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## Robert Brown 200

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Robert Brown in 1850. From the portrait by Maguire. Taken from Mabberley, D.J. (1985) Jupiter botanicus: Robert Brown of the British Museum. (J. Cramer/ British Museum Natural History: Braunschweig / London).

# TELOPEA

A journal of plant systematics

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# Robert Brown 200: Introduction

## David J. Mabberley

*Mabberley, D.J. (Nationaal Herbarium Nederland, University of Leiden, The Netherlands, and National Herbarium of New South Wales, Botanic Gardens Trust, Sydney NSW 2000, Australia) 2004. Robert Brown 200: Introduction.* Telopea *10(2): 497–498.*

This issue of *Telopea* includes a number of papers presented at **Robert Brown 200**, an international conference celebrating Robert Brown's time in New South Wales and his contribution to science. This conference, held at the Royal Botanic Gardens, Sydney on 8–10th May 2002, was one of a series around Australia, to celebrate the successes of Matthew Flinders's voyage, two hundred years after the *Investigator* touched various points in its circumnavigation of the Australian coast.

Robert Brown (1773–1858) was selected by Sir Joseph Banks as naturalist for the voyage (for biographical details of Brown see Mabberley (1985)). On 9th May 1802, the *Investigator* dropped anchor in Sydney Cove, before beginning her circumnavigation of Australia. Little did Robert Brown, the naturalist, know that he was to spend much of the next three years based in New South Wales, a time of avid collecting but also reflection on the enormity of the task ahead of him in bringing order to the materials from the expedition as a whole. For a time he lived in a house on what is now the Domain in Sydney, and we know that he botanised all over the area.

But this conference was not just looking back and celebrating Brown's time here. The meeting used his time in New South Wales as a benchmark from which to consider the systematics of plants and the ecology of Australia in a modern context, and to look forward to the challenges ahead. Robert Brown's interests and influence were broader than the flora of Australia. He had a lasting influence on botanical systematics in general, and his microscopic work led to whole new insights and discoveries beyond systematics in the fundamentals of plant-fertilisation and cytology.

From the standpoint of modern systematics, Brown's re-introduction to the English-speaking world of the natural system of classification was, and is, seen as a major contribution. First set out in his great monograph of Proteaceae, largely concerned with Australian species, it was further elaborated in his *Prodromus florae novae-hollandiae* (1810) and later his appendix to Flinders's account of the *Investigator* voyage (1814). Brown's projected great Flora of Australia was never completed but in monographs later he published a great deal more on Australian plants.

Brown wrote a pioneering monograph of the Asclepiadaceae-Apocynaceae and a great essay on Compositae (1817). He also inserted monographs of families like Sterculiaceae and Gesneriaceae in floristic accounts. He was responsible for the recognition and circumscription of dozens of new families of angiosperms e.g. Chloranthaceae, Winteraceae, Myristicaceae, Pandanaceae, Hypoxidaceae, Hemerocallidaceae, Dioscoreaceae, Marantaceae, Lardizabalaceae, Phytolaccaceae, Hamamelidaceae, Haloragidaceae, Santalaceae, Zygophyllaceae, Celastraceae, Chrysobalanaceae, Oxalidaceae and Connaraceae; Cunoniaceae, Cephalotaceae, Tremandraceae, Casuarinaceae, Combretaceae, Limnanthaceae, Myrsinaceae, Myoporaceae, Pedaliaceae, Escalloniaceae, Pittosporaceae, Stylidiaceae, Goodeniaceae and Calyceraceae, Haemodoraceae and Restionaceae.

Brown also published on mosses and ferns, and clearly distinguished the gymnosperms from the angiosperms (Mabberley 1985, p. 252). He described the biggest flower in the world, *Rafflesia arnoldii* from Sumatra (Mabberley 1985, pp. 219–238), and made important advances in the studies of this and other parasitic angiosperms. Of other angiosperm groups where he made major advances, pre-eminent are the Orchidaceae, particularly collaborating with Ferdinand Bauer, natural history painter on the voyage, and later Ferdinand's brother Franz, especially in the pollination and fertilization studies on which Darwin was to build (Mabberley 1985, p. 158). Another family where he made groundbreaking advances was the grasses.

In Australia we tend to grasp to us Brown, like Bentham later, for his work on our flora, but both men worked monographically and therefore beyond the phytogeographical constraints of Australia. They both also worked floristically on the plants of other parts of the world. For Brown, his greatest plant geography contributions were probably on the flora of Africa — notably the Congo basin, but also west Africa and Ethiopia, besides Madeira. This work had a major influence on von Humboldt, Lyell and through him, Darwin. Brown also worked on Indian, North American and other temperate plants from China and many groups for *Hortus kewensis*, effectively an encyclopaedia of cultivated plants of the period. But to show his truly global influence, it is important that we realise he worked on a flora as distant as it could be from Australia: the Arctic.

The papers presented here deal with a broad range of 'his' plant groups: Apocynacae by Mary Endress; Gesneriaceae and Scrophulariaceae by Tony Weber; Restionaceae by Barbara Briggs; Grasses by Lynn Clark; and Rhamnaceae by Juergen Kellerman.

Other papers relevant to Brown's contribution to our knowledge of the Australian environment, also presented at Robert Brown 200, are to be found in *Cunninghamia* 7(4) 2002.

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Mabberley, D.J. (1985) *Jupiter botanicus: Robert Brown of the British Museum.* (J. Cramer/ British Museum Natural History: Braunschweig / London).

# Restionaceae (Poales) in the footsteps of Robert Brown

Barbara G. Briggs

## Abstract

*Barbara G. Briggs (National Herbarium of New South Wales, Mrs Macquaries Road, Sydney 2000, Australia; barbara.briggs@rbgsyd.nsw.gov.au.) 2004. Restionaceae (Poales) in the footsteps of Robert Brown.* Telopea *10(2): 499–503.* Brown visited major centres of restiad diversity in Africa at the Cape of Good Hope and in Western Australia at King Georges Sound and Lucky Bay; other taxa were collected in northern and eastern Australia, including Tasmania. He described five genera and 36 species now included in Restionaceae, and four genera and 35 species since excluded from that family. His observation, enlightened by fieldwork, was remarkable and some species he named are now recognised again after decades in confusion or synonymy. Mostly he correctly matched dioecious males and females, but for one species these were placed in different genera. Restionaceae has been much cut down in size since Brown's time. In the *Prodromus*, Restiaceae included what are now Anarthriaceae, Centrolepidaceae, Eriocaulaceae and Xyridaceae, as well as Lyginiaceae if this and Hopkinsiaceae are recognised as separate from Anarthriaceae sens. strict. Currently 145 Australian Restionaceae species are recognised, in 31 genera. The 24 species that Brown included in *Restio* (22 of them then newly described) are now distributed among 11 genera, the majority in *Chordifex*, *Baloskion* and *Hypolaena*, while *Restio* is restricted to African and Madagascan species. Anatomy, palynology and especially DNA sequencing have clarified relationships within Restionaceae and between families of Poales. Molecular data indicate that Centrolepidaceae forms the sister-group to Restionaceae, unless it is embedded in the latter.

## Brown's Restiaceae

Among Robert Brown's less publicised achievements was his role in founding an understanding of Australian Restionaceae. At Cape of Good Hope, King Georges Sound and Lucky Bay, Brown visited hot-spots of restiad diversity, collecting 14 species of Restionaceae (and many in closely related families) at King Georges Sound. In northern and eastern Australia, including Tasmania, he saw and collected representatives of genera now recognised but that are not represented in Western Australia or were not collected there (*Dapsilanthus* B.G. Briggs & L.A.S. Johnson, *Baloskion* Raf. and *Empodisma* L.A.S. Johnson & D. Cutler), as well as further species of genera seen in the west, especially of *Lepyrodia* R. Br. and *Sporadanthus* F. Muell.

The family Restionaceae (as Restiaceae) was described by Brown in the *Prodromus* (1810) and was then considerably more inclusive than Restionaceae today. Before Brown's work, only three Australian restiad species, in three genera, had been described, by Labillardière (1806), namely *Restio tetraphyllus*, *Calorophus elongatus* and *Schoenodum tenax*. Labillardière had placed these in the class 'Dioecia triandria', characterised by dioecy and the presence of three stamens. Soon after the *Prodromus*, by the time of Endlicher (1836), the Centrolepidaceae, Eriocaulaceae and Xyridaceae had been excised from Restionaceae. These families, however, remain in Poales as recently recognised (APG 1998, 2003). These excisions left Restionaceae with much the circumscription that it retained until anatomical studies (Cutler 1969) provided the basis for excluding *Ecdeiocolea* F. Muell. and *Anarthria* R. Br. (Cutler & Airy Shaw 1965), and recently DNA data showed *Hopkinsia* W. Fitzg. and *Lyginia* R. Br. to be misplaced in Restionaceae (Briggs & Johnson 2000, Briggs et al. 2000).

Brown described five genera and 36 species now in Restionaceae, and four genera and 35 species since excluded from that family. Like Labillardière, Brown referred some Australian species to *Restio* Rottb., which is now considered to be restricted to Africa and Madagascar (Linder 1985, Linder et al. 1998); indeed classifications of several Restionaceous genera persisted until very recently that treated species on both continents as congeneric.

Most species of Restionaceae are dioecious and difficulties in matching male and female collections have been noted since these were first studied botanically. Mostly Brown correctly matched the male and female plants of the dioecious species, although for *Meeboldina scariosa* (R. Br.) B.G. Briggs & L.A.S. Johnson he placed males in *Restio* (as *R. microstachys* R. Br.) but the corresponding females in *Leptocarpus* R. Br. (as *L. scariosus* R. Br.). Observant field studies prevented more such misplacements. One of the first Australian Restionaceae described, *Schoenodum tenax* Labill., was recognised by Brown as based on material of two collections and these were referred by him to two genera, *Leptocarpus* (female specimen) and *Lyginia* R. Br. (male), now placed in separate families. Since the males and females of both of these genera are remarkably dissimilar, such a mixture of collections is understandable. The male specimen however cannot have come from Tasmania but, as with several other Labillardière specimens attributed to 'van Diemens Land' (Nelson 1974), must have been collected in Western Australia.

At one further point some confusion was generated since Brown named two taxa as '*Restio laxus*' i.e. *Restio* species 3 and 12, now *Chordifex laxus* (R. Br.) B.G. Briggs & L.A.S. Johnson and *Meeboldina laxus* (R. Br.) B.G. Briggs (Briggs 2001).

Brown saw in the field all except one of the 39 species he recognised; his regular annotation '*v.v.*' showing the importance he placed on field study. The one exception was *Leptocarpus ramosus* R. Br. [now *Dapsilanthus ramosus* (R. Br.) B.G. Briggs & L.A.S. Johnson based on a specimen collected by Banks and Solander at the Endeavour River. Brown's observation was remarkable and species he named, such as *Chordifex monocephalus* (R. Br.) B.G. Briggs (*Restio monocephalus* R. Br., synonym *Acion monocephalum* (R. Br.) B.G. Briggs & L.A.S. Johnson), are now recognised after many decades in confusion or synonymy (Morris 1991; Briggs & Johnson 2004). Similarly, *Lyginia imberbis* R. Br. is now recognised after long confusion with *L. barbata* R. Br. The above-ground structures of these *Lyginia* species show some differences but the most reliable characters are in the clumped habit of the former, with culms crowded on the short rhizomes, in contrast to the large patches of sparsely scattered culms connected by elongated rhizomes in *L. barbata*. These differences were clear to the astute field observer but not apparent in specimens that lacked underground parts. Not surprisingly, since he lacked field observation or habit notes, Bentham (1878) synonymised these species.

## Brown's observations

The quality and amazing thoroughness of his observations may be seen in the features Brown used to characterize the Restiaceae. '[The] lenticular embryo being placed at the extremity of the seed opposite to the umbilicus' and 'from Juncaceae it also differs in the order of suppression of its stamina, which when reduced to three are opposite to the inner laciniæ of the perianthium' and the 'simple and unilocular antherae'. Brown was justly notable for endorsing the 'natural system' of Jussieu (1789) and departing from the Linnaean System of plant classification based on the number of reproductive parts in the flowers (Mabberley 1985). Where his classification of Restionaceae was unsatisfactory it was because vestiges remained of classification based on the numbers of floral parts. It is now clear that there has been homoplasious loss of floral parts in many clades and this has obscured relationships (Briggs & Johnson 1999). The small, wind-pollinated flowers do not show great diversity and leaves reduced to sheaths are general throughout the family. Until a wider range of data became available, a satisfactory classification was scarcely possible. *Restio* sens. lat., as Brown recognised it, was polyphyletic but his *Lepyrodia* (now *Lepyrodia* with *Sporadanthus*) and *Leptocarpus* (now *Leptocarpus* with *Apodasmia* B.G. Briggs & L.A.S. Johnson, *Dapsilanthus* B.G. Briggs & L.A.S. Johnson and *Meeboldina* Suess.) correspond reasonably well with clades that are supported by DNA and other data.

In Restionaceae, as in Proteaceae and Myrtaceae, Brown contributed greatly to knowledge of notable Southern Hemisphere families. He commented on the similarities of the South African and southern Australian floras, as well as the proportion of monocotyledons in the floras of different continents and the absence of certain groups from Australia's flora. Unlike Joseph Hooker (1855) who followed him to Australia almost 40 years later, Brown does not appear to have pondered greatly the questions posed by the distribution of these families on separated land masses. In this he was a scientist of his time, decades before evolution opened the way to understanding speciation and diversification, and even longer before plate tectonics gave a new interpretation of the post-Gondwanic Southern Hemisphere.

## Restionaceae today

Now 145 Australian species are recognised (including 21 not yet formally named) in 31 genera (Briggs & Johnson 1999, 2004). Many of those described after Brown's time are from heathlands and shrublands north of Perth and elsewhere in the semi-arid inland of Western Australia, not traversed by botanical collectors till long after his visit. The 24 species that he included in *Restio* sens. lat. (22 of them then newly described) are now distributed among 11 genera, the majority in *Chordifex* B.G. Briggs & L.A.S. Johnson, *Baloskion* Raf. and *Hypolaena* R. Br., while *Restio* is restricted to African and Madagascan species.

DNA sequencing, anatomy, seed morphology, palynology, embryology and phytochemistry are clarifying relationships within Restionaceae and between families of Poales (Cutler 1969; Linder & Ferguson 1985, Rudall & Linder 1988, Briggs & Johnson 1998; Williams et al. 1998, Meney & Pate 1999; Briggs et al. 2000; Linder et al. 2000; Eldenäs & Linder 2000). The genera removed from Restionaceae in recent decades to form the families Ecdeiocoleaceae and Anarthriaceae were distinguished initially on their striking anatomical differences from Restionaceae (Cutler & Airy Shaw 1965). *Lyginia* and *Hopkinsia* WoFitzg., more recently removed from Restionaceae, form a clade with Anarthriaceae but show equally notable anatomical differences from *Anarthria* (Briggs & Johnson 2000).

Within Restionaceae, seed surface patterns are very varied and useful in characterising genera. At a finer level of relationship, seed ornamentation differs markedly among species of *Chordifex*; all have raised patterns of lines of cells but, in *C. chaunocoleus* (F.Muell.) B.G. Briggs & L.A.S. Johnson and the newly described species *C. sinuosus* B.G. Briggs & L.A.S. Johnson and *C. reseminans* B.G. Briggs & L.A.S. Johnson, these form very pronounced ridges (Briggs & Johnson 2004). Differences in seed surfaces were also the initial clue to distinguishing three new species (yet to be formally named) among specimens previously included in *Lepyrodia scariosa* R. Br.

An unresolved question remains under investigation: the status of the Centrolepidaceae. These have highly reduced floral structures; for instance the inflorescences are pseudanthia of several male flowers, each reduced to a single stamen (lacking tepals), and female flowers, each consisting of only a single carpel (Cooke 1998). Some are perennial cushion plants of subalpine or high-latitude habitats, but others are tiny annual plants of seasonally moist sites. Despite the many apomorphic differences from Restionaceae, including differences in anatomy (Cutler 1969) and pollen (Linder & Ferguson 1985), DNA data from several genes show Centrolepidaceae and Restionaceae forming a robustly supported clade, a relationship also indicated by similarities in embryology. The question remains: are the Centrolepidaceae sister to Restionaceae or a specialized neotenous derivative embedded in the latter? Analyses of sequences of different genes have given conflicting results. Briggs et al. (2000) found that *rbc*L data did not separate Centrolepidaceae (represented by *Centrolepis* Labill.) from Restionaceae, and Bremer (2002) obtained a similar result when data from *atp*B were added. Neyland (2002) found a surprising association of *Centrolepis* with *Ecdeiocolea* F.Muell., based on nuclear DNA (26S rDNA), although various recent studies of chloroplast DNA have placed *Ecdeiocolea* in the Poaceae clade, rather than among the closest allies of Restionaceae. Michelangeli et al. (2003) placed Centrolepidaceae (represented by *Aphelia* R. Br.) as sister to Restionaceae on the basis of *rbc*L, *atp*A and morphology). Further data on a wider range of taxa, from *mat*K and *trn*L–*trn*F chloroplast DNA (Marchant & Briggs, in preparation) may, however, still be insufficient to corroborate a position as sister to Restionaceae. Brown's outstanding insight is exemplified in his recognition of the affinities of these plants and inclusion of representatives of the Centrolepidaceae, and other families now in modern Poales, within his Restiaceae.

## Acknowledgments

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# The Grasses (Poaceae): Robert Brown and now

Lynn G. Clark

## Abstract

*Clark, Lynn G. (Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, Iowa 50011-1020, USA) 2004. The grasses (Poaceae): Robert Brown and now.* Telopea *10(2): 505–514.* Robert Brown provided the first account of the Australian grasses in his 1810 *Prodomus*, in which he described a number of new grass genera and species and arranged the genera primarily according to floret number and floral sexuality. Implicit in his circumscription of the family was the recognition of the unique nature of the caryopsis and the specialised grass embryo. In the 1814 *Botany of Terra Australis*, Brown discussed the morphology of grasses and revised his general classification of the family. Brown divided the family into two 'tribes' (what we would today call subfamilies), the Paniceae and Poaceae, and he explicitly noted the trends toward basal reduction in the spikelets of Paniceae and apical reduction in the Poaceae. He described grass spikelets in detail and drew the general conclusions that these were branched structures, and that the lodicules represented perianth parts. Brown also noted that the Paniceae were more diverse in tropical latitudes, and the Poaceae in temperate latitudes. Brown's basic classification persisted without radical modification well into the 20th century. Recent phylogenetic analyses of the grass family demonstrate the paraphyly of Brown's Poaceae, which actually comprises 11 subfamilies, but his Paniceae is retained to a large extent in the modern Panicoideae.

## Introduction

Robert Brown knew the grasses (family Poaceae) as an important component of both the monocots and the Australian flora, noting that grasses comprised about 25% of the known species diversity of both groups (Brown 1810, 1814). Grasses currently comprise approximately 15% of monocot species diversity, and, with about 1320 native and naturalised species in Australia (B. Simon, pers. comm.), no more than 10% of the Australian vascular flora, but an appreciation of the ecological and economic importance of grasses has only continued to grow (GPWG 2001 and references cited therein).

Although Robert Brown studied other plant families in more detail (e.g., Proteaceae, Apocynaceae), he nonetheless made significant contributions to grass morphology and classification. In this paper I will discuss Brown's work on grasses (both descriptive and morphological), the current state of grass systematics, and Brown's contributions to grass systematics.

### Brown and the grasses

Brown (1810) described 32 genera (including one he elevated to generic status) and nearly 200 species of grasses, primarily from the Australian flora. The descriptions emphasised spikelet and floral characters, and were concise and largely parallel. Occasionally comments on distribution, affinities, and/or additional details of spikelet morphology also were included. Larger or more complex genera were often subdivided; for example, the species of *Eriachne* R. Br. were divided into two groups based on whether the lemma was awned or muticous. The description of the family was quite detailed and included both vegetative and reproductive characters, without emphasising one feature over another.

In addition to the purely descriptive aspect of his grass work, Brown (1810) provided an artificial classification of the family that he further refined in 1814. In the earlier work, Brown divided the genera of the family into three major, artificial groups, based primarily on the number of florets and whether the flowers were perfect or unisexual. The first two groups included a majority of the genera, with the third representing a small group of odd genera characterised by three-flowered spikelets, with one floret bisexual and the two 'lateral' florets masculine or neuter. In the later work, Brown focused on the first two groups (his two 'great tribes'), which he formally named the Poaceae and Paniceae, and did not discuss the disposition of the minor third group. He noted that the Poaceae had spikelets with one to many florets and a tendency toward apical reduction (what he called 'imperfection') in the spikelet (Fig. 1a), and that the Poaceae were prevalent in temperate climates. The Paniceae, on the other hand, had two-flowered spikelets, with the lower floret always masculine or neuter and frequently consisting of only a lemma (Fig. 1b), and were more diverse in tropical regions.

Brown made several cogent observations of grass morphology that can be inferred from his 1810 description of the family, and others that were explicitly discussed in the 1814 work. Brown (1810) listed the open leaf sheath, distichous florets within a spikelet, presence of lodicules, caryopsis (fruit with the pericarp adnate to the seed

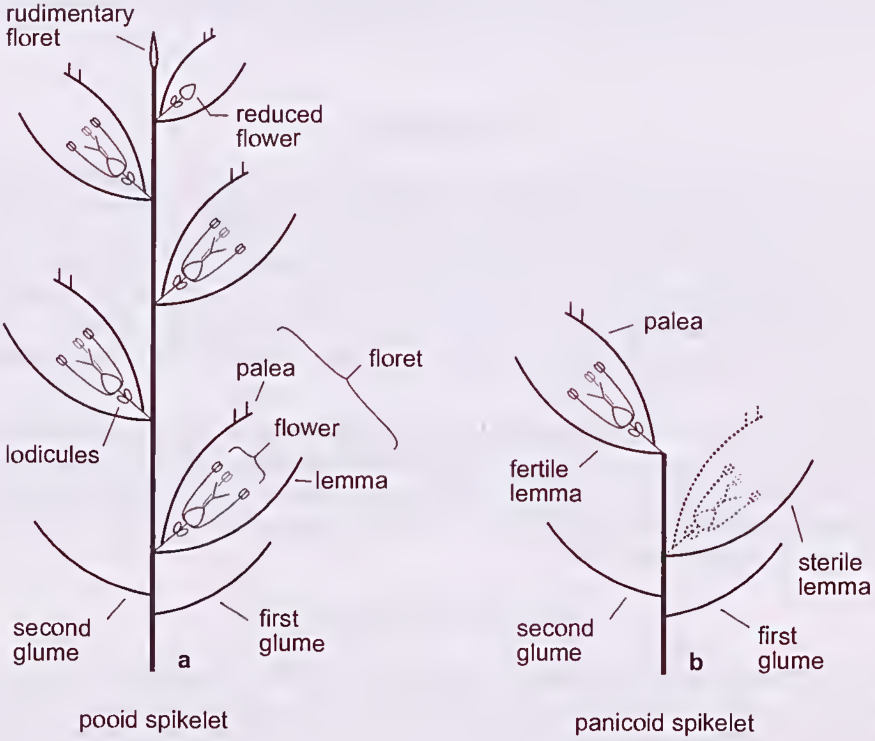

**Fig. 1.** Diagrammatic grass spikelets. **a**, multiflowered pooid (Pooideae) spikelet with apical reduction; **b**, two-flowered panicoid (Panicoideae) spikelets with basal reduction. Dotted lines indicate structures that are usually absent.

coat), specialised embryo in a basal and lateral position, and starchy endosperm among the characters that define the family. With respect to the embryo, Brown referred to the scutellum (which he interpreted as a fleshy, shield-shaped cotyledon), and he also noted the presence of a well-developed shoot with primary leaves. Brown (1814) recognised that the grass spikelet is a branched structure (Fig. 1); he noted that the outer envelope (i.e., the pair of glumes) contained "several flowers with distinct and often distant insertions on a common receptacle." Brown was also interested in the origin of the two valves of the inner envelope (i.e., the lemma and the palea), for which he proposed two alternate hypotheses. According to the floral hypothesis, the lemma and palea were regarded as a modified calyx and corolla (with bilateral symmetry and fusion of parts as seen in other groups of flowering plants), but the origin of the lodicules was unexplained. In the foliar hypothesis, the lemma and palea were considered to be bracts subtending the flower, and thus the lodicules represented the true perianth. He finally settled on an intermediate explanation, in which the lemma and palea represented the calyx, and the lodicules the corolla.

## Current state of grass systematics

A detailed discussion of the history of grass systematics is given in GPWG (2001), but a brief summary is provided here. Subsequent to Brown's work on grasses, various classifications of the family, based on spikelet and inflorescence morphology, appeared in the 19th century. Usually nine or ten tribes (equivalent to modern usage of this term) were recognised. Bentham (1878) formalised Brown's division of the family into two great groups. By the end of the 19th century, some workers were beginning to analyze spikelet structure using an evolutionary perspective (e.g., Čelakovský 1889; Goebel 1895), and additional data sets were accumulating (e.g., leaf anatomical, Duval-Jouve 1875 and embryological, van Tiegham 1897), leading to a broad reassessment of evolutionary relationships. Classification systems based on presumed evolutionary relationships and recognizing three or more subfamilies began to appear as early as the 1930s (e.g., Roshevits 1937; Table 1, GPWG 2001), but Brown's two group system persisted into the 1950s (e.g., Hitchcock & Chase 1950). By the 1980s, usually five to seven subfamilies were recognised, based either on phenetic analyses or presumed evolutionary relationships. A more explicit approach to grass classification and evolution began in the late 1980s with the application of cladistic methodology and the use of molecular data, including both RFLPs (restriction fragment length polymorphisms) and DNA sequences. In recent years, phylogenies derived from DNA sequence data, RFLPs and morphology began to converge, showing in particular that 1) the traditionally recognised bamboos were polyphyletic and included the earliest-diverging lineages of the family, and 2) a group now called the PACCAD clade was strongly supported as having originated from a single common ancestor.

The Grass Phylogeny Working Group (GPWG) was formed in 1996 to combine a series of these existing data sets to produce a comprehensive phylogeny for the grasses, to focus taxon sampling in the development of grass data sets, and to test the existing subfamilial classifications of the grass family based on the results of its phylogenetic analyses. Analysis of eight data sets (four plastid, three nuclear, and one structural) produced a single most parsimonious tree (Fig. 2; GPWG 2000, 2001), and a revised classification recognizing 12 subfamilies was proposed based explicitly on the phylogeny (Fig. 2; GPWG 2001).

This phylogenetic hypothesis and available fossil evidence allow us to explore the evolutionary history of the grasses with greater clarity (GPWG 2001 and references cited therein), although many intriguing questions remain. The oldest known fossils indicate that the family most probably originated some time between 55 and 70 million years ago (mya) in the southern hemisphere. The earliest grasses inhabited

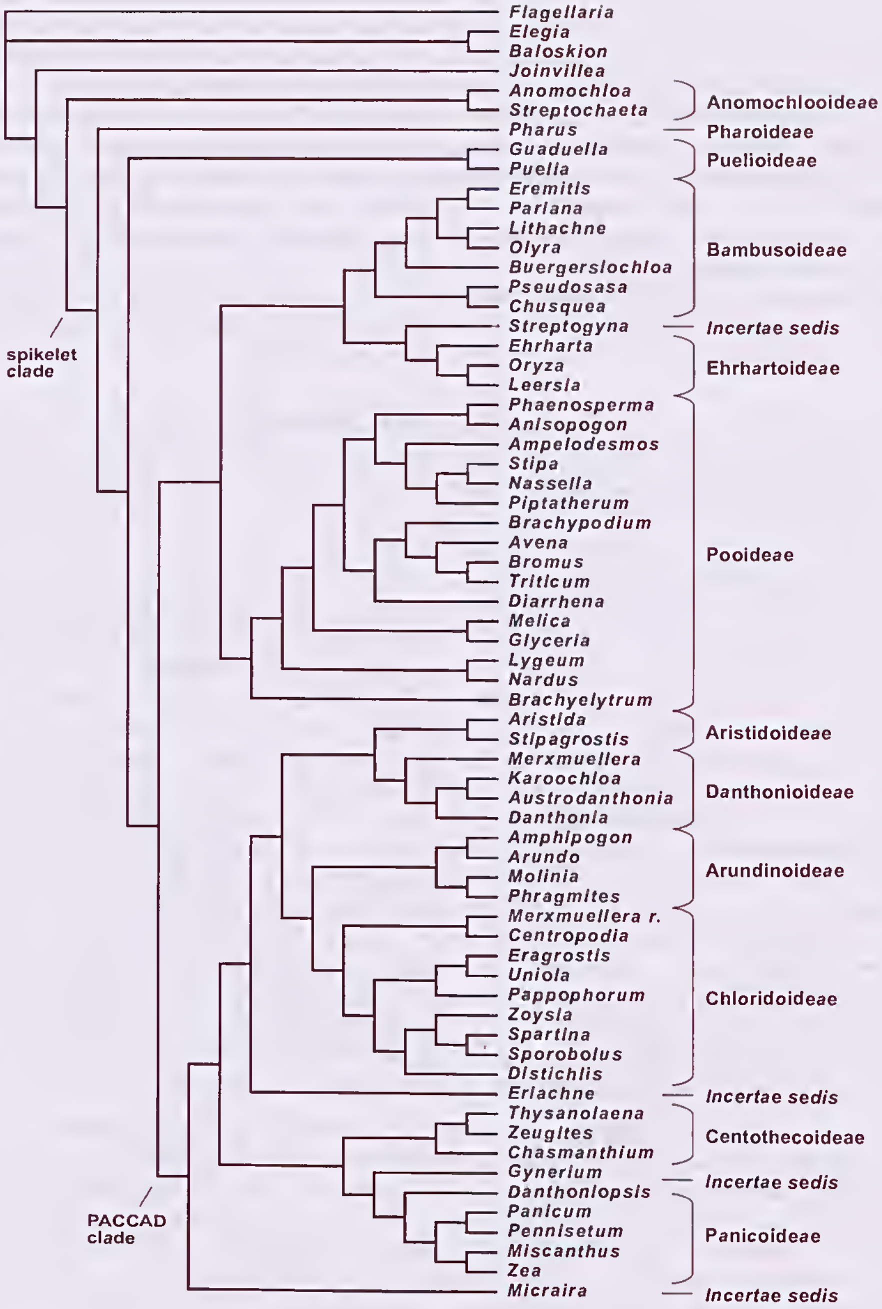

**Fig. 2.** Single most parsimonious tree for the grasses (*Anomochloa* through *Micraira*) and relatives (*Flagellaria* through *Joinvillea*) obtained in the GPWG (2001) analysis, showing the revised subfamilial classification for the grass family.

tropical forests and shared a number of characteristics, including (but not limited to) a rhizomatous, herbaceous, perennial habit; relatively broad, pseudopetiolate leaf blades with fusoid cells in the chlorenchyma; leaves with an open sheath and an adaxial ligule; a bracteate inflorescence and a reduced perianth; spikelets (or spikelet equivalents) with one flower; flowers with six stamens in two whorls; a uniloculate, uniovulate gynoecium with three stigmas; a basic (dry) caryopsis; a specialised, laterally positioned embryo; and $C_3$ photosynthesis. By the mid-Tertiary, as the continental interiors became drier and more open, the grasses began their radiation into more open habitats. At about this time, the number of stamens was reduced to three. All of the major lineages of the grasses were present by the close of the Miocene (about 5 mya); grass-dominated ecosystems also appeared at about that time. The PACCAD clade, which includes all of the $C_4$ lineages, arose no later than 15 mya. One major lineage, the Bambusoideae, either never left the forest habitat or went back to it, and another major lineage, the Pooideae, diversified extensively in cooler climates. Features such as intercalary meristems, drought tolerance, vegetative reproduction, and dispersal mechanisms likely played important roles in the great Tertiary diversification of the grasses, but the evolution of these features is still not well understood.

## Brown's contributions to grass systematics

Brown provided the first significant treatment of Australian grasses, and this publication is still a major reference for anyone working on Australian grass diversity. Twenty-eight (or 87.5 %) of his genera are still accepted (Watson & Dallwitz 1992). Brown's artificial but useful classification of the grasses into two great groups (i.e., subfamilies) persisted until the 1950's without radical modification. Brown's Poaceae is now recognised as paraphyletic, and comprises 11 subfamilies under the most recent proposed classification (GPWG 2001). Brown's Paniceae, however, remains more or less as he circumscribed it and is now recognised as the Panicoideae. The presence of a basal female-sterile floret appears to be a synapomorphy for this subfamily (GPWG 2001). *Holcus* L., which Brown included his Paniceae, shares apical reduction with the Pooideae and as presently circumscribed is classified within that subfamily. The confusion arose because *Holcus*, as understood by Brown, included many andropogonoid genera (e.g., *Sorghum* Moench) and thus his interpretation was consistent; he could not have known that priority was to be made retrospective.

With regard to grass morphology, Brown was correct in his recognition of the caryopsis, the specialised structure of the embryo, and its basal and lateral position as characters that define the grass family. All of these characters are today regarded as synapomorphies for the Poaceae (Fig. 3; GPWG 2001). Brown was the first to recognize that the spikelet is a branched structure, but the implications of this insight for interpretation of the grass inflorescence were largely ignored by subsequent workers. The spikelet, as an aggregation of flowers, is arguably equivalent to an inflorescence (Stapleton, 1997; Judziewicz et al., 1999), but in any case continues to be equated inaccurately to a flower, as seen in the description of grass inflorescences as panicles, racemes, or spikes (e.g., floristic works, Clark & Pohl 1996) at least in part as a means of maintaining consistent usage of terminology. The grass-type spikelet is present in all but the earliest-diverging lineage of the family (the spikelet clade, Fig. 4; GPWG 2001); lemmas are universal within this clade. Brown presciently framed the current debate over the origin of the lemma, the palea, and the lodicules nearly 200 years ago. Currently, the lemma and palea are most commonly regarded as foliar in origin (with the lemma homologous to a subtending bract and the palea homologous to a prophyll) but there is some support for these structures as perianth-like (GWPG 2001). Molecular genetic studies do, however, support the lodicules as petaloid in origin

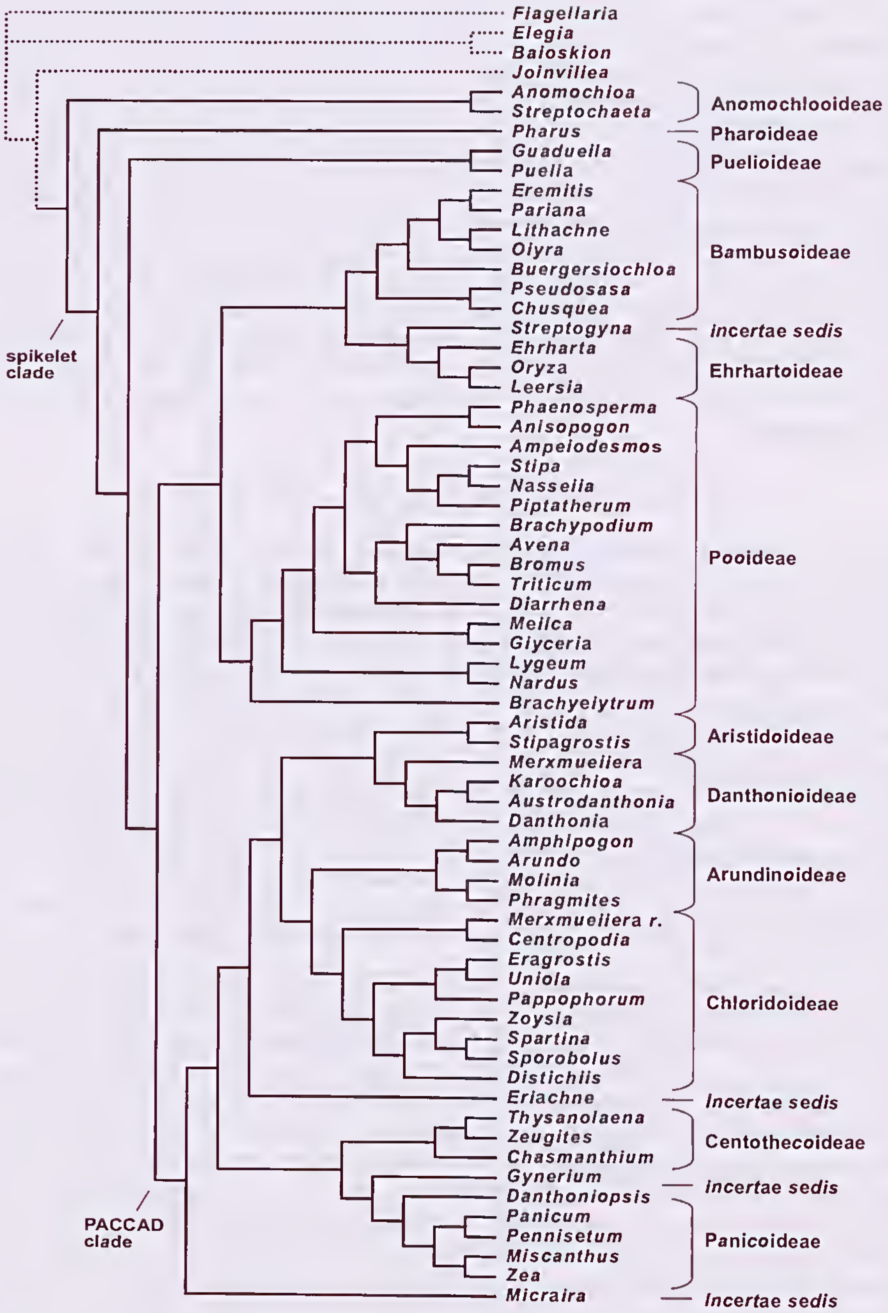

**Fig. 3.** Distribution of the grass-type embryo in the grass family, as optimized on the GPWG (2001) tree. Solid lines = presence of the character.

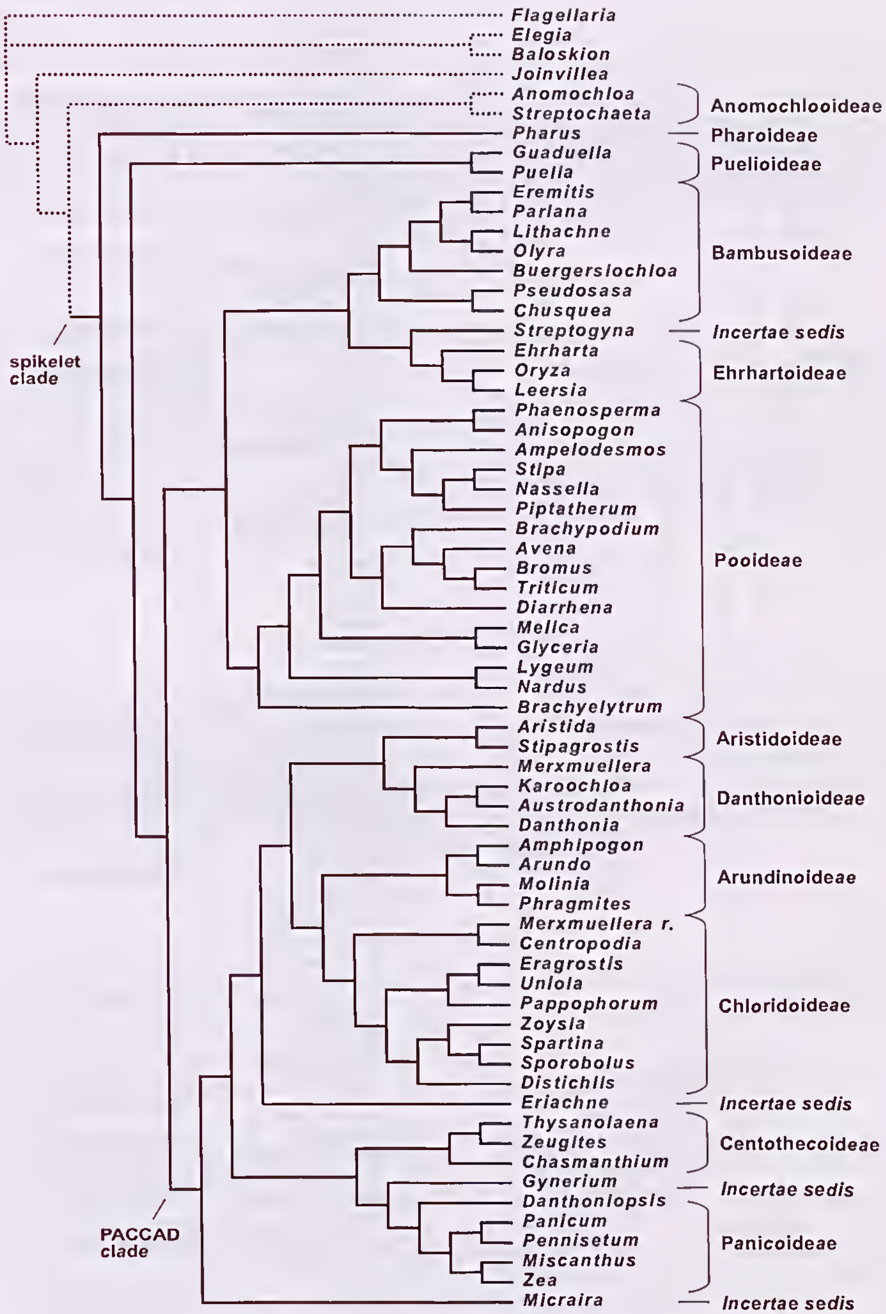

Fig. 4. Distribution of the grass-type spikelet in the grass family, as optimized on the GPWG (2001) tree. Solid lines = presence of the character.

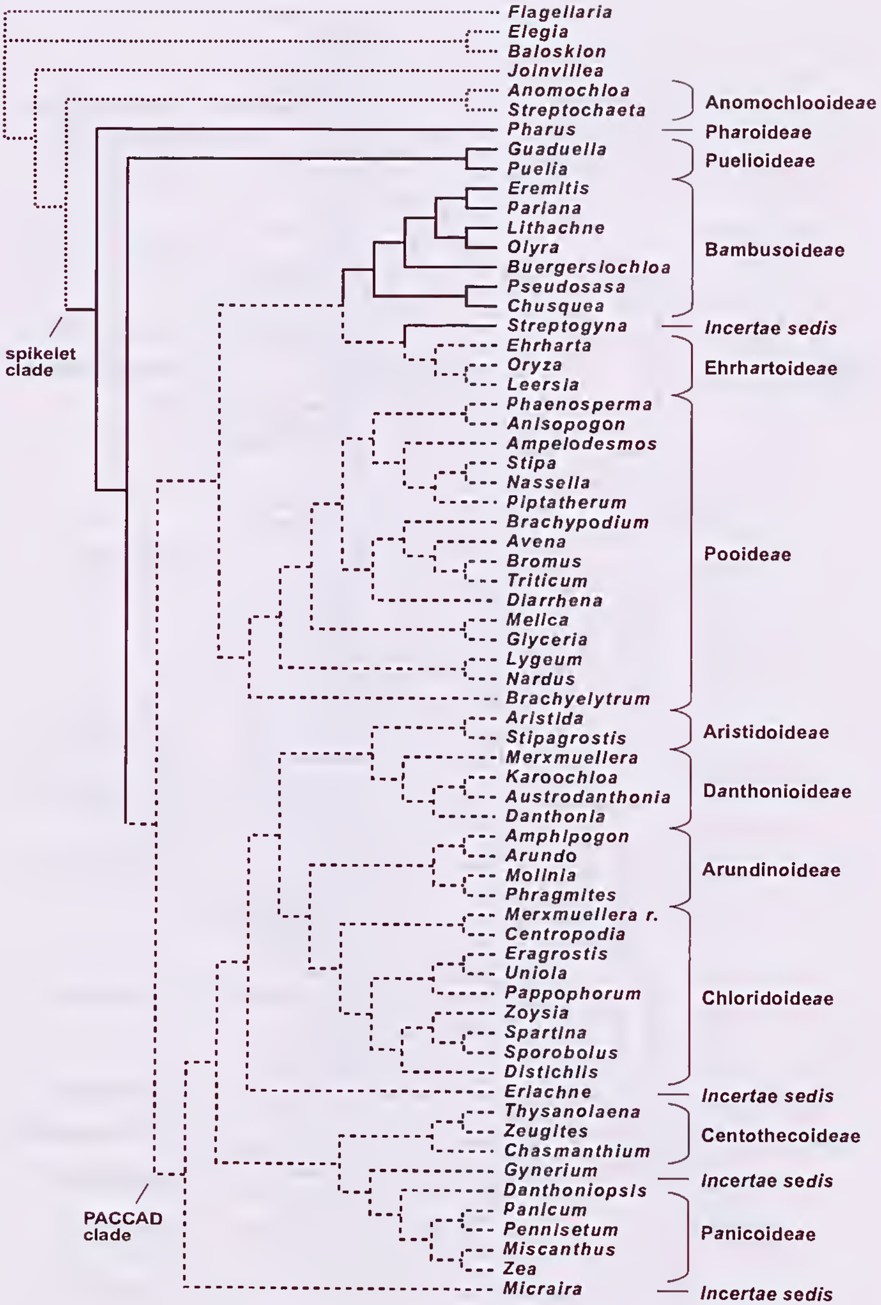

Fig. 5. Distribution of lodicule number in the grass family, as optimized on the GPWG (2001) tree. Dotted lines = lodicules absent; solid lines = three lodicules present; dashed lines = two lodicules present.

(Irish, 1998; Schmidt & Ambrose 1998; Ambrose et al. 2000). At their origin above the earliest-diverging lineage in the grasses (the spikelet clade), there are three lodicules, but above the Puelioideae there are only two, with a reversion to three in the Bambusoideae + Ehrhartoideae lineage (Fig. 5).

When Brown distinguished between the 'tropical' Paniceae and the 'temperate' Poaceae, he was observing the footprint of the evolution of the $C_4$ photosynthetic pathway in the grasses. We now know that all $C_4$ lineages of grasses evolved within the PACCAD clade (Fig. 2), and that the situation is far more complex than Brown could have realised (Sinha & Kellogg 1996; GPWG 2001), but he deserves credit for first recognizing this broad pattern.

## Concluding thoughts

Robert Brown's two published works on grasses amply demonstrate that he was a keen observer of detail who incisively analyzed those observations. It is remarkable that Brown, who spent a comparatively small amount of time on this complex family, could have distilled such accurate morphological patterns from his study of its diversity, but that is exactly what he did. Brown was asking the right questions, especially regarding the origins of the lemma, palea, and lodicules. Perhaps we can now approach more definitive answers using our recently improved understanding of grass evolutionary history (GPWG 2001).

## Acknowledgments

I am grateful to the National Herbarium of New South Wales and the other sponsors of the Robert Brown 200 conference for the invitation to present this paper, and I thank Surrey and Betty Jacobs for their hospitality during my stay in Sydney. An anonymous referee provided helpful comments. Partial support for travel and for final preparation of the manuscript was provided through National Science Foundation grant DEB-9806877 to LGC. Anna Gardner prepared the illustrations.

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# Robert Brown's contributions to Rhamnaceae systematics

Jürgen Kellermann

## Abstract

*Kellermann, Jürgen (School of Botany, The University of Melbourne, Vic 3010, Australia. Email: j.kellermann@pgrad.unimelb.edu.au) 2004. Robert Brown 's contributions to Rhamnaceae systematics.* Telopea *10(2): 515–524.* This paper outlines the taxonomic history of Rhamnaceae Juss. during the first half of the 19th century, with a focus on Robert Brown's contributions. Brown advanced Rhamnaceae systematics in two ways. Firstly, he collected 31 species of the family during his time in Australia (1801–1805); nearly all of them were new to science. Although he did not publish any taxa from these collections himself, they were instrumental for his second contribution. In 1814, Robert Brown gave the family a definition that is still valid today. Brown split Rhamnaceae sensu Juss. into Celastraceae R.Br. and Rhamnaceae s.str. (i.e. sensu R.Br.). Some remaining genera had to be dispersed into a number of other families, such as Aquifoliaceae, Oleaceae or Staphyleaceae.

## Introduction

The Rhamnaceae Juss. is a medium sized plant family, with 900–1000 species worldwide. The taxon was established by Michel Adanson in the *Familles des plantes* as 'Ziziphi' (Adanson 1763), followed by Antoine-Laurent de Jussieu, who treated it as 'Rhamni' in his *Genera plantarum* (Jussieu 1789). Both authors included a variety of genera in their treatments, many of which are now attributed to other families, for example Celastraceae R.Br., Oleaceae Hoffsgg. & Link or Staphyleaceae Martinov (see Table 2 for a detailed analysis of Jussieu's genera). Jussieu seems also to have had doubts about the uniformity of his 'Rhamni' (Harms 1953), since he asks himself: "An indè dividendus ordo?" (Jussieu 1789: 383). After recent molecular systematic analyses (Fay et al. 2001; Richardson et al. 2000a, 2001), the family now contains 52 genera in eleven tribes (Richardson et al. 2000b; Diego Medan, pers. comm., 2002).

In Australia there are currently about 200 species recognised in 21 genera. There is a high level of endemism with approximately 90% of Australian species occurring only on the continent. The Australian members of the family can be divided into four groups, which represent specific biogeographic elements of the family in Australia (Bentham 1863b; Kellermann 2002; Fig. 1):

**Pantropical element -** The first group contains c. 18 species in 11 sub-tropical and tropical genera (*Colubrina* Rich. ex Brongn., *Dallachya* F.Muell., *Emmenosperma* F.Muell., *Gouania* Jacq., *Hovenia* Thunb., *Noltea* Rchb., *Rhamnus* L., *Sageretia* Brongn., *Schistocarpaea* F.Muell., *Ventilago* Gaertn., *Ziziphus* Mill.). Three of these genera, *Hovenia*, *Noltea* and *Rhamnus*, are introduced and naturalised in temperate and sub-tropical regions of Australia.

**Pacific element -** The second group consists of *Alphitonia* Reissek ex Endl., a genus of tropical and sub-tropical trees, which extends from the Malay Archipelago, New Guinea and Australia into the Pacific, as far as Hawaii. Its closest relative is the monotypic genus *Granitites* Rye from granite outcrops in Western Australia (Fay et al. 2001; Kellermann 2002). Fay et al. (2001) assume that *Granitites* is a relict of the rainforest flora that dominated Western Australia in the Cretaceous/Tertiary, resulting in the disjunct distribution of the two genera.

**Endemic element** - The third group is composed of five species-rich genera with a high level of endemism in southern, temperate to semi-arid regions of Australia, namely *Cryptandra* Sm. (30-35 spp.), *Pomaderris* Labill. (65 spp. in Australia and 8 spp. in New Zealand), *Spyridium* Fenzl (c. 35 spp.), *Stenanthemum* Reissek (25–30 spp.) and *Trymalium* Fenzl (c. 15 spp.). These five genera form, together with *Blackallia* C.A.Gardner (2 spp.) and *Siegfriedia* C.A.Gardner (1 sp.), the tribe *Pomaderreae* Reiss. ex Endl. The presence of stellate hairs is a feature that distinguishes this tribe from all other Rhamnaceae species (Kellermann 2001; Richardson et al. 2000b; Suessenguth 1953).

**Gondwanan element** - The fourth group of Australian Rhamnaceae comprises one genus, *Discaria* Hook., with two species restricted to the mountainous regions of south-eastern Australia and Tasmania, one species in New Zealand, and five species in South America (Tortosa 1983). This genus has a Gondwanan distribution.

## Robert Brown in Australia

Under the captaincy of Matthew Flinders, Robert Brown as the naturalist aboard H.M.S. *Investigator*, circumnavigated Australia from 1801 to 1803. When Flinders sailed for England to seek a replacement for the unseaworthy *Investigator*, Brown and Ferdinand Bauer, the botanical artist of the voyage, stayed for another two years in Australia to collect plant specimens and to explore the flora and fauna of the continent. During this time, Brown travelled extensively in the Sydney region, and also to Port Phillip and Tasmania, where he lived for some months. A detailed itinerary of the voyage and a summary of Brown's collection sites are given in Chapman et al. (2001) and Vallance et al. (2001).

When Brown arrived in Australia in December 1801, no Rhamnaceae species had been described from the continent. Two widespread tropical species, which occurred in Northern Australia, *Colubrina asiatica* (L.) Brongn. and *Ziziphus oenoplia* (L.) Mill., were already known. James Edward Smith had given a generic description of *Cryptandra* (Smith 1798), however, he delayed the enumeration and description of species until 1808, with *Cryptandra ericoides* Sm. being the first species described for this genus (Smith 1808).

Brown collected 31 species of Rhamnaceae during his time in Australia from 1801 to 1805, most of them along the south and east coast (Fig. 1; Table 1; an annotated list of his Rhamnaceae collections is in preparation). He gathered 26 species from the endemic tribe *Pomaderreae*, mainly from the genera *Pomaderris*, *Spyridium*, and *Trymalium*, which frequently occur along the coast. Three *Cryptandra* species were found by him during inland trips around Sydney. One species of *Discaria* was collected by Brown in Tasmania. In Northern Australia he found species of *Ziziphus* and *Colubrina*, as well as two species of the genus *Alphitonia*. Thus Robert Brown collected a representative sample of Rhamnaceae species and managed to acquire members of all four biogeographic groups of the family in Australia.

By the time he returned to England, five Australian species had been published by Jaques Julien Houton de Labillardière and Pierre Ventenant (Dryander 1806). Some of the remaining 24 species in Brown's collections had been collected previously on Cook's voyages, but none of them was described or published.

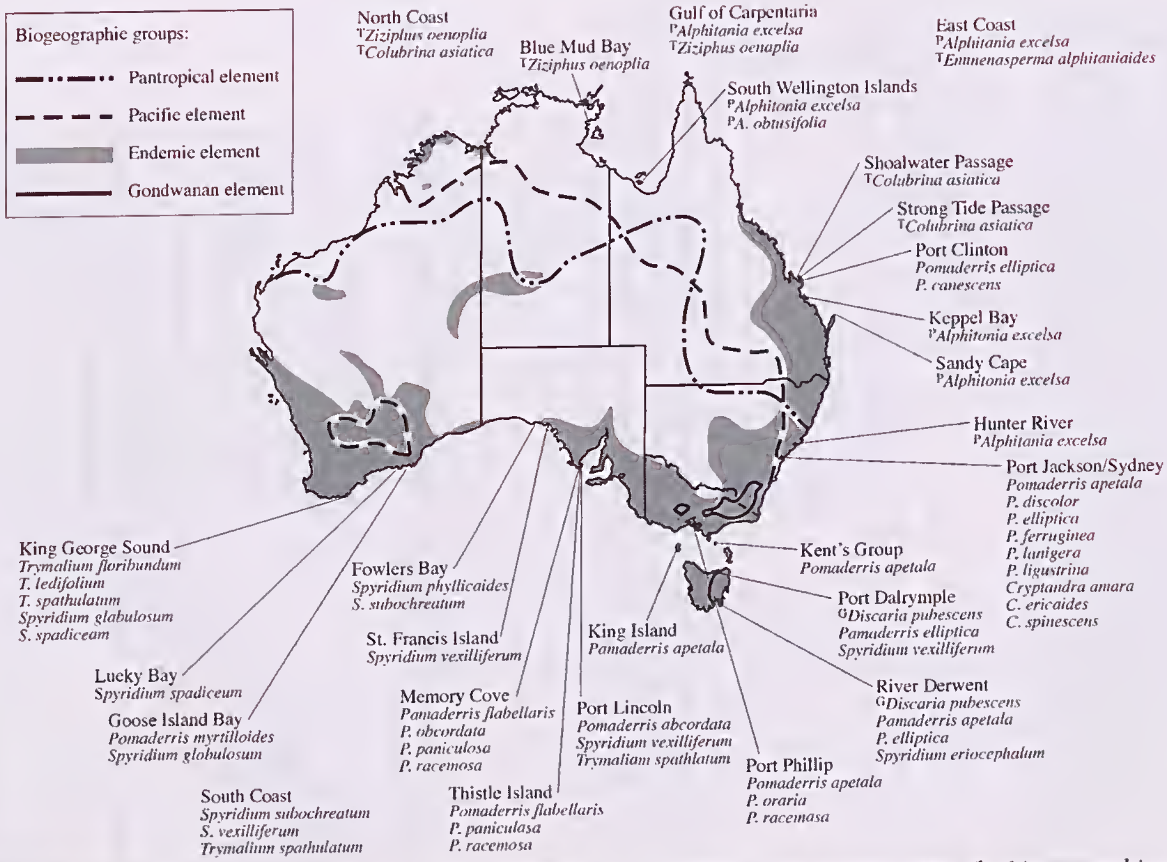


**Fig. 1.** The distribution of Rhamnaceae in Australia, and Robert Brown's Rhamnaceae collections from 1801–1805. The biogeographic regions for Australian Rhamnaceae (Bentham 1863b; Kellermann 2002) are as described in the text. Species names without superscipt symbol belong to the Endemic element; $^{G}$Gondwanan element; $^{T}$Pantropical element; $^{P}$Pacific element. Only locations where Brown collected Rhamnaceae are indicated. Some of his collections only carry approximate locations such as South, East and North Coast, or Gulf of Carpentaria. Data from Bentham (1863b); Moore et al. (2001); BRI, DNA, CANB, MEL, NSW & PERTH.

## The natural system

Robert Brown readily accepted Jussieu's (1789) and later Augustin-Pyramus de Candolle's (1813) natural system (Mabberley 1985). However, when examining his Australian collections he soon realised that Jussieu's classification was not sufficient to accommodate the new genera and species that he had encountered during his voyage. "In arranging the collection", he stated in a letter to Joseph Banks from Sydney, dated 6 August 1803, "I at first follow'd Jussieu's Ord's Naturalis; but I soon found the plants of doubtful affinity so numerous that I judg'd it better to use the Linnean method" (Vallance et al. 2001: 419). Many of Jussieu's family circumscriptions had to be amended and new families had to be described. "It was Brown's first-hand experience of the inadequacies of both systems that led him by his own observations so much to improve Jussieu's [system]" (Stearn 1960: xxviii).

## Brown's publication on Rhamnaceae, and his views on the family

In 1810 Robert Brown published the first volume of his *Prodromus florae Novae Hollandiae et Insulae van-Diemen* (Brown 1810), which dealt with cycads, ferns and fern allies, monocotyledons, and 37 families of dicotyledonous plants. In this book he transferred two genera from Jussieu's Rhamnaceae, *Mayepea* Aublet and *Samara* L., to Oleaceae and Myrsinaceae R.Br., respectively. The fact that *Samara* is allied to *Myrsine* L., and therefore to Brown's family Myrsinaceae, may have been known by botanists for some time, but Brown was the first to publish this information. An annotation by Richard Salisbury in his copy of Brown's *Prodromus* (now held in the library of the Botanic Gardens of Adelaide) states that he was told about the affinity of *Samara* and *Myrsine* by "D$^{r}$. [Dryander] in 1806, & long before when Swartz was here [in London, i.e. 1786–1787]" (Barker & Barker 1990: 51). The second volume of the *Prodromus*

**Table 1. The Rhamnaceae species collected by Robert Brown in Australia. See Fig. 1 for explanation of symbols and source of data.**

$^{P}$*Alphitonia excelsa* (Fenzl.)Benth.
$^{P}$*A. obtusifolia* Braid

$^{T}$*Colubrina asiatica* (L.)Brongn.

*Cryptandra amara* Sm.
*C. ericoides* Sm.
*C. spinescens* Sieber ex DC.

$^{G}$*Discaria pubescens* (Brongn.)Druce

$^{T}$*Emmenosperma alphitonioides* F.Muell.

*Pomaderris apetala* Labill.
*P. canescens* (Benth.)N.A.Wakef.
*P. discolor* (Vent.)Poir.
*P. elliptica* Labill.
*P. ferruginea* Sieber ex Fenzl
*P. flabellaris* (F.Muell. ex Reissek)J.M.Black
*P. lanigera* (Andrews)Sims
*P. ligustrina* Sieber ex DC.
*P. myrtilloides* Fenzl
*P. obcordata* Fenzl
*P. oraria* F.Muell. ex Reissek
*P. paniculosa* F.Muell. ex Reissek
*P. racemosa* Hook.

*Spyridium eriocephalum* Fenzl
*S. globulosum* (Labill.)Benth.
*S. phyllicoides* Reissek
*S. spadiceum* (Fenzl)Benth.
*S. subochreatum* F.Muell. ex Reissek
*S. vexilliferum* (Hook.)Reissek

*Trymalium floribundum* Steud.
*T. ledifolium* Fenzl
*T. spathulatum* (Labill.)Ostenf.

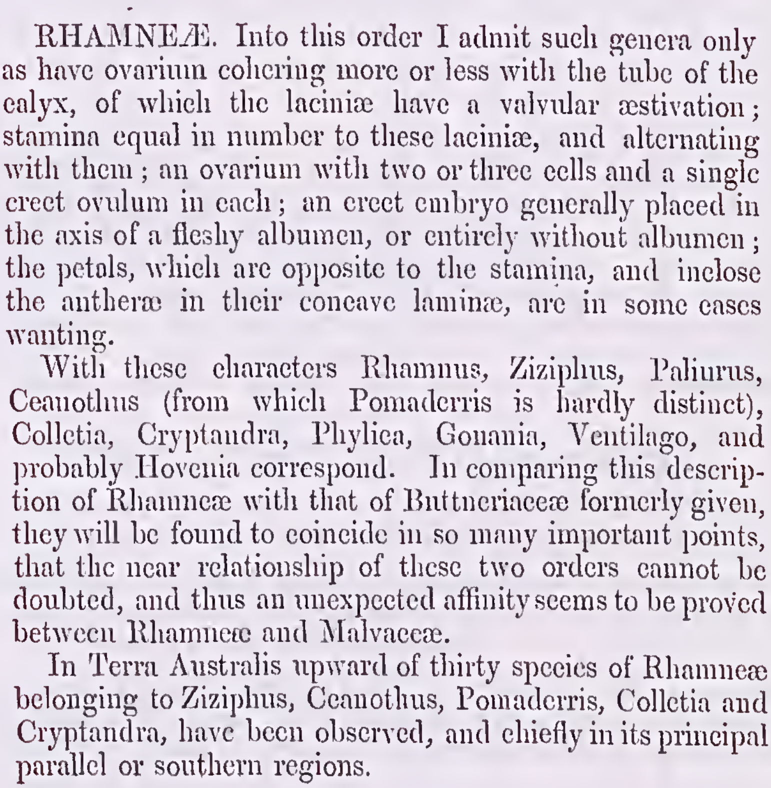
$^{T}$*Ziziphus oenoplia* (L.)Mill.

would have included Brown's treatment of Rhamnaceae and the description of his new species from Australia. Unfortunately, this second volume was never published.

As such, his *General remarks, geographical and systematical, on the botany of Terra Australis,* published in 1814 in the appendix of Matthew Flinders' *A voyage to Terra Australis* (Brown 1814), is the only publication where he expressed his opinion about many of the families not dealt with in his *Prodromus,* including Rhamnaceae. Robert Brown divided the Rhamnaceae of Jussieu into three groups (Grès 1901; Table 2):

(1) The "greater part of the first two sections of the Rhamni of Jussieu" (Brown 1814: 554) formed the newly established family Celastraceae ('Celastrinae' of Brown), which he mainly distinguished from the Rhamnaceae by having flowers with imbricate aestivation of the calyx, and stamens that alternate with the petals.

(2) The third and fourth section of Jussieu's Rhamnaceae, i.e. the genera *Rhamnus, Paliurus, Ziziphus, Ceanothus, Colletia, Hovenia* and *Phylica,* and the genus *Gouania* from section VI made up the redefined family Rhamnaceae ('Rhamneae' of Brown). He also included three genera that had been described after Jussieu, namely *Cryptandra, Pomaderris* and *Ventilago.* Robert Brown's detailed definition of the family is reproduced in Figure 2.



RHAMNEÆ. Into this order I admit such genera only as have ovarium cohering more or less with the tube of the calyx, of which the laciniæ have a valvular æstivation; stamina equal in number to these laciniæ, and alternating with them; an ovarium with two or three cells and a single erect ovulum in each; an erect embryo generally placed in the axis of a fleshy albumen, or entirely without albumen; the petals, which are opposite to the stamina, and inclose the antheræ in their concave laminæ, are in some cases wanting.

With these characters Rhamnus, Ziziphus, Paliurus, Ceanothus (from which Pomaderris is hardly distinct), Colletia, Cryptandra, Phylica, Gouania, Ventilago, and probably Hovenia correspond. In comparing this description of Rhamneæ with that of Buttneriaceæ formerly given, they will be found to coincide in so many important points, that the near relationship of these two orders cannot be doubted, and thus an unexpected affinity seems to be proved between Rhamneæ and Malvaceæ.

In Terra Australis upward of thirty species of Rhamneæ belonging to Ziziphus, Ceanothus, Pomaderris, Colletia and Cryptandra, have been observed, and chiefly in its principal parallel or southern regions.

**Fig. 2.** Robert Brown's definition of Rhamnaceae from his *General remarks, geographical and systematical, on the botany of Terra Australis* (1814). Reproduced from Bennett (1866-1868), vol. 1, p. 26, with permission of the library of the National Herbarium of Victoria (MEL).

(3) The last two sections of Jussieu contained a mixture of genera, which had to be dispersed into a number of different families.

Robert Brown did not state in his *General remarks* nor in any of his published treatises which genera he included in Celastraceae (for collections of his works see Nees von Esenbeck 1825–1834, Bennett 1866–1868). He also gave no indication about the placement of the remaining genera of Jussieu into other families. The only exception was his placement of *Brunia* Lam. in its own family, Bruniaceae Bercht. & J.Presl., in Clarke Abel's *Narrative of a journey in the interior of China* (Brown 1818b).

Since Brown was one of the most influential botanists of his time, he was frequently consulted by others. Table 2 summarises the development of Rhamnaceae classification in Brown's time, from Jussieu (1789) to Endlicher (1836–1840). Brown knew most of the botanists listed in this table and was indeed friends with some of them. Candolle "pestered Brown with questions on the families he was working on for his *Systema* and, later, his *Prodromus*" (Mabberley 1985: 210). Adolphe Théodore Brongniart visited Brown in London during the preparation of his treatment of Rhamnaceae. In the preface to his *Memoire sur la famille des Rhamnées*, the first systematic monograph written on the family, Brongniart expressed his gratitude towards Brown for being allowed access to his herbarium (Brongniart 1826). As such, the treatments of Candolle (1825) and Brongniart (1826) in particular, were most likely written in consultation with Brown. Brown was a friend of Friedrich Wilhelm Heinrich Alexander von Humboldt, and also knew Aimé Jaques Alexandre Bonpland, Karl Siegismund Kunth, Heinrich Gottlieb Ludwig Reichenbach, as well as many other European botanists (Mabberley 1985). It might therefore be appropriate to assume that the data presented in Table 2 also represent Robert Brown's view on Rhamnaceae and Celastraceae.

It is apparent (Table 2) that nearly all genera that Brown, Candolle and Brongniart excluded from Jussieu's Rhamni are still placed in the families to which they were transferred by these authors. The genera included by Brown in the redefined Rhamnaceae are still part of that family. In fact, the definition of Rhamnaceae given by Brown was accepted in all subsequent major treatments of the family (e.g. Reissek 1840, Hooker 1862, Baillon 1875, Weberbauer 1895, and Suessenguth 1953) and is still valid today (e.g. Cronquist 1981, Jones 1993, Mabberley 1997, and Richardson 2000b). Some 19th century German and French authors (e.g. Baillon 1875, 1891, Bischoff 1840) even referred to the family as having been established by Robert Brown.

## Species named by Brown, or from his collections

Robert Brown did not publish from any of his Australian Rhamnaceae collections. There are only two species of Rhamnaceae connected with his name:

*Rhamnus inebrians* R.Br. (*nomen nudum*), which was published without description in James H. Tuckey's *Narrative of an expedition to explore the River Zaire*, in a list of plants collected near the Congo River by Christian Smith (Brown 1818a).

*Cryptandra pyramidalis* R.Br. ex Brongn., a species Brown communicated to Brongniart (1826) presumably from his own collections at the Nepean River and Port Jackson. This is now a synonym of the earlier *Cryptandra spinescens* Sieber ex DC. (Candolle 1825).

Brown's collections were not readily open to other botanists until the 1880's, with the exception of George Bentham (Mabberley 1985; Bentham 1863a), who was given access to them during the preparation of *Flora Australiensis* (Bentham & Mueller 1863–1878). As a result, no other Australian Rhamnaceae species were described from Robert Brown material in the 19th century. In 1925 Kenneth William Braid used Brown

| Jussieu's Rhamnaceae in 1789 | Family classification after Jussieu by Robert Brown's contemporaries<br>Given are the year and author for the first transferral of a genus from Rhamnaceae *sensu* Juss. | Today's classification of Jussieu's genera (APG II 2003) |
|---|---|---|
| I *Staphylea* L.<br>***Celastrus* L.**<br>***Evonymus* L.**<br>***Polycardia* Juss.** | 1825 DC. Staphyleaceae<br>**1814 R.Br. Celastraceae**<br>**1821 Gray Celastraceae**<br>**1825 DC. Evonymeaceae = Celastraceae** | Staphyleaceae<br>**Celastraceae** |
| II ***Cassine* L.**<br>***Myginda* Jacq.**<br>***Rubentia* Comm.**<br>*Goupia* Aublet<br>*Ilex* L.<br>*Prinos* L.<br>*Schrebera* Roxb. | **1824 Spreng. Terebinthaceae = Anacardiaceae**<br>**1825 Kunth Celastraceae**<br>**1825 DC. Evonymeaceae = Celastraceae**<br>* 1840 Endl. Elaeodendreaceae<br>1821 Gray Aquifoliaceae<br>1817 Spreng. Ophiospermaceae = Myrsinaceae<br>1822 Juss. Oleaceae | Goupiaceae<br>Aquifoliaceae<br>Oleaceae |
| III *Mayepea* Aublet<br>*Samara* Sw.<br>***Rhamnus* L.**<br>***Paliurus* Mill.**<br>***Ziziphus* Mill.** | 1810 **R.Br.** Oleaceae<br>1810 **R.Br.** Myrsinaceae | Myrsinaceae<br>**Rhamnaceae** |
| IV ***Ceanothus* L.**<br>***Calletia* Juss.**<br>***Havenia* Thunb.**<br>***Phylica* L.** | **1814 R.Br. Rhamnaceae**<br>**Brown also included the following genera:**<br>***Cryptandra* Sm., *Pomaderris* Labill. and *Ventilaga* Gaertner** | **Rhamnaceae** |
| V *Brunia* Lam.<br>*Bumalda* Thunb. | 1818 **R.Br.** Bruniaceae<br>1825 DC. Staphyleaceae | Bruniaceae<br>Staphyleaceae |
| VI *Aucuba* Thunb.<br>*Carpodetus* Forst.<br>***Gouania* Jacq.**<br>*Plectronia* L.<br>*Votamita* Aublet | 1825 Kunth Caprifoliaceae-Corneae<br>* 1840 Endl. Celastraceae<br>**1814 R.Br. Rhamnaceae**<br>1828 Rchb. Cunoniaceae<br>1828 Rchb. Talineaceae | Aucubaceae/Garryaceae<br>Escalloniaceae<br>**Rhamnaceae**<br>Rubiaceae<br>Melastomataceae |

1790 1800 1810 1820 1830 1840 1850

**Table 2.** The development of Rhamnaceae classification from 1789-1840, compared with today. Genera of Rhamnaceae and Celastraceae are highlighted in bold print. Data from Bennett (1866-1868), Brown (1810), Farr and Zijlstra (1996–2003), Lindley (1846), Mabberley (1993) and Pfeiffer (1873-1874). Brongniart (1826) transferred two genera out of Jussieu's Rhamnaceae without mentioning a new family placement (indicated by an asterisk '*').

specimens to describe *Alphitonia obtusifolia* Braid, using Brown's manuscript name *Ceanothoides obtusifolia* (Braid 1925). Eduard Fenzl described six Australian species (*Pomaderris phylirifolia, P. myrtilloides, P. obcordata, Spyridium eriocephalum, Trymalium majoranifolium, Ziziphus pomaderroides*) from material Ferdinand Bauer gathered during the voyage on the *Investigator* (Fenzl 1837). Whether some of these collections were indeed collected by Bauer and Brown together, and whether some of these collections are also present in Robert Brown's herbarium remains to be seen.

## Conclusion

Robert Brown revolutionised the family concept of Rhamnaceae. He proposed a new definition of the family that is still valid today. Brown's Australian collections played a crucial role in his reassessment of the family concepts of Jussieu. For Rhamnaceae, he mainly gathered specimens of the endemic tribe *Pomaderreae*, nearly all of which were new to science. Although he did not publish names for any of his Rhamnaceae collections, we can assume that these collections, as well as Brown's own field observations on the family during his stay in Australia, would have been quite important for the development of his new definition of the family Rhamnaceae.

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# Apocynaceae: Brown and now

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## Abstract

*Endress, Mary (Institute of Systematic Botany; University of Zurich; Zollikerstrasse 107; 8008 Zurich, Switzerland) 2004. Apocynaceae: Brown and now.* Telopea *10(2): 525–541.* Robert Brown was one of the most important contributors to our understanding of the Apocynaceae sens. lat. He had the prescience to recognise that the asclepiads were more advanced than the Apocynaceae sens. strict., and that together they form a natural series. He chose to split the asclepiads out of Jussieu's Apocineae, and recognised them as a separate family, Asclepiadaceae, on the basis of practicality. Today, following cladistic procedure, the Apocynaceae and Asclepiadaceae are mostly again united into a single family, with five subfamilies recognised: Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae. That Brown's subfamilial classification of the traditional Asclepiadaceae has endured time and cladistics, is a legacy to his sagacity and outstanding skill as a microscopist. Currently, higher level classification in the family is focused mainly on better understanding generic relationships and refining tribal concepts. The great increase in material collected and corresponding increase in the number of known taxa has helped taxonomists to circumscribe natural groups. But the greatest impact has come from the use of phylogenetic methods, especially because they have demonstrated the many instances of parallelisms, which were not recognised as such in traditional classifications. The asclepiads are more homogeneous than are the Apocynaceae sens. strict., and the tribes more clearly defined. Uncertainty still exists as to whether the traditional Asclepiadaceae form a monophyletic group, or if the Periplocoideae are more closely related to the Apocynoideae in the Apocynaceae sens. strict. than they are to the Secamonoideae and Asclepiadoideae. The recognition of four tribes (Fockeeae, Marsdenieae, Ceropegieae and Asclepiadeae) within the Asclepiadoideae is well supported; in addition, great strides have been made in recent years towards a subtribal classification within the tribe Asclepiadeae. Within the Apocynaceae sens. strict., the Rauvolfioideae are especially heterogeneous and have been correspondingly difficult to divide into natural tribes. In the more specialised subfamily, Apocynoideae, on the other hand, genera are much more closely related, and this has proved to be a stumbling block of a different sort for taxonomists, with genera sometimes being differentiated based on whimsical (often 'absence of') characters. In both subfamilies of the Apocynaceae sens. strict., much systematic work remains to be done.

## Introduction

Robert Brown was one of the most influential people in the classification of the Apocynaceae sens. lat. He described more than 40 genera in the family, the great majority of which are still valid today. He segregated the asclepiads out of Jussieu's Apocineae and recognised them as a separate family, which was distinguished by having the pollen coalesced into masses or pollinia and attached to a translator. One of his most significant contributions was his subdivision of the asclepiads into three groups based mainly on the number of pollinia per flower and the type of translator. In Brown's time only 53 genera and some 170 species were known in the Apocynaceae and Asclepiadaceae combined. Today, nearly 200 years later, the Apocynaceae sens. lat. has grown to 395 genera and some 5100 species (Meve 2002, Endress, unpub. data). Brown's three groups are still recognised as the subfamilies Periplocoideae, Secamonoideae and Asclepiadoideae. Since the Apocynaceae sens. strict. are paraphyletic without the Asclepiadaceae, the tendency today is to recognise them as one family. In addition, it is uncertain whether the traditional Asclepiadaceae are a monophyletic group. Many characters have evolved in parallel at various hierarchical levels, the extent of which has only become apparent with the widespread use of phylogenetic analyses, mainly of molecular data.

## Then: Jussieu and Brown

Robert Brown's interest in the Apocynaceae began in 1800, when he was 27 years old. He had just been commissioned by Sir Joseph Banks as naturalist aboard the *Investigator*, the ship captained by Matthew Flinders, which was to circumnavigate Australia (Mabberley 1985). The trip turned into an odyssey of nearly five years. Even before they reached Australia, Brown came into contact with some of the most complex flowers in the asclepiads, when the ship stopped on the way at the Cape of Good Hope in South Africa. One can imagine his fascination with the bizarre Ceropegieae they collected near Table Mountain, which Brown had time to study at length for the next five months until they reached Australia. The Investigator landed first at King George Sound, and then proceeded clockwise around Australia, stopping at various spots along the way (Mabberley 1985). The localities in Australia where Apocynaceae were collected during the *Flinders* Expedition included the Isles of St. Francis (S. A.), Mornington Peninsula and King Island in the the Bass Strait, Port Jackson, Fraser Island, and Moreton Bay (Brisbane). But the great majority were collected in the North, west of Cape York Peninsula, on the mainland as well as islands in the Gulf of Carpentaria.

The chance to see exotic plants in their natural habitat and to study the flowers at length and have them illustrated in great detail by Ferdinand Bauer during the Flinders voyage must have been a great inspiration to Brown. In two important papers – the *Prodromus Florae Novae Hollandiae* (Brown 1810a) and *On the Asclepiadeae* (Brown 1810b) he published on more than 50 genera in Apocynaceae sens. lat., 40 of which were new. In the first of these papers, 14 new genera were described based on plants collected in Australia – ten in Asclepiadeae and four in Apocyneae. Of the 40 new genera Brown described, almost all are still recognised today. (Table 1). *On the Asclepiadeae* (Brown 1810b) contained accounts of a total of 53 genera and 169 species: 38 genera in the Asclepiadeae, and 15 in the Apocyneae. Brown only misplaced one genus, *Cryptolepis*, which has translators so small even he didn't see them, and thus placed it in the Apocyneae, instead of the Asclepiadeae. His *Prodromus* (Brown 1810a) unexpectedly came out a week before *On The Asclepiadeae* (Brown 1810b). So, although the more detailed descriptions are in the latter paper, the type description of the 14 genera indicated in Table 1, as well as those of a number of species (Forster 1991, Forster & Williams 1996, Forster et al. 1996), is in the former.

In *On the Asclepiadeae* Brown (1810b) split the Asclepiadeae out of Jussieu's Apocineae and treated them as separate families. In systematics articles today one often reads that the Apocynaceae is monophyletic if circumscribed in the sense of Jussieu — that is, including the Asclepiadaceae (e.g., Wanntorp 1988, Judd et al. 1994, Civeyrel et al. 1998, Sennblad & Bremer 1996, 2000, Endress & Bruyns 2000, Potgieter & Albert 2001) . Since it was Robert Brown who divided them, one could get the impression that Jussieu was correct, and Brown made a mistake when he separated out the asclepiads as their own family. This is a very naive interpretation of the events. But to understand this, one must take into account what was known about the family as it was circumscribed at the time.

In 1810 the family Apocineae, as circumscribed by Jussieu (1789), contained only 24 genera. These were divided into three groups, based on gynoecium, fruit and seed characters (Table 2). Between his two families Apocineae and Sapotae, Jussieu appended an assemblage of genera, which he described as: genera with an affinity to

**Table 1. Genera of Apocynaceae first described by Robert Brown.**

Alstonia R. Br., Asclepiadeae 64, *nom. cons.* (RAU)
***Balfouria*** R. Br., Prodr. 467, *nom. rej.* = Wrightia R. Br. (APO)
**Wrightia** R. Br., Prodr. 467, (APO)
Holarrhena R. Br., Asclepiadeae 51, (APO)
Isonema R. Br., Asclepiadeae 52 (APO)
Ichnocarpus R. Br., Asclepiadeae 50, *nom. cons.* (APO)
**Parsonsia** R. Br., Prodr. 465, *nom. cons.* (APO)
***Lyonsia*** R. Br., Prodr. 466, *nom. rej.* = Parsonsia R. Br. (APO)
Prestonia R. Br., Asclepiadeae 58, *nom. cons.* (APO)
Cryptolepis R. Br., Asclepiadeae 5B (PER)
Cryptostegia R. Br., Bot. Reg. 5, t. 435 (PER)
**Gymnanthera** R. Br., Prodr. PER
**Secamone** R. Br., Prodr. 464 (SEC)
**Hoya** R. Br., Prodr. 459 (ASC)
**Dischidia** R. Br., Prodr. 461 (ASC)
**Marsdenia** R. Br., Prodr. 460 (ASC)
**Gymnema** R. Br., Prodr. 461 (ASC)
Sarcolobus R. Br., Asclepiadeae 23 (ASC)
Caralluma R. Br., Asclepiadeae 14 (ASC)
Huernia R. Br., Asclepiadeae 11 (ASC)
Leptadenia R. Br., Asclepiadeae 23 (ASC)
Piaranthus R. Br., Asclepiadeae 12 (ASC)
***Microstemma*** R. Br., Prodr. 459 *nom. rej.* = Brachystelma Sims (ASC)
Astephanus R. Br., Asclepiadeae 43 (ASC)
Calotropis R. Br., Asclepiadeae 28 (ASC)
Diplolepis R. Br., Asclepiadeae 30 (ASC)
Ditassa R. Br., Asclepiadeae 41 (ASC)
Eustegia R. Br., Asclepiadeae 40 (ASC)
**Sarcostemma** R. Br., Prodr. 463 (ASC)
Gomphocarpus R. Br., Asclepiadeae 26 (ASC)
Holostemma R. Br., Asclepiadeae 31 (ASC)
Kanahia R. Br., Asclepiadeae 2B (ASC)
Metaplexis R. Br., Asclepiadeae 37 (ASC)
Metastelma R. Br., Asclepiadeae 41 (ASC)
Microloma R. Br., Asclepiadeae 42 (ASC)
Oxypetalum R. Br., Asclepiadeae 30 (ASC)
**Oxystelma** R. Br., Prodr. 462 (ASC)
**Tylophora** R. Br., Prodr. 460 (ASC)
*Daemia* R. Br., Asclepiadeae 39 *nom. rej.* = Pergularia L. (ASC)
Xysmalobium R. Br., Asclepiadeae 27 (ASC)

Names in **bold** are based on plants collected in Australia during Flinders' circumnavigation of the continent. Three-letter acronyms refer to subfamilial position following Endress and Bruyns (2000): APO = Apocynoideae; ASC = Asclepiadoideae; PER = Periplocoideae; RAU = Rauvolfioideae; SEC = Secamonoideae.

Apocyneae, but not lactiferous. Of the five genera included in this assemblage, three (*Strychnos, Fagraea* and *Gelsemium*) are still considered to be among the close relatives of Apocynaceae.

**Table 2. Jussieu's Classification of Apocineae (1789).**

**GROUP 1** (Ovary of 2 free carpels, fruit bifollicular, and seeds without a coma)

1. Vinca L.
2. Matelea Aubl.
3. Ochrosia Juss.
4. Tabernaemontana L.
5. Cameraria L.
6. Plumeria L.

**GROUP 2** (Ovary of 2 free carpels, fruits bifollicular, seeds with a coma)

7. Nerium L.
8. Echites P. Browne
9. Ceropegia L.
10. Pergularia L.
11. Stapelia L.
12. Periploca L.
13. Apocynum L.
14. Cynanchum L.
15. Asclepias L.

**GROUP 3** (Ovary of 2 fused carpels, fruits baccate or rarely capsular, seeds without a coma)

16. Ambelania Aubl.
17. Pacouria Aubl.
18. Allamanda L.
19. Melodinus J.R. & G. Forster
20. *Gynopogon* J.R. Forst. & G. Forst. *nom. rej.* (= Alyxia Banks ex R. Br.)
21. Rauvolfia L.
22. *Ophioxylon* L. *nom. rej.* (= Rauvolfia L.)
23. Cerbera L.
24. Carissa L.

In Jussieu's classification there is a major split between Group 1 and 3 on the one hand, and Group 2 on the other. The taxa in Groups 1 and 3 almost always have corolla lobes contorted to the left, anthers free from the style-head and non-comose seeds. They constitute the Rauvolfioideae in modern classifications. The taxa in Group 2, in contrast, almost always have corolla lobes contorted to the right, anthers postgenitally united with the style-head (forming a gynostegium) and comose seeds. They represent all the other subfamilies in modern classifications: Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae.

Figure 1 shows Jussieu's three Groups where they would come out based on current information. Whereas Group 2 is natural, Groups 1 and 3 are intermixed and thus artificial. It is interesting that Jussieu included *Matelea* in Group 1. This genus is clearly a member of Group 2, and its inclusion elsewhere suggests that the seed depicted in Aublet (1775) belonged to one of the riparian species adapted to water dispersal, in which the seed coma has been lost.

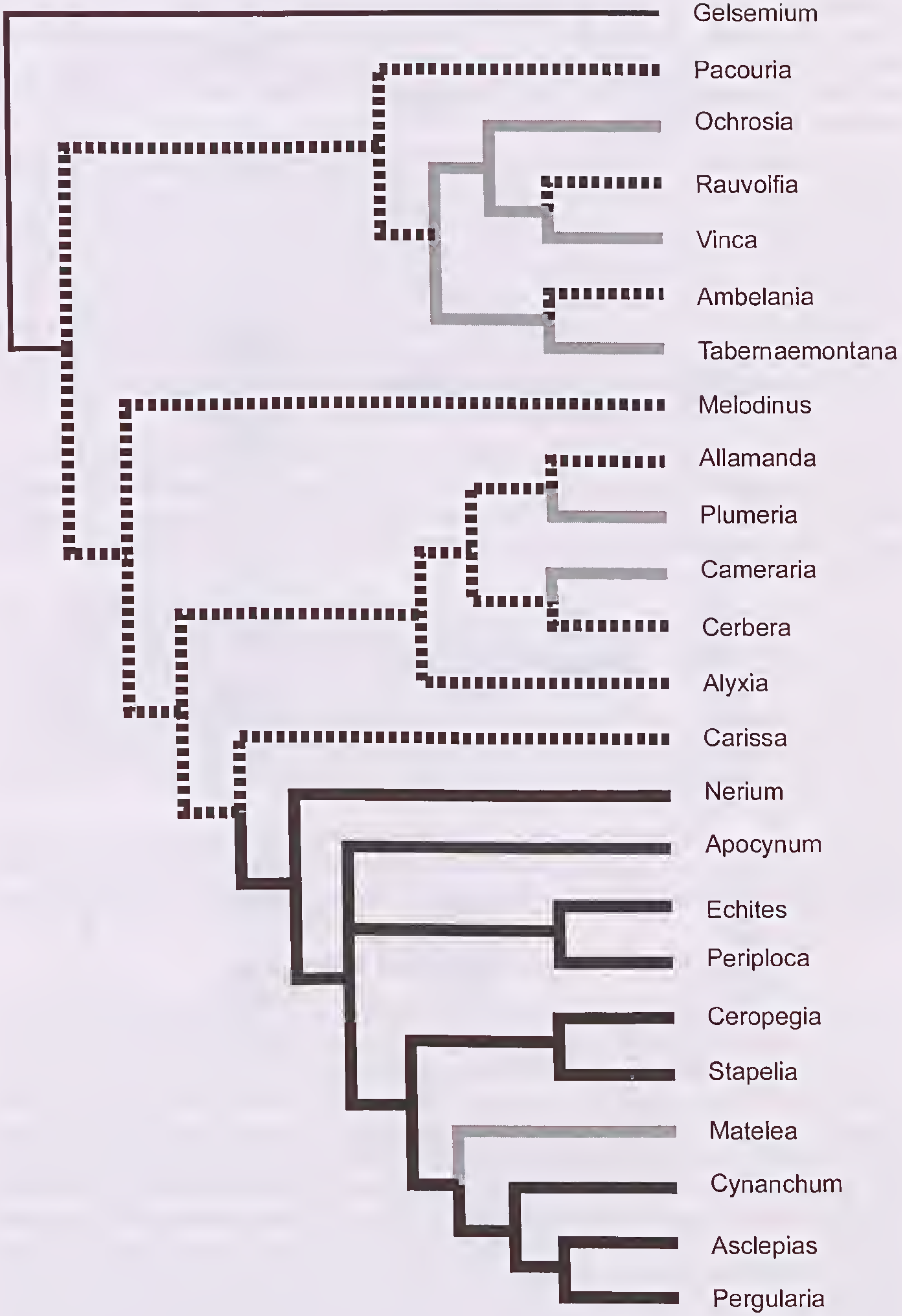

**Fig. 1.** Jussieu's three groups of Apocineae, with the taxa shown where they would come out based on current data. Group 1: grey; Group 2: black; Group 3: interrupted line; outgroup: thin black line.

Brown was fascinated by complex flowers, so he concentrated on Jussieu's Group 2, which contains the most complicated flowers in the family. He was an outstanding microscopist, and did meticulous studies of various developmental stages of the flowers of *Asclepias*. He was the first to realise that the pollinia are produced in the anthers, and only secondarily come into contact with the translator produced by the style-head (Brown 1833). Up until then, it was believed that the pollinia were produced by the style-head.

Brown realised that there were substantial differences among the genera included in Jussieu's group 2. His keen eye discerned and recognised the significance of the different types of pollen presentation and transfer in this assemblage of taxa, and he used this knowledge to order them in a logical fashion. First he excluded the genera that didn't belong, and then elevated Group 2 to a separate family, which he called the Asclepiadeae. He did this based on what he called the'essential character' of the Asclepiadeae: that they have pollen coalesced into masses (pollinia) and that these pollinia are attached to a translator, whereas in the Apocyneae pollen is in single grains. (Definitions for the terminology of some of the key characters found only in Apocynaceae sens. lat. is given in Endress 1994, 2003.)

Brown's greatest contribution to the family, however, was his subfamilial classification within the asclepiads. Because of his careful, detailed studies of the flowers, he had the insight to recognise the meaningful characters to define his infrafamilial groups.The result was a natural classification, recognising three groups, which are given subfamilial status today (Fig. 2):

The 'Asclepiadeae verae'. Pollen is in pollinia. Each anther has two pollen sacs and thus two pollinia. One pollinium each from a theca of two adjacent anthers are attached to a clamp-like translator. This group is known today as the Asclepiadoideae.

An unnamed group, which contained only the genus *Secamone*. Pollen is in pollinia. Each anther has four pollen sacs and thus produces four pollinia. Two pollinia each from a theca of two adjacent anthers are attached to a clamp-like translator. This group is known today as the Secamonoideae.

The 'Periploceae'. Pollen is in tetrads (or rarely in pollinia). Each anther has four pollen sacs. The tetrads (or two pollinia each) from a theca of two adjacent anthers are shed onto a sticky spoon-like translator. This group is known today as the Periplocoideae.

## Now: Grades, Clades and Monophyly

Today, in the Apocynaceae sens. lat. (the Apocynaceae and Asclepiadaceae combined), we estimate there are around 395 genera and some 5100 species. This is more than seven times the number of genera and 30 times the number of species known to Brown in 1810. Despite this significant increase in the number of recognised taxa, the names of most of the genera of Apocynaceae described by Brown are still valid. Of the 40 new genera described by him, only four have been put into synonymy to date (see Fig 1). More significant, however is the endurance of his subfamilial classification within the asclepiads. Today, more than 200 years later, the same three groups, defined using Brown's criteria, represent monophyletic groups and are given subfamilial status. Fig. 3 shows a DNA-generated tree, based on the cholorplast gene *mat*K (taken from Fishbein 2001) with Brown's subfamilies Periplocoideae, Secamonoideae, and Asclepiadoideae mapped on. Brown's accuracy in recognising these three main groups within the asclepiads is quite remarkable, especially when one takes into account the microscope he used at the time, and that he had so few specimens upon which to base his subfamilies.

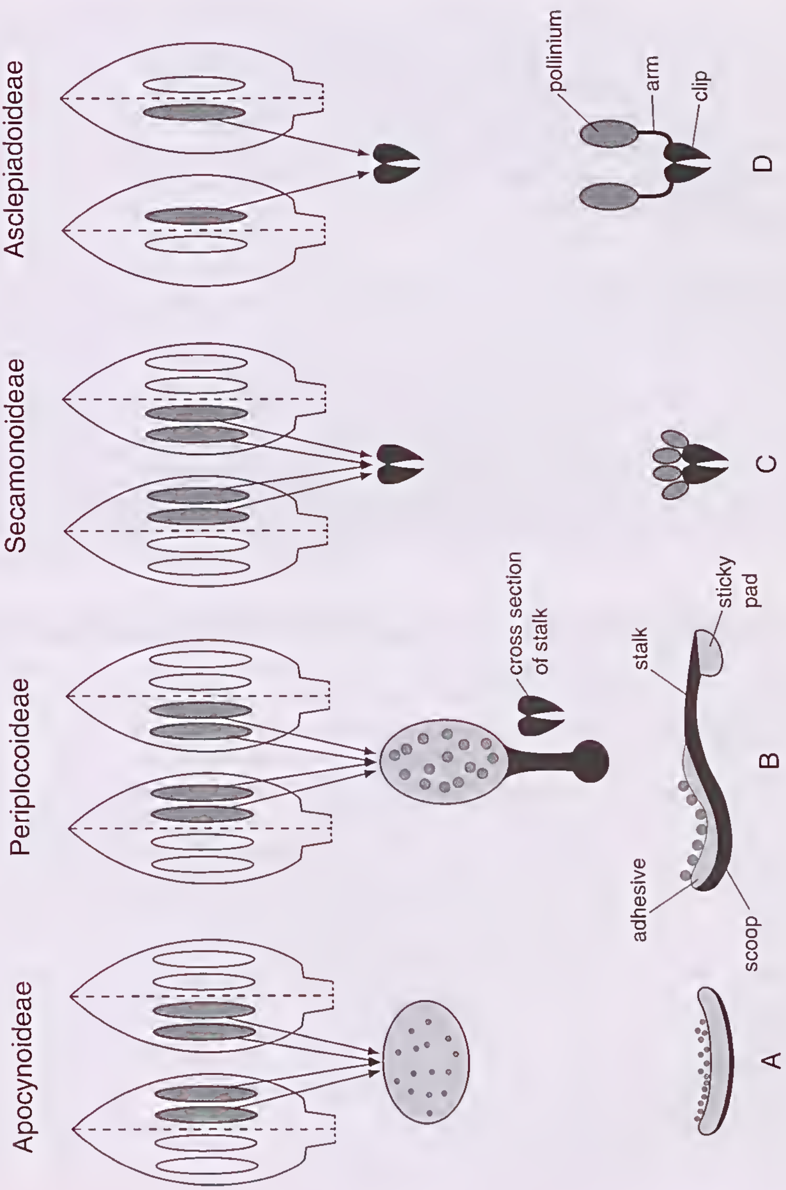

**Fig. 2.** Key characters of the three subfamilies of Robert Brown's Asclepiadeae: translators and pollen masses. Apocynoideae (Apocynaceae sens. strict.) are also shown for comparison. Transition series does not necessarily imply straight-line evolution, only evolutionary stages. A, Apocynoideae: the pollen grains of one theca (containing two pollen sacs) each of two adjacent anthers are shed onto an undifferentiated glob of adhesive situated between two anthers; B, Periplocoideae: the pollen tetrads of one theca (containing two pollen sacs) each of two adjacent anthers is shed onto the adhesive-lined scoop of a morphologically differentiated translator; C, Secamonoideae: the pollen content of one theca (containing two pollen sacs) each of two adjacent anthers is coalesced into pollinia, which become stuck to the dorsal surface of a clip-type translator; D, Asclepiadoideae: the pollen content of one theca (containing one pollen sac) each of two adjacent anthers is coalesced into pollinia, which become stuck to a slender arm attached to the clip-type translator. Pollen: dark grey; black: secretions that are rigid at maturity; light grey: secretions that remain frothy, viscid or tacky at maturity. This figure was first published in Endress (2003), and is reproduced here with permission.

The most dramatic changes in our concepts of the family have occurred within the past ten years, however, and have been brought about by the boom of cladistics and phylogenetic reconstruction, which have changed forever the way we do systematics. Nowadays we strive for monophyletic groups in classification. Since the Apocynaceae sens. strict. are paraphyletic without the Asclepiadaceae, most specialists in the group now unite them into one family, as this is the most straightforward way to achieve a monophyletic group (Goyder 1999, 2001, Endress & Bruyns 2000, Endress & Stevens 2001, Endress 2003). The most recent unified classification is that of Endress and Bruyns (2000), which recognised five subfamilies. This classification was slightly modified by recognition of the tribe Fockeeae by Endress and Stevens (2001) (Table 3): Brown's subfamilies Periplocoideae, Secamonoideae and Asclepiadoideae from the traditional Asclepiadaceae, and in Apocynaceae sens. strict., Rauvolfioideae and Apocynoideae. These last two subfamilies were already recognised in the Apocynaceae by Schumann (1895), although he used the names Plumerioideae and Echitoideae for them, respectively. The main characters used to circumscribe the two subfamilies in the classification are the same as those used by Schumann (1895), and correspond to the major split already present, as mentioned above, in the classification by Jussieu (1789). Thus, there is nothing revolutionary about the circumscription of the subfamilies in the classification by Endress and Bruyns.

**Table 3. Classification following Endress and Bruyns (2000), as modified in Endress and Stevens (2001).**

APOCYNACEAE sens. lat.
RAUVOLFIOIDEAE Kostel.
Alstonieae G. Don
Vinceae Duby
Willughbeieae A. DC.
Tabernaemontaneae G. Don
Melodineae G. Don
Hunterieae Miers
Plumerieae E. Mey.
Carisseae Dumort.
Alyxieae G. Don
APOCYNOIDEAE Burnett
Wrightieae G. Don
Malouetieae Müll.-Arg.
Apocyneae Rchb.
Mesechiteae Miers
Echiteae Bartl.
PERIPLOCOIDEAE R. Br. ex Endl.
SECAMONOIDEAE Endl.
ASCLEPIADOIDEAE R. Br. ex Burnett
Fockeeae Kunze, Meve & Liede
Marsdenieae Benth.
Ceropegieae Orb.
Asclepiadeae (R. Br.) Duby

Another thing that has changed is that the monophyly of the traditional Asclepiadaceae (the Periplocoideae, Secamonoideae and Asclepiadoideae as a natural unit) is no longer indisputable. The tree shown in Fig. 3 includes only two taxa of the Apocynaceae sens. strict., neither of them from the tribe Echiteae (a tribe of the higher Apocynoideae), which some recent analyses (e.g. Sennblad & Bremer 2000) suggest may include some of the closest relatives of the asclepiads. Based on results from the taxa analysed to date, in order to achieve a monophyletic Asclepiadaceae like that shown in Fig. 3, one has to 'not include' critical taxa of the higher Apocynoideae and/or further manipulate the data.

When critical taxa from higher Apocynoideae (Apocyneae and/or Echiteae) are included in the analysis, monophyly of the traditional Asclepiadaceae is equivocal. Figure 4 is a simplified reconstruction of a tree published by Sennblad and Bremer (2000) based on *rbcL* data, which included 77 genera: 53 Apocynaceae and 24 Asclepiadaceae. The relationships shown here are from a combinable component consensus tree from a successive weighting analysis. Noteworthy is that *Periploca* and *Mondia*, both members of the Periplocoideae, form a clade together with *Parsonsia* and *Prestonia*, two genera of Echiteae (Apocynoideae). In addition, *Baissea*, a member of Apocyneae, another tribe of the higher Apocynoideae, is intercalated between Secamonoideae and Asclepiadoideae.

Without successive weighting, relationships among the subfamilies are less clear-cut. The summarised form of the strict consensus tree from the unweighted parsimony analysis from two studies based on cpDNA is shown in Fig. 5. Tree A shows the strict consensus of the tree in Fig. 4 without successive weighting. Except for the basalmost genera, all Apocynoideae, Secamonoideae and Asclepiadoideae form a polytomy (modified from Sennblad & Bremer 2000). Tree B is a summarised form of the strict consensus tree from the unweighted parsimony analysis published by Potgieter and Albert (2001) based on the *trn*L intron and *trn*L-F spacer and six propagule characters. This study is the largest molecular analysis of Apocynaceae sens. lat. to date, and included 117 genera: 72 Apocynaceae sens. strict. (including several taxa of the crucial higher Apocynoideae) and 45 Asclepiadaceae in the traditional sense. *Wrightia* is at the base of the Apocynoideae, and sister to all other Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae. The bulk of the Apocynoideae form a polytomy, in which the Periplocoideae is nested. The crown clade is composed of another group of genera from the tribe Apocyneae (*Urceola, Apocynum, Beaumontia, Trachelospermum* and *Chonemorpha*), which is sister to a clade composed of two subclades: one containing the genus *Baissea*, and the other all the Secamonoideae + Asclepiadoideae (modified from Potgieter & Albert 2001). Results such as those by Sennblad and Bremer (2000) and Potgieter and Albert (2001) are indications that the systematic position of Periplocoideae is still very much unresolved. Nor do we know how to interpret the position of *Baissea*.

The relationship of Secamonoideae to Asclepiadoideae and the relationships among tribes currently recognised in the Asclepiadoideae can be seen in Fig. 3. Secamonoideae, which contains only eight genera (Klackenberg 2001) and is not divided into tribes, comes out fairly consistently as sister to the Asclepiadoideae, if taxon sampling is sufficient (see e.g. Potgieter & Albert 2001). If, with more thorough sampling, it is shown that the unexpected position of *Baissea* in recent analyses is an artifact, Secamonoideae could be reduced to a tribe of the Asclepiadoideae. Based on cladistics alone, there would be nothing to refute this. Considering the degree of the differences in floral structure, however, it is questionable whether including Secamoneae as a tribe of Asclepiadoideae is desirable.

Another thing that has changed significantly since Brown's time, is that we now have a better idea of the tribal relationships within the subfamily Asclepiadoideae. This is

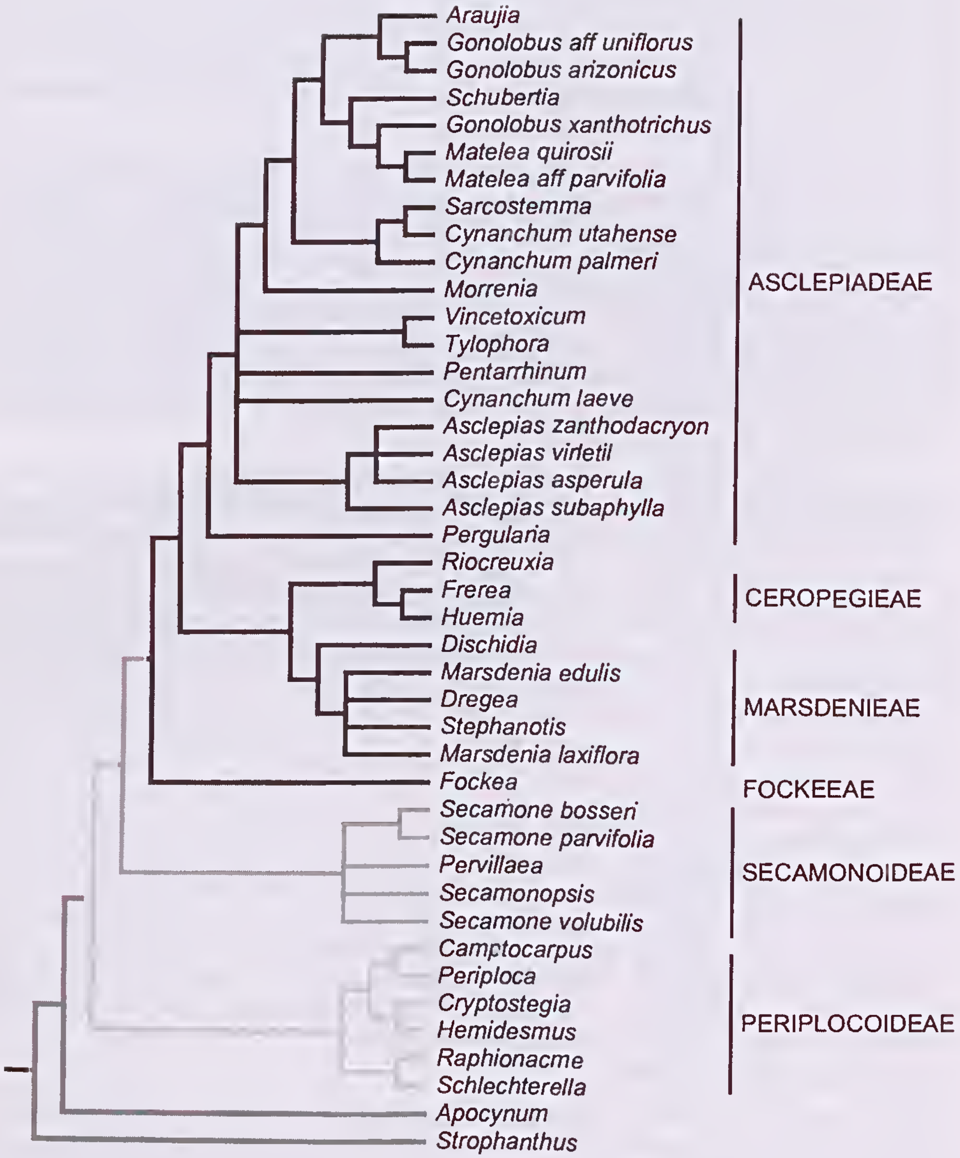

Fig.3. Tree based on maximum parsimony analysis of partial and complete *mat*K sequences published in Fishbein (2001), with Robert Brown's three subfamilies mapped onto it. Periplocoideae: light grey; Secamonoideae: medium grey; Asclepiadoideae, showing the tribes Fockeeae, Marsdenieae, Ceropegieae and Asclepiadeae: black; outgroup (Apocynoideae): dark grey. The traditional Asclepiadaceae is monophyletic.

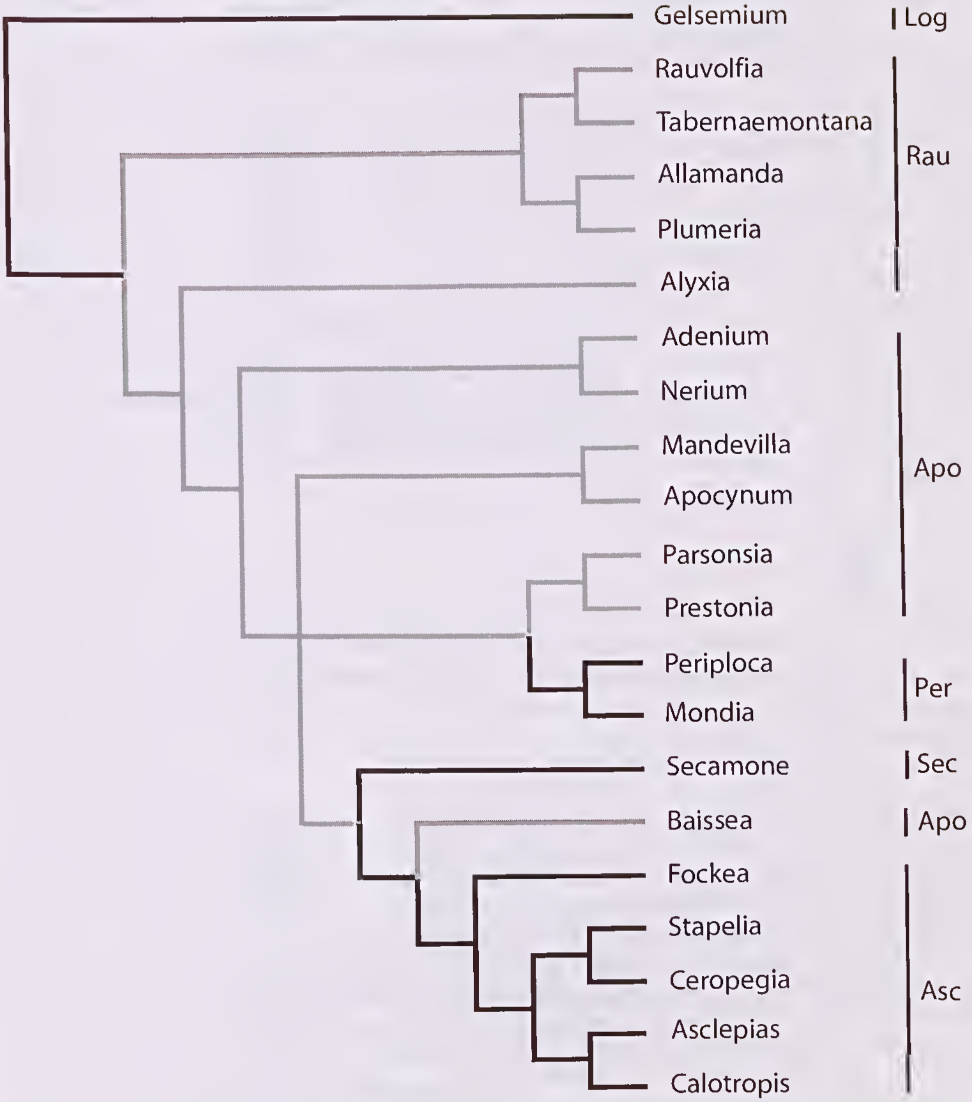

Fig. 4. Simplified reconstruction of the phylogenetic tree of Apocynaceae sens. lat. by Sennblad and Bremer (2000) based on the cholorplast gene *rbc*L with *Gelsemium* (Loganiaceae) as outgroup. 1) The three clades at the apex form an unresolved polytomy; 2) Periplocoideae are sister to *Parsonsia* and *Prestonia* of tribe Echiteae, Apocynoideae, rather than to Secamonoideae + Asclepiadoideae, suggesting that Periplocoideae and Secamonoideae + Asclepiadoideae may not be a natural group; 3) *Baissea* of tribe Apocyneae, Apocynoideae is intercalated between Secamonoideae and Asclepiadoideae, questioning monophyly even within Secamonoideae + Asclepiadoideae. Traditional Apocynaceae: grey; traditional Asclepiadaceae: black.

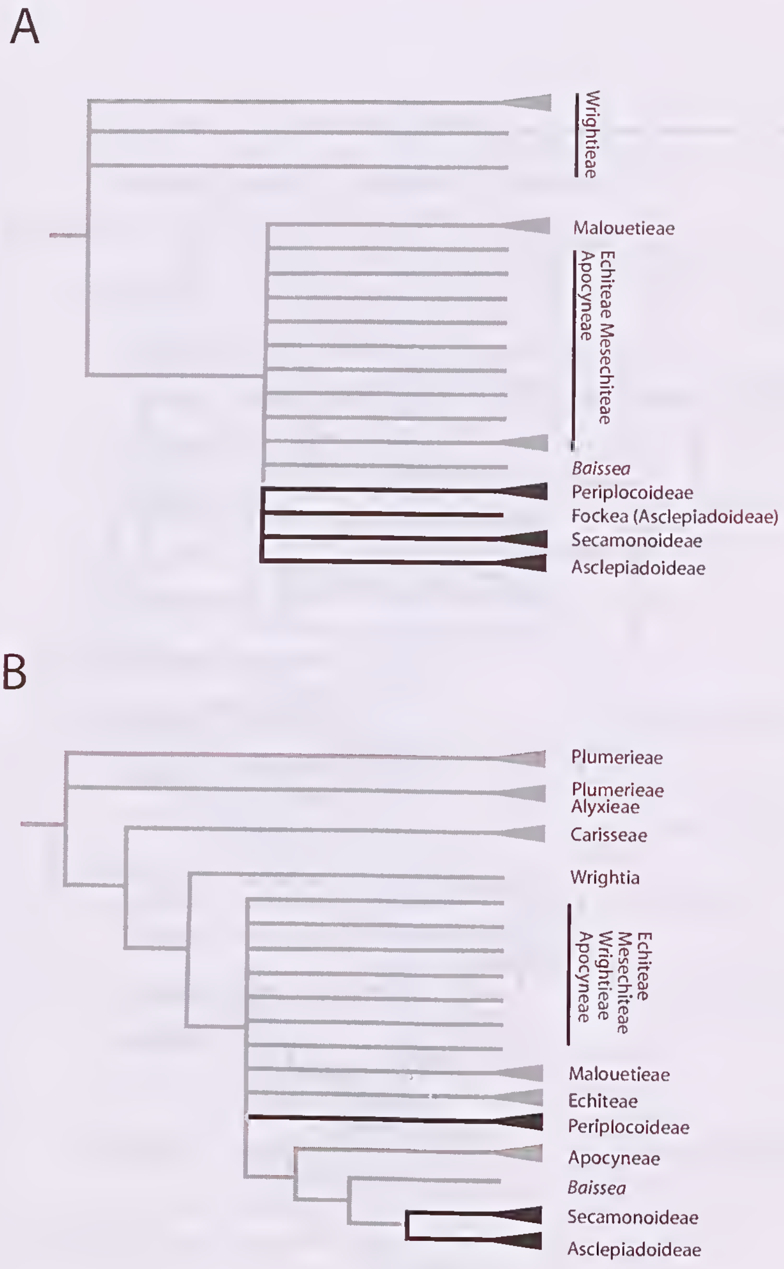

**Fig. 5.** Summarised form of the strict consensus tree from the unweighted parsimony analysis from two cpDNA studies. **A.** Tree based on *rbc*L. The Rauvolfioideae (lower part of the tree) is not shown. Except for the basalmost genera, all Apocynoideae form a polytomy, in which Periplocoideae is nested (modified from Sennblad & Bremer 2000). **B.** Tree based on the *trn*L intron and *trn*L-F spacer and six propagule characters. Except for three of the more advanced tribes of the Rauvolfioideae, the lower part of the tree is not shown. Except for *Wrightia*, at the base, the bulk of the Apocynoideae form a polytomy, in which the Periplocoideae are nested. The crown clade is composed of another group of genera of the tribe Apocyneae, which is sister to the genus *Baissea* on the one hand and the Secamonoideae + Asclepiadoideae on the other (modified from Potgieter & Albert 2001). Traditional Apocynaceae: grey; traditional Asclepiadaceae: black.

partly due to the additional material that has accumulated since then. But the bulk of the new information on relationships among genera is due to the use of DNA data, especially because it has repeatedly revealed convergences that were not realised as such in earlier classifications. This has led to a much more natural delimitation of tribes. Within the Asclepiadoideae four tribes are currently recognised: Fockeeae, Marsdenieae, Ceropegieae and Asclepiadeae (Endress & Stevens 2001). Fockeeae are the basalmost tribe. They contain only two genera – *Fockea* and *Cibirhiza* – and are sister to all the rest of the Asclepiadoideae. The basal position of the Fockeeae is well supported by both morphological as well as molecular data (Kunze 1993, 1994, 1996; Civeyrel et al. 1998, Potgieter & Albert 2001, Verhoeven et al. 2003). The Fockeeae exhibit some unusual ('primitive') features, not found in other Asclepiadoideae, but which are more reminiscent of Secamonoideae (Kunze et al. 1994, Verhoeven et al. 2003). Fockeeae are followed by a major dichotomy, in which all other taxa of the Asclepiadoideae are included. One clade is composed of the Marsdenieae and Ceropegieae (Stapelieae in earlier classifications); the other is comprised of only the large tribe Asclepiadeae (including the taxa, formerly treated as a separate tribe – Gonolobeae) (Bruyns & Forster 1991, Sennblad & Bremer 2000, Fishbein 2001, Potgieter & Albert 2001). Within the ca. 140 currently recognised genera of the Asclepiadeae, work towards a subtribal classification continues to be refined, especially by Sigrid Liede and collaborators. Currently some six subtribes are recognised, though at present taxonomy in the tribe is in a state of flux, and there remains much to do (Liede 1996, 1997, 2001; Liede & Täuber 2000; Liede et al. 2002).

Currently, our ideas about the direction of evolution within the Asclepiadoideae are more or less the reverse of Schumann's (1895), who considered the taxa with pendant pollinia to be less specialised, whereas those with erect pollinia were said to be the 'crowning glory' of the entire family. This interpretation was questioned as early as 1922 by Demeter, based on detailed floral developmental studies of various taxa, and later by Safwat (1962) and Wanntorp (1988). All tribes except Asclepiadeae have erect pollinia. Pendant pollinia are interpreted as an apomorphy and derived state of the tribe Asclepiadeae.

The systematic history of the Apocynaceae sens. lat. is characterised by major categories having repeatedly been based mainly on one or two, easy-to-determine characters – even when other characters suggested that this might not be the best choice. In the Asclepiadoideae, the orientation of the pollinia and the type of corona are the two most important characters that have been used to define tribes (Schumann 1895, Woodson 1941). We have been exceedingly lazy – continuing to use the easy characters, even after there were hints that they might result in artificial groups. A good example of how this illogical clinging to simplistic characters has led us astray is the genus *Astephanus*. Basically, this genus came to be defined by the lack of a staminal corona. As Liede (2001) demonstrated, this condition has apparently arisen at least twice independently in the tribe Asclepiadeae alone. Similarly, *Tylophora* was long included in the Marsdenieae because of the orientation of the pollinia, even though there were other morphological characters, which suggested that it was better placed near *Vincetoxicum* in the Asclepiadeae (Kunze 1996, Liede 1996, Swarpuanandan et al. 1996), a position which has since been confirmed with molecular data (Sennblad & Bremer 2000, Civeyrel & Rowe 2001, Fishbein 2001, Liede 2001).

Within the Apocynaceae sens. strict., the Rauvolfioideae (Plumerioideae in earlier classifications) has almost always been considered to be the more more ancestral, and the Apocynoideae (Echitoideae in earlier classifications) the more derived subfamily. Only Woodson (1930), basing his hypothesis on the assumption that apocarpy is more primitive than syncarpy, considered the Rauvolfioideae to be the more derived subfamily. Morphological characters within the Apocynaceae sens. strict. are much more heterogeneous than in the asclepiads. In the basalmost subfamily, Rauvolfioideae, earlier classifications were almost always based mainly on a few easy to see fruit and seed characters. If the fruit was an indehiscent drupe the plant belonged to the Alyxieae; if it is was an indehiscent berry it was a Carisseae; and if it was dehiscent and had winged seeds, it was a Plumerieae (Pichon 1948, 1949, Leeuwenberg 1994). All of these tribes have now been shown to be polyphyletic (Potgieter & Albert 2001). Selective pressure for dispersal optimisation, means that ovary walls, and even more so, seed surfaces, are evolutionarily remarkably plastic, making them especially poor choices as defining characters for higher taxonomic categories. In addition, syncarpy and thus the taxa with indehiscent berry fruits ('Carisseae') were considered to be 'primitive' in all traditional classifications (e.g. Schumann 1895, Pichon 1948, Leeuwenberg 1994). But results from molecular analyses suggest that the basalmost taxa are more likely those with dehiscent follicles and wind-dispersed seeds (Endress et al. 1996, Potgieter & Albert 2001; but see also Sennblad & Bremer 2000), whereas *Carissa* and *Acokanthera* come out as the most advanced taxa of the Rauvolfioideae in the analysis by Potgieter and Albert (2001). The 'Carisseae' as circumscribed by e.g. Pichon (1948) or Leeuwenberg (1994) are dispersed among three clades in recent molecular analyses (Sennblad & Bremer 2000, Potgieter & Albert 2001), and this division has been followed through in the classification by Endress & Bruyns (2000), with the taxa distributed among four recircumscribed tribes: Willughbeieae, Melodinae, Hunterieae, and Carisseae.

In the more evolved subfamily of the Apocynaceae sens. strict., Apocynoideae, the situation is similar. Results of a combined morphological-molecular analysis (Sennblad et al. 1998) suggest that within the subfamily all the tribes as circumscribed by Leeuwenberg (1994) are not monophyletic. Where morphological differences supported the molecular findings, these were followed through in the classification of Endress and Bruyns (2000) by recognition of the tribe Malouetieae. Because the study of Sennblad et al. (1998) focused only on the basal region of the Apocynoideae, relationships among and within the more advanced tribes of the Apocynoideae (Apocyneae, Mesechiteae, and Echiteae) remain unresolved. To date, all molecular phylogenies of Apocynaceae sens. lat. have been based on chloroplast DNA (*rbc*L, *mat*K, *trn*L), either singly, combined, or in conjunction with a morphological dataset. The two largest studies in the family (Sennblad & Bremer 2000, Potgieter & Albert 2001) suggest that these genes are evolving too slowly to be used alone for sorting out relationships within Apocynoideae. The next logical step is to sequence nuclear genes and combine them with the data from chloroplast DNA. Independent studies, based on previously untried genetic regions, as well as morphological characters, are currently underway, which we hope will help resolve the relationships within the Apocynoideae, including the systematic position of the Periplocoideae. Until more reliable data are available, no satisfactory tribal circumscription within the Apocynoideae is possible.

Even though the tribes within them continue to be refined, both Rauvolfioideae and Apocynoideae are a grade, rather than a clade. Based on current phylogenetic reconstructions, in order to make monophyletic groups in the Apocynaceae sens. strict., one would have to describe a number of additional subfamilies (Sennblad & Bremer 1996, Civeyrel et al 1998, Potgieter & Albert 2001). But to do so at this point would be premature. There are still several areas where relationships are uncertain or where branch support is too low to be useful as the basis for a classification. Once additional genetic regions have been analysed, we should have a better idea of how to proceed. Especially when things are in such a state of flux, it seems best to improve the classification stepwise, as sufficient support is available. The unconventional classification suggested by Sennblad and Bremer (2002), which includes 21 tribes and four rankless taxa, is thought-provoking, if perhaps not palatable for botanists 'in the trenches'.

## Conclusions

1. Robert Brown had a major impact on the classification of the Apocynaceae, especially in the asclepiads. Most of the new genera he described are still in use today. Due to his extraordinary skill as a microscopist and unquenchable desire to understand how complex flowers function, he was able to distinguish the meaningful characters and thus established a subfamilial classification for the traditional Asclepiadaceae that has stood the test of time and cladistics.

2. There has been a manifold increase in the number of known species in the family in the past 200 years. New species are described regularly, and new genera are still being discovered in the tropics of both the Old and New World (Forster 1990, Forster et al. 1997, Zarucchi 1991, Middleton 1995, 1996, Morales 1999, Bruyns 2000). The most profound changes in the family since Brown's time, however, are due to the molecular revolution, which brought to light convergences of characters strongly influenced by ecological factors, which were not obvious using traditional methods. This has resulted in the recircumscription of most tribes in the family, in some cases radically so.

3. We've still got a lot of work to do! Additional studies need to be done in order to come up with satisfactory tribal and subtribal limits in the Rauvolfioideae, Apocynoideae and Asclepiadeae, and we need to explain the anomalous placement of *Baissea* and the Periplocoideae, as well as refine groupings within the Asclepiadeae. When selecting taxa for studies to test the monophyly of the traditional Asclepiadaceae, a sufficient number of taxa of the higher apocynoid tribes should be included in order to make the results meaningful. And authors should have the courage to show the strict consensus tree from the unweighted parsimony analysis. A monophyletic Asclepiadaceae has little meaning if it was only achieved by leaving out critical taxa.

4. Finally, did Robert Brown err when he segregated the Asclepiadeae out of Jussieu's Apocyneae? In the Introduction to *On The Asclepiadeae* he explains his reasons for doing so: "It is true that to the experienced observer, it may still be practicable to refer the greater part, perhaps the whole, of these plants to their proper places in a natural series; but it is, I apprehend, no longer so, to distinguish the two orders by definitions derived from the usual source. ... As, however, both of these families are already too extensive, it becomes expedient rather to attempt their subdivision into smaller groups... .' Thus it is clear that Brown was aware that the Apocyneae and Asclepiadeae form a natural series, but he chose to divide them, because he felt it the more practical way to handle the group. His only mistake, then, was that he was not a cladist. But since he wrote these words more than 100 years before cladistics was invented, I think one can forgive him this indiscretion.

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# Gesneriaceae and Scrophulariaceae: Robert Brown and now

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## Abstract

*Weber, Anton (Institute of Botany, University of Vienna, Rennweg 14, A–1030 Vienna, Austria) 2004. Gesneriaceae and Scrophulariaceae: Robert Brown and now.* Telopea *10(2): 543–571.* Though Robert Brown seems to have seen only one or two species of Gesneriaceae in the field, he understood the family admirably well and had an everlasting influence on it. Apart from contributing to Wallich's 'Plantae Asiaticae Rariores', he prepared a most significant treatment of the family for the 'Plantae Javanicae Rariores' (Bennett & Brown 1838–1852). This treatment appeared as a preprint, entitled 'On Cyrtandreae', in 1839. It was based on Thomas Horsfield's collections from Java and Sumatra, but included also collections from elsewhere. From the two new genera established, only one (*Monophyllaea*) survived, the other (*Loxocarpus*) has been recently reduced to sectional level (*Henckelia* sect. *Loxocarpus*, Weber & Burtt 1998b). The species listed or described as new are briefly surveyed. Brown conceived the family Gesneriaceae in its modern circumscription and presented convincing arguments for the union of the paleotropical Didymocarpaceae D.Don (1822) = Cyrtandraceae Jack (1823) with the neotropical Gesneriaceae. The justification for the union and the monophyly of the family has been confirmed by recent molecular systematic studies. Today, the family includes over 140 genera and over 3500 species. Previous and current classifications are compared, and the four major groups are briefly reviewed using informal names: Coronantheroid, Gesnerioid, Epithematoid and Didymocarpoid Gesneriaceae.

Regarding Scrophulariaceae, Brown's most significant contribution is the treatment of the family in his 'Prodromus florae Novae Hollandiae ...' (1810). This was based on material collected by Brown himself on Flinders' expedition to Australia 1801–1805. Five of the six new genera established there are still in use. There is still much debate on the circumscription of Scrophulariaceae. Partly it is conceived in a very wide sense, including the parasitic Orobanchaceae, and encompassing over 300 genera and 5800 species, yet, based on molecular data, partly it is split into some eight independent families.

## Gesneriaceae

Robert Brown dealt with Gesneriaceae on two occasions. Firstly, he contributed to Wallich's 'Plantae Asiaticae Rariores' in that he permitted Wallich to publish some observations and manuscript notes. Secondly, Brown wrote up the Gesneriaceae for the 'Plantae Javanicae Rariores'. This treatment was published as a separate issue, entitled 'On Cyrtandreae', in 1839. The most significant aspect of this treatment is that Brown formally united the Old World Cyrtandraceae with the New World Gesneriaceae and thus gave the family its present shape. The details are given below.

### The early history of Gesneriaceae

Gesneriaceae was one of the last major families to take on its present form. It was first recognised by Jussieu (1806, quoting Richard), but was formally established much later, by De Candolle (1816)[1]. This group comprised only neotropical plants, namely *Gesneria* and allies. In the eighteen twenties, two new Old World families, Didymocarpaceae (Don 1822, 'Didymocarpeae') and Cyrtandraceae (Jack 1823, 'Cyrtandreae') were established in order to accommodate plants from Asia and the

Pacific. Don (1822, 1825) worked essentially with the plants collected by Nathaniel Wallich and collaborators in Nepal. The family name was based on the genus *Didymocarpus* Wall., which name (and a description) had appeared in a note published by F. Hamilton in 1819. D.Don described the first seven species in 1825. This account comprised two additional genera: *Lysionotus* D.Don (1 sp.) and *Trichosporum* D.Don (the earlier name for *Aeschynanthus* Jack, see below, 2 spp.).[2] William Jack (1823) collected in Penang and Sumatra. When establishing the 'Cyrtandreae' as 'a new natural order of plants' (1823), he recognised four genera: *Cyrtandra* J. & G. Forst. (11 spp.), *Didymocarpus* Wall. (7 spp.; now distributed over four genera: *Didissandra* C.B. Clarke, *Didymocarpus* Wall. s. str., *Chirita* [Buch.–Ham. ex] D.Don, and *Henckelia* Spreng.; Weber & Burtt 1998a,b), *Loxonia* Jack (2 spp.), and *Aeschynanthus* Jack (antedated by *Trichosporum* D.Don, but widely adopted and conserved later; 2 spp.).

According to Burtt (1998a), Don's paper setting up Didymocarpaceae was read to the Wernerian Society in Edinburgh on 26 January 1822 and was published in July 1822; Jack's paper was read at the Linnean Society of London on 7 May 1822, but not published till May 1823. It is clear, therefore, that Don's name Didymocarpaceae has priority over Jack's Cyrtandraceae, yet it was Jack's name that was adopted by those who kept the Old World plants distinct from the American Gesneriaceae, most notably by De Candolle (1845).

In 1829 Martius compared the New World Gesneriaceae with the Old World Cyrtandraceae (incl. Didymocarpaceae). He was apparently the first to notice the close affinity of the two families, but concluded that they could be kept distinct.

Brown recognised clearly that the differences between these two groups did not warrant familial separation. The union of the two families was announced in the manuscript notes he permitted Wallich to publish under the new genus *Aikinia* in the 'Plantae Asiaticae Rariores' (1832, see below)[3].

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[1] Until recently, the formal establishment of Gesneriaceae was attributed to Dumortier (1822), but De Candolle's short reference "Gessnerieae. Rich. et Juss., Ann. Mus. 5, p. 428. Propriétés inconnues." is enough to validate the name and has priority (Greuter & al. 2000, App. IIB).

[2] Don (1922) mentioned in the introduction also the genus *Chirita*, giving enough description to validate the name. However, Don referred the genus to Scrophulariaceae instead of Didymocarpaceae/Gesneriaceae, where it actually belongs.

[3] The conclusion that the two families must be united was reached at about the same time also by David Don (Burtt 1965). In a hidden place, namely in the notes following the description of *Leucocarpus alatus* D.Don (in Sweet, Brit. Fl. Gard. ser 2, 2: t. 124, 1831) he stated: 'I had, formerly, [...] proposed to separate *Didymocarpus*, and certain other genera akin to it, into a distinct family [Didymocarpaceae]; but a more accurate examination has fully convinced me that they must be united to the Gesneriaceae, which again are hardly distinguishable by any tangible character from the *Scrophularinae*'. As neither Brown nor Don referred to each other, it is not clear whether the conclusion was reached independently or who was influenced by whom. As Don confesses in the same paper that the 'inverted embryo' assumed to be characteristic of Didymocarpaceae was based on a misobservation (as pointed out by Brown), it may be assumed that Don's 'more accurate examination' was induced by Brown.

The formal union of Gesneriaceae and Didymocarpaceae/Cyrtandraceae was published several years later by David Don's brother, George Don (1838), without giving reasons or making mention of R. Brown. This publication antedates Brown's formal union of the two families in the 'Cyrtandreae' (1839).

## Brown's contributions to Wallich's 'Plantae Asiaticae Rariores' (1832)

An essential point of Brown's Gesneriad contribution to this important work is the establishment of two genera: *Aikinia* and *Antonia*. Neither name, however, is in use.

***Aikinia*** [R.Br. ex] Wall., Pl. Asiat. Rar. 3: 65, t. 288 (1832)

As was pointed out by Brown himself later (1839, 1840: 104), this is a synonym of Blume's *Epithema* (Blume 1826). Blume had placed *Epithema* in the family Primulaceae on grounds of the *Anagallis*-like fruits (capsules with circumscissile dehiscence) and, therefore, was overlooked by Brown.

Two species were addressed in Wallich: *A. brunonis* and *A. horsfieldii* [now *Epithema horsfieldii* (R.Br.) DC.]. The former was the principal taxon, the latter only appended. Therefore, *Aikinia* was lectotypified with *A. brunonis* (Morton & Denham 1972). Another genus *Aikinia* was published in the same issue (Wall., Pl. Asiat. Rar. 3: 46, t. 273, 1832) as a synonym (this was regarded as invalid by Morton and Denham (1972), but is valid and in fact was a rejection of Wallich; for details see Feuillet (1993)). Wallich had intended to publish a grass genus as *Aikinia*, and had a plate already engraved as *Aikinia elegans* Wall., but found at the last minute that the genus had been previously described by Kunth as *Ratzeburgia*.

When referring to *Aikinia*, Brown was already aware that the Old World Cyrtandraceae and the New World Gesneriaceae did not warrant separation at family level. The reasons for uniting the two families were promised in the 'forthcoming' volume of 'Plantae Javanicae Rariore', which actually came forth six years later, after many complaints by Horsfield at the delays.

***Antonia*** [R. Br. ex] Wall., Pl. Asiat. Rar. 3: 65. 1832, nom. nud., non Pohl (1828–1829) ('1831').

Although sometimes cited as validly published, this is a nomen nudum only. It is stated to be an intended change of name for *Loxotis* R. Br., but *Loxotis* was published only later, by Bentham in 1835. The type was intended to be *Wulfenia obliqua* Wall. (Brown 1839: 104) (Morton & Denham 1972). *Antonia* is a synonym of *Rhynchoglossum* Blume. See also below under *Loxotis*.

## Brown's treatment of Gesneriaceae in the preprint 'On Cyrtandreae' and in the 'Plantae Javanicae Rariores' (collectively referred to here as 'Cyrtandreae')

Details of the history of the admirable 'Plantae Javanicae Rariores' have been reported by Mabberley (1985: 303 ff.; 1986). Here a brief summary, with emphasis on Gesneriaceae, is given. When Brown was librarian for Joseph Banks, he prepared lists of the plant species collected by the American surgeon and naturalist Thomas Horsfield in Java and Sumatra and received in 1814 and 1815. Horsfield proposed that a selection should be made and published under the above title. Brown began preparing the descriptions in 1821. He got John and Charles Curtis to make drawings in the style of the Bauer brothers. One drawing, that of the Gesneriad '*Loxotis obliqua*' (*Rhynchoglossum obliquum*) was from Ferdinand Bauer himself, and we know that the cost for the engraving of this single plate was £3 10s 0d (Mabberley 1986: 309). Horsfield wrote a prospectus, indicating that the first part was to appear in 1831 and the rest to follow in nine-monthly intervals. However, there was much delay, caused by Brown's manifold interests in other subjects. Horsfield suggested that J.J. Bennett, Brown's assistant at the British Museum, should make the book ready for publication. In 1835 Brown made over a number of specimens, drawings and engravings to Bennett. However, by May 1838, the text accompanying plates 24 (Bauer's *Loxotis* *obliqua*) and 25 (the second Gesneriad illustrated, *Loxonia acuminata* R.Br. = *L. hirsuta* Jack, prepared by the Curtis brothers) was still not with the printer. Finally, between July 4th and 7th the first part appeared, consisting of pages 1–104 and plates 1–24, the last being *Loxotis*. In March 1839 the final part of plate 25 (*Loxonia*) had still not reached Horsfield who, not unreasonably, lost his control and complained bitterly that 18 years had elapsed since Brown had started work in 1821. The second part was published in May 1840, consisting of pages 105–196 and plates 25–40, the first one illustrating *Loxonia*.

In the year before (late 1839), a special 'preprint' appeared, consisting of plates 24 (*Loxotis*) and 25 (*Loxonia*) and pages 102–122. This preprint was entitled 'On Cyrtandreae' and covered Brown's remarkable essay on Gesneriaceae. It was subsequently translated into French [(*Ann. Sci. nat. (Bot.)* 13: 149–180 (1840)] and German [*Flora* 25: 193–206, 209–219 (1842)]. A large and more general part of the essay, which is in fact an extensive footnote (pp. 107–112), appeared as a separate paper under the title 'On the relative position of the divisions of stigma and parietal placentae in the compound ovarium of plants' in *Ann. Mag. Nat. Hist.* 11: 35–42 (1843) and in a German translation in *Bot. Zeitg.* 1: col. 193–201 (1843).

In the 'Cyrtandreae', the part on Gesneriaceae starts with the texts accompanying plates 24 (*Loxotis obliqua*) and 25 (*Loxonia acuminata*). In direct connexion, Brown refers to Jack's new family Cyrtandraceae, 'to which *Loxonia* and *Loxotis* belong', to Don's new 'Didymocarpeae', and to Blume's Bignoniaceae. 'It is somewhat remarkable that none of these writers should have adverted the affinity of this new family [Cyrtandraceae] to Besleriaceae of Richard and De Jussieu, now generally named Gesneriaceae' (see, however, footnote 3). He mentions that Martius (1829) 'considers Cyrtandraceae as sufficiently distinct' and starts to discuss the possible affinities of the groups. An important distinguishing feature between the Cyrtandraceae and the Gesneriaceae is seen in the position of the stigma lobes in relation to the position of the placentae. This feature is discussed in a very broad context in the ample footnote already addressed and later published separately.

Brown reaches the conclusion that 'in a natural classification Cyrtandreae must stand next to Beslerieae', one of the two tribes then recognised in Gesneriaceae. In consequence, Brown includes Cyrtandreae as a third tribe in that family. His classification thus reads:

Gesneriaceae: (1) Gesnerieae ('Calyx cum ovario plus minus connatus. Pericarpium capsulare. Semina albumine copioso'), (2) Beslerieae ('Calyx liber. Pericarpium baccatum v. capsulare. Semina albuminosa), (3) Cyrtandreae ('Calyx liber. Pericarpium capsulare v. baccatum. Semina exalbuminosa v. albumine parco'). The latter tribe is characterised in great detail.

In contrast to the general part, the following taxonomic section is in Latin. This is introduced by a survey ('Cyrtandrearum synopsis genera'), in which the genera are enumerated, with indication of their distinctive characters. Two groups are distinguished, one with capsular fruits, the other with berry fruits. In the final part the genera are listed again, giving more morphological details of the respective species, with references and/or brief descriptions.

It is important to note that the taxonomic part is a complete survey of the 'Cyrtandreae' known in Brown's times. The treatment is not only based on Horsfield's collections from Java and Sumatra, but includes many others as well, e.g. Thompson's and Hilsenberg's collections from Madagascar. It covers a huge geographical area from South Africa over Madagascar, India, South China and the Himalayas, the Malay archipelago, to the Pacific.

Brown's revision is almost exclusively based on herbarium material. As far as is known, he encountered only two species of Gesneriaceae in the field: '*Loxotis obliqua*' = *Rhynchoglossum obliquum* (see below), and *Epithema brunonis*, both collected at Coepang in Timor.

## The genera and species treated in the 'Cyrtandreae'

The following list presents the taxa referred to in Brown's treatise. The order of the genera and the species is given as by Brown (but in nomenclaturally updated form), as the sequence clearly reflects Brown's ideas on the affinities. Species synonyms cited by Brown are not given. In the 'synopsis' Brown made a subdivision between the genera with 'pericarpium capsulare' (*Aeschynanthus* to *Rhabdothamnus*) and with 'pericarpium baccatum' (*Fieldia* to *Whitia*).

***Aeschynanthus*** Jack: *A. volubilis* Jack, *A. radicans* Jack, *A. parvifolius* R.Br., *A. fulgens* Wall., *A. parasiticus* (Roxb.) Wall., *A. ramosissimus* [Wall. ex] DC., *A. griffithii* R.Br., *A. horsfieldii* R.Br., *A. bracteatus* [Wall. ex] DC., *A. acuminatus* [Wall. ex] DC., *A. wallichii* R.Br., *A. longicaulis* [Wall. ex] R.Br.

***Tromsdorffia*** Blume [now *Agalmyla* Blume and *Chirita* Buch.-Ham., see Hilliard & Burtt, 2002]: *T. ? elongata* Blume [now *Agalmyla elongata* (Blume) B.L.Burtt].

***Agalmyla*** Blume: *A. staminea* Blume [now *A. parasitica* (Lam.) O.Kuntze].

***Lysionotus*** D.Don: *L. serratus* D.Don.

***Chirita*** [Buch. Ham. ex] D.Don: *C. urticifolia* [Buch. Ham. ex] D.Don., *C. flava* [Wall. ex] R.Br., nom. superfl. (= *Chirita pumila* D.Don), *C. acuminata* [Wall. ex] R.Br. [= *C. oblongifolia* (Roxb.) Sinclair], *C. dimidiata* [Wall. ex] R.Br. [included in *C. anachoreta* Hance by Wood 1974, which is however a later name; but the species is probably distinct, B.L. Burtt, pers. comm.], *C. bifolia* D.Don, *C. macrophylla* Wall., *C. horsfieldii* R.Br. [included in *C. asperifolia* (Blume) B.L.Burtt by Wood 1974, but distinct, Hilliard, 2003], *C. scaberrima* R.Br. [included in *C. asperifolia* (Blume) B.L.Burtt by Wood 1974, but to be included in *C. horsfieldii* R.Br., Hilliard, 2004], *C. caerulea* R.Br., *C. hamosa* R.Br.

***Didymocarpus*** Wall.: D. aromaticus Wall., nom. illeg. [*D. primulifolius* D.Don, see below], *D. villosus* D.Don, *D. oblongus* [Wall. ex] D.Don, *D. punduanus* R.Br., *D. acuminatus* R.Br., *D. pedicellatus* R.Br., *D. macrophyllus* [Wall. ex] D.Don, *D. subalternans* [Wall. ex] R.Br., nom. illegit. [now *D. aromaticus* [Wall. ex] D.Don], D. obtusus [Wall. ex] R.Br., nom. illegit. [now *D. cinereus* D.Don], *D. crinitus* Jack [now *Henckelia crinita* (Jack) Spreng.], *D. serratus* R.Br. [now *Henckelia serrata* (Jack) A.Weber & B.L.Burtt], *D. racemosus* Jack [now *Henckelia racemosa* [Jack] A.Weber & B.L.Burtt], *D. corniculatus* Jack [now *Henckelia corniculata* (Jack) A.Weber & B.L.Burtt], *D. cordatus* [Wall. ex] DC., *D. corchorifolius* [Wall. ex] DC., *D. reptans* Jack [now *Henckelia reptans* (Jack) Spreng.], *D. missionis* [Wall. ex] R.Br. [now *Henckelia missionis* ([Wall. ex] R.Br.) A.Weber & B.L.Burtt], *D. zeylanicus* R.Br. [now *Henckelia zeylanica* (R.Br.) A.Weber & B.L.Burtt], *D. rottlerianus* Wall., nom. illeg. [now *Henckelia incana* (Vahl) Spreng.], *D. frutescens* Jack [now *Didissandra frutescens* (Jack) C.B.Clarke], *D. elongatus* Jack [now *Didissandra elongata* (Jack) C.B.Clarke], *D. lanuginosus* [Wall. ex] R.Br. [now *Corallodiscus lanuginosus* ([Wall. ex] R.Br.) B.L.Burtt].

***Streptocarpus*** Lindl.: *S. rexii* Lindl., *S. hilsenbergii* ['helsingbergii'] R.Br., *S. bojeri* R.Br. [now *S. thompsonii* R.Br. var. *bojeri* (R.Br.) C.B.Clarke], *S. thompsonii* R.Br., *S. paniculatus* R.Br. [now reduced to *S. thompsonii* R.Br.].

***Boea*** Commers.: *B. commersonii* R.Br. [now included in *B. magellanica* Lam.], *B. hygrometrica* R.Br., *B. wallichii* R.Br., *B. multiflora* [Wall. ex] R.Br. [now *Paraboea multiflora* ([Wall. ex] R.Br.) B.L.Burtt.

***Loxocarpus*** R.Br. [now *Heuckelia* sect. *Loxocarpus* (R.Br.) A.Weber & B.L.Burtt]: *L. incanus* R.Br. [now *Heuckelia browniana* A.Weber].

***Epithema*** Blume: *Aikinia* R.Br. in Wall. is cited as a synonym.

***Staurauthera*** Benth.: *Staurauthera grandiflora* Benth., *Staurauthera ecalcarata* R.Br. [now included in *S. caerulea* (Blume) Merr.].

***Loxonia*** Jack: *L. acuminata* R.Br. [now included in *L. hirsuta* Jack], illustrated in tab. 25 (p. 104).

***Glossanthus*** [Klein ex] Benth. [now Rhynchoglossum Blume]: *G. malabaricus* Klein [now *Rhynchoglossum obliquum* Blume], *G. notonianus* (Wall.) R.Br. [*Rhynchoglossum notonianum* (Wall.) B.L.Burtt], *G. zeylanicus* R.Br. [now *Rhynchoglossum gardneri* Theob. & Grupe], *G. mexicanus* R.Br., nom. illegit. [now *Rhynchoglossum azureum* (Schltdl.) B.L.Burtt].

***Loxotis*** Benth. [now *Rhynchoglossum* Blume]: *L. obliqua* (Wall.) Benth. [now *Rhynchoglossum obliquum* Blume], illustrated in tab. 24 (p. 102).

***Monophyllaea*** R.Br.: *M. horsfieldii* R.Br.

***Platystemma*** Wall.: no species is quoted, but the only species known then (and at present) is *P. violoides* Wall.

***Rhabdothamnus*** Cunn.: *R. solandri* Cunn.

***Fieldia*** Cunn.: *F. australis* Cunn.

***Rhynchotechum*** Blume: *Corysanthera* Wall. is cited as a generic synonym, no species are recorded.

***Centronia*** Blume [this is a synonym of *Aeginetia* L., a genus of Orobanchaceae or Scrophulariaceae in the wide sense of Takhtajan 1987 and Fischer 2004, in press]: *C. mirabilis* Blume [now *Aeginetia mirabilis* Levira].

***Cyrtandra*** J. & G. Forster: The manuscript name *Getonia* Banks & Soland. is quoted, but no species are given.

***Whitia*** Blume [now included in *Cyrtandra* J. &. G. Forster]: no species are quoted.

## The new genera

In the 'Cyrtandreae' Brown described two new genera, *Monophyllaea* and *Loxocarpus*. Only the first is still in use at generic level, and this is the only Brown genus that has survived until now.

***Monophyllaea*** R.Br.: This is a most interesting and peculiar genus. As the name indicates, the plant bears only a single, large leaf. Brown did not know the nature of the leaf. The fact that the single leaf of 'unifoliate' Gesneriads represents an enormously enlarged cotyledon ('macrocotyledon') was discovered much later by Caspary (1858) and Crocker (1860) in *Streptocarpus*, and confirmed for *Monophyllaea* by Ridley (1906).

*Monophyllaea* was described by Brown on the basis of a single species and specimen, collected by Horsfield in Sumatra (preserved at BM). Brown named it in honour of the collector *M. horsfieldii*. The species was for the next 20 years the only one known in the genus, until in 1860 a second species, *M. hirtella* Miq., also from Sumatra, was added. In 1883, Clarke raised the species number to six. In 1979, Burtt published a 'preliminary' revision of the genus, adding many new species, and demonstrating a surprising morphological diversity, and a remarkable range and pattern of distribution.

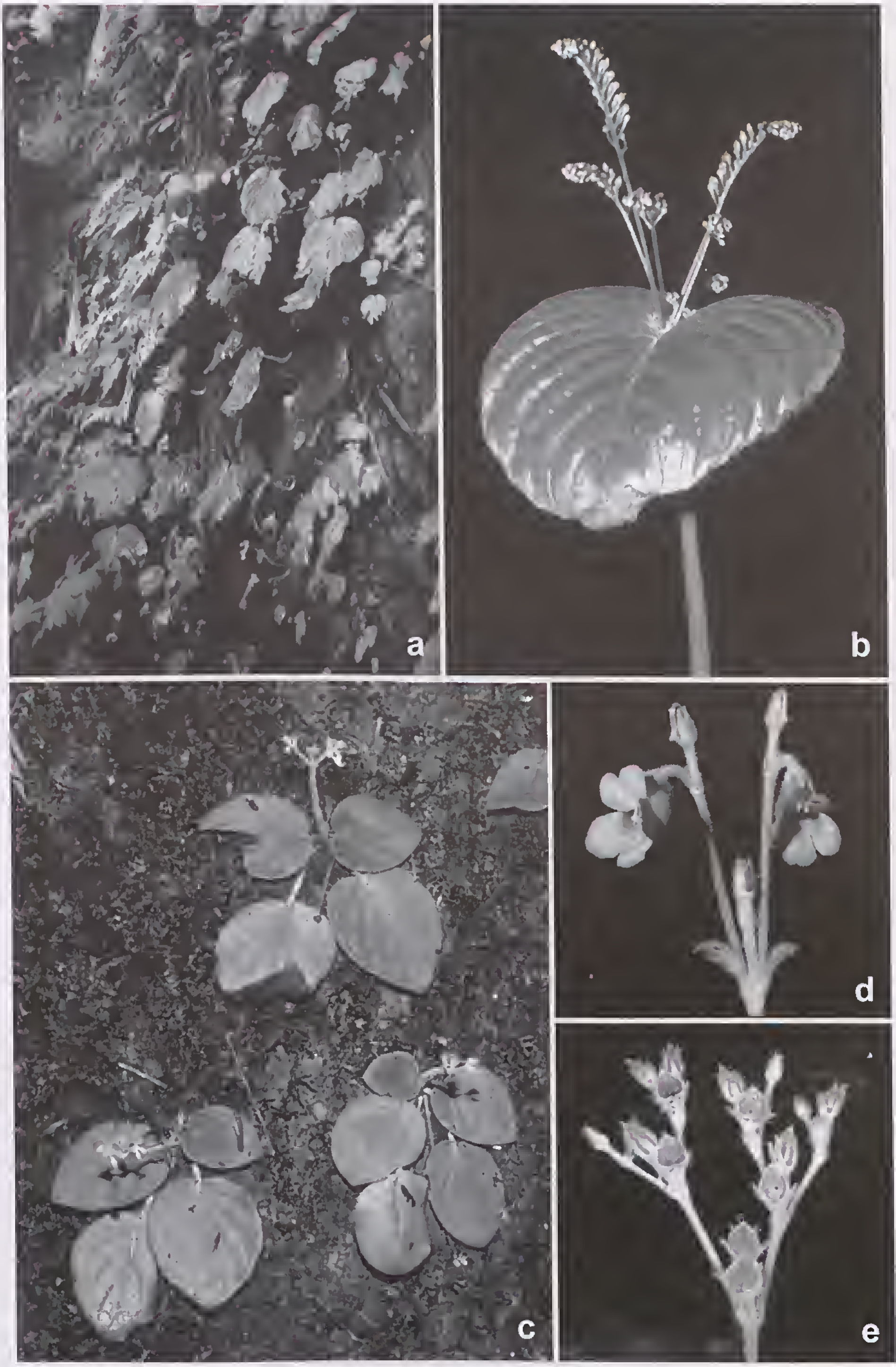

**Fig. 1a,b** *Monophyllaea horsfieldii* R.Br., **a,** plants in their natural habitat (limestone cliffs in rainforest), Peninsular Malaysia, Selangor, Bkt. Takun; **b,** cultivated plant; **c–e** *Henckelia browniana* A.Weber (= *Loxocarpus incanus* R.Br.); **c,** plants in their natural habitat (mossy slopes near streams), Penins. Malaysia, Penang, Penang Hill (Bkt. Penara) (type locality); **d,** flowers; **e,** capsules (seeds mostly washed out by rain); ibid.; all photos by the author.

So far, c. 35 species are known, ranging from the northern part of the Malay Peninsula throughout Malesia to New Guinea. The greatest species number is found in Borneo, while New Guinea has only one species. The species are typically rain-forest plants, growing on rocks and slopes in an everwet climate. Brown's *M. horsfieldii* was later found also on the Malay Peninsula, where it is fairly common on moist limestone rock faces in shady forest (Fig. 1a,b). *M. glabra* Ridl., the northernmost species, is remarkable in its annual habit and the ability to live in a seasonal climate, surviving the dry period only by seeds.

Burtt (1978) showed that the unifoliate habit is not a constitutive feature of the genus: there are some species (*M. caulescens* B.L.Burtt, Sumatra, *M. ramosa* B.L.Burtt, Ceram, and, according to pers. observ. also *M. elongata* B.L.Burtt, Malay Peninsula) that produce several leaves similar to the macrocotyledon and exhibit a phyllomorphic structure.

Certainly the most curious species is the Bornean *M. singularis* (Balf. & Smith) B.L.Burtt, in which the inflorescences (reduced to few-flowered glomerules) are produced along the stalk. As was shown by Weber (1987, 1990) and Imaichi et al. (2001) the inflorescence primordia result from re-embryonalisation of cells on the stalk surface. As in *Streptocarpus* the inflorescence-bearing part corresponds to a mesocotyl (see below).

The morphological analyses of Weber (1975, 1976a) showed that the unifoliate growth pattern of *Monophyllaea* is derived from an anisophyllous-caulescent pattern as is represented in the small South Chinese-Taiwanese genus *Whytockia*. Specific floral characters (Weber 1976a) as well as molecular data (Mayer et al. 2003) show, that *Whytockia* is indeed the closest relative. From this relationship it can be concluded that the origin of *Monophyllaea* was on the Asiatic continent (and not, as suggested by Burtt 1978 on account of geographical considerations, in eastern Malesia). This is in agreement with Burtt's recent view (1998b) of a general E→W expansion of Gesneriaceae (see below).

***Loxocarpus*** R.Br.: This genus is based on a species collected by Wallich in Penang Island (Malay Peninsula) and referred to as *Loxonia ? alata* in his 'Numerical List'. Brown described it as *Loxocarpus incanus*. Bentham (1876) and Clarke (1883) included *Loxocarpus* as a section in *Didymocarpus*. Ridley (1896) followed them at first, but from 1905 onwards he referred to it as a separate genus. Also Burtt (1958, 1962) adopted the generic rank.

Recently, *Didymocarpus* and its allied genera were re-investigated at a broad scale (Weber & Burtt 1998b), with the result that *Didymocarpus* had to be split into three genera: *Didymocarpus* Wall., *Henckelia* Spreng., and *Hovanella* A.Weber & B.L.Burtt. *Didymocarpus* is an essentially Sino-Himalayan genus, *Henckelia* an essentially Malesian genus, and *Hovanella* is confined to Madagascar. The large genus *Henckelia* can be subdivided into five sections, and Brown's *Loxocarpus* is one of them [*Henckelia* sect. *Loxocarpus* (R.Br.) A.Weber & B.L.Burtt]. This section includes about 15 species, most representing small rosette plants with white-silvery indumentum and blue flowers. The fruits are usually short capsules, held horizontally and opening only on the upper side. In most species the fruit base is distinctly 'humped'. One species from Sumatra, *H. caulescens* (B.L. Burtt) A.Weber & B.L.Burtt, deviates from the rosette habit by producing long internodes between the alternate leaves. With the inclusion of Brown's *Loxocarpus incanus* into *Henckelia*, a nomen novum had to be established. The name is now *Henckelia browniana* A.Weber. This is a charming little herb, growing on shady banks of streams in the northern part of the Malay Peninsula. It has blue flowers and short, bowl-shaped fruits which function as rain-splash capsules (Fig. 1c–d).

## The new species

From the new species described by Brown some are still in use in the original form (e.g., all four species of *Aeschynanthus*, some species of *Didymocarpus*, *Boea*, *Streptocarpus* etc. ), some have been transferred to other genera (see below), and a few have been sunk into synonymy.

Some species of *Didymocarpus* deserve special mention, as Brown's (re-)naming caused confusion. Wallich, then director of the Botanical Garden of Calcutta, sent his material (uniformly attributed to 'Wallich, Nepal', but originating from various collectors) to A.B. Lambert in London, whose librarian was David Don. Don prepared the 'Prodromus florae Nepalensis' which was published in 1825, that is before Wallich came to England (1828) and started to prepare his 'Numerical list' (1829). Don usually adopted any manuscript name that Wallich had suggested, and thus Don's published names are in fact Wallich's names. However, probably due to unmounted material and the lack of clear notes, Don attributed a wrong name to a few plants. Brown knew this and reverted in his 'Cyrtandreae' (1839) to Wallich's original names. However, Don's names were published earlier (1825) and have priority. Thus, Don's *D. aromaticus* is not identical with Wallich's and Brown's *aromaticus*, but nonetheless must be retained in Don's sense, while the latter must be referred to as *D. primulifolius* D.Don. Similarly, Wallich's and Brown's *D. obtusus* and *D. subalternans* must be qualified as illegitimate names and referred to Don's *D. cinereus* and *D. aromaticus*, respectively.

## Transfers of Brown's new species to other genera

(1) One species of *Boea* was transferred to the newly segregated *Paraboea* (Burtt 1984). The genus *Paraboea* was established by Ridley (1905) for the accommodation of *Boea*-like plants with straight (not twisted) fruits. Burtt (1984), however, based his definition of *Paraboea* essentially on the interwoven arachnoid tomentum of branched hairs, irrespective of the fruit type. Brown's *Boea multiflora* (with twisted fruits) has the typical indumentum of *Paraboea* and was, therefore, transferred to that genus.

(2) Several species of *Didymocarpus* were transferred to the later-established genera *Didissandra* C.B.Clarke (Clarke 1883), *Corallodiscus* Batalin (see Burtt 1947) and the recently re-established genus *Henckelia* Spreng. (see above under *Loxocarpus*). The essentially Sino-Himalayan *Didymocarpus* s.str. is morphologically characterised by seasonal flowering shoots, cartilagineous bracts and sepals with smooth-polished surface, usually long-tubed, claret-coloured flowers and orthocarpic fruits dehiscing into two valves. Eleven species of Brown's list belong to that genus. From these, three bear Brown's name today: *D. punduanus*, *D. acuminatus*, and *D. pedicellatus*. Some names are illegitimate for the reasons given above. *Henckelia* is an essentially Malesian genus extending (with the type section *Henckelia* which includes Brown's *D. missionis* and *D. zeylanicus*) into South India and Sri Lanka. The plants show a continuous growth, have bracts and sepals of the usual texture (usually hairy), flowers very variable in shape and colour, and plagiocarpic fruits opening only along the upper suture. *Didymocarpus crinitus* is now placed in *Henckelia* sect. *Heteroboea*, *D. serratus* and *D. reptans* in sect. *Didymanthus*, and *D. corniculatus* in sect. *Glossadenia*, a section newly established by Weber & Burtt (1998b).

(3) All species of *Glossanthus* are now placed in *Rhynchoglossum* (Burtt 1962). The generic name *Glossanthus* was established by Klein in Wallich's Numerical list. It was a nomen nudum, but it was later validated by Bentham (1835) and used by G.Don (1838), Brown (1839) and Endlicher (1839). It is, however, antedated by *Klugia* Schltdl. (1833), and that name was used for a long time to accomodate the species similar to *Rhynchoglossum* Blume, but having large flowers with four stamens instead of small

flowers with two stamens. In fact, under *G. mexicanus*, Brown cites *Klugia azurea* as a synonym. In 1962 Burtt united *Klugia* and *Rhynchoglossum* under the latter name, in that he demonstrated in a new species from Borneo (*R. medusothrix* B.L.Burtt) a transitional flower form: a large corolla, and four fertile, but markedly didynamous stamens with the shorter pair having much smaller anthers. The species listed under *Glossanthus* as well as Brown's *Loxotis obliqua* of plate 24 are now all in *Rhynchoglossum*.

As is apparent from the text accompanying the illustration of *Loxotis obliqua*, Brown was well aware of the close relationship of *Loxotis* and *Glossanthus* (p. 104: '... it may be doubted whether *Loxotis* and *Glossanthus* ought to be generically distinguished merely or chiefly on account of the difference in number of their antheriferous stamina, especially as they entirely agree in habit...') and Brown was also aware that his '*Glossanthus mexicanus*' was '...the only plant belonging to Cyrtandreae hitherto observed in any part of America'. The situation is the same at present. Though additional species have been described from the Americas [*R. grandiflorum* (Fritsch) B.L.Burtt, *R. violaceum* (Fritsch) B.L.Burtt] they are believed to be conspecific with Brown's '*Glossanthus mexicanus*' = *Rhynchoglossum azureum* by Wiehler (1983) and thus this species figures as the only representative of Old World Gesneriaceae in the New World. An explanation for the enigmatic distribution is still needed. While Li (1996) suggested that the link between America and Asia was across Africa, the molecular data of Mayer et al. (2003) indicate that *R. azureum* is very close to the South Indian *R. notonianum*, and *R. azureum* is perhaps a rather recent introduction into the Americas.

## The two Gesneriads illustrated in the 'Cyrtandreae'

Brown's treatment of Gesneriaceae contains only two illustrations. These page-sized plates are not only of high scientific accuracy and excellent artistic quality, but depict morphologically very interesting plants. Therefore, a detailed reference is made here.

**'*Loxotis obliqua*** Wall. Benth.' (= *Rhynchoglossum obliquum* Blume). This is the plant of plate 24, prepared by Ferdinand Bauer (Fig. 2). This colour plate shows very accurately the habit and the flower details of the plant. Brown observed it 'in the Island of Timor near Coepang, chiefly in shady places, but sometimes in more exposed situations, in April 1803'. He reports that Horsfield had later collected the plant in many parts of Java and 'if I am correct in referring *Rhinchoglossum obliquum* to our plant, it was observed also by Dr. Blume in mountainous situations of the same island'. This phrase shows that Brown was aware of the possible conspecificity with Blume's *Rhynchoglossum obliquum* (the specific epithet '*obliqua*' seems to have been chosen independently on account of the conspicuous strongly asymmetrical leaves). Further on, Brown refers to other collections, expressing his view that this was a widespread and variable species. In addition, Brown also explains the adoption of the name *Loxotis* in contrast to *Antonia*, and the priority problems involved. 'This difficulty would be easily removed were it absolutely certain that *Rhinchoglossum* of Dr. Blume was identical with *Loxotis*; but from some of the characters ascribed to it I am not entirely satisfied that such is the case'. Today we are satisfied: *Loxotis* is without a doubt identical with *Rhynchoglossum*.

The morphology of *Rhinchoglossum* was studied in the recent past by the author (Weber 1978a,b). The peculiar shape and arrangement of the leaves can be derived from anisophylly of the *Goldfussia*-[*Strobilanthes*]-type (Goebel 1928, Troll 1937) which is found in many Gesneriaceae, and which is characteristic of most 'Epithematoid Gesneriaceae', to which *Rhynchoglossum* belongs. In *Rhynchoglossum*, anisophylly has proceeded to its extreme in that the small leaves are usually completely reduced and only the strongly asymmetrical plus-leaves remain, being placed in two near-distichous ranks. The opposite leaf arrangement, found in the bulk of Gesneriaceae,

**Fig. 2.** Reproduction of plate 24 from Robert Brown, Cyrtandreae (1839), '*Loxotis obliqua* (Wall.) Benth.' = *Rhynchoglossum obliquum* Blume

**Fig. 3.** Reproduction of plate 25 from Robert Brown, Cyrtandreae (1839), '*Loxonia acuminata* R.Br.' = *Loxonia hirsuta* Jack

thus has changed to an alternate-(near-) distichous phyllotaxis (alterniphylly, Weber et al. 1992). Of unique structure are the inflorescences. They have been often regarded as 'pseudo-racemose' equivalents of the cymes of other Gesneriaceae, but represent true racemes, though strongly modified. As in the following genus, *Loxonia*, they are terminal, but the cymes are reduced to single flowers. From the original four ranks of bracts only two are fertile and produce axillary flowers, while the others (sterile minus-bracts) are partly reduced and confined to the dorsal side of the inflorescence axis). Thus there are only two flower-rows present, often (especially in the annual, small-flowered species such as *R. obliquum*) with highly increased flower number.

Formally, *Rhynchoglossum* can be well associated with and derived from the morphological organization of the following *Loxonia*, but molecular data show, that the relationship is not very close: the genus is sister to all other Epithematoid Gesneriaceae (Mayer et al. 2003).

'***Loxonia acuminata*** R.Br.' (= *L. hirsuta* Jack). This plant is depicted in plate 25, prepared by the Curtis brothers (Fig. 3). It was collected by Horsfield in Sumatra, when he accompanied Sir Stamford Raffles from Padang to the Menangaboo (Minankabau) country. Brown was well aware that the plant could be conspecific with Jack's *L. hirsuta* (p. 106): 'I have considered the plant here figured as distinct from *Loxonia hirsuta* of Jack, which, however, it appears from his description to resemble in so many points that it may actually belong to the same species, differing only somewhat in the form of the leaves and in being less pubescent.' Brown was also deterred by the fact that Jack described the phyllotaxis of *Loxonia* as alternate, and therefore he related the plant 'ad eandem sectionem cum *Loxoti*, sed affinitate arctius junctum cum *Staurauthera*' (p. 105). However, Jack simply had overlooked the (often caducous) small leaves in the plants described by him. The conspecifity *of L. acuminata* and *L. hirsuta* was confirmed in the revision of Weber (1977a), who added a third species to the two species described by Jack, *L. burttiana*, occurring in the eastern part of Borneo.

Brown's illustration shows very precisely the flowering shoot portion of a plant and separately some flower and fruit details. The flower colour is given as blue, but this is obviously a fiction, perhaps induced by the general similarity of the plant with *Loxotis/Rhynchoglossum*. No collection of any species records blue flowers. The small flowers of *Loxonia hirsuta* are greenish-white, eventually with a red dot on either side of the mouth, the upper lip is translucent greenish.

*Loxonia* has also strongly asymmetrical and seemingly alternate leaves, but on closer inspection one can see that the leaves are actually placed in pairs, and that one of a pair is reduced to a tiny, heart-shaped, stipule-like structure. The branched inflorescences seem to arise from the axils of the tiny leaves. Jack (1823), Brown (p. 105: 'racemi subcymosi, recurvi, saepe bifidi, ex alis [sic; this should probably read „axillis'] foliorum stipuliformium'), Clarke (1823), Fritsch (1893) and Troll (1964) have definitely stated that it is so. This, however, would be in strong contrast with the also strongly anisophyllous Chinese genus *Whytockia* in which the inflorescences (pair-flowered cymes) emerge clearly from the axils of the large leaves (Weber 1976a). The study of Weber (1977b) resulted in the following findings: the flowering region of *Loxonia* is a sympodium composed of shoot units, each comprising an anisophyllous leaf pair and a terminal (!) inflorescence. The inflorescence is complex in structure. There is a flexuous main axis, bearing two or three tiny bract pairs. Though the bracts of a pair are of equal size and shape, only one is capable of producing an axillary inflorescence. The latter is either a pair-flowered cyme (cincinnus) (*L. discolor*, *L. burttiana*) or a conventional cincinnus with the front-flowers in the pairs reduced (*L. hirsuta*).

## R.Brown's modern concept of Gesneriaceae: the union of Old and New World Gesneriaceae

Brown knew about Jack's Cyrtandraceae and Don's Didymocarpaceae and their identity. He also knew that Martius (1829) was the first to discuss the affinity with the New World family Gesneriaceae. Martius had reached the conclusion that Cyrtandraceae should be kept distinct, essentially on account of (1) the absence of albumen (endosperm) and (2) the 'inverted embryo' (quoted on the authority of Don). Brown added another 'very remarkable' difference: the position of the stigma lobes. In the New World Gesneriaceae the stigma lobes 'are placed left and right in relation to the parts of the flower, and consequently opposite to the lateral parietal placentae, while in Cyrtandraceae the lips of the stigma ... are anterior and posterior, and therefore alternate with the lateral placentae'. Brown knew well about the special situation in *Chirita*, in which the bilobed stigma resembles the stigma of American Gesneriaceae: in this genus the upper lobe is reduced and the lower lobe is bilobed.

Nonetheless, Brown did not think that these characters would warrant strict separation. He knew that the presence/absence of albumen is not 'absolutely constant, there being cases in Cyrtandraceae where the remains of albumen are visible in the ripe seed; and in several Gesneriaceae it exists so sparingly as to become a character of very little value'. Secondly, Brown made clear that the 'embryo inversus' was based on a misobservation (see also footnote 3). Thirdly, he stated that the differences in stigma lobe position 'is certainly not without exception'.

After all, Brown reached the conclusion that Cyrtandraceae and Gesneriaceae should be united and that Cyrtandreae should represent a tribe within the latter family and 'stand next to Beslerieae'. The third tribe recognised in the expanded family was Gesnerieae (with inferior ovary).

It is important to note that Brown did not mix American and Afro-Asian genera in the same tribe. Unfortunately, this was done later by Bentham (1876) and Fritsch (1893–94) (see below).

## Adoption of Brown's union

Apparently the first to adopt Brown's union was Endlicher in his 'Genera plantarum' (1839).

In the 'Prodromus', Auguste P. de Candolle's still followed Martius (1829) and kept Gesneriaceae (published in vol. VII, 1839) and Cyrtandraceae (vol. IX, 1845) distinct. His account on Cyrtandraceae must have been written before publication of Brown's 'Cyrtandreae' in late 1839 for it was made available to Meisner who published in 1840. De Candolle's death in 1841 delayed publication of the Cyrtandraceae until 1845, when vol. IX of the 'Prodromus' was edited by Alphonse de Candolle.

Bentham (1876) was the first to publish an overall account of Gesneriaceae in Brown's sense. He attached primary importance to the position of the ovary: superior or inferior. Genera with inferior ovaries, known only from the New World, formed Bentham's tribe Gesnerieae; but all genera with superior ovaries were classified in tribe Cyrtandreae which thus comprised New World and Old World genera. Fritsch (1893–1894) followed Bentham in this, but his classification was much more detailed. Fritsch raised Bentham's two tribes to subfamilies, and his subtribes to tribes, with the addition of further subtribes. Thus, in contrast to Brown, both these major systems have neotropical and palaeotropical genera mixed together, giving some very improbable groupings.

## Gesneriaceae now: taxa number and distribution

Since Brown's times, Gesneriaceae has grown to a considerable size. At present, between 140 and 150 genera are distinguished (depending on the concept of some genera, a full consensus has not been reached yet, Weber 2004). Species number is around 3500. Distribution is mainly in the tropics and subtropics both of the Old and the New World, with transgressions both to the north (Europe: Pyrenees, Balkan Peninsula; Asia: Himalayas, China incl. N China) and to the south (SE Australia, New Zealand, S Chile).

## Characters distinguishing Gesneriaceae from Scrophulariaceae and linking the New and Old World Gesneriaceae

In fact, it is not very easy to give a morphological definition of Gesneriaceae. Above all, the family is very similar to Scrophulariaceae and there is general agreement that the two families (if Scrophulariaceae are regarded as a single family at all, see below) are most closely allied. The main characters used for separation of the families are largely those binding the New and Old World Gesneriaceae together.

**Ovary structure:** The classical feature distinguishing Gesneriaceae from Scrophulariaceae is the 'unilocular' ovary. Unilocular means that the fused carpel flanks that protrude into the ovary are not fused at the tips and do not form a complete septum. However, in the lower part of the ovary, there is usually a portion with a complete septum ('synascidiate zone') and it is only the expanded upper part of the ovary ('symplicate zone') that exhibits a unilocular structure. Secondly, there are some Gesneriaceae in which the completely septate part makes up the whole ovary (e.g., *Whytockia, Monophyllaea, Asteranthera*) and in which the placentation is axile as in Scrophulariaceae (Weber 1971, Wilson 1974a,b). However, none of these genera is particulary closely allied or transitional to Scrophulariaceae.

**Pair-flowered cymes:** Another significant feature, recognised only recently (Weber 1973), is the branching pattern of the axillary inflorescences. These represent cymes (compound dichasia, double cincinni or cincinni), but each flower is accompagnied by an additional, subsidiary flower ('front-flower'). For this unusual type of cyme the term 'pair-flowered cyme' has been established (Weber 1973, 1995). Pair-flowered cymes are characteristic both of New and Old World Gesneriaceae.

Unfortunately, there are some cases in which difficulties may arise: (a) there exist some genera in Scrophulariaceae which exhibit pair-flowered cymes as well (see Weber 1973): *Penstemon, Russelia, Tetranema, Calceolaria, Jovellana, Stemotria*), (b) there are a few members of Gesneriaceae, in which the 'front-flowers' within the pair-flowered cymes are subject to partial or complete reduction (*Chrysothemis, Loxonia hirsuta, Stauranthera caerulea*, see Weber 1977b, 1978c); (c) in both families the reduction of the cymes to single flower occurs (very common in Scrophulariaceae, rather rare in Gesneriaceae, e.g. *Koellikeria, Diastema*, for the unilateral racemes of *Rhynchoglossum* see above). In these cases a discrimination on grounds of the inflorescence structure is impossible.

## Classification of Gesneriaceae

The infrafamilial classification of Gesneriaceae still poses problems. Traditionally, two subfamilies have been distinguished, the Gesnerioideae and Cyrtandroideae. Bentham (1876) and Fritsch (1893–94) used the ovary position as the primary criterion for their separation, with the consequence that neotropical and paleotropical representatives occurred side by side in some groups. In 1954, B.L.Burtt commenced an important series entitled 'Studies in the Gesneriaceae of the Old World'. In 1963 the firm statement was made that the title was not to be read as a merely geographical restriction: it was (with the exception of Coronanthereae, see below) a taxonomic group: Gesneriaceae subfam. Cyrtandroideae. Thus Burtt reverted principally to the strict geographical separation of Brown. The justification for making a clear break between the New and Old World Gesneriaceae lies in the structure of the seedlings. It has long been known (Caspary 1858, Crocker 1860) that after germination the seedlings of *Streptocarpus* show remarkable growth of one cotyledon while the other remains small and eventually withers. A large-scale study of gesneriaceous seedlings was made by Fritsch (1904), and this showed that anisocotyly was widespread in Cyrtandroideae. Further records were made by Hill (1938) and Burtt and Woods (1958). Lack of evidence of isocotyly in Cyrtandroideae and the absence of any report of anisocotyly in the New World, suggested that anisocotyly provides the best diagnostic character, although in Cyrtandroideae anisocotyly is sometimes only weakly expressed and the larger cotyledon is not long-lived.

Burtt (1963) divided subfam. Cyrtandroideae into five tribes (Cyrtandreae, Trichosporeae, Didymocarpeae, Klugieae and Loxonieae) and later (Burtt & Wiehler 1995), into four by the amalgamation of the two latter tribes.

When comparing this classification with R. Brown's list, it becomes apparent that Brown had a very good feeling about the relationships. Though he divided his 'Cyrtandreae' explicitly only in capsule- and berry-fruited taxa, the sequence of the genera is in good accordance with Burtt's classification: *Aeschynanthus, Tromsdorffia* (= *Agalmyla*), *Agalmya*, and *Lysionotus* represent tribe Trichosporeae; *Chirita, Didymocarpus, Streptocarpus, Boea, Loxocarpus* (= *Henckelia*) represent tribe Didymocarpeae; *Epithema, Stauranthera, Loxonia, Glossanthus* (= *Rhynchoglossum*, formerly *Klugia*), *Loxotis* (= *Rhynchoglossum*), and *Monophyllaea* represent tribe Epithemateae; *Rhynchotechum, Cyrtandra* and *Whitia* (= *Cyrtandra*) represent tribe Cyrtandreae. Out of place is *Platystemma*, a curious tiny herb from the Himalayas. *Rhabdothamnus* and *Fieldia*, now placed in Coronanthereae, are separated by the different fruit type.

As envisaged from morphological characters (Burtt 1977) and now clearly confirmed by molecular data (Mayer et al. 2003), the Klugieae incl. Loxonieae (now called Epithemateae, Burtt 1997) form a very distinct group, sister to the remaining Cyrtandroideae. Informally, the two groups can be referred to as Epithematoid and Didymocarpoid Gesneriaceae.

The small group of Coronanthereae (with *Fieldia* and *Rhabdothamnus* already known to Brown) has, though representing principally a paleotropical group (restricted to E Australia, New Caledonia and some other islands of the SW Pacific), isocotylous seedlings. Burtt (1963) referred it to subfam. Gesnerioideae, together with a closely related new tribe, Mitrarieae, consisting of three monotypic genera from temperate South America. The whole alliance was raised to subfamily rank by Wiehler (1983), distinguished from all other Gesneriaceae by the nectary adnate to the ovary wall (subfam. Coronantheroideae). This group is referred to here as Coronantheroid Gesneriaceae.

The fourth informal group, the Gesnerioid Gesneriaceae, encloses the neotropical Gesneriaceae (Gesnerioideae sensu Wiehler 1983). In the following section the four groups are addressed in some more detail, stressing some salient features.

**Coronantheroid Gesneriaceae:** This small group, comprising 5–6 genera with c. 17 species, was rather neglected for a long time, but has recently received considerable attention in the discussion of the question of the origins of the Gesneriaceae. One hypothesis proposed is that the family is of Chinese (Cathaysian) origin (H.W. Wang 1989). This may appear plausible at first sight because of the many (31) gesneriaceous genera endemic there and the up to three times higher number of genera in mainland Asia as compared to Malesia. However, this opinion does not take into account that (a) the generic concepts of many Chinese genera are very narrow, (b) that the centre of evolutionary diversification is uncritically equated with the centre of origin, and (c) that it is based solely on the consideration of Asiatic Gesneriaceae and ignores other parts of the family such as the neotropical Gesneriaceae. When considering these other parts it is almost inevitable to link the present distribution with continental drift and plate tectonics.

Recently, Burtt (1998b) proposed an interesting 'higly speculative' hypothesis. The essential points are: (1) Gesneriaceae are a family of Gondwanaland origin. (2) The small group of Coronantheroid Gesneriaceae is a relict group that has, by the Australasian members, survived on the Australian plate. (3) This group invaded the Americas via the Antarctis and southern South America and gave rise to the Gesnerioid Gesneriaceae. While the Coronantheroid Gesneriaceae became nearly extinct (the three Chilean genera being the last survivors), the Gesnerioid Gesneriaceae evolved explosively in the American tropics. (4) The Australasian part of Coronantheroid Gesneriaceae gave rise to the present paleotropical Gesneriaceae. These moved northwards on the Indian plate and split very early in the Epithematoid and Didymocarpoid Gesneriaceae. Before the split, one must assume that the mutation(s) resulting in anisocotyly occurred. (5) The presently small group of Epithematoid Gesneriaceae is a relict group that was once much larger and had a much wider distribution in Asia and Africa. *E. tenue* can be considered as the last remnant of Epithematoid Gesneriaceae on the African continent. *Rhynchoglossum* reached America (where it is now represented by *R. azureum*) across Africa, from where it now has completely disappeared. (6) On the way north, a part of Didymocarpoid Gesneriaceae spread to Madagascar and colonised mainland Africa from there. (7) The Indian plate carried the Didymocarpoid Gesneriaceae finally to the Asiatic continent. Here a division took place between the plants of northern India and the south, probably as the result of desiccation. The northern group became established in the Sino-Himalayan area and spread from here, under active evolutionary diversification, east- and south eastwards to China and adjacent areas, as well as westwards to Europe. The southern group spread from south India and Sri Lanka into Sundaland and moved eastwards. Though species reached New Guinea and (*Cyrtandra*) even the Hawaiian islands, time was apparently too short that endemic genera evolved east of Wallace's line.

In this scenario the Coronantheroid Gesneriaceae appear as a relict of the stock from which Gesneriaceae have evolved, giving rise both to the neotropical and the Afro-Eurasian-Pacific Gesneriaceae. Though Burtt's hypothesis appears plausible from the recent distribution patterns of the family, one must not overlook the problems of timing with geological history. It is hard to believe that the family Gesneriaceae originated before or in the early stages of Gondwanaland breakup, 100 or 80 million years ago. Molecular data (Smith et al. 1997, Mayer et al. 2003) are also not in clear agreement with this hypothesis. Though the genera involved form a distinct clade, the clade is not sister to neo- plus paleotropical Gesneriaceae (thus the establishment of a third subfamily is not clearly supported). It occurs either in a sister position to the Gesnerioid Gesneriaceae or (rather basally) nested within this group (Smith et al. 1997, Mayer et al. 2003). No link to the paleotropical Gesneriaceae is apparent in any part of this group, but this is perhaps not too surprising, seeing how little of the Coronantheroid Gesneriaceae has survived. At any rate, this small alliance is of great phylogenetical interest and more studies are needed to get a clearer picture.

**Gesnerioid Gesneriaceae:** This group is very large, comparable in genus and species number to the Didymocarpoid Gesneriaceae. Its classification seems to approach some consensus. The five tribes recognised by Wiehler (Gloxinieae, Gesnerieae, Episcieae, Beslerieae, and Napeantheae) are supported by recent molecular data, and a sixth tribe (Sinningieae, its three genera previously placed in Gloxinieae) was suggested by Smith et al. (1997) and confirmed by Zimmer et al. (2002) and Perret et al. (2003).

There are some notable differences to the paleotropical Gesneriaceae in the biochemical and karyological patterns.

Anthocyanidins such as the widespread pelargonidin and cyanidin, characteristic of red flowers of Old World Gesneriaceae, are not found in the Gesnerioid Gesneriaceae. Here 3-desoxy-anthocyanins are found instead: apigeninidin, luteolinidin and columnidin (Harborne 1966, 1967, Lowry 1972).

The chromosome numbers of the Gesnerioid Gesneriaceae are largely consistent within genera, and, if dysploidy is taken into account, even within tribes: in tribe Gloxinieae most genera have x = n = 13 (a few n = 12, 11 or 10), the number n = 9 is constant almost throughout Episcieae, n = 9 (two genera have n = 8), in Sinningieae n = 13, in Gesnerieae n = 14 (see Wiehler 1983, Burtt & Wiehler 1995). Based on a combination of molecular and karyological data two base numbers are assumed by Zimmer et al. (2002): n = 16 (Beslerieae and Napeantheae) and n = 13. The latter number has been retained in Gloxinieae (with rare reductions to 12, 11 or 10) and Sinningieae, but has been increased to n = 14 (Gesnerieae) and reduced to n = 9 in Episcieae (with further reduction to n = 8). With very few exceptions, polyploidy is unknown in the Gesnerioid Gesneriaceae.

In contrast, in the paleotropical Gesneriaceae the karyological situation is confusingly diverse and no clear patterns can be recognised at present. The larger genera exhibit often two, three or more base numbers. Polyloidy is not uncommon.

There are also striking ecological differences: (1) A large proportion of Gesnerioid Gesneriaceae, especially of tribe Episcieae, is epiphytic (in the paleotropical Gesneriaceae epiphytes are mainly represented in two genera: *Aeschynanthus* and *Lysionotus*). (2) Ornithophily plays a very important role (essentially ornithophilous genera of paleotropical Gesneriaceae are only *Aeschynanthus* and *Agalmyla*, otherwise bird-pollination is found only exceptionally). (3) Seed dispersal by birds is frequent. Soft and fleshy berry fruits are represented throughout Episcieae and in many Beslerieae. In contrast, indehiscent fruits are found only in very few paleotropical Gesneriaceae, soft fleshy berries only in *Rhynchotechum* and the Pacific species of *Cyrtandra*.

**Epithematoid Gesneriaceae:** This small group of paleotropical Gesneriaceae (7 genera, c. 80 species) is notable in several respects. Though the core distribution is in S and SE Asia, there are two remarkable disjunctions: one species of *Epithema* (*E. tenue*) occurs in West Africa, and one species of *Rhynchoglossum* (*R. azureum*) in Central America. In the first case, molecular data indeed indicate an isolated position of *E. tenue* and thus suggest that the disjunction is old. In contrast, *R. azureum* is very close to the South Indian species of *Rhynchoglossum* and its occurence in the neotropics probably due to a rather recent introduction (see above).

The whole group is characterised by a complex and complicated morphology, usually associated with anisophylly. The peculiar morphology of Brown's *Monophyllaea*, *'Loxotis obliqua'* = *Rhynchoglossum obliquum*, and *'Loxonia acuminata'* = *L. hirsuta* has been already addressed above. Also the South Chinese genus *Whytockia* was mentioned, which, despite its caulescent-anisophyllous habit and thus very different appearance, is close to *Monophyllaea* in shoot architecture and apparently represents a relic of the stock from which *Monophyllaea* evolved. Molecular data confirm the close relationship of the two genera (Mayer et al. 2003). *Stauranthera*, described by Bentham (1835), has an architecture similar to *Loxonia*, that is a floral region composed of shoot units with a single strongly anisophyllous leaf pair and a terminal inflorescence in the form of an alternicladic thyrse (Weber 1977b). Though the flowers of the two genera are very different, the molecular data confirm their close relationship. Recently, Wang (1981) described a new genus, *Gyrogyne*, which is apparently very close to *Stauranthera*, but has isophyllous leaves and thus suggests an ancestral position. Most peculiar is also the morphology of the genus *Epithema* (Weber 1976b, 1988). Above the strongly unequal, soon decaying cotyledons a large solitary leaf is formed, resembling the single cotyledonary leaf of *Monophyllaea*. This is followed by one or two ± isophyllous leaf pairs. The inflorescences terminating the main axis and the axillary branches consist of a large cucullate bract embracing a single, much contracted pair-flowered cyme. The last genus, *Rhynchoglossum*, with alterniphyllous leaves and the inflorescences reduced to unilateral racemes, was dealt with above in the context of Brown's illustrations in the 'Cyrtandreae'. The molecular data suggest that this genus is sister to all other Epithematoid Gesneriaceae.

**Didymocarpoid Gesneriaceae:** With regard to classification and relationships of the genera, this large group is the least understood group of Gesneriaceae. It comprises the tribes Didymocarpeae, Trichosporeae and Cyrtandreae in the classification of Burtt (1963) and Burtt and Wiehler (1995). This is a large assemblage of genera from Europe (Pyrenees, Balkan Peninsula), tropical and subtropical Africa, E, S and SE Asia and the Malay Archipelao, the more humid parts of Australia, and the Pacific. The available molecular data (Smith 1997, Mayer et al. 2003, Pfosser et al., unpubl. data) reveal that the current classification cannot be upheld. The tribe Cyrtandreae (2–3 genera with indehiscent fruits) is surely artificial, and the same seems to apply to Trichosporeae (5–6 genera with appendaged seeds). Unpublished data indicate that a small number of Asiatic genera (including *Corallodiscus*) is basal to the European Gesneriaceae, the compact group of African Gesneriaceae and the large rest of Asiatic Gesneriaceae, the relationships of which are still little understood (one of the better demarcated groups is that with twisted fruits). The large genus *Chirita* proves highly polyphyletic, with species turning up in four or five clades.

Not surprisingly, the morphology of the large group of Didymocarpoid Gesneriaceae is extremely diverse. The range of growth patterns is from annual herbs and perennials to shrubs and small trees, from rosette plants to large caulescent plants, and from creepers to climbers and epiphytes. The morphologically most remarkable genus is *Streptocarpus*. Brown knew already Lindley's *S. rexii*, a 'rosulate' representative of the genus. This and its allies have been noted and studied since their introduction into cultivation in the early 19th century (Caspary 1858, Crocker 1860). Significant modern studies include Hilliard and Burtt (1971), Noel and van Staden (1975), Jong (1970, 1973, 1978) and Jong and Burtt (1975).

In subg. *Streptocarpus*, to which *S. rexii* belongs, a wide array of unusual morphologies is found. The most conspicuous is that in which only a single foliar organ is present in the form of a giant and ever-growing macrocotyledon. In these plants a mesocotyl is developed (internode between the macro- and the microcotyledon), but the hypocotyl and the mesocotyl remain short and develop into a stout 'stalk'. The macrocotyledon and the „stalk' form an integrated structure which has been termed 'phyllomorph' by Jong (1970). Growth is by a trinity of meristems: (1) the 'basal meristem' which is situated at the lamina base and which is responsible for the continuous growth of the foliar structure, (2) the 'petiolode meristem' which is an intercalary meristem located in the upper part of the stalk ('petiolode'), and (3) the 'groove meristem' situated at the junction of the petiolode and the lamina. The most remarkable structure is the 'petiolode'. It forms a continuous transition between the axial mesocotyl and the lamina base and represents functionally a petiole. Jong, therefore, regards it as a mixture of leaf-like and stem-like properties.

These 'unifoliate' species of *Streptocarpus*, consisting of the 'cotyledonary phyllomorph' only, are monocarpic, perishing after producing inflorescences, flowers and fruits. Maturity is reached in most species after two or several years growing. In the species living in a marked seasonal climate, a unique mode of survival of the unfavourable dry period has developed: the lamina sheds a large distal part (60% in *S. molweniensis*) through abscission. On the return of favourable conditions growth is resumed from the remaining basal region of the lamina. By this type of unique perennation the basal meristem is safeguarded against a depletion of nutrient and water reserves.

The phyllomorphic organisation is not only characteristic of the unifoliate species, but also of the 'plurifoliate' and 'rosulate' species. Their plant body can be understood as a succession of phyllomorphs. In the plurifoliate species (e.g., *S. polyanthus*) two or few phyllomorphs are produced, each repeating the structure of the cotyledonary phyllomorph. Perhaps the most remarkable plurifoliate species is *S. fanniniae*, in which the curious complexity and morphological unorthodoxy has been studied in detail by Jong (1970) and Jong et Burtt (1975). The plant produces long petiolodes, so that a long-creeping, climbing and trailing habit is reached. From the petiolodes vegetative buds and new branches are produced. By its open and diffuse habit of growth the species helped to lay the foundation of the phyllomorph concept.

'Rosulate' species such as *S. rexii*, *S. gardenii* etc. bear a close resemblance to familiar rosette plants. However, the rosette is not made up of simple leaves, but of phyllomorphs with a distinct petiolode at the lamina base. Within the rosulate species at least two distinct patterns can be recognised: the centric and the excentric pattern. In the first the phyllomorphs are arranged in a spiral phyllotactic sequence on a condensed vertical axis. In the latter the phyllomorphs are arranged in two ranks on the upper surface of a horizontal rhizomatous axis. Here the axis is composed of an aggregation of petiolode bases. These are often pigmented, supplied with stomata and bear roots. The resemblance to a conventional rhizome is largely superficial. Both in the centric and excentric pattern the phyllomorphs produce vegetative buds on the petiolodes and from these buds lateral rosettes or branch 'rhizomes' develop. Roots arise regularly from the base of the petiolodes, so that each phyllomorph is provided with its own root system. Each individual phyllomorph of the rosette is monocarpic and perishes after flowering and fruiting.

All these properties show that the 'rosettes' of rosulate *Streptocarpus* are far from being ordinary rosettes, but consist of subsequent, highly integrated, repetitive units with morphological and developmental features not found in other plants.

The various growth forms found in Streptocarpus seem to have either evolved several times independently, including reversals and intermediate architectures, or are the result of horizontal gene transfer (Möller & Cronk 2001).

## Concluding remarks

With his treatise on Gesneriaceae in the 'Cyrtandreae' and 'Plantae Javanicae rariores', Robert Brown laid an important foundation for the knowledge of one of the most fascinating families of Angiosperms. Apart from describing a number of new taxa, Brown provided strong arguments for the amalgamation of the paleotropical Cyrtandraceae/Didymocarpaceae with the neotropical Gesneriaceae, a conclusion which was reached (independently or induced by Brown?) also by D. and G. Don

(1831 and 1838, respectively). Molecular data confirm that the paleo- and neotropical Gesneriaceae indeed belong together and that Gesneriaceae, unlike Scrophulariaceae, represent a monophyletic family. Each of the four groups recognised here informally, exhibits interesting and uncommon features as to morphology, phytogeography, ecology and/or evolutionary history.

## Scrophulariaceae

To the author's knowledge, Robert Brown's did not discuss or essentially contribute to the circumscription and systematics of Scrophulariaceae. Therefore, this aspect can be kept very brief, and only a comparison is given what Scrophulariaceae have been in Brown's time and what they are now. Brown's importance is to be seen in the establishment of a number of new genera and numerous new species, especially from Australia.

### The Scrophulariaceae in Brown's 'Prodromus'

Robert Brown's most significant contribution to the knowledge of Scrophulariaceae is the treatment of the family in his 'Prodromus florae Novae Hollandiae et Insulae Van Diemen' (1810). This significant early flora of Australia and Tasmania was the result of Robert Brown's personal (and his companions') collections and observations in this then very remote part of the world. Brown went as a naturalist on one of the expeditions of Mathew Flinders to Australia in 1801 (with the ship 'Investigator') and returned to England in 1805. In the subsequent years Brown worked hard on the collected material. In the 'Prodromus', Latin descriptions of 464 genera and ca. 1000 species were provided. 187 genera were described as new, the majority (146) still standing today (Mabberley 1985: 164).

The treatment of Scrophulariaceae, under the name 'Scrophularinae' and including 'Personatarum genera L., Scrophulariae Juss., and Pedicularum genera Juss.', covers 10 pages (433–443) and includes the following genera and species (the names are given here in alphabetical order and in nomenclaturally updated form). Current names are given where easily possible, but no guarantee upon completeness can be given.

***Adenosma*** R.Br.: *A. caerulea* R.Br.

***Buchnera*** L.: *B. asperata* R.Br. [now considered conspecific with *B. linearis* R.Br.], *B. curviflora* R.Br. [now *Striga curviflora* (R.Br.) Benth.], *B. gracilis* R.Br., *B. linearis* R.Br., *B. parviflora* R.Br. [now *Striga parviflora* (R.Br.) Benth.], *B. ramosissima* R.Br., *B. tenella* R.Br., *B. tetragona* R.Br., *B. urticifolia* R.Br.

***Centranthera*** R.Br.: *C. hispida* R.Br.

***Euphrasia*** L.: *E. alpina* R.Br., *E. arguta* R.Br., *E. collina* R.Br., *E. paludosa* R.Br. [now *E. collina* R.Br. subsp. *paludosa* (R.Br.) W.R. Barker], *E. scabra* R.Br., *E. speciosa* R.Br. [now *E. collina* R.Br. subsp. *speciosa* (R.Br.) W.R.Barker], *E. striata* R.Br., *E. tetragona* R.Br. [now *E. collina* R.Br. subsp. *tetragona* (R.Br.) W.R. Barker].

***Gratiola*** L.: *G. latifolia* R.Br. [now *G. peruviana* L.], *G. pedunculata* R.Br., *G. pubescens* R.Br.

***Herpestis*** Gaert.: *H. floribunda* R.Br. [now *Bacopa floribunda* (R.Br.) Wettst.].

***Limnophila*** R.Br.: L. gratioloides R.Br., nom. illegit. [= *Limnophila indica* (L.) Druce, based on *Hottonia indica* L.].

***Limosella*** L.: *L. australis* R.Br.

***Lindernia*** L.: *L. alsinoides* R.Br., *L. scapigera* R.Br., *L. subulata* R.Br.

***Mazus*** Lour.: *M. pumilio* R.Br.

***Microcarpaea*** R.Br.: M. muscosa R.Br., nom. illegit. [now *Microcarpaea minima* (Koen. ex Retz.) Merr.

***Mimulus*** L.: *M. gracilis* R.Br., *M. repens* R.Br.

***Morgania*** R.Br.: *M. glabra* R.Br., *M. pubescens* R.Br.

***Ourisia*** Commers.: *Ou. integrifolia* R.Br.

***Scoparia*** L.: *S. dulcis* L.

***Torenia*** L.: *T. flaccida* R.Br. [now *Lindernia crustacea* (L.) F.Muell.], *T. hexandra* R.Br. [now *Lindernia crustacea* (L.) F.Muell.], *T. scabra* R.Br. [now *Lindernia crustacea* (L.) F.Muell.].

***Uvedalia*** R.Br. [now included in *Mimulus* L.]: *U. linearis* R.Br. [now *Mimulus uvedaliae* Benth.].

***Veronica*** L.: *V. arguta* R.Br., *V. calycina* R.Br., *V. distans* R.Br., *V. formosa* R.Br., *V. gracilis* R.Br., V. labiata R.Br., nom. illegit. [now *Derwentia derwentiana* (Andrews) B.G.Briggs & Ehrend.], *V. perfoliata* R.Br. [now *Derwentia perfoliata* (R.Br.) B.G.Briggs & Ehrend.], *V. plebeia* R.Br.

## The new genera

As is apparent from the list, Brown described six new genera. With the exception of *Uvedalia* all genera still stand today. From these, only *Morgania* is a 'truly' Australian genus, while the others proved to have a wide distribution, with Brown's species occurring rather at the periphery. In the following the genera are briefly surveyed.

***Adenosma***, described by Brown from a single species from Australia (*A. caerulea* R.Br., the type species), is now a genus of some 15 species, with the distribution ranging from China over Indomalesia to Australia.

***Centranthera***: also described from a single Australian species (*C. hispida*, the type), includes now 5–6 species with similar distribution as *Adenosma*.

***Limnophila:*** This is a conserved name, antedated by *Ambulia* Lam. (1789). *Limnophila* is a well-known genus, in which at present c. 35 species are distinguished, occurring mainly in tropical Africa and Asia.

***Microcarpaea***: a monospecific genus distributed in tropical Asia and Australia.

***Morgania:*** this is the only genus with exclusive distribution in Australia. Four species have been described so far. The best known is perhaps *M. glabra* with charming blue flowers (Fig. 4).

***Uvedalia:*** this has been reduced to *Mimulus* by Bentham (1846).

## The new species

Nearly all species listed and described by Brown were new to science - not surprising, of course, as Australia was largely terra incognita at his time.

The few exceptions include: *Scoparia dulcis*, already known to Linnaeus (1753), '*Microcarpaea muscosa*', already described by Koenig (in Retz 1789) as *Paederota minima*, 'Limnophila gratioloides', already known to Linnaeus as *Hottonia indica*, and the illegitimate 'Veronica labiata', for which Brown quoted *Veronica derwentia* as a synonym (see below).

## Transfers and reductions

Two of Brown's species of *Buchnera* have been transferred to *Striga* (Bentham 1835). The only species of *Uvedalia* is now in *Mimulus*, as *M. uvedaliae* Benth. Some of Brown's species of *Euphrasia* have been ranked as subspecies of *E. collina* (Barker 1982). Brown's species of *Lindernia* and *Torenia* have been transferred to *Vandellia* by Bentham (1846), but this is now regarded a subgenus of *Lindernia*. *Veronica perfoliata* and the illegitimate V. labiata (*V. derwentia* Andrews) have been transferred to *Parahebe* (Briggs & Ehrendorfer 1968) and recently to *Derwentia* (Briggs & Ehrendorfer 1992). Recent molecular studies (Albach & Chase 2001), however, point to a union of *Hebe*, *Parahebe* and *Derwentia* with the genus *Veronica*.

## Extinct or threatened species

One of the scrophulariaceous species described by Brown is recorded as extinct on the list of Australia's endangered species: *Euphrasia arguta*

**Fig. 4.** *Morgania glabra* R.Br., ANBG photo no. a4397, phot. M. Fagg, reproduced with permission of Australian National Botanic Gardens.

(http://www.nationalparks.nsw.gov.au/npws.nsf/Content/Euphrasia+arguta+presumed+extinct+species+listing).
*Euphrasia scabra* R.Br. is recorded as endangered
(http://www.nationalparks.nsw.gov.au/npws.nsf/Content/Euphrasia+scabra+a+herb+-+endangered+species+listing) and the same holds true for *E. collina* R.Br. subsp. *muelleri* (Wettst.) Barker
(http://www.nationalparks.nsw.gov.au/PDFs/lost_flora_approved.pdf). Others may be threatened or vulnerable as well, but no information is available at present.

## The Scrophulariaceae in Salt's 'Voyage to Abyssinia' (1814)

In 1809 and 1810, Henry Salt conducted his well known 'Voyage to Abyssinia'. This was primarily for commercial reasons, but Salt had also an eye on the political conditions, customs, folklore, languages, etc. His freight included a number of plants which were collected for Joseph Banks. Banks, however, had died when Salt returned to England and the plant collection was passed to R. Brown. Brown identified the plants and published them in a part of Appendix 4 of Salt's 'Voyage' under the heading 'List of new and rare plants, collected in Abyssinia…'. The list was re-printed in Flora 4(1), 1821. Of the 146 species, all but 15 were new (Mabberley 1985: 193). Unfortunately, the new names are almost exclusively nomina nuda; some species were validly published by others elsewhere. With respect to Scrophulariaceae, the following species names were validated or synonymised later by Bentham (1846):

Buchnera orobanchoides R.Br., nom. nud. = *Striga orobanchoides* R.Br. ex Benth. = *Striga gesnerioides* (Willd.) Vatke

L. gracilis R.Br., nom. nud. = *L. gracilis* R.Br. ex Benth., L. hastata R.Br., nom. nud. = *L. hastata* R.Br. ex Benth., L. propinqua R.Br., nom. nud. [already considered conspecific with *L. gracilis* by Bentham 1846].

Meisarrhenia tomentosa R.Br., nom. nud. = *Anticharis arabica* Endl., Bentham 1846

## New species of *Pedicularis* from the north polar regions

Later, around 1820, Brown was also engaged with collections brought back by William Perry, John Franklin and others from the polar regions. Two new species of *Pedicularis* were named by him: *P. arctica* R.Br. [now *P. langsdorffii* [Fisch. ex] Stev. var. *arctica* (R.Br.) L.I.Ivanina] and *P. nelsonii* R.Br.

## Scrophulariaceae in Brown's time and now

When Brown's 'Prodromus' appeared 1810, Scrophulariaceae was already a considerably large family. Until 1800 around 70 genera had been established, more than 30 genera (mixed with representatives of various other families) were already listed in Linné's 'Species plantarum' (1753). This is in great contrast to Gesneriaceae, but not surprising, as Scrophulariaceae is an essentially temperate family with many genera and species occurring in Europe. In 1846 and 1876, Bentham published his classical treatments on the family, which then were followed by that of Wettstein for Engler and Prantl's 'Natürliche Pflanzenfamilien' (1891). At that time c. 180 genera were known and the species number amounted to about 2600. Many authors followed Bentham's and Wettstein's circumscription and subdivision of the family into three subfamilies: Pseudosolaneae, Anthirrhinoideae and Rhinanthoideae.

Many more genera and species have since been added and the family Scrophulariaceae has grown to a considerable size. Conventional estimates give a number of c. 3000 species, but the actual number is certainly much higher (see below).

Like most large families, the history of the classification of Scrophulariaceae comprises many treatments differing in circumscription of the family (see Olmstead and Reeves (1995)) and the dispute has not come to an end yet. It is impossible to refer in detail to the many attempts to classify this family, the morphological heterogeneity of which is well known.

The molecular data of Olmstead and Reeves (1995), Olmstead et al. (2001), Beardsley and Olmstead (2002), yielded clear evidence that Scrophulariaceae and some other families of the Lamiales are not tenable in the traditional sense and have to be split into several independent families. They suggest the following classification:

(1) Scrophulariaceae s.str. (part or all of the traditional tribes Aptosimeae, Hemimerideae, Leucophylleae, Manuleae, Selagineae, and Verbasceae = Scrophularieae, plus the traditional families Buddlejaceae and Myoporaceae)

(2) Plantaginaceae (= Veronicaceae, the name used by Olmstead et al. 2001, but being not in agreement with the rules of ICBN) (all or part of the scrophulariaceous tribes Angelonieae, Antirrhineae, Cheloneae, Digitaleae, Gratioleae, and Veroniceae plus the conventional families Callitrichaceae, Globulariaceae, Hippuridaceae, and Plantaginaceae).

(3) Orobanchaceae (tribes Buchnereae, Rhinantheae, plus the conventional Orobanchaceae plus *Lindenbergia*, see also Young et al. 1999).

(4) Calceolariaceae (tribe Calceolarieae). This family, newly established by Olmstead et al. 2001) comprises the three genera *Calceolaria, Jovellana* and *Stemotria* (= *Porodittia*). Olmstead's and some other molecular studies indicate that *Calceolaria* / Calceolariaceae occupy a rather basal position within the order Lamiales, only preceeded by Plocospermataceae, Oleaceae and Tetrachondraceae.

(5) Stilbaceae (expanded by the inclusion of *Halleria*).

(6) Phrymaceae (with *Phryma* – formerly placed in Verbenaceae, *Glossostigma, Peplidium, Mimulus* – apparently not monophyletic and indicating that at least six other genera have been derived from within this taxon, *Mazus, Lancea, Hemichaena, Berendtiella* and *Leucocarpus*), see Beardsley and Olmstead (2002).

The most recent treatment of overall Scrophulariaceae is that of E. Fischer for Kubitzki's 'Families and genera of vascular plants' (2004, in press). Formally, Fischer (2004) maintains Scrophulariaceae as a single family, even in a very wide sense with the inclusion of the parasitic Orobanchaceae (following Takhtajan 1997). The number of genera and species is given with 306 and 5850, respectively. Even if Orobanchaceae are excluded, the species number goes far beyond 5000 species.

Informally, however, Fischer divides the Scrophulariaceae into 8 'families', with

(7) Schlegeliaceae (with *Schlegelia, Gibsoniothamnus, Synapsis, Exarata*) and

(8) Paulowniaceae (with *Paulownia* and the possibly congeneric *Shiuyinghua*) additional to those listed above.

Brown's new genera fall into three families: *Adenosma, Limnophila* and *Morgania*: Plantaginaceae (Veronicaceae); *Centranthera*: Orobanchaceae; *Uvedalia* (*Mimulus*) and (?) *Microcarpaea*: Phrymaceae.

## Concluding remarks

With the advent of molecular methods Scrophulariaceae have become a rather bewildering assemblage of plant groups. In contrast to Gesneriaceae, which clearly represent a monophyletic group, traditional Scrophulariaceae obviously must be abandoned and replaced by a series of some 8 families of their own. The morphology of the families and the relationships of the genera within the families are still incompletely understood. Without a doubt, Scrophulariaceae s.l., to which R. Brown has contributed a number of interesting new genera and species, especially from Austrialia, provide a wide and promising field of future research, both in molecular and morphological respects.

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# New Western Australian species of *Hypolaena* (Restionaceae) and a new section

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## Abstract

*Briggs, Barbara G. and Johnson, L.A.S. (National Herbarium of New South Wales, Mrs Macquaries Road, Sydney, NSW 2000, Australia) 2004. New Western Australian species of* Hypolaena *( and a new section* Telopea *10(2): 573–580. Hypolaena* is divided into section **Homeolaena**, consisting only of *H. humilis* (Gilg) B.G. Briggs & L.A.S. Johnson and section *Hypolaena*, including the remaining seven species. Two of these species, **H. viridis** and **H. caespitosa**, are from the south of Western Australia and are newly described and illustrated. The name *H. grandiuscula* F. Muell. is adopted for a further taxon from the same region and a **lectotype** selected. All these three species occur from near Busselton to near Walpole or Denmark; *H. viridis* and *H. caespitosa* are relatively common but *H. grandiuscula* appears to be rare throughout its range.

## Introduction

As currently recognised, *Hypolaena* R. Br. (Brown 1810: 251) includes eight species (Linder et al. 1998, Briggs & Johnson 1999), including the two described here. It is typified by *H. fastigiata* R. Br., (typ. cons., ICBN 1988:170) which occurs in both western and eastern Australia. The other species are limited to the south of Western Australia, as follows: *H. exsulca* R. Br. (Brown 1810: 251), *H. humilis* (Gilg) B.G. Briggs & L.A.S. Johnson (recently transferred from *Leptocarpus*, Briggs & Johnson 1998), *H. robusta* K.A. Meney & J.S. Pate (Meney et al. 1996), *H. pubescens* (R. Br.) Nees and *H. grandiuscula* F. Muell. (name newly adopted here, see below). *Hypolaena pubescens* was originally described as *Restio pubescens* R. Br. (Brown 1810: 247) and was appropriately transferred to *Hypolaena* by Nees (1846: 69) but was, until recently, generally known as *Loxocarya pubescens* (R. Br.) Benth. (Bentham 1878: 242). We drew attention to its affinities to other *Hypolaena* species (Briggs & Johnson 1999), a placement also adopted by Meney et. al. (1999). The species here newly described were included in our conspectus of Restionaceae (Briggs & Johnson 1999); information on them and other *Hypolaena* species is given by Meney et. al. (1999). A description of the genus is provided by Linder et al. (1998) and an account of all species of *Hypolaena* will be given in the Flora of Australia (Briggs, Johnson, Porter & Krauss in preparation).

Although Brown (1810) included only two species, both Australian, when describing the genus, *Hypolaena* was later greatly enlarged, especially by Masters (1869, 1878), by the inclusion of South African species and by Australian species that were originally described in *Calorophus* Labill. and *Loxocarya* R. Br. The African taxa have since been removed, mostly to *Calopsis* (Linder 1985). The Australian species transferred by Masters to *Hypolaena* are now distributed among *Calorophus*, *Desmocladus*, *Empodisma* and *Loxocarya*, while Brown's original two species remain in *Hypolaena*.

## Sectional classification of *Hypolaena*

Bentham (1878) divided *Hypolaena* into section *Hypolaena* (as *Euhypolaena*) and section *Calorophus*. *Calorophus* Labill. is now recognised at generic rank and the three species

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[†] Deceased 1 August 1997.

Bentham placed in the latter section are now divided between *Calorophus* and *Empodisma* L.A.S. Johnson & D.F. Cutler (1973) (Johnson & Briggs 1991). Later, Bentham and Hooker (1883) again divided *Hypolaena* into sections, indicating their distinguishing features but not the species referred to each section. From the features and distributions given, section *Tenues* equates to section *Calorophus* Benth. and section *Africanae* included only African taxa, both groups of species now excluded from *Hypolaena*; while section *Restioideae* included the species now remaining in *Hypolaena*. The past sectional division of the genus has thus been rendered ineffective.

*H. humilis* is, in our opinion, appropriately placed in *Hypolaena* but differs notably from the other species. As foreshadowed previously (Briggs & Johnson 1999), we consider that it is appropriate to establish a section with *H. humilis* as its only member, the other species being placed in the autonomic section *Hypolaena*, typified by *H. fastigiata* R. Br.

**Hypolaena** *section* **Homeolaena** *B.G. Briggs & L.A.S. Johnson*, **sect. nov.**

Type species: *H. humilis* (Gilg) B.G. Briggs & L.A.S. Johnson, Telopea 8: 28 (1998).

A sectione *Hypolaena* combinatione characterum sequentium distinguitur: nuces tepalis bractisque circumcinctae exutae; axis fulcrans floris feminei brevissimus, bracteis haud reductis instructus; tepala nuxem excedentia.

Distinguished from section *Hypolaena* by the whole female spikelet acting as the dispersal unit; dispersed with 4–6 bracts and the six tepals all surrounding the fruit; the female floral axis very short and with a pair of unreduced bracts similar in size and texture to the spikelet bracts and tepals; tepals imbricate and longer than the nut (Fig. 1a, b). In section *Hypolaena* the floral axis abscisses above the spikelet bracts in the fruiting stage; the nut is dispersed with the tepals and, below them, a short fleshy axis that appears to act as an elaeiosome and bears two reduced bracts near the base; tepals not imbricate, longer than the nut or (in most species) much shorter (Fig. 1c, 3c, d, h). Both sections of *Hypolaena* have compound female spikelets, although with a single flower; the compound structure is apparent only by careful dissection and comparison with related genera.

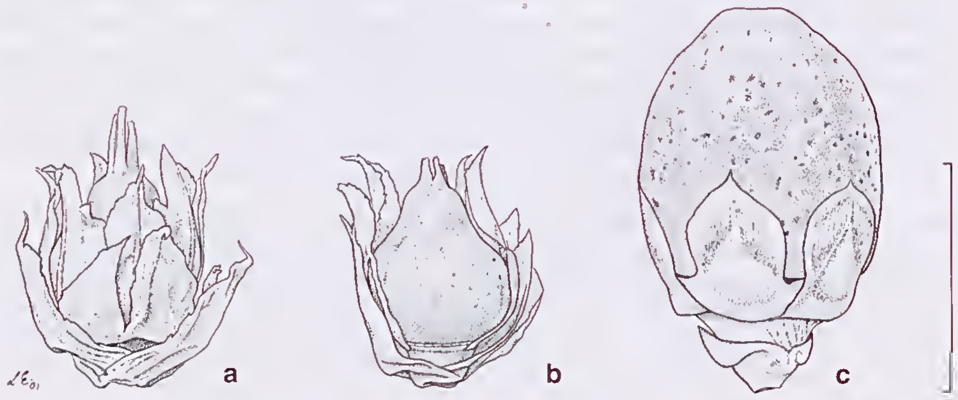

**Fig. 1.** Female spikelets in fruiting stage, **a–b**, *H. humilis*, **a**, as dispersed, nut surrounded by tepals, floral bracts and spikelet bracts; **b**, as (a) but some bracts and tepals removed (48 km SW of Ravensthorpe, *Briggs 460* NSW); **c**, *H. pubescens*, as dispersed, nut with tepals and floral bracts (10 km WNW of Busselton, *Briggs 6463* NSW). Scale bar = 2 mm.

*Homeolaena* is derived from the Greek *homoios*, uniform or similar and *laina*, a cloak, referring to the similarity between the floral bracts, spikelet bracts and tepals.

## New species of section *Hypolaena* and an old name newly adopted

### Hypolaena viridis *B.G. Briggs & L.A.S. Johnson*, sp. nov.

Type: Western Australia: Brockman Highway, 3.3 km W of junction with Sues Rd (c. 27 km E of Karridale), 6 Oct 1984, *B.G. Briggs 7571 & L.A.S. Johnson* ♂ (holo PERTH; iso NSW, AD, CANB, K, MEL, MO, NBG, PRE, RSA).

A *H. exsulca* combinatione characterum sequentium distinguitur: culmi plerumque 1–2 cm separati, concavo-convexi; vaginae culmorum abrupte contractae; bracteae spicularum feminearum non recurvatae.

Rhizome creeping, stout, 4–6 mm diam.; scales glossy orange-brown, partly covering a brown pubescence. Culms spaced mostly 1–2 cm apart on the rhizome, erect to slightly sinuose, compressed and concavo-convex in section, striate, branched, 30–40 cm long, 0.5–1.5 mm wide, mostly glabrous but the lower part with flat multicellular hairs closely appressed to epidermis. Culm sheaths 5–12 mm long, tapering abruptly; with an auriculate, evanescent, membranous margin; lamina usually absent, if present then shortly erect, c. 1 mm long. Male spikelets 1–5(–7) on each of several short slender branches at a few upper nodes of the culm, pedicellate, mostly erect, narrow ovoid, 4.5–7.5 mm long; glumes 15–30, all fertile or with up to 6 sterile lower glumes, ovate, acute to minutely mucronate, concave, glabrous, brown, 1.8–2.3 mm long, with a broad apical hyaline margin. Female spikelets usually solitary and terminal on ± erect, slender branches, very-narrow ovoid, c. 15 mm long, c. 2 mm diam.; glumes 6–8, lanceolate, cuspidate, brown becoming greyish with age, glabrous, 6–13 mm long. Male flowers: tepals 6; outer tepals oblanceolate, truncate; 1.2–1.5 mm long; inner tepals slightly longer, ± flat, lanceolate to oblanceolate, acute to truncate; anthers c. 0.8 mm long. Female flowers: tepals 6, dark brown, oblong, blunt, appressed to the nut, c. 2.3 mm long. Nut: broad cylindrical, tapering distally, rugose, light-brown, 4 mm long. (Fig. 2 e–g).

The epithet is from the Latin, *viridis*, green, referring to the culms; most other *Hypolaena* species have grey-green culms.

**Distribution:** occurs in the south-west of Western Australia from the Busselton and Augusta districts to north of Walpole. Grows near streams, in poorly drained heathy swamps and woodland, on sand or clayey or peaty sand; sites moist most of the year; sometimes in seasonally inundated sites. Resprouts after fire.

**Conservation status:** common, not at risk.

Resembling *H. exsulca* but culms concavo-convex, spaced mostly 1–2 cm apart on the rhizomes; culm sheaths abruptly tapering and with an evanescent membranous margin; male spikelets tapering distally; bracts of female spikelets straight. *H. exsulca* has terete culms, spaced mostly 0.5 cm apart; culm sheaths gradually tapering and with a wide persistent membranous margin; male spikelets almost truncate; bracts of female spikelets becoming recurved. (Fig. 2 h–j).

**Selected specimens examined:** Western Australia; Darling: Jindong, Busselton district, 18 Oct 1948, *R. Royce 2861* ♀, *2862* ♂ (PERTH); Carbunup River, 1.5 miles [2.4 km] SW of Jindong, W.A., 20 Sep 1966, *Briggs 869* ♂ (NSW, MEL); c. 27 km E of Karridale, 6 Oct 1984, *Briggs 7572 & Johnson* ♂ (NSW, BRI, CANB, CBG, HO, K, L, MO, NBG, PERTH, PRE, RSA); Brockman Hwy, 18 miles [29 km] E of Alexandra Bridge, 19 Sep 1966, *Briggs 689* ♀, *692* ♂ (NSW, AD, PERTH); 6.4 km SW of Mt Frankland, 18 Sep 1966, *Briggs 649* ♂ (NSW, CANB); South Western Highway 37.5 km S of Deeside Coast Road, 7 Jan 1989, *K. Meney 4c* ♀ (NSW);12 km N of Walpole on North Walpole Road, 7 Oct 1984, *Briggs & Johnson 7613* ♂ (NSW, CANB, NBG, PERTH, PRE, RSA).

**Hypolaena caespitosa** *B.G. Briggs & L.A.S. Johnson,* **sp. nov.**

Inter species *Hypolaenae* combinatione characterum sequentium distinguitur: habitus caespitosus; culmi numerosissimi, graciles (0.5–1 mm diametro); pili valde appressi culmis ut videtur glabris.

Type: Western Australia: Dennis Road, 5 km S of Brockman Hwy, c. 16 km E of Karridale, 6 Oct 1984, *B.G. Briggs 7590a & L.A.S. Johnson* ♀ (holo PERTH; iso NSW, AD, BRI, CANB, K, MEL, MO, NY).

Caespitose; basal scales brown, partly covering a woolly pubescence. Culms crowded, erect or ascending, usually somewhat compressed but often ± terete towards the base, striate, much-branched, 30–40 cm long, 0.5–1.0 mm diam, appearing glabrous but with flat multicellular hairs very closely appressed to epidermis. Culm sheaths red- or purple-brown when young, glabrous, 0.5–2.0 cm long, ± acute; lamina erect, caducous 2–12 mm long; margin auriculate, evanescent, membranous. Male spikelets 1–7(–12) on each of several short branches from the upper culm nodes, erect or occasionally pendulous, pedicellate, ± ovoid, 3–4 mm long; glumes 10–15, all fertile, ovate to obovate, acute to minutely mucronate, glabrous, brown, 1.5–2.0 mm long, with a broad apical hyaline margin. Female spikelets on slender pedicels arising at several upper nodes of the culm branches, initially very narrow-cylindrical, 6–10 mm long; glumes 5–8, lanceolate, brown, becoming prominently reflexed and hyaline with age, glabrous, 3.0–8.0 mm long. Male flowers: tepals 6; 2 outer tepals slightly longer, broad-oblanceolate, truncate, 0.8–1.0 mm long; inner tepals flat, lanceolate to oblanceolate, acute to truncate; anthers c. 0.8 mm long. Female flowers: tepals 6, light brown with a dark brown base, oblong, blunt, appressed to the nut, 1–1.5 mm long. Nut: narrowly cylindrical, orange-tan, 1.9–3.0 mm long, c. 1 mm wide. (Fig. 2 a–d).

The epithet is from the Latin *caespes*, a tuft or sod of turf, referring to the caespitose habit.

**Distribution:** occurs in the south-west of Western Australia, from near Busselton to east of Augusta. Grows in sedge and heath swamps on peaty sand or sand over ironstone (laterite) pavement; sites seasonally inundated, in more peaty and less well-drained sites than other *Hypolaena* species in the region. Killed by fire.

**Conservation status**: locally common, not at risk.

Distinguished from all *Hypolaena* species except *H. pubescens* by its caespitose habit. Differs from *H. pubescens* in its very numerous slender culms and lack of long (0.5–4 mm) spreading hairs. Related to *H. exsulca* and *H. viridis* which have culms at intervals on long rhizomes and larger spikelets.

**Selected specimens examined:** Western Australia; Darling: 1 km E of Ruabon, 10 Oct 1976, *Briggs 6731* ♂ (NSW, CANB, PERTH), *6732* ♀ (NSW), *6736* ♂ (NSW, PERTH); c. 7 miles (11 km) SE of Busselton, Boallia to Yoongarillup, 21 Sep 1966, *Briggs 795a* ♂ (NSW); Dennis Road, 5 km S of Brockman Hwy, c. 16 km E of Karridale, 6 Oct 1984, *Briggs 7588 & Johnson* ♂ (NSW, CANB, K, MO, NBG, PERTH, RSA), *7589* ♂ (NSW, B, L, MO, PE, PERTH), *7589a* ♂ (NSW, BOL, PERTH), *7590* ♂ (NSW, AD, BRI, CANB, HO, K, MEL, PERTH); Scott River Road, 4 km S of Payne Road, 20 Nov 1994, *K. Wilson 8969 & K. Frank* ♀ (NSW); 1.1 km E of Scott River Road, on Governor Broome Road, c. 16 km ENE of Augusta, 11 Sep 1990, *Briggs 8669, Johnson, K. Meney, J. Pate & P. Linder* ♀ (NSW), *8670* ♂ (NSW, PERTH), *8670a* ♂ (NSW, BOL); 0.5 km S of Brennan Ford, ENE of Augusta, 12 Sep 1977, *E.N.S. Jackson 3282*, ♂ , ♀ (AD, NSW).

**Hypolaena grandiuscula** F. Muell.

(Mueller, Fragm. 8: 85, 1873)

*H. fastigiata* var. *grandiuscula* F. Muell., Fragm. 8: 85 (1873).

**Fig. 2. a–d**, *H. caespitosa*, **a–c**, female: **a**, habit (only a few of the many culms shown); **b**, inflorescence (*Briggs 7590a*); **c**, fruiting inflorescence (*Briggs 6732*); **d**, male inflorescence (*Briggs 6731*); **e–g**, *H. viridis*, e, female fruiting spikelet (*Briggs 689*), f, male: inflorescence, g, culm sheath (*Briggs 869*); **h–j**, *H. exsulca*, **h**, male inflorescence (*Orchard 1394*); **i**, plant habit with female inflorescences (*Wilson 8106*); **j**, culm sheath (Dec 1912, *Koch*). Scale bar: a, i = 5 cm; b–h, j = 1 cm.

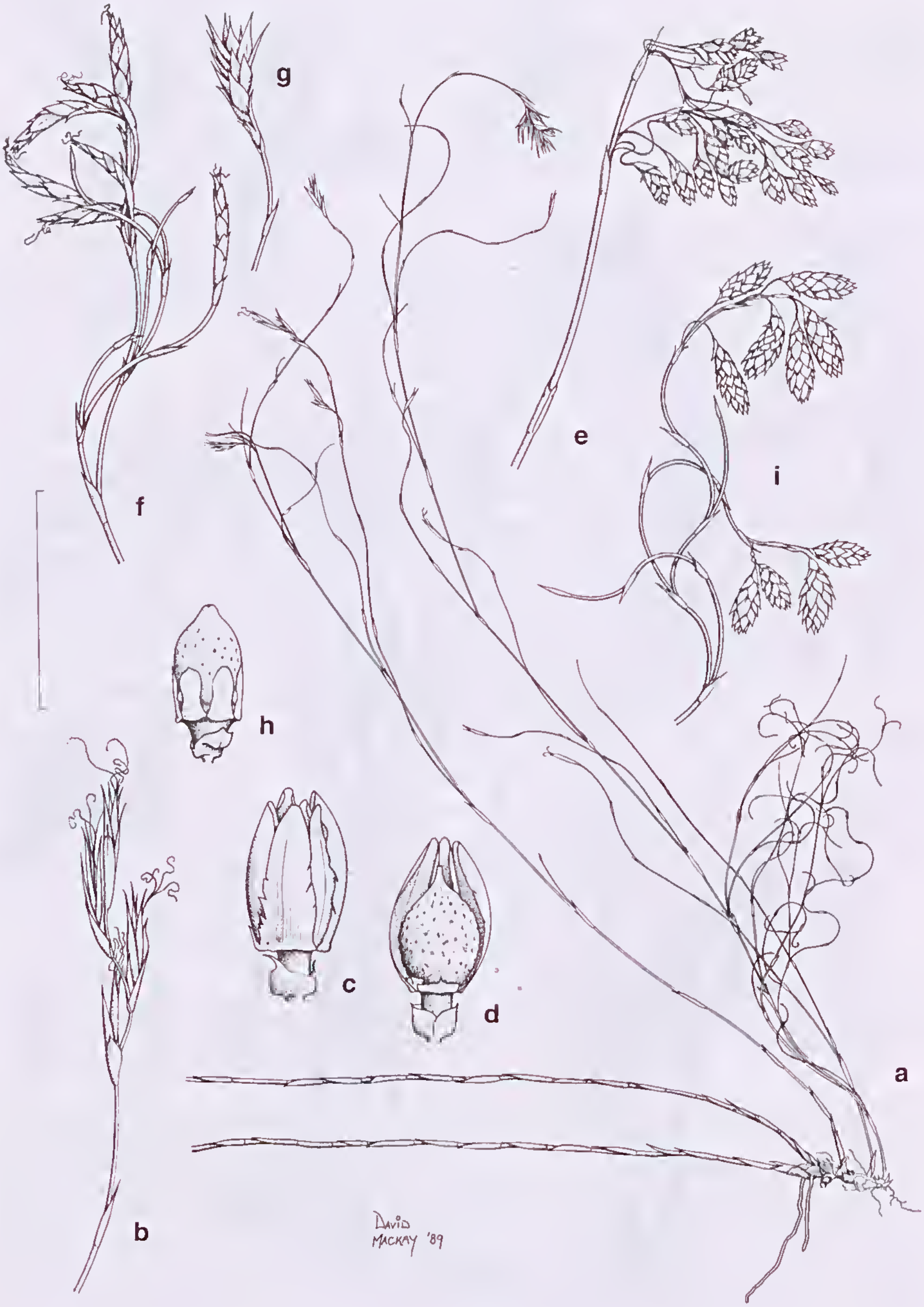

**Fig. 3. a–e**, *H. grandiuscula*, **a–d**, female: **a**, habit, **b**, inflorescence (Bow R., *Gittins 1765b*); **c**, fruit with tepals, **d**, fruit, some tepals removed (Yoongarillup, SE of Busselton, *Briggs 807*); **e**, part of male inflorescence (Bow R., *Gittins 1765a*); **f–i**, *H. fastigiata*, **f–h** female: **f**, part of female inflorescence, **g**, fruiting spikelet (W of Bremer Bay, *Briggs 7847*); **h**, fruit with tepals (SE of Nornalup, *Briggs 7628*); **i**, part of male inflorescence (Bremer Bay, *Briggs 7856*). Scale bar: a = 7.5 cm; b, e–g, i = 2 cm, c, d, h = 0.6 cm.

Type citation: in Australia occidentali prope sinum regis Georgi et montes Stirlingi reperi.

Type: Western Australia: KGS [King Georges Sound], *Oldfield* ♂ (**lectotype, here selected** MEL 14980). Residual syntypes: KGS, *Oldfield* ♂ (MEL 14978, 149879, 14984; 149885); sand near the sea, KGS, *Oldfield* ♂ (MEL 14986); S W Aust, Oct [18]67 ♂ [*Mueller*]. Residual syntype, specific determination doubtful: Stirlings Range, *Mueller* ♂ (MEL 14982)

Mueller simultaneously published alternative names for this taxon at specific and varietal rank; such publication at alternative ranks before 1953 does not invalidate these names (International Code of Botanical Nomenclature Art 34.2). We had previously, however, regarded these as provisional names and had applied the *nomen nudum 'H. macrotepala'* to this species (Briggs & Johnson 1999) and used that name in some herbarium annotations; our usage was also adopted by Meney et al. (1999).

*Hypolaena grandiuscula* (Fig. 3 a–e) resembles *H. fastigiata* R. Br. in its ascending rhizomes and general habit, but differs in the slender orange-brown female spikelets with tepals to 4 mm long (when fruiting) and males with glumes all fertile. It occurs in the south-west of Western Australia on sandy soils from near Busselton to east of Denmark but appears to be rare throughout its range. *Hypolaena fastigiata* (Fig. 3 f–i) has dark red-brown female spikelets with tepals to 1 mm long and males with few to many sterile lower glumes per spikelet; it occurs in the south of Western Australia and in eastern Australia from South Australia and Victoria to Tasmania, and through coastal districts to south-eastern Queensland.

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# *Commersonia rosea* (Malvaceae s.l.: Lasiopetaleae): a new, rare fire-ephemeral species from the upper Hunter Valley of New South Wales

Stephen A.J. Bell and Lachlan M. Copeland

## Abstract

*Bell, Stephen A.J.*[1] *and Copeland, Lachlan M.*[2] *([1]Eastcoast Flora Survey, PO Box 216, Kotara Fair, NSW 2289, Australia, [2]Botany, University of New England, Armidale, NSW 2351, Australia) 2004.* Commersonia rosea *(Malvaceae s.l.: Lasiopetaleae): a new, rare fire-ephemeral species from the upper Hunter Valley of New South Wales.* Telopea *10(2): 581–587.* ***Commersonia rosea*** S.A.J. Bell & L.M. Copel., a fire-ephemeral species from the Central Western Slopes of New South Wales is described as new. Notes on its distribution, ecology and conservation status are given. The species is currently known from just four small populations, totalling c. 200 plants, and is considered endangered.

## Introduction

*Commersonia* J.R. Forst. & G. Forst. is a medium-sized genus with at least 14 published species widely distributed in Australasia and the Pacific Islands (Harden 1990; Short 1996). All 14 species occur in Australia and 12 of them are thought to be endemic (Harden 1990). Although *Commersonia* has traditionally been placed in the Sterculiaceae this family has recently been included within the greatly expanded Malvaceae *s.l.* (Judd & Manchester 1997; Bayer et al. 1999; Whitlock et al. 2001; Wilkins & Chappill 2002). Within Malvaceae *s.l.*, recent molecular and morphological studies suggest that *Commersonia* is best placed within the tribe Lasiopetaleae (Bayer et al. 1999; Whitlock et al. 2001; Wilkins & Chappill 2002).

Since the treatments of Sterculiaceae in the floras of south-eastern Queensland, New South Wales and Victoria (Stanley & Ross 1986; Harden 1990; Short 1996) a number of putative new taxa of *Commersonia* have been discovered. Although some of these taxa have been documented (e.g. Briggs & Leigh 1996; Bell 1997; Henderson 2002) many are yet to be formally described.

During recent vegetation surveys of the Denman-Sandy Hollow area in the Upper Hunter Valley of New South Wales, a distinctive, prostrate taxon with large pink flowers was discovered growing in several disjunct areas around Sandy Hollow. Although originally identified as a species of *Rulingia*, the weakly divided staminodes and the relatively large number of ovules per locule (four to six) suggest that the plant falls within the circumscription of *Commersonia*, following Stanley and Ross (1986) and Short (1996). The presence and shape of the aril also conforms with that indicated for *Commersonia* as depicted in Wilson and Chappill (2002). As the plants did not match any published taxa, an examination of all specimens of *Commersonia* and *Rulingia* in CANB, NSW and NE was conducted (herbarium abbreviations follow Holmgren et al. 1990). This examination supported the recognition of a new species of *Commersonia*.

The species appears to be highly restricted and is currently subject to several threats. For this reason, it was considered appropriate to describe it as new, even though the entire genus of *Commersonia* is in need of revision (C. Wilkins pers. comm. 2002). This paper describes the new species, gives notes on its distribution and ecology and will assist in its conservation.

**Commersonia rosea** *S.A.J. Bell & L.M. Copel.*, **sp. nov.**

*C. melanopetala* F. Muell. et specie inedita (Zamia Range) habitu prostrato similis, sed ab eis floribus paucioribus, majoribus, perspicue roseis et setis capsulae brevioribus differt.

Type: New South Wales: Central Western Slopes: Pikes Gap, 4 km E of Sandy Hollow, 32°20'S, 150°36'E, 250 m alt., *L.M. Copeland 2819 & W.E. Holzinger*, 6 Jan 2001 (holo NSW; iso BRI, CANB, NE).

*Prostrate shrub* 0.1–0.3 m high, producing trailing branches up to 60 cm long. *Branches* terete, densely stellate-hairy (especially on young growth), becoming glabrescent and channelled on older branches; hairs 0.3–0.5 mm long on young growth. *Leaves* petiolate, petioles 4–10 mm long, densely stellate-hairy; stipules linear, 6–9 mm long and 1 mm wide, stellate-hairy, persistent; lamina narrowly oblong to narrowly elliptic, mid-green, (15–) 24–70 mm long, 8–17 mm wide; base obtuse to truncate; margins crenate to toothed; apex obtuse; adaxial surface sparsely to moderately stellate-hairy, with whitish hairs 0.3–0.5 mm long, occasionally mixed with 0.9–1.2 mm long hairs, denser towards leaf margins and along veins; abaxial surface densely stellate-hairy, with whitish hairs of two lengths, 0.3–0.5 mm and 0.9–1.2 mm, longer hairs particularly evident along veins; primary and secondary veins impressed on adaxial surface, raised on abaxial surface. *Inflorescence* a few-flowered, leaf-opposed cyme of 1–3 flowers; peduncle 2–8 mm long; pedicels 2–6 mm long, densely stellate-hairy; bract singular, 0.5–1.0 mm from base of pedicel, linear, 3–10 mm long, persistent, stellate-hairy. *Calyx lobes* 5, 7–9 mm long, pink, abaxial surface densely stellate-hairy with translucent hairs, adaxial surface sparsely to moderately stellate-hairy with translucent hairs. *Petals* 5, free, pink, glabrous, unequally and broadly 3-lobed; 5–7 mm long, 4–5 mm wide at broadest point, linear towards the tips; petal bases broad, truncate and concave about the staminal tube, and then ligulate or tongue-shaped above. *Stamens* 5, almost sessile, opposite the petals: staminal tube white, c. 0.4 mm long; anthers yellow. *Staminodes* 5, white with pink tips, alternating with the stamens, glabrous, each staminode shallowly 3-lobed, the central lobe much wider and more conspicuous than the small, obscure lateral lobes. *Ovary* densely stellate-hairy; styles 5, pale yellowish-green, fused for their entire length; stigmas globular, yellowish-green. *Capsule* globose, lime-green turning pale brown with age, 10–16 mm diameter, densely covered in 2–4 mm long bristles, each bristle sparsely to moderately covered in 2–5 armed stellate hairs, with a 9–16 armed stellate hair apically. *Locules* 5, each with 4–6 ovules. *Seeds* ellipsoid, dark brown, glabrous, warty, 1.5–2.5 mm long; aril basally attached, a creamy-white to pale-brown segmented lobe, 1.0–1.25 mm long. (Fig. 1).

**Selected specimens examined:** New South Wales: Central Western Slopes: Pikes Gap, 4 km E of Sandy Hollow, 32°20'S, 150°36'E, 250 m alt., *L.M. Copeland 1837*, 21 Aug 1999 (NE, NSW); Giants Creek, 2.6 km NW of Sandy Hollow, 32°18'27"S, 150°32'13"E, 340 m alt., *S.A.J. Bell s.n.*, 13 Nov 1996 (NSW); Peberdeys Road, 2.8 km SW of Sandy Hollow, 32°20'50"S, 150°32'32"E, 280 m alt., *S.A.J. Bell s.n.*, 20 Feb 1997 (NSW).

**Illustration**: Bell (1997) *Vegetation survey and mapping of Crown land, south of Manobalai Nature Reserve, upper Hunter Valley*, cover and Pl. 1 (as *Rulingia procumbens*).

**Distribution**: *Commersonia rosea* is currently known from four populations in the Sandy Hollow district of the upper Hunter Valley, New South Wales (Fig. 2). The four localities (Pikes Gap, Giants Creek, Peberdys Road and Boodles Creek) fall within an 8 km radius of Sandy Hollow, within the Central Western Slopes of New South Wales. Specimens from the Boodles Creek population have not been seen by the authors,

**Fig. 1.** *Commersonia rosea* **a,** flowering and fruiting branch; **b,** flower from above, showing calyx lobes and erect, 3-lobed petals; **c,** inflorescence showing flower buds and linear bracts; **d,** capsule with persistent calyx; **e,** capsule bristle with stellate hairs. Scale bar: a = 3 cm; b = 6 mm; c = 8 mm; d = 1 cm; e = 1 mm. (a from *S.A.J. Bell s.n.* 20 Feb. 1997; b, c, d, e from *L.M. Copeland 2819 & W.E. Holzinger.*)

however material has been determined as *Commersonia rosea* (R. Miller, *pers. comm.*). Vegetation surveys in the nearby Manobalai Nature Reserve, Goulburn River National Park, Myambat Logistics Company site, Wollemi National Park and other Crown lands have failed to locate further populations (Bell 1997; Fallding et al. 1997; Hill 1999; Bell 1998; S. Bell *pers. obs*. 2000).

**Flowering:** plants have been observed flowering in August, November, January and February.

**Habitat:** this species occurs on skeletal sandy soils of the Triassic Narrabeen series, in scrub or heath vegetation with occasional emergents of *Eucalyptus crebra, Callitris endlicheri* or *Eucalyptus caleyi* subsp. *caleyi*. Commonly associated understorey species include *Melaleuca uncinata, Acacia triptera, Allocasuarina verticillata, Eucalyptus dwyeri, Acacia doratoxylon, Acacia crassa, Calytrix tetragona, Leptospermum parvifolium, Boronia anethifolia, Melichrus urceolatus, Solanum brownii, Gonocarpus elatus, Hibbertia acicularis, Dampiera purpurea, Cleistochloa rigida, Lomandra glauca, Stypandra glauca, Mirbelia pungens, Halgania brachyrhyncha, Pomax umbellata, Cheilanthes sieberi* subsp. *sieberi* and *Oxylobium pultenaea*. At three of the four sites, fire had occurred within 6–12 months prior to survey (see additional notes below).

**Comparison with similar species:** *Commersonia rosea* is easily distinguished from other species of *Commersonia* in New South Wales by its prostrate habit, smaller leaves, pink flowers, and its few-flowered cymes. Both of the presently recognised New South Wales taxa (*C. fraseri* and *C. bartramia*) are small trees or erect shrubs, with ovate to broad-ovate, 5–17 cm long leaves, possess white flowers in many-flowered cymes, and occur in rainforest or moister eucalypt forest.

Specimens of an undescribed *Commersonia* sp. (*Zamia Range, R.W. Johnson 1398*: Henderson 2002) collected from the Springsure district in Queensland perhaps show the strongest morphological affinities to *C. rosea*. *Commersonia melanopetala* F. Muell. from Western Australia also appears to be similar, and both are compared with *C. rosea* in Table 1. A full revision of the genus is required to better understand relationships between all species.

**Table 1. A comparison of the distinguishing features of *Commersonia rosea* with those of C. sp. (Zamia Range) and *C. melanopetala*.**

| **Character** | ***C. rosea*** | **C. sp. (Zamia Range)** | ***C. melanopetala*** |
|---|---|---|---|
| **Leaf colour (upper surface)** | dark green | pale tan | mid green |
| **Leaf indumentum (upper surface)** | sparsely stellate not velvety | densely stellate hairy, hairy, not velvety | sparsely stellate hairy, appearing velvety |
| **Leaf width** | 8–17 mm | 4–9 mm | 10–25 mm |
| **Capsule diameter** | 10–16 mm | 8–13 mm | 5–8 mm |
| **Flower colour** | deep pink | white to pale pink | pale pink |

*C. rosea* also has larger flowers, fewer flowers per inflorescence and shorter capsule bristles than *C. melanopetala* (which do not differ from the C. sp. Zamia Range specimens).

**Conservation status:** a ROTAP code of 2E (following Briggs & Leigh 1996) is recommended. Two of the four populations are small in size (<15 plants), while a third

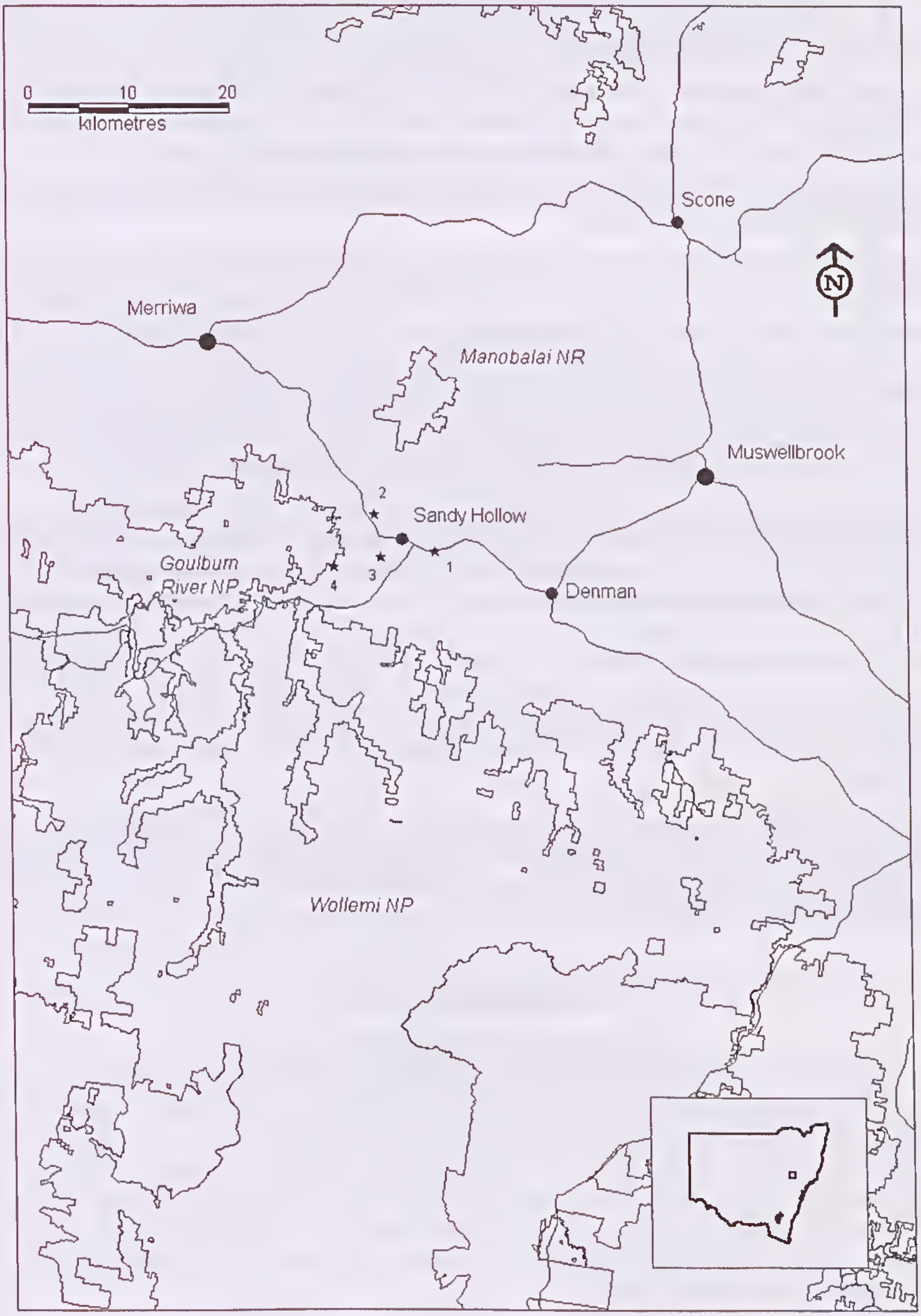

**Fig. 2.** Location of *Commersonia rosea* populations near Sandy Hollow in the upper Hunter Valley, showing existing conservation reserves . ★1 = Pikes Gap, ★2 = Giants Creek, ★3 = Peberdys Road, ★4 = Boodles Creek.

(Peberdys Road) was estimated to contain >100 plants in 1997 (Bell 2001). The species at Boodles Creek was reported to have been locally common over a small area in 1999 (R. Miller, *pers. comm.* 1999). All populations are unreserved and have relatively small occupancy areas. Based on current knowledge, a total population of less than 200 individuals is estimated. The Pikes Gap population occurs along a vehicular track and is particularly threatened by low numbers and physical disturbance through track maintenance. The other three populations occur in Crown land on low ridgetops, and may be threatened by future development should land tenure change.

**Etymology**: The specific epithet *rosea* is from the Latin, and refers to the spectacular deep pink flowers of this taxon.

**Additional notes**: vegetative cuttings taken from the type locality 'struck' particularly easily and have grown quickly. Seed collected from mature fruits have also germinated and produced flowering plants within 18 months under glasshouse conditions. Plants of *C. rosea* appear to be short-lived in cultivation, however, as most plants grown from cuttings flowered, fruited and then died within a 12 month period. Live plants grown from cuttings and/or seed have been donated to the Australian National Botanic Gardens in Canberra, the Hunter Regional Botanic Gardens at Raymond Terrace and Mt Annan Botanic Gardens in south-western Sydney.

All populations have been initially detected after some form of disturbance, either through fire (for Giants Creek, Peberdys Road & Boodles Creek) or roadworks (Pikes Gap). Consequently, *C. rosea* appears to be a fire-ephemeral, flowering and fruiting only after disturbance. A visit to the Peberdys Road site approximately 12 months after the initial observation failed to re-locate the species. In addition, no trace of the species could be found at this location in September 2002, five years after the first discovery. Only two old individuals of the species could be found at the Pikes Gap location in September 2002, these being in poor condition with few leaves and little active growth, possibly as a result of the dry conditions experienced in the upper Hunter Valley at this time.

Bell (2001) briefly discussed three populations of this species (as *Rulingia procumbens*), including reference to the Boodles Creek population. His suggested amendment to the ROTAP conservation code for *R. procumbens* should be disregarded in the light of the recognition here of *C. rosea*.

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# The lichen genera *Cyclographina, Diplogramma, Glyphis, Gymnographa, Medusulina, Sarcographa* and *Sarcographina* (Graphidaceae) in Australia

Alan W. Archer

## Abstract

*Archer, Alan. W. ( Botanic Gardens Trust Sydney, Mrs Macquaries Road, Sydney NSW 2000, Australia).* 2004. *The lichen genera* Cyclographina, Diplogramma, Glyphis, Gymnographa, Medusulina, Sarcographa *and* Sarcographina *(Graphidaceae) in Australia.* Telopea *10(2): 589–605.* The following species are reported from Australia: *Glyphis cicatricosa* Ach., *Sarcographa intricans* (Nyl.) Müll. Arg., *S. labyrinthica* (Ach.) Müll. Arg., *S. oculata* Müll. Arg., *S. subtricosa* (Leight.) Müll. Arg., *S. verrucosa* (Mont. & Bosch) Zahlbr. and *Sarcographina cyclospora* Müll. Arg. The Australian species *Glyphis verruculosa* Zahlbr., *Sarcographa actinota* F. Wilson, *S. colliculosa* (C. Knight) Zahlbr. and *S. kirtoniana* (Müll. Arg.) Müll. Arg. are reduced to synonymy and *Cyclographina platyleuca* (Nyl.) Awasthi & Joshi is restored to *Graphina platyleuca* (Nyl.) Zahlbr. *Diplogramma australienses* is transferred to *Opegrapha* with the new combination **Opegrapha australiensis** and *Gymnographa medusulina* Müll. Arg. is reported as a later synonym of *Phaeographis eludens* (Stirt.) Shirley. The taxonomic position of *Medusulina egenella* (Müll. Arg.) Müll. Arg. remains unclear. A key to the species of *Glyphis, Sarcographa* and *Sarcographina* in Australia is given.

## Introduction

The lichen family Graphidaceae includes 15 genera (Kirk et al. 2001) but includes *Gymnographa* as a synonym of *Sarcographa*; in this present account the two genera are retained, giving a total of 16 genera in the family Graphidaceae. The family in Australia is presently represented by 12 genera, viz: *Acanthothecis* Clem., *Cyclographina* Awasthi & Joshi, *Diplogramma* Müll. Arg., *Glyphis* Ach., *Graphina* Müll. Arg., *Graphis* Adans., *Gymnographa* Müll. Arg., *Medusulina* Müll. Arg., *Phaeographina* Müll. Arg., *Phaeographis* Müll. Arg., *Sarcographina* Müll. Arg. and *Sarcographa* Fée. Of the remaining genera in the family Graphidaceae listed by Kirk et al., *Anomalographis, Gymnographopsis* and *Helminthocarpon* are not recorded for Australia (Filson 1996; McCarthy 2003) and *Gyrostomum* is placed in the family Thelotremaceae (Filson 1996; McCarthy & Elix 1998). A recent, detailed account of the genus *Acanthothecis,* including a description of the single species reported from Australia viz: *A. gracilis* Staiger & Kalb, has been given by Staiger & Kalb (1999). The Australian species in the four major genera have been described elsewhere: *Graphina* (Archer 1999a, 2001a), *Graphis* (Archer 1999a, 2001b), *Phaeographina* (Archer 2000, 2001c) and *Phaeographis* (Archer 2000, 2001d). This leaves the species in the remaining genera found in Australia to be discussed here. *Diplogramma* and *Gymnographa* were previously considered to be monotypic genera, endemic to Australia.

## Material and methods

This account is based on the examination of type and other specimens from BM, G, H, MEL, NSW and WELT and in particular the recent collections made by J.A. Elix and H. Streimann (CANB). The techniques used have been described previously (Archer 1999a, 2000a).

## Key to species of *Glyphis, Sarcographa* & *Sarcographina* found in Australia

1 Ascospores hyaline; lichen compounds absent; ascospores 32–50 μm long, 8–12-locular; widely distributed .................... **Glyphis cicatricosa**

1* Ascospores brown .................... 2

2 Ascospores muriform, 10–13 μm long, 2 × 2-locular; psoromic acid present; endemic .................... **Sarcographina cyclospora**

2* Ascospores septate, with rounded locules, 14–37 μm long, 4-10-locular .................... 3

3 Lichen compounds absent; ascospores 14–18 μm long, 4-locular; Sri Lanka, Northern Territory .................... **Sarcographa subtricosa**

3* Lichen compounds present; ascospores 17–37 μm long .................... 4

4 Norstictic acid present; ascospores 14–21 μm long, (4–)6-locular; South America, Sri Lanka, Borneo, New Zealand, Northern Territory, Queensland .................... **Sarcographa intricans**

4* Stictic acid present; ascospores 17-37 μm long, 4-10-locular .................... 5

5 Ascospores 7–10-locular, 25–37 μm long; endemic .................... **Sarcographa oculata**

5* Ascospores ≤ 6-locular, 17-32 μm long .................... 6

6 Ascospores 17–22 μm long, 4-locular; widely distributed, tropical to temperate .................... **Sarcographa labyrinthica**

6* Ascospores 23–32 μm long, 6-locular; Indonesia, the Philippines, Queensland .................... **Sarcographa verrucosa**

### *Graphina (Cyclographina) platyleuca*

**Graphina platyleuca** (Nyl.) Zahlbr.

(Zahlbruckner 1921: 231).

*Graphis platyleuca* Nyl.

(Nylander 1868: 75).

Type: New Caledonia, Ins. Loyalty, Lifu, *D. Thiébaut s.n.*, 1865 (holo H-NYL 6980).

*Cyclographina platyleuca* (Nyl.) Awasthi & M. Joshi

(Awasthi & Joshi 1979: 174).

*Helminthocarpon platyleucum* (Nyl.) Müll. Arg.

(Müller 1887b: 423).

*Platygrapha*? [sic] *albovestita* C. Knight

(C. Knight 1882: 43).

*Graphina albovestita* (C. Knight) F. Wilson, *nom. nud. in sched.*

*Schismatomma albovestitum* (C. Knight) Zahlbr.

(Zahlbruckner 1923: 553).

Type: New South Wales [near Sydney], C. *Knight vol. 69A, p. 20, no. 26* (holo WELT; iso M).

Thallus greenish-white, corticolous, surface smooth and dull; apothecia lirelliform, white, conspicuous, open, immersed, becoming subsessile, irregular ellipsoid, straight or curved, 1–4 mm long, 0.4–1 mm wide, thalline margin inconspicuous at first, becoming conspicuous and prominent; surface of disc densely white pruinose, revealing the black epithecium when abraded; proper exciple thin or absent, complete, reddish brown to black; hymenium 150–200 $\mu$m tall; ascospores hyaline, densely muriform, 1 per ascus, (100–)125–150(–175) $\mu$m long, 20–30 $\mu$m wide. (Fig. 2b)

**Chemistry:** protocetraric acid.

**Distribution**: occurs in Dominica, Puerto Rico, Florida (USA), New Caledonia and, in Australia, Queensland and New South Wales. It has not so far been reported from Lord Howe Island or Norfolk Island.

**Notes:** *Graphina platyleuca* is characterised by the greenish-white thallus, the conspicuous, open, densely white pruinose, immersed lirellae and the presence of protocetraric acid. The presence of this compound distinguishes the species from other Australian *Graphina* species with open lirellae and large ascospores.

*Schismatomma albovestitium* is listed as a synonym of *G. platyleuca* in the current Catalogue of Australian Lichens (McCarthy 2003).

During a study of the genus *Helminthocarpon* Fée, Awasthi and Joshi (1979) noted several species which lacked the branched, interwoven paraphyses characteristic of that genus. In these species paraphyses of this type were reported to be restricted to the upper part of the hymenium, as in the genus *Cyclographa* Vain., a morphological feature first noted in *Helminthocarpon pruinosa* (Eschw.) Müll. Arg. by Zahlbruckner (Awasthi & Joshi 1979). These *Helminthocarpon* species (which have muriform ascospores) were placed in the new genus *Cyclographina* Awasthi & Joshi (Awasthi & Joshi 1979) (cf. *Cyclographa* with septate ascospores).

Three species of *Cyclographina* were reported from Australia *viz*: *C. lojkana* (Müll. Arg.) Awasthi & M. Joshi, *C. pruinosa* (Eschw.) Awasthi and *C. platyleuca* (Nyl.) Awasthi & M. Joshi (Awasthi & Joshi 1979; Archer 1999b). *Cyclographina lojkana* and *C. pruinosa* are described in detail elsewhere (Awasthi & Joshi 1979) and these two species are currently undergoing detailed study (K. Kalb., *in litt.*, 2001).

*Cyclographina platyleuca*, previousl described as *H. platyleucum* (Nyl.) Müll. Arg.,, was based on *Graphis platyleuca* Nyl. (Nylander 1868). However, Zahlbruckner had indicated that the transfer of *Graphis platyleuca* to *Helminthocarpon* by Müller was incorrect ("mit Unrecht") as the paraphyses were not branched and interwoven, and he transferred this species to *Graphina* (Zahlbruckner 1921). A recent re-examination of several Australian specimens previously identified as *Cyclographina platyleuca* (Archer 1999b), together with additional recent collections, did not show the presence of the branched paraphyses characteristic of the genus *Cyclographina* and the specimens are redetermined as *Graphina platyleuca* (Nyl.) Zahlbr. Wirth and Hale (1978) reported *Graphina platyleuca* from Dominica and made no comment on the paraphyses and a recent account of the Graphidaceae of Florida also reported the taxon as *Graphina platyleuca* (Harris 1995).

The earliest name for this species may be *Graphina leprocarpa* (Nyl.) Zahlbr. Knight sent a specimen of *Platygrapha albovestitum* to Nylander in Paris where it was determined as *Graphis leprocarpa* Nyl. (Nylander 1886), later transferred to *Graphina* by Zahlbruckner (1923). *Graphis leprocarpa* [lectotype: FH] however, has smaller ascospores and does not contain protocetraric acid; it is not an earlier name for *G. platyleuca.*

**Illustrations:** Wirth & Hale, Plate 9e (1978); Awasthi & Joshi, figs. 35, 36 (1979) (as *Cyclographina platyleuca*).

**Specimens examined** (9 out of 18): Queensland: Southport, *F. Wilson s.n.*, no date (NSW); Christmas Pocket, 16 km NW of Kuranda, *J.A. Elix 17586*, Jul 1984 (CANB).

New South Wales: North Coast: Paterson River, *J. Boorman s.n.*, 1906 (NSW); Conglomerate State Forest, 24 km NNW of Coffs Harbour, *A.W. Archer G 205*, Apr 1998 (CANB, NSW 422708); Dorrigo National Park, Wonga Walk, *A.W. Archer G 240*, Apr 1998 (NSW 422707); Byron Bay, SW of Lighthouse, *A.W. Archer G 328*, Nov 1998 (WELT); Evans Head, S bank of Evans River, *A.W. Archer G 331*, Nov 1998 (NSW). Central Coast: Manly, *F. Wilson s.n.*, Sept 1897 (NSW 153559); Tomaga River Estuary, 15 km SE of Batemans Bay, on *Casuarina*, *J.A. Elix 22649*, Aug 1988, (CANB).

## *Opegrapha (Diplogramma)*

**Opegrapha australiensis** *(Müll. Arg. ) A.W. Archer*, **comb. nov.**

Basionym: *Diplogramma australiense* Müll. Arg.

(Müller 1891b: 400).

Type: Australia. Queensland: Brisbane, *F.M. Bailey 510*, 1889 (holo G).

Thallus dull olive-green, thin, cracked, surface smooth and dull; apothecia lirelline, numerous, scattered, straight, curved, or sinuous, sometimes branched, 0.5–2 mm long, 0.3–0.4 mm wide, thalline exciple lacking; proper exciple completely carbonised, sulcate; hymenium divided into two by the carbonised exciple, 40–50 μm tall, paraphyses branched; ascospores 8 per ascus, hyaline, fusiform, 15–18 μm long, 4–5 μm wide, 4-locular. (Fig. 1h, 2e)

**Chemistry:** not known; the type specimen is too small for chemical examination.

**Distribution**: endemic; so far known only from the type specimen.

**Notes**: Müller described the genus *Diplogramma* "as if formed from the longitudinal fusion of two *Opegrapha* lirellae, forming four parallel lips with two parallel hymenia"; in addition the paraphyses were reported to be branched (Müller 1891b). He compared *Diplogramma* with *Ptychographa* Nyl., a lirelline genus with multiple hymenia, but differentiated his species by the septate acospores, in contrast to the simple ascospores in *Ptychographa* (Coppins 1992). In the same paper he described *D. australiense* and compared the new species with *Opegrapha bonplandii* Fée but differentiated the two species by the sulcate lirellae in *Diplogramma*. Although *Diplogramma* is placed in the Graphidaceae (Rogers & Hafellner 1992; Kirk et al. 2001), the morphological features of the genus *Diplogramma*, viz: the sessile lirellae lacking a thalline margin, the ascospores with cylindrical locules characteristic of *Opegrapha* rather than the lenticular locules found in the Graphidaceae, and the branched paraphyses, place the species in the genus *Opegrapha*, as first suggested by Staiger (2000, *in sched.*) Accordingly, the new combination, *Opegrapha australiensis* (Müll. Arg.) A.W. Archer is made here. Multiple hymenia in *Opegrapha* are not unknown; for example, *O. prolificans* Redinger (Redinger 1940) has three hymenia (cf. Redinger. loc. cit. Taf. 1, Fig. 2).

The species resembles the widely distributed *Opegrapha atra* Pers., which also occurs in Australia. This species has similar ascospores to those in *O. australiensis* but is distinguished from that species by the absence of the sulcate proper exciple and the dual hymenia.

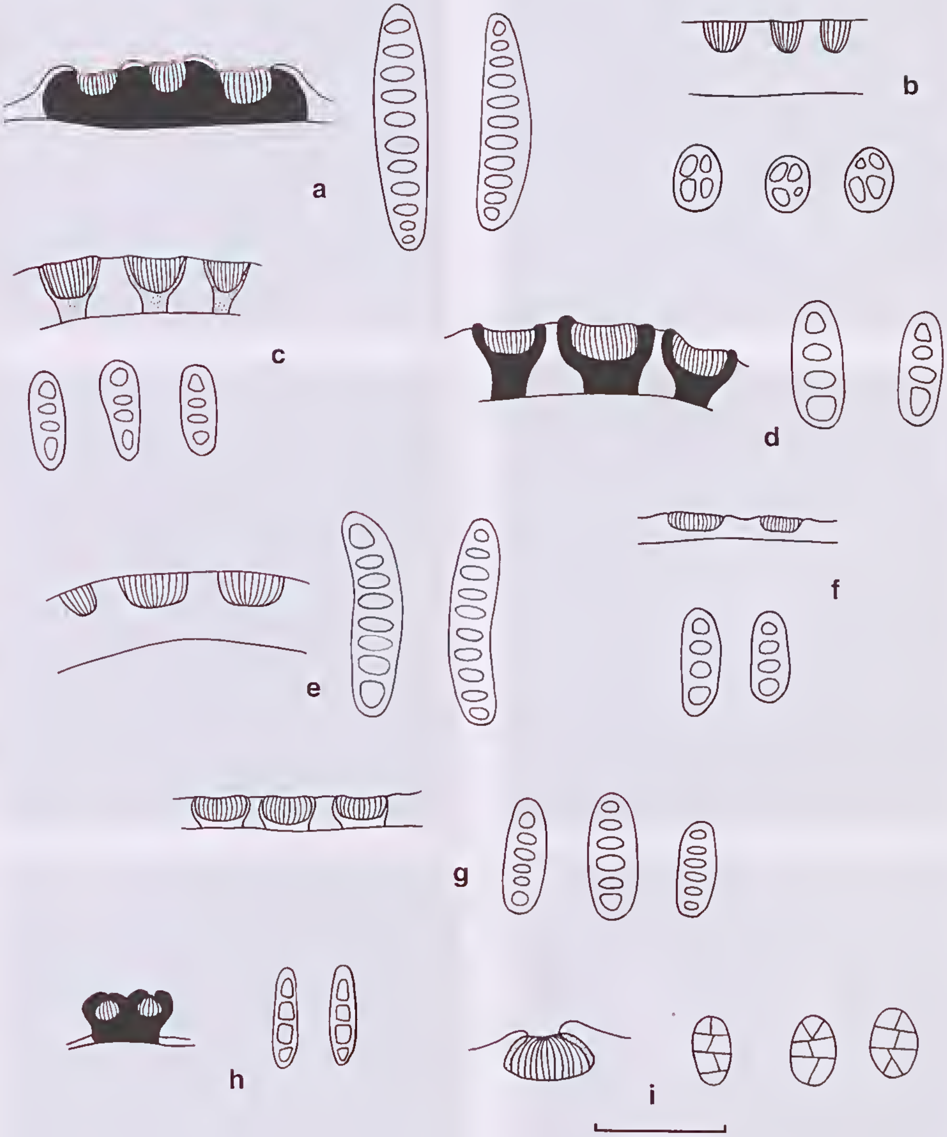

**Fig. 1.** Ascospores and cross-sections of lirellae. **a**, *Glyphis cicatricosa*; **b**, *Sarcographina cyclospora*; **c**, *Sarcographa intricans*; **d**, *S. labyrinthica*; **e**, *S. oculata*; **f**, *S. subtricosa*; **g**, *Sarcographa verrucosa*; **h**, *Opegrapha australiensis*; **i**, *Medusulina egenella* [from Müller (1894) *in sched.*]

lirellae: scale bar = 320 µm; ascospores: scale bar = 20 µm

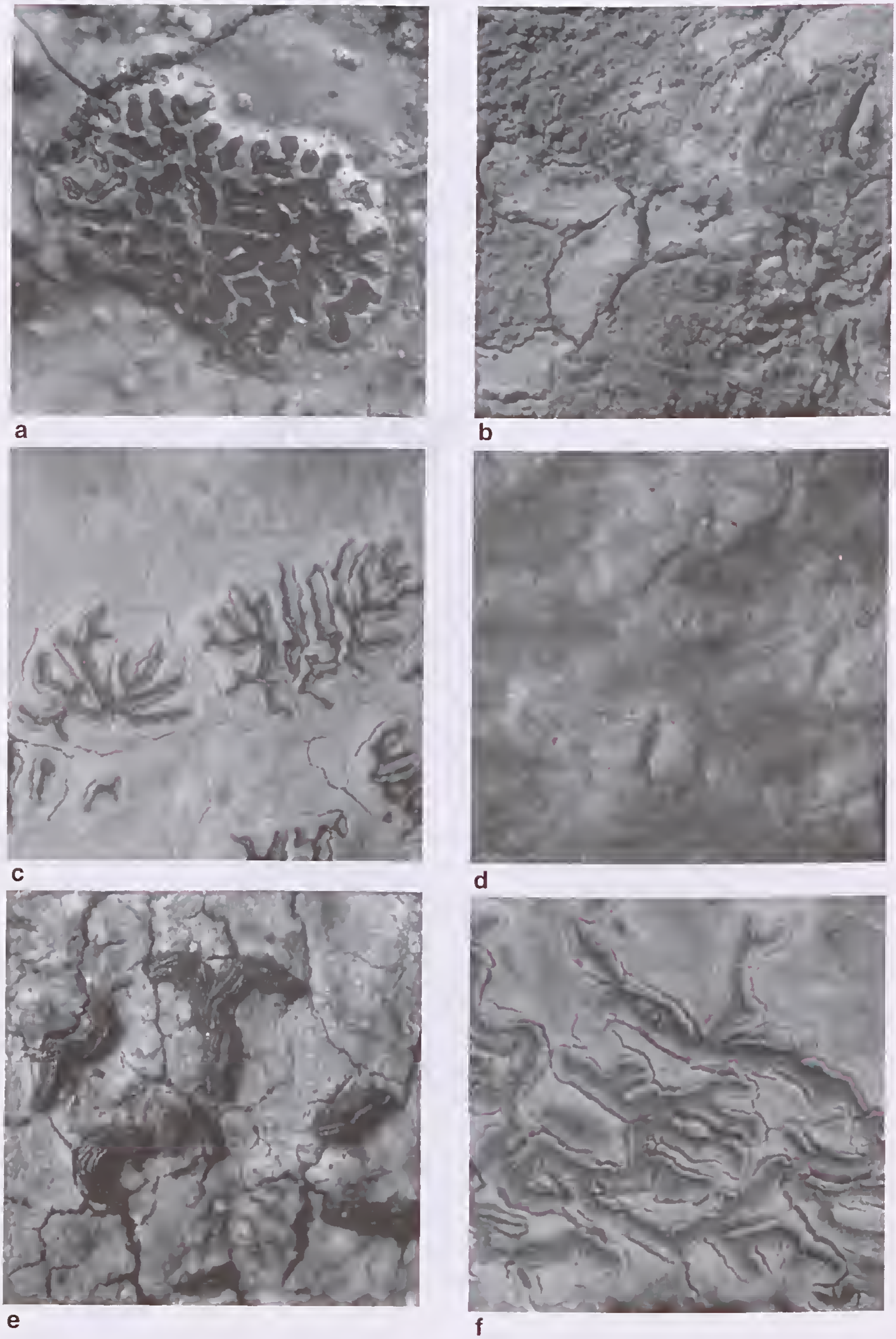

**Fig. 2.** **a**, *Glyphis cicatricosa* Ach. *Archer G 339*; **b**, *Graphina platyleuca* (Nyl.) Zahlbr. *Archer G 330*; **c**, *Gymnographa medusulina* Müll. Arg., holotype (G); **d**, *Medusulina egenella* (Müll. Arg.) Müll. Arg., holotype (G); **e**, *Opegrapha australiensis* (Müll. Arg.) A.W. Archer, holotype (G); **f**, *Sarcographa intricans* (Nyl. ) Müll. Arg., *Elix 16272* (CANB).

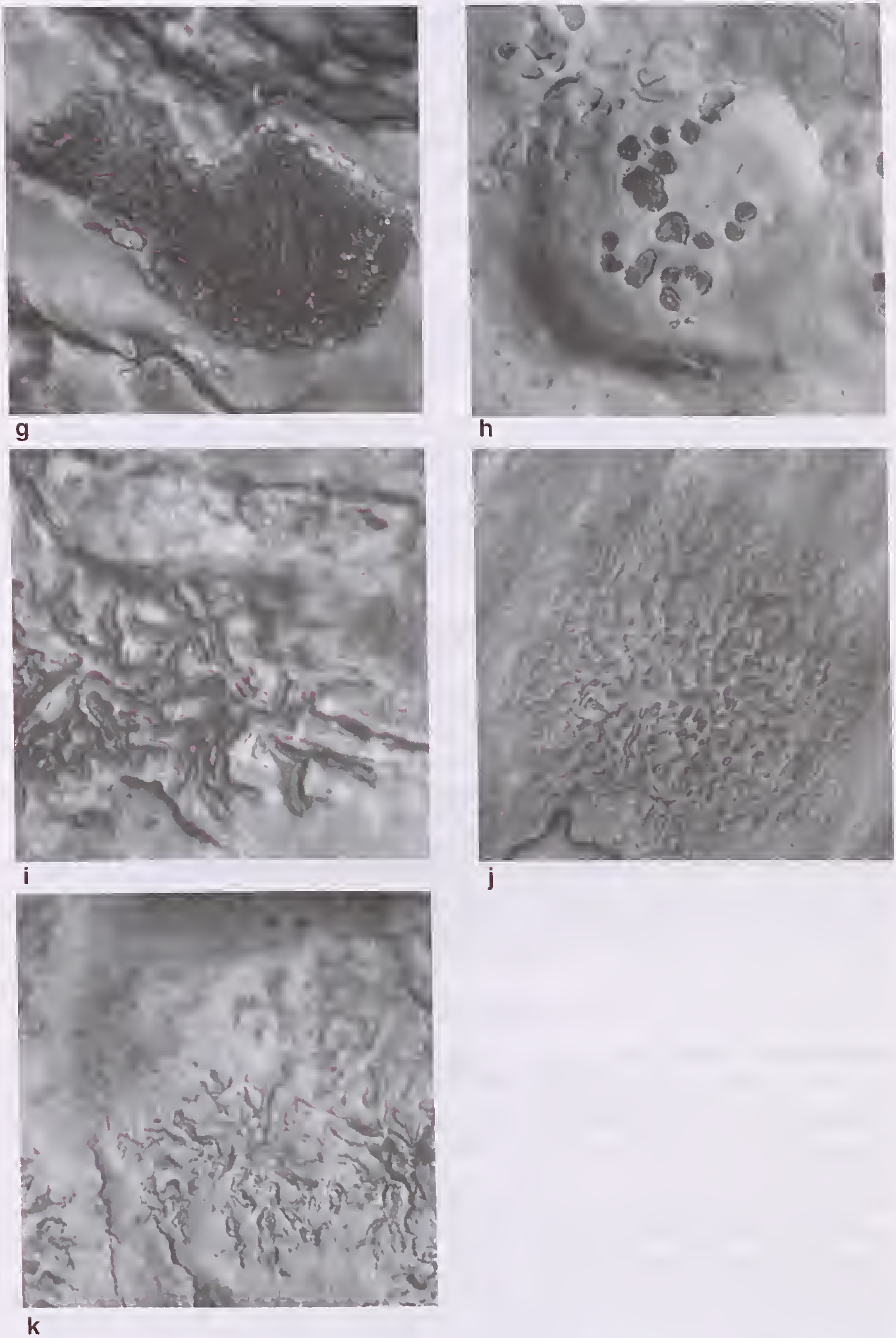

**Fig. 2. g**, *Sarcographa labyrinthica* (Ach.) Müll. Arg., *Archer G 338* (NSW 471723); **h**, *Sarcographa oculata* Müll. Arg., holotype (G); **i**, *Sarcographa subtricosa* (Leight.) Müll. Arg., holotype (BM); **j**, *Sarcographa verrucosa* (Mont. & Bosch) Zahlbr., *F. Wilson s.n.* (NSW 170581); **k**, *Sarcographina cyclospora* Müll. Arg., holotype (G). All ×17.

## *Glyphis*

**Glyphis cicatricosa** Ach.

(Acharius 1814: 107).

Type: Guinea. *s. loc.* no collector, on *Codaria acutifolia* [fide Acharius loc. cit.] (holo H-ACH 887).

*Graphis cicatricosa* (Ach.) Vain.

(Vainio 1921: 265).

*Glyphis verruculosa* Zahlbr.

(Zahlbruckner 1923: 457).

*Glyphis verrucosa* C. Knight

(C. Knight in Shirley 1889: 214).

[nom. inval., non *Glyphis verrucosa* Mont. & Bosch in Junghuhn, *Plant. Junghuhn.*, fasc. 4: 489 (1855)].

Type: Queensland: Brisbane, Sankeys Scrub. *J. Shirley 494,* no date (holo WELT).

*Glyphis cicatricosa* Ach. v. *depauperata* (Müll. Arg.) Zahlbr.

(Zahlbruckner 1923: 456).

*Glyphis favulosa* Ach. v. *depauperata* Müll. Arg.

(Müller 1891a: 54).

Type: Australia. Queensland: Bellenden Ker, *F.M. Bailey 549 p.p.*, 1889 (holo G).

Thallus pale greenish fawn, thin, corticolous, surface smooth and shiny; apothecia lirelline, the lirellae immersed in conspicuous, raised, white stromata; stromata rounded, oval or distorted ellipsoid, 1.5–4 mm wide, black with a thin white coating; lirellae numerous, open, initially rounded, becoming elongate and irregular in outline, finally much branched, crowded and covering the surface of the stromata, 0.1–0.2 mm wide; disc dark reddish brown, epruinose; proper exciple completely carbonised and continuous in the stromata; hymenium 120–160 $\mu$m tall, I-ve; ascospores narrow-ellipsoid, hyaline, irregularly 2-seriate, (32–)40–55 $\mu$m long, 8–12 $\mu$m wide, 8–12-locular, I+ blue. (Fig. 1a, 2a)

**Chemistry:** no lichen compounds found.

**Illustrations:** Acharius, Tab. 2, Fig. 3 (1818), in colour; Redinger, Fig. 1 & Taf. 1 (1933); Nakanishi, p.105, Fig 19A–D (1966); Yoshimura, Plate 44, Fig. 471, in colour (1974).

**Distribution:** a widely distributed tropical to temperate species reported from Brazil, Uruguay, Mexico, the United States (Florida), Japan, the Philippines, Singapore, Indonesia, New Caledonia, Fiji, New Zealand and, in Australia, Christmas Island (McCarthy & Elix 2002), Queensland and northern New South Wales; the species also occurs on Norfolk Island. Reported substrates in Australia include *Acacia, Alphitonia, Casuarina, Citrus, Cryptocarya, Euodia, Grevillea, Hibiscus, Melaleuca, Melia* and *Syzygium.*

**Notes:** *Glyphis cicatricosa* is characterised by the conspicuous stromata with crowded open lirellae, the hyaline *Graphis*-like ascospores and the absence of lichen compounds. The dark reddish brown discs distinguish the species from *Sarcographa labyrinthica,* which has black discs.

The species has several synonyms in addition to various varieties and forms. The varieties and forms were reduced to three forms, viz: f. *depauperata* (Müll. Arg.) Zahlbr. [based on an Australian type specimen, vide supra], f. *intermedia* (Müll. Arg.) Zahlbr. and f. *confluens* (Zenk.) Zahlbr., by Redinger (1933). The three forms, however, are merely stages in the development of the lirellae in the stromata and examples of each form may often be found on the same thallus. Thus the three forms accepted by Redinger, and their synonyms, are all considered to be synonyms of *Glyphis cicatricosa* Ach. The relevant references are reported in Redinger (1933).

**Specimens examined** (13 out of 47): Northern Territory: Channell Point, 23 km NNW of Daly River, *J.A. Elix 27728*, July 1991 (B, CANB).

Queensland: Sankeys Scrub [Brisbane], *F. Wilson s.n.*, Aug 1889 (NSW 170574); Killarney, *F. Wilson 94*, Aug 1890 (MEL 26213); Burleigh Heads National Park, *J.A. Elix 1316*, Aug 1975 (CANB); Yungaburra Road, 2 km SE of Atherton, *H. Streimann 16823*, Feb 1983 (CANB); Conway State Forest, 18 km E of Proserpine, *J.A. Elix 20212*, Dec 1986 (CANB); Stewart Ck, 17 km NNW of Mossman, *H. Streimann 45945*, Dec1990 (B, CANB, NY).

New South Wales: North Coast: Dangar Falls, 2 km N of Dorrigo, *A.W. Archer G 537*, Nov 2000 (NSW 471725); Byron Bay, Cape Byron, *A.W. Archer G 557*, Nov 2000 (NSW 471724); Lord Howe Island: track to Mutton Bird Point, *J.A. Elix 32782*, June 1992 (CANB); *ibid.*, Neds Beach, *J.A. Elix 32883*, Jun 1992 (CANB).

Norfolk Island. Rocky Point Reserve, *J.A. Elix 18238*, Dec 1984 (CANB); Mt Pitt, Mt Pitt Reserve, *J.A. Elix 18814*, Dec 1984 (CANB).

## *Gymnographa*

A saxicolous specimen of the usually corticolous species *Sarcographa medusula* (Spreng.) Fée was reported from Australia by Krempelhuber (1880). This specimen was later made the holotype (Fig.1h) of the new genus *Gymnographa* Müll. Arg. (Müller 1887a).

The only species in this endemic Australian genus, *G. medusulina* Müll. Arg., is based on an old specimen of the Australian taxon *Phaeographis eludens* (Stirt.) Shirley (Archer 2001d) which is described and illustrated elsewhere (Archer Fig. 2c, 2000a). Kirk et al. (2001) record *Gymnographa* as a synonym of *Sarcographa* but the lirellae in the holotype of *G. medusulina* are not immersed in stromatic tissue, as in other *Sarcographa* taxa. Shortly after the publication of *Gymnographa*, Müller reduced *Gymnographa* to section *Gymnographa* in the genus *Melaspilea*, (Müller 1892).

## *Medusulina*

**Medusulina** egenella (Müll. Arg.) Müll. Arg.

(Müller 1894: 93).

*Graphina egenella* Müll. Arg.

(Müller 1891a: 52).

Type: Australia. Queensland: Bellenden Ker, *F.M. Bailey 531 p.p.*, 1889 (holo G).

"Thallus pale yellowish brown, thin, corticolous, immersed, becoming evanescent; lirellae very small, thin, linear, rarely branched, immersed, with a thalline margin; disc 0.05–0.1 mm wide, pale pink and epruinose; perithecium pale brown above, otherwise indistinct; ascospores 8 per ascus, biseriate, hyaline, ellipsoid, 12–14 μm long, 6–8 μm wide, 4 × 2-locular. Similar to *Graphina nitida* (Eschw.) Müll. Arg. but with smaller ascospores with fewer locules." (Müller *loc. cit.* 1891a). (Fig. 1i, 2d)

**Chemistry:** not known; the holotype is too small for chemical examination.

**Distribution:** endemic; the species is so far known only from the type specimen.

**Notes:** *Graphina egenella* was described from a corticolous specimen collected by F.M. Bailey in Queensland. The holotype consists of two small fragments mounted on paper with Müller's annotations. The fragments have conspicuous swellings on the surface but these are part of the substrate. The lirellae are not crowded but are scattered on the surface of the thallus; they are inconspicuous, flattened and only slightly raised, with conspicuous thalline margins and show no stromata. The specimen is too small to permit examination of the ascospores, or chemical examination, but Muller's drawings (*in sched.*; reproduced as Fig. 2i) show small ascospores 12–14 μm long with muriform septation rather than the well-defined locules usually present in *Graphina* species, even those with small ascospores. The internal structure of the ascospores is similar to that of *M. texana*, described by Fink (1935) as transversely and longitudinally septate.

The absence of clustered lirellae or stromata (the distinguishing characteristics of *Medusulina*), the septate rather than locular ascospores and the absence of chemical data and additional specimens, renders the exact taxonomic position of *Medusulina egenella* unclear.

Müller published the genus *Medusulina* to describe the species *M. texana* (Müller 1894). Although *M. texana* was described in detail, the genus itself was briefly and inaccurately described as resembling *Sarcographa* but with hyaline ascospores (Müller, loc. cit.) which, as Redinger pointed out later, makes the genus *Medusulina* identical to the genus *Glyphis* (Redinger 1936: 119). In the same paper Müller transferred *Graphina nitida* (Eschw.) Müll. Arg. (Müller 1888) and *Graphina egenella* Müll. Arg. to the new genus as the corresponding *Medusulina* species. viz: *M. nitida*. and *M. egenella*.

Both *M. nitida* and *M. egenella* are reported to occur in Australia (Weber & Wetmore 1972; Filson 1996; McCarthy 2003). Weber & Wetmore recorded *M. nitida* from Victoria and cited a report by Müller (Müller 1893). However, in that paper Müller referred to *Graphis nitida* Mont. and cited a specimen collected by F. Wilson, no. *884*. A recent examination of this specimen [Victoria, Warburton, on tree, *F.R.M. Wilson* , Dec. 1885, no. *884* (NSW 427010)] revealed the asci to contain hyaline, 4-locular ascospores and confirmed its identity as a *Graphis* species. Apart from the erroneous report above, *Graphina nitida* (Eschw.) Müll. Arg. has not otherwise been reported from Australia and therefore *Medusulina nitida*, so far as is known, does not occur in Australia.

Redinger initially accepted the genus *Medusulina*, which he differentiated from *Graphina* by the presence of stromata in *Medusulina* (cf. *Glyphis* and *Sarcographa*) and described *Medusulina paraguayana* from South America (Redinger 1933). He later rejected the genus on the grounds that it was based on the weak characterisic of "lirellae in crowded clusters" and transferred Müller's *Medusulina* species back to *Graphina* and *Graphis* (Redinger 1936).

## *Sarcographa*

**Sarcographa intricans** (Nyl.) Müll. Arg.

(Müller 1887a: 77).

*Graphis intricans* Nyl.

(Nylander 1863: 473).

Type: Nova Granata [Colombia], Fusagasuga, 1900 m, *A.Lindig 2579*, 1860; (lectotype, **here selected**, H-NYL 7026).

Thallus pale fawn, thin, corticolous, surface smooth and shiny; apothecia lirelliform, immersed in stromata; stromata raised, pale fawn, circular to ovoid, 1–3 mm wide; disc black, fine white pruinose; lirellae thin, intricately branched, 0.05–0.15 mm wide; proper exciple uncarbonised, pale yellow brown, complete, thickened below; hymenium 100–120 $\mu$m tall; ascospores 8 per ascus, irregularly 2-seriate, pale brown, 16–20 $\mu$m long, 5–7 $\mu$m wide, (4–)6-locular. (Fig. 1c, 2f)

**Chemistry:** norstictic acid.

**Distribution:** The species occurs in Brazil, Colombia, Sri Lanka, Borneo and New Zealand; in Australia it occurs in the Northern Territory and Queensland.

**Notes:** *Sarcographa intricans* is characterised by the absence of a carbonised proper exciple, the predominantly 6-locular ascospores and the presence of norstictic acid. The presence of this acid distinguishes *S. intricans* from other Australian *Sarcographa* species.

In the protologue Nylander (loc. cit.) referred to six specimens collected in Colombia (Nova Granata) by A. Lindig; one of these, Lindig 2579 (H-NYL 7026), was collected in 1860 at Fusagasuga (*ca.* 50 km SW of Bogota) and the others were collected in Bogota. Four of the five specimens from Bogota (Lindig 784, 2609, 2610, 2617) are small, unmounted fragments with no annotation and the fifth specimen (Lindig 2718), although mounted and annotated, is only ca. 5 × 10 mm. In contrast, the specimen from Fusagasuga consists of two larger, mounted fragments, (ca. 5 × 2.5 cm & 4.5 × 3.5 cm) with apothecia and is annotated by Nylander with ascospore dimensions and diagrams. This specimen (Lindig 2579, H-NYL 7026) is here selected as lectotype. This specimen has recently (Staiger 2002) been chosen as lectotype but is referred to as H-NYL 7021. However 7021 is the number on the outer packet and the inner sheet on which the specimens are mounted and which was annotated by Nylander bears the number 7026. Thus both numbers refer to the same specimen, Lindig 2579, but Nylander's herbarium number is 7026.

The Nylander Herbarium contains a second specimen labelled Lindig 2579. This specimen (H-NYL pm 6194), which is unmounted, not annotated and has few apothecia, was also collected at Fusagasuga but in 1861.

The lectotype has previously been examined by several lichenologists, including M. Nakanishi, who reported the specimen to contain norstictic acid (Nakanishi, *in sched.* 1973). Each examination, including that of Nylander, found the ascospores to be 6-locular, in contrast to Nylander's published figures of 6–8-locular, but in agreement with the ascospores found in the Australian specimens. A later specimen not cited by Nylander (Nova Granata, Monte del Morro, 2200 m, *A. Lindig s.n.*, 1863, H-NYL 7024) was annotated by Nylander who reported the ascospores to be 5–6-locular. This specimen was also reported to contain norstictic acid (Nakanishi, *in sched.*, 1973).

**Specimens examined:** Northern Territory: Wangi Road, Walker Ck, 68 km SSW of Darwin, *H. Streimann 8802*, Jan 1985 (CANB).

Queensland: Mt. Baldy, 4 km SW of Atherton, *J.A. Elix 16272*, Jun 1984 (CANB); ibid., *H. Streimann 29207* (CANB, US); Upper Coomera, *F. Wilson s.n.*, Sep 1889 (MEL 26179); Killarney, *F.R.M. Wilson s.n.*, Jul 1890 (NSW 170613); Southport, *F. Wilson s.n.*, Aug 1890 (NSW 170614).

**Sarcographa labyrinthica** (Ach.) Müll. Arg.

(Müller 1887c: 62).

*Glyphis labyrinthica* Ach.

(Acharius 1814: 107 ).

*Graphis labyrinthica* (Ach.) Vain.

(Vainio 1921: 230).

Type: Guinea, *s. loc.*, *Afzelius s.n.* fide Müll. Arg. (*loc. cit.* 1887: 63) (holo H-ACH 885).

*Sarcographa colliculosa* (C. Knight) Zahlbr.

(Zahlbruckner 1923: 459).

*Glyphis colliculosa* C. Knight in F.M. Bailey

(C.Knight in Bailey 1886: 75).

Type: type material not located (*fide* Filson 1986).

*Sarcographa kirtoniana* (Müll. Arg. ) Müll. Arg.

(Müller 1887a: 77).

*Glyphis kirtoniana* Müll. Arg.

(Müller 1882b: 516).

Type: New South Wales: Illawarra, *W. Kirton 10 p.p.*, no date (holo G).

*Sarcographa actinota* F. Wilson

(F.Wilson in F.M. Bailey 1891: 33).

Type:Australia. Queensland: Upper Coomera, *F. Wilson s.n.*, 4.ix.1889 (syn NSW 170612).

Thallus pale olive-green, thin, corticolous, surface smooth and shiny; apothecia lirelline, immersed in conspicuous, raised, white stromata; stromata round, oval or distorted ellipsoid, 1–4 mm wide; lirellae numerous, much branched, open, 0.1–0.2 mm wide; disc matt black, epruinose or weakly white pruinose; proper exciple completely carbonised, thick at the base; hymenium 80–110 $\mu$m tall; ascospores 8 per ascus, irregularly 2-seriate, pale brown, 17–21(–23) $\mu$m long, 6–7 $\mu$m wide, 4-locular. (Fig.1d, 2g)

**Chemistry:** stictic acid, cryptostictic acid, hypostictic acid (trace) & constictic acid (trace) [*fide* Staiger *in sched.* 1998].

**Distribution:** a widely distributed, tropical to temperate species reported from South America, Mexico, Colombia, North America (Florida), the Philippines, Indonesia, New Zealand and, in Australia, it occurs in Queensland, New South Wales and Victoria, and on Norfolk Island.

**Notes:** *Sarcographa labyrinthica* is characterised by the highly branched lirellae immersed in conspicuous raised stromata, the 4-locular ascospores and the presence of stictic acid. The species was first reported from Australia by Shirley (Shirley 1889: 214), as *Glyphis labyrinthica*. The syntype of *S. actinota* F. Wilson has pale brown 4-locular ascospores and contains stictic acid, as does the holotype of *Sarcographa kirtoniana* and both species are here reported as synonyms of *S. labyrinthica*. The description of *S. colliculosa* suggests that the species may be based on an old specimen of *S. labyrinthica* and, in the absence of any type material, *S. colliculosa* is also tentatively included as a synonym of *S. labyrinthica*.

*S. actinota* was reported as a synonym of *S. subtricosa* by Shirley (1893) but the syntype material of *S. actinota* from NSW contains stictic acid, in contrast to *S. subtricosa* which lacks lichen compounds.

**Illustrations:** Acharius, Tab II, Fig. 1 (1818); Redinger Taf. VI, Fig. 81 (1936).

**Specimens examined:** Queensland: Darling Downs, Toowoomba, *C.H. Hartmann s.n.*, no date (MEL 26176); Russell River, *W.A. Sayer L 23*, 1886 (MEL 26177); Upper Coomera, *F. Wilson s.n.*, 1889 (NSW 170584); Conway State Forest, 18 km ENE of Proserpine, *H. Streimann 37338*, Jun 1986 (B, CANB); Cape Tribulation Beach, 40 km NE of Mossman, *L. Tibell 14347e*, Oct 1983 (CANB).

New South Wales: South Coast: "Emu Vale", *F. Wilson s.n.*, no date (NSW 170615); Budawang Range, 14 km SE of Nerriga, *D. Verdon 2569*, Aug 1976 (CANB); Clyde Mtn, 18.5 km SE of Braidwood, *D. Verdon 5003*, Sep.1981 (CANB, LSU). Northern Tablelands: New England National Park, Robinsons Knob Trail, 83 km E of Armidale, *A.W. Archer G 338*, Oct 1998 (NSW 471723); Dangar Falls, Dorrigo, *A.W. Archer G 593*, Nov 2000 (NSW 471719). North Coast: Duck Creek Road, 22 km WNW of Buladelah, *J.A. Elix 24421*, Apr 1990 (CANB); Broken Head, track to Seven Mile Beach, *A.W. Archer G 584*, Nov 2000 (NSW 471722). Central Coast: Cumberland State Forest, ca. 25 km NW of Sydney, *A.W. Archer G439*, Apr 2000 (NSW 440787);

Victoria: Woolston, *F. Wilson s.n.*, 1889 (NSW 170620); Cunningham, *F. Wilson s.n.*, Mar 1899 (NSW 170004).

Norfolk Island: Mt Pitt, Mt Pitt Reserve, *J.A. Elix 18806*, Dec 1984 (CANB).

**Sarcographa oculata** Mull. Arg.

(Müller 1895: 323).

Type: Queensland, *s. loc.*, *F.M Bailey 783*, 1893 (holo G).

Thallus pale fawn, thin, corticolous, surface smooth and dull; apothecia lirelline, immersed in scattered, subhemispherical stromata; stromata 1–2 mm diam., the lirellae circular to irregular in outline, 0.2–0.4 mm wide, immersed; disc weakly white pruinose; proper exciple indistinct, uncarbonised; hymenium 100–130 μm tall; ascospores 8 per ascus, brown, (25–)30–36 μm long, 7–8 μm wide, (7–)8–10-locular. (Figs 1e, 2h)

**Chemistry:** stictic acid (*fide* Nakanishi, *in sched.*, 1973).

**Distribution**: endemic; the species is so far known only from the type specimen.

**Notes:** *Sarcographa oculata* is characterised by the sunken rounded lirellae, the 7–10-locular ascospores and the presence of stictic acid. The 7–10-locular ascospores distinguish *S. oculata* from other Australian species of *Sarcographa* with stictic acid.

**Sarcographa subtricosa** (Leight.) Müll. Arg.

(Müller 1887a: 78).

*Glyphis subtricosa* Leight.

(Leighton 1869: 181).

Type: Ceylon [Sri Lanka]: Peradeniya, *G.H.K. Thwaites* (holo BM).

Thallus pale olive green, thin, corticolous, surface smooth and shiny; apothecia lirelline, immersed in ill-defined, flattened, off-white stromata; stromata irregular in outline, ca. 1 × 2 mm; lirellae narrow, immersed, much branched, 0.5–1.5 mm long, 0.15–0.2 mm wide, with slightly raised thalline margins; disc black, white pruinose; proper exciple uncarbonised, inconspicuous; hymenium 60–80 μm tall; ascospores 8 per ascus, brown, 14–18 μm long, 5–6 μm wide, 4-locular. (Figs 1f, 2i)

**Chemistry:** no lichen compounds found (in holotype, *fide* P. James, *in litt.*, 2000).

**Distribution:** the species occurs in Sri Lanka and is reported from Brazil. In Australia it is so far known only from the Northern Territory.

**Notes:** *Sarcographa subtricosa* is characterised by the open lirellae, the absence of a carbonised proper exciple, the 4-locular ascospores and, in particular, the absence of lichen compounds. This last characteristic distinguishes *S. subtricosa* from other Australian *Sarcographa* species, which contain stictic or norstictic acid.

**Specimen examined:** Northern Territory: Litchfield park, 39 km WSW of Batchelor, on fallen palm, *J.A. Elix 27570*, Jul 1991 (CANB).

**Sarcographa verrucosa** (Mont. & Bosch) Zahlbr.

(Zahlbruckner 1923: 467).

*Glyphis verrucosa* Mont. & Bosch,

(Montagne & v.d. Bosch 1855: 489).

*Graphis verrucosa* (Mont. & Bosch) Vain.

(Vainio 1921: 231).

Type: Indonesia. (Java). *s.loc.* (holo: L? n.v.).

*Sarcographa javanica* (Müll. Arg.) Müll. Arg.

(Müller 1887a: 77).

*Glyphis javanica* Müll. Arg.

(Müller 1882a: 333).

Type: Indonesia. (Java). *s.loc.*, no collector (holo G).

Thallus pale fawn, thin, corticolous, surface subtuberculate and slightly shiny; apothecia lirelliform, immersed in white stromata; stromata irregularly ovoid, 4–5(–6) mm long, 2–3.5 mm wide, flattened; lirellae black, crowded, open, not confluent or branched, sub-circular, 0.1–0.15 mm diam.; disc black, fine white pruinose, the pruina often lost due to abrasion; proper exciple complete, thin, dark brown to black; hymenium 120–140 $\mu$m tall; ascospores 8 per ascus, irregularly 2-seriate, pale brown, 24–28(–32) $\mu$m long, 7–8 $\mu$m wide, 6–(–8)-locular. (Fig. 1g, 2j)

**Chemistry:** stictic acid

**Distribution:** the species is reported from Indonesia and the Philippines, and, in Australia, it occurs in Queensland.

**Notes:** *Sarcographa verrucosa* is characterised by the flattened stromata, the discrete lirellae, the 6–8-locular ascospores and the presence of stictic acid. The species is distinguished from other Australian *Sarcographa* species with stictic acid by the 6–8-locular ascospores and the nonconfluent lirellae. The Australian specimen cited below is chemically and morphologically identical to the holotype of *S. javanica* in G. This taxon was reported as a synonym of *S. verrucosa* by Redinger (1936).

**Specimen examined:** Queensland: Korunda [Kuranda], *F. Wilson s.n.*, no date (NSW 170581).

## *Sarcographina*

**Sarcographina cyclospora** Müll. Arg.

(Müller 1887b: 425).

*Glyphis cyclospora* (Müll. Arg.) Shirley

(Shirley 1889: 215).

Type: Queensland, Trinity Bay [Cairns], *W.A. Sayer s.n.* (holo G; iso MEL 26180).

Thallus pale fawn, thin, corticolous, surface smooth and shiny; apothecia lirelline, immersed in stromata; stromata white, immersed, irregularly circular, 2–5 mm wide; lirellae thin, black, open, immersed, in irregular stellate clusters, 0.05–0.1 mm wide; disc black, weakly white pruinose; proper exciple uncarbonised, pale yellow brown; hymenium 80–100 $\mu$m tall; ascospores rounded ellipsoid, initially pale brown, uniseptate, 1-seriate, becoming dark brown, 10–13 $\mu$m long, 6–8 $\mu$m wide, irregularly 2 × 2-locular. (Fig. 1b, 2k)

**Chemistry:** (hplc): psoromic acid (major), 2′-*O*-demethylpsoromic acid (trace) & subpsoromic acid (trace).

**Distribution**: endemic; the species is so far known only from the type specimen from Queensland.

**Notes**: *Sarcographina cyclospora* is characterised by the immersed stromata, with immersed, branched lirellae, the dark brown muriform ascospores and the presence of psoromic acid. Shirley (1889) transfered the species to *Glyphis*, but this is both unnecessary and incorrect.

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# *Cycas candida* (Cycadaceae), a new species from Queensland together with an extension of range and amended description of *Cycas yorkiana*

K.D. Hill

## Abstract

*Hill, K.D. (National Herbarium of New South Wales, Botanic Gardens Trust Sydney, Mrs Macquaries Road, Sydney, NSW 2000, Australia) 2004.* Cycas candida *(Cycadaceae), a new species from Queensland together with an extension of range and amended description of* Cycas yorkiana.. Telopea *10(2): 607–611.* **Cycas candida**, a new species of *Cycas* endemic to Queensland is described, and new records are discussed. The new species is illustrated and mapped, and affinities are discussed. Records of *Cycas media* from Cape Melville have been shown to belong to *C. yorkiana*, previously known only from near Moreton telegraph station in northern CapeYork. An amended description is presented.

## Introduction

Ongoing studies of the genus *Cycas* (Hill 1992, 1994, 1996, 1998) have shown several populations in Queensland of uncertain identity. On closer examination, these proved to be stable and morphologically distinct. These populations are formally validated as a new species here in order to establish nomenclature and to provide conservation authorities with a legitimate name for licensing and management purposes.

Field investigations of a *Cycas* record from Cape Melville previously reported as *Cycas media* (*Wannan 926*, below) have shown this occurrence to belong to *C. yorkiana*, a species previously known only from a single large population near Moreton telegraph station in northern Cape York. A description amended in accordance with the new determination is presented below.

**Cycas candida** *K.D. Hill*, **sp. nov.**

Inter species australienses combinatione characterum sequentium distinguitur: frondes carinatae virides, pinnae carinatae leviter recurvatae, fructus candidus.

Type: Queensland: Rollingstone, *K.D. Hill 5671, L. Stanberg & N. Liu*, 15 Oct 2001 (holo NSW; iso BRI, CANB, IBSC, K, NY, PE).

*Stems* arborescent, 1–3 m tall; base not strongly swollen; bark thick and corky. *Leaves* deep green, semiglossy, 80–145 cm long, moderately keeled (opposing leaflets inserted at 90–130° on rachis), with 180–300 leaflets, with orange tomentum shedding as leaf expands; rachis usually terminated by a spine 3–30 mm long. Petiole 17–40 cm long, glabrous, spinescent for 5–90% of length. Basal leaflets not gradually reducing to spines, 40–140 mm long. *Median leaflets* simple, strongly discolorous, 180–230 mm long, inserted at 55–65° to rachis, decurrent for 2–5 mm, narrowed to 3–4 mm at base, 6–10 mm apart on rachis; section slightly keeled; margins slightly recurved; apex acute, spinescent; midrib flat above, raised below, wide. *Cataphylls* linear, soft pilose or densely floccose, persistent. *Pollen cones* ovoid, orange, 40 cm long, 14 cm diam. Microsporophyll lamina firm, not dorsiventrally thickened, 43 mm long, 14 mm wide; fertile zone 31 mm long, sterile apex 12 mm long, level; apical spine prominent, sharply upturned, 8 mm long. *Seed cones* open at pollination, open as seed set. Megasporophylls 22–32 cm long, grey-tomentose or brown-tomentose, tomentum shedding; ovules 2–6, glabrous; lamina lanceolate, 60–90 mm long, 24–35 mm wide, regularly dentate, with 36-44 pungent lateral spines 1–3 mm long, 1–2 mm wide; apical spine distinct from lateral spines, 15–29 mm long, 3–4 mm wide at base. *Seeds* flattened-ovoid, 36–39 mm long, 29–33 mm wide; sarcotesta orange-brown, strongly pruinose, 3–5 mm thick; fibrous layer absent; sclerotesta smooth; spongy endocarp absent. Fig. 1.

**Etymology:** From the Greek *candida*, white, in reference to the white seeds.

**Historical notes:** Recognised as a distinct species only in 2001.

**Distinguishing features:** Distinguished from other Australian species by the openly keeled leaves with thick, mid to dark green, moderately broad, moderately keeled leaflets with recurved margins, the soft cataphylls with thick orange tomentum, and the waxy, white seeds. Although superficially resembling *C. media* at first sight, the soft floccose cataphylls, the narrow, keeled leaflets with recurved margins and the white ovules and seeds indicate that this species is more allied with *C. cairnsiana* and belongs in that group (subsection *Cairnsianosae*, Hill 1998). Within the subsection, *C. candida* is one of a small group of species with similar cataphylls and keeled but often green leaves that also includes *C. ophiolitica* and *C. megacarpa*. The latter has been previously placed with *C. media* in series Endemicae (Hill 1998) on the basis of green leaves and broad flat leaflets.

**Distribution and habitat:** Known from the Rollingstone district north of Townsville, and a few kilometres north and south of there. This species is locally abundant in grassy woodland or grassland with scattered trees on skeletal gritty sandy soils on steep granite boulder slopes.

**Conservation status:** The range of this species is small, but a substantial part of the population is conserved in the Mount Spec National Park. Although conserved, the range of this species is limited and the habitat may potentially be impacted by too frequent wildfires with the potential to disrupt reproduction. 1994 IUCN Red List of Threatened Plants category **LR cd**. ROTAP category **2RC-** (Briggs & Leigh 1996).

**Selected specimens (from 12 examined): Queensland:** base of Paluma Range, on Paluma road, *Hill 4826*, 15 Oct 1996 (NSW); Rollingstone, *Hill 4827*, 15 Oct 1996 (NSW); 40 km S of Ingham, *Maconochie 2733*, 24 Jun 1981 (DNA, NSW, BRI); Rollingstone, *Maconochie 2735*, 24 Jun 1981 (DNA, NSW, BRI, K).

## Amended description and conservation status of *Cycas yorkiana*

*Cycas yorkiana* K.D. Hill, Telopea 7: 18 (1996).

Type: Queensland: 20.5 km N of Wenlock River crossing on Bamaga road, *K.D. Hill 4711 & L. Stanberg*, 11 Jul 1994 (holo NSW; iso BRI, CANB, DNA, K, L, MEL, NY).

*Stem* to 1.5 m tall, rarely to 3.0 m, 14–20 cm diam. *Leaves* 90–140 cm long, openly keeled in section (opposing leaflet inserted at 150–180° on rachis), with 160–220 leaflet, terminated by a spine 5–20 mm long; petiole loosely orange-brown-woolly or floccose, 15–30 cm long. *Median leaflets* at 60–75° to rachis, 140–200 mm long, 5.5–7.5 mm wide, glabrous or loosely orange-woolly, glossy mid-green, usually falcate, keeled in section with recurved margins, decurrent for 3.0–5.0 mm, narrowed to 4.0–5.0 mm at base (55–80% of maximum width), spaced at 9–11 mm on rachis, apex attenuate; midrib slightly raised above, prominent below. New growth densely woolly with orange-brown trichomes. *Cataphylls* densely orange-brown-woolly or floccose. *Pollen cones* not

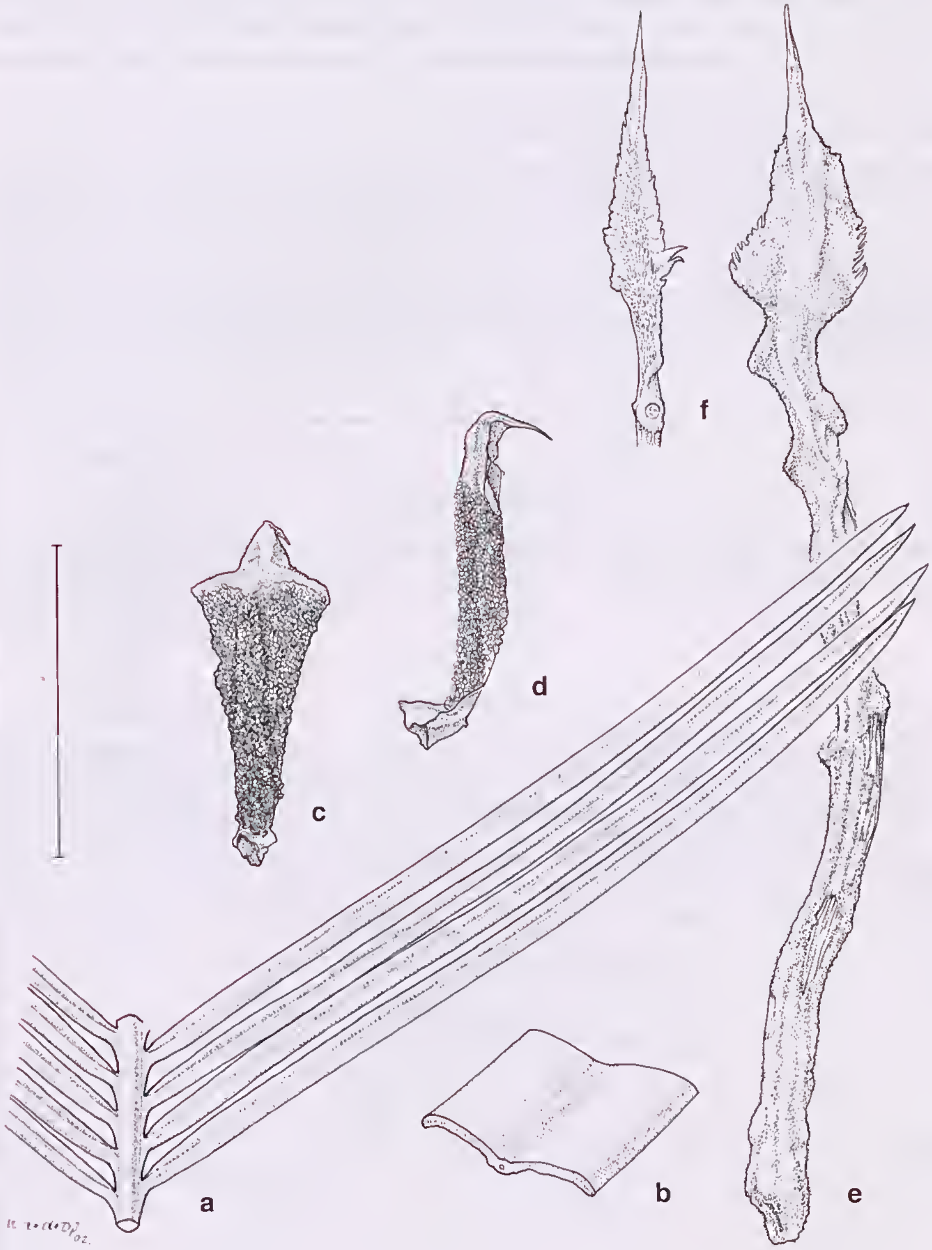

**Fig. 1.** *Cycas candida*. **a**, part of leaf; **b**, section of leaflet; **c**, **d**, microsporophyll; **e**, megasporophyll with stipe; **f**, tip of megasporophyll (a & b from *Hill 5671*, c & d from *Hill 5674*, e from *Hill 5672*, f from *Hill 4827*). Scale bar: a = 6 cm; b = 1 cm; c, d = 4 cm; e, f = 6.6 cm.

seen. Microsporophyll lamina c. 35 mm long, c. 12 mm wide, apical spine c. 6 mm long. Megasporophylls 20–32 cm long, grey- and orange-tomentose, with 2–6 ovules, sterile apex 60–100 mm long, 16–32 mm wide, narrowly triangular, regularly dentate, with 24–32 lateral teeth, apical spine 11–18 mm long, lateral teeth 3–6 mm long. *Seeds* flattened-ovoid, green becoming orange, not pruinose, 28–37 mm long, 26–32 mm diam.; sarcotesta 2–3 mm thick.

**Illustration:** Telopea 7: 19 Fig. 8 (1996).

**Notes:** *Cycas yorkiana* is distinguished from other Australian species by the bright green, keeled leaves with keeled and usually falcate leaflets, the short, soft cataphylls, the thick crown of orange wool around the cataphylls and leaf bases, and the absence of pruinosity in leaves and seeds. The closely allied *C. badensis* differs in having a smaller megasporophyll apex with fewer and shorter lateral spines and a shorter terminal spine, somewhat less orange wool in the crown, and leaflet that are usually

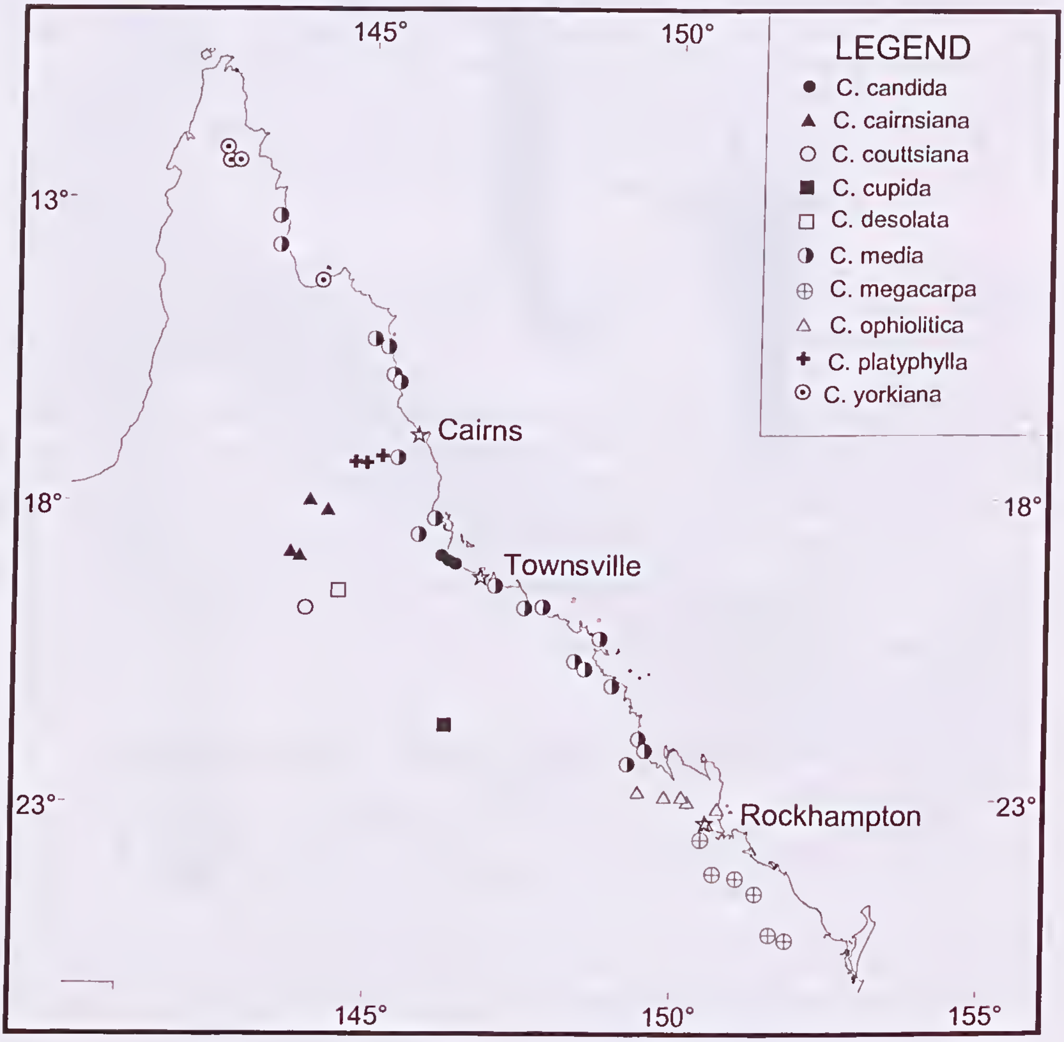

**Fig. 2.** Distribution of *Cycas* species in north-east Queensland: *Cycas candida, C. media, C. platyphylla, C. cairnsiana, C. couttsiana. C. desolata, C. cupida, C. yorkiana.*

straight rather than falcate. The orange wool around the cataphylls readily distinguishes this species in Cape York Peninsula, but also occurs in a number of other species such as C. *cairnsiana* and C. *ophiolitica* further south in Queensland, C. *maconochiei* in the Northern Territory and C. *lane-poolei* in Western Australia. These taxa, however, lack the combination of characters listed above.

**Conservation status:** the newly identified occurrence and consequent range extension necessitates a review of conservation status from the previous 2R- Briggs and Leigh code. The second occurrence is also conserved within the Cape Melville National Park, and this species must now be regarded as not at risk (IUCN 1994 code Low Risk Least Concern).

**Selected specimens:** Queensland: Cook: 31 km N of Wenlock River crossing on Bamaga road, *K.D. Hill 4710 & L. Stanberg*, 11 Jul 1994 (NSW); 3.8 km N of Moreton telegraph station, *Hill 1779*, 22 July 1986 (NSW); 12 km N of Morton Telegraph station, *Maconochie 2692, 2693*, 16 Jun 1981 (DNA); 5.7 km N of Wenlock River on Peninsula Development Road, *Clarkson 5651*, 3 Nov 1984 (BRI, DNA); Rokeby, 45 miles [c. 72 km] NW of Coen, *Gordon s.n.*, Oct 1966 (BRI); Bathurst Bay, *Wannan 926*, 20 Jul 1998 (BRI).

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# Non-marine algae of Australia: 5. Macroscopic Chaetophoraceae (Chaetophorales, Chlorophyta)

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## Abstract

*Skinner, S. and Entwisle, T.J. (Botanic Gardens Trust Sydney, Mrs Macquaries Road, Sydney NSW 2000, Australia. Email: tim.entwisle@rbgsyd.nsw.gov.au) 2004. Non-marine algae of Australia: 5. Macroscopic Chaetophoraceae (Chaetophorales, Chlorophyta).* Telopea *10(2): 613–633.* Five macroalgal genera in the Chaetophoraceae (Chaetophorales, Chlorophyceae) are documented from Australia: *Draparnaldiopsis salishensis* is newly recorded; *Uronema confervicolum* is confirmed and its distribution extended, similarly for *Chaetophora attenuata, C. pisiformis* and *C. elegans.* The distributions of *Draparnaldia mutabilis* and *Stigeoclonium tenue* and *S. farctum* are extended, building on the previous studies by Entwisle (1989a, 1989b) in Victoria. *Stigeoclonium helveticum* is shown to be widespread in New South Wales.

## Introduction

We present here a floristic revision of freshwater macroalgae from the family Chaetophoraceae. Our treatment is based on new collections, mostly from N.S.W., and available herbarium specimens. Quite a number of these species are widely distributed algae, conspicuous as the main species in algal tufts attached to rocks, snags and aquatic vegetation, in streams and standing water. They are frequently included, unvouchered, in species lists e.g. May & Powell (1986), Grimes (1988). Previous workers have identified these algae most commonly by reference to descriptions in floras of other regions of the world (e.g. Prescott 1951).

As often happens in surveys and monitoring of water bodies, the dilemma faced by the scientist or technician has been to find a 'name', fit it to a 'shape', and then be consistent in the application of that 'name'. Our present endeavour involves the morphological fleshing out of those 'names' and their relatives, so bringing the taxonomy up to date. This should permit our scientific and technical colleagues to have greater confidence in their data, and thus be able to compare their results with fellow workers overseas, sure that they are discussing the same or related organisms. However this remains a floristic treatment and no type material has been examined. It is the first necessary step towards understanding Australia's freshwater algal flora. As with our previous papers, the use of the terms 'macroalgae' and 'macroscopic' is pragmatic. We use 'macroalgae' to delimit those entities that can be visible to the naked eye in the field albeit as clumps, tufts or globules of little definition. *Chaetophora* Schrank may be discriminated because of its pulvinate epiphytic habit, the others are

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often seen as bright green to yellowish green streamers in waterways especially on cobbles in riffle banks or on aquatic plants in fast flowing water. We have no material to hand of *Fritschiella* Iyengar or similar terrestrial genera for New South Wales. Not all genera and species in Chaetophorales, included by Printz (1964) in his very diverse Chaetophoraceae, qualify as macroalgae, being encrusting epiphytes, microscopic even in large concentrations. We have included *Uronema* Lagenheim, *Chaetophora*, *Draparnaldia* Bory, *Draparnaldiopsis* Smith & Klyver and *Stigeoclonium* Kützing (including *Cloniphora* Tiffany) as macroalgal representatives of the still inadequately defined Chaetophoraceae.

## Methods

Where specimens have been collected by the authors, or others in recent years, spirit collections were first fixed in 10% Formalin and afterward preserved in 70% Ethanol with 5% Glycerol. Material for microscopic examination (with a Leitz Dialux research microscope) was mounted in 40% corn oil after staining in aniline blue (for general staining), Lugol's Iodine (for chloroplasts and pyrenoids), or safranine (walls and mucilage). Specimens held at NSW have provided the main sources of distributions and biogeographical data, but some specimens have been used from other collections in Australia. Where possible we have compared our material with recognised Exsiccatae, but no attempt has been made to view type material, for, as was noted in Skinner & Entwisle (2001), it is often lost or unobtainable. The general treatment of Printz (1964) for the Chaetophoraceae, and reliable recent treatments for individual genera, have been used to discriminate between taxa.

### Chaetophoraceae

Key to genera and species of macroscopic Chaetophoraceae confirmed for Australia:

1 Thallus not gelatinous; unbranched individual filaments attached by vase-shaped holdfast ........ **1a. Uronema confervicolum**

1* Thallus gelatinous, slippery to touch; ramifying basal system giving rise to branching erect axes ........ 2

2 Thallus globular; filaments much branched, with medulla and cortex ........ **2. Chaetophora**

2* Thallus diffuse; filaments with clearly distinguishable axes and laterals ........ 5

3 Thallus domed but spreading, gel soft, easily dispersed ........ **2a. C. elegans**

3* Thallus hemispherical, gel firm and tough ........ 4

4 Cortical branches consisting of shorter broad cells, L/D 1.5–2........ **2b. C. pisiformis**

4* Cortical branches consisting of longer narrow cells, L/D 3 or more ........ **2c. C. attenuata**

5 Primary and secondary axes distinguished by width, cell diameter tapering gradually; laterals not forming compact clusters ........ **3. Stigeoclonium**

5* Thallus of primary axes and lateral clusters; cells in lateral clusters fusiform or cylindrical, less than half the diameter of axial cells ........ 8

6 Basal system with each cell giving rise to an erect axis as it forms, lower few cells of axis rhizoidal; primary axes distinctly broader than laterals; chloroplast deeply dissected; determinate short secondary laterals sometimes present ........ **3a. S. helveticum**

6* Basal plate of radiating filaments, erect axes concentrated in centre; primary axes grading into secondary laterals; chloroplast ribbon-like; laterals almost always indeterminate ........ 7

7. Basal mat of compact, close-fitting filaments; erect axes few, rarely with secondary branches ........................................ **3b. S. farctum**

7* Basal mat of open, spreading filaments; erect axes numerous, profusely branching **3c. S. tenue**

8 Main axial cells of similar size; opposite or whorled lateral branches arising from upper half of axial cells ........................................ **4a. Draparnaldia mutabilis**

8* Main axial cells of alternating long and short cells; opposite or whorled lateral branches arising from middle of short axial cells ........................................ **5a. Draparnaldiopsis salishensis**

### **1. Uronema** Lagerheim

*Uronema* is a genus of about ten species, of unbranched uniseriate filamentous algae, with an apical seta and a basal vase-shaped holdfast cell, found in freshwater and terrestrial habitats throughout the world. The inclusion of a marine species, *U. marina* Womersley (1984), deserves further investigation. Printz (1964) accepted five species in his world revision, Chaudhery (1979) discusses three of seven species then accepted. Some researchers have disputed the existence of the genus as distinct from *Ulothrix* Kützing (Maddox & Bold, 1962). *Uronema* is now accepted as a member of the Chaetophorales (Silva 1982, Mattox & Stewart 1984) on the basis of structure of flagellar apparatus, a relationship further supported by 18S rRNA gene sequencing (Booton et al. 1998).

*Uronema* has an attachment disc on the bottom of a cup-like basal cell, laminar parietal chloroplasts with 1–4 pyrenoids, a mucronate terminal cell, and 2–4 quadriflagellate zoids. *Ulothrix* (Ulvales) has a rhizoid-like holdfast and is easily detached from its substrate, numerous pyrenoids in the parietal chloroplasts, domed terminal cells and numerous quadriflagellate zoids. *Klebsormidium* Silva, Maddox & Blackwell (Klebormidiales), the other genus from which detached *Uronema* filaments need to be distinguished, is usually free-floating but attaches by mucilage pads along the length of the filament, has a lamellate chloroplast which covers only half the cell at most, containing only one pyrenoids and single, biflagellate zoids.

**1a. Uronema confervicolum** Lagerheim, *Malpighia* 1: 518 (1887).

*Thalli* intertwining to form streamers 20 cm or more. *Basal cell* with disc, narrow cylindrical 3.5–4 μm diam., either without plastid or with chloroplast confined to the upper third of the cell, next one or two cells expanding upward 3–5 L/D; *most cells* short cylindrical, length 4–10(–16) μm, 6–9 μm diameter, chloroplast laminar parietal almost filling the cell, pyrenoids 1–4; *terminal cell*, where retained, length c. 9 μm, c. 3.5 μm diam., prominently mucronate. Reproduction by quadriflagellate zoids, released from vegetative cells by rupture. Fig. 1 a–c.

**Distribution and habitat:** cosmopolitan. Reported previously from Queensland (Möbius 1895), and now from New South Wales and South Australia, probably widespread. In still or slow flowing waters it can be a weedy epiphyte of *Oedogonium* or other filamentous algae, epizoic, or form a green fur on submerged objects. This is not an alga that is likely to be deliberately collected, but rather appears in mixed collections, epiphytic on more conspicuous taxa.

**Notes:** a short distance above the holdfast and at irregular intervals throughout the filament there may be a pinched-in junction between two cells, suggesting that growth is intercalary and there is no fixed meristem. Möbius is quoted in Bailey (1895) as suggesting the Queensland material had a holdfast like var *javanicum* Möbius (1893). Our material does not have such a pronounced holdfast base, and without access to material observed by Möbius, we prefer to avoid intraspecific categories. With a

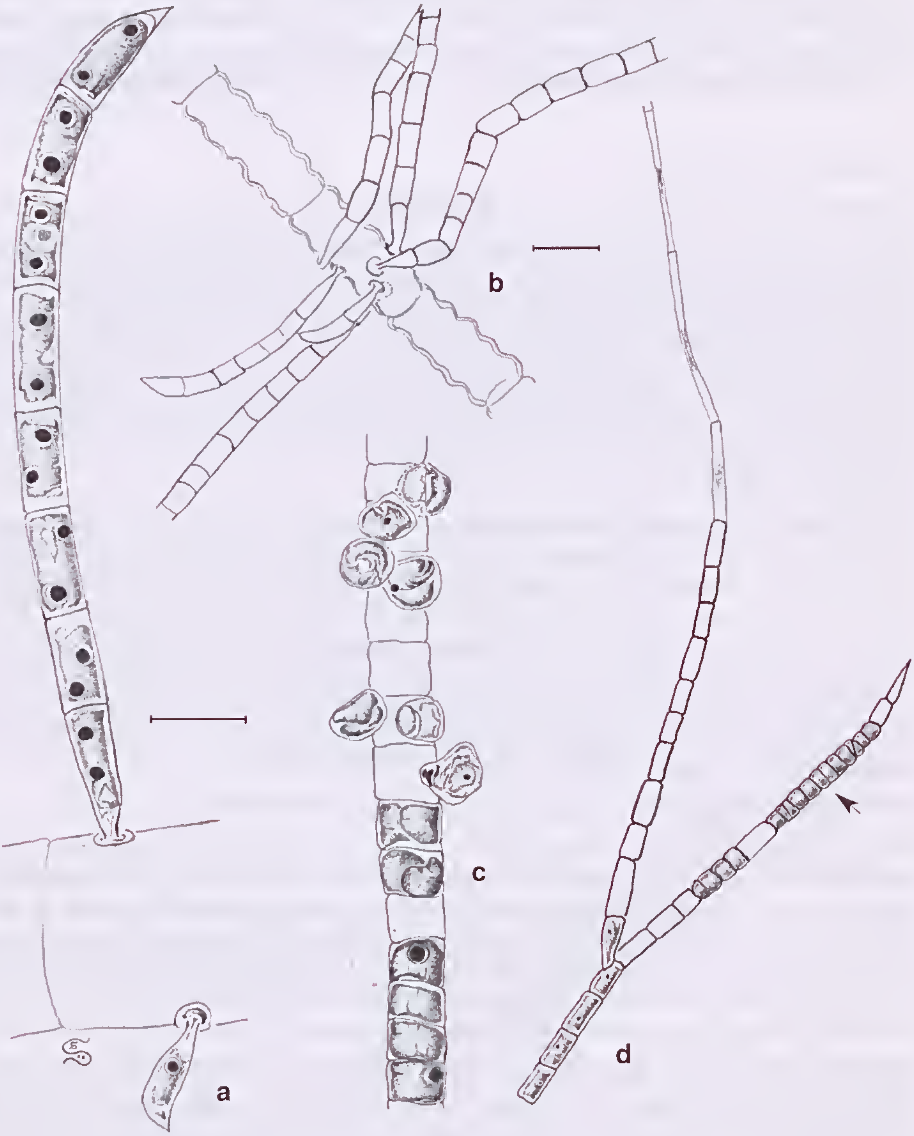

**Fig.1.** ***Uronema confervicolum***: **a**, Whole plant, vegetative; **b**, group of filaments on *Oedogonium*; **c**, filament with reproductive cells, zoids (*Skinner 0411*); ***Stigeoclonium farctum***: **d**, upper filament with hair and sporangia (*Skinner 0228b*). [a,c: scale 10 μm; b,d: scale 20 μm]

limited number of morphological characters on which to make specific distinctions, and comparatively few collections, we feel that all Australian collections so far examined fit the type species.

**Specimens examined:** New South Wales: North Coast: Wrights Ck, Port Macquarie, *Skinner 0014*, 1999 (NSW). Central Coast: aquarium tank, with fish and aquatic plants sourced from Royal Botanic Gardens Sydney, *Skinner 0327*, 5 Jul 2001 (NSW); Bells Ck, Oakhurst, *Coveny 18963*, 14 Oct 2001 (NSW). Southern Tablelands: Queanbeyan R., weir in Queanbeyan, *Skinner 0568*, 2 Jun 2002 (NSW). South West Slopes: Victoria Memorial Gardens, Wagga Wagga, *Skinner 0376, Arnold & Towler*, 26 Sept 2001 (NSW); Deniliquin, *Skinner 0411, Arnold & Towler*, 28 Sept 2001 (NSW).

South Australia: Torrens R., River Torrens Linear Park, Highbury, *Skinner 0278*, 24 Dec 2000 (NSW); Naracoorte Ck, Naracoorte, *Skinner 0458, Arnold & Towler*, 2 Oct 2001 (NSW).

### 2. Chaetophora Schrank

A genus of globose or tubular gel-coated algae that hold their shape out of water, in which Printz (1964) recognised seven species, while Bourrelly (1966) suggested there were about ten. There are four species previously reported from Australia (Day et al. 1995) all but one recollected in this study. *Chaetophora punctiformis* Kützing, from Queensland, has not been confirmed.

### 2a. Chaetophora elegans (Roth) C.Agardh, *Disp. Alg. Suec.* 42 (1812).

*Rivularia elegans* Roth, *Neue Beitr. Bot.* 1: 269 (1802).

*Thallus* globular, or confluent and thus amorphous, gelatinous epiphytic mass on aquatic vegetation, less than 1cm high. *Basal system* of branching filaments of moniliform cells, 7–10 μm diam., 10–12 μm long, impinging on oneanother, giving rise to more or less globular erect basal cells for axes, similar in size, and supporting one or two uniseriate axes. *Erect axes* of elongate barrel-shaped cells, 6–7.5(–8) μm diam., 20–23(–30) μm long; branching well spaced, increasing in frequency towards the outside; meristem subapical; terminal cell a gently curved sharp-pointed but not setaceous cell; hairs, usually arising from inside the axis, of non-pigmented cylindrical cells. *Reproductive laterals* of short, cruciately divided cells among terminal branches. Fig. 2 a–c.

**Distribution and habitat:** cosmopolitan. In Australia previously only recorded from Victoria (Entwisle 1989b), now confirmed from New South Wales and Tasmania as well. Found in still or slow-flowing water.

**Notes:** Hazen (1902) separates *Chaetophora elegans* from *C. pisiformis* based on the much more open branching of the former. Furthermore *C. pisiformis* "usually has a darker green color, and firmer more resistant gelatinous substance; in fact it is often a difficult matter to separate or crush the closely packed filaments. ... This species appears to be less inclined to grow in quiet waters; we have nearly always found it in a strong current." (Hazen 1902, p 213). As *Skinner 0299* was in a pool above a sluggish waterfall and was quite pale and little resistant to squashing it seems to fit Hazen's definition of *C. elegans*. The other mainland specimens are from similar habitats, although sometimes from faster flowing water. The Rodway specimen from Tasmania has numerous short, tumid cells in upper filaments, which Printz (1964) referred to as akinetes, but our specimen shows no wall thickening. This same specimen also showed some accumulation of lime, and many of our specimens, as well as those reported in Entwisle (1989b) are from alkaline waters.

**Specimens examined:** New South Wales: Central Tablelands: rock garden watercourse, Mt Tomah Garden (Royal Botanic Gardens Sydney), *Skinner 0299*, 15 Mar 2001 (NSW); Wombeyan Caves, near Goulburn, *Entwisle 1909*, 7 Feb 1991 (MEL). South Coast: Stony Ck, 3 km S of Bodalla, *Skinner 0497*, 27 Dec 2001 (NSW);

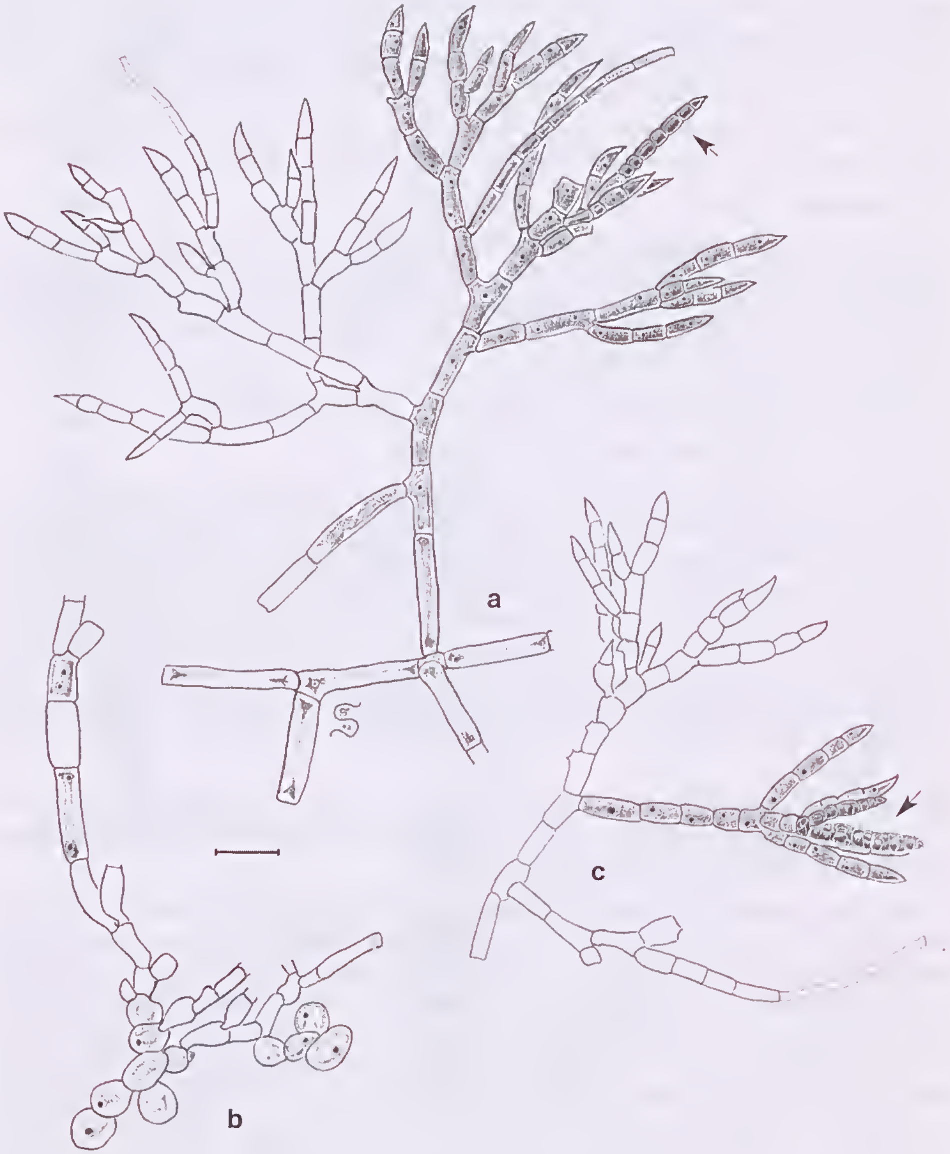

**Fig. 2.** *Chaeophora elegans*: **a**, cortical and medullary filaments; **b**, basal and lower medulla filaments; **c**, cortical branches with hairs and sporangia (*Skinner 0299*). [a–c: scale 20 μm]

Victoria: Old Rocky Ck, near Native Dog Flat, *Entwisle1808*, 29 Oct 1990(MEL); Limestone Ck, Mt Cobberas area, *Entwisle 1804*, 29 Oct 1990 (MEL);

Tasmania: Proctors Road, Hobart, *Rodway s.n.*, Apr 1912 (NSW).

**2b. Chaetophora pisiformis** (Roth) C. Agardh, *Disp. Alg. Suec.* 43 (1812).

*Rivularia pisiformis* Roth, *Neue Beitr. Bot.* 1: 272 (1802).

*Thallus* firm, gelatinous, globose to brain-like, smooth, up to 3 cm diam., on aquatic vegetation or rocks. *Basal system* filamentous, cells irregular cylindrical, 5–8 µm diam., L/D 1.5–3, most supporting erect axes. *Medulla* a system of dichotomously or trichotomously branching erect filaments radiating from base; cells narrow, 6–7 µm diam., L/D 5 or more, rhizoids and clamp-irons (transverse supporting filaments) narrow, multicellular, if rhizoids sometimes forked, arising laterally from middle of axial cells, 5–6 µm diam., L/D 3–5. *Cortex* of short, straight or slightly curved, branched filaments forming a distinct band, cells short, 5–10 µm diam., L/D 1–2 (–2.5), chloroplast laminar parietal, 1–2 (–4) pyrenoids; terminal cell accuminate. Hairs occasional, terminal on cortical filaments. *Sporangia* modified cortical filaments, cells inflated, sometimes with sagittal cross walls. Fig. 3 a–d.

**Distribution and habitat**: cosmopolitan, in Australia only confirmed from the Northern Territory. Specimens collected in both alkaline (*Entwisle 2725*) and more acid waters.

**Notes**: similar to *Chaetophora elegans*, see above. The abundance of rhizoids and clamp-irons in Australian material allies it to *C. pisiformis* var. *hamata* Jao (1940), but our material differs in having mostly straight cortical filaments. We do not recognise infraspecific taxa here, but would ally the Australian material with the type variety if we did so. Reproductive structures are not specifically described or illustrated in literature at hand, but the sporangia described here are similar to those reported for *C. elegans* and in related genera. *Entwisle 2725* harboured many rotifers and had numerous calcium carbonate crystals in the medulla, giving the (preserved) specimens a speckled appearance. Hazen (1902) notes rotifer infestations in both *C. pisiformis* and *C. attenuata* but not *C. elegans*. Printz (1964) separated *C. tuberculosa* (Roth) C. Agardh, which has been reported from Queensland (McLeod 1975, Möbius 1895), from *C. pisiformis* as the former has lateral as well as terminal cortical branch bundles. Hazen (1902) argued for caution, as, in his opinion, European descriptions and Exsiccatae often fitted larger specimens of *C. pisiformis* (and *C. elegans*). We follow Hazen here and do not presently recognise *C. tuberculosa* in Australia.

**Specimens examined:** Northern Territory: Kambolgie Ck, Kakadu N. P., *Entwisle 2741*, 5 Jun 1997 (MEL); Douglas Hot Springs, *Entwisle 2725*, 3 Jun 1997 (MEL); Howard River, upstream of Pioneer Drive, Palmerston, at gauging station, *Dostine, Metcalfe & Padovan 20*, 14 May 2002 (NSW).

**2c. Chaetophora attenuata** Hazen, *Mem. Torrey Bot. Club* 11: 213 (1902).

*Thallus* globose, discrete, firm gelatinous, usually less than 30 mm in radius, epiphytic on aquatic vegetation. *Basal system* of lozenge shaped cells that support the radiating erect filaments. Erect axes of *medulla* similar in diameter throughout, branching infrequent below, but at similar height as adjacent axes, dichotomous, rarely trichotomous; junction cells terminally inflated, with frequent branching rhizoids, arising lateral to cells; upper branching (*cortex*) more frequent, less regular, terminating in attenuated acute ended cells; chloroplast laminar parietal, pyrenoids 1–2, 5–9 µm diam. length (15–)25–45 µm. Reproductive structures not seen. Fig. 4 a–e.

**Distribution and habitat**: also known from North America and New Zealand. Cribb (1986, 1987) reports this species for Kroombit Tops and the Jardine River district in north Queensland, but we could not confirm these records. All collections examined were from fast flowing streams in northern Australia.

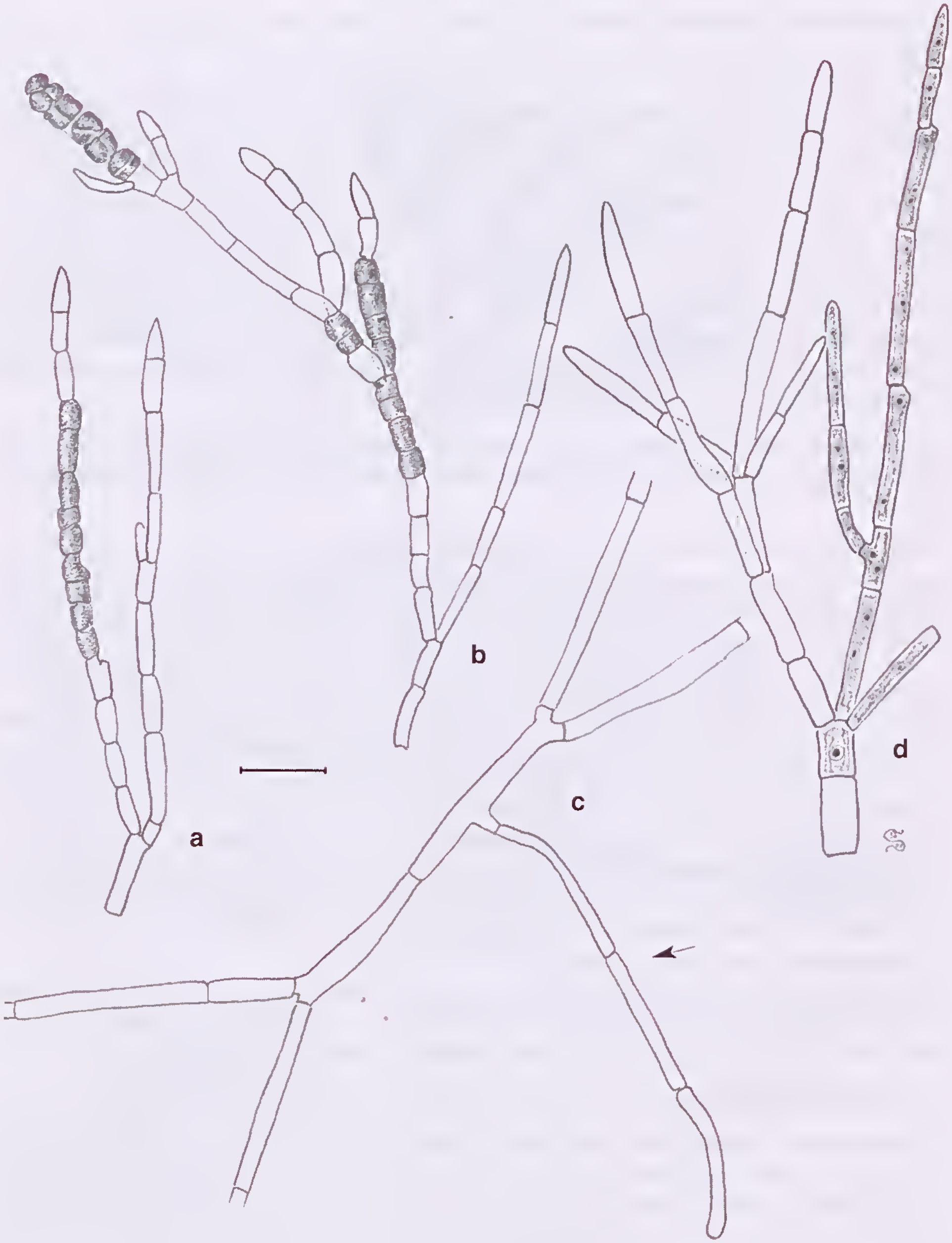

Fig. 3. *Chaetophora pisiformis*: **a**, cortical filament with intercalary sporangium; **b**, cortical filament with terminal and intercalary sporangia; **c**, cortical filaments and upper medulla; **d**, medulla with 3-celled 'clamp-iron' (*Dostine et al., 20*). [a–d: scale 20 $\mu$m]

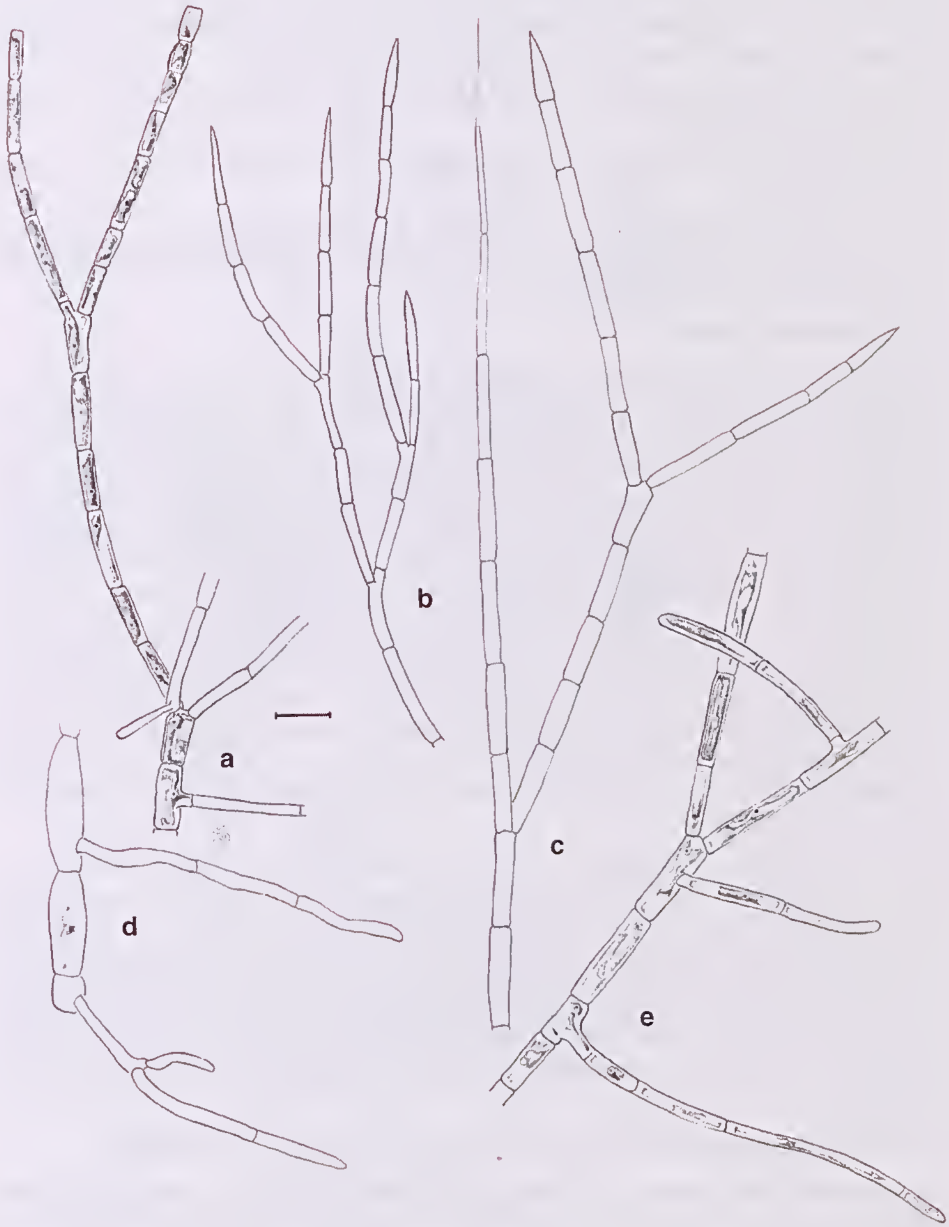

**Fig. 4.** ***Chaetophora attenuata***: **a,** upper medulla, showing branching to support cortex (*Skinner 0106a*); **b,** cortex (*Dostine et al. 42*); **c,** hair-like seta in cortex (*Entwisle 2247*); **d,** basal cells with rhizoids; **e,** lower medulla with 'clamp-irons' (*Skinner 0106a*). [a–e: scale 20 μm]

**Notes:** specimens show the branch-bearing cells and the frequent rhizoids emphasised by Hazen in the protologue, and, at least in the lower filament, long (L/D 5–8), narrow cells, not the shorter ones described by both Printz (1964) and Hazen (1902) for *C. pisiformis* (Roth) C. Agardh. Specimens do show needle-like terminal cells, but many filaments were incomplete. The Australian material appears closer to the type taxon described by Hazen rather than var. *claytonii* of Sarma (1986).

**Specimens examined:** Queensland: Callistemon Cascades, Finch Hatten Ck, Finch Hatten Gorge, *Entwisle 2247*, 8 Sep 1993 (MEL).

New South Wales: North Coast: OBX Ck, old Glen Innes Rd, W of Grafton, *Skinner 0106a, & Cherry*, 23 May 2000 (NSW).

Northern Territory: Elizabeth River, upstream of Elizabeth Valley Rd, Palmerston, *Dostine, Potter & Metcalfe 30*, 15 May 2002 (NSW); Fly Creek, downstream of Old Bynoe Rd, Palmerston, *Dostine, Potter & Metcalfe 42*, 20 May 2002 (NSW).

### 3. *Stigeoclonium* Kützing

Epiphytic or epilithic, mucilage covered, tufted filamentous, bright green algae of diverse freshwater habitats. After many attempts by various authors (e.g. Hazen 1902, Islam 1963, Printz 1964) to circumscribe species in this genus so highly responsive to phenological diversity under variation in ecological conditions, Cox & Bold (1966) defined seven species on the morphology of prostrate systems. Cox & Bold (1966) did not include a list of accepted types in their review, despite Islam (1963) already identifying these, and their graphical comparison of nomenclature is very difficult to follow. Francke (1982) recognised three taxa (*Stigeoclonium aestivale* Hazen, *S. tenue* (C. Agardh) Kützing and *S. farctum* Bertold) and reinforced the value of the prostrate system for morphological comparison of taxa. Francke & Simons (1984) reduced Cox & Bold's seven species to four on similar arguments. Simons et al. (1986) reshuffled the genus into three taxa, *Stigeoclonium helveticum* Vischer, *S. tenue* (including *S. aestivale*) and *S. farctum* on the basis of germination studies both in the field and the laboratory with reference to both the prostrate and the erect axes. Simons & van Beem (1987) provided further support for this system, with reference to the morphology of reproductive tissues.

In Australia Entwisle (1989b) isolated strains from the Yarra River catchment in Victoria and applied the species concepts of Simons et al. (1986). Our recent studies have revealed a wide range of vegetative form in field collections in Australia. For instance, some specimens tentatively included in *S. helveticum*, and resembling Islam's *S. pailiae* (Islam 1963) may represent an Australasian taxon distinct from the European and North American taxa already studied and circumscribed. Without culture studies, however, we prefer to retain the established system of Simons et al. (1986). The descriptions below expand those of Entwisle (1989b) and extend the known distribution.

### 3a. **Stigeoclonium helveticum** Vischer, *Beih. Z. Bot. Centralbl.* 51: 36 (1933).

*Thallus* arising from one or a small group of basal cells, 3–5(–10) cm long, bright green, glutinous to touch. *Primary axis* of cylindrical to slightly tumid cells 15–35(–55) µm diam, 12–70 µm long, chloroplast often fimbriate, parietal ring, several pyrenoids. Short squat junction cells or nodes when present giving rise to opposite new axes, with main primary axis continuing above. Young *secondary axes* markedly narrower than primary axes, cells cylindrical to barrel-shaped, 8–24 µm long, (6–)8–12 µm diam., chloroplast parietal; axes terminated by short, acuminate setae, often subtended by long narrow, 3–6 µm diam., hairs. Short *determinate laterals* ('thorns') arise in association with branching of primary axis or secondary axes, of a few cells only, topped with one or more setae (as in *S. pailiae*). *Rhizoids* arising from the bottom of

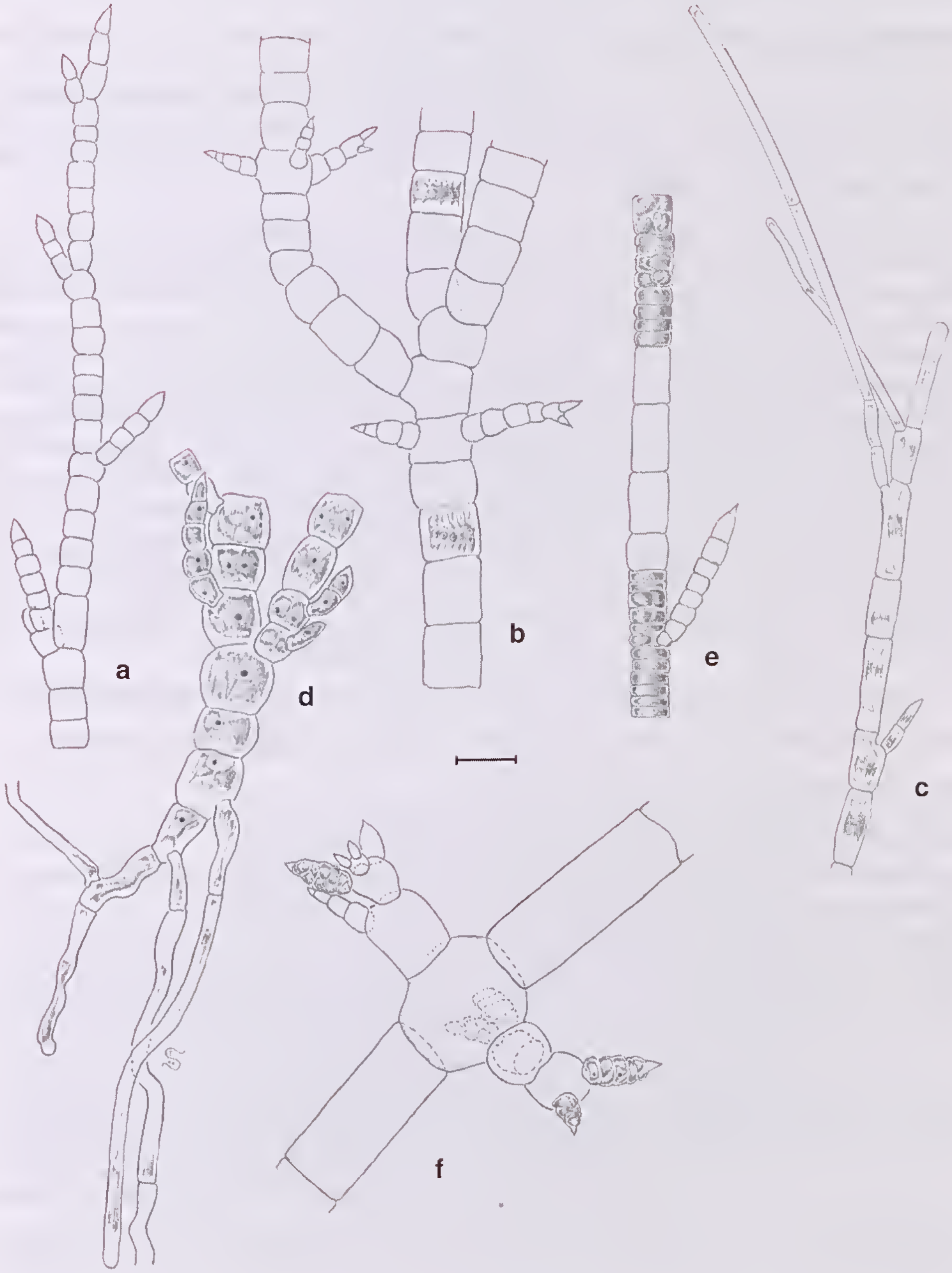

**Fig. 5.** ***Stigeoclonium helveticum*****:** **a**, apex of axis (*Skinner 0141*); **b**, mid-axis, with short lateral initials (*Skinner 0054*); **c**, upper axis with hairs (*Skinner 0507*); **d**, base of axis with rhizoids (*Entwisle 3141*); **e**, intercalary sporangia in main axis (*Skinner 0500*); **f**, 'thorns', modified as sporangia (*S. pailiae* variant, *Skinner 0508*). [a–f: scale 20 $\mu$m]

primary axial cells close to the host surface. *Reproductive regions* intercalary in upper primary or secondary axes, sometimes in laterals and 'thorns', of rows of short, discoid cells L/D 0.5–1.0, sometimes cruciately divided. Fig. 5 a–f.

**Distribution & habitat**: widely distributed throughout the world, and reported from Queensland, New South Wales, Victoria and the Northern Territory. The lack of records from Tasmania, South Australia and Western Australia probably reflects its nondescript appearance and difficulties with species level identification, not its absence. The specimen localities indicate a preference for clear water, in line with observations by other authors.

**Notes**: robust specimens with several degrees of branching, inflated nodes and 'thorns', fit closely Islam's (1963) description of *S. pailiae*. Sarma (1986) transferred this taxon to *Cloniophora*, a genus characterised by the presence of such 'thorns'. Inflation of the nodes, also used to indicate *Cloniophora*, occurs in our collections to varying degrees within a population or even an individual. There does not appear to be any clear ecological or geographic explanation for the coincident expression of these characters, and the plants otherwise fit the Simons et al. (1986) description of *S. helveticum*. *Cloniophora spicata* (Schmidle) Islam, reported for Queensland by McLeod (1975), has not been collected in New South Wales or other states. We therefore find no support for recognising a separate species, let alone genus, in the Australian flora. Our circumscription of *Stigeoclonium helveticum* is based on the key and description of *S. helveticum* (and *S. aestivale*) in Franke and Simons (1984), the description of reproductive structures in Simons and van Beem (1987), and the description of 'the *helveticum* group' in Simons et al. (1986). The following records should be assigned to *S. helveticum* as circumscribed here:

i) *S. amoenum* Kütz. and *S. amoenum* var *novizelandicum* Nordst. (Bailey 1893; Möbius 1892);

ii) *S. askenasyi* Schmidle (1896), (Bailey 1898) = *Cloniophora spicata* (Schmidle) Islam;

iii) *S. flagelliferum* Kütz. (Ling & Tyler 1986);

iv) *S. protensum* (Dillwyn) Kütz. (Möbius 1895, Bailey 1895).

It is clear from the figures and description of *S. subuligerum* Kütz. in Cribb (1984) that his taxon is similar to the *S. pailiae* Islam variant of *S. helveticum*.

**Specimens examined**: New South Wales: North Coast: Nymboidea River, Buccarumbi Bridge, *Skinner 0111*, 23 May 2000 (NSW). Northern Tablelands: Backwater, goldfields, *Wissman* (*Skinner NED014*), Feb 1974 (NE); Round Mountain (Barokee) Rd, Cathedral Rock Nat. Pk., main drain, *Skinner 0169b, and Cherry*, 24 May 2000 (NSW); Beilsdown River, Dangars Falls, Dorrigo, *Skinner 0141, and Cherry*, 23 May 2000 (NSW). North West Slopes: Peel R., Nundle, *Water Resources Commission*, 14 Feb 1978 (NSW). Central Coast: Vaucluse Reserve, *H Jolly s.n.**, 18 Jul 1969 (NSW); Porters Ck, Wyong, *Gartenstein 3a*, 15 Mar 2002 (NSW). Central Tablelands: Lett R., near Hartley, *Brewster s.n.*, no date (NSW) [Islam determined for Valerie May, as *S. amoenum*]; Wollondilly R., *Skinner 0054**, 12 Apr 2000 (NSW). South Coast: Tuross R. at Eurobodalla bridge, *Skinner 0500*, 27 Dec 2001 (NSW); Tuross R., Cadgee area, *Skinner 0507*, 0508**, 27 Dec 2001 (NSW). Southern Tablelands: Widows Ck, Jindabyne, *Entwisle 3141*, 4 Jan 2002 (NSW); Braidwood Lagoon, Braidwood, *May s.n.*, 3 Dec 1969, 24 Nov 1971 (NSW). South Western Slopes: Murrays Rice field, Griffith, *May s.n.*, 6 Dec 1978 (NSW).

Victoria: Loddon Bridge, Guildford, *Skinner 0419, Arnold & Towler*, 29 Sept 2001 (NSW); lake, Royal Botanic Gardens, Melbourne, *Lewis 22*, 22 Oct 1996 (MEL).

* Collections with an asterisk are those most similar to *S. pailiae* Islam (syn. *Cloniophora pailiae* (Islam) Sarma).

**3b. Stigeoclonium farctum** Berthold, *Nova Acta Leopold. Carol.* 40: 201 (1878).

*Erect thallus* arising as a fringe from compact discoid pinnately branching base, less than 1cm high, green, greasy. Erect axes sparsely branched, often terminating in tapering hairs; vegetative cells cylindrical, 6–8 µm diam., 12–22 µm long, chloroplast laminar parietal, one or two pyrenoids. *Reproductive cells* quadrate to shorter than broad, in series in upper filaments. Figs 1 d, 7 d–f.

**Distribution and habitat**: cosmopolitan. So far recorded in Australia from New South Wales and Victoria, there are further specimens at MEL for Victorian localities (see Entwisle 1989b). *S. farctum* tolerated the urban and outer urban areas of the Yarra River catchment, as demonstrated by Entwisle (1989b), but was not a major component of the algal flora. The New South Wales record, below, is from an artificial pond, fed by tap water run-off from a glass-house complex.

**Notes**: Entwisle (1989b) found this species at numerous places in the Yarra River catchment, yet it has been rarely collected elsewhere. Its small size and encrusting habit make it probably less noticeable than the other two species. It is often difficult to separate smallish plants of *S. tenue* from *S. farctum*. As well as usually being much more sparsely branched, *S. farctum* has a tendency to form short, one or two celled leading spurs near tips, while the main axis continues on but slightly laterally displaced, giving upper branches a kinked appearance.

**Specimens examined**: New South Wales: Royal Botanic Gardens, Sydney, pond near Tropical House, *Skinner 0228b*, 21 Jun 2000.

Victoria: Anderson Ck, Warrandyte Rd, *Entwisle 1013*, 16 Dec 1986 (MEL); Merri Ck, Preston, *Entwisle 935*, 29 Oct 1986 (MEL).

**3c. Stigeoclonium tenue** (C. Agardh) Kützing, *Phyc. Gen.* 253 (1845).

*Draparnaldia tenuis* C. Agardh, *Alg. Dec.* 40 (1814).

*Thallus* arising from spreading, irregularly branching *basal plate*, numerous axes together, 3–7 (–15 or more) cm long, bright green, glutinous to touch. *Primary axes* of cylindrical cells, 9–12 µm diam., 12–30 µm long; chloroplast a parietal ring, often incomplete, rarely fimbriate, pyrenoids small, several. *Secondary axes* similar to primary axes, cells, (4–)6–8 µm diam., 9–12 µm long, tapering to pointed cells, rarely setae; chloroplasts laminar parietal. Hairs infrequent, terminal. Rhizoids infrequent. *Reproductive regions* involving much of the upper secondary branches; cells frequently in discrete groups of four, quadrate to inflated, sometimes tangentially, rarely cruciately, divided, opening by rupture. Figs 6 a–c, 7 a–c.

**Distribution & habitat**: cosmopolitan and common. Reported from throughout Australia. Overseas reports (McLean & Benson-Evans 1974, 1977) suggest that *S. tenue* has wide tolerance for turbidity and environmental disturbance; Entwisle (1989a, 1989b) demonstrated similar tolerance in creeks near Melbourne, Victoria. Our collections show a similar tolerance of habitat types.

**Notes**: earlier Australian records, probably referable to *S. tenue*: *Myxonema subsecundum* (Kütz.) Hazen (Playfair 1917), *S. attenuatum* (Hazen) Collins (Moewius 1953), *S. australense* M. Moebius (1892, Bailey 1893, syn. *S. fasciculare* in Islam 1963), and possibly *S. elongatum* Hassall (Cribb 1983, no description).

**Specimens examined**: New South Wales: North Coast: Nymboidea River, Buccarumbi Bridge, *Skinner 0112, and Cherry*, 23 May 2000 (NSW). Northern Tablelands: Little Murray River, Waterfall Way, *Skinner 0146, and Cherry*, 24 May 2000 (NSW). North Western Slopes: Pages River, Arnolds Bridge, Murrurundi, *Skinner 0023*, 11 Dec 1999 (NSW). Central Coast: Nepean River, Yarramundi Bridge, Agnes Banks, *Skinner 0334 and McPherson*, 9 Aug 2001 (NSW); Little Bushells Lagoon, Wilberforce, *Skinner 0345 and McPherson*, 9 Aug 2001 (NSW); wetland , McGraths Hill, *Skinner 0347*

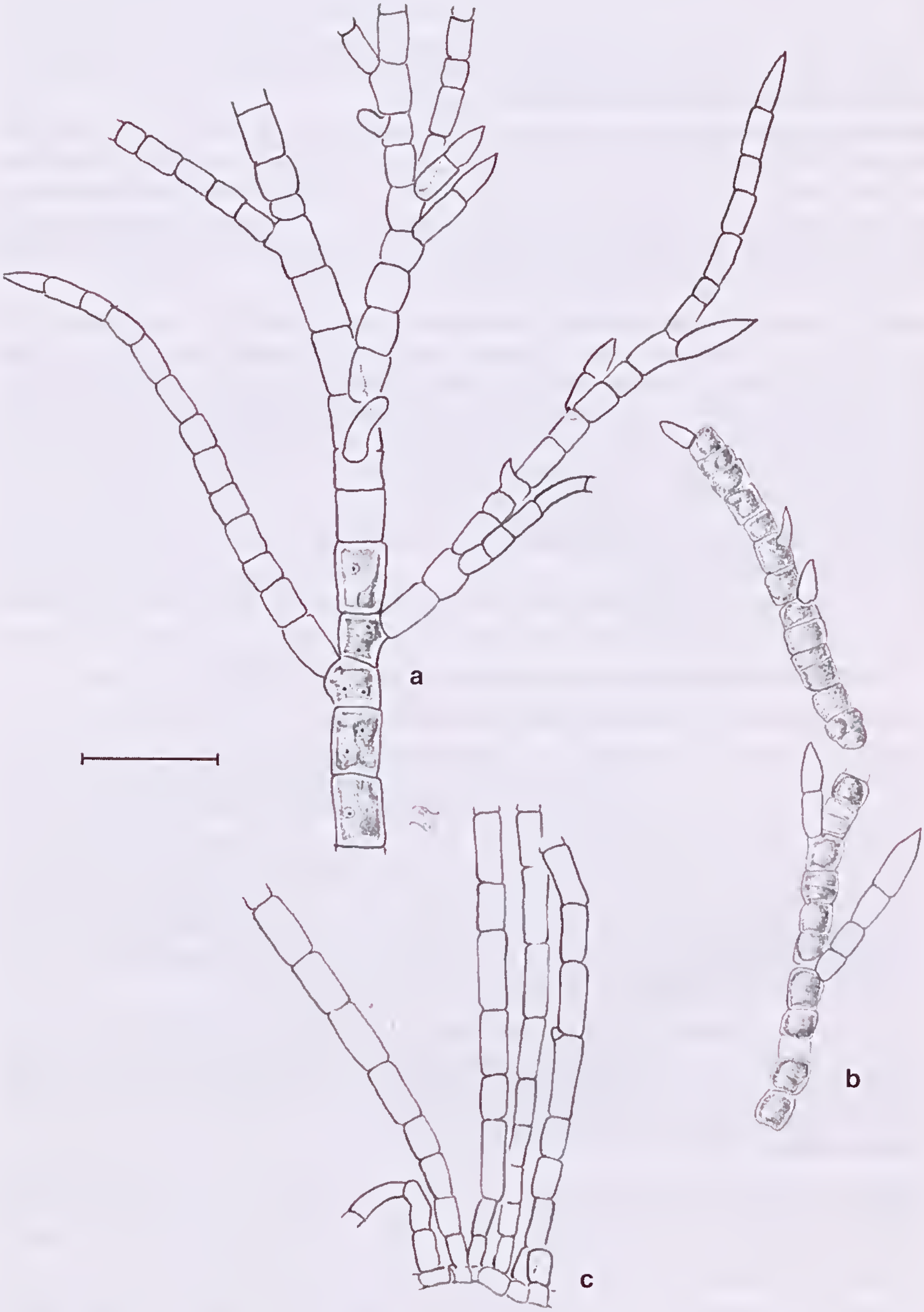

**Fig. 6.** ***Stigeoclonium tenue***: **a,** main axis with laterals; **b,** sporangia transforming lateral tips; **c,** axes arising from basal filament (*Skinner 0334*). [a–c: scale 20μm]

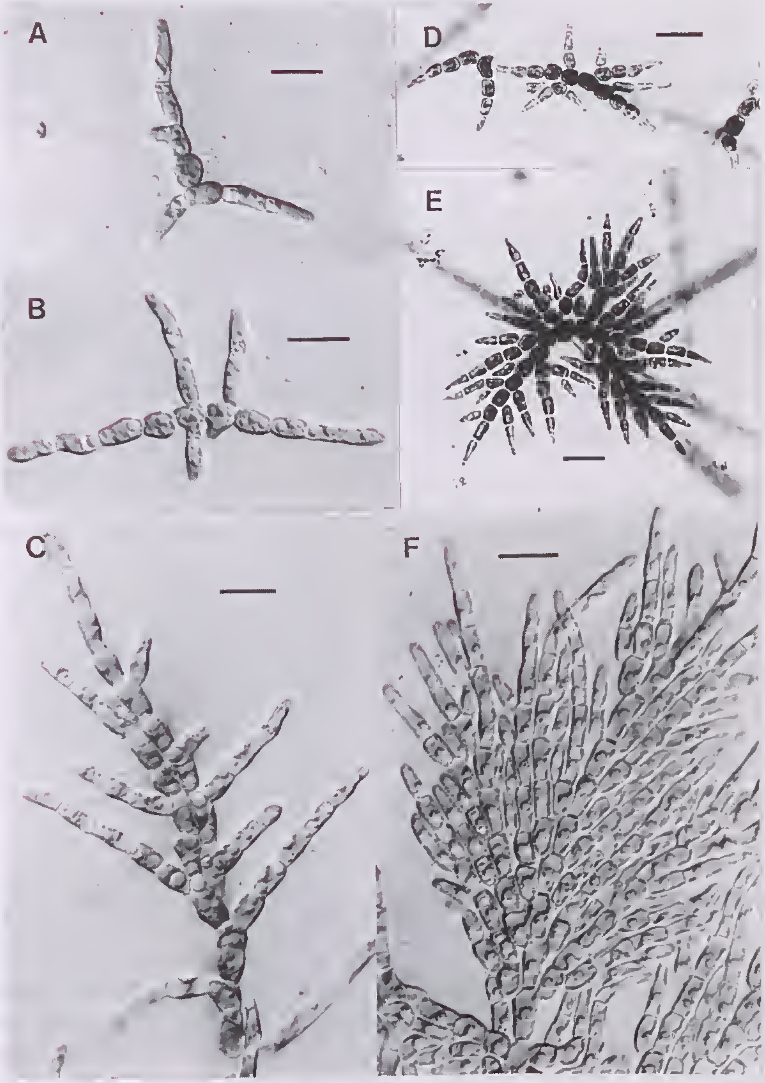

**Fig. 7.** ***Stigeoclonium tenue*****: a,** prostrate development of settled zoospore; **b,** prostrate development with irregular branching; **c,** open prostrate system with irregular branching (*Entwisle 833*). (Note oil globules in a–c.) ***Stigeoclonium farctum*** **d,** prostrate development of zoospore; **e,** pinnate branching of prostrate system; f. pseudoparenchymatous basal system (*Entwisle 935*) [a–f: Scale 20 μm].

*and McPherson*, 9 Aug 2001 (NSW). South Coast: Murrays Beach, Booderee Nat. Pk, Jervis Bay, *Millar s.n.*, 30 Jul 2002 (NSW). Southern Tablelands: Queanbeyan R., below viaduct, Queanbeyan, *Skinner 0563*, 2 Jun 2002 (NSW); Chapmans Dam, Braidwood, *May s.n.*, May 1970, 2 Dec 1970 (NSW); Lords Dam, Braidwood, *May s.n.*, 11 Mar 1973 (NSW). South Western Slopes: Victoria Memorial Gardens, Wagga Wagga, *Skinner 0376, Arnold & Towler*, 26 Sept 2001(NSW); Box Ck Channel, Blighty, *Skinner 0408, Arnold & Towler*, 27 Sep 2001 (NSW).

Victoria: Cockatoo Ck, Avonsleigh, *Entwisle 833*, 24 Sept 1986 (MEL); and see Entwisle (1989b).

Tasmania: St Patricks R., N of Targa, *Entwisle 2633*, 12 Apr 1996 (MEL).

South Australia: Torrens R., River Torrens Linear Park, Highbury, *Skinner 0285*, 25 Dec 2000.

Western Australia: Gingin Brook, 7 Km W of Gingin, *Entwisle 2998*, 5 Dec 1999 (NSW).

### 4. **Draparnaldia** Bory

Gel-coated, dendroid tufted, sparling bright green algae, with a distinct demarcation between axial filaments and much branched determinate laterals, and no pattern of alternation of long and short axial cells. While various authors have accepted numerous species, Johnstone (1978) demonstrated much plasticity in form for the genus. Based on Australian material examined it is considered prudent to follow Johnstone (1978) and the nomenclatural conclusions of Forest (1965), Bourrelly (1966) and Lokhorst (1984) and accept only *Draparnalia mutabilis* (Roth) Bory.

### 4a. **Draparnaldia mutabilis** (Roth) Bory, *Ann. Mus.Hist. Nat.* 12: 402 (1808).

*Conferva mutabilis* Roth, *Cat. Bot.* 1: 197 (1797).

*Thallus* gelatinous coated, branching, growth acropetal, usually attached. *Primary* and *secondary axes* (distinguished on cell width), of cells, evenly sized, cylindrical or tumid cylindrical (10–15–)20–60(–90) µm diam., L/D (1.0–)1.5–2.5(–3); chloroplast central, fimbriate, circular, parietal, pyrenoids 1 to a few. *Branched laterals* alternate, opposite or whorled, arising laterally at the top of axial cells; cells narrowly cylindrical to barrel-shaped, 4–10 µm diam., L/D (1.0–)1.5–3(–4), chloroplast laminar parietal , pyrenoids 1–2; filaments of 3 or 4 cells tipped with a blunt to curved seta or long multicellular hair 3–4(–5) µm diam. *Rhizoids* multicellular, sinuous, 6–8 µm diam., arising with or just below the lateral branches in lower cells of primary, and sometimes secondary, axes. Reproduction by zoids; cells of lateral branches becoming tumid and dividing transversely to form two chambers. Fig. 8 a, b.

**Distribution and habitat**: cosmopolitan. In Australia previously reported in Queensland (McLeod 1975, as *D. glomerata* (Vaucher) C. Agardh), and Western Australia (de Toni & Forte 1922, as *D. glomerata*) and now known from throughout the continent. There are numerous herbarium records from New South Wales, Victoria and Tasmania in MEL, as well as those cited below. Johnstone (1978) contends that *Draparnaldia* prefers to grow alone or with few other macroalgae, yet very few of our collections support this view. Several of them are from swamps and shallow slow flowing water-bodies with numerous unicellular and filamentous algae from diverse groups. Even in collections from rivers and creeks, *Draparnaldia* was not the only alga present, although there were fewer epiphytes in the mucilage of *Draparnaldia* in such specimens.

**Notes**: while even within a specimen there may be degrees of bushiness of laterals, the shape of lateral cells is consistent for that specimen, but ranges from narrow and cylindrical to short, tumid and barrel shaped from collection to collection. Likewise the degree of hairiness ranges from occasional hairs (*Skinner 0355*) to very hairy indeed (*Skinner 0169a; Dingley 30 Mar 2002*). There were indications of occasional intercalary division in axes. Only two of our specimens showed good development of rhizoids (*Skinner 106; Dingley 30 Mar 2002*). The material from the Northern Territory is perhaps

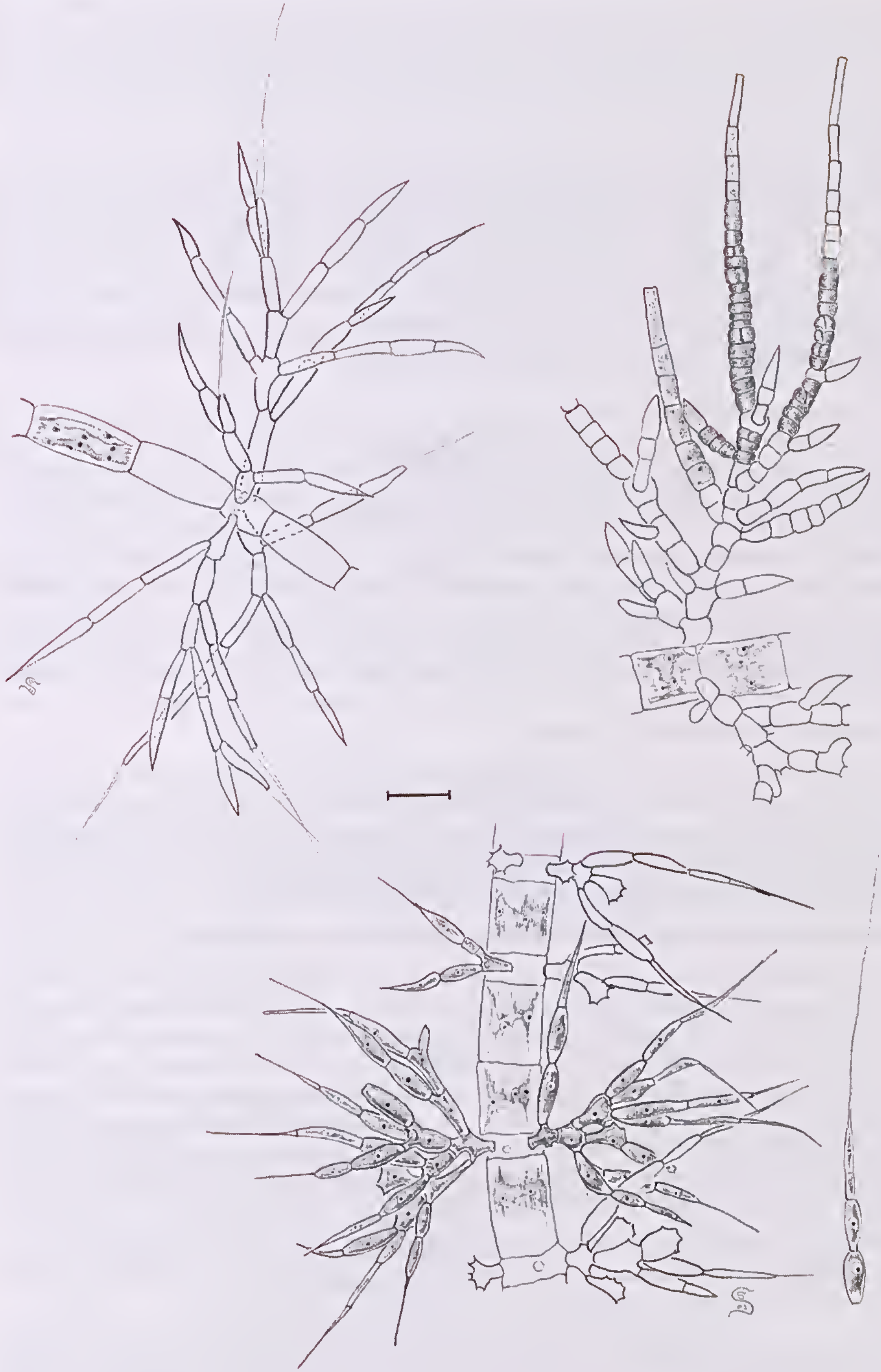

**Fig. 8.** ***Draparnaldia mutabilis*: a,** axial cells with lateral fascicles, *D. judayi* variant (*Dostine* et al. *10*) **b,** lateral filaments modified as sporangia (*Skinner 0453*); ***Draparnaldiopsis salishensis*: c,** main axis and laterals; **d,** four celled branch of lateral, with seta (*Skinner 0500*). [a–d: scale 20 µm]

the most distinctive form, with short laterals topped with spines, as in Prescott's (1944) *D. judayi*, a determination made by Cribb (1993) for material collected on Cape York. However Johnstone (1978) demonstrates that this is a single highly plastic species, and our material fits comfortably within his range of variation. *Skinner 0453* includes fertile filaments.

**Specimens examined:** New South Wales: North Coast: OBX Ck, Old Glen Innes Rd W of Grafton, *Skinner 0106*, & Cherry, 23 May 2000 (NSW). Northern Tableland: Barokee rest area, Catherdal Rock N.P., *Skinner 0169a, & Cherry*, 24 May 2000 (NSW); Polblue Ck, Barrington Tops, *Entwisle 1972*, 10 Feb 1991 (NSW, MEL). Central Coast: Ham Common, Richmond, *Skinner 0339*, 9 Apr 2001 (NSW). Central Tablelands: Bulls Camp Reserve, pond, Woodford, *Dingley s.n.*, 30 Mar 2002 (NSW); Dunns Swamp, *Entwisle 3123, 3127*, 5 Oct 2001 (NSW); Honeyeater Flat, near Glen Davis, *Leishman 73*, 24 Apr 2000 (NSW). Central Western Plains: Wyalong, *Skinner 0355, Arnold & Towler*, 24 Sep 2001 (NSW). South Coast: Yowrie R., Yowrie, *Skinner 0245*, 13 Jul 2000 (NSW). Southern Tablelands: Braidwood Lagoon, Braidwood, *May s.n.*, 3 Dec 1969 (NSW).

Victoria: Upper Yarra catchment, *Entwisle 949*, 17 Nov 1986 (MEL); intersection of Yarra & O'Shannasys R., *Entwisle 859*, 1 Oct 1986 (MEL); Cockatoo Ck, Avonsleigh, *Entwisle 833*, 24 Sep 1986 (MEL); Brandy Ck, Mt Hotham-Omeo road, *Entwisle 690*, 17 Oct. 1984 (MEL, NSW); Limestone Ck, Mt Cobberas area, *Entwisle 1804*, 29 Oct 1990 (MEL); Birch Ck, Newlyn, *Entwisle 178*, 22 Mar 1983 (MEL); creek into McKenzie R., *Entwisle 2467*, 2 Oct 1995 (MEL);

Tasmania: Lachlan R., near New Norfolk, *Robson s.n.*, 17 Feb 1992 (MEL); Inglis R., Takone, *Entwisle 2588*, 7 Apr 1996 (MEL); Lady Baron Falls, Mt Field N.P., *Lewis 6, & Bisby*, 6 Dec 1995 (MEL);

South Australia: Riddock Hwy, Dismal Swamp, *Skinner 0453, Arnold & Towler*, 1 Oct 2001 (NSW).

Northern Territory: Mitchell Creek, downstream of Lambrick Ave, *Dostine, Metcalfe & Padovan 10*, 13 May 2002 (NSW).

### 5. **Draparnaldiopsis** Smith & Klyver

A genus of five species, two from North America, and one each from India, China and New Zealand, superficially similar in form to *Draparnaldia*, but with lateral fasciculate branches arising from only shorter axial cells. *Draparnaldiopsis* has been reported from Queensland and the Northern Territory (Entwisle, 1994) while the description below is of more recently collected specimens from New South Wales.

### 5a. **Draparnaldiopsis salishensis** Prescott, *Hydrobiologia* 7: 52 (1955).

*Thalli* gelatinous coated, tubular, bright green. *Main axis* with alternation of two cell sizes at maturity; longer vegetative cells, which do not give rise to lateral branching systems, singly or more rarely in pairs, chloroplast a ring of shredded ribbon, with a small number of pyrenoids, 23–26 µm diam., L/D 0.75–1.25; shorter lateral branch supporting cells, 23–26 µm diam., L/D 0.3–0.4. *Lateral branches* in whorls of 3, or more rarely 4, stem cells obtriangular and tri- or quadrifurcate, laterals a row of 2–3(–5) spindle-form cells (4–)6–8 µm diam., terminating in a narrow conical cell or in a 3 to 4 celled seta-like hair, each cell having a parietal chloroplast and a prominent pyrenoid. Reproductive structures not observed. Fig. 8 c,d.

**Distribution & habitat**: North America and Australia; reported from Qld and the N.T. (Entwisle & Nairn 1999) as *Draparnaldiopsis* sp., and recently from N.S.W. and Vic., where it occurs in cold water, fast flowing streams, or alpine lakes.

**Notes**: fits the description in both Prescott (1955) and Printz (1964). The main axis has a regular alternation of longer and shorter cells, in common with *Draparnaldiopsis alpinis* Smith & Klyver and *D. indica* Bharadwaja, but fine, drawn-out tips on lateral branchlets, and the lateral branches are in whorls, not paired. *Draparnaldiopsis simplex* Jao, rather like *D. indica*, has no regular pattern for long and short axial cells, and short, penicillate branchlets in opposite laterals. Sarma (1986) has described *D. taylorae* an almost identical species from New Zealand, which, he contends, differs from

*D. salishensis* because *D. taylorae* has whorls of laterals like *Batrachospermum* interspersed with bare patches on axes, and multicellular hairs rather than seta-like hairs. There does not appear to be such patchiness in Australian collections. The hairs of *D. salishensis* visible in the photomicrograph in Bourrelly (1966) are common in *Skinner 0500*, but much less frequent in *Entwisle 3140*, and appear very similar to those illustrated by Sarma (1986). The separation of *D. taylorae* from *D. salishensis* needs to be reviewed. The type locality is described (Prescott 1955) as being 'basic water' with fluctuating water levels, not unlike the New South Wales localities, where seasonal fluctuations in water level would be regularly observed. Prescott (1955, p. 54.) notes the occurrence of 'numerous swarming, gamete-like cells' which arose from the middle cells of the branches, not the tip cells.

**Specimens examined:** New South Wales: South Coast: Tuross R., bridge at Eurobodalla, *Skinner 0500*, 27 Dec 2001 (NSW). Southern Tablelands: Lake Jindabyne, *Entwisle 3140*, 4 Jan 2002 (NSW).

## Conclusion

There is much room for further research into the freshwater filamentous members of the Chaetophoraceae in Australia, especially into *Uronema*, where more species may await discovery, and *Chaetophora*, to confirm some of the older records. We confirm that *Stigeoclonium* has three species in Australia, as in other parts of the world. *Draparnaldia mutabilis* is shown to be widespread and to occur in many aquatic habitats, while one species of *Draparnadiopsis*, *D. salishensis*, is confirmed for Australian waters. It would be interesting to extend our studies in tropical areas of the continent, and compare our northern Australian flora with nearby Asian regions.

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# *Thedachloa*, a new grass genus (Gramineae: Paniceae) from the Northern Kimberley, Western Australia

S.W.L. Jacobs

## Abstract

*Jacobs, S.W.L. (Botanic Gardens Trust, Sydney, Mrs Macquaries Road, Sydney, NSW 2000, Australia) 2004.* Thedachloa, *a new grass genus (Gramineae: Paniceae) from the Northern Kimberley, Western Australia.* Telopea *10(2): 635–637.* **Thedachloa** is described as a new genus with the type species **T. annua.** *Thedachloa* is distinguished by a zone of stiff hairs or bristles on the upper glume and by the deeply-folded or grooved, almost cylindrical lower lemma.

## Introduction

A new grass species was collected in 1996 near Kalumburu, Western Australia. Examination back at NSW indicated that not only was it a new species, but also a new genus. Publication was delayed until further searching allowed a better idea of the distribution and habitat. Further field work in 2002, unfortunately in a very dry year, found no further localities, though it was recollected at the original site. This species so far is only known from c. 200 metres along the bank of a creek north of Kalumburu.

The relationships of *Thedachloa* are not clear. There is a resemblance to *Sacciolepis,* mainly due to the swollen or inflated lower spikelet. The hairs/bristles on the upper glume do not immediately appear similar to the ornamentation of other genera but, when coupled with the folded/grooved lower lemma, may indicate some relationship to the Neurachneae, or perhaps even *Thyridolepis* in particular. It is hoped that DNA sequencing studies may better indicate relationships.

**Thedachloa** *S.W.L. Jacobs* **gen. nov.**

*Sacciolepidi* aemulans, differt fascia longe hispida in gluma superna, lemmate inferno valde sulcato dorsaliter.

Inflorescence a dense ovoid panicle. Spikelets inflated at base, falling entire and fertile floret also separating. Glumes unequal; lower obtuse, inflated, membranous, faintly 3-nerved, rounded on back; upper glume 7-nerved with the lateral nerves closely-spaced, rounded on back, with a band of stiff hairs or bristles above the middle. Lower lemma male or sterile, as long as the spikelet, inflated, 7-nerved with the lateral nerves closely-spaced, deeply grooved or folded on the back below and almost tubular with the innermost tissue of the fold disintegrating on older dried florets; palea well developed. Upper floret bisexual, noticeably shorter than the spikelet, shortly stipitate; lemma shiny, brown, smooth, glabrous, chartaceous, margins slightly inrolled, germination flap weakly developed; palea exposed, shiny, brown, smooth; stigmas brown; anthers pale cream; caryopsis with embryo c. 45% the length.

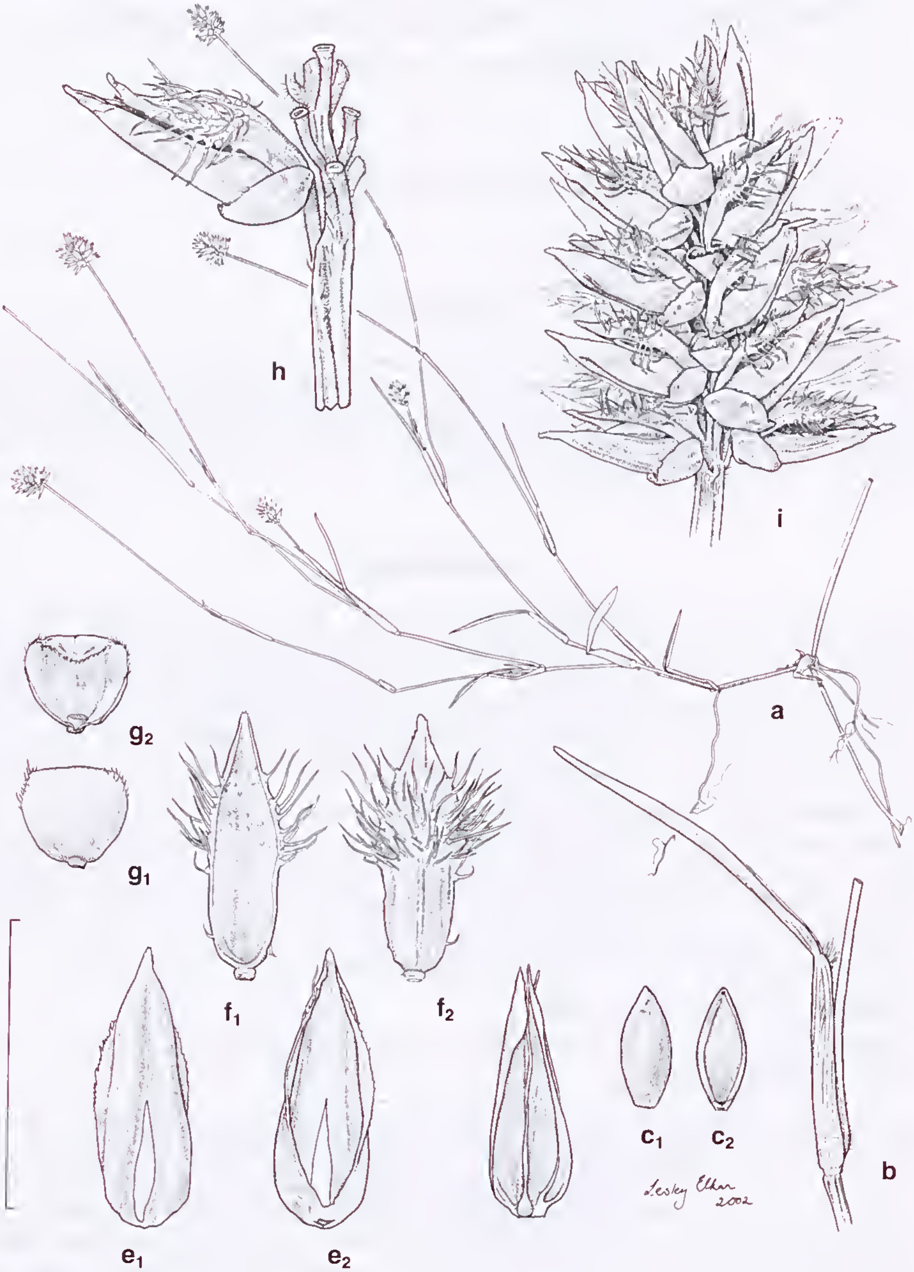

**Fig. 1.** *Thedachloa annua*. Scale bar 2.5 mm unless indicated otherwise. **a**, habit (scale bar 4 cm); **b**, leaf sheath and blade (scale bar 0.6 cm); **$c_1$**, upper or fertile lemma; **$c_2$**, palea of upper lemma; d, palea of lower lemma; **$e_1$**, lower lemma, dorsal view showing groove and gap where tissue has disintegrated; **$e_2$**, lower lemma, ventral view; **$f_1$**,

**Type species:** *Thedachloa annua* S.W.L. Jacobs

**Etymology:** The name is derived from the grazing lease 'Theda' immediately to the south of Kalumburu, in recognition of the contribution made by co-manager Robin Maher to understanding the biology, geology and anthropology of the region.

**Thedachloa annua** *S.W.L. Jacobs* **sp. nov.**

Gramen annuum; inflorescentia densa, ovoidea, 3–5 mm longa; spiculis c. 2 mm longis; gluma superna in dimidio superiore fascia longe hispida (pilis c. 0.5 mm longis); lemmate inferno valde sulcato dorsaliter.

**Holotype:** Western Australia: Northern Botanical Province: Central Gardner: c. 2 km N of Kalumburu, Pago road. 14°16.78' S 126° 37.42' E, *S. Jacobs 8061*, 22 May 1996. Small spreading grass on white sand on bank of ephemeral creek amongst quartzite boulders. (NSW; iso PERTH, US, B).

Stoloniferous scrambling annual; stolons to 20 cm or longer with internodes to 3 cm long, rooting at the nodes, the leaves deciduous from older nodes. Cataphylls absent. Prophyll present in axil, c. 50% sheath length. Culms sometimes branched, glabrous, slender, ridged, compressible; nodes narrower than culm. Leaf sheaths ridged, glabrous except for a few long stiff hairs on upper margins; ligule a fringe of hairs c. 0.5 mm long; blade to 2 cm long, more or less triangular, flat, becoming inrolled on drying, glabrous or sometimes sparsely pubescent near base, veins raised on adaxial surface, smooth on abaxial surface. Inflorescence a dense ovoid panicle 3–5 mm long, c. 4 mm diam. Spikelets 1.7–2.1 mm long, inflated at base, falling entire and fertile floret also separating. Glumes unequal; lower 0.6–0.8 mm long, c. 25% spikelet length, broad, obtuse, inflated, membranous, glabrous except for the ciliate margins, faintly 3-nerved, rounded on back; upper glume 1.6–1.9 mm long, c. 85% spikelet length, slightly inflated at base, 7-nerved with the lateral nerves closely-spaced, rounded on back, with a band of usually tubercle-based stiff hairs or bristles c. 0.5 mm long from about the middle to just below the apex (c. 50–80% of the glume). Lower lemma male or sterile, 1.8–2 mm long, as long as the spikelet, inflated, 7-nerved with the lateral nerves closely-spaced, deeply grooved or folded on the back below and almost tubular with the innermost tissue of the fold absent on older dried florets; palea c. 1.5 mm long. Upper floret bisexual, c. 1 mm long, noticeably shorter than the spikelet, shortly stipitate; lemma shiny, brown, smooth, glabrous, chartaceous, margins slightly inrolled, germination flap present but poorly defined; palea exposed, shiny, brown, smooth; anthers pale cream to pink; stigmas brown; caryopsis c. 0.8 mm long, embryo c. 45% the length. Fig. 1.

**Habitat:** Sandy alluvium along an ephemeral creek.

**Distribution:** Only known from the Type locality in the Northern Kimberley, near Kalumburu, Western Australia.

**Etymology:** Named after its apparently annual habit.

**Specimen examined:** Western Australia: Central Gardner: c. 2 km N. of Kalumburu, Pago rd. 14° 16.806' S 126° 37.432' E, *S. Jacobs 8854*, 3 July 2002 (NSW).

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# The tropical flora of southern China and its affinity to Indo-Malesian flora

H. Zhu & M.C. Roos

## Abstract

*H. Zhu[1] & M. C. Roos (The National Herbarium of the Netherlands, Leiden University branch, P.O.Box 9514, 2300 RA Leiden, the Netherlands. [1]Permanent address: Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences, Kunming 650223, P. R. China) 2004. The tropical flora of southern China and its affinity to Indo-Malesian flora.*Telopea *10(2): 639–648.* A comparative study of floristic composition of the vegetation in South China, i.e. southern Yunnan and Hainan Island, with those in Vietnam, Malay Peninsula and Brunei reveals that: (1) the flora of southern China consists mainly of tropical floristic elements which contribute about 60%, at the family level and more than 80 % at the generic level, of its total flora. The dominant geographical elements of the flora of southern China at the generic level are taxa with a distribution pattern in tropical Asia. This reveals that the flora of southern China is of tropical nature with a strong tropical Asian affinity; (2) most of the dominant families from the flora of southern China are also dominant in the Malesian flora except for the Urticaceae, Fagaceae, Theaceae, Rosaceae and Myrsinaceae. The floristic similarity between the flora of southern China and the flora of western Malesia is over 70% at the family level and more than 50% at the generic level, and between the floras of southern China and Vietnam is more than 84% at the family level and more than 69% at the generic level. This suggests that the tropical flora of southern China has a close affinity not only to the Vietnamese flora but also to the Malesian flora and supports the idea that the flora of southern China, together with the Indochina flora, belongs to Indo-Malesian floristic subkingdom of the Paleotropic kingdom suggested by Takhtadjan (1978) or the Malesian subkingdom of the Paleotropical kingdom as suggested by T.L.Wu et al. (1996); (3) situated at the northern margin of tropical Asia, on the other hand, it is also obvious that the flora of southern China comprises less strictly tropical elements whenc ompared to the Malesian flora, and consequently represents only a marginal type of Indo-Malesian flora; (4) the Vietnamese flora has a closer affinity to the tropical flora of China than to the Malesian flora and therefore is considered also to be a marginal type of Indo-Malesian flora; (5) the close affinity of the flora of southern China to the Indo-Malesian flora can be explained by the geological history of South-East Asia.

## Introduction

Climatologically and biogeographically the tropical area of southern China is located at the margin of tropical Asia, and is composed of south-eastern Xizang (Tibet) (lower valleys of southern Himalayas), southern Yunnan, south-western Guangxi, southern Taiwan and Hainan Island separately. The largest tropical area still covered by forests is in southern Yunnan, the most south-western region of China; followed by south-western Guangxi, also in south-western China, and Hainan Island in south-eastern China. The tropical flora and vegetation of southern China, especially those of mainland south-western China, were only briefly mentioned by C.W. Wang in 1939 for the first time. It was little known until the late 1950s because of poor access. South-western China, for example southern Yunnan, is a mountainous area at the northern

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margin of mainland South-East Asia where there is a slightly lower mean annual temperature (c. 21°C) and lower annual precipitation (average 1500 mm) below 900 m altitude in comparison with the main tropical rainforest areas of the world. For a long time there has been discussion as to whether there is true tropical rainforest in southern Yunnan. If there is tropical rainforest in the region, it would probably be intermediate between classic tropical rainforests and monsoon forests as defined by Schimper (1903), or be a type of subtropical rainforest which differs in various aspects from the truly tropical rainforests described by Richards (1952). After the China-Russia expedition which penetrated deep into areas of south-western China, including southern Yunnan, in the late 1950s, some papers on the tropical rainforest vegetation (Fedorov 1958, Qu 1960, Wang 1961) and tropical flora (Fedorov 1957, Z.Y.Wu 1965) of this part of China were published. It was basically accepted that real tropical rainforests exist in south-western China, but these were considered of a type different from the ones in Indo-Malaysia because of the lack of representatives of Dipterocarpaceae, which dominate the rainforests of Indo-Malaysia . Botanists' interest in these areas was rekindled in the 1970's by the finding of a dipterocarp forest in southern Yunnan and south-western Guangxi. From that finding, the Indo-Malaysian affinity of the tropical flora of China was reconsidered. More and more results from biogeographical and ecological studies on the vegetation and flora of tropical southern China revealed that it is a part of the Indo-Malaysian flora (Zhu 1992, 1993a, 1993b, 1994a, 1994b and 1997, Zhu et al. 1996 and 1997, Zhang & Liu 1980, Fang et al. 1995, T.L. Wu et al. 1996). Also Whitmore (1982) felt that the birds in the tropical rainforest of southern Yunnan sang the same songs as to be heard in the tropical rainforest of Malesia when he was on a short visit to southern Yunnan and he laterconfirmed that there is true evergreen rainforest present in the southern fringe of China (Whitmore 1984).

Van Steenis (1950) recognised Malaysia as a distinct floristic unit, with well-defined demarcation knots, on the basis of generic distribution patterns. The NW frontier of the Malaysian floristic region is about the line Alor Star-Singora a little north of the political border between Malaysia and Thailand where 375 Malaysian genera have their northern-most limit and 200 mainland Asiatic genera have their southern-most limit. Johns (1995) reaffirmed Malesia as a distinct floristic unit. Southern China seems geographically far from the demarcation knot. However, the tropical flora of southern China shows closer affinity to the Malesian flora than to the East-Asian flora because the tropical flora of southern China shows more elements in common with the tropical Malesian flora than with the temperate eastern Asian flora.

In order to investigate the floristic characteristics of the flora of southern China and its affinities, the floristic composition of three well-studied regional floras of southern China, i.e. southern Yunnan, south-western Guangxi and Hainan Island, were concisely enumerated, and their geographical elements were analysed at the generic level. Also the floristic similarities between southern Yunnan and Hainan Island on the one hand, and Vietnam, the Malay Peninsula and Brunei on the other hand, were compared using revised floristic inventories and checklists.

## General background

The tropical flora of southern China mainly consists of three disjunct regional floras, located in southern Yunnan, south-western Guangxi and Hainan respectively.

Southern Yunnan (Xishuangbanna) is the southern part of Yunnan Province in south-western China and lies between 21°09'– 22°32'N and 99°∞58'– 101° 50'E. The region has an area of 19690 km². It borders Burma and Laos, and has a mountainous topography with the mountain ridges running north-south and lowering in elevation southward.

Its altitude varies from 480 m at the bottom of the lowest valley in the south (Mekong River) to 2500 m at the highest mountain top in the north. The region has a typical monsoon climate. In its so-called lowland area, the annual mean temperature is 21 °C, and the annual precipitation is about 1560 mm, of which more than 80% falls during the rainy season, which starts in May and lasts till the end of October. Based on more than 40 years intermittent field collections, 3336 native species of 1218 genera and 207 families of seed plants have been found the region (Li 1996).

South-west Guangxi in south-western China borders on northern Vietnam and lies between 21°30'–23°10'N and 106°–109°∞E. The area has a typical limestone karst topography and most of its area is below 500 m alt. It has also a monsoon climate with an annual mean temperature of 22°C and an annual precipitation of 1200–1600 mm. 4303 species of 1294 genera and 225 families of seed plants are recorded from the region (Fang et al. 1995).

Hainan Island, located in southeastern China, between 18°1'–20∞0' N and 108°∞35–111°∞E, has a mountainous topography with the highest summit of 1867 m alt. In its lower hill area (Jian-fenglin), for example at 800 m alt., there is an annual mean temperature of 19.7°C, and an annual precipitation of 2650 mm. T. L.Wu (1994) recognised 3324 species of 1237 genera and 206 families of seed plants in Hainan Island.

## Floristic composition of the tropical flora of southern China

There is no synthetic and complete floristic material available on the composition and size of the flora of southern China. However, from the available regional floras of southern Yunnan, south-western Guangxi and Hainan Island, a panorama of the flora of southern China can be depicted. The twenty most species-rich families in the floras of southern Yunnan, south-western Guangxi and Hainan are enumerated in Table 1.

It can be seen from Table 1 that the top ranking families in all three regional floras are basically the same. These three regional floras belong to the same floristic unit and represent the tropical flora of southern China. Further analysis shows that most dominant families from tropical southern China are also dominant in Indo-Malesia. For example, Orchidaceae, Rubiaceae, Euphorbiaceae, Lauraceae, Moraceae, Asclepiadaceae, Apocynaceae, Annonaceae, Zingiberaceae etc. are the large tropical families shared by both southern China and Indo-Malesia. The family Dipterocarpaceae is the most characteristic and a dominant family in the Malesian flora. It has only a small number of species in the tropical flora of southern China, but it is the dominant family regarding phytosociological importance (dominant in individuals). Other dominant families in the Malesian flora, such as Guttiferae, Meliaceae, Melastomataceae and Myristicaceae, show a similar pattern to the Dipterocarpaceae. Although the dominant families Urticaceae, Fagaceae, Theaceae, Rosaceae and Myrsinaceae in the tropical flora of southern China, are not among those dominant in Malesian flora, the tropical flora of southern China is basically of Indo-Malesian nature. Excluding cosmopolitan families such as Gramineae, Cyperaceae, Compositae, Labiatae etc., the floristic similarity of tropical southern China to Indo-Malesia is even more obvious.

## Geographical elements at generic level

The distribution types of seed plants from China at the generic level were documented by the Chinese botanist C.Y. Wu (1991) based on the geographical distribution of all genera. From Wu's documentation, the distribution types from these three regional floras at the generic level are quantified and given in Table 2.

**Table 1.** The twenty families most species-rich among the floras of southern Yunnan, south-western Guangxi and Hainan.

| Flora of southern Yunnan, south-western China | | | | Flora of south-west Guangxi, south-western China | | | | Flora of Hainan, south-eastern China | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Name of family | No. of genera | No. of species | %of the flora | Name of family | No. of genera | No. of species | %of the flora | Name of family | No. of genera | No. of species | %of the flora |
| Orchidaceae | 96 | 334 | 10.01 | Leguminosae | 56 | 193 | 4.49 | Gramineae | 109 | 268 | 8.06 |
| Leguminosae | 56 | 182 | 5.46 | Gramineae | 87 | 174 | 4.04 | Leguminosae | 68 | 212 | 6.38 |
| Rubiaceae | 43 | 147 | 4.41 | Rubiaceae | 42 | 170 | 3.95 | Orchidaceae | 69 | 183 | 5.51 |
| Gramineae | 67 | 143 | 4.29 | Compositae | 62 | 150 | 3.49 | Rubiaceae | 51 | 155 | 4.66 |
| Euphorbiaceae | 38 | 119 | 3.57 | Lauraceae | 16 | 142 | 3.30 | Euphorbiaceae | 45 | 143 | 4.30 |
| Compositae | 59 | 107 | 3.21 | Euphorbiaceae | 38 | 141 | 3.28 | Cyperaceae | 23 | 133 | 4.00 |
| Moraceae | 6 | 77 | 2.31 | Orchidaceae | 50 | 124 | 2.88 | Compositae | 57 | 115 | 3.46 |
| Urticaceae | 12 | 72 | 2.16 | Cyperaceae | 22 | 97 | 2.25 | Lauraceae | 15 | 101 | 3.04 |
| Lauraceae | 12 | 68 | 2.04 | Urticaceae | 13 | 90 | 2.09 | Asclepiadaceae | 23 | 70 | 2.11 |
| Zingiberaceae | 15 | 67 | 2.01 | Asclepiadaceae | 24 | 83 | 1.93 | Labiatae | 27 | 59 | 1.77 |
| Asclepiadaceae | 25 | 62 | 1.86 | Theaceae | 10 | 79 | 1.84 | Moraceae | 12 | 58 | 1.74 |
| Apocynaceae | 27 | 61 | 1.83 | Fagaceae | 4 | 79 | 1.84 | Fagaceae | 4 | 58 | 1.74 |
| Labiatae | 29 | 59 | 1.77 | Moraceae | 8 | 71 | 1.65 | Verbenaceae | 13 | 55 | 1.65 |
| Annonaceae | 15 | 52 | 1.56 | Rosaceae | 19 | 69 | 1.60 | Acanthaceae | 26 | 54 | 1.62 |
| Cucurbitaceae | 17 | 50 | 1.50 | Gesneriaceae | 28 | 69 | 1.60 | Urticaceae | 11 | 53 | 1.59 |
| Acanthaceae | 32 | 49 | 1.47 | Myrsinaceae | 6 | 67 | 1.56 | Annonaceae | 18 | 51 | 1.53 |
| Rosaceae | 17 | 49 | 1.47 | Apocynaceae | 21 | 66 | 1.53 | Theaceae | 10 | 50 | 1.50 |
| Fagaceae | 6 | 45 | 1.35 | Liliaceae | 14 | 62 | 1.44 | Myrtaceae | 8 | 50 | 1.50 |
| Araceae | 16 | 43 | 1.29 | Zingiberaceae | 11 | 61 | 1.42 | Myrsinaceae | 6 | 49 | 1.47 |
| Cyperaceae | 13 | 43 | 1.29 | Labiatae | 28 | 58 | 1.35 | Apocynaceae | 26 | 46 | 1.38 |

The tropical Asian distribution, shown by the genera *Alphonsea, Amoora, Pterospermum, Mitrephora, Mycetia, Aganosma, Chukrasia, Crypteronia, Knema* etc., contributes 32.8%, 27.3 and 25.6% to these regional floras respectively and shows the highest percentage among all distribution types. The pantropic distribution, shown by *Gnetum, Beilschmiedia, Cryptocarya, Capparis, Piper, Croton, Dioscorea, Uncaria, Lasianthus, Morinda, Ardisia, Bauhinia, Marsdenia* etc., contributes 22.8%, 20.9% and 25.7% respectively and shows the second highest percentage. Next is the Old World Tropical distribution, shown by *Thunbergia, Dracaena, Pandanus, Ventilago, Stephania, Fissistigma, Polyalthia, Barringtonia, Carallia, Canarium, Chasalia, Uvaria* etc. The tropical Asia to tropical Australia distribution type pertains to genera such as *Ailanthus, Hoya, Argyreia, Dillenia, Lagestroemia, Loeseneriella, Murraya, Toona* etc. The tropical Asia to tropical Africa distribution type includes e.g. *Bombax, Flacourtia, Quisqualis, Bridenia, Premna, Urophyllum, Strophanthus, Mitragyna, Garcinia, Anogeissus, Cymbopogon* etc. The tropical distribution (types 1–6) from the three regional floras comprises 83.5%, 75.9% and 86.8% of the total number of genera respectively. Undoubtedly, the three regional floras are tropical in nature and have strong tropical Asiatic affinity.

## Comparison of floristic similarities

The flora of southern Yunnan (representing the tropical flora of south-western China) and the flora of Hainan (representing southeastern China) are chosen for comparison with Vietnamese and Malesian floras. The Catalogue of the Vascular Plants of Malaya (Turner 1995) and the Checklist of the Flowering Plants and Gymnosperms of Brunei Darussalam (Coode et al. 1996) are the recently up-dated and relatively complete data bases on the regional flora of West Malesia. A revised checklist of plants of Vietnam (Le 1999) is also available. Therefore, a comparison of the floristic similarities at the family and generic levels between southern Yunnan, Hainan Island, Vietnam, Malay Peninsula and Brunei Darussalam was made so as to demonstrate the affinity between the tropical floras of southern China and mainland South-East Asia and Malesia.

**Table 2. Comparison of the distribution-types of genera from the flora of southern Yunnan, the flora of south-west Guangxi and the flora of Hainan (%).**

| Distribution types (Geographical elements) | Southern Yunnan | South-western Guangxi | Hainan |
|---|---|---|---|
| Pantropic | 22.8 | 20.9 | 25.7 |
| Tropical Asia and Tropical America disjunct | 2.4 | 2.4 | 5.0 |
| Old World Tropic (Tropical Africa via Tropical Asia to Tropical Australia) | 10.3 | 9.9 | 11.8 |
| Tropical Asia to Tropical Australia | 6.9 | 7.9 | 10 |
| Tropical Asia to Tropical Africa | 8.4 | 7.6 | 8.7 |
| Tropical Asia or Indo-Malesia | 32.8 | 27.3 | 25.6 |
| North Temperate | 5.2 | 7.2 | 4.3 |
| East Asia and North America disjunct | 3.1 | 3.7 | 2.5 |
| Old World Temperate | 1.5 | 2.7 | 1.5 |
| East Asia | 5.1 | 7.0 | 3.2 |
| Endemic to China | 0.7 | 2.8 | 1.1 |

**Table 3.** The twenty families most species-rich among the floras of Vietnam, Malay Peninsula and Brunei Darussalam.

| Flora of Vietnam | | | Flora of Malay Peninsula | | | Flora of Brunei Darussalam | | |
|---|---|---|---|---|---|---|---|---|
| Name of family | No. of genera | No. of species | Name of family | No. of genera | No. of species | Name of family | No. of genera | No. of species |
| Leguminosae | 121 | 628 | Orchidaceae | 147 | 853 | Rubiaceae | 65 | 269 |
| Orchidaceae | 129 | 621 | Rubiaceae | 79 | 562 | Euphorbiaceae | 42 | 199 |
| Gramineae | 149 | 516 | Euphorbiaceae | 70 | 368 | Dipterocarpaceae | 9 | 177 |
| Rubiaceae | 84 | 425 | Leguminosae | 81 | 298 | Orchidaceae | 54 | 145 |
| Euphorbiaceaee | 67 | 405 | Gramineae | 92 | 238 | Palmae | 25 | 132 |
| Cyperaceae | 26 | 325 | Myrtaceae | 11 | 215 | Araceae | 28 | 120 |
| Compositae | 107 | 293 | Lauraceae | 16 | 214 | Melastomataceae | 25 | 115 |
| Lauraceae | 21 | 244 | Annonaceae | 36 | 202 | Leguminosae | 49 | 110 |
| Fagaceae | 5 | 213 | Palmae | 32 | 198 | Annonaceae | 31 | 96 |
| Acanthaceae | 53 | 195 | Gesneriaceae | 20 | 189 | Zingiberaceae | 13 | 88 |
| Annonaceae | 26 | 168 | Melastomataceae | 22 | 172 | Moraceae | 6 | 84 |
| Apocynaceae | 49 | 155 | Cyperaceae | 29 | 162 | Lauraceae | 14 | 82 |
| Myrsinaceae | 6 | 140 | Acanthaceae | 29 | 158 | Myrtaceae | 9 | 78 |
| Moraceae | 12 | 138 | Dipterocarpaceae | 9 | 156 | Cyperaceae | 20 | 73 |
| Verbenaceae | 25 | 131 | Zingiberaceae | 18 | 150 | Guttiferae | 7 | 70 |
| Labiatae | 45 | 128 | Araceae | 23 | 141 | Gramineae | 45 | 68 |
| Araceae | 27 | 128 | Moraceae | 10 | 138 | Meliaceae | 11 | 58 |
| Rosaceae | 20 | 124 | Guttiferae | 7 | 120 | Myristicaceae | 5 | 56 |
| Zingiberaceae | 24 | 124 | Apocynaceae | 31 | 119 | Anacardiaceae | 16 | 53 |
| Scrophulariaceae | 35 | 117 | Asclepiadaceae | 30 | 116 | Gesneriaceae | 4 | 53 |

The top twenty families regarding species richness from the floras of Vietnam, Malay Peninsula and Brunei Darussalam are listed in Table 3. Except for the Dipterocarpaceae, Melastomaceae, Myristicaceae, Palmae, Guttiferae and Meliaceae, the other species-rich families from Malay Peninsula and Brunei Darussalam are shared with the tropical flora of southern China in the top twenty families. The Vietnamese flora shows a strong similarity to the tropical flora of southern China in the top twenty families.

Comparisons of the floristic similarities at the family and generic levels between southern Yunnan, Hainan, Vietnam, Malay Peninsula and Brunei Darussalam are enumerated in Table 4 and Table 5. The floristic similarity between the floras of southern China and the regional floras of West Malesia is more than 70% at the family level and more than 50% at the generic level, and between the floras of southern China and that of Vietnam is more than 84% at the family level and more than 69% at the generic level. The flora of Hainan from SE China shows higher floristic similarity to the flora of Malay Peninsula than to the flora of southern Yunnan although it is closer to southern Yunnan geographically. These results strongly support the floristic affinity of southern China to Indo-Malesia.

**Table 4. Comparison of floristic similarities at the family level between southern Yunnan, Hainan, Vietnam, Malay Peninsula and Brunei Darussalam.**

| | **No. of families** | **Southern Yunnan** | **Hainan Ilsland** | **Vietnam** | **Malay Peninsula** | **Brunei Darussalam** |
|---|---|---|---|---|---|---|
| | | Shared/S.C. | Shared/S.C. | Shared/S.C | Shared/S.C. | Shared/S.C. |
| Southern Yunnan | 207 | 100/ 100 | | | | |
| Hainan | 206 | 181/ 87.86 | 100/ 100 | | | |
| Vietnam | 249 | 179/84.43 | 187/90.78 | 100/100 | | |
| Malay Peninsula | 215 | 173/ 83.98 | 179/ 86.89 | 202/93.95 | 100/ 100 | |
| Brunei Darussalam | 164 | 119/ 72.56 | 115/ 70.17 | 147/89.63 | 161/ 98.17 | 100/ 100 |

Note: S.C. = Similarity coefficient (%)

Similarity coefficient between A and B = the number of taxa shared by both A and B divided by the lower number of taxa of A or B, multiplied by 100.

**Table 5. Comparison of floristic similarities at generic level between southern Yunnan, Hainan, Vietnam, Malay Peninsula and Brunei Darussalam.**

| | **No. of genera** | **Southern Yunnan** | **Hainan Ilsland** | **Vietnam** | **Malay Peninsula** | **Brunei Darussalam** |
|---|---|---|---|---|---|---|
| | Shared/S.C. | Shared/S.C. | Shared/S.C | Shared/S.C. | Shared/S.C. | Shared/S.C. |
| Southern Yunnan | 1218 | 100/ 100 | | | | |
| Hainan | 1237 | 803/ 65.93 | 100/ 100 | | | |
| Vietnam | 1885 | 1251/69.06 | 1237/85.69 | 100/100 | | |
| Malay Peninsula | 1547 | 786/ 64.53 | 844/ 68.23 | 1547/69.36 | 100/ 100 | |
| Brunei Darussalam | 917 | 446/ 47.80 | 480/ 52.34 | 917/65.98 | 789/ 86.04 | 100/ 100 |

Notes: S.C. = Similarity coefficient (%)

## Conclusion and Discussion

To sum up our conclusions regarding the tropical flora of southern China:

(1) Tropical floristic elements both at the family and generic levels make a major contribution (about 60% at the family level and > 80 % at the generic level) to the total flora of southern China. The dominant geographical element at the generic level is of a tropical Asian distribution. This reveals that the flora of southern China is tropical in nature and has strong tropical Asian affinity.

(2) Most of the dominant families from the flora of southern China are also dominant in the Malesian flora. The floristic similarities between the regional floras of southern China and the regional floras of west Malesia are more than 70% at the family level and more than 50% at the generic level. T.L.Wu et al. (1996) state that the floristic similarity coefficient at the generic level between the flora of South China Sea Islands (with Hainan Island as its core area) and the flora of the Philippines is 78.2%, with Java is 75.0%, with Guangdong of mainland China is 82.3%, and with Taiwan is 70%. Although Hainan Island is almost connected to Guangdong of mainland China, the floristic similarity coefficient between them is just a little higher than the floristic similarity coefficient between Hainan and the far away Philippines and Java. This strongly supports the idea that the tropical flora of southern China is part of the Indo-Malesian flora and belongs to the Indo-Malesia or Malesian floristic region as suggested by Takhtadjan (1978) and T.L.Wu et al. (1996). Although there are clear generic demarcation points between Malesia and mainland SE Asia as found by van Steenis (and certainly there is this kind of demarcation point between southern China and Malesia) the high percentage of taxa shared by both suggests that they should be considered to belong to the same floristic region. This follows the conclusion of van Balgooy et al. (1996) that the number of taxa in common is the first step in surveying floristic affinity.

(3) The flora of southern China occurs on the margin of tropical Asia. Although tropical families and genera contribute most to its total flora, those with a strictly tropical distribution are still underrepresented compared to the Malesian flora. For example, Dipterocarpaceae has only a small number of species in the flora of southern China even though it is the dominant tree in some forest types of southern China. Many Malesian elements reach their northern limits in southern China. This implies that the flora of southern China is a marginal type of the Indo-Malesian flora.

(4) The flora of southern China, in particular south-western China, also has a very close affinity to the India-Burmese flora. Comparisons between regional floras of southern China and India-Burma are not made here because of the lack of up-to-date regional floristic inventories. However, it was demonstrated that the floristic similarity is 97.3% at the family level and 79.7% at the generic level in a comparison between the dipterocarp forest in southern Yunnan and a 10 ha dipterocarp forest in upper Assam of NE India (Zhu 1994a). Comparison between the flora of southern China and Vietnam for the twenty most species-rich families and their similarity at the family and generic levels, shows that the tropical flora of southern China has its closest affinity to the Vietnamese flora and that, floristically, both belong to the Indochina region of the Indo-Malesian subkingdom (as suggested by Takhtadjan (1978)), or of the Malesian subkingdom (as delimited by T.L.Wu et al. (1996)). Although the comparison between the flora of southern China and the flora of Thailand is not made here, the close floristic affinities between them should be high.

(5) From studies on the geological history of SE Asia, it is revealed that the direct land connection between mainland SE Asia and west Malesia existed until early Pliocene (5 million years ago) (Hall 1998), and there was no geographical barrier between

mainland South-East Asia and west Malesia during most of the Tertiary (Morley 1998). This could be the geological explanation for the close affinity between the flora of southern China and the flora of Malesia.

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# Corrigenda — Telopea 9(4)

## Andrew C. Rozefelds. A new species and new combination in *Craspedia* (Asteraceae) from Tasmania.

Page 816: The following table was omitted from the final copy. We apologise to the author.

**Table 1. Comparison of vegetative and reproductive characters in Australian species of *Craspedia* with white florets.**

| | ***C. alba*** **Everett & J.Thompson** | ***C. alpina*** **Backh. ex Hook.f.** | ***C. glabrata*** **(Hook.f.) Rozefelds** | ***C. leucantha*** **F.Muell.** | ***C. preminghana*** **Rozefelds** |
|---|---|---|---|---|---|
| Leaf appearance | White-silvery | White | Green with bluish tinge | Bright green | Green |
| Leaf indumentum (lower surface) | Silvery appressed hairs | White, woolly hairs | Glabrescent or with arachnoid hairs on margin | Glabrous or with fine hairs on margin | Multiseptate and glandular hairs |
| Leaf shape | Oblong to narrowly oblanceolate | Narrowly spathulate | Narrowly oblanceolate | Spathulate | Broadly oblanceolate to to linear |
| Leaf length (cm) | 1.5–5.0 | 7–14 | 3.5–7 | 4–25 | 13–20 |
| Leaf width (mm) | 2–5 | 8–11 | 2.5–4 | 5–25 | 20–34 |
| Compound head diameter (cm) | 1–1.5 | 1.6–2.5 | 0.8–1.2 | 1.0–2.5 | 2.5–3.5 |

## John R. Spence & Helen P. Ramsay. The genus *Anomobryum* Schimp. (Bryopsida, Bryaceae) in Australia.

Page 787: should read as follows:

**5. Anomobryum subrotundifolium** *(A. Jaeger) J.R. Spence & H.P. Ramsay*, **comb. nov.**

*Bryum subrotundifolium* A. Jaeger, *Ber. Tatig. St Gallischen Naturwiss. Ges.* 1877–78: 43 (1879).

*Argyrobryum subrotundum* Hampe, *Linnaea* 40: 312 (1876).

Type: Vic.: Mt Ararat, *Sullivan s.n.* 1875; holo?; iso MEL, NSW ex. MEL. ). **nom. illeg.** non Bridel, *Musc. Recent. Suppl.* 3: 29, 1817. See also page 115 in H.P. Ramsay & J. Seur (1994) Register of type specimens of mosses in Australian Herbaria. *Flora of Australia Supplementary Series*, Number 2 (ABRS: Canberra).

# Instructions for Authors

*Telopea* is published twice a year. It covers systematic botany in Australia and the Asia-Pacific region specialising in the flora of New South Wales. Short Communications are welcome (see previous issues for format).

Deadlines for the submission of papers are **1 June** (for the first issue the following year) and **1 November** (for the second issue).

Authors are expected to have their papers peer-reviewed before submission. All papers will be refereed. Supply full contact details for main author. One hard copy should accompany an electronic file along with originals or electronic files of photographs and figures.

## Formatting

- The title should be explicit and descriptive of the content; a short running head and an abstract (except for Short Communications) should be included.
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- References in the text should be made by giving the author's name with the year of publication in parentheses. For reference list at end of paper see papers in the latest issue for style. Titles of journals should be given in full.
- An index to taxa is useful if the paper is large and deals with many species and synonyms. The author should prepare the basic alphabetic listing including all names in recent use.

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- Cite no more than 20 (except for very widely distributed species) and arrange by Botanical Divisions. Use accepted format: locality, collector & number, date (herbarium code plus institutional number if there is no collector's number) Only latitudes and longitudes on the original labels should be included. Give dates in the following format: 12 Jan 1987, 2 Jun, 30 Jul, 10 Dec etc.

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