

Studies in *Otiophora* Zucc. (Rubiaceae): 4. The taxonomic position of the genus

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ABSTRACT

An evaluation of the characters of *Otiophora* provides conclusive evidence that the genus should be excluded from the Anthospermeae, the tribe in which it has traditionally been placed. Evidence from cytology, anatomy and morphology suggests a placement of the genus in the tribe Hedyotideae, in spite of some features pointing to a link with the Spermaceae. It is, furthermore, pointed out that the tribes Spermaceae and Hedyotideae are perhaps more closely related to each other than previously thought.

Otiophora has been placed traditionally in the tribe Anthospermeae. When Verdcourt (1950) monographed the genus, he stated (p. 35) that it 'shows affinities with *Otomeria*, *Pentas* (Hedyotideae) and *Pentanisia* (Knoxieae), in addition to *Anthospermum* with which it is at present classified', and thus indirectly voiced some doubt as to the true position of the genus. In his remarks on the classification of the Rubiaceae, the same author (1958) occasionally referred to *Otiophora*, but its position in the Anthospermeae was taken for granted.

1965), that of *Otiophora* could be explained as being tetraploidic with $x = 9+9-1$ or $9+8$. A connection to other genera or tribes with $n = 17$ (*Cinchona*/Cinchoneae, or *Posoqueria*, for example) is unlikely because the genus does not share any other characters. The Anthospermeae have a base number of $x = 11$ (Puff, 1982).

INFLORESCENCES

The inflorescences of *Otiophora* invariably consist of paired flowers arranged spirally on the inflorescence axis (Fig. 1a). This arrangement is quite

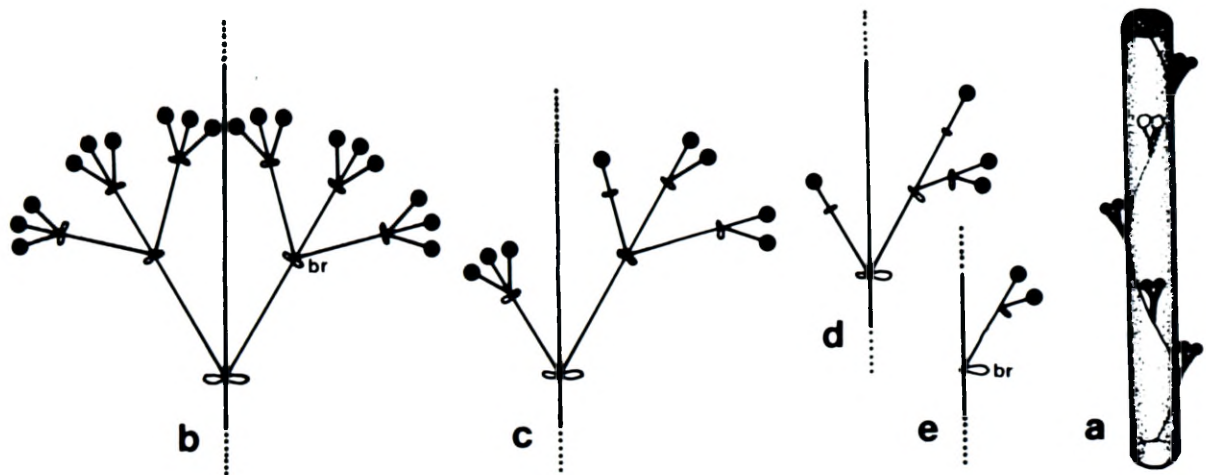


FIG. 1.— *Otiophora*, inflorescence. a, schematic representation of the paired flowers arranged spirally on the inflorescence axis; b–e, main inflorescence axis; with partial inflorescences. Theoretical derivation of two-flowered, alternately arranged partial inflorescences. e, from a typical thyrsopaniculate (see text!) inflorescence; b, (bract: br), the right partial inflorescence is gradually becoming promoted over the left one, and the axes within the partial inflorescences show unequal promotion; the promoted elements arise in the axils of larger bracts. Further explanations in the text.

There is convincing evidence, however, to show that the genus may be better placed in the Hedyotideae and so should be excluded from the Anthospermeae.

CHROMOSOME NUMBER

The chromosome number of *Otiophora* is the most convincing reason for the exclusion of the genus from the Anthospermeae. The genus has a base number of $x = 17$ (–18?) (Puff 1981a,b; $2n = c.36$ for *O. caerulea*, Lewis, 1966). Since the most common base in the Hedyotideae is $x = 9$ (Lewis,

different from the typical opposite arrangement of 'lateral elements' found in the vegetative region. It is a trend encountered frequently in rubiaceous inflorescences and may be explained by the unequal promotion of 'lateral elements' (lateral shoots, partial inflorescences, single flowers, etc.) originating at a node: frequently, a lateral element originates in the axil of only one of the leaves of a leaf pair at a node. If two lateral elements are produced, one is often promoted over (better developed than) the other. This is not infrequently correlated with anisophylly, whereby the promoted lateral element originates in the axil of the larger leaf (bract). The promoted lateral elements — and the larger leaves (bracts) — always seem to follow a spiral (Puff & Mantell, 1982).

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This may result in inflorescences in which (1) the partial inflorescences are monochasial [bracts/prophylls are no longer paired at a node but solitary and arranged alternately; cincinnus and bostryx are common (Weberling, 1977)], and in which (2) the partial inflorescences themselves are alternately (spirally) arranged on the main axis of the inflorescence. Subsequently, bracts/prophylls can be suppressed altogether (as in *Otiophora*) and inflorescences become 'naked' (Troll, 1964).

The theoretical derivation of the paired flowers of *Otiophora* from a typical rubiaceaceous inflorescence (according to Weberling, 1977, the 'central type of rubiaceaceous inflorescences' is a thyrus, but often it is a true panicle or an intermediate thyrso-paniculate inflorescence) is illustrated in Fig. 1. Although the flower pairs have \pm equally long pedicels or are \pm sessile, there is a strong indication that they are borne on axes (pedicels) of unequal rank: it can be observed that one flower of a pair frequently opens slightly earlier than the other.

Similar inflorescences occur in various genera of the Hedyotideae (*Pentas*, *Otomeria* spp., for example) and in other tribes, but are unknown in the Anthospermeae.

FLOWERS, PLACENTATION AND OVULES

The flowers of *Otiophora* are insect pollinated. Heterostyly is absent. Correlations in floral structure between *Otiophora* and the Hedyotideae are numerous: long corolla tubes with stamens inserted near the throat, long style with two filiform stigma lobes, and calyx lobes at least one of which is enlarged and foliaceous are found in genera of both tribes. There are, however, discrepancies in ovary structure and placentation.

Otiophora has only one ovule per locule, which is attached to the base of the septum. The Hedyotideae generally have many ovules per chamber that sit on an often \pm spheroidal stalked placenta (Fagerlind, 1937, Fig. 19) which is inserted at the base, and sometimes to the middle of the septum. Verdcourt (1958) uses 'ovules . . . affixed to the base of the septum' as a distinguishing character of the Hedyotideae but he (1976, e.g. Figs 24 & 27) presents drawings of Hedyotideae ovaries clearly showing placentae being attached to the middle of the septum. Bremekamp (1966) states 'peltate placenta attached to the middle of the dissepiment'.

Characteristic for *Otiophora* is a stalked, shield-like placenta with a single ovule (Figs 2, 3). In literature, such shield-like structures associated with solitary ovules of various rubiaceaceous genera have been given different names ('strophium', 'obturator', 'arillus', 'extraovular growth'). It remains unknown whether they are homologous, i.e. of placental origin (Wunderlich, 1971: p. 351, for references, more detailed information and a discussion of the 'plasticity' of rubiaceaceous placentae and their relationship to the ovules). Such shield-like structures are absent in genera of the Anthospermeae and Paederieae (*Phyllis*, *Putoria*: Fagerlind 1936a, b; *Crocylis*: Puff & Mantell, 1982; Puff, unpublished), but occur in various members of the

Spermacoaceae. *Diodia virginiana*, for example, (Lloyd, 1902) shows a near identical placental and ovule arrangement except that the placenta is attached to the middle of the septum. The shield-like stalked placenta of *Otiophora* may be interpreted as a reduced 'typical' (i.e. \pm spheroidal, stalked) Hedyotideae placenta, in which the reduction in ovule number to one has been accompanied by a reduction in size of the originally spheroidal portion of the placenta. There, nevertheless, is still a remarkable similarity to the placentation in the Spermacoaceae except for the attachment of the placenta. The latter is, by the way, much more variable in the Spermacoaceae than Verdcourt (1958) and Bremekamp (1966) have led us to believe ('ovules affixed to the middle of the septum'). Placentae and ovules sometimes are also attached very near to the base of the septum (e.g. *Richardia scabra*, Verdcourt, 1976, Fig. 56). Refer, in this context, to the comments made above regarding the attachment of the ovules in the Hedyotideae.

SEEDS

As the development of the ovary of *Otiophora* continues, the ovule increases in size, while growth of placental tissue lags behind and eventually ceases. The ovule/young seed becomes much bigger than the shield- (now more rod-)like placental portion (Fig. 3) and grows around the placental tissue (Robbrecht & Puff, 1981: Fig. 4). In the mature seed, the placental tissue remains visible as a longitudinal 'ridge' on the ventral surface of the seed, although this is not always as conspicuous as shown in Fig. 4. The same phenomenon is frequently encountered in seeds of the Spermacoaceae (Wunderlich, 1971, p. 352, and the literature cited there).

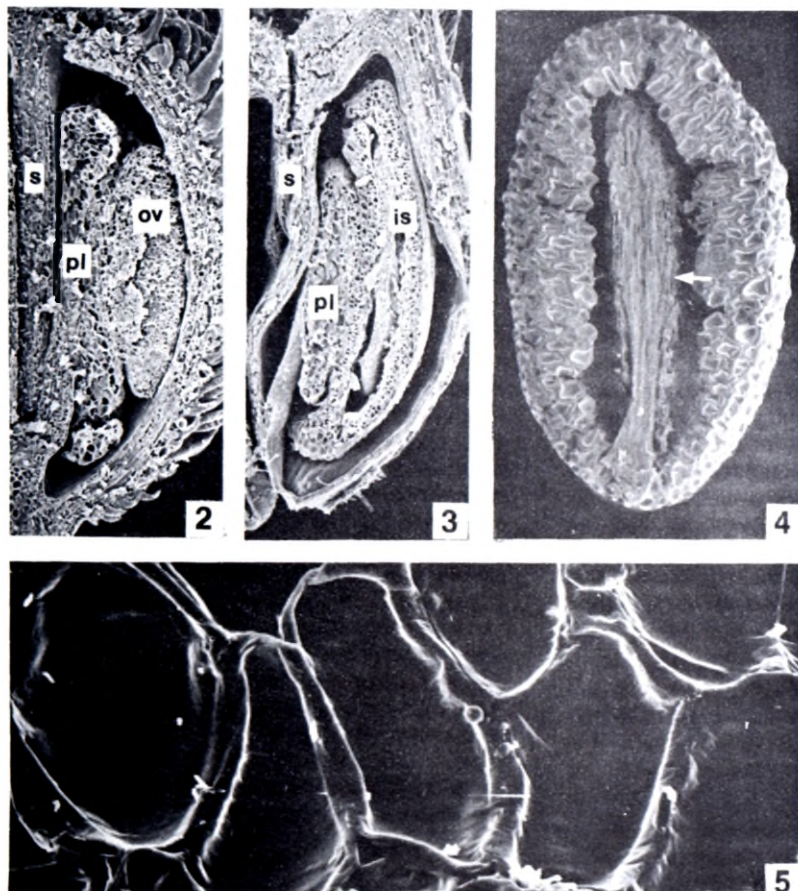
The simple testa cell structure (Fig. 5) matches that of the Hedyotideae (Bremekamp, 1952).

FRUITS

The fruit of *Otiophora* splits into two mericarps, which themselves dehisce to release the actual seeds. In contrast, the seeds of the Anthospermeae always remain enclosed in a hard endocarp, a mericarp, or the fruit as a whole (Puff, 1982). Fruits similar to those of *Otiophora* (i.e. with the same mode of dehiscence) are also found in the Hedyotideae, although capsular fruits are more common (Bremekamp, 1952). On the other hand, *Otiophora*-like fruits are characteristic for many genera of the Spermacoaceae.

POLLEN

Otiophora has subprolate to almost spheroidal, three-colporate pollen grains (Robbrecht & Puff, 1981: Figs 6, 7), the most common type found in the Rubiaceae. Such pollen grains also occur in the Hedyotideae (Lewis, 1965: subspheroidal, infrequently prolate, mostly three-aperturate; 28 African genera) and, for example, in the Anthospermeae and Paederieae (oblate, spherical to prolate, mostly three-colporate or -colpate; Robbrecht, 1982). Palynology, therefore, is of little



FIGS 2 - 5.— 2 & 3, longitudinal sections of ovary/young fruit of *Otiophora cupheoides* (South Africa, Transvaal, Puff 790211-1/1; SEM graphs); 2, young ovary with stalked, shield-like placenta (pl), which, at this stage of development, is larger than the ovule (ov) (s septum; c. \times 55); 3, young fruit with immature seed (is; a portion of the embryo is visible); note that the placenta has remained small (c. \times 35); 4, ventral view of seed of *Otiophora scabra* subsp. *scabra*; the arrow points to the remains of placental tissue (Madagascar, Puff 800814-3/1; SEM graph; c. \times 40); 5, testa of *Otiophora angustifolia* (Zambia, Drummond & Williamson 10046, herb SRGH; SEM graph; c. \times 535).

value to determine the taxonomic position of *Otiophora*. It should be mentioned, however, that the pollen grains of *Otiophora* differ quite clearly from those of the Spermaceae which are mostly oblate and pluricolpate.

LEAVES AND STIPULES

Otiophora is characterized by leaves with stipules which have colleter-tipped fimbriate segments and colleters on both the inside of the stipular sheath and along its actual rim (Robbrecht & Puff, 1981: Fig. 1). According to Krause (1909), colleters are restricted to the tips of fimbriae of the much dissected stipules in the Oldenlandieae (=Hedyotideae), Knoxieae, Paederieae, Anthospermeae and Spermaceae. This can be confirmed for the Anthospermeae and Paederieae, but it is not known whether, in addition to *Pentas lanceolata* (colleters also on the rim of the stipular sheath; Robbrecht, personal communication), there are any other species or genera in the Hedyotideae, or in any of the other tribes mentioned which, like *Otiophora*, also have colleters on the rim and on the inside of the stipular sheath. It must be kept in mind that Krause's survey was limited to relatively few genera. Judging from the wide distribution of colleters within the family it, however, remains doubtful whether this character is of any taxonomic value.

CONCLUSION

In conclusion, it can be said that (1) the genus should definitely be excluded from the Anthosper-

meae and that (2) it may be better placed in the Hedyotideae. It must be stressed, however, that several characters of *Otiophora* are also typical of, and point to 'cross-connections' with genera of the Spermaceae. It appears that, without specifically considering the situation in *Otiophora*, there may be more conspicuous correlations between Spermaceae and Hedyotideae than was originally thought. See, for example, the comments made above on the placentation in the two tribes (a discussion of other characters lies beyond the scope of this article). Perhaps the two tribes should be placed closer to each other, rather than associated with the Anthospermeae. It is suggested that the present, unsatisfactory delimitation of the two tribes be carefully reinvestigated on the basis of the many new data now available.

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UITTREKSEL

'n Evaluasie van die eienskappe van *Otiophora* verskaf afdoende bewys dat die genus uitgesluit behoort te word van *Anthospermeae*, die tribus waarin dit tradisioneel geplaas is. Sitologiese, anatomiese en morfologiese bewyse dui op 'n plasing van die genus in die tribus *Hedyotideae*, ten spyte van enkele kenmerke wat dui op 'n skakel binne die *Spermacoaceae*. Verder word dit aangedui dat die tribusse *Spermacoaceae* en *Hedyotideae* moontlik nader aan mekaar verwant is as wat aanvanklik vermoed word.

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