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REMARKS ON THE TROPICAL ASIAN AND AUSTRALIAN TAXA INCLUDED IN DIPLOSPORA OR TRICALYSIA (RUBIACEAE – IXOROIDEAE – GARDENIEAE)

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SUMMARY

The Asian and Australian species generally included in *Diplospora* or *Tricalysia* are shown to form an artificial assemblage. A few species even do not belong to the Gardenieae–Diplosporinae and need to be transferred to other tribes of the Ixoroideae. So *Diplospora malaccensis*, *Diplospora minahassae*, *Tricalysia purpurea*, and *Tricalysia sorsogonensis* belong to the Hypobathreae. The three Australian *Diplosporas* are members of the Pavetteae and are transferred to *Tarenna*. A survey is given of the characters of the remaining Asian species of *Diplospora/Tricalysia*, demonstrating that 1) these species cannot be accommodated under the African genus *Tricalysia*, and 2) *Discospermum*, since a century included in the synonymy of *Diplospora*, merits to be revived at generic rank. The two genera differ in placentation, fruit size and fruit wall texture, number of seeds per locule, seed shape, and exotestal cell anatomy. Eight necessary new combinations are provided: *Diplospora puberula*, *Diplospora tinagoensis*, *Discospermum abnorme*, *Discospermum beccarianum*, *Discospermum whitfordii*, *Tarenna australis*, *Tarenna cameroni*, and *Tarenna triflora*. An annotated check-list including the more than 100 names involved is given.

1. INTRODUCTION

Present study, undertaken as a short-time postdoctoral research of the first author, intends to settle the problem of the generic position of the Asian species included in *Tricalysia* or *Diplospora* (Rubiaceae–Ixoroideae–Gardenieae–Diplosporinae). Indeed, it is not clear whether the Asian genus *Diplospora* should be separated from *Tricalysia* or not. Robbrecht (1979, 1982, 1983, 1987), when revising the African species of *Tricalysia*, left the question unanswered. In fact, from the nomenclatural viewpoint there was no problem for the African group. Schumann (1891) considered the two taxa to be congeneric and choose the name *Tricalysia* A. Rich. in DC. (1830) associated with an African type species above *Diplospora* DC. (1830) with Asian type; the two genera were published on the same date, and his decision is thus binding in case of merging the taxa into one genus.

During the study, it became apparent that a taxonomic decision on the relationship between the African and the Asian group should involve the comparison of as many species as possible. A complete revision of the Asian group, however, was not pos-

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sible because of the short term of the project. The main aim of the present paper is therefore to give a thorough documentation of the features of the Asian (and the few Australian) species of *'Diplospora'*, and to discuss them in the light of (i) recent concepts of Gardenieae and related tribes (Robbrecht & Puff, 1986) and (ii) known characters of African groups of *Tricalysia* (Robbrecht, 1979, 1982, 1983, 1987).

2. MATERIAL AND METHODS

The study is based on an examination of the herbarium material from BR, L and NY, plus a selection of Indian material from K (abbreviations following Holmgren et al., 1981). Of the many collections seen by us, details and whereabouts are given only for those specimens used for an in-depth morphological and anatomical study (see paragraph 7). The same paragraph contains the information on the sources of the illustrations.

Methods and terminology follow Robbrecht (1988).

3. HISTORICAL SURVEY OF DIPLOSPORA/TRICALYSIA IN ASIA

In 1826, Lindley described a Chinese species under the large paleotropical genus *Canthium*; the specific epithet (*dubium*) expressed his doubt, "in the absence of all knowledge of its fruit", about the correct generic position of his new species. A few years later, De Candolle (1830) erected the monospecific genus *Diplospora* for it and renamed the species (*D. viridiflora*); the correct combination *D. dubia,* under our rules of nomenclature, was provided by Masamune (1939).

In Hooker's (1873) treatment of the Rubiaceae in Genera Plantarum, already 6–8 species were mentioned for *Diplospora,* mainly because of the inclusion, as a synonym, of the genus *Discospermum.* Dalzell described the latter genus from Sri Lanka in 1850.

In a subsequent treatment of *Diplospora,* viz. in the Flora of British India (Hooker, 1880), *Discospermum* was revived to some extent, since *Diplospora* was divided into two sections, *'Eudiplospora'* characterized by apparent sheathing bracteoles embracing the ovary, and sect. *Discospermum* with much smaller free or connate bracteoles.

Bentham (1867) was the first to add an Australian species to *Diplospora, D. australis.* Two more Australian species have later been added, viz. *D. cameroni* and *D. ixoroides.*

Baillon (1876–79) accepted that *Discospermum* is very closely related to *Diplospora,* and proposed *Hypobathrum* section *Diplospora* for the two genera. Baillon, however, made no formal combinations under *Hypobathrum.* As for many other of his genera, his concept of *Hypobathrum* was extremely wide, obviously too wide, and never followed.

Schumann (1891) reduced *Diplospora* to the synonymy of *Tricalysia,* although retaining it as a section; he made no mention of *Discospermum.* His decision was not always followed, and several later authors reinstated *Diplospora* (e.g. Koorders &

Valeton, 1902; Pitard, 1922–24; Chevalier, 1947). The same year, because of the existence of the parahomonym *Diplosporium* Link (1824; Hyphomycetes), Kuntze (1891) took up the generic name *Discospermum* as the correct one in case *Diplospora* and *Discospermum* are merged into synonymy; he consequently made the necessary combinations for the then known species. His decision was never followed and cannot be applied under the present provisions for homonyms (art. 64.3 of the Berlin code). The two names, one in the angiosperms, the other in the Fungi, are not confusing at all.

Since Schumann's decision, many more Asian taxa have been described (in total c. 40 species). As opinions on the generic position were discordant, most Asian *Diplospora* species have an alternative name under *Tricalysia*; for a small number of species, however, only a formal name under *Tricalysia* is at present available.

The taxonomic position of *Tricalysia, Diplospora,* and *Discospermum* is not in need of much comment. Most classical authors placed these genera in the Gardenieae, a previously artificially conceived tribe which became much debated after Bremekamp proposed a more narrow delimitation in 1934. The problems of tribal delimitation in this group of the Rubiaceae were then surveyed and clarified by Robbrecht & Puff (1986). They placed *Tricalysia* and *Diplospora* in the Gardenieae–Diplosporinae, emphasizing that additional work on the delimitation of *Diplospora* is required and that *Discospermum* perhaps merits generic recognition.

4. EXCLUDED TAXA

There are strong overall similarities between the Gardenieae–Diplosporinae and the Hypobathreae. In these taxa indeed, architecture follows Roux's model, with the axillary and opposite inflorescences frequently ± sessile and strongly congested, depicting the appearance of a coffee shrub. Since the flower morphology is also very similar, it is not astonishing that several species described under *Diplospora* or *Tricalysia* in fact belong to the tribe Hypobathreae, as reported in previous literature (e.g. *Diplospora minutiflora*) or found here (e.g. *Diplospora minahassae, Tricalysia sorsogonensis*). The differences between Hypobathreae and Gardenieae are mainly in placentation and fruit morphology (Robbrecht & Puff, 1986). For details on *Diplospora* species transferred to Hypobathreae see paragraph 7.

Kuntze (1891), based on a single flowering specimen of his world trip collection, described one Indian species as *Discospermum parvifolium*. This name was later overlooked; Indian taxonomic or floristic literature never made mention of it. Its type turned up during the present investigation, and showed that this species probably must be excluded from the Rubiaceae. See also paragraph 7.

A close examination of all the Australian taxa showed that they do not belong to the Diplosporinae either. *Diplospora australis* was the first Australian species accommodated in the Asian genus, and two were later added, *D. ixoroides* and *D. cameroni*. The original descriptions (protologues) as well as historical illustrations of these three species (Banks & Solander, 1901: fig. 141; Bailey, 1909: figs. 216, 217) make clear that they belong to the Pavetteae as recently defined (Robbrecht, 1984, 1988),

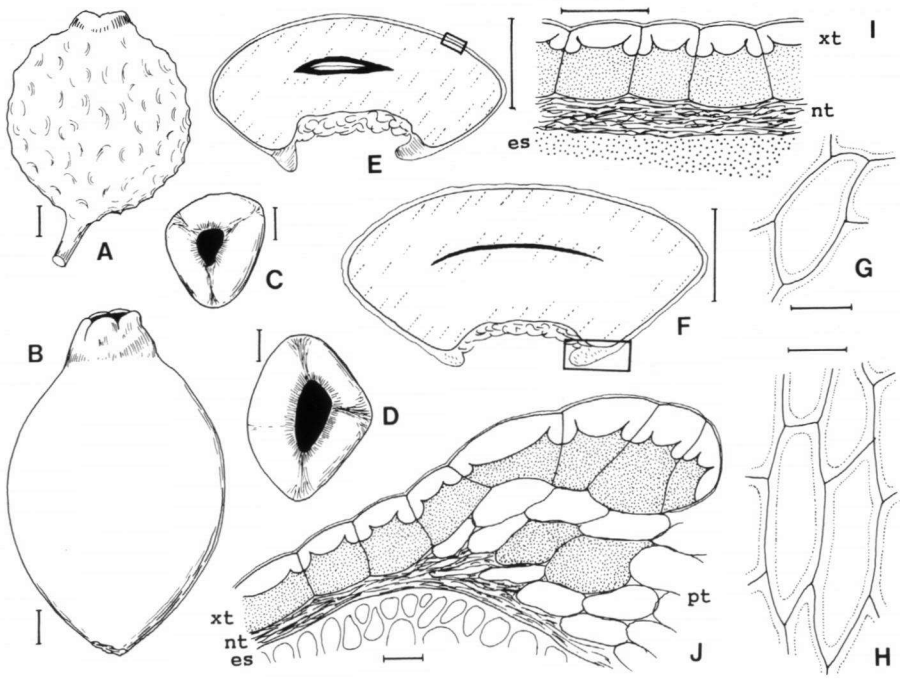

Fig. 1. Fruits and seeds of Australian *'Diplospora'* species (A, C, E, G, I, *Tarenna ixoroides*; B, D, F, H, J, *Tarenna cameroni*): A, B, fruit; C, D, adaxial view of seed; E, F, cross section of seed [from inside to outside: embryo, embryonal cavity (black), endosperm, seed-coat = placental tissue in hilar cavity]; G, H, exotestal cells in surface view; I, cross section of seed-coat, see frame in E (endosperm presented as coarse stippling); J, cross section of seed-coat at place of annular thickening around hilar cavity, see frame in F. Abbreviations to I and J: xt = exotesta; nt = endotesta; es = endosperm; pt = placental tissue; cell-lumina filled with tannins represented by stippling. Vertical scales = 1 mm, horizontal scales = 50 μm.

as the terminal inflorescences alone indicate. They fit well within Bridson's (1979) large concept of the genus *Tarenna*. This is corroborated by our in-depth study (fig. 1) of the fruits of *D. ixoroides* and *D. cameroni* (no fruits of *D. australis* were available to us). The fruits (fig. 1A, B), those of *D. ixoroides* with a characteristic shrivelled appearance in the dried state, contain 2 or 3 ± angular seeds (fig. 1C, D) with a deep, circular, adaxial excavation surrounded by an annular thickening of the seed-coat. The exotestal cells (fig. 1I, G, H) have a conspicuous thickening along the outer tangential wall, provided with a deep intrusion towards the cell-margins; the cell-lumen is copiously filled with tannins. The annular thickening around the hilar cavity results from conspicuous enlargement of the exotestal cells (fig. 1J). This intricate morphological/anatomical pattern fits well with *Tarenna* (see Bridson & Robbrecht, 1985) and makes an inclusion of the Australian species in Bridson's (1979) informal infrageneric group I (= *Tarenna* s.s.) plausible.

The characters of all these excluded taxa are not considered in paragraphs 5 and 6.

5. THE CHARACTERS OF ASIAN DIPLOSPORA/TRICALYSIA COMPARED WITH AFRICAN TRICALYSIA

All comparison with the African taxa is based on Robbrecht (1979, 1982, 1983, 1987). For terminology and a general discussion of rubiaceous features, see Robbrecht (1988).

Vegetative features

All the Asian taxa are shrubs or small trees. The majority of the African species have the same habit; however, in Africa large trees, rheophytes, and geofrutescent species also exist, three categories which are absent in the Asian group.

Leaves and stipules

There are no obvious morphological differences between leaves and stipules of Asian *Diplosporas* and of African *Tricalysias*. Leaves are opposite and provided with sheathing stipules bearing a short to long interpetiolar awn (fig. 2). Most species have elliptic medium-sized (c. 8–14 × 3–5 cm) leaf-blades with a distinct petiole. Domatia are present in many species; they show much variation and belong to the tuft- (e.g. *D. confusa, D. fruticosa*), pocket-, pit- (e.g. *D. abnorme*) or crypt-type (e.g. *D. erythrospora*: crypt with ciliate opening). The occurrence of domatia types has frequently value at the specific level, but some species are quite variable; in *D. sphaerocarpum*, domatia are absent or belong to the pocket- or pit-type.

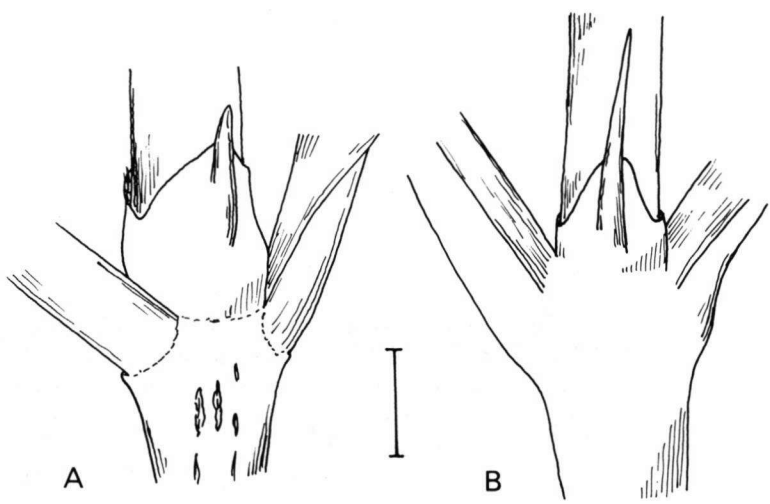

Fig. 2. Stipules of Asian '*Diplospora*' species (A, *Diplospora dubia*; B, *Discospermum sphaerocarpum*). Scale = 2 mm.

Trichomes

Trichome types show only minor variation in Rubiaceae and cannot be expected to have value for the resolution of the taxonomic problems (of generic rank only) here studied. We have thus not investigated trichomes systematically.

(i) External indumentum — While in Africa there is a wide range of variation from *Tricalysia* species with densely hairy vegetative organs to other ones which are completely glabrous, most Asian *Diplospora* species have entirely glabrous vegetative parts. Only a few ones (e.g. *D. siamica, D. tinagoensis*) have the stems (when young) and leaves ± pubescent. The external hairs of the two species quoted above are few-celled, uniseriate, with very thick outer walls and thin septa ('cylindrical' hair-type), and so agree well with African *Tricalysia* hairs and are conform with the standard in Rubiaceae–Ixoroideae.

(ii) Internal indumentum — The trichomes inside corollas observed (e.g. in *D. abnormis, D. siamica*) show no differences (as in African *Tricalysia*) with the standard internal indumentum of Rubiaceae. They are thin-walled, unicellular, long hairs with straight outer walls and striate to verrucate surface.

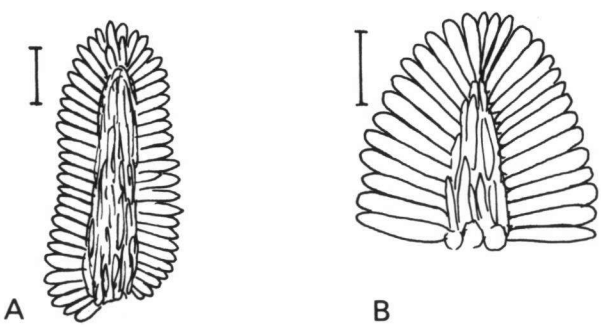

Fig. 3. Colleters of Asian *'Diplospora'* species (A, *Diplospora erythrospora*, from inside of upper bracteolar cup; B, *Discospermum beccarianum*, from inside of calyx). Scales = 50 μm.

Colleters

Colleters of the standard type (fig. 3) occur inside stipules. They are also associated with bracts, bracteoles, and calyces, where they occur on the inside or the margin (see further). The bracteoles and calyces of a particular taxon mostly have a similar arrangement of colleters, but this is not constantly so. In *D. sphaerocarpum*, the calyx has no colleters inside and the bracteoles have their inside completely covered with them.

Raphides

Raphides are absent from both the African and the Asian taxa. However, other Ca-oxalate crystal-types occur in several tissues, e.g. crystal-sand in the endosperm of *D. erythrospora*. We did not investigate systematically the occurrence of crystals.

Inflorescences and flowers

Inflorescences

All the Asian species have the ± sessile flowers densely aggregated in axillary opposite inflorescences, and so in habit strongly resemble most of the African taxa. Coaxillar inflorescences (serial buds), rather common in the African species, seem to lack completely from the Asian ones.

Each flower is normally subtended by a pair of bracteoles, which are free alternate (slightly so in fig. 4C: bf), free opposite (fig. 4A: fh), or fused opposite. In the last case, the bracteoles form a cup (fig. 4D: fh; F: ff) around the base of the flower. Bracteoles are frequently provided with colleters inside (fig. 4F: bc) or at the margin (fig. 4C: br), and their position agrees ± with colleter position on the calyx (see below). In African *Tricalysias*, free bracteoles are rare (almost limited to sections *Empogona* and *Probletostemon*); most African species have the bracteoles fused to cups ('calyculi') which are strongly developed and entirely surround the ovary; in many species, flowers are provided with two or more calyculi.

Flowers

The Asian species have mostly very small or small, rarely (*D. abnorme, D. beccarianum*) medium-sized flowers, the total corolla length varying from c. 5 to 15 mm. The African species are far more variable in this respect, since their corollas vary from small (8 mm) to large (50 mm); small flowers are here very rare (*T. micrantha, T. parva*), however, and the majority of the African species has medium-sized flowers (total corolla length 10–20 mm). The largest flowers (total corolla length 30–50 mm) are found in the east African *T. allocalyx*.

African *Tricalysia*-flowers are mostly 5-pleiomerous, but 4-merous flowers may occur occasionally and even characterize a few species (for a survey of 4-merous flowers in African *Tricalysias*, see Robbrecht, 1985). As regards this feature, the reverse holds for Asian *Diplosporas*: the 4-merous condition has become fixed in their flowers, and characterizes all the species; 5-merous flowers occur only occassionally, together with 4-merous ones, e.g. in *D. tinagoensis*.

Calyx

As in the African group, the shape of the calyx is very diverse and offers interesting identification characters for the species. It normally consists of a tube plus distinct lobes, which are mostly triangular (fig. 4A: fh; C: bf), rarely rounded and overlapping (fig. 4G: fm). Also the tube may only have vague indications of teeth (fig. 4E: fh) or be truncate (fig. 4D: fh). In *D. erythrospora*, the calyx is reduced to a short rim bearing marginal colleters rendering it a very characteristic appearance (fig. 4F: ff).

The calyx is mostly provided with colleters inside (often ± in a row near or at the base, fig. 4A: ov; B: ov; D: ov) or at the margin (fig. 4C: ov; F: bf).

These colleters belong to the standard-type met with in Rubiaceae (fig. 3). In some species, the calyces seem devoid of colleters (fig. 4G: ov), but we have not checked the presence of derived microscopically observable types in such cases.

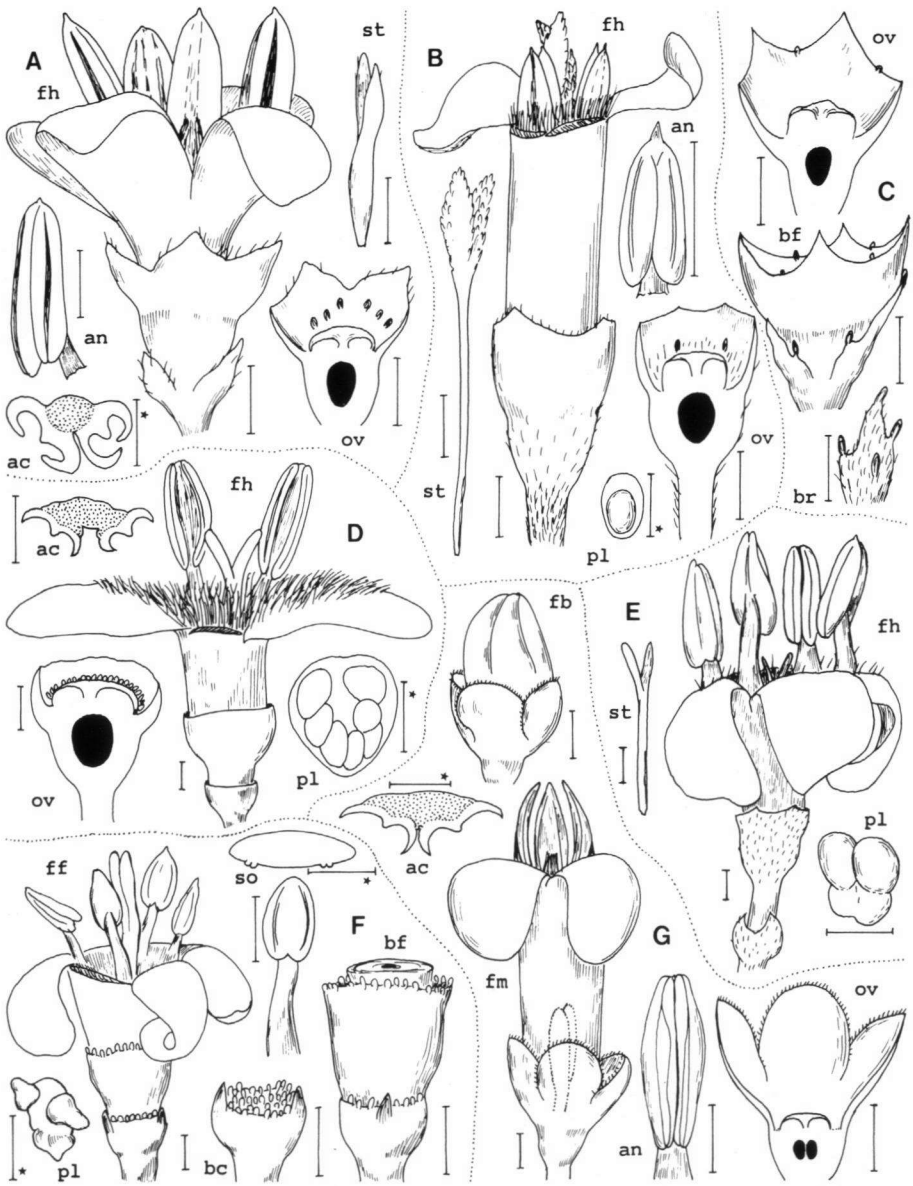

Fig. 4. Flowers of Asian *'Diplospora'* species (A, *Diplospora siamica*; B, *Diplospora tinagoensis*; C, *Discospermum abnorme*; D, *Discospermum beccarianum*; E, *Diplospora dubia*; F, *Diplospora erythrospora*; G, *Discospermum sphaerocarpum*); ac = cross sections of anthers; an = stamens; bc = bracteolar cup; bf = bases of flowers (corollas removed), showing position of colleters; br = bracteole from inside, with colleters; fb = flower-bud showing aestivation contorted to the left; ff = female flower with four ± unequal staminodes; fh = presumably hermaphrodite flowers, with in some cases one or two corolla-lobes removed (only in B drawn without the subtending bracteoles or bracteolar cup); fm = male flower, its reduced included style shown by stippled line; ov = longitudinally opened ovaries + calyces, showing colleter or absence of colleters in G; pl = abaxial views of placentas; so = staminode and its cross section; st = styles. Scales = 1 mm, except those with * = 0.5 mm.

Corolla, androecium, and gynoecium

Besides size and merousness as discussed above, there are no striking differences between African and Asian taxa. The corollas of Asian species are hypocrateriform, with the throat glabrous (fig. 4F: ff) to very hairy (fig. 4D: fh) and the lobe-tips acute, rounded, or emarginate. The anthers (fig. 4: an, ac) are subsessile or borne on a filament and are attached in the corolla-throath. The ovaries are bilocular, exceptionally trilocular, and have in each chamber a ± well-developed placenta bearing (1–)2–15 ovules (fig. 4: pl). A further gynoecium difference between Asia and Africa is the length of the style. The African taxa have long-exserted styles with the two arms well above the anthers; in Asian species the styles are shorter and have the lobes only shortly exserted, below or between the anthers (fig. 4: fh).

Flower biology

Many Asian taxa (e.g. *D. abnorme, D. apiocarpa, D. erythrospora, D. sphaerocarpum*) are dioecious and have male flowers with reduced gynoecium (fig. 4G: fm) and female flowers with staminodes (fig. 4F: ff, so). In male flowers there seems to be a range of variation from flowers with no trace of a gynoecium (such a case very convincingly depicted for *D. apiocarpa* by Beddome, 1872: pl. ccxxiii, male flower cut through vertically, with no sign of ovary) to flowers with a reduced style and empty ovary locules (fig. 4G). Dioeciousness seems sometimes related with inflorescence dimorphism also. Gamble (1921) described that in *D. apiocarpa* male and hermaphrodite flowers are arranged in inflorescences of c. 10 cm in diameter, while those of plants with female flowers are much smaller. Field studies and thorough examination of living material is much needed for further understanding, also since we doubt if stylar pollen presentation (normally present in the whole subfamily Ixoroideae!) is not absent in the Asian *Diplosporas*; the style remains rather short and thus can hardly serve as receptaculum pollinis.

All the African taxa have hermaphrodite flowers, with the exception of a Madagascan group which is in all other characters close to the type section of *Tricalysia* (compare Robbrecht, 1987: table 1); in all the African taxa stylar pollen presentation is present. It thus seems that there are profound differences in the flower biological adaptations of the groups compared here. African *Tricalysias* are melittophilous and probably bee- or butterfly-pollinated; the Asian taxa may well have other pollinators, as the differences in the range of the flower sizes in the two groups also indicate.

Fruits

Fruits are berry-like drupes or ± dry and indehiscent. They are generally sessile, sometimes shortly stalked. Fruit size of the Asian taxa is very variable (fig. 5), from c. 5 mm (*D. dubia*) up to 30 mm in diameter (*D. abnormis, D. polysperma*). Shape (fig. 5) is mostly globose or ellipsoidal, rarely didymous; in a few taxa the fruit surface is weakly ribbed or warty. The colour of the fruits is either red (over yellowish and orange during maturation) or purplish black. The fruit colour is not noted for many species, however; apart from the observations summarized in table 1, red fruits are reported from *D. cuspidata* and *D. mollissima*. The fruits of *D. sphaerocarpum* are reported to have a foetid odour, a feature not observed in any other species. The

Table 1. Comparison of fruit characters in Asian '*Diplospora*' species (sequence based on fruit size).

	fruit size (mm)	fruit shape	fruit colour	calyx	disk	fruit wall	placenta	seeds per locule	seed shape	exotestal cells in surface	exotestal cell thickening
D. wrayi	5 × 3	e	?	n	a	fp	–	0–1	s	*	0
D. fruticosa	4–5	g	red	p	n	fp	±	2–4	f–h	i	b2
D. tinagoensis	5	g	?	p	n	fp	–	1–2	h	e	b2
D. puberula	5	g	red	p	n	fp	–	1	h	e	b2!
D. dubia	5–6	g	red	p	n	fp	–	1–3	a, h	i	b2
D. fasciculiflor	5–7	g	?	p	n	fp	–	1–3	h	i	b2!
D. erythrospora	7	g	?	n	n	fp	±, +	3	a	i	a
D. confusa	7	g	?	p	n	fc	±	5–6	a	i	a
D. siamica	8 × 5	e	?	p	n	fp	±	2	h	i	b2
D. javanica	12–20 × 8–10	e	?	±p	n	±S	++	(1–)3	l	e	e1
D. apiocarpa	18 × 14	e	?	n	a	S	+	3–4	l	i–e	c2
D. abnormis	20	g–d	purplish black	n	a	L–S	++	4–5–many	l	e	e1
D. sphaerocarpa	12–25	g(–e) ±r	?	n	n	L	++	(3–)5–12	l	e	c2
D. whitfordii	20–25	g	?	±p	a	S	±	5–12	l	e	e1
D. beccariana	25	g, ±r	?	p	n	S	++	many	l	i–e	c2
D. polysperma	25–30	g ±r	purplish black	±p	n	S	+	many	l	e	d1 + c2

Specifications: fruit size (approximative, diameter for globose fruits, length × width for ellipsoidal fruits), fruit shape (g = globose; d = ± didymous; e = ellipsoidal; r = ribbed), calyx (p = persistent; n = not), disk (a = accrescent; n = not), fruit wall (fp = with fleshy mesocarp and papery to membranous endocarp; fc, with fleshy mesocarp and chartaceous endocarp; L = fruit wall leathery; S = fruit wall ± sclerified), placenta in fruiting stage (– = undeveloped; ± and + = more or less developed; ++ = much developed), seed shape (l = lenticular; f = flattened; a = angular; h = ± hemispherical or hemi-ellipsoidal; s = ± spherical), exotestal cells in surface (i = ± isodiametric; e = elongated; * = exotesta crushed, see text), exotestal cell thickening type (categories of Robbrecht & Puff, 1986; b2! = variant discussed in text).

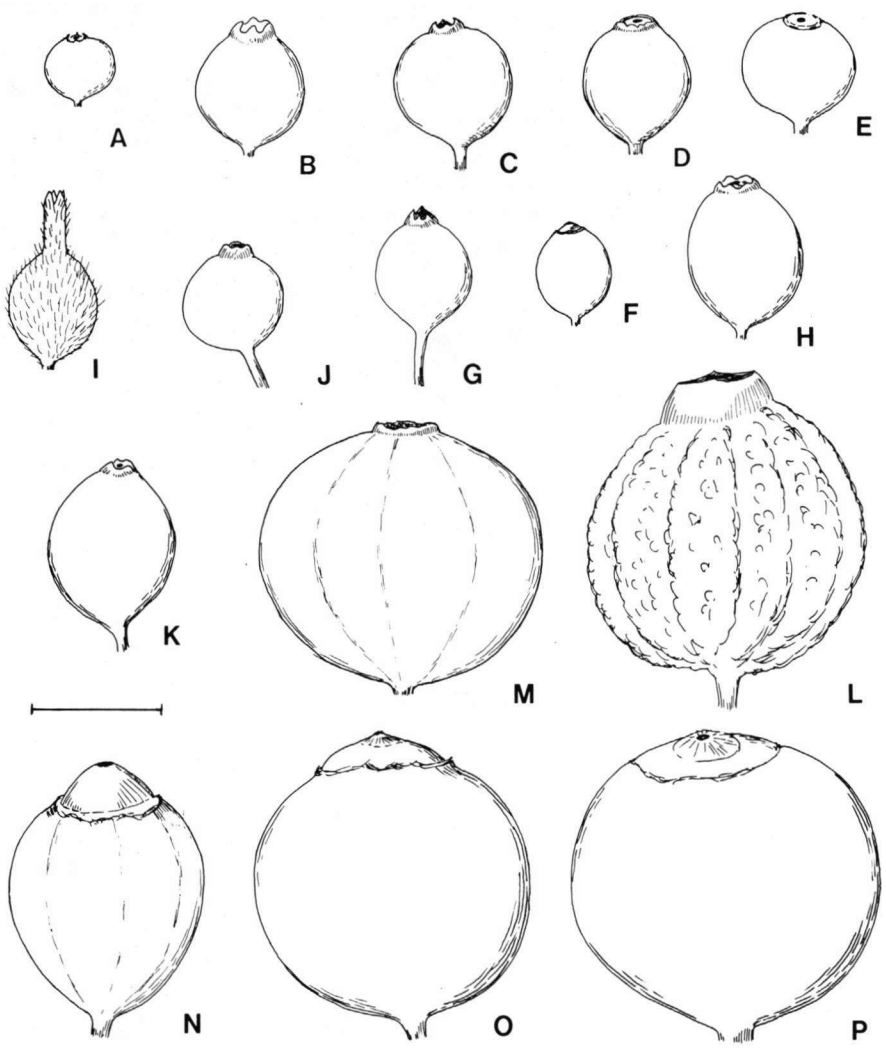

Fig. 5. Fruit size and shape in Asian *'Diplospora'* species (A, *Diplospora fruticosa*; B, *Diplospora confusa*; C, *Diplospora dubia*; D, *Diplospora fasciculiflora*; E, *Diplospora erythrospora*; F, *Diplospora wrayi*; G, *Diplospora siamica*; H, *Diplospora cuspidata*; I, *Diplospora puberula*; J, *Diplospora tinagoensis*; K, *Discospermum javanicum*; L, *Discospermum beccarianum*; M, *Discospermum sphaerocarpum*; N, *Discospermum apiocarpum*; O, *Discospermum abnorme*; P, *Discospermum whitfordii*). All drawings with the same magnification (scale = 10 mm).

fruits are generally crowned with the persistent calyx. Rarely, the calyx disappears while the fruit matures, especially in those species where the disk becomes accrescent (*D. abnorme, D. apiocarpum,* fig. 5N & O). The mesocarp is frequently hard to leathery, especially in the larger fruits; smaller fruits have generally a fleshy mesocarp. The endocarp is papery or chartaceous. In the fruiting stage, the placenta fre-

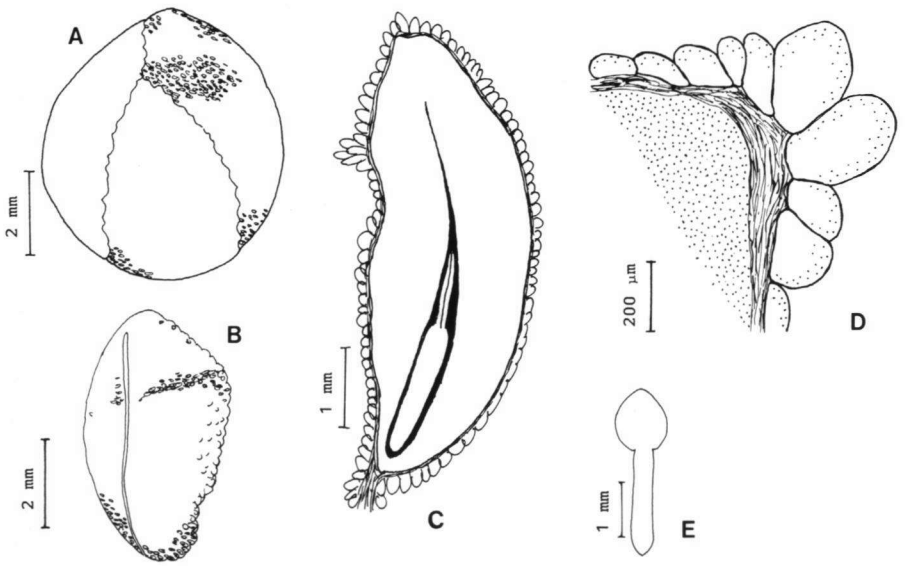

Fig. 6. Seeds of Asian '*Diplospora*' species (*Diplospora erythrospora*): A, three seeds as positioned in a fruit locule, abaxial view; B, seed, adaxial view showing linear hilum; C, longitudinal section of seed; D, the same, detail showing large exotestal cells at edge (endotesta crushed, endosperm depicted by stippling); E, embryo.

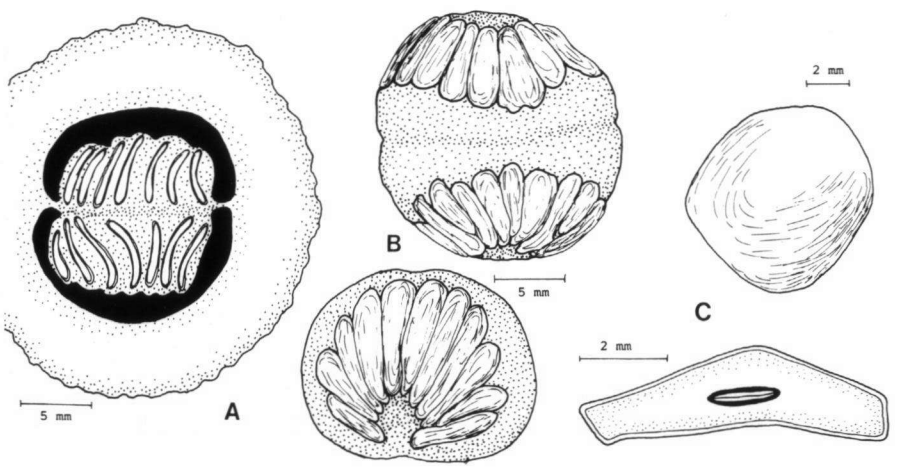

Fig. 7. Seeds of Asian '*Diplospora*' species (A, *Discospermum beccarianum*; B, C, *Discospermum sphaerocarpum*): A, cross section of immature fruit, showing young lenticular seeds embedded in placental outgrowths (black = air-space); B, apical and abaxial view of seed mass removed from fruit [seeds hold together by (stippled) placental outgrowths]; C, lateral view of a lenticular seed and its cross section.

quently grows out into a massive structure, sometimes completely embedding the seeds (*D. beccarianum*, fig. 7A) or forming a tissue around and/or in between them (*D. sphaerocarpum*, fig. 7B). These placental developments are especially common in the large fruits with hard walls.

In the African taxa, a similar fruit variation is met with, but the small fleshy fruit-type predominates and placental outgrowths are nearly absent. Large fruits with a ± sclerified wall are here limited to section *Probletostemon* and a few species (group of *Tricalysia atherura*) of section *Tricalysia*.

Seeds and seed-coat

The number of seeds in each of the two fruit-locules varies from only one to many, in the Asian as well as in the African species. Sometimes, there is only one ± spherical seed in the fruit, apparently by abortion of the ovules in the second locule; *Diplospora wrayi* seems to be the only Asian example of this. The seed shape of the Asian taxa is variable, lenticular (fig. 7C), ± flattened, angular with convex abaxial side (fig. 6), ± hemispherical or -ellipsoidal or ± spherical. As in the African taxa, shape is related to the number of seeds per locule. The lenticular seed shape is characteristic for the large-fruited taxa and, unlike other seed shapes, is absent from African species.

The hilum of the Asian species is generally linear and narrow (fig. 6B), rarely (*Diplospora wrayi*) broad and curved. The endosperm is always entire (fig. 6C), but in a few species (e.g. *D. dubia*) the seed-coat has a weak tendency to intrude in the endosperm at the adaxial side of the seed. This same tendency, and even true rumination, occurs in several African species. In respect to their embryo, Asian species are similar to African ones: embryos (fig. 6C, E) are medium-sized (length attaining about half the length of the seed) and have foliaceous cotyledons somewhat shorter than the embryo-radicle which is directed towards the base (or away from the septum in many-seeded taxa).

As standard in Rubiaceae, the seed-coat is exotestal. In strong contrast to the African taxa which always have seed-coats with parenchyma-like exotestal cells, the anatomy of the exotesta of Asian taxa is quite diverse. The exotestal cells are isodiametric or elongated in surface view; they mostly have conspicuous smooth thickenings, either along the outer tangential walls (*D. siamica, D. dubia*, fig. 8B, C), or along the (base of the) radial walls (*D. javanicum*, fig. 8I). In a number of species the conspicuous radial wall thickenings are accompanied with less-developed outer wall thickenings (*D. sphaerocarpum, D. abnorme, D. apiocarpum*, fig. 8F–H). A peculiar exotestal cell type occurs in *D. fasciculiflora* and *D. puberula* (fig. 8E & F); the large ± isodiametric cells have a rather delicate thickening along the outer tangential wall, continuing, with a single interruption, up to the base of the radial wall. A few species (*D. confusa, D. erythrospora*, fig. 6D, 7A) have parenchyma-like exotestal cells without thickenings. Very rarely (*D. wrayi*) not only the parenchymatic endotestal cells but also the mature exotesta are crushed by the development of the endosperm, so that the seed-coat is reduced to a thin pellicle. This last feature is absent in African *Tricalysias*, but occurs in the related genus *Argocoffeopsis*.

The exotestal cells are mostly ± uniform for the whole of the seed. In a few species, however, edge cells are considerably enlarged (e.g. *D. erythrospora*, fig. 6D).

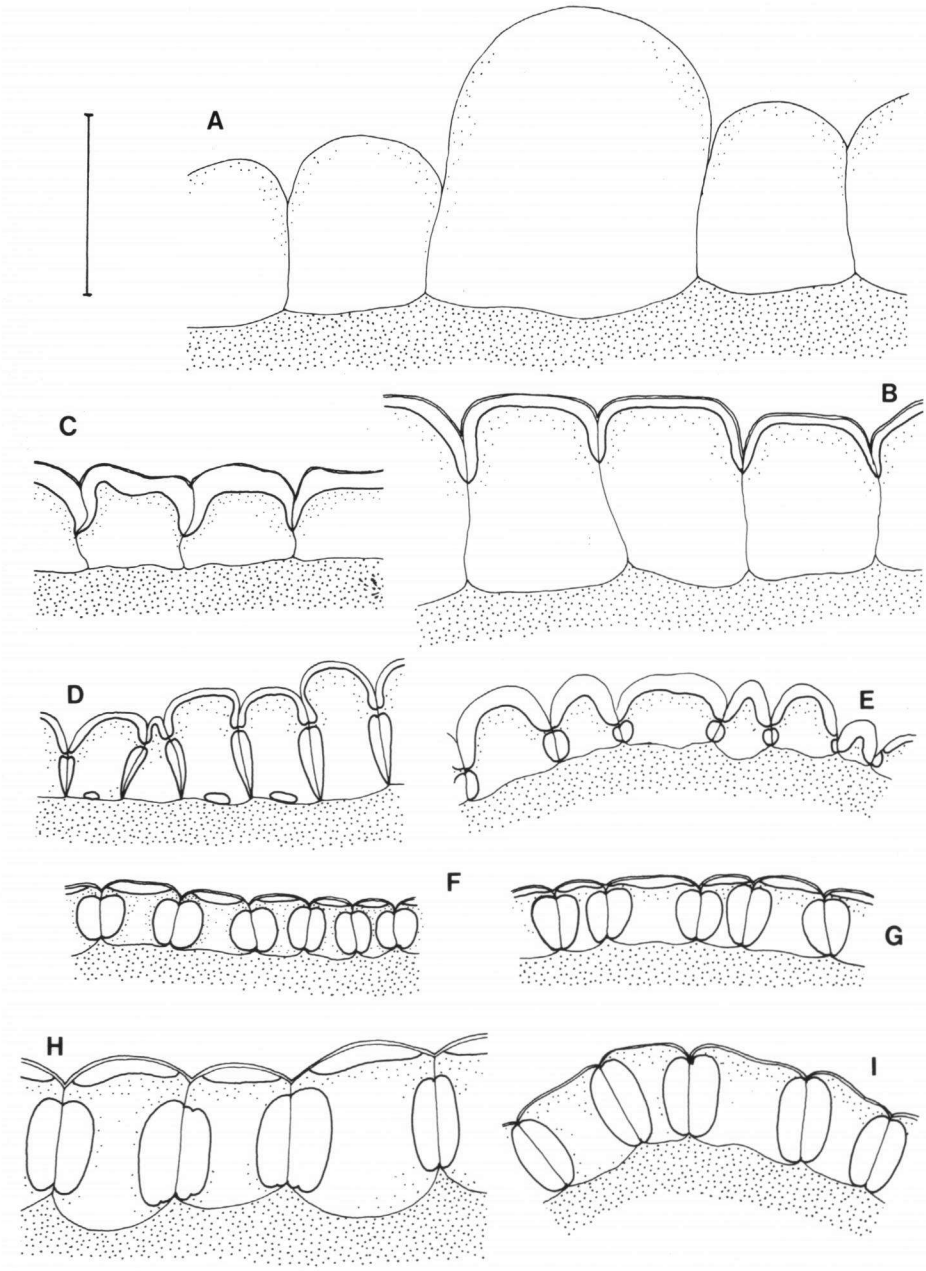

Fig. 8. Exotestal cell anatomy in Asian *'Diplospora'* species (A, *Diplospora erythrospora*; B, *Diplospora siamica*; C, *Diplospora dubia*; D, *Diplospora fasciculiflora*; E, *Diplospora puberula*; F, *Discospermum sphaerocarpum*; G, *Discospermum abnorme*; H, *Discospermum apiocarpum*; I, *Discospermum javanicum*): cross sections of exotestas, adjacent endotesta represented by coarse stippling. All drawings with the same magnification (scale = 100 μm).

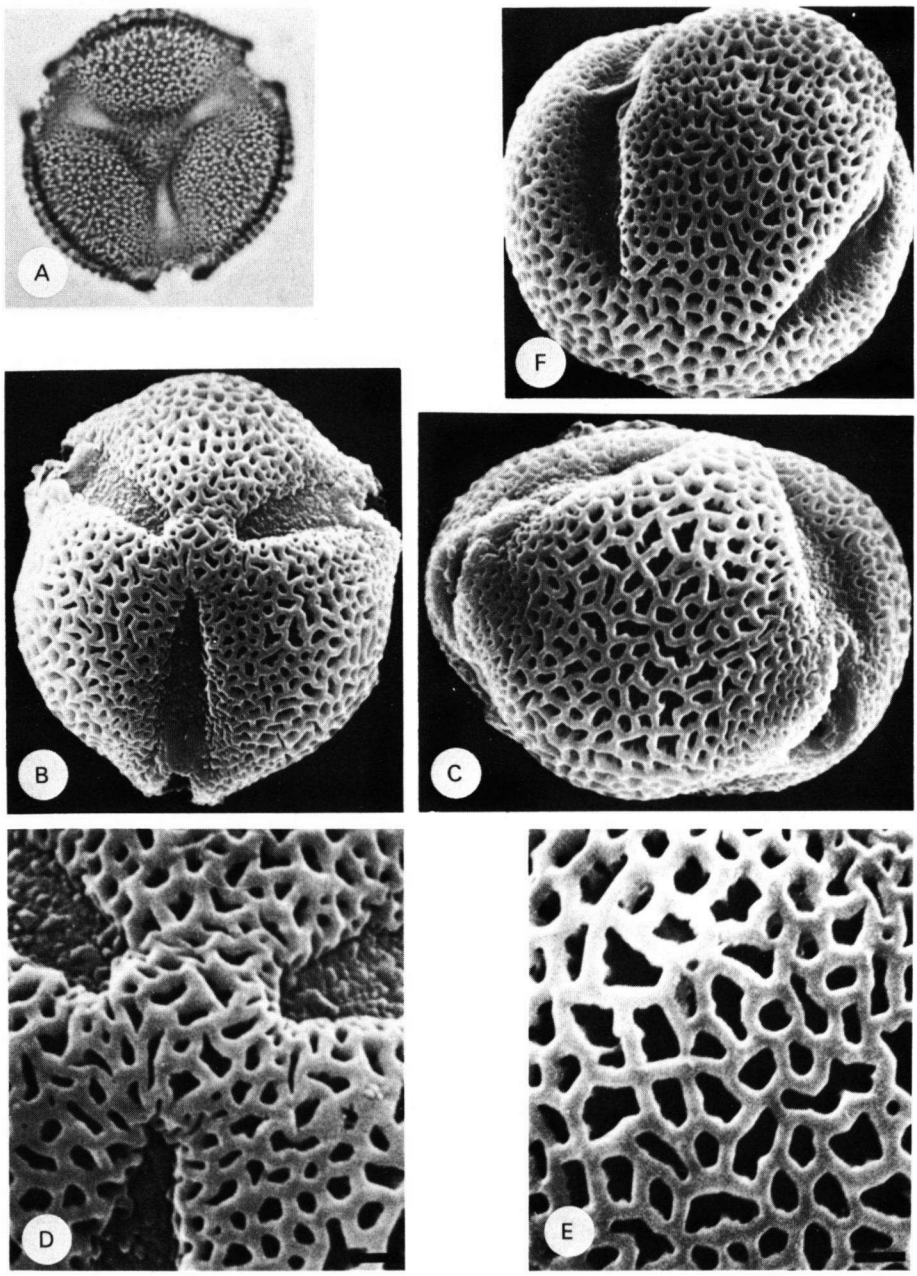

Fig. 9. Pollen grains of Asian '*Diplospora*' species (A–E, *Diplospora dubia*; F, *Discospermum sphaerocarpum*): A, B, polar view; C, equatorial view; D, apocolpium; E, mesocolpium; F, ± equatorial view. A, light micrograph (× 1050); B–F, scanning electron micrographs (B, C, × 2900; D, E, × 6500; F, × 2600).

Pollen

Examination of the pollen of a few species (*D. dubia, D. abnorme, D. sphaerocarpum*) indicates that pollen morphology has probably little value in this group. As in the African *Tricalysias* and in all other members of the Diplosporinae, the pollen grains (fig. 9) are medium-sized, ± spherical, 3-colporate and reticulate (semitectate), without supratectal elements.

Chorology

Like the African species, the Asian *Diplosporas* are essentially tropical. They occur from Sri Lanka and the tropical parts of India to the SE of China and throughout W Malesia, reaching the Philippines, Sulawesi and Java. They are absent from Australia and the Pacific. The most northern point of distribution reached is in the Ryukyu Islands, where *D. dubia* penetrates; this species – centred on the continent (South China) – has the widest distribution of the whole group.

6. TAXONOMIC DISCUSSION

Generic delimitation problems in the groups studied here were in the past solved by attributing a high value to isolated 'technical characters'. So *Diplospora* was distinguished from *Tricalysia* by the number of floral parts (4-merous versus 5-pleiomerous; e.g. Sim, 1907), or *Discospermum* from *Diplospora* (as a section) by the development of the bracteoles (connate and sheathing versus small and sometimes free; Hooker, 1880). It is clear that instead we have to look after groups of correlated characters for a sound delimitation of the genera. Although our morphological and anatomical observations do not include all the species of the groups concerned, there is strong evidence for the following conclusions.

The comparative enumeration of characters above indicates that the African and Asian taxa each have quite divergent tendencies. Major differences are found in:

- colleters: standard colleters characterize the Asian taxa; with few exceptions (sections *Probletostemon* and *Kraussiopsis*) all African taxa, on the contrary, have modified colleter types;
- merousness of the flowers: while the African taxa are predominantly 5-pleiomerous and rarely 4-merous, the Asian taxa are almost consistently 4-merous;
- bracteoles: the Asian species mostly have rather inconspicuous bracteoles; in the African ones there is a strong tendency that the ovaries are completely hidden in 1 or 2 large sheathing bracteolar cups ('calyculi') morphologically resembling the calyx [this situation is alluded to in the name *Tricalysia*];
- flower size: African species have generally larger flowers than the Asian ones;
- flower biology: the strong tendency towards unisexual flowers found in the Asian group is absent, apart from a few Madagascan taxa, in Africa; while stylar pollen presentation no doubt occurs in the African species, it may well be absent in Asia;
- exotestal cell anatomy: Asian species have mostly thickened exotestal cells, a feature occurring in no African species.

The two lineages are discontinuous enough to distinguish them at the generic level. The Asian taxa thus cannot be accommodated under the name *Tricalysia*, the type of which is African.

For the Asian taxa, two generic names have been erected, *Diplospora* and *Discospermum*. Whether the 19th century distinction made between *Diplospora* and *Discospermum* can be maintained or not, is a question that was forgotten as Schumann (1891), in his classical treatment of the family, apparently by inadvertence, made no mention of the second genus.

General habit, inflorescences, and flowers are extremely uniform in the Asian species. The slight variation in the bracteoles, historically used to distinguish *Diplospora* section *Diplospora* and section *Discospermum* (Hooker, 1880), is too continuous to have much taxonomic value. However, fruits show much variation, as shown in table 1. It strongly suggests that easily two groups of species can be recognized.

The first group includes the type of *Diplospora* (*D. dubia*); it is characterized by very small red fruits (diameter c. 5 mm, always under 1 cm) with fleshy mesocarp and few (mostly 1–3, only in *D. confusa* more) seeds in each locule (and of course a pauci-ovulated placenta in flowering stage). The exotestal cells are parenchyma-like or provided with a thickening along the outer tangential wall. Only *D. fasciculiflora* and *D. puberula* have a somewhat different exotestal cell anatomy (see above).

The second group has much larger fruits, 1.2–3 cm in diameter, with a ± sclerified or leathery wall and (2–4–)many lenticular seeds firmly hold together or frequently completely embedded in placental tissue. Fruit colour is missing too frequently on the collectors' notes for certain conclusions, but it is probable that in all the species with large fruits these latter are purplish black when fully mature. The exotestal cells are elongated and have thickenings along the radial walls, in some species also along the outer tangential walls. This group perfectly fits Dalzell's original definition of *Discospermum* ("Semina ... compresso-lenticularia, ... septulis membranaceis vel arillis lamellatis ... Fructus diametro subpollicaris ..."). Dalzell knew two species, *D. apiocarpum* and *D. sphaerocarpum*; the latter we designate here as lectotype, since it fits more closely the original generic description.

The high diagnostic value of rubiaceous fruits in general (Robbrecht, 1988), and particularly in the Ixoroideae (Robbrecht & Puff, 1986), is well known. The differences between *Diplospora* and *Discospermum* are amply sufficient to maintain them as separate genera.

Diplospora DC., Prodr. 4: 477 (1830).

Hypobathrum sect. *Diplospora* (DC.) Baillon, Adansonia 12: 211 (1878).
Tricalysia sect. *Diplospora* (DC.) K. Schum., Nat. Pflanzenfam. 4 (4): 81 (1891).

Shrubs or small trees with decussate leaves, frequently with domatia. Stipules shortly sheathing, provided with ± long interpetiolar awns. Inflorescences axillary and opposite, many-flowered, strongly congested. Flowers 4(–5)-merous, very small to small, hermaphrodite or unisexual (plants polygamo-dioecious); calyx consisting of a short tube with mostly triangular lobes; corolla hypocrateriform, white, greenish, or yellowish, with lobes contorted to the left; anthers ± medifixed, on short filaments attached to the throat; staminodes of female flowers much resembling an-

thers, with empty locules; ovary 2-locular, each axile placenta with 1–3(–6) ovules; locules empty in male flowers; disk annular; style bilobed, shortly exserted except sometimes in male flowers. Drupes turning over yellowish and orange to red, globose or ellipsoidal, very small, 5–7 mm in diameter, mostly with persistent calyx; placental outgrowths mostly absent, rarely (*D. erythrospora, D. lutea*) weakly developed; seeds 1–3(–6) per locule, angular, ± hemispherical, ± spherical, or somewhat flattened, with linear or comma-shaped hilum; embryo-radicle inferior. — Fig. 2A, 3A, 4A, B, E, F, 5A-J, 6, 8A-E, 9A-E.

Type species: *Diplospora dubia* (Lindl.) Masamune.

Other species: see paragraph 7.

Discospermum Dalz., Hooker's J. Bot. Kew Gard. Misc. 2: 257 (1850).

Diplospora sect. *Discospermum* (Dalz.) Hooker, Fl. Brit. India 3: 123 (1880).

Shrubs or small trees with decussate leaves, frequently with domatia. Stipules shortly sheathing, provided with ± long interpetiolar awns. Inflorescences axillary and opposite, many-flowered, strongly congested. Flowers 4-merous, small to medium-sized, hermaphrodite or unisexual (plants polygamo-dioecious); calyx very variable, a short rim, a subtruncate obscurely toothed tube, or a very short tube with large rounded lobes; corolla hypocrateriform, white, with lobes contorted to the left; anthers ± medifixed, on short filaments attached to the throat; ovary 2-locular, each axile placenta with (3–)5–15 ovules; ovary missing or locules empty in male flowers; disk annular; style bilobed, exserted except sometimes in male flowers. Fruits purplish black (colour observations missing in several species), globose or ellipsoidal, sometimes faintly ribbed, large, (12–)20–30 mm in diameter, indehiscent, with ± sclerified or leathery wall; calyx persistent or withering, especially when disk becomes accrescent; placental outgrowth conspicuous, embedding the seeds completely or holding them firmly together; seeds (2–4–)many per locule, lenticular, with long linear hilum along sharp edge of seed; embryo-radicle directed away from septum. — Fig. 2B, 3B, 4C, D, G, 5K-P, 7, 8F-I, 9F.

Type species (lectotype, designated here): *Discospermum sphaerocarpum* Dalz. [Hooker's J. Bot. Kew Gard. Misc. 2: 257 (1850), nomen, sine descr.] ex Hook. f. in Thwaites, Enum. Pl. Zeyl.: 158 (1859). – We consider Hooker's footnote in Thwaites' Enumeratio as the first valid publication of the name *D. sphaerocarpum*, since it contains a short English description. Consequently, the taxonomic synonyms *D. sphaerocarpum* and *D. dalzellii* are of the same date.

Other species: see paragraph 7.

Diplospora and *Discospermum* fit well Robbrecht & Puff's (1986) definition of the Gardenieae–Diplosporinae. *Diplospora* (in the strict sense defined here) is no doubt very closely related to *Tricalysia*, and the two seem to form a pair of sister genera. *Discospermum*, with its large, ± dry fruits, frequently well-developed placental outgrowth around the seeds, and radial exotestal cell-thickenings, seems to occupy a lower level of evolution compared to the other two. In the three features enumerated, it links the Diplosporinae with the Gardeniinae and supports the rank (subtribal) given to these two higher taxa.

7. ANNOTATED CHECK-LIST

In the following list, accepted names are in bold roman, synonyms in italics. The species for which the generic position remains uncertain (no good material at our disposal) are marked with an asterisk.

CANTHIUM

Canthium dubium Lindley = Diplospora dubia.

COFFEA

Coffea schmidtii Schumann = Diplospora schmidtii.

DIPLOSPORA

Diplospora abnormis (Korth.) Valeton = Discospermum abnorme.

*Diplospora andamanica Balakrishnan & Nair

We have not traced the isotype deposited in L or any other specimen. A few elements in the protologue make the position in *Diplospora* suspect: the pendulous ovules and the elongated obovoid fruits suggest a position in the Hypobathreae.

Diplospora apiocarpa (Dalz.) Hook. f. = Discospermum apiocarpum.

Diplospora australis Benth. = Tarenna australis.

Diplospora beccariana King & Gamble = Discospermum beccarianum.

Diplospora buisanensis Hayata = Diplospora dubia.

Diplospora cameroni C.T. White (Australia) = Tarenna cameroni.

Diplospora confusa Hook. f.

Material examined: Burma, *Keenan & al. 776* (K; fr., fig. 5B).

Diplospora cuspidata Valeton

Material examined: Sarawak, *Sinclair & Kadim bin Tassim 10378* (L; fr., fig. 5H). — We could not compare the material examined with the type (from Borneo), but if its identity is correct, this species no doubt belongs to *Diplospora* s.s.

Diplospora dalzellii (Thwaites) Hook. f. = Discospermum sphaerocarpum.

Diplospora dubia (Lindley) Masamune

Material examined: China, *Lau 826* (NY; fr.), *20280* (L; fr.); *McClure 644* (NY; fr., figs. 5C, 8C); *Tsang 24611* (NY; fr., fig. 2A); *Tso 20636* (NY; fl.); *Wang 36190* (NY; fr.); Taiwan: *Gressitt 237* (NY; fr.); Ryukyu Islands: *Fosberg 37343* (L; fr.); *Reid Moran 5061* (BR; fl., figs. 4E, 9A–E). — *Diplospora dubia* is a rather variable species. A monograph is needed to check whether the varieties recognized (see this check-list under *Tricalysia viridiflora*) warrant recognition.

Diplospora erythrospora (Thwaites) Hook. f.

Material examined: Sri Lanka: *Thwaites CP 2510* (isosyntype BR; fl., figs. 3A, 4F), *CP 3481* (isosyntype K; fr., figs. 5E, 6, 8A). — Flowering material is very easily recognized by the extremely short, truncate calyx bearing conspicuous colleters on its margin.

Diplospora fasciculiflora (Elmer) Elmer

Material examined: Philippines, *Williams 1393* (NY; fr., fig. 8D), *1472* (NY; fr., fig. 5D). — This species is frequently confused with *'Tricalysia' sorsogonensis.*

Diplospora fruticosa Hemsley

Material examined: China, *Steward & Cheo 1152* (NY; fr., fig. 5A).

*Diplospora griffithii Hook. f.

Diplospora ixoroides F. Muell. = Tarenna triflora.

Diplospora javanica Miq. = Discospermum javanicum.

*Diplospora kunstleri King & Gamble.

*Diplospora kurzii Hook. f., superfluous substitute name.

When Hooker (Fl. Brit. India 3: 125. 1880) found that *Urophyllum biloculare* Kurz belongs to *Diplospora,* he proposed the substitute name mentioned here. The epithet biloculare was not preoccupied under *Diplospora,* however.

*Diplospora lasiantha Ridley.

Diplospora malaccensis Hook. f. = Hypobathreae (generic position to be determined).

Material examined: Malaya, *Chelliah in Kepong FRI 104432* (L; fr.); *Suppiah 108990* (L; fr.). — Wong (Arborescent Rubiaceae Malaya: 53. 1988) maintained this species in *Diplospora,* but the embryo-radicle directed towards the septum and the folded exotesta with cells thickened along the radial walls (some with additional outer tangential thickenings) doubtlessly make it a member of the Hypobathreae.

Diplospora minahassae Koord. = Hypobathreae (generic position to be determined).

Material examined: Sulawesi, Minahassa (type locality), *de Vogel 2518* (L; fr.). — The large sclerified fruits of this species have the general aspect of *Discospermum* fruits. However, the horizontal arrangement of the seeds, the embryo-radicle position (directed towards the septum), and the seed-coat anatomy (elongated exotestal cells with smooth thickenings along radial walls, some also with minor thickenings along outer tangential walls, and massive endotesta) affirmatively prove that this species belongs to the Hypobathreae, where it seems to occupy a position near *Rhadinopus.*

Diplospora minutiflora Ridley = Hypobathrum sp. 1 (Wong, Arborescent Rubiaceae Malaya: 55. 1988).

*Diplospora mollissima Hutch.
The original description suggests that this belongs to *Diplospora* s. s.

*Diplospora parkinsonii Gangopadhyay & Chakrabarty, see note on page 305.

'*Diplospora parvifolia* Kuntze', sic in Index Kew. (suppl. 1) pro Discospermum parvifolium.

Diplospora polysperma Valeton = Discospermum sp.
Material examined: Origin unknown (? China), cult. in Hort. Bogor. IV.E.130 (holotype L, iso- L, NY; fl., fr.). — Our investigations did not clarify the origin of this very distinct species described from botanic garden material. It may well have received another name in its country of origin, possibly even under a different generic name (e.g. the artificial concept *Randia*), but such synonymy will only be discovered by chance. We therefore refrain making a combination under *Discospermum*.

Diplospora puberula (Merrill) Ali & Robbrecht, comb. nov.
Basionym: *Tricalysia puberula* Merrill, Philipp. Journ. Sci. 10: 113 (1915).
Material examined: Philippines, *Edaño 76009* (NY; fr., figs. 5I, 8E); *Ramos 30205* (NY; fr.); *Ramos & Edaño 75213* (NY; fr.).

*Diplospora pubescens Hook. f.

*Diplospora schmidtii (Schumann) Craib.

Diplospora sessilis Elmer = ? Hypobathreae (generic position to be determined).
Material examined: Philippines, *Elmer 12329* (L; fl.), *13139* (isotype L; fl.). — A number of characteristics make this species very easy to recognize, especially the small, coriaceous and glossy, sessile leaves with cordate bases. The habit is characteristic of the Hypobathreae, inter alia by the blackish discoloration of the leaves in the dried state. However, we could not confirm a position in that tribe since we had only male flowers for examination. A few elements in the protologue ("seeds ... appearing striate or shredded, compressed ...": ? = folded exotesta) corroborate our view.

Diplospora siamica Craib
Material examined: Burma, *J.H. Lace 5788* (K; fl., fig. 4A); Thailand, *Gasnett 1062* (L; fr., figs. 5G, 8B).

Diplospora singularis (Korth.) Valeton = Discospermum abnorme.
See note under *Discospermum javanicum*.

Diplospora sphaerocarpa (Dalz.) Hook. f. = Discospermum sphaerocarpum.

*Diplospora stylosa Ridley.

Diplospora tanakai Hayata = Diplospora dubia.

Diplospora tinagoensis (Elmer) Ali & Robbrecht, comb. nov.
Basionym: *Tricalysia tinagoensis* Elmer, Leafl. Philipp. Bot. 1: 34 (1906).
Material examined: Philippines, *Edaño PNH 15560* (L; fr.); *Zwickey 542* (NY; fr.); Borneo, *Clemens 26869* (NY; fl., fr., fig. 4B); *Elmer 20166* (NY; fr., fig. 5J).

Diplospora vaginata 'Calc.', nom. nud. = Discospermum sp. (*Diplospora polysperma*).

Nomen mentioned in protologue of *D. polysperma*.

*Diplospora velutina King & Gamble.

Diplospora viridiflora DC. = Diplospora dubia.

Diplospora wrayi King & Gamble

Material examined: Malay Peninsula, *Kiah & Stengnell 23976* (NY; fr., fig. 5F).

DISCOSPERMUM

Discospermum abnorme (Korth.) Ali & Robbrecht, comb. nov.

Basionym: *Gynopachys abnormis* Korth., Ned. Kruidk. Arch. 2: 182 (1851).

Material examined: India, N Nicobar, *Chakroborty 2503* (L; fl., fig. 4C); Borneo, *Korthals s.n.* (holotype L; fr); *Kostermans 5606* (L; fr.); *Clemens 28264* (L; fr., figs. 5O, 8G). — The large spherical fruits exceeding 2 cm in diameter and crowned with a characteristic accrescent disk, make the species very easy to recognize in the fruiting stage.

Discospermum apiocarpum Dalz. ex Hook. f.

Material examined: India, Malabar, *Hortes s.n.* (in herb. Hooker & Thompson; L, NY; fr., figs. 5N, 8H).

Discospermum beccarianum (King & Gamble) Ali & Robbrecht, comb. nov.

Basionym: *Diplospora beccariana* King & Gamble, J. As. Soc. Beng. 72: 225 (1903).

Material examined: Borneo: *Anderson S 25516* (L; fl., figs. 3B, 4D); *Benang ak Bubong S 25216* (L; fr.); *F. Krispinus SAN 93841* (L; fr., figs. 5L, 7A). — This species is very easy to recognize by the glossy large leaf-blades with frequently rounded bases.

Discospermum biloculare Kuntze = 'Diplospora kurzii'.

Discospermum confusum (Hook. f.) Kuntze = Diplospora confusa.

Discospermum dalzellii Thwaites = Discospermum sphaerocarpum.

Discospermum dubium (Lindley) Kuntze = Diplospora dubia.

Discospermum erythrosporum Thwaites = Diplospora erythrospora.

Discospermum fruticosum (Hemsley) Kuntze = Diplospora fruticosa.

Discospermum griffithii (Hook. f.) Kuntze = Diplospora griffithii.

Discospermum javanicum (Miq.) Kuntze

Material examined: Borneo: *Reksodihardjo 727* (L; fr.); *Banang 51903* (L; fr., fig. 5K); *Evangelista 703* (NY; fr., fig. 8I), *918* (NY; fr.); *Sayn Elleh 37434* (L;

fr.); Sumatra: *Bartlett 7647* (NY; fr.); Java: *Koorders 30275β* (L; fr.). — Bakhuizen van den Brink Jr. (Beknopte Flora Java 15: 103. 1956) reduced *D. javanica* to the synonymy of *'D. singularis'* (= *Discospermum abnorme*). *Discospermum javanicum* is very different, however, by its much smaller ellipsoid fruits with few seeds in each locule (see Koorders & Valeton, Atlas Baumarten Java 3: fig. 534. 1914).

Discospermum malaccense (Hook. f.) Kuntze = 'Diplospora malaccense'.

Discospermum parvifolium Kuntze = ?

Material examined: India: 'Hinterindien', *O. Kuntze s.n.* (holotype NY; fl.). — This is certainly not a member of the Gardenieae–Diplosporinae, and must probably be excluded from the Rubiaceae. The flower morphology (superior ovary well observed by Kuntze according to his notes with the type, but not mentioned in the protologue) point to Loganiaceae, but the deeply bilobed, well-developed interpetiolar stipules exclude it from that family. Further elucidation is difficult because of the poor state of the type.

Discospermum pubescens (Hook. f.) Kuntze = Diplospora pubescens.

Discospermum singulare (Korth.) Kuntze = Discospermum abnorme.

Discospermum sphaerocarpum Dalz. ex Hook. f.

Material examined: Sri Lanka, *Thwaites 561* (isotypes of *D. dalzellii* BR, K; fl., fig. 4G: ac, G: an, G: fm, fig. 9F); *Hooker & Thomas s.n.* (K, NY; fr.); *Balakrishnan 506* (NY; fr.); *Tirvengadum et al. 481* (NY; fr.), *482* (NY; fr., figs. 5M, 7B & C, 8F); *Wight 1514* (K; fr., fig. 2B), *1515* (K; fl., fig. 4G: fb); *Worthington 2413* (K; fr.). — *Discospermum sphaerocarpum* is a polymorphic species, and at first sight one would recognize a (? shade) variant with larger leaves, sharper leaf-acumens, and longer stipules against one with smaller leaves, more obtuse leaf-acumens, and shorter stipules. We have also seen intermediate materials [*Waas & Tirvengadum 812* (L), *Jayasuriya 2082* (L)].

Discospermum whitfordii (Elmer) Ali & Robbrecht, comb. nov.

Basionym: *Gardenia whitfordii* Elmer, Leafl. Philipp. Bot. 1: 4 (1906).

Material examined: Philippines, *Miranda in For. Bur. 18921* (L; fr., fig. 5P).

GARDENIA

Gardenia daphnoides Hance = Diplospora dubia.

Gardenia whitfordii Elmer = Discospermum whitfordii.

GYNOPACHYS

Gynopachys abnormis Korth. = Discospermum abnorme.

IXORA

Ixora triflora R. Br. ex Benth. = Tarenna triflora.

RANDIA

Randia fasciculiflora Elmer = Diplospora fasciculiflora.

Randia whitfordii (Elmer) Merrill = Discospermum whitfordii.

TARENNA

Tarenna australis (Benth.) Ali & Robbrecht, comb. nov.
Basionym: *Diplospora australis* Benth., Fl. Austral. 3: 413 (1866).
See paragraph 4 for discussion of generic placement.

Tarenna cameroni (C.T. White) Ali & Robbrecht, comb. nov.
Basionym: *Diplospora cameroni* C.T. White, Journ. Bot. 64: 216 (1926).
Material examined: Australia, Yarraman (type locality), *District Forester s.n.* in Queensland Herb. AQ 0010266 (L; fr.; fig. 1B, D, F, H, J). — See paragraph 4 for discussion of generic placement.

Tarenna triflora (R. Br. ex Benth.) Ali & Robbrecht, comb. nov.
Basionym: *Ixora triflora* R. Br. ex Benth., Fl. Austr. 3: 416 (1866).
Synonym: *Diplospora ixoroides* F. Muell. [Fragm. 9: 182 (1875), nomen substit. superfl. pro *Ixora triflora*.]
Material examined: Australia, *L.S. Smith 4760* (L; fr.; fig. 1A, C, E, G, I). — See paragraph 4 for discussion of generic placement.

TRICALYSIA

Tricalysia abnormis (Korth.) Merrill = Discospermum abnorme.

Tricalysia apiocarpa (Dalz. ex Hook. f.) Gamble = Discospermum apiocarpum.

Tricalysia beccariana (King & Gamble) Hand.-Mazz. = Discospermum beccarianum.

*Tricalysia borneensis Merrill
Probably belonging to *Diplospora* s.s.

Tricalysia dalzellii (Thwaites) Alston = Discospermum sphaerocarpum.

Tricalysia dubia (Lindley) Ohwi = Diplospora dubia.

Tricalysia erythrospora (Thwaites) Alston = Diplospora erythrospora.

Tricalysia fasciculiflora (Elmer) Merrill = Diplospora fasciculiflora.

Tricalysia fasciculiflora (Elmer) Merrill var. *oblongifolia* Merrill = Diplospora fasciculiflora.

*'Tricalysia fruticosa (Hemsley) Schumann' = Diplospora fruticosa.
This combination is sometimes (e.g. Pritzel, Bot. Jahrb. 29: 582. 1901 & Iconogr. Cormophyt. Sinicor. 4: 240. 1975) attributed to Schumann, who, however, only placed *Diplospora* in synonymy with *Tricalysia*, without providing formal combinations for the species.

Tricalysia javanica (Miq.) Koord. = Discospermum javanicum.

*Tricalysia lutea Hand.-Mazz.
The description of the fruit in the protologue suggests a position in *Diplospora* s.s.

Tricalysia malaccensis (Hook. f.) Merrill - see Diplospora malaccensis.

*Tricalysia mollissima (Hutch.) H.H. Hu = Diplospora mollissima Hutch.

*Tricalysia negrosensis Elmer.
Presumably to be placed in *Diplospora* s.s.

Tricalysia parvifolia (Kuntze) Merrill = 'Discospermum parvifolium'.

Tricalysia puberula Merrill = Diplospora puberula.

'Tricalysia pubescens (Hook. f.) Schumann' = Diplospora pubescens.
See remark under *Tricalysia fruticosa*.

Tricalysia purpurea Elmer = Hypobathrum purpureum (Elmer) Merrill.
Material examined: Philippines, *Elmer 7616* (NY).

*Tricalysia reticulata Merrill.
Described from fruiting material; possibly a *Discospermum*.

Tricalysia sessilis (Elmer) Merrill - see Diplospora sessilis.

'Tricalysia singularis (Korth.) Schumann' = Discospermum abnorme.
See remarks under *'Tricalysia fruticosa'*.

Tricalysia sorsogonensis Elmer = Hypobathreae (generic position to be determined).
Material examined: Philippines, *Elmer 17164* (NY, fr.), *17261* (isotype NY, fr.).
— Although in habit very similar to *Tricalysia* and *Diplospora*, fruit characters (pendulous seeds with superior embryo radicle, folded exotesta with elongated cells thickened along radial walls) leave no doubt about the placement in the Hypobathreae.

Tricalysia sphaerocarpa (Dalz. ex Hook. f.) Gamble = Discospermum sphaerocar pum.

Tricalysia tinagoensis Elmer = Diplospora tinagoensis.

*Tricalysia versteegii Valeton.

Tricalysia viridiflora (DC.) Matsum. = Diplospora dubia.

Tricalysia viridiflora (DC.) Matsum. var. *buisanensis* (Hayata) Yamamoto = Diplospora dubia.

Tricalysia viridiflora (DC.) Matsum. var. *tanakai* (Hayata) Yamamoto = Diplospora dubia.

Tricalysia whitfordii (Elmer) Merrill = Discospermum whitfordii.

UROPHYLLUM

Urophyllum biloculare Kurz = 'Diplospora kurzii'.

Urophyllum potatorum King = Diplospora kunstleri.
Synonymy fide Wong (Arboresc. Rubiac. Malaya: 52. 1988).

VANGUERIA

Vangueria palembanica Miq. = Discospermum abnorme.
Fide Pitard, Fl. Gén. Indo-Chine 3: 275. 1923.

8. CONCLUSION

Present study has clarified problems of generic delimitation in the Asian Gardenieae–Diplosporinae. Many problems of specific delimitation remain open, however, and a proper monograph or revision of *Diplospora* and *Discospermum* is desirable.

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NOTE — Recently the monospecific genus *Pubistylus* Thothatry has been transferred to *Diplospora*; a new epithet *D. parkinsonii* was thereby provided for *P. andamensis* (Gangopadhyay & Chakrabarty, J. Econ. Tax. Bot. 12: 495. 1988; not seen by us; cited from the citation in the same journal given below). We believe that the new specific name is superfluous (compare with the check-list above: *D. andamanensis* and *D. andamanica* cannot be confused).

However, this *'Diplospora'* is probably yet another member of the Hypobathreae (compare paragraph 5 of the present paper). We previously suspected that *Pubistylus* belongs to the Hypobathreae (Puff, Robbrecht & Randrianasolo, Bull. Nat. Plantentuin Belg. 54: 357. 1984), and this view is corroborated by details given in a paper of Bhakat (J. Econ. Tax. Bot. 14: 215. 1990), who proposed the reinstatement of *Pubistylus*.