

A NEW ANDROECIAL TYPE IN AFRICAN VISCUM

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SUMMARY

An androecial type is reported from *Viscum* aff. *hildebrandtii* (Kenya) which is radically different from other known types in the genus and even in the Order Santalales as currently understood. While in other known species anthers or anther cushions are individually fused with perianth members, those of *V.* aff. *hildebrandtii* are fused into a unified or bilobed, weakly vasculated central synandrium which represents the continuation of the floral axis and lacks any direct contact with perianth members. Somewhat intermediate situations seem to exist in several other African species.

1. INTRODUCTION

The androecium of Viscaceae has undergone some striking modifications which figure prominently in generic delimitations. In all cases but some *Notothixos* (DANSER 1931) where free anthers occur, the anther is fused with the adaxial surface of the perianth member (KUIJT 1969). The anther of *Phoradendron* contains two pollen sacs* which are fused into one in *Dendrophthora*. In *Arceuthobium*, the archesporium is a more or less continuous ring-like zone surrounding a sterile central column, the anther dehiscing by means of an irregular, circular slit. *Notothixos* is superficially similar to *Dendrophthora* in this regard, but has about half a dozen separate pollen chambers which DANSER (1931) believes to have individual apertures but which KUIJT (1969) describes as opening by a common slit. In *Korthalsella* a fusion has taken place of all anthers of the flower, forming a synandrium with a central cavity into which pollen from the thecae collects, and from which the pollen is released to the outside through a small, common pore (MEKEL 1935; SCHAEPPi & STEINDL 1945). Even here, only the anthers are fused, leaving a cavity directly above the floral apex. In *Viscum*, finally, the anther is described as forming a cushion entirely or mostly fused with the perianth member, the cushion differentiating rather superficial, small pollen chambers. The number of pollen chambers, each having its own endothelial jacket and separate aperture, varies somewhat between species, and may reach up to 50 in *V. album*.

During recent work on the palynology of African *Viscum* (Feuer, Kuijt, and Wiens, in preparation) we have discovered a radically different androecial type, which forms the subject of this report. Our observations are based largely on collections made by the second author; details of the collections cited are provided at the end of the paper.

* The letters d and e in *fig. 2–15* of Kuijt (1969) should be transposed.

Earlier studies on the invariably unisexual flowers of *Viscum* were ably summarized for five Eurasian species by SCHAEPPPI & STEINDL (1945). In those species the staminate flower has three or four distinct perianth members arranged in one whorl, the flower terminating in a slightly raised, cushion-like structure in some species, but in a mere depression in at least *V. orientale*. In the mature flower, a slight constriction is present just below the perianth. The resulting slight rim below the constriction has been referred to as a calyculus by SHAEPPPI & STEINDL (1945) and TUBEUF (1923). Since the rim is no more than a local axial expansion, however, the appropriateness of the term calyculus as used in Olacaceae and Loranthaceae (KUIJT 1969) is highly questionable.

In immature stages the anthers press against each other in the species thus far referred to, but there is no hint of any fusion. The mature anther of these species shows various degrees of adherence to the subtending perianth member. The tip of the anther cushion of *V. orientale*, for example, is quite free, while complete fusion has taken place in *V. album*. There is no separate staminal vasculature in *Viscum* (nor, indeed, in other Viscaceae, with the possible exception of those species of *Notothixos* where free stamens exist). However, the vasculature of the perianth member, considering the latter's small size, may be rather elaborate. It is no wonder that such a reduced anther led VAN TIEGHEM (1869) to visualize the staminate flower as a whorl of polleniferous bracts. At any rate, the standard organization of the angiosperm stamen has completely disappeared in *Viscum*.

Taxonomically, the genus remains poorly known notwithstanding extensive work by BALLE (1960, 1964, 1968), BALLE & HALLÉ (1961), DANSER (1941), RAO (1957), BARLOW (1970, 1971a, 1971b), WIENS (1973, 1975), and WIENS & TÖLKEN (1979), as well as a series of cytotaxonomical studies (BARLOW et al. 1978, and literature cited therein) demonstrating an unusual, permanent chromosome translocation system in dioecious species of the genus. *Viscum* contains some 90 species, about two-thirds of which are concentrated in sub-Saharan Africa and Madagascar, the others being distributed in regions of temperate and tropical Eurasia and Australia. The former group is by far the more complex, and is more or less evenly divided between the African landmass and Madagascar; nearly all Madagascan species are endemic to that island, some being related to those of Africa, others appearing to have affinities with Asian species.

2. RESULTS

Superficial inspection of a number of African and Madagascan species showed that the "standard" androecial situation as described by SCHAEPPPI & STEINDL (1945) is of common occurrence. In some flowers, however, there was a considerable variation in the size of the anther. In the majority of flowers of several species an alternation of large and small anthers was frequently noted (for example, in *V. crassulae*, Wiens 5379; *V. combreticola*, Wiens 5271; *V. obscurum*, Wiens 5384; *V. tuberculatum*, Wiens 4452). In *V. anceps* (Wiens 5368) three large anthers and one small one were observed in some flowers, while *V. obovatum* (Wiens 5280) frequently had two large and two small perianth members in

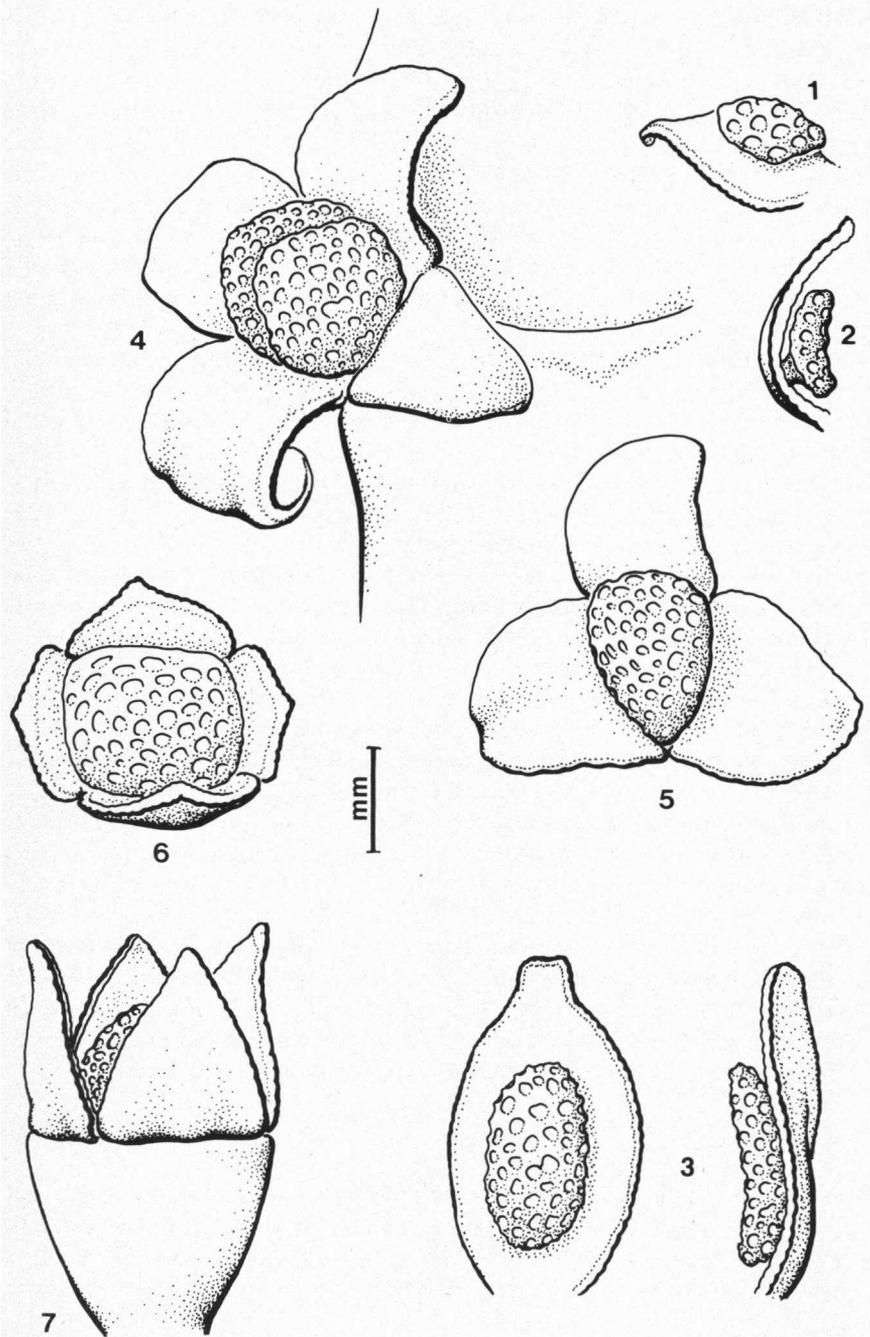


Fig. 1-7. Androecial variation in *Viscum*. Fig. 1. *V. heyneanum*, India (Thomson *s.n.*, K). Fig. 2. *V. cuneifolium*, Madagascar (Baker 5970, K). Fig. 3. *V. combreticola*, Transvaal (Wiens 5271, UT). Figs. 4-7. *V. hildebrandtii*, Kenya (Wiens 5485, UT).

alternating fashion, the latter lacking anthers altogether. In some *V. combreticola* (Wiens 4636) constriction or even subdivision of individual anthers seems to be common. An apparently advanced condition was seen in *V. continuum* (Wiens 5397a). The four anthers, each separately attached to the adaxial surface of a perianth member, are initially in contact with each other, their tips being free from the perianth member. In later stages of anthesis such anthers probably separate, as a probe may easily part them in a mature bud. Interestingly enough, pollen chambers in this species are found on both the abaxial and adaxial flanks of the anther tip. In the Madagascan species, *V. cuneifolium*, the anther is totally distinct and is actually supported on a very short filament, a condition not yet reported for the genus (fig. 2).

It is in *V. hildebrandtii*¹, however, that we discover a radically new androecial type, not just for *Viscum* but also for Viscaceae and indeed for Santalales in general (Wiens 5485, figs. 4–7). The perianth members are devoid of the usual anther cushions, and are smooth to the base. The center is occupied by a variably shaped synandrium which lacks any direct contact with perianth members. The synandrium can take two shapes, even on the same plant. In its simplest form it is a solid, papilla-like central prominence with rounded corners and top, the latter reaching about two-thirds as far as the perianth members. Its shape is conditioned somewhat by the number of perianth members, both the trimerous and the tetramerous conditions being common. The entire surface of the synandrium is covered by numerous small depressions corresponding to pollen chambers, except for its extreme lowest flanks which are smooth. In the more complex form the synandrium is bisected partway down, the resulting two lobes paired with but quite separate from two opposing perianth lobes (fig. 4). In the latter case no pollen sacs occur where the two lobes face each other.

Sections prepared from a few flowers with unified synandria show two to four vascular strands reaching well into the synandrium, but apparently not forming a regular pattern of distribution. The strands are extremely slender, at many levels showing only one very narrow tracheary element with some associated narrow parenchyma cells. No branching has been observed, and we have not been able to ascertain any downward connections with other vascular strands leading into the perianth members. It is well known that the pistillate flower of some Viscaceae has a similar set of unattached central vascular strands which, however, are thought to be a residual carpellary supply (KUIJT 1969).

3. DISCUSSION

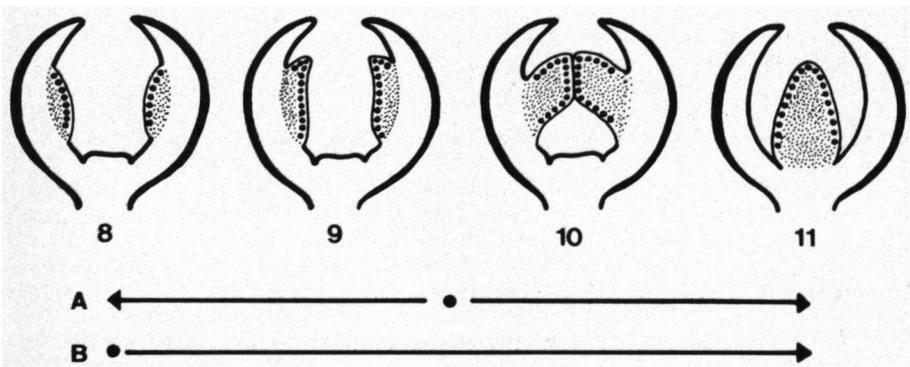
The synandrial type here reported for *V. hildebrandtii* has no known counterpart in the Order Santalales. At first glance it seems similar to that of *Korthalsella*. In that genus, however, the synandrium is clearly perianth-borne, leaving a cavity above the floral apex; dehiscence is introrse into a central cavity which has a

¹The precise identity of our material remains somewhat obscure; it is possible that we are concerned with an undescribed subspecies of, or undescribed species closely related to *V. hildebrandtii*.

single aperture to the outside; and each perianth member bears but two pollen sacs. The synandrium of *V. hildebrandtii* is very different. It represents a transformation of the floral apex itself, and is quite distinct from the surrounding perianth; it is often solid, sometime bilobed; its dehiscence is extrorse, and occurs from numerous small pollen chambers distributed over the surface of the synandrium. The differences are so profound that, in view of the systematic use made of the androecium in the genera of Viscaceae, one might have been tempted to consider elevating the species to the generic level if not other African species seem to form a more or less continuous gradient with it (see below).

It is fortunate that enough androecial variation exists in African *Visca* to provide some insight as to how the synandrium of *V. hildebrandtii* might have evolved. The various species already mentioned above would seem to form an uninterrupted series (figs. 8–11) showing a gradual coalescence of anthers possibly accompanied by a decrease in their number and a redistribution of pollen chambers. It can scarcely be doubted that the new synandrium represents the most highly advanced condition in the genus.

If this be so, the presence of vascular strands in the full-fledged synandrium at first appears to be a stumbling block in interpretation, as the other conditions here described lack androecial vasculature. Are we to believe that the synandrium is traceable back directly to species with free, vasculated stamens the skeleton of which is retained in *V. hildebrandtii*? This is indeed a possibility, as indicated under scheme A in figs. 8–11. An alternative possibility (scheme B of the same figure) envisions a gradual separation of anthers from the perianth members to eventual fusion into a central synandrium. In line with the critical view espoused by CARLQUIST (1969) we do not find it useful to look upon the synandrial vasculature as remnants of ancestral stamens; considering the magnitude of morphological evolution involved it would not be surprising if a *de novo* vasculature had evolved to accommodate the new structure. We also feel that a



Figs. 8–11. Diagrammatic representation of androecia (shaded) as exemplified by *V. album*, *V. heyneanum*, and others (fig. 8), *V. combreticola* (fig. 9), *V. continuum* (fig. 10), and *V. hildebrandtii* (fig. 11).

meaningful view of the evolution of the synandrium of *V. hildebrandtii* would have to be based on a detailed knowledge of pollination of this species and its immediate relatives.

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Collections cited

- Baker 5970, K: *V. cuneifolium* Baker
 Thomson s.n., K: *V. heyneanum* DC.
 Wiens 4452, K, PRE, UT: *V. tuberculatum* A. Rich.
 Wiens 4636, K, PRE, UT: *V. combreticola* Engl.
 Wiens 5271, K, PRE, UT: *V. combreticola* Engl.
 Wiens 5280, K, PRE, UT: *V. obovatum* Harv.
 Wiens 5368, K, PRE, UT: *V. anceps* Sprague
 Wiens 5379, K, PRE, UT: *V. crassulae* Eckl. & Zeyh.
 Wiens 5384, K, PRE, UT: *V. obscurum* Thunb.
 Wiens 5397a, K, PRE, UT: *V. continuum* Sprague
 Wiens 5485, K, PRE, UT: *V. aff. hildebrandtii* Engl.

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