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New names and combinations are printed in **bold**; synonyms are printed in *italics*.

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FLORA
MALESIANA

Edited by
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FOREWORD

Malesia is the equatorial East Asian region stretching from Malaysia to Papua New Guinea. An estimated 40 000 species of vascular plant occur in the region and it is one of the richest, most diverse and valuable concentrations of biodiversity on Earth. Only 50% of the plant species have been defined and named and can currently be identified with certainty. Moreover, this information is readily accessible for only about 20% of these, as yet. This is a fundamental impediment to understanding the ecosystems that this biodiversity makes up, and hence to their sustainable utilisation.

Flora Malesiana is a world-wide network — co-ordinated from Leiden University in The Netherlands and Bogor in Indonesia — of plant scientists and associates whose goal is to break down this impediment. Our core project is to define the plant species of the region, establish their correct names, provide the means of their identification, communicate this information to users, and train new scientists within the Malesian region to pursue this essential work.

The International Flora Malesiana Symposia take place every three years hosted by different institutions involved in Flora Malesiana. They provide the opportunity for FM members to exchange ideas, report research findings and progress, and to workshop issues of progressing and managing the Flora Malesiana Project. The symposia continue to provide a catalyst for dramatically increased output of plant biodiversity information.

The Fifth International Flora Malesiana Symposium, the first to be held in Australia, took place in Sydney in September 2001, immediately preceded by workshops on interactive identification systems and on the family Lauraceae, at Atherton in North Queensland. It both reflects and symbolises the increasing role and relevance Australia, at both Commonwealth and State levels, has in collaborating with neighbouring countries in both research and training in the field of biodiversity.

The Symposium itself differed slightly from earlier Flora Malesiana symposia by including a number of mini-symposia on plant groups of particular significance — including the diversity, geography and ecology of cryptogams which are not covered by the Flora, but which complement research on the vascular flora, palms, orchids and pteridophytes, as well as ethnobotany — which continues to be a strong research focus within the region, and bioinformatics — addressing major issues in information technology and applications for use and management of botanical data. The symposium opened with a mini-symposium of stakeholders representing those who use and fund the generation of information that Flora Malesiana produces, followed by an assessment of the status of botany in the countries of the Malesian region. A very wide variety of papers was also contributed outside the mini-symposium framework and in all, 110 papers were presented, in addition to the plant-family workshops which have become characteristic of Flora Malesiana symposia.

The Symposium could not have gone ahead as it did without the generous assistance of a number of co-sponsors, including Foundation Flora Malesiana, the Royal Botanic Gardens & Domain Trust, the Centre for Plant Biodiversity Research, the Australian Systematic Botany Society, the Australian Academy of Science, the International Association for Plant Taxonomists, Roslyn Oxley^9 Gallery, the Friends of the Gardens, and CSIRO.

This volume represents a broad cross-section of the papers presented in the Symposium. We would like to thank those who contributed to the symposium and those who subsequently contributed manuscripts for the proceedings, the Editorial

Committee of *Telopea* for agreeing to publish the proceedings, and especially Joy Everett for leading the editing of the volume. We are also very grateful to all those who gave their time to review manuscripts.

Dr Alistair Hay
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On behalf of the Organising Committee: Barry Conn, Lyn Craven, Jim Croft, Rogier de Kok, Peter Wilson.

March 2003.

REFEREES

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Sophie Bickford, Alex Chapman, Barry Conn, Lyn Craven, Darren Crayn, Jim Croft, Stuart Davies, John Dowe, Tim Entwisle, Nina Etkin, Ib Friis, Paul Gioia, Caroline Gross, Robin Hide, Ken Hill, Laurie Jessup, David Middleton, Andrew Mitchell, Benjamin Øllgaard, Emma Pharo, Maurizio Rossetto, Martin Sands, Mark Simmons, Alan Smith, Johan van Valkenburg, George Weiblen, Judy West, Peter Weston, Peter Wilson, George Yatskievych.

Flora Malesiana 1991-2001

What has been achieved: revitalisation, momentum? What next?

M.C. Roos

Abstract

M.C. Roos (National Herbarium of the Netherlands, Leiden University branch, P.O. Box 9514, 2300 RA Leiden, The Netherlands; e-mail: roos@nhn.leidenuniv.nl) 2003. Flora Malesiana 1991-2001. Telopea *10(1): 1–10.* An overview is presented of the development of Flora Malesiana since 1991, compared to the progress over the first 40 or so years (from 1948 to 1990). The many things that have been achieved are discussed. Also, the many things that have not been achieved are discussed. The overall picture emerging is a mixture of optimism and pessimism. Some concluding suggestions are presented for ways out of this status quo and to hook on to recent scientific developments for which funding seems a lesser problem.

Introduction

In 1948 the first instalment of Flora Malesiana was published. This implies that the Flora Malesiana project is now a little over a half a century on its way. It is a little over 10 years ago that this series of International Flora Malesiana Symposia started (1989), at the time with heated discussions on the future and prospects of Flora Malesiana. As a result of these discussions, at the Botanical Congress in Yokohama in 1993, Flora Malesiana was called a revitalised flora project. On the occasion of the Fifth International Flora Malesiana Symposium, these seem to me enough reasons to evaluate the present state of affairs and compare that with the situation a decade ago to see whether we really have gained momentum.In 1989 my predecessor in Leiden, the late Rob Geesink, evaluated the progress in Flora Malesiana (Geesink 1990) and he came to the conclusion that the completion of Flora Malesiana would take another 160 years. He regarded that as rather unattainable, and that a considerable increase in funding and efficiency, and a simplified format were necessary for completion within a reasonable time. Otherwise, according to him, Flora Malesiana would loose its credibility. In the following I will discuss what has been achieved since then, and, maybe even more importantly, what has not been achieved, and express some thoughts for future strategies.

What has been achieved

Many things have, of course, been undertaken in the last decade and I will not aim to make an exhaustive list at the risk of leaving things out. I will restrict myself to a few examples which may illustrate the progress made on the various fronts.

- **EU-HCM network — treatment of c. 350 species**

In 1993 the EU approved an application by a network of nine institutes in Britain, the Netherlands, Germany, France, Ireland and Denmark. The grant for three years was one of the largest awarded at the time and four Post-doctoral fellows and five PhD-students could be appointed. In the end, the research funded by this grant yielded the treatment of c. 350 species in families which are still under revision.

• MSc programs

Various MSc programs have been launched. It is fortunate that MSc programs in plant systematics were instituted in the region itself. The efforts made in Malaysia and Indonesia especially deserve mentioning (e.g. University of Bangsi, Malaysia; IPB Bogor, Indonesia). Other programs worth mentioning are those of Reading and Leiden.

• Data bases / checklists (geographic & taxonomic)

The computerisation of taxonomic information has developed enormously in the 1990's. Various databases, either taxon-based or specimen-based, have been developed as special projects or in the course of research projects. To mention just a few: the specimen data base of Euphorbiaceae, the data base on distribution patterns of taxa treated in the FM instalments so far, PROSEA data bases, etc.

• Specimens on Internet

At the risk of a Leiden bias, I first mention the web site on type specimens present in the Dutch herbaria. Many more examples are available (Table 1).

Table 1. Some examples of URLs where collection databases can be consulted.

Http://www.huh.harvard.edu/databases/cms/specimen_index.html (GH/AA)
Http://rathbun.si.edu/botany/types/ (US)
Http://www.bgbm.fu-berlin.de/biodivinf/projects/digitalisierung/default.htm (B)
Http://biodiversity.ukm.my/menu_db.html (Biodiversity Malaysia)
Http://www.botany.net/IDB/botany.html (general Botany Net)
Http://www.nhm.ac.uk/botany/databases/index.html (BM)
Http://nhncml.leidenuniv.nl/rhb/#types (L/U/WAG/AMD)
Http://www.nybg.org/bsci/herbarium_imaging/ (NY)
Http://linnaeus.nrm.se/botany/fbo/welcome.html.en (S-LINN)

• Molecular markers & identification tools

Molecular data are often not regarded as important for flora treatments. However, molecular studies have a great impact on classifications, and consequently on family delimitation (e.g. Apocynaceae, Verbenaceae). Also, molecular information is used to develop identification tools to species or even populations, and this may be of importance for the control of trade (e.g. the screening of products for seriously endangered species, including determination of the area of origin). Furthermore, DNA sequence data will be used increasingly to illuminate the delimitation of species, especially of species complexes.

• CD-ROMs

Increasingly, systematic information is presented on CD-ROM. This is not just another way of presenting the same information published as hard copy, but also aims at using the increased possibilities of an electronic format over the traditional printed presentation, i.e. the inclusion of all kinds of illustrations, user-friendly interactive and pictorial keys, and geographical information on the distribution of species and mapping. A number are mentioned in Table 2.

Table 2. Some examples of CD-ROM's and other electronic identification tools.

Bakker, M.E. (2000) Annonaceae – genera worldwide.

Jarvie, J.K., & Ermayanti. (2001) Trees and shrubs of Borneo.

Newman, M.F., Burgess, P.F., & Whitmore, T.C. (1995-1998) Manual of Dipterocarps for foresters.

Nooteboom, H.P. (2000) Davalliaceae – a family of Old World (sub-)tropical ferns.

Ridder-Numan, J.W.E. & Kort, I. de. (1999) Flora Malesiana: Leguminosae – Mimosoideae of South-East Asia.

Schuiteman, A. & Vogel, E.F. de. (2001) Orchids of New Guinea – Vol. I. Illustrated Checklist and Genera.

• Increased production

Over the past 11 years (1991–2001) 10 instalments have been published, with treatments of over 2 200 species (Table 3). Only in 1999 did no instalment appear (due to practical problems). This is a substantial increase in production, compared to the production of species treatments in the past.

Table 3. List of instalments published between 1991 and 2001.

Year, series	Family	No. species	Accumulated
To 1989			**TOTAL 5761**
1991, II	Tectaria-group	217	217
1992, I	Mimosaceae	158	375
1993, I	Rosaceae + 5	157	532
1994, I	Sapindaceae	235	767
1995, I	Meliaceae	223	990
1996, I	Caesalpiniaceae + 3	264	1254
1997, I	Rafflesiaceae/Loranthaceae + 5	345	1599
1998, II	Polypodiaceae + 6	230	1827
2000, I	Myristicaceae	335	2162
2001, I	Nepenthaceae	83	2247
2001			**TOTAL 8008**

Table 4 gives an overview of the production of treatments according to regions of employment of the authors: figures represent the number of different contributing authors, the number of family treatments they have contributed and the number of species they include per period.

In the first 43 years, the treatment of 5 761 species in total have been published, i.e. 134 species per year on average. The total number of species treated per period and the average number per year per period are presented in Figure 1. It is clear that the 1990's are outstanding in terms of species treated; the average number of species treated per year rose to 204. This is a clear indication that Flora Malesiana can really be regarded as a revitalised project with increased momentum.

Table 4. Overview of the contribution per region and per period in terms of different authors, and families and species treated. NL = Netherlands, EU = other European countries, AUS = Australia, MAL = Malesian countries, ASIA = other Asiatic countries.

Origin	Categories	1948–60	1961–70	1971–80	1981–90	1991–2001
NL	different authors	25	2	14	4	8
	families	82	9	22	12	11
	species	1286	1001	997	251	1038
EU	different authors	7		5	5	6
	families	10	1	6	6	7
	species	254	205	155	594	926
AUS	different authors	1	1	2		1
	families	1	1	2	2	2
	species	4	4	148	89	218
MAL	different authors			2		
	families			3		
	species			285		
ASIA	different authors			1		4
	families			1		6
	species			10		43
USA	different authors			1	2	3
	families			1	5	5
	species			14	465	22

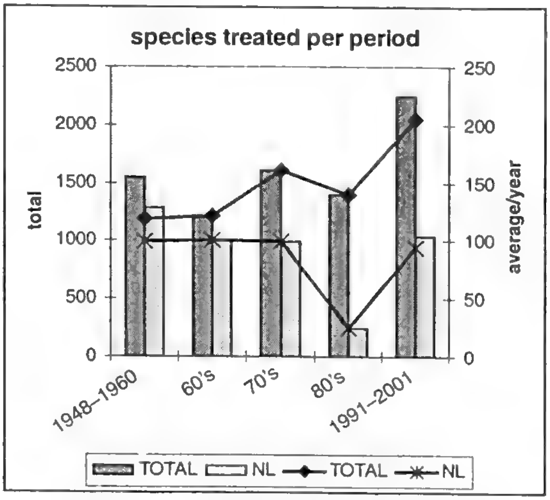

Fig. 1. Number of species treated per period, showing the contribution of Dutch collaborators in relation to the total production: **bars**: total number of species treated in the respective periods, **lines**: average number of species treated per year for each respective period.

Table 5. Species treated by authors according to origin, before and after 1991; in total numbers and percentages.

	No. of species			
	<1990	**1991–2001**	**<1990 %**	**1991–2001 %**
NL	3535	1038	61	46
EU	1208	926	21	41
AUS	245	218	4	10
MAL	285		5	
ASIA	10	43	0.2	2
USA	479	22	8	1
total	**5761**	**2246**	**100**	**100**

Table 6. Number of different contributing authors and their average contribution.

	No. of contributing authors		Species/author	
	<1990	**1991–2001**	**<1990**	**1991–2001**
NL	45	8	79	130
Rest EU	17	6	71	154
AUS	4	1	61	218
USA	3	3	143	
MAL	2		10	11
Rest ASIA	1	4	160	7
Total	**72**	**22**	**80**	**102**

Table 7. Contribution per region in absolute numbers and as percentages.

	Total numbers			Percentages		
	Authors	**Families**	**Species**	**Authors**	**Families**	**Species**
NL	53	135	4572	56	70	57
rest EU	23	29	2134	24	15	27
AUS	5	8	463	5	4	6
USA	6	11	501	6	6	6
MAL	2	3	285	2	2	4
rest ASIA	5	7	53	5	4	1
Total	**94**	**193**	**8008**	**100**	**100**	**100**

- **Increased internationalisation**

Another conclusion that can be drawn from Figure 1 is that except for a real dip in the 1980's, the contribution by Dutch authors has been remarkably constant (c. 100 species/year). Actually, the number of different Dutch authors has dropped in the 1990's relative to the first four periods together (Table 6: 8 in 11years vs. 45 in 43 years), but their average contribution in terms of species has risen by over 60% (Table 4: 130 vs.79). The latter figure, however, should be interpreted with care, as it does not tell how long it has taken to finish the treatment. The increase in production, therefore, comes from a considerable enlargement of the network of cooperating authors outside the Netherlands. This is mainly the result of a substantial increase in the number of contributing authors from other European countries, who also on average contributed double the number of species compared to their colleagues in the first four periods (Table 6: 154 vs. 71); their relative contribution, therefore, has almost doubled in the 1990's (Table 5: 41% vs. 21%). This is a very positive development.

Table 7 gives the total and relative number of species treated by authors arranged by region. Firstly, the Netherlands have made the majority of the contributions, both in terms of authors, families, as well as species. European botanists contributed 80-85% of the treatments. Not surprisingly, there is an obvious correspondence between the number of authors and the number of species treated (compare the percentages in the columns of authors and of species). However, Dutch authors treated relatively small-sized families, whereas authors from elsewhere in Europe contributed larger sized families.

- **Many other relevant publications and treatments**

Many other relevant publications appeared over the past 11 years. It is not feasible to mention them all, but only to highlight a few: the family portraits by van Balgooy, the Tree Flora of Sabah and Sarawak, the Checklist of Brunei, local language guides, the PROSEA series, etc., not to speak of the many electronic formats in development.

What has not been achieved

- **Acceleration towards completion within a few decades**

Table 8 clearly shows, in terms of coverage of the estimated total species richness, that in 2001 we are still at about the same level as in 1990, i.e. c. one quarter of the total flora (leaving the orchids out, following the decision not to include treatments of orchid taxa in series I; they will be covered in a series of CD ROMs – e.g. Schuitemen & De Vogel 2001). It may seem that we are running just to keep up, let alone progress. However, it is, of course, the result of much higher estimations of the numbers of vascular plant species occurring in Malesia (Roos 1993), and taking this into account, we really have made good progress.Still we have to face the rather awkward conclusion: the 1990's have seen a substantial increase in production, nevertheless this does not lead to an accelerated completion of the flora. Figure 2 shows the graph of the production so far, the production needed for completion of Flora Malesiana in 2020 and 2050 respectively (the over-ambitious and 'feasible' — ambitious goals in the action plan as set by the Board), and an extrapolation of the average production of species treatments since 1991 (i.e. 200 species/year). The latter indicates that at the present rate of progress, completion of Flora Malesiana will not be achieved before 2135, which is similar to Geesink's conclusion over a decade ago which prompted the discussion on the format and progress of Flora Malesiana at that time (Geesink 1990, p. 13: 'another 160 years from now'; in Polhill 1990, table 1: 2135).

Table 8. Status of Flora Malesiana for 1990 and 2001.
*** Van Steenis (1948); ** Roos (1993)**

		Taxa treated	Estimated species richness of the flora (*excl. Orchidaceae*)	Coverage (%)
1990	Species	5771	25000*	23
	Families	163	301	54
2001	Species	8008	35000**	23
	Families	193301 (*disregarding new classifications – no new families have been collected*)		64

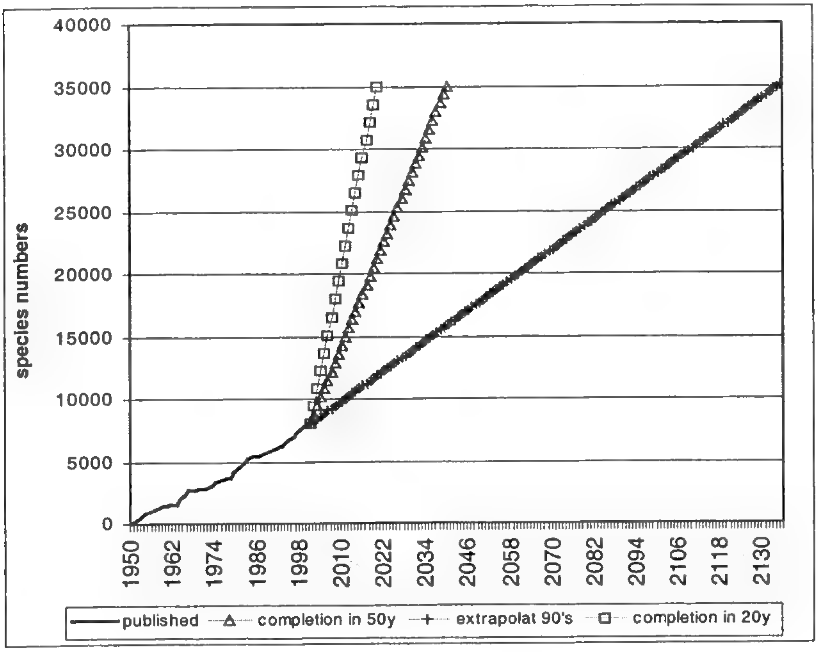

Fig. 2. Graph of 1) the progress in Flora Malesiana so far, in terms of species published, 2) the progress needed for completion in 20 years, 3) completion in 50 years, and 4) extrapolation of the progress of the nineties of last century.

• Allotment of all large-sized families

Large-sized taxa remain a problem, the largest family treatment published in the past decade has been the Myristicaceae, comprising 335 species. This is a major contribution, but still only one of the 18 families with over 500 species has been published so far (Table 9), and the *Tectaria*-group (revised by the late Prof. Holttum) belongs to the list of largest genera (Table 10).

Table 9. Families with >500 species.

	No. of species	Status
Orchidaceae	6500	CD-ROM team
Rubiaceae	2000	p.p. allotted
Euphorbiaceae	1000	working team
Melastomataceae	1000	p.p. allotted
Arecaceae	975	working team
Gesneriaceae	900	
Annonaceae	875	working team
Poaceae	850	p.p. in prep.
Ericaceae	750	1967
Araceae	725	p.p. in press
Myrtaceae	725	working team
Dryopteridaceae	700	
Lauraceae	700	
Zingiberaceae	700	working team
Acanthaceae	625	
Araliaceae	600	
Papilionaceae	575	working team
Moraceae	575	under revision
TOTAL	**20775**	
Cyperaceae	400	1974, 1979
Dipterocarpaceae	390	1982
Myristicaceae	335	2000

Table 10. Genera with >200 species.

	No. of species	Status
Bulbophyllum (Orch.)	1000	1993 p.p.
Dendrobium (Orch.)	700	
Selaginella	500	
Syzygium (Myrt.)	500	allotted
Schefflera (Aral.)	490	checklist
Ficus (Mor.)	475	allotted
Asplenium	400	allotted
Cyrtandra (Gesn.)	400	
Pandanus (Pandan.)	400	
Diplazium (Dryopt.)	300	
Grammitis	300	allotted
Rhododendron (Eric.)	290	1967
Calamus (Arec.)	280	allotted
Diospyros (Eben.)	250	
Eria (Orch.)	250	
Memecylon (Melast.)	250	allotted
Vaccinium (Eric.)	240	1967
Ardisia (Myrs.)	220	allotted
Tectaria (Aspid.)	215	1991
TOTAL	**7460**	
Myristica (Myrist.)	152	2000

- **Substantial overall funding**

A few attempts have been made to raise funds, but in vain. The main funding still comes from the core-funding of participating institutes and project-based funding from national science foundations.

- **Increase in contributions from the Malesian region itself**

The total number of contributions from the Malesian region itself is unfortunately low, much lower than e.g. the contributions from Thai botanists to their (national) Flora of Thailand (Table 5; see for further discussion also Middleton, this volume). It is rather disappointing that in the 1990's no treatments from Malesian authors came out, even though a couple of family treatments in the hands of Malesian colleagues were on the verge of completion already early that decade.

- **Deforestation**

There are no data that the rate of deforestation has decreased significantly. The huge forest fires in Borneo in the second half of the1990's have added their share to the area affected by logging and agriculture. To fulfil one of our main arguments for completing FM, i.e. to provide primary scientific data for better sustainable use and conservation of the plant diversity in the region, more efforts on knowledge transfer and information dissemination is urgently needed, apart from progress towards a complete Flora.

What next?

What can we conclude for the future of Flora Malesiana? Ten years ago the discussion to accelerate the production of instalments essentially focussed on format, efficiency and funding to increase the number of collaborators. What can we add to that discussion? The following are just a few suggestions and thoughts.

- **Format**

Regarding the format, the question still is whether we should hold to voluminous instalments being the sole products of Flora Malesiana, or whether other formats of information on Malesian plant diversity also can be recognised as fitting the goals of Flora Malesiana. After all, the prime goal is a complete survey of the species diversity of vascular plants in the Malesian region, by means of critical revisions of existing knowledge and collections, and including the production of identification tools, and to make this primary scientific information generally accessible. This may allow for a much broader interpretation of the way of presenting the information.

However, the semi-monographic format will most probably remain the ultimate goal of Flora Malesiana as it is highly appreciated as a source of multiple-purpose information by workers in the region. After all, as Geesink (1990), I would like to quote Van Steenis: 'A flora is only useful after it is completed'.

- **Efficiency**

I do not think that we can expect much of a further increase of efficiency in the revision work. The contribution per author seems higher than before, but it needs to be another three times higher, as only when we are able to produce treatments for 600 species per year, will completion in 50 years be in sight. So how can we substantially increase the workforce? Maybe each participant in the network could spend a few percent of his/her time more on flora writing, but everybody is usually over-committed and has to find a compromise between various duties. Moreover, local and special purpose floras depend on the same pool of botanists. I fully understand the national incentives to develop local projects, but in my view, the largest increase in efficiency can be achieved when the research is carried out within regional treatments.

- **Funding**

Table 11 gives some general societal research priorities that may be of relevance for Flora Malesiana and related research in obtaining additional funding. For each of them some suggestions for objectives are given which may be eligible under the respective funding schemes.

Table 11. Some general societal research priorities and possible systematic activities that may fit for grant applications

Societial research priorities	Funding possibilities?
bio-informatics	collection databases sequence databases pattern analysis (old) literature
genomics	infra-specific diversity identification phylogeny and evolution
global change	geographic patterns collection information
biodiversity convention	national monitoring and inventory GIS and geographic scale
increase scientific network	more contributions from the region other scientific disciplines and relevant networks

If there are any possibilities for general funding, e.g. under one or another scheme related to the Biodiversity Convention, the Board will do its best to submit a proposal. Participants in the network are called upon to look for possibilities to submit proposals whenever possible, with a revision component, either as a core activity or as a corollary of the main objectives.

Conclusion

A major point in my eyes is to strengthen the participation of Malesian botanists in the Flora Malesiana network to increase their number of contributions. The largest and most important potential for further accelerating the Flora Malesiana project lies in the region itself. This means that funding of training programs should have high priority. Also, a major drawback for institutes in the region is the low availability of (old) literature. A program to make this information electronically available (e.g. on CD-ROM) will be an important step in enhancing taxonomic work in the region. For a better understanding of the phytodiversity in the region, it will be worthwhile to look for other relevant networks, e.g. in the field of geology, conservation, and geography.

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PROSEA and Flora Malesiana

N. Wulijarni-Soetjipto and B.P. del Rosario

Abstract

N. Wulijarni-Soetjipto[1] *and B.P. del Rosario*[1,2] *([1] PROSEA Foundation Network Office, c/o Herbarium Bogoriense, Jl. Ir. H. Juanda 22, P.O. Box 332, Bogor 16122, Indonesia; [2]-permanent address: Philippine Council for Agriculture, Forestry and Natural Resources Research and Development (PCARRD), Paseo de Valmayor, P.O. Box 425, Los Baños, Laguna 4030, The Philippines) 2003. PROSEA and Flora Malesiana.* Telopea *10(1): 11–27.* About 15 years after its establishment, the PROSEA Programme has published 16 volumes (18 books) of the PROSEA Handbook series of the 20 planned. All together the 18 books cover c. 5615 species in 6515 printed pages. As many as 580 scientists (335 from South-East Asia) have been involved in the preparation of the Handbooks as authors and editors, and more than one quarter contributed to more than one volume. The volumes were published in hardbound and paperback editions. Of the 30 000 copies of all paperback edition printed in 1992–2001, a total of 20 000 copies have been distributed. By April 2003, another 9 books are expected to appear, estimated to include c. 1600 species in more than 2500 pages. From the PROSEA Handbook series, various derived materials intended for education, training and extension were published by and in the PROSEA participating countries in South-East Asia, and training workshops have been carried out. Beyond the year 2000, PROSEA's mission is to become a leading information provider and disseminator on the efficient and sustainable use of the plant resources of South-East Asia. To execute this mission, PROSEA has been seeking linkages with local, regional and international organisations. In the period 2001–2005, a shift to appropriate information and computer technologis will be the preferred dissemination mode to PROSEA's direct and indirect beneficiaries. PROSEA is looking at possibilities to make the information widely available on the internet to reach a broader public. Several ongoing and planned activities, including contacts with other organisations, to reach PROSEA's goal are highlighted. From the start of its programme until today PROSEA has been using the Flora Malesiana series, and PROSEA receives assistance from a number of plant specialists in the Flora Malesiana region. Cooperation between PROSEA and Flora Malesiana will continue to be of mutual benefit. PROSEA's experience in utilising the Flora Malesiana series, and some topics of possible joint activities between the two programmes are presented.

Introduction

PROSEA (Plant Resources of South-East Asia) is:

- an international programme focusing on plant resources of South-East Asia.
- interdisciplinary, covering the fields of agriculture, forestry, horticulture and botany.
- a research programme, making knowledge available for education and extension.
- ecologically focused on promoting plant resources for sustainable tropical land-use systems.
- committed to conservation of biodiversity.
- committed to rural development through diversification of resources and application of farmers' knowledge.

Organisation

PROSEA started in 1986 as a Project initiated by the Wageningen Agricultural University (WAU) in the Netherlands. In 1988 a set of agreements of Cooperation were concluded between WAU and five institutions in five countries in South-East Asia

(Malaysia, Indonesia, Papua New Guinea, the Philippines and Thailand), and in 1990 the Project became a non-profit Foundation under Indonesian law, with an international charter, domiciled in Bogor. In 1991 one institution from Vietnam joined the Foundation.

PROSEA is governed by a Board of Trustees. Members of the Board consist of representatives of the participating institutions, donor agencies and of personal title. The Chairman and Vice-Chairman form the Executive Board, with responsibility for policy-decisions in between meetings of the Board of Trustees. The Board of Trustees meets once a year.

The programme infrastructure, operational since 1988, consists of a Network Office located in Bogor (Indonesia), and a Publication Office in Wageningen (the Netherlands). The Network Office coordinates a network of 6 Country Offices in 6 South-East Asian Countries. The Publication Office coordinates a large informal network of editors and authors of the PROSEA core publications.

Objectives

The PROSEA Programme has four objectives:

- to compile, review and summarise the existing wealth of information on the plant resources of South-East Asia for education, extension, research, and industry.
- to build and maintain a computerised Databank on the plant resources of South-East Asia.
- to publish information on the plant resources of the region in an illustrated, multi-volume handbook.
- to support additional activities that enhance dissemination of this information published in the PROSEA Handbook series or compiled in the Databank.

Participating institutions

The institutions participating in the PROSEA Programme are:

- Forest Research Institute of Malaysia (FRIM), Kepong, Malaysia; hosting the Country Office Malaysia.
- Indonesian Institute of Sciences (LIPI), Jakarta, Indonesia; hosting the Network Office South-East Asia and the Country Office Indonesia.
- Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam; hosting the Country Office Vietnam
- Papua New Guinea University of Technology (UNITECH), Lae, Papua New Guinea; hosting the Country Office Papua New Guinea.
- Philippine Council for Agriculture, Forestry and Natural Resources Research and Development (PCARRD), Los Baños, Laguna, Philippines; hosting the Country Office Philippines.
- Thailand Institute of Scientific and Technological Research (TISTR), Bangkok, Thailand; hosting the Country Office Thailand.
- Wageningen University (WU), Wageningen, the Netherlands; hosting the Publication Office.

Target groups

The target groups of the programme are: *direct users*, i.e. those professionally concerned with plant resources in South-East Asia and working in the fields of education, extension, research, and commercial production. These include, among others, lecturers and students of colleges and universities, scientific staff of Research and Development establishments, subject specialists, and libraries; and *indirect users*, i.e. those in South-East Asia depending directly on plant resources and obtaining relevant information through extension. They are individual farmers applying the information in their actual production activities.

Implementation

Until the year 2000 the programme was implemented in 4 phases. The main activities carried out during each phase are as follows:

Preliminary phase (1985–1986): During this period a feasibility study was made by Wageningen Agricultural University, *Proposal for a handbook* was published in 1986, and promotion of the undertaking was carried out.

Preparatory phase (1987–1990): Network Office South-East Asia was established in Bogor (Indonesia), basic documents for discussion were prepared, PROSEA Databank was established. In this period the First PROSEA International Symposium was held in 1989 in Jakarta (Indonesia) with the objective to discuss the scientific and organisation aspects of the whole PROSEA undertaking based on the experience gained from 1987 to early 1989.

First implementation phase (1991–1995): PROSEA Databank was developed, ten earlier volumes of the PROSEA Handbook were produced. Later in the period, first efforts in producing materials derived from the Handbook were made. The Second PROSEA International Workshop was held in 1994 in Cisarua (Indonesia) with the objectives (1) to highlight the importance of the plant resources of South-East Asia, (2) to review the progress made by the PROSEA Foundation during the First Implementation Phase in achieving international cooperation, in developing a documentation and information system and in publication of the Handbook, (3) to make recommendations for the Second Implementation Phase (1996–2000) on all aspects of the programme, with special attention to dissemination of information.

Second implementation phase (1996–2000): Handbook production and Databank development continued, derived materials were actively produced, and first steps were made in PROSEA Electronics® by producing CD-ROMs. The third PROSEA International Workshop was held in 1999 in Bogor (Indonesia) with the objectives (1) to highlight the importance of the plant resources of South-East Asia and the unique position of PROSEA in this respect, (2) to review the progress made by the PROSEA Foundation during the Second Implementation Phase in achieving its targets, particularly in its electronic and printed-publication programme, and (3) to formulate a new PROSEA mission for a new era while the Publication Office undertakes a Finalisation Phase 2001–2002 for completion of the Handbook.

The historical background, activities and progress of the PROSEA programme from 1987 until today has been reported by our colleague Dr. P.C.M. Jansen (First General Editor of the PROSEA Handbook) in the *Flora Malesiana Bulletin*; these have appeared from Vol. 9 No. 4 onwards. The PROSEA outputs, the activities beyond 2000 and their link with Flora Malesiana will be highlighted in this paper.

PROSEA core outputs

For the years beyond 2000, PROSEA has accumulated information and knowledge on plant resources of South-East Asia in different core outputs and various derived materials. They will be utilised as capital for activities in the period 2001–2005.

The PROSEA Core outputs consist of PROSEA Databank, multi-volume Handbook, the Basic list of species and commodity groupings, Bibliographies, CD-ROMs, and Home page.

The PROSEA databank

The PROSEA Databank at present consists of 7 databases (BASELIST, CATALOG, PREPHASE, ORGANYM, PERSONYM, TEXTFILE, and PHOTFILE). The Databank is physically available and accessible at the PROSEA Offices in South-East Asia and the Netherlands.

- BASELIST: is a database of botanical names and uses of c. 6200 plant resources of South-East Asia. It is based on the books of Heyne (1927), Burkill (1935), Brown (1941–1943), and Reyes (1938). It forms the skeleton of the PROSEA Handbook.
- CATALOG: is a database of international literature references derived from 5 parent databases, i.e. AGRICOLA, AGRIS, BIOSIS Previews, CAB Abstracts and TROPAG. As of July 2001 the database contains 191 830 records.
- PREPHASE: is a database of less-accessible literature references from South-East Asia. It contains information of more localised importance (articles from national journals, reports and books in local languages, student theses, etc.), which are scanned manually by the Country Offices. As of July 2001 it contains 60 340 records, of which more than 30% have abstracts in English.
- ORGANYM: is a database of institutions active in the field of plant resources of South-East Asia. There are 735 records containing basic identification parameters and information on activities and main publications of the respective institutions. This database has been discontinued at regional level.
- PERSONYM: is an expert database, providing information on the research activities and major publications of individual scientists. It contains 5 900 records. This database has also been discontinued at regional level.
- TEXTFILE: is a database containing the text of the PROSEA Handbook volumes, each genus or species article being a record. As of July 2001 the database contains 5 430 records.
- PHOTFILE: is a database containing images of photographs and line-drawings of plant resources. It is particularly intended to make PROSEA CD-ROMs more attractive, but they can also be used for the production of derived materials under proper references. As of July 2001 it contains 6 765 records.

The Handbook

From 1989 until 2000, 18 books of 16 Handbook volumes (of the 20 volumes planned) have been published covering more than 5600 species in 6515 pages (Table 1).

The Handbook volumes are the result of an orchestrated effort of about 580 scientists from 39 countries contributing to the volumes as authors of manuscripts and/or members of the editorial team. Of them 335 are from South-East Asia (Indonesia 134, Malaysia 72, Papua New Guinea 11, Philippines 48, Singapore 2, Thailand 42, Vietnam 26), 106 from the Netherlands, and 245 from other countries. Of the 580 scientists, 167 contributed to more than one volume (Table 2), thus the frequency of their involvement in the Handbook production is more than 935. Taxonomists have played an important role in the preparation of the Handbook.

Table 1. PROSEA Handbook volumes published from 1989 to 2000.

No.	Title	Year published	No. of species	No. of pages
1	Pulses	1989	25	107
2	Edible fruits and nuts	1991	390	447
3	Dye and tannin-producing plants	1991	111	196
4	Forages	1992	359	300
5(1)	Timber trees: Major commercial timbers	1993	596	610
5(2)	Timber trees: Minor commercial timbers	1995	850	655
5(3)	Timber trees: Lesser-known timbers	1998	1778	859
6	Rattans	1993	134	137
7	Bamboos	1995	77	189
8	Vegetables	1994	c. 225	412
9	Plants yielding non-seed carbohydrates	1996	103	237
10	Cereals	1996	40	199
11	Auxiliary plants	1997	213	389
12(1)	Medicinal and poisonous plants	1999	389	711
13	Spices	1999	126	400
16	Stimulants	2000	55	201
18	Plants producing exudates	2000	79	189
19	Essential-oil plants	1999	68	277
Total	**(16 volumes, 18 books)**		**c. 5618**	**6515**

Table 2. Frequency of scientists' contributions to PROSEA Handbook series, 1989–2000.

Contribution	No. of scientists	Frequency
1 book	413	413
2 books	88	176
3 books	38	114
4 books	21	84
5 books	7	35
6 books	7	42
7 books	1	7
9 books	2	18
12 books	1	12
18 books	2	36
Total	**580**	**937**

Of the 580 contributors, 106 scientists from 17 countries were involved in the editing work: 4 scientists (from 2 countries) as general editors of the series, 33 (from 8 countries) as volume editors, and 69 (from 17 countries) as associate editors. In the production of the Handbook effort has been made to keep the number of South-East Asian scientists involved either as authors or as volume editors always in balance with that from outside the region.

The Handbook volumes have been published as hardbound editions for distribution in developed countries and as a paperback low-price edition for distribution in developing countries. A total of 45 895 copies have been printed (hardbound 15 514; paperback 30 380) of which 30 767 have been distributed throughout the world (10 791 for the hardbound, as of end 2000; 19 976 for the paperback, as of July 2001).

The text of the Handbook volumes forms the database TEXTFILE.

Basic list of species and commodity groupings

From the database BASELIST have been published *PROSEA: Basic list of species and commodity grouping: Version 1* (paperback, 1989) and *PROSEA: Basic list of species and commodity grouping: Final version* (hardbound, 1991). The production of *Version 1* involved more than 40 plant taxonomists and other plant specialists from 6 countries (the Netherlands, United Kingdom, Denmark, Germany, United States and Australia). This version was distributed in 1989 within the PROSEA Network only. The production of the *Final version* involved 70 plant taxonomists and other plant specialists from 11 countries (the Netherlands, Austria, Denmark, France, Germany, Norway, United Kingdom, United States, Australia, Indonesia and Malaysia).

This Basic list contains c. 6 200 species and is intended to help editors and authors of the PROSEA Handbook to check correct scientific names, and to decide which species should be considered for inclusion in the Handbook and which commodity group each species can best be assigned to. This list is used as a starting point for each Handbook volume. Besides, it is also used in scanning literature for the CATALOG and PREPHASE databases. It was reprinted in 1993 (paperback) and distributed to those interested in the correct scientific names of useful plants occurring in South-East Asia.

Bibliographies

The database PREPHASE has been extracted to produce PROSEA Bibliographies, each volume of which appeared soon after the publication of the Handbook volume of the same commodity group. Earlier volumes of the Bibliographies were published in printed form, later volumes in CD-ROM. Table 3 shows the Bibliographies that have been published so far.

Table 3. PROSEA Bibliographies.

No.	Commodity group	Year published	No. of records (approximate)
1	Pulses	1990	600
2	Edible fruits and nuts	1993	2 parts 4400
3	Dye and tannin-producing plants	1991	360
4	Forages	1994	950
5(1)	Timber trees: Major commercial timbers	1994	2 parts 260
5(2)	Timber trees: Minor commercial timbers	1996)	1025
5(3)	Timber trees: Lesser-known timbers	1998	1800
6	Rattans	1995	515
7	Bamboos	1996	505
8	Vegetables	1995	2 parts 3100
9	Plants yielding non-seed carbohydrates	1999	in CD-ROM 4700
10	Cereals	1999	in CD-ROM 3625
11	Auxiliary plants	1997	2380
13	Spices	2000	in CD-ROM together with Bibliography 19 3395
19	Essential-oil plants	2000	in CD-ROM together with Bibliography 13 1020
			Total 30 975

CD-ROMs

From the database TEXTFILE, CATALOG, PREPHASE and PHOTFILE the following CD-ROMs have been produced:

- Test Version (1994), containing PROSEA Handbook volumes 1–4, CATALOG 1–4, Bibliography 1–4. PROSEA/Pudoc-DLO, Wageningen, the Netherlands.
- Version 1 (1997), containing PROSEA Handbook volumes 1–8, Bibliography 1–8. PROSEA/Pudoc-DLO, Wageningen, the Netherlands.
- Vegetables (1997), containing PROSEA Handbook 8, Bibliography 8, Photographs. ETI/PROSEA/Pudoc-DLO, Amsterdam, the Netherlands.
- Forestry Compendium (1998); a result of collaboration between CABI, CIFOR and PROSEA, issued by CABI, Wallingford, UK.
- Timber trees (1999/2000), containing PROSEA Handbook volumes 5(1), 5(2), 5(3), Bibliography 5(1), 5(2), 5(3), Photographs, Identification keys for wood properties and anatomy. ETI/PROSEA/Pudoc-DLO, Amsterdam, the Netherlands.
- Fruits and nuts (1999), containing Handbook volume 2, Bibliography 2, Photographs. ETI/PROSEA/Pudoc-DLO, Amsterdam, the Netherlands.
- Forestry Compendium (2000); a result of collaboration between CABI, CIFOR and PROSEA (Global Module), issued by CABI, Wallingford, UK.

Homepage

Information regarding PROSEA in general, PROSEA Databases, PROSEA Newsletter, PROSEA Handbook and spin-off products has been made available on the internet since 1998 (the Netherlands) and since September 2000 (Indonesia) at the following websites: for the Netherlands: http://www.prosea.nl and http://www.prosea.net and for Indonesia: http://www.proseanet.org.

PROSEA derived products

Various products have been produced by the PROSEA Offices derived from the PROSEA Handbook and Databank, i.e. translations, booklet series, non-series booklets, leaflet series, directories, special bibliographies, video presentations, radio broadcasts, game cards, calendars, and other outputs. The PROSEA Handbook and Databank have also been used in workshops/training programmes on certain topics.

Translations

Many local researchers, lecturers and students in South-East Asia, especially in Indonesia, Thailand and Vietnam still have difficulty in understanding texts in English. To reach the wider audience of the PROSEA Handbook series, certain volumes have been translated into local languages and published by the Country Offices. So far 5 volumes have been translated and published in Indonesian, 7 volumes in Thai, 2 volumes in Vietnamese, and 1 volume in Filipino.

Booklet series

For the intermediate beneficiaries (local subject specialists) of the PROSEA Handbook, the Country Office Indonesia publishes *Seri Pengembangan PROSEA* [PROSEA Development Series] in Indonesian. So far the following issues have been published: No. 1–12(1).2 (1993–2000).

Non-series Booklets

Various booklets were published from 1995 to 1998 mostly in local languages:

- *Manual for the cultivation of lowland vegetables* (1995, in Indonesian). Issued by the Country Office Indonesia.
- *Trees for life* (1995, in Indonesian). Issued by the Country Office Indonesia.
- *A guide to root diseases* (1997, in Malay). Issued by the Country Office Malaysia.
- *Forest species for landscaping and urban planting* (1997). Issued by the Country Office Malaysia.
- *Medicinal vegetables in South-East Asia* (1998, in Thai). Issued by the Country Office Thailand.
- *Manual for identification of wood in the fiel*d (1997, in Indonesian). Issued by the Network Office Bogor.
- *Manual for the identification of forest trees in Indonesia* (1998, in Indonesian). Issued by the Network Office Bogor.
- *Techniques for producing planting materials of forest trees* (1998, in Indonesian). Issued by the Country Office Indonesia.
- *Introduction to the efficient and sustainable use of forest trees* (1998, in Indonesian). Issued by the Country Office Indonesia.

Leaflet series

For field extension officers the Country Office Indonesia publishes *Lembaran Informasi PROSEA* [PROSEA Information Leaflet]. The following have been issued: Vol. 1, No. 1–18 (1993–1997); Vol. 2, No. 1–14 (1997–2000).

Another *PROSEA Information Leaflet* has been published in Vietnamese by the Country Office Vietnam. The following issues have appeared: Vol. 1, No 1–5 (1996), Vol. 2, No. 1–6 (1997), Vol. 3, No. 1–5 (1998), Vol. 4, No. 1–6 (1999), No. 1–6 (2000).

The Country Office Philippines published leaflets on edible fruits and nuts in 1992–1997 (81 issues) in English and on vegetables in 1999 (19 issues) in Filipino, intended for farmers.

The Country Office Thailand published leaflets on timber resources in 1997–1998 (14 issues) in Thai.

Directories

Three directories have been issued by the Country Office Philippines based on PERSONYM:

- *PROSEA Philippines' Directory of specialists in agronomy and horticulture 1994.* Issued in 1995.
- *PROSEA Philippines' Directory of specialists in forestry/agroforestry 1997.* Issued in 1997.
- *PROSEA Philippines' Directory of specialists on medicinal and poisonous plants 1998.* Issued in 1998.

Special bibliography

Abstract bibliography *Crop Science Research in the Philippines 1970–1994* was issued by the Country Office Philippines in 1996. It is an extract of the PREPHASE database.

Video presentation

'Know your common trees' (1996), issued by the Country Office Malaysia.

Radio broadcasting

To enhance dissemination of the PROSEA information base to farmers in rural areas, various topics have been broadcast by the Country Office Indonesia in the weekly 'Siaran Pedesaan' [Rural Broadcast] of the RRI (Indonesia Radio Broadcasting) of Bogor.

Game cards

Game cards to introduce plant resources to school children have been issued:

- X-cellent plants fun cards (1998). Issued by the Country Office Philippines.
- Playing cards *Fruits and vegetables* (1999). Issued by the Country Office Indonesia.
- X-cellent trees fun cards 1 (1999). Issued by the Country Office Philippines.
- X-cellent trees fun cards 2 (2000). Issued by the Country Office Philippines.

PROSEA calendars

Three promotional bureau calendars have been issued by the Country Office Philippines in 1998–2000 for the year 1999, 2000 and 2001.

Other outputs

- *Pedoman identifikasi pohon-pohon Dipterocarpaceae.* Kalimantan (1999); Indonesian version of the English edition. Issued by the Country Office Indonesia.
- *Pedoman identifikasi pohon-pohon Dipterocarpaceae.* Sumatera (1999); Indonesian version of the English edition. Issued by the Country Office Indonesia.
- *Pedoman identifikasi pohon-pohon Dipterocarpaceae.* Jawa sampai Niugini (1999); Indonesian version of the English edition. Issued by the Country Office Indonesia.
- *PROSEA Book Reviews 1989–1999.* Issued by the Publication Office, Wageningen.
- *Training Module* (1999) for Summer Environment Youth Camp (Eco-Camp). Issued by the Country Office Philippines.

PROSEA beyond 2000

The PROSEA Programme has been focused and directed from the documentation stage (Handbook production and Databank development) and dissemination stage (production of translations of the Handbook and derived materials) to the utilisation stage of the PROSEA information base for biodiversity conservation, education, industry, agroforestry, planning, extension, etc.

The mission of PROSEA beyond 2000 was, therefore, formulated and recommended during the Third PROSEA International Workshop in November 1999 and states: '*In view of the importance of plant information for mankind and biodiversity conservation, and the unique position of PROSEA in this respect, PROSEA strives to be a leading information provider and disseminator on the plant resources of South-East Asia for their efficient and sustainable use. Emphasis will be on lesser-known plants, and information services will be demand-driven*'.

To carry out the mission, the PROSEA programme activities for the period 2001–2005 will cover:

- Finalisation of Handbook production
- Databank maintenance and development
- Development of PROSEA Electronics® (Webdatabases)
- Active production of derived materials
- Establishment of Country Office websites
- Establishment of Community Websites
- Reduction of the role of Wageningen University (end 2002)
- Extension of PROSEA membership (Laos, Cambodia, Myanmar)

Finalisation of Handbook production

The years 2001–2002 will be a transitional period for the Publication Office that should finalise the production of the Handbook series. Three books are expected to be published before the end of 2001, namely:

No 12(2) : *Medicinal and poisonous plants 2*, treating c. 410 species in c. 780 pages

No 14 : *Vegetable oils and fats*, treating c. 55 species in c. 230 pages

No 15(1) : *Cryptogams: Algae*, treating c. 220 species in c. 320 pages

Another three books, that will be the last to be managed by the Publication Office in Wageningen, are planned to be sent to the printer in Wageningen before the end of 2002, and expected to be ready for distribution in April 2003. Those books are:

No. 12(3): *Medicinal and poisonous plants 3*, treating c. 530 species in c. 660 pages

No. 15(2): *Cryptogams: Ferns and fern allies*, treating c. 100 species in c. 270 pages

No 17: *Fibre plants*, treating c. 250 species in c. 500 pages

Thus, by April 2003, a total of 19 Handbook volumes (comprising 24 books) should be available, covering over 7000 species in more than 9000 pages, involving more than 650 scientists in their production.

After the year 2002, publication activities of the Handbook will be transferred to the Network Office in Bogor. The following volumes are expected after 2003:
No 15(3): *Cryptogams: Fungi*
No 20: *Ornamental plants*

Active production of derived materials

At the Country Office level, production of translations of the Handbook volumes and derived material continues.

Databank maintenance and development

During the period 2001–2005, the existing PROSEA databases TEXTFILE, PREPHASE, PHOTFILE, and CATALOGUE will be maintained and further developed. The text of the newly published Handbook volumes will be incorporated gradually in TEXTFILE. Scanning literature references for PREPHASE continues to pay more attention to lesser-known species. The quality of PREPHASE will be improved through editing work. All line-drawings published in the newly published Handbook volumes will be incorporated in PHOTFILE. Meanwhile, photographs and drawings of species for which no drawing is available yet in PHOTFILE will be sought through contacts with other organisations and individual scientists. It is expected that by December 2002 the TEXTFILE, PREPHASE, PHOTFILE and CATALOG databases will contain about 5950; 67 500; 8 800; and 254 150 records, respectively.

Development of PROSEA electronic products

Three PROSEA databases will be integrated in the PROSEA homepage (http://www.proseanet.org), i.e. TEXTFILE, PREPHASE and PHOTFILE. A trial version of TEXTFILE online was started early in 2001. From 2002 onwards, records in the TEXTFILE database will gradually be accessible online. Complete records of PREPHASE with abstracts will also gradually be put on the internet. PHOTFILE online will cover a selection of images from the off-line PHOTFILE database. For the first few years access to the databases online will be free of charge for personal use. It is expected that by December 2002 the TEXTFILE online, PREPHASE online and PHOTFILE online will contain about 1200, 2 100 and 1 200 records, respectively.

Establishment of Country Office websites

To enhance the distribution and dissemination of the PROSEA information base to the direct and indirect target beneficiaries, Country Office websites are to be established. As of August 2001 two Country Offices have established their respective websites: Philippines and Indonesia.

The website of the Country Office Philippines has been developed as an integral component of the PCARRD-MIKS (Management Information and Knowledge System): http://www.pcarrd.dost.gov.ph/prosea/default.htm. The site has a hyperlink to the PROSEA home page. The website covers the following sections: PROSEA Databases, general information on Country Office Philippines, Publications and services (PROSEA core publications), Country Office publications, and Herbal homepage.

The website of the Country Office Indonesia has been developed as an integral component of the PROSEA homepage: http://www.proseanet.org/Indonesia/. The website covers the sections on general information, publications of the Country Office Indonesia, 'Katalog tumbuhan berguna' [Catalogue of useful plants], Mitra PROSEA [Friends of PROSEA], and collaboration with other organisations. The text is in Indonesian. The website has links to DAFEP (Decentralised Agricultural and Forestry Extension Project) and BIPP (Balai Informasi Penyuluhan Pertanian) [Agricultural Information Extension Center].

Establishment of the Community Websites

Community websites are useful in the chain of information transfer from an international information (knowledge) base to local application. In collaboration with other organisations the Country Office Philippines and Country Office Indonesia have recently established community websites in their own countries.

As a strategy to reduce poverty and improve health situations especially in rural areas, the Country Office Philippines, in collaboration with RED (Rural Enterprise Development) Foundation, has established the PROSEA Herbal Homepage, using *PROSEA volume 12(1): Medicinal and poisonous plants 1* as a source. The homepage is an internet based information service on known medicinal plants which aims to disseminate technologies and information on herbal medicine for alternative health care. The home page forms a section of the website of the Country Office Philippines. The PROSEA Herbal homepage contains 5 main sections: Species list, Techno-catalogue, Indication index, Kitchen technologies, and Frequently asked Questions.

As a strategy to integrate the PROSEA information base into the research-extension mechanism in Indonesia, the Country Office Indonesia in collaboration with DAFEP (Decentralised Agricultural and Forestry Extension Project) of the World Bank in Indonesia established Community Websites in three locations in Central Java, i.e. Bantul, Kulon Progo and Magelang districts. The website of Bantul is http://www.dafep.org/bantul, that of Kulon Progo is http://www.dafep.org/kulonprogo and that of Magelang is http://www.dafep.org/magelang. Each Community Website contains information on organisation, potential of the area, development potential, commodity of top priority, market prices, research-extension network in Indonesia and a hyperlink to the website of the Country Office Indonesia.

Reduction of the role of Wageningen University

When the last six volumes of the Handbook are published, the role of the Publication Office (hosted at Wageningen University) will be terminated and publication activities will be transferred to the PROSEA Network Office in Bogor. The Publication Office will be replaced by a sort of Country Office Netherlands. Meanwhile, Wageningen University will coordinate the PROTA (Plant Resources of Tropical Africa) programme, a sister programme of PROSEA, and will remain a member of the PROSEA Board of Trustees.

Extension of PROSEA membership

South-East Asia also covers Cambodia, Laos and Myanmar. Information on plant resources of these three countries in the PROSEA Databank is very limited. Participation of these three countries in the PROSEA undertaking will surely enrich the PROSEA information base making it beneficial to those outside the three countries. The Third PROSEA International Workshop in 1999 was attended by representatives from Laos and Myanmar who expressed their wish that their respective countries might join the PROSEA Network.

Cooperation with other organisations

In implementing its programme, PROSEA has received cooperation from many national as well as international organisations and individual scientists. Among others, these include:

- PROSEA participating institutions: LIPI (Indonesia), FRIM (Malaysia), PCARRD (the Philippines), TISTR (Thailand), IEBR (Vietnam), UNITECH (Papua New Guinea) and WU (the Netherlands). They coordinate PROSEA activities, provide manpower, working space and facilities for PROSEA Offices, and matching funds.
- Pudoc-DLO, Wageningen, the Netherlands. This Centre of Agricultural Publishing and Documentation provides online service for the development of the CATALOG database, and published and distributed earlier volumes of the PROSEA Handbook and integral CD-ROMs.
- Herbaria in South-East Asia and other countries, by providing authors and editors for PROSEA Handbook volumes, and access to herbarium collection for consultation.
- Research institutes and universities in South-East Asia, by providing authors and editors forPROSEA Handbook volumes, and manpower to scan information sources for the PROSEA Databank.
- ETI (Expert Centre for Taxonomic Identification), University of Amsterdam, the Netherlands, for the production of PROSEA Commodity Groups' CD-ROMs.
- CAB International (Wallingford, Oxon, United Kingdom), for production of the CD-ROM CABI/PROSEA *Crop Protection Compendium*, and together with CIFOR (Center for International Forestry Research, Bogor, Indonesia), for production of the CD-ROM CABI/CIFOR/PROSEA 'Forestry Compendium'.
- ICRAF (International Centre for Research in Agroforestry) South-East Asia, for among others launching of PROSEA 11 *Auxiliary plants*, and in the development of webdatabase on quantitative tree properties.
- Backhuys Publishers (Leiden, the Netherlands), for the publication and distribution of the hardbound edition of later PROSEA Handbook volumes, and the distribution of medium-priced editions of the volumes.
- At the Country Offices' level, with national agencies, NGOs, ministries, industries and others.

The importance of Flora Malesiana for PROSEA

The Flora Malesiana (FM) series is an invaluable source of botanical information and knowledge on plants in the Malesian region (Malaysia, Indonesia, Singapore, Brunei Darussalam, the Philippines and Papua New Guinea), wild as well as cultivated.

PROSEA has used the FM series in the compilation of *PROSEA: Basic list of species and commodity groupings*, a checklist used as a starting point in the preparation of the PROSEA Handbook series. Besides this, the FM series has also been consulted during the preparation of the individual volumes of the Handbook. PROSEA adopted all the family treatments and followed the nomenclature used in the FM series. For families not yet treated in the FM series, PROSEA has to refer to other existing publications.

As a compiler of plant information, PROSEA would not be able to operate without the existence of the FM and other floras of the South-East Asian region such as *Flora of Java*, *Tree flora of Malaya*, *Tree flora of Sabah and Sarawak*, *Flora of Thailand*, and *Flora of Laos*, *Cambodia and Vietnam.* PROSEA is very grateful to the Foundation FM, and to the publishers and editors of the above-mentioned floras for the important botanical sources of information they provide.

Expectations for Flora Malesiana

The following are our expectations and comments based on the first author's and colleagues' experiences in using the FM series during the preparation of the PROSEA Handbook volumes.

For every family in the FM series, useful and cultivated plants of South-East Asia need be given proper treatment, not the same as in the PROSEA Handbook series, but with aspects that will be useful for PROSEA and other users (non-taxonomists) of the series, e.g. taxonomic aspects, correct naming, taxonomy of cultivars, relationship with wild plants, etc. Descriptions of species should not be too brief and should be consistently presented to enable comparison of plant parts. For rather important cultivated plants, information on vernacular names and uses needs to be added.

Cultivars and cultivar groups also need to be more properly treated in other floristic publications in South-East Asia.

FM series is important for plant taxonomists working on the flora of Malesia but it is also important for many other specialists from various disciplines. The knowledge of plant classification is also useful to non-plant taxonomists, e.g. as a tool for identification and registration. Since they are not too familiar with many botanical terms and scientific (Latin) plant names, it will be easier for them (without the help of a plant taxonomist) to use the FM series if a glossary of technical terms and an index of vernacular plant names are available in each volume of the series.

The inclusion of both a glossary and an index will be most welcome. The late Prof. Kalkman, in his paper presented at the First PROSEA International Symposium in 1989, stated that the results of research in plant systematics should not only be beneficial to plant taxonomists but should also be accessible to specialists who are non-plant taxonomists, e.g. horticulturists, foresters, phytochemists, plant breeders, etc. throughout the world, the number of which is much greater than that of the plant taxonomists.

To gain wider usage, the FM series would need to be more attractive and more user friendly. The number of illustrations could be increased to cover more species. The excellent illustrators, herbaria and botanical gardens occurring in South-East Asia could be employed far more.

Cultivated plants need to be better represented in the South-East Asian herbaria to enable people to get a better understanding of cultivars and cultivar groups for their sustainable utilisation and conservation, and to avoid their being described as species.

PROSEA and Flora Malesiana collaboration

Although there is no official collaboration between the PROSEA Foundation and the Foundation Flora Malesiana, collaboration between PROSEA and individual FM specialists has occurred since the start of the PROSEA programme (Preliminary phase: 1985–1986) e.g. in the verification of scientific names, as contributors of manuscripts on certain taxa, as associate editors or editors of certain volumes of the PROSEA Handbook, or of other PROSEA core products, and as instructors in various training courses. PROSEA is very grateful to them, especially since, besides contributing, they are also acting as users of the PROSEA products.

PROSEA will maintain and strengthen collaboration with individual FM specialists and will be pleased to continue collaborating with the Foundation FM and partners for mutual benefit. Some examples of what can be considered activities are:

Update of botanical information in the TEXTFILE database: The PROSEA Handbook volumes will not be revised before 2010. However, information on taxa published in the Handbook which are already in the database TEXTFILE need to be updated and new information added. To develop this database, assistance from botanical specialists is needed.

Contribution and uses of plant images: PROSEA is developing the PHOTFILE database. Of the taxa published in the Handbook volumes many still have no photograph or line-drawing. Contribution of plant images from the FM specialists or organisations to the database is most welcome. On the other hand, images in the PHOTFILE database can be used by FM specialists for illustrating publications on request to the PROSEA Foundation.

Production of booklets and other materials for education: PROSEA core products can be used for producing materials for education. FM specialists together with PROSEA could produce e.g. : (1) Publications on important plant resources (e.g. 100 species per country in South-East Asia) for primary and secondary school children which would cover interesting facts, identification, illustrations, information on how to grow and maintain plants, etc., (2) Good simple botany books for teachers, with numerous familiar examples and correct descriptions of species, (3) Publications on indigenous and imported plant products to be found in local markets, with photographs and drawings, (4) Publications per country or region for tourists interested in plants, e.g. on fruits, flowers, interesting trees, etc., with enough illustrations and details to enable identification.

Training courses at regional and national levels: PROSEA can contribute to training courses on e.g. plant taxonomy, economic botany, para-taxonomy and other topics, especially for young people, by providing e.g. a list of South-East Asian genera which are badly in need of critical taxonomic studies, and by making the PROSEA core products accessible to the trainees and instructors. FM specialists could help in the teaching programmes.

Hyperlink of PROSEA web databases with those of Flora Malesiana: There are three PROSEA databases available online, i.e. TEXTFILE, PREPHASE, and PHOTFILE. These databases can be hyperlinked with those of Flora Malesiana and partners. In that way a gap in certain plant information in the PROSEA Webdatabases can be filled by the Webdatabases of Flora Malesiana or its partners, and vice versa.

Production of PROSEA 20 and PROSEA 15(3): When the time comes, interested FM specialists will be invited to be involved in the production of PROSEA volumes 20 'Ornamental plants' and PROSEA 15(3) 'Cryptogams: Fungi' as members of the task force, authors of manuscripts on certain taxa and as members of the editorial team. PROSEA will be grateful if the Foundation FM and partners could find ways to fund these two publications.

Production of CD-ROMs: In cooperation with ETI (Amsterdam) and Pudoc-DLO (Wageningen) the following PROSEA commodity-groups have been published in CD-ROMs: 'Vegetables' (1997), 'Edible fruits and nuts' (1999) ,'Timber trees' (1999 & 2000), and 'Rattans and Bamboos' (2001). However, in 2001 the PROSEA policy on electronic publishing was shifted to the establishment of Web databases. Depending on the demand and funds available, PROSEA may collaborate someday with FM or other organisations in the production of other CD-ROMs with materials extracted from the PROSEA Web databases, especially TEXTFILE and PHOTFILE online.

Donor agencies

To execute its programme, PROSEA has received financial support from the coordinating institutions (FRIM, Malaysia; LIPI, Indonesia; IEBR, Vietnam; UNITECH, Papua New Guinea; PCARRD, the Philippines; TISTR, Thailand; WU, the Netherlands). It has also received general financial support from the following donor agencies:

- Finnish International Development Agency (FINNIDA): 1991–1995.
- Finnish Department for International Development Cooperation (DIDC): 1996–2000.
- Netherlands Ministry of Agriculture, Nature Management and Fisheries: 1987–1990, 1991–1995, 1996–2000.
- Netherlands Ministry of Education and Science: 1987–1990, 1991–1995, 1996–2000, 2001–2005.
- Netherlands Ministry of Foreign Affairs, Directorate General for International Cooperation (DGIS): 1987–1990, 1991–1995, 1996–2000, 2001–2005.
- Ministry of Forestry, Republic of Indonesia.
- Yayasan Sarana Wanajaya, Indonesia: 1987–1990, 1991–1995, 1996–2000, 2001–2005.

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- Commission of the European Union, DG-1 Programme *Tropical Forests*, Brussels, Belgium: 1996–2000.
- International Tropical Timber Organization (ITTO), Yokohama, Japan: 1991–1995, 1996–2000.
- Tropenbos Foundation, Wageningen, the Netherlands: 1991–1995.
- International Development Research Centre (IDRC), Ottawa, Canada: 1991–1995.
- Glaxo Wellcome

PROSEA would not exist today without financial support from the above-mentioned donor agencies. For the period 2001–2005 we are financially secure for developing PROSEA Electronics® . However, for office management and carrying out other activities, additional financial support from donor agencies is still needed.

PROSEA e-mail addresses

Correspondence with PROSEA offices can be made through e-mail at the following addresses:

- Network Office, Bogor, Indonesia: info@proseanet.org or pran@proseanet.org
- Country Office Indonesia, Bogor: ariebud@indo.net.id or hadi@proseanet.org
- Country Office Malaysia, Kepong: razak@frim.gov.my or philip@frim.gov.my
- Country Office Papua New Guinea, Lae: tbrookings@fo.unitech.ac.pg. or tbrookings@hotmail.com
- Country Office Philippines, Los Baños: prosea@ultra.pcarrd.dost.gov.ph or psfaylon@ultra.pcarrd.dost.gov.ph
- Country Office Thailand, Bangkok: daran@mozart.inet.co.th or proseatha@hotmail.com
- Country Office Vietnam, Hanoi: huyen.prosea@fpt.vn
- Publication Office, Wageningen, the Netherlands: prosea@pros.dpw.wag-ur.nl or Jan.Siemonsma@pros.agro.wau.nl

Conclusion

Entering the phase beyond 2000, PROSEA already has a strong network, various core outputs and derived products. The PROSEA products will be maintained, further developed, and more rapidly distributed and disseminated. With capital in hand, PROSEA is seeking linkages with the Foundation Flora Malesiana and other organisations to reach its various target groups and to accomplish its mission.

Acknowledgments

Special thanks are due to Dr J. West and Dr A. Hay, co-chairs of the 5th International Flora Malesiana Symposium, for the invitation to participate in the Stakeholders Mini-symposium. The first author is grateful to the UNESCO Jakarta Office, especially Prof. Stephen Hill, for financial support that enabled her to participate in the Symposium held in Sydney, Australia. Our thanks are due to Prof. Washington Napitupulu, the Executive Chairman of the Indonesian National Commission for Unesco, for his encouragement and support that made participation of the first author in the Symposium possible. The first author is thankful to the Director PROSEA Network Office, for the opportunity to attend the Symposium and the encouragement in seeking financial support. Many thanks to our colleagues at the PROSEA Network (especially Dr P.C.M. Jansen) for sharing their thoughts. Thanks are also due to Dini Astriani for her assistance in the preparation of transparencies for our presentation at the Symposium.

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Herbarium Bogoriense: present and future activities

Irawati

Abstract

Irawati (Herbarium Bogoriense, Ir. H. Juanda 22, Bogor 16122, Indonesia) 2003. Herbarium Bogoriense: present and future activities. Telopea *10(1): 29–32.* A rehabilitation program at Herbarium Bogoriense supported by the World Bank was completed in September 2000. The main program focused on conservation and curation of specimens, human resources development and information system management. The changes in various aspects of the collection are presented. Taxonomists from different herbaria around the world supported all activities. Rehabilitation activity must be continued as only a part of the collection has been properly curated. Present activities, future programs and challenges faced by the herbarium are discussed.

Introduction

Although it represents a valuable scientific heritage from the previous generation, collections at the Bogor national herbarium have deteriorated over time. The Herbarium Bogoriense (BO) hosts about 2 million specimens of plants and fungi, and is a source of biodiversity information for the Malesian region, especially Indonesia. In 1995 Herbarium Bogoriense and the Museum Zoologicum Bogoriense (MZB) received a five-year grant from the World Bank, through the Global Environment Facility (GEF). This activity was called the Biodiversity Collections Project, which supports the implementation the National Biodiversity Action Plan in Indonesia. The initial development and support of the Biodiversity Collections Project involved five international institutions working together with the Bogor Museum and Herbarium, i.e. Arnold Arboretum of Harvard University, CSIRO–Canberra, The Nationaal Natuurhistorisch Museum – Leiden, the National History Museum–London and the Rijksherbarium/Hortus Botanicus–Leiden.

BO and MZB, with technical assistance from the Arnold Arboretum of Harvard University and the Royal Ontario Museum, assembled and coordinated the activities especially on the rehabilitation of the biodiversity collections and development of the herbarium. The rehabilitation focused on four main aspects:

1. The management system of the herbarium collections
2. The physical condition of the collections
3. Information systems of the herbarium collections
4. Human resources development

The management system of the herbarium collections

The previous herbarium management was under the Botany Development Facilities Section. With limited facilities, only a small part of the herbarium collections was maintained properly by dedicated staff. However the major part of the collections was almost neglected. During the implementation of the project, a Coordinator from the

Botany Division was chosen to take responsibility for the overall rehabilitation activities. The Botany Coordinator was assisted by three Curators.

At the end of the project these activities were transferred to the existing management of the herbarium, i.e. under the Botany Division. To maintain the sustainability of the improvements to the collections, the new curatorial system was continued, and all staff and technicians of the Taxonomy group are involved.

The physical condition of the collections

The main changes can be seen on the second and third floors of the herbarium building, because the tin boxes on wooden shelves were all replaced by cabinets. On each floor a taxonomic laboratory and database room were built.

Rearrangement of the collection was done by separating the monocotyledons from the dicotyledons. The collections were alphabetically arranged as before, according to family, genus, species and location. The collections were mounted on new acid-free papers with new Species Folders and Genus Folders.

The Type specimens were separated from the general collections, with new Type Folders and are stored in an air-conditioned room. During 2000, through the JICA program, a photography course for staff was conducted for the photography of herbarium specimens. This recording activity for all Type specimens has continued.

Mounting and remounting of the 'priority taxa' (Arecaceae, Dipterocarpaceae, Gymnospermae, Lauraceae, Orchidaceae, Sapotaceae), the Type specimens and fragile specimens (including non-priority taxa) were the main activities of the rehabilitation program. With the help of scientists working at the Herbarium Bogoriense, fragile collections were sorted for remounting. Restoration of the spirit collection focused on damaged collections and also on the 'priority taxa'. Some of the collections were transferred to new bottles.

However, at the end of the rehabilitation program only about 13 % of the total collection had been remounted. Therefore, this activity must be continued in the future. In this rehabilitation program, the Herbarium Bogoriense would like to acknowledge the support from Kew Herbarium, Nationaal Herbarium of the Netherlands, CSIRO and other organisations. This is not an easy task, as most of the herbarium materials have to be imported from other countries.

Major changes in the management of the collections were actually on the preservation methods. Mercuric chloride and Paradichlorobenzene were no longer used as preservatives and freezing the herbarium sheets is now used as the primary method of insect control. Without the use of poison, herbaria become vulnerable to insect attack, therefore Integrated Pest Management procedures were applied to monitor the collections for pest infestation. To control insects, fumigation of the specimens is conducted once a year using Phostoxin, the phosphate-based pesticide. Fumigation activity is not carried out on all floors of the herbarium building so the herbarium usually is closed to the public for one month each year, so that specimens can be moved into the fumigation areas and then back into the collection.

Database of the herbarium collections

The previous computer hardware facilities have been upgraded. One server functioning as a back-up domain controller, with seven desktop computers as clients, was provided. A network between the computer room on the first floor, second and third floors has been established. Recently an Internet connection was established between the Herbarium Building and other Indonesian Institute of Sciences offices in Bandung, Cibinong and Jakarta.

The information system team focused on maintaining the application of IBIS 2.0 for the herbarium collections. All information found on the herbarium sheets was entered into the system. The addition of BO number on the herbarium sheet means that the specimen has been recorded in the database. Now about 200 000 collections have been recorded in the database, only 10% of the total collection. Validation remains a slow process in the database activity. Soon part of the Type specimens will appear on the web-site: www.bio.lipi.go.id. Information from other taxonomists is welcome to improve the Type specimen information.

Human resources development

To manage the collection better, the Botany Coordinator and the Collection Managers had the opportunity to study the management systems at other Herbaria (Canberra, Edinburgh, Hawaii, Kew, Leiden, London etc). Some of the herbarium students were also sponsored by the project to attend short-term training programs overseas. Through the GEF scholarship program, Herbarium Bogoriense has successfully recruited 6 new staff and another 2 will be appointed in the future. The newly recruited staff are a significant addition of human resources, because for several years the government has imposed zero growth in government employee numbers.

A mentorship program was an important aspect in human resources development at the Herbarium Bogoriense. Prof. Egon Horak from Zurich started the first group of Agaricales mentorship, followed by Dr. Paul Kessler from the Nationaal Herbarium Netherlands, mentoring on Annonaceae; Dr. Henk van der Werff from Missouri Botanical Garden, St. Louis mentoring on Lauraceae; Mr. Lyn Craven from CSIRO Plant Industry, Australia, mentoring on Myrtaceae; Dr. John Dransfield from Kew Herbarium mentoring on Arecaceae; and Dr. Phillip Cribb from Kew Herbarium mentoring on Orchidaceae. Mentorship programs were also attended by students from the universities and the staff of the Botanic Gardens. Also, through the mentors' participation, many new references were added to the herbarium library.

During the implementation of the project, three internship programs were conducted with a total of 16 participants from universities in Indonesia. The interns studied the herbarium management and the curation of the priority taxa under supervision of the Herbarium Bogoriense senior taxonomists. Through this program Herbarium Bogoriense is trying to broaden the Herbarium's reach throughout the country.

The change from a centralised government system to one of local autonomy has also influenced the management systems for biodiversity collections in Indonesia. Through this program new herbaria in different universities, especially outside Java, were initiated.

Present areas of research of Herbarium Bogoriense staff

Ms. A. Retnowati & Ms. M.A. Rifai (Agaricales of Java & Bali); Dr. B. Sunarno (Myrsinaceae for Malesia); Ms. D. Arifiani (*Ediandra*); Ms. D. Sulistiarini (terrestrial orchids of Sulawesi); Dr. E. A. Widjaja (genetic variation in *Schizostachyum*); Ms. F. I. Windadri (bryophytes); Ms. H. Rustiami (*Daemonorops* sect. *Piptospatha*); Dr. H. Wiriadinata (begonia of Java; flora, charismatic medicinal plants of Lore Lindu); Dr. J.P. Mogea (rattan from Lore Lindu and diversity of *Calamus manna*); Dr. K. Kramadibrata (mycorrhiza); Ms. L. Juswara (*Goodyera* & *Hibiscus*); Dr. N. Utami (Balsaminaceae & anatomy of *Eusideroxylon swageri* embryo); Dr. R. Nasution (Musaceae); Dr. Rugayah & Dr. E. A. Widjaja (the species of *Artabotrys* in Java); Ms. S. Sunarti (*Syzygium* of Java); Ms. T. Djarwaningsih (Solanaceae); Mr. T. Triono (interactive key for Malesian Sapotaceae); Mr. T. Uji (*Micromelum* in Malesia); Mr. U.W. Mahyar (orchids of Halimun Forest Reserve); Ms. Yulita (*Hopea* & *Shorea*).

Exploration activities in Indonesia in 2001 were conducted at Kendawangan (Kalimantan); Bentuang Kehirun (Kalimantan); Nusa Kambangan (Java); G. Ceremai (Java); Bukit Tigapuluh (Sumatra); Flores (East Nusa Tenggara).

Two guidebooks were published during the rehabilitation program, i.e. the *Management Policy of the Herbarium Bogoriense* and a guidebook on the *Processing and Management of the Herbarium Collections and Integrated Pest Management at the Herbarium Bogoriense* (in Indonesian language).

Future activities

Continued contact must be maintained even after the internship program is over. Therefore, during exploration activities in Indonesia, the researchers are encouraged to prepare extra sets of the collections for the local herbaria. We hope that each province in Indonesia will have its own herbarium and understand fully their local flora. I would like to take this opportunity to encourage the Flora Malesiana Foundation to supply references, especially Flora Malesiana, to these newly developed herbaria, which are usually attached to a university.

Improvement in the herbarium collection and additional new staff have put the Herbarium Bogoriense back on track. It is seen in the increasing number of scientists visiting the centre, as well as in the loan and exchange activities.

The Herbarium Bogoriense is known worldwide rather than in the country itself, therefore since 2000 'open house' activities have been conducted once a year during the Flora and Fauna days.

Plant identification services at the Herbarium Bogoriense also need better facilities to encourage students/visitors to learn to identify plants themselves and a Reference Collection was initiated.

Under the coordination of the Nationaal Herbarium Nederland, networking among Malesian herbaria, Leiden and Oxford University will be realized this [2001]year, funded by the European Union. To continue the rehabilitation activities, especially mounting/remounting of the specimens, restoration of the spirit collections and data entry, efforts have been made to raise funds.

Herbarium Bogoriense is open to students from universities especially for those who choose plant taxonomy as their main interest.

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I would like to thank the Organizing Committee of the 5th International Flora Malesiana Symposium for supporting my travel to Sydney. I am also very grateful to Dr. Kartini Kramadibrata who provided valuable information for this article, and to the Biodiversity Information staff for their technical assistance.

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Progress on the Flora of Thailand

David J. Middleton

Abstract

David J. Middleton (Arnold Arboretum, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138, USA) 2003. Progress on the Flora of Thailand. Telopea *10(1): 33–42.* The history, current status and prospects for the Flora of Thailand project are discussed. The need for further collecting in Thailand is highlighted, particularly in Peninsular Thailand, an area covered by both the Flora of Thailand and Flora Malesiana. The rôle that non-South-East Asian botanists have in the Flora of Thailand and Flora Malesiana is discussed and the need for collaboration between the Floras is emphasised.

Introduction

In this paper I want to discuss three topics: the history, progress and future of the Flora of Thailand project; the need for more field work in Thailand; and the rôle of the botanist from outside Asia in the Flora of Thailand and Flora Malesiana. As there is a slight overlap between the areas covered by the Flora of Thailand and Flora Malesiana, from the Isthmus of Kra southwards to the Malaysian border, I thought it would be of particular interest to look more closely at this area.

Thailand has a total population of almost 65 million people and population densities among the highest in South-East Asia. Over the past three decades Thailand has experienced rapid economic growth and a considerable improvement in indicators of social development (Santisuk et al. 1991). Much of this economic development has relied heavily on the utilisation of Thailand's natural resources, including timber, minerals, agriculture, fisheries, and more recently tourism (Arbhabhirama 1987). Thailand has therefore experienced one of the fastest rates of deforestation in the tropics, with significant environmental and economic impacts (Santisuk et al. 1991). Forest cover has declined from over 50% of the total land area in the 1950's to approximately 25% in 2000 (Table 1).

Despite the heavy reliance on natural resources for development, and the rapid rate of ecosystem loss, Thailand's biological diversity and natural ecosystems remain relatively poorly studied. Since 1973 the Thai government has pursued a policy to actively protect as much remaining forest land as possible. Currently there are 115 National Parks and Wildlife Sanctuaries in Thailand which include 6.72 million hectares of land, c. 53% of the remaining forest area or 8% of the total land area of Thailand (Napompeth & Rodcharoen 1998). While the IUCN has listed numerous reptiles, birds and mammals as in danger of extinction in Thailand, little is known of the status of most plant species. According to the IUCN List of Threatened Plants (Walter & Gillett 1998), Thailand has 27 endangered (E), 21 vulnerable (V) and 33 rare (R) species but it is probable that these figures are greatly underestimated due to the lack of data on many plant groups. To quote from Boontawee et al. (1995) "There is an urgent need to explore, identify, protect, and manage the available forest biodiversity properly for future sustainable utilization."

Table 1. Forested areas in Thailand as detected by LANSAT-TM image (from Boontawee et al. 1995 (1976–1991) and the Royal Forest Department web site: http://www.forest.go.th/Botany/Flora/Forest_type.htm (2000)).

Year	Forest area km^2	% Country area
1950	344 000	67
1976	198 417	38.67
1978	175 224	34.15
1982	156 000	30.52
1985	150 866	29.40
1988	143 803	28.03
1989	143 417	27.95
1991	136 693	26.64
2000	129 715	25.28

The Flora of Thailand

Historical Background

Scientific plant collecting began in Thailand in 1778 with the expedition of the Danish botanist J.G. Koenig and continued very sporadically thenceforth until the 20th century when collecting became more extensive. These early collections have been summarized by Kerr (1939). Kerr himself made systematic collections in various parts of Thailand from 1902 to 1932 and collected over 21 500 specimens. His collecting itinerary and other information about this remarkable botanist have been gathered into a review by Jacobs (1962). Early expeditions to Peninsular Thailand, in the area also covered by Flora Malesiana, included those of Curtis between 1889 and 1899. He collected along the Malaysian border and up to Phangnga, although the collections from Thailand are few and mostly from small offshore islands. Ridley collected more extensively in Peninsular Thailand and described many new taxa (Ridley 1920). When Kerr began his collecting in 1902 it is estimated that there were only 4 250 collections from the whole of Thailand. By the time he left Thailand in 1932 there were approximately 35 000 specimens, from his own collecting activities and those of his various colleagues and associates, including collecting trips in Peninsular Thailand on expeditions in 1923 and between 1926 and 1930 resulting in over 7 000 specimens. This increased the density index for Thailand to about 8–9 specimens per 100 km^2 (Jacobs 1962), albeit unevenly spread and with most of the country remaining poorly known. Numerous new taxa were described from these collections, mainly by Craib and by Kerr himself. After Kerr retired not much collecting was done until the Thai Royal Forest Department started new collecting initiatives in the 1950's under the direction of Tem Smitinand. Danish botanists also became involved in the late 1950s and remain active to the present day.

The Flora of Thailand Project

The Flora of Thailand Project was initiated in 1963 under Thai–Danish collaboration and formally launched in 1967. The first part was published in 1970 and additional parts have been produced regularly since then, although not as fast as was at first hoped. To date 16 parts in seven volumes have been published (Smitinand & Larsen

1970, 1972, 1975, 1979, 1981, 1984, 1985a, 1985b, 1987, 1988, 1989, 1990, 1991, 1992, 1993; Larsen 1996; Santisuk & Larsen 1997, 1998, 1999, 2000). It remains a collaborative project with involvement of institutions from Thailand, Europe, Japan and the United States. The current co-editors are Thawatchai Santisuk and Kai Larsen. Submission of manuscripts has increased recently resulting in the hope that the Flora can be completed within 30 years (Parnell 2000), although Santisuk et al. (1991) have suggested that it may take as long as 100 years.

Table 2 gives the figures for the number of taxa that have already been published, or have been accepted for publication, for the Flora of Thailand. Given an estimated number of species for Thailand of 10 250 (my estimate; Parnell (2000) suggests a higher figure of 12 500) then this comprises about 30% of the total number of species. Currently one part is appearing each year. The largest family so far published is the Cyperaceae with 248 species (Simpson & Koyama 1998), followed a long way behind by the Apocynaceae *sensu stricto* (Middleton 1999) with 125 species. However, the account of the Euphorbiaceae is almost complete with c. 400 species. The largest family in the Flora is the Orchidaceae, revision of which is being coordinated by Henrik Pedersen in Copenhagen, building on the work of Gunnar Seidenfaden. Coordinators or authors have been found for nearly all the remaining families with the notable exceptions of the Vitaceae and several small families which might make good projects for Thai students.

In addition to the Flora accounts an extremely useful bibliography to South-East Asian taxonomic treatments has been produced by Alain Mauric and kept up-to-date by Rachun Pooma and Kanlaya Pattarahirankanok. This can be accessed at: http://www.forest.go.th/Botany/BIBLIO/main.htm. Information on the mosses of Thailand can be accessed at http://www.mobot.org/MOBOT/Moss/Thailand/.

One aspect of the Flora of Thailand which has not yet been sufficiently explored is to have web accessible multi-access keys and descriptions. This would be particularly useful for the large families and would be possible to do for many groups from already existing data. Since the Apocynaceae was published (Middleton 1999) two new species have been described (Middleton 2001; Middleton & Santisuk 2001). This is a fact of life for any plant family from an undercollected region like Thailand but need not render previous accounts outdated if the reader is also aware that new taxa and distributions will simply be added to multiaccess keys and descriptions on a web accessible floristic account. As with many aspects of botanical research, this would, of course, be contingent on raising necessary funds and, as yet, no families have been produced in this way. Thailand has a reasonable prospect of completing a written Flora within about 30 years but it may take longer to have it in a web accessible form.

Table 2. Number of taxa published for Flora of Thailand: to volume 7, part 2, plus number of taxa in press or accepted for publication as of August 2001.

	Families	Species
Taxa published	130	2 300
Taxa accepted for publication	25	850
Total number expected	304	10 250

Collecting in Thailand

Thailand remains poorly collected. In the United Kingdom, an average of 17.2 herbarium specimens per km^2 has been collected compared to 0.5 specimens per km^2 in Thailand (Parnell 2000). When one considers that the flora of the UK consists of only about 1500 native species and the flora of Thailand approximately 10250 species, the undercollection of the Thai flora is even worse than the stark figures would suggest. Although the U.K. is considered one of the world's best collected countries, the overall collection density is also low compared to some other parts of South-East Asia (Fig. 1). Collecting densities in all of South-East Asia compare unfavourably with parts of the New World tropics. Recent collecting suggests that the rate for Thailand may be increasing but is still one of the lowest in the tropics (see Parnell et al. in press). This collecting rate has risen to its current rate from one of the lowest in Asia for the period up to 1974 and effectively zero in the period 1974–1981 (Larsen 1979; Parnell et al. in press). Data from both Parnell (2000) and Middleton (1999) show that even in the better known plant groups in Thailand such as the genus *Syzygium* and the Apocynaceae the pattern of collecting within Thailand is extremely patchy. 20% of all collections made in Thailand have been made in a single province, Chiang Mai.

Parnell et al. (in press) also point out that even in those parts of Thailand considered to be reasonably well collected, such as Chiang Mai province, the collections made there are in fact extremely localised on just a few mountains (Doi Sutep and Doi Inthanon) and the surrounding foothills.

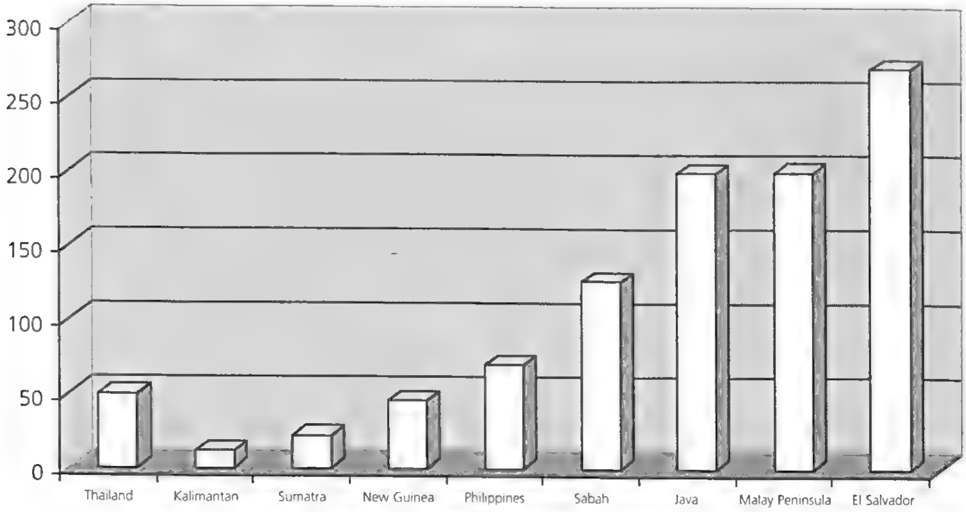

Fig. 1. Number of collections per 100km^2; data from Johns (1995) and Parnell (2000) except Malay Peninsula very roughly estimated by extrapolation from 1972 figure in Johns (1995).

Peninsular Thailand

There have been several recent expeditions to Peninsular Thailand. Shimizu et al. (1980), Phengkhlai and Niyomdham (1991), Larsen (1992), Simpson et al. (1995) and Dransfield (1996) all give accounts of collecting in Peninsular Thailand and have made valuable contributions toward furthering our understanding of this area. These collections are mostly housed in AAU, BK, BKF, K, KYO, PSU and TCD (abbreviations follow Holmgren et al. 1990). However, the area under consideration is large and the overall concentration of specimens from this area remains small.

If one examines the distribution of the Apocynaceae on each side of the border between Malaysia and Thailand it is clear that the Thai side of the border remains terribly undercollected. The majority of species of Apocynaceae are not local endemics so one would expect a reasonably even spread of taxa across the provinces within a region if there were an even spread of collecting. Ten species of Apocynaceae recorded from both Peninsular Thailand and Malaysia have never been collected in the four Thai provinces along the Thai–Malaysia border and yet four species recorded from these four provinces and also in Malaysia are not known anywhere else in Thailand. There are also 44 species of Apocynaceae known from Peninsular Malaysia which are not known in Thailand of which 26 are in at least one of the four Malaysian border states: Perlis, Kelantan, Perak, Kedah (data from Turner 1995; Middleton 1999). Peninsular Thailand includes the important biogeographic transition between Thai seasonal dry evergreen forest and the extremely diverse mixed dipterocarp forest (Van Steenis 1950; Whitmore 1984) characteristic of much of western Malesia. This transition has never been quantitatively described but it is clear that the Isthmus of Kra, the northern limit for Flora Malesiana accounts, is much further north than the edge of this forest type. However, there are areas of it in the southern Thai provinces right on the Malaysian border so one would expect many more of the Malaysian elements to be found in this area if they were better collected. This increased collecting would have two benefits: firstly that taxa found there could be incorporated into the ongoing Flora of Thailand, and secondly that biogeographic studies would have a more accurate pool of data to use in describing this transition zone. Evidence of this is that when more work has been done in Peninsular Thailand numerous papers have resulted, describing new taxa and new country records (e.g., Shimizu et al. 1980; Larsen & Larsen 1993, 1995; Mekanawakul 1996; Sookchaloem 1997; Sookchaloem & Murata 1997; Larsen & Mood 1998; Sawangchote et al. 1999; Triboun & Larsen 1999; J. Dransfield 2001; S. Dransfield 2001). In Larsen and Mood (1998) and S. Dransfield (2000) new genera are even described.

International collaboration

To quote from Pooma (1999), a Thai national and staff member of the Royal Forest Department, "The amount of biological systematic information in *ex situ* collections, such as natural history museums, herbaria and botanic gardens, is very rich in countries poor in biodiversity, and vice versa". He goes on to note the need for technology transfer and data repatriation back to the country of origin. This collaboration requires, of course, willing participants in both the country of origin and the country in which the material is housed. There have been some calls for repatriation of herbarium material back to the country of origin but again as Pooma points out "Specimens are safer in well-maintained and curated major herbaria in developed countries due to the economic, technical, environmental and legal problems in developing countries". Whether this argument remains in years to come will have to be seen but at the moment having data on biological diversity in Thailand available mainly in herbaria outside Thailand poses a responsibility on those herbaria to return that information to Thailand. Pooma reiterates that the completion of a published Flora, including information on species distribution and habitats, and a classification of the vegetation types are necessary for a nation-wide policy and plan for sustainable use and conservation of Thailand's genetic resources. Engaging staff at herbaria in which major Thai collections are housed on a project like the Flora of Thailand does, in part, fulfil that requirement for the repatriation of data and information. Posting images of specimens on the Internet is also a valuable means of making data available worldwide.

Flora of Thailand

Of the families completed for the Flora of Thailand to date (including manuscripts in press or accepted for publication) just under half the families and species have been completed by European botanists (Table 3). This compares well with Flora Malesiana where a very much higher proportion of the taxa have been completed by European botanists. 22% of the species have been revised by Thai botanists.

Table 3. Number of taxa published (or accepted for publication), in the Flora of Thailand, by location of author.

	Families	Genera	Species	% species published
Thai	34	156	680	22
European	75	406	1490	47
Non-Thai Asian	45	196	928	29
Australian	1	11	35	1
North American	6	9	17	<1
Total	**155**	**778**	**3150**	**100**

The dominance of European botanists in completing accounts for Flora Malesiana and, to a lesser extent, the Flora of Thailand is understandable given the concentration of collections in Europe, particularly type specimens, and the resources available for the training of taxonomists in Europe compared to South-East Asia. The important rôle of taxonomists in Europe in ensuring that accounts for the Flora of Thailand are completed is, however, beginning to change with many Thai students having recently been trained in universities in Thailand, Japan and Europe and taking on this rôle themselves. Also many European universities and institutions have changed their emphasis from traditional taxonomic practices to systematics based on molecular studies, or have abandoned systematics altogether. Therefore, the pool of available young European taxonomists to work on the Flora of Thailand has diminished at a time when the available pool of young talented Thai taxonomists is increasing.

One of the best ways forward with large families is to encourage collaboration between experienced taxonomists and students. The Euphorbiaceae with about 400 species has been a collaborative effort with contributors from Thailand and Europe. The larger and more complex genera have been completed by experienced Thai and European researchers whilst the smaller genera have mostly been revised by students as a tool for taxonomic training. This has proved an effective model for the completion of large families that will be continued with the Lauraceae and possibly the Rutaceae. Similar cooperative ventures between experienced taxonomists and students are being conducted for Flora Malesiana, such as in the Apocynaceae and Cucurbitaceae. Students from Thailand or the Malesian countries studying for graduate degrees, within or outside their own countries, may also have the opportunity to work on taxa over wide ranges and in more depth and produce really outstanding work. Testament to this is Indonesian researcher Sidiyasa (1998), who revised the genus *Alstonia* in the Apocynaceae for his PhD at Leiden University, a work which won him the IAPT Silver Engler medal for 1998.

A number of families have been completed by the same authors for both Flora Malesiana and the Flora of Thailand, often in collaboration with other authors. The Sapindaceae (Adema, Leenhouts & van Welzen 1994; van Welzen 1999), Caesalpinioideae (Larsen, Larsen & Vidal 1984; Ding Hou, Larsen & Larsen 1996) and Mimosoideae (Nielsen 1985, 1992), amongst others, are already complete. Other families such as Apocynaceae (Middleton 1999) and Myrsinaceae (Larsen & Hu 1996) have been completed for the Flora of Thailand and are being worked on by the same authors, sometimes in collaboration with others, for Flora Malesiana. Yet others such as the Musaceae and Cucurbitaceae are being worked on simultaneously for both Floras. This cross fertilisation between Flora Malesiana and the Flora of Thailand has proved an extremely efficient way of contributing accounts of both large and small taxonomic groups for both Floras. However, the bulk of this work has been done by botanists from outside South-East Asia, and whereas approximately 65% of species found in Thailand are also found in Malesia the converse is not nearly as true. Malesia is a much larger and more diverse area and it would be a bigger commitment for authors concentrating on the Flora of Thailand to also take on Flora Malesiana. The Ericaceae and Meliaceae are perhaps the most notable examples of large families completed for Flora Malesiana but whose authors will not for various good reasons complete the Flora of Thailand account.

One of the advantages that the Flora of Thailand has over Flora Malesiana is that it is a Flora of a single nation state. Flora Malesiana covers six nations, seven if you include the portion of Thailand to the Isthmus of Kra (and eight if you include the newly independent East Timor). Botanists in Thailand can get national funding to work on their flora and complete accounts whereas resources are not often available within the countries that make up the Malesian region for botanists to work on projects that extend beyond their own national borders. It is highly understandable, although not ideal, that Malaysian botanists have concentrated their efforts of the Tree Flora of Malaya and now the Tree Flora of Sabah and Sarawak and that Philippine botanists have been concentrating on the Philippine Plant Inventory project. Of course collections made in these efforts, new taxa published and accounts produced, will be new sources of information for any future Flora Malesiana account. However, floristic accounts extracted from monographic and semi-monographic revisions, such as Flora Malesiana, invariably lead to more accurate generic and specific delimitation and this has to be weighed in when one is seeking a balance between the urgent need for these accounts and the desire for scientific purity (Roos 1997).

Santisuk et al. (1991), in an international report on the botanical research and conservation needs for Thailand, noted that "one cannot overemphasize the urgent need to inventory all remaining natural vegetation and to complete the Flora [of Thailand] ... ". The same is true for Malesia and, given the common needs and goals of the two Floras and the large overlap in taxa, the collaboration should be further enhanced and encouraged.

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Automated geoparsing and georeferencing of Malesian collection locality data

Reed S. Beaman and Barry J. Conn

Abstract

Beaman, Reed S. (Natural History Museum and Biodiversity Research Center, University of Kansas, 1345 Jayhawk Boulevard, Lawrence, KS 66045, USA) and Conn, Barry J. (Royal Botanic Gardens Sydney, Mrs Macquaries Road, Sydney, NSW 2000 Australia) 2003. Geoparsing and georeferencing of Malesian collection locality data. Telopea *10(1) 43–52.* Some form of geographic reference is almost always present on specimen labels, an essential source of information for mapping species distributions and performing biogeographic analyses. The prospect of databasing large herbarium collections is now reality, but the task of manually georeferencing each specimen would be enormous. The fields of biological informatics and geomatics (biogeomatics) provide tools that streamline and automate acquisition, sharing, analysis, and visualisation of biogeographic data. Digitisation of specimens, particularly type specimens is now commonplace, but specimen imaging and optical character recognition (OCR) may also facilitate the data entry process. Natural language processing of digital data significantly reduces the time required to database and georeference a specimen. A prototype for a geoparsing and georeferencing web service has been developed that utilises a digital gazetteer of over 330 000 Malesian place names. This service is demonstrated using Urticaceae collections from Malesia and comparisons are made between automated and manual georeferencing methods.

Introduction

Biological collections document the diversity and distribution of life on earth. These data are now becoming accessible in networked databases for research, conservation, environmental management and educational uses. Though each discipline has specific data capture needs, every natural history collection shares the problem of transforming descriptive locality information associated with specimens into quantitative spatial values. For most of the last 300 years, specimen locality information has been recorded as cardinal offsets to political or geographical features (eg. '24 km N of Springfield, along a stream bed'). These data can be particularly time-consuming to quantify since they require interpretation and additional resources such as maps and gazetteers in order to be recorded in a standard geographic format (that is, to be georeferenced). Quantitative georeferences for biological specimen localities are the critical data that, in association with the taxon identity and the collection date, allow researchers to visualise and model the known and potential distribution of taxa. This particular area of biological data digitisation offers not only the greatest challenge, but also the greatest potential for a solution that provides significant cost savings for the entire biological collections community. For biological collections, a georeferencing solution must be a cohesive, interoperable system that provides natural language processing, geospatial integration, spatial error analysis, and validation based on species-specific geographic distributions. This paper summarises the development of an automated georeferencing tool for biological collections.

Background

The biological collections held by museums and herbaria worldwide document the biological exploration of the planet and are the primary research archives of biotic diversity. These collections provide the basis for the identification, description, comparison of taxa, and documentation of the occurrence of taxa in space and time. To illustrate the scale of information stored in such collections, there are approximately 6 million botanical collections held by the herbaria associated with the *Council of Heads of Australian Herbaria* (CHAH: Anon. 2001), 500 million specimens of animals and plants in museums and herbaria of the United States of America, and an estimated 2.5 billion natural history specimens in collections worldwide (Duckworth et al. 1993). Specimen data document the identities, habitats, histories, and spatial distributions of the 1.5–8 million described species, and provide the fundamental resource for identifying the estimated tens of millions of species that remain to be discovered and described (Wilson 2000). These essential records are the knowledge foundation for such diverse disciplines as biological systematics, environmental planning, conservation, genetic engineering, and medicine.

HISCOM, the *Herbarium Information Systems Committee* (Conn & Brooks 1998) is an Australian national association of Federal and State/Territory herbaria whose mandate is to develop infrastructure and to complete the process of making herbarium specimen data available to CHAH herbaria and the general public. The HISCOM partners have long been active globally in building interchange standards for botanical collections data (Conn 1996, 2000). The *Council of Heads of Australian Herbaria* currently have funding through to the year 2005 for digital library development as part of the *Australia's Virtual Herbarium* project (AVH), a consortium of Federal and State/Territory agencies in Australia (Barker 1998). The AVH digital library consists of four fundamental strategies; namely, (i) the building, sharing, and preservation of digital collections; (ii) creation of tools (particularly, identification tools) and services; (iii) influencing and supporting innovation in communication between users; and (iv) the development of strategic partnerships for further digital library development. However, the primary deliverables for this funding are the cataloguing of approximately 6.5 million herbarium specimens in Australia and establishing interoperability among the partners to reduce duplication of effort.

Recent developments in distributed database networks (eg. *Australia's Virtual Herbarium* – Barker 1998 and *The Species Analyst* – Anon. 1998) have begun to provide widespread access to biological collections data. However, the AVH is not currently interoperable with U.S.-based digital specimen libraries, such as *The Species Analyst* (Anon. 1998) and *Lifemapper* (Anon. 2002). There is presently a significant duplication of effort between the Australian and U.S. initiatives, and increased collaboration and interoperability are desirable for all parties. In addition, despite the recognised importance of these data, many collections remain largely inaccessible because they are not fully digitised. Internationally, herbaria and museums are participating in the painstaking process of digitally capturing specimen data. Tools to make this process more efficient are desperately needed. Georeferencing and validation are services from which the entire biodiversity community can benefit considerably.

The need for georeferencing of biological collections

Biodiversity is inextricably linked to geography. Common among the data for all biological collections is locality information. It is exactly this common thread of information that forms the basis for the investigation not only of individual species, but also of entire ecological communities. Maier et al. (2000) concluded that the single most important factor influencing work in biodiversity and ecosystem informatics is the problem of complexity, including georeferencing and species referencing. Georeferencing provides the means to link specimen data to the rapidly growing body of spatial environmental data for interdisciplinary research into complex phenomena.

Since most biological collection locality data are written in the form of descriptive localities (often with cardinal offsets), these data do not easily lend themselves to spatial filtering, comparison, or analysis. Locality data interpreted as spatial coordinates with associated measures of uncertainty (accuracy and precision) are more readily queried. Furthermore, the results of such georeferenced data queries are much more readily applied. The importance of capturing localities as spatial data (georeferencing) is recognised as a priority by the 'Digitisation of Natural History Collection Data' Subcommittee of GBIF (GBIF 2002). While it must be remembered that there are limits to the scalability of such data (because collectors were frequently not mindful of computers, analysis or even basic mapping, when they recorded collection information), the development of a method for rapidly digitising locality information in a standard useful form will make a major contribution not only to the digitisation of biological collections worldwide, but also to the vast scientific and public communities that rely on collections information.

Approximately 70% of the herbarium collections held in the *NSW Collections* database of the Royal Botanic Gardens Sydney (NSW) lack georeferences. To illustrate the general lack of georeferenced collections, a sample of 16,300 records from the specialist rapid-entry database (*Rapid*) used by data-processing staff at NSW was analysed (Fig. 1). Almost all collections prior to the 1960s lacked georeferences provided by the collector. The lack of importance attributed to precise spatial data by the collectors, dating back to the earliest collections made by explorers, is difficult to comprehend since many of these specimens were gathered during geographical surveying expeditions and geological exploration. During the 1960s–1980s, the number of botanical collections in Australia increased rapidly. However, the number of collections that were fully georeferenced remained extremely low (Fig. 1), with the majority of georeferences (at least 90%) calculated by curatorial staff or data processors. Since the late 1980s the increased use of detailed topographical maps, followed by hand-held global positioning systems (since the 1990s), has resulted in a significant increase (75% in 1989–1990) in the number of collections that are fully georeferenced. Although the sample size for the period 1991–2000 is too small to provide an accurate comparison with previous years, there is a noticeable increase in the number of collections fully georeferenced (approximately 90%). The available georeferencing tools mean that the qualitative spatial component of the collections can be readily quantified as part of the collection or curation process. Prior to this, there was no reason for providing georeferences because spatial software was not widely available in herbaria for mapping the distribution of these collections. Up until this period, species distribution maps were usually prepared manually. Until recently, general collectors were more interested in the identity of the collection rather than how it fitted into the known distribution of the taxon. Furthermore, herbarium collection databases were not and are still usually not designed to analyse data. The urgent requirement for data and/or the associated resources required to gather these data, on which environmental management decisions are made, frequently precludes the option of re-surveying an area or distribution of a taxon. It is important to make better use of existing collections and to add a higher level of spatial information into these existing historical collections so that they can be used in applications that require georeferenced data.

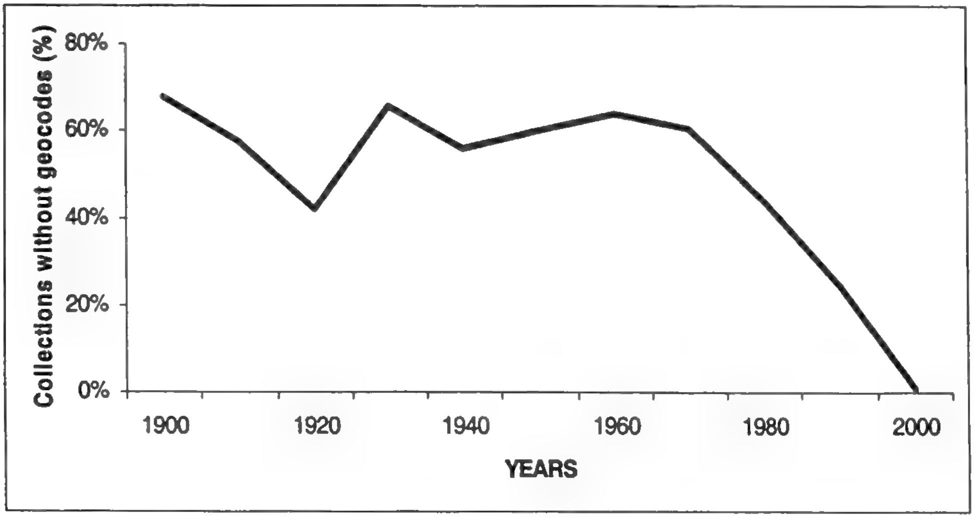

Fig. 1. Percentage of records lacking georeference data taken from a sample of 16 300 herbarium records data processed for the *Australia's Virtual Herbarium* project in the *Rapid* [entry] database (NSW).

It should be noted that given the wide variety and standard of information provided by collectors, the information that is most consistently provided includes the original location of the collection. Other label information is more difficult to interpret across the entire collection because of incompleteness and/or inconsistencies. This information enables the users to answer two important questions, namely, 'What taxa occur in a particular area?' and 'Where does a particular taxon occur?' Both of these questions are fundamental to conservation planning and environmental decision-making.

Impediments to rapid georeferencing

The advent of geographic information systems (GIS) and web-based mapping applications (such as, used by the *Australia's Virtual Herbarium* project) have placed ever-increasing demands on the biodiversity informatics infrastructure to complete digital biological collection catalogues. For example, there are data for approximately 2.3 million specimens available through *The Species Analyst* (Anon. 1998) and *Lifemapper* (Anon. 2002), but less than 30% of these records contains georeferenced locality data. Additional estimates are provided in Table 1. This omission severely limits the value of the specimen data for spatial analyses. Even though most digital data providers recognize the importance of georeferenced specimens, there exist a variety of reasons why these data are not more commonly available. Many of these reasons relate to the cost of this time-consuming task, including the lack of human resources and material resources.

Table 1. Estimates of biological collection size and the percentages digitally catalogued and georeferenced. Note: *The Species Analyst* and *Lifemapper* are both web-based distributed database systems. *NSW Collections* is the botanical specimen database of the National Herbarium of New South Wales (NSW).

Specimen origin	Specimen location	Taxonomic domain	No. of specimens (estimate)	No. digitally catalogued (%)	Number georeferenced (%)
Worldwide	Worldwide	Natural history collections	2.5 billion	< 5	< 5
Worldwide	USA	Natural history collections	0.5–1 billion	< 5	< 2
Worldwide	*The Species Analyst & Lifemapper*	Natural history collections	2.3 million	100	33
Worldwide	USA	Amphibians & reptiles	4.3 million	90	13
Australia	Australia	Vascular plants	6.5 million	22	14
New South Wales	*NSW Collections*	Vascular plants	400000	50	30

At NSW, the process of digitally cataloguing specimens has been ongoing since 1985, with data entry typically requiring 5–30 minutes per specimen. More than half of this time is usually spent on manual georeferencing using paper maps or electronic gazetteers. More recently, desktop geographic information system (GIS) software is being introduced. By using an innovative collaborative georeferencing environment and a well developed set of georeferencing guidelines (Wieczorek 2001), participants in the 'Mammal Networked Information System' (MaNIS 2001) have achieved efficiencies and economies of scale resulting in georeferencing rates of 20 localities per hour. Since MaNIS participants are georeferencing unique localities, each of which refers to an average of about five specimens, the actual rate of specimen georeferencing is closer to 100 per hour. Preliminary results of the prototype automated georeferencing tool (as described here) with MaNIS localities and methodology suggest that the MaNIS georeferencing rate could be increased by an order of magnitude.

Automated georeferencing prototype

Locality information in biological data sets is by no means standardized, but it is to some extent similar across collections, making the task of automated parsing tractable. Similarities notwithstanding, there remain a number of interesting challenges in parsing biological collection locality information. A few examples of textual localities illustrating these challenges are shown in Table 2.

Table 2. Sample textual localities and the challenges posed.

Example textual locality	Challenge posed
Wakarusa, 24 mi WSW of Lawrence	Two or more locations descriptors that are not exactly the same place
Moccasin Creek on Hog Island	Topological nesting
Bupo [?Buso] River, 15 miles [24 km] E of Lae	Complex interpretative description
16 km (by road) N of Murtoa	Linear feature measurement
On the road between Sydney and Bathurst	Linear ambiguity
Southeast Michigan	Vague localities
Yugoslavia	Political borders change over time
British North Borneo	Historical place names

Users of biological collection data have differing needs for spatial resolution, implying that accuracy and precision information need to be captured as integral components of the georeferencing process (Wieczorek 2001). In addition, this information will be essential if biological collection data are to be integrated with other scalable spatial data.

The development of an operational georeferencing prototype using PERL: the Practical Extraction and Reporting Language (Christiansen 2001) to batch process locality data from biological collections is nearly complete. In the original version of this prototype, a query by taxon (e.g., species) to the National Herbarium of New South Wales specimen database (*NSW Collections*) was processed and the results were returned either as a summary report of map-coordinates in HTML, or through a web-based mapping interface. Figure 2 illustrates a sample result in the mapping interface based on a query to the *NSW Collections* database on the genus *Elatostema* (Urticaceae – the stinging nettle family) from Papua New Guinea. Six points (in black) were mapped from data records in which the latitude and longitude were stored in the database. Points in white represent locality data georeferenced by automatic analysis of the descriptive locality data only. In this example, one locality was manually incorrectly georeferenced (as 16°55′S; 155°56′E) (refer black point in the Coral Sea, directly south of Bougainville Island – approximately 1 000 km south). This collection was actually from Buin, Bougainville Island (06°44′S; 155°56′E). Therefore, the manually derived latitude had been either incorrectly calculated or incorrectly data processed. In this example, the automated georeferencing protocols were able to provide some simple error-checking for collections from similar localities. However, it is important to realise that the automated georeferencing protocols are neither more nor less accurate than manually derived georeferences. The main advantage for automating georeferencing is that georeferences can be generated much more rapidly than by manual techniques.

The Western Australian Herbarium (PERTH) have implemented a hybrid system that includes a manual parsing of the descriptive locality into its components during data entry, followed by an automated conversion of these components by appropriate algorithms (P. Goia, pers. comm., 29 November 2002). This approach is expected to remain a useful strategy because manually parsing the locality statement then automating the calculation, is substantially faster than manually calculating the georeference. However, it relies on a high level of operator spatial knowledge.

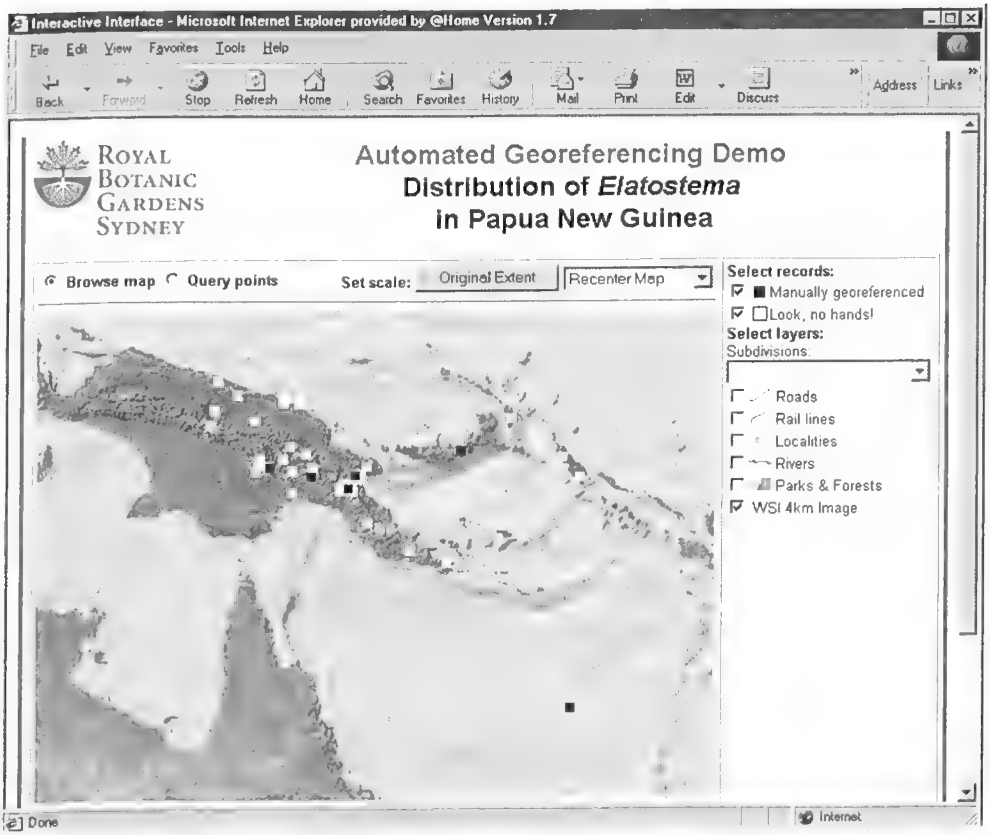

Fig. 2. Web-based mapping results from a specimen database query. Six records (black squares) have mapping coordinates stored in the database, one of which is obviously in error. Automated georeferencing results are shown in white.

The original prototype was based on specimen georeferencing of plants from the Malesian region. However, intensive collaborative interest in georeferencing tools has recently widened the geographic scope of the project to include Australia, through the NSW node of the AVH project. The MaNIS project has recently also started testing the prototype to pre-process mammal biological collections. A georeferencing service has been made available to the MaNIS project through a CGI portal (Beaman 2002) that accepts biological collection data in delimited text format and returns georeferencing results in tab-delimited format.

The automated georeferencing process

The multi-step process involves:

- Pre-processing text for language, locale or project specific anomalies (eg. standardising abbreviations).
- Phrase analysis – the description is compartmentalized by punctuation, prepositions, and stop words into separate phrases. Each phrase is analysed independently.

- Text parsing and pattern matching using regular expressions will involve detecting feature types (e.g., National Park, Island), place names, and their inter-relationships. The web-based prototype (Beaman 2002) queries USA places names from a Geographic Names Information System (USGS 1997). These data are stored locally in a PostgreSQL database.
- Calculation of geographic offsets (e.g., 2.5 km WNW of …).
- Returning results. For the MaNIS project this is done as delimited text. In addition, a PERL/CGI/SOAP interface is currently being designed (by one of us – RSB) for interoperability with *Lifemapper*.

Results of initial tests for MaNIS data from San Bernardino and Placer counties in California (USA), representing the collective data for 17 institutions, are summarised in Table 3 (below). The automated georeferencing results from two samples data sets queried from *The Species Analyst*. A preliminary comparison of the automatically georeferenced Placer County data with georeferences determined manually shows that the mean deviation between results is 0.037 degrees, or about 5.4 km at the latitude of the County. Multiple place-name matches may indicate a higher level of ambiguity in the original text expression. Automated georeferencing of terrestrial vertebrates and birds accurately georeferenced 77–87% of the collections sampled (Table 3), with only 12–26% unable to resolve the descriptive locality because more than one possible georeference was possible (Table 3). These initial tests show that the prototype specimen georeferencing web service is quite promising, but further development and analysis of the results are required to improve the accuracy of the protocol.

Table 3. Summary statistics from automated georeferencing sample data.

Collection(s)	Taxonomic Group	Records tested	Records matched	Records with > than one match
MaNIS	Terrestrial vertebrates	4973	3829 (77%)	861 (17%)
Cornell	Birds	10000	8125 (81%)	1009 (12%)
Univ. of Michigan	Birds	7861	6917 (87%)	2029 (26%)

Conclusion

Individual institutions housing biological collections typically lack the resources or informatics expertise to meet the challenges of georeferencing alone. A community-wide georeferencing solution, equally accessible to all collection-holders, will provide cost-effective added value through economy of scale. Given the scope of both the specimen locality data and the demand for it in a readily usable form, efficiency and accuracy are of prime importance in the task of georeferencing. A multilingual, automated solution that is accessible to individual data providers as well as being interoperable with existing data networks and digital gazetteer services will offer the greatest possible benefit. The solution will need to encompass natural language processing (geo-parsing) to interpret descriptive localities, place-name lookup to register localities with known geographic coordinates, error analysis to self-document uncertainties in the resulting geographic descriptions, and data validation tools with which to analyse the results of georeferencing determinations.

The methodology has shown initial promise for georeferencing biological specimen data, as indicated in Table 3. Based on success rates of up to 87%, future enhancements will initially build upon this model. Research on self-learning for the text parsing module is planned, providing for greater extensibility into other languages. Development will be tailored to the biological collections community through web services made interoperable with other biodiversity community analysis and visualisation applications. Most significantly, error analysis and validation need to be included as integral components of these services. Furthermore, error analysis and validation provide extensive opportunity for testing and further refinement of the geoparsing engine.

The ultimate goal of the project (via the *BioGeoMancer* project, Beaman 2002) is to provide georeferences for natural history collections in a biological context. The research and development for the *BioGeoMancer* project will encompass several research areas within the digital libraries framework. These areas include

- Natural language processing
- Geospatial integration
- Spatial error analysis
- Linkage between geospatial base data and biological classification
- Interoperability between organizations with discordant data standards
- Scalability

In order to achieve our goal, we have assembled a collaborative partnership that provides links to several disciplines: botany, zoology, biodiversity informatics, and computer science engineering. Although the *BioGeoMancer* partners have developed expertise in many disciplines independently, this project provides a unique opportunity to combine resources in a cohesive, productive manner.

Acknowledgments

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Information standards in botanical databases – the limits to data interchange

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Abstract

Conn, Barry J. (Royal Botanic Gardens Sydney, Mrs Macquaries Road, Sydney, NSW 2000 Australia). Information standards in botanical databases – the limits to data interchange. Telopea *10(1) 53–60.* Computers and databases are generally intolerant of inconsistency. Strict standards in data structure and content are necessary to ensure effective management and retrieval of information and communication between databases. The problem in taxonomic botany is not the lack of standards but that there are so many of them from so many different sources that knowing which ones to choose for a particular database situation is difficult. The choice between alternative, competing and often contradictory standards is confusing and can require substantial time in the development of botanical database applications. Botanical databases have been developing rapidly in functionality and content over the past two decades, drawing on international and local standards from other disciplines and creating standards of their own. This paper discusses the practical difficulties of implementing the 'Herbarium Information System and Protocols for Interchange of Data' (HISPID) including problems associated with: data dictionary variants within the standard; implementation of localised standards and styles; data processing errors and impact on data transfer scripting programs; professional work preferences (particularly, the conflict between data capture versus data interpretation, and published versus unpublished data).

Introduction

The Taxonomic Databases Working Group (TDWG) evaluates and endorses standards relevant to biological databases. This Working Group facilities and coördinates the development of new standards when these are needed. The use of such standards is critical to the success of any collaborative *Flora Malesiana* information management project, as it has been for the developing *Australia's Virtual Herbarium* project (Barker 1998). However, the consequence of strict prescriptive adherence to rigid standards is that although it ensures consistency, it constrains innovation. Therefore, a balance between strict adherence to standards and the flexibility offered by non-standardised applications is required. Innovation results in new applications and improved ways of managing botanical data. However, the continual search for improvements reduces the usefulness of standards.

This paper uses as a basis for its discussion the 'Herbarium Information System and Protocols for Interchange of Data' (HISPID) (Croft 1989, Whalen 1993, Conn 1996, 2000).

Institutional abbreviations follow Holmgren et al. (1990).

Importance of Standards

As for other disciplines, data standards provide the common language, rules and protocols for the sharing and interpretation of information. Herbarium collection databases have attempted to incorporate these standards into the structure and management of electronic collection information. However, even when existing databases are unable to comply with the standards, the data interchange protocols (in this case HISPID) have been developed to employ these standards as the common interchange 'language'. For example, even though most Australian herbaria record date information in the form of either DDMMMYYYY (namely, 02 Sep 1978) or DDMMYYYY (02/09/1978), these data are interchanged in HISPID format according to the International time notation (ISO 8601, 2000) of YYYYMMDD (namely, for the above example, 19780902) [HISPID field transfer codes[1] *cdat, cdat2, credit, loadat, texcdat, texvdat, vdat*]. Nomenclatural standards (rules and protocols) (Greuter et al. 2000, Trehane et al. 1995) and standard author abbreviations (Brummit & Powell 1992, Brummit & Davies 1998-) have provided an important framework for referring to plant names within databases. Bisby (1995) developed a specific database information model for plant names to cope with nomenclatural data within a database. Other standards that have been incorporated into database structures or interchange protocols include:

- standard abbreviations for scientific publications (Bridson & Smith 1991; Lawrence et al., 1968; Stafleu & Cowan 1976-);
- official organisational abbreviations (Holmgren et al. 1990) [HISPID – *don*]; and a standard for recording relationships between plants and places (WCMC 1995) [HISPID – *posnat, poscul* and *posint*];
- 'Dublin Core' metadata that have been incorporated into the HISPID transfer protocols for describing multimedia resources (Anonymous 1996);
- transfer of spatial data based on the 'Spatial Data Transfer Standard' (Anonymous 2002). The 'Australian and New Zealand Land Information Council' (ANZLIC) has supported this spatial standard (ANZLIC 2002) for use in Australia and New Zealand.

One of the strengths of the HISPID interchange standard is that it has been able to draw on the expertise incorporated into the many specialised international standards. The actual transfer format of HISPID is based on the 'Abstract Syntax Notation One' standard (ISO/IEC 8824, 1990) that aims at specifying data used in communication protocols. However, the difficulty of incorporating so many standards into a single standard is that they are frequently not completely compatible. Furthermore, some important standards appear to be of limited long-term value. For example, the geographic scheme for describing plant distributions (Hollis & Brummitt 1992) appears to have been largely superseded by more modern geographic information system schemas. The 'Open GIS Consortium' is an industry association that provides a consensus process for adopting spatial data specifications for interfaces and protocols that enable interoperable geoprocessing services, data, and applications (OGC 2002).

Sharing of electronic accession data

The need to manage the storage and retrieval of Australian biological data was first recognised in the 1970s as an important requirement for exchanging data between institutional datasets (Busby 1979). The 'Australian Biotaxonomic Information System' (ABIS) was proposed as a distributed database model, with data management being the responsibility of participating agencies (*loc. cit.*). The ABIS standard was a refinement of the core data standard developed by the 'Australian Biological Resources Study' (Underwood 1975). ABIS standard was further developed through usage by the Australian Museum, the Queensland Herbarium and the Western Australian Museum. Potential participants in ABIS were also involved in its development. The need to share electronic data between herbaria was more generally

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[1] Note: The three- to seven character abbreviations (in italics) refer to the transfer codes used in tag-formatted HISPID3- and HISPID4-files (Conn 1996 & 2000, respectively).

first recognised by the major Australian herbaria in the 1980s. HISPID was first published in 1989 to provide a standard electronic interchange framework for herbarium collections information (Croft 1989). The rationale for sharing electronic herbarium data between Australian herbaria was based on concerns about unnecessary data-entry of replicate material held at each herbarium. This replication of effort not only introduces potential data processing errors, but it also consumes considerable personnel and financial resources, as well as time (Conn 1998). The detailed analysis of data-entry costs provided by Conn (1998) clearly illustrates the financial savings resulting from minimising the unnecessary data processing of the same herbarium label information held in several institutions.

HISPID is a tag-formatted accession-based interchange data-dictionary, even though many fields also refer to taxon-level attributes, such as nomenclature, bibliographic, and typification data (Whalen 1993; Conn 1996, 2000). The botanic gardens community has implemented a similar interchange format (Wyse Jackson et al. 1997). Although HISPID is concerned primarily with electronic data exchange, it has often also been used as a guide in developing database structure. Those agencies that have closely aligned their databases with the standard have been able to readily import and export data using HISPID. Currently, HISPID4 (Conn 2000) is being redrafted as an XML-formatted standard (refer HISPID5 Standard – http://sourceforge.net/projects/big). In part, this will overcome the challenge that HISPID4 presents for data managers, namely, the need to interchange data in a flat-file format. The new HISPID standard will improve the transfer of nested information and repeated elements, such as verification history of the plant name [HISPID – *vhist*] represented by the record.

Data dictionary variants within HISPID

The *Council of Heads of Australian Herbaria* (CHAH) based the development of HISPID on a list of core interchange data fields then recognised. There was unanimous agreement on some core fields, such as the plant name fields; however, other fields included in the standard reflect components of the various CHAH databases. This compromise solution resulted in different ways of transferring some of the same data components. Therefore, even though agencies may be HISPID compliant, data from one database may be difficult to import into another. For example, altitude data (in metres) held in the *NSW Collections* database of the Royal Botanic Gardens Sydney (NSW), including the National Herbarium of New South Wales, is stored as a single value with an associated accuracy field (in metres). Whereas, the *ADHERB* database of the State Herbarium of South Australia (AD) records these data in two fields that represent the altitudinal range of the collection; one for minimum altitude, the other for maximum altitude (both in metres). Therefore, the *NSW Collections* database stores the altitudinal range values of 300 m [minimum altitude: – HISPID transfer code – *alt*] to 500 m [maximum altitude: HISPID – *altx*] from *ADHERB* as an altitude of 400 m [HISPID – *alt*], with a precision code of 100 m (ie. ± 100 m) [HISPID – *altc*]. Although both methods are HISPID compliant, both require conversion by data load scripts prior to incorporation into the other database. Some databases (eg. *MELSIR* – National Herbarium of Victoria and *NSW Collections*) use the aggregate field concept of 'Collection Notes' [HISPID – *cnot*] to store habit/life form, frequency, phenology and other miscellaneous notes about the plant. These data can be transferred either in aggregated form [HISPID – *cnot*] or as the component fields of data [HISPID – *form, fre, phe, misc*]. Both formats are supported by HISPID. However, data sent in either formats may well be stored differently by recipient institutions. Such reorganisation of the data is liable to introduce errors.

Components of descriptive spatial data are another example of alternative data transfer definitions within the HISPID standard. In particular, the transfer of primary recording units (= *pru*) (eg. States or Provinces of Countries) and secondary recording units (= *sru*) (eg. subdivisions of States or Provinces) have two alternative possible formats. Valid values of *pru* are defined as either "... in full or [in] standard abbreviations accepted by ..." (Conn 1996, p. 66). Likewise, the latter field (*sru*) is defined as "written in full or any valid regional code or abbreviation ... (*ibid.*, p. 67). Obviously, a local convention of using abbreviations will result in difficulties for an agency that expects the data in an unabbreviated form. Although the *HERBRECS* database of the Queensland Herbarium (BRI) stores unabbreviated *sru* values, this database appends this information with the qualifier 'District'. For example, *HERBRECS* records 'Burnett District' and 'Gregory District' for two of the official subdivisions of Queensland. These *sru* values are stored in *NSW Collections* database (NSW) as "Burnett" and "Gregory", respectively, without the word "District".

Localised standards and styles

Modifications to an international standard such as HISPID are frequently introduced for a specific, albeit localised reason. Most of these are style format changes that do not impact on the standard; however, some changes do affect the ability to exchange freely data using HISPID. For example, *NSW Collections* capitalises the Family name of the plant record. Other databases (eg. *ANSHIR* of the Centre for Plant Biodiversity Research, Canberra – CANB) use normal sentence case for the plant family name of the record. Although NSW's use of upper-case is only for emphasis, especially when printed on herbarium labels, it means that data load scripts need to account for these data exchange variants.

The *ADHERB* database (AD) uses curly braces "{" and "}" in two different ways. These braces are used to convert the "+" symbol into "±" to represent 'approximately', as in "{+} 8 miles N of ...". This would be printed as "± 8 miles N of ..." on the herbarium label [descriptive locality field: HISPID – *loc*]. The other use of these braces is to enclose text that is to be emphasised by under-lining when printed, eg. "Open {Eucalyptus deglupta} Forest ..." (= Open Eucalyptus deglupta Forest ...") [habitat field: HISPID – *hab*]. The potential problem with the use of these curly braces for data load scripts is that they are reserved as special HISPID standard notation that defines the start of a record (namely, "{") and end of a record ("}"). Therefore, the load scripting has to be sufficiently robust to handle braces that occur within records.

In general, non-standardised abbreviations (with respect to national or international standards) have consequences on data quality within databases. Incoming data needs to be aligned with local database rules by data load scripting. However, inconsistency of data-entry frequently result in abbreviation variants, even though the local syntax is well-understood by the data-processors. Although the accepted protocol in *NSW Collections* is to minimise the use of abbreviations, variants are prevalent because of data-entry inconsistencies. Therefore, both approaches require comprehensive data load scripts to standardise the abbreviations according to the data standard of the local database. Common abbreviations and their variants include: TO, T/O (referring to 'turnoff', an Australian colloquialism for road junction; S, Stn ('station', referring to either an agricultural grazing lease or a railway station; HS (mostly referring to a 'homestead', including the land associated with the home, of a grazing lease, but sometimes referring to a High [Secondary Education level] School); R, Rd (the former usually referring to 'river', but both are used to mean 'road'); SF, S.F. (State Forest reserve); NP, N.P., Nat. Park, Natl Park (National Park reserve). More localised abbreviations that are often difficult to expand are used by particular disciplines TR, T.R. (Timber Reserve); LA, L.A. (logging area); Compart., Cpt. (Forestry compartment area of a timber reserve); dbh, d.b.h. (diameter [of tree trunk] at breast height).

Database structure

The length of database fields frequently causes problems when data are transferred from one institution to another. For example, *Texpress* (KE Software) databases as used by AD, MEL, PERTH and, in part, *EMu* (KE Software) databases (as used by NSW) have fixed length fields that frequently truncate incoming data because of longer field lengths. This is a widespread problem since fixed length fields are the norm for almost all database management systems (eg. also in ORACLE® database systems as used by CANB and DNA). Truncation can result in a corruption of data without appropriate data load scripting and possibly database restructure.

Data entry and data transfer scripting errors

Naturally, data transfer scripts are generally unable to automatically handle data-entry errors without a detailed examination of the data transfer file. This is less of a problem for databases that have highly atomised fields compared to those that group disparate information into single fields. As an example of a potential data load problem, the *MELSIR* database (MEL) is able to store the names of more than one collector in the database's collector's name field. If this information is not separated into the two transfer fields [HISPID – *cnam* and *cnam2*], when exported, then data load scripts will fail during the importing of these data. Likewise, some databases (*eg. MELSIR*) group the abbreviations of the institutions receiving replicate material of a particular record into a single string, according to a defined syntax. The transfer field [HISPID – *desrep*] expects the format to be 'organisation abbreviation1,[space]organisation abbreviation2,[space]organisation abbreviation3,[space] …'. If this format is inconsistently modified within a database during data-entry, then it is difficult for either of the data transfer scripts to correct automatically these modifications. Finally, errors in the export data transfer scripting, especially if related to records that are not in the HISPID-format, are difficult for data load scripts to correct reliably and automatically.

Sociological impediments to data interchange

The exchange of information between herbaria is as old as the exchange of herbarium material itself. However, the exchange of this information in an electronic format has been hampered by an inability of herbaria to donate and receive these data. Prior to the development of HISPID, this was certainly true for herbarium collection information. Indeed, it is still true for taxon-based information. For example, the database information model for plant names developed by Bisby (1995) does not provide an adequate framework for the transfer of botanical nomenclature. However, there are other than technical reasons why the interchange of data continues to be difficult. The reasons given are many; the need to protect the locality of sensitive taxa, regain the financial cost of generating these data, protection of intellectual property held within the data, and more generally, the protection of unpublished information. However, there are a few additional underlying fundamental reasons that impede the ready interchange of digital data. Two frequent reasons include the: (1) conflict that arises between data capture and data interpretation, and (2) status of published and unpublished data. Although these impediments are not directly related to conflicts between the application of data standards, they represent different philosophical approaches to the handling of data and information.

Data capture versus data interpretation

One of the most common conventions enforced on the data-entry process of herbarium label information is the almost universal requirement of capturing these data without modification or interpretation. There are two main reasons why this is regarded as important. Firstly, an electronic record of what the collector actually recorded is regarded as of historical importance. For example, the spelling of many place names has changed over time. Changing these spellings to modern equivalents looses the historical component of the data. Secondly, interpretation of the information is regarded as increasing the likelihood of introducing errors. Attempts to 'compartmentalise' text strings into separate data fields, particularly those describing habitat preferences and plant features, may be extremely difficult to do without changing or corrupting the intended meaning. The use of the square bracket notation (namely, "[" and "]" has been successfully used to identify text modified by the data processor. However, frequently, data interpretation is not done and this can significantly reduce the usefulness of this information. For example, there are currently 27 database records in *NSW Collections* database that record the collector as 'P.G. Wilson'. In Australia, there are two well-known collectors with these initials (namely, Paul G. Wilson – formerly of the Western Australian Herbarium, PERTH and Peter G. Wilson – National Herbarium of New South Wales, NSW). Although most, if not all of these records refer to collections made by the latter, the longer the collector's name is not fully identified, the more difficult it will become. The *MELSIR* database (MEL) has more than 200 database records that refer to the plant collector as 'P.G. Wilson' (P. Neish, *pers. comm.*, 14 October 2002). In this case, most appear to refer to 'Paul G. Wilson'. All of these records are fully HISPID compliant with respect to this data field. Digital images of the botanical specimen, together with any label information and handwritten notes may provide an affordable solution that maximises both integrity of original data and usefulness of electronic data.

Published versus unpublished data

The traditional form by which we share botanical information has been, and continues to be, through publication in paper-based scientific journals and books. Unfortunately, this very limited definition of publication has not been readily expanded to include digital information. In the case of information held within botanical collections, it is assumed that the botanical object needs to be examined so that herbarium label information and other details can be accurately assessed by the user. Indeed, this is probably almost always true for certain applications of this information. Botanical specimens are readily shared between herbaria around the world for professional systematists to examine. This is regarded as an essential activity of all major herbaria. However, the sharing of the collector's information, contained on the herbarium label, in an electronic format raises concerns of ownership and ultimate usage. Although, the concerns appear to be greatest when data requests are made by the general community, commercial environmental consultants and other government agencies, these concerns also exist when electronic data are made available to colleagues at different agencies. Likewise, copyright concerns are actively and vigorously debated when these herbarium collections are presented as digital images, but not when available as physical collections *per se*. The reason for these differences of opinion, based on the nature of the information, is somewhat elusive. However, it may have something to do with our concerns about the lack of rigour in primary scientific data. I suggest that professional botanists are uncomfortable with exposing errors, from typographical to botanical identifications, to our colleagues and the broader community. In particular, the general community is probably unequipped to deal with, or allow for, these errors while using the data.

Paper-based publishing is a very structured (standardised) interactive process between writer, editor and publisher. Paper-printed scientific journals and books are remarkably uniform in structure (format and layout). However, in the botanical world, electronic publication of data (here, including the presentation of digital data as a form of publication) has not involved the general botanical community; but rather, the development has been handed to specialist technical computer experts and linkages to a few botanical specialists. Although it is far from true, there is a tendency for the general botanical community to assume that digital media are largely free-form, unstructured, rapid and not based on international standards. The lack of perceived standards ('controls') reduces electronic data to the status of 'work-in-progress'.

Finally, there is a strong concern that these data will be used by a third party to form the basis of other publications without due recognition of those involved with their creation. This has already happened on many occasions. Although, plagiarism has always been a concern, albeit minor, in all disciplines, measures are in place for controlling the inappropriate use of other workers' information. The more frequent use of joint publications is also providing a solution to this concern.

Conclusion

There is a need for the acceptance of digital data formats as an equally valid information medium for researchers and the general community alike. Data interchange standards are required as the framework for sharing these data. Conflict between available standards must be minimised so that information can be readily transferred between users. Since community groups, at least within Australia, are responsible for the health of the environment, they are demanding access to data and information that was previously only available to professional scientists. Technology is able to deliver these data and information rapidly and in many formats. The challenge for the professionals is to provide supporting explanation, documentation and caveats to assist the community to correctly derive and interpret this information, within the limits of these data sets. An additional challenge for those involved with the free transfer of electronic data is that although data interchange standards were first recognised as important 20 years ago (from 1973), the free exchange of these data has still not been fully realised.

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The role of indigenous parataxonomists in botanical inventory: from Herbarium Amboinense to Herbarium Floresense

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Abstract

Pfeiffer, Jeanine[1,2] *and Yeremias Uril*[3] *([1]Ethnobotanical Conservation Organization for Southeast Asia (ECO-SEA), Post Office Drawer 1710, Davis, California 95617 USA; [2]University of California at Davis, Graduate Group in Ecology, Pomology Department, One Shields Avenue, Davis, California 95616 USA; [3]Pusat Penelitian dan Pendidikan Masyarakat Tado (P3MT), Kotak Pos 3, Labuan Bajo 86554, Nusa Tenggara Timur, INDONESIA) 2003. The role of indigenous parataxonomists in botanical inventory: from Herbarium Amboinense to Herbarium Floresense.* Telopea *10(1) 61–72.* The enormous taxonomic scope of the Flora Malesiana Project is exacerbated by the extremely short supply of trained researchers and taxonomic experts available to undertake this task. The vast number of indigenous botanical experts resident in Malesia represents a potentially valuable, yet largely unrecognised and untapped, resource. By engaging in collaborative research with indigenous parataxonomists, Flora Malesiana researchers can develop field methodologies that enable a more comprehensive and accurate assessment of the botanical resources of the region while simultaneously enrolling local communities in the sustainable, long-term conservation of native biocultural diversity. This paper outlines a number of projects involving indigenous research associates, discusses the advantages of developing a network of parataxonomists, and details ways in which botanists and ecologists can incorporate indigenous expertise into biological inventory and conservation.

The connection between historical and contemporary herbaria collections

Three hundred years following the death of Malesia's most famous ethnobiologist, Rumphius [Georg Everhard Rumpf], the first Eastern Indonesian herbarium to be run by an indigenous community was inaugurated by the Tado clan in a small, thatch-roofed and bamboo-walled building in the southwestern corner of Flores Island. The Tado are the fifteenth generation descendents of Sulawesi islanders who emigrated from the Makassar sultanate to the Bima sultanate sometime during the 16th or 17th century. Rumphius, the author of *Herbarium Amboinense*, relied heavily on the knowledge and expertise of the Tado's ancestors during the 17th century to complete his ethnobiological treatise on the region's biodiversity and ethnoecological traditions. In a unique historical reversal, the descendents of those early ethnobiological informants are now curating their own herbarium as part of a larger project to research and conserve their native biocultural diversity and traditional ecological knowledge. In this paper we assign the temporary name 'Herbarium Floresense' to this new herbarium and research project in order to highlight the parallels between the historical and contemporary involvement of Malesian indigenous communities in botanical inventory. The actual name of the site housing the Tado herbarium, ethnobotanical museum, insect collection and resource library is the Tado Community Research and Training Center (*Pusat Penelitian dan Pendidikan Masyarakat Tado*), part of the Tado Cultural Ecology Conservation Project (*Proyek Konservasi Budaya dan Ekologi Masyarakat Tado*).

The Tado Cultural Ecology Conservation Project, or TCECP, is the flagship project of the California-based ECO-SEA (Ethnobotanical Conservation Organization for

Southeast Asia), a non-profit organization focusing on conservation education, ethnoecological research and institutional strengthening. ECO-SEA prioritises partnerships with local, national and international colleagues on collaborative ventures stressing the equitable sharing of responsibility and benefits. In practical terms, this translates into consortium-based project management teams where local community members have equal standing with national or international researchers. Our research teams, composed of both literate and non-literate collaborators, operate within interdisciplinary programs where data is collected, analysed and critiqued by both informants and researchers; seminars and publications are jointly authoured and published; and financial and material resources are equally and transparently shared.

In this article we employ the term 'parataxonomist', a term coined by Daniel Janzen (Janzen et al. 1993) and related to similar terms (e.g., parabiologists, paraecologists) used by ethnoecological projects (Nabhan 2000) to indicate individuals whose specialisation is based primarily on empirical, rather than academic expertise. An indigenous parataxonomist is an individual native to the area in which the specimens or data are being collected who is intimately familiar with the local flora and fauna, and who conducts biodiversity inventories with support from national and international scientists. Parataxonomists work in parallel with taxonomists in collecting, photographing, sorting, preserving and analysing specimens and data, and carrying on the field and laboratory work locally while maintaining contact with taxonomists. In the pages to follow we present a number of case studies where indigenous parataxonomists play a critical role in generating local community support for regional biodiversity conservation networks.

A predominant theme articulated at the Fifth International Flora Malesiana Symposium in Sydney (2001), by plenary speakers from throughout the bioregion, concerned how the overwhelming nature of the ongoing taxonomic inventory of Malesian flora was exacerbated by the extremely short supply of trained researchers and taxonomic experts available to undertake this task. Given current estimates of the taxonomic scope of the Flora Malesiana project (c. 41 500 plant species), the taxonomic expertise available (around 130 voluntary collaborators), the average productive lifespan of a given individual (approximately 40 years), the time required to complete a taxonomic monograph for a single species (1–12+ months), and the current rates of habitat destruction in the region, we are literally running out of time. Either the current project collaborators will need to be reincarnated several times over to complete the inventory, or Flora Malesiana is in desperate need of a wider network of collaborators if the project is to be completed within our collective lifetimes.

This point is not new—many of us have made similar ironic calculations—but our intellectual hand-wringing is usually conducted within the hearing of our English-speaking, academically trained colleagues. We have not been thinking, or acting, very far 'outside the box.' Given the additional pressing concern that we may be losing an unknown number of species resulting from the ongoing loss of natural habitats in the region, perhaps it is time that our recruitment strategies—the means by which we attract and retain voluntary collaborators—undergo revision. The vast number of indigenous botanical experts scattered throughout the Malesian region—and here we refer primarily to individuals living in rural communities—represent a potentially valuable, yet largely unrecognised and untapped, resource. Yet for almost two millennia, beginning with local inhabitants of the Mediterranean who provided baseline data for the 600 plants described in Dioscorides' *De Materia Medica* in 77 A.D., indigenous peoples have provided substantive source material for taxonomic research. The empirical importance of indigenous expertise to biodiversity studies as specimen collectors, guides and interpreters of local environments is evident in thousands of published works from naturalists such as Rumphius in the 17th century, Linneaus [Carl von Linné] in the 18th century and Alfred R. Wallace in the 19th century. These naturalists relied heavily on indigenous ecological knowledge as a basis for their systematic and theoretical treatises. Ellen and Harris (2000) note that Rumphius' seminal work, *Herbarium Amboinense*, relied in large part on 'indigenous descriptions of plant ecology, growth patterns and habits,' and that Linneaus 'fully adopted the Cochinese classification and affinities in establishing 240 entirely new species' (Ellen and Harris 2000, p.10). Indigenous residents have also played a critical role in 'scientific' discovery. Some of the more well-known cases include Joseph Arnold's 'discovery' of *Amorphophallus* and *Rafflesia*: in both cases, he was led to the plants by native guides (see Bastin 1995 and Zuhud et al. 1998). As Zuhud et al. (1998, p.1) note: '*walaupun* Rafflesia *telah dikenal oleh penduduk pribumi, akan tetapi deskripsinya ditulis oleh seorang naturalis berkebangsaan Inggris* (although *Rafflesia* was well known by native inhabitants, its description was published by a British naturalist).'

The Malesian bioregion is best documented through long-term, repeated, intimate in situ contact, a practice that is rare among many of those who are affiliated with the 'Flora Malesiana' project. Indigenous experts are frequently sought out by Flora Malesiana researchers to act as guides, informants, and/or collectors, but their contributions to the project are usually curtailed when the researcher departs. Given the difficulty many botanists experience in attempting to collect fertile specimens within the extremely limited time most of us are able to spend in the field, versus the phenological realities of the flora we are attempting to collect (i.e., the sporadic flowering nature of many tropical species), it makes sense to involve local, long-term residents in herbarium specimen collection. Once a specimen is tagged by the botanist, local residents trained in specimen collection and curation—especially farmers, many of whom manage a complex portfolio of varied agricultural plots scattered across several ecosystems—could periodically check on the given plant, and collect the flowers, fruits and seeds when the plant enters its reproductive phase.

Locally trained residents can also provide valuable ecological data for species requiring long-term in situ study. The ecology of intermittently flowering or fruiting plants or those with exceptionally lengthy dormancy periods are difficult to investigate, and hence be understood, by temporarily resident or transient researchers. The familiarity of local residents with the native environment of taxa collected for ex situ conservation is also a valuable resource for scientists attempting to replicate the growing conditions (including associated vegetation, symbiotic organisms, soils and microclimatic conditions) in botanical gardens far removed from the plants' origins.

For those of us focusing on ethnobotanically useful plant species (e.g., plants employed for nutritional, medicinal, social, ceremonial, environmental, agricultural, utilitarian or other economic purposes), the expertise of local residents is the starting point for any ethnobotanical inventory. Thousands of ethnobotanical studies published worldwide for the past millennia, including more recent treatises on the extent of native pharmacoepias (Kreig 1964, Plotkin 1993) have relied on indigenous experts for their baseline data. Yet the authors of such studies are not the owners of the knowledge, and it is usually the collectors and translators of the data who receive the credit. Herein lies yet another conundrum facing the Flora Malesiana project. In a recent submission to the *Flora Malesiana Bulletin*, Ng (2002, p. 48) states 'There are almost no contributions from Asian national botanists to the international Flora Malesiana project.' While we would argue this statement underestimates the scientific contributions of national and private universities, herbaria and botanical gardens throughout South-East Asia, the significant disparity between the published taxonomic contributions of 'Western' [non-Asian] botanists versus their Asian counterparts is undeniable. This disparity is due to a complex range of historical, socio-political and economic factors beyond the scope of the 'Flora Malesiana' project, but many of those factors (e.g., an inequitable distribution of resources, among others) are present within current conservation projects and continue to perpetuate an inequitable representation of indigenous experts.

The stark contrast between the relative scarcity of scientific resources available to national researchers resident in the centres of floristic biodiversity (in this case we refer to the nations in the Malesian region) versus the wealth of scientific resources available to researchers residing outside the Malesian region was most poignantly illustrated by the plenary presentation at the Fifth International Flora Malesiana Symposium by Osia Gideon on the current state of affairs in Papua New Guinea. Administrative divisions of Papua New Guinea containing floral megadiversity are served by herbaria staffed by a handful of technicians, and an even smaller number of researchers. Despite the impressive volumes of published taxonomic works completed on Papua New Guinea by a number of experts (many of whom were sitting in the audience during the presentation), there is not a corresponding number of trained national researchers who are able to put these taxonomic works to good use. The question begs to be asked: what good are shelves of books and dried specimens stored outside of Malesia, if we fail to make a sustainable investment in the personnel critical to maintaining the wealth of flora inside Malesia? A more proactive approach to human resource development is called for: one example of such an approach can be found in the Parataxonomist Training Center (located in Madang, Papua New Guinea), which is discussed later in this article as a potential template for similar activities within the Flora Malesiana project. (This example, along with our own work, addresses one of the many challenges faced by researchers in the Malesia region: for a more complete treatment of the impediments to flora documentation and conservation in New Guinea, see Conn 1994.)

As scientists, we frequently bemoan the ongoing loss of native habitat and biodiversity, yet note in the same breath that we do not have enough time or resources to simultaneously conduct our research and actively manage conservation projects. A way of achieving both goals involves making a judicious investment in the training and support of locally based counterparts so that they can continue the field research long after the national or international researchers have left the field. By relying primarily on local personnel and materials, successful community-based collaborations are also extremely cost-effective, enabling a more efficient use of limited funds. By engaging in collaborative research with indigenous parataxonomists, Flora Malesiana researchers can develop field methodologies that not only enable a more comprehensive assessment of the botanical resources of the region, but also enroll local communities in the sustainable, long-term conservation of native biodiversity. Indigenous agrarian communities throughout the Malesian region are facing cultural extinction, a process paralleled by the loss of biological diversity on their ancestral lands (Sponsel 2000). As the following section illustrates, many indigenous communities have a deep-seated, long-term interest in documenting and conserving their native biological diversity as a means to ensuring their cultural survival.

The role of indigenous communities in conserving biological diversity

The Malesian bioregion is renowned not only for its tremendous biodiversity, it is also home to enormous cultural diversity: around 1 900 languages (Grimes & Grimes 2000) are spoken by several thousand ethnic groups inhabiting the region. Each ethnic group is familiar with, and makes use of, different plant assemblages. In addition, each ethnic group has a distinct set of names for the plants used in their culture. Although this linguistic diversity can be a logistical nightmare for a newly arrived botanical researcher (see the following section), the recognition and retention of local biological nomenclature is one of the critical steps to conserving both biological and cultural diversity. The naming of native plant taxa is critical to the maintenance of traditional ecological knowledge and local biological diversity: plants that are locally recognised and/or utilised by resident communities are more likely to be conserved, whereas unknown plants are more vulnerable to accidental loss. In turn, conserving the biological reference points for traditional ecological knowledge (e.g., the taxa associated with the knowledge) helps conserve the cultural history of the indigenous community whose cultural traditions incorporate native plants and animals.

Indigenous agrarian communities practicing swidden ('shifting' or 'slash and burn') cultivation in the tropics are frequently faulted for exacerbating habitat and biodiversity loss (Sponsel et al. 1996), but are rarely recognised for their role in maintaining or enhancing species diversity (Barsh 1999). Indigenous peoples have a history of bringing rare plants into cultivation in order to maintain them (Alcorn 1993), or in tending useful herbaceous plant populations in situ (Anderson & Rowney 1999), promoting population viability and abundance. Backes (2001) and Carrière (2000) have documented the role played by smallholders managing agroforestry systems (homestead gardens, hedgerows, living fences, swidden fields) for the in situ conservation of indigenous trees. Michon et al. (1986) and Aumeeruddy (1995) noted the high species diversity of community-managed agroforestry systems in Sumatra, and the 'natural forest' functions performed by these systems as gene banks and stabilisers against erosion. In describing Ka'apor indigenous forest management in eastern Amazonia, Balée (1994) graphically demonstrated Ka'apor contribution to regional biodiversity: tree species richness in Ka'apor-managed secondary forests following fallow was not significantly different from that of mature forest, and both managed and unmanaged forests accumulated diversity at similar rates. Salick et al. (1999) found a direct relationship between biodiversity maintenance and knowledge of useful plants among the Dusun of Kalimantan (Indonesia).

Indigenous peoples have accumulated several centuries' worth of observational data, much of which is being lost as species become extinct and diverse ecosystems are transformed into monocultures. The efforts to conserve biodiversity need to be in parallel to efforts to conserve traditional ecological knowledge. Senior residents in Eastern Indonesia who can identify an average of 700 plant species (Verheijen 1982) and their associated uses are dying out, while many of the remaining community members find it difficult to recognise any but the most common plants and/or describe the ancestral medicinal and ceremonial practices related to those plants. Researchers working with indigenous communities throughout the Malesian region have published hundreds of studies, but due to the habit of most researchers to work in relative isolation, publish off-site and constantly move on to new areas (Milius 1998), the indigenous owners and managers of this biocultural wealth are often left without the means or methods to effect long-term conservation of the taxa and traditions which are an intrinsic part of their heritage. In the following section we will cite examples of collaborative ventures that involve local communities in the research and conservation of biocultural diversity, and discuss the benefits and challenges of such ventures in greater detail.

Possibilities and challenges in working with indigenous parataxonomists

As we noted above, despite the widespread acknowledgement of traditional ethnoecological expertise (Slikkerveer 1999), indigenous peoples have rarely been recognised for their potential methodological and theoretical expertise in research and analysis of their ancestral ecological and cultural systems. An efficient means to collecting baseline ecological data involves long-term collaborative research with resident indigenous communities, who can provide extensive empirical data and assist with specimen collection and curation, anthropological and ecological surveys, data interpretation and analysis, and editorial review. Traditional ecological knowledge can be incorporated into classical ecological fieldwork exercises such as ecosystem mapping (Robertson et al. 2000), species inventories (Peters 1996), behavioural studies (including competitive, predatory and mutualistic interactions) and historical reconstructions of past anthropogenic and natural disturbances (Martin 1995).

Some of the specific benefits of involving parataxonomists in botanical inventories include:

(a) The collection of higher quality specimens—locals have the time to wait for flowering and fruiting, thus in our case over 90% of the specimens collected and curated by the Tado are fertile, enabling more accurate taxonomic identification of specimens.

(b) The immediate curation of the specimens (drying, pressing and mounting). Rather than collecting large amounts of material and storing it uncurated indefinitely, Tado research associates collect smaller numbers of specimens and mount and catalogue the dried specimens and associated field notes within a few days or weeks of their collection.

(c) The collection of much more complete data regarding the phenology, ecology, surrounding vegetation, and ethnobotanical importance of the taxa. Bassett et al. (2000) note that parataxonomists are able to complete far higher numbers of ecological observations than the temporarily resident researcher, and 'Because of the high spatial and temporal heterogeneity of ecological factors in rain forests, high numbers of replicate observations, even at the expense of lower accuracy, are likely to shed light on interesting biological patterns' (Bassett et al. 2000, p. 907).

(d) The collection of more accurate and reliable data, especially for taxa which are incorporated into traditional customs. Ian Saem Majnep, of the Kalam people (Papua New Guinea) notes that an 'insider' perspective is advantageous linguistically (many native research associates are bi- or trilingual), socially (local community members are part of an extensive social network of potential informants, including persons possessing very specialised knowledge) and methodologically (community associates have more time to track down information and confirm its veracity) (Majnep with Pawley 2001, pp. 353–354).

(e) The more rapid publication of scientific papers. Following extensive biological inventories in Australia, Papua New Guinea and Guyana, Basset et al. (2000) reported being able to decrease the time-lag between initial data collection and publishing from six to seven years without the involvement of parataxonomists, to two years after parataxonomists were involved.

The first internationally funded project to employ parataxonomists on a large scale is the Costa Rican National Biodiversity Inventory, or INBio project. Since 1989, INBio has provided vocational training to a 'small army' of lay people as parataxonomists in the fundamentals of biology, ecology, taxonomy, evolution, collection and preservation techniques, administration and equipment maintenance, and information management. The parataxonomists collect specimens in 23 biodiversity stations scattered across the country and bring them to INBio on a monthly basis. Upon receiving the specimens, technicians pass the information on to a larger network of national and international taxonomy experts. As of 2000, 127 138 plant specimens representing some 8700 species had been collected, in additional to several million collections of vertebrates, invertebrates and microorganisms (INBio 2002). By involving local residents in this national biological inventory, the communities benefit both from the employment opportunities and from the informal education provided by the parataxonomists as they disseminate their knowledge to relatives, neighbours, colleagues, and local schools.

Within the Malesia bioregion, the Parataxonomist Training Center in Papua New Guinea has demonstrated the viability of employing indigenous parataxonomists in large-scale, long-term, biodiversity inventories (Novotny et al. 1997). The encyclopaedic ecological knowledge of indigenous Papua New Guineans (reported by Beehler 1994; Majnep with Pawley 2001) has been harnessed for projects affiliated with the Center, and applied to 'the more esoteric ends of basic ecological research' (Basset et al. 2000). By 1997, over 140 000 insect specimens had been collected and processed by projects affiliated with the Center, which was established in 1994 following the initial efforts of Larry Orsak at the Christensen Research Institution in 1993–1997. Researchers affiliated with the Center note that the efficiency of fieldwork of village collectors in Papua New Guinea is 'comparable with that of professional ecologists' and allows for the simultaneous collection of specimens at multiple locations (Basset et al. 2000, p. 905). Their biological inventories 'take advantage of three elements: knowledge of the environment by local people; recent developments in computer hardware (e.g., speed and mass storage), which make digital photography a useful tool available at a relatively low cost; and higher data quality due to the increased number of replicates and side experiments performed by the parataxonomists' (Basset et al. 2000, p. 907).

Establishing a new model for collaborative fieldwork requires a combination of experience, planning and commitment, especially if the cooperating parties are separated by several thousand kilometres and an ocean or two. Finalising cooperative agreements (often critical to obtaining internal recognition and/or external funding), obtaining funding and visas to permit the research of international researchers on native lands (or enabling indigenous associates to attend overseas conferences) requires years of advance planning and a vast network of support personnel in both home and host nations. When a large group of data collectors are involved in quantitative surveys, additional statistical tests must be performed to sort out enumerator bias from actual variation in the data observations.

Initial reliance on local nomenclature for documenting ethnobotanical uses must be augmented with the positive identification of voucher specimens, an essential but difficult task due to the lack of a one-to-one correspondence between most folk taxonomies and botanical species circumscribed according to Western scientific principles (a common occurrence in Indonesia and elsewhere: see Berlin 1992, Wilkie & Saridan 1999) and the infrequent flowering of a number of the tropical forest species. In the past, indigenous knowledge or traditional ecological knowledge systems have been perceived as parallel, but scientifically inferior, observations of the natural world, especially when indigenous classifications do not match the scientific nomenclature. This intellectual elitism is particularly ironic in cases where Western scientists have mistaken anthropogenically constructed ecosystems for 'natural' landscapes, such as the case of forest islands created by the Kayapó in Brazilian savannahs (Posey 1997) or by Kissidougou pastoralists in Guinean grasslands (Fairhead & Leach 1996). Traditional ecological knowledge may prove critical to researchers working on plant systematics, as historical ecologists are revising long-held definitions of 'natural' vegetation assemblages following research demonstrating centuries-old manipulation of semi-domesticated plant taxa by indigenous forest dwellers (Balée 1994). The sophistication of indigenous ecological classifications has been documented in South America by Fleck and Harder (2000) among the Matses, who distinguish 178 rainforest habitat types, and by the work of Shepard et al. (2001) with the Matsigenka, who delineate 69 vegetationally-defined habitats and 29 abiotically-defined habitats. Yet indigenous ecological terminology tends to vary in meaning and precision, and scientists working with indigenous communities need to consider the cultural context of the indigenous knowledge. A recent report comparing indigenous knowledge with external data sources in Chiapas, Mexico (Hellier et al. 1999) resulted in sufficiently contradictory results for the authors to caution against indiscriminate application of indigenous knowledge to biodiversity assessment.

An example of a cross-institutional collaboration

The Tado clan, whose name is derived from the Tado settlement established by a common ancestor (Pongga) six generations ago, reside in two villages (Golo Leleng, and Nampar Macing) in the Sano Nggoang sub-district, Manggarai district, Flores Island, East Nusa Tenggara province (Indonesia). This province contains the lowest population density (averaging 70 persons/km^2) and greatest degree of poverty in Indonesia outside of West Papua (Badan Pusat Statistik 1998; Republic of Indonesia 1991). The island may be poor economically, but it is rich in biological and cultural diversity. The Tado belong to the Kempo Manggarai linguistic group, one of an estimated 30 dialects (Verheijen 1967, 1982) spoken in Manggarai district. There are approximately 25 000 plant taxa in Indonesia (Suhirman et al. 1994), and species belonging to over 180 plant families have been identified on Flores (Verheijen 1982, Kebun Raya Eka Karya Bali 1994, Simbolon 1998). A recent ecological survey of protected lowland and montane forests in the Sano Nggoang sub-district documented 20 new plant species and a large number of local endemics (Trainer et al. 2000). Ethnobotanical studies conducted by the Tado have identified several hundred useful plant taxa, but the actual floristic diversity is still unknown. Tado lands contain thousands of ethnobotanically important plant species that are required by the Tado for their livelihood, culture, nutrition, income, animal feed, medicine, rituals, sport, myths and legends. Tado elders repeatedly note the connection between the cultural survival of the Tado and the conservation of the ethnobotanical traditions and associated flora.

Although indigenous agrarian communities in Indonesia are well recognised for their exceptional ethnobotanical expertise (Sorenson and Morris 1997, Balitbang Botani 1998), community members have rarely been recognised for their potential applied, theoretical and methodological expertise in research and analysis of their own ecological and cultural systems. Prior to the initiation of the Tado Cultural Ecology Conservation Project (TCECP), this disjuncture between the potential and actual involvement of local communities was also evident in the area we work in. The extensive botanical work in southwestern and central Flores by two long-term resident priests of the Societas Verbi Divini (SVD) order, namely, Fr. Jilis A.J. Verheijen (1967, 1982) and Fr. Erwin Schmutz (1978–80), has resulted in the flora of Manggarai being among the best documented of the Nusa Tenggara region. They followed standard collection protocols and herbarium specimens collected in the district were stored in Herbarium Bogoriense (BO) and Rijksherbarium (L). As Fr. Schmutz worked in an ecoregion (Mbeliling Forest) immediately adjacent to the Tado's ancestral lands and their Catholic congregation, senior Tado residents were familiar with the priest's fieldwork, but were unaware that he and Fr. Verheijen had published ethnobotanical texts and dictionaries translating Manggarai terms into Bahasa Indonesia and scientific nomenclature.

In an effort to augment the seminal work begun by Fr. Verhiejen and Schmutz, ECO-SEA and the Tado have cooperated in a long-term effort to develop an indigenous capacity for conducting ethnoecology research. The Tado Community Training and Research Center was inaugurated in May 2000, and has been equipped with a resource library, herbarium, ethnobotanical museum, scientific equipment and meeting facilities. In addition to training 20 Tado research associates, the TCECP has formalised the involvement of Tado traditional and administrative leaders and residents of the 12 Tado settlements into project design, implementation, analysis and review. Thirty-five 'key' informants (18 women and 17 men ranging in ages from early 40s to over 100) and several hundred 'casual' informants participating in group sessions at their respective settlements have been involved in reporting ethnobotanical uses, sharing historical and cultural narratives, qualitative and quantitative data collection, anthropological and ecological surveys, ecosystem transects, and mapping. Now in its fourth year, the results of the TCECP include: (a) the documentation of some 600 ethnobotanical uses for over 300 plant taxa, (b) the curation of several hundred herbarium specimens onsite in the Tado herbarium, (c) the donation of over 170 mounted and databased duplicate specimens to the UC Davis Tucker Herbarium (and another 20 specimens to the Eka Karya Bali Botanic Gardens), (d) the establishment of an ethnobotanical museum onsite containing over fifty artifacts, (e) the joint presentation of research results at three international conferences, (f) the in-house publishing of six booklets on the cultural ecology of the Tado, (g) the joint authorship of three scientific publications, and (h) the generation of a GPS/GIS-based map of Tado ancestral lands.

The immediately apparent benefits to increasing local participation in our ethnobotanical and ecological surveys include the following:

1. We have been able to expand our research scope and to refine our methodological approach based on the collective advice and ongoing input from several hundred community members.
2. The sophistication and rigor of our qualitative and quantitative survey techniques have been easily maintained due to higher levels of comprehension of the research methods by both data collectors and respondents.
3. We have been able to repeatedly cross-check, augment and deepen our ethnoecological and ethnobotanical narratives through a series of peer-review discussions of our research results.
4. We have developed a low-cost, reliable, 'quick-response' link between Indonesia and the USA to exchange data, specimens, reports and other research products on a regular basis. This has greatly increased our collective productivity and administrative efficiency.
5. We have succeeded in recruiting and retaining a core group of Tado research associates and advisors whose professional performance is linked more to personal motivation and pride in their work than to financial benefit.
6. We are able to establish a direct connection between research results and recommendations, and the implementation of those recommendations to conserve elements of biological and cultural diversity within Tado plant and human communities.

Equipping the Tado with the facilities, tools, training, international exposure, and financial means to conserve their biocultural heritage is only the initial phase of ensuring the sustained maintenance of indigenous customs and native taxa. Strengthening Tado administrative capacity is essential, so that the Tado can continue to manage the Tado Community Research and Training Center independently.

Conclusions

In the words of Robert MacArthur, 'Anyone familiar with the history of science knows it is done in the most astonishing ways by the most improbable people and that its only real rules are honesty and validity of logic, and that even these are open to public scrutiny and correction' (MacArthur 1972, p. 259). Just as Rumphius and Linneaus sparked a scientific revolution in the study of biological and cultural diversity with their extensive accounts of ethnoecological variation, the increased involvement of indigenous communities in botanical inventories could spark a parallel revolution in the research and conservation of biocultural diversity. We salute the efforts of institutions such as the Rijksherbarium, the Royal Botanic Gardens Sydney, the Royal Botanic Gardens Kew, Botanic Gardens Conservation International (BGCI), and the Japanese International Cooperation Agency (JICA) in providing substantive support (infrastructure, equipment, consultancies, in-house and overseas training) to their Asian counterparts; as well as the exemplary work carried out by colleagues such as Paul Keßler, Jan Slikkerveer, Gary Martin, and Glenn Wightman, who have prioritised the field training of Asian and Australian researchers and technicians in taxonomy, ecology and ethnobotany. We have benefited from the extraordinary progress made by the PROSEA project in cataloguing and disseminating Malesian ethnobotanical knowledge to the general public.

As we look forward to the Sixth International Flora Malesiana Symposium, to be held in Los Baños, The Philippines in 2004, we invite our colleagues and sister institutions to support the increased participation of indigenous research associates and parataxonomists at these meetings. Since 2001 Tado research associates and advisors have presented project results at international symposia in Australia and the United States, events that have increased civic pride and heightened the community's confidence in their ability to interact professionally in circles previously beyond their reach. ECO-SEA will be sponsoring two delegates from Tado at the upcoming Flora Malesiana symposium, and we hope to facilitate the attendance of several dozen representatives from other indigenous communities affiliated with research projects conducted by Flora Malesiana affiliates. The ongoing exchange between indigenous community members and Flora Malesiana researchers at national and international institutions represents an opportunity for all of us to adhere more closely to the tenets of mutual benefit and responsibility outlined in international conventions such as the 1988 *Declaration of Belem* by the First International Congress of Ethnobiologists (cited in Martin 1995), the 1992 *Convention on Biological Diversity* (UNEP-CBD 1994) and the 1993 *Principles and Guidelines for the Protection of the Heritage of Indigenous Peoples* by the United Nations Working Group on Indigenous Populations (UN-WGIP 1995). We encourage colleagues who are interested in learning of practical ways to apply specific articles of these conventions to their work to contact us directly.

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An integrated programme for local Floras, conservation research and environmental awareness generation in South India

K. M. Matthew

Abstract

K. M. Matthew (The Rapinat Herbarium, St Joseph's College, Tiruchirapalli 620 002 & The Anglade Institute of Natural History, Shembaganur, Kodaikanal 624 104, India) 2003. An integrated programme for local Floras, conservation research and environmental awareness generation in South India. Telopea *10(1): 73–80.* Three components of the work reported here (local Floras, conservation of endangered species, and a programme for environmental awareness generation involving the neighbourhood community), are integral parts of a holistic eco-restoration programme in South India. It is hoped that this successful model addressing an issue of such vital urgency, especially in the tropics, could be replicated elsewhere at least in essentials. The first component is publishing an affordable, illustrated, modern Flora of the region based on adequate fieldwork. Publication would be initially in English and later in the vernacular. The second component would be a concurrent programme of conservation research on locally endangered species, and the third would be to generate environmental awareness at the local community level.

Local Floras

The technical programme

A modern, illustrated regional Flora of Southern India was the first goal of the programme since all the three previous Floras (Hooker et al. 1872–1897, Gamble & Fischer 1915–1936, Fyson 1932) were out-dated and inadequate. To improve the botanical knowledge of this region, field work was to be done in four zones (Fig. 1) of which the work in Zones 1 & 2 has already been completed. Zone 1, covering the vegetation of the plains and low altitude hills (< 1400 m) including eight out of the nine tribal belts of Tamil Nadu State, was the first zone (Matthew 1981, 1982, 1983 & 1988). A similar illustrated Flora, covered the montane region of the Palni hills (Zone 2). The latter, part of the Western Ghats of India, one of the 25 biodiversity hotspots of the planet (Mittermeier et al. 1998), also suffered from massive introduction of alien species, cultivated or weedy, since the arrival of overseas personnel from the 1840s (Matthew 1996, 1998a & 1999a).

The technical programme for Zones 1 & 2 was described (Matthew 1998c, 1997) under the following headings: 1. The tract and field work; 2. Documentation (Table 1); 3. Illustrations (Table 2); 4. The Flora (Table 3) covering: analysis of materials; taxonomy; nomenclature and synonymy; keys; field notes; world distribution; and phytogeographical findings.

The volumes describing the flora of Zone 1 are now sold out, and instead of reprinting them, we are revising them with a considerable increase in field coverage and re-assessment of the conservation status during the past quarter century. Zone 3, the Coromandel Coast, is being explored separately owing to historical antecedents (Roxburgh 1795–1820, Rottler 1803, Matthew 1993a), and the intense pressure from urbanisation in recent years. Zone 4 extends the area of Zone 1 northwards to the boundary of the State of Andhra Pradesh, and includes the Javadi hills, the only tribal belt of the State not included in Zone 1. From the field data from Zones 1 & 2 a comprehensive conservation report on the extinct, endangered and rare species was published (Matthew 1999b) (Table 4).

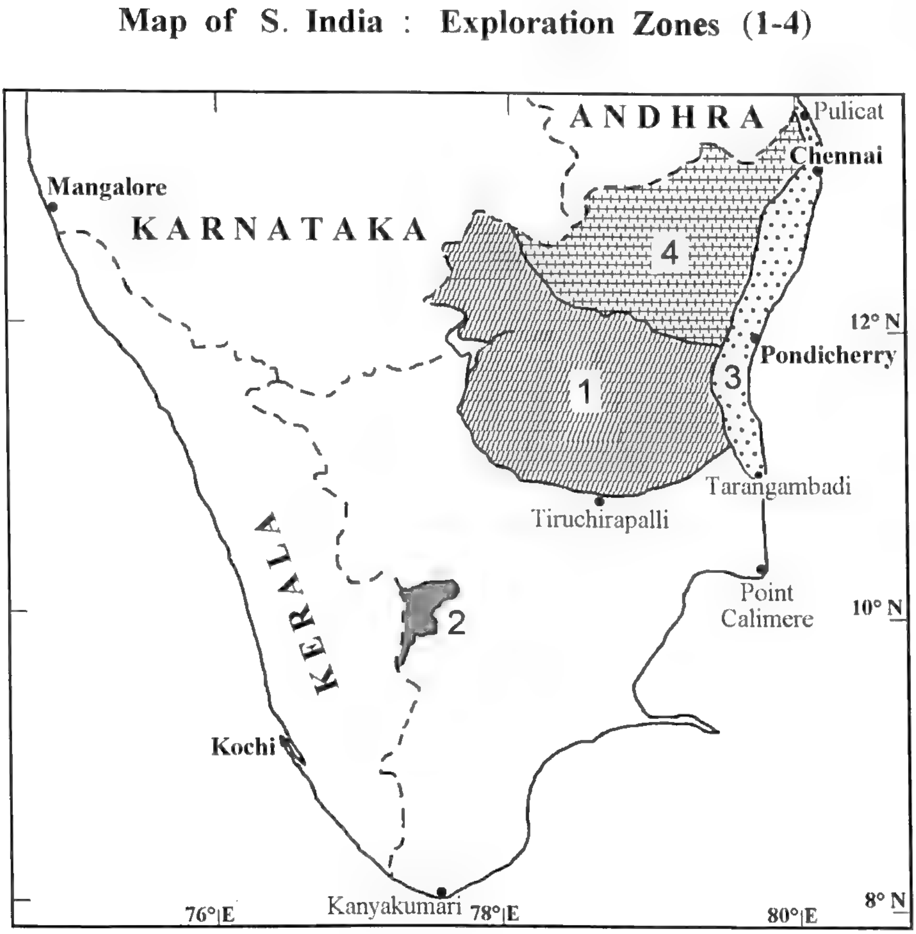

Fig. 1. Map of South India showing the four exploration zones.

Table 1: Details of exploration work.

Zone	Area	Duration	Number of			Publications (Books only)
			Field Days	Collections	Species	
1	*Plains*: low altitute hills	1976–1983	631	30 722	2037	Matthew 1981, 1982, 1983, 1988, 1991, 1993b, 1995, 1998b
2	Palni *hills* (to 2410 m)	1984–1994	323	14 987	2478	1996, 1998a, 1999a
3	Coromandel *Coast*	2000–	52	2177		
4	North Tamil Nadu	1999–	82	3718		

Table 2: Details of plant illustrations.

Publications	Number of	
	Plates	Species
Matthew 1982	960	882
1983	111	14
1988	834	820
1996	950	903
1998a	273	269

Table 3: Classified conspectus of the included taxa.

Zone	Families	Genera (monotypic in brackets)	Species				
			Native	Naturalised	Cultivated	Garden	Total
1	180	990 (486)				2037	
2	202	1137 (377)	1758	161	344	215	2478
3			(Work in Progress)				
4							

Table 4: Conservation status of the endangered taxa (Matthew 1999b).

Area Explored		Status of Species	
	Vulnerable	Presumed extinct	New Record (aliens excluded)
Zone 1	25	3	6
Zone 2	65	13	56
Zone 3		(Work in Progress)	
Zone 4			

Community outreach

(i) Publications

Involving the wider community has been integral to our 'lab to land' vision. Field Floras, first in English (Matthew 1991, 1995), later in the vernacular (Matthew 1993b, 1998b), aimed at 'door delivery' of knowledge of local plants to the wider community. Pricing the publications within the purchasing power (at a quarter of the market rates) of any user, including students, was integral to this process. The issue of booksellers ignoring us because of our minimal pricing policy was initially considered a setback but eventually proved a boon: a direct producer–user link emerged, so that the users procured the publications directly from us, thereby eliminating the hefty profits to booksellers.

(ii) The Herbarium, Library and Conservatory

The long-term significance of the enrichment of the research herbarium (over 100 000 collections added exclusively from the present work) as the indispensable starting point for all future plant-based research in the region, especially monography, cannot be over-emphasised. Furthermore, care has been taken to ensure that our collections are widely represented in overseas herbaria. The complete representation of all our species in the Royal Botanic Gardens Kew (K) will be a valuable extension to its holdings of historical collections from the region. Exchange with overseas centres has notably enriched our infrastructure, especially the library.

A Consultation Herbarium (each species of the region being represented by one or a very few sheets) maintained separately from the Research Herbarium is an easily accessible facility for those in search of names of local plants. This, incidentally, safeguards the latter from improper handling by amateurs.

The library, with a wide representation of periodicals and Floras, is widely used.

A Conservatory representing at least one species from all the local genera of plants, and adjacent to the Herbarium, is much appreciated by outside visitors. Live plants are a welcome change from the stuffy herbarium for ordinary people.

Conservation research

To have known at first hand the endangered plants in the field is the best stimulus to work for their conservation. This work, both *in situ* and *ex situ*, is organised at Kodaikanal, our environment centre. The availability of a high altitude base (1800 m) as a hill laboratory and field station is key to our conservation work, research and education. Such is The Anglade Institute of Natural History at Kodaikanal, 200 km away (from Tiruchirapalli), located inside the Nature Sanctuary of the Palni hills, and equipped with adequate natural history infrastructure.

Ex situ (off site) programmes: *Crotalaria beddomeana* Thoth. & A.A. Ansari, originally described from the nearby Anaimalai hills, and reportedly doing well elsewhere, had nearly disappeared from the Palni hills. From a few seeds collected from a lone local plant, the species has been copiously regenerated and widely planted, so that it is now regarded as out of danger. The widespread planting of this robust shrub (over 3 m tall, with copious soil-enriching root nodules) by the local people, was an excellent example of community commitment to conservation.

Two other successful instances of *ex situ* conservation – *Hoya wightii* Hook.f. subsp. *palniensis* K.T. Mathew and *Sonerila pulneyensis* Gamble, are the work of VOYCE (Vattakkanal Organization for Youth, Community and Environment), a village-based

Conservation Trust organized by R.W. Stewart and Tanya Balcar originally from the United Kingdom, now based near Pambar Shola.

In situ programmes: The *in situ* programmes are taken care of by the the Palni Hills Conservation Council (PHCC), a local conservation agency started in 1985, of which I was the Founder Vice-President. As a result of years of work, the Palni hills are to be declared a Nature Sanctuary contiguous with the Eravikulam National Park of the Anaimalais to the west. However, two constituent units have already been realized. Fencing of the Pambar Shola with the maximum concentration of endangered plants of the Palni hills, completed in 2000, has been decisively important. Replanting of its denuded slopes with local species by VOYCE is already in progress. Hedged in between the Pambar Shola and the 100-hectare campus of the Anglade Institute of Natural History is a notably intact slope with the maximum concentration of the folklore plant *Strobilanthes kunthiana*, probably the best known local plant on all the hills. This tract has been officially declared a "Kurinji (Strobilanthes) Reserve".

Environmental education for the neighbourhood community

The most innovative and successful part of our work has been the generation of mass environmental awareness for the neighbourhood community. The project has been an instant success since its inception in 1984, and has handled some 54 000 trainees in the year-round, 3-day, live-in programmes. This is a free programme because the majority of the trainees cannot pay as they are in a permanent struggle for survival. Student intake figures for 1984–2001 are shown in Table 5.

(a) **Insight**: Starting from the grass-roots level and working upwards ensures lasting results through involvement of people. Particularly in today's environmental crisis, this insight is imperative. Our two main target trainees groups were: 1. Students, the decision-makers of tomorrow, and 2. Villagefolk, the custodians of the environment today.

A 3-step method was adopted: (i) supply of basic environmental information, largely from within the experience of the trainees, or closely related to it; (ii) motivating them to action; and (iii) equipping them with practical action programmes, thereby empowering them to be arbiters of their destiny.

(b) **Objectives:** Built on the 'watershed concept' and the role of primary vegetation in maintaining ecosystem balance, the entire programme was a series of demonstrations of natural processes. Lectures were conspicuous by their absence except for an occasional short keynote presentation, or a summing up of the main points illustrated by practical demonstrations. Eco-restoration is not only possible but imperative on everyone. Blaming someone else for the deteriorating environment is futile; it is time to take matters up oneself.

(c) **Organisation**: As trainees arrive for the 3-day programme (Monday–Wednesday, Thursday–Saturday), they are assured that no previous knowledge of biology is expected, nor even the ability to read or write. All that is expected is an interest in life. The resounding concurrence from the unlettered was a clear indication that we had breached the conventional barriers and reached the core of the trainees. They were engaged, and plunged themselves into the programme.

Day 1: Indoor exposure to the natural riches of the hills as conserved in the Institute: Museum, Gardens, Display Gallery, Reading Room. The intended result was a general appreciation of the riches of nature in the region. A wide selection of videos, also from other parts of the world, reinforced the experience.

Day 2: Outdoor exposure to nature: during half-a-day, visiting some pre-determined spots around Kodaikanal, like intact forests contrasted with others gradually being cleared, monocultures etc., evoking a comparison with the previous day's indoor exposure. The trainees appreciate the urgency of the need of eco-restoration as a personal obligation. This field trip has always remained the high point of the entire programme. The afternoon is given to the Display Gallery where environmental information (regional and global) is displayed through pictures and figures that even illiterate people can follow. A Reading Room with environmental newsletters and periodicals, and some key books, helps to integrate the information. The very successful cultural programme by the trainees on environmental themes is ample proof that the message was getting home.

Day 3: Evaluation and action programmes. That the tax-payer had met the expenses for their taking part in the programme (no charges are made) renders this programme a loan the students had been given, to be returned in the form of service, *noblesse oblige*. The trainees come up with practical steps they can implement back home: nature clubs, greening, dissemination of information in their institutions and neighbourhood, cultural programmes, adopting a neighbourhood village, etc.

Leadership programmes: The need for leadership programmes was discovered in course of time with a view to training of trainers (multiplier effect). Leaders need additional informational inputs and interaction with similar groups elsewhere. Besides one national programme in English, there are at least five zonal programmes in the vernacular (Fig. 3). These are organized by our zonal co-ordinators who are the backbone for quality performance. They carefully screen the applicants and approve only promising ones. Copies of our *Handbook,* in English and in the vernacular (Matthew 1987, 1992, 1994 & 1997), also sold cheaply, are a handy souvenir for the trainees.

(d) **Programme outreach (Figs 2 & 3)**. The 415 centres from where the trainees have come are potential centres for environmental sensitivity to be set into action. This hope was confirmed during the Impact Assessment visits to the trainee centres by our staff. It is essential that this network of environmental initiatives and workers in the region be actively maintained. This is the purpose of *Shola*, our 6-monthly, bi-lingual environmental newsletter (28 issues published so far). Mailing of some 100 copies to overseas centres keeps us in touch with the global pulse.

Table 5: Participation figures 1984–2001

Years	Number of						Total
	Courses	Students	Teachers	Leaders	Activists	Villagers	
1984–2001	1170	36475	2356	1416	2951	10545	53743

Conclusion

The significance of the work reported here is the stepwise integration of three programmes, and relating them to the wider community around who gradually should assume responsibility for their future. The relevance and urgency of this approach, especially in the tropics, the home of the bulk of the planet's green cover now under growing threat, is obvious. The scheme outlined here can easily be replicated anywhere, at least as to its major components.

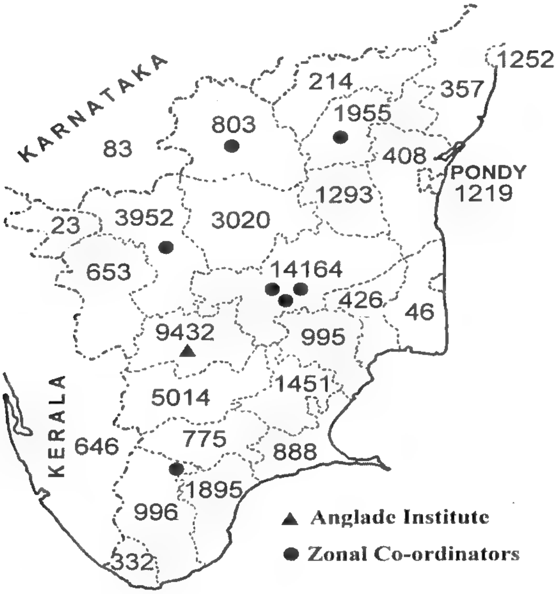

Fig. 2. Map of South India showing the geographical coverage under the Grass-roots Programme.

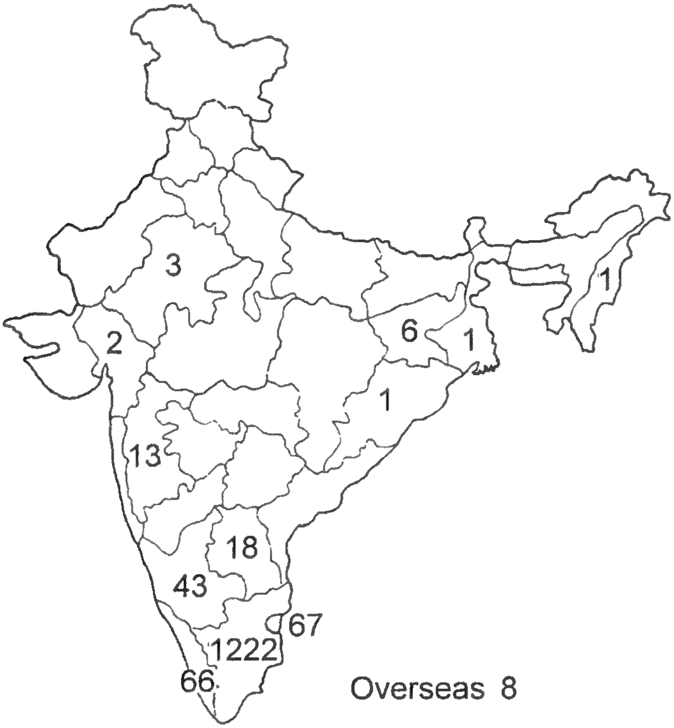

Fig. 3. Map of India showing the geographical coverage under the Leadership Programme.

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An ethnobotanical survey of medicinal and other useful plants of Muruts in Sabah, Malaysia

Julius Kulip

Abstract

Kulip, J. (Ethnobotany Section, Forest Research Centre, Forestry Department Sabah, P.O. Box 1407, 90715 Sandakan, Sabah, Malaysia) 2003. An ethnobotanical survey of medicinal and other useful plants of Muruts in Sabah, Malaysia. Telopea *10(1): 81–98.* This paper presents the results of ethnobotanical studies on medicinal and other useful plants used traditionally by the Muruts in Sabah. They have rich ethnobotanical resources. A total of 91 species of plants were noted and collected during the surveys. Among them are 68 species of medicinal plants and 64 species of other useful plants. Reports from plant informants were obtained during field studies in February 1994, in March 1998, in May 1998, in May 2000 and in February 2001. For each species are given the botanical name, Murut name(s), collection number, medicinal uses, as well as plant part(s) used, and other uses. The popularity of plants with traditional uses among the Muruts is fading due to migration, restriction from religion, lost interest of younger generations and heavy dependence on modern medicine. Opening of forests for agricultural development and timber harvesting makes the resources scarce which is also contributing to the loss of knowledge. Awareness activities in Malaysia's primary and secondary schools on the usefulness of plants and their environment, and government policies on medicinal plants, have contributed significantly towards the preservation of indigenous traditional knowledge of plants.

Introduction

Sabah is one of the 13 states within the Federation of Malaysia and is located in the northernmost part of Borneo. It is the second largest state in Malaysia with a landmass of approximately 7.4 million hectares. The total forested area is 4.7 million hectares. The climate is marine equatorial with an average temperature of 74–88° F (23–32° C). The rainy season, locally called 'Musim hujan', is around November to February. This is also known as the North-east Monsoon. The South-west Monsoon, which is less wet, is from May to October, making the annual rainfall 60–120 inches (1525–3050 mm, or sometimes up to 4500 mm). Sabah, being part of Borneo, is rich in plant biodiversity. There is also an abundance of medicinal plants and other plants for everyday use.

Population in Sabah as at 2000 is about 3.0 million (Dept. Statistics 2000). There are 36 indigenous groups livng in Sabah; the Murut population is estimated at 91,700 and is the third largest. They are distributed in Keningau, Tenom, Nabawan/Pensiangan and Kalabakan districts. These districts are located in the interior and south-eastern parts of Sabah and the territory straddling the borders of Kalimantan (Indonesia) and Sarawak (Fig. 1). The definition of Muruts people adopted here is based on Tombung (1991) and King (1992).

Survey work on Muruts' ethnobotanical resources on medicinal plants and other useful plants in Sabah began in early 1991 by the Sabah Museum and Universiti Kebangsaan Malaysia, Sabah Campus, while at the Forestry Department it began formally in 1999 even though collection of materials started in early 1994. A medicinal plant survey by Guntavid (1992) found that 38 species of plants were used by the Tangala Muruts in Kampung (Kg.) or village Inarad, Ulu Kinabatangan (upper Kinabatangan river). Fasihuddin and Hasmah (1992) found 57 species of plants were used as medicines by Muruts around Nabawan, Sepulut and Pensiangan area.

Medicines, or *Tatapis* (Paste)/*Babas* (antidote) in Muruts' language, from plant resources have been used for a long time by the Murut society to cure their everyday ailments. There is an equally long history of the use of wild plants for food, construction, house utensils, and social and religious functions. In the olden days herbal remedies provided the only relief when modern medicines were not available. Knowledgeable elders or medicine men usually administered the medicine. Depending on the ailments, the healing would often involve some kind of ritual. To the Muruts, the river and the forest represent the world. From them they derive their food, their medicine, their clothing and their house materials.

This paper presents the results of ongoing ethnobotanical research on the Murut people in Sabah. Its purpose is to preserve the precious cultural heritage of the Murut ancestors' use of plants. It is also hoped that further studies on the phytochemical contents of the plants will reveal some useful drugs for the benefit of mankind.

Location and Area of Study

The surveys focus on the various Muruts villages throughout Sabah (Fig. 2). Murut ethnic groups involved in these studies were Keningau Murut, Timugon Murut, Paluan Murut, Kalabakan Murut and Tagal Murut. Villages involved include Kg. (village) Melalap in Tenom district (Timugon Murut); Kg. Melinja and Bahagia B in Nabawan/Pensiangan district (Paluan Murut); Kg. Lingawon in Keningau district (Keningau Murut); Kg. Ulu Kalabakan in Kalabakan district (Kalabakan Murut); and Kg. Murni Empat and Enam in Nabawan/ Pensiangan district (Tagal Murut).

Kg. Melalap is located about 15 km from Tenom town center and consists of about 100 households; Kg. Melinja and Bahagia B are located about five km from Nabawan town center and consists of about 100 households; Kg. Lingawon is located about 10 km from Keningau town center and consists of about 50 households; Kg. Ulu Kalabakan is located about three km from Kalabakan town center and consists of about 50 households; and Kg. Murni Empat and Kg. Enam are located one km from Nabawan town center.

Ethnic groups such as the Murut turn to the forest for their daily needs and also for income. Produce such as wild vegetables, fruits and medicinal plants are gathered and sold in the weekly markets or 'Tamu' for an additional income.

The original vegetation cover of the research area can be classified as lowland mixed dipterocarp forests except for the Pensiangan area. A wet season usually begins in September and can last to January. At higher elevations such as in Pensiangan area, the forest is dominated by species of Fagaceae, Araucariaceae (*Agathis* spp.) and Myrtaceae, while at lower elevations such as in Tenom, Keningau and Kalabakan, species of Dipterocarpaceae, Leguminosae and Euphorbiaceae species predominate.

Methods

Written permission from the office of the District Community Development and verbal permission from the village Chief concerned were usually applied for before entering any villages. Data were gathered by interviewing the plant informant(s), usually the knowledgeable villagers of Muruts elders (men and women) together with some young people who still used plants in their daily life. The interviews were conducted in Murut, which was spoken by all of the members of the Murut communities. The interview process was based on methods described by Martin (1995). Usually after a short interview, the plant informants would take us to their *ladang* (upland agricultural field), backyard gardens and into the forest. Fieldwork was carried out by a team of Ethnobotany Section staff from the Forest Research Centre of the Forestry Department Sabah, Sandakan.

Voucher specimens are deposited at the Ethnobotany Office at the Forest Research Centre Sabah, Forestry Department Sabah, Sandakan. Specimens that were easily identified in the field were not collected, only noted. Unidentifiable specimens were numbered and brought to the herbarium to be examined further.

Villages involved in these studies were namely Kg. Melalap on 1–15th February 1994 where we interviewed Madam Kasium Galawang (62 years); Kg. Melinja and Kg. Bahagia B on 9–23rd March 1998 where we interviewed Mr. Kumalu A. (60 years), Mr. Lasuan Liwau (45 years) and Mr. Muskin Bugan (60 years); Kg. Lingawon on 6–18th May 1998 where we interviewed Madam Murika Gambun (55 years); Kg. Ulu Kalabakan on 8–17th May 2000 where we interviewed Mr. Mantawasa Baukom (60 years); and Kg. Murni Empat and Enam on 14–26th February 2001 where we interviewed Mr. Lintong Eman (45 years). A Murut language translator was used during the surveys. Most interviews lasted four to five hours per day. According to their Native Customary Law, a person must give to the plant informant a *pingkaras* or a kind of compensation. The compensation is normally one black hen and a sum of (RM 20.00) per species of plants. For this survey a sum of RM 20.00 (US$ 5) was paid per day to the informants as a token of appreciation for their kind cooperation during the survey.

Results

Table 1 and Table 2 show the list of medicinal and other useful plants collected during the surveys. In total 91 species of plants were documented. Of these, 68 are indicated by Muruts informants as medicines, 64 as other useful plants (some of which were also used as medicines). Compared to previous collections by authors like Guntavid (1992) and Fassihuddin and Hasmah (1992), there are an additional 50 new records of medicinal plants collected during the present survey. The total number of Murut medicinal plants documented so far for Sabah, amounts to 143 species (Appendix 1) belonging to 44 families. Most prominent among plant families used by the Murut are Euphorbiaceae (10 species documented), followed by Leguminosae (6), Rubiaceae (5) (Appendix 2). There are 94 species found to be indigenous while 34 are introduced, naturalised, or only known from cultivation.

Plants which have a very high value, whether for medicine or other uses, are collected from the forest and often recultivated near the houses or in gardens so that there is a ready supply of the raw materials for future use. That is why many of these plants are quite commonly found in the village. A number of other plants however, can be found in nearby *ladang* (upland agricultural fields), disturbed forest or in relatively undisturbed mixed dipterocarp forest and roadsides.

TABLE 1. PLANTS TRADITIONALLY USED AS MEDICINES BY THE MURUTS COMMUNITIY IN SABAH, MALAYSIA

Botanical name and voucher specimen no. (if any)	Common names (Dialect)	Medicinal uses	Part Used	Method of Use
ACANTHACEAE				
**Justicia gendarussa* L.	Insasahi (Ka)	Stomach ache	Leaves	Leaves are boiled and taken as a tea
AGAVACEAE				
Dracaena elliptica Thumb	Sipak (Ka)	Tonic	Leaves and Flowers	Boiled in water and as a bath
**Cordyline fruticosa* (L.) Goeppert. SAN 138296	Pipisokalaganan (Ti)	Flatulence	Root	Pounded into paste and applied on the stomach
AMARANTHACEAE				
**Amaranthus spinosus* L.	Sansam Sau (P)	Epileptic seizures	Fresh leaves	Boiled in water and as a bath
**Cyathula prostrata* (L.) Bl. SAN 138278	Sansam Bawi (Ti)	Insect bites	Leaves	Pounded into paste and rubbed on the affected area
ANACARDIACEAE				
Semecarpus cuneiformis Blanco.	Kutang	Wounds	Leaves	Burnt to produce smoke to be inhaled
ANNONACEAE				
Desmos teijsmanii (Boert.) Merr. SAN 138271	Molisun Rumungkut (Ti)	Headache	Leaves	Boiled in water and as a bath
Phaeanthus ebrasteolatus (Pers) Merr. SAN 138288	Korokos (Ti)	Eyepain	Sap	Applied directly on eye
Uvaria grandiflora Roxb. SAN 138270	Nolilitan (Ti)	Waist pain and stomach ache	Leaves	Boiled in water to make a tea
APOCYNACEAE				
Alstonia angustifolia Wall ex DC SAN 138289	Tombirog (Ke) Tambailik (Ti & Ta)	Gastritis	Leaves	Boiled in water to make a tea
ARACEAE				
**Acorus calamus* L.	Kusul (P)	Stomach ache & fever	Rhizome	Boiled in water to make a tea
Aglaonema oblongifolium Schoot. FRCSE 424	Pilonos (Ta)	Boils	Leaves	Pounded into paste and applied on the affected area
Alocasia macrorrhizos (L.) G.Don f.	Buntui (Ke)	Itchiness	Sap from the stem	Applied directly to the affected skin
Homalomena propingna Schoot. FRCSE 414	Nyato (Ta)	Feverish cold	Pith	Heated and applied on forehead

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NOTE: *: introduced, naturalised or only known from cultivation; FRCSE: Forest Research Centre Sabah Ethnobotanical Collections Series; SAN: Sandakan Herbarium Series; P: Paluan; Ka: Kalabakan; Ke: Keningau; Ti: Timugon; Ta: Tagal.

Botanical name and voucher specimen no. (if any)	Common names (Dialect)	Medicinal uses	Part Used	Method of Use
ARISTOLOCHIACEAE				
Aristolochia papillifolia Ding Hou. FRCSE 412	Babas Lontong (P & Ta)	Antidote, jaundice, inflammation of liver (Paluon). Diarrhoea (Tagal)	Inner bark	Boiled in water to make a tea
BIGNONIACEAE				
Oroxylum indicum (L) Kurz. SAN 138284	Ulunan Sangku (Ti)	Swelling	Bark	Soaked in hot water and rubbed on the effected area
BIXACEAE				
**Bixa orellana* L. FRCSE 409	Puloh (Ta)	Gastritis	Root's bark	Boiled in water to make a tea
BROMELIACEAE				
**Ananas comosus* (L.) Merr.	Tingkauran (P)	Dandruff	Young leaves	Crushed and rubbed on the head
CECROPIACEAE				
Poikilospermum suaveolens (Bl.) Merr. SAN 13823	Bunatol (Ti)	Post partum treatment	Sap from the stem	Stem is cut to get the sap and drink
COMBRETACEAE				
Combretum nigrescens King SAN 138290	Damat Dumalarom (Ti)	Internal injury	Root	Boiled in water to make a tea
COMPOSITAE				
**Blumea balsamifera* (L.) DC.	Tawawoh (P & Ta)	Runny nose Gastritis Stomach ache Flatulence	Leaves Roots	Boiled in water to make a tea
**B. riparia* (Bl.) DC FRCSE 407	–	Hypertension	Leaves	Boiled in water to make a tea with a mixture of *Hibiscus* sp. (Malvaceae) FRCSE 408
Elephantopus tomentosus L. FRCSE 419	Honsigup (Ta)	Bloody stool	Root	Boiled in water to make a tea
**Synedrella nodiflora* (L.) Gaertn. FRCSE 418	–	Tonic	Whole plant	Boiled in water and as a bath
COSTACEAE				
Costus specious Koen. FRCSE 416	Insasabu (Ka & Ta)	Asthma	Sap from the young stem.	Stem is cut to get the sap and drink
CUCURBITACEAE				
**Trichosanthes cucumerina* L. SAN 138292	Molisun Mamulal (Ti)	Body swelling	Leaves	Pounded into paste and applied to the affected area

Botanical name and voucher specimen no. (if any)	**Common names (Dialect)**	**Medicinal uses**	**Part Used**	**Method of Use**
DILLENIACEAE				
Dillenia grandifolia Wall. Ex. Hk.f. et. Thom.	Dudungin (Ta)	Stomach ache	Roots	Boiled in water to make a tea
DIPTEROCARPACEAE				
Shorea spp. (Eushorea)	Omnompik (Ta)	Food poisoning	Inner bark	Pounded into paste and eaten
EUPHORBIACEAE				
Antidesma montanum Bl. SAN 138297	Damat mandalom (Ti)	Chest pain	Root and leaves	Root is boiled in water to make a tea Leaves are pounded into paste and applied on chest
Baccaurea lanceolata (Miq.) Muell-Arg.	Limposu (P)	Abdomen pain	Fruit	Pounded into paste and applied on the abdomen
Bombax ceiba L.	Kapok (P)	Vomitting blood	Bark	Boiled in water to make a tea
Bridellia stipularis (L) Bl. SAN 138279	Bolingkut (Ti)	Diabetes Mellitus Thrush	Root Fruit	Pounded into paste and applied on the affected area
Eupathorium odoratum L.	Lambaian (P)	Cuts and wounds	Leaves	Pounded into paste and applied on the affected area
Glochidion macrostigma Hk.f. SAN 138273	Sondot Laling (Ti)	Feverish cold	Leaves	Boiled in water and as a bath
**Jatropha curcas* L.	Jarak (Ke)	Gastritis	Leaves	Boiled in water to make a tea
Macaranga gigentifolia Merr.	Binawong (Ka)	Thrush	Sap from the twig	Cut the twig to get the sap and applied on the affected area
**Phyllanthus urinaria* L. SAN 138282	Pilujala (Ti)	Coughing	Entire plant	Boiled in water to make a tea
FLACOURTIACEAE				
Casearia grewiaefolia Vent. var. *grewiaefolia* SAN 138276	Salokdan (Ti)	Swollen pancreas	Leaves	Pounded into paste and applied on the affected area
FLAGELLARIACEAE				
Flagellaria indica L. SAN 138300	Waau (Ti)	Semi-paralysis	Entire plant	Boiled in water and as a bath
GESNERIACEAE				
Cyrtandra aff. *areolata* (Staff.) Bl. Burtt. FRCSE 428 & 431	Pohodo (Ta)	Bloody stool Skin disease	Young stem	Raw stem is eaten and made a tea to treat bloody stool Ashes of burnt stem are applied to treat skin disease

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Botanical name and voucher specimen no. (if any)	**Common names (Dialect)**	**Medicinal uses**	**Part Used**	**Method of Use**
GRAMINEAE				
**Eleusine indica* (L.) Gaetner	Liagon (P)	Food poisoning Broken bones	Entire plant Internodes	For food poisoning entire plant is boiled to make tea For broken bones internodes are crushed and applied
**Cymbopogon citratus* (DC.) Stapf.	Sohumau (P)	Cough	Leaves	Pounded into paste and applied on the affected area
**Imperata cylindrica* (L.) Rausch.	Lalang (Ka)	Bleeding	Young leaves	Pounded into paste and applied on the affected area
Zea mays L.	Halai (Ka)	Stomach ache	Young fruit	Pounded into paste and applied on the stomach
GUTTIFERAE				
**Garcinia mangostana* L.	Timpurog (P)	Vomiting blood	Fruit	Eaten raw
HYPOXIDACEAE				
Curculigo latifolia Dryander	Tambaka (Ta)	Wounds	Sap from the pith of the stem.	Cut to get the sap and applied on the affected area
LABIATAE				
**Hyptis capitata* Jack. SAN 138187	Baing-Baing (Ti)	Stomach ache	Young leaves	Pounded into paste and applied on the affected area
**Orthosiphon aristatus* (Blume) Miq.	Misai Kucing (Ta)	Hypertension	Leaves	Boiled in water to make a tea
LAURACEAE				
Lindera pipericarpa Boerl.	Laindos (P)	Antidote for snake-bite	Leaves, fruits & barks	Pounded into paste and applied on the affected area
Litsea graciae Vidl. FRCSE 420	Novolo (P) Pengolaban (Ta)	Joint dislocation(P) Sprain (Tagal)	Inner barks	Pounded into paste and applied on the affected area
L. odorifera Valeton	Lawang (P)	Gastritis Stomach ache	Bark	Pounded into paste and applied on the affected area
LEGUMINOSAE				
Airgantha borneensis (Oliv.) Brummit SAN 138299	Molisun Matamis (Ti)	High temperature Toothache	Bark	Pounded into paste and boiled in water to make a tea and as a gargle
Cassia alata L.	Emon (Ke)	Ringworm	Leaves	Pounded into paste and applied on the affected area
Milletia nieuwenhuisii FRCSE 389	Ramus (Ka)	Thrush	Sap from the stem	Cut to get the sap and applied on the affected area

Botanical name and voucher specimen no. (if any)	Common names (Dialect)	Medicinal uses	Part Used	Method of Use
LEGUMINOSAE cont.				
**Mimosa pudica* L.	Sikot Mou (Ke) Tenom Molu (Ka)	Stomach ache	Root	Boiled in water to make a tea
Parkia singularis Miq.	Kundai (P)	Kidney cleanser	Fruit	Eaten raw
Spatholobus cf. *gyrocarpus* Benth. in Miq. FRCSE 410	Ramus (Ka)	Thrush	Sap from the stem	Cut to get the sap and applied on the mouth
MALVACEAE				
**Urena lobata* L.I SAN 138286	Injilokot (Ti)	Thrush	Bark	Burnt to ashes and applied
		Bowel movement inducer	Flowers	Pounded into paste and applied on the abdomen
**Sida rhombifolia* L.	Dalupang (P)	Antidote	Leaves	Boiled in water to make a tea
MELIACEAE				
Lansium domesticum Corr. Serr.	Langsat (Ka & P)	Stomach ache Diarrhoea Colic	Bark	Pounded into paste and applied on the abdomen
MENISPERMACEAE				
Coscinium fenestratum (Gaerth.) Cole FRCSE 433	Babas Lingungan (Ta)	Thinning and yellowing skin	Entire plant	Boiled in water to make a tea
Fibraruea tinctoria Lour.	Tolungon (P & Ta)	Anti-malarial (Tagal) Hypertension	Stem	Boiled in water to make a tea
Stephania corymbosa FRCSE 396	– (Ka)	Antidote	Stem	Boiled in water to make a tea
Tinospora crispa (L.) Hook.f. & Thomsen	– (Ka)	Anti-malarial	Stem	Boiled in water to make a tea
RUBIACEAE				
**Jasminum aculeatum* (Blanco.) Merr.	Onsom-onsom (Ti)	Flatulence	Leaves	Pounded into paste with warm water and applied on the affected area
**Psychotria* cf. *sarmentosa* Bl.	Solovondo (Ta)	Itchiness	Stem	Burnt to ashes and rubbed on the affected area
ZINGIBERACEAE				
**Curcuma longa* L.	Kunyit (Ta)	Anti-fungal	Rhizome	Pounded into paste and applied on the affected area
**Zingiber officinale* Roscoe	Halia (Ta)	Flatulence	Rhizome	Pounded into paste and applied on the affected area

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TABLE 2. OTHER USEFUL PLANTS USED BY THE MURUTS IN SABAH, MALAYSIA.

Botanical name and voucher specimen no. (if any)	Common names (Dialect)	Category	Part Used	Method of Use
ARACEAE				
Homalomena propinga Schoot. FRCSE 414	Nyato (Ta)	Fish poison	Pith	Pith is pounded and soaked in water/stream
ANACARDIACEAE				
Mangifera indica L.	Longgom (Ka)	Edible fruit	Mesocarp	Eaten ripe, or unripe as pickle
M. pajang Kost.	Bambangan (Ka)	"	"	Eaten ripe
ANNONACEAE				
Gonoithalamus woodii Merr. FRCSE 390 & 415	Tampaliu (Ka) Kuluor (Ta)	Ghost scare	Whole plant	Hung on the upper main entrance or burnt
BAMBUSOIDEAE				
**Bambusa blumeana* Schult.	Kayawen(Ti)	Vegetable	New shoot	Cooked
Gigantochloa levis	Paling (Ti)	Vegetable Cooking Pot	New Shoot Internode	Cooked Cut
**Schizostachyum brachycladum* Kurz.	Bulu (Ti)	Dart's tip	Internode	Cut
S. pilosum S. Dransf.	Pus (Ka)	Straw	Internode	Cut small
BOMBACACEAE				
Durio graveolens Becc.	Ruyan (Ka)	Edible fruit	Aril	Eaten ripe
D. zibethinus Murray	Lampun (Ka)	"	"	"
BROMELIACEAE				
Ananas comosus (L) Merr.	Tingkauran (P)	Cotton	Leaves	Matured leaves are beaten and woven
CASUARINACEAE				
Casuarina sumatrana Miq.	Silinggaun (Ka)	Ornamental	Entire	Bug tree
CECROPIACEAE				
Poikilospermum suaveolens (Bl.) Merr.	Bunatol (Ti)	Vegetable	Young leaves	Cooked
DIPTEROCARPACEAE				
Shorea parvistipulata Heim. FRCSE 391	Roloi (Ka)	Stimulant	Young leaves	Betel pepper leaf as substitute for gambir
EUPHORBIACEAE				
Baccaurea puberula Merr.	Tampoi kuning (Ka)	Edible fruit	Aril	Ripe
B. lanceolata (Miq.) Muell-Arg.	Lipasu (Ka)	"	Aril & Mesocarp	Ripe aril Mesocarp eaten as pickle
Bombax ceiba L.	Kapok (P)	Pillow	Matured fruit	Fibre for pillows
**Manihot esculenta* Crantz.	Lui (Ka)	Edible	Root (tuber) Leaves	Cook

Botanical name and voucher specimen no. (if any)	Common names (Dialect)	Category	Part Used	Method of Use
EUPHORBIACEAE cont.				
Koilodepas longifolium Hook. f.	Kayu Ulas (Ka)	Bow	Bole	Smaller bole
Macaranga tanarius (L) Muell. Arg.	Daun Bayangan (Ka)	Wrapper	Leaves	To wrap rice
HYPOXIDACEAE				
Curculigo latifolia Dryander. FRCSE 413	Tambaka (Ta)	Edible fuit	Aril	Ripe
GRAMINEAE				
**Saccharum officianarum* L.	Tebu (Ka)	Drinkable	Sap	Matured stem
**Zea mays* L.	Halai (Ka)	Edible fruit	Cotyledons	Cook
GUTTIFERAE				
Garcinia parvifolia (Miq.) Miq.	Kandis (Ka)	Edible fruit	Aril & Mesocarp	Ripe aril Ripe mesocarp dried and cooked as vegetable
FLACOURTIACEAE				
Trichadenia philippensis Merr FRCSE 421	Tulok-Ulok (Ta)	Magical use	Leaves	To make thief's feet bleed; leaves are placed on the sole
LAURACEAE				
Lindera pipericarpa Boerl.	Laindos (P)	Lethal to chicken	Fruits	Ripe
Litsea graciae Vidl. FRCSE 420	Novolo (P) Pengoloban (Ta)	Edible fruit	Aril	Ripe
Eusideroxylon zwageri T. & B.	Belian (Ka)	Blow-pipe	Young bole	A hole made through
LEGUMINOSAE				
Bauhinia kockiana Korth. Var. *kockiana* FRCSE 414	Kulih Bakah (Ta)	Prevent evil-craft from enemy	Entire plant	Fresh
Derris cf. *trifolia* Lour. FRCSE 388	Apa (Ka)	Flavour	Leaves	Cooked
Milletia nieuwenhuisii J.J. Smith	Romus (Ta)	Knife handle	Wood	–
MARANTACEAE				
Donax canniformis (Forst.) Schum	Lias (Ta)	Basketwork	Outer stem & fish trap	Stem split into strips
MELASTOMATACEAE				
Dissochaeta monticula Bl. FRCSE 427	Bina (Ta)	Lethal to mammals	Root's sap	Used as blowpipe poison
MELIACEAE				
Lansium domesticum Corr. Serr.	Langsat (Ka & P)	Edible fruit	Aril	Ripe

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Botanical name and voucher specimen no. (if any)	Common names (Dialect)	Category	Part Used	Method of Use
MENISPERMACEAE				
Pycnarrhena cf. *tumetacta* Miers. FRCSE 388	Apa (Ka)	Flavour	Leaves	Dried and added to cooking
MUSACEAE				
Musa textiles Nee.	Punti (Ka)	Edible fuit Vegetable	Aril Pith & un-opened flowers	Ripe Cook
MORACEAE				
Antiaris toxicaria (Pers.) Lesch.	Paliu (Ka)	Poison	Latex	Poisons darts
Artocarpus communis J.R. & G. Foster	Kemansi (Ka)	Edible fruit	Aril	Ripe
A. elasticus Bl.	Puputul (P)	Bird trap	Latex	
A. odoratissimus Blanco.	Tarap (Ka)	"	"	Ripe
A. integer (Thumb.) Merr.	Luon (Ka)	"	"	Ripe
A. tamaran Becc.	"	Hat or shirt	Bark	Broad strips of bark beaten till flat
Ficus beccarii King. FRCSE 417	Tatali (Ta)	"	"	"
MYRTACEAE				
**Psidium guajava* L.	Kaliabas (P) Liabas (Ka)	Edible fuit	Mesocarp	Raw/ripe
MYRSINACEAE				
Embelia philippinensis A. DC. FRCSE 387	Papaling (Ka)	Edible	Young leaves	Salad
PALMAE				
Areca catechu L.	Kusob (Ta) Pinang (Ka)	Stimulant	Endocarp	Mature fruit eaten raw
Arenga undulitifolia Becc.	Polod (Ta)	Fire starter (tinder)	Soft net	–
Calamus spp.	Rotan lasun, pipit (Ka)	Vegetable Rope	Tip of the plant Cane	Cook Matured cane
**Cocos nucifera* L. Becc.	Piasau (Ka)	Edible fruit Broom	Endocarp/Juice Outer part of old fruit.	Young/matured Matured endocarp used as source of oil
Cryostachys lakka Becc.	Pomutoson (Ka)	Ornamental	Whole plant	
Eugissonia utilis Becc. FRCSE 393	Paluon (Ka)	Edible Sago Dart's cock	Pith Pith	Pressed Matured pith
Licuala spp.	Silan/Tanom (Ta)	Vegetable	Pith	Cooked
Meteroxylon sagu Rottb.	Lumbio (Ta)	Edible sago	"	Pressed
Oncosperma tigillarium (Jack) Ridl	Nibong (Ka)	Vegetable	Tip	Raw or cook

Botanical name and voucher specimen no. (if any)	Common names (Dialect)	Category	Part Used	Method of Use
PALMAE cont.				
Pandanus leuconatus B.C. Stone FRCSE 395	Boboungis (Ka)	Matting	Leaves	Dried and woven
Plectocomiopsis geminiflora (Griff.) Becc. FRCSE 411	Ambarua (Ta)	Vegetable	Stem's shoot	Cooked
SAPINDACEAE				
Lepisanthes fruticosa (Roxb.) Leenh. SAN 138272	Talikasan (Ti)	Edible fruit	Aril	Ripe
Nephelium lappaceum L.	Kayakan (Ka)	"	"	"
N. ramboutan-ake (Labill.) Leenh.	Rumokot (Ka)	"	"	"
SOLANACEAE				
Solanum turvom Sw.	Lintahun (Ta)	Softener	Fruit	Cooked with meat
FUNGI				
Polyporus umbellatus FRCSE 392	Ongkulan (Ka)	Edible mushroom	–	Cooked
Auricularia auricula-judae FRCSE 394	Tondungol (Ka)	"	"	"
Cantharellus cibarius	Sunsulit (Ka)	"	"	"
FERN				
Nephrolepis biserrata (Sw.) Schoot.	Pakis (Ta)	Vegetable	Tip	Cooked

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In most of the treatments with medicinal plants, the herbal preparations are administered orally. The specific amount of material could not be ascertained. The recommended dosage is normally a handful of leaves or few pieces of root, rhizome, stem or bark, flowers, fruits and seeds. For small herbs, the whole plant or a few plants may be used. Leaves are the most common part used. The roots are the second-most common part used in traditional medicine, followed by bark and the reproductive parts. They are used fresh or dry, chewed, or boiled in water and the decoction taken as tea. The herbal preparation is usually taken once or twice daily until the patient recovers. The ailments described by the plant informants have been interpreted according to Pescar and Nelson (1996).

Discussion

The knowledge of medicinal plants in Murut communities is normally passed on from generation to generation but this practice seems to be vanishing. It was estimated that there are only two to three persons in any village who know the many uses of plants, and they were usually the elderly. When asked if they still relied on herbal treatment, the response was that not all of the medicinal plants are used nowadays. Some of the reasons given were:

Only the elderly know most of the plants and where to get them: Some of the very useful medicinal plants are only known by the elderly, but because they are very old and their vision is mostly now poor this makes it difficult for them to recognize the plants. Even if their vision is good they may not be able to walk far.

Preparation of herbs takes time including finding the plants in the forest: The process of looking for the plants in the forest and the preparation of remedies is very laborious compared to buying them at the nearby market or going to the hospital. Each of the districts has its own government district hospital except for Kalabakan district where a government clinic is provided. These modern facilities make rural people dependent on ready-made modern medicines.

Religion: Some religions do not allow the use of any biological material for medicines.

Lost of interest of younger generations: Ancient customs of plant utilization are gradually disappearing. The younger generation is generally unable to recognise the plants nor their traditional use. They are dependent on modern medicines.

Migration to urban areas: Many Muruts people have migrated to urban areas to find paid work and access modern facilities.

Opening of forests: In recent years, Sabah faced a very rapid opening of forest for timber harvesting, development and agriculture. This has caused enormous changes to occur in Murut lives and in the way they utilize plant resources.

Realizing the economic potential of these medicinal and other useful plants and to conserve them, activities at Federal as well as at State level have been launched to save these plants from being neglected. At a Federal level, the Ministry of Education has introduced co-curriculum activities such as establishing a medicinal herb garden. School children at primary and secondary level are encouraged to learn about the medicinal value of some plants, for example, *Eurycoma longifolia* or 'Tongkat Ali' and *Morinda citrifolia* or 'Mengkudu'. The Ministry of Health Malaysia has also conducted a nation-wide campaign on the use and conservation of traditional medicinal plants. To date the Ministry has already registered about 1,300 medicinal plant products that are being sold in the markets. At the State level, the Sabah government has passed a new law this year [2001] concerning the use of indigenous plants; it is called the Sabah Biodiversity Enactment. The purpose is to regulate the studies of useful plants such as medicinal plants and for conservation of natural resources. The Chief Department of Sabah established a working group comprising all State departments, agencies and NGOs called the Sabah Herbal Industry Committee early this year [2001]. The objectives are to act as the Secretariat at State level to systematically document and regulate the utilization of the indigenous medicinal plants in a sustainable manner.

Conclusions

From this survey we have documented a total of 91 species of plants that are being used by Muruts throughout Sabah. Sixty-eight species are medicinal plants and 64 species are other useful plants, which includes wild fruit, handicraft materials, plants for social and religious purposes, and poisons. These plants are available in direct vicinity of the village or in the nearby forest.

The Muruts have a rich ethnobotanical knowledge, but this is fading due to migration to urban areas, a loss of interest among the young, religious restrictions or dependence on modern medicine. Opening of forest areas for agriculture, development and timber harvesting have also made the resources scarce.

The wealth of Murut knowledge of medicinal and other useful plants points to a great potential for research and the discovery of new drugs to fight diseases, new foods and other new uses.

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APPENDIX 1: LIST OF MEDICINAL PLANTS OF MURUTS

Botanical Name	**Murut Name**	**Collection No.**
Acorus calamus L.[3]	Kusul (P)	–
Aglaia rivularis Merr.[1]	Kalambiau	–
Aglaonema oblongofolium Schoot.*	Pilonos (Ta)	FRCSE 424
Agave cf. weberi[3]	Sipak (Ka)	–
Airgantha borneensis (Oliv.) Brummit.[3]	Molisun Matamis (Ti)	SAN 138299
*Alocasia macrorrhizos**	Buntui (Ke)	–
Aloe vera L.[2]	Bunga Raja	–
Alstonia angustifolia Wall ex DC[3]	Tambailik (Ti & Ta) Tombirog (Ke)	SAN 138289
Amaranthus spinosus L.[3]	Sansam Sau (P)	–
Ananas comosus (L.) Merr.*	Tingkauran (P)	–
Annona muricata L.[2]	Lampun Belanda	–
Antidesma montanum Bl.[2]	Damat Mandalom (Ti)	SAN 138297
Areca catechu L.[2]	Kusauh	
Arenga undulitafolia Becc.[3]	Polod (Ta)	–
Aristolochia papillifolia Ding Hou.[3]	Babas Lontong (Pa & Ta)	FRCSE 412
Artocarpus elasticus Reinw ex Bl.[2]	Kikian	
Artocarpus tamaran Becc.[3]	–	–
Baccaurea lanceolata (Miq.) Muell-Arg.[3]	Limposu (Pa)	–
Bauhinia sp.[2]	Pilasang	–
B. semibifida Roxb.[1]	Babaya Songkulibang	–
Begonia sp.[1]	Pamamampang	–
Bixa orellana L.[3]	Puloh (Ta)	FRCSE 409
Blechnum orientale L.*	Paku	–
Blumea balsamifera Harn.*	Tawawoh (P & Ta)	–
B. riparia (Bl) DC[3]	–	FRCSE 407
Bombax ceiba L.[3]	Kapok (Pa)	–
Bridella stipularis (L) Bl.[3]	Bolingkut (Ti)	SAN 138279
Caesalpinia sappan L.[2]	Sapang	–
Calamus pogonacanthus Becc. Ex. K. Winkl.[1]	Sambunil	–
Canarus sp.[2]	Dalat	–
Capsicum frutescens L.[2]	Baras	–
Casearia grewiaefolia Vent. Var. *grewiaefolia*[3]	Salokdan (Ti)	SAN 138276
Cassia alata L.*	Balilang (Pa), Emon (Ke)	–
Centotheca lappacea (Linn.) Desv.[1]	Pampopoi	–
Centella asiatica (L.) Urban*	Pegaga	–
Clausena excavata Burm.[1]	Tataih Nu Manuk	–
Colocasia antiquorum Schott.[1]	Ungkubab Nu Labi	–
Combretum nigrescens King[3]	Damat Durnalarom (Ti)	SAN 138290
Cocos nucifera L.*	Piasau (Ta)	–

P = Paluan, Ka = Kalabakan, Ke =Keningau, Ti = Timugon and Ta = Tagal

[1] = Collected by Guntavid (1992) [2] = Fasihuddin & Hasmah (1992)

[3] = Collected by Kulip (2001) * = Collected by all authors

Botanical Name	**Murut Name**	**Collection No.**
Cordyline fruticosa (L.) Goeppert[3]	Pipisokalaganan (Ti)	SAN 138296
Coscinium fenestratum (Gaerth.) Colebr.[3]	Babas Lingungan (Ta)	FRCSE 433
Costus specious Koen.*	Insasabu (Ka & Ta)	FRCSE 416
Curculigo latifolia Dryander*	Tambaka (Ta)	FRCSE 413
Curcuma domestica Val.[3]	–	–
Cyathula prostrata (L) Bl.[3]	Samsam Bawi (Ti)	SAN 138278
Cymbopogon citratus (Nees.) Stapf.*	Sohumau (Pa)	–
Cyrtandra aff. *areolata* (Staff.)Bl Burtt.[3]	Pohodo (Ta)	FRCSE 428 & 431
Dendrobium umbellatom Reichb.f.[2]	Tingasu	–
Desmos teijsmannii (Boert.)Merr.[3]	Molisun Rumungkut	SAN 138271
Dillenia grandifolia Wall.ex. Hk.f. et. Thorn[2]	Tembakau (Ka)	–
Dillenia sp.[2]	–	–
Dinochloa sp.[2]	Baran	–
D. scabrida S. Dransf.[2]	"	–
Dracaena umbratica Ridl.[1]	Dolol Apui	–
Elephantopus scaber L.[2]	Lambrunai	–
E. tomentosus L.[3]	Honsigup (Ta)	FRCSE 419
Eleusine indica (L) Gaetner.*	Liagon (Pa)	–
Erechtites valerianaefolia L.[2]	Sumayon	–
Eupathorium odoratum L.*	Lambaian (Pa)	–
Eurycoma longifolia Jack.*	Duli (P) Ruli (Ta)	–
Fibraruea tinctoria Lour.[3]	Tolungon (P & Ta)	–
Ficus aurantiacea Griff.[2]	Silabon-rondoh	–
F. deltoidea Jack.[2]	Agolauran	
F. lepicarpa Bl.[3]	Lintotobow (Ke)	–
F. racemosa L. var *elongata*[3]	Tandilan (P)	–
Ficus sp.[2]	Mamponoh	–
Flagellaria indica L.[3]	Waau (Ti)	SAN 138300
Forrestia griffithii C.B. Clarke[1]	Tatapis Da Aputulan	–
Garcinia mangostana L.[3]	Timpurog (Pa)	–
Glochidion macrostigma Hk.f.?	Sondot Laling (Ti)	SAN 138273
Graptophyllum pictum (L.) Griffithi[2]	Lalamih	–
Hanguana malayana Jack.[1]	Tatapis Da Umbir	–
Helecia serrata (R.Br.) Bl.[3]	Andaun Motukal (Ti)	SAN 138291
Hibsicus rosa-sinensis L.[2]	Bunga Raya	–
Hibiscus sp.[3]	–	FRCSE 408
Homalium foetida (Roxb.) Benth[1]	Lulumada	–
Homalomena propingna Schoot.[3]	Nyato (Ta)	FRCSE 414
Homalanthus populneus Geisel.[2]	Sipapaloi	–
Hoya sp.[1]	Pongkukubab	–
Hydnophtyum formicarium Jack[3]	Musalag Noh Kilou (P)	–
Hypoestes sp.[2]	Matopait	–
Hypolytrum nemorum (Vahl) Spreng[1]	Balasan Sungei	–

P = Paluan, Ka = Kalabakan, Ke =Keningau, Ti = Timugon and Ta = Tagal

[1] = Collected by Guntavid (1992)

[2] = Fasihuddin & Hasmah (1992)

[3] = Collected by Kulip (2001)

* = Collected by all authors

Botanical Name	**Murut Name**	**Collection No.**
Hyptis capitata Jack.[3]	Baing-baing (Ti)	SAN 138287
Imperata cylindrica (L) Rausch.*	Lalang (Ka)	–
Ixora capillaries Boern.[3]	Angin Tolunsung (Ti)	SAN 138275
Jasminum aculeatum (Blanco) Merr.[3]	Onsom-Onsom (Ti)	SAN 138285
Jatropha curcas L.[3]	Jarak (Ke)	–
Justicia gendarussa L.[3]	Insasahi (Ka)	–
Kalanchoe pinnata (Lam.) Pers.*	Tanom Tombiog	–
Lansium domesticum Corr. Serr.[3]	Langsat (Ka & P)	–
Leucosyke capitella (Poir.) Wedd.*	Balawian	–
Lindera pipericarpa Boerl.[3]	Laindos (P)	–
Litsea graciae Vidl.[3]	Novolo (P), Pengolaban (Ta)	FRCSE 420
L. odorifera Valeton[3]	Lawang (P)	–
Macaranga gigentifolia Merr.[3]	Binawong (Ka)	–
Micromelum minatum (Frost.) Seem[3]	Kimamansak (Ka)	–
Millettia nieuwenhuisii J.J. Smith[3]	Ramus (Ka)	FRCSE 389
Mimosa pudica L.*	Sikot Mou (Ke), Tanom Molu (Ka)	–
Neonauclea calycina Merr.[3]	Kembalu (P)	SAN 142048
Oroxylum indicum (L) Vent.[3]	Ulunan Sangku (Ti)	SAN 138284
Orthosiphon aristatus (Blume) Miq.[3]	Misai Kucing (Ta)	–
Parashorea malaanonan Merr.[1]	Melapi	–
Parkia singularis Miq.[3]	Kundai (P)	–
Paspalum conjugatum Berg.[2]	Belandak	–
Pavetta sp.[1]	Buntungon	–
Pedilanthus tithymaloides Poit.*	Tatapis Tindukon	–
Phaeanthus ebrasteleolatus (Pres) Merr[3]	Korokos (Ti)	SAN 238288
Phyllanthus urinaria L.[3]	Pilujala (Ti)	SAN 138282
Piper betle L.*	Molur Malat (Ti)	SAN 138277
Piper carinum Bl.*	Kimput-Pilot (Ta)	FRCSE 423
Plectocomiopsis geminiflora (Griff.) Becc.[3]	Ambarua (Ta)	FRCSE 411
Plumeria rubra L.[1]	Campaka	–
Poikilospermum suaveolens (Bl.) Merr.[3]	Bunatol (Ti)	SAN 138230
Polyalthia sp.[1]	Ubat Puru	–
P. bullata King[2]	Serat	–
Praravinia suberosa Merr.[1]	Kingkimut	–
Pronephrium asperum (Prest.) Holtt[2]	Ingkakahas	–
Psidium guajava L.*	Kaliabas (P), Liabas (Ka)	–
Psychotria cf. *sammontosa* Bl.[3]	Solovondo (?)	FRCSE 406
Saurauia longistyla Merr.[1]	Usod-usod	–
Selaginella argentea Sym.[2]	Sondotnulogo	–
Semecarpus cuneiformis Blanco.[3]	Kutang (Kg)	–
Schismatoglottis sp.[1]	Pongongondog	–
Schindapsus perakensis Hook.F.[1]	Pagawangan	–
Scleria bancana Miq.[1]	Onininsil	–
Shorea spp.[3] (Eushorea group)	Omnompik (Ta)	–

Botanical Name	**Murut Name**	**Collection No.**
Sida rhombifolia L.[3]	Dalupang (P)	–
Sindora sp.[2]	Talikakasam	–
Solanum torvum Sw.*	Lintahun (Ka)	–
Spatholobus cf. *gyrocarpus* Benth in Miq.*	Ramus	FRCSE 410
Stachytarpheta jamaicensis (L.) Vahl.[2]	Indalupang	–
Stenochlaena palustris (Brum) Bedd[2]	Kuraunolot	–
Stephania corymbosa (Bl) Wel.P.[3]	–	FRCSE 396
Strychnos ignatii Berg.[1]	Tataga Do Sangi	–
Synedrella nodiflora (L) Gaertn.[3]	–	FRCSE 418
Tetrastigma diepenhostii (Mq)Latiff[3]	Daramatin (Ti)	–
Tinospora crispa (L) Hook.f. & Thomson*	–	–
Trichosanthes cucumerina L.[3]	Molisun Mamulal (Ti)	SAN 138292
Urena lobata L.[3]	Injilokot (Ti)	SAN 138286
Urophyllum nigricans Warnh.[3]	–	FRCSE 425
Uvaria grandiflora Roxb.[3]	Nolilitan (Ti)	SAN 138270
Vitis trifolia (L.) Domin.[1]	Susumoloi	–
Zea mays L.[3]	Halai (Ka)	–

APPENDIX 2: PLANT FAMILIES MOST COMMONLY USED FOR MEDICINAL PURPOSES.

Euphorbiaceae (10 spp.); Leguminosae (6 spp.); Rubiaceae (5 spp.); Araceae (4 spp.); Gramineae (4 spp.); Menispermaceae (4 spp.); Annonaceae (3 spp.); Lauraceae (3 spp.); Moraceae (3 spp.); Malvaceae (3 spp.); Agavaceae (2 spp.); Amaranthaceae (2 spp.); Labiatae (2 spp.); Palmae (2 spp.) and Piperaceae (2 spp.).

One species each:

Acanthaceae , Anarcadiaceae, Apocynaceae, Aristolochiaceae, Asteraceae, Begoniaceae, Bixaceae, Bromeliaceae, Cecropiaceae, Combretaceae, Costaceae, Cucurbitaceae, Dilleniaceae, Dipterocarpaceae, Flacourtiaceae, Flagellariaceae, Gesneriaceae, Guttiferae, Hypoxidaceae, Meliaceae, Myrtaceae, Oleaceae, Proteaceae, Rutaceae, Simaroubaceae, Solanaceae, Vitaceae, Zingiberaceae

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P = Paluan, Ka = Kalabakan, Ke =Keningau, Ti = Timugon and Ta = Tagal

[1] = Collected by Guntavid (1992)

[2] = Fasihuddin & Hasmah (1992)

[3] = Collected by Kulip (2001)

* = Collected by all authors

Considerations for a revision of the fern family Vittariaceae for Flora Malesiana

Stuart Lindsay

Abstract

Lindsay, S. (Arnold Arboretum & Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138, USA) 2003. Considerations for a revision of the fern family Vittariaceae for Flora Malesiana. Telopea *10(1): 99–112.* The Vittariaceae is a family of mostly tropical epiphytic or lithophytic fern species. The family is particularly well represented in Malesia but the number of species present and the genera in which they should be recognised is currently uncertain. This paper explains why. Three factors are discussed: the impact of new molecular data on the traditional concepts of genera in the Vittariaceae; the uncertain taxonomic position of the monotypic (and Malesian endemic) genus *Rheopteris*; and the possibility that unrecorded species, including undescribed ones, exist within the region only as gametophytes.

Introduction

A monographic revision of the fern family Vittariaceae is long over-due. The only monograph in existence is that prepared by Fée and published in 1852 as parts 3 & 4 of his *Mémoires sur la Famille des Fougères*. Part 3 (Fée 1852a) describes c. 60 species (and c. 70 synonyms) of Vittariaceae while part 4 (Fée 1852b) describes c. 25 species (and c. 40 synonyms) of *Antrophyum*. Fée's monograph (which also includes superb illustrations of 27 species) is, undeniably, an impressive account of almost all the Vittariaceae known in the mid-19th century but it cannot now be regarded as representing anything close to a comprehensive treatment of the family. Over the last 150 years or so, c. 220 new species have been described for the family, c. 140 new name combinations have been made, and almost half of the species recognised as Vittariaceae by Fée have been moved to, and accepted in, other fern families (see *Index Filicum* by Christensen 1905-1906, and its seven supplements: Christensen 1913, 1917, 1934; Pichi-Sermolli 1965; Jarrett 1985; Johns 1996, 1997). In total, more than 550 species names have been assigned to various concepts of the Vittariaceae but the family, as recognised today, probably contains no more than 100–130 species.

Species of Vittariaceae are most strongly represented in the damp forests of the New and Old World Tropics (including many islands of the Pacific but not really including tropical Africa where the family is relatively poorly represented). Although the majority of species are tropical, a significant number of species can be found outside the tropics, in places such as south-eastern United States, Argentina, Tristan da Cunha, Easter Island, South Africa, Nepal, China, South Korea and Japan. According to Kramer (1990), the Vittariaceae appear to be a somewhat isolated, very natural (but see discussion of *Rheopteris* later in this paper) group of leptosporangiate ferns, as a whole now well adapted to an epiphytic or lithophytic habitat and therefore probably of secondarily much simplified structure. All of them possess creeping rhizomes (not immediately obvious in some short-creeping species) on which the fronds (usually pendulous, because they lack sclerenchyma) are usually arranged in two rows on the dorsal surface. The fronds of most species are simple and have reticulate venation, but in a few species in which the frond laminae have become much reduced the venation consists simply of a mid-rib with or without a few, free, lateral veins. An interesting feature, which (along with the lack of sclerenchyma) has proved to be a valuable diagnostic character for the family, is the presence of spicule cells (elongated idioblasts containing needle-like crystals; perhaps of silica) in the epidermis of the fronds (Williams 1927). The sporangia are fairly constant in form throughout the family and in most species are assembled in simple or branched soral lines. These soral lines usually also contain paraphyses, the presence/absence, shape or colour of which can be characteristic of certain species or species groups (e.g. Fée 1852a, 1852b; Benedict 1907; Shaffer-Fehre 1996). Little is known about the gametophytes of the Vittariaceae but those of the few species that have been investigated (actually 18 species; 12 New World; 6 Old World) are ribbon-shaped and perennial (gametophytes of most fern species are heart-shaped and short-lived) and all, except one species, bear filamentous gemmae (also rare in ferns) with which they can propagate themselves asexually (Atkinson & Stokey 1964; Nayar & Kaur 1969, 1971; Farrar 1974, 1985; Emigh & Farrar 1977; Sheffield & Farrar 1988). The morphology and ecology of the gametophytes of Vittariaceae are discussed in more detail later in this paper.

Generic delimitation

Traditionally recognised genera

The uniform and simple morphology exhibited by the sporophytes of the Vittariaceae has offered taxonomists few characters useful for classification; disagreement over the interpretation of the few available characters has resulted in the recognition by different authors of between five and 10 genera (e.g. Benedict 1911; Williams 1927; Copeland 1947; Tryon & Tryon 1982; Kramer 1990). That said, most modern texts do agree, at least, with the recognition of five or six main genera based largely on differences in the size and shape of fronds, venation, and soral arrangement. These five or six genera (in order of increasing size) (see Kramer 1990) are: *Rheopteris* Alston (recognised after 1956); *Anetium* (Kunze) Splitg.; *Hecistopteris* J.Sm.; *Monogramma* Comm. ex Schkuhr; *Antrophyum* Kaulf.; and *Vittaria* Sm.

Rheopteris, as currently recognised, is a monotypic genus confined to New Guinea; the single species *Rheopteris cheesmaniae* Alston shares certain characters with other members of the Vittariaceae (e.g. spicule cells), but other characters (especially the pinnate fronds, free venation, and round sori) are so atypical of Vittariaceae that the taxonomic position of *Rheopteris,* and its current inclusion in Vittariaceae, demands further investigation (*Rheopteris* is discussed in more detail later in this paper because of its significance to the generic framework of the Vittariaceae in Malesia).

Anetium is also a monotypic genus; its only species *Anetium citrifolium* (Kunze) Splitg. is widespread in tropical America. *Anetium citrifolium* deviates somewhat from typical Vittariaceae in that the sporangia are not (or are only partially) arranged in soral lines.

Until relatively recently, *Hecistopteris* was also considered to be a monotypic genus widespread in tropical America. However, a second species, currently only known from Ecuador, was described in 1995 (Moran & Øllgaard 1995) and a third species, currently only known from Guyana was described in 1998 (Kellof & McKee 1998). All three species are minute, easily over-looked, epiphytes with fronds that deviate somewhat from typical Vittariaceae in having forked or cleft laminae and dichotomously branched veins.

Monogramma, in its broadest sense, is a genus of eight species found in the warmer parts of the Old World, particularly the east-African islands, Sri Lanka, and the Malesian and Pacific regions. Like *Hecistopteris,* most species of *Monogramma* are also minute, easily overlooked epiphytes. It is in this genus (and to a lesser extent in *Vittaria*) that frond laminae can become so reduced that venation consists simply of a mid-rib. Although not universally accepted, the genus *Monogramma* is sometimes split into two genera: *Monogramma s.s.,* for the two species in which the venation consists simply of a mid-rib, and *Vaginularia* Fée, for the six species in which the venation consists of a mid-rib plus a few (albeit, often indistinct) lateral veins.

Vittaria and *Antrophyum* have always been regarded as the two main genera within Vittariaceae. The size of each of these genera has never been properly established; published estimates of species numbers range from 50–150 for *Vittaria* and from 40–80 for *Antrophyum. Vittaria* (as recognised by most botanists in the 20th century, prior to being re-defined by Crane et al. (1995) and Crane (1995, 1997) — see below) is a genus of tropical (mostly), or warm-temperate species, many of which are not clearly defined. The generic name is derived from the Latin word '*vitta*', meaning 'ribbon', an allusion to the ribbon-like shape of the fronds of most species. Species of *Vittaria* are also commonly referred to as 'Shoestring Ferns', 'Tape Ferns' or 'Grass Ferns'. *Vittaria* is widely acknowledged to be a difficult and confused genus in need of a thorough revision (e.g. Kramer 1990). In addition to having characteristic ribbon-like fronds, species of *Vittaria* are also usually characterised by a pair of long, continuous soral lines, often immersed in grooves in the laminae or covered by the reflexed unmodified leaf margin. Although not universally accepted, the genus *Vittaria* has, sometimes, been split into smaller genera or subgenera. Benedict (1911, 1914) proposed the recognition of two subgenera: subgenus *Radiovittaria* for species with (sub)erect radial stems (all American) and subgenus *Vittaria* for those without (sub)erect radial stems. Maxon (1908) proposed that one *Vittaria* species with particularly unusual venation (*Vittaria angustifolia* (Sw.) Baker; the only *Vittaria* with pluriseriate venation, instead of biseriate venation) should become the sole member of the monotypic genus *Ananthacorus. Ananthacorus angustifolius* (Sw.) Underw. & Maxon (which is still often known by the synonym *Vittaria costata* Kunze, e.g. Moran 1995) is widespread in tropical America.

Antrophyum (as recognised by most botanists in the 20th century, prior to being redefined by Crane et al. (1995) and Crane (1995, 1997) — see below) is a genus of tropical or warm-temperate species best represented in south-east Asia. Fronds of *Antrophyum* are similar in shape to those of *Anetium,* but in *Antrophyum* the sporangia are arranged along the reticulate veins in such a way that the soral lines may join to form a 'soral net'. Many species of *Antrophyum* are ill-defined and this genus is also in need of a thorough revision (Kramer 1990). There have been suggestions (e.g. Moore 1857; Benedict 1907, 1911; Christensen 1925) that the genus *Antrophyum* should be split into several smaller genera or subgenera but, as in *Vittaria,* the proposed subdivisions have not been universally accepted. The four subgenera proposed by Benedict in 1907 were: *Antrophyum s.s.,* for species with tetrahedral spores in which the costa evanesce above the base and in which there are paraphyses amongst the sporangia in the soral lines (only Old World species have this combination of characters); *Polytaenium* (Desv.) Benedict for species with tetrahedral spores in which veins originate from a full-length mid-rib (percurrent costa) and in which there are no paraphyses amongst the sporangia in the soral lines (only New World species have this combination of characters); *Scoliosorus* (T.Moore) Benedict for one fairly widespread New World species (*Antrophyum ensiforme* Hook.) with, among other unusual characters, bilateral spores and paraphyses; and *Antrophyopsis* Benedict for four African 'species' (nowadays recognised as *Antrophyum mannianum* Hook. and three varieties of *Antrophyum boryanum* (Willd.) Spreng.) also with bilateral spores and paraphyses.

Christensen (1925) proposed another subgenus, *Bathia* C.Chr, for three species in Madagascar (unknown to Benedict) that not only have bilateral spores and paraphyses but which, in general morphology and anatomy, are somewhat intermediate between *Antrophyum* and *Vittaria*.

The impact of new molecular characters

The previous section summarized the intrafamilial taxonomy of the Vittariaceae as it was understood in the early 1990's, a few years before the start of the 'molecular revolution' in fern systematics. In 1995, a group of researchers at Iowa State University, U.S.A., published the results of the first (and as yet, only) phylogenetic analysis of *rbc*L gene sequences from 22 species of Vittariaceae (Crane et al. 1995). Despite a bias towards New World species (the material they found easiest to obtain), their analysis clearly indicated that *Vittaria* and *Antrophyum* (as each has traditionally been recognised on the basis of sporophyte morphology) are, respectively, polyphyletic and paraphyletic. This new information could have significant implications for the future classification and content of these genera and the family as a whole. Indeed, by further analyzing their molecular data, Crane et al. managed to re-organize their 22 study species into nine groups (putative 'genera') that were strictly monophyletic (Figure 1).

On the basis of this, and the discovery that the topology of the tree based on *rbc*L sequence data was also well supported by four morphological characters (spore type: tetrahedral or bilateral; shape of the terminal cell on the soral paraphyses: absent, slender, funnel-shaped or round; pattern of gemma development: absent, produced singly or produced in inter-connecting pairs; and the arrangement of the fronds on the rhizome: distichous phyllotaxy or polystichous phyllotaxy) Crane (1997) proposed a revised circumscription of the genera within Vittariaceae (10 or 11 in his opinion) and gave new combinations for 30 species. Of the six main genera traditionally recognised in Vittariaceae on the basis of sporophyte morphology (outlined in the previous section), *Rheopteris, Anetium, Hecistopteris* and *Monogramma* remain unchanged (*Rheopteris* and *Monogramma* were not included in Crane's molecular study). *Antrophyum* (as traditionally recognised) was split into three genera: *Antrophyum* s.s., containing only Old World species; *Polytaenium*, containing only New World species; and *Scoliosorus*, a small genus containing two Old World (African) species and one New World species. Thus the new molecular characters generated by Crane et al. provided additional support for the earlier suggestions of Benedict (and others) that Old and New World species of *Antrophyum* s.l. are different, and that within the Old World the African and Asian species are also different.

Perhaps the most interesting and novel piece of information to come out of this study in relation to *Antrophyum* s.l. is the apparent relationship of the unusual New World species *Antrophyum ensiforme* Hook., (Benedict's subgenus *Scoliosorus*), with the two African species *Antrophyum boryanum* (Willd.) Spreng. and *Antrophyum mannianum* Hook. (Benedict's subgenus *Antrophyopsis*). Benedict was clearly aware of certain similarities between these species (especially in relation to their spores and paraphyses), but there is no evidence in the literature that he had contemplated a close relationship between *Antrophyum ensiforme* in America and the other two species in Africa.

Vittaria (traditionally recognised as the largest genus in the Vittariaceae and pantropical) was also split by Crane into three genera: *Vittaria* s.s. was re-defined as a very small genus containing only six species, five of which are confined to the New World. The exception, *Vittaria isoetifolia* Bory, is confined to Africa and the east-African islands. All the New World species formerly recognised as '*Vittaria*' but now

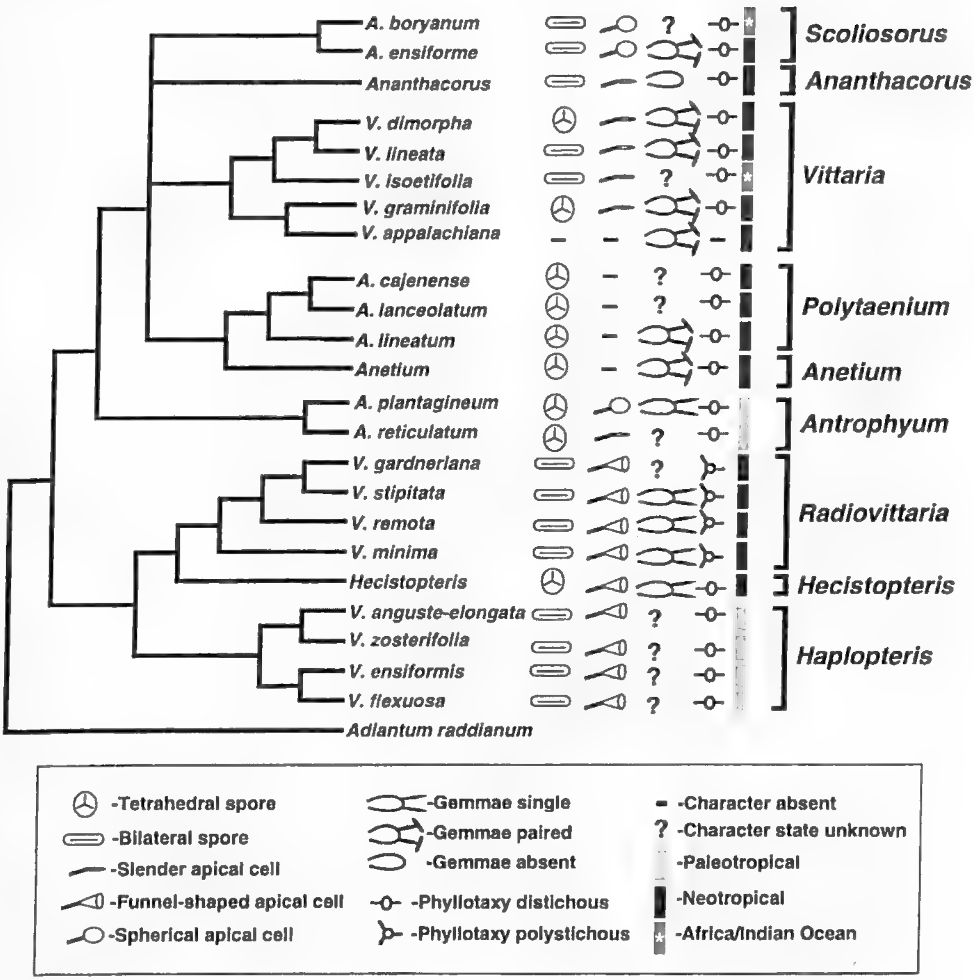

Fig. 1. A strict consensus tree resulting from phylogenetic analysis of *rbcL* gene sequences from 23 species of Vittariaceae (adapted from Crane et al. 1995 and Crane 1997). Symbols showing the states of four morphological characters are mapped onto the tree. These characters (and their states) are: spore type (tetrahedral or bilateral); shape of the apical cell on the soral paraphyses (absent, slender, funnel-shaped or spherical); pattern of gemma development (absent, produced singly or produced in inter-connecting pairs); and the arrangement of the fronds on the rhizome (distichous phyllotaxy or polystichous phyllotaxy). The blocks to the right of the morphology symbols indicate the geographical distribution of each species. Brackets to the far right indicate the revised generic circumscription of Vittariaceae proposed by Crane. Note: (1) The consensus trees shown in Crane et al. (1995) show only 22 species of Vittariaceae because *rbcL* sequence data for *Vittaria appalachiana* was not incorporated into the analysis until a later date. The explanation for why sporophytic morphological characters are absent in this species is given in the 'Independent gametophytes' section of this paper. (2) At the time of Crane's initial molecular analysis *Hecistopteris* was believed to be a monotypic genus; accordingly the label '*Hecistopteris*' in Figure 2 refers to *Hecistopteris pumila* (Spreng.) J.Sm.

excluded from it were placed in the genus *Radiovittaria*. This was the first time that this name had been used at the generic level, but the content of this genus (except for the inclusion of one additional species) is no different from that of subgenus *Radiovittaria* proposed by Benedict almost 90 years ago.

The third segregate genus of *Vittaria* recognised by Crane was *Haplopteris*. In contrast to *Radiovittaria*, this was not the first time that this name had been used at the generic level in Vittariaceae but its previous use was extremely brief and a long time ago (predating but not appearing in Fée's monograph of 1852). *Haplopteris* was resurrected and re-defined by Crane to accommodate nearly all the Old World species formerly recognised as '*Vittaria*'. Eleven of the 20 species that have already been moved to *Haplopteris* are Malesian.

The genus *Rheopteris*

Another factor that must be considered when deciding on the generic framework of the Vittariaceae in the Flora Malesiana region is the currently uncertain taxonomic position of the genus *Rheopteris* Alston. *Rheopteris*, as currently defined, is a monotypic genus known from only three collections in the mountains of West Sepik Province, Papua New Guinea. The genus and its only species, *Rheopteris cheesmaniae* Alston, were described in 1956 based on examination of a specimen (at BM) collected by L.E. Cheesman in the Toricelli Mountains in 1939 (Alston 1956). The other two collections were made by J. Croft et al. in 1982 during a PNG National Herbarium (LAE) Botanical Expedition to the Bewani Mountains (approximately 100 km west of the original collecting locality). Since *R. cheesmanie* was described there has been considerable uncertainty as to what its closest relatives might be. In spite of this, and the fact that Alston himself did not propose a family for his genus, most workers have (albeit, with some reservations) placed *Rheopteris* in Vittariaceae (e.g. Kramer 1990; Tryon & Lugardon 1990; Brummitt 1992).

A revision of the Vittariaceae for Flora Malesiana requires that evidence must be produced to either keep *Rheopteris* in Vittariaceae or exclude it. Anatomical and morphological features including spicular cells, clathrate scales, soral paraphyses, smooth spores, and the absence of indusia do suggest a relationship with Vittariaceae, but the stiff, erect, simply pinnate fronds — with pinnae superficially resembling those of species in the genus *Lindsaea* (Alston 1956) — and circular sori (Figure 2) are distinctive characters not shared with any other species currently recognised in Vittariaceae. *Rheopteris cheesmaniae* also has free veins, a relatively rare character in Vittariaceae.

Resolution of the taxonomic problem surrounding *R. cheesmaniae* would undoubtedly be made a lot easier if the species could be relocated in the wild and frond and viable spore material were collected for laboratory and glasshouse studies. It would be fascinating to see the results of an improved molecular phylogeny of the Vittariaceae that included *Rheopteris* (as well as the two other Old World genera of Vittariaceae missing from Crane's study: *Monogramma* and *Vaginularia*). Studies on the morphology and development of the gametophytes and gemmae (if any?) of *R. cheesmaniae* would also be of particular interest, given the significant correlation of gametophytic and molecular characters demonstrated in Crane's study (Figure 1). Additional field observations of adult plants are also required to provide a more accurate and complete description of *R. cheesmaniae*, the size and growth habit of the sporophyte, and the ecology of both generations. Alston described Cheesman's plant as an 'epiphyte' with a 'creeping rhizome', but as her largest rhizome fragment is only 4 cm long, nothing much can be deduced about its original length or branching pattern. The label of *Croft 1749* (duplicate at A with rhizome fragment 7.5 cm long) states '... climbing fern ...'

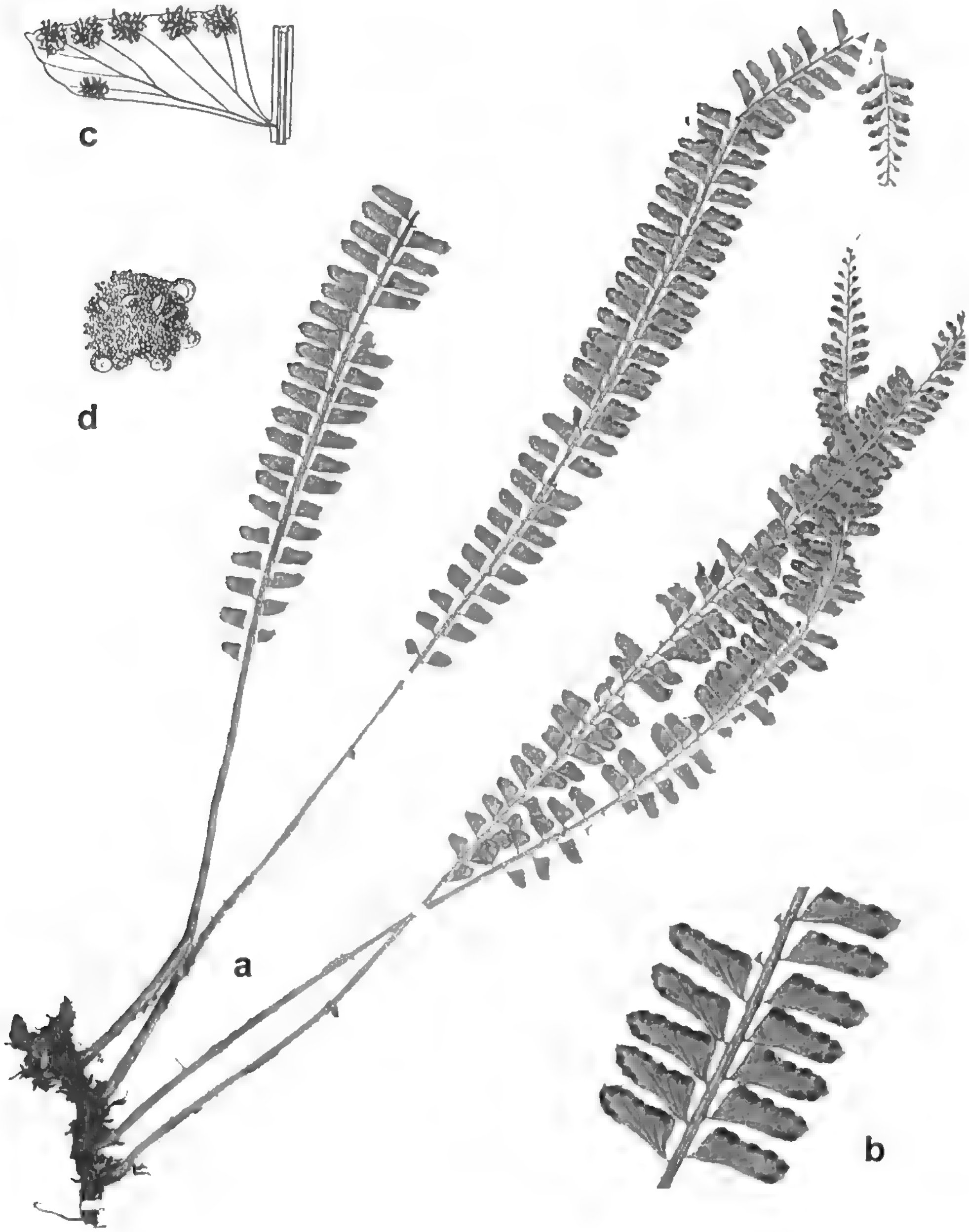

Fig. 2. *Rheopteris cheesmaniae* Alston, the sole representative of the monotypic (and Malesian endemic) genus *Rheopteris*: **a**, scan of the most recent collection of this species: *Croft 1749* collected in the West Sepik Province of Papua New Guinea in 1982 (Duplicates LAE, K, L, NSW, CHR, A - illustrated here); length of rhizome fragment, 7.5 cm; length of longest frond, 44 cm; note that the frond on the left is incomplete and a 4.5 cm section near the tip of the longest frond has been turned over to reveal the dorsal surface; although it is not obvious, this section of the frond is also fertile; **b**, magnified portion of a frond showing pinnules similar in shape to those of *Lindsaea* and round, exindusiate, sori; pinnules c. 1.2 – 1.4 cm long, c. 0.5 cm broad; **c**, illustration of a pinnule showing the free venation and the position of the sori in relation to these; **d**, illustration of a sorus (c. 0.1cm diameter), typically composed of more paraphyses than sporangia. Illustrations (**c**) and (**d**) drawn by Monica Shaffer-Fehre (Royal Botanic Gardens Kew). These and additional line-drawings of *R. cheesmaniae* (including paraphyses and scales) can be found in Johns (1995).

and that of *Croft 1716* (duplicate at A with rhizome fragment 13.5 cm long) states' … climbing epiphyte …' but as with the type specimen there is insufficient material or comments on the labels to understand the original growth habit of the plants. According to the label on the type specimen, Cheesman's plant was growing on the trunk of a fallen tree that was lying in a fast-flowing mountain stream at approximately 600 m. This description does not specifically say whether the plant was in the water, or could have been when the stream was in spate, but it appears that Alston interpreted Cheesman's description as implying a rheophytic existence and this (according to Holltum (1962), though Alston (1956) himself did not say so) is the origin of the name *Rheopteris*. Croft's specimen labels are much more informative than Cheesman's and they reveal, beyond any doubt, that *R. cheesmaniae* is not a rheophyte. *Croft 1716* was discovered as a climbing epiphyte close to (but not in) a stream in mixed lowland hill forest at c. 300 m; *Croft 1749* was even more distant from a rheophytic existence; it was discovered climbing on a small tree in naturally disturbed montane forest on an exposed summit ridge at c. 1100 m.

It is worth noting that a second species of *Rheopteris* (also from New Guinea and perhaps a true rheophyte), was described by Holttum (1962). This species (*R. asplenioides* Holttum) remained in the genus *Rheopteris* for only 13 years before Hennipman (1975) decided that it was better placed in the genus *Austrogramme* (Pteridaceae), section *Aspleniopsis* (Tryon et al. 1990). *Austrogramme asplenioides* (Holttum) Hennipman was renamed *Aspleniopsis asplenioides* (Holttum) Pic.Serm. in 1977 (Pichi-Sermolli 1977).

Tryon and Lugardon (1990) compared spores from the type specimen of *R. cheesmaniae* (wrongly cited by them as being at L but there is no isotype there) with those from *Croft 1716* and noted a size difference. Spores from the type specimen have a diameter of approximately 50 µm whereas those from *Croft 1716* have a diameter of approximately 40 µm. Tryon and Lugardon concluded that this size difference could be an indication of different ploidy levels within the species but until new plants are discovered and living material is collected, cytological analysis and investigation of possible ploidy differences by traditional methods is not possible. Reports of forest destruction in the West Sepik region (due to logging and invasive plant species; B. Waterhouse, pers. comm.) make the rediscovery of *R. cheesmaniae* and the collection of living material and ecological data all the more urgent.

Independent gametophytes

The term 'independent gametophyte' is used in Pteridology to describe a situation in which the gametophyte generation of a particular fern species has established, and is surviving, beyond the known geographical or altitudinal range of the sporophyte generation (Farrar 1985; Rumsey & Sheffield 1996). To date, all independent gametophytes to which species names have been assigned (not an easy task – see Farrar (1978) and below) are members of three families; the Hymenophyllaceae, Grammitidaceae and the Vittariaceae, but it is not yet clear whether gametophytic independence is characteristic of these families or of only certain genera or species within them.

Currently, independent gametophytes are known: in nine species of the Hymenophyllaceae in four genera (*Hymenophyllum, Mecodium, Trichomanes,* and *Callistopteris*); in the Grammitidaceae one species in one genus (*Grammitis, Xiphopteris* or *Micropolypodium,* depending on one's view-point); and in the Vittariaceae two species in one genus (*Vittaria*). The two species of *Vittaria* are *V. graminifolia* Kaulf. and *V. appalachiana* Farrar & Mickel; independent gametophyte populations of both have been found only in the eastern United States (Farrar & Landry 1987; Farrar & Mickel 1991).

In spite of the paucity of information on independent gametophytes (and, in particular, the lack of evidence for them in all but one genus of Vittariaceae) there are good reasons to believe that the phenomenon will, with further study, prove to be widespread in this family. The reasons for believing this are three-fold: First, all the gametophytes of Vittariaceae for which at least some published morphological data is available (18 species representing the genera *Ananthacorus, Anetium, Hecistopteris, Vittaria, Radiovittaria, Haplopteris, Antrophyum, Polytaenium, Scoliosorus,* and *Vaginularia;* see Goebel 1888, 1896; Britton & Taylor 1902; Troll 1932; Stokey 1951; Atkinson & Stokey 1964; Farrar 1974, 1978; and Crane 1997) are ribbon-shaped with multiple marginal meristems that frequently dichotomize (gametophytes of most fern species are heart-shaped, unless old or damaged, with a single recessed apical notch meristem). These features are consistent with a creeping, branching, mat or weft-forming habit and a perennial existence. Second, gametophytes of all but one of the 18 species known (the exception being *Ananthacorus angustifolius* (Sw.) Underw. & Maxon) also produce gemmae by which they can propagate themselves asexually (Goebel 1888 and 1896; Troll 1932; Britton & Taylor 1902; Hughes 1971; Emigh & Farrar 1977; Farrar 1974 & 1978; Sheffield & Farrar 1988; Crane 1997). Reproduction by gemmae enables the gametophyte generation of any species to maintain a presence (and a particular genotype) in a new area, beyond that currently tolerated by the sporophyte generation, even if the original colonizing gametophyte does eventually die. Third, independent gametophytes either confirmed (only for *V. graminifolia* and *V. appalachiana*) or suspected to be those of Vittariaceae have already been reported from the eastern United States, Mexico, Central America, Hawaii, Japan, and northern India (Farrar 1985). As yet, there appear to be no published reports of even the suspected presence of independent gametophytes of Vittariaceae (nor of any other fern family) in South America, Africa, or tropical Asia (including the entire Flora Malesiana region). While there could be a good biological explanation for this, it seems more likely that the apparent absence of independent gametophytes from the regions of the world where ferns in general are most common (and, therefore, where conditions for fern gametophyte establishment must often be favorable) is simply an artifact resulting from inadequate field observations and collections in these regions.

Even if, as suggested by Rumsey and Sheffield (1996), gametophyte independence proves to be more prevalent in species growing at the temperate extremes of this family's largely tropical distribution, the environmental factors that help create the phenomenon in a geographical context might also be expected to operate in an altitudinal context. With this in mind, it might be particularly fruitful to focus initial searches for independent gametophytes in Malesia along an altitudinal gradient incorporating the transition zones between tropical, subtropical, and temperate habitats. It must be emphasized that when independent gametophytes suspected of being Vittariaceae are eventually found in Malesia they will not be easily or quickly identified to species. Confident identification to species may require that the gametophytes be collected alive and cultured long enough to produce identifiable sporophytes. However, there is no guarantee that independent gametophytes will produce sporophytes even in prolonged culture (see below). Identification of independent gametophytes based solely on gametophytic characters would require considerable knowledge of the morphology of the gametophytes of all species of Vittariaceae in, and possibly even beyond, the Flora Malesiana region.

It should not be assumed that any independent gametophytes found in the Flora Malesiana region are those of one of the nearest species represented by sporophytes. *Vittaria graminifolia,* one of the two *Vittaria* species currently confirmed as having independent gametophytes, is known in the United States (in Louisiana), only as gametophytes and the nearest known population of sporophytes is more than 1000 km away in Mexico (Farrar & Landry 1987; Gastony 1980). Similar distances are reported to separate the independent gametophytes of other fern species [e.g. *Grammitis nimbata* (Jenman) Proctor and *Trichomanes speciosum* Willd.] from their nearest known sporophytes (Farrar 1967; Rumsey & Sheffield 1996; F. Rumsey, pers. comm.). It is therefore quite possible that the number of fern species growing on the individual islands in Malesia is actually more than that which is indicated by recording species numbers by sporophyte presence alone. It is also possible that living within the Flora Malesiana region are gametophytes of species not recorded as sporophytes from the region.

One technique that has been used very successfully in the identification of independent gametophytes, and of other morphologically indistinguishable gametophytes (e.g. Lindsay et al. 1992), is isozyme electrophoresis (e.g. Farrar 1985, 1992a, 1992b). Provided that appropriate reference samples are analyzed at the same time this technique can be used to generate and compare isozyme 'finger-prints', and thereby identify or, at least, considerably narrow the search for the identity of morphologically indistinguishable fern gametophytes. For example, the isozyme finger-print of the independent gametophytes found in Louisiana was found to be identical to the isozyme finger-print of those already known to be *Vittaria graminifolia* from Central America and this fact, combined with comparative studies of gametophyte morphology and gemma development, led to the discovery of the true identity of these independent gametophytes (Farrar & Landry 1987).

The discovery of the identity of the only other *Vittaria* species currently confirmed as having independent gametophytes, *Vittaria appalachiana,* was much more complicated (Farrar 1978), so complicated that it was not assigned a species name until 1991, some 60 years after its discovery (Wagner & Sharp 1963; Farrar & Mickel 1991). The main difficulty with attempts to identify this species was that no sporophyte generation could be located and no sporophytes could be raised from cultured gametophytes even under a range of experimental conditions. After years of careful morphological, genetic, and biochemical comparisons with a range of New World (mostly Central American) *Vittaria,* it was eventually concluded that these independent gametophytes from the Appalachians were significantly different from those of all the other species examined and that, quite remarkably, they probably represent the gametophyte generation of an unknown species of *Vittaria* whose sporophyte generation has long since gone extinct (Farrar & Mickel 1991). *Vittaria appalachiana* Farrar & Mickel was the first extant fern species (cf. certain early-Devonian land plants; Remy et al. 1993) to be described based solely on a description of the gametophyte generation. Since then two other species of independent fern gametophytes also with no known sporophytes have been described. These are *Hymenophyllum tayloriae* Farrar and Raine and *Trichomanes intricatum* Farrar (Raine et al. 1991; Farrar 1992b).

Conclusion

Although Crane's sampling of African and Asian Vittariaceae was somewhat limited, the results and conclusions of his molecular study have seriously challenged the traditional concepts of *Vittaria* and *Antrophyum* as two large pantropical genera. If Crane's conclusions are accepted then *Vittaria* s.s. is, in fact, confined (with the exception of one species) to the New World and *Antrophyum* s.s. is confined (with no exceptions) to the Old World. In practice, acceptance of these conclusions will not affect the revision of *Antrophyum* for Flora Malesiana but it will significantly affect the revision of all the Malesian species traditionally regarded as *Vittaria* (20–30 species; Table 1). Eleven Malesian '*Vittaria*' species have already been re-classified by Crane including those as well known as: *Vittaria elongata* Sw. (now *Haplopteris elongata* (Sw.) E.H.Crane); *Vittaria ensiformis* Sw. (now *Haplopteris ensiformis* (Sw.) E.H.Crane); *Vittaria scolopendrina* (Bory) Schkuhr ex Thwaites & Hook. (now *Haplopteris scolopendrina*

	Peninsular Malaysia	Borneo	Philippines	Sulawesi	Moluccas	New Guinea	Sumatra	Java	Lesser Sunda Islands	Malesia
Haplopteris/ Vittaria	11 or 12	11 or 12	12	7	4	8–14	8 or 9	10 or 11	4	20–30
Antrophyum	7	12	11	5	4	11	6	10	4	20
Monogramma	1	1	1	0	0	1	0	0	0	1
Vaginularia	2	2	3	2	0	4	1	2	1	4
Rheopteris	0	0	0	0	0	1	0	0	0	1
Vittariaceae	21 or 22	26 or 27	27	14	8	25–30	15 or 16	22 or 23	9	46–56

Table 1. Preliminary statistics for the number of species in the various genera of Vittariaceae in Malesia. The number of species in the region traditionally recognised as *Vittaria* is 20–30. Crane (1997) moved 11 of these to the genus *Haplopteris* and implied, without listing their names, that most other Malesian '*Vittaria*' species should also be placed in this genus. *Vittaria* as redefined by Crane is a small genus of five New World species and one Old World (African) species.

(Bory) C.Presl); and *Vittaria zosterifolia* Willd. (now *Haplopteris zosterifolia* (Willd.) E.H.Crane). Decisions on whether other Malesian '*Vittaria*' species should be moved to *Haplopteris*, moved elsewhere, or treated as synonyms, will be dependent on the outcome of a thorough comparison of micro-morphological characters. The generation and comparison of new molecular characters, including additional *rbcL* sequence data for a more representative selection of Malesian species and genera, is also highly desirable. Molecular characters could be the key to determining the correct taxonomic position of the monotypic (and Malesian endemic) genus *Rheopteris*.

Independent gametophytes have not yet been reported from the Malesian region but there are good reasons to believe that, with more careful and focused field observations, they will eventually be found. In spite of the novel and important contribution that the confirmed presence and subsequent identification of independent gametophytes would make to our understanding of species numbers and their distribution within Malesia they will not feature in the first account of Vittariaceae for Flora Malesiana. This first account, like the accounts of most fern families in most Floras, will be based almost exclusively on sporophytic data. In reality, a description (with distribution data) of all the fern species present as sporophytes in Malesia is a prerequisite for any future attempts to study and identify independent gametophytes. It is likely to be a long time before any revision of the Vittariaceae (in Malesia or elsewhere) gives a balanced account of both the gametophyte and sporophyte generations.

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Studies in the Miliuseae. V. Review of the taxonomic history of a polyphyletic 'tribe'

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Abstract

J.B. Mols & P.J.A. Keβler (Nationaal Herbarium Nederland, Universiteit Leiden Branch, P.O. Box 9514, 2300 RA Leiden, The Netherlands. Email: Mols@NHN.LeidenUniv.NL) 2003. Studies in the Miliuseae. Review of the taxonomic history of a polyphyletic 'tribe'. Telopea *10(1): 113–124.* This article addresses the problem of the classification of the genera in the Annonaceae. The former classifications within the family based on subsets of morphological data are not congruent with each other and cannot be used to make a clear and uniform classification of the family or subsets of genera. This problem is illustrated here for the tribe Miliuseae Hook.f. & Thomson, which has been defined by a special stamen type (miliusoid) uncommon in the Annonaceae. It is argued that this tribe is not monophyletic and is not "recognised" as such in the classifications using different morphological data sets. The polyphyly of the tribe is also indicated by preliminary molecular studies. Future studies, combining molecular and morphological data, are outlined.

Introduction

The Annonaceae Juss. are a pantropical family consisting of about 130 genera and 2300 species. Most of the species occur primarily in tropical lowland rainforest. The family is often represented by high numbers of individuals and species. In Asia alone about 60 genera and about 1000 species can be found.

The Annonaceae are clearly delimited (e.g. Fries 1959; Keβler 1993) and are regarded monophyletic in all studies including those based on molecular data (Qiu et al. 2000). In contrast to distinct family boundaries, the classification on subfamilial level is unresolved. The genera in the Annonaceae are notoriously difficult to define and to classify into "natural groups". Over the years different authors have subdivided the family into formal and informal groups based on several character sets, such as pollen, flowers, fruits, etc. (e.g. Hutchinson 1923, 1964; Sinclair 1955; Fries 1959; Walker 1971; Setten & Koek-Noorman 1992; Heusden 1992; Keβler 1993; Koek-Noorman et al. 1997). A comparison of these classifications reveals a diversity of conflicting conclusions.

The problem of the classification within the Annonaceae is here illustrated by discussing the position of the genera included in the tribe Miliuseae Hook.f. & Thomson (sub Saccopetaleae) according to Keβler (1993), namely *Alphonsea* Hook.f. & Thomson, *Mezzettia* Becc., *Mezzettiopsis* Ridl., *Miliusa* A.DC., *Orophea* Blume, *Phoenicanthus* Alston and *Platymitra* Boerl. Various alternative character sets that might delimit the tribal boundaries are also discussed. This article is one of a series of studies on this tribe. In previous publications in this series the tribal name Saccopetaleae (articles I–IV) has been used, but a study of the nomenclature has revealed that the correct name should be Miliuseae. This tribe has been chosen as it is the object of the Ph.D. study of the first author.

Miliuseae

The first time the Annonaceae were subdivided was by Dunal (1817). At the time only eight genera (excluding *Kadsura* Juss., now placed in the Schisandraceae) were recognised and, based on fruit characters only, were classified into three groups.

The tribe Miliuseae was first described by Hooker and Thomson in 1855 in their *Flora Indica* and included the genera *Miliusa*, *Saccopetalum* Benn. (= *Miliusa*), and *Alphonsea*. The circumscription of the tribe was based on the following characters: carpels free, petals valvate, stamens loosely imbricate and anthers visible in flower (not concealed). The authors stressed that the tribe differs from the other tribes in the structure of the stamens. In present day taxonomy of the family, this type of stamen is referred to as the miliusoid stamen. Generally the stamens in the Annonaceae are characterized by being narrowly oblong to oblanceoloid with a short filament, two thecae and a shield-like apical prolongation of the connective (**Fig. 1**) (Heusden, 1992). In the miliusoid stamen this apical prolongation is not shield-like and is either small-discoid and not extending over the anthers or absent (**Fig. 2**). The same characters used by Hooker and Thomson are still used to define this tribe. Keβler (1993) recognises a *Miliusa*-group based on sepals and petals being valvate, stamens and carpels few, and connective without a prolonged specialized apex.

The Miliuseae *sensu* Keβler includes six (seven in the original publication) genera which can be determined using the following key and diagnostic descriptions.

Key to the genera in the Miliuseae

1a. Outer and inner petals of (almost) equal length 2

b. Outer petals much smaller than inner petals 5

2a. Sepals connate at the base, inner petals mitreform 3

b. Sepals free, inner petals not mitreform 4

3a. Stamens 6 or 9, ovule(s) 1–2, monocarps up to 1 cm in diameter .. **Phoenicanthus**

b. Stamens 20–35, ovules c. 10, monocarps 1 to 5 cm in diameter .... **Platymitra**

4a. Inner petals saccate at the base, stamens 15–60, carpel(s) 1–15, monocarps stipitate .... **Alphonsea**

b. Inner petals not saccate at the base, stamens 9–21, carpel 1, monocarps sessile .... **Mezzettia**

5a. Sepals and outer petals similar in size and shape 6

b. Sepals and outer petals similar in shape but outer petals much larger, inner petals clawed at base .... **Orophea (incl. Mezzettiopsis)**

6a. Sepals free, inner petals saccate, glandular tissue along middle vein .. **Miliusa s.s.**

b. Sepals connate at the base, inner petals not saccate, glandular ring at base .... **Miliusa p.p. (thought to be a new genus)**

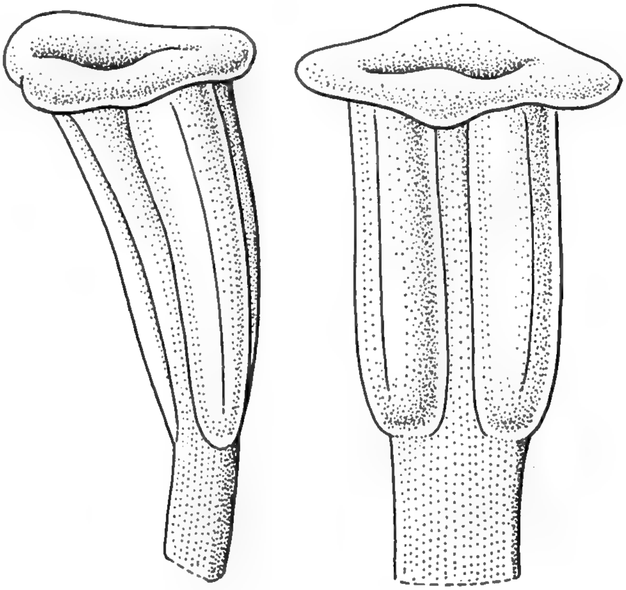

Fig. 1. Stamens of *Phaeanthus nutans* Hook.f. & Thomson (*KEP/FRI 12307 (Whitmore)*). Drawing from Mols & Keßler (2000) by J. van Os.

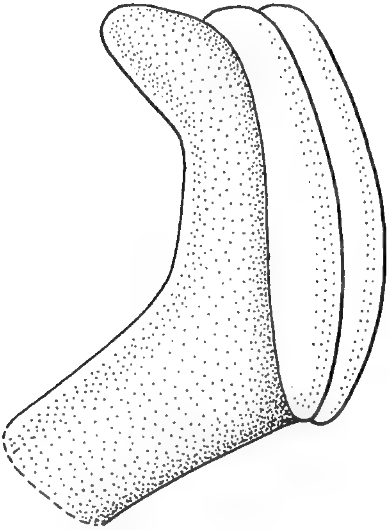

Fig. 2. Stamen of *Miliusa velutina* (Dunal) Hook.f. & Thomson (*Kerr 1078*). Drawing from and by Heusden (1992) (sub *Miliusa villosa*) redrawn and adapted by J. van Os.

Alphonsea Hook.f. & Thomson, Fl. Ind. 1: 152 (1855).

Trees or shrubs; flowers bisexual; sepals 3; petals 6, subequal, inner petals slightly saccate at the base; stamens 15–60, miliusoid; carpel(s) 1 to 15; ovules few, biseriate; monocarps globose to cylindrical, stipitate. Twenty-five species found from mainland Asia (India, Thailand) to Indonesia and the Philippines. Recently revised by Keβler (1996).

Mezzettia Becc., Nuovo. Giorn. Bot. Ital. 3: 187 (1871).

Trees; flowers bisexual; sepals 3; petals 6, inner petals shorter than outer petals; stamens 9–21, miliusoid with truncate dilated apex; carpel 1; ovules 2, biseriate; monocarps globose, sessile. Four species found from Peninsular Malaysia to the Moluccas. Recently revised by Heijden and Keβler (1990). Doubtfully included in the Miliuseae *sensu* Keβler.

Miliusa A.DC., Mem. Anon. (preprint): 37 (1832).

Shrubs or trees; flowers bisexual or unisexual; sepals 3; petals 6, outer petals similar to sepals, inner petals much longer and saccate at the base; stamens few to numerous, miliusoid; carpels few to numerous; ovule(s) 1–10, biseriate; monocarps globose to oblong, stipitate. About 25 to 30 species from mainland Asia (India, China) to New Guinea and Australia. Several species previously included in *Miliusa* differ from the general perception of the genus. The main differences are that the inner petals bases are not saccate in these species but are thickened forming a glandular ring, the sepals are slightly connate at the base and the leaf bases are amplexicaule. These species are thought to form a new genus (to be described) and are referred to in the key as *Miliusa* p.p.. The species of the Flora Malesiana area and Australia have recently been revised (Mols and Keβler, in prep.).

Orophea Blume, Bijdr. Fl. Ned. Ind.: 18 (1825).

Small trees; flowers bisexual; sepals 3; petals 6, inner petals longer than outer ones, inner petals clawed or spoon-shaped; stamens 3–12, miliusoid; carpels 3–18; ovule(s) 1– 6, uni- or biseriate; monocarps globose or cylindrical, stipitate. Fifty species subdivided into two subgenera *Orophea* and *Sphaerocarpon* (latter includes former genus *Mezzettiopsis* Ridl., Kew Bull.: 389 (1912)). Found from mainland Asia (India, China) to the Sunda Islands and the Philippines. The genus has been revised by Keβler (1988a, 1990) and Leonardia and Keβler (2001).

Phoenicanthus Alston in Trimen, Handb. Fl. Ceylon 6: 6 (1931).

Trees; flowers bisexual; sepals 3, slightly connate; petals 6, subequal, inner petals mitreform and concave at the base; stamens 6 or 9, miliusoid with obtuse apex; carpel(s) 1–3; ovule(s) 1–2; monocarps globose, sessile. Two species endemic to Ceylon (Huber, 1985).

Platymitra Boerl., Cat. Pl. Phan. 1: 33 (1899).

Trees; flowers bisexual, ramiflorous; sepals 3, connate at base; petals 6, subequal, inner petals mitreform; stamens 20–35, miliusoid; carpel(s) 1–3; ovules 10, biseriate; monocarps globose to ovoid, sessile. Two species found from Thailand to Java and the Philippines. The genus has been revised by Keβler (1988b).

Classifying the Miliuseae

In the next paragraphs and accompanying Table 1 the position of each genus in the tribe in twelve classifications is shown. These twelve classifications are not all that are known for the family, but are the most widely used or of particular interest in the study of the Miliuseae. The classifications are not always easy to compare because in some cases a genus is missing from a classification simply because it had not been described at the time, did not occur in the area the treatment was dealing with, or because no sufficient data were available. If a genus has been placed in synonymy the most recent circumscription of the accepted genus is recognised.

Reichenbach 1837: After the work by Dunal (1817), the number of genera in the family rose sharply to twenty-four (including some non-Annonaceous genera). The Annonaceae (sub Annoneae) were treated as a tribe of the Ranunculaceae, and based on flower characters primarily three groups were recognised: the Cardiopetaleae, Guatterieae and Annonariae, with the latter group subdivided into three smaller groups, Uvarieae, Bocageae, Annoneae genuinae. The only members of the Miliuseae *sensu* Keßler known up to this point were *Miliusa* and *Orophea*, placed in the Cardiopetaleae because the petals were united at the base in *Miliusa* (in the type specimen, discovered to be genetically atypical, the inner petals were united in some flowers).

Endlicher 1839: Endlicher dealt with a similar number of genera, but the tribal division was somewhat different. Based also on stamen and carpel characters three tribes were recognised: Bocageae, Xylopieae and Annoneae with several genera not allocated to any of these three tribes. The main difference with Reichenbach's system was that the two Miliuseae genera were now placed in the Bocageae, based on having a finite number of stamens. A first indication of the problems concerning the classification was already shown here. The genus *Hyalostemma*, placed in *Miliusa* in modern classifications, could not be accommodated under Endlicher's system.

Hooker and Thomson 1855: As mentioned before, the tribe Miliuseae was first established in the Flora Indica. Based on flower characters alone, Hooker and Thomson recognised six tribes: Annoneae, Uvarieae, Miliuseae (sub Saccopetaleae), Mitrephoreae, Xylopieae and Guatterieae. This classification was based on the plants occurring in India and predominantly dealt with the Asian Annonaceae. But many of the tribal names and characters adopted have been used in later stages as a precursor for the general classification of the Annonaceae. The Miliuseae, defined as having free carpels, valvate petals, and imbricate, miliusoid stamens consisted of *Miliusa, Saccopetalum* (= *Miliusa)*, and *Alphonsea*. The only other genera of Miliuseae *sensu* Keßler classified by Hooker and Thomson were *Orophea* and *Phoenicanthus* (sub *Orophea obliqua*). These genera were placed in the Mitrephoreae, which was defined by having free carpels, valvate petals, inner petals clawed at the base, stamens densely packed together and anthers concealed. This last character state did not apply to *Orophea* and *Phoenicanthus*. The clawed base of the inner petals of *Orophea* (and *Phoenicanthus*) was the reason this genus was placed in the Mitrephoreae, but the stamen characters suggest it should have been placed in the Miliuseae.

Hooker and Thomson 1872: Only slight variations were made from the previous treatment. Five tribes were recognised with the Annoneae included in the Xylopieae. The genus *Guatteria* Ruiz & Pav. was no longer recognised as Asiatic, and the tribe Guatterieae had been renamed Unoneae. The description of the Miliuseae was modified slightly to allow for the fact that the petals could be valvate or imbricate. The stamen characters were again thought to be of more importance and so *Orophea* and *Phoenicanthus* (as *Bocagea obliqua* and *B. coriacea*) were included in the tribe. Additionally, the genus *Lonchomera* Hook.f. & Thomson was first described and placed in the *Miliuseae*, this genus is now considered a synonym for *Mezzettia*. This meant that

Table 1. Overview of the position of the genera included in the Miliuseae sensu Keßler in different classifications. For additional explanation see text (– = not described at time of treatment, N.I. = genus not included in the treatment, N.A. = genus could not be accommodated in the treatment).

	Alphonsea Hook. f. & Thomson	***Mezzettia*** Becc.	***Mezzettiopsis*** Ridl.	***Miliusa*** A.DC.	***Orophea*** Blume	***Phoenicanthus*** Alston	***Platymitra*** Boerl.
Keßler (1993)	Miliuseae	Miliuseae	Miliuseae	Miliuseae	Miliuseae	Miliuseae	Miliuseae
Reichenbach (1837)	–	–	–	Cardiopetaleae	Cardiopetaleae	–	–
Endlicher (1839)	–	–	–	Bocageae	Bocageae	–	–
Hooker & Thomson (1855)	Miliuseae	–	–	Miliuseae	Mitrephoreae	Mitrephoreae	–
Hooker & Thomson (1872)	Miliuseae	Miliuseae	–	Miliuseae	Miliuseae	Miliuseae	–
Ridley (1922)	Miliuseae	Miliuseae	N.I.	Miliuseae	Mitrephoreae	N.I.	–
Sinclair (1955)	Miliuseae	Unoneae	Miliuseae	Miliuseae	Miliuseae	N.I.	Miliuseae
Hutchinson (1923/1964)	Unoneae Xylopineae Hexapetaleae	Unoneae Xylopineae Hexapetaleae	Miliuseae	Miliuseae	Miliuseae & Unoneae Xylopineae Hexapetaleae	(Miliuseae)	Unoneae Xylopineae Hexapetaleae
Fries (1959)	Unoneae Desmos-group	Unoneae Polyalthia-group	Unoneae Orophea-group	Unoneae Polyalthia-group	Unoneae Orophea-group	N.I.	Unoneae Orophea-group
Walker (1971)	Malmea-subfamily Uvaria-tribe	Malmea-subfamily Uvaria-tribe	Malmea-subfamily Uvaria-tribe	Malmea-subfamily Uvaria-tribe	Malmea-subfamily Uvaria-tribe	N.I.	Malmea-subfamily Uvaria-tribe
Setten & Koek-Noorman (1992)	Group 12	Group 5	Group 8	N.A.	Group 8 or 11	N.A.	Group 9
Heusden (1992)	Sageraea-group	N.A.	Mitrephora-group	Miliusa-group	Mitrephora-group	Sageraea-group	Mitrephora-group
Koek-Noorman et al. (1997)	Cluster A	Cluster D	Cluster D	Cluster C	Cluster D	Cluster D	Cluster A

all in all five of seven genera included in the Miliuseae *sensu* Keßler were placed in this tribe, with the other two not yet recognised or described. The genus *Dendrokingstonia* (Hook.f. & Thomson) Rauschert (sub *Kingstonia* Hook.f. & Thomson), with imbricate sepals and petals was included in the tribe. This genus is now usually regarded as related to the genus *Uvaria* L. and allies.

Ridley 1922: In his treatment of Malayan Annonaceae Ridley recognised the same tribes as Hooker and Thomson based on mostly the same floral characters. The main difference was that Ridley again put the emphasis on petal shape instead of the stamens when dealing with *Orophea* and placed it back in the Mitrephoreae. The miliusoid stamen was in fact not mentioned as a defining character for the Miliuseae that included *Miliusa, Alphonsea, Mezzettia* and *Dendrokingstonia* (sub *Kingstonia*). Ridley included *Phaeanthus* Hook.f. & Thomson in the Miliuseae because it also had small sepals and outer petals and large inner petals, this difference between the two whorls of petals becoming the main character to place all genera together. In *Mezzettia* this difference is only slight, the inner petals often being smaller than the outer.

Sinclair 1955: This treatment dealt also only with the Annonaceae of the Flora of Peninsular Malaysia, but is regarded as one of the main references dealing with Asian Annonaceae as it is the most complete overview of the family in the region. The tribes used were the same as Ridley's with a slight difference in the composition of the tribes. *Platymitra* had been described in the meantime and was added to the tribe. Furthermore Sinclair stated (p. 175) that the stamen characters are probably better suited to be used than the corolla characters to base the relationships between the genera in the Miliuseae, this in contrast with the other tribes. He thought that sexual organs are more likely to be static and less liable to variation over time. For this reason *Orophea* was transferred (back) to the Miliuseae, and Sinclair noted that, based on petal structure, *Orophea* and *Platymitra* were considered to be closely linked to the Mitrephoreae. The stamens of *Mezzettia* on the other hand were not regarded to be miliusoid and the genus was transferred to the Unoneae. The stamens of *Mezzettia* are slightly different as the apex is truncately dilated, but presently are regarded by us to be more related to the miliusoid type than any other.

Hutchinson 1923 & 1964: Hutchinson (1923) used the ideas of Hooker and Thomson for the entire family (nearly 100 genera and more than 1000 species). But using the same characters for all Annonaceae genera resulted in an artificial classification. Hutchinson recognised two subfamilies Annonoideae and Monodoroideae. Within the Annonoideae three tribes Uvarieae, Miliuseae and Unoneae were recognised. The latter was divided into two subtribes Annonineae and Xylopineae, the latter of which was divided into three series Hexapetalae, Tetrapetalae and Tripetalae (group A, B, and C in Hutchinson, 1964). *Miliusa, Orophea* and *Mezzettiopsis* were in the Miliuseae based on the valvate petals and a large differentiation between the inner and outer petals together with the Asian genera *Phaeanthus, Trivalvaria* Miq., *Marsypopetalum* Scheff., the American genera *Heteropetalum* Benth. and *Cymbopetalum* Benth. as well as the African genera *Piptostigma* Oliv. and *Brieya* De Wild. (now included in *Piptostigma*). The genera *Mezzettia, Platymitra* and *Alphonsea* were placed in the Unoneae, subtribe Xylopineae, series Hexapetalae, based on having 6 petals, the outer petals similar or larger than the inner petals and free carpels. The miliusoid stamen character was only used to define the genera *Mezzettiopsis, Miliusa, Orophea* and *Saccopetalum*. This classification is artificial because *Orophea* was placed in two tribes, the Miliuseae and the Unoneae, subtribe Xylopineae, series Hexapetalae. The 1964 treatment only differed by the addition of some (not all!) newly described genera. To the Miliuseae *Fenerivia* Diels (Africa) and *Anomianthus* Zoll. (Asia) were added, with the latter placed also in the tribe Uvarieae.

Fries 1959: This treatment is generally seen as the standard work of the Annonaceae on a global scale. It is based primarily on floral characters, but more characters were used, probably producing a better classification, especially for the South-American genera, as Fries revised almost all the Neotropical species known at that time. Fries also recognised two subfamilies: the Annonideae and the Monodoroideae. The Annonideae were subdivided into three tribes and 15 groups, the Uvarieae (with 5 groups), the Unoneae (with 9 groups), and the Tetramerantheae. All genera now in the tribe Miliuseae *sensu* Keβler, based on having valvate petals, were placed in the Unoneae but subdivided into three groups. *Miliusa* and *Mezzettia* were placed in the Polyalthia-group with eight other genera. This group was recognised based on having petals in 2 whorls, flowers having bracts, apocarpous fruits, inner petals not enclosing the sexual organs and touching each other at the base, and axillary inflorescences. *Orophea* (including *Mezzettiopsis*) and *Platymitra* were placed in the Orophea-group, which, although similar to the Polyalthia-group, differed in having inner petals that enclose the sexual organs being fused at the tip to form a dome. In this group twelve additional genera were included. The genus *Alphonsea* was placed in the Desmos-group together with four other genera. This group differs from the Polyalthia-group in having leaf-opposed inflorescences. As can be concluded from this short summary the interpretation of the characters is different and some are used at another level as in previous treatments.

Walker 1971: Walker introduced a major change in the general classification trend within the family. He used pollen morphology to classify the Annonaceae into three subfamilies, the Malmea, Fusaea and Annona subfamilies. The first and last of these subfamilies were subdivided further; the Malmea subfamily into three tribes, the Malmea tribe, Uvaria tribe and Guatteria tribe, and the Annona subfamily into four tribes, Hexalobous tribe, Asimina tribe, Annona tribe and Cymbopetalum tribe. The Miliuseae were placed in the Uvaria-tribe which was defined by having solitary globose pollen grains which are apolar, radiosymmetric and inaperturate of medium-size to large with well-developed to reduced columellae and often verrucate exine. Based on these characters the tribe included c. 60 genera, including all genera in the Miliuseae *sensu* Keβler (except *Phoenicanthus* which was not included in the treatment).

Setten and Koek-Noorman 1992: These authors studied fruit and seed characters, and recovered 16 groups from the observed variation patterns. This suggested a different set of relationships among the genera. Unfortunately only four of seven genera in the Miliuseae *sensu* Keβler were accommodated in these groups. *Mezzettia* was placed in group 5 because it has large monocarps with two lateral seeds with thick walls and stout lamellate ruminations in often more than 4 parts. *Mezzettiopsis* (= *Orophea*) was placed in group eight based on a low number of pitted lateral seeds with spiniform ruminations. This group was said to be closely related to the genus *Polyalthia* and the members of group 9. This latter group included *Platymitra* and was different from 8 in having its seeds in 2 rows. *Alphonsea* was accommodated in group 12 which was defined by having lamellate rumination in four parts with a smooth seed wall and having no oil cells in the endosperm. This group was also said to be closely related to *Polyalthia*. *Phoenicanthus* was not accommodated, as data available was not sufficient to suggest any placement. Fruit and seed characters are very diverse in *Miliusa* and *Orophea*. *Orophea* was found to consist of two sections one of which could be placed in group 8 (together with *Mezzettiopsis*) and the other in group 11. *Miliusa* was so diverse that the authors did not accommodate the genus, but proposed it should be placed in the centre of the scheme connecting the groups, together with *Polyalthia*, with which it also shares some features.

Heusden 1992: In this study the flower characters were partly reevaluated, new characters were used and the significance of more traditional characters to the classification of the genera was reinterpreted. Nineteen groups were recognised and the members of the Miliuseae *sensu* Keßler were distributed across three groups. *Mezzettia* could not be accommodated in any of the nineteen groups. *Miliusa* was included in the Miliusa-group along with *Marsypopetalum* and *Phaeanthus*. The sepals and outer petals being of similar size and shape characterized this group. The author indicated that this group was closely related to the Mitrephora-group, which included the genera *Orophea, Mezzettiopsis,* and *Platymitra,* and was defined by valvate sepals, two whorls of petals that are of slightly different size and shape and mostly several lateral ovules. The genera *Alphonsea* and *Phoenicanthus* were placed in the Sageraea-group based on a large number of broadly defined characters. Heusden also stated that this group was ill-defined but the genera could not be placed better in any group other than together. Some connection was shown with the *Miliusa*-group as *Alphonsea* has similar stamens and carpels to the genera in this group. The author concluded that the groups could be recognised only through a combination of several character states but in many instances the genera did not fall neatly into any particular group.

Koek-Noorman et al. 1997: This study combined the two previous datasets and performed a cluster analysis on the data thus making it the first treatment to use both flower and fruit/seed characters to group the genera within the family. The phenetic analysis clustered *Alphonsea* and *Platymitra* together in group A. *Miliusa* was placed in group C forming in this group a cluster with *Mitrephora* (Blume) Hook.f. & Thomson and *Desmopsis* Saff. All other genera in the Miliuseae *sensu* Keßler were placed in group D, along with *Phoenicanthus* (based on flower characters only) and *Mezzettia,* and *Orophea* and *Mezzettiopsis* closely also clustering together.

This comparison of earlier classifications clearly shows that when switching the emphasis from one character (state) or data set to another the composition of resulting groups or tribes changes considerably. Our conclusions are therefore similar to those of Koek-Noorman et al. (1990). No single character set gives a clear picture of the relationships of the genera within the family. One needs to combine the different datasets (e.g. fruit, pollen, flower, etc.) into a complete data set, which should be used in a phylogenetic analysis. Doyle and Le Thomas (1994, 1996) performed such an analysis of 79 morphological characters. This data set produced 180 most parsimonious trees belonging to two islands, which showed a high level of homoplasy, and therefore the relationships between the groups obtained remained unclear. However in the rooting of these cladograms and in the formation of the major clades the pollen characters were phylogenetically most informative. This idea was strengthened in their later studies (Doyle and Le Thomas, 1997) because of the phylogenetic differences found between the cladograms before and after removal of the pollen data from the overall morphological data set in the analysis. It must be stated that their studies only included c. 36 out of 130 genera of the Annonaceae worldwide, which means that many possibly morphologically intermediate genera were omitted. Because only one genus (*Miliusa*) of the *Miliuseae sensu* Keßler was included this study has not been used in the previous comparison of classifications.

Preliminary ideas based on molecular data

In recent years research has been more directed towards the use of molecular data to determine relationships within the family. Zuilen (1996) was the first to use molecular data but she only dealt with one genus in the family. Bygrave (2000) and Chatrou et al. (in prep.) have made phylogenetic analyses based on respectively *rbc*L and *rbc*L & *trn*L-F DNA sequence data. Although many of the groupings found are not well supported and the overall resolution of parts of the cladograms obtained is rather poor, the cladograms have shown some interesting aspects. When dealing with such a "primitive" family within the angiosperms, the closest relative of a certain genus might not be found on the same continent. For instance, a close relative of the Asiatic genus *Miliusa* appears to be the Central American genus *Sapranthus* Seeman. Classifications on a regional scale will not identify these possible relationships. The importance of this has already been referred to by other authors (e.g. Setten & Koek-Noorman 1992; Heusden 1992; Koek-Noorman et al. 1997; Keβler 1993).

Furthermore even though the resolution in the end clades is poor, these early molecular studies provide a basis for future research. They indicate larger subsets of genera that can be the subjects of further research into the relationships between these genera. A preliminary phylogenetic analysis based on *rbc*L and *trn*L-F DNA sequence data (Chatrou et al., in prep.) suggests that the Miliuseae *sensu* Keβler are not monophyletic and that the closest relatives of *Miliusa* might be any of the following genera: *Fitzalania* F.Muell., *Ancana* F.Muell., *Sapranthus, Neo-uvaria* Airy Shaw, *Sageraea* Dalzell, *Enicosanthum* Becc., *Alphonsea, Platymitra, Phaeanthus, Popowia* Endl. and *Polyalthia* Blume p.p. Of these genera only *Alphonsea* and *Platymitra* are included in the Miliuseae *sensu* Keβler and all genera except *Sapranthus* have an Asiatic distribution. Only some *Polyalthia* species ended up in this clade. The few species of *Polyalthia* included (c. 10 of 150) in the analyses (Bygrave, 2000; Chatrou et al., in prep.) were divided over several clades. Not surprisingly the genus *Polyalthia* is regarded as polyphyletic, because based on morphology alone it was already considered to be an ill-defined genus.

In none of the classifications examined and surveyed above, is the molecular grouping of these twelve genera closest to *Miliusa* suggested or found. For instance different stamen types can be found (miliusoid, various stamens with a shield-like prolongation of the connective, etc.), some genera have two whorls with similar petals, while others have similar sepals and outer petals, and also the fruits come in many different shapes and sizes.

To solve this question a combined analysis of molecular and morphological data needs to be performed. Doyle et al. (2000) performed such analysis by combining Bygrave's *rbc*L data and Doyle and Le Thomas' morphological data. In their article the morphological characters were plotted on the cladogram based on the *rbc*L data and the datasets were combined and phylogenetically analyzed. Only the taxa included in the studies by Doyle and Le Thomas were used, all other genera studied by Bygrave were omitted. Of the possible relatives of *Miliusa* based on the work by Chatrou et al. (in prep.) mentioned previously, *Ancana, Sapranthus,* several *Polyalthia* species and *Miliusa* itself were included. The combined analysis showed a better resolution than the cladogram based solely on molecular data and *Miliusa, Sapranthus, Ancana* and several *Polyalthia* species ended up in one clade (the miliusoids) in the consensus cladogram of each of the three islands. This corroborates the preliminary ideas based on the work by Chatrou et al. (in prep.). When looking at the morphological characters it seems that the pollen characters again are phylogenetically most informative. It would be interesting to see whether the other genera thought to be closely related to *Miliusa* would also end up in this miliusoid clade based on morphology and molecular data.

Conclusions

From the evidence presented here, it is clear that classifications of the Annonaceae, based on subsets of morphological data are not satisfactory as they do not recognise monophyletic groups unambiguously. In debating the status of the tribe Miliuseae it seems evident that the Miliuseae as variously recognised by different authors is not a monophyletic group, which also seems to be supported by the molecular data. It is envisaged that the tribe in the present circumscription of Keβler does not comprise a natural group.

In order to find out which morphological characters are phylogenetically informative one must not look at the subsets of morphological data independently but rather combine them to a complete data set, preferably supplemented with molecular data. Within the Annonaceae several such studies are now being carried out.

In our further studies we will keep a focus on the genera included in the tribe Miliuseae *sensu* Keβler. By using molecular data we want to establish whether this tribe is really polyphyletic. For this purpose a number of genera will be included (up to 30, from Asia, Central-America and Africa) apart from the genera included in the Miliuseae. Based on the work by Bygrave (2000) we will select which genera are the most relevant in elucidating the relationships. If the tribe is really polyphyletic we will then further study the clade containing the genus *Miliusa* s.s., because this genus has recently been studied morphologically by the authors (Mols & Keβler, in prep.). In this further study on the *Miliusa*-clade more taxa will be added, from *Miliusa* as well as related genera, and when needed, additional genes will be sequenced. At the same time a morphological data set will be constructed for the genera included in the *Miliusa*-clade by combining the available morphological subsets supplemented with additional data scored from literature and by a survey of herbarium collections. By combining the molecular data set and the complete morphological data set (when congruent), and performing a combined phylogenetic analysis we hope to find which morphological characters (states) are phylogenetically most informative. This information might then be used in further revealing the relationships between the Annonaceae as a whole.

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A taxonomic revision of the Australian *Ficus* species in the section *Malvanthera* (*Ficus* subg. *Urostigma*: Moraceae)

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Abstract

Dixon, D.J. (Tropical Plant Sciences, School of Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia. Rainforest CRC, James Cook University, Cairns, Queensland 4870, Australia. Permanent address: Parks and Wildlife Commission of the Northern Territory, P.O. Box 496, Palmerston, NT 0831, Australia.) 2003. A taxonomic revision of the Australian Ficus *species in the section* Malvanthera (Ficus *subg.* Urostigma: *Moraceae*). Telopea *10(1)*: *125–153.* A revision of the Australian *Urostigma* sect. *Malvanthera* Corner (*Ficus*: Moraceae) is presented. Seventeen taxa in fourteen species are recognised. These are: *Ficus atricha* D.J.Dixon, *F. brachypoda* (Miq.) Miq., *F. cerasicarpa* D.J.Dixon, *F. crassipes* F.M.Bailey, *F. destruens* F.Muell. ex C.T.White, *F. lilliputiana* D.J.Dixon f. *lilliputiana*, *F. lilliputiana* f. *pilosa* D.J.Dixon, *F. macrophylla* Desf. ex Pers. f. *macrophylla*, *F. macrophylla* f. *columnaris* (C. Moore) D.J.Dixon, *F. obliqua* G.Forst., *F. platypoda* (Miq.) A.Cunn. ex Miq., *F. pleurocarpa* F.Muell., *F. rubiginosa* Desf. ex Vent. f. *rubiginosa*, *F. rubiginosa* f. *glabrescens* (F.M.Bailey) D.J.Dixon, *F. subpuberula* Corner, *F. triradiata* Corner, and *F. watkinsiana* F.M.Bailey. *F. watkinsiana* F.M. Bailey is lectotypified. *Malvanthera* subser. *Hesperidiiformes* is raised to the rank of series. The taxonomy of *Urostigma* sect. *Malvanthera* is strongly supported by the pollinator wasp association. Pollinator wasp associations are given for each species. A formal rearrangement of the Australian and the New Guinea species in *Urostigma sect. Malvanthera* is presented. Keys to the series and species now recognised in *Urostigma* sect. *Malvanthera* are provided. Descriptions, notes, and distribution maps are provided for the Australian species.

Introduction

Ficus is a large pantropical genus divided by Corner (1959a, 1959b, 1959c, and 1959d) into four subgenera, two of which, *Ficus* subgen. *Ficus* and *Ficus* subgen. *Urostigma* are well represented in Australia. The two remaining subgenera, *Ficus* subgen. *Pharmacosycea* and *Ficus* subgen. *Sycomorus* are each represented by only one species, *F. albipida* (Miq.) King and *F. racemosa* L. respectively. The taxa associated with the *Ficus* subgen. *Ficus* are commonly referred to in Australia as sandpaper figs while the members of the *Ficus* subgen. *Urostigma* are called stranglers or banyans. Each subgenus is further divided into sections, series and subseries. In a modification of the classification by Corner (op. cit.), Ramirez (1977a) rearranged the infrageneric classification to better reflect the wasp specificity and morphology, and the pollination ecology, morphology and physiology of the figs. In this classification Ramirez (1977a) expanded *Ficus* subg. *Sycomorus* to include among others, the *Ficus* sections *Adenosperma* and *Neomorphe*, each with representatives in Australia. Similarly, Berg (1989) discussed the validity of Corner's classification and proposed two groups within *Ficus* based on morphological and functional traits connected with the pollination ecology of the figs. In the classification of Berg (1989), two main groups were recognised, a monoecious group consisting of the *Ficus* subgenera *Pharmacosycea* and *Urostigma*, and a mainly (gyno)dioecious group consisting of the subgenera *Ficus* and *Sycomorus*. Weiblen (2000) provided phylogenetic insights into *Ficus* classification based on ITS sequences and morphology agreeing in part with Ramirez (1977a) and

Berg (1989). Despite the fact that infrageneric rearrangements have been proposed subsequent to Corner (op. cit.), the monophyly of *Urostigma* sect. *Malvanthera* has been maintained by Weiblen (2000).

Ficus has previously been treated in the *Flora of Australia* (Chew 1989) and was considered to consist of 41 species. Since the *Flora of Australia* treatment various taxa in the *Urostigma* sect. *Malvanthera* as well as their associated pollinator wasps have been revised (Dixon 2001a; Dixon 2001b; Dixon 2001c; Dixon et al. 2001; Lopez-Vaamonde et al. 2002). In addition, the species *Ficus subnervosa* Corner, previously considered to be endemic to Papua New Guinea, has been found on Cape York Peninsula, such that the key to *Ficus* by Chew (1989) may prove unworkable. This work finalises the taxonomic account of the Australian taxa in the *Urostigma* sect. *Malvanthera* providing a better understanding of the relationships between the fig taxa and their pollinator wasp(s) species.

Methods

This revision of the Australian *Urostigma* sect. *Malvanthera* is based on the examination of 1638 herbarium collections from AD, BM, BRI, CANB, DNA, FI, G, JCT, K, L, LAE, MANCH, MEL, NSW, PERTH, QRS, SING, and U. I have seen and collected all Australian species including their pollinator wasps. These specimens are at JCT and DNA.

Taxonomic History

Fig species occurring in the *Ficus* subgen. *Urostigma* can be distinguished primarily by their habit. This subgenus is perhaps the easiest of the four subgenera to recognise for this is the banyan or strangling group of *Ficus* (Ramirez, 1977b). The epiphytic and lithophytic habit of the species in this subgenus, commonly produce aerial, adventitious, or creeping root systems. In addition, the wall of the syconium has an inner and outer layer of scleritic cells. Corner (1959a) established the *Urostigma* sect. *Malvanthera*, based on the following characters: an ostiole with two or three lobes with inflexed bracts; syconia with two or three basal bracts; reniform unilocular anthers with crescentic or transverse dehiscence; ovaries that are attached by their base to the wall of the syconium, or embedded in the wall of the syconium; a red spot at the apex or the base of the ovary; and a stigma that is either simple or bifid. The section was further subdivided into two series:

1. Malvanthera ser. Malvanthereae: with reniform anthers that dehisce crescentically, containing four subseries. Members of this series are wide-spread, being distributed throughout Australasia and eastern Malaysia (Corner 1965).

(i) *Malvanthereae* subser. *Malvanthereae:* with 2 (3?) large caducous basal bracts; pedunculate syconia; ovaries that are partially immersed in the wall of the syconium. The taxa included are: *F. macrophylla* Desf. ex Pers., *F. glandifera* Summerh., *F. watkinsiana* F.M. Bailey, *F. baileyana* Domin, and *F. rhizophoriphylla* King.

(ii) *Malvanthereae* subser. *Platypodeae*: with 2 or 3 large caducous basal bracts; pedunculate or sessile syconia; ovaries that are attached by their base to the wall of the syconium. The taxa included are: *F. platypoda* (Miq.) A.Cunn. ex Miq., *F. leucotricha* (Miq.) Miq., *F. obliqua* G. Forst., *F. subpuberula* Corner, *F. destruens* F. Muell. ex C. T. White, and *F. rubiginosa* Desf. ex Vent.

(iii) *Malvanthereae* subser. *Hesperidiiformes*: with 3 small persistent basal bracts. The taxa included are *F. hesperidiiformis* King, *F. augusta* Corner, *F. xylosycia* Diels, *F. mafuluensis* Summerh., *F. heteromeka* Corner, *F. pleurocarpa* F. Muell., and *F. crassipes* F. M. Bailey.

(iv) *Malvanthereae* subser. *Eubracteatae*: with 3 large persistent basal bracts; pedunculate or sessile syconia; ovaries that are attached by their base to the wall of the syconium. Represented by one species, *Ficus triradiata* Corner.

2. **Malvanthera ser. Cyclanthereae:** with depressed globose anthers that dehisce transversely; ovaries that are partially immersed in the wall of the syconium. Represented by one species, *Ficus sterrocarpa* Diels which is restricted to eastern New Guinea (Corner 1965).

Difficulties with the infrasectional classification

There are approximately equal numbers of species in three of the four subseries, the exception being *Ficus triradiata* which is the sole member of *Malvanthereae* subser. *Eubracteateae.* It is the only species with large persistent basal bracts. The three remaining subseries, the subser. *Malvanthereae,* subser. *Hesperidiiformes,* and subser. *Platypodeae* were defined rather loosely by persistence and size of the basal bracts. Thus it was easy to distinguish *Malvanthereae* subser. *Hesperidiiformes,* with small inconspicuous persistent basal bracts, from *Malvanthereae* subser. *Malvanthereae* and *Malvanthereae* subser. *Platypodeae* which have relatively larger caducous basal bracts. However, distinguishing the latter two subseries from each another is much more difficult. The only difference was whether the ovaries were attached by their base to the wall of the syconium, or were partially imbedded in the syconium wall (Corner 1959a). Also Corner (1965) may have later doubted the validity of his classification as he included *F. crassipes* and *F. pleurocarpa* in the key to the subser. *Malvanthereae* as well as the subser. *Hesperidiiformes.* A new infrasectional classification is proposed.

There are 14 Australian species recognised in the *Urostigma* sect. *Malvanthera.* A comparison of the classification of Chew (1989) and this research is presented in Table 1. *Ficus lilliputiana* was treated by Dixon (2001a), *F. macrophylla* (Dixon 2001b), *F. obliqua* and *F. rubiginosa* (Dixon et al. 2001), and *F. atricha, F. cerasicarpa, F. platypoda* and *F. brachypoda* (Dixon 2001c). Species descriptions are presented for the following taxa: *F. crassipes, F. destruens, F. pleurocarpa, F. subpuberula, F. triradiata,* and *F. watkinsiana.* For each species there is a discussion on etymology, nomenclature where necessary, distribution and ecology, and conservation status. Distributional ranges are provided for each taxon. In species where infraspecific taxa are described, a key to their identification is given. Plates and illustrations found in other texts are listed so that these texts can be updated with the correct nomenclature where necessary. The pollinator wasp of each *Ficus* species is also given. The author abbreviations for the plant taxa follow Brummitt and Powell (1992).

Table 1. A comparison of the classification of Chew (1989) and this research.

***Ficus* taxa recognised by Chew (1989)**	**Accepted name this research**
F. platypoda var. *minor* *F. platypoda* var. *lacnocaulon* *F. obliqua* var. *puberula*	*F. brachypoda*
F. platypoda var. *cordata*	*F. atricha*
F. rubiginosa *F. platypoda* var. *leichhardtii* *F. obliqua* var. *petiolaris* *F. baileyana*	*F. rubiginosa* f. *rubiginosa*
Not recognised	*F. rubiginosa* f. *glabrescens*
F. obliqua var. *obliqua*	*F. obliqua*
Not recognised	*F. cerasicarpa*
F. platypoda var. *platypoda* *F. leucotricha* var. *leucotricha* *F. leucotricha* var. *megacarpa* *F. leucotricha* var. *sessilis*	*F. platypoda*
Not recognised	*F. lilliputiana* f. *lilliputiana*
Not recognised	*F. lilliputiana* f. *pilosa*

Morphology

Basal bract form: The developing syconia are axillary and occur in pairs. At its junction with the peduncle, the syconium is subtended by either two or three basal bracts. These bracts are valvate or imbricate, either large and completely enclosing the developing syconium, or reduced and never enclosing the developing syconium. For the majority of the species these bracts are caducous; however, in two species they remain persistent for the life of the fig. In previous taxonomic treatments on this section, the basal bract number was considered to be fixed for each species and was used as an important character in delimiting some species, especially *F. obliqua* and *F. platypoda* with supposedly two and three basal bracts respectively (Corner 1965). I have found that the basal bract number is variable within some species in this section of *Ficus* and is therefore not a reliable character for species delimitation.

Basal veins of lamina: There may or may not be distinct lateral veins present at the base of the lamina. These veins diverge from the midvein at a different angle from the remainder of the lateral veins and were measured separately. The measurement taken was the displacement from the midrib. Basal veins are very distinct in the rainforest species, but indistinct in the deciduous vine thicket species.

Number of lateral veins: Both the major and minor lateral veins diverging from the midvein were counted. I could never consistently agree with the number of lateral veins recorded by Corner in his descriptions. Thus for consistency I counted both the major and minor lateral veins diverging off the midrib. The major lateral veins curve inside the margin and join with the next major vein. The minor lateral veins are those between two major veins.

Habit: The *Urostigma* sect. *Malvanthera* contains species that are hemi-epiphytic trees, erect free-standing trees or shrubs, lithophytic trees or shrubs, or lithophytic prostrate shrubs.

Intercostal region of lamina: The intercostal region between the tertiary veins on the abaxial surface of the lamina can either be sunken to form areolae as is found in *F. cerasicarpa* and *F. platypoda*, or flat as is found in the remainder of the species in the *Urostigma* sect. *Malvanthera.*

Key to the series in *Urostigma* sect. *Malvanthera*

1. Basal bracts imbricate.. **1. ser. Malvanthereae**
   Basal bracts valvate .... **2. ser. Hesperidiiformes**

Series Descriptions

1. Malvanthera ser. Malvanthereae Corner, *Gard. Bull. Singapore,* 17: 375 (1959). Type: *Ficus macrophylla* Desf. ex Vent.

Malvanthereae subser. *Platypodeae* Corner, *Gard. Bull. Singapore,* 17: 375 (1959). Type: *Ficus platypoda* (Miq.) A.Cunn. ex Miq.

Basal bracts imbricate. Stigma simple.

For included species refer to Table 2.

Malvanthera ser. Malvanthereae

This series consists of taxa, with imbricate basal bracts. The Australian species in this series are *F. platypoda, F. cerasicarpa, F. atricha, F. subpuberula, F. lilliputiana, F. brachypoda, F. destruens, F. macrophylla, F. rubiginosa, F. obliqua,* and *F. watkinsiana.* With the exception of *F. obliqua* and *F. brachypoda* all species are endemic to Australia.

Table 2. The infrasectional arrangement of the taxa belonging to the *Urostigma* sect. *Malvanthera*.

Malvanthera* ser. *Malvanthereae	***Malvanthera* ser. *Hesperidiiformes***
Species with imbricate basal bracts	Species with valvate basal bracts
F. macrophylla	*F. hesperidiiformis*
F. platypoda	*F. triradiata*
F. cerasicarpa	*F. sterrocarpa*
F. atricha	*F. mafuluensis*
F. subpuberula	*F. heteromeka*
F. lilliputiana	*F. crassipes*
F. brachypoda	*F. xylosycia*
F. destruens	*F. augusta*
F. rubiginosa	*F. glandifera*
F. obliqua	*F. pleurocarpa*
F. rhizophoriphylla	
F. watkinsiana	

Biogeography: There appear to be two diverging groups in this series, a hemi-epiphytic rainforest group represented by *F. destruens, F. watkinsiana,* and *F. macrophylla,* and a lithophytic deciduous vine thicket group represented by *F. platypoda, F. brachypoda, F. cerasicarpa, F. atricha,* and *F. lilliputiana.* The later group also shows strong biogeographical support with all the taxa found in deciduous vine thickets on the sandstone escarpments of central and north-western Australia. *Ficus rubiginosa* and *F. obliqua* are not obligate hemi-epiphytes, neither are they restricted to rainforest. They can also occur as lithophytes and hemi-epiphytes in deciduous vine thickets. *Ficus destruens* is also not restricted to the rainforest. It is often found as a hemi-epiphyte in ecotonal areas adjacent to rainforest. These taxa suggest the occurrence of transition species between the hemi-epiphytic taxa and the lithophytic taxa and thus preclude the recognition of two subseries within the series.

2. Malvanthera ser. Hesperidiiformes (Corner) D.J.Dixon **stat. nov.**

Malvanthereae subser. *Hesperidiiformes* Corner, *Gard. Bull. Singapore,* 17: 375 (1959). Type: *Ficus hesperidiiformis* King.

Malvanthera ser. *Cyclanthereae* Corner, *Gard. Bull. Singapore,* 17: 375 (1959). Type: *Ficus sterrocarpa* Diels.

Malvanthereae subser. *Eubracteatae* Corner, *Gard. Bull. Singapore,* 17: 375 (1959). Type: *Ficus triradiata.*

Basal bracts valvate. Stigma bifid except *F. glandifera.*

For included species refer to Table 2.

Australia has high levels of endemism in the *Urostigma* sect. *Malvanthera* (Corner 1958). Berg (1989) considered northern Australia to be the centre of distribution for the section.

Malvanthera ser. Hesperidiiformes

This series consists of taxa with valvate basal bracts. All the species in this series are rainforest hemi-epiphytes from Australia, New Guinea, and the New Britain, Solomon, and New Hebrides island groups. Three species, *F. triradiata, F. crassipes,* and *F. pleurocarpa,* are endemic to the closed forests of the Australian wet tropics.

Pollinator Wasps

The group of wasps that pollinate the florets of the numerous *Ficus* species belong to the Hymenopteran subfamily *Agaoninae.* At the sectional level of *Ficus,* with all but a few exceptions, Wiebes (1994) was able to show that related *Ficus* species have related genera of pollinator wasps. The *Ficus* species in the *Urostigma* sect. *Malvanthera* are pollinated by wasps of the genus *Pleistodontes* Saunders (Wiebes 1994). The Indo-Australian fig wasps have recently been treated by Wiebes (1994) who provided keys and descriptions of the wasp species presently known. Within the *Urostigma* sect. *Malvanthera* Wiebes (1994) recorded the same species of pollinator wasp from different species of *Ficus* and as such provided evidence for exceptions to the 1: 1 rule for fig wasp/host specificity. With the revision of the Australian *Urostigma* sect. *Malvanthera* and the pollinator wasp genus *Pleistodontes* now complete, I consider that much of the confusion over the wasp/host specificity was generated by unsatisfactory and incomplete taxonomies. For example, Table 3 compares the discrepancies that existed between the classifications of Chew (1989) and Wiebes (1994) and how the taxa are treated by this research and Lopez-Vaamonde et al. (2002).

Table 3. The Ficus species of the Urostigma sect. Malvanthera and the taxa recognised by Chew (1989) with their wasp pollinators (*Pleistodontes* spp.) as recognised by Wiebes (1994) compared with this research and the classification of Lopez-Vaamonde et al. (2002).

Ficus **taxa recognised by Chew (1989)**	***Pleistodontes*** **spp. recorded by Wiebes (1994)**	**Accepted name this research**	***Pleistodontes*** **spp. recorded by Lopez-Vaamonde et al. (2002)**
F. rubiginosa	*P. imperialis*	*F. rubiginosa*	*P. imperialis*
F. obliqua var. *obliqua*	*P. greenwoodi*	*F. obliqua*	*P. greenwoodi* *P. xanthocephalus*
F. obliqua var. *petiolaris*	*P. imperialis*	*F. rubiginosa*	*P. imperialis*
F. obliqua var. *puberula*	not known	*F. brachypoda*	*P. macrocainus*
F. platypoda var. *platypoda*	not known	*F. platypoda*	*P. cuneatus*
F. platypoda var. *not determined*	*P. proximus*	*F. lillputiana*	*P. proximus*
F. platypoda var. *angustata*	*P. imperialis*	*F. rubiginosa*	*P. imperialis*
F. platypoda var. *minor*	*P. greenwoodi*	*F. brachypoda*	*P. macrocainus*
F. platypoda var. *lachnocaulos*	not known	*F. brachypoda*	*P. macrocainus*
F. platypoda var. *cordata*	not known	*F. atricha*	not known
F. leucotricha var. *leucotricha*	not known	*F. platypoda*	*P. cuneatus*
F. leucotricha var. *not determined*	*P. cuneatus*	*F. platypoda*	*P. cuneatus*
F. leucotricha var. *megacarpa*	not known	*F. platypoda*	*P. cuneatus*
F. leucotricha var. *sessilis*	not known	*F. platypoda*	*P. cuneatus*
F. macrophylla ssp. *macrophylla*	*P. froggatti*	*F. macrophylla* f. *macrophylla*	*P. froggatti*
F. macrophylla ssp. *columnaris*	*P. froggatti*	*F. macrophylla* f. *columnaris*	*P. froggatti*
F. pleurocarpa	*P. nitens*	*F. pleurocarpa*	*P. regalis* *P. deuterus*
F. crassipes	*P. addicotti*	*F. crassipes*	*P. addicotti* *P. nitens*
F. watkinsiana	*P. nigriventris*	*F. watkinsiana*	*P. nigriventris*
F. destruens	*P. rigisamos*	*F. destruens*	*P. rigisamos*
F. baileyana	not known	*F. rubiginosa*	*P. imperialis*
F. subpuberula	not known	*F. subpuberula*	*P. austrobocheilus*
F. triradiata var. *triradiata*	not known	*F. triradiata*	*P. schizodontes*
F. triradiata var. *sessilicarpa*	not known	*F. triradiata*	*P. schizodontes*
Not recognised		*F. cerasicarpa*	*P. macrocainus* *P. athysanus*

Key to the species of *Urostigma* sect. *Malvanthera* in Australia

This key has been developed to reflect the characters that will best delimit the taxa involved. It is recommended that fertile material be used when at all possible and that the combination of characters in each couplet be matched conclusively.

1. Plants hemi-epiphytic (stranglers), lithophytic, or free-standing large trees to 50 m; leaves with basal veins more or less conspicuous; distribution eastern Queensland (eastern edge of the Mitchell Grass Plains) and New South Wales; habitat rainforest, vine thicket, rarely woodland 2

   Plants lithophytic, small trees to 13 m, or prostrate shrubs; leaves with basal veins more or less inconspicuous; distribution western Queensland (western edge of the Mitchell Grass Plains), Northern Territory, South Australia, and Western Australia; habitat vine thickets 9

2. Stipules, petiole (may only be scattered at base), and twigs with ascending hyaline hairs, adaxial lamina surface glabrous 3

   Stipules, petiole, and twigs with ascending hyaline hairs interspersed with weak ferruginous hairs, adaxial lamina surface with weak ferruginous hairs at least when young 5

3. Abaxial lamina surface glabrous, syconia small (4–12 mm long, 4–11 mm in diameter), ellipsoid, obloid, spheroid; widespread along eastern seaboard of Australia, from Cape York Peninsula to south-eastern New South Wales .... **1. F. obliqua**

   Abaxial lamina surface with ascending hyaline hairs, syconia large (39–68 mm long, 15–32 mm in diameter), 3 to 10-angled 4

4. Abaxial lamina surface with weak ferruginous hairs restricted to the intercostals (tomentose to felted), ascending hyaline hairs along mid and basal pair of veins, syconia 5 to 10-angled, red to orange, ostiole gibbose forming a crown with up to four unequal lobes; found from Cape Tribulation south to the Atherton Tablelands of Queensland........................... **2. F. pleurocarpa**

   Abaxial lamina surface glabrous or with ascending hyaline hairs scattered at base of lamina, syconia 3-angled, brownish yellow, ostiole probosciform with three unequal lobes; restricted to the Atherton Tablelands of Queensland.. **3. F. crassipes**

5. Abaxial lamina surface with a dense covering of weak ferruginous hairs only, tomentose (may appear white in very young growth) 6

   Abaxial lamina surface glabrous or with weak ferruginous hairs that are either interspersed with ascending hyaline hairs, scattered over lamina surface (not tomentose), or very sparsely scattered at base of lamina 7

6. Abaxial lamina surface appearing glabrous but with felted to tomentose ferruginous hairs restricted to intercostals, petiole glabrous, syconia 18–25 mm long, 15–24 mm in diameter, ostiole with three lobes (triradiate), distribution south-eastern Queensland, eastern New South Wales, and Lord Howe Island .... **4. F. macrophylla**

   Abaxial lamina surface with weak ferruginous hairs (may appear white in very young growth), petiole with weak ferruginous hairs with or without ascending hyaline hairs, syconia 13–20 mm long, 11–16 mm in diameter, ostiole umbonate with two lobes (bilabiate), distribution closed forest from Cape Tribulation to Eungella Range, may also be found in ecotonal areas adjacent to rainforest .... **5. F. destruens**

7. Abaxial and adaxial lamina surface, petiole, stipule, twigs, basal bracts, syconia, and peduncle with ascending hyaline hairs, or with weak ferruginous hairs (may have combination of both) (if abaxial and adaxial lamina surface, petiole, twigs, and basal bracts, are glabrous then stipule and syconia with weak ferruginous hairs); syconia 7–18 mm long, 7–18 mm in diameter; widespread along eastern Australia from Cape York Peninsula to south-eastern New South Wales .... **6. F. rubiginosa**

   Abaxial and adaxial lamina surface and petiole glabrous, stipule with hyaline ascending hairs or glabrous, syconia 21–37 mm long, 15–29 mm in diameter... 8

8. Stipules glabrous, or with ascending hyaline hairs, or with weak ferruginous hairs, basal bracts persistent, glabrous, syconia, yellow or pink-orange; restricted to the Mt. Windsor Tableland, Mt. Lewis, and lowland rainforest of Cape Tribulation .... **7. F. triradiata**

Stipules with ascending hyaline hairs interspersed with weak ferruginous hairs, never glabrous, basal bracts caducous with weak ferruginous hairs, syconia deep purple to black; two disjunct populations, Atherton Tablelands to Paluma Range and south-eastern Queensland/north-eastern New South wales .... **8. F. watkinsiana**

9. Intercostals of abaxial lamina surface strongly sunken, abaxial leaf lamina densely covered with ascending hyaline hairs (pilose, villous), ... 10

Intercostals of abaxial lamina surface not strongly sunken, abaxial leaf lamina glabrous or (minutely) puberulous, pilose, ... 11

10. Basal bracts 2–8 mm long, peduncles slender (1–2 mm in diameter), western Queensland, northern Northern Territory, occasionally Western Australia .... **9. F. cerasicarpa**

Basal bracts 6–29 mm long, peduncles thick (2–5 mm in diameter), northern Northern Territory, northern Western Australia. .... **10. F. platypoda**

11. Mature plants prostrate shrubs; restricted to the escarpments around Kununurra, Western Australia, and the adjacent Keep River National Park, Northern Territory ...... **11. F. lilliputiana**

Mature plants erect trees 12

12. Lamina mealy, grey-green in colour, syconia yellow, distributed from Lawnhill National Park in Queensland across the Top End of the Northern Territory, to the Kimberley region of Western Australia .... **12. F. subpuberula**

Lamina glabrous or with weak ferruginous hairs, ascending hyaline hairs may be present, syconia red or reddish brown 13

13. Plants glabrous in all parts; distributed across Kakadu plateau, Northern Territory, to the Kimberleys of Western Australia .... **13. F. atricha**

Plants with parts variously pubescent; widely distributed from western Queensland, across the Northern Territory and Western Australia, extending south into northern South Australia .... **F. brachypoda**

Species descriptions

1. Ficus obliqua G.Forst. *Fl. Ins. Austral.* 77 (1786). A full description for this species is presented in Dixon et al. (2001).

Pollinator wasp(s): Two pollinator wasps have been recorded by Lopez-Vaamonde et al. (2002) for *F. obliqua*. They are *Pleistodontes greenwoodi* Grandi and *Pleistodontes xanthocephalus* Vaamonde, Dixon, Cook & Rasplus.

2. Ficus pleurocarpa F.Muell., *Fragm.* 8: 246 (1874). Type: Johnson River, QLD, *W. Hill s.n.* (holo *n.v.*).

According to Stafleu and Cowan (1976) the type of *F. pleurocarpa*, being a Mueller name, should be at MEL; however, efforts to locate it at MEL have failed. Attempts to locate the type at K or the British Museum (BM) were unsuccessful. There is a specimen of *F. pleurocarpa* with a Mueller label at K, it has the correct locality details, but it lacks the collector's name of 'W. Hill' as cited by Mueller (1874) in the protologue, which would authenticate this specimen as the type.

Ficus cylindrica Warb., *Repert. Spec. Nov. Regni Veg.* 1: 72 (1905). Type: Barron River, QLD, 22 May 1902, *L. Diels 8382* (holo B).

Hemi-epiphyte to 25 m. *Twigs* glabrous, or pilose to villous with ascending hyaline hairs, glabrescent. *Leaves* alternate, narrowly oblong to ovate; apex acute; base cuneate to rounded. *Lamina* 150–257 mm long, 49–100 mm wide; abaxial surface with ascending hyaline hairs restricted to the mid vein and basal pair of veins, puberulous to pilose, lamina surface tomentose with ferruginous hairs restricted to the intercostals; adaxial lamina surface glabrous. *Lateral veins* 75–121 pairs, 64°–84°, basal veins distinct, 30°–56°. *Petiole* 44–102 mm long, 1–5 mm wide; pilose with ascending hyaline hairs, glabrescent. *Stipules* 120–245 mm long; glabrous, or pilose to villous, with ascending hyaline hairs, glabrescent. *Syconia* 39–61 mm long, 19–27 mm in diameter; oblong to ovoid, 5–10-angled; orange or red; glabrous, or with weak ferruginous hairs, glabrescent; punctate; ostiole lobes 4, of unequal size. *Basal bracts* 3, valvate, much reduced; caducous; puberulous, with ascending hyaline hairs. *Peduncle* 10–30 mm long, puberulous to pilose with ascending hyaline hairs. *Female florets* sessile, tepals 3 or 4; stigma bifid; male florets pedicellate, tepals 3–5, anthers 1 with crescentic dehiscence, interspersed with the female and gall florets; gall florets pedicellate, tepals 3 or 4. *Interfloral bracts* present.

Selected specimens examined: Queensland: Cook: Hewet's Property, Cooper Creek, *D. Dixon PHD93*, 26 Apr 1996 (JCT); Eastern Slope of Mount Sorrow, Cape Tribulation, 16°05S 145°27E, *G.D. Weiblen 209*, 25 Feb 1993 (BRI); Vacant Crown Land, near Noah Creek, 16°10S 145°10E, *B.P.M. Hyland 5978*, 11 Apr 1972 (QRS); Mt. Pieter Botte, 16°41S 145°25E, *R. Russell 20*, 30 Mar 1992 (BRI); Copper Lode Falls dam area, Cairns, 17°00S 145°40E, *W.R. Birch 18*, 07 Dec 1972 (BRI); State Forest Reserve 185, Buchan Logging Area, 17°08S 145°37E, *B. Gray 2574*, 13 May 1982 (QRS); State Forest Reserve 310, Gadgarra, Tardent Logging Area, Compartment 4a, 17°18S 145°43E, *G.L. Unwin 256*, 24 Mar 1977 (QRS); Road to Bartle Frere walking track, off Lake Eacham Road, Atherton Tablelands, 17°22S 145°42E, *D. Dixon PHD338*, 21 Nov 1996 (JCT); Timber Reserve 1230, Boonjie Logging Area, 17°23S 145°45E, *B.P.M. Hyland 13326*, 12 Nov 1987 (QRS); Wallace Road near commencement of State Forest Reserve 755, 17°25S 145°40E, *A.K. Irvine 1303*, 26 Mar 1975 (QRS); Elinjaa Road, Millaa Millaa District, 17°28S 145°40E, *A.K. Irvine 2218*, 09 Jul 1982 (QRS); 1.8 km along Theresa Creek Road from Millaa Millaa side, Atherton Tablelands, 17°29S 145°36E, *D. Dixon PHD343*, 21 Nov 1996 (JCT); Timber Reserve 1231, Djallan Logging Area, 17°34S 145°43E, *B. Gray 2928*, 13 Jan 1983 (QRS); Palmerston Highway, *H. Cooke s.n.*, 18 Dec 1976 (JCT); Palmerston National Park, N Johnstone River 17°36S 145°46E, *L.W. Jessup 743*, 10 Dec 1984 (BRI); State Forest Reserve 756, Maple Logging Area (between Tully River and S Johnston River), 17°40S 145°40E, *A.W. Dockrill 29*, 29 Apr 1971 (QRS).

Etymology: The epithet *pleurocarpa* is derived from the Greek prefix *pleuro-* meaning ribbed, and the Greek adjectival suffix *–carpus*, and refers to the syconia that have 5–10 ribs running from the base to the tip of the syconium.

Distribution and Ecology: *Ficus pleurocarpa* is a hemi-epiphytic species restricted to the lowland and upland wet tropic rainforests of north-east Queensland (Fig. 1) with an altitudinal range from near sea level to 1000m (Hyland & Whiffin 1993). *Ficus pleurocarpa* is endemic to Australia.

Notes: Commonly referred to as Banana Fig, it is easily identified by its large orange to red cylindrical syconia that bear up to 10 ribs running from base to tip. The ostiole bears four, sometimes indistinct, lobes often forming a crown at the apex of the syconium.

Conservation Status: *Ficus pleurocarpa* is well conserved in national parks and state forests throughout its distributional range, therefore no conservation code is recommended.

Illustrations: *Williams, K.A.W., 1979,* Native Plants Queensland, *Volume 1, p. 124; Chew, W., 1989, Moraceae,* Flora of Australia *3: 48 fig. 31C; Christophel, D.C. & Hyland, B.P.M., 1993,* Leaf Atlas of Australian Tropical Rain Forest Trees, *p. 166, plate 103a; Cooper, W., and Cooper, W.T., 1994,* Fruits of the Rainforest, *p. 134, Fig. 268.*

Pollinator Wasp(s): Two pollinator wasps have been recorded by Lopez-Vaamonde et al. (2002) for *F. pleurocarpa*. They are *Pleistodontes regalis* Grandi and *Pleistodontes deuterus* Vaamonde, Dixon, Cook & Rasplus. This association constitutes one of the few examples where two pollinator species have been reared from the same syconium of a *Ficus* species.

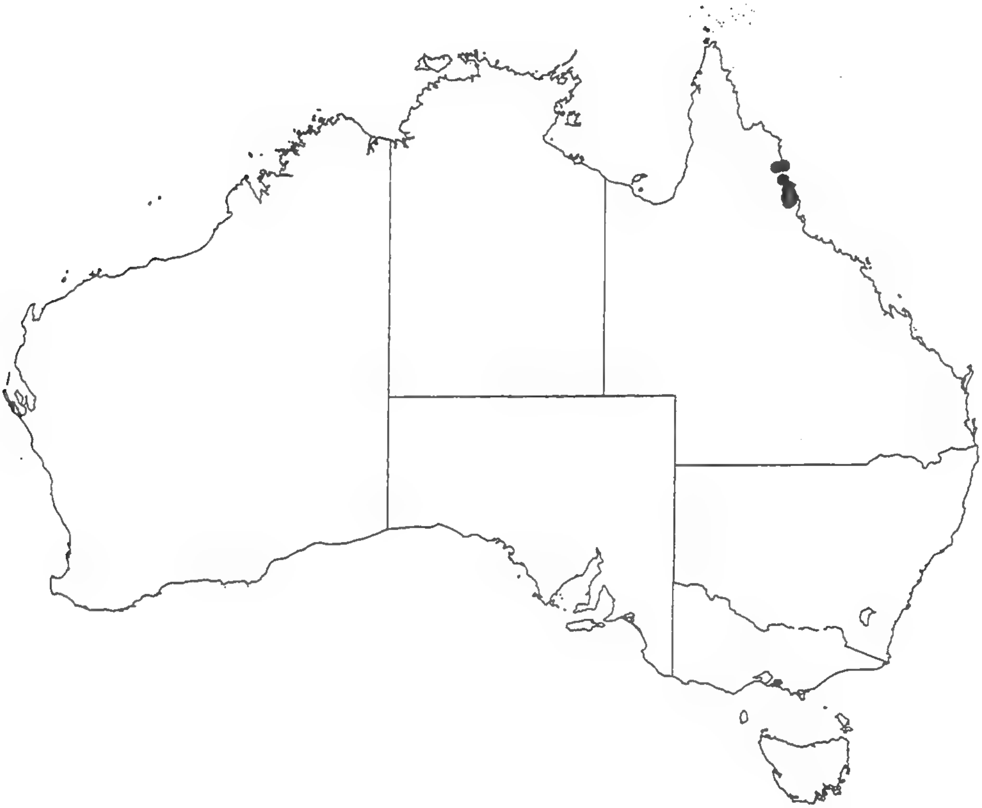
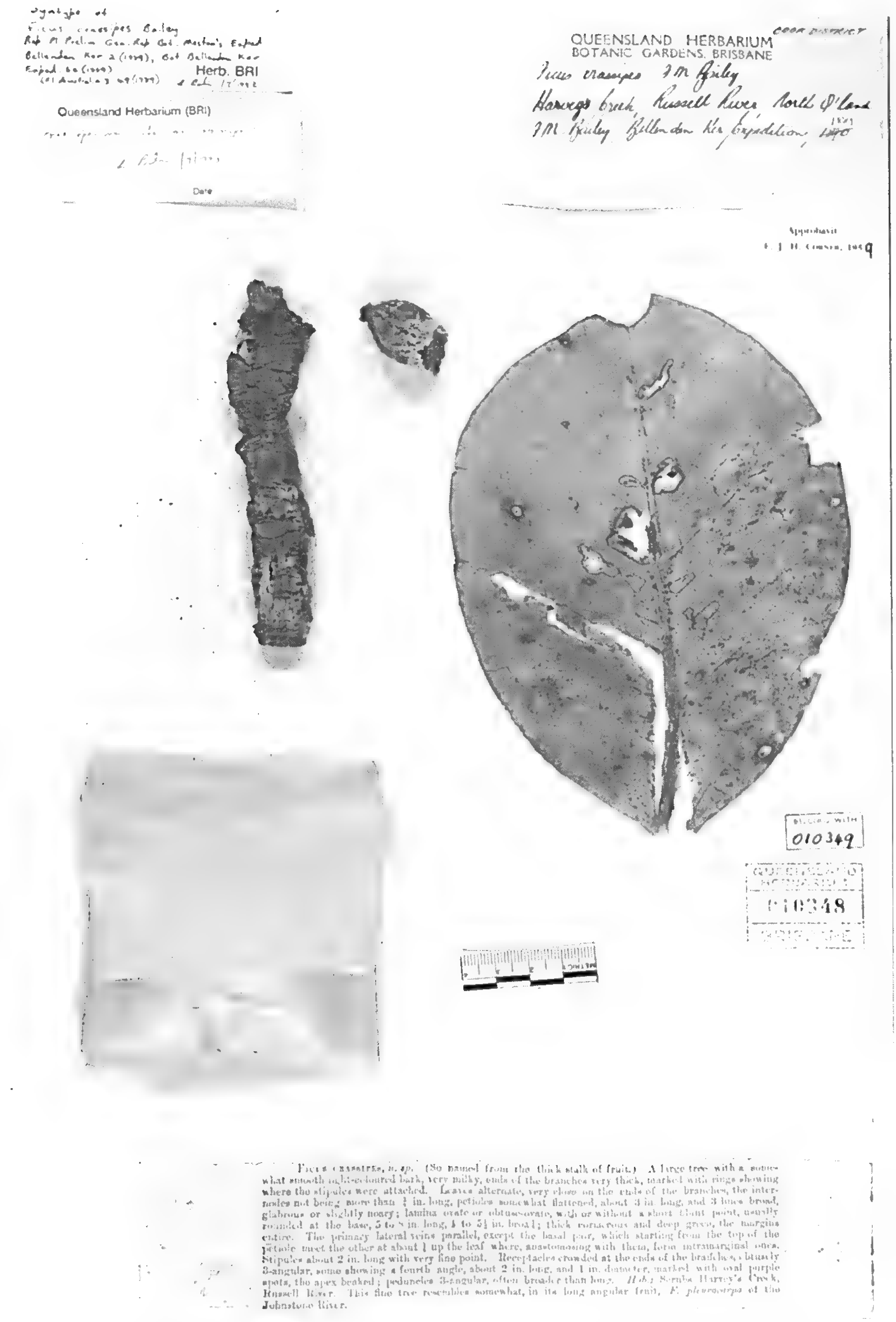


Fig. 1. The distribution of *Ficus pleurocarpa* based on available collection data.

3. Ficus crassipes F.M.Bailey, *Rep. Pl. Prelim. Gen. Rep. Bot. Meston's Exped. Bellenden Ker* 2 (1889); *Bot. Bellenden Ker Exped.* 60 (1889). Type: Harvey Creek, Russell River, QLD, *F.M. Bailey & E. Meston s.n.* (holo BRI; iso MEL) (Fig. 2).

Hemi-epiphyte to 20 m. *Twigs* pilose with ascending hyaline hairs interspersed with weak ferruginous hairs, or puberulous to pilose with ascending hyaline hairs only. *Leaves* alternate, ovate, oblong, elliptic, widely elliptic, obovate, widely obovate; apex obtuse, rounded; base obtuse, rounded. *Lamina* 76–218 mm long, 53–154 mm wide; abaxial and adaxial surface glabrous or with scattered ascending hyaline hairs at the junction of the petiole and lamina. *Lateral veins* 36–68 pairs, 38°–70°, basal veins distinct, 26°–57°. *Petiole* 38–138 mm long, 3–5 mm wide; glabrous, or puberulous to pilose with ascending hyaline hairs, glabrescent. *Stipules* 81–125 mm long; pilose to villous with ascending hyaline hairs interspersed with weak ferruginous hairs, or pilose, to villous with ascending hyaline hairs only. *Syconia* 43–68 mm long, 15–32 mm



Ficus crassipes, *n. sp.* (So named from the thick stalk of fruit.) A large tree with a somewhat smooth light-coloured bark, very milky, ends of the branches very thick, marked with rings showing where the stipules were attached. Leaves alternate, very close on the ends of the branches, the internodes not being more than ½ in. long, petioles somewhat flattened, about 3 in. long, and 3 lines broad, glabrous or slightly hoary; lamina ovate or obtuse-ovate, with or without a short blunt point, usually rounded at the base, 5 to 8 in. long, 4 to 5½ in. broad; thick coriaceous and deep green, the margins entire. The primary lateral veins parallel, except the basal pair, which starting from the top of the petiole meet the other at about ⅓ up the leaf where, anastomosing with them, form intramarginal ones. Stipules about 2 in. long with very fine point. Receptacles crowded at the ends of the branchlets, obtusely 3-angular, some showing a fourth angle, about 2 in. long, and 1 in. diameter, marked with oval purple spots, the apex beaked; peduncles 3-angular, often broader than long. *Hab.:* Scrubs, Harvey's Creek, Russell River. This fine tree resembles somewhat, in its long angular fruit, *F. pleurocarpa* of the Johnstone River.

Fig. 2. The holotype of *Ficus crassipes* F.M.Bailey. The specimen consists of two sheets of which only sheet one is shown. The original description, as it appeared in the original publication in 1889, is near the bottom margin.

in diameter; lanceoloid, ovoid, oblong, narrowly oblong, often 3-angled; yellow-brownish-orange, orange-brown, brown, dark purple, with dark brown spots; puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs, or puberulous to pilose with ascending hyaline hairs only; punctate, ostiole probisciform, triradiate. *Basal bracts* 3, valvate, much reduced, persistent; pilose with ascending hyaline hairs interspersed with weak ferruginous hairs, or puberulous to pilose with ascending hyaline hairs only. *Peduncle* 7–17 mm long; pilose with ascending hyaline hairs interspersed with weak ferruginous hairs, or puberulous to pilose with ascending hyaline hairs only. *Female florets* imbedded in wall of receptacle, sessile, subsessile, tepals 3 or 4, stigma bifid; male florets pedicellate, tepals 3 or 4, anthers 1 with crescentic dehiscence, interspersed with the female and gall florets; gall florets imbedded, sessile, subsessile, pedicellate, tepals 3 or 4. *Interfloral bracts* present.

Selected specimens examined: Queensland: Cook: 14.9 km along Ravenshoe to Millaa Millaa, Scenic Route, Atherton Tablelands, 17°34S 145°36E, *D. Dixon PHD333*, 19 Nov 1996 (JCT); Timber Reserve 146, Fritz Logging Area, between gap and Three Jims Creek, 15°45S 145°20E, *B.P.M. Hyland 6779*, 25 Jul 1973 (QRS); Kennedy Highway, Evelyn Central, 17°29S 145°30E, *R. Elick 62*, 18 May 1988 (QRS); Wallace Road, 17°24S 145°40E, *R. Jensen 726*, 13 May 1996 (QRS); Millaa Millaa, 200m along Theresa Creek Road, Atherton Tablelands, 17°30S 145°36E, *D. Dixon PHD330*, 18 Nov 1996 (JCT); Topaz, near Malanda, 17°25S 145°43E, S.T. *Blake 15204*, 25 Aug 1943 (BRI); Road to Butcher Creek on the Topaz Road to Bartle Frere, Atherton Tablelands, 17°21S 145°41E, *D. Dixon PHD340*, 21 Nov 1996 (JCT); Glen Allyn, 17°27S 145°42E, *A.W. Dockrill 131*, 16 Jun 1971 (BRI; QRS); Timber Reserve 1230, Boonjie Logging Area, 17°25S 145°45E, *B.P.M. Hyland 6591*, 04 Dec 1972 (QRS); Hugh Nelson Range, 19 miles S of Atherton, 17°26S 145°29E, *J.W. Wrigley & I.R. Telford NQ554*, 02 Jun 1972 (CANB); Evelyn Tableland, 26 miles S of Atherton, 17°30S 145°30E, *J.W. Wrigley & I.R. Telford NQ572*, 02 Jun 1972 (CANB); Jaggan, S of Malanda, *L.S. Smith & J. Webb 3340*, 17 Aug 1947 (BRI); Mt. Lewis, approx 7 km from top, *A. Cairns s.n.*, 23 Jun 1996 (JCT).

Etymology: The epithet *crassipes* is derived from the Latin adjective *crassus* meaning thick, and refers to the thick peduncle on the syconia of this species (Meston 1889).

Distribution and Ecology: *Ficus crassipes* is a hemi-epiphytic species restricted to upland areas of the wet tropic rainforests of north-east Queensland (Fig. 3). It has an altitudinal range of 650–1000 m (Hyland & Whiffin 1993) and is endemic to Australia.

Notes: Commonly referred to as Round Leaf Banana Fig, *F. crassipes* is sometimes confused with *F. pleurocarpa*, it is easily identified by its large brownish cylindrical syconia, the very small persistent papery basal bracts, and the probosciform triradiate ostiole.

Conservation Status: Although much of the rainforest of the Atherton Tablelands has been cleared, *F. crassipes* is still commonly encountered and is well-conserved in state forests throughout its distributional range. Therefore no conservation code is recommended.

Illustrations: *Williams, K.A.W., 1979,* Native Plants Queensland, Vol. 1, p. 122*; Chew, W., 1989, Moraceae,* Flora of Australia *3: 48, Fig. 31A–B; Christophel, D.C. & Hyland, B.P.M., 1993,* Leaf Atlas of Australian Tropical Rain Forest Trees, *p. 160, plate 98b; Cooper, W. and Cooper, W.T., 1994,* Fruits of the Rainforest, *p. 130, Fig. 259.*

Pollinator Wasp(s): Two pollinator wasps have been recorded by Lopez-Vaamonde et al. (2002) for *F. crassipes*. They are *Pleistodontes nitens* Grandi and *Pleistodontes addicotti* Wiebes. Together with the pollinators of *F. pleurocarpa* this is one of the few instances in which two pollinator species have been reared from the same syconium of a *Ficus* species. Wiebes (1994) cited *F. pleurocarpa* as the host of *P. nitens*; however Vaamonde et al. (2002) stated that previous treatments had misinterpreted *P. nitens*.

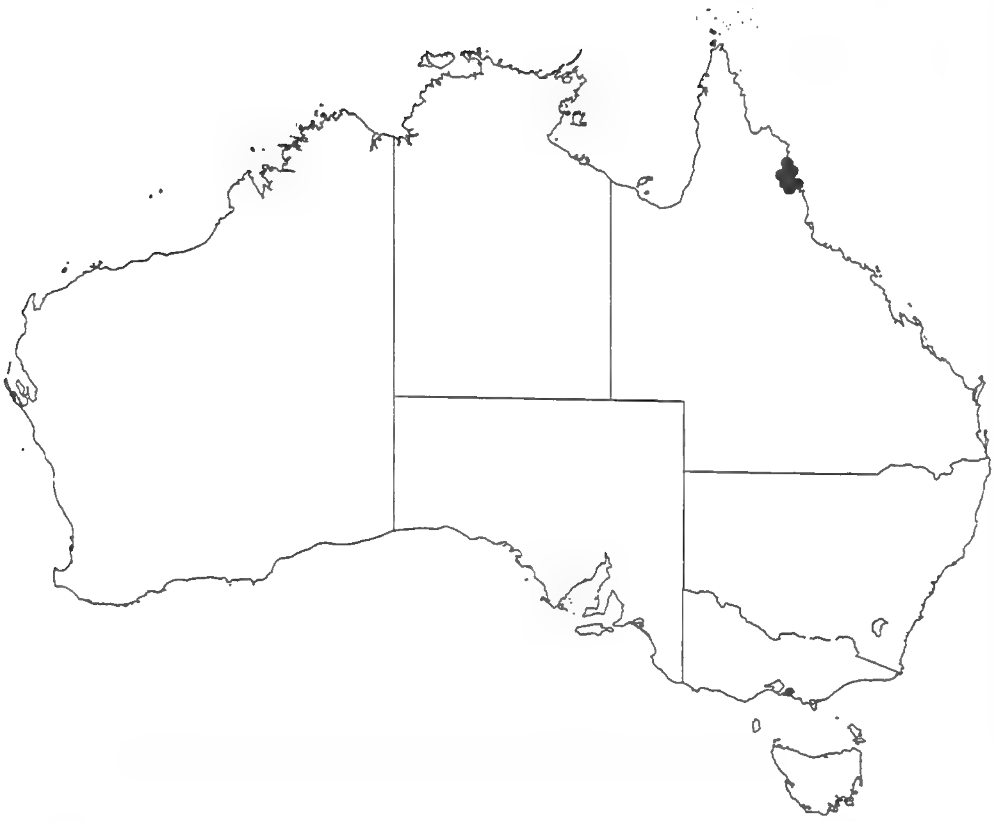


Fig. 3. The distribution of *Ficus crassipes* based on available collection data.

4. Ficus macrophylla Desf. ex Pers. *Syn. Pl.* 2: 609 (1807). A full description is presented in Dixon (2001b).

There are two forms which are distinguished as follows:

1. Free-standing tree, endemic to mainland Australia .... f. *macrophylla*
 Hemi-epiphtye with no obvious main trunk, endemic to Lord Howe Island .... f. *columnaris*

Pollinator Wasp: The pollinator wasp of *F. macrophylla sens. lat.* is *Pleistodontes froggatti* Mayr (Lopez-Vaamonde et al., 2002).

5. Ficus destruens F.Muell. ex C.T.White, *Contr. Arnold Arbor.* 4: 16 (1933). Type: Gadgarra, Atherton Tableland, QLD, 8 June 1929, *S.F. Kajewski 1087* (holo BRI) (Fig. 4).

Hemi-epiphyte to 32 m. *Twigs* pilose to villous with ascending hyaline hairs interspersed with weak ferruginous hairs, glabrescent. *Leaves* alternate, narrowly oblong, narrowly elliptic, oblanceolate, lanceolate; apex acute; base cuneate, obtuse. *Lamina* 51–194 mm long, 16–63 mm wide; abaxial surface tomentose with ferruginous hairs restricted to the intercostals, glabrescent; adaxial surface glabrous in older leaves, or tomentose

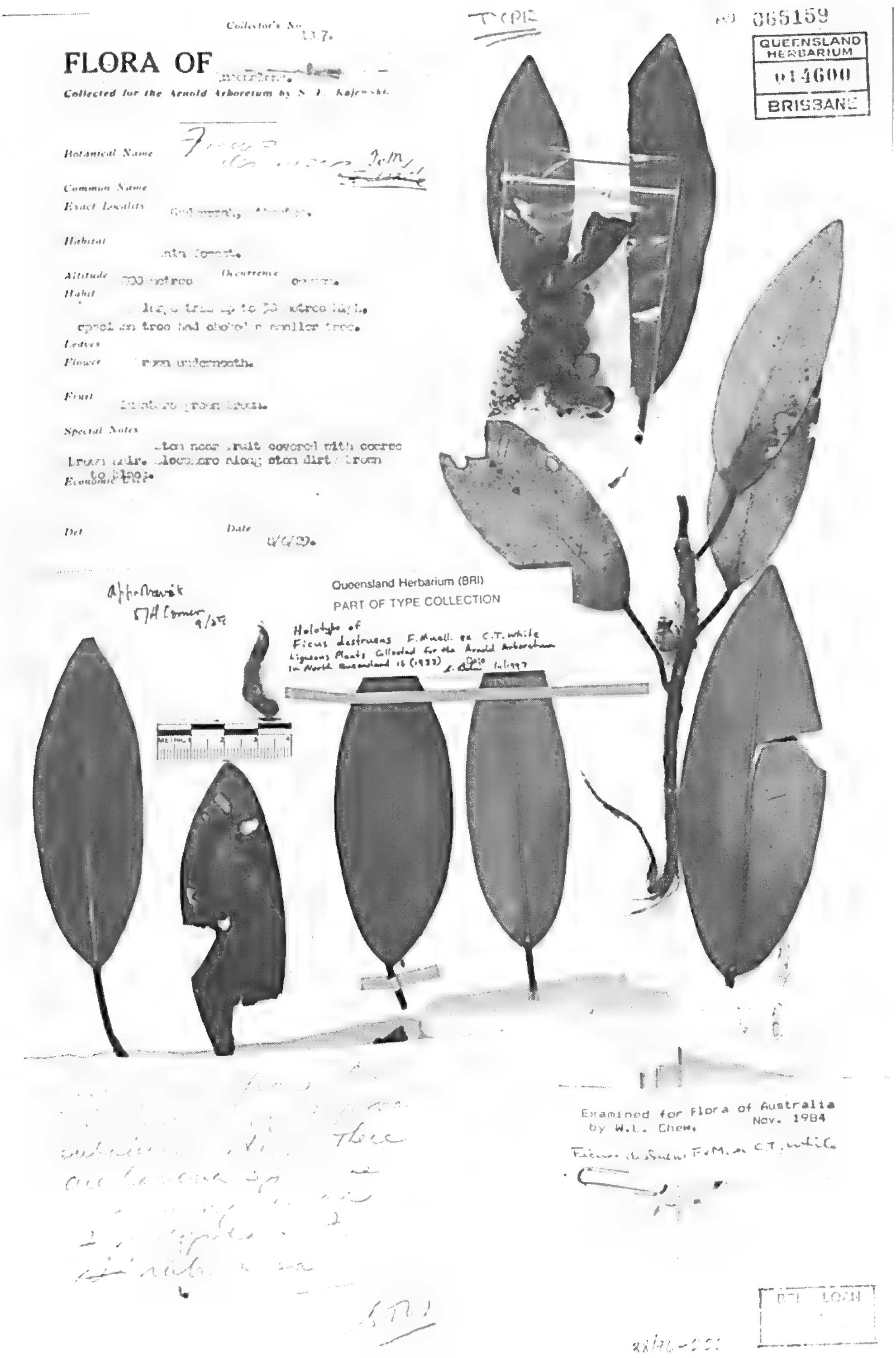


Fig. 4. The holotype of *Ficus destruens* F.Muell. ex C.T.White.

with ferruginous hairs, glabrescent in the younger leaves. *Lateral veins* 20–53 pairs, 49°–74°, basal veins distinct, 28°–52°. *Petiole* 12–64 mm long, 2–5 mm wide; puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs, glabrescent, or tomentose with ferruginous hairs, glabrescent. *Stipules* 46–74 mm long; pilose to villous with ascending hyaline hairs interspersed with weak ferruginous hairs. *Syconia* 13–19 mm long, 11–16 mm in diameter, often compressed laterally; broadly oblong to broadly ellipsoid, ellipsoid, spheroid; orange, red; tomentose with ferruginous hairs, glabrescent; punctate, ostiole bilabiate. *Basal bracts* 2, imbricate, puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs, glabrescent, or tomentose with ferruginous hairs. *Peduncle* 3–6 mm long; pilose with ascending hyaline hairs interspersed with weak ferruginous hairs, glabrescent. *Female florets* sessile, subsessile, tepals 4 or 5, stigma simple; male florets pedicellate, tepals 5–7, anthers 1 with crescentic dehiscence, interspersed with the female and gall florets; gall florets sessile, pedicellate, tepals 3–6. *Interfloral bracts* present.

Selected specimens examined: Queensland: Cook: 52.2 km along Palmerston Highway, heading towards Palmerston, on S side of road, Atherton Tablelands, *D. Dixon PHD94*, 27 Apr 1996 (JCT); Hope Vale Aboriginal Reserve, 15 km SW of McIvor River mouth, Cooktown, 15°13S 145°07E, *D.G. Fell & J.P. Stanton DGF3838*, 17 Nov 1993 (BRI); 4 km W of Isabella falls on Battle Camp Road, 15°16S 144°59E, *L.W. Jessup, G.P. Guymer & H.A. Dillewaard GJD3025*, 30 Nov 1989 (BRI); State Forest Reserve 78, Dagmar, 16°13S 145°17E, *B.P.M. Hyland 9224*, 01 Dec 1976 (QRS); State Forest Reserve 144, Cockatoo Logging Area, 0.5 km past W Spencer Creek Forestry Camp, 33 km NNW of Mount Carbine, 42 km NW of Mossman, Mount Windsor Tableland, 16°15S 145°02E, *L.W. Jessup, G.P. Guymer & W.J. McDonald GJM1199*, 01 Nov 1988 (BRI); 3 miles from Kuranda towards Mareeba, 16°15S 145°36E, *J.W. Wrigley & I.R. Telford NQ1229*, 16 Jun 1972 (CANB); Whyanbeel on road to Devils Thumb, 16°23S 145°22E, *R. Russell 7*, 01 May 1993 (BRI); Mossman Gorge National Park, 16°27S 145°18E, *L.W. Jessup, G.P. Guymer & H.A. Dillewaard GJD3331*, 04 Dec 1989 (BRI); Kuranda, 16°49S 145°38E, *B.P.M. Hyland 3063*, 06 Feb 1964 (BRI); Davies Creek, 16°54S 145°33E, *J.G. Tracey 15330*, 01 Dec 1963 (BRI); Copper-lode Falls Dam Site, Cairns, 16°56S 145°34E, *C.H. Gittens 2216*, 13 Sep 1970 (NSW); State Forest Reserve 185, Robson Logging Area, Experimental Plot 9, 17°10S 145°35E, *K. Sanderson 135*, 25 May 1972 (QRS); Lake Tinaroo, 41.6 km along Danbulla Forest Drive from dam end, Atherton Tablelands, 17°13S 145°39E, *D. Dixon PHD329*, 13 Nov 1996 (JCT); Russell Road, 17°19S 145°43E, *P.I. Forster & S.J. Figg 17127*, 04 Jul 1995 (BRI); State Forest Reserve 310, Windin Logging Area (Windin Creek, a tributary of W Mulgrave River), 17°20S 145°45E, *A.W. Dockrill 80*, 06 May 1971 (QRS); Boulders, Babinda, 17°21S 145°52E, *B. Jago 44*, 16 Nov 1988 (QRS); Topaz Road, 2.5 km NE of Bartle Frere Road junction, 17°22S 145°41E, *P.H. Weston, P. Hind, D. Healey & G. Sankowsky 883*, 21 Aug 1986 (NSW); 1.7 km along Theresa Creek Road from Millaa Millaa side, Atherton Tablelands, 17°29S 145°36E, *D. Dixon PHD342*, 21 Nov 1996 (JCT); Gotack Road, 17°31S 145°29E, *R. Elick 49*, 21 Jan 1988 (QRS); State Forest Reserve756, Velvin Logging Area, 17°40S 145°55E, *B.P.M. Hyland 1646*, 01 Aug 1968 (BRI). North Kennedy: Paluma Range, Dotswood Holding, 19°15S 146°25E, *B.P.M. Hyland 7266*, 11 Jun 1974 (QRS). South Kennedy: Rick and Brenda Parker's property, Bee Creek, off Bee Creek road, Eungella Range, *D. Dixon PHD98 & I. Champion*, 03 Jun 1996 (JCT); Eungella-Dalrymple road, 0.5 km N of Black's road turnoff, *D. Dixon PHD97 & I. Champion*, 03 Jun 1996 (JCT); near Boundary State Forest Reserve 62, Gamma, on Eungella Road, 21°05S 148°35E, *B.P.M. Hyland 8211*, 09 May 1975 (QRS).

Etymology: The species epithet is Latin for destroy, and refers to the ability of this species to destroy its host. *Ficus destruens* is a strangler fig eventually killing its host thus securing its place in the canopy of the rainforest.

Distribution and Ecology: *Ficus destruens* is found mainly in upland areas of the wet tropic rainforests of north-east Queensland at altitudes between 350 and 1000 m (Hyland & Whiffin 1993). However, I have observed it growing in the tropical lowland rainforests at Broadwater State Forest, north of Ingham. It extends from the Atherton Tablelands, south to Eungella Range west of Mackay (Fig. 5). It is a hemi-epiphytic species that is occasionally found as a strangler on *Eucalyptus grandis* W.Hill ex Maiden in the wet sclerophyll forests of Eungella Range (Chew 1989), and on other eucalypt species around Cairns (White 1933). *Ficus destruens* is endemic to Australia.

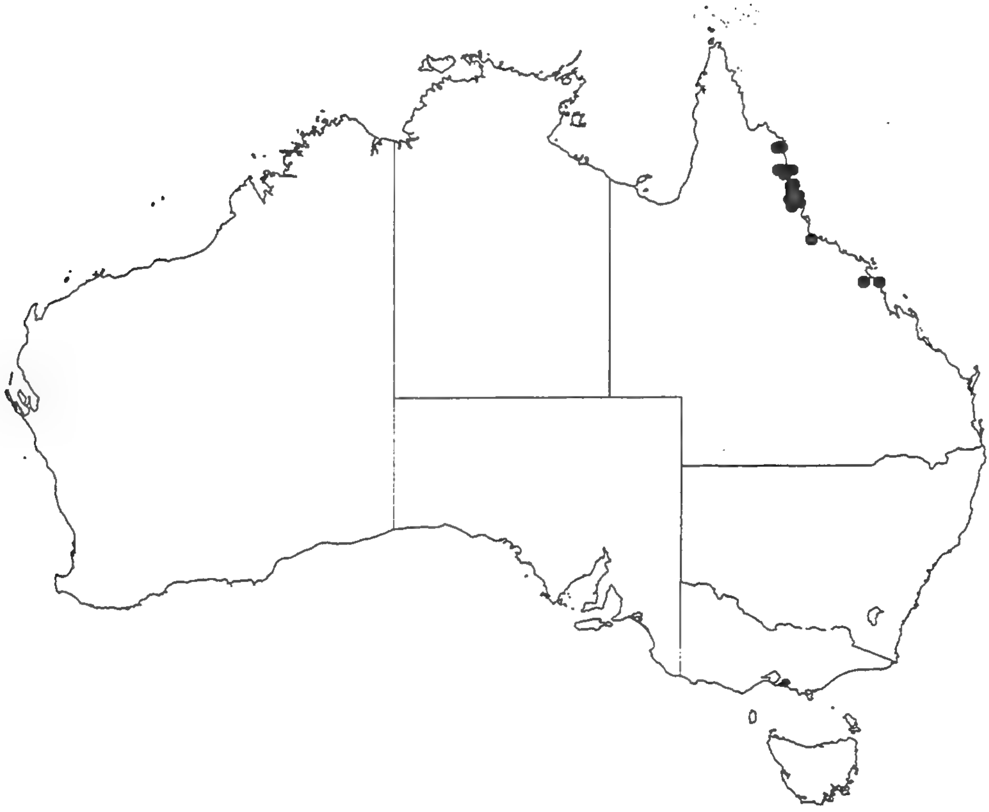


Fig. 5. The distribution of *Ficus destruens* based on available collection data.

Notes: *Ficus destruens* is easily identified in the rainforest by its bilabiate syconia and the somewhat dense covering of weak, often tomentose, ferruginous hairs on the abaxial surface of the leaf. The older leaves may appear glabrous at first glance but on closer inspection some ferruginous hairs can be found at the base of the lamina. Commonly referred to as Rusty Fig.

Illustrations: Williams, K.A.W., 1984, *Native Plants Queensland*, Vol. 2, p. 136; Pearson, S., & Pearson, A., 1992, *Rainforest Plants of Eastern Australia*, p. 108; Christophel, D.C. & Hyland, B.P.M., 1993, *Leaf Atlas of Australian Tropical Rain Forest Trees*, p. 160, plate 98b; Cooper, W., and Cooper, W.T., 1994, *Fruits of the Rainforest*, p. 130, Fig. 259.

Pollinator Wasp: The pollinator wasp of *F. destruens* is *Pleistodontes rigisamos* Wiebes (Lopez-Vaamonde et al., 2002).

6. Ficus rubiginosa Desf. ex Vent., *Jard. Malm.* 114 t. 114 (1805). A full description is presented in Dixon et al. (2001).

There are two forms which are distinguished as follows:

1. Leaves variously hairy.. f. *rubiginosa*
   Leaves glabrous.. f. *glabrescens*

Pollinator Wasp: The pollinator wasp of *F. rubiginosa* sens. lat., is *Pleistodontes imperialis* Saunders (Lopez-Vaamonde et al., 2002)

7. Ficus triradiata Corner, *Gard. Bull. Singapore* 17: 401 (1959). Type: Mount Spurgeon, QLD, *C.T. White 10536* (holo BRI; iso MEL) (Fig. 6).

Ficus triradiata var. *sessilicarpa* Corner, *Gard. Bull. Singapore* 17: 401 (1959). Type: Mount Finnegan, QLD, *L.J. Brass 20052* (holo BRI; iso L, SING).

Hemi-epiphyte to 25 m. *Twigs* glabrous, or puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs, or with weak ferruginous hairs, glabrescent, or minutely puberulous with ascending hyaline hairs. *Leaves* alternate, oblanceolate, narrowly elliptic, obovate, elliptic or oblique; apex obtuse or acute; base cuneate. *Lamina* 33–163 mm long, 10–66 mm wide; abaxial and adaxial surface glabrous. *Lateral veins* 20–51 pairs, 51°–70°, basal veins distinct, 20°–37°. *Petiole* 5–50 mm long, 1–5 mm wide; glabrous, or puberulous with ascending hyaline hairs, glabrescent. *Stipules* 35–92 mm long; puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs, glabrescent, or with weak ferruginous hairs, glabrescent, or with ascending hyaline hairs at base. *Syconia* 21–26 mm long, 15–26 mm in diameter, very broadly ovoid to ovoid, occasionally spheroid; cream, yellow, orange or pink, with orange spots; glabrous, or with weak ferruginous hairs, glabrescent; punctate; ostiole triradiate. *Basal bracts* 3, valvate, persistent; glabrous. *Peduncle* 1–8 mm long; glabrous, or with weak ferruginous hairs, glabrescent, or puberulous with ascending hyaline hairs. *Female florets* imbedded, sessile, pedicellate, tepals 3 or 4, stigma bifid; male florets pedicellate, tepals 3 or 4, anthers 1 with crescentic dehiscence, interspersed with the female and gall florets; gall florets sessile or pedicellate, tepals 3 or 4. *Interfloral bracts* present.

Selected specimens examined: Queensland: Cook: Timber Reserve 146, Tableland Logging Area, 15°45S 145°15E, *B.P.M. Hyland 8336*, 9 Jul 1975 (QRS); Mount Finnigan, W slopes, 15°49S 145°17E, *L.J. Brass 20052*, 6 Sep 1948 (BRI); Little Cooper Creek, end of Turpentine Road, Daintree, *D. Dixon PHD87*, 26 Apr 1996 (JCT); Eastern ridge of Mount Sorrow, Cape Tribulation, 16°05S 145°27E, *G.D. Weiblen 212*, 25 Feb 1993 (BRI); Creek beside forestry hut, Mt. Windsor, 20°21S 146°10E, *D. Dixon PHD354*, 9 Dec 1996 (JCT); Adeline Creek road, Mt. Windsor, 16°14S 145°04E, *D. Dixon PHD367*, 10 Dec 1996 (JCT); State Forest Reserve 144, Whypalla, Bower Bird Logging Area, 16°15S 145°01E, *B.P.M. Hyland 13466*, 22 Dec 1987 (QRS); Timber Reserve 142, Zarda Logging Area (Roots Creek), 16°25S 145°15E, *B.P.M. Hyland 6881*, 25 Sep 1973 (QRS); Mount Spurgeon, 16°26S *145°12E C.T. White 10536* 1 Sep 1936 (BRI; MEL); Mt. Lewis State Forest, 16°32S 145°16E, *D. Dixon PHD369*, 11 Dec 1996 (JCT); Mount Lewis Road, South Mary Logging Area, 16 km NNW of Mount Molloy, 16°32S 145°17E, *L.W. Jessup, G.P. Guymer & W.J. McDonald GJM1589*, 1 Nov 1988 (BRI).

Etymology: Corner (1959a) did not give a derivation for the species epithet. However, it is most likely in reference to the three large persistent basal bracts found on the syconia of this species.

Nomenclatural Notes: In his comments concerning the infraspecific taxa of this species, Chew (1989) suggested that the two varieties, *F. triradiata* var. *triradiata* and *F. triradiata* var. *sessilicarpa*, may represent different developmental stages of the same taxon. It has become evident during the studies on the *Urostigma* sect. *Malvanthera* that the peduncle of many species is often quite variable in length and is not a good taxonomic character. The figs present on the type specimen of *F. triradiata* var. *sessilicarpa* do appear sessile; however, they are much smaller than the mature figs of this species. The size of the syconia on the type specimen of *F. triradiata* var. *sessilicarpa* (12–15 mm long, 11–13 mm in diameter), are outside the range of dimensions for the mature syconia of this species (21–26 mm long, 15–26 mm in diameter). Thus I have concluded that *F. triradiata* var. *sessilicarpa* was described from a specimen with immature syconia and have accordingly reduced it to synonymy under the type species.

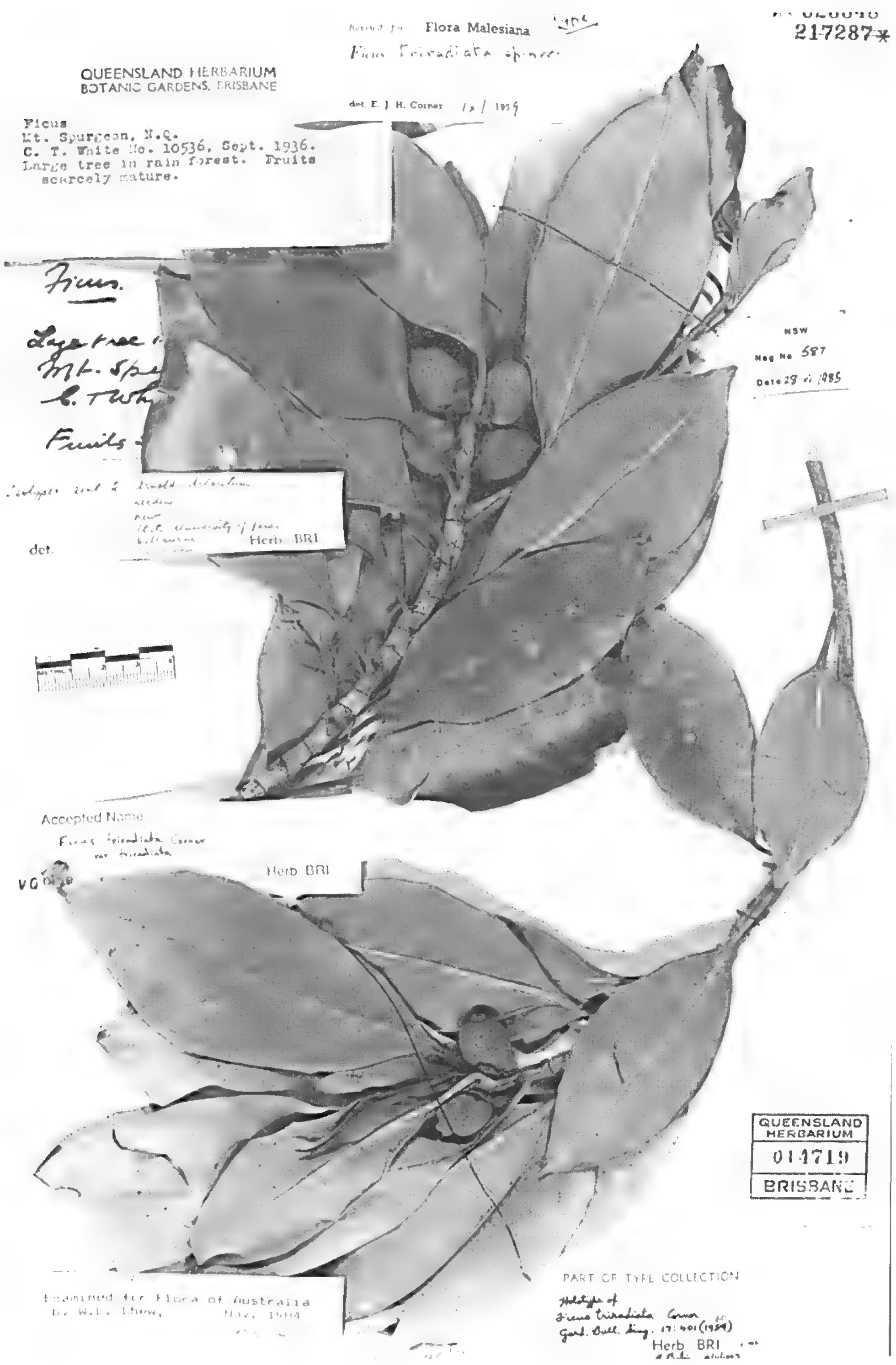


Fig. 6. The holotype of *Ficus triradiata* Corner.

Distribution and Ecology: *Ficus triradiata* is found in lowland and upland wet tropical rainforest of north-east Queensland (Fig. 7), at an altitudinal range from near sea level to 1300 m (Hyland and Whiffin, 1993). This species is hemi-epiphytic and is endemic to Australia.

Notes: It is an attractive species with peach to apricot coloured figs and is commonly referred to as Red Stipule Fig. The common name is a misnomer as the stipules are translucent white when mature. The stipules are only red in colour when the growing point is inactive. It is easily identified by the syconia always having three large persistent basal bracts.

Conservation Status: *Ficus triradiata* has been relatively poorly collected and was considered poorly known (Staff, Queensland Herbarium, 1994) and given a conservation coding of 2K by Briggs and Leigh (1996). However, it is commonly encountered throughout its limited distributional range between Mount Molloy and Cooktown. During a field trip to the Windsor Tablelands in December 1996, 103 individuals were encountered along a 24.6 km section of logging road. Twenty-one individuals were encountered along a three kilometre section of road on Mount Lewis. *Ficus triradiata* also occurs in the rainforests of Cape Tribulation and is adequately conserved in forestry reserves across its entire range. No conservation code is necessary at this present time.

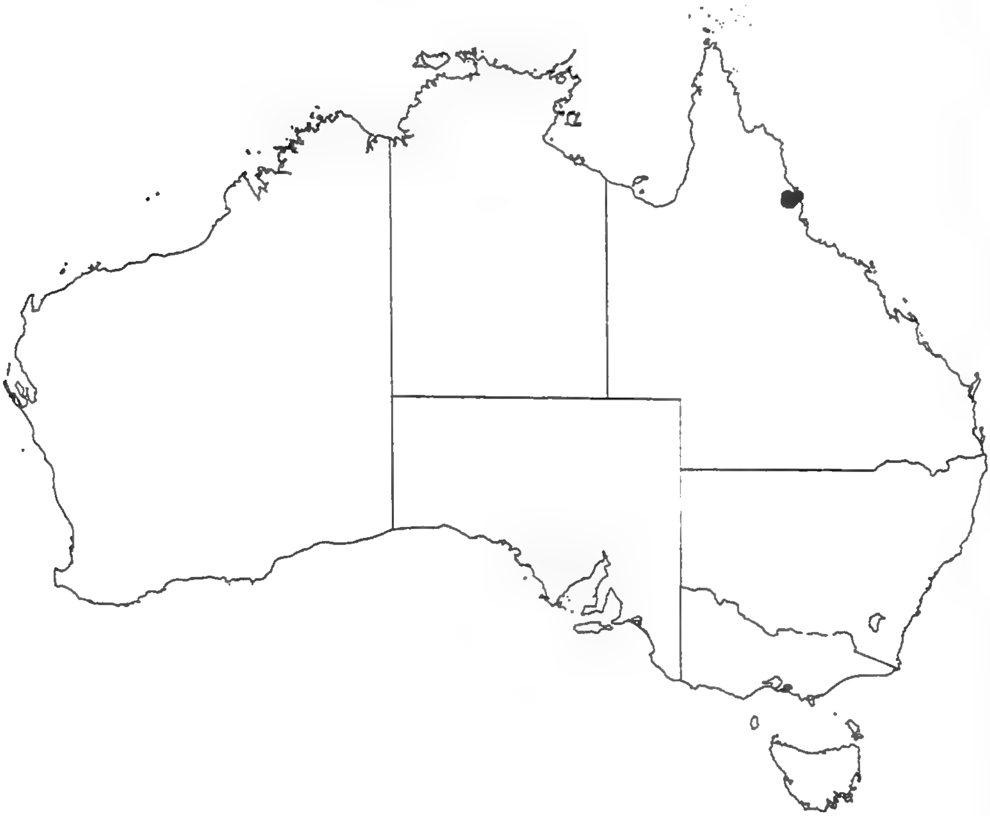


Fig. 7. The distribution of *Ficus triradiata* based on available collection data.

Illustrations: Christophel, D.C. and Hyland, B.P.M., 1993, *Leaf Atlas of Australian Tropical Rainforest Trees*, p. 166, plate 104e; Cooper, W., and Cooper, W.T., 1994, *Fruits of the Rainforest*, p. 135, Fig. 272.

Pollinator Wasp: The pollinator wasp of *F. triradiata* is *Pleistodontes schizodontes* Vaamonde, Dixon, Cook & Rasplus (Lopez-Vaamonde et al. 2002).

8. Ficus watkinsiana F.M.Bailey, *Queensland Bot. Bull.* 2: 18 (1891). Type: Mooloolah, QLD, Dec 1890, *Field Naturalists AQ66925* (lecto BRI, **here designated**) (Fig. 8); top of Bunya Mountains, QLD, *H. Tryon* (syn: *n.v.*); top of Blackall Range, QLD, *A. Anderson* (syn: *n.v.*).

Ficus bellingeri C. Moore in C. Moore & E. Betche, *Handb. Fl. New South Wales* 81 (1893). Type: Bellinger R., N.S.W., *collector unknown* (holo BM).

Ficus simmondsii F.M.Bailey, *Queensland Agric. J.* 25: 234 (1910). Type: Coolangatta, *J.H. Simmonds s.n.* (holo BRI).

Hemi-epiphyte to 35 m. *Twigs* minutely puberulous to puberulous, with ascending hyaline hairs interspersed with weak ferruginous hairs, glabrescent. *Leaves* alternate, narrowly oblong to elliptic; apex acute; base cuneate, rounded. *Lamina* 51–217 mm long, 26–97 mm wide; abaxial surface glabrous, or with ascending hyaline hairs interspersed with weak ferruginous hairs at junction of lamina and petiole, or with ascending hyaline hairs at junction of lamina and petiole; adaxial surface glabrous. *Lateral veins* 30–78 pairs, 52°–77°; basal veins distinct, 32°–49°. *Petiole* 20–87 mm long, 1–4 mm wide; glabrous, or with ascending hyaline hairs, glabrescent. *Stipules* 62–95 mm; minutely puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs, or with weak ferruginous hairs only, glabrescent. *Syconia* 24–37 mm long, 18–29 mm in diameter; very broadly ovoid to ovoid, oblong, narrowly oblong, ellipsoid, narrowly ellipsoid; with ascending hyaline hairs interspersed with weak ferruginous hairs, or with weak ferruginous hairs, glabrescent; deep purple to black; punctate; ostiole triradiate. *Basal bracts* 2 or 3, imbricate, caducous, puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs, or with weak ferruginous hairs, glabrescent. *Peduncle* 9–25 mm long; puberulous with ascending hyaline hairs interspersed with weak ferruginous hairs. *Female florets* imbedded in the wall of the receptacle, sessile, tepals 3 or 4, stigma simple; male florets pedicellate, tepals 3 or 4, anthers 1 with crescentic dehiscence, interspersed with the female and gall florets; gall florets pedicellate, tepals 3 or 4. *Interfloral bracts* present.

Selected specimens examined: Queensland: Cook: State Forest Reserve 144, Windsor Tableland, 16°15S 145°05E, *B.P.M. Hyland 5534*, 04 Oct 1971 (QRS); Hunter Creek, Julatten, 16°38S 145°19E, *B. Gray 4514*, 17 Jun 1987 (QRS); Lake Barrine, Atherton Tableland, 17°15S 145°38E, *S.F. Kajewski 1122* (BRI); State Forest Reserve 191, Barron, 17°19S 145°30E, *B.P.M. Hyland 13476*, 21 Jan 1988 (QRS); Keough's Scrub, Evelyn Portion 52v, Parish of Herberton, 17°40S 145°30E, *B.P.M. Hyland 5522*, 22 Sep 1971 (QRS); State Forest Reserve 418, 19°10S 146°05E, *B.P.M. Hyland 3991*, 23 Feb 1968 (BRI). North Kennedy: Birthday Creek crossing, Paluma Dam road, on E side of road, on boundary of loggers hut, *D. Dixon PHD61 & A. Cairns*, 14 Feb 1996 (JCT); Mt. Spec, 19°00S 146°05E, *B.P.M. Hyland 1572*, 23 Jul 1968 (BRI); Mount Dryander, 20°15S 148°33E, *Kilner & Fitzalan* s.n. (MEL). Wide Bay: Cooloola State Forest R451, E of Gympie, approx 3 miles W of Rainbow Beach, *E.J. Carrol & I.R. Telford EJC1083*, 24 May 1967 (CANB); Elanda Point, Lake Cootharaba, 26°15S 153°01E, *K.A.W. Williams 78034*, 11 May 1978 (BRI); Base of Mount Kandanga, Imbil, 26°27S 152°35E, *E. Rider 82*, 09 Jan 1990 (BRI); Eumundi, N Coastline, 26°29S 152°57E, *C.T. White* s.n., 01 Jan 1911 (BRI); Blackall Range, 6 miles from Mapleton, towards Cooloolabin, 26°35S 152°50E, *E.J. Carroll & I.R. Telford EJC1107*, 25 May 1967 (CANB); Didillibah Road, Bli Bli, near Paynters Creek, 26°38S 153°01E, *A.R. Bean 8655*, 26 May 1995 (BRI). Moreton: Mistake Mountains, *L.S. Smith & L.J. Webb 3649*, 25 May 1948 (BRI); D'Aguilar Range, approx. 1 km NW of Mount Glorious, 27°20S 152°46E, *I.R. Telford 9685*, 17 Apr 1984 (CANB); Lamington National Park, 28°10S 152°59E, *R.F. Thorne 25517*, 17 Mar 1960 (BRI); Roberts Plateau, track to W Canungra Creek, 28°13S 153°07E, *I.R. Telford 9787*, 26 Apr 1984 (CANB). New South Wales; North Coast: Clarence River, 29°30S 153°06E, *A. Camara* s.n. (MEL). Central Coast: Sydney, 33°53S 151°13E, *C. Moore* s.n. (MEL).

Fig. 8. The lectotype of *Ficus watkinsiana* F.M.Bailey AQ66925 (BRI). The specimen consists of two sheets of which only sheet one is shown.

Etymology: Named in honour of George Watkins who was a collector of Queensland plants (Bailey, 1891).

Distribution and Ecology: *Ficus watkinsiana* is a hemi-epiphytic species found in upland rainforest. This species occurs in two disjunct populations, one in north-eastern Queensland between Cairns and Townsville, and the other in south-eastern Queensland and north-eastern New South Wales (Fig. 9). *Ficus watkinsiana* is endemic to Australia.

Notes: Commonly referred to as Watkin's Fig or Green-leaved Moreton Bay Fig, *F. watkinsiana* is easily recognised in the rainforest. At first glance the leaves resemble those of *F. pleurocarpa*, however, they lack the tomentose to felted covering of ferruginous hairs and the leaves are on average smaller in size being 51–217 mm long, 26–97 mm wide in *F. watkinsiana* compared to 150–256 mm long, 49–100 mm wide in *F. pleurocarpa*. The syconia of *F. watkinsiana* are dark purple to black when mature and lack ribs compared to those of *F. pleurocarpa* which have up to 10 longitudinal ribs and are orange-red when mature.

Conservation Status: *Ficus watkinsiana* is adequately conserved throughout its distributional range and therefore no conservation code is recommended.

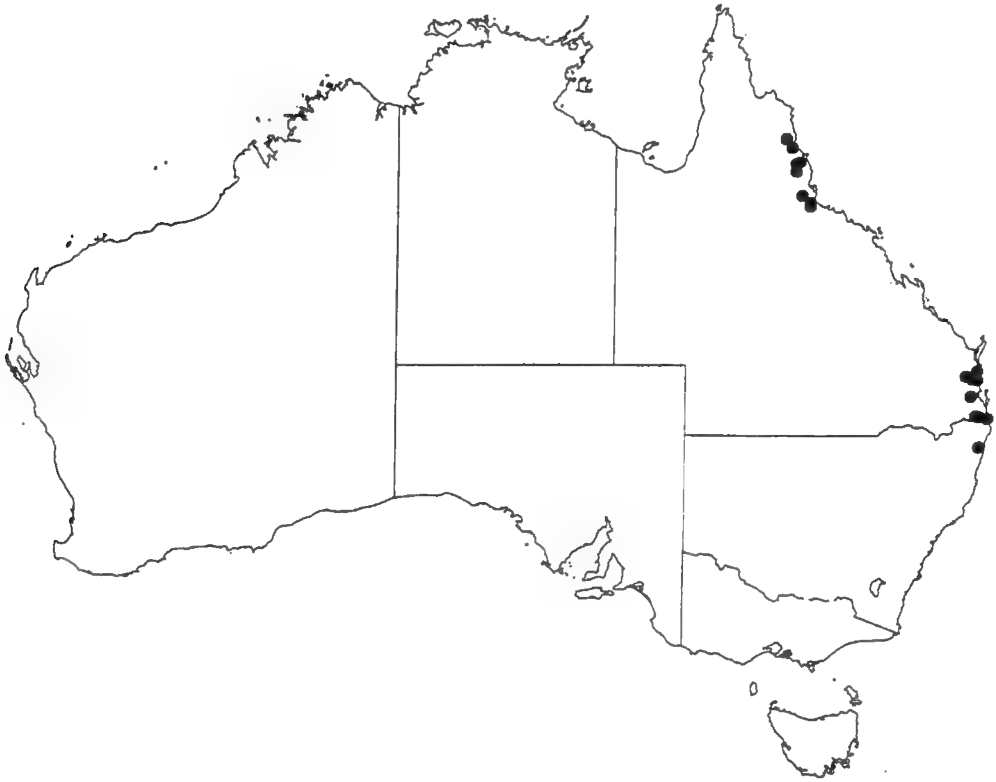


Fig. 9. The distribution of *Ficus watkinsiana* based on available collection data.

Illustrations: Chew, W.L.,1989, *Flora of Australia*, Vol. 3, p. 34; Williams, K.A.W., 1984, *Native Plants Queensland*, Vol. 2, p. 138; Christophel, D.C. and Hyland, B.P.M., 1993, *Leaf Atlas of Australian Tropical Rainforest Trees*, p. 168, plate 106b; Cooper, W., and Cooper, W.T., 1994, *Fruits of the Rainforest*, p. 139, Fig. 275.

Pollinator Wasp: The pollinator wasp of *F. watkinsiana* is *Pleistodontes nigriventris* (Girault) (Lopez-Vaamonde et al., 2002).

9. Ficus cerasicarpa D.J.Dixon. *Aust Syst. Bot.* 14: 535–563 (2001). A full description is presented in Dixon (2001c).

Pollinator Wasp: Lopez-Vaamonde et al. (2002) reported that *Ficus cerasicarpa* is associated with two species of pollinator wasp, *Pleistodontes macrocainus* Vaamonde, Dixon, Cook & Rasplus and *Pleistodontes athysanus* Vaamonde, Dixon, Cook & Rasplus. *Pleistodontes athysanus* is mainly recorded from *F. brachypoda;* however, two specimens were also identified from a collection of *Pleistodontes macrocainus* reared from *F. cerasicarpa* collected at Mount Isa (Dixon & Champion, PhD 405), see Dixon (2001c) for exact location details.

10. Ficus platypoda (Miq.) A.Cunn. ex Miq. *Ann. Mus. Bot. Lugduno-Batavum* 3: 287 (1867). A full description is presented in Dixon (2001c).

Pollinator Wasp: The pollinator wasp of *F. platypoda* is *Pleistodontes cuneatus* Wiebes (Lopez-Vaamonde et al., 2002)

11. Ficus lilliputiana D.J.Dixon. *Nuytsia* 13: 457–464 (2001). A full treatment of this species is presented in Dixon (2001a).

There are two forms which are distinguished as follows:

1. Leaves and other parts glabrous .... f. *lilliputiana*
   Leaves hairy, other parts variously hairy .... f. *pilosa*

Pollinator Wasp: The pollinator wasp of *F. lilliputiana* is *Pleistodontes proximus* Wiebes (Lopez-Vaamonde et al., 2002).

12. Ficus subpuberula Corner, *Gard. Bull. Singapore* 17: 403 (1959). *Urostigma puberulum* Miq. *London Journal of Botany* 6: 562 (1847); *Ficus puberula* (Miq.) Miq. *Annales Musei Botanici Lugduno-Batavi* 3: 287 (1867). Type: York Sound [WA], *A. Cunningham s.n.* (holo K; iso U) (Fig. 10).

Lithophytic tree to 13 m. *Twigs* glabrous or minutely puberulous to pilose with ascending hyaline hairs, glabrescent. *Leaves* alternate, widely ovate, ovate, narrowly elliptic to widely elliptic, lanceolate; apex acuminate, acute or obtuse; base cuneate, obtuse, rounded or cordate. *Lamina* 27–143 mm long, 11–68 mm wide; abaxial surface glabrous or mealy to minutely puberulous with ascending hyaline hairs; adaxial surface glabrous or mealy to minutely puberulous with ascending hyaline hairs. *Lateral veins* 16–49 pairs, 49°–80°; basal veins indistinct. *Petiole* 7–81 mm long, 1–3 mm wide, glabrous, minutely puberulous to pilose with ascending hyaline hairs. *Stipules* 20–65 mm long, caducous, glabrous, minutely puberulous to puberulous with ascending hyaline hairs. *Syconia* 10–24 mm long, 9–23 mm in diameter, widely oblong, broadly oblong, oblong to narrowly oblong, spheroid or broadly ellipsoid; yellow, orange or red; glabrous or minutely puberulous to puberulous with ascending hyaline hairs; ostiole triradiate. *Basal bracts* 3, imbricate, caducous, glabrous, minutely puberulous to pilose with ascending hyaline hairs. *Peduncle* 3–27 mm long, glabrous, minutely puberulous to pilose with ascending hyaline hairs. *Female florets* sessile or pedicellate, tepals 3 or 4, stigma simple; male florets pedicellate, tepals 2 or 3, anthers 1 with crescentic dehiscence, interspersed with female and gall florets; gall florets pedicellate, tepals 4 or 5. *Interfloral bracts* present.

Fig. 10. The holotype of *Ficus subpuberula* Corner.

Selected specimens examined: Queensland: Burke: Westmoreland Station, 17°20S 138°15E, *C.H. Gittons 837*, 1 Jun 1963 (BRI). Lawn Hill, 18°42S 138°29E, *C. O'Keefe 11*, 10 Nov 1987 (BRI). Northern Territory: Barkley Tableland: Barkley Tableland, Nicholson River Area, near Dry Creek Gorge in China Wall, 17°44S 137°47E, *A. Kanis 1811*, 11 Jun 1974 (CANB); Cox River Station, Tanumbirini Creek, 16°01S 134°47E, *P.K. Latz 7296*, 10 Jul 1977 (DNA); Echo Gorge, Wollogorang Station, 17°11S 137°43E, *B.G. Thompson 796*, 27 Nov 1984 (DNA). DARWIN AND GULF DISTRICT: 12°19S 133°14, *E M. Lazarides 7547*, 06 Jul 1972 (CANB); 1.5 miles SW of Cannon Hill, 12°23S 132°57E, *P. Martensz AE673*, 02 Feb 1973 (DNA); 10 km NW of Bauhinia Downs Station, 16°07S 135°24E, *J. Russell-Smith & Lucas 6276*, 30 Oct 1988 (DNA); 1 km on Koongarra side of Jump Up, 12°51S 132°51E, *M.O. Rankin 1411*, 13 Sep 1978 (DNA); 2.5 km SW of Mount Gilruth, 13°03S 133°02E, *M. Lazarides 7944*, 28 Feb 1973 (CANB); 24 miles SE of Oenpelli, 12°32S 133°19E, *L.G. Adams 2753*, 07 Jul 1972 (CANB); 2 km N of Nabarlek Airstrip, 12°17S 133°19E, *M.O. Rankin 2187*, 26 Apr 1979 (DNA, MEL); 40 km NE of Beswick, 14°19S 133°24E, *B.G Thompson 2810*, 16 Jan 1989 (DNA); 5 km N of Paradise Pool, Balbirini, 16°47S 135°22E, *J. Russell-Smith 7058*, 30 Jan 1989 (DNA); Approx. 40 km SSW of Nathan River Homestead, 15°56S 135°20E, *P.K. Latz 10107*, 27 Aug 1985 (DNA); Bessie Spring, Macarthur River Station, 16°45S 135°50S, *G. Wightman 1646*, 09 Jul 1984 (DNA); Cannon Hill, 12°22S 132°57E, *M. Parker 650*, 17 Jul 1975 (DNA); Canopy Rock, Mountain Valley Station, *R. Swinbourne 687*, 25 Feb 1963 (DNA, MEL); E Alligator River, 1 km N of Cahills Crossing, 12°25S 132°58E, *J.C. Cardale* s.n., 07 Jun 1973 (CANB); Redbank Creek, *L. Brass 391*, 01 Nov 1923 (BRI); Edith Falls, *D.J. Dixon PHD419 & I. Champion*, 16 Oct 1997 (JCT); Kakadu National Park, 1 km S of Obiri Rock, 12°24S 132°57E, *I.R. Telford & J.W. Wrigley IRT8385*, 15 Aug 1980 (CANB); Liverpool Meteorite Crater, 12°25S 134°03E, *M.J. Clarke 1147*, 28 Jul 1987 (DNA); Magela Creek, 12°40S 133°03E, *C.R. Dunlop 3370*, 25 Feb 1973 (DNA, MEL); Mount Borridale, Arnhem Land, 12°05S 132°50E, *K. Metcalfe* s.n., 19 Jul 1995 (DNA); Moyle River, 65 km E of Port Keats, 14°19S 130°06E, *P. Latz & C.R. Dunlop 13764*, 10 Jun 1994 (DNA); Nathan Spring, Nathan River, 15°35S 135°26E, *J. Russell-Smith 6712*, 19 Jan 1989 (DNA); Tabletop Range near Mount Tolmer, 13°13S 130°44E, *C.R. Dunlop 6780*, 19 May 1985 (DNA); Tanum Creek, Cox River Station, 16°01S 134°47E, *P.K. Latz 7296*, 10 Jul 1977 (DNA); Upper Mann River, 12°39S 134°08E, *J. Russell-Smith & Lucas 4016*, 07 Nov 1987 (DNA); Upper Wilton River, 13°17S 134°12E, *J. Russell-Smith & Lucas 4058*, 11 Nov 1987 (DNA). Victoria River District: Headwaters of Lalngang Creek, 15°05S 130°10E, *I. Cowie & N.G. Walsh 5082*, 16 May 1994 (MEL). Western Australia: Gardner: 0.5 miles E past Grey's Cave, Glenelg District, *C.A. Gardner 9638*, 14 Jul 1950 (PERTH); 13 km W of Kununurra off highway on track to Blackrock waterhole, 15°39S 128°39E, *D.J. Dixon PHD442 & I. Champion*, 20 Oct 1997 (JCT); 25.3 km W of old Mount Elizabeth Homestead on Panter Downs track, 16°11S 125°59E, *K. Hill 966*, 27 Jul 1984 (NSW); 4.2 km NW of Gibb River-Kalumburu Road intersection, travelling along old Mitchell River Station Road, 15°09S 126°10E, *B.L. Koch 560*, 08 Jun 1987 (PERTH); El Questro Station, 15°50S 128°20E, *C. Done 742*, 10 Jul 1986 (PERTH); Langi, 4 km S of Prior Point and 33 km SSW of Kuri Bay, Kimberley Coast, 15°45S 124°24E, *K.F. Kenneally 11058*, 14 Jul 1990 (PERTH); Lennard River Gorge, King Leopold Range, +/-130 km ENE of Derby, *G.W. Carr & A.C. Beauglehole 4021*, 22 Jul 1974 (PERTH); Prince Regent River Reserve, 15°34S 125°36E, *K.F. Kenneally 2025*, 14 Aug 1974 (PERTH); Solea Falls, Drysdale River National Park, 14°40S 127°00E, *A.S. George 13428*, 05 Aug 1975 (PERTH); Summit of Mount Derberh, King Leopold Range, *W. Fitzgerald* s.n., 01 May 1905 (PERTH); Surveyor's Pool area, Mitchell Plateau, 14°41S 125°43E, *J.S. Beard 8395*, 24 Feb 1979 (PERTH); SW Osbourne Island, Bonaparte Archipelago, 14°26S 125°56E, *P.G. Wilson 11161*, 29 Jul 1973 (PERTH). Hall: Kimberlite Pipe area at source of Smoke Creek, SW of Lake Argyle, 16°45S 128°30E, *A.S. Weston 12294*, 05 May 1980 (PERTH); N Gorge, Bungle Bungle National Park, 17°25S 128°35E, *I. Solomon 866*, 20 Oct 1993 (PERTH).

Etymology: Corner (1959a) did not provide a derivation for the epithet. However, it most likely applies to the leaves of *F. subpuberula* being 'almost pubescent'.

Distribution and Ecology: *Ficus subpuberula* is a lithophytic species restricted to sandstone gorges and rock crevices. It occurs from Lawn Hill National Park, on the extreme western edge of Queensland west across the Top End of the Northern Territory to the Kimberley area of Western Australia (Fig. 11). It is endemic to Australia and has previously not been recorded from Queensland.

Notes: *Ficus subpuberula* is easily recognised. The foliage is often sparse, pendulous, and a dull grey green colour. The figs are a lemon-yellow colour when mature.

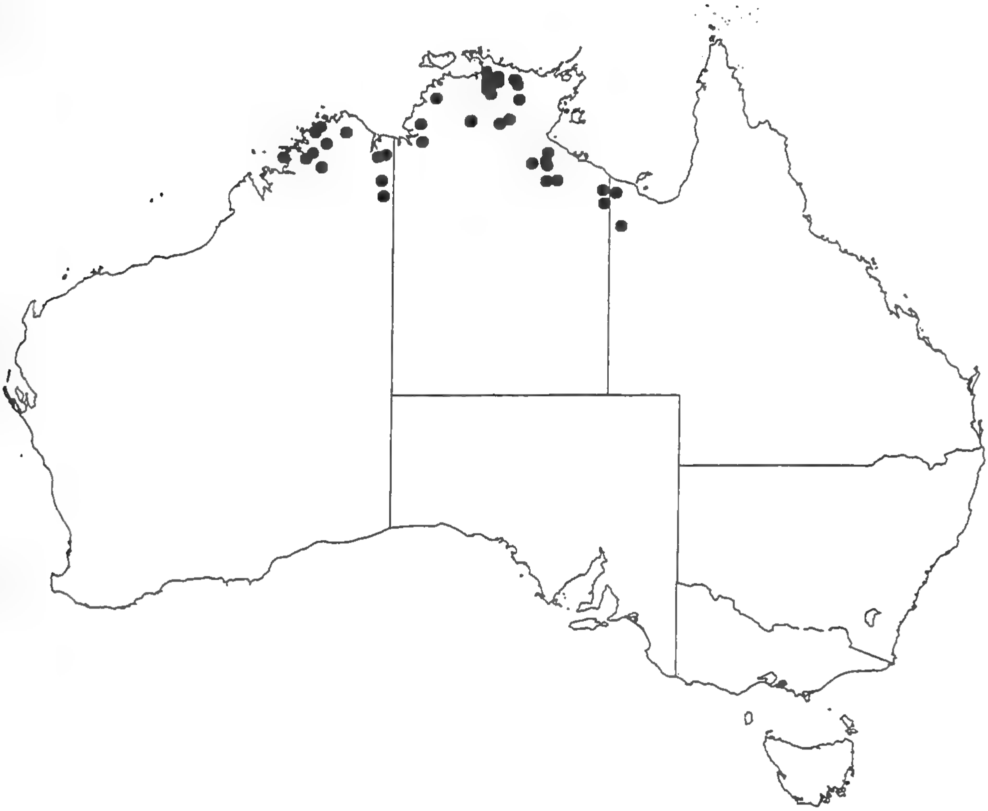


Fig. 11. The distribution of *Ficus subpuberula* based on available collection data.

Conservation Status: *Ficus subpuberula* is adequately conserved in national parks of Queensland, the Northern Territory, and Western Australia, therefore no conservation coding is recommended.

Illustrations: Wheeler, J.R. (ed.) 1992, *Flora of the Kimberley Region*, p 81, Fig. 18f.

Pollinator Wasp: The pollinator wasp of *F. subpuberula* is *Pleistodontes austrobocheilus* Vaamonde, Dixon, Cook & Rasplus (Lopez-Vaamonde et al., 2002).

13. Ficus atricha D.J.Dixon. *Aust. Syst. Bot.* 14: 535–563 (2001). A full description is presented in Dixon (2001c).

Type: Another isotype of *R.L. Specht 449* was recently found at NSW. The holotype is at BRI, other isotypes are held at L, PERTH, MEL).

Pollinator Wasp: The pollinator wasp of *F. atricha* has yet to be collected.

14. Ficus brachypoda (Miq.) Miq., *Ann. Mus. Bot. Lugduno-Batavum* 3: 268 (1867). A full description is presented in Dixon (2001c).

Distribution and Ecology: In Dixon (2001c) I stated that this species was endemic to Australia. I have since found that this is not the case. *Ficus brachypoda* also occurs in the Lesser Sunda Islands and Timor.

Additional specimens examined: Lesser Sunda Islands: Flores Island, *J.A.J. Verheijen 2313* (L); Sumba Island, Waingapu, Kemiru R., *Kostermans & Wirawan 256*, 6 Apr 1965 (L); Roti Island, *J.A.J. Verheijen 2443*, 1969 (L).

Timor: Soenda Eil., *E. Schmutz 2393*, 20/08/1969 (L).

Pollinator Wasp: The pollinator of *F. brachypoda* is *Pleistodontes macrocainus* (Lopez-Vaamonde et al., 2002).

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Reinstatement of *Gymnosporia* (Celastraceae): implications for the Flora Malesiana region

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Abstract

Jordaan, Marie[1] *and van Wyk, A.E.*[2] *([1]National Botanical Institute, Private Bag X101, Pretoria, Republic of South Africa 0001; e-mail: marie@nbipre.nbi.ac.za; [2]Department of Botany, University of Pretoria, Pretoria, Republic of South Africa 0002; e-mail: avanwyk@postino.up.ac.za) 2003. Reinstatement of* Gymnosporia *(Celastraceae): implications for the* Flora Malesiana *region.* Telopea *10(1): 155–167.* The reinstatement of the genus *Gymnosporia*, comprising all the spiny members previously included in the genus *Maytenus*, has implications for the Flora Malesiana region. An account is given of six species and two varieties in the region (*Gymnosporia curtisii, G. diversifolia, G. inermis, G. littoralis, G. nitida, G. spinosa* var. *spinosa* and var. *parva*). The new combination **G. littoralis** (Backer) Jordaan is made (based on *Gymnosporia montana* var. *littoralis*) and a **neotype** and **lectotype** designated for two other taxa. *G. emarginata* from India and Sri Lanka is also included since this name was previously misapplied to plants in the Flora Malesiana region. *Maytenus rapakir* is mentioned as probably belonging to *Gymnosporia. Maytenus cupularis*, which has a racemose inflorescence, is related to the Australian species of *Maytenus* s. lat. and is retained in *Maytenus.*

Introduction

The Celastraceae account for the Flora Malesiana was published by Ding Hou in 1962 and 1964. His genus concepts coincide with those of Exell (1952, 1953), Blakelock (1956), Marais (1960) and Robson (1965, 1966 & 1994) in that he considers *Gymnosporia* and *Maytenus* to be congeneric. New research on the family suggests that larger genera need to be recircumscribed into smaller segregate ones. The genus *Gymnosporia* (Wight & Arn.) Hook.f. has recently been reinstated (Jordaan & Van Wyk 1999, Archer & Jordaan 2000) to include all its spiny members, previously placed under *Maytenus* Molina sens. lat. A study of *Gymnosporia* (the southern African species) was undertaken and the subdivision of the genus into eight sections was proposed (Jordaan 1995), based mainly on fruit and seed morphology as well as leaf anatomy; a monographic study covering the genus on a worldwide basis is currently in progress. All the *Gymnosporia* species in the Flora Malesiana region have seed with a basal aril and are placed in *G.* section *Tenuispina* M.Jordaan ined. Diagnostic characters of *Gymnoporia* include the presence of brachyblasts and spines, leaves which are in fascicles or alternate, the inflorescence which is a dichasium, the flowers which are mostly functionally unisexual, the fruit which is a dehiscent capsule and the seeds which have an aril.

Gymnosporia is an Old World genus of suffrutices, shrubs and trees. It comprises about 108 members, occurring in the whole of Africa, Madagascar and adjacent islands, southern Spain, the near Middle East, Afghanistan, Pakistan, India, Sri Lanka, Thailand, Vietnam, S China, Taiwan, Ryukyu Islands (Japan), Malesia, and Queensland (Australia), with *G. vitiensis* (A.Gray) Seem. endemic to the Polynesian Islands.

The genus has two main centres of diversity on the Afro-Arabian continent: (i) NE tropical Africa and tropical Arabia and (ii) southern Africa. There is a high degree of regional endemism at both specific and sectional level and there are only a few widespread species in the genus. Five members of *Gymnosporia* occur on the Philippines, which is the highest level of species diversity in the Flora Malesiana region. The purpose of this contribution is to provide an account of the members of *Gymnosporia* native to the Flora Malesiana region.

Taxonomy

Key to the species

1a Plants with spines of two kinds: axillary ones and lateral branches ending in a spine:

  2a Capsules 2-valved:

    3a Leaves usually smaller than 30 mm; China, Taiwan, Ruykyu Islands and N Philippines .... **6. G. diversifolia**

    3b Leaves usually longer than 30 mm; Thailand, Malaysia and Java .... **5. G. littoralis**

  2b Capsules 3-valved:

    4a Plants totally glabrous; India and Sri Lanka .... **7. G. emarginata**

    4b Plants with puberulous or muricate branches; Thailand, Malaysia and Java .... **5. G. littoralis**

1b Plants usually without spines or when spines present then only axillary ones, lateral branches not ending in a spine:

  5a Pericarp of capsules thick (± 1.5 mm), woody .... **4. G. nitida**

  5b Pericarp of capsules thin, papery (less than 1 mm):

    6a Leaf apex acute to short-acuminate; Thailand and Malaysia .... **3. G. curtisii**

    6b Leaf apex obtuse, rounded to emarginate; Taiwan, Philippines, Indonesia, New Guinea, Australia:

      7a Brachyblasts usually present; leaves coriaceous; capsules longer than 6 mm .... **1. G. inermis**

      7b Brachyblasts usually absent; leaves membranous; capsules shorter than 6 mm .... **2. G. spinosa**

1. Gymnosporia inermis *Merrill & Perry*

(Merrill & Perry 1939: 335).

Type: Papua New Guinea: Western Division: Tarara, Wassi Kussa River, *Brass 8690*, Jan 1937; holo A; iso L!, LAE!, US!

Gymnosporia montana sensu Benth.

(Bentham 1863: 400), non M.A.Lawson (M.A.Lawson 1875: 621).

Maytenus emarginata sensu Ding Hou

(Ding Hou 1962: 241), quoad specimens from N Queensland, Philippines, Celebes, Moluccas and New Guinea; sensu Jessup (Jessup 1984: 164).

Scandent shrub or small tree, up to 5 m high, glabrous in all parts, with spines when young, becoming spineless with age; brachyblasts well developed on older branches; branches angular when young, grey, with inconspicuous lenticels. Leaves alternate on young branchlets, fasciculate on older ones, ovate, elliptic or oblong, (30–)40–110(–140)

× (15–)20–76(–110) mm, apex rotundate to retuse, or subacute to emarginate, base cuneate to rotund, margin distinctly crenulate-serrate, reticulate venation prominent on both sides; petioles up to 12 mm long, sometimes pinkish-tinged. Inflorescence axillary, solitary or few-flowered in short cymes; peduncle ± 10 mm long, pink-tinged; pedicels up to 4 mm long, pink-tinged, bracts lanceolate. Flowers white or cream-coloured, 5–7(–9) mm in diameter, fragrant. Sepals semi-orbiculate. Petals oblong-ovate, 2–3(–4) × 1–2 mm, apex obtuse, margin fimbriate. Male flowers: stamens slightly shorter than petals; pistillode short; stigmas absent. Disc green, 5-lobed. Female flowers: staminodes shorter than stamens of male flowers: ovary 3-locular, green; style as long as ovary, 3-branched. Capsule 3-valved, obconic-trigonous, 3-angled, 6–12 mm long, green becoming red. Seed ellipsoid, glossy, 3.5–5.5 × 2–4 mm; aril reddish, reduced to a basal rim. (Fig. 1).

Diagnostic characters: plants when young with spines, but spines not developing on older stems; well developed brachyblasts present; leaves coriaceous and losing spines with age; well developed brachyblasts present; leaves coriaceous and usually longer than 40 mm, apex rounded, obtuse to emarginate or subacute; capsules 3-valved, red; seed with a basal aril.

Distribution and ecology: (Celebes and Moluccas) Indonesia, New Guinea, East Coast of the Philippines, Taiwan and Queensland (Australia). Growing at elevations from near sea level and locally abundant on the coast on sand at the edge of mangrove forest, or secondary forest, at forest margins, in thickets on beaches and hillsides and on sea cliffs, often on limestone.

Selected specimens examined: INDONESIA: Kei Island (Kai Kecil), *Jensen 80*, 25 Mar 1922 (GH, L); Tanimbar Islands: Selaru, Namtabung, *Van Borssum 3176*, 17 Mar 1956 (K, L); Moluccas: Sula Islands, Tandjong Baliha, *Bloembergen 4389*, 28 July 1939 (GH, SING); Aru Islands: Pulau Trangan, Kp. Kerei, *Turner 115*, 17 Apr 1993 (GH, L). Sulawesi (Celebes): Tukangbesi, Binongko, *Elbert 2559*, 23 July 1909 (L).

NEW GUINEA: West Papua: Radjah Ampat, Waigeo Island, Lupintol on SW coast of Majalibit Bay, *Van Royen 5454*, 8 Feb 1955, (L); Merauke, *Koch Expedition 1904–1905* (L).

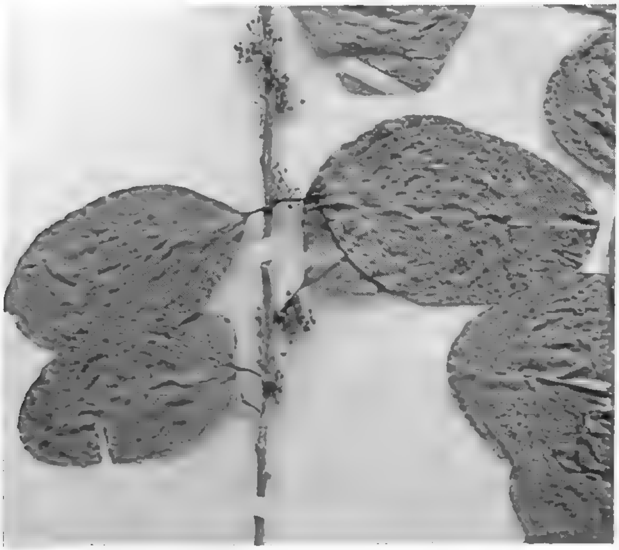

Fig. 1. *Gymnosporia inermis*. Sulawesi (Celebes): Binongko, Pulau, *Elbert 2559* (L).

Papua New Guinea: Tarara, Wassi Kussa River, *Brass 8690*, Jan 1937 (L, LAE, US); Lea Lea, NW of Pt. Moresby, *Pullen 3359*, 19 July 1962 (CANB, LAE); Daru Island, *Brass 6229* 29 Mar 1936 (L); Nanuk Island, East New Britian Prov., *Nagari UPNG 7303*, 3 Nov 1981 (LAE).

PHILIPPINES: Dalupiri Island: Babuyan Group, 19°10'N 121°15'E, *Bartlett 15075, 15168*, 31 Oct–5 Nov 1935 (GH); **Luzon**: Isabela Prov: Palanan municipality, Dipoduanaw Point, 17°06.8'N 122° 31.1'E, *Leonardo Co 3393, 3394*, 18 Apr 1991 (GH, K, L, PNH); Luzon: Sierra Madre Mountains of Dingalan, sea level, 15° 29' N 121° 23' E, *Jacobs 7772*, 16 Mar 1968 (L).

AUSTRALIA: Queensland: Jack Jacky Ck, Cape York, 10° 58' S 142° 30' E, *Jones 3821*, 25 Oct 1965 (CANB); Portland Roads, 12° 35' S 143° 25' E, *Dockrill 468*, 4 July 1972 (BRI, K); Cairns: *Webb & Tracey 8193*, June 1965 (BRI, CANB).

2. Gymnosporia spinosa *(Blanco) Merrill & Rolfe*

(Merrill & Rolfe 1908: 109); (Merrill 1918: 235); (Loesener 1942: 151).

Cupania spinosa Blanco

(Blanco 1837: 184).

Type: Philippines: Luzon Island: Bulacan Prov., Angat, *Merrill: Species Blancoanae 349*, Sep 1913; neo US! **(designated here)**; isoneo GH!, L!

var. **spinosa**

Selected specimens examined: PHILIPPINES: Luzon: Cagayan Prov.: Nabanagan, *Pacheco 29523*, Mar 1923 (GH); Bulacan Prov.: Angat, *Merrill: Species Blancoanae 349*, Sep 1913 (L, US); Rizal Prov.: San Juan del Monte, Pr Manila, *Vidal 189* (GH); Lubang Islands: *Merrill 978*, Apr 1903 (GH); Panay: Port Iloilo, *Vidal 189*, Nov–Dec 1958 (GH).

var. **parva** *Merrill & Rolfe*

(Merrill & Rolfe 1908: 110).

Type: Philippines: Luzon Island: Rizal Province, Montalban, Mariquina River, *Merrill 5070* March 1905; holo PNH†; iso K!, L!, NY! US!

G. philippinensis Vidal (Vidal 1885: 103), nom. nudum quoad specimen *Cuming 1575* (L). Rolfe (1886) stated that this is just a manuscript name and not validly published.

Selected specimens examined: PHILIPPINES: Luzon: *Cuming 1575* (L); Rizal Prov., Montalban, *Elmer 12573*, Jan 1910 (GH, L); *Merrill 5070*, Mar 1905 (K, L, NY, US).

Plants sometimes with small thin axillary spines, even on fruiting branches. A distinct species with two varieties, which can be separated from *G. inermis* by axillary spines more often present, its membranous leaves (20–35 × 8–20 mm) which are narrower, more elliptic and thinner. It has 3-valved capsules like *G. inermis*, but the capsules are smaller, shorter than 5 mm. The difference between the two varieties lies in the size of the leaves; var. *parva* has smaller leaves, shorter and narrower than 20 mm. (Fig. 2).

Distribution: apparently endemic to the Philippines.

Notes: Merrill and Rolfe (1908) stated, and we agree, that *G. spinosa* is not the same as *G. montana* (Roth ex Roem. & Schult.) M.A.Lawson from India, which is the type species of the genus *Gymnosporia*.

Merrill and Perry (1939) stated that *G. inermis* is closely related to *G. spinosa* but lacks the spines of the latter species. *G. inermis* and *G. spinosa* are indeed very closely related. Specimens of *G. spinosa* var. *spinosa* and var. *parva* have often short axillary spines, lack brachyblasts, their leaves are thinner in texture and the reticulate venation on both surfaces of the leaves is more prominently raised than in *G. inermis*; their capsules are smaller (usually less than 6 mm long).

Blanco (1837) originally described *G. spinosa* in *Flora de Filipinas*, but apparently there is no original material in PNH of Blanco's names of new taxa. Merrill's specimen at US is therefore selected here as a neotype, following the recommendation of Nicolson and Arculus (2001).

3. Gymnosporia curtisii *King*

(King 1896: 353); (Prain 1904: 198); (Ridley 1922: 451).

Type: Malaysia: Kedah Prov., Polo Tanyury Piri, *Curtis 2500*, Sep 1890; holo K!

Maytenus curtisii (King) Ding Hou

(Ding Hou 1962: 240).

Illustration: Ding Hou (1962: fig. 2a–d).

Erect or scandent shrub or small tree; spines robust, in axils of leaves. Leaves coriaceous, elliptic, sometimes broadly elliptic, 62–85 (–110) × 27–36 (–90) mm, base cuneate, tapering into petiole, apex acute to short-acuminate, rarely obtuse, margin crenulate, principal lateral veins 7–9(–15), obliquely spreading towards margin and curved upwards, reticulate venation obvious above; petiole 5–9 mm long. Inflorescences cymose, usually crowded towards apex of brachyblasts, axillary, puberulous when young; peduncle 5–10 mm long; bracts lanceolate, short-fimbriate; pedicels 2–5 mm long. Flowers white. Sepals deltoid or semi-orbicular, 0.5–0.75 mm in diameter, margins sparsely ciliate. Petals ovate or obovate-oblong, 2.5–3.2 × 1.5 mm, obtuse, ± entire. Disc fleshy, rounded, 1.5–2.0 mm in diameter. Male flowers with stamens ± 2.5 mm long; anthers broad-ovoid, 0.5 mm long, slightly apiculate; pistillode with short style, stigmas absent. Female flowers with staminodes very short or abortive; ovary trilocular; style longer than ovary; stigma 3-lobed. Capsule 3-valved, obconic-trigonous, concave at tip, ± 15 × 13 mm. Seed ellipsoid, slightly irregularly rugose, 7–8 × 4–5 mm; aril ± flat or shallowly disc-like and attached laterally at base.

Diagnostic characters: plants usually with axillary spines; leaf apex acute to short-acuminate; capsule 15 mm long, 3-valved; seed with a flat or shallowly disc-like aril, laterally attached at base.

Distribution and ecology: Thailand and Malaysia. It occurs on limestone at sea level, or in lowland forests.

Fig. 2. *Gymnosporia spinosa* var. *parva*. Philippines: Rizal Province, Montalban, *Elmer 12573* (L).

Selected specimens examined: THAILAND: Doi Chiengdao, *Put 380* (K); Kelantan Prov., Gua Jaya, Jenera, *Whitmore FRI4261* (K).

MALAYSIA: Kedah Prov., Polo Tanyury Piri, *Curtis 2500* (K); Kedah Prov., Pulau Dayang Bunting, *Soepadmo & Mohmud 1229* (K); Langkawi Island, Selat Panchor, Pulau, *Henderson 21368* (K).

4. Gymnosporia nitida *Merrill*

(Merrill 1914: 31), non *Maytenus nitida* Mart.

Type: Philippines: Luzon Island: Pangasinan Prov., *Domingo FB11836*, 1912–1913; holo K!; iso L, US!

Maytenus crassa Ding Hou, *nom. nov.*

(Ding Hou 1962: 242).

Ding Hou (1962) described it as having small, short, axillary spines and said that it occurred in the Philippines, but it was found only once. *Gymnosporia nitida* has 3-valved capsules, but the distinguishing character seems to be the thick pericarp (± 1.5 mm) of the dehiscent fruits.

Specimen examined: PHILIPPINES: Luzon Island: Pangasinan Prov., *Domingo FB11836*, 1912–1913 (K, US).

5. Gymnosporia littoralis *(Backer) Jordaan*, comb. et stat. nov.

Gymnosporia montana var. *littoralis* Backer (Backer 1908: 55; 1911: 235); (Koorders 1912: 524).

Type: Java: Batavia, Tandjong Priok, *Backer 34926*, Dec 1905; holo BO!

Lax scandent shrub, up to 3 m high; branches subangular, puberulous, muricate to glabrous, dark brown or pale grey, with lenticels, spinescent; spines glabrous or puberulous, up to 15 mm long, of two kinds: spines short, axillary and spines terminating short lateral shoots. Leaves fasciculate on brachyblasts, subcoriaceous, glabrous or with few scattered hairs, obovate, oblanceolate, or broad-obovate, 12–60 × 10–20 mm, subcoriaceous, apex obtuse, rounded or emarginate, base attenuate narrowed into the petiole, margin sparsely denticulate or crenulate; petiole up to 4 mm long, puberulous to glabrous. Inflorescences fasciculate or solitary, axillary or crowded at upper part of a short-shoot, shorter than leaves; peduncles puberulous, 4–6 mm long; bracts elliptic, short-fimbriate; pedicels 1–6 mm long. Flowers small, greenish-white. Sepals deltoid or suborbicular, 0.5–0.7 mm long, margins short fimbriate. Petals oblong or elliptic, obtuse, 1–3 mm long, margin subentire. Disc cupular. Male flowers: stamens ± 1.2 mm long; pistillode flask-like, ± 1 mm long; style very short; stigma obscure. Female flowers: staminodes very small or abortive; ovary subglobose, narrowed into a distinct, 2(3)-branched style. Capsule 2(3)-valved, obconic-trigonous, red, 4–6 × 5–7 mm. Seeds 2 or 3, ellipsoid, ± 3 × 1.5 mm, smooth and glossy; aril at base. (Figs 3 & 4).

Diagnostic characters: plants with axillary and/or terminal spines (short lateral branches ends in a spine); stems, spines, petioles and often peduncles puberulous or muricate; leaves glabrous or with few scattered hairs, laxly arranged on stems, obovate-oblong, oblanceolate or broad-obovate, apex obtuse; ovary 2(3)-locular; disc cupular; capsules obconic-trigonous, usually smaller than 6 mm.

Distribution and ecology: S Thailand, Malaysia and Java. It occurs mainly along seashore, in marsh thicket.

Selected specimens examined: THAILAND: ¼ mile SW of Vayama, *Maxwell s. n. L430468*, 24 Jan 1969 (L); Samut Sakhon, Ban Khlong Su, *Van der Kevie 19*, 26 June 1960 (L). **MALAYSIA:** S Tukong, S Johore, *Spare F958* (SING); Pulau Sibu, Johore, June 1991, *Wong 101* (SINU).

JAVA: Batavia, Tandjong Priok, *Backer 34926*, Dec 1905 (BO); Anjol near Tandjong Priok, *Djerro Kotan 85* (L); no precise locality, 16 Oct 1903, *Sargent s.n.* (GH).

Note: specimens from Malay Peninsula (Johore) and Java determined by Ding Hou as *Maytenus emarginata* in 1962, belongs to this species.

6. Gymnosporia diversifolia *Maxim.*

(Maximowicz 1881: 459); (Loesener 1941: 149); (Ding Hou 1950: 177).

Type: Japan: Archipelagi Lu-schu Islands (Ryukyu Islands): U-shima, *Charles Wright s.n.*, 1853–1856; holo? NY468032!; iso? US16301.

Celastrus diversifolia (Maxim.) Hemsl.

(Hemsley 1886: 123).

Celastrus buxifolia L. var. *subdidymocarpus* Kuntze

(Kuntze 1891: 115).

Type: Annam (Vietnam), Bai Turong (Bai Thuong), 24 Feb 1875, *Kuntze 3642*; lecto NY! **(designated here)**; isolecto K!

Maytenus diversifolia (Maxim.) Ding Hou

(Ding Hou 1962: 242); (Li 1977: 629); (Lu & Yang 1993: 654).

Illustration: Li (1977: pl. 754), Lu & Yang (1993: pl. 338).

Scandent or erect shrub, up to 4 m high; branches zigzag, puberulous to muricate, spinescent. Spines up to 15 mm long, of two kinds: spines short, axillary and spines terminating short lateral shoots. Leaves mainly alternate, subcoriaceous; lamina obovate, oblanceolate, or broad-obovate to round, 17–30 × 10–20 (–25) mm, apex obtuse, rounded or emarginate, base attenuate narrowing into the petiole, margin sparsely denticulate or crenulate, or sometimes subentire, principal lateral veins 3 or 4; petiole very short or subsessile. Inflorescences fasciculate or solitary, sometimes 1-flowered, axillary or crowded at upper part of a short-shoot, shorter than the leaves,

Fig. 3. *Gymnosporia littoralis*. Thailand: ¼ mile SW of Vayama, *Maxwell s.n. L430469* (L).

10–20 mm long; peduncles 4–6 mm long; bracts elliptic, short-fimbriate; pedicels 1–4 mm long. Flowers small, greenish white. Sepals deltoid or suborbicular, 0.5–0.7 mm long, margins short-fimbriate. Petals oblong or elliptic, obtuse, 1–3 mm long. Disc cupular. Male flowers with stamens ± 1.2 mm long; pistillode flask-like, ± 1 mm long; style very short; stigma obscure. Female flowers: staminodes very small or abortive; ovary subglobose, narrowing into a distinct style, style 2-branched. Capsule 2-valved, compressed-obcordate, ± inflated, red, 5–6 × 5–8 mm. Seeds 2 or 3, ellipsoid, ± 3 × 1.5 mm, smooth and glossy; aril at base.

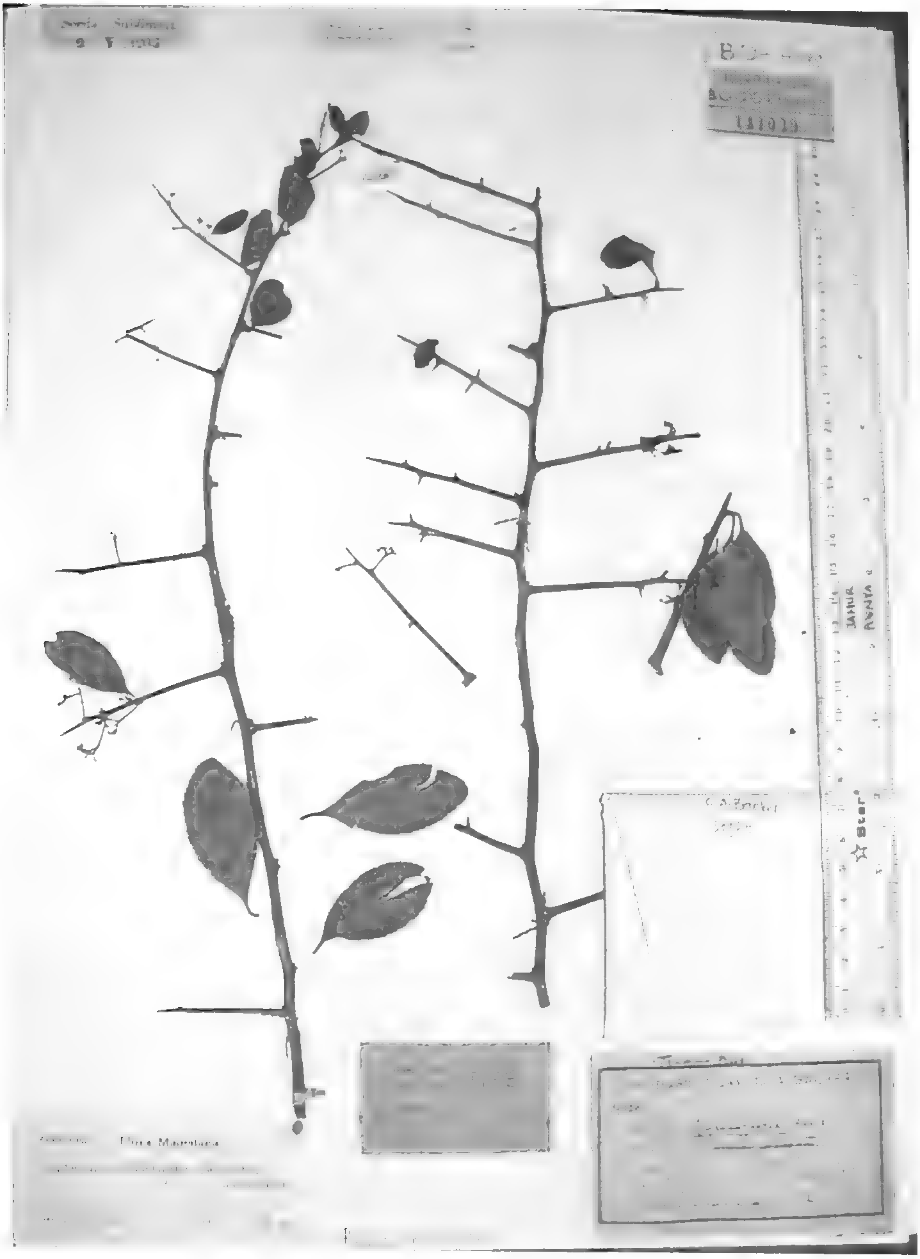

Fig. 4. *Gymnosporia littoralis* (type). Java: Batavia, Tandjong Priok, *Backer 34926* (BO).

Diagnostic characters: plants with axillary and/or terminal spines (short lateral branches ending in a spine); leaves obovate-oblong, oblanceolate or broadly obovate, apex obtuse; ovary bilocular; disc cupular. Differs from *G. inermis* in having smaller leaves and 2-valved capsules.

Distribution and habitat: Philippines, Taiwan, S China (Xiamen), Ryukyu Islands (Japan) and Vietnam. It occurs mainly in coral places or dry thickets along the seashore.

Selected specimens examined: PHILIPPINES: Luzon: Ilocos Norte Prov., Burgos, *Ramos 27204*, Feb–Mar 1917 (GH).

TAIWAN: Kaohsiung, *Playfair 271* (K).

CHINA: Fukien: Amoy (Xiamen), *Ching 777*, 1922 (SING).

JAPAN: Ryukyu Islands: S of lighthouse, *Fosberg 38585* (K); Loo-Choo Islands (Ryukyu Islands), *Wright 53* (K), *Wright s.n.* (NY468032, US16301).

VIETNAM: Bai Turong (Bai Thuong), *Kuntze 3642*, 24 Feb 1875 (K, NY).

7. Gymnosporia emarginata *(Willd.) Thwaites*

(Thwaites 1864: 409); (M.A.Lawson 1875: 621); (Loesener 1902: 471); (Loesener 1942: 150).

Celastrus emarginatus Willd.

(Willdenow 1798: 1128); (Wight & Arnott 1834: 160).

Type: Eastern India, *B. Heyne s.n. Herb. Willdenow 4752*; holo B (microfiche at PRE!).

Catha emarginata (Willd.) Don

(Don 1832: 9); (Walpers 1842: 532).

Maytenus emarginata (Willd.) Ramam.

(Ramamurthy 1983: 74); (Matthew 1995: 85); (Wadhwa 1996: 83); non Ding Hou (1962: 241); non Li (1977: 629); non Jessup (1984: 164); non Lu. & Yang (1993: 654).

Shrub or small tree up to 6 m high; bark pale brown, smooth, cracked; branches terete, with pale lenticels; spines axillary or terminating short lateral shoots. Leaves thick, coriaceous, shining above, paler beneath; lamina narrowly lanceolate to obovate, oblanceolate to rotundate, rarely elliptic-oblong, 25–40 (–70) × 15–30 mm, apex rounded or obtuse, usually emarginate, margin thickened, usually entire or remotely crenate in distal part, reticulate venation usually obscure above, prominent below; petiole short, 1–3 mm long. Inflorescence axillary, often on spines, few-flowered; peduncle short, 1.0–2.5 mm long; pedicel very slender, glabrous, 7–9 mm long. Flowers pale greenish-yellow or white, sweet-scented, ± 4 mm in diam. Sepals deltoid, ± 1 mm long, apex obtuse, margin ciliate. Petals obovate-oblong or oblong, 2–3 × 1.0–1.5 mm, twice as long as sepals, apex subacute, often reflexed, margin entire or uneven. Disc very broad, fleshy, sinuate-lobed. Male flowers: stamens slightly shorter than petals, inserted slightly beneath the disc margin; anthers broadly ovoid; pistillode globose, small, style unbranched. Female flowers: staminodes shorter than stamens in male flowers; ovary semi-immersed in disc, 3-locular; style cylindrical, 3-branched, spreading. Capsule obconic-trigonous, inflated, flat-topped, apiculate, 3-valved, 3–5 × 6–12 mm, red or dull purple. Seed ovoid or ellipsoid, red and shining, 2.5–3.5 × 2.0–2.5 mm; aril white, fleshy, a basal rim. (Fig. 5).

Distribution and habitat: S India and Sri Lanka. Growing in scrub, on coastal plains, up to 500 m.

Diagnostic characters: leaf apex is usually emarginate, margin is entire or only remotely crenate in the distal part; peduncles short (up to 2 mm long) and pedicels long and slender (up to 9 mm), which is unusual for this genus (usually with long peduncles and short pedicels); capsule 3-valved.

Note: this name is now considered to apply only to plants from India and Sri Lanka. The name is therefore misapplied to plants in the Flora Malesiana region. Specimens previously named *Maytenus emarginata* by Ding Hou in 1962, occurring in Malesia (Philippines, Celebes, Moluccas and New Guinea) and northern Queensland in Australia now belong to *Gymnosporia inermis*.

Selected specimens examined: INDIA: South Arcot: Ulundurpet, 4 km to Pulloorkkadu, *Matthew & Perumal RHT 20070*, 12 Dec 1978 (L, RHT); Vallampadugai, *Ramamurthy 90458*, 16 Mar 1989 (BSI).

SRI LANKA: Northern Province: Jaffna District, SE Point Pedro, near Kaddaikadu, *Bernardi 14253*, 16 Mar 1973 (L); Central Province: Matale District, Laggala, altitude ± 900 m, *Cramer 5005*, 25 Nov 1977 (K); Central Province: Peradeniya Botanic Garden, 7° 16' N 80 ° 37′ E, *Kostermans 27823*, 3 Oct 1979 (K).

8. **Maytenus rapakir** *Loes.*

(Loesener 1936: 217); Loesener 1942: 140)

Type: Bismarck Archipelago (New Ireland): Neu-Mecklenburg, Namatanai, *Peekel 433*, flowers and fruits in May; (holo B, probably destroyed).

Leaves ovate, papery, 85–130 long. Inflorescence cymose, many-flowered. Capsules 3-valved, 7–8 mm long and seed with basal aril.

Fig. 5. *Gymnosporia emarginata*. Sri Lanka: Matale District, Laggala, *Cramer 5005* (K).

Note: Ding Hou (1962) mentioned this name and said that it is distinct because of the broadly ovate-oblong to ovate leaves. Loesener (1936) when he described this species placed it in *Maytenus* section *Fasciculatae* and noted that the flowers appeared to be unisexual, thus suggesting that it may be an intermediate between the genera *Maytenus* and *Gymnosporia*. However, according to the description (large ovate to oblong leaves and cymose inflorescences), it agrees with *Gymnosporia* and also fits into its overall distribution pattern; it seems to be close to *G. inermis* and *G. vitiensis* (A.Gray) Seem.

Sleumer (1960) mentioned that most of Peekel's type specimens collected in the Bismarck Archipelago, which he sent to Berlin Herbarium, were destroyed during World War II. 'Rapakir' is probably a native name added to the generic name, as was Peekel's custom. The authors of this paper were unsuccessful in tracing any duplicates of the type material or other authentic material of this species.

10. Maytenus cupularis *Ding Hou*

(Ding Hou 1962: 243).

This species has a racemose inflorescence and has a cupular disc and is related to the Australian members of *Maytenus* s. str. All the *Gymnosporia* species in this region are spiny shrubs, up to 5 m high, growing near sea level at the edge of mangroves or along the seashore, whereas this species is a 30 m rainforest tree.

Conclusions

As currently circumscribed, the genus *Maytenus* Molina, even after the reinstatement of *Gymnosporia* (Jordaan & Van Wyk 1999), is still clearly a heterogeneous assemblage which will have to be split into more natural genera, a view also supported by Rogers et al. (1999), Simmons & Hedin (1999), Simmons et al. (2001a) and Simmons et al. (2001b). Species remaining in *Maytenus* do not have spines and their leaves are always alternate, not fascicled, their inflorescence type varies from racemose, fascicled to monochasial cymes and their flowers are bisexual. The Celastraceae of the Flora Malesiana region needs revision, especially at the generic level. There are six species and two varieties of *Gymnosporia*, and one species of *Maytenus* s.lat, in this region.

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Fruit characters in Malesian Euphorbiaceae

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Abstract

Esser, H.-J. (Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138, USA; current address: University of Hamburg, Institute of General Botany, Ohnhorststrasse 18, 22609 Hamburg, Germany). 2003. Fruit characters in Malesian Euphorbiaceae. Telopea *10 (1): 169–177.* It is argued that zoochory is more abundant in Malesian Euphorbiaceae than in any other tropical area, and probably played a more significant role in the diversification of the family in Malesia than elsewhere.

Introduction

The Euphorbiaceae are among the larger families of flowering plants with c. 300 genera and 8000 species (Webster 1994, Radcliffe-Smith 2001). They are usually recognised by their unisexual flowers and typical fruits, although a phylogenetic diagnosis with morphological characters is still difficult. Recent studies, using molecular characters, indeed indicate that they may not be monophyletic (Savolainen et al. 2000, among others).

For many anatomical and morphological characters, comparative studies have been published covering the whole family or at least some of the five subfamilies, summarised with detailed references by Webster (1994). This includes vegetative, floral and seed characters. The fruits, however, never received much attention, and were hardly discussed by Webster.

These fruits are superior, three-locular, dry schizocarps, dehiscing violently along the septa into three mericarps ('cocci'); the mericarps consist of pericarp and two septal parts, and contain one or two dry seeds each, the seeds with or without a caruncle. The dispersal of Euphorbiaceae is usually considered to be autochorous by explosion of the ballistic fruits, and diplochorous in combination with myrmechory (Berg 1975 a, b).

It is often implied that fruits are quite uniform within the family (e.g., Dilcher & Manchester 1988). Nevertheless Berg (1975b) published the only detailed anatomical and morphological analysis of euphorbiaceous fruits. He found structures unique in flowering plants. They could be a strong argument for the possible monophyly of Euphorbiaceae. Unfortunately comparative studies throughout the family have never been published.

Fruit diversity

Fruit diversity can be studied under various viewpoints. There are clearly historical, phylogenetic aspects, such as the distinction in bi-ovulate and uni-ovulate Euphorbiaceae. Another aspect is the occurrence of fleshy or indehiscent fruits. The Philippine *Balakata luzonica* (Vidal) Esser, for instance, has one-seeded berry-like drupes and was originally described as a species of *Myrica* (Myricaceae), and was later re-described as Icacinaceae (Esser 1999).

The aim of this contribution is a comparison of the occurrence of fleshy diaspores between various tropical areas. In some Euphorbiaceae, the whole fruit becomes fleshy and will attract animals (e.g., in *Antidesma* Burm. ex L.), whereas in others the dry fruit wall falls off easily, exposing fleshy and attractively coloured seeds (e.g., in *Sapium* Jacq. and *Triadica* Lour.). For the purpose of this study I will distinguish between 'typical' fruits of Euphorbiaceae (i.e., dry seeds and fruits, and most probably autochorous), and probable adaptations to zoochory (including fleshy or indehiscent fruits as well as fleshy seeds). In most cases, dispersers will probably be birds (ornithochory), but this will not be distinguished here.

The recognition of zoochory is sometimes difficult from herbarium collections alone, and it is also not strictly distinguished in nature. Several Euphorbiaceae have basically dry and woody fruits that show reddish colours and may be dispersed by birds if small enough, although not clearly adapted to ornithochory (observed in scattered field notes and herbarium labels).

Spiny-echinate fruits can be found in numerous genera in all tropical areas (such as *Mallotus* Lour. or *Chaetocarpus* Thwaites). These fruits are usually dry, which could indicate epizoochory, but could also be a protection of autochorous fruits against herbivory.

The absence or presence of a caruncle on the seeds is not analysed here. It has a probable phylogenetic background, because a caruncle is consistently absent in Phyllanthoideae but variable and often present in other subfamilies, without an obvious correlated distinction in ecology etc. between the subfamilies. It is also variable within numerous genera of the family (such as *Croton* L., *Euphorbia* L.), and it is therefore difficult to compare at the genus level.

Methods

Data on the generic diversity of Euphorbiaceae were extracted from published accounts for Malesia and three other tropical areas for which recent and reliable revisions are available. Cultivated, exotic taxa were omitted.

The family is currently under revision for Flora Malesiana, and data on diversity in Malesia (Table 1) are taken from the regularly updated Malesian Euphorbiaceae Newsletter (Welzen 1997, 2000), separate revisions cited therein, and own unpublished estimations for *Breynia, Croton* and *Euphorbia*. The species numbers exclude Thai taxa not known from Malesia.

Data for extra-Malesian regions were taken, unchanged, for Tropical East Africa (Table 2, after Carter & Radcliffe-Smith 1988, Radcliffe-Smith 1987), Costa Rica (Table 3, after Burger & Huft 1996), and the Venezuelan Guayana (Table 4, after Webster et al. 1999). These areas are much smaller than Malesia, and the focus is therefore not on absolute numbers of taxa.

Diaspores were distinguished into presumably autochorous and zoochorous. These data were extracted from the cited references and usually verified in the herbarium. For Malesia, however, a considerable part of the family has not been revised yet (more than 60 genera are listed as such by Welzen 2000), and here the data are based on own observations on herbarium specimens only.

Because of the mentioned uncertainties (ongoing studies of Malesian Euphorbiaceae, sometimes problematic classification of dispersal syndromes in certain genera) no further statistics will be applied, and the data should be understood as preliminary at this stage.

Results and Discussion

Although this study was mainly based on a compilation from available publications, it leads to some conclusions that have not been discussed much before. The comparison of Tables 1 to 4 shows a number of interesting patterns:

Although there is a considerable range of fruit types within Euphorbiaceae as a whole, only very few genera are variable in their fruit type: *Alchornea, Mallotus, Omphalea, Phyllanthus,* and *Shirakiopsis*. The largest ones of these (*Mallotus* and *Phyllanthus*) are probably unnatural in their present circumscription (Slik & Welzen 2001, K. Wurdack pers. comm.). *Alchornea* is mentioned here with some doubt because only in the Neotropics do the fruits tend to show a slightly fleshy pericarp, tardily dehiscent, but are not clearly zoochorous. Variation in dispersal syndrome as distinguished here is usually found above the genus level only.

In Malesia the proportion of genera and species with fleshy, presumably zoochorous diaspores is higher than in Africa or the Neotropics (Table 5). This difference is even more obvious in species numbers than in numbers of genera. Whereas in all regions compared more than 50% of all genera have dry and dehiscent fruits, it is only in Malesia that the majority of species of Euphorbiaceae has zoochorous diaspores.

A large proportion of the genera endemic to, or most diversified in, Malesia shows zoochory, in particular most of the largest Malesian genera (such as *Antidesma, Macaranga*). This is very different in the African and American regions compared, where the most species-rich genera have 'typical' dry schizocarps.

Most pantropical genera of Euphorbiaceae have dry, dehiscent fruits (such as *Acalypha, Croton, Euphorbia, Microstachys*) or are variable, with a large proportion of autochory (such as *Phyllanthus*). All of these are comparatively poorly diversified in Malesia, with the centre of diversity in other continents. The only pantropical zoochorous genera are *Drypetes* (which probably has to be excluded from the family, as discussed by, e.g., Wurdack & Chase 1996) and *Margaritaria* (which is the smallest of the pantropical genera with 14 species).

Webster (1994: 18, table 3) included a brief comparison between geography and dispersal type in genera of Euphorbiaceae, and concluded that ornithochory is prevalent in tropical Asia and in Africa/Madagascar in contrast to the other continents. His data could not be confirmed in the present contribution. At the genus level, autochory is prevalent on all continents, although there seems to be a difference between Old World and New World. The diversification of zoochorous Euphorbiaceae is however certainly more obvious in Malesia than in Africa when numbers of species are considered, as done here.

Schizocarps and autochory were most probably the plesiomorphic conditions in Euphorbiaceae (Webster 1994). It can therefore be postulated that zoochorous dispersal (in most cases probably ornithochory) played a significant and underestimated role in the evolution and diversification of Malesian Euphorbiaceae, much more than it did on other tropical continents.

This contribution is only a first and preliminary step in the comparative study of Euphorbiaceae fruits, focussing on one particular aspect. It is nevertheless apparent that additional studies are desirable. For instance, a more detailed distinction between forest and savanna ecosystems and their respective dispersal syndromes within the regions compared here might be interesting. A more detailed comparison of 'typical' dry schizocarps within the family will be undertaken in a forthcoming publication.

Table 1. Malesian genera of Euphorbiaceae and the presence of zoochorous diaspores. Nomenclature follows Radcliffe-Smith (2001). Genera are sorted according to their species number. a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type	Overall number of species	Distribution
175	***Macaranga***	**z**	280	Africa to Pacific Islands
150	***Glochidion***	**z**	300	Madagascar to Pacific Islands
108	*Phyllanthus*	v	800	pantropical
70	***Antidesma***	**z**	170	Africa to Pacific Islands
63	***Drypetes***	**z**	200	pantropical
61	*Mallotus*	v	150	Indopacific
60	***Claoxylon***	**z**	80	Madagascar to Indopacific
60	*Cleistanthus*	a/d	140	Africa to Pacific Islands
55	*Croton*	a/d	800	pantropical
52	***Aporosa***	**z**	80	India to Malesia
42	*Trigonostemon*	a/d	50–60	India to Australia
39	***Baccaurea***	**z**	43	India to Pacific Islands
30	*Euphorbia* (incl. *Chamaesyce*)	a/d	2000	worldwide
28	*Acalypha*	a/d	450	pantropical
21	***Breynia***	**z**	35	India to New Caledonia
15	*Actephila*	a/d	20	Australasia
15	***Bridelia***	**z**	60	Africa to Asia
14	*Codiaeum*	a/d	16	Malesia to Pacific Islands
12	***Homalanthus***	**z**	20	Malesia to Pacific Islands
12	***Ptychopyxis***	**z**	12	Thailand and Malesia
12	***Sauropus***	**z**	80	India to China and Australia
11	***Endospermum***	**z**	12	India to China and Australia
10	*Alchornea*	a/d	60	pantropical
10	*Dimorphocalyx*	a/d	20	India to Malesia
9	*Koilodepas*	a/d	10–12	India to China
8	*Cleidion*	a/d	25	pantropical
7	*Blumeodendron*	a/d	6	Burma to Malesia
6	***Galearia***	**z**	6	Burma to Malesia
6	*Neoscortechinia*	a/d	6	Burma to Malesia
6	***Suregada***	**z**	31	Africa to Asia
5	*Agrostistachys*	a/d	10	India to Malesia
5	*Cephalomappa*	a/d	6	China to Malesia
5	*Excoecaria*	a/d	35	Africa to Polynesia
5	*Jatropha*	a/d	175	pantropical
4	*Cnesmone*	a/d	12	Southeast Asia
4	*Omphalea*	v	20	pantropical
4	***Pimelodendron***	**z**	6–8	Malesia to Australia
3	***Distichirhops***	**z**	3	endemic
3	*Epiprinus*	a/d	6	India to Malesia
3	***Micrococca***	**z**	12	Africa to Asia
3	*Shirakiopsis*	v	6	Africa to Asia
3	*Trigonopleura*	a/d	3	endemic
2	***Aleurites***	**z**	2	India to Pacific Islands
2	***Ashtonia***	**z**	2	endemic
2	***Balakata***	**z**	2	India to Malesia
2	*Chondrostylis*	a/d	2	Thailand to Malesia
2	*Dalechampia*	a/d	110	pantropical

Number of species	Genus	Diaspore type	Overall number of species	Distribution
2	*Erismanthus*	a/d	2	Malesia to China
2	***Flueggea***	**z**	15	Paleotropics, temperate Eurasia
2	***Fontainea***	**z**	6	New Guinea to Australia
2	*Gymnanthes*	a/d	45	pantropical
2	*Lasiococca*	a/d	5	India to China
2	*Leptopus*	a/d	10	Asia, Australia, America
2	***Margaritaria***	**z**	14	pantropical
2	*Spathiostemon*	a/d	4	Thailand to Malesia
2	*Syndyophyllum*	a/d	2	endemic
2	*Wetria*	a/d	2	Burma to Malesia
1	*Alphandia*	a/d	3	Malesia to New Caledonia
1	*Annesijoa*	a/d	1	endemic
1	*Austrobuxus*	a/d	20	Malesia to Fiji and Australia
1	*Baliospermum*	a/d	12	India to China
1	***Bischofia***	**z**	1	Malesia to Pacific Islands
1	*Blachia*	a/d	15	India to Southeast Asia
1	*Borneodendron*	a/d	1	endemic
1	*Botryphora*	a/d	1	Burma to Malesia
1	*Chaetocarpus*	a/d	13	America, Madagascar, Asia
1	*Cheilosa*	a/d	1	endemic
1	*Choriceras*	a/d	2	New Guinea to Australia
1	***Chrozophora***	**z**	10	Mediterranean to East Asia
1	*Cladogynos*	a/d	1	Southeast Asia
1	*Clonostylis*	a/d	1	endemic
1	*Dicoelia*	a/d	1	endemic
1	***Doryxylon***	**z**	1	endemic
1	*Elateriospermum*	a/d	1	Thailand to Malesia
1	***Erythrococca***	**z**	50	mostly Africa
1	***Falconeria***	**z**	1	India to Malesia
1	***Homonoia***	**z**	2	India to Malesia
1	*Hymenocardia*	a/d	9	Africa to Asia
1	*Kairothamnus*	a/d	1	endemic
1	*Loerzingia*	a/d	1	endemic
1	***Megistostigma***	**z**	5	Burma to Malesia
1	***Melanolepis***	**z**	2	Malesia to Indochina
1	***Microdesmis***	**z**	10	Africa to Asia
1	*Microstachys*	a/d	17	pantropical
1	*Moultonianthus*	a/d	1	endemic
1	***Neotrewia***	**z**	1	endemic
1	***Octospermum***	**z**	1	endemic
1	*Ostodes*	a/d	1–3	Himalaya to Malesia
1	*Pachystylidium*	a/d	1	India to Malesia
1	*Paracroton*	a/d	3	India to Malesia
1	***Petalostigma***	**z**	6	New Guinea to Australia
1	*Plukenetia*	a/d	15	pantropical
1	*Reutalis*	a/d	1	endemic
1	*Richeriella*	a/d	2	Malesia to China
1	*Stillingia*	a/d	27	nearly pantropical
1	*Strophioblachia*	a/d	1	Malesia to China
1	***Sumbaviopsis***	**z**	1	India to Malesia
1	*Tapoides*	a/d	1	endemic
1	***Trewia***	**z**	1	India to China
1	***Triadica***	**z**	3	India to China
1	*Vernicia*	a/d	3	Burma to East Asia

Table 2. Genera of Euphorbiaceae in tropical East Africa and the presence of zoochorous diaspores. Genera are sorted according to their species number.
a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type
208	*Euphorbia*	a/d
52	*Phyllanthus*	v
30	*Acalypha*	a/d
27	*Tragia*	a/d
23	*Croton*	a/d
22	*Jatropha*	a/d
15	***Erythrococca***	**z**
10	***Drypetes***	**z**
8	***Bridelia***	**z**
8	***Macaranga***	**z**
7	*Clutia*	a/d
6	*Zimmermannia*	a/d
5	*Alchornea*	a/d
4	*Dalechampia*	a/d
4	***Micrococca***	**z**
3	***Caperonia***	**z**
3	*Meineckia*	a/d
3	*Pycnocoma*	a/d
3	***Suregada***	**z**
3	*Thecacoris*	a/d
3	*Tragiella*	a/d
2	*Argomuellera*	a/d
2	*Cephalocroton*	a/d
2	*Cleistanthus*	a/d
2	*Excoecaria*	a/d
2	***Maprounea***	**z**
2	*Neoboutonia*	a/d
2	***Oldfieldia***	**z**
2	***Ricinodendron***	**z**
2	*Spirostachys*	a/d
2	***Tetrorchidium***	**z**
1	*Andrachne*	a/d
1	*Aristogeitonia*	a/d
1	*Cavacoa*	a/d
1	***Chrozophora***	**z**
1	*Crotonogynopsis*	a/d
1	***Discoclaoxylon***	**z**
1	***Discoglypremna***	**z**
1	*Flueggea*	a/d
1	***Givotia***	**z**
1	*Heywoodia*	a/d
1	***Maesobotrya***	**z**
1	***Mallotus***	**z**
1	*Mareya*	a/d
1	***Margaritaria***	**z**
1	*Mildbraedia*	a/d
1	*Necepsia*	a/d
1	*Neoholstia*	a/d
1	*Omphalea*	a/d
1	*Paranecepsia*	a/d
1	*Pseudagrostistachys*	a/d
1	*Pseudolachnostylis*	a/d
1	*Savia*	a/d

Table 2 cont.

Number of species	Genus	Diaspore type
1	*Sclerocroton*	a/d
1	*Shirakiopsis*	a/d
1	***Sibangea***	**z**
1	*Spondianthus*	a/d
1	*Tannodia*	a/d

Table 3. Genera of Euphorbiaceae in Costa Rica and the presence of zoochorous diaspores. Genera are sorted according to their species number.
a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type
32	*Croton*	a/p
32	*Euphorbia* (incl. *Chamaesyce*)	a/p
19	*Acalypha*	a/p
13	*Phyllanthus*	v
10	*Dalechampia*	a/p
6	*Jatropha*	a/p
6	***Sapium***	**z**
5	*Alchornea*	v
4	***Tetrorchidium***	**z**
4	*Manihot*	a/p
3	***Cnidoscolus***	**z**
3	***Drypetes***	**z**
3	*Mabea*	a/p
3	*Tragia*	a/p
2	*Bernardia*	a/p
2	***Caperonia***	**z**
2	*Gymnanthes*	a/p
2	***Hieronyma***	**z**
2	*Plukenetia*	a/p
1	*Acidoton*	a/p
1	*Actinostemon*	a/p
1	*Adelia*	a/p
1	*Adenophaedra*	a/p
1	***Alchorneopsis***	**z**
1	*Amanoa*	a/p
1	*Aparisthmium*	a/p
1	*Argythamnia*	a/p
1	*Astrocasia*	a/p
1	*Caryodendron*	a/p
1	*Conceveiba*	a/p
1	*Dysopsis*	a/p
1	*Garcia*	a/p
1	***Hippomane***	**z**
1	*Hura*	a/p
1	***Margaritaria***	**z**
1	*Microstachys*	a/p
1	*Omphalea*	v
1	*Pausandra*	a/p
1	*Pedilanthus*	a/p
1	*Pera*	a/p
1	***Richeria***	**z**
1	*Sagotia*	a/p
1	*Stillingia*	v

Table 4. Genera of Euphorbiaceae in the Venezuelan Guayana and the presence of zoochorous diaspores. Genera are sorted according to their species number.
a/d = autochorous/diplochorous diaspores; **z** = presumably zoochorous diaspores; v = variable diaspore type.

Number of species	Genus	Diaspore type
45	*Croton*	a/d
43	*Phyllanthus*	v
15	*Mabea*	a/d
14	*Dalechampia*	a/d
11	*Euphorbia* (incl. *Chamaesyce*)	a/d
9	*Acalypha*	a/d
7	*Micrandra* (incl. *Cunuria*)	a/d
6	*Amanoa*	a/d
6	*Manihot*	a/d
6	*Pera*	a/d
5	*Alchornea*	v
5	*Plukenetia* (incl. *Apodandra*)	a/d
4	*Conceveiba*	a/d
4	*Hevea*	a/d
4	***Sapium***	**z**
3	*Discocarpus*	a/d
2	*Actinostemon*	a/d
2	*Dendrothrix*	a/d
2	***Drypetes***	**z**
2	***Hieronyma***	**z**
2	*Jatropha*	a/d
2	***Maprounea***	**z**
2	*Piranhea*	a/d
2	*Sagotia*	a/d
2	*Sandwithia*	a/d
2	*Senefelderopsis*	a/d
2	*Tragia*	a/d
1	*Acidoton*	a/d
1	*Adelia*	a/d
1	*Adenophaedra*	a/d
1	***Alchorneopsis***	**z**
1	*Aparisthmium*	a/d
1	*Astrococcus*	a/d
1	*Bernardia*	a/d
1	***Caperonia***	**z**
1	*Celianella*	a/d
1	*Chaetocarpus*	a/d
1	***Cnidoscolus***	**z**
1	*Ditaxis*	v
1	*Gavarretia*	a/d
1	***Glycydendron***	**z**
1	*Gymnanthes*	a/d
1	*Haematostemon*	a/d
1	*Hura*	a/d
1	***Jablonskia***	**z**
1	***Margaritaria***	**z**
1	*Microstachys*	a/d
1	*Omphalea*	a/d
1	*Pausandra*	a/d
1	*Pedilanthus*	a/d
1	*Podocalyx*	a/d
1	*Pogonophora*	a/d
1	*Pseudosenefeldera*	a/d
1	***Richeria***	**z**
1	*Savia*	a/d
1	***Tetrorchidium***	**z**

Table 5. Numerical comparison of fleshy (incl. indehiscent) diaspores between different tropical regions, summarising Tables 1–4.

	Malesia	**Tropical East Africa**	**Costa Rica**	**Venezuelan Guayana**
Total number of genera	101	59	44	56
Total number of species	1288	494	177	238
Genera with dry fruits and seeds	58 (= 57.4%)	39 (= 66.1%)	32 (= 72.7%)	42 (= 75%)
Species with dry fruits and seeds	371 (= 28.8%)	375 (= 75.9%)	135 (= 76.3%)	173 (= 72.7%)
Genera with fleshy fruits/seeds	39 (= 38.6%)	19 (= 32.2%)	10 (= 22.7%)	12 (= 21.4%)
Species with fleshy fruits/seeds	741 (= 57.5%)	67 (= 13.6%)	24 (= 13.6%)	17 (= 7.1%)
Variable genera	4	1	2	2
Species of variable genera	176	52	18	48

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Endosperm condition and the paradox of *Ptychococcus paradoxus*

Scott Zona

Abstract

Zona, S. (Fairchild Tropical Garden, 11935 Old Cutler Road, Coral Gables, FL 33156-4242, USA. e-mail: szona@fairchildgarden.org). Endosperm condition and the paradox of Ptychococcus paradoxus. Telopea *10(1): 179–185.* Endosperm condition, whether homogeneous or ruminate, is an easily-observed character that is widely used in species level taxonomy of palms, although it appears to be a poor indicator of relationships at higher levels. Palms are routinely described as having homogeneous or ruminate endosperms; however, all endosperm ruminations may not be homologous. My experience with the palm genus *Ptychococcus* (Arecaceae: Arecoideae) suggests that misinterpretations of endosperm variation have led to taxonomic confusion. I have examined herbarium specimens of lowland *Ptychococcus* and conclude that variation in endosperm condition is continuous, from completely homogeneous to slightly ruminate to deeply ruminate. In the absence of contradictory evidence from other characters, I conclude that the various taxa defined solely by their endosperm condition cannot be maintained and that only one species of *Ptychococcus*, *P. paradoxus*, should be recognized from the lowlands of New Guinea. The paradox of *P. paradoxus* lies in the variability of its endosperm, which has been confounding botanists for over a century.

Introduction

Endosperm condition, whether ruminate or homogeneous, has long been recognized as a useful and often diagnostic character state in angiosperms. A ruminate endosperm is characterized by in-growths or invaginations of the endosperm by the seed coat (Bayer & Appel 1996, Werker 1997). A homogeneous endosperm lacks such in-growths. Obvious examples of ruminate endosperms are found in the seeds of nutmeg, *Myristica fragrans* Houtt. (Myristicaceae), and betel nuts, *Areca catechu* L. (Arecaceae).

A recent survey of Angiosperms by Bayer and Appel (1996) found 58 families in which the ruminate endosperm condition is known to occur, and van Balgooy (1997) listed those Malesian seed plants with the ruminate condition (although he also included exalbuminous taxa with convoluted embryos, which are usually termed 'labyrinth seeds'). Prominent on both of those lists is the palm family (Arecaceae). Within the palm family, 51 genera (out of nearly 200) have at least one species with ruminate endosperm, and 23 of these genera occur in the Malesian region (Table 1).

Ruminate endosperm morphology has been used successfully in the classification of some groups, e.g. Annonaceae (van Setten & Koek-Noorman 1992), but the morphology of endosperm ruminations in palms has not been carefully examined. Although the presence or absence of ruminate endosperm is much used at the species level in palms, it appears to be homoplasious when used for higher level classification. Ruminate endosperm occurs in four different subfamilies of palms and numerous tribes and subtribes (Table 1), an observation suggesting that it has evolved and/or been lost many times in the course of palm evolutionary history.

Table 1. Occurrence of ruminate endosperm within the Arecaceae (Uhl & Dransfield 1987, with modifications from Dowe & Cabalion 1996, Barrow 1998, Uhl and Dransfield 1999 and Dransfield et al. 2000). Genera occurring in Malesia are marked with an asterisk (*).

CORYPHOIDEAE
Chamaerops
Copernicia
Chuniophoenix p.p.
*Kerriodoxa**
Phoenix p.p.*
Medemia
Satranala

CALAMOIDEAE
Korthalsia p.p.*
*Daemonorops**
Calamus p.p.*
Raphia

CEROXYLOIDEAE
Synechanthus

ARECOIDEAE
Caryota p.p.*
Wettinia p.p.
Reinhardtia p.p.
Dypsis p.p.
Euterpe p.p.
Prestoea p.p.
Neonicholsonia
Oenocarpus p.p.
Archontophoenix
Laccospadix
Calyptrocalyx p.p.*
Drymophloeus p.p.*
Normanbya
*Adonidia**
Ptychosperma p.p.*
Ptychococcus p.p.*
Loxococcus
Lemurophoenix
*Siphokentia**
Hydriastele p.p.*
Gulubia p.p.*
*Nenga**
Pinanga p.p.*
*Areca**
Iguanura p.p.*
Heterospathe p.p.*
*Rhopaloblaste**
Dictyospermum
*Actinorhytis**
Physokentia p.p.*
*Oncosperma**
Verschaffeltia
Roscheria
Phoenicophorium
Nephrospermum
Beccariophoenix
Syagrus p.p.
Lytocaryum p.p.
Polyandrococos

Development of ruminations

The ruminate endosperms of palms have been the subject of several anatomical studies, although the topic is not yet exhausted. Periasamy (1962) classified ruminate palm seeds as 1) the *Annona* type: possessing localized meristematic activity in a multi-layered seed coat that produces in-growths in the endosperm, or 2) the *Myristica* type, which is similar but the in-growths have vascular tissue or are subadjacent to vascular tissue. Examples of the *Annona* type include *Caryota* and *Heterospathe* (Werker 1997); examples of the *Myristica* type include *Adonidia* and *Bentinckia* (Murray 1971, Padamanabham & Regupathy 1981). Examples of Periasamy's other five types of ruminate endosperm, which differ in the number of integument layers and layers of the seed coat, have not been found in the Arecaceae.

Werker (1997) noted additional variation in the development of palm seed ruminations. The endosperm of some palm seeds, at an early stage of development becomes quiescent while the seed coat and integuments develop irregularities. When at a later stage, the endosperm again commences growth, it fills in the around the seed coat. One might say that the seed coat leads, and the endosperm follows. In contrast, ruminations in other palms develop as a result of unequal and localized cell division of the nucellus (megagametophyte). The nucellus throws the seed coat into irregular folds, and then the seed coat hardens. As the embryo sac enlarges and absorbs the nucellus, it conforms to the shape of the seed coat. In this case, the nucellus leads, and the seed coat follows.

Endosperm condition and palm taxonomy

Until well into the 20th century, endosperm condition was used at the generic level in palm classification. In other words, pairs of genera that differed primarily in endosperm condition were recognized (Hooker 1883; Drude 1887; Burret 1953). Examples of these generic pairs are *Phloga* (ruminate) and *Neophloga* (homogeneous), *Coleospadix* (ruminate) and *Drymophloeus* (homogeneous), *Rhyticocos* (ruminate) and *Syagrus* (homogeneous) and *Jessenia* (ruminate) and *Oenocarpus* (homogeneous). In all of these examples, the generic pairs are now recognized as congeneric (Uhl & Dransfield 1999). A broadening of generic concepts allowed the recognition of genera that include species with ruminate endosperms alongside species with homogeneous endosperms. Of the 51 genera with ruminate endosperms listed in Table 1223 genera also include species with homogeneous endosperms.

Endosperm condition, however, is sometimes not so easily interpreted, and the dichotomy between ruminate and homogeneous is not always clear-cut. The following example presents evidence that, in the case of *Ptychococcus paradoxus* (Sheff.) Becc., endosperm condition varies continuously from homogeneous to ruminate, and over-emphasis on this one character has led to taxonomic confusion. I conclude that, for *Ptychococcus paradoxus,* the species concept must be broadened to allow this single species to accommodate both homogeneous and ruminate endosperms.

The case of *Ptychococcus paradoxus*

The type specimen of *Ptychococcus paradoxus* was collected by J. E. Teijsmann in July, 1871, from New Guinea. He collected only fruits, which he brought back to the Buitenzorg (now Bogor) Botanic Garden for propagation. One fruit or endocarp was the basis for Scheffer's (1876a) description; later descriptions of vegetative characters were based on juvenile plants grown from the seeds of these fruits. When Scheffer (1876a; p. 53) proposed the name *Drymophloeus ? paradoxus,* he described the endosperm as 'subaequalibe' (sub-homogeneous), yet just a few lines later, he wrote that the endosperm was not ruminate. At the time, *Drymophloeus* was thought to comprise only species with homogeneous endosperms. In a consecutive publication (Scheffer 1876b, p. 121), he suggested that his *D. paradoxus* may belong to the same genus as *Ptychosperma capitis-yorkii* H. Wendl. & Drude [= *P. elegans* (R. Br.) Blume], a taxon noteworthy for its deeply ruminate endosperm. By pages 155 and 156, Scheffer (1876b) was calling his taxon *Ptychosperma paradoxa* and admitting that his first description was incorrect, that his type was in poor condition and difficult to interpret and that additional material had ruminate endosperms.

How did Scheffer come to have better material of this taxon in the course of 102 pages? The additional material then at his disposal was produced on plants grown from Teijsmann's seeds (Scheffer 1876b, p. 156). Scheffer's (1876a) work, including the description of *Drymophloeus ? paradoxus* on p. 53, described the interesting plants brought back by Teijsmann from New Guinea. It was likely prepared for publication in 1871, immediately upon receiving Teijsmann's collections, perhaps with the intention of including it in his first publication on Areceae (Scheffer 1871). For reasons unknown, publication of the work was delayed, and it did not appear until 1876. Rather than rewrite the description drafted earlier, Scheffer published it as it stood and later (1876b) emended his description. By that time, the seeds collected by Teijsmann and planted in the botanic garden had grown and provided additional material for Scheffer's examination.

In December 1999, a search of the Herbarium Bogoriense (BO) for the type specimen of *Ptychococcus paradoxus* revealed a bag of fruits among the carpological collections bearing Teijsmann's name (J. Dransfield, pers. com.). The seeds of the fruits showed, according to Dransfield, 'absolutely no signs of rumination'. This specimen, however, cannot be the type, as Scheffer (1876b) said he had only one fruit and that this was in such bad condition he had difficulty in interpreting the endosperm condition. In addition, the specimen located by Dransfield does not match the protologue (Scheffer 1876a) for this species. The type of *P. paradoxus* has not yet been located. Perhaps Scheffer destroyed the specimen, believing it to be in poor condition and unrepresentative.

Upon describing a new species, *Ptychococcus arecinus* (Becc.) Becc. (as *Ptychosperma arecina* Becc.), Beccari (1877) noted that the endosperm of *P. paradoxus* was less ruminate than that of his new species. Clearly, the degree of endosperm rumination was influencing species concepts and taxonomic decisions for Beccari at a time when the endosperm condition was often taken to have generic-level significance. For Beccari, with only a handful of specimens to compare, differences in endosperm condition, together with supposed differences in trunk and andreocium characters, seemed highly significant.

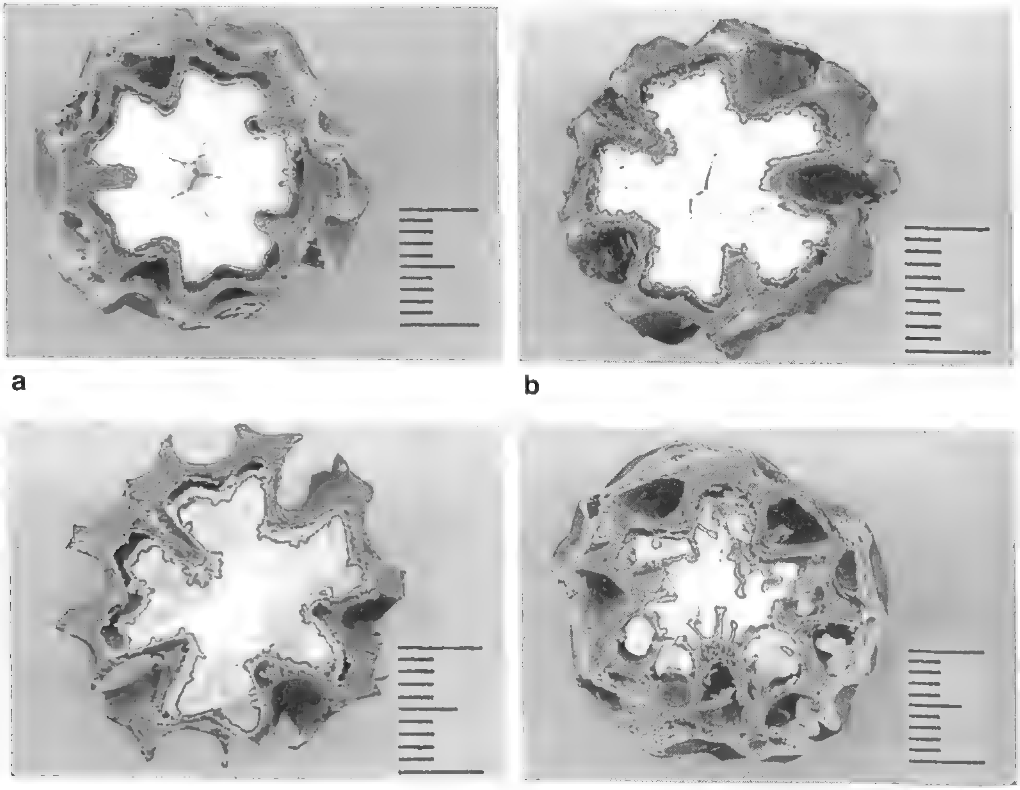

Fig. 1. Transverse sections through dried fruits and seeds of *Ptychococcus paradoxus* showing variation in endosperm condition. **a**, endosperm homogeneous (with slight intrusion visible along rapheal side of seed, at right); **b**, slight marginal rumination; **c**, slight rumination; **d**, profoundly ruminate endosperm. (**a** from *Baker 597*; **b** from *Raffill s.n.*; **c** from *Furtado X-D-32*; **d** from *Heatubun CH195*. All specimens at K). Scale bars = 10 mm.

As new material came to hand from collectors in Papua New Guinea, additional species were described. In the early years of the 20th century, Beccari described three taxa, and Burret added two more, bringing to seven the number of taxa in the genus. Burret (1939) used endosperm condition to subdivide the genus into two sections, one ruminate and the other homogeneous.

Pichi-Sermoli (in Beccari & Pichi-Sermoli 1955) cast doubt on the usefulness of the endosperm character. He did not accept the subdivisions of Burret (1936), believing that there was overlap between the two subgenera and that species with superficially ruminate endosperm would be difficult to classify in Burret's sections. Pichi-Sermoli is the first botanist to question the usefulness of endosperm condition in classifying palms and to suggest that the distinction between the two conditions was not black and white. He offered no reason for his apostasy, but perhaps his careful examination of seeds, especially noticing those with superficial ruminations, which most botanists would call 'homogeneous', led him to his new stance.

After examining a series of 20 specimens (many more than were available to Scheffer, Beccari or Pichi-Sermoli), I too began to doubt the usefulness of endosperm condition as a means of distinguishing species in *Ptychococcus*. Specimens appearing identical in vegetative and floral features differed only in the condition of the endosperm (Figs. 1a–d), from completely homogeneous (*Pullen 1077* at A or *Baker 597* at K, Fig. 1a) to slightly ruminate around the edges (*Raffill s.n.* and *Furtado s.n.* at K, Figs. 1b and 1c, respectively) to strongly ruminate (*Heatubun CH195* at K, Fig. 1d). Previously recognized differences in stamen number evaporated when a large series of specimens was examined; likewise, stem diameter appears to be a highly plastic character, depending on local growing conditions. I saw no way in which these specimens can be easily and unambiguously separated into species groups. Therefore, I believe that specimens cannot be unambiguously assigned to Burret's subgenera and that his classification should be abandoned. Available evidence suggests the lowland species of *Ptychococcus* should be recognized as a single species, *P. paradoxus*.

An end to endosperm condition as a taxonomic character?

The recognition of just one species of *Ptychococcus* in lowland New Guinea brings an end to some of the taxonomic confusion surrounding these palms. Moreover, this taxonomic disposition resolves the proliferation of names for every endosperm variant. Should other groups of palm species be re-examined to determine if they too should include both ruminate and homogeneous endosperms?

The endosperm condition of *Ptychococcus lepidotus* H. E. Moore from the highlands of New Guinea is also controversial. Few seed specimens of *P. lepidotus* are available for study, so the degree to which its endosperm condition varies is unknown. Moore (1965), in describing the species, noted 'shallow marginal ruminations on the lobes and a deep intrusion on the rapheal lobes'. Ferrero (1996) reported that the endosperm was ruminate. However, one specimen (*Hoogland 9033* at K and L) appears to have a homogeneous endosperm. Additional material of *P. lepidotus* is greatly desired.

The variable endosperm condition described for *Ptychococcus* is not unique in the family. Another palm, *Synechanthus fibrosus* (H. Wendl.) H. Wendl., is a species in which the endosperm condition is variable. *Synechanthus* is a genus of two species from Mexico and Central America allied to *Chamaedorea* and *Hyophorbe*. Moore (1971) described *S. fibrosus* as having a 'homogeneous or minutely and marginally ruminate endosperm'.

Henderson and Galeano (1996), in a revision of *Prestoea*, a genus of Central and South America, described the endosperm of *P. pubens* H. E. Moore as 'lightly (then almost homogeneous) to deeply ruminate'. In the same publication, they described *P. longepetiolata* (Oersted) H. E. Moore as comprising three varieties. Two varieties have ruminate endosperms, but *P. longepetiolata* var. *cuatrecasasii* (H. E. Moore) Henderson & Galeano is said to have a homogeneous endosperm.

Do these examples sound the death knell for the usefulness of endosperm condition in the classification of palms? Not at all; endosperm condition will continue to be an important and useful character. It is a helpful 'spot-character' (van Balgooy 1997) and an easily-observed character for use in keys. Moreover, more detailed study of endosperm condition may reveal previously overlooked characters that may prove useful in phylogenetic classifications. Nevertheless, the taxonomic history of *Ptychococcus paradoxus* is a cautionary tale. The paradox of *P. paradoxus* lies in the variability of its endosperm, which has been confounding botanists for over a century.

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Morphological diversity of the genus *Licuala* (Palmae)

L.G. Saw, J. Dransfield and D.M. Keith-Lucas

Abstract

L.G. Saw[1]*, J. Dransfield*[2] *& D.M. Keith-Lucas*[3] *([1]Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia, Email: sawlg@frim.gov.my; [2]Royal Botanic Gardens Kew, Kew, Surrey TW9 6AB, UK; [3]School of Plant Sciences, University of Reading, Whiteknights, PO Box 221, Reading, Berkshire RG6 6AS, UK) 2003. Morphological diversity of the genus* Licuala (Palmae). Telopea *10(1): 187–206*. There are about 141 described species of *Licuala*. Structurally, the genus has very consistent vegetative and fertile characters. As the genus undergoes revision, it is becoming clear that it contains great morphological variation within the strict vegetative and reproductive character constraints found in the genus. This paper describes the variation found in the genus and its significance in taxon delimitation.

Introduction

There are about 141 species of *Licuala*, distributed mainly in the Malesian region. High species diversities are centred on two main areas, one within the Sunda Shelf in Malaya and Borneo, the other centred on the Sahul Shelf on the island of New Guinea. *Licuala* is a distinct genus with well-defined characters (Uhl & Dransfield 1987). In the process of revising the genus, it has became apparent that the genus contains wide morphological variation within a rather strict set of morphological themes. It is important to understand this variation to define the taxa better. The paper was written mainly from detailed study of herbarium specimens of species found in Thailand, Malaya, Sumatra, Java, Borneo and New Guinea. The first author has also made extensive field observations on the variation of *Licuala* in Malaya (Saw 1997) and to some extent in Borneo.

Habit

The absence of any secondary vascular and mechanical tissue in palms has largely limited the growth habit of palms. As a result, palms tend to have fixed crown sizes, and aerial branching is rare (Tomlinson 1990). In general, vegetative branching is largely restricted to the base of the original trunk. The crown restriction has also produced plants displaying very simple architectural models. Palms on the whole are represented by only four (out of the total of 23) architectural models, as defined by Hallé et al. (1978). Nevertheless, there is still a surprising diversity of growth form in the family when consideration is given to the size, nature of the growth axis and basic branching patterns. These reflect the varied ecological adaptations found in the members of the family. Dransfield (1978) discussed the different growth forms found in the family and divided them into four basic categories.

1. Tree palms (palms that reach the main forest canopy).
2. Shrub palms (low palms found in the forest undergrowth).

3. Acaulescent palms (palms without a visible trunk or caudex, the true stem either being subterranean or, if aerial, very short).
4. Climbing palms (palms with narrow stems and long internodes which are not self supporting, but climb by grapnel hooks).

Licuala displays indeterminate growth and flowering is interfoliar, i.e. it has a pleonanthic habit. Following the architectural models of Hallé et al. (1978), *Licuala* manifests two models: Corner's model for solitary members and Tomlinson's model for clustering members. These models are, however, not very descriptive of the growth habits found in these palms. Some species for example can exhibit both models in different populations. *Licuala modesta* Becc. on the hill at Bukit Larut, Peninsular Malaysia, for example, expresses Tomlinson's model towards the summit of the hill but is solitary, i.e. exhibiting Corner's model, near the foot of the hill. In many clustering species, there is a transition from solitary forms in juveniles to clustered forms in adults; the architectural model thus changing. If size and the nature of clustering habit is taken into consideration, there is indeed a surprising range of growth habits in *Licuala*, which is not reflected by the definition of the tree architectural models, factors which these models do not account for. In Dransfield's categories, *Licuala* exhibits the first three groups listed above, particularly categories 2 and 3.

Members of this genus range from trees to shrubs to acaulescent palms, but none is climbing. They are small to medium palms. All are understory plants of the rainforest. The smallest amongst them, such as, *L. triphylla* Griff. or *L. kiahii* Furtado, are no more than a metre tall, while the largest are never large emergent trees but may be over 10 metres tall and can dominate the lower part of the forest canopy, e.g. *L. ramsayi* Domin of Australia (Dowe 1992).

Licuala species may be solitary or clustering, with erect aerial stems ('stemmed') or acaulescent. There is, therefore, a possible combination of four basic themes in habits of *Licuala*. In general, these combinations of habits are rather taxon specific but, as discussed above, some taxa express overlapping forms. Within these basic themes, there are some degrees of variation that can be quite consistent within taxa. These habits are good field characters in determining taxa. Figure 1 gives a diagrammatic representation of the habits seen in *Licuala*.

1. Stemmed and solitary (Figure 1a)

In the simplest form, the plant is solitary and with an erect stem. In Malaya and Borneo, it is one of the commoner habits, and species with this habit include small to larger species. Smallest among them, such as *L. scortechinii* Becc. and *L. cameronensis* L.G.Saw, have stems no more than a metre tall. The larger species, such as *L. peltata* Roxb. ex Buch.-Ham., *L. longipes* Griff., *L. valida* Becc. and *L. fractiflexa* L.G.Saw are among the largest species of *Licuala* in Malaya and Borneo.

2. Stemmed, clustering with one to a few dominant shoots (Figure 1b)

Species with this habit have one to a few dominant shoots and a number of suckers at the base. Generally, the dominance of the main shoots is obvious in the field and it is only these that are fertile. Shoot dominance is probably the result of suppression of the basal suckers, as long as the dominant shoots are functioning. In some species, for example, *L. ridleyana* Becc., *L. malajana* Becc. and *L. terengganuensis* L.G.Saw, only 1–2 shoots remain dominant. In the summit population of *L. modesta* at Bukit Larut, there is a tendency for individual clumps to form clusters with a larger number of co-dominant shoots.

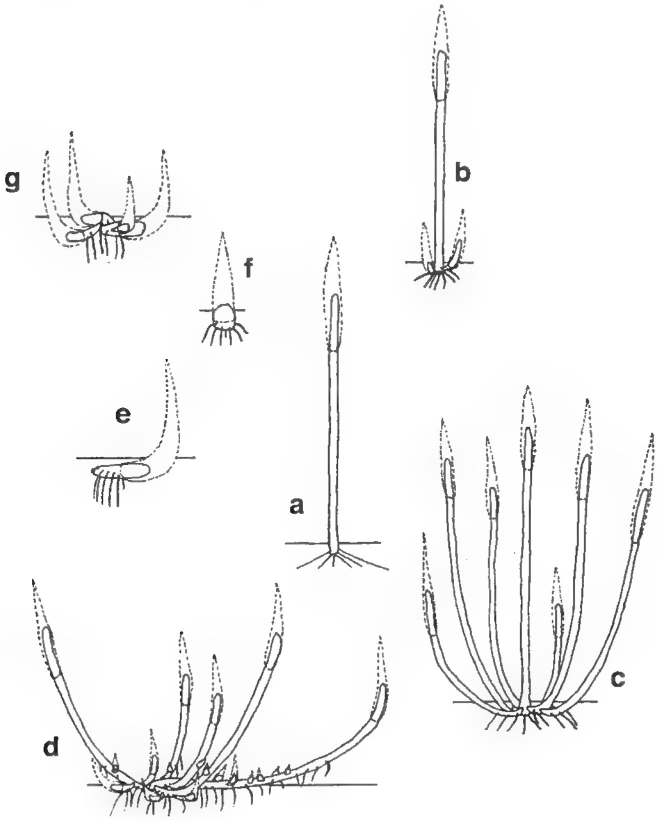

Fig. 1. A diagrammatic representation of the growth habits of *Licuala* species (solid line represents stem, broken line represents crown shaft). **a,** Stemmed and solitary. **b,** Stemmed, clustering with one to a few dominant shoots. **c,** Stemmed, clustered with ± equal erect shoots. **d,** Stemmed, clustered with ± decumbent shoots. **e,** Acaulescent and solitary, stem plagiotropic and **f,** with orthotropic stem. **g,** Acaulescent and clustered.

Species that are stemmed and solitary, as described above, will occasionally also produce small suckers at the base. This is suspected to be stress-related; for example, in Pasoh Forest Reserve, Malaysia, individuals of *L. longipes* that have crowns damaged by pigs, were seen to produce suckers. However, these suckers do not grow to a large size as seen in this group.

3. Stemmed, clustered with subequal erect shoots (Figure 1c)

This is an extension of the above category but instead of a distinct dominance of a few shoots, there is a cluster of subequal shoots. Here, suckering occurs early in the life of the young plant and its ramets grow at about the same rate as the mother shoot. Species in this group form large clusters. It is difficult to locate the mother shoot in older clumps. Reproductive structures are found on most of the ramets that are large enough. Only two species are known in this group, *L. spinosa* Wurmb and *L. paludosa* Griff.

4. Stemmed, clustered with about equal decumbent shoots (Figure 1d)

Very similar to category 3 but here the stems are erect to spreading and often decumbent, producing a 'colonial' habit. The stems are thin and nodes are wide apart, suggesting a rather fast growth rate. As the stem grows from an initial erect position, the stem gradually reclines onto the ground under its own weight, with its apex constantly curving up at its tip. In very old shoots, the stem may be of a considerable length, prostrate on the ground. In the former two groups with clustered habits, the suckers are formed quite close to the base of the stems. In this group, however, while there are suckers close to the base of the stem, suckers are also formed along the stems away from the base. This occurs mainly in older prostrate stems that are in contact with the ground. Adventitious roots sprout along these stems. It is not a common habit. In Malaya, it is only observed in *L. sallehana* L.G.Saw; in Kalimantan, Borneo, *L. hallieriana* Becc. has been reported to exhibit this habit. *Licuala reptans* Becc., also from Kalimantan, has been described with decumbent habit but it is solitary.

5. Acaulescent and solitary (Figures 1e & f)

Here the stem is 'unseen'. The acaulescent habit in *Licuala* is of the plagiotropic adult form as defined by Tomlinson (1990). The apical axis of the palm is oblique with unequal growth of the leaf bases (Figure 1e). This keeps the stem underground. In younger plants, the stems tend to be orthotropic (Figure 1f) but as the stem becomes more prominent, the axis becomes plagiotropic. Together with this growth habit, the nodes are also very close together, thus making very little stem height increment with every new leaf, even when the growth is orthotropic. Occasionally, as with the stemmed and solitary form, suckers may form when the plant is stressed, e.g. damaged by animals. This is another common habit in *Licuala* of Malaya. Most species with this habit are very small, e.g. *L. triphylla* Griff., *L. kiahii* Furtado, *L. tenuissima* L.G.Saw, *L. kamarudinii* L.G.Saw and *L. khoonmengii* L.G.Saw. Only one species that is considered large by *Licuala* standards has this habit, viz.: *Licuala ferruginea* Becc.

6. Acaulescent and clustered (Figure 1g)

Similar in habit to category 5 but the plant clusters. The plagiotropic growth habit is also maintained in the suckers, making the shoots of the ramets subterranean. The subsequent ramets will continue to produce further suckers. This mode of growth can result in a rather large clump of shoots from a single mother plant. Only three Malayan species have this habit, namely, *L. ahlidurii* L.G.Saw, *L. bayana* L.G.Saw and *L. lanuginosa* Ridl..

In *Raphia hookeri* G.Mann & H.Wendl. (Profizi 1985) and *Oenocarpus mapora* Karst. (De Steven 1989), suckers are reported to occur only in the young axis of the plant. Both these species are rather large clustering palms. Such suckers and in some cases bulbil formation are seen in mature reproductive stems of *Licuala*. Sucker production in *Licuala* may not be totally confined to young axes as in the case of species of *Raphia* and *Oenocarpus* mentioned above.

Tomlinson (1990) defines the colonial habit in palms, as a habit in which the palm initially has suckers that are horizontal and usually subterranean for some distance before turning erect, as distinct from the clustered habit. The axes are dimorphic as the horizontal portions bear only scale leaves and are non-flowering, whereas the erect portions bear foliage leaves and distally, inflorescence units. This definition is, of course, easily applicable to plants that show a distinct stoloniferous habit, a habit not observed in *Licuala*. The dimorphic axes, however, exist in at least the growth forms of acaulescent and clustering species and possibly also in the clustered and equal-stemmed ones. In these last two categories, the axillary suckers grow horizontally for a very short distance from the mother shoot before forming the aerial shoots. Whether this short stem can be defined as a stolon is of course open to debate. In this instance the stem remains subterranean. True scale leaves are lacking but in the short-stemmed phase of the axillary suckers, the leaves are much reduced to be almost scale-like, the earliest-formed ones lacking laminae while the older ones have juvenile-like laminae, Dransfield (1978) reported that *L. paludosa* forms open colonies in Malesian peat swamp forest. They however do produce long stolons.

The Leaf

The plicate and usually split leaf is the most distinctive organ of the palm family and more than any other structure links palms together (Dransfield et al. 1990). The use of the characters of leaf form and the nature of the leaf splits and their relevance to the classification of palms has been the subject of much discussion (e.g. Saakov 1954, Satake 1962, and more recently Dransfield & Uhl 1986, Uhl & Dransfield 1987, Dransfield et al. 1990). The subfamily *Coryphoideae* has a wider range of leaf form than any of the six other palm subfamilies. In the subtribe *Livistoninae*, the leaves are usually palmate or costapalmate, and there are two very distinctive leaf forms which are unknown elsewhere in *Coryphoideae*, the diamond-shaped leaf of *Johannesteijsmannia* and some species of *Licuala*, and the wedge-shaped segments with 'reduplicate' margins found in almost all species of *Licuala* (Uhl & Dransfield 1987).

The leaf sheath of *Licuala* does not abscise and at maturity its original tubular nature is often no longer obvious; a ligule is absent. This corresponds to the *Trachycarpus* type of sheath, according to Tomlinson's (1962) definition of leaf sheath types, where the ventral leaf sheath tissue persists as a fibrous mat. In immature leaves, a pair of auricles enclose the younger developing leaves. The auricles in most cases are rather fragile and may disintegrate in mature leaves. In some species, the auricles are not noticeable in the crown as they disintegrate very early while in others such as *L. glabra*, they may persist for a while in the crown. However, these too soon break away. The ventral leaf sheath of *Licuala* consists of two broad categories of fibre types. They are rather constant in each species. In a number of smaller species, the ventral leaf sheath breaks up finely into a network of fine fibres consisting of mainly individual strands; examples are *L. sallehana* and *L. kamarudinii*. In most of the larger species, the ventral leaf sheath breaks up into a network of rather coarse fibres consisting of bundles of flat tape-like strands, e.g. *L. glabra* Griff., *L. paludosa*, *L. ridleyana*.

The petiole is variable in length. In very small species, it can be less than 10 cm long, but in larger species petioles can exceed 3 m long. The length in any individual often depends on the vigour of the plant and on the amount of shade received and hence the amount of etiolation. The petiole is convex abaxially, but the adaxial side is concave or channelled towards the base, flattened to slightly convex towards the apex. It is normally covered with deciduous scales on the adaxial surface, but glabrous abaxially. On older fronds, the scales may drop off leaving behind black to dark brown dot or dash-like scars on the surface. The scales do not seem to be very useful taxonomically as they are variable. The petiole will dry with distinctive colours in different shades of brown. The colours are quite useful in distinguishing species. The petioles of most species dry a light bleached or greenish brown, e.g. *L. acutifida* Mart., *L. spinosa*, *L. ferruginea* and *L. modesta*. Petioles of *L. terengganuensis*, *L. fractiflexa*, *L. bintuluensis* Becc. and *L. longipes*, however, dry a very distinctive, dark reddish brown.

The petioles are normally armed with spines along the lateral margins. Spines in palms have a number of morphological origins but functionally they serve as protective organs (Tomlinson 1962, Fisher 1981, Tomlinson 1990). The spines on the lateral margins of the petioles in *Licuala* are typified as emergences and are not associated with any organs. This feature is very common among the fan-leafed Coryphoid palms (Tomlinson 1990). They are normally distributed along the margins of the lower part of the petiole. At the petiole base, they continue beyond but outside the leaf sheath. In *L. spinosa* and *L. peltata*, the spines are distributed along the whole length of the petiole. In *L. moyseyi* Furtado, the petiole is unarmed. Spines may be large, some to well over 1.5 cm long, but in most species they are less than 1 cm long. They are generally larger near the base of the petiole and become smaller distally. They are variously curved but generally curving towards the base; they may be regularly or irregularly sized and spaced. They can be quite variable in some species, e.g. *L. malajana*, while in others the spines can be quite distinctive, e.g. *L. paludosa* has distinctive small black spines found on the proximal half of the petiolar margins.

The leaf blades are the most conspicuous and distinctive organs of *Licuala*. They are palmate and in most species orbicular. The hastula is well developed on the adaxial surface but absent on the abaxial surface. It is usually triangular and is not useful in distinguishing taxa at any level. The blade of *Licuala* is basically induplicate as in most members of Coryphoideae. However, unique to *Licuala*, superimposed on the induplicate splits along the outer margin, are the more obvious abaxial lateral splits (Figure 2). These abaxial lateral splits divide the blade right to its insertion into compound or very rarely single-fold reduplicate segments (Dransfield et al. 1990) (e.g. in *L. bidentata* Becc. and in the Gunong Ledang population of *L. glabra* (Saw 1997)). These abaxial splits on the lateral margins of segments occur very early in the development of the leaf, while the induplicate splits on the outer margin, usual in the subfamily, occur much later (Dransfield 1970). The abaxial lateral splitting appears to be a specialised development, at least in *Licuala*. The abaxial lateral splits are unusual in being the only ones in the subfamily to reach the insertion of the blade, except in the central divisions.

Most species have segmented leaves. The number of segments in the leaf is usually variable and in most cases is not very useful in species identification. Similarly, the number of veins or costae in the segments is constant in some species, but in other species is quite variable. Segments range from single folds to many folds. Overall, segmentation is rather constant within populations but can vary between populations of the same species.

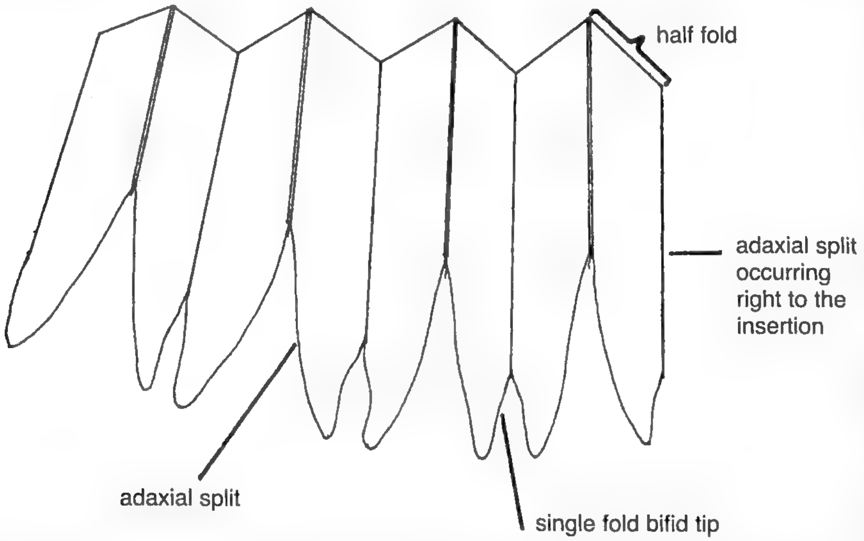

Fig. 2. Induplicate fold of *Licuala* with the abaxial splits (redrawn from Uhl & Dransfield (1987)).

Leaf forms found in *Licuala* are given in Figure 3. The eophyll of *Licuala* is simple and strap-like (Figure 3a). Its apex is truncate to rounded. This type corresponds to Tomlinson's (1960) 'Class 2' type of induplicate-leafed palms. This condition is common among the Coryphoid palms. Tomlinson (1960) further attempted to explain the phylogenetic significance of the development of the seedling series and the subsequent development of the adult leaves. In the following paragraphs, we have attempted to correlate the different leaf forms of *Licuala* with their development.

The juvenile form, lanceolate or narrowly cuneate-based and undivided, is retained in the adult leaves (neoteny) (Figure 3b) of *L. sallehana* var. *sallehana*. In *L. thoana* L.G.Saw & J.Dransfield, the juvenile-leafed form is also found in young adult reproductive individuals. However, in older individuals of this species, the blade may be segmented, generally with about two, to sometimes four, very narrow lateral segments. The mid-segment remains spathulate, and is much larger than the lateral one, very much like the juvenile-leafed form of the young adults.

If one follows the ontogeny of segmented leaves of *Licuala* species, the seedling leaves are replaced by larger and similarly shaped juvenile leaves; subsequently segmented leaves are produced. As the plant builds up its base, the older leaves become larger and the number of segments also increases. Unlike *L. thoana*, segmentation of the leaf occurs quite early, even in very young juveniles. This increment continues until the maximum number is attained for that particular species. Most species of *Licuala* in Malaya have this leaf type (Figure 3c). The lateral margin of the segments of most species is straight but in a few species, they can be curved (Figure 3i).

In most species, the central segment is prominent; it is larger than the lateral segments, while in others they are about the same size. Rarely are the mid-segments much smaller than the lateral segments (so far, only known in *L. mattanensis* Becc. var. *paucisecta* Becc. from Borneo). The central segment is very often undivided and sessile. It, however, may be petiolulate (Figure 3d). This character is not consistent in Malayan *Licuala*. It is quite common in *L. triphylla*, rare in *L. longipes*, *L. spinosa* and *L. malajana*. However, in Borneo, *L. petiolulata* consistently has a petiolulate mid-segment. In both *L. triphylla* and *L. petiolulata*, there is sometimes a further extension of the mid-segment to include one or two leaflets giving a pinnate leaf arrangement for the central 2 or 3 leaflets (Figure 3e). In describing *Licuala stenophylla* Hodel, Hodel (1997) included a form of *L. triphylla* with pinnate mid-segments (Barfod & Saw, in press). This variation, as mentioned previously, is not consistent and cannot be used as a singular character to define a taxon. The mid-segment can also be divided. In most instances, it is bifid (Figure 3f), a situation more common than normally realized. It occurs for example, in *L. glabra* var. *selangorensis*, *L. peltata* and *L. paludosa*, etc. While *L. glabra* (form found in Bukit Bauk, Terengganu, Malaysia (Saw 1997)) has a mid-segment that is normally bifid, is also sometimes further split from one of the inner sides of the bifid segment to include another segment giving a trifid segmentation. This differs from the pinnate segmentation described earlier in *L. triphylla* and *L. petiolulata*. In the Bukit Bauk population of *L. glabra*, the inner split is about the same size as the other adjacent segments of the central segmentation. In some specimens of *L. collina* L.G.Saw (ined.), the inner splits are much smaller than the adjacent segments (Figure 3h), giving it an attractive tail-like segmentation. This smaller central tail-like segmentation is again different from the central segmentation described earlier in *L. mattanensis* var. *paucisecta*. A further modification in this leaf form is the loss of the lateral segments leaving only the bifid mid-segment (Figure 3g). This unusual segmentation is also found again in some individuals of *L. collina*.

The only Malayan species with simple and orbicular leaves is *L. peltata* var. *sumawongii* L.G.Saw (Figure 3j). The other frequently cultivated species with this leaf form is *L. grandis* H. Wendl. from Vanuatu. In Borneo, at least four taxa are known to have orbicular or near orbicular fronds, *L. orbicularis* Becc., *L. cordata* Becc., *L. micholitzi* Ridl.

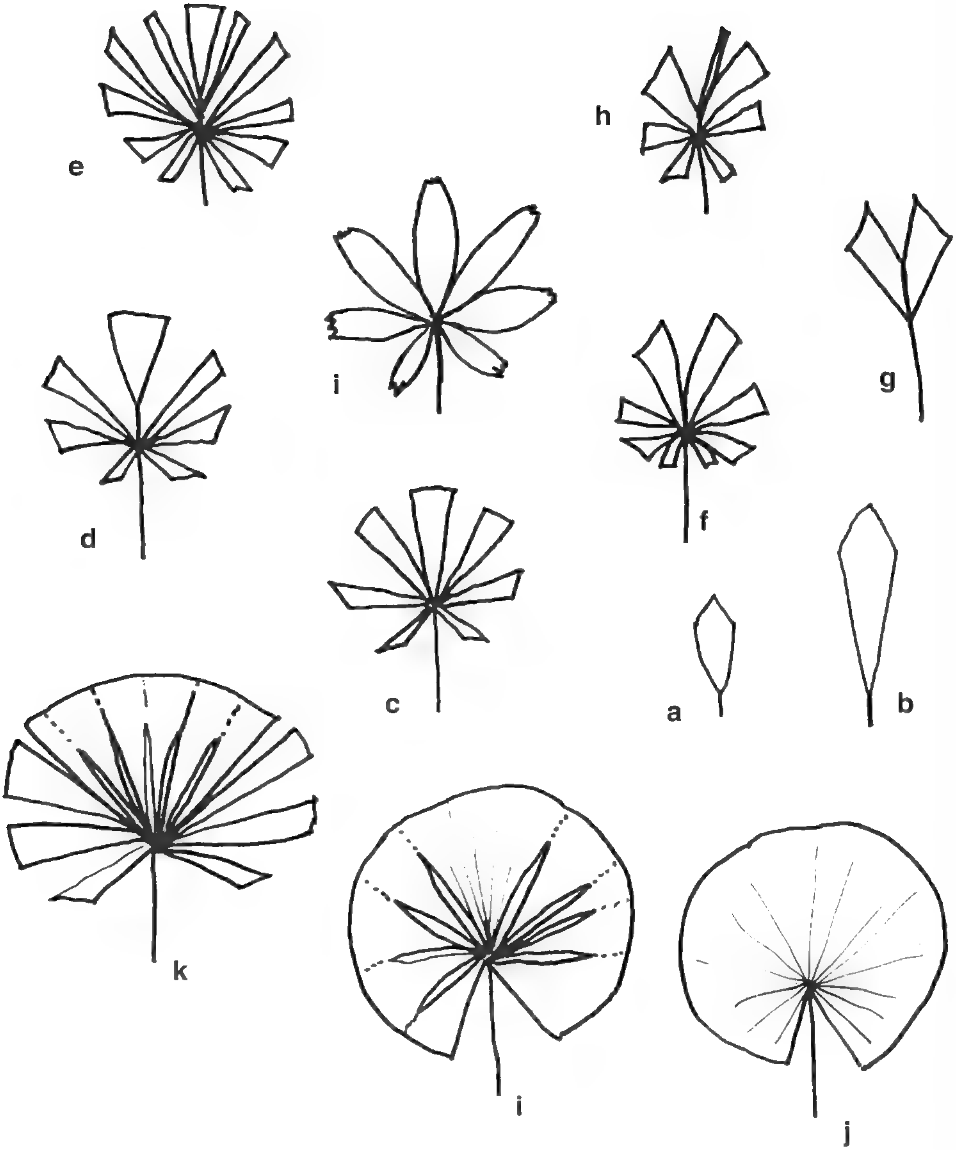

Fig. 3. Leaf types of *Licuala* species. **a,** Eophyll. **b,** Adult juvenile type or neoteny (juvenile leaf form retained in adult plants). **c.** Segmented adult leaf type. **d** ,Segmented type with petiolulate mid-segment. **e,** Segmented type with pinnate mid-segment. **f,** Segmented type with bifid mid-segment. **g,** Segmented type with bifid mid-segment with loss of lateral segments. **h,** Segmented with bifid mid-segment including a further split. **i,** Segments with curved lateral sides. **j,** Entire. **k,** Fronds with mid-segment perforated with windows. **l,** Entire leaf with windows. (See text for explanation).

var. *micholitzi* and *L. yiiana* L.G.Saw (ined.). We believe, the development of the simple leaf in this type is quite distinct from the retention of the juvenile leaf type found in *L. sallehana* var. *sallehana*. The simple leaf arises from the loss of lateral splits from two possible processes.

The suggestion for this is found in two phenomena observed in the leaves of some *Licuala* species. The first author has seen juveniles of *L. peltata* var. *sumawongii* with lateral splits that do not reach the insertion of the blade. It is known that the lateral splits occur very early in the leaf development (Dransfield 1970). Therefore, in these individuals, the incomplete splits must be part of the early development of the leaves, indicating a reversion to its ancestral form of segmented leaves as juveniles. They, however, will subsequently grow into adults with undivided leaves by the loss of the splits. In *Licuala ashtonii* L.G.Saw (ined.), a different form of splitting occurs, the margin remains entire (i.e. not broken into segments) but within the blade, splits occur from the hastula to near the edge of the frond, forming window-like splits (e.g. *P.S. Ashton* S 18263) (Figure 3l). Similar splits in *Licuala* fronds have also been observed in *L. sabahana* L.G.Saw (ined.) and the form of *L. valida* Becc. from Sepilok, Sabah (*L.G. Saw* FRI 37691 & FRI 37692) and observed on a juvenile plant of *L. ramsayi* in Singapore Botanic Gardens (first author's observation) (Figure 3k). In these last examples, however, the windows are restricted to the mid-segments, these species have segmented fronds.

The Inflorescence

Although palm inflorescences can be quite elaborate and often massive, appearing very complicated, they are relatively easy to describe because they usually conform to very basic patterns. They are largely made up of repeating units, each unit with the same construction, and with gradual but progressive changes along any given axis (Tomlinson 1990). These have been well described and discussed by a number of authors (e.g. Tomlinson & Moore 1968, Moore & Uhl 1982, Uhl & Dransfield 1987, Tomlinson 1990).

Licuala overall shows a surprising degree of variation in its reproductive characters. Although the vegetative characters are sometimes rather variable within taxa and difficult to use, the reproductive characters are numerous and remain quite consistent in the different species. It is even possible to determine species with old infructescences. This is quite difficult with vegetative characters.

Inflorescences of *Licuala*, like those of the rest of the Coryphoid palms show a very simple construction (Uhl & Dransfield 1987). The size is variable: in small species, they may be less than 15 cm long while in large species, the inflorescence can be well over 3 m long. The inflorescence is interfoliar, consisting of a main axis and branches to two, or very rarely three orders. Figure 4 gives an example of an inflorescence of *Licuala*.

The inflorescence is displayed variously. Most species have their inflorescences displayed within the crown – that is, they are shorter than the leaves. In others, the inflorescences are much longer than the leaves, for example in *L. spinosa* and *L. paludosa*. The inflorescence is also variously positioned. This is sometimes not very obvious on herbarium specimens. The character can be quite useful in species identification, as it is quite consistent within species. Most species have spreading inflorescences. In *L. lanuginosa* and *L. ahlidurii*, the inflorescences are erect. *Licuala cameronensis* and *L. mustapana* L.G.Saw have spreading and pendulous inflorescences. The former has a very thin rachis and the inflorescence hangs over as it grows. The latter has rather long spreading inflorescences which also hang over under their own weight as they grow.

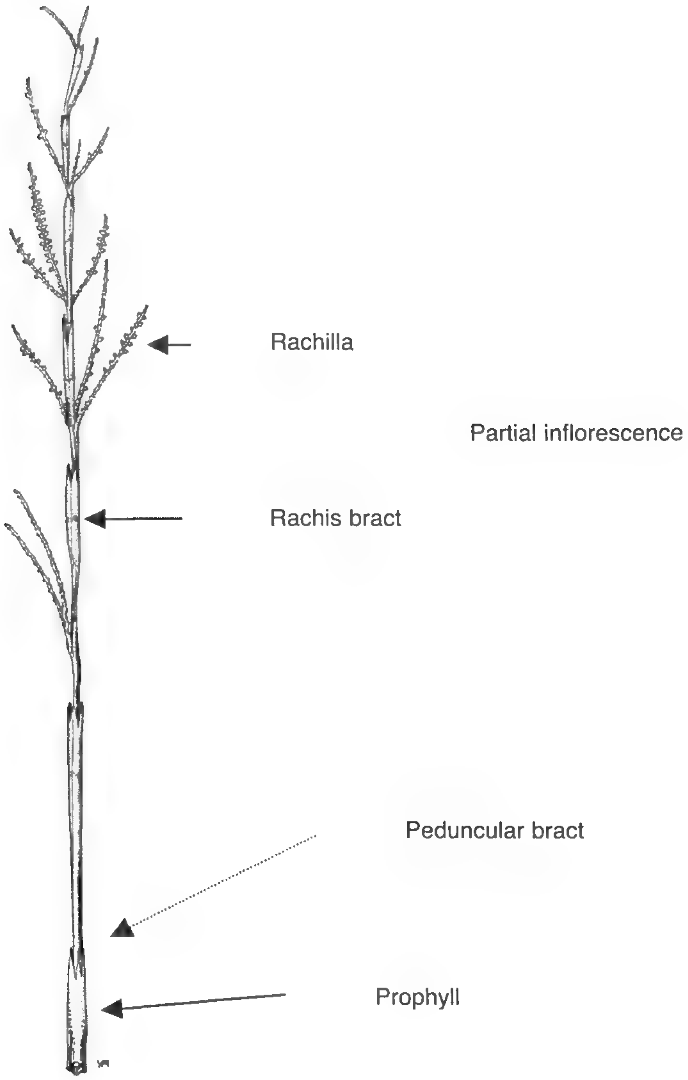

Fig.4. Inflorescence structure of *Licuala*. In this example, the species *L. egregia* lacks peduncular bract, here marked in dotted arrow. (Drawing from Saw, 1997 of *L. egregia* L.G.Saw).

The first bract of the inflorescence is a tubular, two-keeled prophyll. The prophyll is often not seen in the crown, as it usually remains hidden by the subtending foliage leaf. A number of tubular peduncular bracts may further sheath the peduncle before the first inflorescence branch occurs. In some species peduncular bracts may be absent. The number or absence of peduncular bracts appears to be quite consistent within species. However, very often this is not properly noted in herbarium specimens or when collected, they are not collected properly. Each primary branch is subtended by a rachis bract. The rachis bracts are also tubular. In some species, the rachis bract is reduced and is not tubular, but narrowly triangular in shape, e.g. *L. scortechinii* Becc. and *L. kingiana* Becc. In most species, these bracts are cylindrical, constricted abruptly near their bases, and are rather tightly sheathing. In other species, such as *L. mirabilis* Furtado, the bracts are inflated, funnel-shaped and loosely sheathing. The mouths of the rachis bracts split obliquely and widely to one side while in others, they split only at the apex quite perpendicular to the axis of the rachis. The mouth can be fibrous, breaking open into untidy strands of fibres. In *Licuala ferruginea* Becc., for example, the bracts have this type of mouth. In most other species, the mouths are neatly irregularly split, giving an impression of being toothed.

The rachis axis is rather straight and rigid in a number of species, while in others it is flexible. In a few other species, the rachis axis is sinuous, bending at the junctions of the primary branches, e.g. *L. mirabilis*.

The first order branch complement subtended by the rachis bract is sometimes referred to as the partial inflorescence. This term is useful to describe the basic structure of the *Licuala* inflorescence. Based upon the arrangement of the partial inflorescences, four major inflorescence types are recognized (Figure 5). The simplest, corresponding to most species of Coryphoid palms is the type with a few superposed (i.e. one above another) branched partial inflorescences (Type 1 of Figure 5). In this type, the partial inflorescences can be highly branched, e.g. *L. patens* Ridl., *L. longipes* Griff. ex Mart. and *L. fractiflexa* L.G.Saw, while in others they only have a few branches, e.g. *L. ferruginea*, *L. malajana*, *L. tenuissima*. Based on Saw (1997) and Saw (in prep.), this inflorescence type is found in about 46% of the species from Malaya and Borneo (Table 1). In reducing the number of rachillae in each partial inflorescence to one (spicate), we have the Type 2 inflorescence. This inflorescence type is quite common among Malayan and Bornean *Licuala* species. A further variant of this inflorescence type is found in *L. punctulata* Burret; here it appears that the proximal two spicate partial inflorescences have merged into a single partial inflorescence giving the proximal partial inflorescence a bifurcating branch with the loss of one rachis bract (see figure 5, Type 2a). So far, this condition is only seen in this species. In both Types 1 and 2 inflorescences, there can be reduction in the number of peduncular bracts from a few to none at all. These numbers, as mentioned previously, are quite consistent within species and if properly recorded can be useful in distinguishing species.

Table 1. Comparison of inflorescence types found in Malaya and Borneo (data extracted from Saw (1997) and Saw (in prep.)).

Inflorescence type	Region		Common to both regions	Total number of species	%
	Malaya	Borneo			
1	20	22	4	38	46.34
2	19	12	0	32	37.80
3	1 (+1*)	6 (+2*)	0	7 (+3*)	8.54
4	1	5	0	5	7.32
Total	41	~46	4	82	100

* Overlapping inflorescence types, see text for explanation.

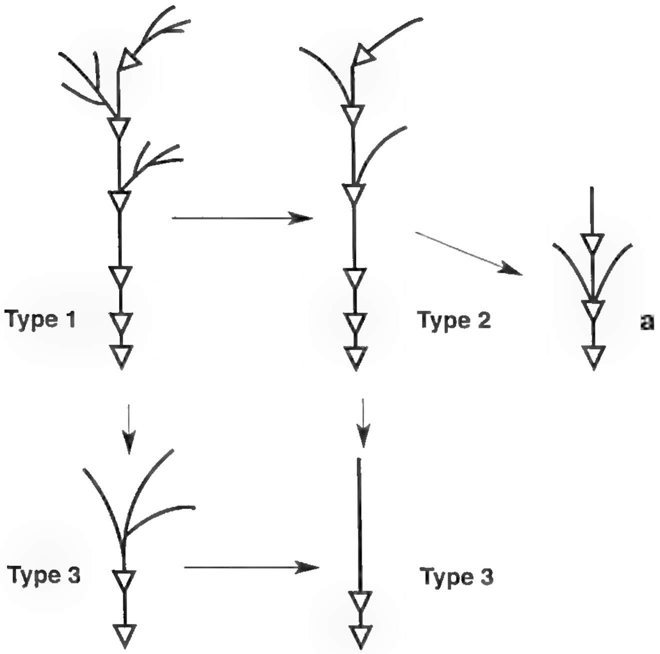

Fig. 5. Diagrammatic presentation of inflorescence types found in *Licuala*, triangles represent bracts. Possible trends of reduction of organs indicated by arrows. See text for further details.

When the inflorescence is reduced to one partial inflorescence, two inflorescence types are possible: Type 3, where the partial inflorescence is branched; and Type 4, where the inflorescence is a spike. Both Types 3 and 4 inflorescences are not very common in *Licuala*. In Malaya, only *Licuala scortechinii* has strictly a Type 3 inflorescence. There are eight other species in Borneo with this inflorescence type (Table 1). *Licuala kingiana*, *L. mattanensis* Becc. and *L. collina* L.G.Saw (ined.) (former from Malaya and the latter two from Borneo) have spicate inflorescences, i.e. Type 4 inflorescences, but sometimes these branch into two rachillae, i.e. Type 3 inflorescences. However, *Licuala spicata* Becc. and *L. elliptica* L.G.Saw (ined.) in Borneo consistently have spicate inflorescences. Although the typification of inflorescences is useful in understanding likely evolutionary processes in the genus, these types, as already obvious in the earlier discussions, are not mutually exclusive within particular species. However, in the majority of species, they are constant, making this character very useful in species identification. Species of *Licuala* in both Borneo and Malaya with Types 3 or 4 inflorescences all lack peduncular bracts. Further reduction in inflorescence bracts is seen in a number of Bornean species (e.g. *L. micholitzii* Ridl., *L. yiiana* L.G.Saw (ined.), *L. collina* L.G.Saw (ined.)) where the inflorescence bears only a prophyll and no other bract on the rachis. At least six species in Borneo have this condition.

Table 1 also indicates a trend of reduction in inflorescence parts with corresponding lower species numbers.

The rachilla takes on various forms in different species. It can be rather wiry, commonly among the smaller species. In other species, the rachilla is wiry when immature, but will become swollen and thick as the inflorescence matures. The rachillae in most species are not ornamented. In some, they are ornamented with pits with flowers, regular ridges between the flowers, tubercles supporting flowers and short floral stalks (Figure 6). In one species, *L. whitmorei* L.G.Saw, the rachilla surface is regularly cracked when dried (Saw 1997). The rachilla on the whole may be glabrous (a rather uncommon condition, e.g. in *L. glabra*) or it may be hairy (varying in density, length and colour). Each flower is subtended by a bracteole and a floral bract, although sometimes only one of these is obvious. The rachilla characters are found to be quite useful in differentiating taxa.

We have differentiated the pedicelliform base of the flower and the floral stalk which carries the flower. The term pedicel is deliberately not used because it might cause confusion by its general usage. The floral stalk, being part of the rachilla is defined as the stalk just below the articulation with the flower (Figure 6e). The pedicelliform base, being part of the calyx, fused to the receptacle, is the part above the articulation of the flower with the rachilla. It is important to differentiate these because the stalk below the flower of some species (e.g. in some forms of *L. glabra*) consists of these two elements, while in others consists of only one element but of different origin (e.g. *L. acutifida* has a floral stalk but its calyx is not pedicelliform).

The flowers are arranged spirally all along the rachilla. In most species, the flowers are very closely packed, whereas in others they are arranged loosely on the rachilla. The flowers are strictly solitary in a number of species (Figure 7a), while in others, they are in groups near the base of the rachilla but are solitary distally. In a number of species, the cincinni are on branched floral stalks. Each cincinnus can have up to seven flowers arising from a single branched stalk, for example in *L. sallehana* (Figures 7b). In *L. tenuissima*, the flowers are also in groups but they are sessile (Figure 7c). Flowers mature about the same time in inflorescences of most species and open within a short period of each other. This is rather obvious in the herbarium specimens, as they are all about the same size and at about the same stage of development. In a number of others, common only in species that have flowers in groups, different stages of floral development are found within each cincinnus. This gives an inflorescence a more staggered period of flowering (Figure 7c).

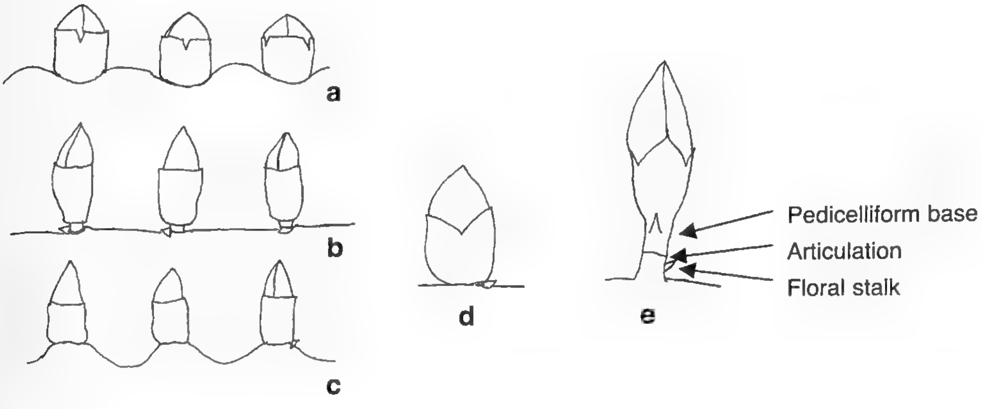

Fig. 6. Ornamentation on rachilla surfaces and floral types. **a,** Flowers in pits. **b,** Surface unornamented. **c,** Flowers on tubercles. **d,** Sessile flower. **e,** Stalked flower showing pedicelliform base, articulation and floral stalk.

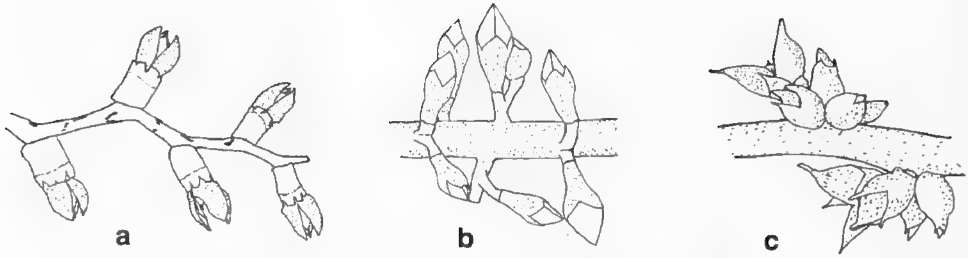

Fig. 7. Cincinni of *Licuala*. **a,** Flowers singly. **b,** Flowers in groups of 1-few on floral stalks. **c,** Flowers in groups of 3 or more, sessile.

The Flowers

Palm flowers with the basic trimerous construction are similar to those of many monocotyledonous families. Perfect (hermaphroditic) flowers which are regularly trimerous and with three separate carpels are considered to represent the ancestral condition (Tomlinson 1990). This construction is found in *Thrinacinae* and has been considered by Moore (1973), and Moore and Uhl (1982) as evidence that the *Coryphoideae* are closest to ancestral palms. These conclusions will need to be reconsidered in the light of recent phylogenetic analyses. This floral construction is also considered to be the least specialized among the palms (Uhl and Dransfield 1987). In *Livistoninae,* however, the carpels are free basally but united at the style. The fusion of the style probably represents a derived state from free carpels of the *Thrinacinae.* While the flowers of *Licuala* are of simple construction, there is a surprising array of variation in the flower, even within the strict trimerous construction, i.e. three sepals, three petals, six stamens (in two whorls of three), and three carpels.

Licuala in general has hermaphroditic flowers. Dioecy is very rare in *Licuala,* but is known in at least one, and suspected in a few other species. *Licuala gracilis* Blume from west Java has some plants with only female flowers; i.e. they have a gynoecium and staminodes but no anthers. In the same population, other individuals have what seem to be hermaphroditic flowers (collection *J. Dransfield* 1433 in Kew). One of us (JD) has observed that these individuals do not produce fruits and are functionally male plants. *Licuala hexasepala* Gagnep. from Vietnam also has a similar flower differentiation. For example, in the collections made by M. Newman 177 is female, while 179 is hermaphroditic (both numbers are in Kew). The ovary of the hermaphroditic flowers is similar to those of the female flowers. Whether the hermaphroditic flowers are also functional males as in *L. gracilis,* needs to be confirmed by field observation. There is another species with only female flowers from South China (*C.F. Wei* 123257). This new species, planted in South China Botanical Garden, was introduced from Guangxi province. It appears that a similar syndrome of dioecy has occurred in a few species of *Licuala.* We further suspect that there may be more species with this syndrome when a fuller survey of the genus is carried out.

There are two main flower tissue types found in *Licuala.* They are quite easy to recognise in dried specimens. Species with rather succulent or fleshy flowers when dried will shrink to some extent and the calyx and corolla become membranous with the calyces often loosely enclosing the corolla. These flowers also often dry dark brown to black. The second flower type is lignified. These flowers dry various shades of brown, often light brown. On drying, the calyces continue to enclose the corolla tightly.

The calyx is sometimes stalk-like at the base, tubular, truncate, irregularly splitting or with three neat triangular lobes, glabrous or variously hairy. There are very good diagnostic characters in the calyces, particularly in the shape, striation and hairiness. They are, overall, quite constant but in some species can be quite variable and can cause confusion in the definition of taxa. *Licuala glabra*, for example, has quite variable calyces ranging from cylindrical to cyathiform to urceolate (Saw 1997). Their bases are sometimes pedicelliform and sometimes swollen. These infra-specific variations are quite constant within populations. In spite of these variations in shape, they are united in the constantly glabrous calyx with very short pointed lobes at the apex.

Striation on the calyx is normally more obvious in dried specimens than in fresh. In some species this character is very distinctive, e.g. *L. pahangensis* and *L. terengganuensis.* In species with hairy calyces, the hairs are always spreading. Although this is also a constant character in most species, there is an exception, in most of the range of *Licuala terengganuensis*, the calyx is glabrous but on Bukit Bauk, Terengganu, there are some individuals with hairy calyces together with those with usual glabrous calyces. Although there are some differences between this population and the main population outside Bukit Bauk, Saw (1997) considered them conspecific. In *L. lanuginosa* and *L. cameronensis,* the hairs are very long and shaggy. In *L. ferruginea* and related species, the hairs are distinctively ferruginous.

The corolla is usually considerably larger than the calyx, tubular at the base, and divided into three rather thick, triangular, valvate lobes. It is glabrous to variously hairy, and its adaxial surface is usually marked near the tip with the impression of the anthers. The petal shape is rather constant, i.e. triangular, this character not being very useful in defining taxa. However, *L. terengganuensis* outside the population at Bukit Bauk has corolla lobes that are strongly incurved. Most other species of *Licuala*, including the population of *L. terengganuensis* at Bukit Bauk have spreading or gradually incurving corolla lobes.

There are eight species in Malaya and *c.* 20 species in Borneo of *Licuala* with glabrous corollas. It is also interesting that all these species also have glabrous ovaries. We have found that the hairiness of the corolla to be a useful character. The hairs are all simple, but they can be orientated differently. Three types are recognized; spreading hairs (Plate 1a), spreading and appressed hairs (Plate 1b) and strictly appressed hairs (Plates 1c & d). Spreading hairs are most common amongst species with hairy corollas. There are five species in Malaya with strictly appressed hairs. The hairs appeared to be glued to the corolla surface. In some cases, when it is both densely hairy and strongly appressed, the corolla surface appears superficially glabrous. When Beccari (1921) and Kiew (1989) described *L. ridleyana* Becc. and *L. dransfieldii* Kiew (both are now considered conspecific), they had erroneously described the corollas as glabrous. The categorization of hair orientation would be rather straightforward had there been only these two types. There are, however, a few species that are intermediate between the spreading and appressed hair types. These are referred to as having corollas with appressed and spreading hairs (Plate 1b). Hair lengths and density can also be good characters. In general, similar hairs are found on both the calyx and corolla, if both are hairy.

The androecium is represented by six epipetalous stamens with somewhat distinct flattened filaments adnate to the throat of the corolla tube. The point of fusion is generally just below the base of the corolla lobes. The filaments may be free or may be united to form a staminal ring. Furtado (1940) used the nature of the androecium formation to classify the subgenera. Figure 8 gives a diagrammatic presentation of the androecium found in *Licuala*.

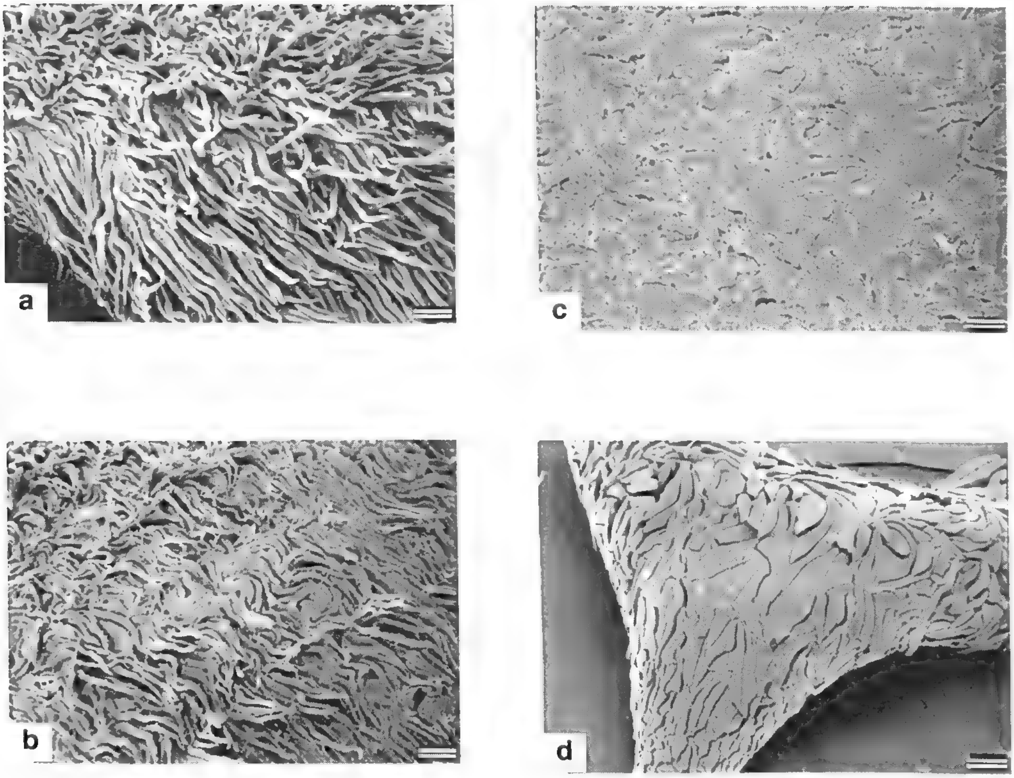

Plate 1 Corolla hair types.

a. *Licuala ahlidurii*, hairs are spreading (*L.G. Saw* FRI 39860). Scale bar = 0.1 mm

b. *Licuala fractiflexa*, hairs are appressed and spreading (*L.G. Saw* FRI 37585). Scale bar = 0.1 mm

c. *Licuala stongensis*, strictly appressed hairs (*T.C. Whitmore* FRI 12469). Scale bar = 50 mm.

d. *Licuala kingiana*, strictly appressed hairs (*R. Kiew* RK 2581). Scale bar = 0.1 mm.

In Furtado's classification, the subgenus *Licuala* includes species with stamens united at the base into a conspicuous ring adnate to the corolla throat and the staminal ring is rather uniform in height, with its filaments of about equal size (Figure 8a). It has a wide distribution, occurring in most of the range of the genus in Indo-China, Thailand, Malaya, Borneo, Philippines and Indonesia. The highest concentration of species is in Malaya and Borneo. Species with rather large flowers, about 15 mm or more long, with 6 equal free stamens adnate to the corolla tube and lacking a staminal ring are placed in subgenus *Libericula* (Figure 8b). This subgenus includes *L. peltata* Roxb. and *L. distans* Ridl. Finally, in the subgenus *Pericycla*, the staminal ring consists of three lobes, the lobes are emarginate with one filament in the notch at the apex of each lobe and one in each sinus between the lobes (Figure 8c). Most species are found in New Guinea and the islands surrounding it, east of the Wallace's line but there are two aberrant species described by Burret (1940 & 1941) with staminal rings which are slightly trilobed, which occur in South China and North Vietnam.

Two more types, representing new taxa are also included in the figure. Both of these were observed in collections made from Borneo. Figure 8d represents an androecium type where the staminal ring has filaments of two different heights alternating in two whorls. The anthers are basifixed and joined to the whole dorsum of the filament. This construction is observed in a new species collected from Brunei (*J. Dransfield*

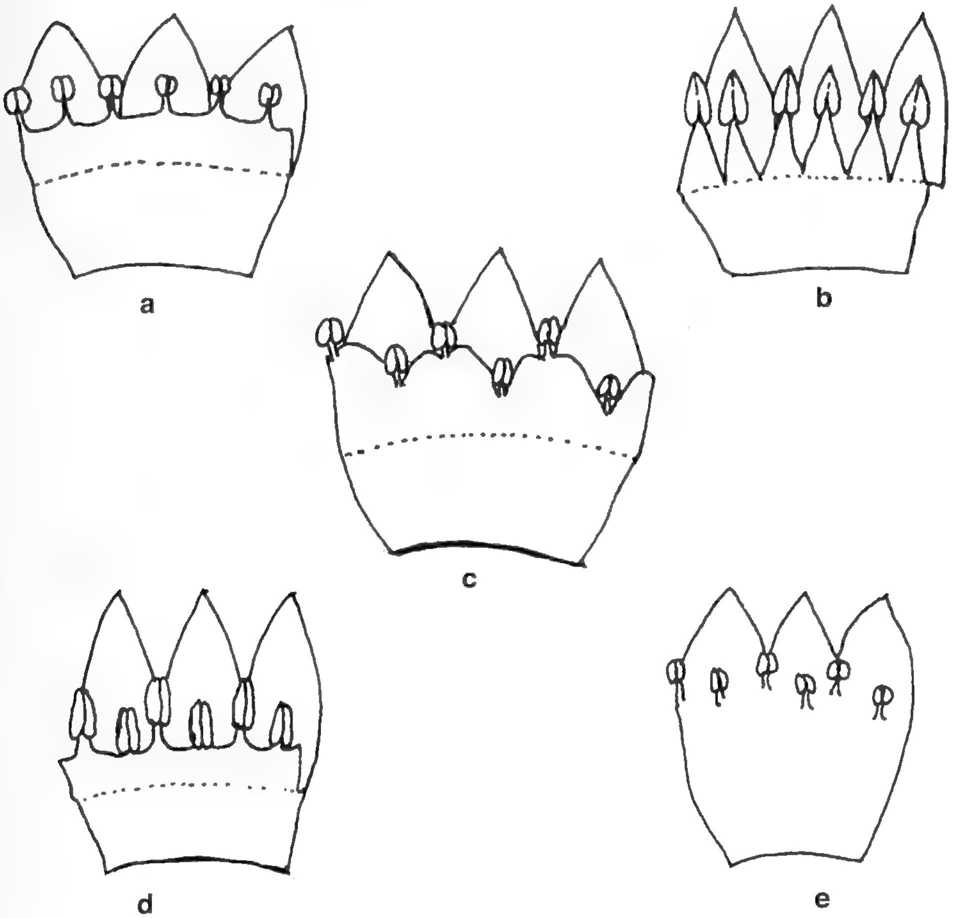

Fig. 8. A diagrammatic representation of androecium types of *Licuala* species. **a,** Regular staminal ring with equal sized filaments. **b,** Stamens free but joined at the base. **c,** Staminal ring trilobed, stamens on ridges and valleys of lobes. **d,** Staminal ring regular, filaments in two alternating lengths. **e** Filaments completely free from each other.

794); *L. bruneiana* L.G.Saw (ined.). Figure 8e represents yet another androecium type that is unlike any other we have seen. Here, the stamens are very small; the filaments are adnate to the corolla wall a short distance below the corolla lobes. What is strange about this construction is that the filaments are completely free from each other. Although the filament lacks a staminal ring in the subgenus *Libericula,* they still contact each other at the base. The flower shape on the whole is also very 'un-*Licuala*-like', i.e. its shape is ovoid and the corolla lobes split away from the calyx with a very small mouth. The species is also new and was collected by P.C. Yii (S 42003) from Bako, Sarawak (*L. flammula* (L.G.Saw (ined.)). *L. flammula* is unusual among Bornean *Licuala,* as the species appears to be dioecious, the species is currently only known by its type and the flowers of the specimen (S 42003) has female flowers, the anthers are present but appear to be empty.

Anthers can be basifixed or dorsifixed. All Malayan species of *Licuala* have dorsifixed anthers. The anthers can be either versatile or rigid. Most anthers that are dorsifixed are also versatile. When the anthers are basifixed, they are always rigid, e.g. *L. bidentata* Becc. from Borneo. There are a few species with dorsifixed anthers that are rigid too. The filament ends in a discoid apex joined to the anthers quite rigidly – so far only known from *L. fatua* Becc. and *L. hexasepala* Gagnep., both species from Indo-China. *Licuala reptans* Becc. from Borneo has inflexed anthers, and here the filament is bent twice, carrying the long, very narrowly linear pendulous anthers.

The ovary consists of three uniovulate carpels, which are fused at their apices into a single style. They are variously shaped; cylindrical, turbinate, fusiform to globular. The apex is sometimes sculptured by the impression of the anthers, giving it a truncate and channelled top. When the ovary develops with little contact with the anthers, its apex is rounded. These features appear to be constant within the species. The surface can be glabrous to hairy. A glabrous ovary is the more common situation in the genus. Out of the c. 44 species of *Licuala* found in Borneo, only two species have hairy ovaries, while the rest have glabrous ovaries (Saw, in prep.). These two are *L. triphylla* from Peninsular Malaysia and *L. pilosa* L.G.Saw (ined.), the only endemic Bornean species with a hairy ovary. Species with hairy ovaries appear to be more restricted in distribution. They are restricted to Malaya and Sumatra, though more common in Malaya. In Sumatra, the three species with hairy ovaries are also found in Malaya or are closely related to Malayan taxa, i.e. *L. longipes*, *L. ferruginea* and *L. ferruginoides*. Hairs are mostly globally distributed on the whole ovary. In some species, they may be restricted only to the upper parts. For example, *L. thoana* has an ovary with hairs in a ring around the rim of the apex of the ovary, but in closely related species, *L. ferruginea* the whole ovary is covered in hairs.

Usually only one carpel develops into a fruit, but in some species, two or even all three carpels in a flower will develop into independent drupes. Whether this character is species-specific, is still uncertain. The style is filiform or narrowly conical. The stigma is very shortly 3-lobed but sometimes it is difficult to discern the lobes.

The Fruits

The fruits are usually small and are drupaceous, usually globose or ovoid, rarely ellipsoid. Very few species are known with long ellipsoid fruits, e.g. *L. kiahii* Furtado from Malaya and *L. mattanensis* Becc. from Borneo. Immature fruits are green in most species of *Licuala* but in *L. ferruginea* and its alliance, the immature fruits are distinctively pink. Most species with green immature fruits will ripen orange to red. However, in *L. ferruginea* and its alliance, the young fruit is pink and then ripens black. In *L. densiflora* Becc., similar to *L. ferruginea*, the immature fruit is pink to red but here it matures white. Fruit surfaces or the exocarps are generally smooth but they can be shagreen (e.g. *L. tenuissima* L.G.Saw and *L khoonmengii* L.G.Saw from Malaya) to even corky warty (e.g. *L. bintuluensis* Becc. and *L. bruneiana* L.G.Saw (ined.) from Borneo). Mesocarps are usually pulpy when ripe and non-fibrous. The fruits are animal dispersed and the most likely dispersal agents are birds and small forest mammals. Most seeds are globose and some are ellipsoid, following the shape of the fruits. Endocarp surfaces are smooth in most *Licuala* species and are usually crustaceous. The endocarp usually adheres quite strongly to the seed in fresh specimens and is difficult to separate. Shrinkage of the seeds as a result of drying, for example in herbarium specimens, can result in the endocarp loosely enclosing the seed. The testa is usually very thin, brown and is strongly adherent to the seed in both fresh and dried specimens but may peel off from the seed after prolonged boiling.

In New Guinea, the fruits of some species are rather large and endocarps are rather thick and ornamented with regular longitudinal ridges, quite unlike any others (e.g. *L. beccariana* Furtado, *L. lauterbachii* and *L. crassiflora* Barfod). There are, however, other species with smooth endocarps in New Guinea. The ornamented endocarp may represent a different line of fruit types in *Licuala*. It will be very interesting to see if this condition is correlated with characters of New Guinean *Licuala* species. Ferrero (in letter to J. Dransfield, 1994) suggested that the fruits of *Licuala* with longitudinal ridges are dispersed by cassowaries.

The seed consists of a uniform endosperm, usually white and very hard when mature. Embedded in the endosperm are two structures clearly visible in longitudinal section, viz.: the chalaza that intrudes into the endosperm (as a postament) like a large inverted comma at the base of the seed and the embryo, located variously, usually about dorsal to the axis of the fruit. The embryo is straight and cylindrical, rounded distally comprising the cotyledon and flattened proximally, comprising the apical meristem and radical.

Conclusion

In conclusion, *Licuala* is shown to have rather strict morphological construction. Although vegetative characters can be useful in taxon delimitation, as often they are not. Inflorescence and floral characters are most useful.

Acknowledgments

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Contrasting pollination modes in three species of *Licuala* (Arecaceae: Coryphoideae)

A. S. Barfod, T. Burholt and F. Borchsenius

Abstract

Barfod, A.S., Burholt, T. and Borchsenius, F. (Dept. of Systematic Botany, Institute of Biological Sciences, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark) 2003. *Contrasting pollination modes in three species of* Licuala *(Arecaceae: Coryphoideae). Telopea 10(1): 207–223.* The pollination modes of *Licuala spinosa, L. distans* and *L. peltata* were studied in Peninsular Thailand. The differences in flowering behaviour and mechanisms that promote pollination are described. The pollen counts and frequent visits of calliphorid flies and halictid bees suggest that these are the most likely pollinators in *L. spinosa* followed by eumenid wasps and tachinid flies. Species of *Trigona* bees collected in the flowers of *L. distans* and *L. peltata* had high pollen loads. They were present during both anthesis and the receptive phase of the flowers and are probably responsible for pollination.

Introduction

About 14% of all palm species bear perfect flowers (Uhl 1969). This is lower than the corresponding 65% for rain forest trees in general (Bawa 1979). Most of the perfect flowered palms are found in the tribe Corypheae, which comprises 31 genera. In this tribe only the two monotypic genera *Guihaia* and *Kerriodoxa* have unisexual flowers. *Licuala* belongs to the subtribe Livistoninae that includes twelve genera, all with hermaphroditic flowers. The gynoecium is composed of three carpels that are free at the base but joined in the stylar region. The genus consists of more than 150 species distributed in SE Asia from India in the west to Vanuatu in the east. It is the most species-rich genus of fan palms. Based on floral morphology, Furtado (1940) divided the genus into three subgenera: subgenus *Libericula* Furt. with discernible staminal filaments, subgenus *Licuala* with filaments fused into an androecial tube and all anthers inserted at the same level, and subgenus *Pericycla* (Bl.) Drude with anthers in two levels and an androecial tube.

Species of *Licuala* are typically palmlets or rosette palms growing in rainforest under low light conditions. One exception is *L. spinosa* Wurmb, which thrives in light, open and often disturbed habitats. Other species are found exclusively in habitat types such as freshwater swamp forests and limestone outcrops. The typical *Licuala* has armed petioles of differing lengths that position the fan-shaped blades at various levels and angles. The inflorescence varies from erect and overtopping the crown to short and hidden between the leaves. The inflorescence rachis has one to several nodes. At each node, a long tubular bract subtends a partial inflorescence that is either ramified or unbranched. The flowers are generally hermaphroditic and dichogamous but dioecy has been reported in a few instances (Uhl & Dransfield 1987, Saw 1997, Barfod pers. obs.). Pollen morphology is very uniform throughout the genus (Ferguson 1987, Ferguson & Harley 1993, Ambwani & Kumar 1993).

Studies of the reproductive biology of palms have revealed a wide range of plant adaptations that match the behavioural characteristics of their pollinators (Henderson 1986, Zona 1987, Andersson et al. 1988, Herrera 1989, Olesen & Balslev 1990, Barfod

1991, Búrquez et al. 1987, Scariot et al. 1991, Listabarth 1992, Borchsenius 1993, Ervik 1993, Bernal & Ervik 1996, Bøgh 1996, Listabarth 1996, Ervik & Feil 1997, Küchmeister et al. 1997, Anstett 1999, Howard et al. 2001). The most common pollen dispersing agents are beetles followed by bees and flies. Except for Knuth (1904) who reported abundant nectar production in the flowers of *Licuala grandis* H. Wendl., and listed some insects as likely pollinators, nothing has been published about pollination within this large genus.

Materials and methods

Study organisms

Licuala spinosa Wurmb (subgenus *Licuala*) is an understorey palm often with a large production of suckers. It is found in a range of habitats from ditches to forest understorey. It forms a dense crown and the petioles are armed with long spines. Inflorescences are typically erect and visible above the crown. The partial inflorescences are branched with up to seven rachillae (Fig. 1a).

Licuala distans Ridl. (subgenus *Libericula*) is a solitary palm restricted to the peninsular part of Thailand from Ranong in the north to Krabi in the south. It occurs in hill dipterocarp forest where it is locally very common, especially on ridges. The appearance of the crown is less dense than *L. spinosa* and the petioles are longer and more slender, and only armed basally. The lamina is finely divided into up to 35 segments, each folded two to three times. The inflorescences are gracefully bending and visible under the crown. The partial inflorescences are branched with up to five pendent rachillae (Fig. 1b).

Licuala peltata Roxb. ex Buch.-Ham. (subgenus *Libericula*) is also a solitary palm, widely distributed from India in the west to Peninsular Thailand in the east, barely extending across the border with Malaysia. It occurs in lowland dipterocarp forest where it is typically associated with limestone formations or local outcrops of calcareous rock. The crown carries only 5–10 leaves and the petioles are armed along their entire length. The number of segments per lamina varies from one in var. *sumawongii* L.G. Saw to 21, this figure being relatively constant throughout a population. The segments in divided leaves are 50–90 cm long, narrowly wedge-shaped to triangular. The inflorescences are erect and visible among the leaves. The partial inflorescences are spicate and pendent (Fig. 1c).

Morphological and anatomical features of importance for interaction with pollinating insects are summarised in Table 1.

Study sites

Licuala spinosa was studied at two sites in Peninsular Thailand (Fig. 2), the Khao Nor Chuchi Lowland Forest Project (KNC), located within the Khao Phra Bang Kham Wildlife Reserve in the Province of Krabi (99° 15' E 07° 55' N, 20–80 m elevation) and the Thung Kai Arboretum (TKA) in the Province of Trang (99° 38' E 07° 27' N; 0–10 m elevation). At both sites *L. spinosa* was abundant. The study site at Khao Nor Chuchi is situated in a landscape of limestone hills covered with evergreen forest vegetation. Lime is precipitated in the soil in many places forming a water impermeable layer that causes flooding in the rainy season. Thung Kai Arboretum is situated near the sea. Here *L. spinosa* occur in open parkland vegetation dominated by *Melaleuca cajuputi* Powell, sedges and grasses. Patches of thicket are common composed of low trees and

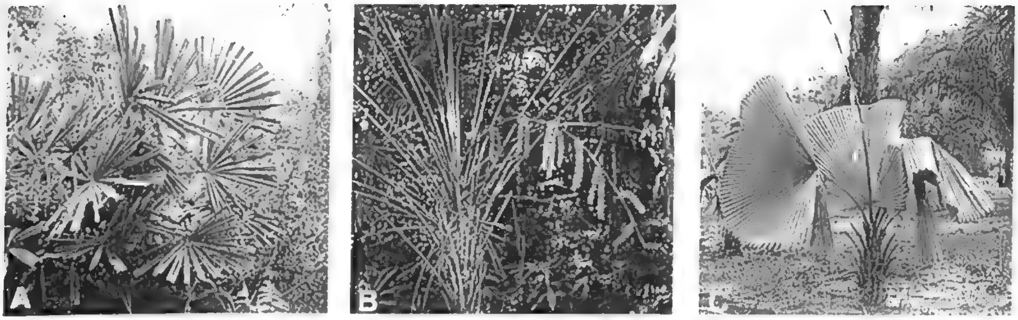

Fig. 1. *Licuala* habit. **a,** *L. spinosa.* **b,** *L. distans.* **c,** *L. peltata.*

Table 1. Comparison of *Licuala spinosa, L. peltata and L. distans.*

Diagnostic feature	***Licuala spinosa***	***Licuala distans***	***Licuala peltata***
growth form	clustering	solitary	solitary
average no. of rachillae per partial inflorescence	3.4 (n=13)	2.8 (n=5)	1.0 (n=5)
average length of rachillae (cm)	14.7 (n=122)	21.4 (n=31)	31.2 (n= 5)
average density of flowers (number per cm rachillae)	9.61 (n=311)	4.05 (n=5)	5.98 (n=5)
average length of flower (mm)	4.0 (n=10)	9.5 (n=10)	13.0 (n=10)
haircovering, calyx	dense	scattered	dense
haircovering, corolla	hairy	glabrous	hairy
sclereids, corolla	absent	present	absent
filaments	fused into tube	fused basally	fused basally
raphide ideoblasts in staminal tube	present	present	absent
anther length (range in mm)	0.6-0.8	2.6-2.8	3.0-3.2
average pollen/ovule ratio in thousands (range in parentheses, n=2)	12 (0)	210 (166-253)	67 (62-73)
pollen grain, length (range in µm)	28-32	27-31	32-36
pollen grain, exine sculpturing	perforate	perforate	foveolate
average diam. of perforations of pollen grains (µm, n=5)	0.2	0.5	1.2
ovary, haircovering	glabrous	glabrous	hairy
ovary, sclereids	absent	absent	present

shrubs. The terrain is characterized by poorly drained soils that are inundated in the rainy season. Lower lying terrains are permanently under water and dominated by *Nypa fruticans* Thunb. and *Acrostichum aureum* L.

Observations on *Licuala distans* were made at the Sri Phangnga National Park (SPNP) where this species is locally common. *Licuala peltata* var. *sumawongii* was observed in the Peninsular Botanical Garden in Khao Chong (PBG), Province of Trang, near the fringes of the surrounding hill Dipterocarp forest.

Field observations

Field observations were conducted in Oct–Nov 1992. A 10 × 10 m plot was established at both the study sites for *Licuala spinosa*. All reproductive individuals found within these plots were marked (n=8 at TKA; n=9 at KNC). Phenology and inflorescence development were studied on the individuals at KNC during the period 5–24 Oct. All inflorescences were labelled and growth rates of peduncle, rachis, first-order branches, and rachillae monitored. Numbers of flowers, buds per rachilla, number of rachillae per inflorescence, and number of inflorescences per palm were counted. Detailed studies of flowering biology and insect visitation were conducted at both study sites by continuous observation over a 24 hour period. Close-up photographs of flowers in different phases were taken (Fig. 3) and the adhesive capacity of the pollen grains tested by touching the anthers with a clean glass slide. The presence and relative quantity of nectar was determined and numbers and behaviour of visiting insects noted. In addition a representative sample of insect visitors were caught and preserved in alcohol for later identification and determination of pollen load. At TKA flowers in different developmental stages were collected and fixed in Navashin's solution for study of changes on the stigmatic surfaces. Insects were identified to family using Jensen (1987), Ross (1965) and Unwin (1981, 1984).

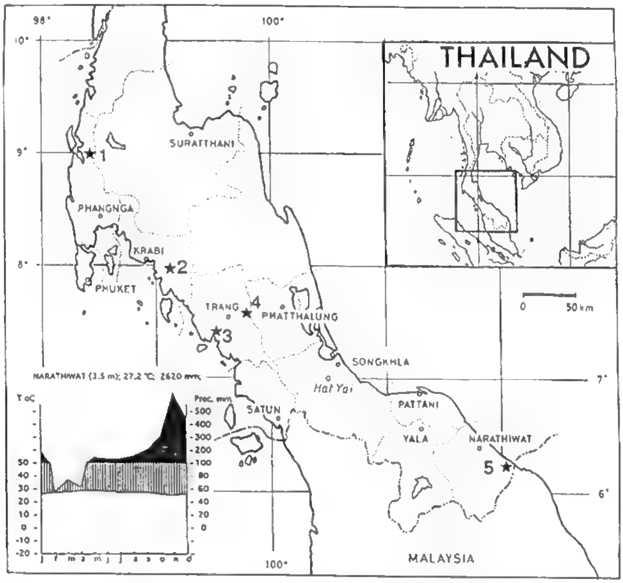

Fig. 2. Study sites in Peninsular Thailand. **1**. Sri Phangnga National Park. **2**, Khao Nor Chuchi Lowland Forest Project (KNC). **3**, Thung Kai Arboretum (TKA). **4**. Peninsular Botanical Garden in Khao Chong (PBG). **5**, Narathiwat.

Observations of inflorescence development, flowering biology and insect visitors of *L. distans* and *L. peltata* var. *sumawongii* were made over a few days in late October. For both species the number of flowers per rachilla and per inflorescence were determined and flowers sampled for later studies of morphology, anatomy and P/O ratio. For *L. distans* a number of flowers in different phases were additionally collected and fixed in Navashin's solution for later study of flower development.

Voucher specimens of *L. spinosa* and *L. distans* from all study sites are deposited in AAU, BKF and K.

Laboratory analysis

Flowers fixed in Navashin's solution were prepared for anatomical study by desilicification in hydrofluoric acid for 1 or 2 days. After this treatment, they were gradually dehydrated with ethanol and embedded in Technovit 7100™. Serial sections 7–8 microns thick were prepared on a Reichert™ rotary microtome. The sections were stained with toluidine-blue or ferric chloride for examination of tannin content and mounted in Euparal™. For scanning electron microscopy (SEM) the dehydrated flowers were critical point dried using a BIO RAD CPD 750™, sputter coated with platinum, and examined with a Jeol JSM-840™ scanning electron microscope. To estimate the pollen:ovule (P/O) ratio all pollen grains in one anther were extracted and counted. The estimates were based on anthers from at least two different

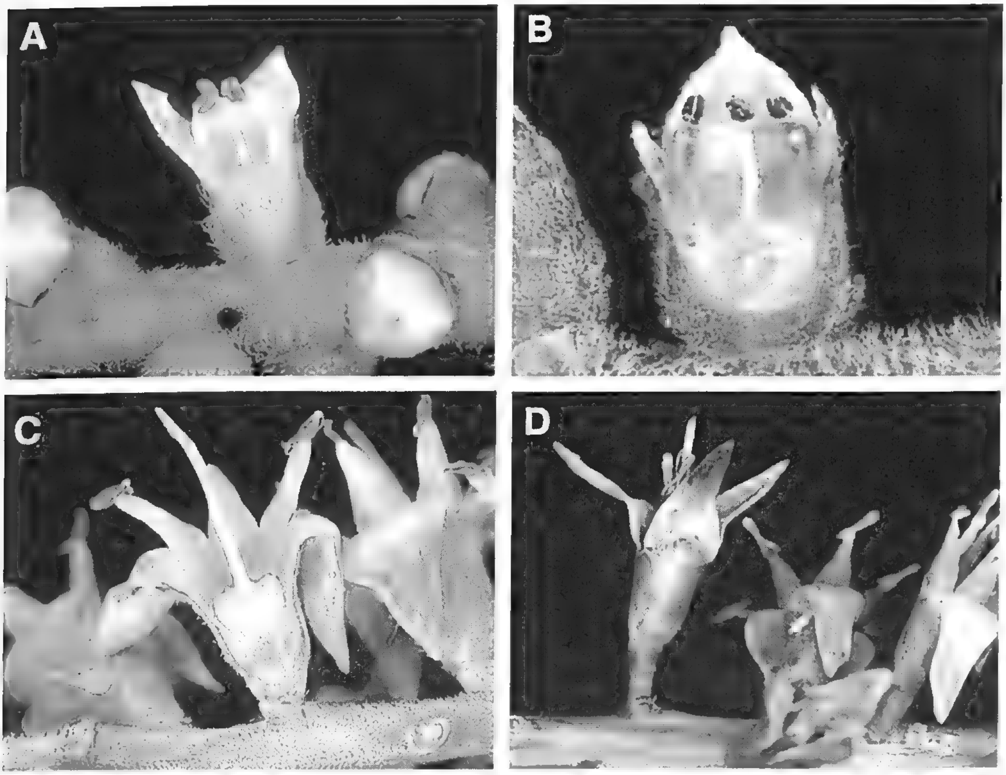

Fig. 3. *Licuala* flowers. **a,** *L. spinosa*. LS of flower in early male phase. **b,** *L. spinosa*. LS of flower in receptive phase. **c,** *L. peltata*. LS of flower in late male phase. **d,** *L. distans*.

individuals. Surface pollen load of insect visitors was determined by ethanol washing followed by centrifugation. The pellet was smeared on glass slides, embedded in glycerine, and the number of *Licuala* and foreign pollen, respectively, counted under a light microscope.

Results

Phenology

Flowering of the three *Licuala* species studied is synchronized with rainfall patterns. In *Licuala spinosa* flowering is apparently triggered by the onset of the rainy season. *Licuala peltata* flowered at the end of the rainy season, whereas *L. distans* flowered at the beginning of the dry season in 1994. It should be noted, however, that variation in phenological patterns occur within *L. spinosa*, probably as a facultative response to differing growth conditions. Thus in KNC, sun-exposed individuals flower once a year, whereas we did not observe an annual flowering cycle in shaded individuals growing nearby.

The first individuals of *Licuala spinosa* studied at KNC were in an advanced state of flowering on Oct 14. The last palm to flower had about 40% of its flowers in bud on Oct 25. On this basis, we estimate that flowering of the entire population lasted from mid September to mid November in 1992, peaking in October. Fruits of *L. spinosa* are normally mature in February. Prior to anthesis the rachillae elongated fast, while the length of the peduncle and rachis increased only negligibly. The rachillae on the proximal partial inflorescence grew faster than those of the distal partial inflorescence. After onset of anthesis, longitudinal expansion almost ceased.

Flowering in *Licuala spinosa* proceeded in an acropetal pattern. The first flowers to open were typically found on the distal rachillae of the proximal partial inflorescences. The proximal partial inflorescences still presented flowers when anthesis started in the distal partial inflorescence. The opening of the single to paired flowers is not synchronized. Two pulses of flowering usually occur on each rachilla, the first pulse being the most intensive. The number of flowers opening per day in one rachilla varied from 1–27 (n=311). Detailed phenological observations were made on four inflorescences that began to flower immediately after we arrived on Oct 5. The total number of flowers that open per day, per inflorescence, increases steadily to about 150–250 during the first 8–10 days of anthesis. Hereafter, the number begins to decline. Based on these observations we estimate that one inflorescence stays in anthesis for about 30 days.

Inflorescence development and flowering in *L. distans* and *L. peltata* followed a pattern different from that observed in *L. spinosa*. The proximal spicate rachilla branches flowered first. The overall sequence of flowering is thus acropetal. Flowering of the individual rachillae, however, was basipetal and of short duration. On the first day of flowering, only a few buds in the distal end of the rachilla opened (mean 5.20, range 1–7, n=5). The next three days about one-third of the remaining flowers opened each day (mean 30.75, range 25–40, n=4) in the following way: on the second day of flowering all remaining buds in the distal third part of the rachilla opened; on day 3 the flowers in the central third of the rachilla opened; and on day 4, the flowers in the basal third part opened.

Flowering biology

Flowers of all three species were protandrous (Fig. 3). In *L. spinosa* the buds opened in the morning of day 1 and in most cases dehiscence of the anthers started 2 hours hereafter (Fig. 4). Sometimes the anthers dehisced immediately after opening of the bud. Dehiscence occurred earlier and proceeded faster in flowers that were exposed to the sun. Flowers emitted a sweet, honey-like scent, and a small amount of nectar was observed around the ovaries of the flowers. The androecium started wilting early at night on day 1. It gradually turned dark brown, as did the anthers and the petals.

In *Licuala distans* and *L. peltata* flowers were still open on day 3 and the stigmas were probably receptive. Abundant nectar production was observed both during staminate and pistillate phases (3 µl was easily sucked up using a micropipette). The nectar had a sweet taste and a glucose test showed positive reaction. Anthesis was accompanied by a sweet, honey-like scent, resembling that observed in *L. spinosa.*

To estimate the duration of the receptive phase, flowers of *Licuala spinosa* were collected in different stages of development and fixed (Fig. 5). The starting point is the late bud, approximately one day before anthesis (*phase 0*). At this stage the stigma has three conspicuous lobes that are closely bunched together (Fig. 5a). *Phase I* corresponds to the newly opened flower at 07:20 with just a few dehisced anthers. At this stage the stigma lobes are straight. Only the papillae at the apex are exposed with few pollen grains adhering to them (Fig. 5b). Flowers in *phase II* were collected at 13:45 on day 1 of flowering. All the anthers had dehisced. The stigma lobes are slightly more reflexed and conspicuous. The papillae have enlarged, but few pollen grains adhere to the stigmatic surface (Fig. 5c). *Phase IIIa* corresponds to stages collected at 01:00 on day 2 of flowering. At this time, the staminal tube has turned light brown and a dense layer of newly germinating pollen covers the stigma (Fig. 5d). Adhesion of the pollen grains is probably facilitated by a combined effect of the glutinous stigmatic fluid and the enlarged papillae. The stigmas are thus receptive before the arrival of the first insect visitors to the flowers at dawn. Early germination of the pollen grains makes self-pollination a possibility, provided that the flowers are self-compatible. Later, in *phase IIIb & c,* an enlargement of the papillae is visible (Figs 5e, 5f) and even more pollen grains adhere to the stigma. *Phase IV* stages were collected at 06:00 on day 2 of

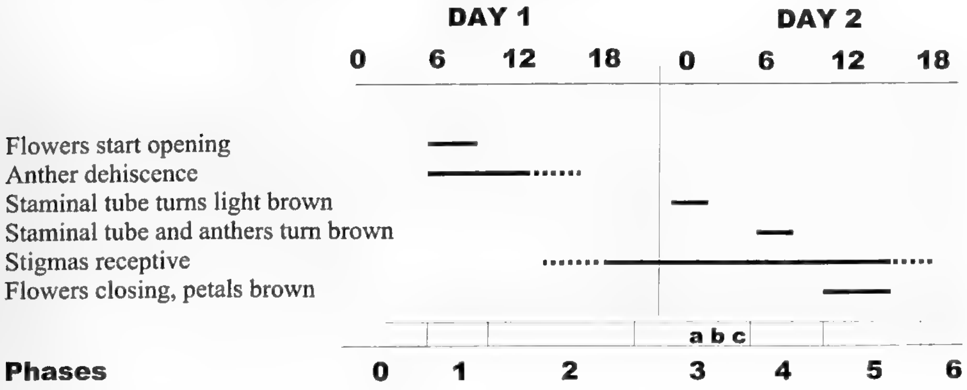

Fig. 4. Phenological events in *Licuala spinosa.*

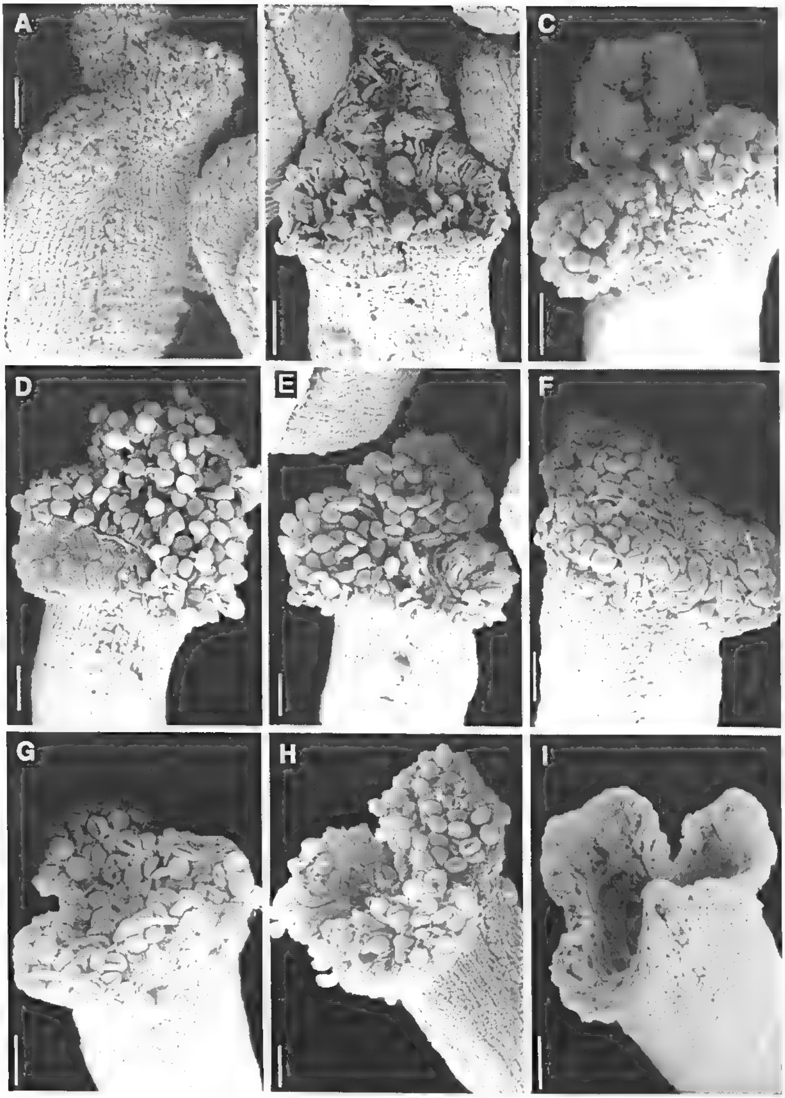

Fig. 5. Development of receptivity in *Licuala spinosa*. **a,** *phase 0*. Stigma in the late bud, approximately one day before anthesis. At this stage the stigma has three lobes that are closely bunched together. **b,** *phase I*. Stigma in a newly opened flower at 7:20 am. The flower is in the ealy male phase with a few dehisced anthers. The stigmatic lobes are little reflexed with only a few pollen adhering to them. **c,** *phase II*. Stigma at 1:45 pm on day 1 of flowering. All the anthers have dehisced. The stigma is slightly reflexed and slightly three-lobed. Notice also the enlarged papillae in this stage. **d,** *phase IIIa*. Beginning of female phase at 01:00 am on day 2 of flowering. The staminal tube has turned light brown. The stigma is covered with newly germinating pollen. The stigmatic lobes are clearly discernible and reflexed at this stage. Early receptivity and germination of the pollen makes self-pollination a possibility in this stage. **e–f,** *phases IIIb & c*. The staminal tube and the stamens have turned brown and the papillae are further enlarged. **g,** *phase IV*. At 06:00 am on day 2 of flowering, a shallow depression appears on the stigma. The stigma is still covered with pollen and the lobes are further reflexed. The pollinating insects are reappearing at this stage. **h,** *phase V*. The flower passes into this phase when the petals turn brown and close the flower by curving inward. **i,** *phase VI*. The flowers are closed, dark-brown and past the receptive phase. The papillae have desintegrated so that the opening of the stylar canal is visible. Scale bar = 50 μm.

flowering. The staminal tube and the stamens are brown (Fig. 5g). The insects start reappearing at this stage. The pollen load on the stigma is heavy and the stigmatic lobes are further recurved. The flower passes into *phase V* when the petals turn brown and close the flower by curving inward. At this time, a depression appears on the stigma (Fig. 5h). In a few cases reopening of the flowers took place on day 3 (*phase Va*). No apparent changes were recorded in the stigma relative to the previous phase. *Phase VI* corresponds to the closed and dark-brown flowers past the receptive phase (Fig. 5i). The papillae have disintegrated so that the opening of the stylar canal is visible.

Changes in the stigma during the different phases of flowering were also studied in *Licuala distans*, but in less detail. In this species the receptive surfaces are lining the inside of the tubular stylar canal. At staminate anthesis on day 1, the rim surrounding the opening of the stylar canal is curved inwards. Few pollen grains were observed on the reduced stigmatic surface at this point (Fig. 6a). During the receptive phase on day 2, only a slight reflexion of the stigmatic margins occurs (Fig. 6b). On day 3, a shallow depression on the stigmatic surface is seen (Fig. 6c). The stigma of *L. peltata* is morphologically very similar to that of *L. distans* and probably passes through the same stages. The stigmatic surfaces of both species are less reflexed than those of *L. spinosa* and have fewer adhering pollen grains.

Insect visitors

Licuala spinosa. A range of insects belonging to eight different orders visited the flowers (Table 2). The first insects arrived at the flowers just after sunrise around 06:00 and insect activity continued until sunset, apparently peaking somewhere between 10:00 to 11:00 with a maximum of 20 visits per hour. During the night there was almost no activity and only one moth and one *Thysanoptera* were observed. Apart from insects, Orange-Bellied Flowerpeckers (*Dicaeum trigonostigma*) and a few spiders were also observed among the visitors, probably preying on the insects. Representatives of *Anisoptera* and *Zygoptera* apparently used the inflorescence as a resting place and were not observed to be in contact with the inner parts of the flowers. *Cicadoidea, Formicidae, Lepidoptera* and *Thysanoptera* were also recorded but their presence was erratic. Potentially important pollinators should consequently be looked for among insects of the orders *Coleoptera, Diptera* and *Hymenoptera.*

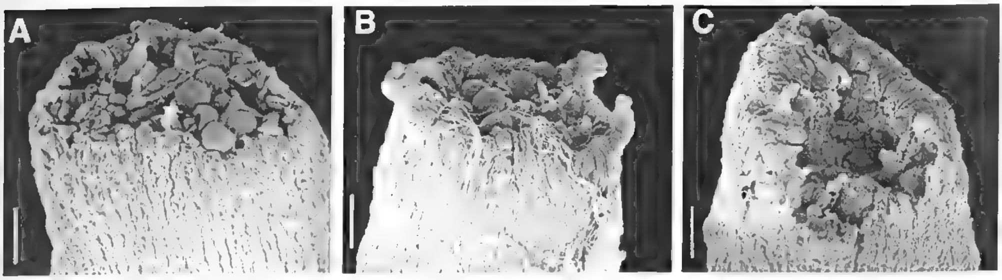

Fig. 6. Development of receptivity in *Licuala distans*. **a**, At male phase on day 1, the rim surrounding the opening of the stylar canal is curved inwards. Few pollen grains were observed on the reduced stigmatic surface in this stage. **b**, During the female phase on day 2, the stigmatic margins are only sligthly recurved. **c**, On day 3, a shallow depression on the stigmatic surface is seen. Scale bar = 50 µm.

Some differences in insect visitor activity were noted between the two sites where *L. spinosa* was studied. In KNC a larger number of insect species was observed whereas a higher number of individuals were present in TKA.

Surface pollen loads of insect visitors (Table 3) varied from 0–785 pollen of *Licuala spinosa* per individual. The highest values were recorded for halictid bees and some species of the *Calliphoridae*. However, Halictid bees were only observed in flowers in the staminate phase. Calliphorid and also Tachinid flies were both observed with their proboscises inserted deep into the flowers throughout all phases, presumably engaged in extracting nectar.

Licuala distans. At 09:40 there was activity of bees around the inflorescence. The bees were mostly stingless *Trigona* spp. but also a few *Apis* were observed. No flies were seen in the flowers. The stingless bees arrived continuously until 11:20 when observations stopped and visited flowers both in the staminate and the pistillate phases. Examination of the surface pollen loads of the visiting *Trigona*-bees showed that these had relatively high loads (Table 3).

Table 2. Visiting insects to the inflorescences of *Licuala spinosa*

Order	Family	Number of individuals of visting insects	
		Khao Nor Chuchi	Thung Kai Arboretum
Anisoptera		1	
Coleoptera	Cerambycidae	3	
Diptera	Calliphoridae	14	33
	fam. unknown 1	1	
	fam. unknown 2		42
	fam. unknown spp.	6	19
	Empididae	2	
	Platystomatidae		1
	Tachinidae	8	11
Hemiptera	Cicadidae	4	
	Membracidae	1	
Hymenoptera	Eumenidae	9	16
	Formicidae	2	
	Halictidae	6	20
Lepidoptera		4	18
Thysanoptera		2	1
Zygoptera		5	

Table 3. Average pollen loads for visiting insects (insects that do not not carry pollen grains of the species of *Licuala* visited have been excluded)

Order	**Family**	**Average pollen load per visitor**			
		Licuala spinosa **Khao Nor Chuchi**		***Licuala spinosa*** **Thung Kai Arboretum**	
		own	**alien**	**own**	**alien**
Araneae		3	7	0	2
Coleoptera	Cerambycidae sp. 1	105	9		
	Cerambycidae sp. 2	5	21		
	Cerambycidae sp. 3	7	12		
Diptera	Calliphoridae sp. 1	0	6		
	Calliphoridae sp. 2	483	53		
	Calliphoridae sp. 3			42	7
	Calliphoridae sp. 4			65	5
	Empipidae	6	24		
	Platystomatidae			6	71
	Tachinidae	123	41		
	fam. unknown sp. 1			10	17
	fam. unknown sp. 2			1	7
	fam. Unknown sp. 3	20	21		
Hemiptera	Membracidae	8	7		
Hymenoptera	Eumenidae sp. 1	86	57		
	Halictidae sp. 1	4	20		
	Halictidae sp. 2	785	776		
	Halictidae sp. 3	269	2		

		Licuala peltata **cultivated**		***Licuala distans*** **Sri Phangnga**	
		own	**alien**	**own**	**alien**
Hemiptera	Meridae			0	0
Hymenoptera	Apidae, Trigona sp. 1			111	1
	Apidae, Trigona sp. 2			283	1
	Apidae, Trigona sp. 3			167	7
	Apidae, Trigona sp. 4			641	210
	Apidae, Trigona sp. 5			1547	22
	Apidae, Trigona sp. 6	1584	19		
	Apidae, Trigona sp. 7	2106	36		
	Eumenidae sp. 2	29	107		

Licuala peltata. Only a few insects were observed near flowering individuals of *L. peltata* var. *sumawongii* cultivated in the palm field of the Peninsular Botanical Garden in Khao Chong (observations made from 08:00 to 11:30). A few honey bees (*Apis*) were seen collecting pollen from flowers in the staminate phase (3 observations). A large wasp belonging to the *Eumenidae* was seen moving around in the flowers of the palm (4 observations). The *Trigona*-bees were the most frequent visitors in flowers both during staminate and pistillate phases and had the highest pollen load (Table 3).

Test for selfing in *Licuala spinosa*

Rachillae bagged with nets impenetrable to insects (6 rachillae with a total of 187 flowers) showed a fruiting success of 3.4%, comparable with that of unbagged inflorescences from adjacent palms growing in shady conditions (5.5%; 2 rachillae with a total of 145 flowers). *Licuala spinosa* is thus potentially self-compatible.

Pollen/Ovule ratio

The variation of P/O ratios within palms often reflects pollination mode since pollen is offered as a reward particularly in the case of bee pollination. The following ratios were recorded for the species studied: *Licuala distans* 210 (range 166–253, n=2); *L. peltata* 67 (range 62–73, n=2) and *L. spinosa* 12 (no variation, n=2). In *L. peltata*, many undeveloped pollen grains were observed. These were not included in the calculation.

Floral anatomy

Sections of the flowers of all three species of *Licuala* (Fig. 7) revealed the presence of idioblasts containing bundles of needle-shaped calcium oxalate crystals (raphides), which probably serve to protect the flowers from herbivory during their prolonged phase of anthesis. Raphides were found mostly in the staminal tube, but they also occur in the ovary and the fleshy part of the sepals. All three species had tannins evenly distributed throughout the floral parts and the calyx was heavily sclerified. Numerous sclereids were found in the petals of *L. distans* and in the ovary of *L. peltata*.

Cross-sections of the flowers revealed the presence of two types of nectaries. In some species the nectar flow is raised by undulation and convolution of the septal nectaries. This labyrinthine kind of nectary (Schmid 1983) is found in *L. distans* and *L. peltata* (Figs. 7a & c). In *L. spinosa* nectar secretion only occurs in the cavities created by the adjoining septal radii of the ovary (simple type). The nectar is discharged at the base of the ovary. The outline in transverse section is like a circle with three T-formed appendices (Figs. 7b & d).

Discussion

The study of pollination modes within the subgenera *Licuala* and *Libericula* respectively has revealed fundamental differences.

Licuala spinosa, the only representative from subgenus *Licuala* included in this study, is characterised by having ramified partial inflorescences, small and inconspicuous flowers and an erratic flowering sequence. The entire inflorescence constitutes a functional unit that flowers for approximately one month. Limited amounts of nectar are discharged from secretory epithelial cells that are located at the bottom of the septal slits. The flowers are well protected during the long exposure in bud by structural and chemical defences such as sclerified tissues and tannin. The narrow opening of the staminal tube assures that only small insects get access to the nectar. Interestingly the staminal tube has a higher concentration of raphide containing idioblasts than the two other species in this study.

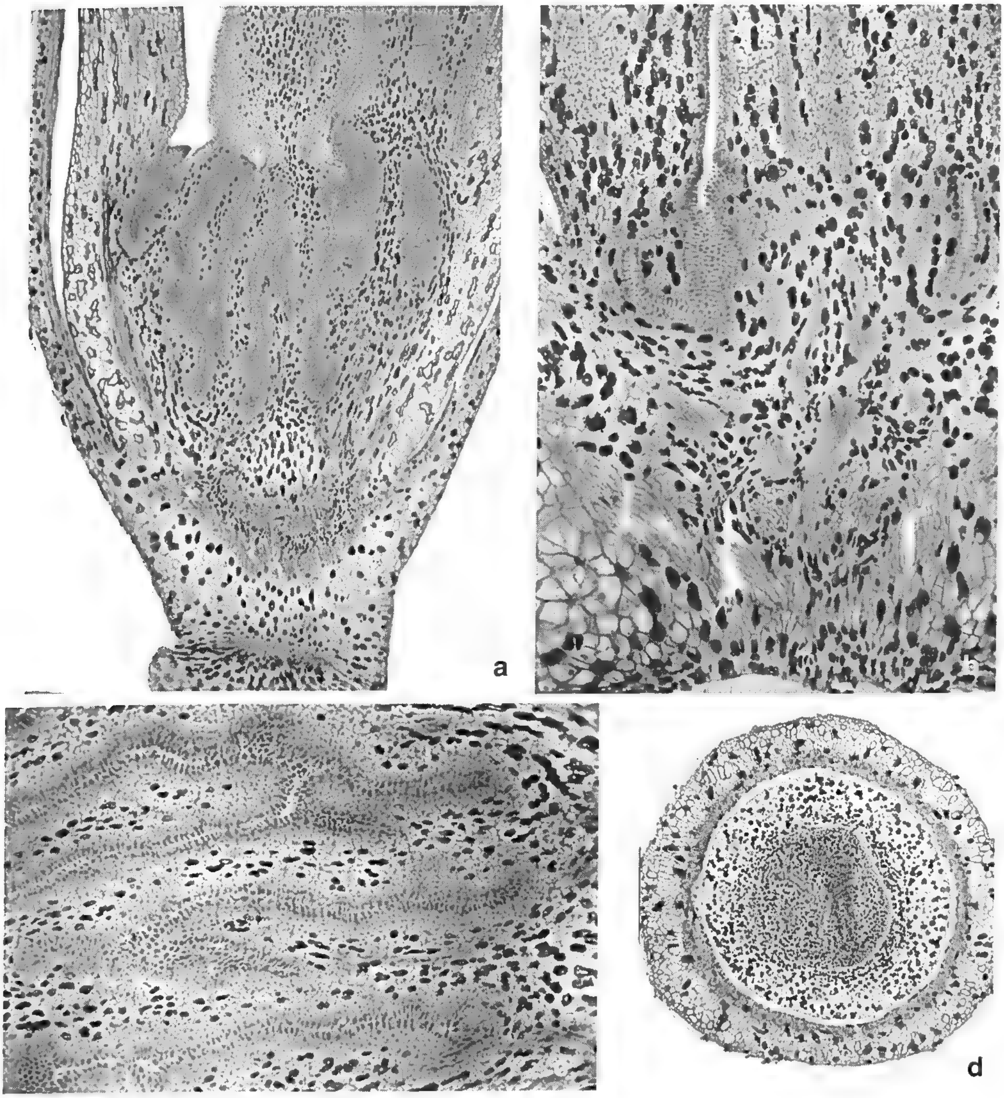

Fig. 7. Anatomical preparations of *L. spinosa* and *L. distans*. **a,** *L. distans*. LS of basal part of flower. Notice the densely staining labyrinthine nectaries below the gynoecium and the dark coloured tannin-containing cells scattered throughout. **b,** *L. spinosa*. LS of flower. Notice the densely staining nectaries in the bottom of the septal slits and the dark coloured tannin-containing cells scattered throughout. **c,** *L. distans*. Detail of LS of labyrinthine nectaries. **d,** *L. spinosa*. CS of the flower. The nectaries line the bottom of the septal slits. Notice their T-shape towards the periphery of the gynoecium.

Brown (1982) observed that sub-canopy trees of *Sabal palmetto* Lodd. *ex* Schult. f. flowered later compared to trees exposed to sunlight. In many fly-pollinated species there has been reported a lack of seasonality in the flowering of several species (Kwan 1959, Skov & Balslev 1989, Borchsenius 1993, Schmid 1970). This is probably an effect of the stable microclimatic conditions that prevail throughout the year in the understorey of mature phase forest patches where these species typically occur. In KNC we observed sun-exposed individuals of *L. spinosa* that flowered in annual cycles. Flowering is apparently triggered by the first rains of the rainy season. Individuals of the same species occurring in the forest nearby produced inflorescences throughout the year. Observations throughout Thailand have shown that *Licuala spinosa* is a versatile species that thrives well under both light open and forest conditions, as long as there is a constant water supply. Other species of *Licuala* probably have a more uniform phenology and require shaded and undisturbed conditions.

The study of populations of *L. spinosa* in two contrasting habitats revealed variation in the populations of visiting insects. In both the light-open Parklands at TKA and in the forest understorey at KNC flies and eumenid and halictid bees were numerous. We ascribe the bees a minor role in transferring pollen grains since they were only observed in flowers in the male phase. In the forest situation the diversity of visitors was greater but the total number of visits smaller. The pollination success was limited corresponding to that of inflorescences bagged for selfing. The detailed study of receptivity further shows that self-pollination is possible during an overlap between the male and female phases before the insects reappear at sunset (*phase III*). The stamens and the stigma are situated closely to each other in the flower (Figs 3a & b). The pollen loads carried by the visiting insects further indicate the dominating role of especially calliphorid and tachinid flies in transferring pollen grains in this species. The low P/O ratio combined with the low amount of nectar confirms that the award offered to visiting bees is limited.

In *L. peltata,* the partial inflorescences are spicate and function as distinct units. The flowers are large and conspicuous. The filaments are fused basally only and form a wide cup-like structure. Opening of the flowers is under strict control and proceeds as a basipetal pulse that last 4–5 days. *Licuala distans* is similar to *L. peltata* in most of the above-mentioned aspects. The flowering is, however, more intensive in this species due to more inflorescences at anthesis at the same time and branching of the partial inflorescences. A high concentration of sclerified tissue is found in the petals of *L. distans* and in the ovary of *L. peltata*. The staminal tube of *L. peltata* is characterized by an almost lack of raphide containing idioblasts. Based on morphological and anatomical features, it is tempting to conclude that specialisation of pollination has proceeded further in *L. peltata*. This assumption is, however, contradicted by the fact that the P/O ratio is higher in *L. distans*. Compared with *L. spinosa* self-pollination is less likely in subgenus *Libericula* since the stigmas are well separated from the anthers in the flower (Figs 3 c & d). The inward curved rim that surrounds the opening of the stylar canal at anthesis furthermore restricts the receptive surfaces of the stigma.

The *labyrinthine* nectaries are situated below the gynoecium in both *L. distans* and *L. peltata*. Copious amounts of nectar are produced thanks to undulations and convolutions of the nectariferous tissues. This makes the flowers attractive to insects with high energy requirements such as bees. Additional ontogenetic studies by Barfod and Stauffer (in progr.) will hopefully throw more light on the origin of this specialized type of nectary. Interestingly, a member of subgenus *Licuala, L. merguensis* Becc. (syn. *Licuala hirta* Hodel), has been observed to have a labyrinthine type of nectary (Barfod & Saw 2002). This species is characterized by having yellow flowers, a colour that is often found in bee-pollinated palm species.

The mutualistic interaction between pollinating insects and flowers is mediated by the scent and colour of the flower and the nutritional value of nectar and pollen grain (Harborne 1988). Pollination by flies or myophily has been reported in a wide range of palms such as *Aiphanes eggersii* Burret (Borchsenius 1993), *Geonoma irena* F Borchsenius and *G. cuneata* H. Wendl. ex Spruce (Borchsenius 1997). Flies do not nurse their brood and only need food for their own consumption, usually in the form of energy-rich nectar. Representatives of the families *Calliphoridae*, *Syphidae* (hover flies) and *Drosophilidae* (fruit flies) have often been reported as visiting palms. Although hover flies and fruit flies are often listed among the visitors to palm inflorescences they rarely have a major role in transferring pollen. In *Licuala spinosa* the evidence strongly suggests that Calliphorid flies probing for nectar are the major contributors to pollination. Promiscuity is probably widespread as evidenced by the little overlap between pollinators at the two study sites. Myophily is particularly widespread in understorey palms. Flies are not busy food collectors and are inefficient pollinators compared to insects that nurse their brood. Myophily is considered the least specialized type in the family (Howard et al. 2001).

Pollination by bees or melittophily is a widespread phenomenon in the tropics. Especially *Trigona* bees (stingless bees or sweat bees) are well known as visitors to palms (Bullock 1981, Bøgh 1996). However, they often act as pollen thieves (Búrquez et al. 1987) or can be ruled out as pollinators because they only visit male flowers (Essig 1971, Beach 1984, Barfod 1991, Kiew & Muid 1989). The bees are attracted by a combination of pollen that is used for nursing the brood and sugar-rich nectar to satisfy a high energy demand. Usually the specificity of the interaction between bees and palms is low. The palm thus shares pollinators with a wide range of other plant species. In two species of subgenus *Libericula* studied, there was no overlap in the visiting species of *Trigona*. The stingless bees both collected pollen from the relatively large anthers and probed for nectar. The hoarding instinct of higher, social hymenoptera makes them more effective than flies as pollinators. Bees are typically attracted to brightly coloured zygomorphic flowers with mild scent. In palms they are typically found in species that allow for extensive foraging due to bunched flowers and large anthers that are easy to handle. Both *Licuala distans* and *L. peltata* match the behavior of *Trigona* bees well in their adaptations to pollination.

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Assessment of the hybrid status of some Malesian plants using Amplified Fragment Length Polymorphism

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Abstract

R. Kiew [1]*, L.L. Teo and Y.Y. Gan* [2] *(*[1] *The Herbarium, Singapore Botanic Gardens, Singapore;* [2] *Division of Biology, National Institute of Education, Nanyang Technological University, Singapore). Assessment of the hybrid status of some Malesian plants using Amplified Fragment Length Polymorphism.* Telopea *10(1): 225–233.* Compared with temperate regions where hybrids are common, hybrids reported from the Malesian region are few. In addition, almost none has been the subject of quantitative or experimental study, either because they are rare or inaccessible or are difficult to grow or have long life cycles. Amplified fragment length polymorphism (AFLP) has proved useful in determining whether taxa suggested as hybrids based on their morphological intermediacy between two putative parents are indeed hybrids. The results of AFLP analysis confirmed the hybrid status of taxa in the following genera, *Begonia* (Begoniaceae), *Mangifera* (Anacardiaceae) and *Nepenthes* (Nepenthaceae), while disproving the hybrid status of duku-langsat, *Lansium* (Meliaceae).

Introduction

Natural hybrids are relatively common in temperate floras, for example Stace (1991) considered that 21.7% of the native British flora are hybrids, so it is not surprising that some of these species have been intensively studied, both qualitatively and experimentally, for many years.

In contrast, in the Malesian tropics, natural hybridization is very rare and confined to very few genera, such as *Cryptocoryne* (Araceae), *Globba* (Zingiberaceae), *Nepenthes* (Nepenthaceae), *Rhododendron* (Ericaceae), and a few other isolated instances. For almost all of these, hybrid status has been suggested by their intermediate morphology between two other species that are presumed to be the putative parents. Very few hybrids, e.g. in *Globba* (Lim 1973), and *Begonia* (Teo & Kiew 1999) have been subject to quantitative study using a hybrid index to assess this morphological intermediacy and even fewer have been subject to cytological study, e.g. *Globba* (Lim 1972).

Experiments involving growing these hybrids and their putative parents and reconstituting the hybrids are nil. This is not surprising because of several factors: knowledge of how to grow these species is often lacking, e.g. in the case of trying to grow deep shade forest plants or for montane plants to survive in the lowlands or crossing experiments of trees involves an unacceptably long time frame or the ratio of botanists to species in the Malesian region is so small that there is not sufficient manpower for detailed experimental work or there is a lack of expertise, e.g. in fields such as cytology.

To overcome these impediments and, in particular, to be able to assess the genotype rather than the phenotype, Amplified Fragment Length Polymorphisms (AFLP) were used to test whether this would be a suitable method for assessing hybrid status and to identify the putative parents. Molecular markers can be used to discover species-specific genetic markers for the presumed parental taxa and the distribution of these markers in plants of different phenotypes can be examined to ascertain whether they are hybrids or not. AFLP is a DNA-fingerprinting technique developed by Vos et al. (1995). With AFLP, it is possible to obtain information for many loci randomly distributed throughout the genome in a single assay so it is therefore a powerful means of fingerprinting individuals and establishing genetic relationships of plants based on genetic similarity. According to Morell and Rieseberg (1998), due to extinction of parental alleles following the initial hybridization event, additivity in the molecular markers can often only be detected by analysis of multiple loci, thus making AFLP a suitable technique for studying hybridization. In our study, bands specific to each parent were identified and the inheritant patterns of the hybrid samples were studied. Hybrids commonly have an additive inheritant pattern of parental alleles (Crawford 1990). Beisman et al. (1997) have already used AFLP successfully to distinguish a hybrid of *Salix* (Salicaceae) and its parents as have Suh et al. (1997) for *Aconitum* hybrids (Ranunculaceae).

The hybrids we assessed covered a range of life forms: trees (*Mangifera* and *Lansium*), climbers (*Nepenthes*) and perennial herbs (*Begonia*) and habitats (*Begonia* is montane, the others lowland).

1. Kuwini, *Mangifera odorata* Griff. (Anacardiaceae)

Ding Hou (1978) suggested that kuwini, *Mangifera odorata*, was a hybrid between the mango (*M. indica* L.) and the strong-tasting horse mango (*M. foetida* Lour.). In Malaysia, the horse mango is a wild species that is sometimes grown in villages, while kuwini is a common village fruit tree but has never been confirmed as growing wild.

Leaf samples were taken from 5 *Mangifera odorata* trees from Sabah and Sarawak, 5 trees of *M. foetida* from Sabah and 10 trees of of different clones of *M. indica* from Sabah, Sarawak and Singapore. Using AFLP, seven primer pairs were used resulting in 380 unambiguous bands with 84% polymorphism (Teo et al. 2002), of which 22 were specific to *M. indica* and 28 specific to *M. foetida*. Kuwini had no unique bands but had 16 of the *M. indica* species-specific bands and 20 of those of *M. foetida*. The AFLP results therefore confirm that *M. odorata* is a hybrid between these two species. Since *M. indica* is an introduced species, this is clearly a case of an anthropogenic hybrid, where geographical isolation has broken down.

Interestingly, the index of similarity showed that kuwini is closer to *M. foetida* (76% similarity) than it is to *M. indica* (66%). In this case, similarity in genotype is manifested in the phenotype, as morphologically it is difficult (if not impossible) to distinguish sterile plants of kuwini from *M. foetida* (Corner 1988).

2. Duku-langsat, *Lansium domesticum* Correa (Meliaceae)

Duku-langsat is a popular local fruit. Its fruits are morphologically intermediate between those of langsat and duku, which have variously been treated as a single aggregate species, *Lansium domesticum* (Mabberley 1985) or as distinct species — duku, *Aglaia dokoo* and langsat, *A. domesticum* (Kostermans 1966) — or as races of *L. domesticum* with duku-langsat as a hybrid between them (Corner 1988). While it is difficult to distinguish the trees when they are not fruiting, the fruits are distinct and in fact sell for different prices in the market. Langsat has smaller, ellipsoid, yellow, thin-skinned fruits, which do not split but ooze a lot of latex when broken. Duku is larger, rotund, brown, very thick-skinned, but splits open and has no latex. It also has thicker and sweeter flesh. Duku-langsat is intermediate in size, is round, brownish and has a skin that splits but which is much thinner than that of duku. This is the preferred fruit and the most expensive among the three.

To ensure correct identification of samples, we used the seeds of five fruits per batch bought at several local markets in Peninsular Malaysia and Singapore. Batches of langsat were bought in markets in Johore Baru and Yong Peng (Malaysia) and Singapore, and duku-langsat and langsat from markets in Johore Baru and Singapore.

Five primer pairs were used resulting in 269 unambiguous bands. Ten bands were specific to duku and 20 bands were found in all the langsat and duku-langsat samples, while 78 bands were common to all three. Neither langsat nor duku-langsat had any unique bands.

In addition, the genetic similarity between samples was very high: 91.5–100% for duku and 85.5–100% for langsat/duku-langsat. This can be ascribed to duku and langsat being apomictic (Prakash et al. 1977). This high level of similarity indicates that langsat, duku and duku-langsat belong to a single species. The conclusion of Mabberley (1985) that they are cultivars of a variable species, *L. domesticum*, probably best reflects the taxonomic status of these three fruit types. Langsat is considered the wild form as it is a widespread understorey tree.

3. *Nepenthes* hybrids (Nepenthaceae)

Three pitcher plant hybrids that occur naturally in Singapore were investigated: *Nepenthes* x*hookeriana* Lindl., which as early as 1928, on morphological intermediacy, had been suggested by Danser as a hybrid between *N. rafflesiana* Jack and *N. ampullaria* Jack; *N.* x*trichocarpa* Miq. that Holttum (1940) considered a hybrid between *N. gracilis* Korth. and *N. ampullaria,* and the less common hybrid between *N. gracilis* and *N. rafflesiana* reported by Tan et al. (1997).

Six primer pairs were used in the AFLP analysis which yielded 372 unambiguous bands of which 74 bands were common to all three species, *N. ampullaria, N. gracilis* and *N. rafflesiana. N. gracilis* had most species-specific bands (34), followed by *N. rafflesiana* (22) and *N. ampullaria* (14). *N.* x*trichocarpa* had 22 bands in common with *N. gracilis* and 14 in common with *N. ampullaria* but no unique bands, while the third putative hybrid had 20 bands in common with *N. gracilis* and 14 in common with *N. rafflesiana* and no unique bands. *Nepenthes* x*hookeriana* additively inherited 16 bands from *N. rafflesiana* and 14 from *N. ampullaria* with one unique band occurring in half the samples that could either be due to unsampled diversity in the parental plants or to a mutation in the hybrid. The AFLP results therefore confirm the hybrid status of these three taxa and confirmed the parents suggested on morphological grounds.

4. *Begonia* hybrid (Begoniaceae)

A natural begonia hybrid between *Begonia decora* Stapf and *B. venusta* King is found in several populations at Cameron Highlands, Peninsular Malaysia, where these two species grow sympatrically in upper montane forest. A quantitative study on plants in the hybrid zone showed that there are hybrid swarms displaying an almost complete continuum between the two putative parents from decora-like hybrids to intermediate hybrids to venusta-like hybrids for both morphological and leaf anatomical characters (Teo & Kiew 1999). In addition, the hybrids were highly fertile both for pollen viability (91–100%) and seed viability (98%).

For the AFLP analysis, three populations were studied. Two at higher elevations, one where *B. decora* and *B. venusta* grew sympatrically, the other comprising a hybrid swarm; and the third, at a lower elevation comprised *B. decora* only. *B. venusta* was not found growing alone. Six primer pairs produced 502 unambiguous bands of which six were species-specific for *B. decora,* while none were specific to *B. venusta,* which was always found growing together with *B. decora* and/or hybrids. This suggests that through introgression *B. venusta* is no longer genetically distinct from the venusta-like hybrids. However, the phenograms produced were instructive for the two populations with hybrids.

The phenogram (Fig. 1) for the population where both species grew sympatrically (Berinchang) showed that *B. decora* plants clustered with the decora-like hybrids, while the *B. venusta* plants clustered with the venusta-like hybrids. In the second population (Beremban), while ten years ago (1990) a few plants of *B. decora* were recorded, none could be located in the vicinity when this study was carried out (2000). In the phenogram for this population (Fig. 2), the intermediate hybrids clustered together with the decora-like hybrids, but the separation between the decora-like and venusta-like hybrids was not complete. In this population, it appears that through introgression neither *B. decora* nor *B. venusta* are any longer distinct. That introgression has occurred over several generations is further supported by the presence of unique bands in a few of the hybrids (Fig. 3).

Apart from *B. decora* growing over a wider altitudinal range (as low as 1200 m as opposed to 1700–2000 m altitude for *B. venusta*), there are no discernable differences in the physical habitat requirements of these two species. Being a hill resort, there is some disturbance by the opening up of roads and pathways though the montane forest but this does not appear to have affected the begonias, which do not invade the more exposed areas. The breakdown in reproductive isolation between these two species is probably due to habitat changes that affect their common pollinator, a *Trigona* bee. With pathways opened up the pollinators could move unobstructed over greater distances, which would promote hybridization between contiguous populations.

Discussion

These case studies show that AFLP is a useful method for identifying hybrids and their parents and confirms the hybrid status of the taxa of *Mangifera*, *Nepenthes* and *Begonia*, while disproving the status of duku-langsat as a hybrid. In addition, it shows that AFLP has potential to tackle the problem of species complexes, such as that of *Lansium domesticum*.

The number of naturally occurring hybrids in the Malesian region is negligible (probably less than 1%), compared with their frequency in temperate regions (e.g. 21.7% for the British flora) or even Hawaii with 9.3% hybrids reported from the flora (Ellstrand et al. 1996).

Various reasons for this have been suggested. One is the observation that in temperate regions many hybrids occur in disturbed or open areas whereas open areas are relatively few in tropical rain forest. However, both rhododendrons and pitcher plants occupy this niche in montane areas where landslips are relatively frequent. For example, Argent et al. (1988) report that on Mt Kinabalu, some rhododendron hybrids form hybrid zones where they are common and abundant. Indeed, pitcher plants and, to a lesser extent rhododendrons, have invaded disturbed man-made areas, such as roadsides. On the other hand, Ashton (1969) ascribed the great rarity of hybrids among Malesian trees in part due to the inability of primary forest species to become established in the exposed conditions of gaps or open areas so that this niche not available to them. Interestingly, hybridization among native secondary forest species, which effectively invade gaps and open areas, has not been recorded at all.

Over recent geological time, however, Malesia has seen drastic fluctuations in climate and changes in sea level that would create widespread open niches (Morley 1999) but there is no evidence that this has caused hybridization followed by speciation.

Hybridization is often associated with lower fertility of the F1 generation. This may be the case in *Nepenthes* where hybrids are widespread and occur between almost all species, but where they are often found as single or a few plants and are nowhere

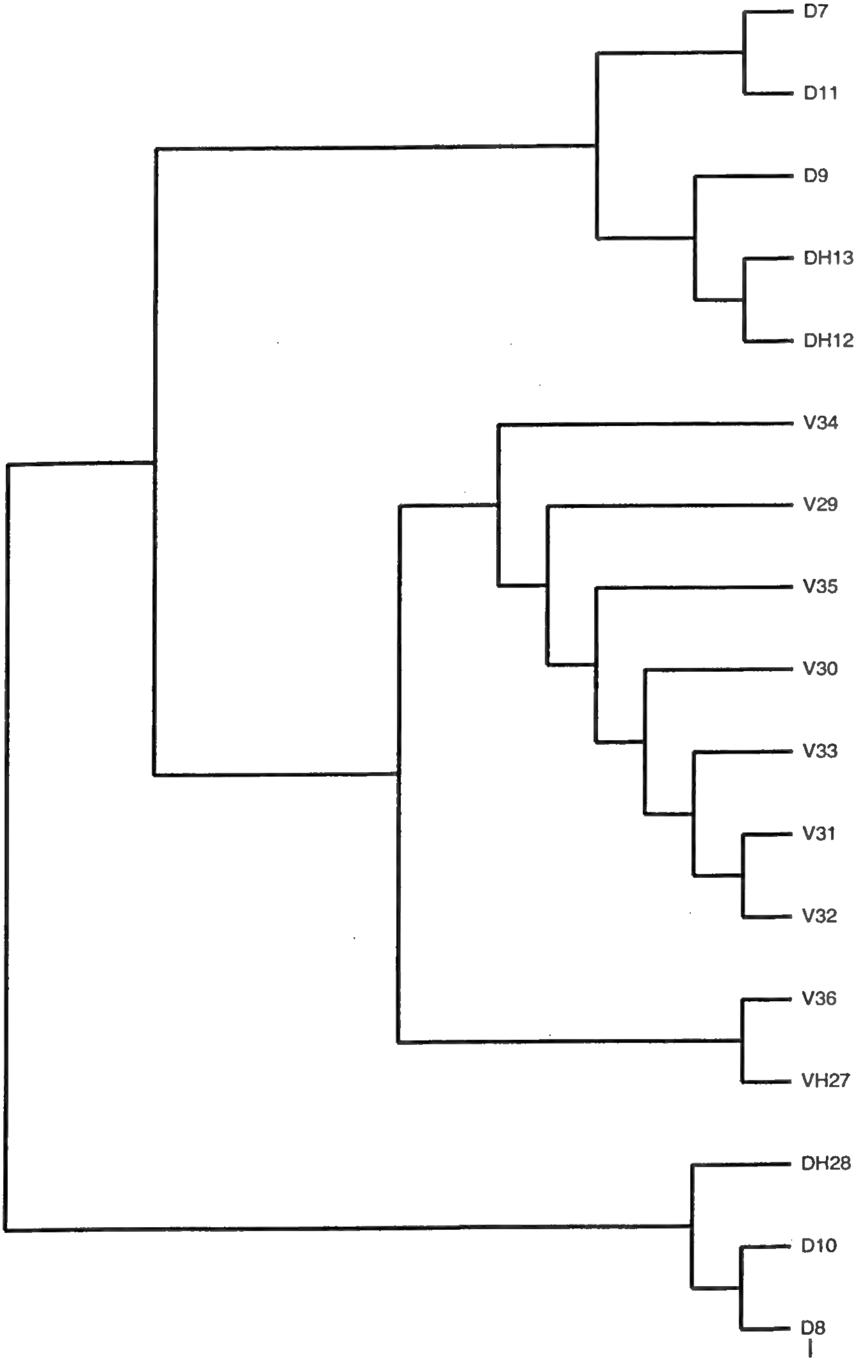

Fig. 1. UPGMA cluster analysis of AFLP data generated by six primer combinations for *Begonia* samples from Berinchang.

(D:*B. decora;* DH: decora-like hybrids; V: *B. venusta;* VH: venusta-like hybrid).

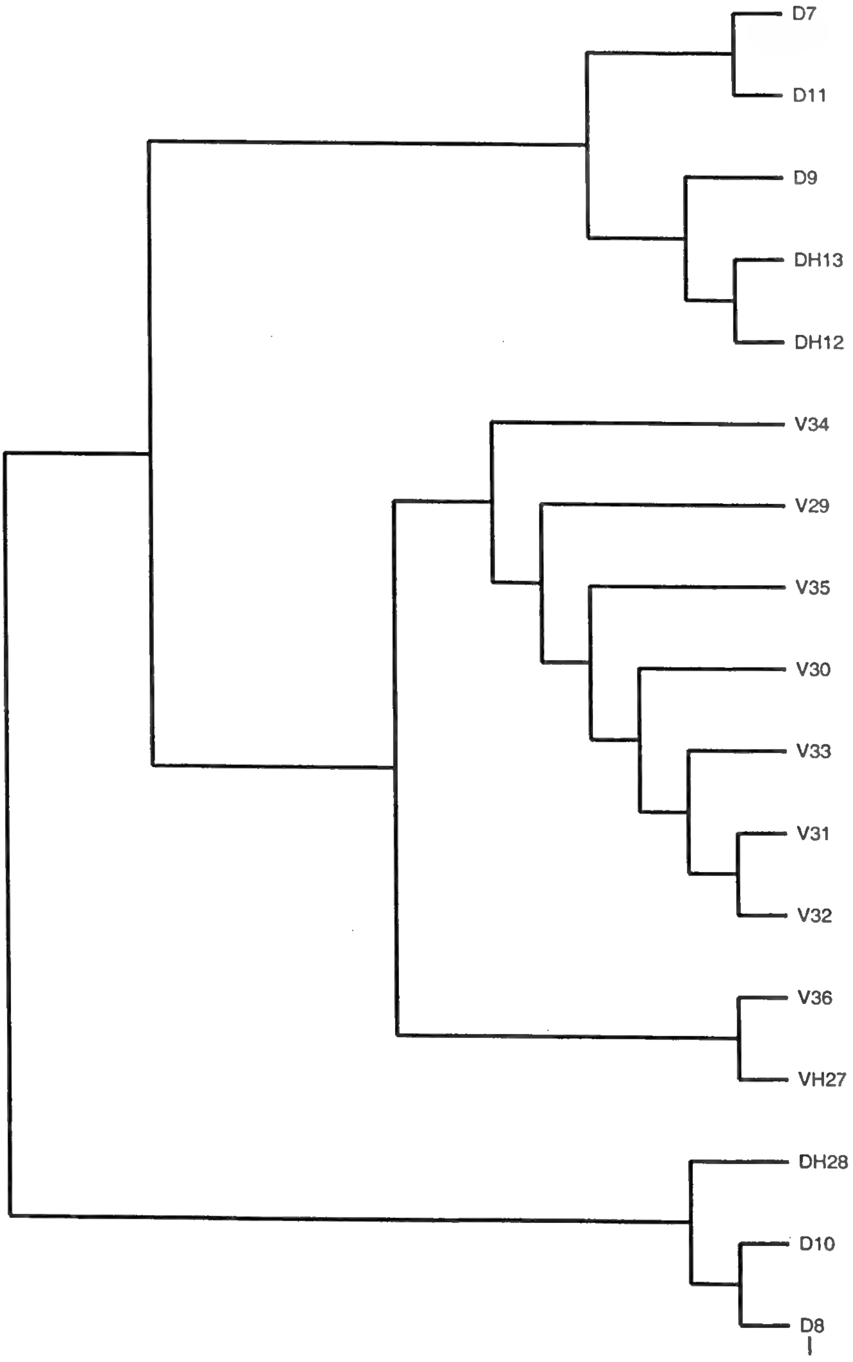

Fig. 2. UPGMA cluster analysis of AFLP data generated by six primer combinations for *Begonia* samples from Beremban.

(DH: decora-like hybrid; IH: intermediate hybrid; VH: venusta-like hybrid).

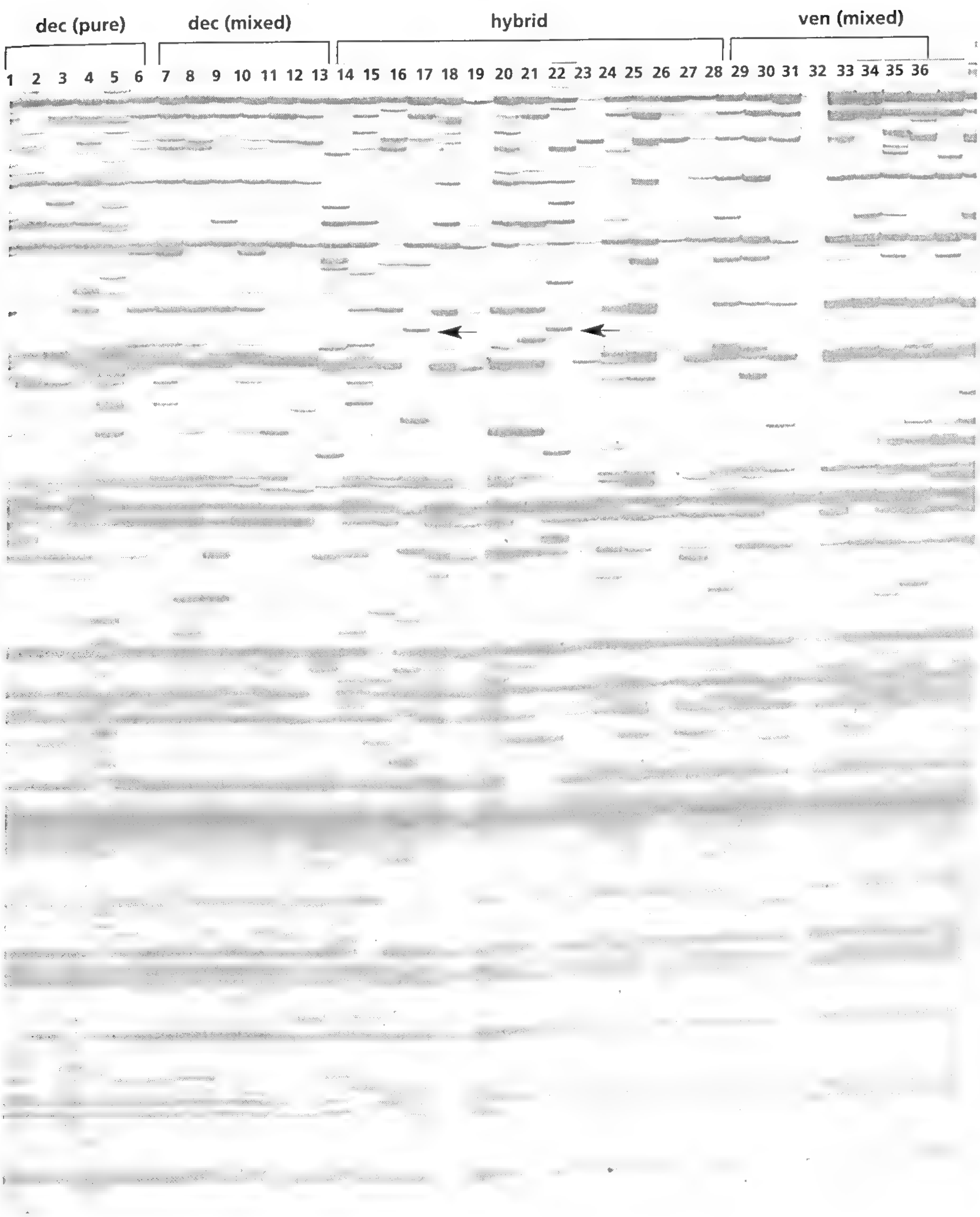

Fig. 3. AFLP profile of begonias using primer pair P10.

(Lanes 1–6: *Begonia decora* (single species population); lanes 7–13: *B. decora* (mixed populations); lanes 14–28 hybrids; lanes 29–36 *B. venusta* (mixed poulations). Arrows indicate unique bands present in the hybrid.

abundant. Polyploidy is often associated with hybridization as allopolyploidy is one way of overcoming the sterility barrier in the F1 generation. Briggs and Walters (1997) drew attention to the lower occurrence of polyploidy in tropical floras compared with temperate floras and cited the example of 53% of the British flora being polyploid as compared with only 26% in West Africa. Levels of polyploidy in the Malesian flora are, however, not known as chromosome numbers for the majority of taxa are still lacking.

A generally held view is that hybrids will be less well adapted to either of the parents' niche so, for example, in conditions of extreme competition in the biodiverse rain forest, the less well adapted hybrids will be selected against. However, Arnold (1997) holds the opposite view as, in his opinion, hybrids are often more fit due, not only to the combination of genotypes from the parents, but also due to the fact that hybridization often produces novel genotypes that may be more fit under certain environmental conditions, particularly disturbed or novel environmental conditions. For species that grow sympatrically, it is often difficult to discern without detailed experimentation what are the critical differences between the niche requirements of the parents.

In the tropics, it may be that pollinator specificity is more important than the physical environment. In this study, the breakdown of reproductive isolation between the two begonia species is more likely to be due to change in pollinator behaviour associated with habitat disturbance than the direct effect of disturbance on the begonias themselves. Clarke (2001) has suggested that in *Nepenthes* differences in pollinators of the parents may be important in preventing backcrossing between the hybrid and parents.

Another viewpoint suggested by Ashton (1969) for forest trees is that gregarious flowering that is temporally separated between species is also an isolating mechanism that precludes hybridization and is a factor that explains why hybrids are exceedingly rare among rainforest trees.

One thing that is quite clear is that we still know extremely little about the reproductive biology of Malesian plants.

Conclusion

This study shows that AFLP is a convenient method of analyzing the genotype of putative hybrids and their parents. In addition, the fact that fruit material can be used shows that AFLP has great potential in studying plants where the differences between cultivars and varieties are often defined by fruit characters. However, much still remains unknown about the genotypes and breeding systems of Malesian plants. Our concept of a species is still very much the taxonomic species defined by morphology rather than the biological species. In fact, hybrids have sometimes been invoked when taxa were poorly understood, as in the case of *Pentaphragma ellipticum* Poulsen, which Airy Shaw (1963) suggested was a hybrid between *P. acuminatum* Airy Shaw and *P. horsfieldii* (Miq.) Airy Shaw (Kiew 1989). AFLP provides a convenient method for providing data on hybrid status and can therefore bring us a step closer towards understanding more fully what the taxa we call species really are.

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Phylogeny of *Elatostema* (Urticaceae) using chloroplast DNA data

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Abstract

Hadiah, Julisasi T.[1,2]*, Christopher J. Quinn*[2] *and Barry J. Conn*[2] *(*[1]*School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia;* [2] *Royal Botanic Gardens Sydney, Mrs Macquaries Road, Sydney, NSW 2000, Australia) 2003. Phylogeny of* Elatostema *(Urticaceae) using chloroplast DNA data.* Telopea *10(1) 235–246.* Phylogenetic analyses of the Urticales, based on chloroplast DNA data, support the monophyly of the Urticaceae, *Boehmeria, Pilea* and *Procris,* but not of *Elatostema*. Our result suggests that the circumscription of *Procris* is to be extended or included within *Elatostema*. At the tribal level, both Boehmerieae and Lecantheae appear paraphyletic, although this may be an artefact of the low taxon sampling. Preliminary analyses of relationships within *Elatostema* do not support the recognition of the subgenus *Pellionia*.

Introduction

Friis (1989 & 1993) provides a detailed comparison of morphological features of the Urticaceae at the familial, infrafamilial, and generic levels with a brief discussion of higher-level relationships based on previous classical taxonomic approaches. Recent phylogenetic studies involving the Urticaceae have concentrated on ordinal relationships. The circumscription of the Urticales has been relatively stable since the mid 1800s when Weddell (1856) included Artocarpeae, Cannabineae, Moreae, Ulmaceae and Urticaceae in the order. This classification was used by Thorne (1992) and Takhtajan (1997). Barbeyaceae was added by Dickison and Sweitzer (1970) and followed by Cronquist (1981), Dahlgren (1989), and Friis (1993). Cecropiaceae was proposed by Berg (1978) and placed close to Moraceae and Urticaceae. The reconstructed high-level phylogenies of Chase et al. (1993), using the DNA sequences of the chloroplast gene *rbc*L, support the monophyly of the Urticales with Cannabaceae, Moraceae, Ulmaceae and Urticaceae included. However, subsequent analyses including additional loci (Angiosperm Phylogeny Group 1998; Soltis et al. 2000) and non-molecular data (Judd et al. 1999) have shown this group to be nested within the Rosales. All these authors consider Cannabaceae, Celtidaceae, Cecropiaceae, Moraceae and Ulmaceae to be the closest families to Urticaceae.

Weddell (1854, 1856, 1869) revised the familial and infrafamilial classification of Urticaceae devised by Gaudichaud (1830) and recognised five tribes, namely, Lecantheae, Urereae (= Urticeae *sensu* Friis 1989), Boehmerieae, Parietarieae and Forskohleae (= Forsskaoleae *sensu* Friis 1989), renaming the tribe Lecantheae to Procrideae (Weddell 1856). Friis (1993) accepted Weddell's circumscription of these five tribes; however, he reversed the name Procrideae to Lecantheae (as accepted here). Friis (1989, 1993) characterised the Lecantheae as having staminodes that eject the mature achenes; leaves which are opposite, anisophyllous to completely reduced; intrapetiolar and fused stipules; and uniformly linear cystoliths. The Urticeae was characterised by the presence of stinging hairs. However, he questioned the distinctiveness of the other three tribes, and suggested further work may lead to a taxonomic rearrangement at the tribal level (Friis 1989).

Phylogenetic reconstruction of the Urticaceae using morphological data (Beaman 2000, Fig. 3-3), as part of a study of *Elatostema* from Mt Kinabalu (Malaysia), provided support for the monophyly of Lecantheae and Urticeae, but suggested that the Boehmerieae is polyphyletic. The Lecantheae consists of seven genera (Friis 1993), including *Elatostema,* the focus of our study. The genus consists of approximately 300 herbaceous to shrubby species (Friis 1993) that are characterised by having the female flowers arranged on a flattened discoid or lobed receptacle.

Schröter and Winkler (1935) recognized four subgenera within *Elatostema,* namely *Elatostema* (as *'Euelatostema'*), *Elatostematoides, Pellionia* and *Weddelia,* based on several features, but particularly the nature of leaves, stipules, inflorescence, and presence and form of the receptacle. Friis (1989, 1993) made no comment on the subgenera, but the analyses of Beaman (2000, 2001) did not support the arrangement.

This paper summarises the preliminary evaluation of different regions of the chloroplast genome for estimating relationships within Urticaceae, in general, and within *Elatostema,* in particular. As part of our continuing Urticaceae research program, we also aim to test the monophyly of the Lecantheae and *Elatostema.*

Materials

Plant materials used for the molecular work were either collected specifically for this project (namely from Indonesia — Sumatera, Java and Bali; and Australia — New South Wales, including Lord Howe Island) or are part of the horticultural collections at Royal Botanic Gardens Sydney. Fresh leaf material, particularly from the young shoots, cleaned and stored in airtight plastic bags with silica gel, was used for DNA analysis. These samples were stored at -20°C. The voucher specimens for DNA extracts are listed in Appendix 1 (all held at NSW).

Methods

Three regions of the chloroplast genome were selected for this study. The *rbc*L gene was chosen to test the monophyly of the family because of the availability in GenBank of sequences for representatives of several of the related families. Two potentially more informative regions were chosen to examine relationships within the family: the *atpß-rbc*L intergenic spacer and a region including the *trn*L intron, the *trn*L-F intergenic spacer, and the intervening *trn*L exon. For simplicity, the latter is henceforth referred to as *trn*.

DNA was extracted from 0.2-0.25 g silica gel dried leaves and purified using the protocol of Gilmore et al. (1993). The three regions were amplified by polymerase chain reaction (PCR) in an FTS-4000 Thermal Sequencer (Corbett Research, Mortlake NSW) using 20 µM of the primers as listed in Appendix 2. All the PCR products were purified using CONCERT™ Rapid PCR Purification System (protocol provided by manufacturer). The cleaned PCR products were auto-sequenced at SUPAMAC (Sydney University Prince Alfred Macromolecular Analysis Centre). The DNA sequences were edited and aligned using Sequencher 3.1.1. (Gene Codes Corp., Inc., Ann Arbor, Michigan) with subsequent manual adjustment. Sequences were then viewed in MacClade Version 4.03 (Maddison & Maddison 2001) to assist with the positioning of segments affected by insertion/deletion mutations (indels). Deleted segments were treated as missing data in the analyses.

Our data for *rbc*L and *trn* were supplemented by sequences of the following taxa obtained from GenBank: *Celtis sinensis* (Ulmaceae), *Dorstenia psilurus, Ficus pretoriae, Morus alba* (2 accessions) and *M. rubra* (Moraceae), *Cannabis sativa* and *Humulus lupulus* (Cannabaceae) as indicated in Appendix 1. Since Chase et al. (1993, figs 11B & 16) and Soltis et al. (2000, fig. 7) concluded that the Urticaceae, Cannabaceae, Moraceae and Ulmacaeae (Celtidaceae *sensu* Soltis et al.) form a strongly supported clade, species from the latter three families have been used for outgroup comparison in the *rbc*L analysis. This analysis was used to test the monophyly of Urticaceae. Outgroup choice for each of the other two data sets was based on the *rbc*L analysis, as set out below.

Heuristic searches were performed in PAUP* Version 4.0b10 (Swofford 2002) using tree bisection reconnection branch-swapping and the MULPARS option, with all characters equally weighted to find the most parsimonious trees. Analyses involved 100 replicates of random taxon addition in order to search for multiple islands of equally parsimonious trees. Branch lengths for trees were calculated using the ACCTRAN (accelerated transformation optimisation) option in PAUP. Relative support for the clades identified by parsimony analysis was estimated by jackknife with 10000 replicates of fast stepwise addition using 33% character deletion and 'emulate jac resampling'.

Results

The *rbc*L database

Sequences were generated for 9 ingroup taxa from the Urticaceae, and another two ingroup and seven outgroup sequences were added from GenBank. A total of 1346 aligned positions was included in the analyses, of which 226 (16.8%) were variable and 140 (10.4%) parsimony informative. Missing data constituted 6.5% of the database, the taxon with the most missing data being *Ficus pretoriae* (33%). Initial heuristic analyses gave a topology that did not accord with the family level relationships and cast doubt on the identity of two of the outgroup sequences obtained from GenBank: *Morus alba* L01933 and *Dorstenia psilurus.* A BLAST search (NCBI November 2002) placed the former among a group of *Prunus* sequences (Rosaceae), and the latter among Rhamnaceae. A further outgroup sequence belonging to *Prunus persica* (Table 1) was obtained from GenBank and added to the data set, and the analysis repeated using the two Rosaceae sequences as root.

Heuristic search found a single island of two trees of 374 steps, consistency index (CI) = 0.606 without uninformative characters, retention index (RI) = 0.708, and rescaled consistency index (RC) = 0.496. The strict consensus tree is shown in Figure 1. The names of the misidentified taxa are shown within inverted commas. There is strong support (95% jackknife) for a sister relationship between Urticaceae and the clade comprising Moraceae, Cannabaceae and Ulmaceae. The two sequences of each of *Elatostema* and *Procris* are strongly grouped (jackknife support $\geq$ 95%), as are the four sequences of *Boehmeria* (94% support), and there is 82% support for the monophyly of Urticaceae. *Pilea pumila* is placed sister to *Urtica dioica* (89% support) rather than with the other genera of the tribe Lecantheae, *Elatostema* and *Procris. Myriocarpa longipes*, of the Boehmerieae, is placed closer to all four of the above genera (80% support) than to the *Boehmeria* clade.

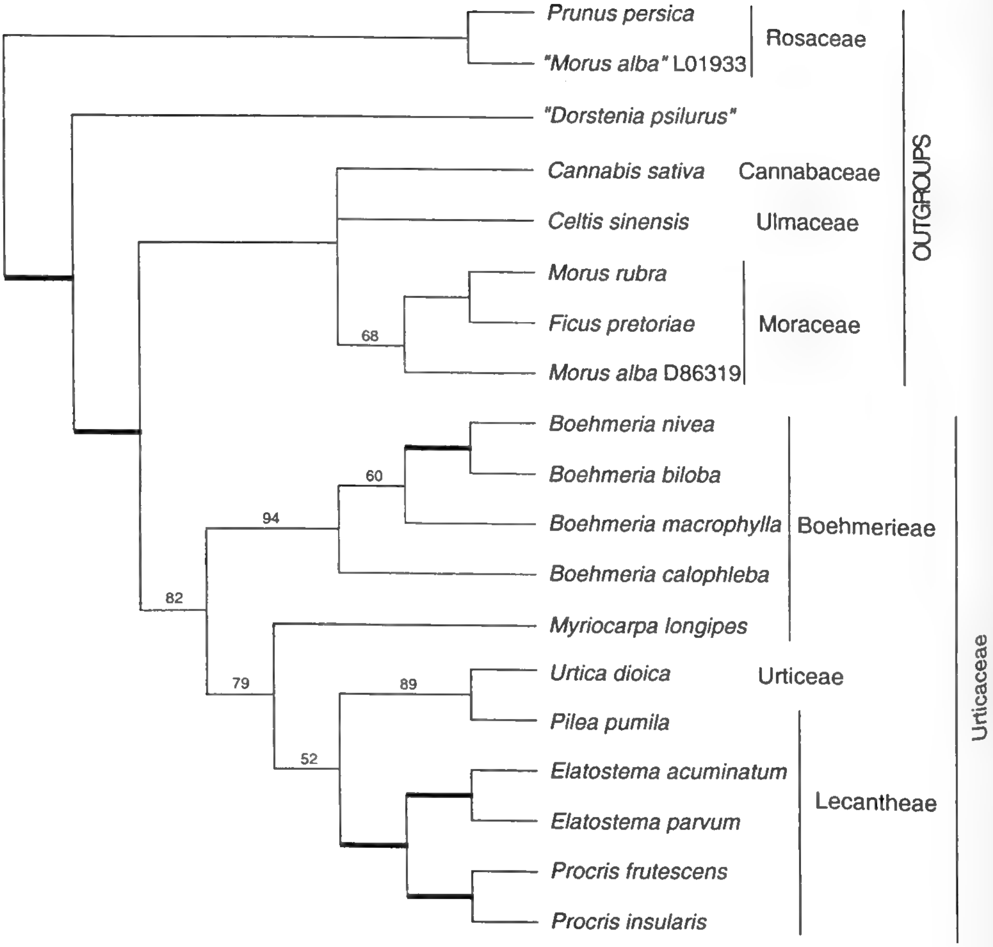

Fig. 1. Strict consensus of two equally parsimonious trees of 374 steps found from heuristic search of the *rbc*L data. CI = 0.606 excluding uninformative characters; RI = 0.708; RC = 0.496. Thick branches received >95% support; other jacknife values >50% shown above the clades.

The *atpß-rbc*L database

Fourteen species of Urticaceae were sequenced, thirteen representing Lecantheae (*Elatostema, Procris* and *Pilea*), and *Myriocarpa longipes* from the Boehmerieae *sensu* Friis (1993). The latter was used to root the analysis. Alignment required numerous indels ranging from 1-69 bp. The aligned data constituted 962 positions. There were 168 variable positions (17.5%), of which 84 (8.7%) were potentially informative. Six potentially informative indels, ranging from 1-10 bp, were scored as additional characters (sequence present/absent) and added to the database. Missing data constituted 14.9% of the data set.

Heuristic search found a single island of ten trees of 191 steps, CI = 0.922 excluding uninformative characters, RI = 0.948, RC = 0.908. The strict consensus of these trees is shown in Figure 2. The distributions of informative indels have been mapped on the tree. Both *Elatostema* and *Procris* are very strongly supported as monophyletic groups (100% and three and two indels, respectively), and there is 95% support for a sister relationship between them.

The *trn* database

Sequences were generated for 24 taxa representing 16 species or species groups of *Elatostema* and eight other species of Urticaceae. Sequences of two outgroup species, namely *Humulus lupulus* and *Cannabis sativa*, were taken from GenBank. A total of 1108 aligned positions were included in the analyses, which included 582 base pairs (bp) of the *trn*L intron, 50 bp of the *trn*L exon, and 449 bp of the *trn*L-F intergenic spacer (the last 4 bp of the spacer were omitted). Alignment required numerous indels involving from 1-101 bp. Missing characters constituted 16.2% of data, with the taxon having the highest proportion of missing data being *Cannabis sativa* (39.6%). Thirty-one potentially informative indels, ranging from 1-51 bp, were scored as sequence present or absent and added to the database. There were 431 (38.9%) variable positions, 258 of which (23.3%) were potentially informative.

Heuristic search found a single island of two equally parsimonious trees of 663 steps, CI = 0.733 excluding uninformative characters, RI = 0.846, RC = 0.688. The strict consensus of these trees is shown in Figure 3. The distributions of informative indels have been mapped on this cladogram (Fig. 3). The species pairs representing *Boehmeria, Pilea* and *Procris* are each strongly grouped (100%), but *Elatostema* appears paraphyletic, with *E. curtisii* and *E. repens* placed sister to *Procris* with 99% support, whereas the remaining members of *Elatostema* constitute a very robust clade (100% support). There is good support (91%) for a sister relationship between these two clades. Once again, *Urtica dioica* is placed sister to *Pilea*, but jackknife support for this relationship is very weak (54%).

Discussion

Friis (1993) provides a detailed discussion of morphological characters of the Urticaceae. He circumscribed the family as having basal ovaries and stamens that are elastic and reflexed (Friis 1989, 1993). However, he does not provide a phylogenetic interpretation of these data. The monophyly of the Urticaceae was tentatively supported by Beaman (2000), based on morphological characters.

The analysis of the *rbc*L data, which places all Urticaceae within a clade that is sister to the five taxa belonging to three of the other five families of the order Urticales *sensu* Cronquist (1981), provides support for the concept of the family. The ingroup clade, which comprises 11 sequences drawn from six genera and three of the five tribes, receives 82% jackknife support. The current tribal arrangement, however, receives no

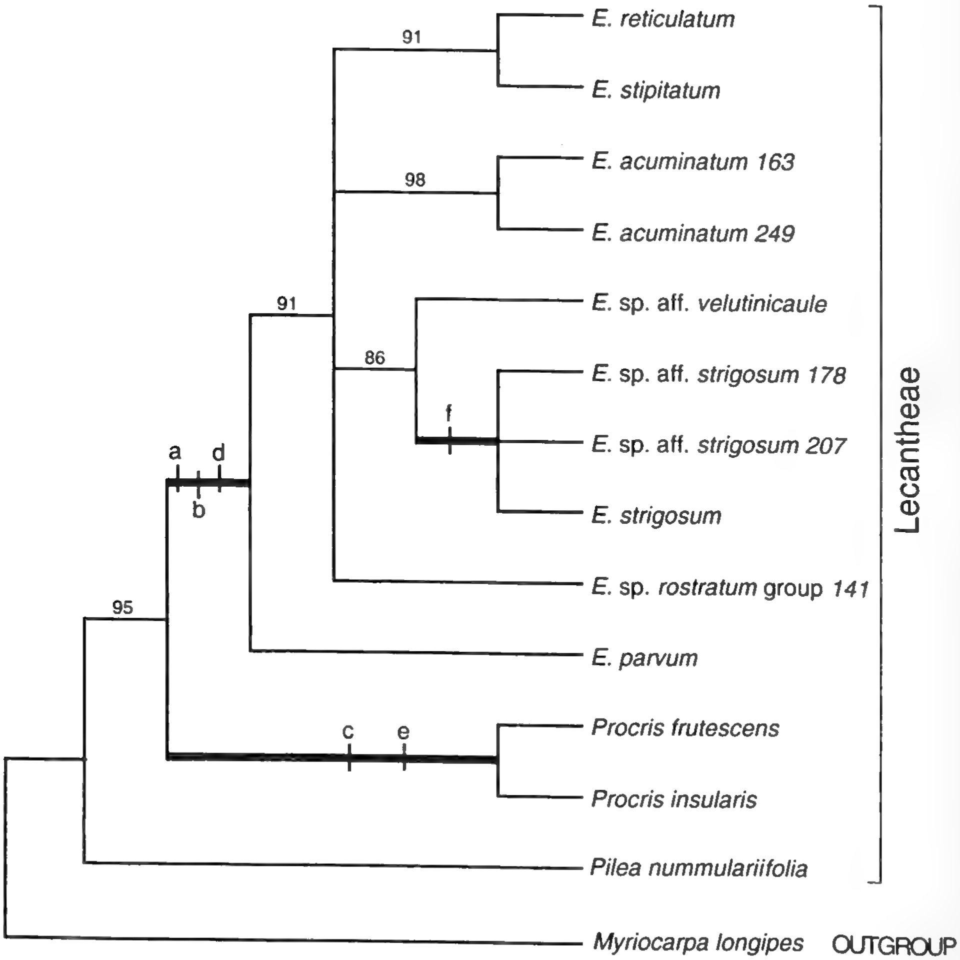

Fig. 2. Strict consensus of the 10 equally parsimonious trees of 191 steps found from heuristic search of the *atpß-rbc*L spacer data set; CI = 0.922 excluding uninformative characters; RI = 0.948; RC = 0.908. Thick branches received 100% jackknife support; other values > 50% shown above the branches. Distributions of indels a-f are mapped on the tree. *E.*, *Elatostema*.

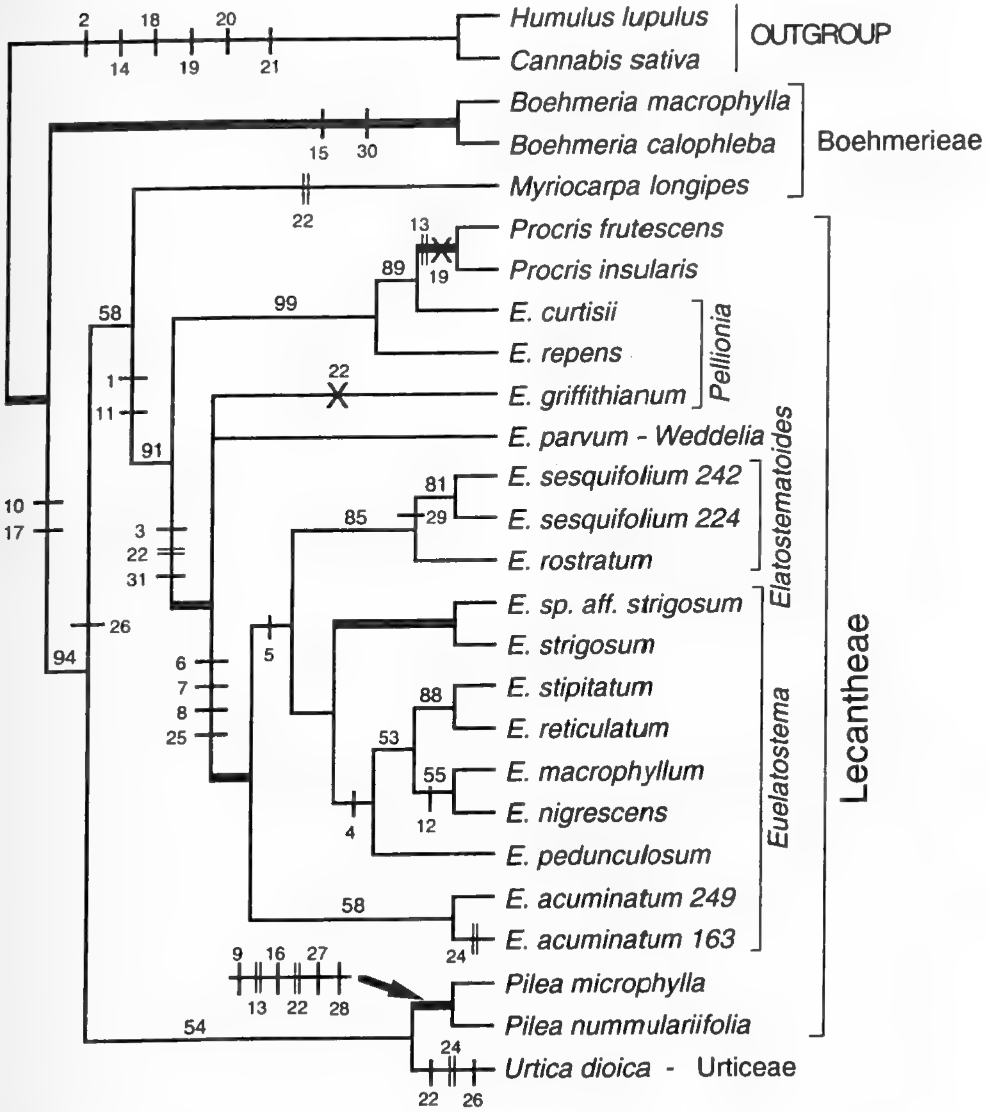

Fig. 3. Strict consensus of two equally parsimonious trees of 663 steps found from heuristic search of the *trn* data set; CI = 0.733 excluding uninformative characters; RI = 0.846; RC = 0.688. Thick branches received 100% jackknife support; other values >50% shown above the branches. Distributions of 31 scored indels have been mapped on the tree; single bar indicates unique origin; double bar indicates homoplasy; X indicates reversal. *E.*, *Elatostema*.

support. In both Figures 1 and 3, the Lecantheae (*Elatostema, Pilea* and *Procris*) and Boehmerieae (*Boehmeria* and *Myriocarpa*) are paraphyletic. Constraint analyses of the *trn* data set revealed that an extra 15 steps are required over and above the most parsimonious tree to render the Lecantheae monophyletic, and a total of 31 extra steps are needed to make both tribes monophyletic. It can be concluded, therefore, that there is considerable strength in these data to reject the present tribal arrangement of these genera. The grouping of *Pilea* with *Urtica*, however, which is apparent in both analyses, may well be an artefact of the low taxon sampling. It is only weakly supported on the *trn* data (54%), and both genera are on very long terminal branches (data not presented here).

The monophyly of *Boehmeria, Pilea* and *Procris* received high levels of jackknife support in all the analyses where more than one species was included, but the more extensive sampling of *Elatostema* in the *trn* analysis revealed it to be paraphyletic with respect to *Procris*. Support for the grouping of *Elatostema curtisii* and *E. repens* with *Procris* is very robust (99%).

Support for the '*Elatostema-Procris*' clade is high in all three data sets. The placement of the latter genus within *Elatostema* in the *trn* analysis, supports the broader concept of *Elatostema* adopted by Hallier (1896) and Winkler (1922). An alternative conclusion is that the current circumscription of *Procris* should be extended such that this group could be maintained as a separate genus. It is clear from Figure 3 that even as a subgenus, the limits of *Procris* need to be extended to include further species (eg. *Elatostema curtisii* and *E. repens*) currently assigned to *Elatostema*. The robust grouping (100%) of *E. griffithianum* with species of subgenera *Elatostema, Elatostematoides* and *Weddelia* indicates that the morphological basis for the recognition of subgenus *Pellionia* (Schröter & Winkler 1935 & 1936) (or as a distinct genus – as classified by Weddell 1856, Robinson 1910, Friis 1989), at least, is not supported by the molecular data. Beaman (2000, 2001), using morphological features, also concluded that subgenus *Pellionia* was not distinct from the other subgenera. Furthermore, the current circumscriptions of the first three subgenera are also not supported by molecular data.

Overwhelmingly, the distributions of indels are congruent with the estimate of the phylogeny obtained primarily from the substitution data, and they can be seen to support many of the clades: e.g. both species of *Pilea* are characterised by four unique indels (9, 16, 27 & 28) and another two (13 & 22) that also arise on other lineages (Fig. 3). All six of the informative indels in atpß-*rbc*L required only a single origin when their distributions were mapped on the strict consensus tree (Fig. 2), and only three of the 31 informative indels (13, 22 & 24) in the *trn* region required more than one origin (Fig. 3). Two of these (indels 13 and 24) involved the gain or loss of a single base pair from non-coding regions. Multiple origins of such indels in intergenic spacers have been frequently observed (e.g. Golenberg et al. 1993, Lowrey et al. 2001). Indels 19 and 22 required reversals (Fig. 3), but resolution of the trichotomy so that *Elatostema parvum* diverged after *E. griffithianum* would remove the need for the reversal in the latter case. The outgroup (Cannabaceae) differ from the ingroup by six indels (2, 14, 18, 19, 20 & 21), although indel 19 (a 6 bp insertion) has been subsequently lost in both species of *Procris*. This case of homoplasy (reversal or parallel origins) is interesting, since the indel is not a duplication of adjacent sequence, a type that has been observed to be common in spacer regions (Golenberg et al. 1993, Kelchner & Clark 1997). It is possible that secondary structure of the *trn*L-F spacer region may be responsible for the loss of the inserted region in its entirety, although there was no evidence of complementary segments of sequence on either side of the insertion which might promote the formation of a loop (Kelchner & Wendel 1996).

Sequences for all three regions could be confidently aligned across the family. Both the *trn* and *rbc*L data sets could be rooted outside the family, and yielded good resolution of generic relationships. The latter, however, provided only low levels of variability: e.g. the uncorrected pairwise sequence divergence between *Elatostema acuminatum* and *E. parvum* was only 0.7%. As a result, jackknife support for clades was often relatively low even in this small taxon set. It is concluded that this region of the chloroplast genome is insufficiently variable to provide robust resolution of relationships within the genus. The *trn* region provided the highest proportion of variable characters: the uncorrected pairwise divergence between *E. acuminatum* and *E. parvum* was 5.1%. Hence, this is the most promising of the three regions trialled here for resolving interspecific relationships within *Elatostema*. Even within this region, however, relationships were not fully resolved in a very limited taxon sample (Fig. 3), and pairwise divergences between species are frequently very low: e.g. 0.02% for *E. reticulatum* cf. *E. stipitatum*, 0.04% for *E. rostratum* cf. *E. sesquifolium*. It therefore appears that robust resolution of species relationships within the genus will require a more variable region of DNA. The nuclear encoded intergenic transcribed spacer region of the rDNA is currently being investigated for this purpose.

Finally, the recognition of the misidentification of two of the outgroup sequences highlights the caution that must be exercised about the authenticity of sequences lodged in GenBank and the importance of including voucher details when sequences are lodged — in this case no voucher was provided by either author.

Conclusion

Phylogenetic analyses of the Urticales, based on chloroplast DNA sequences, provided support for the monophyly of the Urticaceae, but not for the tribe Lecantheae. However, the apparent paraphyletic nature of the tribe may be an artefact of low taxon sampling, particularly in the Urticeae. Although *Boehmeria* is monophyletic, the Boehmerieae is polyphyletic, with the tribal position of *Myriocarpa* uncertain. The genus *Elatostema*, a member of the Lecantheae, has been shown to be paraphyletic, having the segregate genus *Procris* embedded within it. The preliminary analyses of infrageneric relationships within *Elatostema* do not support the recognition of the subgenus *Pellionia*.

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Appendix 1. List of voucher specimens for DNA extracts and GenBank numbers for sequences. (Classification of Urticaceae follows Friis 1989, 1993).

Taxa	**Voucher No.**	***rbc*L**	***atp*B-*rbc*L**	***trn* region**
CANNABACEAE				
Cannabis sativa		AJ390068		AJ390367
Humulus lupulus				AB033889 — intron AB033890 — spacer
MORACEAE				
"Dorstenia psilurus"		AJ390066		
Ficus pretoriae		AJ390067		
Morus alba		D86319		
"M. alba"		L01933		
M. rubra		U06812		
ROSACEAE				
Prunus persica		AF206813		
ULMACEAE				
Celtis sinensis		D86309		
URTICAEAE				
Boehmerieae				
Boehmeria biloba		AJ390069		
B. calophleba	Hadiah 393	AY208700		AY208723
B. macrophylla	Hadiah 394	AY208701		AY208722
B. nivea		AJ235801		
Myriocarpa longipes	Hadiah 395	AY208705	AY208720	AY208724

Appendix 1. cont.

Taxa	Voucher No.	*rbc*L	*atp*B-*rbc*L	*trn* region
Lecantheae				
Elatostema – Elatostemoides				
E. rostratum	Hadiah 144			AY208743
E. rostratum group	Hadiah 141		AY208714	
E. sesquifolium	Hadiah 224			AY208742
E. sesquifolium	Hadiah 242			AY208741
Elatostema – Elatostema				
E. acuminatum	Hadiah 163		AY208710	AY208745
E. acuminatum	Hadiah 249	AY208702	AY208711	AY208744
E. macrophyllum	Hadiah 245			AY208739
E. nigrescens	Hadiah 256			AY208740
E. pedunculosum	Hadiah 312			AY208738
E. reticulatum	Perkins 00/01		AY208708	AY208737
E. stipitatum	Perkins 00/02		AY208709	AY208736
E. strigosum	Hadiah 159		AY208717	AY208735
E. sp. aff. *strigosum*	Hadiah 178		AY208715	AY208734
E. sp. aff. *strigosum*	Hadiah 207		AY208716	
E. sp. aff. *velutinicaule*	Hadiah 183		AY208713	
Elatostema – Pellionia				
E. curtisii	Hadiah 427			AY208731
E. griffithianum	Hadiah 351			AY208732
E. repens	Hadiah 445			AY208730
Elatostema – Weddelia				
E. parvum	Hadiah 154	AY208703	AY208712	AY208733
Pilea microphylla	Hadiah 398			AY208726
P. nummulariifolia	Hadiah 389		AY208721	AY208727
P. pumila		AF206811		
Procris frutescens	Hadiah 149	AY208704	AY208718	AY208728
P. insularis	Hadiah 390	AY208706	AY208719	AY208729
Urticeae				
Urtica dioica	Hadiah 391	AY208707		AY208725

Appendix 2. Primers use for PCR (P) and sequencing (S); F, forward; R, reverse.

Region	Use	Primer	Reference or sequence
*rbc*L	P/F	*rbc*L 1	GGGATTTATGTCACCACAAACAGA – P. Gadek, unpubl.
	P/R	*rbc*L 2	GATCTCCTTCCATACTTCACAAGC – P. Gadek, unpubl.
	S/F	861	TGGACCACTGTTTGGACCGA – P. Gadek, unpubl.
	S/F	381	GCAGTTATTGACAGACAAAGAAATCATGGT – P. Gadek, unpubl.
	S/R	497	ACCATGATTCTTCTGCCTATCAATAACTGC – P. Gadek, unpubl.
*atp*ß-*rbc*L	P/F	377	Crayn & Quinn (2000)
	P/R	520	O'Brien et al. (2000)
	S/F	2603	Crayn & Quinn (2000)
	S/R	2604	Crayn & Quinn (2000)
	S/R	2607	Crayn & Quinn (2000)
*trn*L-F	PS/F	B49317	Taberlet et al. (1991)
	PS/R	CalTabF	GTCCTCTGCTCTACCAACTG – A. Perkins, unpubl.
	PS/R	A50272	Taberlet et al. (1991)
	S/F	AdTabB2	Briggs et al. (2000)
	S/R	A49855	Taberlet et al. (1991)

Molecular phylogenetic systematics in the Dendrobiinae (Orchidaceae), with emphasis on *Dendrobium* section *Pedilonum*

M.A. Clements

Abstract

Clements, M.A. (Centre for Plant Biodiversity Research, Australian National Herbarium, G.P.O. Box 1600, Canberra, A.C.T. 2601, Australia) 2003. Molecular phylogenetic systematics of the Dendrobiinae (Orchidaceae), with emphasis on Dendrobium *section* Pedilonum. Telopea *10(1): 247–298.* Molecular systematic research using the internal transcribed spacer (ITS) region of the 18–26S nuclear ribosomal DNA repeat unit, on representatives of most taxonomic units within the Dendrobiinae has provided independent support, in addition to morphological and biological data, for the phylogenetic reassessment of the taxon. At a broad level, the Dendrobiinae is polyphyletic with *Epigeneium* forming an independent clade; *Dendrobium* section *Oxystophyllum* is deeply embedded within one of the outgroups, subtribe Eriinae: Podochileae; and the remaining taxa isolated into two major groups, viz the Asian and Australasian clades. A detailed study of part of the Asian clade, with emphasis on representatives of the morphologically based *Dendrobium* section *Pedilonum*, groups species into seven major clades. *Dendrobium* section *Pedilonum* is shown to be non-monophyletic with most species previously interpreted as belonging to it being well isolated from *D. secundum*, the designated type of that taxon, and interspersed amongst representatives of *D.* section *Calcarifera, Calyptrochilus, Cuthbertsonia, Dendrobium, Dolichocentrum, Oxyglossum* and *Platycaulon*. *Dendrobium* section *Rhopalanthe*, which separates the two major clades containing representatives of *D.* section *Pedilonum*, is itself paraphyletic with representatives of sections *Aporum* and *Bolbidium* embedded within it. These molecular results, combined with morphological data, provide a strong basis for a reassessment of the phylogeny of part of the study taxon. A reclassification of this part of the Dendrobieae and Podochileae is provided in Appendix 2, including: re-instatement of the genus *Oxystophyllum* (Eriinae: Podochileae); the recognition and description of subtribes Epigeneiinae and Grastidiinae (Dendrobieae); recognition or re-instatement of the genera *Aporum, Callista, Ceraia, Coelandria, Eurycaulis, Distichorchis, Pedilonum* as distinct from *Dendrobium*; the elevation of *Anisopetala* to generic status; and where necessary the transfer of the appropriate species from *Dendrobium* to these genera.

Introduction

The Dendrobiinae Lindl. comprises a diverse group of epiphytic, lithophytic and terrestrial herbs classified in six genera in current usage containing approximately 1150 species (Dressler 1993). Species within these genera are distributed predominantly throughout paleotropical regions with extensions to temperate Asia (Seidenfaden 1985, 1992, Seidenfaden & Woods 1992), the Philippines (Ames 1908, Quisumbing 1934), the Malay archipelago (Smith 1905, Comber 1990, Wood et al. 1993), New Guinea (Schlechter 1912, van Royen 1979), Australia (Rupp 1947, Dockrill 1969, Jones 1999), New Caledonia (Hallé 1997), south-west pacific islands (Lewis & Cribb 1989, 1992, Kores 1991, Cribb & Whistler 1996), and New Zealand (Moore 1972). Members of the Dendrobiinae vary considerably in their floral and vegetative morphology, especially in the southern part of their range, making them prime candidates for studies of character evolution. The subtribe has already been the focus of a broad taxonomic study (Brieger 1981) and phylogenetic studies based on analysis of chloroplast DNA restriction sites (Yukawa et al. 1993, 1996) and chloroplast DNA sequences (Yukawa et al. 2000).

The subtribe Dendrobiinae was created in 1829, as a section within the tribe Malaxideae Lindl., accompanying the description and illustration of *Dendrobium secundum* (Blume) Lindl. in the Botanical Magazine (Lindley 1829). Thereafter Lindley enumerated his concept of Dendrobiinae, embracing 20 genera and grouping them together on the possession of two, four or eight pollinia (Lindley 1830). *Dendrobium* Sw. was grouped together with ten other genera including *Aporum* Blume, *Macrostomium* Blume, *Bulbophyllum* Thouars and *Polystachya* Hook. on account of the possession of four naked pollinia. Most subsequent authors including Lindley (1851), Reichenbach (1861), Bentham (1881), Bentham and Hooker (1883), Pfitzer (1882, 1889), Schlechter (1905, 1912, 1926), Dressler and Dodson (1960) and Dressler (1972, 1979, 1981), have progressively narrowed the interpretation of the Dendrobiinae so that Dressler (1993), in his most recent classification of the family, recognised only six genera with approximately 1150 species within the subtribe, viz *Cadetia* Gaudich. (67 spp.), *Dendrobium* (c. 900 spp.), *Diplocaulobium* Kraenzl. (94 spp.), *Epigeneium* Gagnep. (12 spp.), *Flickingeria* A. Hawkes (70 spp.) and *Pseuderia* Schltr. (4 spp.).

However, the systematic position and presumed monophyly of the Dendrobiinae *sensu* Schlechter (1926) was questioned when Brieger (1981) published an account of the group as part of a revised classification of the family. He noted that Lindley had united a great number of taxa into two huge collective genera, *Dendrobium* and *Eria*. Thereafter, with the description of many additional species, it became necessary to create a sometimes complex, infra-generic structure to accommodate the various forms being described within each of these large genera, e.g. Bentham and Hooker (1880), Pfitzer (1889), Kraenzlin (1910), Schlechter (1912). However, in Kraenzlin's complex, and confusing thesis on the Dendrobiinae, he proposed the re-instatement and recognition of several segregate genera within the subtribe, *viz. Callista* Lour., *Inobulbum* (Schltr.) Schltr. et Kraenzl. [as *Inobulbon*], *Sarcopodium* Lindl., *Diplocaulobium* (Rchb.f.) Kraenzl. and *Desmotrichum* Blume. Thereafter, the situation changed slightly with a push towards the acceptance or recognition of several of these segregate genera, so that by 1980 typically in the scientific literature six genera were recognised within the Dendrobiinae and eight in the Eriinae (Dressler 1981). Brieger (1981) took the classification of the subtribes Dendrobiinae and Eriinae to new levels of confusion, combining them into one large subtribe containing six informal categories that he termed 'Genera-Series' based on overall perceived similarities of vegetative and floral morphology. He also reinstated, recognised and described many new genera within this framework. The systematic position of the Dendrobiinae also came under scrutiny as a result of studies of embryological development, from representatives of the Orchidaceae including the Dendrobiinae (Clements 1995, 1996, 1999, unpublished). These studies provided independent evidence that the Dendrobiinae, and more particularly *Dendrobium*, was polyphyletic with respect to the Eriinae (Podochileae), where different embryo types were identified within these taxa. Results from phylogenetic analyses of *rbc*L and *mat*K plastid sequences and cpDNA restriction sites in the Dendrobiinae (Yukawa et al. 1993, 1996, 2000, Yukawa & Uehara 1996) also supported similar conclusions. These authors concluded that the Dendrobiinae is polyphyletic and comprises four major clades: (i) *Pseuderia* which was shown to belong to the Podochilinae [?](Yukawa et al. 1996); (ii) *Epigeneium*; (iii) *Dendrobium* Clade 1 containing species predominantly inhabiting mainland Asia, including the type of the genus; and (iv) *Dendrobium* Clade 2 containing taxa including *Cadetia, Diplocaulobium* and *Flickingeria* widespread mostly in Australasia and the Pacific Islands. It was on the basis of these results and some unpublished data that genera such as *Dockrillia* Brieger (Clements & Jones 1996), *Grastidium* Blume (Clements & Jones 1997), *Inobulbum* (Schltr.) Schltr. et Kraenzl. (Clements & Jones 1998a), *Tetrodon*

(Kraenzl.) M.A.Clem. et D.L.Jones (Clements and Jones 1998a), *Winika* M.A.Clem., D.L.Jones et Molloy (Clements et al. 1997), and *Cannaeorchis* M.A.Clem. et D.L.Jones (Clements & Jones 1998b) from the Malesian and Australasian regions have been recognised, reinstated or described.

Dendrobium section *Pedilonum*

One characteristic group of species in *Dendrobium*, often with extremely colourful flowers, and frequently encountered throughout the Malesian region, which as yet has received little attention at the molecular level, is *Dendrobium* section *Pedilonum* and its associated sections *Calyptrochilus, Cuthbertsonia* and *Oxyglossum*. Brieger (1981) treated these taxa in genus series *Dendrobia,* all as part of the genus *Pedilonum,* and he added two further sections formerly treated as part of *Dendrobium*, section *Sanguinolenta* and section *Platycaulon*. *Dendrobium* section *Pedilonum* was described by Blume in 1825 but then, almost immediately, he treated it at generic rank (Blume 1825). Blume considered *Pedilonum* distinct from *Dendrobium* by the absence of an articulate, slipper shaped labellum and included six species in the genus. He divided *Pedilonum* into two unnamed sections: one, containing *P. kuhlii* and *P. hasseltii,* was distinguished by possession of an elongate, laterally compressed sack formed by fusion of the lateral sepals not adnate to the labellum claw; the second, containing *P. secundum, P. undulatum, P. biflorum* and *P. erosum,* was distinguished by lateral sepals forming an elongate spur often adnate to the labellum claw. Over 140 species have since been assigned to *Pedilonum* all as *Dendrobium,* mainly by Miquel (1859), Pfitzer (1888), Hooker (1890), Ridley (1896), Bailey (1902), Kraenzlin (1910), Schlechter (1905, 1912), and Seidenfaden (1985).

Kraenzlin (1910) in his monograph of *Dendrobium* divided the genus into ten subgenera, including subgenus *Pedilonum,* all roughly equivalent to the sections of earlier authors. He treated 137 species within subgenus *Pedilonum* and further divided it into five sections, viz. *Secunda, Glomerata, Capitata, Ceratobium* and *Brevisaccata*. Of these five sections only the first three contain species closely related to *Pedilonum* as considered by authors such as Schlechter (1910, 1911a & b, 1912, 1914, 1921, 1923a & b, 1925), Smith (1908b, 1909, 1910a,b & c, 1911a, b & c, 1912, 1913, 1916, 1917, 1918, 1919, 1020, 1922, 1924, 1925, 1926, 1927a & b, 1928a,b & c, 1929, 1930, 1933a & b, 1934a ,b & c) and van Royen (1979).

Schlechter (1912), in his account of *Dendrobium* in the Orchids of German New Guinea, considered section *Pedilonum* to be part of subgenus '*Eu-Dendrobium*', which he distinguished as those taxa possessing: leaves upon distinct sheaths; stems pseudobulbous or fleshy for their whole length; and the absence of any longitudinal splitting of the labellum into well defined lobes. He also considered that section *Pedilonum* shared these characteristics with sections *Dendrobium, Platycaulon, Calyptrochilus, Cuthbertsonia* and *Oxyglossum*. He further characterised section *Dendrobium* as having the habit of two- to multi-flowered lateral inflorescences with spreading flowers, and an undivided, rotund labellum in most cases internally finely papillate. Section *Platycaulon* was characterised by the much-flattened, compressed pseudobulbs and the labellum veins thickened frequently into ridges. Section *Calyptrochilus* was characterised by the labellum, which at the apex is turned inwards and cucullate, and with finely serrate margins, an elongated column-foot adnate with the margins of the labellum forming a spur. Section *Cuthbertsonia* included species with short pseudobulbs but with a peculiar papillose covering of the leaves and outside of the flowers, particularly the ovaries; the flowers werecharacteristic of those found in the previous section minus the serrate inward facing labellum apices. Section *Oxyglossum* was also characterised by the short pseudobulbs, two but occasionally multi-flowered inflorescence, an ovary with three to ten, sharp wings, and an attenuate labellum with a brightly coloured, sharp apex.

By comparison, Brieger (1981) recognised *Pedilonum* at generic rank with six sections, viz. *Pedilonum, Calyptrochilus, Cuthbertsonia, Oxyglossum, Sanguinolenta (Calcarifera)* and *Platycaulon*. Section *Sanguinolenta* was created by Brieger (1981) to account for a group of species typified by *D. sanguinolentum*, possessing 'stem axes uniformly cylindrical, with numerous leaves, rarely non-uniformly thickened, not flattened; labellum narrow at base, broadening and with erect margins, indistinct, rarely distinctly trilobed'. The section is more or less equivalent to Smith's *D.* section *Calcarifera* which he characterised as differing from section *Pedilonum* by the labellum which is larger, broader, and usually more or less lobed and has a tooth protruding into the mentum. Based upon Brieger's interpretation of the subtribe, Rauschert (1983) made hundreds of automatic transfers to various genera including *Pedilonum* although authors such as Seidenfaden (1985) and Cribb et al. (1985) criticised these taxonomic changes.

Since there is obviously much confusion surrounding the status and circumscription of *Pedilonum* and associated taxa, I decided to investigate furthur the relationships of such a prominent member of the Dendrobiinae in the Malesian region. The main purpose of this study was therefore to: (i) contribute to our understanding of the phylogenetic relationships in the Dendrobiinae; (ii) determine if *Pedilonum* and associated taxa are monophyletic, based on analyses of the internal transcribed spacer (ITS) region of 18-26S nuclear ribosomal DNA, an independent data set; and (iii) clarify the status of *Pedilonum* and allied taxa. This study also offers the opportunity to further unravel the confusion that currently surrounds the status of *Dendrobium* sens. lat., and subtribe Dendrobiinae and tribe Dendrobieae of which it is a part.

Methods

Plant material. Material of 75 species representative of genera in the Dendrobiinae and sections within *Dendrobium*, but in particular those associated with section *Pedilonum*, were used in this study. Outgroups were chosen on the basis of previous studies and are roughly equivalent to those used by Yukawa et al. (1996, 2000) and comprised species of *Bryobium*, *Eria* (Eriinae: Podochileae), *Adelopetalum*, *Bulbophyllum*, *Oxysepala* (Bulbophyllinae: Dendrobieae), *Liparis* (Malaxideae) and *Drymoanthus* (Aeridinae: Vandeae) (Appendix 1). Species used in this study were carefully chosen from amongst representatives of the c. 290 species in the study group for which sequences were available. Fresh leaf samples were collected either in the field or from cultivated plants of known provenance. All collections are vouchered and deposited at the Australian National Herbarium (CANB) (Appendix 1).

DNA extraction and PCR and sequencing procedures. Genomic DNA extraction and sequencing procedures used are the same as those described in the preparation of material for the analyses of the Diurideae (Clements et al. 2002). The complete sequence of the ITS1–5.8S–ITS2 region for each sample was edited and assembled from the sequencing chromatograms using Sequencher 3.0 software (Gene Codes Corporation). The sequences have been submitted to GenBank and given accession numbers as shown in Appendix 1.

Method of alignment and sequence analysis. Sequences were first aligned using the EclustalW program supplied by the Australian National Genomic Information Service (ANGIS) Multiple alignment parameters were set at the default values; a gap opening penalty of 10 (range 1–100), a gap extension penalty of 5 (range 0.10–100) and gap separation penalty of 8 (range 1–50). Sequences were manually re-aligned, using

BioEdit version 4.7.8. The re-aligned files were converted to PAUP/NEXUS format, exported to MacClade and analysed using PAUP version 4.0b4a. The most parsimonious trees were determined using a heuristic search algorithm with 100 replicates of random taxon entry, TBR branch swapping and the 'Multrees' option. Successive weighting (Farris 1969) was applied through recalculation of the rescaled consistency indices until a stable position was attained. Bootstrap analyses were done for both unweighted and weighted trees to determine the relative support for the resultant clades (Felsenstein 1985), and all minimal length trees saved. These equally parsimonious trees were summarised by generating a consensus tree.

Results

An overall assessment of the Dendrobieae, centered on the Dendrobiinae, was first undertaken through a sequence analysis of 23 species, representative of most major taxonomic groups used in previous studies of the group (Yukawa et al. 1993) including seven outgroup species, viz. *Bryobium, Eria* (Eriinae: Podochileae), *Adelopetalum, Bulbophyllum* and *Oxysepala* (Bulbophyllinae: Dendrodieae), *Liparis* (Malaxideae) and *Drymoanthus* (Aeridinae: Vandeae). The alignment used contained 786 nucleotide sites of which 324 were potentially parsimony-informative. Analysis of this computer based alignment produced 3 equally parsimonious trees; tree length = 1440; consistency index (CI) = 0.5743; retention index (RI) = 0.4853; and rescaled consistency index (RC) = 0.2787. One of these trees is shown in Figure 1.

These results show a polyphyletic Dendrobiinae with: (i) *Dendrobium* section *Oxystophyllum* deeply embedded within the strongly supported (100% bootstrap support) Eriinae (Podochileae), (ii) a strongly supported (96% bootstrap support) monophyletic *Epigeneium* sister to the remainder of the Dendrobiinae, and (iii) the remaining representatives of the Dendrobiinae separated into two major groups, the Australasian and Asian clades. Excluding *Dendrobium* section *Oxystophyllum* these results reveal only weak support (<50% bootstrap support) for the monophyly of the remainder of the ingroup including *Epigeneium*. Conversely there is moderately strong support for monophyly of *Epigeneium*, the Australasian (85% bootstrap support) and Asian (91% bootstrap support) clades. These results also show that the Dendrobieae is polyphyletic when the Bulbophyllinae is included, with the Eriinae (Podochileae) deeply embedded within it.

A more comprehensive molecular phylogenetic analysis was then undertaken based on the inclusion of an additional 52 species, mostly representative of the Asian clade from within the Malesian and Australasian regions, and in particular those attributed in the literature to *Dendrobium* section *Pedilonum* and associated taxa *viz.* sections *Aporum, Calcarifera, Cuthbertsonia, Calyptrochilus, Dendrobium, Dolichocentrum, Oxyglossum and Rhopalanthe.* This analysis, based on an alignment of 768 nucleotide sites of which 444 were potentially parsimony-informative, produced 122 equally parsimonious trees; tree length = 2726; consistency index (CI) = 0.3899; retention index (RI) = 0.6719; and rescaled consistency index (RC) = 0.2620. Successive weighting was then applied resulting in three trees, all with the same general topography. One randomly selected tree is shown as a phylogram in Fig. 2. These results again show the polyphyletic condition of the Dendrobiinae and its fragmentation into two separate component groups, the larger of which is only weakly supported by both nuclear and plastid molecular analyses but contains three major, well-supported clades. *Dendrobium* section *Oxystophyllum* with *Epigeneium* remain isolated from the main body of the Dendrobiinae. Some of the species that were added in the more comprehensive analyses (*Winika cunninghamii, Cannaeorchis fractiflexa, Dendrobium*

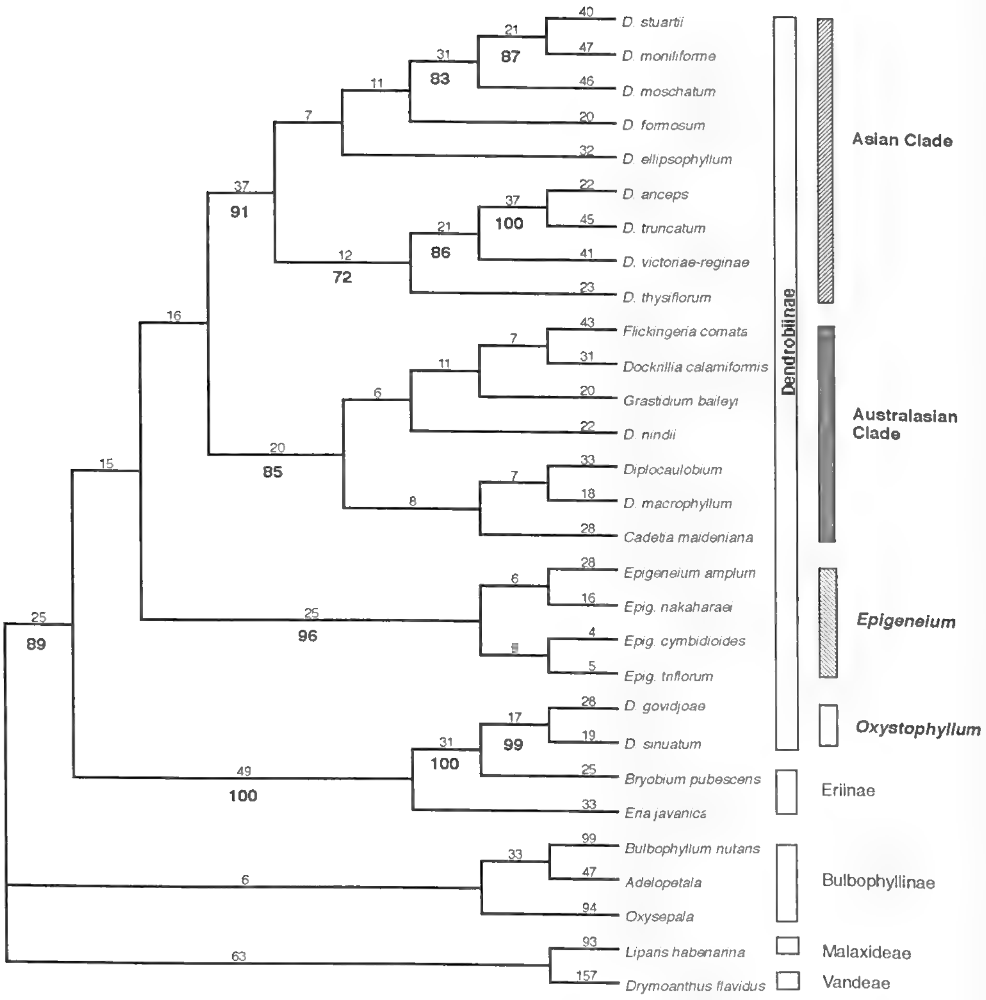

Fig. 1. One of three most parsimonious trees generated from the broad based data matrix based on nuclear ITS sequences, showing the composition of the Dendrobiinae with *Oxystophyllum*, *Epigeneium* and Australasian and Asian clades identified relative to 7 outgroup species: L. = 1440, CI = 0.5743, RI = 0.4853. Numbers above branches are branch length estimates (ACCTRAN optimalization); bootstrap percentages greater than 50% are given below in bold.

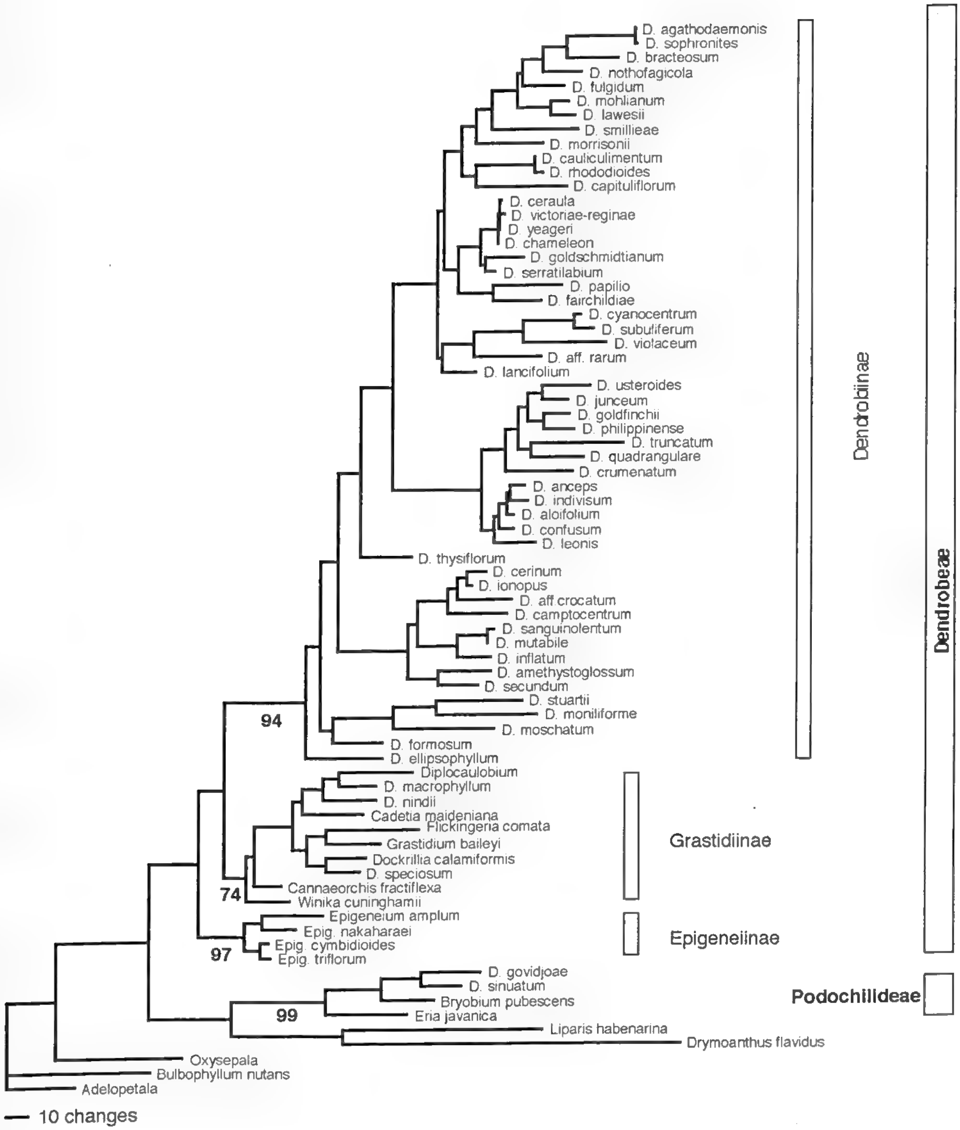

Fig. 2. A phylogram of one of the three most parsimonious successively weighted trees from the ITS analysis of a study of the Dendrobiinae and outgroup taxa based on 75 species: L = 2728, CI = 0.3897, RI = 0.6715, showing the relationships between groups when all study species are included. Bootstrap percentages (50% or more) for the four main taxa containing elements of the Dendrobiinae are in bold.

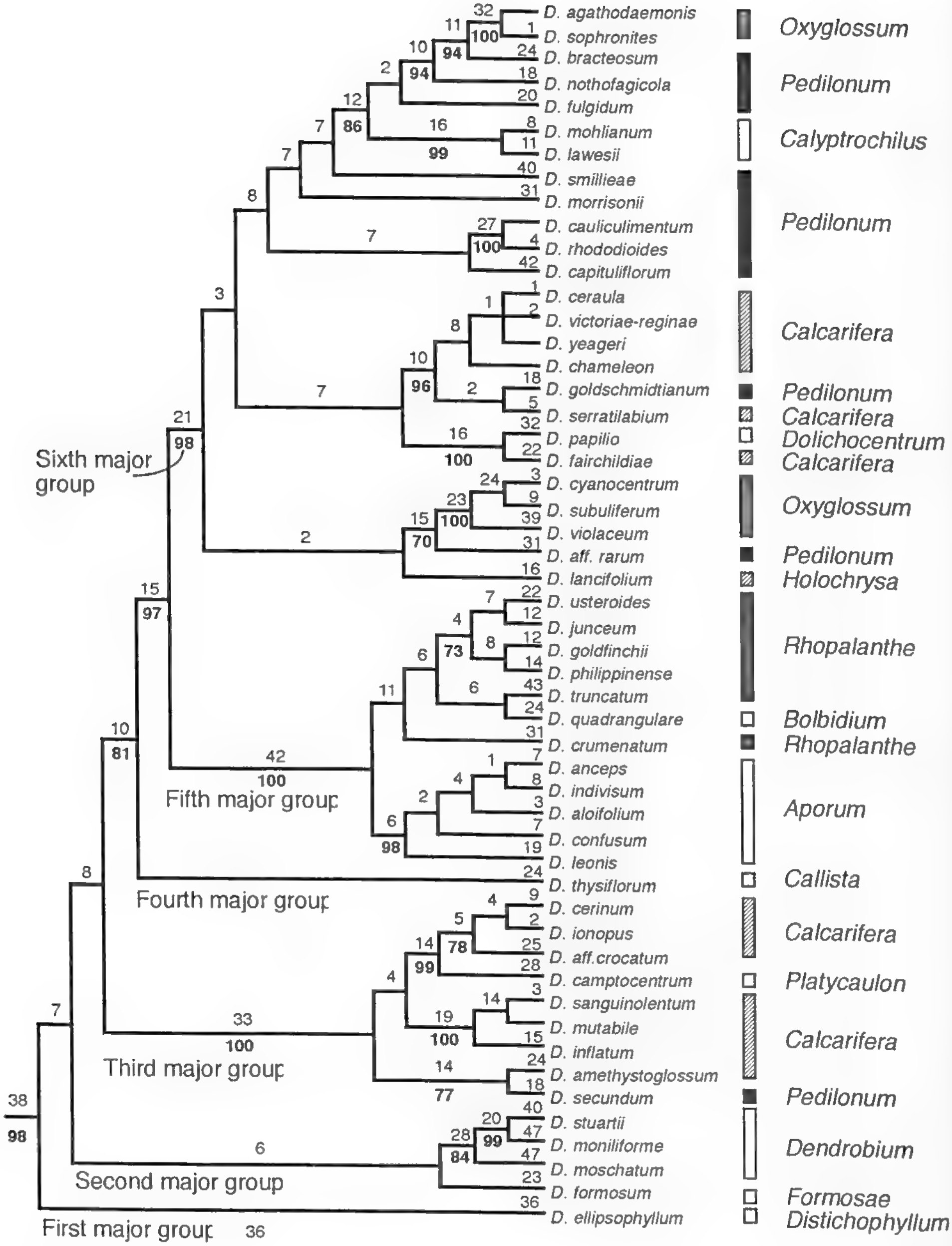

Fig. 3. Details of the Asian clade portion of Fig. 2 showing one of the 3 most parsimonious successively weighted trees from the ITS analysis of the Dendrobiinae, and proposed arrangement of the six major groups within: L = 2728, CI = 0.3897, RI = 0.6715. Sections in which species have historically or are currently placed are shown on the right hand side column. Numbers above branches are branch length estimates (ACCTRAN optimalization); bootstrap percentages greater than 50% are given below in bold.

nindii, D. macrophyllum and *D. speciosum*), group with *Cadetia, Diplocaulobium, Dockrillia, Flickingeria* and *Grastidium* into the moderately supported Australasian clade (74% bootstrap support) thus rendering *Dendrobium* in its current interpretation, polyphyletic. All remaining species cluster into a strongly supported monophyletic Asian clade (94% bootstrap support) also shown in Figure 3. Within the Asian clade there are six major groupings. The first contains a single species *Dendrobium ellipsophyllum* representative of section *Distichophyllum*. The second major group contains representatives of section *Formosa* and section *Dendrobium* including *D. moniliforme*, the designated type of the genus. All four remaining major groups are all clearly isolated and strongly supported (81–100% bootstrap values) from each other. The third major group contains representatives of sections *Pedilonum, Calcarifera* and *Platycaulon* while the fourth major group contains a single species *D. thysiflorum* representative of section *Callista*. The fifth and sixth major groupings are grouped together with strong support (97% bootstrap value). Representatives of sections *Aporum, Bolbidium* and *Rhopalanthe* comprise the fifth major group. The sixth major group comprises a large assemblage of species, most of which have been assigned to section *Pedilonum* or the allied sections *Calyptrochilus, Calcarifera* and *Oxyglossum*, in addition to representatives of section *Dolichocentrum*. These results reveal the non-monophyletic nature of many sections within this part of the Dendrobiinae but in particular, sections *Calcarifera* and *Pedilonum*. Additionally, section *Rhopalanthe* is paraphyletic with a representative of section *Bolbidium* embedded within it. Section *Oxyglossum* is polyphyletic whereas section *Aporum* represents a monophyletic group.

Discussion

These current analyses, based on ITS nrDNA sequence data, provide an insight into the phylogeny and overall structure in the Dendrobieae including a significant portion of the Dendrobiinae, in particular the Malesian elements of the Asian clade. At the broader level, using a similar range of species to that used in previous molecular systematic studies (Yukawa et al. 1993, 1996a, 1996b, 2000), the present results strongly corroborate the overall phylogeny of the Dendrobiinae based on analyses of plastid DNA data (restriction sites and *rbc*L and *mat*K sequences). Both sets of results show representatives of *Epigeneium* grouped together in a strongly supported clade (96–100% bootstrap support) and sister to the remainder of the Dendrobiinae. They also show the remainder of the Dendrobiinae split into the same two major groupings, the Australasian and Asian clades. The strong correlation between both sets of results suggests the taxonomic status of this group needs reconsideration. On the basis of both independent sets of results the continued recognition of *Epigeneium* in a separate genus would seem appropriate.

Dendrobium section *Oxystophyllum*

Of particular note in these ITS sequence analyses is the grouping of *Dendrobium govidjoae* and *D. sinuatum* with *Eria javanica* and *Bryobium pubescens*, two representatives of the Eriinae (Podochileae). *Dendrobium govidjoae* and *D. sinuatum* are members of the taxon *Dendrobium* section *Oxystophyllum* and this group historically has been treated either as a separate genus *Oxystophyllum* (Blume 1825, Lindley 1830), as a section of *Dendrobium* (Miquel 1859, Smith 1908, Kraenzlin 1910, Schlechter 1912), or as a section of the genus *Aporum* (Reichenbach 1861, Hooker 1890, Brieger 1981) all within the tribe Dendrobieae, subtribe Dendrobiinae. When treated within *Dendrobium*, section *Oxystophyllum* has been interpreted as allied to sections *Aporum* and *Rhopalanthe* (Schlechter 1912) on account of similarities of vegetative features most notably the equitant leaves and the abbreviated, lateral inflorescences formed in the axils of the leaf-sheaths along the leafy part of the stem. The position of *Oxystophyllum* outside the Dendrobieae renders that tribe polyphyletic unless the Eriinae is included within it. Additionally, inclusion of *Oxystophyllum* within the Eriinae contradicts the interpretation that possession of eight pollinia can be used as a defining character for that subtribe (Dressler 1993). Careful examination of *Dendrobium govidjoae* and *D. sinuatum* plus other species in the group, both as living or herbarium specimens, reveals the existence of key morphological characters that correlate with, and support, the proposed alignment with the Eriinae rather than with the Dendrobiinae. Characters possessed by *D.* section *Oxystophyllum* include: pensile habit; roots wiry, hirsute, rusty brown, with a purplish growing apex; leaves equitant, rigid, falcate to lanceolate, with abscission layer towards base, apex sharply acute and with vascular traces confined to adaxial surface; inflorescences compressed, simple or compound, indeterminate, lateral or terminal, racemes, covered with persistent equitant, imbricate bracts, the solitary flowers arising intermittently; flowers sombre coloured, with short, acute, thick, rigid tepals, lateral sepals contiguous and adnate to column-foot, saccate; labellum ligulate, on a short hinge, thick, fleshy and secreting sticky fluids at base; pollinia four, in two separate sets of two, small, irregularly shaped, pinkish cream, and with prominent caudicles. Two of these characters in particular (the roots, wiry, hirsute, rusty brown, with a purplish growing apex; and the pollinia, with prominent caudicles) are more consistent with those present in various members of the Eriinae than with those in the Dendrobiinae. Although unusual in the Eriinae, the equitant leaf habit is present in *Eria* section *Aporodes* (Schlechter 1912, Cootes 2001), another example of convergent evolution within the Orchidaceae. Aside from the obvious similarities of habit and vegetative morphology, characters possessed by species in *D.* section *Aporum* are: roots white or green, thin, glabrous; vascular traces scattered randomly throughout the leaf tissue; compressed simple or compound inflorescence lacking; bracts equitant, imbricate, persistent; flowers with a well defined column-foot; labellum non-articulate, lacking any secretory processes; pollinia yellow, four in two tightly appressed hemi-pollinia lacking caudicles. On the basis of these ITS sequence analyses and the cited morphological characters, it is proposed that *Oxystophyllum* as originally interpreted by Blume (1825), should again be recognized at generic rank within the subtribe Eriinae (Podochilideae) rather than in the Dendrobieae (see below). Additionally, the definition of the Eriinae should be adjusted to include: pollinia, eight (rarely four) in two sets of four (two), with caudicles.

Epigeneium

Although there is strong support for the monophyly of *Epigeneium* (96% bootstrap support) in the present ITS analyses, there is only weak support for its position as sister group to the remaining members of the Dendrobiinae, a result that was also found in analyses of *rbc*L and *mat*K sequences and cpDNA restriction sites (Yukawa et al. 1993, 1996a, 2000). Treatment of the group as part of, but sister to, the bulk of the Dendrobiinae is not unreasonable (see below). Many species in this group were first treated under the epithet *Sarcopodium* Lindl. (Lindley 1850, Rolfe 1910, Kraenzlin 1910) or as a section of *Dendrobium* (Hooker 1890, Schlechter 1912), based on *Dendrobium amplum*. However, none of these authors was apparently aware that the name *Sarcopodium* was a later homonym of a fungal genus. Later Gagnepain (1932) described *Epigeneium* to accommodate a small group of morphologically distinct *Dendrobium* species typified by *D. fargesii*, because of their *Bulbophyllum*-like habit but having flowers reminiscent of a *Coelogyne*. Because of the unavailability of the name *Sarcopodium*, Hawkes (1956) proposed the alternative name *Katherinea*, overlooking, or not making the connection to, the earlier published legitimate name *Epigeneium*. The name *Epigeneium* has since been taken up and applied, using a broader circumscription, to all species in the group (Summerhayes 1957, Seidenfaden 1980, Garay & Romero-Gonzalez 1999) although some authors prefer to maintain the distinction between *Epigeneium* and *Katherinea* (Balakrishnan & Chowdhury 1966). Based on detailed morphological study of both living and herbarium material, species in the *Epigeneium* clade can be circumscribed by the following combination of characters: plants epiphytic or lithophytic; stems rhizomatous terminating in a single internode pseudobulb; leaves conduplicate, coriaceous, 1–3, terminal; inflorescence subterminal, determinate, single or multi-flowered, erect or pedant, arising from a prominent erect, imbricate bract; flowers long-lasting, with spreading segments, non-articulate labellum, a prominent long column-foot, petals obliquely attached for greater part or not, glabrous elongate column, with prominent apical often ornate anther attachment (see below).

In addition, there are three well-supported, morphologically distinct groups within the *Epigeneium* clade. These three taxa, represented in Figure 1 by (a) *E. nakaharaei*, (b) *E. amplum*, and (c) *E. cymbidioides* and *E. triflorum*, more or less correspond to those identified as sections by Garay and Romero-Gonzalez (1999), *viz E.* section *Epigeneium*, *E.* section *Katherinea* and *E.* section *Racemosum*. Briefly these are characterised as follows:

(a) section *Epigeneium*: epiphytic herb with reptant habit; stems pseudobulbous, pseudomoniliform, terminated by solitary leaf; inflorescence one-flowered, arising from new growth, shorter than leaves; dorsal and lateral sepals well separated and petals obliquely attached for greater part along a prominent long column-foot that is 2–3 times longer than the broadly concave column.

(b) section *Katherinea*: epiphytic herb with *Coelogyne*-like habit; stems rhizomatous terminating in erect, pseudobulbs; leaves erect, two to three per pseudobulb; inflorescence one-flowered, arising only from old growth, shorter than leaves; flowers large, *Coelogyne*-like; column approximately equal to the column-foot; column-foot porrect, narrow.

(c) section *Racemosum*: epiphytic herb often in large clumps; stems rhizomatous, often markedly so, terminating in suberect to ascending, pseudobulbs; leaves two or three per pseudobulb erect or spreading; inflorescence racemose, terminal to subterminal, multi-flowered, erect to pendulous, commonly much exceeding the leaves; flowers stellate, the lateral sepals not joined at base and labellum contiguous with column-foot; column narrowly concave approximately equal to the column-foot; a porrect, narrow column-foot.

In addition to highlighting the isolation of the *Epigeneium* clade as distinct from the remainder of the Dendrobiinae, results from these ITS analyses also provide a basis for alternative interpretations on the taxonomic status of the three identified groups within the clade. Since the whole group is monophyletic, one option is to maintain all three groups as a single genus under the name *Epigeneium* in line with the proposal of Garay and Romero-Gonzalez (1999). Another equally plausible and tempting option is to recognise all three sections at generic rank. There is, however, a problem with this option. *Epigeneium* section *Racemosa* is typified by *E. acuminatum* for which no material was available for sequencing. Without ITS sequence data it would be presumptive to suggest that *Epigeneium* section *Racemosa*, based only on study of *E. cymbidioides* and *E. triflorum*, represents a monophyletic taxon. One unacceptable option, based on these ITS sequence analysis results, is the recognition of just two genera in the group, as proposed by Balakrishnan and Chowdhury (1966), because acceptance of section *Katherinea* at generic rank would render *Epigeneium* paraphyletic. On the basis of all available evidence (and recognising that further research is require) for the present it is proposed to recognise only *Epigeneium* within the Epigeneiinae.

This leaves the remainder of the Dendrobiinae spread amongst the relatively strongly supported Australasian and Asian clades, a situation consistent with the results based on *rbc*L and *mat*K sequence and plastid restriction site analyses (Yukawa et al. 1996, 2000). Several taxonomic options are apparent; the *status quo*.unfortunately is not one of them.

Australasian clade

Focusing firstly on the Australasian clade in results from the present ITS analyses, the presence of the long-accepted, established genera *Cadetia, Diplocaulobium* and *Flickingeria*, deep within the well-supported Australian clade (85% bootstrap support), renders the current concept of the genus *Dendrobium* polyphyletic.

Cadetia was first described by Gaudichaud (1826) but it was Schlechter (1912) who finally established its status as distinct from *Dendrobium*. He characterised *Cadetia* by the possession of: the *Pleurothallis*-like habit; formation of a spur through cohesion anteriorly in the lower half of the lateral sepals; papillae in front of the column and labellum.

Since its proposal as a genus *Diplocaulobium* (Kraenzlin 1910) has gradually gained acceptance as separate from *Dendrobium* based on possession of the following characters: closely spaced single internode pseudobulbs; flowers mostly solitary, pedicellate, arising from a conspicuous bract at base of single terminal leaf, stellate, flowers lasting one day (rarely longer), with distinct mentum and articulate labellum (Lavarack et al. 2000)

Flickingeria, which was originally described under the illegitimate name *Desmotrichum* (Blume 1825), has similarly regained acceptance as a separate genus having in the interim been treated as a section of *Dendrobium* (Schlechter 1912) and under the generic name *Ephemerantha* (Hunt & Summerhayes 1961). The genus *Flickingeria* is characterised by: rhizomes irregularly branched, creeping, terminating in an erect pseudobulbous internode with a terminal non-sheathing leaf; inflorescences single or multi-flowered, terminal or subterminal to pseudobulb, both adaxial and abaxial to leaf, and covered by persistent sheathing bracts; flowers ephemeral; labellum midlobe fimbriate plicate, or bilobate (Seidenfaden 1980) Since the type species for *Dendrobium* is embedded within the Asian clade, one option is to accept that all species in the Australasian clade are representatives of genera other than *Dendrobium.* A second option is to re-include *Cadetia, Diplocaulobium* and *Flickingeria* in a broadly defined *Dendrobium* that includes both the Australian and Asian clades. However, there is only very weak support from the present analyses for treating the Australasian and Asian clades together as one large monophyletic group, and including these well-established, morphologically well-defined genera in an extremely broad concept of the genus *Dendrobium* would lead to much confusion and be unpopular with users. It would also leave Dendrobium as a huge (c. 1800 spp) unwieldy genus. A third option, to treat the Australasian and Asian clades as two separate genera, is likewise unhelpful. Such a proposal requires, in the case of the Australasian clade, the reduction of *Cadetia, Diplocaulobium* and *Flickingeria,* as well as all other members of this clade, to synonyms of the morphologically disparate and distinct *Grastidium* (Blume, 1825), as it represents the oldest named genus in the clade.

As shown previously, *Grastidium* is easily separated from other Dendrobiinae by the possession of: laterally flattened stems of pseudo-indeterminate growth; synchronous flowering; lateral inflorescences emerging from a node opposite a leaf lamina and breaking through its subtending sheath; inflorescences emerging with the protection of two indurated, laterally compressed sheathing bracts; inflorescence a much reduced, geminate raceme with terminal, inward-facing flowers; flowers ephemeral (Clements & Jones 1997). These characters, or combinations thereof, are also absent from the remaining species in the Australasian clade and the aggregation of all species into a single genus under the name *Grastidium* would create more confusion and uncertainty than presently exist. Yukawa et al. (1993) arrived at similar conclusions with respect to the integrity and maintenance of representatives within the Australasian clade (including the genera *Cadetia, Diplocaulobium* and *Flickingeria*) although they refrained from formally recognising any other genera in the clade. Taxonomic and systematics treatments of most taxa within the Australasian clade are already well-advanced with the recognition of 35 genera:

> *Abaxianthus* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Australorchis* Brieger (Brieger 1981), *Bouletia* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Cadetia* Gaud. (Schlechter 1912), *Cannaeorchis* M.A.Clem. et D.L.Jones (Clements & Jones 1998b); *Cepobaculum* M.A.Clem. et D.L.Jones, *Ceratobium* (Lindl.) M.A.Clem. et D.L.Jones, *Davejonesia* M.A.Clem, *Dendrobates* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Dichopus* Blume, *Diplocaulobium* (Rchb.f.) Kraenzl. (Kraenzlin 1910), *Dockrillia* Brieger (Clements & Jones 1996), *Durabaculum* M.A.Clem. et D.L.Jones, *Eleutheroglossum* (Schltr.) M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Eriopexis* (Schltr.) Brieger (Brieger 1981, Clements & Jones 1997), *Euphlebium* (Kraenzl.) Brieger (Brieger 1981), *Exochanthus* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Flickingeria* A.Hawkes (Seidenfaden 1980), *Grastidium* Blume (Clements & Jones 1997), *Herpethophytum* (Schltr.) Brieger (Brieger 1981), *Inobulbum* (Schltr.) Schltr. et Kraenzl. (Clements & Jones 1998a), *Kinetochilus* (Schltr.) Brieger (Brieger 1981), *Leioanthum* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Microphytanthe* (Schltr.) Brieger (Brieger 1981), *Monanthos* (Schltr.) Brieger (Brieger 1981), *Sarcocadetia* (Schltr.) M.A.Clem. et D.L.Jones (Clements and Jones 2002), *Sayeria* Kraenzl. (Rauschert 1983), *Stelbophyllum* M.A.Clem. et D.L.Jones, *Tetrabaculum* M.A.Clem. et D.L.Jones (Clements and Jones 2002), *Tetrodon* (Kraenzl.) M.A.Clem. et D.L.Jones (Clements & Jones 1998a), *Thelychiton* Endl. (Clements and Jones 2002), *Trachyrhizum* (Schltr.) Breig. (Brieger 1981), *Tropilis* Raf. (Rauschert 1983, Clements and Jones 2002), *Vappodes* M.A.Clem. et D.L.Jones (Clements and Jones 2002) and *Winika* M.A.Clem., D.L.Jones et Molloy (Clements et al. 1997).

A full account of the phylogeny of these taxa based on the results of molecular analyses is in preparation. The present ITS sequence analyses, and the plastid DNA analyses of Yukawa et al. (1996, 2000), also provide a basis for the recognition of both the Australasian and Asian clades at higher taxonomic rank within the Dendrobieae (examined below).

Asian clade

The remaining element of the Dendrobiinae, the Asian clade, forms a strongly supported monophyletic group (94% bootstrap support value), which strongly correlates with the results of Yukawa et al. (1996, 2000). Presence of *Dendrobium moniliforme*, the designated type species for the genus *Dendrobium* (Holttum et al. 1982) automatically means that in any classification system this clade must be included within the Dendrobiinae. Focussing on the elements of this clade, there are three strongly supported major groupings, all with 98–100% bootstrap support values, as well as two isolated species and another major group that contains *D. moniliforme*. Once again, although the species used in this study are not fully representative of all the groups considered to make up the Asian clade, they nevertheless provide an insight into the phylogeny of the group as a whole and in particular many of the Malesian elements of the Dendrobiinae with emphasis on representatives of *Dendrobium* section *Pedilonum*.

First major group: The first major group comprises a single species *Dendrobium ellipsophyllum*, that historically has been treated as: part of *Dendrobium* subgenus *Dendrobium* (Lindley 1851, Smith 1905); in section *Chrysantha* (Reichenbach, 1861); in section *Revoluta*; in subgenus *Grastidium* (Kraenzlin 1910); but more typically in section *Distichophyllum* (Hooker 1890, Schlechter 1912, Seidenfaden 1985, Brieger 1981). Hooker (1890) established section *Distichophyllum* to accommodate those species with the habit of the genus *Appendicula* and flowers solitary or in short leaf-opposed racemes, a short, spur-like mentum as long as, or longer than, the lateral sepals and with broad recurved side lobes. Despite the taxon being represented by a single species in the present ITS sequence analyses (in order to keep a direct compatability with the species used by Yukawa et al. (1993)), the isolation of *D. ellipsophyllum* from the other major groups supports it recognition as a distinct from *Dendrobium sens. str.* Sequence analyses of other species from within the group, *D. austrcaledonicum, D. revolutum*, and *D.* aff. *sculptum*, are in progress. Examination of fresh and herbarium material of *D.* section *Distichophyllum*, including many type collections, has revealed additional key characters to those cited above present in all species in this taxon. Key characters for the taxon are: stems slender non-pseudobulbous, often angular; leaves pedicellate and clasping; inflorescence a highly reduced, lateral periodically developing raceme; flowers solitary (rarely two), each with a papery sheath that persists in the sheathing bracts after anthesis; labellum trilobed, with broadly bilobed mid-lobe, fleshy, minutely papillate and spongy at base on lamina callus, forming a closed, conspicuous, nectiferous spur with basal half to the column-foot; column with centra groove; column-foot concave, papillose on inner surface; and protocorm discoid type. On the basis of these broader results this taxon has been recognised as a distinct genus and given the name *Distichorchis* (Clements & Jones 2002).

Second major group: The type species for the genus *Dendrobium* together with *D. formosum, D. moschatum and D. stuartii*, are contained within the second major group but there is only weak support (<50% bootstrap support) for its acceptance as a monophyletic taxon. Internally however, there is good support for separation of *D. formosum* from the remaining species in the group. *Dendrobium formosum* belongs to a group commonly referred to as section *'Nigrohirsutae'* on account of possession of black hairs on the leaf sheaths of most species (Lindley 1859), but correctly the sectional name *Formosae* should be applied to it (Seidenfaden 1985). Authors such as Lindley (1859) and Reichenbach (1861) treated *D. formosum* and morphologically similar species belonging to section *Dendrobium*, in the subgenus *Nigrohirsuta* (Kraenzlin 1910), or in section *Oxygenianthe* (Schlechter 1912). However, not all species currently placed within *D.* section *Formosae* (e.g. Seidenfaden 1985, 1992, Seidenfaden & Wood 1992, Cootes 2001, Wood et al. 1993, Wood & Cribb 1994, Lavarack et al 2000, Comber 2001) possess the characteristic black hairs on the leaf sheaths, which suggests that further research is required as the taxon may not be monophyletic. The phylogeny and systematics of the group will be the subject of a separate paper. The remaining species in the second major group have historically been included in *D.* section *Eu-dendrobium* (Lindley 1851, Bentham & Hooker 1883, Kraenzlin 1910), section *Planifolia* (Reichenbach 1861), but more recently been treated as members of *D.* section *Dendrobium* (Seidenfaden 1985) although the nomenclatural history, taxonomy and systematics of the group is very complex and will be the subject of a separate paper. Representatives of this taxon are particularly scarce towards the eastern part of the Malay archipelago and in New Guinea are represented by three species and in Australia by a solitary species, *D. stuartii.*

Third major group: The third major group contains *D. secundum*, the designated type of the genus *Pedilonum*, plus eight other species representative of sections *Calcarifera* and *Platycaulon* of *Dendrobium* (Smith 1908, Schlechter 1912). Other species representative of *Pedilonum* are, however, scattered amongst three separate subclades in the sixth major group of the ingroup. This renders *Pedilonum* polyphyletic in any traditional or modern sense with the bulk of representative species well removed from *D. secundum.* Additionally, the proposed arrangement of species bears little relationship to any proposed infrageneric classification of the Dendrobiinae, which has been based on perceived differences in floral morphology. Sister to *D. secundum*, and with moderately strong bootstrap support, is *D. amethystoglossum.* This proposed arrangement of these two species seems unusual; firstly, because of the presumed lack of similarity of the two species, and secondly, because historically the possibility has barely been considered. For example, Kraenzlin (1910) included *D. amethystoglossum* with 28 other species, in the subgenus *Pedilonum* section *Glomerata* subsection *Mesocentra*, whereas *D. secundum* was treated in the adjacent section *Secunda* in subgenus *Pedilonum*. Other authors such as Schlechter (1912), Brieger (1981), Rauschert (1983) and Seidenfaden (1985), did not offer an opinion on the phylogenetic position of *D. amethystoglossum*. By comparison, Cootes (2001) in the latest account of the orchids of the Philippines, and Comber (2002), treat the endemic *D. amethystoglossum* as a member of *D.* section *Calcarifera*. On my examination it was found that *D. secundum* and *D. amethystoglossum* shared several morphological features in particular: stems erect or porrect, pseduobulbous, soft, fleshy, long and tapering, covered with leaf sheaths; leaves thin, fleshy, deciduous, the sheath persistent and with slightly thickened red veins; lateral sepals connate in basal half, forming a saccate spur; labellum non-articulate, long, narrow, rigid, with median cross-laminar ridge or spur and concave in basal half forming a nectary with concave column foot and connate lateral sepals; rostellum protruding, acute and rigid; pollinia oblong-orbicular, bright yellow. Other species in this major grouping cluster into two separate clades. One contains *D. inflatum*, *D. mutabile* and *D. sanguinolentum* while the second comprises *D. camptocentrum*, *D.* aff. *crocatum*, *D. ionopus* and *D. cerinum*. Apart from *D. platygastrium*, all the other species have been treated as part of the poorly understood and often overlooked *D.* section *Calcarifera* (Smith 1908, Comber 1990, 2001, Lavarack et al. 2000), which is characterised by possession of flowers with a long mentum directed away from the pedicel and ovary; a moderately wide labellum that narrows abruptly towards the base where adnate to the column foot for most of its length and with a small protuberance on the upper surface. In comparison, although superficially florally similar *D. platygastrium* is a member of section *Platygastrium*, so called because of the characteristic flattened, compressed pseudobulbs. There is an historical link within this entire major grouping.

Blume (1825) when describing *Pedilonum* considered it distinct from *Dendrobium* by the absence of an articulate labellum and with flowers with a slipper shaped labellum, dividing the six species in the genus into two sections. The second of these two sections which was distinguished by lateral sepals forming an elongate spur often adnate to the labellum claw, contains *P. secundum* as well as *P. undulatum*, *P. biflorum* and *P. erosum*. Two of these species, *P. undulatum* (as *D. hymenophyllum*) and *P. biflorum* (as *D. gemellum*), have since been transferred to *Dendrobium* and are now treated as members of section *Calcarifera* (Comber 1990, 2001) so Blume's interpretation of presumed relationships between this group of species perhaps has some basis. Blume (1825) also described *Onychium lamellatum*, with its characteristic laterally flattened pseudobulbs. This species has since been transferred to *Dendrobium* (Lindley, 1830) as well as designated as the type of *Dendrobium* section *Platycaulon* (Schlechter 1905), with close affinities to section *Eugenanthe* (Schlechter 1912) Opinions are divided on how to treat this group of species. It has been variously maintained in *D.* section *Platycaulon* (Kraenzlin 1910, Comber 1990, 2001, Lavarack et al. 2000), in *D.* section *Calcarifera* (Wood & Cribb 1994), transferred the genus to *Pedilonum* (Brieger 1981), or incorporated within *D.* section *Pedilonum* (Seidenfaden 1985, 1992, 1997, Seidenfaen & Wood 1992). Comber (2001) recently suggested that the only difference between *D. lamellatum* and species in section *Calcarifera* is the vegetative character of flattened stems. In these ITS sequence analyses *D. platygastrium* groups with species possessing flowers with a long narrow mentum that is adnate to the column foot in the basal half, rather than those species with a similarly inflated mentum and labellum attached only at the base of the column foot. *Dendrobium platygastrium* and its relatives also lack any form of basal protuberance on the labellum. Presence of a representative of this section in this clade does, however, render section *Calcarifera* paraphyletic. All these data provide a framework for the recognition of the separate sections *Platycaulon-Calcarifera* as distinct from the first group of section *Calcarifera*. Furthermore, whilst there is very strong support for these two individual *Calcarifera* groups (100% and 95% bootstrap support), there is by comparison only poor support for the recognition of these two groups as sister taxa.

The remaining species in this major grouping, *D. mutabile, D. sanguinolentum* and *D. inflatum*, which have also been considered part of *Calcarifera* (Comber 2000), are clearly separated in a well-supported clade (100% bootstrap support). Historically, these species were described by Blume (1825) in the illegitimate genus *Onychium* and then transferred to *Dendrobium* (Lindley 1830). Blume's description of *Onychium* agrees closely with Smith's concept of section *Calcarifera* and two of the species originally described in *Onychium*, namely *O. mutabile and O. nudum* (similar to *D. inflatum*), have since been transferred to this section. Characteristically, this group of species have flowers with an inflated spur; a more membranous labellum that is more or less continuous with the base of the column foot forming a short nectiferous spur; and uniformly obovate-elongate pollinia. Interestingly, the pollinia differ significantly from those found in representatives of the first described group in *Calcarifera*, where they are irregularly shaped, undulate structures. These data together suggest that *Calcarifera* is not a monophyletic group in its current form and that these various elements of the group are deserving of higher taxonomic status separate from that of *Pedilonum*.

Fourth major group: The fourth major group contains a single species, *D. thysiflorum*, representative of a group of species commonly referred to section *Callista* (Reichenbach, 1868, Schlechter 1912, Seidenfaden 1985) or as a separate genus *Callista* (Kraenzlin 1910, Brieger 1981) The genus *Callista* was described by Loureiro (1790) and predates *Dendrobium* by nine years. One consequence of the amalgamation of many genera into *Dendrobium* and recognition by Reichenbach (1868) that *Callista* was synonymous with it, was that by the rules of the International Code of Botanical Nomenclature (ICBN), *Callista* had priority over *Dendrobium*. It was on this basis that Kuntze (1891) automatically transferred most species described in *Dendrobium* to *Callista*. To counteract this, a decision was made at the Second International Botanical Congress to conserve *Dendrobium*. All of this of course is based on the assumption that *Callista* is part of *Dendrobium*, which is easy to understand considering the similarity of floral morphology between species in the two groups. However, on the basis of the results generated in these ITS studies, where *Callista* is separated from *Dendrobium* sens. str. by the third major group containing morphologically disparate species, it would appear that these perceived similarities are yet another example of convergent evolution within the Dendrobieae, or that the floral similarities are symplesiomorphic. Apart from floral morphology, *Callista* is characterised by the possession of erect, angular, fusiforme, pseudobulbous stems, coriaceous, terminal to subterminal leaves, and development of the inflorescence as though being extruded like paste from the original stem bud. Furthermore, in broader based studies the addition of sequences obtained from four morphologically similar species considered part of this group, *D. amabile* (the type species for *Callista*), *D. griffithianum* and *D. palpebrae*, confirmed the group was a strongly supported monophyletic taxon well isolated from *D.* section *Dendrobium*. The combined characteristics of *Callista* enunciated above coupled with its isolated position in these ITS sequence analyses results, provides good evidence that Loureiro's original concept should again be adopted.

Fifth major group: Species in the fifth major group form a strongly supported clade (100% bootstrap support) isolated from the remainder of the ingroup. Within this major grouping are two subgroups, only one of which is strongly supported (98%

bootstrap support) In the strongly supported subgroup, *D. leonis, D. aloifolium, D. indivisum* and *D. anceps* have been treated by most authors as the genus *Aporum* (Blume 1825, Lindley 1830, 1847, Pfitzer 1889, Brieger 1981) or as section *Aporum* (Lindley 1851, Reichenbach 1861, Bentham & Hooker 1883) or subgenus *Aporum* (Kraenzlin 1910) within *Dendrobium. Dendrobium aloifolium* was also originally described by Blume (1825) in the monotypic genus *Macrostomium* while *D. anceps* was treated as the type for another monotypic genus *Ditulima* (Rafinesque 1836). In contrast to these four species, *D. confusum* belongs to an assemblage of species treated under the sectional name *Strongyle* (Smith 1905, Seidenfaden 1985), first devised by Lindley (1851) to account for those species within *Dendrobium* possessing terete leaves. The similarities between species in section *Aporum* and *Strongyle* had been noted by Schlechter (1912) who treated the latter as a part of *Aporum*. Despite some diversity in the origins of the inflorescence and floral morphology, the group is held together on its vegetative characters, in particular: possession of equitant leaves; lack of any form of thickening of the ensheathed wiry stems; production of persistent, compact, lateral and terminal inflorescences with persistent indeterminate meristematic regions from which are generated single (occasionally multiple) flowers. Possession of these common characters and the fact that all these representative species are embedded within a single tight cluster suggests they should be treated as representative of a single taxon, the earliest and most commonly applied generic or sectional name being *Aporum*.

In the second (although poorly supported) subgroup within the fifth major group, all but *D. quadrangulare* have been treated either in the section or subgenus *Crumenata* (Pfitzer 1889, Kraenzlin 1910), or in the (more widely used name) section *Rhopalanthe* in *Dendrobium* (Schlechter 1912, Seidenfaden 1985), or as a component of *Aporum* (Brieger 1981). By comparison, *Dendrobium quadrangulare* is a representative of *D.* section *Bolbidium* (Schlechter 1912, Seidenfaden 1985). In Schlechter's system of classification of the Dendrobiinae, section *Bolbidium* was placed in the first subgenus *Anthecebium* well removed from the third subgenus *Rhopalobium* that contained *D. crumenata*. No species in this group has previously been considered to be closely related to section *Pedilonum*. Careful study of the two subgroups identified by these ITS sequence analyses reveals that although they appear to represent groups of species with different gross vegetative characteristics they nevertheless share many features. For example, the equitant leaf habit common to all species in the first subgroup, section *Aporum*, is also present in species such as *D. goldfinchii* and *D. philippinense* in the second subgroup. A persistent inflorescence covered in the persistent remains of successive floral bracts, and containing an indeterminate meristem that permits the successive production of flowers from the same point on the stems, is however common to all species in the fifth major group. All species in the second, poorly supported subgroup are also united by the common possession of one to several swollen, near-basal, leafless internodes. For those representative species possessing one to several swollen, near basal leafless internodes, the vegetative form varies from the crassulate duplicate two leaved form found in *Bolbidium*, to the conduplicate thin leaves of *D. truncatum*, the thicker multi-leaved stems of *D. crumenatum*, the rigid, terete leaves of *D. junceum* and *D. usteroides*, to the flattened equitant leaves of *D. goldfinchii* and *D. philippinense*. Possession of these features was also noted previously when Loureiro (1790) described *Ceraia simplissisima*, which predates the description of *Dendrobium* by nine years.

Although the type specimen of *Ceraia simplissisima* now lacks any floral material, it is undoubtedly representative of a group of species similar to *D. crumenatum*. Brieger (1981) recognised these differences as significant and raised the taxon to generic rank. Schlechter (1912) also created the solitary section *Rhopalanthe* in his subgenus *Rhopalobium* within *Dendrobium*, for those species with pseudobulbs or stems thickened on 1–3 internodes only. In so doing he recognised its affinities with *Aporum* and proposed the subsection name *Aporopsis* to accommodate the species with equitant leaves that he was about to describe as distinct from *D. crumenatum* (which has conduplicate leaves and undoubtedly considered by him typical of the subgenus). The affinities of vegetative morphology aside, species in the whole group are characterised by the near-membranous flowers which last only one to several days and synchronous flowering habit; the broad, membranous, concave column foot, very short column, and the thin, spreading labellum with a broadly lobed apex. Also embedded within this general group is *D. quadrangulare*, which is representative of *D.* section *Bolbidium* (Lindley 1850), *D.* subgenus *Bolbidium* (Kraenzlin, 1910 (although he included a large number of *Cadetia* species in the taxon)), *D.* subgenus *Athecebium* section *Bolbidium* (Schlechter 1912) and *Bolbidium* (Brieger 1981). With *Bolbidium* embedded deeply within the whole group, Schlechter's concept of subgenus *Rhopalobium* is rendered paraphyletic. Recognition of *Bolbidium* at the generic rank, such as has been proposed by Brieger (1981), would seem premature on the basis of these ITS sequence analyses results. If additional studies using a greater range of species representatives of the various groups were to establish that *Bolbidium* needed to be treated as a separate genus, it would necessitate the acceptance of at least three other genera including *Ceraia*. If we apply a broader generic concept to this group as a whole, then the first available name is *Ceraia*, despite the uncertainties surrounding the determination of the species described as the type. Either scenario necessitates the re-recognition of the genus *Ceraia*, as distinct from *Dendrobium*, something both the molecular results and morphological data strongly support. There is one further piece of information concerning the group as a whole. All species in this major group, studied to date, including those referred to the subgroup *Aporum*, are also defined by possession of an isobilateral protocorm (Clements 2000), a feature known to be absent from the remainder of the Asian clade. Although further research is clearly needed using a greater range of species, possession of the defining characters and isolation of the group in these ITS results, provides a strong basis for the re-instatement of the group as a whole and recognition of at least two genera therein.

Sixth major group: The sixth major group is strongly supported (99% bootstrap support) and represents a complex of taxa with many different vegetative and floral forms. Historically most species in the complex have been placed in at least ten different infrageneric taxa within *Dendrobium*, including section *Pedilonum* or those sections considered closely related to it, e.g. *Calyptrochilus*, *Cuthbertsonia* and *Oxyglossum* (Schlechter 1912, Brieger 1981, Reeve & Wood 1989). Since the type of *Pedilonum* (*D. secundum*) is isolated in the third major group in these analyses, it is apparent that *Pedilonum* as taditionally defined, is entirely artificial. Isolated at the base of the sixth major group is a clade containing *D. lancifolium*. This species is characterised by possession of a cluster of thin stems with lanceolate, grape-like leaves and has short lateral or terminal inflorescences of one to a few pink flowers. It has variously been included in section *Chrysantha* (Reichenbach 1861), subgenus *Pedilonum* section *Glomerata* and subgenus *Grastidium* section *Revoluta* (Kraenzlin 1910), or section *Calcarifera* (Schlechter 1925, van Bodegom 1973, O'Byrne 2001, Cootes 2001) of *Dendrobium*. Reichenbach's section *Chrysantha* is a renamed and expanded version of the ill-defined and often overlooked *Dendrobium* section *Holochrysa* of Lindley (1859). D*endrobium section Holochrysa* was first described to accommodate a small group of Indian species with 'stems on all sides leafy and flowers entirely yellow' but Reichenbach expanded its limits to cover many more species including *D. lancifolium* which has pink and white, rather than yellow, flowers. Most subsequent authors have never seriously considered using Reichenbach's system of classification for *Dendrobium* because it is confusing (Seidenfaden 1985). Kraenzlin (1910), in his much critised monograph of the Dendrobiinae, was clearly confused about the relationship of *D. lancifolium* as he simultaneously included it as 'Species dubia' under *D.* subgenus *Pedilonum* section *Glomerata* and then again in *D.* subgenus *Grastidium* section *Revoluta*. Both taxa are highly artificial, containing species that, in more modern accounts of *Dendrobium*, are treated in many different taxa including some that are now recognised as representative of distinct genera such as *Grastidium sens. str.* (Clements & Jones 1998) and *Cannaeorchis* (Clements & Jones 1999). The non-monophyletic nature of section *Calcarifera* has been dealt with above and the isolation of the *D. lancifolium* group from those in the third major group in the present ITS results provides further evidence of the artificiality of that taxon. The isolation of *D. lancifolium* from any other subgroups of species in this major group suggests it should be recognised as a separate genus or infraheneric taxon,but further study is required. Clustered with *D. lancifolium* is *D.* aff. *rarum* from Vanuatu, a representative of section *Pedilonum*, and three species representative of *D.* section *Oxyglossum* (Schlechter 1912). Reeve and Woods (1989), in their revision of the group considered species belonging to sections *Oxyglossum* and *Cuthbertsonia*, on account of the overall similarity of floral features, should be amalgamated into a single taxon under the name *D.* section *Oxyglossum*. Results from the present ITS studies reveal the exact opposite, where *D. sophronites* and *D. agathodaemonis* are present in another arm of the sixth major group, rendering Reeve and Woods' concept of section *Oxyglossum* polyphyletic. There is, however, strong ITS and morphological support for the monophyly of the *Oxyglossum* group for which *D. cyanocentrum* is the type. These species are readily recognised by possession of short tapering pseudobulbs with a few terminal to subterminal leaves, and one- to multi-flowered inflorescences, multi-ribbed ovaries, and flowers with acute to acuminate segments including the labellum. In comparison, species in the *Cuthbertsonia* group possess, amongst other things, flowers with an obtuse labellum apex. *Dendrobium* aff. *rarum* possesses some floral features common to those found in section *Oxyglossum*, but differs in plant habit where the elongate, thinly pseudobulbous stems are semi-pendulous. The weak–moderate level of support for the inclusion of *D.* aff. *rarum* into section *Oxyglossum* suggests this presumed relationship needs further investigation.

All remaining species in the sixth major grouping fall into two weakly supported clades (bootstrap values below 50%), but with several strongly supported subgroups in each. The first of these weakly supported clades comprises *D. fairchildiae, D. papilio, D. serratilabium, D. goldschmidtianum, D. chameleon, D. ceruela, D. yeageri* and *D. victoriae-reginae*, in two strongly supported groups (96% and 100% bootstraps values). Ames and Quisumbing (1932) in describing *D. fairchildiae*, placed it in section *Calcarifera*w while *D. papilio* has been considered to have affinities to section *Virgatae* (Ames 1908), subgenus *Crumenata* (Kraenzlin 1910), section *Calcarifera* (Lavarack et al. 2000), and section *Dolichocentrum* (Cootes 2001). Only the last of these proposals are supported on the basis of these ITS sequence analyses. As indicated above, section *Calcarifera* was created by Smith (1908), when describing *D. pedicellatum*, and this species equates to the clade containing *D. mutabile, D. sanguinolentum* and *D. inflatum* in the third major grouping of these results. The treatment of *D. fairchildiae* as a member of section *Calcarifera* renders that section polyphyletic in the present analysis, and the relationship is clearly artificial. Section *Virgatae* (Hooker 1885) and the subgenus *Crumenata* are both roughly equivalent to section *Rhopalanthe* of Schlechter (1912) and contain species grouped together in the fifth major group of these ITS analyses, rendering that taxon paraphyletic. Cootes (2001), in assigning *D. papilio* to section *Dolichocentrum*, relied heavily on the similarities in both vegetative and floral morphology to those of *D. furcatum*, the type of the taxon, in particular the thin wiry stems with grass-like leaves, elongate spur formed through fusion of the base of the lateral sepals. The furthur addition of the vegetative and florally similar species, *D. auriculatum* and *D. miyasakii* seems logical. On the basis of these ITS results, the treatment of section *Dolichocentrum* by Brieger (1981) as a separate genus seems premature and further research is needed to clarify its relationship with *D. fairchildiae* and similar species. A second strongly supported clade (96% bootstrap support) accounts for all remaining species in this sub grouping, *viz. D. serratilabium, D. goldschmidtianum, D. chameleon, D. ceraula, D. yargeri* and *D. victoriae-reginae.* Internally the clade is divided into two subgroups. Historically these species have variously been treated as: belonging to section *Dendrobium* (Reichenbach 1877), subgenus *Pedilonum* section *Revoluta* (Kraenzlin 1910); section *Pedilonum* (Williams 1937); section *Calcarifera* (Lavarack 2000, Cootes 2001); or remained unassigned to any particular taxon within *Dendrobium* (Schlechter 1919, Ames & Quisumbing 1931, Liu & Su 1978); or were treated as part of the genus *Pedilonum* (Rauschert 1984). In describing *D. ceraula* Reichenbach (1877) considered it belonged to *Dendrobium* presumably on account of possession of the clustered, lateral inflorescences. Species representative of *Dendrobium* are by necessity related to *D. moniliforme* the designated type of the genus. As shown in these ITS sequence analyses, *D. moniliforme* sits well away from the sixth major group so its presumed alliance with species in this grouping is entirely artificial. As stated earlier, *Pedilonum* is polyphyletic with the type within the third major group, well-isolated from *D. ceraula* and other presumed members of the taxon. Furthermore, the inclusion of *D. goldschidtianum* renders this group paraphyletic. Cootes (2001) treated *D. serratilabium, D. chameleon, D. ceraula, D. yargeri* and *D. victoriae-reginae* in section *Calcarifera,* on account of the plants branching along the pseudobulb and their pendulous habit. Typical members of section *Calcarifera* are only present in one clade within the third major group identified in these ITS analyses. Treatment of this group of species in section *Calcarifera* again renders that taxon polyphyletic. Apart from similarities in plant habit, species in the group have an elongate, narrow labellum spur.

The remaining weakly supported group contains a mixture of strongly as well as weakly supported subgroups and isolated species, with some similarities in floral and vegetative morphology. Part of this group is a poorly supported clade (<50% bootstrap support) containing an isolated *D. capituliflorum* (with thickened canes, capitulate inflorescence, and rigid, concave cymbidiform labellum with an acute apex), and a strongly supported clade (100% bootstrap support) containing *D. cauliculimentum* and *D. rhododioides* (with a pendulous, much-branched habit, and flowers with thin texture). On the basis of these results, species in these two clades are representative of two distinct taxa, well isolated from the type of *Pedilonum.* Sister to the clade containing the proceeding three species is a chained lineage arm of the group with *D. morrisonii* and *D. smillieae* at the base. *Dendrobium smillieae,* with its distinctive large thickened elongate canes, bottlebrush-like inflorescences, and thick, rigid, concave cymbidiform labellum, was described as a separate genus, *Coelandria* (FitzGerald 1882) but typically is included within sections of *Dendrobium,* viz. section *Dendrocoryne* (Bentham 1873), or section *Pedilonum* (Schlechter 1912, Dockrill 1969, 1992, Lavarack et al. 2001). Results of these ITS sequence analyses do not support its continued placement within section *Pedilonum,* rather they support recognition as a separate genus *Coelandria,* which is the oldest available generic name for any taxon within the sixth major group. *Dendrobium morrisonii* has also been treated as a typical member of section *Pedilonum* (Lewis & Cribb 1989) but again these results do not support this proposal.

Dendrobium mohlianum and *D. lawesii* are typically treated as members of section *Calyptrochilus* on account of possession of highly visible colourful flowers with an elongate column foot pressed to the ovary, lateral sepals forming an elongated spur, and labellum adnate to the base of the column foot, and labellum apex in turned with lacerate margins. These species are representative of one of the most characteristic taxonomic groups within the Dendrobiinae, comprising over 70 species. Possession of these features coupled with the very strong molecular support for the clade adds weight to the concept of their treatment as a separate taxon. This leaves a strongly supported clade containing *D. sophronites* and *D. agathodaemonis;* and three species – *D. fuligidum, D. nothofagicola* and *D. bracteosum*, that have been treated as members of section *Pedilonum*. Although clearly part of the broader (but weakly supported), major grouping, the true phylogenetic relationship of these three species awaits the study of additional species. What is clear however, is that this is yet another example of the polyphyly of section *Pedilonum*.

Aside from providing support for the overall taxonomic conclusions about the study taxa, there is also a suggestion of some biogeographical groupings within the study taxa. For example the clade containing *D. fairchildiae, D. papilio, D. serratilabium, D. mayakei, D. chameleon, D. ceruela, D. yargeri* and *D. victoriae-reginae* are all representative of species that are endemic to the Philippines and Taiwan. Likewise the remaining major elements of that same clade are all predominantly species found in the New Guinea region of Malesia. These groupings are suggestive of radiation from these regional centres, a feature not uncommon in other orchid genera, e.g. most genera in the tribe Diurideae (Jones & Clements 2001).

Conclusion

The overall results obtained in these ITS sequence analyses coupled with data on the morphology of study species, provides a basis for a clearer understanding of the phylogeny of a major part of the Dendrobiinae. At the broadest level, the present ITS results correlate strongly with those produced from analyses of *rbc*L and *mat*K chloroplast DNA sequences and chloroplast DNA restriction sites (Yukawa et al. 1993, 1996, 2000). This support confirms that a fundamental division exists within the Dendrobiinae into three separate major lineages, viz (i) *Epigeneium,* (ii) a predominantly Australasian group, and (iii) a predominantly Asian group. The isolation of *Dendrobium* section *Oxystophyllum* in the Eriinae is new, providing yet further strong evidence of the polyphyletic nature of the Dendrobiinae. Considering the constant recurrence of these three strongly supported clades in results in all molecular studies, it now seems appropriate and necessary to formally recognise these three distinct lineages of the Dendrobieae. Additionally these results provide evidence for the following: (i) that Brieger's interpretation of *Pedilonum* is polyphyletic; (ii) that the subsequent automatic transfer by Rauschert (1983) of most species to *Pedilonum,* and other genera within the Dendrobiinae, is not supported; (iii) that Blume's original concept of *Pedilonum* had merit; (iv) that Schlechter's concepts of sections *Oxyglossum, Calyptochilus* and *Cuthbertsonia* appear monophyletic, whereas his concept of section *Pedilonum* does not; (v) that Schelchter's interpretation of a close relationship between these four taxa, excluding the type of *Pedilonum,* was fundamentally sound; (vi) and that section *Calcarifera* defined by Smith (1908) and later authors is polyphyletic. Consequently these data provide evidence for the recognition and reinstatement of the long established genera *Ceraia* and *Pedilonum,* as well as the recognition of several other monophyletic groups at generic rank. Whilst in some authors' opinions the formal recognition of these monophyletic taxa at generic rank might seem premature, the strong body of molecular and morphological evidence from independent data sets and different sources of plant material provides ample support for the proposed reclassification of many of these taxa. In many cases this simply involves the elevation of infrageneric taxa ,but in other cases it involves the redefinition or description of these taxa. Recognition, at generic rank, of major monophyletic taxa within the Dendrobiinae, also provides a far more realistic framework for understanding phylogenies than exists at present. The alternative, of maintaining all these taxa within a greater *Dendrobium,* is not practical in terms of the complexities of classification now required to account for all variation known to exist within this very large and diverse assemblage of species. Additionally, recognition of a broadly circumscribed *Dendrobium* would sink several well-established useful genera.

Appropriate formal taxonomic changes follow in Appendix 2. The present results have also identified complex areas requiring further research before their phylogeny and systematics can be fully enunciated.

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Appendix 1. Collection details of the species used for these analyses.

Species	Provenance	Collection No.	GenBank Accession No.
Adelopetalum bracteatum Fitzg.	cult. ex Qmo*; Queen Mary Falls NP	Crane 2138	AY239945
Bryobium pubescens Lindl.	cult. ex Christmas Island	Ziesing 307	AY239946
Bulbophyllum nutans Thouars	cult. ex Mauritius	Clements 8108	AY239947
Cadetia maideniana (Schltr.) Schltr.	cult. ex Qco*;	Jones 4311	AY239948
Cannaeorchis fractiflexa (A.Finet) M.A.Clem. Et D.L.Jones	cult. ex New Caledonia; Yaté Road	Clements 9348	AY239949
Dendrobium agathodaemonis J.J.Sm.	cult. ex Indonesia; Irian Jaya	Rose (S 926)	AY239950
Dendrobium aloifolium (Blume) Rchb.f.	cult. ex Thailand	Clements 9168	AY239951
Dendrobium amethystoglossum Rchb.f.	cult. ex Philippines	Cootes(ORG 1482)	AY239952
Dendrobium anceps Sw.	cult. ex Philippines	Clements 9309	AY239953
Dendrobium bracteosum Rchb.f.	cult. ex Papua New Guinea (PNG)	CBG 750451	AY239954
Dendrobium camptocentrum Schltr.	cult. ex New Caledonia	Clements 5830	AY239955
Dendrobium capituliflorum Rolfe	cult. ex PNG; Wassabamal	Clements 6319	AY239956
Dendrobium cauliculimentum R.S.Rogers	cult. ex PNG	ORG 3598	AY239957
Dendrobium ceraula Rchb.f.	cult. ex Philippines	ORG 2921	AY239958
Dendrobium cerinum Rchb.f.	cult. ex Philippines	Cootes (ORG 3585)	AY239959
Dendrobium chameleon Ames	cult. ex Philippines	ORG 3590	AY239960
Dendrobium confusum Schltr.	cult. ex PNG	Banks (ORG 1391)	AY239961
Dendrobium aff. *crocatum* Hook.f.	cult. ex Indonesia; Sumatra	Smedley s.n.	AY239962
Dendrobium crumenatum Sw.	cult. ex Thailand	Clements 4890	AY239963
Dendrobium cyanocentrum Schltr.	cult. ex PNG	Spence (Clements 8709)	AY239964
Dendrobium ellipstophyllum T.Tang et F.T. Wang	cult. ex Thailand	Banks (ORG 3581)	AY239965
Dendrobium fairchildiae Ames et Quisumb	cult. ex Philippines; Bukidnon	Cootes (Clements 1485)	AY239966
Dendrobium formosum Roxb. ex Lindl.	cult. ex Thailand	Phillips 457	AY239967
Dendrobium fulgidum Schltr.	cult. ex PNG	Banks (ORG 3599)	AY239968

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* Abbreviations for Australian Botanical Districts: Nsc = New South Wales, South Coast; Qco = Queensland, Cook; Qmo = Queensland, Moreton.

ORG = Orchid Research Group.

CBG = Canberra Botanic Gardens (now the Australian National Botanic Gardens).

RBGS = Royal Botanic Gardens Sydney

Species	**Provenance**	**Collection No.**	**GenBank Accession No.**
Dendrobium goldfinchii F.Muell.	cult. ex PNG; Wassabamal	Clements 5860	AY239969
Dendrobium goldschmidtianum Kraenzl.	cult. ex Taiwan	ORG 3465	AY239970
Dendrobium govidjoae Schltr.	cult. ex PNG; Garassa	Clements 6810	AY239971
Dendrobium indivisum (Blume) Miq.	cult. ex Malaya; Langkawi	Vaughn (Clements 5822a)	AY239972
Dendrobium inflatum Rolfe	cult. ex Indonesia; Bali	Clements 5820	AY239973
Dendrobium ionopus Rchb.f.	cult. ex Philippines	Cootes (ORG 3589)	AY239974
Dendrobium junceum Lindl.	cult. ex Philippines	ORG 3588	AY239975
Dendrobium lancifolium A.Rich.	cult. ex Indonesia; Sulawesi	Clements 9176	AY239976
Dendrobium lawesii F.Muell.	cult. ex PNG	Spence D54	AY239977
Dendrobium leonis (Lindl.) Rchb.f.	cult. ex Thailand	ORG 1983	AY239978
Dendrobium macrophyllum A.Rich.	cult. ex Philippines?	Spence (Clements 8704)	AY239979
Dendrobium mohlianum Rchb.f.	cult. ex Fiji	ORG 3603	AY239980
Dendrobium moniliforme (L.) Sw.	cult. ex Japan	no collector 3544	AY239981
Dendrobium morrisonii Schltr.	cult. ex Vanuatu	Phillips 1069	AY239982
Dendrobium moschatum (Buch.-Ham.) Sw.	cult. ex Thailand	Clements 5808	AY239983
Dendrobium mutabile (Blume)	cult. ex Indonesia; Java	ORG 3608	AY239984
Dednrobium nindii W.Hill	cult. ex Qco*; Daintree River	Jones 4285	AY239985
Dendrobium nothofagicola T.M.Reeve	cult. ex PNG	ORG 3600	AY239986
Dendrobium papilio Loher	cult. ex Philippines	Cootes (Clements 9202)	AY239987
Dendrobium philippinense Ames	cult. ex Philippines	ORG 1499	AY239988
Dendrobium quadrangulare Parish & Rchb.f.	cult. ex Thailand	ORG 1277 (s#3500)	AY239989
Dendrobium aff. *rarum* Schltr.	cult. ex Vanuatu; Espirato Santo	Clements 5613	AY239990
Dendrobium rhododioides P.Royen	cult. ex PNG	ORG 3601	AY239991
Dendrobium sanguinolentum Lindl.	cult. ex Malaya;	Vaughn s.n.	AY239992
Dendrobium secundum (Blume) Lindl.	cult. ex Thailand	Clements 5377	AY239993
Dendrobium serratilabium	cult. ex Phillipines; Luzon, Laguna	Cootes & L.O.Williams (Clements 9180)	AY239994
Dendrobium sinuatum (Lindl.) Lindl. ex Rchb.f.	cult. ex Thailand;	ORG 3615	AY239995
Dendrobium smillieae F.Muell.	cult. ex Qco*; Captain Billy Ck	Jones 8795	AY239996
Dendrobium sophronites Schltr.	cult. ex PNG;	Spence s.n.	AY239997
Dendrobium speciosum Sm.	cult. ex Nsc*; Pidgeon House Mountain	Clements 5058	AY239998
Dendrobium stuartii F.M.Bailey	Qco*; Mt Finnigan	Roberts s.n.	AY239999

Species	**Provenance**	**Collection No.**	**GenBank Accession No.**
Dendrobium subuliferum Schltr.	cult. ex PNG; Torricelli Mts	Clements 9523	AY240000
Dendrobium thysiflorum Rchb.f.	cult. ex Thailand	Clements 5163	AY240001
Dendrobium truncatum Lindl.	cult. ex Malaya; Tamannegara	Vaughn (Clements 5806)	AY240002
Dendrobium usteroides Schltr.	cult. ex Philippines; Bulalacao	ORG 3000	AY240003
Dendrobium victoriae-reginae Loher	cult. ex Philippines	Cootes (ORG 1484)	AY240004
Dendrobium violaceum Kraenzl.	cult. ex PNG	ORG 3597	AY240005
Dendrobium yeageri . Ames et Quisumb	cult. ex Philippines	ORG 3580	AY240006
Diplocaulobium ischnopetalum (Schltr.) Kraenzl.	cult. ex PNG; near Lae	Clements 7270	AY240007
Dockrillia calamiformis (Lodd.) M.A.Clem. et D.L.Jones	cult. ex Qco*	ORG 3469	AY240008
Drymoanthus flavidus St.George et Molloy	New Zealand; Pounawea	Molloy 207/00	AY240009
Epigeneium amplum (Lindl.) Summerh.	cult. ex India	Banks s.n.	AY240010
Epigeneium cymbidioides (Blume) Summerh	cult. ex Indonesia; Java	Banks s.n. (ORG 3609)	AY240011
Epigeneium nakaharaei (Schltr.) Summerh	cult. ex Taiwan	Clements 9167	AY240012
Epigeneium triflorum (Blume) Summerh.	cult. ex Indonesia; Java	ORG 3591	AY240013
Eria aff. javanica (Sw.) Blume	cult. ex PNG	CBG 740854	AY240014
Flickingeria comata (Blume) A.Hawkes	cult. ex Qco*; Iron Range	Wrigley 354	AY240015
Grastidium baileyi (F.Muell.) Rasuchert	cult. ex Qco*	Jones 4165	AY240016
Liparis habenarina (F.Muell.) Benth.	cult. ex Qco*; Stony Creek	Roberts (ORG 2154)	AY240017
Oxysepala ovalifolia Wight	cult. ex Thailand	RBGS 810771	AY240018
Winika cunninghamii (Lindl.) M.A.Clem., D.L.Jones & Molloy	cult. ex New Zealand; Lincoln	Molloy 061/98	AY240019

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* Abbreviations for Australian Botanical Districts: Nsc = New South Wales, South Coast; Qco = Queensland, Cook; Qmo = Queensland, Moreton.

ORG = Orchid Research Group.

CBG = Canberra Botanic Gardens (now the Australian National Botanic Gardens).

RBGS = Royal Botanic Gardens Sydney

Appendix 2: Taxonomy

Some essential taxonomic and nomenclatural changes arising as a result of these analyses are provided as the next step towards the re-classification of this scientific, horticultural and commercially important group within the Orchidaceae.

Tribe: Podochileae Pfitz., *Entw. Nat. Anord. Orch.* 101 (1887) (as 'Podochilinae').

Type: *Podochilus* Blume

Subtribe: Eriinae Benth., *J. Linn. Soc., Bot.* 18: 287 (1881).

Type: *Eria* Lindl.

Oxystophyllum Blume, *Bijdr.* 335–336 (20 Sep–7 Dec 1825).

Type species: *Oxystophyllum rigidum* Blume, *vide* Brieger (1981).

Dendrobium Sw. sect. *Oxystophyllum* (Blume) Miq., *Fl. Ind. Neerl. Bat.* 3: 644 (1855).

Dendrobium Sw. subg. *Aporum* (Blume) Kraenzl. sect. *Holophylla* Karenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 201, 203–204 (1910), *pro parte min.*
Type species: not designated.

Aporum Blume sect. *Oxystophyllum* (Blume) Brieger, *Schltr. Die Orchideen* 3, Aufl. 1: 670, 676 (1981).

Epiphytic, erect, reptant to pendulous herbs. Roots thin, wiry, hirsute, rusty brown, the growing apex purplish, arising from the base or from internodes along the stem. Stem thin, flexible, covered with equitant leaf sheath. Leaves equitant, rigid, falcate to lanceolate, with abscission layer towards base, apex sharply acute. Inflorescence simple or compound, compressed raceme, lateral or terminal, equitant, indeterminate, the solitary flowers arising intermittently from the developing raceme; floral bracts persistent and often forming dense tufts. Flowers with sombre colours and thick, fleshy and rigid, with short, acute dorsal sepal and petals, the larger lateral sepals adnate to column-foot forming a saccate base with the labellum. Labellum ligulate, on a short hinge, thick fleshy, and secreting sticky fluids on upper surface. Column very short and with a long, broad curved column-foot. Pollinia 4 in two separate sets of 2, small, irregularly shaped, pinkish cream, and with prominent caudicles.

Distribution: South-East Asia and Malesia as far east as the Solomon islands.

Oxystophyllum acianthum (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium acianthum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 572–572 (1912).

Oxystophyllum ambotiense (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ambotiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 466–467 (1928).

Oxystophyllum araneum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium araneum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 397 (1913).

Oxystophyllum atropurpureum Blume, *Rumphia* 4: 41. t. 193. f. 4; 198 f. C (1858); *Dendrobium atropurpureum* (Blume) Miq., *Fl. Ind. Bat.* 3: 644 (1855).

Oxystophyllum atrorubens (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium atrorubens* Ridl., *J. Linn. Soc., Bot.* 32: 247 (1896).

Oxystophyllum bipulvinatum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bipulvinatum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 397 (1913).

Oxystophyllum buruense (J.J.Sm.) M.A.Clem., ***comb. et stat. nov.***
Basionym: *Dendrobium excavatum* (Blume) Miq. var. *buruense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 466 (1928).

Oxystophyllum capitellatum M.A.Clem., ***nom. nov.***
Basionym: *Dendrobium capitellatum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 215 (1910), non J.J.Sm. (1906).

Oxystophyllum carnosum Blume, *Bijdr.* 335 (1825); *Dendrobium carnosum* (Blume) Rchb.f. in Walp., *Ann. Bot.* 6: 280 (1861), non Presl. (1827), nec Teijsm. et Binn. (1853).

Oxystophyllum changiiangense (S.J.Cheng et C.Z.Tang) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium changiiangense* S.J.Cheng et C.Z.Tang, *Acta Phytotax. Sin.* 18(1): 98–99, f. (1980).

Oxystophyllum cultratum (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cultratum* Schltr., *Repert. Spec. Nov. Regni Veg.* 10: 71–72 (1911).

Oxystophyllum cuneatipetalum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cuneatipetalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 157–159 (1927).

Oxystophyllum deliense (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium deliense* Schltr., *Repert. Spec. Nov. Regni Veg.* 11: 143 (1912).

Oxystophyllum elmeri (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium elmeri* Ames in Elmer, *Leafl. Philipp. Bot.* 5: 1573 (1912).

Oxystophyllum excavatum Blume, *Bijdr.* 335 (1825); *Dendrobium excavatum* (Blume) Miq., *Fl. Ind. Bat.* 3: 644 (1855).

Oxystophyllum floridanum (Guillaumin) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium floridanum* Guillaumin, *Bull. Mus. Hist. Nat. Paris* (ser. 2), 37: 199 (1965).

Oxystophyllum govidjoae (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium govidjoae* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 572 (1912).

Oxystophyllum hagerupii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hagerupii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 78–79 (1922).

Oxystophyllum helvolum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium helvolum* J.J.Sm., *Bot. Jahrb. Syst.* 48: 99 (1912).

Oxystophyllum hypodon (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hypodon* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 502 (1910); *Aporum hypodon* (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Oxystophyllum kaudernii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kaudernii* J.J.Sm, *Svensk Bot. Tidskr.* 20: 475–477 (1927).

Oxystophyllum lepoense (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lepoense* Schltr., *Repert. Spec. Nov. Regni Veg.* 9: 285–286 (1911).

Oxystophyllum lockhartioides (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lockhartioides* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 507 (1910).

Oxystophyllum longipecten (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium longipecten* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 61–62 (1928).

Oxystophyllum minutigibbum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium minutigibbum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 13: 3 (1914).

Oxystophyllum moluccense (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium moluccense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 13: 11 (1914).

Oxystophyllum nitidiflorum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium nitidiflorum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 396 (1913).

Oxystophyllum oblongum (Ames et C.Schweinf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium oblongum* Ames et C.Schweinf., *Orchidaceae* 6: 108 (1920).

Oxystophyllum oligadenium (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium oligadenium* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 502–503 (1910).

Oxystophyllum paniferum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium paniferum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 14: 34 (1914).

Oxystophyllum rigidum Blume, Bijdr. 336 (1825); *Dendrobium rigidum* (Blume) Miq., *Fl. Ind. Neerl. Bat.* 3: 644 (1859), *nom illeg.*, non R.Br. (1810), *nec* Lindl. (1830); *Aporum rigidum* (Blume) Brieger, *Schltr., Die Orchideen* 3, Aufl. 1: 676 (1981).

Oxystophyllum sinuatum (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Aporum sinuatum* Lindl., *Edwards' Bot. Reg. 27;* Misc. 3 (1841).

Oxystophyllum speculigerum (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium speculigerum* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 507–508 (1910).

Oxystophyllum subsessile (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium subsessile* Schltr., *Repert. Spec. Nov. Regni Veg.* Beih. 1: 571–572 (1912).

Oxystophyllum torricellianum (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium torricellianum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 215–216 (1910), *nom.*; *Aporum torricellianum* (Kraenzl.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983). *Dendrobium atrorubens* Schltr. in K.Schum. et Lauterb., *Nachtr. Fl. Deutsch. Südsee* 175 (1905), *nom. illeg.* non Ridl. (1896); *Dendrobium simile* Schltr., *Repert. Nov. Spec. Regni Veg.* 3: 80 (1906), *nom. illeg.*, non Schltr. (1905).

Oxystophyllum tropidoneuron (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tropidoneuron* Schltr., *Bot. Jahrb. Syst.* 45, Beibl. 104, 32 (1911).

Oxystophyllum tumoriferum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tumoriferum* J.J.Sm., *Bull. Dep. Agric. Indes Néerl.* 39: 11 (1910).

Oxystophyllum validipecten (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium validipecten* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 59–60 (1928).

Tribe: Dendrobieae Endl., *Gen. Pl.* 190 (1837).
Type: *Dendrobium* Sw.

Subtribe: Epigeneiinae M.A.Clem., ***subtribus nov.***

Dendrobiinis affinis, sed *Bulbophylli* et *Coelogyne* habitu; pseudobulbis turgidis uninodis, aggregatis vel repenti rhizomati separato; pseudobulbis terminalibus foliis 1–3; inflorescentia terminali, uni- vel multiflora; petalis latera columnae adnatis; mento prominenti, differt.

Type: *Epigeneium* Gagnep. **(here designated)**

Plants epiphytic or lithophytic; stems rhizomatous terminating in a single internode pseudobulb; leaves conduplicate, coriaceous,1–3, terminal; inflorescence subterminal, determinate, single or mutli-flowered, erect or pedant, arising from a prominent erect, imbricate bract; flowers long-lasting, with spreading segments, non-articulate labellum, a prominent long column-foot, petals obliquely attached for greater part or not, glabrous elongate column, with prominent apical often ornate anther attachment.

Distribution: The subtribe comprises one genus distributed throughout South-East Asia and much of the Malaya archipelago.

Note: A full account of the subtribe is in preparation. For further details of the genera *Epigeneium* and *Katherinea* A.D.Hawkes, see Balakrishnan and Chowdhury (1966) and Garay and Romero-Gonzalez (1999).

Subtribe: Grastidiinae M.A.Clem., ***subtribus nov.***

Dendrobiinis affinis sed caulibus vel praecipue durobaculoidibus vel pseudobulbis elongatis et duris; inflorescentia racemosa laterali vel subterminali, abbreviata vel prolongata, uni- vel multi-flora; labello articulato, raro pedi columnae adnato; protocormis discoidis vel globosis, raro late isobilateralibus, differt.

Type: *Grastidium* Blume. **(here designated)**

Terrestrial, lithophytic or epiphytic herbs. Stems comprising one to many internodes, hard, wiry, slender or forming pseudobulbs, indeterminate or determinate. Leaves distichous, duplicate, ligulate, terete or sagittate, articulate, with or without sheaths at base. Inflorescence, lateral or pseudoterminal, usually upper axillary, racemose, rarely paniculate. Flowers solitary, in pairs or numerous, ephemeral, or lasting a few days to several weeks, resupinate or non-resupinate, conspicuous. Sepals, laterals dissimilar to dorsal. Petals similar. Labellum showy, trilobed, sometimes obscurely so, articulate, or fused at base to column-foot, with central callus ridges. Column elongate or short, glabrous, entire. Anther fleshy, glabrous. Pollinia hard, waxy, glabrous, four, in two pairs appressed together. Protocorms discoid or globose rarely isobilateral-globose.

Distribution: Genera in the subtribe are distributed mainly in Australasia and Malesia with a small number of representative species reaching the Asian mainland.

Note: The Grastidiinae comprises the following genera and for most the taxonomy and nomenclature has been dealt with preliminarily elsewhere. A full account of all taxa within these genera based primarily on the results of molecular analyses of ITS sequence data is in preparation.

Abaxianthus M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 485 (2002).
Type species: *Desmotrichum convexa* Blume.

Australorchis Brieger in Schltr., *Die Orchideen* 1(11–12): 741 (1981).
Type species: *Australorchis monophylla* (F.Muell.) Brieger (= *Dendrobium monophyllum* F.Muell).

Bouletia M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 485 (2002).
Type species: *Dendrobium finetianum* Schltr.

Cadetia Gaud. in Freycinet, *Voy. Uranie* 422, t. 33 (1826 [Sept. 1829]).
Type species: *Cadetia umbellatum* Gaud.

Cannaeorchis M.A.Clem. et D.L.Jones, *Lasianthera* 1(3): 132 (1998).
Type species: *Dendrobium fractiflexum* Finet.

Cepobaculum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 486 (2002).
Type species: *Dendrobium canaliculatum* R.Br.

Ceratobium (Lindl.) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 486 (2002).
Type species: *Dendrobium antennatum* Lindl.

Davejonesia M.A.Clem, *Orchadian* 13(11): 487 (2002).
Type species: *Dockrillia lichenastra* (F.Muell.) Brieger.

Dendrobates M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 487 (2002).
Type species: *Dendrobium virotii* Guillaumin.

Dichopus Blume, *Mus. Bat.* 2: 176 (1856).
Type species: *Dichopus insignis* Blume.

Diplocaulobium (Rchb.f.) Kraenzl., *Pflanzenreich Orch.-Mon.-Dendr.* 45: 331 (1910).
Type species: *Diplocaulobium nitidissimum* (Rchb.f.) Kraenzl. (= *Dendrobium nitidissimum* Rchb.f.).

Dockrillia Brieger, *Schltr., Die Orchideen* 3(1): 745 (1981).
Type species: *Dendrobium linguiforme* Sw.

Durabaculum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 487 (2002).
Type species: *Dendrobium undulatum* R.Br.

Eleutheroglossum (Schltr.) M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 489 (2002).
Type species: *Dendrobium eleutheroglossum* Schltr.

Eriopexis (Schltr.) Brieger, *Schltr., Die Orchideen* 3 (1): 656 (1981).
Type species: *Dendrobium eriopexis* Schltr. (= *Eriopexis schlechteri* Brieger).

Euphlebium (Kraenzl.) Brieger, *Schltr., Die Orchideen* 3(1): 722 (1981).
Type species: *Dendrocolla spurium* Blume.

Exochanthus M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 496 (2002).
Type species: *Dendrobium pleianthum* Schltr.

Flickingeria A.Hawkes, *Orchid Weekly* 2(46): 451 (6 Jan. 1961).
Type species*: Desmotrichum angulatum* Blume (= *Flickingeria angulata* (Blume) A.D.Hawkes), a substitute name for *Desmotrichum* Blume 1825 (*nom. rej.*), non Kuetzing 1845 (*nom. cons.*).

Grastidium Blume, *Bijdr.* 7: 333 (1825).
Type species: *Grastidium salaccense* Blume.

Herpethophytum (Schltr.) Brieger, *Schltr., Die Orchideen* 1(11–12): 660 (July 1981).
Type species: *Herpethophytum schlechteri* S. Rauschert, (= *Dendrobium herpethophytum* Schltr.).

Inobulbum (Schltr.) Schltr. et Kraenzl. in Engl. *Pflanzenreich, Orch.-Mon.-Dendr.* 1: 316 (1910).
Type species: *Inobulbum muricatum* (Finet) Kraenzl. (= *Dendrobium muricatum* Finet).

Kinetochilus (Schltr.) Brieger, *Schltr., Die Orchideen* 1(11–12): 686 (July 1981).
Type species: *Kinetochilus pectinatus* (Finet) Brieger (= *Dendrobium pectinatum* Finet).

Leioanthum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Dendrobium biflace* Lindl.

Microphytanthe (Schltr.) Brieger, *Schltr., Die Orchideen* 3(1): 742 (1981).
Type species: *Dendrobium bulbophylloides* Schltr.

Monanthos (Schltr.) Brieger, *Schltr., Die Orchideen* 3(1): 660 (1981) (as '*Monanthus*').
Type species: *Monanthos biloba* (Lindl.) Brieger (= *Dendrobium bilobum* Lindl.).

Sarcocadetia (Schltr.) M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Cadetia funiformis* (Blume) Schltr.

Sayeria Kraenzl., *Ost. Bot. Zeitsch.* 44: 257–59 (1894).
Type: *Sayeria paradoxa* Kraenzl.

Stelbophyllum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Dendrobium toressae* F.M.Bailey.

Tetrabaculum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Dendrobium tetragonum* A.Cunn.

Tetrodon (Kraenzl.) M.A.Clem. et D.L.Jones, *Orchadian* 12(7): 310 (1998).
Type species: *Eria oppositifolia* Kraenzl. (= *Dendrobium oppositifolium* (Kreanzl.) N. Hallé.

Thelychiton Endl., *Prod. Fl. Norf.* 32 (1833).
Type species: *Thelychiton macropus* Endl.

Trachyrhizum (Schltr.) Breiger, *Die Orchideen* 3(1): 687 (1981).
Type species: *Dendrobium chalmersii* F. Muell.

Tropilis Rafin., *Fl. Tell.* 2: 95 (1837).
Type species: *Dendrobium aemulum* R.Br. (= *Tropilis emulum* (R.Br.) Rafin.).

Vappodes M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 492 (2002).
Type species: *Dendrobium bigibbum* Lindl.

Winika M.A.Clem., D.L.Jones et Molloy, *Orchadian* 12(5): 214 (1997).
Type species: *Dendrobium cunninghamii* Lindl.

Subtribe: Dendrobiinae Lindl., *Gen. Sp. Orch. Pl.* 45 (1830) (as Section II. Dendrobieae).
Type: *Dendrobium* Sw., *fide* Butzin (1971: 323).

First major group

Distichorchis M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 487 (2002).

Basionym: *Dendrobium* Sw. sect. *Distichophyllum* Hook.f., *Fl. Brit. India* 5: 711 (1890).
Type species: *Dendrobium uniflorum* Griffith, *fide* Brieger (1981).

Dendrobium Sw. subgen. *Grastidium* (Blume) Kraenzl. sect. *Revoluta* (pars 2) Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 181 (1910), *pro parte max.*
Type species: *Dendrobium revolutum* Lindl.

Epiphytic or lithophytic herb. Stems psuedobulbous or non-pseudobulbous to c. 80 cm long. Inflorescence a highly reduced, lateral, periodically developing raceme, protected in a terminal sheathing bract. Flowers solitary, one, occasionally two per inflorescence, each with a papery sheath that persists in the sheathing bracts after anthesis. Labellum fleshy, minutely papillate, towards base on lamina callus, forming a closed, conspicuous, nectiferous spur at the base through fusion of basal half to the column-foot. Column short, concave, papillose on inner surface. Column-foot longer than column. Pollinia four, obliquely-obovate, elongate, glabrous, bright yellow. Capsules near globular, glabrous or hirsute, splitting open longitudinally when mature. Discoid protocorm-seedling type.

Distribution: South-East Asia, Malesia and South-west Pacific Islands.

Notes: The following species are transferred to this genus following detailed research of types and the literature.

Distichorchis angusta (Quisumb.) M.A.Clem., ***comb. et stat. nov.***
Basionym: *Dendrobium uniflorum* Griff. var. *angustum* Quisumb., *Philipp. Orch. Rev.* 3(3): 9, t. 1 (1950).

Distichorchis angustipetala (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium angustipetalum* J.J.Sm., *Orch. Ambon* 59 (1905).

Distichorchis barisana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium barisanum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 45–46 (1917).

Distichorchis bifaria (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bifarium* Lindl., *Wall., Cat.* N. 2002 (1828); *Gen. Sp. Orch. Pl.* 81 (1830).

Distichorchis bihamulata (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bihamulatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 43–45 (1917).

Distichorchis cerina M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 487 (2002).
Basionym: *Dendrobium cerinum* Schltr., *Bot. Jahrb. Syst.* 39: 72 (1906), non Rchb.f. (1879); *Dendrobium austrocaledonicum* Schltr., *Repert. Spec. Nov. Regni Veg.* 3: 80 (1906), *nom.*

Distichorchis connata (Blume) M.A.Clem., ***comb. nov.***
Baisonym: *Onychium connatum* Blume, *Bijdr.* 328 (1825).

Distichorchis dissitifolia (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium dissitifolium* Ridl., *Trans. Linn. Soc., Bot.* 9: 168 (1916).

Distichorchis distachya (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium distachyon* Lindl., *J. Linn. Soc., Bot.* 3: 13 (1859).

Distichorchis elephantina (Finet) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium elephantinum* Finet, *Bull. Soc. Bot., France* 50: 373, t. 11, f. 20–31 (1903).

Distichorchis ellipsophylla (T.Tang et F.T. Wang) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ellipsophyllum* T.Tang et F.T. Wang, *Acta Phytotax. Sin.* 1, 1: 81 (1951).

Distichorchis hepatica (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hepaticum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 48 (1917).

Distichorchis igneonivea (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium igneoniveum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 161 (1927).

Distichorchis kenepaiensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kenepaiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 46–47 (1918).

Distichorchis lambii (J.J.Wood) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lambii* J.J.Wood, *Kew Bull.* 38(1): 79, f. 1 (1983).

Distichorchis lamriana (C.L.Chan) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lamrianum* C.L.Chan, *Sandakania* 5: 67–77, f. 1–2 (1994).

Distichorchis maraiparensis (J.J.Wood et C.L.Chan) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium maraiparense* J.J.Wood et C.L.Chan in C.L.Chan, A.Lamb, P.S.Shim and J.J.Wood, *Orch. Borneo* 1: 119, f. 25, t. 5E (1994).

Distichorchis melanotricha (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium melanotrichum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 558–559 (1912).

Distichorchis mellicolor (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium mellicolor.*J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 160 (1927).

Distichorchis metachilina (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium metachilinum* Rchb.f., *Bonplandia* 3: 222 (1855).

Distichorchis moquetteana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium moquetteanum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2) 25: 50–51 (1917).

Distichorchis multicostata (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium multicostatum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 5: 11 (1907).

Distichorchis nabawanensis (J.J.Wood et A.Lamb) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium nabawanense* J.J.Wood et A.Lamb in J.J.Wood et P.J.Cribb, *Checklist Orch. Borneo* 258, f 32 (1994).

Distichorchis olivacea (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium olivaceum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 8: 41 (1912).

Distichorchis osmophytopsis (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium osmophytopsis* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 172 (1910).

Distichorchis ovatifolia (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ovatifolium* Ridl., *J. Linn. Soc., Bot.* 31: 271 (1896).

Distichorchis pachyantha (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pachyanthum* Schltr., *Repert Spec. Nov. Regni Veg.* 9: 290 (1911).

Distichorchis pahangensis (Carr) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pahangense* Carr, *Gard. Bull. Straits Settlements* 5: 126 (1930).

Distichorchis pandaneti (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pandaneti* Ridl., *J. Linn. Soc., Bot.* 32: 257 (1896).

Distichorchis piranha (C.L.Chan et P.J.Cribb) M.A.Clem. et D.L.Jones, ***comb. nov.***
Basionym: *Dendrobium piranha* C.L.Chan et P.J.Cribb in C.L.Chan, A.Lamb, P.S.Shim et J.J.Wood, *Orch. Borneo* 1: 127, f. 28, t. 6B (1994).

Distichorchis pluricostata (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pluricostatum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 557–558 (1912).

Distichorchis quadrisulcata (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium quadrisulcatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 49–50 (1917).

Distichorchis refracta (Teijsm. et Binn.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium refractum* Teijsm. et Binn., *Tijdschr. Nederl. Ind.* 24: 315–316 (1862).

Distichorchis revoluta (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium revolutum* Lindl., *Edwards' Bot. Reg.* 27; Misc. 51 (1840).

Distichorchis rupicola (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rupicolum* Ridl., *J. Fed. Mal. States Mus.* 1: 174 (1915).

Distichorchis sandsii (J.J.Wood et C.L.Chan) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sandsii* J.J.Wood et C.L.Chan in C.L.Chan, A.Lamb, P.S.Shim et J.J.Wood, *Orch. Borneo* 1: 129, f. 29, t. 6C (1994).

Distichorchis siberutensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium siberutense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 82–83 (1922).

Distichorchis spathipetala (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium spathipetalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2) 13: 20 (1914).

Distichorchis striatiflora (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium striatiflorum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 114 (1913).

Distichorchis torquisepala (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium torquisepalum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 187 (1910).

Distichorchis uniflora (Griff.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium uniflorum* Griff., *Notul.* 3: 305–306 (1851); *Icon. Pl. Asia.* t. 303 (1851).

Distichorchis xanthophaea (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium xanthophaeum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 558 (1912).

Second major group

Dendrobium *Sw., Nov. Act. Soc. Sci. Upsal.* 6: 82 (1799) (nom. cons.).
Type species: *Dendrobium moniliforme* Sw. (type cons. *vide* Holttum et al. 1979).

Ormostema Raf., *Fl. Tellur.* 4: 38 (1836).
Type species: *Ormostema purpurea* Raf. (*Epidendrum moniliforme* L. = *Dendrobium moniliforme sensu* Lindl. ≡ *D. linawianum* Rchb.f.); *O. albiflora* Raf. (*Epidendrum monile* Thunb. = *Dendrobium monile* (Thunb.) Kuntze ≡ *Dendrobium moniliforme* (L.) Sw.)

Peirardia Raf., *Fl. Tellur.* 4: 41 (1836).
Type species: *Peirardia bicolor* Raf. (= *Dendrobium pierardii* Roxb.).

Dendrobium Sw. sect. *Dendrobium* Lindl., *Edwards' Bot. Reg.* 30: misc. 62 (1844); Lindl. et Paxton in Paxton's *Fl. Gard.* 1: 135 (1850–51), (as 'sect. Eudendrobium').

Dendrobium Sw. subgen. *Dendrobium* (Lindl.) Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dend.* 1: 26–27 (1910), (as 'subg. Eudendrobium').

Dendrobium Sw. subgen. *Dendrobium* (Lindl.) Kraenzl. sect. *Eugenanthe* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 445 (1912).

Epiphytic or lithophytic herbs. Roots thick and fleshy, white, arising at base of new growths. Stems pseudobulbous, thickest near the middle, often with aerial growths. Leaves duplicate, deciduous; sheaths not overlapping. Inflorescence lateral, determinate racemose, with one to five flowers lasting several to many days. Flowers usually showy, erect with spreading segments. Petals and sepals glabrous, spreading, often similar in size and shape, but petals may also be broader. Labellum fleshy, showy, distinctly different to petals, continuous with the column-foot, non-articulate, forming a cavity at their base, obscurely trilobed, covered in papillae, sometimes granular in appearance. Column short, concave, broad nearest the base, glabrous. Anther cap large and ornate. Pollinia elongate, lunate, four (2 x 2) appressed together, yellow glabrous. Capsule elongate, fusiform. Elongate protocorm-seedling type.

Distribution: Found throughout South-East Asia, Malesia and Australia (represented by a single species).

Note: Furthur systematics of this group will be published separately (Clements et al. in prep.).

Third major group

Anisopetala (Kraenzl.) M.A.Clem., ***gen. et stat. nov***.

Basionym: *Dendrobium* Sw. subgen. *Dendrobium* sect. *Anisopetala* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 27, 68 (1910).
Type species: *Dendrobium mutabile* (Blume) Lindl., *vide* Brieger (1981: 698).

Pedilonum Blume sect. *Sanguinolenta* Brieger, *Schltr., Die Orchideen* 3(1): 681 (1981).
Type species: *Pedilonum sanguinolentum* (Lindl.) Brieger (= *Dendrobium sanguinolentum* Lindl.).

Plants epiphytic herbs. Stems elongate, narrow, relatively fleshy. Leaves along almost their entire length when young, deciduous prior to flowering. Inflorescence lateral, the peduncles short and usually pendulous, bearing 1–14 flowers. Flowers showy, with a distinct mentum fusion of the basal part of the lateral sepals, and always held away from the ovary and pedicel; free parts of sepals and petals spreading; labellum with distinct claw, with or without a small projection on the upper surface near the base, the apical part spreading, usually without distinct sidelobes, and with a bilobed apex.

Distribution: South-East Asia, western Malesia and the Philippines.

Notes: The following species are transferred to this genus following detailed research of types and the literature.

Anisopetala acutimenta (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium acutimentum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 53–54 (1917).

Anisopetala annae (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium annae* J.J.Sm, *Orch. Java* 354–355 (1905).

Anisopetala biflora (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Pedilonum biflorum* Blume, *Bijdr.* 1: 322 (1825).

Anisopetala calicopis (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium calicopis* Ridl., *J. As. Soc. Straits* 39: 72 (1903).

Anisopetala filicaulis (Gapnep.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium filicaule* Gagnep., *Bull. Mus. Hist. Nat. Paris* (ser. 2), 21: 741 (1949).

Anisopetala fulminicaulis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fulminicaule* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 51–53 (1917).

Anisopetala hughii (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hughii* Rchb.f., *Gard. Chron.* (new ser.) 17: 764 (1882).

Anisopetala inflata (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium inflatum* Rolfe, *Kew Bull.* 61 (1895).

Anisopetala lucens (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lucens* Rchb.f., *Bot. Zeit. (Berlin)* 21: 128 (1863).

Anisopetala montana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium montanum* J.J.Sm., *Orchid. Java* 363–364 (1905).

Anisopetala mutabilis (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium mutabile* Blume, *Bijdr.* 324 (1825).

Anisopetala nuda (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium nudum* Blume, *Bijdr.* 324 (1825).

Anisopetala rigida (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium rigidum* Blume, *Bijdr.* 324 (1825).

Anisopetala sanguinolenta (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sanguinolentum* Lindl., *Edwards' Bot. Reg.* 28: 62, misc. 73 (1842).

Anisopetala spathilinguis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium spathilingue* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 9: 64 (1913).

Anisopetala transtillifera (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium transtilliferum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 85–86 (1922).

Eurycaulis M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 490 (2002).

Basionym: *Dendrobium* Sw. sect. *Platycaulon* Schltr. in K.Schum. et Laut., *Fl. Schutzg. Südsee, Nachtr.* 150 (1905) (as '*Platybulbon*', orth. error).
Type species: *Dendrobium lamellatum* (Blume) Lindl. (as 'lamellatus').

Dendrobium Sw. sect. *Dendrocoryne* Lindl.. *Edwards' Bot. Reg.* 28: Misc. 76 (1842).
Type species: *Dendrobium compressum* Lindl.

Pedilonum Blume sect. *Platycaulon* (Schltr.) Brieger, *Schltr., Die Orchideen* 3(1): 685 (1981).
Type species: *Onychium lamellatum* Blume ≡ *Dendrobium lamellatum* (Blume) Lindl. ≡ *Pedilonum lamellatum* (Blume) Brieger

Dendrobium Sw. subgen. *Dendrocoryne* (Lindl.) Kraenzl. sect. *Platycaula* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 242, 266–267 (1910).
Type species: *Dendrobium platycaulon* Rolfe.

Notes: The following species are transferred to this genus following detailed research of types and the literature. The genus comprises two subgenera based on the results of these studies.

Eurycaulis subgen. Eurycaulis

Plants epiphytic; stems elongate, fusiform, narrowest in basal half, laterally flattened, fleshy; leaves thin, conduplicate, alternate, present in upper half, deciduous prior to flowering; inflorescence short lateral, peduncles short and usually pendulous, bearing 1–14 flowers; flowers showy, or if not opening widely these usually being cleistogamous, forming a distinct mentum fusion of the basal part of the lateral sepals and always held away from the ovary and pedicel; free parts of sepals and petals spreading; labellum with distinct claw, with or without a small projection on the upper surface near the base, the apical part spreading, without distinct sidelobes, and with bilobed apex.

Distribution: Malesia as far east as the Solomon Islands.

Eurycaulis camptocentrus (Schltr.) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 490 (2002).

Eurycaulis compressus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium compressum* Lindl., *Edwards' Bot. Reg.* 28, Misc. 76 (1842).

Eurycaulis discocaulon (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium discocaulon* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 501 (1912).

Eurycaulis lamellatus (Blume) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 490 (2002).
Basionym: *Onychium lamellatum* Blume, *Bijdr.* 526 (1825).

Eurycaulis lamprocaulon (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lamprocaulon* Schltr. in K. Schum. et Laut., *Nachtr. Fl. Deutsch. Südsee* 166 (1905).

Eurycaulis milaniae (H.Fessel et E.Lückel) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium milaniae* H.Fessel et E.Lückel, *Orchidee* 47(3): A131 (1996).

Eurycaulis platycaulon (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium platycaulon* Rolfe, *Kew Bull.* 139 (1892).

Eurycaulis platygastrius (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium platygastrium* Rchb.f., *Otia Bot. Hamb.* 55 (1878).

Eurycaulis praetermissus (Seidenf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium praetermissum* Seidenf., *Contr. Orch. Fl. Thailand* XIII: 34, f. 7 (1997).

Eurycaulis remiformus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium remiforme* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 111 (1913).

Eurycaulis septemcostulatus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium septemcostulatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 8384 (1920).

Eurycaulis treubii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium treubii* J.J. Sm., *Orch. Ambon* 65 (1905); *Ic. Bogor.* 3: 29–30, t. 212 (1906).

Eurycaulis ypsilon (Seidenf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ypsilon* Seidenf., *Opera Bot.* 83: 158 (1985).

Eurycaulis subgen. Calcariferus (J.J.Sm.) M.A.Clem., ***subgen. et stat. nov.***

Basionym: *Dendrobium Sw.* sect. *Calcarifera* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 15: 14 (1908).
Type species: *Dendrobium pedicellatum* J.J.Sm.

Plants epiphytic; stems elongate, narrow, relatively fleshy; leaves along almost their entire length, deciduous prior to flowering; inflorescences lateral, the peduncles short and usually pendulous, bearing 1–14 flowers; flowers showy, forming a distinct mentum fusion of the basal part of the lateral sepals and always held away from the ovary and pedicel; free parts of sepals and petals spreading; labellum with distinct claw, with or without a small projection on the upper surface near the base, the apical part spreading, without distinct sidelobes, and with bilobed apex.

Distribution: South-East Asia and Malay archipelago.

Eurycaulis acutifolius (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium acutifolium* Ridl., *J. Fed. Mal. States Mus.* 8: 91–92 (1917).

Eurycaulis annamensis (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium annamense* Rolfe., *Kew Bull.* 113–114 (1906).

Eurycaulis anthrene (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium anthrene* Ridl., *J. Linn. Soc., Bot.* 31: 272 (1896).

Eurycaulis appendiculoides M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium appendiculoides* Ames, *Orchidaceae* 7: 93–94 (1922), *nom. illeg.*, non J.J.Sm. (1913).

Eurycaulis arcuatus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium arcuatum* J.J.Sm., *Orch. Java* 357 (1905).

Eurycaulis atjehensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium atjehense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 12: 137 (1932).

Eurycaulis bicallosus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bicallosum* Ridl., *J. Fed. Mal. States Mus.* 8(4): 92–93 (1917).

Eurycaulis boumaniae (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium boumaniae* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 8: 55–56 (1926).

Eurycaulis calcariferus (Carr) M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium calcariferum* Carr, *Gard. Bull. Straits Settlement* 8: 107–108 (1935).

Eurycaulis cerinus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cerinum* Rchb.f., *Gard. Chron.* (ser. 2), 12: 554 (1879).

Eurycaulis cinereus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cinereum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 78–79 (1920).

Eurycaulis compressimentus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium compressimentum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 63–64 (1928).

Eurycaulis corallorhizus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium corallorhizon* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 140–141 (1931).

Eurycaulis courtauldii (Summerh. ex J.J.Wood) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium courtauldii* Summerh. ex J.J.Wood, *Orchid Rev.* 89(1056): 322 (1981).

Eurycaulis crabro (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium crabro* Ridl., *J. As. Soc. Straits* 50: 133 (1908).

Eurycaulis crassimarginatus (L.O.Williams) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium crassimarginatum* L.O.Williams, *Bot. Mus. Leafl. Harvard Univ.* 5: 42–44 (1937).

Eurycaulis crocatus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium crocatum* Hook.f., *Fl. Brit. Ind.* 6: 185 (1890).

Eurycaulis croceocentrus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium croceocentrum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 75–76 (1920).

Eurycaulis cumulatus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cumulatum* Lindl., *Gard. Chron.* 756 (1855).

Eurycaulis curvus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium curvum* Ridl., *J. Fed. Mal. States Mus.* 8: 91 (1917).

Eurycaulis cymbiformis (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cymbiforme* Rolfe, *Kew Bull.* 192 (1898).

Eurycaulis cymboglossus (J.J.Wood et A.Lamb) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cymboglossum* J.J.Wood et A.Lamb in J.J.Wood et P.J.Cribb, *Checklist Orch.Borneo* 247–248, f. 29, t. 8C (1994).

Eurycaulis derryi (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium derryi* Ridl., *Mat. Fl. Mal. Penins.* 1: 52 (1907).

Eurycaulis diffusus (L.0.Williams) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium diffusum* L.0.Williams, *Bot. Mus. Leaf. Harvard Univ.* 5: 44–45 (1937).

Eurycaulis endertii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium endertii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3),11: 138 (1931).

Eurycaulis exilicaulis (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium exilicaule* Ridl., *Fl. Mal. Penins.* 4: 50 (1924).

Eurycaulis fimbrilabius (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fimbrilabium* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 81–82 (1920).

Eurycaulis foetens (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium foetens* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 77–78 (1910).

Eurycaulis foxii (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium foxii* Ridl., *J. Bot.* 38: 70 (1900).

Eurycaulis grastidioides (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium grastidioides* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 80–81 (1920).

Eurycaulis groeneveldtii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium groeneveldtii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 79–80 (1920).

Eurycaulis guerreroi (Ames et Quisumb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium guerreroi* Ames et Quisumb., *Philipp. J.. Sci.* 49: 489 (1932).

Eurycaulis hamatus (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hamatum* Rolfe, *Kew Bull.* 183 (1894).

Eurycaulis hamaticalcar (J.J.Wood et Dauncey) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hamaticalcar* J.J.Wood et Dauncey in J.J.Wood, Baeman et Beaman, *Pl. Mt Kinabalu* 2, Orch. 168, f. 20 (1993).

Eurycaulis huttonii (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium huttonii* Rchb.f., *Gard. Chron.* 686 (1869).

Eurycaulis hymenanthus M.A.Clem., ***nom. nov.***
Basionym: *Dendrobium hymenanthum* Hook.f., *Fl. Brit. Ind.* 5: 732 (1890); Icon. Pl. t. 2032 (1890); 6: 185 (1890), *nom. illeg.*, non Rchb.f. (1855).

Eurycaulis intricatus (Gagnep.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium intricatum* Gagnep., *Bull. Mus. Hist. Nat. Paris* (ser. 2), 2: 236 (1930).

Eurycaulis ionopus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ionopus* Rchb.f., *Gard. Chron.* 2: 808 (1882).

Eurycaulis kentrochilus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kentrochilum* Hook.f., *Fl. Brit. Ind.* 5: 731(1890); Icon. Pl. t. 2030 (1890).

Eurycaulis kruiensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kruiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 8: 56–57 (1926).

Eurycaulis lampongensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lampongense* J.J.Sm., *Bull. Dépt. Agric. Néerl.* 15: 14–15 (1908).

Eurycaulis lankaviensis (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lankaviense* Ridl., *J. As. Soc. Straits* 54: 49 (1910).

Eurycaulis leucochlorus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium leucochlorum* Rchb.f., *Gard. Chron.* 1: 202 (1879).

Eurycaulis lilacinus M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium lilacinum* Rchb.f., *Gard. Chron.* 674 (1865), non Teijsm. et Binn.(1864).

Eurycaulis lucens (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lucens* Rchb.f., *Bot. Zeit. (Berlin)* 21: 128 (1863).

Eurycaulis maierae (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium maierae* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 76–78 (1920).

Eurycaulis megaceras (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium megaceras* Hook.f., *Fl. Brit. Ind.* 5: 713 (1888); Icon. Pl. t. 2031 (1890).

Eurycaulis modestus M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium modestum* Ridl., *J. Bot.* 211(1898), non Rchb.f.(1855)

Eurycaulis multiflorus M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium multiflorum* Ridl., *Journ. As. Soc. Straits* I: 134 (1908), non Par. et Rchb.f. (1874).

Eurycaulis nieuwenhuisii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium nieuwenhuisii* J.J.Sm., *Ic. Bogor.* 3: 25–27: t. 211 (1906).

Eurycaulis obrienianus (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium o'brienianum* Kraenzl., *Gard. Chron.* (ser. 3), 11: 266 (1892).

Eurycaulis paathii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium paathii* J.J.Sm., *De Orchidee (Bandoeng)* 4: 183 (1935); Orch. Rev. 43: 290, in obs (1935); *Gard. Bull. Straits Settlements* 9: 90 (1935).

Eurycaulis panduriferus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium panduriferum* Hook.f., *Fl. Brit. India* 6: 186 (1890).

Eurycaulis pedicellatus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pedicellatum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 15: 13 (1908).

Eurycaulis peralu (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium peralu* Rchb.f., *Hamb. Gartenz.* 21: 298 (1865).

Eurycaulis pictus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pictum* Lindl., *Gard. Chron.* 548 (1862).

Eurycaulis profusus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium profusum* Rchb.f., *Gard. Chron.* 1: 510 (1884).

Eurycaulis rantii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rantii* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 36: 114–115 (1934).

Eurycaulis rappardii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rappardii* J.J.Sm., *Blumea* 5: 308 (1943).

Eurycaulis rhodocentrum (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rhodocentrum* Rchb.f., *Gard. Chron.* 426 (1872).

Eurycaulis roseatus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium roseatum* Ridl., *J. Linn. Soc.* 32: 261 (1896).

Eurycaulis singalanensis (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium singalanense* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 167 (1910).

Eurycaulis subflavidus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium subflavidum* Ridl., *J. Linn. Soc., Bot.* 38: 324 (1908).

Eurycaulis tropaeoliflorus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tropaeoliflorum* Hook.f., *Fl. Brit. Ind.* 6: 186 (1890).

Eurycaulis undulatus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Pedilonum undulatum* Blume, *Bijdr.* 322, t. 36 (1825).

Eurycaulis ventrilabius (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ventrilabium* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 84–85 (1922).

Eurycaulis viriditepalus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium viriditepalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 54–56 (1917).

Eurycaulis viridulus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium viridulum* Ridl., *J. Linn. Soc.* 32: 259 (1896).

Eurycaulis zamboangensis (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium zamboangense* Ames, *Orchidaceae* 5: 145 (1915

Pedilonum (Blume) Blume, *Bijdr. Fl. Ned. Ind.*: 320 (1825)

Dendrobium Sw. sect. *Pedilonum* Blume, *Bijdr. Fl. Ned. Ind.*: tab. 4 (1825).
Type species: *Dendrobium secundum* (Blume) Lindl. ex Wall., *vide* Rafinesque (1836: 44).

Dendrobium Sw. sect. *Dendrobium* subsect. *Pedilonum* (Blume) Pfitzer in Engl. and Prantl, *Nat. Pflanzenfam.* 2(6): 174 (1888).

Dendrobium Sw. subgen. *Pedilonum* (Blume) Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 96 (1910).

Erect to pendulous epiphytic herb. Stems stout, clustered, cylindric to more or less cylindric-fusiform. Leaves coriaceous, somewhat twisted at base, linear-oblong to elliptic-ovate. Inflorescence densely multi-flowered, arising from upper nodes of leafless stems. Flowers secund, waxy, purple, pink, rarely white, the labellum lamina usually orange or yellow; pedicellate ovary cylindric-clavate. Dorsal sepal slightly concave, ovate-triangular to elliptic-oblong, acute. Lateral sepals obliquely falcate to tringular, elliptic-oblong, acute to acuminate; mentum equalling or slightly longer than free part, fused to labellum, saccate. Petals small, obliquely linear-obovate to narrowly elliptic, acute. Labellum linear-spathulate, lamina narrowly linear-elliptic to obovate-cuneate, acute to acuminate, saccate for basal two-thirds, shallowly concave above, fused to column-foot, transverse callus V-shaped to semilunate. Column short, laterally dilated toward apex, with sunken stigma, and protruding hard, plate-like rostellum. Column-foot curved, slightly thickened below stigma, with basal nectary. Capsule oblique ellipsoidal-ovoid.

Distribution: South-East Asia and the Malesian Archipelago.

Pedilonum amethystoglossum (Rchb.f.). M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium amethystoglossum* Rchb.f., *Gard. Chron.* 109 (1872).

Pedilonum secundum Blume, *Bijdr. Fl. Ned. Ind.*: 322 (1825).

Fourth major group

Callista Lour., *Fl. Cochinch.* 2: 519 (1790).
Type species: *Callista amabilis* Lour.

Endeisa Rafin., *Fl. Tellur.* 2: 52 (1836)[1837].
Type species: *Endeisa flava* Raf. (= *Dendrobium densiflorum* Lindl.).

Dendrobium Sw. sect. *Densiflora* Finet, *Bull. Mus. Nat. Hist. (Paris)* 9: 295–303 (1903).
Type species: *Dendrobium densiflorum* Lindl.

Dendrobium Sw. sect. *Callista* (Lour.) Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 444–445 (1912).
Type species: *Callista amabilis* Lour.

Epiphytic herbs. Roots thick, fleshy, white. Stems erect, fusiforme to clavate, often angular, pseudobulbous, comprising several to many internodes; Leaves one to five, coriaceous, terminal to subterminal, near sheathless. Inflorescence pendant, multi-flowered, arising from near terminal nodes, development as though being extruded like paste from the stem buds. Flowers yellow, white or pink, with or without contrasting orange or yellow labellum. Lateral sepals similar and thin textured, spreading. Petals broader and often with serrate erose margins. Labellum broadly orbicular with constricted base, lacking side lobes, the base continuous with column-foot, flexible but non-articulate; the upper surface papillose-pubescent, basal transverse callus, and concave base. Column short with prominent sunken stigma. Column-foot relatively short, with prominent shortly falcate staminodia and with distal, glabrous, shiny, basal nectiferous cavity. Anther cap elongate, glabrous. Pollinia four in two groups of two, obovate-elongate, thin, glabrous, light yellow.

Distribution: South-East Asia.

Notes: The following species were recognized as belonging to this genus following detailed research of types and the literature.

Callista amabilis Lour., *Fl. Cochinch.* 2: 519 (1790).

Callista densiflora (Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 654 (1891).

Callista farmeri (Paxt.) Kuntze, *Rev. Gen. Pl.* 2: 654 (1891).

Callista griffithiana (Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 654 (1891).

Callista guibertii (Carriere) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium guibertii* Carriere, *Rev. Hortic.* 48: 430 (1876).

Callista palpebrae (Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 655 (1891).

Callista thyrsiflora (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium thyrsiflorum* Rchb.f. in Andre, *Illustr. Hortic.* 22: 88, t. 207 (1875).

Fifth major group

Ceraia Lour., *Fl. Cochinch.* 2: 518 (1790) (as '*Ceraja*').
Type species: *Ceraia simplicissima* Lour.

Dendrobium Sw. sect. *Crumenata* Pfitz. in Engl. et Prantl, *Pflanzenr.* II (6): 174 (1889).
Type species: *Dendrobium crumenatum* Sw.

Dendrobium Sw. subgen. *Crumenata* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dend.* 1: 224 (1910).

Aporum Blume sect. *Crumenata* (Pfitz.) Brieger, *Schltr., Die Orchideen* 1(11–12): 671 (1981).

Dendrobium Sw. sect. *Ampullaria* Pfitz. in Engl. et Prantl, *Pflanzenr.* II (6): 174 (1889).
Type species: *Dendrobium planibulbe* Lindl.

Dendrobium Sw. subgen. *Rhopalobium* Schltr. sect. *Ceraia* Schltr., *Repert. Spec. Nova. Regni Veg.*, Beih. 1: 442, 449 (1914).
Type species: *Dendrobium crumenatum* Sw.

Aporum Blume sect. *Linearifolia* Brieger in Schltr., Die. *Die Orchideen* 674 (1981).
Type species: *Onychium gracile* Blume (= *Dendrobium linearifolium* Teijsm. et Binn.).

Dendrobium Sw. sect. *Rhopolanthe* Schltr. subsect. *Aporopsis* Schltr., *Repert Spec. Nov. Regni Veg.*, Beih. 1: 565 (1912), *nom. nud.*

Aporum Blume sect. *Aporopsis* (Schltr.) Brieger, *Schltr., Die Orchideen* 674 (1981), *nom. inval.*
Type species: *Onychium tetraedre* Blume

Aporopsis (Schltr.) M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 485 (2002), *nom. inval.*
Type species: *Dendrobium macfarlanei* F.Muell.

Dendrobium Sw. sect. *Virgatae* Hook.f., *Fl. Brit. Ind.* 5: 711, 726 (1890), *pro parte min.*

Epiphytic or lithophytic herb; pseudobulbous stems to c. 1m long, the swollen part comprising three or four nodes and internodes at least four nodes from the base of a shoot; aerial growths arising above the swollen pseudobulb, capable of forming a swollen pseudobulb; roots arising from the nodes at the base of each shoot; sheaths overlapping; inflorescence enclosed in a covering sheath, a highly reduced indeterminate, raceme; flowers one to three per inflorescence, spontaneous at any time following a drop in air temperature, and synchronous for all plants in the same area; flowers lasting only a few hours in a single day, of superficial substance; very fragrant perfume; labellum non-articulate, attached directly to base of column-foot where it forms a short spur containing nectar; column-foot longer than column. Stelidia reduced not divided. Pollinia four, obliquely elliptical, loosely held together in two groups of two. Capsule fusiforme. Protocorm-seedling type, narrowly isobilateral.

Distribution: Frequent throughout South-East Asia, and the Malay archipelago including Christmas Island which is an Australian Territory, and as far east as Papua New Guinea.

Notes: The following species are transferred or recognised as belonging to this genus following detailed research of Types and the literature.

Ceraia acaciifolia (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium acaciifolium* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 34–36 (1917).

Ceraia acicularis (Lindl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium aciculare* Lindl., *Edwards' Bot. Reg.* 26: 81, misc. 188 (1840).

Ceraia alabensis (J.J.Wood) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium alabense* J.J.Wood, *Lindleyana*, 5(2): 90 (1990).

Ceraia aurantiflammea (J.J.Wood) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium aurantiflammeum* J.J.Wood, *Orchid Rev.* 106: 337–342, f. (1998).

Ceraia batanensis (Ames et Quisumb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium batanense* Ames et Quisumb., *Philipp. J. Sc.* 47: 200, f. (1932).

Ceraia boothii (Teijsm. et Binn.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium boothii* Teijsm. et Binn., *Natuurk. Tijdschr. Ned.-Indie* 24: 318 (1862).

Ceraia bukidnonensis (Ames et Quisumb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bukidnonense* Ames et Quisumb., *Philipp. J. Sc.* 59: 5 (1936).

Ceraia calceola (Roxb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium calceolum* Roxb., *Hort. Beng.* 63 (1814), *nom. nud.*; *Fl. Ind.* 3: 488 (1832).

Ceraia carinata (L.) M.A.Clem., ***comb. nov.***
Basionym: *Epidendrum carinatum* L., *Sp. Pl.* 1350 (1753); *Dendrobium carinatum* (L.) Willd., *Sp. Pl.* 4: 133–134 (1805).

Ceraia chrysotainia (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium chrysotainium* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 508 (1910).

Ceraia cinnabarina (Rchb.f.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium cinnabarinum* Rchb.f., *Gard. Chron.* 14: 166 (1880).

Ceraia clavator (Ridl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium clavator* Ridl., *J. Linn. Soc.* 32: 255 (1896).

Ceraia compressicaulis (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium compressicaule* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 57–58 (1928).

Ceraia confunda (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium confundens* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 205 (1910).

Ceraia cultrifolia (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cultrifolium* Schltr., *Repert. Spec. Nov. Regni Veg.* 16: 111 (1919).

Ceraia cuneata (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cuneatum* Schltr., *Bull. Herb. Boiss.* (ser. 2) 6: 454–455 (1906).

Ceraia cuneilabra (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium cuneilabrum* J.J.Sm., *Icon. Bogor.* 3: 11–12, t. 205 (1906).

Ceraia cymbulipes (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium cymbulipes* J.J.Sm., *Mitt. Inst. Bot. Hamburg* 7: 51, t. 8, f. 41 (1927).

Ceraia dentata (Seidenf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium dentatum* Seidenf., *Nordic J. Bot.*, 1(2): 206 (1981).

Ceraia eboracensis (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium eboracense* Kraenzl., *Oest. Bot. Zeitschr.* 44: 419 (1894).

Ceraia ephemera (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium ephemerum* J.J.Sm. in Merrill, *Interpr. Rumph. Herb. Amboin.* 174 (1917).

Ceraia equitans (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium equitans* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 228 (1910).

Ceraia exilis (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium exile* Schltr., *Repert. Spec. Nov. Regni Veg.* 2: 85 (1906).

Ceraia facifera (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium faciferum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 15: 10 (1908).

Ceraia fimbriata (Blume) M.A.Clem. ***comb. nov.***
Basionym: *Onychium fimbriatum* Blume, *Bijdr.* 325 (1825); *Dendrobium blumei* Lindl., *Gen. Sp. Orch. Pl.* 88 (1830), *nom.*

Ceraia fugax M.A.Clem., ***nom. nov.***
Basionym: *Dendrobium fugax* Schltr., *Bull. Herb. Boiss.* (ser. 2), 6: 455 (1906), *nom. illeg.*, non Rchb.f. (1871).

Ceraia gedeana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium gedeanum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 8: 29 (1907).

Ceraia gerlandiana (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium gerlandianum* Kraenzl., *Repert. Spec. Nov. Regni Veg.* 6: 317 (1909).

Ceraia goldfinchii (F.Muell.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium goldfinchii* F.Muell., *Wings South Sc. Record* 3: 4 (Jan. 1883).

Ceraia gracilis (Blume) M.A.Clem. ***comb. nov.***
Basionym: *Onychium gracile* Blume, *Bijdr.* 327 (1825).

Ceraia grootingsii (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium grootingsii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 33–34 (1917).

Ceraia gynoglottis (Carr) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium gynoglottis* Carr, *Gard. Bull. Straits Settlements* 8: 105 (1935).

Ceraia humboldtensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium humboldtense* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 11: 131 (1912).

Ceraia hymenocentra (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hymenocentrum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 567 (1912).

Ceraia hymenopetala (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hymenopetalum* Schltr., *Bot. Jahrb. Syst.* 45, Beibl. 104: 33 (1911).

Ceraia hypopoga (Kraenzl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium hypopogon* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 232–234 (1910).

Ceraia inconcinna (Ridl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium inconcinnum* Ridl., *J. Linn. Soc.* 32: 255 (1896).

Ceraia inconspicua (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium inconspicuum* J.J.Sm. in L. S. Gibbs, *Phytogeogr. & Fl. Arfak Mts.* 205 (1917).

Ceraia incurvociliata (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium incurvociliatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 11: 137–138 (1931).

Ceraia juncea (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium junceum* Lindl., *Edwards' Bot. Reg.* 28, Misc. 11 (1842).

Ceraia juncifolia (Schltr.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium juncifolium* Schltr., *Repert. Spec. Nov. Regni Veg.* 10: 76 (1911).

Ceraia koeteiana (Schltr.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium koeteianum* Schltr., *Bull. Herb. Boissier* (ser. 2), 6: 456 (1906).

Ceraia kohlmeyeriana (Teijsm. et Binn. ex Miq.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium kohlmeyerianum* Teijsm. et Binn. ex Miq., *Choix, Pl. Jard. Buitenzorg* t. 24. f.1 (1867).

Ceraia kurashigei (T.Yakawa) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium kurashigei* T.Yakawa, *Lindleyana* 13(1): 28–30, f.2 (1998).

Ceraia lagara (Schltr.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium lagarum* Seidenf., *Opera Bot.* 83: 187 (1985).

Ceraia lamatochila (Seidenf.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium lamatochilum* Seidenf., *Nordic J. Bot.* 1(2):206 (1981).

Ceraia lamellifera (Carr) M.A.Clem. **comb. et stat. nov.**
Basionym: *Dendrobium cinnabarinum* Rchb.f. var. *lamelliferum* Carr, *Gard. Bull. Straits Settlem.* 8: 103 (1935).

Ceraia lamellulifera (J.J.Sm.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium lamelluliferum* J.J.Sm., *Mitt. Inst. Bat. Hamburg* 7: 52, t. 8, f. 42 (1927).

Ceraia lanciloba (J.J.Wood) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium lancilobum* J.J.Wood, *Lindleyana* 5(2): 90 (1990).

Ceraia lawiensis (J.J.Sm.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium lawiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 3: 60 (1912).

Ceraia limii (J.J. Wood) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium limii* J.J. Wood in J.J.Wood et P.J.Cribb, *Checklist Orch. Borneo* 254–255, f. 31 (1994).

Ceraia linearifolia (Teijsm. et Binn.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium linearifolium* Teijsm. et Binn., *Tijdschr. Nederl. Ind.* 24: 318 (1862).

Ceraia litoralis (Schltr.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium litorale* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 567 (1912).

Ceraia macfarlanei (F.Muell.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium macfarlanei* F.Muell., *Papuan Pl.* 1: 29 (1875).

Ceraia macrapora (J.J.Sm.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium macraporum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 8: 38 (1912).

Ceraia maleolens (Kraenzl.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium maleolens* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 54 (1910).

Ceraia minima (Ames et C.Schweinf.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium minimum* Ames et C.Schweinf., *Orchidaceae* 6: 107, t. 91 (1920).

Ceraia modesta (Rchb.f.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium modestum* Rchb.f., *Bonplandia* 3: 222 (1855).

Ceraia multiramosa (Ames) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium multiramosum* Ames, *Orchidaceae* 5: 129 (1915).

Ceraia odorata (Schltr.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium odoratum* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 503–504 (1910).

Ceraia ovatipetala (J.J.Sm.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium ovatipetalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 12: 134–135 (1932).

Ceraia papilionifera (J.J.Sm.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium papilioniferum* J.J.Sm., *Orch. Ambon* 49 (1905).

Ceraia parviflora (Ames et C.Schweinf.) M.A.Clem. **comb. nov.**
Basionym: *Dendrobium crumenatum* Sw. var. *parviflorum* Ames et C.Schweinf., *Orchidaceae* 6: 100–101 (1920).

Ceraia patentiloba (Ames et C.Schweinf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium patentilobum* Ames et C.Schweinf., *Orchidaceae* 6: 110–112 (1920).

Ceraia peculiaris (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium peculiare* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 58–59 (1928).

Ceraia philippinensis (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium philippinense* Ames, *Philipp. J. Sc.* Bot. 8: 424 (1914).

Ceraia planibulbis (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium planibulbe* Lindl., *Edwards' Bot. Reg.* 29: 70, misc. 54. (1843).

Ceraia platybasis (Ridl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium platybasis* Ridl., *Trans. Linn. Soc., Bot.* 9: 165 (1916).

Ceraia plebeja (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium plebejum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 5: 6–7 (1907).

Ceraia polytricha (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium polytrichum* Ames, *Orchidaceae* 2: 183–184 (1908).

Ceraia pseudocalceola (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudocalceolum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 5: 34 (1907).

Ceraia pseudoequitans (H.Fessel et E.Luckel) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudoequitans* H.Fessel et E.Luckel, *Die Orchidee* 51(1): 83–85, t. (2000).

Ceraia pseudotenella (Guillaumin) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudotenellum* Guillaumin, *Bull. Mus. Hist. Nat. Paris* (ser. 2), 36: 697 (1965).

Ceraia puberilinguis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium puberilingue* J.J.Sm., *Mitt. Inst. Allg. Bot. Hamburg* 7: 53, t. 8., f. 43 (1927).

Ceraia ridleyana M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium ridleyanum* Kerr, *Kew Bull.* 218 (1927) nom. illeg, non Schltr. (1905).

Ceraia robinsonii (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium robinsonii* Ames, *Philipp. J. Sc., Bot.* 8: 425 (1914).

Ceraia saaronica (J.König) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 486 (2002).
Basionym: *Epidendrum saaronicum* J.König, *Retz. Obs.* 6: 58 (1791). *Angraecum crumenatum* Rumph., *Herb. Amb.* 6: t. 472 (1750), nom. illeg. (pre 1753). *Dendrobium crumenatum* Sw., *Schrad. J. Bot.* 2: 237 (1799).

Ceraia sanguinea M.A.Clem. ***nom. nov***.
Basionym: *Dendrobium sanguineum* Rolfe, *Gard. Chron.* (ser. 3) 18: 292 (1895), non Sw. (1799).

Ceraia scirpoides (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium scirpoides* Schltr., *Repert. Spec. Nov. Regni Veg.* 9: 103 (1911).

Ceraia setifera M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium tenellum* (Blume) Lindl. var. *setifolium* Guillaumin, *Bull. Mus. Paris* (ser. 2), 28: 484 (1956).

Ceraia setifolia (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium setifolium* Ridl., *J. Linn. Soc.* 31: 270 (1896).

Ceraia simplicissima Lour., Fl. Indoch. 578 (1790). *Dendrobium podagraria* Hook.f., *Fl. Brit. Ind.* 5: 728 (1890); *Icon. Pl.* t. 2026 (1890).

Ceraia stelidiifera (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium stelidiiferum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 66–67 (1920).

Ceraia strigosa (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium strigosum* Schltr., *Bot. Jahrb. Syst.* 45, Beibl. 104, 34 (1911).

Ceraia tenella (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium tenellum* Blume, *Bijdr.* 327 (1825).

Ceraia tenuis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tenue* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 31–33 (1917).

Ceraia tenuicaulis (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tenuicaule* Hook.f., *Fl. Brit. Ind.* 6: 184 (1890).

Ceraia tetraedris (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium tetraedre* Blume, *Bijdr.* 327 (1825).

Ceraia torajaensis (O'Byrne) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium torajaense* O'Byrne, *Malayan Orchid Rev.* 33: 45–46, 95, f., t. (1999).

Ceraia tricuspis (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium tricuspe* Blume, *Bijdr.* 326 (1825).

Ceraia tridentata (Ames et C.Schweinf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tridentatum* Ames et C.Schweinf., *Orchidaceae* 6: 115–117 (1920).

Ceraia truncata (Lindl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium truncatum* Lindl., *J. Linn. Soc.* 3: 15 (1859).

Ceraia usterii (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium usterii* Schltr., *Bull. Herb. Boiss.* (ser. 2), 6: 458–459 (1906).

Ceraia usterioides (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium usterioides* Ames, *Orchidaceae* 5: 142 (1915).

Ceraia ventricosa (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ventricosum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 209 (1910).

Ceraia ventripes (Carr) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ventripes* Carr, *Gard. Bull. Straits Settlem.* 8: 103 (1935).

Aporum Blume, *Bijdr.* 6: f. 39; 7: 334 (1825).
Type species: *Aporum lobatum* Blume (*vide* Brieger 1981), non *Aporum indivisum* Blume (*vide* Seidenfaden 1985).

Macrostomium Blume, *Bijdr.* 335 (1825); *Aporum* Blume sect. *Macrostomium* (Blume) Bieger, *Schltr., Die Orchideen* 3 (ed. 1): 676 (1981).
Type species: *Macrostomium aloifolium* Blume

Schismoceras Presl, *Rel. Haenk.* 1: 96–97, t. 13, f. 2a–e (1827).
Type species: *Schismoceras disticha* Presl.

Ditulima Rafin., *Fl. Tellur.* 4: 41 (1836)[1838].
Type species: *Ditulima anceps* Raf. (= *Dendrobium anceps* Sw.)

Dendrobium Sw. sect. *Aporum* (Blume) Lindl. in Paxt., *Fl. Gard.* 1: 134 (1851).

Aporum Blume sect. *Aporum* Brieger, *Schltr., Die Orchideen*, 3 Aufl. 1: 677 (1981).

Erect, porrect or pendulous, small to large, epiphytic or lithophytic, herbs. Roots thin wiry, divided. Stems thin, wiry, covered with lead sheaths for most of their length but exposed in most species towards the apex, often branching. Leaves equitant, hard, fleshy, broadest near the basal half of each stem, then tapering towards the apex, with a distinct abscission layer, apices acute, persistent for several years, those nearest the apex becoming increasingly smaller and bract like. Inflorescence lateral on exposed apical part of stem, the bract from successive flowering forming a tuft at each node, comprising one or a few flowers. Flowers solitary arising from a lateral meristematic persistent inflorescence, lasting only a few days, synchronous with other plants of the same species in the immediate vicinity; fleshy. Lateral sepals connate at base and spreading towards the apices, together with the labellum and column-foot forming a small spur or saccate base. Dorsal sepal free often much smaller than the lateral sepals. Petals free and often smaller than the dorsal sepal. Labellum fleshy, sessile, rigid with distinct thickened callus of small glands on the laminar surface. Column short with truncate apex, and prominent staminodes. Pollinia small, hard waxy, yellow in two globose hemipollinia. Protocorm-seedling type narrowly isobilateral.

Distribution: throughout South-East Asia and Malesia.

Aporum acinaciforme (Roxb.) Griff., *Cal. J. Nat. Hist.* 5: 370 (1845).

Aporum albayense (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium albayense* Ames, *Philipp. J. Sc., Bot.* 7: 14 (1912).

Aporum aloifolium (Blume) Brieger, *Schltr., Die Orchideen*, 3 Aufl. 1: 676 (1981).

Aporum anceps (Sw.) Lindl., *Gen. Sp. Orch. Pl.* 71 (1830).

Aporum auyongii (T.Yukawa) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium auyongii* T.Yukawa, *Lindleyana* 13(1): 28, f.1 (1998).

Aporum babiense (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum banaense (Gagnep.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum basilanense (Ames) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium basilanense* Ames, *Philipp. J. Sc., Bot.* 7: 14–15 (1912).

Aporum bicornutum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum bilobulatum (Seidenf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium bilobulatum* Seidenf., *Opera Bot.* 83: 218, f. 147 (1985).

Aporum brevimentum (Seidenf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium brevimentum* Seidenf., *Opera Bot.* 83: 225–226, f. 154 (1985).

Aporum calceolariae (J.König) M.A.Clem., ***comb. nov.***
Basionym: *Epidendrum calceolariae* J.König, *Retz. Obs.* 6: 45 (1791). *Dendrobium acerosum* Lindl., *Edwards' Bot. Reg.* 30: misc. 86 (1841).

Aporum capitellatoides (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum capitellatum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum cochinchinense (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum compressistylum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum concavum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum confusum (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium confusum* Schltr., *Repert. Spec. Nov. Regni Veg.* 10: 72 (1911).

Aporum crucilabre (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum curviflorum (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium curviflorum* Rolfe, *Kew Bull.* 281(1805).

Aporum dalatense (Gagnep.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum diaphanum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum distichum (Presl.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum escritorii (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium escritorii* Ames, *Orchidaceae* 5: 123 (1915).

Aporum ferdinandi (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ferdinandi* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 209 (1910).

Aporum flexile (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum fuscum (O'Byrne) M.A.Clem., ***comb. et stat. nov***.
Basionym: *Dendrobium indivisum* (Blume) Miq. var. *fuscum* O'Byrne, *Malayan Orch. Rev.* 31: 21–22, 77, t. f. (1997).

Aporum grande (Hook.f.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum indivisum Blume, *Bijdr.* 6: 334. t. 39 (1825).

Aporum jenkinsii Griff., *Calc. J. Nat. Hist.* 5: 367, t. 25 (1854). *Dendrobium parciflroum* Rchb.f. ex Lindl., *J.Linn. Soc.* 3: 4 (1859).

Aporum jennae (O'Byrne) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium jennae* O'Byrne, *Malayan Orch. Rev.* 30: 24 (1996).

Aporum keithii (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium keithii* Ridl., *J. Linn. Soc.* 32: 247–248 (1896).

Aporum kentrophyllum (Hook.f.) Brieger, *Schltr., Die Orchideen* 3 (ed. 1): 676 (1981).

Aporum kiauense (Ames et C.Schweinf.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium kiauense* Ames et C.Schweinf., *Orchidaceae* 6: 103–105 (1920).

Aporum kjellbergii (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum korthalsii (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum kuyperi (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum leonis Lindl. in Edwards', *Bot. Reg.* 26: misc. 59–60 (1840).

Aporum litoreum (F.M.Bailey) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium litoreum* F.M.Bailey, *Queensl. Agric. J.* 16: 411 (1906).

Aporum lobatum Blume, *Bijdr.* 6: 334 (1825).

Aporum lobbii M.A.Clem., **nom. nov.**
Basionym: *Dendrobium lobbii* Lindl., *J. Linn. Soc.* 3: 3 (1859), non Teijsm. et Binn. (1853).

Aporum lobulatum (Rolfe ex J.J.Sm.) Brieger, *Schltr., Die Orchideen* 3 Aufl. 1: 677 (1981).

Aporum lunatum (Lindl.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium lunatum* Lindl., *J. Linn. Soc.* 3: 4 (1859).

Aporum macgregorii M.A.Clem., **nom. nov.**
Basionym: *Dendrobium macgregorii* Ames, *Philipp. J. Sc., Bot.* 7: 17–18 (1912), non F.Muell. et Kraenzl. (1894); *Dendrobium quisumbingii* A.D.Hawkes et A.H.Heller, *Lloydia* 20: 123 (1957), *nom.*

Aporum mannii (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum marivelense (Ames) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum merrillii (Ames) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium merrillii* Ames, *Orchidaceae* 2: 181–182, f. (1908).

Aporum mindanaense (Ames) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium mindanaense* Ames, *Philipp. J. Sc., Bot.* 8: 423 (1914).

Aporum mirandum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum modestissimum (Kraenzl.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium modestissimum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 206–207 (1910).

Aporum nathanielis (Rchb.f.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium nathanielis* Rchb.f. in Schill., *Cat. Orch.* (ed. 3). 26 (1857).

Aporum nycteridoglossum (Rchb.f.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum pendulicaule (Hayata) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum porphyrophyllum (Guillaumin) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium porphyrophyllum* Guillaumin, *Bull. Mus. Hist. Nat. Paris* (ser. 2), 27: 395 (1955).

Aporum prostratum (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum pseudoaloifolium (J.J.Wood) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium pseudoaloifolium* J.J.Wood, *Kew Bull.*, 39(1): 82–84, f. 7 (1984).

Aporum pseudoequitans (H.Fessel et E.Lückel) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium pseudoequitans* H.Fessel et E.Lückel, *Orchidee* 51(1): 83 (2000).

Aporum quadrilobatum (Carr) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum ramificans (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum reflexibarbatulum (J.J.Sm.) M.A.Clem., **comb. nov.**
Basionym: *Dendrobium reflexibarbatulum* J.J.Sm., *Mitt. Inst. Bot. Hamburg* 7: 54, t. 8., f. 44 (1927).

Aporum reflexitepalum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum rhodostele (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum rhombopetalum (Kraenzl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum rosellum (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum roseonervatum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum roseostriatum (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum sagittatum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum salicornioides (Teijsm. et Binn.) Brieger in Schlechter *Die Orchideen*, 1(11–12): 676 (1981).

Aporum sambasanum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sambasanum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 22: 25 (1909).

Aporum shompenii (B.K.Sinha et P.S.N.Rao) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium shompenii* B.K.Sinha et P.S.N.Rao, *Nordic J. Bot.*, 18(1): 27–30, f. (1998).

Aporum sinuosum (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sinuosum* Ames, *Orchidaceae* 7: 96 (1922).

Aporum smithianum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum spatella (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium spatella* Rchb.f., *Hamb. Gartenz.* 21: 298 (1865).

Aporum sphenochilum (F.Muell. et Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sphenochilum* F.Muell. et Kraenzl., *Oest. Bot. Zeitschr.* 44(7): 254–255 (1894).

Aporum subpandifolium (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum subulatoides (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum subulatum (Blume) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum teloense (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum teres Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum terminale (Par. et Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium terminale* Par. et Rchb.f., *Trans. Linn. Soc.* 30: 149 (1874).

Aporum tetralobum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum thysanophorum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum uncatum (Lindl.) Brieger in Schltr., *Die Orchideen* 3 (ed. 1): 676 (1981).

Aporum vanhulstijnii (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 443 (1983).

Aporum wenzelii (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium wenzelii* Ames, *Orchidaceae* 5: 144 (1915).

Aporum xanthoacron (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium xanthoacron* Schltr., *Bull. Herb. Boiss.* (ser. 2), 6: 459–460 (1906).

Aporum xiphophyllum (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium xiphophyllum* Schltr., *Repert. Spec. Nov. Regni Veg.* 9: 291–292 (1911).

Sixth major group

Species in this clade are in need of much additional study. Present evidence suggests that the group as a whole could be treated as a single genus with a number of infrageneric taxa, the first available name being *Coelandria*. However, further study is required on the remaining species in this major group before a decision can be made on their phylogenetic relationships and status. In the interim, it is here proposed that only those species that clearly fall into a small group directly containing *Coelandria smillieae*, be transferred to that genus.

Coelandria Fitzg., *Austral. Orch.* 1(7): [t. 2] (1882).

Type species: *Coelandria smillieae* (F. Muell.) Fitzg.

Erect, spreading to pendulous epiphytic, occasionally lithophytic herb. Stems robust, clustered, cylindric to cylindric-fusiform, not branching. Leaves membranous to leathery, seasonally deciduous, slightly recurved, linear-ovate to elliptic; sheaths slightly shorter to longer than internodes, papery, persistent. Inflorescences densely multi-flowered, bottle-brush like, lateral, usually on leafless stems; peduncle short, thick, cylindrical. Flowers, rigid, shiny, glabrous, white, pink, purple, orange, green, the labellum often contrasting in colour. Dorsal sepal small, ovate to obovate-oblong. Lateral sepals obliquely narrowly obovate to somewhat spatulate, fused at apex, truncate. Petals small, similar to dorsal sepal. Labellum cymbidiform, thick, fleshy, parallel to column-foot, embracing column, constricted nearest the base, fused to column-foot along basal margin, transverse callus. Column short, thick fleshy and very short stelidia, the stigma sunken, a prominent tooth-like, hard, rostellum, with large viscidia. Column-foot with central longitudinal groove, and nectary at base. Pollinia four, fused together, obovate, concave, light brown to blackish-blue, smooth waxy.

Distribution: Malesia and Australia.

Coelandria andreemillariae (T.M.Reeve) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium andreemillarae* T.M.Reeve, *Orchadian* 7: 130, f. 1 (1982).

Coelandria chrysoglossa (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium chrysoglossum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 509–510 (1912).

Coelandria coccinea (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium coccineum* Kraenzl. in Engl., *Plfanz. Orch.-Mon.-Dendr.* 1:129–130 (1910).

Coelandria concavissima (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium concavissimum* J. J. Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2) 2: 11 (1911).

Coelandria fornicata (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fornicatum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 509 (1912).

Coelandria fracta (T.M.Reeve) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fractum* T. M. Reeve, *Orchadian* 7: 133–134, f. 3 (1982).

Coelandria glomerata (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium glomeratum* Rolfe, *Kew Bull.* 1894: 155 (1894); *Gard. Chron.* 1: 653, f. 80 (1894).

Coelandria obtusa (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium obtusum* Schltr. in K. Schum. et Lauterb., *Nachtr. Fl. Schutzgeb. Südsee* 177 (1905), non Rchb. f. (1861).

Coelandria smillieae (F. Muell.) Fitzg., *Austral. Orch.* 1(7): t. 2 (1882).
Basionym: *Dendrobium smillieae* F. Muell., *Fragm.* 6: 94 (1867); *Callista smillieae* (F. Muell.) Kuntze, *Revis. Gen. Pl.* 2: 655 (1891); *Pedilonum smillieae* (F. Muell.) Rauschert, *Feddes Repert.* 94: 464 (1983).

Colonisation of orchids on the Krakatau Islands

Tukirin Partomihardjo

Abstract

Partomihardjo, T. (Bidang Botani, Puslit Biologi-LIPI, Jalan Juanda 22, Bogor-Indonesia) 2003. Colonisation of orchids on the Krakatau Islands. Telopea *10(1): 299–310.* Orchids are the most diverse and attractive of the flowering plant families. Most of them grow as epiphytes. In forest communities of the Krakataus, Indonesia, epiphytic orchids are more abundant than terrestrial ones. However, during early succession of the Krakataus, terrestrial orchids were more common than epiphytes. The role of orchids in succession has received little attention. Changes in orchid communities on the Krakatau Islands during the last 115 years provide an insight into colonisation patterns in a vegetation regenerating towards tropical rain forest. In surveys of the Krakataus between 1981 and 1998, at least 63 species of orchids colonising the islands have been noted. All orchids on Krakatau Islands are wind-dispersed. Rakata, the highest and least disturbed island in the group, carries the greatest diversity of orchids. The orchid flora of Krakatau is a disharmonic subset of the mainland (Southeast Asia) pool and certain genera e.g. *Agrostophyllum, Dendrobium, Eria,* and *Grammatophyllum* are relatively under-represented. Comparison between Javanese and Sumatran species, and the proportion of species common between the islands of Sebesi-Sebuku and the Krakatau Islands, indicates that the orchid flora of the Krakataus has been chiefly derived from Java rather than from Sumatra, even though two 'stepping stone' islands exist between the Krakataus and Sumatra.

Introduction

After the eruption of the volcanic island Krakatau in the Sunda Strait in 1883, it is believed that no living thing existed on the three remaining islands. The flora of the Krakatau Islands has been investigated ever since the first higher plant was observed growing on the islands within 3 years after the eruption. The documenting of plant colonisation on the islands, from the earliest successional stage, has provided a unique record of island recolonisation. The vegetation studies on the Krakataus thus have a special place in the theory of primary succession of bare ground (Docters van Leeuwen 1936, Borssum Waalkes 1960, Whittaker & Bush 1993). A survey made in 1896, 13 years after the explosion, revealed that among the pioneer plant species, three orchids were found on Krakatau. One year later (1897), four terrestrial species of orchids were collected (Docters van Leeuwen 1936). By 1935 the number of species of orchids reached 25 and by 1989 the number of species recorded on the islands had increased to 59 (App. 1, 2, 3). The species record of orchids thus increased continuously in conjunction with vegetation succession on the islands.

Orchids are among the most numerous and attractive flowering plants in the tropical region. They can be found in a variety of habitats from open grasslands, dense forests, hot and cold deserts, on damp or dry areas, on trees or rocks that hang over the ocean and are subjected to salt spray, underground, on floating vegetation and other habitats that can support flowering plants (Arditti 1992). They grow in mountains, flatlands and valleys. They can grow in the soil (terrestrial) and on other plants as epiphytes. A number of terrestrial orchids can colonise bare soil as pioneers, as noted for the Krakatau Islands by Docters van Leeuwen (1936).

Despite their importance in the colonising flora, the occurrence of orchids in the Krakatau Islands appears to have received relatively little attention. The Krakatau Islands provide a unique opportunity to assess the role of orchids in a colonisation record spanning a period of over 100 years. This paper reports on records of orchid colonisation on the islands, since the earliest succession stage. It is of interest to compare the species establishment of the early succession stages and the recent developed forest situation.

Study Area

The Krakatau Islands are situated in about the middle of Sunda Strait, about 40 km from each of the biologically rich mainlands of Java and Sumatra (Fig.1). Three of the four islands, Rakata, Sertung and Panjang are believed to have been totally sterilized by the devastating eruption of Krakatau in 1883. The fourth island, Anak Krakatau, emerged from the submarine caldera of Krakatau in about 1930. This youngest island suffered self-devastating eruptions in 1952/3, 1967/8, 1992–4, with the most recent occurring in 1995–6. Rakata, with an elevation of about 780 m, is the southern half of what was Krakatau's highest volcano. Rakata, Sertung and Panjang are now covered by species-poor mixed forest. Anak Krakatau's vegetated area is only some 17 % concentrated along the eastern coastal areas. The remainder of the island is composed of barren ash and lava flows.

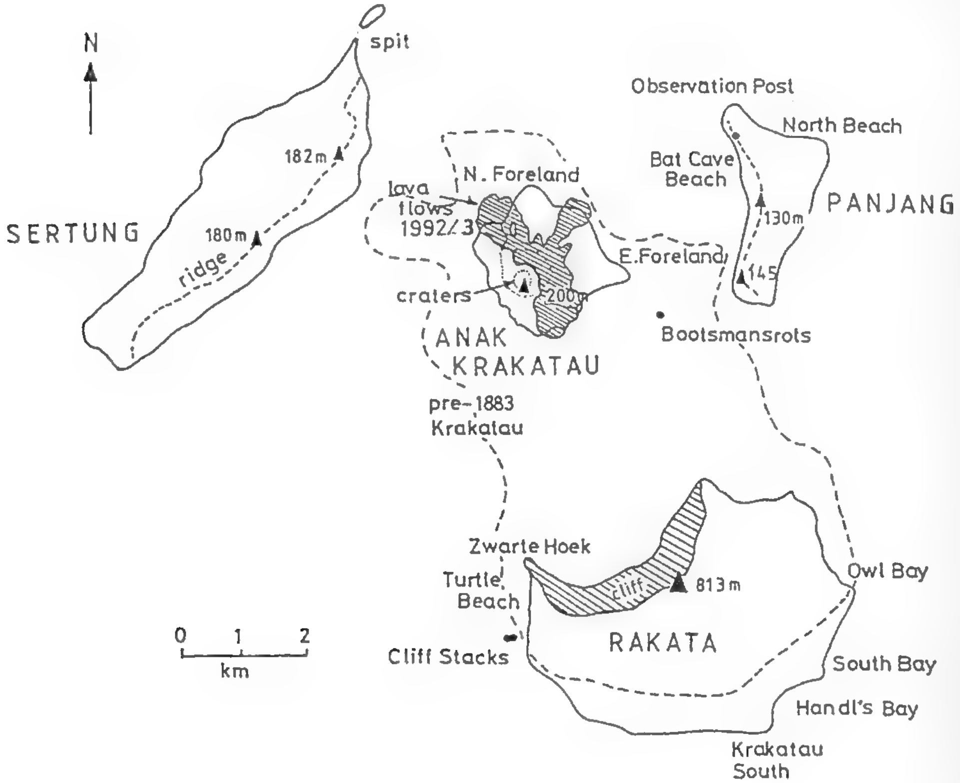

Fig. 1. The Krakatau Islands in 1994 showing the tip of Sertung spit which split off and then disappeared in 1995. Broken lines indicate the island shape before the 1883 eruption.

Methods

The analyses are based upon the complete flora lists for Rakata, Sertung, and Panjang (Docters van Leeuwen 1936, Borssum Waalkes 1960, Whittaker et al. 1989, Partomihardjo 1995). Unpublished flora data from the complete lists of various expeditions are also included (University groups from Kagoshima, Oxford, La Trobe). The flora of Anak Krakatau was taken from investigations by the author since 1981 (Partomihardjo et al. 1992, Partomihardjo 1995). The floristic surveys of Krakatau have been somewhat irregular and not all surveys are comparable in collecting effort, therefore some surveys have been grouped together for comparative purposes (as Whittaker et al. 1989, Partomihardjo 1995). The period 1992 to 1998 is treated as a single block for the older islands because over this period a fairly comprehensive survey has been carried out. The number of species of flowering plants recorded from various expeditions between 1989 and 1998 currently stands at 306, consisting of 65 orchids and 131 other species of Spermatophytes, although it should be stressed that these are conservative estimates.

Four plots of 30 × 30 m were established, one each at 10, 100, 300 and 500 m a.s.l. and one plot of 20 × 20 m at 700 m a.s.l. on Rakata Island, to observe the occurrence of epiphytic orchids at different altitudes. The plots were established in 1992 and almost every two years were monitored.

Results and Discussion

The history of orchid colonisation

The first orchids: Among the first higher plants to arrive on the Krakataus were three orchids. *Cymbidium finlaysonianum*, a common epiphytic orchid in the Indo-Malayan region, was found by Boerlage on Panjang in 1896, where it grew on a steep ravine wall. *Spathoglottis plicata* and *Arundina graminifolia*, both terrestrial pioneer orchids, were also recorded in 1896. One year later Penzig found two of them, growing on Rakata (Docters van Leeuwen 1936). Besides the three species mentioned above, he also recorded *Phayus* sp. on Rakata and Panjang. Four terrestrial orchids in total were found on all three islands, and they have been recorded in all subsequent surveys (Docters van Leeuwen 1936). During the first 20 years, the epiphytic orchids were restricted to *C. finlaysonianum*, whilst five species of terrestrial orchids were recorded. In 1908, Backer reported *Nervilea aragoana* growing in the south east of Rakata above 200 m, and collected *Eulophia graminea* on the beach at Zwarte Hoek (Rakata) and on Sertung. The *Arundina* and *Spathoglottis* were common in 1908, the latter species in particular covered steeply sloping areas. These heliophilous plants are restricted to areas sparsely covered with vegetation and to the recent landslides. Although the shade of the developing tree layer affected the heliophilous orchids, this denser shading and the larger quantities of humus made it possible for a number of other terrestrial orchids to settle. Seven species of orchids had colonised the Krakataus by 1908, two of them were terrestrial, *A. graminifolia* and *S. plicata*, and the others were epiphytes. These epiphytic orchids have been a continuous component of the epiphytic flora of Krakatau since their arrival. *Dendrobium crumenatum* and *D. mutabile*, are epiphytic orchids, which successfully colonised the canopy of the beach forest. Another important orchid first found in 1905–08 was an *Eria* species, which Docters van Leeuwen (1936) reported from both the beach and the 'grass-jungle' before 1919. It was also observed growing as an epiphytic orchid, and by the end of the 1920s it had become a common component of the epiphytic flora on the islands. There were a number of new epiphytic species growing in the higher part of Rakata, especially in the *Cyrtandra* shrubland. In 1934, Boedijn found a holo-saprophytic orchid, *Galeola kuhlii* growing on a decayed tree trunk on Rakata (Docters van Leeuwen 1936).

Early diversification: In the early 20th century, as the Krakatau flora continued to diversify on all three islands, the Orchidaceae was the most speciose family with 17 species being recorded as of 1920. A young forest developed on each of the islands offering support for the epiphytic orchids. Docters van Leeuwen (1936) reported that the early-arrival air-dispersed species tended to spread to all three islands by the early 1930s, a pattern evident in the orchid data set presented in Table 1. The number of orchids species continuously increased, and by 1933 it reached 31. The colonisation of the orchid flora on the Krakataus was relatively rapid within the early stage of the succession process because the distance from the mainland of Java is only 40 km. Most orchids recorded in the early diversification were terrestrial. Because of the limited availability of the usual tree habitat, the epiphytic orchids recorded during the early stages grew on rock or ash faces, particularly in steep gullies.

Table 1. Appearance of orchids on Krakataus following the explosion of 1883

Event	1883	1886	1896	1908	1932	1951	1979	1989	1998
Explosion	x	-	-	-	-	-	-	-	-
Number of species recorded	-	0	3	5	21	10	15	17	40
Elapsed time, years since									
Previous count	-	-	10	12	24	18	28	10	9
Explosion	-	3	13	25	49	68	96	106	115
Increase in species number									
Previous count	-	-	3	1	30	13	11	32	43
Explosion	-	-	3	5	31	36	44	55	65
Increase per year since									
Previous count	-	-	0.3	0.08	1.2	0.7	0.4	3.2	4.8
Explosion	-	-	0.23	0.2	0.5	0.5	0.5	0.5	0.56

Actual and cumulative number of orchid species on the Krakatau Islands from various expedition records are summarised in Table 2. The epiphytic orchid species of the Krakataus had increased to about 40 species (61% of the total orchids flora) by 1994, although some of the early epiphytic orchids species may have become extinct from the islands (Appendix 1). Over the period of 1979 to 1989 the increase of species was relatively slow, compared to the total enrichment of vascular plants on the islands, in particular for the terrestrial orchids. This might be due to the seasonal vegetative appearance of the terrestrial orchids, which makes it difficult to detect them in certain periods of the year. However, in the 1991–1993 field survey, four species of epiphytic orchids *Eria verruculosa, Flickingeria angustifolia, Glomera erythrosma* and *Pholidota articulata* were newly recorded. Based on herbarium collections, the two species *Eria verruculosa* and *Glomera erythrosma* are known so far only from Java.

Partomihardjo et al. (1992) mentioned that vegetation communities on Anak Krakatau are still in a very early stage of succession, where diversity of potential host trees is very low. The first orchid recorded from Anak Krakatau since it emerged from the sea in 1930 was *Dendrobium crumenatum*. This epiphytic orchid was found growing on the cliff of an eroded gully. Six additional species of orchids were recorded on the island from 1981 to 1991 (Appendix 2). The epiphytic orchids *Acriopsis javanica* and *Cymbidium finlaysonianum* were found growing at the base of clumps of wild sugarcane (*Saccharum spontaneum*: Poaceae), and in recent observations they were recorded with *C. pubescens*, on *S. spontaneum*. This condition reflects the limited availability of their usual tree habitat. In the early stages of succession on the Krakatau Islands, epiphytic orchids did not grow on trees because there were none. Whittaker et al. (1992) demonstrated that the forest communities on the Krakataus are still accumulating new families and genera of plants. The forests are still relatively immature, with a large potential pool of immigrants. Vascular plants still continue to colonise the islands.

Table 2. Orchids on Krakatau Islands: cross-tabulation of terrestrial and epiphytic orchids, with island combinations indicated by the letter codes: R=Rakata, S=Sertung, P=Panjang.

	RSP	RS	RP	SP	R	S	P	Total
1886–1934								
Terrestrial	5	4	2	0	7	0	0	18
Epiphyte	1	2	0	0	12	1	0	16
Total	**6**	**6**	**2**	**0**	**19**	**1**	**0**	**34**
1935–1979								
Terrestrial	0	0	0	0	8	0	0	8
Epiphyte	0	0	0	0	10	0	0	10
Total	**0**	**0**	**0**	**0**	**18**	**0**	**0**	**18**
1980–1998								
Terrestrial	5	3	1	1	5	1	0	16
Epiphyte	3	1	0	0	26	0	0	30
Total	**8**	**4**	**1**	**1**	**31**	**1**	**0**	**46**
1886–1998								
Terrestrial	7	4	2	1	11	1	0	26
Epiphytes	3	3	0	0	32	0	0	38
Total	**10**	**7**	**2**	**1**	**43**	**1**	**0**	**64**

Over the period 1951 to 1983, gradual vegetation change took place on Rakata, from a poor mixed secondary forest to a taller forest with a more diverse canopy. On Panjang and Sertung, which were disturbed by the eruption of Anak Krakatau, the forests remained less diverse, with lower, sparser canopy than in forests of Rakatau. The vegetational development was accompanied by an increase in the number of plant species. This increase in vegetation diversity was accompanied by a build-up in the diversity of orchid species, which mostly are epiphytes. Actual and cumulative number of orchid species on the Krakatau Islands from various expeditions are summarized in Figure 2.

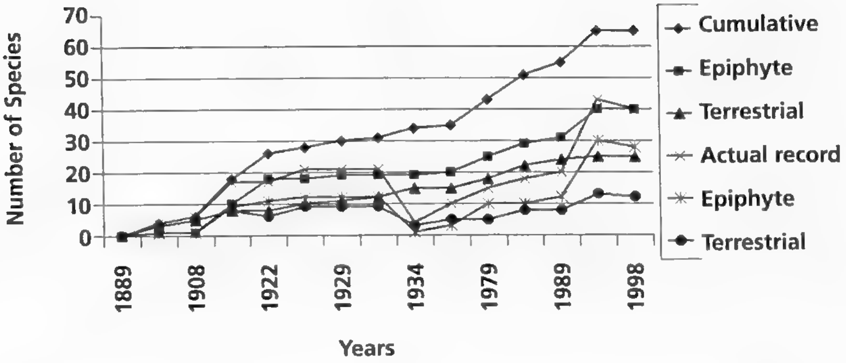

Fig. 2. Colonisation of orchids on the Krakatau Islands. Data recorded from various expeditions.

Ash-fall and species depletion of orchids: Since 1934, orchids colonisation on Rakata has continued at a faster rate than on Sertung and Panjang (Table 2), increasing the disparity in species diversity between the islands. Of the 45 species of orchids currently recorded on the three older islands, all occur on Rakata, three on Panjang and two on Sertung (Table 2). These data are consistent with the whole flora pattern and are interpreted as a consequence, in part, of repeated disturbance by post-1930 ash falls from Anak Krakatau, depressing colonisation (Whittaker et al. 1989, 1992, Bush et al. 1992, 1995). The thick ash accumulation on Panjang and Sertung, followed by a severe dry season, will possibly have killed all ground cover vegetation including the orchids. Consequently, species with local distributions on Sertung and Panjang, particularly terrestrial orchids, may have been eliminated by these disturbances, whereas Rakata has been unaffected.

The record of orchids in the forest of Krakatau after 115 years: The commonest orchid within the interior forest is *Dendrobium crumenatum*. This species is also known as the most cosmopolitan and abundant epiphytic plant throughout the islands. First recorded on Rakata and Sertung in 1920, this orchid was not recorded on Panjang until 1951. *Grammatophyllum speciosum*, a giant epiphytic orchid that might occur growing on the ground in early colonisation, is unlikely to be missed by any visitor: was recorded as epiphytic on the beach vegetation in 1994 and 1998; was not found on Sertung until 1991; and is not documented from Panjang. Recently, the commonest orchid in Panjang is *Dendrobium crumenatum*. This species was also recorded from Anak Krakatau in 1981, growing on the wall of gullies. Judging by its population size on Panjang and Sertung, it seems to have colonised recently. These inter-island differences of orchids are most parsimoniously explained by the disturbance regimes of Anak Krakatau activities. Most of the terrestrial orchids both on Sertung and Panjang were covered by the accumulation of ash fall during each eruption of Anak Krakatau. In contrast, the arboreal orchids are mostly found in the cloud forest of Rakata, i.e. the summit area down to about 500 m, and the same is true for other epiphytic plants. Despite an overall increase in the abundance of epiphytes as the forest becomes moister above 500 m elevation, the number of terrestrial orchids is also noticeably larger.

A means of estimating forest maturity is based on epiphytes, mostly consisting of orchids. It has been suggested that in well-established forests epiphytic species (mostly orchids) are abundant, and that as the forest matures epiphytic species become proportionally more abundant, particularly on trees of > 30 cm dbh (Benzing 1981). In mature dipterocarp forests at Wanariset, East Kalimantan, 50% of the epiphytes were orchids (Partomihardjo 1995). It has been mentioned that the epiphytic orchids have a wide distribution within the trees. For example, epiphytic orchids can be found to grow on the terminal branches of the canopy layer to the very base of large trees. Interestingly, the rate of increasing of epiphytic and terrestrial orchids is somewhat anomalous.

Dispersal mechanisms and limits to colonisation: The cumulative survey data of orchids from 1883 to 1998 shows 24 to 41 species of terrestrial and epiphytic respectively. On Krakatau, orchids are assumed to have colonised through wind dispersal (anemochorous). Dressler (1981) suggested that most orchid seeds are well-suited for wind dispersal. Measurements of the air space inside seeds in the laboratory and the time needed for them to fall 1.5 m in a glass tube, indicate that long-distance travel by air is clearly possible for orchid seeds (Arditti 1992). Air transport of orchid seeds on the feathers or legs of birds has been suggested by Went (1990) and Ridley (1930), although Arditti (1992) argued that the chance is very small. This evidence is supported by the fact that large numbers of common species of orchids have no correlation with the bird migration roots. Wind dispersal seems the only mode of orchid dispersal, because all species recorded on the Krakataus have capsules that open and release the seeds free to float on the air. Dispersal by sea as suggested by Ridley (1930) seems very unlikely.

Most orchids are very sensitive to altitude, which really means temperature and moisture regimes (Comber 1990). Because the mountain on Krakatau is relatively low, there is only a narrow range of temperatures available to suit the needs of many orchids. Moisture condensation in the form of rain or mist on the highest point of Rakata is much greater than at the lower altitudes, because this island is surrounded by sea, and it is continuously swept by moist winds which cool as they rise and release their rain water on the summit area. So it has been found that most of the orchids recorded in Krakatau grow exclusively on the trunks and branches of trees at high altitude, where they only have a few ferns as competitors.

Sebesi is the closest island to the Krakatau group and is of similar altitude to Rakata. Sebesi was less badly damaged by the eruptions of 1883. As of 1921 its inland forests were in a more advanced state of recovery than on Krakatau, and possessed a larger number of orchids (Docters van Leeuwen 1936). At least nine other species occurring there have not yet been recorded for Krakatau. This simple comparison suggests that further additions to the Krakatau orchid assemblage can be expected.

Altitudinal distribution and species richness of epiphytic orchids: At higher altitudes on Rakata a greater diversity of epiphytic orchids is present than in lower areas. To investigate the altitudinal variation of the orchid species, plots were set up at 10, 100, 300, 500 and 700 m a.s.l. (Table 3). The total number of species counted within each plot were 2, 2, 7, 9 and 14 species respectively. The population was highest in the 500 m plot, with the number of individuals declining to 50.75 per 100 m^2 at the summit. In the 300 m plot there were only 8.5 individuals per 100 m^2. An altitudinal preference was evident in some species of orchids. The epiphytic species *Appendicula reflexa* and *Pholidota articulata* were recorded in the highest plot only. The common species *Dendrobium crumenatum* tends to be more abundant in the lower areas, while *D. mutabile* grows at higher altitude.

Table 3. Epiphytic orchids recorded at different altitudes in forest plots on Rakata

Species	10 m a.s.l.	100 m a.s.l.	300 m a.s.l.	500 m a.s.l.	700 m a.s.l.
Agrostophyllum bicuspidatum	0	0	0	4	0
Agrostophyllum denbergerii	0	0	0	2	5
Appendicula reflexa	0	0	0	0	66
Bulbophyllum purpurascens	0	0	7	99	1
Bulbophyllum unguiculatum	0	0	0	16	2
Bulbophyllum sp.	0	0	3	0	8
Coelogyne rochussenii	0	0	0	7	0
Dendrobium accuminatissimum	0	0	0	14	1
Dendrobium sp.	0	0	0	0	1
Dendrobium crumenatum	88	95	24	22	0
Dendrobium mutabile	75	12	19	295	96
Dendrobium secundum	0	0	3	0	1
Eria retusa	0	0	0	0	1
Flickingeria angustifolia	0	0	0	2	14
Malaxis latifolia	0	0	2	0	1
Phaius tankervilleae	0	0	0	0	1
Pholidota articulata	0	0	0	0	5
Thixspermum merguense	0	0	2	0	0
Total of species per plots	**2**	**2**	**7**	**9**	**14**
Total of individuals per plot	**161**	**107**	**60**	**461**	**203**

The greater number of orchid species in upland Rakata, compared to the lowlands, might be explained in terms of the wetter conditions on the upper slopes. The forest above 500 m, as indicated by the moss communities, can be regarded as cloud forest (Whittaker et al. 1989). The large increase in population size and species richness in the 500 m plot compared to the 300 m plot is correlated with an increase in daily cloud cover and humidity at this altitude. Therefore, the species richness of orchids in the mossy forest of Rakata is not very different from the summit area, although the population density in the latter is much lower. Whitmore (1992) noted that moisture from cloud and mist are important for colonisation of epiphytes (orchids). The increase in species richness with altitude in the series of closed-forest plots on Rakata can be attributed to increasing average daily period of cloud cover and humidity, with increasing altitude. It is doubtful that the humidity associated with cloud cover alone accounts for the high diversity of the epiphytic orchids on Rakata, for it is evident that many integrated factors affect the epiphytic population. Although there is no detailed study, it seems likely that the abundance of mosses covering the bark, with their considerable water-holding capacity, promote the germination of epiphytic orchid seeds. In the mainland areas (Java and Sumatra) such altitudes are usually free from fog and the cloud belt is situated at an altitude of about 2000 m. This phenomenon of lowered and compressed zonations on islands may be caused by increasing air humidity due to the surrounding sea-water (van Steenis 1972): changes in temperature, relative humidity and rain-fall all being related to small altitudinal differences.

Orchids on Sebesi-Sebuku and the Krakatau Islands: In 1996, 17 species of orchids were collected from Sebesi, bringing the cumulative total for the island to 21 species from 7 genera. Prior to the 1996 survey, 15 species of orchids were recorded from Sebesi in 1886 (Docters van Leeuwen 1936). Of these, 11 species were also found in 1996. This island was less badly damaged by the eruptions of 1883, than were the Krakatau Islands themselves. As of 1921, its inland forests were in a more advanced state of recovery than Krakatau, and possessed a larger number of orchids (Docters van Leeuwen 1936). At least eight other species occurring there were not recorded for Krakatau at that time. This simple comparison indicates that further additions to the Krakatau orchids can be expected.

On the Krakatau Islands, 64 species of orchids consisting of 7 species of terrestrial and 58 species of epiphytic orchids were recorded during the period from 1886 to 1996.

Common species on Sebesi-Sebuku and Krakatau Islands: Four species out of the 17 species that were recorded in 1996 on Sebesi-Sebuku have never been recorded from the Krakatau Islands (Table 4), and all species of orchid found on Krakatau were also recorded from Java. This suggests that there have been more frequent dispersals of orchid species from Java to the Krakatau and then on to Sebesi-Sebuku, than in the opposite direction. According to Comber (1990), the flowering season of orchids on Java mostly occurs between May and June. The capsule fruits ripen during the end of dry season from August to September. During this season easterly winds are prominent. Consequently the species of orchids colonising the Krakataus appear likely to be biased towards Javan elements rather than those of Sebesi-Sebuku.

Table 4. Comparison between species belonging to Javanese and Sumatran components in the proportion of species common on Sebesi and Krakatau Islands

Distributional category	Recorded on Sebesi/Sebuku	Recorded on Krakatau Islands
Javanese	13 (80%)	9 (75%)
Sumatran	4 (20%)	0 (0.0 %)
Total	**17(100%)**	**9 (75%)**

Conclusion

This study finds that orchids colonising in the immediate aftermath of the eruption episode were drawn from the terrestrial group. The appearance of epiphytic orchids in the early succession processes was associated with grass clumps featuring as temporary host plants. The availability of host trees undoubtedly promoted the colonisation rate of epiphytic orchids, while deadwood provided substrates for saprophytic species establishment. As generally the case for forest taxa, which are still accumulating, new records of orchids are still being made. However, the colonisation rate is likely to slow since the natural forests of surrounding areas on mainland Java and Sumatra are being depleted.

The wide-spread distribution of most orchids throughout the islands, indicates that dispersal mode is not the limiting factor for orchid colonisation. The distribution of species richness seems to be affected by moisture availability and habitat quality. The lower and less diverse population of orchids on Panjang and Sertung is probably due to the volcanic activities of Anak Krakatau and the topography of the islands, which lacking high upland regions are less suitable for orchid establishment.

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Appendix 1. The species list of Orchidaceae recorded on the Krakatau Islands (1883–1998) from various expeditions. Survey data are combined: R=Rakata, S=Sertung, P=Panjang. (Anak Krakatau data are listed separately in Appendix 2).

Species	1889	1897	1908	1920	1922	1924	1929	1932	1934	1951	1979	1982	1989	1994	1998
Acanthephippium parviflorum Hassk.	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-
Acriopsis javanica Reinw. ex Bl.	-	-	-	-	R	R	-	-	-	-	R	R	-	RSP	RSP
Agrostophyllum bicuspidatum J.J.Sm.	-	-	-	-	R	R	R	R	-	-	-	-	-	R	R
Agrostophyllum denbergeri J.J.Sm.	-	-	-	-	R	r	-	-	-	R	R	R	R	R	R
Appendicula reflexa Bl.	-	-	-	-	-	-	-	-	-	R	R	R	R	R	R
Arundina graminifolia (D.Don)Hochr.	-	RP	RP	RS	R	R	RSP	RS	-	-	-	S	-	R	R
Bulbophyllum purpurascens T.& B.	-	-	-	-	-	-	R	R	-	-	-	-	-	R	R
Bulbophyllum unguiculatum Rchb.f.	-	-	-	-	-	-	-	-	-	?	-	-	-	R	-
Bulbophyllum sp.	-	-	-	-	-	-	-	-	-	-	*	-	-	R	-
Calanthe angustifolia (Bl.)Lindl.	-	-	-	-	-	-	-	-	-	-	-	P	-	P	P
Calanthe sp.	-	-	-	-	-	-	-	-	-	-	*	-	S	-	-
Coelogyne longifolia (Bl.)Lindl.	-	-	-	-	-	-	-	-	-	-	-	R	-	R	R
Coelogyne rochusseni De Vr.	-	-	-	-	-	-	-	-	-	-	R	-	R	R	R
Cymbidium aloifolium (L.)Sw.	-	-	-	-	-	-	-	-	-	-	R	-	-	R	R
Cymbidium bicolor Lindl.	-	-	-	S	-	-	R	-	-	-	-	-	-	R	R
Cymbidium finlaysonianum Lindl.	-	P	R	RS	R	R	R	-	-	-	-	-	R	RSP	RSP
Dendrobium acuminatissimum Lindl.	-	-	-	-	-	-	-	-	-	-	-	R	-	R	R
Dendrobium crumenatum Swartz	-	-	-	-	R	r	R	R	-	?	-	RS	RS	RSP	RSP
Dendrobium mutabile Lindl.	-	-	-	-	R	R	R	R	-	R	-	R	R	R	R
Dendrobium secundum Lindl.	-	-	-	-	R	R	R	R	-	-	-	R	-	R	R
Dendrobium sp.	-	-	-	-	-	-	-	-	-	-	*	-	-	R	R
Eria annulata Bl.	-	-	-	-	-	-	-	-	-	-	-	R	-	R	R
Eria oblitterata Rchb.f.	-	-	-	-	-	-	-	-	-	-	-	-	R	R	R
Eria retusa Rchb.f.	-	-	-	-	-	-	-	-	-	-	-	R	-	R	RS
Eria verruculosa J.J.Sm.*	-	-	-	-	-	-	-	-	-	-	-	-	-	R	R
Eulophia graminea Lindl.	-	-	RS	-	-	-	-	-	-	-	-	S	-	S	RSP
Eulophia macrostachya Lindl.	-	-	-	RS	R	R	RSP	RSP	-	-	-	-	-	RSP	RSP
Eulophia nuda Lindl.	-	-	-	-	-	R	RP	P	R	-	-	R	-	-	-
Eulophia zollingeri J.J.Sm.	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-
Flickingeria angustifolia (Bl.)A.D. Hawkes	-	-	-	-	-	-	-	-	-	-	-	-	-	R	R
Galeola nudifolia Lour.	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-
Geodorum densiflorum (Lamark)Schltr.	-	-	-	-	-	-	RP	-	-	R	-	S	P	RSP	RP
Glomera erythrosma Bl.	-	-	-	-	-	-	-	-	-	-	-	-	-	R	R
Goodyera colorata (Bl.)Bl.	-	-	-	-	-	-	-	-	-	-	-	-	R	R	R
Goodyera rubens-grandis (Bl.) Bl.	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
Goodyera sp.	-	-	-	-	-	-	-	-	-	-	r	-	-	-	-
Grammatophyllum speciosum Bl.	-	-	-	S	-	-	-	-	-	-	-	-	-	R	R
Habenaria sp.	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Liparis viridiflora Lindl.	-	-	-	R	R	R	R	R	-	-	-	-	-	R	R
Liparis wrayii Hook.f.	-	-	-	RS	R	R	Rs	Rs	-	-	-	-	-	R	-
Liparis sp.	-	-	-	-	-	-	-	-	-	-	-	-	r	-	-
Macodes petola Lindl.	-	-	-	-	-	-	-	-	-	-	-	-	R	R	R
Malaxis latifolia Sm.	-	-	-	S	R	R	R	R	-	-	-	-	-	-	-
Nervilia aragoana Gaudich.	-	-	R	RS	R	R	RSP	RSP	-	R	-	RS	RS	RS	RSP
Nervilia punctata Makino	-	-	-	-	-	-	-	-	R	R	-	-	-	-	-
Oberonia monstruosa Lindl.	-	-	-	-	R	R	R	R	-	-	-	-	R	R	R
Oberonia sp.	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Peristylus goodyeroides Lindl.	-	-	-	-	-	R	-	-	-	R	-	-	RS	R	R
Peristylus gracilis Bl.	-	-	-	RS	-	R	R	R	-	-	R	-	-	-	-
Peristylus grandis Bl.	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Phaius tankervilliae (Banks ex I.Herit)Bl.	-	RS	R	S	-	R	R	R	-	-	-	-	R	RS	R
Phaius sp.	-	-	-	-	-	-	-	-	-	-	-	-	**		-
Pholidota articulata Lindl.	-	-	-	-	-	-	-	-	-	-	-	-	-	R	R
Pholidota imbricata Hook.	-	-	-	-	-	-	-	-	-	-	R	-	R	R	R
Podochilus gracilis Lindl.	-	-	-	-	-	-	-	-	-	-	R	-	-	R	-
Spathoglottis plicata Bl.	-	RP	RSP	RS	R	R	RS	RSP	-	R	-	S	RS	RSP	RSP
Taeniophyllum sp.	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-
Thrixspermum merguense (Hook.f)O.Kuntz	-	-	-	-	R	R	R	R	-	-	-	-	-	-	-
Thrixspermum sp.1	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Thrixspermum sp.2	-	-	-	-	-	-	-	-	-	-	r	-	-	-	-
Trichotosia annulata Bl.	-	-	-	-	-	-	-	-	-	-	-	R	-	R	R
Tropidia curculigoides Lindl.	-	-	-	-	-	-	-	-	-	-	R	-	-	R	R
Vrydagzynea albida Bl.	-	-	-	-	-	-	-	-	-	-	R	-	RP	R	R
Vrydagzynea sp.	-	-	-	S	R	R	RSP	RSP	-	-	-	-	-	-	-
Zeuxine gracilis Bl.	-	-	-	R	-	-	-	R	-	-	-	-	-	-	-
Total	**0**	**4**	**6**	**17**	**17**	**21**	**21**	**21**	**4**	**10**	**15**	**19**	**20**	**44**	**40**

Appendix 2. List of species of orchids recorded on Anak Krakatau from various expeditions.

Species	1963	1971	1979	1981	1982	1983	1989	1990	1991	1994	1998
Acriopsis javanica Reinw.	-	-	-	-	-	-	-	+	+	-	-
Calanthe sp.	-	-	+	+	-	-	-	+	+	-	-
Cymbidium finlaysonianum Lindl	-	-	-	-	-	-	-	+	+	-	-
Dendrobium crumenatum Swartz.	-	-	+	+	-	+	+	+	+	-	-
Eulophia graminea Lindl.	-	-	-	-	+	+	+	+	+	-	-
Eulophia pulchhra (Thou.) Lindl.	-	+	-	-	-	-	-	-	-	-	-
Spathoglottis plicata Bl.	-	-	-	+	-	-	-	+	+	-	-

Appendix 3. List of species of orchids recorded on Sebesi-Sebuku and common to Krakatau Islands (from van Leeuwen (1921) and author's data for 1989, 1994).

Species	Sebesi-Sebuku	Krakatau
Agrostophyllum majus J.J.Sm.	+	-
Bulbophyllum multiflorum (Breda) Krzl.	+	-
Bulbophyllum scheffleri Schlechter.	+	-
Calanthe zollingeri Rchb.f.	+	-
Coelogyne miniata Lindl.	+	-
Corymbis veratrifolia Rchb.f.	+	-
Cymbidium finlaysonianum Lind.	+	+
Dendrobium crumenatum Lindl.	+	+
Dendrobium mutabile Lindl.	+	+
Dendrobium tenellum Lindl.	+	-
Eulophia macrostachya Lindl.	+	+
Eulophia squalida Lindl.	+	-
Goodyera colorata Bl.	+	+
Liparis sp.	+	+
Macodes petola Lindl.	+	+
Nervilia aragoana Gaudich.	+	+
Oberonia monstruosa Lindl.	+	+
Phaius tankervillae (Banks ex l.Herit) Bl.	+	+
Spathoglottis plicata Bl.	+	+
Vrydagzynea sp.	+	+
Zeuzine sp.	+	+

Ericaceae in Malesia: vicariance biogeography, terrane tectonics and ecology

Michael Heads

Abstract

Heads, Michael (Science Faculty, University of Goroka, PO Box 1078, Goroka, Papua New Guinea. Current address: Biology Department, University of the South Pacific, P.O. Box 1168, Suva, Fiji. Email: heads_m@usp.ac.fj) 2003. Ericaceae in Malesia: vicariance biogeography, terrane tectonics and ecology. Telopea *10(1): 311–449.* The Ericaceae are cosmopolitan but the main clades have well-marked centres of diversity and endemism in different parts of the world. *Erica* and its relatives, the heaths, are mainly in South Africa, while their sister group, *Rhododendron* and relatives, has centres of diversity in N Burma/SW China and New Guinea, giving an Indian Ocean affinity. The Vaccinioideae are largely Pacific-based, and epacrids are mainly in Australasia. The different centres, and trans-Indian, trans-Pacific and trans-Atlantic Ocean disjunctions all indicate origin by vicariance. The different main massings are reflected in the different distributions of the subfamilies within Malesia. With respect to plant architecture, in *Rhododendron* inflorescence bracts and leaves are very different. *Erica* and relatives with the 'ericoid' habit have similar leaves and bracts, and the individual plants may be homologous with inflorescences of *Rhododendron*. Furthermore, in the ericoids the 'inflorescence-plant' has also been largely sterilised, leaving shoots with mainly just bracts, and flowers restricted to distal parts of the shoot. The epacrids are also 'inflorescence-plants' with foliage comprised of 'bracts', but their sister group, the Vaccinioideae, have dimorphic foliage (leaves and bracts). In Malesian Ericaceae, the four large genera and the family as a whole have most species in the 1500–2000 m altitudinal belt, lower than is often thought and within the range of sweet potato cultivation. The same belt is also most diverse for ferns, birds-of-paradise and bowerbirds. Distribution maps of Malesian Ericaceae are presented, with related species indicated. Concentric patterns of distribution are frequent and could be attributable to evolution around shrinking seas. In New Guinea the main axial range is a composite structure, with the southern part formed by the old Australian craton and the northern and eastern parts formed from 32 tectonostratigraphic terranes or microplates. These formed independently and then docked with each other and the craton. The tectonic boundary between the craton and the accreted terranes is also an important biogeographic boundary. Many taxa have distributions linking different accreted terranes but are not on the craton. Movement and integration of island arcs and more substantial terranes has led to complex patterns of disjunction throughout Malesia, but there is an underlying parallel-arc structure, seen clearly in New Guinea. The tectonic provinces in Borneo are also reflected in the two main biogeographic tracks: Kuching—Kinabalu and Kutei Mts./Mt. Kemul–Kinabalu, the Lupar River boundary and the Meratus Mts. centre. The islands of the Riouw Pocket (Corner 1978a) are notably surrounded by many groups which are absent there, including mangrove and Ericaceae species. However, other mangrove and coastal taxa occur along a CW Sumatra – Riouw Pocket – SW Borneo track. In Malesia, *Rhododendron* and *Vaccinium* mangrove and coastal species are mainly restricted to the west, in Sumatra–Borneo and often the Riouw Pocket; and are represented in New Guinea by related montane taxa. Van Steenis (1963, 1984) drew attention to mangroves uplifted by tectonics and the Malesian Ericaceae in general could be largely derived from mangrove forms. *Rhododendron* species occur as epiphytes in mangrove, and many Ericaceae occur in calcareous and saline sites. The very rapid rates of tectonic uplift occurring in New Guinea would raise a mangrove community or a coastal 'padang' to the upper montane zone in just one million years.

CONTENTS

'Fortune reigns in gifts of the world, not in the lineaments of nature'.

– Shakespeare, *As You Like It*.

Introduction

Rhododendron L. (c. 900 species) and *Erica* L. (c. 860 species) are the largest genera in Ericaceae. Both are ecologically important and widely cultivated in Europe, but they are not highly speciose there. *Erica* has a clear centre of diversity in Cape Province, South Africa, and *Rhododendron* has one in N Burma/SW China and a second in New Guinea.

Ericaceae (including Epacridaceae) are hardy plants, better able than most families except grasses to withstand the environmental extremes of mountain tops, arctic conditions, volcanoes, swamps, rocks, tree trunks and branches, and acid, oligotrophic soil which is often sandy or peaty. However, apart from a few saprophytic members they nearly all require high light levels, and many need a good supply of moisture.

This paper deals with the Ericaceae of the lands between Asia and Australia (the East Indies) that botanists refer to as Malesia.

The affinities of Ericaceae with other families

From the 1960s to the 1980s the Russian–American (Takhtajan–Cronquist) classification of the dicotyledons (e.g. Cronquist 1981) was widely taught and very influential. However, the three largest groupings — Dilleniidae, Rosidae and Asteridae — were often not adopted by tropical botanists. Philipson (1974, 1975, 1977), for example, placed Ericales (Dilleniidae), and Cornales, Araliales, and Pittosporaceae (Rosidae) together with the Asteridae on the basis of ovule morphology. (Philipson revived and extended Warming's early observations which had fallen into disrepute through van Tieghem's uncritical and complete reliance on them). Philipson (1977) also removed Ebenales, Primulales and Theales from Dilleniidae to a position near this group, and a broad Ericales, including these orders, is also supported by palynology.

This vast group of all the Asteridae plus many 'dilleniid' and 'rosid' families comprises about a third of the dicots (Olmstead et al. 2000). Although Philipson's work drastically undermined the Cronquist–Takhtajan groups, it was soon taken up by Dahlgren (1980). (Anderberg's 1992 claim that the new grouping of Ericales s.l. with Asteridae was 'definitely an innovative approach' of Dahlgren was perhaps a little over-enthusiastic).

Recent results from molecular studies are much more closely aligned with the Philipson–Dahlgren system than with the Russian–American classification: for example Olmstead et al. (2000) indicated a broad Ericales (including Actinidiaceae, Primulales, Ebenales, Theales and Lecythidaceae etc.) as the sister group of the Euasteridae.

It is interesting that both the Philipson–Dahlgren ideas and the DNA cladograms resemble the classic systems of a century ago rather than the long detour of the Russian–American system. Bentham and Hooker's (1862–1883) Gamopetalae and Engler and Prantl's (1887–1914) Sympetalae both included all of the Ericales, Ebenales and Primulales with 'Asteridae'. It seems rather confusing to call this very large group 'Asteridae' when it is nothing like the original Asteridae and is much more like Sympetalae, an older and very well-known name.

A study of *rbc*L, *atp*B and 18S RNA in 560 angiosperms (Soltis et al. 2000) had Ericaceae sister to Actinidiaceae, and this pair with Clethraceae, Cyrillaceae and insectivorous Sarraceniaceae. Roridulaceae of South Africa was sister to a very large Ericales (including Theaceae, Sapotaceae, Ebenaceae, Myrsinaceae, etc.).

In a study of *rbc*L in 589 dicots, Savolainen et al. (2000) had Ericaceae sister to Roridulaceae, as was earlier proposed by Anderberg (1992). This pair is sister to a clade comprising Actinidiaceae and the Sarraceniaceae (cf. Judd and Kron 1993). Sister to all these is a clade comprising Cyrillaceae, Camellieae and Clethraceae. Ericales as a whole again included Theaceae, Sapotaceae, Ebenaceae and Myrsinaceae. 'C.A.R.-G.' (in Sleumer 1966) pointed out the strong similarities in wood anatomy between Ericaceae and Theaceae, families often associated ecologically in the montane tropics.

Roridula L., a possible sister of Ericaceae, comprises two shrub species of southwest Cape Province, South Africa. The leaves bear tentacle-like, glandular trichomes superficially similar to those of *Drosera*, and *Roridula* was long regarded as insectivorous. However, the secretion proved to contain resins rather than enzymes (Lloyd 1976). *Roridula* also contains latex with a relatively high percentage of rubber. *R. gorgonias* grows in *Sphagnum*-covered seeps on cloudy montane slopes, whereas *R. dentata* has some xeromorphic features and occurs on drier, sandy flats (Carlquist 1976). Soils in both habitats are highly acidic and low in nitrates, as in standard Ericaceae habitat. *Roridula*, like Ericaceae, is mycorrhizal, which may have permitted the loss of any digestive function in the secretion.

In a study of five genes (Anderberg et al. 2002), a strict consensus tree included an 'ericoid clade' in which a group Actinidiaceae, Roridulaceae and Sarraceniaceae was sister to a group Clethraceae, Cyrillaceae and Ericaceae. The 'ericoid clade' as a whole shows a strong centre around the Pacific Ocean: Actinidiaceae comprises *Actinidia* Lindl. of E Asia, *Saurauia* Willd. of tropical Asia and America, and *Clematoclethra* Maxim. in west and central China. Clethraceae (comprising *Clethra* L. only) has a classic trans-Pacific track, China to New Guinea, and SE United States to Colombia and Brazil, with one species in Madeira. Cyrillaceae comprises two genera of the SE United States, and *Purdiaea* Planch., mostly in Cuba, and also in central and South America (Mexico, Colombia, Brazil).

Subfamilies of Ericaceae and their biogeography

Hutchinson (1959) emphasized the 'great concentration' of *Erica* in southern Africa and *Rhododendron* in W China. Cullen (1978) reiterated this: the two genera show 'remarkable concentrations of species in relatively small areas. *Rhododendron* has a massing of about 700 species in the area where China, Tibet, Burma, and Assam all meet – the area where the great rivers of eastern Asia (the Brahmaputra, Irrawaddy, Salween, Mekong and Yangtse) break though the Himalayan chain. The genus also has a secondary centre of almost 300 species in New Guinea ['Malesia' is possibly meant] ... *Erica* has an even more remarkable concentration of species in southern Africa, where about 450 species occur, many of them restricted to the Cape Province ... '.

Cullen (1978) pointed out that in Ericaceae *Gaultheria* also has an interesting distribution as it rings the Pacific Ocean almost completely.

Cullen also noted that Ericaceae s.s. are absent from most of Australia: there are only two *Agapetes* and two *Rhododendron* species in NE Queensland, and five *Gaultheria* in Tasmania and the highlands of Victoria/New South Wales (Beadle 1981). There are no Ericaceae s.s. in Western Australia, despite many suitable environments there; conversely, Epacridaceae are most diverse in SW Western Australia and SE Australia/New Zealand.

Cullen (1978) concluded that distributions of the main Ericaceae clades as outlined 'present challenges to plant geographers and students of evolution, and no generally acceptable explanation of them has so far been proposed.'

The taxonomy of the Ericaceae is notoriously controversial from family level down, making biogeographic analysis complex. However, DNA results are now appearing for many groups, and these tend to give clear patterns of vicariance. In particular, the subfamily or equivalent clades in Ericaceae indicated in Kron's (1996, 1997) studies have vicariant main massings, implying they have probably evolved by allopatric evolution during a phase of immobilism. The main clades in the family, with the location of their main species massings (Fig. 1), are the following.

Enkianthus Lour., a genus of shrubs and small trees in the Himalayas, southern China and Japan, is sister to all the other Ericaceae (Anderberg 1992, 1993, 1994, Judd and Kron 1993, and subsequent DNA studies).

The next branch is Ericaceae subfam. Monotropoideae s.l. (including Pyroloideae and Arbutoideae), a small group mainly in the Northern Hemisphere (with three genera in Peninsular Malaysia/N. Sumatra, also sister to all the other Ericaceae. Recently Hileman et al. (2001) concluded that the Mediterranean – North American disjunction in this group is the result of mid-Tertiary vicariance on the basis of age of fossils, and so the actual date is at least this age.

The rest of the family comprises two large clades. The first is a large, mainly Indian Ocean clade: (ericoids + 'phyllodocoids') + (rhododendroids + empetroids (formerly Empetraceae)). Ericoideae is mainly in South Africa and also occurs in tropical Africa, Madagascar and the Mascarenes, with a secondary massing, about 20 species, in Europe). The small phyllodocoid branch for *Phyllodoce* Salisb. and relatives has several monotypic or oligotypic genera in the Northern Hemisphere, especially the United States. The only large genus is the basal *Bejaria* L. with 30 species in tropical and subtropical America, indicating a possible Atlantic Ocean baseline for the clade.

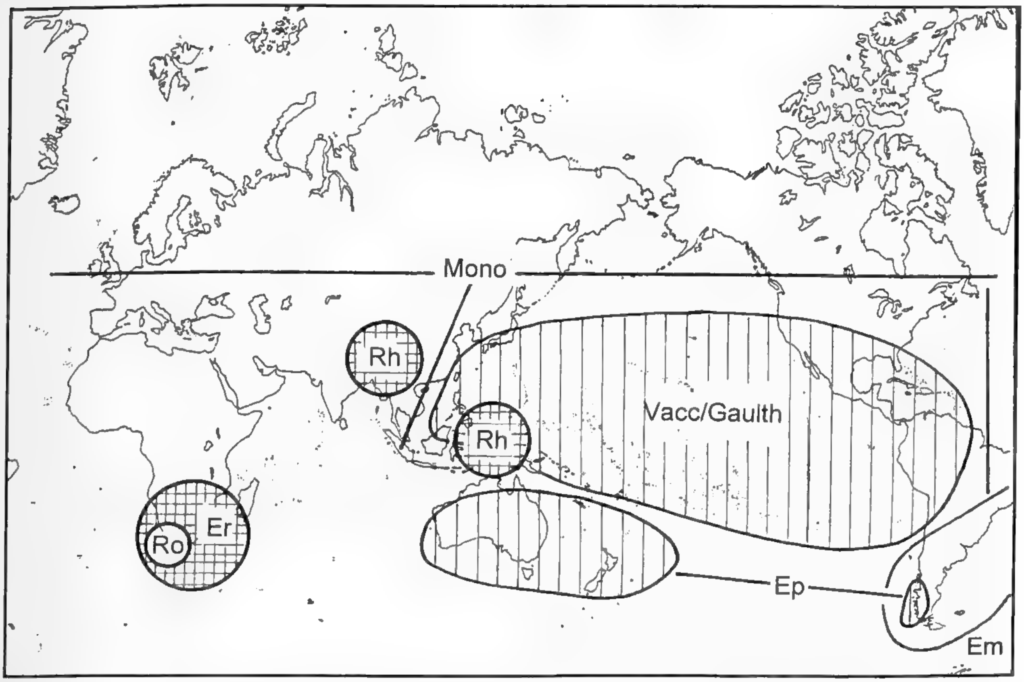

Fig. 1. Main centres of diversity in Roridulaceae (Ro), ericoids (Er), rhododendroids (Rh), Vaccinioideae (Vacc/Gaulth), epacrids (Ep) and Empetraceae (Em).

Rhododendroideae has main massings in N Burma/S China and New Guinea, and is also in Eurasia (one or two species of *Rhododendron* occur as far south as the Nilghiris and Sri Lanka) and America. The 'Empetraceae' branch is in southern South America and the Northern Hemisphere.

The ericoid-rhododendroid clade is sister to the second large group in the family, the *Vaccinium–Gaultheria–Lyonia*–epacrid clade, referred to here as subfam. Vaccinioideae (Kron, Judd and Crayn 1999). Unlike the first group, this has a large, if not the main, massing around the Pacific. Epacrids, formerly the family Epacridaceae, are now seen as the sister of the other vaccinioids. They are in Australasia and Chile, with a few species in the Pacific and SE Asia and possibly as fossils in South Africa (Namaqualand) (Coetzee 1993).

1. Ericoideae

Oliver (1991, 2000) has sunk 23 genera into a broadened *Erica* which now covers virtually all of the subfamily's range. Oliver (1989) accepted just three genera in Ericeae: *Calluna* Salisb. (one species widespread in Europe to the Urals), *Erica* s.l. (860 species, Africa and Europe) and *Daboecia* D.Don, Atlantic Europe and Azores. Oliver (1989) gave a very useful map of Ericeae (although the only record for West Africa was mapped in northern Ghana instead of at the Ivory Coast/Liberia/ Guinea border). Outside mainland Africa *Erica* also ranges (with '*Philippia*' only) in Madagascar (45 species, including some on calcareous rocks), the Comoros, and the Mascarenes (Perrier de la Bâthie 1927). '*Philippia*' also occurs on mainland Africa and at sea-level on Mafia Island off Tanzania (at 8° lat.), a site which is neither temperate nor tropical-montane, where most Ericaceae occur. There is a second centre of *Erica* in Europe (20 species).

In southern Africa there is a dramatic increase in the number of *Erica* species towards the southern tip of the continent which Oliver (1991) called 'the most remarkable distribution phenomenon in the plant kingdom' and the concentration of *Erica* species in the SW Cape is 'unequalled [for any genus] anywhere in the world.'

Of 657 southern African *Erica* species, Schumann et al. (1992) illustrated 468 from South Africa. They cited 625 species present in southern Cape Province, and 235 in Caledon District alone. The term Caledon Centre (Croizat 1965) has been taken up by most authors for this region, one of the most dramatic centres of diversity in the world.

At a finer scale than that of district, Oliver et al. (1983) mapped species numbers of Cape genera in 1/4° × 1/4° grid squares (about 20 km × 20 km), and showed *Erica* reaching a maximum at 175 species in a square just east of Cape Town which includes the town of Somerset West and the Hottentots-Holland Mountains. The same square is richest for Ericaceae as a whole, Restionaceae, Diosmeae (Rutaceae) and Bruniaceae, first equal for Penaeaceae, and is adjacent to the richest square for Proteaceae.

Other Ericoideae are of special morphological interest. In '*Nagelocarpus*' Bullock, monotypic in the SW Cape, the ovary is half-inferior to the corolla and stamens but superior to the calyx — N.E. Brown (1905) described this as unique in the vegetable kingdom. Oliver (1991) illustrated bizarre forms of '*Philippia*' from Madagascar in which the very large stigmatic lobes form an immense funnel that can take up the whole mouth of the corolla, similar to species in *Erica* sect. *Arsace* of South Africa which also have very large, shield-like stigmas. These are wind-pollinated and often form a dominant part of the 'fynbos' or heath.

Oliver (1991) concluded that 'explanations for the great concentration of so many species of *Erica* just in the Cape have not been forthcoming'. In this paper the concentration is attributed to activity early in the history of the Ericales along the major tectonic features, the Zwartberg and Cedarberg Fold Belts (cf. Craw et al. 1999). These run at right angles to each other and intersect at the SW Cape, by the Caledon Centre. This massing, the high diversity in East Africa and Madagascar (45 species), and the occurrence at the Mascarenes all indicate an old SW Indian Ocean centre vicariant with the NE Indian Ocean centre in *Rhododendron* and SE Indian Ocean centre in epacrids. Oliver (1991) commented that 'Ericoideae were always put forward as a clear-cut example of a northern [sub]family because of the strong connection to the north and none to the west or east. This is in contrast to the families Proteaceae or Restionaceae.' However, DNA studies emphasize instead the vicariance of Ericoideae with Rhododendroideae and Vacciniodeae/epacrids in the east, and *Bejaria* etc. in the west.

2. Rhododendroideae

The ericoid – rhododendroid clade basically follows an Africa–Eurasia–America track. *Rhododendron* itself has a primary centre of diversity in the Sino-Himalaya region and a second in New Guinea, like groups such as *Ficus* sect. *Sycidium* (Corner 1938, 1963) and also extends to Europe and North America (south to the US/Mexico border). The clade is notably absent from the central and south Pacific, in contrast with the vaccinioid-epacrid clade, and has only two *Rhododendron* species in Queensland and none in the mountains of New Caledonia or New Zealand. Members of this group that are remarkably ericoid vegetatively include *Ledothamnus* Meissn. in Venezuela/Guyana and *Rhododendron ericoides* on Mount Kinabalu.

3. 'Empetraceae'

This is the sister group of Rhododendroideae and here the flowers are 3-merous, unisexual and wind-pollinated. The group ranges throughout the Northern Hemisphere north of lat. 40°N, in bogs, moors, and pine barrens. However, *Empetrum* is also in the Southern Hemisphere, from the southern Andes, the Falkland Islands, Juan Fernandez and Tristan da Cunha. The north-south disjunction is aligned along the Mid-Atlantic Ridge. There are three genera: *Empetrum* L. holds the family range, *Ceratiola* Michx. is a SE United States monotype, and *Corema* D.Don occurs in eastern North America, the Azores, the Canary Islands, and SW Europe in a classic trans-Atlantic pattern.

4. Vaccinioideae (incl. *Gaultheria* L. and *Lyonia* Nutt.)

Vaccinioideae traditionally includes the Ericaceae with an inferior ovary, many of which are found around the Pacific region. *Vaccinium* is widespread around the world with about 450 species, especially in the north, but has over half its species (242) in Malesia, and half of these are in New Guinea. In South America it is not found south of Bolivia (Cochabamba), and in Chile it is replaced by epacrids (*Lebetanthus* Endl.). In Africa it has only half a dozen species and occurs in southern Africa only in Malawi (one species) and eastern Transvaal, near Barberton (one species). South of here it is replaced by the great diversity of *Erica*.

Vaccinium and its immediate relatives, the tribe Vaccinieae D.Don, comprise 30–35 genera that are especially diverse in southeast Asia and Malesia, and Central and South America (Kron, Fuller et al. 1999). Stevens (1971) concluded that many of the South American genera share a complex of anatomical characters with the Malesian genera *Costera* J.J.Sm., *Dimorphanthera* F.Muell. and *Agapetes* subg. *Paphia* (Seem.) Stevens. In the Vaccinieae, Atkinson et al. (1995) found diploids in western Malesia and mainland Asia, whereas polyploids are recorded from New Guinea, Australia, and the Neotropics in a trans-Pacific disjunction.

Kron, Fuller et al. (1999) concluded that Vaccinieae are monophyletic, although *Agapetes* and *Vaccinium* as currently accepted are both polyphyletic. In a possible Atlantic Ocean affinity (cf. Empetraceae), *Vaccinium* sect. *Neurodesia* of the Andes and North America may be close to *V.* sect. *Cinctosandra* of Africa and Madagascar. In *Vaccinium*, the group containing *Dimorphanthera* and *Agapetes* subg. *Paphia* (both diverse in Malesia) may be more closely related to New World Vaccinieae than to the other Old World taxa in a trans-Pacific affinity, although the data support for this is still weak (Kron pers. comm., in press).

Another Pacific group, *Gaultheria* and relatives, has often been treated with Vaccinieae, and this is supported by Kron, Judd and Crayn (1999) and Kron, Fuller et al. (1999). Camp (1947) mapped the distribution of this group as 'the *Gaultheria* ring', and this follows the plate margins and the volcanic 'ring of fire' around the Pacific. The *Gaultheria* group includes the well-supported clade (Kron, Judd and Crayn 1999):

Gaultheria L. (incl. *Pernettya* Gaudich.). Circumpacific, also west to W Himalayas and S India, east to E US and E Brazil;

Diplycosia Blume. Malesia (throughout);

Tepuia Camp. Venezuela.

The other genera in the *Gaultheria* group mainly occur around the north Pacific.

A third Pacific affinity, the *Lyonia* group, was accepted by Kron, Judd and Crayn (1999) as sister to the *Vaccinium–Gaultheria* group (cf. Stevens 1971). *Lyonia* itself occurs in East Asia, Malesia (only in Peninsular Malaysia) and North America, *Craibiodendron* W.W.Smith is in SE Asia, and *Pieris* D.Don is in East Asia and North America. The *Lyonia* group thus ranges around the north Pacific, complementing the *Vaccinium* group in the north and central Pacific, and the *Gaultheria* group wide in the Pacific.

5. Epacrids

These shrubs and trees are distinctive through their leaf venation which is branched near the base, parallel and 'open' — almost monocotyledean (Sleumer 1964). In many ways the leaves are similar to bracts. In tribe Richeae, the aptly-named Tasmanian 'grass-tree' and the New Zealand 'pineapple-scrub' are vegetatively much like monocots, and one member, *Dracophyllum* Labill., was named after *Dracaena* L. The 'epacrids' were formerly known as Epacridaceae, but now appear to be nested well within Ericaceae, as sister to the other Vaccinioideae (Kron 1996, Crayn et al. 1998, Crayn and Quinn 2000, Kron et al. 1999). Garcin (1890) pointed out that the fruit in *Vaccinium* is a drupe (the inner epidermis of the pericarp sclerifies), as in many epacrids. Kron, Fuller et al. (1999) concluded that their studies suggest 'possible biogeographic links between the Southern Hemisphere taxa of Ericaceae s.l.'.

Within the epacrids (Watson 1967, Crayn et al. 1998) the tribe Prionoteae in Tasmania and southern Chile is sister to the rest. Oligarrheneae in SW Western Australia in turn is sister to the remaining five tribes. All these five tribes are shared by Australia and western South Island, New Zealand. Of the five, Richeeae also extends to New Caledonia and has important endemism on the Chatham Islands, and Styphelieae ranges widely, but with few species, in the Pacific and Malesia north to Vietnam. The epacrids are thus centred around SW Western Australia – southern Tasman Sea – Chile, and are poorly represented in Malesia. They are not present in the Bismarck Archipelago at all (where there are five *Rhododendron* species), and in the geographical Solomon Islands they are only on Bougainville with a single species (Sleumer 1964).

In the Styphelieae Sleumer (1963) sunk several genera (*Astroloma* R.Br., *Cyathodes* Labill., *Leucopogon* R.Br. and *Melichrus* R.Br.) under *Styphelia* (G.Forst.) Sm. This was not accepted by many Australasian botanists, and following detailed morphological studies Weiller (1996a,b,c, 1999) accepted the old genera and also described new ones. However, beyond the basal *Pentachondra*, none of the branches in the *Styphelia* group (which involve the genera synonymised by Sleumer) are supported by molecular data (Crayn et al. 1998, Crayn and Quinn 2000). In fact these data may even support extending Sleumer's lumping to include additional genera in a broad *Styphelia*.

Coetzee (1993) reported that pollen evidence from the sediments of the Arnot kimberlite pipe in Namaqualand (western South Africa) indicate the occurrence there during the Paleocene of an 'open-canopied dry subtropical forest with an understorey of Ericaceae, Epacridaceae, Thymelaeaceae, and Restionaceae'. This rather modern-sounding community (the understorey resembles assemblages in, for example, SW New Zealand) ties the epacrids to the most important centre for the family, in South Africa.

Conclusion on biogeography of the subfamilies

In conclusion, the subfamilies of Ericaceae show clear global vicariance of main massings. One of the main subjects of this paper is the relevance of these massings for distributions within Malesia. Analysing the land-snail fauna of Vanuatu, Solem (1958) recognised three elements which can also be seen in Malesian Ericaceae: Paleo-Oriental or Malayan (cf. Rhododendroideae), Southern Relict or Australasian (cf. epacrids), and Pacific Ocean or Polynesian (cf. Vaccinioideae). The last element is often ignored (see below), but is crucial for E Malesian groups in particular.

As Hutchinson (1959) wrote, the Ericales are most highly represented in the Southern Hemisphere. However, there are also important centres in the Northern Hemiphere, such as Japan, SE United States and Europe, and it is probably not a question of migration between one and the other, but rather of independent evolution. In fact, there is no evidence indicating a restricted centre of origin of the family Ericaceae followed by migrations; the complex is more simply derived by subdivision of an already global ancestral complex. *Roridula* and *Erica* in SW Cape Province, *Rhododendron* in Burma – New Guinea, the Vaccinioideae around the Pacific, and epacrids around the Tasman Sea all indicate Gondwanic origins for the group (although there are no direct Madagascar – Sri Lanka/India links).

It should be noted here that a 'basal' group is simply a small sister group, it does not imply that the 'basal' group is the ancestral group from which the others were derived, or that it has a 'primitive' morphology, or that it occurs at the 'centre of origin'. For example, *Roridula* might be sister to Ericaceae, but this is not evidence that Ericaceae had a centre of origin in South Africa and then migrated by physical movement across the world. Nevertheless, the South African region is clearly crucial in the evolution of the group, and the plants there cannot be secondarily derived from a centre of origin elsewhere.

Global biogeography

Many other taxa with very different ecology and means of dispersal show distributional similarities to the Ericaceae, across both the Indian and Pacific Oceans.

1. Indian Ocean affinities

Hooker (1860) observed that many 'Indian' groups, such as Melastomataceae, are absent or rare in Australia, while related groups like Myrtaceae are very diverse there. The opposite situation holds in Africa–Asia, where Melastomataceae are rich but there is a surprising lack of Myrtaceae. Likewise, Hooker noted that Campanulaceae are diverse in South Africa, while the related Goodeniaceae and Stylidiaceae are diverse in Australia, and Ericaceae in South Africa are 'represented' (Darwin's term) in Australia by Epacridaceae. These are all examples of vicariance around the Indian Ocean.

The connection between the main massings of *Erica* (South Africa) and *Rhododendron* (Burma/Yunnan – New Guinea) is another standard Indian Ocean disjunction, in which India/Sri Lanka are mainly avoided (although there are a few *Rhododendron* species in the Nilghiris and Sri Lanka).

Clarke (1997) discussed the classic Indian Ocean distribution of *Nepenthes* L. in Madagascar, Seychelles, Sri Lanka, India, S China and Malesia (by far the most species), the lowlands of far northern Queensland and New Caledonia (Fig. 2). For Clarke, the theory of a centre of origin in SE Asia has 'a number of problems'. For example, 'it seems astounding that no *Nepenthes* have reached the highlands of northern Australia' (cf. the paucity of *Rhododendron* there), and this is not explained in the centre of origin model. Clarke continued: 'The second theory, put forward by Danser (1928) … assumes that *Nepenthes* is a much older genus, their ancestors having arisen perhaps as much as 70 million years ago … *Nepenthes* could have originated at a time when Madagascar, the Seychelles, Sri Lanka and India were breaking away from Gondwanaland …'. Clarke (1997) found the second theory to be the more plausible.

Malesian palms have both Indian Ocean (*Veitchia*, Fig. 3) and SW Pacific Ocean (*Orania*, Fig. 3) disjunctions.

Madagascar–Burma connections occur in many plants, for example: Sleumer (1942) keyed out *Desmostachys* Planch. (Icacin.) of tropical Africa and Madagascar with *Pittosporopsis* Craib. of Upper Burma, Yunnan, and Thailand. (The fact that taxa are keyed together does not necessarily mean they are closely related, but it does indicate that some characters are shared).

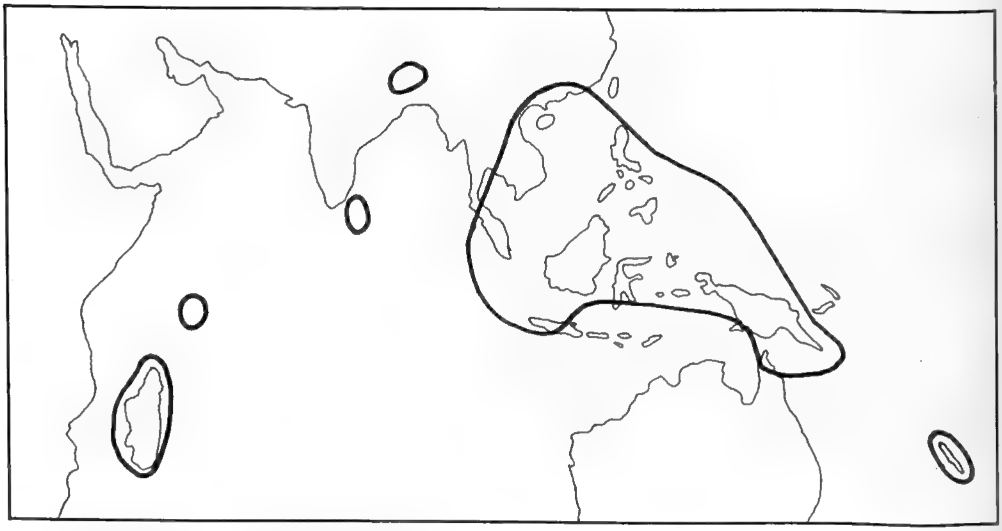

Fig. 2. *Nepenthes* L. (Nepenth.) (Juniper et al. 1989).

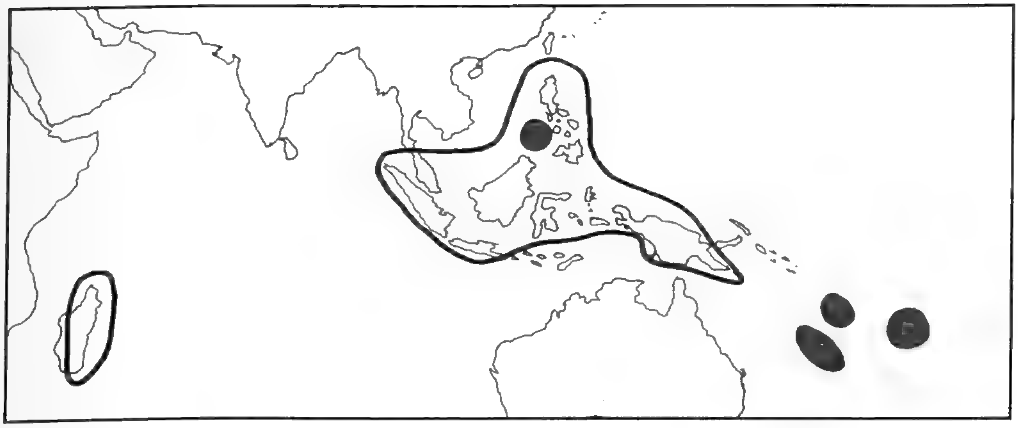

Fig. 3. *Orania* Zippel. (line) and *Veitchia* H. Wendl. (black) (Palmae) (Baker et al. 1998).

Afzelia Sm. (Caesalpin.) has seven species in Africa, three in Burma–China, and three in Malesia. (Brenan 1967).

In birds, *Gymnobucco* (Capitonidae) of Africa is usually placed with *Calorhamphus* of S Burma, Malaysia, Sumatra, and Borneo (Howard and Moore 1984). *Zoonavena* (Apodidae) is in Africa, Madagascar, and India to Burma. *Raphidura* (Apodidae) is in Africa and S Burma to Sumatra, Java and Borneo.

The distance between Aceh and Madagascar is the same as between Aceh and PNG, and both sectors represent important disjunctions. Madagascar–Sumatra examples include the following.

Aralidium Miq. comprises a single pachycaul species endemic to the lowlands of W Malesia: southern Thailand (south of the Kra Isthmus), Peninsular Malaysia, Sumatra, Singapore, Anambas Is., and Borneo (widespread). It was formerly treated in Araliaceae but Philipson and Stone (1980) created a new family, Aralidiaceae, for it. This is supported by DNA studies (Savolainen et al. 2000) in which it appears as the sister group of Melanophyllaceae of Madagascar.

Dapania Korth. (Oxalid.) (Veldkamp 1971) has the same 'remarkable' but 'characteristic' disjunction: West Malesia – Madagascar.

Quassia borneensis Nooteboom (Simaroub.) of peat-swamp forest and lowland rainforest in central Sumatra and Borneo is 'obviously closely allied' to African species (Nooteboom 1964).

In *Crossonephelis* Baill. (Sapind.), the Madagascar species is 'possibly the most primitive' of the living species (Leenhouts 1973) and seems allied on one hand to the continental African species and on the other to the most widespread and 'least specialised' of the Malesian species, *C. palawanicus* (Sumatra to New Guinea).

In addition to Madagascar-Sumatra and Madagascar-Burma tracks, many plants illustrate the connections between NE Assam and Malesia (van Steenis 1962b) (cf. *Rhododendron*), either through N Sumatra (*Primula prolifera*, cf. *Gaultheria*) or via Kinabalu and the Philippines (*Haloragis micrantha*).

2. Pacific Ocean affinities

Even though van Steenis (1962) devoted a long paper to trans-tropical Pacific distributions, accepting significant Polynesian endemism or trans-Polynesian biogeographic connections has generally remained taboo. When they are admitted, trans-central Pacific connections are traditionally explained by long distance dispersal (e.g. Vijverberg et al. 1999, on *Microseris* D.Don, Compositae) although the same pattern may be shared by many taxa with different means of dispersal, indicating instead a vicariance origin (Chin et al. 1991 on *Microseris*, marine algae, etc.).

Luteyn (2002) recorded the highest diversity of Neotropical Ericaceae in Antioquia, NW Colombia (23 genera, over 100 species, especially Vaccinieae). Luteyn attributed this to 'adaptive radiation' in the very wet climate there, but did not refer to the regional geological history of terranes accreted from the Pacific side. In fact, a similar pattern occurs in pantropical marine groups, such as fiddler crabs (*Uca*), which have maximum diversity around the coasts of NW Colombia (Crane 1975). This pattern and its occurrence in both marine and alpine groups could easily be explained as the result of terrane accretion.

In Ericaceae there are several trans-Pacific tracks and it is not possible to understand the group in Malesia without considering these. There are southern connections in *Gaultheria* (several groups), central connections in *Dimorphanthera* – New World *Vaccinium, V.* sect. *Macropelma*, and possibly in the *Gaultheria–Diplycosia–Tepuia* clade, and northern Pacific connections in *Rhododendron*, *Vaccinium*, *Gaultheria*, and the *Lyonia* group.

Clethraceae, with about 64 species, is closely related to Ericaceae, as mentioned above, and is another typical Pacific group. It ranges in tropical Asia (SE China and Japan through Malesia to New Guinea) and mainly tropical America (SE US to Brazil), with one species in Madeira (Sleumer 1971b).

The pantropical *Casearia* and its relatives comprise the sister group to Flacourtiaceae s.s./Salicaceae (Savolainen et al. 2001). *Casearia pachyphylla* Gilg of NE New Guinea (mossy mountain forest in the Schrader Mts. and Saruwaged Mts.) is unique among the 60 Malesian *Casearias* by its peduncled inflorescence, a character otherwise known only in some Brazilian species (Sleumer 1954).

Van Steenis (1962a) cited and mapped many trans-Pacific plant groups. The following are some other, recently-studied examples.

Citronella D.Don (Icacin.) is in Malesia, E Australia, SW Pacific islands, and South America. Old World and New World species have been placed in separate sections, but Sleumer (1971) found that the characters used to discriminate the two are rather vague or do not hold.

Deplanchea Vieill. (Bignon.) has affinities with American plants (van Steenis 1977).

Castanopsis Spach and *Lithocarpus* Blume (Fagaceae), dominant in many Malesian forests, have virtually identical distributions: SE Asia/Malesia – NW United States (Soepadmo 1972). *Mitrastema* Makino (Rafflesiaceae) is parasitic on these and other Fagaceae such as *Quercus*, but ranges only from NE India to Japan and New Guinea, and in S Mexico (Chiapas)/Guatemala and NW Colombia (Antioquia) (Meijer and Veldkamp 1993).

In *Solanum* L., Symon (1986) cited direct links between New Guinea and central America species in each of sections *Cypellocalyx* Bitter, *Lasiocarpa* (Dunal) D'Arcy, *Micrantha* Dunal and *Torva* Nees.

The tribe Schismattoglossideae of Araceae ranges between China and Vanuatu, with a centre on Borneo, but also has three species in the Neotropics (Hay 1996).

Oreomyrrhis andicola (Kunth) Hook. s.l. (Umbelliferae) is recorded from Kinabalu, New Guinea, and is widespread in the Andes (Dransfield 1987).

The tribe Moutabeeae of Polygalaceae comprises *Eriandra* Royen & Steen. of New Guinea and Solomon Islands, *Balgoya* Morat & Meijden from New Caledonia, and three genera of tropical South America (van Royen and van Steenis 1952, van der Meijden 1988, Balgooy and van der Meijden 1993). Although Eriksen (1993a) indicated that the tribe Moutabeeae is polyphyletic, he and van der Meijden (1988) both accepted that the sister of *Eriandra* is *Diclidanthera* Mart., one of the American genera. Eriksen (1993b) accepted the Moutabeeae as previously defined and had it as sister to *Xanthophyllum* Roxb., diverse throughout Malesia.

Spondias L. (Anacard.) has 10 species occurring naturally in the Indo–Malesian and American tropics (four species are widely cultivated through the tropics) (Ding Hou 1978).

In legumes (Verdcourt 1979), *Oxyrhynchus* Brandgee (Papilionoideae) (incl. *Peekelia* Harms) has one species in Papuasia, and three or four from Texas to Colombia and the West Indies. *Inocarpus* J.R. & G.Forst. (Caesalpinioideae) (Malesia, Pacific Islands) and *Etaballia* Benth. (Brazil, Venezuela, Guyana) are either congeneric or closely related.

Discussing Kinabalu ferns, Holttum (1964) mapped taxa restricted to both sides of the tropical Pacific (*Gleichenia* subg. *Diplopterygium* Diels and *Cibotium* Kaulf.), and both sides of the tropical and South Pacific (*Schizaea fistulosa, Paesia* A. St-Hil., *Dicksonia* L'Hérit. (also one species in St Helena), and *Culcita* Presl. (also one species in Portugal–Azores)).

Pacific basin distributions are also well-known in animals (higher order groups include the millipede superfamily Conotyloidea (comprising 9–10 families) (Eskov and Golovatch 1986), and trans-tropical Pacific distributions even occur repeatedly within taxa such as the ponerine ants (Lattke, in press).

Amphi-Pacific distributions are probably related to distributions restricted to the Central Pacific, like that of Campanulaceae subtribe Sclerothecinae: Hawaii, Tahiti, Cook Islands (Raynal 1976), or the palm *Pritchardia* Seem. & H.Wendl.: Hawaii, Tuamotus and Fiji (Corner 1966).

Sommieria Becc. (New Guinea), *Pelagodoxa* Becc. (Marquesas) and *Manicaria* Gaertn. (tropical America, West Indies) form a group of related palms (Corner, 1966).

Vaccinium sect. *Macropelma* Klotzsch is endemic to Hawaii and SE Polynesia (Marquesas, Society, Rapa, and Cook Islands). It occurs in what Vander Kloet (1996) called two 'disparate' island groups, but the Hawaiian and SE Polynesian islands are probably not really disparate — that is, 'essentially different, ... incommensurable, without comparison or relation, ... so unlike that there is no basis for their comparison' (Oxford English Dictionary). In a brief panbiogeographic analysis (Heads 1983) Hawaii and Marquesas were shown to be connected by a standard track. Sleumer (1941) related *V.* sect. *Macropelma* to sect. *Myrtillus* (greatest diversity along the Pacific rim from Japan to Mexico (Vander Kloet 1996)) and this is confirmed by analyses of DNA (Kron in press).

West of *Vaccinium* sect. *Macropelma*, *Vaccinium* species on Vanuatu (one is indicated in *Oarianthe* III; Fig. 49) are related to Malesian plants. In Fiji, between Vanuatu and the central Pacific *Macropelma*, there is no *Vaccinium* and the only Ericaceae is *Paphia* (shared with Queensland, New Caledonia and New Guinea). Across the plate margin in Samoa, *V. whitmeei* is of 'unknown sectional affinity'.

Unlike many authors who have denied that there is a true Polynesian flora, Philipson (1970) argued that plants such as *Meryta* J.R. & G.Forst., *Tetraplasandra* A.Gray (both Araliaceae), *Fitchia* Hook.f. (Compositae), *Sclerotheca* A.DC., *Vaccinium* sect.

Macropelma, 25 endemic species on Rarotonga, and many others indicate that 'the southern Pacific islands must be credited with a flora specific to this region … Clearly land has been present for long periods in this area of the Pacific because well-marked genera are endemic to it. The flora characteristic of this region could survive provided a few oceanic volcanoes projected above the sea at all times. Such oceanic islands characteristically rise and fall relative to sea-level so that they are precarious footholds for a flora, but collectively they form a secure base'. In this view, vicariants could also maintain their respective ranges in adjacent archipelagoes, as long as new volcanoes and atolls constantly appear to replace vanishing ones. New individual islands will be colonised by ordinary, everyday movement, an observable ecological phenomenon which functions using ordinary means of survival.

This is a very different process from the (imaginary) biogeographic dispersal which relies on theoretical jumps, freak events, extraordinary and mysterious 'means of dispersal', epic voyages by waifs and strays, etc., to explain standard patterns. Not surprisingly, even its adherents often admit that this process can be rather mysterious, especially in taxa with limited means of dispersal. Conversely, the albatrosses range at ease over thousands of kilometres of open ocean but always return to very specific localities to breed (e.g. on mainland New Zealand only at Dunedin) and these are vicariant with their relatives' breeding localities in standard biogeographic patterns.

Ideas on the survival of flora discussed by Philipson find parallels in zoological work. For example, 'It is virtually universally accepted now that the Polynesian Islands have been populated by overseas dispersal in quite recent times … Yet the highly endemic and antique nature of the Pacific Island snail fauna … cannot be dismissed' (Solem 1976).

Discussing the Fiji lizard fauna and criticising the usual interpretation of their derivation by long distance dispersal, Zug (1991) wrote that 'The persistence of ancient taxa and their speciation on different island groups indicate the continual presence of emergent islands throughout the long history of Indoaustralian-Pacific plate interactions.'

Shoot architecture and habit

The main topic of this paper involves the evolution of Ericaceae in space, time and form. Evolution of form in biology is usually interpreted teleologically in terms of 'purpose' — a structure is seen to have evolved 'in order to' achieve a certain end. In this paper, however, particular morphologies are instead interpreted as the results of morphogenetic trends which are primarily structural and due to processes such as molecular drive (Craw et al. 1999). In this view, any particular adaptation is a secondary aspect of a main trend, a single point on a series or trajectory of morphologies as seen, for example, in the many species of a large genus. Of course, any observed morphology must have attained a certain level of viability or it would not occur. The morphogenetic trends (the antithesis of random mutation) take place largely independently of the environment and may eventually lead to subviable morphologies and extinction. Thus the trends (Darwin's 'laws of growth' (Grehan and Ainsworth 1985)) are of primary importance, and supply the raw material on which natural selection can bring about secondary 'pruning'.

Morphological structure, like biogeography, is usually interpreted as beginning from a restricted centre of origin, for example a leaf, gland or scale beginning as a small 'outgrowth' and developing by 'selection pressure' into a large, more complex structure. Instead, organs in Ericaceae are interpreted here mainly as the results of prior trends in suppression, reduction and fusion of parts.

For example, the angiospermous flower may be the result of reduction of a complex strobilar structure involving the 'telescoping' of parts. If this reduction has been even with respect to the different radial sectors, a regular flower results. If the process has been uneven, zygomorphy, often cryptic, is produced. Both states are alternatives, neither more 'advanced' than the other, derived from a more complex ancestral pre-floral condition. It is not a question of a zygomorphic flower being 'derived' from a radial flower. Ericoids and rhododendroids differ in floral morphology, notably in the obvious zygomorphy of many *Rhododendron* species. However, flowers of *'Grisebachia'* and *'Acrostemon'* (both now *Erica* s.l.) can be slightly oblique (Brown 1905). In other *Erica* spp. (*'Philippia'*) a bract is more or less recaulescent with the pedicel. In some species the bract becomes totally recaulescent and forms part of the calyx as the apparent abaxial sepal, the sepal itself disappearing (Oliver 1991). Below the flower the 'pedicel + bract base' is a compound structure of fused stem and leaf, a hypoclade (Bugnon 1955). Pichi Sermolli and Heiniger (1952) illustrated the dimorphic *P. abyssinica* which has both zygomorphic and actinomorphic flowers. The 'false' zygomorphy (Oliver 1989, 1991) in *'Philippia'* can be contrasted with 'real' zygomorphy in Rhododendroideae etc., but a similar telescoping process in the origin of the flower may also be responsible for the zygomorphy in these plants.

Ericoid shrubs as largely sterilised inflorescences

Rhododendron and *Erica* have very different shoot architecture. Rhododendroideae have inflorescences usually terminating the main branches, while in Ericoideae inflorescences may apparently terminate the main branches but in reality are 'intercalary' and always include a vegetative bud (Cullen 1978). Philipson (1966) interpreted the apex as periodically vegetative and reproductive. In other 'ericoid' plants (e.g. *Kelleria*, Thymelaeaceae) different species in the same genus can show intercalary or terminal inflorescences (Heads 1990).

In addition to inflorescence position, there are other important architectural distinctions between *Erica* and *Rhododendron*. *Rhododendron* has dimorphic foliage of large foliage leaves, and much smaller bud scales (perulae) with open venation. For example, the perulae of *R. javanicum* differ in colour, size, shape, texture and venation from the foliage leaves. They resemble epacrid foliage, as do the bracts of other *Rhododendron* and *Vaccinium* species (Fig. 4). In contrast to *Rhododendron* and its dimorphic foliage, ericoid shrubs (incl. ericoids, epacrids, 'Empetraceae', Monotropoideae s.s.) have only one kind of foliage: the vegetative leaves are similar, often very similar, to the floral bracts and both are bract-like.

A possible explanation is that the whole plant in ericoid shrubs is equivalent to an inflorescence of *Rhododendron* (itself highly telescoped) or, more obviously, *Vaccinium* – the newly expanding inflorescences of many New Guinea *Vaccinium* species closely resemble vegetative shoots of epacrids.

In the ericoid 'bract-plants' there is (a) a 'reduction' of the plant to just an inflorescence, and (b) a sterilisation of most of the bracts with flowering restricted to the end of the shoots/sterilised peduncles (or basally on the branches as in *Acrotriche ramiflora* R.Br. and relatives (Paterson 1960)).

Oliver (1991) recorded an interesting 'limit case' in *Calluna*, half-way between a 'bract plant' and a 'normal' plant with dimorphic foliage. The inflorescence was described by Webb (1972) as a terminal or intercalary raceme or panicle, but by Stevens (1970) as axillary and usually single-flowered (cf. *Gaultheria* spp.).

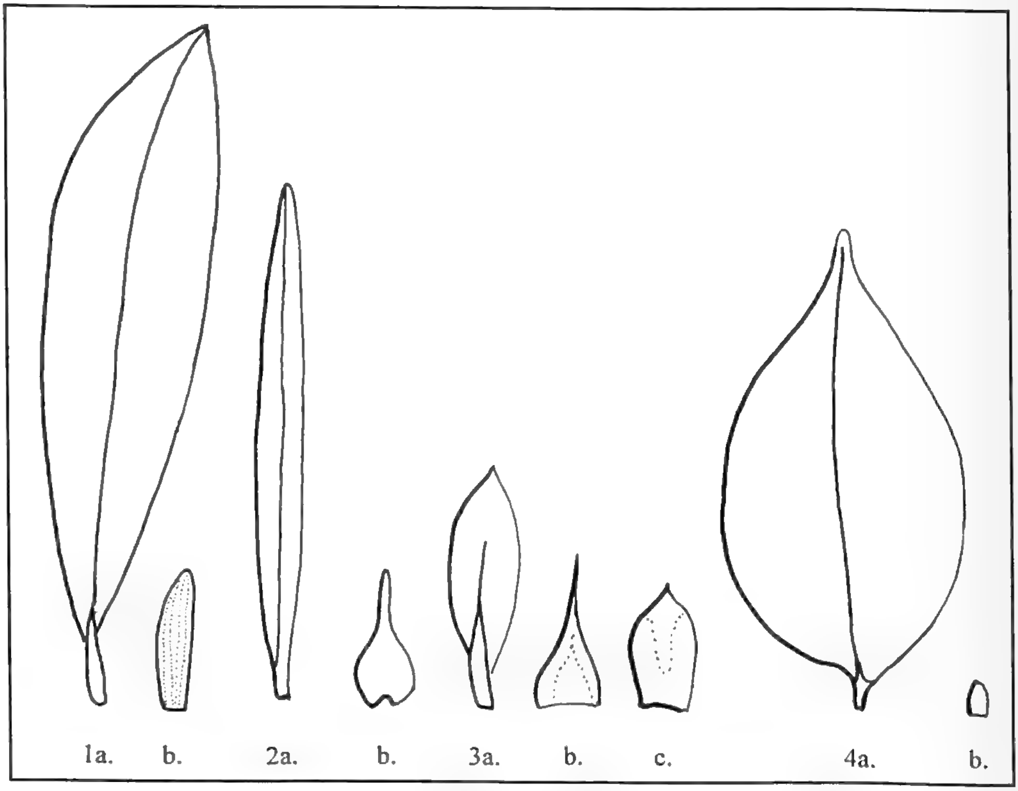

Fig. 4. Leaves (a) and perulae (b) in 1. *Rhododendron javanicum* (van Steenis 1962), 2. *R. caliginis* (Kores 1984), 3. *R. capellae* (Kores 1978) (b. outer perula, c. inner perula) and 4. *Vaccinium* cf. *albicans* (*Heads s.n.*).

Epacrids are largely 'bract plants', while their sister group, the Vaccinioideae, have dimorphic foliage. Both groups are recorded from both Africa and the Pacific, and so seem to contradict the trend in ericoids/rhododendroids, in which bract-plants are in the west, and their normal, dimorphic-foliage relatives in the east. However, epacrids are recorded from SW southern Africa (fossil) whereas *Vaccinium* only reaches the Transvaal, and in the central Pacific the Vaccinioideae have a greater massing than the epacrids, and at least some of the epacrids here (e.g. on New Caledonia, see below) are dimorphic.

In Monotropoideae s.s. the scale-like leaves and their bracts are more or less identical, whereas foliage in their relatives, Pyroloideae and Arbutoideae is normal and dimorphic.

Other 'bract-plants' are found in New Zealand, northern Australia (described next), South and East Africa and Madagascar. North and east of New Zealand and New Caledonia there are notably very few on the Pacific islands (from New Guinea and Chatham Islands east).

In *Dracophyllum* Labill. (epacrids), the species with racemes or panicles have distinct bracts, and these are most highly differentiated from the leaves in the tree species (Oliver 1928), especially in the massive New Caledonian *D. involucratum* Brongn. & Gris. comprising subgen. *Cordophyllum* W.R.B. Oliver. Here the inflorescence is a 40 cm long spike, with flowers borne in dense fascicles each on a separate pedicel/peduncle covered with numerous bracts. The opposite morphological extreme is shown by the prostrate mats and cushions of subgen. *Oreothamnus* (F.v.Muell.) Oliver with terminal, solitary flowers, especially *D. muscoides* Hook.f. (southern South Island New Zealand) and *D. minimum* F.Muell. (Tasmania). In these dense, hard 'cushion plants' only a few centimetres in diameter, the leaves are very small (2–3 mm long in *D. muscoides*) and the bracts are very similar. As Oliver (1928) perceived: 'Each flowering peduncle [in *Cordophyllum*] might be compared with a separate branch of such a species as *D. minimum*'.

Pachynema DC. (Dilleniaceae) comprises xerophytic, broom-like shrubs of northern Australia and is usually affiliated with *Hibbertia* Andr. Beyond the seedling or coppice stage the often flattened stems are leafless but bear bracts. Some species have rhizomes, which occur elsewhere in the family only in *Acrotrema* Jack (Sri Lanka, southern India, Burma and Peninsular Malaysia).

Craven and Dunlop (1992) observed that: 'Unlike the other genera of Dilleniaceae, *Pachynema* rarely exhibits a distinct vegetative phase followed by a distinct flowering phase or inflorescence … The presence of basal, functional leaves in three species … suggests to us that perhaps the bracts on the aerial stems may not represent reduced leaves on a vegetative stem but may be equivalent to the inflorescence bracts described for other genera, e.g. *Dillenia* (Corner 1978b)'. The aerial stems (above the short leafy section if present) are interpreted by Craven and Dunlop 'as elaborate inflorescences which have been modified into largely non-flowering, 'vegetative' stems'. The morphogenetic relationship between *Dillenia* and *Pachynema* is the same as that between the large- and small-leaved taxa of *Dracophyllum* compared by Oliver (1928).

The branches of *Ginalloa* Korth. and *Notothixos* Oliv. (Visc.) bear both normally developed leaves and rudimentary cataphyll-like ones, often in successive pairs, but in *Ginalloa* the pattern is more variable, and some species bear very few normal leaves (e.g. *G. nuda* Danser, a Kinabalu endemic) (Barlow 1997). Inflorescence bracts in these plants are small and arranged in pairs forming a boat-liked cupule (like the rudimentary leaves), and these bract-plants may have a similar origin to those already cited.

Three lepidocaryoid palms have flagelliform inflorescences which can develop as individual plants. The inflorescences are up to 2 m long and the ultimate branches lie on the surface of the soil (Dransfield 1978) where they take root and grow a new shoot. This eventually becomes established as a separate plant.

In the *Hebe* complex (Scrophulariaceae), Bentham (1846) compared the habit of the ericoid, whipcord hebes with that of *Andromeda* and *Cassiope* species. The ericoid hebes (*Leonohebe* Heads) have been interpreted as the equivalent of sterilised inflorescences of the large-leaved, orthotropic *Hebe* (Heads 1994a). The ericoid *Olearia* sect. *Divaricaster* Heads (Compositae) and the small-leaved *Coprosma* J.R. & G.Forst. (Rub.) species also differ from their large-leaved relatives in similar ways: plagiotropy, determinate long shoot axes, and differentiation of brachyblasts. They have been interpreted in the same way as the plants in the *Hebe* complex (Heads 1996, 1998).

Frankeniaceae and Tamaricaceae are sister families in the otherwise mainly insectivorous clade which is sister to Centrospermae (Savolainen et al. 2000). They are both heath-like shrubs centred in Africa and Eurasia (they are absent in Malesia) and favour sandy or salty places, both maritime and inland. *Frankenia* L. has leaves with inrolled margins like *Erica* and bracts which are no different from the leaves. *Tamarix* L. also has scale-like leaves and bracts but in addition has more mesophyllous 'juvenile' foliage like that of *Leonohebe* and certain Cupressaceae (Heads 1994a).

Summing up, dwarf shrubs, whether coastal or alpine, are often not simply miniature trees. Their whole morphology is different and closely related plants such as *Erica* and *Rhododendron* can have quite different architecture, leaf and bract morphology, and 'inflorescence structure. Perhaps it is simpler for the plant to change into an 'inflorescence-' or 'bract-plant' than for the whole plant to be miniaturised.

It may be relatively simple morphogenetically to suppress the large-leaved part of a shoot, leaving only the inflorescence, possibly with a few residual ('juvenile') leaves basally. It may also be relatively simple to sterilise a large part of this 'inflorescence-plant', leaving only the scales over most of it and restricting flowers to (usually) branch tips. The result is a microphyllous, xerophytic shrub with all the ecological adaptability of this life form, and able to survive in many extreme environments.

There is abundant other evidence from the Ericales suggesting evolution of architecture by the suppression and sterilisation of parts. For example, everyone agrees that the typical umbelliform *Rhododendron* inflorescence is a condensed structure, evolved from an earlier racemose arrangement as seen in many Vaccinioideae. The 'telescoping' in the flower of *Erica* (*'Philippia'*) was mentioned above. In some epacrids Watson (1964) pointed out that at least the distal bracts are aborted inflorescences, recalling epiphyllous inflorescences in *Chisocheton* Bl. (Melia.), Flacourtiaceae tribe Phyllobotryeae and others. Oliver (1991) also recorded clear evidence for reduction and fusion in floral parts in *Erica*, especially in the former minor Cape genera.

The different forms of scales and hairs on the leaves of *Rhododendron* seem to characterise large geographic and phylogenetic groups, but their history in the evolution of the leaf is unknown. These structures and others, such as the glands at the base of the lamina in *Vaccinium* and *Dimorphanthera* species, and the laticiferous system in *Roridula*, may not be superficial, secondary features, added on to an otherwise fully-evolved leaf or shoot, but rather relictual traces of prior, largely suppressed morphology and physiology. This agrees with Schwendt's (1907) important general concept of a gland as a region of hemmed-in growth.

* Malesian Ericaceae include the whole sequence from densely branched cushions (148: *Rhododendron saxifragoides*) and prostrate mats to decumbent shrubs, scandent shrubs/lianas (*Dimorphanthera*, 3: *Vaccinium fissiflorum* Sleum., etc.), and erect shrubs and trees (*D. pulchra* J.J.Sm. is a small tree up to 15 m high in primary forest). Species cited as 'hemi-epiphytes' (Sleumer 1967: Fig. 115) begin life as epiphytes, but by sending roots down the host tree may reach the soil and become terrestrial as lianes.

A number of Ericaceae species may be erect shrubs, trailing shrubs, or vines, depending on the habitat. All of these may be epiphytic or terrestrial. In 'moss forest' (often there are more liverworts) the plants often grow on more or less dead, half-fallen tree-trunks, and here the distinction between epiphytic and terrestrial wears thin. Authors like Parris (1983) distinguish three main habitats for plants in these forests, rather than two: epiphytic, terrestrial and rupestral. The distinctions between these mainly involve light and drainage.

In Ericaceae, Hallé et al. (1978, citing Temple 1975), recognised the architectural models of Holttum (*Dracophyllum*), Leeuwenberg (*Dracophyllum, Erica, Rhododendron, Pieris*), Scarrone (*Arbutus, Rhododendron*), Rauh (*Styphelia, Erica, Calluna*), Mangenot (*Vaccinium*), and Troll (*Leucothoe*). A liane species of *Pieris* had no known model. Numerous southern African Ericoideae species examined in the wild proved difficult to assign clearly to any known models (A.Temple pers. comm., cited in Oliver 1991).

*** Species numbers given here follow Sleumer's *Flora Malesiana* treatments and are cited to allow easy reference to the large genera in Sleumer's work and to the maps below.**

Stevens (1981) observed that many, if not all, *Rhododendron* species and also *Gaultheria pullei* have architecture conforming to Leeuwenberg's model. Scarrone's model differs from this only in its monopodial trunk and is common in Ericaceae, and intermediates between the two models occur. Many other New Guinea Ericaceae are similar but also show abortion of the shoot apex. Sleumer (1967) illustrated this in *Diplycosia pinifolia* and *Vaccinium leptospermoides*, and it also occurs in *Gaultheria*, *Dimorphanthera* and *Agapetes* (Stevens 1981). The lianoid species (?Champagnat's model) also have determinate shoot apices. Vaccinioideae in general tend to share abortion of the apical buds of the vegetative shoots (Kron, Fuller et al 1999) and *Rhododendron* axes are determinate by flowering.

In *Rhododendron*, Asian species vary from trees up to 20 m tall with a trunk 60 cm diameter (Noshiro and Suzuki 2001) to small shrubs 5–10 cm tall. In Malesia plants are usually 1–2 m high shrubs, sometimes small trees up to 12 m tall (e.g. sp. 249: 1–12 m New Guinea; sp. 251: 6–15 m Kinabalu; sp. 278: 3–12 m Malesia). Many species grow to 6 m tall. Species 23 is a 'small crumpled tree' with a trunk c. 35 cm d.b.h. Sp. 225 has a 'writhed' trunk, as seen in Asian species and recalling liane stems.

In the models of Leeuwenberg, Scarrone and Rauh all axes are orthotropic. However, plagiotropy is evident in Ericaceae with spreading and decurved branches (e.g. *Vaccinium varingiaefolium*), and is widespread in epacrids such as the mat species of *Dracophyllum*. Plagiotropy is absent in many *Rhododendron*, but present in the dwarf, spreading forms, which are epiphytic (140: *R. caespitosum*, forming 10 cm high cushions on tree fern trunks in alpine grassland, branches rooting), sprawl over rocks (139: *R. gracilentum*), or are cushion plants in alpine peat-bogs (148: *R. saxifragoides*). In Malesia, smaller *Rhododendron* species include dwarf shrublets of the Latimodjong Range (33), Mt. Kinabalu (19), and Irian Jaya (102) which may be decumbent (142, 147, 152, 153). Other smaller species also show marked plagiotropy: sp. 5 is a 5 cm to 1 m tall xerophytic shrub, prostrate on limestone at Wilhelmina, 139, 10–60 cm, is subprostrate and also recorded from limestone and other prostrate or creeping species include: 8, 53 (on limestone), 137 (5–10 cm high).

The presence of rhizomes, an aspect of plagiotropy, is an important polyphyletic trend in the Ericaceae. In Malesian species rhizomes occur in *Rhododendron* (*R. anagalliflorum*), *Pyrola*, *Gaultheria*, *Vaccinium*, *Agapetes*, and *Diplycosia* (mostly in open, high altitude grasslands) (Stevens 1981). In *Erica* there are also prostrate marsh forms with rhizomes (Oliver 1991).

How can the presence of both orthotropy and plagiotropy in the same lineage be rationalised morphogenetically? Many plants, for example palms, whose stems are otherwise purely orthotropic show striking plagiotropy in their inflorescences, and plagiotropy may be another feature inherited by bract-plants (cf. plagiotropic axes in divaricate *Coprosma*, Heads 1996).

The smallest *Erica*, *E. petrophila* L.Bolus (SW Cape), is 100 mm tall and covers only 400 mm in cracks on large boulders or rock faces. Other *Erica* species grow on damp rock ledges and form moss-like matted plants (*E. physophylla* Benth., *E. ophylla* Benth.) (Oliver 1991). Plagiotropy is often associated with limestone, and the plagiotropy may have been inherited from mangrove-associate ancestors.

Another aspect of plagiotropy is seen in the 34 *Rhododendron* species described by Sleumer as having 'divaricate' branches. Other *Rhododendron* species have more or less sprawling or scandent divaricate branches (46, 51, 79, 109, 135, 136, 138, 255). 'Corymbose' architecture is seen in the flat-topped shrubs of 165 (Sleumer 1966: Fig. 35) and *Gaultheria* 11 (Sleumer 1967: Fig. 64).

'Divaricate shrubs' is a term used universally in New Zealand for plants with a very specific architecture in which brachyblasts are differentiated and apex abortion occurs in the long shoots, giving 'cymose' architecture (e.g. *Olearia* sect. *Divaricaster* (Compositae) (Heads 1998a), many *Coprosma* spp. (Rubia.) (Heads 1996)). Plants with this syndrome are 'bract-plants' (above), and are especially abundant in southern and east Africa and Madagascar. As noted above, many Malesian taxa have the shoot-tip abortion which is always present in the New Zealand-African 'divaricates'. Unlike these plants, however, Malesian Ericaceae show no sign of brachyblast differentiation. Some South African ericas do show differentiation of brachyblasts (e.g. *E. ribisaria* Guthrie and Bolus) and in general the New Zealand–African 'divaricate' plants and ericoids are 'bract-plants' (see above/below) like Ericoideae, unlike most Rhododendroideae, despite their divaricate branching.

The root system of Malesian Ericaceae, particularly in crater fields and near solfataras, is very horizontal, and roots may attain large dimensions in such places. This is of course common to all plants growing on sterile, rocky, impervious or badly drained soils. Such roots also have a distinctly corky bark (Sleumer 1966).

The hypocotyl and lignotuber

Swollen stem-bases and adjacent roots, developed from the hypocotyl and capable of storing water and resprouting occur in many Ericaceae. Describing the California chaparral, where resprouting species of *Arctostaphylos* Adans. are important, Wells (1969) noted that the habit is generally regarded as a specialised trait, evolved in response to fire as a selecting agent. However, he concluded that 'The truth of the matter is that the capacity to sprout vegetatively from older wood, stumps, or underground parts following destruction of the tops by fire is a widespread and probably ancestral trait among angiosperms.' In Malesia crown-resprouting is important, especially in epiphytic species of *Vaccinium* and the related genera *Agapetes, Costera* and *Dimorphanthera*. Thickened roots occur in *Rhododendron*, e.g. 52 (Sleumer 1966: Fig. 12), 152, 168, 205. The thickening often 'superficially resembles a lignotuber' (Sleumer 1966) with several stems arising from it and heathland species in general often have lignotubers (Specht and Womersley 1979). Lignotubers, root-crowns, or burls are enlarged, bulbous structures formed by the root-shoot 'interface tissue', and equivalent to xylopodia (Brazil), souches (France), and toucas (Portugal). These are well-known in *Erica arborea* as they are used for making pipes, and *Rhododendron* or *Kalmia* burls in North America can weigh more than 200 kg. Malesian species like *Vaccinium varingiaefolium* and *V. striicaule* in particular persist after fire because shoots develop from the root crown. Sleumer (1967 Figs. 72, 75, 99) illustrated *Diplycosia* cf. *kinabaluensis* (from temporarily inundated rocks), *Diplycosia* 65, and *Vaccinium* 114 with a swollen hypocotylar bases and thickened roots.

In the Ericoideae the vast majority of species regenerate only from seed after a veld fire — fewer than 10% of *Erica* species in the Cape Floristic region resprout from a lignotuber, although this is common among Euro-Mediterranean species (Ojeda 1998). Ericaceae species in Malesia also have igneous and pioneer ecology, but there are no comparable figures for resprouting species vs. seed reproducers. In the Cape, the highest number of resprouters occurs in the eastern Cape, while the lowest is in the SW Cape. Lignotubers occur in the widest ranging South African *Erica* (*E. cerinthoides* L.) and a very few others. The few that resprout do so at ground level from 'swollen stem bases or root stocks referred to as burls or lignotubers ... In the Cape species this lignotuber may reach up to 100 mm in diameter for plants only 150 mm tall. In the very variable *E. coccinea* most forms only regenerate from seed, but the form occurring on the limestone flats near Agulhas is a resprouter ... ' (Oliver 1991). *Erica trichostigma* Salter, of sandveld, 'produces a number of stems from a common root underground' (Schumann et al. 1992).

The hypocotyl is morphologically intermediate in structure as well as position between shoot and root. However, in addition to the well-known variation giving rise to epigeal and hypogeal germination it develops in many ways and may represent something more than simply a transition zone.

In a typical 'pan-adaptationist' view (the dominant paradigm at least in the Anglophone countries) it has been argued that 'the purpose of lignotubers in neotropical Ericaceae appears to be for the production of buds ... ' (Luteyn 2002). However, plant structure is not accepted here as having evolved because it has a 'purpose'. Rather, a particular series of biological structures, with some 'adaptive' and some 'neutral,' is the result of prior structural trends. Luteyn (2002) also suggested that lignotubers 'probably also provide an advantage to new seedlings', but any 'advantage' is interpreted here strictly as a secondary consequence of the primary morphogenetic trend.

The main trends in hypocotyl morphology which may have led to the ericaceous hypocotyl/lignotuber and the consequent ecology, can be indicated with a summary of variation in the hypocotyl of the angiosperms.

The hypocotyl takes many different forms. In African Caesalpinioideae the following variations occur in the seedling at germination (Léonard 1957):

- the hypocotyl may lengthen or not;
- the stem/root axis may be central or lateral to the cotyledons;
- the collet or collar at the hypocotyl/root junction may or may not bear an 'appendix' — a ring-shaped lateral spur.

The different combinations of these three features characterise the different genera. Léonard (1957) also emphasised the importance of the hypocotyl in other plants, such as in *Hura* L. and *Dichostemma* Pierre (Euphorbiaceae) in which it grows to 20 cm long while the cotyledons remain in the testa, as in mangroves.

The hypocotyl in subtribe Myrtinae (Myrtaceae) may be greatly swollen, rendering interpretations of embryo morphology in these plants controversial (Landrum and Stevenson 1986). At the lower end of the hypocotyls, ring-shaped protuberances, often bearing absorbing hairs, occur in *Myrtus* L., *Leptospermum* J.R.& G.Forst., *Melaleuca* L., *Callistemon* R.Br., and *Angophora* Cav., and these even take the form of bizarre 'coleorrhizae' enclosing the radicle in *Eucalyptus* L'Hérit. (Baranov et al. 1955, Baranov 1957). Baranov cited the last as 'the full expression' of the trend, but even this may be a largely reduced relic. Baranov cited a similar expanding hypocotyl base in the mangrove *Bruguiera* Lam. (Rhizophoraceae).

Caesalpinioideae, at least co-dominant in most woodlands and forests of Africa, and the mallee *Eucalyptus* species, dominant in many parts of Australia, are characterised by lignotubers that begin to develop at the seedling stage. In *Eucalyptus* these usually develop at the top of the hypocotyl in the cotyledonary axils, as in *Quercus* (Molinas and Verdaguer 1993a,b), but they may also develop from the hypocotyl below the cotyledons (Kerr 1925). The varied forms of xylopodia developed by cerrados plants in South America are similarly effective in achieving drought resistance.

The trunk of the frankincense tree (*Boswellia* Colebr. spp., Burseriaceae) of northern Somalia, Yemen and Oman has a basal swelling which often, especially in rock-inhabiting plants, forms a ± disc-shaped plate up to 70–80 (–100) cm in diameter (Thulin and Warfa 1987). This develops at a very early age and is initially almost entirely confined to the hypocotyledonary region.

The many other possible outcomes of hypocotyl development include the following.

The viviparous axis of the mangrove seedling is well-known for its precocious development and is generally interpreted as hypocotyl, although in these plants it grows geotropically.

In the aquatic family Podostemonaceae Schnell (1970) wrote that there is no true root, instead haptera and rhizoids develop from the hypocotyl.

In Madagascan Hydrostachyaceae, also aquatics, studies of seed germination showed an important development of the hypocotyl as 'a sort of rhizome' (Koechlin 1967).

The seedling of *Streptocarpus* has a hypocotyl which ends at the base in an enlarged disc. This produces a crown of rhizoids (Rhizoidenkranz) before eventually elongating to form a central root (Schenk 1942).

The seedling of *Elatine hexandra* (Elatin.), a plant of periodically submerged mud, develops a ring of 'prop-hairs' or 'prop-roots' to form a skirt-like flange at the base of the hypocotyl (Salisbury 1967).

In *Phylloxylon* Baill. of Madagascar (Papilionoideae) the cotyledons are fused, and this involves the disappearance of the apical meristem; growth takes place instead from adventitious buds on the hypocotyl axis (Peltier 1970).

In *Cucurbita pepo* L., the marrow, the withdrawal of the cotyledons from the seed is aided by the development of a 'lateral outgrowth or peg' fom the lower surface of the hypocotyl (Purseglove 1988). A similar 'talon' occurs in other Cucurbitaceae as well as in *Mirabilis* L. (Nyctaginaceae). Likewise, in *Scabiosa* L. (Dipsac.) a 'thickened, projecting ledge' at the base of the hypocotyl pins the involucel to the ground at germination (Lubbock 1907).

In *Marah* Kellogg (Cucurbit.) the cotyledon petioles emerge from the seed fused into a single tube which bears apparently functional absorbing hairs on its outer epidermis. This tube flares out at the base into a 'flange-like cap' (Hill 1916).

In *Hippuris* L. (Hippurid.) 'there is considerable divergence of opinion as to the meaning and function of the ring of hairs produced at the collet.' (Good 1924).

A swollen zone in the hypocotyl and other 'geophilous features' occur at the root/shoot collet in Sapotaceae (Smith 1909).

In *Linaria* Mill. (Scroph.) the hypocotyl proliferates by means of buds which eventually grow stronger than the primary stem. The seedling can still grow by this means even if the top of the hypocotyl and the cotyledons are removed after germination (Lubbock 1892). Likewise, in the South African *Galopina* Thunb. (Rub.) innovation shoots develop from accessory cotyledonary and hypocotyledonary buds (Puff 1986). At first these grow plagiotropically underground, later they become ascending.

In the rainforest trees *Garcinia, Barringtonia* and *Anisophyllea* both cotyledons and endosperm remain undeveloped, the storage function being undertaken by the hypocotyl alone (Ng 1978).

In southern African *Eriospermum* (Eriospermaceae) the hypocotyl forms a globose or irregularly-shaped perennating tuber, sometimes bearing a proliferation of 'rhizomes' or 'stolons' (Perry 1994).

Hypocotyledonary tubers are also a feature of herbaceous Aristolochiaceae growing in seasonal climates (Huber 1993).

'Macropodous' embryos with a conspicuously swollen radicle or hypocotyl occur in several basal families of monocots (submerged aquatics in Alismatiflorae, and several Araceae) (Dahlgren and Clifford 1982).

In the Loranthaceae Bhatnagar and Johri (1983) reported that there is no true radicle and the 'radicular end' represents the hypocotyledonary extension. This may bear a 'fringe of lateral processes including hair-like structures'. In *Viscum* (Santal.) (Sallé 1983) and *Amyema* (Loranth.) (Calder 1983), the swollen, glandular meristematic apex of the hypocotyl bends towards the host and when it touches flattens to form an adhesive 'attachment disc' or 'holdfast' (developing into the first haustorium; cf. Barlow 1997).

Hypocotyl variation can have a geographic basis: American material of *Vigna vexillata* (L.) Benth. (Legum.) has epigeal germination in which the hypocotyl elongates, while Old World material of the same species has hypogeal germination in which the hypocotyl does not elongate (Vanderborght 1989).

The epiphytic 'ant-plants' in *Hydnophytum* Jack, etc. (Rub.) have characteristic large, rooting, aerial tubers formed from the hypocotyl and often covered with spines, probably aborted rootlets (pers. obs.). Labyrinthine cavities in the tuber house the ants. For Schnell (1970) these bizarre plants are 'incontestably very evolved, the last word, the most perfected', but instead the tubers may be just another one of a range of alternative possibilities in hypocotyl development.

All these different phenomena are points in a series, quite different morphologies but aligned on a single morphogenetic trajectory. The different structures may enhance the ability to survive in different environments, whether aquatic, terrestrial, arid, epiphytic or parasitic. However, each particular morphological 'adaptation', whether the disc of frankincense, the holdfast of the Loranthaceae, the talon of Cucurbitaceae, the tuber of the ant-plants, the 'rhizoids' of the Hydrostachyaceae, or merely, as in most plants, a slightly thickened or coloured 'collet' at the hypocotyl base, is a secondary consequence of the underlying morphogenetic trend in hypocotyl development.

These particular morphologies have important ecological consequences, for example in woodlands of America, Africa and Australia, aquatic communities in southern Africa, and Ericaceae–Myrtaceae heath communities and epiphyte communities in Malesia. These are all occupied or dominated by 'hypocotyl plants' with lignotubers and/or thickened stem bases. Perhaps the thickening of the hypocotyl/lignotuber represents the last trace of what was a well-developed system of hypocotyledonary rhizoids and more elaborate organs formerly widespread in seed-plants.

Ericaceae ecology

Ericaceae are well-known as plants of cold, high places, where the soil is acid and infertile. Ericaceae have endotrophic mycorrhiza present in their root cortex which at least partly explains their ability to survive on soils poor in nutrients, especially nitrogen and phosphorus. The peculiar mucilaginous sheath which surrounds the root-tip in Ericaceae (Leiser 1968) may also be ecologically significant. Ericaceae are usually characteristic of well-drained rocky sites: Malesian *Rhododendron* occur in sandy and rocky sites, on moss-covered rocks, rocky ridge-crests, white acid sand, clay, open gravelly or clayey ground of old gold workings, sluiced areas, edges of precipices, exposed summits (e.g. 119, 123), crevices in granite (e.g. 19: granite fissures to the very top of Mount Kinabalu, 4096 m), and cliffs (e.g. 157: *Vaccinium horizontale*).

However, Ericaceae also occur in other habitats. Monotropideae s.s. are without chlorophyll and are totally saprophytic; and they are also mycorrhizal. They live on the forest floor in full shade. Other taxa occupy a wide range of sites: hot or cold, well- or poorly-drained, and in acid or basic soil.

Malesian Ericaceae species are often gregarious terrestrially on steep slopes and ridge crests, volcanic terrain, glades and other sterile places in the mountains (Sleumer 1966). For example, on Mt. Kerinci above 3000 m there is a brushwood consisting largely of of *Gleichenia, Vaccinium miquelii, Rhododendron retusum* and *Gaultheria leucocarpa*. On volcanoes in Bengkulu *V. miquelii* can have a diameter up to 40 cm. Sleumer (1966, 1967) described similar communities from Kinabalu, W Java (*R. retusum, V. varingiaefolium*) and New Guinea (*R. brassii, R. inconspicuum, R. herzogii, R. christianae, V. dominans*). Sleumer (1967) cited species of *Vaccinium* which may form pure stands or even vegetation-belts in the upper montane zone, and Archbold et al. (1942) illustrated the interior of closed subalpine *Vaccinium* forest at Lake Habbema.

Gardeners cultivate vireyas in conditions which recreate a tectonic setting of well-drained areas such as alluvial terraces around peaty swamp forest in regions of uplift and vulcanism, and a climate with high atmospheric moisture and free movement of air. Good drainage and a very open potting mix are essential. Materials such as tree fern fibre, pine bark, coarse river sand, and scoria all help to keep the mix open, while use of peat-moss and leaf-mould open the soil up and also help retain moisture. At Kew, vireyas are grown in an open mixture of two parts coarse peat and one part coarse sand or grit, to which some charcoal has been added (Halliday 2001).

Specht and Womersley (1979) wrote that Malesian Ericaceae s.l. occur in the following oligotrophic environments: 1. Tree crowns, 2. Forest floor, 3. Breaks in the rainforest (tree fall gaps, landslides and man-made clearings) as pioneer plants, 4. Above the timberline, in the alpine zone, and 5. Low altitude kerangas and padangs. These provide useful headings for further notes, as follows.

1. Tree crowns

Vascular epiphytes, especially shrubby epiphytes, are a distinguishing feature of rain forest (Richards 1952). Richards interpreted the structure and ecology of epiphytes (and most other rainforest plants) in terms of pre-adaptation. He argued that epiphytes' extraordinary specialisations 'may not be adaptations which have evolved by gradual modification in the habitat the plant now occupies' and cited rainforest Bromeliaceae inheriting absorbing hairs from arid-dwelling ancestors. Richards concluded that 'The plants from which the epiphytes arose were thus 'pre-adapted' and families without the required preadaptations, such as legumes with their heavy seeds, have simply not given rise to epiphytes.'

One of the key preadaptations of Malesian Ericaceae for life as epiphytes is the thickening of the hypocotyl, permitting water storage and resprouting.

One of the features of the Malesian Vireya rhododendrons that struck botanists when they were first described is that so many are epiphytic, growing high on forest tree limbs with mosses and orchids (Withers 1984). Sleumer (1966) recorded the following species from primary ('primaeval') forest, and these are mainly epiphytic: *Rhododendron* spp: 22, 23, 25 var. 11, 46, 73, 150, 154, 213, 223, and *Vaccinium* 221 ('virgin forest'). In the vaccinioids, *Gaultheria* is exclusively terrestrial while its close relative *Diplycosia* is predominantly epiphytic. Many species of *Rhododendron* will grow in either situation. All species found growing as epiphytes have been found growing as terrestrial plants, but a number of terrestrial species have never been found growing as epiphytes. Vireya rhododendrons grow as terrestrial plants in open habitat, but when growing in dense forests in competition with other trees they occur as epiphytes, as they require high light levels and tolerate rapid drainage.

At and above tree-line a 'heathland' high in the trees descends to the ground (Fig. 5), with associated plants such as ant-plants (Hydnophytineae, Rubiaceae); ant-plants are terrestrial only above the tree-line, and this only occurs in Irian Jaya (An exceptional new, undescribed species of *Hydnophytum* from Mt. Michael breaks both rules by being terrestrial in forest and in PNG (M. Jebb pers. comm.)).

In *Nepenthes*, 12 Malesian species are recorded from both epiphytic and terrestrial sites (Cheek and Jebb 2001), and of these sp. 46. is noted as terrestrial in thin woodland, 44. is terrestrial in swamp grassland, ridge tops, open forest on white sand, and ultramafic soils, and 38., the highest *Nepenthes*, is terrestrial in alpine scrub and grassland in Irian Jaya.

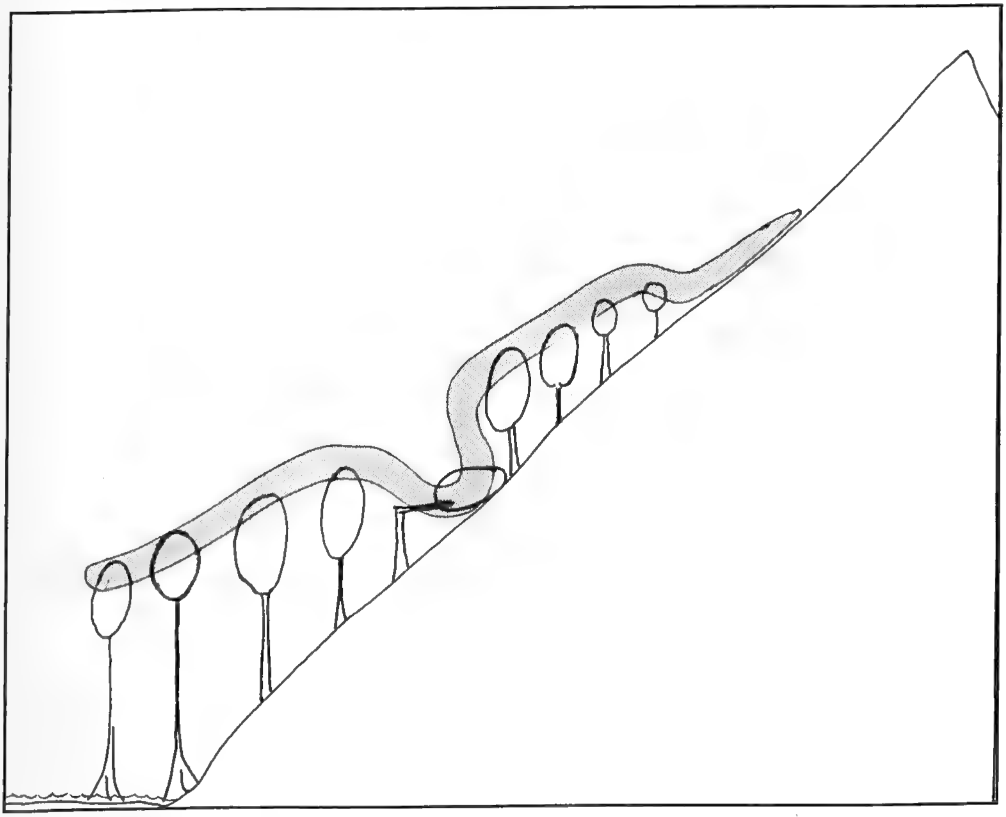

Fig. 5. Ecology and altitude in Ericaceae, ranging from epiphytic in mangrove to terrestrial in forest gaps and above tree-line.

The habitat of epiphytes is similar to that of plants growing on rocks, and several species of *Rhododendron* occur as epiphytes and also terrestrially on rocks. Other epiphytic-terestrial transitions are seen in the following *Rhododendron* species:

9: generally epiphytic, but also terrestrial in swampy (i.e. open) shrub-covered places, or in alpine scrub.

37: epiphytic just below true moss forest, terrestrial on edge of cloud forest.

51: epiphytic in moss forest or on tree ferns in grassland, terrestrial in more open *Nothofagus*, *Podocarpus*, and *Pandanus* forest, along banks of creeks, edges of bogs, natural or artificial clearings, landslides, cliff faces.

54: high epiphyte in *Castanopsis / Nothofagus* forest, terrestrial in openings or grassy slopes.

71. (*R. truncicolum* Sleum.): epiphytic on giant emergent trees of *Araucaria cunninghamii*, terrestrial in open vegetation on sandy, riverine flats and sharp ridges (Stevens 1981).

112 (cf. 115): epiphytic in rather dense forest, terrestrial in more or less open, devastated *Nothofagus* summit forest or scrub.

131: epiphytic in ridge forest, terrestrial in kerangas and elfin woodland,

176: epiphytic in moss forest, terrestrial in open places on moss cushions.

172: epiphytic in low forest, terrestrial in shrub vegetation.

139: epiphytic in *Nothofagus* forest, terrestrial on old gold workings.

250: epiphytic in primary forest, secondary forest and mangrove, terrestrial on rocks, in kerangas etc.

Diplycosia 92: is epiphytic in mossy low forest, terrestrial on open serpentine ridges.

In *Vaccinium* the following are all epiphytic, but terrestrial in the named habitats: 10, 27: on limestone, 21: on boulders, 57, 58: on open ground with rocks, 73: amongst grass in moist places, 132, 139: on rocks, 157: growing horizontally from eroded cliff face, and 204: at forest edges.

In *Dimorphanthera* (Stevens 1981), 28: at 850 m is epiphytic, at 1200 m is a high climbing liane in oak forest, and at 2150 m is a shrub in mossy forest/dense scrub.

D. amplifolia is epiphytic at lower altitude, terrestrial in subalpine forest on peaty soil.

Similar patterns of epiphytic/terrestrial habitat are seen in *Grammitis* (Parris 1983), in which otherwise epiphytic species are terrestrial on limestone, boulders in streams and (again, usually rupestral) in subalpine–alpine shrubland and grassland.

2. Forest floor in closed forest

This is an unusual environment for Ericaceae, but is occupied by the two saprophytic genera.

3. Breaks and open places in forest

Malesian *Rhododendron* species are recorded from low, light, or thin forest, *Casuarina* forest (sp. 92), degraded or devastated *Nothofagus* forest, ridge-crest forest, stunted/dwarf forest, dense subalpine forest, mossy forest (i.e. low and well-lit): dwarf mossy forest, light moss forest, moss cushions of old fallen trees, rotten stumps, open banks of streams in mossy forest, shrubby openings in forest, elfin woodland, and forest edge (Sleumer 1966, 1967).

4. Above the timberline

Several *Rhododendron* species occur on exposed rocky bluffs in open grassland (e.g. 96), in alpine grassland and in subalpine shrubland (e.g. 142). *Rhododendron* species are also recorded from other kinds of shrubland: low dense shrubland, scrub-forest, heath plains, and in open mossy thickets on exposed ridges,

5. Low altitude kerangas and padangs

Rhododendron spp. are recorded from low, scrubby kerangas vegetation on bare sandstone eroding into white sand (25 var. 9, 131).

Ericaceae as weeds of active margins

In addition to the habitats listed above, Ericaceae are characteristic in several habitat types associated together at active margins.

1. Secondary grassland and forest

Neotropical Ericaceae are often found in disturbed sites such as recent landslides, or in disturbed habitats created by man (Luteyn 1989, 2002). Likewise, many Malesian Ericaceae occur in secondary vegetation. Habitats include land-slides, old gold workings, high road banks (*Rhododendron:* 182, 198, 201), earthen cliff faces, land-slides ... heath, infertile sandy or clayey soil; fern regrowth, sluiced areas or gullies in old gardens (31: *R. herzogii*), *only* in secondary vegetation (201), moss forest, also open sunny places and landslides (227), *Miscanthus* regrowth (*Dimorphanthera:* 4), 'blukar' (secondary) and grass vegetation (*Vaccinium:* 116), steep road cutting, old gold working (*Vaccinium:* 163), 'ladang' - land cleared for farming, shrubbery or fern scrub (*Vaccinium:* 195). *Rhododendron:* 232 is a locally endemic (Wissel Lakes) weed: 'secondary forest, locally common'.

242. *R. macgregoriae* is fairly common and locally abundant in primary forest, secondary brush, *Imperata* grassland, dry sunny sites, along creeks, on precipitous stream banks, landslides, formerly cultivated land, invading artificial clearings (airstrips), and on sand, peaty or stony soil, clay, and limestone.

2. Volcanoes

Many *Vaccinium, Rhododendron* and epacrid species in Malesia are closely associated with active or recently active volcanoes and their highly disturbed environs. Approaching almost every crater or solfatara field in Sumatra, Java and the Lesser Sunda Islands the percentage of the Ericaceae component increases, and they are among the plants which come closest to the sulphur vents. *V. varingiaefolium* is also able to withstand partial burial by acid volcanic mud. To a certain extent the Ericaceae may also be fire resistant (e.g. pure stands of 3–4 m high *R. vanvuurenii* in pyrogenous grassland in the Latimodjong Ra.).

This igneous ecology is also seen elsewhere. Neotropical Ericaceae are also frequently found near the craters of volcanoes (Luteyn 1989, 2002). In New Zealand, *Gaultheria oppositifolia* Hook.f., the only member of its genus with opposite leaves, ranges in the North Island in rocky and open places north of a line: Mt Egmont/Taranaki – National Park (Waimarino) – East Cape, to Tarawera, Matamata and Mayor Island, with a stronghold in the Rotorua-Taupo region (Franklin 1962). This distribution is closely aligned with a region (the 'volcanic plateau') dominated by Quaternary and recent volcanic activity of different kinds. Other endemics on the North Island volcanic plateau include taxa in *Parahebe* W.R.B.Oliver and *Olearia* Moench (Heads 1994b, 1998). *Scaevola gracilis* Hook.f. (Goodeniaceae), as revised by Sykes (1998), is endemic to volcanic areas of the same subduction zone further north, being known only from the Kermadec Is. and Tonga. Elsewhere in the Pacific, Ericaceae are endemic to isolated volcanic islands, e.g. *Gaultheria* (*'Pernettya'*) *howellii* endemic at higher altitudes on Mt Crocker in the Galapagos Islands. These species are obviously well-adapted to life around subduction zones and, within their sector, have probably been colonising new volcanoes as they appeared for millions of years — much longer than the age of any individual volcanic island.

In Malesia, *Rhododendron* has the following species recorded at and around craters: 87 (only known from one collection, near a crater in W Java), 92 (crater walls, near solfataras etc.), 98 (dry sulfur stone slope), 125 (on volcanoes, in sandy grit or volcanic soil), 133, 136 (open, rocky places on old, dry volcanic soil, always near solfataras, capable of standing SO_2 this is *R. jasminiflorum*, also known from sea-level in the Sarawak R. delta), 135 (narrow ridge in stunted forest on crater rim (New Georgia), 221, 225, and 267.

Several rhododendrons and *Diplycosia* 13 are recorded in burnt (i.e. open) ridges and summits. Other 'igneous' Ericaceae include *Gaultheria* 2, 10, and 15 in volcanic debris and near active craters and volcanic gases. *Vaccinium* 22 is on mudflows, 110 on stony mud flows, 89 is with *Eucalyptus* near the edge of craters (Timor), 109 on volcanic soil, *Vaccinium* 132 and 228 near cold solfataras, and 169 at crater edges.

Vaccinium 115 (*V. varingiaefolium*, photos in Sleumer 1967) occurs in old craters and on very young volcanic soil. 'It forms the main co-dominant in stands mixed with *Eurya*, *Symplocos* etc. of the subalpine forest on all (or most) Javanese mountain tops, chiefly above 1800–2000 m, not rarely in the form of a belt, growing as a tree in forest with rich humus as well as a shrub in open, extremely stony and rather dry places. It is a pioneer on ashy or volcanic soil of crater ridges, common in the vicinity of solfataras and hot mud-wells, and in such localities it descends to 1400 m [this lower altitude on active volcanoes supports Philipson's ideas, cited above, about survival of plants on oceanic volcanoes]. It becomes a small, more or less prostrate shrub in high, wind-exposed bare slopes up to 3340 m, growing closely appressed to the ground. As a tree it is almost fire-proof; even when the whole trunk is charred, buds at the base of the stem may still sprout, thus holding its ground even in large numbers on mountains which are continually subject to bush fires.' (Sleumer 1967). Sleumer (1967 Fig. 104) illustrated prostrate shrubs in the crater of Mt. Papandajan, caused by the combined action of wind and sulphurous vapours from solfataras and but there is possibly also a genetic component. Studies of cultivated plants would be of interest.

3. Ophiolite/Ultramafic terrane (= ultrabasics, serpentine)

Stevens (1985) noted there are as many as five endemic species of *Rhododendron* from serpentine areas on Doormantop (including the distinctive 2: *R. taxoides*) and three species and one variety are endemic to Cyclops Mts., another area where serpentine occurs. Waigeo I. is an ophiolite terrane and has endemics like *Rhododendron* 160, *Vaccinium* 234. There is also notable bird endemism here (Heads 2002a). Other ultramafic endemics in *Rhododendron* include 157B: *R. rousei* (Argent and Madulid 1998) and 264C (Argent 1998) from the Philippines (177 is endemic to the same mountain as 264C and is probably another ultramafic endemic), and 268D (Argent and Barkman 2000) from Kinabalu. Also on ultramafics are *Diplycosia* 44 and 92, and *Vaccinium* 130 (all on both serpentine and granite), and *Styphelia* 156. *S. abnormis* is at Waigeo and nearby Gebe Islands on red clay with nickel and chrome. Elsewhere, the epacrids *Dracophyllum uniflorum* Hook.f. and *Styphelia nesophila* (DC.) Sleum. (= *Cyathodes fraseri* (A.Cunn.) Allan) are recorded on ultramafics in New Zealand (Mark and Adams 1979).

The New Guinea orogen is characterised by abundant outcrops of ultramafic rocks. The largest of these, the Papuan Ultramafic Belt (Bowutu terrane) covers an area 400 × 40 km and is one of the world's most spectacular ophiolites. It forms a series of subsidiary mountain ranges north of the main ranges of the Papuan Peninsula and its emplacement must have been a major tectonic event.

Botanists have long recognised that these northern New Guinea ultramafics were strong foci of endemism (e.g. *Kairothamnus* Airy Shaw, Euphorb. (Airy Shaw 1980), *Calophyllum streimannii* Stevens, Guttiferae – (Stevens 1974b), *Dioscorea* sp. aff. *nummularia* Lamk. (Johns and Hay 1981), *Freycinetia takeuchii* Huynh, Pandan. (Huynh 2000)), and it was assumed that much of this endemism was due to edaphic rather than historical factors. However, Polhemus (1996) pointed out that many animals show similar patterns and that this correlation greatly weakens the edaphic hypothesis. Instead, Polhemus (1996) regarded the ophiolites as biogeographically significant because they are arc terrane markers. The most mature phase of arc collision is seen in old arc fragments now deeply embedded in modern mainlands such as New Guinea and the Philippines. The remnants of these Mesozoic arc systems have been crushed between even older arcs or continents but have left a biological signature in the disjunct distributions of living taxa.

Like the five *Rhododendron* species endemic there, *Vaccinium* 127 is on Doormantop, a high mountain with exposed ultramafic rock, and also 100 km to the east near Bernhard Camp, on the edge of the vast swamp-forest of the Meervlakte. The three species of the *Grammitis mesocarpa* group are restricted to the same sites (Parris 1983). The two localities might seem to have little in common ecologically, but both are on the Rouffaer terrane (Fig. 6), which consists of the Irian Jaya Ophiolite (Pigram and Davies 1987). Ultramafic rocks are only part of an ophiolite sequence, and with closer mapping 'ultramafic endemics' may prove, as here, to be 'ophiolite terrane endemics', restricted to the terrane and not just ultramafic-derived soils. The vegetation at Doormantop and that at Bernhard Camp represent two ecological aspects of the same terrane. Montane plants of the Doormantop show many dramatic disjunctions, but so do lowland plants such as *Dacryodes* (Burser.), a W Malesian group, known in Moluccas–New Guinea only from one record from the Idenburg R.(Leenhouts 1956).

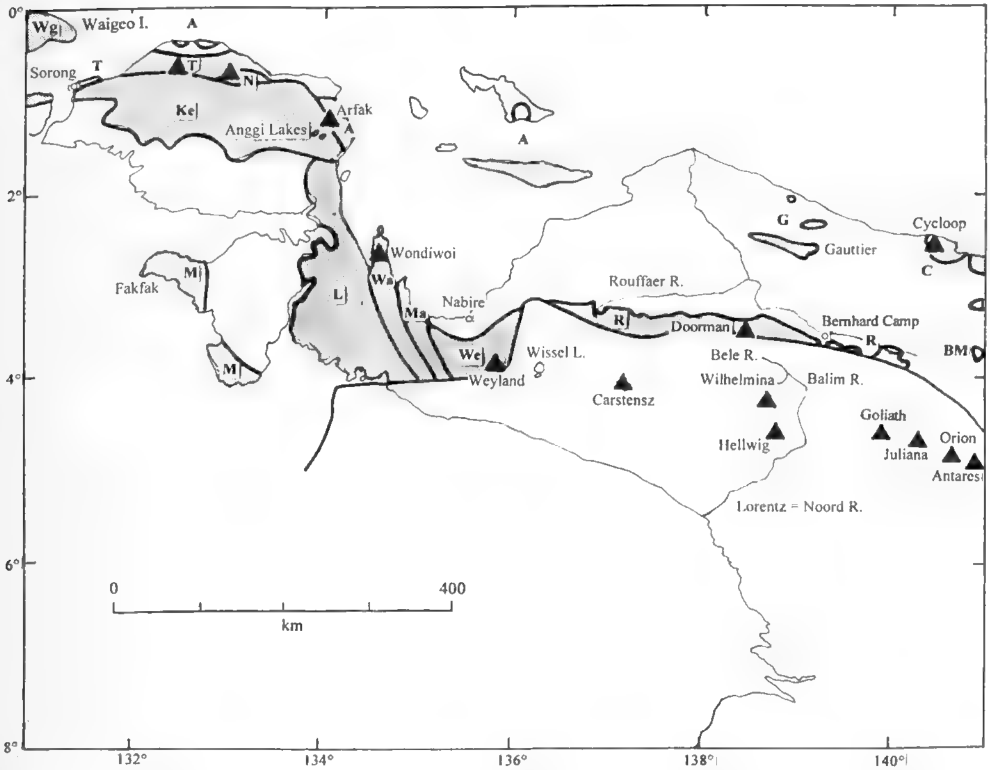

Fig. 6. West New Guinea (Irian Jaya, = West Papua) showing localities mentioned in the text, and accreted terranes (stippled) with abbreviations as follows: Wg, Waigeo; M, Misool; T, Tamrau; N, Netoni (with Nettoti Mts.); A, Arfak; Ke, Kemum; L, Lengguru; Wa, Wandammen; Ma, Mangguar; We, Weyland; R, Rouffaer; G, Gauttier; C, Cyclops; BM, Border Mountains. Former craton margin as heavy line to the south of the accreted terranes (Pigram and Davies 1987).

4. Limestone

Plants which can tolerate basic sites have the potential to be very widespread in coastal areas in the tropics. Uplifted coral reefs and associated coral rubble ('karanas') and carbonate platforms occur throughout the northern coastal areas of New Guinea, for example, as well as further inland. Extensive carbonate sedimentation occurs in tropical waters while colder waters are undersaturated with $CaCO_3$ and shells there dissolve on the death of the organism.

Thoughout the world most Ericaceae appear to be confined to acidic, quartzite- or sandstone-derived soils (Oliver 1991). However, there is a significant number of species recorded on limestone. The collector George Forrest reported the widespread occurrence of rhododendrons overlying limestone in western China, although at the time botanists in Britain took little notice. Kinsman (1998) measured soil pH at limestone sites with rhododendrons in Yunnan, and these were mostly below 6. Most species had their roots in the upper, acid part of the soil. Kinsman showed that in areas like Yunnan with an evenly distributed rainfall a water deficit is never developed and so water percolates downward through the soil profile at all seasons of the year. This water is generally acid through decay of organic detritus, and rainfall itself is acid. The plant is not exposed to the alkalinity of the underlying rock, whereas in areas like Great Britain a net water deficit, and thus an upward flux of water, often occurs.

Nevertheless, Kinsman (1998) found one species, *R. primuliflorum*, commonly anchored into small joints and cracks within the limestone, often hanging precariously off shear limestone cliffs. The plants had generally accumulated a small quantity of organic debris at their base, but even this material had a measured pH of 7.4–7.9.

Luteyn (1989, 2002) cited several Neotropical Ericaceae species on serpentine and limestone, growing in humus filled crevices.

Sleumer (1966) revealed the large number of Malesian Ericaceae species growing on limestone, including 23 species of *Rhododendron* (5b, 22, 30, 34, 39, 41, 50, 51, 53, 67, 72, 80, 95, 102 (stony areas), 105, 137, 139, 148 (Sleumer's 1973 record from 'griky' limestone hill is possibly a misreading of 'slimy'), 183, 204, 214 (abundant on limestone), 240, 242, 250, 255 and 271. 250. *R. longiflorum* and *Vaccinium uniflorum* can grow with some direct contact with bare limestone (Argent 1982). *R. caliginis* Kores (Hindenburg Ra., Victor Emanuel Ra., Laiagam–Porgera; 2400–2850 m) is a rather striking species both in its morphology and 'its apparent predilection for limestone outcrops' (Kores 1984).

Vaccinium species on limestone include: 7, 8, 10 (epiphyte in submontane heath forest, terrestrial on limestone), 16, 26, 27, 51, 72 (dry calcareous soil), 104, 185 (from seashore to 2400 m, epiphyte in mossy forest, terrestrial on rather dry limestone rocks and near solfataras or chalk tuff terraces), 195 (forest; limestone rocks etc.), and 211 (primary forest, limestone).

Dimorphanthera 15 is in primary forest and on limestone, *Dimorphanthera* 33 is 'maybe on limestone ridges' (Sleumer 1967).

In *Erica* most species in southern Africa grow in quartzitic or sandstone habitats, but other species occur on the limestone or at least calcareous ridges of the south coastal plains. In pockets in calcrete there Oliver (1991) recorded a pH of 7.6 near the plants' roots and cited 30: *Erica mariae* Guth. & Bol., 285: *E. oblongiflora* Benth. and species in *Syndesmanthus* Klotzsch and *Thoracosperma* Klotzsch (now treated under *Erica*) as endemics here (the species numbers follow Guthrie & Bolus's 1905 *Flora Capensis* system, used also by Schumann et al. 1992). In Europe species such as *E. carnea* L., *E. multiflora* L. and *E. sicula* Guss. prefer, or are confined to, calcareous habitats.

Erica in South Africa has many species in moist, sandy areas, especially flats, but there are quite a number of ericas which are confined to the limestone/calcified dune habitats that crop up along the coast from False Bay to near Mossel Bay (E.G.H. Oliver in litt. Dec. 2001). Schumann et al. (1992) recorded the following limestone species:

Sp. 29: On limestone hills as well as sandstone ('refuting the generalisation that some erica species grow exclusively on limestone whereas others prefer Table Mountain sandstone.')

Sp. 89: Riviersonderend Range and Caledon, reaching the coast at the limestone hills and flats near Pearly Beach.

Sp. 285: Very localised: limestone hills and stable dunes SW of Bredasdorp on or near outcrops or slabs of limestone.

Sp. 310: Widely distributed on sandy flats, on the Cape Peninsula associated with limestone deposits.

Sp. 311: Limestone hills and flats, sometimes forming dense colonies.

Sp. 399.1: (*E. occulta* E.G.H. Oliver): On rock ledges and boulders in limestone hills near Pearly Beach. The photograph of this 'most extraordinary' erica shows a plant growing directly out of a hairline crack in the bare, vertical rock.

Sp. 418.1: Only in limestone hills around Pearly Beach and nearby Stanford (both in W Bredasdorp District).

Sp. 418.2.: (*E. calcareophila* E.G.H. Oliver): only in limestone hills near Pearly Beach, usually prostrate where it grows on rocks.

Sp. 424: Limestone hills and rocks in the SW part of Bredasdorp District.

Sp. 448.3: Confined to a single reserve in Bredasdorp District: 'Along the shore of De Hoop Vlei [a small lake] it occurs on the limestone cliiffs (calcified dunes), whereas away from the vlei it may be found near watercourses, but still on limestone.'

E. sect. *Gypsocallis* D.Don, as the name indicates, the species occur mainly on limestone, in sandy, sometimes seepage areas.

Many of the calciphilous endemics in the Cape flora have vicariads on adjacent quartzite substrates (Cowling 1983), and this may also occur in Malesian Ericaceae although it does not seem to be documented.

Rouse (1985) noted that most rhododendrons are calcifuges; lime will kill them and lime leaching out of concrete will cause chlorosis. However, Rouse also observed that added calcium appears to improve the health and vigour of small seedlings as well as larger plants of *Rhododendron*, and that the leaves of healthy plants contain about 1% dry weight as calcium. It may be relevant that the presence of calcareous debris from coral and shells in the soil seems to be essential for the proper development of mangroves, particularly in areas of high salinity (Percival and Womersley 1975). As calcium reduces the level of internal sodium the presence of calcium ions seems to reduce or prevent any damage which may be done to the plant by an excess of sodium ions.

Many plants occur around both ultramafic rock and limestone or coral. Examples include *Swintonia schwenkii* (Anacard., Ding Hou 1978), *Illigera celebica* Miq. (Hernand., Duyfjes 1996), and *Alocasia cuprea* (C.Koch & Bouché) C.Koch (Araceae, Hay 1998), from Malesia, and there are many others in New Caledonia and New Zealand. This relationship may reflect some similarity in the basic soils derived from these.

5. Swamps

In West New Guinea, Archbold et al. (1942) described the Bernhard Camp vegetation cited above as an example of ophiolite vegetation. Here 'Pure stands of a six to seven-metre high small *Nauclea* species, remarkably like a low *Sonneratia alba* mangrove community in appearance, covered flat islands in the upper end of the lagoon and sometimes fringed its banks. They grew on ground submerged to a depth of about 2.7–3.7 meters by the highest flood. Complete flooding was therefore the average condition from January 1 to May 8.' At the nearby Araucariakamp, 'flood resistant, low *Ficus* L. trees of two species and a *Syzygium* Gaertn., alike in their wide-spreading, horizontal branches, appeared on gravel bars and low banks as representatives of a stream community found everywhere in the low mountains of New Guinea.'.

Although many Malesian Ericaceae require good drainage and light, and so are lithophytes or epiphytes, a significant number occur in sites that are at least periodically waterlogged, such as semi-swampy open places, peat moor, peat bogs, and wet ground with mosses and lichens (a particularly ancient habitat). Swamp habitats are characteristic of rifted areas and plate margins, e.g. the Mamberamo-Sepik-Ramu depression in New Guinea, and along the Alpine Fault Zone in New Zealand.

Many Ericaceae are recorded in swampy habitats. For example, *Rhododendron* is in shrubland on poor impervious white clay (28), moss forest in damp ground or swampy places (30), swampy jungle on white sand podsols at low elevation (233, Sarawak), swamps near lake-shore (248, Sleumer 1966: Fig. 40), *Agathis* forest, waterlogged white acid sands and on granite rock faces (274), and along rivulets, rocky places by rivers, and in riverine forest (229).

Costera is in acid, waterlogged sandy soil, sometimes with *Agathis* (4, 8).

Vaccinium is recorded in open marshy places (6), marshy forest (22), and *Miscanthus* grass swamp (33, 95).

Other swampy habitats include: swampy forest (*Diplycosia* 3, *Vaccinium* 75), semi-swampy alpine thickets (*Diplycosia* 33), marshy flats, bogs or wet flats in alpine grassland (*Vaccinium* 56), sandy or swampy soil (*Vaccinium* 61), swampy shrub vegetation and swampy *Dacrydium* forest (*Vaccinium* 66), boggy area in *Nothofagus* forest, also *Miscanthus* grass swamp (*Vaccinium* 95), swamp (*Vaccinium* 121), *Agathis* and *Quercus* forest on acid, waterlogged sand, kerangas, low scrub (*Vaccinium* 151), and swampy sites (*Vaccinium* 207).

Dimorphanthera 38 occurs on the margin of *Metroxylon* (sago-palm) swamp, *Dimorphanthera* 28, 30 and 31 are all riverine.

The 'marsh ericas' of South Africa are a diverse group with slender, wiry branches and distant leaves (Schumann et al. 1992). Most (e.g. species 147.1, 147.2, 149, 149.2, 149.3, 149.4, 149.5) are confined to a very small area, sometimes a single marsh. Sp. 334 grows in sandy soil which may be moist in winter, but quite dry in summer. 341: grows in hard, gravelly soil that is usually wet in winter.

a. Mangrove

Eighteen Malesian Ericaceae species occur below 100 m and many of these are associated with maritime conditions. For example, *Rhododendron* 250 (*R. longiflorum*) of Sumatra and Borneo is epiphytic in high trees in mangrove, along rivers and in primary and secondary forest, terrestrial in poor forest in stagnant water, in extreme kerangas heath forest, and on quartzite ridges and sandstone pavement.

Rhododendron 276 (*R. brookeanum*, Borneo) occurs from sea-level, where it is epiphytic on mangrove or on rocks, to 1525 m altitude in moss forest, especially on trees along rivers.

136: *R. jasminiflorum*, usually epiphytic, has named varieties at Mt Ophir, Peninsular Malaysia (sometimes terrestrial on rocks in more open places), the Cameron Highlands, the summit of Mount Apo, Mindanao (ridge forest, moss forest and thicket), and the Gajo Lands (open rocky places and old dry volcanic soil always near solfataras, where it is able to withstand SO_2). The fifth variety is known from the Peninsular Malaysia and Borneo where it normally occurs in mountain forest, but it was once found 'almost at sea level' in the delta of the Sarawak River (whether epiphytic or terrestrial is not recorded).

New Guinea species of old sandy clearings in mossy forest (*Rhododendron* 189) and forest opening of long standing (*Vaccinium* 122) may be taxa of gaps on the uplifted coastal land surfaces which are abundant in New Guinea, for example Neon Basin in the Owen Stanley Mts. (formed at sea-level but currently at 2800 m).

Vaccinium 27 is recorded from mangrove near Kuching, and other species are on sandy coasts.

In the Neotropics, Ericaceae are most common in areas of cloud forest at 1000–2000 m altitude and some extend up to 4000 m. However, 'a few' occur as epiphytes in mangrove swamps (Luteyn 2002, citing Smith 1946). Luteyn (2002) also observed vivipary in several New World Ericaceae.

Many taxa are found in close association with mangrove, but not always in the main mangrove swamp, and Mepham and Mepham (1985) made the reasonable suggestion that a broad definition of mangrove is desirable. In New Guinea, mangroves in a fairly broad sense include species like *Cerbera manghas* L.: swamp forests near the sea or beach formations, preferring well-drained sandy soils, and *Dolichandrone spathacea* (L.f) Sch.: in areas only flooded by spring tides, usually on the coastal dunes separating freshwater lagoons from the sea, although it can form almost pure stands behind the mangrove in swamp soils (Percival and Womersley 1975).

Continuously water-logged mangrove peat soils and other saline peats and muds of the coast have a neutral to alkaline reaction in saturated conditions, becoming acid on aeration (Bleeker 1983). In New Guinea mangroves Percival and Womersley (1975) noted that the pH of the soil in the *Avicennia* and *Rhizophora* zones is alkaline, while that of the *Nypa* zone falls gradually to an acid level.

Erica (*'Philippia'*) occurs at sea-level on Mafia Island, Tanzania, and maritime species of *Erica* in South Africa include the following (Schumann et al. 1992):

Sp. 70: This shows apparent resistance to salt spray. It never grows very far from the sea and is sometimes (e.g. at False Bay) found amongst rocks so close to the breakers that in stormy weather it becomes quite wet.

Sp. 256: (*E. subdivaricata* Bergius) has a spreading habit, and grows on level ground in sandy conditions that may be marshy in winter. The plants are not inhibited by salt air or spray and may even grow quite well only a few hundred yards from the sea.

Other Malesian Ericaceae occurring under 100 m are listed below, under 'Altitude'.

b. Freshwater swamp forest

22: *Vaccinium acuminatissimum* and 87: *V. bracteatum* occupy the lowland fresh-water swamp forest of Peninsular Malaysia (Corner 1978a). This type of forest shows clear affinities with the mangrove, as indicated by the massive stilt roots, flanges, fluting and buttresses (spectacular photographs in Corner 1978a and Ding Hou 1978 Figs 25, 26). Freshwater swamp forest in New Guinea (for example, in the Sepik Valley) with *Myristica, Calophyllum, Eugenia, Terminalia* and *Campnosperma* is flooded daily, at least near the coast, and 'is well-termed 'freshwater mangrove" (Johns 1972, Paijmans 1976). The distinction between mangrove and freshwater swamp forest may have been even less in the past if the salinity of sea-water has been constantly increasing.

c. Peat-swamp forest

Acid soils usually occupied by Ericaceae are poor in nutrients but those of marshes, seeps, or streambanks are high in organic humus (Oliver 1991). In Europe, *Calluna* and *Erica* can grow where most other shrubs cannot, in pure organic matter such as *Sphagnum* peat. In South America, a plant of *Lyonia* was growing in soil measured at pH 2.8 (Luteyn 1989). Here and elsewhere Ericaceae share this habitat with other 'heathland' families such as Myrtaceae, Droseraceae, Nepenthaceae and Restionaceae.

The tallest vegetation on peat in Malesia is peat swamp forest (Anderson 1963). This is the acidic environment equivalent of mangrove and is widespread along the coasts and deltas of Malesia. It is considered to be 'an outcome of fresh-water swamp-forest, behind the mangrove and nipa, where for some reason the water-logged soil is no longer subject to tidal inundation or disturbed by the passage of streams' (Corner 1978a). The forest debris accumulates into huge thicknesses of peat and there is no enrichment of the soil with silt. The swamp water is tea-coloured, extremely acid and anaerobic. Peat swamp forest covers 12% of the land in Sarawak, and also large areas in Sumatra and southern New Guinea (Anderson 1963). The Rejang Delta is the largest in Sarawak and each island in it forms a self-contained peat-swamp unit, bounded by a fringe of mangrove or riparian forest. Anderson (1963) recorded *Vaccinium borneense* in peat swamp forest only in the Rejang Delta, but throughout Sarawak and Brunei in heath forest.

Also recorded in peaty sites are *Rhododendron* 29 (temporarily inundated grass-plain on peaty soil), *Diplycosia* 66 (padang, peat swamp forest, kerangas with *Shorea albida*, 60–800 m), *Diplycosia* 77 (peaty, swampy quartzite, open forest), *Diplycosia* 97 (secondary *Dacrydium* forest or heath vegetation or in swamps, temporarily covered by water, on peaty soil), *Diplycosia* 96 (swampy or peaty sites), *Vaccinium* 24 (submontane and moss forest but also in 'low country', in the shrub layer of a *Shorea albida* padang on peat swamp), *Vaccinium* 113 (peaty quartzite plateau), wet, peaty openings in forest, open shores of lake, long grass in open marsh (*Vaccinium* 54) and *Dimorphanthera* 21 (peat swamp).

d. Kerangas forest and padang

These are coastal and lowland communities. Kerangas, or closed heath-forest, occurs in Borneo and other parts of Malesia on poor sandy soils which are strongly podzolised or even seasonally waterlogged to form humus podzols and ground-water humus podzols. Like mangroves they are periodically inundated. On increasingly poor sites, e.g. areas with a rapidly fluctuating water table, or in sandy soil on rocks with excessive drainage, the kerangas is replaced by open shrubland or padang.

In Borneo, heath forest occurs between peat-swamp forest and lowland dipterocarp forest (map in Mackinnon et al. 1996).

Altitude

Fig. 5 indicates the major altitudinal sequence in Malesian Ericaceae from epiphytes in mangrove and lowland forest to terrestrial plants at and above alpine tree-line and in forest gaps. This ecological 'track' follows a zone of high light. Ericaceae occupy the zone because they possess critical morphological/physiological features:

- They are smaller, woody plants seldom forming a trunk that reaches the canopy.
- They are light-demanding.
- They tolerate a low supply of mineral nutrients.
- They have thick, water-storing, mycotrophic roots and coriaceous, xeromorphic leaves, and they tolerate high drainage.

It is often thought that all Ericaceae in the tropical regions thrive in the mountains. This is indeed the case for the bulk of the species but in the four largest Malesian genera, *Rhododendron, Diplycosia, Vaccinium* and *Dimorphanthera,* many species occur below 1000 m altitude and some of these, e.g. 87: *V. bracteatum*, thrive mainly in the tropical lowland at sea-level.

Table 1. Numbers of species of Malesian Ericaceae in 500 m altitudinal bands. Based on literature records.

ALTITUDE/m	**0–500**	**500–1000**	**1000–1500**	**1500–2000**	**2000–2500**	**2500–3000**	**3000–3500**	**3500–4000**	**4000–4500**
Rhododendron	13	46	98	143	131	96	81	28	3
Andresia	.	.	1	.					
Monotropastrum	.	.	1	1					
Pyrola	.	.	.	.	.	1			
Lyonia	.	1	1	1	1				
Pernettyopsis	.	.	1	2	1	1			
Gaultheria	.	.	5	8	11	16	13	5	1
Diplycosia	3	16	38	56	41	32	17	6	
Costera	3	6	7	2					
Vaccinium	28	55	91	121	98	73	51	23	2
Agapetes	.	.	3	4	8	6	6	3	.
Dimorphanthera	12	20	24	32	22	13	13	5	1
Styphelia	3	3	2	3	3	4	3	1	1
Decatoca	.	.	.	.	.	1	1	1	
Trochocarpa	.	1	1	4	5	7	5	5	
TOTAL	**62**	**148**	**273**	**377**	**321**	**254**	**190**	**77**	**8**

Table 1 shows that the four largest Ericaceae genera in Malesia and the family as a whole have most of their species in the 1500–2000 m band, in the lowest part of the montane zone. This is within the range of sweet potato (kaukau) cultivation (below about 2400 m) and so is potentially very vulnerable. Highest diversity for ferns (Parris 1996), birds-of-paradise and bowerbirds (Heads 2001c), and Ericaceae occurs in the same 1500–2000 m band. Of the other Ericaceae, *Agapetes* is most diverse at 2000–2500 m, and *Gaultheria* and the three epacrid genera, all with small leaves, have maximum diversity at the highest altitudes, in the 2500–3000 m belt.

Takeuchi (1999a) observed that the lowland-montane ecotone around 1500 m has been somewhat neglected in Papuasia, but cited recent unpublished findings suggesting that floristic richness in Papuasia peaks at or near this altitude. (It may be more useful to focus on these altitudinal centres of diversity, rather than defining supposed 'breaks' between 'lowland', 'lower-', 'mid-', and 'upper-montane', and 'subalpine'). Stevens (1981) noted elevations of 1500 m or more in New Guinea during the Miocene, 15 million years BP, and it is of interest that this is the belt with most diversity of Ericaceae.

To explain the large-scale variations in altitude discussed below, a general explanation for the altitudinal sequence of taxa is needed. Many authors have discussed affinities between the flora of mangroves and that of the montane zone. Van Steenis (1934b) cited the 'instructive case of altitudinal vicariism' seen in *Bulbophyllum tenellum* Lindl., only in mountain forest at 1000–1500 m, and its nearest relative, *B. xylocarpi* J.J.Sm., only at sea-level on mangroves, but how is this to be explained?

Van Steenis (1934b) noted that 'In the Malaysian lowland there are peculiar, natural open sandy plains called padangs … They are situated mostly near sea-level … several plants descend here to their lowest altitude'. A comparison can be drawn with the Awarua plains of southern New Zealand. Van Steenis took a fundamentally geological approach to the problem and reasoned that 'The possibility of the occurrence of mountain plants at abnormally low altitudes on account of secular sinking cannot be denied.' Van Steenis (1934b) cited possible tectonic lowering of mountains and plant communities in SE Sumatra (for the Riouw Pocket (Corner 1978a), see below). In a classic but forgotten paper Krašan (1883) discussed sinking land in SE Asia and Malaysia in relation to plants having a lower altitude in Sumatra than in Java, and rejected the idea that climate could be responsible – rightly, according to van Steenis.

Conversely, van Steenis (1934b) cited 'abnormally high altitudes [of taxa] in regions which are gradually elevated' and cited Krašan's (1883) studies on tectonic uplift of oak forest in the European Alps. Later, van Steenis (1963, 1984) recorded mangroves in Malesia which have been stranded inland through tectonic uplift, and Hossfeld (1964, cited in Löffler 1977) recorded a former tidal mangrove at Aitape (NW coast of PNG), 13 km inland and 52 m above sea-level. In fact, current uplift rates in northern New Guinea (3 mm/yr) would move a mangrove or a coastal padang to the high montane (3000 m) in just one million years. Kinabalu is said to have risen at 5 mm/yr.

Although it might appear that birds and rhododendrons move freely and the mountains stay still, birds and rhododendrons may actually stay in their own locality, while the mountains move up, down and sideways.

Another example from Malesia is *Scolopia rhinanthera* (Benn.) Clos (Flacourtiaceae), which always grows in humid or marshy soil along the land-side of mangrove forests or more inland on riversides, at margins of pools or in temporarily inundated soil, usually at 0–15 m. 'Quite out of this area' are two specimens growing at 900 m south of Lake Toba in northern Sumatra (van Slooten 1925).

Hydrophiidae, the sea-snakes, are widespread in tropical seas, but there are two species confined to freshwater lakes (Dunson 1975). One is in Lake Taal in southern Luzon, which occupies an ancient crater and is itself occupied by the volcano Taal (Smith 1926). The other is in a lake on an uplifted coral island (Rennell I.) in the Solomon Islands (a 'distributional anomaly' (Minton 1975)).

Nearly a century ago in the upper Ramu Valley at Kenejia, Schlechter was surprised to find typical sea-shore plants such as the orchid *Dendrobium antennatum* Lindl. (Schlechter 1982). Schlechter also noted uplifted coral at 600 m on the Huon Peninsula and reasoned correctly that the Ramu–Markham valley was previously flooded by the sea, but that subsequently an 'enormous elevation' had joined the Huon Peninsula to the mainland.

Brookfield and Hart (1971) described the raised beaches on the Huon Peninsula and also observed that on the southern plain of New Guinea some forest is being actively transformed into swamp forest through depression along axes transverse to the central cordillera.

In New Guinea plants many other 'altitudinal anomalies' are known in which a group has unusual altitude at certain geographic localities.

At Kiunga in the upper Fly River, Stevens (1981) described 'altitudinal irregularities' in the flora; species of otherwise montane genera, or species otherwise known at higher altitude are present here on ridges at only 100 m elevation (*Dimorphanthera, Vaccinium, Podocarpus, Lithocarpus, Calophyllum*). In the same area montane birds also occur at anomalously low altitude (Heads 2001b).

At another site in southern New Guinea, in the Lakekamu basin SW of Wau, Takeuchi and Kulang (1998) reported 'unexpected' montane genera in families such as Ericaceae, Monimiaceae, Elaeocarpaceae, Winteraceae, Ternstroemiaceae and Pittosporaceae at anomalously low altitude (175 m), very near the alluvial-coastal plain. Individual species are found there far below their previously known lower limit. Takeuchi (2000) described a new subspecies of 133: *Rhododendron loranthiflorum* from the site and inferred 'the apparent displacement of an entire montane assemblage to the Papuan lowland environment where the non-conforming elements now coexist in disparate combination with the conventional lowland flora.' As Takeuchi and Kulang (1998) noted, these records are 'rather provocative and deserving of further enquiry'.

Whether the 'montane' elements occur at low altitude through downwarping of terranes bearing these populations, or because there has been relatively little uplift there compared with the main central mountains, it seems unrealistic to discuss the altitudinal range of communities and taxa without reference to the changes of a site's altitude caused by orogenic and epeirogenic uplift, vulcanism, sedimentation, downwarping and erosion.

The following species of Malesian Ericaceae are of interest as they occur at or below 100 m:

Rhododendron:

136: *R. jasminiflorum.* Aceh to Mindanao, 'Almost at sea-level in the Sarawak R. delta'; also in thicket, open rocky places, mountain forest, sea-level – 3100 m.

163: *R. nieuwenhuisii.* Borneo, dense forest along river, heath forest, 100–800 m.

250: *R. longiflorum.* Sumatra, Peninsular Malaysia, Borneo, including Riouw pocket, mangrove etc., sea-level – 750 m.

255: *R. zoelleri.* Moluccas and New Guinea, sandy and clayey soil, limestone, sea-level – 2000 m.

276: *R. brookeanum.* CW Sumatra and widespread in Borneo, mangrove etc., sea-level–1750 m.

Vaccinium:

21: Borneo, on boulders, 5–200 m.

27: Sarawak, limestone, mangrove, sea-level – 700 m.

87: Burma to Java, common locally on sandy coasts, padang, sea-level – 1830m.

88: Sulawesi, dry forest, sea-level – 850 m.

158: Sumatra, Riouw Pocket, Borneo, beach, padang, kerangas, sea-level – 1700 m.

165: Borneo, padang, acid sand, sea-level only.

185: (*V. littoreum* Miq.), Sumatra, Malay Peninsula, Java (not Riouw) limestone etc., sea-level – 2400 m.

Diplycosia:

52: Borneo, Sarawak, mossy and *Agathis* forest, acid, sandy-loam soil or sandstone, 20–1000 m.

65: Sarawak, padang, kerangas, 60–800 m.

Dimorphanthera:

3 (included under sp. 7 by Stevens 1974): lower Mamberamo R., Irian Jaya, primary forest, 75–100 m.

66: *D. tedentii* Stevens. 80 m (Fly River 528 Mile Camp) – 835 m.

Styphelia

3: Indo-China to Borneo (including Riouw, Banka, Billiton, and Karimata Islands),

exposed cliffs or rocks, sandy beach plains, 'blukar' (secondary vegetation) behind coconut groves near the sea, kerangas, padang, etc., sea-level – 2745 m.

7: Borneo, Sulawesi, Moluccas, Waigeo I., xeromorphic vegetation on red, nickel- and chrome-containing clay, sea-level – 1000 m.

Summarising, of the 18 Ericaceae more or less definitely recorded from below 100 m, only three (16%) occur in New Guinea, one ranges between Borneo and Waigeo, while 14 (78%) occur in W Malesia.

A very similar pattern is seen in *Nepenthes*. This genus has 82 species in Malesia (Cheek and Jebb 2001) of which 13 occur at sea-level. All of these 13 are in W Malesia except one at the Vogelkop (Sorong) and nearby Misool I., and only this species and one wide are in New Guinea. As in the Ericaceae, coastal species are much more frequent in W Malesia. In Ericaceae there are mangrove species in Sumatra: Borneo, *Nepenthes* is recorded in the mangrove at Sulawesi. The distribution of another species, *N. mirabilis*, illustrates the general pattern: at low altitude in the west, but at anomalously high altitude in New Guinea.

This pattern in the two families could be attributable to Mesozoic ancient invasion of the Malesia/SW Pacific region from the Indian Ocean by mangrove and coastal forms, followed eventually by great uplift of these in E Malesia during the Neogene. This is compatible with the sea-level species *Nepenthes danseri* of Ceram being sister to the Madagascan species (Jebb pers. comm. 2001).

In a similar example, *Buchanania macrocarpa* (Anacard.) is widespread in E Malesia through the Moluccas, New Guinea, and the Solomons, occurring in the lowlands up to 450 m. However, it was once collected at 900 m in northern PNG (Morobe) (Ding Hou 1978). Still in Anacardiaceae, a similar W–E altitudinal cline in New Guinea is seen in *Rhus caudata* Laut. This ranges in New Guinea mossy montane forest at 900–2400 m, but was once found at 10 m on Biak Island on a wet, coastal coral limestone ridge (Ding Hou 1978).

Likewise, *Meliosma pinnata* subsp. *macrophylla* (Merr.) Beus. (Sabia.) is a tree of primary rain forest with buttresses to 2.5 m high, fairly common from E Borneo (within Borneo it is sharply delimited against the W Malesian ssp. *ridleyi*) through Sulawesi, the Moluccas, New Guinea and New Britain (van Beusekom 1971). It occurs on loam, sandy soil, volcanic and limestone soil, and rarely in occasionally submerged areas. It was reported once on peaty soil (in New Guinea) where it was developing stilt roots. In Borneo it only occurs below 100 m, but further east it ranges up to 1100–1200 m, and in W New Guinea it has been collected at 1800 m.

Xylosma G.Forst. (Flacourt./Salicaceae) has four species in Malesia. The two in W Malesia have serrate leaves and occur from the sea-shore (thickets back of the beach etc.) to 200 and 1200 m respectively; the two species in New Guinea (one is also in W Malesia) have entire leaves and are at distinctly higher altitudes: 400–1600 m and 1070–2200 m (Sleumer 1954).

Floral biology

Stevens (1976, 1985) described the great variety of flower types in Papuasian *Rhododendron*. These are not distributed at random, either geographically or altitudinally. For example, in Papuasia there are 36 species with red, tubular, zygomorphic, scentless flowers, and with one exception (199B: *R. yongii* of Sabah) this type is only known from here. Another 40 species in Papuasia have similar flowers but with little zygomorphy and this type occurs in some W Malesian species.

In Papuasia nearly 50 red-flowered species grow above 3000 m, but only 9 species with flowers of other colours grow much above this altitude. Birds remain active at all temperatures and are probably more important pollinators at this altitude than insects, and Ericaceae may be an important source of nectar for groups such as Meliphagidae. Below 3000 m white-flowered, moth-pollinated species also occur. (The absence of alpine lepidoptera in New Guinea compared with their abundance in New Zealand is striking).

Ericaceae in Malesia – systematic treatment

The Ericaceae of Malesia have been treated by Sleumer (1966, 1967, 1973) with 737 species, of which 236 were newly proposed by him (van Steenis 1979). Sleumer (1964) also treated Malesian Epacridaceae (18 species), here included in Ericaceae. Other authors have since described 32 new species, and *Dimorphanthera alba* J.J.Sm. and *D. arfakensis* J.J.Sm. have been reinstated. Six *Rhododendron* species are now regarded as hybrids by Argent and colleagues, and six *Dimorphanthera* species have been synonymised. This gives a total of 737 + 18 + 34 -12 = 777 species in Malesia. Photos of the types of most of Sleumer's taxa and many other Malesian Ericaceae are available at www.nationaalherbarium.nl

New taxa have been described from New Guinea by Stevens (1972, 1974a, 1977, 1978a, 1982), Kores (1978,1984), Veldkamp (1979, 1991), Craven (1980), and Takeuchi (2000). *R. heptaster* Gilli 1980 and *R. sleumeri* Gilli 1980 were synonymised by Kores (1984).

Two important floristic studies by Takeuchi (1999a,b) have several interesting Ericaceae records, as does Streimann (1983).

Working on *Rhododendron* in Borneo, Argent and co-workers (1982–2000) have described nine new species, six new subspecies and varieties, changed the status or made new combinations for ten taxa, and have treated six of Sleumer's species as hybrids. Argent et al. (1996) listed all the species in *R.* sect. *Vireya*, with synonyms. Argent (1982) also described a new species in each of *Costera, Vaccinium, Diplycosia* and *Pernettyopsis*, all from Sabah.

Van Royen and Kores (1982) treated the many species of Ericaceae found above 3000 m in New Guinea. This valuable supplement to Sleumer's work included many new localities, altitudinal records, habit photographs, and drawings showing important features such as perulae. Stevens (1976, 1981, 1985) studied many aspects of morphology, architecture, ecology, biogeography and evolution in New Guinea Ericaceae. Argent et al. (1988) treated the Sabah species of *Rhododendron.*

Middleton (1991) gave a detailed revision of the infrageneric classification of *Gaultheria*, including *Pernettya.*

Species described after Sleumer (1973).

Sleumer's (1973) new species are listed in the maps with the number of their putative relative and a suffix 'A' (or 'B' in cases where there is more than one new, related species), but are not listed separately here. Other authors' new species are listed here, with a suffix, and are also mapped. 131A was first named by Sleumer, then lumped by him in the *Flora Malesiana* ('partly under the influence of badly prepared material'), but later revived (Sleumer 1973).

Rhododendron

23A: *R. capellae* Kores (1978).

41A: *R. caliginis* Kores (1984).

82A *R: lamrialianum* Argent & Barkman (2000).

105A: *R. roseiflorum* Stevens (1975).

131B: *R. alborugosum* Argent & Dransf. (1989).

137A: *R. rubineiflorum* Craven (1980).

155A: *R. burttii* Woods (1978).

157B: *R. rousei* Argent & Madulid (1998).

192A: *R. meijeri* Argent, Lamb & Philipps (1984).

199B: *R. yongii* Argent (1982).

227A: *R. sarcodes* Argent & Madulid (1995).

264B: *R. madulidii* Argent (1998).

268C: *R. baconii* Argent, Lamb & Philipps (1984).

268D: *R. tuhanensis* Argent & Barkman (2000).

Agapetes

2A: *A. prostrata* Stevens (1972).

3A: *A. kudukii* Veldk. (1991).

9A: *A. sleumeriana* Stevens (1972).

11A: *A. shungolensis* Stevens (1972).

Vaccinium

2A: *Dimorphanthera albida* Stevens (1977). (Sect. *Pachyanthum* is retained here in *Vaccinium* instead of being transferred to *Dimorphanthera*).

54A: *V. candidum* Veldk. (1991).

23A: *V. tenax* Argent (1982).

58A: *V. altiterrae* Veldk. (1979).

Dimorphanthera

11A: 17A. *D. tedentii* Stevens (1974a).

44A: *D. viridiflora* Stevens (1974a).

51A: *D. bracteata* Stevens (1974a).

52A: *D. glauca* Stevens (1974a).

54A: *D. papillata* Stevens (in van Royen and Kores 1982).

55A: *D. longistyla* Stevens (1974a).

64A: *D. napuensis* Stevens (1977).

64B: *D. wisselensis* Stevens (1977).

Pernettyopsis megabracteata Argent (1982).

94A: *Diplycosia microsalicifolia* Argent (1982).

The distributions of the Malesian Ericaceae species are mapped here and related to the geological structure of SE Asia–Malesia, summarised in terrane maps (Figs. 6, 7 and 8). Many of the sutures between the terranes are Jurassic, a time during which an important phase of modernisation took place in the flora and fauna of the world (cf. Heads 1989, Parenti 1991).

Rhododendron L.

Many of the papers cited below are available at the outstanding website devoted to the Vireyas, www.vireya.net. *Rhododendron* species range from *R. rex* of western China with leaves up to 37 cm in length, to the miniature *R. caespitosum* from Irian Jaya with leaves 0.6 cm long, *R. stenophyllum* of Kinabalu in which the leaves resemble pine needles, and *R. ericoides* of Kinabalu which is like a heath. The largest flowers in the genus belong to two northern New Guinea species, 238: *R. leucogigas* (Cyclops Mts. and Hunstein Mts.) with flowers trumpet shaped and 14 cm long, and its sister species 237: *R. schlechteri* (Bismarck and Kani Mts.) with a corolla 15–17 cm long. Style length varies from 4 mm (*R. anagalliflorum*) to 100 mm (*R. leucogigas*).

Halliday (2001) illustrated 121 species representing all the subsections and series in the genus. Apart from *Vireya*, Halliday illustrated many species from SE Xizang (= Tibet) – NE Upper Burma – N Yunnan. Sikkim, Bhutan and Sichuan (Szechuan) are also very diverse. The 'centre of gravity' of *Rhododendron* was previously thought to lie in the Himalayas, but after the collecting of the French missionaries it was acknowledged to lie further east, in Yunnan/Sichuan (Philipson and Philipson 1974).

There are many morphological and ecological parallels with the vireyas elsewhere in *Rhododendron*. The following examples are cited from Halliday (2001).

R. hippophaeoides Balf.f. & W.W.Sm.: Yunnan, SW Sichuan, boggy ground, spread over vast tracts of land forming an ankle-deep carpet. Up to 4800 m.

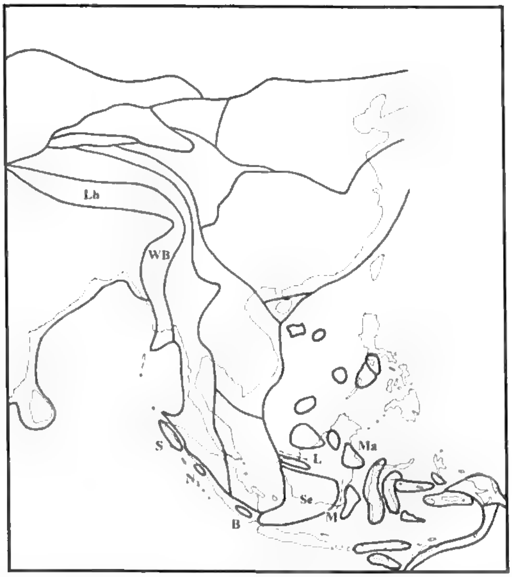

Fig. 7. Continental allochthonous terranes and principal sutures of SE Asia. The following examples are labeled: Lh, Lhasa terrane; W B, West Burma terrane; S, Sikuleh terrane; N, Natal terrane; B, Benkulu terrane; L, Lupar suture; Se, Semitau terane; M, Meratus suture; Ma, Mangkalihat terrane (Metcalfe 2001).

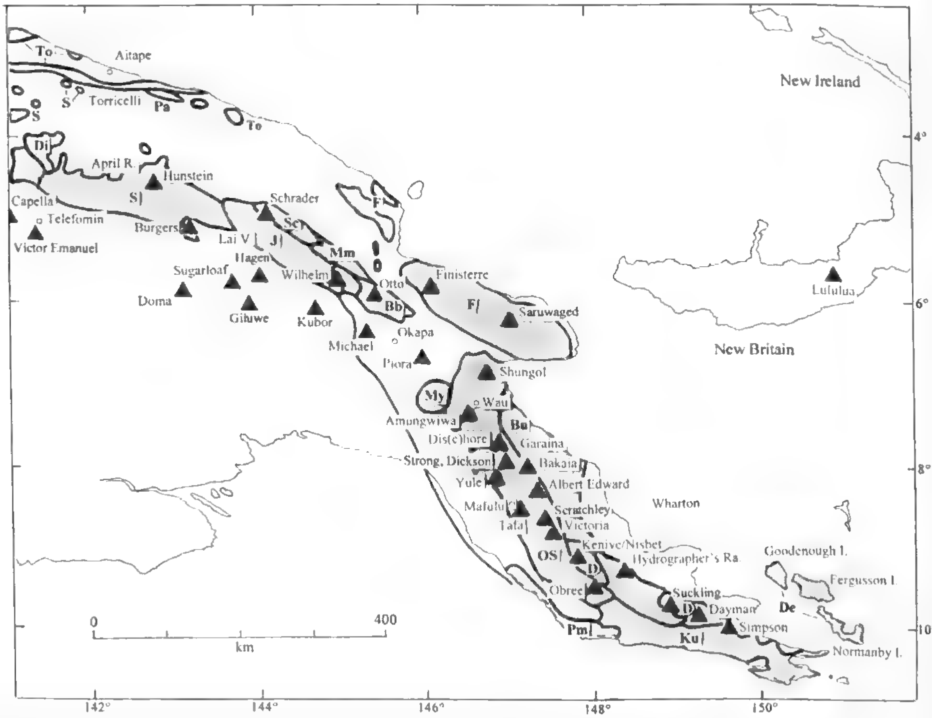

Fig. 8. Papua New Guinea, showing localities mentioned in the text, and accreted terranes (stippled) with abbreviations as follows: To, Torricelli; S. Sepik; LS, Landslip; Di, Dimaie; Pa, Prince Alexander; Tu, Mount Turu; J, Jimi; Sc, Schrader; Mm, Marum; Bb, Bena Bena; F, Finisterre; My, Menyamya; OS, Owen Stanley; Bu, Bowutu; D, Dayman; PM, Port Moresby; Ku, Kutu; De, D'Entrecasteaux; Wo, Woodlark. Former craton margin as heavy line to the south of the accreted terranes (Pigram and Davies 1987).

R. hirsutum L.: European mountains, dry, stony situations in calcareous areas. It vicariates with the other 'Alpenrose', *R. ferrugineum*, which prefers acid soil and shady locations.

R. calostrotum Balf.f. & K.Ward (the 'pygmy rhododendron with the giant flowers'), Burma, Assam, SW China, prostrate or mat-forming shrub, to 4800 m. It has a var. *calciphilum* which grows on limestone. Other species range up to 4900 m.

R. afghanicum Aitch. & Hemsley (Afganistan/Pakistan border) creeping among rocks, usually gneiss or limestone.

Several species in Nepal–China are gregarious and form impenetrable thickets.

R. floccigerum Franchet: (Yunnan, Xizang) grows in open pine forest and on limestone cliffs and rocks.

Rhododendrons are usually plants of open, rocky, well-drained sites but several species occur in swamps (*R. canadense* (L.) Torrey, *R. venator* Tagg) or bogs (*R. sanguineum* Franchet). *R. simsii* Planchon of China and Japan to Thailand grows on hillsides, cliffs and river-banks, sometimes in places where it is submerged during the rainy season.

Dwarf, creeping species include *R. forrestii* Diels of China and Burma which is usually no more than 15 cm high and occurs up to 4500 m altitude.

According to the sample of 121/900 species in Halliday (2001), subgen. *Hymenanthes* is more widespread in C and E China than subgen. *Rhododendron*, which is mainly in the Xizang-Yunnan-Sichuan area, possibly indicating an overall vicariance between the subgenera.

A recent molecular study (Kurashige et al. 2001) found that within *Rhododendron* (incl. *Menziesia* but not *Therorhodion*), subgenera *Hymenanthes* and *Tsutsusi* are monophyletic, *Azaleastrum* and *Pentanthera* are polyphyletic, and *Rhododendron* is monophyletic (if subsect. *Ledum* is excluded).

Subg. *Rhododendron* is characterised by peltate epidermal scales but no other multicellular hairs (Stevens 1985). The subgenus is represented in Malesia by sect. *Vireya* only.

Nearly all the Malesian rhododendrons belong to sect. *Vireya*, which ranges from East Asia (subsect. *Pseudovireya* only), through Malesia to Queensland and the Solomon Islands and includes about a third of the species in the genus. According to Kron and Judd (1990) sect. *Vireya* is well-embedded in *Rhododendron*. Species are often locally common. Some are both widespread and common, many others are only known from a single collection.

Stevens (1985) gave a very useful overview of sect. *Vireya*, noting its distinctive features: geographic separation, a corolla which lacks zygomorphic markings, and seeds with tails, or at least points, at either end (subsect. *Pseudovireya* is variable). In addition, the capsule valves twist after dehiscence (Brown et al. 2001, citing Sleumer 1980). Other characters useful in separating sect. *Vireya* include the absence of a rachis (axis) in the inflorescence, the absence in the flowers of blue pigment and of spots (although a similar effect caused by the presence of scales on the corolla can be seen on a small number of species, e.g. *R. variolosum*), and an ovary in which the upper end tapers gradually into the style, without a marked junction.

The introduction to the vireya.net website notes that most of the species are to be found in the cool montane forests, where many species grow as epiphytes high in the trees with mosses and orchids, and are normally only seen as fallen corollas. Higher still, on more open ground, other species can be found growing terrestrially. On the Bulldog Road near Wau, gouged through the mountains and thick forest during World

War II and now reduced to a narrow track, Black (1966) observed many *Rhododendron* species on the steep cuttings in the hillsides, and to a lesser extent on the road itself. The roots penetrated up to 60 cm in the case of small plants about 90 cm high, with very little surface rooting. In all the species Black observed the roots were thick and of a soft consistency, pruning shears sliding through them with ease. He wrote that these roots seem capable of storing a considerable amount of water, enabling the plants to survive on hot dry banks during dry spells. Though it was the driest part of the season, many of them were putting on new growth.

In the upper reaches of the Fatima River, Eastern Highlands, Black recorded that the vegetation was so thick on either side that they waded up the river bed, sometimes up to the armpits in swirling water. Many rhododendrons grew in the gravel and among the rocks on the banks, and in one place where the river had changed its course there were quite a number colonizing the old river bed, which appeared to be pure sand and gravel.

Section *Vireya* and the genus *Rhododendron* reach their southern limit with two species in NE Queensland at 910–1520 m (Withers 1992, Craven and Withers 1996). On the Bellenden Ker Range, *R. lochiae* F.Muell. sens. str. grows as a terrestrial plant hanging over the side of the rocky razor-back at the top of Mt Bellenden Ker, and on Mt. Bartle Frere it is rooted in deep cracks in or between rocky boulders. Apparently it also occurs on Bell Peak in the adjacent Malbon Thompson Range. Further north, a second species, previously identified as *R. lochiae,* is quite widespread and common in rocky areas at 910–1330 m, growing in accumulated litter on or between rocks, and also epiphytically. (Craven, 1996, proposed a new type for *R. lochiae* so that the name would continue to apply to this widespread, well-known plant, but the proposal was rejected; L.Craven pers. comm.). It occurs around Thornton Peak, Mt Finnigan, Mount Windsor Tableland and the Main Coast Range). The largest plants grew in the forest but were invariably associated with rocks. On Mt. Finnigan this *Rhododendron* was found growing at the top of a large mound of rocks around the base of a rock along with the sprawling *Agapetes meiniana.* Although mainly growing as a terrestrial plant, on Mt. Spurgeon it mostly grows as an epiphyte on the tops of large *Syzygium* trees.

Classification of Malesian rhododendrons

Stevens (1985) noted that distinguishing between subsects. *Pseudovireya* and *Siphonovireya* can be difficult, but that subsects. *Malayovireya, Albovireya* and *Phaeovireya* all seem coherent and largely monophyletic. The long, narrowly tubular corolla of *Solenovireya* and *Siphonovireya* is distinctive, but it is unclear whether these two (especially former) are monophyletic. In subsect. *Vireya* (as subsect. *Euvireya* Copel. in Sleumer 1966), the separation of ser. *Buxifolia* from ser. *Javanica* is doubtfully useful, but the Papuasian members of the two together form a single group (with the New Guinea species of *Stenophylla* Stevens 1981), perhaps including *Siphonovireya,* ser. *Saxifragoidea,* and the West Malesian members of subsect. *Vireya.*

Van Royen and Kores (1982) also made changes in the composition and species order in subsect. *Vireya.*

Based on detailed study of the Borneo species, Argent (1982, 1985, 1988) gave a tentative classification of sect. *Vireya* in just two subsections:

1. Subsect. *Vireya*

Ser. *Vireya,* ser. *Albovireya,* ser. *Phaeovireya.* Incl. Solenovireya.

2. Subsect. *Pseudovireya*

Ser. *Pseudovireya,* ser. *Malayovireya.* Incl. Siphonovireya.

Argent based this on four characters, as follows.

In 1., the epidermal scales have a small point-like centre, in 2. they have a large, cushion-like centre (cf. Sleumer 1966: Fig. 2).

In 1., the vegetative buds are well-developed. The bud scales are sheathing, relatively broad and thin, and characteristically persistent for some time on resting buds but quickly shed when the branch begins to grow. In 2., vegetative buds remain small and unspecialised. Bud scales are virtually absent and the young shoots develop in a naked manner. Where present, the bud-scales are slender, hardly broader than thick, and often persistent as subulate cataphylls on the elongated stems for some time after the branch has grown.

In 1., the floral bud scales (perulae of Sleumer 1966) rarely have simple hairs (if these do occur, they rarely form a fringe at the edge, and rarely have epidermal scales except at the edges) In 2., the perulae are almost always fringed with simple hairs and are often very scaly as well.

In 1., the exocarp peels irregularly from the woody 'valves' (mesocarp and endocarp) before dehiscence, while in 2. the exocarp remains firmly attached to the underlying tissues.

The four characters correlate well in the species studied, and divide *Vireya* into two groups. *R. buxifolium, R. stapfianum, R. variolosum* and *R. herzogii* are exceptions with incongruent character combinations and this may indicate ancient hybridism.

In Argent's scheme, Sleumer's subsections were redesignated as series with the exception of the long, white, tubular-flowered groups *Solenovireya* and *Siphonovireya.* Argent did not accept these two at any rank as they are largely based on corolla shape, which he considered a very plastic character.

According to Argent (1985), Stevens (1985) may be right that *Phaeovireya* should incorporate series *Dendrolepidon* Argent, Lamb & Phillips, the main differences between these two being whether the scales sit on epidermal protuberances or not.

Spethmann (1987) reverted from section to subgenus *Vireya* (Bl.) Clarke while retaining Sleumer's seven subsections at the same rank unaltered.

Brown et al. (2001) sequenced DNA of 22 species of Malesian *Rhododendron*. Two clades emerged and formed a trichotomy with the outgroup (sect. *Maddenia*): *Pseudovireya* (but with a bootstrap value of only 55%), and a clade formed from the other three subsections sampled (bootstrap value 99%). The second is equivalent to a broadened *Euvireya* (including *Solenovireya* and *Phaeovireya* as paraphyletic). *Rhododendron arfakianum* appears as 'basal' in this second clade, which then divides into one group of five west Malesian species and one of 13 species from east Malesia, Solomons, and NE Australia.

Biogeography of *Rhododendron*

Sleumer and Stevens (1981) have published very useful maps showing sections and subsections of Malesian Ericaceae, but so far fewer than 20 species have been mapped (Croizat 1968, Argent 1988, van Welzen 1997, Takeuchi 2000). Sleumer's stupendous treatment (the only full treatment available) is beautifully laid out, with actual localities (not just provinces) cited. Sleumer's keyed groups indicate related recombinations of characters and putatively related species, and are indicated on the maps here by lines connecting species localities. It is the characters underlying the taxa, not the taxa per se, which are stressed in the hypocladistic approach followed here.

Other authors who have proposed new taxa and localities are cited above.

In the maps provided here all the species but not all the varieties are shown; where they are, they are indicated with lower-case suffices. Upper-case suffices indicate new species described after Sleumer (1966–1967).

Rhododendron subsect. *Pseudovireya* (Clarke) Sleum. I. (Fig. 9). There are two main centres which are also important for the genus as a whole: north Sumatra/Peninsular Malaysia (from here connections are also possible with Madagascar, Burma etc.) and western New Guinea. East and West Malesian taxa are connected via Mount Bonthain (= Mt Lompobattang) in SW Sulawesi. The group is notably absent from Kinabalu and the Philippines, in contrast with the next. Doormantop in Irian Jaya (Rouffaer terrane) is associated with major disjunction to Sumatra–Java. Within New Guinea there is a disjunction between the Vogelkop and the Owen Stanley terrane (Mt Dickson/Bakaia). Concentric distributions around Mt. Carstensz, Doormantop and Oranje Mts. possibly indicate evolution around regressing seas.

Rhododendron subsect. *Pseudovireya* II. (Fig. 10). A Sumatra/Peninsular Malaysia group (spp. 14–16) is sister to the rest and an Aceh – Snow Mountains (Carstensz–Oranje Mts.) track again defines the group and the disjunction sp. 17 – 18 (cf. podocarps etc. listed below). East and west Malesia are connected north of the last group, and in Sulawesi are centred on Latimodjong. 19: *R. ericoides* grows in subalpine shrubland of Kinabalu with *Leptospermum* and *Dacrydium* as a 3 m high shrub, and ranges right to the summit in rock cracks where it is ultimately just 15 centimetres high.

Rhododendron subsect. *Siphonovireya* Sleum. (Fig. 11). Sp. 32: (*R. incommodum* Sleum., the name referring to its uncertain position) crosses the great Markham Valley, but stops at Okapa. This is inexplicable by current geography, but is closely correlated with the former margin of the Australian craton (this feature is shown here on all the New Guinea maps). The remaining five local endemics are all on the craton. Although the group is most diverse in western New Guinea, it does not occur outboard of the craton margin in the Vogelkop. Stevens (1976) viewed the placement of 32: *R. incommodum* (1830–1950 m) in *Siphonovireya* with suspicion because of the flower, which is identical to that of 250: *R. longiflorum* (Borneo-Sumatra, sea-level to 1500 m).

Rhododendron subsect. *Phaeovireya* Sleum. I. (Fig. 12). This ranges: Doormantop/Oranje Mts. – Latimodjong. 41: *R. hooglandii* has a stronghold on Kubor Mountains, south of the craton margin, and on Mount Kerigomna (more or less on the margin), but is notably absent from Mt. Wilhelm (north of the craton margin). It is closely allied to 41A., also restricted to the craton.

Rhododendron subsect. *Phaeovireya* II. (Fig. 13). Latimodjong – Upper Sepik (Dimaie terrane). The Sulawesi-New Guinea disjunction is involved here with accreted terranes. Like *Siphonovireya,* the group is notably absent from the Vogelkop and is more diverse in PNG (four species) than in Irian Jaya (one species).

Rhododendron subsect. *Phaeovireya* III. (Fig. 14). There are two disjunctions between the accreted terranes of the northern Vogelkop (especially Arfak terrane) and those of PNG: one to sp. 67 on Lagaip limestone (on the craton but close to the margin), and one to sp. 66 on Mt Kaindi (Owen Stanley terrane).

Overall, *Phaeovireya* masses more or less evenly in Irian Jaya and PNG, which is unusual in *Rhododendron*. Subsect. *Solenovireya* is even more unusual as it has most species in PNG.

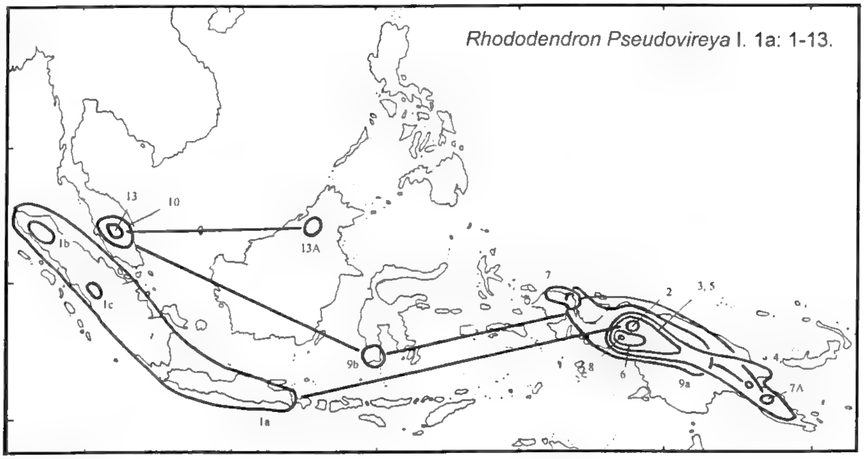

Fig. 9. *Rhododendron* subsect. *Pseudovireya* I. For sp. 11, see 94. For sp. 12., see 183.

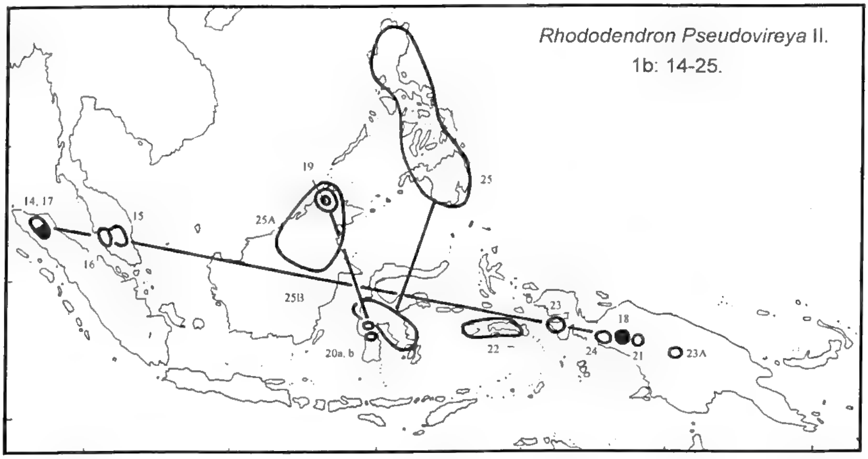

Fig. 10. *R. subsect. Pseudovireya* II. 25A *R. borneensis* (J.J. Sm.) Argent, Lamb & Phillips (three varieties) and 25B *R. cuneifolium* Stapf (two varieties) are split off from 25 *R. quadrasianum sensu* Sleumer (Argent, Lamb and Philips 1984).

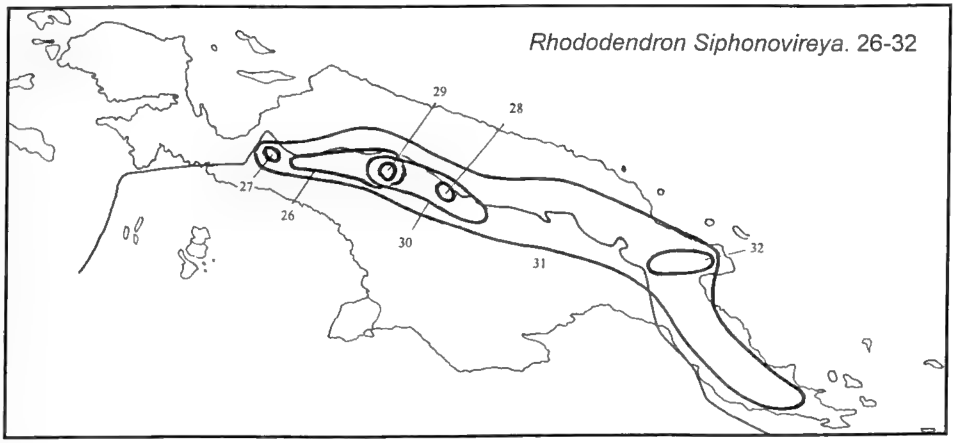

Fig. 11. *Rhododendron* subsect. *Siphonovireya*.

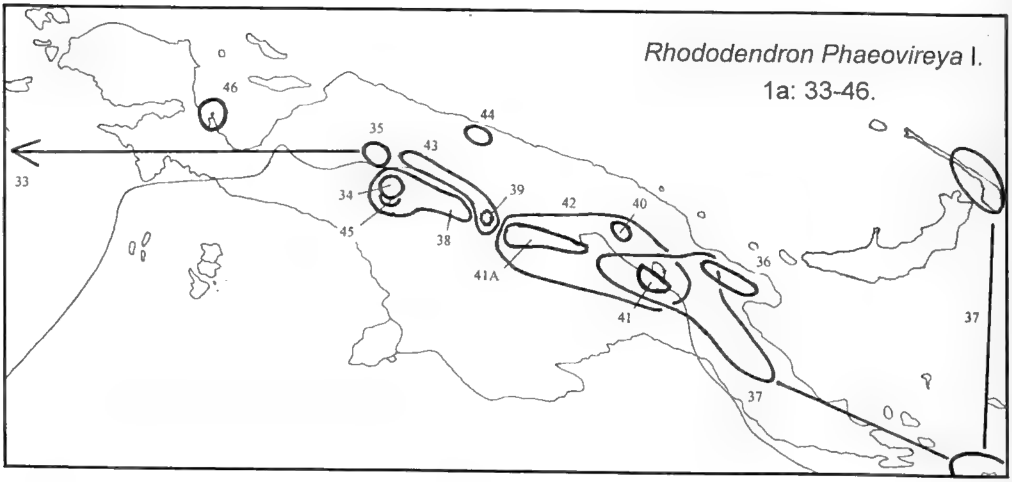

Fig. 12. *Rhododendron* subsect. *Phaeovireya* I.

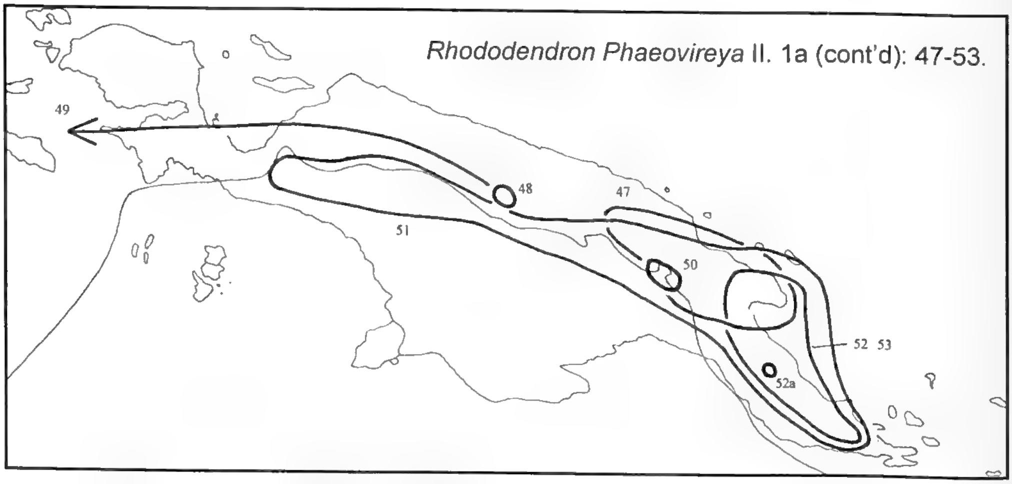

Fig. 13. *Rhododendron* subsect. *Phaeovireya* II. 52 includes 53 as a variety (Argent 1995).

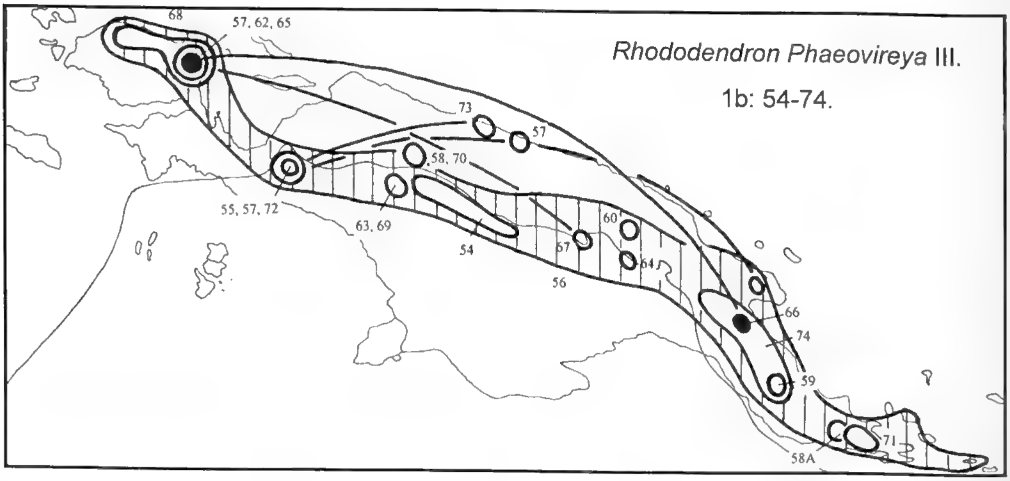

Fig. 14. *Rhododendron* subsect. *Phaeovireya* III. 56 includes 57 as a variety (Argent 1995).

Rhododendron subsect. *Malayovireya* Sleum. (Fig. 15). There is a strong massing on northern Borneo. The group was placed with *Euvireya*, *Albovireya* and *Solenovireya* by Sleumer (1966), but with *Pseudovireya* by Argent (1985).

Rhododendron subsect. *Albovireya* Sleum. (Fig. 16). Latimodjong is central in the distribution and is the most diverse area. There are three separate connections between here and New Guinea, with the Vogelkop, the PNG mountains, and Mts. Albert Edward/Scratchley/Victoria, respectively. The group is absent from Borneo. The parallel arcs in SW Sumatra/W Java are noteworthy, as are two identical disjunctions: Snow Mts – Mt Victoria (Owen Stanley terrane) (spp. 95–96, and 101–102).

Rhododendron subsect. *Solenovireya* Copel. I. (Fig. 17). There is a Snow Mountains – Mt Victoria disjunction, as in the last. The Kinabalu–Vogelkop disjunction here is vicariant with the disjunct arcs Philippines – New Guinea and Sulawesi – New Guinea in the next map, giving three parallel tracks.

Rhododendron subsect. *Solenovireya* II. (Fig. 18). The New Guinea range comprises three parallel arcs:

* N Sumatra/Peninsular Malaysia – S Philippines (Palawan, Mindanao) – Lae/New Britain. The sister group is in N and W Borneo.

* CE Borneo (Mt. Kemul) – Sulawesi – Mt Carstensz (cf. *Buxifolia* IV).

* Disjunction within New Guinea between terranes in the far west (Tamrau/Tohkiri/Nettoti Ranges and Wissel Lakes) and the far east (Goodenough Island). This last island is D'Entrecasteaux terrane, which may be an easterly extension of Owen Stanley terrane (Pigram and Davies 1987). The substantial massing on the Milne Bay mountains (Dayman, Simpson and Suckling) is unique in Ericaceae. In *Vaccinium* sect. *Bracteata* XI and *Styphelia* this node is connected with the Philippines and Marianas Is. respectively.

The Borneo group (130–131, 131A, 131B) forms an arc between the Meratus Mts. and Kinabalu.

Species 133 has subspecies in New Britain and Lakekamu, separated by the New Guinea orogen.

Solenovireya is unique in *Rhododendron* as it has more species in PNG (13) than in Irian Jaya (7).

Rhododendron subsect. *Vireya* (= subsect. *Euvireya* Copel.):

Like *Diplycosia*, below, this group virtually defines Malesia, with slight extensions to southern Vietnam and the Solomons, and absences in Timor and the northern Moluccas.

Rhododendron ser. *Linnaeoidea* Sleum. (Fig. 19). The concentric distributions on Oranje Mts. as in *Pseudovireya* I could be the result of evolution around the margins of shrinking seas. Nine of the 11 species are in Irian Jaya, all but one on the craton. There are only three in PNG, a pattern like *Siphonovireya*.Sp. 137 is disjunct between Mt. Carstensz and Bismarck Range NW of Mt. Wilhelm (Takeuchi 1999a). Craven (1980) originally listed sp. 137A from Star Mts. to Wharton Range but van Royen and Kores (1982) list it east to New Britain.

Rhododendron ser. *Saxifragoidea* Sleum. (Fig. 20). This occurs only along the northern rim of the craton, from Mt. Carstensz to Mt. Giluwe.

Rhododendron ser. *Taxifolia* Sleum. (not mapped). Only on Luzon (Mts. Pulog and Tabayoc). This group is sister to the next.

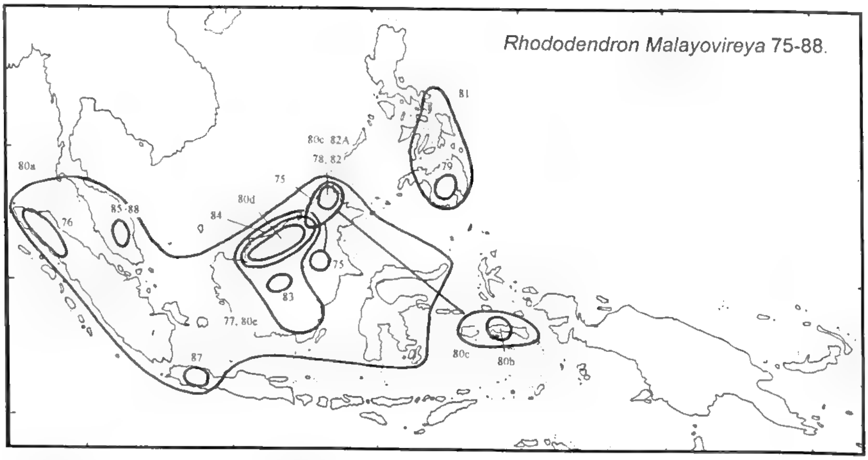

Fig. 15. *Rhododendron* subsect. *Malayovireya.*

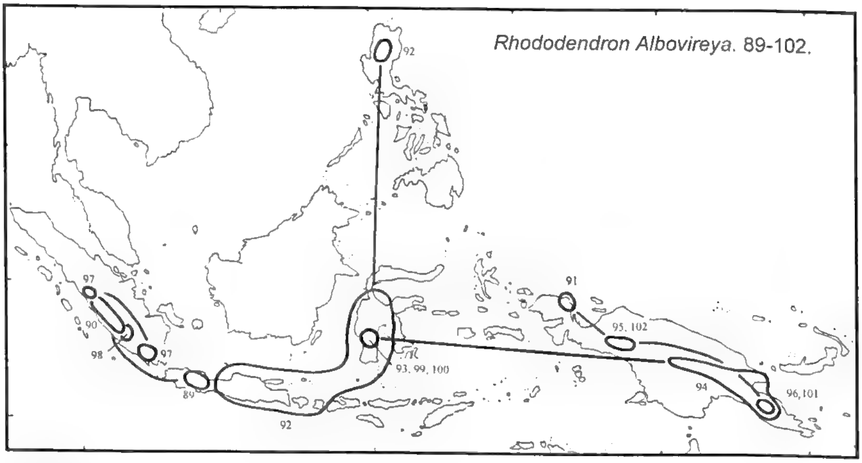

Fig. 16. *Rhododendron* subsect. *Albovireya.*

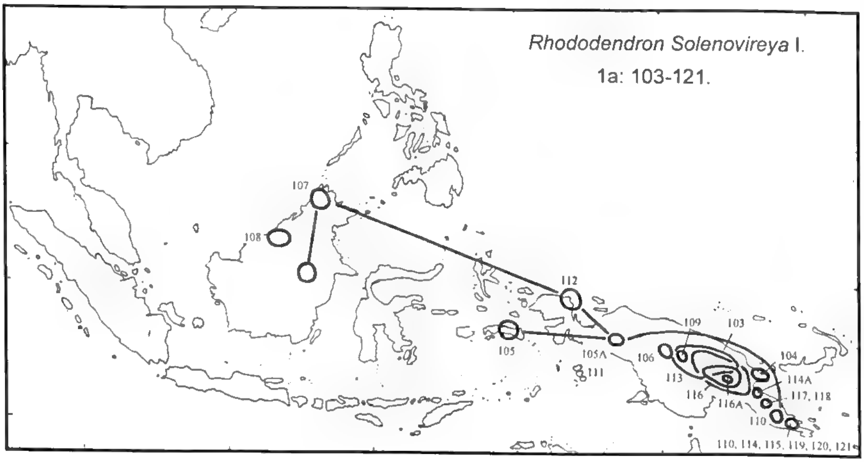

Fig. 17. *Rhododendron* subsect. *Solenovireya* I.

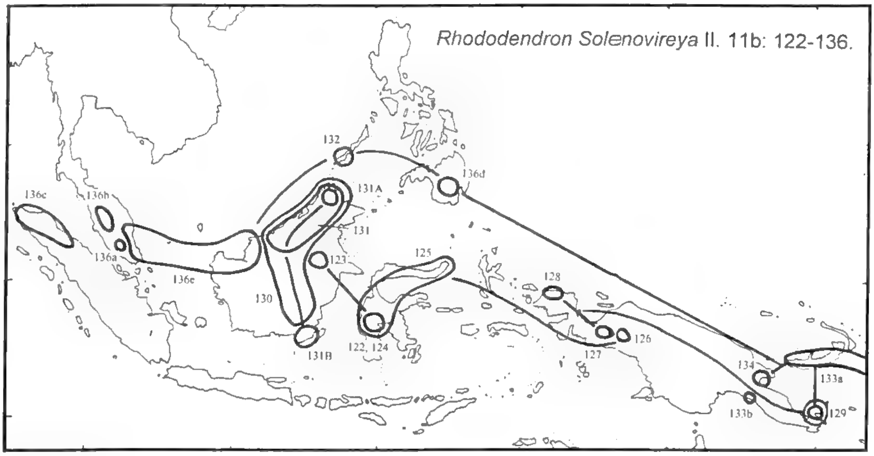

Fig. 18. *Rhododendron* subsect. *Solenovireya* II. 135 is included in 133. 133a is *R. loranthiflorum* var. *lakekamuensis* Takeuchi.

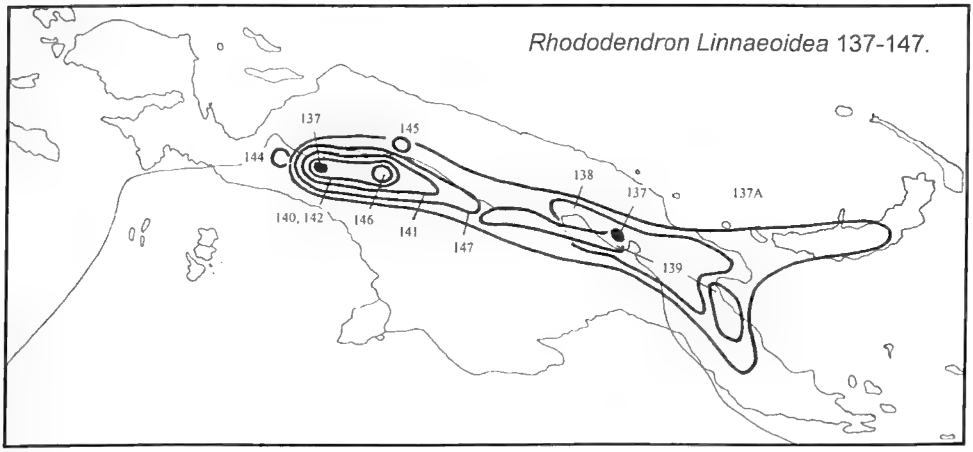

Fig. 19. *Rhododendron* ser. *Linnaeoidea*.

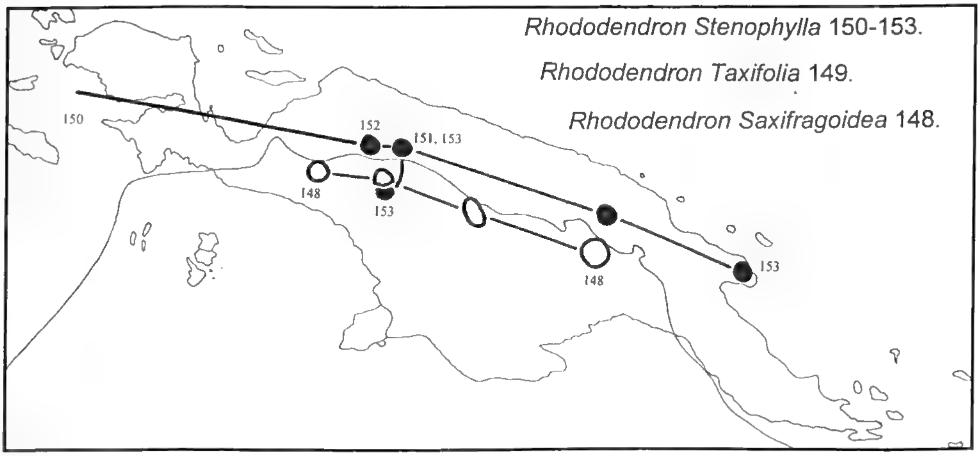

Fig. 20. *Rhododendron* ser. *Saxifragoidea*, *R.* ser. *Stenophylla*, *R.* ser. *Taxifolia*.

Rhododendron ser. *Stenophylla* Sleum. (Fig. 20). This occurs north of the craton only, except for a single record at Perameles Bivaque (Went Mts.) south of Mt. Wilhelmina. The group is disjunct in Borneo. Stevens (1976) suggested that the New Guinea species are probably allied instead with Papuasian members of Ser. *Javanica* and *Buxifolia*, but did not indicate a position for the Borneo species.

Rhododendron ser. *Citrina* Sleum. (Fig. 21). This comprises a single species of Sumatra and Java, keyed as sister to the remaining 122 Malesian *Rhododendron* species.

Rhododendron ser. *Buxifolia* Sleum. I. (Fig. 22). As in the last, a Sumatra species (155, Gajo Lands) is sister to the rest. The three New Guinea tracks (Luzon –Waigeo; Latimodjong – PNG mountains; Peninsular Malaysia – Snow Mts.) show New Guinea deconstructed into an amalgamation of island arcs and other terranes (cf. subsect. *Solenovireya* II, ser. *Saxifragoidea*/ser. *Stenophylla*). The map of sp. 162 is reproduced from Argent (1988).

Rhododendron ser. *Buxifolia* II. (Fig. 23). The Irian Jaya species is south of the former craton margin, sp. 173A tracks the margin. Both these are related to E and C Sulawesi species, rather than to the PNG species 170 and 171 which are outboard of the craton.

Rhododendron ser. *Buxifolia* III. (Fig. 24). This comprises a Vogelkop species sister to an outer arc of four species: Aceh (Gajo Lands) – Palawan (Mt Mantalingahan, cf. *Solenovireya*) – Owen Stanley Mts. This and the next map show three vicariant arcs.

Rhododendron ser. *Buxifolia* IV. (Fig. 25.). The Aceh (Gajo Lands) species is sister to the rest, and there are precedents for a direct Aceh–Kinabalu connection (e.g. *Potentilla borneensis* (Stapf) Kalkman (Rosa.), known only from the two localities and related to species of the Himalayas/Taiwan on one hand, and of Sulawesi/New Guinea on the other (Kalkman 1993)). There are two other significant disjunctions: 1. Kinabalu – Oranje Mts. (craton), and 2. Latimodjong – Oranje Mts.

Rhododendron ser. *Javanica* Sleum. I. (Fig. 26). This group is in Borneo (Sabah-Sarawak) and New Guinea, mainly on the craton, and absent from the Vogelkop, Huon Peninsula, and Milne Bay. The Nassau/Oranje/Treub Mts. – Wilhelm disjunction in 202 resembles differentiation in *Drimys piperita* Hook.f. (Winter.) discussed below. The NW Borneo – W New Guinea disjunction is seen in alpines such as *Kelleria* Endl. (Thymel.) (Fig. 127) and lowland plants such as *Dactylocladus* (Oliv.) (Crypteron.) (van Beusekom-Osinga 1977) (although in both of these the W New Guinea records are on Rouffaer terrane, rather than at Mts. Carstensz/Wilhelmina like the Rhododendrons). *Dactylocladus* forms trees up to 40 m tall with pneumatophores, and is one of the most characteristic taxa in the lowland peat swamp forests of W Borneo. Pollen has been reported in a Miocene deposit in Brunei with the same associates as to-day. As van Beusekom-Osinga noted, 'It is remarkable that whereas this type of peat forest ranged unbrokenly at least from the Miocene to the Present, *Dactylocladus* is not found in Sumatra and Malaya …'. The only other record of the genus is in New Guinea, in peat forest along the Rouffaer R. where it is 'the only large tree in this forest type'. Van Beusekom-Osinga (1977) argued logically that the absence of peat forest between New Guinea and Borneo is no explanation of the disjunction, as the same gap occurs in taxa such as *Koompassia* (Legum. – Caesalpin.) which are not peat-dwellers.

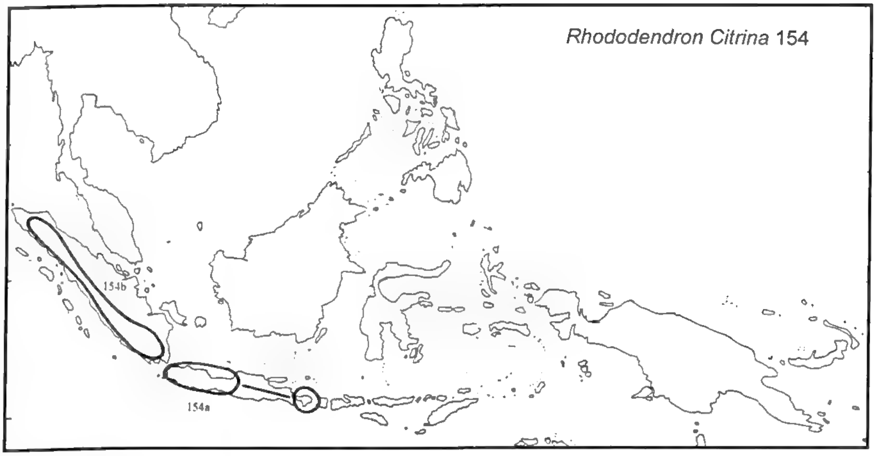

Fig. 21. *Rhododendron* ser. *Citrina*.

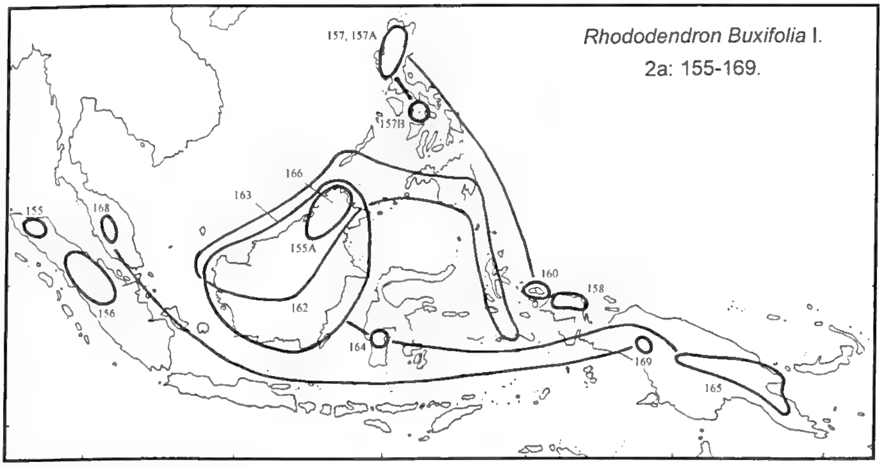

Fig. 22. *Rhododendron* ser. *Buxifolia* I. 159 is included in 170, 161 and 167 are hybrids. Distribution of 162 is from Argent (1988, 1998).

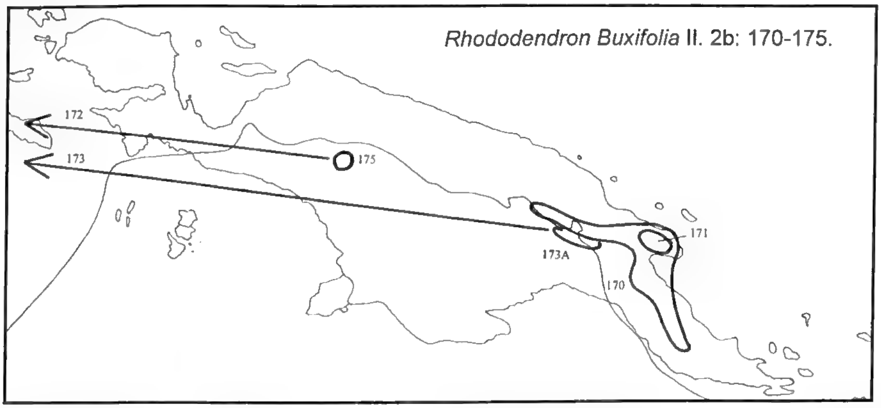

Fig 23. *Rhododendron* ser. *Buxifolia* II. 172 is also in C Sulawesi (Kambuno). 173 is in E–C Sulawesi: Lumut. 173A is 'to be inserted near 172 and 173', but is 'markedly different' (Sleumer 1973).

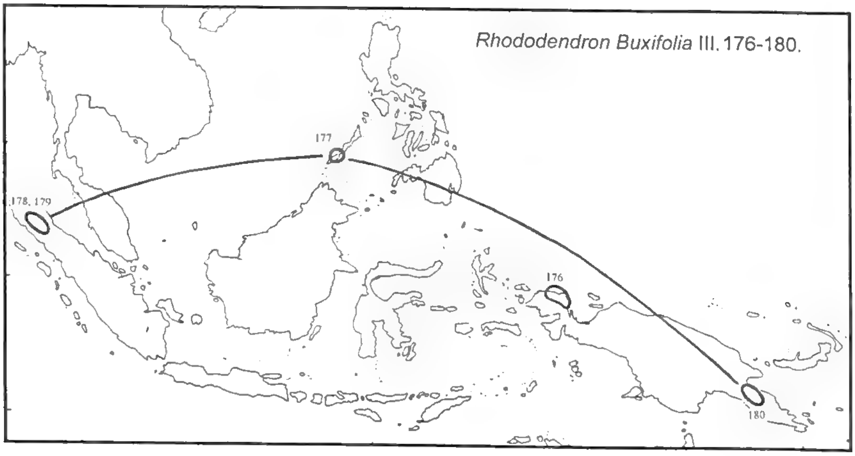

Fig. 24. *Rhododendron* ser. *Buxifolia* III. van Royen and Kores (1982) transferred 180 to ser. *Javanica*, but did not refer to the other species mapped here.

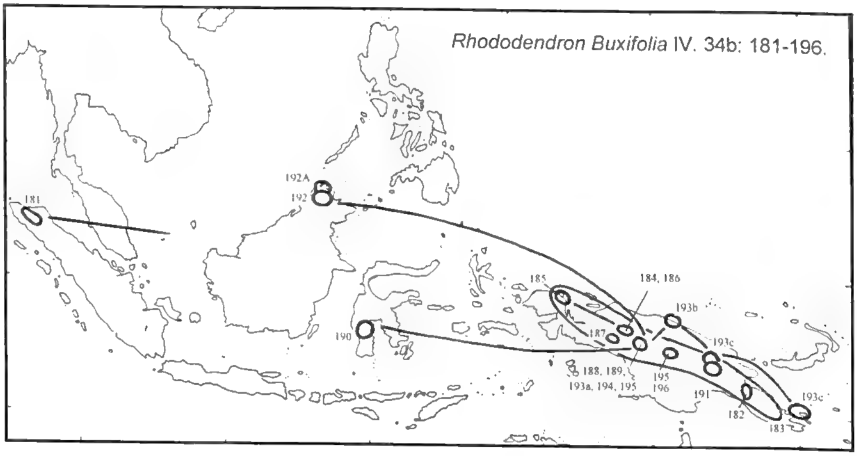

Fig. 25. *Rhododendron* ser. *Buxifolia* IV.

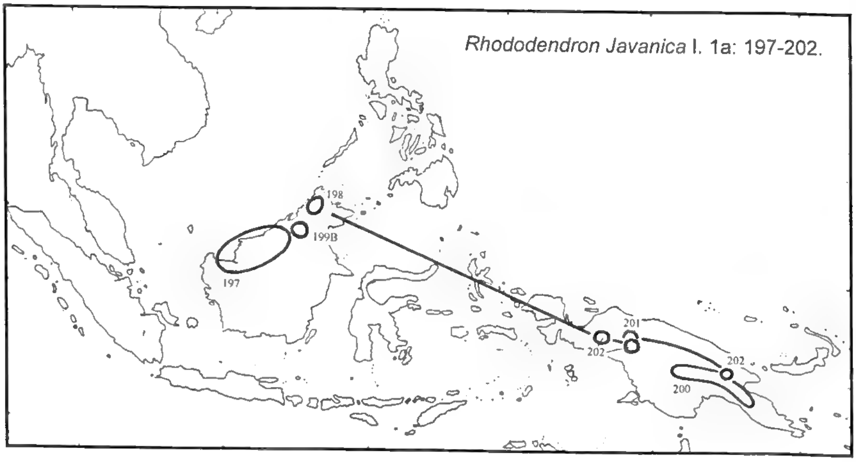

Fig. 26. *Rhododendron* ser. *Javanica* I. 199 is a hybrid.

Rhododendron ser. *Javanica* II. (Fig. 27). This group surrounds Borneo from the east. In PNG the group is only on accreted terranes, with sp. 204 on Finisterre terrane and 206 on Mt Obree, by the contact of Owen Stanley and Dayman terrane. (The large block of Dayman terrane lying east of Mt. Kenive(= Nisbet) and Mt. Obree (Pigram and Davies 1987) is shown on Bain et al.'s (1972) map as Owen Stanley terrane). Both PNG species are related to craton species in Irian Jaya (cf. the honeyeater *Macgregoria* etc.). However, the two PNG species are keyed together in Sleumer's key; instead there are two parallel arcs: NE Sulawesi – Wichmann Mts. – Huon Peninsula, and S Moluccas – Balim Valley/Mt Goliath – Mt Obree.

Rhododendron ser. *Javanica* III. (Fig. 28). Here a group on N Sumatra – N Philippines – Moluccas (214–218, hatched) surrounds Borneo, as does the group 219–225 (wide-spaced hatching) except for a record at Mt Kemul, central E Borneo. Spp. 219–225 are sister to 226–227. The CW Sumatra (Kerintji, 226) – Borneo (227) connection is also seen in the mangrove *R. brookeanum* (276). Sp. 268: *R. culminicolum* var. *angiense* occurs east to the Star Mts.; plants on New Ireland (Hans Meyer Ra.) are an undescribed variety (Johns and Argent 1995) which keys out to var. *angiense.*

Rhododendron ser. *Javanica* IV. (Fig. 29). The Latimodjong – New Guinea distribution is like that of *Phaeovireya* I and II. Sp. 229 holds an outer arc in PNG: Torricelli Mts. (Torricelli terrane) – Maboro Range (not located) – Waria R. (Bowutu or Owen Stanley terrane).

Rhododendron ser. *Javanica* V. (Fig. 30). 250: *R. longiflorum* occurs in the Mentawei Islands, W Sumatra, Riouw Pocket (Bangka I., where there is an endemic variety; Karimata Is.) and Borneo, where it is widespread but apparently not on Kinabalu (Sleumer 1973) (cf. *Costera, Vaccinium* sect. *Rigiolepis*). It is an epiphyte in primary and secondary forest and mangrove, and is terrestrial on rocks, in kerangas and in poor forest in stagnant water. It is keyed with 244–249 of New Guinea and the Solomon Islands (with a related species in NE Queensland). As suggested above, this is possibly the result of an Indian Ocean group occupying Malesia in an ancestral stage, and for the most part being largely uplifted in the New Guinea orogen — van Steenis's (1978b) observations on uplifted mangroves can be applied to the whole flora. The Arfak Mts – Mt. Dayman disjunction (247–248) is an outer arc parallel to the Snow Mts – Owen Stanley Mts seen in groups like *Albovireya* and *Solenovireya* I. spp. 237–238 (Cyclops terrane – Bismarck Mts) are the largest-flowered rhododendrons, both occur only on accreted terrane.

Rhododendron ser. *Javanica* VI. (Fig. 31). There are two arcs: Philippines – accreted terranes of PNG (Jimi Valley – Jimi terrane; Bulolo/Wau – Owen Stanley terrane); and New Guinea – southern Moluccas.

Rhododendron ser. *Javanica* VII. (Fig. 32). The double tracks here again indicate the hybrid nature of Borneo, Sulawesi and New Guinea.

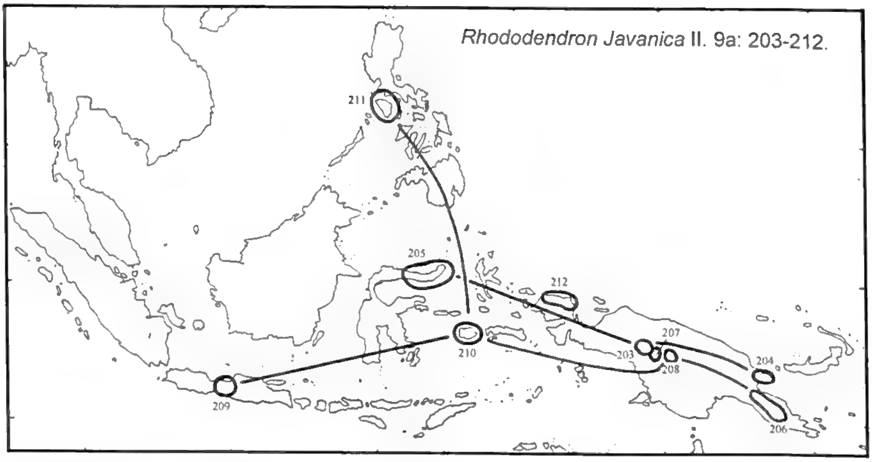

Fig. 27. *Rhododendron* ser. *Javanica* II.

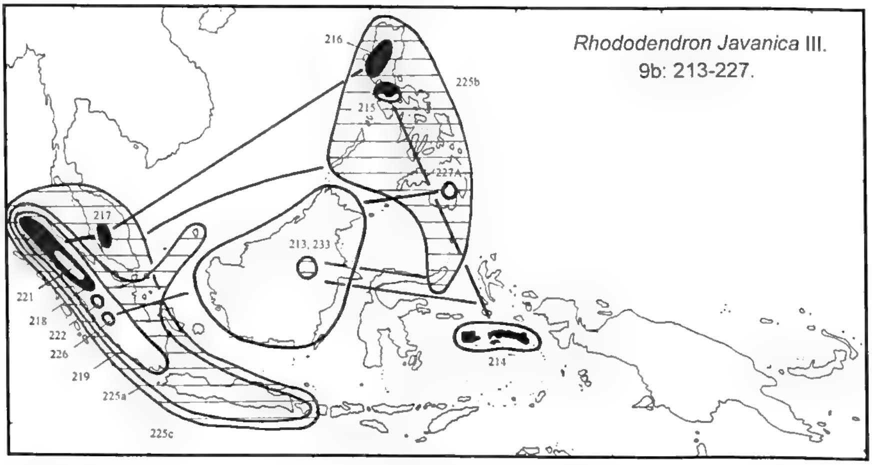

Fig. 28. *Rhododendron* Ser. *Javanica* III. 220 is included in 227. Taxon 224 is a variety of 276.

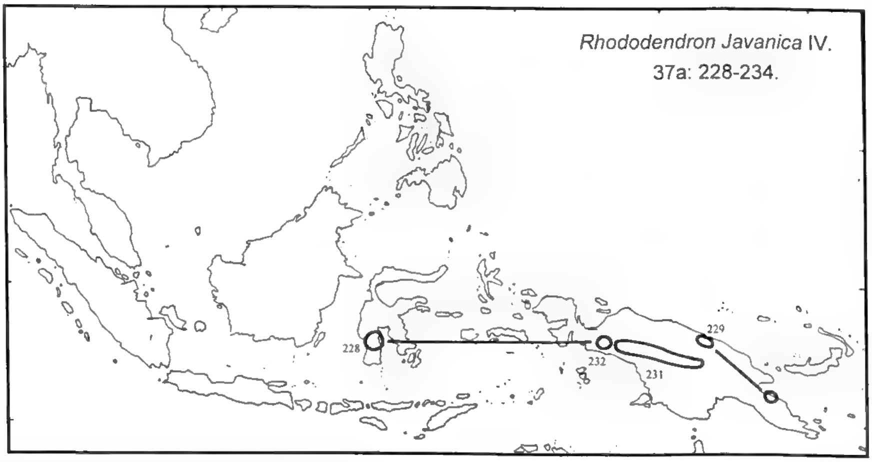

Fig. 29. *Rhododendron* ser. *Javanica* IV. Sp. 230 is recorded only from 'New Guinea' and has not been mapped. 233 and 234 are included in 250.

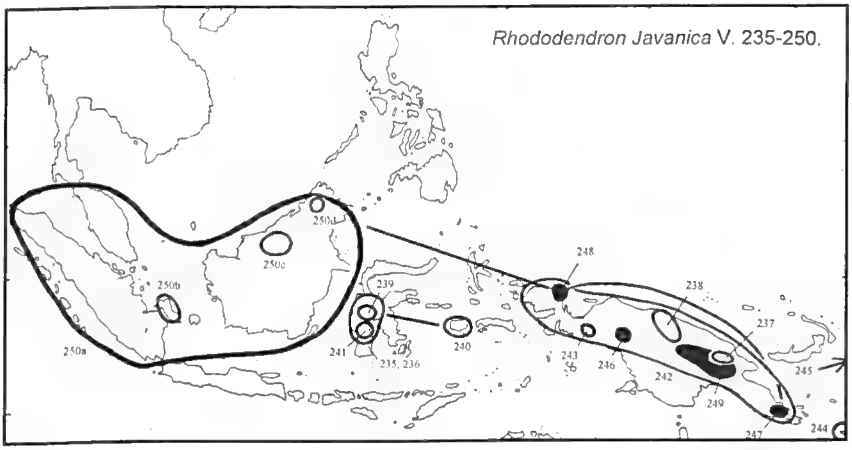

Fig. 30. *Rhododendron* ser. *Javanica* V. Sp. 244 of Sudest I. is closest to the Queensland species. Within the Malesian species it is keyed with 245 of Bougainville, New Georgia and Guadalcanal (Sleumer 1966).

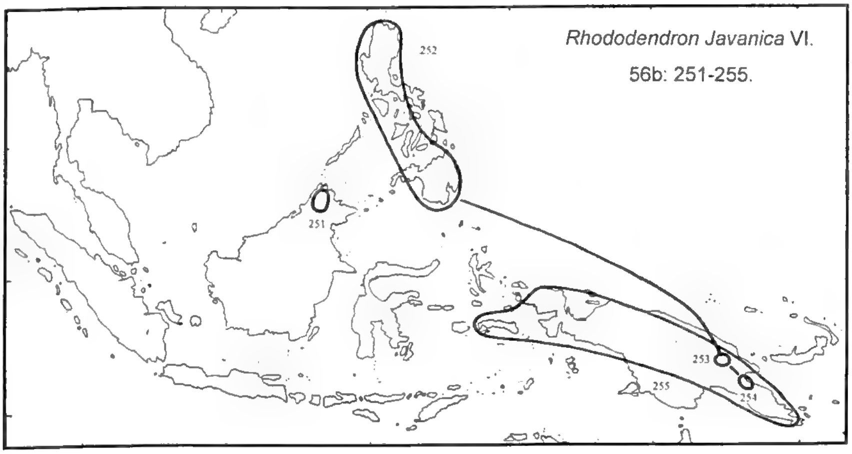

Fig. 31. *Rhododendron* ser. *Javanica* VI. Argent (1992) suggested 251 might be better placed with 198.

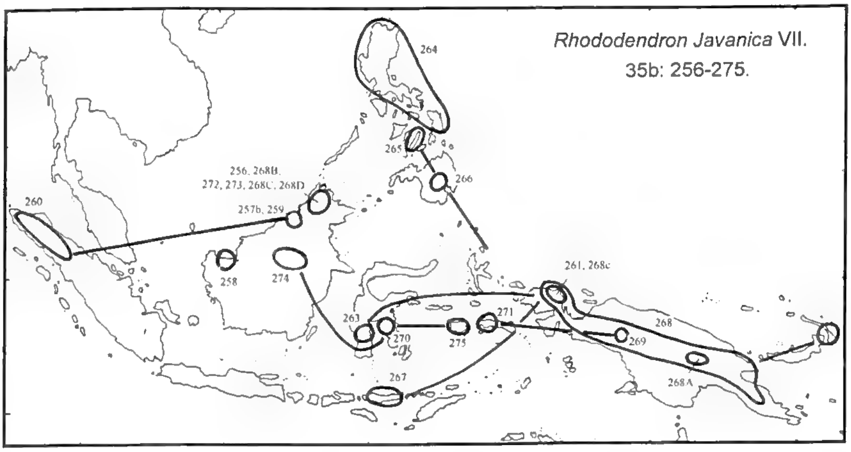

Fig. 32. *Rhododendron* ser. *Javanica* VII. 262 is a hybrid.

276. *Rhododendron brookeanum*, (Fig. 33), recorded from mangrove, is in CW Sumatra and widespread in Borneo (cf. 227). It is shown separately here for convenience, but belongs with *Javanica* VII with which it is largely vicariant. However, Argent (1988) described material from E. Sabah which shows remarkable similarity to the Javan form of 225: *R. javanicum* and is very distinct from most other forms of *R. brookeanum* in Sabah. Argent had earlier synonymised these two, but later accepted them as distinct. However, recent acquisition of new material from Sumatra 'throws back all the old problems of making distinctions of more than one character that do not have exceptions in wide ranging low altitude species'. The fluidity of the situation in these widespread, low altitude W Malesian mangrove/volcano plants perhaps resembles that of the ancestral complex out of which the large diversity of montane, more or less local endemics in E Malesia 'precipitated'.

The following three Asian subgenera occur only at the northern and western margins of Malesia:

Rhododendron subgen. *Hymenanthes* (Bl.) K.Koch (Fig. 34). N Sumatra/Peninsular Malaysia.

Rhododendron subgen. *Tsutsutsi* (G.Don) Pojarkova (Fig. 34). Luzon.

Rhododendron subgen. *Azaleastrum* Planch. (Fig. 35). Peninsular Malaysia.

Monotropoideae

Monotropoideae is not mapped here. *Andresia* Sleum., *Monotropastrum* Andres and *Pyrola* L. (the latter formerly in Pyroloideae) each have one species in Malesia: in Peninsular Malaysia, N Sumatra (Tapanuli, Gajo Lands), and Peninsular Malaysia respectively.

Lyonia Nutt. was treated by Sleumer with *Pyrola*, but the DNA studies cited above support a position with Vaccinioideae. It is in Malesia only in Peninsular Malaysia.

Pernettyopsis King & Gamble. (Fig. 36). Peninsular Malaysia – N Sarawak (Mt Mulu, Argent (1982)). It is keyed by Sleumer (1966) with *Gaultheria* and *Diplycosia*.

Gaultheria L. I. (Fig. 36). *Gaultheria* has Malesian centres of diversity in Sumatra and New Guinea and only one species out of 24 in Borneo. This is vicariant with its near relative *Diplycosia* which has almost half its 97 species in Borneo, and secondary centres in Sulawesi and New Guinea. Middleton (1991) revised the infrageneric classification of *Gaultheria*, which occurs in east Asia, Australasia and the Americas. Four of the ten sections in the genus are represented in Malesia.

G. sect. *Brossaeopsis* Airy Shaw comprises three series. One is monospecific in the Himalayas. Ser. *Dumicolae* Airy Shaw occurs in the Himalayas, Yunnan (*G. notabilis*) and disjunct in Sumatra (spp. 7–9). Ser. *Atjehenses* Airy Shaw comprises spp. 2 and 3 from Sumatra and Java. Sleumer wrote that sp. 2 is 'remarkably near' *G. notabilis* and the Himalaya/Yunnan – Sumatra disjunction is notable. The section is closest to plants of the Andes.

G. sect. *Monoanthemona* Middleton (wide hatching on map) is a trans-Pacific group comprising three series. The first is monospecific for 10: *G. nummularioides*: Himalayas to W Szechuan and Upper Burma, disjunct to Sumatra, Java and Bali. This is 'difficult to separate' from ser. *Antipodae*, comprising 11: *G. mundula* of New Guinea, and plants of Tasmania, New Zealand and western South America. The last series is in SE Brazil.

Gaultheria II. (Fig. 37). North Sumatra – Peninsular Malaysia – Vogelkop. Again, Borneo is hardly involved in this pattern, and has no endemics.

G. sect. *Brossaea* (L.) Middleton, by far the largest in the genus, ranges from Asia to Australasia and America. The Malesian species 1, 4–6 (see *Gaultheria* I) and 12–22 were treated here by Middleton in two series which show little biogeographic separation. The disjunction between the Vogelkop (16) and 17–19 may be to Peninsular Malaysia (17, 19) or Sumatra/Java (18).

G. sect. *Chiogenopsis* Middleton includes 23: *G. novaguineensis* (New Guinea) and 24: *G. pernettyoides* (Gajo Lands) (both fine hatching on map), both allied with Himalayan/Chinese species (cf. *Pseudovireya* II, *Buxifolia* I). The section is elsewhere known from Japan and North America.

Diplycosia Bl. I. (Fig. 38). There are two parallel arcs: Luzon – Vogelkop (Arfak terrane) – April R. (Sepik terrane); and Borneo – Vogelkop (Tamrau terrane) – Star Mts. The taxa in the second are related to a third E Borneo track: Kinabalu – Mt. Kemul. There is a strong massing on Kinabalu as in *Diplycosia* IV and V. In addition to these montane plants, the Kinabalu region has endemic lowland species, such as *Caesalpinia oppositifolia* Hattink: open spaces in primary forest, up to 600 m, Kinabalu and Sandakan (NE Sabah) (Hou, Larsen and Larsen 1996). A Philippines – New Guinea connection similar to that of *Diplycosia* 10–11 is seen in the fern *Belvisia platyrhynchos* (Kunze) Copel. (Polypod.) of Luzon, Mindoro, Mindanao, and Japen I. (Hovenkamp 1998), the last locality comprising part of the Arfak terrane.

Diplycosia II. (Fig. 39). The species shown here do not comprise a single group, but rather four basal groups in, respectively: Latimodjong Range; Kinabalu; the Gajo Lands; and CE Sulawesi – N Borneo. The last range illustrates Wallace's Line as a centre of endemism, rather than a boundary line (cf. Tan 1998).

Diplycosia III. (Fig. 40). These species largely surround Borneo to the north and are vicariant with groups in *Diplycosia* I, IV and V which mass in Borneo. New Guinea disintegrates into the following tracks: Philippines – Vogelkop; Wandammen – Cyclops terrane; North Sumatra (Gajo Lands) – Sepik terrane (Hunstein Mts./Sepik Basin); Mt. Bonthain – old cratonic New Guinea (Kubor Mts). Two species (34, 41) show the important break between Tamrau and Netoni terranes (cf. *Diplycosia* I), and the two varieties of sp. 28 show the same break, with one in the Tamrau and Tohkiri Mts. (Tamrau terrane), the other in the Nettoti Mts. (Netoni terrane) and Arfak Mts. (Arfak terrane)

Diplycosia IV. (Fig. 41). This group is massed in northern Borneo and the Latimodjong/Paloppo/Makale region of C Sulawesi, and again Wallace's Line (77–78) appears as a centre of endemism in its own right, rather than simply as a boundary. New Guinea is held by two parallel arcs: Aceh–Vogelkop (cf. *Diplycosia* III, *Gaultheria* II etc.) and Mindanao–Doormantop. Like these arcs, spp. 69–78 (black in figure) also largely surround the massing of species in Sarawak.

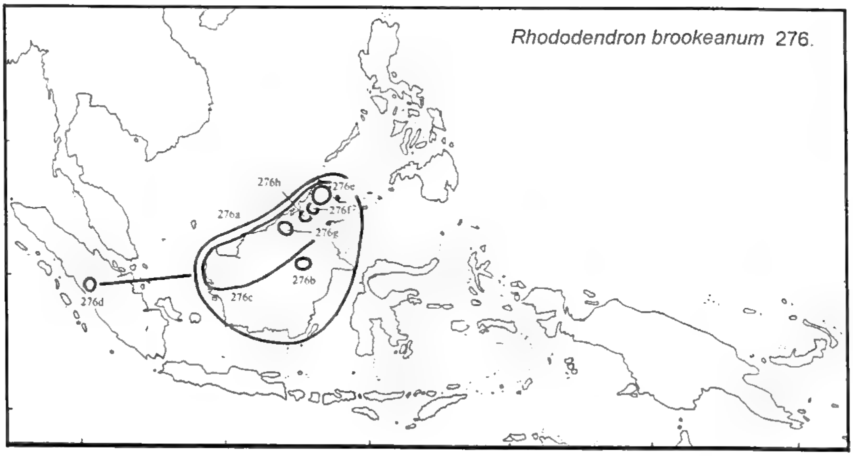

Fig. 33. *Rhododendron brookeanum*. 276c is *R. b. var kinabaluense* (Argent, Lamb and Philips) Argent; 276f is *R.b.* subsp. *cockburnii* (Argent, Lamb and Philips) Argent; 276g is *R. b.* subsp. *gracile* (Lindl.) Argent; 276h is *R. b.* var. *moultonii* (Ridl.) Argent.

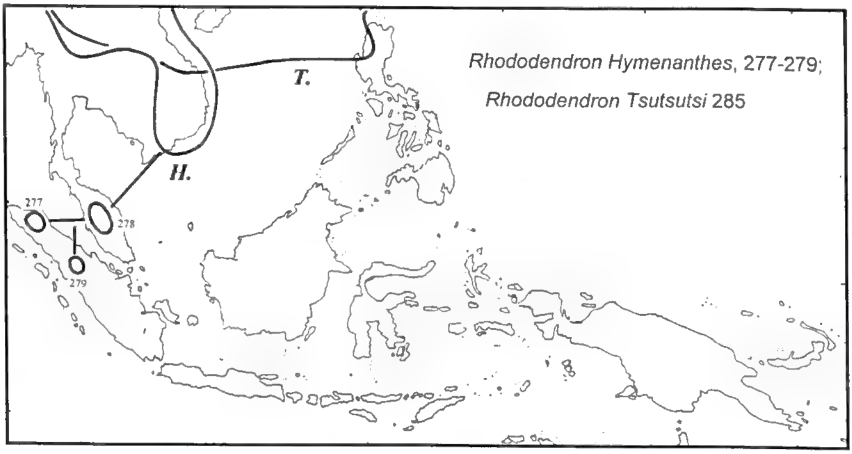

Fig. 34. *Rhododendron* subgen. *Hymenanthes*, and *R.* subgen. *Tsutsutsi*.

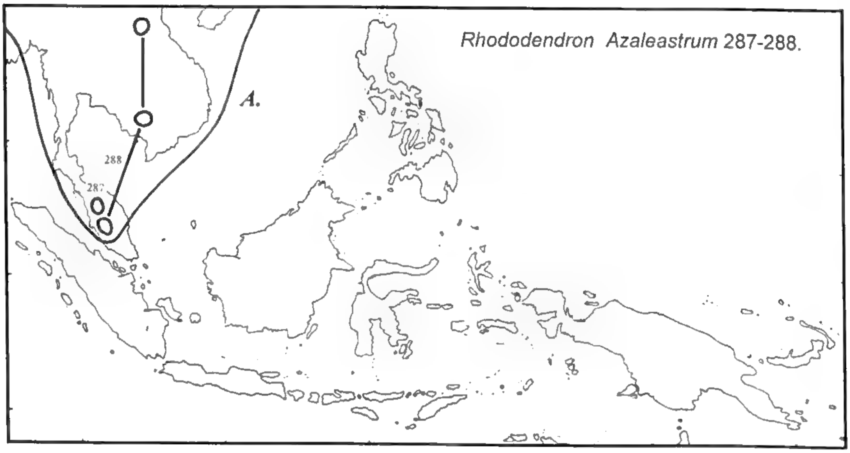

Fig. 35. *Rhododendron* subgen. *Azaleastrum*.

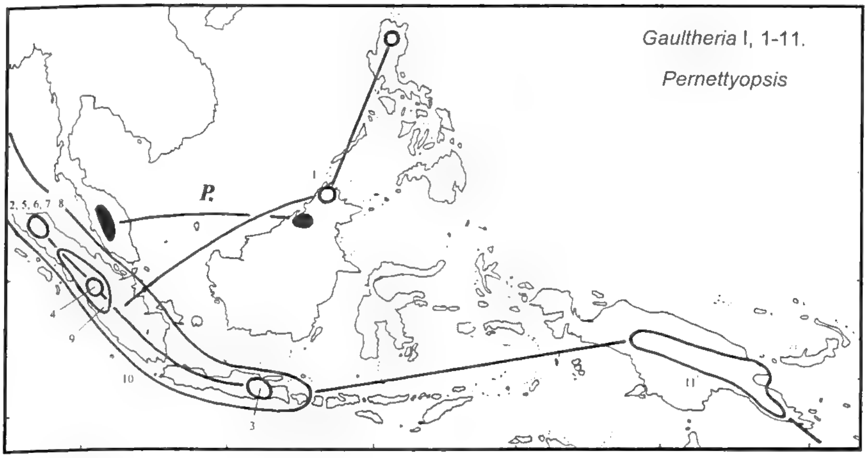

Fig. 36. *Pernettyopsis* and *Gaultheria* I.

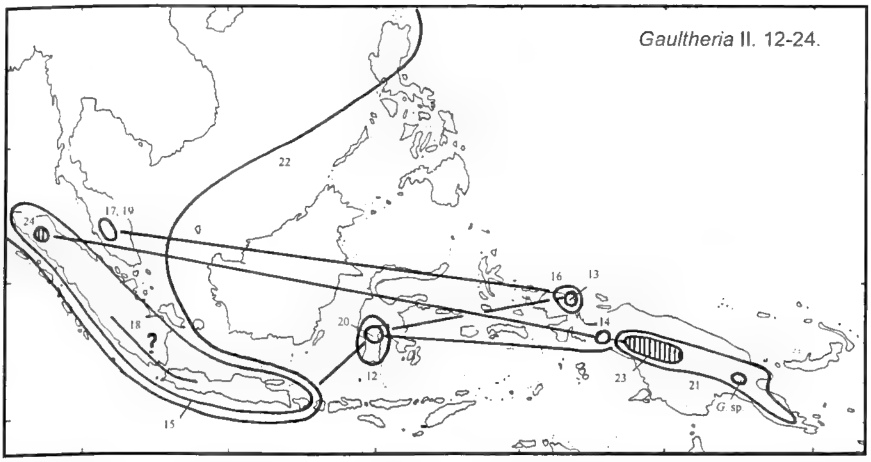

Fig. 37. *Gaultheria* II. The distribution of 18 is given as 'Java (Merapi) or Sumatra (Lower Tapanuli)'. *Gaultheria* sp from Crater Mountain (indicated on the map) 'could be new' (Takeuchi 1999b).

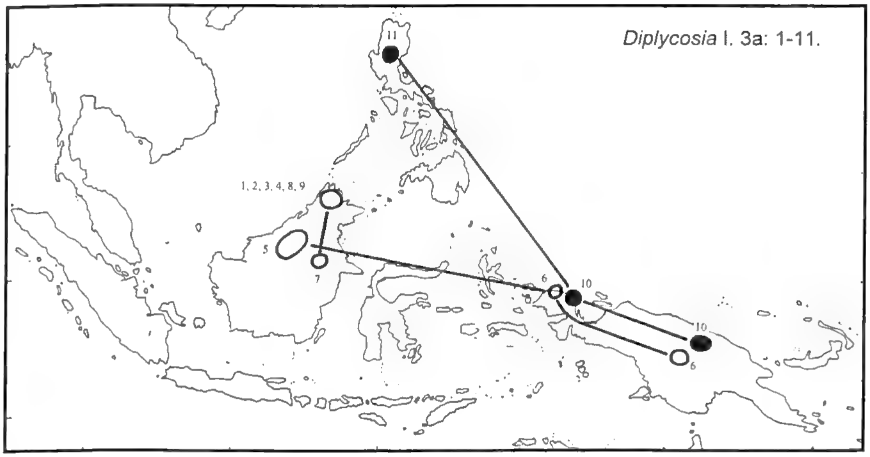

Fig. 38. *Diplycosia* I.

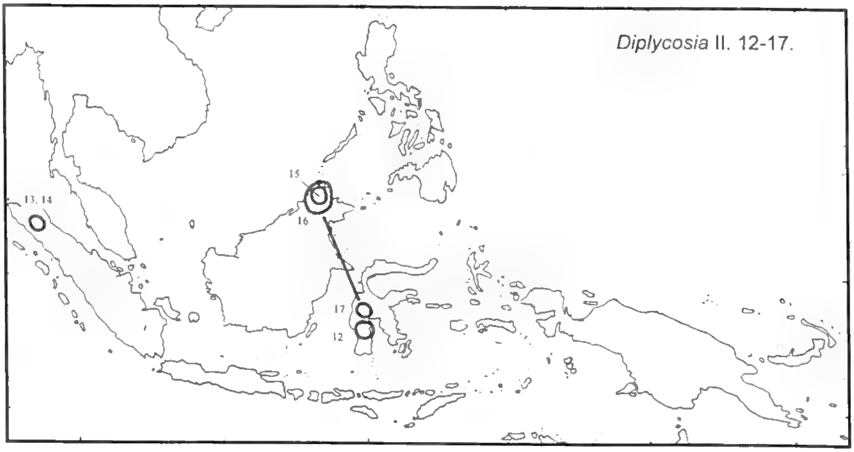

Fig. 39. *Diplycosia* II.

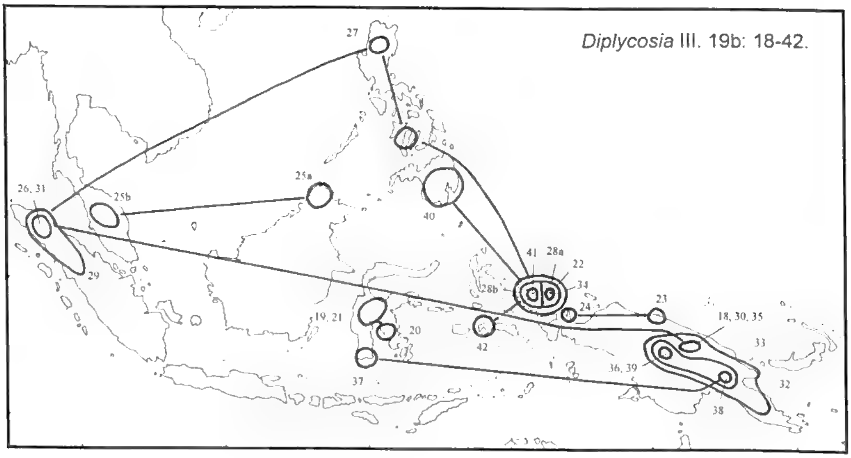

Fig. 40. *Diplycosia* III.

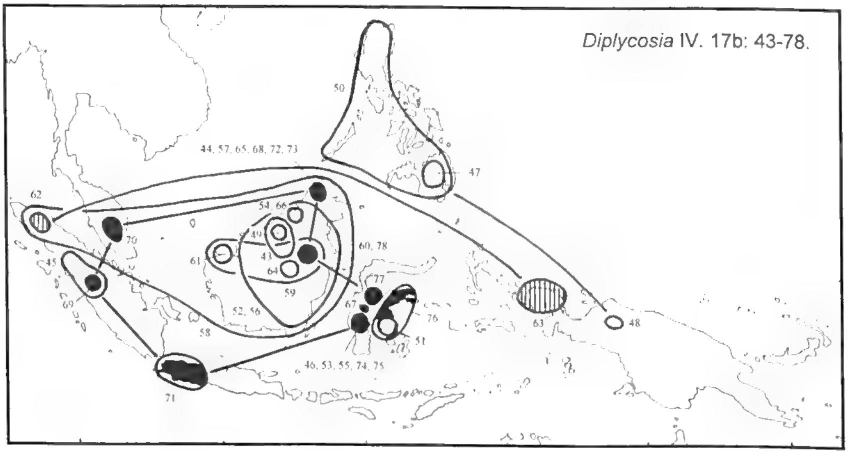

Fig. 41. *Diplycosia* IV.

Diplycosia V. (Fig. 42). The group is divided into largely eastern (79–90) and western (91–96) groups, but sp. 80 in W Sumatra is allied with the eastern group. The map is very similar to that of *Vaccinium* sect. *Bracteata* IX, below. The large disjunction Kinabalu – PNG (Finisterre and Owen Stanley terranes) is also seen in *Grammitis clemensiae* (Copel.) Parris (Parris 1983). A similar pattern is seen in *Phytocrene* Wall. (Icacin.) which extends east past Borneo to Sulawesi, and is disjunct from there to PNG: Morobe (Boana) and Mt Victoria (Sleumer's 1971a map does not quite match the text), and cf. *Lamiodendron* (Fig. 130).

Costera J.J.Sm. (Fig. 43). The widespread species 9 ranges around the Riouw Pocket, as does the track: SW Sumatra – Karimata I. (cf. *Diplycosia* V). The Mt. Kemul area is crucial here, but Kinabalu, where *Diplycosia* has its main massing, has no endemics.

The presence of *Costera* (Vaccinioideae, Pacific Ocean) in the northern Moluccas is significant as *Rhododendron* (Rhododendroideae, Indian Ocean) is only in the southern Moluccas, indicating local vicariance of the two subfamilies.

Vaccinium in Malesia

Vaccinium has six sections in Malesia, of which three — *Pachyanthum*, *Neojunghuhnia* and *Oarianthe* — are in the east. Sect. *Bracteata* is similar, with about two thirds of its species in the Philippines, Moluccas and New Guinea. In contrast, sects. *Rigiolepis* and *Galeopetalum* are concentrated in the west. The Himalaya–China region is an important centre for *Vaccinium* with about 100 species but this is quite distinct from the Malesia centre, and only two sections (*Bracteata* and *Galeopetalum*) occur in both.

Vaccinium sect. *Pachyanthum* Sleum. (Fig. 44). Stevens (1974a) transferred this distinctive group to *Dimorphanthera*, but molecular studies indicate that it is closer to '*Agapetes*' subgen. *Paphia* (Seem.) Stevens and here it is retained in *Vaccinium*. PNG has all six species (five between Doma Peaks and Mt Victoria); and apart from one on the border, Irian Jaya has none. This pattern is unlike any *Rhododendron* group, but recalls '*Agapetes*' subgen. *Paphia* (below). This is probably a reflection of the Pacific base of Vaccinioideae absent in *Rhododendron*.

Vaccinium sect. *Galeopetalum* (J.J.Sm.) Sleum. (Fig. 45). This ranges all the way from SE Tibet through Indochina and Malesia to W Java, but it is not in Borneo. However, it is keyed with the next group, sect. *Rigiolepis*, which has 19 of its 25 species in Borneo – mainly in Sarawak and Kalimantan (there is only one at Kinabalu).

Vaccinium sect. *Rigiolepis* (Hook.f.) J.J.Sm. (Fig. 46). Sp. 22c is endemic to the Mentawei Islands where there are also high rates of endemism in other plants, birds and primates. Sp. 27 is terrestrial on limestone rocks, epiphytic on mangroves; and follows the common mangrove track: Riouw Pocket (e.g. Lingga Archipelago) – SW Borneo, but neither this widespread species nor its many Borneo relatives, occur around Kinabalu. The Kinabalu species is related not to other Borneo species but to one from Sulawesi.

This and the last group, both in W Malesia, are sister to the remaining *Vaccinium* groups (spp. 30–239), widespread in Malesia.

Vaccinium sect. *Oarianthe* Schltr. I. (Fig. 47). As in *Diplycosia* III, plants of the Tamrau terrane (39) are distinct from those of the Arfak and Netoni terranes (36). There is a disjunction (in 40) between the Schrader terrane/Upper Minj R. and the Owen Stanley terrane, and also one (in 30) between the Arfak and Bismarck Mts. (Takeuchi 1999a).

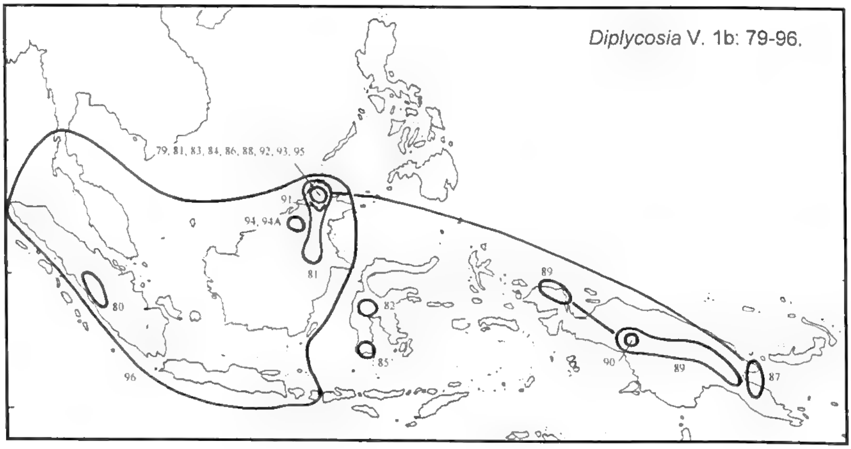

Fig. 42. *Diplycosia* V.

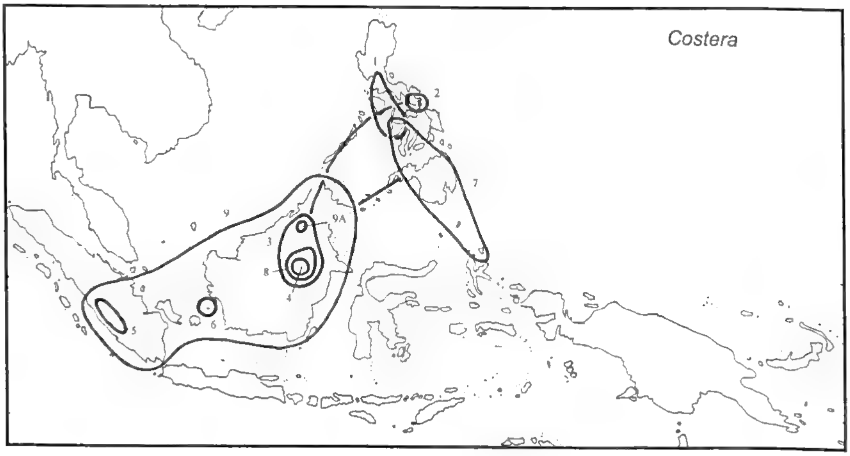

Fig. 43. *Costera*.

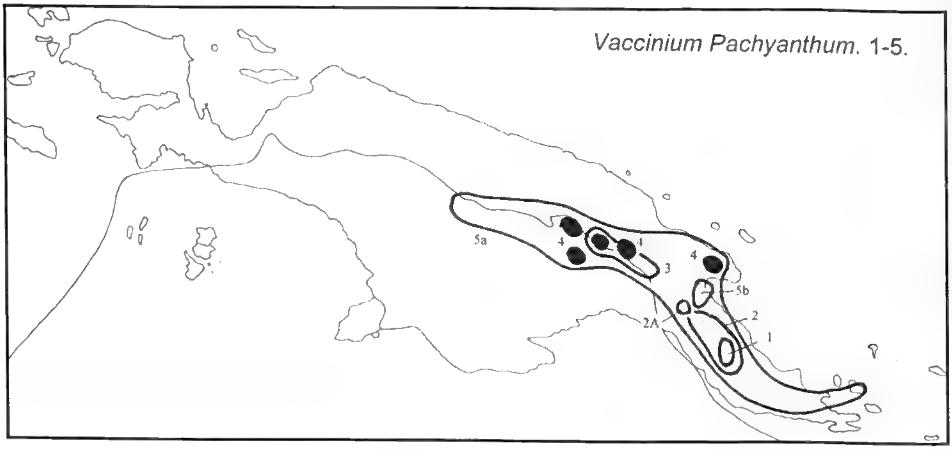

Fig. 44. *Vaccinium* sect. *Pachyanthum*.

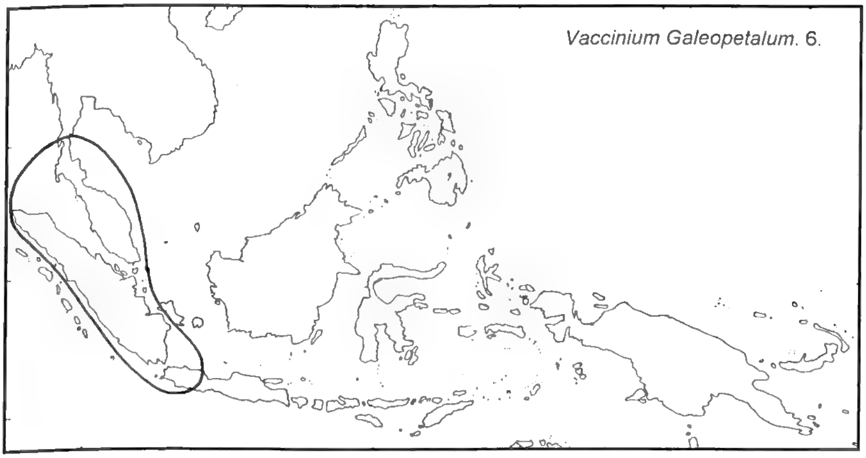

Fig. 45. *Vaccinium* sect. *Galeopetalum.*

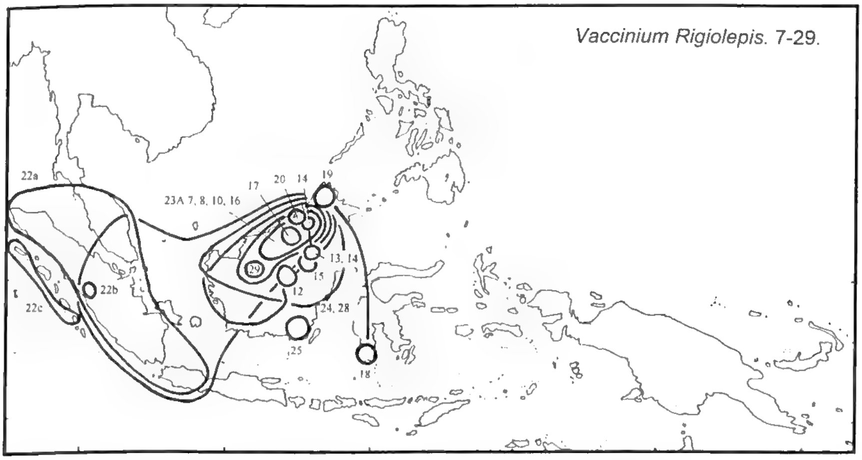

Fig. 46. *Vaccinium* sect. *Rigiolepis* Four species have not been located: 11. C Borneo (Amai Ambit), Sarawak (Ulu Mayeng, Sg. Kakus), 12. C Borneo (Batu Lesong, U. Kapuas). 23. Sarawak (Gat, U. Rejang R.), 26. Sarawak (Mt. Api).

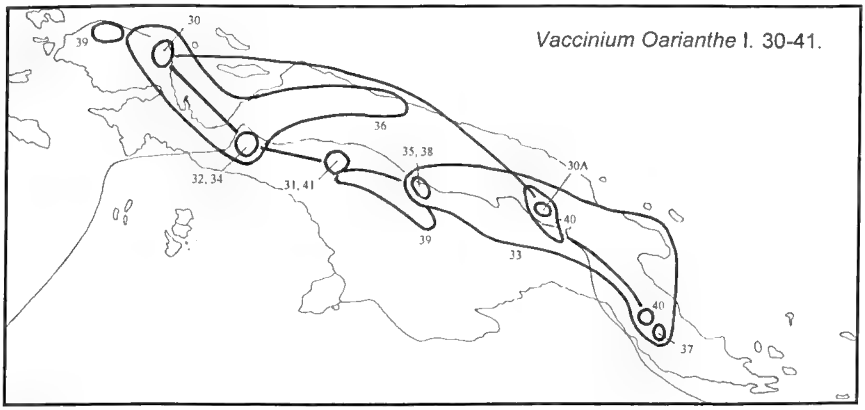

Fig. 47. *Vaccinium* sect. *Oarianthe* I. The Bismarck Mts. record of *Vaccinium* sp. aff. 30 is from Takeuchi (1999).

Vaccinium sect. *Oarianthe* II. (Fig. 48). This comprises four parallel arcs: Vogelkop–Cyclops terrane etc.; Wandammen – upper Sepik (10 km south of Landslip terrane: known from the type only, lost); Ceram – W Nassau Mts – Doormantop (the last locality with the most dramatic disjunction, as usual) – Bougainville; Snow Mts – Saruwaged Mts.

Vaccinium sect. *Oarianthe* III. (Fig. 49). The outer arc species at Philippines/Moluccas – Vanuatu is sister to the rest in W New Guinea, five of which have concentric distributions on Doormantop – Oranje Mts. A similar striking disjunction occurs in *Ginalloa arnottiana* Korth., of Borneo, Sulawesi, the Philippines and Moluccas, and also the Solomons (Barlow 1997). The intervening area in New Guinea and New Britain is occupied by the related *G. flagellaris* Barlow. Species of *Dacrydium* (Fig. 80) and *Podocarpus* (Fig. 87) show the same Moluccas – Solomons disjunction.

Vaccinium sect. *Oarianthe* IV. (Fig. 50). Sp. 60 has the disjunct range: Arfak – Wondiwoi – Wissel Lakes, on the edge of the craton. This group and the last are poorly represented in PNG (unlike sect. *Oarianthe* V (next), sect. *Pachyanthum*, etc.).

Vaccinium sect. *Oarianthe* V. (Fig. 51). N Philippines – PNG, like *Solenovireya* II and *Javanica* VI (and cf. *Oarianthe* II: Philippines-Vogelkop). The Huon Peninsula species (72) is more closely related to the Irian Jaya species than to the other PNG species, as in *Oarianthe* II.

Vaccinium sect. *Neojunghuhnia* (Koord.) Sleum. (Fig. 52). One group (74–77) has three of its four species on widely disjunct accreted terranes (Arfak terrane, Sepik terrane (April R.), Owen Stanley terrane (Mafulu)), and one on the craton in the Oranje Mts at Mt Resi. The other group (78–86) is only on the craton.

Vaccinium sect. *Bracteata* Nakai. This group (Sleumer 1967: Fig. 95) is most diverse in New Guinea (74 species) and Philippines (28), with only 16 in Borneo. The Philippines-New Guinea axis (a standard connection in Pacific groups, see below) contrasts with the main centres of Malesian *Rhododendron* - New Guinea and Borneo. East of the New Guinea mainland *V.* sect. *Bracteata* is at New Caledonia (and Vanuatu), a connection also seen in plants like *Hunga* Prance (Chrysobalan.) (Prance 1989).

Vaccinium sect. *Bracteata* I. (Fig. 53). sp. 87 (to Burma and China) and 88 are on seashores, sandy coasts and padang around the Riouw Pocket (Bangka, Billiton, Lingga Islands etc.) and in Sulawesi. Spp. 89 and 90 reach higher altitudes in Sulawesi. Borneo is surrounded and not occupied, although the group is on nearby Karimata Island.

Vaccinium sect. *Bracteata* II. (Fig. 54). Peninsular Malaysia – Mindanao – PNG (cf. *Buxifolia* III, *Solenovireya* II). Not in Borneo.

Vaccinium sect. *Bracteata* III. (Fig. 55). There are massings in Aceh, Luzon and Irian Jaya, and Borneo is surrounded, as in *Bracteata* I.

Vaccinium sect. *Bracteata* IV. (Fig. 56). This ranges in Central Sulawesi and New Guinea, with the usual disjunction: Irian Jaya craton (Oranje Mts.) – PNG accreted terrane (Mt Victoria) (in 120). Sp. 125 (type only, lost) is at the West Range (Landslip and Dimaie terranes) (cf. 128, next).

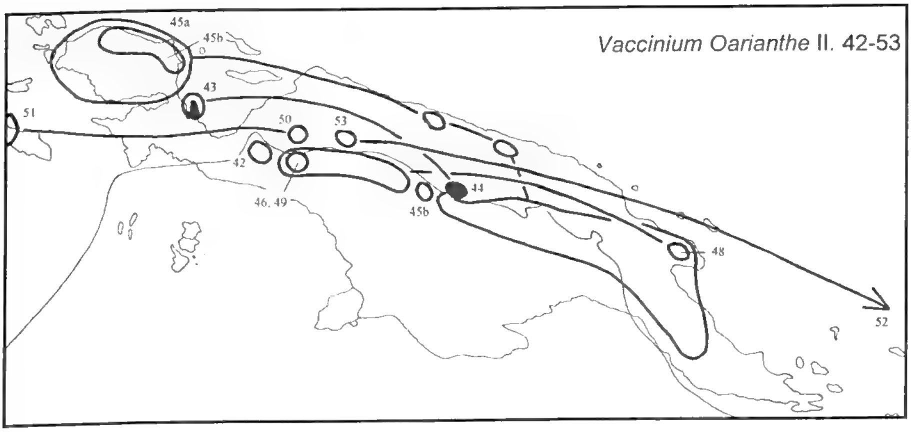

Fig. 48. *Vaccinium* sect. *Oarianthe* II.

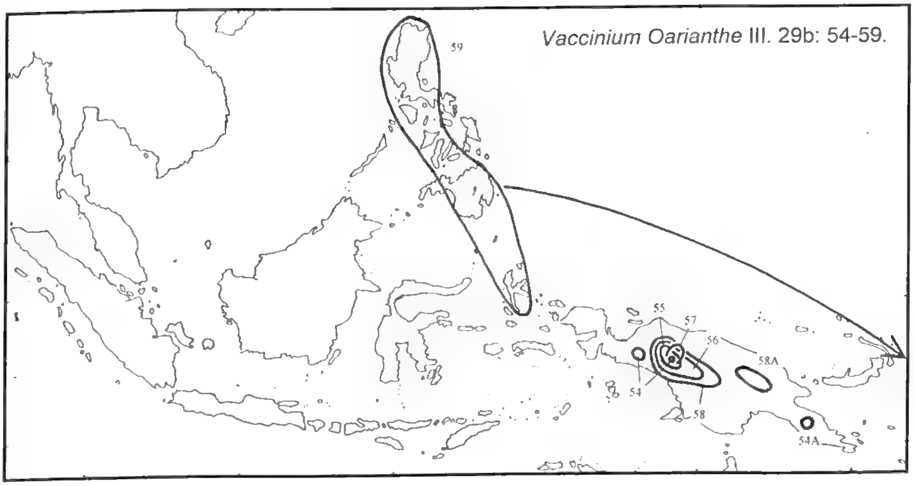

Fig. 49. *Vaccinium* sect. *Oarianthe* III.

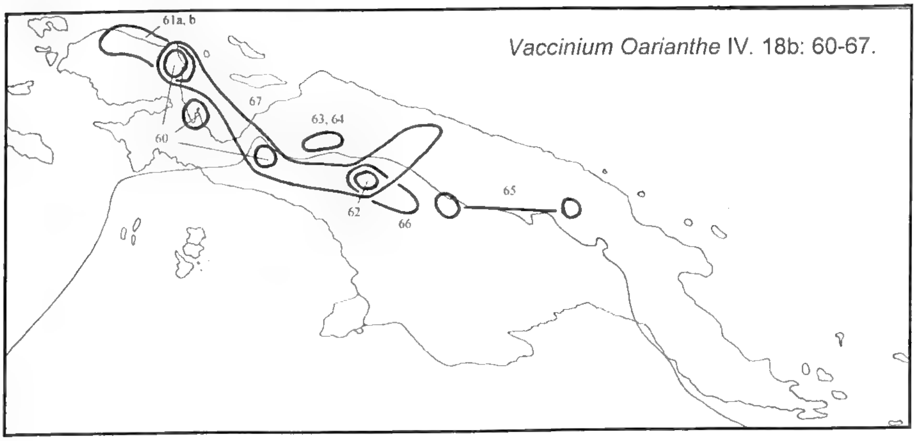

Fig. 50. *Vaccinium* sect. *Oarianthe* IV.

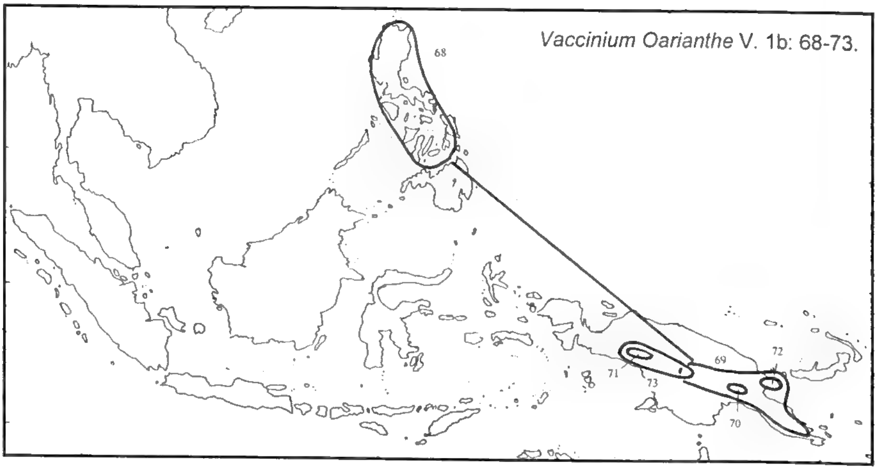

Fig. 51. *Vaccinium* sect. *Oarianthe* V.

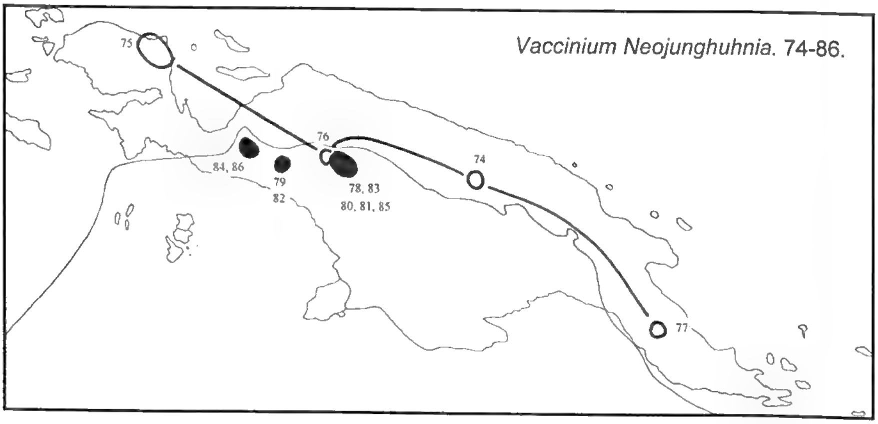

Fig. 52. *Vaccinium* sect. *Neojunghuhnia.*

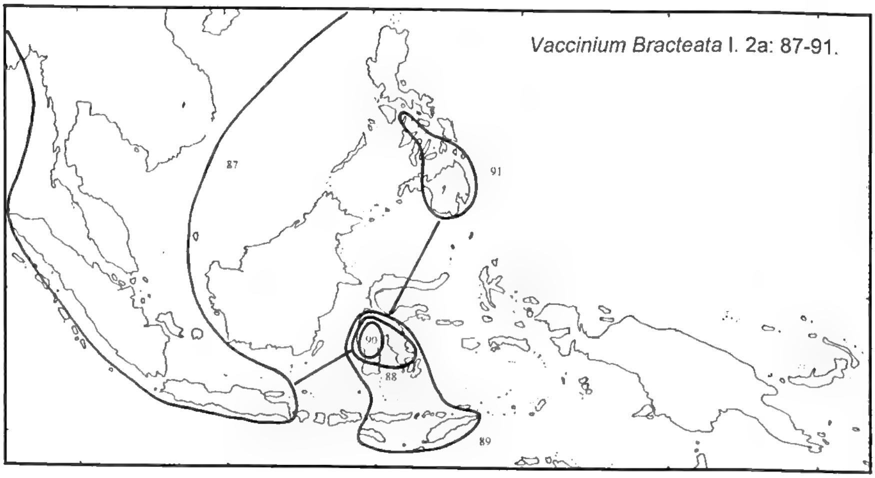

Fig. 53. *Vaccinium* sect. *Bracteata* I.

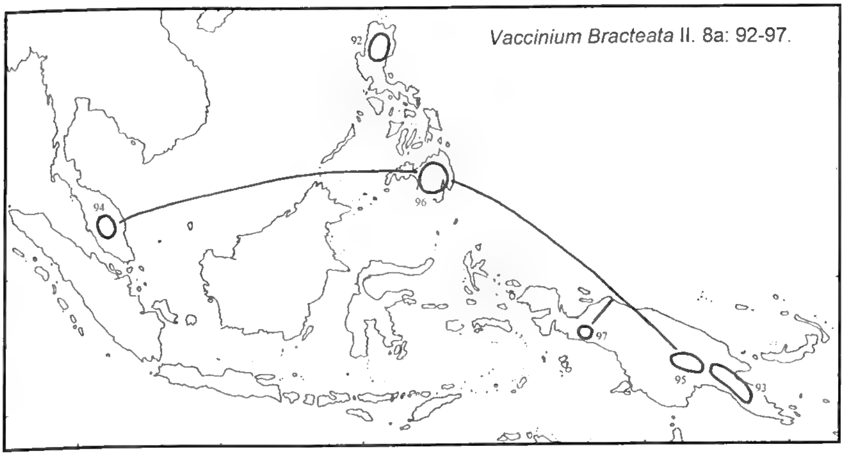

Fig. 54. *Vaccinium* sect. *Bracteata* II.

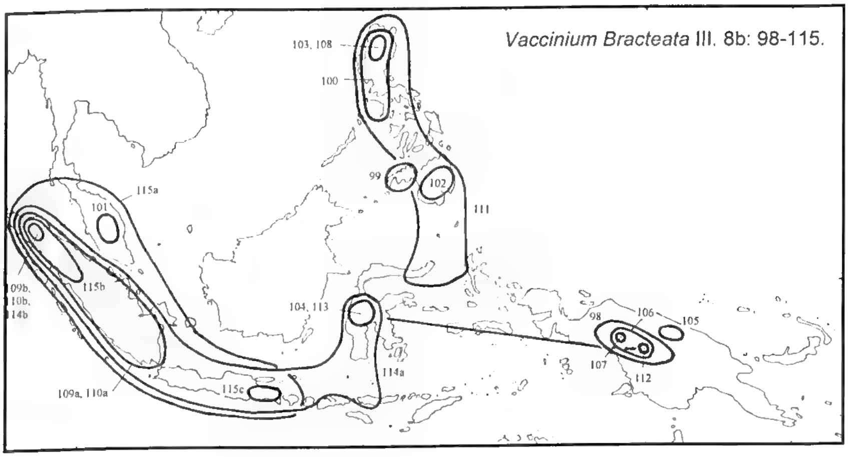

Fig. 55. *Vaccinium* sect. *Bracteata* III.

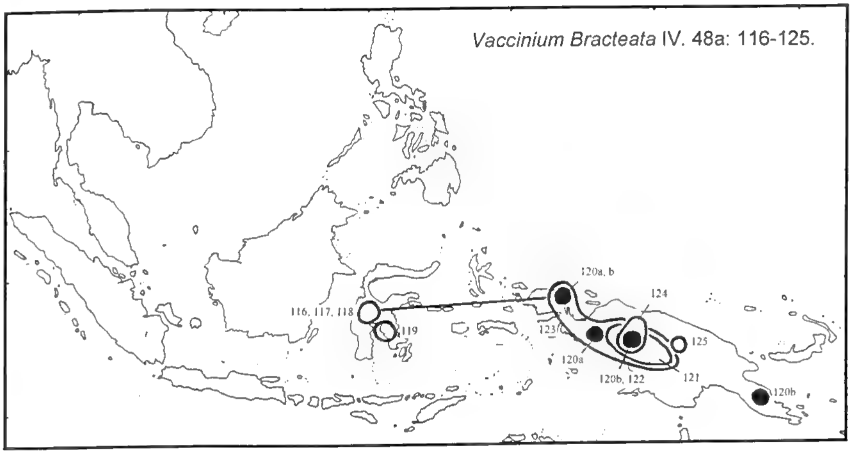

Fig. 56. *Vaccinium* sect. *Bracteata* IV.

Vaccinium sect. *Bracteata* V. (Fig. 57). There are three parallel arcs: Rouffaer R. – Torricelli Mts – Hunstein Mts (Sepik terrane) (126); Doormantop – near Bernhard Camp (127, both localities on Rouffaer terrane) and Lake Habbema (129) – West Range (128, type only, lost).

Vaccinium sect. *Bracteata* VI. (Fig. 58). The two species are at Kinabalu, and Batu Tiban – Mt Dulit. They are distinctive through their cordate leaves and appear in the key as sister to the rest of the genus (the next 107 species). Like *Bracteata* VIII and IX this is a Borneo group, vicariant with the next.

Vaccinium sect. *Bracteata* VII. (Fig. 59). Borneo/Sulawesi are surrounded. PNG has eight species (plus varieties), Irian Jaya only two and the group is not in the Snow Mts. The track: Rouffaer R. (143) – Aitape (144) can be compared with the distribution of sp. 126 in *Bracteata* V.

Vaccinium sect. *Bracteata* VIII. (Fig. 60). N Borneo – southern Philippines. This is an important pattern in which SW Borneo (Riouw Pocket) and SE Borneo (Meratus suture) are not involved.

Vaccinium sect. *Bracteata* IX. (Fig. 61). 158a (dunes and rocks by sea-shore) has the usual mangrove track: CW Sumatra and Borneo. This can be compared with the range of *Vaccinium* 27 (mangrove), *Diplycosia* 80, 81, *Costera*, and *Rhododendron* 226–227, 276 (mangrove). The disjunction: Borneo – Owen Stanley terrane (157, NW Owen Stanley Range, up to 2300 m altitude), again implies uplift of mangrove in East Malesia. The eastern species 153 (SE Owen Stanley Range, specimens from Mt. Obree differ from the others) is sister to the rest of the group, a Pacific-oriented pattern not seen in *Rhododendron* but present in both epacrid groups (below).

Vaccinium sect. *Bracteata* X. (Fig. 62). There are four separate groups shown here: the pair 160–161 centred on N Luzon is sister to the rest of sect. *Bracteata*, another Pacific pattern not seen in *Rhododendron*. Species 162 (West Ra., Hunstein - Schrader Mts.); 163–168, and 169–170 are each in turn sister to the rest of the genus. The disjunction between Doormantop (163) and the Papuan Peninsula (164), enclosing 162 in central PNG, is seen elsewhere in groups like *Potentilla adenophylla* Merr. & Perry (Rosa.) of Doormantop and the Papuan Peninsula (Central and Milne Bay Provinces), which encloses the related *P. brassii* Merr. & Perry of the New Guinea main range (Kalkman 1993). The Aceh–Palawan connection is also seen in *Rhododendron* 177, 178, 179. The Borneo species is in swamp forest on sandy soil at sea-level, while its relatives in New Guinea are montane in the Vogelkop, Doormantop and the Owen Stanley Mts.

Vaccinium sect. *Bracteata* XI. (Fig. 63). This comprises two parallel arcs: Luzon – Mindanao – Talaud Islands – Vogelkop (Netoni terrane); and N Luzon – Negros – Milne Bay (Dayman terrane). This shows the composite structure of both the Philippines and New Guinea.

Vaccinium sect. *Bracteata* XII. (Fig. 64). In Sumatra, in forest near the seashore and on limestone rocks (sp. 185); but in New Guinea in the mountains (with the highest record in PNG, at 3745 m). The New Guinea distribution is in four parallel arcs: Luzon – Goodenough I., Vogelkop – Mt. Ambua/Mt. Otto – Mt. Dickson; Sumatra – Hunstein Mts – Mt. Tafa; and, on the craton, Wissel Lakes – Mt. Goliath.

Vaccinium sect. *Bracteata* XIII. (Fig. 65). Borneo (including endemism on Mt. Kutei) – Arfak Mts.

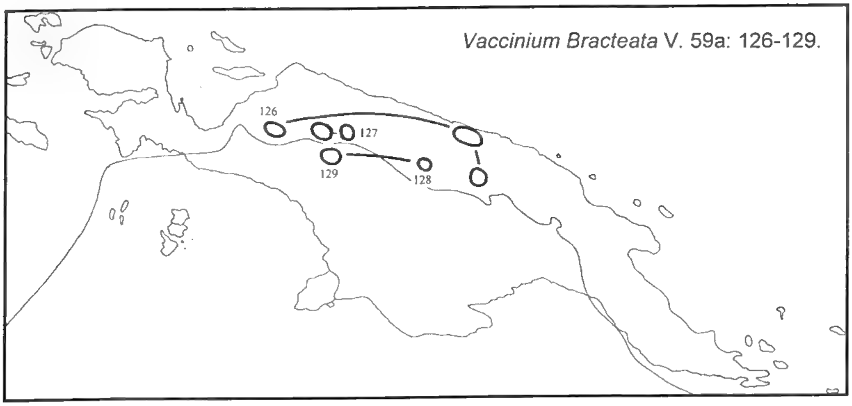

Fig. 57. *Vaccinium* sect. *Bracteata* V.

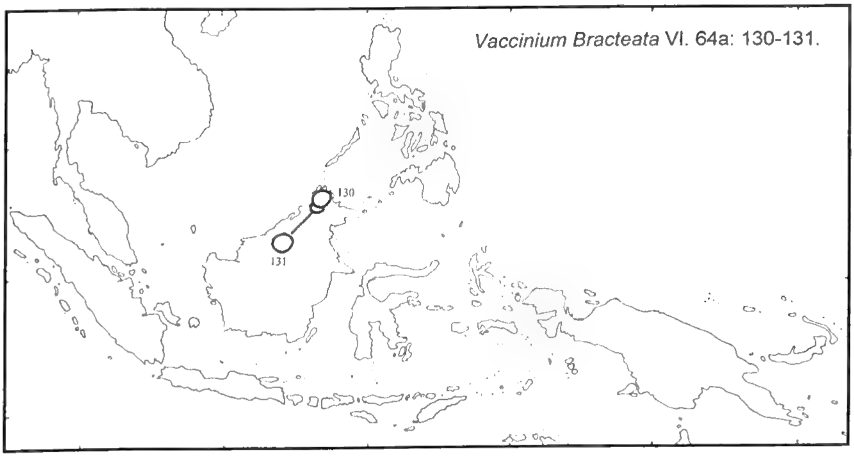

Fig. 58. *Vaccinium* sect. *Bracteata* VI.

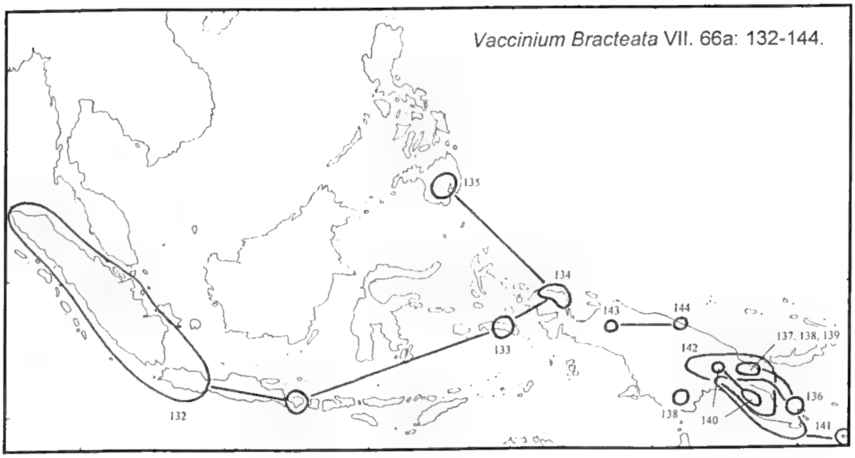

Fig. 59. *Vaccinium* sect. *Bracteata* VII.

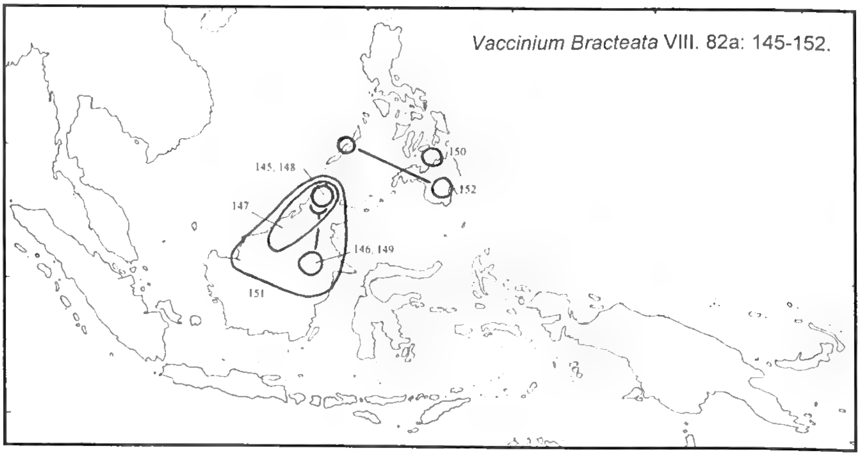

Fig. 60. *Vaccinium* sect. *Bracteata* VIII. The following localities for 149 were not located: Amai Ambit (C Borneo), Ulu Majong (Sarawak).

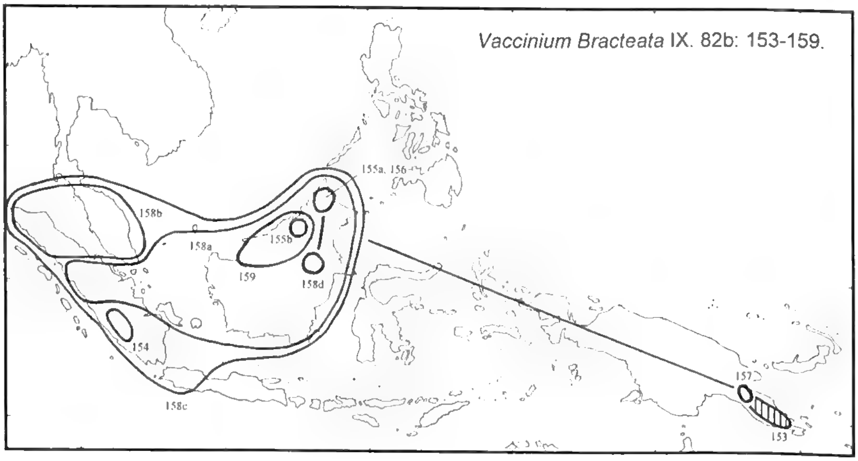

Fig. 61. *Vaccinium* sect. *Bracteata* IX. 155b is *V. coriaceum* var. *hirsuticalyx* Argent.

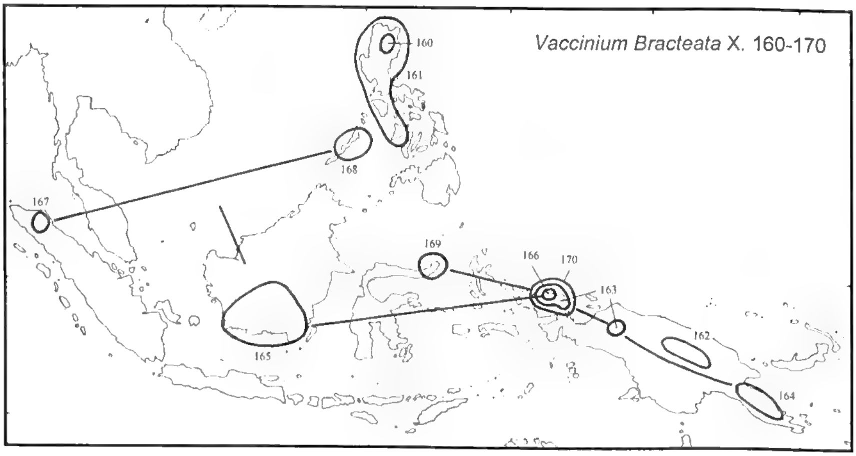

Fig. 62. *Vaccinium* sect. *Bracteata* X.

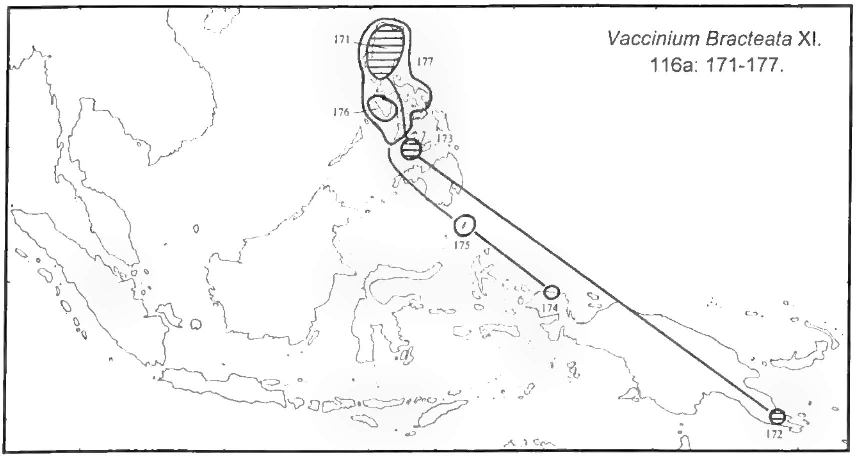

Fig. 63. *Vaccinium* sect. *Bracteata* XI.

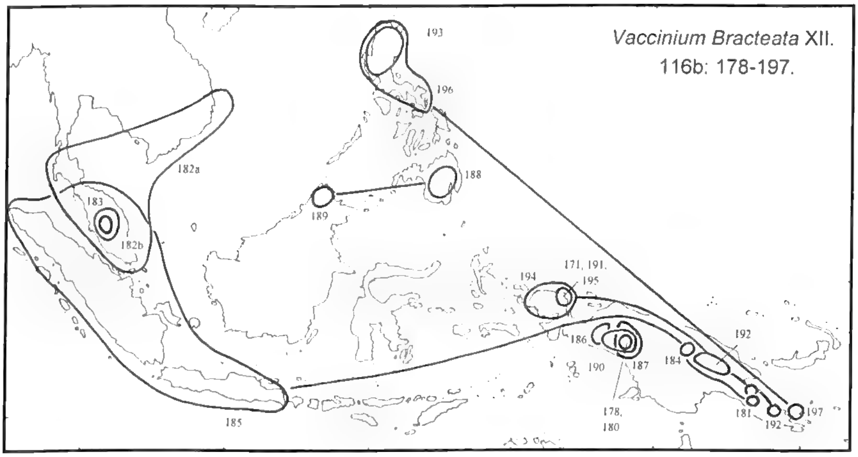

Fig. 64. *Vaccinium* sect. *Bracteata* XII.

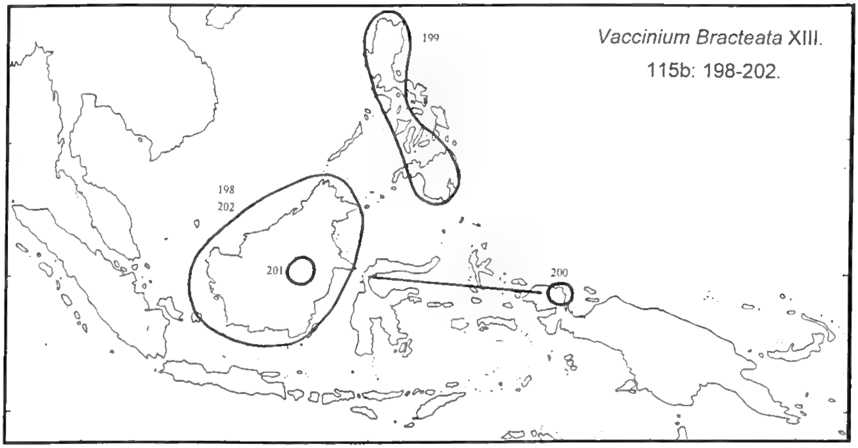

Fig. 65. *Vaccinium* sect. *Bracteata* XIII.

Vaccinium sect. *Bracteata* XIV. (Fig. 66). There are endemics on the craton (e.g. the trio 203–205) and also on some of the accreted terranes, but no representation on Arfak or Finisterre terranes.

Vaccinium sect. *Bracteata* XV. (Fig. 67). Two parallel tracks, running Aceh – Philippines – New Guinea – Sulawesi/W Malesia, largely surround Borneo, which has no endemic species. Species 219 (N Sumatra) and 220 (New Guinea) are keyed together, as are 222 (Doma Peaks, Mt. Hagen, and Mt. Giluwe, all Quaternary volcanoes on the craton), and 223 (Latimodjong Ra).

Agapetes subgen. *Paphia* (Seem.) Stevens (Fig. 68). Thirteen out of the 14 species occur between Mt. Amungwiwa/Mt. Shungol and Mt. Victoria (Stevens 1972, 1981), a 250 km-long sector of the Owen Stanley terrane.

Dimorphanthera I. (Fig. 69). Philippines–PNG. The Vogelkop–Owen Stanley disjunction is similar to the Vogelkop–Huon disjunction seen in birds-of-paradise (Heads 2001b, 2002a). Species 1 and 2 comprise sect. *Pteridosiphon* Wernh., confined to Mt Carstensz. The other species on this map (3–15) comprise sect. *Dimorphanthera.* The remaining species of the genus make up sect. *Trochilanthe* Schltr.

Dimorphanthera II. (Fig. 70). This is on the craton in the west, with only two species out of eight. In PNG there are six species, on both the craton and the accreted terranes.

Dimorphanthera III. (Fig. 71). Three tracks converge near Mount Wilhelm: Torricelli Mts – Wabag – Okapa (25, 26); Vogelkop – Mt Piora (28–32); and a craton track (24; this species is sister of the first two groups). The middle track crosses a litle way onto the craton at Lake Kopiago (29), but here the species differs through its glabrous corolla.

Dimorphanthera IV. (Fig. 72). This comprises one widespread species, three endemics on the craton, and two on the accreted terranes forming a disjunction between Nassau Mts and the Owen Stanley, Port Moresby and Kutu terranes in PNG.

Dimorphanthera V. (Fig. 73). This is keyed out next to the last and has many endemics on the accreted terranes. 49: *D. collinsii* var. *collinsii* is on Mts Michael, Otto, Kerigomna and possibly Wilhelm (all off the craton). *Dimorphanthera collinsii* var. *montis-wilhelmi* is on Mts. Otto, Kerigomna, and Wilhelm, and also on the craton at the Minj-Nona Divide in the Kubor Mts. However, at this last locality it has a slightly different form, with less prominent basal glands on the lamina (Stevens 1974a). This recalls sp. 29, last map, and *Rhododendron* 191 (*Buxifolia* IV) which also show slight but possibly significant differences between the populations on the craton and those on accreted terranes.

Dimorphanthera VI. (Fig. 74). There are disjunctions between Irian Jaya species on the craton, and PNG species on accreted terranes. This resembles the disjunction in *Macgregoria* etc., but occurs here in three vicariant affinities. Species 65A is in the Hydrographer's Range (= Sibium Mts) (Bowutu ophiolite terrane).

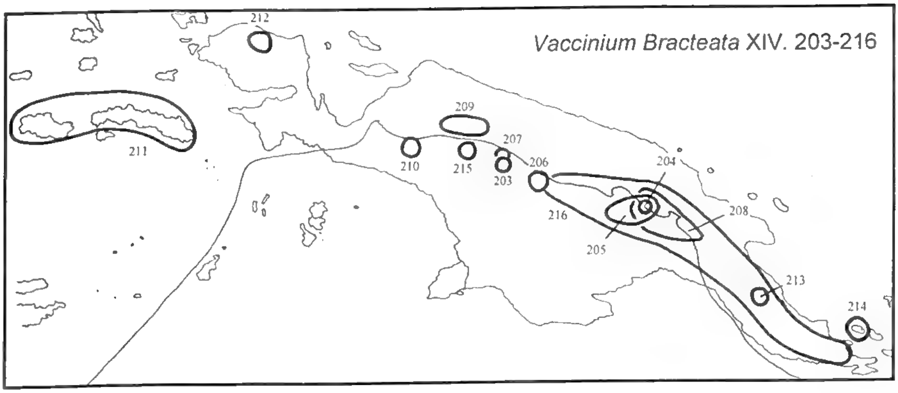

Fig. 66. *Vaccinium* sect. *Bracteata* XIV.

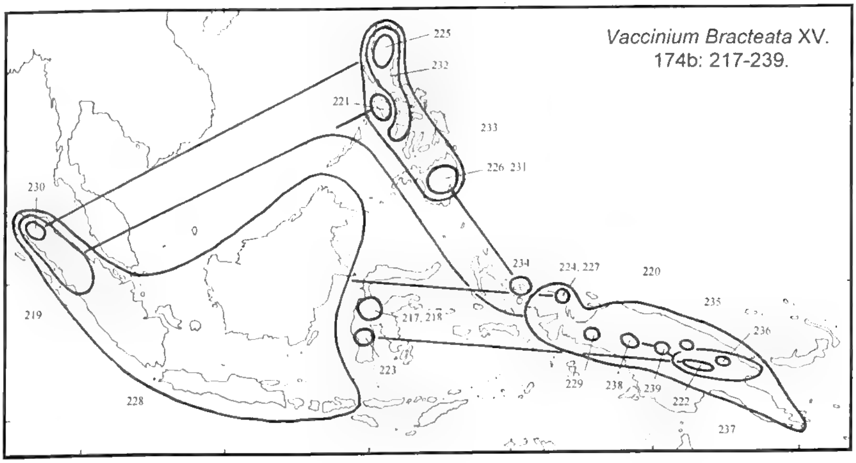

Fig. 67. *Vaccinium* sect. *Bracteata* XV.

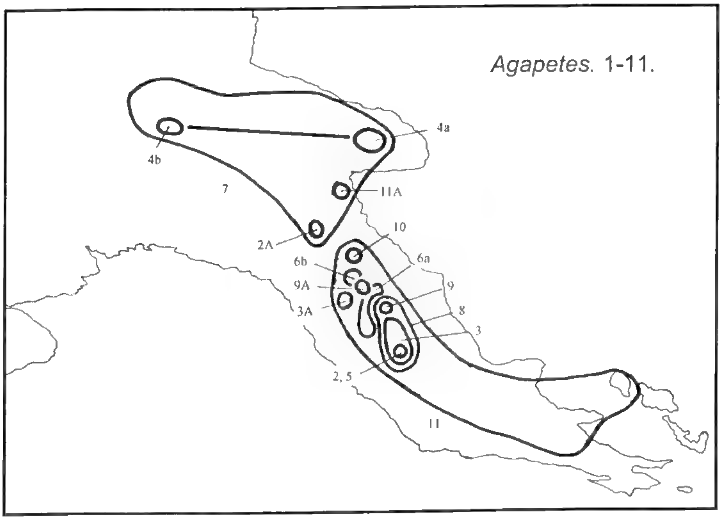

Fig. 68. *Agapetes*. 6b is *A. brassii* var. *serratifolia* Stevens.

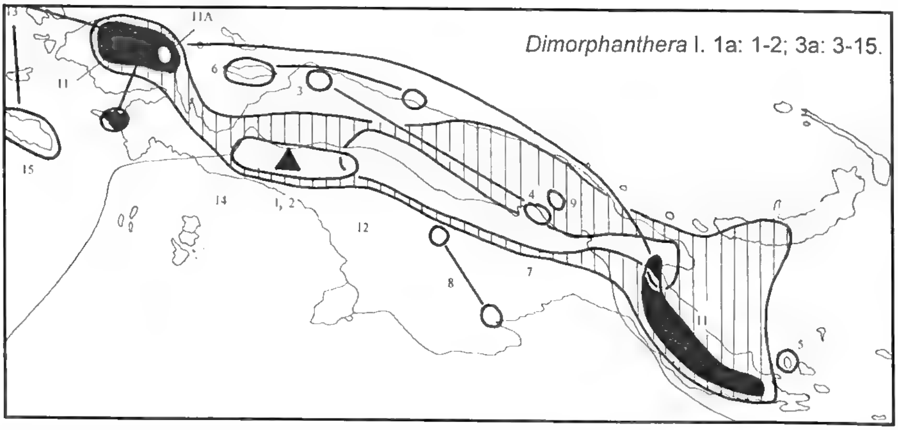

Fig. 69. *Dimorphanthera* I. 3 and 4 are included in 7 by Stevens (1974a) but are shown here as the possible cline is of geographic interest. 11A is the reinstated *D. arfakensis* J.J. Sm. 13 is included in 10 as a variety. 14 is a variety of 11.

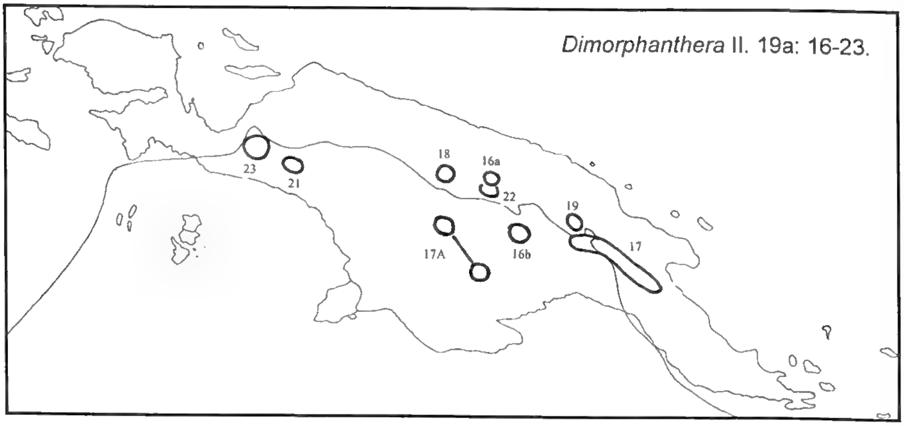

Fig. 70. *Dimorphanthera* II. 20 is included in 35.

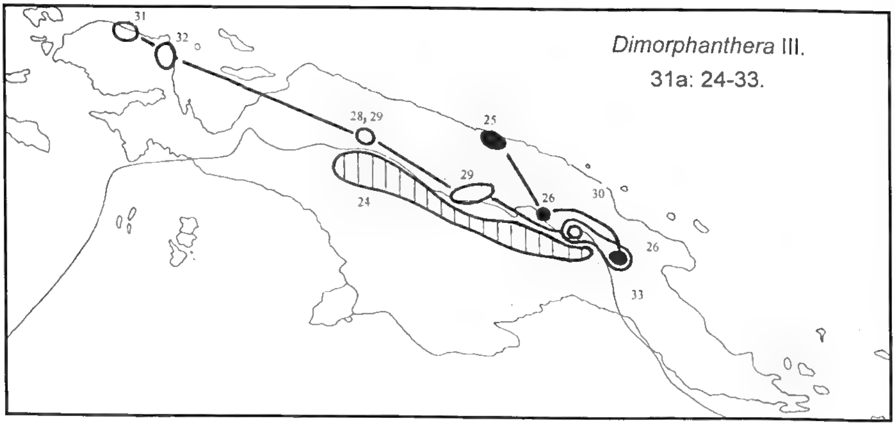

Fig. 71. *Dimorphanthera* III. 27 is included in 40.

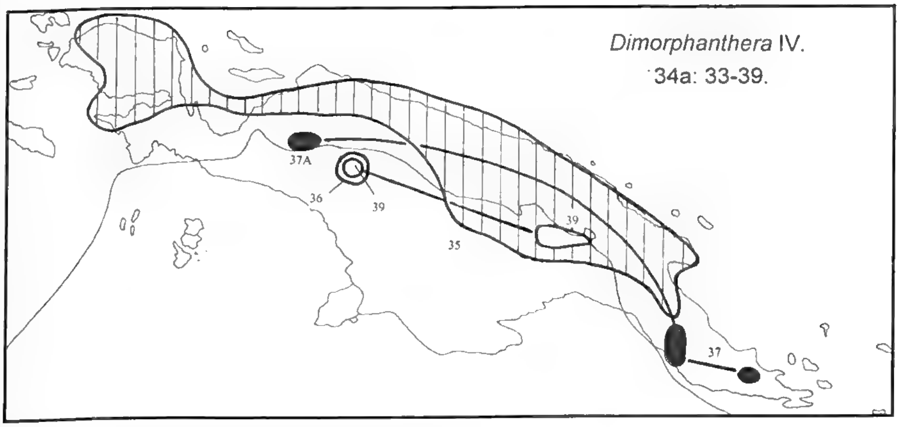

Fig. 72. *Dimorphanthera* IV. 37A is the reinstated *D. alba* J.J. Sm. Species 34 (and 20) are included in 35. Species 38 is a variety of 50 (Stevens 1974a).

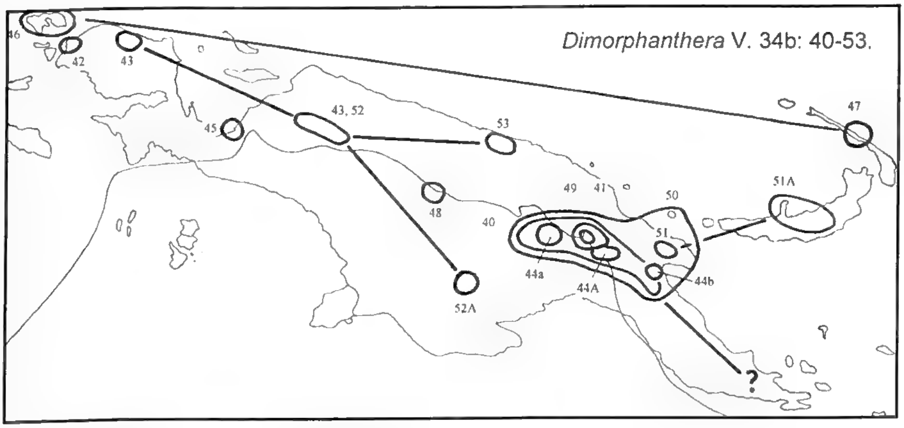

Fig. 73. *Dimorphanthera* V. 44A is *D. viridiflora* Stevens. 44b is *D womersleyi* var. *continua* Stevens. 51A is *D. bracteata* Stevens. 52A is *D. glauca* Stevens.

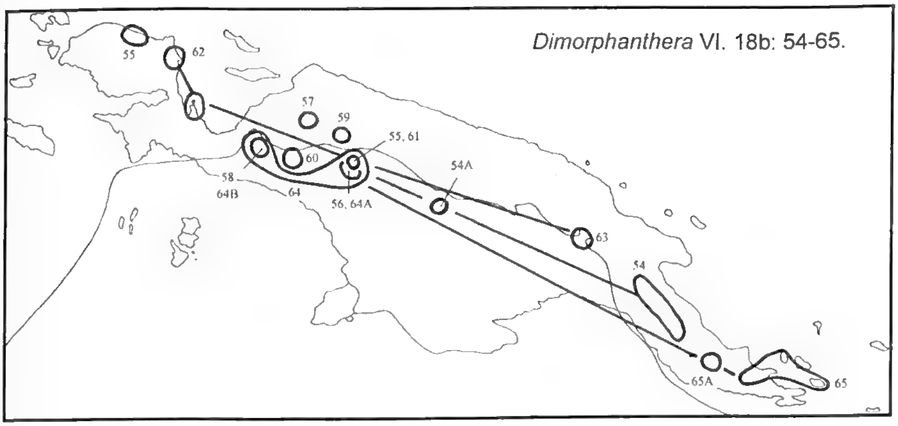

Fig. 74. *Dimorphanthera* VI.

Epacrids.

The three Malesian Epacrid genera are all in tribe Styphelieae (Watson 1967).

Styphelia J.E.Sm. (Fig. 75). This ranges around the Riouw Pocket (including Riouw, Billiton, and Karimata Islands) like several other mangrove associates, and has a W Malesia – Cyclops terrane disjunction resembling that of *Diplycosia* V and *Bracteata* IX. The E PNG – Marianas group (subgen. *Cyathodes* (Lab.) Drude) is sister to the rest (subgen. *Leucopogon* (R.Br.) Drude).

Decatoca F.Muell. (Fig. 76). Finisterre and Owen Stanley terranes (cf. subgen. *Cyathodes*, last map).

Trochocarpa R.Br. (Fig. 76). New Guinea, Sulawesi, Borneo. (*Decatoca* and *Trochocarpa* are paired in Sleumer's key). 1–7 comprise *T.* subgen. *Trochocarpa*. *Trochocarpa* subgen. *Pseudocyathodes* Sleum. (8 and 9) is disjunct: (Arfak Mts. – Doormantop – central PNG (Mt. Hagen to Mt. Scratchley)). *Trochocarpa* is also in Queensland and New South Wales.

Both *Styphelia* and *Decatoca/Trochocarpa* are E Malesian. Also, both have close ties with Australia and the main massing of the subfamily, and in both a widespread Malesian group has its sister-group in SE Papua – unlike *Rhododendron* which usually has sister groups of widespread taxa in the west (*Vaccinium* has at least one in the east and one in the Philippines).

Epacrids are another Australasian group which is much more diverse in PNG than in Irian Jaya (twice as high at the subgeneric level). This pattern is also seen in groups such as birds-of-paradise (Heads 2001b). 'Asian' or 'Old World' groups (e.g. *Rhododendron*) are usually more diverse in Irian Jaya.

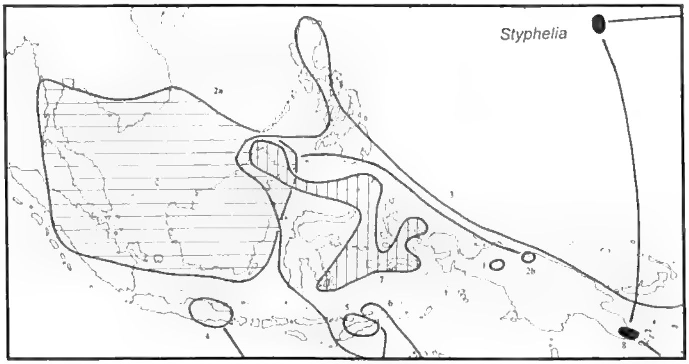

Fig. 75. *Styphelia.*

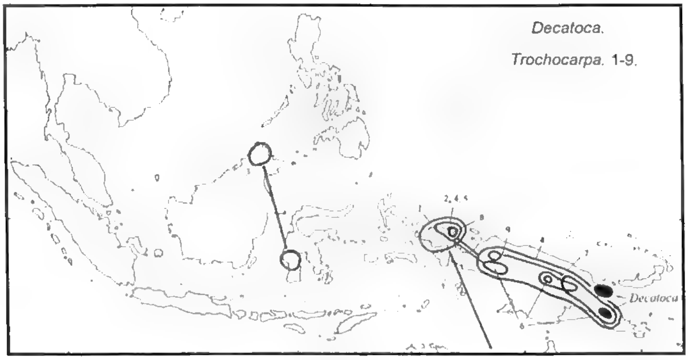

Fig. 76. *Decatoca* and *Trochocarpa.*

Biogeography of the Malesian mountain flora and the myth of long distance dispersal

The dispersalist tradition of Holarctic centres of origin — the 'great evolutionary workshops of the north' — has dominated Australasian biogeography for over a century. A particularly well-preserved, well-explored and well-publicised fossil record in North America has meant that even today marsupials are assumed to have colonised Australasia and E Malesia from North America via South America and Antarctica. In other groups, Malesia/Australasia is supposed to have been invaded from the north directly, via Asia.

However, an alternative view has existed alongside the orthodoxy ever since biogeography came into existence as a global science. Already in the eighteenth century Willdenow (1798, cited in Weimarck 1934) was discussing biogeographic affinities between the Cape region of South Africa and Australia. This affinity among southern lands is totally unexpected in the orthodox explanation of dispersal from northern centres of origin. Because of the relationship between the floras Willdenow concluded that Australia and the Cape were once connected.

In an analysis of Borneo phytogeography, van Steenis (1964) referred to Hooker's idea of a 'continuous current of vegetation' between Scandinavia and Tasmania (e.g. *Carex pyrenaica* Wahl.: New Zealand – Pyrenees). In this 'current', Hooker observed that the Himalayan element (e.g. *Rhododendron*) stops abruptly in New Guinea, while going the other way the Antarctic element disappears more or less on the Bornean Alps (e.g. *Kelleria* Endl. (Thymel.)), or has very small numbers in Malaysia and SE Asia (e.g. epacrids). Likewise, van Steenis (1934b) observed that the rich region of Ericaceae (in the narrow sense) extends from the Himalayan-Chinese region through Borneo to New Guinea where it ends rather abruptly. Australia, especially, is surprisingly poor in Ericaceae sens. strict. Van Steenis wrote that 'This is a very peculiar phenomenon as there is hardly any climatic evidence which can be put forward to explain the absence of a rich Ericaceae flora in Queensland for instance … . It is very peculiar that whereas Papua has a swarm of species Australia is so extremely poor in rhododendrons [only two species known], the more so as the dispersal of the minute seed must apparently go easily'. Further, the genus is very tolerant of the volcanic environment, and it is not immediately clear why are there no more species on, for example, Java, New Britain, or Bougainville, a high (2743 m), wet, volcanic island with only two species.

What is the reason for these globally significant breaks at New Guinea and Borneo? They are attributed here to vicariance at the origin of the groups, for example in the case of Ericaceae absent in Australia, the vicariance is with the epacrids. Vicariance developed naturally from the conclusions of van Steenis as he showed clearly that, first, the groups are much older than current topography, and second, that long distance dispersal is not an acceptable concept.

Van Steenis (1964) concluded that the array of mountain species on Kinabalu is a distinctly and essentially relict one, a fragment of what must have been there before, not necessarily on Kinabalu itself, but on the old mountains in its vicinity from which it derived its present flora.

Significantly, a few plants otherwise known only from Kinabalu are found on summits of lower, worn down ranges notably Kong Kemul in central east Borneo. Van Steenis cited plants such as Clethraceae; the *Clethra* species of eastern Borneo (Mt. Kinabalu, Mt. Murud (northernmost Sarawak) and Kemul (not cited by Sleumer 1971b), is related to plants on Palawan and Vogelkop–Wissel Lakes (Sleumer 1971b).

Van Steenis (1964) concluded that 'not much can be added to Stapf's [1894] grand theory on the origin of the Malaysian mountain flora'. Stapf and Warburg's (1891) ideas on ancient mountain ranges in Malaysia were perhaps simplistic compared to modern geological ideas, and alpine plants may not actually need very high mountains, but van Steenis agreed with these authors in dismissing long distance dispersal and emphasising, instead, location and geological history. Later, van Steenis (1978a) even headed a section 'The myth of long-distance dispersal' and his whole approach to this subject was a major contribution to analytical biogeography.

The critique of 'dispersal' is counter-intuitive: Holloway and Hall (1998) wrote that 'To a geologist the dismissal of the role of dispersal seems bizarre'. It probably also seems bizarre to the layman, but is based on the simple observation that distribution of taxa and their means of dispersal show no correlation. The same distribution is held by many taxa with many different means of dispersal, while taxa with similar means of dispersal have quite different distributions. In his classic study of the Kinabalu flora, Stapf (1894) 'clearly showed the fallacy of invoking long distance dispersal' after finding no relation between size of range and dispersal mechanisms (van Steenis 1962b).

Van Steenis (1934b) argued that 'the effect of present dispersal can give no clue to an explanation of the present distribution of mountain plants in Malasia' and concluded (van Steenis 1936) 'there is no evidence that long distance dispersal has played a role in the origin of this flora ... *On the whole I cannot trace any relation between distribution and what is known of* [means of] *dispersal'*. (emphasis in the original).

If means of dispersal were important for establishing range, van Steenis (1964) reasoned, 'One would suppose that *Radermachera ramiflora* (Bignon.) with winged seed and the endemic species of *Nepenthes* and endemic orchids with dust seed would not be endemic on Kinabalu. [The *Radermachera* is closest to a Yunnan species]. Furthermore, plants with sympatric range and similar ecology often possess entirely different methods of dispersal, for example the conifer genus *Phyllocladus* Mirb. and the ferns *Blechnum fraseri* (A. Cunn.) Luerssen and *B. fluviatile* Salomon which occur in New Zealand, New Guinea, the Philippines and Kinabalu (the ferns extend to North Sumatra, *Phyllocladus* to Peninsular Malaysia). Moreover, strength of botanical affinities is often out of proportion with distances ... Finally the remarkable regularities in plant ranges and affinities of plants outlaw the idea of 'chance' dispersal otherwise than at very short distance.'

Writing on Malesian mountain plants in general, van Steenis (1934b) found that 'The regularity of the plant invasion tracks is so well-pronounced ... that I can hardly attribute that to the rather irregular effect of typhoons', and 'The Malaysian mountain flora exhibits a rigid scheme of tracks which is opposed to any idea of randomness'. (van Steenis 1962a).

Kalkman (1979) was rather sceptical of what he called the 'anecdotic' view that there is no correlation between distribution and means of dispersal. He undertook a much larger analysis than any done previously, including just over 3000 species from the *Flora Malesiana*. Apart from a correlation in a small number of species, he felt 'the conclusion must be, at least for the time being, that the dispersal method is of subordinate importance for areogenesis ... On the other hand, I still cannot quite accept that dispersal efficiency ... would not be mirrored in the areas covered by the species if the sample taken is large enough'. However, the facts again are clear enough, although perhaps unexpected.

Van Steenis's (1934b) conclusions agreed with those of Stapf (1894), as indicated, and also contemporary authors such as Lam (1929), who felt the distribution of Papuan mountain plants 'to some extent cannot be explained in another way than by reference to historic plant geography.' Lam's (1930) prescient synthesis of Wegener's geological ideas and plant geography has been overlooked by American plant geographers since they 'rediscovered' continental drift in the 1960s–1970s. Likewise, Skottsberg (1940) concluded that the alpine plants of Hawaii or their ancestors 'antedate the formation of the volcanoes which are their present home', and Ridley (1930) wrote that it is 'impossible' that the connection between the mountain floras of the Peninsula Malaysia and Kinabalu can be explained by seed being blown across the South China Sea. Instead, these two areas and their floras are relics of a once more continuous region. Symington (1936) agreed with Ridley that dispersal between Peninsular Malaysia and Kinabalu by wind, water etc. is 'much more difficult to credit than the, perhaps less obvious, relic hypothesis ... To explain these relics it is probably necessary to go back to Cretaceous times ...'.

Discussing Ericaceae of South America and tropical Africa, Stevens (1970) agreed with van Steenis' critique of long distance dispersal: 'plants can disperse from one old almost eroded-away mountain to another younger one, so the age of taxa inhabiting isolated mountains and mountain systems may bear no relation to the age of the physiographic features themselves.'

Thus in contrast with the ideas of the dispersalist school, as expressed mainly in the writings of temperate botanists, tropical botanists have often taken a more critical look at 'dispersal'.

The view that distributions reflect non-random processes leads to critical analysis of the distributions themselves, ecology, evolution, systematics and paleogeography. Van Steenis (1964) wrote: 'It is surely a miracle that some [Malesian mountain species] like *Euphrasia* and *Haloragis micrantha* still bear testimony of the ancient pathway ... we can easily deduce that temperate taxa could only survive by transfer from decaying mountains and ranges to new ones coming up. ... From this it follows that many plant taxa will be older than the bedrock of the mountains on which they are now found'. This is a very important process, although mountains can also inherit biota from lower land in situ (see below), as 'mountain plants' do not always need mountains to survive. Van Steenis gave an example: 'The Snow Mountains [Irian Jaya] of possible Pliocene uplift must have received their alpine flora from another, older higher range in decay, probably along the northern Papuan coast'.

Kinabalu is an anomaly, the youngest exposed granite intrusion in the world, uplifted very rapidly just 1–2 million years ago. As it rose it would have inherited flora from the Crocker Range through which it burst. Although the Crocker Range is now less than 1000 m high, Meijer (1974) wrote that during the Miocene (7 Ma) it was part of a much higher range which had a temperate conifer belt above a subtropical forest zone. The sediments comprising the Crocker Range were themselves deposited and uplifted 15–5 million years ago, and as they rose would have inherited local flora and fauna from any adjacent land, details of which are by now largely lost from the geological record.

Corner (1964) gave the following sequence: 1. L. Cretaceous – Eocene: deposition of alluvial 'geosynclinal' strata (Wariu Formation) which later became the base of Kinabalu; 2. Oligocene (35 Ma): first emersion of the Wariu Formation; 3. Pliocene (11–9 Ma): intrusion of granodiorite; 4. Mid-Pliocene: emersion of the batholith.

Meijer (1974) described the 185 species in the lower montane tree flora of Kinabalu and concluded that: 'the ecological plant geographical potential of such a mountain flora is certainly great – it contains plants adapted to acid sandy podsolic soil ... Some of these plants are not very sensitive to high temperatures, and can live as well at sea-level. In fact they are as much a part of the coastal sandy forests and peat swamps as of the submontane flora.' Meijer cited as examples *Vaccinium bancanum* and species in *Agathis, Tristania* and *Xanthophyllum*. In addition to `geographical potential', the survival potential of this flora is great enough to allow its persistence more or less in situ, highly modified of course, through several generations of mountain building and erosion.

In this view, features such as the centres and breaks in distribution in Borneo and New Guinea cited above are explained primarily by vicariance and accretion, as mediated by tectonics. In another example, there is a sharp floristic demarcation between Taiwan and Luzon, with the very rich conifer flora of Taiwan quite different from that of Luzon-Borneo, Van Steenis (1964) presented this 'remarkable relation' as an 'unsolved problem'. A major break in Sulawesi constitutes what van Steenis (1972) called 'another problem for the geologists': the existence of a floristic boundary between South and Central Sulawesi. Van Steenis (1936) observed that, the number of typical New Guinea track plants is much higher in the Central Sulawesi Latimodjong Range compared with Mount Bonthain in the south. Conversely, of 150 mountain species of Java, 80 occur in the Lesser Sunda Islands, and no fewer than 50 are also found on Bonthain volcano, while none occurs on the Latimodjong Range [S Central Sulawesi].

In practice, the concept of dispersal — the process giving rise to distribution — as physical movement due to 'means of dispersal' (rather than evolution of earth and life together) has only lead to endless, desultory debate. For example, Stevens (1981) noted that only three species of *Rhododendron* occur south and east of New Guinea, 'although there is no obvious ecogeographic reason for such an abrupt cut-off ... Hence it seems reasonable to postulate movement from west to east through Malesia.' (cf. Irving and Hebda 1993). However, Specht and Womersley (1979) observed that about half the species of the section *Vireya* are in New Guinea, and so *Vireya* 'must have developed on the Australasian tectonic plate and then migrated into the Malay Archipelago when the two areas became contiguous in the late Miocene' – the exact opposite of what Stevens decided.

Through the 1980s long distance dispersal made an insidious return with the rise of the non-systematics-based ecologists who were probably unfamiliar with most of the data that van Steenis and the others had worked with. For example, Cain et al. (2000) studied long-distance dispersal in plants and concluded, predictably enough, that more observations are needed and that genetic methods should be applied. However, Veldkamp (2001) noted that in this paper `curiously, van Steenis's many arguments against [long distance dispersal] are nowhere mentioned'. There seems to have been a loss of hard-won knowledge over a single generation. The critique of dispersal was one of the few things that the great tropical botanists Corner, Croizat and van Steenis all agreed on, and their views should at least be cited in discussion of a problem which is clearly and unfortunately still not resolved.

The long distance dispersal hypothesis continues to attract criticism from many different fields. In molecular studies, for example, Füchter (2001) supported the nunatak hypothesis of survival of European flora during glaciation, often supposed to 'wipe clean' a region. Disjunctions in Malesian vascular plants were discussed by Baker et al. (1998) who concluded that these 'probably require a tectonic explanation'. Likewise, Tan (1998) suggested that disjunctions in Malesian mosses `can now be better explained by relating them to local plate tectonic movements than by the long-distance dispersal hypothesis', and 'the majority of Malesian species of mosses ... have evolved *in situ* during the geological formation of the various island groups, notably Borneo and New Guinea.'

Studies of the palms illustrate the differences between dispersal and vicariance analyses.

Hahn and Sytsma (1999) treated *Caryota* in three main clades. The geographic pattern is clear and simple: the *rumphiana* clade (southern India, Sri Lanka, Borneo, E Malesia) and the *mitis* clade (SE Asia, W Malesia) are sisters, and overlap on Borneo and Sulawesi, whereas the *rumphiana* clade and the basal *maxima* clade (SE Asia, Sumatra, Java) are precise geographic vicariants, with the latter sandwiched between the disjunct locations of the former. Although Hahn and Soltis observed accurately that 'Broad patterns of relationship among the three principal clades correlate well with vicariance coupled with the geologic history of SE Asia', they did not actually describe the vicariant pattern, or observe that it does not occur between sister groups. Instead, they gave a lengthy discussion of Huxley's Line and two versions of Wallace's Line, none of which coincide with either the western or eastern boundaries of any of the three clades. They could have mentioned the precise vicariance that is actually in evidence between two of the three clades, which does not lie along the famous lines but along the boundary between the Peninsular Malaysia, Sumatra and Java on one hand, and Borneo on the other.

Authors often invoke chance dispersal to explain what they feel to be anomalous distributions. Hahn and Sytsma (1999) are no exceptions and immediately after correlating the origin of the principal clades with vicariance and geology, they proposed a 'general model' for the genus in which it migrated from a centre of origin in (presumably mainland) SE Asia eastwards through Malesia. No reason for this is offered apart from the fact that previous authorities have suggested it.

In fact the major Borneo–Java break in *Caryota* is a standard one seen in very many Ericaceae and other organisms. For example, in areas such as Indonesia with strong ocean currents, it has usually been assumed that populations of coral reef organisms with pelagic larvae will be genetically connected and interbreeding. However, among populations of a mantis shrimp from 11 reefs in Indonesia, Barber et al. described 'southern' and 'northern' clades in the Java and Flores Seas, which 'may be relics of [respectively] Indian and Pacific Ocean populations' like the Malesian Ericaceae.

Although Hahn and Sytsma (1999) concluded overall in the usual way, supporting 'a combination of vicariance and dispersal', no evidence for `dispersal' is given, apart from supposed 'anomalies' of distribution. Instead of focusing on the actual patterns of distribution and phylogeny the authors centred their discussion around Wallace's and Huxley's Lines, that are famous but not relevant, and on what some other authors have said about palm dispersal. In the last paragraph Hahn and Sytsma drop their initial, radical idea of broad patterns of relationship being correlated with vicariance and geology, and suggest that, after all, 'dispersal has played a very large role' in the evolution of the genus.

In contrast with Hahn and Sytsma's (1999) approach, Corner (1966) regarded panbiogeography as 'the most positive contribution to palm biogeography', and Rodd (1998) interpreted another palm genus in the area, *Livistona* R. Br., simply in terms of vicariance. This genus has most species in Australia and ranges through the Solomon Islands and Malesia to Japan and Assam. There is also a disjunct population in NE Africa. Rodd (1998) argued against Miocene dispersal, as 'this rather brief time scale hardly seems sufficient to account for the great diversity of form found in Australian *Livistona*, especially when taken in conjunction with the concentration of most of the species in refugia often associated with far more ancient land surfaces'. Rodd proposed as an alternative 'that proto-*Livistona* had already emerged by the time Laurasia and Gondwana began to separate'. As further support, Rodd cited the biogeography and Upper Cretaceous fossils already attributable to the modern, morphologically specialized palm genus *Sabal* Adans.

Biogeography of regions in Malesia

Mentawei Islands

These islands lie 100 km off Aceh and central Sumatra and are an important centre for many groups. 22: *Vaccinium acuminatissimum* forma *ellipticum* (J.J.S.) Sleum., is endemic to Simalur and Sipora Is. Sumatra has nine endemic mammal species (including one primate), while the Mentawei Islands have 11 endemics, including four primates. The biogeographic status of these islands is probably related to their position in the Indian Ocean. The following examples are taken from bird data (Howard and Moore 1984), the best-known of any group and invaluable for resolving most biogeographic problems.

The parakeet genus *Psittacula* ranges in a northern Indian Ocean triangle: Sudan/Somalia – Afghanistan/Tibet – Borneo, with endemic species on Sri Lanka, Mauritius etc. *Psittacula alexandri* is disjunct between north India/southern China/Indochina and Java/Bali, and although absent from Sumatra, is present on the Andaman and Mentawei Islands (Simalur, Lasia and Babi, and Nias), skirting Sumatra to the west.

Borneo is held with *Psittacula longicauda*, with one widespread subspecies on Sumatra, Malaysia and Borneo, and endemic subspecies on each of Andaman Is., Nicobar Is., Mentawei Is. (Enggano), and Riau and Natuna (Bunguran) Islands. The island subspecies would usually be assumed to have been derived by 'chance dispersal' from the mainland to the islands followed by 'peripheral isolation'. Here they, along with *P. alexandri* and the Mauritius and Sri Lanka species, are taken to represent relics of the former Indian Ocean/Riouw Pocket base from which the mainlands, as they took shape, were invaded.

The nightjar *Europodus macrotis* has subspecies at: Assam to W. China, Indochina and N Malaysia; S India; Mentawei Is. (Simalur I.); Philippines; and Sulawesi. Here the connection S India – Mentawei Islands is likely, while Sumatra and Java are not involved. The related *E. temminckii* is in Malaysia, Sumatra, and Borneo.

Distributional arcs skirting Sumatra to the west are well-known in other birds (*Treron* pigeons, Fig. 77), cf. *Hemiprocne longipennis thoa*: Batu I, Pagi Is., Enggano I., possibly *Halcyon chloris chloroptera* 'West Sumatran Is.'; and plants (*Phaleria* Jack., Ding Hou 1960). *Citronella* D. Don is disjunct between Simalur I. and Java (Sleumer 1971a), recalling *Chisocheton aenigmaticus* D.J.Mabberley endemic to Simalur I., but apparently related to New Guinea species (Mabberley 1979),

Aceh

For Sumatra, Whitten et al. (1987) wrote that 'perhaps the most surprising zoogeographic boundary, because it is not obviously caused by a river or a strait, is that which runs SW/NE through Lake Toba [just south of the Aceh border]. Seventeen bird species are found only to the north of Lake Toba and ten only to the south.' Three mammals (including the orang-utan) occur only in the much smaller area to the north (Aceh), four only to the south.

The geological map shown above (Fig. 6, from Metcalfe 2001) shows the part of Aceh west of the Sumatra fault as comprising the Sikuleh terrane, occurring to the north of the Natal terrane. These two are more or less equivalent to the Aceh and Mentawai microplates of Malod and Kemal (1996), bounded in the west by the Mentawai fault.

Absences are often neglected in systematic studies and not properly documented, but they contribute to the phenomena seen at a biogeographic node. For example, Gillett (1974) observed 'significant voids' in the distribution of Melanesian *Cyrtandra* and referred to the `paradox' of these absences. Danser (1928) wrote that 'it seems strange' that *Nepenthes* does not occur in the northern part of Sumatra (Aceh, according to his map). Danser suggested that with more collecting it may prove to occur there, but Cheek and Jebb (2001) recently wrote that the genus is still not known in the `northern tip' of Sumatra. As *Nepenthes* is most diverse in W. Malesia, with dozens of species in secondary, swamp, and heath forest as well as montane habitats, and also occurs in Sri Lanka and NE India, its absence from Aceh has all the hallmarks of a `significant void'.

Taxa of Aceh, especially the Gajo Lands (Mt. Losir etc.) in central Aceh, show important biogeographic connections with Madagascar and Sri Lanka. Direct (disjunct) ties with Himalaya/N Burma/Yunnan 2000 km to the north are shown in *Gaultheria*. A similar example from timber trees is *Terminalia myriocarpa* Heurck & Müll. Arg. (Combret.), known from NE India, Upper Burma and Yunnan, and also in Aceh (Gajo Lands) (Exell 1954).

Aceh – New Guinea connections are very important in Ericaceae, e.g. *Pseudovireya* I and II. Van Steenis (1964) noted that a small but distinct set of Australia–New Zealand high-mountain taxa is found as an outlier on the ancient Losir massif. Examples include *Oreobolus* R.Br. (Cyperaceae) (Fig. 120, here and Peninsular Malaysia, Kinabalu, Sulawesi, New Guinea, and around the Pacific); *Centrolepis* (Centrolepid.); *Patersonia* R. Br. (Irid.), and *Monostachya* Merr. (Gramineae: Losir, Philippines, New Guinea). This pattern represents a classic biogeographic 'problem' (van Steenis 1964) as long distance dispersal seems such an unlikely explanation. The pattern is also seen in the many N Sumatra – New Guinea disjunctions in Ericaceae and others; Schouten and Veldkamp (1985) described this disjunction in the following:

Anthoxanthum horsfieldii. In this species the populations from N Sumatra and New Guinea (from Mt. Carstensz to Mt. Dayman) are 'especially close.'

Agrostis infirma Buse. In this species a variety found in Sumatra, Java and New Guinea 'clasps' the ones on the islands in between (Veldkamp 1982) (Fig. 78).

Centrolepis fascicularis is in Sumatra, and disjunct in New Guinea (Wissel Lakes, Lake Habbema, Mt. Suckling) and Australia.

Schouten and Veldkamp concluded their discussion with the query: 'Why does it seem as if a taxon can 'jump' from New Guinea to Sumatra and is then, once there, apparently unable to disperse further along the Bukit Barisan?'

Other N Sumatra – New Guinea disjunctions are seen in *Lindsaea* (Fig. 79), Podocarpaceae (Fig. 80), *Rhopaloblaste* (Palmae) (Fig. 81), *Grammitis ornatissimum* (Fig. 82), *Papuama* (Diptera) (Fig. 83) and *Grammitis padangense* (Fig. 84), the last also on Mt. Kinabalu and Mt. Apo. *Canarium hirsutum* and allies (Burser.) (Fig. 85) show a related pattern, with one species widespread through Malesia and the others in Sumatra/Peninsular Malaysia and in New Guinea.

Central W Sumatra is biogeographically closely related to Aceh and like Aceh is also an important site of disjunction. *Nepenthes sumatrana* (Miq.) Beck, endemic there, is 'remarkably similar' to *N. treubiana* Warb, of New Guinea (Check and Jebb 2001). (Danser, 1929, included the former in the latter).

Impatiens L. (Balsamin.) is widespread globally and in Sumatra has 29 species, most of which are local endemics in the montane forest (Grey-Wilson 1989). This occurs along the entire western seaboard of Sumatra, where a long series of active and extinct volcanoes set within the rift of a chain of more ancient mountains provides sufficient altitude for a rich flora. Apart from one widespread species, Aceh has 8 species of *Impatiens*, North Sumatra 6, West Sumatra 13, Bengkulu 2, South Sumatra 5, and Lampung 1. The maximum number is in West Sumatra (especially Mt. Kerinci which has three endemic species and one variety). Red-flowered species occur only on a standard track: Africa, Madagascar, Sri Lanka, southern India and Aceh.

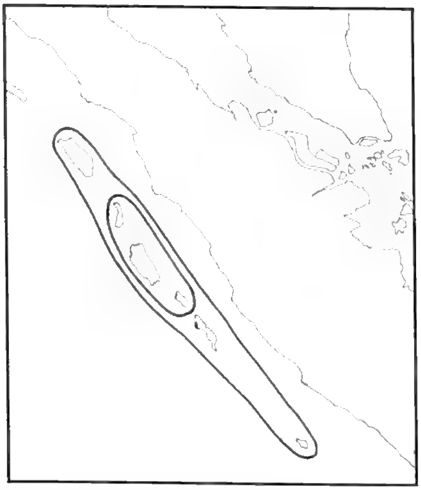

Fig. 77. The green pigeons *Treron curvirostra smicra* (central) and *T. vernans mesochloa* (more widespread) (Columbidae) (Howard and Moore 1984).

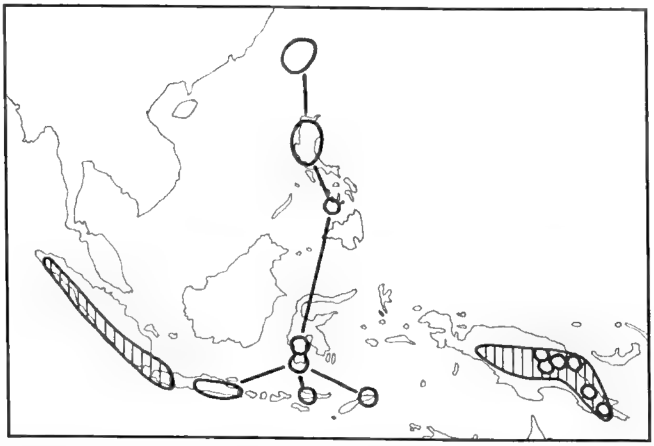

Fig. 78. *Agrostis infirma* Buse var. *infirma* and var. *remota* (Buse) Veldk. (hatched), (Gramineae) (Veldkamp pers. comm.; the two varieties were cited in Veldkamp 1982 as '*A. rigidula* Steudel var. *rigidula*' and 'var. *remota* (Buse) Hoynck & Linden').

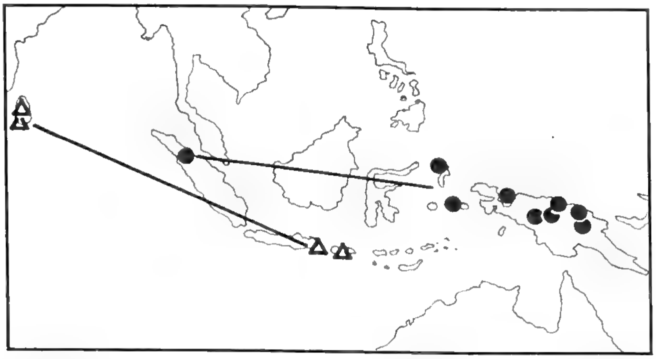

Fig. 79. *Lindsaea werneri* Rosenstock (circles) and *L. glandulifera* v.A.v.R. (triangles) (Dennstaedt.) (Kramer 1971).

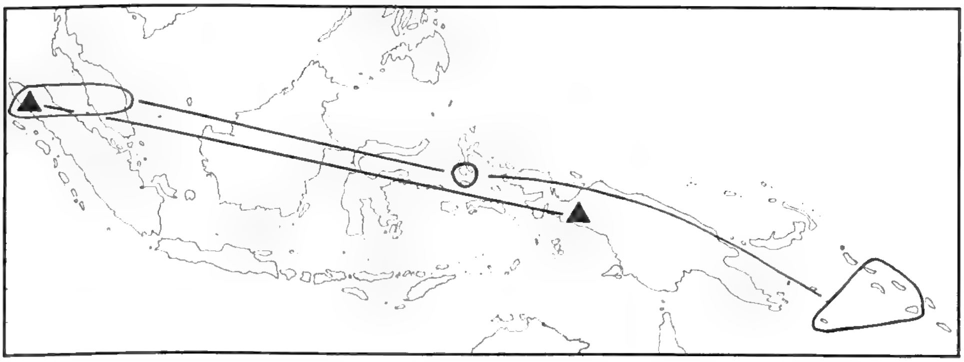

Fig. 80. *Podocarpus atjehensis* (triangles); *Dacrydium medium* de Laub. (Sumatra, Peninsular Malaysia) and its sister species *D. magnum* de Laub. (Moluccas, Solomon Is.) (de Laubenfels 1988).

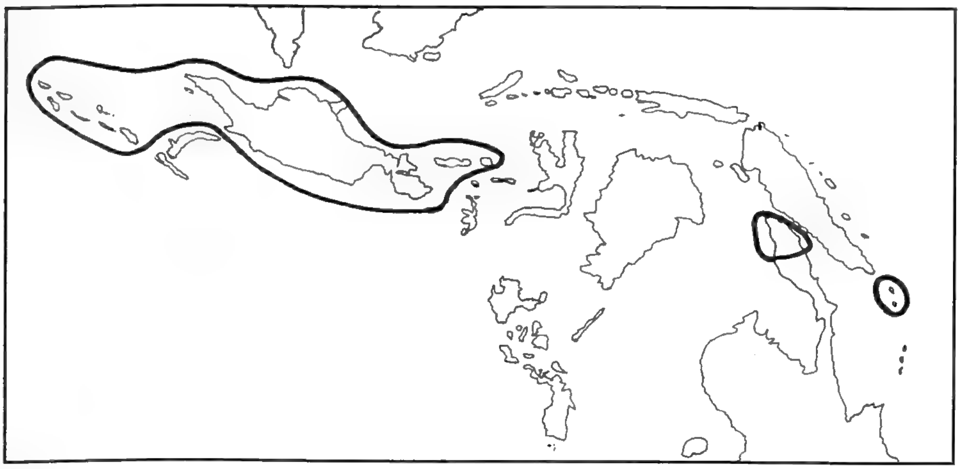

Fig. 81. *Rhopaloblaste* Scheff. (Palmae) (Baker et al. 1998).

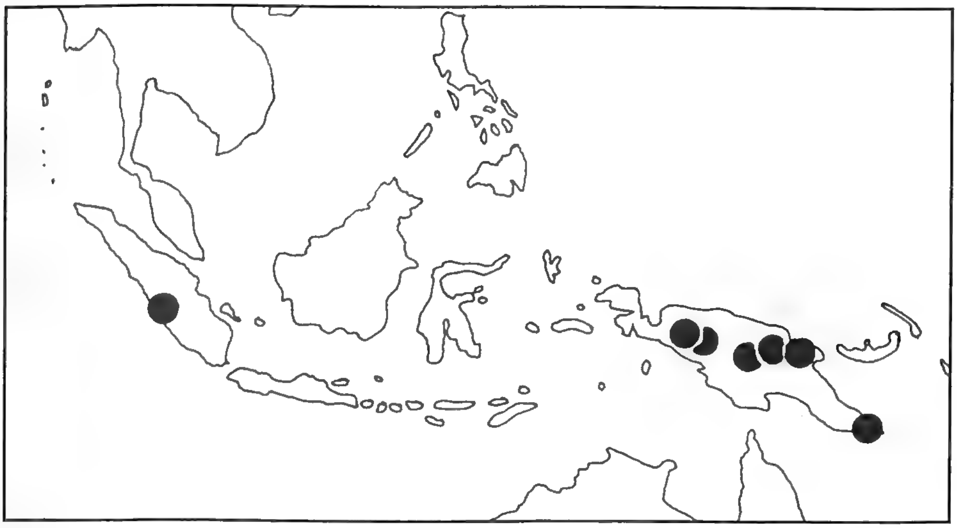

Fig. 82. *Grammitis ornatissismum* Rosenst. (Grammitid.) (Parris 1983).

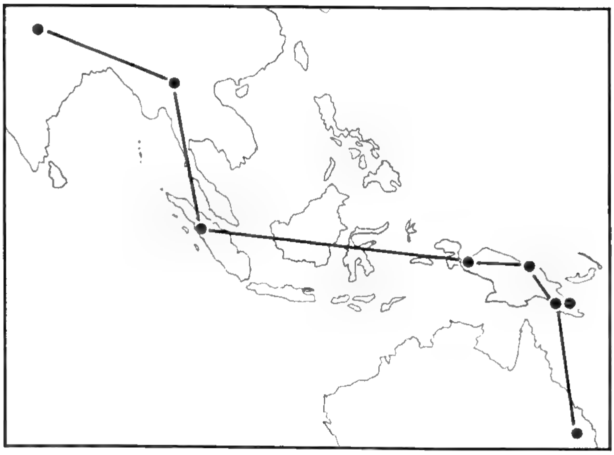

Fig. 83. *Papuama* Mathis and Zatwarnicki (Diptera: Ephydridae) (Mathis and Zatwarnicki 2002).

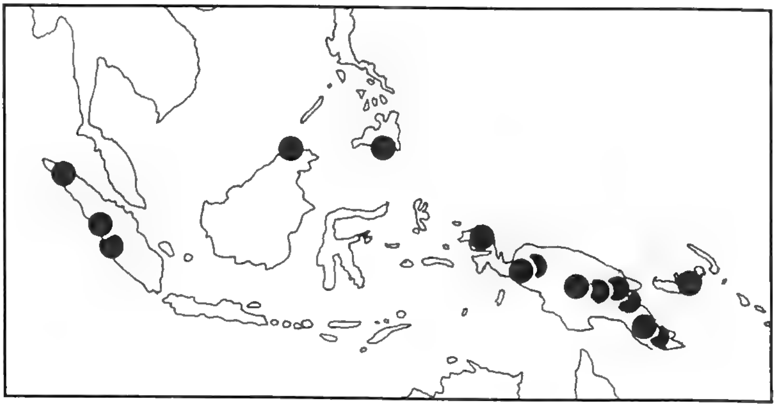

Fig. 84. *Grammitis padangense* Baker (Grammitid.) (Parris 1983).

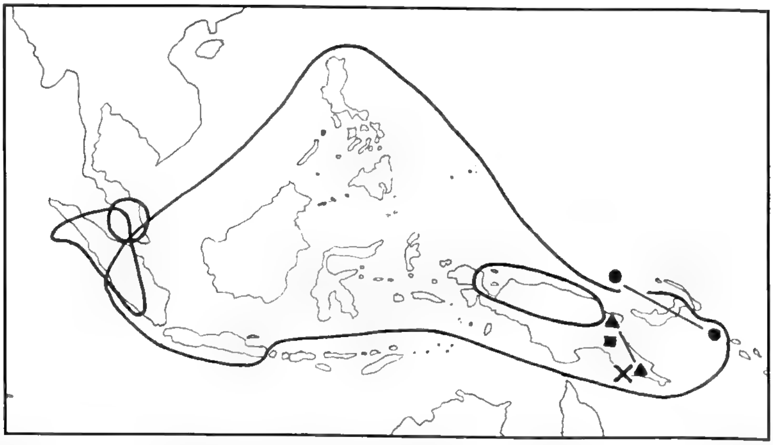

Fig. 85. *Canarium hirsutum* and allies (Burser.) (Leenhouts et al. 1956). Note the concentration of species in the far west and east of Malesia, and the suggestion of parallel arcs in Papua New Guinea.

Impatiens eubotrya Miq. of West Sumatra and *I. steenisii* Grey-Wilson of Aceh have a bilaterally assymmetrical corolla lip, and are closely allied, not with other Sumatran plants, but with a group of species centred on the Himalayas, Burma, Assam, and Yunnan. This disjunction recalls that seen in *Gaultheria* and others.

Describing a related disjunction, Ding Hou (1964) wrote 'it is rather remarkable' that *Euonymus benguetensis* Merr. (Celastr.), is known only from Central Sumatra (Mt. Kerinci) and Luzon. However, this track is vicariant with the species keyed with *E. benguetensis*, *E. japonicus*, which also runs between CW Sumatra and Luzon (and points north), but instead of a direct connection occurs through Java and Sulawesi. *E. javanicus* also largely surrounds Borneo, and is present there only in the N Meratus Mts. (Fig. 114). *E. acuminifolius* (forests 700 m–3200 m) is only known from CW Sumatra, Kinabalu, and SW Sulawesi, again, largely surrounding Borneo and this time present there only at Kinabalu.

The *E. benguetensis* track (Central/North Sumatra – Luzon) is also seen in several Ericaceae affinities (*Rhododendron* ser. *Javanica* III, *Diplycosia* III, *Vaccinium* sect. *Bracteata* XV, and cf. *Bracteata* X). Likewise, *Norrisia* Gardn. (Logan.) consists of two species: *N. malaccensis* is in CW Sumtra/Peninsular Malaysia and Philippines (Suibuyan/Mindanao), its vicariant *N. major* fills the gap in southern Sumatra and Borneo (Leenhouts 1962).

West Sumatra – Philippines connections skirting W Borneo are seen in taxa such as *Xanthophytum ferrugineum* (Rub.) (Axelius 1990) (Fig. 86).

In southwest Sumatra, species in *Rhododendron* subsect. *Albovireya* show an interesting pattern of disjunctions which may have been caused by dextral transcurrent movement along the Sumatra fault. This massive fracture runs along the entire length of west Sumatra following the active volcanic arc (Hall 1998). Detailed mapping of the species in relation to the fault is needed.

West Sumatra includes arc and ophiolitic material accreted in the Cretaceous (Hall 1998).

Peninsular Malaysia

Like N. Sumatra, Peninsular Malaysia shows disjunctions with E. Malesia. *Podocarpus spathoides* (Podocarp.) (Fig. 87) ranges in Penisular Malaysia (Mt. Ophir) – Rossel Is.: these populations have buds half the length of the remaining two populations: N. Moluccas (Morotai) – Solomon Islands (de Laubenfels 1989). *Parsonsia curvisepala* (Apocyn.) (Fig. 89) is a widespread, well-collected species in Peninsular Malaysia and E Malesia but is not in Borneo, W. Philippines, or N. Sulawesi (Middleton 1991).

Bruguiera hainesii C.G. Rogers (Rhizoph., dry side or inland of mangrove) is found along the Burma and Thailand coast to Peninsular Malaysia, with a disjunct population in Papua (Ding Hou 1958, Percival and Womersley 1975). Other species are widespread through Malesia.

Leptocarpus R. Br. (Restion.) is disjunct in Malesia between Hainan, Cambodia and Peninsular Malaysia (one species) and Aru I. and southern New Guinea (two species). Elsewhere (Heads 1985a) this was shown to be one of many groups which cross Wallace's Line, but not as the result of chance dispersal.

In animals, the *Ponera taipingensis* species group (Hymenoptera: Formicidae) has a single species in each of Peninsular Malaysia, Papua New Guinea, and Fiji, and two in Samoa (Fig. 88) (Taylor 1967).

Riouw Pocket

The Riouw Pocket (Corner 1938, 1960, 1978a) includes SE Sumatra (Riau, Jambi and Sumatera Provinces), south Johore, the SW corner of Borneo, and the islands in the region (Riouw, Lingga, Bangka and Billiton). Corner noted the strange absence here of several otherwise very widespread plants (e.g. *Ficus tinctoria*, near mangrove, on coral rock etc.; *F. subulata*, related to the last but in rainforest, shade-loving, often epiphytic; *F. fulva, F. glabberima, F. parietalis, F. uniglandulosa, F. hispida)*, but also the presence there of many range-restricted taxa (*F. deltoidea* var. *deltoidea, F. d.* var *ovoidea, F. microstoma, F. acamptophylla* Miq., *F. microsice* Ridley, *Tristaniopsis* sp., *Pandanus corneri*). *Ancistrocladus tectorius* (Fig. 90) in Malesia is largely restricted to the Riouw Pocket. An example of local endemism is *Indovethia* Boerl. (Ochn.), Central East Sumatra (Riouw Province), westernmost Kalimantan and Sarawak (1st Div.) (Kanis 1971). This is a rare lowland monotype recorded from the edge of a lake and above a torrent in forest. *Gonystylus bancanus* (Thymel.) (Fig. 91) is the most valuable timber tree in the area and also an endemic. Likewise the bird *Setornis* (Pycnonotidae) is only known from E. Sumatra, Bangka I. and Borneo.

As many as 57 species of dipterocarp reach their eastward or westward limit at the Lupar R. (by Kuching) Ashton 1969, Corner 1978a), at the boundary of the Riouw Pocket. The Semitau terrane (Fig. 6) occupies the Kuching corner of Borneo, and is bounded in the north by the Lupar suture (like the dipterocarps) and in the south by the Boyan suture, dated at Late Cretaceous (Metcalfe 1998). Hutchison (1996) and Morley (2002) provided more data on the tectonics of the 'Lupar Line'.

The incense tree *Aetoxylon* Airy Shaw (Thymel.) was known to Airy Shaw (1953) only from 1–200 km around Kuching. Riouw pocket disjunctions include those of *Nephthytis* Schott (Araceae), known only from tropical West Africa and near Bintulu in central W. Sarawak (Hay et al. 1994). *Gymnanthes* Sw. (Euphorb.) occurs around the Riouw pocket (widespread in Borneo, especially the west) and is also in Cameroun/Congo and America (Esser 1999). *Lindsaea walkerae* (Kramer 1971) (Fig. 92) shows both Riouw Pocket – Sri Lanka and Riouw Pocket – Vogelkop disjunctions.

In a broader sense the Riouw Pocket involves most of Sumatra and west Borneo. *Aralidium* Miq. (Aralid.), *Pentastemona* Steenis (Pentastemon.), *Scaphocalyx* Ridley (Flacourt.) and *Scyphostegia* Stapf (Flacourt.) are all W. Malesia endemics from here, centred on the Riouw pocket. The last two have morphologically challenging flowers. Van Heel (1973) observed that the unique ovary of *Scaphocalyx*, with two radially alternating whorls of ovules one above the other, cannot be understood under the classical theory of the carpel as a modified leaf (like heretical 'sterile carpels' in *Styphelia*; Paterson, 1961). The seed of *Scaphocalyx* has features (nucellar beak, three-layered testa etc.) that are frequent in gymnosperms, but rare in angiosperms, indicating that the Riouw pocket may act as a centre of relictual characters. The morphogenetic significance of *Scyphostegia*, with structures intermediate between ovule and ovary (and 'blossoms' intermediate between flower and inflorescence), has been discussed elsewhere (Heads 1984).

Michaux (1995) analysed the biogeography of 384 Borneo vertebrates and invertebrates, and interpreted their distribution in terms of West Malesian geological terranes. His 'Pattern 3', numerically the most strongly defined, is identical to Corner's (1978a) Riouw Pocket and also the East Malaya terrane (as mapped by Michaux 1995).

A good example of the Riouw pocket avoided by a mangrove associate is *Sauropus bacciformis* (L.) Airy Shaw (Euphorb.) ('along or near beaches ... along path through mangrove ... tidal flats, open waste ground' etc.) (van Welzen, in press) . This largely vicariates with other Euphorbiaceae such as *Neoscortechinia philippinensis* (Merr.) van Welzen (freshwater swamp forest, along mangrove etc.) which invades the lands

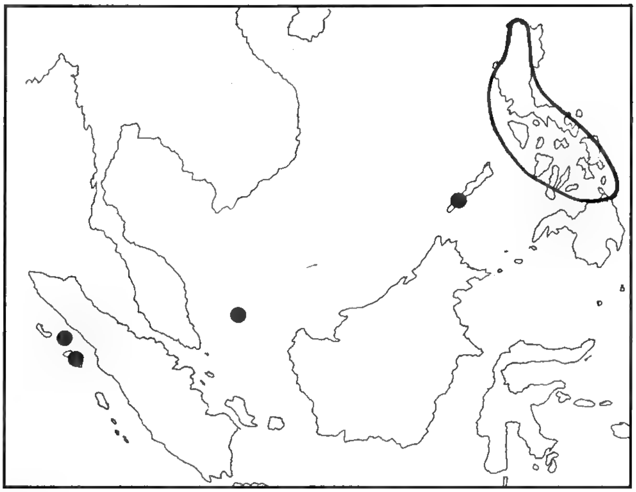

Fig. 86. *Xanthophytum ferrugineum* (DC) Merrill (Rub.) (Axelius 1990).

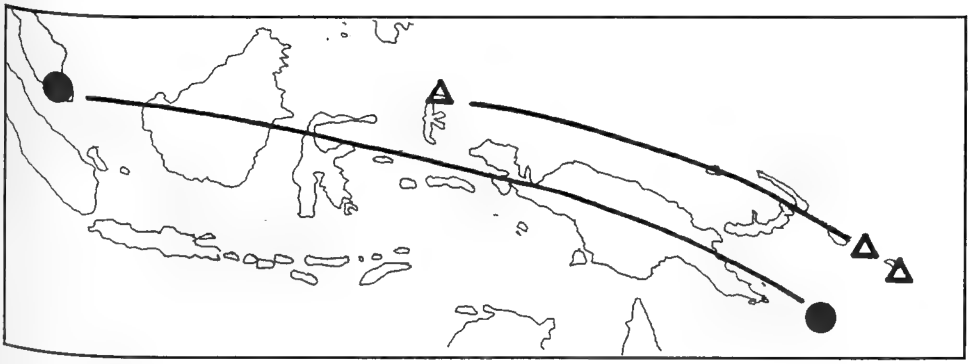

Fig. 87. *Podocarpus spathoides* de Laub. Peninsular Malaysia and Rossel I. populations have foliage buds up to 3 mm long, Moluccas and Solomons plants have buds twice as long (de Laubenfels 1988).

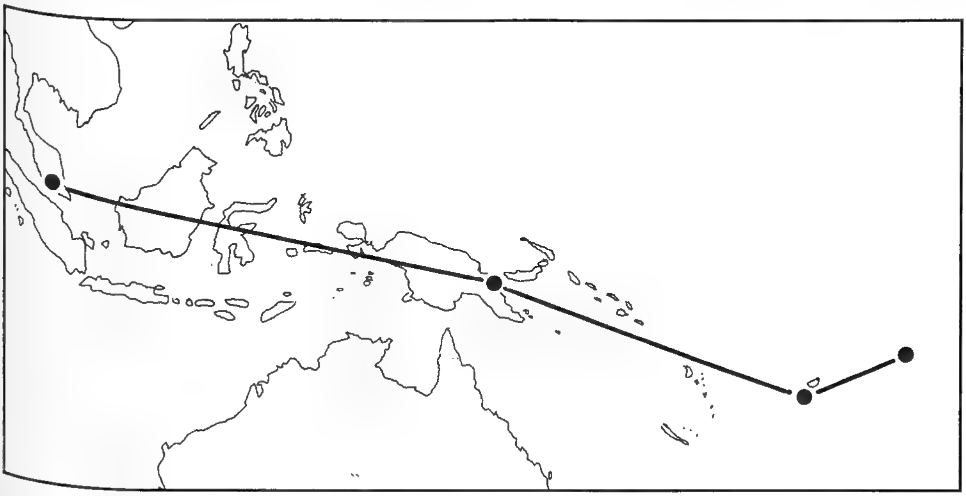

Fig. 88. *Ponera* Latreille (Hymenoptera: Formicidae) (Taylor 1967).

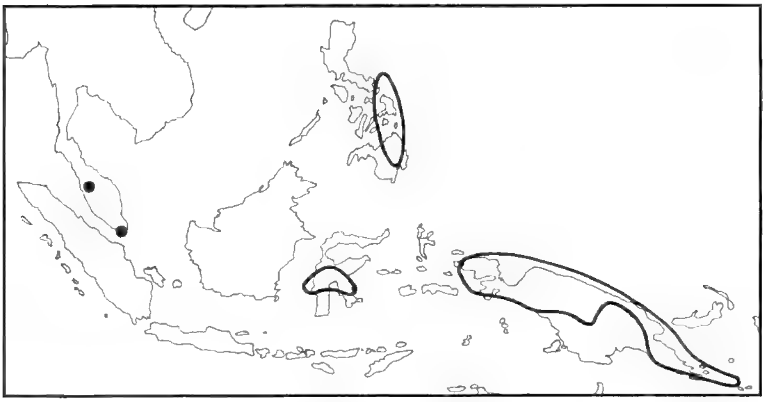

Fig. 89. *Parsonsia curvisepala* (Apocyn.) (Middleton 1991).

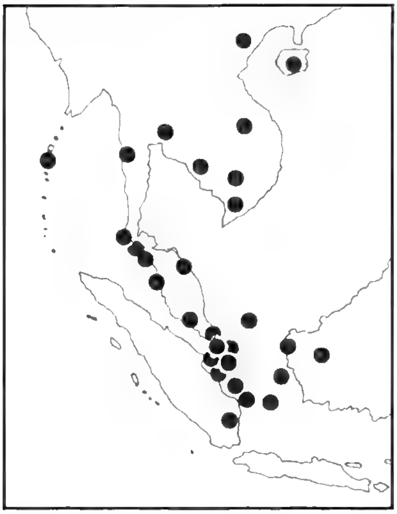

Fig. 90. *Ancistrocladus tectorius* Merr. (Ancistroclad.) (the only Malesian member of the family) (van Steenis 1948).

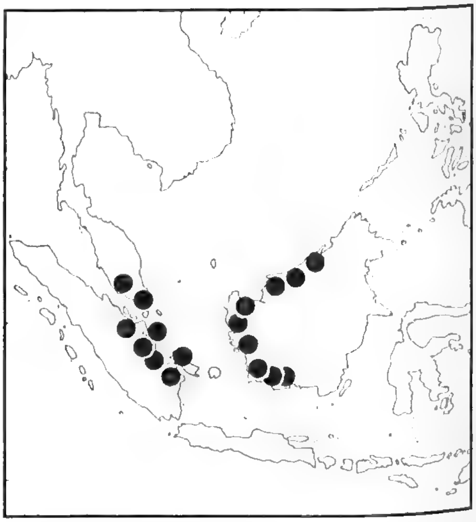

Fig. 91. *Gonystylus bancanus* (Miq.) Kurz (Thymel.) (Airy Shaw 1953).

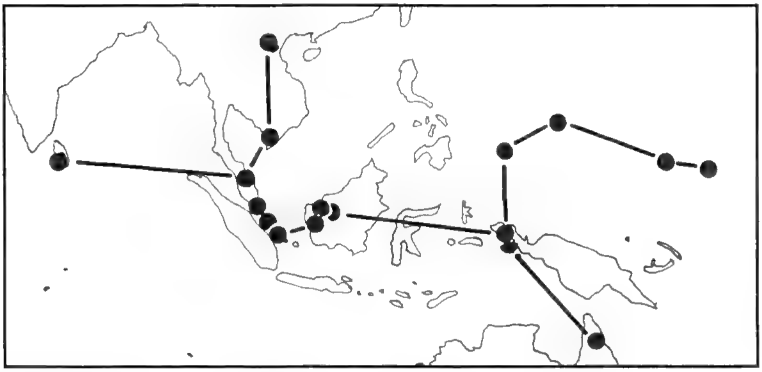

Fig. 92. *Lindsaea walkerae* Hook. (Dennstaedt.) (Kramer 1971).

around the Riouw pocket (van Welzen 1994a). Thus plants with mangrove ecology may invade the Riouw pocket, or not. These alternative distributions would seem to have little to do with ecology, and are presumably due to different histories.

W. Sumatra – W. Borneo Mangrove Track

An example of this pattern is given above in *Rhododendron brookeanum*. An especially interesting W Borneo species, *Podocarpus micropedunculatus* de Laub., is found in N. Sarawak, Brunei, and Sabah. It ranges from sea level to 500 m on humic peaty podzols of raised beaches, in peat-swamp forest, kerangas, and *Agathis* forest and is a major element in thickets along the margins of clearings (de Laubenfels 1988). It propogates by rhizomes which spread under the forest litter — a remarkable character otherwise unknown among erect conifers. The distribution, habitat and the plagiotropy all suggest a weedy, mangrove relic.

In an example from insects, Holloway and Hall (1998) recorded the *Antheraea frithi* complex of emperor moths from mangrove in W Sumatra (Tapanuli), Belitung [Billiton] Island (Riouw pocket), the W. Borneo coast and Palawan, following the usual mangrove track. Elsewhere the moths are in hill and montane forest in mainland Asia, Mentawei Islands, Sumatra, Borneo (where the montane species is also at low altitude in heath forest on river terraces), and Sulawesi.

Borneo

Like many Ericaceae, other plants also surround Borneo without occurring on it (Figs. 93–106). Other examples include *Strophioblachia* Boerl. (Euphorb.) (Thin et al. 1998) and invertebrates such as the spider genus *Fecenia* (Levi 1982). The pattern has been attributed to ecological factors (for example, there is no significant dry season in most of Borneo), but this seems unlikely as the taxa concerned show the entire range of ecologies. An example of a mangrove associate avoiding Borneo is *Sauropus villosus* (Blanco) Merr. (Euphorb.) (open thickets, often near the sea-shore etc.: N Sumatra, Peninsular Malaysia, Philippines) (van Welzen, in press). In fact, biogeography may determine ecology: taxa restricted to, say, drier parts of the Lesser Sunda Islands, Sulawesi and Philippines due to biogeographic/geological reasons may be forced to survive there (or go extinct).

Corner (1961) argued that 'Distribution must have been a geologically slow process. This point of view is repeatedly argued by Croizat (1958) who points to Cretaceous geography as the guide even to modern details of distribution. In Sarawak, where forest is still so abundant, the force of his argument can be appreciated: localization of plants, unable to spread, makes the flora a complicated mosaic …'

Several terranes in Borneo appear to be of biogeographic significance. Kinabalu is discussed above. Biogeographically, and perhaps geologically, Kinabalu belongs largely with the Philippines mountain systems rather than with the rest of Borneo.

Sarawak and Kutei Mts./Mt. Kemul in Kalimantan are important centres that both interact with Kinabalu but not each other.

The well-documented W. Borneo track: Sarawak-Brunei-Sabah is seen in many Ericaceae, and possibly represents a direct extension of the Riouw Pocket distributions. In another example, *Indovethia* (Ochn.), cited above in connection with the Riouw Pocket, is possibly closest to *Schuurmansiella* Hall, a monotypic genus in Sarawak (1st and 4th Div.) (Kanis 1971). In Borneo *Soulamea* Lam. (Simaroub.) (Nooteboom 1964) has a restricted distribution in the west and north (Fig. 107). *Steenisia* Backh.f. (Rub.) is only in central, north and west Borneo, and the Natuna Islands, west of Borneo (Bremer 1984).

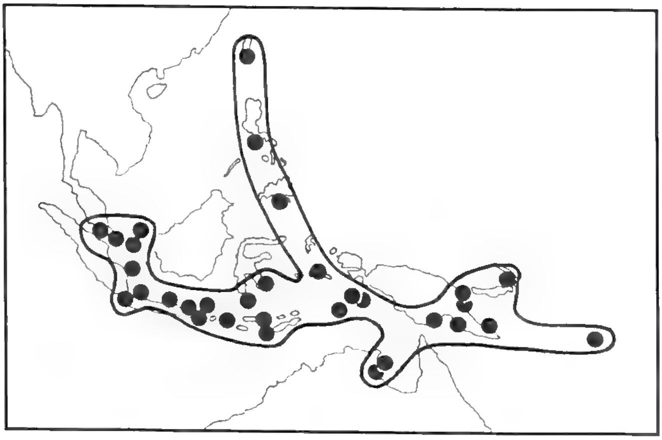

Fig. 93. *Rhizophora stylosa* Griff. (Rhizophor.) (Ding Hou 1958).

Fig. 94. *Codiocarpus* Howard (hatched) and *Medusanthera* Seem. (Stemonuraceae – Sleumer 1971a, Kårehed 2002). *Medusanthera* is in coastal swamp forest, primary and secondary forest etc. and on limestone and coral, at 0–300 (900) m. It was once found in Western Highlands Prov., PNG, at 1740 m.

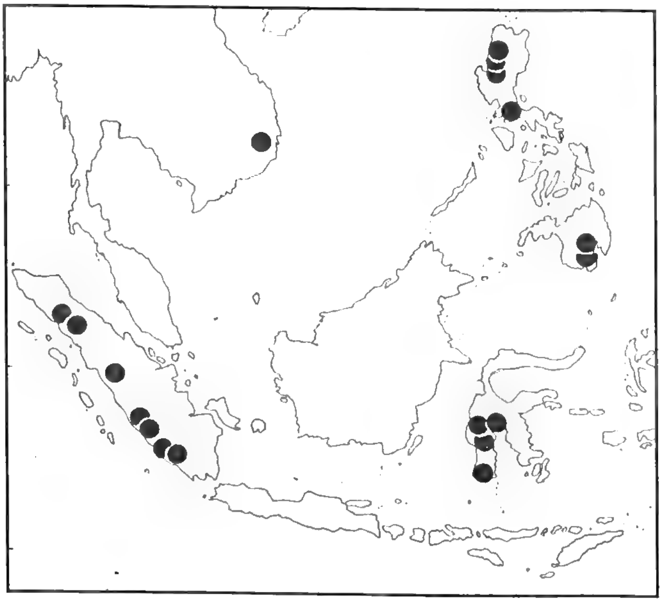

Fig. 95. *Taxus sumatrana* (Miq.) de Laub. (de Laubenfels 1988)

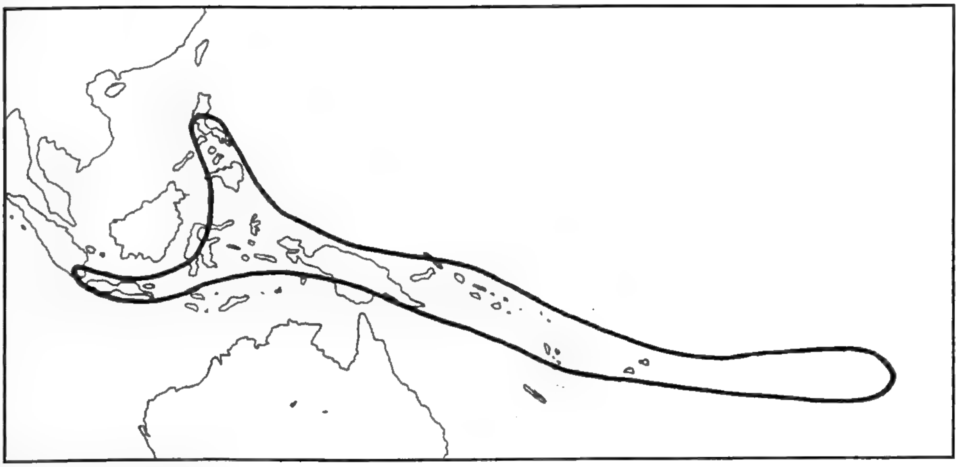

Fig. 96. *Parasponia* Miq. (Ulm.) (Soepadmo 1977).

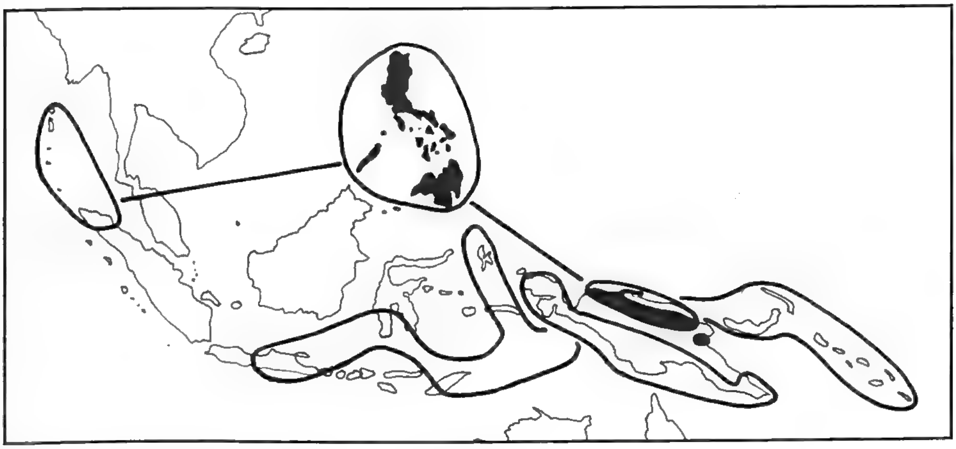

Fig. 97. *Lepidopetalum* Blume (Sapind.) (van Welzen 1993).

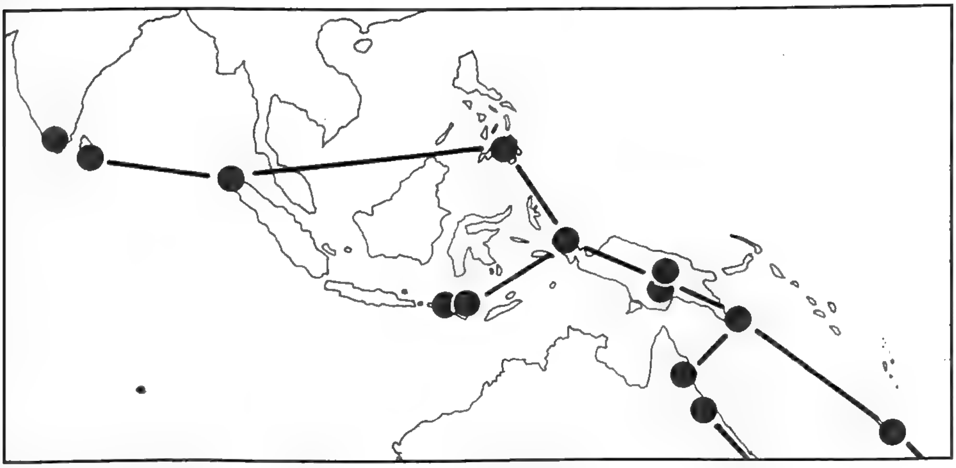

Fig. 98. *Orthorrhynchium elegans* (Hook. f. and Wils.) Reichdt. (Musci) (Tan 1998).

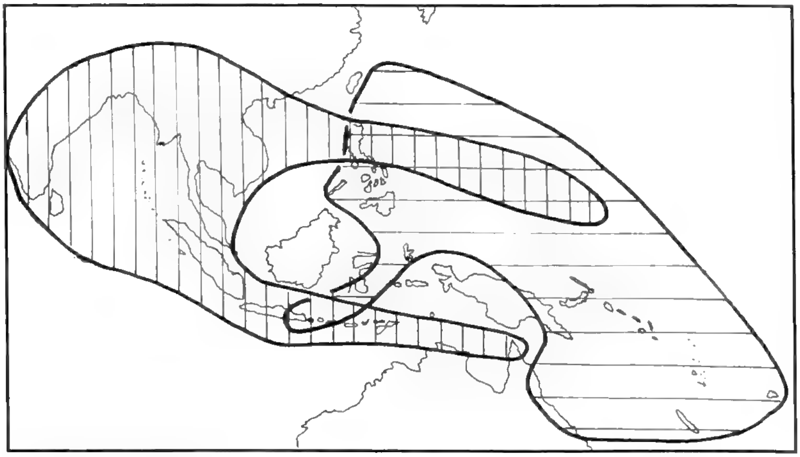

Fig. 99. *Balanophora fungosa* J.R. & G. Forst. ssp. *fungosa* (east), and ssp. *indica* (Arn.) Hansen (west) (Balanophor.) (Hansen 1974).

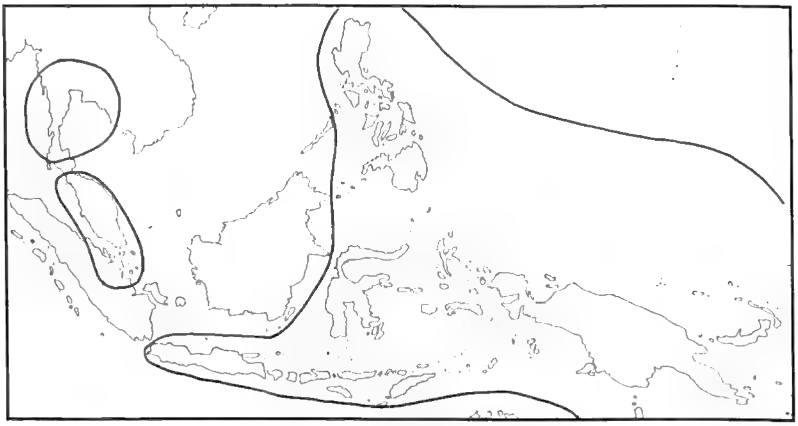

Fig. 100. Tribe Bannisterieae (Malpighiaceae) in Malesia: *Brachylophon* Oliv. in the west (also in East Africa); *Rhyssopteris* Blume ex A.Juss. in the east (to Queensland and New Caledonia) (Jacobs 1954).

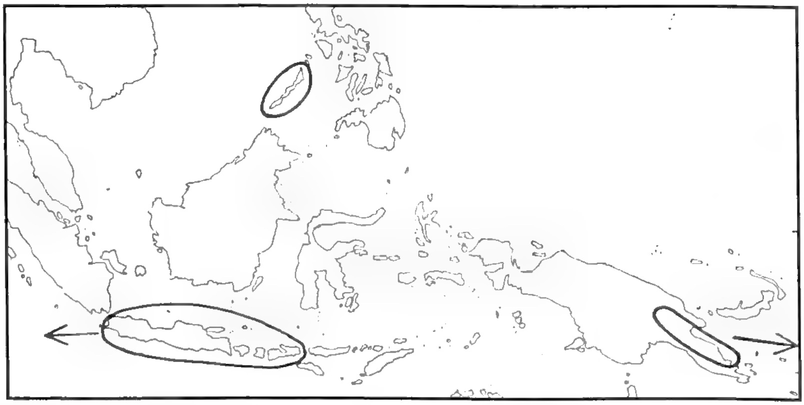

Fig. 101. *Protium* Burm.f. (Burser.) in Malesia (also in Madagascar, Mascarenes, SE Asia, and America (Leenhouts et al. 1956).

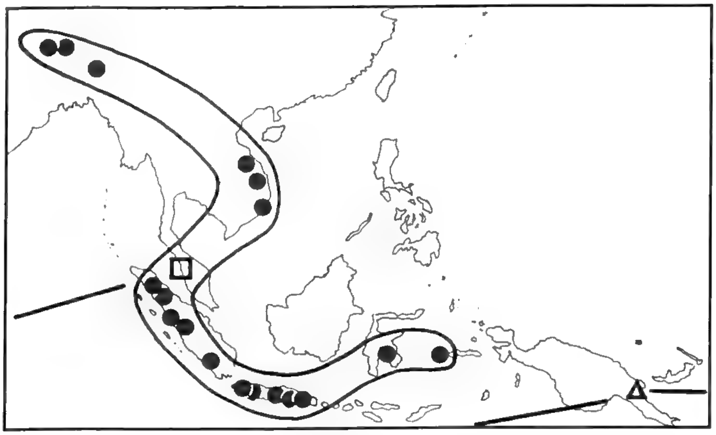

Fig. 102. *Rhopalocnemis* Jungh. (Himalaya – Moluccas), *Ditepalanthus* Fagerl. of Madagascar; *Exorhopala* Steen. (square); and *Langsdorffia* Mart, (also in Madagascar and Central and South America) (Balanophoraceae) (Hansen 1974).

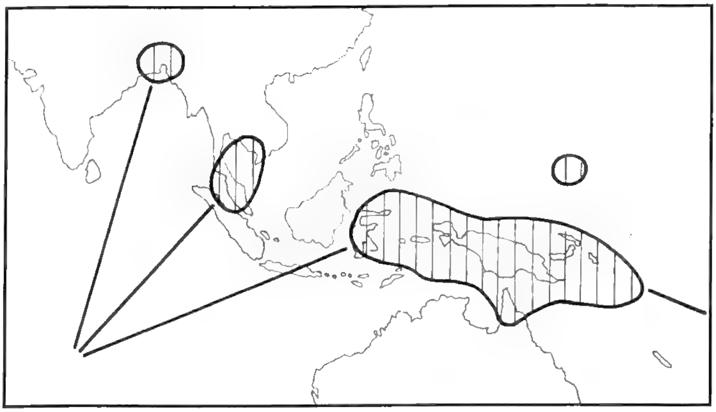

Fig. 103. *Maniltoa* Scheff. (Legum.) (de Vogel 1975c).

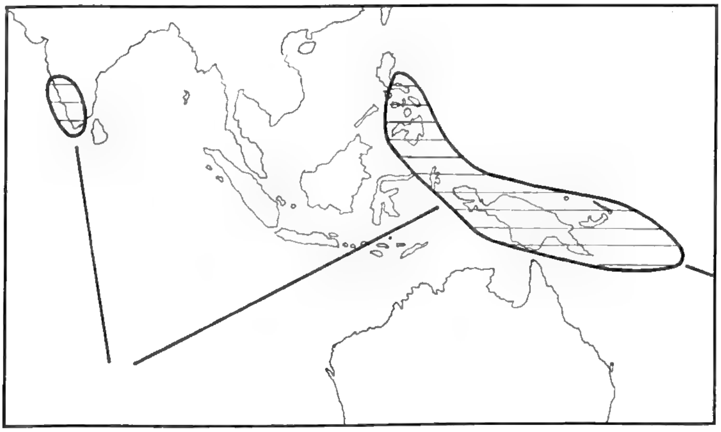

Fig. 104. *Kingiodendron* Harms (Legum.) (de Vogel 1975b).

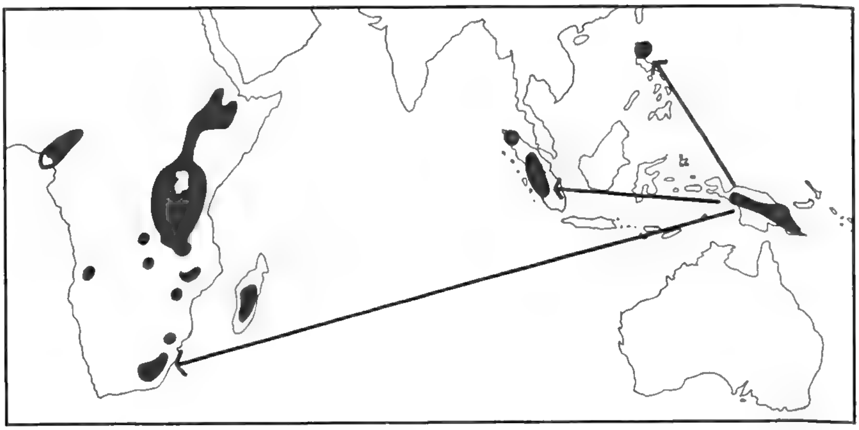

Fig. 105. *Hypericum* sect. *Humifusoideum* (Robson 1981).

Fig. 106. *Ehrharta* Thunb.: s.s. Africa (broken dotted line); s.l. including *Microlaena* R.Br. (continuous line). *Tetrarrhena* R.Br. (dotted line), *Petriella* Zotov (broken line). (Gram.) (Willemse 1982).

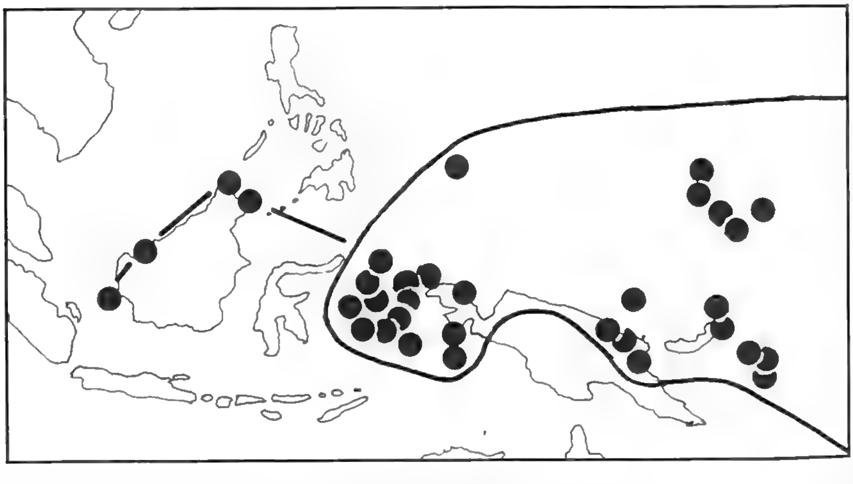

Fig. 107. *Soulamea* Lam. (Simaroub.) in Malesia (Nooteboom 1964).

The eastern Borneo track: Kinabalu–Kemul is shown in Ericaceae and Fagaceae endemic to Kinabalu/Kutei (*Castanopsis endertii* Soepadmo) and Kinabalu/Crocker Range/Kemul (*C. densinervia* Soepadmo) (Soepadmo 1972). The Mangkalihat Mountains give their name to the Mangkalihat terrane which extends from CE Borneo inland to about Mt. Kemul (Metcalfe 1999, 2001).

Taxa restricted to the NE of Borneo include *Podocarpus rumphii* Bl. (Fig. 108), *Serianthes* Benth. (Leg.) (Fig. 109), *Lophopyxis* (Lophopyxid.) (Fig. 110) and *Hugonia L.* (Lin.) (Fig. 111). In the central-eastern part of Borneo are *Deplanchea glabra* (Steen.) Steen. (Fig. 112) and *Podocarpus* sect. *Gracilis* de Laub. (Fig. 113).

East Borneo and West Sulawesi appear to be underlain by accreted arc and ophiolitic material as well as continental crust and this material was accreted during the Cretaceous (Hall 1998).

Hall (2001) wrote that 'Some of the biogeographic patterns in SE Asia at present are difficult to relate simply to geology, for example, the distance between Borneo and Sulawesi (Wallace's line and equivalents) should have been as easy to cross as the barriers between Australia and Sulawesi.' Actually the records (not the Wallacean theory) show that it was. For example, 25B: *Rhododendron cuneifolium* Stapf, *Trochocarpa* 3, and the pairs *Rhododendron* 123 and 124, *Diplycosia* 16 and 17, and *Vaccinium* 18 and 19 all show this sector of Wallace's line (Makassar Strait) not as a boundary but as a centre of endemism. The real boundary is between E and W Borneo. This pattern is also recorded in vertebrates: the freshwater fishes of the region 'are not distributed according to existing land. Those of Sumatra and western Borneo are more alike than those of the western and eastern sides of Borneo' (Darlington 1957).

In SE Borneo, the region of the Meratus suture, *Rhododendron* 131B (on sandstone) and *Vaccinium* 25 (collected once, in 1836) are endemic to the Meratus Mts. These, with the nearby Pulo Laut, include the only ophiolite complexes in Kalimantan and here the process of obduction (the opposite of subduction) has produced large upthrust slabs of oceanic crust. The Meratus Mountains are floristically distinct from other regions and are a site of plant richness and endemism. Local endemics include *Nepenthes boschiana* Korth. of limestone hills (Cheek and Jebb 2001) and the region is especially rich in orchids (Mackinnon et. al. 1996, citing E. de Vogel, pers. comm.), such as *Porphyrodesme* Schltr., only known from there and New Guinea. The Meratus Mts. appear to be one of the places where Borneo is 'entered' by tracks from the south and east, like Mt. Kemul further north. The Meratus Mts. represent a suture between the SW Borneo and Paternoster terranes dated as Late Cretaceous (Metcalfe 1998).

Euonymus javanicus B1. (Celastr.) (Fig. 114), *Lumnitzera racemosa* (Combret.) (Fig. 115) and *Agrostistachys capitata* Dalzell (Euphorb.) (Sevilla and van Welzen 2001) are restricted in Borneo to the southeast (Meratus suture region), and *Phaleria capitata* (Thymel.) (Fig. 116) is largely restricted to the southeast. *Calophyllum lanigerum* Miq. (two varieties) and *C. dasypodum* Miq. show an interesting set of parallel arcs converging on SE Borneo (Fig. 117).

The large area of mélange in the centre of Borneo is less well-understood. This is a zone of broken rocks, often including fragments of ophiolite, but its width and extended geological age (late Mesozoic to older Tertiary) are 'difficult to explain in terms of simple plate tectonics' (Mackinnon et al. 1996).

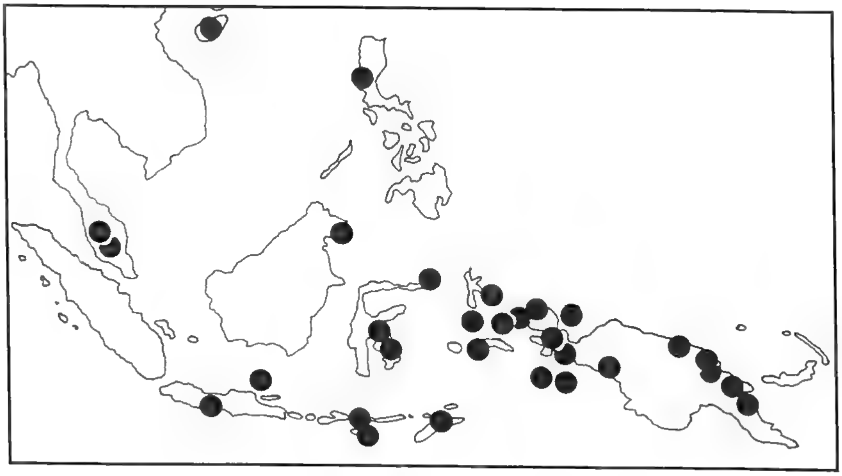

Fig. 108. *Podocarpus rumphii* Bl. (de Laubenfels 1988).

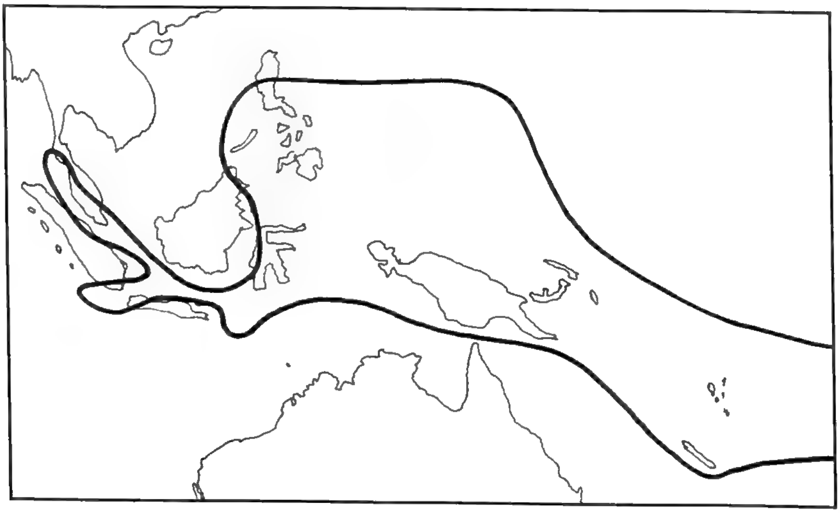

Fig. 109. *Serianthes* Benth. (Legum.) (van Balgooy and Nielson 1993).

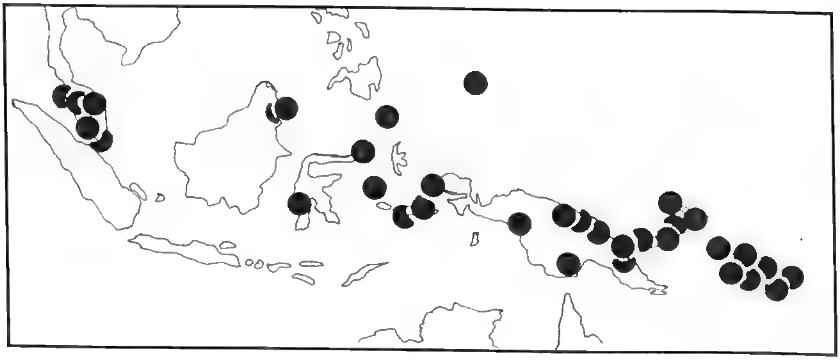

Fig. 110. *Lophopyxis* Hook. f. (Lophopyxid.) (de Vogel 1975).

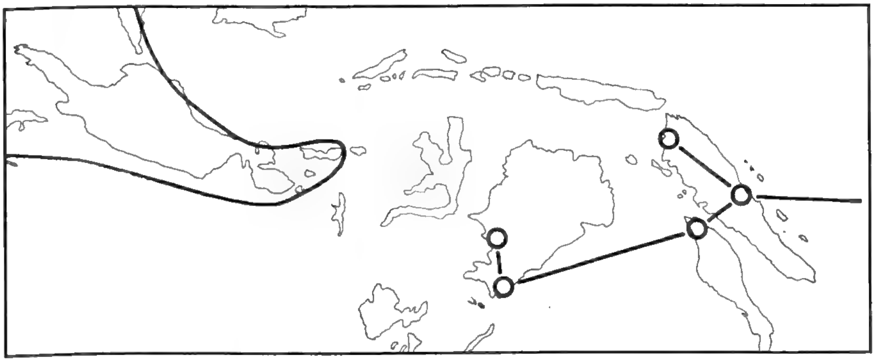

Fig. 111. *Hugonia* L. (Lin.) in Malesia (two species) (van Hooren and Nooteboom 1988). Other species are in Sri Lanka, India, Madagascar and Africa.

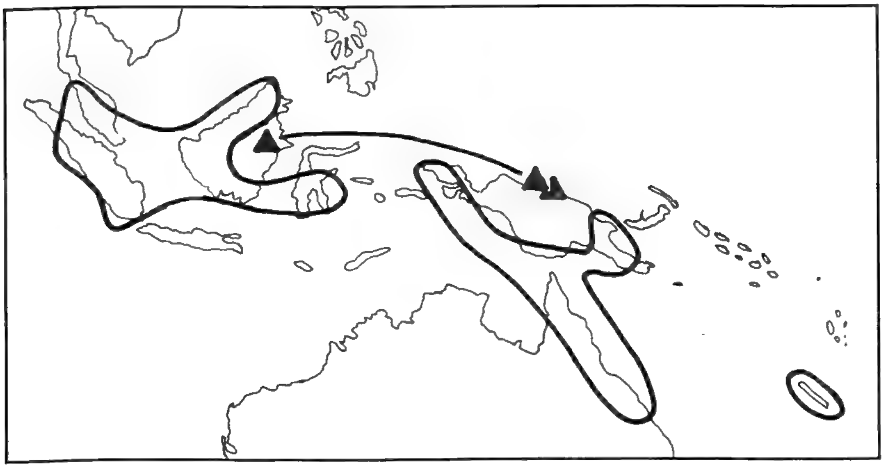

Fig. 112. *Deplanchea* Vieill. (Bignon.) (Avé 1984).

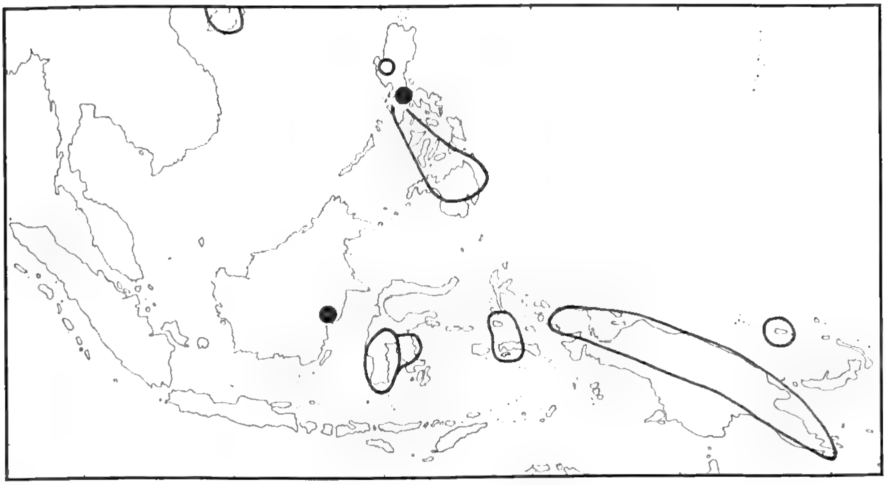

Fig. 113. *Podocarpus* sect. *Gracilis* de Laub. (Podocarp.) (de Laubenfels 1988).

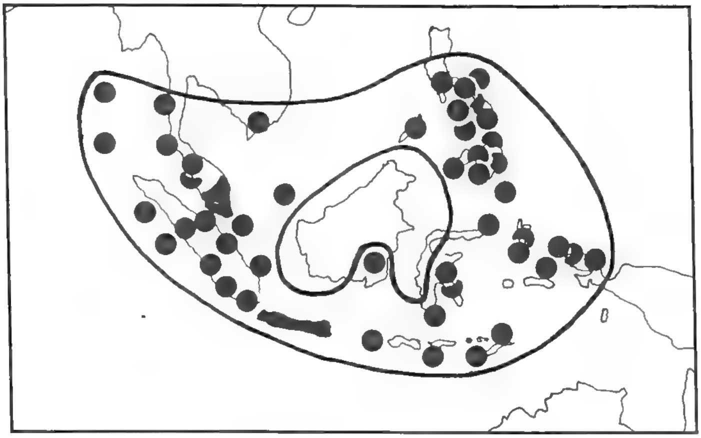

Fig. 114. *Euonymus javanicus* Bl. (Celastr.) (Ding Hou 1964).

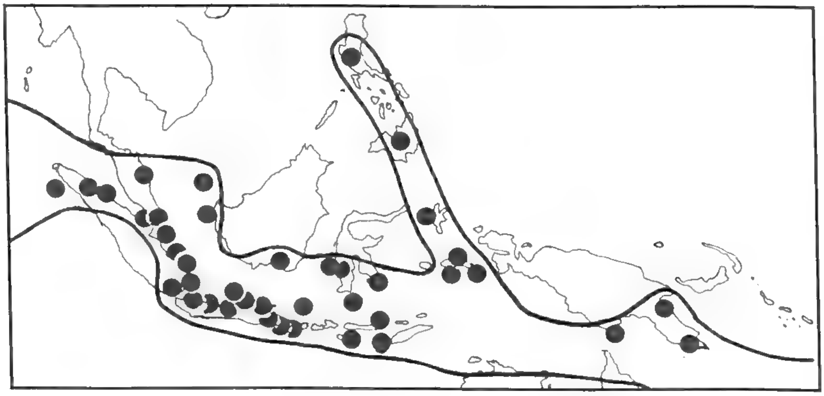

Fig. 115. *Lumnitzera racemosa* (Combret.) (Exell 1954).

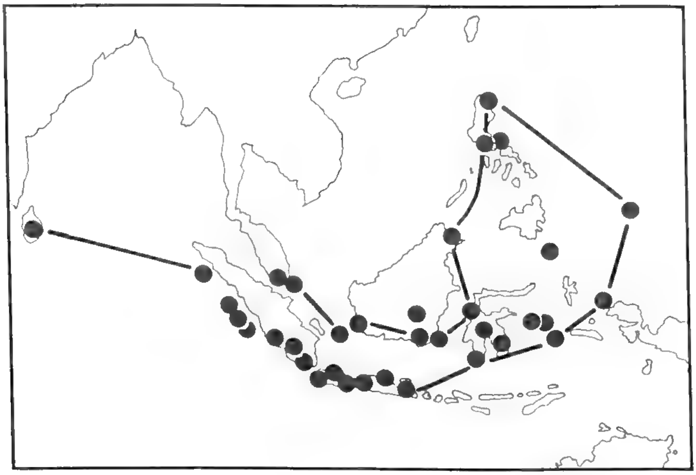

Fig. 116. *Phaleria capitata* Jack (Thymel.) (Ding Hou 1960).

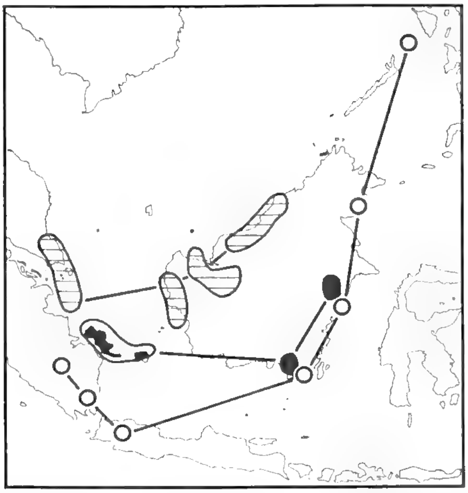

Fig. 117. *Calophyllum lanigerum* Miq. var. *austrocoriaceum* (T.C.Whitmore) P.F.Stevens (hatched); *C. lanigerum* var. *lanigerum* (solid black); *C. dasypodum* Miq. (open circles) (Guttiferae) (Stevens 1980).

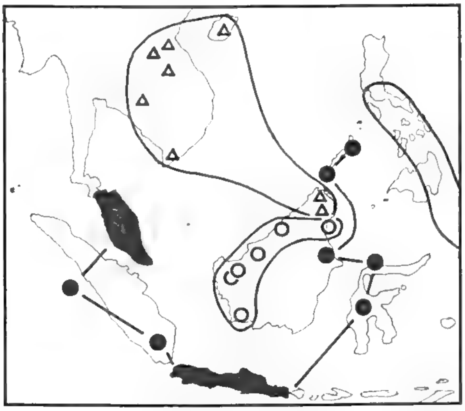

Fig. 118. *Myxoporum* Bl. (Olea.) (Kiew 1984) in W. Malesia: three subspecies of *M. nervosum*, all in Borneo and *M. ovatum* (Philippines).

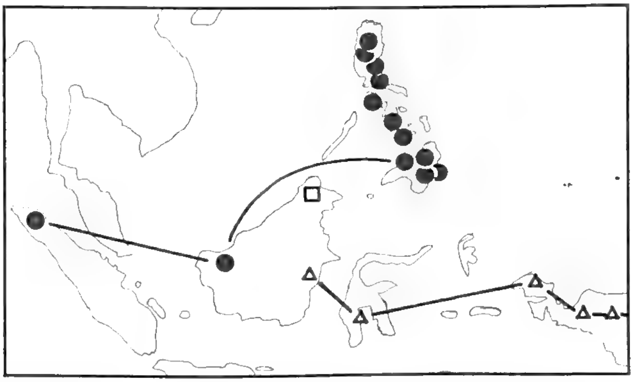

Fig. 119. Three related species in *Dacrycarpus* (Podocarp.) (de Laubenfels 1988): *D. cumingii* (dots), *D. steupii* Wasscher de Laub. (triangles), *D. kinabaluensis* (Wasscher) de Laub. (square).

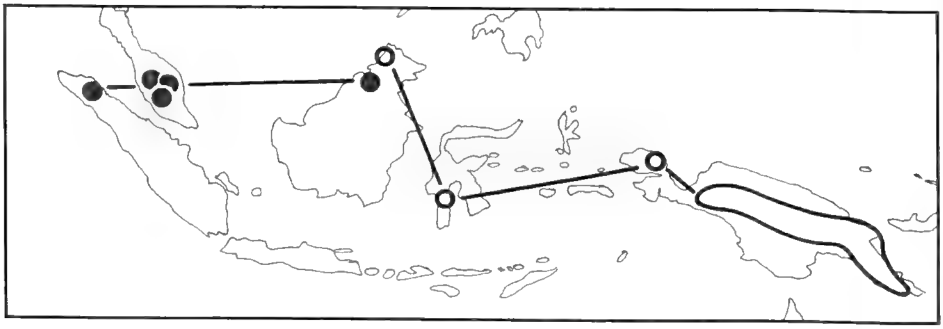

Fig. 120. *Oreobolus* R.Br. (Cyper.) in Malesia (Seberg 1988). Two species are mapped, the third is also in the New Guinea mountains.

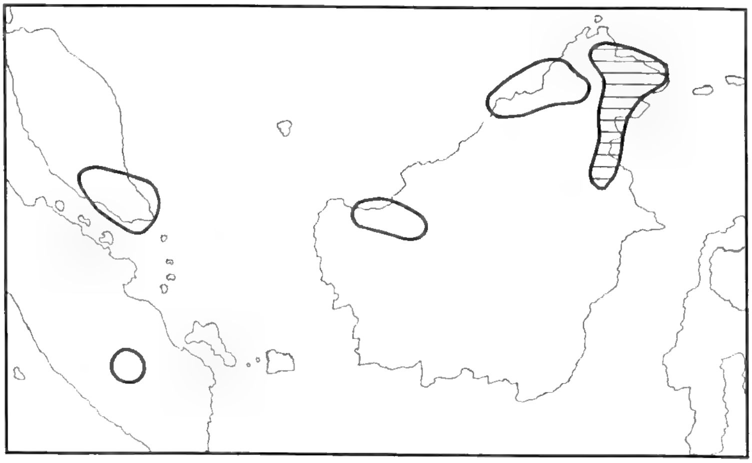

Fig. 121. *Neoscortechinia sumatrensis* (west) and *N. angustifolia* (east) (Euphorb.). The genus also includes two other W Malesian species and one in New Guinea (van Welzen 1994a). Note the distribution of *N. sumatrensis* centred around the Riouw pocket.

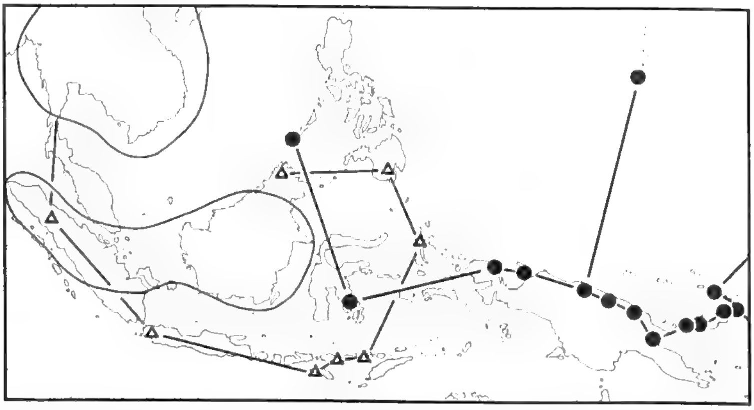

Fig. 122. *Apodytes* Am. (Icacinaceae s.s.) (SE Asia and triangles), *Cantleya* Ridl. (Sumatra-Borneo) and *Merrilliodendron* (dots) (Stemonuraceae) (Sleumer 1971a, Kårehed 2001).

The deconstruction of Borneo into western, northern and eastern sectors is illustrated by differentiation in *Myxoporum* (Olea.) (Fig. 118), *Dacrycarpus* (Podocarp.) (Fig. 119), *Oreobolus* (Cyper.) (Fig. 120), *Neoscortechinia* Hook.f. ex Pax (Euphorb.) (Fig. 121) and Icacinaceae/Stemonuraceae (Fig. 122). In *Calophyllum*, good examples are seen in *C. alboramulum* P.F.Stevens (Peninsular Malaysia, central West Borneo) and *C. blancoi* Planchon & Triana (N and CE Borneo, Philippines) (Stevens 1980, Map 3).

Why is *Rhododendron* so much more diverse in New Guinea (especially Irian Jaya) than in Borneo when it is not even a Pacific group? (Note that the number of *Rhododendron* species in Borneo in Sleumer's (1966 Fig. 1) map, i.e. 28, does not agree with the number of species in the text – 37). Borneo does not have many really high mountains, but as indicated, the altitudinal centre of diversity for *Rhododendron* is only 1500–2000 m. It seems likely that *Rhododendron* is much less diverse in Borneo than in New Guinea for the same reasons that many groups largely or totally avoid Borneo — not because of means of dispersal but because of different ancestral massings in the different groups. Alternative nodes and tracks, such as Borneo-wide endemism vs. tracks peripheral to Borneo, are held by different organisms not because of different means of dispersal or ecology but because the different groups evolved there, on the different sectors.

Philippines

The Philippines (except for Palawan) represent an amalgamation of island arc terranes and juxtaposition of these against fragments of continental (Eurasian) margin (Pubellier et al. 1996). Belts of ultramafics are shown in Fig. 123 (from Brooks 1987), indicating aspects of the arc structure. In the Eocene parts of the archipelago lay south-east of their present position (Hartley 2001). Hall's (1998, 2000) reconstruction of the region for 30 Ma shows the east Philippines, northern Moluccas and north New Guinea terranes (including New Britain) forming a relatively continuous arc, running parallel with and 1–2000 km north of New Guinea, before moving south and west and docking. This would go some way to explaining the close connections among these regions and also the great difference between the northern and southern Moluccas. Excellent animations illustrating this model are available at http://www.gl.rhul.ac.uk/seasia/movies.

Nevling (1961) wrote that the Philippines – New Guinea disjunction seen in *Enkleia paniculata* (Merr.) Hallier f. (Thymel.) (Luzon – Vogelkop) is 'puzzling indeed'. However, as shown above in the Ericaceae, there are many direct Philippines – New Guinea ties. These are seen in groups such as the bird *Mearnsia* (Philippines and New Guinea only) and the plant *Mearnsia* Merr. (Myrt.) (Philippines, New Guinea, New Caledonia, New Zealand). 57 ferns are known only from the Philippines and New Guinea (Copeland 1950). Bonds between species of Mindanao and East New Guinea are seen in *Legnephora* Miers (Menisperm.) (Forman 1986), and Philippines – Manus/New Ireland connections in particular are well-documented, for example in the ferns *Culcita straminea* (Labill.) Maxon (Holttum 1963), *Coryphopteris squamipes* (Copel.) Holttum (Holttum 1981), *Ctenitis pallens* (Brackenr.) M.G. Price, and *Tectaria tabonensis* M.G. Price/*T. subcordata* Holttum (Holttum 1991). Sets of parallel arcs involving the Philippines, the Moluccas and PNG are observed in a group of *Casearia* spp. (Flacourt.) (Sleumer 1954) (Fig. 124). Related patterns include those of the *Makota* generic complex (Hemiptera) (Soulier-Perkins 2000) (Fig. 125), the *Orisema uchancoi* species group (Philippines – PNG) (Hymenoptera) (Heraty 1995), and a Mindanao–Fergusson I. (Milne Bay) disjunction is seen in *Licania* Aubl. (Chrysobalan.) (Prance 1989).

Luzon – Sulawesi (cf. *Pseudovireya* II, *Albovireya*) is one of the few `longitudinal' tracks in Malesia. Van Steenis (1978a: Fig. 18) illustrated it with *Biophytum microphyllum* Veldk. and wrote that this 'rather peculiar range pattern ... has received too little attention'. George (1987) pointed out that it is now known to occur in plants, amphibians, birds, and mammals. A similar track occurs in Euphorbiaceae such as *Doryxylon* Zoll. (van Welzen 1999) and *Shirakiopsis sanchezii* (Merr.) Esser (Esser 1999), and in *Semecarpus longifolius* Bl. (Anacard.) (the latter with additional records from Java, the Moluccas and Taiwan) (Ding Hou 1978).

Sulawesi

In dispersal biogeography Sulawesi is merely a stepping stone or transition zone for plants 'invading' eastwards or westwards, but many authors (e.g. Stevens, 1985, on *Rhododendron*) have been struck by the unexpectedly high diversity there. Likewise, of the 380 bird species in Sulawesi, 'no less than 96 of these are endemic to the region, an incredible 25% of the avifauna' (Holmes and Phillips 1996). Plants of the Latimodjong Range are central in many Ericaceae distributions and are closely related to plants of the New Guinea orogen.

New Guinea

Within New Guinea, Stevens (1981) noted that the geographic concentrations of diversity in several groups, such as *R.* ser. *Linnaeoidea* and *R.* subsect. *Pseudovireya* are in Irian Jaya. This is also true for *Vaccinium* sect. *Oarianthe, V.* sect. *Neojunghuhnia*, and *Rhododendron* as a whole — the vireya.net website lists 161 *Rhododendron* species in New Guinea, with 100 in Irian Jaya, but only 81 in Papua New Guinea (cf. 47 in Borneo, 28 in Sulawesi, 25 in Sumatra, 19 in the Philippines).

The western bias in New Guinea is typical of 'Asian' groups, whereas 'Australian' groups such as birds-of-paradise (Paradisaeidae) are more diverse in the eastern half of the island (PNG). PNG groups like *Vaccinium* sect. *Pachyanthum* and *Agapetes* subgen. *Paphia* mean that Vaccinioideae are almost as rich in PNG (134 spp.) as in Irian Jaya (143 spp.). In *Vaccinium* PNG has 134/143 (94%) of the number of species in Iran Jaya, compared with *Rhododendron* in which PNG has only 81/100 (81%) of the number of species in Irian Jaya. This is probably the result of *Vaccinium* being a fundamentally Pacific group, whereas *Rhododendron* is an Indian Ocean group, and thus stronger on the western side of the island.

The Irian Jaya biota is also more diverse for birds in general (e.g. 32 mainland bird endemics vs. 15 on mainland PNG).

West and east New Guinea have interacted in complex ways. The folded and faulted mountain ranges of the spine of New Guinea form the New Guinea orogen (Fig. 7, 8). This mountainous belt was formerly regarded as the result of a simple continent-island arc collision, but Pigram and Davies (1987) gave a radical reinterpretation. They described the orogen as consisting of a southern part, the former northern margin of the Australian craton, and a northern part made up of at least 32 tectonostratigraphic terranes, fault-bounded geological provinces with independent histories. The New Guinea terranes, including intrusive and metamorphic rocks, formed and sometimes amalgamated with others some distance from their present position and subsequently accreted to the craton margin. (In ordinary English the craton grows by accretion; in geological English it is the terranes which accrete or, more usually, 'are accreted'). Accretion history in the Vogelkop involves mainly continental terranes. The central Kemum terrane was detached from Gondwana by the early Cretaceous and then had a history of movement independent of the Australian craton until the Miocene. In central New Guinea, the Sepik and Rouffaer terranes had docked with the craton by the Late Oligocene, when the New Guinea orogeny was initiated. In eastern PNG

Fig. 123. Ultramafic outcrops of the Philippines (black) and ophiolite belts (Brooks 1987).

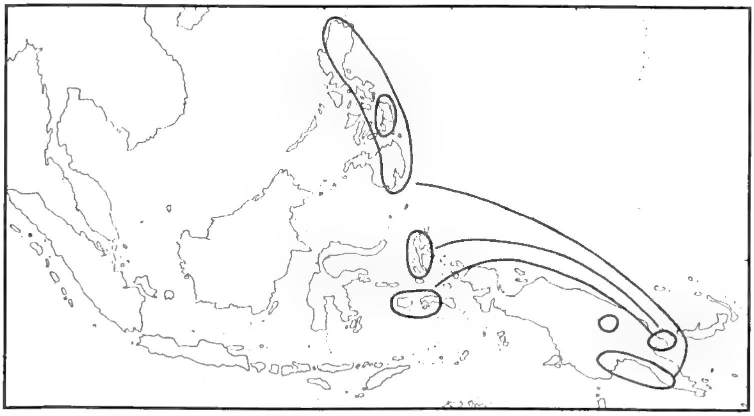

Fig. 124. *Casearia* Jacq. (Flacourt.): a group of eight species (53–60) keyed together by Sleumer (1954). (The gap in Irian Jaya is filled by 11 other species).

Fig. 125. The *Makota* goup of five genera (Hemiptera: Lophopidae) (Soulier-Perkins 2000).

several terranes of diverse origin amalgamated in the Paleogene (Early Eocene if this process caused the metamorphism of the proto-Owen Stanley terrane), and this composite terrane then docked with the Australian craton in the Miocene (cf. Crowhurst et al. 1996). Finally, the Finistere terrane was accreted to the mainland at 3.0–3.7 Ma (Abbott et al. 1994), and rapid uplift continues there. Probably New Britain will dock next. Pigram and Davies (1987) discussed transcurrent movements on faults, and suggested left-lateral offsets of up to 300 km along the Ramu-Markham and the Bundi Fault Zones.

In Hall's (1998, 2000) model, after the Papua and Sepik ophiolites were emplaced in Paleocene/early Eocene, the North New Guinea are terranes originated as the South Caroline Arc, about 4000 km north of New Guinea in the central Pacific. They converged on New Guinea and eventually docked, but continued to be translated west in the major left-lateral shear zone.

The importance of the craton margin as a biogeographic marker has been stressed above for Ericaceae. It is also important in many other groups, such as *Drimys piperita* Hook.f. (Winter.) (Fig. 126), where the craton margin separates the different infraspecific 'regional complexes', some of which appear to have been laterally displaced ('d' in Fig. 126). The complex, hybrid nature of New Guinea is also shown by the three species of *Kelleria* (Thymel.) there (Fig. 127) (Heads 1990). One species is in New Guinea only on Mt. Carstensz and Mt. Wilhelmina but is also in SE Australia and New Zealand. A second is not on Carstensz or Wilhelmina in the west, or Mts. Scratchley, Victoria and Kenive/Nisbet in the east, but is widespread centrally and in the north at Doormantop, Saruwaged Mts. and Mt. Kinabalu. The third species is a New Guinea endemic sandwiched between the two; it is not on Doormantop or Saruwaged Mts., but is present on Scratchley, Victoria and Kenive. This ecologically inexplicable juxtaposition of the three species deconstructs the geographic entity 'New Guinea' and may be a direct result of the geological formation of the island from separate terranes, and subsequent massive strike-slip movement.

The Ericaceae show the biogeographic structure of New Guinea (and the Philippines) to be one of nested parallel arcs, reflecting massive disjunctions among terranes, and among terranes and the craton (cf. New Zealand, Heads 1989). The parallel arcs structure of New Guinea involves more than two or three arcs (the Inner and Outer Melanesian Arcs of some authors); perhaps there are six or seven (cf. Croizat 1958).

Many other groups also show parallel distribution arcs in E Malesia, inside and outside New Guinea, from the coast to the high alpine, and show the `deconstruction' of New Guinea clearly. The 'ericoid' Thymelaeaceae (tribe Gnidieae, including *Kelleria*, above) (Heads 1990) are one example. Another is provided by the three species of mosses in Cyrtopodaceae (Sastre-De Jesús, 1987). The monotypic *Cyrtopus* (Bridel) Hook.f. is in the D'Entrecasteaux Islands, New Zealand, and Hawaii, *Bescherellia elegantissima* Duby is in the central PNG Highlands and New Caledonia, and *B. cryphaeoides* (C. Muller) Fleischer is in the Owen Stanley Mts., Mindanao, CE Australia and Fiji. Here, vicariance within New Guinea is matched by vicariance outside the island.

Cyrtandra J.R. & G. Forst. (Gesner.) has 500–600 species (Atkins et al. 2001) ranging from Malaysia to Polynesia. The species of W Malesia have hard crustaceous fruit, whereas those of the Pacific turn soft and white at maturity. The meeting ground is in New Guinea and the Solomon Islands (Burtt 1970), where most species have western affinities but a few are allied with species further east. This sort of pattern is usually explained as the result of a 'double invasion' of a modern New Guinea from different centres, but again may be related to the structurally hybrid nature of New Guinea.

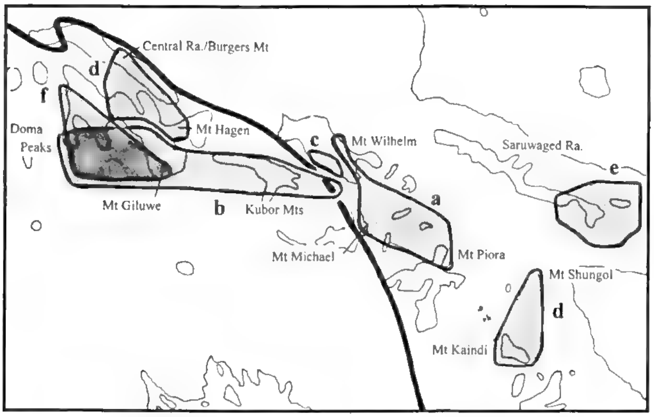

Fig. 126. Regional complexes of *Drimys piperita* Hook, f. (Winter.) in the PNG Highlands (Vink 1970). Note the two disjunct populations of 'd'. Land over 2400 m in fine line, fomer craton margin as thick line.

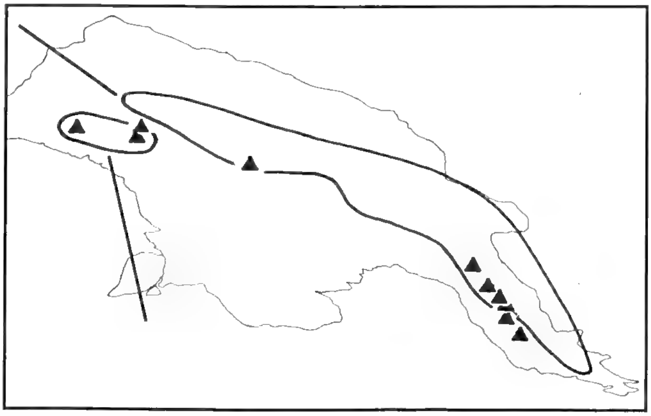

Fig. 127. *Kelleria* Endl (Thymel.) in New Guinea (Heads 1990). Continuous line at west: *K. dieffenbachii* (Hook.) Endl., also in SE Australia and New Zealand; continuous line to the east: *K. ericoides* (Hook.f.) Berggren, also on Kinabalu; triangles: *K. patula* Merr. & Perry (whole distribution shown).

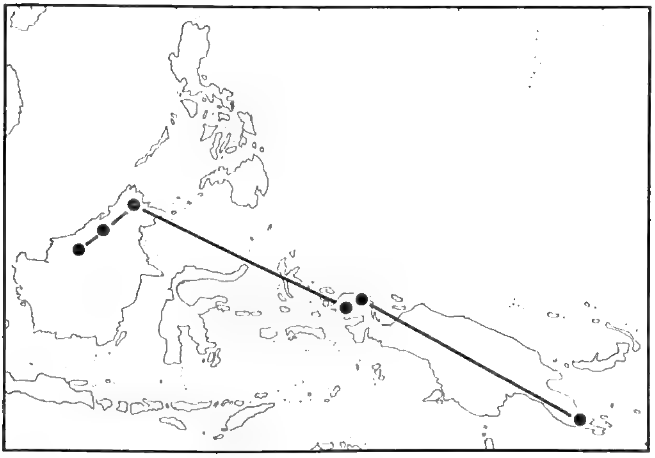

Fig. 128. *Distichirops* Haegens (Euphorb.) (Haegens 2000).

The Treubiaceae (Hepaticae) comprise two Pacific genera (D. Glenny pers. comm.). *Treubia* is throughout Malesia and widespread in the South Pacific, while *Apotreubia* occurs north of here in SE Asia and North America, but also with one species in the Sepik/Madang area of PNG. This is the only place where the two genera overlap.

Vogelkop

The Vogelkop region is biogeographically quite distinct from the rest of New Guinea. *Knema* Lour. (Mysristic.) is through the Philippines, Sulawesi and the Moluccas, but is known in New Guinea only from the Vogelkop (de Wilde 2000). The owl *Otus* is widespread through the Old and New Worlds, but occurs in New Guinea only at nearby Biak Island (Arfak terrane). However, the Vogelkop is geologically composite. In Ericaceae, the distinction between Arfak/Nettoti Mts. (Arfak and Netoni terranes) and Tamrau/Tohkiri Mts. (Tamrau terrane) is seen clearly in *Diplycosia* I and III (Figs. 38, 40).

It is probably significant that while the Tamrau terrane is unlike any of the other terranes in western Irian Jaya, there are similar sequences with mid-Miocene intermediate volcanics on the northern flank of the central ranges in eastern Irian Jaya and PNG (Pigram and Davies 1987) (cf. *Diplycosia* I). This recalls the proposed massive westward movement of the Halmahera arc (Heads 2001b, 2002a).

Holloway and Hall (1998) noted that while de Boer (1995) reviewed geological evidence for a previous more easterly position of the Bird's Head, near the Solomons, other patterns (*Myrmephytum* Becc.(Rub.), *Aporosa* Blume (Euphorb.)) are consistent with a westerly position for the Bird's Head (cf. Hall 1998, 2000). Holloway and Hall concluded that 'An alternative most parsimonious hypothesis might be that dispersal occurred ….'. However, before bringing in 'dispersal', it should be acknowledged that the Vogelkop is a geological and biogeographical composite, and even within the northern Vogelkop, the Arfak/Netoni terranes have biogeographic affinities quite different from those of the Tamrau terrane.

The plants and animals of the Vogelkop show many interesting disjunctions. The disjunction between taxa of the Vogelkop terranes (outboard of the craton margin) and those of the Papuan Peninsula terranes (often the Owen Stanley terrane) is seen in plants such as the following (any west Malesian records not given here):

Rhododendron 65: Arfak Mts. – 66: Owen Stanley terrane (Mt. Kaindi).

Dimorphanthera 11. Vogelkop, and Lae to Milne Bay.

Homonoia Lour. (Euphorb.). Nabire (on the Bird's Neck), disjunct on the Papuan Peninsula (van Welzen 1998). (This plant is a rheophyte and is also found along coasts — seeds germinate in salt water. The plant has superb anchorage).

Distichirops Haegens (Euphorb.). Vogelkop, disjunct at Mt Suckling (Dayman terrane) (Fig. 128). (Haegens 2000).

Hartleya Sleum. (Stemonur.). Vogelkop, disjunct south of Lae at Mounts Shungol and Kaindi (Sleumer 1971a, Kårehed 2001).

Picrasma Blume (Simaroub.). Vogelkop, disjunct at the Huon and Papuan Peninsulas (Nooteboom 1964).

Koompassia Benth. (Legum.). Vogelkop, disjunct at Morobe, Gulf and Central Provinces (Verdcourt 1979).

Lycianthes subg. *Polymeris* sect. *Asiomelanesia* Bitt. (Solan.). Vogelkop, disjunct at Huon and Papuan Peninsulas (Symon 1984).

Sauropus macranthus Haask. (Euphorb.). Vogelkop, disjunct at the Huon and Papuan Peninsulas and NE Queensland (van Welzen, in press).

Aglaia teysmanniana (Melia). Vogelkop, disjunct at Huon and Papuan Peninsulas (Pannell 1992).

Alyxia subser, *Clusiaceae* Markgr. (Apocyn.). Vogelkop and Meos Num Island in Geelvink Bay, disjunct at Bulolo (Markgraf 1977).

Amyema queenslandica (Blakely) Danser (Loranth.). Vogelkop, disjunct at Mount Kaindi and points southeast of there (Barlow 1992).

Polyscias australiana (F.v.M) Philipson (Aral.). Vogelkop and `Southern District, Papua' (Philipson 1979).

Xanthophytum Reinw. (Rub.). Vogelkop, disjunct at Morobe and the Papuan Peninsula (Axelius 1990).

Romnalda P.F. Stevens (Laxmann.). Japen Island, disjunct at the southern Morobe coast (Stevens 1978b).

Rapanea minutifolia Knoester, Wijn & Sleumer (Myrsin.). Vogelkop, disjunct at Mount Kaindi, Mount Amungwiwa and Milne Bay (Sleumer 1986).

Xanthomyrtus angustifolia A.J. Scott (Myrt.). Sulawesi, Vogelkop, Mount Kaindi, and (possibly) Normanby Island (Scott 1979).

Calophyllum sil Lauterb. variant (Guttif.). Moluccas and Vogelkop, disjunct at upper Ramu R. and New Britain (Stevens 1980).

Oplismenus hirtellus subsp. *imbecillis* f. *imbecillis* (Gram.). Disjunct between Waigeo I. and the Morobe south coast and near Port Moresby (the gap is filled by f. *lanceolatus*) (Scholz 1981).

In birds:

Melanocharis arfakiana (Finsch) (Dicaeidae) is known only from Vogelkop (Arfak Mountains) and north of Port Moresby (Matsika, halfway between Kairuku and Mount Albert Edward), with sight records on the nearby Kokoda trail (Beehler et al. 1986).

In the birds-of-paradise (Paradisaeidae), Vogelkop – Huon disjunctions occur in species pairs in each of three genera (*Astrapia*, *Paradisaea* and *Parotia*) (Heads 2001b, 2002a).

Zosterops minor tenuifrons (Greenway) is in the Vogelkop (Tamrau Mountains) and also SE New Guinea (Herzog Mountains to Hydrographer's Mountains) (Rand and Gilliard 1967) and a related Vogelkop – Papuan Peninsula disjunction is seen in *Pitohui* (Dumbacher and Fleischer, 2001).

Similar disjunctions are seen in insects such as the *Euops quadrifasciculatus* group of Coleoptera (Vogeklkop, Papuan Peninsula) (Riedel 2001).

Diamond (1972) referred to five 'drop-out' bird species which are on the Vogelkop and in PNG but not in the Irian Jaya mountains. Like the Ericaceae 'drop-outs', these disjunctions can be explained by movement and accretion of terranes rather than extinction of central populations.

Possible connections between the Vogelkop and the D'Entrecasteaux Archipelago, 2100 km to the east, are indicated by two pairs of *Rhododendron* species keyed together by Sleumer (1966):

Rhododendron 128: Vogelkop and Wissel Lakes, 129: Goodenough I.

Rhododendron 248: Arfak Mts, 247: Milne Bay.

Archidendron tenuiracemosum Kanchira & Hatusima (Legum.) (Moluccas, Vogelkop) is a `very close' sister species of *A. hooglandii* Verdcourt (D'Entrecasteaux Archipelago) (Nielsen et al. 1984).

Salacia forsteniana Miq. (Celastr.) is disjunct between the Moluccas/Waigeo and Normanby I., Milne Bay (Ding Hou 1964).

In *Kibara* Endl. (Monim.) a group of four species in Philipson's (1986) key (under couplet 8b) are only on the Vogelkop and the D'Entrecasteaux/Louisiade islands.

The form of *Podocarpus spathoides* cited above disjunct between the Moluccas and the Louisiades has a similar pattern.

Pandanus amboinensis Warb. (Pandan.) occurs at the Moluccas and Vogelkop (Manokwari) and is disjunct at Milne Bay (Mt Dayman, Goodenough I., Woodlark I.) (Stone 1992).

A similar disjunction (Vogelkop–D'Entrecasteaux) occurs in the perciform fish *Plesiops corallicola* (Mooi 1995).

A related Vogelkop disjunction is illustrated by other Araliaceae, in which Frodin (1998) recorded *Osmoxylon* Boerl. disjunct between the Vogelkop and the Bismarck Archipelago, and *Gastonia serratifolia* (Miq.) Philipson disjunct between the Vogelkop and the central Solomons. Frodin concluded that these patterns possibly relate to movement along the Sorong Fault, a strike-slip zone initiated at 20 Ma.

A similar disjunction in *Dimorphanthera* V: Waigeo I. (off the Vogelkop) – New Ireland, recalls that of *Epithema* Blume (Gesner.): Geelvink Bay – Solomon Islands (Rennell I.) (Burtt 1998) and the genus *Japenoides* Oldroyd (Diptera: Tabanidae): northern Vogelkop, Biak and Japen Is., disjunct at New Britain, the Solomons, Vanuatu and Fiji (Mackerras 1971).

The parallel arcs connecting different parts of New Guinea with different parts of the Philippines, C Sulawesi etc. all show the deconstruction of New Guinea. In a similar way, Australia does not really exist as a biological or geological entity; for example, in Proteaceae, NE Australia taxa are allied with South American plants, whereas SW Australian plants are allied with African taxa (Croizat 1964, Hoot and Douglas 1998).

The former craton margin in New Guinea

Kalkman and Vink (1970) compared the Ericaceae floras of four neighbouring mountain ranges in the Highlands of PNG (Doma, Giluwe, Wilhelm, and Kubor). They discussed both the 'conspicuous absences' and the 'remarkably high' number of taxa known from only one of the ranges (and other parts of New Guinea). They clearly demonstrated the great differentiation between ranges, but showed that this is not due simply to local endemism on every mountain top — a common misconception.

Many biogeographic breaks in the Ericaceae of this region occur at the former craton margin where similar breaks occur in many other taxa. For example, the shrub *Drimys piperita* entity *'reducta'* (Diels) Vink: Wissel Lakes, Mount Wilhelmina, Mount Giluwe and the Kubor Mountains, and entity *'subalpina'* Vink: Mount Wilhelm, act as a pair of 'replacing taxa' (Vink 1970). Vink reported the `unexplained circumstance' that the form of *reducta* most distinct from *subalpina* is found at the Kubor Mountains (the locality closest to Mount Wilhelm), while the form which connects the two morphologically, entity *'subpittosporoides'* Vink, is restricted to Mount Wilhelmina. A very similar pattern is seen in the closely related pair *Grammitis ceratocarpa* Copel. (Snow Mts., Mt. Wilhelm, Huon Pen.) and *G. salticola* Parris (Mt. Giluwe) (Parris 1983). Again, this arrangement could be explained by (right-) lateral movement of terranes. (Movement is right-lateral or dextral if rock on the other side of the fault from the observer has moved to the right).

Other examples of plant differentiation around the former craton margin include species of orchids (*Corybas* Salisb., *Dendrobium* Sw., mapped in Heads 2001b: Fig. 32; *Glossorhyncha* Ridl., Fig. 33), *Rhododendron* (Fig. 34), Compositae (*Tetramolopium* Nees., Fig. 35; *Olearia* Moench, Fig. 36) and Rubiaceae (*Amaracarpus* Blume, Fig. 37).

Stevens (1985) listed seven species distributions in the PNG Highlands which 'suggest that long distance dispersal or extinction has produced anomalous distribution patterns.'

Of these, 41. *R. hooglandii* is known from the Kubor Mountains and Mount Kerigomna, but not on the nearby Mount Wilhelm. This absence is an 'apparent anomaly' and the floristic differences among the mountains are 'apparently inexplicable' and 'particularly perplexing'. But this overlooks the major tectonic division in New Guinea, lying between the craton and the accreted terranes, and marked in this area by the Bismarck Fault Zone (for terranes etc. see maps in Heads 2001b). Diamond (1972) overlooked this same tectonic boundary in accounting for differences between the birds of Okapa and Mount Karimui. The Wilhelm batholith and associated metatamorphics form a separate block from the former craton (Kubor Mountains etc.) and Mt. Kerigomna is right on the margin.

Sp. 191 *R. atropurpureum* is known only from the Kubor Mountains and Mount Wilhelm, but the two populations shows interesting differentiation, with the Kubor Mountains plants having smaller flowers (P.F. Stevens pers. comm. 28-8-01; Stevens does not believe current introgression from *R. womersleyi* is a likely explanation for this).

Sp. 170 *R vitis-idaea* is on Mts. Wilhelm, Sarawaged, Amungwiwa etc. (as mapped in Heads 2001b), and there is an additional record from Porget (*R. 'vandeursenii'*). This is a classic example which ranges right up to the former craton margin from the north and east.

Sp. 148 *R. saxifragoides* comes right up to the margin from the west, reaching Giluwe but notably absent on Mt. Wilhelm.

Thus at least four otherwise inexplicable distributions all show a break at the main tectonic boundary in New Guinea.

Sepik terrane

Steven (1985) noted the importance of the Sepik Basin, PNG, where many endemics occur on accreted terranes. These include poorly known taxa such as *Rhododendron* 48 (near Mt Stolle), *Vaccinium* 235 (Hunstein Mts), *Dimorphanthera* 9 (Schrader Mts.) and 18 (Sepik), all known only from their types which were all destroyed in World War II. Huynh (1999) has recently described as many as six new endemic species of *Freycinetia* Gaudich. (Pandan.) from the Hunstein Mts (all collected by Wayne Takeuchi) and the monotypic *Paramyristica* de Wilde is endemic to the Sepik basin (de Wilde 2000).

Northwestern Owen Stanley terrane: upper Watut Valley

The northwestern margin of the Owen Stanley terrane is well-marked biogeographically, for example by *Dimorphanthera* 11: Port Moresby – Lae/Bulolo area. Affinities skirting the northwestern edge of the Owen Stanley terrane are also seen in plants of drier areas (D. Frodin pers. comm., *Rhynchosia minima* (L.) DC. (Legum.), *Capparis quiniflora* DC., van Steenis 1978a: Figs. 14, 21), as well as mangroves (*Osbornia* F. Muell. (Myrt.), van Steenis 1978a; Fig. 22) and aquatic taxa (*Torrenticola* Domin (Podostemon.), known from Queensland, Port Moresby (Roona: Laloki R.) (van Steenis 1949), and Baiune R. near Bulolo (pers. obs. 1981)).

Many other plants of SE New Guinea reach their northwest limit here, for example, distinctive genera in Sapotaceae (*Magodendron* Vink, Vink 1995), Rubiaceae (*Anthorrhiza* Huxley & Jebb, Huxley and Jebb 1991), Monimiaceae (*Kairoa* Philipson, Philipson (1980) and Malvaceae (*Cephalohibiscus* Ulbr.) (Fryxell 1980, possibly also on the Huon Peninsula).

The upper Watut area is the northern limit of the Owen Stanley terrane schists and is marked by mid-Tertiary granodiorite intrusions which form the mountains bounding the Watut catchment: Shungol, Missim, Kaindi, and Amungwiwa. Each of these is a centre of endemism for different groups, such as *Rhododendron* 66 (Mt. Kaindi), sp. 254 (Wagau, Mapos (Snake R.), Zenag, Wau, Kaisenik), *Dimorphanthera* (= *Vaccinium* sect. *Pachyanthum*) 2A (Bulldog Road), var. 44b (Gurakor), and *Agapetes* var. 2a (Mt. Amungwiwa), 11A (Mt. Shungol).

There are as many as six *Solanum* species locally endemic in the upper Watut (Symon 1985). Other plants here include *Langsdorffia* Mart., known only from Mount Missim, Madagascar, and tropical America (Hansen 1974, Streimann 1983), and *Hartleya* Sleum. (Stemonur.), known only from Mount Shungol with sterile specimens from the Vogelkop and its nearest relative, *Gastrolepis* Tiegh, in New Caledonia (Sleumer 1971a, Kårehed 2001). As well as being a boundary, Mount Missim and the Herzog Mountains (= Mount Shungol etc.) comprise a centre of endemism for bird subspecies in *Mirafra, Pachycephala, Colluricincla, Melidectes,* and *Rhamphocharis* (Rand and Gilliard 1967).

Other groups showing craton/accreted terrane differentiation include the following:

Dendrobium sect. *Latouria* Bl. (Orchid.) has 48 species, all except four of which are in New Guinea (Cribb 1983). Within New Guinea it has important centres of diversity on the accreted terranes. There are 8 species groups, of which the following five are more or less restricted to the accreted terranes: Group 1 (except one species widespread from Java to Samoa), Group 2 (except one record in the Upper Fly R.), Group 3 (tracking the margin at Weyland Mts., Wissel Lakes, and Chimbu Province), Group 6 (except one record on Wilhelmina, in PNG ranging up to the margin at Central Range and Wapenamanda), and Group 8 (ranging up to the margin at Rouffaer R., Central Range, Minj, and Kundiawa).

Only Group 5 occurs mainly south of the craton margin.

Only Group 4 and Group 7 (one species only) are widely recorded both north and south of the craton margin.

Helmholtzia F. Muell. (Philydr.) is in the Moluccas, the Vogelkop (Fakfak), Bernhard Camp (Rouffaer terrane), Hunstein Mts. (Sepik terrane) and NE Queensland (Johns and Hay 1981). Its closest relative is *Orthothylax* (Hook.f.) Skottsb. of SE Queensland, and this connection between the accreted terranes and the McPherson-Macleay Overlap (also accreted terrane) is standard (cf. the main diversity of bowerbirds, Ptilonorhynchidae), complementing the other track between southern cratonic New Guinea and the far north of Queensland (cf. the main diversity of birds-of-paradise, Paradisaeidae; Heads 2001c) .

In a similar pattern to that of *Helmholtzia, Sphenostemon arfakensis* (Gibbs) Steen. & Erdtman of the Vogelkop (Arfak Mountains) is closest to *S. lobosporus* (F.v.M.) L.S. Smith of Jimi Valley (Jimi terrane), Milne Bay and Queensland (van Steenis 1986).

Following an assessment of biodiversity of *Grammitis* Sw. in Heads (2001a) based on data in Parris (1983), Dr. B. Parris (pers. comm.) commented that *Grammitis* seems more diverse on Mounts Giluwe and Hagen, and probably the main Irian Jaya mountains (all these are on the craton), than on Mt. Wilhelm – Saruwaged Mts. This recalls the distribution of 148. *Rhododendron saxifragoides* which stops mysteriously at Mt. Giluwe and is not on Mt. Wilhelm. A similar pattern is seen in *Coprosma brassii* (Rubiaceae), widespread from Mt. Carstensz to Mt. Hagen (Gardner 2002).

However, several groups in *Grammitis* show a different pattern, vicariant to this one and skirting the main ranges and the craton to the north on the accreted terranes. Thus, the *G. adspersa* subgroup is in the Arfak Mts. – Doormantop – Hunstein Mts. – Owen Stanley terrane, vicariant with the New Britain – New Caledonia link in the *G. pseudaustralis* subgroup. The Doormantop species is also in SE Sulawesi, Java and Aceh. G. *plerogrammoides* also avoids the main (craton) ranges, but ranges right up to the border from the north at the Baiyer–Jimi divide north of Mt. Hagen. Likewise, the *G. reducta* subgroup is only north of the craton (Doormantop, Star Mts on the margin, Watut/Aseki Divide), and the *G. lasiosora* subgroup (Arfak Mts. – Doormantop – Mt. Piora) also avoids the craton. It seems unlikely that this pattern can really be explained by ecology.

Parris (1983) described *G. collina* Parris, endemic at Baiyer-Jimi divide just outboard of the craton, as `superficially similar' to *G. rupestris* Parris endemic to Laloki near Port Moresby, also just outboard of the craton. Parris treated the two together, but felt they are probably not closely related. Whether or not they are in fact close, this tracking of the craton margin is a common biogeographic connection despite the totally different ecology (altitude, rainfall etc.) at these two sites, and resembles the western limit of G. *oblanceolata*: Astrolabe Range, Aseki, and Kum (Mt. Hagen).

Chronology

Specht and Womersley (1979) concluded 'It is probable that the forerunners of Malesian heathland elements had already evolved on the supercontinent of Gondwanaland before it began to break up into tectonic plates ... The heathland species of Malesia appear to have been derived from the ancient flora which existed on the northeast section of Gondwanaland. Two distinct groups resulted when Gondwanaland split assunder — one on the Indian plate, the other on the Australian-New Guinea plate'. This view (although it overlooks the main massings of Ericoideae in South Africa and Vaccinioideae around the Pacific) is supported here.

In the fossil record *Rhododendron* seeds have been recorded as far back as the Paleocene of southern England (Collinson and Crane 1978). This early Tertiary 'age of fossilisation' could easily indicate an 'age of existence' in the upper Mesozoic, which is compatible with Nixon and Crepet's (1992) report of the oldest fossil flower of Ericalean affinity from mid-Cretaceous (Turonian, 87 Ma) deposits. This supports the idea that Mesozoic tectonics are fundamental in explaining the main global pattern of the large genera and tribes in Ericaceae.

The age of the angiosperms is unknown. Gymnosperms have a much older fossil record (320 million years) than angiosperms (130 million years). However, recent work (Chaw et al. 2000, Bowe et al. 2000) indicates the extant gymnosperms are a monophyletic group. Chaw et al. (2000) concluded by asking 'Are the angiosperms substantially older than the current fossil record indicates, or did they arise in the Jurassic from the Bennettitales, Caytoniales, or some other extinct group of seed plants?' Likewise, Boew et al. (2000) wrote that their own study 'implies that angiosperms originated some time along a very long stem lineage. This would reach back possibly to the Carboniferous ...'.

Modern phylogeography (Avise 2000) often claims to be testing whether a distribution is due to dispersal or vicariance. However, the molecular divergences are nearly always calibrated using a literal reading of the fossil record, that is, a group whose oldest fossil x is y years old is assumed to actually be y years old. This is a key procedure of the dispersalist school, so a study based on it can hardly be considered an unbiased test of dispersal vs. vicariance. Occasionally authors have calibrated the sequence data using a simple equation of biogeography and geology. For example, trans-Tasman Sea disjuncts have been taken to be the same age as the opening of the Tasman. This approach is better but still simplistic, as trans-Tasman taxa could be much older than the opening of this sea.

Mangrove ancestry of Malesian Ericaceae

The occurrence of *Rhododendron* and other Ericaceae in the mangroves of W Malesia (but not E Malesia) is usually assumed to have resulted from a secondary invasion of the mangrove after the evolution of the group. However, many Ericaceae seem quite at home there. *R. brookeanum* (photos at www.vireya.net/R.brookeanum.htm) and *R. longiflorum* (there is a plant growing in the Royal Botanic Gardens Sydney) even look like mangroves, with long, elliptic, acute, coriaceous leaves like, say, a *Bruguiera*. The mangrove and coastal Ericaceae species do not comprise a related group, but may retain relictual traces of an ancestral ecology.

Gentry (1987) criticised the common misconception in which 'Mangrove epiphytes are implied to be basically plants from nearby terrestrial communities that transgress into the mangroves', and emphasized that many epiphytes, such as the entire genus *Tuberostylis* Steetz. (Compositae), seem unique to mangroves.

The mangrove and back-mangrove are much richer than is often realised. For example, in Sapindaceae, 9 of the 42 Malesian genera (21%) occur in or around mangrove and 11 others (26%) are known from coastal cliffs and sands (data from Adema et al. 1994). In New Guinea Euphorbiaceae 11 out of 47 genera (25%) are recorded in or around mangrove (Airy Shaw 1980). In Malesia, Icacinaceae (Sleumer 1971a) have 6/12 genera in or around mangrove or on coral limestone at sea-level, Celastraceae s.l. (Ding Hou 1964) have 5/19 and Simaroubaceae (Nooteboom 1964) 5/9 genera represented in similar habitats. In birds of paradise, at least five out of 14 genera of Paradisaeinae (35%) are found in mangrove and associated vegetation.

In these and other birds and trees the New Guinea mangrove shows clear affinities with terrestrial rainforest, drier forest and secondary forest, and there is also an obvious link between mangrove and the more or less freshwater swamp forests and peat swamp forests found along the Mamberamo–Sepik depression in New Guinea. In the coastal lowlands, mangrove, beach forest, 'lowland rainforest' and freshwater swamp forest species often grow together in different microhabitats in a complex association not shown in text-books.

There are also important phylogenetic ties between dry-land plants and those of shore and aquatic environments. For example, the mangrove palm *Nypa* Steck. is basal to all the other palms (except Calamoideae) (Hahn 2002). In dicots, molecular studies (Savolainen et al. 2000) indicated that the mangrove family Rhizophoraceae (with Erythroxylaceae) is basal to a very large group of 34 families (termed the Malpighiales by Savolainen et al., 2000, but including the Euphorbiaceae — much larger and better known than Malpighiaceae, Flacourtiaceae, etc.). Again, this seems less consistent with a secondary 'invasion' of the mangrove than with Church's ideas (Mabberley 1981) on the evolution of land plants from shore plants through tectonic uplift ('The discussion of any theory of 'migration' should be preceded by the examination of the possibilities of a mechanism of '*transition in situ*'').

A good example of a coastal plant possibly stranded inland is *Chaetocarpus* Thw. (Euphorb.), which ranges from India and Sri Lanka to Peninsular Malaysia and Borneo. It is common along the coast in NE Malaysia and according to van Welzen (1994b) the many inland collections 'may reflect old Pleistocene shorelines'.

For many years it was thought that angiosperms must have originated in the mountains (thus explaining the lack of fossils), but paleobotanists (Retallack and Dilcher 1981) have supported a coastal origin of the group. Plants of the mangrove, back-mangrove and freshwater swamp occur in a wide range of oligotrophic, periodically inundated soils, including both acid sands and basic, calcareous material derived from coral reefs. Plants of the shore and its hinterland, including cliffs and rocks, are often tolerant of some drought. The very diverse flora has a high potential as an ancestral community, especially during phases of marine transgression, in contrast with the climax vegetation of the high montane cloud forest and its narrow endemics committed to a 'specialist' environment.

Evidence of uplift and stranding of taxa inland and on mountains cited above for Malesia can be seen in many countries. For example, in Nijmegen in the Netherlands 'for some mysterious reason the gulls have chosen one of the numerous fens on the western edge of the city as their breeding place. A biological memory from primeval times, when the sea had here her strands?' (Seveke 1955).

In Australia, 'a considerable portion of southern and central Australia was submerged by sea in Mesozoic and Tertiary times.' Specht (1981) inferred that 'Remnants of the salt-marsh flora along the estuarine parts of the Tertiary coastline remained far inland when the sea retreated'. Specht cited *Avicennia marina* stranded 40 km inland from the Western Australian coast, and also saltmarsh floras 500 km inland.

Salicornia L. (Chenopod.) and Frankeniaceae are usually maritime shrubs, but in the Andes both have cushion species occurring at over 4200 m altitude (Ruthsatz 1978).

In the West Indies, Stoddart et al. (1973) described inland mangrove vegetation in Babuda including *Laguncularia* Gaertn.f., *Conocarpus* L. and a closed woodland of *Rhizophora* L. on old lithified beach ridges that have no connection with the sea. This raises 'problems of the history and development of these communities ... It is clear, however, that mangroves, including *Rhizophora*, can grow in environments very different from those usually associated with mangrove vegetation'.

The Russian author Tolmachev (1970) described the process of formation of highland floras, in which `the height rises with its vegetational cover, namely with its flora, which will ultimately become orophytic ... the adaptational amplitudes of the different species and their hereditary conservatism varies. Accordingly, some species of the rising highland will remain without any apparent changes in their nature, whereas other species, adapting to their new conditions, will be transformed into new 'daughter' species, and finally, other species, being unable to adapt to the changing conditions, will perish'. Tolmachev emphasized the fundamental significance of the 'Floral and vegetational character of a certain area on the earth's crust before its rise to the ultimate altitude. The importance of this moment is frequently not fully appreciated in investigations of the origin of orophytic floras, although their nature (especially that of the more recent formations) will largely depend on it'.

Personal observations made clambering through mangrove and subalpine forest in New Guinea indicate that these densely-branched, sometimes impenetrable communities share architectural similarities, and may supply equivalent habitat for birds. For example, stilt and prop-roots are frequent in both (e.g. montane Rhizophoraceae, *Crossostylis* J.R. & G.Forst.; Soepadmo's 1972: Figs 19, 29 showing montane *Lithocarpus* spp.). In birds, taxa such as the bird-of-paradise *Manucodia comrii* Sclater occur in both mangrove and subalpine forest.

Why are there no mangrove Ericaceae in E Malesia? Perhaps they have all been uplifted, as seems to be the case for species like 238. *R. leucogigas* in northern New Guinea. *Lamiodendron* Steen. (Fig. 129), a 'most remarkable bignoniaceous tree' (van Steenis 1957, 1977), is a monotype from Milne Bay (Normanby I., Rossel I., Alotau) and Popondetta, and is 'geographically unexpected and rather isolated'. Its affinities are probably with the African – SE Asiatic – W Malesian genera *Fernandoa* Seem., *Radermachera* Zoll. & Mor. and *Stereospermum* Cham., plants of rocky coasts, limestone, rainforest and drier forest, but it differs from all these in its exceedingly showy flowers (the tree is 'worthy of introduction into cultivation'). In Normanby I. it was found 'forming a community on a gravel bank behind the beach fronting swamp forest', and it is also known from sago swamps, lowland rainforest and disturbed forest. It appears to be a relic mangrove-associate, left stranded in the east far from its western relatives, the whole lineage having been unable to survive any uplift at all in central New Guinea (unlike other Bignoniaceae such as *Tecomanthe*).

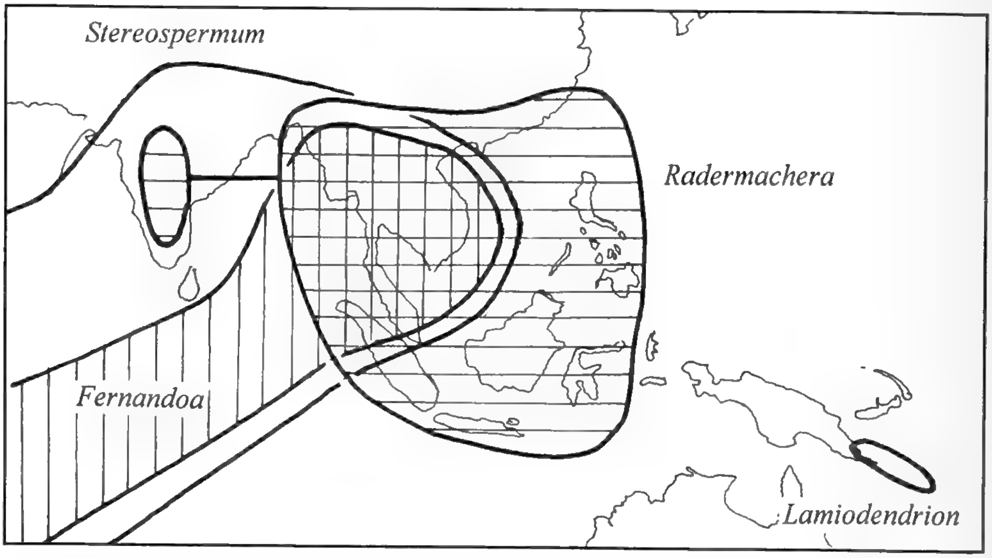

Fig. 129. Four related genera of Bignoniaceae tribe Tecomeae: *Stereospermum* Cham., *Radermachera* Zoll. & Mor., *Fernandoa* Seem. and *Lamiodendrion* Steen. (van Steenis 1977).

Terrane tectonics and biogeography

Van Steenis (1934a) made the crucial point that 'Plant geography does not need to be tied to the apron strings of other branches of natural history. It is an independent study having at its disposal important objective material, which enables it to develop and come to conclusions of its own'. This approach is in contrast with that of chance-dispersal biogeography, which remains in thrall to phylogeny, geology, ecology, and anthropology etc. and has no principles of its own, except a concept of 'chance' in which, given enough time, anything becomes possible. Van Steenis's alternative approach is essential if a real science of biogeography, capable of analysing localities and the relations among them, is to advance.

In fact, biology has potentially far more spatial information than geology; most of the different rock types on earth are composed of only a hundred or so minerals in combination, whereas the living communities involve millions of organic species. In addition, life is less easily eroded than inorganic strata and often remains more or less in situ during phases of uplift, erosion, subduction, metamorphism, intrusion, vulcanism etc., using its ordinary means of survival (cf. Craw et al. 1999, Figs. 2–5, 2–12). The problem is that biology often does not analyse the spatial data it already has available (e.g. for Ericaceae) simply because 'chance-dispersal' is assumed to have rendered distributions meaningless and there cannot be any pattern by definition. It should be remembered that biogeographic data were used to argue for continental drift decades before this was 'discovered' by American geologists in the 1960s.

It is easy to show that geographical distribution has been neglected in biology. There is no equivalent in Biology courses of the standard first-year mapping project in Geology and distribution maps did not even become a common feature of taxonomic monographs until the 1960s. Many modern monographs and floras have no maps at all.

The first integrations of biogeography and terrane tectonics, in New Zealand (Craw 1982, 1985, Heads 1989, 1997, 1998), gave interesting results, and biologists have recently begun to use accreted terranes in explaining distributions of New Guinea plants (van Welzen et al. 1992, van Welzen 1997, Vermeulen 1993, Turner 1995, Heads 1999, 2001a), invertebrates (de Boer 1995, de Boer and Duffels 1996a, b, Polhemus 1996, Polhemus & Polhemus 1998, Novotny & Missa 2000) and vertebrates (Michaux 1994, Heads 2001b,c, 2002a,b).

Discussing mammals, Flannery (1995) wrote that 'tectonic movements have been the prime cause of many of the zoogeographic patterns that we see in New Guinea today'. The northern coastal ranges include `the most peculiar and inexplicable mammal distributions found anywhere in New Guinea'. For example, the range of the marsupial *Pseudochirops albertisii* (Peters) (Arfak Mountains, Japen Island, Weyland, Cyclops, Bewani and Torricelli Mountains) is 'quite enigmatic … Without massive tectonic movements its distribution would be inexplicable, as its present distribution is disrupted by ocean (Geelvink Bay), massive rivers (e.g. the Mamberamo) and swamp (the Meervlakte). Not even the most extreme late Pleistocene climatic change could account for its present distribution. Yet the tectonic changes necessary to produce its distribution are so massive … as to be breathtaking'.

In traditional plate tectonics Malesia is interpreted as the suture zone of just two continental blocks, with 'Asian' groups like *Rhododendron* entering Papuasia from the west within the last 20 Ma. Hall (1998) agreed that there were originally two principal biogeographic regions, Australasia and Asia, which were physically separated and subsequently became connected, and that up to at least 15 Ma there was 'probably very little land' between Borneo and Australia. This seems unrealistic, and terrane models with their potentially great complexity are more satisfactory for biogeography than earlier, more simplistic plate models. For example, the 32 accreted terranes in New Guinea all have endemics and are of general biogeographic interest.

Hall (2000) warned that while the idea of terranes is a popular one, sometimes the terranes are interpreted as simply the carriers of land plants and animals. It is probably more complex than this, with the terrane margins (e.g. as zones of suturing, metamorphism and physiographic change) being more important than the terranes as geographical entities.

As Hall (2000) wrote, 'New Caledonia serves to remind us all of some fundamental geological and biogeographic problems in the region ... there is apparently an ancient Gondwanic flora, and other strange features of the flora and fauna seem to imply some land there since the late Cretaceous. On the other hand it is difficult to find any geological evidence that New Caledonia was above sea-level until the late Eocene. How do we resolve this dilemma?' Hall suggested that 'it indicates that we should remain cautious about simple and definitive answers ... and we should all remain critical of our data and beliefs ...', which is true of course but gives no real answer. Instead it is suggested here that in places like New Caledonia and New Guinea the biological evidence is much more complete than the geological, due to removal of strata by erosion, tectonic narrowing, and subduction.

Corner (1963) argued that the fig flora of New Caledonia holds a 'master key' to the past: it has high and peculiar endemism but lacks nearly all the species and sections which would be expected if it had simply been an extension of the Papuan, Queensland or Solomon Islands flora. 'Such precise evidence, negative and positive, must deny any hypothesis of chance colonisation ... Croizat's victory is the defeat of chance dispersal: he has given us whereon to stand'.

Discussing 'Wallacea', or the central Malesia region, Hall (2000) emphasized that important tectonic features can disappear within short periods leaving almost no trace, and that 'In areas of volcanicity there is always the possibility there might have been ephemeral land ...'. Individual volcanoes are geologically ephemeral, usually lasting less than 1 Ma, but even small, transient volcanoes can be very effective in preserving flora and fauna, as Philipson (1970) noted for the central Pacific. Tectonic narrowing in New Zealand and New Guinea has led to many terranes (much larger units than volcanoes) being much smaller now than they were originally. Some are merely remnant slivers, while others have probably disappeared entirely. However, their biota, like that of the volcanoes, may be able to survive great physiographic change by being 'scraped off' at subduction zones.

Hall (2000) suggested that biogeographers could contribute to testing tectonic models 'by, for example, mapping distributions of fossil plants and interpreting their environment'. However, both these approaches are probably of rather limited value; Hall himself noted that the fossil record is poor or non-existent for most plants and animals and this is actually true for the vast majority. It is much more important to map the living organisms, especially the diverse groups.

Holloway and Hall (1998) wrote that 'The reluctance of some biogeographers to consider the palaeontological data is something that geologists find difficult to understand.' Much palaeontological data and interpretation (unlike work on tectonics) are riddled with dispersalist assumptions, but panbiogeographic studies make a point of integrating data from fossil (when available) and extent taxa (e.g. Heads 1989: Fig. 16d showing fossil and extent brachiopod taxa; Fig. 19 comparing Mesozoic molluscs and the plant *Coriaria* L.). What perhaps riles palaeontologists is the fact that panbiogeographic analysis does not privilege the fossil data to the great extent that the centre of origin theory does. In this theory, the oldest known fossil of a group represents the ancestor and occurs at the place and time of the group's origin. Fossil data can provide essential evidence for morphogenetic studies but are almost always woefully inadequate for biogeographic analysis. For example, fossil data of Ericaceae, or any plants for that matter, contribute practically nothing to analyzing the relationships among the mountain floras of New Guinea. Despite this, Holloway and Hall (1998) claimed that 'Hypotheses of strict terrane fidelity by biotas are not well supported by fossil evidence ... ', which is probably true, but only because there is hardly any fossil evidence of these groups to begin with.

Hall (2000) also suggested that for biogeographers to test tectonic models 'there must be a focus on plants and animals which have difficulty in dispersing'. But this makes unnecessary assumptions. It is better to study a wide range of well differentiated groups without making prior assumptions about dispersal. In any case, as dispersalists know, all organisms, even snails and worms disperse, and given enough time any distribution becomes possible.

Centre of origin biogeography often takes as key just two parts of geology, which are arguably among the weaker in the subject and which are both based on negative evidence. Centre of origin models take the age of fossils to represent the age of taxa, when in fact there is no relationship (except fossils will nearly always be younger than their taxon); and when geologists say there is no evidence for land during a certain period, centre of origin biologists take this to mean there is evidence for no land. Neither assumption is accepted here.

Holloway (1998) suggested that 'The types of distribution patterns in the New Zealand biota that have been related to tectonic arc structures in the islands (e.g. Craw 1989) are also manifest in the distributions of plants introduced by Europeans, and suggested for these to have a climatic basis (Wilson et al. 1992)'. Holloway and Hall and (1998) wrote that these introduced plants 'can reproduce in response to climate the 'parallel arcs' patterns shown by indigenous plants', and this supposed similarity is used to support their conclusion of 'absence of widespread terrane fidelity'. The distributions of the introduced species mapped by Wilson et al. (1992) reflect the west-east decrease in rainfall in the South Island and the hot, sunny climate of the central regions, as indicated by Wilson et al. (1992). Despite Holloway's claim, these introduced plants and the local climatic zones they follow do not have similar distributions to the highly complex but repeated patterns of the local and regional endemics. This is why the biogeography of the last groups is so interesting (Heads and Patrick, in press) and why for many years ecologists have invoked different kinds of historical factors to explain the distributions.

Holloway and Hall (1998) suggested that panbiogeographers such as Heads (1989) 'postulate a high degree of terrane fidelity by biota', but correlations of a great number of New Zealand and New Guinea endemics with terranes is more of an observation than a hypothesis. Holloway and Hall (1998) concluded by admitting that: 'Some degree of terrane fidelity is suggested ... for groups such as cicadas (de Boer 1995), some plant taxa (Ridder-Numan 1998, on Borneo) and water bugs (Polhemus and Polhemus 1998), but it might be dangerous to extrapolate this to a generality.' It would certainly be dangerous for dispersal theory. Birds-of-paradise (Heads 2001b,c, 2002a) and Ericaceae are two more groups which illustrate a high degree of geological control.

Centres of origin, chronology and adaptation

This paper has questioned certain current concepts in biology. With respect to the spatial component of evolution, a concept of `dispersal' as physical movement from a point centre of origin is best replaced by one of vicariance mediated by tectonics, especially rifting, accretion and uplift. As George (1987) pointed out, it was discrepancies between theories of centres of origin, in particular how one derived the centre of origin, that led to the development of the generalised tracks/vicariance approach. Authors like Darwin (1859), Matthew (1915), Frey (1993) and Briggs (1999, 2000) assume that the most advanced species occur at the centre of origin (and out-compete the primitive ones which migrate away), whereas other authors such as Mayr (1942), Hennig (1966) and the modern phylogeographers (Avise 2000) assume that the most primitive taxa occur at the centre of origin, and the advanced ones have migrated away ('Progression Rule'). This stand-off within the dispersal school has not even been recognised yet and may well continue for another 140 years, but neither assumption is used in vicariance cladistics (e.g. Platnick 1981) or panbiogeography.

Other phenomena are also difficult to understand under the centre of origin/migration theory: 232: *Rhododendron cuspidellum* Sleum is a weedy, pioneer species, locally common in secondary forest, but it is also a very local endemic known only from the Wissel Lakes on the edge of the craton. Some very localised species of *Erica* are also abundant in their area, for example, *Erica urna-viridis* H. Bolus is known only from one plateau on the Cape Peninsula, but is very common were it does grow and forms fairly large colonies (Schumann et al. 1972).

In a centre of origin view of ecology, Luteyn (2002) concluded that Ericaceae became epiphytes as a result of 'canopy invasion', and likewise 'migrated into higher-altitude, Andean habitats, which were unoccupied'. Instead, it is suggested here that the canopy was always, already occupied by epiphytes such as the ancestors of Ericaceae, and likewise that the 'Andean' habitats were always, already occupied by the ancestors of Ericaceae, even before they were uplifted to alpine heights.

With respect to the chronology of evolution, it now seems that while Quaternary events may have locally modified distributions and abundances they have had little effect on the evolution of modern groups, which is the result of Mesozoic and Tertiary events. Hall argued that `DNA studies offer one way of determining a time-scale for biological development', but this is probably one of the few things it doesn't offer, as molecular biologists feel themselves obliged to rely on the age of fossils to calibrate their 'clocks'.

Cladistics was an attempt to get away from using absolute degree of difference. But now, as before, number of base pairs etc. as degree of difference is supposed to be meaningful, especially with respect to time. Degree of divergence, whether molecular or morphological, may have very little to do with either the age of a group or the time involved in its evolution, and may be determined rather by the evolutionary potential of the group. Under this view, in any given phase of evolution, for example, during a period of rifting, some groups will diverge to species level, others to generic level, while yet others may diverge only cryptically or not at all. This explains why the same biogeographic track is always held by taxa of obviously different rank.

In studies on form, a concept of evolution by 'adaptation' in response to selection pressure can be replaced with one of molecular drive (Craw et al. 1999), morphogenetic series, and pre-adaptation. The synthetic concept of 'adaptive radiation' relies on two of the older concepts, adaptation and the centre of origin.

Rhododendron: adaptive radiation or non-adaptive amalgamation?

Many tropical botanists have taken a critical view of the significance of 'adaptation'. For example, van Steenis (1958) gave a classic demolition of a textbook orthodoxy — 'adaptive features' in mangrove hypocotyls. One of Richards' (1952, 1992) main themes in his account of tropical rainforest was a critique of 'adaptationism'. He suggested that any usefulness or 'advantage' in a feature is incidental — a consequence and not a cause. Biological structure is the way it is primarily because of prior morphogenetic trends or Darwin's 'laws of growth', 'pruned' only secondarily by natural selection (Grehan and Ainsworth 1985) (and mediated spatially by tectonics). This approach was taken in the analysis of the hypocotyl, above. In another example, red pigments in the young leaves of tropical trees are often assumed to have an adaptive value. However, Richards (1992) cited work giving no support to the view that anthocyanins give a selective advantage to the tree and suggested instead that they may be 'merely byproducts in the synthesis of flavonoid compounds in the young leaves.

In tropical rainforest, rainwater falling on the leaves runs off the acuminate drip-tips found in so many species there. The classic view is that the drip-tips have evolved in order to facilitate this. However, Richards (1992) cited authors who give a number of reasons why drip-tips have unwettable leaf surfaces, some species have drip-tips on some leaves and not on others, and some plants with long drip-tips grow in dry environment.

Richards (1992) concluded that 'The crude teleological 'explanations' [of rainforest leaf morphology] of the last century are no longer acceptable', and this is correct; however, Richards continued: 'but there is as yet little to put in their place'. This is probably less correct, as there is much relevant work on morphogenesis. This has not been widely recognised as the primary factor because 'selective pressure' is usually regarded as determining morphology and is invariably cited in the popular media as one of the 'wonders of nature'.

It is hard to imagine that the different forms of scales on the *Vireya* leaf or the peculiar glands at the base of the leaf in *Vaccinium* represent any selective advantage. However, they may date back to the origin of the leaf and represent traces of earlier structures largely suppressed during the evolution of the modern leaf from a sterilized inflorescence, rather than something superficial added on later for no apparent reason to an already formed leaf (cf. epiphyllous inflorescences, Watson (1964) on epacrid bracts, etc.).

Rhododendron may be a colossal genus, but is it an 'adaptive radiation', as is often suggested? There is no evidence that it is a radiation from a single point centre of origin, or from a single species (or parent pair). (For a critique of the Darwinian/Hennigian view that clades are descended from a single ancestral species, see Heads 1985b). Despite the claims of both pan-adaptationism and cladistics, probably nothing important in biology happens only once. So-called 'uniquely-derived' characters may only occur in one group, but that is not evidence for their only having evolved once. Neither is there a convincing argument for the great diversity in *Erica, Rhododendron* or *Vaccinium* having evolved through adaptation mediated by selection pressure. Rather than New Guinea *Rhododendron* being the result of an adaptive radiation, it seems more likely to represent the result of amalgamation and juxtaposition, developing during terrane accretion and the formation of modern New Guinea. The next event will be the docking of the 450 km-long New Britain and its distinctive flora with the mainland. Only forms that were pre-adapted survived uplift in New Guinea, others went extinct.

Within *Vireya* there are no barriers to compatibility (if temperate species in subsect. *Pseudovireya* are excluded) (Rouse 1985) and reproductive barriers are breached in cultivation. Apomixis does not occur. The *Rhododendron* keys are based on recombinations of just a few characters, often concerning indument of ovary, style and corolla (presence/absence, lepidote/hairy or both). This recombination is compatible with the group being the direct descendants of a very old, widespread, ancestral hybrid swarm, now largely 'frozen' in place, at least in the wild.

Many *Rhododendron* taxa are only slightly differentiated, and this is often taken to be the sign of a young group, and an explosive radiation. As emphasized, there is no reason to assume degree of difference is related either to the age or time of form making. Just as subtly different lithology may indicate the presence of an important tectonic feature, minor differences in, for example, anther glands, may represent the frozen trace of an ancient landscape and its flora. Of course, the *age* of the biological form-making may have little or no relation to the *time* it involved.

Vireya seed can be stored for 3 to 5 years (cold, over calcium chloride); light is essential for germination. *Rhododendron* is a classic weed, dwelling on the ecological and geological margins, these are 'plants of tomorrow', infinitely flexible (within the heliophilic limitation), and most unlikely to ever go extinct in the New Guinea region whatever happens geologically, unlike 'fixed' monotypic or oligotypic groups, even widespread ones like Trimeniaceae (Philipson 1986b).

Conclusions: biogeography and evolution in Ericaceae

Ericaceae are well known in Europe and North America and they are widespread and conspicuous in the barren wastelands of the far north. Because of this, the family is often portrayed as mainly temperate in distribution and more or less restricted to cold, acid sites. For example, *Rhododendron* was introduced recently as comprising '850 species native to the northern hemisphere' (Halliday 2001). The subtext here supports the concept of a northern centre of origin (Matthew 1915) and this theme was explicitly and clearly developed in Irving and Hebda's (1993) review. They cited oldest Ericaceae fossils (pollen) at 68 Myr and oldest *Rhododendron* fossils (leaves) at 50 myr, and took these to represent the age of the groups. They also assumed that the location of the oldest *Rhododendron* fossil (Alaska) represents a centre of origin in North America/Eurasia, from which 'founder populations' migrated into the present main centre, N Burma/Yunnan. They wrote that 'upland terrain seems to be an essential ingredient of rhododendron habitats, and that rhododendrons probably did not originate in [N Burma/Yunnan or Malesia] (where they are now most abundant and most diverse) because these regions did not exist 50 million years ago'. But both these conclusions may well be matters for discussion. Geologists have identified Tibet, most of China, and Burma. Thailand as former parts of Gondwanaland which rifted and separated from that continent (Fig. 6). Amalgamation and accretion of Gondwanaland derived Asian terranes occurred progressively between the Late Devonian and Cretaceous and many sutures are dated as Jurassic, perhaps the most important time for angiosperm evolution.

In fact there is much more diversity in the family than the boreocentric characterisation allows. Ericaceae are highly speciose in the tropics (for example, there are some 777 species in Malesia) and in the southern hemisphere (e.g. in New Guinea, with 161 *Rhododendron* species), are widespread on the coast even in the tropics, and often grow on limestone or ultramafics in potentially basic sites. This flexibility, within the heliophilous constraint, bestows great potential for survival.

Apart from the early northern hemisphere fossils, which are probably unknown in the southern hemisphere simply due to sampling error in the fossil record (cf. Cracraft 2001 for birds), there is no evidence for a northern centre of origin with subsequent dispersal south. Australian authors, influenced by the abundance of Epacridaceae in Australian and of Ericaceae in New Guinea, have argued against the northern centre of origin idea (Specht and Womersley 1979). Recently, Kron et al. (1999), pointed out that epacrids were sister to the 'vaccinioids' and indicated that this relationship among southern groups was of 'great biogeographic interest' (cf. Willdenow 1798), that is, it contradicts the northern centre of origin.

In fact, the subfamilies of Ericaceae *sens. lat.* comprise the classic example in plants of global vicariance among well-known, highly speciose groups. Although there is considerable overlap of the groups in some areas, such as Malesia, the different locations of the main massings are clear and of fundamental significance, as recognized by Hutchinson (1959) and Cullen (1978). The simplest explanation is that there is no point centre of origin and the groups have developed by vicariance in immobilism of an already global ancestral complex. There is no need to invoke any large scale 'migrations' of any of the subfamilies, simply vicariance around the Indian Ocean (Ericoideae-Rhododendroiodeae), Pacific Ocean (Vaccionioideae, epacrids), and Atlantic Oceans (empetrads). The recognition that the SW Cape *Roridula* is a sister group to Ericaceae gives strong support to the vicariance interpretation, but would not be predicted in the northern centre of origin/dispersal theory.

Why does current biodiversity follow Mesozoic and Tertiary orogens? Possibly because these are zones of accreted terranes. Many of the patterns seen in New Guinea, for example, between craton and accreted terrane biotas, and in dextral offsets, also occur in New Zealand (Heads 1989). Recent ideas on the structure of the Andes are similar to those suggested here for the New Guinea orogen, in particular the Andes are now seen as tectonically more complex than previously thought. J. Flynn (quoted in Moffat 1996) cited the importance of lateral, as well as vertical, movement on faults and emphasized that 'The Andes are not homogeneous, biologically or geologically ... There is no such thing as 'the Andes''. The great diversity of rock types seen in the New Zealand and New Guinea orogens is reflected in an Ericaceae flora which can survive on acid as well as basic, ultrabasic and saline terrain, in well-drained lithophyte and epiphyte communities as well as swampy or periodically inundated sites, and from the mangrove to the high alpine. The ability to tolerate this wide range of heliophilous habitats is probably of long-standing in the family, and it is not surprising that the distributions of taxa in a family characteristic of peaty, sandy regions and sometimes coasts, deltas and swamps should track oil-belts so closely (for example in Aceh and around Makassar Strait). Bituminous sequences and new taxa are often created at the turning points in paleogeographic history (Heads 1989).

Within New Guinea, birds-of-paradise and rhododendrons show many parallels in their ecology and biogeography. The same altitudinal band is most diverse for both, they also show the same disjunctions, breaks in ranges (e.g. the old craton margin), centres of endemism and sites of altitudinal anomalies, all despite very different means of dispersal. None of these are predicted in the chance-dispersal models, but the rejection of 'centres of origin', 'means of dispersal', 'adaptive radiation' and Pleistocene evolution, allows a productive reappraisal of forest ecology and of what Victor Hugo called 'the secret intimacy of bird and tree'.

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Appendix:

Associates of Malesian Ericaceae cited by Sleumer (1966, 1967)

These will usually be at least co-dominant: *Sphagnum* L., *Gleichenia* Sm., *Pteridium* Scop., tree ferns (the Ericaceae are usually epiphytic on these), conifers (*Agathis* Salisb., *Papuacedrus* Li, *Dacrydium* Soland., *Podocarpus* Pers., *Pinus* L. (N Luzon)), Proteaceae (*Grevillea* R. Br.), Pandanaceae (*Pandanus* L.f.), Palmae (*Metroxylon* Rottb.), Fagaceae (*Castanopsis* (D. Don) Spach, *Lithocarpus* Blume, *Quercus* L.), Casuarinaceae (*Casuarina* Adans.), Nothofagaceae (*Nothofagus* Blume), Myrsinaceae (*Rapanea* Aubl.), Saxifragaceae (*Quintinia* A.D.C.), Myrtaceae (*Leptospermum* J.R. & G. Forst., *Xanthomyrtus* Diels, *Tristania* R.Br.), Ternstroemiaceae/Symplocaceae (*Eurya* Thunb. and *Symplocos* Jacq.), and other Ericaceae (especially *Vaccinium* and *Rhododendron*).

Archbold (1942) recorded that a white-flowered liane of *Dimorphanthera* brought together numbers of flower-feeding birds, the most persistent being *Charmosyna josefinae, Philemon meyeri, Myzomela eques, Melanocharis bicolor* and *Lorius.* Stevens (1976) recorded *Melidectes fuscus, M. princeps,* and *Ptiloprora pestriata* (all Meliphagidae) feeding on, and probably pollinating, *Rhododendron* flowers. The berries of *Vaccinium paradisearum* are eaten by *Oreopsittacus* and *Charmosyne* (Loriidae) (Sleumer 1967).

The distribution of Grammitidaceae (Filicales) inside and outside Malesia

B.S. Parris

Abstract

B. S. Parris (Fern Research Foundation, 21 James Kemp Place, Kerikeri, Bay of Islands, New Zealand) 2003. Distribution of Grammitidaceae (Filicales) inside and outside Malesia. Telopea *10(1): 451–466.* Over 750 species of Grammitidaceae are known. At least 250 occur in the New World and at least 450 are found in the Old World. Of the Old World species, 262 are in Malesia, 127 in the Pacific including Australia and New Zealand, 63 in Asia excluding Malesia and 54 in Africa including Macaronesia, Madagascar and the Mascarene Islands. *Lomaphlebia* (2 spp.) and *Luisma* (1 sp.) are endemic to the New World; *Ceradenia* (54 spp.), *Cochlidium* (16 spp.), *Enterosora* (10 spp.), *Melpomene* (25 spp.) and *Terpsichore* (57 spp.) are centred in the New World, each with less than half their species in Africa; *Micropolypodium* (25 spp.) is New World-centred with 3 Asian/Malesian species; *Lellingeria* (63 spp.) is New World-centred with 11 African species and 2 Pacific species; *Grammitis* s. str. has 11 New World species, 7 African species and 4 Pacific species; *Zygophlebia* has 7 African species and 7 New World species. *Acrosorus* (5 spp.), *Calymmodon* (30 spp.), *Chrysogrammitis* (2 spp.), *Prosaptia* (53 spp.), *Scleroglossum* (10 spp.) and *Themelium* (7 spp.) are centred in Malesia and extend to Asia and/or the Pacific, as are several species groups of *Ctenopteris*, *Grammitis* s. lat. and *Xiphopteris*. *Adenophorus* (9 spp.) is endemic to the Pacific. Two species groups of *Grammitis* s. lat. are endemic to Africa. The *Ctenopteris blechnoides* species group has 11 species in the Asia-Malesia-Pacific region and 5 in Africa. The *Grammitis billardierei* species group is largely in Old and New World south temperate regions (16 spp.), with 1 species in Malesia and 2 in Africa. Numbers of groups, species and endemic species are given for the 93 countries in which the family occurs. Old World countries with the most species are Indonesia (162), Papua New Guinea (131), Malaysia (97) and Philippines (68). New World countries with the most species are Venezuela (86), Colombia (83), Ecuador (82) and Costa Rica (78). 364 species are endemic to a single country. Old World countries with the most endemics are Indonesia (48), Papua New Guinea (46) and Australia, Malaysia and Hawaiian Islands (all with 13). New World countries with the most endemics are Brazil (19), Venezuela (17), Peru (12) and Colombia (11).

Introduction

The fern family Grammitidaceae is a characteristic and important component of rainforest in tropical montane regions of the Old World and the New World, extending to the north and south temperate zones. In the northern hemisphere it does not occur beyond c. 40°N, but in the southern hemisphere it extends to 56°S. Seasonal dryness is the major limiting factor in its distribution within both tropical and temperate regions. In the tropics the average daily lower limit of cloud formation is an important demarcator of the lower altitudinal limits of distribution. A few species are found in tropical lowland forest associated with rivers, either as epiphytes on trees overhanging the water or as facultative rheophytes on rocks in and by water.

For many years Grammitidaceae was one of the least studied of large groups of ferns, but in the last three decades it has been the subject of numerous taxonomic studies, some still ongoing, and including both morphological and molecular investigations. More than 750 species are now known (Parris 1998c). Floristic treatments, many recent and written by taxonomists who have prepared monographic accounts of the family, are also available. Enough is now known about the taxa of Grammitidaceae to enable a preliminary compilation of their distribution and centres of diversity to be made, although our knowledge is as yet incomplete. In the light of current concerns on the loss of biodiversity it is also useful to highlight the areas with high species numbers and endemicity.

In the New World 11 genera of Grammitidaceae are currently recognised, nearly all of which have been recently revised or described. They are *Ceradenia* L.E.Bishop (Bishop 1988), *Cochlidium* Kaulf. (Bishop 1978), *Enterosora* Baker (Bishop & Smith 1992), *Grammitis* Sw. sect. *Grammitis* (Bishop 1977), *Lellingeria* A.R.Sm. & R.C.Moran (Smith et al. 1991), *Lomaphlebia* J.Sm. (Smith 1875), *Luisma* M.T.Murillo & A.R.Sm., *Melpomene* A.R.Sm. & R.C.Moran (Smith & Moran 1992), *Micropolypodium* Hayata (Smith 1992), *Terpsichore* A.R.Sm. (Smith 1993) and *Zygophlebia* L.E.Bishop (Bishop 1989).

Redefinition of generic limits in the Old World is as yet incomplete, with 18 genera currently accepted (Parris 2001, 2002, Moran & Smith 2001, Smith 1992). They are *Acrosorus* Copel., *Adenophorus* Gaudich., *Calymmodon* C.Presl, *Ceradenia, Chrysogrammitis* Parris, *Cochlidium, Enterosora, Grammitis* s. str. (sect. or subgenus *Grammitis*), *Lellingeria, Melpomene, Micropolypodium, Prosaptia* C.Presl, *Scleroglossum* Alderw., *Terpsichore, Themelium* (T.Moore) Parris and *Zygophlebia; Ctenopteris* s. lat., *Grammitis* s. lat. and *Xiphopteris* p.p. (Old World) have also been accepted, with the proviso that within *Ctenopteris* and *Grammitis* a number of distinct species groups can also be recognised (Parris 2001). As the type species of *Ctenopteris, C. venulosa* Blume ex Kunze, is now treated as *Prosaptia venulosa* (Blume ex Kunze) M.G.Price (e.g. Parris 2001), the type species of *Xiphopteris, X. serrulata* (Sw.) Kaulf., has been transferred to *Cochlidium* (Bishop 1978) and *Grammitis* is now only accepted as a genus in the strict sense (e.g. Moran & Smith 1995), the remaining species of these three genera in the Old World need to be assigned to other genera.

Thirty-two groups of Grammitidaceae have been recognised for this paper. Some groups are genera that have already been described, while most (or all) of the others may be described as genera in the future. The groups are listed in Table 1, together with the number of species in each.

Table 1. Groups of Grammitidaceae and the number of species in each group.

Acrosorus	5 (Parris unpublished data)
Adenophorus	9 (Palmer 2002)
Calymmodon	20 (Parris unpublished data)
Ceradenia	54 (Bishop 1988, Parris 2002)
Chrysogrammitis	2 (Parris 1998a)
Cochlidium	16 (Bishop 1978)
Enterosora	10 (Bishop & Smith 1992, Parris 2002)
Grammitis s. str.	22 (Bishop 1977, Parris 1997a, Parris unpublished data)
Lellingeria	63 (Smith et al. 1991, Parris 2002, Parris unpublished data)
Lomaphlebia	2 (Parris unpublished data)
Luisma	1 (Murillo & Smith 2003)
Melpomene	25 (Smith & Moran 1992)
Micropolypodium	25 (Smith 1992)
Prosaptia	53 (Parris unpublished data)
Scleroglossum	10 (Parris unpublished data)

Terpsichore	57 (Smith & Moran 1995, Parris 2002)
Themelium	7 (Parris 1997b, Parris unpublished data)
Zygophlebia	14 (Bishop 1989, Parris 2002)
Ctenopteris blechnoides (Grev.) W.H.Wagner & Grether group	16 (Parris unpublished data)
Ctenopteris curtisii (Baker) Copel. group	10 (Parris unpublished data)
Ctenopteris lasiostipes (Mett.) Brownlie group	2 (Parris unpublished data)
Ctenopteris mollicoma (Nees & Blume) Kunze group	9 (Parris unpublished data)
Ctenopteris nutans (Blume) J.Sm. group	10 (Parris unpublished data)
Ctenopteris repandula (Mett.) C.Chr. & Tardieu group	27 (Parris unpublished data)
Ctenopteris whartoniana (C.Chr.) Copel. group	4 (Parris unpublished data)
Grammitis billardierei Willd. group	16 (Parris unpublished data)
G. cryptophlebia (Baker) Copel. group	2 (Parris unpublished data)
G. pervillei (Mett. ex Kuhn) Tardieu group	4 (Parris unpublished data)
G. reinwardtii Blume group	c. 146 (Parris unpublished data)
G. samoensis (Baker) Ching group	7 (Parris unpublished data)
G. universa (Baker) Copel. group	4 (Parris unpublished data)
Xiphopteris hieronymusii (C.Chr.) Holttum group	6 (Parris unpublished data)

Distribution

It is convenient to divide the world into five regions for the purpose of examining the distribution of Grammitidaceae: 1, New World (North, Central and South America, the West Indies and the islands of the Galapagos, Falklands and South Georgia); 2, Africa (continental Africa, Madagascar and the islands of the Azores, Canaries, Ascension, St Helena, Tristan da Cunha group, Seychelles, Comoros, Mauritius, Réunion, Marion, Crozets and Kerguelen); 3, Asia excluding Malesia (India, Sri Lanka, Nepal, Thailand, Cambodia, Laos, Vietnam, China, Taiwan and Japan); 4, Malesia (Malaysia, Singapore, Brunei Darussalam, Indonesia, Philippines and Papua New Guinea), and 5, Pacific (Australia, New Zealand and the islands of Micronesia, Melanesia and Polynesia).

A provisional world list of Grammitidaceae species and their distribution has been compiled (Parris, unpublished) from the sources listed in Table 1, together with the following: Baksh-Comeau (2000), Bishop (1995), Bishop & Smith (1995), Braithwaite (1986), Brown and Brown (1931), Brownlie (1969, 1977), Christensen (1943), Copeland (1932), Dorr et al. (2000), Iwatsuki (1995), Kato and Parris (1992), Kramer (1978), Labiak (2000, 2002), Manickam and Irudayaraj (1992), Mickel and Beitel (1988), Moran and Smith (1995a, 1995b, 1995c, 1995d), Parris (1983, 1990, 1993, 1997a, 1998b, 1998c, in press), Parris and Given (1976), Parris and Glenny (in prep.), Parris and Latiff (1997), Ponce (1996), Proctor (1977, 1985, 1989), Rodriguez (1995), Sledge (1967), Smith (1985, 1995a, 1995b), Smith and Bishop (1995), Smith et al. (1999), Stolze (1981), Tagawa and Iwatsuki (1989), Tardieu-Blot and Christensen (1941), Tryon and Stolze (1993), Werff and Smith (1980), Zhang (2000). Parris' unpublished data cited in Table 1 is based on fieldwork in Malesia and the study of herbarium material from the institutes acknowledged below, particularly for Africa, Malesia and the Pacific.

The provisional world list was used as the basis for the data in Figure 1, which shows the number of groups, species and endemics in each of the phytogeographical regions. It should be noted that Table 1 does not include monotypic groups and distinct species

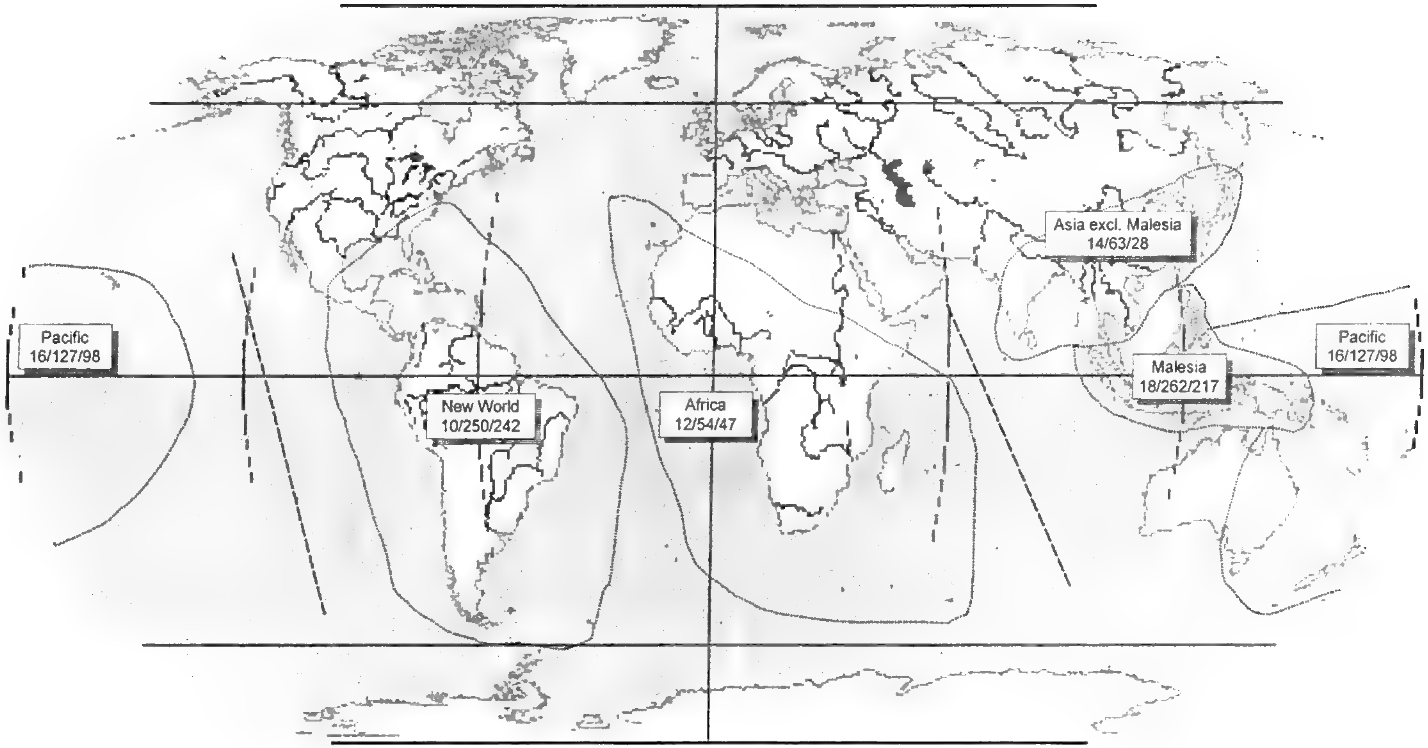

Fig. 1. Groups of Grammitidaceae, number of species and number of endemic species, in each of the five phytogeographical regions, and the two major phytogeographic boundaries.

whose affinities are not yet clear; however, they are included in the following species counts for the phytogeographical regions. Taxa in unresolved species complexes in African *Ceradenia* and *Zygophlebia*, Malesian and Pacific *Calymmodon*, Malesian *Ctenopteris* and undescribed species from South America (particularly Bolivia, Paulo Labiak and Alan Smith pers. comm.) are not included in the counts. Preliminary investigations suggest that more than 60 species are involved and they bring the number of species in the family to over 750.

The groups, their disposition in the five regions, the number of species in each region and the number of species endemic to each region, are shown in Table 2..

Table 2. Distribution of groups of Grammitidaceae showing the number of species and the number of endemic species in each region.

Group	New World	Africa	Asia	Malesia	Pacific
Lomaphlebia	2/2	-	-	-	-
Luisma	1/1	-	-	-	-
Ceradenia	48/46	8/6	-	-	-
Cochlidium	16/15	1/0	-	-	-
Enterosora	9/8	2/1	-	-	-
Melpomene	25/24	1/0	-	-	-
Terpsichore	55/55	2/2	-	-	-
Zygophlebia	7/7	7/7	-	-	-
Grammitis billardierei	3/0	3/1	-	1/0	15/11
Grammitis s. str.	11/11	7/7	-	-	4/4
Lellingeria	50/50	11/11	-	-	2/2
Micropolypodium	22/22	-	2/2	1/1	-
G. cryptophlebia	-	2/2	-	-	-
G. pervillei	-	4/4	-	-	-
Ctenopteris blechnoides	-	5/5	4/1	6/2	6/4
Acrosorus	-	-	2/0	5/2	1/0
Calymmodon	-	-	4/1	20/14	7/5
Chrysogrammitis	-	-	2/0	2/0	1/0
Prosaptia	-	-	11/4	40/32	12/10
Scleroglossum	-	-	2/0	8/5	5/2
Themelium	-	-	1/0	7/5	2/0
Ctenopteris mollicoma	-	-	3/0	7/4	3/2
Ctenopteris repandula	-	-	6/4	23/18	4/2
G. reinwardtii	-	-	16/8	105/94	40/31
Ctenopteris curtisii	-	-	1/0	10/9	-
G. universa	-	-	1/1	3/3	-
Xiphopteris hieronymusii	-	-	1/0	6/5	-
Ctenopteris nutans	-	-	-	8/8	2/2
G. samoensis	-	-	-	2/2	5/5
Ctenopteris whartoniana	-	-	-	4/4	-
Adenophorus	-	-	-	-	9/9
Ctenopteris lasiostipes	-	-	-	-	2/2
Unassigned	**1/1**	**1/1**	**7/7**	**6/6**	**7/7**
Total	**250/243**	**54/47**	**63/28**	**262/217**	**179/98**

Table 2 shows that there are two major phytogeographic zones for Grammitidaceae: the New World and Africa, and Asia-Malesia-Pacific. The boundaries between them lie 1) in the Pacific Ocean, between the New World/African groups that extend no further west than continental Central and South America and the Galapagos Islands, and the Asia-Malesia-Pacific groups that extend no further east than the Hawaiian Islands and the Marquesas, and 2) in the Indian Ocean, between the New World/African groups that extend no further east than Madagascar, the Mascarene Islands and the Seychelles, and the Asia-Malesia-Pacific groups that extend no further west than Sri Lanka and India. They delimit the New World-centred and the Malesian-centred areas of diversity within the family and are marked on Figure 1.

Twenty-seven of the 32 groups dealt with here do not cross either of the boundaries, only five of the groups do, and they show several distribution patterns. *Lellingeria* and *Grammitis* s. str. both occur in Africa, the New World and the Pacific, but do not extend into Asia-Malesia; *Lellingeria* is mainly New World, with 11 species endemic to Africa, one (*L. saffordii* (Maxon) A.R.Sm. & R.C.Moran) endemic to the Hawaiian Islands and one (*L. subcoriacea* (Copel.) A.R.Sm. & R.C.Moran) found on the Society Islands and the Marquesas; *Grammitis* s. str. has 11 species in the New World, seven species endemic to Africa and four species endemic in the Pacific, ranging from Vanuatu (New Hebrides) to the Marquesas. *Micropolypodium* is another mainly New World genus that does not extend into the Pacific, but has c. three species in Asia-Malesia. The group of *Ctenopteris blechnoides* has 11 Asian-Malesian-Pacific species, and five endemic to Africa. In contrast to all other groups of Grammitidaceae, which are largely restricted to the tropics, the group of *Grammitis billardierei* is essentially south temperate and circum-antarctic in distribution, with one species (*G. stenophylla* Parris, syn *G. kairatuensis* M.Kato & Parris) extending to the tropics of Australia and Seram in the Moluccas.

All 17 groups occurring only in the Asia-Malesia-Pacific areas are most diverse in Malesia, as is the group of *Ctenopteris blechnoides*. Of the groups found in Asia, Malesia and the Pacific, only six occur in all of the regions of Malesia: Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands, Borneo, Sulawesi, the Moluccas, the Philippines and New Guinea. They are the *Grammitis reinwardtii* group, *Prosaptia*, the *Ctenopteris repandula* group, *Scleroglossum*, the *Ctenopteris mollicoma* group and the *Ctenopteris blechnoides* group. *Acrosorus, Calymmodon, Chrysogrammitis* and *Themelium* are found in Asia, the Pacific and part of Malesia. The groups of *Ctenopteris curtisii* and *Grammitis universa, Micropolypodium*, and the group of *Xiphopteris hieronymusii* are present in Asia and part of Malesia, but are absent from the Pacific; in contrast, the groups of *Ctenopteris nutans, Grammitis billardierei* and *Grammitis samoensis* are absent from Asia, but are in part of Malesia and in the Pacific. The group of *Ctenopteris whartoniana* is endemic to part of Malesia.

It is constructive to examine the distribution of diversity and endemicity within the family in detail for each of the regions to establish which countries are richest in terms of species numbers and numbers of endemics and are thus important for conservation. The provisional world checklist for the family has been used to build tables for each of the regions. Information on the distribution of species within countries is sometimes unavailable in floras, although endemic status is usually cited. In the discussion of endemics following each table, distribution is cited at the level of primary political unit within a country, when known, with the number of endemics followed by the total number of species, except for Sri Lanka, where distribution of Grammitidaceae is confined to a small area delimited by co-ordinates, and Tanzania, Madagascar and Malesia, where distribution is cited by major geographical units, sometimes within major political units. Countries without endemic species are omitted from the regional tables, but are listed above them, with the number of groups preceding number of species for each. They are countries at the edge of the distribution of the family or apparently with little suitable habitat. A few have limited information available (Hispaniola, Guyana and French Guiana).

Table 3 shows the distribution of Grammitidaceae endemic to New World countries. The regions can be subdivided into areas that are often treated as floristic units based upon species distribution and numbers of endemics. They are listed here, but space prohibits a detailed discussion of regional endemicity. Data on endemics in the following New World list is sometimes limited to country level and for countries where floristic accounts are unavailable it has been acquired from monographs. Countries without endemics are United States (1/1), Belize (4/7), Honduras (8/30), Nicaragua (7/21), El Salvador (6/26), Hispaniola (9/34), Tobago (2/3), Guyana (7/25), Surinam (7/18), French Guiana (3/8), Argentina (2/4), Chile (1/3), Falkland Islands (1/1) and South Georgia (1/1).

Table 3. Distribution of New World Grammitidaceae.

Area	No. of groups in area	No. of species in area	No. of species endemic to area
Southern Mexico & Central America	9	101	25
Mexico	7	37	3
Guatemala	7	38	1
Costa Rica	9	78	3
Panama	9	68	2
Antilles	10	67	26
Greater Antilles	10	62	17
Cuba	8	23	3
Jamaica	10	50	6
Puerto Rico	7	20	2
Lesser Antilles	9	28	5
South America	11	192	111
Trinidad	5	12	1
Brazil	8	55	19
Colombia	10	83	11
Venezuela	9	86	17
Ecuador	9	82	7
Peru	9	72	12
Bolivia	9	55	7

Mexican endemics are found in Chiapas (1/37) and Oaxaca (3/33). The sole Guatemala endemic comes from Alta Verapaz (1/23) and Huehuetenango (1/9). For Costa Rica and Panama the distribution of endemic taxa within the country is unknown.

In Cuba the majority of species (or all?) including endemics occur in Oriente; no modern account is available. In Jamaica the majority of species and all endemics occur in St Andrew (2/29), Portland (6/36) and St Thomas (2/30) in the Blue Mountains, John Crow Mountains and the Port Royal Mountains. The Puerto Rico endemics and the majority of species are found in Jayuya (1/10), Naguabo (1/10) and Río Grande (1/12); the endemics are also known from Adjuntas (1/3), Caguas (1/2) and San Lorenzo (1/3). In the Lesser Antilles the majority of species and the endemics occur on St Kitts (2/10), Montserrat (1/5), Nevis (1/6), Guadeloupe (5/22), Dominica (4/17), Martinique (3/16), St Vincent (2/14) and Grenada (2/12). The New World endemic genus *Lomaphlebia* is restricted to the Greater Antilles, with one species in Cuba and one in Jamaica.

The Trinidad endemic and most other species are restricted to the Northern Range in St George. Brazil's endemic species are found either in the north or in the southeast, and most of the other species are restricted to either or both of these areas. No modern account is available for Colombia and the distribution of endemic taxa within the country is unknown. The monotypic endemic *Luisma* is known only from the Colombian type. Venezuela endemics and the majority of species, occur in Amazonas (5/46) and Bolívar (8/51) in the Venezuelan Guayana and in Aragua (2/21), Mérida (1/24), Tachira (1/13) and Trujillo (3/27) in the Venezuelan Andes. In Ecuador the endemics and the majority of species are found in Azuay (3/16), Carchi (1/28), Loja (1/20), Pichincha (2/42), Tunguragua (1/26) and Zamora (1/23). Peruvian endemics and most species are in Amazonas (1/22), Cuzco (7/40), Huánuco (2/28), Pasco (2/27) and San Martín (1/21). No modern account is available for Bolivia and the distribution of endemic taxa within the country is unknown. The New World Grammitidaceae are most numerous in the Andes from Venezuela to Bolivia, with 141 species known from the mountain chain.

The distribution of Grammitidaceae in African countries having endemic species is shown in Table 4. Countries with no endemic species are Azores (2/2), Canary Islands (1/1), Guinea (3/3), Sierra Leone (3/3), Liberia (4/4), Ivory Coast (3/3), Ghana (1/1), Cameroon (6/6), Bioko (5/5), Equatorial Guinea (1/1), Annobon (1/1), Popular Republic of the Congo (2/2), Democratic Republic of the Congo (4/4), Rwanda (3/3), Uganda (1/1), Kenya (3/3), Zimbabwe (3/3), Mozambique (3/3), Mauritius (9/10), South Africa (2/2), South Atlantic Ocean Islands (2/2) and South Indian Ocean Islands (1/1).

Table 4. Distribution of Grammitidaceae in African countries having endemic species.

Area	No. of groups	No. of species	No. of species endemic
San Tomé & Principe	5	6	1
Gabon	3	3	1
Ethiopia	2	2	1
Tanzania	9	14	3
Malawi	6	6	1
Madagascar	12	28	12
Comoro Islands	2	2	2
Seychelles	4	4	1
Réunion	11	12	2
Ascension Island	1	1	1
St Helena	1	1	1

Cochlidium serrulatum (Sw.) L.E.Bishop, *Lellingeria oosora* (Baker) A.R.Sm. & R.C.Moran, *Melpomene flabelliformis* (Poir.) A.R.Sm. & R.C.Moran) and *Terpsichore elastica* (Bory ex Willd.) A.R.Sm. are widespread in tropical Africa. Some or all four occur in the countries without endemics listed above. The endemic species of San Tome, Gabon, Ethiopia and Malawi are each known from a single gathering. In Tanzania an endemic species and the majority of other species are found on the Uluguru Mounts (1/10). The other endemics occur on Kilimanjaro (1/2) and the Nguru Mounts (1/6). Madagascar endemics and other species are known from Ambazinana (1/3), Ambohimitombo (2/3), Andrangovalo (2/5), Anjenaharibe (2/4), Andohahela (1/4), Andringitra (2/4), Ankafina (2/6), Befingotra (3/7), Manongarivo (4/13), Mantadia (2/7), Marojejy (2/7), Ranomafana (3/8) and Tsaratanana (2/6). The Comoro endemics are found on Anjouan (2 species) and Grande Comore (1 species). All Seychelles species including the endemic are known from Mahé while one species is also found on Silhouette. The endemic and other species of Réunion are found in forest, often above 800-1000 m (Badré and Cadet 1978). The endemic species of Ascension Island and St Helena occur on the summit peaks of the islands. Two groups are endemic to Africa, those of *Grammitis cryptophlebia* and *G. pervillei.* The former extends from San Tomé to Mauritius and Réunion while the latter occurs in Tanzania, Madagascar and the Seychelles.

The distribution of Grammitidaceae in Asian countries, excluding Malesia, having endemic species is shown in Table 5. Bhutan (1/1), Nepal (2/2), Thailand (11/27), Cambodia (3/4) and Laos (1/1) have no endemic species.

Table 5. Distribution of Grammitidaceae in Asia (excluding Malesia), having endemic species.

	No. of groups	No. of species	No. of species endemic
Japan	4	6	5
China	7	13	1
Taiwan	10	19	1
North & Northeast India	3	3	1
South India	5	8	2
Sri Lanka	9	22	9
Vietnam	10	19	1

Japanese endemic and other species are found in Honshu (2/3), Shikoku (1/2) and Kyushu (3/4), while the species of Ryukyu (2/2) and Iwo-jima (1/1) are all endemic. In China the endemic and other species occur in Fujian (1/3), Guangxi (1/3) and Zhejiang (1/2). Hainan (6/8) is the most species-rich area of China. The endemic species of Taiwan is known from Takaio (probably in southern Taiwan), where the majority of species are found. The Indian endemic occurs in Meghalaya and Assam, while the other two Indian species are in Sikkim (2), Manipur (1), Meghalaya (1) and Nagaland (1). In South India the endemic species and all other species are in Tamil Nadu. The Sri Lanka endemics and the majority of other species are confined to the upland areas between c. 6°30'–7°30'N 80°20'–81°20'E. In Vietnam the endemic species occurs in Nhatrang (1/13), as do the majority of other species, but no groups are endemic to this area.

The distribution of Grammitidaceae in Malesian phytogeographic regions having endemic species is shown in Table 6. Singapore (1/1) and the Lesser Sunda Islands (6/17) have no endemics.

Table 6. Distribution of Malesian Grammitidaceae.

Area	No. of groups	No. of species	No. of species endemic
Peninsular Malaysia	13	48	6
Sumatra	12	57	4
Java	10	50	5
Borneo	16	91	14
Sulawesi	14	45	5
Moluccas	13	66	9
Philippines	13	68	12
New Guinea	14	161	91

In Peninsular Malaysia the endemic and other species are found in Pahang/Selangor (Cameron Highlands (1/23), Gunung Tahan (1/21), Fraser's Hill (1/19), Gunung Ulu Kali (1/11)), Perak (Larut Hills (1/17), Melaka (Gunung Ledang (1/6)), Johor (Gunung Belumut (2/4), Gunung Mering (1/3)) and Kedah (Gunung Jerai (1/3)). Sumatran endemics and most other species occur on Gunung Kerinci/Gunung Tujuh (1/22), Gunung Singalang (1/17) and Gunung Kemiri (1/16); other endemics are known from Gunung Dempo (2/2), Laë Pondom (1/8), Goh Lembuh (1/4) and Bukit Sipitai (1/3); Gunung Losir has 12 species, none endemic. In Java nearly all of the species, and all endemics are on Mount Gede/Pangrango (5/41); the only other site with more than 5 species is Gunung Patuha (1/7). In Borneo most endemics and the majority of species occur on Mount Kinabalu in Sabah (10/77); other endemics are known from Gunung Mulu (3/40+), Pueh Range (1/11), Mount Penrissen (1/8), Mount Dulit (2/7), Ba Kelalan (1/3) and Kelabit Highlands (1/3) in Sarawak, the Crocker Range (1/13) in Sabah, Gunung Besar (1/5), Bukit Raja (1/4), Gunung Murud (1/3) and Gunung Kemul (1/2) in Kalimantan, and Mt Galegas (1/1) in Brunei. Sulawesi endemics and the majority of species occur on Mt Roroka Timbu (3/25), while other endemics are known from Gunung Matinang (1/2) and Mt Busu (1/1). In the Moluccas all of the endemics and nearly all of the species are found on Seram (9/60). The Philippine endemics and the majority of other species are found on Luzon (5/44), Mindanao (7/48) and Mindoro (1/12), with the greatest number of species occurring on Mount Apo (27) and Mount Dulang-Dulang (17) in Mindanao, and Mount Banahaw (18) and Mount Pulog (16) in Luzon. In New Guinea the endemics are found in 79 localities, the most important of which are Mount Jaya (9/50), Mount Trikora (3/15), Lake Habbema (4/24) and Mount Doorman (6/21) in the Central Ranges of West Papua, and Mount Hagen (7/36) in Western Highlands, Tari Gap (4/15) in Enga District, Mount Giluwe (6/36) in Southern Highlands District, Mount Wilhelm (3/24) in Simbu District, Mount Otto (4/12) and Mount Piora (3/17) in Eastern Highlands District, Aseki (4/21), Matap (3/17), Rawlinson Range (8/32), Saruwaged Range (9/38) and Ekuti Range (3/20) in Morobe District, Boridi (3/7) and Mount Albert Edward (3/15) in Central District, Mount Suckling (5/20), Fergusson Island (3/12) and Normanby Island (3/8) in Milne Bay District, Papua New Guinea. The group of *Ctenopteris whartoniana* is endemic to East Malesia and ranges from Seram in the Moluccas to Papua New Guinea.

For Malesia the diversity and endemicity figures presented above are arranged in the floristic units that are recognised in the literature for Flora Malesiana, but it is expedient to list them also by political rather than geographic boundaries for conservation purposes (Table 7).

Table 7. Distribution of Malesian Grammitidaceae by country.

Country	No. of groups	No. of species	No. of species endemic
Malaysia	15	97	13
Singapore	1	1	0
Brunei Darussalam	8	12	1
Indonesia	16	162	48
Philippines	13	68	12
Papua New Guinea	14	131	46

Table 8 shows the distribution of Grammitidaceae in the Pacific countries with endemic species. Tonga (1/1) has no endemic.

Table 8. Distribution of Pacific Grammitidaceae.

Area	No. of groups	No. of species	No. of species endemic
Australia	7	24	13
New Zealand	1	12	5
Solomon Islands	10	28	5
Vanuatu	8	14	3
New Caledonia	7	11	5
Fiji	7	16	7
Samoa	9	18	8
Cook Islands	2	2	1
Rapa	2	2	2
Society Islands	9	15	10
Marquesas Islands	7	8	4
Hawaiian Islands	3	14	13
Federated States of Micronesia	7	9	6

In Australia the highest number of species and endemics are in northeast Queensland, mostly between 16–19°S 145–146°E (9/14), other endemics are on Lord Howe Island (3/3) and Tasmania (1/7). The endemic and the majority of other species in New Zealand are in North Auckland (2/6), South Auckland (3/8), Taranaki (2/7), Gisborne (2/7), Wellington (2/8), Nelson (2/8), Marlborough (2/7), Westland (2/7), Canterbury (2/7), Otago (1/7) and Southland (3/10), endemics are also known from Stewart Island (2/6), Auckland Islands (2/6), Antipodes Island (1/3) and Chatham Islands (1/3). In the Solomon Islands the endemic and most of the other species occur on Guadalcanal (2/16), Kolombangara (2/14) and Bougainville (2/13); another endemic is on San Cristobal (1/3). In Vanuatu the endemic and most other species are on Espiritu Santo (2/8) and Tanna (1/4); Aneitum also has 8 species, none endemic. The Grammitidaceae of New Caledonia, including the endemic species, are distributed in the forest areas along the centre and east of the island in numerous localities. The Fijian endemic and most other species are on Viti Levu (4/12), Vanua Levu (4/11), Taveuni (2/6) and Ovalau (1/3). In Samoa the endemics and the majority of species occur on Upolu (5/14) and Savai'i (5/13); other islands with endemic species are Tutuila (2/5), T'au (1/4) and Olosina (1/3). The species of the Cook Islands are restricted to Rarotonga (1/2) and the two endemic species of Rapa are known only from Mount Perahu. In the Society Islands the endemics and most of the species are found on Raiatea (6/8) and Tahiti (5/11), with endemics also occurring on Huahine (2/3) and Tahaa (2/3). The Marquesas Islands endemics and most of the species are known from Nuku Hiva (3/5) and Hiva Oa (2/6), with another endemic on Ua Pou (1/2). In the Hawaiian Islands the endemics and all species are found on Hawaii (6/7), Kauai (12/13), Lanai (7/8), Maui (8/9), Molokai (8/9) and Oahu (9/10). The endemic and all other species in the Federated States of Micronesia are found on Ponape, Caroline Islands (3/6) and Babeldoab, Palau Islands (3/4). In the Pacific the group of *Ctenopteris lasiostipes* is endemic to New Caledonia and *Adenophorus* is endemic to the Hawaiian Islands.

Discussion

This treatment of the distribution of Grammitidaceae must be regarded as preliminary, providing an outline of the areas of group and species richness and indicating areas of species endemism. Essentially it summarises our current knowledge concerning what is where and is of course incomplete. The hows and whys of distribution within the family may be addressed with some hope of success later, when we have a family phylogeny.

Grammitidaceae are known from a total of 93 countries. The countries with the highest number of groups in the Old World are Indonesia (16), Malaysia (15) and Papua New Guinea (14); in the New World they are Colombia (10) and Jamaica (10). Old World countries with the most species are Indonesia (162), Papua New Guinea (131), Malaysia (97) and Philippines (68). New World countries with the most species are Venezuela (86), Colombia (83), Ecuador (82) and Costa Rica (78). It is useful to compare the areas of high diversity in Grammitidaceae with the areas identified by Groombridge and Jenkins (2002) as important centres of plant diversity at regional and global levels. In Indonesia areas of significant diversity are Murkele Ridge in Seram, Moluccas (55 species), Mount Jaya in West Papua (50 species), and Mount Gede/Pangrango (3000 m) in Java, Indonesia (41 species). Mount Jaya is identified as important by Groombridge and Jenkins (2002), but the other two Indonesian areas are not. In Papua New Guinea the Saruwaged Range (38 species) and Mount Hagen and Mount Giluwe in Papua New Guinea (both with 36 species) are important for Grammitidaceae and also important for plant diversity as a whole. In Malaysia, Mount Kinabalu in Sabah (77 species), Gunung Mulu in Sarawak (40 species) and Cameron Highlands in Peninsular Malaysia (23 species) are important for Grammitidaceae and also for plant diversity in general. In the Philippines, Mount Apo (27 species) and Mount Dulang-Dulang (17 species) in Mindanao, and Mount Banahaw (18 species) and Mount Pulog (16 species) in Luzon have the greatest diversity of Grammitidaceae. None of these areas is identified as important by Groombridge and Jenkins (2002). In the New World, areas of diversity in Colombia and Costa Rica have not been identified because of the paucity of information about distribution within these countries. In Venezuela the states of Amazonas (46 species) and Bolívar (51 species) in the Venezuelan Guayana (total 54 species), and Trujillo (27 species) and Mérida (24 species) in the Venezuelan Andes are important centres for Grammitidaceae. The Venezuelan Guayana is identified as important by Groombridge and Jenkins (2002), but not the other two. In Ecuador, Pichincha (42 species), Carchi (28 species) and Tunguragua (23 species) are richest in Grammitidaceae. Parts of these areas have been identified as important by Groombridge and Jenkins (2002). It is evident that on a world scale areas of diversity in Grammitidaceae do not overlap completely with those of plants as a whole. Apart from the areas cited above with high species numbers there are other locations, e. g. in Cuba, Tanzania and Madagascar that are important for Grammitidaceae rather than plants in general. It is hoped that their diversity and endemicity is adequately protected.

Old World countries with the most endemics are Indonesia (48), Papua New Guinea (46) and Australia, Malaysia and Hawaiian Islands (all with 13). New World countries with the most endemics are Brazil (19), Venezuela (17), Peru (12) and Colombia (11). It is interesting to compare the percentage of endemics in countries with high numbers of endemic species in Grammitidaceae with the figures for plant endemicity cited by Groombridge and Jenkins (2002) in their survey of biodiversity at country level. Indonesia has the highest number of endemic species in the family, comprising 30% of the total, which is similar to the figure of 27% for plants as a whole there. Papua New Guinea has 35% of Grammitidaceae endemic, but no figures are available for plants. Australia has high plant endemism (90%) but the figure for Grammitidaceae is much lower, 54%. Malaysian endemic Grammitidaceae are 13% of the total, compared with 23% for plants in general. The Hawaiian Islands have the highest percentage of endemism in Grammitidaceae (93%). Separate figures for Hawaiian Islands plants are not provided by Groombridge and Jenkins (2002), but Palmer (2002) gives a figure of 77% for endemicity in Hawaiian Islands pteridophytes and Wagner et al. (1990) cite a figure of 89% for angiosperms. Brazil endemic Grammitidaceae form 35% of the total, but no plant figures are available. The proportion of Grammitidaceae in Venezuela (20%), is much lower than that of plants in general (37%), in Peru 17% of Grammitidaceae are endemic, compared with 31% of plants and in Colombia 13% of Grammitidaceae are endemic, compared with 29% of plants.

The percentage figures for endemicity in Australia, Colombia, Malaysia, Peru and Venezuela for Grammitidaceae are probably lower than those for plants in general because of the greater vagility of wind-blown spores. The figure for the Hawaiian Islands Grammitidaceae is high largely because of the species radiation of *Adenophorus*.

The total number of species endemic to a single country is 364, i. e. 49% of species in the family. It is likely to rise when the unresolved complexes in *Calymmodon, Ceradenia, Ctenopteris* and *Zygophlebia* are dealt with. The taxonomic status of some endemic species in groups yet to be revised needs to be confirmed, and the continued existence of some endemics needs to be verified. For example, *Grammitis tomensis* Schelpe has not been recorded during the 20th century (Figueiredo 2000), and *Terpsichore kirkii* Parris is known only from the type, collected in the 19th century. Many endemic species are known only from the type collection or from one locality and their conservation status remains unknown. Some may well be extinct. It is matter of some urgency to document them more fully.

The pteridophyte flora of Seram has been estimated by Kato (1990) as over 700 species, a surprisingly high figure. The number of species of Grammitidaceae, 60, is also unexpectedly high. The Murkele Ridge, including Gunung Binaiya (3000 m), supports 55 species, but even much lower areas, such as Gunung Kobipoto (16 species) and Gunung Roihelu (13 species) that are c. 1500 m alt., have significantly greater numbers of species than areas of similar altitude elsewhere. The Moluccas lie between the two great centres of botanical diversity in eastern and western Malesia and part of the species richness of Seram is due to an overlap of elements from both centres. Elsewhere in the Moluccas there appear to be far fewer species of Grammitidaceae.

Ambon has 4, Bacan 6, Buru 4, Halmahera 4 and Tidore 3, but based on the figures for Seram, far more would be expected. Another of the reasons for Seram's diversity appears to be that the four botanical expeditions responsible for nearly all of the material gathered there have included experienced pteridologists who have been assiduous in collecting the smaller and less obvious species. If the collecting of Grammitidaceae were carried out to the same standard elsewhere it would probably lead to a significant increase in the numbers of species in most areas, an increase in new species and possibly significant range extensions of already described species.

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Review of the bryofloristic connections of New Guinea Island

S. Piippo & T. Koponen

Abstract

S. Piippo[1] *& T. Koponen*[2] *(*[1]*Botanical Museum, P.O. Box 47, FIN-00014 University of Helsinki, Finland;* [2]*Mailantie 109, FIN-08800 Kirkniemi, Finland) 2003. Review of the bryofloristic connections of New Guinea Island.* Telopea *10 (1): 467–476.* The bryoflora of New Guinea has connections to Indonesia and Malaysia, and less stongly to Australia and New Zealand. This pattern is more evident in hepatics than in mosses, in which a pantropical element is more prominent. Vertical distribution also has clear connection with ranges, e.g. endemism is high at 1500–3000 m, disjunct boreal, temperate, and bipolar taxa occur at the highest altitudes, and pantropical or widely distributed taxa at the lowest altitudes. A preliminary attempt is made to compare the limits of vegetation zones in New Guinea and in Hunan Province of China, based on the vertical distribution of bryophyte species.

Material and Methods

Our studies on Western Melanesian bryoflora began in 1981 when D. H. Norris and T. Koponen made several field excursions in New Guinea in order to collect bryophytes. The original idea was to publish a list of the collections from the Huon Peninsula area but the target gradually changed toward a complete flora of Western Melanesia. We included Papua New Guinea, West Irian of Indonesia, and the Solomon Islands in our revisions and some of those revisions grew into world monographs of the genera studied. In total, Koponen and Norris collected c. 17 500 specimens in Madang, Morobe, and West and East Sepik Provinces of New Guinea (Fig. 1). Koponen and Norris are responsible for the study of the mosses and S. Piippo for the hepatics. Additionally we have had many collaborators (see the acknowledgments). The revisions are being published in Annales Botanici Fennici (Vols. 20–36) and Acta Botanica Fennica (Vols. 125–165) in three series: 'Bryophyte flora of the Huon Peninsula, Papua New Guinea' (67 parts published), 'Bryophytes from Frieda River, East and West Sepik Provinces, Papua New Guinea' (4 parts published), and 'Annotated catalogue of Western Melanesian bryophytes' (1 part published, 1 ms.). Additionally, with our colleagues we have published many papers dealing with the bryogeography, ecology, rarity and frequency of taxa, and human influence based on the collections or research (Koponen 2000).

Chinese bryoflora has been studied again (after V. F. Brotherus', 1849–1929, studies) in Helsinki beginning 1970, based on Finnish herbarium collections and new material (a total of 32 000 specimens) collected during Finnish-Chinese bryological expeditions. In addition to taxonomic research we have published checklists and floras of different provinces of China, such as Jiangxi (Fang et al. 1998), Guangdong (Li & Piippo 1994), Hainan (Lin et al. 1992), Hubei (Peng et al. 2000), Sichuan and Yunnan (Piippo et al. 1997, 1998), and checklist of the hepatics of the whole of China (Piippo 1990).

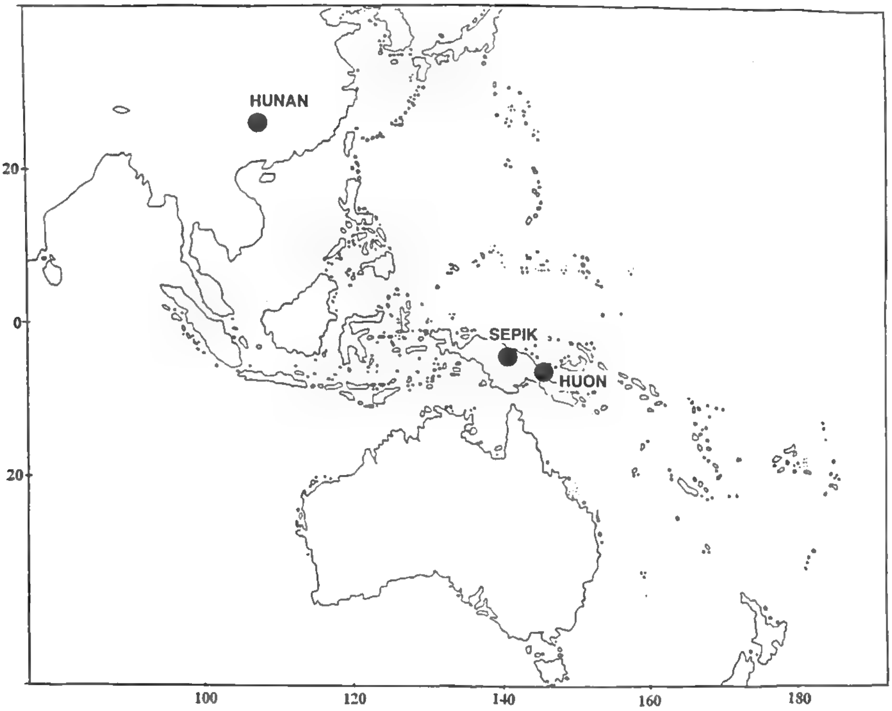

Fig. 1. The research localities in Western Melanesia (Sepik and Huon) and China (Hunan).

Results

1. Present state of study: Major taxonomic results from Western Melanesia are: Families studied 88, genera studied 296, species studied and published 1058, taxa new for science in total 87 (5 genera and 76 species), new combinations 65, new synonyms 446, first records for Western Melanesia of genera 44 and species 225. During these 20 years, 72 taxonomic revisions have been published (see Koponen et al. 1992, Koponen 2000, Gradstein et al. 2002). Today Anthocerotophyta and all the other families of Hepaticae except Aneuraceae and the genus *Bazzania* S. Gray of the Lepidoziaceae have been published, Lejeuneaceae are under revision. Most of the remaining families of Musci such as Hookeriaceae, Hypnaceae, Hypopterygiaceae, and Sematophyllaceae are under revision.

In 1997, our latest project in Hunan province, China, began (Fig. 1). The major objective is to compile bryophyte flora of the Hunan province and, in addition, to focus on ecology and phytogeography. A checklist of Hunanese bryophytes was published by Rao et al. (1997) and other records and revisions so far published are Koponen et al. (2000) and Potemkin (2000).

2. **Bryofloristic connections of New Guinea:** Hyvönen (1989) reviewed the bryofloristic connections of Western Melanesia. His review was based on 309 moss species and they showed that floristic affinities were to Asia, Oceania, and Australia, but to some extent also to South America and Africa. Enroth (1991) carried out a similar study on hepatics and showed that hepatics had much less affinity to Australia than mosses. Piippo (1992) and Piippo and Koponen (1997) studied the affinities of the bryophyte floras using Kroeber's similarity index. They compared 2900 species and 250 genera of hepatics in Western Melanesia, Australia, New Zealand, Borneo, Philippines, Taiwan, mainland China, Japan, Korea, and Bhutan; and 4 755 species and 550 genera of mosses in Western Melanesia, Australia, New Zealand, Philippines, Borneo, Lesser Sunda Islands, Peninsular Malaysia, Society Islands, Ceylon, Indochina, Taiwan, Korea, and Bhutan (Fig. 2). The plate tectonics behind the affinities were also discussed (see also Tan 1984, 1996, 1998, Tan & Engel 1990, Tan et al. 1988). Even though New Guinea belongs to the Australian plate, and the island is located much closer to Australia than to continental Asia, Western Melanesian hepatic flora is more closely related to the Laurasian flora than to the floras of Australia or New Zealand. This pattern is more clearly visible in species than in genera. Western Melanesian species shared with Indomalaysia and Asia are pantropical, Laurasian Asian widespread, or old Gondwanic elements speciated in Western Melanesia. China, Japan, Taiwan, Korea, and Bhutan are dominated by a Sino-Japanese temperate and warm-temperate element that is rather widespread also at high elevations in New Guinea. The affinities of Western Melanesian mosses to those of Indomalaysia are not as striking as those of the hepatics, even though the same pattern can be detected. The moss genera *Hypnodendron* (Touw 1971), *Dawsonia* (Zanten 1973), and *Desmotheca* (Vitt 1990) are examples of Gondwanic distribution types. Whitmore (1981) shows the same patterns in vascular plant distributions, such as Dipterocarpaceae and climbing palms (Laurasian), and Winteraceae (Gondwanic).

3. **Vertical distribution of bryophytes in New Guinea and in Hunan:** Enroth (1990) studied the vertical distribution of hepatics and mosses on the Huon Peninsula, and Piippo (1994a, 1994b, see also Piippo et al. 1987) those of endemic hepatics and epiphyllous Lejeuneaceae. All groups (hepatics and mosses and endemics) are most common at altitudes of 1200–2700(–3000) m, in mid-mountain forests, mossy forests and to some extent in high mountain forests. Only the epiphyllous Lejeuneaceae occur at 500–2300 m; they occur in lowland rainforests, and are more widespread due to better means of dispersal, their monoicous state, and due to their Laurasian origin. Endemism is high especially among Western Melanesian hepatics, c. 38%, due e.g. to the isolation of mountain-tops, and they are most common in montane forests. Asian-Oceanian and pantropical taxa prevail in lowland forests (0–300m) and foothill forests (300–1200 m); endemics prevail in SE Asiatic and Asian–Australian mid-mountain forests (1200–c. 2200 m), and mossy forests (c. 2200–c. 2800 m). At higher altitudes Southern and Northern Hemisphere taxa become more common. Norris et al. (1999) listed the disjunct occurrence of 21 boreal to temperate northern hemisphere taxa and 17 bipolar taxa at high altitudes of New Guinea.

4. Comparison of New Guinea and Hunan Province of China: Our results allow a bryofloristic and altitudinal comparison of the Huon Peninsula of New Guinea and Hunan Province of China (Figs. 3–5). The line in the Hunan maps shows the upper limit of the middle meridional (evergreen forest) zone. Based on this fact, of the hepatics: *Acrobolbus ciliatus* (Mitt.) Schiffn. (Fig. 3) is temperate; *Jungermannia comata* Nees, subtropical-meridional (Fig. 3); the very common species *J. truncata* (Mitt.) Amakawa, subtropical-temperate (Fig. 3); *J. virgata* (Mitt.) Steph., subtropical-meridional (Fig. 4); and *Notoscyphus lutescens* (Lehm.) Mitt., subtropical-meridional-temperate (Fig. 4), (but this species has severe taxonomic problems). *Schistochila blumii* (Nees) Trevis. is subtropical-meridional (Fig. 4). Of the mosses: *Palamocladium leskeoides* (Hook.) Britt. is meridional-temperate (Fig. 5); *Rhodobryum giganteum*, meridional-temperate (Fig. 5); and *Racopilum cuspidigerum* (Schwaegr.) Ångstr., tropical-subtropical (Fig. 5). Huon lies at the equator and Hunan at c. 25–30°N. The dots at c. 25°N in Hunan represent Mangshan, the only locality in Hunan that has subtropical elements.

Discussion

The altitudinal mapping of bryophyte distributions is a useful tool in two ways. Firstly, if the altitudinal maps do not correspond, two different taxa may be present. For instance, if a widely distributed species in Hunan occurs only in temperate areas, but is constantly subtropical or tropical on the Huon Peninsula, we can start to suspect the species concept (e.g. *Palamacladium leskeoides*, Fig. 5). There may be two related taxa in question, which can be confirmed by morphological comparison. Secondly, altitudinal distributions may support the vegetation zonal systems created by other parameters such as temperatures and temperature sums. Examples have been published from the northern hemisphere (e.g. Hämet-Ahti et al. 1974).

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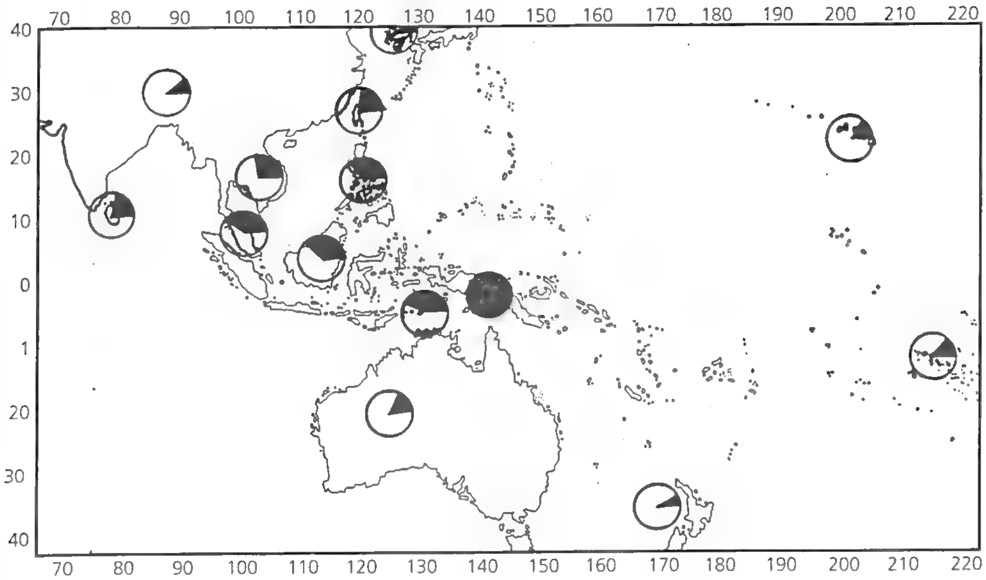

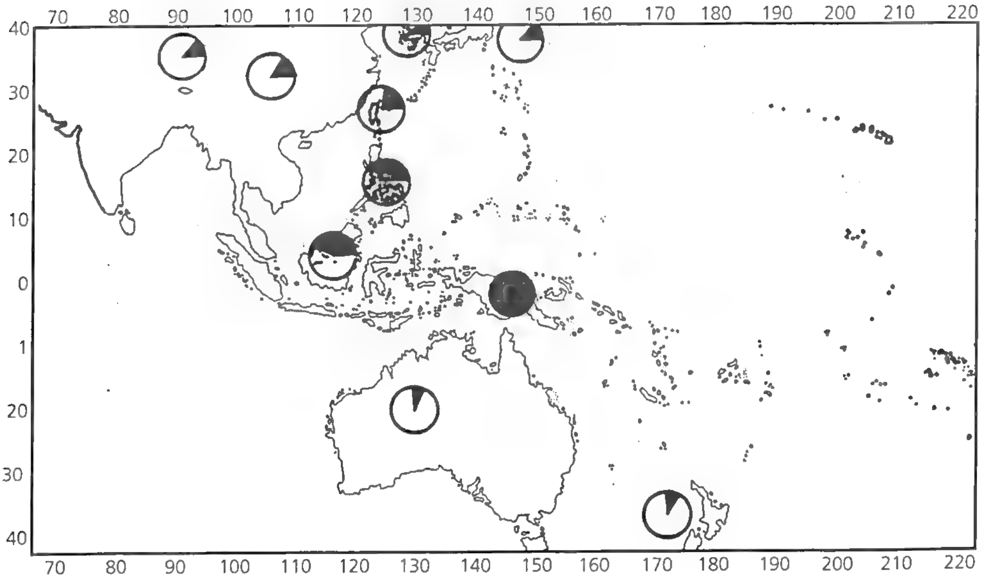

Fig. 2. Affinities of Western Melanesian moss species to other areas studied (above) and affinities of Western Melanesian hepatic species (below). First published in Piippo (1992) and Piippo & Koponen (1997).

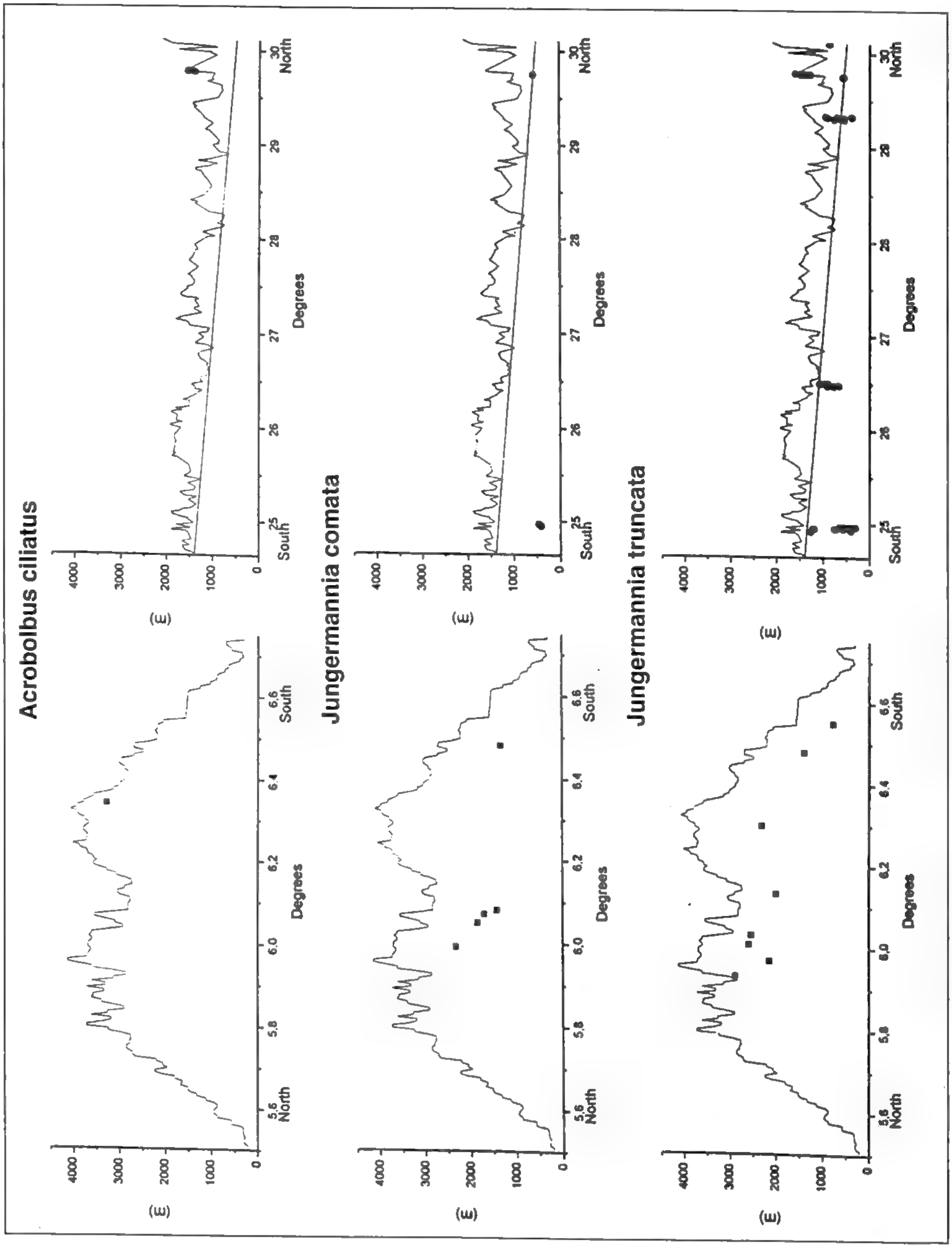

Fig. 3. Vertical distribution of *Acrobolbus ciliatus, Jungermannia comata,* and *J. truncata* on the Huon Peninsula and Hunan Province. The line in the Hunan map shows the upper limit of the middle meridional (evergreen forest) zone. The determinations of *Acrobolbus* and *Jungermannia,* are based on unpublished manuscripts by Koponen et al. and Váňa et al.

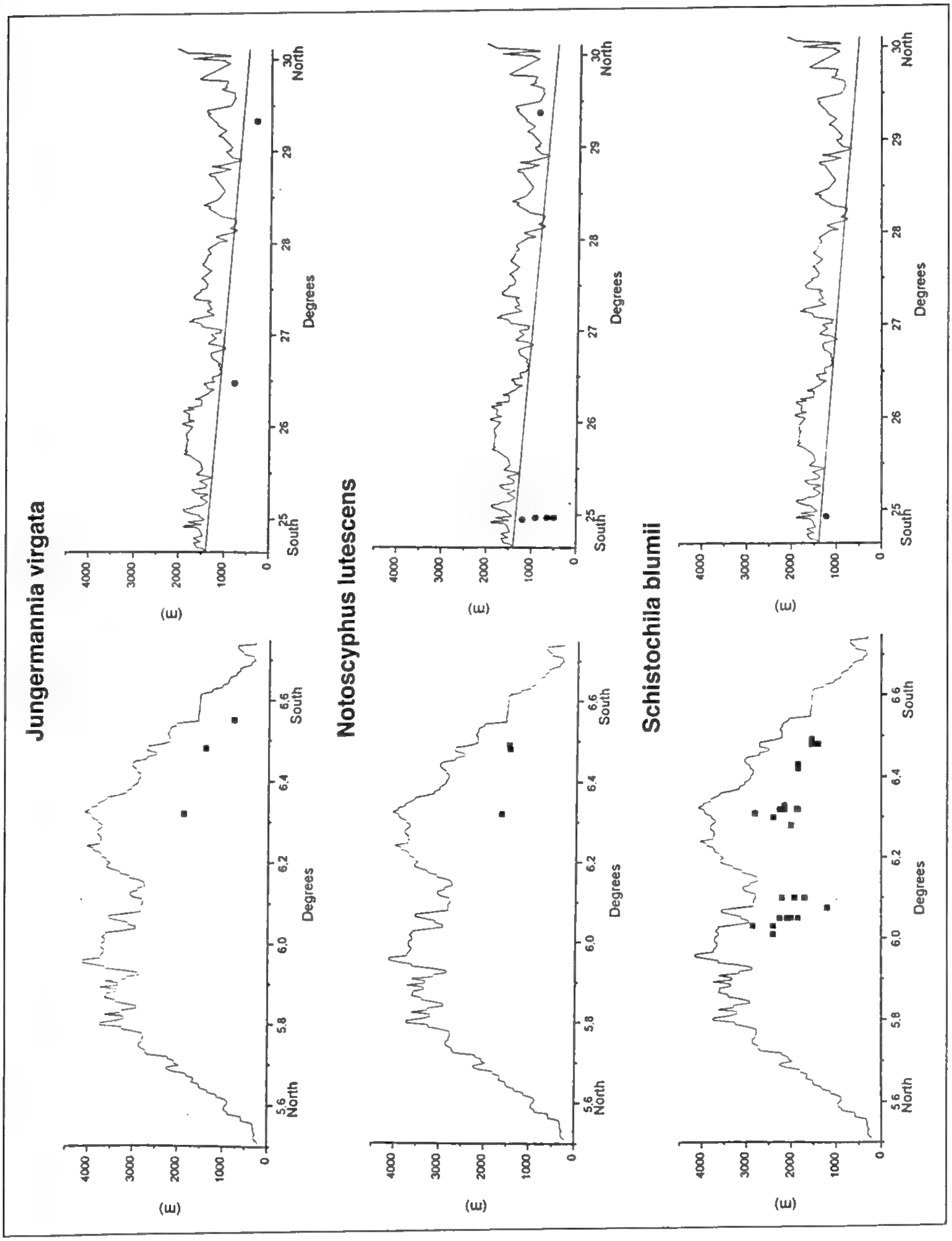

Fig. 4. Vertical distribution of *Jungermannia virgata, Notoscyphus lutescens*, and *Schistochila blumii* on the Huon Peninsula and Hunan Province. The line in the Hunan map shows the upper limit of the middle meridional (evergreen forest) zone. The determinations of *Jungermannia, Notoscyphus* and *Schistochila* are based on unpublished manuscripts by Váňa et al and Koponen et al.

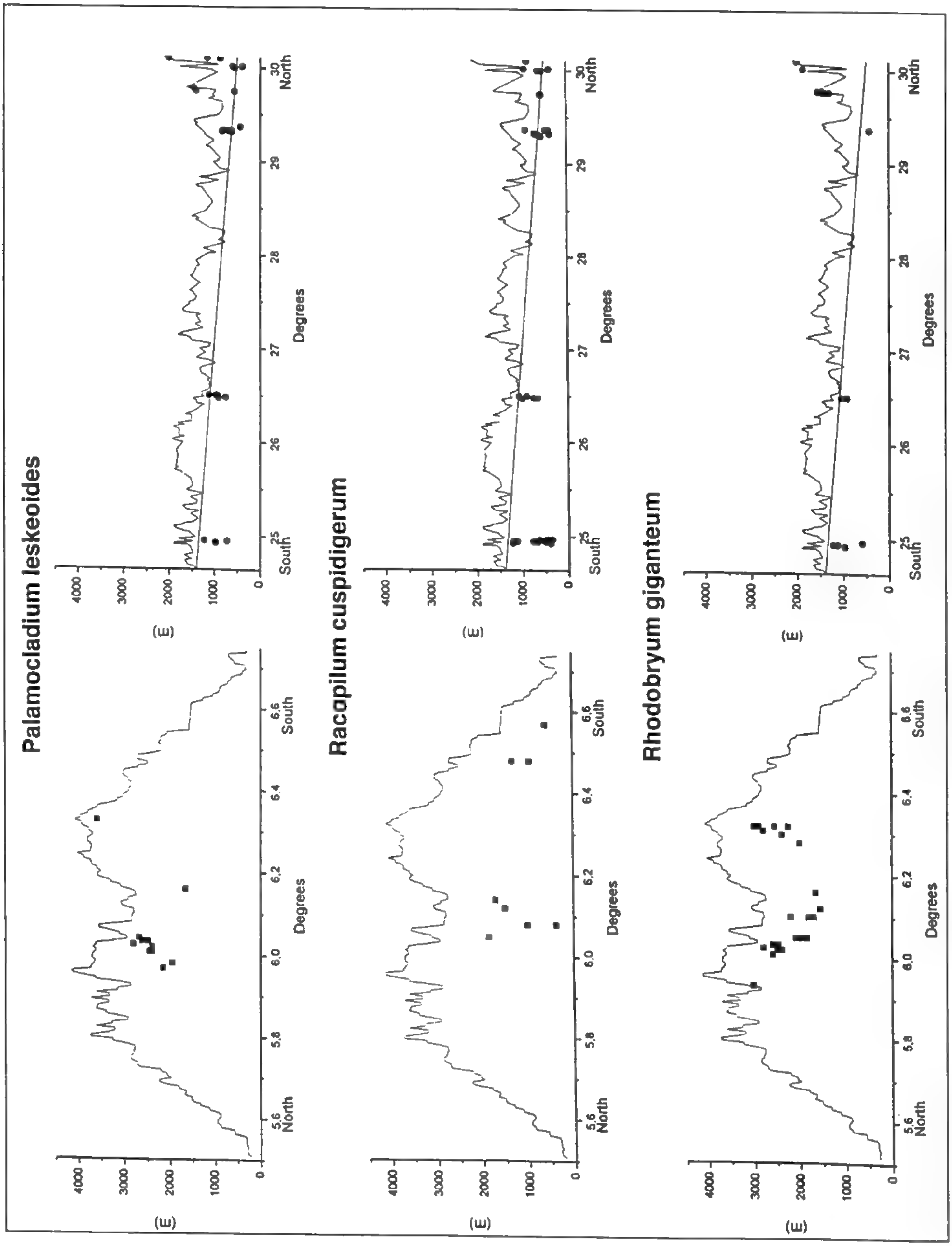

Fig. 5. Vertical distribution of *Palamocladium leskeoides, Racopilum cuspidigerum,* and *Rhodobryum giganteum* on the Huon Peninsula and Hunan Province The line in the Hunan map shows the upper limit of the middle meridional (evergreen forest) zone. The determinations of *Palamocladium, Racopilum* and *Rhodobryum* are based on unpublished manuscripts by Ignatov et al. and Koponen et al.

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Know your enemy: recent records of potentially serious weeds in northern Australia, Papua New Guinea and Papua (Indonesia)

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Abstract

Waterhouse, B.M. (AQIS, PO Box 1054, Mareeba, Qld 4880, Australia) 2003. Know your enemy: recent records of potentially serious weeds in northern Australia, Papua New Guinea and Papua (Indonesia). Telopea *10(1): 477–485.* Botanical collectors rarely specialise in introduced species. Consequently weeds are usually under-represented in herbaria, and comprehensive current checklists of local and regional weed floras are lacking. Potentially serious new weeds are often overlooked until they are widely naturalised and having a harmful impact on agricultural production or the environment. Weed surveys conducted under the auspices of the Northern Australia Quarantine Strategy (NAQS) have documented additions to the weed flora of northern Australia, Papua New Guinea (PNG), and the Province of Papua (Indonesia). New distribution records for the serious tropical weeds *Chromolaena odorata* (L.) R.M. King & H. Rob. (Asteraceae), *Mikania micrantha* Kunth (Asteraceae), *Cleome rutidosperma* DC. (Capparaceae), *Limnocharis flava* (L.) Buchenau (Limnocharitaceae), *Clidemia hirta* (L.) D.Don (Melastomataceae) and *Piper aduncum* L. (Piperaceae), as well as two previously 'unknown' weeds *Chromolaena squalida* (DC.) R.M. King & H. Rob. (Asteraceae) and *Praxelis clematidea* (Griseb.) R.M. King & H.Rob. (Asteraceae) are discussed. Early detection and response to new invaders offers the best opportunity for cost-effective intervention. In PNG and Papua, detection of *Chromolaena odorata* facilitated expansion of an ACIAR-funded biological control program to include these regions. In north Queensland, infestations of *Chromolaena odorata, M. micrantha, L. flava* and *Clidemia hirta* are targets of eradication campaigns. Even though scarce resources and differing priorities prevent responses against every new invader, it is hoped that collection and dissemination of information on the spread of potentially serious weeds will have benefits for the entire region.

Introduction

Weeds are widely regarded as plants growing where they are not wanted and thus have nuisance value. This broad definition encompasses species that are either introduced or native to a region. For purposes of this paper, weeds are defined as introduced plant species that have become naturalised and invasive, with consequent potential for causing economic and environmental harm. Habitat degradation, loss of biodiversity, reduced water quality, animal and crop losses, increased production costs, increased incidence of herbicide resistance, contamination of produce and harmful effects on human and animal health are among the deleterious impacts of weeds.

Early recognition of new weeds presents the best opportunity for timely and cost-effective intervention. Botanists should play an important role in drawing attention to new or recent naturalisations, but weeds are often under-represented in herbarium collections, and up-to-date checklists of local and regional weed floras are lacking. Serious 'new' weeds are often overlooked until they become conspicuous and widespread, by which time it is too late to prevent or mitigate their economic and environmental impacts; where early detection and appropriate response might have provided a different outcome. In northern Australia, botanists working under the auspices of the Northern Australia Quarantine Strategy (NAQS — a sub-program of the Australian Quarantine and Inspection Service), focus on collecting specimens of naturalised species in addition to native taxa. In this way NAQS surveys have provided a unique opportunity to consolidate knowledge of the weed flora of northern Australia, and to supplement and update information on the weed floras in neighbouring regions of PNG and Indonesia. Overseas surveys have also provided NAQS botanists with the opportunity to become familiar with weed species previously thought not to occur in Australia, thus increasing the likelihood of their detection in Australia.

Methods

Target lists

'Target lists' are used to help focus NAQS survey efforts and to promote awareness of potential threats (Mitchell 2001). These are lists of serious pests, diseases and weeds not yet recorded or of very limited extent and under official control in Australia, and known to occur in the adjacent region. Additional information and references for each target species accompany the lists. Regular revision and updating of the information is essential. The current NAQS weed target list (Waterhouse and Mitchell 1998) contains 41 species, several of which have been detected in northern Australia since completion of the list. During surveys attention is paid to any new weed irrespective of whether it is on the target list.

Field surveys

The primary objective of all NAQS survey activities is to detect new threats or incursions before they become well established, thus enabling implementation of preventative or remedial strategies at relatively low cost and with a high probability of success. In northern Australia, multi-disciplinary plant and animal health teams visit coastal and near-coastal settlements at a frequency determined by the perceived likelihood of quarantine incursions. This varies from twice yearly at some high risk Torres Strait islands to once every five years at low risk sites. Disturbed sites around habitation, road verges, cultivated plots, plantations, rubbish dumps, culverts and stream banks are searched thoroughly for weeds. Attention is paid to the vicinity of disembarkation points such as boat ramps and airstrips. Common and well-known weeds are recorded on checklists. Species that are poorly represented in collections, unknown weeds, or weeds thought to be recent arrivals are collected. Voucher specimens are submitted to state and national herbaria for identification or verification and permanent storage. To supplement survey activities, state and local government weeds officers and the general public are also encouraged to submit weed specimens for identification by the NAQS botanists.

Botanists or weed scientists from collaborating organisations in PNG and Indonesia participate in NAQS surveys in those countries. In PNG these survey activities are confined to the western border region of Western and Sandaun Provinces, and the coastal fringe adjacent to the Torres Strait islands. The same procedures are followed for documentation of the weed flora at each site. Local authorities and residents are asked which weeds have the greatest economic or ecological impact, and whether they have noticed any 'new' invaders. Voucher specimens are deposited in the PNG National Herbarium (Lae) or in Herbarium Bogoriense (Bogor).

Important records arising from NAQS surveys

1. Weeds with a 'history' elsewhere

Chromolaena odorata (L.) R.M. King & H. Rob. (Asteraceae)

Chromolaena odorata justifiably has a reputation as one of the world's worst tropical weeds (Holm et al. 1977). Originating from Central and South America, it is an aggressive invader of pastures and plantation crops, and is a major environmental weed, suppressing and smothering underlying vegetation. Seasonal dieback after flowering creates highly combustible fuel, promoting hot fires in vegetation that would otherwise rarely burn, including rainforests. *Chromolaena odorata* is one of the most damaging weed species throughout the Malesian region. In Australia, *C. odorata* would thrive along much of the coastal margin and adjacent hinterland from northwest Western Australia, through the Northern Territory and Queensland to northern New South Wales.

Prior to 1991, *C. odorata* was suspected to be present in Irian Jaya (now Papua) and known to be present in East New Britain (PNG) but had not yet been recorded on the PNG 'mainland'. Its presence near Jayapura and Merauke (Papua) was reported anecdotally in November 1991 and July 1993 respectively (J. Turner pers. comm.) following NAQS surveys for insect pests of crops in Papua. Following up the earlier report from the Jayapura district, a NAQS survey confirmed its presence just east of the PNG border at Wutung and Bewani near Vanimo (Sandaun Province) in June 1992. Voucher specimens were collected and submitted to LAE and BRI, and PNG and Australian authorities were notified. The record from Sandaun Province prompted botanists and weed scientists to search elsewhere, locating infestations near Lae and in other mainland provinces. The population of *C. odorata* has 'exploded' in the vicinity of Jayapura and Vanimo in recent years, probably influenced by deforestation and unusually dry spells (accompanied by fire) during *El Nino* weather cycles. This serious weed now threatens native vegetation, subsistence farming and other agricultural pursuits throughout the region.

The discovery of *C. odorata* in Papua and PNG led to the inclusion of both regions in a pre-existing biological control project funded by the Australian Centre for International Agricultural Research. Since 1997 two agents have been released: a leaf-feeding Arctiid moth *Pareuchaetes pseudoinsulata* Rego Barros in PNG only; and a stem-galling tephritid fly *Cecidochares (Procecidochares) connexa* Macquart in PNG and Papua (Orapa, Bofeng & Donnelly 2000, Wilson & Widayanto 2000). To date, only the fly appears to have established readily. NAQS weed surveys in Papua since 1997 have recorded *C. odorata* in other regional centres including Timika, Nabire and Sorong. It is hoped that local personnel will redistribute populations of the stem-galling fly to these centres.

In July 1994, numerous small to extensive infestations of *C. odorata* were discovered in the vicinity of Bingil Bay and along the lower Tully River valley of north Queensland (Waterhouse 1994). Experience gained previously in PNG ensured instant recognition at this unexpected location. The discovery was reported to Australian authorities and an immediate search of the surrounding district determined that the infestations, while scattered over several hundred square kilometres, were confined to two adjacent catchments. Investigations and the discovery of two other related species from the same region (see below) led to the conclusion that *C. odorata* seeds were accidentally introduced in the late 1960s as a contaminant of pasture seed imported from Brazil. In view of the predicted broad distribution, ecological and economic impacts of *C. odorata* throughout tropical and sub-tropical Australia, a national consultative committee recommended that eradication should be attempted (Waterhouse 1994, 1996). The eradication program commenced in August 1994 and continues with annual reviews. The *C. odorata* population has been reduced substantially using herbicides, fire and mechanical control, although occasional small stands of mature plants continue to be discovered. The presence of viable seed in the soil is problematic and necessitates ongoing vigilance and treatment. To date, the eradication effort has been jointly funded by federal and state governments, including a proportion from those states likely to become infested in the absence of control. Large infestations of *C. odorata* were unexpectedly found on West and Home Islands of the Cocos Keeling group in 2000 (A. Mitchell pers. comm. 2000). It had been misidentified in 1987 and remained so for 13 years.

Mikania micrantha Kunth (Asteraceae)

Mikania micrantha is a rapidly growing perennial vine with small wind-borne seeds. It is native to Central and South America and widely naturalised in the Malesian region where it is regarded as a serious pest of plantations and pastures. Climbing to the canopy, dense infestations shade and inhibit the growth of native vegetation in forest gaps and margins. In Australia its potential distribution includes the more humid coastal regions of the Northern Territory, much of eastern Queensland and extends into northeastern New South Wales. In the weeds literature (eg. Holm et al. 1977), *Mikania micrantha* has been confused with the related species *Mikania cordata* (Burm.f.) B.L. Rob., which is native in South-East Asia and New Guinea. Although the latter species is also weedy, it has probably been displaced across parts of its range in Indonesia by the more aggressive *M. micrantha* (Soekisman Tjitrosemito pers. comm. 1997).

On the basis of specimens lodged at LAE, Henty and Pritchard (1988) noted records of *Mikania micrantha* from Bougainville, New Britain and the Central districts of PNG, suggesting a limited distribution in New Guinea. Recent NAQS surveys have recorded *M. micrantha* in the Merauke, Timika, Nabire and Sorong districts (Papua) and the Vanimo and Tabubil districts of PNG. This species is undoubtedly much more widespread in the region than our records suggest. *Mikania micrantha* is generally regarded as being a weed of the humid tropics. Discovery of a small but expanding infestation of *M. micrantha* in Merauke was unexpected because Merauke has a seasonal wet/dry climate with an average annual rainfall of only c. 1200 mm, mostly falling between December and April. If this infestation persists and spreads, a much larger area of south-western PNG and northern Australia might also be vulnerable to invasion than is predicted by current eco-climatic models.

Although known to occur in Christmas Island, Indian Ocean (Du Puy et. al 1993) *Mikania micrantha* was first recorded in mainland Australia in June 1998, with the discovery of three small infestations at Bingil Bay, Mission Beach and Forrest Beach in north Queensland (Waterhouse 1999). In 2001, several additional infestations were discovered at Speewah and Ingham, also in north Queensland, but the total (known) infested area remains at less than 30 hectares. Several of the infestations abut rainforests of the Wet Tropics World Heritage Area. Although their origin is unclear, the infestations at Bingil Bay, Mission Beach and Forrest Beach were related. At Mission Beach and Forrest Beach plants had been intentionally cultivated for use as an herbal remedy for skin infections (C. Runow pers. comm. 1998). The origin of the Ingham infestation is unknown. Circumstantial evidence suggests a separate introduction to Speewah, possibly as a contaminant of imported palm seeds. All known *M. micrantha* infestations are now targets of an eradication campaign.

Cleome rutidosperma DC. (Capparaceae)

Cleome rutidosperma is a perennial herb native to Africa. It has recently become an important weed of crops and disturbed sites throughout South-East Asia, with particularly rapid expansion of its range in Indonesia (Soerjani et al. 1987). Elaiosomes on the seeds encourage dispersal by ants, and plants are often observed growing as epiphytes on cliff faces, stone walls and trees. *Cleome rutidosperma* was discovered for the first time on the New Guinea landmass during recent NAQS surveys in Papua, where it was recorded as a weed of annual crops (eg. peanuts), abandoned cultivation, roadsides and amenity areas in Jayapura, Merauke, Timika, Nabire and Sorong. Although not yet recorded from PNG, it will probably spread eastwards across the border as an accidental contaminant with cross-border traffic.

Several small populations of *C. rutidosperma* infesting an area of less than 10 hectares were discovered in Darwin, Northern Territory by NAQS botanist A. Mitchell in August 2000. In low numbers this species is relatively cryptic and difficult to locate amongst other herbaceous vegetation, so other infestations may remain undetected. Work has commenced to eradicate the infestations (A. Mitchell pers. comm 2000). *Cleome rutidosperma* has not yet been recorded elsewhere in mainland Australia, although it is reported as locally common in Christmas Island, Indian Ocean (Du Puy & Telford 1993).

Limnocharis flava (L.) Buchenau (Limnocharitaceae)

Limnocharis flava is a clump-forming, perennial, aquatic herb native to Central and South America. Seeds and vegetative plantlets are dispersed by flowing water. Possessing attractive foliage and flowers it was probably introduced to the Malesian region as an ornamental species. It has subsequently naturalised and become a serious weed in padi rice, irrigation canals and wetlands in South-East Asia, where it is sometimes also cultivated as a green vegetable or pig fodder. Its potential distribution in Australia encompasses the humid tropical regions of the Northern Territory and Queensland.

Soerjani et al. (1987) noted that *Limnocharis flava* had not yet been reported from Irian Jaya (Papua). NAQS surveys in Papua in 1997 and 1999 recorded cultivated and naturalised populations of *L. flava* in the Jayapura, Merauke, Timika, Nabire and Sorong districts. It was probably intentionally introduced by Javanese transmigrants. Movement across the border into PNG as a source of food is inevitable, if it isn't there already. When allowed to grow unchecked, *L. flava* is a very invasive environmental weed of streams and wetlands. The RAMSAR-listed wetlands in Wasur National Park and the contiguous Tonda Conservation Area around the Bensbach River floodplain in PNG will be under direct threat of invasion if *L. flava* becomes widely established east of Merauke.

Limnocharis flava was recorded for the first time in Australia in June 2001, when several cultivated plants were discovered in an ornamental pond near Cairns, north Queensland. The source was traced to a wild population in a Cairns lake. Publicity about its potential weed status led to further detections in the Cairns and Townsville districts. The known infestations occupy an area of less than 3 hectares, but other plants are almost certainly lurking in suburban gardens and there may be undiscovered wild populations. *Limnocharis flava* has become the focus of an eradication campaign where plants are removed by hand and destroyed by deep-burial. Infested sites will require regular ongoing inspection to locate and remove seedlings.

Clidemia hirta (L.) D.Don (Melastomataceae)

Clidemia hirta is a highly invasive shrub that is a pest of plantations and pastures and a serious environmental weed in humid tropical regions. Native to Central and South America it is widely naturalised in the Malesian region and Pacific islands. To date there have been no formal records of its occurrence in either Papua or mainland PNG, although Henty and Pritchard (1988) state that *C. hirta* had been reported recently from southern Bougainville. It is likely to have established elsewhere in New Guinea. Its potential distribution in Australia includes humid coastal sites in the Northern Territory and much of northeast Queensland.

Clidemia hirta was discovered for the first time in Australia in August 2001. A tiny infestation of at least several hundred plants was found at Julatten, north Queensland, while searching for *Mikania micrantha* (as follow-up to the recent discovery at Speewah). Avian and flood-borne dispersal of seeds was evident, with mature plants and seedlings scattered throughout a former palm nursery and along the banks and bed of an ephemeral stream running through the property. The source and duration of the infestation have not been determined. Every observed *C. hirta* plant was destroyed during a search of the area, but the characteristics of shade tolerance and bird-dispersed seed have increased the difficulty of detection of all plants. The infested area abuts extensive tracts of rugged forested land in the Wet Tropics World Heritage Area. Regular follow-up to locate and destroy seedlings, accompanied by an effective awareness campaign, will be essential for successful eradication.

Piper aduncum L. (Piperaceae)

Piper aduncum L. is a shrub or small tree, native to Central and South America but now naturalised and invasive in South-East Asia and some Pacific islands. Henty and Pritchard (1988) reported that it was already widespread at low elevations in New Guinea. Outside its native range it has been cultivated as an ornamental shrub, and the timber is reported to have been used to manufacture match-sticks in Papua (D. Suweny pers. comm. 2002). NAQS surveys have recorded *P. aduncum* near Jayapura, Nabire and Sorong in Papua, and the Vanimo, Tabubil and Lae districts of mainland PNG. We have also recorded it in the early stages of invasion in southern Bougainville. Anecdotal evidence suggests that it is much more widespread in both regions. *Piper aduncum* is a serious environmental weed. Mature plants often comprise multiple vertical stems arising from a horizontal stem growing across the surface of the ground. Dense infestations thus become impenetrable. Individual fruiting spikes contain huge numbers of tiny seeds that are dispersed by birds and mammals, and as contaminants of vehicles and logging equipment (Waterhouse & Mitchell 1998). 'Wheatfield' regeneration of *P. aduncum* seedlings has been observed along roadsides, and in forest clearings in the Vanimo district. It rapidly invades disturbed sites and recently logged forests. At sites near Lae, *P. aduncum* has been reported to out-compete *Chromolaena odorata* (W. Orapa pers. comm. 2001).

Piper aduncum has not yet been recorded on the Australian continent, but is expected to be invasive in humid coastal regions of northern Australia. Recognition of its potential weed status in Australia has facilitated recent placement of *P. aduncum* on national and Queensland 'Prohibited plant' lists. However, like each of the other weeds discussed above, it may be already present and awaiting discovery. Du Puy (1993) recorded *P. aduncum* as a naturalised species on Christmas Island, Indian Ocean. A small population of about ten plants was still present there in 2000 (A. Mitchell pers. comm. 2001).

2. Previously 'unknown' weeds

Chromolaena squalida (DC.) R.M. King & H.Rob. (Asteraceae)

State government officers responsible for the eradication of *Chromolaena odorata* from north Queensland, discovered a 0.5 hectare infestation of an unrecognised shrub, within the eradication zone. Leaf and flower morphology suggested that it might be a species of *Chromolaena*, but these plants were small (to 1.5 m tall), usually single-stemmed and generally did not appear to be invasive. Specimens could not be identified at Queensland Herbarium and were subsequently identified at the Smithsonian Institute as *Chromolaena squalida*, not previously recorded outside its native range in S. America (H. Robinson pers. comm. 2001). There is little doubt that *C. squalida* also arrived in north Queensland as a contaminant of pasture seeds imported from Brazil. Although it does not appear to be as serious a weed as its congener, it has been included in the *C. odorata* eradication campaign.

Praxelis clematidea (Griseb.) R.M. King & H.Rob. (Asteraceae)

Praxelis clematidea is a relatively unknown weed, which poses an imminent threat of invasion to the Malesian region. It is an annual or short-lived perennial herb native to South America. Its native range overlaps with that of *Chromolaena odorata* and *Chromolaena squalida* in southern Brazil. It had not been recorded outside its native range until 1993/1994 when specimens from the Innisfail and Tully districts of north Queensland and Hong Kong were identifed almost simultaneously at KEW (N. Hind pers. comm.). Ironically, although *P. clematidea* had probably been present at both locations for at least 10 years, correct identification was delayed because it had been mistaken for the widespread and common species *Ageratum conyzoides* L. and *Ageratum houstonianum* Mill. (Waterhouse & Corlett 1996, Waterhouse 2000). Veldkamp (1999) has published a description and ecological notes about *P. clematidea* (under the name *Eupatorium catarium* Veldk) to help draw attention to its imminent arrival in South-East Asia.

In the Hong Kong region, *Praxelis clematidea* has also been recorded in neighbouring southern China and Macau and in Taiwan. (J.F. Veldkamp pers. comm.). The origin of the Hong Kong and neighbouring infestations is unknown. The most plausible explanation for the introduction of *P. clematidea* to north Queensland is that it was also a contaminant of pasture seeds imported from Brazil, along with *Chromolaena odorata* and *Chromolaena squalida*. However, if this assumption is correct, *P. clematidea* has demonstrated greater dispersal and establishment capacity than *C. odorata* over a similar timeframe, and is now abundant in the region between Townsville and Mossman (latitude 16°–19.5° S), including the Atherton Tablelands. This area encompasses sites from near sea level to 800 metres elevation, and average annual rainfall 900–4000 mm. Frost resistance has been demonstrated in Hong Kong and is suggested by occurrence of plants on higher parts of the Atherton Tableland. NAQS surveys have recently recorded small infestations at remote sites in Cape York Peninsula and on Thursday and Badu islands in Torres Strait. *Praxelis clematidea* is rapidly approaching New Guinea from the south!

In north Queensland, *Praxelis clematidea* is an abundant weed of roadsides, stream banks and pastures. It encroaches upon sugarcane plantations and other cultivated areas and is able to invade the understorey of relatively undisturbed woodlands. Seeds are readily spread as contaminants of vehicles, building and landscaping materials and garden mulch. Air-borne seed dispersal also seems to be effective over short distances.

In this case, *Praxelis clematidea*'s lack of 'history' as a weed, and the fact that it was already widespread by the time it was correctly identified, means that it was not considered as a suitable candidate for eradication (or indeed any response). Landholders and concerned botanists are seeking implementation of local control measures to prevent or delay its further spread. It now threatens much of northern Australia (including more southerly parts of Queensland and northern New South Wales), New Guinea, South-East Asia and the Pacific Islands.

Discussion

Early recognition and reporting of new weeds can lead to implementation of eradication or control programs at an early stage in the invasion process. By actively seeking, collecting and reporting weedy taxa, individual botanists can make a huge difference to the ecological and economic future of a region. For example, the early recognition and reporting of *Chromolaena odorata* in Queensland, probably represents a saving of millions of dollars annually (in the long term) and means that this species is unlikely to become a widespread and intractable pest in northern Australia (at least in the foreseeable future). Up-to-date inventories of the weed flora, validated by voucher specimens in major herbaria are essential for prioritising weed management activities in any region.

The relatively brief and infrequent NAQS surveys in Papua and PNG are unlikely to identify every new weed that has arrived, but hopefully will help draw attention to some of the major and emerging weed problems in the region.

Acknowledgments

Congratulations are due to the Australian Quarantine and Inspection Service for having the foresight to implement and continue to support 'early warning' surveys for weeds and other pests in northern Australia and adjacent regions. I would also like to thank our collaborating organisations in Papua and PNG who have facilitated surveys in those regions. Finally I would like to acknowledge the exceptional efforts of personnel in Queensland Natural Resources and Mines, who are responsible for a daunting list of eradication efforts. Collection and identification was the easiest part of the process!

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Recognition of cryptic species in the *Asplenium nidus* complex using molecular data — a progress report

Yoko Yatabe and Noriaki Murakami

Abstract

Yatabe, Yoko and Murakami, Noriaki (Department of Botany, Graduate School of Science, Kyoto University, Kitashirakawa-Oiwake-cho, Kyoto 606-8502, Japan) 2003. Recognition of cryptic species in the Asplenium nidus *complex using molecular data — a progress report.* Telopea *10(1): 487–496. Asplenium nidus* is an epiphytic fern species with large simple leaves found throughout the Old World tropics. A large amount of variation of *rbc*L sequences found in plants identified as *A. nidus* sensu Holttum (1974), suggested that multiple cryptic species might be within this species. We tested this hypothesis using *rbc*L sequences. In previous studies, we found five *rbc*L sequence types from populations of *A. nidus* in West Java, Indonesia. Based on ecological comparison and allozyme analysis, it is suggested these five *rbc*L types may be potential cryptic species. Crossing experiments among these *rbc*L types revealed that they are also reproductively isolated. Here we extend the investigation area from West Java to the West Malesian region in order to evaluate furthur the species diversity in the *A. nidus* complex. In this paper, we review our previous studies on recognition of cryptic species in the *A. nidus* complex and report our recent progress.

Introduction

In systematic research on the homosporous ferns, data from cytotaxonomic and enzyme electrophoretic studies have uncovered cryptic species in many lineages such as *Adiantum, Botrychium,* and *Pityrogramma* (see Paris et al., 1989). Recently, in various fern species such as *Asplenium nidus, Hymenasplenium obliquissimum, H. cheilosorum* (Aspleniaceae), *Stegnogramma pozoi* (Thelypteridaceae), *Osmunda cinnamomea, O. claytonia, O. regalis* (Osmundaceae) and *Cheiropleuria bicuspis* (Dipteridaceae), a large amount of *rbc*L sequence variation has been reported (Murakami et al. 1998a, Murakami et al. 1998b, Yatabe et al. 1998, Yatabe et al. 1999, Kato et al. 2001). The substitution rates of *rbc*L in Osmundaceae were estimated to be on average approximately 7×10^{-8} nucleotide substitutions per year (Yatabe et al. 1999). Considering this slow evolutionary rate for *rbc*L, the large amount of *rbc*L sequence variation within a single morphological species may suggest that these species contain several cryptic species that are reproductively isolated from each other. Here we have tried to recognize cryptic species in ferns using chloroplast DNA, including *rbc*L sequences in *Asplenium nidus.*

Asplenium nidus is assigned to *Asplenium* sect. *Thamnopteris,* a group of epiphytic ferns with simple leaves, found throughout the Old World tropics. In this group, only tetraploid species (2n = 144) have been recorded so far (Bir 1960, Abraham et al. 1962, Koul 1970, Kawakami 1970, Tsai & Shieh 1983, Yatabe et al. 2001). Murakami et al. (1999a) examined *rbc*L sequences of this group and found that the difference among *rbc*L sequences reached 4–5% in plants identified as *A. nidus* sensu Holttum (1974). We tested the hypothesis that *A. nidus* may contain several cryptic species using *rbc*L sequences as a first step. In West Java, five *rbc*L sequence types were found from plants identified as *A. nidus* according to Holttum's (1974) classification (Murakami et al. 1999b). We call these *rbc*L types A, B, C, D and E. From phylogenetic analysis, these five *rbc*L sequence types turned out to be distantly related in *Asplenium* sect. *Thamnopteris* (Murakami et al. 1999b, Fig. 1). If each *rbc*L sequence type is a biologically distinct assemblage, we can conclude that *A. nidus* contains several cryptic species.

In order to clarify whether these *rbc*L types are ecologically differentiated, their habitats were compared. The results suggest that the habitats of these five *rbc*L types differ in altitude or in the position where they grow on the tree trunk, although the boundaries of the habitat were not necessarily clear (Murakami et al. 1999b, Yatabe et al. 2002, Fig. 2). In order to clarify whether *rbc*L sequence types are genetically differentiated in their nuclear genomes, we examined allozyme polymorphism using the Single Strand Conformation Polymorphism (SSCP) method. The results showed some loci where the allele frequencies significantly deviated from each other for every pair of the *rbc*L types (Yatabe et al. 2002). Nei's genetic distance (D) and genetic identity (I) were also calculated among *rbc*L types (Table 1). Soltis and Soltis (1989) reported the range of genetic identity (I) between congeneric species to be 0.00–0.85, and between conspecific populations of homosporous pteridophytes to be 0.78–0.996. All of the genetic identity (I) estimated fell into the range of that between congeneric species though the value estimated between Type C and E fell into the range of that between conspecific populations as well. Thus, it is suggested that the five *rbc*L types distributed in West Java are ecologically and genetically well differentiated, separate species.

Table 1. Genetic Identity (above diagonal) and genetic distance (below diagonal).

	A	B	C	D	E
A	-	0.599	0.702	0.596	0.659
B	0.513	-	0.621	0.379	0.693
C	0.353	0.476	-	0.401	0.806
D	0.517	0.970	0.913	-	0.516
E	0.417	0.366	0.215	0.663	-

Yatabe et al. (2001) also conducted artificial crossing experiments among *rbc*L types. These artificial crossing experiments were designed to examine the frequencies of hybrid formation, and the allozyme polymorphisms were used to identify hybrid plants based on their heterozygous patterns combining those of their parents. Details are provided in Yatabe et al. (2001). The results of five data sets showed that the pairing of Type A and B fail to form hybrid plants and that these are reproductively isolated. It has also been suggested by the results of the same artificial crossing experiments that hybrid plants may not be formed between Type A and C (Yatabe et al. 2001), B and C, and C and E (unpublished data). Thus, the plants classified as *A. nidus* consist of several cryptic species, and *rbc*L sequences are useful as a first step to recognize cryptic species in *A. nidus*.

It becomes, however, more difficult to interpret the molecular data when we extend our investigation area and take the allopatric populations into consideration. Now we are investigating cryptic species distributed in West Malesia as well as West Java. In order to clarify the distribution of the potential cryptic species found from West Java, it is necessary to investigate the distribution of the *rbc*L types in areas adjacent to West Java. In this paper, we report the results of investigation at two areas in West Malesia, the Malay Peninsula and West Sumatra (Fig. 1).

By comparing the habitats of *rbc*L types distributed in the Malay Peninsula and West Sumatra, we addressed the following questions: 1) Is ecological differentiation observed among *rbc*L types in these areas as well as West Java? 2) Do individuals of the same *rbc*L type keep their habitat preference constant throughout their distribution area?

Materials and Methods

Materials

Between 1997 and 2002, we collected fresh leaves from 87 and 37 individuals of *Asplenium nidus* in the Malay Peninsula and West Sumatra, respectively. We also collected fresh leaves from 26 individuals in West Java in addition to the 40 individuals in a previous study (Yatabe et al. 2002). For all the individuals collected from West Java and West Sumatra, and 73 individuals collected from the Malay Peninsula, we recorded their habitats, such as altitude and position on the tree trunk where they grew. Details of the localities are provided in Table 2. We used small parts of fresh leaves for *rbc*L sequencing and kept the rest as vouchers in the herbarium of the Graduate School of Science, Kyoto University (KYO). Full voucher details will be available on completion of the project.

Fig. 1. Map of the West Malesian region. **WJ**, West Java, **WS**, West Sumatra, **PM**, Malay Peninsula.

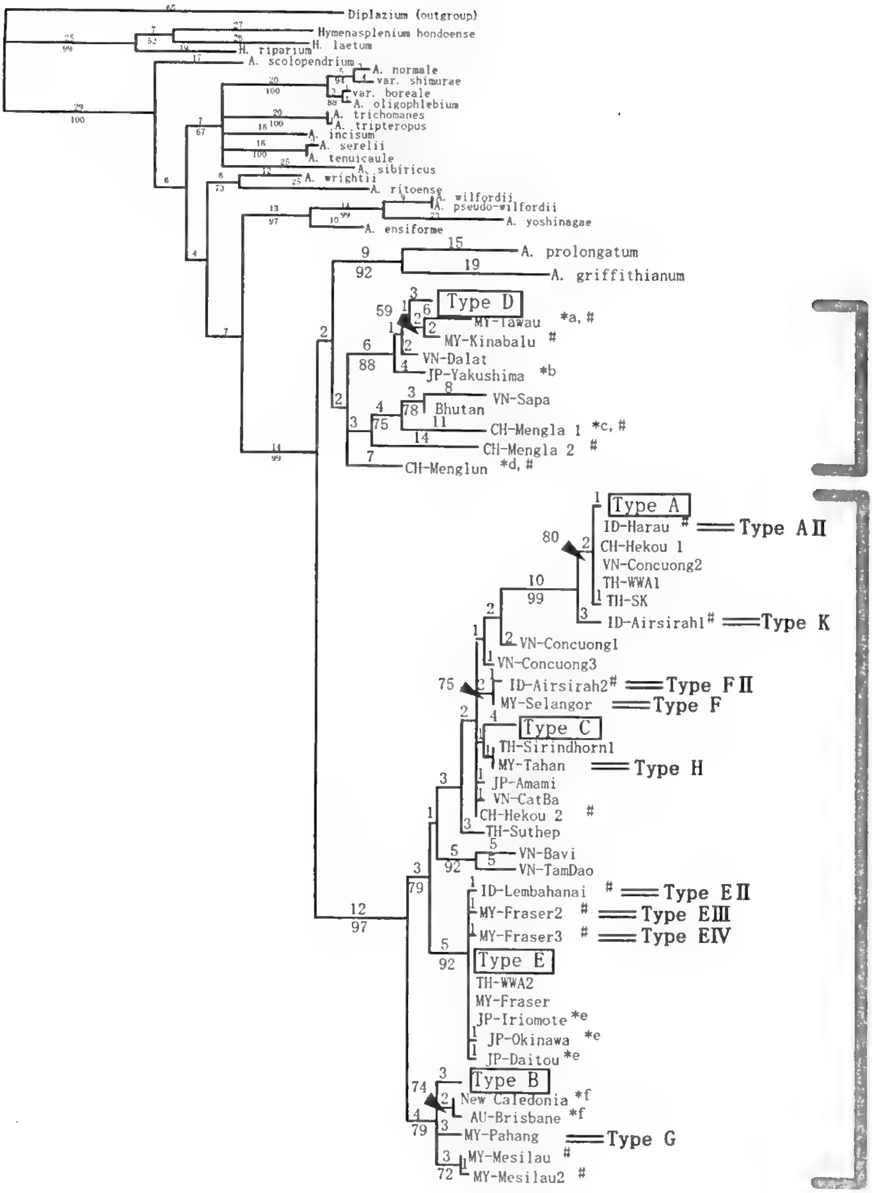

Fig. 2. The strict consensus of the four most parsimonious trees (length = 700 steps; consistency index = 0.587; retention index = 0.815) obtained in the phylogenetic analysis using PAUP ver. 3.1.1 based on the *rbc*L sequence data of *Asplenium* sect. *Thamnopteris*. Information on each accession is available in Yatabe et al. (2001) except for those indicated by #. The numbers above and below the branches are the number of nucleotide substitutions (ACCTRAN optimisation) and bootstrap percentages respectively. *a is identified as *A. cymbifolium*; *b as *A. antiquum*; *c as *A. phyllitidis*; *d as *A. antrophyoides*; *e as *A. setoi*; *f as *A. australasicum*.

Table 2. *Rbc*L sequence type and the number of individuals of each *rbc*L sequence type found in the West Malesia region.

Locality	*rbc*L sequence type (number of individuals)
West Java	
Halimun National Park, West Java, Indonesia*	A(n=16), B(n=10), C(n=15), D(n=8), E(n=4)
Gunung Gede Pangrangro National Park, West Java	C(n=22), D(n=8)
Bogor Botanical Garden, West Java*	E(n=5)
Malay Peninsula	
Cameron Highland, Malaysia	AII(n=1), E(n=17), F(n=27), G(n=9), H(n=5)
Fraser's Hill, Malaysia	AII(n=3), E(n=12), EIII(n=1), EIV(n=1), F(n=5), G(n=2)
Mt. Tahan, Malaysia	E(n=1), F(n=1)
Kuala Lumpur	G (n=2)
West Sumatra	
within a radius of 50 km from Padang City, West Sumatra, Indonesia	AII(n=2), E(n=11), EII(n=1), F(n=12), FII(n=1), G(n=3), K(n=4)
Lembah Harau Natural Reserve, West Sumatra, Indonesia	AII(n=2), E(n=3)

*indicates the data provided in the previous study (Yatabe et al. 2002)

*Rbc*L sequencing

Total DNA was extracted using a 2X CTAB (hexadecyl trimethyl ammonium bromide) solution according to the method of Doyle and Doyle (1987). PCR (polymerase chain reaction) amplification of *rbc*L fragments followed Murakami et al (1999a). The PCR products were purified using a GENE CLEAN III kit (BIO101, Vista, California, USA) after electrophoresis in 1.0% agarose gel, and then used as templates for direct sequencing. Sequencing reactions were prepared using a Big Dye terminator cycle sequencing kit (Perkin Elmer Applied Biosystems, Foster, California, USA). The reaction mixtures were analyzed on an Applied Biosystems Model 377 automated sequencer (Perkin Elmer Applied Biosystems). For phylogenetic analyses, sequences were aligned using Sequence Navigator Software (Perkin Elmer Applied Biosystems). GenBank numbers will be published on completion of the project.

Phylogenetic analysis

The *rbc*L sequence data matrix contained data from 68 accessions, including that of *Diplazium esculentum* and those of 22 species in Aspleniaceae other than those of the *Asplenium nidus* complex. *Diplazium esculentum* (Woodsiaceae) was used as the outgroup. Phylogenetic analysis was performed by the Maximum Parsimony method using PAUP (Phylogenetic Analysis Using Parsimony) version 3.1.1 (Swofford 1993). A branch and bound search was conducted to find the most parsimonious trees. A bootstrap analysis with 10 000 replications was performed in order to estimate the reliability for various clades.

Results

*Rbc*L types in West Java, Malay Peninsula and West Sumatra

We determined *rbc*L nucleotide sequences of 1194 bp for a total of 192 individuals and found 14 *rbc*L types including the five types reported from West Java – Types A, B, C, D and E. We named the other types as Type AII, EII, EIII, EIV, F, FII, G, H, and K. The number of individuals of each *rbc*L type found from each locality are shown in Table 2. We found only a small number of individuals, one to four, of Type EII, EIII, EIV, FII, H and K. In Mt. Gede, West Java, we found two types, Type C and D, which had been already found from Mt. Halimun National Park. In the Malay Peninsula and West Sumatra, seven and six types were found, respectively. Four types, AII, E, F and G, were distributed in both the Malay Peninsula and West Sumatra. While Type E was found from the Malay Peninsula and West Sumatra as well as West Java, the other four types reported from West Java (A, B, C and D) have not been found from these other areas.

Phylogenetic analysis

For phylogenetic analysis, we used 1191 nucleotide characters because the outgroup did not show 1194 bp nucleotides. This gave 75 equally most parsimonious trees (length = 700 steps; consistency index = 0.587; retention index = 0.815). The strict consensus tree with bootstrap percentages is shown in Fig. 2. The general topology of the tree for Aspleniaceae is the same as that in Murakami et al. (1999c). The plants identified as *Asplenium nidus* were, however, not supported as a monophyletic group because *A. griffithianum* and *A. prolongatum* were nested within the *A. nidus* complex (Fig. 2). In *A. nidus* two major clades were formed, one clade (Clade B) which has high bootstrap support (97%), includes *A. australasicum* from New Caledonia and Australia, *A. setoi* from Japan and *A. nidus* from various localities in Asia (Fig. 2). The sequence of *A. setoi* from Iriomote Is. is the same as that of Type E. The other clade (Clade A) which is closely associated with *A. griffithianum* and *A. prolongatum*, includes *A. antiquum* from Japan, *A. cymbifolium* from West Malesia, *A. phyllitidis* and *A. antrophyoides* from China, and some populations of *A. nidus* from Asia, including West Malesia, Bhutan and Vietnam (Fig. 2).

Ecological observation

The altitude where the individuals grew, and the distribution of each *rbc*L type in West Java, the Malay Peninsula and West Sumatra, is shown in Figs 3, 4 and 5, respectively. On Mt. Gede, West Java, at altitudes above 1400m, we found the two types, Type C and D, which had been found above 1300m in Mt. Halimun National Park, West Java (Fig. 3). In Mt. Gede and Mt. Halimun National Park, Type D was not found below 1600 m (Fig. 3). Type C and D were not found in the Malay Peninsula or West Sumatra.

Type E, found in areas lower than 1100 m alt. in West Java, was found in the Malay Peninsula and West Sumatra. In the Malay Peninsula or West Sumatra, Type E was not found above 1200m (Figs 4, 5). Besides Type E, Type AII, F and G were found in both the Malay Peninsula and West Sumatra. All but one individual of Type G were found at altitudes lower than 600m, and the only individual found at 1100m in Cameron Highland, the Malay Peninsula, was a sterile plant without sori (Fig. 4). Type AII was found at altitudes below 1000m (Figs 4, 5) and always grew on tree trunks below the 2 m level. In striking contrast to Types AII, E and G, Type F was found at higher elevations in the Malay Peninsula and West Sumatra (Figs 4, 5).

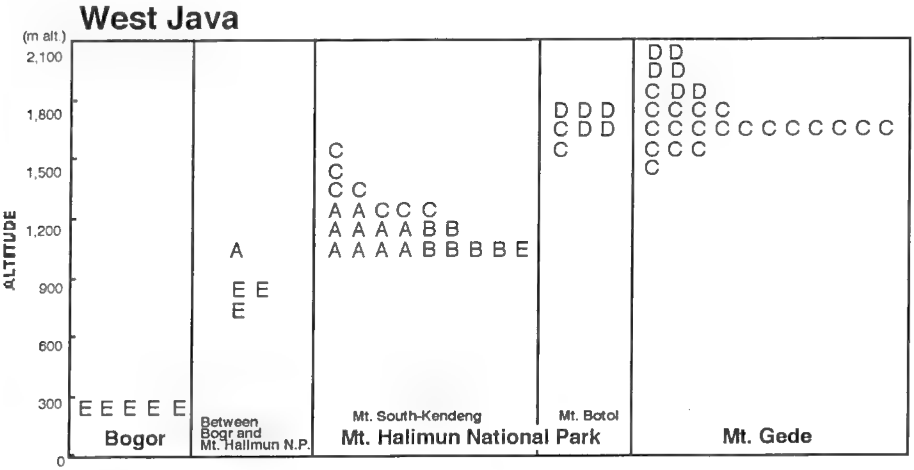

Fig. 3. The distribution of each *rbc*L type in West Java. The *rbc*L type is indicated for each individual examined. Each *rbc*L type is concordant with those in Fig. 2.

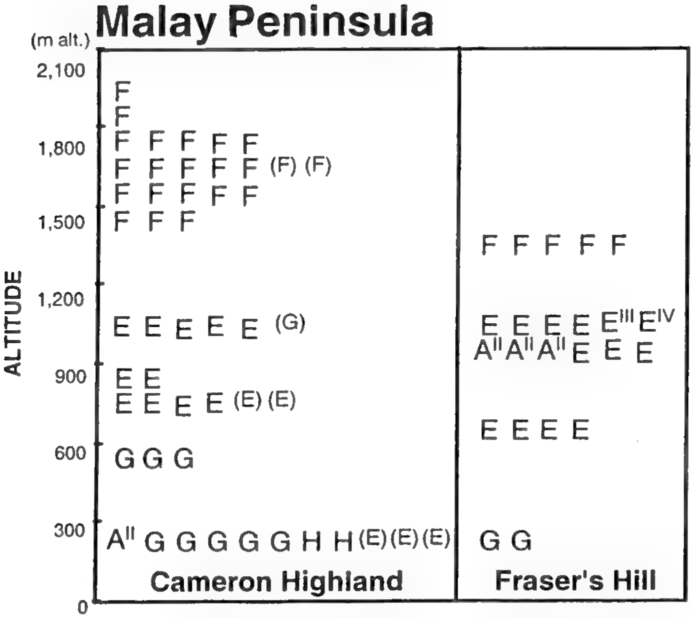

Fig. 4. The distribution of each *rbc*L type in the Malay Peninsula. The *rbc*L type is indicated for each individual examined. Parentheses indicate the individuals that lack sori. Each *rbc*L type is concordant with those in Fig. 2.

Discussion

DNA sequence data have been used for analysing phylogenetic relationships among species, or higher taxa. In particular, maternally inherited chloroplast DNA was considered to be appropriate for phylogenetic analysis from many aspects. One of the superior features of chloroplast DNA is its small effective population size, which is one quarter of that of nuclear DNA. Since genetic drift excludes genetic variation from a gene pool more effectively in chloroplast DNA than in nuclear DNA, it is less feasible that ancestral polymorphism and lineage sorting cause disagreement between a gene tree and a species tree (Moore 1995). In recognising reproductively isolated assemblages, chloroplast DNA, where variations are efficiently excluded, may provide appropriate information as well. In previous studies, using *rbc*L sequences as the first step, we recognized five potential cryptic species in the populations of *Asplenium nidus* in Mt. Halimun National Park and the surrounding area (Murakami et al. 1999b, Yatabe et al. 2001, Yatabe et al. 2002). It was suggested that these potential cryptic species would be ecologically and genetically differentiated, and some pairs of them have been already tested for reproductive isolation by artificial crossing experiments. Thus, *rbc*L sequences may be useful as a first step in revealing cryptic species hiding in the populations of *A. nidus* at particular localities.

It is, however, necessary to take allopatric populations into consideration as well as sympatric and parapatric populations in order to evaluate species diversity in *Asplenium* sect. *Thamnopteris*. As a result of our investigations in the Malay Peninsula and West Sumatra show, Type E turns out to be widely distributed in lowland areas of West Malesia. In addition to this the *rbc*L sequence of *A. setoi* from Iriomote Is. was found to be the same as that of Type E. In order to clarify the relationship between *A. setoi* distributed in Japan and Type E found from West Malesia, further investigations, such as artificial crossing experiments and morphological comparisons, will be required. The other four types found from West Java, Type A, B, C and D, have not

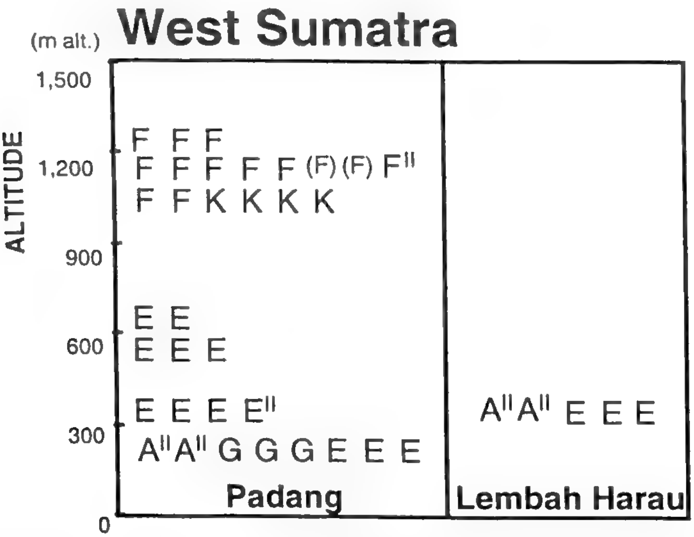

Fig. 5. The distribution of each *rbc*L type in West Sumatra. The *rbc*L type is indicated for each individual examined. Parentheses indicate the individuals that lack sori. Each *rbc*L type is concordant with those in Fig. 2.

been found outside West Java. Therefore, the geographical distributions of these four potential cryptic species are still unknown.

In the Malay Peninsula and West Sumatra, we also investigated the habitat in the same way as we did in West Java (Murakami et al. 1999b, Yatabe et al. 2002, Fig.2). In West Java, the habitats were well differentiated between the five *rbc*L types in altitude or in position on the tree, though the boundaries of the habitat were not necessarily clear. Also in the Malay Peninsula and West Sumatra, differences in habitat among *rbc*L types were observed. The four types, Type AII, E, F and G, were distributed in both the Malay Peninsula and West Sumatra (Table 2). The habitat of Type F was suggested to differ in altitude from the other three types, Type AII, E and G (Figs 4, 5). The difference in habitat between Type F and the other three types was clear because Type F was never found at the same elevation as the other three types. Type F was, however, found together with Type FII in the Malay Peninsula and with Type K in West Sumatra, so ecological comparison will be required between these sympatrically distributed pairs of *rbc*L types. Ecological differentiation between Type E and G was obscure because these two types were sometimes found together at the same elevation. As far as the distribution of mature individuals of these two *rbc*L types is concerned, Type G has an inclination to grow at a lower elevations than Type E does (Figs 4, 5). When we take it into consideration that an immature plant was found at an altitude of 1100m in the Malay Peninsula (Figs. 4), it is possible that Type G may grow well at lower elevations than Type E. In Halimun National Park, West Java, between Type A and B, difference in the position where they grow on tree trunks was reported, and Type A was suggested to prefer deeply shaded places (Murakami et al. 1999b). Comparing the three types, Type E, F and G, with Type AII in the Malay Peninsula and West Sumatra, Type AII grew on relatively low sections of tree trunk where it is deeply shaded. Therefore, it is suggested that Type AII also may prefer deeply shaded places. Thus, ecological differentiation was observed between some pairs of *rbc*L types also in the Malay Peninsula and West Sumatra. Moreover, as far as Type AII, E, F and G are concerned, it is suggested that individuals of the same *rbc*L type may not differ in their habitat preference between the Malay Peninsula and West Sumatra.

In order to understand species diversity in *Asplenium* sect. *Thamnopteris*, it will be necessary to increase investigation localities and to continue recognizing potential cryptic species by analyzing molecular data, such as *rbc*L sequence and allozymes, and ecological comparison. Crossing experiments will also be required to investigate reproductive isolation among potential cryptic species. At present we are conducting artificial crossing experiments between various pairs of *rbc*L types collected widely from the West Malesian region and other localities, including not only the plants identified as *Asplenium nidus* but also related species in *Asplenium* sect. *Thamnopteris*. Once we obtain hybrid plants, we will grow them in order to examine their fertility. These kinds of data will provide more information on the systematics of *Asplenium* sect. *Thamonopteris*.

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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.

Reference

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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

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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

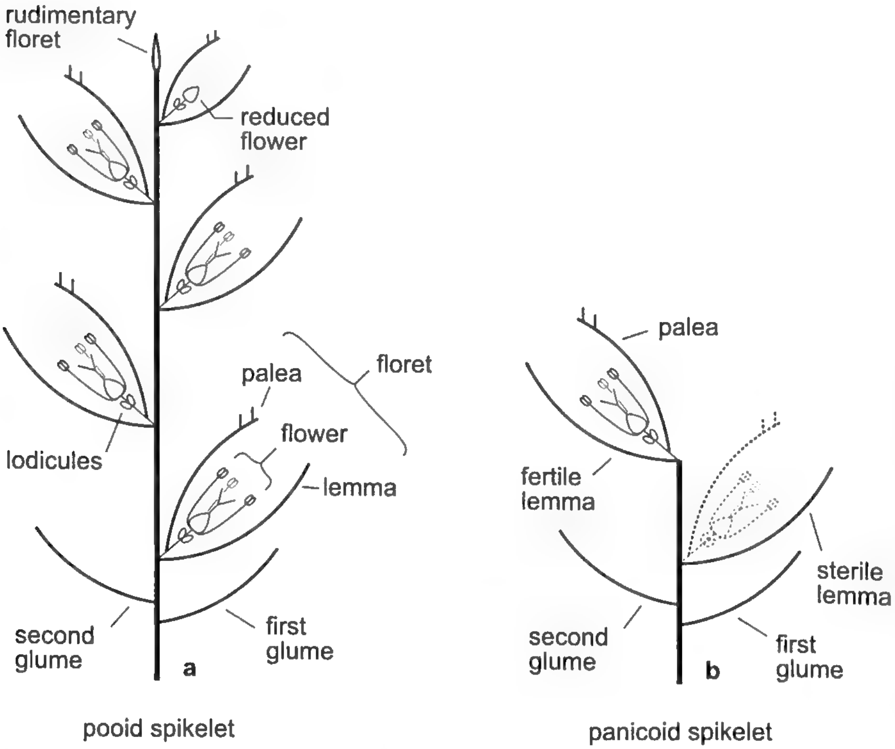

Fig. 1. Diagrammatic grass spikelets. **a,** multiflowered pooid (Pooideae) spikelet with apical reduction; **b,** two-flowered panicoid (Panicoideae) spikelets with basal reduction. Dotted lines indicate structures that are usually absent.

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

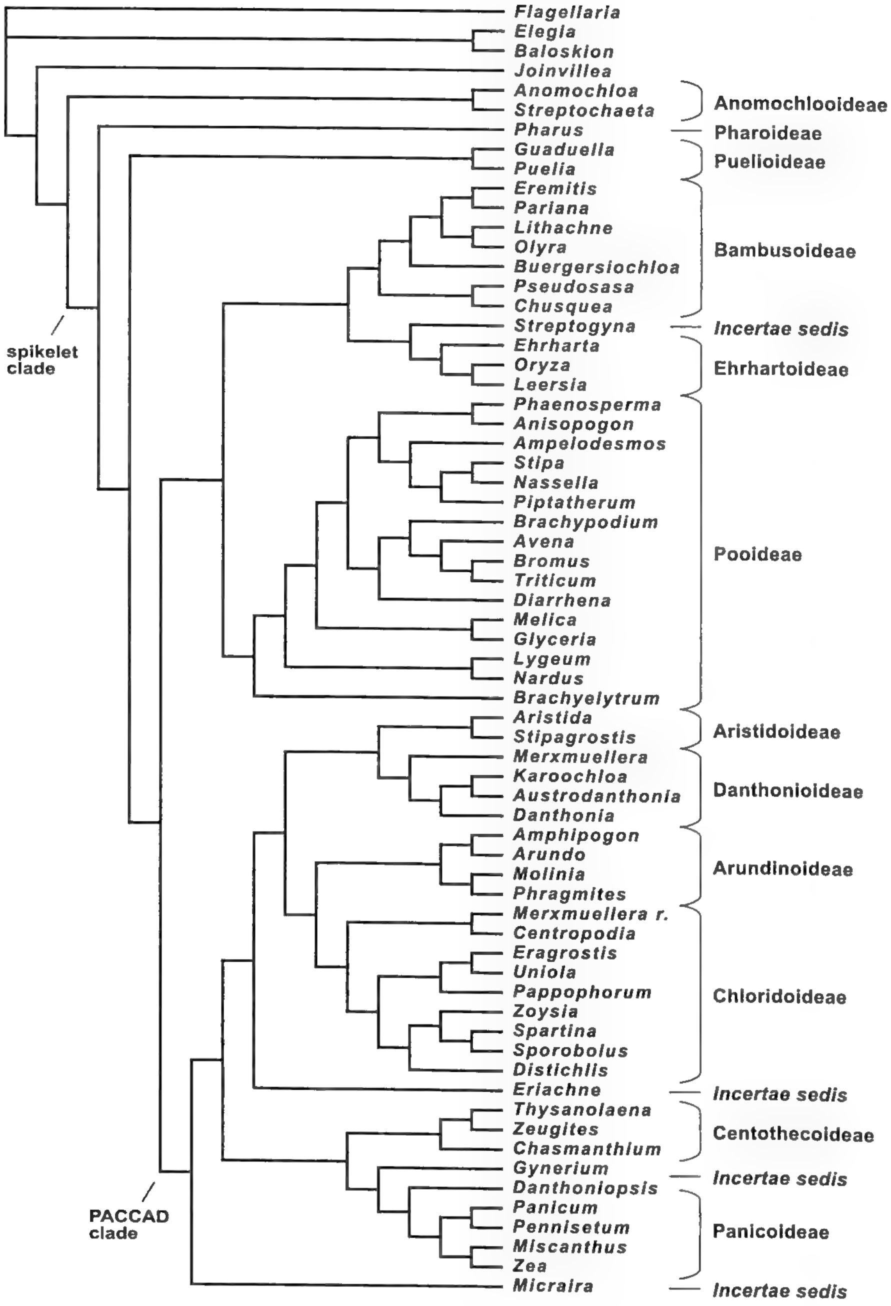

Fig. 2. Single most parsimonious tree for the grasses (*Anomochloa* through *Micraira*) and relatives (*Flagellaria* through *Joinvillea)* obtained in the GPWG (2001) analysis, showing the revised subfamilial classification for the grass family.

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

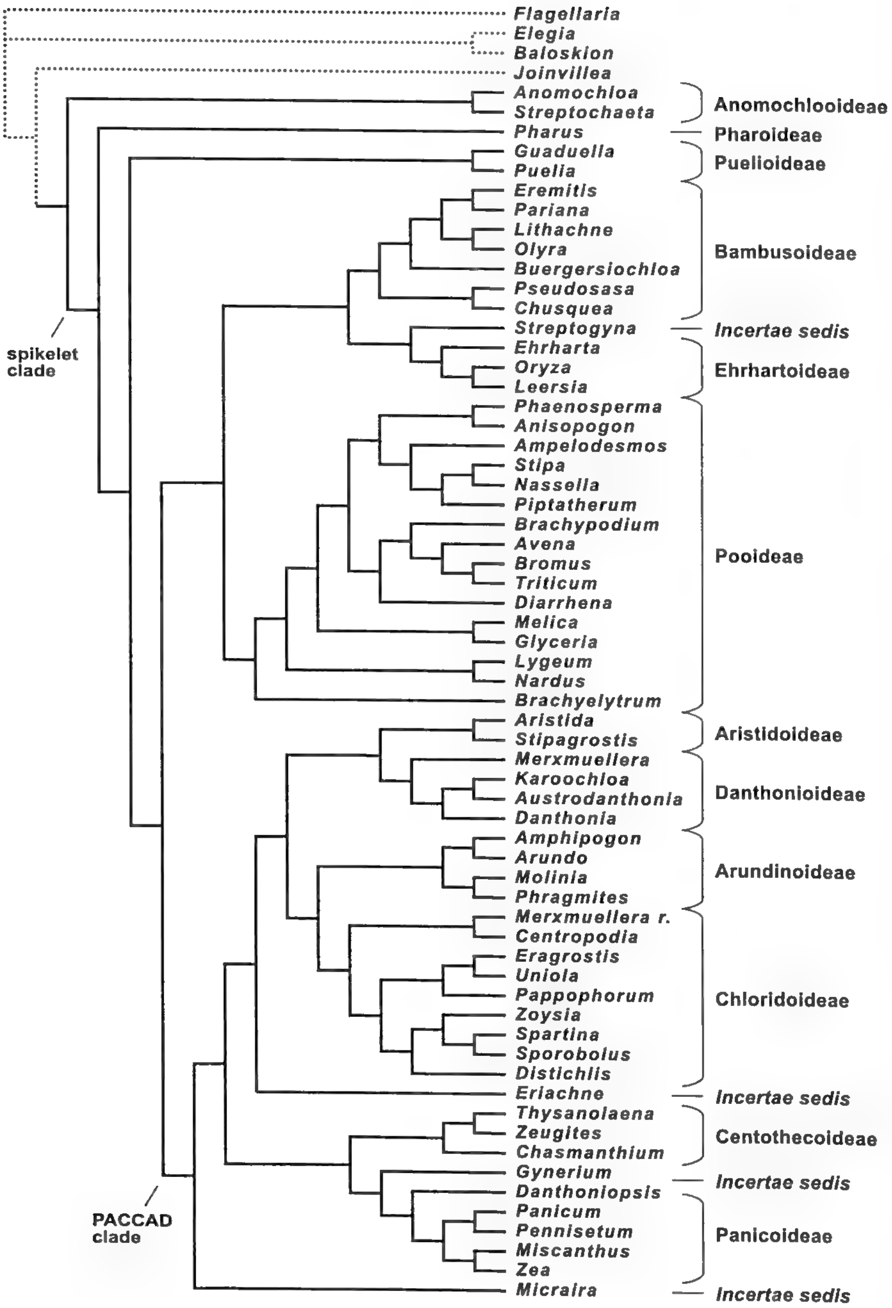

Fig. 3. Distribution of the grass-type embryo in the grass family, as optimized on the GPWG (2001) tree. Solid lines = presence of the character.

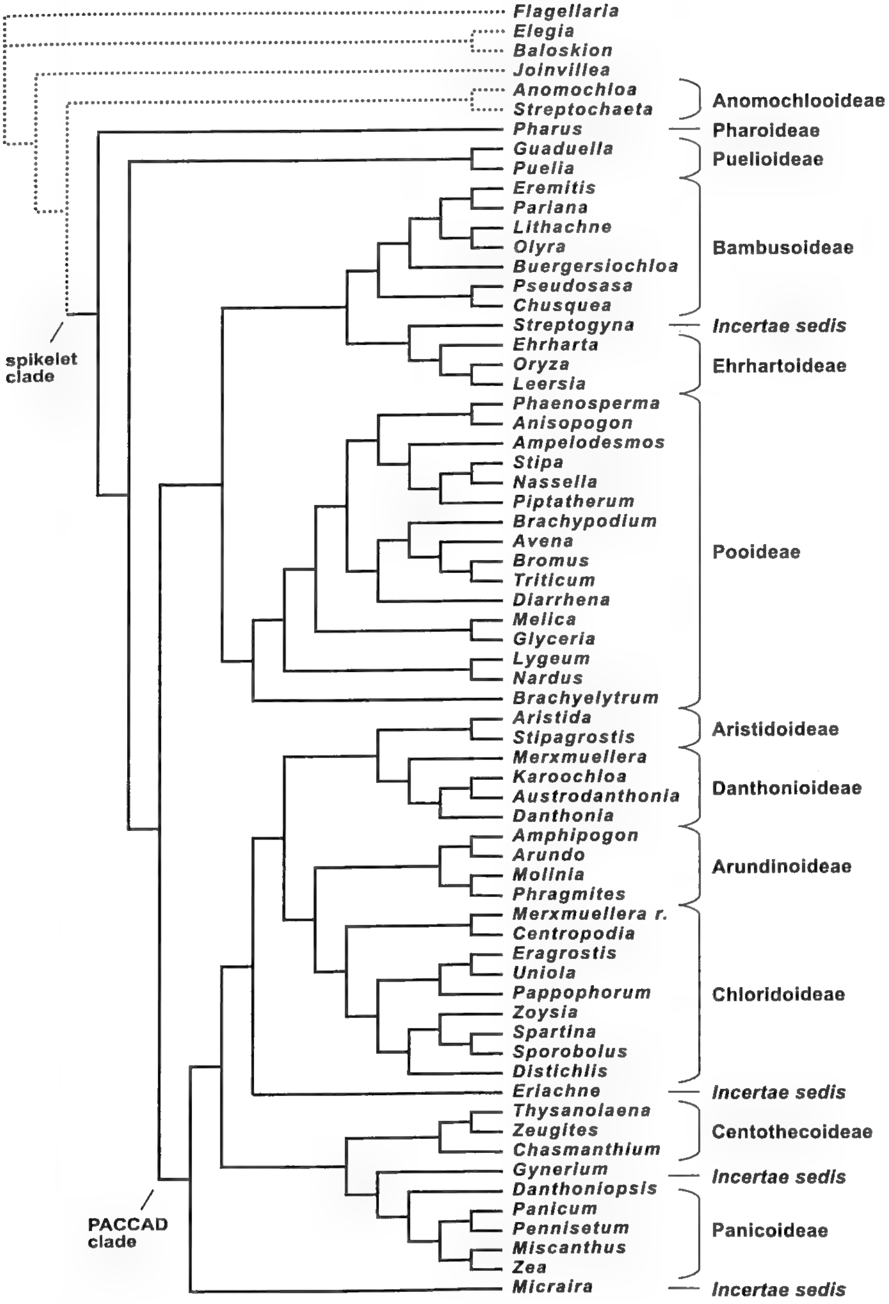

Fig. 4. Distribution of the grass-type spikelet in the grass family, as optimized on the GPWG (2001) tree. Solid lines = presence of the character.

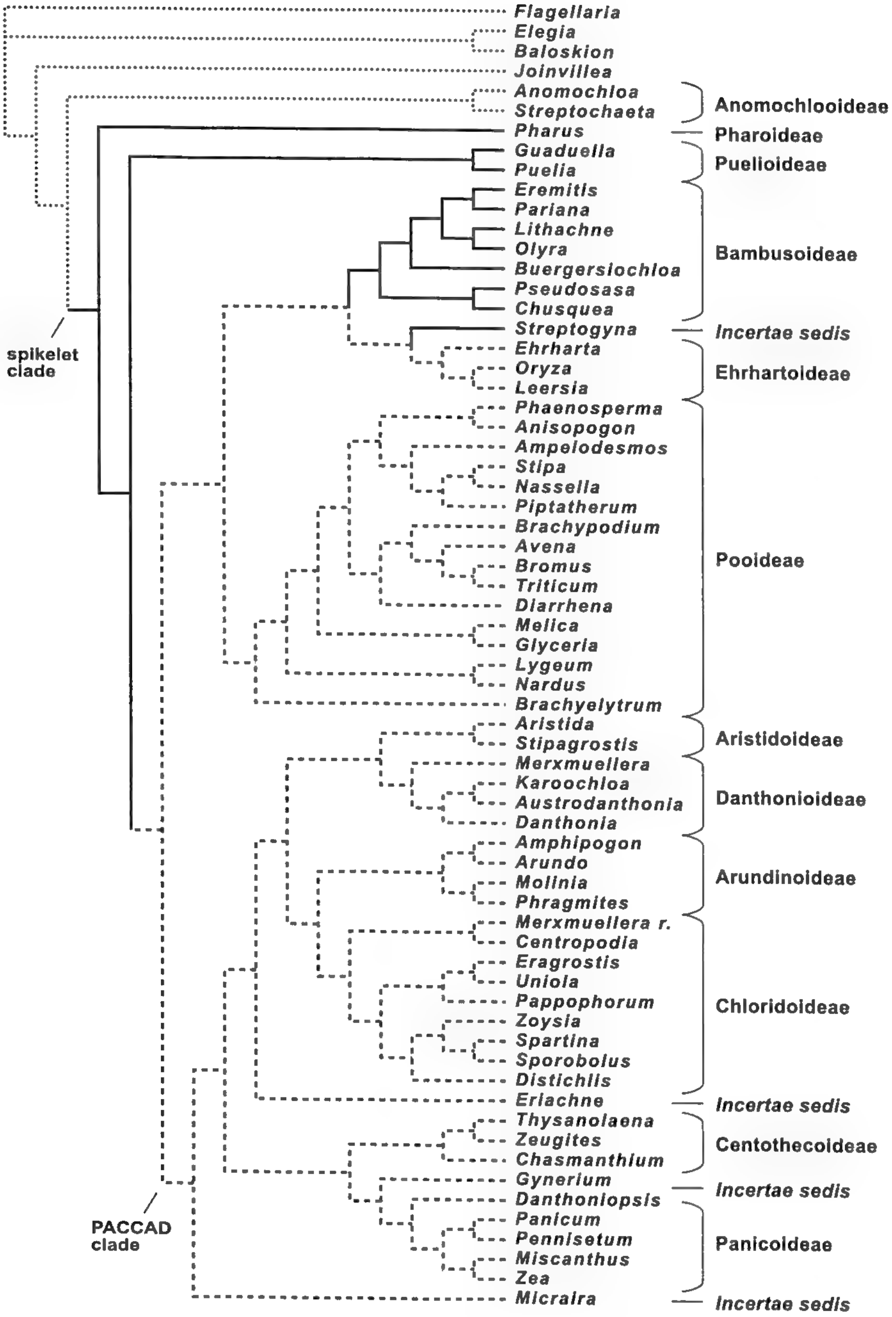

Fig. 5. Distribution of lodicule number in the grass family, as optimized on the GPWG (2001) tree. Dotted lines = lodicules absent; solid lines = three lodicules present; dashed lines = two lodicules present.

(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.

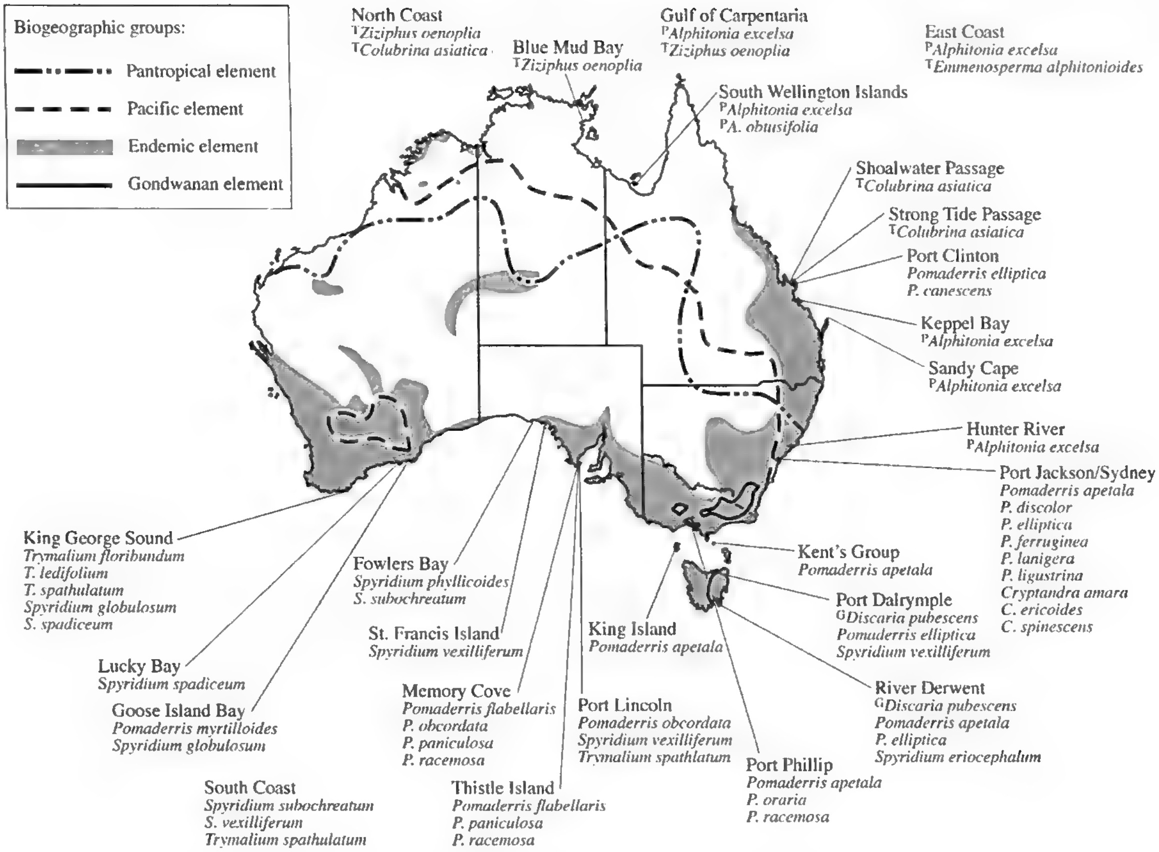


Fig. 1. The distribution of Rhamnaceae in Australia, and Robert Brown's Rhamnaceae collections from 1801–1805. The biogeographic regions for Australian Rhamnaceae (Bentham 1863b; Kellermann 2002) are as described in the text. Species names without superscipt symbol belong to the Endemic element; ^{G}Gondwanan 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.

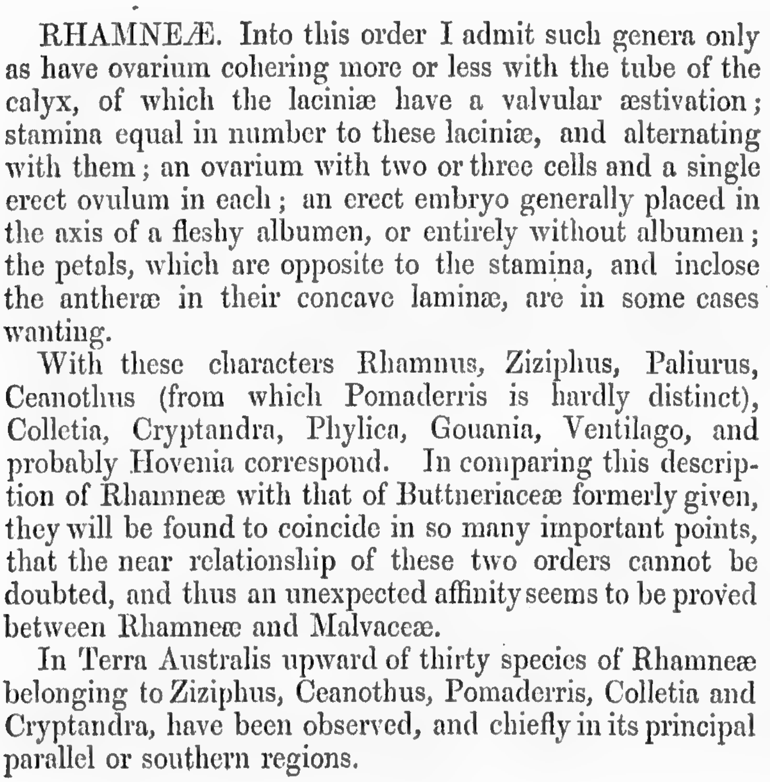
^{T}*Ziziphus oenoplia* (L.)Mill.

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 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.	1825 DC. Staphyleaceae	Staphyleaceae
	***Celastrus* L.**	**1814 R.Br. Celastraceae**	**Celastraceae**
	***Evonymus* L.**	**1821 Gray Celastraceae**	
	***Polycardia* Juss.**	**1825 DC. Evonymeaceae = Celastraceae**	
II	***Cassine* L.**	**1824 Spreng. Terebinthaceae = Anacardiaceae**	
	***Myginda* Jacq.**	**1825 Kunth Celastraceae**	
	***Rubentia* Comm.**	**1825 DC. Evonymeaceae = Celastraceae**	
	Goupia Aublet	* 1840 Endl. Elaeodendreaceae	Goupiaceae
	Ilex L.	1821 Gray Aquifoliaceae	Aquifoliaceae
	Prinos L.	1817 Spreng. Ophiospermaceae = Myrsinaceae	
	Schrebera Roxb.	1822 Juss. Oleaceae	Oleaceae
III	*Mayepea* Aublet	1810 **R.Br.** Oleaceae	
	Samara Sw.	1810 **R.Br.** Myrsinaceae	Myrsinaceae
	***Rhamnus* L.**	**1814 R.Br. Rhamnaceae** **Brown also included the following genera:** ***Cryptandra* Sm., *Pomaderris* Labill. and *Ventilago* Gaertner**	**Rhamnaceae**
	***Paliurus* Mill.**		
	***Ziziphus* Mill.**		
IV	***Ceanothus* L.**		
	***Colletia* Juss.**		
	***Hovenia* Thunb.**		
	***Phylica* L.**		
V	*Brunia* Lam.	1818 **R.Br.** Bruniaceae	Bruniaceae
	Bumalda Thunb.	1825 DC. Staphyleaceae	Staphyleaceae
VI	*Aucuba* Thunb.	1825 Kunth Caprifoliaceae-Corneae	Aucubaceae/Garryaceae
	Carpodetus Forst.	* 1840 Endl. Celastraceae	Escalloniaceae
	***Gouania* Jacq.**	**1814 R.Br. Rhamnaceae**	**Rhamnaceae**
	Plectronia L.	1828 Rchb. Cunoniaceae	Rubiaceae
	Votomita Aublet	1828 Rchb. Talineaceae	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 58 (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 28 (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.

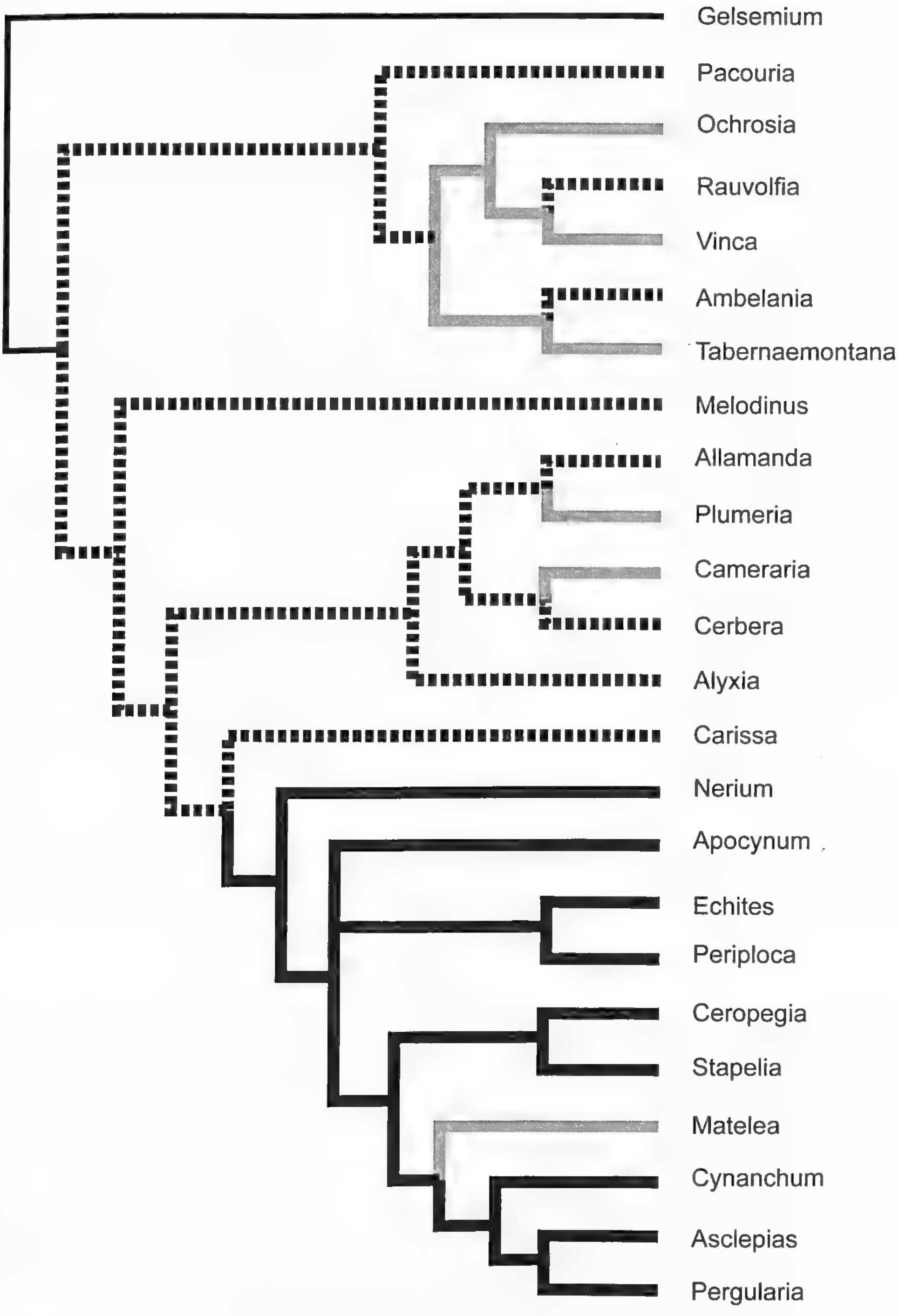

Fig. 1. Jussieu's three groups of Apocineae, with the taxa shown where they would come out based on current data. Group 1: grey; Group 2: black; Group 3: interrupted line; outgroup: thin black line.

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.

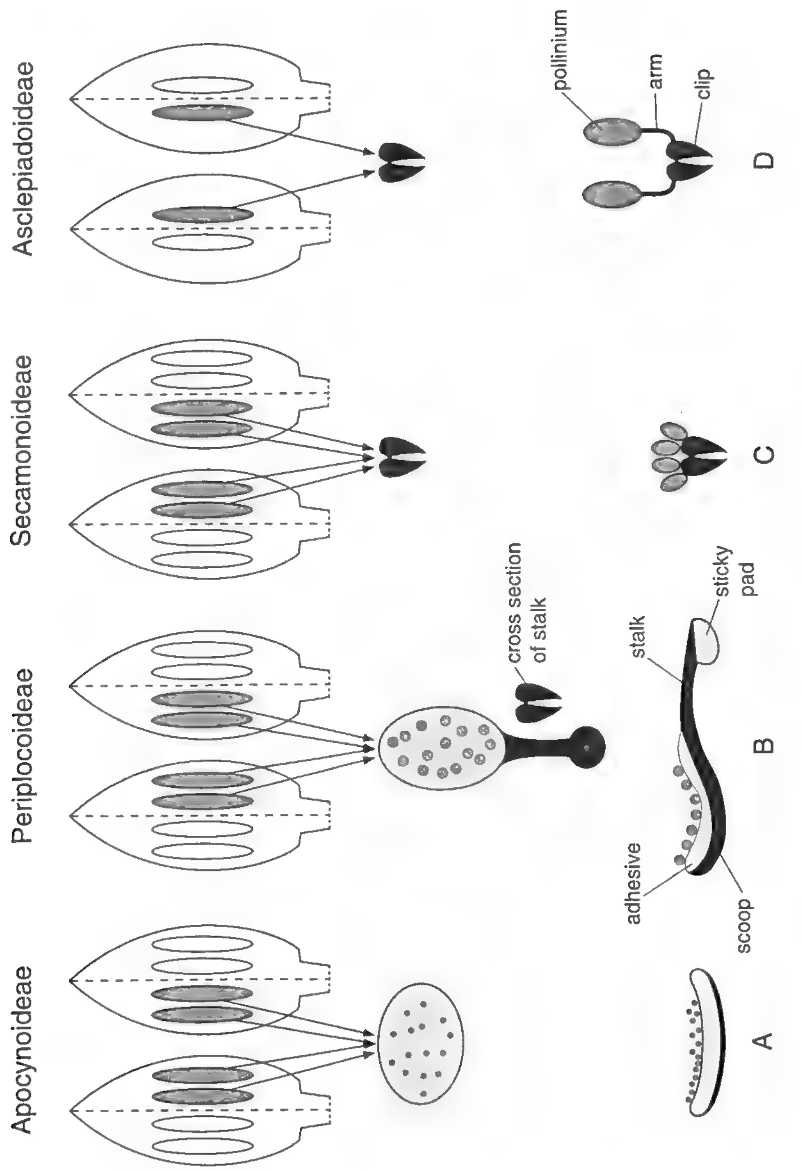

Fig. 2. Key characters of the three subfamilies of Robert Brown's Asclepiadeae: translators and pollen masses. Apocynoideae (Apocynaceae sens. strict.) are also shown for comparison. Transition series does not necessarily imply straight-line evolution, only evolutionary stages. A, Apocynoideae: the pollen 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

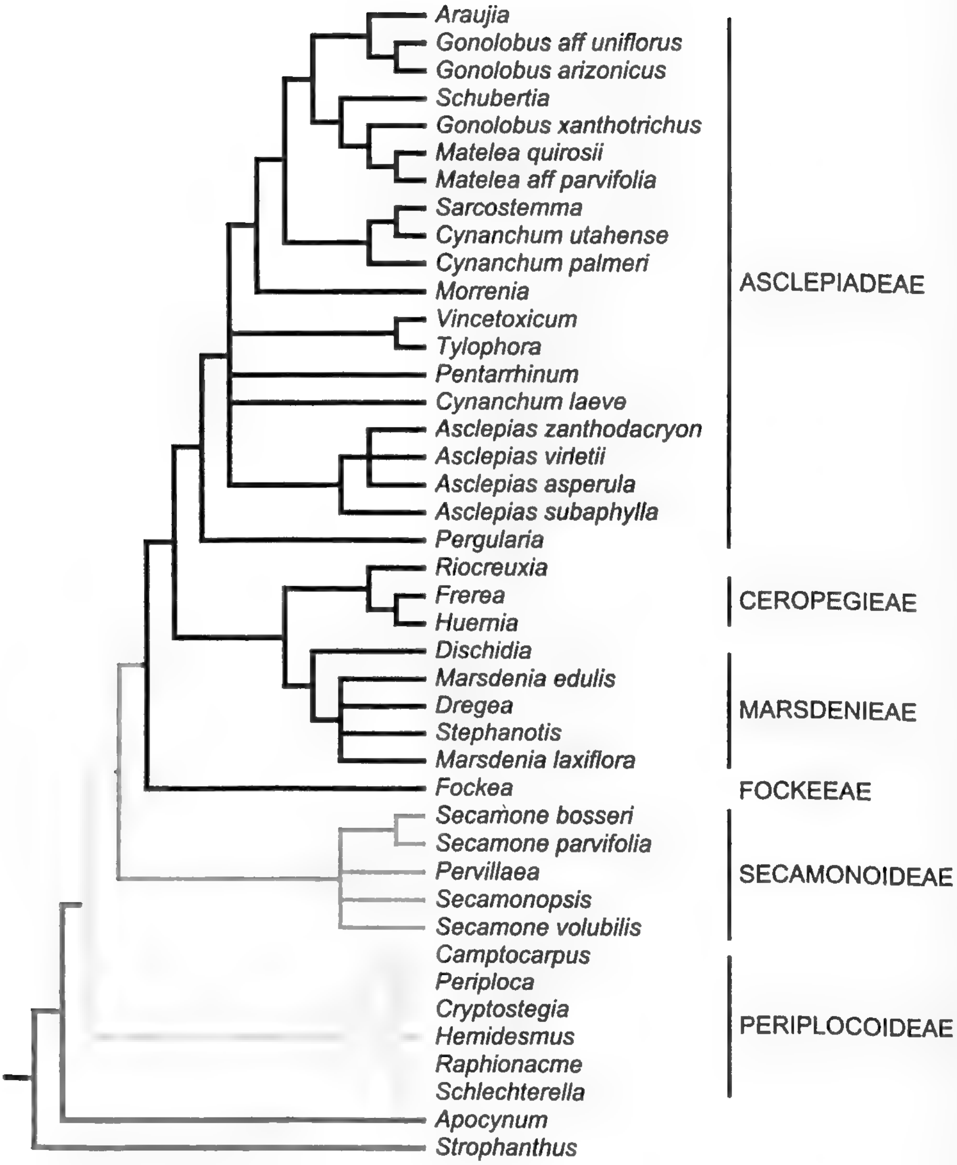

Fig.3. Tree based on maximum parsimony analysis of partial and complete *mat*K sequences published in Fishbein (2001), with Robert Brown's three subfamilies mapped onto it. Periplocoideae: light grey; Secamonoideae: medium grey; Asclepiadoideae, showing the tribes Fockeeae, Marsdenieae, Ceropegieae and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

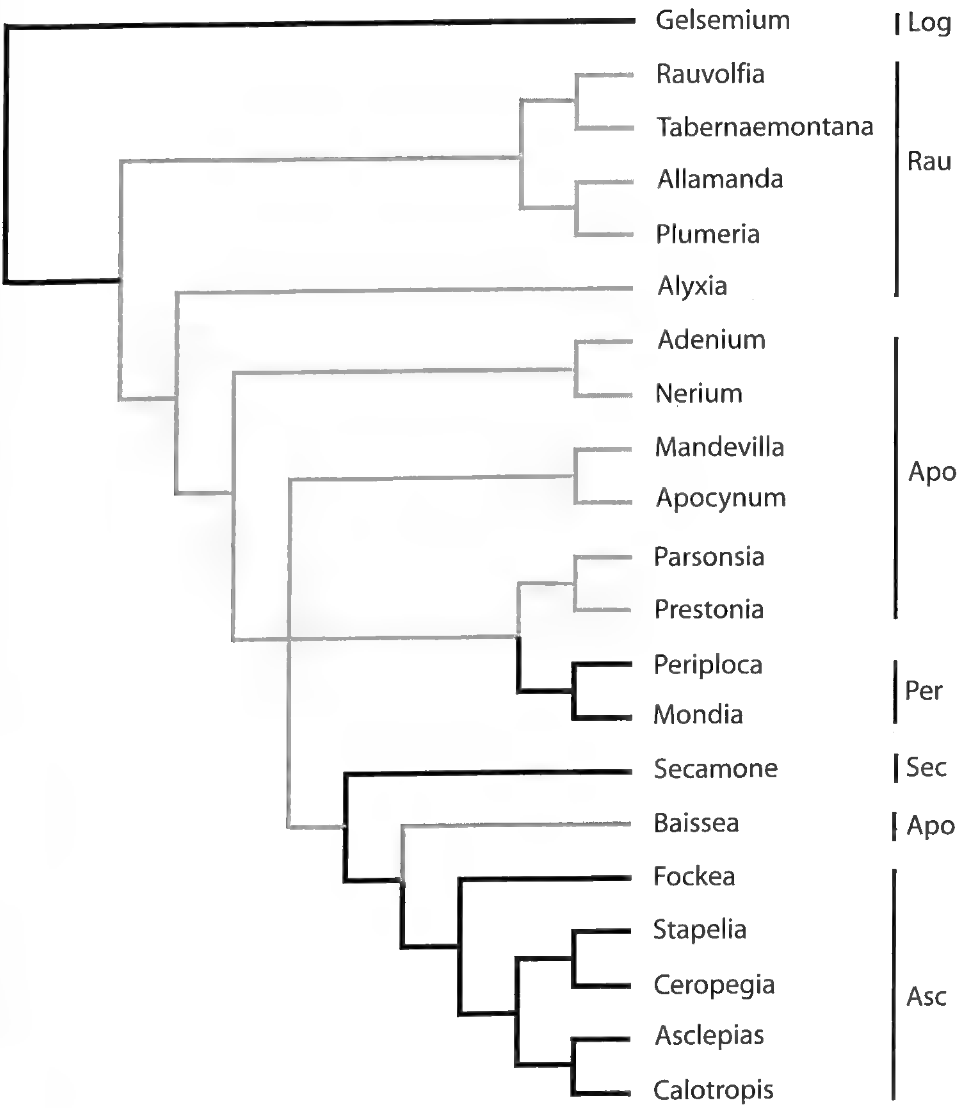

Fig. 4. Simplified reconstruction of the phylogenetic tree of Apocynaceae sens. lat. by Sennblad and Bremer (2000) based on the cholorplast gene *rbc*L with *Gelsemium* (Loganiaceae) as outgroup. 1) The three clades at the apex form an unresolved polytomy; 2) Periplocoideae are sister to *Parsonsia* 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.

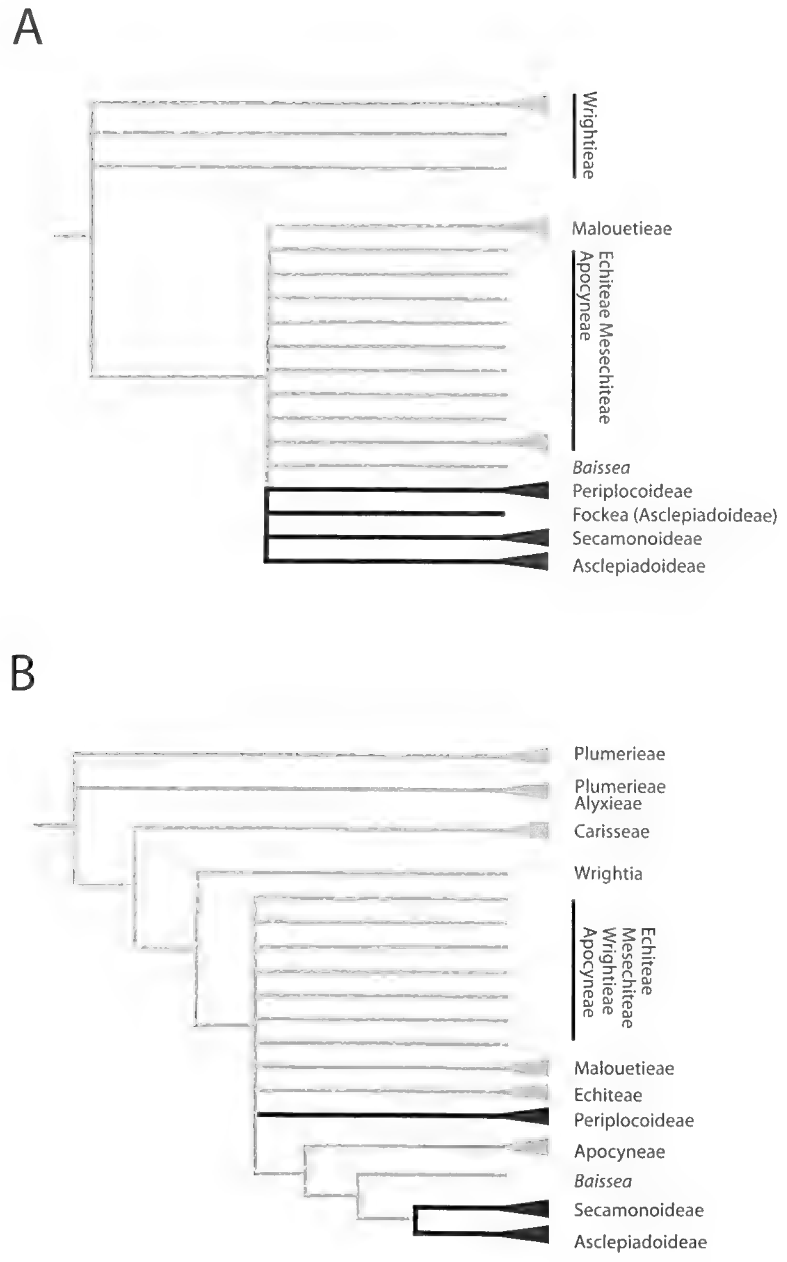

Fig. 5. Summarised form of the strict consensus tree from the unweighted parsimony analysis from two cpDNA studies. **A**. Tree based on *rbc*L. The Rauvolfioideae (lower part of the tree) is not shown. Except for the basalmost genera, all Apocynoideae form a polytomy, in which Periplocoideae is nested (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.

Acknowledgments

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

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

Stauranthera Benth.: *Stauranthera grandiflora* Benth., *Stauranthera 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.

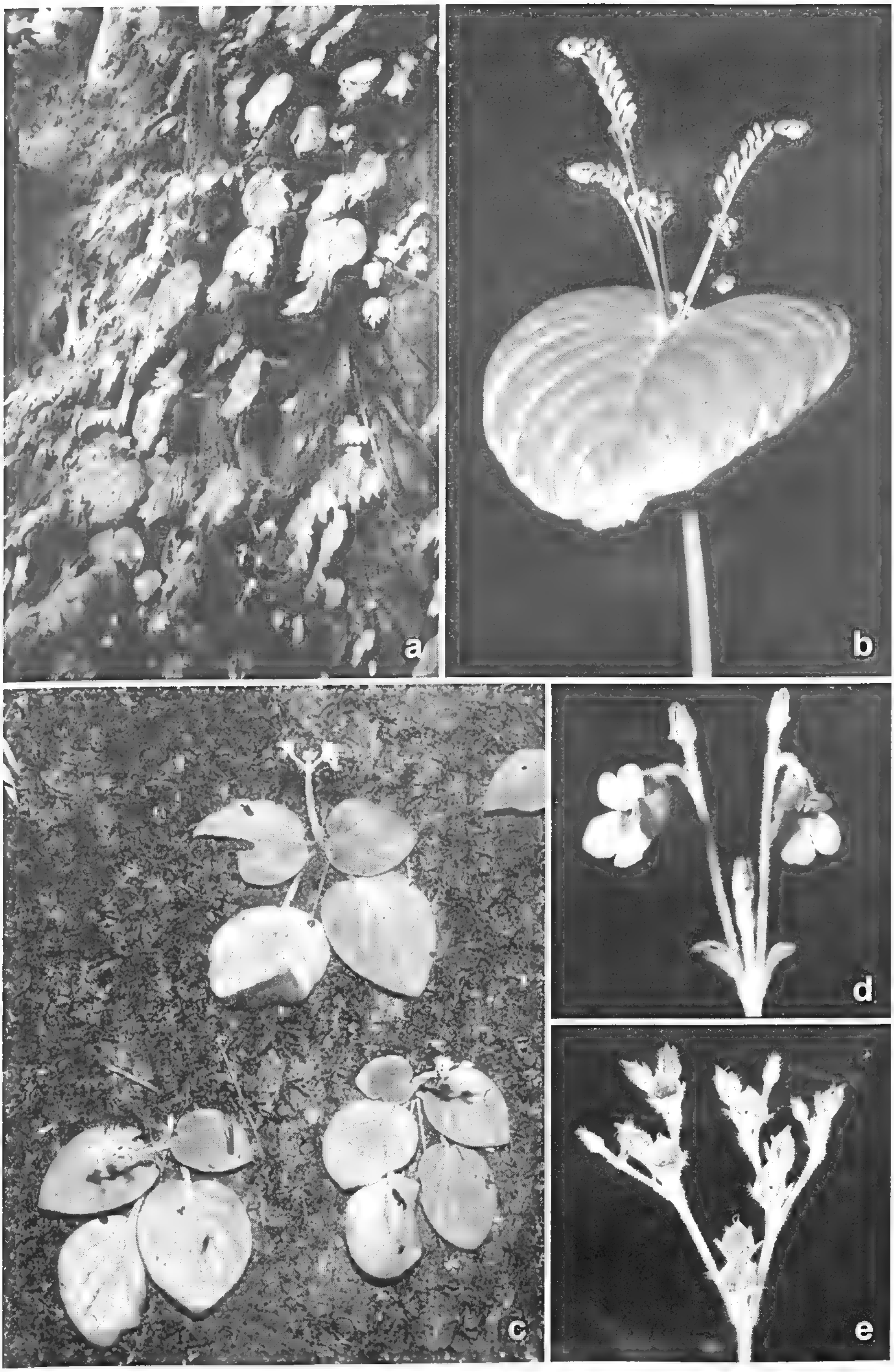

Fig. 1a,b *Monophyllaea horsfieldii* R.Br., **a,** plants in their natural habitat (limestone cliffs in rainforest), Peninsular Malaysia, Selangor, Bkt. Takun; **b,** cultivated plant; **c–e** *Henckelia browniana* A.Weber (= *Loxocarpus incanus* R.Br.); **c,** plants in their natural habitat (mossy 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

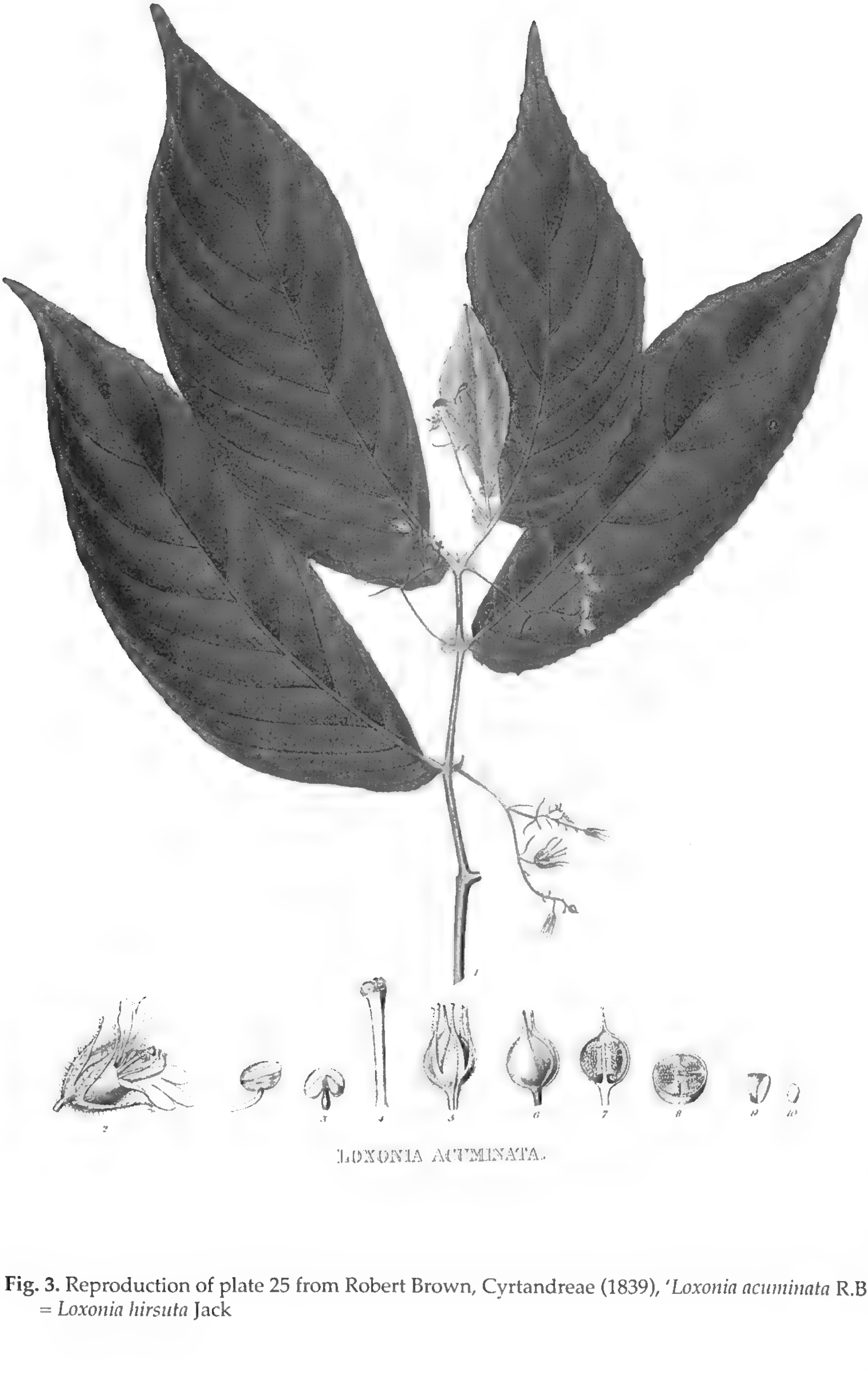

Fig. 3. Reproduction of plate 25 from Robert Brown, Cyrtandreae (1839), '*Loxonia acuminata* R.Br.' = *Loxonia hirsuta* Jack

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 *Stauranthera*' (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

Barbara G. Briggs and L.A.S. Johnson†

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 Bussleton 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* Homeolaen*a* *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.

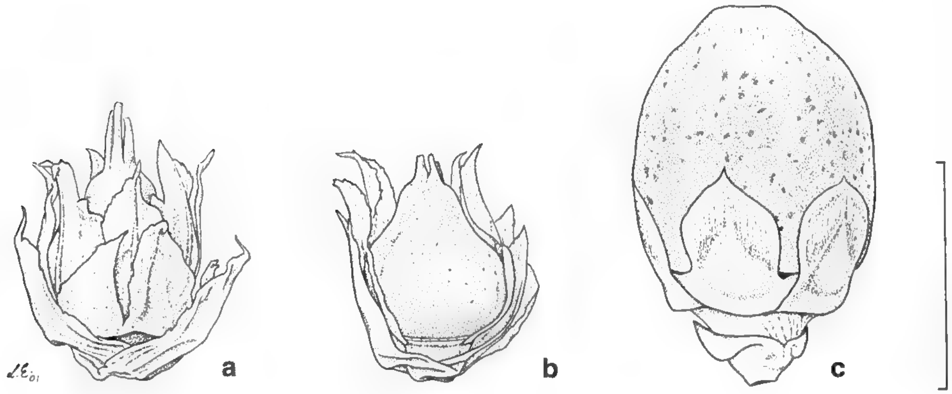

Fig. 1. Female spikelets in fruiting stage, **a–b**, *H. humilis*, **a**, as dispersed, nut surrounded by tepals, floral bracts and spikelet bracts; **b**, as (a) but some bracts and tepals removed (48 km SW of Ravensthorpe, *Briggs 460* NSW); **c**, *H. pubescens*, as dispersed, nut with tepals and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

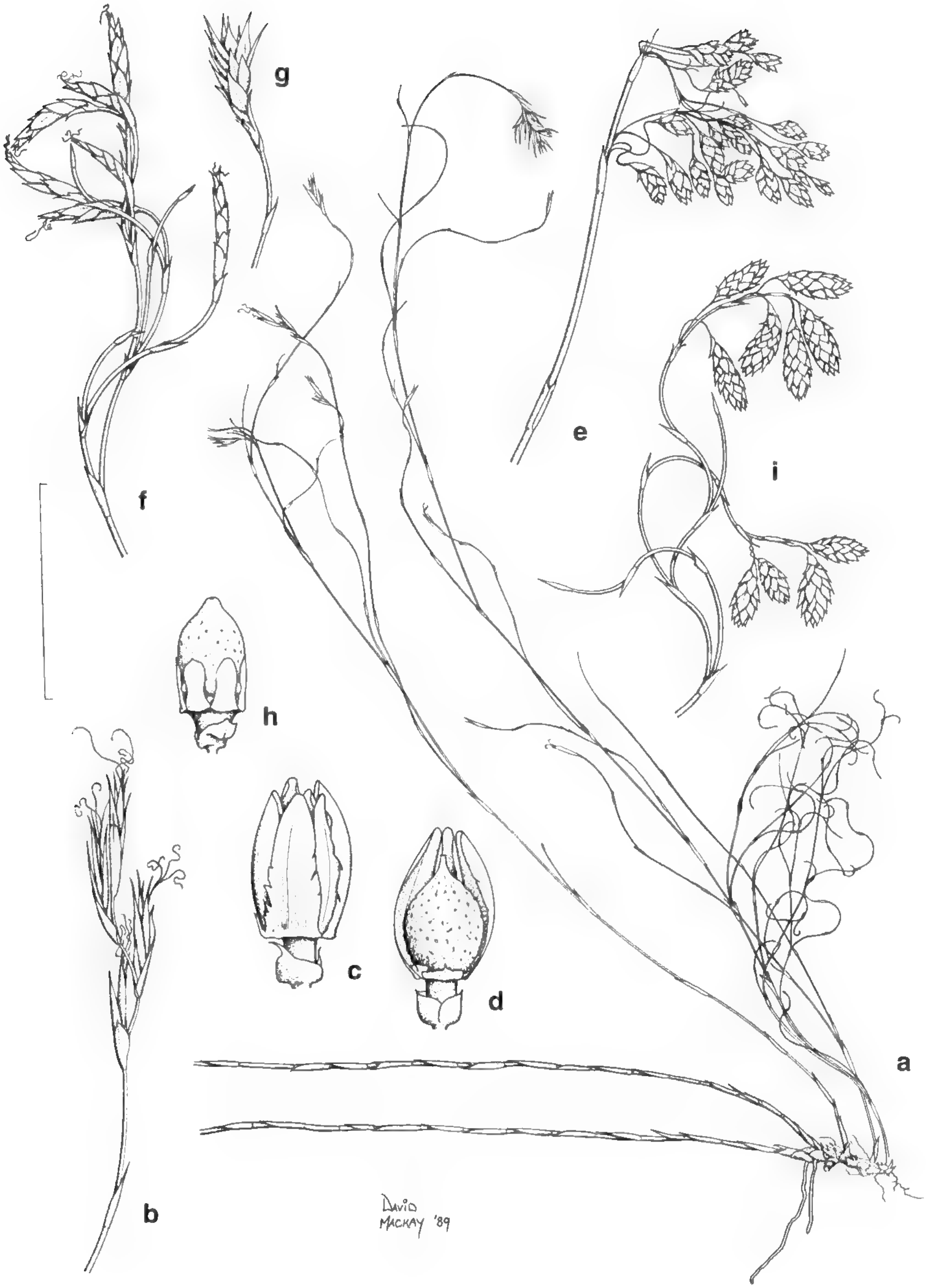

Fig. 3. a–e, *H. grandiuscula*, **a–d**, female: **a**, habit, **b**, inflorescence (Bow R., *Gittins 1765b*); **c**, fruit with tepals, **d**, fruit, some tepals removed (Yoongarillup, SE of Busselton, *Briggs 807*); **e**, part of male inflorescence (Bow R., *Gittins 1765a*); **f–i**, *H. fastigiata*, **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.

Acknowledgments

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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,

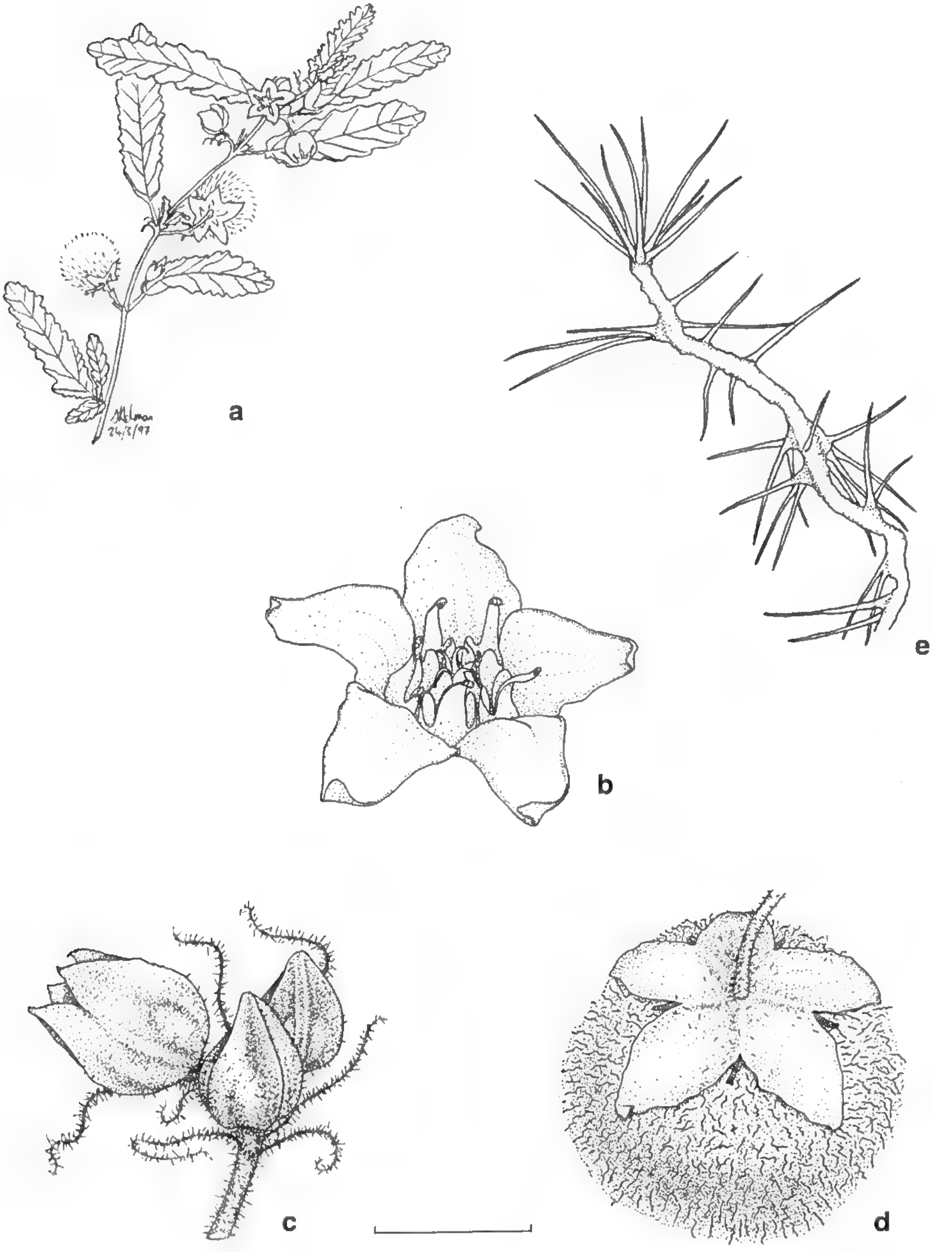

Fig. 1. *Commersonia rosea* **a,** flowering and fruiting branch; **b,** flower from above, showing calyx lobes and erect, 3-lobed petals; **c,** inflorescence showing flower buds and linear bracts; **d,** capsule with persistent calyx; **e,** capsule bristle with stellate hairs. Scale bar: a = 3 cm; 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 brachyryhncha, 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

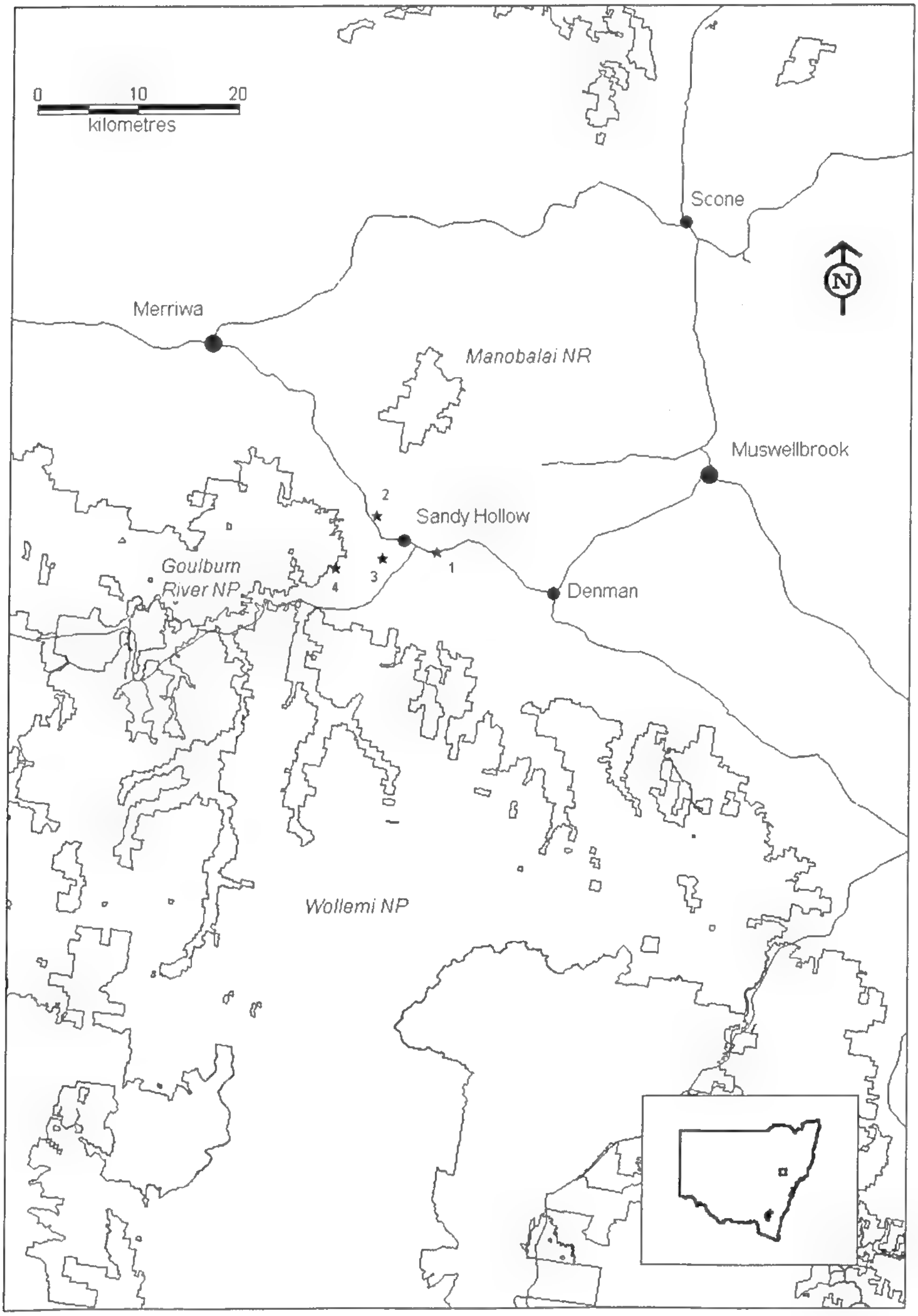

Fig. 2. Location of *Commersonia rosea* populations near Sandy Hollow in the upper Hunter Valley, showing existing conservation reserves . ★1 = Pikes Gap, ★2 = Giants Creek, ★3 = Peberdys Road, ★4 = Boodles Creek.

(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*.

Acknowledgments

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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 μm tall; ascospores hyaline, densely muriform, 1 per ascus, (100–)125–150(–175) μm long, 20–30 μm 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.

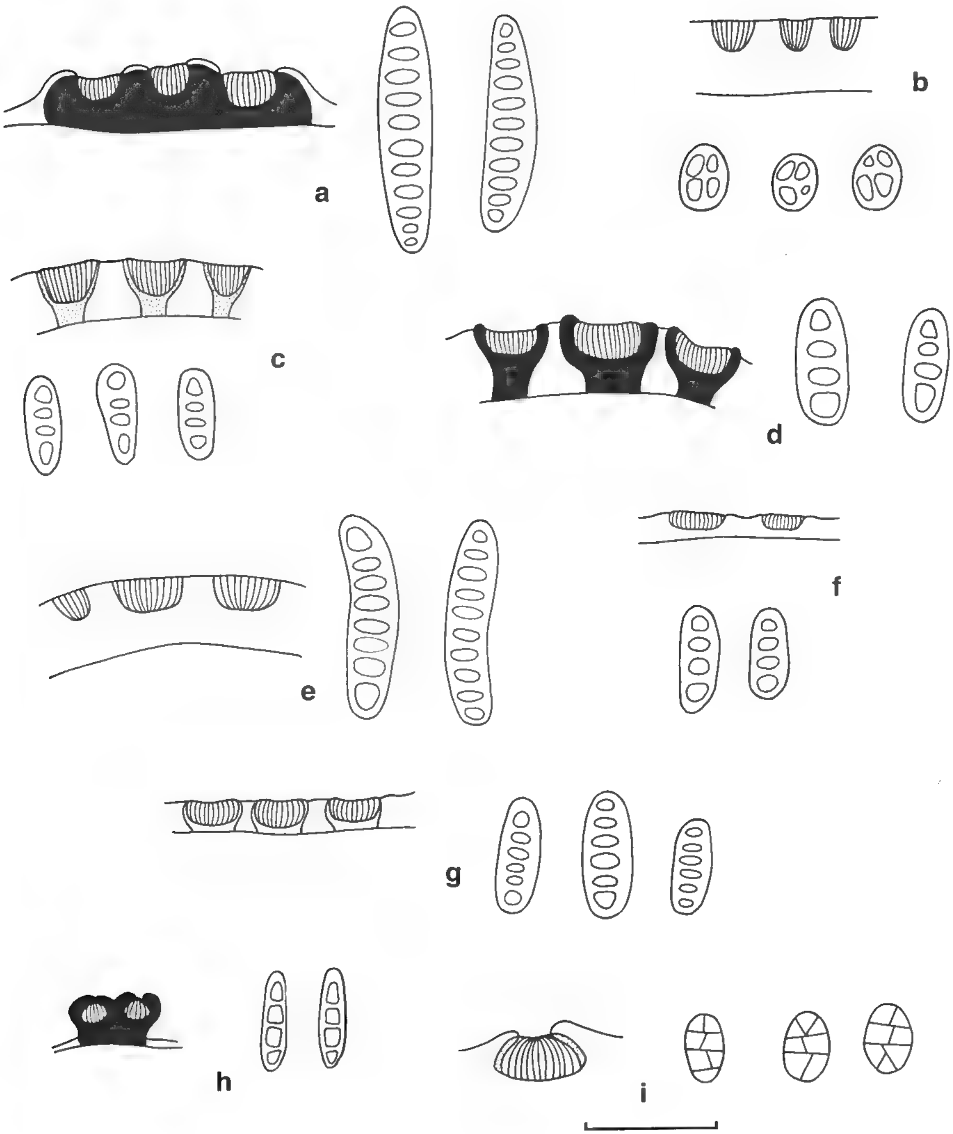

Fig. 1. Ascospores and cross-sections of lirellae. **a**, *Glyphis cicatricosa*; **b**, *Sarcographina cyclospora*; **c**, *Sarcographa intricans*; **d**, *S. labyrinthica*; **e**, *S. oculata*; **f**, *S. subtricosa*; **g**, *Sarcographa verrucosa*; **h**, *Opegrapha australiensis*; **i**, *Medusulina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

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

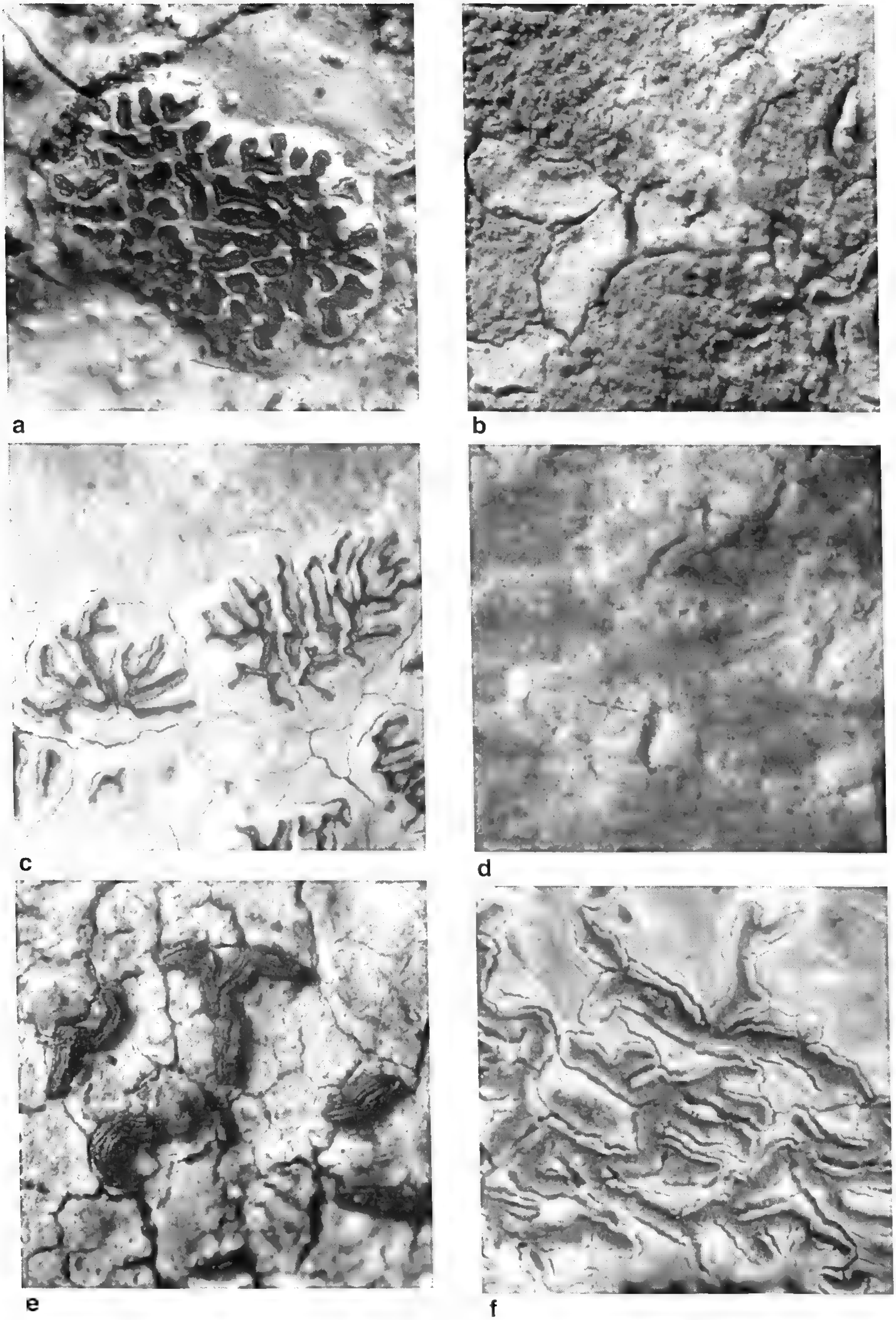

Fig. 2. **a**, *Glyphis cicatricosa* Ach. *Archer G 339*; **b**, *Graphina platyleuca* (Nyl.) Zahlbr. *Archer G 330*; **c**, *Gymnographa medusulina* Müll. Arg., holotype (G); **d**, *Medusulina egenella* (Müll. Arg.) Müll. Arg., holotype (G); **e**, *Opegrapha australiensis* (Müll. Arg.) A.W. Archer,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

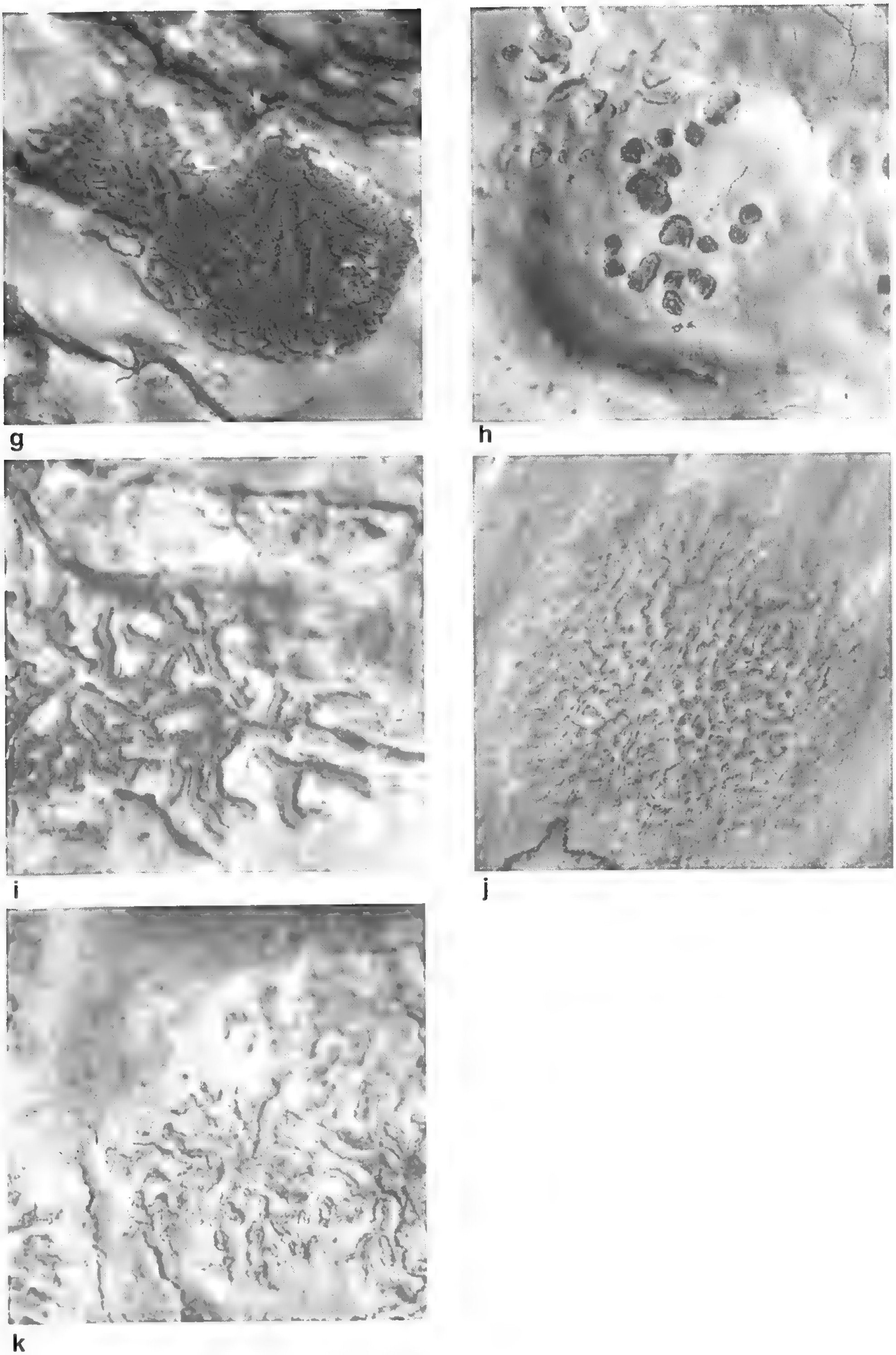

Fig. 2. g, *Sarcographa labyrinthica* (Ach.) Müll. Arg., *Archer G 338* (NSW 471723); **h**, *Sarcographa oculata* Müll. Arg., holotype (G); **i**, *Sarcographa subtricosa* (Leight.) Müll. Arg., holotype (BM); **j**, *Sarcographa verrucosa* (Mont. & Bosch) Zahlbr., *F.Wilson s.n.* (NSW 170581); **k**, *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 μm tall, I-ve; ascospores narrow-ellipsoid, hyaline, irregularly 2-seriate, (32–)40–55 μm long, 8–12 μm 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 µm tall; ascospores 8 per ascus, irregularly 2-seriate, pale brown, 16–20 µm long, 5–7 µm 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 μm tall; ascospores 8 per ascus, irregularly 2-seriate, pale brown, 17–21(–23) μm long, 6–7 μm 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 μm tall; ascospores 8 per ascus, irregularly 2-seriate, pale brown, 24–28(–32) μm long, 7–8 μm 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 μm tall; ascospores rounded ellipsoid, initially pale brown, uniseptate, 1-seriate, becoming dark brown, 10–13 μm long, 6–8 μm 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

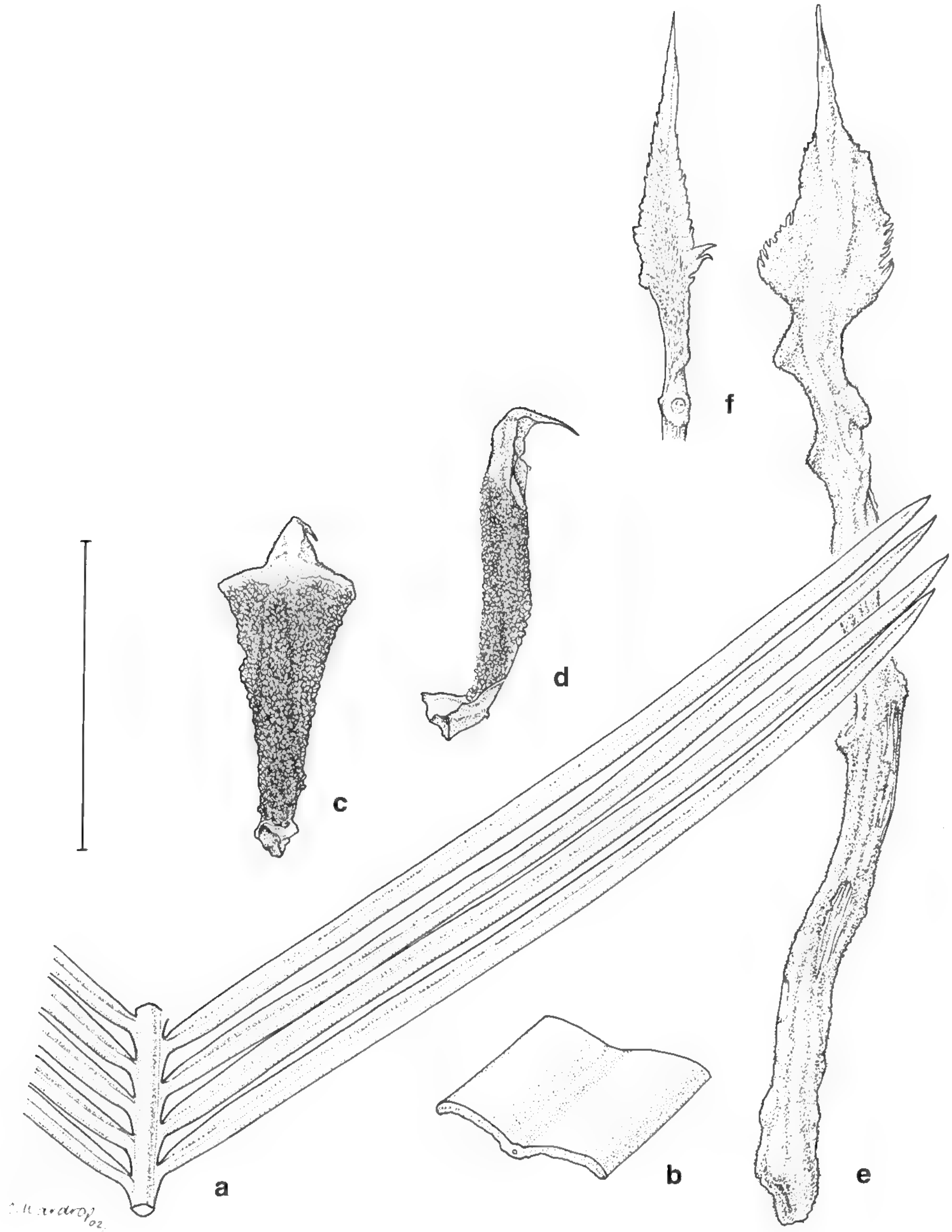

Fig. 1. *Cycas candida.* **a,** part of leaf; **b,** section of leaflet; **c, d,** microsporophyll; **e,** megasporophyll with stipe; **f,** tip of megasporophyll (a & b from *Hill 5671,* c & d from *Hill 5674,* e from *Hill 5672,* f from *Hill 4827*). Scale bar: a = 6 cm; b = 1 cm; c, d = 4 cm; e, f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

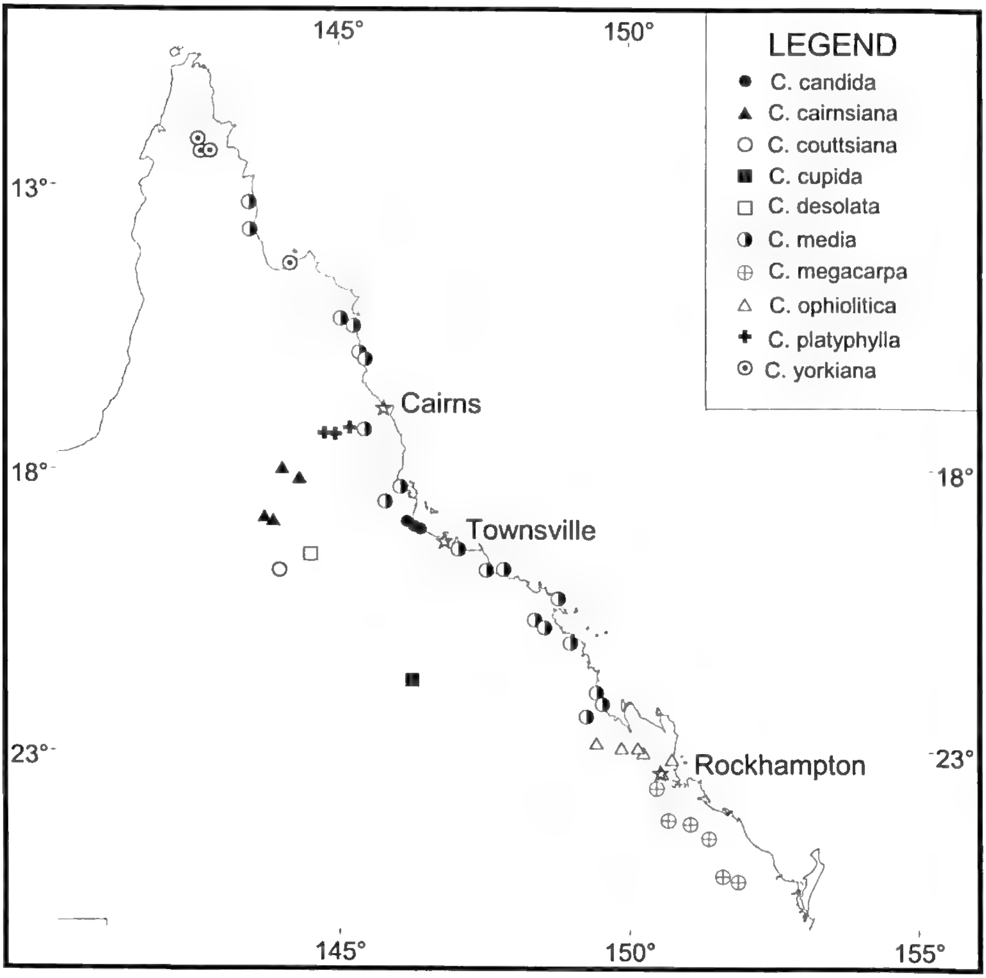

Fig. 2. Distribution of *Cycas* species in north-east Queensland: *Cycas candida, C. media, C. platyphylla, C. cairnsiana, C. couttsiana. C. desolata, C. cupida, C. yorkiana.*

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)

Stephen Skinner and Timothy J. Entwisle

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 confevicolum* 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

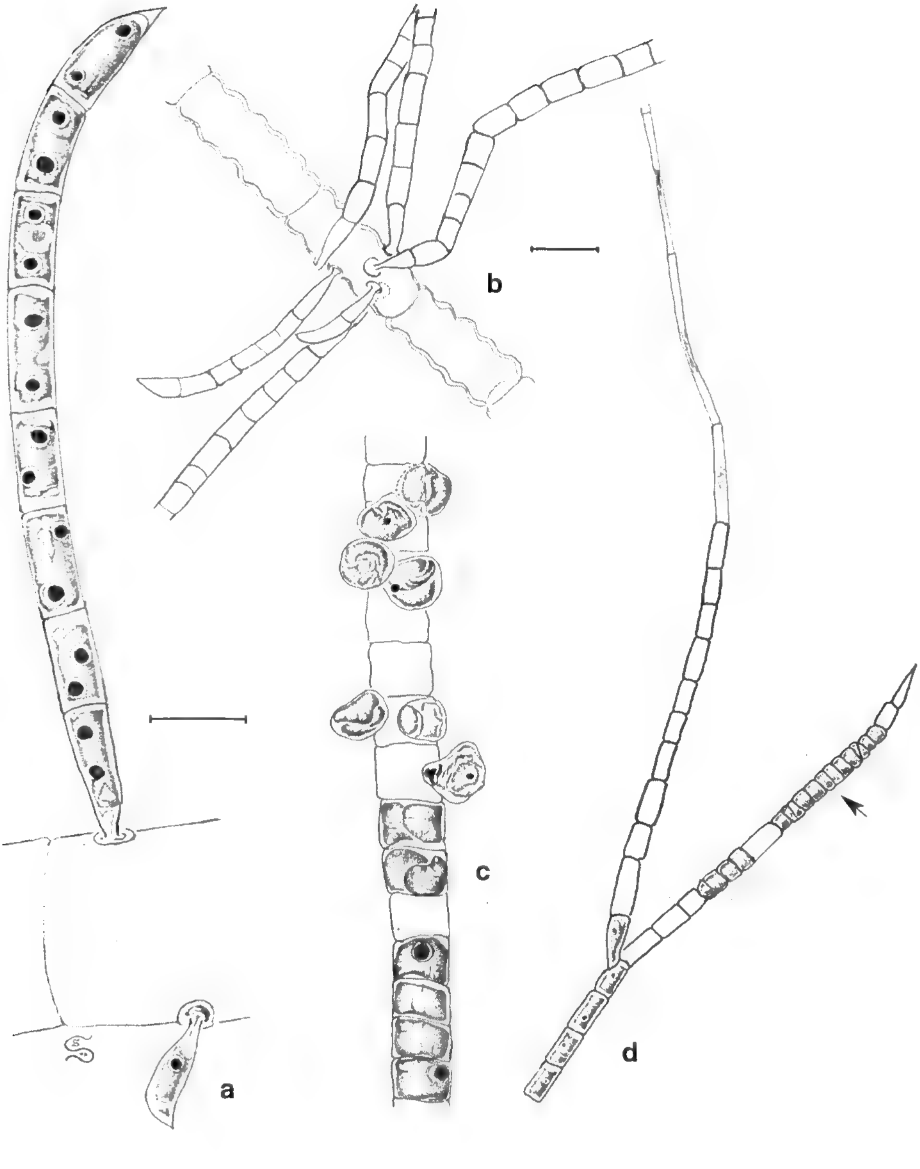

Fig.1. ***Uronema confervicolum*****: a,** Whole plant, vegetative; **b,** group of filaments on *Oedogonium*; **c,** filament with reproductive cells, zoids (*Skinner 0411*); ***Stigeoclonium farctum*****: d,** upper filament with hair and sporangia (*Skinner 0228b*). [a,c: scale 10 μm; b,d: scale 20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

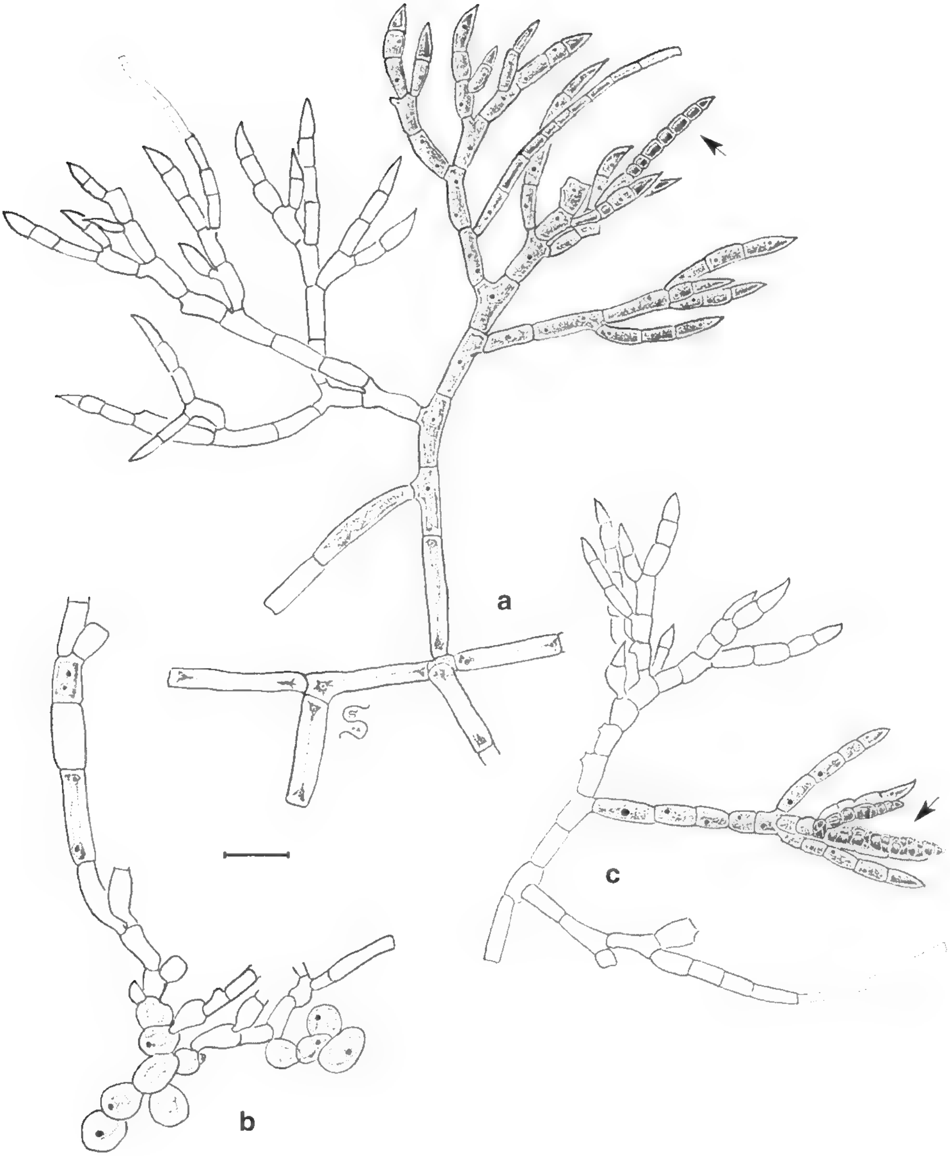

Fig. 2. ***Chaeophora elegans***: **a,** cortical and medullary filaments; **b,** basal and lower medulla filaments; **c,** cortical branches with hairs and sporangia (*Skinner 0299*). [a–c: scale 20 μm]

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.

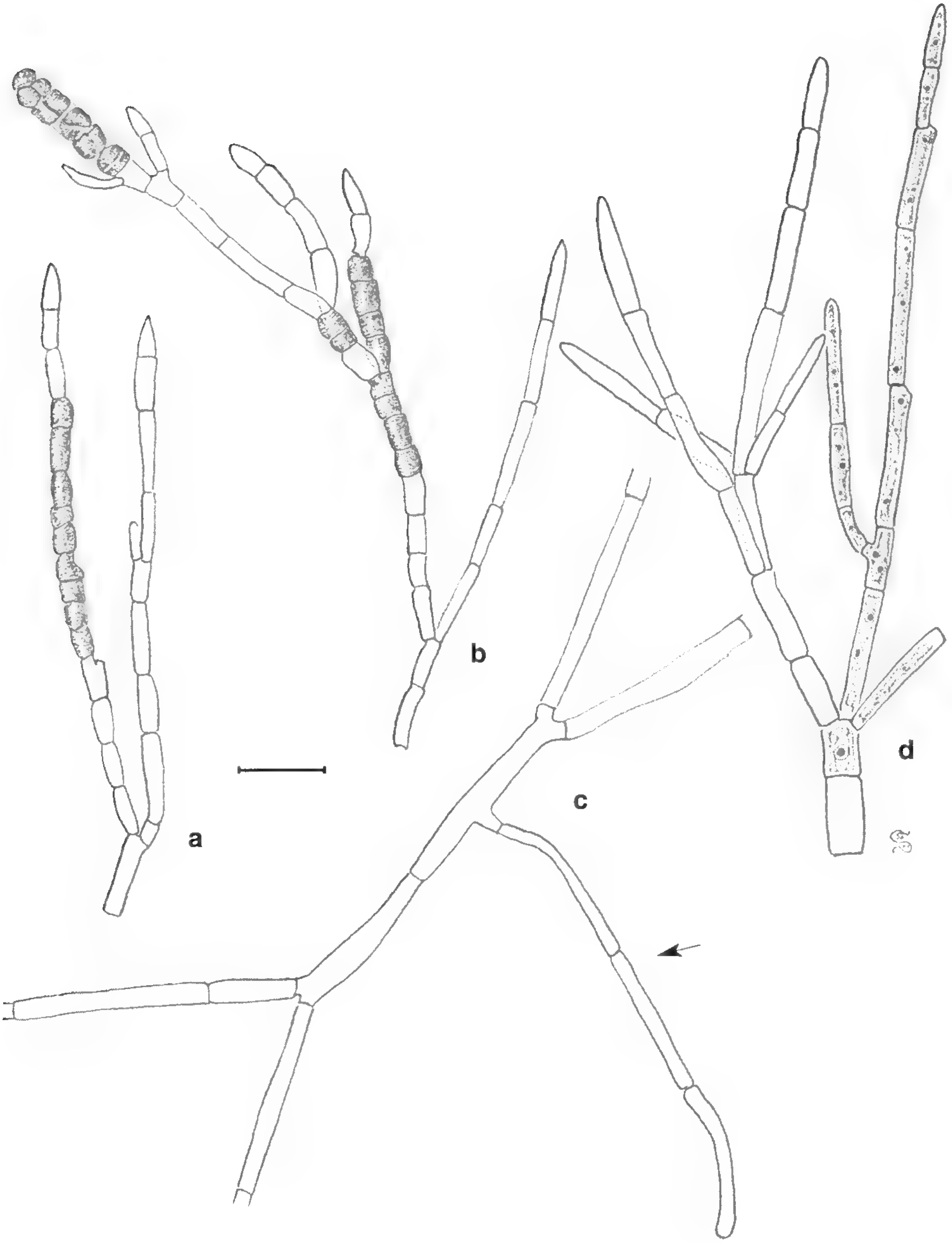

Fig. 3. ***Chaetophora pisiformis*****: a,** cortical filament with intercalary sporangium; **b,** cortical filament with terminal and intercalary sporangia; **c,** cortical filaments and upper medulla; **d,** medulla with 3-celled 'clamp-iron' (*Dostine et al., 20*). [a–d: scale 20 μm]

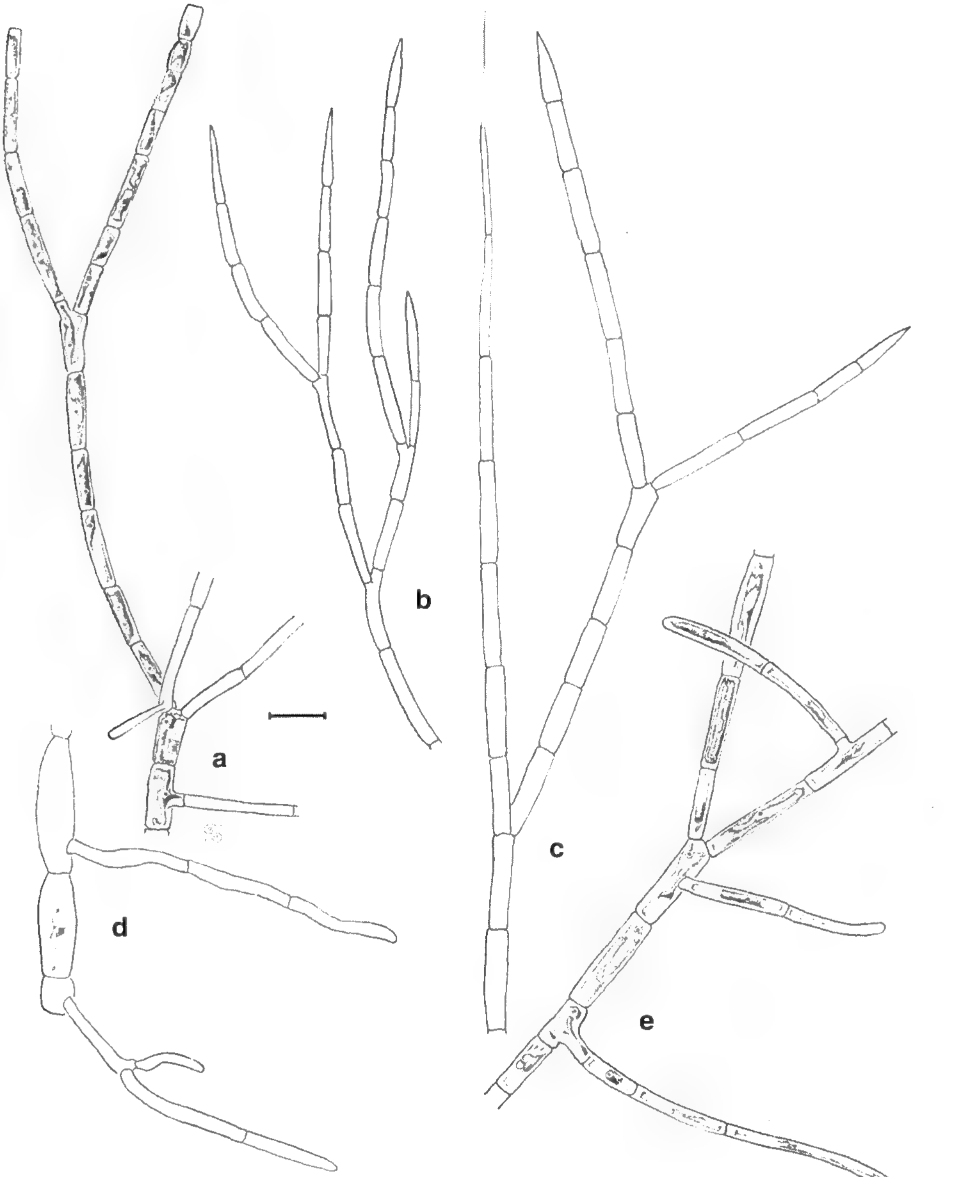

Fig. 4. ***Chaetophora attenuata***: **a,** upper medulla, showing branching to support cortex (*Skinner 0106a*); **b,** cortex (*Dostine et al. 42*); **c,** hair-like seta in cortex (*Entwisle 2247*); **d,** basal cells with rhizoids; **e,** lower medulla with 'clamp-irons' (*Skinner 0106a*). [a–e: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

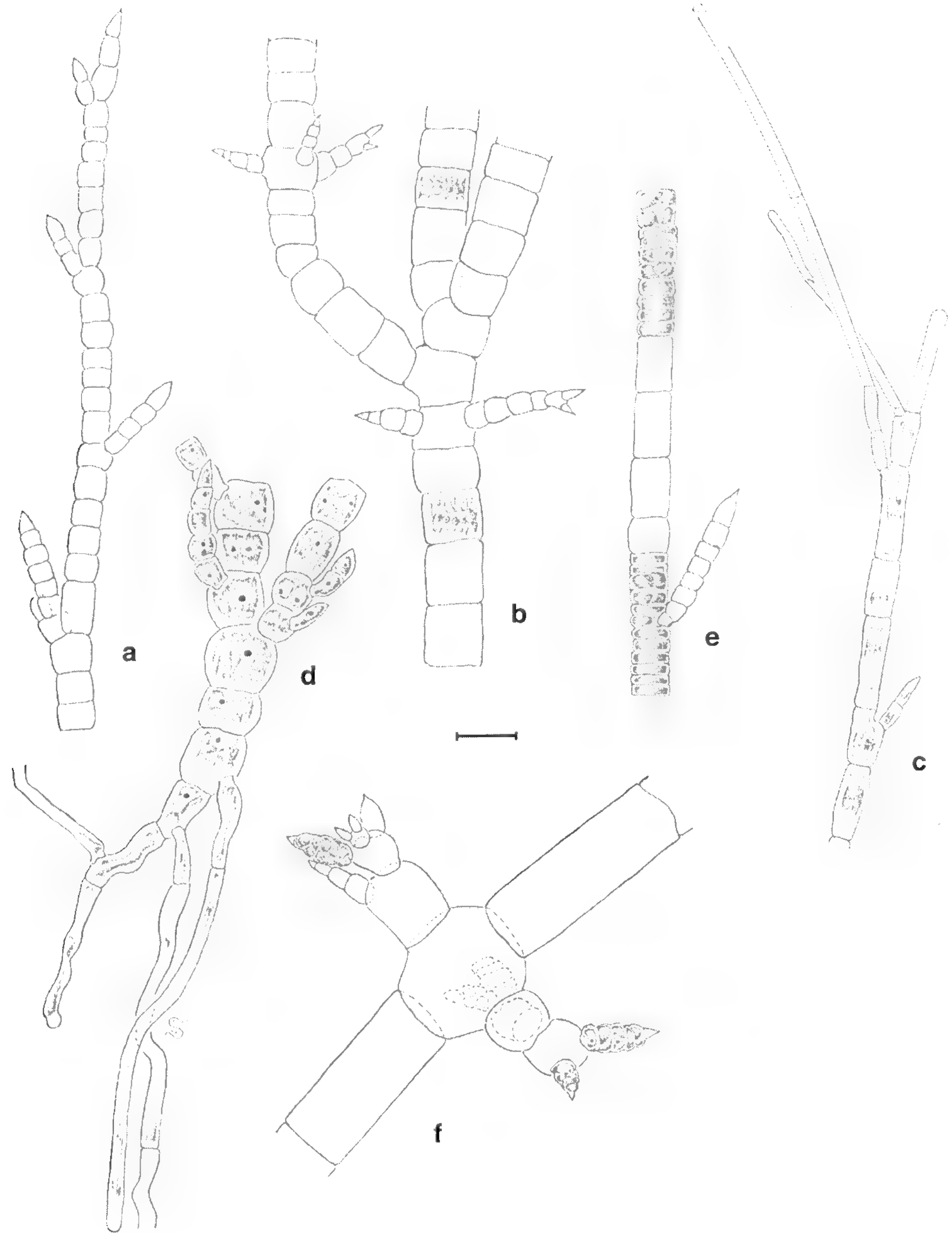

Fig. 5. ***Stigeoclonium helveticum*****:** **a,** apex of axis (*Skinner 0141*); **b,** mid-axis, with short lateral initials (*Skinner 0054*); **c,** upper axis with hairs (*Skinner 0507*); **d,** base of axis with rhizoids (*Entwisle 3141*); **e,** intercalary sporangia in main axis (*Skinner 0500*);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

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. paihiae*. 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. paihiae* 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. paihiae* Islam (syn. *Cloniophora paihiae* (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*

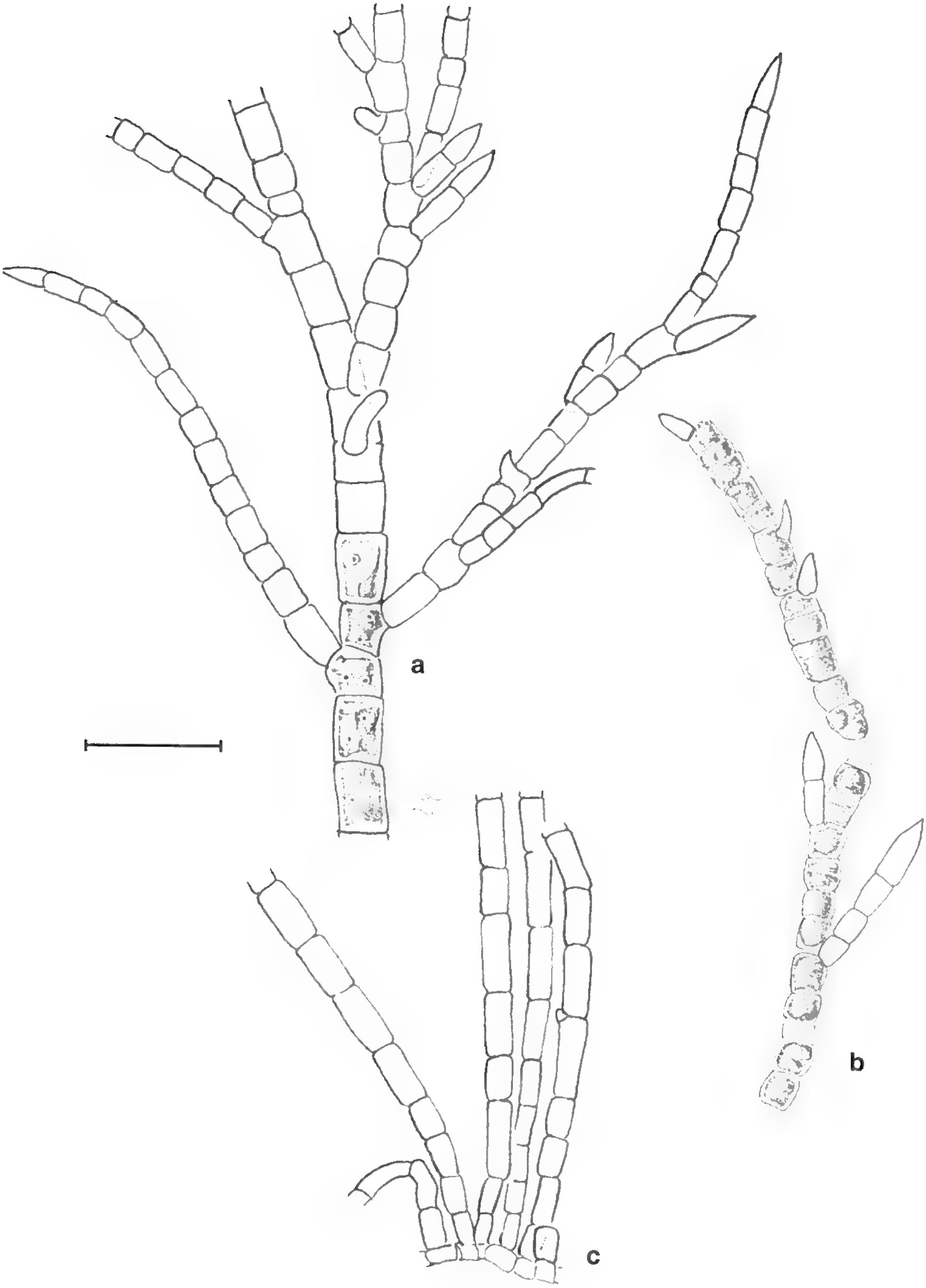

Fig. 6. ***Stigeoclonium tenue***: **a,** main axis with laterals; **b,** sporangia transforming lateral tips; **c,** axes arising from basal filament (*Skinner 0334*). [a–c: scale 20µm]

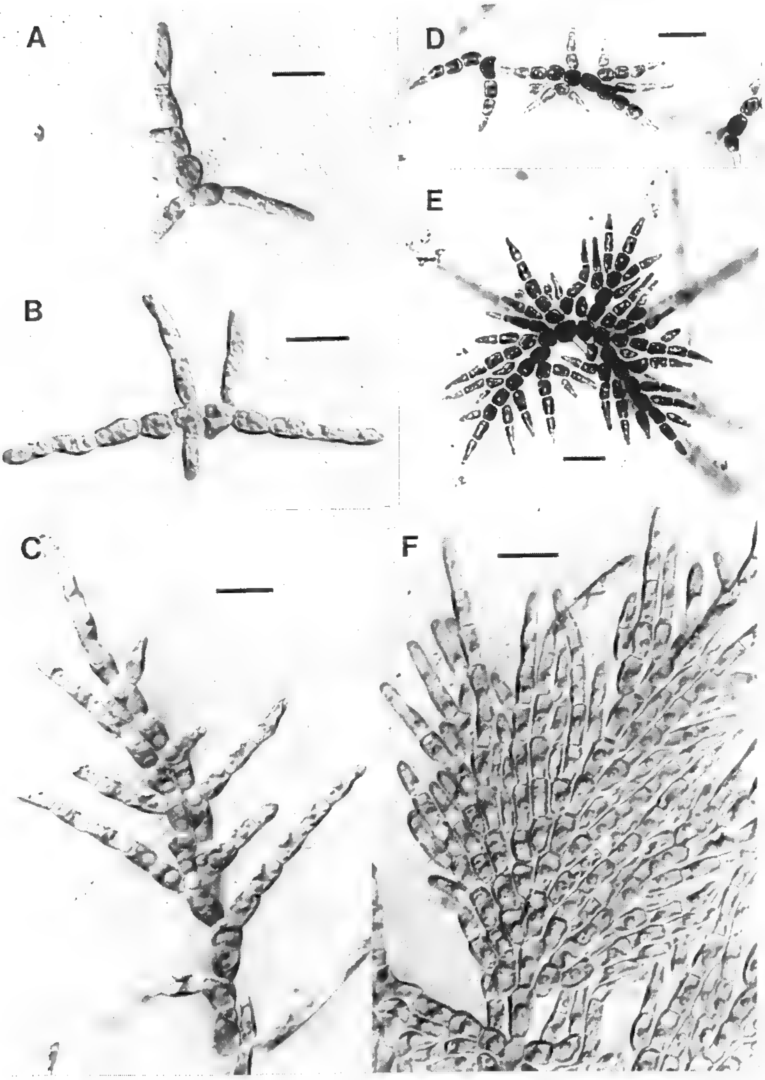

Fig. 7. ***Stigeoclonium tenue***: **a,** prostrate development of settled zoospore; **b,** prostrate development with irregular branching; **c,** open prostrate system with irregular branching (*Entwisle 833*). (Note oil globules in a–c.) ***Stigeoclonium farctum*** **d,** prostrate development of zoospore; **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

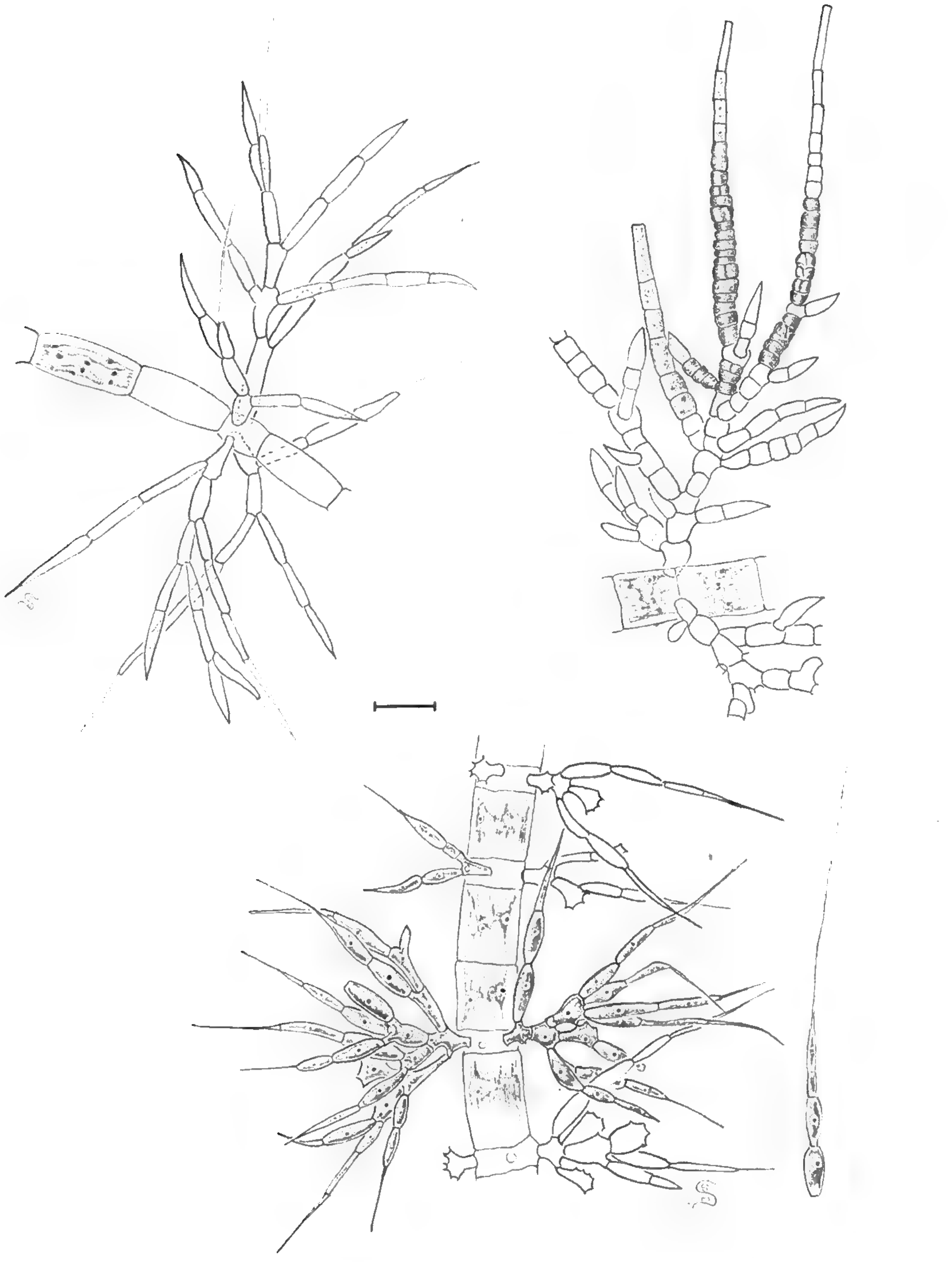

Fig. 8. ***Draparnaldia mutabilis***: **a,** axial cells with lateral fascicles, *D. judayi* variant (*Dostine* et al. *10*) **b,** lateral filaments modified as sporangia (*Skinner 0453*); ***Draparnaldiopsis salishensis***: **c,** main axis and laterals; **d,** four celled branch of lateral, with seta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

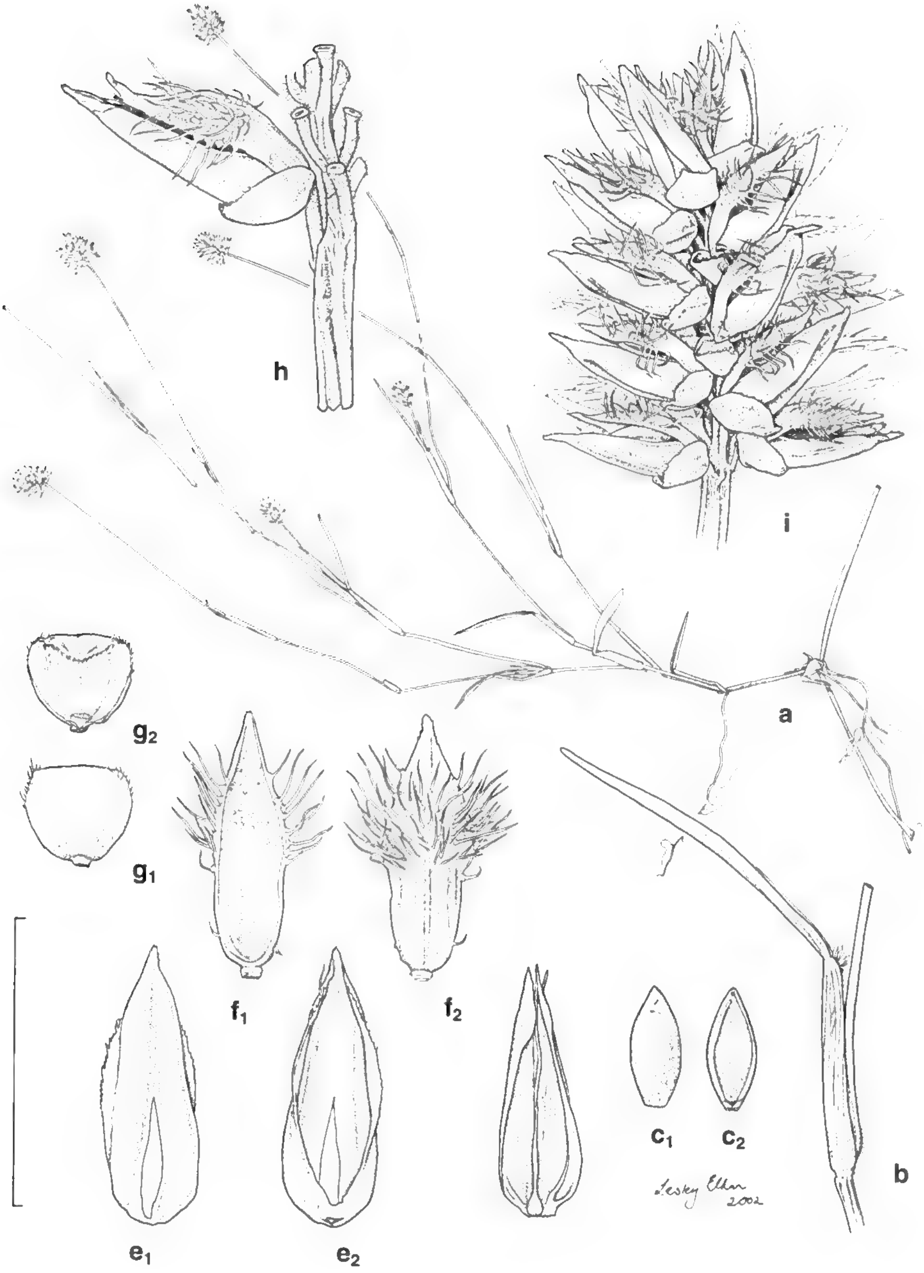

Fig. 1. *Thedachloa annua*. Scale bar 2.5 mm unless indicated otherwise. **a**, habit (scale bar 4 cm); **b**, leaf sheath and blade (scale bar 0.6 cm); **c_1**, upper or fertile lemma; **c_2**, palea of upper lemma; **d**, palea of lower lemma; **e_1**, lower lemma, dorsal view showing groove and gap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

Paper from the 5th International Flora Malesiana Symposium 2001.

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 km^2. 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, Loesenneriella, 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.

Acknowledgments

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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).

A revision of the Indigofereae (Fabaceae) in Australia. 1. *Indigastrum* and the simple or unifoliolate species of *Indigofera*

Peter G. Wilson and Ross Rowe

Abstract

Wilson, Peter G.[1] *and Rowe, R.*[1, 2] (*[1]National Herbarium of New South Wales, Royal Botanic Gardens, Sydney NSW 2000, Australia; [2]present address: Environment Australia, GPO Box 787, Canberra ACT 2601, Australia) 2004. A revision of the Indigofereae (Fabaceae) in Australia. 1.* Indigastrum *and the simple or unifoliolate species of* Indigofera. Telopea *10(3): 651–682.* The first part of a revision of Australian representatives of the tribe Indigofereae (Fabaceae) is presented. Two genera are recognised for Australia, *Indigastrum,* with one variable species, *Indigastrum parviflorum,* and *Indigofera.* In this paper, we give a general introduction to the tribe and treat *Indigastrum* and those species of *Indigofera* with simple or unifoliolate leaves; the remainder of the species of *Indigofera* will be covered in a future publication. The twelve species of *Indigofera* (ten endemic, one native and one introduced) with simple or unifoliolate leaves are fully described and one species complex is indicated as worthy of further in-depth study. Where relevant, typification, variation, and conservation status are discussed. Five new species of *Indigofera* are described and illustrated: **Indigofera ixocarpa, I. rupicola, I. petraea, I. pilifera** and **I. triflora**. Two synonyms of *Indigastrum parviflorum* are lectotypified.

Introduction

Indigofera and its allies are now widely considered to constitute a group of tribal rank, the Indigofereae (Rydberg 1923, Polhill 1981b, Schrire 1995); the tribe is predominantly one of the Old World tropics. Polhill (1981a: 199, fig. 4) considered it to be derived from a broadly defined, woody 'Tephrosieae' (=Millettieae) and *rbc*L sequence data (Doyle et al. 1997) appear to confirm that this is the case. In the latter study, two diverse representatives of the Indigofereae (*Indigofera* and *Phylloxylon*) form a strongly-supported clade that is associated with representatives of the Psoraleeae, Phaseoleae, Desmodieae, Abreae and two representatives of a polyphyletic Millettieae (*Tephrosia* and *Derris*); however, this association is not strongly supported by the *rbc*L data. In two more recent studies, of the Milletieae (Hu et al. 2000) based on sequence data from the *trn*K region, and of the genistoid tribes (Crisp et al. 2000) based on ITS sequence data, the tribe was well-supported but the topology of that part of the tree varied.

Schrire (1995) carried out a phylogenetic analysis of the tribe based predominantly on taxa from the Africa–Madagascar region. As a result he recognised seven genera, *Indigofera* plus *Cyamopsis, Indigastrum, Microcharis, Phylloxylon, Rhynchotropis* and *Vaughania,* compared with the four accepted by Polhill (1981b). Schrire's study reviews the history of the classification of the Tribe and the various taxonomic schemes proposed for the genus *Indigofera,* and provides a revised system of Sections and Subsections for taxa from the African region. Schrire's classification accommodates a number of widespread taxa and he (Schrire 1995, pers. comm.) has suggested sectional and subsectional positions for a number of Australian taxa. Barker et al. (2000) followed this study with a molecular survey of the tribe based on sequences from three regions, chloroplast *trn*L and *trn*K introns, plus the nuclear ITS spacers, using outgroups from the core Milletieae. Their analysis confirmed that *Phylloxylon* is sister to the rest of the tribe. It also supported the generic segregates accepted by Schrire (1995) with the exception of *Vaughania*, which was nested in the *Indigofera* clade as sister to the anomalous species *Indigofera ammoxylum*. Barker et al. (2000) conclude that further research on the position of *Vaughania* is required. Schrire et al. (2003) conducted a combined analysis of molecular (ITS) and morphological data from 87 species of *Indigofera* that confirmed the findings of Barker et al. (2000) for the tribe Indigofereae. Schrire et al. (2003) also found four monophyletic clades within *Indigofera* itself: the Cape clade, the Boreotropical clade, the Paleotropical clade, and the Pantropical clade. All except the Boreotropical clade showed strong bootstrap support in parsimony analyses but all four received high likelihood scores under Bayesian analysis. The three endemic Australian species in the study (*I. pratensis*, *I. rugosa* and *I. australis*) were members of the Pantropical clade and formed a monophyletic group under both parsimony and bayesian analyses. Of the three widespread native species included, *I. trita*, *I. trifoliata* and *I. colutea*, the first two were members of the Boreotropical clade and the latter of the Paleotropical clade.

Bentham (1864) was the first to give a full account of the Australian species of *Indigofera* then known. He did not adopt any formal subgeneric classification; he did not use the sections set up by de Candolle (1825) or in any way anticipate the subgenera he adopted later (Bentham 1865). Bentham merely separated the species into two groups labelled 'Herbaceous Species' and 'Shrubby Species'. Apart from the contribution of Domin (1926), who described a number of new species and proposed a few nomenclatural changes, there has been little revisionary study of the genus in Australia.

Davidson and Davidson (1993) consider the possible time of establishment and development of various Australian genera of legumes. Their hypothesis is that one group of genera, including *Indigofera*, first became established in Australia during the late Miocene (5–11 Ma) with the widespread appearance of sclerophyllous vegetation. They suggest that radiation of these early, established genera may have entered a new phase during the early Pleistocene (post 2.5 Ma) during a time of rising temperatures and development of more open vegetation types. The most widespread Australian species, *Indigofera australis*, has the distribution, ecological preference and variability consistent with a long history in Australia. *I. australis*, and a number of other Australian species with ± glabrous fruits, would fall in Schrire's sect. *Psiloceratiae*, a relatively unspecialised group judging by its position in his published morphological analysis (Schrire 1995). Schrire et al. (2003) carried out rate analyses that estimated the age of the Pantropical clade to be about 12–20 Ma, which would be consistent with the estimate given above for the age of the Australian endemic element.

Schrire (1995) presents two hypotheses of relationships for the tribe Indigofereae: a cladogram and a preferred phylogenetic tree one step longer. There is no major difference between these hypotheses. According to this analysis, the other genera in the tribe are basal and are either restricted to, or centred on, the Africa–Madagascar region. There are around 540 species of *Indigofera* in the same area and it should be noted that, within the genus, the widespread species and many of the tropical Asian and Australian species fall into the more derived groups. Schrire does not specifically mention American endemic species but, from his treatment of the sections set up by Rydberg (1923), these seem to fall into a variety of basal and derived groups. This clearly points to an origin of the tribe in West Gondwana with *Indigofera* itself extending to Australia and South America where it has diversified further. The later analysis of Schrire et al. (2003) does not contradict these general conclusions. Species from northern Africa and Asia seem to belong to either more derived or to pantropical groups. This could indicate a more recent radiation of species by way of northern Africa to Asia and from there to Australia. Although most of the non-endemic species in Australia have distributions consistent with this hypothesis, there is no easy explanation for the absence of *Indigastrum parviflorum* (formerly *Indigofera parviflora*) from Burma (Sanjappa 1985) and other parts of Southeast Asia (de Kort & Thijsse 1984).

Schrire (1995) recognised infrageneric taxa for African species of *Indigofera* and had suggested (in litt. 1992) placement of some Australian species in this scheme. However, as a result of the analyses presented in Schrire et al. (2003), some of the relationships suggested in the earlier paper have been questioned and the classification system requires modification. So, in the present paper, the affinities of many Australian taxa are be suggested (in notes under individual species) but placement of endemic Australian species in sections or informal groups is not attempted in any systematic way.

Morphology

Schrire (1995) discusses a large number of morphological characters as a prelude to his cladistic analysis. We will consider only some of these characters, and then mostly in relation only to endemic Australian taxa.

Habit

As indicated by Schrire, the type of habit is likely to be of phylogenetic importance. The Australian species can be divided roughly into three categories based on habit. Plants that could be described as shrubs or large shrubs, such as *Indigofera brevidens, I. australis, I. adesmiifolia* and some members of the *I. pratensis* group, occur predominantly on the east coast in more mesic habitats or on better soil types. This accords well with Schrire's designation of this type of habit as plesiomorphic. Next, there are those species that occur as subshrubs or perennial herbs, for example *I. efoliata, I. baileyi, I. triflora,* the *I. georgei* and *I. rugosa* groups, and other members of the *I. pratensis* group; these occur in the more arid or seasonally dry parts of Australia. Annual herbs are apparently uncommon amongst the endemic species, with only two annual species, *I. haplophylla* and *I. ammobia*; these occur in the monsoon tropics (*I. haplophylla*) and the Tanami and Great Sandy Deserts (*I. ammobia*). The native species with wide extra-Australian distributions, particularly *I. colutea, I. hirsuta, I. linnaei, I. linifolia* and *Indigastrum parviflorum,* occur in a wide variety of habitats, mostly towards the northern parts of the continent, and often in disturbed sites. It is highly likely that these taxa now occupy a greater range than they did before European settlement and there is also a strong possibility that the Australian populations of these species have been augmented by the introduction of seed from non-Australian sources.

Trichomes/emergences/'glands'

The tribe Indigofereae is characterised by biramous hairs. This is one of only a few morphological synapomorphies for the tribe. The biramous hairs predominantly have arms of equal lengths but in some species unequally biramous hairs occasionally occur. *Indigofera hirsuta* is well documented as having very unequally biramous hairs (Gillett 1958, 1971: fig. 45/13, Prabhakar et al. 1985: figs 7–9, Schrire 1995: plate 3e) to the extent that they may superficially appear simple.

There are a number of different types of multicellular trichomes or emergences found in the tribe. These have long been recognised at species level and were used by Rydberg (1923) to define two Sections in *Indigofera*. The first kind of multicellular hair is the sticky, gland-tipped type found in *I. colutea* and *I. adenotricha*. In *I. colutea*, the density of these hairs varies markedly; some specimens are very heavily clothed in them, in others they are virtually restricted to the fruit, and in rare cases they seem to be lacking altogether. In the few available specimens of *I. adenotricha*, the gland-tipped hairs occur on all parts of the plant; the glandular tips of the hairs are about twice the size of those found in *I. colutea*.

Schrire (1995) includes the other prominent types of multicellular emergence under the category 'pearl bodies' but the definition of pearl bodies that he gives (citing O'Dowd 1982, see also Uphof 1962: 165) does not seem appropriate for the various structures observed in Australian species. None are lustrous and pearl-like, and none appear to be filled with lipid. However, Schrire (1989: 241) records that he had personally observed small, red, multicellular 'glands' in the leaf axils of some African species being 'milked' by ants; we have not observed this in any Australian species. Both O'Dowd and Uphof acknowledge that these structures are of heterogeneous origin in dicots and there is no evidence to indicate whether or not the main forms that occur in *Indigofera* are homologous. Schrire recognises two main classes, the clavate to cylindrical type and the hollow-discoid type, and he himself treats them as independent characters in his analysis. These structures are both commonly called 'glands' in the literature but it has not been demonstrated that they have any glandular function. In this study we avoid use of the terms 'gland' and 'pearl body' for these structures and refer to these emergences merely as multicellular hairs or trichomes.

The clavate type of multicellular hair is very common in Australian species, although they are often inconspicuous and only occur in conspicuous clumps in a few species, viz. *I. adesmiifolia, I. australis, I. bancroftii, I. brevidens, I. centralis* ms., *I. coronillifolia, I. haematica* and *I. helmsii*. They also form conspicuous clumps in the axils of the stipules in many specimens in the western Australian form of *I. australis*. These structures are orange-red to deep red in colour, the colour darkening with age. In a few species, clavate emergences may occur scattered on other parts of the plant, particularly on inflorescence axes and sepal margins (for an example of this, see Schrire 1995: fig. 6f). A variation of the usual clavate type occurs in *I. circinella* where they are more conical than club-shaped.

A probable variant of the clavate type is found in a few species. In these taxa the multicellular trichomes are uniseriate rather than multiseriate and are less rigid; they appear pointed. They are borne in similar places to the clavate type, i.e. on the rachis between leaf pairs and at the leaf axil. These linear trichomes are characteristic of, and well-developed in, *I. decipiens* ms. but are found to varying extents in a range of other species.

The hollow-discoid type of emergence (Prabhakar et al. 1985) is characteristic of *I. trifoliata* and *I. glandulosa*; they are visible on the undersurface of the leaflets as yellow to dark brown spots.

Two Australian species, *I. ixocarpa* and *I. verruculosa*, have small, wart-like, multicellular emergences that are found on most aerial parts of the plant; to our knowledge, emergences like these have not been recorded for any extra-Australian species. They do not appear to be stalked and may arise from depressions in the epidermis in the same way as the hollow-discoid type; anatomical investigation is needed to confirm this. In *I. ixocarpa* these structures appear to be the source of a viscid exudate that covers the stems, leaves and fruits while in *I. verruculosa* no such exudate is produced.

Leaves

Leaves are pinnate (imparipinnate), trifoliolate, unifoliolate or simple. Unifoliolate and simple leaves have arisen many times in unrelated species by reduction. Gillett (1958) stresses that the distinction between simple and unifoliolate leaves should not be given too much significance, as the distinction is not always easy to apply. However, for the Australian species, we will maintain the distinction: unifoliolate leaves are defined as having a distinct articulation in the 'petiole', in many cases with stipellae present; the distal portion of the 'petiole' is homologous with the petiolule or leaflet stalk. Simple leaves, on the other hand, are defined as having a short, uniform petiole.

Leaflets are usually opposite on the rachis but are markedly alternate in a few species. In a few cases (*I. efoliata* and *I. adesmiifolia*) they are reduced and ± caducous leaving phyllode-like rachises. This phenomenon is variable in *I. adesmiifolia* and is best developed in those populations with wider rachises and smaller leaflets. Stipellae are usually small or absent, but are conspicuously present (regularly 1 mm or more long) in at least seven species and are smaller, but discernible, in many others. In *I. oxyrachis*, the weakly spinescent rachis-tip appears to have been formed by fusion of the distal pair of stipellae.

Stipules are mostly small, ± triangular and inconspicuous but some are more elongated, verging on setaceous. Stipules with scarious margins are found in one widespread native species (*I. linnaei*), and a few introduced species (*I. circinella, I. cordifolia, I. hendecaphylla* and *I. spicata*). It is worthy of note that all these species, except the simple-leaved *I. cordifolia*, have leaflets that are alternate on the rachis. Two other species, in particular, have rather specialised stipules. *I. helmsii* has broad triangular stipules that become recurved, hardened and somewhat spinescent. *I. cornuligera* ms. has stipules that are linear and tapering but become thickened at the base to produce a hardened horn-shaped organ.

Flowers

Schrire (1995) gives a very detailed account of the variation in floral morphology in the tribe Indigofereae. He remarks that the more plesiomorphic taxa in the tribe, and in *Indigofera* itself, have calyx lobes that are shorter than to ± equal to the length of the tube. Bentham (1864) recognised this and used the length of the calyx lobes relative to the tube as a major key character in his Flora Australiensis.

Schrire scores pink to mauve or white flowers as plesiomorphic in the tribe. The Australian species have flowers that are predominantly pink to mauve in colour but a few are red-flowered. *I. haematica* has a maroon standard but the other petals are pinkish. Occasional white-flowered forms of usually red-flowered species have also been recorded (e.g. in *I. erubescens* ms.).

Corolla indumentum is one of the main distinguishing characters between *Indigofera* and *Indigastrum* with the latter characterised by a glabrous corolla. In *Indigofera,* the back of the standard and the apex and upper margin of the keel are usually noticeably hairy, sometimes with dark-coloured hairs. Apart from the lack of hairs, *Indigastrum parviflorum* also has a keel that is open and somewhat spathulate at the apex; Schrire calls this a 'prolonged rostrum'.

The keel also has what Schrire (1995) calls 'lateral prominences' which take the form of pockets or spurs and which may interlock with the wings to produce a platform level with the upper margin of the keel. Nair and Tewari (1975) show that the tips of the spurs in *Indigofera enneaphylla* (= *I. linnaei*) are glandular and apparently exude nectar. In *Indigastrum* these pockets are rather shallow while in species of *Indigofera* they are prominent and spur-like. The interlocked wings and keel have long been known to be tripped by probing at the base of the flower (e.g. Henslow 1867) with the stamens and style remaining in their former position (see Fig. 3c). The falling platform releases a cloud of pollen that may effect self-pollination but may also serve to deposit pollen on the abdomen of an insect. Hence, the tripping of the flower may increase out-crossing although many, perhaps all, species are self-compatible. Standard length and staminal tube length have been stressed in the keys and descriptions since the tripping of the flowers very often results in the wings and keel falling from the flower. The staminal tube is persistent and can usually be measured in fruiting specimens.

Schrire considers that a synapomorphy for many groups of herbaceous taxa in *Indigofera* is the combination of short ovary and long style; however, he does not quantify this. In species found in Australia, some species that have few-seeded fruits, and therefore short ovaries, do have relatively long styles but this is not restricted to herbaceous taxa; in fact, the introduced herb *I. sessiliflora* has a style shorter than the ovary. Amongst the native, shrubby taxa, *I. rugosa* and *I. tryonii* have styles 1–2 times longer than their ovaries while *I. pilifera* has a style that is over twice the length of the ovary.

Anthers of *Indigofera* species almost always have a dark coloured connective. They are usually glabrous but in some species there are tufts of hairs at the base and sometimes at the apex as well, as is the case in the introduced species *I. decora*. These hairs have also been recorded in *I. rugosa*. A few hairs at the base of the anther have occasionally been observed in a few species (including *I. baileyi*) but Schrire scores hairs absent or few as plesiomorphic in the tribe. In this study, green anthers were observed in at least some specimens of the related species *I. haplophylla* and *I. ammobia*.

Pollen

In a survey of the pollen morphology of the Indigofereae, Ferguson and Strachan (1982) sampled six species from specimens collected in Australia. Three of these species were endemics, viz., *Indigofera australis*, *I. 'brevidens'* (=*I. gilesii* ms.) and *I. 'haplophylla'* (=*I. rupicola*). The first two were classed as Type I, Subtype IC and the third was classed as Type III. The only taxon from Australia with Type IV pollen was the widespread *I. linnaei*. Ferguson and Strachan comment that Type I pollen occurs in predominantly woody groups and that there is a transition to Type III in more shrubby taxa, while Type IV occurs in more herbaceous groups which they consider as likely to be morphologically derived. Schrire (1995) considered that Types I and III graded into each other and that they represented the plesiomorphic state compared with Type IV pollen.

Wu and Huang (1995) propose a somewhat different classification of pollen in their study of Taiwanese *Indigofera* species and recognise five types rather than four. They include a number of species that occur in Australia, either as adventives (*I. tinctoria* [Type I], *I. spicata* [IV] and *I. suffruticosa* [V]) or as natives (*I. hirsuta* [Type II], *I. linifolia* [III] and *I. trifoliata* [IV]). The only species common to the two studies was *I. trifoliata*, which Ferguson and Strachan (1982) put into their type III. Wu and Huang (1995) also consider Type I pollen to be plesiomorphic and that both Types III and IV have arisen through modification of Type II pollen; Type V may be derived from Type IV or, perhaps, from a sub-type of Type I (Wu & Huang 1995: Fig 117).

Schrire and Sims (1997) examined pollen of 86 species in the tribe Indigofereae from Africa and Madagascar. Based on a phenetic analysis of pollen features, these authors recognised three groups within *Indigofera* itself, which they call groups A–C. Comparing these groups to the pollen types of Ferguson and Strachan (1982) they found Group A to be most comparable to Type 1C, Group B to Type 3 and Group C to Type 4C. Compared to the phylogenetic analysis of Schrire (1995) they found that in sect. *Indigofera* the larger-flowered, more plesiomorphic species had Group A pollen, while the more derived, smaller-flowered species were referable to Group B. Group C pollen characterises many of the derived tropical members of the genus.

Pod

Schrire (1995) discusses features of the fruit relevant to the Australian taxa and these will not all be repeated here. De Kort and Thijsse (1984: 93) were the first to recognise that all species have a persistent fruit-base that remains with the calyx and staminal tube after the valves of the open pod have fallen. Schrire considers this a synapomorphy for the tribe.

There is much variation in size, orientation and indumentum. Schrire scores glabrous pods as apomorphic. Pods that are glabrous or have very few hairs occur fairly commonly in Australian species. Orientation, the angle at which the pod is held on the axis of the infructescence, is often distinctive for a species but in other cases the angle seems to vary. Most endemic species have terete pods but pods are noticeably subtorulose in at least one species, *I. chamaeclada* ms., and slightly so in some others.

Virtually all endemic species have endocarp tannins present. The exceptions, apart from *I. ewartiana* and *I. polygaloides*, which are members of the *I. trita* group (Wilson & Rowe 1994), are *I. baileyi* and *I. mackinlayi* ms. However, the last two species are variable in this and faint spots are visible in some specimens.

Chromosome numbers

The base chromosome number for *Indigofera* is x=8 (Frahm-Leliveld 1966, Goldblatt 1981) with occasional tetraploids (2n=32); *Indigastrum* has a base number of x=7. As far as we can determine, there is only one chromosome count for an endemic Australian species, although counts exist for all widespread native and introduced species. Gupta and Agarwal (1982) record n=8 for *I. brevidens*, but this name has been one of the most widely misapplied *Indigofera* names in Australia so, in the absence of a voucher, it is uncertain which species they examined. Further investigation would be required to establish whether species from arid Australia show a higher incidence of polyploidy, as implied by Frahm-Leliveld (1966).

Toxicity

Non-protein amino acids: two toxic non-protein amino acids occur in *Indigofera*, canavanine and indospicine, both analogues of arginine. Canavanine is fairly toxic to some insects but is apparently harmless to mammals. Indospicine, on the other hand, is a strong hepatotoxin. An analysis of numerous seed samples (Charlwood et al. 1984) found measurable levels of indospicine in only six species, including *I. trita*, *I. hirsuta* and *I. spicata*. The delimitation of *I. spicata* has been reassessed (Du Puy et al. 1993) and *I. hendecaphylla* is now recognised as separate from it. It is not certain that both these species have been implicated in poisoning cases, but some published records (e.g. Morton 1989) definitely refer to *I. hendecaphylla*. As far as we are aware, there have been no reports of poisoning by *I. trita* or *I. hirsuta*. *Indigofera linnaei* is known to cause the condition 'Birdsville Disease' in horses, and although this species does contain indospicine (Dowling & McKenzie 1993: 78, Bruneton 1999: 279), which can affect dogs fed with contaminated horsemeat, this 'disease' is a neurological disorder and is not caused by Indospicine.

Aliphatic nitrocompounds: compounds derived from β-nitropropionic acid (NPA) have been recorded from very many species of *Indigofera* and may even occur in all of them. It has been suggested that NPA could be toxic by causing methaemoglobinaemia (through oxidation of haemoglobin hence blocking its oxygen-carrying ability). Similar nitrocompounds in *Astragalus* are known to have this effect but there is no evidence that any *Indigofera* species does. Although the precise cause of 'Birdsville Disease' is not known, some researchers (e.g., Majak et al. 1992) have suggested that NPA is implicated in some way.

Systematic treatment

Where possible, taxa have been lectotypified. Nomenclatural issues and questions were addressed in accordance with the *International Code of Botanical Nomenclature* [ICBN] (Greuter et al. 2000).

Key to genera of Indigofereae in Australia

Standard glabrous; keel rostrate; fruit somewhat bilaterally flattened, partitions between seeds membranous, endocarp never spotted .... **Indigastrum**

Standard with hairs on back; keel not rostrate; fruit ± round (rarely somewhat tetragonal) in section, partitions between seeds (when present) usually pithy, endocarp often spotted .... **Indigofera**

Indigastrum

Indigastrum Jaub. & Spach, Ill. Pl. Or. 5: 101, t. 492 (1856)

Indigofera 'group' *Indigastrum* (Jaub. & Spach) Bak. f., Leguminosae Trop. Afr. 1: 161 (1926)

Indigofera subg. *Indigastrum* (Jaub. & Spach) Gillett, Kew Bull., Add. Ser. 1: 123 (1958)

Type: *I. deflexum* (A. Rich.) Jaub. & Spach (= *I. parviflorum*).

Annual herbs or subshrubs. Indumentum of equally two-armed hairs, appressed; multicellular and glandular hairs absent. Leaves pinnate, rarely 1–3-foliolate (but never exclusively unifoliolate); stipellae absent. Stipules present, not persistent or spinescent. Inflorescence a pedunculate axillary raceme; flowers pedicellate; bracts caducous. Calyx lobes 5, equal to or longer than the tube, with a broad u-shaped sinus between the upper lobes. Corolla pink, mauve or white; standard glabrous, base narrow, gradually tapering to the claw; wings glabrous; keel glabrous, lateral pockets pouch-like, apex open, ± spathulate. Stamens 10, 9 filaments connate and 1 free; filaments alternating long and short; anthers apiculate, glabrous or anthers of the shorter stamens rarely with scales at the base. Ovary sessile, pubescent; ovules numerous. Style shorter than the ovary, incurved; stigma oblique. Pod usually straight and descending, linear, terete to slightly bilaterally flattened; endocarp never spotted. Seeds cylindrical or cuboidal, never globose, separated by papery outgrowths of the endocarp. Chromosome number 2n = 14.

Indigastrum parviflorum (Wight & Arn.) Schrire, Bothalia 22: 168 (1992)

Indigofera parviflora Heyne ex Wight & Arn., Prod. Fl. Pen. Ind. Or.: 201 (1834)

Type citation: '*Heyne! in Wall.! L. n.* 5457; *Wight*! *cat. n.* 859.—Mysore; *Heyne*. Cunnawady.'

Type (*fide* Schrire 1992): India, in herb. Wallich no. 5457, *Heyne s.n.* (K).
Anila parviflora (Wight & Arn.) Kuntze, Rev. Gen. Pl. 2: 939 (1891)

Indigofera oxycarpa F. Muell., Fragm. 3: 103 (1862) nom. illeg., non Desv. (1814)

Type citation: 'In collibus petraeis nec non ripas glareosas secus flumina Victoriae et Sturt's Creek.'

Lectotype (**designated here**): Sturts Creek, *F. Mueller s.n.* (MEL 586188, fruiting element).

Indigofera brachyodon Domin, Biblioth. Bot. 89 (3): 189 (1926)

Type citation: 'Queensland: Grassflächen der Rolling Downs zwischen Hughenden und Mt. Walker (DOMIN II. 1910)'.

Lectotype (**designated here**): Locis graminosis in collibus Rolling Downs inter opp. Hughenden et Mt. Walker, *Domin 4532*, Feb 1910 (PR 527209).

Illustrations (all as *Indigofera parviflora*): Hacker (1990: 184) photo; Milson (1996: 50) photo; Wilson (1992) fig. 125B.

Erect, annual herb 0.2–0.75(–1.5) m high, with taproot. Young stems ridged, green, strigose; hairs moderately dense, appressed, equally biramous. Leaves pinnate, rarely uni- or trifoliolate; leaflets (1–)5–11. Petiole (3–)7–15(–20) mm long. Rachis furrowed; multicellular hairs between leaflet pairs absent; stipellae absent. Leaflets linear to narrowly elliptical or ovate, (10–)20–45 mm long, 1–6 mm wide, opposite. Upper surface of leaflet green, glabrous, or rarely sparsely hairy; hairs (if present) appressed. Lower surface of leaflet green, hairs sparse to moderately dense, appressed. Discoid glands on lower surface absent. Veins not prominent. Apex obtuse and shortly mucronate. Stipules narrowly triangular or subulate, 1–1.9 mm long, sparsely pubescent, not persistent or spinescent. Inflorescence (2–)10–30(–40) mm long, shorter than the leaf. Peduncle 0.5–0.9 mm long. Bracts ovate, 0.3–1.1 mm long. Flowers purplish to pinkish to red or orange. Pedicel 0.5–0.9 mm long. Calyx 1.5–3 mm long; hairs sparse to moderately dense, white, appressed; lobes equal to or longer than the length of the tube, unequal to subequal. Standard reddish, obovate, 5.9–6.5(–7.2) mm high, (3.5–)4.5–5.2 mm wide. Wing narrowly obovate, 6.5–8 mm long, (2.0–)2.7–3.5 mm wide. Keel 5.5–7.7 mm long, 1.2–1.5 mm wide, glabrous; apex spathulate, drawn out from body of the keel (1.0–)1.4–2.2 mm. Lateral pockets present but inconspicuous, 0.1–0.3 mm long. Stamens colourless. Staminal tube 3–3.8 mm long. Ovary moderately hairy with fine hairs. Pod descending, somewhat bilaterally flattened, (12–)20–40(–48) mm long, 2–3 mm deep, yellowish or brown, strigose; hairs moderately dense, appressed; apex upturned, shortly beaked; endocarp not spotted. Seed (10–)14 per fruit.

Notes: the basionym *Indigofera parviflora* is yet to be lectotypified. Although a particular specimen was indicated by Schrire (1992), there are a number of specimens at Kew that are consistent with the citation in the protologue; a lectotype is to be chosen from these syntypes (Schrire pers. comm.).

Although a poor specimen in other respects, we have chosen the fruiting element on the sheet MEL 586188 as lectotype of *Indigofera oxycarpa*. The fruits are unquestionably of *Indigastrum parviflorum* and Mueller's taxon was named for the distinctive fruit shape. The other two sheets at Melbourne (MEL 586184, 586185) and the two at Kew, all from the Upper Victoria River, consist only of flowering specimens.

Domin (1926) recognised *I. brachyodon* as distinct from *I. parviflora* based only on the short calyx lobes of his specimen. There are three sheets at PR containing type material; the material is presumably all part of a single collection (the 'collecting numbers' were added later). Of these, we have chosen the sheet PR 527209 as lectotype. This sheet consists of a single plant, including roots, that is both flowering and fruiting; PR 527210 has two flowering stems, without roots, that may not come from the same plant, and PR 527208 is a mixed sheet.

A few specimens from near Pine Creek, one from Litchfield National Park, and a few from north-eastern Queensland have only 1–3 leaflets and these seem also to have a more slender habit. In Africa, a separate subspecies (subsp. *occidentalis*) is recognised for populations with a lower leaflet number. A more detailed analysis of Australian populations might lead to the recognition of infraspecific taxa, but a study of the species across its entire range would be desirable to place this variation in context.

Distribution and habitat: Queensland, Northern Territory, and Western Australia: recorded from heavy black or red clay soils, gravelly loams or sand in grasslands and open savanna woodlands. It often occurs on roadsides and disturbed sites and is thus considered a weed (Lazarides et al. 1997). Beyond Australia it is recorded from north-eastern to southern Africa and India.

Selected specimens: Queensland: Burke: Mount Walker, S of Hughenden, *Wilson UNSW 13453 & Puttock*, 23 Apr 1982 (NSW, UNSW); 35 km N of Julia Creek on the Normanton road, *Pullen 10425*, 21 Mar 1977 (CANB); 67 km WNW of Mount Isa, 6 km N of Mingera, *Harris 647*, 9 Mar 1991 (NSW). Cook: 45 km from Walsh River crossing on Mungana–Wrotham Park road, *Clarkson 3020*, 9 Mar 1980 (BRI); 2 km NE of Marina Plains turn-off on the Musgrave to Lakefield road, *Clarkson 7111 & Simon*, 9 May 1987 (BRI, NSW, QRS); 36.3 km from Dixie Station on the track to Killarney, *Clarkson 8155 & Neldner*, 5 June 1989 (NSW); 24.2 km S of Batavia Downs on the Peninsula Development Road, *Clarkson 8327 & Neldner*, 19 Apr 1990 (NSW); 2.8 km from Lappa on road to Sunnymount, *Clarkson 9197*, 23 Feb 1992 (NSW). Gregory North: Mimong, *Blake 11512*, 16 May 1936 (AD, BRI). Leichhardt: Tanderra (Nardoo), c. 45 miles SW of Springsure, *Johnson 1315*, 15 Feb 1960 (BRI, CANB). Maranoa: Mt Abundance, 1.5 miles [c. 2.5 km] from Mitchell Highway, *Martin s.n.*, 25 May 1962 (BRI). Mitchell: Athol, c. 20 miles W of Blackall, *Everist 3805*, 28 May 1949 (BRI); 13.5 km east of Hughenden on road to Charters Towers, *Blaxell 89/059, Johnson & D'Aubert*, 26 July 1989 (NSW). Warrego: Morven, *Blake 10992*, 2 Apr 1936 (BRI, CANB).

Western Australia: Fitzgerald: Inglis Gap, Gibb River Road, *Wilson 220*, 10 May 1988 (NSW, PERTH). Fortescue: 1.9 km WNW of Wittenoom turn-off, North West Coastal Highway, *Wilson 1007, Rowe & Mitchell*, 10 Sep 1991 (NSW, PERTH, PRE, K, L); c. 30 km W of Millstream homestead on Pannawonica road, c. 2 km N of McCarthys Bore, *Mitchell PRP203*, 31 Mar 1994 (NSW). Gardner: above and about Port Warrender, *Symon 10240*, 29 May 1975 (PERTH); 40 km E of Kununurra, *Andrew 287*, 17 Jan 1979 (DNA).

Northern Territory: Barkly Tableland: 3 miles [c. 4.8 km] NW Alexandria homestead, *Chippendale NT 1896*, 22 Mar 1956 (BRI, DNA, NSW). Central North: 8 miles [c. 12.8 km] S of Tobermorey Homestead, *Latz 2536*, 22 May 1972 (CANB, DNA); approx. 2 miles W of Argadargada H.S., *Nelson 168*, 27 Mar 1962 (DNA). Central South: 13 miles [c. 20.8 km] S Hamilton Downs Station, *Maconochie 85*, 7 Apr 1967 (NSW); Mt Riddoch area, Harts Range, *Beauglehole 44426*, 25 May 1974 (MEL, NSW). Darwin & Gulf: c. 15 miles [24 km] NE of Pine Creek township, *Lazarides 157 & Adams*, 11 Mar 1965 (CANB, DNA); Fossil Head, *Leach 4226*, 23 Feb 1994 (NSW); Kapalga, *Dunlop 6056 & Taylor*, 9 Mar 1982 (NSW); *Dunlop 7676*, 29 Feb 1988 (NSW). Victoria River: 3 km W of Timber Creek, *Wilson 198 & Jacobs*, 7 May 1988 (NSW, BRI, DNA); Middle Creek, Top Springs–Victoria River Downs road, c. 25 km E of VRD, *Beauglehole 54563*, 10 July 1976 (DNA, MEL); 67.7 miles NE Tanami, *Chippendale NT 5703*, 13 Apr 1959 (CANB, DNA).

South Australia: Lake Eyre: 9 km S of Cordillo Downs, *Williams 8304*, 2 June 1976 (AD); 2 miles SE Alka-Seltzer Bore, Mt Dare Station, *Latz 4762*, 3 Apr 1974 (CBG, DNA).

Indigofera

Indigofera L., Sp. Pl. 2: 751 (1753)
Anil Mill., Gard. Dict. ed. 4: 95 (1754)
Indigo Adans., Fam. Pl.: 326 (1763)
Anila Ludwig ex Kuntze, Rev. Gen. Pl. 1: 159 (1891)
Type: *I. tinctoria* L. (lectotype designated by Britton & Brown 1913: 371)

Sphaeridiophorum Desv., J. Bot. 1: 125 (1813)
Type: *S. linifolium* (L.f.) Desv. [= *I. linifolia* (L.f.) Retz.]
Indigofera subg. *Sphaeridiophora* Benth., in Benth. & Hook. f., Gen. Pl. 1: 494 (1865)
Bremontiera DC., Ann. Sci. Nat. sér. 1, 4: 94 (1825)
Type: *B. ammoxylum* DC. [= *I. ammoxylum* (DC.) Polhill]

Hemispadon Endl., Flora 15: 385 (1832)
Type: *H. pilosus* Endl. [= *I. pilosa* Poir.]

Oustropis G. Don, Gen. Syst. 2: 214 (1832)
Type: *O. microphyllus* (Hook.) G. Don [= *I. gracilis* Spreng.]

Eilemanthus Hochst., Flora 29: 593 (1846)
Type: *E. strobilifer* Hochst. [= *I. strobilifera* (Hochst.) Bak.]

Acanthonotus Benth., in Benth. & Hook., Fl. Nigrit.: 293 (1849)
Type: *A. echinatus* (Willd.) Benth. [= *I. nummulariifolia* (L.) Alston]
Indigofera subg. *Acanthonotus* (Benth.) Benth., in Benth. & Hook. f., Gen. Pl. 1: 494 (1865)

Indigofera subg. *Amecarpus* Benth. ex Harv., in Harv. & Sond., Fl. Cap. 2: 201 (1862)
Type: *I. sessilifolia* DC. (lectotype designated by Gillett 1958: 9)

Annuals, subshrubs or shrubs. Indumentum typically of two-armed, sometimes with multicellular and/or gland-tipped hairs as well. Leaves simple, unifoliolate, trifoliolate or pinnate, discolorous; stipellae present in some species, persistent. Stipules present, sometimes spinescent and persistent. Inflorescence a pedunculate axillary raceme; flowers pedicellate; bracts usually deciduous, occasionally persistent. Calyx lobes 5, subequal or the lowermost longer; sinus between upper lobes v- to u-shaped. Corolla red or pink to purple; standard hairy on adaxial surface, base abruptly tapering to the claw; wings variously hairy; keel hairy at apex and upper margin fringed, lateral pockets spur-like. Stamens 10, 9 filaments connate and 1 free; filaments alternating long and short; anthers apiculate, glabrous or with tufts of hairs at the apex and/or the base. Ovary sessile, usually pubescent; ovules 1, 2 or numerous. Style longer, or sometimes shorter, than the ovary, incurved; stigma capitate. Pod straight or curved, spreading to descending, rarely ascending, globose to linear, terete or sometimes angular, usually dehiscent; endocarp very often spotted. Seeds globose to cylindrical or cuboidal, separated by papery or pithy outgrowths of the endocarp. Chromosome number 2n = 16, 32.

Key to species

1 Leaves all unifoliolate or apparently simple 2
1 Leaves pinnate or trifoliolate ....see Part 2 (Wilson & Rowe, in prep.)

2 Leaves apparently simple 3
2 Leaves unifoliolate, articulate on the petiole 9

3 Pod at least 10 mm long; flowers pink to purple 4
3 Pod up to 3 mm long; flowers red 8

4 Stems covered with small wart-like protuberances; fruits viscid .... **1. I. ixocarpa**
4 Stems lacking wart-like protuberances; fruits not viscid 5

5 Stipules mostly ≤ 1 mm long 6
5 Stipules 1.2–3.5 mm long 7

6 Leaves usually 3 mm wide .... **2. I. haplophylla**
6 Leaves linear, 1 mm wide .... **3. I. ammobia**

7 Leaves linear to narrowly elliptical, ≤ 8 mm wide.......... **4. I. triflora**
7 Leaves obovate or elliptical (rarely oblong), usually > 10 mm wide .... **5. I. rupicola**

8 Leaves linear to narrowly elliptical .... **6. I. linifolia**
8 Leaves broadly ovate to elliptical, cordate .... **7. I. cordifolia**

9 Pod usually < 20 mm long, 4–5-seeded 10
9 Pod usually > 20 mm long, 6–10-seeded 12

10 Leaf surface with long, spreading hairs .... **9. I. pilifera**
10 Leaf surface densely tomentose 11

11 Leaf with conspicuously impressed veins; calyx lobes 3.5–5.5 mm long; corolla 6–10 mm long .... **8. I. rugosa**
11 Leaf lacking conspicuously impressed veins; calyx lobes 1.4–2.3 mm long; corolla 3–4 mm long .... **10. I. petraea**

12 Petiole 3–9 mm long; staminal tube 5–7 mm long .... **11. I. monophylla**
12 Petiole 9–21 mm long; staminal tube 3–4 mm long .... **12. I. schultziana**

Systematic treatment – species with simple or unifoliolate leaves

The simple-leaved taxa appear to fall into two groups: the species with long pods (spp. 1–5) into sect. *Planisiliquae* Wight & Arn., Prod. Fl. Ind. Or. 1: 200 (1834), and those with short pods (spp. 6, 7) into sect. *Brachycarpae* Wight & Arn., Prod. Fl. Ind. Or. 1: 198 (1834). The unifoliolate taxa, likewise do not constitute a single relationship group. Schrire (pers. comm.) has suggested that most of them should be distributed through a number of subsections of sect. *Psiloceratiae* (Gillett) Schrire, but that *I. rugosa* is not related to the rather similar-looking plants in the *I. monophylla* complex. In the case of *I. schultziana*, it is clear that this species is closely allied to *I. saxicola* and is, therefore, a unifoliolate member of the *I. pratensis* group. So, the simple and the unifoliolate taxa do not form two natural groupings and most, if not all, species considered here are thought to be related to species with pinnate leaves.

1. **Indigofera ixocarpa** *Peter G. Wilson & Rowe*, **sp. nov.**

Ramuli foliaque verrucis parvis numerosis instructa; folia simplicia lamina conduplicata et apice recurvato; inflorescentiae longae, folia excedentes; flores parvi, malvacei; fructus viscidi.

Holotype: Western Australia: Beatons Pool, 1 km NW of Nullagine, *Newbey 10092*, 31 Mar 1984 (PERTH). Isotypes: NSW, K.

Spreading somewhat rounded shrub, 0.4–0.8 m high; young stems terete, green and covered with small green, red or black warts which also occur on the leaf margin and lower surface, stems, stipules and bracts; hairs sparse, appressed, equally biramous. Leaves simple; stipules triangular to linear, 0.4–3 mm long, glabrescent, not spinescent, not persistent, adnate to the leaf base and falling with it; petiole 0.7–1.5 mm long; multicellular hairs in the leaf axils lacking; stipellae absent. Lamina very narrow and obovate, or linear, 20–47 mm long; 1–3(–6.0) mm wide, with the sides folded upwards about the midrib with the edges usually meeting and the mucronate apex distinctly down-turned or hooked; upper surface green, with sparse, appressed hairs; lower surface green with sparse, appressed hairs; veins not prominent. Inflorescences 80–180 mm long, longer than leaves; peduncle 15–22 mm long; bracts triangular, 0.7–1.2 mm long; flowers pink to purple; pedicel 0.5–0.8 mm long. Calyx 1.8–2.5 mm long, with subequal lobes equal to the length of the tube, and moderately dense, white, appressed hairs. Standard pink, elliptical to obovate, 3.5–4.5 mm high, 3 mm wide. Wings oblong, 3.5–4 mm long, 1–1.3 mm wide. Keel 4–4.8 mm long, 1.5 mm deep; lateral pockets 0.8–0.9 mm long; apex beaked; hairs moderately dense, golden to brown, along the bottom. Staminal tube 2.5–3 mm long, colourless. Ovary sparsely hairy. Pod ascending to descending, terete, 16–26 mm long, 2.5–3.5 mm deep, brown, glabrous but covered with sticky fluid; apex shortly pointed; endocarp spotted; seed 6 per fruit. (Fig. 1).

Notes: *I. ixocarpa* is likely to be most closely related to *I. verruculosa* from Arnhem Land by reason of the shared occurrence of the small warty protuberances, although the sticky coating on the fruits and young stems of *I. ixocarpa* does not occur in *I. verruculosa*. The simple (rather than unifoliolate) leaves, the long inflorescences, the small pink flowers and the ± glabrous fruits of this species also suggest an affinity with *I. ammobia* and *I. haplophylla* and their allies.

The epithet is derived from the Greek *ixos*, birdlime, in reference to the sticky fruit.

Distribution and habitat: this species is only known from four localities in the Fortescue District where it occurs on variably-drained stony and gritty alluvium and wash-out gravels. It has been collected in the bed of a small drainage line (near Nullagine) and also on the open stony slopes and summit of Mount Nameless and Marandoo Hill; it was formerly on the Mount Tom Price mine site.

Conservation status: Briggs and Leigh (1996) code this species 3KC–. Its conservation status is given as 'Priority Two' on *FloraBase* (Western Australian Herbarium 1998–2003). According to this source, a P2 rating is given to species that 'are known from one or a few (generally <5) populations, at least some of which are not believed to be under immediate threat (i.e. not currently endangered)'.

Other specimens examined: Western Australia: Fortescue: Tom Price mine, *Atkins HI-691*, 4 July 1980 (KARR); Beatons Pool, Nullagine, *Deighton 325*, 6 Oct 1982 (PERTH); Marandoo Hill, Hamersley Range, *van Leeuwen 1240*, 20 May 1992 (CANB, NSW, PERTH), *van Leeuwen 1320*, 19 Aug 1992 (NSW, PERTH); c. 1.8 km from summit of Mt Nameless, *Wilson 1080 & Rowe*, 14 Sep 1991 (CANB, K, MO, NSW, PERTH), *Wilson 1081 & Rowe*, 14 Sep 1991 (NSW).

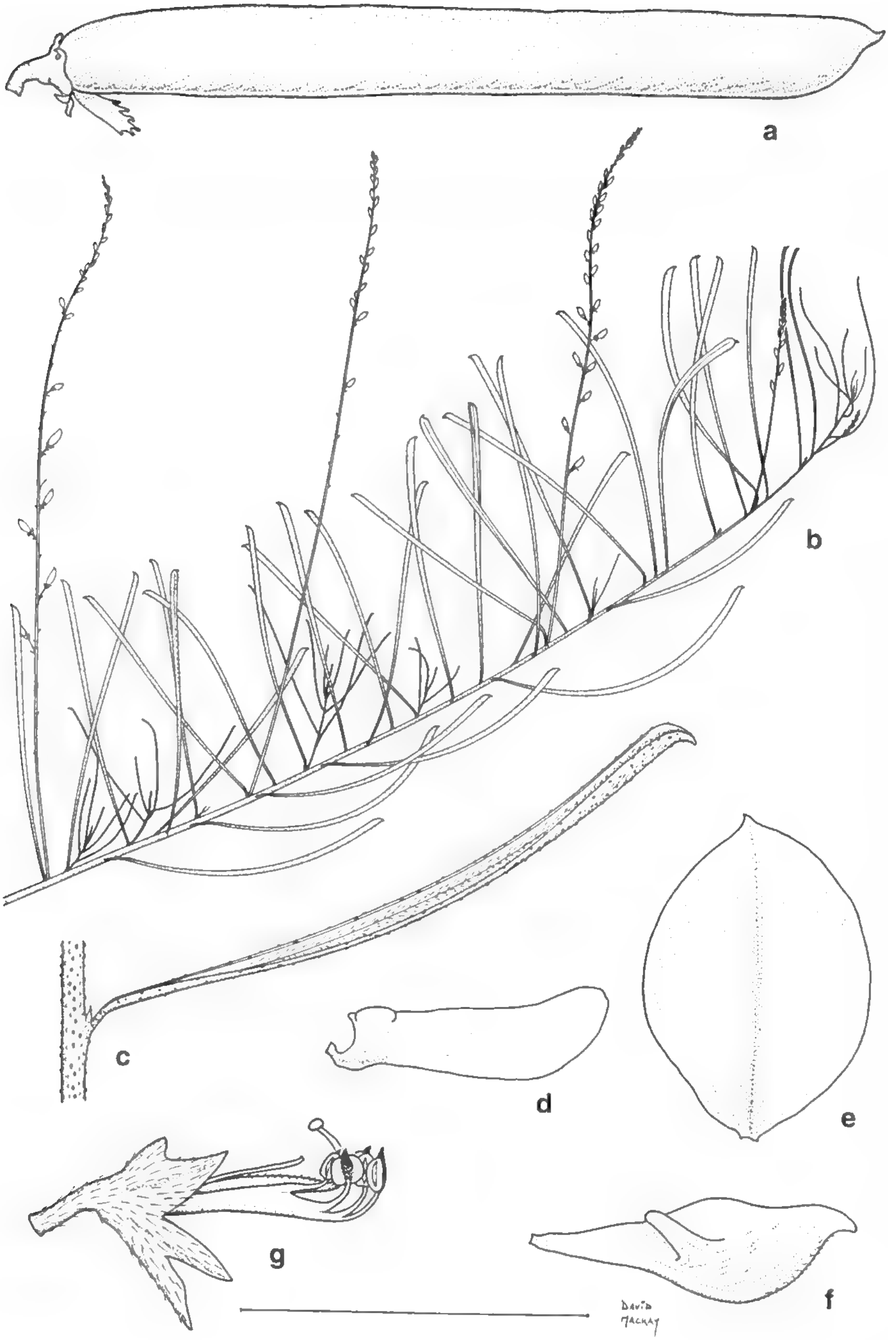

Fig. 1. *Indigofera ixocarpa*. **a**,fruit; **b**, habit; **c**, leaf; **d**, wing; ; **e**, standard; **f**, keel; **g**, lateral view of calyx and androecium. (a, c–g from *Newbey 10092*; b from *Deighton 325*). Scale bar: a, d–g = 50 mm; b = 10 mm; c = 15 mm.

2. Indigofera haplophylla F. Muell., Fragm. 3: 102 (1862)

Type citation: 'Ad fontes rupestres torrentesque exarescentes montium ad originem fluminis Victoriae.'

Holotype: Upper Victoria River, *F. Mueller s.n.* (K).

Anila haplophylla (F. Muell.) Kuntze, Rev. Gen. *Pl.* 2: 939 (1891)

Erect or spreading annual herb, 0.2–0.5(–0.85) m high, with taproot; young stems slightly ridged, green, strigose with sparse to moderately dense, appressed or rarely short spreading, equally biramous hairs. Leaves simple; stipules triangular, 0.3–1 mm long, pubescent, not spinescent, persisting but not woody; petiole 1–3 mm long; rachis terete; multicellular hairs absent to moderately dense in the leaf axils, inconspicuous, red, club-shaped; stipellae absent. Lamina elliptical to narrowly ovate, (10–)20–50(–65) mm long, (1–)3–8(–12) mm wide; upper surface green with sparse, appressed hairs, rarely glabrous; lower surface green (paler than above), with sparse, appressed hairs; apex acute or obtuse and apiculate; veins not prominent. Inflorescences 25–80(–125) mm long, shorter to longer than leaves; peduncle (1–)5–15(–27) mm long; bracts triangular to ovate, 0.3–0.7(–1.0) mm long; flowers pink to purple; pedicel 1–2(–4.0) mm long. Calyx 2–2.8 mm long, with subequal lobes equal to or longer than the length of the tube and sparse to moderately dense, grey appressed hairs. Standard purple, ovate or obovate to orbicular, 4.5–5.7 mm high, 3.7–4.2 mm wide. Wings oblong to narrowly obovate with some hairs at base, 4.8–5.5 mm long, 1.5–1.7 mm wide. Keel 4.5–5.3 mm long, 1.7–1.8 mm deep; lateral pockets 0.6–1 mm long; apex rounded or rarely beaked; glabrous or with sparse hyaline hairs mostly along the bottom. Staminal tube 3.2–3.5 mm long, colourless. Ovary glabrous. Pod ascending to descending, terete, (10–)20–35 mm long, 2–2.5(–3.0) mm deep, brown, glabrous; apex shortly pointed or shortly beaked; endocarp spotted; seed (4–)7–9(–10) per fruit.

Notes: A specimen collected from near 'Shamrock' Station (*Mitchell 2757*), shows some features intermediate between this species and *I. ammobia*, particularly the rather narrow leaves.

Distribution and habitat: Queensland, Northern Territory and Western Australia; occurs in a wide range of habitats, from ridge tops to creek lines, and in a range of substrates, although it is generally found on gravelly or sandy soil in open woodland.

Selected specimens examined: Queensland: Burke: Spring Creek Scree Site, 23 km N of Mt Isa, *Harris 280*, 10 Mar 1989 (BRI).

Western Australia: Dampier: 5 km N of Shamrock Station Hsd at horticult. block, *Mitchell 2757*, 10 Nov 1992 (NSW 272404, BROOME). Fitzgerald: Lennard River Gorge, *Wilson 327*, 4 June 1988 (NSW 209870); Fern Creek, King Leopold Range, *Dunlop 7781 & Simon*, 9 Apr 1988 (BRI, NSW, PERTH); Tyra Islands, King Sound, *Mitchell 3982*, 31 May 1995 (NSW); Sunday Island, *Mitchell 2222*, 31 Mar 1992 (BROOME, NSW). Gardner: 1.9 km along Mulligans Lagoon Road, Kununurra (to N of Hidden Valley National Park), *Wilson 836 & Rowe*, 29 Aug 1991 (BRI, CANB, PERTH); Headwaters of Packsaddle Creek, Northern Carr Boyd Ranges, *Hartley 14355*, 7 Mar 1978 (CANB, PERTH); Longini Landing, near Kalumburu Mission and on coastline, *Symon 10195*, 16 May 1975 (AD, NSW, PERTH).

Northern Territory: Darwin & Gulf: Fitzmaurice River, *Leach 4068*, 20 Feb 1994 (MEL, NSW); 94 m [c. 120 km] E of Daly Waters, *Byrnes 2508*, 18 Mar 1972 (CANB, DNA, BRI); Cox River Station, *Latz 7329*, 12 July 1977 (DNA, CANB); Bukalara Plateau, *Rice 2291*, 12 Feb 1976 (CANB); Mt Gilruth, *Craven 8315 & Wightman*, 28 Mar 1984 (CANB, NSW); 36 km W of Cape Crawford, Carpentaria Hwy, *Cowie 1731 & Wilson*, 1 May 1991 (NSW). Victoria River: Keep River National Park, *Dunlop 5732*, 23 Feb 1981 (NSW, MEL); Victoria River District, *Evans 3182*, 13 Apr 1990 (MEL, NSW).

3. Indigofera ammobia Maconochie, J. Adelaide Bot. Gard. 2: 325 (1980)

Holotype: Western Australia: just S of Tobin Lake, Great Sandy Desert, *A.S. George 15644*, 6 May 1979 (PERTH). Isotypes: CANB, DNA.

Illustration: Maconochie (1980: 326).

Erect annual to short-lived perennial herb, 0.15–0.7 m high, with taproot; young stems terete, dull green, strigose, with moderately dense, appressed, equally biramous hairs. Leaves simple; stipules narrow and triangular, 0.3–1 mm long, glabrescent or sparsely pubescent, not persistent; petiole 0.5–1 mm long; multicellular hairs absent to sparse in the leaf and stipule axils, inconspicuous, red, club-shaped; stipellae absent. Lamina linear, (10–)20–45 mm long, 0.3–1 mm wide, the surface furrowed or margins in-rolled; upper surface dull green with sparse, appressed (rarely shortly spreading) hairs; lower surface dull green with sparse, appressed hairs; apex acute; veins not prominent. Inflorescence (5–)15–35(–55) mm long, shorter or rarely longer than leaf; peduncle 3–15 mm long; bracts triangular; 0.5–0.7 mm long. Flowers pink to purple; pedicel 0.5–1.5 mm long. Calyx (1.3–)1.5(–1.8) mm long, with subequal lobes equal to or longer than the length of the tube and moderately dense, grey, appressed hairs. Standard pink, obovate to orbicular, 3–3.2 mm high, 2.8–3 mm wide. Wings spathulate to narrowly obovate, 2.8–3.3 mm long, 1.1–1.3 mm wide. Keel 3.3–3.5 mm long, 1.3–1.5 mm deep, with lateral pockets 0.3–0.4 mm long; acute apex; hairs moderately dense, hyaline, at the tip and along the bottom. Staminal tube 1.8–3.2 mm long, colourless. Ovary glabrous. Pod ascending to spreading, terete, 15–30 mm long, 2–3 mm deep, brown, glabrous; apex shortly pointed; endocarp spotted; seed (5–)8(–10) per fruit.

Distribution and habitat: Northern Territory and Western Australia; red sand dunes and plains.

Conservation status: Albrecht et al. (1997) and White et al. (2000) give this species a conservation coding of 3k indicating that it is poorly known in the Northern Territory. This species occurs in the Great Sandy and Tanami Deserts and, although collected only occasionally, is probably not at risk. A coding of 3R is probably more appropriate.

Selected specimens examined: Western Australia: Canning: North of Dragon Tree Soak, Great Sandy Desert, *George 14769*, 10 Aug 1977 (AD, BRI, DNA, NSW). Fortescue: about 10 km E of Nimingarra Outcamp, near Shay Gap, *Mitchell PRP 895*, 24 Oct 1995 (NSW). Mueller: Wolfe Creek Meteorite Crater, *Wilson 865 & Rowe*, 31 Aug 1991 (NSW, PERTH, CANB).

Northern Territory: Tanami Sanctuary, *Henshall 1253*, 28 May 1976 (DNA); c. 40 km SSE of the Granites, *Latz 8708*, 23 June 1981 (DNA); Aboriginal soak, 20 km WNW of Lake Surprise, Tanami Desert, *Latz 10071*, 27 June 1985 (CANB [ex CBG]).

4. Indigofera triflora *Peter G. Wilson & Rowe*, **sp. nov.**

I. haplophylla affinis sed habitu perspicue perenni, stipulis longioribus et inflorescentia plerumque triflora differt.

Holotype: Queensland: North Kennedy: Warrigal Siding, *Peter G. Wilson 610 & R. Rowe*, 9 Sep 1990 (NSW). Isotype: BRI.

Erect perennial herb, 0.15–0.45 m high, with woody rootstock or taproot; young stems ridged, green, strigose with sparse, appressed to shortly spreading, equally biramous hairs. Leaves simple; stipules narrowly triangular to linear, 1.2–4 mm long, glabrescent, not spinescent, ± persistent; petiole 1–2 mm long; multicellular hairs absent to sparse in the leaf axils, inconspicuous, red, club-shaped; stipellae absent. Lamina narrowly ovate to narrowly elliptical or linear, (15–)25–55(–70) mm long, (0.9–)1.5–5(–8.0) mm wide; upper surface green, glabrous or with sparse, appressed hairs; lower surface green (paler than above), with sparse, appressed hairs; apex

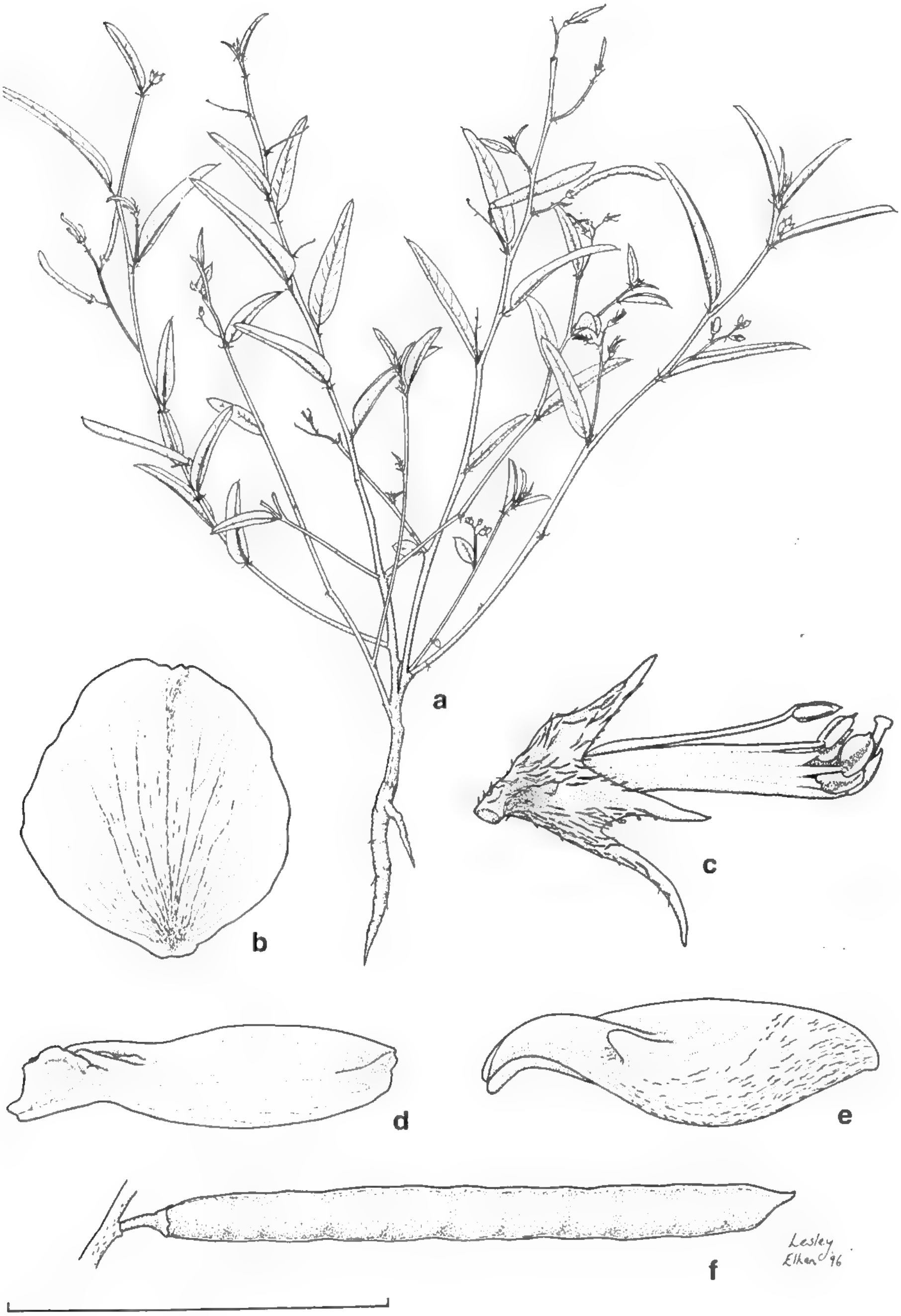

Fig. 2. *Indigofera triflora*. **a**, habit; **b**, standard; **c**, lateral view of calyx and androecium; **d**, wing; **e**, keel; **f**, fruit. (a–e from *Wilson 610 & Rowe*; f from *Blake 8585*). Scale bar: a = 75 mm; b–e = 5 mm; f = 20 mm.

obtuse or acute and apiculate; veins not prominent. Inflorescences (3–)13–30 mm long, shorter than leaves, generally with 3, very rarely 2 or 4, flowers; peduncle (1.0–)8–20(–28) mm long; bracts triangular, (0.4–)0.8–1.5 mm long, sometimes persistent; flowers pink to purple; pedicel (0.7–)1–2 mm long. Calyx 2–3(–3.3) mm long, with subequal lobes equal to or longer than the length of the tube and sparse, white to grey, appressed hairs. Standard pink, obovate to orbicular, 4.1–5.2 mm high, 3–4(–4.9) mm wide. Wings narrowly obovate, (4.0–)5–6 mm long, 1–2 mm wide. Keel 4.7–5.7 mm long, 1.5–2 mm deep; lateral pockets 0.5–1 mm long; apex beaked; glabrous or with sparse, hyaline hairs along the bottom. Staminal tube (2.0–)2.5–4 mm long, colourless. Ovary glabrous. Pod ascending, terete, (10–)20–30(–38) mm long, 2–2.5 mm deep, brown, glabrous; apex shortly beaked; endocarp spotted, sometimes faintly; seed (2–)7–9 per fruit. (Fig. 2).

Notes: This species has formerly been included in *I. haplophylla* but is easily distinguished from that species by its longer stipules, short, 3-flowered inflorescences and perennial habit. It also approaches *I. ammobia* in leaf morphology in parts of its range but can also be distinguished from that species by the stipule length. In *I. ammobia* the leaves are linear and up to 0.9 mm wide, while in *I. triflora* they are usually narrowly ovate to narrowly elliptical and at least 2 mm wide. However, specimens collected near St George, towards the southern end of its range, have leaves that are only 0.9–1.5 mm wide. The inflorescences are about the same length, but *I. ammobia* has a higher flower number (3–7). In any case, the species are allopatric and the perennial habit of *I. triflora* will distinguish it from *I. ammobia*, which appears to be an annual.

The epithet is derived from the Latin *triflorus*, 3-flowered, in reference to the predominantly 3-flowered inflorescences.

Distribution and habitat: recorded from the southern part of the Cook District of Queensland and extending into New South Wales in the Yetman area, where it is known from only a single collection. The few detailed site descriptions indicate that this species grows on sandy soil in open forest, often in disturbed areas like roadsides.

Conservation status: despite the geographic range of this species, specimens have been collected only rarely, so the conservation status remains uncertain. The plants are small, easily overlooked and growth from the rootstock may be seasonal and is evidently subject to grazing. The senior author has attempted to relocate the species in the Yetman area on about four occasions but without success.

Selected specimens examined: Queensland: Cook: Black Rock (Lynd), *Horsup 113*, Apr 1988 (BRI). North Kennedy: near source of Poison Creek, about 90 miles N of Hughenden, *Blake 8585*, 12 Apr 1935 (BRI, CANB). Mitchell: 10–18 km E of Torrens Creek, *Rebgetz 715*, May 1981 (BRI). Leichhardt: Gainsford, *Bowman s.n.* (MEL 585913, 586580). Maranoa: 26.1 km W of St George, *Bean 14475*, 28 Dec 1998 (BRI, NSW).

New South Wales: North Western Plains: 3 miles [c. 4.8 km] from Yetman on Texas road, *K. Wilson 796, Johnson & Jacobs*, 20 Nov 1974 (NSW).

5. Indigofera rupicola *Peter G. Wilson & Rowe*, sp. nov.

Habitus decumbens vel adscendens; stipulae 1.2–3.5 mm longae; folia plerumque obovata, apice obtuso apiculatoque; bracteae inflorescentiae semipersistentes; fructus plerumque 10–25 mm longi.

Holotype: Northern Territory: 70 km NE Pine Creek, *Wightman 1749*, 5 Mar 1985 (NSW). Isotypes: BRI, CANB, DNA, K.

[*Indigofera* sp. 3, Brennan (1996: 54)]

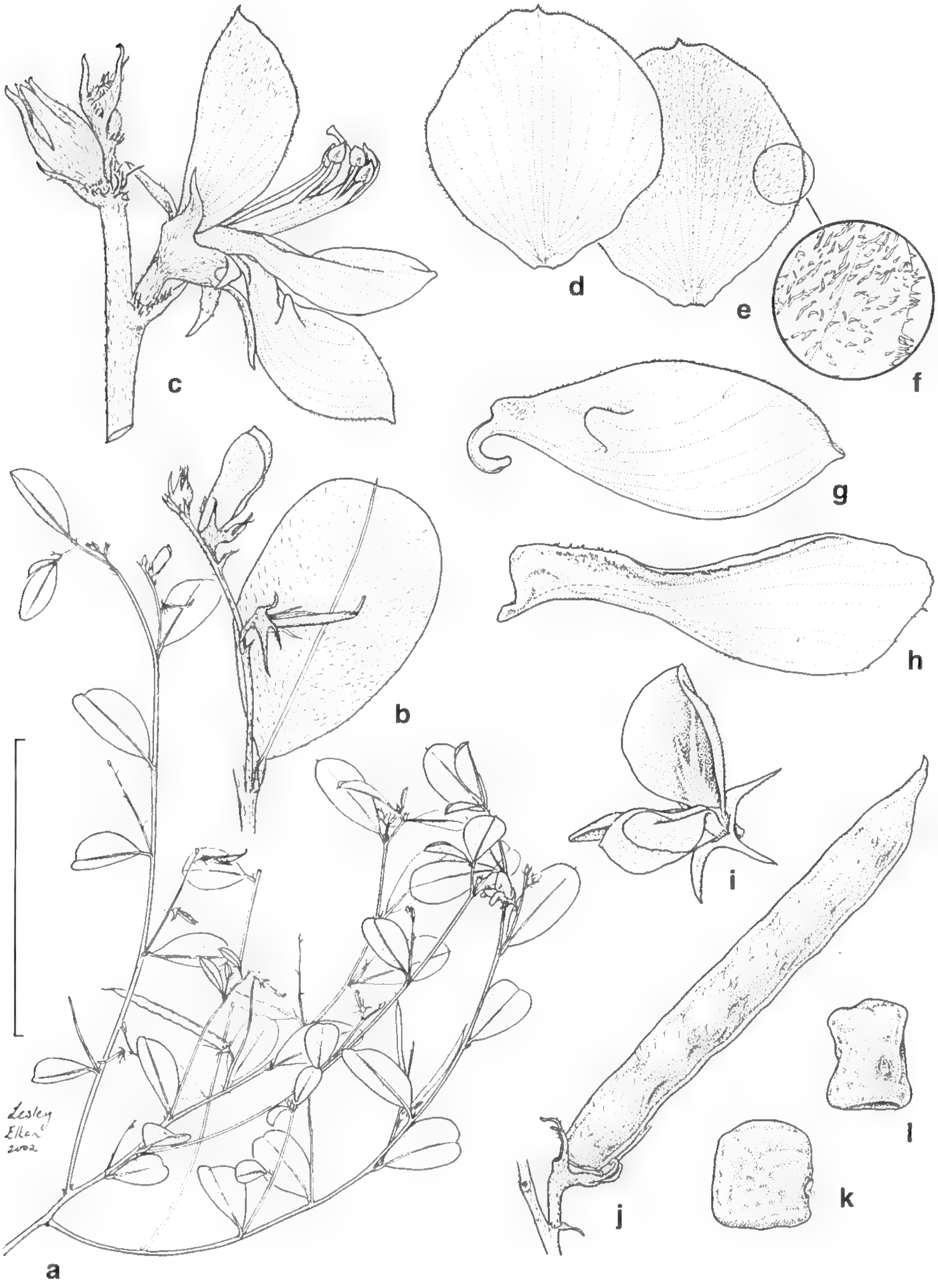

Fig. 3. *I. rupicola*. **a**, habit; **b**, inflorescence and leaf; **c**, bud and 'tripped flower'; **d**, **e**, **f**, front, back and detail of standard; **g**, keel; **h**, wing; **i**, flower; **j**, fruit; **k**, **l**, seed (lateral and ventral view). (a, b from *Dunlop 3404*; c–h, j–l from *Wightman 1749*; i from photograph of cultivated plant). Scale bar: a = 50 mm; b = 10 mm; c–e = 6 mm; f = 2.5 mm; g–h, k–l = 4 mm; i–j = 10 mm.

Decumbent to spreading, annual or perennial herb or subshrub, 0.05–0.45 m high, with woody rootstock or taproot; young stems ridged, green, strigose with moderately dense, appressed to shortly spreading, equally biramous hairs. Leaves simple; stipules linear, 1.2–3.5 mm long, glabrescent, not spinescent, not persistent (but not falling early); petiole 1–2 mm long; rachis terete, multicellular hairs in the leaf axils lacking; stipellae absent. Lamina obovate to elliptical, rarely oblong, narrowly elliptical or narrowly ovate, (5–)10–25(–40) mm long, (3–)5–10(–17) mm wide; upper surface green, glabrous or with sparse, appressed hairs; lower surface green, paler than above, with sparse, appressed hairs; apex obtuse and apiculate; veins not prominent. Inflorescences 5–35(–80) mm long, shorter than or equal to leaf, rarely longer; peduncle 1–10(–20) mm long; bracts triangular to ovate, 0.7–2 mm long, often persistent; flowers pink to purple, pedicel 0.5–2 mm long. Calyx 2.2–3(–3.8) mm long, with subequal lobes longer than the length of the tube and moderately dense, white, appressed, rarely shortly spreading hairs. Standard pink to purple, suborbicular, 4.8–6.5 mm high, 4–5.5 mm wide. Wings narrowly obovate, 5–6.5 mm long, 1.5–2.5 mm wide. Keel 5–6 mm long, 1.5–2.5 mm deep; lateral pockets 0.6–1 mm long; apex acute; hairs sparse to moderately dense, hyaline to white, at the tip and along the bottom; margin ciliate. Staminal tube 3–4.5 mm long, colourless. Ovary glabrous or moderately densely hairy when young. Pod ascending to spreading, terete, (8–)10–25(–33) mm long, 2 mm deep, brown, strigose to glabrescent; hairs sparse, appressed; apex shortly beaked; endocarp spotted; seed (4–)6–8 per fruit. (Fig. 3).

Notes: this new species is clearly related to the *I. haplophylla* group of species but may be distinguished from the other Australian taxa in this group by the more spreading, prostrate to ascending annual to perennial habit and the usually obovate leaves. The inflorescence bracts are also persistent in many cases, as in *I. triflora*.

There is some convergence in leaf shape with *I. haplophylla* in the specimen from Katherine Gorge and the one from Queensland, but the habit and stipule length indicate that they are both *I. rupicola*. Also, these two species appear to be ecologically distinct and seem not to occur sympatrically. On the other hand, specimens of *I. haplophylla* from Sunday Island, NNW of Derby, have broader leaves that approach *I. rupicola* in width but they have stipules that are typical of *I. haplophylla*.

There is a collection from Kununurra (*Andrew 436*, BRI, CANB, DNA) that was collected on sandy soil, and is somewhat different in aspect from the rest of the specimens, having longer and broader leaves, longer inflorescences and ± prostrate habit. It is retained here, with some doubt, pending further collections.

The epithet is derived from the Latin *rupicola*, rock-dweller, an allusion to the sandstone plateaux where most specimens have been collected.

Distribution and habitat: Western Australia, Northern Territory and Queensland; generally in savannah woodland on sandy soils of sandstone escarpments.

Selected specimens examined: Western Australia: Gardner: About 3 km E of Mitchell Falls in sandstone country, *Mitchell 3353*, 15 Mar 1994 (NSW, PERTH).

Northern Territory: Darwin & Gulf: Twin Falls, 1 km upstream, *Fensham 818*, 24 Mar 1988 (DNA); East Alligator River, *Dunlop 3404*, 2 Mar 1973 (BRI, DNA, MEL, NSW); 55 miles [c. 88 km] E of Pine Creek, *Byrnes 1333*, 29 Jan 1969 (BRI, DNA); Plum Tree Creek crossing, *Menkhorst 226*, 15 Feb 1989 (DNA); Katherine Gorge National Park, *Byrnes 2159 & Dunlop*, 23 Mar 1971 (CANB, DNA, NSW).

Queensland: Cook: Donkey Spring Creek, Bulleringa National Park, 80 km NW of Mt Surprise, *Forster 22496 & Booth*, 22 Apr 1998 (BRI, NSW).

6. Indigofera linifolia (L.f.) Retz., Obs. Bot. 4: 29 (1786)

Hedysarum linifolium L.f., Suppl. 331 (1781)

Holotype: India (LINN 921.5).

Sphaeridiophorum linifolium (L.f.) Desv., J. Bot. 3: 125 (1813)

Anila linifolia (L.f.) Kuntze, Rev. Gen. Pl. 1: 160 (1891)

Illustration: Banks and Solander (1900: t.55); Weber (1986) fig. 309A; Urban (1990: 96) photo; Hacker (1990: 183) photo; Anderson (1993: 167) photo; Milson (1996: 49) photo.

Prostrate or spreading, perennial herb, 0.1–0.3(–0.5) m high, with taproot; young stems ridged, green, strigose with dense, appressed, equally biramous hairs. Leaves appearing simple, with no apparent articulation; stipules triangular, 1–3 mm long, pubescent, not spinescent, not persistent though occasionally persisting beyond leaf fall; petiole 0.5–1 mm long; multicellular hairs in the leaf axils lacking; stipellae absent. Lamina linear or narrowly lanceolate to narrowly oblanceolate, (6–)10–35(–50) mm long, 1–3(–4.0) mm wide; both surfaces green to grey-green, with moderately dense or dense hairs; apex acute and shortly mucronate; veins not prominent. Inflorescences (2–)5–15(–25) mm long, shorter than leaves; peduncle 0.5–1 mm long; bracts ovate with scarious margin, 0.7–1.5 mm long; flowers red; pedicel 0.5 mm long. Calyx 1.5–4 mm long, with subequal lobes longer or much longer than the length of the tube, and dense, grey, appressed hairs. Standard red, obovate to orbicular, 2.5–3.5 mm high, 1.7–3 mm wide. Wings narrowly obovate, 2.5–3 mm long, 0.7–1.2 mm wide. Keel 2.5–3.8 mm long, 0.8–1.1 mm deep; lateral pockets 0.3–0.7 mm long; apex acute or rounded; glabrous. Staminal tube 2.5–3 mm long, free ends pigmented. Ovary densely hairy. Pod ascending, globular, 2–3 mm long, 1.5–1.8 mm deep, white or grey, strigose; hairs dense, appressed; apex shortly beaked; endocarp not spotted or rarely some pale blotches; seed 1 per fruit.

Distribution and habitat: in Australia the species is found in Queensland, Northern Territory, Western Australia, South Australia, and New South Wales. It is found in a wide range of habitats, especially on disturbed sites like roadsides but also occurs on sand or rocky ridges in open woodland or grassland; it is considered to be a weed in some areas (Lazarides et al. 1997). The species has a wide distribution and is found in north-eastern Africa, through southern Asia to southern China, Ryukyu and Taiwan, and south through Thailand to Malesia.

Selected specimens examined: Queensland: Burke: Yelvertoft Station, *Gittins 782*, May 1963 (BRI, NSW); Shell Ridge, N end of Wernadinga Station, *Pullen 8996*, 1 May 1974 (BRI, CANB); Whitecliff Gorge Creek, *Wilson 626 & Rowe*, 10 Sep 1990 (NSW); North end, Bentick Island, South Wellesley Islands, *Tindale s.n. & Aitken*, June 1963 (AD 97306383). Burnett: Junction of Barambah Creek and Burnett River, 5 miles [c. 8 km] NE of Gayndah, *Lebler 35 & Durrington*, 22 Jan 1970 (BRI, CANB, NSW). Cook: 1 km north of Nassau River mouth, 300 m east of the beach, *Neldner 3034 & Clarkson*, 15 June 1990 (NSW); Flinders Island, c. 7 km N of Bathurst Head in the S end of Princess Charlotte Bay, *Clarkson 2295*, 11 June 1978 (BRI, CANB, NSW); Walsh River crossing on Burke Development Road, c. 11 km NW of Rookwood Homestead, c. 16 km NE of Mungana, *Conn 1329 & De Campo*, 3 June 1983 (CANB, MEL, NSW). Gregory North: Ardmore, 25 miles [c. 40 km] W of Dajarra, *Everist 3207*, 20 Nov 1947 (BRI). Gregory South: 47.8 km W of Windorah, *Wilson 423 & Pickering*, 23 Sep 1989 (BRI, NSW); Charleville, *Blake 5360*, 19 Apr 1934 (BRI 335782). Leichhardt: Apis Creek, Bruce Highway, 40 km W of Marlborough, *Halliday 356*, 5 Apr 1975 (BRI, HO); Tanderra (Nardoo); c. 45 miles [c. 72 km] SW of Springsure, *Johnson 1317*, 15 Feb 1960 (BRI 232917). Maranoa: Mitchell, *Blake 5778*, 4 May 1934 (BRI). Mitchell: 6 km NW of Malvernton (60 km W of Blackall) on stock route from Malvernton to Gowan Hills, *Johnson 3022*, 10 Nov 1975 (BRI 194173); Torrens Creek, *White 8670*, 19 Mar 1933 (BRI 232925). Moreton: Near Somerset Dam, *Blake 13972*, 26 Feb 1939 (BRI, CANB); Colleges Crossing, 6 miles [c. 9.6 km] NE of Ipswich, *Henderson 165*, 18 Jan 1967 (BRI, CANB). North Kennedy: West Point, Magnetic Island, *Forster 12765 & Bean*, 18 Jan 1993 (NSW); Ritson's plots, Lansdown Pasture Research Station, *Lazarides 7155*, 5 Apr 1965 (BRI, CANB); Burdekin River area above Dalbeg on track to Gorge Weir, 20.9 km S of Expedition Pass Creek bridge, *Staples 2101*, 16 Apr 1975 (BRI, CANB). Port Curtis: Biloela, at experimental farm, *Smith 3469*, 22 Oct 1947 (BRI, NSW); Curtis Island, *Blake 22517*, 26 Mar 1966 (CANB). South Kennedy: Red Mountain, c. 40 km W of Clermont, *Wilson 559 & Rowe*, 7 Sep 1990 (NSW, BRI, PRE); Newry Island, *Hegerl N233 & Trinder*, 9 Dec 1986 (BRI, MEL). Warrego: 'Gilruth Plains', Cunnamulla, *McKee 10358*, 13 Apr 1963 (BRI, NSW); 46 km SE of Charleville along Boatman road, *Purdie 93 & Boyland*, 23 Mar 1976 (BRI). Wide Bay: Bundaberg, *Stanley 906*, 17 Mar 1980 (BRI).

New South Wales: North Coast: 'Plain Station', 10 miles [c. 16 km] S of Tabulam, *Atkinson s.n. & Quirk*, 5 Feb 1973 (NSW 299180). North Western Plains: MacIntyre River, Yetman, *Coveny 12540, Dunn & Plat*, 28 Mar 1987 (NSW, BRI, KYO, L, MEL, PERTH). North Western Slopes: edge of boat ramp, Lake Keepit, *Hosking 1049 & Wicks*, 28 Nov 94 (NSW).

South Australia: Lake Eyre: 5 miles [c. 8 km] N of Cordillo Downs, *Filson 3404*, 2 Oct 1960 (AD, MEL, NSW).

Western Australia: Ashburton: Foot of Mt Augustus, *Wittwer 1076*, 19 Aug 1973 (PERTH); Jigalong [Jiggalong] Depot, Tropic of Capricorn, *Royce 1974*, 7 June 1947 (PERTH). Canning: Anketell Ridge, Great Sandy Desert, *A.S. Mitchell 1183*, 14 May 1979 (DNA). Carnarvon: 29 miles N of Learmonth, *George 2538*, 3 June 1961 (PERTH); 10 miles S of Onslow, *George 1151*, 28 Aug 1960 (PERTH). Dampier: Mt Anderson Station, Fitzroy River, *Royce 6912*, 7 May 1962 (BRI, PERTH); 4 km S of Cape Bertholet, Dampierland, *Kenneally 6038*, 19 Apr 1977 (CANB, PERTH). Fitzgerald: Same Creek crossing, Gibb River Road, *Wilson 255 & Jacobs*, 17 May 1988 (NSW, PERTH); 18.3 km NE of Mary River crossing, *Beauglehole 53262*, 19 June 1976 (PERTH). Fortescue: 6.2 km along track to Carawine Gorge, *Wilson 921 & Rowe*, 5 Sep 1991 (NSW, PERTH, PRE); 10 km SW of Boodarie Hsd on delta of Turner River, *A.A. Mitchell 1752*, 11 Apr 1989 (PERTH, NSW); 12 km N of Millstream, towards Mt Herbert, *Keighery 730*, 23 May 1976 (PERTH). Gardner: 1 km SW of Peanut Mill, Kununurra, *Wilson 203 & Jacobs*, 8 May 1988 (NSW, AD, MEL, PERTH); Tunnel Creek, Napier Range, *Dunlop 7742 & Simon*, 8 Apr 1988 (BRI, PERTH); South East Osborne Island, Bonaparte Archipelago, *Paul Wilson 11084*, 26 June 1973 (PERTH). Giles: Pass of the Abencerrages, Rawlinson Ranges, *Paul Wilson 2403*, 3 Aug 1962 (AD). Hall: Ord River at Blue Holes, Bungle Bungle National Park, *Menkhorst 613*, 13 July 1989 (DNA); Topyard Bore, 'Cherrabun', *Wolfe 115 & Martin*, 8 June 1970 (CANB). Keartland: Rudall River, *George 10753*, 21 May 1971 (CANB, PERTH). Mueller: Near Wolfe Creek Crater, *George s.n.*, Apr 1979 (DNA, PERTH).

Northern Territory: Barkly Tableland: 4.2 miles ESE of Frewina, *Perry 662*, 29 Apr 1948 (BRI, CANB, DNA); Kilgour Gorge, Mallapunyah Station, *Thomson 551*, 17 May 1984 (CANB, DNA); Elliott, *Chippendale NT 1065*, 10 Mar 1955 (AD, BRI, DNA, MEL, NSW). Central North: 11 miles NNE Donald Downs Station, *Perry 3414*, 12 Mar 1953 (BRI, CANB, DNA); 20 miles N of Barrow Creek, Stuart Highway, *Latz 177*, 23 Feb 1968 (AD, DNA, MEL); 46 miles [c. 73.5 km] SW of Mongrel Downs Homestead, *Latz 727*, 1 Aug 1970 (AD, DNA); Kollola Bore [=Cooloola Well], 4 miles [c. 6.4 km] NW Numagalong homestead, *Nelson 1 & Swinbourne*, 26 Aug 1965 (BRI, DNA, NSW); 15 miles [c. 24 km] N of Devils Marbles, *Chippendale NT 941*, 8 Mar 1955 (BRI, DNA); Boomerang Waterhole, Lander River, 42 miles NW of Willowra Homestead, *Chippendale NT4780*, 30 July 1958 (BRI, DNA, NSW). Central South: Finke River near Glen Helen, *Leach 531*, 24 Feb 1985 (CANB, AD, MEL, NSW); Docker River township, *Henshall 2896*, 26 Mar 1980 (AD, DNA); McGrath Flat, 30 miles N of Alice Springs, *Nelson 1659*, 13 Feb 1968 (AD, BRI, DNA); Mt Liebig, north side, *Carr 2357 & Beauglehole 46136*, 28 June 1974 (DNA, MEL). Darwin & Gulf: Mataranka, Stuart Highway, *Maconochie 569*, 18 Feb 1968 (AD, BRI, CANB, DNA); 1 km N of Pandanus Creek, c. 75 km SW of Borroloola, *Leach 561*, 5 May 1985 (CANB, DNA, MEL); 41 miles [c. 65.5 km] E of Pine Creek, *Nelson 300*, 13 Apr 1962 (AD, BRI, DNA, MEL, NSW); Hempel [Hempel] Bay, Groote Eylandt, *Specht 358*, 4 May 1948 (AD, BRI, MEL, NSW); Elcho Island, *Maconochie 2075*, 2 July 1975 (CANB, DNA). Victoria River: Auvergne Station, 35 km NW Timber Creek, *Must 1621*, 14 July 1977 (CANB, DNA); 13 miles [c. 15 km] NW of Wave Hill Police Station, *Perry 2188*, 21 June 1949 (BRI, CANB, DNA); 50 miles [c. 80 km] NE Tanami, *Chippendale NT 5675*, 12 Apr 1959 (DNA, MEL, NSW).

7. *Indigofera cordifolia Heyne ex Roth, Nov. Pl. Sp. 357 (1821)

Type: Ind. Or., *Heyne s.n.* (K, n.v.).

Anila cordifolia (Heyne ex Roth) Kuntze, Rev. Gen. Pl. 1: 160 (1891)

Prostrate perennial herb or subshrub, 0.1–0.3 m high, with taproot; young stems terete, greenish white, hirsute with dense to very dense, hyaline, spreading, unequally biramous hairs. Leaves simple; stipules triangular, fused to base of petiole, 1 mm long, pubescent with scattered long hairs, not spinescent, persistent, scarious; petiole 0.4–0.6(–1.0) mm long; multicellular hairs in the leaf axils lacking; stipellae absent. Lamina ovate to orbicular, cordate, 2.5–6.2(–7.0) mm long, 2.7–5.7(–6.5) mm wide; upper surface green with moderately dense, spreading hairs; lower surface green to white with moderately dense, spreading hairs; apex obtuse and apiculate; veins not prominent. Inflorescences 3–4 mm long including flowers, the axis c. 0.5 mm long, shorter than leaves (± sessile); bracts subulate, 1.5–2 mm long; flowers red; pedicel 0.2–0.5 mm long. Calyx 2.2–2.5 mm long, with subequal lobes ± free to the base and dense, white, spreading hairs. Standard red, obovate to spathulate, 2.6–3 mm high, 1.5–2 mm wide, with obtuse apex and moderately dense, hyaline to white hairs at tip. Wings narrowly spathulate, c. 3 mm long, 0.5–0.6 mm wide, keel 2.8–2.9 mm long, 0.5–0.7 mm wide; lateral pockets 0.2–0.25 mm long; apex acute; glabrous. Staminal tube 2 mm long, colourless. Ovary densely hairy. Pod globular, 1.5–2 mm long, 1.2–1.5 mm deep, white or grey, strigose; hairs dense, shortly spreading to spreading; apex shortly beaked with persistent sterile ovary tip; endocarp very faintly spotted; seed spherical, irregularly 1–2 per fruit.

Notes: Bentham (1864: 196) recorded this species for Australia and cited a specimen (Port Essington, *Armstrong*). For many years, no other Australian collection of the species was known and the Armstrong collection could not be located at K or BM (Schrire pers. comm.). It is also known that some of Armstrong's collections were made in Timor but mislabelled as to locality (Bean 1996). However, the species has recently been recollected on the Cobourg Peninsula, in the vicinity of the original Port Essington settlement. It occurs on disturbed sites and is almost certainly an early introduction, perhaps from Timor, that has persisted in areas with some continuing human activity.

Distribution and habitat: in Australia, known only from the Cobourg Peninsula in the Northern Territory where it is found around camp sites near the coast. It is otherwise known from tropical Africa to India and eastern Indonesia.

Selected Specimens examined: Northern Territory: Darwin & Gulf: Cobourg Peninsula; Fort Wellington, Raffles Bay, *Cowie 3759*, 20 Apr 1993 (DNA, CANB, NSW); Cobourg Peninsula; Port Bremer pearling base, *Cowie 3704*, 19 Apr 1993 (DNA, AD, BRI, CANB, MEL, NSW, PERTH, K, L).

8. Indigofera rugosa Benth., Fl. Aust. 2: 199 (1864).

Type citation: 'Bed of the Fortescue river, N.W. coast, *F. Gregory's Expedition (Herb. F. Mueller).*'

Holotype: Fortescue River, *Maitl. Brown* (MEL).

Erect shrub, 0.2–1 m high; young stems terete or ridged, white or yellowish, tomentose to hirsute with very dense, spreading, equally or unequally biramous hairs. Leaves unifoliolate; stipules linear or subulate, 2–6 mm long, pubescent, not spinescent, not persistent; petiole 3–8 mm long; rachis furrowed, appearing terete; multicellular hairs at point of articulation sparse, inconspicuous, red to brown, club-shaped to pointed linear. Leaflet lacking stipellae; lamina broadly ovate to obovate or orbicular, (7–)13–28 mm long, 7–25 mm wide; upper and lower surface white to grey, with dense, spreading hairs; apex obtuse and mucronate; veins prominent below and impressed above. Inflorescences 10–40 mm long, shorter than or rarely longer than leaves; peduncle 0.5–2 mm long; bracts triangular to subulate, 2–3.5 mm long; flowers pink to purple; pedicel 2–3.5 mm long. Calyx 4–7 mm long, with subequal lobes longer than to much longer than the length of the tube, and dense, white, spreading hairs. Standard purple or pink, ovate to orbicular, 7–10 mm high, 6.5–8.5 mm wide. Wings narrowly obovate or spathulate, 6–8 mm long, 2–3 mm wide. Keel 6–9 mm long, 2–3 mm deep; lateral pockets 1–1.5 mm long; apex acute or rounded; hairs dense, white at the tip and along the bottom; margin ciliate. Staminal tube 4–5.5 mm long, colourless. Ovary glabrous to densely hairy. Pod ascending to descending, terete, (5–)10–22 mm long, 3–4 mm deep, white, tomentose or hirsute; hairs dense, spreading; apex shortly pointed, the style often persisting; endocarp spotted; seed 4 or rarely 5 per fruit.

Distribution and habitat: Western Australia: in spinifex and mixed open shrubland on well drained, stony red sandy loams in ironstone country of the Hammersley region.

Conservation status: although uncommon, this species does not appear to be under threat.

Selected specimens examined: Western Australia: Fortescue: Gregory Range, opposite abandoned mine, *Wilson 946 & Rowe*, 5 Sep 1991 (NSW, CANB, PERTH); SE of Camp Anderson, Hamersley Range, *Wilson 1024 & Rowe*, 11 Sep 1991 (NSW, AD, CANB, K, MO, PERTH, UPS); About 85 km S of Munjina roadhouse, Newman road, *Pringle PRP 635*, 4 Sep 1995 (NSW).

9. Indigofera pilifera *Peter G. Wilson & Rowe*, sp. nov.

I. rugosae affinis sed ab ea stipellis praesentibus, lamina non rugosa, calyce corollaque minore, fructibus hirsutis vice tomentosis distinguitur.

Holotype: Western Australia: Carr Boyd Range, 20 km ENE of Dunham River HS, *M. Lazarides 8520*, 12 Mar 1978 (NSW). Isotypes: BRI, CANB, DNA, PERTH.

Spreading shrub, 0.3–0.4 m high, 1 m wide; young stems terete, white or green to yellowish, hirsute with dense, spreading, unequally biramous and scattered linear multicellular hairs. Leaves unifoliolate; stipules narrowly triangular to subulate, 2–3.5 mm long, pubescent, not spinescent, persistent; petiole 2–5.5 mm long; rachis terete, or slightly furrowed; multicellular hairs at point of articulation sparse, inconspicuous, orange or red, pointed linear. Leaflet with conspicuous stipellae 1–2 mm long; lamina ovate to elliptical, 10–28 mm long, 6–16 mm wide; upper surface pale grey to green, with moderately dense, spreading hairs; lower surface grey to green, paler than above, with moderately dense, spreading hairs; apex acute or obtuse and mucronate; veins prominent below. Inflorescences 35–90 mm long, longer than leaves; peduncle 2–7 mm long; bracts narrowly triangular, 1.5–2 mm long; flowers pink to purple; pedicel 0.5–0.8 mm long. Calyx 2.5–3.9 mm long, with subequal lobes longer than the length of the tube and moderately dense, white, spreading hairs. Standard purple or pinkish mauve, broadly elliptical to orbicular 4.5–5.5 mm high, 4–5 mm wide. Wings spathulate, 4–5 mm long, 1–1.5 mm wide. Keel 4.5–5.5 mm long, 1.5 mm deep; lateral pockets 0.5 mm long; apex acute; hairs moderately dense, hyaline to white, at the tip and along the bottom. Staminal tube 3–3.5 mm long, colourless. Ovary densely hairy. Pod descending to deflexed, terete, 8–12 mm long, 2.5–3 mm deep, brown, hirsute; hairs moderately dense, spreading; apex shortly pointed, the style sometimes persisting; endocarp spotted; seed cuboid, 4 per fruit. (Fig. 4).

Notes: the epithet is derived from the Latin *pilifer*, bearing hairs, in reference to the pilose leaves.

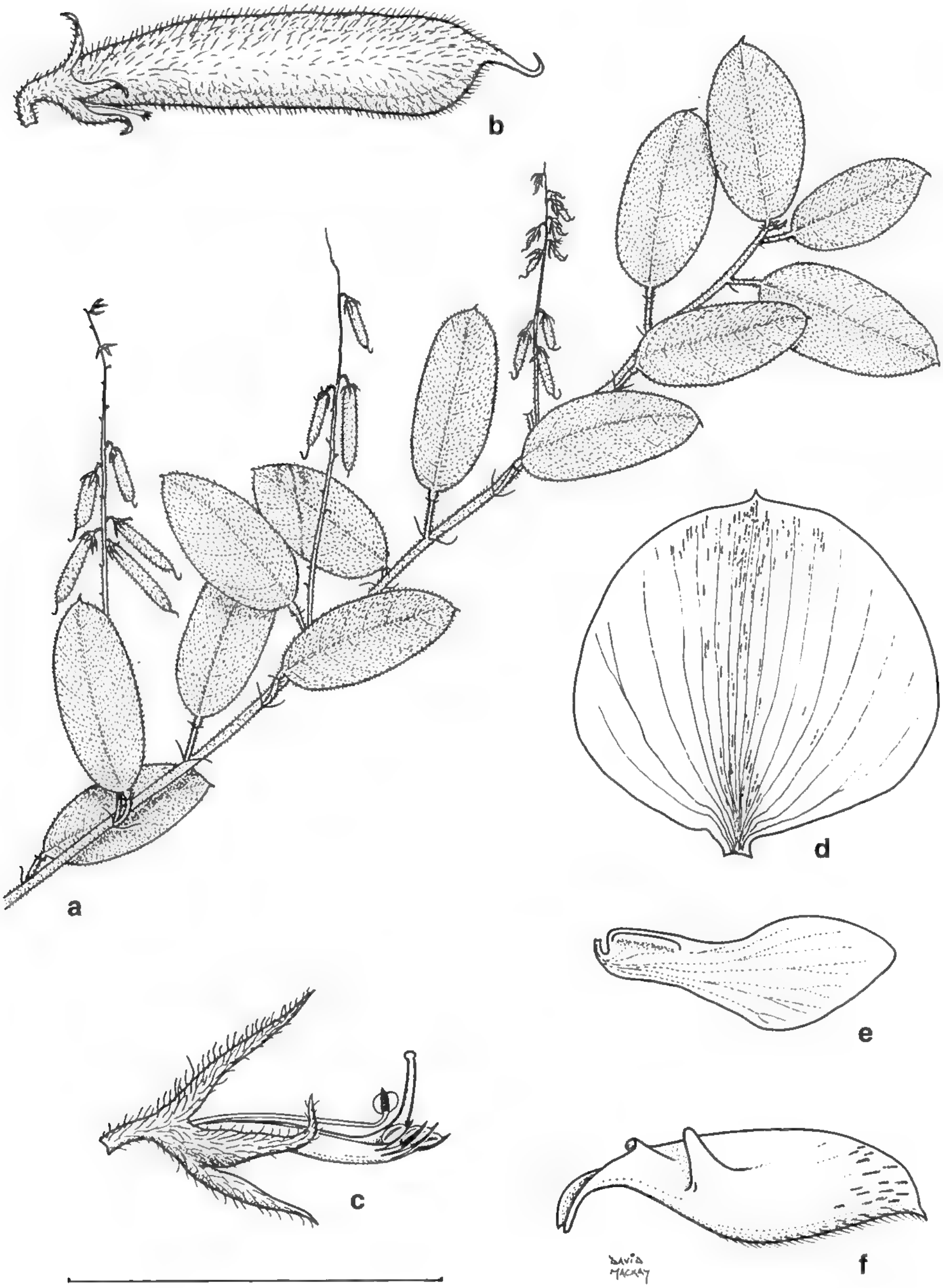

Fig. 4. *I. pilifera*. **a**, habit; **b**, fruit; **c**, lateral view of calyx and androecium; **d**, standard; **e**, wing; **f**, keel. (all from *Lazarides 8520*). Scale bar: a = 50 mm; b = 10 mm; c–f = 5 mm.

Distribution and habitat: *I. pilifera* is only known from a few collections from ranges in the vicinity of Kununurra, between 15°30'S and 16°30'S, where it is recorded as occurring on steep sandstone hills in open woodland.

Conservation status: although this species is poorly collected, it occurs in areas that are, as far as is known, not under any immediate threat. Further surveys will be necessary to assess distribution and population size for this species.

Other specimens examined: Western Australia: Gardner: Ivanhoe Station, East Kimberleys, *Langfield 378*, [c. 1952] (PERTH); Deception Range, *Wilson 841 & Rowe*, 30 Aug 1990 (NSW, CANB, K, PERTH).

10. Indigofera petraea *Peter G. Wilson & Rowe*, sp. nov.

I. rugosae foliis dense tomentosis similis sed lamina non rugosa, calyce corollaque minore, distinguitur.

Holotype: Western Australia: Barlee Range Nature Reserve, *S. van Leeuwen 1545*, 11 Aug 1993 (NSW 403825). Isotypes: KARR, PERTH.

Erect shrub 0.7–1.5 m high; young stems terete, yellowish becoming white to grey, tomentose with very dense, spreading, equally biramous (stalked) hairs. Leaves unifoliolate; stipules linear to subulate, 3.5–5 mm long, pubescent, not spinescent, not persistent; petiole 2.5–6.5 mm long; multicellular hairs at point of articulation sparse, conspicuous or inconspicuous, red to brown, pointed linear. Leaflet with inconspicuous to conspicuous setaceous stipellae 1–2.5 mm long; petiolule 1.5–3.5 mm long; lamina broadly elliptical, 10–27 mm long, 8–18 mm wide; upper and lower surface grey to white with dense, spreading hairs; apex obtuse (with small, dark mucro); veins not prominent above (laterals prominent below). Inflorescences 20–45(–55) mm long, shorter than to longer than leaves; peduncle 4–10 mm long; bracts ovate and subulate, 2.5–3.6 mm long; flowers deep pink to dark purple-red; pedicel c. 1 mm long. Calyx 3–3.8 mm long, with subequal lobes equal to or longer than the length of the tube, 1.4–2.3 mm long and dense, white or grey to brown, spreading hairs. Standard obovate, 3.3–4 mm high, 3–4.5 mm wide; hairs dense, hyaline or brown; apex obtuse with small apiculum. Wing oblong, 1.7–4.1 mm long, 0.6–1.1 mm wide. Keel 3–4 mm long, c. 1 mm deep; lateral pockets c. 0.5 mm long; apex rounded; hairs dense, white or brown, along the bottom. Stamens colourless or pigmented at the distal end; tube 2.0–3.5 mm long. Ovary densely hairy, 2–2.5 mm long. Pod descending, terete, 13–18 mm long, 2.5–3.5 mm deep, yellowish to white, pubescent; hairs dense, spreading; apex shortly pointed; endocarp spotted (confined to pithy partitions); seed cuboid, 3–6(–7) per fruit. (Fig. 5).

Notes: the epithet is taken from the Latin *petraeus*, growing among rocks, in reference to the rocky habitat.

Distribution and habitat: Western Australia: apparently confined to the Barlee Range where it occurs in skeletal sandy soil over massive silcrete in shrubland with *Triodia*.

Conservation status: this species has only recently been discovered but does not appear to be under any immediate threat. It is conserved within the Barlee Range Nature Reserve.

Other specimens examined: Western Australia: Ashburton: Barlee Range, 8.2 km S of Wongida Well, 34.4 km N of Mt Maitland, 17.5 km SSW of Mt Florry, *van Leeuwen 2190*, 6 Sep 1995 (KARR, NSW, PERTH); Barlee Range Nature Reserve, 5.1 km S of Yadiyugga Claypan, 18.7 km SSW of Mt Florry, 9.9 km ESE of Minnie Spring (on Henry River), 17.4 km N of Joy Helen Mine, *van Leeuwen 5081*, 31 Jul 2002 (KARR, NSW, PERTH); Glenflorrie Station, 1.4 km north of boundary to Barlee Range Nature Reserve, 6.3 km NNE of Yadiyugga Claypan, 8.5 km SW of Mt Florry, 14.8 km NE of Minnie Spring (on Henry River), 28.5 km NNE of Joy Helen Mine, *van Leeuwen 5082*, 31 Jul 2002 (KARR, NSW, PERTH).

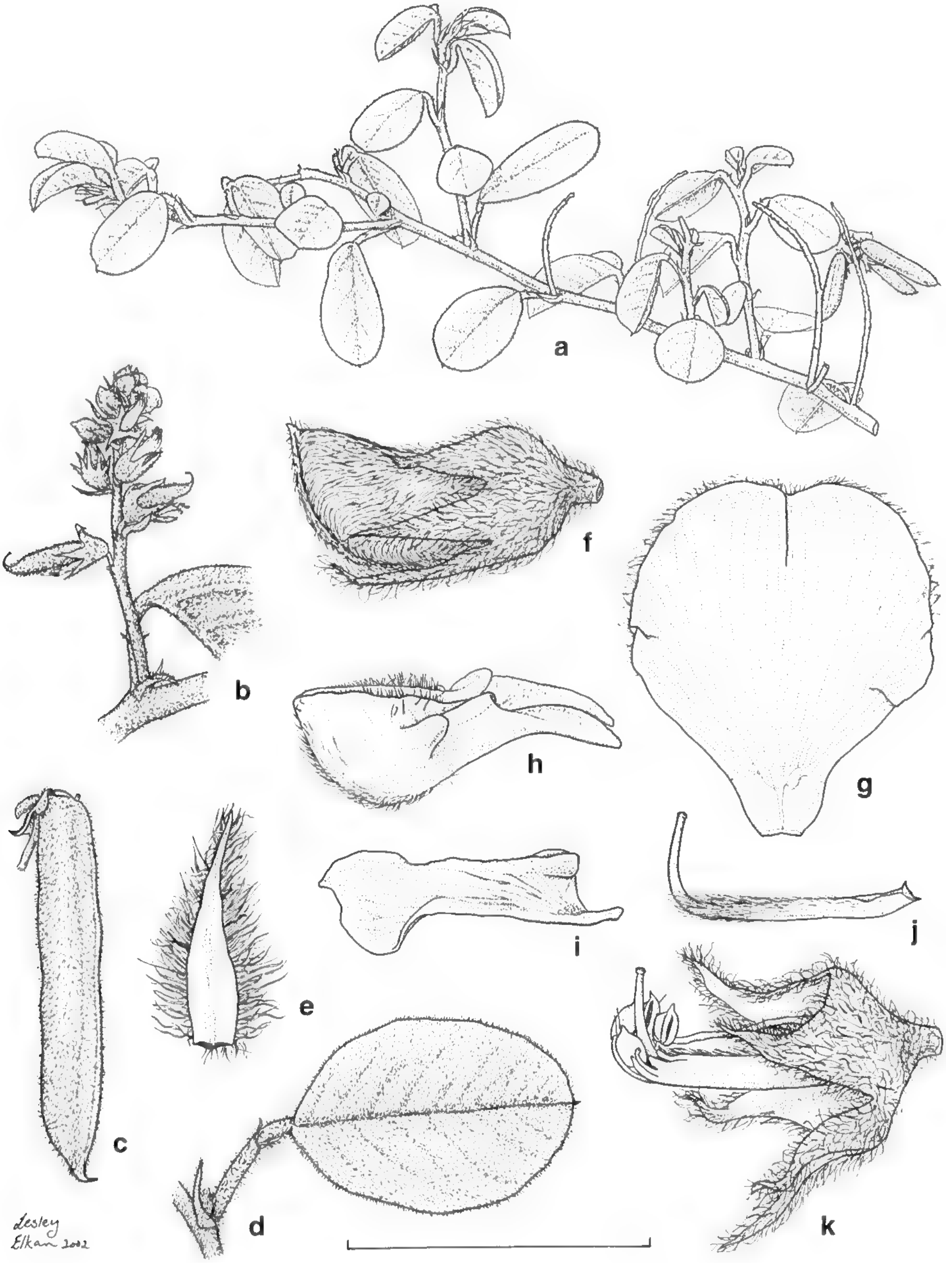

Fig. 5. *I. petraea*. **a**, habit; **b**, inflorescence; **c**, fruit; **d**, leaf; **e**, bract (adaxial view); **f**, bud; **g**, standard; **h**, keel; **i**, wing; **j**, ovary; **k**, lateral view of calyx and androecium. (a, c from *van Leeuwen 2190*; b, d, j from *van Leeuwen 1545*; e, f–i, k from *van Leeuwen 5082*). Scale bar: a = 60 mm; b, d = 20 mm; c = 15 mm; e–k = 4 mm.

11. Indigofera monophylla DC., Prod. 2: 222 (1825).

Type citation: '? in Novae Hollandiae orâ orientali.

Holotype: Nouvelle Hollande, côte ouest (G-DC *n.v.*, NSW microfiche).

Erect to prostrate shrub or subshrub, 0.2–1(–2.4) m high, with woody rootstock; young stems terete to ridged, white to brown, strigose or tomentose with dense to very dense, appressed to spreading, equally biramous hairs. Leaves unifoliolate; stipules triangular, often narrowly, (0.5–)1–4.5(–8.0) mm long, pubescent, not spinescent, persistent or not; petiole (1.0–)3–9(–12) mm long; rachis furrowed, often slightly; multicellular hairs at point of articulation absent to moderately dense, conspicuous or inconspicuous, red to dark brown, club-shaped. Leaflet with inconspicuous to conspicuous stipellae (0.2–)0.5–1 mm long; lamina ovate, elliptical, obovate or orbicular; (4.5–)10–30(–45) mm long, (3.5–)8–25(–33) mm wide; upper surface grey, white or green with sparse to dense, appressed to spreading hairs; lower surface grey, white or green with sparse to dense, appressed to spreading hairs; apex obtuse and mucronate; veins prominent or not prominent. Inflorescences (10–)20–120(–210) mm long, equal to, or longer than the leaf; peduncle (1.5–)4–20(–43) mm long; bracts triangular (0.5–)1–2.5(–6.0) mm long; flowers pink to purple or red; pedicel 0.5–1.8 mm long. Calyx (1.5–)2–3(–4.0) mm long, with unequal to subequal lobes less than to longer than the length of the tube and moderately dense or dense, white to almost black, appressed to shortly spreading hairs. Standard red, purple or pink, ovate to orbicular, 6.5–8.5(–9.4) mm high, 5.3–7.6 mm wide. Wings spathulate or narrowly obovate, 6–8.9 mm long, 2–3 mm wide. Keel 6.8–8.9(–9.5) mm long, 2–3 mm deep; lateral pockets 0.7–2 mm long; apex acute or rarely rounded; hairs moderately dense to dense, grey to dark brown, at the tip and along the bottom; margins ciliate. Staminal tube 5–7.3 mm long, colourless or free ends and tube pigmented. Ovary moderately to densely hairy. Pod spreading to descending, terete, (12–)18–30(–37) mm long, 3–4 mm deep, grey to brown, strigose to tomentose; hairs moderately dense to dense, appressed to spreading; apex pointed; endocarp spotted; seed (4–)8–10 per fruit.

Notes: as accepted here, this taxon is extremely variable. It varies in habit from an almost prostrate multi-stemmed shrub to a tall shrub over 2 m high and is variable in leaf size and morphology. There are apparently two common forms: one that occurs on rocky hills that has prominent lateral venation and another that occurs mostly on plains and has much less conspicuous lateral venation; there is a possible correlation of flower colour with these forms. The type is of the more prominently-veined form. There are a couple of other variants as well (Trudgen pers. comm.), including *Indigofera* sp. Bungaroo Creek, and this complex requires further in-depth study to clearly define segregate taxa.

Distribution and habitat: Northern Territory and Western Australia: found on rocky hills including limestone, the Great Sandy Desert, red sand and Pindan country, also loamy plains, watercourses and roadsides.

Conservation status: not at risk.

Selected specimens examined: Northern Territory: Central North: 45 km W of Sangsters Bore, Tanami Desert, *Latz 8115*, 28 Sep 1978 (NSW, CBG, K, MO, NSW); Central Mount Stuart, *Maconochie 707*, 26 June 1969 (AD, DNA, NSW); Vaughan Springs, *Winkworth 430*, 4 July 1954 (CANB). Central South: Laura Vale, *Tietkens s.n.*, 24 May 1889 (AD, DNA, MEL). Victoria River: Birrundudu Station, *Lang 5*, 22 July 1993 (NSW).

Western Australia: Ashburton: 30 km E of 'Three Rivers' Homestead, Great Northern Highway, *Mitchell 1651*, 24 Apr 1988 (NSW); Postcutters Bore, *Beard 6094*, 22 Aug 1970 (NSW). Austin: 100 m N of Yoothapina turn-off, on Great Northern Hwy, *Wilson 1150 & Rowe*, 18 Sep 1991 (NSW, PERTH, PRE); 16 miles SW of Mannine [Nannine], *Speck 724*, 8 Sep 1957 (CANB); 48 miles [c. 77.75 km] from Wiluna on Sandstone road, *Bennett 21*, July 1941 (PERTH). Canning: 52.6 km N of Shay

Gap, *Wilson 898 & Rowe*, 4 Sep 1991 (NSW 246773, PERTH); Anketell Ridge, Great Sandy Desert, *A.S. Mitchell 1111 & 1209*, 14 May 1979 (AD, DNA). Carnarvon: 53.0 km SW of Nanutarra, *Wilson 1111 & Rowe*, 15 Sep 1991 (NSW, PERTH); Cape Range - Rough Range at 20.0 km on road to coast from Learmonth, *Briggs 8812 & Johnson*, 6 Aug 1991 (NSW, L, MEL, MO, PERTH); Middle Gascoyne River Crossing, *Symon 9997*, 15 May 1975 (NSW, PERTH). Dampier: Edgar Range, SE of Broome, *Kenneally 5523*, 7 Aug 1976 (CANB, PERTH); Great Northern Highway, 35.5 km S of Lagrange Mission turn-off, *Wilson 885 & Rowe*, 3 Sep 1991 (NSW, E, PERTH, PRE, US). Fitzgerald: Great Northern Highway, c. 25 km W of Wolfe Creek turn-off, *Wilson 868 & Rowe*, 31 Aug 1991 (NSW, K, L, PERTH, RSA); 10 miles [c. 16 km] E of Margaret River Station, *Lazarides 6328*, 13 July 1959 (NSW, AD, BRI, DNA, MEL). Fortescue: Duck Creek, out from Mt Brockman, *Blockley 311*, 9 July 1966 (CANB, PERTH); 1.1 km W of Oakover River, *Wilson 950 & Rowe*, 5 Sep 1991 (NSW, MO, PERTH, UPS); Dolphin Island, Dampier Archipelago, Royce 7204, 5 June 1962 (PERTH). Hall: 6 miles NE of Gordon Downs Station, *Perry 2446*, 13 July 1949 (BRI, CANB, MEL, NSW); East Branch of Wolf Creek, c. 60 km S of Halls Creek, *Carr 3567 & Beauglehole 47345*, 13 July 1974 (PERTH). Keartland: Near Rudall R., *George 10859*, 24 May 1971 (CANB, NSW); 1 mile [c. 1.6 km] N of Googhenama Rockhole, *Royce 1811*, 19 May 1947 (PERTH). Mueller: Dovers Hills, *George 8984*, 27 July 1967 (NSW, PERTH); Djaluwon Creek, near S end of Lake Gregory, *George 15421*, 26 Apr 1979 (DNA, PERTH).

12. **Indigofera schultziana** F. Muell., Fragm. 7: 105 (1870)

Type citation: 'Prope portum Darwinii; Schultz (482).'

Holotype: Port Darwin, *Schultz 482* (MEL 586275). Probable isotypes: AD, E.

Erect subshrub, 0.3–0.6 m high; young stems slightly four-angled or ridged, grey and green, or brown, strigose with sparse to moderately dense, small, appressed, equally biramous hairs. Leaves unifoliolate with a conspicuous point of articulation; stipules triangular, 0.5–1 mm long, pubescent, not spinescent, not persistent; petiole 9–21 mm long; rachis furrowed; multicellular hairs at point of articulation moderately dense, inconspicuous, dark brown, club-shaped. Leaflet with inconspicuous stipellae, 0.2–1 mm long; lamina ovate to orbicular, 25–103 mm long, 20–60 mm wide; upper surface grey and green, glabrous or with sparse, very small appressed hairs; lower surface grey and green, paler than above, glabrous or with sparse, very small appressed hairs; apex obtuse or acute and apiculate; veins visible but not prominent. Inflorescences 35–115 mm long, longer than leaves; peduncle 6–24 mm long; bracts triangular, 5–8 mm long; flowers pink to purple; pedicel 2.5–3.5 mm long. Calyx 1.5–2.3 mm long, with subequal lobes less than or equal to the length of the tube, and moderately dense, hyaline, white or brown, appressed hairs. Standard pink or lavender, ovate; 6–8 mm high, 5.3–6.5 mm wide. Wings spathulate to narrowly obovate, 5.3–8 mm long, 1.5–2.5 mm wide. Keel 6.3–8 mm long, 1.5–2 mm deep; lateral pockets 0.6–1 mm long; apex acute; hairs sparse to moderately dense, hyaline to golden along the bottom; margin ciliate. Staminal tube 3.2–4 mm long, free ends, or free ends and tube, pigmented. Ovary moderately hairy. Pod ascending to descending, terete, 21–40 mm long, 2.5–3 mm deep, brown, strigose; hairs very small, moderately dense, appressed; apex shortly beaked; endocarp spotted; seed 6–8 per fruit.

Notes: *I. schultziana* is most closely related to *I. saxicola* and there are a number of specimens that represent probable intergrades between these two species. These will be discussed more fully under *I. saxicola* in part 2 of this revision.

Distribution and habitat: only known from a small area of the Northern Territory in the Finniss River area.

Conservation status: Leach et al. (1992) and Briggs and Leigh (1996) code this species 2R. It is listed as 'Rare' in the *IUCN 1997 Red list of Threatened Plants*.

Selected specimens examined: Northern Territory: Darwin & Gulf: Finnis River area, *Parker 153*, 12 Aug 1973 (BRI, CANB); NE of Finnis River crossing, *Dunlop 3122*, 16 Jan 1973 (CANB, DNA); 9 miles [c. 14.5 km] from Rum Jungle, *Blake 16738*, 8 Aug 1946 (BRI, DNA).

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New combinations in *Chordifex* (Restionaceae) from eastern Australia and new species from Western Australia

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Abstract

Briggs, Barbara G. and Johnson, L.A.S. (Royal Botanic Gardens, Mrs Macquaries Road, Sydney, NSW 2000, Australia) 2004. New combinations in Chordifex *(Restionaceae) from eastern Australia and new species from Western Australia.* Telopea *(10)3: 683–700.* New combinations in *Chordifex* are provided for two species from New South Wales (**C. dimorphus** and **C. fastigiatus**) and two Tasmanian endemics (**C. hookeri** and **C. monocephalus**), extending the distribution of the genus to eastern Australia. Phylogenetic analysis of chloroplast DNA data has shown these species to be embedded in *Chordifex*, so that the latter is paraphyletic if they are excluded. These species were previously included in *Restio* and subsequently divided among the genera *Acion*, *Guringalia* and *Saropsis* which are now synonymised under *Chordifex*. The main concentration of *Chordifex* is in the south of Western Australia where there are sixteen species. Ten of these were formerly transferred from *Restio* and a further five of them are now described and illustrated. **C. microcodon** (occurring from near Eneabba south almost to Perth) and **C. sinuosus** (from near Geraldton to Perth and Yarloop) are widespread species, **C. capillaceus** (around South Stirling and Wellstead) is relatively common in a more restricted area, while **C. reseminans** (near Eneabba to Cataby) is endangered and **C. jacksonii** (near Walpole) vulnerable. The colliculate or ridged seed type of *Chordifex* contrasts with the smooth seeds of *Baloskion*; while the strongly ridged seeds of *C. sinuosus*, *C. reseminans* and *C. chaunocoleus* are compared with the colliculate seeds of other *Chordifex* species. Seed surface features show greater congruence with results from DNA data than does the presence or absence of the conspicuous culm anatomical feature of pillar cells in the chlorenchyma.

Introduction

Extensive studies from a variety of approaches, but especially morphological and anatomical (Johnson & Briggs 1981; Linder 1984, 1985; Linder et al. 1998, 2000; Briggs & Johnson 1999), and DNA sequencing studies (Briggs et al. 2000, Eldenäs & Linder 2000) have resulted in classifications in which no genera of Restionaceae are common to the Australasian and the African regions. Since *Restio* is typified by an African species, and the Australian species previously referred to *Restio* are a diverse assemblage, the latter were divided among several genera (Briggs & Johnson 1998a, b). The majority of eastern Australian species were transferred to *Baloskion* Raf., while the largest group of Western Australian species were placed in the newly-described genus *Chordifex*, typified by the new species *C. stenandrus* B.G. Briggs & L.A.S. Johnson. Thus *Chordifex* has been regarded as a Western Australian endemic and included *C. abortivus* (Nees) B.G. Briggs & L.A.S. Johnson, *C. amblycoleus* (F. Muell.) B.G. Briggs & L.A.S. Johnson, *C. chaunocoleus* (F. Muell.) B.G. Briggs & L.A.S. Johnson, *C. crispatus* (R. Br.)

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* BGB is responsible for the new combinations published here; the newly described species were distinguished and studied by both authors.

† Deceased 1 August 1997.

B.G. Briggs & L.A.S. Johnson, *C. gracilior* (F. Muell. ex Benth.) B.G. Briggs & L.A.S. Johnson, *C. isomorphus* (K.W. Dixon & K.A. Meney) B.G. Briggs & L.A.S. Johnson, *C. laxus* (R. Br.) B.G. Briggs & L.A.S. Johnson, *C. leucoblepharus* (Gilg) B.G. Briggs & L.A.S. Johnson, *C. ornatus* (Steud.) B.G. Briggs & L.A.S. Johnson and *C. sphacelatus* (R. Br.) B.G. Briggs & L.A.S. Johnson.

When we described *Chordifex* we also segregated from *Restio* three new, small genera, *Acion*, *Guringalia* and *Saropsis* (Briggs & Johnson 1998a) and transferred two species into *Acion* and one each into the latter two genera. These species differed from *Chordifex*, as it was then circumscribed, in lacking the distinctive and very prominent culm anatomical feature of pillar cells (Cutler 1966, Briggs & Johnson 1998a, 1999) extending across the chlorenchyma. These thick-walled cells divide the chlorenchyma into linear segments and produce a striated culm surface. They were among the major features characterising the anatomical groups distinguished by Cutler (1969) within *Restio* as then broadly circumscribed and defining a major multi-generic lineage in a tentative phylogeny of Restionaceae (Johnson & Briggs 1981). The presence of uninterrupted chlorenchyma led to comparisons of these four species being made principally with *Baloskion*, which also shares an eastern Australian distribution, rather than with *Chordifex*. Inflorescence, floral, and seed coat features (Figs 1, 2) all distinguish these species from *Baloskion*, while features of culm branching, culm sheaths, single or multiflowered spikelets, and numbers of cell layers in the chlorenchyma characterised each of the segregate genera.

Phylogenies based on DNA data for three segments of the chloroplast genome (*rbc*L, *trn*L-*trn*F and *mat*K) strongly support the distinctness of the African and Australian lineages and the separation of *Chordifex* and *Baloskion*., but show *Acion*, *Guringalia* and *Saropsis* embedded within *Chordifex* (Briggs et al. 2000, Marchant pers. com.). Referring to these four eastern Australian species, Briggs et al. (2000) observed that 'It is notable that these associate with the south-western Australian genus *Chordifex*, which they resemble in seed ornamentation, rather than with *Baloskion*' and 'The phylogeny inferred from these [DNA] findings suggests that a prominent and distinctive feature of culm anatomy, the presence of pillar cells, may have been lost in several separate clades'. Thus pillar cells are now considered have evolved early in the diversification of Australian Restionaceae (although after divergence of *Lepyrodia* group) and presence or absence of pillar cells is considered to be unreliable basis for characterising monophyletic groups in Australian Restionaceae. Seed-coat characters, however, are given prominence by their congruence with DNA data in corroborating relationships that were previously considered unlikely on grounds of culm anatomy and biogeography. Other vegetative and reproductive features of the three eastern genera are compatible with those of *Chordifex*, which already includes a relatively diverse array of species. These three genera are therefore placed in synonomy and new combinations in *Chordifex* provided for the relevant species.

Congeneric with the named species of *Chordifex* are five Western Australian species that are described here. These were not collected until recent decades or were not distinguished from related species. The names now published were included (without formal description) in the conspectus of our classification of Australian Restionaceae (Briggs & Johnson 1999). Information on their features and biology, in advance of formal naming, was also given by Meney, Pate & Hickman (1999), who provide excellent illustrations of these and the already-named species. Further information on the biology, ecology and conservation of various species is given in other chapters of Meney and Pate (1999). An account of all species of *Chordifex* will be given in the *Flora of Australia* (Briggs, Johnson, Porter & Krauss, in preparation).

Baloskion and *Chordifex* seed surface patterns

Seed surfaces in those Restionaceae with indehiscent or late-dehiscent fruit are mostly smooth or almost so. Where the seed is the disseminule, the seed surfaces show much variation and provide features that are synapomorphies of clades or assist in characterising genera (Linder 1984, Briggs & Johnson 1998a, 1999). In *Baloskion* the pedicel of the flower is fused to the subtending glume and the seeds are mostly dispersed within the late-dehiscent capsule, still attached to the glume, and the seed surface is almost smooth (Fig. 1). In most seed-dispersed species the outer cellular layer is white, fragile and easily removed. In most *Chordifex* species this layer is colliculate, with lines of convex cells with a thick cuticle, and these often also bear a pattern of smaller angular cells, apparently the imprint of the cells of the inner layer of the pericarp. Such features are shown by the four eastern Australian species transferred to *Chordifex* (Fig. 2) and by three of the newly described species: *C. capillaceus, C. microcodon* and *C. jacksonii* (Figs 3, 4). A small group of *Chordifex* species, however, have strikingly ridged seeds, as in the two new species *C. sinuosus* and *C. reseminans* (Figs 5, 6). Such seed ornamentation, seen also in *C. chaunocoleus,* but not in the somewhat similar species *C. sphacelatus* and *C. laxus*, appears to be an apomorphic development from the more widespread colliculate character state. The ridge- or colliculate-pattern is still clearly shown on the inner surface of the capsule wall after the seeds have been shed.

Synonymy and new combinations in *Chordifex*

Chordifex B.G. Briggs & L.A.S. Johnson, *Telopea* 7: 356 (1998).

Synonyms: *Acion* B.G. Briggs & L.A.S. Johnson, *Telopea* 7: 353 (1998); *Guringalia* B.G. Briggs & L.A.S. Johnson, *Telopea* 7: 353 (1998); *Saropsis* B.G. Briggs & L.A.S. Johnson, *Telopea* 7: 355 (1998).

New combinations

Chordifex dimorphus *(R. Br.) B.G. Briggs,* **comb. nov.**

Basionym: *Restio dimorphus* R. Brown, Prodr.: 246 (1810).

Synonym: *Guringalia dimorpha* (R. Br.) B.G. Briggs & L.A.S. Johnson, *Telopea* 7: 353.

Chordifex fastigiatus *(R. Br.) B.G. Briggs,* **comb. nov.**

Basionym: *Restio fastigiatus* R. Brown, Prodr.: 246 (1810).

Synonym: *Saropsis fastigiata* (R. Br.) B.G. Briggs & L.A.S. Johnson, *Telopea* 7: 356.

Chordifex hookeri *(D.I. Morris) B.G. Briggs,* **comb. nov.**

Basionym: *Restio hookeri* D.I. Morris in M.R. Banks et al. (eds), *Aspects Tasmanian Bot., Tribute to Winifred Curtis*: 33 (1991).

Synonym: *Acion hookeri* (R. Br.) B.G. Briggs & L.A.S. Johnson, *Telopea* 8: 22 (1998).

Chordifex monocephalus *(R. Br.) B.G. Briggs,* **comb. nov.**

Basionym: *Restio monocephalus* R. Brown, Prodr.: 245 (1810).

Synonym: *Acion monocephalum* (R. Br.) B.G. Briggs & L.A.S. Johnson, *Telopea* 7; 355 (1998).

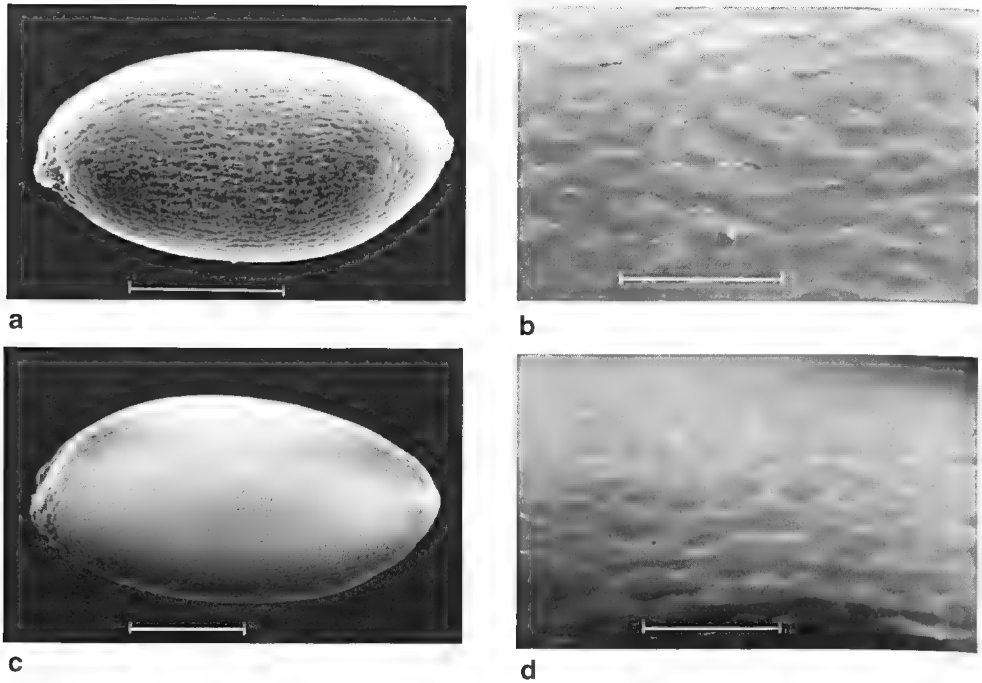

Fig. 1. Seed surfaces. **a, b**, *Baloskion pallens* (R. Br.) B.G. Briggs & L.A.S. Johnson (Bowenia State Forest, Qld., 5 May 1981, *Johnson 8656* [NSW]); **c, d**, *Baloskion tetraphyllum* (Labill.) B.G. Briggs & L.A.S. Johnson subsp. *meiostachyum* (L.A.S. Johnson & O. Evans) B.G. Briggs & L.A.S. Johnson (Kendall, NSW, *Bailey*, Sep 1932 [NSW 47937]). Scale bars: a, c = 200 μm; b, d = 50 μm.

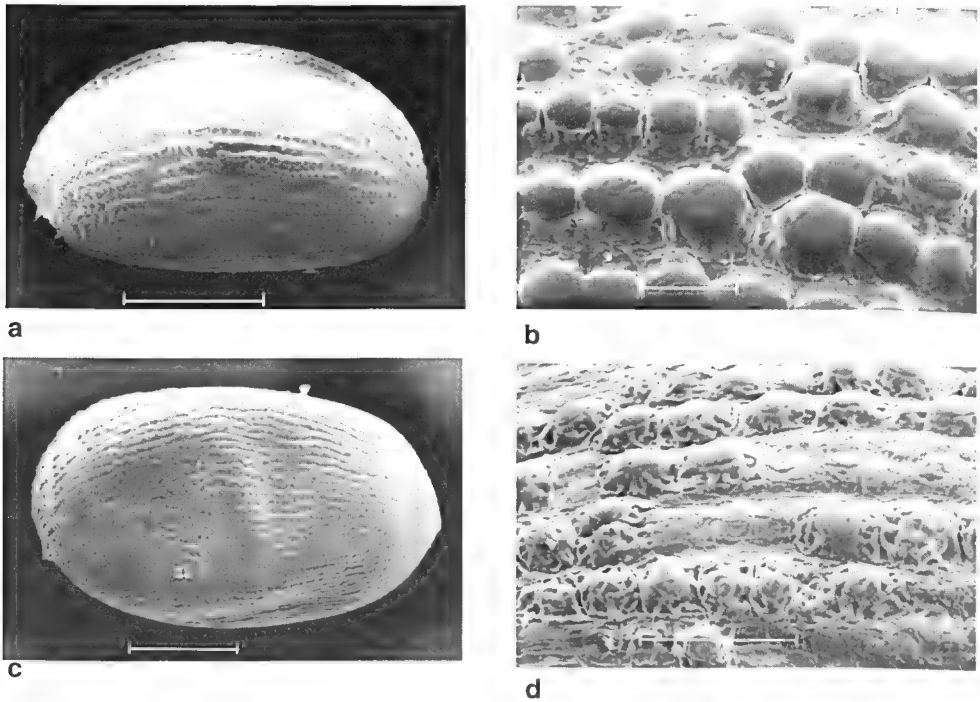

Fig. 2. Seed surfaces. **a, b**, *C. dimorphus*. (Ku-ring-gai Chase, Constable 18 Sep 1958 [NSW 48845]); **c, d**, *C. hookeri* (Mt Tim Shea, Tasmania, 18 Jan 1962, *J. Vickery* [NSW 57045]). Scale bars: a = 500 μm; b = 50 μm; c = 300 μm; d = 100 μm.

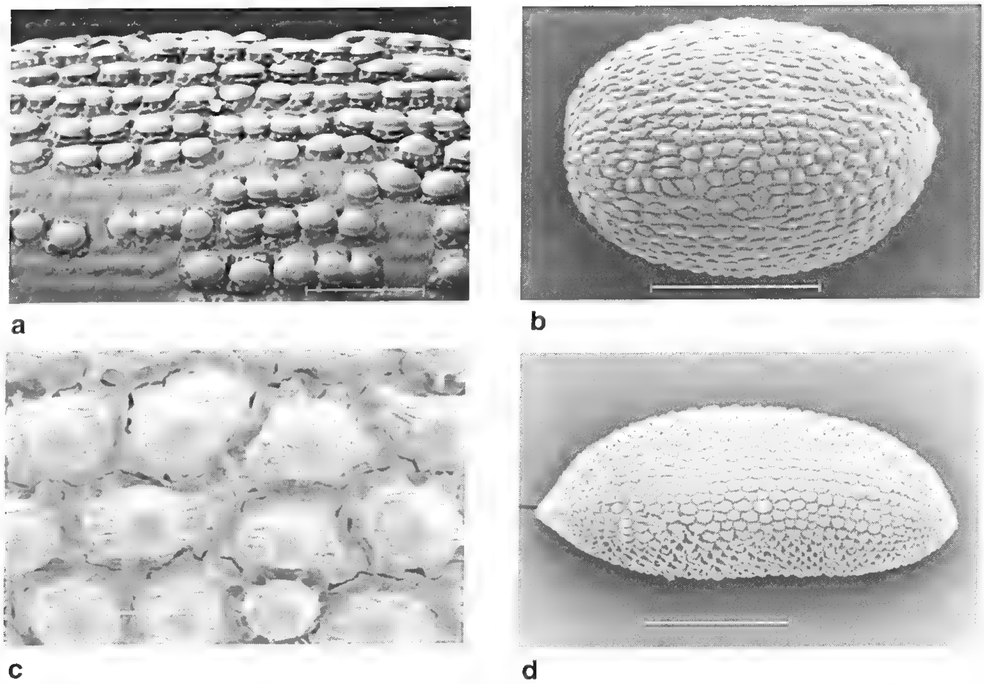

Fig. 3. Seed surfaces. **a**, *C. capillaceus* (*Briggs 7662*); **b**, **c**, *C. microcodon* (*Briggs 7491*); **d**, *C. jacksonii* (*Briggs 9442*). Scale bars: a = 80 µm; b = 500 µm; c = 50 µm.

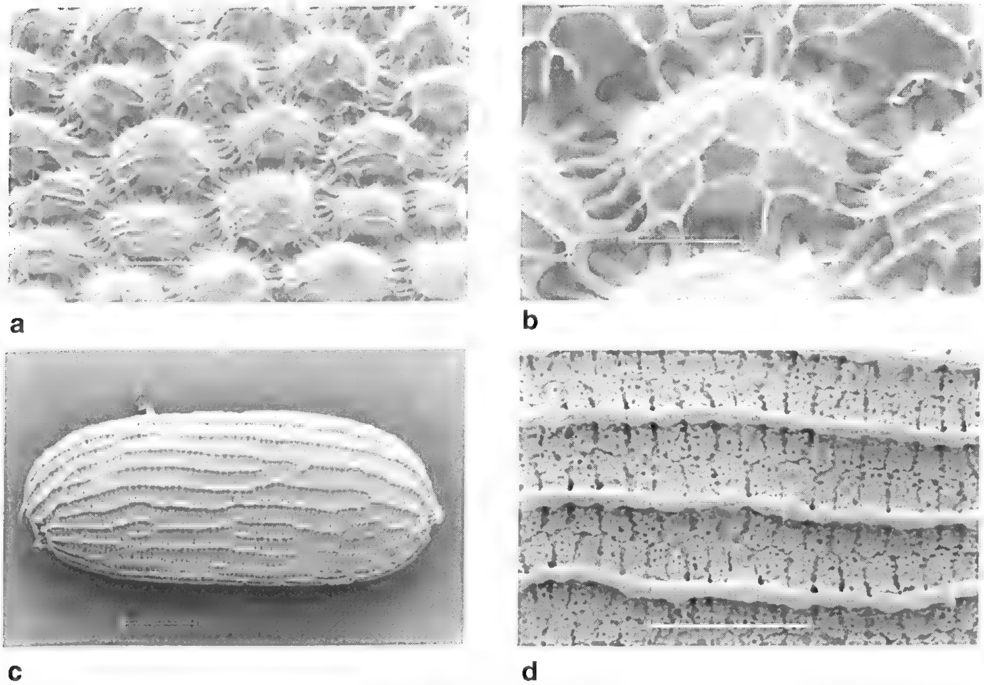

Fig. 4. Seed surfaces. **a**, **b**, *C. jacksonii* (*Briggs 9442*); **c**, **d**, *C. amblycoleus* (21 Km ENE of Karridale, 6 Oct 1984, *B. Briggs 7575 & L. Johnson* [NSW]). Scale bars: a = 50 µm; b = 20 µm; c = 200 µm; d = 100 µm.

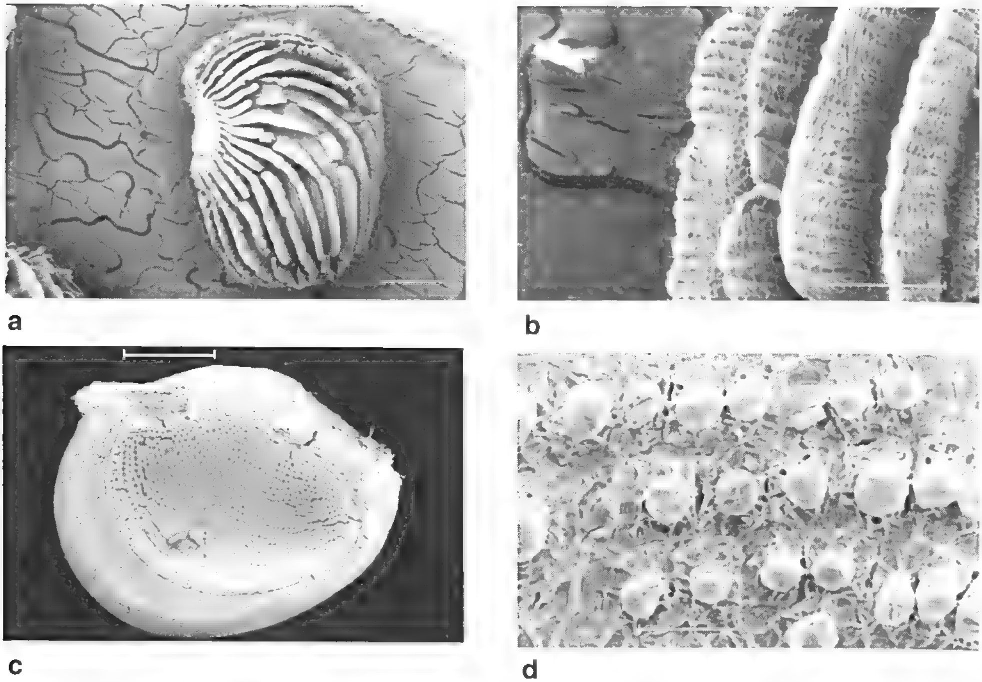

Fig. 5. Seed surfaces. **a, b**, *C. sinuosus* (*Briggs 7445*); **c, d**, *C. sphacelatus* (12 km WNW of Wellstead, 13 Sep 1990, *Briggs et al. 8710* [NSW]). Scale bars: a = 400 µm; b = 170 µm; c = 500 µm; d = 50 µm.

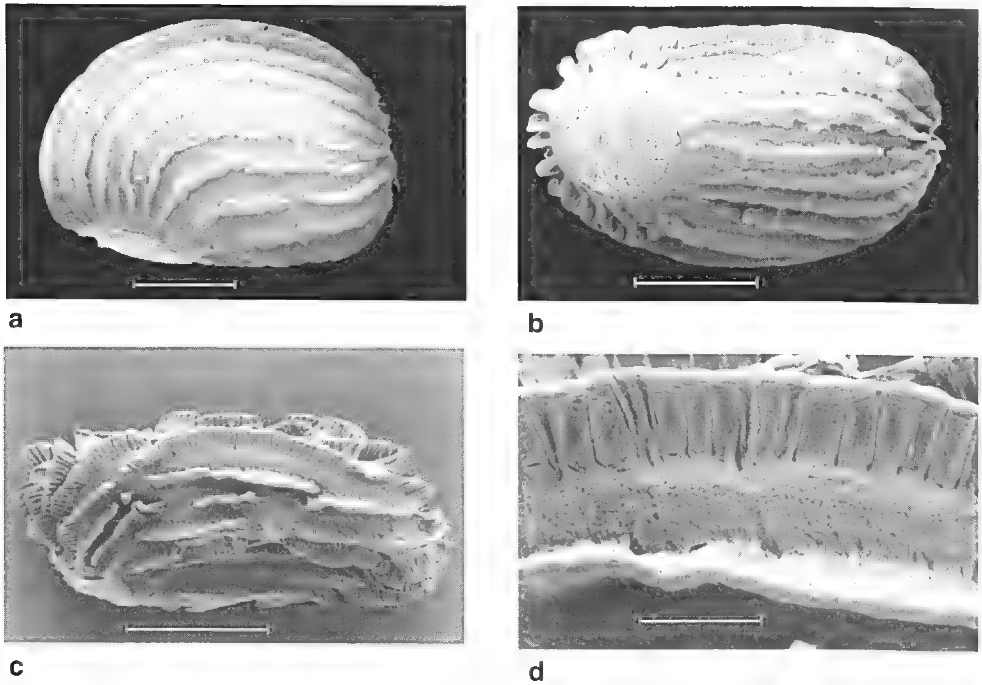

Fig. 6. Seed surfaces. **a, b**, *C. reseminans* (*Briggs 9376*); **c, d**, *C. chaunocoleus* (c. 8 km SW of Toodjay, 28 Sep 1990, *Briggs et al. 8636* [NSW]). Scale bars: a, b, c, = 500 µm; d = 50 µm.

Description of new species

Chordifex capillaceus *B.G. Briggs & L.A.S. Johnson*, **sp. nov.**

Inter species *Chordificis* combinatione characterum sequentium distinguitur: rhizomata gracilia (1–1.5 mm diam.); culmi graciles (0.3–0.7 mm diam.); spiculae femineae fructiferae graciles elongataeque.

Type: Western Australia: 1 km W of South Stirling at north end of Pfeiffer Road, W.A., 8 Oct 1984, *B.G. Briggs 7662 & L.A.S. Johnson* ♀ (holo: NSW; iso AD, CANB, K, MO, MEL, PERTH).

Plants mostly forming a dense small clump. Rhizomes slender, horizontal, much branched and intertwined, to c. 15 cm long, c. 1.0–1.5 mm diam., red-brown and sparsely pubescent, with small brown, scarious, appressed scales. Culms slender, numerous and closely spaced on the rhizomes, 1.3–8 mm apart, erect, terete, 0.5–0.7 mm diam., glabrous above the lowest internode, striate; fertile culms mostly unbranched below the inflorescence, 5–20(–40) cm long, usually simple but occasionally branched, nodes (below the inflorescence) 1–3, the lowest internode mostly more slender (0.3–0.5 mm diam.) and often sparsely pubescent; sterile culms mostly shorter, repeatedly branched, the branches erect or flexuose and terete to compressed. Sheaths appressed; basal sheaths light-brown; cauline sheaths 4–10 mm long, green to brown, ciliate, smooth or slightly ribbed, acute with a caducous lamina c. 1 mm long. Male inflorescence of 1–3 erect or pendulous spikelets, lower spikelets on peduncles to 8(–15) mm long, upper spikelets sessile or shortly pedunculate; subtending bracts similar to culm sheaths. Female inflorescence of 1–2(–4) erect spikelets at the uppermost node(s). Male spikelets ovoid, 4–15 mm long, 2.5–6.0 mm wide; 3–15 glumes, all fertile, lanceolate, light-brown, glabrous or lowest glume apically pubescent, acute, 4.0–4.5 mm long. Female spikelets very narrow oblong, 8–15 mm long, 1.5–3.0 mm wide; glumes 3–5, all fertile, similar to males, 4.0–5.5 mm long; spikelet axis elongating in fruit to 15(–25) mm long, so that the flowers are widely separated. Male flowers: tepals 5, lanceolate, acute, membranous, pale, 2.6–3.0 mm long; outer tepals keeled, occasionally pubescent; inner tepals flat, glabrous; stamens 3, filaments 3.0–3.5 mm long, anthers (1.3–)1.8–2.1 mm long. Female flowers shortly pedicellate; tepals 5, similar to males; staminodes 3; styles 2, free almost to the base, mostly stigmatic. Capsule c. 1–2 mm long, smooth, brown. Seed oblong-cylindrical, c. 1.3 mm long, colliculate with lines of convex cells. (Figs 3a, 7).

The epithet is from the Latin *capillus,* a hair, referring to the very slender culms.

Distribution: occurs in the south of Western Australia from South Stirling to Chillinup and Wellstead, c. 100 km NE of Albany. Grows in heathy shrubland on yellow sand, often with laterite gravel; in somewhat poorly drained situations in a low-rainfall region.

Conservation status: common (Meney, Pate, Dixon, Briggs & Johnson 1999) and moderately widespread.

Fire response: killed by fire.

Note: Somewhat resembling *C. ornatus*, but culms shorter and more slender, with less branching of the vegetative culms; with small appressed culm sheaths; male spikelets ovoid, with fewer glumes and glumes acute. Culms of *C. ornatus* are 20–35 cm tall, 0.5–1 mm diam., with lax sheaths 8–17 mm long; the male spikelets are globular with 20–55 glumes and the glumes aristate. *Chordifex ornatus* occurs near Tambellup and the Stirling Range.

Selected specimens examined: Western Australia: Eyre: South Stirling, just W of township, 4 Oct 1976, *B. Briggs 6586* ♂, *6602* ♀ (NSW, CANB, K, PERTH, RSA), *6603* ♂ (NSW, CANB, PERTH); 1 km W of South Stirling at N end of Pfeiffer road, 8 Oct 1984, *B.G. Briggs 7661 & L.A.S. Johnson* ♂ (NSW, AD, B, BOL, CANB, K, MEL, MO, PE, PRE, PERTH, RSA); Wellstead, Hassell Hwy, Apr 1992, *K. Meney & J. Pate* (NSW 254925); 2 km E of Wellstead, 29 Aug 1998, *B.G. Briggs 9453*♂, *9454* ♀ (NSW); 13 km NW of Black Head, 23 Sep 1973, *K. Newbey 3840* ♀ (PERTH, NSW); 3.7 km along the Boat Harbour road from the turn-off on the Hassell Hwy, 25 Jun 1976, *D.J. McGillivray 3498 & A.S. George* ♀ (NSW, K, MO, PERTH), *3499* ♂ (NSW, AD, PERTH).

2. Chordifex microcodon *B.G. Briggs & L.A.S. Johnson*, **sp. nov.**

Inter species *Chordificis* combinatione characterum sequentium distinguitur: planta caespitosa; culmi crassi (1.5–2.3 mm diam.), teretes, ramosi; spiculae campanulatae; spiculae masculae plerumque pendulae.

Type: Western Australia: 22.8 km E of Brand Hwy on Green Head–Coorow Road, Alexander Morrison Natl Park, 30 Sep 1984, *B.G. Briggs 7733 & L.A.S. Johnson* ♀ (holo: NSW; iso: K, PERTH).

Plant caespitose, the base with short brown scales partly covering a dense pale woolly pubescence. Culms numerous, densely clumped on the very short rhizomes, branched, mostly erect, ± terete, 40–70 cm long, main culms 1.5–2.3 mm diam., striate, basally pubescent with white appressed hairs; the branches straight or flexuose or occasionally convoluted and then usually barren; internodes several, 4.5–9.0 cm long. Sheaths lax, open, flaring from the base, 0.6–1.9 cm long, scarious, smooth to striate, dark tan, glabrous, obtuse to truncate, lamina c. 1–1.8 mm long. Inflorescence with long (to 15 cm), spreading lower branches and short upper branches, spikelets numerous; the males mostly pendulous on short, filiform pedicels; females erect; subtending bracts similar to culm sheaths. Male spikelets campanulate, 7–10 mm long, 3–4 mm wide; sterile lower glumes 15–21; fertile upper glumes 10–16, lanceolate, brown, usually glabrous, acuminate, 2.5–7.5 mm long; mucro 0.5–0.9 mm long. Female spikelets campanulate, slightly shorter than males; sterile lower glumes 6–13; fertile upper glumes 1–3(–11), similar to males, broad-lanceolate, 2–5 mm long; mucro c. 1 mm long. Male flowers: tepals 5, linear, membranous; outer tepals keeled, c. 3.5 mm long, sparsely pubescent; inner tepals slightly shorter, flat, glabrous; stamens 3; filaments filiform, 3.0–4.5 mm long; anthers 2.0–2.4 mm long, becoming spirally twisted. Female flowers: tepals 5, narrow lanceolate, rigid, acute; outer tepals keeled, c. 3.5 mm long, sparsely pubescent; inner tepals slightly shorter, flat, glabrous; staminodes 3; styles 2, mostly free, half-stigmatic. Capsule compressed, 2.0–2.5 mm long. Seed globose, c. 1.3 mm long, colliculate with lines of convex cells. (Figs 3b, c; 8).

The epithet is from the Greek, *mikros*, small, and *kodon*, a bell, referring to the shape of the spikelets after anthesis.

Distribution: occurs in Western Australia from Eneabba to Regans Ford district and south to near Wanneroo. On deep sand, or sand over laterite, in heath and woodland, mostly in well-drained sites.

Conservation status: common and widespread.

Fire response: killed by fire.

Note: A distinctive species, differing from other *Chordifex* species by the following combination of characters: habit caespitose; culms stout, terete, branching; spikelets campanulate and often pendulous. *Chordifex microcodon* is a host to a pathogenic smut fungus tentatively identified as a species of *Tolyposporium* (Sieler et al. 1999); smutted male plants may produce infertile inflorescences similar in appearance to those of female plants.

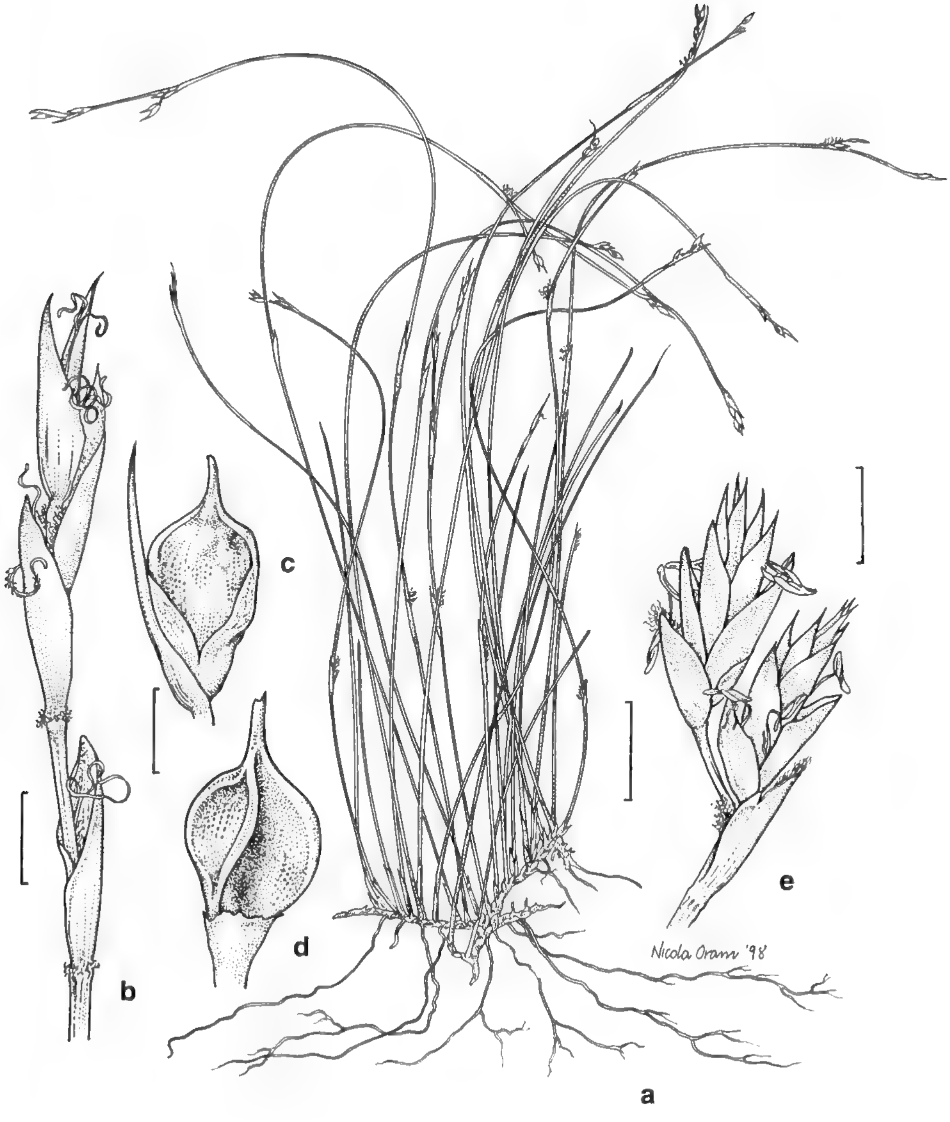

Fig. 7. *Chordifex capillaceus.* **a–d**, female (*Briggs 7662*): **a**, habit; **b**, spikelet; **c**, capsule; **d**, dehisced capsule;. **e**, male spikelet (*Briggs 6586*). Scale bars: a = 2 cm; b = 3 mm; c, d = 1 mm; e = 3 mm.

Fig. 8. *Chordifex microcodon*. **a–c**, female (*Briggs 7733 & Johnson*): **a**, habit (part of a plant with many culms); **b**, flower; **c**, dehisced capsule with emerging seed; **d, e**, male (*Briggs 7490 & Johnson*): **d**, inflorescence; **e**, spikelet. Scale bar: a, d = 8 cm; b, c = 4 mm; e = 1.5 cm.

Selected specimens examined: Western Australia: Irwin: 25 miles [40 km] W of Winchester to Eneabba, 30 Sep 1966, *E.M. Bennett 1405* ♂ (PERTH, NSW); 29 km S of Eneabba on Brand Highway, 29 Sep 1984, *B. Briggs 7490 & L. Johnson* ♂, *7491* ♀ (NSW, CANB, NBG, PERTH); 22.8 km E of Brand Hwy on Green Head–Coorow Road, Alexander Morrison Natl Park, 30 Sep 1984, *B.G. Briggs 7732 & L.A.S. Johnson* ♂ (NSW, PERTH); 5 km SE of Badgingarra, 10 Sep 1979, *G.J. Keighery 2554* ♂ (PERTH, NSW); 6.5 km S of New Badgingarra, Badgingarra Natl Park, 25 Sep 1976, *B. Briggs 6312* ♂ (NSW, CANB, K). Darling: 19 km WNW of Mogumber, 23 Sep 1966, *B.G. Briggs 857* ♂ (NSW, K, PERTH), 858 ♀ (NSW); 1.5 miles [2.4 km] S of Regans Ford on Gingin road, 23 Sep 1966, *B. Briggs 852* ♀ (NSW, K, MEL, PERTH); Bullsbrook, May 1944, *F.M. Bailey* ♀ (PERTH); Neaves Rd, c. 15 km NE of Wanneroo, 18 May 1983, *B. Briggs 7236 & L. Johnson* ♂ (NSW, CANB, PERTH, K, MEL, RSA), *7237* ♀ (NSW, CANB, PERTH).

3. Chordifex jacksonii *B.G. Briggs & L.A.S. Johnson*, sp. nov.

A *C. amblycoleo* combinatione characterum sequentium distinguitur: culmi graciles (c. 1 mm diam.); vaginae culmorum acutae, lamina filiformis; spiculae parvae globosaeque; semina colliculosa.

Type: Western Australia: near Mt Frankland, 13 Feb 1913, *S.W. Jackson* ♂ (holo: NSW 78864; iso: CANB, K, MEL, AD, MO, PERTH).

Plant tufted; the base with brown, scarious scales covering a pale woolly pubescence. Culms few, erect, straight, terete or slightly compressed, simple, 40–100 cm long, c. 1 mm diam., striate, glabrous. Sheaths imbricate, closely appressed, 1.6–2.2 cm long, striate, light-brown to straw-coloured, tapering into a filiform lamina (2–)4–7 mm long. Inflorescence of up to 5 spikelets on each of several long, filiform, occasionally branched peduncles; subtending bract usually apically ciliate, similar to culm sheaths or shorter. Male spikelets ovoid to globose, c. 5 mm long, 3–5 mm wide; sterile lower glumes 15–38, fertile upper glumes 4–14, oblong-ovate to spathulate, apex sparsely ciliate, 1.5–2.5 mm long; mucro erect or spreading, 1.5–2.2 mm long; uppermost c. 5 glumes smaller and sterile. Female spikelets similar to males. Male flowers: tepals 6, red-brown; 2 outer tepals keeled, sparsely pilose along keel; lanceolate, usually obtuse, 2.2–2.8 mm long; inner tepals and 3rd outer tepal, glabrous, 1.9–2.7 mm long; stamens 3; filaments 2.5 mm long; anthers c. 1.2 mm long. Female flowers: tepals similar to males, glabrous; staminodes 3; styles 2, free, almost wholly stigmatic. Capsule 2.5 mm long. Seed ellipsoid, white, 1.9 mm long, colliculate with lines of convex cells. (Figs 3d; 4a, b; 9).

The epithet commemorates Sydney William Jackson (1873–1946), a noted collector of bird and plant specimens. He first collected this species, as his handwritten specimen label states: 'on low damp sandy flat near Mt Frankland … under great difficulties'.

Distribution: occurs in the south of Western Australia, near and west of Mt Frankland, NW of Walpole. Grows in wet heaths on damp, sandy flats.

Conservation status: vulnerable, known from few localities, CALM conservation status P2 (Meney, Pate, Dixon, Briggs & Johnson 1999; Wheeler et al. 2002).

Fire response: killed by fire.

Note: *Chordifex jacksonii* resembles the more widespread and robust species *C. amblycoleus* (F. Muell.) B.G. Briggs & L.A.S. Johnson, although these do not appear as sister species among *Chordifex* species sampled in DNA-based phylogenetic analyses (Marchant pers. com.). *Chordifex jacksonii* has more slender culms, acute culm sheaths that taper into a filiform lamina and small ovoid or globular spikelets that do not elongate in fruit. *Chordifex amblycoleus* has culms 1–2 mm diam., truncate sheaths with lamina absent or minute, and ovoid or narrow ovoid spikelets 6–23 mm long, elongating in fruit; it occurs near Jindong (Busselton region) and from Augusta to Walpole. The seed surfaces of the species differ; seeds of *C. jacksonii* are colliculate with lines of large convex cells whereas *C. amblycoleus* seeds have narrow, widely spaced ridges (Figs 4c, d).

Selected specimens examined: Western Australia: Darling: Beardmore Rd intersection with South Western Hwy, 34 km W of Walpole, Oct 1990, *S. Pignatti* ♀ (KPBG); 0.3 km E of Beadmore Rd and South Western Highway intersection, 28 Aug 1998, *B. Briggs 9442* ♀ (NSW); 3.5 km E of South Western Hwy on Beardmore Rd, 14 Oct 1992, *B.G. Briggs 9078 & K. Meney* ♂ (NSW, CANB, PERTH), *9079* ♀ (NSW); Pingerup Rd, c. 4 km NE of Marron Rd junction, 5 May 1991, *N. Gibson & M. Lyons 630* ♀ (PERTH); near Mt Frankland, 13 Feb 1913, *S.W. Jackson* ♀ (NSW 91597).

4. Chordifex sinuosus *B.G. Briggs & L.A.S. Johnson*, sp. nov.

A *C. sphacelatus* combinatione characterum sequentium distinguitur: vaginae culmorum mucrone 1–2 mm longo instructae; mucro glumae 1–1.7 mm longus; culmi teretes (autem rami compressi); semina valde porcata.

Type: Western Australia: 34 km NNW of Gingin on Brand Hwy, *B.G. Briggs 7445 & L.A.S. Johnson* ♀ (holo: NSW; iso PERTH, CANB, K, MO).

Forming diffuse tussocks or large patches of widely spaced culms. Rhizome horizontal to c. 20 cm long or more, stout, 3–5 mm diam., with scarious, pale- to dark-brown, appressed scales partly covering a pale, thick, woolly pubescence. Culms at intervals of c. 0.5–1.0 cm on the rhizome, usually much branched, initially erect but sinuose distally, terete, 20–45 cm long, c. 1 mm diam., striate, grey-green, mostly glabrous or the basal internodes occasionally pubescent; branches short, sinuose or convoluted, terete or compressed, often barren; internodes numerous, 2.5–5.5 cm long. Sheaths loosely appressed, 0.6–1.2 cm long, initially red-brown or blackish, often grey and weathered with age; apex obtuse or truncate, shortly ciliate; margins narrow, caducous, membranous; mucro 1–2 mm long. Inflorescence of 1–4 spikelets, the spikelets terminal on the culm or on short lateral branches, or sessile at the upper nodes; subtending bracts similar to culm sheaths but shorter. Male spikelets ovoid, 5–10 mm long, 3–4 mm wide; sterile lower glumes 5–12; fertile upper glumes c. 15–18, broad-ovate, mostly glabrous, brown, acute, 3.0–4.0 mm long, outer margin with a few hairs; mucro 1–1.7 mm long. Female spikelets elliptic to ovoid, 6–8 mm long, 3.0–4.0 mm wide; 11–21 sterile lower glumes and 2 or 3 fertile upper glumes, similar to males, obtuse to acute, 2.5–4.5 mm long, occasionally with a few short hairs on margin. Male flowers: tepals 5 or 6, pale-brown, membranous, 2.5–3.0 mm long; outer tepals keeled, pubescent; inner tepals flat, narrow-lanceolate, acute; stamens 3; filaments stout and basally dilated and spongy, 3.0–4.0 mm long; anthers c. 1.5–2.0 mm long. Female flowers: tepals 5, brown, lanceolate, 4.0–5.7 mm long; 2 outer tepals keeled and pubescent; inner tepals flat; staminodes 3, 1.2–1.5 mm long; styles 2, bases connate. Capsule 2.2–2.8 mm long, smooth, brown. Seed ovoid, c. 2 mm long, prominently ridged. (Figs 5a, b; 10).

The epithet is from the Latin *sinuosus*, full of bendings, referring to the flexuose culms.

Distribution: occurs in Western Australia from Walkaway near Geraldton south to Perth and Yarloop. Grows in heaths and woodland on sand, in dry or seasonally moist sites.

Conservation status: common and widespread.

Fire response: resprouts after fire.

Note: *Chordifex sinuosus* resembles *C. sphacelatus*, which occurs from Kulin and Albany to Israelite Bay, but differs in the longer mucro on culm sheaths and glumes, the culms terete in the upper half (though culm branches ± compressed) and the seeds being very strongly ridged. *Chordifex sphacelatus* has the mucro on culm sheaths < 0.5 mm long and on glumes absent or minute; the upper culms (as well as the branches) are compressed and the seeds are colliculate with lines of convex cells (Fig. 5c, d). Both these species are hosts to smut fungi tentatively identified as a species of *Tolyposporium* (Sieler et al. 1999). Some of the spikelets on both male and female plants affected by

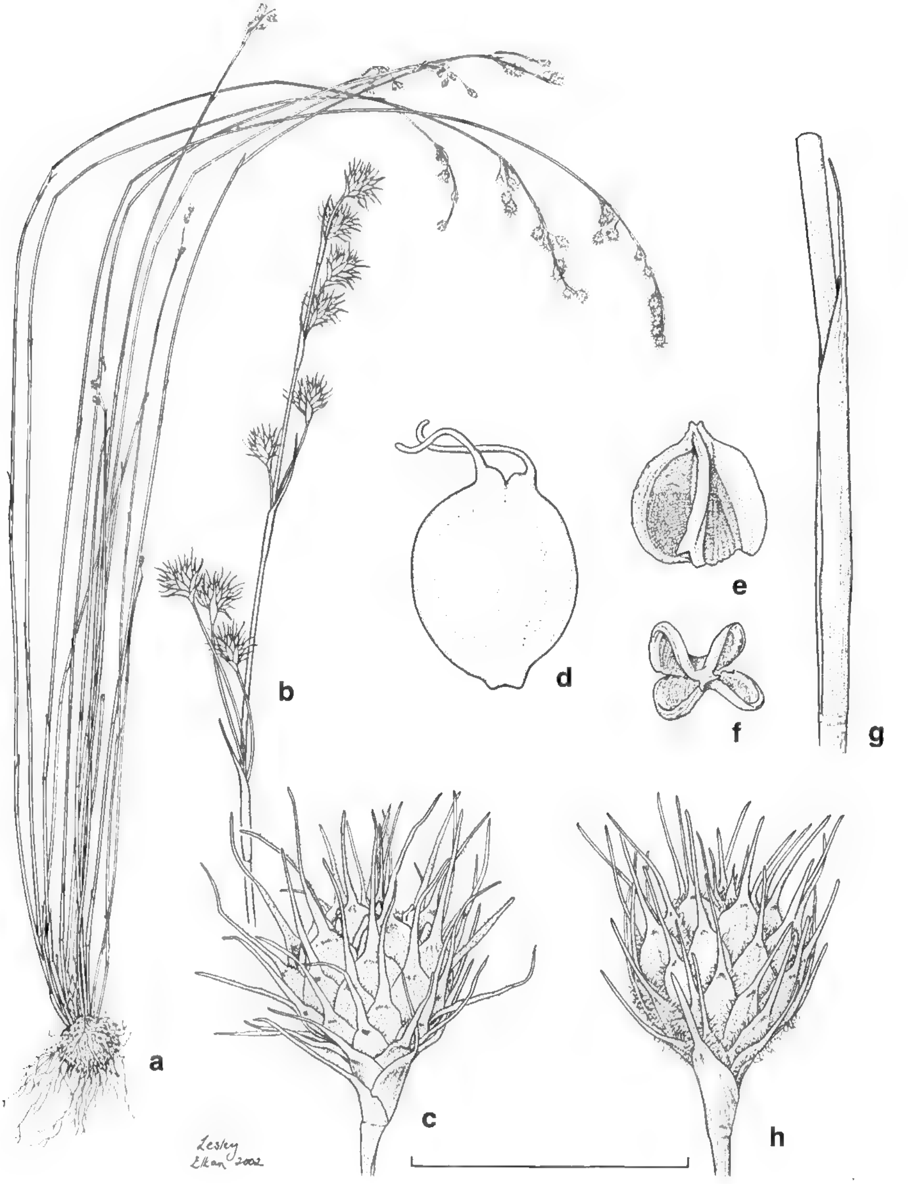

Fig. 9. *Chordifex jacksonii.* **a–f**, female (*Briggs 9079*): **a**, habit; **b**, inflorescence; **c**, spikelet; **d**,capsule; **e**, **f**, dehisced capsule, side and top views; **g–h** male (*Jackson NSW 78864*): **g**, culm sheath. **h**, spikelet. Scale bar: a = 9 cm; b = 3 cm; c,h = 1 cm; d, e, f = 0.3 cm; g = 0.5 cm.

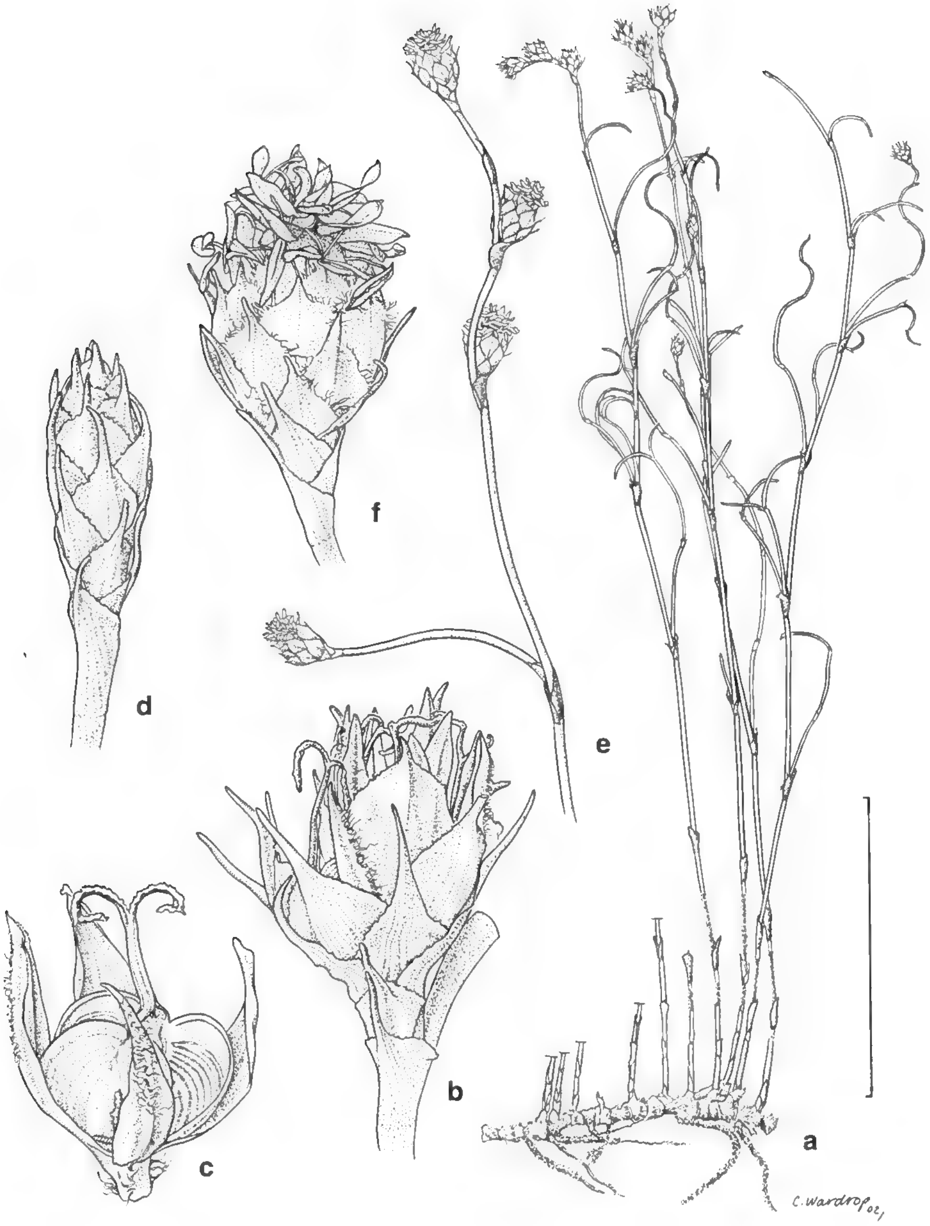

Fig. 10. *Chordifex sinuosus*. **a–d**, female: **a**, habit; **b**, spikelet; **c**, dehisced capsule with tepals, showing ridges on inner surface of pericarp (holotype); **d**, young female spikelet (*Krauss 142 & Howitt*); **e**, male inflorescence **f**, male spikelet (*Pate & Meney NSW 255721*). Scale bar: a = 10 cm, b = 1 cm, c = 0.6 cm, d, f = 0.75 cm, e = 3 cm.

this inflorescence-smut are enlarged (to 16 mm long and 11 mm wide) and infertile, with the glumes modified in shape and lacking a mucro. Largely because of such smut infection, female plants of *C. sphacelatus* are often infertile and few specimens bear seeds or well-developed capsules. Occasional uninfected plants, such as *Briggs 8710 et al.* bear abundant capsules and seed.

Selected specimens examined: Western Australia; Irwin: Burma Rd, 13.3 km SE of Nangetty–Walkaway Rd, 13 Aug 1991, *B. Briggs 8894 & L. Johnson* ♀ (NSW, PERTH); 27 km SE of Dongara, 26 Oct 1981, *K. Newbey 9379* ♂ (PERTH); 31 km NNW of Eneabba on Brand Highway, 22 Apr 1989, *S. Krauss 142 & L. Howitt* ♀ (NSW, CANB, K, MO, PERTH); 11.7 km S of Eneabba Road on Brand Highway, 6 Oct 1995, *B.G. Briggs 9374* & J. Pate ♂, 9373 ♀ (NSW, PERTH); Brand Highway 12.3 km S of Eneabba, May 1992, *J. Pate & K. Meney* ♂ (NSW 255721), ♀ (NSW 255721). Darling: c. 1.5 km NE of Mt Lesueur, 24 May 1983, *L.A.S. Johnson 8719a* ♂, *8719b* ♀ (NSW); 30 km E of Jurien Bay, 2 Sep 1976, *R.G. Coveny 8005 & B.R. Maslin* ♂, 8020 ♀ (NSW); 6 km S of Regans Ford, N of Gingin, 23 Sep 1966, *B.G. Briggs 845* ♀ (NSW, K, MEL, PERTH); 34 km NNW of Gin Gin on Brand Highway, 28 Sep 1984, *B. Briggs 7445 & L. Johnson* ♀ (NSW); High Wycombe, 31 May 1998, *M. Hislop 1056A* ♀, *1056B* ♂ (PERTH, NSW); Maida Vale Rd, Kewdale, 7 Sep 1976, *R.G. Coveny 8224* ♂ (NSW, AD, MEL); 0.8 km N of Yarloop, *B. Briggs 7528 & L. Johnson* ♀ (NSW, AD, CANB, PERTH).

5. **Chordifex reseminans** *B.G. Briggs & L.A.S. Johnson*, **sp. nov.**

A *C. sphacelato* combinatione characterum sequentium distinguitur: planta caespitosa; rhizomata brevia; inflorescentiae spiculis numerosis instructae; a C *chaunocoleo* sic distinguitur: rami inflorescentiae producti; mucro glumae brevis (usque 1.5 mm longus).

Type: Western Australia: 11.7 km S of Eneabba Road on Brand Highway, 6 Oct 1995, *B.G. Briggs 9375 & J. Pate* ♂ (holo NSW; iso CANB, K, MO, NBG, PERTH, RSA).

Plants caespitose, forming dense clumps to 30 cm diam. Rhizomes short, horizontal, much-branched and interlaced, up to 3 cm long on specimens, c. 3 mm diam., with short straw-coloured scales covering a pale pubescence. Culms crowded, initially erect and unbranched, with 3–4 long internodes, but usually branched and sinuose distally, terete, 30–60 cm long, 1.0–1.4 mm diam., striate, mostly glabrous or the basal internodes occasionally pubescent; branches at several upper nodes, sinuous, terete or compressed. Sheaths loosely appressed, (0.8–)1–2 cm long, initially red-brown but becoming grey and weathered with age; apex obtuse or truncate, shortly ciliate, with narrow, caducous, membranous margins; lamina 1.5–3 mm long. Inflorescence: lateral branches to 10 cm long, each with 2–10 (males) or 1–4 (females) sessile or pedicellate spikelets near the apex; subtending bracts similar to culm sheaths but shorter. Male spikelets ovoid, 4.5–6 mm long, 3–4 mm wide; sterile lower glumes c. 12–15; fertile upper glumes c. 11–16, broad-ovate, brown, acute, 3.0–3.7 mm long, mostly glabrous but distal margin with a few hairs; mucro to 1.2 mm long; Female spikelets elliptic to ovoid, 6–8 mm long, 3.0–4.0 mm wide (when fruiting up to 6–7 mm wide); sterile lower glumes 11–25; fertile upper glumes 2 or 3, similar to males, obtuse to acute, 3.5–6.0 mm long, occasionally with a few short hairs on margin; mucro to 1.5 mm long. Male flowers: tepals 5 or 6, pale-brown, membranous, 2.5–3.0 mm long; outer tepals keeled, pubescent; inner tepals flat, narrow-lanceolate, acute; stamens 3; filaments stout, dilated and spongy at the base, 3.0–4.0 mm long; anthers c. 1.5–2.0 mm long. Female flowers: tepals 5, brown, lanceolate, 4.7–6.3 mm long; 2 outer tepals keeled and pubescent; inner tepals flat; staminodes 3, 1.1–1.5 mm long; styles 2, bases connate. Capsule (2.2–)2.4–2.8 mm long, smooth, glossy, brown. Seeds ovoid, 1.4–2 mm long, prominently striated. (Figs 6a, b; 11).

The epithet is from the Latin *re-*, again or very, and *semen*, a seed, (plural *semina*), referring to the reproductive habit of establishing from seed, rather than resprouting, after fire or disturbance.

Fig. 11. *Chordifex reseminans*. **a–d**, male: **a**, habit; **b**, flower; **c**, spikelet; **d**, inflorescence (holotype). **e**, **f**, female: e, young spikelet; f, old spikelet with dehisced capsule showing ridges on inner surface of pericarp (*Pate & Meney NSW 255720*). Scale bar: a = 7.5 cm, b = 0.4 cm, c, e, f = 0.75 cm, d = 3 cm.

Distribution: occurs in Western Australia from near Eneabba to Cataby. Grows in dry heath, shrubland and woodland on white sand.

Conservation status: endangered, rare and restricted in distribution (Meney, Pate, Dixon, Briggs & Johnson 1999; Meney, Pate & Hickman 1999), known from few localities, in a region where there has been much loss of natural habitat. Especially vulnerable because of its fire sensitivity.

Fire response: killed by fire.

Note: Differs from *C. sinuosus* in the caespitose habit with culms crowded on short, interlaced, branching rhizomes, longer culm sheaths, more branching in the inflorescence; more spikelets per culm and recovery after fire by seed rather than resprouting. The two species sometimes occur together (e.g. *Briggs 8917b* and at the type locality). In habit and fire response it resembles *C. chaunocoleus* but the inflorescence branches are longer and the glume mucro shorter. *Chordifex chaunocoleus* has inflorescence branches to 2.5 cm long, glumes with a mucro 0.8–2.4 mm long, and occurs in isolated localities near Badgingarra and Toodyay. All three species have similar, strongly ridged seeds (Figs 5, 6).

Specimens examined: Western Australia: Irwin: 11.7 km S of Eneabba Road on Brand Highway, 6 Oct 1995, *B.G. Briggs 9376, 9377* & *J. Pate* ♀ (NSW, PERTH, NBG); Brand Highway, 12.3 km S of Eneabba, May 1992, *J. Pate & K. Meney* ♂ (NSW 255717), ♀ (NSW255720); 16 km N of Cooroo Road on Highway 1, 15 Aug 1991, *B.G. Briggs 8917b & L.A.S. Johnson* ♂ (NSW, PERTH, BOL); 29 km N of Tootbardi Road, Badgingarra, 31 Nov 1990, *K. Meney / K. Dixon 911* ♀ (KPBG, NSW); Bibby Road, N boundary of Badgingarra National Park (Reserve 31809), W of Badgingarra, 7 Dec 1992, *E.A. Griffin 8321* ♀ (PERTH); Cataby, Apr 1992, *K. Meney & J. Pate* ♂ (NSW 416522), ♀ (NSW 254918).

Acknowledgments

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The tribe Triodieae (Chloridoideae: Gramineae)

S.W.L. Jacobs

Abstract

Jacobs, S.W.L. (Royal Botanic Gardens Sydney, Mrs Macquaries Road, Sydney, NSW 2000, Australia) 2004. The tribe Triodieae (Chloridoideae: Gramineae). Telopea *10(3): 701—703.* The tribe **Triodieae** is formally published and delimited, and a key to the four genera provided.

Introduction

The *Flora of Australia* series requires that the names for all levels of taxa must be formally published before they can be used.

Bentham (1881) described the subtribe *Triodiinae* within his *Festuceae* (Pooideae: Gramineae). Bentham circumscribed his subtribe on the basis of >2 (fertile) florets per spikelet, lemmas rarely >3-nerved, and ending in 3 teeth, lobes or awns. He included *Triodia, Diplachne, Triplasis, Scleropogon, Eremochloa* and *Triraphis,* genera now usually placed in three different subfamilies: *Triodia, Diplachne, Triplasis* and *Triraphis* are all usually placed in the subfamily Chloridoideae (Watson and Dallwitz 1992); *Scleropogon* is retained in the Pooideae; and *Eremochloa* is usually placed in the Panicoideae. Of Bentham's original defining characters, the only one that more or less still holds for the current usage of *Triodieae* is the 'lemmas … ending in 3 teeth, lobes or awns'.

Triodia is the only genus of Bentham's subtribe *Triodiineae* retained in the tribe *Triodieae* as currently used, and is here selected as the lectotype of the subtribe. Watson and Dallwitz (1980) seem to have been the first to actually use the name *'Triodieae'* for a tribe containing *Triodia* and related genera, the same sense in which it is used here. The tribal name has been used elsewhere (Wheeler et al. 1982, 2002, Macfarlane 1992) with many authors not concerned about the formal publication of names above the genus level. Walsh (1994) retained subtribe *Triodiineae* but transferred it to the tribe *Eragrostideae* (Chloridoideae) and interpreted it in the same sense as used here for *Triodieae. Triodia* and its relatives are now generally accepted as being Chloridoid grasses (Jacobs 1971, Watson & Dallwitz 1980, 1992, Jacobs & Pickard 1981, Wheeler et al. 1982, 2002, Macfarlane 1992, Walsh 1994, Lazarides 1997).

Triodieae *(Benth.) S.W.L. Jacobs* **stat. nov.**

Subtribe *Triodiineae* Benth. (1881: 30) in part; Walsh (1992: 555).

Lectotype, **here designated,** *Triodia* R.Br.

Plantae perennes pro parte maxima habitu hemisphaerici ramis aeriis. Laminae foliorum planae ad initium sed plicatascentes permanente ubi ariditate afflictiones, anatomia 'Kranz' cellulis vaginarum fasciculatarum mesophyllum vice fasciculorum vascularium cingentibus.

Perennials, mostly hummock-forming. Leaves: sheaths often resinous; ligule a row of hairs or teeth, or sometimes a narrow, fringed membrane; blade originally flat, permanently folding when stressed, sometimes resinous; anatomically C_4 with distinctive parenchymatous bundle-sheath cells that arch well away from the vascular bundle to surround the mesophyll; the stomatal grooves either distributed evenly on both surfaces and then the leaves rigid, pungent when dry and usually non-resinous ('Hard' Spinifex), or the grooves distributed all over the adaxial surface and with few near the midrib or none on the abaxial surface and then the blades comparatively soft, usually resinous and non-pungent ('Soft' Spinifex). Inflorescence a panicle, or a single 2- or 1-sided raceme or spike, sometimes reduced to 1 or a few spikelets. Glumes 2, 1–many-nerved, ranging from ±equal to distinctly unequal, persistent. Florets 1–many; fertile bisexual florets 1–many, sometimes with incomplete florets or an extended, naked rhachilla above; rhachilla disarticulating below each floret and above the persistent glumes. Lemma 3–many-nerved, the nerves often in 3 groups; apex variously lobed, emarginate, mucronate, awned (1–3), or almost entire.

Notes: An apparently isolated tribe confined to Australia and dominant in the hummock grasslands of arid Australia, but while some species have the Chloridoid-type bicellular microhairs, others have the Panicoid-type bicellular microhairs, as do some other Chloridoid grasses (Jacobs 1987). In this treatment, the tribe is kept in subfamily Chloridoideae and comprises at least four genera, *Triodia, Plectrachne, Monodia* and *Symplectrodia*. Lazarides (1997) suggested that *Plectrachne* be included in *Triodia* but supplied data supportive of dividing both genera into three new genera, with possibly even more genera in *Triodia* s. str., based on leaf morphology and lemma apex characters. To these characters could be added the bicellular microhairs and silica cells of the epidermes.

Key to genera

1 Spikelets with 1 floret; rhachilla prolonged beyond the floret, the extension naked; lemma with a single terminal awn .... **Monodia**

1* Spikelets with more than 1 floret 2

2 Fertile floret 1 only, at base of spikelet, with 2 or more incomplete florets widely separated on a very long rhachis above it; florets becoming longer towards tip of rhachis .... **Symplectrodia**

2* Fertile florets more than 1, usually 3–many, closely or loosely imbricate, becoming progressively smaller towards tip of rhachis and, if many, upper few often incomplete 3

3 Glumes usually shorter than the florets; lemma apex variously emarginate, lobed, toothed or nearly entire, not with distinct long capillary awns .... **Triodia**

3* Glumes usually longer than the florets; lemma apex with three capillary awns .... **Plectrachne**

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Boronia hapalophylla (Rutaceae), a new and restricted species from north-eastern New South Wales

Marco F. Duretto, John Edwards and Patricia Edwards

Abstract

Duretto, Marco F. [1]*, John Edwards and Patricia Edwards*[2] *([1]Tasmanian Herbarium, Tasmanian Museum and Art Gallery, Private Bag 4, Hobart, Tasmania 7001. Email: marco.duretto@tmag.tas.gov.au; [2]PO Box 179, South Grafton, New South Wales 2460) 2004.* Boronia hapalophylla *(Rutaceae), a new and restricted species from north-eastern New South Wales. Telopea 10(3): 705–710.* **Boronia hapalophylla** Duretto, F.J.Edwards & P.G.Edwards, a narrow endemic of the Grafton area, north-eastern New South Wales, is newly described and illustrated, and notes on its relationships are given.

Introduction

Fieldwork in the Grafton area by two of the authors (J. & P. Edwards) located an undescribed species of *Boronia* series *Valvatae* that is newly described and named below as *B. hapalophylla* Duretto, F.J. Edwards & P.G. Edwards. This species is one of a number of undescribed taxa, eg. in *Grevillea* (Proteaceae) and *Bertya* (Euphorbiaceae), that have been identified from the area. The opportunity is taken here to publish a formal description and a more detailed account of the species before the forthcoming *Flora of Australia* treatment of the genus. A cladistic analysis of *B.* section *Valvatae* was completed to help ascertain the relationships of the species within *B.* series *Valvatae.*

Materials and Methods

Field surveys were conducted by J. and P. Edwards in 2002 and 2003 and herbarium material was collected in 2003.

To determine the phylogenetic position of *B. hapalophylla,* it was scored for the data set of *B.* section *Valvatae sensu lato* that was analysed by Duretto and Ladiges (1999) with the additions of Duretto (2003). All taxa and characters of these analyses were used following the methods as outlined for the third analysis of Duretto and Ladiges (1999). The data set was analyzed using PAUP 4.03ba (Swofford 1998) and *B.* section *Alatae, B.* section *Algidae* and *B.* subsection *Ternatae* were used as outgroups. As it is difficult in some species of *Boronia,* including this one, to determine if the leaves are petiolate or sessile a number of analyses were completed: leaves were scored as being both sessile and petiolate, just sessile or just petiolate (Character 12).

Taxonomy

Boronia hapalophylla *Duretto, F.J.Edwards & P.G.Edwards,* **sp. nov.**

A *Boronia rosmarinifolia* Endl. et *B. ledifolia* (Vent.) DC. sepalis maioribus (5–10 mm longis, 3–7 mm latis; cf. 2–4.5 mm longis, 1.5–3.5 mm latis) et foliis indumento stellato sparso vel denso superficiali (cf. glabris vel indumento sparso) differt.

Type: Near Grafton [precise information withheld], 16 Sep 2003, *F.J. Edwards A* (holo HO 523452; iso BRI, NSW).

Erect, much branched shrub to 3 m tall, very open and spindly, often supported by other species when tall. Multiangular stellate hairs sessile, with up to 15 rays; rays to 0.5 mm long, unicellular, free, firm, straight, glossy, smooth, white to yellow. Branches terete to slightly quadrangular in cross section, decurrent leaf bases lacking, not obviously glandular, with no massive cork development, with a moderately dense stellate indumentum, becoming glabrous with age, regrowing from a rootstock after disturbance. Leaves simple, opposite, rarely sub-opposite or in whorls of three, not conspicuously glandular, sessile to subsessile, leaf base so strongly attenuate as to appear petiolate, apparent petiole to 1.5 mm long; lamina narrow-elliptic to elliptic to lanceolate, (13–)18–50(–70) mm long, (1–)3.5–12 mm wide, strongly discolourous, paler beneath, dorsiventral, with palisade mesophyll above and spongy mesophyll below; tip acute; base strongly attenuate; margins entire, slightly recurved to revolute; midrib prominently raised abaxially, with tightly packed parenchyma with secondary thickening between midvein and abaxial epidermis, impressed adaxially; adaxial surface with a sparse to moderately dense, stellate indumentum; abaxial surface with a dense, heterogenous indumentum of two hair types: a moderately dense layer of multiangular stellate hairs over a dense layer of peltate stellate hairs. Inflorescence axillary, 1–5-flowered, with a dense stellate indumentum; peduncle absent, or sometimes 2–5 mm long in inflorescences with 3–5 flowers; prophylls minutely unifoliolate, often leaf-like, 1.5–7(–20) mm long, with a dense stellate indumentum, or indumentum as leaves; anthopodia [pedicels] 2–6.5 mm long. Sepals broadly ovate-deltate, shorter and narrower than petals, acuminate, valvate in bud, 5–7 mm long, 3–4.5 mm wide, enlarging to 10 mm long and 7 mm wide with mature fruit, persistent; adaxial surface densely and minutely pubescent, becoming glabrous towards base; abaxial surface with a dense stellate indumentum. Petals pink, valvate in bud, (6–)8–10 mm long, enlarging to 15 mm long with mature fruit, with midvein raised abaxially, persistent; adaxial surface sparsely pilose, becoming glabrous towards base; abaxial surface with a dense stellate indumentum. Stamens all fertile, filaments bearing stiff, simple hairs abaxially and on margins below glandular tip; sepaline filaments clavate, tapering to anther connective, 2–2.5 mm long, the distal 0.5–1 mm prominently glandular; petaline filaments, c. 1.5 mm long, the distal end glandular; anthers monomorphic, glabrous; anther appendage erect or reflexed. Disc entire, glabrous, rarely with slight swelling opposite sepaline stamens. Ovary glabrous or rarely with few stellate hairs at apex; style glabrous or rarely with scattered stellate hairs at base; stigma slightly wider than style. Cocci c. 7 mm long, c. 3.5 mm wide, glabrous or hirsute. Seeds black, shiny, 5–6 mm long, 2.5–3 mm wide; surface at magnification tuberculate; tubercles free. (Fig. 1).

Specimens examined [precise information withheld]: Near Grafton, 16 Sep 2003, *F.J. Edwards B* (HO, NSW); *ibid*, 16 Aug 2003, *P.G. & F.J. Edwards 1, 4–7* (HO); *ibid*, 16 Aug 2003, *P.G. & F.J. Edwards 2, 3* (HO, NSW); *ibid*, Aug 2003, *F.J. & P.G. Edwards 1–4* (HO).

Distribution and ecology: *Boronia hapalophylla* is restricted to a single sandstone rise near Grafton, north-eastern New South Wales. Populations are usually found in open Eucalypt woodland generally with an open understorey though the species is sometimes found in thick gully vegetation dominated by *Leptospermum* and *Banksia*. The species appears to flower throughout the year with a main flowering and fruiting period in Spring.

Conservation status: *Boronia hapalophylla* occurs in scattered numbers in a very limited area of approximately five by three kilometers. Some areas do have dense populations, eg. one with 200 plants in a 300 m × 20 m area has been recorded. It is found sparingly in one Nature Reserve. Supporting infrastructure (roads etc) for a proposed dam in the

Fig. 1. Holotype of *Boronia hapalophylla*: herbarium specimen × 0.4; flowers × 2 (*F.J. Edwards A*, HO *523452*).

area threatens a significant number of the known populations. *Boronia hapalophylla* appears to be isolated, taxonomically, in *B.* series *Valvatae*, and does have any close relatives in New South Wales (see 'Relationships' below): increasing its conservation significance for the state. A conservation code (following Briggs and Leigh 1996) of 2E seems appropriate.

Boronia hapalophylla is found with other rare and restricted species such as *Eucalyptus tetrapleura* L.A.S.Johnson, *Angophora robur* L.A.S.Johnson & K.D.Hill, the endangered *Melichrus hirsutus* J.B.Williams MS, and the undescribed taxa in *Grevillea* and *Bertya* as mentioned above. It is also found with the *Corymbia trachyphloia* (F.Muell.) K.D.Hill & L.A.S.Johnson subsp. *trachyphloia* / *Eucalyptus psammitica* L.A.S.Johnson & K.D.Hill (Brown Bloodwood/Sandstone Mahogany) community which has been recently declared as an Endangered Ecological Community.

Derivation of name: The epithet is derived from the Greek, *hapalo* (soft to touch), and *phyllus* (leaf), and refers to the stellate indumentum on the adaxial surface of the leaves that can make them soft in appearance and to the touch unlike the other species of *Boronia* in the area.

Notes: *Boronia hapalophylla* differs from the closely related species *B. rosmarinifolia*, *B. ledifolia* and *B. chartacea* P.H.Weston by the large sepals (5–10 mm long, 3–7 mm wide; cf. 2–4.5 mm long, 1–3.5 mm wide) and the sparse to dense indumentum on the adaxial surface of the leaves (cf. glabrous, *B. rosmarinifolia* and *B. chartacea*, or with a sparse indumentum, *B. ledifolia*).

The density of the indumentum on the adaxial surface of the leaves is variable with plants to the south generally having a denser indumentum. Plants from the more southern populations may also have a stellate indumentum on the ovary tip and/or style, and hirsute fruit whereas these organs are usually glabrous.

Relationships: The species, with two different types of stellate hairs on the abaxial surface of the leaves, axillary inflorescences, sepals and petals that are both valvate in bud and persistent with mature fruit, and petals with a prominently raised midrib, clearly belongs in *B.* series *Valvatae* (as defined by Duretto 1999). This is a large series that in previous cladistic analyses (Duretto & Ladiges 1999; Duretto 1999, 2003) has proven to be very sensitive to character and taxon deletions and additions. Indeed, the internal structure of the clade is supported mainly by homoplasious characters and/or reversals. *Boronia hapalophylla* is similar to the *B. rosmarinifolia* species-group (Qld, NSW) in that it usually has sessile, simple leaves. Some specimens of *B. hapalophylla*, though, do have subsessile leaves and the leaves are very attenuate and so can appear petiolate, as found in the *B. foetida* Duretto species-group (Qld), but not to the same degree. With this latter group *B. hapalophylla* shares the acuminate sepals. It differs from both the *B. rosmarinifolia* and *B. foetida* species-groups, and from *B. chartacea* (north-eastern NSW), by having an indumentum on the adaxial surface of the leaves as do some members of the *B. lanceolata* F.Muell. species-group (NT, Qld) and *B. ledifolia* (NSW, Vic.). It differs from the other species-group found in series *Valvatae* (viz. the *B. alulata* Benth. species-group) in having broadly ovate-deltate sepals and simple leaves.

The cladistic analysis, where *B. hapalophylla* was scored as having both sessile and petiolate leaves, produced 55 most parsimonious trees, each of 205 steps. The strict consensus tree (not shown) is exactly like the strict consensus tree as shown by Duretto (2003: p. 117) except for the addition of *B. hapalophylla*. This species was placed in *B.* series *Valvatae* in the *B. foetida* species-group where it formed a trichotomy with *B. jensziae* Duretto and another trichotomy containing *B. bella* Duretto, *B. excelsa* Duretto and *B. foetida*. The *B. foetida* species-group, with *B. hapalophylla*, is part of a trichotomy with *B. chartacea* and the *B. rosmarinifolia* species-group. This clade of simple-leaved species is sister to a clade containing all the pinnate-leaved taxa in *B.* series *Valvatae* and *B. lanceolata* (viz. *B. ledifolia*, *B. lanceolata* species-group, *B. alulata* species-group). When the leaves of *B. hapalophylla* were scored as being petiolate the results did not change except, of course, for the length of the trees. When the leaves were scored as being sessile then 2161 most parsimonious trees were found, each of 206 steps. In the strict consensus tree of this analysis the clade containing the simple-leaved species identified above collapsed and formed a polytomy with *B. ledifolia* and another polytomy of the *B. lanceolata* species-group and a resolved clade of the *B. alulata* species-group. The 50% majority-rule consensus tree of this analysis was identical to the strict consensus trees of previous analyses.

The analyses confirm the placement of *B. hapalophylla* in *B.* series *Valvatae* and indicate it is part of the simple-leaved clade that contains *B. chartacea* and the *B. rosmarinifolia* and *B. foetida* species-groups. It appears to be more closely related to the *B. foetida* species-group than to the *B. rosmarinifolia* species-group or *B. chartacea*. The geographically closest member of the *B. foetida* species-group, *B. foetida*, is found nearly 500 km to the north. Interestingly, *B. rosmarinifolia* and *B. chartacea* are each found only a few tens of kilometers away.

Boronia series *Valvatae* was redefined and revised in 1999 (Duretto 1999) and since then two additional species have been described, *B. beeronensis* Duretto (Duretto 2003) and *B. hapalophylla* here. In *Boronia* section *Valvatae* the series is notable for its size (24 species, of c. 65 in the section, and c. 150 in the genus), the poor support of the internal structure within the series, and the associated lack of a formal internal classification. *Boronia beeronensis* was easily classified into one of the informal species-groups but offered little additional information regarding the classification of the series. *Boronia hapalophylla*, on the other hand, is not easy to classify in the series and if anything offers poorer elucidation of relationships. Like *B. beeronensis* though, it is a large flowered species restricted to a small, though hardly isolated, area of south-eastern Australia highlighting again that much needed basic field survey work and research are still required to accurately document Australia's biodiversity.

Keys

Previously published keys for *Boronia* section *Valvatae* (Duretto 1999) and for *Boronia* in New South Wales (Weston & Duretto 2002) can be amended to accommodate *B. hapalophylla* by inserting the following.

For Duretto (1999, p. 12):

Note: additions have already been made to this area of the key by Duretto (2003).

60. Leaf with glandular punctate margin; sepals narrowly ovate-deltate, at least twice as long as wide; rays of stellate hairs usually dull and flexuous .... **17. B. repanda**

60. Leaf with smooth margin; sepals ovate-deltate, less than twice as long as wide; rays of stellate hairs shiny and usually more or less straight

  61A. Adaxial surface of leaves with a sparse to dense indumentum

    61AA. Sepals acute, 2.5–3 mm long; petals 4–7(–10 with fruit) mm long (western slopes of NSW) .... **38. B. glabra**

    61AA. Sepals acuminate, 5–10 mm long; petals (6–)8–10(–15 with fruit) mm long (NE NSW) .... **B. hapalophylla**

  61A. Adaxial surface of leaves glabrous or glabrescent

    61. Leaves usually glabrescent, slightly discolourous; fruit hirsute (inland Qld, western slopes of NSW) .... **38. B. glabra**

    61. Leaves strongly discolourous, adaxial surface of leaves glabrous and shiny, abaxial surface with a dense, stellate indumentum; fruits glabrous or densely hirsute.......

For Duretto (1999, p. 13):

70. Adaxial surface of petals with a sparse to moderately dense indumentum of simple hairs

  73. Adaxial surface of leaves glabrous or with few hairs along midrib; petals 5.5–7(–8.5 with fruit) mm long; leaf base strongly attenuate (Hinchinbrook Is. of N Qld) .... **39. B. jensziae**

  73. Adaxial surface of leaves with a sparse to dense stellate indumentum; petals (4–)6–12(–15 with fruit) mm long; leaf base strongly attenuate or obtuse (central Qld, NSW, Vic.)

    73A. Sepals acuminate, 5–10 mm long, 3–4.5(–7 with fruit) mm wide; leaf base strongly attenuate (north coast of NSW) .... **B. hapalophylla**

    73A. Sepals acute, sometimes acuminate, 2–4.5 mm long, 1.5–2.5(–3.5 with fruit) mm wide; leaf base usually obtuse (central Qld, NSW, Vic.)

      74. Leaf-lamina elliptic, plane or margin slightly recurved (becoming revolute on drying); peduncle less than 2 mm long; anthopodium 1–5 mm long; petals 5–7 mm long (central inland Qld) .... **32. B. odorata**

      74. Leaf-lamina narrowly elliptic to elliptic, plane or margin recurved to revolute; peduncle (1–)2–10 mm long; anthopodium 7–11 mm long; petals (5–)8.5–12 mm long (central coastal ?Qld, NSW, Vic.) .... **21. B. ledifolia**

For Weston and Duretto (2002, p. 266; GROUP 1):

1* All leaves simple or 1-foliolate

  11A Sepals broadly ovate-deltate, acuminate, 5–10 mm long, 3–7 mm wide; upper surface of leaves with a sparse to dense indumentum of large stellate hairs .... **B. hapalophylla**

  11A* Sepals ovate-deltate or narrowly deltate, acute, 2–5 mm long, 1–3 mm wide; upper surface of leaves glabrous, glabrescent or with a sparse indumentum, or rarely with a dense indumentum of minute stellate hairs

    11 Leaves sessile.....

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Multivariate analysis of morphological variation in *Eucalyptus* series *Psathyroxyla* Blakely (Myrtaceae): taxonomic implications

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Abstract

B.E. Pfeil[1] *and M.J. Henwood (John Ray Herbarium, School of Biological Sciences, Heydon-Laurence Building (A08), The University of Sydney, NSW 2006, Australia;* [1]*Present Address: Department of Plant Biology, 228 Plant Science Bld., Cornell University, Ithaca NY 14853, U.S.A.) 2004. Multivariate analysis of morphological variation in* Eucalyptus *series* Psathyroxyla *Blakely (Myrtaceae): taxonomic implications.*Telopea *10(3): 711–724.* Characters used in recent treatments to separate members of *Eucalyptus* series *Psathyroxyla* Blakely (scribbly gums) show a considerable degree of overlap. Multivariate analyses of 79 individuals were used to examine morphological variation in up to 35 characters, in order to resolve this problem. These analyses revealed the presence of three taxa, not five as previously described. Furthermore, two of these taxa show significant morphological overlap which is best explained by introgression. Problems regarding the type specimens are discussed. *Eucalyptus haemastoma* Smith, *E. racemosa* Cav. ssp. *racemosa* and **E. racemosa** subsp. **rossii** (R.T. Baker & H.G. Smith) B.E.Pfeil & Henwood **comb. et stat. nov.** are recognised here.

Introduction

Four species of *Eucalyptus* were recognised by Blakely (Blakely 1934) as constituting the series *Psathyroxyla*. The series became commonly known as the scribbly gums, on account of the characteristic insect 'scribbles' that cover their otherwise smooth bark. Apart from the markings on the bark, the scribbly gums are further distinguished by their raised fruit disc, mostly hemispherical fruit, and their small seed (Ladiges et al. 1992). Despite Chippendale's (1988) more inclusive definition of the series, Ladiges et al. (1992) confirmed that the scribbly gums constituted a monophyletic group. The most recent flora treatment of the group (Hill, 1991) recognises five species: *Eucalyptus haemastoma* Smith, *E. racemosa* Cav., *E. rossii* R.T. Baker & H.G. Smith, *E. sclerophylla* (Blakely) L.A.S.Johnson & Blaxell, and *E. signata* F. Muell.

Scribbly gums are trees or mallees restricted to woodlands on the coast of southern Queensland (south from Fraser Island) and New South Wales (north from Jervis Bay), and the tablelands and south-western slopes of N.S.W. (Figs 1 and 2). The western geographic limit of the scribbly gums is near Wagga Wagga on the N.S.W. south-western slopes (Fig. 2). Whilst the group is geographically relatively widespread, species are locally frequent but patchy in their distribution. They are usually confined to infertile, sandy or stony soils on ridge tops or rises with rare occurrences on sandy and sometimes swampy flats in coastal N.S.W. (Hill 1991).

The most recent taxonomic treatments of the scribbly gums are those by Hill (1991) and by Bean (Bean 1997). Hill (1991) recognised five species, the diagnostic characters of which overlap, e.g. fruit length and width, and adult leaf width. In Hill's key, leaf glossiness, fruit width and the location of populations are used to separate the species. Bean (1997), however, found that leaf glossiness can vary within a population, and is thus not diagnostic. The overlap of many morphological characters has meant that the geographic location of an individual is the primary method of positive identification.

Bean (1997) included *E. signata* and *E. sclerophylla* within the circumscription of *E. racemosa*, but did not provide a formal analysis of character variation for this action. He stated that "there appear to be no significant differences between the entities *E. racemosa, E. sclerophylla* and *E. signata*" (Bean 1997, p.133).

As with many species complexes, one must always be aware of the possibility that phenotypic plasticity might be masking otherwise diagnostic characters in at least some individuals of some taxa. Testing the extent of phenotypic plasticity in adults by way of traditional common garden experiments is particularly problematic in relatively long-lived taxa like the scribbly gums. However, the use of seedlings can provide an environmentally independent set of characters by which to assess the taxonomic limits of species under consideration (Wiltshire et al. 1992). The character differences (or similarities) which may be present should, therefore, be due more to underlying genetic differences than to phenotypic plasticity. A preliminary assessment of scribbly gum seedling characters has indicated that a range of morphological variation exists within the group (Brooker & Kleinig 1990; Chippendale 1988; Hill 1991).

The current study aims to provide an empirical analysis of the character variation encountered in the scribbly gums, with the aim of assessing the taxonomic distinctness of any entities present. Multivariate analysis of morphological (and thereby phenotypic) variation is a suitable method to accomplish this aim.

Methods

Sampling

Twenty-five populations were sampled, covering the geographic range of the species (Fig. 1, Table 1). Over half of the populations (14 of 25) were drawn from the central coast and central tablelands, as these regions are where scribbly gums species with the most narrow circumscriptions (Hill, 1991) have the greatest overlap in their distributions. An ambiguous population from the Bruxner highway in the northern tablelands was also targeted, as individuals from this area have been alternatively assigned to *E. signata* and *E. rossii*, the only suspected area of overlap between those species. Other populations were spread over the range of scribbly gum species to maximise capture of the variation among populations over a wide geographic range, although the furthest extremes of the distribution were not sampled due to practical limitations.

Five individuals were sampled from each apparently monomorphic population, with the exception of two populations where only single individuals (represented by herbarium specimens with viable seed) were available. Populations with a range of morphotypes (e.g. those potentially containing two or more species) were sampled more intensively in order to capture the range of observable morphological variation (up to ten individuals). Generally, one branch, consisting of numerous branchlets, was sampled for each individual. From each branch, numerous fully expanded leaves and a range of available reproductive material were collected and dried. Seed was subsequently removed from the fruit and stored at room temperature in paper bags. A total of 130 individuals were sampled in this way.

Table 1: Population localities.

Population Name	Region	Latitude S		Longitude E	
		Deg	Min	Deg	Min
Bungendore Turnoff	ST	35	10	149	17
Marulan	ST	34	44	149	51
Tallong	ST	34	43	150	03
Jerrabomberra Hill	ST	35	22	149	12
Black Mountain (ACT)	ST	35	16	149	06
Penrose	CT	34	40	150	15
Sutton Forest	CT	34	28	150	19
Mudgee*	CT	32	26	149	50
Running Stream	CT	33	04	149	56
Bruxner H'way	NT	28	56	152	13
Nowra Air Base	SC	34	57	150	31
North Nowra	CC	34	51	150	34
Wilton	CC	34	17	150	43
Mount White	CC	33	27	151	12
Somersby	CC	33	21	151	18
Bucketty	CC	33	09	151	12
Mandalong	CC	33	07	151	28
Nord's Wharf	CC	33	08	151	36
Munmorah SRA	CC	33	11	151	35
Charmhaven	CC	33	14	151	29
Hornsby Heights	CC	33	31	151	07
Nabiac	NC	32	07	152	25
Copperabung Ck	NC	31	13	152	49
Red Rock	NC	29	59	153	13
Queensland*	-	26	24	153	06

*Populations represented by a single herbarium sheet.

Character selection

A data set comprising 18 adult leaf, bud, fruit and seed characters was generated (Table 2). Data included characters used traditionally in the identification of these species (eg. fruit width) as well as additional characters such as bud dimensions. The appropriate sample size for fruit characters was determined by plotting the variances of these measurements against sample size for each of five individuals. Variance estimates become more accurate as sample size increases, although the rate of accuracy-gain is reduced simultaneously. The estimate of the variance of all the individuals was found to peak at a sample size of about 50 fruit. A sample size of 30 fruit per individual was considered to be a reasonable combination of morphological variation captured for time expended.

Six fully expanded leaves, each subtending a floral bud, were selected to represent the foliar characters for each individual. Leaves at the apex of a growing shoot were not used. Five unopened buds on an umbellaster with at least one open flower (to minimise ontogenetic variation) were chosen for hand-sectioning.

Twenty seeds from each individual were sorted from the chaff and sown into five replicate pots each containing four, equally spaced seeds. Pots were randomly arranged within a single glasshouse. A variation of Hoagland's Solution (after Mowatt 1981) was used to fertilise the seedlings. Four to five seedlings per individual were subsequently chosen at random, and these were used to derive a total of 17 seedling characters for each individual (Table 3). Pots were randomised once a month, and each pot was rotated by 90° at this time.

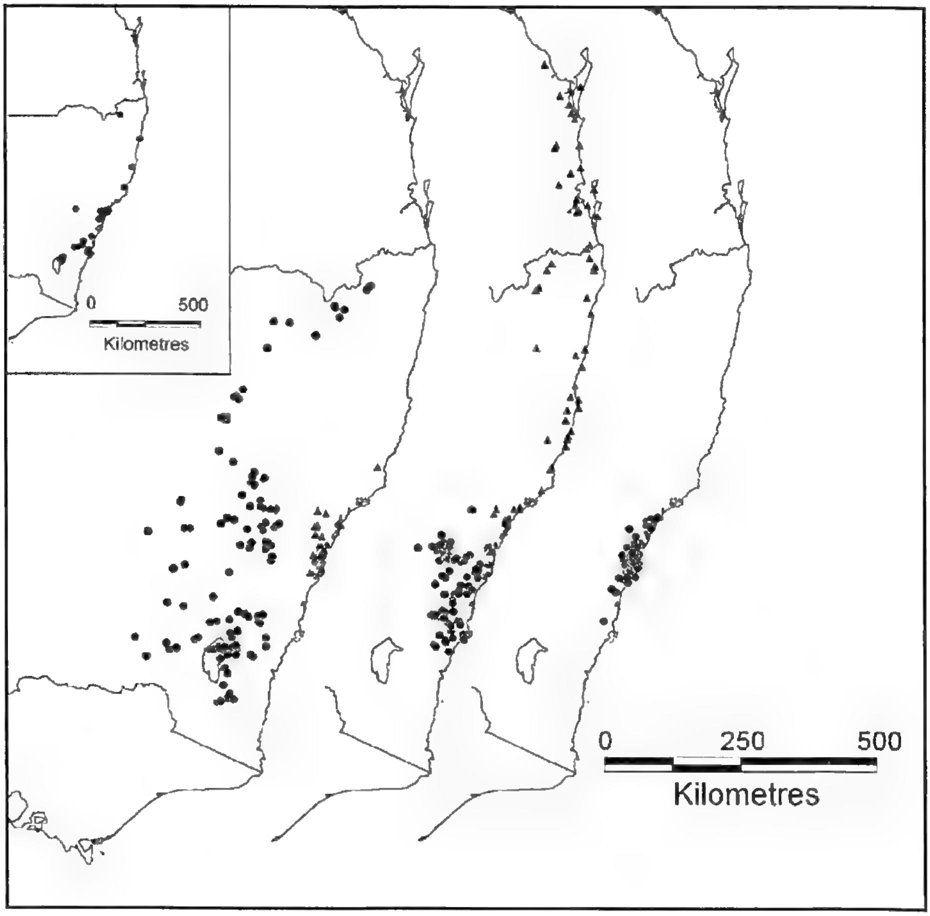

Fig. 1. Distribution of scribbly gums *sensu* Hill (1991). Left: *Eucalyptus rossii* (●), *E. racemosa* (▲). Centre: *E. sclerophylla* (●), *E. signata* (▲). Right: *E. haemastoma* (●) . Inset: sites sampled in this study

Table 2. Adult characters.

Character name	Abbreviation	Sample size
Leaf characters		
Petiole Length	(LPE)	6
Leaf Length	(LLN)	6
Maximum Width	(LMW)	6
Length to Width Ratio	(LLW)	6
Fruit Characters		
Maximum Width	(FMW)	30
Width of Disc	(FDW)	30
Fruit Length	(FLE)	30
Degree of Disc Emergence	(FDE)	30
Shape of Base	(FSB)	30
Length to Width Ratio	(FLW)	30
Fruit Width to Disc Width Ratio	(FWD)	30
Seed Characters		
Seed Colour	(SCO)	1*
Chaff Colour	(SCC)	1*
Bud Characters		
Ovary Chamber Height	(BOC)	5
Floral Chamber Height	(BFH)	5
Floral Chamber Width	(BFW)	5
Style Length	(BSL)	5
BSL/BFH	(BSF)	5

* seed and chaff were pooled for each individual.

Data analysis

There is wide agreement that multi-dimensional scaling (MDS), and, in particular, the non-metric form (N-MDS), is recommended above Principle Component Analysis (PCA) for taxonomic studies (Crisp 1991; Faith et al. 1987; Pimentel 1981). In contrast with PCA, N-MDS assumes a much less restrictive model of relationships between an association measure and the ordination space (Coxon 1982; Austin 1985).

The program PATN (Belbin 1991) was used for all analyses. In the case of MDS, PATN uses a semi-strong monotonic transformation (a type of N-MDS), with the option of using a linear transformation (M-MDS) for smaller association matrix ranks (i.e. for smaller distances between individuals). This scaling - termed hybrid scaling - is most appropriate for ecological data. The hybrid nature of the scaling refers the linear relationship between values in an association matrix (based on robust association measures) and the distance between points in an ordination when distances are small. When distances become large, a monotonic relationship holds, over a number of different species response models (Faith et al. 1987).

Table 3: Seedling characters.

Character name	Abbreviation	Sample Size
At 1st bud emergence		
Cotyledon Maximum Width	(CMW)	5
At 3rd bud emergence		
1st Leaf Pair Maximum Width	(1W3)	4
1st Leaf Pair Length	(1L3)	4
Length / Width Ratio of 1st Leaf Pair	(1LW)	4
2nd Leaf Pair Maximum Width	(2W3)	4
Internode Trichome Type	(TC1)	4
2nd Leaf Margin Trichome Type	(T2M)	4
1st Leaf Primary Vein Trichome Type	(T1P)	4
At 6th bud		
2nd Leaf Pair Maximum Width	(2W6)	4
2nd Leaf Pair Length	(2L6)	4
Length / Width Ratio of 2nd Leaf Pair	(2LW)	4
3rd Leaf Pair Maximum Width	(3W6)	4
3rd Leaf Pair Length	(3L6)	4
Length / Width Ratio of 3rd Leaf Pair	(3LW)	4
2nd Leaf Pair Margin Undulation	(MU2)	4
3rd Leaf Pair Margin Undulation	(MU3)	4
3rd Leaf Pair Base Contact	(BC3)	4

No such models for taxonomic data have been assessed in this way (an exception being the limited study by Pimentel 1981). Therefore, for the current study it was decided to initially employ the least restrictive transformation available in PATN (semi-strong monotonic scaling) to transform the association matrix values into ordinations.

Shepard plots (Shepard 1974) based on 2-dimensional N-MDS ordinations were examined for each of the analyses. The shape of these plots indicated that a linear relationship existed between the inter-item distances in the association matrix and the inter-item distances in the ordinations ($n=3080$, $r=0.95$, $p<0.05$). Therefore, M-MDS was used in all subsequent analyses. In all cases Gower's metric (Gower 1971) was used as the association metric.

Three analyses were conducted. After removing individuals for which insufficient material was available to score characters (due to seedling mortality, insufficient fully expanded adult foliage, etc.), most populations were represented by three individuals, with the variable populations represented by up to ten individuals. The analyses, therefore, used a total of 79 individuals.

Analysis 1: Combined adult and seedling characters

Analysis 2: 17 seedling characters

Analysis 3: 18 adult characters

Results

Analysis 1: All characters

Figure 2 shows two distinct groups (group 1 and 2). Individuals from each population are contained entirely within either group 1 or group 2 and are connected by lines. Variation in group 1 can be summarised as fruit ≥ 8 mm wide, whereas group 2 can be characterised as having fruit ≤ 7 mm wide. The morphological distinctness of each group is paralleled by a congruent geographic distribution. Group 1 forms a geographically cohesive group, the four populations all being located on the central coast of NSW, between Botany Bay and Lake Macquarie. The populations of group 2 span a broader geographic area than those of group 1. Group 2 ranges from the coast of southern Queensland to southern NSW, and from the coast to the western slopes in NSW.

Populations with small fruit (group 2) form two sub-groups (groups 2a and 2b; Fig. 2). Sub-group membership is defined primarily by a combination of mean adult leaf width (sub-group 2a = 5–13 mm; sub-group 2b = 11.5–24 mm) and mean adult leaf

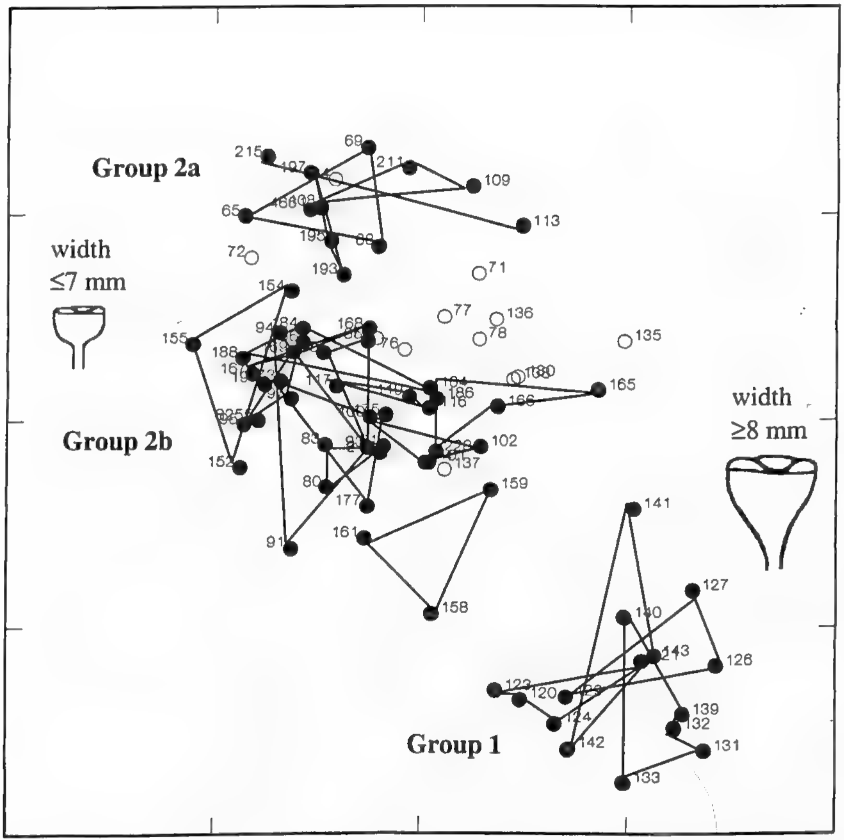

Fig. 2. A 2-dimensional M-MDS ordination based on Analysis 1 (35 characters, 79 individuals). Stress = 0.17. Individuals from any one population are connected by lines. Groups of morphologically similar populations (overlapping in the ordination) discussed in text are labelled. Individuals marked by open circles (○) come from two intermediate populations as discussed in text. Relative fruit size for large vs. small fruited groups is shown diagrammatically.

length (2a = 5–9.5 cm; 2b = 8–13.5 cm). These differences are diagrammatically represented on Fig. 3. Each sub-group, however, is linked by individuals from populations of mixed morphology. These 'linking' populations are also from geographically intermediate localities. The morphologically heterogeneous populations contain individuals that fall within either sub-group, as well as individuals that fall between the sub-groups. We were only able to locate two such populations in the field; one from near Bucketty (central coast, NSW) and the other from near Marulan (southern highlands, NSW). Individuals from these populations are shown by open circles (Fig. 2).

Analysis 2: Seedling characters only

Analysis of seedling data, revealed two non-overlapping groupings of morphological homogenous populations (Fig. 3). In contrast with the analysis of all characters (Fig. 2), the seedling data did not strongly separate individuals with large fruit (group 1 of Fig. 2, shown as stars in Fig. 3) from those with small fruit (group 2 of Fig. 2, other symbols in Fig. 3). Individuals from the morphologically heterogeneous populations cross the previously identified sub-group boundaries (shown as open circles, Fig. 3).

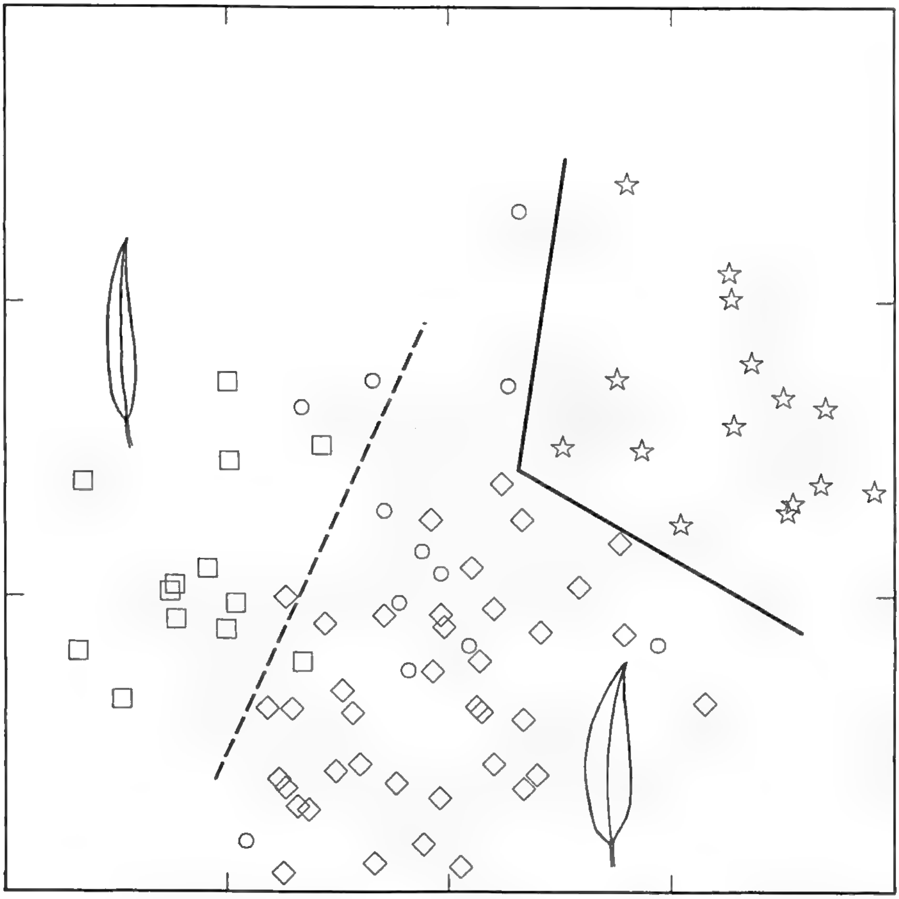

Fig. 3. A 2-dimensional M-MDS ordination based on Analysis 2 (17 seedling characters, 79 individuals). Stress = 0.15 Stars (★) = large-fruited (≥ 8 mm wide) individuals. Diamonds (◆), squares (■) and circles (●) = small-fruited (≤ 7 mm wide) individuals. Relative adult leaf size for large vs. small leaved sub-groups (within the small-fruited group) is shown diagrammatically.

Analysis 3: Adult characters

As with seedling data, the adult data (Fig. 4) mostly maintained the group membership observed in Figure 2 (all characters). An exception to this pattern is that one individual from one population (Charmhaven), previously clustered within group 2, is now located amongst group 1 individuals (shown as a diamond in Fig. 4). This population is located in the same general area as group 1 populations (central coast, NSW).

Discussion

Our results reveal the presence of two distinct groups of scribbly gums, characterised by large and small fruit (group 1 and 2 respectively, Fig. 2). Furthermore, the group with small fruit is divisible into two sub-groups with small and large adult foliage (group 2a and 2b respectively, Fig. 2).

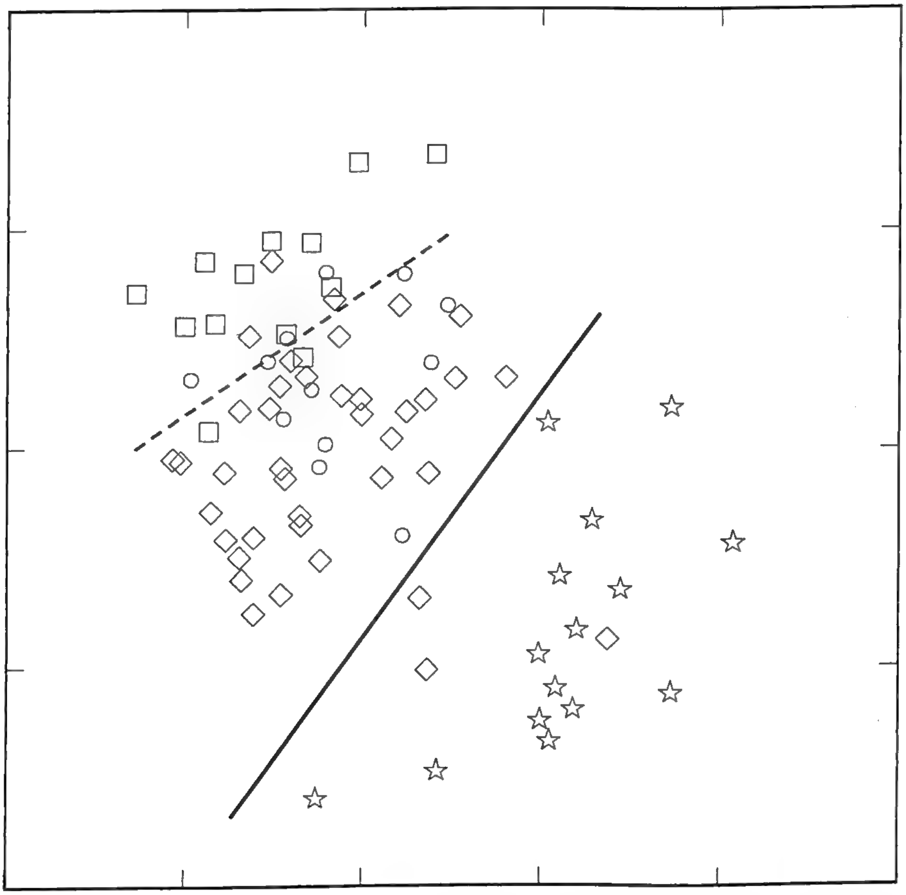

Fig. 4. A 2-dimensional M-MDS ordination based on Analysis 3 (18 adult characters, 79 individuals). Stress = 0.22 Stars (★) = large-fruited (≥ 8 mm wide) individuals. Diamonds (◆), squares (■) and circles (●) = small-fruited (≤ 7 mm wide) individuals.

The morphologically heterogeneous populations at geographically intermediate locations are particularly informative with respect to the relationships between the two sub-groups of group 2 (plants with small fruit). In adult, seedling and combined analyses, the presence of both intermediate individuals as well as individuals closely resembling 'core' members of both sub-groups strongly suggests that introgression is occurring at these sites. This pattern of variation is inconsistent with the presence of a cline, where all individuals would be expected to possess a morphology intermediate between both sub-groups.

The population at Bucketty, the only population that unambiguously contains members of group 1 and group 2, shows clear separation between individuals of both groups in all analyses. No introgression or cline between groups 1 and 2 appears to be present at this site.

One population (Charmhaven), however, occupies an ambiguous morphological position in relation to groups 1 and 2 (Fig. 2). This population is in the same region as all of group 1 (central coast, NSW). One individual from this population appears to have adult morphology of the large-fruited group, whereas its seedlings are more similar to those of the small-fruited group. It is possible that this population is mixed, with only a few group 1 individuals introgressing with a larger pool of group 2 individuals. This would give an overall position that is intermediate between group 1 and 2, but closer to group 2. It is also possible that the adult morphology is convergent due to the similar environment, whereas the seedling morphology more accurately reflects genetic affinities. Both processes may be operating together. Despite this single ambiguous population, there is no strong evidence that widespread introgression is occurring between individuals of group 1 and group 2. Furthermore, herbarium specimens and field observations indicated that populations within a morphological group, as determined in these analyses, do not flower synchronously.

Thus, rather than the five species recognised by Hill, our analyses have indicated the presence of only three taxa. Whilst this broadly corresponds with Bean's treatment (1997), we consider that the entities revealed here are not of equivalent taxonomic rank to those of Bean. These differences in concept are the result of several factors. Firstly, the use of a larger number of characters to resolve taxa; secondly, the use of seedling characters grown under controlled conditions; and thirdly, the use of multivariate statistics to summarise character information.

Prior treatments have relied upon an intuitive interpretation of a limited number of adult morphological characters. However, the overlap of many 'diagnostic' characters which led to the use of geographic location of an individual to make identifications is a clear sign that the complex variation in this group was not adequately dealt with by intuitive taxonomic methods. The power of multivariate analyses to accurately summarise morphological information from a large number of characters is particularly useful as an aid to taxonomic decision-making in such situations.

Furthermore, whilst neither adult nor seedling data sets alone provided resolution of component taxa with any certainty, the combination of these data led to the clear resolution of three taxa in this group. Our conclusions are strengthened by the fact that our data set contains information from two independent sources, of which the seedling information should be significantly less susceptible to phenotypic plasticity. Seedling data can only be expected to have these properties when derived from an appropriate sampling strategy coupled with germination and growth under controlled environmental conditions. Only then can environmentally induced effects be teased from genotypic variation.

Scribbly gums with large fruit (group 1) are here assigned the rank of species, as is the group with small fruit (group 2, Fig. 2). The two sub-groups of group 2 are assigned sub-specific rank. The types of all species of series *Psathyroxyla* were examined, with the exception of that of *E. rossii* which could not be located at NSW where it is believed to be held (Chippendale 1988).

The isotype of *Eucalyptus haemastoma* has smaller fruit than that of members of the large-fruited species (to which the name has been thus far applied). Examination of additional specimens from the northern suburbs of Sydney revealed a number of plants with morphology intermediate between the large- and small-fruited species of scribbly gum. The fruit of the *E. haemastoma* isotype fell within this intermediate set of specimens. The large number of intermediate collections found suggests that our sampling regime may have missed a critical zone of genetic exchange between the large- and small-fruited species. As such, we are reluctant to suggest any alteration to the name of the large-fruited group, despite the type not being entirely consistent with this group.

The small-fruited species currently has the names *E. racemosa* and *E. rossii* applied to it. *Eucalyptus racemosa* has priority at the rank of species as it was published in 1797. As the type of *Eucalyptus rossii* is currently missing, a specimen from Bungendore in N.S.W. discussed by the authors (Baker & Smith 1920) as being chemically and morphologically similar to the holotype is here chosen as the lectotype. This specimen is a very close match for our subspecies and for *E. rossii* as described by Baker and Smith (1920).

Descriptions of taxa

The taxa found here are accommodated by Bean's (1997) circumscriptions, although the exact limits of *E. haemastoma* are uncertain (as discussed above). Our sampling found a more narrowly definable core group of individuals (centred around Lake Macquarie), but the uncertainties in being able to assign specimens from northern Sydney reliably to either species makes this narrow concept difficult to justify. The uncertainties revealed here must await resolution after further study.

Taxonomy

E. haemastoma Smith, *Trans. Linn. Soc. London* 3: 286 (1797). Type: *J. White s.n.*; holo: LINN, iso: G!.

Eucalyptus racemosa Cav., *Icones* 4: 24 (1797).

Type: *L. Née s.n.*; holo: MA; iso: MEL (photo BRI!).

E. haemastoma var. *capitata* Maiden, *Crit. Revis. Eucalyptus* 1: pp.319 (1909). Type: *J.H. Maiden s.n.*; holo: NSW!; iso: FRI.

E. haemastoma var. *sclerophylla* Blakely, *Key Eucalypts* pp. 218 (1934). Type: *J.H. Maiden s.n.;* holo: NSW!; iso: FRI.

E. micrantha DC., *Prodr.* 3: pp. 217 (1828). Type: *F.W. Sieber 497*; holo: G; iso: G, W.

E. signata F. Muell., *J. Proc. Linn. Soc., Bot.* 3: pp. 85 (1859). Type: *F. Mueller s.n.*; holo: MEL!; iso: K.

Eucalyptus racemosa *ssp.* **rossii** *(R.T. Baker & H.G. Smith) B.E.Pfeil & Henwood* **comb. et stat. nov.**

E. rossii R.T. Baker & H.G. Smith, *Res. Eucalyptus* 70 (1902). Type: *R.T. Baker s.n.*, March 1901, Cow Flat, Bathurst; holo: NSW (missing); **lectotype here chosen**: *Baker and Smith s.n.*, Bungendore, N.S.W., March 1899; NSW!.

Distribution of taxa

Maps of the distributions of these taxa based on CANB and NSW collections, and the collections made during this study, are presented in Figure 5.

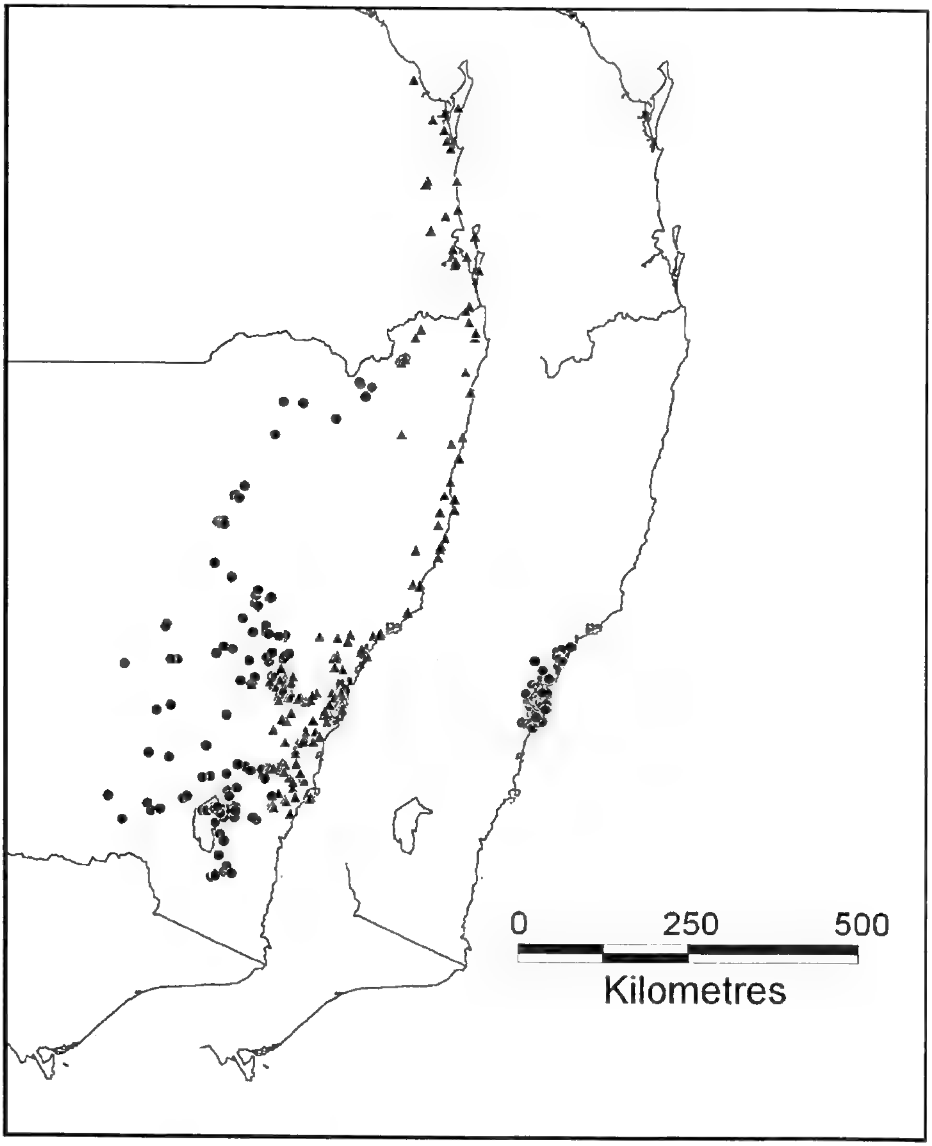

Fig. 5. Distribution of scribbly gums *sensu* Pfeil and Henwood. Left: *Eucalyptus racemosa* subsp. *rossii* (●), *E. racemosa* subsp. *racemosa* (▲). Right: *E. haemastoma* (●).

Key to species of *Eucalyptus* series *Psathyroxyla*

1 Fruit ≥ 8 mm wide, pyriform (occasionally almost hemispherical), discs ≥ 1.6 mm wide. Raised oil glands of seedling internodes (at 2nd leaf pair stage) usually adorned with small stellate hairs, raised oil glands of the 2nd leaf pair margin prominent and those nearest the petiole often adorned with small stellate hairs .... ***Eucalyptus haemastoma***

1* Fruit ≤ 7 mm wide, hemispherical (rarely almost pyriform), discs ≤ 1.6 mm wide. Raised oil glands on seedling internodes (of the 2nd leaf pair stage) usually unadorned or rarely adorned with small stellate hairs; raised oil glands on 2nd leaf absent or present .... ***E. racemosa* ... 2**

2 Leaves subtending buds 5–13 mm wide × 50 mm–95 mm long; usually more than 7 times as long as wide; raised oil glands on 2nd leaf margin usually absent, if present then unadorned .... ***E. racemosa* subsp. *rossii***

2* Leaves subtending buds 11.5–24 mm wide × 80 –135 mm long; usually less than 7.5 times as long as wide; raised oil glands on the 2nd leaf margin usually present and occasionally adorned with small stellate hairs near the petiole .... ***E. racemosa* subsp. *racemosa***

Aknowledgments

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A key to *Dysoxylum* (Meliaceae) in Australia, with a description of a new species from Far North Queensland

D.J. Mabberley

Abstract

Mabberley, D.J. (Nationaal Herbarium Nederland, University of Leiden, The Netherlands, and National Herbarium of New South Wales, Royal Botanic Gardens Sydney, Mrs Macquaries Road, Sydney 2000, Australia) 2004. A key to Dysoxylum *(Meliaceae) in Australia, with a description of a new species from Far North Queensland.* Telopea *10(3): 725–729.* A key to the known 15 species of *Dysoxylum* in mainland Australia is presented. **Dysoxylum pumilum** from Far North Queensland is illustrated and described as new.

Introduction

The continuing delay in publishing my submitted account of Meliaceae for *Flora of Australia* (see Mabberley 1998) has given the opportunity to revise the account of the family in the light of new discoveries. One of these is a new species of *Dysoxylum* Blume from Far North Queensland, here described. Publication of this has been prompted by the imminent appearance of a new edition of William and Wendy Cooper's *Fruits of the Rain Forest* (Cooper & Cooper 1994) in which the species will be figured.

With 15 indigenous species, the genus *Dysoxylum* is the biggest in the family in Australia and, as no modern account of it is accessible, the opportunity is taken to provide a key to the identification of its species here. Descriptions of the 12 species not restricted to Australia were published by the author in Mabberley et al. (1995: 61-133). Descriptions of the remaining two species in mainland Australia, *D. fraserianum* and *D. rufum*, are to be found, in Stanley and Ross (1983: 481) and Taylor and Harden (2002). The indigenous species of Lord Howe Is. (*D. pachyphyllum* Hemsl., endemic) and Norfolk Is. (*D. bijugum* (Lab.) Seem.), not considered here, are described in Green (1994).

Key to the species

Note: The fruits are often characteristic but are rarely well represented in herbaria. Illustrations of most are provided by Cooper and Cooper (1994: tt. 192–203) and are indicated in the key below.

1 Leaves decussate

  2 Leaflets with scarcely discernible lateral veins; capsule 5–8 cm diam., glabrous .... ***Dysoxylum acutangulum*** Miq. subsp. ***foveolatum*** (Radlk.) Mabb.
  northern Australia, Solomon Is. to Sumatra

  2* Leaflets with conspicuous lateral veins; capsule c. 2 cm diam., finely hairy .... ***Dysoxylum oppositifolium*** F. Muell.
  north-east Queensland, New Guinea to Philippines
  Cooper and Cooper [1994: t. 198]

1* Leaves in spirals

3 Leaves in bud stiletto-like

4 Leaves 3- or 4-jugate; capsule c. 5 cm long, pyriform, usually strongly veined *in sicco*, lacking rostrum .... ***Dysoxylum latifolium*** Benth.
northern Australia, Solomon Is., New Guinea [and Ternate?]
Cooper and Cooper [1994: t. 196]

4* Leaves usually 2-jugate; capsule c. 3.5-4 cm long, subspherical, ± veined in sicco, distinctly rostrate .... ***Dysoxylum pumilum*** Mabb.
north-east Queensland

3* Leaves in bud fist-shaped

5 Leaves paripinnate, sometimes with a terminal spike

6 Domatia present .... ***Dysoxylum fraserianum*** (A. Juss.) Benth.
Queensland, New South Wales

6* Domatia absent

7 Petals less than 2 mm long .... ***Dysoxylum papuanum*** (Merr. & L.M. Perry) Mabb.
north Queensland, New Guinea, Solomon Is.
Cooper and Cooper [1994: t. 199]

7* Petals more than 5 mm long

8 Bracts and bracteoles 1–1.5 mm long; petals 6–15 mm long; capsule to 2.5 cm diam., foliage not garlic- scented .... ***Dysoxylum klanderi*** F. Muell.
north-east Queensland
Cooper and Cooper [1994: t. 195]

8* Bracts and bracteoles minute; petals 5–8 mm long; capsule to 7.7 cm diam., foliage garlic-scented .... ***Dysoxylum alliaceum*** (Blume) Blume
Queensland, Solomon Is. through Malesia
to peninsular Thailand and Andaman Is.
Cooper and Cooper [1994: t. 192]

5* Leaves imparipinnate

9 Calyx of free sepals

10 Calyx glabrous or subglabrous .... ***Dysoxylum gaudichaudianum*** (A. Juss.) Miq.
Queensland to Java, Christmas Is. and Samoa
Cooper and Cooper [1994: t. 194]

10* Calyx densely hairy .... ***Dysoxylum rufum*** (A. Rich.) Benth.
Queensland, New South Wales
Cooper and Cooper [1994: t. 202]

9* Calyx a tube

11 Fruit densely hairy .... ***Dysoxylum setosum*** (Span.) Miq.
north Queensland, New Guinea, Timor
Cooper and Cooper [1994: t. 203]

11* Fruit glabrous

12 Flowers on bole and branches, rarely in axils too

13 Petals 15–20 mm long .... ***Dysoxylum parasiticum*** (Osb.) Kosterm.
Queensland, Solomon Is. through Malesia to Taiwan
Cooper and Cooper [1994: t. 200]

13* Petals 8–9 mm long .... ***Dysoxylum pettigrewianum*** F.M. Bailey
Queensland, Solomon Is. to Moluccas
Cooper and Cooper [1994: t. 201]

12* Flowers in axils

14 Flowers 4-merous .... ***Dysoxylum mollissimum*** Blume subsp. ***molle*** (Miq.) Mabb.
Queensland, New South Wales, New Guinea west to Celebes, north to Carolines and east to Niue
Cooper and Cooper [1994: t. 197, as *D. muelleri*]

14* Flowers 5-merous .... ***Dysoxylum arborescens*** (Blume) Miq.
Queensland, Vanuatu and Malesia north to Taiwan
Cooper and Cooper [1994: t. 193]

Dysoxylum pumilum, a new species from Far North Queensland

Dysoxylum pumilum *Mabb.*, species nova

Arbor pumila, gracilis, foliis saepissime bijugatis; Dysoxylum, D. latifolium Benth. affine, foliolis majoribus forte acuminatis, inflorescentiis longioribus, fructibus subsphericis, rostratis, seminibus majoribus, distincta est.

Typus: Australia, Queensland, Cook, SFR 755, Gosschalk L.A., 17°25'S, 145°47' E, 360 m, *B. Hyland 8792*,18 May 1976, fls (holo QRS; iso NSW).

Small understorey tree to 8 m; bole to 8 cm diam. Bark smooth; inner bark white to yellow or brown with no latex. Leafy twigs 3 mm diam., glabrous; apical buds stiletto-like. Leaves 14–25 cm long, 2 (3)- jugate, with terminal spike or its scar, dark glossy green adaxially, alternate (or subopposite); petiole 7.5–10 cm, ± angled, subglabrous, drying blackish; leaflets 12–34 × 5–12 cm, ovate to oblong, chartaceous, glabrous, opposite to alternate, bases weakly asymmetric, acute to obtuse, apices acute to acuminate, the acumen to 8 mm long, costae 8–14 on each side, pale and prominent abaxially in sicco, arcuate, obscure near margin, intercostals subprominent; petiolules 5–8 mm, weakly swollen. Thyrses axillary, sometimes in axils of undeveloped leaves, 8–35 cm long, subspiciform; axis subglabrous to finely sericeous, bearing cymules of 1–3 flowers, rectangular in bud; bracts c. 0.5 mm, triangular, pubescent, caducous; pedicels 3–4 mm long, pubescent, articulated with short pseudopedicels. Calyx c. 2 mm long, 3–4 mm diam., shallowly cupular, margin weakly 4-toothed. Petals 4, 5–6 mm × c. 2.5–3 mm, oblong, cream. Staminal tube narrowed towards apex, subglabrous, cream, margin very shallowly crenulate to ± dentate; anthers 8, c. 1mm long, included. Disk c. 1 mm tall, glabrous, margin undulate. Ovary finely pubescent, 4-locular; style pubescent in proximal 2/3; stylehead subcapitate. Capsule c. 3.5–4 cm long, 3.5–4 cm diam., subspherical, abruptly rostrate, ± veined in sicco, yellow-green, orange-yellow within. Seeds 2 or 3, c. 2.5–3 cm long, 2–2.5 cm wide, 1–1.5 cm thick, flattened ellipsoid to hemispherical; sarcotesta glossy, orange-brown; cotyledons collateral, dark green.

Other material examined: Queensland, Cook: SFR 755, Gosschalk L.A., EP/34, 17°26'S, 145°46'E, 380 m, *D. Fitzsimon 222*, 30 Nov 1976 (QRS), sterile, and *D. Fitzsimon 2757*, Dec 1976, (QRS), fr.; SFR 755, Gosschalk L.A., 17°24'S, 145°46'E, 380 m, *B. Gray 786*, 9 Nov 1977 (NSW, QRS), fr.; Chuklunga [Chuck Lunga] Creek, 17°25'S, 145°46'E, 360 m, *A.K. Irvine 1939*, 11 July 1979 (QRS), fr.; SFR 755, Bartle Frere, Russell River, 17°23'S, 145°47'E, 380 m, *B. Gray (Hyland no. 25903RFK)*, 7 Dec 1995 (QRS), buds; idem, *B. Gray (Hyland no. 25904RFK)* (QRS), sterile; idem, *B. Gray 6468* (QRS), fr., seedlings; SFR 755, Bartle Frere, Gosschalk L.A., 17°24'S, 145°46' E, 400 m *B. Gray 6765*, 30 May 1996 (QRS), fls; ibid, *B. Gray 6808*. 21 June 1996 (NSW – spirit only, QRS), fls, and *6809* (QRS), fr.; Russell River at junction with Chuck Lunga Creek, 17°26'S, 145°46'E, 160 m, *W. Cooper 1624*, 4 Dec 2001 (QRS), sterile.

Distribution and ecology: an understorey tree known only from the above collections from the Bartle Frere area of north-east Queensland. By comparison, the very closely allied *D. latifolium* is a widespread tree of rain forest and semi-deciduous thicket (Port Moresby region of Papua New Guinea) to 1200 m. It is frequently reported as a common canopy tree in New Guinea and the Solomon Is.

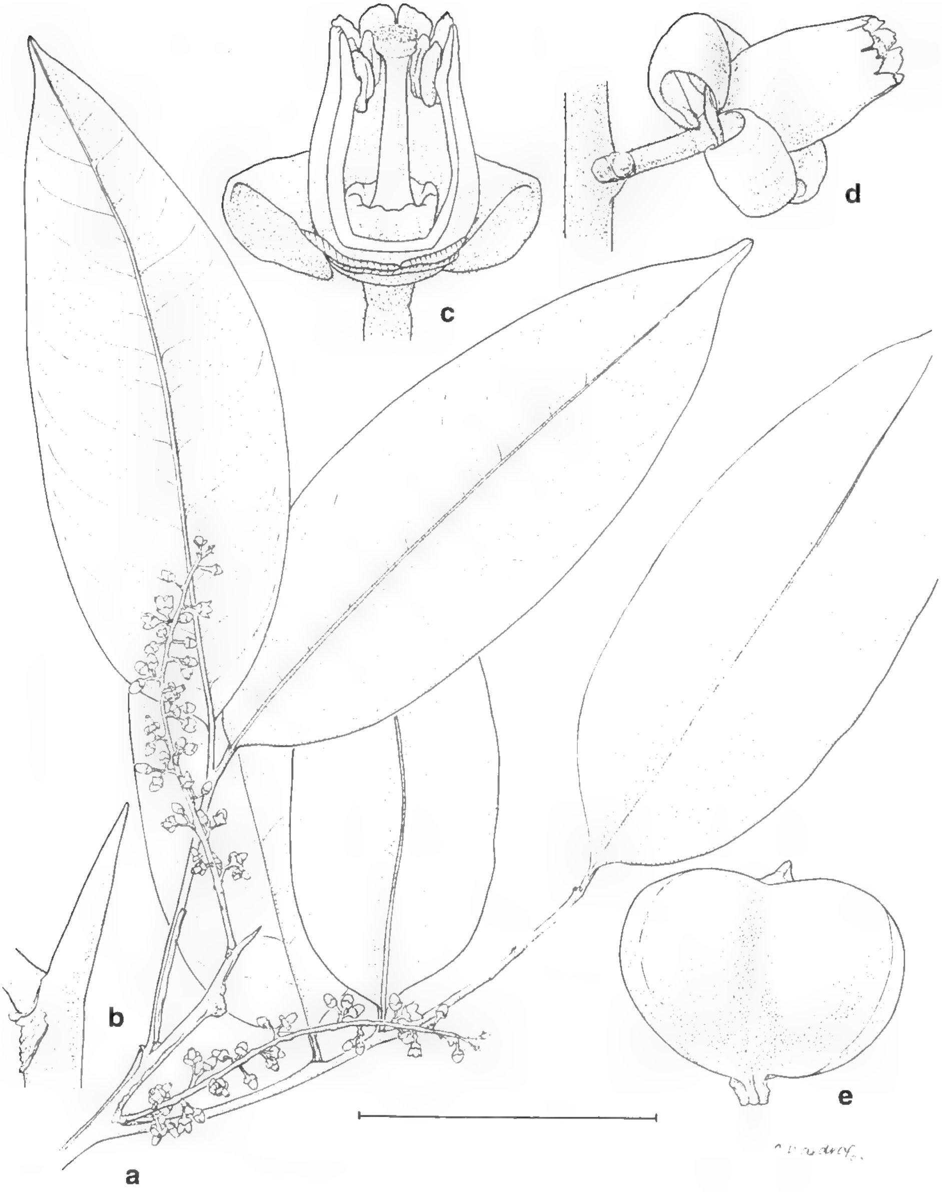

Fig. 1. *Dysoxylum pumilum.* **a,** habit; **b,** apical bud; **c,** flower (dissected); **d,** flower; **e,** fruit: a, b, *Hyland 8792*; c, d, *Gray 6808* (spirit material); e, *Gray 786*. Scale bar: a = 8.5 cm; b = 1.5 cm; c = 0.75 cm; d = 1.2 cm; e = 4 cm.

Etymology: The specific epithet refers to the small size of the treelet.

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Non-marine algae of Australia:
6. Cladophoraceae (Chlorophyta)

Stephen Skinner and Timothy J. Entwisle

Abstract

Skinner, S. and Entwisle, T.J. (Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney NSW 2000, Australia. email: tim.entwisle@rbgsyd.nsw.gov.au) *2004. Non-marine algae of Australia: 6. Cladophoraceae (Chlorophyta).* Telopea *10(3): 731–748.* Five species of *Cladophora* and one each of *Rhizoclonium*, *Pithophora* and *Wittrockiella* are reported for freshwater habitats in Australia. *Rhizoclonium riparium* (= *R. heiroglyphicum*) is shown to be widespread in coastal and near coastal areas of eastern Australia, while the range of *Pithophora oedogonia* is extended and a new variety, var. **calcarata** is described. *Cladophora globulina* and *C. kosterae* are reported for the first time from Australia, and the presence of *C. glomerata*, *C. aegagropila* and *C. fracta* is confirmed and their distribution extended. *Wittrockiella salina var.* **kraftii** is newly described from freshwater habitats on Lord Howe Island.

Introduction

Despite Martin Möbius' (1895) comment that *Cladophora*, common in European freshwater, was relatively rare in the samples sent to him from Australia, records suggest that taxa in the Cladophorales, particularly *Cladophora* species, are both widespread and common in freshwater habitats in all States and Territories. Members of the group tend to prefer mineral-rich waters with pH values greater than seven, but may also be found in neutral and slightly acid waters, especially where there are elevated levels of dissolved salts. It is likely that increased eutrophication of Australia's inland waterways over the last century has actually favoured the spread of this genus.

The Cladophorales is one of the very few groups of macro-green algae that flourish in both marine and freshwater habitats, and its members have structural and phenological characteristics which suit both milieux. The cell walls are strongly reinforced; the cell structure is siphonous, each cell containing two to dozens or hundreds of nuclei and an open peripheral reticulum of chloroplasts associated with numerous pyrenoids. Individuals in general are perennial, their reproduction variously involving fragmentation of the thallus, the formation of thick-walled akinetes, or the release of sexual or asexual zoids.

Many freshwater representatives of the order are considered nuisance algae or weeds. In garden or other artificial water features, *Cladophora* — and more rarely *Rhizoclonium*

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or *Pithophora* – may be the first macroscopic organism to thrive in pioneer conditions. Physical removal of plants that leads to a subsequent increase in vegetation complexity is the main element of human control that usually keeps such populations in check. Both *Cladophora* and *Pithophora* can become weedy in irrigation channels, drains and flood mitigation schemes, as well as river systems where control measures may involve management of nutrient input from catchment groundwater.

Methods

Where specimens have been collected by the authors or have been sent by others in recent years to the Royal Botanic Gardens and Domain Trust for classification, spirit collections have first been fixed in 10% formalin and afterward preserved in 70% ethanol with 5% glycerol. Specimens have been mounted in 40% Karo after staining in aniline blue (0.5 g water soluble aniline blue in 100 ml distilled water and 5 ml conc. acetic acid) for general staining, Lugol's Iodine for chloroplasts and pyrenoids, or safranine for walls and mucilage. Specimens held at NSW have provided the main sources of distributional and biogeographical data, but some specimens from other collections in Australia have also been examined and cited. Where possible, we have compared our material with authenticated Exsiccatae. No attempt has been made to view type material, however, for, as was noted in Skinner & Entwisle (2001), types are either mostly lost, unobtainable, or in poor condition and are there instances where a type and/or a type locality may never have been designated.

As authorities for identification of Australian species, the monographs or substantial genus revisions of Nienhuis (1975) have been followed for *Rhizoclonium*, van den Hoek (1963) for *Cladophora* (both marine and freshwater species), and Pankow & Täuscher (1980) for *Pithophora*.

Key to the genera in Cladophoraceae from non-marine habitats in Australia

1\. Filaments unbranched, or with rhizoidal branching only 2
1\. Filaments variously branched 3

2\. Cells less than 70 m diameter; marine or freshwater .... **1. Rhizoclonium**
2\. Cells greater than 70 μm diameter; marine only .... **Chaetomorpha***

3\. Branching opposite and often perpendicular to bearing axes, akinetes alternating with vegetative cells .... **2. Pithophora**
3\. Branching alternate or dichotomous at acute angles?, akinetes in segments of filaments or absent 4

4\. Cells more-or-less uniform in diameter .... **3. Cladophora**
4\. Cells variable in diameter .... **4. Wittrockiella**

* no species described, see note under *Rhizoclonium riparium*, below.

1. Rhizoclonium Kützing
This is a genus of unbranched filamentous algae growing attached or floating in marine, estuarine and freshwater habitats. Unicellular or short multicellular rhizoids arise (often very infrequently) both from the base and in intercalary positions on or as extensions of conspicuously bent cells ('knees'). Cell diameter does not exceed 70 μm, and the number or nuclei per cell is usually <10, these being the characters which distinguish *Rhizoclonium* from the more usually marine genus *Chaetomorpha*, in which

rhizoids are absent, nuclei are usually many more than 10 per cell, and the only modified cell in the filament (in attached species) is the basal holdfast cell.

One widespread species in Australia (see below).

Rhizoclonium riparium (Roth) Harvey, *Phycologia brittanica* IV: Pl. 138 (1846) emend. Nienhuis, *Biosys. Ecol. Rhizo.* 63 (1975)

Rhizoclonium hieroglyphicum (C. Ag.) Kütz., *Tab. phyc.* 206 (1845)

Thallus a long unbranched filament, with or without a basal rhizoid and/or intercalary one- or two-celled rhizoids, the filaments becoming detached and either free-floating or entangled with age. Cells cylindrical L/D (0.75–)1–6(–10), (14–)20–32(–46) µm diam., nuclei two to four per cell, chloroplast a reticulum of interconnected strands, pyrenoids frequent, the cell wall lamellate and often moderately thick. Reproduction by fragmentation, akinetes (often occurring in short terminal or intercalary series), or by zoids discharged through pores at the upper ends of sporangia or gametangia of cells. Figs 1a–h.

Distribution and habitat: cosmopolitan in fresh, brackish or marine habitats. Reported from all Australian states and territories. New South Wales records are predominantly coastal and frequently from sites in close proximity to salt water, as are those presented here for Victoria and South Australia. This is a similar to the pattern of distribution in the Netherlands as reported by Koster (1955) and Nienhuis (1975). Plants are usually encountered as green to yellowish-green rafts, often mixed with other filamentous algae (Zygnematales and Oedogoniales commonly) among aquatic vegetation or occurring as 'curls', thick mats in which the surface has an undulating form like wet curly hair, at the margins of shallow water bodies. Some collections showed concretions of lime.

Notes: Entwisle & Nairn (1999) listed seven species of unbranched Cladophoraceae as occurring in Australia, although there were no records for New South Wales at that time. *Rhizoclonium capillare* Kütz., *R. fontanum* Kütz. and *R. hookeri* Kütz. were names applied by Cribb (1965) or McLeod (1975) to material from Queensland localities, the vouchers for these records, held in BRI, not having been examined in the present study. Although not included by Koster (1955) in her revision of Dutch taxa, *R. capillare* and *R. fontanum* appear to be synonymous with *R. riparium* (sensu Nienhuis 1975), whereas *R. hookeri* may be conspecific with *R. africanum* Kütz., which Kraft (2000) records from the mouth of Soldiers Creek on Lord Howe Island.

Nienhuis (1975) redefined *R. riparium* to include all specimens from both estuarine and freshwater habitats with filaments 8–43 µm in diameter and L/D 1–11. Within it he included *R. implexum* (Dillw.) Kütz., which Koster (1955) had maintained for narrow (8–15 µm diameter) specimens, and *R. hieroglyphicum,* to which most freshwater collections have usually been referred. Kraft (2000) attributed a somewhat coarser (filaments 44–48 µm thick) but otherwise similar taxon from a euryhaline habitat on Lord Howe Island to *R. africanum* Kütz., a species and range of filament diameters not otherwise recorded in Australia. The two recent collections from Lord Howe Island cited here have cells less than 44 µm diameter. Wide variation in diameter has been observed in collections listed below, and we prefer to follow Nienhuis (1975) in placing them all in *R. riparium.*

Parodi & Cáceres (1993) preferred to continue to employ the name *R. hieroglyphicum* for freshwater specimens from Argentina and, by implication, Europe, emphasising the number of nuclei at 2(–4) as a reliable character, claiming the taxon was clearly defined, without making a clear distinction between *R. hieroglyphicum* and *R. riparium* other than to separate them on habitat choice. The name *R. hieroglyphicum* is also retained in recent freshwater floral treatments (John et al. 2002, Wehr & Sheath 2003)

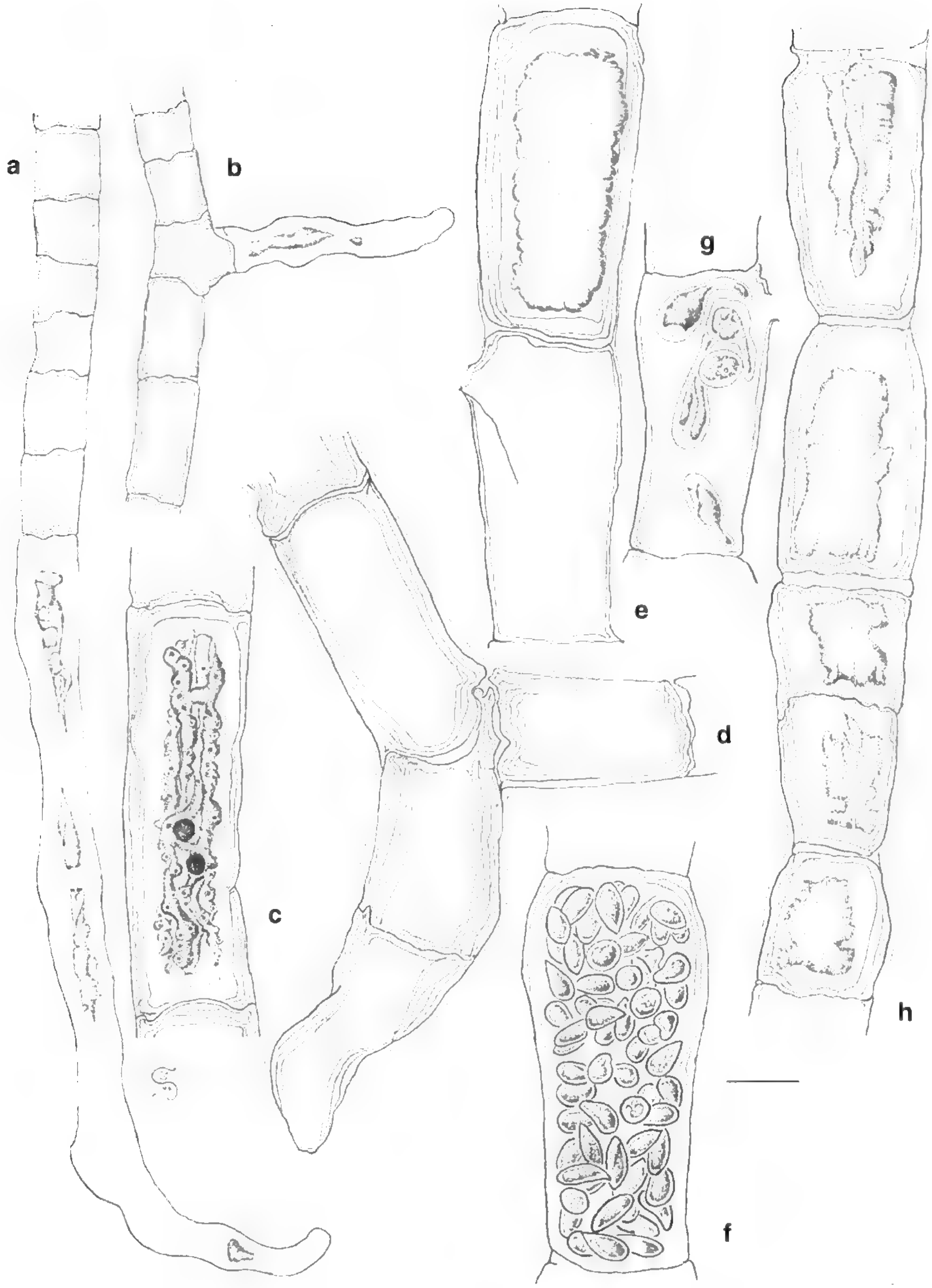

Fig. 1. *Rhizoclonium riparium* **a, b,** basal and lateral rhizoids (*Skinner 0348*); **c,** mature cell, after staining, showing two nuclei and pyrenoids (*Skinner 0452*); **d,** rhizoidal branch (*Conn 4360, &* Brown); **e, f, g,** immature, ripe and discharging sporangia (premature germination among zooids late to leave sporangium in g) (*Hacking,* sample C); **h,** akinetes (*Skinner 0452, Arnold & Towler*). (Scale = 20 µm)

from the northern hemisphere. Rather than use three names, two freshwater (*R. implexum* and *R. hieroglyphicum*) and one marine and estuarine (R. riparium), all morphically intergrading, it appears preferable to follow Nieuhuis (1975) and call all similar collections *R. riparium.*

Selected specimens examined: New South Wales: North Coast: Deep Ck, Valla Beach, *Hacking, sample C,* – Jan 2001(NSW). Central Coast: Lotus pond, Royal Botanic Gardens, Sydney, *Skinner 0017,* 26 Jun 2000 (NSW); quarry, Clovelly Bowling Club, Shark Point, *Skinner 0062, & Entwisle,* 12 May 2000 (NSW); McKell Park, Darling Point, *Skinner 0316,* 18 Apr 2001 (NSW); Cadigal Reserve, Hawthorne Canal, Summer Hill, *Skinner 0348,* 12 Aug 2001 (NSW). Central Tablelands: road gutter, Bowral, *Small s.n.* Apr 2002 (NSW). South Coast: Congo Ck, *K.L.Wilson 10030,* 20 Dec 2001 (NSW); culvert, Long Point St., Potato Point, *Skinner 0494,* 27 Dec 2001 (NSW); Dry R., Quaama, *Skinner 0526,* 2 Jan 2002 (NSW). Southern Tablelands: Queanbeyan R., Queanbeyan, *Skinner 0510,* 28 Dec 2001 (NSW).

Lord Howe Island: NW of Kim's Lookout, *Conn 4268, Brown, Downs, & Hutton,* 9 Nov 2000 (NSW); small freshwater creek, Boat Harbour, *Conn 4360, & Brown;* 16 Nov 2000 (NSW). Victoria: Barwon Valley Park, Belmont Common, *Skinner 0012,* 1 Feb 1986 (NSW); Wagon Bay, Tower Hill, *Skinner 0429, Arnold & Towler,* 30 Sep 2001 (NSW); east main lake, Tower Hill, *Skinner 0430, Arnold & Towler,* 30 Sep 2001 (NSW).

South Australia: 'Heatherdale', Sellicks Hill, *Skinner 0557, & Thomas,* 12 Nov 1976 (NSW); fly-ash lagoons, Port Augusta, *Kokkim s.n.,* – Nov 1982 (NSW); Mrs Cuttings Lake, Allandale East, *Skinner 0450, 0452, Arnold & Towler,* 1 Oct 2001 (NSW).

Chaetomorpha linum (O. Müll.) Kütz. has been collected (and confirmed in this study) in coastal areas of western Victoria and adjacent South Australia (for example *Thurgate 10*), in what was reported as fresh water, but recent collections from the area (for example *Skinner 0430, 0450, Arnold & Towler*) have only revealed *Rhizoclonium riparium.* The *Thurgate 10* specimen is indeed *C. linum,* but it may have been blown/washed into the ponds during very rough weather as the outlet is onto the beach through a low sandhill.

Specimen examined: South Australia: Piccaninnie Ponds, *Thurgate* 10, Feb 1993 (MEL 2034318).

2. Pithophora Wittrock

A genus of vigorously growing, much branched, multinucleate multicellular filaments that favour still or slow-flowing waterbodies and are highly tolerant of eutrophication. A single cosmopolitan species has been reported previously for Australia (Entwisle & Nairn 1999).

Pithophora oedogonia (Montagne) Wittrock, *Nova acta Regiae Soc. Sci. Upsal.* 3: 55 (1877) var. **oedogonia**

Thallus a tangle of uniseriate branching filaments forming anchored by akinete wall and rhizoids or free-floating rafts of a few to 20 or more cm across, the mats yellow- to dark green in colour. Main filaments cylindrical (50–)60–100(–120) µm diameter, cells L/D > 20; chloroplast an open to compact peripheral reticulum with numerous pyrenoids; branching opposite or irregular, arising distally on and forming nearly right angles to their bearing cells; terminal cells of main and lateral axes tapering gradually to an obtuse point. Akinetes intercalary or terminal, when intercalary solitary, in pairs or threes, cylindrical, barrel-shaped or inflated on one side, 200–300 µm long, 70–125 µm diam.; terminal akinetes solitary or, more rarely, in short series, hastate to piliate (with a short or long point), 125–300µm long, 55–80 µm diam. Rhizoids and haptera rare, basal; helicoid structures at branches not observed in Australian material. Figs – see Entwisle & Price (1993) Fig. 1a.

Distribution and habitat: This species has been reported from throughout the Australian continent (Entwisle & Nairn 1999). Entwisle & Price (1993) particularly noted its high tolerance for warm, shallow, alkaline water that is rich in nitrogen and phosphorus at Queensland sites. The most recent collections also come from such habitats, one a transient stream in an urban area, others being shallow riverine lagoons within canefields. Western Australian and New South Wales collections are from artificial ponds or the streams feeding them that are similar to Queensland sites in physical and chemical characteristics.

Notes: terminal akinetes in our collections are usually hastate and obtuse rather than pointed, whereas intercalary akinetes are usually solitary, never in groups of more than three. Our specimens thus conform well to both van den Hoek's (1959) and Pankow & Täuscher's (1980) circumscriptions of *P. oedogonia*. Pankow & Täuscher (1980) recognise two broadly defined taxa and have suggested synonymy or doubtful status for many if not most of the previously described fifteen species. They defined *Pithophora roettleri* (Roth) Wittr. as having rows of variously shaped intercalary akinetes (up to seven/row) and rounded terminal akinetes, whereas in their opinion *P. oedogonia* has one or two [3–7 in var *polyspora* (Rendle & West) Pankow & Täuscher] barrel-shaped to cylindrical intercalary akinetes and pointed terminal akinetes. Van den Hoek (1959) had earlier separated four Caribbean taxa on the basis of akinete shapes and main-filament diameters, but Pankow & Täuscher (1980) included all of van den Hoek's taxa in one or other of the two species that they recognised.

Fresh specimens may have a distinct smell of cats' urine.

Specimens examined: Queensland: Anderson Park, Townsville, *Price s.n.*, 9 Aug 1990 (JCT); James Cook University Campus Ck, Townsville, *Dell s.n.*, 11 Nov 2002 (NSW); Castanelli's Lagoon, near Burdekin R., *Reid s.n.*, 14 Nov 2002 (NSW); Healeys lagoon system, off Woodstock Rd, *Reid 270103.10*, 27 Jan 2003 (NSW).

New South Wales: Central Coast: Mullet Ck, North Narrabeen, *Entwisle 2920* (NSW); Fairlight, *McCune s.n.*, 4 Apr 2003 (NSW).

Western Australia: Berkerley R., *Kenneally 11878*, 13 Jun 2003 (NSW); Broome airport, *Kenneally 11900, 11901*, 21 Jun 2003 (NSW).

Pithophora oedogonia var. **calcarata** *Skinner and Entwisle* **var. nov.**

Akineta intercalaria terminaliaque frequenter calcari breviore vel extentiore extrudete a latere.

Intercalary and terminal akinetes frequently with a short to extended spur projecting? from the side; otherwise morphology as for var. *oedogonia*. Fig. 2.

Type: type locality: as turf in concrete drain, Pieter van Hasselt Park, Shalvey, 33°43'S; 150°48'E, N.S.W. *Coveny 18551 & Sherring*, 24 April 2000 (NSW).

Etymology: *calcar* (latin) is a spur, so *calcaratus, a, um* meaning spurred.

Distribution & habitat: coastal hinterland of New South Wales, in sluggish, often warm, shallow freshwater disturbed by storm-water or agricultural runoff..

Notes: there is much variation in the form of the akinetes, both intercalary and terminal, in *Coveny 18550*, including some with lateral spurs, but most intercalary akinetes fit the 'meist tonnenförmig, selter zylindrisch bis subzylindrisch' specifications of *P. oedogonia* (Pankow & Täuscher 1980). As well, there are plenty of the short hastate terminal akinetes that are characteristic of that species. The spurs that confer the varietal name are pronounced and more uniform than the irregular lateral projections in *O. aequalis* Wittr. (as illustrated by van den Hoek 1959), which we consider synonymous with *P. oedogonia*.

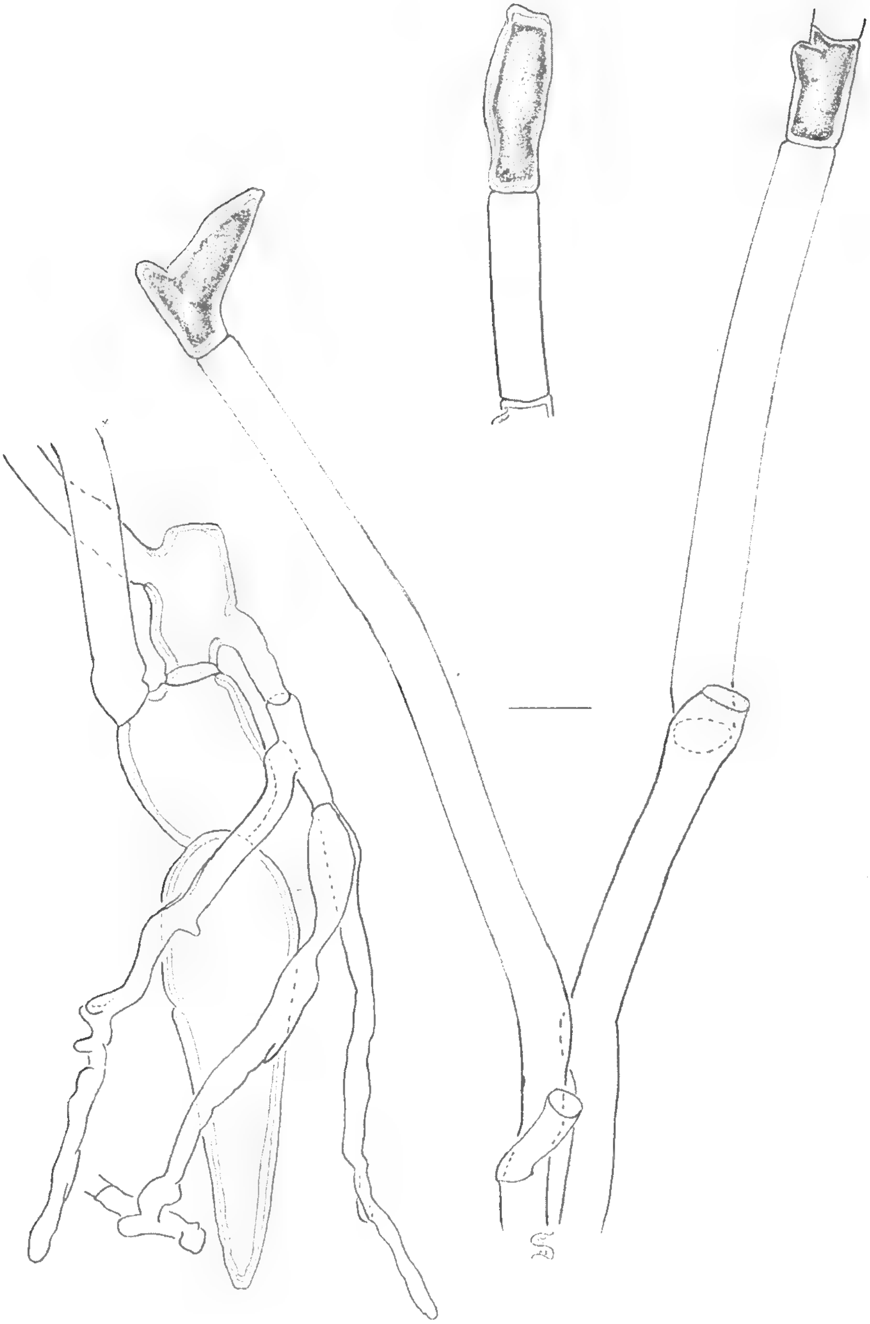

Fig. 2. *Pithophora oedogonia* var. *calcarata*: germinating akinete series, with intercalary and apical spurred akinetes in germling (*Coveny 18551 & Sherring*). (Scale = 100 µm)

Short series of akinetes, including the hastate terminal one, have been found in *Coveny 18551* showing production of both new axes and tendril-like haptera. It would appear that the empty akinete chambers, with their thick walls, act as an anchor for the new thallus.

Specimens examined: New South Wales: North Coast: Nabiac, *Skinner 0352*, 28 Aug 2001 (NSW). Central Coast: Pieter van Hasselt Park, Shalvey, *Coveny 18550, 18551 & Sherring*, 24 Apr 2000 (NSW); Bells Ck, Oakhurst, *Coveny 18963*, 14 Oct 2001 (NSW).

3. Cladophora Kützing

A large genus of branching, filamentous algae, with multinucleate cells with reticulate parietal chloroplasts, numerous pyrenoids, and frequently thickened walls. Although most species-rich and morphologically diverse in marine habitats, at least nine members are credited by van den Hoek (1963) to euryhaline or freshwater habitats in Europe, of which three or four have been reported in Australian inland aquatic systems. There are nine names used in Entwisle & Nairn (1999), many are synonyms for the five species documented below, which probably represent the full range of morphological variation in Australia.

Key to freshwater *Cladophora* in Australia

1. Basal system prostrate and extensive; secondary laterals making acute angles (<45°) with main axes .... **3a. C. kosterae**

1. Basal system, where present, rhizoidal; secondary (and higher order) laterals with wide (>45°) adaxial angles ....

2. Lateral filaments laterally inserted subapically; rhizoids, if present, arising adventitiously; cells large, with thickened walls .... **3b. C. aegagropila**

2. Lateral filaments inserted at apical ends of bearing cells; rhizoids confined to basal areas; cells sizes variable, with or without thickened walls 3

3. Thalli sparsely branched and finely constructed, with even gradations from main axes to higher orders of branching .... **3c. C. globulina**

3. Thalli repeatedly branched and often coarse, with distinct size differences between diameters of main axes and ultimate branch orders 4

4. Thalli attached, or faculatively free-floating; apical cells 20–90 µm diam., main axes often more than 100 µm diam. .... **3d. C. glomerata**

4. Thalli usually free floating, apical cells 16–27 µm diam., main axes less than 85 µm diam. .... **3e. C. fracta**

3a. Cladophora kosterae van den Hoek, *Revision of the European species of Cladophora*: 37 (1963)

Erect axes arise from an extensive prostrate base and give rise to opposite or alternate laterally inserted secondary axes. Main axes are often very long, sometimes with pairs of parallel, tangentially inserted cells, often subtending branching, L/D 3–10, 47–72 µm diam. Secondary branches inserted below end-walls at acute adaxial angles, such that secondary branches often appear to lie parallel to main axis, at least for the first cell in a branch, 50–54 µm diam. Apical cells tapering, tip more-or-less blunt, 25–29 µm diam. Groups of intercalary or subterminal swollen sporangia 65–72 (–90) µm long, 58–65 µm diam. opening by a supramedian lateral pore. Fig. 3 a–c.

Distribution and habitat: van den Hoek (1963) reports this species from France and the Netherlands. In Australia it has only been collected in the South Creek catchment of the Cumberland Plain, west of Sydney, always from sluggish, weed-infested waterbodies in suburban developments.

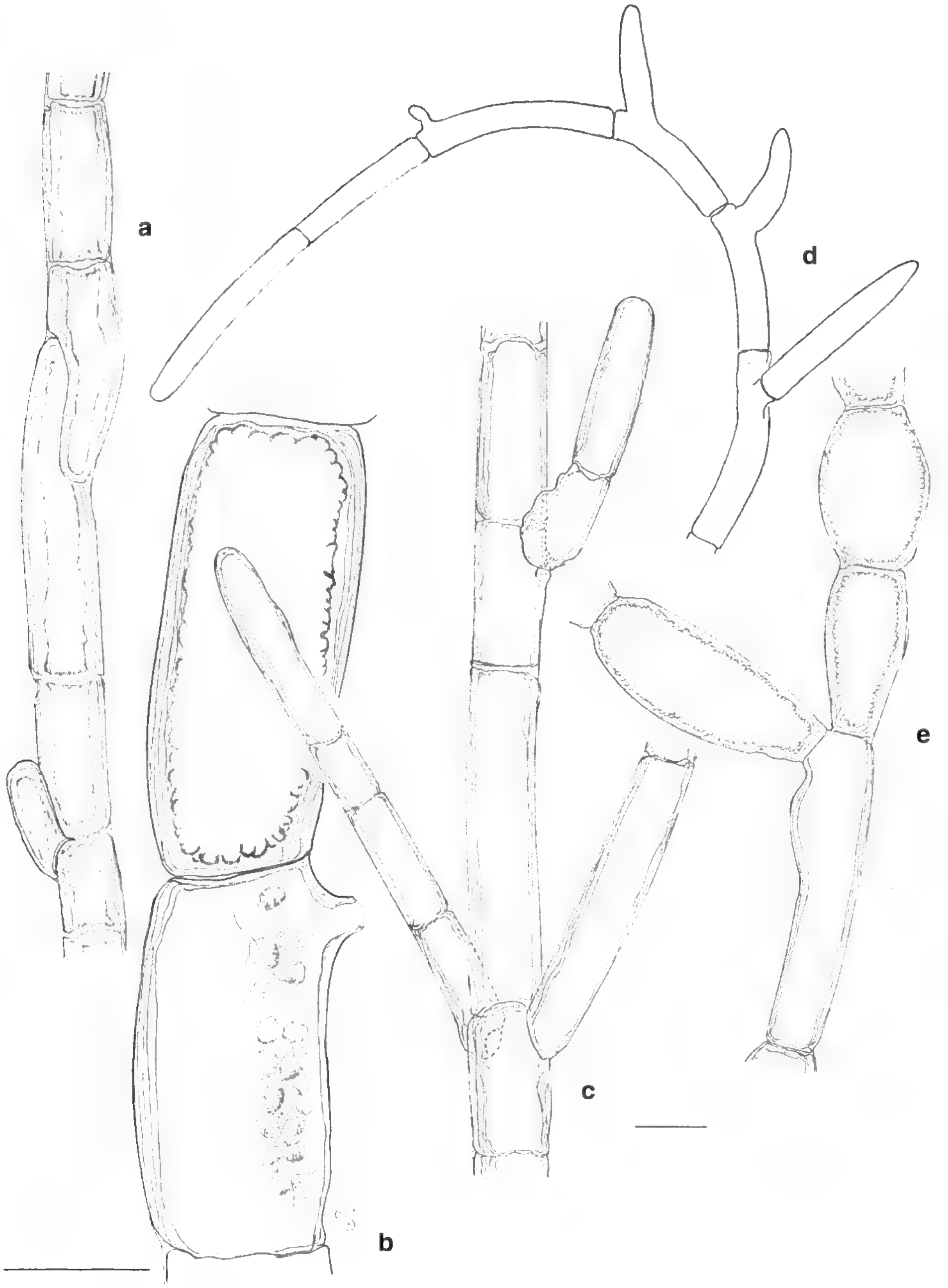

Fig. 3. *Cladophora kosterae:* **a,** primary filament with tangentially disposed cells (*Coveny 18546*); **b,** sporangia, the lower one with mature zooids (*Coveny 18550*); **c,** filament with opposite and alternate laterals, showing narrow adaxial angle (*Coveny 18550*); *C. aegagropila*: **d,** growing tip with maturing laterals (*Skinner 0371*); **e,** akinetes (*Reid 270103.5*). (Scale a,c–e = 20 µm at 250×; b = 20 µm at 400 ×)

Notes: Although the extensive basal mat described by Hoek for *C. kosterae* has not been seen in Australian specimens, the reproductive structures fit its description well. The almost parallel secondary branches are distinctive, and the occasional oblique septation of cells, described by van den Hoek as being particularly numerous in parts of the prostrate system, are also present.

Ducker (1958) described as *Basicladia ramulosa* Ducker populations from Victoria and Queensland that appear similar to *C. kosterae,* the plants growing obligately on the carapaces of the freshwater turtle *Chelodina longicollis* (Shaw). We do not have any specimens to hand of turtle carapaces with epizoic Cladophoraeae and thus cannot reassess the position of Ducker's taxon. Van den Hoek (1963) considered both the obligate epizoic taxa and the similar *Cladophora kosterae* and *C. okamurai* (Ueda) Hoek, to belong to section *Basicladia* of the genus *Cladophora.*

Specimens examined: New South Wales: Central Coast: Bells Ck, Oakhurst, *Coveny 18963,* 14 Oct 2001 (NSW); Peter van Hasselt Pk, Shalvey, *Coveny 18550;* Emerton, *Coveny 18546,* 9 Apr 2000 (NSW).

3b. Cladophora aegagropila (L.) Rabenh, *Flora europaea algarum aquae dulcis et submarinae* III 343–344. (1868)

Conferva aegagropila Linnaeus, *Sp. pl.* II 1167–1168. (1753)

Cladophora parvula Möbius, *Abh. seneckenberg. naturf. Ges.* 18: 328 (1895).

Thallus attached or, commonly, free floating, yellowish to dark green. Apical cells L/D 5–24, 30–70 µm diam.; ultimate branch cells L/D 3–15; 30–100 µm diam.; main axes L/D 1.5–15, 125–200 µm diam.; wall 2.5–8 µm thick at tip, 20 µm in main axes. Lateral branches inserted laterally and a little below upper end-wall of axis cell, retaining this position with maturity. Rhizoids may sprout from most parts of thallus. Reproduction only by fragmentation or akinete formation. Akinetes in series, ovoid to elliptical, 100–190 µm long, 70–80 µm diam. with strongly lamellate walls. Fig. 3 d,e, 4. a–c.

Distribution and habitat: cosmopolitan. Collection localities in Australia are often alkaline streams with at least moderate flow rates, often in association with improved pasture.

Notes: there are two distinct groups of specimens: those that conform to the 'European' *C. aegagropila,* and those that have a similar branching pattern but narrower apical cells and generally less robust form throughout, thus fitting the description of Möbius (1895) for *C. parvula. Cladophora parvula,* from Warwick, Queensland, is described by Möbius (1895) as less than 8 mm long. Without culture and field work it would be decidedly premature to describe a variety or, alternatively, to ressurect the ill-defined epithet *parvula,* but it may be beneficial for future workers if the collections to hand are filed separately.

Entwisle 1507 was previously reported (Entwisle 1994) as *Chaetomorpha linum,* as the filaments are very rarely branched and the cells are broad, moderately short (L/D 2.5–3.5) and thick-walled. Comparison with perennial fragments in other collections (*Skinner 0041, Thurgate 21*) and the occasional subterminal branch initial or scar suggest that it may be better referred to *Cladophora aegagropila.*

Specimens examined: Queensland: Burdekin R., Hwy crossing, *Reid 270103.05,* 27 Jan 2003 (NSW).

New South Wales: Northern Tablelands: MacDonald R., Bendemeer, *Skinner 0074, & Cherry,* 21 May 2000 (NSW); Falconers Ck, Backwater Rd, near Guyra, *Skinner NED027,* Dec 1974 (NE); Apsley R., Walcha, *Skinner 0201 & Cherry,* 25 May 2000 (NSW); Apsley R., Apsley Falls, *Skinner 0203b & Cherry,* 25 May 2000 (NSW); Tia R., Tia Falls, *Skinner 0214 & Cherry,* 25 May 2000 (NSW). Central Coast: McKell Park, Darling Point, Port Jackson, *Skinner 0314,* 18 Apr 2001 (NSW); Yarramundi Bridge, Nepean R., *Skinner 0334 & McPhearson,* 9 Aug 2001 (NSW). Central Tablelands: Wingecarribee R., Berrima, *Skinner 0317,* 25 Apr 2001(NSW). Central Western Plains: Arnolds bridge, Page R.,

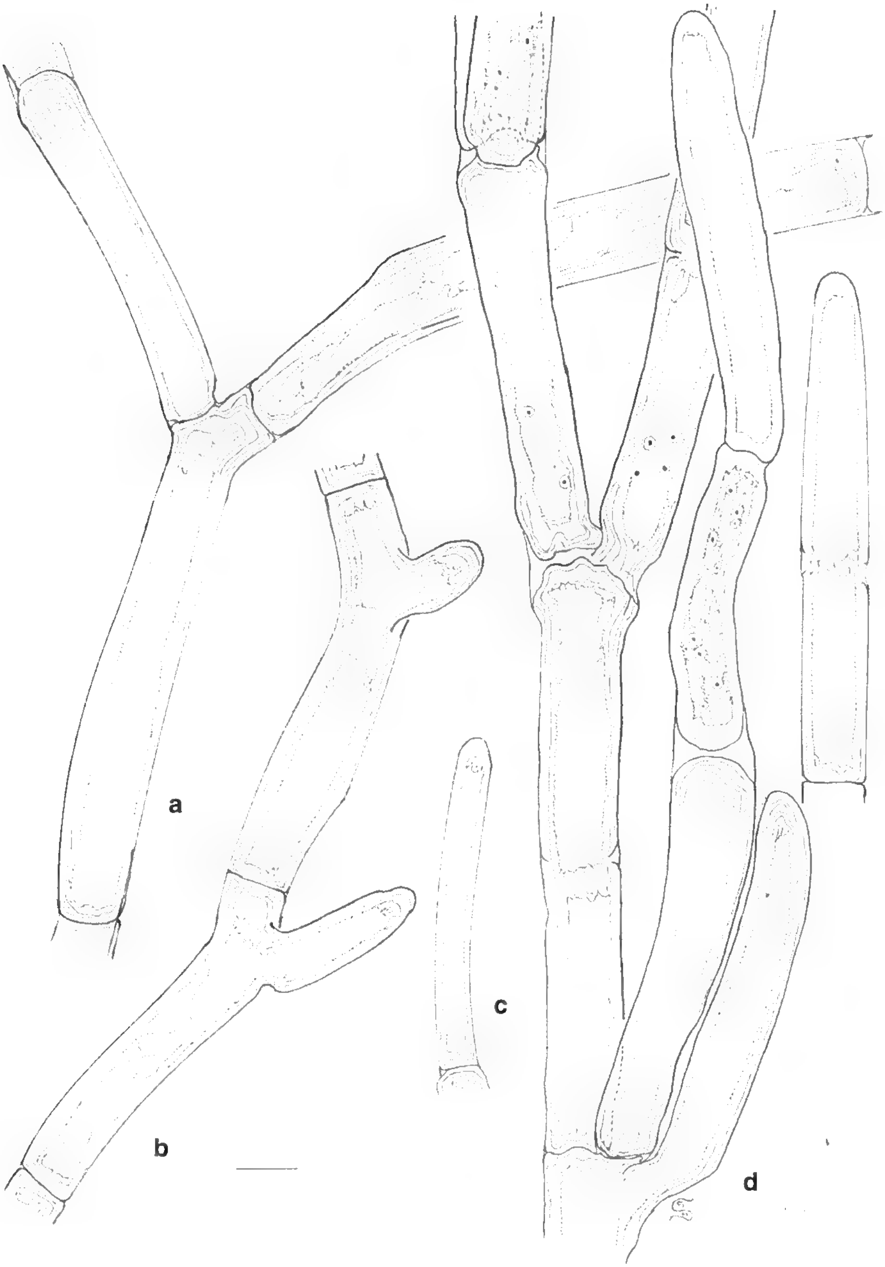

Fig. 4. *Cladophora aegagropila:* **a, b,** lateral branching ; **c,** apical cell (*Skinner 0317*); *C. glomerata*: **d,** pseudodichotomous branching; **e,** apical tip (*Skinner 0408, Arnold & Towler*). (Scale = 20 µm)

Murrurundi, *Skinner 0021*, 11 Dec 1999 (NSW); Lake Cargelligo, *Skinner 0476*, Arnold & Towler, 4 Oct 2001 (NSW).

Victoria: Barwon R., Barwon Valley Park, Belmont, *Skinner 0012*, 1 Feb 1986 (NSW); Lake Cooper, near Shepparton, *Gar?ia AG 30.09.01.1Al*, 30 Sept 2001 (NSW); Korkuperrimul Ck, Bacchus Marsh, *Entwisle 1507*, 14 Jul 1988 (MEL).

South Australia: 'Heatherdale', Sellicks Hill, *Skinner 0557, & Thomas*, 12 Nov 1976 (NSW, AD); Torrens R., River Torrens Linear Park, Paradise, *Skinner 0276*, 24 Dec 2000 (NSW); Torrens R., RTLP, Highbury, *Skinner 0278*, 24 Dec 2000(NSW); Eight Mile Ck, *Skinner 0041*, 6 Dec 1989 (NSW); Ewans Ponds, *Thurgate 21*, –Feb 1992 (MEL); Goulden Hole *Thurgate 12*, – Feb 1992 (MEL); Piccaninnie Ponds, *Skinner 0032, 00033*, 15 Nov 1989 (NSW); main pond, Piccaninnie Ponds, *Skinner 0445, Arnold & Towler*, 1 Oct 2001 (NSW); Piccaninnie Ponds, *Thurgate (Entwisle 1540)*, –Oct 1988 (MEL).

Doubtful determinations: New South Wales: Eastern Ck, *Coveny 18856*, 16 Apr 2001 (NSW); Macdonald R., Bendemeer, *Skinner 0071, 0072 & Cherry*, 21 May 2000 (NSW); RBG Mt Annan, *Coveny 18890*, 22 Nov 2001 (NSW) may all be referable to *C. parvula*, but are much, much bigger plants than the Type (as described in Möbius 1895).

3c. Cladophora globulina (Kütz.) Kütz., *Phyc. germ.* 219 (1845).

Conferva globulina Kütz., *Alg. aq. dulc. germ.*, no. 20 (1833).

Filaments are long and delicate, with almost no branching; apical cells tapering sharply to a bluntly rounded end , L/D 7–10, 17–20 µm diam., cells of filaments thin walled, L/D 10–12, to 35 µm diam.; insertion of branches rare, at first lateral but becoming sub-dichotomous with age in lower parts of axes. Reproduction by fragmentation or akinetes, as well as zoids. Fig. 5 a—d.

Distribution and habitat: Continental Europe; newly recorded for Australia from central and south coast of New South Wales, where it is found in artificial ponds and a sluggish, seasonally shallow to dry river.

Notes: The Quaama and Camperdown specimens conform well vegetatively to the description in van den Hoek (1963), the Camperdown collection being additionally actively reproductive, releasing large numbers of zoids. Van den Hoek (1963) comments on the 'thorn-like' appearance of young branch initials and the swelling of the cell ends in older parts of the filaments, both of which features can be seen in Australian material. Confusion with *Rhizoclonium* can be largely avoided in fresh material by looking for nuclei, as most cells have four, six or even ten as opposed to 2–4, in *Rhizolclonium riparium*.

Specimens examined: New South Wales: Central Coast; Victoria Park, Camperdown, *Skinner 0554*, 24 Mar 2002 (NSW); garden pond, Penrith, *Cammack s.n.*, 17 Jan 2000 (NSW); Lake Nadungamba in Mount Annan Botanic Garden, *Coveny 18980*, 22 Nov 2001 (NSW). South Coast: Dry R., Quaama, *Skinner 0524, 0526*, 2 Jan 2002 (NSW).

3d. Cladophora glomerata (L.) Kütz., *Phyc. gen.* 226 (1843).

Conferva glomerata Linnaeus, *Sp. pl.* II:1167 (1753)

Cladophora chartacea Grunow, *Reise…Novara*, vol.I, *Sporenpflanzen. Heft I Algae* 1 (1867)

Rhizoids basal, often grouped into a fascicular holdfast. Axes repeatedly branched, insertion either terminal or lateral but at the apical ends of cells, becoming co-terminal and so forming pseudo di-or trichotomies; growth intercalary to acropetal; main axes 100–275 µm diam., L/D (7–12)–(1.5–5), ultimate branch cells (22–34)–(68–100) µm diam., L/D (5–10)–(1.5–3.5), apical cells (21–31)–(58–91) µm diam., L/D (6–13)–(1.5–5). Reproduction by fragmentation, by intercalary akinetes, and zoids formed in terminal and sub-terminal cells of upper lateral branches, opening by sub-terminal or terminal pore. Figs 4 d,e, 5 e,f.

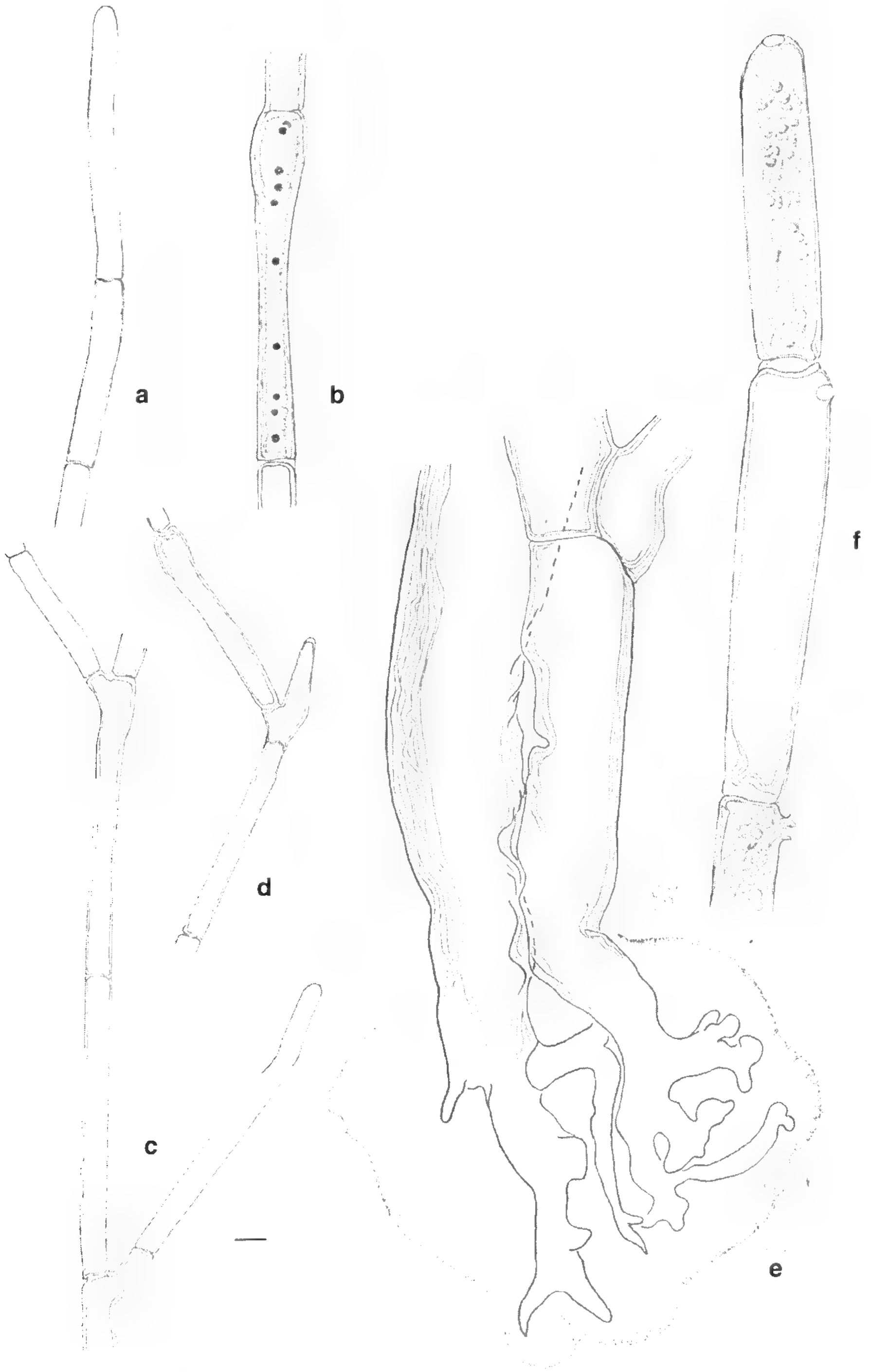

Fig. 5. *Cladophora globulina:* **a,** apical tip; **b,** terminally thickened cell, showing distribution of nuclei; **c,** branching pattern; **d,** thorn-like branch initial (*Skinner 0554*); *C. glomerata:* **e,** rhizoidal system; (Woods s.n.) **f,** series of sporangia (*Skinner 014*). (Scale = 20 μm)

Distribution and habitat: cosmopolitan, reported from freshwater and saline habitats in all states and territories of Australia. Widely distributed in New South Wales, where it favours neutral to alkaline, often weedy waterways, but can also be found in seepages and other almost aerophylic conditions. A similar distribution is to be expected in other States, as is indicated by the South Australian collections examined.

Notes: This is a very variable and frequently perennial species, so that some specimens may have much variation in dimensions between old and new growth that probably reflect responses to changes in environmental conditions.

Cladophora chartacea Grunow (1867), based on a collection by Frauenfeld at Naraby (most likely an orthographic error for Narrabeen) Lagoon, Port Jackson, is a good example of the blanket-weed form of *C. glomerata*. The dried material does show the alternating imploded cells of Grunow's figure, but on regaining turgidity it displays the expected form of the species. When growing rapidly, specimens often show a predominance of conspicuously shortish cells in the new-growth parts.

Specimens examined: New South Wales: North Coast: Wrights Ck, Port Macquarie, *Skinner 0014*, 1999 (NSW). Northern Tableland: Wollomombi R., Waterfall Way bridge, *Skinner 0190 & Cherry*, 24 May 2000 (NSW). North West Slopes: Chaffy Dam, Peel R., near Nundle, *May s.n.* 14 Feb 1978 (NSW). Central Coast: BB Ck, Manly Dam, no collector name 22 Sep 2000 (NSW); Middle Harbour Ck, St Ives, *Entwisle 2962*, 20 Mar 1999(NSW); Panania, *Pinner s.n.*, 2 Jul 2000 (NSW); Tropical House pond, RBG Sydney, *Skinner 0228a*, 21 Jun 2000 (NSW); stairs between Lower Fort St & Hickson Rd, Dawes Point, Sydney, *P.G. Wilson 1578*, 20 Feb 2003 (NSW); West Wollongong, *Garcia s.n.* 14 Mar 2002 (NSW); Nor-West Business Park, Baulkham Hills, *Rooney s.n.*, 10 Jul 2003 (NSW); Lake Nadungamba in Mt Annan Botanic Garden, *Ling, J. s.n.*, 22Oct 2001 (NSW). Central Western Plains: Lake Cargelligo, *Skinner 0477, Arnold & Towler*, 4 Oct 2001 (NSW). South Coast: Narira Ck, Cobargo, *Skinner 0233*, 13 Jul 2000 (NSW); Jemersons Beach, Potato Point, *Skinner 0496*, 27 Dec 2001 (NSW). South West Slopes: Botanic Gardens, Wagga Wagga, *Skinner 0378, Arnold & Towler*, 26 Sept 2001 (NSW). South West Plains: Yenda, *Skinner 0359, Arnold & Towler*, 24 Sep 2001 (NSW); Box Ck channel, Blighty, *Skinner 0408, Arnold & Towler*, 27 Sep 2001 (NSW).

Also: Naraby Lagoon, Port Jackson, *Frauenfeld 884*, 1858? (NSW) = Coll. Grunow 15411, 32416, 32417, 32418. (WEIN).

Victoria: Lake Cooper, Shepparton, *Garcia AG 30-09-01-1 A1*, 30 Sep 2001 (NSW).

South Australia: Inman R., billabong, Encounter Bay, *Skinner 0005*, Oct 1978 (NSW); Brownhill Ck, Fullerton Rd., *Woods s.n.*, 18 Jun 1978 (NSW); Torrens R., Reeds Rd ford, Highbury, *Skinner 0004*, 4 Feb 1986 (NSW); Bool Lagoon site 1, *Lloyd s.n.*, 5 Nov 1982 (NSW).

Northern Territory: Roper R. at Moraok Station, *Townsend A1,A2*, 12 Sept 2000 (NSW).

Western Australia: Swan R., Wanganga NP, *Entwisle 2994*; Loch Ness, Yanchep Inn area, *Entwisle 3000.*

3e. Cladophora fracta (Müll. ex Vahl) Kütz., *Phyc. gen.* 263–264 (1843)

Conferva fracta Müller ex Vahl, *Flora danica* 16: 946 (1787)

Basal rhizoids often present, although plants not usually attached; branching frequent, insertion terminal; vegetative cell walls usually not heavily lamellated, growth mostly acropetal. Apical cells L/D 3.5–25, 14–27 µm diam.; ultimate branch cells L/D 3–17, 17.5–38 µm diam.; main axes L/D 1.5–14, 45–85 µm diam. Reproduction asexual. Sporangia in laterals, tumid, L/D 5–8; 29–36 µm diam. opening by terminal pore. Akinetes not seen. Fig. 6 a,b.

Distribution and habitat: world-wide but apparently uncommon, rare or under-collected in Australia. Favours coastal localities with fluctuating balance of salt and fresh water such as estuaries and sand dune marshes.

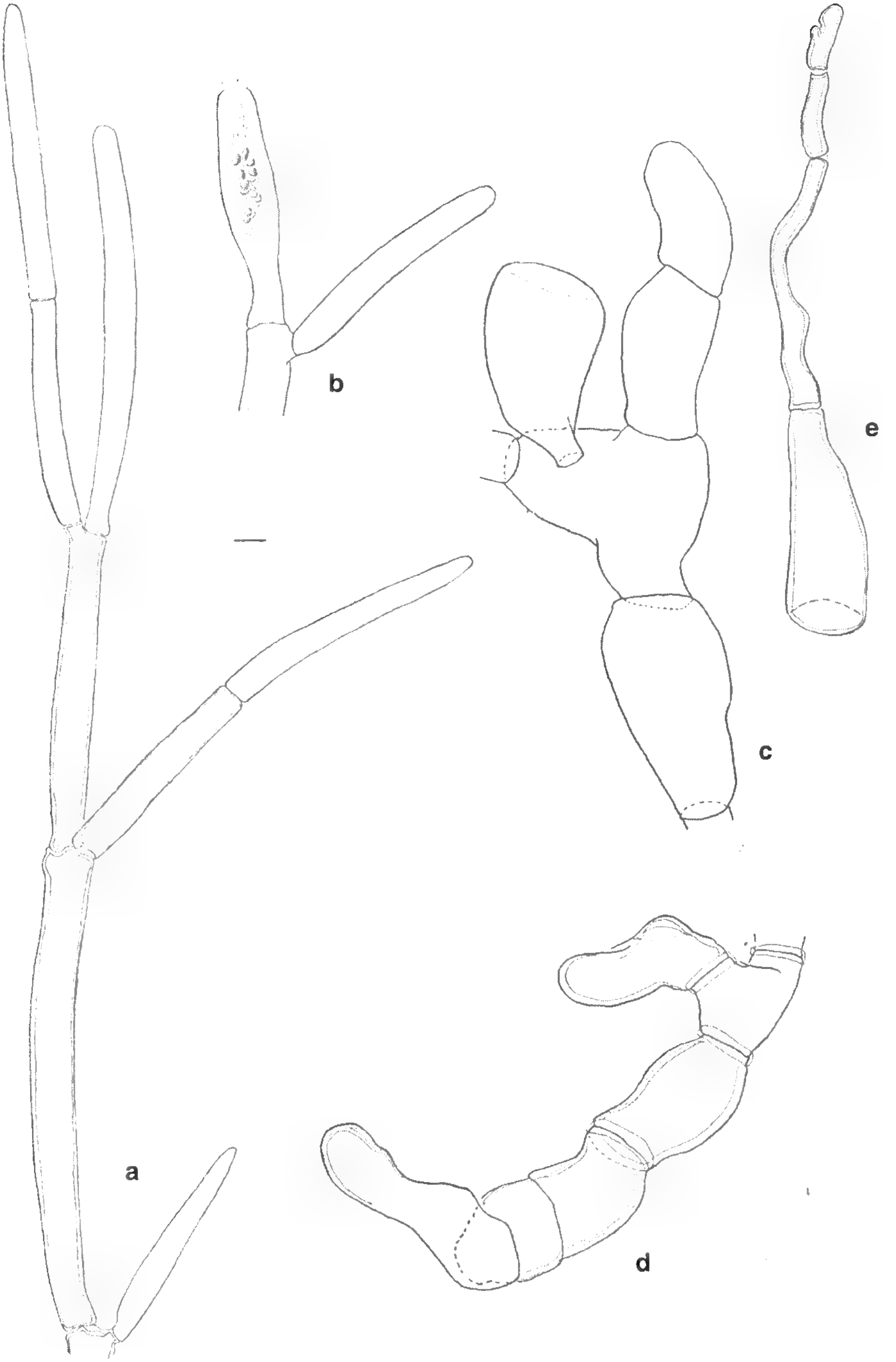

Fig. 6. *Cladophora fracta:* **a**, branching filament, including immature sporangium (third branch); **b**, discharging sporangium (*Skinner 0512*); *Wittrockiella salina* var. *kraftii:* **c**, **d**, prostrate system; **e**, erect filament (*Brown 2000/157 et al.*). (Scale a, b = 20 µm, c–e = 50 µm)

Notes: both specimens of the NSW collections are from the same estuarine system from sites where the water was only slightly salty to taste and direct communication to the sea only intermittent during spring tides.

Specimens examined: New South Wales: South Coast: estuary between Lake Brunderee and Potato Point beach, *Skinner 0512*, 29 Dec 2001 (NSW); Lake Brunderee, *Skinner 0515*, 31 Dec 2001 (NSW).

4. Wittrockiella Wille

A small genus of a few species that are most often encountered in specialised coastal and estuarine habitats. The prostrate and erect systems are photosynthetic, and there is little uniformity in cell shape, rather a fitting to spaces between surrounding cells Most previous records in Australia and from overseas are from saline habitats or the brackish-water interfaces between fresh and salt water in coastal rivers.

Wittrockiella salina Chapman, *Farlowia* 3: 495 (1949) var. **kraftii** *Skinner & Entwisle* **var. nov.**

Filamentibus prostratis ad varietati implicitae aestuariis mentiens sed in aquam dulcem processibusque erectis intricatis sinuatis sineque pilis.

Type: New South Wales: Lord Howe Island, Dinner Run, at base of lowest falls, *Brown 2000/157, Conn, Downs & Hutton*, 11 Nov 2000 (holo: NSW).

Thallus a mat of entangled, freely branching prostrate filaments (with some suggestion of anastomoses) and erect processes rhizoid-like in appearance. Prostrate filaments of short broad, cylindrical to irregular cells, L/D 1–2.5(–3), 200–260 µm diam.; terminal cells broadly obtuse and short, 100–150 µm diam. Erect processes arising laterallyor sub-apically, erect, sinuous, narrow, much longer than broad, 25–90 µm diam. Reproduction unknown. Fig. 6c–e.

Etymology: named in honour of Dr G. T. Kraft who has contributed much to the study of marine and freshwater Cladophorales in Australia, and has a continuing special interest in the algal flora of Lord Howe Island.

Notes: var. *kraftii* does not show either the regular erect processes in *W. salina* or the hairs, especially when compared to the ball form from the Lake Brunderee estuary near the Tuross River delta. It has more elongate erect processes and, at least in its Type collection, a contrasting habitat preference. *W. salina* var. *kraftii* does not compare well with the description and illustration in Harvey (1855) for *W. lyallii* (as *Cladophora lyallii* Harvey) from New Zealand, but has some similarity to the figures of *W. lyallii* (Harvey) van den Hoek, Ducker & Womersley that are given in van den Hoek et al. (1984). *W. lyallii* has apical cells 250—510 µm diam. and intercalary cells 250—450 µm diam. (van den Hoek et al 1984), however, which are much larger dimensions than those of *W. salina* var *kraftii*, and in addition form as a turf at high water or form floating 'moss' balls.

The type variety is an estuarine populant of south eastern Australia and New Zealand. As noted by van den Hoek et al. (1984), it is often found in lower salinities than marine habitats. *Skinner 0514*, from the estuarine creek flowing out of the almost freshwater Lake Brunderee, is the 'moss-ball' form. The creek mouth was closed to all but spring tides in summer 2001–2002, but the water tasted salty at the place, close to the road to the mouth of the Tuross, where the moss balls formed a carpet on top of the water. Other records from the south coast of New South Wales (*Verdon 1091, 1097*) are of the turf form from margins of coastal waterways.

***Wittrockiella salina* var. *salina* examined:** New South Wales: South Coast: estuarine creek into Lake Brunderee, Potato Point, N.S.W., *Skinner 0514*, 30 Dec 2001 (NSW), Little Malua Bay Beach, Malua Bay, *Verdon 1091*, 10 Apr 1975 (CANB); Lilli Pilli Beach, 8 km S of Batemans Bay, *Verdon 1097*, 10 Apr 1975 (CANB).

There are a number of other infrequently encountered freshwater genera in Cladophoraceae, including *Cladophorella* Fritsch, *Cladostroma* Skuja, *Arnoldiella* Miller and *Chaetonella* Schmidle and more (Bourrelly 1966,1988). *Arnoldiella* and *Cladostoma* are taxa with compact thalli, whereas *Cladophorella* has some morphological similarities to *Wittrockiella*, but is distinct in forming terminal akinetes, and having its erect processes composed of regular cylindrical cells like those of short filaments in *Cladophora*. None of these mostly middle-European taxa have yet been reported from Australia.

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Thanks are also due to many of our colleagues here in Sydney (especially the Lord Howe Island team led by Dr Elizabeth Brown) and in other states and territories (especially Dr Kevin Kenneally, Dr Simon Townsend, and David Reid) for many of the collections. We also thank the National Herbarium of Victoria for the loan of numerous specimens and Dr G.T. Kraft for discussions of various taxa, and especially the loan of references on *Rhizoclonium*. This research was funded through the *NSW Biodiversity Strategy*.

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Notes on the geography of South-East Asian *Begonia* and species diversity in montane forests

W. Scott Hoover, Carrie Karegeannes, Harry Wiriadinata and James M. Hunter

Abstract

Hoover, W. Scott[1], Karegeannes, Carrie[2], Wiriadinata, Harry[3], Hunter, James M.[4] ([1]New England Tropical Conservatory; [2]American Begonia Society; [3]Herbarium Bogoriense; [4]New England Tropical Conservatory) 2004. Notes on the geography of South-East Asian Begonia *and species diversity in montane forests.* Telopea *10(3): 749–764.* Field reconnaissance of *Begonia* in lower montane forests of Sumatra and Sulawesi, Indonesia was undertaken in 1995 and 1998, with formal research expeditions being conducted in lower montane forests of West Java in 2000 and 2001. Forty-seven mountains have been explored in Indonesia, by mostly single samplings along elevational gradients on each mountain. Taxonomic determinations have been made for most of the *Begonia* collected in 2000 and 2001 and species of the section *Sphenanthera* were recognised, observed and photographed in Sumatra and Sulawesi. In 1977 and 1978, wet tropical forest at the Carpentaria mining exploration site at the Frieda River, West Sepik, Papua New Guinea was explored for *Begonia*. Many different *Petermannia* species were diversified along elevational gradients. Field observations at this West Sepik site suggest populations of individual species were often restricted to one or several small, localised colonies along stream margins within the 25 km^2 site.

Introduction

The important horticultural genus *Begonia* is unusual among angiosperms from a number of standpoints:

1. It is ranked the 16th largest genus of vascular plants by Minelli (1993), who lists *Begonia* as having 900 species. According to Smith et. al. (1986) and Doorenbos et. al. (1998), the genus is estimated to include 1400 species, equalling *Solanum* and *Psychotria* in size. *Begonia* is now considered to be one of the five largest genera of vascular plants with up to 1600 species (Sands, 2001).
2. The taxonomy of the Begoniaceae has been very difficult and historically controversial, (for example, Irmscher 1915, Lawrence 1951). Sands' (1977, 1982, 1990 and 2001) taxonomic work on South-East Asian *Begonia* has been extensive and he has described many valuable horticultural species including *B. amphioxis* Sands and *B. chlorosticta* Sands.
3. Though many species of *Begonia* have singly occurring stomata (Hoover 1990a) many other species are observed to have stomatal clusters and a hypoderm (Fellerer 1892, Hoover 1986).
4. Medullary and cortical vascular bundles in the petiole and stem of many *Begonia* species represent an anatomical pattern more like monocotyledons than dicots (Esau 1965).

Paper from the 5th International Flora Malesiana Symposium 2001.

5. Physiologically, *Begonia* is distinct for the presence of oxalic acid in cytoliths, another characteristic limited in the angiosperms (Pireyre 1961).

Most botanical exploration of SE Asian countries has occurred at lower elevations, leaving higher montane forests largely unexplored. *Begonia* is highly diversified in SE Asian montane forests (Bates 1978, Hoover 1990b, 1998; Hoover et. al. 2000) and, to such a degree, that the genus may be an indicator of overall floristic diversity. In these notes we identify the number of *Begonia* species per section and their geographical distribution in SE Asian countries.

Methods

Counts for number of species per country, region or island were initially evaluated from Barkley's (1972) list, and then updated from Doorenbos et al. (1998) sectional assignment (Table 1), although Sands regards the total number of species per country as low (Sands, pers. comm). More detailed figures for the Flora Malesiana region can be found in Sands (2001).

Botanical exploration of Indonesian montane forests and the Frieda River, West Sepik, Papua New Guinea area involved standard herbarium specimen acquisition and data recording. The first set of specimens were deposited within the countries of origin, a second set of duplicates were deposited with Harvard University Herbarium (HUH) with additional duplicate sets distributed to different herbariums by HUH. Due to great species variation in *Begonia,* often up to 10 duplicates were collected, thus providing many specimens for taxonomic specialists. Determinations have not been made on most of these collections, though many West Javan collections are believed to be identified correctly.

Accessing the remaining montane forests covering volcanoes in Indonesia involved determining which roads lead to the highest point on the mountain, hiking a couple of hours through agricultural land until reaching forest, which often was disturbed, especially in West Java Province. Sumatran and Sulawsian lower montane forests were generally not disturbed. Hunting trails network these forests. Local guides lead collectors to trails that were close to streams so there would be a higher probability of finding *Begonia*. Roads leading to the higher elevations generally stopped at 1000m. Collectors would usually hike another 200m until reaching forest, and spend the rest of the morning and early afternoon collecting from roughly 1200 to 2000m, depending upon the mountain. For safety reasons, collecting always stopped around 2:00pm.

Collecting at the Frieda River involved working at the Carpentaria Exploration Base Camp, located at approximately 4°35'S/142°E. Access to the remote, low elevation stream valleys was accomplished through use of the mining companies helicopter. Three weeks were spent conducting botanical exploration at the approximately 25 km^2 gold and copper exploration site. Collection sites were identified by geologist Ron Britten based on different soil conditions. Dr. Ted Henty of the Lae Forestry Department suggested that we conduct the general botanical exploration of the Frieda site because of its unusual flora, stating he had visited the site briefly and observed that floristic composition was more like that of lower montane forests even though elevation ranged generally from 400–1000m.

Results

The 18 sections of SE Asian *Begonia* include about 576 species. 94.6% of the species were placed in 6 sections, in order of size: *Petermannia* (189), *Diploclinium* (133),

Table 1. Taxonomic sections of SE Asian *Begonia*: Estimated numbers (and percentages) of species from different geographic areas.

Section	Indian region*	China with Taiwan	Malaysia (Peninsular)	Indochina region*	Myanmar (Burma)	Philippines	New Guinea* region	Borneo*	Sumatra	Java	Sulawesi (Celebes)	Worldwide Total species/ section
Alicida					3							3
Apterobegonia					1							1
Baryandra						1						1
Bracteibegonia									2			2
Coelocentrum		12										12
Diploclinium	19 (14.3)	39 (29.3)	2 (1.5)	11 (8.3)	4 (3.0)	36 (27.1)	9 (6.8)	6 (4.5)				133
Haagea	1											1
Heeringia			1									1
Lauchea					2							2
Monophyllon			1									1
Monoptera	2											2
Petermannia			5 (2.6)	1 (.53)		59 (31.2)	55 (29.1)	40 (21.2)	12 (6.4)	4 (2.1)	13 (6.9)	189
Platycentrum	25 (22.7)	45 (40.9)	21 (19.1)	4 (3.6)	6 (5.5)	4 (3.6)		1 (0.91)				110
Putzeysia	1											1
Reichenheimia	4 (9.3)	7 (16.3)	5 (11.6)	6 (14.0)	2 (4.7)			3 (7.0)	6 (14.0)	5 (11.6)	5 (11.6)	43
Ridleyella			2									2
Parvibegonia	5 (13.9)	2 (5.6)	10 (27.8)	9 (25)	7 (19.4)						3 (8.3)	36
Sphenanthera	7 (19.4)	6 (16.7)	2 (5.6)	4 (11.1)	2 (5.6)	2 (5.6)	1 (2.8)					36
Total number of species	64	111	49	35	29	102	65	50	30	15	26	576

*Indian region includes India, Nepal and Sri Lanka. Indochina Region includes Cambodia, Laos, Thailand and Vietnam. New Guinea region includes Papua, New Guinea, Irian Jaya and Solomon Islands. Borneo includes Kalimantan and Malaysian Sarawak and Sabah, plus Brunei.

Platycentrum (110), *Reichenheimia* (43), *Sphenanthera* (36), and *Parvibegonia* (36) (Table 1). The first three sections accounted for 74.7% and the latter three sections representing 19.9%. The 12 minor sections include 31 species. The few species not assigned to sections are excluded from tabulations.

South-East Asian sections have distinct geographical distribution patterns (Table 1). In *Petermannia,* 154 species representing 81.5% of the section are observed in the Philippines, New Guinea and Borneo. The remaining 35 species are distributed between Sulawesi, Sumatra, Peninsular Malaysia, Java and Indochina region, while no species of *Petermannia* were collected in Myanmar, China or the Indian region. *Diploclinium* is concentrated primarily in China, with 39 species (29.3%), and The Philippines, with 36 species (27.1%). Nineteen species (14.3%) are observed from the Indian region; these three geographical areas account for 70.7% of this section's distribution. The remaining species of this section are somewhat equally distributed between the Indochina region, New Guinea region, Sumatra, Borneo, Myanmar and Peninsular Malaysia. No species of *Diploclinium* have been described from Java or Sulawesi, though several unidentified species of this section may have been observed on these islands (Hoover 1995, 1998). The section *Platycentrum* is predominately of mainland distribution, having 82.7% of the section distributed between China (45 species, 40.9%), Indian region (25 species, 22.7%) and Peninsular Malaysia (21 species, 19.1%). Small numbers of species are observed in Myanmar, Indochina region, The Philippines, Sumatra, Borneo and Java, with no species in this section found in the New Guinea region or Sulawesi

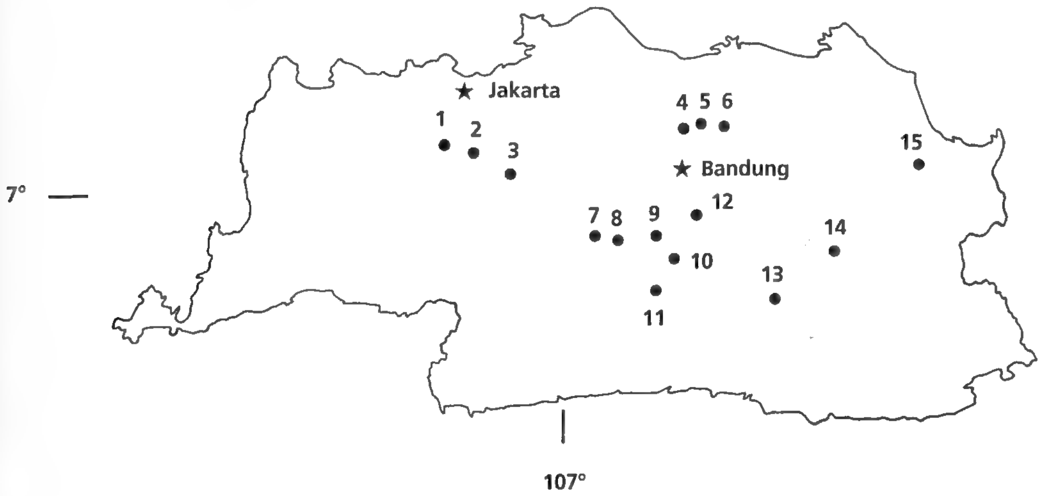
The sectional distributions of *Reichenheimia* and *Sphenanthera* indicate no single country, region or island is represented by more than 20% of their respective species. *Reichenheimia* is distributed throughout SE Asia, with no species found in the Philippines or New Guinea region. *Sphenanthera* is distributed somewhat equally among the India and Indochina regions, Java, Sulawesi and China, with a few species found in Peninsular Malaysia, the Philippines, New Guinea region and Sumatra. *Parvibegonia* is primarily a mainland Asian section, with 3 species observed in Sulawesi. Our team may have recently collected one or 2 species of *Parvibegonia* on Java (pers. comm., Tebbitt), possibly being the first collections of this section from Java.

Table 2 lists the number of *Begonia* collections our team has made in SE Asia since the late 1970's. Figures 1–4 indicate the geographical locations for field work in Indonesia. Appendix 1 provides detailed information on each of the mountains we explored in Indonesia.

Table 2. Hoover and team's SE Asian *Begonia* field collections.

Country/year of expedition & duration	No. of collections	No. of estimated species
Papua New Guinea Nov. 1977–Mar. 1978	84	46
Thailand Jan.–Feb. 1990	32	14
Peninsular Malaysia March 1990	31	10
Sumatra, Java, Bali, Indonesia Jan.–Mar. 1995	36	17
Sumatra, Sulawesi, Java, Indonesia Feb.–Apr. 1998	53	20
Java, Indonesia Feb.–Mar. 2000	138	13
West Java Province, Indonesia Apr.–May 2001	85	9
Total	459	N.A.

Several field observations appear relevant to the geography of *Begonia* in these countries. It appears the most common and geographically widespread species in Indonesia are found at the lower to middle elevations, exemplified by the following: *Begonia isoptera* Dry, *B. multangula* Blume, *B. longifolia* Blume, and possibly *B. muricata* Blume. The taxonomy of these common species may be difficult due to local variation. As species characteristics are not stable, taxonomic confusion exists as noted by many botanists observing *Begonia* in the field. As elevation increases, endemism seems to be more prevalent and individual species morphological characteristics appear more stable and more clearly defined. Individual mountains at the upper elevational limits for *Begonia* (about 1800–2000m) may harbour endemic species particular to an individual mountain or a group of adjacent mountains. Sections *Sphenanthera* and *Petermannia* appear to include the most endemic species in Java and Sumatra. Species that may be new appear to be local endemics whose populations are restricted in size as well. Local endemics are found in small populations along stream margins or less frequently along ridges and forest areas between streams. The more common species of *Begonia* have been identified with reasonable certainty, but less common species remain unidentified. A number of species photographed in Sumatra and Sulawesi on the reconnaissance expeditions did not appear to be represented by any collection in the Bogor or Harvard University Herbariums. This does not mean they may not be represented in European Herbariums.



Map Legend

1. Mt. Salak
2. Mt. Pangrango
3. Mt. Gede
4. Mt. Burangrang
5. Mt. Tangkubanperahu
6. Mt. Bukittunggu
7. Mt. Patuha
8. Mt. Waringin
9. Mt. Tilu
10. Mt. Windu
11. Mt. Kancana
12. Mt. Malabar
13. Mt. Cikuray
14. Mt. Telagabodas
15. Mt. Ciremay

Fig. 1. *Begonia* exploration site in West Java. Indonesia.

At the Frieda River, West Sepik, Papua New Guinea, *Begonia* was highly diversified with seemingly local *Petermannia* endemics, ranging between 400 –1000m. The 25 km2 Carpentaria exploration site received an average of 550 inches of rainfall per year, data accumulated over the duration of the site's existence, which was first explored by geologists in 1968. The three weeks of fieldwork allowed Hoover to explore an estimated 60% of the larger streams at the site, thus offering a reasonably good opportunity for examining the distribution of *Begonia*. An estimated 20 species of *Begonia* were collected at the Frieda River area, with only one species of *Platycentrum* being common, and that was at the uppermost elevations between 800 to 1200m. Furthermore, the species occurred as a vine or an epiphyte growing to several meters along tree trunks, characteristics that were not exhibited in the other begonias at Frieda. Only one or two of the Frieda River species were observed elsewhere in Papua. *Platycentrum* species are not generally distributed in New Guinea (see Table 1). Except

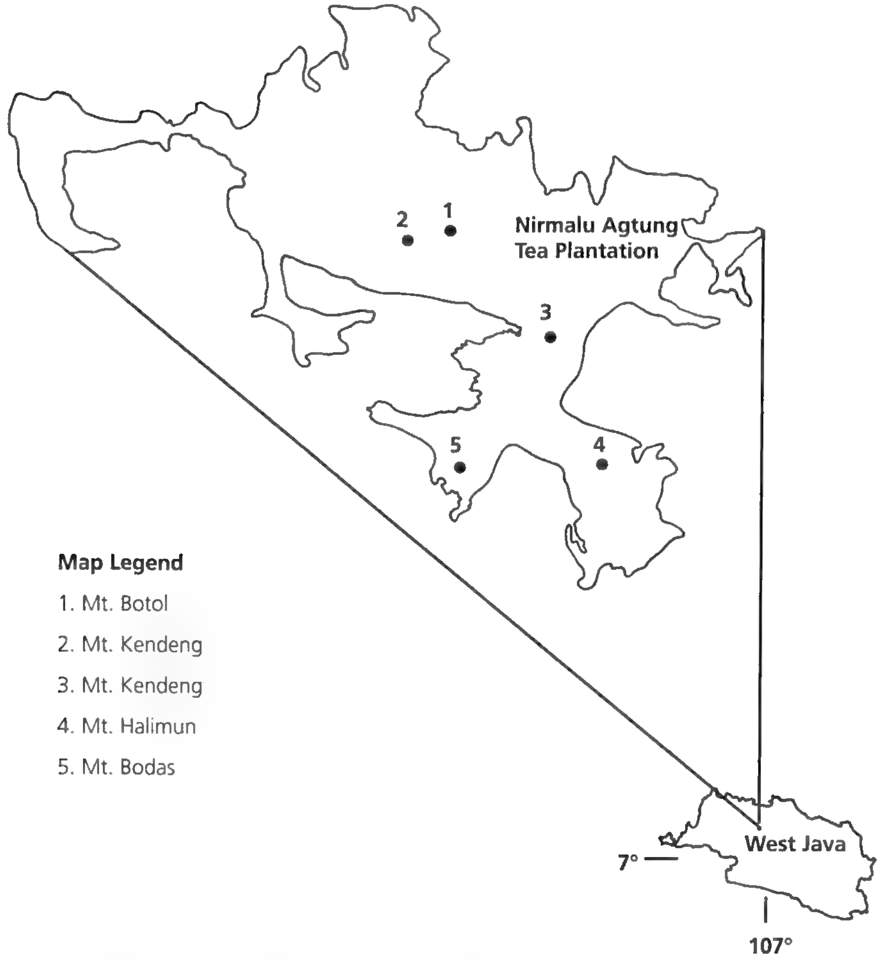


Fig. 2. *Begoina* expolration sites in Halimun National Park, West Java, Indonesia.

for the common *Platycentrum*, the distinct impression resulting from observations on Frieda River *Begonia* was that individual species appeared limited to a single population or to several, with each local population consisting of a few individual plants or small colonies. Over an elevational range of usually several hundred meters along streams, one could observe between four to six different species per stream. Individual streams had different *Begonia* species compositions, even when streams were adjacent or within close proximity to one another. This *Begonia* species diversity is the highest Hoover has ever observed in a small geographical area, though similar high-density species diversities among *Piper*, *Anthurium* and *Philodendron* in Carchi and Esmeraldes Provinces, Ecuador were observed. Croat (pers. comm.) has made similar observations for these genera of the Araceae in Western Colombia and Ecuador as well.

1. Mt. Siluatan
2. Mt. Lubukrya
3. Mt. Malintang
4. Mt. Ophir
5. Mt. Singgulang
6. Mt. Merapi
7. Mt. Talang
8. Mt. Patiacermin
9. Mt. Kerenci
10. Mt. Sumbing
11. Mt. Seblat
12. Mt. Keba
13. Mt. Dempo
14. Mt. Nani
15. Mt. Pugnug
16. Mt. Sekkau
17. Mt. Ulusabak
18. Mt. Tanggamus
19. Mt. Ratai

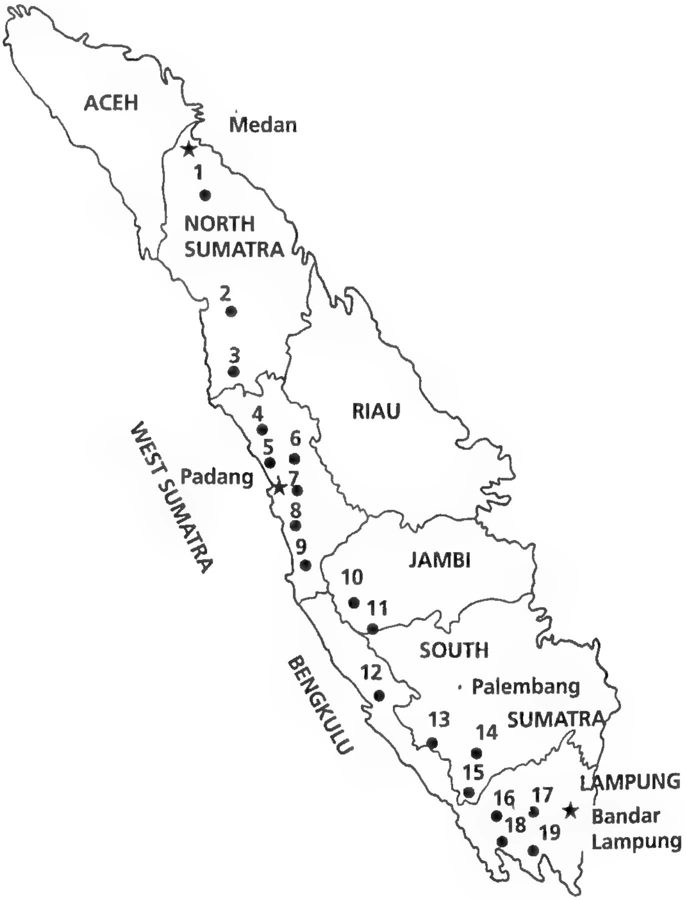


Fig. 3. Exploration sites in Sumatra, Indonesia.

Discussion

Most SE Asian begonias were collected in the past from lower elevations when forest cover was nearer its original size. The logistics required to do botanical collecting in lowland tropical forest during the 1800's to early 1900's was difficult enough, without trying to reach mountain forests large distances away along steep slopes. Deforestation has provided the unfortunate benefit in modern times of access to some montane forests, though not without considerable logistical effort. Montane forests of Java, Sumatra and Sulawesi are restricted to about 280 mountains over 1500m (unpublished data). Few of these mountains appear to have been explored scientifically.

Field observation on *Begonia* in lower montane forests of Indonesia and Papua New Guinea indicate species prefer stream margin habitats. And the steep, rocky embankments directly above streams are the habitats preferred over forest slope areas or mountain ridges. When undertaking field expeditions to collect *Begonia*, the decision was made to search out streams along elevational gradients. Stream margins are subject to regular disturbances caused by rise and fall of water level in the stream.

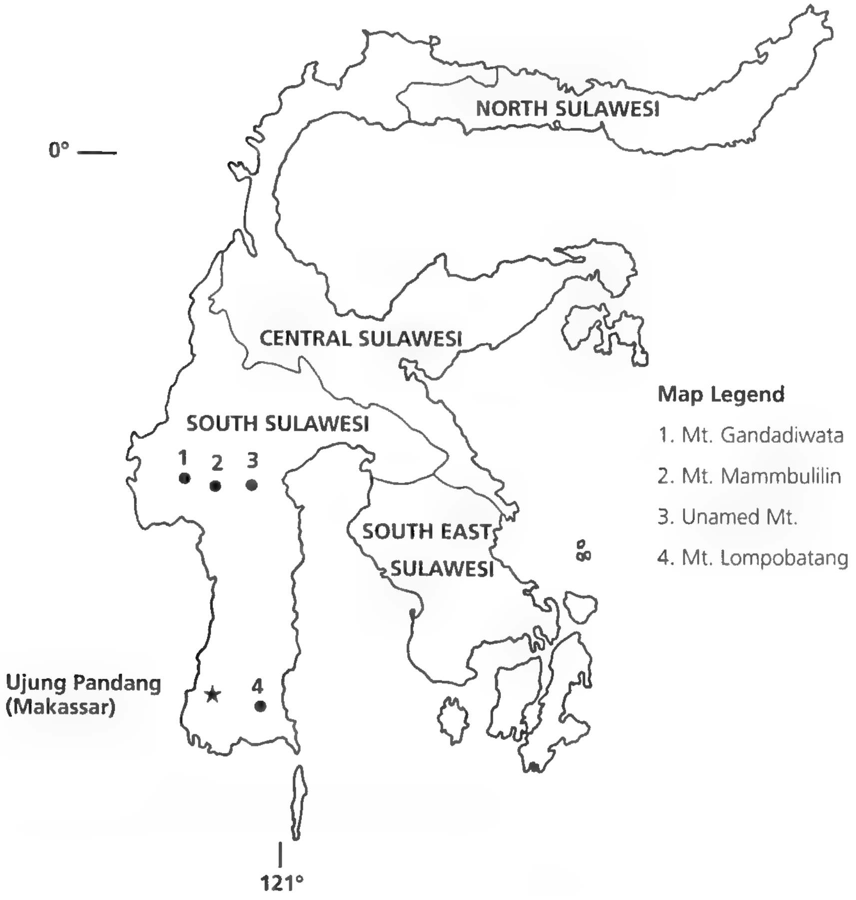


Fig. 4. *Begonia* exploration sites in Sulawesi, Indonesia.

A line of vegetation is frequently observed along stream banks, due to rainfall running off mountain slopes, filling streams and stripping the vegetation off embankments. It is also observed that light ranges from deep shade to sunny gaps along streams. These light gaps appear to be microhabitats being places where a stream levels out forming a pool or where a small flattened area is found along the mountain slope, allowing running water to spread out over a larger area, or where pools form at the base of larger waterfalls. Gaps, of course, are observed where trees fall across streams opening the canopy.

This constancy and variation of habitat disturbance, both from water and light, may be relevant to understanding high species diversity in the genus. Though not directly applicable to *Begonia* species diversity, but possibly relevant, is the "intermediate disturbance hypothesis" tested by Molino and Sabatier (2001) for tropical forest trees on Barro Colorado Island, Panama. Patch size, tree fall gaps are recognised to cause disturbance in tropical forests and are believed to harbour a greater diversity of plants than in surrounding forest. *Begonia* appears to colonise disturbed habitats in natural forest as well as along roadside embankments in lower montane forest. Could the constant disturbance of *Begonia*s environment be part of the cause for the genus being so diverse?

Having observed dozens of streams and their vegetation in lower montane tropical forests of SE Asia, the impression is that light gaps along streams are pockets of higher plant diversity than stream areas without gaps. Light gaps along streams appear to be more diverse than in forests on slopes or ridges. If indeed such an observation were confirmed through data collecting, the explanation might well be the same as for higher plant diversity caused by tree fall gaps. Unlike tree fall gaps, light gaps along streams are much older, having natural histories based on geomorphic time scales. After volcanic eruptions, streams begin to erode mountain slopes and plant colonisation begins. Some of these stream habitats may indeed be quite ancient. One often observes the same herbaceous plant groups colonising these light gaps along streams: Aroids, *Begonia*, ferns, Gesneriads (particularly *Cyrtandra*), to name a few common groups.

Field observations and herbarium specimens indicate many species of *Begonia* are local or regional endemics. Though fieldwork in the ultra-wet Frieda River was limited to the Carpentaria Site, it appeared the entire area was dominated by local endemics. In Indonesia, endemism seems to be at the regional level with individual species distributed on several mountains, often adjacent to one another. Endemic species also seem to have very narrow elevational ranges. An observation by van Steenis (1969) adds perspective to issues regarding tropical plant species endemism. "This leads me to conclude that endemic, and even, local-endemic, species in the Malesian tropics must be defined as 'species that have not yet been found elsewhere', expressing thereby that exact floristic knowledge of distribution is hard, if even possible, to attain in tropical forest." *Begonia* will continue to offer many surprises.

Acknowledgments

We are always grateful to the Bogor Herbarium and LIPI for extending us the opportunity to obtain permits and work in Indonesia. Rizali Indrakasuma and the Consulate General's Office in New York have been most helpful over the years and we thank them for their efforts.

Much appreciation is extended to the American Begonia Society for grants supporting our expeditions. Though it is not possible to list all our ABS patrons we extend special thanks to Gene and Ann Salisbury, Tim and Thelma O'Reilly, Tom Keepin and friends, Howard and Barbara Berg and Peter and Carol Notares.

Though Dr. Peter Ashton is not responsible for any conclusions or opinions drawn in these notes, none of this would have been done without his prompting, for which we are most grateful. The patience and assistance of Bob Cook, John Burly, David Middleton, and the Harvard University Herbarium staff is most appreciated.

Hoover wishes to acknowledge his respect for Dr. Bernice Schubert, her scholarly work on *Begonia* and her viewpoints regarding the value of taxonomy.

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Appendix 1. Indonesian mountains explored or exploration attempted by Hoover, Hunter and Wiriadinata.

Island Name of mountain Province	Lat./long. & elevation (m)	Date climbed or attempt made	Approximate elevation reached (m)/% of mtn ht	No. of *Begonia* species observed ^{A} or collected^B	Notes and impressions
SUMATRA					
Mt. Lubukraya N. Sumatra	1°28'N/ 101°10'E 1886	3/19/95	1500/80%	3^A	Quite dry. Upper 2/3s of mtn forested
Mt. Singgalang W. Sumatra	0°20'S/ 100°2'E 2877	3/17/95 1/3–2/13/98	2200/77%	7^A	2 new species likely collected. Upper half of mtn forested
Mt. Merapi W. Sumatra	0°42'S/ 100° 18'E 2891	3/24/95 2/11–2/18/98	2200/73%	6^A	3 new species likely collected. Upper half of mountain forested, mild volcanic activity causing deforestation on upper 10% of mtn
Mt. Talang W. Sumatra	1°13'S/ 101° E 2599	3/26/95	2200/85%	2^A	1 new species likely Upper 2/3s of mtn forested
Mt. Patiacermin W. Sumatra	1°28'S/ 101° 12'E 2690	1/27/98	1300/47%	4^A	3 new species likely collected. Upper half of mtn forested Remote
Mt. Kerlnchi Jambi	1°45'S/ 101° 20'E 3800	3/14/95 1/26/98	2350/63%	7^A	4 new species likely collected. Large tea plantation covering lower half of mtn, national park on upper half
Mt. Keba Bengkulu	3°28'S/ 102° 30'E 1983	3/12/95 1/23/98	1500/76%	3^A	1998 trip a new road to top of mtn. Mild volcanic activity causing deforestation on upper 25% of mtn
Mt. Dempo Sumatra	4°25'S/ 103°10'E 3159	3/10/95% 1/19–21/98S	2000/76%	4^A	1 new species likely collected. Large tea plantation covering lower half of mtn

Island Name of mountain Province	Lat./long. & elevation (m)	Date climbed or attempt made	Approximate elevation reached (m)/% of mtn ht	No. of *Begonia* species observed ^{A} or collected^{B}	Notes and impressions
Mt. Sekkau Lampung	5°55'S/ 104°18'E 1718	1/18/98	1500/88%	1 ^{A}	Considerable deforestation at upper elevations from coffee plantations
Mt. Tanggamus Lampung	5°30'S/ 104°37'E 2102	1/16/98	1300/61%	-	Quite dry
Mt. Ratai Lampung	0°10'S/ 105°15'E 1681	3/4/95	1600/60%	2^{A}	Rice fields to 75% of mtn
JAVA					
Mt. Botol W. Java	6°42'S/ 106°28'E 1785	3/3–20/00	1785/100%	3^{B}	Tea plantation to mid elevations and expanding into nat. park
Mt. Kendeng W. Java	6°43'S/ 106°27'E 1867	3/3–20/00	1867/100%	2^{A}	Entire mtn forested. One possible new species collected
Mt. Kendeng W. Java	6°46'S/ 106°31'E 1764	3/3–20/00	1764/100%	3^{B}	Entire mtn forested
Mt. Halimun-South W. Java	6°50'S/ 106°31'E 1744	4/15/01	1046/60%	4^{B}	Very steep mountain
Mt. Bodas W. Java	6°52'S/ 106°28'E 966	4/17/01	862/89%	4^{A}	Forest still intact
Mt. Salak W. Java	6°28'S/ 106°35'E 2211	2/22–24/00	1775/81%	5^{B}	1 new species likely collected Upper 1/3 of mtn forested

Island Name of mountain Province	**Lat./long. & elevation (m)**	**Date climbed or attempt made**	**Approximate elevation reached (m)/% of mtn ht**	**No. of *Begonia* species observed ^{A} or collected^{B}**	**Notes and impressions**
Mt. Pangrango W. Java	6°45'S/ 106°52'E 3018	4/11/01	1569/52%	3^{A}	Rich forest, undisturbed at upper elevations
Mt. TalagWarna W. Java	(Pangrango complex)	4/11/01	1569/52%	4^{B}	Very disturbed throughout mtn complex
Mt. Gede W. Java	6°25'S/ 106°50'E 2958	4/3/95	1400/47%	4^{B}	Top 25% of mtn still forested
Mt. Burangrang W. Java	6°48'S/ 107°33'E 2064	3/10/01 3/26/01	1723/84%	3^{A}	Quite dry
Mt. Tangkubanperahu W. Java	6°49'S/ 107°34'E 207	3/27/01	1877/90%	2^{A}	Quite dry
Mt. Bukittunggu W. Java	6°49'S/ 107°44'E 2205	3/28/01	1754/80%	1^{A}	Quite dry
Mt. Patuha W. Java	7°15'S/ 107°17'E 2434	2/11–16/00 3/14/01	2277/94%	3^{B}	1 new species likely collected. Tea plantation covers 2/3 of mtn
Mt. Puncak W. Java	(Mt. Patuha complex)	2/16/00 3/14/01	2000/80%	1^{B}	1 new species likely collected. Only very top ~50m forested; encroached by tea plantation
Mt. Ranca Upas W. Java	(Mt. Patuha complex)	3/6/00 3/15/00	1700	5^{B}	2 possible new species
Mt. Triangularis W. Java	(Mt. Patuha complex)	3/6/00 3/15/00	1900	2^{B}	Part of volcanic crater rim

Island Name of mountain Province	Lat./long. & elevation (m)	Date climbed or attempt made	Approximate elevation reached (m)/% of mtn ht	No. of *Begonia* species observed ^{A} or collected^B	Notes and impressions
Mt. Cadaspang W. Java	(Mt. Patuha complex)	3/6/00 3/15/00	1900	2^B	Part of volcanic crater rim
Mt. Kawahputih W. Java	(Mt. Patuha complex)	3/6/00 3/15/00	1800	2^B	Part of volcanic crater rim
Mt. Kolotok W. Java	(Mt. Patuha complex)	3/6/00 3/15/00	1800	1^B	Part of volcanic crater rim
Mt. Tikulur W. Java	(Mt. Patuha complex)	3/6/00 3/15/00	1900	2^B	Part of volcanic crater rim
Mt. Waringin W. Java	7°10'S/ 107°25'E 2140	4/9/01	1846/86%	3^B	New logging near upper slopes
Mt. Tilu W. Java	7°12'S/ 107°31'E 2040	4/8/01	1508/74%	3^B	Very rich forest; undisturbed
Mt. Windu W. Java	7°14'S/ 107°42'E 2054	4/7/01	1539/75%	3^B	New agriculture on upper slopes
Mt. Abig W. Java	(Mt. Kancana complex)	4/7/01	1939/89%	2^B	Encroaching tea plantation
Mt. Kancana W. Java	7°18'S/ 107°35'E 2182	4/8/01	1939/89%	2^B	Encroaching tea plantation
Mt. Malabar W. Java	7°07'S/ 107°38'E 2321	4/9/01	\1908/82%	4^B	Well preserved, montane forest intact
Mt. Merapi Central Java	7°28'S/ 110°22'E 2911	4/5/95 3/20/00	1000 1200	3^B	2 tuberous species collected

Island **Name of mountain** **Province**	**Lat./long. & elevation (m)**	**Date climbed or attempt made**	**Approximate elevation reached (m)/% of mtn ht**	**No. of *Begonia* species observed [A] or collected[B]**	**Notes and impressions**
Mt. Lawu Central Java	7°25'S/ 111°10'E 3265	4/7/95	1900	2[B]	1 new tuberous species collected
Mt. Cikuray W. Java	7°19'S/ 107°52'E 2821	3/22/01	1939/69%	3[A]	Rich forest, wet
Mt. Telagabodas W. Java	7°09'S/ 108°03'E 2201	3/21/01	1692/77%	2[A]	Very disturbed forest
Mt. Pasripis W. Java	(Telagabodas complex)	3/20/01	1754/80%		Very disturbed forest
Mt. Ciremay W. Java	6°58'S/ 108°26'E 3078	3/24/01	11415/46%	2[A]	Forest intact from 1200m to top of mountain
SULAWESI					
Mt. Gandadiwata S.E. Sulawesi	3°15'N/ 119°30'E 2382	3/4/98	1388/58%	2[A]	Forest intact, undisturbed
Mt. Mammbulilin S.E. Sulawesi	2°55'N/ 119°275'E 2865	3/5/98	1839/64%	2[A]	Forest intact, undisturbed

Island Name of mountain Province	Lat./long. & elevation (m)	Date climbed or attempt made	Approximate elevation reached (m)/% of mtn ht	No. of *Begonia* species observed [A] or collected[B]	Notes and impressions
Unnamed mt. S.E. Sulawesi	2°59′N/ 121°52′E 1916	3/12/98	1420/74%	2[A]	New road being constructed on lower slope of mtn from Mamasa to Ramtapo
Mt. Lompobatang S.E. Sulawesi	5°45′N/ 119°58′E 2871	3/1/98	1613/56%	1[A]	Upper half of mtn forested
LOMBOK					
Mt. Rijani	8°28′S/ 116°39′E 3726	4/23/01	1169/31%	5[A]	Dry forest: well preserved

A new species of *Agrostis* (Poaceae) endemic to Tasmania

D.I. Morris

Abstract

Morris D.I. (Tasmanian Herbarium, Hobart, Tasmania 7000 Australia) 2004. A new species of Agrostis *(Poaceae) endemic to Tasmania.* Telopea *10(3): 765–767.* **Agrostis diemenica** is newly described and illustrated. It is endemic to Tasmania, and has previously been known as *Agrostis* aff. *australiensis.*

Introduction

When the section on *Agrostis* was being prepared for Part 4B of *The Student's Flora of Tasmania* (Curtis and Morris 1994) a number of specimens were found which did not fit the descriptions of any named species. These, all regarded as native, were described under various 'aff.' names. Of these, aff. *hiemalis*, aff. *parviflora* and aff. *scabra* have now been included in the four species described by Jacobs (2001). A fourth, dsignated aff. *australiensis*, is here described as a new species.

Agrostis diemenica *D.I. Morris* **sp. nov.**

A. australiens Mez. similis sed lamina folii plana, usque ad 2 mm latam, lemmate 2–2.5 mm longo, antheris 0.5–1.6 mm longis differt.

Holotype: AUSTRALIA: Tasmania: Lake 1/2 km NW of Second Bar Lake (41°47'S 146°31'E), *A. Moscal 6946*, 12 Mar 1984 (HO 100671). (Fig. 1)

Loosely tufted glabrous perennial up to 35 cm high. Leaf sheaths ribbed, becoming loose; ligules 1–3 mm long, membranous, truncate, entire or shortly erose; blades flat, often becoming involute distally, up to 12 cm long and 2 mm wide, subsmooth to scaberulous on both surfaces. Culms smooth, sometimes scaberulous below the panicle. Panicle up to 10 cm long, at first partially enclosed in the uppermost leaf-sheath, later exserted, branches whorled or binate at the lower nodes, upper nodes binate, ± stiffly spreading, bare in the proximal half, few-flowered, the spikelets loosely arranged at the tips of the secondary branches. Spikelets purplish, occasionally green. Glumes subequal to unequal, acute, keels scabrous; lower glume 2–3 mm long, upper glume 1.75–2.75 mm long. Lemma shorter than to shortly exceeding the glumes, 2–2.5 mm long, the nerves obscure or purplish and obvious. Palea minute. Callus minutely bearded. Anthers 0.5–1.6 mm long Caryopsis c. 1.25 mm long.

This is the *A.* sp. aff. *australiensis* Mez. described in *The Students Flora of Tasmania* (Curtis & Morris 1994), and recorded in *A Census of the Vascular Plants of Tasmania* (Buchanan 1999).

Habitat: edges of lakes, marsh or streams, seepage areas and damp areas in open situations.

Distribution: Central Highlands and Mount Field National Park at altitudes between 900 and 1350 metres. (Fig. 2)

Etymology: from Van Diemens Land, an early name for Tasmania.

Fig. 1. Photograph of holotype of *Agrostis diemenica*.

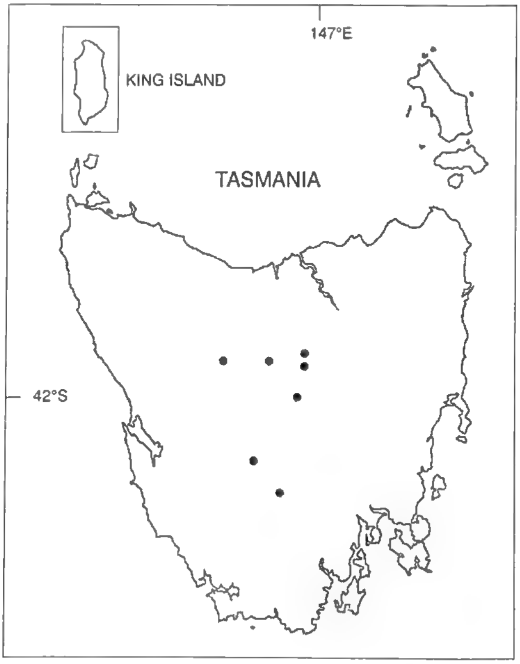

Fig. 2. Map of distribution of *Agrostis diemenica* in Tasmania.

Selection of specimens examined: Tarn, Wombat Moor, National Park, *O. Rodway 101*, 26 Mar 1922 (CANB 1097-1); Mother Lords Plains, *A. Moscal 585a*, 2 Feb 1981 (HO 58896); St Patricks Plains, *A. Moscal 6540*, 28 Feb 1984 (HO 100440); Wild Dog Tier, *A. Moscal 6848*, 9 Mar 1984 (HO 99281); close to the summit of Wylds Craig, *P. Collier 4613*, 3 Mar 1990 (HO 142895).

Conservation status: apart from the Mother Lords Plains and St Patricks Plains specimens, which are in highland grazing areas, all specimens are in National Parks or Conservation Areas.

Acknowledgments

My thanks are due to Surrey Jacobs (NSW)and to Austin Brown, Department of Primary Industries, State Chemistry Laboratory, Werribee, for examining and commenting on this problem group and especially to Surrey for allowing me to see his draft of a key to the genus to be used in the *Flora of Australia*. Thanks also to Lyn Cave for the preparation of Figures 1 and 2.

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SHORT COMMUNICATION

New combinations in *Eurycaulis* and *Ceraia* (Orchidaceae: Dendrobiinae), and corrections to Clements (2003)

M.A. Clements

There are some errors in Appendix 2 of Clements (2003), concerning taxonomic and nomenclatural changes, that I correct here.

Eurycaulis lucens *(Rchb.f.)M.A.Clem.*, **comb. nov.**

Basionym: *Dendrobium lucens* Rchb.f., *Bot. Zeit. (Berlin)* 21: 128 (1863).

Synonyms: *Anisopetala lucens* (Rchb.f.)M.A.Clem., *Telopea* 10(1): 283 (2003), *nom. inval. Eurycaulis lucens* (Rchb.f.)M.A.Clem., *Telopea* 10(1): 287 (2003), *nom. inval.* Combinations invalid under ICBN, Art 34.2 as both were published in the same article based on *Dendrobium lucens* Rchb.f.

Ceraia pseudoequitans *(Fessel et Lückel)M.A.Clem.*, **comb. nov.**

Basionym: *Dendrobium pseudoequitans* Fessel et Lückel, *Die Orchidees* 51(1): 83–85, t. (2000).

Synonyms: *Aporum pseudoequitans* (Fessel et Lückel)M.A.Clem., *Telopea* 10(1): 296 (2003), *nom. inval. Ceraia pseudoequitans* (Fessel et Lückel)M.A.Clem., *Telopea* 10(1): 293 (2003), *nom. inval.* Combinations invalid under ICBN, Art 34.2 as both were published in the same article based on *Dendrobium pseudoequitans* Fessel et Lückel.

Page 283: *Anisopetala lucens* — see *Eurycaulis lucens* (Rchb.f.)M.A.Clem.

Page 287: *Eurycaulis lucens* — see *Eurycaulis lucens* (Rchb.f.)M.A.Clem

Page 287: *Eurycaulis panduriferus* — should read *Eurycaulis pandurifer* (Hook.f.)M.A.Clem.

Page 287: *Eurycaulis peralu* — should read *Eurycaulis perula* (Rchb.f.)M.A.Clem., comb. nov. Basionym: *Dendrobium perula* Rchb.f, …

Page 288: *Eurycaulis undulatus* (Lindl.)M.A.Clem. — should read *Eurycaulis undulatus* (Blume) M.A.Clem. — treated as a bibliographic error of citation so the combination is still valid according to ICBN, Art. 33.4.

Page 290: Basionym: *Epidendrum carinatum* L., *Sp. Pl.* 1350 (1753). — should read *Epidendrum carinatum* L., *Sp. Pl.* 953 (1753).

Page 290: *Ceraia confunda* — should read *Ceraia confundens* (Kraenzl.)M.A.Clem.

Page 291: *Ceraia hypopoga* — should read *Ceraia hypopogon* (Kraenzl.)M.A.Clem.

Page 292: *Ceraia lagara* (Schltr.)M.A.Clem. — should read *Ceraia lagara* (Seidenf.)M.A.Clem. — treated as a bibliographic error of citation so the combination is still valid according to ICBN, Art. 33.4.

Page 292: *Ceraia lamatochila* — should read *Ceraia lomatochila* (Seidenf.)M.A.Clem., comb. nov. Basionym: *Dendrobium lomatochilum* Seidenf., …

Page 293: *Ceraia pseudoequitans* — see *Ceraia pseudoequitans* (Fessel et Lückel)M.A.Clem.

Page 295: *Aporum confusum* (Schltr.)M.A.Clem., comb. nov. — should read *Aporum confusum* M.A.Clem., ***nom. nov***. Basionym: *Dendrobium confusum* Schltr., *Repert. Spec. Nov. Regni Veg*. 10: 72-73 (10 Nov.1911), *non* J.J.Sm. (Mar.1911).

Page 296: *Aporum pseudoequitans* — see *Ceraia pseudoequitans* (Fessel et Lückel)M.A.Clem.

Acknowledgment

I thank Katherine Challis at Kew for drawing these to my attention.

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Additions to the lichen flora of Fiji and Vanuatu based on Graphidaceae in the F.R.M. Wilson collection at the National Herbarium of New South Wales

Alan W. Archer

Abstract

Alan W. Archer (Royal Botanic Gardens, Mrs. Macquaries Road, Sydney, NSW 2000, Australia) 2004. Additions to the lichen flora of Fiji and Vanuatu based on Graphidaceae in the F.R.M. Wilson collection at the National Herbarium of New South Wales. Telopea *10(4): 771–776.* Six species in the family Graphidaceae are added to records of the lichen flora of Fiji, and 12 species in the same family are added to records of the lichen flora of Vanuatu. A key to identification is provided. All the specimens are from the Wilson lichen collection at NSW.

Introduction

The recent *Catalogue of the Lichens of the Smaller Pacific Islands* (Elix & McCarthy 1998) lists one taxon in the family Graphidaceae from Vanuatu, viz: *Graphis assimilis* f. *ochracella* Räs., and three species in the family from Fiji, viz: *Graphina insulana* Müll. Arg., [= *G. subserpentina* (Nyl.) Müll. Arg.], *Graphis fagorum* (A. Massal.) Kremp. and *Phaeographina heterocarpoides* (Nyl.) Zahlbr.

The Reverend Francis R.M. Wilson collected lichens in Fiji and Vanuatu in 1892, and again in 1895 in Vanuatu when he visited his son-in-law T.W. Leggatt (Ralston 2001). The Wilson collection also includes specimens sent to him in Australia by Leggatt from Mallecola [Malekula], Vanuatu. A recent examination of this collection, housed at NSW, has found it to include six species in the family Graphidaceae previously unreported from Fiji, and 12 species previously unreported from Vanuatu. The species are here listed and briefly described.

Key to the Wilson Graphidaceae from Fiji and Vanuatu

1 Ascospores hyaline 6
Ascospores pale brown or brown 2

2 Ascospores muriform, 45–110 µm long .... **Phaeographina quassiicola**
Ascospores with linear, lenticular locules 3

3 Ascospores 4-locular, 16–20 µm long, lichen compounds absent .... **Phaeographis tremulans**
Ascospores 5–9-locular, 16–37 µm long 4

4 Lirellae immersed in conspicuous stroma, ascospores 16–20 µm long, norstictic acid present .... **Sarcographa intricans**
Lirellae not immersed in stroma 5

5 Stictic acid present .... **Phaeographis dendroides**
Lichen compounds absent .... **Phaeographis exaltata**

6 Ascospores with linear, lenticular locules, exciple carbonised or not 12
Ascospores muriform, exciple uncarbonised 7

7 Ascospores < 20 μm long, lirellae closed 8
Ascospores > 20 μm long, lirellae open or closed 9

8 Lirellae conspicuous, ascospores 11–16 μm long; salazinic acid present .... **Graphina colliculosa**
Lirellae inconspicuous, ascospores 9–16 μm long, norstictic acid present .... **Graphina dimorphodes**

9 Ascospores < 70μm long, lirellae closed, stictic acid present 10
Ascospores > 70 μm long, lirellae open, stictic or norstictic acid present 11

10 Lirellae inconspicuous, immersed, exciple red-brown, ascospores 28–35 μm long .... **Graphina abdita**
Lirellae conspicuous, sessile, exciple lacking, ascospores 22–30 μm long .... **Graphina austenensis**

11 Hymenium Iodine + blue, ascospores 70–105 μm long, norstictic acid present .... **Graphina mendax**
Hymenium Iodine -ve, ascospores 80–145 μm long, stictic acid present .... **Graphina pallido-ochracea**

12 Lirellae immersed in conspicuous stroma; ascospores 32–55 μm long .... **Glyphis cicatricosa**
Lirellae sessile or immersed in thallus, not immersed in stroma 13

13 Ascospores 62–80 μm long, 13–16-locular, lichen compounds absent .... **Graphis longula**
Ascospores ≤ 40 μm long, norstictic acid present 14

14 Lirellae immersed, ascospores 24–26 μm long, 6–8-locular .... **Graphis schiffneri**
Lirellae sessile, ascospores 28–40 μm long, 8–11-locular .... **Graphis apertella**

The family Graphidaceae from Fiji and Vanuatu

Glyphis cicatricosa Ach., *Syn. Meth. Lich.*: 107 (1814)

Lirellae crowded, open, immersed in conspicuous stromata; ascospores hyaline, 32–55 μm long, 8–12 μm wide, 8–12-locular; chemistry: no lichen compounds found. A detailed description is given by Archer (2004).

Distribution: a widely distributed tropical to temperate species from Brazil, Uruguay, Mexico, the United States (Florida), Japan, the Philippines, Singapore, Indonesia, New Caledonia, Fiji, Vanuatu, New Zealand, Australia (Queensland, northern New South Wales) and Norfolk Island.

Specimens examined: Vanuatu: *F. Wilson s.n.*, 1895 (NSW L4984 p.p.); *F. Wilson s.n.* (NSW L 5051 p.p.).

Graphina abdita A.W. Archer, A.W. Archer, *Mycotaxon* 77: 160 (2001)

Lirellae inconspicuous, fissurine, immersed, scattered; exciple pale reddish-brown; ascospores hyaline, muriform, 28–35 μm long, 8–10 μm; chemistry: stictic acid. A detailed description and illustration are given by Archer (loc. cit.).

Distribution: Fiji, the Solomon Islands and Australia (Queensland).

Specimen examined: Fiji: *s. loc.*, *F. Wilson s.n.* (NSW 426676).

Graphina austenensis A.W. Archer, *Mycotaxon* 83: 361 (2002)

Lirellae conspicuous, white pruinose, sessile; carbonised exciple absent; ascospores hyaline, muriform, 22–30 µm long, 11–14 µm wide; chemistry: stictic acid. A detailed description is given by Archer (loc. sit.).

Distribution: Fiji, Indonesia and the Solomon Islands. It has not been found in Australia.

Specimen examined: Fiji, *s. loc., Leucographina suvana, nom. nud., in sched., F.R.M. Wilson s.n.*, (NSW 426694).

Graphina colliculosa (Mont.) Hale, *Smithsonian Contr. Bot.* 40: 34 (1978)

= *Sclerophyton colliculosum* Mont., *Ann. Sci. Nat., Bot.* sér. 3, 16: 61 (1851)

Lirellae numerous, conspicuous, proper exciple uncarbonised; ascospores hyaline, muriform, 11–16 µm long, 5–7 µm wide, 4 × 1–2-locular; chemistry: salazinic acid. A detailed description and illustration are given by Wirth and Hale (loc. cit.1978).

Distribution: pantropical and is reported from India, the Philippines, Indonesia, Tahiti, Fiji, Papua New Guinea, Hong Kong and Vanuatu. It has not been found in Australia.

Specimen examined: Vanuatu: Malo Island, *F. Wilson s.n.*, 1895 (NSW L4983).

Graphina dimorphodes (Nyl.) Zahlbr., *Cat. Lich. Univ.* 2: 404 (1923)

= *Graphis dimorphodes* Nyl. in Leighton, W.A., *Trans. Linn. Soc. London* 27: 176 (1869)

Lirellae inconspicuous, proper exciple uncarbonised; ascospores hyaline. muriform, 9–16 µm long, 5–8 µm wide, 4–5 × 1–3-locular; chemistry: norstictic acid.small muriform ascospores and the presence of norstictic acid. A detailed description and illustration are given by Nakanishi et al. (2001).

Distribution: Sri Lanka, India, Thailand, the Solomon Islands and Vanuatu. It has not been found in Australia.

Specimen examined: Vanuatu: *F. Wilson s.n.*, 1895 (NSW 43851 p.p.)

Graphina mendax (Nyl.) Müll. Arg., *Rev. Mycol.* 10: 177 (1888)

= *Graphis mendax* Nyl., *Ann. Sci. Nat. Bot., sér.* 4, 11: 244 (1859)

Lirellae inconspicuous, open; epithecium white pruinose; ascospores hyaline, muriform, 70–105 µm long, 20–35 µm wide; chemistry: norstictic acid. A detailed description with synonyms is given elsewhere by Archer (2001a).

Distribution: Fiji, Vanuatu, the Philippines, India, Tahiti, Thailand, Indonesia, New Caledonia, Vanuatu and in Australia (Northern Territory and Queensland).

Specimens examined: Fiji: *s. loc., F. Wilson s.n.*, (NSW 499956); Vanuatu: *F. Wilson s.n.*, 1895 (NSW L4981).

Graphina pallido-ochracea (Kremp.) Zahlbr., *Cat. Lich. Univ.* 2: 417 (1924)

= *Graphis pallido-ochracea* Kremp., *Nuovo. Giorn. Bot. Ital.* 7: 32 (1975)

Lirellae conspicuous, open, discs pruinose; carbonised proper exciple absent; large ascospores muriform, hyaline, 80–145 µm long, 20–45 µm wide; chemistry: stictic acid. A detailed description, with synonyms, is given by Archer (2001a).

Distribution: Sarawak, the Philippines, the Solomon Islands, Vanuatu, and in Australia (Queensland, New South Wales).

Specimens examined: Vanuatu, Malokola [Malekula], *F. Leggatt s.n.*, Mar. 1890 (NSW 438458 p.p.); *s. loc.*, *F. Wilson s.n.*, 1895 (NSW).

Graphis apertella A.W. Archer, *Aust. Syst. Bot.* 14: 258 (2001)

Lirellae, conspicuous, open, disc slightly pruinose; proper exciple laterally carbonised; ascospores 28–40 µm long, 6–9 µm wide, 8–11-locular; chemistry: norstictic acid. A detailed description and illustration are given by Archer (2001e).

Distribution: occurs in Australia (Queensland, New South Wales, Lord Howe Island) and on Norfolk Island and Vanuatu.

Specimen examined: Vanuatu: Mallecola [Malekula], *F. Leggatt s.n.*, Mar. 1890 (NSW 438458 p.p.); *s. loc.*, *F. Wilson s.n.*, 1895 (NSW 4985 p.p.).

Graphis longula Kremp., *Flora* 59: 414 (1876)

Lirellae, numerous, thin, sub-immersed; proper exciple weakly striate, completely carbonised; ascospores hyaline, 62–80 µm long, 8–11 µm wide, 13–16-locular; chemistry: no lichen compounds found. A detailed description is given by Archer (2001d).

Distribution: occurs in Brazil, Mexico, Costa Rica, Dominica, Vanuatu, and in Australia (Queensland, northern New South Wales).

Specimen examined: Vanuatu: *F. Wilson s.n.*, 1895 (NSW)

Graphis schiffneri Zahlbr., *Ann. Cryptog. Exot.* 1: 127 (1828)

Lirellae, thin, black, immersed; proper exciple completely carbonised; ascospores hyaline, 24–26 µm long, 7–9 µm wide, 6–8-locular; chemistry: norstictic acid. A detailed description is given by Redinger (1936).

Distribution: occurs in Indonesia and Vanuatu.

Specimen examined: Vanuatu: *F. Wilson s.n.* (NSW L 4986 p.p.).

Phaeographina quassiicola (Fée) Müll. Arg., *Mém. Soc. Phys. Genéve* 29: 47 (1887)

= *Thecaria quassiicola* Fée, *Essai Crypt.*: 97 (1824)

Lirellae conspicuous, pale grey, raised, open (cup-like); proper exciple completely carbonised; ascospores muriform, pale brown, 45–110 µm long, 15–25 µm wide; chemistry: no lichen compounds found. A detailed description and illustration are given by Archer (2001b).

Distribution: occurs in Madagascar, India, Sri Lanka, Thailand, the Philippines, Japan, Indonesia, the Solomon Islands, New Caledonia, Fiji, Australia (Queensland) and on Norfolk Island.

Specimens examined: Fiji: Suva, *F. Wilson s.n.*, Aug. 1892 (NSW 438692); *s.loc.*, F. Wilson (NSW L5032; 499951).

Phaeographis dendroides (Leight.) Müll. Arg., *Flora* 65: 208 (1882)

= *Platygrapha dendroides* Leight., *Trans. Linn. Soc. London* 27: 179 (1869)

Lirellae conspicuous, black, open, with a thalline margin; ascospores pale brown, 25–37 µm long, 6–10 µm wide, 5–9-locular; chemistry: stictic acid. A detailed description and illustration are given by Archer (2001c).

Distribution: occurs in Sri Lanka, Thailand, Indonesia, the Philippines, Hawaii, Tahiti, New Caledonia, the Solomon Islands, Fiji, Vanuatu and Australia (Queensland, New South Wales).

Specimens examined: Fiji, *s. loc., F. Wilson, s.n.* (NSW 438744); *ibid., F. Wilson, s.n.* (NSW L 4997 p.p.); *ibid., F. Wilson, s.n.* (NSW L 5002; 499959); Vanuatu: *F. Wilson s.n.*, 1895 (NSW 438451 p.p.).

Phaeographis exaltata (Mont. & Bosch) Müll. Arg., *Flora* 65: 336 (1882)

= *Lcanactis exaltata* Mont. & Bosch, in Junghuhn, F., *Plant. Junghuhnianae* 4: 475 (1855)

Lirellae conspicuous, black, open with thalline margins; ascospores pale brown, 21–33 µm long, 7–11 µm wide, 6-locular; chemistry: no lichen compounds. A detailed description and illustration are given by Archer (2001c).

Distribution: a widely distributed species found in Mexico, Dominica, Brazil, Guadalupe, Thailand, Japan, Hawaii, Western Samoa, Sabah, India, the Philippines, Indonesia, Papua New Guinea, the Solomon Islands, New Caledonia, Fiji, Vanuatu, New Zealand and in Australia (Queensland, New South Wales, Victoria, Tasmania).

Specimens examined: Fiji: *s. loc., F. Wilson s.n.*, (NSW 4997 p.p.); Vanuatu: *F. Wilson s.n.*, 1895 (NSW 438451 p.p.).

Phaeographis tremulans Müll. Arg., *J. Linn. Bot. Soc.* 30: 460 (1895)

Lirellae much branched, open; proper exciple completely carbonised with a thick base; ascospores pale brown, 16–20 µm long, 6–8 µm wide, 4-locular; chemistry: no lichen compounds found. A detailed description is given by Müller (1895).

Distribution: occurs in Indonesia, Fiji and Vanuatau. It has not been found in Australia.

Specimen examined: Vanuatu: *F.Wilson s.n.*,1895 (NSW L5051 p.p.); Fiji: *s. loc., F. Wilson s.n.*, 1892 (NSW L4998; 499953).

Sarcographa intricans (Nyl.) Müll. Arg., *Flora* 70: 77(1887)

=*Graphis intricans* Nyl., *Acta. Soc. Sci. Fenn.* 7: 473 (1863)

Lirellae branched, immersed in conspicuous stromata; carbonised proper exciple absent; ascospores pale brown, 16–20 µm long, 5–7 µm wide, 6-locular; chemistry: norstictic acid. A detailed description and illustration are given by Archer (2004).

Distribution: occurs in Brazil, Colombia, Sri Lanka, Borneo, Vanuatu, New Zealand and Australia (Northern Territory, Queensland).

Specimen examined: Vanuatu: *F.Wilson s.n.*,1895 (NSW L5051 p.p.).

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Scaevola archeriana (Goodeniaceae), a new species from the Esperance Plains bioregion of Western Australia

L.W. Sage

Abstract

Sage, L.W. (Swan Coastal District, Department of Conservation and Land Management, 5 Dundebar Road, Wanneroo WA 6065) 2004. Scaevola archeriana *(Goodeniaceae), a new species from the Esperance Plains bioregion of Western Australia.* Telopea *10(4): 777–779.* A new species, **Scaevola archeriana** from Western Australia, is described and illustrated. A comparison to the related species, *S. depauperata* and *S. basedowii*, is provided and conservation status discussed. The species requires listing as Priority 1 with the Conservation and Land Management Codes and 2K- with ROTAP (Briggs & Leigh 1996).

Introduction

Two unusual plant collections related to *Scaevola depauperata* and *S. basedowii* from the Esperance Plains bioregion were made by William R. Archer in the 1990s. The collections were found to differ enough from these taxa to warrant recognition at the species level.

These collections differ from *Scaevola depauperata* in the absence or reduction of a beard under the indusium, a smaller corolla, smaller bracteoles, simple-hairy stems and cauline leaves that are sometimes obovate and toothed.

Scaevola archeriana *L.W. Sage*, **sp. nov.**

Scaevola depauperata barba sub indusio reducta vel absenti, corolla minore, foliis caulinis interdum obovatis dentatis recedit.

Type: Australia, Western Australia. Esperance Plains bioregion [precise locality withheld for conservation purposes], *W.R. Archer 2512952*, 25 December 1995 (holo PERTH; iso MEL, not seen).

[*Scaevola* sp. Esperance (*W.R. Archer* 2512952)]

Erect resprouting, multi-stemmed, clonal herb to c. 45 cm tall; stems striate with stiff, antrorse, simple hairs, becoming scattered above and adpressed. Basal leaves obovate, dentate, c. 8 × 3 mm (few seen), apparently glabrous. Cauline leaves ± triangular and usually dentate or obovate and serrate or toothed, to c. 10 mm long and c. 5 mm wide; hairs simple, stiff, antrorse. Flowers in thryses or racemes; bracts and bracteoles triangular, to c. 2 mm long; peduncle 12–22 mm long; hairs simple, stiff, antrorse. Sepals ± triangular, to c. 1.3 mm long, connate below lower third; hairs simple, stiff, antrorse, and minute and glandular. Corolla mauve, 12–16 mm long, densely bearded inside with thin barbulae and with simple, non-adpressed hairs outside; lobes c. 5mm long; wings 0.2–0.9 mm wide. Stamen filaments linear. Anthers without hairs at apex. Ovary 2.5–3.9 mm long, with simple, stiff and glandular hairs. Indusium c. 2.5 mm wide, beard significantly reduced or absent, long simple hairs below not equalling lips, lips with short bristles. Fruit obovoid to ellipsoidal, tuberculate, ribbed below sepals, c. 6.5 mm long, with stiff simple and glandular hairs. Seeds not seen.

Table 1. Comparison of *Scaevola archeriana, S. depauperata* and *S. basedowii*.

	S. archeriana	*S. depauperata*	*S. basedowii*
Indumentum on stems	simple, becoming scattered higher up	mostly glabrous, sometimes some glandular hairs	glandular and few simple or glabrous
Cauline leaves	triangular or obovate	triangular	triangular
margin	mostly dentate or serrate	entire	entire
Sepals	triangular	triangular	widely triangular
apex	acute	acute	rounded
outside indumentum	glandular & simple	glandular & simple	glandular
separation	connate below ⅓	connate below ⅓	connate ⅓–½
Beard under indusium	reduced or absent	stiff, ± equalling mouth	stiff, ±equalling mouth
Distribution	south-west WA	All southern states except WA	Central Australia

Specimens examined: Western Australia: Esperance Sandplain bioregion: NNE of Mount Heywood, [precise locality withheld for conservation purposes], *W.R. Archer 103924*, 1 March 1992 (MEL, PERTH).

Distribution and habitat: known only Western Australia, *S. archeriana* is recorded from sandy and sand-clay loam soils north east of Esperance. Research into the habitat preference of this species is essential.

Scaevola depauperata is found in all southern mainland states except Western Australia (Carolin 1992). *Scaevola basedowii* is known from central Australia (Carolin 1992).

Notes: distinguished from *S. depauperata* by a significantly reduced or absent beard under the indusium not equalling the lips, a smaller corolla (to 16 mm compared to a minimum of 20 mm), stems that have scattered hairs and cauline leaves that are sometimes obovate and toothed (compared to only ± triangular). The new species is distinguished from *S. basedowii* by sepals that have an acute apex, simple and glandular indumentum on the outside sepal surface and stems that have only a simple indumentum.

Etymology: the specific epithet honours the only collector to date of the new species, William R. Archer, of WA Nurseries in Merivale, Western Australia.

Conservation status: apparently uncommon and not known from any conservation reserves. This species, like many *Scaevola* species, spreads by underground roots and is most likely fire responsive (L.W. Sage, unpublished data). This is supported by the label of W.R. Archer 103924, '…after fire'. In the absence of fire or an appropriate fire regime the true abundance of *S. archeriana* may be hard to determine. Research into the longevity of soil stored seed and the reproductive biology of the species may be required.

Because it has a highly restricted distribution and is currently known from only two populations, the new species requires a Priority One listing under the CALM Conservation Codes for Western Australian Flora and coding as 2K- under Briggs & Leigh (1996). Urgent surveys are required to gain a better understanding of the true conservation status of *S. archeriana*.

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Dendrobium crassilabium (Orchidaceae: Dendrobieae), a new species from Papua New Guinea, Northern Province

Phil Spence

Abstract

Spence, Phil (PO Box 3525, Wamberal NSW 2260, Australia) 2004. Dendrobium crassilabium *(Orchidaceae: Dendrobieae), a new species from Papua New Guinea, Northern Province.* Telopea *10(4): 781–785.* A new species, **Dendrobium crassilabium**, discovered in the Northern Province of Papua New Guinea, is described and illustrated. It is distinguished from other members of section *Lautouria* by having green flowers with a thick and fleshy, narrowly spathulate labellum midlobe, and spreading narrow sidelobes.

Introduction

In 1994 I collected material of an unnamed species of the genus *Dendrobium* section *Latouria* from dense forest about 10 km from the nearest small village of Waja, near the mission station of Sangara, which is about half way along the road from the towns of Popondetta and Kokoda in the foot-hills of the Kekend mountains in the Guava Range, Northern Province, Papua New Guinea. Most plants in this region were destroyed when Mount Lamington erupted on 21 January 1951. This small, dense colony of plants survived a c. 200° C flash that killed the entire village population and burnt the forest badly. The ground was covered with volcanic ash to the extent that when the trees started to grow they produced a new root system in the ash several meters above the old forest floor. Some 40 years later the roots remain and most of the ash has been washed away, leaving a trampoline-like structure of roots several meters above the forest floor. In this forest at the edge of the Roduna River (which is a tributary of the Kumusi River) nine plants were removed with the consent of the land owners and the village people. Export and import permits were arranged, and plants were quarantined for approximately four months at a registered quarantine nursery. Four plants did not survive fumigation.

These plants were not in flower when found and did not flower until several months after being released from Quarantine. I compared these plants with the type specimens of the following closely related species at CANB (then on loan from BO and AMES): *Dendrobium euryanthum* Schltr., *Dendrobium subquadratum* J.J.Sm. and *Dendrobium sikini* Schltr. In addition, observation of live plants of *Dendrobium sikini* Schltr. in the wild and pressed flowers in my personal herbarium, supported the view that this was a new undescribed species. Comparisons were also made with the drawings and descriptions of *Dendrobium euryanthum, subquadratum, sikini,* and other related species, obtained from Smith (1911: 553, 1913:42, 1929:417) and Schuiteman and de Vogel (2002). As a result of this research, it was clear that these plants are representatives of an unnamed species and accordingly it is described here as new. It should be noted that in the future this species may be placed in the genus *Sayeria* (Clements, pers. comm.).

Dendrobium crassilabium *P. Spence*, **sp. nov.**

Ab alliis speciebus sectionis Latouriae labello crassissimo calosissimoque differt.

Type: cultivated Sydney, 19 Aug 1994, *P. Spence & Clements 8190* (holotype: NSW; iso: CANB, Herb. P. Spence 37). Ex Papua New Guinea, Dense forest, at edge of Roduna River about 10 km from the nearest small village of Waja, near the mission station of Sangara. On tree boughs, alt. c. 2500 m, *P. Spence s.n.*, 1994.

Epiphytic herb, erect or somewhat spreading, 12 to 28 cm tall. *Rhizome* abbreviated 0–0.2 mm long. *Roots* threadlike, glabrous. *Stems* pseudobulbous, cylindrical, slightly attenuated towards the base, finely furrowed lengthwise, with 1–3 leaves, 3–8 mm diam. *Leaves* terminal to sub-terminal, spreading at an angle of about 45° to the vertical, lanceolate to elliptic, acutely tapering from inwardly curved sides to a narrow point, cuneate at the base, 12–18 cm long, widest at or below the middle, 3–5 cm wide. *Inflorescence* terminal or sub-terminal, shorter than the leaf, 6–10 cm long slender, slightly thickening along the rachis: rachis 4–8 cm long with 4–14 flowers; peduncle thin 20–40 mm long, 1.8 mm diam.; bracts ovate or elliptic, shortly acuminate, glabrous, 3 to 4 times shorter than the pedicels, at a c.15° angle to rachis at base, 3–4 mm long. *Flowers* at a c. 45° angle to rachis, with sepals and petals light apple-green to almost olive-green; labellum similar or darker. *Lateral sepals* oblong, slightly falcate, acute, 12 mm long, 8 mm wide, apex cuspidate. *Dorsal sepal* oblong, acute, apex apiculate to cuspidate, 14 mm long, 6–8.5 mm wide. *Petals* obliquely lanceolate, acute or acuminate, c. 11 mm long, 3–4 mm wide. *Labellum* 3-lobed; attached at the based by a narrow claw, non-articulate; lateral lobes small, spreading, oblong, slightly falcate, obtuse, 3 mm long, 2.5 mm wide; mid-lobe much larger, porrect, with slightly intoned margins, c. 12 mm long, c. 7 mm wide; epichile fleshy, rigid, medially sulcate, transversely elliptic-reniform, thick for the section, cordate to almost square, truncate with a downturned apicule, 6.5 mm wide, not exceeding the lateral lobes; callus ligulate, expanded and thickened in front, abruptly obtuse, extending from the base of the labellum to base of the mid-lobe. *Column* broadly elliptical, hooded, exceeding length of the lateral lobes of the labellum, 8–9 mm long, 0.28–0.3 mm wide. *Anther* broadly elliptical, hooded, slightly truncated, glabrous, c. 0.12 mm long × 0.18–0.2 mm wide. *Ovary* thick for the size of the flower, almost cylindrical, 4–6 mm long, 3.4–4 mm wide, tapering to a slender pedicel, 8 mm long, 2 mm wide. Fig. 1.

Derivation of name: the Latin for 'wood-like labellum'.

Habitat and ecology: Epiphytic on main trunk and heavy boughs of trees overhanging a fast flowing river. This species forms large colonies on its host trees and was found in the humus of long ribbon ferns that secured its roots. The plants that I observed were exposed to full sun and constant high humidity that was lifting from the fast-flowing water not far below.

Distribution: Papua New Guinea, Northern Province, Guava Range near Sangara, at the base of Kekend mountains. Only known from type locality. The cultivated plants from which the holotype and isotype duplicates were made, were originally separate plants adjacent on the same bough; these are considered duplicates under Article 8.3, ICBN St Louis 1999.

Notes: The new species differs, and can be readily distinguished, from the closely related species, *D. subquadratum* (J.J. Smith 1908), and *D. sikini* (Schlechter 1912) as shown in Table 1.

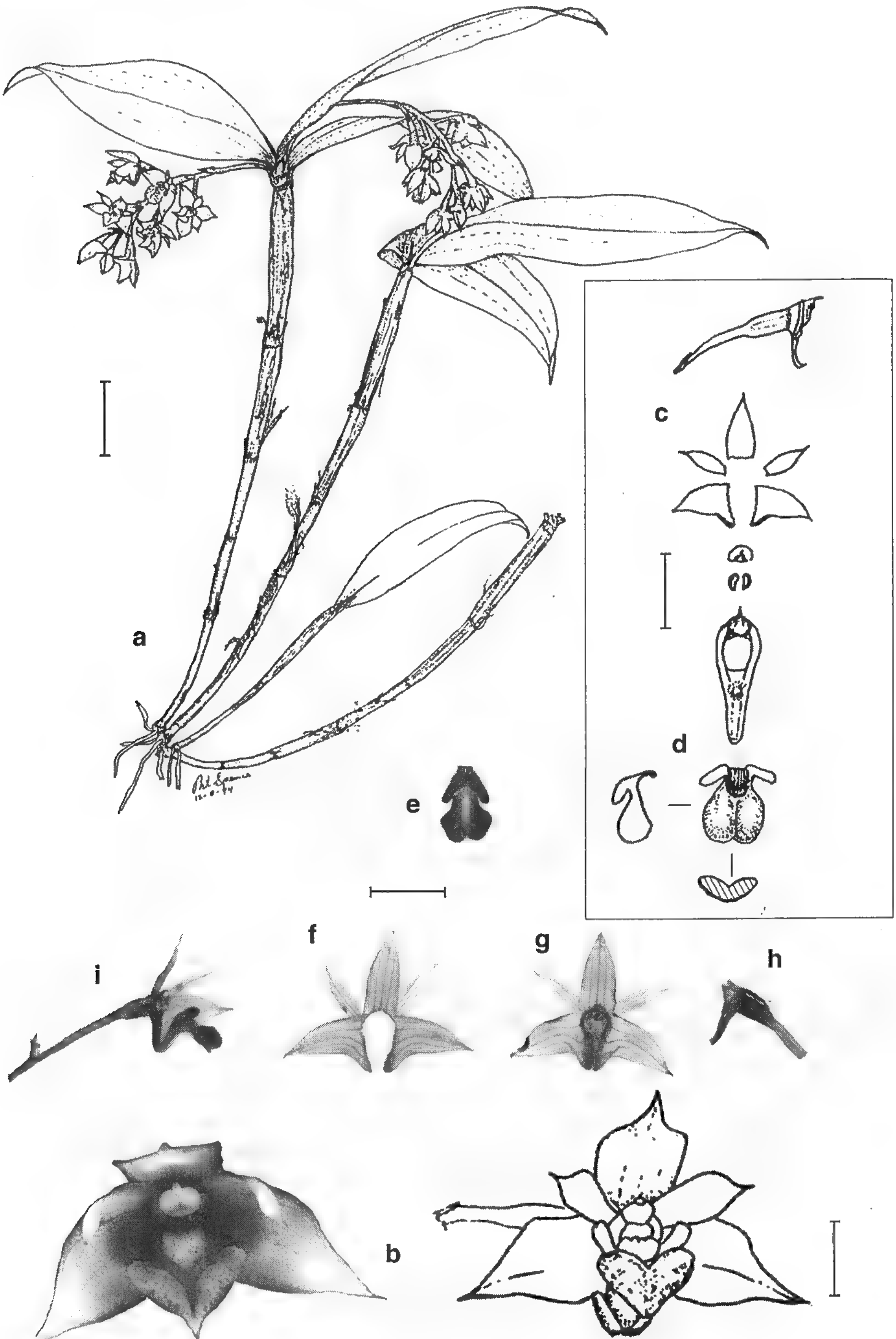

Fig. 1. *Dendrobium crassilabium* P. Spence. **a,** habit; **b,** flower; **c,** flower dissection; **d,** labellum with cross-sections (latitudinal below, longitudinal to left); **e,** labellum pressed flat; **f,** sepals and petals with column removed; **g,** sepals and petals with column, front view; **h,** column, column foot, pedicle and ovaries; **i,** complete flower, longitudinal section, pressed flat. Scale bars: a= 3.4 cm, b= 0.57 cm, c–i = 0.8 cm.

Table 1. Comparison chart for *Dendrobium subquadratum, D.sikini,* and new species, *D. crassilabium.*

	D. subquadratum	***D. sikini***	***D. crassilabium***
Plant habit	pendent	pendent	erect, spreading
No. of flowers	8	1–5	4–14
Inflorescence length, cm	12	5–8.5	6–12
Callus, mm	15.5	8.5	5
Ovary width, mm	-	2.5	3.4–4
Dorsal sepal, width at base, mm	13.5	12.2	8.5
Dorsal sepal, length, mm	15	9.2	14
Pedicel length including ovary, mm	20	8.8	11.5–12
Colour petals and sepals	white-pale green to orange	white-yellow	white-pale green
Colour labellum	pale green-yellow to dark orange	deep yellow	olive green–brown green

The proposed new species is an erect-growing plant whereas the other two are pendent, and *D. crassilabium* generally has significantly more flowers.

The sepals and petals are similar on all three species. From the above table it can be seen that there are marked differences in the length and width of the dorsal sepals. The ovary of *D. crassilabium* is shorter and wider than in *D. sikini.*

The callus on the labellum of *D. crassilabium* is yellow and fleshy and much shorter than in the other two species. The side lobes of the middle extension of the labellum are thicker, with a more pronounced wood-like texture than in the other two species. The side lobes of the labellum of *D. subquadratum* are much wider than in the other two species.

Cultural notes: The plant was raised from seed and distributed under the horticultural name of 'Nuff' (as it came from the village of a Mr. Nuffield). *Dendrobium crassilabium* responds to pot culture and is extremely easy to cultivate. I use a medium-sized pine bark being careful not to cover the rhizome as new growths have a tendency to tunnel rather than grow erect especially if good light is not provided from directly above. My plants are housed in a glasshouse with a minimum winter temperature of 8° C. The plants grow best with high humidity and air movement and hung just under the glass. This species is very free-flowering and is almost constantly in flower. Flowers will last up to two or more months.

Acknowledgments

I wish to thank Royal Botanic Gardens Sydney, especially Dr Peter Weston for overseeing this manuscript and Dr Peter Wilson for constructing the Latin diagnosis of *Dendrobium crassilobium.* Dr Mark A. Clements (CANB) assisted with herbarium material and provided advice. Ed Wilson assisted with the manuscript.

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Phebalium bifidum (Rutaceae), a new species from the Capertee Valley, New South Wales

Peter H. Weston and Margaret Turton

Abstract

Weston, P.H.[1] *and Turton, M.*[2] *(*[1]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia;* [2] *PO Box 186 Wentworth Falls, NSW 2782, Australia) 2004.* Phebalium bifidum *(Rutaceae), a new species from the Capertee Valley, New South Wales.* Telopea *10(4): 787–792.* **Phebalium bifidum** P.H.Weston & M.Turton, is named, described and distinguished from its closest relatives, *P. obcordatum* and *P. glandulosum.* Illustrations, a distribution map, and modifications to existing keys are provided.

Introduction

In September 1998, the second author was conducting a survey of populations of the vulnerable taxon *Grevillea obtusiflora* subspecies *fecunda* in the Capertee Valley. During the course of this survey, a specimen was collected of an unusual *Phebalium.* This specimen and subsequent observations and collections by Margaret Turton and Haydn Washington, were sent to Peter Weston for identification. After examination, Weston confirmed that these specimens belonged to a rare, unnamed taxon, which had not previously been collected. Approximately 230 plants are known from two populations about three kilometres apart. Pending formal taxonomic description, it was given the informal 'phrase name' *Phebalium* sp. 'Capertee' (NSW 481881). It is named and described in this paper, using the morphological terminology discussed by Wilson (1970, 1998). The most recent taxonomic treatment of *Phebalium* (Wilson 1998) is an update of Wilson's earlier comprehensive revision of the genus (Wilson 1970). Wilson (1998) narrowed the circumscription of the genus to that of *Phebalium* section *Phebalium* of his earlier revision (Wilson 1970). Wilson (1970) formally recognised infraspecific variation at either varietal or subspecific rank in four polymorphic species in *Phebalium.* Our new taxon is morphologically distinct from all others that have been described, but it most closely resembles two other eastern Australia species, *P. obcordatum* and *P. glandulosum,* the latter of which is polymorphic, with four formally recognised subspecies.

Before describing the new taxon we wanted to clarify its relationships to other taxa and thus determine the most appropriate rank at which to recognise it. Consequently, we tried to conduct a preliminary cladistic analysis of *Phebalium,* using qualitative morphological characters that Wilson (1970) found to be taxonomically informative in the genus. This attempt failed, yielding hundreds of thousands of equally parsimonious trees, the strict consensus of which was almost completely unresolved (results not shown). The problem of the precise position of the new taxon could, in principle, be investigated as part of the molecular phylogenetic analysis of *Phebalium* that is now in progress (see Mole 2004) but that would be a major task. Preliminary results from that project (Mole 2004) suggest that a well resolved phylogeny down to subspecific level would require the sequencing of multiple genetic loci. Given our present inability to resolve detailed relationships amongst taxa in *Phebalium,* it seemed wisest to apply Wilson's (1970) criterion of phenetic distinctness in choosing the taxonomic rank at which to recognise this taxon. Consequently, we decided to recognise this new taxon at specific rank, rather than to arbitrarily include it as a subspecies within one of the other known species that it closely resembles.

Taxonomy

Phebalium bifidum *P.H.Weston & M.Turton*, **sp. nov.**

Frutex erectus; ramuli teretes, glandibus non protrudentibus. Folia adulta bilobata, 3.5–14 mm longa; lobi 0.5–3.0 mm longi, 0.6–1.2 mm lati; pagina adaxialis laminae costa impressa glandibus parum protrudentibus; pagina abaxialis laminae dense lepidota. Inflorescentia 2–11 floribus; pedicelli 2.5–7.5 mm longi; calyx cupulatus 0.9–1.5 mm longus, 2.0–2.5 mm latus, truncatus vel obtuse lobatus; petala 5 plus minusve elliptica, 3.0–3.5 mm longa, 1.4–1.8 mm lata, pagina adaxiali cremea vel vivida citrina; apiculum antherae glandiferum.

Type: New South Wales: Central Tablelands: Capertee Valley, *P.H. Weston 2609, D. Crayn, J. Allen & H. Washington*, 29 Aug 2003 (holo NSW 608407; iso CANB, BRI, K, MEL, MO, PERTH) [exact location withheld for conservation purposes].

Erect shrubs 0.2–1.5 m high. Branchlets erect to spreading, terete, densely covered in glossy, scale-like compound trichomes, which vary in colour when young from cream with a scattering of ferruginous scales to uniformly ferruginous, discolouring to matt grey with age; oil glands not raised, covered by scales. Leaves of sexually immature shoots ('juvenile leaves') at first cuneate, with a slightly emarginate apex, successive leaves developing a distinctly bilobed apex, the largest leaves reaching 16 mm long, 3.5 mm wide, with an apical sinus 1 mm deep, densely lepidote on abaxial surface. Leaves of sexually mature shoots ('adult leaves') spreading to erect, shortly petiolate, Y-shaped, bilobed, 3.5–14 mm long; petiole 0.3–1.0 mm long, densely covered in scales; adaxial surface of lamina dark green when fresh, fading to olive or greyish green when dried, with distinctly impressed midvein, with oil glands protruding slightly above surrounding epidermis, sparsely to moderately covered in scales when young, glabrescent with age; margins entire, revolute; abaxial surface of lamina densely covered in glossy cream scales and a scattering of ferruginous scales when young, the scales discolouring to grey with age, the midvein protruding slightly to prominently; basal part of lamina (proximal to the lobes) narrow-oblong to narrow-cuneate, 2–10 mm long, 1–1.8 mm wide, 0.5–0.85 the length of the whole lamina; lamina lobes oblong or tapering slightly to a truncate to obtuse tip, straight or laterally incurved, 0.5–3.0 mm long, 0.6–1.2 mm wide, diverging from each other at an angle of 25–90°; sinus between lobes v-shaped to u-shaped, 0.5–2.5 mm deep, 0.5–3.5 mm wide. Inflorescences umbelliform, sessile or rarely shortly pedunculate, terminal or rarely axillary, 2–11-flowered. Pedicels c. 0.4–0.5 mm thick at base, c. 0.7–0.8 mm thick at apex, 2.5–7.5 mm long, densely covered in glossy cream scales and usually a few scattered ferruginous scales. Mature bud broadly obovoid, c. 2.5 mm long, c. 2.0 mm wide. Calyx cupulate, 0.9–1.6 mm long, 2.0–2.5 mm wide, smooth or verrucose with slightly protruding oil glands, densely lepidote with scales grading in colour from predominantly cream at the base to ferruginous at the upper margin, truncate to obtusely lobed. Petals 5, spreading, ±elliptical, 3.0–3.5 mm long, 1.4–1.8 mm wide, cream to bright lemon yellow on adaxial surface, densely lepidote on abaxial surface with glossy cream scales in the basal half and ferruginous scales in the apical half. Stamens divergently and symmetrically spreading, cream to bright lemon yellow; staminal filaments filiform, 5.0–5.5 mm long, c. 0.1 mm thick; anthers elliptical, glandular-apiculate, 0.6–1.2 mm long. Ovary subspherical, 0.9–1.1 mm high, densely covered in shiny, colourless, semi-

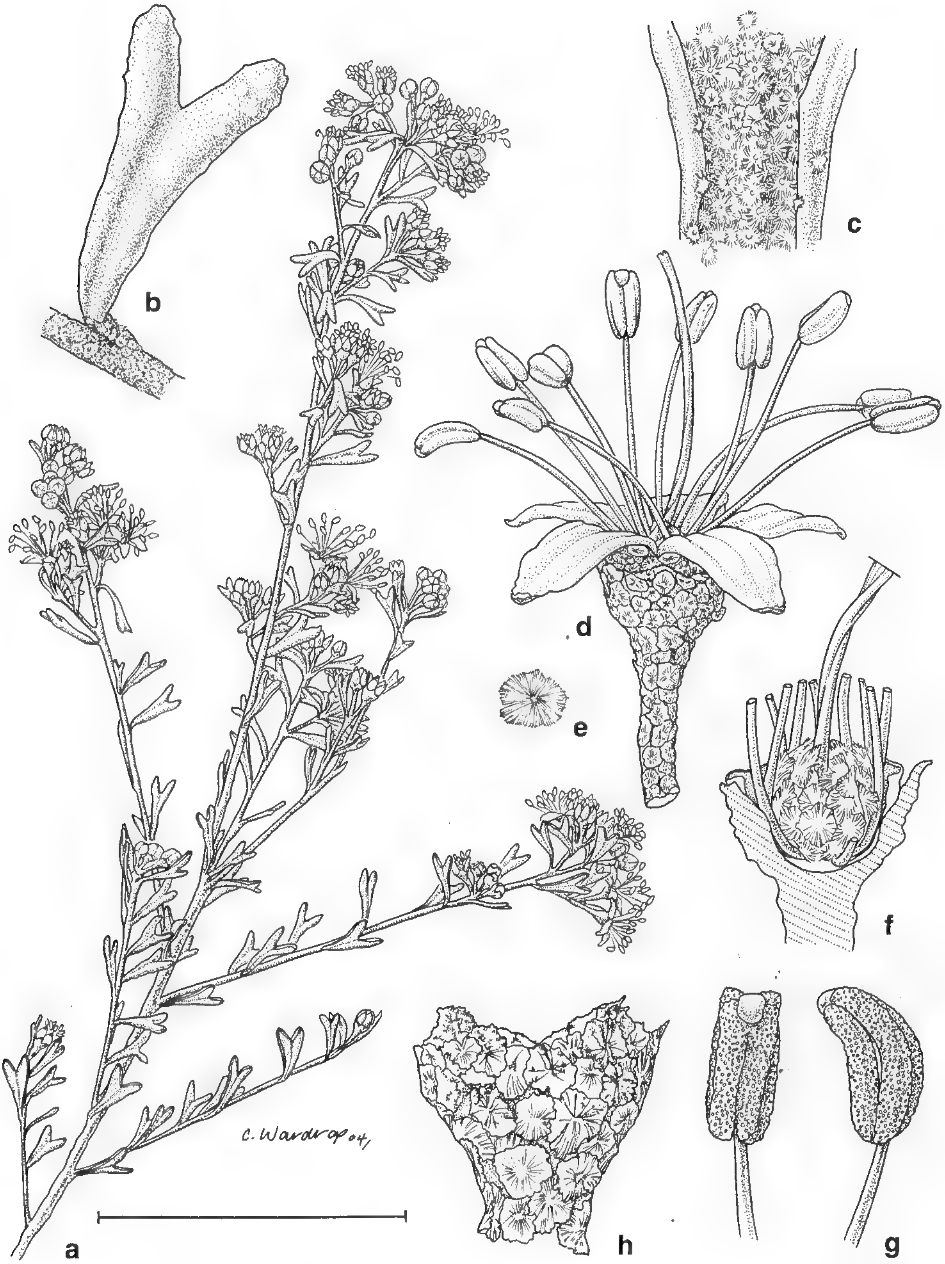

Fig. 1. *Phebalium bifidum* P.H.Weston & M.Turton. **a**, flowering shoot; **b**, adaxial surface of adult leaf; **c**, indumentum of scales on abaxial surface of adult leaf; **d**, flower; **e**, scale (trichome); **f**, ovary; **g**, anthers, lateral and abaxial views; **h**, calyx and tip of pedicel. From *NSW 496205* and photographs supplied by Haydn Washington. Scale bar: a = 4 cm, b = 7.5 mm, c = 4 mm, d = 5 mm, e, g, h = 2.5 mm, f = 3.3 mm.

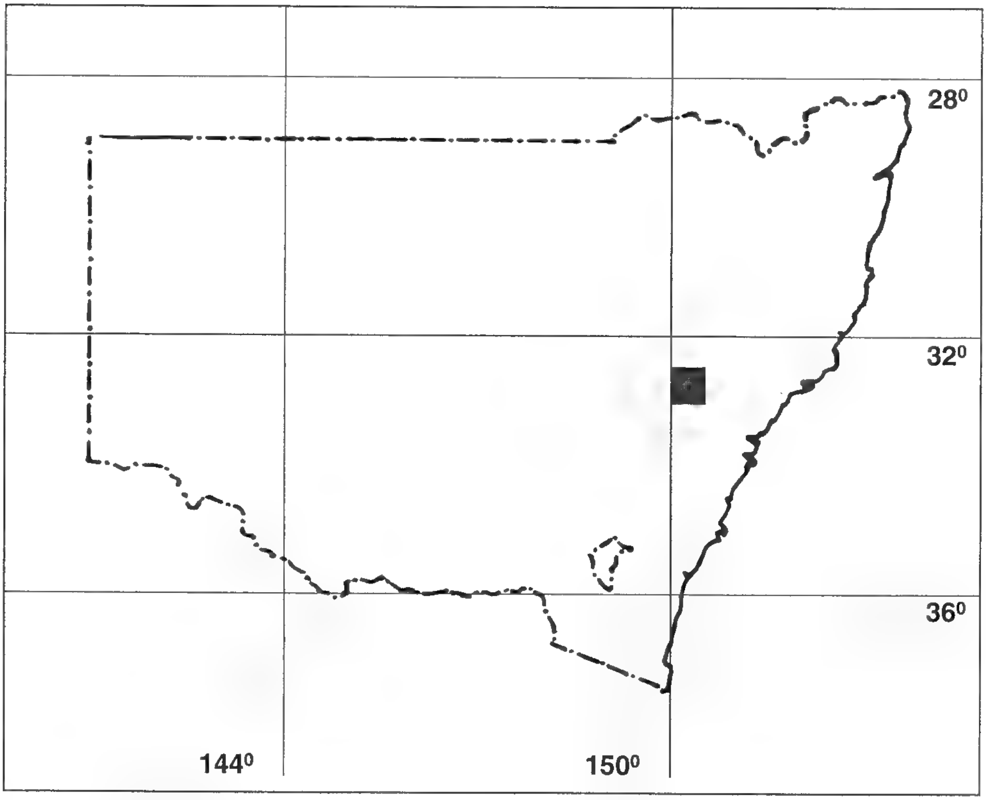

Fig. 2. Distribution of *Phebalium bifidum* (■) shown on a map of New South Wales.

transparent scales; style glabrous, ± equal to stamens, cream to bright lemon yellow. Fruits and seeds not known. Fig.1.

Specimens examined: New South Wales: Central Tablelands: Capertee, *M. Turton*, 24 Sep 1998 (NSW 483804); Capertee, *M. Turton*, 11 Jun 2001 (NSW 483808); Capertee, *M. Turton*, 3 Oct 2001 (NSW 483809); Capertee Valley, *M. Turton*, 7 Oct 2002 (NSW 496205); Capertee Valley, *H. Washington*, 29 May 2001 (NSW 481881).

Derivation of epithet: From the Latin bi- (two) and -fidus (divided); referring to the bifid adult leaves, which distinguish this species most readily from its closest relatives.

Flowering period: August to October.

Habitat: dry sclerophyll woodland or heath, the former dominated by *Callitris endlicheri*, *Eucalyptus fibrosa*, and one or more other eucalypts, such as *E. crebra*, *E. punctata*, *E. tenella* and *E. macrorhyncha*, with shrubby and herbaceous species including *Acacia buxifolia* subsp. *buxifolia*, *Cryptandra amara*, *Grevillea obtusiflora* subsp. *fecunda*, *Leptospermum parvifolium*, *Leucopogon muticus*, *Leucopogon virgatus*, *Lissanthe strigosa* subsp. *subulata*, *Persoonia linearis* and *Stypandra glauca*, on structured loam soil derived from shale, siltstone, conglomerate and sandstone associated with the geology of the Permian, Shoalhaven Group (Bembrick 1980), at 460–500 m altitude. The area experiences hot, dry summers and moist to wet winters, with an average rainfall of 750–850 mm.

Distribution: known from only two populations of about 230 plants, about 3 km apart (Fig. 2).

Proposed conservation status: geographically restricted, endangered, not conserved (2E coding of Briggs & Leigh 1996). Clearing and habitat fragmentation are the most obvious threatening processes that endanger this species. *Phebalium bifidum* is known only from roadside verges and private land in a moderately disturbed rural area.

Notes: *Phebalium bifidum* most closely resembles *P. obcordatum* (as implicitly recircumscribed by Wilson, 1998) and *P. glandulosum*. It is most easily distinguished from both of those species by its strongly bilobed, Y-shaped leaves (broadly obcordate; sinus between lobes to 0.3 mm deep in *P. obcordatum*, linear to narrowly or broadly oblong-cuneate with a truncate to obcordate apex; sinus between lobes absent or up to 0.7 mm deep in *P. glandulosum*) and foliar oil glands protruding only slightly above the surrounding epidermis (protruding, hemispherical glandular pustules or undulate swellings in *P. obcordatum* and *P. glandulosum*). It also has a higher proportion of ferruginous to cream-coloured scales on lepidote organs than either *P. obcordatum* or *P. glandulosum*. From *P. obcordatum* it is also distinguished by its longer leaves (2.0–4.0 mm long in *P. obcordatum*), with the midvein being distinctly impressed on the adaxial surface (slightly sulcate with no definite midrib in *P. obcordatum*), the margins being revolute (flat to recurved in *P. obcordatum*), longer pedicels (2–3 mm long in *P. obcordatum*), and longer petals (to 2.5 mm long in *P. obcordatum*). From *P. glandulosum* it is also distinguished by its branchlets lacking raised oil glands (minutely to prominently glandular-verrucose in *P. glandulosum*).

P. bifidum is allopatric to both *P. obcordatum* and *P. glandulosum*, occurring 210 km east of the nearest populations of *P. obcordatum* and 65 km south of the nearest populations of *P. glandulosum* (subsp. *angustifolium*). It shares few associated species with either *P. obcordatum* or *P. glandulosum* although it does occur in structurally similar communities on similarly siliceous, nutrient-poor, well-drained soils.

Amendments to published keys to *Phebalium*: The keys published by Wilson (1970), Weston and Porteners (1991) and Weston and Harden (1995) need to be altered to accommodate *P. bifidum*. In all three keys, a couplet is reached where neither lead applies satisfactorily to *P. bifidum:* in Wilson (1970) 'Sectio 1. *Phebalium*: South Australian, Eastern Australian, and Tasmanian Species' at couplet 1; in Weston and Porteners (1991) at couplet 6; and in Weston and Harden (1995) at couplet 4. This part of all of these keys can be amended by inserting a new couplet prior to the problematic couplets listed above:

> 'A Leaves strongly bilobed, Y-shaped, the sinus between the lobes 0.5–2.5 mm deep, with oil glands protruding only slightly above surrounding epidermis; branchlets lacking protruding oil glands .... *P. bifidum*
>
> A* Leaves either entire (sometimes with glandular-undulate margins), or shallowly bilobed (sinus between the lobes to 0.7 mm deep) but then branchlets and adaxial leaf surface covered in prominently protruding, hemispherical, oil glands.'

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Towards a taxonomic revision of *Pteridium* (Dennstaedtiaceae)

John A. Thomson

Abstract

Thomson, J.A. (National Herbarium of NSW, Royal Botanic Gardens and Domain Trust, Sydney, NSW 2000, Australia) 2004. Towards a taxonomic revision of Pteridium *(Dennstaedtiaceae).* Telopea *10(4): 793–803.* Controversy concerning typification of the bracken fern *Pteridium aquilinum* (L.) Kuhn is here resolved and an **epitype** proposed. Bracken taxa recognised in current European and Asian regional floras can for both land masses be placed in two morphologically and genomically distinct groups: an 'aquilinum' group and a 'latiusculum' group. Limited, presumably ongoing, gene flow between 'aquilinum' and 'latiusculum' morphotypes is attested in field situations of sympatry or parapatry by the presence of stands of intermediate morphotype, and by DNA fingerprinting. In Europe, 'aquilinum' morphotypes are referable to *P. aquilinum* subsp. *aquilinum*; in Asia, to *P. aquilinum* subsp. *wightianum* (Wall. ex J. Agardh) Shieh. To facilitate consistent, objective systematic treatment of 'latiusculum' morphotypes in Europe and Asia, *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén is redefined to include only specimens from the North American region, and **paratypes** designated. Similar morphotypes from Europe are referred to **P. aquilinum** subsp. **pinetorum** (C.N. Page & R.R. Mill) J. A. Thomson, and those from north-east Asia are referred to *P. aquilinum* subsp. *japonicum* (Nakai) Á. Löve & D. Löve for which a **lectotype** is chosen and **syntypes** identified. The endemic Hawaiian bracken morphotype is here formally recognised at subspecies rank as **P. aquilinum** subsp. **decompositum** (Gaudich.) Lamoureux ex J.A. Thomson.

Introduction

The cosmopolitan bracken fern genus *Pteridium* Gled. ex Scop. (Dennstaedtiaceae) forms a readily delimited taxonomic entity (Tryon 1941; Cooper-Driver 1976:16) consistent with its probable origin through ancient allopolyploidy (Thomson 2000a, b). In contrast, infrageneric systematic treatment of the many morphotypes has proved extremely difficult, contentious and unstable. Factors contributing to this problem include phenotypic plasticity in relation to environmental variables, a dearth of useful taxonomic characters, and the widespread occurrence in the field of morphological intermediates between definable morphotypes (for references, see Thomson 2000a, b). These difficulties are exacerbated by inconsistencies in the application and/or definition of infraspecific taxonomic designations.

Within *Pteridium*, one major discontinuity stands out, allowing the diploid (based on 2n = 104) southern hemisphere brackens, *P. arachnoideum* (Kaulf.) Maxon of C and S America and *P. esculentum* (G. Forst.) Cockayne, to be distinguished morphologically and genetically from the essentially northern hemisphere diploid bracken morphotypes of C and N America, Europe, Africa and Asia, that are currently placed collectively in *P. aquilinum* (L.) Kuhn (Thomson 2000a, b). This genetic discontinuity is reflected in the presence of the northern/southern allotetraploid (based on 4n = 208) species *P. caudatum* (L.) Maxon in C and S America, and the analogous allotetraploid *P. semihastatum* (Wall. ex J. Agardh) S.B. Andrews (*P. yarrabense* (Domin) N.A. Wakef.) in South-East Asia/Australia (Thomson & Alonso-Amelot 2002).

Two problems are examined here in preparation for publication of several collaborative re-evaluations of the taxonomic status of bracken morphotypes from

C and N America, Europe, Africa and Asia. The first concerns controversy surrounding typification of *Pteridium aquilinum* (L.) Kuhn, a question central to taxonomic treatment of the whole genus. The second relates to current polemics on recognition of *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén as a pan-boreal taxon distributed from N America and northern Europe into north-east Asia (Karlsson 2000), versus treatment of the N European morphotype of this series as a distinct full species, *P. pinetorum* C.N. Page & R.R. Mill (Page & Mill 1995a, b; Page 1997; Hutchinson & Thomas 1996).

Towards an attempt to standardise infraspecific nomenclature in *Pteridium*, subspecies are here regarded as morphologically, biochemically and/or geographically distinct assemblages that are partially isolated genetically from other such assemblages, interbreeding between them being restricted to narrow contact zones. Varieties are here treated as distinct assemblages of populations that are morphologically, biochemically or geographically distinct, or only weakly distinct, with a greater area of overlap within which intermediate forms indicative of genetic exchange are encountered. Varieties may be grouped into subspecies that, in their totality, are significantly more distinct morphologically, biochemically and geographically (see Cronquist 1988). Increasing use in recent years of biochemical (including molecular) characters to supplement, or even in some cases to replace, morphology in these infraspecific contexts presents no logical difficulty. As Mabberley (2002:795) has written in another context: 'Should infrageneric groupings be recognised... such clades can, if necessary, be defined by molecular parameters, thereby obviating the need for botanists having to strive to find ever more obscure 'morphological features', which are ever more unusable for the layman trying to identify 'taxa' given names associated with ranks. There is, after all, no theoretical reason to suppose that all clades will be recognisable by eye, for evolution may act on chemical constitution, disease resistance etc., ...'

Typification of *Pteridium aquilinum*

Conflicting opinions concerning typification of *Pteridium aquilinum* (L.) Kuhn have recently been expressed in the literature, a problem of particular significance because of the central role of this taxon in structuring any systematic treatment of this cosmopolitan genus. Tryon's (1941) selection of Fuchs' 1542 illustration of *Filix femina* as the type for the basionym *Pteris aquilina* L. is explicit, even to consideration of the critical characters that it illustrates (Tryon 1941:18). Tardieu-Blot (1964) later named *Hort. Cliff. 473, no. 6* (BM) as lectotype for this basionym without specifying whether she was referring to *Hort. Cliff. 473, Pteris. 6?* (since numbered BM000647565) or to *Hort. Cliff. 473, Pteris 6* (now numbered BM000647566). *Hort. Cliff. 473 Pteris 6?* is, as noted by both Sheffield et al. (1989) and Page and Mill (1995b), typical of central-southern 'mid-latitude' European *P. aquilinum* subsp. *aquilinum* as currently understood. In contrast, *Hort. Cliff. 473 Pteris 6* is labelled in Gronovius' hand 'Ex Nova Anglia attalit Dr Du Bois 5136' and is typical of *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén from N America. As Linnaeus clearly states in the protologue for *Pteris aquilina* 'Habitat in Europae sylvis, praesertim caeduis', BM000647566 is ineligible, so Tardieu-Blot's (1964) choice must be taken as BM000647565. Subsequent to Tardieu-Blot's publication, *Hort. Cliff. 473 Pteris 6?* was labelled 'Lectotype of *Pteris aquilina* L. Determinavit B. Parris 12.2.1980' and regarded as such by Parris (1985:1884; B. Parris pers. comm. 2004) under ICBN rules pertaining before implementation of the Berlin Code of 1988. Presumably in view of introduction of the Berlin Code, Sheffield et al. (1989) in referring to Parris' annotation wrote: ' ... as far as we know no formal publication of this lectotypification has been made, and we do so here'. Page and Mill (1995b) commented in detail on, and supported, the action taken by Sheffield et al.

(1989). Bobrov's (1984:19) nomination of *Herb. Linn. 1246.13* (LINN) as the type of *P. aquilinum* is superfluous and in any case inappropriate as this specimen is referable to subsp. *pinetorum* as defined below (see discussion in Page and Mill, 1995b:240), rather than to subsp. *aquilinum*.

Verdcourt (2000) recently re-examined the question of lectotypification of *P. aquilinum*. Although he describes Tardieu-Blot's (1964) selection as 'the more sensible choice', Verdcourt (2000:5) concluded that Tryon's choice of Fuchs' illustration is valid and must stand. S. Cafferty and C.E. Jarvis of the Linnaean Plant Name Typification Project (BM) concur with Verdcourt's opinion (S. Cafferty pers. comm. 2003), noting the absence of serious discrepancy between Tryon's selection and the protologue. Fuchs' plate provides little diagnostic detail; for instance it does not show nectaries at the pinna bases, and it is not clear from the outline drawing whether marginal sori are indicated or not. The illustration does, however, accord generally with *Pteridium aquilinum* in regard to frond lamina proportions and cutting, presence of a false indusium and in rhizome features. Page and Mill (1995) comment that: 'The frond as drawn is slightly stunted and is typical of a *P. aquilinum* plant growing in a somewhat dry place'. In view of the taxonomic complexities of , the availability of unequivocal type material of *P. aquilinum* (L.) Kuhn is particularly desirable. This end appears best reached by designation of *Hort. Cliff. 473 Pteris 6*? as epitype to support Fuchs' plate as the type of *P. aquilinum* as follows:

Pteridium aquilinum (L.) Kuhn in von der Decken, *Reisen Ost Afrika* 3(3):11 (1879).

Basionym: *Pteris aquilina* L., *Species Plantarum* 2:1075 (1753).

Type: [icon.] *Filix femina*, Fuchs, *Historiae Stirpium*: 596, misprinted 569 (1542), lectotype selected by Tryon (1941) [photograph seen, NSW].

Epitype: *Hortus Cliffortianus 473 Pteris 6*? (BM 000647565), **selected here**, [photograph seen, NSW].

Type locality: Europe.

Notes: Linnaeus' use of the specific name 'aquilina' for European bracken has been widely regarded as referring to the transitory eagle-like appearance of the apical pinnae during frond expansion (e.g. Page 1997:344). More likely, however, the name alluded to the widespread belief of Middle Age scholars (including Erasmus) and herbalists that the dark irregular outlines of the fibrovascular bundles evident in sections of bracken stipes and rhizomes symbolised either a double-headed eagle or an oak tree (Britten 1882). (Fig. 1).

The *'latiusculum'* problem

Tryon's (1941) monograph established the concept that two principal bracken taxa, *P. aquilinum* var. *aquilinum* (his var. *typicum*) and *P. aquilinum* var. *latiusculum* (Desv.) Underw. ex A. Heller are represented in Europe, while in north-east Asia the two main taxa are, in Tryon's scheme, *P. aquilinum* var. *wightianum* (J. Agardh) R.M. Tryon and *P. aquilinum* var. *latiusculum*. The former is currently accorded subspecific rank as *P. aquilinum* subsp. *wightianum* (Wall. ex J. Agardh) W.C. Shieh, the latter as *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén with a pan-boreal distribution.

Subsequent to Page's (1989) identification of *P. aquilinum* subsp. *latiusculum* in Scotland, Page and Mill (1995a, b) controversially (see Rumsey et al. 1991) named the Scottish and continental European 'latiusculum' as a new full species, *P. pinetorum* C.N. Page and R.R. Mill. These authors also moved the 'latiusculum' morphotype *P. aquilinum* var. *osmundaceum* Christ into *P. pinetorum* as *P. pinetorum* subsp.

osmundaceum (Christ) C.N. Page. This treatment of northern European 'latiusculum' morphotypes has received wide coverage in British floras, most notably in *Welsh Ferns* (Hutchinson & Thomas 1996) and *The Ferns of Britain and Ireland* (Page 1997). More widely accepted, however, is the contrasting treatment of *Pteridium* in *Flora Nordica* (Karlsson 2000) that places all European brackens into either *P. aquilinum* subsp. *aquilinum* or *P. aquilinum* subsp. *latiusculum* and describes the scope of phenotypic variation within them.

Karlsson (2000) rejects Page's taxonomic treatment of European *Pteridium* in the following terms: 'However, there is no biological foundation for such a narrow species concept, and the distinctness of the N European plant (*P. pinetorum*) from the N American one (*P. latiusculum*) is not documented.' On the other hand, treatment of the 'latiusculum' morphotypes as comprising a single pan-boreal taxonomic entity, whether as a full species, *Pteridium latiusculum* (Desv.) Hieron. ex R.E. Fr., or as a subspecies, *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén, is also untenable in the light of recent morphological and molecular studies.

A number of lines of molecular evidence now support the conclusion that the N American, European and NE Asian 'latiusculum' morphotypes do not form a monophyletic assemblage, either overall or considered pairwise. This is consistent with morphological evidence of genetic exchange within each of these regions between the local 'latiusculum' and other morphotypes (Tryon 1941, Page 1989, Harmaja 1990, Karlsson 2000, Shorina & Perestoronina 2000).

These include:

(i) Isozyme analyses of 'aquilinum' morphotypes from Britain and 'latiusculum' morphotypes from Scotland (later ascribed to *P. pinetorum*), Denmark (Møn Island) and New Hampshire made by Rumsey et al. (1991) show that overall the 'latiusculum' plants are genetically more similar to each other than to the 'aquilinum' accessions tested. The European 'latiusculum' samples are more closely related to each other than to those from N America, and show isozyme patterns suggesting introgression from 'aquilinum'. These findings are consistent with the suggestion that the European and

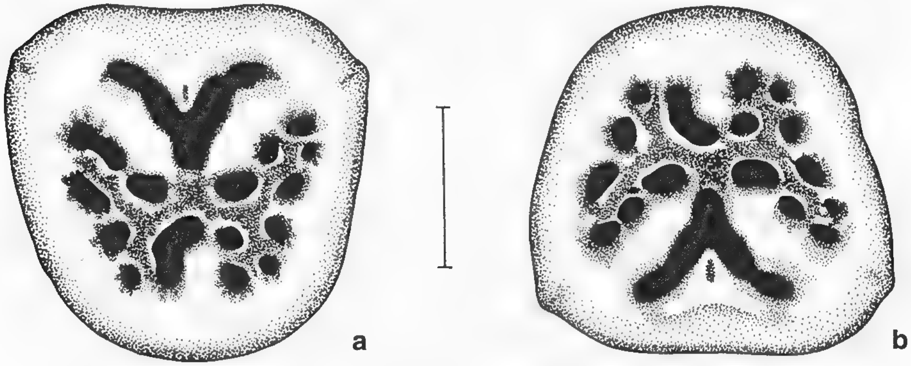

Fig. 1. *P. aquilinum* subsp. *aquilinum* , Wales UK. **a**,**b**, transverse sections of stipes close to their base, oriented to show patterns of fibrovascular bundles supposedly resembling **a**, double-headed eagle; **b**, oak tree; scale bar = 3 mm.

Table 1. Distribution of 45S rDNA restriction-site haplotypes in diploid morphotypes of *Pteridium*, compiled from data used by Thomson et al. (1995).
([1]estimated fragment lengths in kb; [2]in parentheses: number of accessions/number examined)

Haplotype	**Diagnostic restriction fragments**[1]	**Occurrence**[2]
A	*Bgl* II (7.9); *Bst* EII (7.5)	all morphotypes (23/23)
B	*Bgl* II (5.4 + 2.5); *Bst* EII (9.0); *Bam* HI (3.02 + 2.32 +1.70); *Sac* I (1.38 + 1.23)	*P. esculentum* (3/3), *P. arachnoideum* (1/1)
C	*Bam* HI (2.88 + 1.64)	NE Asian 'latiusculum' (4/4)
D	*Sac* I (1.55 + 1.41 + 1.17); probably also *Bam* HI (2.66)	*P. aquilinum* subsp. *wightianum* (4/4)
E	*Sac* I (1.46 + 1.25)	all N hemisphere morphotypes (15/15) **except** *P. aquilinum* subsp. *wightianum* (4/4)
F	*Bam* HI (2.24)	some European 'aquilinum' (2/5), some NE Asian 'latiusculum' (2/4), African 'aquilinum' (2/2), *P. aquilinum* subsp. *wightianum* (4/4), N American 'latiusculum' (1/1), European 'latiusculum' (1/1)

American 'latiusculum' morphotypes may not constitute a single taxon (Rumsey et al. 1991).

(ii) Comparative sequencing studies of the chloroplast genomes of N American and European brackens separate an 'aquilinum' clade from a *'latiusculum'* clade (Speer 2000), a finding in agreement with an earlier restriction site analysis (Wolf et al. 1995). Within the 'latiusculum' clade, accessions from Scotland (*P. pinetorum* subsp. *pinetorum* from its type locality), Sweden and Russia group more closely with each other than with N American samples, again suggesting genetic differentiation between the American and European forms, albeit at a level too low to warrant species-level treatment of either (Speer 2000).

(iii) Analysis of restriction endonuclease sites in the 45S rDNA sequences of bracken morphotypes (Thomson et al. 1995) leads to identification of six haplotypes (A-F, Table 1). Of these, haplotype A is found in all *Pteridium* taxa examined, together with haplotype B in *P. esculentum* and *P. arachnoideum*; with haplotypes C, E and/or F in NE Asian 'latiusculum'; with haplotypes D and F in *P. aquilinum* subsp. *wightianum*; with haplotypes E and F in 'latiusculum' from Europe (Ukraine) and N America; with haplotypes from E and/or F in other N American bracken taxa and in European *P. aquilinum* subsp. *aquilinum*. While these 45S rDNA haplotype patterns do not allow distinction between N American and European 'latiusculum', haplotype C is unique to NE Asian 'latiusculum'.

(iv) Phenetic clustering analysis of DNA-fingerprint band patterns of the nuclear genome of *Pteridium* taxa obtained using Arbitrarily-Primed (A-P) PCR (Thomson 2000a, b) groups NE Asian 'latiusculum' more closely with *P. aquilinum* var. *decompositum* (Gaudich.) R.M. Tryon from Hawaii than with N American 'latiusculum', while *P. pinetorum* clusters with European 'aquilinum' morphotypes.

Nomenclature of 'latiusculum' morphotypes

Given that treatment of 'latiusculum' morphotypes as a single pan-boreal taxonomic entity as currently understood (Karlsson 2000) is untenable (whether as a full species, *Pteridium latiusculum* (Desv.) Hieron. ex R.E. Fr., or as a subspecies, *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén), three regional subspecies are recognised here, restricted respectively to N America, Europe and Asia.

Pteridium aquilinum *(L.) Kuhn* subsp. **pinetorum** *(C.N. Page & R.R. Mill) J.A. Thomson*, **stat. nov.**

Basionym: *Pteridium pinetorum* C.N. Page & R.R. Mill, *Bot. J. Scotl.* 47:140 (1994, publ. February 1995).

Type: *C.N. Page 17049*, Scotland, 4 June 1983, (holo: E 00026882 [seen]; iso: ABD, GL, PTH). Holotype cited by C.N. Page as voucher of *P. aquilinum* subsp. *latiusculum*, Watsonia 17:431 (1989).

Type locality: Scotland: East Inverness-shire, Rothiemurchus Forest near Loch an Eilein.

Synonymy: *Pteridium aquilinum* (L.) Kuhn var. *osmundaceum* Christ, *Beitrage Krypt. Schweiz* 1(2):54 (1900); *Pteridium pinetorum* C.N. Page & R.R. Mill subsp. *osmundaceum* (Christ) C.N. Page, *Bot. J. Scotl.* 47:140 (1994, publ. February 1995);

Pteridium aquilinum (L.) Kuhn var. *pinetorum* (C.N. Page & Mill) Perest. in N.I. Shorina and O.N. Perestoronina, Proc. Intl Bracken Group Conference, Manchester 1999, Bracken Fern: Toxicity, Biology and Control Ch. 7:51 (publ. August 2000).

Distribution: Restricted to N, C and E Europe, ranging from Scotland to Siberia, Scandinavia, Switzerland, Northern Italy and Northern Ukraine. Localities as for *P. aquilinum var. osmundaceum* (Christ 1900), *P. pinetorum* (Page & Mill 1995a, b; Hutchinson & Thomas 1996; Page 1997), *P. aquilinum* var. *pinetorum* in N and C Russia and Ukraine (Shorina & Perestoronina 2000) and *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén in Scandinavia (Karlsson 2000). Not in Crimea and the Caucasus Mountains (Shorina & Perestoronina 2000) or Armenia (Gabrieljan & Greuter 1984).

Chromosome complement (sporophyte): diploid, implied by the results of Rumsey et al. (1991); 2n = 104 (Sorsa 1961).

Notes: Christ's name 'osmundaceum' is not available at subspecific level in *P. aquilinum* under ICBN (Saint Louis Code) Art. 11.6. Nakai (1925) was aware that Christ (1900:54) had described a variety of *P. aquilinum* from Europe, but apparently he did not see the original description, and gives the following citation: '*Pteridium aquilinum* var. *osmundoides* Christ apud Lévéille in *Bull. Acad. Geogr. Bot.* 3 ser. XIX. p.9 (1910), nihil aliud.' Tryon (1941, p. 23) lists this as a nomen nudum; var. *osmundoides* appears to be an erroneous reference to var. *osmundaceum*. Had Nakai had access to Christ's original (1900) paper, his comments might well have been interesting, and may have encouraged recognition of *P. aquilinum* var. *osmundaceum* in Europe, for he comments (Nakai 1925) that 'There are a few distinct varieties of *Pteris aquilina* (*Pteridium aquilinum*) in Europe. The variety from North Europe (including Up[p]sala) has similar lobes as var. *osmundoides* ...', and makes no reference to use of the name for Japanese material (Bonaparte 1918: 72, see below). For morphometric data on *P. aquilinum* in Eastern Europe see Shorina and Perestoronina (2000). Genetic analysis of populations in Scotland referred here to *P. aquilinum* subsp. *pinetorum*, has been reported by Bridges et al. (1998).

Pteridium aquilinum (L.) Kuhn subsp. **japonicum** (Nakai) Á. Löve & D. Löve, *Taxon* 26:325 (1977).

Basionym: *Pteridium aquilinum* (L.) Kuhn var. *japonicum* Nakai, *Bot. Mag.* (Tokyo) 39 (461):106 (1925).

Type: *Torama Yoshinaga* [s.n.], July 19th 1886, *Pteris aquilina* L. *Pteridium aquilinum* Kuhn [the latter identification in Nakai's handwriting], (**lectotype selected here**: TI [photographs seen, NSW]); **syntypes designated here:** *C. Owatari* s.n., 1 Nov. 1896, Keelung, Taiwan; *K. Miyake* s.n., 16 Oct. 1899, Taihoku, Taiwan; *Nikai 720*, 1910, Honshu, Japan; *T. Nakai 4096*, 31 May 1917, Korea; *T. Nakai 6578*, 28 Oct. 1917, Korea; *T. Nakai 10460*, 19 Jun. 1921, Korea; *T. Nakai 10461*, 28 Jun. 1921, Korea; (all TI [photographs seen, NSW]).

Type locality: Japan:Shimizu-toge, Echigo Province (now Niigata Prefecture), Honshu Island.

Synonymy: *Pteridium japonicum* (Nakai) Tardieu-Blot & C. Chr., *Fl. Gen. Indo-Chine* 7: 138 (1939–1951).

Distribution: The N E Asian region only, as specified for *P. aquilinum* var. *japonicum* by Nakai (1925), and as part of *P. aquilinum* var. *latiusculum* by Tryon (1941) and others, in Japan, Russia (Kamchatka, Amur, Sakhalin), Korea, China (extending west to Manchuria), Taiwan, North Vietnam, South Vietnam, Cambodia, Laos.

Chromosome complement (sporophyte): diploid, 2n =104 (Takahashi 1961, Kurita 1963).

Notes: Many sheets in TI carry the label *Pteridium aquilinum* var. *japonicum* Nakai in Professor Nakai's handwriting; none appears to have been so annotated before publication of this taxon in 1925 (H. Ohba, pers. comm. 2003). The lectotype is a well-spread, well-preserved, fertile frond from Japan, chosen from about 12 specimens in TI that can be identified as original material. A specimen from Sakhalin (*Père Urbain Faurie 304*, not seen) listed by Bonaparte (1918:72) as *P. aquilinum* var. *osmundaceum* Christ should presumably be referred to *P. aquilinum* subsp. *japonicum*.

Plants intermediate in morphology between *P. aquilinum* subsp. *japonicum* and *P. aquilinum* subsp. *wightianum* are well documented, particularly from China (e.g. Tryon 1941:44-5).

Pteridium aquilinum (L.) Kuhn subsp. **latiusculum** (Desv.) Hultén, *Lunds Univ. Arssk.* N.F. Avd 2, 37 no.1; 43 (1941) [*Flora of Alaska and Yukon*].

[*Pteridium aquilinum* (L.) Kuhn subsp. *latiusculum* (Desv.) Hultén ex R.T. Clausen, *Cornell Univ. Agric. Exper. Stat. Mem.* 291: 7 (1949)].

Basionym: *Pteris latiuscula* Desv., *Mém. Soc. Linn. Paris* 6(2): 303 (1827).

Type: 'Pteris latiuscula Desv.', Desvaux' Herbarium (holo: P 00347485); 'Pteris latiuscula Desv.' from de Vaillant's Herbarium (**new paratype:** P 00347522); 'Pt. caudata SCHK.' from the Herbarium of Danty d'Isnard (P00347486), (**new isoparatype**). [photographs seen, NSW].

Type locality: Canada: St. Pierre, Newfoundland.

Synonyms: *Pteridium latiusculum* Hieron. ex R.E. Fr., *Wiss. Erg. Schwed. Rhodesia-Kongo-Exped.* 1911–1912 1 : 7 (1914); *Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex A. Heller, *Cat. N. Am. Pl.*, 3 ed., 17 (1909); *Pteridium aquilinum* (L.) Kuhn subsp. *latiusculum* (Desv.) C.N.Page, *Watsonia* 17: 429,431 (1989).

Distribution: Circumscription of *P. aquilinum* (L.) Kuhn subsp. *latiusculum* (Desv.) Hultén is amended here to include only specimens from the N American region, encompassing plants from localities as specified for *P. aquilinum* var. *latiusculum* (Desv.) Underw. ex A. Heller by the following and other authors: Canada (Lellinger 1985, Cody & Britton 1989); USA (most abundantly in eastern and northern regions (Tryon 1941, Jacobs & Peck 1993, Lellinger 1985, Speer & Hilu 1999); Mexico (Nuevo Léon, Jacobs & Peck 1993).

Chromosome complement (sporophyte): diploid, 2n = 104 (Britton 1953, Cody & Mulligan 1982).

Notes: The original material for *Pteris latiuscula* Desv. consists of three specimens in P. On P 000347485, the printed label 'HERB. MUS. PARIS' reads 'Herbier de A. N. DESVAUX Donné par Mme Vve LAVALLÉE en 1896' [Desvaux' initials N. A. presumably having been inadvertently transposed]. Other labels read 'Pteris Aquilina variété Occidentalis T. N et St. Pierre' [Terre Neuve = Newfoundland]; 'Pteris latiuscula Desv.' and 'Habitat in America boreali'. These annotations exactly match specifications in the protologue. P 00347522 ('Herbier de Vaillant') and P 00347486 ('Herbier de Danty d'Isnard') are both labelled 'Filix ramosa major …' and 'No. 84 ex Canada' in the same hand and are evidently duplicates. P 00347522 carries in addition a bluish-coloured label 'espèce distincte, Pteris latiuscula Desv.' This specimen, sent to Vaillant in Paris during 1770 (Boivin 1977, 1978), was clearly used and probably annotated by Desvaux. P 00347486 is marked 'Pt. caudata SCHK.', which is listed as a synonym in the protologue for *Pteris latiuscula* Desv. It therefore appears appropriate to regard P 000347522 as a paratype and P 000347486 as an isoparatype of *Pteris latiuscula* Desv. (F. Rakotondrainibe (P), pers. comm. 2004).

The combination *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén (1941) was not accepted initially because Hultén made no reference to the basionym, leading Clausen (1949) to republish the combination. However, Hultén's combination is now considered valid under the ICBN (Saint Louis Code) Arts 33.2 and 33.3 (as it was published before 1 January 1953), rendering Clausen's later publication unnecessary. *P. aquilinum* subsp. *latiusculum* as defined in the present paper is genetically close to *P. aquilinum* subsp. *pseudocaudatum* (Clute) Hultén (*P. aquilinum* var. *pseudocaudatum* Clute) (Speer & Hilu 1999, Speer et al. 1999, Thomson 2000a, b), with which it hybridises at points of contact in the field (Speer et al. 1999).

Nomenclature of the endemic Hawaiian bracken fern

The endemic Hawaiian bracken morphotype, locally known as kīlau, has until recently been referred to *Pteridium aquilinum* var. *decompositum* (Gaudich.) R.M. Tryon, or to *P. decompositum* Gaudich. [nomen nudum] (Rumpf et al. 1994). A number of contemporary accounts of the fern flora of the Hawaiian Islands [e.g. Valier (1995), see also synonymy given by Palmer (2002)] have used the more appropriate rank *P. aquilinum* subsp. decompositum attributed to C.H. Lamoureux. This name, used in a draft list [Charles H. Lamoureux 1988, *Draft Checklist of Hawaiian Pteridophytes*, p.5] appears not to have been published before the untimely death of its author (C. Puttock, pers. comm. 2004), and is therefore formally published here.

Pteridium aquilinum (L.) *Kuhn* subsp. **decompositum** (*Gaudich.*) *Lamoureux ex J.A. Thomson*, **stat. nov.**

Basionym: *Pteris decomposita* Gaudich., Freyc. Voy. Bot. 393 (1829).

Type: '17. pteris Decomposita. iles Sandwich 1819: C. Gaudichaud' [sic] in Herb. Muséum d'Histoire Naturelle (holo: P 00347589, [photographs seen, NSW]).

Type locality: Hawaiian Islands.

Synonymy: *Pteridium capense* (Thunb.) Krasser var. *decompositum* (Gaudich.) Nakai, Bot. Mag. (Tokyo) 39 (461): 106 (1925); *Pteridium aquilinum* var. *decompositum* (Gaudich.) R.M. Tryon, Rhodora, 43: 40 (1941).

Distribution: Known only from the Hawaiian Islands (except Ni'ihau, Kaho'olawe).

Chromosome complement (sporophyte): diploid, 2n = 104 (Sheffield et al. 1995).

Notes: P00347589 is the only original material so far identified. Provenance of P00347587 'Gaudichaud Iles Sandwich' to the Herbarium of E. Drake (P) is uncertain; this sheet may have dated from either the Uranie or Bonite voyages. Gaudichaud himself collected P00347586, 'Voyage de M. Gaudichaud sur la Bonite. 1836-1837. Iles Sandwich. Septembre et Octobre, 1836' but this post-dated his description of *Pteris decomposita*. P00347588, O'Wai'he, M. Botta s.n., 1829 is also excluded by the date of collection.

DNA fingerprinting indicates that *P. aquilinum* subsp. *decompositum* shares a unique combination of genomic elements otherwise found in subsp. *wightianum* and subsp. *japonicum* (Thomson, 2000a, b). Sequencing studies of the chloroplast genome suggest a close relationship with *P. aquilinum* subsp. *lanuginosum* (Bong.) Hultén (*P. aquilinum* var. *pubescens* Underw.) of western N America (Speer et al. 2002). Systematic crosses made by Klekowski (1973) have indicated that bracken from the Hawaiian Is. is intersterile with *P. arachnoideum* from the Galapagos Is., although at least partially fertile in crosses with certain S and C American accessions of *P. arachnoideum* and *P. caudatum*.

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A new species of *Leionema* (Rutaceae) from south-eastern New South Wales

Neville G. Walsh

Abstract

Walsh, N.G. (Royal Botanic Gardens, Birdwood Ave, South Yarra, Victoria 3141, Australia) 2004. A new species of Leionema *(Rutaceae) from south-eastern New South Wales.* Telopea *10 (4): 805–810.* A new species, **Leionema ceratogynum**, is described from montane to subalpine localities in south-eastern New South Wales. Specimens of this species were previously included in *L. phylicifolium*. The new species is discussed in relation to *L. phylicifolium* and *L. lachnaeoides*. It is illustrated and its ecology and conservation status are discussed.

Introduction

In an investigation into the variation of *Leionema phylicifolium* (F. Muell.) Paul G. Wilson, a number of specimens of a distinct taxon were encountered, apparently confined to Wadbilliga National Park and occurring in different plant communities from those usually occupied by *L. phylicifolium*. No mention was made of this taxon in the *Flora of New South Wales* (Weston & Porteners 1991, Weston & Harden 2002). Wilson (1998) made reference to what is probably this taxon in notes under *Leionema lachnaeoides*, but referred specimens representing it to *L. phylicifolium*. The opportunity is here taken to recognise formally this entity.

Leionema ceratogynum *N.G. Walsh*, **sp. nov.**

A *L. phylicifolia* ovario manifeste rostrato glabro vel pilis simplicibus vestito, foliis scabridiusculis supra costis prominentibus infra differt. A *L. lachnaeoide* inflorescentibus trifloris, foliis majoribus marginibus minus revolutis pagina supra scabridiuscula vice scabra differt.

Type: AUSTRALIA: New South Wales: Wadbilliga Fire Trail, Wadbilliga National Park, *T.R. Lally 185*, 28 Oct 1993; holo CANB; iso MEL, NSW.

Dense shrub to c. 2.5 m high; branchlets strongly ridged by leaf decurrencies when young, stellate-puberulous with hairs 0.3–0.5 mm long; hairs retained for several years. Leaves oblong-elliptic, (8–)12–21(–30) mm long, 1.3–2.5 mm wide, apex acute to obtuse, sometimes very shortly apiculate; upper surface minutely scabridulous by the raised epidermal cells, and somewhat tuberculate by the raised oil-glands, glabrous or with very sparse, scattered stellate hairs; lower surface smooth, white stellate-puberulous, sometimes with a few longer hairs along the raised midrib; margin revolute; petiole 1.5–3 mm long. Inflorescence a compact axillary triad (rarely a single flower), produced along distal 5–15 cm of branches; peduncles and pedicels glabrous, or very sparsely indumented with hairs like those of subtending branches; peduncles 0–1 mm long, terminated by 2 pairs of narrowly triangular, hispidulous bracts 0.5–1.3 mm long; pedicels 1–2 mm long, each with 1 or 2 narrowly triangular bracteoles 0.4–0.7 mm long in the proximal half. Calyx obturbinate, 1–1.5 mm long, glabrous, lobes deltoid, about half the length of the entire calyx; petals valvate, narrow-elliptic, 4.5–5 mm long,

HOLOTYPE
National Herbarium of Victoria
Leionema ceratogynum N.G. Walsh
Det.: N.G. Walsh Feb 2004

AUSTRALIAN NATIONAL HERBARIUM (CANB)
Commonwealth Scientific & Industrial Research
Organisation; Australia

RUTACEAE

Phebalium phylicifolium

AUSTRALIA : New South Wales

[redacted] Wadbilliga National Park.

36° 23 ' S 149° 38 ' E Alt: 1100 m

Rise in moist clay soil with much leaf litter; in closed Eucalyptus fraxinoides forest.

Shrub 1.5 m high, 2 m wide, forming dense hedge; flowers yellow.

Dupl. to: NSW,MEL.

T.R. Lally 185 28 Oct 1993

Fig. 1. Type specimen of *Leionema ceratogynum* (*Lally 185*, CANB).

pale yellow, glabrous, gland-dotted; stamens 6–8 mm long; style slightly shorter than or equal to stamens; disc not apparent; ovary glabrous or with a few simple hairs to c. 1.5 mm long, rarely villous, each carpel terminated by a linear sterile process (rostrum) 1.5–2 mm long at anthesis. Follicles 5 or fewer by abortion, erect, the fertile portion ± ellipsoid, 3.5–4 mm long, the sterile process 3–4 mm long at maturity. Seed D-shaped to slightly reniform, 2.5–3.3 mm long, angled dorsally, testa shining dark brown, smooth or obscurely patterned with low tubercles, raphe (sensu Wilson 1998) shield-like, c. 1.5 mm long and wide, appressed to testa.

Distribution: Known only from a small area within Wadbilliga National Park in the catchments of the Brogo and Wadbilliga Rivers, east and north-east of Kybean (ESE of Cooma). Populations have been recorded over a linear range of about 11 km.

Habitat: Structural communities in which *L. ceratogynum* occurs have been described on herbarium sheets as open forest, scrub, mallee and heath with common associates *Eucalyptus fraxinoides, E. kybeanensis, E. paliformis, Acacia obliquinervia, Banksia canei, Leucopogon lanceolatus, Oxylobium ellipticum* and *Tasmannia lanceolata*. Soils are sandy loams derived from Devonian sediments. Most populations occur on or near the ridgeline. The altitudinal range is from c. 1100 to 1300 m a.s.l.

Conservation status: All populations known to me are contained within Wadbilliga National Park. No herbarium specimens seen to date indicate precise population numbers, but extrapolating from populations seen by me in January 2004, an estimate of 300–2000 individuals distributed between about 5 populations seems reasonable. On the basis of these estimates, the conservation status is assessed as 2Vat or 2Rat (sens. Briggs & Leigh 1996) or VU (sens IUCN 1994). Given that these plants are almost certainly obligate seed regenerators, the most likely threat to populations would appear to be successive fires with insufficient time between to allow for replenishment of the soil seed bank.

Etymology: The epithet is from the Greek (*ceras* = horn & *gyne* = female) and alludes to the prominently beaked carpels. Although not a unique character within *Leionema* it is chosen to emphasize the difference between this species and its presumed nearest relative *L. phylicifolium*.

Notes: Differs from *L. phylicifolium*, to which it appears most closely related, in the beaked carpels and follicles, in the slightly roughened leaf upper surfaces with more prominent oil glands (in fresh and dried material), and in the longer indumentum and raised midrib on the leaf lower surfaces. When present, the hairs on the ovary of *L. ceratogynum* are relatively long (to c. 1.5 mm) and simple, in contrast to the fine stellate furze (under 0.2 mm long) characteristic of *L. phylicifolium* (very rarely the ovary is glabrous in *L. phylicifolium*). Different plants within the same population of *L. ceratogynum* may have either glabrous or villous ovaries.

The terminal sterile appendage on the ovary and follicle, and the scabridulous foliage suggest a relationship with *L. lachnaeoides*, a localised endemic in the Blue Mountains, but that species differs significantly from *L. ceratogynum* (and *L. phylicifolium*) in having single-flowered inflorescences. The leaves of *L. lachnaeoides* are generally smaller (to c. 15 mm long, 1 mm wide) than those of *L. ceratogynum*, usually slightly arcuate, more pronouncedly scabrous and have margins more strongly revolute (usually obscuring the entire lower surface).

In its generally dry, elevated habitat, *L. ceratogynum* differs from *L. phylicifolium* which is typically a species of margins of watercourses or lower valleys in subalpine areas. In some instances *L. phylicifolium* occurs on low ridges (e.g. Mt Jagungal region of Kosciuszko National Park, New South Wales and Mt Cobberas in the Alpine National Park, Victoria) but these sites are at higher elevations (above 1500 m a.s.l.) than those

Fig. 2 Flowers of *L. ceratogynum* showing rostrate carpels (glabrous form) (*Lally 185*, CANB).

Fig. 3 Developing fruits of *L. ceratogynum* (form with villous gynoecium) (*Telford 3660*, CANB).

occupied by *L. ceratogynum* and receive higher effective precipitation. Typical *L. phylicifolium* occurs within 10 km of the type locality of *L. ceratogynum*. The habitat of *L. lachnaeoides* in the Blue Mountains is perhaps more comparable to that of the new species, being principally in drier, elevated habitats (to c. 1000 m a.s.l.) on shallower soils derived from sandstone.

Selected specimens examined (Precise locality details withheld): New South Wales, Southern Tablelands; Wadbilliga National Park (all): *A.M. Lyne 1248, I.R. Telford & A. Young*, 23 Sep 1993 (AD, BISH, BRI, HO, MEL, NSW, PERTH); *I.R. Telford 3660*, 19 Nov 1973 (BRI, CANB, MEL, NSW, PERTH); *I.R. Telford 3656*, 19 Nov 1973 (A CANB, K, L, NSW, PERTH); *A.N. Rodd 6171, M. Kennedy & A. Whitehead*, 25 Jan 1991 (CANB, NSW, P); *M.F. Duretto 712*, 1 Oct 1995 (MEL, NSW PERTH); *J.D. Briggs 1826 & P.H. Weston*, 27 Mar1985 (CANB); *N.G. Walsh 6009*, 12 Feb 2004 (CANB, MEL, NSW); *M.D. Crisp 1236 & I.R. Telford*, 30 Sep 1975 (AD, BRI, CANB, MO); *M.D. Crisp 1241 & I.R. Telford*, 30 Sep 1975 (CANB, NSW, PERTH); *P. Gilmour W070*, 23 Apr 1983 (CANB); *P. Beesley 351 & D. Binns*, 27 Mar 1985 (CANB).

The key to *Leioinema* in Weston and Harden (2002, p. 306) may be modified to include *L. ceratogynum* by replacing lead '5*' with the following:

5* Apex of leaves entire, leaves 0.8–2(–3) cm long, margins entire; inflorescences usually < 10 mm long, 1–3-flowered

  6 Ovary globose, white stellate-pubescent or rarely glabrous; ripe follicles obtuse or apiculate, to 3.5 mm long; leaves smooth; southern alpine and subalpine regions (ST) .... **2 L. phylicifolium**

  6* Ovary rostrate, glabrous, pilose or rarely villous; ripe follicles 6 mm long or more; leaves minutely scabridulous

Fig. 4. Dehisced follicles of *L. ceratogynum* (Walsh 6009, MEL, photographed *in situ*).

6a Inflorescences 3-flowered, rarely some (never all) 1-flowered; leaves straight, mostly 12–21 mm long, undersurfaces apparent; Kybean area (ST) ...... **2a L. ceratogynum**

6a* Inflorescences 1-flowered; leaves slightly up-curved, mostly 7-15 mm long, undersurfaces mostly obscured by revolute margins; Blue Mountains (CT) .... **3 L. lachnaeoides**

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Utricularia sandersonii (Lentibulariaceae), a new record for Australia

Barry J. Conn, Elizabeth A. Brown and Alan T. Fairley

Abstract

Conn, Barry J.[1], *Brown, Elizabeth A.*[1] *and Fairley, Alan T.*[2] *([1]National Herbarium of New South Wales, Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia; [2]PO Box 148, Oatley, NSW 2223, Australia) 2004.* Utricularia sandersonii *(Lentibulariaceae), a new record for Australia.* Telopea *10(4): 811–814.* The species *Utricularia sandersonii* Oliver is recorded for the first time in Australia, from the Blue Mountains area of New South Wales. It belongs in section *Calpidisca* otherwise known from Africa, Madagascar, Mexico and India. A full description, illustration and a key to distinguish it from *U. uliginosa* and *U. lateriflora* are provided.

Introduction

During November 2001, one of us (ATF) discovered a small population of what appeared to be a new *Utricularia* species in a Blue Mountains City Council reserve, south of Blackheath, New South Wales (Australia). It was not possible to fully evaluate the status of this taxon until recently, when flowers became available (on cultivated material). The identity of this species appears to be *Utricularia sandersonii*, a species native to South Africa (Taylor 1989). This species is commonly cultivated and it would appear to be a naturalised introduction in the Blue Mountains.

Utricularia sandersonii *Oliver*, Journ. Linn. Soc. 9: 155 (1867)

Small, perennial lithophytic herb, 20–40 mm high. Rhizoids numerous, capillary, to c. 10 mm long, to c. 0.3 mm wide. Stolons present, glandular. Leaves few, obovate, long-petiolate; lamina c. 10 mm long (including petiole), 2–3 mm wide, apex entire; venation indistinct, dichotomously branched. Traps few, on rhizoids and leaves, subglobular, stalked, 0.5–0.8 mm long; mouth slightly lateral to subterminal, dorsal appendage distinct, rounded, long-stipitate glandular, ventral appendage very short, forming a small stipitate glandular lip; internal glands 4-partite (lobes obloid, ± equal, 0.05–0.06 mm long, c. 0.01 mm wide) and widely spaced. Inflorescence erect, simple, solitary, 2–7 cm high, 1- to c. 4-flowered; peduncle terete; non-floral bracts ('scales' *sensu* Taylor 1989) basifixed, ovate, 0.7–1 mm long, c. 0.3 mm wide; pedicel 1.5–2 m long; bracts triangular, c. 1 mm long, c. 0.5 mm wide, apex subacute; bracteoles 2, basifixed, c. 0.7 mm long, c. 0.1 mm wide, white with tinge of purple along their length, apex subacute. Calyx 2-lobed, cucullate; lower and upper lobes ovate to subcircular, divergent, 2.2–2.4 mm long (upper lobe larger than lower), c. 1 mm wide, apex subentire to slightly irregular. Corolla 11–12 mm long, white with faint lilac tinge; spur curved forward (porrect) and directed slightly upwards, c. 10 mm long, cylindrical, slightly tapered, apex obtuse; lower lip obovate, c. 7 mm long, 4.5–5 mm wide, white, with green-yellow crescent-like marking near mouth (distinctly white-papillose medially between 'curve' of crescent - on 'palate' *sensu* Taylor 1989), more distally with two lateral (narrow) lilac markings, then with additional, but indistinct green-yellow marking medially, and most distally with broad, darker lilac marking (darker laterally); lateral ridges 2, prominent, white; central ridges absent; margin slightly irregular to notched (crenate) distally; upper lip deeply 2-lobed, each lobe slightly obovate, divergent, 3.5–4 mm long, c. 1 mm wide, white with lilac strip medially. Staminal filaments curved, c. 1 mm long; anther locules subdistinct. Gynoecium: ovary ovoid, c. 1.2 mm long; style and stigma c. 2 mm long; stigma 2-lobed, lower lip semi-circular, upper lip deltoid, about as long as lower lip, receptive. Capsule unknown. (Fig. 1).

Habitat: This species grows on a wet, vertical sandstone rock wall with *Zoopsis setulosa* and *Riccardia crassa*, in the splash-zone of a waterfall. It also occurs with *Drosera binata, Blechnum ambiguum* and *Schizaea rupestris* nearby. This site is thought probably not to receive direct sunlight. The flowering time for this species is not known, except in cultivation. Plants 'grown-on' in cultivation flowered in November, December and April. Plants at the Blue Mountains site have not been observed flowering during November and December, but a few plants were observed to have old inflorescences (lacking flowers). No fruiting material has been observed in the wild.

Distribution: Native to South Africa. This species is widely cultivated by carnivorous plant growers.

Australian specimen examined: Cult. Sydney, Australia ex Australia: New South Wales: Central Tablelands: Blue Mountains City Council Reserve, S of Blackheath, (orig. coll. *A.T. Fairley s.n.*, November 2001), *A.T. Fairley s.n.* (NSW 612660).

Notes: This species belongs to the section *Calpidisca*. This section of eleven species was previously known from Africa and Madagascar, with *U. livida* E.Meyer extending to Mexico and *U. arenaria* A.DC. extending to India (Taylor 1989). The recording of *U. sandersonii* in the Blue Mountains represents the first record of this section from Australia. The trap appendage and ventral lip are fringed with rows of multicelled gland-tipped hairs; the 4-partite internal glands of the traps; and corolla coloration are all characteristic of section *Calpidisca*. The Blue Mountains material tends to differ slightly from plants of *U. sandersonii* from South Africa. For example, the former plants have slightly smaller traps (less than 1 mm long cf. 1–1.5 mm long), a shorter spur (c. 1.5 times length of lower lip of corolla cf. 2–3 times) that is more strongly curved upwards than in *U. sandersonii*. The morphology of this material is, however, similar to a form of *U. sandersonii* that is common in cultivation (including in Australia).

To include this species in the key to species of *Utricularia* occurring in New South Wales, the key in *'Flora of New South Wales'* Volume 3 (Rowe and Brown 1992, p. 599) couplet 5 is modified to incorporate this species. Couplet 6 has also been modified to assist in distinguishing *U. lateriflora* from *U. uliginosa*:

'5 Bracts basifixed, bracteoles present.

5A Spur c. 1.5 times length of lower lip of corolla; upper lip of corolla deeply divided into 2 divergent lobes .... **U. sandersonii**

5B Spur about as long as lower lip of corolla or very slightly longer; upper lip of corolla more or less emarginate

  6 Bracts much broader than bracteoles; spur directed at ± 90° to lower lip of corolla .... **U. uliginosa**

  6* Bracts not, or not much broader than bracteoles; spur directed forward and slightly curved upwards .... **U. lateriflora**

5* Bracts basisolute…'

Conservation status: Although the Blue Mountains site appears to be relatively natural and unmodified, the probability of this population being a garden escape cannot be dismissed. Taylor (1989, p. 230) reports that this species has 'proved to be easily cultivated in Europe and elsewhere'. This species is not known to have a long-

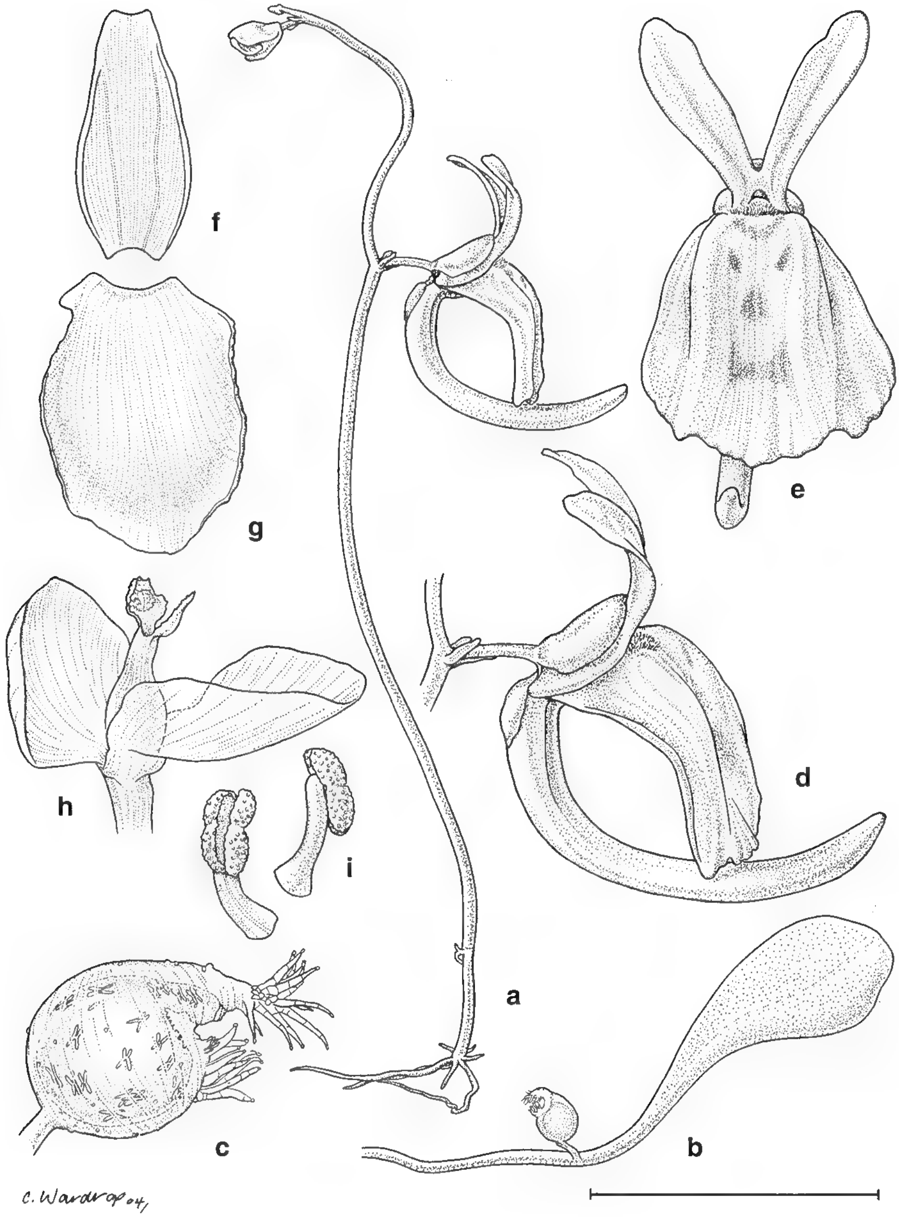

Fig. 1. *Utricularia sandersonii*. **a**, habit; **b**, leaf with attached trap; **c**, trap; **d**, flower in lateral view; **e**, flower in frontal view; **f**, lower lobe of calyx; **g**, upper lobe of calyx; **h**, gynoecium with pedicel and calyx (corolla removed); **i**, stamens. (all from *Fairley s.n.* Nov. 2001). Scale bar: a= 12.5 mm; b= 6 mm; c= 1 mm; d, e= 7.5 mm; f–i= 2.5 mm.

distance dispersing mechanism (Laurent Legendre pers. comm., 27 April 2004). Therefore, if this were a natural occurrence in Australia, it would represent an unusual disjunct extension of range for *U. sandersonii*. The geographic origin of the Blue Mountains population will be investigated by a comparison of molecular characteristics with those of other populations of *U. sandersonii.*

Only one population of this species is known from the Blue Mountains, consisting of several thousand plants, in an area of approximately 0.3 × 0.2 m^2. The impact that this apparently introduced species will have on the natural vegetation is unknown.

Acknowledgments

Dr W.R. (Bill) Barker (AD) confirmed the generic identity of this material. Leahwyn Seed and Bob Coveny (both NSW) identified the associated liverworts. Catherine Wardrop (NSW) skillfully illustrated this species. We thank Dr Barry Rice (DAV) for clarifying the identity of this taxon as *Utricularia sandersonii* and its morphological variation.

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Leionema scopulinum (Rutaceae), a new species from Wollemi National Park

Bryony M. Horton, Darren M. Crayn, Steve W. Clarke and Haydn Washington

Abstract

Bryony M. Horton[1], Darren M. Crayn[1], Steve W. Clarke[2] and Haydn Washington[3] ([1] National Herbarium of New South Wales, Botanic Gardens Trust, Sydney, NSW 2000, Australia; [2] School of Science, Food and Horticulture, University of Western Sydney, Hawkesbury Campus, Richmond, NSW 2753, Australia; [3] Lot 35, Widden Trail, Nullo Mountain, Rylstone, NSW 2849, Australia.* [1]*for correspondence: darren.crayn@rbgsyd.nsw.gov.au) *2004.* Leionema scopulinum *(Rutaceae), a new species from Wollemi National Park.* Telopea *10(4): 815–822.* **Leionema scopulinum** B.M. Horton & Crayn is described and compared with related species. Illustrations, a distribution map and a modified *Flora of New South Wales* key are provided along with notes on the ecology of the species.

Introduction

Over two weeks beginning on June 19, 2003, one of us (SWC), collected specimens of an interesting and unfamiliar shrub bearing striking greenish-yellow flowers from narrow, rocky ridges in the Lee Creek catchment (Wollemi National Park, New South Wales). The specimens keyed out to *Leionema* (plants lacking scales, having five, free, valvate sepals, five valvate petals, and versatile anthers with a retuse apex that lack an apical gland), but did not match any of the currently recognised species (Wilson 1998, Weston & Harden 2001). Coincidentally, another one of us (HW) independently discovered another occurrence of the novelty in the vicinity of Nullo Mountain on August 6. Since November 2003 a further 22 occurrences have been discovered, bringing the total number to 29.

Until recently *Leionema* was treated as a section of *Eriostemon* (e.g. Mueller 1882, 1889) or *Phebalium* (e.g. Bentham 1863, Wilson 1970). Wilson (1998) raised this section to generic rank based on floral and seed morphology. With the addition of the species described herein, *Leionema* (F.Muell.) Paul G. Wilson comprises 24 species, 23 in the eastern states of Australia and one species (*Leionema nudum* (Hook.) Paul G. Wilson) in New Zealand. Two other undescribed species are known from the Colo River (central coast of New South Wales; *Leionema* sp. 'Colo' [Weston 2423]) and the Macleay River (north coast of New South Wales), respectively. These will be dealt with separately. Terminology in this paper follows Wilson (1998), however it should be noted that the hairs in this species should probably be described as branched rather than stellate since they lack a consistently star-like morphology.

Taxonomy

Leionema scopulinum *B.M. Horton & Crayn* **sp. nov.**

Frutex scopulos inhabitans. Ramuli angulares, stellato-pubescentes. Lamina plerumque serrulato-marginata, 24–65 mm longa, 4.5–10.0 mm lata. Inflorescentia erecta floribus 9–32. Aestivatio petalarum valvata, petalis denique 6.6–8.1 mm longis, 1.5–2.0 mm latis, virido-citrinis vel citrinis. Cocci 5.5–7.0 mm alti, rostris 1.5–3.0 mm longis.

Type: New South Wales: Central Tablelands: Wollemi National Park: *D. Crayn 595, J. Allen, H. Washington, P. Weston*, 28 Aug 2003 (holo NSW 612970; iso CANB, K, MEL, PERTH). (Specific locality details withheld for conservation purposes).

Erect shrub 0.5–3 (–4) m high, usually about 1.5 m. Branchlets angled due to leaf decurrencies, sparsely to densely hairy, often more densely so toward tips, the hairs white, stellate, about 0.1 mm diameter. Leaves strongly aromatic, narrowly elliptic to very slightly oblanceolate (widest point 0.5–0.6 lamina length from base), dark green, glossy above, paler and somewhat duller below; petiole 1.5–5.5 mm long, 0.6–1.2 mm wide, winged, usually stellate-hairy especially on adaxial surface; lamina 24–65 mm long (mostly longer than 40 mm), 4.5–10 mm wide (length:breadth 5.5–7.5:1), mostly glabrous, often stellate-hairy along midrib near base, the occasional hair near midrib or margin, midrib impressed above but prominently raised below, other venation often visible but not prominent, both surfaces moderately glandular-punctate (density 200–300 glands/cm^2), the glands c. 0.5 mm diameter, pale yellow to pale green, raised (although flush with leaf surface or slightly impressed in a few dried specimens); apex obtuse to emarginate (and slightly asymmetric); base decurrent; margin entire to serrulate (especially in distal ½), ± flat (fresh) to slightly recurved (dried). Inflorescence cymose, erect, 9–32-flowered; pedicels 3.5–8.0 mm long, angled, stellate-hairy, glandular-punctate, the glands green to brown. Bracteoles small, linear, c. 0.5 mm long, stellate-tomentose, inserted ⅓–⅔ along pedicel from base. Sepals fused in proximal half, thick, approximately 1 mm long, stellate-pubescent, green when fresh, greenish brown when dried, glandular-punctate; lobes deltoid, 0.9–1.4 mm wide at base; apex acute. Petals free, lemon yellow to greenish yellow, elliptic-lanceolate, keeled (especially in distal ½) and sometimes somewhat recurved, 5.0–8.1 mm long, 1.5–2.0 mm wide (length:breadth ratio 4–5:1), tip slightly inflexed, glabrous, glandular-punctate, the glands yellow, sometimes greenish when dried. Stamens yellow, arising from calyx base, up to about twice as long as petals (shorter when immature); filaments terete, glabrous, varying in length up to 3× within individual flowers, 3.0–14.0 mm long, 0.3–0.7 mm wide; anthers 1.0–2.0 mm long, each locule c. 0.5 mm wide. Pollen ellipsoid, c. 300 µm long, tricolpate, exine reticulate. Ovary ± cylindrical, slightly swollen at base; carpels 5, fused at base, green, glabrous, glandular-punctate, 1.4–1.6 mm high, 0.5–0.9 mm wide (length:breadth c. 3:1), apex sterile and rounded; style arising from the centre of the carpels, pale yellow, glabrous, slightly longer than stamens, 6.0–14.5 mm long, 0.2–0.4 mm thick; stigma small. Fruit a schizocarp capsule, cocci 5, erect, mid-green to lemon yellow maturing to dark brown, 5.5–7.0 mm high, transversely corrugated, apex rounded and prominently rostrate (beaked) on outer angle, rostrum 1.5–3.0 mm long. Seeds dark brown to black, sub-reniform, 3.0–4.3 mm long, 1.6–2.0 mm wide, the surface smooth; raphe white, flattened, 1.8–2.0 mm long, up to ½ seed length, positioned opposite micropyle. (Figs 1a–g, 2).

Juvenile plants differ from adults in having larger leaves (petiole 5–8 mm long, lamina 53–83 mm long) that tend to be slightly more oblanceolate (widest point 0.6–0.7 lamina length from base) with consistently serrulate to serrate margins. (Fig. 1b).

Selected specimens examined: New South Wales: Central Tablelands: Wollemi National Park: Lee Creek and upper Growee River catchments [specific locality details withheld for conservation purposes]: *S. Clarke s.n.*, 19 Jun 2003 (NSW 613315); *S. Clarke s.n.*, 29 Jun 2003 (*NSW 613314*); *H. Washington s.n.*, 21 Aug 2003, (NSW 613338); *D. Crayn 595, J. Allen, H. Washington, P. Weston*, 28 Aug 2003 (NSW, CANB, K, MEL, PERTH); *S. Clarke s.n.*, 27 Nov 2003, (NSW *613307, 613312, 613313*); *D. Crayn 771, 773–778, J. Allen, S. Clarke, B. Horton, C. Pavich, H. Washington*, 4 Dec 2003 (NSW).

Derivation of epithet: from the Latin *scopulinus* (Greek: *skopelos*, a projecting point of rock, rock, cliff, crag, shelf or ledge) meaning 'pertaining to cliffs' referring to the species' preference for rocky ledges and clefts associated with sandstone 'pagoda' formations.

Flowering period: Flowers have been recorded in April–September with fruits reaching full maturity in December.

Habitat: Found on shallow sandy soils derived from Triassic Narrabeen sandstone (Bembrick 1980) on small ledges or in sloping clefts, at 780–900 m altitude, along narrow 'pagoda' ridge tops. It grows in heath under a sparse over-storey of *Eucalyptus oreades* and *E. sparsifolia*. This community has similarities with Narrabeen Talooby Pagoda Rocky Heath-Scrub as defined by Bell (1997) but does not fit readily into that community, and may be distinct. Species commonly associated with *Leionema scopulinum* include *Acacia obtusifolia, A. terminalis, A. ulicifolia, Allocasuarina distyla, Amperea xiphoclada, Boronia anemonifolia, B. angustisepala, Callitris endlicheri, Calytrix tetragona, Caustis pentandra, Coopernookia barbata, Dampiera adpressa, Dillwynia retorta, Eucalyptus rossii, Epacris reclinata, Exocarpus cupressiformis, Goodenia decurrens, Hibbertia monogyna, Isopogon anemonifolius, Leptospermum arachnoides, L. parvifolium, L. sphaerocarpum, Leucopogon muticus, L. setiger, Logania albiflora, Monotoca scoparia, Ochrosperma oligomerum, Persoonia linearis, Phebalium squamulosum* subsp. *gracile, Philotheca salsolifolia* subsp. *salsolifolia, Platysace linifolia, Pseudanthus pimelioides*. It also grows with four rare plants listed under ROTAP (Briggs & Leigh 1996); *Prostanthera hindii* (coded 2KC-), *Epacris coriacea* (3RC-), *Banksia penicillata* (3RC-), *Homoranthus cernuus* (2RCa) and grows near the endangered *Pultenaea* sp. 'Olinda' (Schedule 1, NSW Threatened Species Conservation Act 1995) and *Pultenaea* sp. aff. *glabra* (*P. glabra* is vulnerable listed under ROTAP; 3VCa).

Distribution: Very restricted range, being found to date only in 29 sites in the north-west of Wollemi National Park around the headwaters of Lee Creek and the Growee River, Central Western Slopes, New South Wales (Fig. 3). Targetted searches of similar habitat nearby by SWC and HW have failed to find further occurrences of this species.

Proposed conservation status: This species comprises fewer than 1500 plants and is restricted geographically to an area 14 km (N-S) by 7 km (E-W). All known populations occur within Wollemi National Park. The species occurs only in relatively inaccessible sites such as ledges and clefts on rocky ridgetops which might indicate sensitivity to fire, but which also appears to protect it from feral browsers such as goats. Strict application of ROTAP (Briggs & Leigh 1996) criteria would lead to rare listing (2RCit). However, other species in the area having similar or greater distributions and population sizes are listed under the NSW Threatened Species Conservation Act 1995 as endangered (Schedule 1, e.g. *Pultenaea* sp. 'Olinda') or vulnerable (Schedule 2, e.g. *Eucalyptus cannonii, Grevillea evansiana, Persoonia marginata*). Since *Leionema scopulinum* does not appear to be any more secure than those species, Schedule 2 (vulnerable) or even Schedule 1 (endangered) listing is considered appropriate.

Notes: *Leionema scopulinum* most closely resembles *L. ralstonii, L. sympetalum* and *L. viridiflorum* but can be distinguished from all those species by the following attributes: the erect inflorescence (the inflorescence is nutant in the other three species), the larger size of the leaves and the larger size of the coccus beak (Wilson 1970, Weston & Harden 2001). *Leionema scopulinum* is restricted to ridge tops in the Lee Creek and upper Growee River catchments (Wollemi National Park) where it grows on ledges and in clefts associated with sandstone 'pagoda' formations. *Leionema sympetalum*, which grows on rocky outcrops in dry sclerophyll forest east of Rylstone (Weston & Harden 2001), is the only species which occurs near *L. scopulinum*.

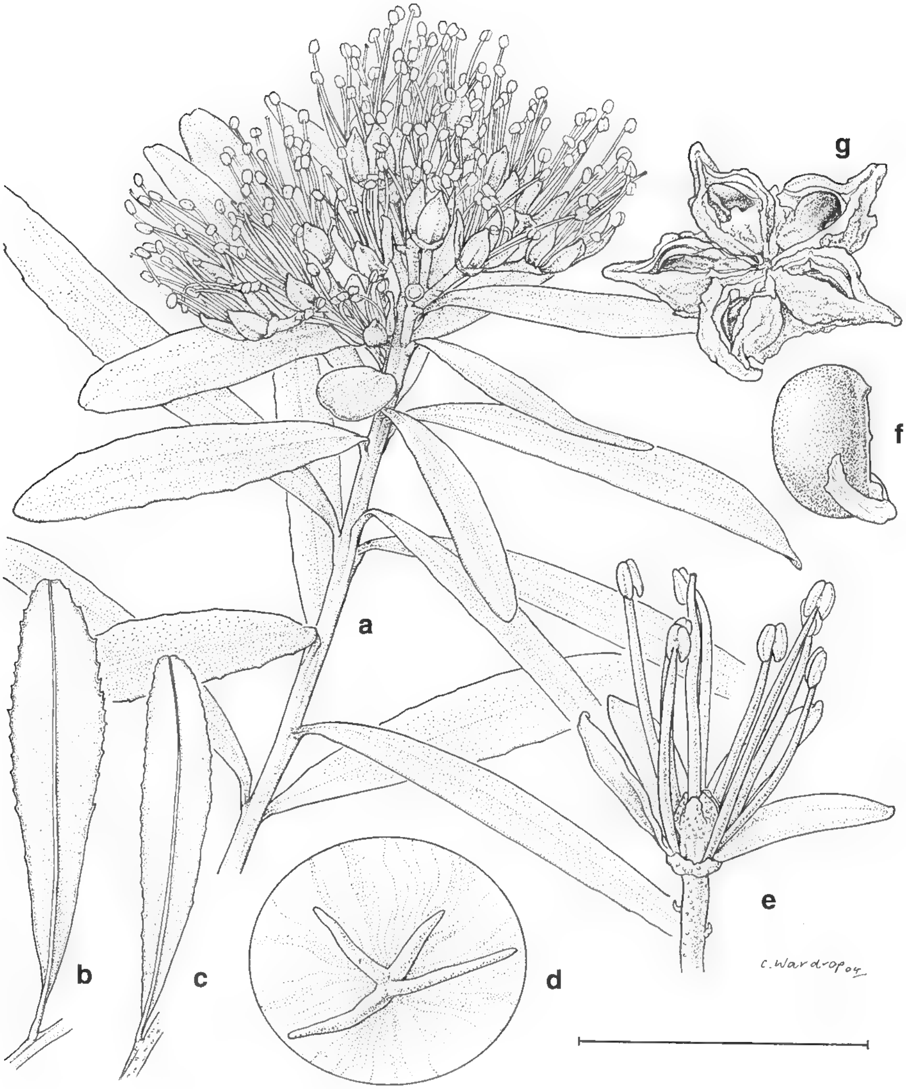

Fig. 1. *Leionema scopulinum* **a,** flowering branchlet (*S. Clarke s.n.*, NSW *613314*); **b,** juvenile leaf (*S. Clarke s.n.*, NSW *613313*); **c,** mature adult leaf (*D. Crayn 595 et al.*); **d,** stellate hair (*D. Crayn 595 et al.*), **e,** flower (*D. Crayn 595 et al.*); **f,** seed (*D. Crayn 778 et al.*); **g,** fruit including seeds (*D. Crayn 778 et al.*). Scale bar a = 3.75 cm, b, c = 4 cm, d = 275 µm, e = 1.2 cm, f = 0.5 cm, g = 1 cm.

However, in addition to the attributes mentioned above, the tubular flowers and glabrous branchlets of *L. sympetalum* prevent the two species being confused. *Leionema ralstonii* grows in open forest and on ridges in the Bega to Eden district and *L. viridiflorum* grows in heath and on trachyte outcrops in the Warrumbungle and Mt Kaputar National Parks (Weston & Harden 2001).

Modified *Flora of NSW* key to some species of *Leionema*

The following replaces the second lead of the first couplet in the *Flora of NSW Leionema* key (Weston & Harden 2001).

1* Petals usually > 7 mm long, erect; stamens considerably exceeding petals.

  12 Petals fused .... **13 L. sympetalum**

  12* Petals free

    13 Stems glabrous, strongly angled .... **12 L. ralstonii**

    13* Stems hairy, ± terete or angled.

      14 Leaves ± spreading, ovate to lanceolate, c. 10 mm long, obtuse; stems pilose .... **11 L. carruthersii**

      14* Leaves ± erect, narrow-oblong to elliptic, 20–65 mm long, obtuse to retuse; stems stellate pubescent to tomentose.

        15 Stems ± terete; leaves 20–40 mm long, margins entire; inflorescence nutant; coccus beak 1.5 mm long .... **14 L. viridiflorum**

        15* Stems angled; leaves 24–65 mm long, margins frequently serrulate; inflorescence erect; coccus beak 1.5–3 mm long .... **15 L. scopulinum**

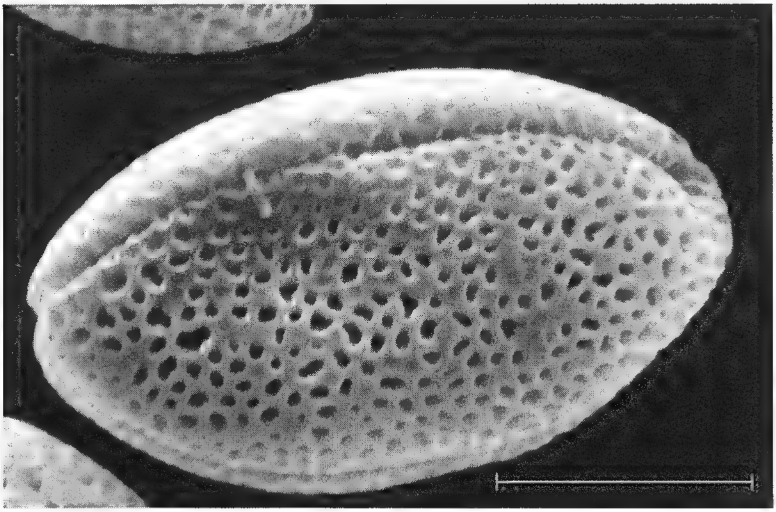

Fig. 2. SEM micrograph of a pollen grain (voucher *D. Crayn 595 et al.*). Scale bar = 10 μm.

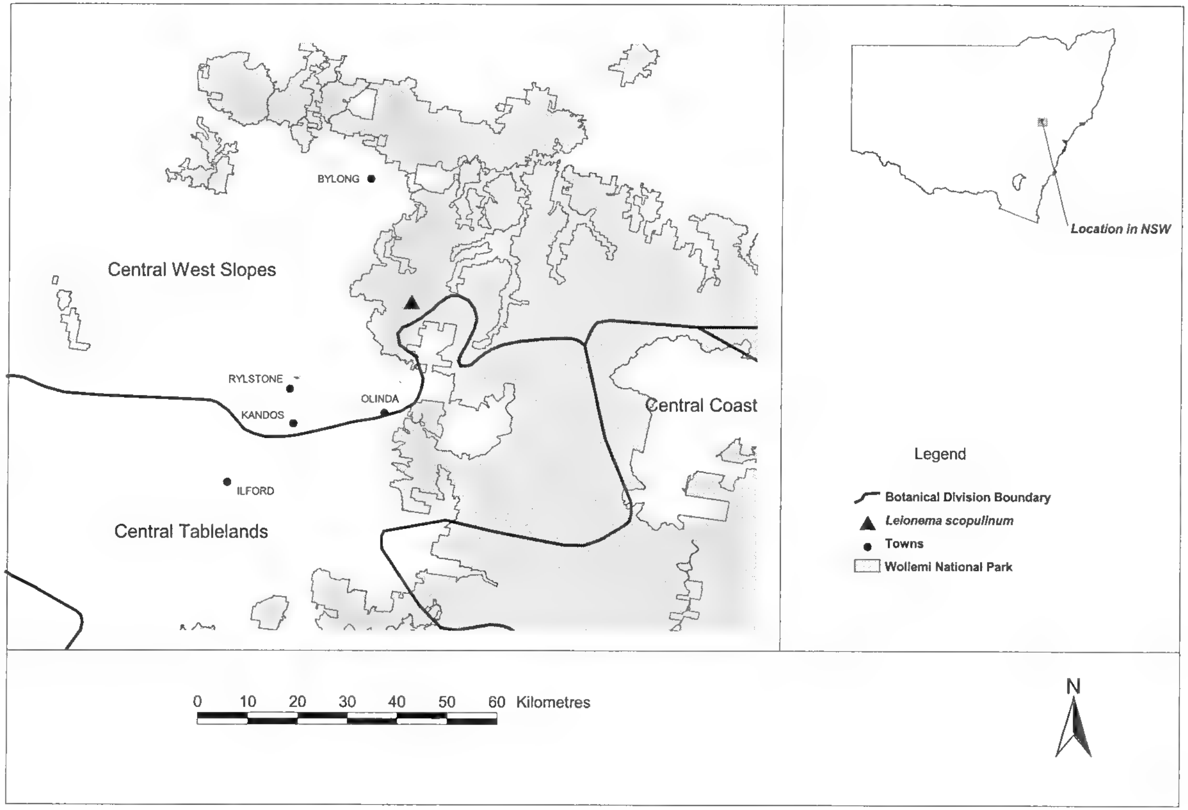

Fig. 3. Approximate location of the known populations of *Leionema scopulinum*.

Table 1. Comparison of selected characteristics of *Leionema scopulinum* and the three species most similar to it, based on the literature (Wilson 1970, Weston & Harden 2002) and observations on specimens held at NSW.

	L. scopulinum	***L. ralstonii***	***L. sympetalum***	***L. viridiflorum***
Branchlets	angled	angled	terete	terete
Branchlet Indumentum	stellate-hairy	glabrous	glabrous	stellate-hairy
Leaf Lamina Shape	elliptic to slightly oblanceolate	oblanceolate to narrowly obovate	obcuneate to elliptic	narrowly oblong to elliptic
Lamina Length	24–65 mm	25–50 mm	15–35 mm	20–40 mm
Lamina Width	4.5–10 mm	5–8 mm	4–8 mm	4–8 mm
Leaf Margin	mostly serrulate	entire	serrulate toward apex	entire
Inflorescence	erect	nutant	nutant	nutant
Flowers per Inflorescence	9 to 32	4 to 7	1 to 3	6 to 12
Petal Fusion	petals free	petals free	petals fused	petals free
Petal Length	up to 8 mm	up to 8 mm	up to 15 mm (including tube)	up to 10 mm
Petal Indumentum	glabrous	glabrous	glabrescent	stellate-hairy
Coccus Height	5.5–7 mm	4–5 mm	c. 4 mm	c. 6 mm
Coccus Beak Length	1.5–3 mm	up to 1 mm	up to 1.5 mm	up to 1.5 mm
Geographical Distribution (NSW)	Wollemi National Park, Central Western Slopes	Bega to Eden, South Coast	Ranges east of Rylstone, Central Tablelands	Warrumbungle and Mt. Kaputar National Parks (mainly), Northern Tablelands and North Western Slopes

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BMH is the grateful recipient of a Janet Cosh studentship from the Botanic Gardens Trust, during which the majority of this work was completed. Jan Allen, Chris Pavich and Peter Weston provided assistance and companionship in the field and helpful general discussions. Jan Allen and Peter Weston provided useful comments on the manuscript, Catherine Wardrop drew the illustrations, Peter Wilson helped with the Latin diagnosis and Carolyn Porter assisted with the electron microscopy.

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Spyridium burragorang (Rhamnaceae), a new species from New South Wales, with new combinations for *Spyridium buxifolium* and *Spyridium scortechinii*

K.R. Thiele and J.G. West

Abstract

K.R. Thiele[1] and J.G. West (Australian National Herbarium, Centre for Plant Biodiversity Research, GPO Box 1600, Canberra, ACT 2601, Australia. [1]Corresponding author) 2004. Spyridium burragorang *(Rhamnaceae), a new species from New South Wales, with new combinations for* Spyridium buxifolium *and* Spyridium scortechinii. Telopea *10(4) 823–829. Spyridium* comprises c. 40 species from southern temperate Australia, characterised by cymose inflorescences, a distinctive floral disk, and schizocarpic fruits in which an indehiscent, papery pyrene containing the seed is shed as the disseminule. Three species from New South Wales, previously included in *Cryptandra,* belong in *Spyridium* where they form a small, distinctive group. One of these, **Spyridium burragorang** K.R.Thiele, is described as new, while new combinations are provided for **Spyridium buxifolium** (Fenzl) K.R.Thiele and **Spyridium scortechinii** (F.Muell.) K.R.Thiele.

Introduction

The Australian and New Zealand genera *Pomaderris* Labill., *Siegfriedia* C.A.Gardner, *Cryptandra* Sm., *Spyridium* Fenzl, *Stenanthemum* Reissek and *Trymalium* Fenzl form a natural tribe in Rhamnaceae (tribe Pomaderreae Reissek ex Endl.; see Richardson et al., 2000) characterised by a stellate indumentum on at least some vegetative or floral parts (a few species in some of these genera lack stellate hairs, but this is almost certainly a secondary loss). However, taxonomic boundaries between genera in this group have been unstable and ill-defined for many years. Bentham (1863: p. 410) noted that '... most [genera], even the most natural ones, are difficult to characterize. The differences in their flowers and fruits are very trifling; they often pass into one another by the finest gradations, and habit, foliage and inflorescence must often be relied upon for fixing generic limits'. Such difficulties have been reiterated by subsequent authors (e.g. Conn, 1983; Wheeler, 1987).

Mueller (1882) followed Hooker (1855) in the most extreme rearrangement of species, by reducing *Trymalium, Spyridium* and *Stenanthemum* to synonymy under a very broadly defined *Cryptandra,* and accepting only the two genera *Cryptandra* and *Pomaderris.* Subsequent authors (e.g. Rodway, 1903; Black, 1926; Ewart, 1930) mostly disregarded this with respect to *Trymalium* and *Spyridium,* although species of *Stenanthemum* remained in *Cryptandra* (or *Spyridium*) until Rye (1995) reinstated the genus.

Such taxonomic fluidity may be expected to result in misplaced taxa and confusion over generic boundaries. Work towards a *Flora of Australia* treatment of Rhamnaceae has allowed an assessment of morphological characters across the family as a whole. While a complete reappraisal of generic concepts in the group awaits a DNA sequence analysis to elucidate areas where morphological characters are inadequate, some misplacements are clear. This paper transfers two species currently misplaced in *Cryptandra* to *Spyridium*, and describes a related species as new.

Spyridium and *Cryptandra*

Spyridium and *Cryptandra* each comprise c. 40 species mostly from southern-temperate Australia, with centres of species diversity in south-eastern Australia, South Australia and south-western Western Australia. Some species of *Cryptandra* (at least as currently circumscribed) extend north into the subtropics.

Traditionally, *Spyridium* and *Cryptandra* have been defined on the basis of a single character of floral morphology, *Cryptandra* flowers having a distinct hypanthium tube and *Spyridium* flowers having only a very short tube or apparently lacking a hypanthium altogether. The hypanthium, however, varies widely and there is a continuous grade in both genera from species in which the tube is very short or indistinct to species in which it is distinct.

A survey of characters throughout the Australian Rhamnaceae, however, shows that three other morphological features can very adequately separate species of *Cryptandra* sensu stricto[1] from *Spyridium* (Table 1; see also Mueller, 1862; Barker, 1995; Coates & Kirkpatrick, 1999).

Although a formal cladistic analysis of these characters is not presented here, the disseminule structure of *Spyridium* and the inflorescence, floral disk and stipule morphology of *Cryptandra* are putative synapomorphies, as each is unique in the tribe Pomaderreae, and indeed in the entire family.

On the basis of these characters, three species of *Cryptandra* from New South Wales, *C. scortechinii*, *C. buxifolia* and the undescribed *C.* sp. A *sensu* Harden (1990) are misplaced and are here transferred to *Spyridium*. All three species have the typical *Spyridium* inflorescence, floral disk and disseminule structure. The three are morphologically closely related, sharing an unusual leaf shape and flowers with a longer free hypanthium tube than other *Spyridium* species (the latter feature explaining their misplacement in *Cryptandra*). Preliminary DNA sequence analyses of the Australian stellate-haired Rhamnaceae support the placement of these species in *Spyridium* (J. Kellermann, June 2004, pers. comm.) and confirms their close relationship as a small monophyletic clade.

Spyridium burragorang *K.R.Thiele*, **sp. nov.**

Type: Wollondilly River, 2 Sep. 1994, *K.R.Thiele 2509*; holo: CANB; iso: AD, MEL, NSW, PERTH. (exact details withheld for conservation purposes).

Cryptandra sp. A, G.J. Harden, in G.J. Harden, *Flora of New South Wales* 1: 371 (1990).

Species nova combinatione sequenti distinguenda foliis oblongis vel anguste oblongis, hypanthio tubuliformi 1.8-2.5 mm longo pilis stellatis solum dispositis distaliter, et disco breviter coalito circum basim tubi hypanthii.

Evergreen shrub 0.2–1.5 m high, diffusely multi-stemmed from base. Young stems densely and shortly greyish- or yellowish-stellate, sometimes with intermixed long, curved or flexuose, simple hairs, the stellate indumentum persisting to older stems of current season's growth. Leaves alternate, distinctly discolorous; lamina oblong to narrowly oblong, (10–)15–25(–30) mm long, (3–)4–6 mm wide, entire, with narrowly recurved to revolute margins, smooth, glabrous and dark green above, densely and closely greyish stellate-pubescent beneath, sometimes also with sparse, ± straight,

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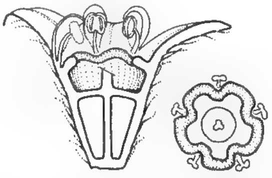
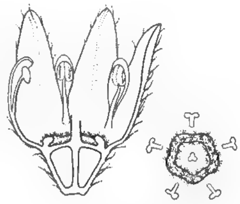
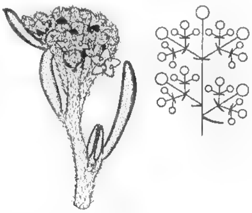
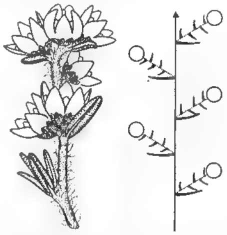
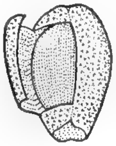
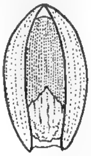
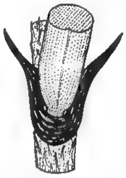
[1] *Cryptandra* as currently circumscribed contains a number of misplaced taxa, particularly from Western Australia; these will be reassigned once DNA sequence analyses make their affinities clear.

Table 1. Diagnostic characters in *Spyridium* and *Cryptandra* s.s.. (Features in bold text are unique to the respective genera and are considered to be synapomorphies)

Spyridium	***Cryptandra***
 Floral disk glabrous, lining the hypanthium and forming a shelf-like projection notched adjacent to the staminal filaments	 **Floral disk usually pubescent, forming a sinuate annulus around the base or summit of the ovary**
 Flowers arranged in loose or dense compound cymose inflorescences, with cymose bracts	 **Inflorescence comprising a single flower subtended by several to many spirally-arranged bracts**
 **Disseminule an indehiscent pyrene with a thin and papery (often ± translucent) wall covered with a crystal layer, the seed loose within the pyrene and lacking an aril*** 	 Disseminule a seed, the pyrenes ± persistent in the mature fruit, splitting along their inner face to release the arillate seed
 Stipules membranous or chartaceous, free from each other and lying between the petiole and stem	 **Stipules indurate, connate around the base of the petiole**

* *Trymalium* also sheds an indehiscent pyrene as disseminule, but in that genus the pyrene wall is crustaceous rather than thin and papery, and lacks the crystal layer of *Spyridium.*

appressed, simple hairs along the midrib, veins and leaf margins; venation penninerved, obscure; base cuneate to obtuse; apex obtuse, minutely apiculate, straight to recurved; petiole 2–4 mm long; stipules 3–6 mm long, persistent, scarious, triangular to narrowly triangular or rectangular, acute, free, glabrous except along the midrib, dark reddish-brown to almost black. Inflorescences comprising terminal, loose or dense, cymose panicles to 1 cm long by 2 cm wide with 30–50 flowers, subtended by whitish floral leaves; inflorescence axes densely stellate-pubescent like the young stems; bracts rich brown, 3–5 mm long, persistent, ovate or triangular, acute, ciliate on the margins, densely pubescent along the midrib, otherwise ± glabrous. Flowers bisexual, sessile, white or cream, 5-merous. Hypanthium tube 1.8–2.5 mm long, 0.8–1.0 mm diameter, sparsely greyish-pubescent or -villous, with mixed simple and stellate hairs; stellate hairs restricted to the distal third. Sepals 1.0–1.2 mm long, spreading, densely pubescent with short, greyish, stellate hairs overtopped by a few long, flexuose, loosely appressed or spreading simple hairs. Petals 0.6–0.7 mm long, erect, cucullate, clawed. Stamens erect, 0.5–0.6 mm long including the 0.4–0.5 mm long anthers. Disk conspicuous, shortly lining the hypanthium tube at the base, smooth, glabrous, notched adjacent to the bases of the staminal filaments and with broad, obtuse, ± free, emarginate lobes between the filament bases. Ovary inferior at anthesis, remaining so after anthesis; ovary roof stellate-pubescent; carpels 3; style glabrous, 2.0–2.6 mm long, with an obscurely 3-lobed stigma. Fruit maturing c.12 months after flowering, a black or grey, obovoid or ellipsoid, schizocarpic capsule c. 2 mm long; pyrenes indehiscent, pale reddish-brown covered with pale crystals, shed from the capsule at maturity. Seed 1.8–2.0 mm long, uniformly reddish-brown; aril lacking or nearly so. (Fig. 1).

Derivation of epithet: Derived from the place name 'Lake Burragorang'.

Distribution and habitat: Endemic to New South Wales in the Wollondilly and adjacent Nattai River valleys, particularly around the upper parts of Lake Burragorang, at 150–300 m altitude. Found on dry, low ridges in *Eucalyptus crebra* forest with a shrubby understorey, in shallow soil over soft sandstone. Often moderately common, but very restricted and most populations cover only a small area. Flowers June–July; fruits the following year.

Notes: *Spyridium burragorang* is closely related to *S. buxifolium* (Fenzl) K.R.Thiele, which differs in having broadly elliptic, acute leaves, pale brown stipules, a hypanthium tube that is densely stellate-pubescent to the base, and in lacking whitish floral leaves. It is also related to *S. scortechinii* (F.Muell.) K.R.Thiele, which differs in its smaller leaves, denser inflorescences lacking whitish floral leaves, and white-woolly flowers.

Spyridium burragorang was first collected by George Caley during one of several expeditions through the Burragorang Valley, following the route of the explorer Barralier. In 1806 Caley travelled upstream along the Wollondilly River to Douglas Flat (Andrews, 1996), the site of one of the main current populations of *Spyridium burragorang*. The specimen collected by Caley bears a label annotated 'Dicky Robinson's, September 1808'. No references to 'Dicky Robinson's' can be found, and the date is presumably in error, as Caley's last expedition from Sydney was in 1807 (Webb, 1995). No further collections are known until those collected in the mid-1960's.

Conservation Status. Although geographically restricted, the species is relatively secure. All populations are in National Parks or restricted-access catchment areas. A conservation code of 2RCa (following the codes of Briggs & Leigh, 1996) is suggested.

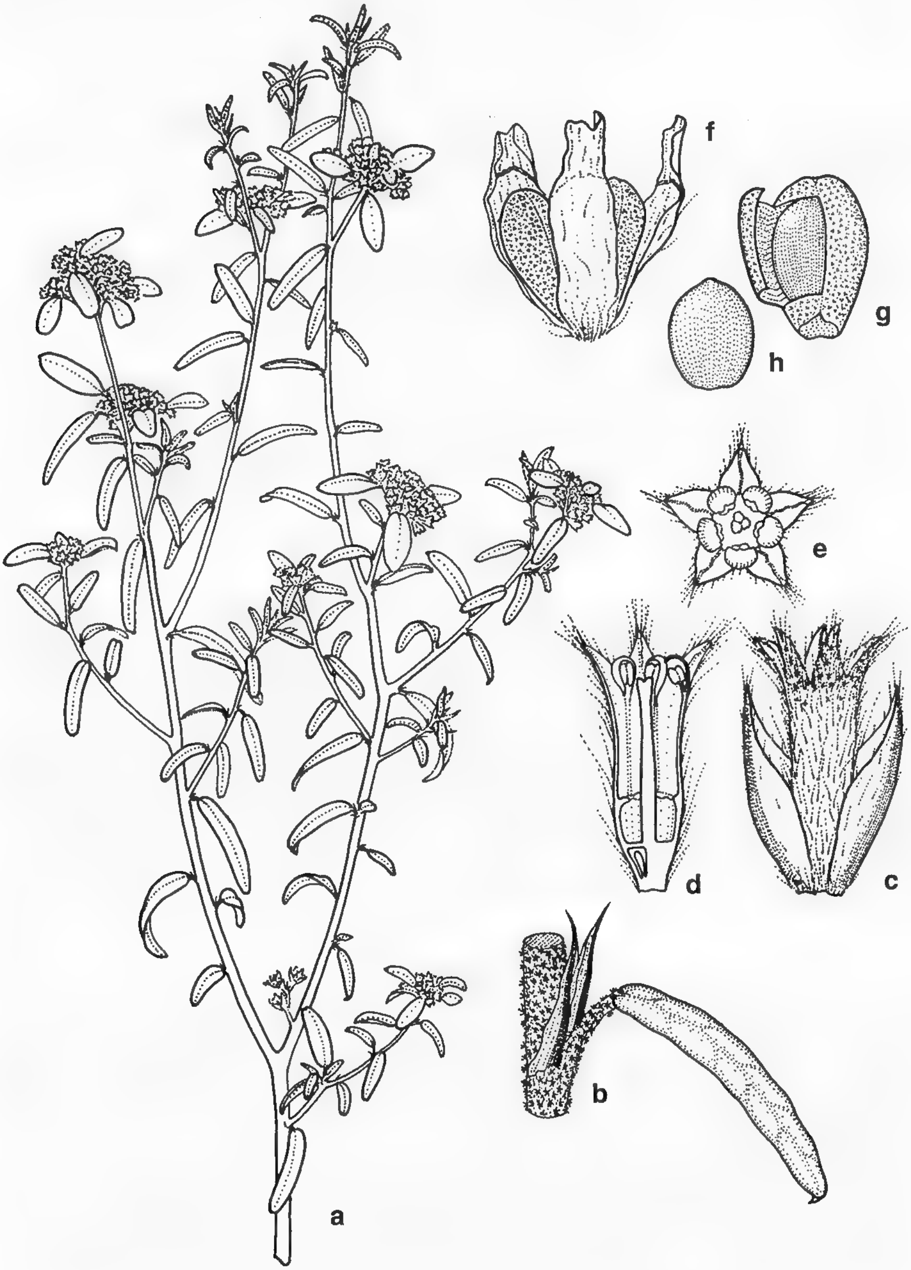


Fig. 1. Spyridium burragorang a, habit × 0.5; **b**, leaf and stipule × 5; **c**, flower with bracts × 10; **d**, flower in LS × 10; **e**, flower from above × 10; **f**, fruit, showing pyrenes within the schizocarpic hypanthium × 10; **g**, pyrene, opened to show the seed × 10; **h**, seed × 10.

Other specimens examined (exact details withheld for conservation purposes): NSW 'Dicky Robinson's', Sep 1808, *G. Caley s.n.* (NSW); Burragorang Valley, 26 Feb 1967, *L.A.S. Johnson & A Rodd 441* (CANB, NSW); Nattai River, 29 Jun 1974, *I. Olsen 2162* (NSW); E of Warragamba Dam, Feb 1969, *R. Mitchell s.n.* (CANB, NSW); Between Tonalli R. and Byrnes Ck, 17 Aug 1966, *R. Mitchell 411* (NSW).

New Combinations

Spyridium buxifolium *(Fenzl) K.R.Thiele*, **comb. nov.**

Cryptandra buxifolia Fenzl in S.F.L.Endlicher, *Enum. Pl.* 23 (1837).

Type: New South Wales, *A. Cunningham s.n.*; **lecto**: K (Hunter's River) (!)- **here designated**; syn (!): K, BRI 70463, BRI 70464, CBG 7800636 at CANB, CBG 7800637 at CANB.

Spyridium scortechinii *(F.Muell.) K.R.Thiele*, **comb. nov.**

Cryptandra scortechinii F.Muell., *Australas. Chem. Druggist* 6: 72 (1884); *Stenanthemum scortechinii* (F.Muell.) Maiden & Betche, *Proc. Linn. Soc. New South Wales* 27: 57 (1902).

Type: On the Severn, *B. Scortechini s.n.*; holo: MEL 2223246; iso: NSW(!).

Acknowledgments

We thank Dennis Ashton and Roger Lembit for advice on the distribution of *Spyridium burragorang* and Sydney Water Board for permission to enter the Lake Burragorang catchment area. Alan Fairley provided useful information on Caley's expedition, and Jürgen Kellermann shared his early results of a DNA sequence analysis of the Pomaderreae. Ian Telford and Frank Udovicic provided comments on the manuscript, Ian Brooker translated the Latin diagnosis, and Kirsten Cowley searched the reference material. The director of NSW allowed access to herbarium material for study. Two anonymous reviewers provided useful comments. This paper arises from work preparatory to a *Flora of Australia* treatment for Rhamnaceae, supported by the Australian Biological Resources Survey.

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Three new species of *Leptospermum* (Myrtaceae) from Queensland and northern New South Wales

A.R. Bean

Abstract

Bean, A.R. (Queensland Herbarium, Brisbane Botanic Gardens Mt Coot-tha, Mt Coot-tha Road, Toowong, Queensland 4066, Australia) 2004. Three new species of Leptospermum *(Myrtaceae) from Queensland and northern New South Wales.* Telopea *10(4): 831–838.* The new species **Leptospermum anfractum, Leptospermum benwellii** and **Leptospermum barneyense** are described and illustrated. Herbarium and field keys to the identification of taxa beloging to *L. brachyandrum* subgroup are presented.

Introduction

In her revision of *Leptospermum,* Thompson (1989) established informal taxonomic subgroups within the genus. In the *L. brachyandrum* subgroup, she included six species from south-western W.A. and six species from north-eastern Australia and New Guinea. Since this time, *L. madidum* and *L. pallidum* have been added (Bean 1992), and two of the species described here (*L. anfractum, L. benwellii*) belong to this subgroup. As the subgroup has considerably increased in number since Thompson's treatment, it seems appropriate to present new identification keys for it.

The third species described here (*L. barneyense*) belongs to the *L. polygalifolium* subgroup.

Leptospermum anfractum *A.R.Bean* **sp. nov.**

affinis *L. brachyandro* autem cortice decidua ad planitiem soli, maronina ante exuentem; pedicellis glabris 1.3—2.8 mm longis, petalis sine glandulis olei differt.

Type: Queensland. North Kennedy District: Mount Stuart, 9 km S of Townsville, 14 December 1991, *A.R. Bean* 3867 (holo BRI; iso: MEL, QRS).

Spreading shrub to 2 m high, trunks and stems twisted and contorted; bark smooth and deciduous throughout, purple to maroon coloured, shedding to white. Branchlets sparsely pubescent, glabrescent, stem flanges present, conspicuous. Leaves alternate, subsessile, discolorous, linear, 17–30 × 1.8–4.4 mm, apex acute to acuminate; appressed indumentum persistent on lower surface; upper surface glabrous. Inflorescence axillary, comprising 1–6- bracteolate monads, floral bracts shed before anthesis. Flowers 5–7.5 mm diameter; pedicels 1.3–2.8 mm long at anthesis; hypanthium glabrous, 1.9–2.4 mm long; sepals obtuse, c. 0.6 mm long, margin ciliate; petals white, obovate to orbicular, 1.8–2.6 mm long, oil glands absent. Stamens 0.7–1.0 mm long, anthers versatile, cells parallel; stigma capitate; roof of ovary glabrous. Ovary 3-locular. Fruit thin-walled, glabrous, campanulate to hemispherical, 1.8–2.2 mm long, 2.9–3.4 mm diameter, sepals persistent. Seeds pale brown, narrowly obovoid to cuneate, reticulate, 0.9–1.1 mm long. (Fig. 1).

Distribution: *L. anfractum* is endemic to Queensland. The main area of distribution is from Cardwell to Proserpine, including some continental islands, and there is a disjunct population near Laura on Cape York Peninsula.

Habitat: It inhabits rocky ridges and cliff-lines of sandstone, rhyolite or granite.

Phenology: Flowers are recorded from August to January; fruits from November to May.

Affinities: I had originally included *L. anfractum* within *L. brachyandrum* (Bean 1992), but additional material has persuaded me that it is distinct at species level. *Leptospermum anfractum* differs from *L. brachyandrum* by having bark deciduous to ground level (lower stems rough-barked for *L. brachyandrum*), recurved leaf margins (vs. flat), leaves with only the midvein visible (3–5 longitudinal veins visible for *L. brachyandrum*), new growth appearing glabrous to naked eye (conspicuously silky-hairy for *L. brachyandrum*), upper leaf surface glabrous (with appressed hairs, except on old leaves for *L. brachyandrum*), pedicels 1.3–2.8 mm long (0.6–1.1 mm long for *L. brachyandrum*), petals without oil glands (oil glands readily visible for *L. brachyandrum*), and fruits 1.8–2.2 mm long (2.5–2.7 mm long for *L. brachyandrum*). The habitat of *L. anfractum* (rocky ridges and cliff-lines) is also very different to that of *L. brachyandrum* (riparian communities with sandy soil).

Conservation status: *Leptospermum anfractum* is present on several coastal mountains and on some continental islands, including at least three populations within national parks. The places where this species grows are totally unsuitable for agriculture or grazing, hence it is not considered to be under any threat.

Etymology: from the Latin *anfractus* meaning bending, winding or crooked. This is in reference to the contorted stems and branches of the species in its natural habitat.

Specimens examined: Queensland. Cook District: Turtle Rock, SE of Laura, *A.R. Bean 5512 & P.I. Forster*, 22 Jan 1993 (BRI, K); at Turtle Rock lookout on Split Rock walking trail, 14 km S of Laura, *V.J. Neldner 3887*, 28 Jun 1992 (BRI, DNA, NSW). North Kennedy District: S end of Gloucester Island, *G.N. Batianoff 940522 & H. Dillewaard*, 11 May 1994 (BISH, BRI, CANB, MEL, NSW); Cockatoo Creek area, Mt Elliot, S of Townsville, *A.R. Bean 3588*, 11 Aug 1991 (BRI, CANB, K, MEL, NSW, PERTH); Mt Abbot, 50 km W of Bowen, *A.R. Bean 4244*, 29 Mar 1992 (BRI); Mt Abbot, 50 km W of Bowen, *A.R. Bean 4872*, 2 Aug 1992 (BRI, MEL); Mingela Bluff, *R. Cumming 9294*, 21 Sep 1989 (BRI); Cape Upstart peninsula, *Hinson* CU4, Jun 1967 (BRI); SF461, Five Mile Ck, c. 6.5 km S of Cardwell, *Thorsborne* 476 & *Travers*, 7 Oct 1978 (BRI); Stonehaven Bay, Hook Island, *C. Warrian CW706*, 14 Jul 1985 (BRI). South Kennedy District: Scawfell Island NP, 50 km ENE of Mackay, *G.N. Batianoff 6103 & E. Hegerl*, 17 Nov 1986 (AD, BRI, CANB, DNA, MEL, NSW).

Leptospermum benwellii *A.R.Bean* sp. nov.

Affinis *L. luehmannii* autem costis elevatis caulis conspicuis, ramulis glabris praeter margines costium elevatarum, foliis trivenatis, petalis glandulis olei praeditis, pedicellis fructuum 1.3–1.9 mm longis differt.

Type: New South Wales. North Coast: just NE of Munningyundo Mountain, Nymboida N.P., between Grafton and Glen Innes, *A.R. Bean 20113*, 22 March 2003 (holo BRI; iso CANB, NSW).

Spreading shrub to 3 m high; bark smooth and deciduous throughout, orange or green coloured, peeling in ribbons. Branchlets with conspicuous stem flanges, pubescence sparse and mainly on margins of stem flanges. Leaves alternate, subsessile, discolorous, narrowly-elliptic, 18–25 × 2.7–5.0 mm, apex obtuse or mucronate; margins of young leaves with silky hairs, otherwise glabrous. Inflorescence axillary, comprising 1–3 bracteolate monads, floral bracts shed before anthesis. Flowers with pedicels c. 1.2 mm long at anthesis; hypanthium glabrous, c. 3 mm long; sepals obtuse, 1.2–1.4 mm long, inner and outer surfaces glabrous, margin ciliate; petals white, obovate to orbicular, 2.6–2.7 mm long, oil glands present. Stamens 1.5–2 mm long, anthers versatile, cells parallel; stigma capitate; roof of ovary glabrous. Ovary 3-locular. Fruit thin-walled, campanulate to hemispherical, 2.5–3 mm long, 4–4.7 mm diameter, glabrous; sepals sparsely hairy, persistent. Seeds pale brown, obovoid to ellipsoidal, reticulate, 0.8–0.9 mm long. (Fig. 2).

Fig. 1. Leptospermum anfractum a, flowering branchlet × 1; **b**, leaf, abaxial surface × 4; **c**, flower × 8; **d**, infructescence × 6. a, c from *Bean 3867* (BRI); b, d from *Bean 11562* (BRI).

Distribution and habitat: Known only from the type locality, where it grows on steep slopes of acid volcanic rock, in an open shrubland community. Associated species include *Acacia falciformis, Xanthorrhoea malacophylla, Ozothamnus diosmifolius, Plectranthus graveolens*, and stunted specimens of *Eucalyptus campanulata* and *E. notabilis*.

Phenology: Flowers are recorded for November; fruits from March to May.

Affinities: *Leptospermum benwellii* is closely related to *L. luehmannii* F.M.Bailey, but differs by the presence of conspicuous stem flanges (stem flanges absent for *L. luehmannii*), branchlets mostly glabrous except for margins of stem flanges (branchlets silky hairy *L. luehmannii*), leaves 1–3-veined (5–7 veined for *L. luehmannii*), leaves 2.7–5 mm wide (4.1–7.4 mm wide for *L. luehmannii*), petals with oil glands (oil glands absent for *L. luehmannii*), fruiting pedicels 1.3–1.9 mm long (0.5–1.3 mm long for *L. luehmannii*) and fruiting valves at rim level (exserted for *L. luehmannii*)

Conservation status: The only known population comprises about 50 mature-aged plants, if one includes those regenerating from a recent fire. Using the guidelines of the IUCN (IUCN, 2001), a category of Endangered is proposed (criterion EN D).

Etymology: Named for Andrew Samuel Benwell, a talented botanist and ecologist, who discovered this species during a survey of montane heathlands in northern New South Wales.

Specimens examined: New South Wales. North Coast: Mt Munningyundo, Nymboida N.P., west of Grafton, *A. Benwell* 4, May 2000 (BRI).

Herbarium key to *Leptospermum* species from northern and eastern Australia, belonging to the *L. brachyandrum* subgroup

1. Flowers and fruits 4–20, sessile, in congested clusters 2
   Flowers and fruits 1–3 per inflorescence, not tightly clustered, with pedicels >0.5 mm long 3

2. Leaves 7–11 mm wide, base obtuse; fruits 5–6.5 mm diameter .... **L. speciosum**
   Leaves 3–5 mm wide, base cuneate; fruits 3–4 mm diameter .... **L. whitei**

3. Stem flanges present on young branchlets 4
   Stem flanges absent 7

4. Leaves 7–13 mm long, lower surface with dense appressed hairs .... **L. purpurascens**
   Leaves 20–50 mm long, those remote from apex of shoot glabrous or with scattered hairs on lower surface 5

5. Leaf apex obtuse or mucronate .... **L. benwellii**
   Leaf apex acute to acuminate 6

6. Leaves with only midvein visible; new growth appearing glabrous to naked eye; pedicels 1.3–2.8 mm long; petals without oil glands .... **L. anfractum**

   Leaves with 3–5 longitudinal veins; new growth conspicuously silky-hairy; pedicels 0.6–1.1 mm long; petals with oil glands .... **L. brachyandrum**

7. Ovary 5-locular; fruits 5-locular, with conspicuous dome; pedicels and peduncles longer than 3 mm .... **L. pallidum**
   Ovary 3-locular; fruits 3-locular, valves at about rim level; pedicels 0.5–1.3 mm long, peduncles absent 8

8. Leaves 7–10 times longer than broad, apex acute; fruits 3–4 mm diameter .... **L. madidum**
   Leaves 3.5–4.5 times longer than broad, apex obtuse; fruits 4.5–5 mm diameter .... **L. luehmannii**

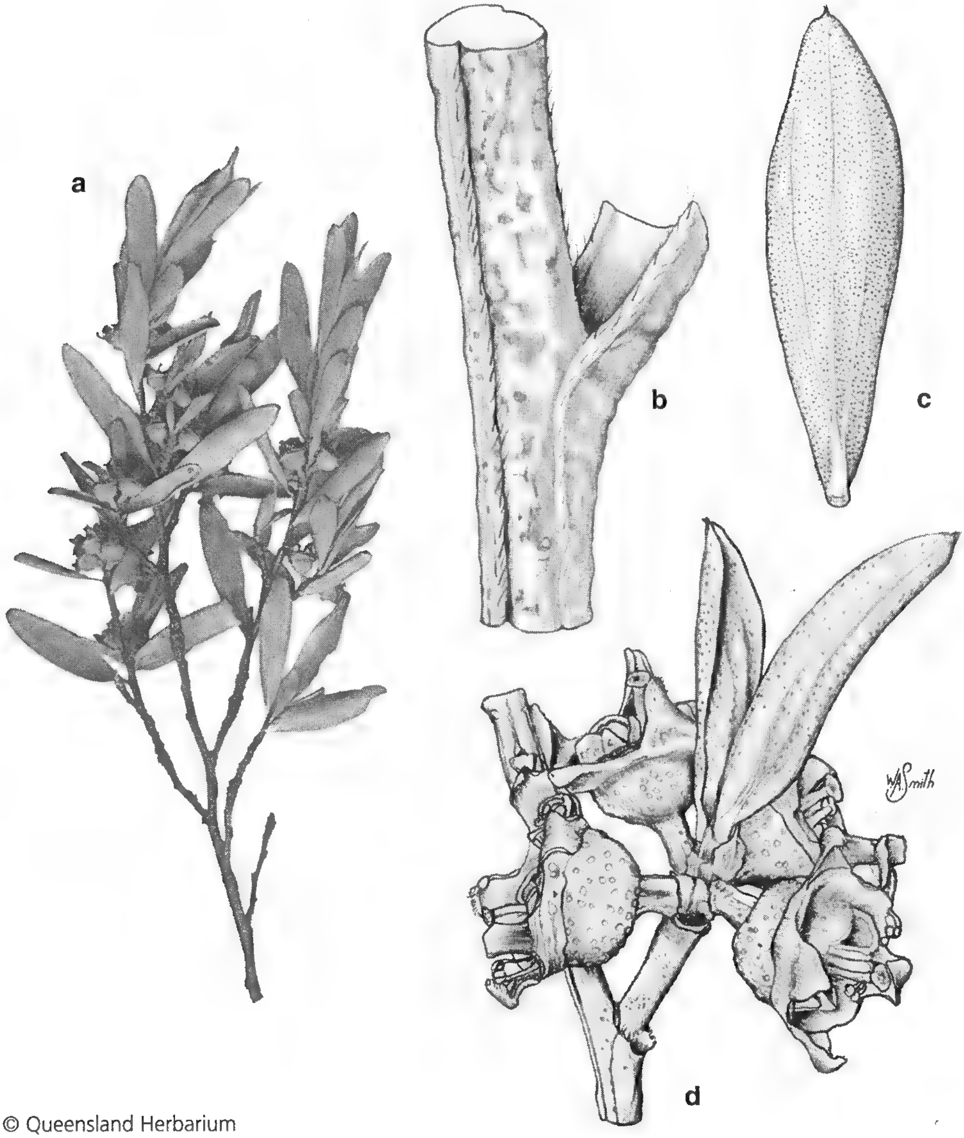

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Fig. 2. Leptospermum benwellii a, flowering branchlet × 1; **b**, branchlet, showing stem flanges with hairs along margin × 18; **c**, leaf, abaxial surface × 4; **d**, infructescence × 6. All from *Bean 20113* (BRI).

Field key to *Leptospermum* species from northern and eastern Australia, belonging to the *L. brachyandrum* subgroup

1. Bark rough, grey, persistent throughout 2
   Bark smooth and deciduous throughout, or with some rough bark at the base 4

2. Leaves quickly glabrescent, yellowish-green; fruits 5-locular, pedicellate .... **L. pallidum**
   Leaves persistently hairy, grey-green; fruits 3-locular, in sessile clusters 3

3. Leaves 7–11 mm wide, base obtuse; dried fruits 5–6.5 mm diameter .... **L. speciosum**
   Leaves 3–5 mm wide, base cuneate; dried fruits 3–4 mm diameter .... **L. whitei**

4. Bark rough at base, especially in larger plants; young leaves and branchlets conspicuously hairy .... **L. brachyandrum**
Bark smooth throughout; young leaves (upper surface) and branchlets appearing glabrous to the naked eye 5

5. Branchlets fully pendulous; riparian habitats on Cape York Peninsula, N.T. Top End, and Kimberley .... **L. madidum**
Branchlets not or somewhat pendulous; growing on rocky hillsides or clifflines; eastern Qld and north-eastern NSW 6

6. Leaves 10–15 mm long, lower surface densely hairy .... **L. purpurascens**
Leaves 20–50 mm long, lower surface glabrous or with scattered hairs 7

7. Newly exposed bark white; leaves linear, 7–10 times longer than wide, apex acute to acuminate; dried fruits 2.9–3.4 mm diameter .... **L. anfractum**
Newly exposed bark green; leaves narrowly elliptic, 3.5–7 times longer than wide, apex obtuse or mucronate; dried fruits 4–4.7 mm diameter 8

8. Leaves 2.7–5 mm wide, 1–3- veined; fruiting valves at rim level .... **L. benwellii**
Leaves 4.1–7.4 mm wide, 5–7 -veined; fruiting valves exserted .... **L. luehmannii**

Leptospermum barneyense *A.R.Bean* **sp. nov.**

affinis *L. variabili* autem fructibus longioribus latioribusque et sessilibus, foliis latioribus (2.8–5 mm latis), sepalis plerumque roseis, hypanthio in fructu longiore tholo a valvis exsertis formato differt.

Type: Queensland. Moreton District: North Ridge, Mt Barney National Park, *A.R. Bean 7743 & D. Halford*, 16 July 1994 (holo BRI; iso MEL, NSW).

Shrub to 2.5 m high, stems somewhat gnarled; bark rough and fibrous throughout, grey in colour. Branchlets glabrous, with conspicuous stem flanges. Leaves alternate, subsessile, concolorous, oblanceolate, 17–23 × 2.8–5.0 mm, flat except near apex where distinctly incurved, apex apiculate or mucronate; younger leaves hairy towards base on lower surface, otherwise glabrous. Inflorescences comprising a single flower on modified shoots in leaf axils; floral bracts shed before anthesis. Flowers 17–25 mm diameter, sessile; hypanthium glabrous, 3.5–4.3 mm long; sepals obtuse, 2.9–3.8 mm long, with abundant oil glands, glabrous, usually pink; petals white or occasionally pink, obovate to orbicular, 5.5–7.8 mm long, oil glands present. Stamens 2.5–3.0 mm long, anthers versatile, cells parallel; stigma capitate; roof of ovary glabrous. Ovary 5-locular. Fruit thick-walled, glabrous, 5.5–8 mm long, 8.0–11.5 mm diameter, sessile; hypanthium hemispherical, exserted valves forming a dome, height of dome always less than hypanthium, sepals tardily deciduous. Seeds brown, narrowly cuneiform, striate, 2.5–3.0 mm long. (Fig. 3).

Distribution: Confined to Mt Barney and Mt Maroon in extreme south-eastern Queensland.

Habitat: It grows at altitudes between 600 and 1350 metres, in montane heathland or low eucalypt woodland on rhyolite.

Phenology: Flowers are recorded between June and October; fruits may be found at any time of the year.

Affinities: *Leptospermum barneyense* is closely related to *L. variabile*, but differs by the fruits 5.5–8 × 8–11.5 mm (4.5–5.5 × 6.7–8 mm for *L. variabile*), the sessile flowers and fruits (pedicel 0.4–1.5 mm long for *L. variabile*), the leaves 2.8–5 mm wide (1.8–2.9 mm wide for *L. variabile*), the fruiting hypanthium longer than the dome formed by exserted valves (hypanthium equal to or shorter than dome for *L. variabile*) and the usually pink sepals (white for *L. variabile*).

Conservation status: There are some thousands of plants present within the Mt Barney N.P.

Etymology: The epithet refers to the Mount Barney National Park, where the species is endemic.

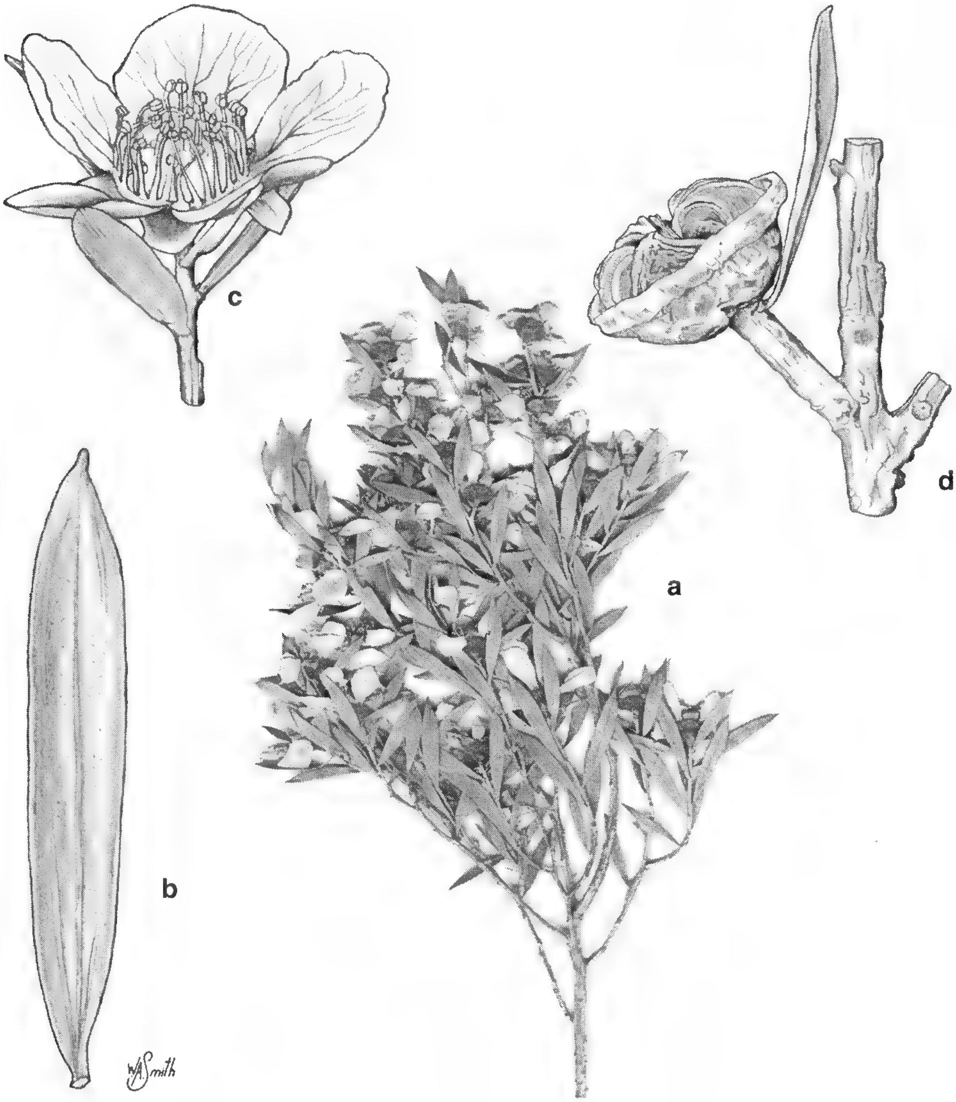

Fig. 3. Leptospermum barneyense a, flowering branchlet × 0.8; **b,** leaf, abaxial surface × 6; **c,** flower × 3; **d,** fruit × 4. a, b, d from *Bean 6665* (BRI); c from *Bean 7743* (BRI).

Selected Specimens examined: Queensland. Moreton District: Mt Maroon, SW of Rathdowney, *A.R. Bean 6665*, 3 Oct 1993 (BRI, CANB, MEL, NSW); Mt Barney, *S.L. Everist 1360*, 13 Oct 1935 (BRI); Mt Barney, *S.L. Everist 4134*, 25 Sep 1949 (BRI); Mt Maroon, *S.L. Everist 7031*, 28 Jan 1962 (BRI); Mt Barney, summit area East Peak, *P.I. Forster PIF15723*, 4 Sep 1994 (BRI, CANB, MEL); Mt Barney, S of Ipswich, *N. Michael 2630*, Sep 1936 (BRI); Mt Maroon, NNE of Mt Barney, *V. Moriarty 484*, Sep 1970 (BRI, CANB); Mt Barney, east peak summit area, *J.M. Powell 1003 & J. Armstrong*, 26 Sep 1977 (BRI, NSW).

Acknowledgments

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SHORT COMMUNICATION

Lectotypification of *Alisma oligococcum* F. Muell. (Alismataceae)

S.W.L. Jacobs

For forthcoming treatments of Australian aquatic plants and the *Flora of Australia* it is necessary to lectotypify *Alisma oligococcum* F.Muell., the basionym of *Caldesia oligococca* (F.Muell.) Buchenau.

Alisma oligococcum F.Muell. *Fragm.* 1: 23 (1858).

T: Upper Victoria River, s.d., *F.Mueller* (MEL 501493, **lectotype, selected here**).

Basionym of *Caldesia oligococca* (F.Muell.) Buchenau. *Botanische Jahrbucher für Systematik, Pflanzengeschichte und Pflanzengeographie* 2: 479 (1882).

Remaining syntype: Moreton Bay, s.d., *W. Hill* (MEL).

Notes: When Mueller described *A. oligococcum* he listed three collections, (i) Upper Victoria River, (ii) Moreton Bay (W. Hill) and (iii) 'in vicinia sinus Gulf of Carpentaria'; consequently it is necessary to lectotypify the name. The first two collections can be recognised readily in MEL and are identifiable as this species. There are a few possibilities for the last in MEL, but none have the exact label details as cited. The specimen from Upper Victoria River (MEL 501493) best matches the description and maintains current usage and is therefore selected as the lectotype.

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SHORT COMMUNICATION

A new combination in *Lachnagrostis* (Gramineae)

S.W.L. Jacobs

The new combination, *Lachnagrostis punicea*, was validly made in Jacobs (2002). Unfortunately, there was also a combination for a subspecies of this species (*L. punicea* subsp. *filifolia*) made in Jacobs (2001) that was not validly published. This combination is made here.

Lachnagrostis punicea (A.J. Brown & N.G. Walsh) S.W.L. Jacobs (837: 2002)

Type: Tasmania: New Norfolk, 15 Nov 1840, *Ballantine 1446* (K).

Based on: *Agrostis billardieri* var. *setifolia* Hooker (115: 1858); *Agrostis punicea* A.J. Brown & N.G. Walsh (83–86: 2000).

Agrostis aemula var. *setifolia* (Hook. f.) Vickery (1941).

Lachnagrostis punicea *subspecies* **filifolia** (*Vickery*) *S.W.L. Jacobs*, **comb. et stat. nov.**

Basionym:: *Agrostis billardieri* var. *filifolia* Vickery (110: 1941).

Type: Victoria: Hawkesdale, Dec 1901, *Williamson* (K).

Agrostis punicea var. *filifolia* (Vickery) A.J. Brown & N.G. Walsh (2000)

Acknowledgments

Thanks to Marco Duretto and Werner Greuter who kindly pointed out the problem with my treatment of *Lachnagrostis* (Jacobs 2001).

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SHORT COMMUNICATION

Lectotypifications of five Australian species of floating-leaved *Potamogeton* (Potamogetonaceae)

Sabine E. Papassotiriou

The following lectotypifications are required for a forthcoming *Flora of Australia* treatment.

Potamogeton australiensis A. Bennett, *Journal of Botany* 48: 149 (1910).

Type: Merrigang [Merrigig] Creek, near Barwon River, Vic, *J.B. Wilson s.n.*, 1883 (BM, specimen reference no. 2500, **lectotype, selected here**), labelled *P. coloratus* var. *jamaicensis* Griseb.

Remaining syntypes: Merrigang [Merrigig] Creek, near Barwon River, Vic, *J.B. Wilson s.n.*, 1883 (NSW 3755), labelled *P. coloratus* var. *jamaicensis* Griseb.; New South Wales, *J.H. Maiden s.n.*, 25.7.1898 (NSW 3809), labelled *P. coloratus* var. *jamaicensis* Griseb.

Notes: In his description of *P. australiensis*, Arthur Bennett stated that 'Lately Mr. Maiden, the Director of the Sydney Botanic Gardens, has sent me numerous unnamed Australian specimens. Among them a good sheet of what has passed for *P. coloratus* Hornem. var. *jamaicensis* Griseb., containing many specimens.'

Both specimens at NSW are annotated as *P. australiensis* A. Bennett in Bennett's handwriting. Neither specimen matches the description completely, although both specimens clearly belong to the same species.

The collection at the BM also contains several specimens collected at 'Merrigang [Merrigig] Creek, near Barwon River, Vic', labelled *P. coloratus* var. *jamaicensis* Griseb. and also annotated by Arthur Bennett. Of these specimens, the specimen with reference no. 2500 is the most complete specimen and is a good match for the protologue. I have therefore selected this specimen as the lectotype.

Potamogeton reduncus Hagstrom, *Kungl. Sv. Vet. Akademiens Handlingar* Vol. 55(5): 172 (1916).

Type: S. Western Australia, *James Drummond ex Mueller s.n.*, s.d. (S, specimen no. 4255, **lectotype, selected here**), 'not been refound' F. v. Mueller written on a herbarium label of Arthur Bennett, F.L.S. England. Annotated by Hagstrom '! O.H. 07'.

Notes: Hagstrom described *P. reduncus* citing the following specimen: 'S. Western Australia (hb. Stockholm). On the label Mr. Ar. Bennett has noted: >not yet refound. f. Baron v. Mueller; leg. James Drummond ex Mueller< etc and has determined it as *P. drummondii* Benth.'

The Director of S kindly loaned a specimen that fits the label information given in the protologue. The annotation '! O.H. 07' above the label indicates that Hagstrom saw this sheet in 1907, prior to the publication of the description of this species in 1916. The herbarium label identifies it as a specimen from Arthur Bennett's herbarium, and it is therefore reasonable to assume that this is from Bennett's collection, which may also explain its poor condition. However, efforts to find another, better, specimen fitting Hagstrom's citation, in herbaria around Australia and Europe were fruitless. I have therefore selected the specimen no. 4255 from the herbarium at S as lectotype.

Potamogeton similis A. Bennett, *Journal of Botany* 40: 146 (1902).

Type: Swan River Colony (Nouvelle Hollande), *J. Drummond 117*, 1847 (G8006-1, **lectotype, selected here**).

Remaining syntypes: Swan River, *Mr Drummond 117*, 1847 (G806-2), Scripsit Boissier, Conservatoire botanique, Genêve, Herbier BOISSIER, séries n'ayant pas servi Bla réduction du *Flora Orientalis; Mr Drummond*, 1847 (G8006-3), Conservatoire botanique, Genêve, Herbier BOISSIER, séries n'ayant pas servi Bla réduction du *Flora Orientalis.*

Notes: Arthur Bennett described *P. similis* citing the following specimens from Western Australia as well as Tasmania: 'Swan River, W. Australia; Drummond, no. 117, 1847 and 1851; Tasmania: Swanport, Dr. Story, ex. F. Mueller; Lagoon, York Plains, near Oatlands, Herb. Boissier.'

The Director at K kindly lent a sheet filed as the type but labelled as 'Southport (Tasmania), Story, Herb. F. Mueller;. It is possible that this is the specimen Bennett referred to as collected at 'Swanport'. Dr Story lived near Swansea, about 60 km north of Swanport. It also appears that there is no Southport in Tasmania. However, this sheet also contains a mixed collection of what appears to be *P. cheesemanii*, the senior synonym to *P. similis*, and a fragment of P. australiensis, which was annotated by Bennett as *P. cheesemanii.*

The three sheets at G, kindly on loan by the Director at G, match the protologue of *P. similis* well, are uniform and in good condition. Sheet G8006-1 is tied with a handwritten label bearing the number 117. Sheet G8006-2 has a herbarium label with the number 117, whereas sheet G8006-3 bears no collection number. I have selected the sheet G-8006-1 as the lectotype.

Potamogeton sulcatus A. Bennett, *Annalen des K. K. Naturhistorischen Hofmuseums, Vienna* 7: 294 (1892).

Type: Murray River, *Erkrit s.n.*, 1892 (BM, **lectotype, selected here**), copiously annotated by A. Bennett.

Remaining syntypes: New South Wales: Sydney (Port Jackson), *Robert Brown s.n.*, 1802-1805 (BM, 2 sheets) on the label of one the remark: 'Potamogeton sulcatus A. Bennett (Type collection)'.

Notes: *P. sulcatus* was described by Arthur Bennett citing four specimens: 'Australien, Victoria, Murray River l. Dr. v. Wawra (Reise des Prinzen Philipp August v. Sachsen-Coburg um die Welt, 1872-1873, Nr. 476); Murray River l. J.P. Erkrit 1892 ex Baron F. v. Mueller in herb. A. Bennett; Queensland, Brisbane l. Bayley in herb. A. Bennett; Port Jackson l. R. Brown in herb. Mus. Brit.'

Inquiries produced three potential lectotypes: The Murray River specimen collected by J.P. Erkrit in 1892 and two sheets collected by Robert Brown at Port Jackson. All specimens are located at BM. The best match for the description is the larger of the two Robert Brown specimens, which appears to have been regarded traditionally as the type.

Erkrit's Murray River specimen is the only specimen annotated by Arthur Bennett. It also appears to have come from Arthur Bennett's original herbarium. The Erkrit specimen at BM is not as complete as the larger R. Brown specimen and does not match the original description quite as well for some of the taxonomically less significant characters, e.g., length of stem and description of submersed leaves. However, due to its extensive annotation by Arthur Bennett, and because it is the best match for the (admittedly limited) past and current use of the name, I have selected the Erkrit 1892 specimen as the lectotype.

Potamogeton tenuicaulis F. Mueller, *Fragmenta Phytographiae Australiae,* Vol. 1: 90 (1859)

Type: Gulf of Carpentaria, *F. Mueller s.n.,* s.d. (MEL 1585739, **lectotype, selected here**), determined as *P. tenuicaulis* by F. Mueller.

Notes: When F. Mueller described *P. tenuicaulis* in 1859 he cited no specimens. Instead he gave the location 'in lacubus, fluviis stagnisque a sinu Carpentaria usque ad regiones Australiae orientales' [in lakes and stagnant rivers of the Gulf of Carpentaria as well as other regions of eastern Australia].

The collection at MEL contains one specimen (MEL 1585739) collected at the Gulf of Carpentaria and identified by F. Mueller as *P. tenuicaulis.* However, the specimen is not dated and bears no further annotations. This specimen is complete with both submersed and floating leaves, inflorescence and infructescence and is a good example of the species. I have selected it as the lectotype.

Potamogeton tepperi A. Bennett, *Journal of Botany* 25: 178 (June 1887).

Type: Pool 500 miles north of Brisbane, Queensland, *F.M. Bailey s.n.,* s.d. (BRI, **lectotype, selected here**).

Notes: *Potamogeton tepperi* was described by A. Bennett in 1887. Bennett cites two specimens in his description: 'Pool 500 miles north of Brisbane, Queensland, F.M. Bailey.Neighbourhood of Pioneer River?' & 'River Cygnet, Knicks [Kinch's Station], South Australia, J.G.O. Tepper'.

The specimens which could serve as types unfortunately belong to two different species. The protologue describes features from both specimens and therefore of both species. The description of the floating leaves refers to the species with southern distribution, now known as *P. cheesemanii.* On the other hand the description of the submersed leaves and the description of the fruit is clearly a mixture of both species while the description of the inflorescences fits the specimen from South Australia. The first part of the description of the fruit fits the Queensland specimen. The second half of the fruit description, however, mentions 'projecting processes irregularly distributed on the outer angles', which are not really present on either species, but on a third.

Potamogeton tepperi is a later name than *P. cheesemanii* and would be lost to synonymy under that species. Using the name *P. tepperi* for the northern species, which otherwise appears to lack a name, means no new name would be required. *P. tepperi* has been used only rarely. Where it has been used, however, it was misapplied to yet another species, *P. sulcatus.* By using *P. tepperi* for the northern species, I do not contradict current usage and avoid adding yet another name to the already long list of names for Australian species. I have, therefore, selected the F.M. Bailey specimen as the lectotype.

Potamogeton tricarinatus F. Mueller & A. Bennett, *Journal of Botany* 30: 229 (1892).

Type: Van Alpin River, Mueller s.n., s.d. (K, Herbarium Hookerianum no. 1897, **lectotype, selected here**). Annotations: 'P. tricarinatus Mueller, a good species, A.B.' [Arthur Bennett's handwriting], 'I shall compare this plant ?? carefully in Melbourne with my Europ. specimens' [F. Mueller's handwriting].

Remaining syntypes: MEL1585749, duplicate of the lectotype, with a remark that the Van Alpin River is now known as the Robinson River.

Notes: When Arthur Bennett described *P. tricarinatus* he cited two specimens: 'Australia. In the Yas [Yass] and Murambridge [Murrumbidgee] country, 1831, G. Bennett in Herb. Mus. Brit.! Van Alpin River, F. Mueller in Herb. Kew!'

Inquiries with BM and K yielded only one specimen, the Van Alpin River specimen of Mueller. This specimen has been annotated by Arthur Bennett as '*P. tricarinatus* Mueller' and has obviously been seen by both authors. It is an excellent match for the fairly lengthy type description.

The name *P. tricarinatus* has been used at some stage for all of the floating-leaved *Potamogeton* species in Australia, with the exception of *P. octandrus* [*P. javanicus*]. Selection of the Van Alpin River specimen requires no fewer changes to current usage than any other selection. It also means that no new names appear to be required for any of this group. I have, therefore, selected the specimen at K as the lectotype.

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