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Cytoevolutionary patterns in *Rutaceae*

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Abstract: Chromosome numbers for 9 tribes and 73 genera of *Rutaceae* are examined for the probable chromosome base numbers in these taxa. There is abundant dysploidy and infrageneric polyploidy in the large *Rutoideae*/*Toddalioideae* complex. We found that x = 18 was typical for the tribes *Zanthoxyleae* and *Toddalieae*; probably ancestral in the *Boronieae* and perhaps in the *Ruteae, Diosmieae*, and *Cusparieae*; and characteristic of subfamily *Flindersioideae*. Considering the basic position of elements of *Zanthoxyleae* and *Toddalieae* in the family it appears that diploid x = 18 is ancestral in the *Rutaceae*. The morphologically advanced *Citroideae* are invariant for x = 9 and may be a product of dysploid reduction.

The *Rutaceae* are a large, widely distributed family of trees and other woody plants comprising about 150 genera and some 180 species. Engler (1931) created 7 subfamilies and 12 tribes, but the family is in need of taxonomic revision and here we include only 6 subfamilies and 11 tribes. The family is likely to be of southern origin (Armstrong 1983). It contains species of economic significance for timber, edible fruit, and aromatic oils. There is substantial chromosome number variation in *Rutaceae*, and aspects of cytoevolution are discussed here with respect to the probable chromosome base number in the family and likely phylogenetic trends in the subfamilies, tribes and genera.

Smith-White (1954, 1959) proposed x = 9 as the basic chromosome number in the *Rutaceae*, since x = 9 is "characteristic of all tribes except the *Boronieae*", and suggested that this basic cytotype had originated and established prior to the beginning of the Tertiary era. Subsequent authors (Darlington & Wylie 1955, Federov 1969, Raven 1975, Grant 1982) have endorsed x = 9 for the *Rutaceae*. Ehrendorfer (1976) in a review of chromosomal differentiation patterns in the family has argued x = 9 to be a dysploid derivative of x = 7 and that the original chromosome number in the *Rutaceae* was x = 7. All these authors postulated paleopolyploidy as an essential stage in the cytoevolution of chromosome numbers higher than their proposed base number. James (1981) has questioned whether polyploidy can produce new genera. On this view higher chromosome numbers may be true diploids, and ancestral to lower chromosome numbers through dysploid decrease.

We have collated all available chromosome numbers in the *Rutaceae*. There is an absence or paucity of data in some tribes and subfamilies, and this survey may stimulate additional research in those groups to test the conclusions which we have reached from the present data.

Chromosome base number hypothesis. We follow the general cytoevolutionary principles discussed below in deducing the original base numbers of groups.

1. High frequency and ubiquity of a particular chromosome number can be a strong indicator that it is ancestral in the group. In certain families a clear pattern can be discerned, e.g., in the *Myrtaceae* x = 11 is strongly conserved (RYE 1979). However others show considerable variation in chromosome numbers, which may have substantial systematic and phylogenetic information, but which increases the difficulty of determining the chromosome base number in the family, e.g., *Leguminosae* (GOLDBLATT 1981).

2. The ancestral chromosome base number for a family may be sought in the genera and species considered to be the least specialised on morphological or ecological grounds. Identifying these taxa is facilitated by cladistic models of phylogeny, but does not guarantee that they have conserved the ancestral chromosome number for the genus, tribe or family. However, the repeated association of a particular chromosome number with such taxa can be strong corroborative evidence for the probable base chromosome number in the larger group.

3. Commonly, cytoevolution at the diploid level can achieve stepwise reductions in chromosome number (dysploid falls) by translocating chromosome segments onto other chromosomes followed by loss of a centromere, resulting in one fewer linkage groups and one fewer haploid chromosomes. This may occur sequentially to produce an extended dysploid series, in which the highest chromosome number is the oldest.

4. Less frequently, diploid cytoevolution may result in stepwise increases in chromosome number (dysploid rises), sometimes involving centromere fission and perhaps subsequent translocation onto the duplicated centromeres. In such a series, the lowest chromosome number is the oldest.

5. Cytoevolution through polyploidy can occur from any of the original or derived diploid chromosome numbers. Polyploidy involves the addition of whole diploid genomes, and generates euploid increase. Euploid decreases are rare. Polyploidy as a process may yield chromosome races (infraspecific auto-allopolyploidy) or species (infrageneric allopolyploidy) but typically each polyploid race of species has had its own independent origin (neopolyploidy).

6. Although polyploidy is often stated to be of restricted evolutionary potential, occasionally whole genera are found with an elevated chromosome number which could be interpreted as extensive speciation from a putatively polyploid ancestor (paleopolyploidy). This interpretation requires adequate proof of polyploidy, such as: demonstrating diploid progenitors; or cytological or genetic evidence of polyploidy. In the absence of other proof, or even the expectation of proof, high chromosome number alone is not adequate evidence of paleopolyploidy. In the present paper we suggest that diploidy is the superior genetic system for macroevolutionary processes, and that polyploidy is an inferior genetic system for long-term evolution.

7. Dysploid decrease or increase from very high chromosome numbers is difficult to distinguish from aneuploid changes at high ploidy levels.

Methods

Information on chromosome numbers in *Rutaceae* is extremely fragmented and dispersed in the literature. SMITH-WHITE (1954) provided a classical cytological study of the Australasian tribe *Boronieae*, in which chromosome numbers were reported for 69 species and 11 genera. Since then cytological data have accumulated in various studies and are collated in Appendix 1.

There are numerous examples of unreliable counts in the early literature due mainly to species misidentification, need for taxonomic revision, technical faults, and errors of approximation (GUERRA 1984). In preparing a table of chromosome numbers for genera we point out conflicting accounts and update the nomenclature (Appendix 1).

Results and discussion

In the *Rutaceae*, chromosome numbers are known for 73 out of 150 genera (49%) and approximately 250 out of 1800 species (14%). Considerable variation in chromosome number is observed, and the distribution of chromosome numbers in the family is presented in Table 1, and of generic chromosome numbers in Fig. 1.

In the following, the chromosome numbers and cytoevolutionary patterns are considered for each tribe under the relevant subfamily (mostly sensu ENGLER 1931). Within the largest subfamily *Rutoideae*, only the tribes *Ruteae* and *Boronieae* are relatively well known cytologically, but these need more cytological information. The large subfamily *Toddalioideae* is sampled inadequately. Minimal information is available for the small Australasian subfamily *Flindersioideae*, but no counts are

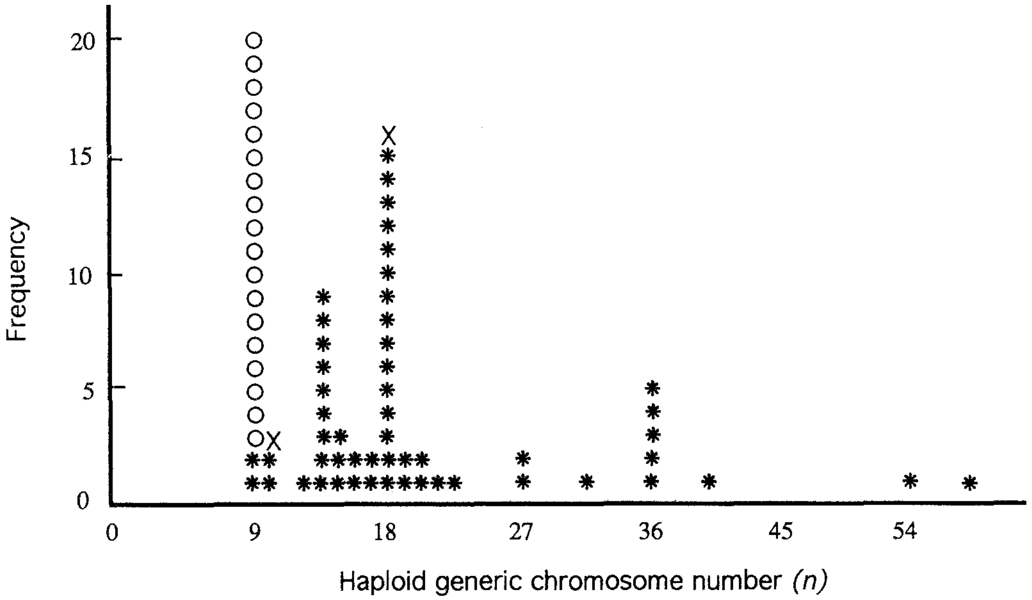

Fig. 1. Distribution of generic chromosome numbers in subfamilies of *Rutaceae*. * *Rutoideae*/*Toddalioideae*. X *Flindersioideae*. O *Citroideae*

Table 1. Chromosome numbers in subfamilies, tribes, subtribes, and genera of *Rutaceae*

Subfamily Tribe Subtribe Genus	No. genera counted*	No. spp. counted	Species numbers (n)	Generic number (n)
RUTOIDEAE	40/88	172/1321		
Zanthoxyleae	12/30	40/541		
Euodiniinae				
Comptonella		1/8	18	18
Evodiella		1/3	18	18
Melicope		8/150	12, 18, 19?	18
Tetradium		4/9	18, 36–40	18
Zanthoxylum (incl. *Fagara*)		19/200	16, 18, 32–36, 66, 68	18
Acradenia		1/2	19	19
Orixa		1/1	20	20
Geijera		1/7	54, 81	54?
Pelea		1/75	36	36
Lunasiinae		0/1		
Decatropidinae		0/7		
Choisynae				
Platydesma		2/6	18	18
Choisya		1/6	27	27?
Pitaviinae				
Pitavia		1/1	18	18
Ruteae	6/6	11/89		
Rutinae				
Haplophyllum		3/70	9	9
Thamnosma		1/6	9	9
Boenninghausenia		1/1	10	10
Ruta		7/7	10, 20, 40	10
Cneoridium		1/1	18	18
Dictaminae				
Dictamnus		1/1	18	18
Boronieae	14/22			
Boroniinae				
Boronia s.l.		34/100	7, 8, 9, 10, 11, 12, 16, 18, 36	18
Zieria		17/26	18, 36	18
Eriostemoninae				
Asterolasia		2/11	13, 14	14
Drummondita		1/4	14	14
Geleznowia		1/1	14	14
Philotheca s. l.		12/34	14, 28	14
Phebalium s. l.		13/49	16, 32	16
Eriostemon s. str.		1/1	17	17
Crowea		2/3	19	19
Aff. *Eriostemon*		1/1	20	20
Correinae				
Correa		6/11	16	16

Table 1 (continued)

Subfamily Tribe Subtribe Genus	No. genera counted*	No. spp. counted	Species numbers (n)	Generic number (n)
Nematolepidinae				
Chorilaena		1/1	14	14
Muriantha		1/1	14	14
Diplolaeninae				
Diplolaena		3/6	13, 14	14
Diosmeae	6/11	18/260		
Diosminae				
Agathosma		3/136	13, 45/2	13
Euchaetes		1/23	14	14
Adenandra		8/18	14, 19, 21, 24, 25	14?
Diosma		3/26	15	15
Coleonema		2/8	17, 18?	17
Calodendrinae				
Calodendrum		1/1	27	27
Empleurinae				
Cusparieae	5/19	5/167		
Moniera		1/2	15	15
Pilocarpinae				
Pilocarpus		1/22	22	22
Esenbeckia		1/38	32	32
Cuspariinae				
Ravenia		1/18	18	18
Erythrochiton		1/8	58	58
TODDALIOIDEAE	8/23	22/234		
Toddalieae	8/23	22/234		
Phellodendrinae				
Phellodendron		5/10	39	39
Ptelinae				
Ptelia		3/3	21	21
Oriciinae				
Diphasia		2/5	36	36
Toddalinae				
Skimmia		6/8	15	15
Acronychia		4/46	17, 18	18
Casimiroa		1/6	18	18
Toddalia		1/1	18, 36	18
Vepris		1/10	36	36
Amyridinae				
Teclea		1/30	36	36
DICTYLOMATOIDEAE	0/1	0/2		
Dictylomataceae	0/1	0/2		
FLINDERSIOIDEAE	2/2	5/18		
Flindersieae	2/2	5/18		
Flindersia		4/15	18, 54	18
Chloroxylon		1/1	10	10

Table 1 (continued)

Subfamily Tribe Subtribe Genus	No. genera counted*	No. spp. counted	Species numbers (n)	Generic number (n)
SPATHELIOIDEAE	0/1	0/10		
Spatheliae	0/1	0/10		
CITROIDEAE	18/33	50/217		
Clauseneae	4/5	12/97		
Micromelinae				
Micromelum		3/9	9	9
Clauseninae				
Clauseana		4/23	9, 18	9
Glycosmis		2/43	9	9
Murraya		2/11	9	9
Merrillinae				
Citreae	14/28	38/130		
Triphasiinae				
Triphasia		1/3	9	9
Citrinae				
Atlantia		4/11	9	9
Citropsis		2/11	9	9
Citrus		16/16	9, 18, 27	9
Eremocitrus		1/1	9	9
Fortunella		4/4	9, 18	9
Hesperenthus		1/1	9	9
Microcitrus		2/6	9, 18	9
Poncirus		1/1	9, 18	9
Severina		1/6	9	9
Balsamocitrinae				
Aegle		1/1	9, 18	9
Aeglopsis		1/1	9	9
Afraegle		1/4	9	9
Feronia		2/2	9	9

* Missing genera:

Australasia: *Bauerella, Bosistoa, Bouchardatia, Brombya, Clymenia, Dutaillya, Euodia* s. s., *Halforida, Lunasia, Pentaceras, Medicosma, Microcybe, Monanthocitrus, Myrtopsis, Nematolepis, Neobyrnesia, Oxanthera, Rhadinothamnus, Sarcomelicope, Zieridium.*

South-east Asia: *Burkillanthus, Feroniella, Limnocitrus, Lunasia, Maclurodendron, Merope, Merrillia, Pleispermum, Swinglea, Tetractomia, Wenzelia.*

East Asia: *Psilopeganum.*

South Asia: *Luvunga, Pamburus, Paramignya.*

Africa: *Acmadenia, Araliopsis, Balsamocitrus, Empleurum, Fagaropsis, Humboltodendron, Macrostylis, Oricia, Oriciopsis, Phyllosma, Sheilanthera, Thamnosma, Toddaliopsis.*

Central America: *Amyris, Decatropis, Decazyx, Galipea, Helietta, Jahnia, Lubaria, Megastigma, Peltostigma, Plethadenia, Polyaster, Raputia, Sargentia, Spathelia, Stauranthus.*

South America: *Adiscanthus, Almeida, Angostura, Balfourodendron, Dictyoloma, Euxylophora, Hortia, Naudinia, Raputia, Rauia, Raveniopsis, Spiranthera, Ticorea.*

available for two small subfamilies, the South American *Dictylomatioideae* and the West Indian *Spathelioideae*. The subfamily *Citroideae*, containing the economic tribe *Citreae*, has the most extensive record.

The *Rutoideae/Toddalioideae* complex. The subfamilies *Rutoideae* and *Toddalioideae* are treated together as a complex, due to the inadequacy of ENGLER's circumscription of these two groups. There are notable similarities between the pantropical tribes *Zanthoxyleae* and *Toddalieae* in their phytochemistry and morphology (WATERMAN 1983, DA SILVA & al. 1988) and, as shown here, in their cytoevolutionary patterns.

Tribe *Zanthoxyleae*. Although there are data for 14 of the tribe's 29 genera, those exhibiting the most generalised morphologies (e.g., *Bouchardatia, Bosistoa*) remain uncounted. Cytotypic diversity occurs within and between genera. For 10 genera with single counts only, n = 18, 20, 27, and 36, mostly n = 18 and n = 36, occur. A similar range is found in three genera with counts for several species, but species with n = 36 are congeneric with n = 18. Infraspecific chromosome number variation is reported in *Geijera, Melicope*, three *Tetradium* species, and four *Zanthoxylum* species. In *Tetradium* and *Zanthoxylum* infraspecific aneuploid or dysploid variation is relatively common at the tetraploid level. In *Xanthoxylum* abundant infrageneric tetraploids ranging from n = 32–36 possibly result from various allotetraploid combinations of n = 16 and n = 18, extending to octoploids of n = 66–68.

In *Geijera* (n = 54, 81) the data might suggest a base of x = 27, but the high polyploid n = 81 requires re-examination as the genus may prove to be based on x = 18. The report of n = 27 in a pollen and seed sterile species of *Choisya*, possibly triploid on x = 18, also requires re-examination in relation to its probable generic number.

In the tribe *Zanthoxyleae* the data strongly suggest that x = 18 is ancestral (found in seven genera), with dysploid falls to n = x − 2 = 16 in *Zanthoxylum* and to n = x − 6 = 12 in *Melicope*, and dysploid rises to n = x + 1 = 19 (in *Acradenia* and *Melicope*) and n = 4 + 2 = 20 (in *Orixa*); and with frequent infrageneric euploid increases to n = 2x = 36 (four genera), or other multiples of n = 18 (*Geijera*?), sometimes with subsequent aneuploidy or dysploidy especially around the n = 2x = 36 level (in *Tetradium* and *Zanthoxylum*). The absence of lower chromosome numbers, such as n = 9, suggests that in the *Zanthoxyleae* x = 18 is diploid.

Tribe *Toddalieae*. In nine cytologically known genera in this tribe, the most frequent number is n = 18 (3 genera) or n = 36 (3 genera with single counts only), suggesting that x = 18 is fundamental in this tribe. Two remaining genera may be derived by dysploidy from x = 18: *Ptelia* n = x + 3 = 21 and *Skimmia* n = x − 3 = 15; but dioecious *Phellodendron* n = 38–40 may be tetraploid on x = 19 (SANTAMOUR 1966) plus accessary chromosomes. Infrageneric dysploidy is shown in *Acronychia* (n = 18, 17), analogous to the proposed generic dysploidy from x = 18 in the tribe. It may be concluded that this large and heterogeneous assemblage appears to be based on x = 18, which from the absence of n = 9, may be regarded as diploid.

Tribe *Boronieae*. With 14 of its 22 genera and 36% of the species counted, the Australasian tribe *Boronieae* is relatively well known cytologically. Its five subtribes demonstrate abundant cytoevolution especially through dysploidy. Generic chromosome numbers are x = (9?), 14, 16, 17, 18, 19, 20; most notably x = 14 which occurs in 7 genera and 3 subtribes. It is the *Boronieae*, in particular the genus *Boronia*, which best exemplifies the debate between x = 18 and x = 9 as the original chromosome number for the tribe and perhaps the family.

Boronia, the largest and most widespread genus in the tribe, occurs in many open forest and heathland communities around Australia. It shows n = 18, 16, 12, 11, 10, 9, 8, 7 in counts for 34 species particularly n = 9 (11 species, mostly Western Australian) which Smith-White (1954) nominated as the likely primitive number in *Boronia* (Fig. 2 a) and in the *Boronieae*. A phylogenetic analysis of *Boronia* (Weston & al. 1984) shows a marked downward trend in chromosome numbers with increasing numbers of advanced characters (Fig. 3). The trend starts from n = 18 in sect. *Cyanothamnus*, through n = 16, 10, 9 in sect. *Valvatae*, to n = 11, 9, 8, 7 in sect. *Boronia*. Progressive dysploid falls appear to be a real phylogenetic

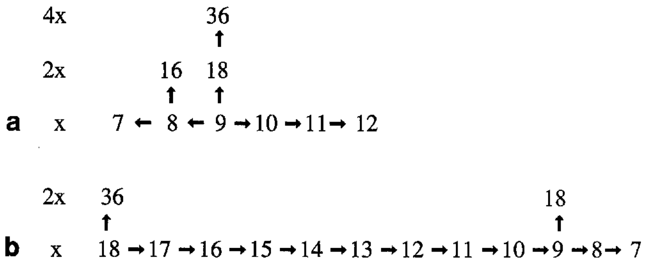

Fig. 2. Two models for cytoevolution in the genus *Boronia*. (a) x = 9 and paleopolyploidy, after Smith-White (1954, 1959). (b) x = 18 and dysploidy: two origins of n = 18 are shown. Other models combining or extending these two models are possible

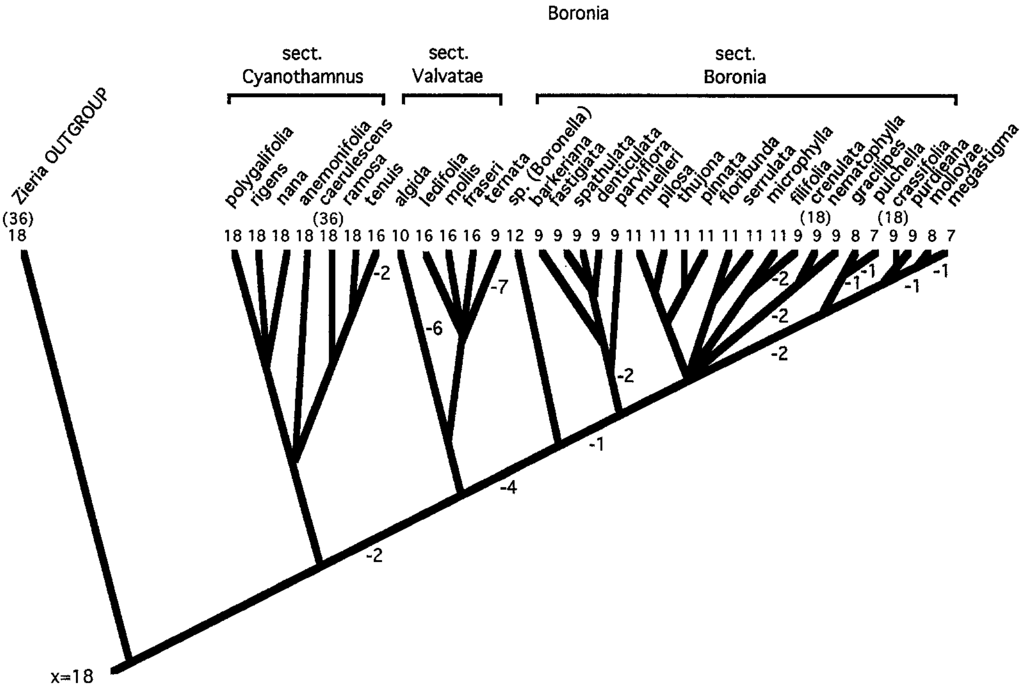

Fig. 3. Morphological cladogram of *Boronia* (from Weston & al. 1984, redrawn) showing cytologically known species and their evolution from x = 18. See text for further explanation

correlate in *Boronia*. This trend is consistent with an original x = 18 in the genus, with progressive dysploid falls to n = 7 (Fig. 2 b).

Hennigian analysis of chromosome data in the cladogram (Fig. 3) compares four models for the ancestral chromosome number of *Boronia*:

1. x = 18 with dysploidy to n = 7 requires 34 steps (34 dysploid falls).

2. x = 9 with dysploidy to n = 18 and n = 7 requires 38 steps (13 dysploid falls, 25 dysploid rises).

3. x = 9 with neopolyploidy to n = 18 and n = 16 and dysploidy to n = 12 and n = 7 requires 37 steps (6 dysploid falls, 11 dysploid rises, 10 neopolyploid rises, and 10 non-detections or extinctions).

4. x = 9 with paleopolyploidy to n = 18 and n = 16 and dysploidy to n = 12 and n = 7 requires 28 steps (14 dysploid falls, 10 dysploid rises, 2 paleopolyploid rises, and 2 extinctions).

The fourth model, advocated by Weston & al. (1984), explains the aggregation of n = 18 in *Cyanothamnus* and of n = 16 in *Valvatae*, but the underlying hypothesis of paleopolyploidy with rediploidization and speciation from a polyploid ancestor is extremely complex and requires independent evidence that it has occurred in *Boronia*. The third model supposes that the several cases of n = 18 in *Cyanothamnus* and of n = 16 in *Cyanothamnus* and *Valvatae*, are neotetraploids whose diploids were not detected in the study. We may assign a probability P that non-detection of diploids can occur purely by chance in any one case. The probability that it has occurred by chance in 10 cases is P^{10}. If $P < 0.6$ the hypothesis could be rejected at the 1% level.

If paleopolyploidy and neopolyploidy are each judged implausible as explanations for the chromosome numbers in the cladogram, then x = 18 (the first hypothesis) is more parsimonious than x = 9 (the second hypothesis) for the ancestral number in *Boronia*. Furthermore x = 18 produces falls far outnumbering rises, a result consistent with findings in other Australian plant groups, e.g., *Brachyscome* (Smith-White & al. 1970), *Loranthaceae* (Barlow & Wiens 1971), *Calotis* (Stace 1978), *Stylidium* (James 1979), *Myrtaceae* (Rye 1979) and with theoretical considerations (James 1992).

Data in closely related genera (outgroup comparison) may distinguish whether x = 18 or x = 9 is likely to be ancestral in *Boronia*. In subtribe *Boroniinae, Zieria* is x = 18, and it is widespread in both tropical forests and heathlands. Two wet forest genera, *Medicosma* and *Euodia* s. str., may be closer to *Boronia* and hence incorrectly placed in *Zanthoxyleae* (Hartley 1977, 1985) but, with the allied *Neobyrnesia*, are cytologically unknown (Armstrong & Powell 1982). However, x = 18 as the likely ancestral chromosome number in *Boronia* would be consistent with a current cladistic analysis of its position in the tribe (Fig. 4), and here we accept x = 18 as the base number in *Boronia* (Table 1) and the *Boronieae*.

In the subtribe *Eriostemoninae* generic chromosome numbers of x = 14, 16, 17, 19, 20 occur, predominantly n = 14 in four (or five) genera. *Eriostemon* has reports of n = 14, 17, 20 but a cladistic analysis (Fig. 4) indicates that this genus is polyphyletic, and may be more correctly treated as a monophyletic genus *Eriostemon* s. str. (n = 17) closely allied to *Crowea* (n = 19), another genus aff. *Eriostemon* (n = 20), with the majority of species (n = 14, 28) placed in *Philotheca* s. lato (n = 14). Three smaller subtribes show n = 14 occurring in three genera and n = 16

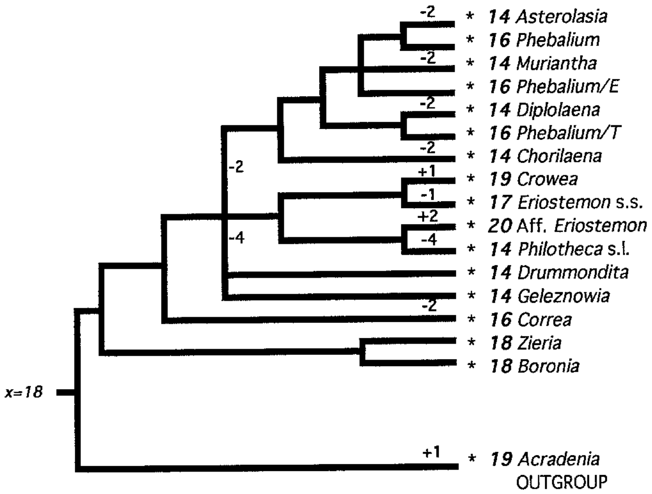

Fig. 4. Morphological cladogram of generic relationships in the *Boronieae* (from Armstrong 1987 and unpubl.) showing cytologically known taxa and their derivation from x = 18

in one. Dibasic chromosome numbers are found in *Asterolasia* and *Diplolaena* (n = 14, 13) in which n = 13 is presumably a dysploid reduction from n = 14. It is possible that some of Engler's (1931) subtribes of *Boronieae* are unnatural.

Published interpretations of cytoevolution in the *Boronieae* proposed that x = 9 was basic in the tribe (Smith-White 1954, 1959) with ancient reductions to n = 8 and n = 7 and subsequent paleopolyploidy to n = 18, n = 16, and n = 14, with secondary dysploidy to n = 19, 17, and 13 (see also Ehrendorfer 1976, 1982). Alternatively, James (1981) has argued in principle that these generic numbers are the products of primary dysploid cytoevolution. This view is consistent with evidence supporting x = 18 as the original number in the *Boronieae* and its related tribes, and with the likely dysploid derivation of other generic numbers in the tribe (Fig. 4). It is consistent also with the absence in the *Boronieae* of lower generic chromosome numbers, such as n = 8 and n = 7 (and n = 9 in related tribes), which in the Smith-White and Ehrendorfer models are presumed extinct. The balance of current evidence strongly suggests that x = 18 is ancestral in the *Boronieae* with cytoevolution through dysploidy and infrageneric neopolyploidy. There is no necessity for postulating paleopolyploidy for cytoevolution in *Boronia*, or in the tribe *Boronieae*.

Ultimately the further assessment of these competing models requires new cytogenetic and molecular information in addition to chromosome number determinations. Whether n = 14 as a recurring generic chromosome number has evolved once or several times is amenable to investigation by modern isozyme or DNA genetic analyses. A similar comparison could be made for n = 16 found in *Boronia-Valvatae, Phebalium*, and *Correa*, and for n = 18 found in *Zieria* and *Boronia-Cyanothamnus*. Such data could resolve for each of these groups the question of putative paleopolyploidy or descending dysploidy during their cytoevolution.

Tribe *Diosmeae*. The available cytological data for the mainly South African *Diosmeae* are meagre with only 7% of taxa counted, but two general points emerge. In four genera of subtribe *Diosminae* generic base numbers are n = 17, 15, 14, 13, suggesting dysploid falls from a putative x = 18 (Goldblatt & Williams 1987), particularly the two close genera *Diosma* (n = 15) and *Euchaetes* (n = 14). The genus *Adenandra* demonstrates a wider range from n = 14 to n = 25, for which the data do not readily suggest a generic base number except that n = 14 appears in 2 species. In the subtribe *Calodendrinae, Calodendrum* (n = 27) might be hexaploid on x = 9, but requires re-examination as it may be the product of dysploid increase from a putative x = 18. Detailed cytoevolutionary and phylogenetic studies in the *Diosmeae* would be considerable value.

Tribe *Ruteae.* This small tribe is relatively well known with its 6 genera counted, although species sampling (18%) is inadequate. Generic chromosome numbers of n = 9 (*Haplophyllum, Thamnosma*), n = 10 (*Boenninghausenia, Ruta*), and n = 18 (*Dictamnus, Cneoridium*) appear to be reliable (GUERRA 1984, RAVEN & al. 1965, WARD 1984). Polyploidy occurs in *Ruta* (n = 10, 20, 40), sometimes with aneuploidy around n = 40 (2n = 76–81) which may be stabilised by apomixis.

The traditional cytoevolutionary interpretation may suggest a base number of x = 9 in *Ruteae* (with n = x = 9 in *Haplophyllum* and *Thamnosma*, and dysploid rises to n = x + 1 = 10 in two other genera) and generic polyploidy n = 2x = 18 in *Cneoridium* (*Rutinae*) and *Dictamnus* (*Dictaminae*). However, we suggest the hypothesis that diploid x = 18 is ancestral in the *Ruteae* with dysploid reductions to n = 10 and n = 9 in the subtribe *Rutinae*. The large genus *Haplophyllum* (70 spp.) might demonstrate the role of dysploidy in the cytoevolution of the group.

Tribe *Cusparieae.* The cytological information for the South American tribe *Cusparieae* is insufficient to allow any realistic assessment of cytoevolutionary patterns. With only 2% of the species sampled the diversity of reported chromosome numbers (n = 15, 18, 22, 32, 58) suggests that it could prove to be as variable as the preceding tribes of comparable size.

In the *Rutoideae-Toddalioideae* considerable cytoevolution is observed. Comparing generic chromosome numbers in the tribes that typically contain wet forest genera (*Zanthoxyleae* and *Toddalieae*) with tribes that have radiated into heathlands of Australia, South Africa, and Eurasia (*Boronieae, Diosmeae*, and *Ruteae*) indicates a trend towards lower generic chromosome numbers in the latter (e.g., Table 2). In the tribes *Zanthoxyleae, Toddalieae*, and *Boronieae*, and perhaps *Cusparieae, Diosmeae*, and *Ruteae*, x = 18 appears fundamental and probably ancestral. In the tribes *Boronieae* and *Ruteae* n = 9 occurs but is derived probably by dysploidy from x = 18. There is little support for x = 9 as a primitive chromosome number in this large association of tribes and genera of the *Rutaceae*.

Subfamily *Flindersioideae.* The base number of x = 18 is firmly established in this predominantly Australasian subfamily. Species of genus *Flindersia* are chiefly rainforest trees with n = 18 but one species *F. australis* has entered the arid zone and is reported as n = 54 (hexaploid). The monotypic genus *Chloroxylon*, usually placed in *Flindersioideae*, is n = 10, which MORAWETZ (1986) suggested was derived by dysploidy from x = 9 but which is more likely derived from x = 18.

Subfamily *Citroideae.* The two tribes in this subfamily are relatively well known cytologically, due partly to the economic significance of the tribe *Citreae*. Despite the great diversity of morphological characters, chromosome numbers in the *Citroideae* are largely constant.

Tribe *Clauseneae.* A base number of x = 9 is indicated in this tribe, as it accounts for almost all the counted species. One *Clausenia* species is n = 18 and is probably an infrageneric tetraploid; no cases of infraspecific polyploidy are reported despite

Table 2. Cytological comparison of indigenous Australian genera in two contrasting plant communities. **Closed forest:** Northern Australia: *M* monsoon; Eastern Australia: *T* tropical, *S* subtropical, *W* warm temperate, *C* cool temperate. **Sclerophyll heathlands:** *N* Northern Australia; *W* South-western Australia; *E* South-eastern Australia; *A* Alpine Australia. *X* genus present in habitat (Specht 1981); *n* generic chromosome numbers, except *Boronieae* where other species numbers are also shown

Tribe Genus	Closed Forest					Heathlands				n
	M	T	S	W	C	N	W	E	A	
Clauseneae										
Glycosmis	X	X	X							9
Micromelum	X	X	X							9
Murraya	X	X	X							9
Clausena		X								9
Citreae										
Paramignya	X									–
Microcitrus		X	X	X						9
Flindersieae										
Flindersia	X	X	X							18
Toddalieae										
Acronychia		X	X	X						18
Halfordia		X	X	X						–
Zanthoxyleae										
Geijera	X									54
Lunasia	X	X	X							–
Zanthoxylum	X	X	X	X						18
Brombya		X								–
Euodia s. str.		X								–
Evodiella		X								18
Bosistoa		X	X							–
Medicosma		X	X							–
Melicope s. l.		X	X	X						18
Sarcomelicope		X	X	X						–
Bouchardatia			X							–
Pentaceras			X							–
Acradenia			X		X					19
Boronieae										
Zieria		X	X	X	X	X		X		18
Phebalium			X	X	X	X	X	X	X	16
Correa					X		X	X	X	16
Neobyrnesia						X				–
Drummondita						X	X			14
Philotheca s. l.						X	X	X		14
Boronia						X	X	X	X	18, 16, 11, 10, 9, 8, 7
Diplolaena							X			14, 13
Galeznowia							X			14
Muriantha							X			14
Rhadinothamnus							X			–
Nematolepis							X			–
Microcybe							X	X		–
Asterolasia							X	X	X	14, 13
Eriostemon s. str.								X		17

numerous investigations in the tribe. There are no unchallenged cases of dysploidy in the tribe or subfamily.

Tribe *Citreae.* Clearly x = 9 is basic in this tribe, and n = 9 accounts for most counted taxa. Occasional infraspecific tetraploids (n = 18) have developed in *Triphasia, Fortunella, Poncirus*, and *Aegle*. Some karyotypic rearrangements on n = 9 are shown in *Citrus* hybrids (NAITHANI & RAGHUVANSHI 1958, 1963). Isolated instances of aneuploids (n = 19/2, 21/2), triploids (n = 27/2), tetraploids (n = 18), and hexaploids (n = 27) also occur in *Citrus*. Such infraspecific variants are associated with apomixis; triploid forms occurring as unreduced gametic seedlings, and tetraploids as nucellar seedlings or somatically in growing points of stems (FROST 1948). Most taxonomic species and cultivated varieties of *Citrus* are diploid agamic complexes, and perhaps only *C. halimii, C. grandis, C. media*, and *C. reticulata* are true sexual species (SCORA & KUMAMOTO 1983).

Cytologically, the subfamily *Citroideae* is markedly distinct from the preceding subfamilies of *Rutaceae*. It is believed to have originated in Southeast Asia or Central Africa, perhaps from ancestors in the *Toddalieae* (WATERMAN 1983). Its cytoevolutionary origins are obscure, but would appear to be derived by dysploidy probably from the x = 18 in other subfamilies. Genera of *Citroideae* in northern Australia (Table 2) are likely to be extensions of the Malesian flora during the late Tertiary or Quaternary (ARMSTRONG 1975, BARLOW 1981).

The original chromosome number in *Rutaceae*

This review of chromosome numbers clearly points to x = 18 as being the probable basic number in the *Rutaceae*, rather than x = 9 as proposed by SMITH-WHITE (1954).

In *Rutaceae* there is a periodicity of generic numbers on n = 9, 18, 27, and 36 (Fig. 1), a feature noted by SMITH-WHITE (1954) and subsequent authors who endorsed x = 9 as being basic in the family, and suggestive of polyploidy on x = 9. We make three observations on these data.

Only in the *Citroideae* is n = 9 abundant. The *Citroideae* are morphologically derived (ARMSTRONG 1975) and are not good corroborative evidence for x = 9 being ancestral in the *Rutaceae*. In other *Rutaceae* n = 9 is infrequent, and occurs in three genera only, *Boronia* (*Boronieae*), *Haplophyllum*, and *Thamnosma* (*Ruteae*). Certainly in the *Boronieae*, n = 9 may be interpreted as a dysploid fall from x = 18, and this might also apply to the *Ruteae*, and, presumably, to the *Citroideae*. Our analysis of chromosome numbers in *Rutaceae* suggests that n = 9 represents a second, presumably modern, mode of cytoevolution, and that once the genome reaches this new level of organisation, speciation rates are enhanced, as shown by *Boronia*, perhaps *Haplophyllum*, and the *Citroideae*.

Generic chromosome numbers of n = 36 in the tribes *Zanthoxyleae* and *Toddalieae* are likely to resolve to n = 18 after further counts in congeneric species. In both tribes n = 18 predominates, with similar modes of cytoevolution from x = 18. Their basic position in the *Rutaceae* strongly suggests that the ancestral diploid number in the *Rutaceae* was x = 18. Furthermore x = 18 is characteristic of the *Flindersioideae*, and is probably ancestral in *Boronieae*, and perhaps also in *Diosmeae, Ruteae*, and *Cusparieae*. On the criteria of high frequency, ubiquity and presence in least specialized groups, x = 18 must be accepted as the most likely diploid ancestral chromosome number in the *Rutaceae*.

Nowhere in the family does x = 7 or x = 8 occur as a generic chromosome number. In the genus *Boronia* the hypothesis that x = 7 is plesiomorphic (original) and gave rise by dysploid increase to an apomorphic (derived) x = 9 is not sustained by a phylogenetic analysis of the genus (WESTON & al. 1984). Furthermore x = 14 (a supposed paleopolyploid derivative of x = 7) is prevalent only in the tribe *Boronieae* where it characterises mostly small genera displaying derived ecological and morphological features, i.e., *Chorilaena, Diplolaena, Muriantha, Geleznowia, Philotheca, Drummondita, Asterolasia* (ARMSTRONG 1987, CLAUSSEN-BOCKOFF & al. 1991). The cytoevolution of n = 14 and other generic chromosome numbers in *Boronieae* is probably by dysploidy from x = 18.

Finally, paleopolyploidy was proposed also for *Epacridaceae* and *Proteaceae* (SMITH-WHITE 1959) but in *Epacridaceae* POWELL (pers. comm.) finds higher chromosome numbers amongst the morphologically least specialised groups, and JAMES (1981) noted higher chromosome numbers amongst the ecologically less specialised *Proteaceae* of the old gondwanan forests of Eastern Australia. It is likely that other major plant families will show similar correlations of cytoevolution through dysploidy with phylogenetic and ecological development, as discussed here for *Rutaceae*.

Conclusions

We have compared three models of cytoevolution in the *Rutaceae*, two of which propose x = 9 or x = 7 as basic in the family with higher generic chromosome numbers derived by paleopolyploidy, and one which proposes a higher ancestral diploid chromosome number for the family with new generic chromosome numbers produced by dysploidy. We find that x = 18 is widespread in the family including two pantropical tribes that may be central in the *Rutaceae*. The derivation of various generic chromosome numbers from diploid x = 18 is relatively parsimonious without invoking paleopolyploidy. Most of the primitive *Rutaceae* are wet forest trees and have received less cytological attention than the more advanced groups which have extended the family into temperate climates, or which contain economic species. Impressions that the *Rutaceae* are based on lower chromosome numbers possibly reflect the far greater abundance of cytological observations in these derived groups.

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Appendix 1. Chromosome numbers in the *Rutaceae*. Species are listed as currently accepted taxa. Changes from those in the cytological literature, citing taxonomic author, are listed under comments. For *Citrus* all described taxa are listed under comments

Species	n	References*	Comments
Tribe *Zanthoxyleae*			
Acradenia			
frankliniae	19	**44**	From *Boronieae*? (HARTLEY 1977)
Comptonella			
drupaceae	18	**34**	
Evodiella			
hooglandii	18	**8**	
Geijera			
parviflora	54	**100**	
	81	**97**	Cult., India (**97**)
Melicope s. lato			
confusa	12	**42**	As *Euodia confusa* (HARTLEY, pers. comm.)
	18	**78**	As *Euodia confusa*
	19?	**78**	As *Euodia confusa*
mantellii	18	**85**	
micrococca	18	**100**	As *Euodia micrococca* (HARTLEY 1990)
retusa	18	**78**	As *Euodia retusa*

Appendix 1 (continued)

Species	n	References*	Comments
semecarpifolia	18	**78**	As *Euodia semecarpifolia* (Hartley, pers. comm.)
simplex	18	**36, 85**	
spec.	18	**65**	As *Euodia roxburghiana* (Hartley, pers. comm.)
ternata	18	**34, 36, 85**	
villamilii	18	**78**	As *Euodia villamilii* (Hartley, pers. comm.)
wawreana	36	**34**	As *Pelea wawreana* (Hartley & Stone 1989)
Orixa			
japonica	20	**34**	
Tetradium			
daniellii	36	**10**	As *Euodia daniellii* & *E. hupehensis*
	38	**34**	As *Euodia hupehensis* (Hartley 1981)
	39	**34**	As *Euodia danielli* (Hartley 1981)
	40	**19, 20**	As *Euodia danielli*
fraxinifolium	36	**10**	As *Euodia fraxinifolium* (Hartley 1981)
	39	**63**	As *Euodia fraxinifolium*
glabrifolium	18	**63**	As *Euodia meliaefolia* (Hartley 1981)
	36	**20**	As *Euodia glocii* (= *glauca*?) (Hartley 1981)
ruticarpum	c. 38	**34**	As *Euodia ruticarpa* (Hartley 1981)
	39	**34**	As *Euodia officinalis* (Hartley 1981)
Zanthoxylum (incl. *Fagara*)			
acanthopodium	32	**63**	
armatum	33	**97**	As *Z. alatum*
	33	**63, 64**	
	33	**89**	+ 0–4 B chromosomes
	68	**34**	
americanum	34	**117**	
	68	**20**	
bungei	16	**20**	
clava-herculis	c. 36	**9, 10**	
naranjillo	36	**104**	
nitidum	34	**63**	
ovalifolium	18	**63**	
	34	**63**	
	c. 68	**63**	
oxyphyllum	36	**63, 64**	
piperitum	35	**34, 68, 99, 117**	
rhetsa	34	**63**	As *Z. limonella* (Hartley 1970)
scandens	34	**63**	
simulans	c. 66	**34**	
spec.?	12	**77**	As *Fagara schlechteri*
spec.?	32	**61**	As *Fagara atchoum*
spec.?	32	**59, 61**	As *Fagara macrophylla*
spec.?	33	**34**	As *Fagara* spec.
spec.?	34	**6**	As *Fagara coco*
tetraspermum	c. 35	**65**	
zanthoxyloides	36	**34**	As *Fagara zanthoxyloides* (Hartley 1966)
Choisya			
ternata	27	**19**	Pollen sterile (**19, 21**) perhaps triploid
Platydesma			
rostratum	18	**12, 34**	

Appendix 1 (continued)

Species	n	References*	Comments
Pitavia			
puncata	18	**111, 113**	
Tribe *Ruteae*			
Boenninghausenia			
albiflora	9	**108, 109, 110**	Doubtful (**34**)
	10	**34, 51**	
Cneoridium			
dumosum	18	**86**	
Haplophyllum			
dauricum	9	**37**	
obtusifolium	9	**34**	
perforatum	9	**27**	
Ruta			
angustifolia	18	**76**	As *R. chalepensis* var. *angustifolia*; doubtful (**34**)
	20	**18, 34, 74**	
chalepensis	18	**76**	Doubtful (**34**)
	20	**34**	
corsica	9	**15, 16, 17**	Doubtful (**34**)
	10	**115**	
	18	**39**	Doubtful (**34**)
graveolens	36	**75, 76, 87**	Doubtful (**34**)
	38	**34**	
	39	**34**	
	40	**34**	
	81/2	**34, 87**	
montana	18	**76**	Doubtful (**34**)
	20	**34**	
oreojasme	18	**11, 39**	Doubtful (**34**)
patavina	9	**15, 76**	Requires checking
pinnata	20	**34**	
Thamnosma			
texana	9	**116**	
Dictamnus			
albus s. lato	15	**76**	Doubtful (**34**)
	18	**9, 10, 34, 54, 55**	
	18	**20**	As *D. dasycarpus*; reinterpreted (**34**)
	18	**7, 34, 56, 62, 119**	As *D. fraxinella, gymnostylis, tadshikorum*
Tribe *Boronieae*			
Boronia s. lato			
algida	10	**104**	
anemonifolia	18	**100**	
barkerana	9	**100**	
caerulescens	18	**100**	
	36	**100**	
crassifolia	9	**100**	
	18	**100**	
crenulata			
var. *gracilis*	9	**100**	As *B. viminea* (WILSON 1971)
var. *crenulata*	18	**100**	As *B. crenulata* (WILSON, pers. comm.)

Appendix 1 (continued)

Species	n	References*	Comments
denticulata	9	**100, 104**	
fastigiata	9	**100**	
filifolia	9	**104**	
floribunda	11	**100**	
fraseri	16	**100**	
gracilipes	8	**100**	
ledifolia	16	**100**	Also as *B. triphylla* (ARMSTRONG 1981)
megastigma	7	**100**	
microphylla	11	**100**	
mollis	16	**100**	
molloyae	8	**100**	As *B. elatior* (WILSON, pers. comm.)
muelleri	11	**104**	
nana	18	**104**	
nematophylla	9	**100**	
parviflora	9	**100**	
pilosa	11	**100**	
pinnata	11	**100**	
polygalifolia	18	**100**	
pulchella	7	**100**	
purdieana	9	**100**	
ramosa	18	**100**	
rigens	18	**100**	
serrulata	11	**100**	
spec.	12	**101**	As *Boronella* spec. (WESTON & al. 1984)
spathulata	9	**100**	
tenuis	9	**100**	Possible misidentification (**103**)
	16	**103**	
thujona	11	**100**	
Zieria			
adenodonta	18	**104**	
aspalathoides	36	**100**	
caducibracteata	18	**104**	
citriodora	18	**104**	
covenyi	54/2	**104**	Sterile triploid hybrid (n = 18 × n = 36)
cytisoides	36	**100, 104**	
fraseri	18	**104**	
furfuracea	18	**104**	
involucrata	18	**104**	
laevigata	36	**100**	
laxiflora	18	**100**	As *Z. laevigata* (ARMSTRONG 1991)
	18	**104**	
minutiflora	18	**104**	
odorifera	18	**104**	
pilosa	18	**100**	
robusta	18	**104**	
smithii	18	**100**	Possible misidentification (**104**)
	36	**34, 100, 104**	
southwellii	18	**104**	
veronicea	18	**104**	

Appendix 1 (continued)

Species	n	References*	Comments
Asterolasia			
correifolius	14	**100**	
pallida	13	**100**	As *A. dielsii* (Wilson 1987)
Crowea			
angustifolia	19	**100**	As *C. dentata* (Wilson 1970)
saligna	19	**100**	
Drummondita			
miniata	14	**100**	As *Philotheca miniata* (Wilson 1971)
Eriostemon			
australasius	17	**100**	As *E. lanceolatus* (Wilson 1970)
brevifolius	28	**100**	
buxifolius	14	**100**	
difformis	c. 30/2	**104**	
hispidulus	14	**100, 104**	
myoporoides	14	**100, 104**	
obovalis	14	**100**	
scaber	14	**100**	
spicatus	28	**100**	
virgatus	c. 14	**104**	
Aff. *Eriostemon*			
pallidus	20	**34**	As *Eriostemon pallidus* (Wilson 1970)
Galeznowia			
verrucosa	14	**100**	
Phebalium			
bullatum	16	**100**	As *P.* spec. (Wilson 1970)
coxii	16	**104**	
dentatum	16	**100**	
diosmeum	16	**100**	
drummondii	32	**100**	
elatius	16	**104**	
ellipticum	c. 16	**104**	
glandulosum	16	**100**	
microphyllum	32	**100**	
nottii	c. 16	**104**	
nudum	16	**36**	
ralstonii	16	**100**	
squameum	16	**100**	As *billardieri* & *P. squameus* (Wilson 1970)
squamulosum	16	**100, 104**	
subsp. *ozothamnoides*	32	**100**	As *P. ozothamnoides* (Wilson 1970)
Philotheca			
salsolifolia	14	**100**	As *P. australis* & *P. reichenbachiana* (Armstrong 1981)
tubiflora	14	**47**	
Correa			
alba	16	**100**	
backhousiana	16	**19, 20**	
glabra	16	**1**	
lawrenciana	16	**100**	
reflexa	16	**34, 100**	As *C. speciosa* or *C. virens* (Wilson 1961)
schlechtendalii	16	**1**	

Appendix 1 (continued)

Species	n	References*	Comments
Chorilaena			
quercifolia	14	**100**	Also as *C. hirsuta* (WILSON, pers. comm.)
Muriantha			
hassellii	14	**47**	
Diplolaena			
ferruginea	14	**48**	
grandiflora	13	**100**	
microcephala	14	**48**	
Tribe *Diosmeae*			
Calodendrum			
capense	27	**40, 100**	
Adenandra			
coriaceae	25	**106**	
dahligrenii	24	**106**	
fragrans	21	**33, 106**	
gummifera	14	**106**	
multiflora	c. 25	**106**	
obtusata	14	**33, 106**	
odoratissima	c. 21	**106**	
uniflora	19	**106**	
Agathosma			
apiculata	13	**34**	
crenulata	c. 45/2	**88**	As *Barosma crenulata* (PILLANS 1950)
lanceolata	13	**34**	As *Barosma lanceolata* (PILLANS 1950)
Coleonema			
album	17	**34**	
pulchellum	17	**34**	
	18	**100**	As *C. pulchrum*; perhaps doubtful (**34**)
Diosma			
aristata	15	**33**	
oppositifolia	15	**33**	
subulata	15	**33**	
Euchaetes			
avisylvera	14	**33**	
Tribe *Cusparieae*			
Esenbeckia			
febrifuga	32	**46**	
Moniera			
trifolia	15	**35**	
Pilocarpus			
pennatifolius	18	**36**	Perhaps doubtful (**34**)
	22	**34, 46**	
Erythrochiton			
brasiliense	c. 45	**38**	Doubtful (**34**)
	58	**34**	
Ravenia			
spectabilis	18	**29**	

Appendix 1 (continued)

Species	n	References*	Comments
Tribe *Toddalieae*			
Phellodendron			
amurense	38	**91**	Male plant (**91**)
	39	**34**	
chinense	39	**34**	
japonicum	39	**34**	
lavallei	38	**91**	Male plant (**91**)
sachalinense	40	**20**	
Ptelea			
baldwinii	21	**34**	
isophylla	21	**34**	
lutescens	21	**34**	
nitens	21	**34**	
serrata	21	**34**	
trifoliata	18	**75**	Doubtful (**34**)
	21	**20, 34**	
Diphasia			
angolensis	36	**60**	
klaineana	36	**61**	
Acronychia			
oblongifolia	18	**91**	As *A. laevis* (Hartley 1974)
pedunculata	18	**63**	
pubescens	17	**34**	
suberosa	18	**34**	
Casimiroa			
edulis	18	**73**	
calderonii	18	**14**	
Skimmia			
anquetifolia	15	**45**	
arborescens	15	**45**	
formannii	16	**20**	Doubtful (**45**)
fortunei	30	**96**	
japonica	15	**34, 96, 45**	
	30	**45**	
laureola	15	**63, 45**	
	30	**45**	
rubella	15	**96**	
veitchii	15	**96**	
Toddalia			
aculeata	36	**32**	
asiatica	18	**63**	
	36	**81**	
Vepris			
undulata	36	**34**	
Teclea			
grandiflora	36	**60**	
verdoorniana	36	**61**	

Appendix 1 (continued)

Species	n	References*	Comments
Tribe *Flindersieae*			
Flindersia			
australis	54	**100**	
bourjotiana	18	**100**	
schottiana	18	**100**	Also as *F. pubescens* (HARTLEY 1969)
	18	**34**	As *F. pubescens*
xanthoxyla	18	**100**	As *F. oxleyana* (HARTLEY 1969)
Chloroxylon			
swietena	10	**73, 65, 98**	
Tribe *Clauseneae*			
Micromelum			
cyelanicum	9	**34**	
integerrimum	9	**63**	
tephrocarpum	9	**118**	
Clausena			
dentata	9	**26**	
lansium	9	**49**	
wampi	9	**97**	
willdenowii	18	**32, 82**	
Glycosmis			
arborea	9	**3, 93**	
pentaphylla	8	**73**	Doubtful (**34**)
	9	**20, 21, 28, 29, 34, 57, 65, 102**	
Murraya			
koenigii	9	**43, 81, 90, 92**	
paniculata	9	**34, 41, 49, 112**	
	9	**34, 79, 81, 90**	As *M. exotica*
Tribe *Citreae*			
Triphasia			
trifolia	9	**49, 53**	
	18	**49**	
Atalantia			
buxifolia	9	**34, 75**	
citroides	9	**49**	
monophylla	9	**32**	
racemosa	9	**32**	
Citropsis			
articulata	9	**59, 61**	
schweinfurthii	9	**49, 53**	
Citrus			
spp.	9	**2, 4, 22, 23, 24, 30,**	As *C. acida, assamensis, aurantifolia, aurantium,*
	9	**31, 34, 49, 52, 53,**	*bergamia, bigaradia, celebica, decumana, genshos-*
	9	**66, 67, 69, 70, 72,**	*kan, deliciosa, depressa, erythrosa, grandis, halimii,*
	9	**75, 83, 84, 94, 95,**	*hybridus, hystrix, inodora, ichangensis,*
	9	**105, 107, 109, 111,**	*jambhiri, japonica, junos, karna, kinokunii,*

Appendix 1 (continued)

Species	n	References*	Comments
	9	**112, 114, 118**	*kotokan, leiocarpa, limetta, limon, limonia, limonium, macroptera, madurensis, maxima, medica, mediglobosa, mitis, obovata, oleocarpa, paradisi, pectinifera, penivesculata, ponderosa, poonensis, pyriformis, reticulata, rugulosa, sinensis, succosa, sunkii, surcata, tachibana, tamurana, tangerina, tankan, verrucosa, webberi, yatsushior*
	19/2	**94**	As *C. acida*
	21/2	**94**	As *C. decumana*
	27/2	**2, 49, 50, 52**	As *C. aurantifolia, limonia, nobilis, paradisi*
	14	**2, 49**	As *C. medica*; doubtful (**34**)
	18	**22, 23, 24, 49, 52, 69, 70**	As *C. deliciosa, grandis, limon, maxima, madurensis, mediglobosa, ponderosa, reticulata, sinensis, tankan*
	27	**52**	As *C. ponderosa*
Eremocitrus			
glauca	9	**118**	
Fortunella			
crassifolia	9	**53, 71**	
hindsii	9	**53, 71**	
	18	**53**	
japonica	9	**30, 53**	
margarita	9	**34, 52, 53, 71**	
obovata	9	**71**	
Hesperenthusa			
crenulata	9	**97**	As *Limonia acidissima*
Microcitrus			
australasica	9	**49**	
australis	9	**?**	
Poncirus			
trifoliata	9	**34, 52, 53, 96**	
	27/2	**25**	
	18	**52**	
Severina			
buxifolia	9	**53**	
Aegle			
marmelos	9	**5, 58, 73, 81, 90**	
	18	**43**	
Aeglopsis			
chevalieri	9	**53, 61**	
Afraegle			
gabonensis	9	**49**	
Feronia			
elephantum	9	**30, 90**	
limonia	9	**112**	
Tribe *Rhabdodendrae*			To *Rhabdodendraceae* (Cronquist 1981)
Rhabdodendron			Excluded from *Rutaceae* (Da Silva & al. 1988)
microphyllum	10	**80**	

Cytological references. Those noted (*D & W*) or (*G*) are cited in full in Darlington & Wylie (1955) or Guerra (1984) and are not listed in the References section of this review. **1**. Anderson (1975). **2**. Bacchi (1940, *D & W*). **3**. Baguar (1967). **4**. Bamerji (1954). **5**. Banerji & Pal (1957). **6**. Bernardello (1983). **7**. Bolhovskih & al. (1969, *G*). **8**. Borgmann (1964). **9**. Bowden (1940, *D & W*). **10**. Bowden (1945, *D & W*). **11**. Bramwell & al. (1971, *G*). **12**. Carr (1985). **13**. Capelletti (1929, *D & W*). **14**. Chiang & Gonzalez-Medrano (1981). **15**. Contandriopoulis (1957 a, *G*). **16**. Contandriopoulis (1957 b, *G*). **17**. Contandriopoulis (1962, *G*). **18**. Dahlgren & al. (1971, *G*). **19**. Desai (1955). **20**. Desai (1960, *G*). **21**. Desai (1962, *G*). **22**. *F*rost (1925 a). **23**. Frost (1925 b). **24**. Frost & Krug (1942, *D & W*). **25**. Fukumoto (1960). **26**. Gajapathy (1962). **27**. Ghafferi (1987). **28**. Ghosh (1960, *G*). **29**. Ghosh (1966, *G*). **30**. Gill & al. (1979). **31**. Gill & al. (1981). **32**. Gill & al. (1984). **33**. Goldblatt & Williams (1987). **34**. Guerra (1984). **35**. Guerra (1986). **36**. Hair & Beuzenberg (1960). **37**. Hanelt (1973). **38**. Heitz (1926, *G*). **39**. Honsell (1954, *G*). **40**. Honsell (1957, *G*). **41**. Hsu (1967). **42**. Hsu (1968). **43**. Janaki Ammal (1945, *D & W*). **44**. Jackson, pers. comm. **45**. Johnson & Taylor (1989). **46**. Kaastra (1978, *G*). **47**. Keighery (1978). **48**. Keighery (1982). **49**. Krug (1943). **50**. Krug & Bacchi (1943, *D & W*). **51**. Kurosawa (1966). **52**. Lapin (1937, *D & W*). **53**. Longley (1925, *D & W*). **54**. Love & Kvellqvist (1974, *G*). **55**. Lovka & al. (1971, *G*). **56**. Majovsky & al. (1974, *G*). **57**. Malla & al. (1979, *G*). **58**. Malla & al. (1981). **59**. Mangenot & Mangenot (1957). **60**. Mangenot & Mangenot (1958). **61**. Mangenot & Mangenot (1962). **62**. Matveeva & Tikhonova in Federov (1969). **63**. Mehra & Khosla (1969). **64**. Mehra & Sareen (1969). **65**. Morawetz (1986). **66**. Naithani & Raghuvanashi (1958). **67**. Naithani & Raghuvanshi (1963). **68**. Nakajima (1937, *D & W*). **69**. Nakamura (1934 a, *D & W*). **70**. Nakamura (1978, *G*). **71**. Nakamura (1941, *D & W*). **72**. Nakamura (1942, *D & W*). **73**. Nanda (1962, *G*). **74**. Natarajan (1978, *G*). **75**. Negodi (1937, *D & W*). **76**. Negodi (1939, *D & W*). **77**. Paiva & Leitao (1989). **78**. Pancho (1971). **79**. Pathak & al. (1949, *D & W*). **80**. Puff & Weber (1976). **81**. Raghavan (1957). **82**. Raghavan & Arora (1958). **83**. Raghuvanshi (1962 a). **84**. Raghuvanshi (1962 b). **85**. Rattenbury (1957). **86**. Raven & al. (1965). **87**. Revell (1945, *D & W*). **88**. Riley & Hoff (1961). **89**. Sandhu & Mann (1988). **90**. Sanjappa (1979). **91**. Santamour (1966). **92**. Sarkar & al. (1975). **93**. Sarkar & al. (1982). **94**. Sharma & Bal (1957). **95**. Simmonds (1954). **96**. Simonet & Miedzyrzecki (1932, *D & W*). **97**. Singhal & al. (1980). **98**. Singhal & Gill (1984). **99**. Sinoto (1929, *D & W*). **100**. Smith-White (1954). **101**. Smith-White (1959). **102**. Sobti & al. (1979). **103**. Stace & Patrick (1993). **104**. Stace & Armstrong (1992). **105**. Stone & al. (1973). **106**. Strid (1972). **107**. Sugiura (1931, *D & W*). **108**. Sugiura (1936 a, *D & W*). **109**. Sugiura (1936 b, *D & W*). **110**. Susuka & Koriba (1949, *D & W*). **111**. Torres (1966). **112**. Toxopeus (1933, *D & W*). **113**. Tschishow (1956). **114**. Vasil (1962). **115**. Vitek in Guerra (1984). **116**. Ward (1984). **117**. Walker (1942, *D & W*). **118**. Yarnell (1940). **119**. Zakharyeva & Astanova (1948).