
KRISTINA L. LEMSOM

Department of Botany, The University of Western Australia, Nedlands, W.A. 6907, Australia

Received: 3 February 1995 Accepted: 4 October 1995

Andersonia R.Br. is a genus of small to medium-sized shrubs endemic to the south west of Australia. It currently comprises 22 recognized species and is one of three closely related genera which form the tribe Cosmelieae. Andersonia is distinct from the closely related Sprengelia Sm., but serious problems in the subgeneric taxonomy have been identified. A strict application of the current descriptions of two subgeneric divisions does not include two species, and a full assessment of the homologies of the leaf-organs on which these sections are based has never been made. At species level a large number of new taxa have been identified, and some previous combinations are questionable. This paper outlines these problems and ways in which they are being addressed. Some urgency is attached to the taxonomic work because of the threat posed to the genus by dieback caused by the fungus Phytophthora cinnamomi.

Key words: Andersonia, Epacridaceae, systematics.

INTRODUCTION

Andersonia R.Br. is a genus of 22 small to medium-sized woody shrubs endemic to the south west of Australia. All species prefer an open position with sandy soils and occur in heathlands, open forest glades, on and around granite outcrops, or in winter-wet depressions.

It is over 30 years since the genus was reviewed (Watson, 1967) and a large volume of material collected since has revealed a number of previously undescribed taxa and serious shortcomings in the current taxonomy. The resolution of these taxonomic difficulties, most especially completion of revision at species level, are of importance to the future conservation of Andersonia. Wildfire dieback caused by the fungus Phytophthora cinnamomi Rands represents a real threat to the continued existence of several species. The ecological preferences and life histories of Andersonia species place them collectively as the most susceptible group within a highly susceptible family. Two as yet undescribed species of Andersonia are listed as Declared Rare Flora and regarded as endangered (Keighery, 1981; Anonymous, 1994). Western Australian legislation for the protection of endangered flora allows for only identified and named taxa and so clear taxonomic boundaries and understanding of species variation are a necessary requirement for conservation efforts to be best targeted and of greatest benefit.

GENERIC CIRCUMSCRIPTION

Andersonia was originally described by Brown (1810) and has since been treated as both a genus in its own right (Brown, 1810; de Candolle, 1839; Sonder, 1845; von Mueller, 1859; Bentham, 1868) or as a section of the closely related Sprengelia Sm. (von Mueller, 1867, 1873; Drude, 1889) with some debate over the distinction between the two genera. Recent work has focused on the place of Andersonia within the family as a whole (Watson, 1967; Powell, Chapman and Doust, 1987). Andersonia, Sprengelia and the closely related Cosmelia R.Br. share a number of characteristics including sheathing leaf bases, an absence of leaf scars and pattern of leaf fibre bundles (Table 1) and have been placed in recent times together in the tribe Cosmelieae on this basis (Watson, 1967; Powell et al., 1987), although the subfamilial placing of the tribe was different.

Consideration of characters used to separate the genera shows Cosmelia to be clearly distinct on the basis of several characters (Table 1). The single species, Cosmelia rubra R.Br. has characteristics similar to both Andersonia and Sprengelia, but differs from both of them in having filaments adnate to the tube and pendulous flowers (Table 1). Sprengelia has been distinguished by an absence of floral nectary scales, glabrous corolla, corolla lobes imbricate in the bud and a tube which may split to form petal claws, whilst Andersonia has nectary scales at the base of the ovary, a pubescent corolla, valvate corolla lobes and a tube which is continuous for at least one third of the corolla length. Further work on several characters listed (Table 1) is warranted, however, as the consideration of new material of Andersonia calls them into question. Whilst the corolla lobes in Andersonia are never split to the base there are collections of new species where the tube is very short. The tube in Andersonia is formed by congenital fusion of the petals and lengthens by intercalary growth quite late in development. It is intriguing to consider what the controls on this process are, especially when Sprengelia incarnata Sm. is recorded as having a short tube or the petals free (Curtis, 1963) and S. distichophylla (Rodw.) W. M. Curtis as having a tube 2 mm long with lobes ‘slightly longer’ (Curtis, 1963). Sprengelia has also been characterized as having anthers cohering around the style (Watson, 1962). However, this too does not appear to occur in all species—the anthers in S. distichophylla are described as spreading or free (Curtis, 1963). The anthers in S. incarnata cohere at their margins.
but the join appears only superficial and the anthers are easily separated. This character should be considered of dubious value until further investigation is complete. *Sprengelia* has been reported with anthers in which the longitudinal slits remain separate, in contrast to other Epacridaceae where the thecae become confluent and form a single, central slit (Paterson, 1961). *Andersonia bifida* L. Watson has anthers that are divided at the apex, and the slits apparently continue as separate to the base of the anther. Despite these questionable characters, the distinction between *Andersonia* and *Sprengelia* should remain until a full reappraisal is complete. Cladistic analysis is in progress in an attempt to clarify phylogenetic relationships between the three genera using the Richeae (*Richea R.Br.*, *Dracophyllum* Labill., and *Sphenotoma* Sweet) (Powell *et al.* 1987) as outgroups.

**SUBGENERIC DIVISION**

*Andersonia* has traditionally been divided on the basis of flower position, beginning with Brown (1810) who observed a fundamental difference in flower position between species within *Andersonia*. In seven species (Table 2) the flowers are terminal on a short lateral shoot clothed with a number of leaf-like structures, which differ in shape and size from normal leaves. The last 8–15 of these form a series in which the shape gradually changes from leaf-like to sepal-like and the decurrent base of the sheath is reduced and lost. In the remaining 15 species (Table 2) the flowers occur in the axils of leaves on the main stem, subtended by a pair of folded and keeled leaf-like structures differing markedly in shape and size from the vegetative leaves. Brown (1810) assigned his five species to two groups based on this difference in subtending leaves but made no formal descriptions of subgeneric groups.

Sub-generic divisions were formalised by Sonder (1845). The monotypic *Aitherocephala* D.C. (de Candolle, 1839)
(synonymous with \textit{Andersonia aristata} Lindl.; Lindley, 1839) was placed alone in a section of the same name, and the remaining species allocated to \textit{Euandersonia}. The latter was subdivided into sections on the lines observed by Brown (1810), and formally named Multibracteatae (flowers terminal with multiple bracts) and Bibracteatae (axillary flowers subtended by two folded and keeled bracts). Bentham (1868) also subdivided the genus, with \textit{Cephalanthus} described as having ‘flowers in terminal heads, each one solitary and sessile in the axil of the floral leaf or subtending bract, between two keeled and complicated bracteoles’ and \textit{Monanthus} with ‘flowers solitary and terminal, surrounded by numerous bracts without distinct bracteoles’. However there was a subtle difference in the interpretation made by Bentham (1868) and previous authors (Brown, 1810; de Candolle, 1839; Sonder, 1845; von Mueller, 1859, 1864), in that Bentham (1868) regarded the keeled leaves in \textit{Cephalanthus} as qualitatively different from the organs clothing the lateral shoots in the \textit{Monanthus}, referring to them using different terms, whilst the others did not. Later workers (Drude, 1889; Druce, 1917; Watson, 1962) maintained sub-generic division with the most recent (Watson, 1962) using Sonder’s (1845) terms Bibracteatae and Multibracteatae for two sections, although not with precisely the same content.

The most serious problem with these interpretations is the lack of consideration of homologies between the leaf-organs which subtend the flower, a clear comprehension of which is necessary to make a meaningful analysis of any need for sub-generic division. Imprecise and interchangeable uses of the terms bract and bracteole have not contributed to a clarity of understanding on this account. ‘Bracteole’ was originally used by Bentham (1868) only in reference to the keeled and folded organs which immediately subtend the flowers in his \textit{Cephalanthus}, but was later also used by Watson (1962) for the leaves preceding the flower on the lateral shoot in the alternative section. ‘Bract’ has been used in reference to organs in both these positions and to the structure on the main stem which subtends axillary flowers in the Bibracteatae (Watson, 1962). It is interesting in this context to note that although Watson (1962) used the term bracteole in reference to the keeled structures the name of the section was maintained as ‘Bibracteatae’ rather than ‘Bibracteolae’. Clear and consistent definitions and usages of terminology are needed for a deeper analysis of these criteria for generic division, as each of these leaf-like structures is morphologically distinct.

In species with terminal flowers, the leaves on the lateral shoots may be considered as three separate classes. The proximal leaves are two folded, and sometimes keeled, prophylls. These are usually less than half as long as the subsequent leaves. The leaves above the prophylls are morphologically similar to leaves on the main stem, sometimes differing slightly in shape and usually smaller, whereas those which immediately precede the flower change in shape towards the shoot apex, and lose the decurrent sheathing base, and are inserted in the same fashion as the sepals. The question must be posed as to which, if any, of these are homologous to the keeled leaves in axillary flowers of the Bibracteatae. In terms of morphology and position, the keeled leaves of the Bibracteatae have most in common with the vegetative prophylls found at the bases of all lateral shoots in all species, a point noted but not elaborated on by Watson (1962). If this is the case the axillary structures in the Bibracteatae may represent a reduced inflorescence.

Inflorescence structure in the Multibracteatae has proven more complicated than suggested by previous studies. In species examined thus far, each axillary shoot produces more than one flower. The initial flower forms at the apex of a side shoot with the second and subsequent flowers produced below this flower in the axils of sheath-based leaves. Above the last of these flowers the series of leaves before the apical flower commences changing to the sepal-like form. Second-order laterals lack sheath-based leaves altogether, with the flowers preceded only by a pair of prophylls and the series of non-sheathing leaves.

A significant further complication when considering subgeneric division is the ambiguous treatment of \textit{A. carinata}. L. Watson and \textit{A. simplex} (Stschég.) Druce. Both these species frequently, if not always, have inflorescences in which both types of flowers occur. Sub-terminal flowers are subtended by two keeled leaves but the single apical flower is surrounded by a series of leaves which follow the same pattern as those subtending flowers in the Multibracteatae, that is, they change in shape in a series and lose the sheathing base. These two species were placed in the Bibracteatae by Watson (1962) despite this anomaly, and without discussion of the significance of the multibracteate apical flower. \textit{A. carinata} and \textit{A. simplex} do not fit easily into a strict division on the basis of flower position, and raise the question as to the validity of a split based on this feature.

**SPECIES-LEVEL TAXONOMY**

The 30 years since the last revision of \textit{Andersonia} has seen the collection of large volumes of new material which highlight difficulties with species-level taxonomy. Apart from the collection of specimens which represent up to 25 new species, field observations have shown that herbarium specimens, on which the last revision was exclusively based, give little or no indication of characteristics that can delineate closely related species. The most striking of these are colour characteristics, particularly of the corolla and calyx, but also the anther, pollen, ovary and corolla hairs. Corolla tube shape ranges from a narrow cylinder with parallel sides to urceolate or virtually campanulate and is also not preserved in dried specimens. Environmental scanning electron microscopy on fresh floral and leaf materials has revealed some previously unreported variation in features such as nectary scales, sculpturing on corolla hairs, surfaces of the corolla and seed and ovule numbers. This examination also calls into question some previously made distinctions such as that between hairs and papillae and the divisions between various terms for pubescence used by Watson (1962).

This new information suggests a reappraisal of combinations of taxa made by other workers. Watson (1962) sank \textit{A. pubescens} Sond. within \textit{A. lehmanniana} Sond. (as \textit{A. lehmanniana} subsp. \textit{pubescens}) emphasising flower size and
shapes of anther and filaments. However fresh material of these two taxa suggests they may be distinct species. *Andersonia lehmanniana* subsp. *lehmanniana* has a bright to pale blue, urceolate tube with a narrow mouth, incurved anther filaments and anthers which converge around the style among thick hairs at the tube mouth. *Andersonia lehmanniana* subsp. *pubescens* has a pink tube with parallel sides, straight filaments and sparse hairs. These features place the taxon much closer to *A. sprengelioides* R.Br. of which the two taxa within *A. lehmanniana* were once regarded as subspecies (Bentham, 1868; Diels and Pritzel, 1905).

The most immediate practical problem at species level was created by the merging of seven taxa into *A. caerulea* R.Br. (Watson, 1962) resulting in a taxon with a broad range of variation, and a large volume of quite disparate material has since been referred to it. It now seems clear that *A. caerulea sensu* Watson (1962) encompasses several groups. While some of Watson’s recombinations might be justified from herbarium specimens, not all of his changes to *A. caerulea* are supported by observations of live plants. A large proportion of material ascribed to *A. caerulea* has the typical pink calyx and blue corolla of *A. caerulea sensu stricto*, but there is significant variation in the extent and nature of corolla colouration. Corolla colour at anthesis varies from bright blue to a mixture of blue and pink on the same flower to pure white. Colour changes also occur as the flower ages, fading to white as anthesis ends and the flower withers. In some populations, corolla colour hardly varies between individuals, in others there is strong variation in both colour and intensity over a short geographical distance. There are also groups where both the calyx and corolla are the same colour. Two populations near Narrogin differ strikingly in having deep magenta corolla and calyx and no blue colouring at all, fitting the description of *A. concinna* N. E. Brown. Furthermore, marked differences in habit, flower size, corolla shape and ecological preferences occur, again over short distances. It is interesting to consider the basis of these variations, and the species as presently defined represents an opportunity for population-based studies. Chromosome counts of various grouping are in progress, to test phylogenetic relationships amongst the species and the monophyly or otherwise of previously defined subgeneric groupings.

**ACKNOWLEDGEMENTS**

This work forms part of a PhD project in the Department of Botany, The University of Western Australia under the supervision of Dr J. A. Chappill. The work is supported by a University of WA Postgraduate Award. I am grateful to Dr H. M. Stace, Ms Carol Wilkins and two referees for their comments.

**LITERATURE CITED**


