

**Chromosome numbers of Malayan and other paleotropical
Gesneriaceae. II. Tribes Trichosporeae, Cyrtandreae and
Epithemateae.**

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**Chromosome numbers of Malayan
and other paleotropical Gesneriaceae.
II. Tribes Trichosporeae, Cyrtandreae and Epithemateae**

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(With 1 figure)

Keywords: Gesneriaceae, Scrophulariaceae, *Aeschynanthus*, *Agalmyla*, *Cyrtandra*, *Cyrtandromoea*, *Epithema*, *Loxonia*, *Monophyllaea*, *Rhynchoglossum*, *Rhynchotechum*, *Stauranthera*, *Whytockia*. – Cytology, karyology, chromosome number. – Borneo, China, Indonesia, Malaya, Malaysia, Malesia.

Abstract

Chromosome numbers (including first counts for 18 species and 4 genera) and additional karyological data are reported for Malayan and a few additional paleotropical Gesneriaceae belonging to the following genera: *Aeschynanthus*, *Agalmyla* (tribe Trichosporeae); *Cyrtandra*, *Rhynchotechum* (tribe Cyrtandreae); (*Whytockia*), *Monophyllaea*, *Loxonia*, *Stauranthera*, *Rhynchoglossum*, *Epithema* (tribe Epithemateae = Klugieae), *Cyrtandromoea* (Gesneriaceae-Epithemateae?, Scrophulariaceae?). The data are discussed with regard to their taxonomic significance.

Zusammenfassung

Für malaiische und einige weitere palaeotropische Vertreter der Triben Trichosporeae, Cyrtandreae und Epithemateae (= Klugieae) werden Chromosomenzahlen und ergänzende karyologische Daten mitgeteilt und im Hinblick auf ihre taxonomische Bedeutung diskutiert.

Introduction

This paper is a continuation of KIEHN & al. (1998) and deals with chromosome numbers of the tribes Trichosporeae, Cyrtandreae and Epithemateae (= Klugieae, BURTT 1997). The bulk of data comes from the Malay Peninsula (W. Malaysia), the additional ones mainly from Borneo.

Materials and methods

Collecting data for the investigated taxa are included in Table 1. Vouchers are deposited in the herbarium of the University of Vienna (WU), or in the herbaria mentioned in Table 1. Permanent slides for the counts are deposited in the collection of MK. For fixation conditions, plant tissues used, staining procedures and other technical background see KIEHN & al. (1998).

Table 1
Results of chromosome counts.

Explanation of the abbreviations and signs: n = haploid chromosome number, $2n$ = diploid chromosome number; ° first count for the species, °° first count for the genus,

- result deviating from literature data.

Investigated plant part/division stage: a = shoot apex, fl = flower-buds, EMC = embryo sac mother cells, ov = ovary, P = pollen mitosis, PMC = pollen mother cells, rt = root tip.

Pretreatment: 8HQ = 8-hydroxy-quinolin

Staining technique: F = Feulgen, G = Giemsa.

WU = Herbarium of the Institute of Botany, University of Vienna.

Taxon Locality ¹ , voucher specimen (herbarium)	n	$2n$	tissue; pretreatment	staining
Trichosporeae				
<i>Aeschynanthus</i>				
<i>A. parvifolius</i> R. Br. Perak, Larut distr; Maxwell's Hill to G. Hijau; WEBER 860816-1/3 (WU).	-	32	ov	F
- Selangor/Pahang border; Fraser's Hill; road to Telekom Station; WEBER 870504-6/1 (WU).	-	32	a	F
- Selangor/Pahang border; Fraser's Hill, Pine Tree Hill area; WEBER 870614-1/16 (WU).	-	64	ov	F
<i>A. radicans</i> Jack Kedah, Kuala Muda distr.; Gunung Jerai, southern foot, Sg. Bujang (c. 500 m); WEBER 860813-1/5 (WU).	16	32	EMC, ov	F

¹ If not stated otherwise, the country is Malaysia.

Table 1 (continued)

Taxon	<i>n</i>	<i>2n</i>	tissue; pretreatment	staining
Locality, voucher specimen (herbarium)				
<i>A. rhododendron</i> Ridl. Perak, Larut distr.; Maxwell's Hill to G. Hijau; WEBER 860816-1/6 (WU).	-	32°	ov	F
<i>A. rhododendron</i> Ridl. s.l. Pahang, Cameron Highlands; G. Berembun; WEBER 860819-2/2 (WU).	-	32°	ov	F
- Pahang; Gunung Jasar, Hilltop Bungalow; WEBER 870622-3/5 (WU).	-	32	ov	F
<i>Agalmyla</i> <i>A. parasitica</i> (Lam.) O. Kuntze Selangor/Pahang; Fraser's Hill; WEBER 870505-5/4 (WU).	-	32	fl	F
Cyrtandreae				
<i>Cyrtandra</i>				
<i>C. dispar</i> A. DC. Perak; Gunung Keledang, middle part; WEBER 860818-2/2 (WU).	-	34°	fl	F + G
<i>C. pendula</i> Blume Negeri Sembilan, Kuala Pilah distr.; Hutan Rekreasi; Jeram Toi (W of Kuala Pilah); WEBER & ANTHONYSAMY 860730-1/2 (WU).	17	-	PMC	F
- Negeri Sembilan, Kuala Pilah distr.; Hutan Rekreasi; Jeram Toi (W of Kuala Pilah); WEBER & ANTHONYSAMY 860730-1/3 (WU).	17	34	PMC, fl	F
<i>C. splendens</i> C. B. Clarke Borneo, cult. HBV sub no. GS-89-04 (WU).	-	34	rt; 8HQ	F + G

ed in Table 1. Vouchers are
a (WU), or in the herbaria
are deposited in the collec-
d, staining procedures and

s.
chromosome number, $2n =$
cies, ° first count for the

, fl = flower-buds, EMC =
PMC = pollen mother cells,

of Vienna.

tissue; staining
pretreatment

ov F

a F

ov F

EMC, ov F

Table 1 (continued)

Taxon Locality, voucher specimen (herbarium)	<i>n</i>	<i>2n</i>	tissue; pretreatment	staining
<i>C. wallichii</i> (C. B. Clarke) B. L. Burt Perak; Gunung Keledang, middle part; WEBER 860818-2/1 (WU).	17°	-	EMC	F
<i>Rhynchotechum</i>				
<i>R. parviflorum</i> Blume Pahang, Pulau Tioman; above Kg. Tekek; WEBER 840726-5/2 (WU).	-	18-20°	fl	F
Epithemateae				
<i>Epithema</i>^{oo}				
<i>Epithema membranaceum</i> (King) Kiew Pahang, Lipis distr.; Gua Bama (13 km NW of Kuala Lipis); WEBER 870508-2/1 (WU).	-	24°	fl	F
- Pahang, Lipis distr.; Gua Bama (13 km NW of Kuala Lipis); WEBER 870508-2/2 (WU).	-	24-26°	fl	F
<i>E. cf. membranaceum</i> Trengganu, Ulu Trengganu distr.; Bukit Lading (S of Ajil); WEBER & ANTHONYSAMY 860828-2/1 (WU).	-	(24)-26°	a	F
<i>E. saxatile</i> Blume Perlis; Bukit Bintang; WEBER 860809-1/1 (WU).	8°	16°	P, ov	F
- Perak, Kinta distr.; Sg. Siput Sela- tan, near Chinese temple; WEBER & ANTHONYSAMY 870521-1/1 (WU).	9°	-	EMC	F
- Perak, Kinta distr.; Kg. Kepayang (between Gopeng and Ipoh); WEBER & ANTHONYSAMY 870521-3/2 (WU).	-	18°	fl	F

Table 1 (continued)

tissue; pretreatment	staining	Taxon Locality, voucher specimen (herbarium)	<i>n</i>	<i>2n</i>	tissue; pretreatment	staining
EMC	F	<i>E. saxatile</i> Blume (cont.) Selangor, Batu Caves, N. Kuala Lumpur; WEBER 790801-1/1 (WU).	-	18°	rt; 8HQ	G
		- Kedah, Baling distr.; Baling; STONE, SAW & WEBER 870424-5/1 (WU).	-	18°	ov	F
fl	F	- Pahang; Gunung Panching (Banleng) [= Bt. Cheras]; WEBER 840811-1/3 (WU).	-	18°	fl	F
		<i>Loxonia</i> ^o				
fl	F	<i>L. hirsuta</i> Jack Pahang; Pulau Tioman, path from Kg. Tekek to Juara Bay; W of Juara bay; WEBER 870602-1/5 (WU).	22°	-	P	F
		<i>Monophyllaea</i>				
fl	F	<i>M. albicalyx</i> A. Weber Perak, near Sungai Siput Selatan; WEBER & ANTHONYSAMY 870518-1/2 (WU).	-	20°	a	F
a	F	<i>M. glauca</i> C. B. Clarke var. <i>hirta</i> B. L. Burtt Sarawak, First Div., Padawan distr., Tiang Bekap; VOGEL & WEBER 790902-2/2 (WU).	c. 12°	20 - 24°	PMC, fl	F
P, ov	F	<i>M. hendersonii</i> (B. L. Burtt) A. Weber Pahang, Bukit Charas (Panching Caves); WEBER 840811-1/2 (WU).	-	24°	rt, 8HQ	F
EMC	F	- , <i>ibid.</i> ; WEBER & ANTHONYSAMY 860825-1/2 (WU).	-	20 (22°)	rt	F
fl	F	- , <i>ibid.</i> ; WEBER 870516-1/1 (WU).	12°	-	PMC	F
		- , <i>ibid.</i> ; WEBER 870608-1/2 (WU).	-	24°	rt, 8HQ	F

Table 1 (continued)

Taxon Locality, voucher specimen (herbarium)	<i>n</i>	<i>2n</i>	tissue; pretreatment	staining
<i>M. hirticalyx</i> Franch. Kelantan, (10) - 15 km N of Gua Musang; WEBER 870512-2/2 (WU).	11°	-	PMC	F
- Perak, limestone rocks and caves N of Ipoh; WEBER 860818-1/2 (WU).	-	22°	rt, 8HQ	F
- Perak, Gunung Rapat, Sam Poh Tong Temple (a few km S. of Ipoh); WEBER 870522-2/2 (WU).	11°	22°	PMC, rt; 8HQ	F
- Perak, South of Ipoh; VOGEL & WEBER 790821-3/1 (WU).	10°	-	PMC	F
- Pahang, Lipis district, Gua Rusa (limestone area c. 40 km S of Gua Musang; WEBER 870510-1/11 (WU).	11°	-	PMC	F
- Selangor, Gua Batu, at base, temple cave; CHIN & WEBER, CHIN 2107 (KLU).	10 (11°)	20°	PMC, fl	F
- var. <i>furcata</i> A. Weber Perak, Sg. Siput Selatan, near Chi- nese temple; WEBER & ANTHONYSAMY 870521-1/4 (WU).	11°	22°	PMC	F
<i>M. horsfieldii</i> R. Br. Kelantan, limestone outcrops N of Ladang Sungai Terah (between Gua Musang and Bertam); WEBER 870511-1/2 (WU).	10°	-	PMC	F
- Kelantan, (10 -)15 km N of Gua Musang; WEBER 870512-2/1 (WU).	10°	-	EMC	F
- Perak, Bkt. Kepayang (betw. Gopeng and Ipoh); WEBER 21. V. 1987 (fixation only).	10°	-	PMC	F

Table 1 (continued)

tissue; pretreatment	staining	Taxon Locality, voucher specimen (herbarium)	<i>n</i>	<i>2n</i>	tissue; pretreatment	staining
PMC	F	<i>M. horsfieldii</i> R. Br. (cont.) Perak, near Sungai Siput Selatan; WEBER & ANTHONYSAMY 870518-1/3 (WU).	10 ⁻	-	PMC	F
rt, 8HQ	F	- Perak, Sungai Siput Selatan, near Chinese temple; WEBER & ANTHONYSAMY 870521-1/5 (WU).	10 ⁻	20°	PMC, fl	F
PMC, rt; 8HQ	F	- Selangor, Batu Caves; WEBER 25. VI. 1987 (fixation only).	10 ⁻	20°	PMC, fl	F
PMC	F	- Selangor, Ulu Gombak, Genting Simpah, 18th mile; WEBER 840713-1/2 (WU).	10 ⁻	-	PMC	F
PMC	F	<i>M. musangensis</i> A. Weber Kelantan, Ulu Kelantan, Gua Musang; WEBER 870511-2/2 (WU).	20°	c. 40°	PMC, P, fl	F
PMC, fl	F	<i>M. tetrasepala</i> B. L. Burtt Sarawak, First Div., Padawan distr., Gunung Manok; VOGEL & WEBER 790904-1/2 (WU).	-	20 - 24°	ov	F, G
PMC	F	<i>Rhynchoglossum</i> <i>R.</i> (cf.) <i>obliquum</i> Blume Pahang, Lipis district; Gua Rusa (limestone area c. 40 km S. of Gua Musang); WEBER 870510-1/3 (WU).	-	22 ± 2 ⁻	a	F ²⁹¹
PMC	F	<i>Stauranthera</i> ^{oo} <i>S. grandiflora</i> Benth. Pahang; Pulau Tioman, above Kg. Tekek; WEBER 870602-1/1 (WU).	18 - 20°	-	P	F
PMC	F					

Results and discussion

The data presented in Table 1 refer to 26 species from 9 genera. In some cases chromosome analysis proved difficult due to the small size and/or high number of chromosomes. Moreover, metaphase chromosomes of field fixations often clumped together and the exact chromosome number could not be established. As approximate numbers allow at least the assessment of the ploidy level, it seemed worthwhile to communicate them.

In the following, the taxa investigated and their tribal affinities and placement are briefly commented on and the taxonomic significance of the karyological data is discussed.

Trichosporeae

At present, the tribe comprises the following genera: *Aeschynanthus*, *Agalmyla*, *Loxostigma*, *Lysionotus* and *Micraeschynanthus*. The latter monotypic genus is doubtful, being possibly based on a floral anomaly of a species of *Aeschynanthus* (see BURTT 1968). WANG & PAN (1982; see also WANG 1990 and WANG & al. 1992) included also the genus *Anna* in the tribe Trichosporeae because of the long, tapering ovules and seeds which they regard as representing the first stage of the formation of hair-like appendages characteristic of the seeds of Trichosporeae. The inclusion needs confirmation. The monotypic genus *Oxychlamys* from New Guinea has recently been reduced to *Aeschynanthus* by VAN ROYEN (1983).

Chromosome data are presently available for *Aeschynanthus*, *Agalmyla* and *Lysionotus* (see SKOG 1984). In Peninsular Malaysia the tribe is represented only by *Aeschynanthus* and *Agalmyla*.

Aeschynanthus

Aeschynanthus is one of the cytologically best known genera of palaeotropical Gesneriaceae, chromosome data being available for c. 25 species. Currently, 6 sections are distinguished, based essentially on the number and shape of seed appendages. The Malayan species belong to the following sections: sect. *Aeschynanthus*, sect. *Haplotrichium*, sect. *Polytrichium* and sect. *Microtrichium*.

Table 2

Chromosome numbers in the genus *Aeschynanthus*

	<i>n</i>	<i>2n</i>	Reference
Sect. <i>Aeschynanthus</i>: <i>x</i> = (15), 16			
<i>A. boschianus</i> De Vriese	32		EBERLE 1956 [as <i>A. lamponga</i> Miq.]
<i>A. obconicus</i> C. B. Clarke	16		RATTER & PRENTICE 1964
<i>A. parvifolius</i> R. Br.		32	HELLMAYR 1989
		32	this paper
	32		EBERLE 1956 (as <i>A. lobbianus</i> Hort. Veitch ex Hook.)
		64	RATTER & MILNE 1970
		64	HELLMAYR 1989
		64	this paper
<i>A. praelongus</i> Kraenzl.	16		RATTER & MILNE 1970
<i>A. pulcher</i> (Blume) G. Don		60	ROGERS 1954
	32		EBERLE 1956
		64	RATTER 1963
<i>A. radicans</i> Jack	32		EBERLE 1956 [as <i>A. javanicus</i> Hort. Rollisson ex Hook.]
	15		RATTER & MILNE 1970
		32	RATTER & MILNE 1970
		32	HELLMAYR 1989
	16		this paper
<i>A. tricolor</i> Hook.	16		EBERLE 1956
		32	RATTER & MILNE 1970
Sect. <i>Diplotrichium</i>: <i>x</i> = 15, 16			
<i>A. lineatus</i> Craib		30	MILNE 1975
<i>A. parasiticus</i> (Roxb.) Wall.	16		EBERLE 1956 [as <i>A. grandiflorus</i> (D. Don) K. Spreng.]
		30	ROGERS in LEE 1962
			[as <i>A. grandiflorus</i> (D. Don) K. Spreng.]
	16		MALLA & al. 1978
<i>A. parviflorus</i> (D. Don) K. Spreng.		32	RATTER 1963
<i>A. sikkimensis</i> Stapf		32	RATTER 1963
		32	RATTER & MILNE 1970
Sect. <i>Haplotrichium</i>: <i>x</i> = 15, 16			
<i>A. hosseussii</i> Pellegr.		32	RATTER 1963
<i>A. longiflorus</i> (Blume) DC.		30	FUSSELL 1958
		30	RATTER 1963
<i>A. perakensis</i> Ridl.		30	RATTER & PRENTICE 1964
		(28, 21)	
<i>A. speciosus</i> Hook.	32		EBERLE 1956

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Table 2 continue

	<i>n</i>	<i>2n</i>	Reference
Sect. <i>Microtrichium</i>: <i>x</i> = 16			
<i>A. ellipticus</i> Lauterb. & K. Schum.		64	RATTER 1963
		96	RATTER & PRENTICE 1964
		32	MILNE 1975
<i>A. guttatus</i> P. Woods		32	MILNE 1975
<i>A. horsfieldii</i> R. Br.		32	MILNE 1975
<i>A. longicalyx</i> Ridl.		32	MILNE 1975
		32	HELLMAYR 1989
<i>A. nummularius</i> (Burk. & S. Moore) K. Schum.		64	RATTER 1963
		64	RATTER & MILNE 1970
<i>A. papuanus</i> (Schltr.) B. L. Burt		32	MILNE 1975
<i>A. rhododendron</i> Ridl.		32	this paper
<i>A. rhododendron</i> Ridl. s.l.		32	this paper
Sect. <i>Polytrichum</i>: <i>x</i> = (14), 15, 16			
<i>A. albidus</i> (Blume) Steud.		30	MILNE 1975
<i>A. fecundus</i> P. Woods	16		RATTER & MILNE 1970 (as <i>A. sp. nov.</i>)
<i>A. longicaulis</i> R. Br.		30	ROGERS 1954 (as <i>A. marmoratus</i> T. Moore)
	14		EBERLE 1956 (as <i>A. marmoratus</i> T. Moore)
		30	RATTER & MILNE 1970 (as <i>A. marmoratus</i> T. Moore)
		64	MILNE 1975
<i>A. myrmecophilus</i> P. Woods		64	MILNE 1975
Sect. <i>Diplotrichium</i> × <i>Haplotrichium</i>			
<i>A. x splendidus</i> T. Moore		32	RATTER 1963 [as <i>A. parasiticus</i> (Roxb.) Wall.]
		32	RATTER & PRENTICE 1964 [as <i>A. parasiticus</i> (Roxb.) Wall.]

In Table 2 the cytologically known species are listed and (as far as possible) referred to their respective sections. The genus apparently exhibits two² different basic numbers: $x = 15$ and $x = 16$. As Table 2 shows, the basic numbers do not precisely match the sections. A possible explanation is that the sectional circumscription is inadequate and needs revision. This view is supported to some degree by recent studies of structure and development of the seeds (LASSNIG, pers. comm.). One also has to consider that particular (ill-known) species may be simply misplaced.

Though at present no definite decision can be made which of the two basic numbers is the primitive one (the other being an dysploid derivative), the following arguments can be quoted in favour of $x = 16$: (1) This number is found throughout sect. *Microtrichium*; no species has $x = 15$. This section is characterized by a single appendage at both ends of the seed, the appendage being short and \pm as broad at the base as the seed (but never filiform); it may, therefore, occupy a basal position within the genus. (2) In the other Trichosporeae counted so far [species of *Agalmyla* (see below) and *Lysionotus*] only $x = 16$ has been found³.

Sect. *Aeschynanthus* is probably homogeneous with respect to chromosome number ($n = x = 16$). Two deviant counts with $x = 15$ could not be confirmed by later investigations (Table 2) and are probably erroneous. At any rate, the relevant species are not allied to any other species of the genus exhibiting $x = 15$.

A closer affinity between the species with $x = 15$, which presently appear scattered over several sections, should be considered. Based on seed surface characters, for instance, the species *A. longiflorus* (incl. *A. perakensis*), *A. parasiticus*, *A. albidus* (and \pm also *A. longicaulis*) can be grouped together. *A. fecundus* should be checked again: it is morphologically closely related to *A. longicaulis* (seed morphology is identical), but is said to have $x = 16$.

Aeschynanthus is one of the few Gesneriaceae in which polyploidy apparently plays a significant role in evolutionary diversification. Polyploidy (mostly $4x$) is not only characteristic of particular species, but evidently also occurs within clearly defined species. Such differentiation into diploid and tetraploid chromosomal races is now definitely known in the Malayan *A. parvifolius*. In the New Guinean *A. ellipticus* even three different ploidy levels have been reported (see Table 2).

² A single record for *A. longicaulis* indicates $x = 14$ ($2n = 28$, EBERLE 1956). As two further counts for the same taxon revealed $x = 15$ ($2n = 30$; ROGERS 1954, RATTER & PRENTICE 1964), the existence of $x = 14$ within *Aeschynanthus* is most doubtful.

³ It may be noted that a dysploid change from 16 to 15 is in contrast to *Streptocarpus*, where morphology suggests a change from 15 to 16.

33
 PRENTICE 1964
 5
 5
 5
 1989
 13
 MILNE 1970
 5
 5
 MILNE 1970
 ov.)
 14 (as *A. marmoratus*
 6 (as *A. marmoratus*
 MILNE 1970
voratus T. Moore)
 3 [as *A. parasiticus*
 1.]
 PRENTICE 1964
iticus (Roxb.) Wall.]

With regard to chromosome size, *Aeschynanthus* is characterized by very small chromosomes. In the diploids investigated, their length does not exceed 1,5 μm in mitotic metaphase; in the tetraploids they are even shorter, 0,6 μm at maximum.

Agalmyla

This genus (in the emended sense of BURTT 1968) is still inadequately known with regard to species number and species delimitation. On the Malay Peninsula there is only one species, *A. parasitica*, which is widespread in W. Malesia. The present result ($2n = 32$) confirms the counts of FUSSELL (1958) and RATTER (1963). The number matches those known for *A. borneensis* and two species (one unidentified, the other reported as *Dichrotrichum amabile* S. Moore) from New Guinea (RATTER & PRENTICE 1964, 1967).

In *Agalmyla* the chromosomes are distinctly larger than in the species of *Aeschynanthus* investigated, measuring nearly 3 μm in mitotic metaphase.

Concluding remarks: A closer affinity of *Aeschynanthus*, *Agalmyla* and *Lysionotus* is supported by the shared basic number $x = 16$. This number is the sole basic number in *Agalmyla* and is probably the primitive one in *Aeschynanthus*. It is also the only number reported for *Lysionotus* (see SKOG 1984). The considerable difference in chromosome length between *Aeschynanthus* and *Agalmyla* is remarkable. This character distinguishes these two ornithophilous genera cytologically. It is remarkable that the DNA sequences of the *ndhF* chloroplast gene do not support a close relationship between *Aeschynanthus*, *Agalmyla* and *Lysionotus* (SMITH & al. 1997b), while in a cladistic analysis based on morphological characters these genera formed a well-supported monophyletic clade (SMITH 1997).

Cyrtandreae

The genus *Cyrtandra* with more than 600 species makes the Cyrtandreae quite a large tribe. In contrast, the number of genera is very small and the inclusion of some of them is problematic or obsolete. BURTT (1963), defining the tribe by the indehiscent fruit, listed 5 genera: *Cyrtandra*, *Protocyrtandra*, *Sepikaea*, *Rhynchotechum* and *Hexatheca*. *Protocyrtandra* is reduced to *Cyrtandra* in the meantime (GILLET 1970), and the same will happen with the monotypic *Sepikaea* from New Guinea (BURTT, pers. comm.). Re-investigation of better material of *Hexatheca* showed that the fruits are thin-walled and dehiscent by breaking into pieces. It, therefore,

does not match the definition of the tribe and has to be excluded and transferred into Didymocarpeae (BURTT, pers. comm.). *Rhynchotechum* has berry fruits (but by its fleshy consistence rather recalling those of Hawaiian species than those of W. Malesia), but floral and anatomical (indumentum) characters seem to indicate a closer relationship with *Boeica* (Didymocarpeae) (BURTT, pers. comm.). Thus it may well be, that after thorough revision the tribe Cyrtandreae will turn out as monotypic.

Cyrtandra

This immensely species-rich genus ranging from the Nicobar Islands, the Malay Peninsula and Taiwan southwards to Sumatra and Java, and eastwards throughout the Pacific to the Hawaiian Islands, is represented on the Malay Peninsula by less than 10 species. This low number (as compared, for instance, with Borneo harbouring at least 150 species) indicates that the genus is here (and in Sumatra) fading out at its western border. It is noteworthy that the few species are scattered over several sections (as far as they can be assigned to any). Karyology of the genus in its whole geographical area is presently under study (KIEHN 1991, LUEGMAYR & KIEHN 1991, KIEHN in prep.). Chromosome numbers are now known for about 50 species (roughly half of them from Hawaii, the others scattered over the whole distribution area). With the exception of three counts by BORGMANN (1964: unidentified taxa from New Guinea, $2n = 32$), all counts revealed $n = x = 17$ and $2n = 34$.

The present results obtained for four species, three from Peninsular Malaysia (*C. pendula*, $n = 17$, $2n = 34$; *C. wallichii*, $n = 17$; *C. dispar*, $2n = 34$) and one from Borneo (*C. splendens*, $2n = 34$), are in full agreement with $x = 17$ as the basic number of *Cyrtandra*.

Rhynchotechum

From this genus of roughly a dozen species (with great difficulties in distinguishing them) the chromosome number of *R. discolor* (Maxim.) B. L. Burtt has been reported as $2n = 20$ (RATTER 1963). The number obtained for the Malayan *R. parviflorum* ($2n = 18 - 20$) approximates RATTER's count reasonably well.

Concluding remarks. The new chromosomal data provide further evidence that the evolutionary diversification of *Cyrtandra* took place exclusively at a single ploidy level and without any changes in the chromosome number. The number of *Rhynchotechum*, $2n = 18 - 20$, is markedly different from that of *Cyrtandra*. This supports BURTT's suspicion that the genus is probably misplaced in Cyrtandreae (BURTT, pers.

comm.). The indehiscent berry-like fruit (which, moreover does not specifically match the sclerocarpous fruits of the W. Malesian species of *Cyrtandra*) may be only a verbal correspondence.

According to RATTER & MILNE (1970), *Hexatheca* has the same chromosome basic number ($x = 17$) as *Cyrtandra*. This might be taken as a possible indication of relationship. However, one must not forget that this number recurs also in some genera of Didymocarpeae (*Opithandra*, *Ornithoboea*, *Petrocosmea*, *Ridleyandra*, some spp. of *Chirita*; see SKOG 1984, KIEHN & al. 1998). This chromosomal coincidence again raises the question of the origin of *Cyrtandra* and Cyrtandreae within or outside Didymocarpeae. Both morpho-cladistical (SMITH 1997) and molecular data indicate a position within the Didymocarpeae (SAMUEL & al. 1997b; these studies, however, do not include one of the $n = 17$ -genera of Didymocarpeae).

Epithemateae

This tribe, formerly known as Klugieae (cf. BURTT 1997), is the only one that can be kept clearly separate within paleotropical Gesneriaceae. This does not only hold true for the morphological situation (no clearly intervening characters to other tribes, particularly to Didymocarpeae; see also the morpho-cladistic analysis of SMITH 1996), but also for molecular data (SMITH & al. 1997b, SAMUEL & al. 1997a)⁴. All genera of Epithemateae are morphologically well marked (the most curious genus being *Monophyllaea* with its unifoliate habit) and sharply separated from one another. With the data presented here and counts for *Whytockia* (WANG, Y. Z., pers. comm.) chromosome numbers are now known for representatives of all genera of the tribe (for a summary see Table 3).

The genus *Cyrtandromaea* is also briefly discussed in an appendix; because the DNA-data of SMITH & al. (1997a) suggest that it belongs to Gesneriaceae, to be placed next to Epithemateae⁵.

⁴ Up to now molecular data for only two genera of Epithemateae (*Monophyllaea*, *Rhynchoglossum*) are available. DNA-analyses of the *ndhF* chloroplast gene (SMITH & al. 1997b) even suggest that Epithemateae are sister to all other Gesneriaceae (that is including the neotropical ones). Morphology, especially the marked anisocotily, relates Epithemateae clearly to the paleotropical subfamily Cyrtandroideae. In the study of SAMUEL & al. (1997a; analysis of *atpB/rbcL* cpDNA intergene region) only *Monophyllaea* was included and proved clearly distant to the investigated species of *Cyrtandra*, *Didissandra* and *Didymocarpus*. The additional inclusion of *Rhynchoglossum* (SAMUEL & al. 1997b) placed this genus also distant to Didymocarpeae.

⁵ SMITH & al. (1997a: 65) even say that "*Cyrtandromoea* belongs to the Klugieae". Their cladogram, however, shows *Cyrtandromoea* only sister to the clade with *Monophyllaea* and *Rhynchoglossum*.

Table 3
Chromosome numbers in the Epithemateae

	<i>n</i>	<i>2n</i>	Reference
<i>Epithema</i>			
<i>E. membranaceum</i> (King)			
Kiew		24, 24 - 26	this paper
<i>E. cf. membranaceum</i> (King)			
Kiew		(24 -) 26	this paper
<i>E. saxatile</i> Blume	8, 9	16, 18	this paper
<i>Loxonia</i>			
<i>L. hirsuta</i> Jack	22		this paper
<i>Monophyllaea</i>			
<i>M. albicalyx</i> A. Weber		20	this paper
<i>M. glauca</i> C. B. Clarke			
var. <i>hirta</i> B. L. Burt	c. 12	20 - 24	this paper
<i>M. hendersonii</i> (B. L. Burt)			
A. Weber	12	20 (- 22), 24	this paper
<i>M. hirtella</i> Miq.	10	20	OKADA 1990
<i>M. hirtella</i> x <i>M. horsfieldii</i>		21	OKADA 1990
<i>M. hirticalyx</i> Franch.	10, 11	20, 22	this paper
<i>M. h.</i> var. <i>furcata</i> A. Weber	11	22	this paper
<i>M. horsfieldii</i> R. Br.	16	32	OEHLEKERS 1923
	10		RATTER & PRENTICE 1964
	10	20	this paper
	11	22	OKADA 1990
<i>M. musangensis</i> A. Weber	20	c. 40	this paper
<i>M. tetrasepala</i> B. L. Burt		20 - 24	this paper
<i>Rhynchoglossum</i>			
<i>R. gardneri</i> Theobald & Grupe	10		RATTER & PRENTICE 1967
<i>R. notonianum</i> (Wall.)		20	EBERLE 1956 (as <i>Klugia notoniana</i> Wall.)
B. L. Burt			
<i>R. obliquum</i> Blume	21		RATTER & PRENTICE 1967 (as <i>R.</i> sp. from Thailand).
	18		VASUDEVAN 1976
		22 ± 2	this paper
<i>R. omeiense</i> W. T. Wang	27	54	WANG, Y. Z., pers. comm.
<i>R. papuae</i> Schltr.	27		RATTER & PRENTICE 1967

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Table 3
Chromosome numbers in the Epithemateae

	<i>n</i>	<i>2n</i>	Reference
<i>Stauranthera</i>			
<i>S. grandiflora</i> Benth.	18 - 20		this paper
<i>Whytockia</i>			
<i>W. hekouhensis</i> Y. Z. Wang		18	WANG, Y. Z., pers. comm.
<i>W. purpurascens</i> Y. Z. Wang		18	WANG, Y. Z., pers. comm.
<i>W. tsiangiana</i> (Hand.-Mazz.) A. Weber var. <i>wilsonii</i> A. Weber		18	WANG, Y. Z., pers. comm.

Epithema

This genus is rather isolated in the tribe. It comprises over 20 species (for new species and names see HILLIARD & BURTT 1997, a revision of the genus is in preparation), one of them (*E. tenue*) occurring in W. Africa. On the Malay Peninsula three taxa are present, all with very similar habit: *E. saxatile* (long known), *E. membranaceum* (recognized by KIEW 1985), and *E. parvibracteatum* (recently described by HILLIARD & BURTT 1997). So far, no karyological data for the genus have been reported. In the course of the present study chromosome numbers were obtained for two species and proved heterogeneous.

Four populations of *E. saxatile*, from different localities in Perak and Selangor, revealed $x = n = 9$, $2n = 18$ chromosomes. Examination of plants of one population from Perlis revealed $n = 8$, $2n = 16$. All figures were obtained from several counts of clear mitotic and/or meiotic stages and erroneous counts can be excluded. Therefore, *E. saxatile* indeed seems to be cytologically heterogeneous.

Though not easy to distinguish morphologically, *E. membranaceum* clearly differs in its chromosome number from *E. saxatile*. The precise number could not be established for all available accessions, the haploid number is $n = 12$ (- 13), the diploid $2n = 24$ (26) (Fig. 1a). A possible explanation for the discordant basic number may be stabilization of an originally triploid chromosome set.

Loxonia

The genus comprises three species, one in S. W. Sumatra, one in the eastern half of Borneo, and one (*L. hirsuta*, examined here) with a wide

distribution from Sumatra to the western half of Borneo (WEBER 1977a). Curiously enough, *L. hirsuta* has not been found on the mainland of Peninsular Malaysia, but only on the island Pulau Tioman off the east coast. Its haploid number, $n = 22$ (Fig. 1b), is amongst the highest in the Epithemateae (tetraploidy on $x = 11$). The basic number $x = 11$ also occurs in some species of *Monophyllaea* and *Rhynchoglossum*. The chromosomes of *Loxonia* also resemble those of *Monophyllaea* in size and structure, while those of the *Rhynchoglossum obliquum* accession studied by us are very different (see below).

Monophyllaea

To date, the chromosome numbers of only two species and one hybrid were known: *M. hirtella* ($n = 10$, $2n = 20$, OKADA 1990), *M. horsfieldii* ($n = 16$, $2n = 32$, OEHLKERS 1923; $n = 10$, RATTER & PRENTICE 1967, $2n = 22$, OKADA 1990) and *M. hirtella* × *M. horsfieldii* ($2n = 21$, OKADA 1990). In the present paper cytological data are given for 8 species from Peninsular Malaysia and Borneo, 7 of them being first reports.

In *M. horsfieldii* the number $n = 10$, $2n = 20$, established by RATTER & PRENTICE 1967 for plants from the Malay Peninsula (Perak, Ipoh), was confirmed by the examination of plants from seven localities, covering roughly the whole distribution area in Peninsular Malaysia (Fig. 1f, g). OEHLKERS' count (1923) (plant material of unknown origin⁶) is apparently erroneous (even when explaining the high number with the accidental investigation of an abnormal polyploid plant, the basic number $x = 8$ – so far unknown in *Monophyllaea* – would still remain problematic). The situation with OKADA's record ($2n = 22$), however, is different. OKADA's material came from W. Sumatra (near Padang), and there may be cytological (and unknown morphological) differences between the Sumatran and Malayan representatives of the same(?) species. Indeed, OKADA records the flowers as purple, which colour has never been recorded in the Malayan plants. Re-collection and re-examination of Sumatran plants is needed to resolve the problem.

Certainly closely allied to *M. horsfieldii* is the new *M. albicalyx* (WEBER 1998), differing from the former in the white sepals and larger flowers with a yellow palate. Its chromosome number $2n = 20$ is in agreement with that of *M. horsfieldii*.

⁶ An attempt has been made to trace the origin of the plants cultivated in the twenties in the Botanical Garden of Munich. A definitive answer cannot be given, but there is some probability that the plants came via England from the Malay Peninsula.

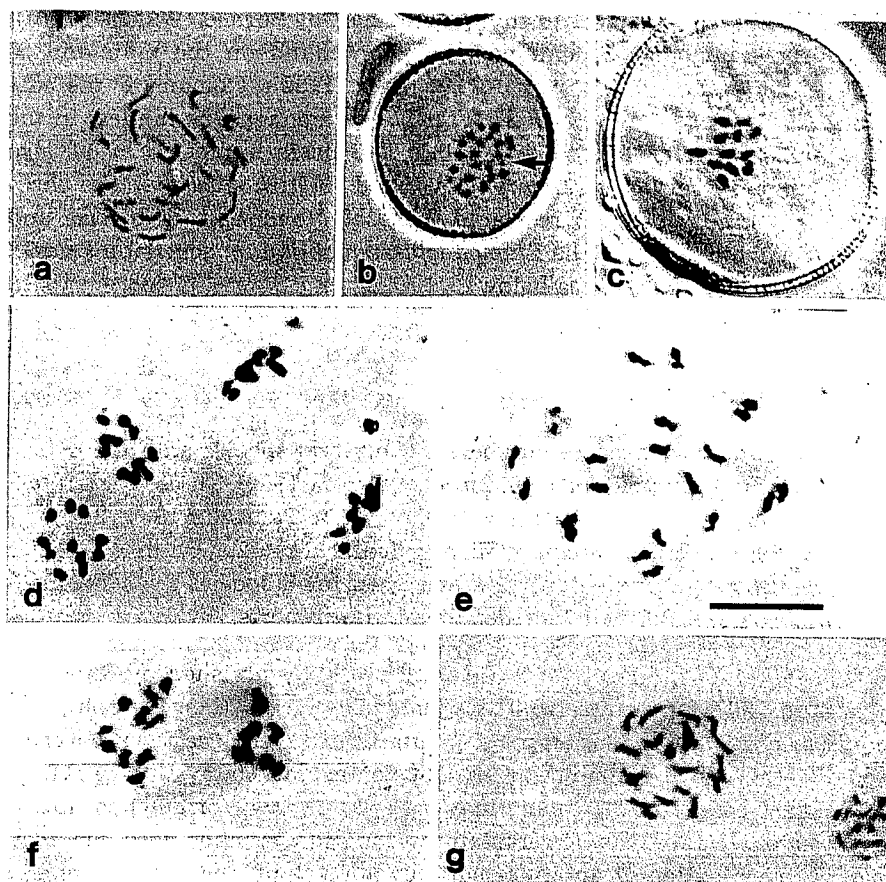


Fig. 1. a *Epithema membranaceum* (WEBER 870508-2/1), $2n = 24$, mitotic prometaphase; b *Loxonia hirsuta*, $n = 22$, metaphase of 1st pollen mitosis, note two prominent satellites (arrow); c *Monophyllaea hendersonii* (WEBER 870516-1/1), $n = 12$, metaphase of 1st pollen mitosis. d *M. hirticalyx* (WEBER 870512-2/2), $n = 11$, pollen mothercell (PMC), ana-telophase of 2nd meiotic division; e *M. hirticalyx* (WEBER 870522-2/2), $n = 11$ II, PMC, meta-anaphase of 1st meiotic division; f *M. horsfieldii* (WEBER 870511-1/2), $n = 10$, PMC, ana-telophase of 1st meiotic division; g *M. horsfieldii* (WEBER & ANTHONYSAMY 870521-1/5), $2n = 20$, mitotic prometaphase. - Bar 10 μm .

M. hirticalyx is a species of more slender habit and has extremely thin leaves adapted to an absolutely constant humidity and low light intensity. It is often found in the immediate vicinity of *M. horsfieldii*, but is ecologically well separated. Plants from seven localities were investigated. In five cases (populations from Kelantan, Perak, and Pahang) a number of $n = 11$, $2n = 22$ was established (Fig. 1d, e). In two cases, how-

ever, a basic number of $x = 10$ ($n = 10$, $2n = 20$) was found. One of these results (based on VOGEL & WEBER 790821-3/1, Perak, S of Ipoh) was obtained from the first mitotic division in pollen. As no cell divisions in other tissues could be found to confirm this number, and irregularities of divisions during pollen mitosis are known to occur, this count is perhaps not reliable. The second report (based on CHIN 2107, Selangor, Batu Caves) is, however, based on counts from several cells in different tissues of a single plant. While $x = 11$ is certainly the predominant basic number in *M. hirticalyx*, at least the Batu Caves population should be studied more thoroughly in order to find out if the plants really have a different basic number or if the present count of $x = 10$ was based on an abnormal individual.

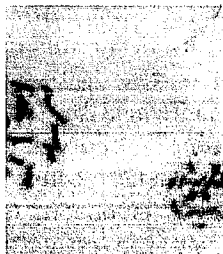
The basic number $x = 11$ ($n = 11$, $2n = 22$) also occurs in a curious plant which is identical with *M. hirticalyx* in stature and in floral characters, but has inflorescences showing regular dichotomous branching (not known in any other species of the genus). Two populations were found near the small village Sg. Siput Selatan (S. Perak). It was described as *M. hirticalyx* var. *furcata* by WEBER 1998.

M. hendersonii exhibits the highest basic number in the genus: $x = n = 12$, $2n = 24$ (Fig. 1c). This taxon was originally described as a variety of *M. horsfieldii* (BURTT 1978), but re-collection and re-examination showed that it is morphologically quite distinct from that species and merits specific rank (WEBER 1998). The different basic number supports this view.

The chromosome number of *M. glauca* var. *hirta* from Borneo could not be established precisely. All we can say is that it is diploid and that its basic number is in the range of the genus ($n = c. 12$, $2n = 20 - 24$).

The highest chromosome number for a *Monophyllaea* was found in *M. musangensis* with $n = 20$ (tetraploidy based on $x = 10$). This is a tiny hairy plant collected on the limestone massif of Gua Musang (Kelantan). At first sight it was taken for a dwarf form of *M. hirticalyx*, but later turned out to be a distinct taxon. Its affinity is certainly not with *M. hirticalyx* or *M. horsfieldii*, but could be with the (cytologically unknown) annual *M. glabra* occurring in NW. Malaysia and SW. Thailand (WEBER 1998).

The basic numbers found in *Monophyllaea* can be arranged in the sequence $n = 10, 11, 12$. Should this be interpreted as an increasing or decreasing series of dysploidy? The morphology of the respective species yields some argument in favour of increase: the Bornean *M. glauca* ($n = 12$?) belongs to subg. *Moultonia*, which by the fruits ('not breaking up into valves, dehiscence porose by fall of style with swollen base', BURTT



24, mitotic prometaphase, note two prominent chromosomes (870516-1/1), $n = 12$, 2-2/2), $n = 11$, pollen 1. *hirticalyx* (WEBER 1998); f *M. horsfieldii* (BURTT 1978); g *M. horsfieldii* (BURTT 1978) mitotic prometaphase. -

was extremely thin and low light intensities were investigated, and Pahang) a In two cases, how-

1978: 22) and the indumentum (hairs in certain species forked, dendroid or stellate) may occupy a more advanced position⁷.

More conclusive is perhaps the fact that both in *M. hirticalyx* ($x = 11$) and *M. hendersonii* the pedicels of the paired flowers become reflexed postflorally, the one winding around the base of the other (WEBER 1975), which is certainly an advanced feature not found in *M. horsfieldii*. Additionally, in *M. hendersonii* the inflorescences get displaced onto the hypocotyl – a first step to the curious situation found in the Bornean *M. singularis*, in which numerous small flower clusters arise along one side of the 'hypocotyl' (BALFOUR & SMITH 1915, BURTT 1978).

The series of morphological advancement *M. horsfieldii* (and the closely related *M. albicalyx*) → *M. hirticalyx* → *M. hendersonii* could be well paralleled by the series of increasing dysploidy $x = 10, 11, 12$.

WANG's report for *Whytockia* fits well into that interpretation. Its chromosome number $x = 9$ (a basic number found in many paleotropical Gesneriaceae) may be the ancestral number in the series of increasing dysploidy. Thus cytology substantiates the phylogeny of *Monophyllaea* suggested by morphological characters.

All species of *Monophyllaea* investigated are very similar in their chromosome morphology. They all have relatively large chromosomes (between 1.5–3 μm long and up to 1 μm wide in mitotic metaphase; Fig. 1c–g, compare also OKADA 1990, Fig. 4). Thus the chromosomes of *Monophyllaea* are amongst the largest found in paleotropical Gesneriaceae. As mentioned below, *Whytockia* is also reported to have exceptionally large chromosomes.

Rhynchoglossum

Counts from five species of *Rhynchoglossum* (including *Klugia*, BURTT 1962) have been reported so far (see Table 3). EBERLE (1956) described the structure of pachytene chromosomes of *Klugia notoniana* (= *Rhynchoglossum notonianum*) as being unique in the Gesneriaceae (p. 310: "Die Gattung *Klugia* mit *Klugia notoniana* weist Chromosomentypen auf, wie sie sonst bei Gesneriaceen nicht beobachtet werden konnten"). However, his studies did not include other genera of Epithemateae. While the number $n = 10$, $2n = 20$ for the tetrandrous *R. gardneri* and *R. notonianum* (both formerly placed in *Klugia*) appears to be settled, there is

⁷ The ovary structure, however, may be more advanced in subg. *Monophyllaea*. Moreover, in the Malayan plants of *M. horsfieldii* fruit dehiscence is similar as described for subg. *Moultonia* (WEBER 1976a).

much inconstancy in diandrous *Rhynchoglossum*, especially in *R. obliquum*, which is the type species of the genus.

R. obliquum in the current circumscription is a very widespread species, ranging from India over the whole Malesian area. It is an annual, and virtually a weed in some habitats. It apparently includes several chromosomal races. The present count of $2n = 22 \pm 2$ for a Malayan plant is exceptional in comparison with the much higher numbers reported so far (see Table 3).

There are marked differences in chromosome morphology between the $x = 10$ -taxa formerly placed in *Klugia* (having more elongated, larger chromosomes measuring up to $1 \mu\text{m}$ in mitotic metaphase) and the diandrous *R. obliquum* and *R. papuae* (having smaller, 'dot-like' chromosomes). Perhaps these differences are due to elimination of homologous DNA after polyploidisation.

Stauranthera

This genus is distributed from NE. India, S. China and the Philippines southwards to Java with a disjunct species in Papua New Guinea. Five species can be recognized, one, the widespread *S. caerulea*, apparently being composed of several varieties or micro-species (WEBER, in prep.). The present count is the first for the genus. The chromosome number ($n = 18 - 20$) indicates tetraploidy.

The chromosomes are relatively large (c. $1 \mu\text{m}$ in metaphase of first pollen mitosis) and are very similar to those of *Monophyllaea* and *Loxonia* at the same stage. The cytological findings are thus in accordance with the morphology: *Stauranthera* and *Loxonia* have the same sympodial architecture and a similar inflorescence structure in common (WEBER 1977). The idea of a rather close relationship between the two genera is thus supported.

Whytockia

Though *Whytockia* is not a Malayan genus (the species occur in S. China and one in Taiwan, WEBER 1982, WANG 1995, WANG & LI 1997) and though its chromosome number has not been established by the present authors, the genus deserves mention here. It is apparently the most primitive genus of the tribe Epithemateae, being specially close (ancestral) to *Monophyllaea* (see WEBER 1976b, 1982). WANG YIN-ZHENG (pers. comm.) recently established the chromosome number of *Whytockia tsiangiana*, *W. hekouhensis* and *W. purpurascens* with $2n = 18$. This number does not occur in the genus *Monophyllaea*, but may represent the lowest number in a series of

increasing dysploidy (see discussion under *Monophyllaea*). Of special interest is WANG's communication that the chromosomes of *Whytockia* "are larger than most of the other taxa in Gesneriaceae". This conforms remarkably with the chromosome size of *Monophyllaea*.

Concluding remarks: In the Epithemateae chromosome size and morphology seem to be more conservative than basic numbers and ploidy levels, and appear to be characteristic of certain groups. The present findings accord well with the morphological diversity of the genera of Epithemateae. The generic relationships emanating from morphological analyses (WEBER 1976 - 1988) are well supported by chromosome data. The genera *Whytockia*, *Monophyllaea*, *Loxonia*, and *Stauranthera* (and possibly also the $x = 10$ taxa of *Rhynchoglossum*) share relatively large and similarly structured chromosomes that are very unusual for Gesneriaceae. With regard to both morphology and chromosomes, *Epithema* seems to occupy an isolated position within the Epithemateae. *Rhynchoglossum* requires further study; the small chromosomes of the diandrous species of *Rhynchoglossum* appear to indicate an advanced position. In the cytologically better known genera (*Monophyllaea*, *Epithema*, *Rhynchoglossum*) different basic numbers and/or ploidy levels are found. This indicates speciation also taking place at the chromosomal level. Such changes in the constitution of the chromosome set may create crossing barriers between sympatric individuals. These barriers apparently do not totally exclude hybridisation (cf. *Monophyllaea*, OKADA 1990).

Appendix: *Cyrtandromoea*

This genus was originally ascribed to Gesneriaceae, but transferred to Scrophulariaceae by BURTT (1965). In contrast to typical Scrophulariaceae it is centered in tropical SE. Asia and comprises true rain forest species. The molecular data of SMITH & al (1997a), however, indicate that the genus should be placed in Gesneriaceae, next to Epithemateae. First chromosome data (relating to *Cyrtandromoea grandis*) have been reported by HELLMAYR & al. (1995): 11 - 12 bivalents were recognized in the 1st meiotic division of a pollen mother cell, and $2n = 22 - 24$ were found in a mitotic prophase from ovary tissue. While these numbers are in accordance with representatives of Epithemateae, the interphase nucleus types and the chromosome structures are different: while the chromosomes of typical Epithemateae are comparatively large (between 1,5 - 3 μm in mitotic metaphase) and \pm homomorphic (meta- to submetacentric), *Cyrtandromoea* exhibits a somewhat heteromorphic karyotype with numerous small chromosomes less than 1 μm long and some more

elongated ones not exceeding 1,5 μm in mitotic prometaphase. These findings are not in accordance with a close relationship between *Cyrtandromoea* and the Epithemateae.

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Note added in proof: The following paper communicating the chromosome numbers and karyotypes of species of *Whytockia* has appeared in the meantime: WANG, Y. Z., GU, Z. H. & D. Y. HONG: Karyotypes of *Whytockia* (Gesneriaceae). — Acta Phytotax. Sin. 36: 28 - 35 (1998).

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