood of the sea at Circular Head and Woolnorth, flowering during the latter part of October and early in Novb. In my earlier collections I am afraid I have sadly confounded different species of Euphrasia, and to commence clearing up matters, I give this a new number to begin with. K(p.p.); isolectotypus: BM (n.v.). Syntypus possibilis isosyntypusve: *Gunn 181432, 30.x.1837 & 6.xi.1837. Sandhills, Circular Head. NSW10838; syntypi alteri: Baxter s.n., K (King George's) Sound N. Holl. K(p.p.)." Specimina a Labillardière in ore meridionali Australiae . . . lecta" (n.v.). See Typification.


Fig. 67. *E. collina* ssp. ‘Northwest Tasmania’, Barker 990 (scale 5cm).

Fig. 68. Lectotype of *E. muelleri* Wettst. (scale 5cm).
Studies in Euphrasia


Erect perennial herb or undershrub (14.5)17-46(47)cm tall, with many ascending or erect branches arising from a single erect stem, flowering in first year, subsequently dying back to upper branches. Stem or, after first year, main inflorescence-bearing branches (10)12-37(41)cm high to base of inflorescence, simple for (0.2)0.25-0.95 of height of inflorescence from ground level; upper (0)2-8(9) internodes as long as or longer than upper leaves, the longest internode (0.75)1.3-4.1(4.3) times length of upper leaves; axes in upper parts bearing two rows or four lines of sparse to dense, very short to moderately long eglandular hairs decurrent from between leaf bases, sometimes with sparse eglandular hairs between, in lower parts usually sparser and shorter, often glabrous. Leaves: uppermost leaves of stem or main inflorescence-bearing branches (4.6)5.5-13.8(14.3) x 1.8-6.0(9.6)mm, with sessile glands confined to distal (0.35)0.4-0.85 of underside, otherwise glabrous, except sometimes for sparse to dense, short eglandular hairs on upper surface, with blade ovate-elliptic to obovate-elliptic, sometimes narrowly or broadly so; base narrowly cuneate to rounded; teeth (0)1-2(4) along each margin, confined to distal (0)0.15-0.5(0.6) of leaf, usually bluntly obtuse or acute, rarely sharply acute, the longest tooth (0.1)0.2-1.5(2.4)mm long; apical tooth (0.2)1.3-3.5(3.8) x (0.8)1.0-3.1(5.2)mm, usually bluntly acute or obtuse, rarely truncate; leaves lower down glabrous. Inflorescences racemes, except sometimes for widely-spaced lower 1-2 nodes, usually dense, sometimes moderately dense, rarely lax in flower and fruit, with (12)18-52(80) flowers, with lowest node sometimes bearing a single flower; pedicels at lowest node (0.6)0.7-5.0(7.0)mm long, shorter higher up; rachis with indumentum similar to upper part of axis, but sometimes denser; internodes elongating prior to anthesis such that capsules usually reach past, sometimes well below base of calyx above; apical bud cluster usually narrowly cylindrical to narrowly conical-cylindrical, sometimes ovoid, initially 1.0-4.0cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after flowers at first 5-29 nodes have reached anthesis. Bracts glabrous, except often for eglandular hairs on upper surface, shorter than calyx, except sometimes for those at lowest 2(4) nodes, usually those at lower 2-11(23) nodes toothed with distal ones entire, rarely all entire, those at lowest nodes similar to upper leaves in shape and size. Calyx (4.7)4.9-9.3(10.0)mm long, externally glabrous or with a small patch of eglandular hairs decurrent from base of median clefts, internally with moderately dense to dense, short to moderately long eglandular hairs on distal part of tube and lobes. Corolla (9)11-16(17)mm long along upper side, white or pale to deep mauve, pink, purple, lilac, violet, lavender or blue, with yellow to orange blotch behind lowest lobe, usually also with smaller blotch at base of each anterior filament, sometimes with blotches in the two areas coextensive; tube (6.2)7-10(12)mm long; hood (2.6)3.5-6(6.8)mm long; upper lobes emarginate or shallowly so, with rear surface glabrous; lower lip (5.2)6-10.5(13)mm long; lower lobes usually emarginate or deeply so, rarely shallowly emarginate, externally glabrous. Stamens with anthers (1.5)1.7-2.5(3.0)mm long, with connectives surrounded by usually dense, sometimes moderately dense, rarely sparse, long to very long eglandular hairs; rearmost pair of awns (0.1)0.2-0.5mm long. Capsules 7.5-12mm long, in lateral view elliptic to obovate-caudate, 2.5-3.0mm broad, in median view narrow obovate-acuminate, glabrous or with a few short setae at very apex; apex in lateral view obtuse to truncate-obtuse, sometimes obliquely so; seeds (7)55-105, (0.5)0.6-0.9(1.0) x 0.3-0.4mm, ellipsoid, oblong or ovoid, often obliquely so. Figs 7, 48F, G, 69, 70.

Typification
1. E. tetragona R.Br. Although the BM specimen seen is undoubtedly part of the type collection described in Brown's (unpubl.) manuscript and the protologue (Brown 1810),
there are grounds for doubting that the specimen is the same as that designated and described by Du Rietz (1948b) as the "holotype". Du Rietz makes no mention of Brown’s collection of *E. tetragona* from Memory Cove, South Australia, which is mounted with the above collection. In fact, he considered that *E. tetragona* was a “geographically very isolated member of the *collina-paludosa* group (which does not seem to be represented at all in South Australia)”. It is likely that the collections were mounted together on the one sheet before Du Rietz’s visit to BM in 1930-1931 as photographs in Du Rietz’s (1948a,b) publication’s of Brown’s holotypes of *E. collina* and *E. striata* show that the specimens are arranged identically to their present state. Several explanations for this anomaly come to mind, the first being that he saw a duplicate of this sheet. The existence of a duplicate may be indicated also by the fact that unlike all Brown’s other holotype sheets of *Euphrasia*, this one lacks locality annotations in Brown’s handwriting. Alternatively however this may be the sheet seen by Du Rietz; either he may have considered that the Memory Cove collection belonged to “*E. tetragona*” and did not know that Memory Cove was in South Australia, or he may well have considered that it belonged to *E. collina* (sensu Brown 1810). In support of the latter, Brown had annotated the Memory Cove collection “*Euphrasia cfr. collinam*” and Du Rietz may have agreed.

2. *E. multicaulis* Benth. Gunn’s collection from Herbarium Hookerianum is the obvious choice as lectotype since it forms the basis of the initial diagnosis (Bentham 1846). The other two syntypes were described as hardly differing from the species as described. The Baxter collection, although almost vegetative, clearly belongs to ssp. *tetragona*. From the locality cited it is probable that the other syntype also belongs to this subspecies.

The lectotype as designated is apparently a combined collection from Circular Head and Woolnorth, two locations in north-west Tasmania. There seems no chance nor little point to assigning the three specimens in the combined collection to their correct provenance, as together they form a homogeneous assemblage. Nevertheless, the two smaller plants may have come from one locality and the larger from the other. The lectotype is mounted with the collection *Gunn 8" ge22* of ssp. *diemenica* from New Norfolk.

It is probable that BM also has an isolectotype as Du Rietz (1948b, p.354) discussed the K lectotype specimen, strangely without mention that it was a type of *E. multicaulis*, and noted that the collection was also represented in BM.

A search for *Euphrasia* in the region of Circular Head was unsuccessful. The sand dunes in the area appear to be covered almost exclusively with marram-grass (*Ammophila arenaria*), which was introduced by the Van Diemen’s Land Co. in the early or mid 1800s to stabilize dune areas (Mr D. Steane, pers. comm. 1971).

*Distribution* (fig. 51): *E. collina* ssp. *tetragona* is restricted mainly to the coastal regions of south-west Western Australia and South Australia with an inland extension into the sandy-mallee heaths of the 90-Mile Desert in South Australia and the Little Desert and Big Desert of western Victoria. A few old collections come from Tasmania, the only specific localities being at Woolnorth and Circular Head (or Stanley) on the north-west coast. In South Australia, there are three isolated, possibly relict occurrences at Mt Kitchener in the Mt Lofty Ranges, Mt Remarkable in the southern Flinders Ranges and in the Gawler Ranges (fig. 51: note 4). Altitude, sea level to c. 150m; there are no records for the isolated inland populations in South Australia.

*Ecology:* The subspecies commonly occupies sandy soil, in the mallee-heaths of the inland plains of south-eastern South Australia and western Victoria, in heathland of
coastal cliff-tops with underlying limestone on southern Yorke Peninsula, Kangaroo Island and possible southwest Western Australia, and on coastal dunes and the swales between across southern Australia. The unusual population on West Cape, southern Yorke Peninsula, grows in very limited soil in cracks in the exposed limestone cliff-top (note 3: fig. 70). Atypical records of habitat are “Lateritic soils. Eucalyptus cladocalyx dominant” (D. Smith 309A) and “Granite rock” (Lullfitz 3558).

Flowering occurs between August and February, with a single record of March (Staer NSW10949). Capsules begin to form from September.

Conservation status: considered not at risk.

Notes: 1. Muir 1783 from Wilsons Promontory in Victoria (fig. 51) has been tentatively placed under ssp. tetragona, even though it constitutes the most easterly locality of the subspecies well apart from the nearest known occurrence of the subspecies in the Little Desert of western Victoria. Although the single plant is typical of ssp. tetragona, it is possible that it is an extreme variant of populations related to ssp. paludosa and ssp. collina which occur on Wilsons Promontory. A study of populations in the region as part of a general revision of the lowland Victorian members of E. collina is required to clarify the situation.

2. Within ssp. tetragona there is geographical variation in leaf shape and the extent of branching into the upper parts of the stem and main inflorescence-bearing branches.

This variation is illustrated in the graph (fig. 69) of the length:breadth ratio of the upper leaves of the main axes plotted against the proportion simple of the height of the inflorescence on the main axis above ground level. It should be noted that the selection of specimens in some cases is neither complete nor random, but has been
based on an attempt to obtain the whole range of variation. The Kangaroo Island populations are represented by all entire plants in the available herbarium material. In addition, although incomplete, the only plants from the northern side of the island (Ashby 1400) are included, as they appear to relate more to the mainland populations than those from the southern coast of the island.

The graph demonstrates that except for the inland collections, which are apparently relict (see note 4), a very atypical collection (Eichler 14044) from Corny Point, and the collection Mueller MEL41408 from the extreme east of the mainland occurrences of ssp. tetragona (but see note 1), the south coast Kangaroo Island populations differ from the mainland populations by their extremely high aerial branching on the main inflorescence-bearing axes. They also have a tendency to have broader leaves than their counterparts on the neighbouring peninsulas, although the differences may not prove statistically significant (fig. 7: Eichler 15384, Barker 1355). However, it is clear that plants from the sandy mallee heaths of the 90-Mile Desert, the Little Desert and the Big Desert in the eastern part of the mainland range of distribution, diverge from populations to the west by their narrower upper leaves (fig. 7: Barker 1450). These leaves are very similar in shape and size to those found in ssp. collina in the adjacent areas of inland western Victoria (fig. 6: Barker 1439, 1443, 1446), and reflect the close taxonomic affinities of the two subspecies.

Growing on the extreme tip of West Cape, south-western Yorke Peninsula, occurs a population of ssp. tetragona (Barker 1374, fig. 70) unique in its large broad, very fleshy leaves (fig. 7), calyces and bracts, and short inflorescence-bearing branches. The plants grow with other succulent plants in very exposed conditions in sparse soil in crevices of the limestone which tops the promontory. Plants (Barker 1375) typical of coastal populations of southern Yorke Peninsula occur behind the headland in the more protected slopes of sand dunes. The increased fleshiness in the cliff-top plants is probably because of the greater exposure to sea-spray, a response often exhibited by plants in such areas (e.g. Specht 1972). Plants on less-exposed cliffs such as those near Corny Point are typical of the subspecies. Whether there is any genetic basis to these differences is not known.

In South Australia ssp. tetragona is recorded well to the north of its common range of distribution (fig. 51) in three widely disjunct mountain areas, the Gawler Ranges (Sullivan MELA1413 and a possible duplicate Anon. MELA1752), Mt Remarkable in the southern Flinders Ranges (Mueller HBG, p.p.), and Kaisersstuhl (now Mt Kitchener) in the Barossa Range (Mueller MELA1488 and possibly Mueller MELA1513, which is so similar it may be a duplicate). Despite the individual records probably being based on single old collections, the coincidence of three such isolated locations in the same general region points to their authenticity. The three mountain ranges have been proposed as part of a series of refugia for plants formerly occupying lowlands between in wetter climatic periods (Crocker & Wood 1947; Boomsma 1972; Parsons 1973; Kraehenbuehl unpubl.). This pattern of distribution in ssp. tetragona would seem to be unusual, as it involves a predominantly sandy mallee-heath plant apparently with isolated occurrences in what are basically refuges for montane sclerophyll forest or woodland taxa.

The statement by Sprengel (1825) that “E. tetragona” (now E. collina ssp. tetragona) was restricted to Tasmania (“Terra Diemen”) is clearly an error, since the remainder of the text on E. tetragona, like the other five species confined to Australia, is a copy with some rearrangement of Brown’s (1810) description. Either Sprengel mistakenly substituted “Terra Diemen” for the southern coast of Australia (“Ora Meridionalis”) cited by Brown for the species, or he intended to extend the distribution of the species into Tasmania and omitted reference to localities already known.

*Decayed branches from the previous year indicate that the branching may have been much lower then, with the proportion of the height of the inflorescence above ground level simple about 0.60. This may point to some unusual seasonal effect.
Fig. 70. *E. collina* ssp. *tetragona*, West Cape, Yorke Peninsula (Barker 1374). A, population on exposed limestone cliff-top; B, very fleshy-leaved specimen; C, inflorescence showing white corollas with broad yellow blotch on lower side of mouth, scale 1 cm.
Selected and cited specimens


AUSTRALIA. WITHOUT LOCALITY (5 seen).

LOCALITY DOUBTFUL (2 seen): Anon s.n., s.dat. N.S. Wales. AD9701201 (p.p.).—Woolls s.n., s.dat. Par[r]lamatta. MEL41424.

Specimen with affinities to ssp. tetragona


11e. ssp. trichocalycina (Gandoger) Barker, comb. & stat. nov.


Erect perennial herb or undershrub (15)26-50(62)cm high, with branches erect or rapidly ascending, arising from a single erect stem, terminated by an inflorescence in first year and then dying back to upper branches. Stem or, after first year, main inflorescence-bearing branches (13)22-43(55)cm high to base of inflorescence, simple for (0.05)1.0-0.45(0.75) of height from ground level to inflorescence; upper (1)4-9(10) internodes as long as or longer than upper leaves, the longest internode (1.0)2.2-4.2(7.0) times length of upper leaves; axes in upper parts covered by two rows or four lines of dense, short to moderately long eglandular hairs decurrent from between leaf bases, rarely with sparser eglandular hairs between, sometimes mixed with usually sparse, rarely dense, very short to moderately long glandular hairs all around, lower down with similar eglandular indumentum, rarely with dense, short glandular hairs all around. Leaves: uppermost leaves of stem or main inflorescence-bearing branches (5)7-14(15.8) x (1.7)2.3-4.4(5.4)mm, with blade linear or narrowly ovate-oblong to obovate-oblong, with sessile gland patches confined to distal (0.5)0.55-0.7(0.75) of lower surface,
otherwise usually glabrous, sometimes covered by sparse to moderately dense, very short to short glandular hairs; base rounded or narrowly cuneate; teeth (0)1(2) along each margin, confined to distal (0.15)0.25-0.45(0.5) of leaf, usually sharp, sometimes blunt, usually acute, rarely obtuse, the longest tooth 0.8-2.0(2.4)mm long; apical tooth (1.2)1.7-3.0(3.4) x (0.8)1.0-1.9(2.3)mm, usually blunt, rarely sharp, acute or obtuse; leaves lower down glabrous but rarely for leaves near base which bear very sparse, short glandular hairs. Inflorescences racemes, except for widely-spaced lower (0)1-3(5) nodes dense in bud, moderately dense to dense in flower and fruit, with (14)20-40(48) flowers, rarely with lowest node bearing a single flower; pedicels at lowest node (0.5)1.0-3.7(7.5)mm long; rachis with eglandular indumentum similar to uppermost part of axis, but sometimes denser or slightly longer, sometimes with sparse to dense, very short to moderately long glandular hairs all around; internodes elongating prior to anthesis such that, except at widely spaced lower nodes, capsules usually reach or extend past node above, sometimes just below it; apical bud cluster except for widely-spaced lower nodes narrow cylindrical or narrow conical to ovoid, initially (1.5)2-3.4cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after flowers at lower (4)6 or more nodes have reached anthesis. Bracts similar to uppermost leaves in size and shape, usually bearing sparse to very dense, very short to short glandular hairs, rarely glabrous, those at all but the lower (2)3-6(9) nodes entire, those at all but the lower 0-4(5) nodes shorter than or equal to calyx. Calyx (3.5)4.4-6.0(7.8)mm long, externally covered by very sparse to dense, usually very short to short, rarely moderately long glandular hairs most dense on teeth and extending to their margins, with short eglandular hairs on inside of teeth, rarely extending to outer surface. Corolla (9)9.5-12.5(14.5)mm long along upper side, white, or lavender to lilac with white lobes, or lavender to lilac and whitish behind lobes, with yellow blotch lacking; tube (5.5)6-9.5(10)mm long; upper lobes obtuse or shallowly emarginate with rear surface bearing moderately dense to dense, very short glandular hairs, very short to short glandular hairs, sometimes throughout, sometimes confined to base; lower lip (3.9)4.3-7.5(8.0)mm long, with moderately dense to dense, short glandular hairs, sometimes mixed with sparse to moderately dense, short eglandular hairs, the indumentum usually all over, sometimes only at base; lower lobes usually emarginate to shallow emarginate, sometimes praemorse-obtuse. Stamens with anthers (1.4)1.5-1.9(2.2)mm long, with connectives surrounded by dense, long to very long eglandular hairs, the area about front ones sometimes somewhat sparser; rearmost pair of awns (0.1)0.2-0.4(0.5)mm long. Capsules (6.5)6.9-8.7(9.2)mm long, in lateral view usually elliptic to oblong-elliptic, sometimes narrow or obovate or somewhat caudate and slightly deflexed, (1.8)1.9-2.6mm broad, in median view ovate- to elliptic-acuminate, usually glabrous, sometimes with a few to moderately dense, short to long setae confined to apex; apex in lateral view acute to truncate-obtuse, sometimes obliquely so; seeds (23)55(123), (0.5)0.7-1.0(1.3) x (0.2)0.3-0.5(0.6)mm, ellipsoid, oblong, ovoid or reniform, often obliquely so, sometimes broadly so. Fig. 7.

Distribution (fig. 52): E. collina ssp. trichocalycina is confined mainly to central and western Victoria. It is also known in the south-east of South Australia. Altitude, 0-800m.

Ecology: Mostly details of habitats of ssp. trichocalycina have been recorded from the Grampians. On their lower slopes populations occur in sandy soil in open areas of heath in low Eucalyptus forest/woodland (Barker 1432). On the higher slopes they inhabit low Eucalyptus scrub with a dense shrub understory in shallow sand between exposed bedrock (Barker 1438, 1439p.p.), tall dense shrubbery bordering tall Eucalyptus forest (Barker 1442) or a "heathy flat" (Symon 263). Elsewhere the subspecies has been found in Eucalyptus forest (Willis MEL41472) and swamps (Mueller MEL41512, Cleland AD).
Flowering begins from probably as early as August to early November and continues possibly into January. Copiously fruiting plants have been recorded in September. Flowering period is affected greatly by altitude, since towards the end of October the population seen on the lower slopes of the Grampians had all but finished flowering while those higher up had hardly begun to flower.

Conservation Status: 3V/R, C.

Note: The type diverges somewhat from most other representatives of the subspecies by its elliptic upper leaves with short teeth extended almost into the basal half and its lax habit. However, the short glandular indumentum restricted to the upper parts, the short rearmost anther awns (0.2mm) and the subglabrous capsules ally the specimen with the other members of the subspecies.

Mueller MEL41512 from "Swamps about Forest Creek" and Thorn MEL41391 from "Upper Goulbourne River" contain single specimens which like the holotype are related to the major portion of ssp. trichocalycina by their glandular indumentum, their branching above ground level, their rearmost anther awns 0.2-0.3mm long and their subglabrous capsules, but diverge from them by their upper leaves with 2-3 teeth along each margin. The glandular indumentum of the former (c. 0.5mm on calyx and leaves, 0.2mm on rachis and axis) is unusual in that it is very sparse on the calyx but moderately dense on the bracts, rachis, leaves and axis almost to ground level; the upper leaves bear 3 teeth extended well down each margin. The Thorn specimen bears glandular hairs (0.2mm long on the calyx) confined to the upper parts and has upper leaves with 2 pairs of teeth restricted to the distal half. It seems probable that the type came from the western part of the eastern highlands of Victoria where these two allied collections were made. Further collections of the subspecies are required outside the Grampians to determine whether two distinct taxa are present.

Specimens examined


11f. ssp. 'tasmanica'

Collections from the east coast of Tasmania (fig. 52) from heath in open Eucalyptus woodland at St Helens (George Bay) which include the holotype of E. tasmanica (Simson 58: see p. 160) and from well to the south on the Forestier and Tasman Peninsula, belong to the group of glandular subspecies of E. collina branched in the
upper parts and with few-toothed leaves. There are three subspecies recognized in this group. From ssp. *trichocalyxina* these plants differ by their fewer-flowered inflorescences, shorter rearmost anther awns and the shorter apices and teeth of their uppermost leaves (fig. 8: Barker 892). The plants differ from ssp. *gunnii* by their denser inflorescences, usually glabrous capsules, rarely sparingly setose at the apex, and the short glandular indumentum, if present, at the base of the plant. From ssp. *deflexifolia* the plants are distinguishable by their fewer-flowered inflorescences, subglabrous capsules and the short glandular indumentum (if present) at the base of the plant.

It is likely that these plants represent a distinct subspecies, but as only one “mass” collection (Barker 892) has been made from populations its formal taxonomic recognition in such a closely knit complex of subspecies is considered premature.

Lilac-flowered individuals from a mud flat beside a swamp on the Freycinet Peninsula (Barker 969, Himson HO(p.p.)) differ significantly from this apparently distinct subspecies only in flower colour. However only two specimens exist in herbaria. They have a short sparse glandular indumentum confined to the rachis, bracts and calyces, an inflorescence apparently moderately dense in flower, and ovaries which are either glabrous or with a few short setae at the very apex. There is no evidence that the two plants are hybrids between ssp. *collina* and the nearby populations of ssp. *deflexifolia* as postulated by Dr W.M. Curtis (in letter with Himson HO). Ssp. *collina* is unknown along the east coast of Tasmania, and the original population was apparently about 1km away from the nearest plants of ssp. *deflexifolia* (pers. observ.; Mr A. Himson, pers. comm. 1970). In addition there was a low percentage of sterile pollen in the single anther tested from Barker 969 (PS8).

**Specimens examined**


**11g. ssp. gunnii (Du Rietz) Barker, comb. & stat. nov.**


*E. collina* R.Br.: Benth. in DC., Prodr. 10 (1846) 553 (at least as to Gunn 1220, Scott K); Hook.f., Fl. Tasm. 1 (1857) 296, p.p. (as to Gunn 1220, Hooker MEL14460); Benth., Fl. Austral. 4 (1868) 520, p.p. (as to Tasm. collections incl. Hooker 778, Gunn 1220; Wettst., Monogr. Gatt. Euphrasia (1896) 254, p.p. (as to pl.5.f.404-409, Gunn 1220, Cunningham G, and probably other specimens cited except Labillardière G).


Erect perennial *herb or undershrub* (19)24-43(45)cm tall, with branches erect or rapidly ascending, arising from a single erect stem, terminated by inflorescence in first year, then dying back to upper branches. *Stem* or, after first year, *main inflorescence-
bearing branches (12)17-30(36) cm high to base of inflorescence, simple for (1)2-9(22) nodes below inflorescence, i.e. for 0.2-0.6(0.7) of height from ground level to inflorescence; upper (2)3-12(20) internodes longer than or as long as uppermost leaves, the longest internode (2)2.5-5(6) times length of upper leaves, those lower down shorter than leaves; axes in upper parts bearing two rows of dense, usually short to moderately long, rarely long eglandular hairs decurrent from between leaf bases, rarely with sparse eglandular hairs between, mixed all around with sparse to dense, short to long glandular hairs, lower down with eglandular indumentum similarly distributed but shorter, with glandular hairs lacking or sparse to moderately dense, short to long all around, in lowest parts with sparse to dense, very short to very long eglandular hairs often mixed with sparse to dense, moderately long to very long glandular hairs. Leaves: uppermost leaves of stem or main inflorescence-bearing branches (4.2)4.9-10.0(11.3) x (1.9)2.1-3.2(4.2) mm, narrowly oblong to oblanceolate in outline, with sessile gland patches extended over distal (0.6)0.7-0.8(0.9) of lower surface, covered by sparse to dense, short to long glandular hairs, sometimes mixed with sparse to moderately dense, very short to moderately long eglandular hairs; base narrow cuneate to rounded-cuneate; teeth 1(2) along each margin, confined to distal (0.15)0.2-0.5(0.6) of leaf, usually blunt, rarely sharp, acute or obtuse, the longest lobe 0.6-1.1(1.5) mm long; apical tooth usually blunt, rarely sharp, acute or obtuse, (0.9)1.1-2.0(2.6) x (0.8)0.9-1.4(1.8) mm; leaves lower down glabrous or covered by sparse to moderately dense, short to long glandular hairs, sometimes mixed with moderately dense, short scabrous eglandular hairs; lowest leaves usually covered by sparse to dense, very short to moderately long glandular hairs, sometimes with sparse to dense short scabrous eglandular hairs along margins, sometimes glabrous. Inflorescences racemes, usually dense, sometimes moderately dense in bud, lax to moderately dense in flower, with (10)12-24(28) flowers, sometimes with lower 1(4) nodes bearing a single flower or none at all; pedicels at lowest node (0)1.5-6(7.5) mm long, shorter higher up; rachis with eglandular hairs usually as for upper parts of axis, sometimes denser, with moderately dense to dense, moderately long to very long glandular hairs all around; internodes elongating prior to anthesis and sometimes greatly after, such that capsules well below node above; apical bud cluster narrowly cylindrical to conical or conical-ovoid, initially c. 1.0-2.2 cm long, hidden by or hardly emergent from corollas of uppermost flower pair after flowers at initial 3-6 nodes have reached anthesis. Bracts covered by moderately dense to dense, short to moderately long glandular hairs, sometimes mixed with sparse to moderately dense, short to long glandular hairs, those at lowest nodes similar in size and shape to uppermost leaves, shorter higher up, all bracts, except rarely for lower 1-2 pairs, shorter than or equal to calyx, those at lower 3-6 or more nodes toothed, distally entire. Calyx (3.2)3.5-5.5(6.3) mm long, externally covered by usually moderately dense to dense, rarely sparse, short to long glandular hairs, densest on teeth, sometimes extending onto inner surface of teeth where mixed with short to moderately long glandular hairs. Corolla (8.0)9-12(12.5) mm long along upper side, white or white with pink or lilac extremities, lacking yellow blotch; tube (5.0)6-8.5(9.3) mm long; hood (2.2)2.8-4.0(5.0) mm long; upper lobes usually obtuse or shallowly emarginate, sometimes emarginate, with rear surface usually ± glabrous, sometimes covered by sparse to dense, very short eglandular hairs or glandular hairs; lower lip (4.0)5.3-9(11.0) mm long; lower lobes usually emarginate or shallowly so, sometimes truncate or obtuse and then often praemorse, externally usually bearing sparse to dense, very short to moderately long eglandular hairs, often mixed with sparse to moderately dense, very short to short glandular hairs, sometimes ± glabrous. Stamens with anthers (1.2)1.4-1.9(2.1) mm long, with connectives of posterior pair surrounded by usually dense, sometimes moderately dense, long to very long eglandular hairs, those of anterior pair with indumentum sometimes similar, sometimes very sparse to sparse; rearmost pair of awns (0.1)0.2-0.3(0.4) mm long. Capsules (6.5)7-8(10) mm long, in lateral view usually obovate or elliptic, sometimes
obliquely so or shortly caudate, 2.1-3.2mm broad, in median view elliptic-acuminate, usually with dense setae 0.1-0.2mm long in upper 1/3-1/6, sometimes with a few at apex, rarely glabrous; apex in lateral view usually obtuse to truncate, sometimes obliquely so, rarely shortly broad acuminate; seeds (41 in one capsule of Tenison-Woods MEL) 0.8-1.0 x 0.35-0.6(0.7)mm, oblong, ellipsoid, ovoid or reniform, usually obliquely so. Fig. 8.

Typification

_E. gunnii_ Du Rietz  
The holotype chosen by Du Rietz (1948b) to typify his species clearly contains at least two different collections. However, together the specimens make up an homogeneous group, and satisfy the requirements for a holotype under Article 7 of the ICBN (see also definition of “element” in McVaugh, Ross & Stafleu 1968). Gunn’s practice of combining collections of his concept of a species under the one “species number” (Burns & Skemp 1961) makes the recognition of isotypes difficult. The only specimens seen which could possibly be isotypes are cited.

The holotype is mounted on the same sheet as a collection Hooker 778 of the subspecies, but it is almost certain that Hooker’s collection only consists of the right-hand specimen on the sheet (mainly in bud and with the initials “JDH” next to it), while Gunn’s collections comprise the other three specimens (mainly in flower and fruit, and with “VDL Gunn” written next to them well apart from the other specimen). Mr P.S. Green (pers. comm. 1973) has indicated that the association of labels and annotations with specimens on Kew collections of the past is usually reliable, especially when supported by the appearance of the specimens.

Of the type material the NSW specimen provides the most precise locality information. It is probable, however, that Gunn made collections from a number of places about Launceston.

Distribution (fig. 52): _E. collina_ ssp. _gunnii_ is apparently restricted to Tasmania, where it is known at present only from the region of Launceston, where collections are reasonably plentiful but mainly old, and from a single collection Hooker 778 from about 180km to the south at Grass Tree Hill on the northeastern outskirts of Hobart. There is no reason to doubt the authenticity of Hooker’s record, for he collected in Tasmania outside the localities of other collections of _ssp. gunnii_ (cf. _ssp. deflexifolia_). Altitude, possibly near sea level to a few hundred metres (no actual records).

Ecology: The subspecies has only been recorded “On cleared land of _Eucalyptus_ dry sclerophyll forest—either on grassy roadside, or inside fence where trees felled. Growing in litter in dark brown loam on dolerite and ironstone” (Barker 913).

Flowering occurs between late August and the end of December.

Conservation Status: 3 ?E. Although Gunn on the holotype label described the plant as common in the Launceston region, only two collections of the subspecies (_Barker 913, Curtis HO_) have been made in the last sixty years (I am grateful to the late Mr H.J. King of Launceston for directing me to one locality). Assessment of the endangerment of the subspecies is retarded by the low collecting activity in its provenance in recent times.

Note: The basic colour of the corolla in _ssp. gunnii_ is white. The yellow colour attributed to the subspecies by Wettstein (1896), under _E. collina_, and Du Rietz (1948a,b) and Curtis (1967), under _E. gunnii_, is clearly based on the colour of the dried flower.
Specimens examined

11h. ssp. deflexifolia (Gandoger) Barker in Stones & Curtis, End. Fl. Tasm. (1978) 477, 432, pl. 137

Erect perennial herb or undershrub, (25)26-51(76) cm high, with branches erect or rapidly ascending, arising from a single erect stem terminated by inflorescence in first year, dying back to upper branches in subsequent years. Stem or, after first year, main inflorescence-bearing branches (19)20-41(68) cm high to base of inflorescence, simple for (1)3-15(22) nodes below inflorescence, i.e. for (0.1)0.2-0.55(0.6) of height from ground level to inflorescence; upper (0)3-9(17) internodes longer than or as long as upper leaves, the longest internode (0.75)1.8-5.0(6.0) times length of upper leaves, those lower down shorter than leaves; axes in upper parts with two rows of moderately dense to dense, short eglandular hairs decurrent from between leaf bases, sometimes with sparse eglandular hairs between, mixed all around with sparse to dense, short to very long glandular hairs, lower parts with eglandular indumentum shorter and slightly sparser, with glandular hairs usually lacking or sparse, sometimes similarly dense and long, in lowermost parts with eglandular hairs often long, sometimes similar to middle parts, with glandular hairs usually moderately dense, moderately long to long, sometimes absent. Leaves: uppermost leaves of stem or main inflorescence-bearing branches (4.0)5.6-10.0(12.5) x (2.5)2.9-6.0(7.4) mm, crenate-serrate, oblong to oblong-elliptic to obovate in outline, with sessile gland patches extended over distal (0.5)0.55-0.8(0.85) of undersurface usually covered by sparse to dense, short to long glandular hairs, mixed rarely with sparse short eglandular hairs, rarely glabrous; base rounded to rounded-cuneate; teeth 1-2(4) along each margin, confined to distal (0.15)0.3-0.65(0.7) of leaf, sharply or bluntly acute to obtuse, the longest tooth (0.2)0.9-1.5 (1.9) mm long; apical tooth (0.5)1.1-2.1(2.6) x 1.1-2.1(2.4) mm, bluntly or sharply truncate-obtuse to acute; leaves lower down with sparser, shorter indumentum or glabrous; lowermost leaves usually covered by sparse, short to moderately long glandular hairs, sometimes bearing sparse to dense short eglandular hairs or glabrous. Inflorescence racemes, dense in bud, moderately dense to dense in flower; those of stem or main branches with (16)18-40(46) flowers, with usually two flowers at each node, rarely a single flower only at lowest node; pedicels at lowest node (0.5)1.0-3.0 mm long,
shorter higher up; *rachis* as for upper parts of axes, but indumentum denser and slightly longer; *internodes* elongating slightly or greatly before and possibly after anthesis, such that capsules well below or reach past node above; *apical bud cluster* narrow cylindrical to ovate-cylindrical or broad ovate-elliptic, initially 1.0-2.0cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after first 5-14 pairs of flowers have reached anthesis. *Bracts* at lowermost nodes similar in shape and indumentum to uppermost leaves, shorter higher up, never extending past calyx, those at lower 6-14 or more nodes toothed, distal ones entire. *Calyx* (3.8)4.3-6.5(7.8)mm long, externally covered by dense, short to very long glandular hairs, with short to long setose eglandular hairs on inside of teeth. *Corolla* (9.4)11-13(14)mm long along upper side, white or white with pinkish extremities, lacking yellow blotch; *tube* (6)7-8.5(9)mm long; *hood* (3.0)3.5-5(5.3)mm long; *upper lobes* obtuse or praemorse-obtuse to emarginate, with rear surface usually covered by sparse to dense, very short to short glandular hairs, sometimes all over by moderately dense to dense, short eglandular hairs or a mixture of both, rarely the indumentum confined to base; *lower lip* (5.0)6-10(11)mm long; *lower lobes* usually emarginate to shallowly emarginate, sometimes truncate or almost obtuse, externally covered all over by a moderately dense to dense indumentum of short to moderately long glandular hairs or short to long eglandular hairs or a mixture of both. *Stamens* with *anthers* 1.4-2.1(2.5)mm long, with *connectives* surrounded by usually dense, rarely moderately dense, long to very long eglandular hairs; rearmost pair of *awns* (0.1)0.15(0.3)mm long. *Capsules* (6)7-9(9.5)mm long, in lateral view obovate to ovate, (2.0)2.3-3.4(3.5)mm broad, in median view ovate to elliptic, sometimes narrowly so, usually acuminate, with distal (1/5)1/8-1/6 or less covered by dense setae, 0.1-0.2(0.3)mm long, *apex* in lateral view truncate to obtuse; *seeds* (3)39(82), (0.6)0.8-1.1(1.5) x (0.3)0.4-0.6(0.9)mm, obliquely ellipsoid, ovoid, oblange or reniform, sometimes broadly or narrowly so. Figs 8, 71.

**Distribution** (fig. 52): *E. collina* ssp. deflexifolia is known only from the east coast of Tasmania from the St Marys-Scamander region and about 80km further to the south on the Freycinet Peninsula. However, J.D. Hooker's collection of the subspecies (GHp.p.) must have come from outside this area of distribution, for he and Dr Lyall collected only "in the Derwent, and in the Lake District of Tasmania, and at Port Arthur" (Hooker 1859b, p. cxvii). Altitude, 0-200m.

**Ecology:** The subspecies occupies sand or sandy loam, in heath and dry sclerophyll (*Eucalyptus*) forest or woodland with a dense low heath understory. Except for *Barker 977*, the subspecies was seen on the granite outcrops of the Freycinet Peninsula. It may prefer granite-based soils such as on the granite mountains of the Freycinet Peninsula for the Scamander River and Falmouth localities have extensive areas of granite of a similar geological age within at the most a few kilometres (Banks 1965, map 4).

From the condition of herbarium specimens, all collected in November, flowering begins in October to November, and continues to December and possibly early January.

**Conservation status:** 2V, C.

**Note:** Some plants in *Barker 977* which appear depauperate and grazed have retained nevertheless the leaf characters used to distinguish the subspecies from its closest relatives (fig. 8).

**Specimens examined**


Barker 943, 9.xi.1970. Freycinet Nat. Park: on the track across The Hazards from Coles Bay to Wineglass Bay, c. 100m up the southern side of the saddle. AD.

Barker 948, 9.xi.1970. At the end of the track from Coles Bay, on the hill above Sleepy Bay, c. 3km SE of Coles Bay. AD.

Barker 949, 9.xi.1970. C. 4km NW of Coles Bay on the road to Bicheno. AD.


Fig. 71. E. collina ssp. deflexijolia. Inflorescence showing entirely white corollas, Freycinet Peninsula, Tasmania (Barker 939), scale 1cm.


E. glacialis Wettst. var. eglandulosa Willis, Muelleria 1 (1967) 146, p.p. (as to Darbyshire 73).


"E. aff. glacialis Wettst.": Burbidge & Gray, 1. c. 328.

"E. aff. glacialis Wettst. var. eglandulosa J.H. Willis": Burbidge & Gray, 1. c. 329.
Erect perennial *herb*, (10)18-45(56)cm tall, usually with few to many ascending branches, arising from lower part of stem or prostrate parts of other branches, with stem sometimes in first year bearing inflorescence, subsequently dying back to near ground level, sometimes reduced and never extending above branches near ground level. *Stem* or, if reduced, *main inflorescence-bearing branches* (7)10-26(50)cm high to base of inflorescence, simple for (1)4-21(31) nodes below inflorescence, i.e. for (0.35)0.8-1.0 of distance from inflorescence to ground level; upper (2)4-8(12) *internodes* as long as or longer than upper leaves, the longest (1.3)2.0-4.0(4.5) times length of upper leaves, those lower down much shorter; *axes* in upper parts bearing two rows of dense, short to moderately long eglandular hairs decurrent from between leaf bases, sometimes with somewhat sparser eglandular hairs between, sometimes glabrous between, sometimes (in plants of subalpine grasslands) mixed with sparse to dense tiny subsessile glands, with indumentum in lower parts sometimes similar, sometimes sparser and shorter or even lacking at base, rarely with sparse to dense moderately long glandular hairs. *Leaves:* *uppermost leaves* of stem or main inflorescence-bearing branches (5.6)7.4-13.5(23.0) x (2.4)3.4-7.0(8.0)mm, in outline usually elliptic or oblong-elliptic, sometimes ovate or obovate, serrate to crenate-serrate, with sessile gland patches extended over distal (0.6)0.7-0.85(0.9) of undersurface, sometimes glabrous, sometimes with margins lined with sparse to dense, very short to short, hard eglandular protuberances or sparse to moderately dense, short to moderately long eglandular hairs, sometimes (in plants of subalpine grasslands) also bearing very sparse to dense, tiny sessile glands *base* usually rounded to rounded-cuneate, sometimes narrow cuneate; *teeth* 1-3(6) along each margin, confined to distal (0.2)0.3-0.65(0.85) of leaf, usually blunt, rarely sharp, usually acute, sometimes obtuse, the longest tooth (0.5)0.7-2.0(2.8)mm long; *apical tooth* (1.1)1.3-2.8(4.3) x (0.9)1.4-2.5(5.1)mm, usually bluntly acute, sometimes sharp or obtuse, rarely shortly acuminate; leaves *lower down* with similar indumentum, at base rarely with sparse, moderately long glandular hairs. *Inflorescences* racemes, dense in bud (except for more widely spaced lower (0)1-3(5) nodes), moderately dense to dense in flower and fruit with (14)20-40(55) flowers, sometimes with lowest node bearing a single flower; *pedicels* at lowest node (0.6)1.3-5.5(9.2)mm long, shorter higher up; *internodes* elongating prior to anthesis; *rachis* as for upper part of axis; *apical bud cluster* cylindrical to conical or ovoid, usually narrowly so, with apex ± acute, initially (1.3)2.0-3.0(5.0)cm long, hidden by or hardly emergent from corollas of uppermost flower pair after flowers at first 3-23 nodes have reached anthesis. *Bracts* at lowest nodes like uppermost leaves in size, shape and indumentum, shorter higher up, those at lower 0-5(20) nodes extended past calyx, distal ones shorter, those at lower (2)4-9 (rarely all) nodes toothed, distal ones entire. *Calyx* (3.8)4.4-7.0(9.0)mm long, usually glabrous but for sparse to dense, very short to moderately long, lax to scabrous eglandular hairs on inner surface and margins of teeth, sometimes (in plants of subalpine grasslands) also with sparse to dense tiny subsessile glands on outer surface. *Corolla* (8.5)9.5-13.5(15)mm long along upper side, white, or coloured palely or deeply in blue, lavender, violet, lilac, purple, mauve or pink, with colour sometimes confined to tube and veins, sometimes on lobes and tube with broad white area behind lower lobes, sometimes all over but often paler behind lower lobes, with yellow blotch sometimes present on lower lip behind lobes, rarely also at point of insertion of filaments, sometimes absent; *tube* (6)7-10(11)mm long; *hood* (2.5)3.2-4.0(4.5)mm long; *upper lobes* usually obtuse, sometimes truncate to shallowly emarginate, rarely emarginate, with rear surface usually bearing sparse to dense, very short to short glandular hairs, sometimes confined to base of lobes, sometimes mixed with moderately dense to dense short eglandular hairs, sometimes glabrous; *lower lip* (4.4)5.5-7(8.5)mm long; *lower lobes* usually obtuse to truncate, sometimes shallowly emarginate, rarely emarginate, covered by usually moderately dense to dense, rarely sparse indumentum of short to moderately long glandular or eglandular hairs or both, rarely confined to proximal parts. *Stamens* with *anthers* (1.3)1.6-1.9(2.1)mm long,
with connectives surrounded by dense, long to very long eglandular hairs; rearmost pair of awns (0.15)0.2-0.3(0.4)mm long. Capsules (7.2)7.5-10.5(11.3)mm long, in lateral view (1.8)2.0-2.9(3.2)mm broad, usually elliptic or oblong, sometimes ovate or obovate or somewhat deflexed, rarely linear, in median view ovate-caudate to elliptic-acuminate, sometimes narrowly so, glabrous or bearing very sparse to dense, very short setae at apex only; apex in lateral view usually obtuse, sometimes truncate or acute, rarely shallowly emarginate-truncate, sometimes obliquely so; seeds (5)26-58(93), oblong to ellipsoid, sometimes obliquely so, (0.5)0.7-1.3(1.5) x (0.2)0.3-0.5(0.7)mm. Figs 8, 62.

**Typification**

*E. paludosa* R.Br. Two collections, one in K, the other in BM, are identified in Brown's handwriting as *E. paludosa* and are clearly the material upon which Brown (1810) based his description of the species. The two syntypes belong to the same subspecies of *E. collina*.

Both collections fit the protologue in morphology and distribution (the distribution designation "J" in the protologue was used by Brown to denote the area of his Sydney-based collections). The K specimen was described in Brown's (unpubl.) manuscript. Although there is no reference to the BM specimen in the manuscript, the protologue was presumably based on both.

The BM specimen is chosen as lectotype on several grounds. Stearn (1960) considered that lectotypes of Brown's species should be the most complete specimen in BM, it follows the view of Du Rietz (1948b) who called the BM specimen "holotypus" (however there is no evidence that he saw the K syntype), and the BM specimen is of superior quality.

**Distribution** (fig. 53): *E. collina* ssp. *paludosa* is widely spread in eastern Australia from the Mt Lofty Ranges of South Australia to the very south of Queensland. There is one doubtful record from Hobart, Tasmania (note 4).

The subspecies is most common in the montane and subalpine regions of eastern Victoria and New South Wales. In southern Queensland it is known from only two old collections. In South Australia the subspecies was confined to the Mt Lofty Ranges, which is a noted refuge area for plant species common in the wetter climates of south-eastern Australia and apparently more widespread in previous cooler and wetter times (e.g. Parsons 1973); it is now apparently extinct. Ssp. *paludosa* also occurs in the regions of Victoria between Port Phillip and Warrnambool and probably near Maryborough (note 1), and in the coastal regions of New South Wales, north of Botany Bay. Altitude, near sea level to 1900m.

**Ecology:** Ssp. *paludosa* occupies a wide range of habitats. In the subalpine zone of south eastern Australia it is common in sparse to dense snowgum (*Eucalyptus pauciflora*) woodland and sod-tussock grassland, but sometimes also occurs in heath or areas of shrubs in sparse snowgum woodland, or in grassy areas associated with bogs or swamps. On the summit of Mt Speculation, Victoria, it occurs above the tree-line in a herbfield with scattered shrubs (*Barker 1543*). In lower mountain regions of south-eastern Australia it is common in wet or dry sclerophyll forest or grassy clearings between, but has also been recorded in association with swamps or in "damp heath". In western coastal regions there are records from heath and swampy sites. Finally, there is one record (Anon. 44) from a sand hill apparently near Walmer in the south-western plains of New South Wales. There are no data concerning the South Australian localities.

The subspecies has been recorded in sandy to clay soils associated commonly with granite, but also with shale, sandstone or sedimentary rocks.
The time of flowering varies with the climatic zone. In lowland and montane regions it occurs mainly between the beginning of August and the start of December. The specimens in *Brown K*, collected at the end of June from Botany Bay, had begun to flower. In subalpine regions flowering often is later and occurs mainly between late September and early February, with one record (*Gray 5087*) of plants flowering in mid March.

*Conservation status:* considered not at risk.

*Notes:* 1. There are problems in assessing the extent to which morphological distinctions between ssp. *paludosa* and ssp. *collina* are maintained in central and southern Victoria and the distribution of the two subspecies there. See ssp. *collina*: note 1.

2. Ssp. *paludosa* is one extreme of a polymorphic complex involving ssp. *speciosa* and ssp. *diversicolor* (see *E. collina*: Intraspecific Polymorphism). The possibility of its involvement in the part of the complex involving ssp. *speciosa* and an allied variant in lowland and montane New South Wales is discussed under ssp. *speciosa* (note 1). Its general lack of intergradation with ssp. *diversicolor* and an allied variant, apart from one instance of hybridization, is detailed under *E. collina*: Intraspecific Polymorphism.

Ssp. *paludosa* shows polymorphism in the indumentum of the axes, leaves, bracts and calyces. Variation in presence or absence of subsessile glands in higher altitudes of the southern tablelands of New South Wales cannot be dealt with formally (note 3). However, in the subalpine and alpine grasslands of the Mt Howitt-Mt Wellington region of Victoria's eastern highlands, these subsessile-glandular types are replaced by populations including plants with longer glandular hairs. A comparison of the variation in diagnostic characters in the two glandular variants recognized informally from these regions and typical ssp. *paludosa* is given in table 9.

In the Mt Wellington region non-glandular populations of ssp. *paludosa* occur in the areas of wet sclerophyll forest (*Barker 1489*) while the predominantly glandular “Mt Wellington variant” occupies nearby subalpine snowgum woodland and tussock grassland. Similarly the two collections of the glandular “Mt Howitt variant” were apparently collected from the summit region above the tree-line. Populations of non-glandular ssp. *paludosa* (*Barker 1504, 1505, 1510, 1511*) are prevalent within snowgum woodland in the same region.

Pollen sterility tests have been made on plants from the Mt Howitt glandular populations (PS302-304), the glandular (PS294-301) and non-glandular (PS42-44) plants of the Mt Wellington populations, and the related glandular (PS286) and non-glandular (PS287-288) plants from the region between Mt Wellington and Mt Howitt. There is no evidence that any of these populations are hybrid swarms. There were occasional plants with high sterility but their low frequency indicates that this is probably caused by other factors unrelated to hybridism.

These variants almost certainly have their own genetically based independent variability, but in view of the apparently poor morphological distinction between them, a wider study of populations in the region in the context of a critical study of the whole complex is needed to clarify whether any formal taxonomic recognition, possibly at a varietal level, is warranted.

3. In ssp. *paludosa* there are variations in characters of indumentum and seed size which are apparently related to altitude and geographical distribution.

Subsessile glandular hairs (see p. 13) are confined to populations at higher altitudes particularly in the Snowy Mountains of New South Wales, and are especially dense on
plants of the higher parts of the Mt Kosciusko region near Charlottes Pass (e.g. Barker 1700, Johnson & Constable NSW15760). They are much sparser or sometimes completely absent on plants of lower subalpine areas, both in the Mt Kosciusko region and in the extensive tussock grass-lands to the north. Occurrences of these hairs outside the Snowy Mountains seem limited to two localities. Specimens in the subalpine woodland of the Brindabella Range (e.g. Barker 1644) bear subsessile glandular hairs mainly on the calyx; in other subalpine or montane sites only non-glandular plants seem to occur. In the summit populations of Mt Speculation, Victoria (Barker 1542-1543), rare plants have subsessile glandular hairs mainly confined to the lower leaves, but the majority lack these glands.

Seeds are generally larger in ssp. paludosa in the Kosciusko region (usually 1.0-1.4mm long), where plants invariably bear a sparse to dense indumentum of subsessile glandular hairs. This, however, seems to be an independent altitudinal phenomenon as elsewhere populations with subsessile glandular hairs have the more normal smaller seeds (usually 0.6-1.1mm long). Similar reduction in seed size with lower altitude is seen in other taxa and groups of taxa in the genus in Australia (p. 35).

Because of the large number of populations with only a partial incidence of the scattered subsessile glandular hairs and the lack of a strong correlation of their presence with other character differences, formal taxonomic recognition is unwarranted.

4. In ssp. paludosa branching is restricted to the regions of the axes at or near ground level throughout most subalpine and montane areas. However, specimens with branches or shoots occurring well up the main axes are rather common in the montane regions of northern New South Wales and southern Queensland. This type of habit also predominates in the collections from the coastal areas of New South Wales north of Newcastle, Mt Stanley (Canning 364) and Mt Granya (Wallner MEL1306) which are isolated mountains of north-eastern Victoria, East Gippsland (Sayer MEL1323, MEL1324), and the Dandenong Ranges and other more westerly montane and lowland areas on the edge of the eastern highlands of Victoria (Gargurevich MEL1373, Walter NSW10944, AK30649).

The record of ssp. paludosa from Hobart is doubtful as it is represented only by Caley MEL1441. Since Caley also collected in the Sydney region, where in his time ssp. paludosa was apparently prevalent, the specimens could have come from there. However, the possible occurrence in south-east Tasmania cannot be ruled out completely as the surroundings of Hobart, especially on the east side of the Derwent, do not appear to have been extensively botanized (see E. collina ssp. gunnii and ssp. deflexifolia).

Selected and cited specimens


NEW SOUTH WALES (156 seen): Anon. 44, 18.ix.1860. Wolmar [?Walmer]. MEL(p.p.).—Barker s.n., 14.x.1896. Sydney. LY (holotype of E. novae-cambriae); BISH.—Barker 1662, 21.i.1972. Long Plain, which is along the east side of The Fiery Range; c. 20km NNE of Rules Point. AD.—Barker 1666(p.p.), 1670(p.p.), 22.i.1972. SE end of Toolong Range, on top of southern ridge of Mt Jagungal, c. 50m below and c. 1¼-1½km S of summit. AD (2 specimens).—Barker 1680, 23.i.1972. Three Mile Creek; c. 5km SW of Kiandra; near the road to Cabramurra. AD.—Barker 1690, 1693, 26.i.1972. C. 1½km E of The Smiggins Holes, c. 50m of bridge across Pipers Creek. AD.—Barker 1695, 26.i.1972. Perisher Valley; on slopes of hill E of bridge across Perisher Creek on North Perisher Road. AD.—Barker 1700, 26.i.1972. C. 50m NW of bridge across Spencers Creek on Kosciusko Summit Road, c. 3km ENE of Charlotte Pass. AD.—Beckler s.n., s.dat. Hastings River. MEL1427, MEL1477.—Boorman s.n., viii.1909. Smoky Cape. NSW10934.—Boorman s.n., ix.1911. Port Stephens. W27532.—R. Brown 2721, s.dat. Port Jackson. BM (lectotype of E. paludosa).—R. Brown s.n.,
Studies in Euphrasia


E. collina R.Br.: Benth., Fl. Austral. 4(1868) 520, p.p. (as to Wilhelmi MEL41377 and a number of other specimens


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Erect perennial herb (9.5)21-33(41)cm tall, with several to many, erect or ascending annual branches arising usually from perennating base, sometimes somewhat higher up from other branches. Stem reduced; main inflorescence-bearing branches (7.0)13.5-27(29)cm high to base of inflorescence, simple for (6)7-26(42) nodes below inflorescence, i.e. for (0.55)0.75-1.0 of height of inflorescence above ground level; upper (0.3)3-7(8) internodes as long as or longer than upper leaves, the longest internode (0.8)2.3-3.3(4.5) times the length of upper leaves, those lower down shorter than leaves; axes in upper parts bearing two rows of dense, short to moderately long eglandular hairs decurrent from between leaf bases, often with sparser eglandular hairs between, lower down with eglandular indumentum usually sparser and shorter or absent, rarely (Mueller MEL41511) dense and long and mixed with dense, short to long glandular hairs. Leaves: uppermost leaves of main inflorescence-bearing branches ovate-elliptic to obovate-elliptic in outline, (5.9)6.5-11.5(14) x (1.8)0.5-7.6(7.6)mm, serrate to pinnatifid-serrate, with sessile gland patches confined to distal (0.35)0.55-0.9(0.95) of leaf, otherwise usually moderately densely to densely scabrous or scaberulous all over, rarely sparsely so, or glabrous; base rounded-cuneate to narrow-cuneate; teeth (1)2-3(4) along each margin, confined to distal (0.25)0.35-0.65(0.75) of leaf, blunt or sharp, usually acute, rarely obtuse, the longest tooth (0.5)0.7-1.8(2.1)mm long; apical tooth (0.9)1.2-2.8(3.2) x (0.8)1.0-1.7(2.0)mm, usually blunt, sometimes sharp, usually acute, rarely obtuse; middle leaves like upper leaves but usually with shorter scabridity or glabrous; lowest leaves sometimes glabrous, sometimes sparsely or scaberulous, sometimes bearing moderately dense to dense, very short (subsessile) to moderately long glandular hairs, rarely slightly scabrous or glabrous; inflorescences racemes, excluding widely-spaced flowers at lowest (0)1-2(5) nodes dense in bud, usually moderately dense to dense, rarely sparse in flower and fruit, with (22)26-46(50) flowers, sometimes with lowest node supporting a single flower; lowermost pedicels (0.7)1.0-3.7(4.7)mm long; rachis as for upper parts of axis; apical bud cluster usually narrowly cylindrical to narrowly ovoid- or conical-cylindrical, rarely broadly ovoid, initially c. 1.5-4cm long, hidden by or hardly emergent from corollas of uppermost flower pair after first (3)5-15 pairs of flowers have reached anthesis. Bracts similar in size and shape to uppermost leaves, usually moderately densely to densely scabrous or scaberulous all over, rarely sparsely so, those at lower (5)9-15 or more nodes toothed, distal ones entire, with all bracts, except sometimes for those at lower 2-5(7) nodes shorter than or equal to calyx. Calyx (3.5)3.6-6.5(6.7)mm long, with external surface covered by moderately dense to dense, very short to long, usually stiff, rarely lax eglandular hairs, sometimes with indumentum denser on teeth, sparser towards base. Corolla (9.4)9.8-13.5(14.8)mm long along upper side, apparently (from dried material) purplish or lilac, sometimes with a paler tube and lower lip behind lower lobes, with incidence of yellow blotch on lower lip unknown; tube 6-8.5(10)mm long; hood 3-5(6.5)mm long; upper lobes usually shallowly emarginate, sometimes truncate or obtuse or praemorse, rarely emarginate, with rear surface covered by moderately dense, very short glandular hairs, or moderately dense to dense, very short to moderately long eglandular hairs, or a mixture of both; lower lip (4.5)6-10.5(12)mm long; lower lobes usually emarginate or deeply so, rarely shallowly emarginate or praemorse obtuse, externally covered by a dense indumentum usually of very short to long eglandular hairs, rarely of very short glandular hairs or a mixture of both. Stamens with anthers (1.4)1.5-1.8(1.9)mm long, with connectives surrounded by dense, long to very long eglandular hairs; rearmost pair of anther awns 0.15-0.3(0.35)mm long. Capsules c. 6.5-8mm long, in lateral view ovate-elliptic to obovate, often narrowly so, or ± caudate, 1.5-2.5mm broad, in median view narrowly ovate-caudate to narrowly elliptic-acuminate, usually with dense, very short to moderately long setae over
distal ($\frac{2}{3}$) or less, sometimes sparsely setose at apex only, or glabrous; apex in lateral view acute, obtuse or truncate, often obliquely so; seeds c. 19-96, (0.35)0.4-0.8 x 0.2-0.4(0.5)mm, ellipsoid, oblong, ovoid or reniform, often obliquely or broadly so. Fig. 68.

Typification

_E. muelleri_ Wettst. Wettstein (1896) combined plants of three subspecies of _E. collina_ under his new species _E. muelleri_. It is clear from the protologue, including the key and the illustration, that the species was characterized by "bracteae et tubus calycis setis tninutis dense obsiti". Neither _Wilhelmi W71487_, which is related to _ssp. collina_, nor one fragment of _ssp. trichocalycina_ in _Walter W3912_ have eglandular hairs on the bracts and the outer surface of the calyx. All the other syntypes seen were considered for lectotypification as each have this indumentum, although sometimes it diverges slightly from the protologue by being sparse on the bracts and tube. The choice of lectotype from among these specimens was based primarily on the quality of the material.

Distribution (fig. 53): Old collections of _E. collina_ ssp. _muelleri_ indicate that the subspecies was once widely distributed on the mainland of Australia from northern New South Wales near the Queensland border throughout mainland south-eastern Australia, and westwards as far as the Mt Lofty and Southern Flinders Ranges of South Australia. For one erroneous record (_Stuart MEL41509_) from Tasmania see ssp. _osbornii_; note 2.

There are many more collections from central and western Victoria than from New South Wales and South Australia, which, from the many collections made of _Euphrasia_ in the respective areas in the 19th century, indicates the subspecies was rare outside these parts of Victoria. Only two collections have been made since 1907; they came from Frankston, a Melbourne suburb on the western side of Port Phillip Bay, in 1947 and 1949. Only an active search for material of this subspecies will indicate whether it is truly extinct or not.

Altitudinal data are lacking; it occupied lowland and at least low mountain habitats.

Ecology: There are insufficient ecological data on herbarium labels to gain a picture of the range of habitats which have been occupied by ssp. _muelleri_. Those available (_Stirling 166; Mueller MEL41378_) indicate an open meadow habitat. The annotations on two mixed herbarium sheets, possibly also pertaining to ssp. _muelleri_, refer to damp places (_Mueller MEL41379, Anon. MEL41410_).

Flowering material has been collected mainly between August and November, with capsules being present from September. One collection from northern New South Wales (_Boorman G_) was collected in July and bears buds, flowers and fruits.

Conservation status: 3E/X (see distribution).

Note: A few collections diverge in the indumentum of the calyces, bracts and upper leaves from typical ssp. _muelleri_ (fig. 53). Several collections from western Victoria and south-eastern New South Wales (_Mueller GHp.p., Crouch MEL41431, Eckert 29, Reader 9, Rodd 886, Sullivan 43, Whan NSW10940_) bear sparse to dense glandular hairs, 0.05-0.1mm long, mixed with the moderately densely to densely eglandular scabrous or scaberulous indumentum characteristic of ssp. _muelleri_. Still other forms apparently confined to the Southern and Central Tablelands and South-western Slopes regions of New South Wales, and possibly in Victoria near the Snowy Mountains, bear woolly eglandular hairs 0.2-0.5mm long on the upper parts, with the indumentum shorter lower down (_Bull MEL41486, Rawes 34, Curran MEL41719_). There are two similar specimens (mounted with a densely glandular plant related to ssp. _speciosa_) in _Anon. MEL41503_ from nearby in New South Wales; they bear dense woolly eglandular hairs c. 0.2mm long mixed with very short glandular hairs on the bracts and rachis, and also differ from typical ssp. _muelleri_ by their
very elongated inflorescences with long pedicels and long narrow leaves with 1-2 pairs of teeth. The long woolly eglandular variants lacking glandular hairs may be extremes of variation in normal populations of ssp. muelleri; Mueller MEL41375 and French MEL41748 contain some plants with the scabrous indument typical of the subspecies, and others with a longer, more lax indumentum in the upper parts. However, the glandular variants of ssp. muelleri are more likely to represent one or two distinct taxa or intergrades with ssp. speciosa. To establish the true relationships between ssp. muelleri and these variants surviving populations of each must be found.

Selected and cited specimens


Specimens with affinities to ssp. muelleri


WITHOUT LOCALITY: Sullivan 43, s.dat. MEL41704.

11k. ssp. nandewarensis Barker, subspecies nova

Subspecies nova Euphrasia collinae prope ssp. paludosam et ssp. diemenicam indumento non-glanduloso in calyce rami simplices super terram, sed differt a duabus foliis multidentatis indumento glanduloso semper in partibus inferis, etiam a ssp. diemenica lobis corollae plerumque obtusis usque truncatis interdum ita praemorse, foliis summis apice acuto usque subcaudato et dentibus secus multum longitudinis distribuit, seminibus brevioribus.


Erect perennial herb, c. 30-50 cm tall, with ascending branches arising from stem near ground level or prostrate parts of other branches (stem reduced in plants seen). Main inflorescence-bearing branches c. 20-35 cm high to base of inflorescence, simple for 15-70 nodes below inflorescence, i.e. for 0.85-1.0 of distance from inflorescence to ground level; upper 0-11 internodes longer than or as long as upper leaves, the longest internode c. 1.0-2.5 times length of upper leaves, those lower down shorter; axes in upper parts
Fig. 72. Holotype of *E. collina* R.Br. ssp. *nandewarensis* Barker, ssp. nov. (scale 5cm).

Fig. 73. Holotype of *E. collina* R.Br. ssp. *osbornii* Barker, ssp. nov. (scale 5cm).
bearing very short to short eglandular hairs, sparse to dense in two rows or four lines
decurrent from between leaf bases, sparser in between, or dense all around, in lower parts
with similar eglandular indumentum, but in lower $\frac{1}{2}$ also bearing short to long glandular
hairs, which are moderately dense to dense near base. Leaves: uppermost leaves of main
inflorescence-bearing branches 9-18 x 4-9.5mm, elliptic to ovate in outline, serrate,
sometimes deeply so, with sessile glands on undersurface extending over distal 0.65-1.0 of
leaf, with margins lined by dense, very short, scabrous white eglandular protruberances,
often also on upper surface and veins of lower side, otherwise glabrous; base rounded-
cuneate to cuneate; teeth 4-6 along each margin, confined to distal 0.65-0.85 of leaf, sharp or
blunt, usually acute to caudate, rarely obtuse, the longest tooth c. 0.9-4(5)mm long; apical
tooth c. 1.8-3.2 x 0.7-2.5mm, usually blunt, rarely sharp, usually acute, sometimes almost
caudate; leaves lower down with similar eglandular indumentum, on leaves of basal $\frac{1}{2}$ of
axes bearing very short to moderately long glandular hairs, moderately dense to dense at
base, grading to very sparse distally. Inflorescences racemes, dense in bud, usually
moderately dense to dense, rarely sparse in flower and fruit, with c. 35-50 flowers, with basal
node sometimes bearing only one flower; pedicels at lowest node c. 0.4-3.0mm long, shorter
higher up; rachis as for upper parts of axis; internodes elongating prior to anthesis;
apical bud cluster narrowly cylindrical to ovoid, c. 2.5-4cm long, with apex rounded or acute,
becoming hidden by or hardly emergent from corollas of uppermost flower pair after first c.
14 or more flowers have reached anthesis. Bracts at lowest nodes similar in shape and
indumentum to uppermost leaves, shorter higher up, extending past calyces at lowest 1-8
nodes, shorter higher up, with all bracts toothed. Calyx c. 5-7.5mm long, externally glabrous
often except for eglandular protuberances similar to those lining margins of leaves. Corolla
(the lowermost corollas of main inflorescences not seen) similar in size to ssp. paludosa,
white, very pale lilac or “white, becoming pink on drying” (Johnson & Constable NSW
30524), (presence of yellow blotch on lower side not known); lobes obtuse to truncate,
sometimes praemorse, with rear of upper lobes ± glabrous, or covered by sparse, very short
glandular hairs, with external surface of lower lobes covered by sparse to dense, moderately
long to long eglandular hairs, sometimes mixed with a few short to moderately long
glandular hairs. Stamens with anthers c. 1.5-2.3mm long, with connectives surrounded by
dense, long to very long eglandular hairs; rearmost pair of awns 0.2-0.3mm long. Capsules c.
7.5-14.5mm long, in lateral view c. 2.9-3.8mm broad, ± elliptic, sometimes obliquely so, in
median view elliptic-acuminate to ovate-caudate, glabrous except sometimes for very short
to short setae, very sparse and confined to apex, or moderately dense along lines of
dehiscence of distal $\frac{1}{2}$; apex in lateral view usually obtuse, sometimes narrow acuminate;
seeds c. 12-60, c. (0.5)0.6-0.9 x 0.3-0.6mm, ellipsoid to reniform-ellipsoid, sometimes
broadly so. Figs 8, 72.

Distribution (fig. 54): E. collina ssp. nandewarensis is apparently confined to the Nandewar
and Warrumbungle Ranges, two ranges about 80km apart and to the west of the main part
of the Great Dividing Range in northern New South Wales. Altitude, 1155-1490m in
Nandewar Range; no data from the Warrumbungles which only reach about 1200m.

Ecology: From annotations provided the subspecies occurs in Eucalyptus sclerophyll forest
or Eucalyptus pauciflora snowgum woodland, at least sometimes in areas of grass, herbs or
low shrubs.

Both the Warrumbungles and the Nandewar Ranges have apparently very similar late
Tertiary volcanic origins (Morcombe 1969). Accordingly the restriction of the subspecies to
these ranges may reflect soil preference.

Flowering occurs between October and January, although one plant (Briggs NSW) with
a few flowering branches amongst fruiting ones, was collected in April from high on Mt
Kaputar. Fruits begin to form between about October and January and possibly later.
Studies in *Euphrasia*

**Conservation status**: 2V/R, C.

**Specimens examined**


**111. ssp. speciosa (R. Br.) Barker, comb. & stat. nov.**


Erect perennial *herb*, often woody at base, (15)26-40(50)cm high, with branches either ascending, arising from near ground from reduced stem or prostrate parts of other branches, or rapidly ascending and arising from lower nodes of single erect stem flowering in first year, then dying back to near ground level, and lower parts of other branches. Stem or, if stem reduced, main inflorescence-bearing branches (12)15-30(35)cm high to base of inflorescence, simple for (4)5-32(53) nodes below inflorescence, i.e. for (0.5)0.7-1.0 of height from ground level to inflorescence; upper (2)4-8 internodes longer than or as long as leaves, the longest internode (1.8)2.3-6.0(7.0) times length of upper leaves, those lower down shorter than leaves; axes in upper parts with usually two rows, sometimes four lines of sparse to dense, short or moderately long glandular hairs recurrent from between leaf bases, sometimes with sparser eglandular hairs between, mixed all around with usually moderately dense to dense, sometimes sparse, moderately long to very long glandular hairs, lower down with glandular indumentum almost always extending to very base of plant, often denser, rarely sparser, rarely absent from lower parts, with eglandular hairs somewhat sparser and shorter. Leaves: uppermost leaves of stem or main inflorescence-bearing branches (4.8)5.4-16.0(17.0) x (2.6)3.0-8.0(10.0)mm, usually ovate or broadly so to ovate-elliptic, sometimes obovate-elliptic, serrate or crenate, with sessile gland patches on undersurface, covered by usually dense, rarely very sparse (Baeuerlen 215) or absent (Fletcher NSW10907), usually short to moderately long, rarely long glandular hairs, with margins lined by dense, short, white scabrous eglandular hairs, with upper surface covered by similar, but sometimes sparser and somewhat more lax eglandular hairs; base usually broadly rounded to rounded-cuneate, sometimes cuneate; *teeth* 2-5(8) along each margin,
spread over distal (0.45)0.55-0.9 of leaf, usually bluntly acute, sometimes sharp or obtuse, the longest tooth (0.6)0.7-2.5(3.3)mm long; apical tooth (1.0)1.3-3.4(4.0) x (0.9)1.1-2.5(3.5)mm, usually blunt, sometimes sharp, acute or obtuse; leaves lower down with glandular indumentum usually continuing to very base of plant, where often dense, rarely very sparse, rarely absent from lowest leaves, with eglandular indumentum similar to uppermost leaves. Inflorescences racemes dense in bud, usually sparse to moderately dense, rarely dense in flower and fruit, those of stem or main inflorescence-bearing branches with (20)22-40(56) flowers, with usually two flowers at each node, rarely only one at lowest node; pedicels at lowest node (0.5)0.7-4.0(5.5)mm long, shorter higher up; rachis as for upper parts of axis, but indumentum slightly denser and longer; internodes elongating prior to anthesis; apical bud cluster usually ovoid-conical or cylindrical, or narrowly so, usually with apex rounded, rarely acute, initially c. 2.5-3.5(6.5)cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after first (4)7-14 or more flowers have reached anthesis. Bracts at lowest nodes similar in shape and indumentum to uppermost leaves, shorter higher up, rarely extending past calyx and then only at lowest 1-2 nodes, with all toothed. Calyx (3.2)4.2-7.8(8.5)mm long, externally covered by dense, usually short to moderately long, sometimes long glandular hairs, often mixed on margins with dense moderately long eglandular hairs sometimes extending over outer surface, internally with sparser similar glandular hairs towards tooth apices, with sparse to dense eglandular hairs towards base of teeth and in distal part of tube. Corolla (9)11-15.5mm long along upper side, bluish, violet or purple, with mouth and tube lacking yellow blotch (Brown, unpubl.: under "E. coerulea"), behind lower lobes often apparently whitish (yellowish in dried material, e.g. Woolls MEL41494); tube (5)7-9.5(11.5)mm long; hood (2.3)2.8-5.0(6.5)mm long; upper lobes usually obtuse, sometimes truncate or praemorse, with rear surface sometimes with sparse to dense, usually short, rarely long glandular hairs, sometimes with sparse to dense, very short to moderately long glandular hairs, the indumentum sometimes confined to proximal parts, rarely ± glabrous; lower lip (4)6-10(11)mm long; lower lobes usually obtuse or truncate, sometimes emarginate and then usually shallowly so, externally bearing usually moderately dense to dense, rarely sparse indumentum of very short to moderately long glandular or eglandular hairs or both. Stamens with anthers (1.3)1.5-1.9(2.2)mm long with connectives surrounded by dense, long to very long eglandular hairs; rearmost pair of awns (0.1)0.2-0.3(0.4)mm long. Capsules 5.5-9(13)mm long, in lateral view usually ovate to obovate-elliptic, sometimes narrowly so, rarely ± linear, 2.0-3.3mm broad, in median view ovate to ovate-caudate, sometimes narrowly so, with usually dense, rarely moderately dense setae 0.1-0.2(0.25)mm long, covering distal (1/4)1/3-1/2; apex in lateral view acute, obtuse or truncate, sometimes obliquely so; seeds (0)35-80(140), 0.4-0.9(1.0) x 0.2-0.4(0.5)mm, ovoid to ellipsoid or oblong, often obliquely so. Fig. 9.

Typification

E. speciosa R.Br. The BM specimen is clearly a syntype as it bears the name “E. speciosa” in Brown's handwriting, and agrees with the protologue (Brown 1810) in morphology. There is no reason to doubt that Brown's (unpubl.) manuscript description of “E. coerulea” is the basis for the initial diagnosis of E. speciosa, and that the K specimen is a duplicate. The manuscript description of “E. coerulea” was based on plants collected by Brown at Port Jackson on 14th May, 1802. It clearly agrees with the K and BM syntypes as well as with the protologue of E. speciosa. The other seven species described in Brown's (1810) 'Prodromus' had a matching description of type material in the manuscript. This is the only description in the manuscript that could correspond to E. speciosa, as defined by the BM syntype and the brief description in the protologue. If this is so, the K specimen is definitely a syntype (and almost certainly a duplicate of the BM specimen) as not only does it come from the locality cited in the manuscript and protologue, but it was also identified by Brown as “E. decussata”, a name which Brown initially used in his manuscript description, but which he subsequently crossed out and replaced with “E. coerulea”.

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The BM collection is chosen as lectotype on the basis of its superior quality and Stearn's (1960) recommendation that lectotypes of Brown's species come from BM.

**Distribution (fig. 54):** *E. collina* ssp. *speciosa* is at present known in New South Wales from the Central and Southern Tablelands (including the Australian Capital Territory), from the coastal areas between Bulladelah and Jervis Bay, and from the eastern part of the Central Western Slopes in the region of Mudgee. In Victoria it is known from several old collections from the eastern part of the western highlands between Ballarat and Heathcote. Altitude, 0-1370m.

Plants allied to ssp. *speciosa* (see note 1) are apparently confined to New South Wales but are otherwise similarly distributed.

**Ecology:** In montane areas ssp. *speciosa* grows in open *Eucalyptus* sclerophyll forest or woodland, swampy areas, or (Constable NSW48942) a “rocky bank above creek”. In the coastal region near Sydney it has been found associated with sandstone “in sandy soil; rather moist open situation” (Evans SYD). There are no data from Victoria.

The variant allied to ssp. *speciosa* (see note 1) occupies similar montane and lowland sites, with additional records from coastal heath. There are several references to sand or sandstone.

Flowering occurs mainly between August and December, although the holotype, collected in May (Brown unpubl.), contains flowers and young fruits. Capsules form from September.

**Conservation status:** 3 R, C.

**Notes:** 1. Ssp. *speciosa* is an extreme variant of the polymorphic complex which also encompasses ssp. *paludosa* and ssp. *diversicolor*. The overall variation in the complex and its taxonomic problems are discussed under *E. collina* (Intraspecific Polymorphism). In New South Wales, between the Lithgow area of the Blue Mountains and Jervis Bay (fig. 54), occur plants partially linking ssp. *speciosa* with ssp. *paludosa*. The most extreme variants in collections of these plants are characterized by glandular hairy upper parts and non-glandular lower parts, subglabrous capsules, and leaves resembling ssp. *paludosa* by their narrower width and usual confinement of teeth to the distal half. Collections of plants such as these may also contain intermediate individuals, some with glandular hairs extending down to the very base, but with subglabrous capsules, others with capsules densely setose in the distal $\frac{1}{3}$-$\frac{1}{2}$, yet with glandular hairs confined to the upper parts. Two collections (Gauba 7859, 9245; Constable NSW126378) contain plants resembling ssp. *speciosa* in addition to others with glabrous capsules and a limited glandular indumentum.

The significance of these collections which form a partial intergradation between ssp. *speciosa* and ssp. *paludosa* is indefinite. Further study may show them to be the components closest to ssp. *speciosa*, of a cline between the two subspecies. As such they may be remnants of an evolutionary link between them. Alternatively, they may result from an introgression of characters of ssp. *paludosa* into populations of ssp. *speciosa*. This could explain the apparent lack of a full intergradation between the two subspecies. A pollen sterility test (PS181) showed no high incidence of sterility in the intermediates. On the other hand the populations from which the collections came may have a stabilized inherent variation in the above characters, and, whatever the past origin of this variation, may now be spatially and genetically independent of populations of ssp. *speciosa* and ssp. *paludosa* to maintain this variation. If further study shows this to be the case, it is suggested that they be recognized as a distinct variety of ssp. *speciosa*.

2. Possible intergrades with ssp. *muelleri* are discussed in the note under that subspecies.
Selected and cited specimens


NEW SOUTH WALES (47 seen): Anon. s.n., capitaine Baudin) s.n., of this component partially purplish, not yellow). Anon. S. NEW SOUTH WALES (47 seen): AUSTRALIAN CAPITAL TERRITORY (4 seen):

Selected and cited specimens


Subspecies nova Euphrasiae collinae, proxima ssp. speciosam indumento glandulosum, capsula dense setosa, foliisque summis multidentatis in axe principalis inflorescenti, sed differt rami surculivse super terram, plurumque sic multimum, pilisque glandulosii a basi plantae saepe absensibus; etiam ssp. trichocalycinae, ssp. gunni, ssp. deflexifoliaeque similares indumentum glandulosum habituque, sed differt dentibus multis secus multum longitudinis foliorum, seminibus minoribus, et corollis maioribus.

11m. ssp. osbornii Barker, subspecies nova


Subspecies nova Euphrasiae collinae, proxima ssp. speciosam indumento glandulosum, capsula dense setosa, foliisque summis multidentatis in axe principalis inflorescenti, sed differt rami surculivse super terram, plurumque sic multimum, pilisque glandulosii a basi plantae saepe absensibus; etiam ssp. trichocalycinae, ssp. gunni, ssp. deflexifoliaeque similares indumentum glandulosum habituque, sed differt dentibus multis secus multum longitudinis foliorum, seminibus minoribus, et corollis maioribus.

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Erect perennial herb, woody at base, (13)25-47(60)cm high, with branches erect or rapidly ascending, arising from single erect stem, terminated by inflorescence in first year, dying back to upper branches in subsequent years. Stem or after first year, main inflorescence-bearing branches (8.5)15-35(45)cm high to base of inflorescence, simple for (1)3-14(32) nodes below inflorescence, i.e. for (0.15)0.3-0.75(0.85) of height from ground level to inflorescence; upper (3)4-7(10) internodes longer than or as long as leaves, the longest internode (1.5)2.0-3.2(4.1) times length of upper leaves, those lower down shorter than leaves; axes in uppermost parts with two rows of dense, eglandular hairs (0.1)0.2(0.3)mm long decurrent between leaf bases, with usually only slightly sparser, rarely sparse eglandular hairs between, with sessile gland patches on undersurface often obscure, but when apparent extended over distal 0.8 to entire length of leaf surface, covered by usually dense, rarely moderately dense glandular hairs, 0.1-0.2(0.5)mm long, sometimes mixed with sparse to moderately dense, very short to short scabrous eglandular hairs confined to margins and upper surface; base truncate or broadly rounded; teeth (1)3-6(8) along each margin, spread over distal (0.35)0.5-1.0 of leaf, usually blunt, sometimes sharp, usually acute, rarely obtuse, the longest tooth (0.4)0.9-1.7(2.9)mm long; apical tooth (1.1)1.2-2.9(3.3) x (0.8)1.0-1.8(2.3)mm, usually blunt, rarely sharp, usually acute, rarely obtuse; leaves lower down with glandular indumentum sparser from point (0.15)0.25-0.6(0.8) of distance from base of inflorescence to ground, absent from point (0.25)0.6-0.9(1.0) of same distance below inflorescence, with glandular hairs on lowest leaves usually very sparse or absent, rarely dense, 0.1mm long or less, with eglandular hairs usually absent from lower leaves, rarely dense to moderately dense and very short. Inflorescences racemes, dense in bud, moderately dense to dense in flower and fruit, sometimes with lowest 1-2 nodes more widely spaced, those of stem or main branches with (20)24-56(60) flowers, with usually two flowers at each node, sometimes only one at lowest node; pedicels at lowest node (0.7)1.0-2.7(4.8)mm long, shorter higher up; rachis as for upper parts of axes, but indumentum slightly denser and slightly longer; internodes elongating prior to anthesis but very little after, such that capsules reach up to or past base of calyx above; apical bud cluster usually ovoid to ovoid-cylindrical or narrowly so, with rounded apex, rarely conical-cylindrical with acute apex, initially c. 2.5-3.5cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after first 9-12 or more pairs of flowers have reached anthesis. Bracts at lowest nodes similar in shape and indumentum to uppermost leaves, shorter higher up, rarely extending past calyx and then only at lower 1-2 nodes, with all, rarely except for the very distal ones toothed. Calyx (4.0)4.6-7.0(7.5)mm long, externally covered by glandular hairs 0.1-0.25(0.3)mm long, dense on teeth and distal part of tube, often sparse towards base, with eglandular hairs lacking except towards base of tube, internally with similar but sparser glandular indumentum on teeth, often mixed with very short to short eglandular hairs, sparse on teeth, denser on distal part of tube. Corolla (9.2)13-17.5mm long along upper side, white or pink, purple or lavender, with colour sometimes only on veins and base of tube and with rest white, sometimes on lobes and tube and with broad white area behind...
lower lobes, sometimes all over, occasionally also with yellow blotch behind lower lobe; tube (6)9-13mm long; hood 3-5mm long; upper lobes acute, obtuse or shallowly emarginate, with rear surface usually covered by very short to short glandular hairs, very sparse to dense at base, sparser or absent distally, rarely mixed with moderately dense short eglandular hairs; lower lip (4.8)7-10.5(16)mm long; lower lobes usually emarginate or shallowly so, sometimes truncate or obtuse, externally usually bearing short glandular hairs, very sparse to dense in proximal parts, sparser or absent distally, sometimes mixed with short eglandular hairs, rarely with eglandular hairs only. Stamens with anthers (1.5)1.7-2.2mm long, with connectives covered by dense, long to very long eglandular hairs; rearmost pair of awns (0.1)0.2-0.4mm long. Capsules (5.2)6.0-8.0mm long, in lateral view ovate to ovate-elliptic, often obliquely so, sometimes narrowly so, 1.6-2.9mm broad, in median view.
ovate-caudate, with distal $(_{3}^{1/3})$ covered by dense setae 0.1-0.3mm long, often extending almost to base along lines of dehiscence; apex in lateral view truncate, obtuse or acute, usually obliquely so; seeds $(22)_{66}^{(112)}$, $0.5-0.7(0.8) \times (0.3)0.4-0.5(0.6)$mm, usually obliquely ellipsoid or broad-oblong, sometimes almost spherical. Figs 9, 48A-C, 73, 74.

**Typification:** The type locality, on private property, was in several acres of natural scrub surrounded by cleared farming land. It has since been cleared and placed under cultivation.

**Distribution** (fig. 54): *E. collina* ssp. *osbornii* is confined to South Australia in the Upper South-East, Kangaroo Island (Dudley Peninsula), Fleurieu, Yorke and Eyre Peninsulas, and in the Flinders Ranges apparently as far north as Burra in the Mid North. Records are notably absent from the western half of Kangaroo Island, and the southern parts of Yorke and Eyre Peninsulas; this accords with Wood's (1930) floristic analysis of the gulf region of South Australia. Two apparently erroneous records from Tasmania are discussed in note 2.

Altitude: sea level to 600m.

**Ecology:** Ssp. *osbornii* has been recorded mainly from the mallee (*Eucalyptus*) scrublands common throughout most of its range. In higher parts of the Mount Lofty Ranges it occurs in heathy openings in wet sclerophyll forest (Mr D.J.E. Whibley, pers. comm. 1974). At Square Waterhole near Mt Compass "plants [are] scattered through . . . a *Calorophus* swamp" (Chinnock 1342, apparently an extension of the [former] populations of the "dry stony hills adjoining the swamp" (Tepper 48).

Flowering usually begins in August or October, although June (Eichler 13872) and March (Kaspiew 66) collections of plants beginning to flower have been made. Fruits first appear in October to November.

**Conservation status:** 3E, ?C. Despite the many collections, most are old, and only about six montane and six lowland sites have been collected from in the last decade.

**Notes:** 1. Within ssp. *osbornii* there is a geographical variation in the colour and coloration of the corolla. Mt Lofty Range populations are predominantly off-white, although pink tinting sometimes occurs in buds or in the veins of the lobes and at the base of the tube of open corollas; senescent corollas may also deepen in colour. References to pink (Anon. AD97331115, Hunt 3314) and "pale heliotrope" (Hunt 3280) flowers may be the only records of markedly non-white corollas in the Mt Lofty Ranges. In the remainder of the area of distribution of the subspecies on either side of the Mt Lofty Ranges, corollas are coloured in lilac or mauve or similar shades, with only the lower side of the mouth white. Predominantly white corollas are rare in populations.

The incidence of the yellow nectar guide behind the lowest corolla lobe is also apparently geographically demarcated. In the white-flowered Mt Lofty Range populations yellow blotches seem to occur only in the Square Waterhole populations near Mt Compass (Chinnock 1342; Tepper 48, 49) where it apparently occurs in all individuals (Mr R.J. Chinnock, pers. comm. 1974). Among the purplish-flowered populations of the lowland areas, yellow blotches have been recorded only from the eastern plains near Yumali in the Upper South-East of South Australia (Barker 1464; Gooden AD97147041) in a population in which plants with corollas lacking the yellow spots were far more frequent. There is an occasional slight yellowing of the white patch on the lower side of the corolla in populations near Curramulka on Yorke Peninsula (Barker 1346).

On these bases there is perhaps some justification for recognizing several infra-subspecific taxa within ssp. *osbornii* as circumscribed in the current revision. However, because no supporting characters are apparent and since data on corolla colour and the incidence of the yellow nectar guide are generally absent (it is especially difficult to discern the latter from dried specimens), this has not been considered advisable.
The apparent confinement of populations with an incidence of the yellow spot to the eastern side of the Mt Lofty Ranges may be related to the partial overlap in geographical distribution of at least the more easterly populations with those of ssp. *tetragona*, plants of which apparently always possess the yellow blotch in this region. The occurrence of the yellow blotch in these populations may be produced by introgression into ssp. *osbornii* of genes determining this character in ssp. *tetragona*, or it may be a product of convergent evolution, perhaps under competition for a common pollinator. There is apparently no breakdown in the other characteristic differences, apart from an unusually high frequency of many-toothed leaves in populations of ssp. *tetragona* in the region.

2. Indications that ssp. *osbornii* and ssp. *muelleri* of *E. collina* occur in Tasmania based upon herbarium labels on two old specimens collected by Stuart, are considered to be erroneous. The sheet *Stuart MEL41509* consists of a mixture of material of both subspecies. The one accompanying label is annotated by Mueller with both a South Australian locality “Ad fluv. Torrens” in a region where both subspecies are known to have occurred, and the inscription “V.D.L. F.M.”.

Labels of Stuart’s collections from South Australia were sometimes annotated by Mueller with confirmation of the occurrence in Tasmania (Van Diemen’s Land) of the species collected, e.g. by “V.D.L. explor. F.M.” (Barker 1977). The annotation on *MEL41509* is undoubtedly a further contraction of this. In the absence of other records of the two subspecies from Tasmania, it is likely that the specimen *Stuart HBG* of ssp. *osbornii*, allegedly from Tasmania, is a duplicate of this or another Stuart collection from South Australia.

Selected and cited specimens (122 seen)

11n. ssp. diversicolor Barker, subspecies nova


Subspecies nova Euphrasiae collinae proxima ssp. speciosam et ssp. lapidosam indumento glanduloso longo in partibus superis, ramificatione solum prope terram, foliisque plerumque multi-dentatis, sed a duabus differt seminibus maioribus antherisque maioribus; etiam differt a ssp. speciosa aristis postremis antherarum longioribus, partibus inferis saepe non-glandulosis, capsulisque interdum glabris, et a ssp. lapidosa internodiis longioribus in partibus superis, quorum internodium longissimum bis longitudine foliorum maior est, altitudine maiore, basique foliorum latiore.

Holotypus (fig. 75): W. R. Barker 1684, 25.1.1972. Kosciusko National Park. C. 2km ENE of Mt Kosciusko summit; on slope below and c. 50m N of Seaman’s Hut, along snowpole line to Lake Albina. Tall alpine herbfield; Euphrasia-Celmisia-Poa (tussock grass) -dominated. Altitude c. 6600 feet (2000m). AD97221170. Isotypi: CANB, CGE, GH, K, NSW, W.

Erect perennial herb, (10)15-30(45)cm tall, with stem reduced, or erect or ascending and flowering in first year, then dying back to ground, with many densely crowded ascending branches arising from base of stem or prostrate parts of other branches, rarely (except when in sphagnum bogs) rooting in proximal regions of prostrate parts. Stem, if erect and flowering, or main inflorescence-bearing branches (8)12-25(30)cm high to base of inflorescence, simple above ground level, i.e. for (11)13-28(33) nodes below inflorescence; upper (2)4-8(13) internodes longer than or as long as upper leaves, the longest internode (1.8)2.2-4.0(4.3) times length of upper leaves; axes in upper parts bearing two rows or four lines of dense, short to long eglandular hairs, sometimes with sparse eglandular hairs between, usually mixed all around with sparse to dense, short to long glandular hairs, with glandular hairs lacking. Leaves: uppermost leaves of stem or main inflorescence-bearing branches (5)8-12(17) x (3.5)5-10(13)mm, usually ovate-elliptic to obovate-elliptic, usually broadly so, sometimes ovate or broadly ovate, with sessile glands confined to distal (0.55)0.75-0.95 of lower side, with marginal rows of glands along either side of apical tooth and proximal side of each marginal tooth with lateral branches which are finally directed towards leaf base and usually reach level of upper side of base of tooth below, otherwise usually covered by usually moderately dense to dense, sometimes sparse, short to moderately long glandular hairs, with margins and upper surface, sometimes also lower surface, covered by sparse to dense, short to long woolly eglandular hairs, sometimes ± glabrous; base usually rounded, sometimes truncate or rounded-cuneate, rarely cuneate; teeth (1)2-4(6) along each margin, confined to distal (0.25)0.4-0.8(0.85) of leaf, the longest tooth (0.9)1.1-2.4(3.0)mm long, usually bluntly or sharply acuminate or acute, rarely bluntly obtuse; apical tooth (1.3)2.0-4.0(6.0) x (1.4)2.5-4.0(6.5)mm, usually blunt, rarely sharp, usually acuminate or broadly so to acute, sometimes obtuse or broadly so; leaves lower down with sparser shorter indumentum, at base usually glabrous, rarely with sparse short woolly eglandular hairs lining margins. Inflorescences racemes, dense in bud, flower and fruit except sometimes for wider-spaced lower I(3) nodes,
Fig. 75. Holotype of *E. collina* ssp. *diversicolor* Barker, ssp. nov. (scale 5 cm).

Fig. 76. Holotype of *E. collina* ssp. *lapidosa* Barker, ssp. nov. (scale 5 cm).
with (6)12-22(26) flowers, two at each node; pedicels at lowest node (1.4)1.5-3.0(6.2)mm long, shorter higher up; rachis with indumentum similar to uppermost parts of axis or slightly denser and longer; internodes elongating prior to anthesis such that capsules reach to or past base of calyx above; apical bud cluster ± spherical to conical-ovoid, sometimes broadly so, initially c. 1.0-2.5cm long, becoming hidden by or hardly emergent from corollas of uppermost flower pair after flowers at first 1-4(6) nodes have reached anthesis. Bracts covered by dense mixture of glandular and woolly eglandular hairs, at lower nodes similar in shape, size and indumentum to uppermost leaves, shorter than or equal to calyx except rarely at lowest node, toothed at all nodes. Calyx (5.8)6.0-9.8(12.0)mm long, externally covered by dense, usually moderately long, sometimes short, long or very long glandular hairs, extending also onto inner surface of teeth, mixed with long to very long, woolly eglandular hairs, dense on margins and inner surface of teeth, sparse to dense and often shorter on outer surface. Corolla (9)11:16(17)mm long along upper side, either white or purple-violet to pink often with colour confined to lobes and with tube and area behind lower lobes white, with yellow blotch behind lowest lobe often large and extending behind lateral lobes and coextensive with yellow blotches in tube at base of anterior filaments; tube (6.5)7.5-11(12)mm long; hood (3.0)3.5-5.3(5.5)mm long; upper lobes usually obtuse, sometimes truncate, rarely shallowly emarginate, often praemorsely so, with rear surface ± glabrous but for short, moderately dense glandular hairs at base; lower lip (7)8-12(13)mm long, externally covered by a mixture of short glandular and short to moderately long eglandular hairs, extending well out onto lobes, denser on lateral ones; lower lobes usually truncate to shallowly emarginate, sometimes obtuse or emarginate. Stamens with anthers (1.7)2.0-2.6(3.0)mm long, with connectives surrounded by usually dense, rarely moderately long to very long, flexuose eglandular hairs; rearmost pair of awns (0.25)0.3-0.5(0.6)mm long. Capsules (6.3)7.5-10.5(13.3)mm long, in lateral view elliptic to ovate-elliptic, sometimes broadly so or somewhat caudate, (2.6)3.0-4.0mm broad, in median view ovate- to elliptic-acuminate, sometimes narrowly so, glabrous or with a few to moderately dense setae 0.1-0.2mm long or less, confined to apex or upper 1/4; apex in lateral view usually shallowly emarginate or truncate to obtuse, sometimes obliquely so, rarely acuminate; seeds (18)41(71), (0.9)1.1-1.7(1.9) x 0.5-0.8 (1.1)mm, obliquely ovoid to ellipsoid or oblong, sometimes flattened or broadly so. Figs 9, 48D, 61, 62, 75, 77, 78.

Distribution (fig. 55): _E. collina_ ssp. _diversicolor_ is endemic to the alpine and subalpine zones of the Snowy Mountains of south-eastern New South Wales. It is apparently absent from the subalpine zone on the summit of the Brindabella Range even though it occurs on the lower-lying northward extension of the subalpine grasslands of the Snowy Mountains which reach the base of these mountains (note 4). The absence of typical forms of _ssp. diversicolor_ from the Gibbo-Pinnibar-Pilot-Cobberas mountain system has probably stemmed from the lack of botanical collecting in the area, although a closely-related but divergent form from the Cobberas indicates that it is possibly absent from at least some alpine areas in the region (note 2). An old record from Mt Feathertop, Victoria is probably erroneous (note 5). Altitude, 1370-2230m.

Ecology: In the alpine zone _ssp. diversicolor_ is especially common in tall alpine herbfield (fig. 77), but sometimes occurs in heath and (Costin et al. 1979) drier sites of sod tussock grassland.

In subalpine regions the subspecies is less common and generally grows on the margins of sphagnum bogs (fig. 78). It avoids sod tussock grassland, a principal habitat of _ssp. paludosa_. However, at Spencers Creek crossing on the Kosciusko summit road it was found not only on bog margins, but also in a community apparently similar to tall alpine herbfield. Similarly, on Long Plain, north of Kiandra, a lone population (Barker 1663) was confined to a small area of herbfield within extensive sod tussock grassland (note 4).
Fig. 77. *E. collina* ssp. *diversicolor*, Mt Kosciusko region, New South Wales (Barker 1686). A. Population in tall alpine herbfield; B. Habit, scale 5 cm wide; C. Inflorescences showing white corolla with lilac flush and with yellow blotch on lower side of mouth, scale 1 cm.
Flowering occurs mainly between December and the middle of February, although flowering specimens have been collected as early as the beginning of September (*Stead NSW64341*) and as late as the end of March (*Wimbush NSWNP*). Mature fruits are evident at the start of January.

**Conservation status:** considered not a risk while under reservation and with no grazing pressure.

**Notes:** 1. Ssp. *diversicolor* is sympatric with ssp. *glacialis*, ssp. *lapidosa* and ssp. *paludosa* in parts of its range. It retains its morphological and ecological differences, except where there is ecotonal intergradation into ssp. *glacialis* and in a single known instance of hybridization with ssp. *paludosa* (see *E. collina*: Intraspecific Polymorphism).

2. Ssp. *diversicolor* is an extreme of a polymorphic complex which encompasses ssp. *paludosa* and ssp. *speciosa*. The overall complex is discussed under *E. collina*: Intraspecific Polymorphism.

Plants of this complex collected from The Cobberas, which lies south of the range of distribution of ssp. *diversicolor* diverge from ssp. *diversicolor* by the shorter glandular indumentum, 0.05-0.1(0.2) mm long, which always seems to extend to the base of the plant, and the usual absence of long woolly eglandular hairs lining the bracts, leaves and calyces. The Cobberas populations also differ in their subalpine snowgum woodland habitat, from which ssp. *diversicolor* is not known.

It is probable that populations related to either or both ssp. *diversicolor* and The Cobberas plants occur elsewhere in the Gibbo-Pinnibar-Pilot-Cobberas mountain system, but only The Cobberas with its very limited alpine zone (Costin 1957b) appears to have been significantly botanized. Wider expanses of alpine herbfld, which are potential habitats for ssp. *diversicolor*, occur on Mt Pinnobar (Costin 1957a) and apparently The Pilot (Costin 1954, from f. 31). Until extensive collections are made in these regions it is not clear whether The Cobberas populations belong to a distinct variety or represent a divergent woodland extension of the typically alpine ssp. *diversicolor*.

3. Populations from tall alpine herbflds in the Kosciusko area and the higher mountains to the north are characterized by large, broad leaves, often broadest near the base and often with bluntish-tipped apical and marginal teeth (fig. 9: Barker 1684, 1703, 1704), long calyces and long corollas with long broad lower lips (fig. 77C).

Plants found growing in sphagnum bogs (fig. 78) in the upper parts of the subalpine zone about Kosciusko have smaller leaves with typical teeth but with less truncate bases (fig. 9: Barker 1701) and flowers which tend to be smaller with narrower lower corollas lobes (fig. 78B). The plants often set less fruit, and the roots and lower branches, which are encased in sphagnum, are very slender. Such bogs occur at Spencers Creek near the Mt Kosciusko road. The plants growing in the bog area but not within the sphagnum itself (fig. 9: Barker 1702) have uppermost leaves more similar to those of plants within the sphagnum (fig. 9: Barker 1710) than those of plants within the nearby herbfld (fig. 9: Barker 1703). However their root system and leafy lower parts of branches resemble the latter.

In the watersheds of the lower altitudes to the north where tussock grasslands mainly replace the herbflds of the higher regions, plants of ssp. *diversicolor* are usually associated with sphagnum bogs, although they do not grow within the sphagnum. These plants (e.g. fig. 9: Barker 1677) tend to be intermediate between the sphagnum and herbfld forms of the Kosciusko region in leaf and floral characters.
4. The absence of ssp. *diversicolor* from the Brindabella Range on the north-east perimeter of its area of distribution is worthy of note. This range rises to an altitude of about 1900m, which is within the altitudinal range of the subspecies, but well above the elevation of the nearest population of ssp. *diversicolor* (*Barker 1663*) occurring in sub-alpine herbfield (see Ecology) at about 1370m altitude and about 15km west of Mt Bimberi and 7km from the nearest spurs of the range. The range lacks a true alpine zone (*Lang 1970, f. 5*) but is topped by extensive areas of subalpine snowgum woodland in which some sphagnum bogs occur. That ssp. *diversicolor* has never been recorded from...
these bogs, while it occurs predominantly in such habitats on the subalpine plains below and to the south and east, can be explained by one or more of the following hypotheses: (a.) The bogs of the Brindabella Range are unsuitable for colonization by ssp. diversicolor (this could be tested by transplant experiments); (b.) The bogs are not extensive enough to have housed with certainty relict populations of the subspecies which may have been widespread in the area during Pleistocene glaciations; (c.) Such subalpine bog populations in order to survive, require replenishment of seed (via the watershed) from self-sufficient alpine populations, which do not exist in the Brindabella Range; (d.) Seed cannot be dispersed against gravity from the populations on the plains up the mountain slopes across the presumably effective migratory barriers of montane forest and subalpine woodland.

5. The sheet MEL41549 bears three specimens of ssp. diversicolor mounted together with Mueller’s label “Mount Hotham”. Mueller’s Mount Hotham is apparently the present-day Mt Feathertop (Carr 1962). As this is far outside the known range of the subspecies, this locality is considered very doubtful.

**Selected and cited specimens (107 seen)**

**NEW SOUTH WALES:** Ashby 838, 14.i.1964. Charlotte Pass, near Mt Kosciusko. AD.—Ashby 4424, 1.xii.1971. Boggy Plain, E of Tantangara Mtn, near Kiandra. AD.—Barker 1663, 21.i.1972. Long Plain, which is along the E side of The Fiery Range, c. 16km NNE of Rules Point. AD.—Barker 1165, 1168 (p.p.), 22.i.1972. SE end of Toolong Range; on side and top of southern ridge of Mt Jagungal, c. 70m and 50m below and c. 1/2km S of the summit. AD.—Barker 1677, 22.1.1972. Toolong Range; on the Grey Mare Trail between Round Mtn & Mt Jagungal, c. 3km NW of the intersection with the track to Happy Jacks. AD.—Barker 1683, 24.1.1972. C. 100m E of the top of Dead Horse Gap at the headwaters of the Crackenback River. AD.—Barker 1684, 25.1.1972. C. 2km ENE of Mt Kosciusko summit; on slope below and c. 50m N of Seamus Hut, along snowline to Lake Albina. AD (holotype); CANB, CGE, GH, K, NSW, W.—Barker 1686, 25.1.1972. C. 2km ENE of Mt Kosciusko summit; on valley below and c. 400m NW of Seamus Hut, along snowline to Lake Albina. AD.—Barker 1691, 26.i.1972. C. 1/2km E of The Smiggin Holes, c. 50m S of bridge across Pipers Creek. AD.—Barker 1692, 26.i.1972. C. 1/2km E of The Smiggin Holes, c. 100m S and c. 30m above bridge across Pipers Creek. AD.—Barker 1694, 26.i.1972. Perisher Valley; near the bridge across Perisher Creek on the North Perisher Road. AD.—Barker 1698, 1699, 26.i.1972. C. 50m N and NW of bridge across Spencers Creek on Kosciusko Summit Road, c. 3km ENE of Charlottes Pass. AD.—Barker 1701-1703, C. 50m S of bridge across Spencers Creek on Kosciusko Summit Road, c. 3km ENE of Charlottes Pass. AD.—Barker 1704, 27.i.1972. On top of Etheridge Range, c. 1/2km W of Seamus Hut, c. 1km E of Mt Kosciusko summit; above large quarry by Kosciusko Summit Road. AD.—Barker 1709 (p.p.), 27.i.1972. C. 2km NE of Mt Kosciusko summit; in the second valley c. 1km NW of Seamus Hut along snowline to Lake Albina. AD(p.p.).—Barker 1711 (p.p.), 1713, 27.i.1972. C. 2km NE of Mt Kosciusko summit; c. 1km N of Seamus Hut along snowline to Lake Albina; at bottom of valley immediately S of Mt Northcote. AD(p.p.).—Burbridge 3934, 3935, 3938, 24.i.1955. Mt Kosciusko, near summit. CANB.—Carroll 154, 17.i.1966. Happy Jack's Plain, Snowy Mountains. 2 miles along Happy Jack's Road from Grey Mare Track. CBG.—Gittins 433, 1.x.1962. The Kerries. NSW102594.—Gray & Todderdell 6570, 19.ii.1972. Near Lake Cootapatamba, Mt Kosciusko. CANB.—Johnson & Constable s.n., 20.i.1951. Club Lake, Mt Kosciusko.—McVean s.n., xii.1966. Mueller's Peak, Kosciusko area. CANB.—Rodd 708, 28.xii.1968. Grey Mare Range, about 1 mile NE of The Grey Mare. NSW.—Salasoo 3575, 23.i.1969. SE slope of Mt Guthrie, NE of Mt Kosciusko. NSW103008.—Stead s.n., 1.x.1964. Charlottes Pass, Kosciusko. NSW64341, BISH.—Willis s.n., 5.i.1946. Hedley Tarn, below the Blue Lake, Kosciusko Plateau. MEL41541.—Wimbush s.n., 22.iii.1957. Mt Carruthers. NSWNP.

**LOCALITY DOUBTFUL. VICTORIA:** [Mueller] s.n., s.dat. Mount Hotham [now Mt Feathertop]. MEL41549.

**Specimens with affinities to ssp. diversicolor**

**10.** *sssp. lapidosa* Barker, *subspecies nova*


Subspecies nova *Euphrasiae collinae* proxima *sssp. diversicolorem* et *sssp. speciosam* indumento glanduloso longo in partibus superis, ramificatione solum prope terram, foliisque plerumque multidentatibus, sed a duabus differt internodiis brevioribus in partibus superis, quorum internodium longissimum bis longitudine foliorum minus est, et altitudine breviore; etiam differt a *sssp. speciosa* partibus inferis non-glandulosi, floribus pauciioribus, aris et postremis antherarum longioribus, capsulis sape glabris, seminibus maioribus, et a *sssp. diversicolori* basi foliorum summorum angustiore, antheris brevirioribus seminibusque minoribus.

**Holotypus** (fig. 76): W.R. Barker 1706, 27.i.1972. Kosciusko National Park. On top of Etheridge Range, c. 1/2km W of Seaman's Hut, c. 11/2km E of Mt Kosciusko summit; above large quarry by the Kosciusko Summit Road. In pure fjaeldmark on slight slope; growing usually amongst the extremities of prostrate woody bushes or occasionally in the stone chips between. Altitude c. 6950 feet (2120m). AD97221206. *Isotyphi*: CANB, SYD.

Erect perennial herb, (3)5-9(11)cm tall, with stem reduced or ascending and flowering in first year, then dying back to ground, with few to many ascending branches arising from base of stem or prostrate parts of other branches, often rooting in prostrate parts of branches. *Stem*, if flowering, or main inflorescence-bearing branches (1.2)1.5-6.5(7.5)cm high to base of inflorescence, simple above ground level, i.e. for (5) 10-30(33) nodes below inflorescence; upper 0-3(4) internodes as long as or longer than upper leaves, the longest internode (0.3)0.5-1.8(2.1) times length of upper leaves; axes in upper parts with two rows or four lines of dense, short to very long eglandular hairs decurrent from between leaf bases, sometimes with sparse eglandular hairs between, short to very long glandular hairs decurrent from between leaf bases, sometimes with sparse eglandular hairs between, mixed all around with moderately dense to dense, short to very long glandular hairs, lower down with glandular hairs absent and eglandular hairs sometimes shorter and sparser, sometimes absent on prostrate parts. *Leaves*: uppermost leaves of stem or main inflorescence-bearing branches (4.5)6.5-10.5(12.5)x (3)4.5-7(9)mm, elliptic to obovate, sometimes broadly so, with sessile gland patches extended over distal (0.6)0.65-0.75 of lower side, otherwise covered by very sparse to dense, short to very long glandular hairs, sparser or lacking towards apex, often with short lax eglandular hairs on margins, sometimes extended onto upper side; *base* usually narrow-cuneate, shortly attenuate or attenuate, sometimes rounded or cuneate; *teeth* 2-3(4) along each margin, confined to distal (0.45)0.5-0.6(0.65) of leaf, usually sharp, rarely blunt, usually acute, sometimes acuminate, the longest tooth (1.0)1.3-2.0(2.5)mm long; *apical tooth* (1.0)1.2-2.0(2.6)x (1.2)1.6-2.5(3.2)mm, usually sharp, sometimes blunt, usually acuminate, sometimes broadly so or acute, rarely obtuse; *leaves* lower down glabrous. *Inflorescences* racemes, dense in bud, flower and fruit, with (6)10-16 flowers, two at each node; *pedicels* at lowest node (0.1)0.2-2(4)mm long; *rachis* with indumentum similar to uppermost part of axis, but sometimes denser; *internodes* elongating prior to anthesis such that capsule extends past base of calyx above; *apical bud cluster* very broadly ovoid, initially c. 1.5cm long, hidden by or hardly emergent from corollas of uppermost flowers after corollas of first 1-2 flowers have reached anthesis. *Bracts* covered by dense, short to long mixture of glandular and lax eglandular hairs, at lowest node similar in shape and size to uppermost leaves, shorter than or equal to calyx except rarely at lowest node, toothed at all nodes. *Calyx* (5.5)6.2-8.0(9.0)mm long, externally covered by dense, usually moderately long to very long, rarely short glandular hairs, extending to inner surface of teeth, mixed with short to long woolly eglandular hairs, dense on margins and inner surface of teeth, sparser or absent on outer surface. *Corolla* (8.5)9.5-13(14)mm long along upper side, pale to deep lilac or mauve-pink, with tube and area behind lower lobes
white, with yellow blotch behind lowest lobe and two smaller blotches in tube at base of anterior filaments; tube (6.5)-9(9.5)mm long; hood (2.6)-4.5(5)mm long; upper lobes usually emarginate to truncate or praemorse-obtuse, rarely obtuse, with rear surface usually glabrous, except sometimes for sparse to dense, very short to short glandular hairs at base, rarely with sparse mixture of very short glandular and eglandular hairs all over; lower lip (5.4)-7.5-9.5(10)mm long, externally covered by sparse to dense, short to long eglandular hairs, sometimes mixed with sparse short glandular hairs, the indumentum often restricted to base of lobes, sometimes all over; lower lobes usually emarginate or shallowly so, sometimes praemorsely truncate, rarely obtuse. Stamens with anthers (1.5)-1.6-1.9(2.0)mm long, with connectives usually bearing very sparse to moderately dense, short to long eglandular hairs, sometimes glabrous; rearmost pair of awns (0.25)-0.3-0.5(0.6)mm long. Capsules (7.0)-7.3-12(13.5)mm long, in lateral view ovate-elliptic to obovate-elliptic, 2.8-4.8mm broad, in median view ellipsoid-acuminate, sometimes narrowly so, glabrous or with very sparse to moderately dense, short to moderately long setae at very apex; apex emarginate to obtuse, sometimes obliquely so; seeds (18)-32(48), (0.8)-0.9-1.2(1.4) x 0.4-0.6mm, oblong to ellipsoid, often obliquely so. Figs 10, 76, 79.

Distribution (fig. 55): E. collina ssp. lapidosa is known only from the alpine zone in the Kosciusko region of the Snowy Mountains, south-eastern New South Wales. Altitude, 1920-2130m.

Ecology: Ssp. lapidosa is almost exclusively confined to areas of Epacris-Chionohebe fjældmark (fig. 79: Costin et al. 1979), a sparsely vegetated community of prostrate, woody shrubs on stony, wind swept ridges above 6500 feet (1980m: Barrow, Costin & Lake 1968).

The one known site at a lower altitude (fig. 60: Barker 1710) consists of two small fjældmark-like stony areas, on top of small elevated platforms cut out by intersecting streams in the broad valley floor south of Mt Northcote. The stony area is covered by apparently the same Epacris species that occurs throughout the fjældmark on the ridges but its dominant in those localities, Chionohebe densifolia, appeared absent.

Flowering begins in December and is probably completed by early February. Ssp. lapidosa flowers earlier than the two subspecies of the surrounding herbfields (see E. collina: Intraspecific Polymorphism).

Conservation status: 2V,C.

Note: I wish to record my thanks to Mr Max Gray (CANB) for informing me of the presence of this distinct subspecies. His collections of the three alpine subspecies of E. collina, which he had recognized to be distinct taxa, provided an excellent preview for my field work in the Kosciusko area.

Specimens examined
Fig. 79. *E. collina* ssp. *lapidosa*, Etheridge Range, New South Wales (Barker 1706, holotype). A, B, plants growing in stony exposed fjaeldmark community, with corollas lilac and with white mouth yellow-blotched on lower side. (Scales: A, 1cm wide; B, 1cm).
Studies in *Euphrasia*


Erect perennial herb, (3.5)7-12(18)cm tall, with stem reduced, or ascending and flowering in first year, then dying back to ground, with few to many ascending branches arising from base of stem or prostrate parts of other branches, in larger plants often rooting along prostrate parts. *Stem*, if flowering, or *main inflorescence-bearing branches* (2.5)3.5-9.5(13)cm high to base of inflorescence, simple above ground level, i.e. for (5)13-22(25) nodes below inflorescence; upper (0)3-6 internodes as long as or longer than upper leaves, the longest internode (0.9)1.7-3.0(3.5) times length of upper leaves; *axes* in upper parts with two rows or four lines of dense, short to long eglandular hairs decurrent from between leaf bases, sometimes with sparser eglandular hairs between, usually mixed with sparse to dense, short to very long glandular hairs, lower down with eglandular hairs sparser and shorter, often absent at base, with glandular hairs absent. *Leaves*: uppermost leaves of stem or inflorescence-bearing branches (3.5)5.5-9(11) x (2)4-6(8)mm, usually elliptic, sometimes obovate, ovate or oblong, often broadly so, with sessile gland patches extended over distal (0.6)0.7-0.85(0.9) of lower side, with marginal rows of glands along either side of apex and proximal side of each tooth with lateral branches which are finally directed towards leaf base and usually reach level of upper side of base of leaf below, otherwise usually bearing very sparse to dense, short glandular hairs, with sparse to dense, short woolly eglandular hairs on margins, also often on upper side, rarely on lower side, the indumentum towards apex sparser, often absent; *base* usually rounded to rounded-cuneate, sometimes very shortly attenuate, rarely truncate; *teeth* (0)1-2(3) along each margin, confined to distal (0.9)1.2-2.5(3.5) x (1.6)2.0-3.2(3.8)mm, usually blunt, sometimes sharp, usually acute, sometimes acuminate, rarely obtuse, the longest tooth (0.2)0.9-1.5(2.0)mm long; *apical tooth* (0.9)1.2-2.5(3.5) x (1.6)2.0-3.2(3.8)mm, usually blunt, sometimes sharp, usually acuminate, sometimes broadly so or acute, rarely obtuse; leaves *lower down* glabrous. *Inflorescences* racemes, dense in bud, flower and fruit, sometimes except for widely-spaced lowest node, with c. 6-12 flowers, two at each node; *pedicels* at lowest node (0.1)0.3-2.0(2.5)mm long, shorter higher up; *rachis* with indumentum similar to highest parts of axis; *internodes* apparently elongating prior to anthesis such that capsules reach past base of calyx above; *apical bud cluster* spherical to very broadly ovoid, initially c. 1.0cm long, hidden by or hardly emergent from uppermost corollas after flowers at first node have reached anthesis. *Bracts* at lowest node similar in shape and

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size to uppermost leaves, but covered by dense, short to long mixture of glandular and woolly eglandular hairs, shorter than or equal to calyx except rarely at lowest node, apparently toothed at all nodes except when leaves rarely entire or bear one very short tooth. Calyx (3.5)5-7.5(9)mm long, externally covered by dense, short to long glandular hairs, extending onto inner surface of teeth, mixed with short to long woolly eglandular hairs, dense on margins and inner surface of teeth, on outer surface sometimes sparser and often shorter, sometimes absent. Corolla (8.5)10-12(13.5)mm long along upper side, usually white, rarely lilac in bud and becoming white as it opens, with yellow blotch on lower lip behind middle lobe, sometimes extending to behind lateral lobes, often continuous with two small yellow blotches at base of anterior filaments; tube (6.0)7.6(10.0)mm long; hood (2.5)3.6(5.0)mm long; upper lobes usually emarginate, often shallowly so, rarely obtuse, with rear surface usually glabrous, sometimes with very short glandular hairs at very base; lower lip (5.6)8.4(13.0)mm long; lower lobes usually emarginate, sometimes shallowly so, usually with very sparse to moderately dense, short to long eglandular hairs confined to base, rarely extending all over, sometimes mixed with sparse to moderately dense, short glandular hairs. Stamens with anthers 1.4-2.0mm long, with connectives surrounded by sparse to dense, usually short to long, rarely very long eglandular hairs, with rearmost pair of awns (0.3)0.4-0.5(0.65)mm long. Immature capsules 6.5-8.0mm long, in lateral view obovate to elliptic, 2.5-4.0mm broad, ± glabrous; apex in lateral view usually truncate to shallowly emarginate, sometimes obtuse; young seeds c. 12-40, c. 1.1-2.0mm long. Figs 10, 61, 80.
Typification

1. *E. glacialis* Wettst. The type specimens appear to have come from a single homogeneous collection. The selection of lectotype from the two syntypes, each of which bear Wettstein's determinavit slip, is based only on quantity of material present.

All type specimens are labelled "E. alpina R.Br. var. nivalis F. Muell." by Mueller, but Mueller apparently never published this name.

The Munyang Mountains was the general term for the Kosciusko region in Mueller's time (M. Willis 1949).

2. *E. maidenii* Gandoger. The holotype of *E. maidenii*, the BISH specimen and much of the material in the NSW collections clearly belong to ssp. *glacialis* and could represent a single collection of the subspecies. However, in all three NSW specimens 1-3 specimens of ssp. *diversicolor* are present. The occurrence of both a label identical to the holotype and a discordant label (*Maiden & Forsyth s.n.*, i.1900. Mt Kosciusko) on *NSW10831* indicates that at least two collections have been mixed. One of the two sheets of *NSW10855* (it was divided in order to send type material to BISH) has an 1899 label identical to the holotype. The BISH material must have been separated from this material. It is by no means certain that all NSW material of ssp. *glacialis* comes from the one 1899 collection; some could have been collected in January 1900. These specimens should be considered only possibly as isotypes.

Distribution (fig. 55): *E. collina* ssp. *glacialis* is confined to the alpine zone of the Snowy Mountains in south-eastern New South Wales in the region of Mt Kosciusko at altitudes of above 1920m (6300 feet).

Ecology: Ssp. *glacialis* occupies depressed areas in sod tussock grassland, short alpine herbfield (a specialized community associated with snow patches), and the short turf beside streams (figs 60, 80) and of the "wet flushes" which occur in depressions within tall alpine herbfield.

Flowering occurs between mid December and late February.

Conservation status: 2V,C.

Note: Ecotonal intergradation into ssp. *diversicolor* is discussed under *E. collina*: Intraspecific Polymorphism.

Specimens examined

W. R. Barker


Holotype: C. Walter s.n., 1902. Australia, Victoria. LY; probable isotypes: BISH (2 specimens, one fragments only); NSW10845. See Typification.


Perennial herb (6)10-20(30)cm tall, with many crowded ascending branches arising from reduced stem or prostrate parts of other branches, with proximal prostrate parts sometimes rooting. Stem reduced; inflorescence-bearing branches with distal erect parts simple, (4)9-18(23)cm high to base of inflorescence; internodes in upper parts usually longer than or as long as upper leaves, the longest internode (2/3)1-2(3/2) times length of upper leaves, in lower parts shorter than leaves; axis often reddened, in upper parts bearing four lines of dense short eglandular hairs decurrent from between leaf bases, sparser in lower parts, sometimes also with glandular hairs, dense in lower parts, sparse or lacking in upper parts. Cotyledons not seen. Leaves often reddened, cleft or serrate; uppermost leaves of inflorescence-bearing branches usually ovate-elliptic to elliptic, rarely obovate-elliptic, (7)8-13(16) x (4)5-8(10)mm, glabrous except for sessile gland patches which are confined to distal (0.7)0.8(1.0) of lower side and the usually dense, short to long woolly eglandular hairs lining margins; base usually rounded-cuneate, sometimes truncate or shortly attenuate; teeth 1-3(5) along each margin, usually confined to distal 1/6-2/3, rarely over entire length, bluntly or sharply subacuminate to acute to obtuse, (0.2)0.3-1.2(1.7)mm long; apical tooth broad, usually obtuse to shortly acuminate, sometimes acute, blunt or sharp at very tip, (0.5)1.0-3.0(3.7) x (1.7)2.1-4.2 (5.2)mm; leaves lower down inflorescence-bearing branches and those on young shoots smaller, with eglandular hairs on margins sparse to dense or absent, sometimes bearing glandular hairs. Inflorescences racemes, dense but for widely spaced lower 1-3 nodes, bearing c. 20-40 flowers; rachis similar to upper axis; internodes elongating only slightly after anthesis such that (except for lower widely spaced nodes) top of calyces level with node above; pedicels of upper flowers 1/2-2mm long, those of lowermost flowers longer; apical bud cluster conical, ± acute, initially (0.5)1.5(3.0)cm long, hidden by or hardly emergent from uppermost corollas after first 4-6 pairs of flowers have reached anthesis. Bracts similar to uppermost leaves, with margins lined by dense, long to very long woolly eglandular hairs, sometimes mixed with glandular hairs. Calyx 5.0-8.5mm long, glabrous but for dense, long to very long woolly eglandular hairs on margins and inner surface of distal part of teeth, rarely also with glandular hairs on margins; teeth bluntly or sharply acute; lateral clefts 2-4mm deep, usually shorter than, sometimes equal to median clefts which are 2.5-5mm deep. Corolla (9)10-14.5(16)mm long along upper side, white to pale or deep lilac or purple, with yellow blotch on lower lip behind lowest lobe, sometimes flanked by two smaller ones, with two smaller blotches in tube at base of anterior filaments, with purple striations lacking or faint and confined to tube and hood or distinct and extending well out onto all lobes; tube 5-9mm long, for initial 3-6mm to base of anterior filaments narrow cylindrical, then expanded laterally and ventrally, externally glabrous on abaxial side and elsewhere almost up to anterior filaments, distally on adaxial and lateral surfaces covered by dense, short to long down-

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turned eglandular hairs, with a small patch of short glandular hairs behind lateral cleft, internally glabrous or with short to moderately long eglandular hairs, very sparse about bases of filaments or dense and decurrent from them to top of ovary; hood c. 3.2-5.2 x 6.7-9.5mm (including lobes), 3.5-4.2mm wide (excluding lobes), externally on top and front covered by dense, moderately long to long, downturned eglandular hairs, on sides mixed with dense short glandular hairs, internally with dense long flexuose eglandular hairs behind sinus, and sparse to moderately dense, short glandular hairs above anthers or all over; upper lobes coplanar or almost so, obtuse to praemorse-truncate to emarginate, with rear surface covered by glandular hairs, dense near base, sparser to glabrous distally, with margins usually glabrous, sometimes lined by short eglandular hairs near base, with front surface glabrous, with cleft between lobes (2.1)2.7(3.3)mm deep; lower lip concave from above, downcurved at anthesis such that ± perpendicular to upper side, (6.0)8.2(10.0) x (12.7)16.3(19.5)mm, externally usually glabrous, sometimes bearing very few eglandular hairs, internally usually glabrous, rarely with patch of eglandular hairs behind lateral lobes; lower lobes obtuse or praemorse-obtuse to emarginate, usually shallowly so, with clefts between (4.2)4.9(6.4)mm deep. Stamens  with filaments glabrous, the anterior pair 4.2-6.5mm long, the posterior pair 2.0-3.5mm long; anthers (1.5)1.8-2.5 x (0.9)1.0-1.5(1.6)mm, with connectives glabrous or surrounded by sparse to dense, long flexuose eglandular hairs, with awns of rearmost pair (0.3)0.4-0.5(0.6)mm long, longer than those of anterior 3 pairs. Ovary slightly compressed laterally, in lateral view ovate-oblong to elliptic-oblong or oblong, in median view ovate to elliptic-ovate, usually glabrous, sometimes with short to long, sparse to moderately dense setae at very apex and extended slightly down lines of dehiscence; apex in lateral view truncate to obtuse, often obliquely so; ovules 40-100. Capsules slightly compressed laterally, (5)6-8.5(9.5)mm long, in lateral view ovate-elliptic or ovate-oblong to obovate-elliptic or obovate-oblong, (1.8)2.0-3.2(3.5)mm broad, in median view usually ovate, sometimes narrowly ovate or elliptic, usually glabrous, rarely setose at apex; apex in lateral view usually obtuse to truncate, sometimes shallowly emarginate, often oblique; seeds (3)10-40(62), ellipsoid or obovate to obvoid, (0.8)1.0-1.7(1.8) x (0.3)0.5-0.8(0.9)mm. Chromosome number: n= c. 27-30 (Barker 1590, 1593).

Typification

E. crassiuscula Gandoger. The holotype consists of a single branch broken off from about ground level and terminated by an inflorescence containing buds, flowers and very young capsules. A number of leaves are missing, but otherwise the specimen is in good condition. A discordant fragment, definitely not Euphrasia, is also mounted on the sheet. There seems no reason to doubt that material in BISH is isotypic, as it is similarly annotated and bears material of similar age. One herbarium sheet bears a branch with only flowers; all leaves are present, but the upper ones have been insect-eaten. The other sheet contains the fragments of two flowers, a bract and a young capsule.

While there is no doubt about the affinities of the holotype at the species level, the material on the holotype sheet does not allow a confident selection of a type subspecies. The holotype has white corollas with lobes not distinctly striated and sparsely hairy anther backs. This combination of characters is not common in either of the nonglandular subspecies to which the holotype is clearly allied, and occurs more frequently in the rare populations which are intermediate between them.

The type has not been placed with the intermediate populations for two reasons. Firstly, because of their rarity there is only a low probability that Walter by chance made his collection from such populations. Secondly, if the two taxonomically determined subspecies were erected excluding the holotype, a ssp. crassiuscula including the
holotype would still have to be established for nomenclatural reasons (ICBN, Art. 26); this would produce a taxonomically unnatural classification.

As a consequence it is necessary to base the selection of the type subspecies upon the characteristics of the apparent isotypes in NSW and BISH. The NSW specimen is clearly a different plant as internodes are shorter and anther backs are more densely hairy than in the holotype; its corollas, allowing for drying, were similarly white and lacking striations. The BISH material has been segregated from the LY (as fragments) and NSW specimens. Densely hairy anther backs are frequent in one subspecies, but extremely rare (and then only probably by way of introgression) in the other. The type has accordingly been allotted to the subspecies characterized by sparsely to densely hairy anther backs.

**Distribution** (figs 55, 81): *E. crassiuscula* is confined to two neighbouring mountain areas in the Victorian Alps. It is most diverse in the region bound on the south by the extensive Bogong High Plains and the higher regions of the Dargo High Plains, on the north-east by Mt Bogong, which is the highest mountain in Victoria, and on the west by the Mt Feathertop-Mt Hotham-The Twins ridge. It also occurs on the isolated granitic Mt Buffalo plateau which is north-west of the “main divide” of the Alps. Altitude, 1200-2000m.

**Ecology:** *E. crassiuscula* occurs in dense local populations from the subalpine zone to the tops of the highest summits. It has been recorded from subalpine snowgum (*Eucalyptus pauciflora*) woodland, where it favours the more open areas, from alpine heath, especially in areas of low shrubs, although it is sometimes found in tall dense shrubberies, and from tall alpine herbfield. It appears to be absent from the subalpine tussock grassland in the Mt Cope-Pretty Valley area of the Bogong High Plains.

Flowering mainly occurs between mid-December and late February, with mature capsules being produced from early to mid-January and onwards.

**Conservation status:** see subspecies.

**Note:** *E. crassiuscula* is distinguished from all other Australian species of *Euphrasia* with non-glandular calyces and bracts by its conspicuous dense long woolly fringe of eglandular hairs which line the leaves, bracts and calyces, and by its often broad, shortly lobed leaves. It is remarkable in that it varies in the presence of hairs on the anther backs and the presence of striations on the corolla, the very characters which distinguish Sect. *Australes* and Sect. *Striatae* (see Sect. *Australes*: note 2).

**Intraspecific polymorphism**

1. **The pure populations of the taxa.** Three subspecies are recognized under *E. crassiuscula*. Their altitudinal occurrence and areas of distribution (fig. 58) are different, but overlapping. Figure 81 portrays the known distribution of the three taxa concerned and their intermediates. In addition it shows the variation in the diagnostically important characters of anther pilosity, corolla colour, and indumentum in often extensive population samples covering much of the range of the species.

   The distribution and altitudinal range of pure populations of ssp. *glandulifera* are very similar to ssp. *eglantulosa*, although populations of the former are much rarer than those of either of the other subspecies. In contrast to the other two subspecies, ssp.

Fig. 81. Variation in diagnostic characters separating the three subspecies of *E. crassiuscula* in the eastern highlands of Victoria. Variation in extent of corolla striations is not portrayed. Collections used are cited by collector and number, Barker collections only by number.

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Indumentum on anther backs

- ssp. crassiuscula
- ssp. glandulifera
- ssp. eglandulosa
- ssp. crassiuscula-ssp. glandulifera
- ssp. crassiuscula-ssp. eglandulosa

Indumentum on axes and leaves

- dense
- sparse
- very few
- glabrous
- white
- white to lilac
- pale to deep lilac
- non-glandular
- glandular

Corolla colour

- Studies in Euphrasia
Crassiuscula occupies a lower altitudinal range and its range of distribution hardly overlaps with them. There is little apparent difference in the ecological preferences of ssp. eglandulosa and ssp. crassiuscula. Both occur in alpine heath and subalpine woodland. Ssp. glandulifera, however, has not been recorded from snowgum woodland communities.

A geographical variation pattern in the density of the woolly marginal indumentum of the leaves, bracts and calyces seems evident. All populations of both ssp. crassiuscula (Barker 1601) and ssp. glandulifera which occur in the Bogong High Plains area exhibit a denser indumentum than their populations to the west. These latter plants have a density similar to that of ssp. eglandulosa throughout its range. The taxonomic and phylogenetic significance of this is unclear.

2. Intergradation between the taxa. The two similarly distributed taxa, ssp. eglandulosa and ssp. glandulifera, apparently remain completely distinct from each other. On Mt Nelse (Barker 1595, 1596; Willis MEL41551, MEL41553) and Mt Feathertop (Barker 1573, 1574) they are found as easily distinguishable populations with no detectable intergradation.

Populations intermediate between each of these taxa respectively and the generally allopatric ssp. crassiuscula occur in the Feathertop-Hotham area. Except for possibly one case on Mt Loch (see below), populations of the two eastern taxa apparently never occur beside populations of ssp. crassiuscula without morphological intergradation.

Ssp. crassiuscula and ssp. glandulifera intergrade in alpine and subalpine localities on The Razorback between Mts Hotham and Feathertop (Barker 1579) and on the slopes of Mt Feathertop itself (Barker 1575). It is unclear whether the two subspecies remain as distinct populations or are intermixed near the summit of Mt Loch (Barker 1561; Briggs NSW126383).

The differences between ssp. eglandulosa and ssp. crassiuscula break down to some extent on the rounded summit area of Mt Hotham (Barker 1551, 1553/4) and on the saddle between Mt Hotham and Mt Loch (Barker 1563)*. Two variants occur on Mt Hotham (Barker 1974). The populations apparently allied to ssp. eglandulosa by their white, frequently extensively striated corollas, encompass the variation in anther back indumentum typical of both subspecies (fig. 81). In contrast, ssp. crassiuscula retains its integrity, even in a situation where populations of both variants overlap while flowering simultaneously.

Unlike other intergrades between Australian taxa of Euphrasia (e.g. E. gibbsiae, E. collina, E. caudata: q.v.) variation in the characters separating ssp. crassiuscula and ssp. eglandulosa are not associated with any obvious topographical or ecological gradient. In fact, extremes in one diagnostic character were seen associated with either extreme of another in neighbouring plants. On this basis it seems that the characters of anther pilosity, corolla colour and extent of corolla striations are controlled by separate genes and the extremes of variation in each are real genetic differences rather than environmental effects. In addition, some barrier to interbreeding must be involved.

Possibly populations intermediate between ssp. crassiuscula and ssp. eglandulosa are relicts of an ancestral population from which either or both subspecies evolved.

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*The record from Mt St Bernard (Robbins 145) of plants intermediate between ssp. eglandulosa and ssp. crassiuscula is doubtful. Mt St Bernard, about 1500m high, is much lower than the other known occurrences of such intermediates (c. 1800-1860m), and it is about 8km from the nearest of these occurrences in an area where only ssp. crassiuscula has been found.
On the other hand, they may be of hybrid origin through a unilateral breakdown of sterility barriers, resulting in the introgression of characters of ssp. crassiuscula into the local populations of ssp. eglandulosa. In such a case the lack of lilac or lilac-tinted corollas in the intermediate populations could occur through a dominance (epistatic) of the gene determining white corolla colour in ssp. eglandulosa over the white/lilac “locus” of ssp. crassiuscula.

The possibility that the extensive grazing and erosion which have occurred over the past century in these areas (Costin 1957a, 1962; Carr & Turner 1959) may have caused a breakdown of ecological barriers should also be considered.

A genecological study of the intraspecific variation which occurs in E. crassiuscula is required. Such a study may have even wider implications at the sectional level because two of the characters involved in the variation (extent of corolla striations and anther hairiness) distinguish the sections with which E. crassiuscula has the closest affinities.

Specimens intermediate between ssp. crassiuscula and ssp. glandulifera
VICTORIA: Barker 1561, 3.i.1972. From c. 20-30m below and from c. 200-400m S of the summit of Mt Loch, which is c. 3km NE of Mt Hotham. AD.—Barker 1575, 4.i.1972. C. 1km SW of and c. 400-500 feet (120-150m) below the summit of Mt Feathertop on the saddle across to Mt Little Feathertop; c. 9km N of Mt Hotham. AD.—Barker 1579, 4.i.1972. C. 2km S of the Twin Knobs by the track along the Razorback; c. 41/2km S of Mt Hotham. AD.—Briggs s.n., 31.xii.1952. Mt Loch near Mt Hotham. AD97123081, NE004731, NSW126383(n.v.).

Specimens intermediate between ssp. crassiuscula and ssp. eglandulosa
VICTORIA: Barker 1551, 1551A, 2.i.1972. From c. 1/2-1km ENE of the summit of Mt Hotham above the Alpine road. AD.—Barker 1553 & 1553A, 1554, 2.i.1972. C. 1/2km W of the summit of Mt Hotham, c. 1/2km E of Diamantina Hut. AD.—Barker 1563, 1563A, 3.i.1972. On N-facing slope overlooking Derrick Col, halfway between carpark by the Alpine Road at Mt Hotham and the summit of Mt Loch. AD.—Whaite 1978, 25.i.1960. Mt Hotham. NSW(s.n.). LOCALITY DOUBTFUL: Robbins 145, c. 1950. Mt St Bernard. BEAUGLEHOLE.

Key to the subspecies of E. crassiuscula

1a. Anther backs usually glabrous, sometimes with a few hairs about each connective. Corollas white, with purple striations usually on tube and hood, often extending onto lobes, sometimes lacking. .................................................. c. ssp. eglandulosa (p. 245)

1b. Anther backs usually densely hairy, sometimes sparsely hairy about each connective. Corollas white to lilac on lobes to deep lilac or purple throughout, with purple striations on tube and hood only or completely absent.

2a. Glandular hairs absent except on corolla. Corollas white to deep lilac or purple. .................................................. a. ssp. crassiuscula (p. 241)

2b. Glandular hairs present on axes and leaves of lower parts, sometimes extending onto upper leaves, bracts, calyx margins and rachises. Corollas pale to deep lilac or purple. .................................................. b. ssp. glandulifera (p. 242)

12a. ssp. crassiuscula

E. glacialis Wettst. var. eglandulosa auct. non Willis: Willis, Muelleria 1 (1967) 146, p.p. (as to Tadgell MEL41547; Willis MEL41552, MEL41555, MEL41554).

Plant lacking glandular hairs on vegetative parts, rachis, bracts and at least outer surface of calyces. Corolla white or pale lilac with white mouth and tube with purple striations confined to tube and hood or absent, or deep lilac or purple and lacking striations; tube covered by moderately dense to dense eglandular hairs below and between bases of filaments. Anthers with connectives surrounded by usually dense, sometimes sparse, long eglandular hairs below and between bases of filaments. Figs 10, 81.
Distribution (figs 55, 81): Ssp. crassiuscula occupies the Mt Feathertop-Mt Hotham-The Twins ridge, with an outlying occurrence on the southern (highest) part of the Mt Buffalo plateau, which lies about 30km to the north-west. No collection has been made east of the east branch of the Kiewa River, where the majority of populations of ssp. eglandroidosa and ssp. glandulifera occur. Altitude, 1200-1900m; usually over 1350m in the Hotham region.

Ecology: Ssp. crassiuscula mainly inhabits subalpine localities, especially grassy areas, in or near snowgum woodland, often between shrubs. It also occurs in low alpine heath.

Conservation status: 2R,C.

Note: The Mt Buffalo populations are characterized by elongated branch and inflorescence internodes and white flowers. I consider these plants do not warrant the separate taxonomic distinction suggested by Willis (1967, 1973). While ssp. crassiuscula in the Bogong-Hotham region differs in its greater variability, all populations there contain some plants with similarly elongated internodes, or white flowers, or both. In fact, at the lowest altitudes plants with such internodes are very common (e.g. Barker 1581, 1583). The Mt Buffalo plants would appear to be a very homogeneous extreme of an elsewhere more variable subspecies.

Specimens examined

VICTORIA: Barker 1545, 31.xii.1971. Mt Buffalo Plateau; beside the road to the Horn; c. 1/2km S of the Tatra Inn. AD.—Barker 1546, 2.i.1972. C. 50m below the summit of C.R.B. Hill, above the Mt Hotham Alpine Road, c. 5km SW of Mt Hotham. AD.—Barker 1547, 2.i.1972. On Little Blowhard, which is on the southern slopes of Mt Blowhard, c. 3km SW of Mt Hotham; c. 20m above the Alpine Road. AD.—Barker 1548, 2.i.1972. On the upper slopes of Mt Little Ballyd, which is c. 1km NE of Blowhard Hut and c. 2km SW of Mt Hotham summit. AD.—Barker 1549, 2.i.1972. C. 200m NW to N of the summit of Mt Hotham above the Alpine Road. AD.—Barker 1550, 3.i.1972. C. 1/2km S of the summit of Mt Hotham. AD.—Barker 1558, 3.i.1972. By Alpine Road on top of saddle between Mt Higginbotham and Mt Little Higginbotham, c. 3km SE of Mt Hotham. AD.—Barker 1559, 3.i.1972. On the upper ESE slopes of Mt Higginbotham, which is c. 3km SE of Mt Hotham. AD.—Barker 1560, 3.i.1972. On the W end of the summit of Mt Higginbotham, near water tanks; c. 3km SE of Mt Hotham. AD.—Barker 1564, 3.i.1972. C. 20m W of the cairn on the NW end of the mountain of The Twins, which is at the E end of the Barry Mountains, c. 6km SW of Mt Hotham. AD.—Barker 1571, 3.i.1972. On the southern slopes of Mt St. Bernard beside the track to The Twins, which is at the E end of the Barry Mts, c. 6km SW of Mt Hotham. AD.—Barker 1578, 4.i.1972. On the W slopes of Mt Little Feathertop; c. 8km N of Mt Hotham. AD.—Barker 1580, 4.i.1972. Near the summit of one of the peaks of The Razorback, c. 3km S of the Twin Knobs; c. 3km N of Mt Hotham. AD.—Barker 1581, 5.i.1972. On the Dargo Road, c. 8km from the turnoff of the Harrietville-Mt Hotham road. AD.—Barker 1583, 5.1.1972. On the Dargo road, c. 10km from the Harrietville-Mt Hotham Alpine Road. AD.—Barker 1601 9.1.1972. C. 50m E of and c. 15m below summit of Mt Niggerhead. AD.—Cambage 3707, 17.3.1913. Summit of Mt Hotham. NSW10842.—Ford s.n., 13.3.1959. Below the Horn, Mt Buffalo. NSW102588, BISH. —Hill 1286, 31.xii.1963. Mt Buffalo Plateau. AD.—Hill 1337, 2.1.1964. Mt Hotham area. AD.—Tadgell s.n., xii.1914. Razor Back, Feathertop . . . towards Mt Hotham. MEL41547.—Tadgell A, xii.1914. Towards Mt Hotham. NSW10846.—Tadgell B, xii.1917. Mt Feathertop (North of Mt Hotham). NSW10843.—Tadgell C, xii.1917. Mt Feathertop (North of Mt Hotham). NSW10844.—Walter s.n., 1902. Victoria. LY (holotype); BISH (2 spec.); NSW10845.—Willis s.n., 18.ii.1963. Mt Buffalo Nat. Park. Along southern foot of The Bluff (SW portion of plateau). MEL41552.

12b. ssp. glandulifera Barker, subspecies nova


Subspecies nova prope ssp. crassiusculam eglandroidosamque sed differt indumento glandulosi, breve usque longo, parce usque denso, plerumque in foliis humilissimis, foliis surculorum regionibusque humilissimis axium, interdum in ramis foliosae totis, marginibus bracteatarum calyciumque, rachidibusque. Plantae corollae lilacini purpureivae, pallidis usque profundiis, interdum albis post lobos inferos et in tubo; connectivis antherarum pilis eglandroidiosi, plerumque densis, raros parcis circumcinctis.
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Fig. 82. Holotype of E. crassiuscula Gandoger ssp. glandulifera Barker, ssp. nov. (scale 5cm).

Holotypus (fig. 82): W. R. Barker 1596, 8.1.1972, Victoria, Eastern Highlands. Bogong High Plains; from c. 30-60m below & c. 100-150m S of Mt Nelse summit (southern peak); near snow-pole line. Altitude c. 6000ft (1830m). AD97220027. Isotypi: CANB, CGE.

Plant with short to long, sparse to dense glandular hairs, usually on lowermost leaves, leaves of young shoots and lower parts of axes, sometimes extending over all vegetative parts as well as bracts, calyx margins and rachises. Corollas pale to deep lilac or purple, sometimes white behind lower lobes and on tube; tube densely hairy between and below bases of filaments. Anthers with connectives surrounded by long eglandular hairs, usually dense, rarely sparse. Figs 11, 81-83.

Distribution (figs 55, 81): Ssp. glandulifera occurs in distinct populations on the higher summit areas of the Bogong-Hotham mountain system. The subspecies has not been found on Mt Bogong itself, but in view of its apparent rarity in comparison with the other subspecies, collections of E. crassiuscula from this apparently little-botanized mountain are too few to make any conclusions about its presence there. Altitude, 1650-1950m.

Ecology: Most collections of ssp. glandulifera come from tall alpine herbfield or the probably equivalent “alpine meadow”. It has also been recorded from alpine heath grading into tall alpine herbfield (fig. 83: Barker 1596), and from open grassy situations, sometimes on stony terrain. It has not been cited from below the tree-line, although collections from the Bogong High Plains (Eichler 14696, MUMC CBG011562) come from areas with extensive snowgum woodland.

Conservation status: 2V/R,C. The greater rarity of this subspecies compared with the others and the practice of grazing on the High Plains may make it vulnerable.

Note: That Willis overlooked the glandular indumentum which is distinctive of this subspecies is clear from his published work (Willis 1967, 1973), in which he outlined the features of his E. glacialis var. eglandulosas (= E. crassiuscula), and from his annotations of his collections of ssp. glandulifera (MEL41555, on label; MEL41554, on outer folder). He described both his varieties and the specimens of ssp. glandulifera as “non-glandular”. It is equally clear, however, from his annotations on the type of ssp. eglandulosa that on
Fig. 83  *E. crassiuscula* ssp. *glandulifera*, near summit of Mt Nelse, Victoria *(Barker 1596, holotype). A, population in alpine heath; B, inflorescence with lilac corollas with yellow blotch on lower side of mouth, scale 1 cm.
his 1946 visit to Mt Nelse he recognized the distinctiveness of populations of ssp. eglandulosa and ssp. glandulifera.

**Specimens examined**

VICTORIA: Barker 1574, 4.i.1972. C. 100m SW of and c. 50 feet (15m) below the summit of Mt Feathertop on the track to Little Feathertop; c. 9km N of Mt Hotham. AD.—Barker 1576, 4.i.1972. C. 1/2 km NE of and c. 150 feet (50m) below the summit of Mt Feathertop, on the lowest part of the saddle across to Mt Feathertop; c. 9km N of Mt Hotham. AD.—Barker 1596, 8.i.1972. Bogong High Plains; from c. 30-60m below and c. 100-150m S of Mt Nelse summit (southern peak); near snowpole-line. AD (holotype); CANB, CGE.—Craven 1607, 1608, 22.xii.1969. Summit area of Mt Feathertop. CANB.—Eichler 14696, 3.ii.1958. Bogong High Plains. Rocky Knobs. AD.—Ford s.n., 12.i.1959. Below Mt Loch (c. NE of Mt Hotham). NSW102589, BISH.—M. U. M. C. s.n., 1.i.1965. Above Cope Hut, Bogong High Plains. CBG011562, AD97345098.—Muir 1039, 11.i.1960. Bogon High Plains. Summit of Mt Nelson. MEL.—Willis s.n., 12.i.1946. Summit of Mt Nelse (Nelson), Bogong High Plains. MEL41555, HO.—Willis s.n., 15.i.1947. NW slopes of Mt Nelse (“Nelson”), Bogong High Plains. At source of the Big River. MEL41554.

12c. ssp. eglandulosa (Willis) Barker, **comb. & stat. nov.**


Plant with glandular hairs usually absent, rarely (see note) present sparsely on lower vegetative parts. Corolla white, with purple striations usually on tube and hood, often extending well out onto lobes, rarely absent; tube with eglandular hairs about base of each filament and decurrent from it, rarely sparsely hairy between. Anthers usually glabrous on back, sometimes with a few hairs about each connective. Figs 11, 81, 84.

**Distribution** (figs 55, 81): Except for occurrences on Mt Feathertop, the highest mountain west of the Kiewa River, ssp. eglandulosa is confined to regions east of the Kiewa River from the Bogong High Plains to Mt Bogong. Altitude, (71500)1650-2000m.

**Ecology:** Ssp. eglandulosa occurs in low alpine heath and tall alpine herbfield (fig. 84) usually in grassy areas, but occasionally in stony tracts. Occasionally the subspecies has been collected within areas of shrubs in sparse snowgum (Eucalyptus pauciflora) woodland or in wide areas of heathland between snowgums. Only a single plant (Barker 1605) has been found in dense woodland.

**Conservation status:** 2R,C.

**Note:** Barker 1572 contains a few plants with glandular hairs on the lower vegetative parts within a population sample mainly of non-glandular individuals typical of ssp. eglandulosa.

**Specimens examined**

VICTORIA: Aston 247B, 30.xii.1958. Mount Bogong, 20 yards N of Summit Hut. MEL.—Barker 1572, 4.i.1972. C. 20m E of cairn on the summit of Mt Feathertop; c. 9km N of Mt Hotham. AD.—Barker 1573, 4.i.1972. C. 100m SW of and c. 50 feet (15m) below the summit of Mt Feathertop on the track to Little Feathertop; c. 9km N of Mt Hotham. AD.—Barker 1577, 4.i.1972. C. 1/2km NE of and c. 150 feet (50m) below the summit of Mt Little Feathertop, on the lowest part of the saddle across to Mt Feathertop; c. 9km N of Mt Hotham. AD.—Barker 1588, 1588A, 7.i.1972. Bogong High Plains; on the upper E slopes of Mt Cope, c. 10-50m below the summit. AD.—Barker 1590, 7.i.1972. Bogong High Plains; on the upper W slopes of Mt McKay, c. 30m W of the road to the summit. AD.—Barker 1591, 1591A, 7.1.1972. Bogong High Plains; beside road along N edge of Rocky Valley Reservoir, c. 1/2-1km E of causeway. AD.—Barker 1593, 1593A, 8.i.1972. Bogong High Plains; on top of Bakers Spur, which is a ridge WNW of Mt Nelse summit leading to Spion Kopje; c. 1km W of Mt Nelse North. AD.—Barker 1594, 1594A, 8.i.1972. On pole line between summits of Mt Nelse North and Mt Nelse (southern peak), c. 100m S of Mt Nelse North. AD.—Barker 1595, 8.i.1972. On the lowest part of the pole line between Mt Nelse North and Mt Nelse (southern peak) and c. 1/2km from each; c. 100m W of and 15m below the eastern peak of Mt Nelse summit region. AD.—Barker 1597, 8.i.1972. C. 300m N of turnoff to Kelly’s Hut along track to Mt Nelse. AD.—Barker 1599, 8.i.1972. On

Specimens of E. crassiuscula inadequate for infraspecific determination


V. Sect. Lasiantherae Barker

For synonymy, Latin and English description, typification and distribution see p. 85. Fig. 85.

The section is endemic to south-eastern mainland Australia, and consists of three very distinct species, endemic to successive and disjunct mountain areas in the Australian Alps (fig. 86).

Note: Sect. Lasiantherae is remarkable for the pattern of distribution of its species. The morphological transition from E. lasianthera to E. eichleri and thence to E. alsa corresponds with the transitions in their geographical distribution and in their altitudinal and ecological occurrences from montane-alpine to subalpine-alpine to alpine habitats, respectively.

Key to the species of Sect. Lasiantherae

1a. Perennial; flowering stem usually lacking, present at least sometimes in first-year plants, with branches ascending and produced only from ground level. Anthers (1.9)2.0-2.5 (2.7)mm long; rear awns of posterior pair (0.4)0.5-0.7(0.8)mm long; area about connectives of anterior anthers ± equally as hairy as in posterior anthers. Anterior filaments 5.0-6.5(7.5)mm long. Ovary sparsely to densely setose in apical region; ovules (31)60(97). Capsule sparsely to densely setose over distal 1/2; seeds (6)17-70, 0.9-1.4(1.5)mm long. [Corolla with two prominent yellow spots at base of anterior filaments, but lacking yellow blotch on lower lip. Uppermost leaves of inflorescence-bearing branches crenate-serrate to serrate, with length:breadth ratio of (0.9)1.3(1.6):1, with (1)2-4(7) teeth along each margin.…………………………………………………………………………………………………………………………………………………………………….. 13. E. lasianthera (p. 250)

1b. Annual; flowering stem present, with branches ascending or erect, developing in a basipetal sequence, initially from upper parts of stem. Anthers 0.9-2.0(2.2)mm long; rear awns of posterior pair 0.1-0.4(0.5)mm long; area about connectives of anterior anthers less hairy than in posterior anthers. Anterior filaments 2.2-5.0mm long. Ovary densely setose over distal 1/2; seeds 10-35(40). Capsules densely setose in upper 1/2; seeds c. 4-15, 1.5-2.5mm long.

Fig. 84. E. crassiuscula ssp. eglandulosa. A, population in tall alpine herbfield, near summit of Mt Feathertop, Victoria (Barker 1573); B, plant near summit of Mt Nelse, Victoria (Barker 1593), scale c. 2cm; C, variation in size of white corollas, yellow blotched on lower side of mouth, and extent of purple striations (Barker 1593), scale 1 cm.
Fig. 85. Sect. *Lasiantherae* (*E. lasianthera*). A. front view of flower (*y* = yellow blotch); B. side view of flower; C. dorsal view of corolla with stigma; D. oblique ventral view of corolla; E. external view of anthers on one side of flower, with an anterior anther on left and a posterior anther on right; F. internal view of a posterior anther (on right) and part of an anterior anther; G. lateral view of capsule; H. median view of capsule; I. abaxial view of uppermost leaf of main inflorescence-bearing axis (*s* = sessile gland patch). (A–F, I: Barker 1498, holotype; G, H: Beauglehole 40774).
Fig. 86. Distribution of species of Sect. *Lasiantherae*. 5000ft (1520m) contour.

2a. Stem to base of inflorescence (2.5)-5-11(14)cm long, bearing (5)-6-8(12) pairs of leaves. Indumentum on calyces, bracts, rachis, axis and leaves (0.2)-0.4-0.7(1.0)mm thick. Uppermost stem leaves serrate to serrate-crenate, with length (1.8)-2.6(3.3) times breadth, with (2)-3-4(5) teeth along each margin. Corolla (6.5)-8.2-11.5(13.0)mm long along upper side; hood (2.1)-2.7-4.0(4.5)mm long; cleft between upper lobes (2.0)-2.5-4.0(4.5)mm deep; lower lip (5.0)-7.0(10.0) x (11.0)-14.0(18.0)mm; clefts between lower lobes (3.0)-4.0-6.0(7.8)mm deep; inner surface of tube densely eglandular hairy between bases of filaments and decurrent from them. Anthers (1.2)-1.6-2.0(2.2)mm long; rearmost pair of awns (0.25)-0.3(0.5)mm long. Anterior filaments 3.5-5.0mm long. Ovules (20)-30(40).

2b. Stem to base of inflorescence 1.3-5(6)cm long, bearing (1)-3-4(5) pairs of leaves. Indumentum on calyces, bracts, rachis, axis and leaves c. 0.1-0.3mm thick. Uppermost stem leaves pinnatifid to pinnatifid-serrate, with length (1.1)-1.7(2.7) times breadth, with (1)-2(3) teeth along each margin. Corolla (5.5)-7.0-9.0(10.2)mm along upper side; hood 1.5-2.8mm long; cleft between upper lobes 0.8-2.2mm deep; lower lip (3.0)-3.5-5.0(6.5) x (6.5)-7.5-12.0(12.7)mm; clefts between lower lobes 1.6-4.0mm deep; inner surface of tube glabrous. Anthers 0.9-1.3mm long; rearmost pair of awns 0.1-0.2(0.25)mm long. Anterior filaments 2.2-2.9mm long. Ovules 10-12(15).
13. Euphrasia lasianthera Barker, species nova


Species nova Sectionis Lasiantherarum ab speciebus duobus alteris differt duratione perenni, ramis multis ad terram restrictis, filamentis longioribus, antheris maioribus pare postremo aristarum longiore connectivisque subaequaliter pilosis, ovario non nisi ad apicem setoso, ovulis seminibus pluribus, et seminibus minoribus.

Holotypus (fig. 87): W.R. Barker 1498, 25.xi.1971. Victoria, Eastern Highlands. C. 2½km NW of Howitt Hut on the road to Macalister River headwaters, c. 1km SE of turnoff to Macalister Springs. roadside; cleared areas near semi-closed snowgum woodland or in the shade of the snowgums in low shrub stratum and grassy undergrowth. Altitude ca. 5000 feet (1520m). AD97218059. Isotypi: B, BM, BRI, CANB, CGE, E, GH, HO, K, L, NY, W.

Perennial herb, (10)16-30(35)cm tall with many densely crowded ascending branches arising from very reduced stem, lacking roots on prostrate parts. Stem terminated just above ground; main inflorescence-bearing branches initially prostrate for length of (0)4-18(25)cm, abruptly or gradually erect, (6)11-18(25)cm high to base of inflorescence, branched in proximal prostrate parts, simple distally; internodes in upper parts (1)1½-2(3) times length of upper leaves, lower down shorter than leaves; vegetative branches shorter, either similarly robust with leaves of similar size often clustered towards apex or more slender with smaller leaves; axes in upper parts covered by usually moderately dense to dense, rarely sparse, long to very long glandular hairs [(0.2)0.4-0.5(0.6) mm long], mixed with short to moderately long eglandular hairs usually in four lines, sometimes in two rows different from between leaf bases, the indumentum slightly sparser and shorter in lower parts. Cotyledons not seen. Leaves: uppermost leaves on inflorescence-bearing branches usually broadly obovate to broadly ovate, sometimes circular, crenate-serrate to serrate, (5)8-12(14) x (4)5-8(14)mm, light green, rarely reddened, with margins recurved and sessile gland patches distributed over almost entire length of underside, covered on both surfaces by moderately dense to dense, usually long, rarely short glandular hairs mixed with sparse short eglandular hairs, usually denser towards leaf base; base rounded-cuneate to truncate, with margins clasping axis; teeth (1)2-4(7) along distal (1/2)½(1) of each margin, usually bluntly acute to acuminate, rarely obtuse, 1.0-2.5(4.3)mm long; apical tooth usually bluntly acute to obtuse, sometimes bluntly short acuminate, (1.0)1.2-2.7(3.0) x (1.5)2.0-3.5(4.0)mm; leaves lower down smaller with sparser indumentum. Inflorescences but for lowermost 1 to several pairs of flowers dense showy racemes bearing (14)20-26(30) or more flowers; rachis similar to axes but with slightly longer indumentum; internodes elongating after anthesis such that fruiting calyces extend to base of calyx above or past it; pedicels (0.5)1.5-5.5(7.0)mm long, longest towards base of inflorescence; apical bud cluster (excluding buds at widely spaced lower nodes) cylindrical to conical-cylindrical, rounded, initially up to 1.5(1.8)cm long, after flowers of first 3-6 pairs have reached anthesis usually hidden by uppermost corollas, rarely remaining extended up to lcm above corollas. Bracts similar to uppermost leaves of inflorescence-bearing branches but with bases more attenuated. Calyx (5.5)6-8(9)mm long, externally with indumentum (0.1)0.2-0.3(0.4)mm thick comprising moderately dense to dense, usually moderately long to long, rarely short glandular hairs, sometimes mixed with sparse to moderately dense, short to moderately long eglandular hairs, internally with tube usually glabrous, sometimes bearing a mixture of glandular and eglandular hairs, with teeth usually with indumentum similar to but somewhat shorter than external surface, usually confined to distal part and margins or over whole length, rarely glabrous; teeth ± sharply acute to shortly acuminate; lateral clefts 2.0-5.0mm deep, shorter than median clefts which are 3.0-6.0mm deep and often somewhat unequal. Corolla (10) 11-14(15)mm long along upper side, white to pale lilac to deep pink, with 3-5 red-purple striations on each lobe, usually conspicuous, rarely faint, converging together deep in
Fig. 87. Holotype of *E. lasianthera* Barker, sp. nov. (scale 5cm).

Fig. 88. Holotype of *E. eichleri* Barker, sp. nov. (scale 5cm).

Studies in *Euphrasia*
tube, often also with broad red-purple band lining base of lobes, especially lower ones, with small intense yellow blotch at base of each anterior filament; tube 6-10mm long, cylindrical for initial 3-5mm to base of anterior filaments, distally expanded laterally and ventrally, externally glabrous at base, distally on adaxial and lateral surfaces covered by dense long eglandular hairs sometimes mixed with sparse glandular hairs, with patch of moderately dense to dense, short to long glandular hairs behind lateral clefts, on abaxial surface covered by mixture of glandular and eglandular hairs, internally glabrous at base, distally covered by dense, short to moderately long eglandular hairs below and between base of filaments sometimes mixed with a few glandular hairs; hood (3)3.5-5mm long, externally covered by moderately long to long eglandular hairs, dense on top, sparser on sides, mixed with short to moderately long glandular hairs, usually sparse or absent, sometimes moderately dense on top, moderately dense to dense on sides, internally with short glandular hairs, usually moderately dense to dense, sometimes sparse above anthers, sparser or absent towards bases of filaments, mixed with eglandular hairs, dense, long to very long at sinus, usually lacking farther back, rarely sparse, moderately long above anthers; upper lobes coplanar, obtuse to praemorse-obtuse to shallowly emarginate, with rear surface covered by short glandular hairs, sparse to moderately dense towards base, sparse to absent distally with front surface and margins glabrous, with cleft between (3.0)4.2(5.5)mm deep; lower lip usually 3-lobed, sometimes 5-7 lobed by subdivision of lobes, concave from above, downturned from base but finally curved forward, (8)10-13(16) x (12)15-20(22)mm, externally covered in proximal parts by a sparse to moderately dense mixture of glandular and eglandular hairs, distally with indumentum sparser, sometimes almost glabrous, internally and on margins glabrous; lower lobes usually emarginate to praemorse-truncate to truncate, sometimes broadly obtuse, with clefts between (4.0)5.0-7.0(8.5)mm deep. Stamens with filaments glabrous, the anterior pair 5-6.5(7.5)mm long, the posterior pair 2-3.5 (4.5)mm long; anthers (1.9)2-2.5(2.7) x (1.2)1.3-1.6(1.7)mm, with connectives surrounded by dense long flexuose eglandular hairs, the pilosity ± equal on each anther, rearmost pair of awns (0.4)0.5-0.7(0.8)mm long, longer than anterior six awns. Ovary in lateral view ovate to oblong, somewhat compressed laterally, in median view ovate, usually glabrous but for very few to dense, short to long setae in apical region, rarely glabrous all over; apex in lateral view truncate to oblong, sometimes obovate-oblong (3)3.5-4(5)mm broad, in median view ovate to oblong-elliptic, with few to moderately dense, short to long setae confined to the upper 1/4 or at the very apex; apex in lateral view usually truncate to broadly obtuse, rarely acute, often oblique; seeds (6)17-70, oblong to ellipsoid, usually obliquely so, sometimes broadly so, 0.9-1.4(1.5) x 0.5-0.8(1.0)mm. Chromosome number: n=c. 38-47 (Barker 1535, 1536).

Distribution (fig. 86): E. lasianthera occurs in the western part of Victoria's eastern highlands. It is endemic to a small dissected highland region of interconnected ranges and small plateaux bounded to the west, north and south by Mts Buller, Speculation and Arbuckle, respectively. Altitude, c. 1500-1800m.

Ecology: The species, as far as is known, occurs on mountain sides, on plateau areas and on rocky summits. It occurs in dense local populations in grassy areas in a variety of habitats, namely alpine herbfield, alpine grassland, alpine heath, subalpine snowgum (Eucalyptus pauciflora) woodland in glades or under overhanging trees, and (Barker 1538) sclerophyll forest. It occasionally occupies disturbed situations such as roadsides.

Flowering apparently begins in late November and continues until early February. Mature capsules are increasingly apparent after the start of January.
Fig. 89. *E. lasianthera*, Macalister River headwaters, Eastern Highlands, Victoria. Habit (*Barker* 1498, holotype), scale 5cm long.

**Conservation status**: 2R,C.

*Note:* *E. lasianthera* is one of the few Australian perennials with the character combination of hairy anther backs and prominently striated corollas (fig. 85). It is also distinctive in the sharply demarcated yellow blotches, one at the base of each anterior filament. They form the centre point of the flower and are highlighted by the convergent striations on the corolla lobes (fig. 85A). It may share this character with some populations of its close ally, the annual *E. eichleri* (*q.v.*: Intraspecific Polymorphism). Unlike other Australian perennials with striated corollas, *E. lasianthera* lacks a yellow blotch behind the lowest corolla lobe.
Specimens examined


14. Euphrasia eichleri Barker, species nova


Species nova Sectionis Lasiantherarum, ab E. lasianthera differt inter aliis duratione annua, caule uno ramificatione in partibus superioribus, filamentis antherisque minoribus, parte maiore ovarii setosa, ovulis paucioribus et seminibus maioribus, ab E. alsa caulibus altioribus folia plura ferentibus, indumento longiore, foliis angustioribus dentibus pluribus, corolla maiore in basi tubi pilosa, antheris filamentisque maioribus, et seminibus pluribus.

Holotypus (fig. 88): Hj. Eichler 14825, 13.ii.1958. Victoria, Bogong High Plains. Surroundings of Mt Nelse; ca. 1900m alt. AD96105007. Isotypi: CANB, CGE, K.

Annual herb, (4)7-14.5(16)cm tall, higher when fruiting, erect, occasionally with herbaceous parts reddened. Stem to base of inflorescence (2.5)5-11(14)cm long, bearing (5)6-8(12) pairs of leaves, with branches forming in axes of cotyledons (at least in the few sufficiently mature plants seen) and all leaf axes up to (1)(2)3 nodes below inflorescence; branches later-flowering, with upper ones developing first, bearing (1)(2)3-4(leaf) pairs, the lower pairs themselves usually subtending shoots (fully developed lower branches not seen); axes with indumentum usually extending to below cotyledons, consisting of mixture of glandular hairs and lax eglandular hairs, arranged in four rows decurrent from leaf bases, alternately dense, long, i.e. (0.2)0.4-0.7(1.0)mm, and moderately dense, short to long, the eglandular hairs sometimes lacking or shorter than the glandular hairs. Cotyledons 2-5 x c. 1½-2mm, spatulate to elliptic, entire, glabrous, usually persisting until after flowering time. Leaves: uppermost stem leaves (8)10-16(20) x (2.9)3.5-6.5(8.5)mm, serrate to crenate-serrate, usually elliptic, sometimes ovate-elliptic or obovate-elliptic in outline, with margins recurved, with upper surface covered by dense glandular hairs, short in apical half grading to moderately long towards base, mixed with short eglandular hairs, dense and ± scabrous in apical region, especially upon recurved margins, grading to sparse and lax towards base, with lower surface usually covered by sparse to moderately dense, moderately long...
glandular hairs, sometimes mixed with sparse to moderately dense, short to moderately long ± lax eglandular hairs; base usually rounded-cuneate to narrowly cuneate, sometimes rounded; teeth (2)3-4(5) along each margin, bluntly acute or obtuse, (0.5)1.5 (2.5)mm long; apical tooth bluntly obtuse or acute, (2.0)2.5-4.0(6.5)mm long; leaves in middle of stem similar; lowest leaves smaller, fewer-toothed and with more attenuated bases, but with similar indumentum. Inflorescences dense racemes, that of stem with usually more than 15 flowers; rachis with indumentum similar to axis but denser; internodes elongating somewhat after anthesis such that fruiting calyces extend past bases of calyces above, sometimes lower ones slightly longer; pedicels 0-1.0(2.5)mm long, hardly elongating after anthesis; apical bud cluster hemispherical, hardly extending above corollas of initial flower pair (i.e. extended less than 0.5cm). Bracts similar to uppermost leaves or somewhat shorter, with longer, occasionally more numerous teeth and denser indumentum. Calyx (5.3)6.2-8.7(9.5)mm long, externally bearing dense long glandular indumentum, (0.3)0.4-0.6(1.0)mm thick, with apices of teeth covered by short setose to moderately long lax, moderately dense to dense, upturned eglandular hairs, internally with dense, short to long glandular hairs above median clefts mixed with short to moderately long glandular hairs, usually confined to apices of teeth, sometimes all over teeth and onto tube; teeth ± sharp, linear, acute or caudate, with margins somewhat recurved at least when dried; lateral clefts (2.0)2.5-3.9(4.8)mm deep, shorter than median clefts which are (3.0)3.5-5.0(5.8)mm deep. Corolla (6.5)8.2-11.5(13.0)mm long along upper side, white to lilac with 3-5 indigo to deep red-purple striations on each lobe, those on upper lobes extending onto hood, sometimes with yellow blotch at the base of the lower lip, sometimes only with two distinctive yellow patches at base of each anterior filament; tube (4.5)6.4(8.0)mm long, for initial (3.3)3.6(5.7)mm to base of anterior filaments narrowly cylindrical, then expanded laterally and ventrally, externally glabrous or with dense, short to long downturned eglandular hairs on distal ½-⅓ of adaxial and lateral surfaces, usually also with dense patch of short to moderately long glandular hairs behind lateral clefts, internally with dense, short to moderately long eglandular hairs on upper half of tube about bases of filaments and decurrent from them; hood (2.1)2.7-4.0(4.5)mm long, externally on top covered usually by dense long eglandular hairs, sometimes by dense, short to moderately long glandular hairs, on sides covered usually by dense long eglandular hairs, sometimes by moderately dense, moderately long glandular hairs, internally bearing moderately dense to dense, short to moderately long glandular hairs above anthers, together with a dense patch of usually moderately long to long, occasionally short, flexuose eglandular hairs in area of sinus, sometimes also with sparse line of short eglandular hairs down middle of hood, with upper lobes ± coplanar, usually shallowly to deeply emarginate, sometimes praemorse-truncate, with front surface and margins glabrous, with rear surface usually glabrous, sometimes bearing sparse glandular hairs on proximal half, with cleft between (2.0)2.5-4.0(4.5)mm deep; lower lip (5.0)7.0(10.0) x (11.0)14.0(18.0)mm, concave from above, curved downward from tube, externally covered behind lobes usually by sparse to dense mixture of moderately long glandular and eglandular hairs, sometimes by eglandular hairs alone, lobes usually bearing a sparser indumentum, sometimes glabrous, with margins and inner surface glabrous, with lower lobes usually emarginate or deeply so, rarely shallowly to deeply emarginate, with clefts between (3.0)4.0-6.0(7.8)mm deep. Stamens with filaments usually glabrous, rarely with one or two short eglandular hairs, anterior pair 3.5-5.0mm long, posterior pair 1.5-2.5mm long; anthers (1.2)1.6-2.0(2.2) x 0.8-1.1mm, with connectives of anterior pair glabrous or surrounded by usually sparse, rarely moderately dense, short flexuose eglandular hairs, less hairy than those of posterior pair, which are surrounded by very sparse to dense, short to moderately long flexuose hairs, with rearmost pair of awns (0.25)0.3(0.5)mm long, always longer than other three awn pairs. Ovary laterally compressed, in lateral view ovate to oblong-elliptic to oblong-ovobovate, with upper ½-⅔ covered by dense, long to very long setae;
apex in lateral view obtuse to truncate-obtuse; ovules (20)30(40), often with somewhat different number in each cell. Immature capsules obovate to oblong-elliptic to oblong-ovate in lateral view, laterally compressed, attaining a length of 7mm and breadth of 4mm and then still shorter than calyx, with upper $\frac{1}{3}$ to $\frac{3}{4}$ clothed by dense setae, short towards base, long at apex; apex in lateral view shallowly emarginate to truncate; immature seeds c. 4-15, obliquely ellipsoid, 1.5-2.0 x 0.5-1.2mm. Chromosome number: unknown. Figs 11, 88.

Distribution (fig. 86): E. eichleri is confined to alpine and subalpine tracts of the Victorian Alps between Mt Bogong and the Bogong High Plains, and on the Dargo High Plains to the south. Altitude, c. 1370-1890m.

Ecology: Ecological data on this species are very poor. It has been recorded from "low open shrubland dominated by Orites lancifolia" (Adair AD98117251), grassland (Sneddon 10) and sphagnum bogs (Willis MEL41664).

Flowering apparently begins from mid January to early February. Only the type, which was collected in mid February, bears capsules on the stem. The remaining collections were gathered earlier. Flowering probably continues until at least April.

Conservation status: 2V,C. The effect of cattle grazing on this restricted species must be investigated.

Intraspecific polymorphism

Coloration of the corolla may have taxonomic significance at an infraspecific level in E. eichleri. Corollas of Sneddon 10 from the Bogong High Plains have a yellow patch behind the lowest lobe (? extending to the base of the filaments), typical of E. alsa and many other species. In the dried state, Backen MEL exhibits a small but distinctive yellow patch at the base of each anterior filament. Such patches are strongly demarcated in E. lasianthera. A field study of variation in corolla coloration is needed.

Specimens examined


LOCALITY VERY DOUBTFUL: Stead s.n., 13.i.1962. New South Wales. Charlottes Pass, Kosciusko area. NSW60818 (presumably from her visit to Bogong High Plains a week earlier).


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E. zelandica auct. non Wettst.: Ewart, Fl. Vict. (1931) 1024, pro syn. "zealandica".

Annual herb, 2-6(7)cm tall, reaching c. 12cm when fruiting, erect, with vegetative parts as well as calyces, bracts and rachises often red-purple, greener in more luxuriant plants. Stem to base of inflorescence 1.3-5.0(6.5)cm high, bearing (1)3-4(5) pairs of leaves, with branches in axils of cotyledons and leaves up to (1)2(3) nodes below inflorescence, the upper ones developing first; branches later-flowering, bearing 0-2 leaf pairs, sometimes themselves branched; axes with indumentum c. 0.1-0.3mm thick, consisting of moderately dense, short to moderately long glandular hairs and two broad bands of dense, short to moderately long eglandular hairs decurrent from between leaf bases. Cotyledons broad, ovate-elliptic to elliptic, 2-5mm long, entire, glabrous, persistent. Leaves: uppermost stem leaves in outline usually obovate or elliptic, rarely broadly so, pinnatifid or pinnatifid-serrate, (4.6)-10(15) x (2.3)-5.7(9)mm, with blade usually elliptic to elliptic-ovate or narrowly so, sometimes lanceolate with margins recurved, with upper surface and margin covered by sparse short glandular hairs mixed with eglandular hairs, with lower surface covered by mixture of moderately dense, moderately long glandular hairs and sparse to moderately dense, short to moderately long eglandular hairs decurrent from between leaf bases. Base narrow cuneate to rounded-cuneate; teeth (1)2(3) along each margin, bluntly acute or obtuse, (0.7)1.2-2.5(3.5)mm long; apical tooth blunt, usually acute, sometimes obtuse, (1.0)1.5-3.5 (5.0)mm long; lower leaves near the cotyledons smaller, fewer-toothed, with a sparser shorter indumentum; leaves on branches similar to uppermost stem leaves, but rather smaller. Inflorescences dense racemes; flowers of inflorescence terminating stem c. 15-30, fewer on depauperate plants less than 3cm high and in inflorescences terminating branches; rachis with indumentum similar to axis; internodes elongating slightly after anthesis such that apices or capsules extend past bases of calyces above, with lowestmost 1-2 internodes longer; pedicels 0.3-1.5(2.0)mm long; apical bud cluster hemispherical, extending (0.1)0.3-0.8mm above initial flower pair, hidden by or hardly emergent from uppermost corollas after flowers of first (0)2-3(6) pairs have opened. Bracts of similar shape to the uppermost leaves but longer, broader, sometimes more toothed and with a denser similar indumentum. Calyx (4.0)4.5-7.0(7.7)mm long, broadening as capsule forms, with external indumentum 0.1-0.3(0.4)mm thick, consisting of a mixture of moderately dense to dense, short to moderately long glandular hairs and sparse, very short to short eglandular hairs, with inside of teeth bearing very sparse to dense, short to moderately dense eglandular hairs mixed with sparse short eglandular hairs behind the apex only or extending to bases of clefts, with margins lined with moderately dense, eglandular hairs, with inner surface below teeth glabrous; teeth ± bluntly narrow acute, with margins not recurved; lateral clefts (1.7)2.0-3.2(3.6)mm deep, shorter than median clefts which are (2.0)2.3-4.0(4.5)mm deep. Corolla (5.5)7.0-9.0(10.2)mm long along upper side, white to lilac, with three red-purple striations on each lobe, those on upper lobes extending onto hood, with yellow blotch on lower lip behind lobes extending deep into throat to point of insertion of stamens; tube (4.8)6.0(8.0)mm long, for initial (3.4)4.5(6.0)mm to base of anterior filaments narrowly cylindrical, then expanded laterally and ventrally, externally glabrous but for short to moderately dense, eglandular hairs on dorsal and lateral surfaces of distal half and small patch of dense, moderately long glandular hairs behind lateral clefts, internally glabrous; hood 1.5-2.8mm long, externally with dense, moderately long eglandular hairs on dorsal...
surface and sides, with sparse glandular hairs occasionally at base of lobes, rarely along middle of dorsal surface, internally with sparse to dense, very short to short glandular hairs above anthers mixed with moderately long, moderately dense eglandular hairs below sinus between lobes, with upper lobes ± coplanar, glabrous, usually emarginate or shallowly so, rarely ± obtuse, with cleft between 0.8-2.2mm deep; lower lip (3.0) 3.5-5.0(6.5) x (6.5)7.5-12.0(12.7)mm, concave from above, markedly downturned from tube, externally covered behind lobes by dense, moderately long eglandular hairs, sometimes mixed with sparse to moderately dense, moderately long glandular hairs, on middle lobe by sparse to moderately dense, moderately long eglandular hairs, rarely mixed with sparse short glandular hairs, with indumentum on lateral lobes similar to that of lower lobe but sparser, internally and on margins glabrous, with lower lobes usually emarginate, sometimes broadly or deeply so, with clefts between 1.6-4.0mm deep. Stamens with filaments glabrous, anterior pair 2.2-2.9mm long, posterior pair 0.7-1.2mm long; anthers 0.9-1.3 x 0.6-1.0mm, with connectives of anterior pair glabrous or surrounded by a few to sparse, short flexuose eglandular hairs, less hairy than those of posterior pair which are surrounded by sparse to dense, short to moderately long flexuose hairs, with rearmost pair of awns 0.1-0.2(0.25)mm long, always longer than other 3 pairs. Ovary laterally compressed, in lateral view elliptic to oblong-elliptic, with upper ⅓ covered by dense, moderately long to long setae; apex in lateral view usually broadly obtuse, sometimes truncate to slightly emarginate; ovules 10-12(15), equal in each cell of ovary or with one more in dorsal cell. Capsules laterally compressed, in lateral view elliptic, 7.0-8.5 x c. 4mm, usually shorter than calyx, sometimes slightly protruding with upper ⅓(⅔) clothed with dense long setae; apex in lateral view broad, truncate to obtuse, sometimes shallowly emarginate; seeds (4)7-11(12), ± ellipsoid, 1.8-2.5mm long. Chromosome number: n=27 (Barker 1696). Figs 11, 15, 90.

Typification: The sheets of E. alsa collected by Mueller from the "Munyang Mountains", now the Snowy Mountains of New South Wales, are very homogeneous and were apparently collected at a similar time (all are at a similar stage of development). However, it is impossible to determine whether they come from the one gathering. Most have annotations similar to or only slightly differing from the very general distribution cited in the protologue (Mueller 1855), "Gregarious on the highest stoney summits of the Munyang Mountains—(6000 feet)". Many of the syntypes have an extended altitudinal range of "5-6000 feet". Many also are identified as E. antarctica Benth. in keeping with Mueller's acceptance of the name after its publication in Bentham's 'Flora Australiensis' (1868).

MEL41669 was chosen as lectotype since it alone bears all the following attributes: a label in Mueller's handwriting worded the closest to the protologue, Mueller's annotation "Euphrasia alsa Ferd. Muell." rather than E. antarctica Benth., and no other slightly discordant labels on the same sheet. Some of the syntypes have been dated January 1855 by Mueller. Dr J.H. Willis has annotated other MEL type collections with this date. This does not appear justified. Since there is no reason to assume that all syntypes come from the one gathering, and as Mueller climbed the summit of Mt Kosciusko or a neighbouring peak on New Year's Day, 1855 (M. Willis 1949), some collections may have been made in late December, 1854.

Distribution (fig. 86): E. alsa is endemic to the Snowy Mountains of south-eastern New South Wales. Most collections come from the Kosciusko region in the south of the distributional range. Not only may this be because the higher mountains of this region provide a greater area of potential habitat, but it may also reflect its greater accessibility to collectors. Altitude, 1700-2100m or more.
Fig. 90. *E. also*, at Spencers Creek, Snowy Mountains, New South Wales (*Barker* 1696). A, population in small open areas in low (sub)alpine heath, scale 5cm wide; B, plant with white corolla with purple striations and yellow blotch on lower side of mouth, line scale 1cm.
Ecology: *E. alsa* in the alpine zone tends to occupy small bare stony areas between shrubs of low heath, tall alpine herbfield, sod tussock grassland, and *Epacris-Chionohebe fjaeldmark*, its most common habitat (Costin et al. 1979).

In its rare occurrences within the subalpine zone, *E. alsa* may occur in pockets of characteristically alpine vegetation rather than subalpine types. At Spencer's Creek, at about 1770m, it occurs in a community resembling low alpine heath (fig. 90: Barker 1696). Burbidge (6322) records it also from “alpine heath” at the even lower Piper’s Gap (probably about 1730m high).

Flowering of the stem inflorescence begins between late December and late January or even early February. Mature fruits are apparent from mid January. Branch inflorescences may still be found in early April as they are at an early stage of flowering in *Costin & Skottsberg NSW10873* and *Gauba GAUBA7854, GAUBA7855*, all collected in mid March.

Conservation status: 2R,C.

Note: *E. alsa* is most closely related to *E. eichleri*, the other annual of Sect. *Lasiantherae*, and *E. caudata* (q.v.: note 1) of Sect. *Scabrae*.

Specimens examined


VI. Sect. *Scabrae* (Du Rietz) Barker

For synonymy, description, typification and distribution see p. 86. Fig. 91.

Sect. *Scabrae* is to endemic to temperate southern and eastern Australia. It consists of five species, *E. scabra* which is widespread throughout southern Australia (fig. 93), *E. caudata* which is restricted to the Australian Alps (fig. 92), and four other species confined to north-eastern New South Wales (fig. 94). There is some evidence for a possible undescribed taxon in the Blue Mountains region of New South Wales which links *E. arguta* and *E. caudata* (see *E. arguta*: note 1). Several species are apparently extinct or facing extinction.
Fig. 91. Sect. Scabrae. A, front view of flower; B, side view of flower; C, dorsal view of corolla, showing position of anthers; D, ventral view of corolla; E, F, external view of the anthers on one side of flower, with an anterior anther on the left and a posterior anther on the right; G, internal view of a posterior anther (on right) and part of an anterior anther; H, lateral view of capsule; I, median view of capsule; J, abaxial view of an uppermost leaf on the main inflorescence-bearing axis (s = sessile gland patch). (A-D, F, G, J, E. caudata: Barker 1649; E, E. ciliolata: Pullen 3792; H, I, E. caudata: Hoogland 8481, type).
Figs 92-93. Distribution of the species and subspecies of Sect. Scabrae (1). 5000ft (1520m) contour.
Fig. 94. Distribution of the species and subspecies of Sect. Scabracae (2). 3000ft (910m) contour.
Note: In the Australian Alps, populations of *E. scabra* approach *E. caudata* in some characters. The two species may be distinguished on flower colour and length of the glandular indumentum of the axes, leaves and calyces. See *E. scabra* (Intraspecific Polymorphism).

**Key to the species of Sect. Scabrae**

1a. Outer surface of calyx scaberulous to shortly scabrous, sometimes also bearing a few tiny mm long).

2a. Uppermost stem leaves with (2)3-4(5) teeth along each margin, the longest tooth (1.5) 3.0(5.5)mm long. Lowermost calyces of stem inflorescence (5.3)6.3(8.2)mm long. [Corollas white to lilac to ?purple, at least sometimes with yellow patch on lower lip.] ................................................................. 19. *E. arguta* (p. 282)

2b. Uppermost stem leaves with (0)1(2) teeth along each margin, the longest tooth 0.05-1.5mm long. Lowermost calyces of stem inflorescence (2.8)3.5-5.4(6.9)mm long.

3a. Corollas blue to mauve, with midline of lower lip at least sometimes yellow. Capsules usually with upper \( \frac{1}{3} \)\(-\frac{1}{2} \) covered by sparse to moderately dense setae less than 0.1mm long, sometimes glabrous. Seeds (0.9)1.0-1.2(1.4)mm long. Rearmost pair of anther awns (0.3)0.4-0.5(0.6)mm long. .................. 20. *E. ciliata* (p. 285)

3b. Corollas yellow. Capsules with upper \( \frac{1}{3} \)\(-\frac{1}{4} \) covered by dense setae more than 0.2mm long. Seeds (0.4)0.5-0.8(0.9)mm long. Rearmost pair of anther awns (0.1) 0.2(0.3)mm long. ................................................................. 18b. *E. orthocheila* ssp. peraspera (p. 280)

1b. Outer surface of calyx covered by prominent glandular hairs, moderately dense to dense at least on teeth, usually 0.1-1.0mm long, rarely subsessile (with large glands), mixed with very short to long, scabrous to lax eglandular hairs.

4a. Lower corolla lobes usually emarginate, rarely truncate, with glabrous margins. Seeds (0.9)1.2-2.0(2.5)mm long. Capsules porrect, with apices in lateral view shallowly emarginate-truncate to broadly obtuse. [Corollas usually violet to pink, sometimes paler or white, with yellow to red streak along midline of lower lip. Capsules with upper \( \frac{3}{4} \)\(-\frac{3}{4} \) covered by dense setae more than 0.3mm long. Glandular hairs dense over calyx, (0.1)0.2-0.4(0.6)mm long.] ................................................................. 16. *E. caudata* (p. 265)

4b. Lower corolla lobes usually obtuse to truncate and often shortly apiculate, sometimes shallowly emarginate, with margins sparsely to densely lined by short eglandular hairs or glabrous. Seeds (0.4)0.5-0.8(1.0)mm long. Capsules usually slightly downcurved, rarely porrect, with apices in lateral view acute to obtuse.

5a. Uppermost stem leaves (4)6-8(11) x (0.5)1.2-2.0(2.5)mm, with 0-1(2) teeth along each margin, the longest tooth 0.05-0.5(0.6)mm long. Lowermost calyces of stem inflorescence (2.8)3.5-4.5(4.9)mm long. Lowermost capsules of stem infructescence (3.4)4.0-5.0mm long. [Corollas yellow.] ................................................................. 18a. *E. orthocheila* ssp. orthocheila (p. 280)

5b. Uppermost stem leaves (6)7.5-14(20) x (1)2.5-10(13)mm, with (1)2-3(5) teeth along each margin, the longest tooth (0.4)0.7-4.0(5.5)mm long. Lowermost calyces of stem inflorescence (4.3)5.5-7.0(9.0)mm long. Lowermost capsules of stem infructescence (4.0)5.0-8.0(9.3)mm long.

6a. Corollas yellow. Capsules with upper \( \frac{3}{4} \)\(-\frac{3}{4} \) covered by dense setae more than 0.3mm long. Stem nodes (6)8-18(24). Glandular hairs on calyx prominent, (0.05)0.1-0.2(0.3)mm long. Rearmost pair of anther awns (0.1)0.2(0.3)mm long. ................................................................. 17. *E. scabra* (p. 270)

6b. Corollas white to lilac to ?purple, at least sometimes with yellow blotch on lower lip. Capsules usually with upper \( \frac{1}{4} \)\(-\frac{1}{4} \) covered by moderately dense to dense setae 0.1-0.3mm long, extending slightly further down lines of dehiscence, sometimes glabrous but for a few setae at very apex. Stemnodes (18)24(30). Glandular hairs on calyx tiny (less than 0.05mm long). Rearmost pair of anther awns (0.2)0.3-0.4(0.5)mm long. ................................................................. 19. *E. arguta* (p. 282)


Erect annual herb, (7.5)12-34(40)cm tall. Stem to base of inflorescence (3.5)7-24 (30)cm high, bearing (5)8-14(17) pairs of leaves, with axillary branches developing from (1)2-6(10) nodes above cotyledons to (2)3-5 nodes below inflorescence, with length of stem between inflorescence and uppermost branches more than half length of entire stem to base of inflorescence; branches flowering later than stem and developing in a basipetal sequence, lower branches bearing up to c. 4-10 leaf pairs, uppermost pair bearing (1)2-5(7) leaf pairs, with all but upper and occasionally lowermost leaf pairs subtending shoots; axes covered by moderately dense, moderately long to long glandular hairs over whole length, mixed with short to moderately long eglanular hairs, which are mainly confined in upper parts to two dense rows discernent from between leaf bases or four dense lines discernent from sides of each leaf, sparse in between, more scattered and sparse to moderately dense lower down. Cotyledons oblong to broad oblong, c. 1.0-2.5mm long, entire, glabrous, hardly persisting or deciduous at flowering. Leaves: uppermost stem leaves in outline ovate-elliptic, usually pinnatifid, sometimes serrate-crenate, (6)12-24(36) x (1.7)3.3-7.0(9.5)mm, with margins recurved, with blade (excluding teeth) lanceolate, covered by usually moderately dense to dense, rarely sparse, short to moderately long scabrous indumentum on upper surface and margin, often sparser on lower surface, usually mixed especially towards base with sparse to dense, moderately long to long glandular hairs; base rounded to rounded-cuneate; teeth 2-3(5) along each margin, usually bluntly or sharply acute, rarely obtuse, reaching (0.5)1.2-3.0(5.0)mm long; apical tooth bluntly or sharply acute, (2.0)4.0-10.0(14.8)mm long; leaves lower down somewhat longer than uppermost leaves with shorter teeth and with similar indumentum; those at very base much smaller; leaves of branches in similar positions similar in shape but somewhat smaller. Inflorescences dense racemes, that of stem with (10)18-24(32) flowers, those of branches producing fewer, those of depauperate plants with 10 or less flowers; rachis covered by dense rows of down-turned, moderately long to long eglanular hairs mixed with sparse, short to long glandular hairs discernent from between bracts, alternating with a mixture of sparse, short to long eglanular hairs and moderately dense, moderately long to long glandular hairs; internodes elongating after anthesis such that capsules are well below or just reach node above; pedicels hardly elongating after anthesis, 0.2-0.9(1.5)mm long, those at lowermost 1-3 nodes longer; apical bud cluster rounded-conical, bracteose, extended c. 0.5-2.0cm above initial flower pair, becoming hidden after 3-12 or more pairs of flowers have opened. Bracts similar to uppermost leaves but somewhat shorter and broader, with similar indumentum. Calyx (3.8)5.5-8.0(9.5)mm long, externally covered by a mixture of dense, usually moderately long to long, rarely short [i.e. (0.1)0.2-0.4(0.6)mm long] glandular hairs and sparse to dense, short to long eglanular hairs, internally with teeth covered by moderately long to long glandular hairs, moderately dense to dense at apex, sparser or absent below mixed with short to long, upturned appressed eglanular hairs, usually sparse to dense or sometimes absent at base of teeth, sparser or absent towards apex, glabrous below.
teeth; teeth usually sharply, occasionally bluntly acute; lateral clefts (2.0)2.6-3.7(5.5)mm deep, shorter than the median clefts which are (2.3)3.2-4.5(6.2)mm deep. Corolla (9.0)11.8-16.0(19.0)mm long along upper side, usually violet to mauve to pink, rarely paler or white, with broad groove extending from behind lower lobes to narrow part of tube at least usually white with a usually yellow to orange-brown, rarely red streak down its midline; tube (6.3)8.2(10.0)mm long, laterally and somewhat medially broadened at bases of anterior filaments, which are (4.2)5.4(6.8)mm from base of corolla, externally glabrous at base, distally except for proximal part of abaxial groove covered by moderately dense to dense, moderately long to long glandular hairs, sometimes with dense patch of short to moderately long glandular hairs behind the lateral clefts, sometimes extending as far as base of anterior filaments, internally glabrous to summit of ovary, distally covered by moderately dense to dense, short to moderately long glandular hairs up to bases of posterior filaments; hood (3.4)4.8(6.3)mm long, externally covered by moderately dense to dense, moderately long to long glandular hairs, often mixed with short to moderately long glandular hairs, usually restricted to sides or front where sparse to moderately dense, occasionally dense all over, internally covered by moderately dense to dense, short to long glandular hairs at the sinus, often extended to above anthers, usually lacking elsewhere, sometimes sparse along midline of hood, sometimes also with sparse short glandular hairs, with upper lobes usually emarginate or deeply or broadly so, sometimes shallowly emarginate or truncate, with rear surface usually glabrous, sometimes covered by sparse to dense short to moderately long glandular hairs or both, with front surface and margins glabrous, with cleft between (1.0)1.8(2.6)mm deep; lower lip (5.0)8.0(11.0) x (8.0)11.8(17.0)mm, ± flat crosswise, initially porate, often later bent downwards distally, probably after anthesis, always longer than upper lip, externally covered by sparse to dense, moderately long to long glandular hairs, occasionally mixed with moderately dense to dense, short to moderately long glandular hairs, internally at base bordered by glandular hairs of tube, otherwise glabrous, with margins glabrous or with one or two glandular hairs towards base of clefts, with lower lobes usually emarginate or deeply so, rarely truncate, with clefts between (2.5)4.1(5.5)mm deep. Stamens with filaments usually glabrous, rarely with dense glandular hairs covering lower third of anterior filaments, anterior pair (4.0)6.0(8.6)mm long, posterior pair (2.0)3.1(5.2)mm long; anthers (1.2)1.7(2.1) x (0.9)1.1(1.5)mm, with connectives of anterior pair surrounded by usually very few to moderately dense, long to very long, rarely dense or short downturned glandular hairs, less hairy than or equally as hairy as those of posterior pair, which bear sparse to dense, long to very long glandular hairs, with rearmost pair of awns (0.2)0.3(0.4)mm long, longer than the anterior three pairs. Ovary laterally compressed, in lateral view usually oblong-obovate to oblong-ovate, sometimes ovate or elliptic, with upper 1/2-2/3 covered by dense erect setae, very long about apex, long lower down; apex in lateral view usually obtuse or ± truncate, rarely broad acute; ovules (20)30-110. Capsules slightly compressed laterally, in lateral view oblong-ovate to oblong-elliptic, (5.2)5.5-8.5(9.5) x (3.0)3.9(4.3)mm, with upper 1/2-2/3 covered by dense long erect setae, very long about apex; apex in lateral view obtuse to truncate or even slightly emarginate; seeds 9-80, usually ± ellipsoid, sometimes angular-ellipsoid, (0.9)1.2-1.5(2.0) x (0.5)0.6-0.9(1.0)mm. Chromosome number: n = 27 &/ or 28 &/ or 27II + 2I &/ or 725I + 2II (Barker 1649). Figs 11, 15, 16, 91A-D, F-J, 95.

Typification

_E. scabra_ R.Br. var. caudata_ Willis  Three plants on the type sheet, less branched than normal for the species, were labelled as isotypes by Willis on 11.i.1966. The fourth plant, more typical of the species, was designated as the holotype. One of these isotypes is also unusual in that the stem has apparently been truncated near the base, with the pair of branches in the axils of the uppermost of the remaining leaves developing equally in its place.
Distribution (fig. 92): *E. caudata* is confined almost entirely to the Brindabella Range of New South Wales and the Australian Capital Territory, the Snowy Mountains of New South Wales, and the Victorian Alps to the east of Omeo. There are isolated collections from Mt Wellington, Victoria (note 2) and the “Brown Mountains near Littleton” (*Betche NSW/10868*) about 100km east of Mt Kosciusko. Altitude, 1070-1980m.

Ecology: The majority of collections of *E. caudata* come from the subalpine zone, where it is often associated with sphagnum swamps, streams or other damp situations. It frequently grows in open grassy areas or in grassy or shrubby areas under snowgums (*Eucalyptus pauciflora*). One montane habitat is recorded: “Steep mountain side in fairly tall scrub in Eucalypt forest” (*Ford NSW47104*). No ecological data are available for the dwarf variant at Charlottes Pass, Kosciusko region (see Intraspecific Polymorphism), but it possibly extends into the alpine zone.
Flowering begins usually in January, rarely in early December. Stems finish flowering from February to March, but primary and secondary branches may continue to flower well into April or May.

Conservation status: considered not at risk.

Notes: 1. *E. caudata* is closely related to *E. ciliolata*, *E. arguta* and *E. scabra*. Differences are given in the key to the species of Sect. Scabrae. In addition, the separation of *E. caudata* and *E. scabra* is discussed under *E. scabra*: Intraspecific Polymorphism.

*E. caudata* approaches *E. alsa* and *E. eichleri* of Sect. Lasiantherae by its emarginate corolla lobes, glandular indumentum, densely setose capsules with broadly obtuse to truncate or emarginate apices, and its large seeds. *E. alsa*, which also approaches *E. caudata* in leaf shape (figs. 11, 12) differs by its smaller habit, fewer stem nodes, shorter indumentum, smaller striated corollas lacking a groove on the lower side and with a downturned lower lip, and by its smaller anthers. In the one known location where *E. alsa* and *E. caudata* meet, highly sterile hybrids are common (p. 290). *E. eichleri* differs by its serrate to crenate-serrate leaves (fig. 11), its fewer stem nodes, its shorter striated corollas lacking a groove on the lower side, with a downturned lower lip and with longer lobes, and its shorter filaments.

2. A single plant, collected by Mueller (MEL41653) in 1861 from Mt Wellington, Victoria (fig. 92), far to the west of the main area of distribution of *E. caudata*, is distinctive for its glabrous-backed anthers and its leaf apices and teeth which are rather blunter than normal. Otherwise the plant resembles *E. caudata*. Although the corollas have dried yellow, they seem to have originally been the purple or white of *E. caudata*. This is suggested not only by the brownish colour of the anthers, a commonly associated attribute, but also by the fact that Mueller (1865) placed the specimen (of his own collecting) under *E. brownii*, which he distinguished from *E. scabra* by its non-yellow corollas. Further collections are required to determine whether the plant represents a distinct subspecies of *E. caudata*.

Intraspecific polymorphism

In *E. caudata* there is evidence for the existence of a dwarf variant apparently confined to the higher parts of the Kosciusko massif around and above Charlotte's Pass (fig. 92), in the subalpine zone and possibly extending into the alpine zone. Normal, larger sized plants, which occur throughout much of the Australian Alps, are extensive in the Kosciusko region below Charlotte's Pass.

The collection Stead 7 from Spencer's Creek (fig. 92) comprises plants which are intermediate between the two variants. The sites at Spencer's Creek are only at a slightly lower altitude than Charlotte's Pass. The locality is somewhat intermediate between the habitats typical of both variants as, while it is surrounded by tree-covered slopes, there are also areas of communities resembling tall alpine herbfield and low alpine heath. Plants of this intermediate population as well as plants of both normal and dwarf habits were tested for possible evidence of hybridism. All bore a high percentage of apparently normal pollen (PS51, 92, 98-103).

A comparison of the morphological variation in the two variants and the intermediate population, as well as the possible differences in habitat are summarized in table 11.

In the absence of a combined ecological and genetical study of the two variants it is not possible to determine whether their morphological differences reflect true genetic differences or alternatively, the different influences of their respective habitats upon very similar genotypes. However, while the differences between the two variants are all
Table 11. A summary of morphological variation within *Euphrasia caudata* in various habitats in the Kosciusko region of the Australian Alps.

<table>
<thead>
<tr>
<th>Known localities in Kosciusko area</th>
<th>Mt Kosciusko 6500 feet, Charlottes Pass, The Chalet (at Charlottes Pass)</th>
<th>Spencers Creek</th>
<th>Dead Horse Gap, Thredbo River Gorge, Guthega, Guthega Dam, Waste Point</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimated altitudinal range</td>
<td>1800-2000m</td>
<td>1770m</td>
<td>1000-1600m (-1800m in Brindabella Ra.)</td>
</tr>
<tr>
<td>Probable general habitat</td>
<td>subalpine and/or alpine vegetation</td>
<td>area supports alpine and subalpine vegetation</td>
<td>subalpine (rarely alpine) vegetation</td>
</tr>
</tbody>
</table>

**HABIT**

<table>
<thead>
<tr>
<th>Plants sampled</th>
<th>12</th>
<th>15</th>
<th>50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height</td>
<td>(7.5)12.0(14.5)cm</td>
<td>(13.5)18.6(26.0)cm</td>
<td>(10)15-34(40)cm</td>
</tr>
<tr>
<td>Stem height</td>
<td>(3.5)6.7(11.0)cm</td>
<td>(10.0)13.5(17.5)cm</td>
<td>(7.3)11.0-24.0(30.0)cm</td>
</tr>
<tr>
<td>Number of nodes above inflorescence</td>
<td>(5)6-8(9)</td>
<td>8-10(12)</td>
<td>(8)10-14(17)</td>
</tr>
<tr>
<td>Number of nodes below inflorescence</td>
<td>0-1(3)</td>
<td>(1)2-3(4)</td>
<td>(1)2-4</td>
</tr>
<tr>
<td>Number of nodes on uppermost branches</td>
<td>1-2(4)</td>
<td>c. 2-3</td>
<td>(3)5(7)</td>
</tr>
</tbody>
</table>

**UPPERMOST STEM LEAVES**

<table>
<thead>
<tr>
<th>Plants sampled</th>
<th>6</th>
<th>7</th>
<th>66</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf length</td>
<td>(12.0)16.7(20.5)mm</td>
<td>(7.5)13.6(17.5)mm</td>
<td>(6)12-24(36)mm</td>
</tr>
<tr>
<td>Leaf breadth</td>
<td>(2.2)4.6(8.0)mm</td>
<td>(2.2)3.5(5.1)mm</td>
<td>(1.7)3.5-7.0(9.5)mm</td>
</tr>
<tr>
<td>Apical tooth length</td>
<td>(3.2)4.0(5.2)mm</td>
<td>(2.8)4.9(7.5)mm</td>
<td>(2.0)5.3-10.0(14.8)mm</td>
</tr>
<tr>
<td>Number of teeth along each margin</td>
<td>2-3(4)</td>
<td>2-3(5)</td>
<td>2-3(4)</td>
</tr>
<tr>
<td>Length of longest tooth</td>
<td>(0.6)1.3(1.7)mm</td>
<td>(0.5)1.2(2.0)mm</td>
<td>(0.5)1.2-3.0(5.0)mm</td>
</tr>
</tbody>
</table>

**STEM INFLORESCENCE**

**UPPER FLOWERS**

<table>
<thead>
<tr>
<th>Plants sampled</th>
<th>10 plants</th>
<th>11 plants</th>
<th>59 plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of flowers</td>
<td>(10)18(26) : 10 plants</td>
<td>(12)20(32) : 11 plants</td>
<td>(12)24(32) : 59 plants</td>
</tr>
<tr>
<td>Calyx length</td>
<td>(4.5)6.0(8.0)mm ; 19 plants</td>
<td>(5.3)7.1(8.0)mm ; 11 plants</td>
<td>(3.8)5.3-8.0(9.5)mm ; 59 plants</td>
</tr>
<tr>
<td>Corolla length along upper side</td>
<td>(9.0)11.1(15.7)mm : 16 plants</td>
<td>Longer than 9-10mm (upper flowers only) : 7 plants</td>
<td>(9.5)12.5-16.0(19.0)mm : 56 plants</td>
</tr>
<tr>
<td>Anther length</td>
<td>(1.4)1.6(2.0)mm ; 7fls</td>
<td>(1.3)1.6(2.0)mm ; 7fls</td>
<td>(1.2)1.7(2.1)mm ; 10fls</td>
</tr>
<tr>
<td>Rearmost awn length</td>
<td>(0.2)0.3(0.4)mm ; 7fls</td>
<td>(0.2)0.3(0.4)mm ; 6fls</td>
<td>(0.2)0.3(0.4)mm ; 10fls</td>
</tr>
<tr>
<td>Number of ovules</td>
<td>(20)37(45) ; 7fls</td>
<td>—</td>
<td>(30)62(110) ; 10fls</td>
</tr>
<tr>
<td>Capsule length</td>
<td>(5.5)6.1(8.3)mm ; 20 capsules</td>
<td>6.5-9.0mm ; 3 capsules</td>
<td>(5.2)7.7(9.5)mm ; 0.25 capsules</td>
</tr>
<tr>
<td>Number of seeds</td>
<td>9-30 : 6 capsules</td>
<td>29.40 : 2 capsules</td>
<td>(10)30-80 : 8 capsules</td>
</tr>
<tr>
<td>Seed length</td>
<td>(0.9)1.2-1.5(1.9)mm ; c. 30 seeds</td>
<td>(0.9)1.2-1.6(1.7)mm ; c. 20 seeds</td>
<td>(1.0)1.3-1.5(2.0)mm ; c. 50 seeds</td>
</tr>
</tbody>
</table>

Quantitative, the organs do not show correlated changes in all characters measured in them. Thus, although the dwarf variant has leaves with, on average, shorter teeth and apices than those of the typical, the leaf length and the number of leaf teeth are much the same. Similarly, the two variants are characterized by anthers of like size and show only slight differences in calyx size, even though their flowers show greater divergence in corolla size and number of ovules. Furthermore, depauperate plants of *E. caudata* from other regions (e.g. in Willis *MEL41656*) are very slender, bear a few small flowers and show no tendency to branch. Plants of the dwarf variant have a similar
number of stem nodes, but can be readily distinguished by their strong development of inflorescence-bearing branches. It does seem possible, then, that the differences have a genetic basis.

Selected and cited specimens


Specimens examined of dwarf variant of E. caudata


LOCALITY ERRONEOUS: Anon. s.n., s.dat. Mt Alexander [Western Highlands, Victoria]. MEL41607 (p.p., annotation must apply to E. scabra specimen on sheet).


17. Euphrasia scabra R.Br., Prodr. (1810) 437

[...]

270
Erect annual herb, becoming brittle, (8.5)15-35(50) cm tall. Stem to base of inflorescence (7.5)11-25(45) cm high, bearing (6)8-18(24) pairs of leaves, usually with axillary branches forming in region from (1)2-7(14) nodes above cotyledons to 1-2(3) nodes below inflorescence, with length of stem between inflorescence and uppermost branches (0.03)0.21(0.48) length of entire stem to base of inflorescence, sometimes simple (mainly if plant depauperate); branches flowering later than stem and developing basipetally, lower ones bearing up to 7(9) nodes, upper ones bearing 1-3(5) nodes, with leaf pairs finally subtending shoots; axes reddish-brown to yellow-brown, usually covered by short white eglandular hairs, dense in upper parts but sparser or absent lower down, sometimes with short glandular hairs in upper parts, sparse and then absent down stem, sometimes with moderately dense, short to moderately long glandular hairs on lower parts. Cotyledons oblong, glabrous, sometimes persisting. Leaves: uppermost stem leaves in outline usually ovate-elliptic to elliptic, rarely linear-lanceolate, pinnatifid to serrate-crenate, (6)7.5-14(20) x (1)2.5-6.5(9.5) mm, covered by dense, short to moderately long scabrous eglandular indumentum, sometimes mixed with sparse, short glandular hairs, with margins recurved; base usually rounded cuneate, rarely truncate; teeth (1)2-3(5) along each margin, usually bluntly obtuse or acute, rarely acuminate, with longest tooth (0.4)0.7-2.6(4.0) mm long; apical tooth usually bluntly obtuse or acute, rarely sharply acute, (1.8)3.0-6.0(9.0) mm long; leaves in middle of stem only slightly longer, sometimes with 1 more tooth along each margin, lacking glandular hairs; lowermost ones much shorter, with scabrous indumentum rarely mixed with sparse, short to moderately long glandular hairs; leaves in similar positions on branches similar but somewhat smaller. Inflorescences dense racemes, that of stem producing (10)14-32(54) flowers; rachis covered usually by a dense mixture of short to moderately long glandular and eglandular hairs, sometimes by dense eglandular hairs; internodes elongating variably, such that apices of capsules well below to well above node above; pedicels 0-0.3(0.6) mm long, reaching 1.2(1.6) mm on lowest flowers; apical bud cluster rounded, cylindrical to conical, that of stem 0.3-1.9 cm long, remaining extended above uppermost corollas until 2-11 or more pairs of flowers have reached anthesis. Bracts like uppermost leaves, but somewhat shorter and broader, bearing densely scabrous indumentum often mixed with dense, short to moderately long glandular hairs, denser on underside. Calyx (4.3)5.5-7.0(9.0) mm long, externally covered by dense, usually short to moderately long, rarely subsessile or long [i.e., (0.05)0.1-0.2(0.3) mm long] glandular hairs, mixed with dense, short to moderately long scabrous eglandular hairs, sparser on tube, internally covered on teeth by moderately dense to dense, subsessile to short glandular hairs, often also by moderately dense to dense, upturned appressed short glandular hairs, elsewhere glabrous; teeth sharply acute to acuminate; lateral clefts 1.7-3.9 mm deep, shorter than median clefts which are 2.2-5.6 mm deep. Corolla (8.0)9.0-12.0(14.0) mm long along upper side, with lower side broadly grooved, yellow, sometimes with 3 red-brown striations present (at least in dried material) on hood and lower lip behind each lobe; tube (6.0)7.0(8.3) mm long, broadened laterally and somewhat medially at or below bases of anterior filaments, which are (4.0)5.0(5.9) mm from base of corolla, with basal part glabrous on inside and outside, with distal parts covered externally by dense, moderately long eglandular hairs sometimes mixed behind lateral clefts with sparse to dense, short glandular hairs, internally by eglandular hairs, sometimes sparse to dense, short to moderately long and confined to region between
Fig. 96. Lectotype and other syntype of *E. scabra* R.Br. (scale 10cm long).

Fig. 97. Holotype of *E. orthocheila* Barker, *sp. nov.* (scale 5cm).
Studies in *Euphrasia*

filaments, sometimes moderately dense to dense, short to moderately long around and below bases of filaments and behind lower lip; **hood** (3.3)4.4(5.5)mm long, externally covered by moderately long eglandular hairs, dense towards rear, sparser at front, mixed with short glandular hairs, dense in front half or only above sinus, absent towards rear, internally with moderately long to long eglandular hairs densely covering entire surface or restricted to area about sinus, sometimes with a patch of subsessile glandular hairs also at sinus, with **upper lobes** obtuse or acute, with front surface ± glabrous or covered by dense short eglandular hairs, with rear surface moderately densely to densely covered by short to moderately long eglandular hairs or by short to moderately long eglandular hairs or by both, in which case former tend toward base, latter toward tip, with margins glabrous or lined with sparse to moderately dense, short eglandular hairs, with cleft between 0.4-1.0mm deep; **lower lip** (3.4)6.9(8.3) x (4.9)8.0(15.0)mm, porrect, externally covered by sparse to dense, moderately long to long eglandular hairs, usually mixed with dense, moderately long eglandular hairs, sometimes with glandular hairs restricted to parts of lip or absent, internally ± glabrous or with dense, short to moderately long eglandular hairs all over or confined to area behind lobes, with margins glabrous or lined with sparse to dense, short eglandular hairs, with **lower lobes** usually obtuse to truncate, often shortly apiculate, sometimes shallowly emarginate, with clefts between 1.0-3.0mm deep; **Stamens** with filaments glabrous, anterior pair (4.2)4.8(6.2)mm long, posterior pair (1.8)2.5(3.0)mm long; **anthers** (1.1)1.2-1.5(1.6) x (0.7)0.8-1.0(1.1)mm, with connectives of anterior pair, glabrous or with sparse to dense, short to long eglandular hairs, less hairy than or as hairy as those of posterior pair which are usually surrounded by sparse to dense, short to long flexuouse eglandular hairs, sometimes glabrous, with rearmost pair of awns (0.1)0.2(0.3)mm long, usually longer than those of other three pairs, rarely ± equal to them. **Ovary** laterally compressed, in lateral view elliptic to oblong-elliptic or ovate-elliptic, covered in upper 3/4 by dense upturned setae, moderately long to long at base, long to very long at apex; **apex** in lateral view acute, often obliquely so, to obliquely obtuse; **ovules** (57)90(140). **Capsules** in lateral view oblong-elliptic to ovate-elliptic, usually ± declinate, (5.0)6.7(9.3) x (2.0)2.4(3.0)mm, in upper 3/4 covered by dense long upturned setae; **apex** in lateral view usually acute to obtuse, often obliquely so, rarely truncate; **seeds** (29)60-90, ± ellipsoid to oblong-ellipsoid, often somewhat angular, (0.4)0.5-0.8(1.0) x (0.2)0.3(0.6)mm. **Chromosome number**: unknown. Figs 12, 96.

**Typification**

*E. scabra* R.Br. Both type collections belong to the one species. Initially (fig. 96) the Port Dalrymple collection had been called “*Euphrasia lutea*” by Brown, while the Port Phillip material he annotated “*Euphrasia lutea? an sp. divers?”*, indicating that at some stage Brown considered that the two collections may not have been conspecific. The Port Dalrymple material alone was renamed “*E. scabra*” by Brown on both the BM specimen (fig. 96) and in the manuscript (Brown unpubl.). It also was cited as the basis for the extensive manuscript description. The BM sheet of the Port Dalrymple collection is accordingly chosen as lectotype. The selection thus conforms with Stearn’s (1960) recommendation that BM material be used as lectotypes of Brown’s species.

The lectotype locality “Lagoon beach” is near a fresh-water lagoon 4km south-east of Low Head on the shores of Port Dalrymple.

**Distribution** (fig. 93, also 94): *E. scabra* occurs throughout most of temperate, non-arid Australia and Tasmania, reaching as far north as Sydney on the east coast, and extending into the south-west of Western Australia.

It ranges in altitude from sea level up to 1100m in Tasmania and to about 1500m on the Australian mainland, including some subalpine or high montane sites (see Intraspecific Polymorphism).
Ecology: *E. scabra* has been found in a wide range of habitats. From specimen annotations it appears most frequent in open grassy situations, possibly ones which are wet. However, it is perhaps less common in permanently wet sites than the closely allied *E. caudata, E. ciliolata* and, possibly, *E. orthocheila*. It has also been recorded from sand associated with dunes and salt lakes along the coasts of South and Western Australia, and in dry heath and dry forest land in south-eastern Australia and Tasmania.

Flowering times seem to vary considerably throughout the range of the species. Plants begin flowering between early October and February. The main stem inflorescences cease bearing flowers by November to March, but those of the branches continue to produce them until early January to April or even longer. From the few records available, in the Australian Alps the flowering times are towards the later part of the stated ranges of time. This is in keeping with the later seasons in the high mountain regions.

Conservation status: 3E. Although described in the last century as flourishing throughout extratropical Australia but not as abundantly as the sympatric perennial species (Mueller 1865), nowadays *E. scabra* appears to have become very rare as it has been seldom collected in this century. During the past 70 years it has most often been recorded from the hills west of Hobart, the latest collections being Carolin 1770 in 1960 and Ratkowsky AD97349029 in 1973. Elsewhere in Tasmania it was found by Rees (HO) in 1929 at St Marys and Moscal (HO) south of Fingal in 1979. The only mainland Australian records during that period have been Ashby 4354, 4928 respectively from near Lake Muir and at Yorn Creek in south-west Western Australia in 1971 and 1973, together with Willis MEL41654 from Buckety Plain in the Victorian Alps, collected in 1946, which is from the divergent high-mountain populations (see Intraspecific Polymorphism). The contrast between numbers of collections in each century indicates that the species may be threatened with extinction.

Notes: 1. Populations of *E. scabra* in the Australian Alps (fig. 93) approach *E. caudata* in some characters but there is no full intergradation between the two species (see Intraspecific Polymorphism).

2. There is little purpose giving three unusually tall and slender plants of *E. scabra* from Tasmania (Mueller MEL41678p.p.; Stuart MEL41645p.p., MEL41570) varietal status as suggested by Mueller's annotations, since they appear to be extremes of the range of variation in stem length in *E. scabra*, perhaps produced by a shaded position or by growth between tall grasses. The latter Stuart collection contains a specimen of normal habit as well as the slender plant. Mueller (MEL41573) collected a similarly slender plant from South Australia.

3. Two old specimens apparently of *E. scabra*, show some differences from typical forms of the species. Both Anon. GH (“N.Holl., E. arguta R.Br.”) and Anderson G (“Nouvelle-Holland”), identified as *E. scabra* by Wettstein, are characterized by short but broad capsules which are symmetrically ovate in lateral view, a shape not otherwise found in the species. The G collection also diverges by its shallowly emarginate lower corolla lobes, an attribute only occasionally found in the species. While there is little doubt that the G specimen had the yellow corollas (with reddish striations apparent) of *E. scabra*, the GH specimen has dried a colour atypical of herbarium material of the species. Although it has yellow anthers, an attribute often found in plants with yellow corollas, the association of these characters is too loose to enable the corolla colour to be determined with any certainty. If it was originally a non-yellow colour, it may be allied to “*E. arguta* Wettst.” (see *E. arguta*: note 2). There is no evidence for hybridism being involved as a high percentage of pollen sampled appears normal (PS132-134).
Intraspecific polymorphism

In the Australian Alps between the Mt Kosciusko region and the Bogong High Plains there is a breakdown of a number of the many morphological differences between *E. scabra* of lowland and lower montane sites and *E. caudata*. These differences are detailed in Table 12.

The specimens intermediate between *E. scabra* and *E. caudata* all appear to possess the yellow corollas of the former species, although this is largely determined from the dried state. Only in one of the collections (*Willis MEL41654*) is this feature noted. Of the nine collections involved, seven are only slightly divergent from *E. scabra* while two are more or less intermediate between the two species.

The seven specimens only slightly atypical of *E. scabra* have character states which rarely occur elsewhere in lowland Australia, but occur more frequently in the region of the Australian Alps. *Martin MEL41660, MEL41614* and *Findlay MEL41661* diverge from *E. scabra* only by their emarginate lower corolla lobes, those in *MEL41660* being very deeply incised. *Baeuerlen NSW10885* and *Howitt MEL41681* show a rather extensive cover of glandular hairs over the herbaceous parts, rarely seen elsewhere in *E. scabra*; in addition they diverge slightly in the approximately symmetrical lateral view of the capsules, the rather large seeds (0.9-1.1mm long) and the rather large anthers (1.4-1.9mm long). Finally, there are two poor specimens which show characters somewhat atypical of *E. scabra*. Lower corolla lobes in *Baeuerlen 57* are emarginate. *Merrah MEL41352*, which bears many capsules and no flowers, has a glandular indumentum extending farther down the stem than usual in *E. scabra* and capsules with broadly obtuse apices. In all other respects, except where a character cannot be observed because of the inadequacy of material, the above specimens are characteristic of *E. scabra*.

Perhaps of greatest importance are the two collections *Willis MEL41654* and *Anon. 116*. These specimens tend in many respects towards *E. caudata*. Thus, their lower corolla lobes are emarginate, branching begins at the second to as low as the sixth node below the main stem inflorescence at a point rarely less than halfway down the stem,

Table 12: A comparison of the characters distinguishing *E. caudata* from populations of *E. scabra* outside the Australian Alps.

<table>
<thead>
<tr>
<th><strong>E. caudata</strong></th>
<th><strong>E. scabra</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Corollas usually violet to pink, rarely paler or white</td>
<td>Corollas yellow</td>
</tr>
<tr>
<td>Lower corolla lobes usually emarginate, often deeply so, rarely truncate</td>
<td>Lower corolla lobes usually obtuse to truncate, often shortly apiculate, occasionally shallowly emarginate</td>
</tr>
<tr>
<td>Anthers (1.2)1.4-1.8(2.1) x (0.9)1.0-1.3(1.5)mm</td>
<td>Anthers (1.1)1.2-1.5(1.6) x (0.7)0.8-1.0(1.1)mm</td>
</tr>
<tr>
<td>Capsules densely setose in upper 1/3-2/3, in lateral view piorrect, with apex usually emarginate to broadly obtuse, rarely broadly acute</td>
<td>Capsules densely setose in upper 3/4 or more, in lateral view downcurved or somewhat so, with apex asymmetrically narrow acute to obtuse, rarely broadly obtuse to truncate or ± symmetrical</td>
</tr>
<tr>
<td>Seeds (0.9)1.2-1.5(2.0)mm long</td>
<td>Seeds (0.4)0.5-0.8(1.0)mm long</td>
</tr>
<tr>
<td>Upper (1)2-4 stem nodes lacking branches and occupying more than half of stem</td>
<td>Upper 0-1(2) stem nodes lacking branches and occupying upper (0.03)0.21(0.48) of stem</td>
</tr>
<tr>
<td>Glandular indumentum all over vegetative parts, rachis, bracts and calyces, but sometimes sparse in middle section of stem or branches</td>
<td>Glandular indumentum usually confined to rachis, bracts and calyces, sometimes at base of plant or on axis for some distance below inflorescence, sometimes on upper leaves, rarely on lower leaves</td>
</tr>
<tr>
<td>Glandular indumentum on above parts usually moderately long to very long, rarely short, e.g. on calyx (0.1)0.2-0.4(0.6)mm</td>
<td>Glandular indumentum on above parts usually short to moderately long, rarely long, e.g. on calyx (0.05)0.1-0.2(0.3)mm</td>
</tr>
</tbody>
</table>
the glandular hairs cover all herbaceous parts, although very sparsely in the upper middle regions, and the ovaries appear symmetrical in lateral view. However, bending in the ovary is more obvious in the capsule stage. In addition anthers are rather large for *E. scabra* (1.3-1.7mm long). The specimens approach *E. scabra* by their yellow corollas and short to moderately long eglandular hairs. Unfortunately, capsules and seed are absent.

There appears to be a relationship between the ecological ranges of the atypical specimens of *E. scabra* and those of *E. scabra* and *E. caudata*. *E. caudata* is confined to the subalpine and alpine zones. Typical forms of *E. scabra* occur below these zones in montane or lowland habitats. Similarly, the seven slightly divergent specimens all appear to occur well below the subalpine zone. On the other hand, it is likely that the two collections intermediate between *E. scabra* and *E. caudata* occur in the subalpine zone, where *E. caudata* abounds. The locality, altitude (1520m) and habitat (sphagnum bog) of *Willis MEL41654* from the Bogong High Plains clearly indicate that it came from this zone. It should be noted that there is no authentic record of *E. caudata* from this extensive much-botanized alpine region. If the location "Nunionyong" cited for *Anon. 116* is identical to the Nunniong Plateau, Victoria, to the south of Mt Kosciusko, then a subalpine occurrence is also quite likely. Hogg (1970) refers to "large areas of open snowplain" there, and *E. caudata* occurs in this region.

It is possible, therefore, that the two species, *E. scabra* and *E. caudata* actually represent the extremes of a cline along an altitudinal and ecological gradient, with the above collections representing relictual intergrading forms (p. 65). An alternative explanation based on hybridism seems unlikely as there is no real evidence that the two species grow together and there seems little variation in the intergrade specimens. In addition, pollen sterility tests show only a very low percentage of sterile pollen in all but one (*Martin MEL41614*) of the nine intergrade plants sampled (PS127-131, 136-139). The present evidence points to a group of variable high mountain populations for which an intraspecific classification at this stage is impossible to justify or determine. The lack of a full intergrade into *E. caudata* precludes its union with *E. scabra* into one highly variable species.

**Selected and cited specimens**


WITHOUT SPECIFIC LOCALITY (5 seen): Anderson s.n., [prior to 1893]. Nouvelle-Hollande. G.—Anon. s.n., s.dat. N. Holl. GH.

Specimens of E. scabra approaching E. caudata


18. Euphrasia orthocheila Barker, species nova


Species nova Sectionis Scabrarum corollam flavam E. scabrae tenens, sed differt foliis plerumque brevioribus angustioribus dentibus paucioribus brevioribus, et calycibus capsulisque plerumque minoribus.

Holotypus (fig. 97): Dr Beckler s.n., s.dat. Mt. Mitchell. MEL41595. See Typification.

Erect annual herb, becoming brittle, (18.5)20-43(60)cm tall. Stem to base of inflorescence (15)17.5-37(50)cm high, bearing (10)13-30(36) pairs of leaves, with axillary branches forming in region from 0-1(6) nodes above cotyledons to (1)3(4) nodes below inflorescence, sometimes with 1-5 stem-like branches developing at basal 1-2 nodes if stem growth suppressed; branches flowering later than stem and developing basipetally, lower ones bearing up to 7(10) nodes, upper ones bearing 1-2 nodes, with all leaf pairs except uppermost subtending shoots; axes reddish-brown to yellow-brown, covered by short down-turned white eglandular hairs, more or less evenly distributed about axis or in four rows, with one or two dense alternating with two sparse, with sparse rows decurrent from leaf bases. Cotyledons oblong, glabrous, sometimes persisting. Leaves: uppermost stem leaves usually narrow-linear to linear, sometimes oblong-lanceolate, broadest towards base, densely scaberulous or shortly scabrous eglandular indumentum, often deeply reddened, with margins recurved, sparingly lobed or cleft, or entire, (4)6-8(11) x (0.5)1.2-2.0(2.5)mm; base rounded-cuneate; teeth 0-1(2) along each margin, obtuse, 0.05-0.5 (0.6)mm long; apical tooth usually sharply, rarely bluntly acute, when leaf toothed along margin (2.3)2.5-5.0(5.5)mm long; lower leaves longer and broader, crenate with 2-3(4) teeth along each margin and with longer scabrous indumentum; leaves in similar positions on branches similar but somewhat smaller. Inflorescences ± dense racemes, that of stem bearing (15)25-40 flowers, with some flowers not forming fruits; rachis bearing dense downturned eglandular hairs or moderately dense to dense, subsessile to short glandular hairs; internodes hardly elongating after anthesis such that apices of capsules reach or extend past node above except at lowermost 1-2 nodes; pedicels c. 0.1-0.8mm long; apical bud cluster conical, that of stem 0.3-1.3cm long, remaining extended above the uppermost corollas after 7-12 pairs of flowers have reached anthesis. Bracts like uppermost leaves, but shorter, broader at base, with dense, scaberulous or shortly scabrous indumentum, sometimes mixed with subsessile glandular hairs. Calyx (2.8)3.5-4.5(4.9)mm long, externally densely scaberulous or only sparsely so and then mixed with moderately dense to dense, subsessile to short glandular hairs, internally glabrous well below clefts with region above usually covered by a mixture of sparse to dense, upturned appressed short eglandular hairs and sparse to dense, subsessile...
glandular hairs, sometimes lacking glandular hairs; teeth usually sharply, rarely bluntly acute; lateral clefts 1.1-1.8mm deep, shorter than median clefts which are (1.3)1.6-2.6mm deep. Corolla (9.5)11.0-13.5(15.0)mm long along upper side, with lower side broadly grooved, yellow, sometimes (at least in dried material) with 3 red-brown striations on hood and lower lip behind each lobe; tube 5.4-7.0(8.5)mm long, broadened laterally and somewhat medianally at or below bases of anterior filaments, which are (3.5)4.7(6.0)mm from base of corolla, with basal part glabrous, with distal parts covered externally by dense, short to moderately long eglandular hairs mixed behind lateral clefts with moderately dense to dense, short glandular hairs, internally by moderately dense to dense, short to moderately long eglandular hairs; hood (3.8)5.9(7.2)mm long, covered externally by dense, short to moderately long eglandular hairs, internally by sparse to dense, moderately long to long flexuose eglandular hairs all over or along midline only, sometimes mixed above anthers with sparse, very short glandular hairs, with upper lobes usually obtuse or acute, sometimes acuminate, with cleft between (0.4)0.8(1.5)mm deep, with front surface ± glabrous, with rear surface glabrous or proximally with a few very short glandular hairs and distally sometimes with sparse to dense, short eglandular hairs, with margins lined densely or very sparingly with short eglandular hairs; lower lip (5.0)6.1(8.0) x (4.8)6.8(10.0)mm, porrect, somewhat shorter to somewhat longer than upper lip, covered externally by dense, short to moderately long eglandular hairs, sometimes mixed with sparse short glandular hairs, internally glabrous except usually for sparse to dense eglandular hairs behind lobes, with margins very sparsely to densely lined with short eglandular hairs, with lower lobes shallowly emarginate to truncate or obtuse, sometimes praemorse or shortly apiculate, with clefts between (1.0)1.8(2.5)mm deep. Stamens with filaments usually glabrous, sometimes with a few eglandular hairs at very base, anterior pair (4.8)6.7(8.2)mm long, posterior pair (2.7)3.8(5.0)mm long; anthers 1.2-1.5(1.6) x (0.6)0.7-1.0(1.1)mm, with connectives of anterior pair usually surrounded by sparse to dense, short to long flexuose eglandular hairs, sometimes glabrous, less hairy than or as hairy as those of posterior pair which are surrounded by moderate to dense to dense, moderately long to long downturned flexuose eglandular hairs, with rearmost pair of awns (0.1)0.2(0.3)mm long, usually longer than anterior three pairs, sometimes equal to them. Ovary laterally compressed, in lateral view usually ovate to ovate-elliptic, sometimes elliptic, covered in upper 2/3-3/4 by dense, moderately long upturned setae; apex in lateral view usually acute, sometimes obtuse or obliquely so; ovules (20)45-100. Capsules in lateral view obovate-elliptic to ovate-elliptic, usually with lower side straighter than upper, (3.4)4.0-5.0 x (0.8)1.3-1.7mm, with moderately long to long, dense setae over upper 2/3-3/4; apex acute or obtuse in lateral view; seeds (4)15-40, ± ellipsoid or oblong-angular, (0.4)0.5-0.8(0.9) x 0.3-0.4(0.5)mm. Chromosome number: unknown.

**Typification:** Mt Mitchell is in the New England tablelands. The type collection was made prior to 1868 (it was cited in Bentham's "Flora Australiensis" of that date).

**Distribution** (fig. 94): *E. orthocheila* is known mainly from the Northern Tablelands of New South Wales and the very south of Queensland. Two subspecies are recognized. Although evidence is poor, the species may have been collected further south in the region of Sydney (Mueller MEL41587). It also possibly occurred in the vicinity of the Blue Mountains, although the localities, Castlereagh and "Orange district", only doubtfully apply to *E. orthocheila* (note 3). From the distribtuional range of the species, its altitudinal range is possibly between about 750m and (Coveny 8964) 1350m in the Northern Tablelands and lower in the south.

**Ecology:** Ecological annotations, confined to only four collections, suggest that *E. orthocheila* grows in moist or wet, apparently open situations.
From the few dated collections seen, it appears that flowering begins in November to December, although one specimen just beginning to flower (Porter MEL41644) is alleged to have been collected in March. The stem ceases flowering in about the February-March period. Plants with branches still flowering have been gathered as late as May (Crawford 19).

Conservation status: see subspecies. From the number of collections of *E. orthocheila* made up to the 1917 collection Boorman NSW10878, the species was apparently relatively common. Covery 8964 and Sharpe & Williams 1060 represent the only records of the species since that time. Both subspecies may be threatened with extinction.

Notes: 1. The two subspecies of *E. orthocheila* approach most closely different species of Sect. Scabrae. *E. scabra* is clearly allied to ssp. *orthocheila* by many characters including its yellow corollas and short glandular indumentum. *E. ciliolata* clearly resembles ssp. *peraspera* by its lack of glandular hairs from the calyces, bracts, rachises and at least upper vegetative parts, by its scaberulous calyces, and its leaves with few short teeth. Ssp. *peraspera* may represent a stabilized hybrid derived from two ancestral forms similar to ssp. *orthocheila* and *E. ciliolata*, respectively (p. 65).

2. There are a number of examples in the collections of *E. orthocheila* of the apparent suppression of growth of the main stem apex with a consequent replacement by lateral growth alone. In some cases (Heron NSW10880, Boorman NSW10878, Stuart MEL 41593) the stem is very reduced and is mounted by a number (2-5) of often equally-developed stem-like branches. In others (e.g. Stuart 49, Hartmann 59) it is the very upper part of the stem that has not properly developed; a short length of dead stem may still remain. One plant of Beckler MEL41595 is terminated by a dead main stem inflorescence which had apparently died before it could develop significantly despite concurrent or subsequent flowering on many branches. These phenomena may result from grazing.

3. Woolls 3, allegedly from Orange (fig. 94, locality B), is placed under *E. orthocheila* ssp. *orthocheila* rather than *E. scabra* because of its small upper leaves, calyces and capsules. However, the fragmentary nature of the specimen and the uncertainty as to whether the branches present have arisen from a stem or a branch make this determination questionable. The specimen is also unusual for its extremely dense pubescence and the thickening of its leaf and bract margins.

Another herbarium sheet Woolls MEL41489, which is annotated Castlereagh (fig. 94, locality A), comprises a mixture of two species, namely *E. orthocheila* and *E. collina* ssp. *paludosa*. It is impossible to determine to which species the locality applies.

4. The epithet “orthocheila” refers to the porrect lower corolla lip found in this species. This is one of several characteristics which together describe the corolla shape apparently peculiar in the genus to *E. orthocheila* and its closest relatives in Sect. Scabrae.

Intraspecific polymorphism

Two subspecies distinguishable by the presence or absence of glandular hairs in the inflorescence, are apparent under *E. orthocheila*. Although many of the collections contain more than one plant, there is no instance of a mixing of the plants of the two subspecies. It is therefore likely that they are confined to separate populations. There is insufficient information to judge whether there are any associated ecotypic differences.

Key to the subspecies of *E. orthocheila*

1a. Glandular indumentum present in the inflorescence, [always on calyx, sometimes on bracts, usually on rachis]. .................................................. a. ssp. *orthocheila* (p. 280)

1b. Glandular indumentum lacking from inflorescence. .......................... b. ssp. *peraspera* (p. 280)
18a. ssp. orthocheila

Inflorescences with rachis usually bearing moderately dense to dense, subsessile to short glandular hairs, rarely bearing dense downturned eglandular hairs. Bracts covered by a dense scabrous to shortly scabrous eglandular indumentum, occasionally mixed with sparse to moderately dense subsessile glandular hairs. Calyx externally covered by subsessile to short glandular hairs, dense at least on lobes, and short scabrous hairs, sparse or dense, mainly on lower part of tube. Figs 12, 97.

Distribution & ecology: see under species.


Specimens examined


QUEENSLAND: Anon. s.n., s.dat. Warwick. MEL41596(p.p.).—[Mr B] s.n., s.dat. Stanthorpe. MEL41591.—Bailey s.n., xii.1875. Stanthorpe. BRI.—Huttman 59, 1873. Severn. MEL.

WITHOUT SPECIFIC LOCALITY: Anon. s.n., s.dat. MEL41602(p.p.).—Sieber 490, s.dat. Fl. Novae Holl. L.

18b. ssp. peraspera Barker, subspecies nova

Subspecies nova prope ssp. orthocheilam sed differt inflorescentiis rhachide pilos densos deflexos eglandulosos ferentibus, bracteis indumentum dense brevique scabrum ferentibus, calyceque extra dense scaberulo.

Holotypus (fig. 98): Wilcox s.n., xi.1875. Clarence River MEL41718. Isotypus: MEL41589.

Inflorescences with rachis bearing dense downturned eglandular hairs. Bracts covered by dense, scaberulous to shortly scabrous eglandular indumentum. Calyx externally densely scaberulous. Figs 12, 98.

Typification: Judging by the distribution of the subspecies, the type locality is probably nearer the source of the Clarence River, in the Northern Tablelands of New South Wales, rather than downstream.

Distribution & ecology: see species.

Conservation status: 3 ?E. See species.

Specimens examined


QUEENSLAND: Sankey s.n., ii.1913. Stanthorpe. BRI.—Sharpe & Williams 1060, South Bald Rock near Wallangarra. BRI.

LOCALITY EXTREMELY DOUBTFUL (Barker 1974): Smith s.n., vi.1902. Launceston. Tasmania. HBG.

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Fig. 98. Holotype of *E. orthocheila* Barker ssp. *peraspera* Barker, ssp. nov. (scale 5cm).

Fig. 99. Holotype of *E. cilio/clata* Barker, sp. nov. (scale 5cm).
19. Euphrasia arguta R.Br., Prodr. (1810) 437


?E. scabra fi arguta (R.Br.) Benth. in DC.. Prodr. 10 (1846) 554 (possibly as to name only: see note 1).

Erect brittle annual herb, (17)28(45)cm high. Stem to base of inflorescence (12)22 (33)cm tall, bearing (18)24(30) pairs of leaves, with axillary branches developing from (6)8(12) nodes above cotyledons to 1-2(5) nodes below inflorescence, sometimes with an extra shoot along underside of branch in axils of upper leaf pair; branches flowering later than stem, developing in basipetal sequence, lower branches bearing up to c. 13 leaf pairs, uppermost pair bearing 0-1(4) leaf pairs, with all leaf pairs subtending shoots; axes in upper parts covered equally all around by dense to moderately dense, short to moderately long, downturned eglandular hairs, often very dense on young shoots, somewhat sparser to very sparse lower down stem. Cotyledons caducous. Leaves: uppermost stem leaves in outline ovate to elliptic, often broadly so, pinnatifid to deeply pinnatifid, (6.8)10.7(14.5) x (3.5)8.3(13.0)mm, usually densely eglandular-scarburous, sometimes sparser on lower side or with a few tiny glandular hairs, rarely densely scabrous on upper surface and margins, with blade lanceolate to elliptic or narrowly so, with margins ± recurved; base rounded-cuneate to narrowly cuneate; teeth 2-3(4) along each margin, sharply acute to acuminate with longest (1.5)3.0(5.5)mm long; apical tooth (2.5)4.5 (7.5)mm long, sharply acute to long acuminate; lower leaves similar to upper leaves, but occasionally with somewhat longer ciliates or somewhat shorter teeth; leaves in similar positions on branches similar but somewhat smaller. Inflorescences dense racemes with that of stem producing (30)50-90 or more flowers, those of branches somewhat fewer; rachis of same pilosity as upper stem; internodes hardly elongating after anthesis so that capsules usually extend well past or sometimes just reach node above; pedicels (0.2)0.3-0.5(1.1)mm long, remaining the same length after anthesis; apical bud cluster rounded, up to 1.5cm long, emergent above flowers even after inflorescence has produced many flowers. Bracts similar in dimensions to uppermost leaves, but usually with broader blade, usually moderately densely to densely scabrous, often also bearing a few tiny glandular hairs, rarely densely scabrous. Calyx (5.3)6.3(8.2)mm long, externally usually densely scabrous, usually also bearing very few to moderately dense tiny glandular hairs, rarely densely scabrous, internally bearing sparse to dense, very short to moderately long, appressed upturned eglandular hairs mixed with sparse to moderately dense, very short glandular hairs, the indumentum on the teeth shorter or sometimes lacking; teeth sharp-tipped usually very narrowly acuminate, sometimes narrowly acute; lateral clefts (2.0)3.0(4.0)mm deep, shorter than the median cleft which are (2.6)4.1(6.3)mm deep. Corolla (10.0)11.6(14.0)mm long along upper side, with lower side ± broadly grooved, white (Brown) to lilac (Musson) and, at least in plants seen by Brown, with yellow area on lower side of mouth; tube (6.7)7.7(8.5)mm long, laterally and somewhat medianly narrowly broadened from below bases of anterior filaments, which are (4.0)5.0(6.0)mm from base of corolla, externally glabrous at base, distally covered by dense, moderately long to long eglandular hairs, usually with dense patch of short glandular hairs behind lateral cleft extended towards base of anterior filaments, internally glabrous to summit of ovary, distally covered by dense, short to long downturned eglandular hairs up to bases of posterior filaments; hood (3.0)4.1(5.5)mm long, covered externally by dense, moderately long to long eglandular hairs, sometimes mixed with dense, very short glandular hairs on sides, internally with moderately long to long

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flexuose eglandular hairs, dense at sinus, sparser above anthers and usually lacking proximally, mixed with very few to moderately dense, very short glandular hairs, with upper lobes usually obtuse, occasionally acute or shortly apiculate, with front glabrous or covered by moderately dense to dense, very short to short eglandular hairs, with rear usually covered by sparse to dense, short to long eglandular hairs, rarely glabrous, with margins lined by moderately dense to dense, short to moderately long eglandular hairs, with cleft between (1.0)1.5(2.5)mm deep; lower lip (4.5)5.8(9.0) x (8.2)9.6(13.0)mm, ± flat cross-wise, apparently distally bent downwards, always longer than upper lip, externally covered by dense, moderately dense to long eglandular hairs, internally covered behind lobes by sparse to dense, short to moderately long eglandular hairs, on lobes usually sparser and shorter, sometimes lacking, with margins lined by moderately dense to dense, short to moderately long eglandular hairs, less hairy or equally as hairy as those of posterior pair which bear dense long eglandular hairs, with rearmost pair of awns (0.2)0.3-0.4(0.5)mm long, longer than anterior three pairs. Ovary laterally compressed, in lateral view ovate-elliptic, elliptic or oblong-elliptic, glabrous but for dense upturned setae in apical $\frac{1}{8}$, long at very apex, very short to short below; apex in lateral view usually acute or somewhat shortly acuminate, rarely obliquely obtuse; ovules c. 35-80. Capsule laterally compressed, in lateral view usually broadly elliptic and declinate, sometimes obovate-elliptic, rarely ovate-elliptic, (4)5-7(7.5) x (1.8)2.1(3.2)mm, usually with setae, dense to moderately dense over upper $\frac{1}{4}$-1 of and dense along upper $\frac{1}{2}$-2 of lines of dehiscence, short to long at apex, shorter lower down, occasionally glabrous but for a few setae at very apex; apex in lateral view usually acute or obtuse, rarely acuminate; seeds (8)23(50), usually more or less oblong-ellipsoid, sometimes broadly so, (0.4)0.6-0.8 (1.0) x (0.3)0.4-0.6(0.9)mm. Chromosome number: unknown. Fig. 12.

Typification

E. arguta R.Br. As the holotype is in very poor condition, the manuscript description (Brown unpubl.) was taken into account in determining its identity. The locality cited under E. arguta in the manuscript is "In prato prope ripas Paterson's River. inter Mt Anna et Mt Elizabeth. Oct. 1804. No. 58". The location of the two mountains is unknown, but Dr L.A.S. Johnson and Mr D.J. McGillivray (pers. comm. 1973) suggested that the locality would not be in highland areas, nor would it be near the headwaters of the two rivers as Brown "did not venture very far inland... and it is unlikely that he went north of 32° 35' S."

Distribution (fig. 94): E. arguta is recorded from a small area inland and to the north and west of Sydney. The area of distribution covers part of the Central Western Slopes, the Northern Tablelands, and the North Coast regions of New South Wales. The altitudinal range is unknown.

Ecology: Nothing is known of the ecology of E. arguta other than Brown's record of its occurrence in meadows near rivers.

Although data are poor, flowering plants are recorded from October to January, with one collection with branches still flowering in June.

Conservation status: 3 ?X. In 1865 Mueller wrote of the evident rarity of E. arguta; to
that time he had seen only a single specimen, *Woolls MEL41394* from Mudgee. To date only about 14 collections have been made, apparently none in the past 75 years. It is likely that the species is endangered, if not already extinct.

**Notes:**

1. Bentham (1846, see also 1868) and Wettstein (1896) both misapplied the name *E. arguta*. I have been unable to study the specimen "Ad Portum Jackson (A. Cunningham)" upon which Bentham's misapplication was based, nor those upon which Wettstein based his concept of the species, namely "Australia orientalis (Hügel; H. Hofm. [W]—Sieber [490]; H.Hofm. [W], H.U.P. [PRC]), Alpes Australiae (Cunningham; H.Flor. [FL]), Blaue Berge (Lesson; H.Berl. [B])." Wettstein's description was based mainly on the Huegel collection.

Wettstein described *E. arguta* as having stems which bore glandular hairs mixed with lax eglandular hairs, leaves and calyces covered by a mixture of long glandular hairs and scabrous eglandular setae, and bracts covered by a mixture of long glandular and eglandular hairs. His illustration of a fruiting calyx (Wettstein 1896, pl.6 f.453) shows exactly these attributes. This description of the length of the indumentum and density and size of the glandular hairs is in absolute discord with that of the same attributes in the true *E. arguta*. Thus the glandular hairs of *E. arguta*, if present on the leaves, bracts and calyces, are very sparse and extremely small, the stem never bears glandular hairs, and the uppermost leaves, bracts and calyces are usually densely scaberulous and only rarely densely scabrous.

Wettstein's description does not fit any species outlined in this work. It differs from *E. scabra* in the dull purple (when dried) corolla colour, the restriction of the capsule hairs to the apical region and the "obovate-cuneate" capsule shape. From *E. caudata* it differs in the integrity of the corolla lobes (unusual in *E. caudata*) and the restriction of the capsule setosity. While one of the two specimens cited by Wettstein with specific localities came from the "Alpes Australes" (*Cunningham FL*) and could possibly have been confused with *E. caudata*, another comes from the Blue Mountains (*Lesson B*), an area from which I have seen only one questionable record of an annual species (see *E. orthocheila*: note 3). The other two specimens cited by Wettstein under *E. arguta*, those of Huegel and Sieber, as well as a further possible representative of this putatively distinct taxon from "Nouvelle Hollande" referred to under *E. scabra* (note 3), could have come from this latter region. The shape and indumentum of the capsule of the glandular forms of *E. collina* which occur in the Blue Mountains, is often similar to that described and illustrated by Wettstein for *E. arguta*. However, it is very doubtful that Wettstein would have mis-identified plants of this species as he saw much material of it and its habit is very different. It seems possible that Wettstein's *E. arguta* represents an undescribed Blue Mountains taxon intermediate between *E. caudata* and *E. arguta* both in morphology and geography (see also p. 65).

2. The two specimens of *E. arguta* collected by Sieber under his number 490 which I have seen are obviously two different collections. The plants come from New South Wales (Sieber spent seven months there during 1823: Dietrich 1881, Maiden 1908). While the NY specimen has a sparse external corolla indumentum and the L plant has a dense scabrous indumentum longer than any other specimen seen, both clearly belong to *E. arguta*.

3. *Boorman NSW10934* has one plant atypical of *E. arguta* by its glabrous leaves, bracts and calyces, and its large seeds (1.2-1.4mm long). Pollen from a flower of this plant is almost entirely functional in appearance (PS113). The other four plants appear typical of *E. arguta*. However, while one plant also had a high percentage of normal pollen (PS112), another had an estimated 54% sterile pollen (PS114). It is possible that the plants are of hybrid origin with *E. arguta* and perhaps *E. collina* the parent species.
Specimens examined


20. Euphrasia ciliolata Barker, species nova

Species nova Sectionis Scabrarum E. orthocheilae ssp. perasperae et E. argutae calycibus scaberulis usque breve scabris, raro pilos glandulosos paucos minutissimos ferentibus affinis, ab hoc differt corolla caerulea usque malvina, interdum macula flava, aristis postremis longioribus, capsulis plerumque non nisi in dimidio superiore setosis, interdum glabris, seminibus longioribusque, ab illo foliis dentibus paucioribus brevioribusque et calycibus brevioribus.


Erect annual herb, (19)22-32(45)cm tall. Stem to base of inflorescence (11)16-23 (25)cm long, bearing (10)13-16(19) pairs of leaves, usually with axillary branches forming in region from (2)5(10) nodes above cotyledons to (1)3-4(7) nodes below inflorescence, sometimes also with 1-2 stem-like branches developing early in axils of basal 1-2 leaf pairs, rarely simple; branches flowering later than stem, developing basipetally, bearing (3)5-8(10) leaf pairs, many of these subtending shoots or branches; axes in upper parts bearing short down-turned white eglandular hairs in four rows, two of dense indumentum alternating with two of sparse indumentum, with sparse rows recurrent from leaf bases, in lower parts with similar indumentum mixed rarely with short to long, sparse to moderately dense glandular hairs. Cotyledons elliptic, entire, rarely persisting. Leaves: uppermost stem leaves (5.2)5.5-11.0(13.0) x (2.0)2.4-4.5 (5.5)mm, crenate to serrate, usually ovate to elliptic, sometimes oblong-elliptic, usually glabrous, rarely (Constable NSW56101, Lowry NSW55199) scaberulous, with somewhat recurved margins; base usually rounded-cuneate, occasionally narrowly cuneate; teeth (1)2(3) along each margin, usually bluntly, rarely sharply, acute or obtuse, 0.2-1.5mm long; apical tooth usually sharply acute, sometimes blunter acute or obtuse, (1.4)2.8(4.5)mm long; lower leaves larger, more toothed, scabrous to scaberulous, the lowermost ones occasionally also bearing short to long, sparse glandular hairs; leaves in similar positions on branches similar but somewhat smaller. Inflorescences ± lax racemes, that of stem bearing (10)16-26(36) flowers, the upper ones usually not forming fruits; rachis with indumentum similar to upper part of axis but denser; internodes elongating after anthesis such that apices of capsules do not reach node above; pedicels 0.5-2.5mm long, hardly elongating after anthesis; apical bud cluster rounded-conical 0.8-1.7cm long, hardly extended past corollas of uppermost pair of flowers after 3-7 pairs of flowers have reached anthesis. Bracts like uppermost leaves. Calyx (3.0)4.0-5.4 (6.0)mm long, externally densely scaberulous, internally bearing sparse to dense, short to long upturned eglandular hairs mixed with sparse to dense, short glandular hairs extending to clefts or well below them; teeth sharply acute; lateral clefts (0.8)1.2-2.0mm deep, shorter than median clefts which are (1.4)1.8-2.8mm deep. Corolla (10.5)12-15.5 (16.5)mm long along upper side, blue, purple, deep purple or mauve, with lower side broadly grooved and white except on lobes, with mid-line of lower lip, at least occasionally (Briggs 3167, Pullen 3792, White 11596) yellow; tube (6.0)8.0(9.8)mm long, laterally and somewhat medially narrowly broadened well below bases of anterior filaments, which are (3.5)4.2(5.8)mm from base of corolla, glabrous proximally, distally covered externally by dense short eglandular hairs, between bases of anterior filaments and lateral clefts mixed with dense short glandular hairs, internally by dense short...
eglandular hairs up to bases of posterior filaments; **hood** (4.0)5.3(6.5)mm long, covered externally by dense short eglandular hairs, mixed on sides with dense short glandular hairs, internally in area below upper cleft by dense, short to moderately long eglandular hairs, sometimes along midline of hood by dense short glandular hairs or from base of filaments to the anthers by dense short eglandular hairs, with **upper lobes** usually obtuse and entire, rarely acute or praemorse, with cleft between (0.6)1.2(1.8)mm deep, on front surface glabrous or covered by dense, very short eglandular hairs, on rear surface covered proximally with dense short glandular hairs, distally with dense short eglandular hairs which also line margins; **lower lip** (4.2)5.9(7.2) x (6.0)7.9(12.0)mm, flat, directed ± straight out from tube, slightly shorter to slightly longer than upper lip, covered externally by dense short glandular hairs, often sparser in middle, mixed towards margin with dense short glandular hairs, with margin lined with similar eglandular hairs, internally by dense eglandular hairs, usually short, sometimes very short behind lateral lobes with region behind middle lobe glabrous, with **lower lobes** obtuse, usually shortly apiculate, with clefts between (0.8)1.9(3.0)mm deep. **Stamens** with **filaments** usually glabrous, sometimes with lower ½-1mm of anterior pair covered by short eglandular hairs, anterior pair 6.0-9.0mm long, posterior pair 3.0-5.0mm long; **anthers** (1.3)1.5-1.8(2.0) x 0.9-1.4mm, with **connectives** of anterior pair glabrous or with a few short to long eglandular hairs, less hairy than those of posterior pair which are surrounded by moderately dense to dense, moderately long to long down-turned flexuose eglandular hairs, with rearmost pair of **awns** (0.3)0.4-0.5(0.6)mm long, always longer than the anterior three awn pairs. **Ovary** laterally compressed, usually ovate, sometimes elliptic-ovate in lateral view, clothed by dense, very short to short, upturned setae in apical region only or in upper ½-⅓; **apex** in lateral view obtuse or acute; **ovules** c. 30-75. **Capsule** 4.0-6.8mm long, hardly compressed laterally, in median view usually ovate, sometimes narrow ovate, porrect or slightly declinate, in lateral view ovate-elliptic to obovate-elliptic, 1.8-2.5(3.0)mm broad, usually covered in upper ½-⅓ by sparse to moderately dense, very short to short setae, occasionally glabrous, **apex** in lateral view obtuse, usually obliquely so; **seeds** (14)30(63), (0.9)1.0-1.2(1.4) x (0.4)0.5-0.6(0.8)mm, more or less ellipsoid, often angled. **Chromosome number:** unknown. Figs 12, 91E, 99.

**Distribution** (fig. 94): *E. ciliolata* is restricted to montane and subalpine zones in the Northern Tablelands of New South Wales. It is especially well-collected in the Barrington Tops-Gloucester Tops area. Altitude, c. 900-1550m, elevations above about 1000m being recorded from the southern localities.

**Ecology:** The species is recorded frequently from open grassy situations or near bogs or swamps in a variety of communities, namely sclerophyll forest, *Eucalyptus pauciflora* snowgum woodland, grasslands, meadows and herbfield.

Plants begin flowering in early January, with branches still bearing flowers in May or even August.

**Conservation status:** 3 ?R,C. Possibly not at risk.

**Notes:** 1. **Carolin 487** consists of plants which resemble *E. collina* by their many-seeded, large capsules (7-9mm long) and long upper leaves and bracts with two teeth along each margin. The pubescence of the calyces, corollas, and anther backs, the shape of the corolla, the presence of axillary branches on the erect stem, and the lack of evidence that the plants are perennial clearly show the specimens to be most closely allied to *E. ciliolata*. Whether they are hybrids between the two species, or an extreme variant of *E. ciliolata* cannot be determined.
2. The specific epithet refers to the short eglandular hairs which densely line the margins of the corolla lobes in this species. Only in *E. arguta* does this pilosity occur with similarly high density and consistency.

**Specimens examined**


**Interspecific hybrids**

Hybridization between Australian species of *Euphrasia* is rare. Only four definite cases have been found (three of these recognized from field study), which clearly indicate that the barriers to interspecific hybridization are great. In each case hybrids show reduced pollen fertility and are scarce in comparison with the prolific population(s) of the parent species in the area. It seems significant that the only hybrids so far detected have arisen from the crossing of species from different sections. This is to some extent a reflection of two facts. Firstly, where intergradation, generally of an ecotonal nature, involves allied taxa with no evidence of increased pollen sterility in the intermediates, this has been used as one of the criteria for distinction of the taxa at an infraspecific level (p. 96). Secondly, in at least the areas visited, there is always an ecological separation between sympatric species of the same section. Nevertheless, in the past interspecific hybrids may have given rise to stabilized intermediate populations (p. 97).

4 x 11b. *E. striata* x *E. collina* ssp. *diemenica*

Populations of *E. striata* (Sect. *Striatae*) and *E. collina* ssp. *diemenica* (Sect. *Australes*) grow together on the Central Plateau and Mt Wellington in Tasmania (figs 35, 50). They represent the only cases known to the author of overlap of populations of taxa from Sect. *Striatae* and Sect. *Australes*.

On the Central Plateau in an extensive area of alpine heath near Lake Augusta (fig. 35), sporadic hybrids occur among abundant populations of the two species. The two species differ in flowering time, with *E. striata* flowering earlier. The hybridization between them is probably effected mainly by the native bees which were seen visiting flowers of both species and the hybrids. The hybrid individuals were intermediate in the characters separating the two species, namely the presence of striations on the corolla, the presence of hairs on the anther backs, the bluntness of the leaf teeth, the overall leaf shape, and the incidence of a glandular indumentum on the upper and/or lower parts. The hybrids were mainly detected in the field by their only partially striated corollas. Pollen tests (PS28, 29, 226-227, 229-230, 261-265) showed the hybrids to be highly sterile. *E. striata* (PS18, 26, 27, 228, 258-260, 269) and in general *E. collina* ssp. *diemenica* (q.v.: note 1) show pollen which is mainly functional in appearance.

Hybrids have been collected also on the Central Plateau (fig. 35) from the Ironstone
Mountains (Rodway NSW22281p.p.) and near Breona (Barker 1065). In both instances pollen from the hybrid was highly sterile (PS231, 267).

A putative hybrid from Mt Wellington was not tested for pollen sterility because of the paucity of flowers.

Specimens examined

Putative hybrid
TASMANIA: L. Rodway s.n., i.1914. Mt Wellington. HO.

11g x 13. E. collina ssp. paludosa x E. lasianthera

E. lasianthera (Sect. Lasiantherae) and E. collina ssp. paludosa (Sect. Australes) hybridize near the headwaters of the Macalister River in the eastern highlands of Victoria (fig. 86). Prolific populations of both species grow in close proximity on a flat ridge-top covered by snowgum (Eucalyptus pauciflora) woodland (fig. 100). On the cleared grassy roadside verge on the summit of the ridge, plants of the two species were commonly found within twenty metres of each other, and cases of plants of either species growing side by side were not uncommon. The two species were flowering simultaneously (although E. lasianthera was at a more advanced stage), and native bees similar to those observed visiting flowers of E. collina ssp. paludosa (Barker 1492, 1495) several kilometres away were seen among the flowers of E. lasianthera (fig. 17). With the plants of the two species clearly distinguishable on the characters of corolla coloration (the plants of E. collina in this region all bore a yellow blotch on the lower corolla lip) and indumentum, numerous plants of both populations were studied for evidence of hybridism. Only four plants (fig. 100: Barker 1505A, 1507, 1508, 1512) were discovered with a mixture of characters of both species. Three of these proved to be certain hybrids as their anthers contained an abnormally low percentage of functional pollen (PS30, 31, 35, 46). The pollen of the sympatric populations of E. collina ssp. paludosa is mainly functional in appearance (PS32, 38-41, 45).

Clearly there must be some substantial barriers to interbreeding between the species. It is possible that the two species have only come together in the disturbed roadside situation which provides an intermediate habitat between the open tussock grasslands in which E. collina was observed to abound, and the snowgum woodland where E. lasianthera was generally seen.

Specimens examined
VICTORIA (EASTERN HIGHLANDS): Barker 1507, 1508, 26.xii.1971. C. 3km NW of Howitt Hut on the Macalister Headwaters road, c. 100m SE of the turnoff to Macalister Springs. AD.—Barker 1512, 26.xii.1971. C. 2km NW of Howitt Hut on the Macalister Headwaters road, c. 1km SE of the turnoff to Macalister Springs. AD.

Putative hybrid
Barker 1505A, 26.xii.1971. As for Barker 1507. AD.
Fig. 100. *E. collina* ssp. *paludosa x E. lasianthera*, Macalister River headwaters, Eastern Highlands, Victoria. A, disturbed site with plant each of *E. lasianthera* (Barker 1506, at front), *E. collina* ssp. *paludosa* (Barker 1505, right rear), and a hybrid (Barker 1507, left rear), scale 5cm high; B, inflorescence of hybrid (Barker 1507) with lilac corolla with reddish-purple striations and deep yellow patch at the base of each anterior filament, scale 1cm.
?I1g x 18a. ?E. collina ssp. paludosa x E. orthocheila ssp. orthocheila

The three plants of *Cambage 1594* from Stannum in north-eastern New South Wales (fig. 94) resemble *E. orthocheila* ssp. *orthocheila* (Sect. *Scabrae*) by their yellow corollas, small capsules, branching apparently well up the stem, the high degree of secondary branching, and the glandular-scaprous indumentum of the herbaceous parts of the inflorescence. They tend, however, towards Sect. *Austerales* mainly in the shape and indumentum of the corollas. The corollas possess lower lips which are large and apparently downcurved, while their pilosity is much sparser and less extensive than is typical in *E. orthocheila*.

In addition, two of the plants are abnormal in other characters. One plant, the only one which still retains a good set of leaves, has leaves uppermost on the main axes rather larger than normal for *E. orthocheila*, and these bear two teeth along each margin. The capsules are typical of *E. orthocheila* in indumentum and shape, while the seeds are rather large at c. 0.9mm long. This plant has mainly functional pollen (PS110, 123). The capsules of a second plant (with the best display of fruits but lacking in leaves) are very long (c. 5.8mm) for ones occurring on branches, have obtuse apices, and have a moderately dense cover of setae over only the upper half. The seed size is also large (c. 1.0mm). In all these capsule characters it diverges from *E. orthocheila*. The pollen sterility estimates for this plant are abnormally high at 46-51% (PS109, 124). The third plant resembles *E. orthocheila* but for the unusual corollas mentioned above. The pollen appears almost entirely functional (PS108, 125).

On the basis of the above evidence it is very probable that these plants are hybrid in origin. One parent taxon is clearly *E. orthocheila* ssp. *orthocheila*. The sympatric *E. collina* ssp. *paludosa* (Sect. *Austerales*) may be the other parent.

**Specimen examined**


15 x 16. *E. alsa* x *E. caudata*

These hybrids are known only at Spencer's Creek, near Mt Kosciusko (fig. 86). Mrs J. Thompson (pers. comm. 1980) states that *E. alsa* (Sect. *Lasiantherae*), *E. caudata* (Sect. *Scabrae*) and their hybrid are all common in this area which has been much disturbed by trampling and earth-moving operations. All hybrids show a high degree of pollen sterility (PS49, 50, 86-91, 93-94). On the other hand, *E. alsa* and *E. caudata* show a high percentage of normal pollen (PS48, 51-53, 82-85, 92, 97, 104). The hybrid collection *Barker 1697* was made at the edge of a population of *E. alsa* in low heath beside the river bank. The plants were very distinctive by their larger habit and more faintly striated corollas. The intermediacy of leaf variation in the hybrid compared with the two parent species is shown in fig. 11. No ecological differences between the hybrid and *E. alsa* were observed.

**Specimens examined**

NEW SOUTH WALES: *Barker 1697*, 26.i.1972. C. 50m N of bridge across Spencers Creek, on the Kosciusko Summit Road, c. 3km ENE of Charlottes Pass. AD.—Stead 3, 13.i.1966. Spencer's Creek, Kosciusko area. MEL.—Stead s.n., 22.i.1964. Spencer's Creek, Kosciusko. NSW64342.

**Possible further interspecific hybrids**

The hybrid status of the following is by no means certain. The relevant plants may equally or more likely be extremes of variation of a taxon, or an undescribed taxon.

7 x III. *E. hookeri* x *E. sp.* (Sect. *Striatae*)

Studies in Euphrasia

19 x ?11. E. arguta x ?E. collina

11 x III. E. collina x E. sp. (Sect. Striatae)
Tasmania: Port Cygnet. See E. collina: note 3.

11 x 20. E. collina x E. ciliolata

E. Index to Australian collections
Included in this index are numbered collections and those (unnumbered) collections of Ferdinand von Mueller which bear dates.

The first number, in italics, is the collectors number or, in the case of Mueilleri, the date. The second designation is the code of the taxon to which the collection belongs (see below). Where the collection is referred to in a note under a particular taxon, the code of the taxon, the symbol “N” and the note number are given in that order. Type specimens (excluding paratypes) are designated by “(T)”. Hybrids are denoted by “x” between the codes of the parent taxa. Intermediates between taxa are designated by “-” between the codes of the taxa. Where a collection is inadequate for determination to a lower rank this is designated by “Q” (= questionable).

1. E. ramulosa
2. E. phragmostoma
3. E. gibbsiae
   a. ssp. gibbsiae
   b. ssp. psilantherea
   c. ssp. wellingtonensis
   d. ssp. comberi
   e. ssp. kingii
   f. ssp. microdonta
   g. ssp. discolor
   h. ssp. pulvinestris

4. E. striata
5. E. sp. ‘Southport’
6. E. semipicta
7. E. hookeri
8. E. bella
9. E. sp. ‘Tamworth’
10. E. bowdeniae
11. E. collina
   a. ssp. collina
   b. ssp. diemenica
   c. ssp. ‘Northwest Tasmania’
   d. ssp. tetragona
   e. ssp. ‘tasmania’

12. E. crassiuscula
   a. ssp. crassiuscula
   b. ssp. glandulifera
   c. ssp. eglandulosa

13. E. lasianthera
14. E. eichleri
15. E. alsa
16. E. caudata
17. E. scabra
18. E. orthocheila
   a. ssp. orthocheila
   b. ssp. peraspera
19. E. arguta
20. E. ciliolata

Acknowledgments to Australian collections
Ackland 3111d, 189/II; Adams 510/11, 1645/11i, 254/116; Ainsworth 1/1, 2/1, 3/1; Alcock 1648/11d; Alkinson 141/11a; Anderson 3111b, 8/3f, 251111; Andrews 83111d; Anon. 3111, 3111la, 4/h i, 5/11a, 42/117, 45/11i, 49/1111, 5/111, 66/111, 67/111, 102/111, 110/111, 111/111, 11/116; A.M. Ashby 858/11n, 3166/116, 3757/111, 4354/117, 442/111, 4928/117; Ashby 1400/11d; Aston 2478/112c, 754/11a, 1020/111; Atkinson 15111i.

Baeuerlen 57/117, 64/115, 215/111, 511/11; Barker 853/11m, 854/11m, 856/11m, 861/11m, 862/11m, 863/11m, 864/11m, 869/11m, 873/11m, 877/11m, 880/11m, 913/11m, 923/11m aff. b, 939/11m, 940/11m, 942/11m, 945/11m, 946/11m, 947/11m, 953/11m, 955/11m, 960/6, 962/6, 963/6(T), 967/6, 968/11m, 975/11m, 977/11m, 978/11m, 980/11m, 982/11m, 990/11m, 992/3e, 994/3e, 995/4 x 11m, 999/11mb, 1000/11mb, 1002/11mb, 1003/11mb, 1004/3x, 1008/3c(T), 1011/4, 1012/3c, 1015/11b, 1016/4, 1020/11b, 1021/4 x 11b, 1023/11b, 1040(p.p.)/4, 1040(p.p.)/4 x 11b, 1041/11b, 1042/11b, 1044/3x, 1045(1)&(2)/11b, 1046/11b, 1047/11b, 1048/4 x 11b, 1049(1)&(2)/11b, 1050/11b, 1051(1)&(2)/11b, 1052/4 x 11b, 1053(1)&(2)/11b, 1058/11b, 1060/4, 1061/4, 1062/11b, 1064/3x, 1065/4 x 11b, 1066/4, 1067/4, 1068/11b, 1069/4, 1070/11b, 1071/4, 1073/11b, 1074/4, 1078/11b, 1079/11b, 1080/11b, 1095/11b, 1097/11b, 1098/11b, 1105/11b, 1107/11b, 1112/11b, 1113/11b, 1119/11a, 1123/3c, 1124/3b, 1128/11b, 1137/11b, 1138/11a-b, 1141/11b, 1146/11b-a-b, 1147/11b-a-b, 1149/11a-b, 1151/4, 1151/4, 1154/4, 1157/3a, 1158/3a, 1164/3a, 1165/3a, 1166/3i, 1167/3i, 1168/3i, 1169/3a, 1170/3i, 1173 & 1173A/3a-d, 1174(1)&(2)/3a-d, 1175/3a-d, 1176/4, 1177/3a, 1178/4, 1178A/4, 1181/3d(T), 1182/3i, 1183/4, 1184/3a-d, 1185/3a-d, 1186/4, 1187/3aff. g, 1188/4, 1189/3a, 1191/3d-e, 1193/3d-e, 1194/3d-e, 1201/4, 1202/4, 1203/4, 1204/3, 1205/3a, 1206/3m, 1207/7, 1208/4, 1209/4, 1210/4, 1211/7, 1212/7, 1214/7, 1215/7, 1216/3a, 1218A/3h(T), 1218B/3a, 1222/7, 1224/4, 1225/4, 1227/7, 1228/4, 1231/4, 1232/4, 1233/4, 1346/11m(T), 1345/11d, 1356/11d, 1374/11d, 1375/11d, 1431/11a, 1432/11a, 1438/11e, 1439(p.p.)/11e, 1439(p.p.)/11a, 1440/11a, 1441/11a, 1442/11e, 1443/11a, 1446/11a,
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Kantvilas 9/3d-e; Kaspiew 40/11m, 66/11m, 700/12c, 1365/11n, 1366/11n; Kraehnbeul 138/11d, 1250/11d.

VI. ACKNOWLEDGEMENTS

This work is based on a thesis (Barker 1974) which was submitted to the Botany Department, University of Adelaide and produced under the tenure of a Commonwealth Post-Graduate Award in the State Herbarium of South Australia and the Botany Department, University of Adelaide. Considerable modifications were made subsequently from 1976 during employment in the State Herbarium.
I am grateful to the National Parks and Wildlife Service of New South Wales, the National Parks Authority of Victoria, the State Electricity Commission of Victoria, the Forests Commission of Victoria, and the Tasmanian Parks and Wildlife Service for permission to enter areas under their authority, and to the herbaria (p. 3) which forwarded loans of specimens.

To the following people I extend my sincere thanks: to Mr A.C. Beauglehole and Dr & Mrs D.A. Ratkowsky for assistance in obtaining a large number of collections; to Miss I. Bowden, Dr & Mrs I.J. Edwards, Mrs I. Grubb, Dr & Mrs D. Hamilton, Mr A. Himson, Miss D. Hunt, Mr K. Rogers, Dr J.H. Wills and Mr & Mrs D.J. Wimbush for guidance and/or the supply of accommodation on field trips; to Mr L. Dutkiewicz for spending much personal time in producing the figures 30, 31, 48, 85 and 91; to Miss K. Stove for assistance with photography; to Miss B.A. Welling and Mrs E.M. Kosmala for typing manuscript; to Dr J.P. Jessop for support and editorial assistance; to other staff of the State Herbarium of South Australia and Adelaide Botanic Gardens; and to other people who provided special information or assistance acknowledged in the text.

I am very grateful to the late Miss C.M. Eardley for her advice and encouragement.

To Dr P.J. Garnock-Jones, Dr S.D. Hopper, Dr P.H. Raven, Professor C.G.G.J. van Steenis and Dr P. Wardle I am thankful for constructive comments and criticisms on an earlier draft of the evolution chapter, and to Professor D.I. Axelrod for a beneficial discussion.

Mrs J. Thompson spent considerable time suggesting ways of tightening up the large manuscript. I gratefully acknowledge her thoroughness and comments on all facets of the revision.

To Dr Hj. Eichler I am very thankful for his beneficial discussions and ready assistance. His sound judgement, high standards and perseverance have been always appreciated.

Finally, I wish to express my deepest gratitude to my wife, Robyn, for her considerable assistance, personal sacrifices and continued encouragement.

VII. REFERENCES

Brown, R. (unpubl.). "Botanical Descriptions (Manuscript) of Australian Plants held by the British Museum (Natural History)". (Positive microfilm: 22 reels at AD).


Kraehenbuehl, D.N. (unpubl.). Distribution and inter-relationships of the flora and fauna in the Tothill Range, South Australia. (Unpublished manuscript).


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