Pl. Syst. Evol. 211: 71–92 (1998)

—Plant—
Systematics
and
Evolution

Collapse of *Isertieae*, re-establishment of *Mussaendeae*, and a new genus of *Sabiceeae* (*Rubiaceae*); phylogenetic relationships based on *rbc*L data

BIRGITTA BREMER and MATS THULIN

Received November 21, 1996; in revised version February 25, 1997

Key words: *Gentianales, Rubiaceae, Isertieae, Mussaendeae, Sabiceeae, Tamridaea.* – Chloroplast DNA, *rbc*L, phylogeny, Socotra.

Abstract: The circumscription of the *Isertieae* has been under debate for a long time and recently a phylogeny based on morphological data has been presented (ANDERSSON 1996), contradicting the classification of ROBBRECHT (1988, 1993). Our investigation of molecular data neither supports the phylogeny of ANDERSSON nor the classification of ROBBRECHT, but instead indicates totally new relationships of *Isertieae, Mussaendeae*, and *Sabiceeae*. The *Isertieae* are a bigeneric tribe of subfam. *Cinchonoideae*, while *Mussaendeae* and *Sabiceeae* are two separate tribes of subfam. *Ixoroideae*. We have also referred a species from Socotra (Yemen) with disputed position to the tribe *Sabiceeae* and we place it in a new genus, *Tamridaea*, with the single species *T. capsulifera* comb. nov. New *rbc*L sequences of 20 taxa are presented and analysed, from *Gentianaceae*: *Gentianella*; from *Loganiaceae*: *Spigelia*; and from *Rubiaceae*: *Amphidasya, Aoranthe, Chomelia, Coussarea, Gonzalagunia, Heinsia, Hippotis, Isertia* (three taxa), *Mussaenda, Pseudomussaenda, Pseudosabicea, Rondeletia, Sabicea, Schradera, Tamridaea*, and *Virectaria.*

One or many seeds, fleshy or dry fruits are characters easily recognised and commonly used to split taxonomic groups in halves, natural or not. These characters have played a significant role in plant classification, also in the *Rubiaceae*. BREMEKAMP (1934: 249–250) was, long before parsimonious interpretations of sets of characters became common in systematics, critical of the general approach of using presence or absence of single characters to split taxonomic groups, and said "that dichotomous classifications are almost always unnatural. This is caused by the circumstance that they are usually (as in our case) based on a quantitative contrast in a single character, very often on its presence or absence." As a consequence he was particularly critical of the subfamily classification of the *Rubiaceae*, based on seed number, but he was more positive towards the tribal classification (of HOOKER 1873, and SCHUMANN 1891). However, he proposed to split some of the heterogeneous tribes (BREMEKAMP 1934), e.g. *Isertieae* (under the synonymous name *Mussaendeae* – for a long period of time the illegitimate name *Mussaendeae* was used instead of *Isertieae* for *Isertia, Mussaenda*, and allied genera, as shown by DARWIN 1976). The remaining part of the *Isertieae* was still mainly characterised by single or few characters, e.g., fleshy fruits with many small angular seeds.

The circumscription of the *Isertieae* (*Mussaendeae*) has differed distinctly between different authors. Initially the tribe was restricted to three genera (DE CANDOLLE 1830), *Isertia*, *Gonzalea* (now *Gonzalagunia*), and *Metabolos* (now placed in *Psychotrieae* PUFF & IGERSHEIM 1994), but later in the same century many more genera were added (HOOKER 1873, SCHUMANN 1891). BREMEKAMP (1934) pointed out that the wide circumscription of the tribe was unnatural, proposed to exclude several genera, and placed them in new tribes, e.g. *Sabicea* to *Sabiceeae*, *Schradera* to *Schradereae*, and *Coccocypselum* to *Coccocypseleae* (cf. BREMER & JANSEN 1991, NATALI & al. 1995). After BREMEKAMP most authors have treated the *Isertieae* as a relatively small tribe of about ten or fewer genera (VERDCOURT 1958; BREMEKAMP 1966; HALLÉ 1966, 1970; KIRKBRIDE 1979, 1981). ROBBRECHT (1988, 1993) on the other hand widened the *Isertieae* again, to include about 25 genera. With ROBBRECHT's wide circumscription of *Isertieae* as a starting point, ANDERSSON (1996) conducted a cladistic analysis based on morphological characters. His conclusion was that the *Isertieae* of ROBBRECHT are highly polyphyletic. ANDERSSON found that several genera are more closely related to other parts of the family and he sorted the remaining genera into two separate tribes, *Isertieae* and *Sabiceeae*. The *Isertieae* were restricted to the seven genera *Aphaenandra*, *Heinsia*, *Isertia* (incl. *Yutajea*), *Mussaenda*, *Neomussaenda*, *Pseudomussaenda*, and *Schizomussaenda*, and *Sabiceeae* to the nine genera *Acranthera, Amphidasya, Ecpoma, Pentaloncha, Pittierothamnus, Pseudosabicea, Sabicea, Schizostigma,* and *Temnopteryx*.

One taxon of the *Isertieae*, endemic to Socotra (Yemen), has had a disputed taxonomic position. We treat it as a new genus, see under *Sabiceeae*, but it was first described as *Mussaenda capsulifera* BALF. f. (BALFOUR 1882). BALFOUR (1888) observed that this species, together with *M. luteola* DEL., is aberrant in this otherwise fleshy-fruited genus by its dehiscent fruits. WERNHAM (1916) erected the genus *Pseudomussaenda* for *M. capsulifera* and three other species with capsular fruits, including also *M. luteola*, an illegitimate name now replaced by *P. flava* VERDC. (VERDCOURT 1952: 377). WERNHAM placed his new genus in the tribe *Condamineeae* and compared it most closely with the New World genera *Pinkneya* and *Pogonopus*. VERDCOURT (1988: 467) in his treatment of *Pseudomussaenda* for Flora of Tropical East Africa indicated that "the very aberrant species *P. capsulifera* with emarginate corolla-lobes and diverse capsule from Socotra may need placing in a separate genus". VERDCOURT (1958, 1988) placed *Pseudomussaenda* in the tribe *Isertieae* (including *Mussaendeae*). He regarded *Pseudomussaenda* and *Mussaenda* as very closely related, and BACKER & BAKHUIZEN VAN DEN BRINK (1965) even suggested that the two should be merged. HALLÉ (1961), in contrast, suggested an affinity of *Pseudomussaenda* with the tribe *Hedyotideae*, while ROBBRECHT (1988), following the original suggestion by WERNHAM (1916), placed it in *Condamineeae*. PUFF & al. (1993b) made a detailed morphological

Table 1. rbcL sequences analysed in this paper. All taxa except *Ligustrum* (L11686) have been sequenced by B. Bremer, or in her laboratory

Family	Species	Accession EMBL/ GenBank	New acçession EMBL/ GenBank	Source/voucher information
Apocynaceae	*Kopsia fruticosa*	L14402		
Gentianaceae	*Anthocleista grandiflora*	L14389		
	Gentianella rapunculoides		Y11862	Ecuador, Bremer & al. 3369 (QCA, QCNE, UPS)
Loganiaceae	*Spigelia anthelmia*		Y11863	Ecuador, Bremer & al. 3377 (QCA, QCNE, UPS)
	Strychnos nux-vomica	L14410		
Gelsemiaceae	*Mostuea brunonis*	L14404		
Oleaceae	*Ligustrum vulgare*	L11686		
Rubiaceae	*Amphidasya ambigua*		Y11844	Ecuador, Clark & Watt 736 (MO, QCNE, UPS)
	Anthospermum herbaceum	X83623		
	Antirhea lucida	X83624		
	Aoranthe penduliflora		Y11845	Herb. material, Iversen & Steiner 86776 (UPS)
	Argostemma hookeri	Z68788		
	Bertiera breviflora	X83625		
	Calycophyllum candidissimum	X83627		
	Catesbaea spinosa	X83628		
	Cephalanthus occidentalis	X83629		
	Chiococca alba	L14394		
	Chomelia sp.		Y11846	Ecuador, Bremer & al. 3354 (MO, QCA, QCNE, UPS)
	Cinchona pubescena (succirubra)	X83630		
	Coccocypselum hirsutum	X87145		
	Coffea arabica	X83631		
	Coussarea macrophylla		Y11847	Ecuador, Bremer & al. 3339 (MO, QCA, QCNE, UPS)
	Cubanola dominguensis	X83632		
	Erithalis fruticosa	X83635		
	Exostema caribaeum	X83636		
	Faramea multiflora	Z68796		
	Gardenia thunbergia	X83637		
	Gonzalagunia affinis		Y11848	Ecuador, Bremer & al. 3350 (MO, QCA, QCNE, UPS)
	Guettarda uruguensis	X83638		
	Hamelia cuprea	X83641		
	Heinsia crinita		Y11849	Gabon, McPherson 16188A (MO)
	Hillia triflora	X83642		
	Hippotis sp.		Y11850	Ecuador, Clark & Watt 825 (MO, QCNE, UPS)
	Hoffmannia refulgens × *ghiesbreghtii*	X83644		
	Hydnophytum formicarum	X83645		
	Isertia cf. *laevis*		Y11852	Ecuador, Bremer & al. 3360 (QCA, QCNE, UPS)
	I. laevis		Y11853	Ecuador, Bremer & al. 3364 (QCA, QCNE, UPS)
	I. pittieri		Y11851	Ecuador, Delprete 6394 (LL, TEX, UPS)
	Ixora coccinea	X83646		
	Ladenbergia pavonii	Z68801		
	Lasianthus pedunculatus	Z68802		
	Meyna tetraphylla	X83649		
	Mitriostigma axillare	X83650		
	Morinda citrifolia	X83651		
	Mussaenda arcuata		Y11854	Gabon, McPherson 16213 (MO)
	M. erythrophylla	X83652		
	Mycetia malayana	Z68806		
	Nauclea orientalis	X83653		
	Nertera granadensis	X83654		
	Neurocalyx zeylanicus	Z68807		
	Oldenlandia cf. *corymbosa*	X83655		

Table 1 (continued)

Family	Species	Accession EMBL/ GenBank	New acçession EMBL/ GenBank	Source/voucher information
	Ophiorrhiza mungos	X83656		
	Pauridiantha paucinervis	Z68811		
	Pentagonia macrophylla	X83658		
	Pentas lanceolata	X83659		
	Pogonopus speciosus	X83662		
	Pseudomussaenda flava		Y11855	Cult. Copenhagen, NISSEN s.n. (UPS)
	Pseudosabicea arborea		Y11856	Herb. material, BORHIDI & al. 82262 (UPS)
	Psychotria kirkii (bacteriophila)	X83663		
	Rachicallis americana	X83664		
	Rondeletia odorata		Y11857	Cult. Uppsala, BREMER & ANDREASEN 3504 (UPS)
	Rubia tinctorum	X83666		
	Sabicea villosa		Y11858	Ecuador, DELPRETE 6396 (LL, TEX, UPS)
	Schradera subandina		Y11859	Ecuador, CLARK & WATT 783 (MO, QCNE, UPS)
	Tamridaea capsulifera		Y11860	Socotra, THULIN & GIFRI 8663 (Aden Univ., E, K, UPS)
	Theligonum cynocrambe	X83668		
	Uncaria rhynchophylla	X83669		
	Vangueria madagascariensis	X83670		
	Virectaria major		Y11861	Herb. material, REEKMANS 10916 (UPS)

analysis of *Pseudomussaenda* [based on material of *P. flava* and *P. stenocarpa* (HIERN) PETIT], *Schizomussaenda* [with the only species *S. dehiscens* (CRAIB) LI], and *Mussaenda* (based on material of four species). The conclusion by PUFF & al. (1993b) was that *Pseudomussaenda* (with five species in tropical Africa), *Schizomussaenda* (with one species in SE Asia), and *Mussaenda* (with about 100 species widespread in the Paleotropics) form a close alliance belonging to the *Isertieae* (including *Mussaendeae*). However, they also stated that "it may well turn out that, after a thorough reinvestigation of the *Isertieae*, the *Mussaenda-Pseudomussaenda-Schizomussaenda* complex (and other genera) will have to be removed from the tribe in its strict sense". PUFF & al. (1993b: 37) also explicitly excluded *P. capsulifera* from their study and indicated that this species "may need placing in a separate genus".

The present study was initiated for two different reasons: (1) to test the proposed phylogeny (ANDERSSON 1996) and the wide circumscription of ROBBRECHT'S *Isertieae* (1988, 1993) with molecular data, and (2) to resolve the phylogenetic relationship and taxonomic position of the disputed and morphologically aberrant endemic species from Socotra which was described as a species of *Mussaenda* and later transferred to *Pseudomussaenda*.

Materials and methods

The strategy of taxon sampling for the cladistic analysis was to investigate the disputed Socotran taxon and as many genera as possible from what has been included in *Isertieae* (*Mussaendeae*), and to analyse these in the context of a broad and even sampling from the whole family *Rubiaceae*. The analysis includes 69 sequences (Table 1)

Table 2. Investigated genera that have been or are associated with the *Mussaendeae-Isertieae-Sabiceeae* complex. New taxonomic positions according to the *rbc*L data printed bold face; *?* indicates uncertain position according to the quoted author

Genera	Schumann (1891)	Bremekamp (1934, 1966)	Verdcourt (1958, 1975)	Kirkbride (1979, 1981)	Robbrecht (1988, 1993)	Andersson (1996)	*rbc*L-support
Amphidasya				*Isertieae*	*Isertieac*	*Sabiceeae*	**subfam. RUBI**
Aoranthe					*Isertieae?*	subfam. IXOR	subfam. IXOR
Bertiera	*Gardenieae*	*Mussaendeae*	*Hamelieae*	incertae sedis	subfam. IXOR	subfam. IXOR	subfam. IXOR
Coccocypselum	*Mussaendeae*	*Coccocypseleae*	*Coccocypseleae*	subfam. RUBI	*Coccocypseleae*	subfam. RUBI	**subfam. RUBI, close to *Coussareae*** (Bremer 1996)
Gonzalagunia	*Mussaendeae*	*Mussaendeae*	*Mussaendeae*	*Isertieae*	*Isertieae*	subfam.?	**subfam. CINC, close to *Rondeletieae* or *Guettardeae***
Heinsia	*Gardenieae*	*Mussaendeae*	*Mussaendeae*		*Isertieae*	*Isertieae*	***Mussaendeae***
Hippotis	*Mussaendeae*	incerteae sedis		*Hippotideae*	*Hippotideae*	subfam.?	**subfam. IXOR**
Hoffmannia	*Mussaendeae*	*Hamelieae*			*Hemelieae*	subfam. RUBI	**subfam. CINC** (Bremer & al. 1995)
Isertia	*Mussaendeae*	*Mussaendeae*	*Mussaendeae*	*Isertieae*	*Isertieae*	*Isertieae*	*Isertieae*
Mussaenda	*Mussaendeae*	*Mussaendeae*	*Mussaendeae*	*Isertieae*	*Isertieae*	*Isertieae*	***Mussaendeae***
Mycetia	*Mussaendeae*	*Hedyotideae*	*Hedyotideae?*		*Isertieae*	subfam. RUBI	**subfam. RUBI, close to *Argostemma*** (Bremer 1996)
Pauridiantha	*Mussaendeae*	*Pauridiantheae*	*Urophylleae*		*Pauridiantheae*	subfam. RUBI	**subfam. RUBI,** (Bremer 1996)
Pentagonia	*Mussaendeae*	incertae sedis		*Hippotideae*	*Hippotideae*		**subfam. IXOR** (Bremer & al. 1995)
Pseudomussaenda		*Mussaendeae*	*Mussaendeae*		*Isertieae*	*Isertieae*	***Mussaendeae***
Pseudosabicea					*Isertieae*	*Sabiceeae*	*Sabiceeae*
Sabicea	*Mussaendeae*	*Sabiceeae*	*Mussaendeae*	*Isertieae*	*Isertieae*	*Sabiceeae*	*Sabiceeae*
Schradera	*Mussaendeae*	*Schradereae*	*Schradereae*	subfam. RUBI	*Schradereae*	subfam. RUBI	subfam. RUBI, **close to *Psychotrieae* and *Morindeae***
Tamridaea							***Sabiceeae***
Virectaria		*Ophiorrhizeae*	*Virectarieae*		*Hedyotideae*		***Sabiceeae***

representing seven outgroup genera of *Gentianales* (excluding *Rubiaceae*) and 62 sequences from all major clades of the *Rubiaceae* (Bremer & al. 1995) representing a majority of the tribes, and includes the new genus *Tamridaea*, the genus *Virectaria* and 17 genera that have been associated with the tribes *Isertieae, Mussaendeae,* and *Sabiceeae* (Table 2).

The *rbc*L gene has been sequenced from 20 taxa (Table 1); sequences are accessioned in EMBL as Y11844 to Y11863. One sequence has been extracted from GenBank (*Ligustrum* L11686) and the other 48 sequences have earlier been published by the first author alone or in collaboration with co-authors (Olmstead & al. 1993, Bremer & al. 1995, Bremer 1996).

DNA was extracted, amplified, and sequenced following the protocols in Bremer & al. (1995). The *rbc*L data matrix in the phylogenetic analyses comprises characters corresponding to each nucleotide position (27 to 1428, position 1–26 are excluded as they are the 5′ PCR primer site) of the *rbc*L sequence.

Parsimony analyses were conducted using PAUP version 3.1.1 (Swofford 1993) on a PowerMac 8100/80, with all character changes weighted equally. Only phylogenetically informative characters were included. The methods for the searches were heuristic, with random stepwise addition of sequences and 100 replications, and TBR branch swapping. To estimate the support for each clade bootstrap (with 10000 replicates; Felsenstein 1985) values were calculated.

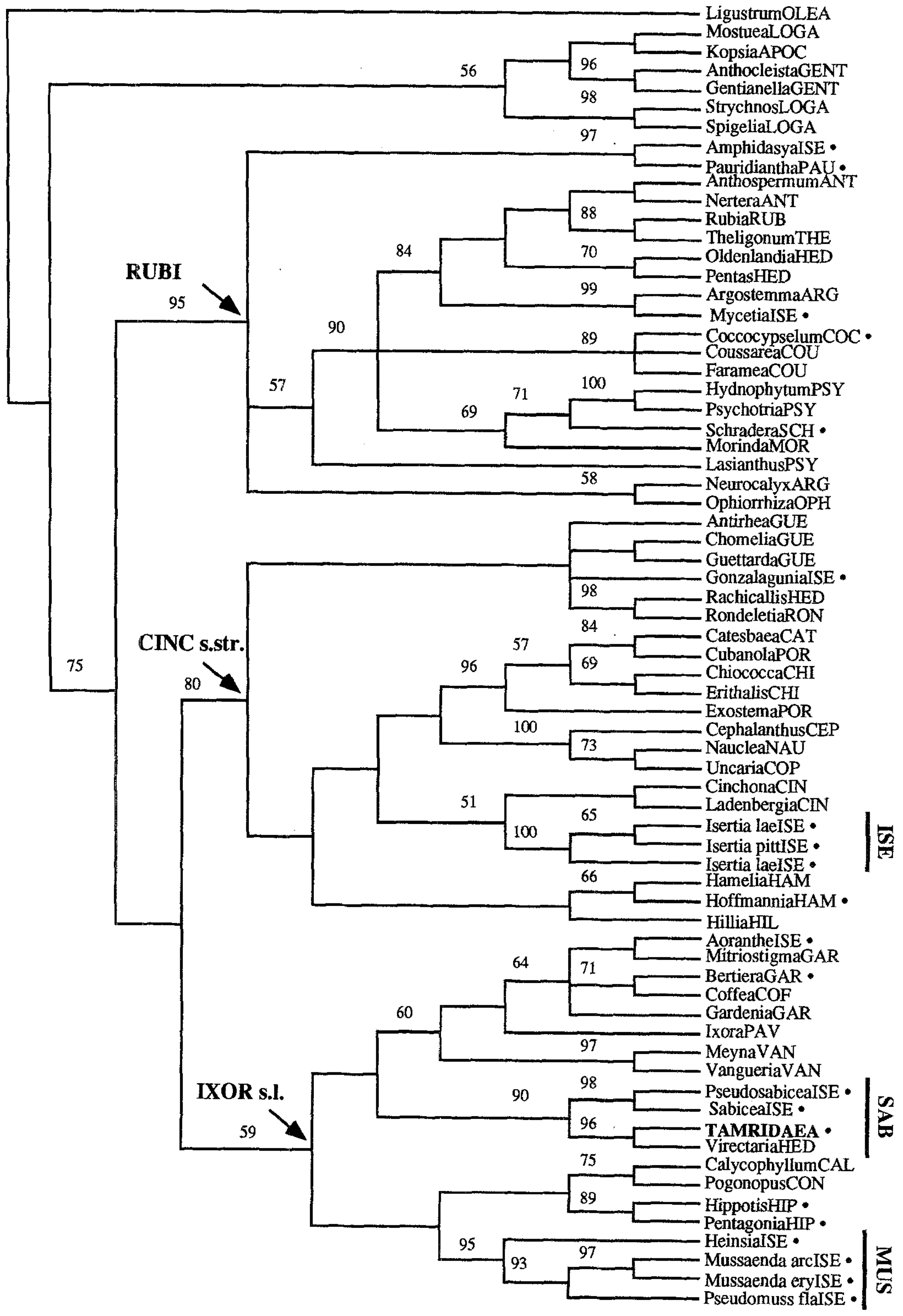
The account of *Tamridaea* is based on the study of herbarium material im BM, E, K, and UPS (acronyms according to Holmgren & al. 1990), as well as on field observations (M. Thulin).

Results

In the cladistic analysis of the 69 included taxa, 520 nucleotide positions were variable and of these 340 were phylogenetically informative. The heuristic search with 100 random addition sequences, including only the phylogenetically informative characters, resulted in 36 equally parsimonious trees 1318 steps long (minimal possible steps 456) with a consistency index (ci) of 0.346 and a retention index (ri) of 0.640. The strict consensus tree is much resolved with a majority of all branches supported by high bootstrap values (above 63%).

The included species associated with the tribe *Isertieae* (*Mussaendeae*) were distributed on all the three subfamilies, *Rubioideae, Cinchonoideae* s. str., and *Ixoroideae* s. l., into ten different, not closely related groups (Fig. 1A, B). *Mycetia, Schradera, Coccocypselum, Amphidasya,* and *Pauridiantha* are all nested within subfam. *Rubioideae* (cf. Bremer & Jansen 1991, Bremer & al. 1995, Bremer

Fig. 1a. Strict consensus tree of 36 equally parsimonious trees illustrating the position of the new genus *Tamridaea* and the positions of the tribes *Isertieae, Mussaendeae, Sabiceeae* of the *Rubiaceae* based on *rbc*L sequences. Vertical bars and corresponding letters represent ISE=*Isertieae*, MUS=*Mussaendeae*, and SAB=*Sabiceeae*; the arrows and corresponding letters represent CINC s. str.=subfam. *Cinchonoideae* s. str., IXOR=subfam. *Ixoroideae* s. l., and RUBI=subfam. *Rubioideae*. Tribal positions are indicated by a three-letter suffix corresponding to the tribes in Robbrecht (1993). Black dots indicate taxa earlier associated with the tribe *Isertieae* (*Mussaendeae*). Numbers above the branches indicate bootstrap values above 50%


LigustrumOLEA
MostueaLOGA
KopsiaAPOC
AnthocleistaGENT
GentianellaGENT
StrychnosLOGA
SpigeliaLOGA
AmphidasyaISE •
PauridianthaPAU •
AnthospermumANT
NerteraANT
RubiaRUB
TheligonumTHE
OldenlandiaHED
PentasHED
ArgostemmaARG
MycetiaISE •
CoccocypselumCOC •
CoussareaCOU
FarameaCOU
HydnophytumPSY
PsychotriaPSY
SchraderaSCH •
MorindaMOR
LasianthusPSY
NeurocalyxARG
OphiorrhizaOPH
AntirheaGUE
ChomeliaGUE
GuettardaGUE
GonzalaguniaISE •
RachicallisHED
RondeletiaRON
CatesbaeaCAT
CubanolaPOR
ChiococcaCHI
ErithalisCHI
ExostemaPOR
CephalanthusCEP
NaucleaNAU
UncariaCOP
CinchonaCIN
LadenbergiaCIN
Isertia laeISE •
Isertia pittISE •
Isertia laeISE •
HameliaHAM
HoffmanniaHAM •
HilliaHIL
AorantheISE •
MitriostigmaGAR
BertieraGAR •
CoffeaCOF
GardeniaGAR
IxoraPAV
MeynaVAN
VangueriaVAN
PseudosabiceaISE •
SabiceaISE •
TAMRIDAEA •
VirectariaHED
CalycophyllumCAL
PogonopusCON
HippotisHIP •
PentagoniaHIP •
HeinsiaISE •
Mussaenda arcISE •
Mussaenda eryISE •
Pseudomuss flaISE •
ISE
SAB
MUS
RUBI
CINC s.str.
IXOR s.l.
56
96
98
97
88
70
84
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95
90
89
100
71
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69
58
98
84
57
69
96
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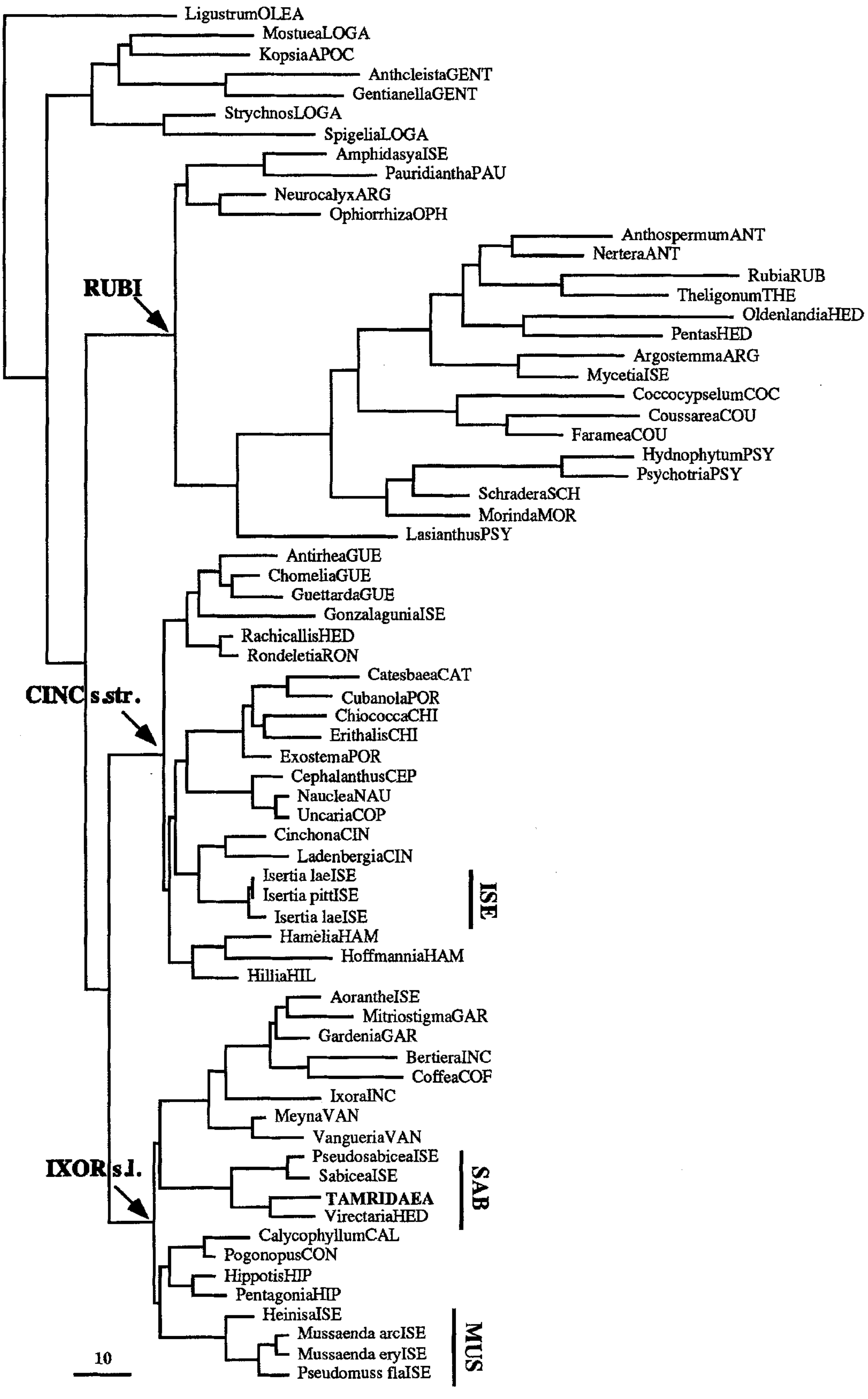
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MostueaLOGA
KopsiaAPOC
AnthcleistaGENT
GentianellaGENT
StrychnosLOGA
SpigeliaLOGA
AmphidasyaISE
PauridianthaPAU
NeurocalyxARG
OphiorrhizaOPH
AnthospermumANT
NerteraANT
RubiaRUB
TheligonumTHE
OldenlandiaHED
PentasHED
ArgostemmaARG
MycetiaISE
CoccocypselumCOC
CoussareaCOU
FarameaCOU
HydnophytumPSY
PsychotriaPSY
SchraderaSCH
MorindaMOR
LasianthusPSY
RUBI
AntirheaGUE
ChomeliaGUE
GuettardaGUE
GonzalaguniaISE
RachicallisHED
RondeletiaRON
CatesbaeaCAT
CubanolaPOR
ChiococcaCHI
ErithalisCHI
ExostemaPOR
CephalanthusCEP
NaucleaNAU
UncariaCOP
CinchonaCIN
LadenbergiaCIN
Isertia laeISE
Isertia pittISE
Isertia laeISE
ISE
HameliaHAM
HoffmanniaHAM
HilliaHIL
CINC s.str.
AorantheISE
MitriostigmaGAR
GardeniaGAR
BertieraINC
CoffeaCOF
IxoraINC
MeynaVAN
VangueriaVAN
PseudosabiceaISE
SabiceaISE
TAMRIDAEA
VirectariaHED
SAB
IXOR s.l.
CalycophyllumCAL
PogonopusCON
HippotisHIP
PentagoniaHIP
HeinisaISE
Mussaenda arcISE
Mussaenda eryISE
Pseudomuss flaISE
MUS
10

1996). The first three genera are closely related to the tribes *Argostemmateae, Psychotrieae*, and *Coussareae*, respectively, and *Amphidasya* and *Pauridiantha* together form a distinct clade. *Gonzalagunia* and *Isertia* are nested in the *Cinchonoideae* s. str. *Isertia* is not closely related to *Mussaenda*, which instead together with the remaining investigated taxa is nested within the *Ixoroideae* s. l. *Aoranthe* and *Bertiera* are closely related to the *Ixoroideae* s. str. *Heinsia, Mussaenda*, and *Pseudomussaenda flava* constitute one clade, *Hippotis* and *Pentagonia* another, and the endemic taxon from Socotra is closely related to *Virectaria*, also a genus of disputed taxonomic position, and these are close to *Sabicea* and *Pseudosabicea* of the *Sabiceeae*. The endemic Socotran species is not closely related to *Pseudomussaenda* or *Mussaenda*, as earlier proposed, and differs distinctly from the sister taxon *Virectaria*. Hence, it is described as a new genus *Tamridaea*.

Discussion and description of the new genus *Tamridaea*

The present investigation does not support a wide circumscription of the *Isertieae*, as proposed by Robbrecht (1988, 1993), Schumann (1891), or Hooker (1873), nor the more narrow circumscription of Andersson (1996). Instead the molecular data support a very small tribe *Isertieae*, excluding the "*Mussaenda-Pseudomussaenda-Schizomussaenda* complex", an idea earlier mentioned by Puff & al. (1993b), and excluding also most other genera earlier associated with the tribe. A particularly interesting result from the present analysis concerns the phylogenetic relationship of *Isertia*; it is not close to *Mussaenda* or *Sabicea*, nor to any other taxon earlier included in the former tribe *Isertieae* (*Mussaendeae*), but instead is most closely related to *Cinchoneae* of subfam. *Cinchonoideae* s. str. As a consequence, *Isertieae* need a new circumscription.

Among the other investigated taxa the molecular data support two larger groups: one around the genus *Mussaenda* (with *Isertia* excluded the name *Mussaendeae* is legitimate and should be re-established), and another group around *Sabicea* (*Sabiceeae*). These two groups were first identified by Bremekamp (1934; but then *Isertia* was included in *Mussaendeae*) and recently supported by morphological data (Andersson 1996). Our results differ from Bremekamp's classification and Andersson's analysis mainly in the totally different phylogenetic relationships for each group. In our molecular analysis both groups around *Mussaenda* and *Sabiceeae* belong to subfam *Ixoroideae* s. l. (cf. Bremer & al. 1995), but in Andersson's analysis only the *Sabiceeae* group was close to *Ixoroideae* and these together are more closely related to subfam. *Rubioideae* than to the *Mussaenda* group (included in *Isertieae*).

Fig. 1b. Sample phylogram, one of the 36 equally parsimonious trees. Branch lengths are proportional to the number of substitutions supporting a node (scale bar equal to 10 substitutions). Vertical bars and corresponding letters represent ISE=*Isertieae*, MUS=*Mussaendeae*, and SAB=*Sabiceeae*; the arrows and corresponding letters represent CINC s. str.=subfam. *Cinchonoideae* s. str., IXOR=subfam. *Ixoroideae* s. l., and RUBI=subfam. *Rubioideae*. Tribal positions are indicated by a three-letter suffix corresponding to the tribes in Robbrecht (1993)

The endemic and disputed taxon from Socotra is not related to either of the genera that it has been included in before, *Mussaenda* or *Pseudomussaenda*, but instead is more closely related to the *Sabiceeae*, and it is sister taxon to *Virectaria*, another genus with disputed taxonomic position.

In our analysis the remaining investigated taxa with earlier associations to the *Isertieae-Mussaendeae-Sabiceeae* are distributed widely among subfamilies and tribes, partly in concordance with earlier suggestions (cf. Bremekamp 1934, 1966; Verdcourt 1958; Robbrecht 1988; Bremer & al. 1995; Andersson 1996; Bremer 1996). *Mycetia, Schradera, Coccocypselum, Pauridiantha,* and *Amphidasya* are all nested within subfam. *Rubioideae. Mycetia* is sister taxon to *Argostemma* of the *Argostemmateae* as shown and discussed in Bremer (1996).

Schradera (or *Schradereae*), by many regarded as an isolated genus (Bremekamp 1966), was recently re-examined by Puff & al. (1993a). The morphological investigation is careful and detailed, but their cladistic analysis is not. Only one of the nodes is supported by their data (98% bootstrap value for the node with *Schradera* and *Lucinaea*). Their tree indicates that the tribe *Schradereae* is sister taxon to *Hillia* of subfam. *Cinchonoideae*, but their conclusion is to maintain it provisionally in subfam. *Rubioideae*. Our analysis shows that *Schradera* belongs to subfam. *Rubioideae* (supported by a bootstrap value of 95%), and also that it occupies a position close to *Psychotrieae* and *Morindeae* or *Psychotrieae* s. l. (Bremer 1996; a large group of taxa in need of molecular investigations). If this molecular tree reflects the true phylogeny, *Schradera* represents a very rare or unique case in *Rubiaceae* of a berry-fruited genus nested within a large group of drupaceous taxa, or evolution of a taxon with many-seeded carpels from an ancestor with one-seeded carpels (cf. Bremer & Eriksson 1992 and Bremer 1996).

Another isolated genus is *Coccocypselum*, which Robbrecht (1988) suggested may belong to the same group of genera as *Schradera*. This is not supported in our analysis, instead *Coccocypselum*, representing a monogeneric tribe *Coccocypseleae*, is closely related to the tribe *Coussareae* (cf. Bremer 1996). The fruits of *Coccocypselum* are berries with many seeds and according to some floras the *Coussareae* seem to have very different fruits, berries or drupes with solitary seeds (cf. Steyermark 1974). However, recent studies have shown (C. Taylor, pers. comm.) that both *Coussarea* and *Faramea* have berries with thin endocarps, and seed number reduction only is an evolutionary change that has occurred several times within the family (cf. Bremer & Eriksson 1992, Bremer 1996).

The basal position of *Pauridiantha* in the *Rubioideae* has been discussed (Bremer 1996), but the sequence of *Amphidasya* is new and our results contradict Andersson (1996), who placed it in the *Sabiceeae*. Our data strongly support a position close to *Pauridiantha* within subfam. *Rubioideae*. Several morphological characters support such a placement of *Amphidasya* in the *Rubioideae*, e.g. occurrence of small raphids in the fruit walls and in the calyx lobes (e.g. *A. ambigua*, Ecuador, Clark & Watt 736 at MO, QCNE, UPS), testa structure without pits, and fringed stipules (very typical for several tribes of the *Rubioideae*).

The genus *Gonzalagunia*, which was placed in the *Isertieae* in Robbrecht's (1988) system, was excluded by Andersson (1996), who suggested a position close to *Rondeletia* or *Sipanea* (even if his tree does not show that) of subfam.

Cinchonoideae. Our results indicate that *Cinchonoideae* is the correct subfamilial position for *Gonzalagunia* and our data indicate a relationship to *Rondeletieae* or *Guettardeae*. Our results also agree about the exclusion of *Aoranthe* from *Isertieae* (*Mussaendeae*), and its transfer to subfam. *Ixoroideae* s. str.

***Isertieae* s. str.** The *rbc*L data position *Isertia* in a totally new relationship, not close to any of the other genera earlier included in the tribe *Isertieae* (*Mussaendeae*) but close to *Cinchona* and *Ladenbergia* of the tribe *Cinchoneae*. Such a novel result must, of course, be tested carefully to exclude the risk of error by contamination of DNA or misidentification of material. To eliminate the possibility that our sequence did not represent *Isertia*, but a contamination, we investigated two more samples, one representing the same species, *I. laevis* ("lower surface of leaf blade with white canescent vestiture", Boom 1984: 430) and one specimen of *I. pittieri* ("lower surface of leaf blades glabrescent or pubescent, but never with white canescent vestiture"). All three sequences are very similar and clearly represent closely related taxa; all are placed close to *Cinchoneae* in the analysis. Two of the sequences are almost identical but belong to specimens identified to different species (according to the key and description in Boom 1984), while the two specimens identified as the same species differ in DNA; perhaps the genus needs further revision. The investigated taxa of *Isertia* belong to subg. *Cassupa*, which was treated initially as a separate genus by de Candolle (1830). There is strong morphological support for the inclusion of *Cassupa* in *Isertia* and for the monophyly of this genus (including also the former genus *Yutajea*, Andersson 1996), e.g. the anthers are septate with many small chambers. This condition is rare in *Rubiaceae* but has been reported from *Isertia* (Boom 1984, Kirkbride 1985) and from other genera (from taxa of the *Gardenieae* and *Pavetteae*, Robbrecht 1981, 1984, and from *Kerianthera* of the *Condamineeae*, Kirkbride 1985). However, in all other genera, the anther organisation is different from that in *Isertia*. In the *Gardenieae* and *Pavetteae* the small chambers are arranged in four rows in each anther (Kirkbride 1985; Robbrecht 1984: Fig. 1G). For *Kerianthera* and *Isertia* Kirkbride (1985: 115) stated that "the locelli are, in general, smaller than those of the African taxa [*Gardenieae* and *Pavetteae*] and do not exhibit an organization into rows oriented from base to apex". However, we note that Kirkbride (1985) and probably Delprete (1996) misinterpreted the condition found in *Isertia* and *Kerianthera*, respectively. In *I. laevis*, at least, each anther (with two thecae) is divided into about 160 small chambers, oval in outline, and these are arranged in eight (four in each theca) distinct longitudinal rows from apex to bottom (the eight rows of chambers make the cross-section of the anther look like an anther with eight loculi, Fig. 2).

Is it possible to find morphological or chemical support for a position of *Isertia* close to *Cinchoneae*? Or conversely, how strong is the support for a position of *Isertia* close to *Mussaenda* and allied genera as proposed in the study by Andersson (1996)? Despite many differences in morphology, e.g. in fruit structure, stipule shape, and aestivation between *Isertia* and the *Cinchoneae*, there are several morphological and chemical similarities. There is support in occurrence of alkaloids; complex indole alkaloids have been found rather frequently in the *Rubiaceae*, but when compared to the phylogenetic tree they occur only in taxa

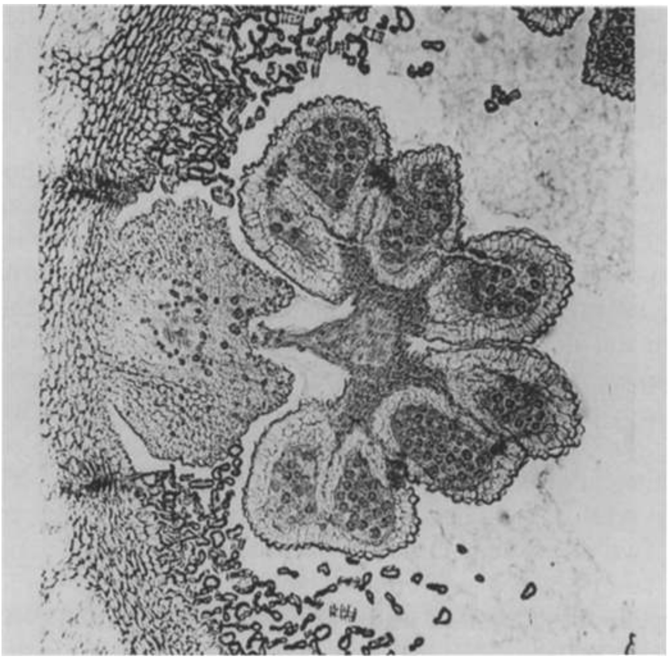

Fig. 2. *Isertia laevis*. Cross-section of flower bud showing one of the six anthers with eight rows of loculi, centre of bud to the right; from BREMER & al. 3360 (UPS)

from the *Cinchonoideae* s. str. (BREMER 1996). HEGNAUER (1973) and KISAKÜREK & al. (1983) reports alkaloids of the corynanthean type in the *Cinchoneae*, *Naucleeae*, and *Guettardeae* only, all of subfam. *Cinchonoideae*, and also in *Isertia* but not from other parts of the family like the *Ixoroideae* s. l. (BREMER 1996) to which *Mussaenda* and allied genera belong. Turning to the morphology SOLEREDER (1899) reported secretary canals in *Cinchona* and relatives and also in *Isertia* and *Mussaenda*. The pollen of *Isertia* is different from *Mussaenda*, but shows similarities to *Cinchoneae* (as interpreted from pictures in ANDERSSON 1993, 1996).

In a recent reinvestigation of *Kerianthera*, DELPRETE (1996) found several morphological characters, in addition to the septate anthers, that support a movement from *Condamineeae* to a position close to *Isertia* in the *Isertieae*. We have not investigated this genus but we feel convinced by DELPRETE'S description and illustration that *Kerianthera* is close to *Isertia*. Interestingly, several of the morphological characters of *Kerianthera* do not occur in *Isertia* but are found in *Cinchoneae*, e.g. the capsular fruit, the dorsiventrally flattened winged seeds with irregular outline, and the 4–5-colporate pollen grains.

The aestivation is valvate in *Cinchoneae* as well as in *Kerianthera* and in some species of *Isertia*, which also has imbricate species. In the phylogeny presented by BREMER & al. (1995) and BREMER (1996) almost all taxa with imbricate aestivation are found in one monophyletic group identified as *Cinchonoideae* s. str. (including *Cinchoneae*, *Chiococceae*, *Guettardeae*, *Naucleeae*, *Rondeletieae*, *Hamelieae*, and *Hillieae*), with a few exceptions of taxa outside this group that are imbricate (e.g. *Heinsia*). A chromosome survey (KIEHN 1995) showed that *Isertia* differs from the

Mussaenda-Pseudomussaenda-Heinsia group by different basic number and also by ploidy level (*Isertia* is tetraploid with x = 10 in contrast to diploidy and x = 11), on the other hand *Isertia* differs from *Cinchona* (x = 17; diploids and tetraploids) and *Ladenbergia* (x = 17, 18 diplids).

In the fruit walls of *Isertia* idioblasts with ruby- or brown-coloured substances, probably tannins, are common, very similar to the idioblasts in *Mussaenda* and *Pseudomussaenda* and also reported from *Ixoroideae* s. str., e.g. *Oxyanthus, Tricalysia* (Robbrecht & Puff 1986), and *Rytigynia* (Robbrecht 1988). One of the main reasons for placing *Isertia* in the same tribe as *Mussaenda* was the occurrence of fleshy fruits, but several investigations have shown that fleshy fruits have evolved many times in the family (Bremer & Eriksson 1992, Bremer 1996). Fleshy fruits occur in several places in subfam. *Cinchonoideae*, e.g. in *Hamelieae, Guettardeae*, and *Chiococceae*.

In Andersson's (1996) cladistic analysis of the tribe, *Isertia* becomes the sister group to the rest of *Isertieae* (*Mussaenda* and allies). He admits a low support for this grouping but writes "in spite of the poor support for clade 115 in the bootstrap runs, I would prefer to recognize this clade as tribe *Isertieae*, rather than subdividing the group into a monotypic *Isertieae* and a very narrowly circumscribed *Mussaendeae*" (Andersson 1996: 156). The bootstrap value of the branch uniting the *Isertieae* (in Andersson 1996) is 53%. All values below 63% are low (cf. Sennblad & Bremer 1996), and the six characters (membranaceous leaf texture; paniculate, corymbose, or thyrsoid inflorescences; white- or cream-coloured corollas; sterile process of anther tip present; fruit indehiscent; mesocarp fleshy) supporting the node are all homoplastic (with ci between 0.083 and 0.571), and have evolved or been lost many times. Nevertheless, Andersson's hypothesis is that *Isertia* is most closely related to the *Mussaenda* group. The support value of our *Isertia-Cinchona-Ladenbergia* clade is also very low (51%; Fig. 1A), but to unite *Isertia* with the *Mussaenda* group requires 19 extra steps in our analysis and is thus very unparsimonious. We conclude that *Isertia* is very distant from the *Mussaenda* group and that the tribe *Isertieae* needs a new circumscription.

***Isertieae* A. Rich. ex DC.**, Prodr. **4**: 342, 435 (1830). Type: *Isertia* Schreber.

Shrubs or trees with subrotund or quadrangular branchlets. Stipules interpetiolar or intrapetiolar, usually deeply bifid. Raphids absent. Inflorescences terminal. Flowers 5- to 8-merous, without (*Isertia*) semaphylls or with (*Kerianthera*); corolla tube cylindrical, short or elongate, the throat villous inside; aestivation valvate or imbricate; stamens 4–8 with septate anthers. Fruit indehiscent with fleshy mesocarp, 2-6(-7)-celled with many seeds, berries or drupes (*Isertia*), or a dry and dehiscent 2-locular capsule with many winged seeds (*Kerianthera*); fruit-walls with tanniniferous (?) idioblasts (*Isertia*); seeds small unwinged, with inner exotesta walls with small pits and knobs (*Isertia*); seeds small unwinged, with inner exotesta walls with small pits and knobs (*Isertia*) or dorsiventrally flattened and winged seeds (*Kerianthera*). Reported (Kiehn 1995) basic chromosome number x = 10 vith 4x ploidy level (*Isertia*).

Genera included: *Isertia* (including *Yutajea*), *Kerianthera*.

Genera excluded: (i) To *Mussaendeae*: *Aphaenandra* (cf. Andersson 1996), *Heinsia, Mussaenda, Pseudomussaenda, Neomussaenda* (cf. Andersson 1996), *Schizomussaenda* (Puff & al. 1993b). (ii) To *Sabiceeae*: *Sabicea, Pseudosabicea,* and *Schizostigma* (cf. Puff & al., oral presentation at the Flora Malesiana Symposium, Kew 1995, Andersson 1996). (iii) To the subfamily *Ixoroideae* s. str. *Aoranthe*. (iv) To subfam. *Rubioideae*: *Amphidasya* (close to *Pauridiantha*), *Coccocypselum* (close to *Coussareae*), *Mycetia* (close to *Argostemma*), *Schradera* (close to *Psychotrieae* and *Morindeae*). (v) To subfam. *Cinchonoideae*: *Gonzalagunia* (close to *Guettardeae* or *Rondeletieae*).

Mussaendeae. In the present analysis the genus *Mussaenda* (represented by two species, one with and one without semaphylls), together with *Heinsia* and *Pseudomussaenda*, form a well supported monophyletic group, not closely related to *Isertia* in the *Cinchonoideae*, but placed within the *Ixoroideae* s. l. (cf. Bremer & al. 1995). These taxa and probably a few more genera, yet to be sequenced, correspond to a smaller tribe *Mussaendeae*, that is established when *Isertia* has been excluded. There are several studies indicating that the taxonomic group around *Mussaenda* should include also *Aphaenandra* (Bremekamp 1937), *Schizomussaenda* (Puff & al. 1993b), and *Neomussaenda* (Tange 1994). The monophyly of this unit is supported in Andersson's analysis (1996), though in his analysis *Mussaenda* and allied genera are not closely related to the *Ixoroideae*. However they possess several characteristic features that are very common in the *Mussaendeae*, even if these are not restricted to this group, e.g. bifid stipules, shaggy hairs, terminal inflorescences, heterostyly, semaphylls, corolla lobes with tail-like projections, discoid placentas, and fruits with tanniniferous idioblasts. One problem in diagnosing this group of taxa is that several commonly used characters in tribal classification are highly variable in the group. For example, aestivation is imbricate (*Heinsia*), reduplicate valvate (*Mussaenda, Aphaenandra*) or induplicate valvate (*Neomussaenda, Pseudomussaenda, Schizomussaenda*); fruits are dry or fleshy, dehiscent or indehiscent with thin or hard endocarps; testa cells are usually provided with thickenings in the inner wall and with large pits, or as in *Schizomussaenda* with very small pits (Puff & al. 1993b). This high variability is obvious also in Andersson's analysis, where the group is supported by six characters (hererostyly; not truncate calyx; aestivation induplicate; corolla lobes with tail-like apex; anthers dorsifixed near base; annular thickening around os), all of which are homoplastic (ci values between 0.120 and 0.500).

***Mussaendeae* J. D. Hooker in Bentham & Hooker,** Gen. Pl. **3**: 8, 15 (1873).
Type: *Mussaenda* L.

Shrubs or small trees. Stipules bifid. Raphids absent. Inflorescences terminal. Flowers (4-)5-merous, often with semaphylls, corolla salver- or funnel-shaped, the throat villous inside; aestivation reduplicate-valvate, induplicate-valvate or imbricate; stamens (4-)5. Fruit indehiscent with fleshy mesocarp or dry capsules with loculicidal dehiscence, 2-celled with many seeds; fruit walls with tanniniferous idioblasts common; seeds small, with inner exotesta walls with large or small pits (*Schizomussaenda*, Puff & al. 1993b) and also knobby (*Neomussaenda*). Reported basic chromosome number (Kiehn 1995) x = 11 with 2x, 4x (*Neomussaenda*, Tange 1994) or doubtfully 6x ploidy level.

Genera included (here investigated): *Heinsia, Mussaenda, Pseudomussaenda. Aphaenandra* (material kindly provided by C. Puff has recently been sequenced and the genus is nested within *Mussaendeae* if analysed with the DNA data matrix of this study).

Genera that probably also belong to this tribe: *Neomussaenda, Schizomussaenda.*

Sabiceeae. The tribe *Sabiceeae* was monogeneric when described by Bremekamp (1934). It was excluded from the *Isertieae* (*Mussaendeae*) because of the simple stipules, axillary inflorescences, and very narrow testa cells (Bremekamp 1966). Most authors did not accept this tribe (Verdcourt 1958; Kirkbride 1979, 1981; Robbrecht 1988, 1993), but Andersson (1996) has shown that it forms a monophyletic group not related to *Isertieae*, but more closely related to the *Ixoroideae*. He included nine genera in the tribe and of these we have only sequenced three, *Pseudosabicea, Sabicea*, and *Amphidasya.* There is a close relationship between *Pseudosabicea* and *Sabicea*, but these two genera are not close to *Amphidasya* which according to our analysis instead belongs to subfam. *Rubioideae* (see above). We are more uncertain of the other genera that Andersson included in *Sabiceeae*, e.g. *Acranthera* may perhaps also belong to the *Rubioideae* as the testa structure is very different from that in *Sabicea* and *Pseudosabicea* but similar to that of *Amphidasya.* In *Sabicea, Pseudosabicea*, and *Stipularia* (Andersson 1996: Fig. 2) the testa structure is very distinct with narrow cells, distinct thickenings on the radial walls, and with large pits and knobs.

The molecular analysis strongly supports the relationship between *Sabicea* and *Pseudosabicea* and also between these genera and *Virectaria* and the new genus *Tamridaea* (see below). Except for the relationship between *Sabicea* and *Pseudosabicea*, these relationships have never been proposed before, but there are several morphological traits that support an affinity between *Virectaria* and *Tamridaea* and their relationship to *Sabicea* and *Pseudosabicea.*

Tamridaea Thulin & B. Bremer, gen. nov.

Type: *T. capsulifera* (Balf.) Thulin & B. Bremer

Frutex ad 1 m altus. Folia opposita vel interdum verticillata; lamina elliptica vel oblongo-elliptica vel obovata, integra, supra glabra, infra pubescens pilis brevibus appressis; petiolus ad 1 mm longus; stipulae integrae triangulares mucrone centrali. Flores fragrantes, hermaphroditi, heterostyli, sessiles vel subsessiles. Calycis lobi 5, lineares vel spathulati, subaequales vel plus minusve inaequales, persistentes. Corolla hypocrateriformis, alba; tubus anguste cylindricus, 25–33 mm longus extus pubescens fauce dense pilosus; lobi 5, reduplicato-valvati, plus minusve obcordati, emarginati et mucronati. Stamina 5, inclusa, antheris linearibus dorsifixis fere sessilibus. Stylus stigmate bilobo lobis lineari-oblongis, incluso in floribus brevistylis, breviter exserto in floribus longistylis. Ovarium biloculare utroque loculo ovulis numerosis. Fructus capsularis loculicidalis. Semina angularia compressa subtiliter reticulata.

Shrub up to c. 1 m tall; young stems terete or somewhat tetragonous, appressed pubescent with short stiff hairs. Leaves opposite or lower ones sometimes in whorls of 3; blade elliptic to oblong-elliptic or obovate, up to 55×25 mm, with entire and slightly revolute margins, obtuse to acute or shortly acuminate at the apex, cuneate to attenuate at the base, glabrous above, pubescent with short appressed hairs beneath, particularly on the veins; venation prominent beneath, with 4–6 pairs of arching lateral veins not reaching the margin of the leaf; petiole up to c. 1 mm long; stipules entire, broadly triangular with a central mucro c. 0.5 mm long. Flowers fragrant, in few- to several-flowered terminal generally dichasial corymbose cymes, hermaphrodite, 5-merous (or very rarely 4-merous), heterostylous, sessile or subsessile; peduncles up to c. 20 mm long; bracts filiform, up to c. 1.5 mm long, or the lower ones sometimes foliose. Calyx-tube cup-shaped to obovoid, 1.5–2 mm long, appressed-pubescent; lobes 5, erect or somewhat spreading, linear to spathulate, subequal or ± unequal, 4–8 mm long, enlarging up to c. 10×2 mm after anthesis, persistent. Corolla salver-shaped, white; tube narrowly cylindrical, 25–33 mm long, striate, slightly widened in the upper part, pubescent with ± appressed ± short stiff hairs outside, densely hairy in the throat and more sparsely hairy inside the tube with longer soft hairs with 1–3 small globular cells at the tip; lobes reduplicate-valvate in bud and forming a deeply 5-lobed structure with a truncate-emarginate tip, at anthesis ± obcordate, c. 6–10×4–8 mm, emarginate and mucronate at the apex, glabrous or pubescent in lower part outside, forming a flat limb. Stamens included in uppermost part of corolla-tube in short-styled flowers, reaching 2–3 mm from the top of the tube in long-styled flowers; anthers linear, c. 3–3.5 mm long, including an apical projection from the connective c. 0.2 mm long, dorsifixed, practically sessile. Pollen 4-colporate with indistinct colpi. Style ± half the length of the corolla-tube in short-styled flowers, equalling the corolla-tube and with stigma shortly exserted in long-styled flowers; stigma green, 2-lobed with thick linear-oblong lobes 1.5–2 mm long. Ovary 2-locular, each locule with numerous ovules born on oblong fleshy peltate placentas; top of ovary with a low annular disk. Fruit a ± ovoid capsule with loculicidal dehiscence mainly in the apical part, 4–6.5×3–4.5 mm, appressed pubescent. Seeds angular, oblong to obovate in outline, flattened, c. 1.2–1.4×0.6–0.8 mm, finely reticulate with mostly narrowly oblong exotesta cells with large pits.

Genus of a single species confined to Socotra (Yemen).

Etymology. *Tamridaea* is derived from Tamrida, an old name for the capital of Socotra (now Hadiboh).

Typification of *Pseudomussaenda*. Greuter & al. (1993) stated that the name *Pseudomussaenda* is not typified. If this is true any of the four species originally included in the genus by Wernham (1916), one of them being *P. capsulifera*, are potential types of the name. On the other hand, Index Nominum Genericorum (Farr & al. 1979) stated that *Pseudomussaenda* was lectotypified by Verdcourt (1952: 378), but he merely said in passing that Wernham "when founding his new genus *Pseudomussaenda* for Delile's yellow-flowered plant" (i.e. *P. flava* Verdc.). This was obviously not regarded as a lectotypification by Greuter & al. (1993) in NCU-3, and we agree on this. However, Hallé (1966) in his treatment of *Pseudomussaenda* for Flore du Gabon stated that "on peut considerer le *P. monteiroi* (Wernh.) Wernh. comme l'espèce type de genre". This, in our opinion, is sufficient to be regarded as a lectotypification of *Pseudomussaenda* and fixes the name for the group of tropical African taxa currently included in the genus.

Thus, if *P. capsulifera* is regarded as a genus of its own, a new generic name is needed.

Tamridaea capsulifera **(Balf. f.) Thulin & B. Bremer, comb. nova** (Fig. 3).

Mussaenda capsulifera Balf. f. in Proc. Roy. Soc. Edinb. **11**: 836 (1882); in Trans. Roy. Soc. Edinb. **31**: 116, tab. 29 (1888); Hooker in Bot. Mag. tab. 7671 (1899); Balfour in Forbes, Natural History of Socotra and Abd al-Kuri: 478 (1903). – *Pseudomussaenda capsulifera* (Balf. f.) Wernham in J. Bot. **54**: 299 (1916).

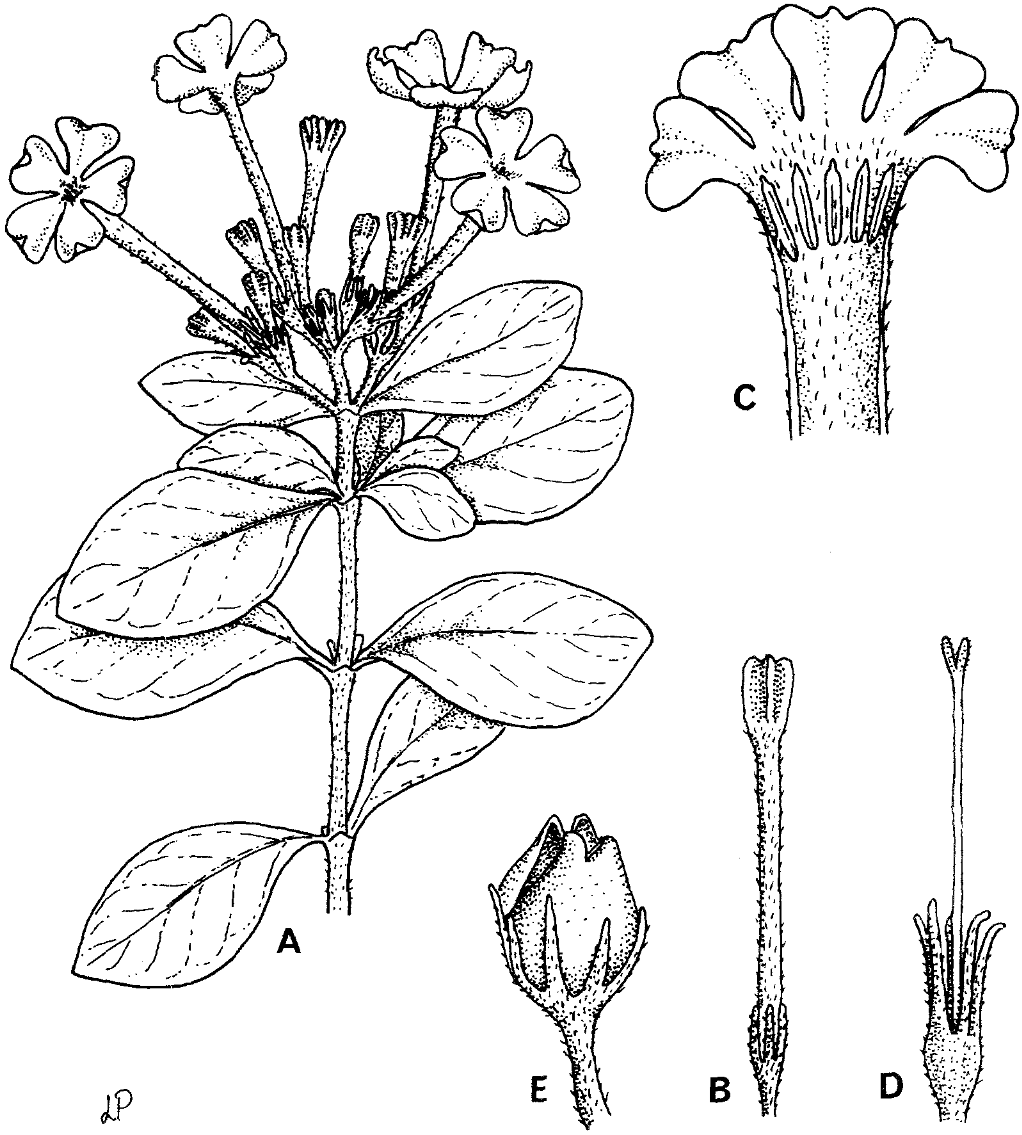

Fig. 3. *Tamridaea capsulifera*. *A* Flowering branch, × 1, *B* bud, × 2, *C* upper part of the corolla tube, opened up, × 3, *D* calyx and style of short-styled flower, × 3, *E* capsule, × 3. From Thulin & Gifri 8663, photographs and illustrations in Balfour (1888) and Hooker (1899)

Type: Yemen, Socotra, Haggier Mts. Feb.-Mar. 1880, BALFOUR, COCKBURN & SCOTT 550 (K lectotype, designated here, BM, E, K isolectotypes).

Note on typification. Two collections, BALFOUR, COCKBURN & SCOTT 550 and SCHWEINFURTH 455, were cited in the protologue of *Mussaenda capsulifera.* BALFOUR, COCKBURN & SCOTT 550 is the better of the two and shows both flowers and fruits, while SCHWEINFURTH 455 is in fruit only. In Kew two sheets of BALFOUR, COCKBURN & SCOTT 550 are present, one mounted together with SCHWEINFURTH 455 and 571, and one mounted on a separate sheet. The latter specimen is here selected as the lectotype.

Description as for the genus.

Distribution and habitat. *Tamridaea capsulifera* is locally a fairly common species apparently confined to the north-central and north-eastern part of Socotra. The species is found in rocky places on both limestone and granite, often growing in rock crevices, at altitudes between 100 and 1100 m a.s.l.

Additional collections. Yemen. Socotra: Keregnigiti, 20 Apr. 1881, SCHWEINFURTH 455 (K): above Kischen, 20 Apr. 1881, SCHWEINFURTH 571 (K); without precise locality, NIMMO s.n. (K), 1897, BENT s.n.; Homhil, 1899, OGILVIE, GRANT & FORBES 171 and 182 (E); Adho Dimeelus, Feb. 1899, OGILVIE, GRANT & FORBES 218 (E); Hammaderoh, small valley leading W of plateau, 12°35′N, 54°17′E, 7 April 1967, SMITH & LAVRANOS 298 (K); N facing slope of Jebel Rughid, 12°37′N, 53°58′E, 13 April 1967, SMITH & LAVRANOS 376 (K); Jebel Chthliheh, above Muqadrihon, 24 May 1967, SMITH & LAVRANOS 775 (K); 3 km SW of Hadiboh, 18 Feb, 1989, MILLER, GUARINO, OBADI, HASSAN & MOHAMED 8215 (E, K); wadi Ayhaft, 8 km SW of Hadiboh, 25 Jan. 1990, MILLER, BAZARA'A, GUARINO & KASSIM 10027 (E, K); Muqadrihon Pass c. 10 km SW of Hadiboh, 26 Jan. 1990, MILLER, BAZARA'A, GUARINO & KASSIM 10087 (E, K, UPS); Mumi village, 12°30′N, 54°20′E, 21 Jan. 1994, THULIN & GIFRI 8663 (Aden Univ., E, K, UPS); 12°22.8′N, 53°47.5′E, 5 March 1996, MILLER & al. 14095 (E).

Initially BALFOUR (1882, 1888) stated that "*Mussaenda capsulifera*" is a small tree, but subsequent collectors have recorded it as small shrub. HOOKER (1899), judging from the collections then available, believed it to be a small shrub, and also reported that cultivated material, grown from seeds collected by BENT, was fully developed and flowering at a height of 18 inches. MATS THULIN observed the species on Socotra several times in 1994, and it was not seen taller than about 0.5 m. The tallest plants recorded were up to 1 m high (MILLER & al. 14095). BALFOUR'S statement therefore must be a mistake. Another erroneous statement by BALFOUR (1882, 1888) is that the stipules in "*Mussaenda capsulifera*" are dentate. As pointed out by HOOKER (1899) the stipules are entire and triangular, and this is also obvious from BALFOUR'S (1888: tab. 29) own illustration. BALFOUR (1888) also erroneously stated the flower colour of the plant to be yellow. As pointed out by HOOKER (1899) the flowers are pure white. Another statement by BALFOUR (1888) is that the leaves of "*Mussaenda capsulifera*" are "obscure pellucido-punctulata". We have not been able to confirm this in any of the available collections.

HOOKER (1899) stated that the aestivation in "*Mussaenda capsulifera*" is "induplicate-valvate", which would agree with the aestivation in *Pseudomussaenda,* but the aestivation actually is reduplicate-valvate. The aestivation thus constitutes a clear difference between *Tamridaea* and *Pseudomussaenda.* A reduplicate-valvate aestivation, however, is typical for *Mussaenda* (PUFF & al. 1993b). The emarginate corolla-lobes appear to be a unique trait in *Tamridaea,* *Pseudomussaenda*, for example, has corolla-lobes with filiform appendages. The stipules in *Tamridaea* are broadly triangular with a single usually rigid mucro, while in *Pseudomussaenda* (as well as in *Mussaenda* and *Schizomussaenda*) the stipules are typically bifid (Puff & al. 1993b). In *Tamridaea* there are no enlarged, coloured and petaloid calyx-lobes, while in *Pseudomussaenda* (as well as in *Schizomussaenda* and most *Mussaenda*) one to several of the flowers in an inflorescence have petaloid calyx-lobes. The stigma-lobes in *Tamridaea* are linear-oblong, while they are more or less ovate in *Pseudomussaenda.*

According to the molecular analysis *Tamridaea* is more closely related to *Virectaria* (tropical Africa), *Sabicea* (pantropical), and *Pseudosabicea* (tropical Africa) than to *Pseudomussaenda* and its allies. All these genera lack petaloid calyx-lobes in contrast to the *Mussaenda-Pseudomussaenda* clade, and they all have valvate aestivation of the corolla, narrow testa cells with knobs and pits, as well as entire stipules. The fruit types differ, however, *Tamridaea* and *Virectaria* having capsular fruits and *Sabicea* and *Pseudosabicea* having fleshy fruits. *Tamridaea* also agrees with *Sabicea* and *Pseudosabicea* in its always white corolla. *Tamridaea* and *Virectaria* differ markedly from almost all members of *Sabicea* and *Pseudosabicea* apart from in their capsular fruits, also in their herbaceous to shrubby (not lianescent) habit, in their terminal (not axillary) inflorescences, and in their different flowers with emarginate corolla-lobes (*Tamridaea*) or much exserted stamens (*Virectaria*). From *Sabicea* they also differ in their 2-locular (not 4-5-locular) ovaries. The pollen grains are rather similar in *Sabicea* and *Pseudosabicea* (3-porate or colporate with indistinct colpi) but different in *Tamridaea* (4-colporate with indistinct colpi) and *Virectaria* (3-colporate with distinct colpi). However, according to Andersson (1996) the variation within *Sabiceeae* is rather high from 3- to 4-aperturate and from porate to colpate pollen.

Tamridaea differs from *Virectaria* in being a shrub (not a herb) with heterostylous (not homostylous) flowers with a flat corolla-limb (not with suberect corolla-lobes) and with a distinctly hairy (not practically glabrous) throat, inserted (not much exserted) stamens, 2-lobed (not subcapitate) stigma, inconspicuous disk, and different capsules dehiscing in upper part only (not to the base into 2 valves), and in the different pollen type.

The taxonomic position of *Virectaria* also has been controversial. At its publication (Bremekamp 1952) it was included in the tribe *Ophiorrhizeae*, but Bremekamp (1952: 21) also stated "it can not be said that this genus shows a very striking resemblance to *Ophiorrhiza* and *Spiradiclis*". Verdcourt (1958) disagreed with the position of *Virectaria* close to *Ophiorrhiza*, mainly due to the lack of raphids in *Virectaria.* His conclusion was instead that *Virectaria* belongs to subfam. *Cinchonoideae*, close to the tribe *Rondeletieae*, and later he (Verdcourt 1975) placed it in a new tribe *Virectarieae*, while *Ophiorrhiza* (*Ophiorrhizeae*) was placed in subfam. *Rubioideae*, because of its raphids. Robbrecht (1988, 1993), partly based on Darwin (1976), moved *Virectaria* to the tribe *Hedyotideae* of subfam. *Rubioideae.* Our analysis strongly supports the opinion of Verdcourt with a position of *Virectaria* outside subfam. *Rubioideae*, though its close affinity to the new genus *Tamridaea* and to the *Sabiceeae* was not expected.

Only a few of the genera of the *Sabiceeae* (sensu Andersson 1996) have been investigated in this analysis and the phylogeny of this part of the family is rather preliminary. Still, we tentatively propose the inclusion of *Virectaria* and *Tamridaea* in the *Sabiceeae.*

We appreciate all kind of help we have got to carry out this study; for providing plant material (living or herbarium specimens) we thank J. Clark, P. Delprete, R. Moberg, G. McPherson, K. Pharsen, and all directors of the botanical gardens and herbaria listed in Table 1 and under Materials and methods, for comments on the manuscript K. Andreasen, K. Bremer, D. Olmstead, C. Puff, C. Taylor, and one anonymous reviewer, for technical assistance J. Rönnholm, U.-B. Sahlström, and for the drawing in Fig. 3 L. Petrusson. This research was supported by the Swedish Natural Science Research Council (NFR) grants to BB for molecular work and to MT for the field work on Socotra.

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Address of the authors: BIRGITTA BREMER and MATS THULIN, Department of Systematic Botany, Uppsala University, Villavägen 6, S-752 36 Uppsala, Sweden.

Accepted March 13, 1997 by F. EHRENDORFER