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VISCACEAE

(B.A. Barlow, Canberra, Australia)[1]

Viscaceae Batsch, Tab. Aff. Reg. Veg. (1802) 240, '*Viscinae*'; Miers, Contrib. Bot. (1851) 39, nom. provis.; Miq., Fl. Ind. Bat. 1, 1 (1856) 803; Agardh, Theoria Syst. Pl. (1858) 114; Tiegh., Bull. Soc. Bot. France 43 (1896) 247; Barlow, Proc. Linn. Soc. New S Wales 89 (1964) 269; Kuijt, Brittonia 20 (1969) 138. — *Loranthaceae* subfam. *Viscoideae* Engl., Nat. Pflanzenfam. 3, 1 (1889) 177; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 236. — Type genus: *Viscum* L.

[For additional synonymy see Barlow, Proc. Linn. Soc. New S Wales 89 (1964) 269].

Perennial evergreen or leafless plants, hemiparasitic on tree branches; attachment to the host by a single primary haustorium. *Stem* internodes terete or often angular or flattened, especially in species without developed leaves, often green. *Leaves* or their rudiments opposite, always simple; stipules absent. *Inflorescences* axillary or terminal; uniflorescence a simple cyme or a single flower, these sometimes aggregated to racemose or spicate compound inflorescences or expanded into dense clusters. *Flowers* small (mostly less than 2 mm long), monochlamydeous, unisexual; plants monoecious or (not in Malesia) dioecious. *Tepals* 2–4, valvate. *Stamens* as many as and opposite the tepals, epitepalous or free; anthers basifixed, free or sometimes united into a synandrium, 1- to many-celled, opening by pores or rarely slits; pollen spherical. *Ovary* inferior, 1-locular, with a short placental column; ovules absent; sporogenous cells located at the base of the placental column; stigma simple, sessile, nipple-like. *Fruit* berry-like, with a single seed covered by a sticky layer which develops in a zone internal to the vascular bundles.

DISTRIBUTION

Seven genera and about 400 species, predominantly tropical with fewer species in temperate regions. In *Malesia* 4 genera and 26 species, distributed throughout the region, without any distinct centre of species richness. For biogeography see below.

HABITAT

Mostly in tropical and warm temperate habitats; rare in seasonally cold temperate situations. In *Malesia* distributed through a range of forest habitats from lowland to tropicsubalpine at 3000 m altitude. They occur in all major forest types (everwet and seasonal, closed and open, humid and dry, primary and secondary, evergreen and deciduous).

An important element of habitat for *Viscaceae* is the host; see below for discussion of host specificity.

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1) With contributions by P. Baas (leaf anatomy), R.W.J.M. van der Ham (palynology), and L. van den Oever (wood anatomy). Drawings adapted from various earlier publications and redrawn at CSIRO Plant Industry Visual Resources Unit, Canberra, principally by Sandie McIntosh, with contributions by Sue Percival and Carl Davies. Photographs are from different sources as indicated.

ECOLOGY

Like *Loranthaceae*, *Viscaceae* exhibit a suite of remarkable adaptations associated with the hemiparasitic habit; for additional details see under morphology below.

Except for *Korthalsella* and *Arceuthobium*, effective seed dispersal is by fruit-eating birds, and involves similar adaptations to those found in *Loranthaceae* (for details see there). In *Viscaceae* the fruits and seeds are usually smaller than those of *Loranthaceae*, but they have the same general architecture. In *Korthalsella* the fruits are mostly less than 2 mm long, and the minute seeds are released by a weak explosive mechanism (Stevenson 1934); dispersal is probably achieved by attachment to the feet or feathers of birds. In *Arceuthobium* a more powerful explosive mechanism propels projectile-shaped seeds considerable distances (Hinds et al. 1963; Hinds & Hawksworth 1965), and local dispersal from tree to tree is probably abiotic. See further discussion under plant geography.

Host preference and specificity vary widely within the family. Most *Viscaceae* grow on dicotyledonous hosts, but one genus (*Arceuthobium*) is specialized for and confined to coniferous hosts, and some species of *Dendrophthora*, *Korthalsella*, *Phoradendron* and *Viscum* also occur on conifers. In mixed forests with high tree species diversity many species of *Viscaceae* tend to have low host specificity, occurring on a broad range of host species; this is the case for several species in Malesia. However, other species show some specificity, including *Notothixos cornifolius*, which appears to have a strong host preference for species of *Sterculiaceae*. Also notable is the tendency for many species, especially of *Notothixos* and *Viscum*, to grow on other mistletoes, both of *Loranthaceae* and *Viscaceae*. The latter situation probably reflects the ease with which mistletoes can form haustorial attachments on related species, but may be adaptive in that it involves shared use of the same seed dispersal agents.

In open forests or woodlands with low tree species diversity the viscaceous flora tends to exhibit higher host specificity, sometimes involving differentiation of host races. Infraspecific variation or differentiation of host races in *Arceuthobium* and *Viscum*, for example, is linked with specificity for different hosts (Kuijt 1960; Wiens 1964; Hawksworth 1987; Nickrent & Stell 1990). In other cases, close adaptation for very unusual hosts occurs, for example in *Viscum minimum* of South Africa, which parasitizes succulent *Euphorbia* species, and in which only a fertile shoot c. 3 mm long emerges above the surface of the host (Wiens & Tölken 1979). *Viscum minimum* may thus be one of the smallest dicotyledons. High host specificity in *Viscaceae* is not generally associated with close visual resemblance to the preferred host, as occurs in some *Loranthaceae* (see there), although some species of *Phoradendron* closely resemble their preferred hosts in North America (Atsatt 1979).

The syndrome of floral characters indicates that pollination is consistently by insects. This contrasts with the adaptations of most *Loranthaceae*, which are predominantly bird pollinated. Pollinator guilds are unknown, at least for Malesia.

References: Atsatt, P.R., Second Symp. Parasitic Weeds (1979). — Hawksworth, F.G., in S.J. Corley, Proc. 34th Western Int. For. Disease Work Conf. (1987) 45. — Hinds, T.E. & F.G. Hawksworth, Science 148 (1965) 517–519. — Hinds, T.E., F.G. Hawksworth & W.J. McGinnies, Science 140 (1963) 1236–1238. — Kuijt, J., Univ. Calif. Publ. Bot. 30 (1960) 337–436. — Nickrent, D.L. &

A.L. Stell, Biochem. Syst. Evol. 18 (1990) 267–280. — Stevenson, G., Trans. Roy. Soc. New Zealand 64 (1934) 175–190. — Wiens, D., Brittonia 16 (1964) 11–54. — Wiens, D. & H.R. Tölken, Fl. Southern Africa 10 (1979) 1–59.

MORPHOLOGY

Haustorial system — The haustorial system in *Viscaceae* shows fewer primitive characters than that in *Loranthaceae* (see there). No species of *Viscaceae* are terrestrial root parasites, and none produce secondary haustoria on long epicortical runners. The absorbing connection to the host is therefore provided only by the primary haustorium developed on the embryo, although secondary sinkers to the host xylem may be produced from strands of tissue which spread in the cortex of the host (Gill & Hawksworth 1961). In some cases the primary haustorium becomes large and complex, with a convoluted contact surface and cortical strands. However, when species of *Viscaceae* parasitize other mistletoes the haustoria may be very simple and sometimes externally imperceptible.

Stems and leaves — In many species of *Viscaceae* the stems remain green, even in the case of leafy species. The stems are often sharply angular or flattened, both in leafy and leafless species. In genera in which both leafy and leafless species occur, habit and inflorescence characters suggest that the leafless state may have arisen many times, and it may therefore have a relatively simple genetic basis. The closest relatives of individual leafless species are usually leafy species, and sometimes such species pairs show few other differences.

Inflorescences — There are some parallel trends in inflorescence structure in *Viscaceae* and *Loranthaceae*, although inflorescences in the former family are generally less complex than in the latter. A common inflorescence unit widespread in *Viscaceae* is a simple dichasium (triad), although it is often amplified by sequential development of additional flowers in lateral positions, forming cymose fans or clusters, and sometimes it is reduced to a single flower. In monoecious species the individual cymules usually bear both male and female flowers, with the central flower (or flowers) being of one gender and the lateral flowers of the other; however, entirely female cymules are common in many species. In many cases the cymules are aggregated into larger conflorescences, which are mostly racemose or spicate.

Flowers and fruits — Ovary structure and embryology in *Viscaceae* are distinguished by some unusual features (Johri & Bhatnagar 1960). Comparable reductions in ovary structure occur in *Loranthaceae* (see there), but there are several differences which have been used to support distinction of *Loranthaceae* and *Viscaceae* as separate families (see below). There are no ovules, and the ovary shows very little internal differentiation. A small central placenta (mamelon) is present in *Arceuthobium*, *Korthalsella* and *Phoradendron*, but is much reduced or lacking in *Viscum*. Two to several sporogenous cells differentiate at the base of the mamelon. The embryo lacks a suspensor except in *Vis-*

cum, where it is very short. Normally only one embryo develops in the pseudoseed, and the viscous layer develops from a zone in the ovary wall internal to or within the vascular zone.

References: Gill, L.S. & F.G. Hawksworth, USDA Tech. Bull. 1242 (1961), 87 pp. (haustorial system). — Johri, B.M. & S.P. Bhatnagar, Proc. Nat. Inst. India 26B (1960) 199–220 (embryology).

VEGETATIVE ANATOMY

(P. Baas, leaf anatomy & L. van den Oever, wood anatomy)

Leaf anatomy — The leaf anatomy of Malesian *Viscum* is very poorly known. Stomata paracytic. Groups of silicified cells present in the mesophyll. Sclereid cells common (Engler & Krause 1935). Vascular bundles of the veins supported by arcs of collenchyma (Metcalfe & Chalk 1950).

Wood anatomy — The description given below is based on literature data (Metcalfe & Chalk 1950; Fahn et al. 1986) and original observations on three species. Only one of the specimens is from a tropical region and may be used as best reference for the Malesian area (*Viscum* sp., *Geesink 7817*, Thailand), the others are from Europe. Quantitative features given below are mainly restricted to the tropical specimen. The description must be considered as preliminary at best.

Growth rings faint to distinct. Vessels diffuse 20–30/mm^2, in radial multiples and solitary, tangential diameter up to 100 μm, vessel member length up to 350 μm; in the temperate species the vessel elements are very short (c. 100 μm) and storied together with the axial parenchyma strands. Perforations simple. Intervessel pits very small alternate, vessel-ray and vessel-parenchyma pits alternate, similar in shape and size to intervessel pits. Ground tissue composed of relatively thin-walled libriform fibres with minutely bordered pits mainly confined to the radial walls (in *Geesink 7817*), in the other specimens libriform fibres are scanty and the ground tissue is composed of vessel elements and axial parenchyma.

Parenchyma predominantly apotracheal, diffuse, partly scanty paratracheal, in strands of 2–5 cells.

Rays mainly uniseriate and heterocellular in the tropical specimen; in the other species up to 6-seriate and often compound.

Crystals solitary, infrequent in non-chambered ray or axial parenchyma cells.

References: Engler, A. & K. Krause, Loranthaceae. Nat. Pflanzenfamilien, ed. 2, 16b (1935) 103–105. — Fahn, A., E. Werker & P. Baas, Wood anatomy and identification of trees and shrubs from Israel and adjacent regions (1986) 126–127; Israel Academy of Sciences. — Metcalfe, C.R. & L. Chalk, Anatomy of the Dicotyledons 2 (1950) 1188–1194.

POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

Pollen of the *Viscaceae* is rather poorly known. Only that of *Viscum*, including four of the species occurring in Malesia, has been thoroughly described by Feuer & Kuijt (1982) and Feuer et al. (1982). These studies contain scanning as well as transmission electron micrographs. Pollen of *Korthalsella* is dealt with in several regional accounts, e.g.: Madagascar: Muller et al. (1989); China: Liu & Qiu (1993); New Zealand: Moar (1993). The pollen of *Ginalloa* and *Notothixos* is unknown. The pollen morphology of the predominantly neotropical *Arceuthobium* was monographically studied by Hawksworth & Wiens (1996), but not published in a comprehensive way. Regional data were provided by Quiroz-García et al. (1986) and, including one of the Old World species, Liu & Qiu (1993). The pollen of the large exclusively neotropical genera *Dendrophthora* (Rizzini 1956) and *Phoradendron* (Quiroz-García et al. 1986) is very incompletely known.

In contrast to the pollen of most *Loranthaceae*, which is oblate and triangular, *Viscaceae* pollen is usually spheroidal to subprolate with a more or less rounded equatorial outline. Only that of African *Viscum* is often suboblate with a lobate outline. *Arceuthobium* pollen may be distinctly 6-lobate when the three pseudocolpi are invaginated. *Viscum* has the largest pollen grains in the family: largest diameter from 32 to 55 µm; that of other genera ranges from 17 to 33 µm. Except for a number of African *Viscum* species that show (3-) 4–6-aperturate grains, the pollen of *Viscaceae* is 3-aperturate. In one African *Viscum* species (5–)7–10-rugorate pollen was found. The apertures are usually compound, though the ectoaperture is sometimes short and indistinct and the endoaperture not always well-defined. Simple, colpate apertures occur in a few African *Viscum* species and possibly all *Arceuthobium* species. Pseudocolpi are present in *Arceuthobium* and a few *Viscum* species (Feuer & Kuijt 1982: fig. 14; Feuer et al. 1982: fig. 1–3, 37, 60). Exine ultrastructure has been studied in *Viscum*. The exine is 3-layered (tectum, infratectum, nexine). An endexine is present throughout the grain. The infratectum is finely granular, or granular at the poles and columellate in the equatorial parts, or columellate throughout. The tectum is nearly closed, sometimes very thin or restricted to 'supratectal' elements. Ornamentation in *Viscaceae* pollen is either psilate to scabrate or verrucate (*Dendrophthora, Korthalsella, Phoradendron, Viscum*), sometimes suprareticulate (*Viscum*), or more or less echinate, showing a loose to dense cover of usually conical pointed elements (*Arceuthobium, Viscum*). The four *Viscum* species occurring in Malesia (Feuer & Kuijt 1982) all have scabrate/verrucate pollen; the nearest echinate *Viscaceae* pollen reported is that of *V. alniformosanae* from Taiwan (Feuer & Kuijt 1982) and *A. chinense*, *V. coloratum* and *V. nudum* from China (Liu & Qiu 1993).

According to Feuer et al. (1982) the basic characters of *Viscum* pollen are subprolate, rounded equatorial outline, 3-colporate aperture system, non-uniform columellate/granular exine structure and non-uniform non-prominent ornamentation, which features are all represented in Asian *Viscum*. Due to the lack of detailed data of the other genera no intrafamilial relationships can be established on the basis of pollen morphology. There is no clear relationship between the pollen of *Viscaceae* and *Loranthaceae*. The *Viscaceae* do share a number of characters with the *Eremolepidaceae*: 3-colporate aperture system, exine structure (finely granular infratectum) and echinate ornamentation (Feuer & Kuijt 1978).

Fossil pollen that might be assigned to the *Viscaceae*, and much alike that of the extant *Arceuthobium oxycedri*, was described as *Spinulaepollis arceuthobiodes* from early

Eocene to Pliocene strata in central Europe (Muller 1981: *Arceuthobium* type). Hawksworth & Wiens (1972) listed Miocene to Holocene finds of *Arceuthobium* pollen from North America and later added further details on records from Europe, Asia and North America, from Eocene to Holocene (Hawksworth & Wiens 1996). Selling (1947) recorded *Korthalsella* pollen from the Holocene of Hawaii. Fossil *Viscum* pollen is known from the Pliocene of the Netherlands and Germany (Muller 1981).

References: Feuer, S.M. & J. Kuijt, Can. J. Bot. 56 (1978) 2853–2864; Amer. J. Bot. 69 (1982) 1–12. — Feuer, S.M., J. Kuijt & D. Wiens, Amer. J. Bot. 69 (1982) 163–187. — Hawksworth, F.G. & D. Wiens, Biology and classification of dwarf mistletoes (Arceuthobium). USDA Agric. Handb. (1972) 401; Dwarf mistletoes: biology, pathology and systematics. USDA Agric. Handb. (1996) 709. — Liu, L.F. & H.X. Qiu, Guihaia 13 (1993) 235–245. — Moar, N.T., Pollen grains of New Zealand dicotyledonous plants (1993). — Muller, J., Bot. Rev. 47 (1981) 1–142. — Muller, J., M. Schuller, H. Straka & B. Friedrich, Trop. Subtrop. Pflanzenwelt 67 (1989) 5–17. — Quiroz-García, D.L., R. Palacio-Chávez, M. de la Luz Arreguín-Sánchez & D. Ramos-Zamora, Phytologia 60 (1986) 373–382. — Rizzini, C.T., Rodriguésia 30/31 (1956) 87–234. — Selling, O.H., Spec. Publ. B.P. Bishop Mus. 38 (1947).

CHROMOSOMES

Chromosomal characters have made a significant contribution to phylogenetic knowledge of the family, especially in relation to the origin and maintenance of dioecy in *Viscum*. The primary basic chromosome number is x = 14, and the other basic numbers of x = 15, 13, 12, 11 and 10 indicate progressive dysploid increase or reduction, usually within genera (Wiens & Barlow 1971, 1979). Polyploidy is rare, but some species have very large chromosomes, the largest equalling those of *Loranthaceae* and any others in the plant kingdom.

In *Viscum* sex-associated and floating chromosome translocation complexes are characteristic of dioecious species, but are virtually absent in monoecious species (Wiens & Barlow 1979; Barlow 1981; Aparicio 1993). This suggests that the translocations are primarily associated with the origin and establishment of dioecy, by bringing non-allelic male- and female-determining factors into genetic linkage. The inception of dioecy appears to have initiated a significant secondary radiation of *Viscum*, especially in Africa (Barlow 1983).

References: Aparicio, A., Bot. J. Linn. Soc. 111 (1993) 359–369 (sex-associated translocations). — Barlow, B.A., Bot. Mag. Tokyo 94 (1981) 21–34 (sex-associated translocations, dioecy); in D.M. Calder & P. Bernhardt (eds.), The Biology of Mistletoes (1983) 19–46, Academic Press. — Wiens, D. & B.A. Barlow, Taxon 20 (1971) 313–332 (karyology); Heredity 42 (1979) 201–222 (karyology, dioecy).

PHYTOCHEMISTRY AND CHEMOTAXONOMY

Much of the phytochemical study of mistletoes has been undertaken at a time when the *Loranthaceae* and *Viscaceae* were treated as a single family *Loranthaceae* sens. lat. Furthermore many of the studies have involved comparative work in several genera of both families, identifying similarities and differences between the groups then considered subfamilies. For this reason the phytochemistry of the two families has been considered together, to identify the contribution of chemotaxonomy to the current treatment of the two families. As might be predicted, phytochemical studies have shown a number of shared features between the two families. However they have also revealed significant differences which support their distinction. For details see the introductory section on phytochemistry and chemotaxonomy for the family *Loranthaceae* (p. 217).

USES

Mistletoes, including *Viscaceae*, feature prominently in folk legend and medicine (Kanner 1939; Barlow 1987). For general discussion, see introduction to *Loranthaceae*. The traditional European mistletoe *Viscum album* is prominent in mythology, for which it has an extensive literature. The Golden Bough of classical Roman mythology was probably this species, as was the killer of the sungod, Balder, of the Germanic peoples, and the heavenly plant worshipped by the Celts. Some of the beliefs surrounding European mistletoe have been transferred to *Phoradendron* in the New World.

A detailed review of uses of mistletoes (primarily *Viscaceae* but also *Loranthaceae*) was provided by Kanner (1939). Along with many magical uses are therapeutic applications which appear to reflect genuine properties of the plants. Institutes which focus specifically on researching medicinal properties of *Viscum album* have been established, with a strong emphasis on cancer research; for brief historical summaries and experimental studies see, for example, Sallé (1980) and Hülsen & Mechelke (1982).

References: Barlow, B.A., Biologist 34 (1987) 261–269. — Hülsen, H. & F. Mechelke, Arzneim.-Forsch. Drug Res. 32 (1982) 1126–1127. — Kanner, L., Bull. Hist. Med. 7 (1939) 875–936. — Sallé, G., Planta Medica 38 (1980) 43–49.

TAXONOMY

General acceptance of *Viscaceae* as a family distinct from *Loranthaceae* dates from about 1960. As early as 1802 Batsch distinguished the group at this level, and was followed by Miers, Miquel, Agardh and Van Tieghem. Other influential authors, including Engler, Danser and Krause relegated the group to subfamily rank within *Loranthaceae*. More recent sources of data supporting distinction at family level include embryology (Johri & Bhatnagar 1960; Dixit 1962), karyology (Barlow 1964; Wiens & Barlow 1971) and morphology (Kuijt 1968, 1969). The brief diagnostic key to the two families presented at the end of this section covers all Malesian taxa.

Further to the strong grounds for treating *Viscaceae* as a family distinct from *Loranthaceae*, there is some evidence that the two families may not even be directly related (Kuijt 1968). Some genera of *Santalaceae* and *Olacaceae* also show reductions in ovary structure, and aerial stem parasitism also occurs in other families of *Santalales*. Some of the striking features of haustorial structure, ovary structure and growth habit in *Loranthaceae* and *Viscaceae* may therefore be parallel developments (and divergent specializations) acquired from different direct ancestors in *Santalales* (possibly in *Olacaceae* and *Santalaceae* respectively), so that their common ancestor may be phyletically more remote.

Within the *Viscaceae* generic limits have remained relatively stable. However, there is no consensus on the relationships between all genera and their arrangement into subfamilies or tribes. In contrast to *Loranthaceae*, karyology provides little useful data. Various inflorescence and floral characters have been applied in assessing relationships between genera, but differences in weighting lead to different arrangements. Because of the small number of genera in the family, and their obvious affinities with each other, there seems little merit in establishing subfamilial taxa, and none are utilized here.

At the species level there are difficulties in several genera. Many species show considerable morphological variability, some of which may be responses to different growing conditions. In Malesia the greatest difficulties are in *Korthalsella*, for which Molvray (1990) has argued a substantial reduction in the number of species recognized by Danser (1937, 1940), and in *Viscum*, in which apparently widespread species show considerable polymorphy. Like *Loranthaceae*, narrow species concepts in the past have led to segregate taxa being recognized. For Malesia many names have been placed in synonymy, especially by Danser (1931, 1935, 1937, 1940, 1941).

Phylogenetic analysis of *Viscaceae* is difficult, owing to uncertainties about generic relationships, and to the limited number of characters for which polarity states are evident, and applicable at the generic or natural group level. A possible phylogenetic relationship of the genera is indicated by the biogeography of the family (see below).

KEY TO THE FAMILIES

1a. Perianth monochlamydeous, with tepals mostly less than 2 mm long; flowers unisexual, with male and female flowers usually in the same inflorescence; pollen spherical; fruit with the viscous layer inside the vascular bundles; embryo suspensor very short or absent .... **Viscaceae**

b. Perianth dichlamydeous, with the calyx reduced to a limb at the apex of the ovary and the corolla (2.5–)10–150 mm long; flowers mostly bisexual, rarely functionally unisexual and then with vestigial organs of the other sex present and plants mostly dioecious; pollen trilobate; fruit with the viscous layer outside the vascular bundles; embryo suspensor long, multiseriate .... **Loranthaceae** *(p. 209)*

References: Barlow, B.A., Proc. Linn. Soc. New S Wales 89 (1964) 268–272 (family status). — Danser, B.H., Bull. Jard. Bot. Buitenzorg III, 11 (1931) 233–519; 14 (1937) 115–159; 16 (1940) 329–342; Philipp. J. Sc. 58 (1935) 1–128; Blumea 4 (1941) 261–319 (all taxonomy). — Dixit, S.N., Bull. Bot. Surv. India 4 (1962) 49–55 (embryology). — Johri, B.M. & S.P. Bhatnagar, Proc. Nat. Inst. Sci. India 26B (1960) 199–220 (embryology). — Kuijt, J., Brittonia 20 (1968) 136–147 (family status); The biology of parasitic flowering plants (1969), Univ. California Press (family status). — Molvray, M., PhD Thesis, Tulane Univ., Louisiana, USA (1990), 159 pp. — Wiens, D. & B.A. Barlow, Taxon 20 (1971) 313–332 (karyology).

PLANT GEOGRAPHY

Because of the nature of seed dispersal mechanisms in most genera of *Viscaceae*, their dispersability is normally very low. With the striking exception of *Korthalsella*, the family has a strongly continental distribution, and the present distribution of the family has probably been achieved largely by migration over continuous land surfaces. This allows confidence in the correlation of area, migration and phylogeny. *Korthalsella* is remarkable among all mistletoes for its wide distribution to, and diversification on, remote oceanic islands, perhaps attributable to dispersal of the minute seeds on the feet and feathers of migratory birds rather than by ingestion. Determining the centre of origin of *Korthalsella* is therefore difficult, and contributes little to an analysis of the entire family.

At least four of the seven genera of *Viscaceae* appear to be centred in the southeast Asian/Malesian region (Barlow 1983). A fifth genus, *Arceuthobium*, whilst species-rich in North America, is probably Asian in origin (Hawksworth & Wiens 1972, 1996). An eastern Asian origin for *Viscaceae* has therefore been postulated (Barlow 1983), with *Arceuthobium*, *Dendrophthora* and *Phoradendron* reaching the New World via the Tertiary Beringian land connection, associated at least in part with migration of the preferred hosts. The family may ultimately be of Gondwanan origin (Barlow 1990), but its major diversification was probably a Tertiary palaeotropic Laurasian event.

All four genera of *Viscaceae* in Malesia are centred there or in Southeast Asia, and show some attenuation across Charles's Line to Papuasia, Australia and the Pacific. They are probably all components of the one floristic element, a tropical one with a primary centre in SE Asia, which has diversified in the Malesian region (up to generic level), and which is represented further southeastwards in Australia only as an intrusive stock.

References: Barlow, B.A., in D.M. Calder & P. Bernhardt (eds.), The Biology of Mistletoes (1983) 19–46, Acad. Press; in P. Baas et al. (eds.), The Plant Diversity of Malesia (1990) 273–292, Kluwer Academic Publ. — Hawksworth, F.G. & D. Wiens, Biology and classification of dwarf mistletoes (Arceuthobium). USDA Agric. Handb (1972) 401; Dwarf mistletoes: biology, pathology and systematics. USDA Agric. Handb. (1996) 709.

KEY TO THE GENERA

1a. Plants leafy 2
b. Plants lacking normally developed leaves 3
2a. Plants densely white to golden or brown stellate-hairy, especially on the young parts .... **Notothixos** *(p. 425)*
b. Plants glabrous or nearly so 4
3a. Flowers minute (mostly less than 0.5 mm long); anthers 3, fused into a single unit; fruits up to 3 mm long; [in Malesia plants mostly less than 20 cm long; internodes in most species flattened in the one plane to form a cladode] . **Korthalsella** *(p. 418)*
b. Flowers small (mostly 0.5–2 mm long); anthers 3 or 4, free from each other; fruits more than 3 mm long; [in Malesia plants mostly reaching more than 30 cm length; internodes in most species terete or when angular or flattened with the succeeding ones at right angles] 4
4a. Inflorescence a spike of decussate single flowers or 3-flowered cymes; anthers opening by slits; tepals persistent on the fruit .... **Ginalloa** *(p. 412)*
b. Inflorescence a single 3- or 5-flowered cyme, sometimes with subsidiary cymes or flowers arising within or below the first; anthers opening by several pores; tepals not persistent on the fruit (except in *V. loranthi*) .... **Viscum** *(p. 432)*

GINALLOA

Ginalloa Korth., Verh. Bat. Genootsch. 17 (1839) 260. — Type species: *Ginalloa arnottiana* Korth.

Aerial stem-parasitic shrubs, glabrous. *Stems* much-branched, striate or longitudinally wrinkled. *Leaves* opposite, with normally developed ones and rudimentary cataphyll-like ones borne on each branch; normally developed leaves entire, unifacial, curvinerved, with 1–5 veins usually visible on both surfaces; rudimentary leaves forming a boat-shaped collar encircling the stem. *Inflorescences* terminal and axillary, a spike of decussate pairs of cymules (triads) or single flowers; central flowers usually female; lateral flowers female or male; bracts small, in pairs forming a boat-shaped cupule (like the rudimentary leaves) subtending each cymule; bracteoles of the lateral flowers (when present) small, free, entire to densely fimbriate. *Male flowers* globose or somewhat flattened, 0.5–1 mm long, 3-merous; tepals triangular, valvate; anthers disc-shaped, 2-loculate, opening by slits, on a short filament. *Female flowers* cylindric or narrowly ellipsoid, at anthesis usually less than 2 mm long, usually 3-merous; tepals triangular; stigma small, nipple-shaped. *Fruit* narrow-ellipsoid to ellipsoid, smooth or tuberculate, crowned by the persistent tepals. — **Fig. 1, 2.**

Distribution — Perhaps 9 species distributed from Sri Lanka eastwards and southwards to New Guinea and Solomon Islands. In *Malesia* 6 species, without a distinct centre of diversity.

Habitat & Ecology — Mostly in closed humid forests but extending to open woodlands and disturbed habitats, common in lowlands but extending to 2100 m altitude in New Guinea. Host specificity is low.

Morphology — In most species of *Ginalloa* the stems long remain green. *Ginalloa* is similar to *Notothixos* in producing both normally developed and rudimentary cataphyll-like leaves on each branch system but in *Ginalloa* the pattern is more variable, and some species bear very few normal leaves.

The basic inflorescence unit is a small 3-flowered dichasium (cymule), usually with both male and female flowers, although all-female cymules are sometimes produced when flowering is prolific. The spicate arrangement of the cymules is consistent in the genus *Ginalloa*, although in several species the cymules are often or always reduced to solitary flowers.

Phylogeny — *Ginalloa* is probably the least specialized genus of *Viscaceae*. It shows clear links to each of the other three genera in Malesia, supporting the view that Malesia may be a major centre of diversification for the family (see phytogeography discussion above).

Taxonomy — There is no critical revision of the entire genus, and the taxonomic status of species from Burma and the Andaman Islands is uncertain.

KEY TO THE SPECIES

1a. Inflorescence up to 10 mm long; cymules mostly 1-flowered 2
b. Inflorescence more than 10 mm long; cymules mostly 3-flowered 3

2a. Plants with normally developed and rudimentary leaves in successive pairs; normal leaves 5–40 mm long; inflorescences mostly terminal, with 3–16 pairs of cymules .... **4. G. linearis**

b. Plants seemingly sparsely leafy or leafless, with rudimentary leaves produced at most or all nodes; normal leaves 30–50 mm long; inflorescences mostly axillary, mostly with 2 or 3 pairs of cymules .... **5. G. nuda**

3a. Bracteoles densely fimbriate, forming a tuft of white hairs surrounding the flowers; spikes 80–200 mm long with internodes 8–20 mm long; fruit white .... **3. G. flagellaris**

b. Bracteoles entire or serrate; spikes 20–90 mm long with internodes 2–7 mm long; fruit yellow to red 4

4a. Normal leaves linear to narrowly lanceolate, less than 10 mm wide .... **1. G. angustifolia**

b. Normal leaves narrowly to broadly ovate or elliptic, more than 10 mm wide ... 5

5a. Normal leaves thickly coriaceous, broadly elliptic or broadly ovate; rudimentary leaves 2–4 mm above each leafy node, ragged at the margin; spikes 20–35 mm long with 8–10 pairs of cymules .... **6. G. siamica**

b. Normal leaves thinly coriaceous, narrowly ovate to ovate; rudimentary leaves mostly 7–25 mm above each leafy node, entire at the margin; spikes 30–90 mm long with 9–40 pairs of cymules .... **2. G. arnottiana**

1. Ginalloa angustifolia (Merr.) Danser

Ginalloa angustifolia (Merr.) Danser, Philipp. J. Sc. 58 (1935) 132. — *Ginalloa cumingiana* var. *angustifolia* Merr., Philipp. J. Sc., Bot. 4 (1909) 153. — Type: *Banks BS 1139*, Negros.

Plant slender, probably pendulous, to 0.6 m long. *Stems* with rudimentary leaves on each growth segment; internodes terete, (7–)25–40 mm long, 0.5–2 mm in diameter. *Leaves* rudimentary and normally developed in successive pairs; normally developed leaves linear to narrowly lanceolate, often falcate, attenuate at the base to an obscure petiole 2–4 mm long, attenuate and finally shortly rounded at the apex, 3-nerved, with veins visible on both sides, 40–60 by 2–8 mm; rudimentary leaves (7–)10–25 mm above each leafy node, c. 0.5 mm high. *Inflorescences* commonly terminal, often in threes, sometimes axillary, 10–40 mm long, a spike of 4–10 pairs of triads or single flowers; internodes 2–7 mm long; bracteal cup c. 1 mm long; bracteoles acuminate, serrate, 0.4–0.8 mm long. *Fruit* ellipsoid, smooth or slightly rugose, orange or red.

Distribution — *Malesia:* Philippines (Luzon, Negros, Palawan).

Habitat & Ecology — 0–1300 m altitude; only recorded host *Garcinia.*

Note — Closely related to *G. arnottiana*, differing in the narrow, more or less falcate 3-veined leaves shortly rounded at the apex and the shorter inflorescence. Also similar to *G. spathulifolia* of Sri Lanka, differing in the cataphyll-like rudimentary leaves being less consistently positioned near the stem bases, smaller persistent tepals on the fruits and shorter more sharply differentiated inflorescences.

2. Ginalloa arnottiana Korth.

Ginalloa arnottiana Korth., Verh. Bat. Genootsch. 17 (1839) 260; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 449; Philipp. J. Sc. 58 (1935) 130. — Type: *Korthals s.n.*, Borneo, Kalimantan, Tandjoeng Djawa.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 449; Philipp. J. Sc. 58 (1935) 130].

Plant slender to moderately robust, erect, 50–80 cm in diameter. *Stems* usually with rudimentary leaves on each growth segment; internodes terete or slightly dilated and flattened upwards, (2–)15–80 mm long, 1–3 mm in diam. *Leaves* usually rudimentary and normally developed in successive pairs; normally developed leaves narrowly ovate to ovate or elliptic, attenuate at the base to an obscure petiole 2–8 mm long, often undulate at the margin, more or less acuminate and finally shortly rounded at the apex, 3-nerved, with veins visible on both sides, 40–90(–110) by 10–30 mm; rudimentary leaves rarely lacking, rarely in two successive pairs, (2–)7–25 mm above each leafy node, c. 1 mm high. *Inflorescences* commonly terminal, often in threes, sometimes axillary, 30–90 mm long, a spike of 9–25(–40) pairs of triads or sometimes single flowers; internodes 2–5 mm long; bracteal cup c. 0.5 mm long, spreading; bracteoles acuminate, almost entire to serrate, rarely (not in Malesia) densely fimbriate, 0.4–1 mm long. *Fruit* narrowly ellipsoid to ellipsoid, smooth or rarely finely verrucose, yellow to red. — **Fig. 1a.**

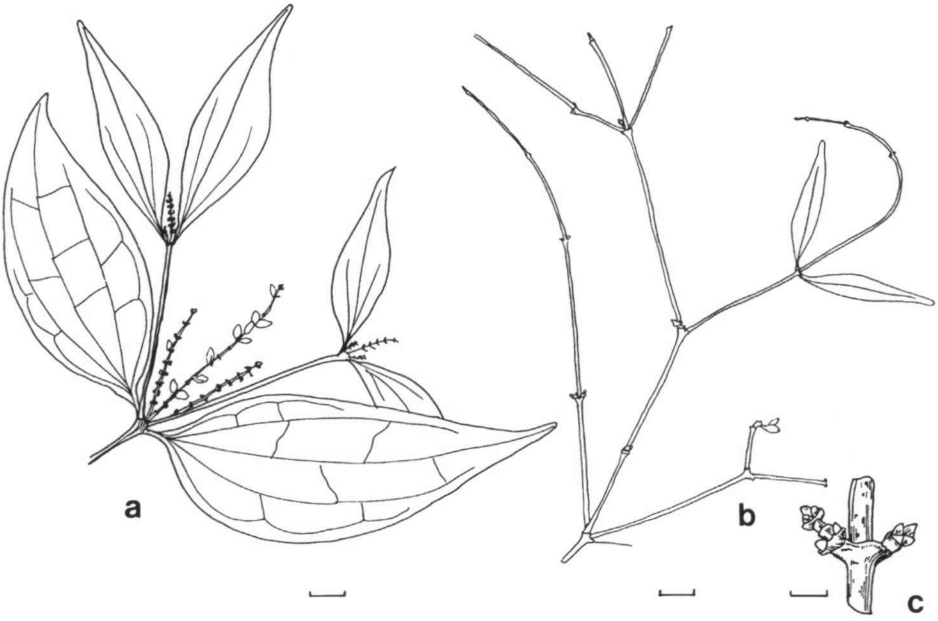

Fig. 1. *Ginalloa arnottiana* Korth. a. Twig with inflorescences. — *G. nuda* Danser. b. Habit; c. inflorescences (a: *Winkler 2437*; b, c: *Clemens 31538*). Redrawn from Danser (1931, 1934). Scale bars represent 1 cm (a, b), resp. 1 mm (c).

Distribution — Solomon Islands; *Malesia:* Borneo, Philippines, Celebes, Lombok, Moluccas. See note on disjunct distribution.

Habitat & Ecology — Primary and secondary humid forests and disturbed sites, from 0 to 2100 m altitude; recorded hosts include *Citrus, Eugenia, Mallotus, Mitrephora, Parinari, Schima, Shorea.*

Note — There is a striking disjunction in the species area between the Moluccas and the Solomon Islands, with the intervening area in New Guinea occupied by *G. flagellaris* (see note there). In the Solomon Islands *G. arnottiana* shows the strongly fimbriate bracteole character which is otherwise diagnostic of *G. flagellaris.*

3. **Ginalloa flagellaris** Barlow

Ginalloa flagellaris Barlow, Blumea 41 (1996) 339. — Type: *Womersley & Whitmore NGF 19070,* Papua New Guinea, Wau.

Ginalloa arnottiana auct. non Korthals: Danser, Blumea 3 (1938) 54.

Plant slender to moderately robust, pendulous, to 0.6 m long. *Stems* with rudimentary leaves on each growth segment; internodes terete, 20–60 mm long, 1–3 mm in diam. *Leaves* mostly rudimentary or sometimes rudimentary and normally developed in successive pairs; normally developed leaves often falling early, narrowly to broadly elliptic, attenuate or cuneate at the base to an obscure petiole 5–10 mm long, attenuate to acuminate and acute at the apex, 5-nerved, with veins visible on both sides, 80–160 by 25–60 mm; rudimentary leaves 0.8–1.5 mm high. *Inflorescences* commonly terminal, often in threes, also axillary, often branching near the base, often not strongly differentiated from vegetative stems, 80–200 mm long, a spike of 15–25 pairs of triads; internodes 8–15 (–20) mm long; bracteal cup c. 1 mm long, spreading; bracteoles densely fimbriate, forming a tuft of white hairs surrounding the flowers. *Fruit* ellipsoid, smooth, white. — **Fig. 2.**

Distribution — *Malesia:* New Guinea, New Britain.

Habitat & Ecology — Humid forests from 400 to 1860 m altitude; *Garcinia* is a commonly recorded host; others include *Antidesma, Castanopsis, Vavaea.*

Note — Geographically replaces *G. arnottiana,* from which it is possibly derived but distinct in several characters, including larger and fewer normally developed leaves not undulate, longer inflorescences and inflorescence segments, and especially the white fruits. *Ginalloa flagellaris* is also distinct in its densely fimbriate bracteoles, forming a tuft of white hairs surrounding the flowers; the occurrence of this character in *G. arnottiana* in the Solomon Islands may be a result of introgression.

4. **Ginalloa linearis** Danser

Ginalloa linearis Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 451. — Type: *Hallier B3049,* Borneo, Kalimantan, Liang Gagang.

Ginalloa applanata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 448. — Type: *Hallier B1780,* Borneo, Kalimantan, Mt Kenepai.

[*Ginalloa tenuifolia* Tiegh., Bull. Soc. Bot. France 42 (1895) 647, nom. nud. — Types: *Beccari 1971 & 2348,* Borneo].

Fig. 2. *Ginalloa flagellaris* Barlow. a. Habit; b. inflorescence node with two triads (*Womersley & Whitmore NGF 19070*). Drawing by L. Spindler, reproduced from Blumea 41. Scale bars represent 1 cm.

Plant slender, erect, 50–80 cm in diam. *Stems* usually with rudimentary leaves on each growth segment; internodes terete or flattened upwards, (0–)10–25(–45) mm long, 0.5–2 mm in diam. *Leaves* usually rudimentary and normally developed in successive pairs; normally developed leaves linear to narrowly elliptic, attenuate to contracted at the base, more or less sessile, often undulate at the margin, rounded at the apex, obscurely 1-nerved, with veins usually not visible, (5–)10–40 by 1.5–4 mm; rudimentary leaves rarely lacking, rarely in two successive pairs, (0–)4–12 mm above each leafy node, 0.3–0.5 mm high. *Inflorescences* mostly terminal, mostly solitary, rarely in threes, rarely axillary, 1.5–10 mm long, a spike of 3–9(–16) pairs of single flowers or sometimes triads; internodes 0.5–1.5 mm long; the bracteal cup c. 0.3 mm long; bracteoles (when present) acute to truncate, almost entire or weakly serrate, c. 0.4 mm long. *Fruit* ellipsoid to almost globose, smooth, red.

Distribution — *Malesia:* Sumatra, Borneo.

Habitat & Ecology — Recorded in primary forests from 50 to 300 m altitude; recorded hosts include *Croton, Garcinia.*

Notes — 1. Rudimentary leaves sometimes quite basal, resembling true cataphylls.

2. When flowers are produced in triads the lateral flowers may develop later than the central one, which may be either male or female.

5. **Ginalloa nuda** Danser

Ginalloa nuda Danser, Rec. Trav. Bot. Néerl. 31 (1934) 229. — Type: *Clemens 31538*, Borneo, Sabah, Mt Kinabalu.

Plant slender, pendulous, 30–60 cm long. *Stems* with rudimentary leaves predominant on each growth segment; internodes terete, 15–60 mm long, 0.3–2 mm in diam. *Leaves* usually rudimentary, sometimes normally developed without regular pattern; normally developed leaves lanceolate, attenuate at the base to an obscure petiole 1–3 mm long, attenuate and finally shortly rounded at the apex, obscurely 3-nerved, 30–50 by 5–10 mm; rudimentary leaves 0.5–0.8 mm high. *Inflorescences* commonly axillary, sometimes terminal, solitary, 1.5–3 mm long, a spike of 2–3(–4) pairs of single flowers; internodes 0.6–1.2 mm long; bracteal cup c. 0.5 mm long, spreading. *Fruit* narrowly ellipsoid, smooth, red. — **Fig. 1 b, c.**

Distribution — *Malesia:* Borneo, recorded only from Mt Kinabalu.

Habitat & Ecology — 900–1350 m altitude; no hosts recorded.

Note — Similar to *Viscum* spp. in the predominantly leafless state and short inflorescence, but the anther structure and persistent tepals are characteristic of *Ginalloa.* Similar to *G. linearis*, differing in larger leaves and mostly shorter, predominantly axillary inflorescences.

6. **Ginalloa siamica** Craib

Ginalloa siamica Craib, Kew Bull. (1911) 455; Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 47. — Type: *Kerr 1300*, Thailand, Chiangmai.

Ginalloa siamica var. *scortechinii* Gamble, J. As. Soc. Beng. 75, ii (1914) 383; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 451. — Type: *Scortechini s.n.*, Perak.
Ginalloa ovata Danser, Philipp. J. Sc. 58 (1935) 133. — Type: *Oro FB 30844*, Luzon.

Plant moderately robust, erect, 50–80 cm in diam. *Stems* with rudimentary leaves on each growth segment; internodes terete or slightly dilated upwards, those bearing normally developed leaves 30–65 mm long, 1–5 mm in diameter. *Leaves* rudimentary and normally developed in successive pairs; normally developed leaves broadly elliptic to broadly ovate, cuneate at the base to an obscure petiole 2–4 mm long, rounded at the apex, 3- or 5-nerved, with veins visible on both sides, 25–60 by 20-40 mm; rudimentary leaves in pairs alternating regularly with normally developed leaves, 2–4 mm above each leafy node, ragged, c. 1 mm high. *Inflorescences* commonly terminal, often in threes, sometimes axillary, 20–35 mm long, a spike of 8–10 pairs of triads; internodes 1.5–5 mm long; bracteal cup c. 1 mm long, spreading; bracteoles acute, irregularly serrate, c. 0.5 mm long. *Fruit* ellipsoid, smooth or finely verrucose, not seen mature.

Distribution — Thailand, Cambodia; *Malesia:* Peninsular Malaysia, Philippines.

Habitat & Ecology — 400–1080 m altitude; the only recorded host is *Pentacme.*

KORTHALSELLA

Korthalsella Tiegh., Bull. Soc. Bot. France 43 (1896) 83, 163. — Type species: *Korthalsella remyana* Tiegh.
[For additional synonymy see Barlow, Brunonia 6 (1983) 37. The type species there cited for *Bifaria* should be *B. japonica* (Thunb.) Tiegh., not *B. rubra*].

Aerial stem-parasitic small perennials, entirely glabrous except for the floral cushions. *Stems* green or yellowish, usually articulated at the nodes; internodes terete or compressed or most often strongly flattened in one plane forming a cladode. *Leaves* opposite, rudimentary, each pair forming a border mostly less than 1 mm high at each node and subtending the flower clusters. *Flowers* developing successively in lateral clusters, usually surrounded and separated by multicellular sparsely branched thick-walled hairs (derived from floral bracts) which often form a raised mound (floral cushion); flower clusters sometimes coalescing and completely encircling the stem at each node; first-formed flower arising in an axillary position and usually male; subsequent flowers developing laterally to the first and often also in further transverse rows below the first, mostly female. *Male flowers* globose to obconic in bud, c. 0.5 mm in diam., attenuate at the base and shortly stipitate, 3-merous; tepals persistent, triangular, valvate; anthers 3, 2-locular, introrse, united into a synandrium with a common apical pore. *Female flowers* globose to pear-shaped, usually less than 0.5 mm in diam., 3-merous; tepals triangular; persistent at the top of the ovary. *Fruit* pear-shaped or ellipsoid, seldom reaching 3 mm in length, crowned by the persistent tepals. — **Fig. 3, 4.**

Distribution — 7–25 species (see below) distributed from Japan to Australia and New Zealand, extending eastwards to several Pacific archipelagos and westwards to Indian Ocean islands and Ethiopia. In *Malesia* 5 species, without a distinct centre of diversity.

The genus is exceptional among mistletoes for its range over remote islands, apparently the result of its atypical fruit structure and mode of dispersal (see under ecology, p. 404). The apparently fragmented distributions of some species may simply reflect their crypsis in the field (see below).

Habitat & Ecology — Mostly in closed humid forests but extending to open woodlands and disturbed habitats (especially outside Malesia). In Malesia apparently most common in highlands above 1500 m but also known from lowland forests. The recorded occurrences may be to some extent an artifact of collecting because the minute plants may be rarely observed in the crowns of tall lowland rain forest trees, where they are usually found only when the host is sampled. The hosts are mostly dicotyledons, rarely conifers; for most species host specificity is low.

Morphology — *Korthalsella* is homogeneous in inflorescence and floral characters, but the species vary strikingly in general appearance owing to differences in vegetative characters and in the degree of differentiation of flower-bearing stems. In species with terete or weakly compressed internodes, the successive leaf pairs may be distichous or decussate. In species with strongly flattened internodes, the successive ones of each stem are always flattened in one plane. In some species virtually all nodes bear flower clusters, whereas in others flowering may be restricted to lateral stems or distal parts of stems. In such cases the flowering stems may be less flattened than the vegetative ones. The extreme of this development is illustrated by *K. geminata* (Fig. 3c,d), in which strongly flattened cladodes produce spike-like conflorescences in which the internodes are very short and terete. For additional illustrations of plant form in *Korthalsella* see Barlow, Brunonia 6 (1983) 40, 45, 50, 53.

The hairs which form the floral cushion are probably very densely fimbriate floral bracts, and therefore are homologous with the hairs in the inflorescences of some *Ginalloa* species (see there). In *K. geminata*, which lacks floral cushions, floral bracts are visible and are barely ciliate. Dissected floral bracts can also be seen in *K. japonica* and *K. papuana.*

Taxonomy — The most recently published revision of the entire genus is that of Danser, Bull. Jard. Bot. Buitenzorg III, 14 (1937) 115; 16 (1940) 329. The Australian species were revised by Barlow, Brunonia 6 (1983) 37. Danser recognized 23 species in the genus, and additions by Barlow only slightly outnumber reductions to synonymy, thus bringing the total to 25 species. Danser's and Barlow's treatments were based largely on external morphology, ecology and integrity of geographic occurrence. Touw, in Blumea 29 (1984) 525, reported a study of vascular structure in *Korthalsella*, and in subsequent unpublished work (Molvray 1990, see above) she used this as a major data set for a taxonomic revision. Although she accepted only 7 species in the genus, the nomenclatural implications for Malesia are minor, affecting only one species. However, Molvray's treatment of the entire genus has raised complex issues regarding species circumscription, and it has not been followed here.

For additional notes on taxonomic history, see Danser, Bull. Jard. Bot. Buitenzorg III, 14 (1937) 115 and Barlow, Brunonia 6 (1983) 37. Apart from the work of Danser the most significant earlier work was that of Van Tieghem in Bull. Soc. Bot. France 43

(1896) 83–87, 162–179. He was first to recognize *Korthalsella* as a genus distinct from *Viscum*, and subsequently distinguished two more genera, *Bifaria* and *Heterixia*, and more than 60 species. The latter genera are now regarded as congeneric with *Korthalsella*, and most of Van Tieghem's species names have been reduced to synonymy.

KEY TO THE SPECIES

1a. Flowers in terete spicate conflorescences which arise singly or in threes, terminally and laterally, these sharply distinct from the strongly flattened vegetative cladodes 2
b. Flowers produced at nearly all nodes, or predominantly on more slender lateral cladodes, but not in strongly differentiated spicate conflorescences (the internodes of flowering branches showing a gradual rather than an abrupt transition in shape from the lower non-flowering ones) 3
2a. Flowers 3 in each cluster; conflorescences commonly lateral, sometimes terminal; conflorescence internodes 1–1.5 mm long .... **2. K. geminata**
b. Flowers 40 or more in each cluster; conflorescences rarely lateral, mostly terminal; conflorescence internodes 1.5–7 mm long .... **4. K. papuana**
3a. Internodes terete, without visible veins; plants very slender, up to 3 cm long; hosts conifers .... **1. K. dacrydii**
b. Internodes compressed or flattened in one plane, with 1–3 veins visible as raised ribs; plants slender to robust, mostly more than 5 cm long; hosts dicotyledons . 4
4a. Largest internodes usually 1-ribbed, 5–12 mm long; plants mostly less than 10 cm long; flowers usually 8 or fewer in each cluster .... **3. K. japonica**
b. Largest internodes usually 3-ribbed, 10–27 mm long; plants mostly more than 10 cm long; flowers usually more than 10 in each cluster .... **5. K. rubra**

1. Korthalsella dacrydii (Ridl.) Danser

Korthalsella dacrydii (Ridl.) Danser, Rec. Trav. Bot. Néerl. 31 (1934) 759; Bull. Jard. Bot. Buitenzorg III, 14 (1937) 124; Backer & Bakh. f., Fl. Java 2 (1965) 75. — *Arceuthobium dacrydii* Ridl., J. Fed. Malay States Mus. 6 (1916) 170; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 455. — Type: *Ridley 16094*, Malaya, Pahang, Mt Tahan.

Plants minute, to 3 cm long, slender, sparsely branched, not differentiated into distinct vegetative and flowering axes. *Stems* terete, to 10-noded; basal internode 2–3 mm long, 0.7–1 mm in diam.; succeeding internodes of the main stems to 9 mm long; distal flower-bearing internodes 1–3 mm long; venation not visible. *Rudimentary leaves* together encircling the node, c. 0.5 mm high, membranous, acute at the apices. Hairs of the *floral cushion* few, scarcely protruding, reddish. *Flowers* in 1 to 2 rows, 3–7 per cluster, the opposite clusters meeting and encircling the stem; male flowers solitary or with 2 subsidiary ones developing beside the first.

Distribution — *Malesia:* Sumatra, Peninsular Malaysia, Borneo, Java, Timor; recorded sporadically, possibly more widespread but overlooked owing to the very small size of the plants.

Habitat & Ecology — 950–1650 m altitude; apparently exclusively parasitic on conifers; recorded hosts are *Dacrydium* spp. and *Podocarpus imbricata* (*Dacrycarpus imbricatus*).

Note — Very similar to *K. salicornioides* of New Zealand and New Caledonia, differing in the prominent acute tips of the rudimentary leaves, and in its specificity for coniferous hosts. Differs from *K. grayi* of Australia in the same characters, together with the predominantly decussate phyllotaxy.

2. **Korthalsella geminata** (Korth.) Engl.

Korthalsella geminata (Korth.) Engl., Nat. Pflanzenfam., Nachtr. (1897) 138; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 453; 14 (1937) 129; 16 (1940) 331. — *Viscum geminatum* Korth., Verh. Bat. Genootsch. 17 (1839) 259. — *Heterixia geminata* Tiegh., Bull. Soc. Bot. France 43 (1896) 178. — Type: *Korthals s.n.*, Borneo, Mt Sakumbang.

Plants to 18 cm long, sparsely-branched vegetatively, differentiated into distinct vegetative and flowering axes. *Stems* with 8–12 vegetative internodes; basal internode usually terete or slightly angular, 2–3 mm long, 2–3 mm in diam.; succeeding internodes of the main stems progressively more strongly flattened, the largest ones narrowly to broadly elliptic or rarely almost linear, (10–)15–25 by (3–)6–15 mm; the vegetative branches mostly flattened in the same plane as the parent stem; venation with 3–7 veins distinct and raised and connecting veins usually visible. *Rudimentary leaves* together encircling the node, c. 0.5 mm high, leathery, acute at the apices. *Flower-bearing stems* forming terete spike-like conflorescences to 35 mm long, these usually solitary in the axils and sometimes terminal in threes; internodes 1–1.5 mm long; floral bracts c. 0.5 mm long, acute, sparsely and shortly ciliate. Hairs of the *floral cushion* absent. *Flowers* in 1 row, 3 per cluster; the male flower solitary and central. — **Fig. 3c, d.**

Distribution — *Malesia:* Sumatra, Peninsular Malaysia, Borneo, Flores; recorded sporadically, possibly more widespread but overlooked owing to the small size of the plants.

Habitat & Ecology — Recorded from 1450 to 1740 m altitude; recorded hosts include *Garcinia*, *Rhodamnia* and *Syzygium.*

Note — Similar and probably related to *K. papuana*, differing in the characters set out in the key.

3. **Korthalsella japonica** (Thunb.) Engl.

Korthalsella japonica (Thunb.) Engl., Nat. Pflanzenfam., Nachtr. (1897) 138; Backer & Bakh. f., Fl. Java 2 (1965) 75. — *Viscum japonicum* Thunb., Trans. Linn. Soc. Lond. 2 (1794) 329. — Type: *Herb. Thunberg.*

Korthalsella brassiana Blakely, Proc. Roy. Soc. Queensland 47 (1936) 79. — *Korthalsella japonica* subsp. *brassiana* (Blakely) Barlow, Brunonia 6 (1983) 47. — Type: *Brass 2298*, Queensland, Thornton's Peak.

Viscum opuntia Thunb., Fl. Jap. (1784) 64, nom. superfl. — *Korthalsella opuntia* (Thunb.) Merr., Bot. Mag. Tokyo 30 (1916) 68, comb. illeg.; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 453; 14 (1937) 134; 16 (1940) 333; Philipp. J. Sc. 58 (1935) 134.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 14 (1937) 134, excluding *K. articulata* and names with epithets *breviarticulata*, *howensis* and *rubra*; Barlow, Brunonia 6 (1983) 48].

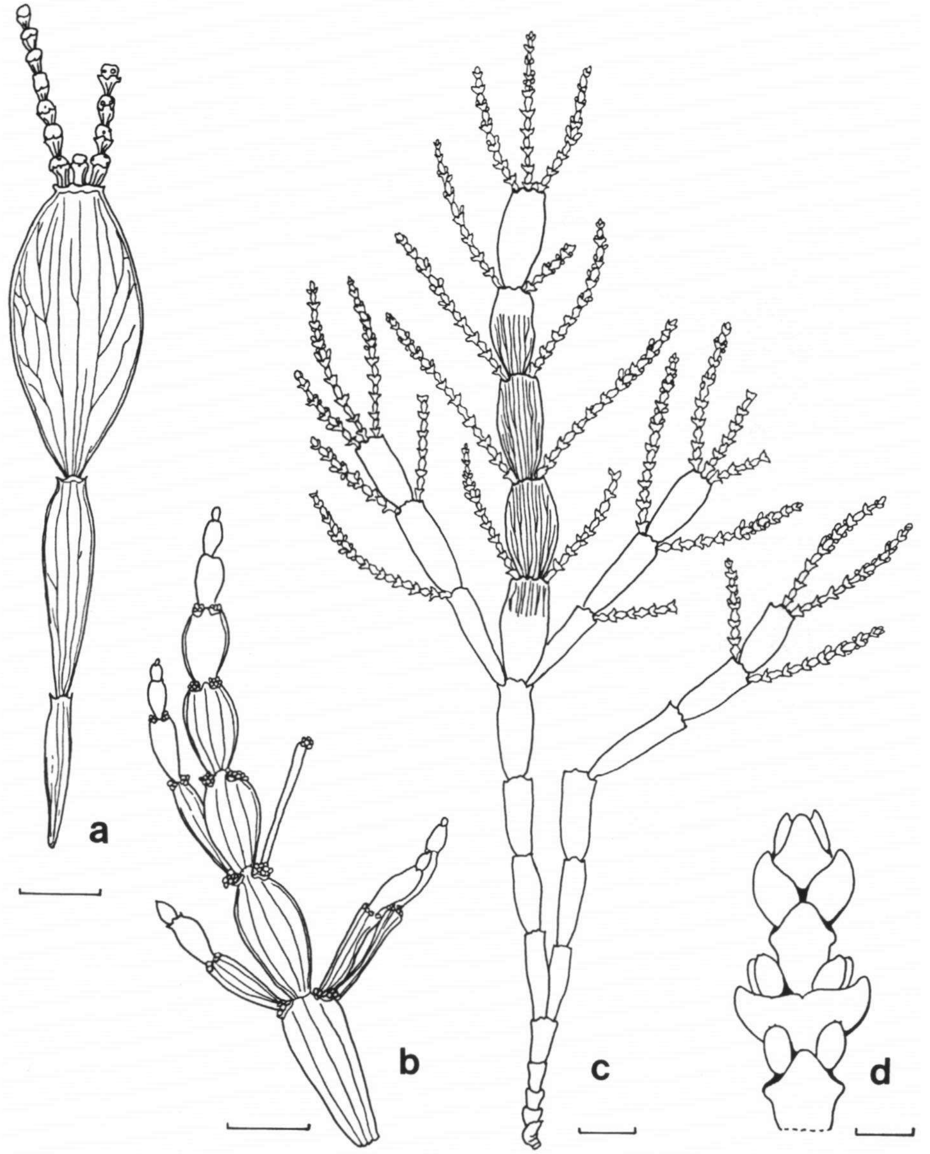

Fig. 3. *Korthalsella papuana* Danser. a. Habit. — *K. rubra* (Tiegh.) Engl. b. Habit. — *K. geminata* (Korth.) Engl. c. Habit; d. part of inflorescence (a: *Hyland 8007*; b: *Hyland 6460*; c, d: *Korthals s.n.*). Redrawn with permission from Flora of Australia 22 (a, b), and (c, d) from Danser (1937). Scale bars represent 1 cm (a, b, c), resp. 1 mm (d).

Plants 4–10(–20) cm long, relatively slender, much-branched, variable in appearance, sometimes with all branches similar to the main stems and sometimes with flowering branches distinctly narrower than the main vegetative ones although not strongly

Fig. 4. *Korthalsella japonica* (Thunb.) Engl. Photograph B. A. Barlow, 1982, macrophotograph from herbarium specimen. Reproduced with permission from Brunonia 6.

differentiated into abruptly distinct vegetative and flowering axes. *Stems* with 8–25 internodes; basal internode 2–12 mm long, terete and 1–2 mm in diameter when shorter, terete at the base and flattened up to 4 mm wide towards the apex when longer; succeeding internodes of the main stems flattened or compressed, narrowly cuneate to narrowly obovate, 5–12 by 2–4 mm; branches mostly flattened transversely to the plane of flattening of the parent stem; venation with 1 vein distinct and raised. *Rudimentary leaves* together encircling the node, 0.2–0.5 mm high, usually thin, truncate. Hairs of the *floral cushion* few or absent, developed from very small bracts, scarcely protruding, reddish. *Flowers* in 1 or 2 rows, c. 8 per cluster, the opposite clusters meeting and encircling the stem; male flowers usually solitary. — **Fig. 4.**

Distribution — Japan southwards to Australia, westwards to India and Indian Ocean islands, and possibly eastwards to Pacific islands; recorded sporadically, possibly more widespread and continuous but overlooked owing to the small size of the plants; in *Malesia:* Sumatra, Peninsular Malaysia, Java, Philippines.

Habitat & Ecology — In Malesia recorded from mossy forest and ericoid brushwood from 1400 to 2700 m altitude; recorded hosts include *Diplycosia, Eurya, Rhododendron, Symplocos, Ternstroemia, Vaccinium.*

Notes — 1. For distinction as a species, see Barlow, Brunonia 6 (1983) 48.

2. In some specimens, especially from Sumatra, internodes of the flowering stems are short (1.5–2 mm long) and slightly compressed or almost terete, thus showing a gradation into spicate flowering axes, but not the abrupt transition present in *K. geminata* and *K. papuana.*

4. **Korthalsella papuana** Danser

Korthalsella papuana Danser, Blumea 3 (1938) 53; Bull. Jard. Bot. Buitenzorg III, 16 (1940) 331. — Type: *Carr 15120*, Papua, Main Range NW of The Gap.

Plants to 18 cm long, relatively unbranched vegetatively when young, branched at nearly every node when older, differentiated into distinct vegetative and flowering axes. *Stems* with 3–6 vegetative internodes; basal internode 2–3 mm long, terete and 1–2 mm in diameter, or up to 25 mm long and terete at the base and flattened up to 4 mm wide towards the apex; succeeding internodes of the main stems strongly flattened, the largest ones narrowly to broadly obovate, 16–55 by 10-22 mm; vegetative branches mostly flattened transversely to the plane of flattening of the parent stem; venation with 3–5 veins distinct and raised and connecting veins visible. *Rudimentary leaves* together encircling the node, c. 0.5 mm high, leathery, acute at the apices. *Flower-bearing stems* forming terete spike-like conflorescences 20–30(–50) mm long, these usually terminal in threes and sometimes solitary in the axils; the internodes 1.5–5(–7) mm long; floral bracts c. 0.3 mm long, coarsely dissected. Hairs of the *floral cushion* absent or few, coarse, scarcely protruding, red or black. *Flowers* in c. 4 rows, more than 40 per cluster, the opposite clusters meeting and encircling the stem in dense whorls; male flowers in the upper whorl. — **Fig. 3a.**

Distribution — Australia (Queensland); *Malesia:* New Guinea.

Habitat & Ecology — In Malesia from 2000 to 2900 m altitude; there recorded hosts include *Macaranga, Syzygium, Xanthomyrtus.*

Note — Similar and probably related to *K. geminata*, differing in the characters set out in the key.

5. **Korthalsella rubra** (Tiegh.) Engl.

Korthalsella rubra (Tiegh.) Engl., Nat. Pflanzenfam., Nachtr. (1897) 138. — *Bifaria rubra* Tiegh., Bull. Soc. Bot. France 43 (1896) 173. — Type: *Mueller s.n.*, New South Wales, Richmond River.
[For additional synonymy see Barlow, Brunonia 6 (1983) 51].

Plants 10–23 cm long, relatively robust, much-branched in the lower part with long unbranched extremities. *Stems* with 12–20 internodes; basal internode varying from terete, 5–12 mm long and 2–3 mm in diameter to flat, narrowly cuneate, to 18 mm long and 4 mm wide; succeeding internodes strongly flattened, narrowly cuneate to narrowly obovate, 10–18(–27) by 3–10 mm; branches often with subsidiary ones arising from the same node, mostly flattened transversely to the plane of flattening of the parent stem; venation mostly with 3 veins distinct and raised. *Rudimentary leaves* together more or less encircling the node, 0.2–1 mm high, leathery, truncate. Hairs of the *floral cushion* sparse to dense, usually protruding, usually red or white. *Flowers* in 2–5 rows, 10–80 per cluster, the opposite clusters not meeting to encircle the stem; male flowers few in all rows. — **Fig. 3b.**

Distribution — Eastern Australia, Lord Howe I.; *Malesia:* New Guinea (New Ireland, Lousiade Archipelago); possibly more widespread in New Guinea but overlooked owing to the small size of the plants.

Habitat & Ecology — Closed and open forests; in Malesia in humid forests at 0–1000 m altitude; there recorded hosts include *Aceratium, Planchonella, Platea* and *Rhodamnia.*

Note — For distinction as a species see Barlow, Brunonia 6 (1983) 52. In unpublished work, Molvray (1990) has proposed the inclusion of *K. rubra* in a more broadly circumscribed species under the name *K. taenioides.*

NOTOTHIXOS

Notothixos Oliv., J. Linn. Soc. Bot. 7 (1864) 92, 103. — Type species: *Notothixos subaureus* Oliv., lecto.
[For additional synonymy see Barlow, Brunonia 6 (1983) 2].

Aerial stem-parasitic shrubs, densely velvety tomentose on young parts. *Stems* much-branched; branches with a pair of prophylls at the base of the first internode and a decussate pair of rudimentary leaves (cataphylls) just above the base. *Leaves* opposite, petiolate, entire, bifacial, curvinerved, usually with 3 or 5 veins visible on the upper surface. *Inflorescences* terminal, of 1 or more fan-shaped cymules, these solitary or in a racemose or spicate arrangement; cymules with 3–13 flowers developing successively from the centre outwards, with the central flowers male and the lateral flowers female; bracts small, triangular, in pairs subtending each cymule. *Male flowers* globose, c. 1 mm in diam., shortly stipitate, usually 4-merous; tepals triangular, valvate; anthers depressed-ovoid or reniform, many-loculate, opening by pores, on a short filament. *Female flowers* cylindric or barrel-shaped, usually less than 2 mm long, 4-merous; tepals triangular; stigma small, nipple-shaped. *Fruit* narrowly ellipsoid to almost globose, crowned by the persistent tepals. — **Fig. 5–8.**

Distribution — Eight species distributed from Sri Lanka eastwards and southwards to eastern Australia and the Santa Cruz Islands. In *Malesia* 6 species, with a centre of diversity in New Guinea.

Habitat & Ecology — Mostly in closed humid forests but extending to open woodlands and disturbed habitats, common in lowlands but extending to 2000 m altitude in New Guinea. For most species host specificity is low.

Morphology — All species of *Notothixos* have a dense, copious indumentum on the young parts, usually persisting at least on the leaf undersides, inflorescences and flowers. This easily distinguishes the genus from *Viscum*, in which all species are glabrous. The tomentum is creamy white to brown, often golden, and comprises mixed unicellular and multicellular hairs. The unicellular hairs are stellate, sometimes dilated into peltate scales. The multicellular hairs are dendritic, consisting of several to many stellate cells in series. For discussion and illustration see Barlow, Brunonia 6 (1983) 5.

The basic inflorescence unit is a small cymose cluster subtended by a pair of small bracts. It becomes fan-like as successive flowers develop laterally. In some species the inflorescence is a single terminal cymule, but in others it is expanded in racemose or spicate fashion, usually with decussate pairs of cymules. In some cases these complex inflorescences are determinate, producing a terminal cymule, and in other cases are indeterminate. For discussion and illustration see Barlow, Brunonia 6 (1983) 6.

Taxonomy — For a revision of the genus and discussion of relationships and biogeography, see Barlow, Brunonia 6 (1983) 1.

KEY TO THE SPECIES

1a. Inflorescence a single terminal cymule; indumentum consisting of peltate scales mixed with dendritic hairs .... **4. N. malayanus**
b. Inflorescence of 3 or more cymules on a common axis; indumentum lacking peltate scales among the dendritic and stellate hairs 2
2a. Inflorescence of 3 or 4 decussate cymules, each produced from the central bud of the one below it .... **5. N. papuanus**
b. Inflorescence of 3 to many cymules on a common axis, borne laterally in 1 or more decussate pairs, with or without a terminal cymule 3
3a. Lateral cymules pedunculate, each with 5–11 flowers 4
b. Lateral cymules sessile, each 3-flowered 5
4a. Tomentum cream to brown, mostly golden, persisting as a dense felt on the lower leaf surfaces; cataphylls narrowly triangular, not sheathing the stem, not at a visible nodal articulation .... **3. N. leiophyllus**
b. Tomentum white or tawny, becoming sparse on lower leaf surfaces with age; cataphylls broadly triangular, partly sheathing the stem, often at a nodal articulation .. .. **1. N. cornifolius**
5a. Young leaves with tomentum similar on both sides; leaf lamina 12–15(–20) mm wide; inflorescence axis 15–20(–40) mm long with 7–10 pairs of triads .... **2. N. floccosus**
b. Young leaves usually with tomentum paler on the upper side; leaf lamina (5–)22–30 (–50) mm wide; inflorescence axis 30–60 mm long with 9–14 pairs of triads .... **6. N. sulphureus**

1. Notothixos cornifolius Oliv.

Notothixos cornifolius Oliv., J. Linn. Soc. Bot. 7 (1864) 103; Barlow, Brunonia 6 (1983) 18. — Type: *Cunningham 50*, New South Wales, Liverpool Plains.
[For additional synonymy see Barlow, l.c.].

Indumentum short, white or tawny, sparse on mature parts with only scattered hairs remaining. *Stem* prophylls c. 0.3 mm long, broadly acute; cataphylls c. 1 mm long, acute, partly sheathing the stem. *Leaf* lamina narrowly elliptic or ovate, (3.5–)4.5–7(–9) by (1–)1.5–2.5(–4) cm, sometimes falcate, attenuate at the base to a petiole 5–10 mm long, somewhat attenuate and rounded to acute at the apex. *Inflorescence* an indeterminate raceme of 4–11 decussate pairs of cymules, often with subsidiary racemes at the base; axis 25–60(–90) mm long; peduncles of the cymules 2–5 mm long; cymules 5- to 11-flowered with the central 1–5 flowers male. — **Fig. 5b, c.**

Distribution — Eastern Australia; *Malesia:* eastern New Guinea.

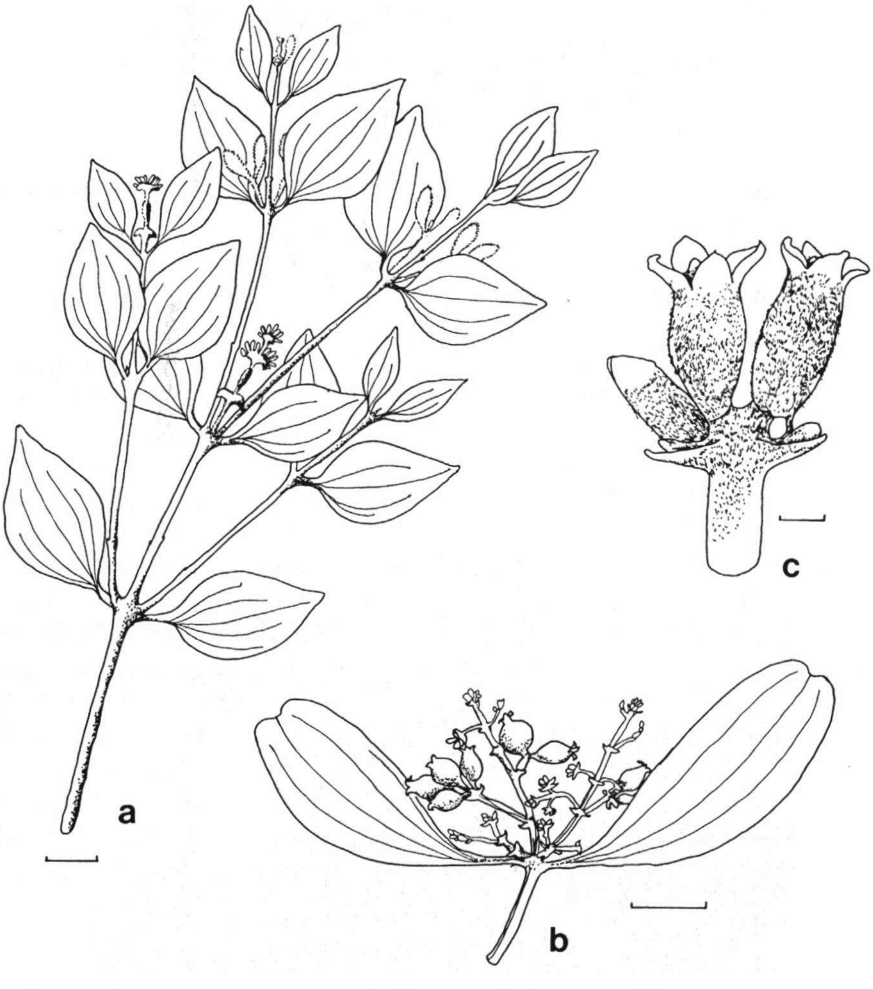

Fig. 5. *Nothothixos papuanus* Danser. a. Habit. — *Nothothixos cornifolius* Oliv. b. Branchlet with flowers and fruits; c. cymule from inflorescence (a: *Carr 15403*; b, c: *Barlow 3742*). Redrawn with permission from Flora of Australia 22 (b, c), and (a) from Danser (1938). Scale bars represent 1 cm (a, b), resp. 1 mm (c).

Habitat & Ecology — 0–1680 m altitude; other habitat details not known for Malesia; in Australia in open and closed forests, almost exclusively parasitic on *Sterculiaceae* (*Argyrodendron, Brachychiton, Sterculia*); also recorded on *Jagera.*

Note — Common in eastern Australia but known from only a single collection in New Guinea.

2. Notothixos floccosus (Thwaites) Oliv.

Notothixos floccosus (Thwaites) Oliv. ex Hook. f., Fl. Brit. India 5 (1885) 227; Barlow, Brunonia 6 (1983) 19. — *Viscum floccosum* Thwaites, Enum. Pl. Zeyl. (1864) 418. — Type: *Thwaites CP 3654,* Sri Lanka, between Ambalangoda and Ratnapura.

Notothixos curranii Merr., Philipp. J. Sc., Bot. 4 (1909) 152; Danser, Philipp. J. Sc. 58 (1935) 136. — Type: *Merritt & Curran FB 12402,* Luzon, Mt Limay.

Notothixos spicatus K. Krause, Bot. Jahrb. 57 (1922) 465, 492; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 458; Backer & Bakh. f., Fl. Java 2 (1965) 75. — Type: *Ledermann 9841,* New Guinea, 'Etappenberg'.

Notothixos merguiensis Danser, Blumea 3 (1940) 392. — Type: *Braybon's Collector 201,* Burma, Leipok Chuang.

Indumentum dense, cream to greenish gold or light pinkish brown, becoming dull with age and soon disappearing from vegetative parts. *Stem* prophylls and cataphylls narrow, acute, up to 0.5 mm long, appressed, apparently deciduous. *Leaf* lamina ovate to broadly ovate or broadly elliptic, 1.5–3(–4) by 1.2–1.5(–2) cm, attenuate or cuneate at the base to a petiole c. 5 mm long, shortly attenuate and rounded or rarely acute or obtuse at the apex. *Inflorescence* an indeterminate spike of 7–10 decussate pairs of cymules; axis 15–20(–40) mm long, with tufts of hairs prominent at the nodes; cymules 3-flowered with the central flower male and a bract under each flower.

Distribution — Sri Lanka, Burma; in *Malesia:* from Philippines, Borneo and Java to New Guinea.

Habitat & Ecology — 0–1600 m altitude; recorded hosts include *Elaeocarpus* and *Gironniera.*

Notes — 1. Closely related to *N. sulphureus*; for differences see Barlow, Brunonia 6 (1983) 22.

2. For distinction as a species and conspecificity of *N. curranii, N. merguiensis* and *N. spicatus,* see Barlow, l.c.: 20.

3. Notothixos leiophyllus K. Schum.

Notothixos leiophyllus K. Schum. in K. Schum. & Lauterb., Fl. Deutsch. Schutzgeb. Südsee, Nachtr. (1905) 260; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 456; Philipp. J. Sc. 58 (1935) 130; Barlow, Brunonia 6 (1983) 15. — Type: *Parkinson 105,* New Britain.

Notothixos philippense Elmer, Leafl. Philipp. Bot. 2 (1908) 47. — Type: *Elmer 10114,* Negros Or., Cuernos Mts.

Notothixos schlechteri K. Krause, Bot. Jahrb. 57 (1922) 465, 493; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 458. — Type: *Schlechter 17662,* New Guinea, Kani Mts.

Notothixos ledermannii K. Krause, Bot. Jahrb. 57 (1922) 465, 494. — Type: *Ledermann 6975,* New Guinea, near Malu.

Fig. 6. *Notothixos leiophyllus* K. Schum. Leafy branches with one young inflorescence. Queensland, Kuranda. Photograph W.N.B. Quick, 1982, with permission.

Fig. 7. *Notothixos leiophyllus* K. Schum. Inflorescence, detail, with immature fruits. Queensland, Card well. Photograph M.F. Braby, 1991, with permission.

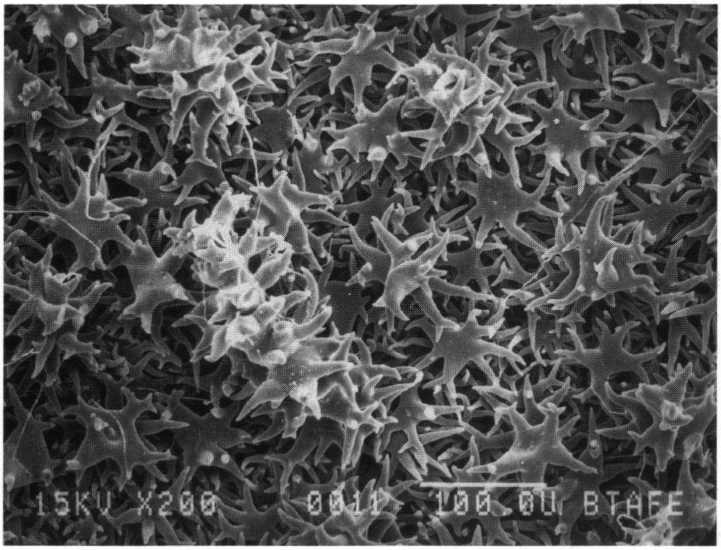

Fig. 8. *Nothothixos leiophyllus* K. Schum. Scanning electron micrograph of lower leaf surface, showing dendritic and stellate hairs. Reproduced with permission from Brunonia 6.

Indumentum short, creamy to golden or rarely rusty, becoming dull with age and soon disappearing from stems and leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, c. 1 mm long, the cataphylls often unequally accrete 1–4 mm above the base of the internode. *Leaf* lamina narrowly to broadly elliptic or ovate, (4–)5–10(–15) by 2–4(–7) cm, cuneate to truncate at the base to a petiole 5–10 mm long, acuminate and rounded at the apex with a short blunt mucro. *Inflorescence* an indeterminate raceme of 6–12 decussate pairs of cymules, often with subsidiary cymules developing below them in the axils of the same bracts, rarely determinate with a terminal cymule; axis up to 10 cm long; peduncles of the cymules 2–5 mm long; cymules 5- to 9-flowered with the central 0–3 flowers male. — **Fig. 6–8.**

Distribution — Northeastern Queensland, Solomon Islands, Santa Cruz; in *Malesia:* from Philippines southwards to Flores and eastwards to New Guinea.

Habitat & Ecology — Primary and secondary humid forests and cultivated lands, from 0 to 1200 m altitude; recorded hosts include *Aegle, Citrus, Decaisnina, Dendrophthoe, Elaeocarpus, Gironniera, Haplolobus, Macaranga, Pangium, Pometia, Prunus.*

Note — For distinction as a species, differences from *N. cornifolius* and conspecificity of *N. ledermannii, N. philippinense* and *N. schlechteri*, see Barlow, Blumea 6 (1983) 16.

4. **Notothixos malayanus** Oliv.

Notothixos malayanus Oliv. in Hook., Ic. Pl. 16 (1886) t. 1519; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 457; Barlow, Brunonia 6 (1983) 10. — Type: *Curtis 233*, Penang.

Indumentum dense, of peltate, stipitate, disc-shaped unicellular scales each with 4–8 scattered tooth-like processes, mixed with scattered dendritic hairs, disappearing with age from stems and leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, c. 0.7 mm long. *Leaf* lamina elliptic to broadly elliptic, 2.5–4 by 2–3 cm, attenuate or cuneate at the base to a petiole 3–5 mm long, rounded at the apex. *Inflorescence* a single pedunculate cymule of c. 7 flowers with the central 1–3 flowers male; peduncle c. 2 mm long, elongating to c. 6 mm long in fruit.

Distribution — *Malesia:* Peninsular Malaysia (Penang I.).

Habitat & Ecology — 0–210 m altitude; no hosts recorded.

Note — Apparently not collected since 1910; assessment of the conservation status of the species is desirable.

5. **Notothixos papuanus** Danser

Notothixos papuanus Danser, Blumea 3 (1938) 56; Barlow, Brunonia 6 (1983) 13. — Type: *Carr 13660*, Papua, Alola.

Indumentum dense, golden, becoming sparse on leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, 0.5–1 mm long, almost obscured by the indumentum, with the cataphylls accrete up to halfway along the basal internode. *Leaf* lamina ovate to broadly ovate, 2.5–4 by 1.5–3 cm, cuneate at the base to a petiole 3–5 mm long, acute and sometimes shortly acuminate at the apex. *Inflorescence* spike-like, actually a determinate series of 3 to 4 decussate pedunculate cymules, each produced from the central bud of the one below it; axis with a basal internode 8–10 mm long and succeeding internodes 4–8 mm long; cymules up to 12-flowered with the central 2–6 flowers male. — **Fig. 5a.**

Distribution — *Malesia:* New Guinea.

Habitat & Ecology — Closed humid forests from 1200 to 2100 m altitude; recorded hosts include *Palaquium* and *Planchonella.*

Note — For discussion of inflorescence structure see Barlow, l.c.

6. **Notothixos sulphureus** Merr.

Notothixos sulphureus Merr., Philipp. J. Sc., Bot. 4 (1909) 152; Danser, Philipp. J. Sc. 58 (1935) 137; Barlow, Brunonia 6 (1983) 22. — Type: *Whitford & Hutchinson FB 9132*, Mindanao, Zamboanga.

Indumentum long and dense, cream to golden or rusty, mostly paler on young leaf upper surfaces, soon disappearing from the stems and leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, c. 1 mm long, the cataphylls often unequally accrete (2–)4–7(–40) mm above the base of the internode. *Leaf* lamina ovate to broadly ovate, (2–)2.5–4(–6) by (1.5–)2–3(–5) cm, cuneate to slightly cordate at the base to a petiole (1–)3–5(–7) mm long, rounded but sometimes shortly attenuate at the apex. *Inflorescence* an indeterminate spike of 9–14 decussate pairs of cymules; axis 3–6 cm long, with dense tufts of hairs prominent at the nodes; cymules 3-flowered with the central flower usually male and a bract under each flower.

Distribution — *Malesia:* Borneo, Philippines (Mindanao), Celebes.

Habitat & Ecology — 0–1220 m altitude; no hosts recorded.

Note — Closely related to *N. floccosus*; for differences see Barlow, l.c.

VISCUM

Viscum L., Sp. Pl. 2 (1753) 1023; Gen. Pl., ed. 5 (1754) 448. — Type species: *Viscum album* L.
Aspidixia (Korth.) Tiegh., Bull. Soc. Bot. France 43 (1896) 191. — *Viscum* sect. *Aspiduxia* Korth., Verh. Bat. Genootsch. 17 (1839) 235. — Type species: *Viscum articulatum* Burm. f.

Aerial stem-parasitic shrubs, glabrous, monoecious or (not in Malesia) dioecious. *Stems* much-branched; internodes terete or compressed or flattened decussately, often longitudinally ridged or striate. *Leaves* opposite, normally developed or rudimentary; normally developed leaves entire, unifacial, curvinerved, usually with 3 or 5 veins visible; rudimentary leaves bract-like, c. 1 mm long. *Inflorescences* terminal or axillary, basically a 3-flowered cymule, sometimes reduced to 1 flower or enlarged by development of adventitious flowers; bracts small, triangular, in pairs forming a boat-shaped cupule subtending each cymule. *Male flowers* flattened, 0.5–1.5 mm long, 4-merous; tepals triangular, valvate; anthers disc-shaped, many-loculate, opening by pores, sessile and fused to the tepal. *Female flowers* cylindric, at anthesis usually less than 2 mm long, 4-merous; tepals triangular; stigma small, nipple-shaped. *Fruit* narrow-ellipsoid to globose, smooth or tuberculate; tepals usually caducous, rarely persistent as a crown on the fruit. — **Fig. 9–13.**

Distribution — Genus of c. 100 species distributed in Europe, throughout Africa, and eastwards to eastern Asia, Malesia and Australia. In *Malesia* 9 species, of which probably 4 are endemic, without a distinct centre of species richness.

Habitat & Ecology — Occurs in a range of habitats from closed humid forests to open woodlands and disturbed habitats; in *Malesia* usually in lowlands to 1500 m but reaching 2300 m in Java. For most species host specificity is low, but some species occur commonly or exclusively on other mistletoes of the families *Loranthaceae* and *Viscaceae.*

Morphology — In most species of *Viscum* the stems long remain green. The basic inflorescence unit is a small 3-flowered dichasium (cymule), in Malesia usually with both male and female flowers, although all-female cymules are sometimes produced when flowering is prolific. In some monoecious species the male flowers are central in the cymule; in others they are lateral. Cymules often develop successively at each node.

Biogeography — The greatest diversity in *Viscum* occurs in Africa and southern Asia. Dioecy is a derived state which has probably arisen in Africa and spread to Europe and temperate Asia, but has not reached Malesia. The Malesian species probably represent an earlier phase of expansion of the monoecious stocks from a Laurasian source, with a gradual attenuation of species richness southeastwards to Australia. For discussion see Barlow in Calder & Bernhardt (eds.), The Biology of Mistletoes (1983) 19–46; in Baas et al. (eds.), The Plant Diversity of Malesia (1990) 273–292.

Taxonomy — For a revision of Asian and Malesian species, see Danser, Blumea 4 (1941) 261–319.

KEY TO THE SPECIES

1a. Plants seemingly leafless 2
b. Plants leafy 6
2a. Inflorescence with a peduncle 2–4 mm long; fruit tuberculate .... **2. V. exile**
b. Inflorescence sessile or nearly so; fruit smooth or papillose 3
3a. Fruit papillose, with persistent tepals at the apex .... **4. V. loranthi**
b. Fruit smooth, without persistent tepals at the apex 4
4a. Stem internodes quite flat, 3–10 mm wide .... **5. V. nepalense**
b. Stem internodes terete or if flattened distinctly angular, 0.5–3(–5) mm wide .. 5
5a. Fruit globose, white; internodes angular .... **1. V. articulatum**
b. Fruit ellipsoid, yellow; internodes terete or angular, distinctly longitudinally ribbed .... **8. V. stenocarpum**
6a. Fruit tuberculate 7
b. Fruit smooth or minutely punctate 8
7a. Leaves linear, less than 3 mm wide, soon falling .... **2. V. exile**
b. Leaves narrowly elliptic to obovate, 10–35 mm wide, long persistent .... **6. V. ovalifolium**
8a. Male flowers, when present, central in the inflorescence .... **3. V. katikianum**
b. Male flowers, when present, lateral in the inflorescence 9
9a. Leaves linear, 3–5 mm wide .... **7. V. scurruloideum**
b. Leaves spathulate to obovate, 12–25 mm wide .... **9. V. wrayi**

1. Viscum articulatum Burm. f.

Viscum articulatum Burm. f., Fl. Indica (1768) 211; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 460; 16 (1938) 56; Philipp. J. Sc. 58 (1935) 141; Blumea 4 (1941) 280; Backer & Bakh. f., Fl. Java 2 (1965) 76. — Type: *Pryon s.n.*, Java.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 460; 16 (1938) 48; Philipp. J. Sc. 58 (1935) 141; Blumea 4 (1941) 280].

Plant slender, pendulous. *Stem* internodes at maturity decussately flattened or compressed, quadrangular or double-edged with a raised angular rib on each face, 15–50 mm long, 0.5–3 mm wide below, widened to 1–5 mm above. *Leaves* rudimentary, spreading, c. 0.5 mm long. *Inflorescence* axillary, a sessile cymule of 1 flower subtended by a cupule c. 1 mm long, with subsidiary cymules developing lateral to the first one, with the first-formed flower female and the lateral flowers female or male. *Fruit* globose, sessile, smooth, white. — **Fig. 9a, 10.**

Distribution — Eastern India eastwards to Vietnam and southwards to eastern Australia; *Malesia:* widespread throughout the region.

Habitat & Ecology — Open and closed forests from 0 to 1500 m altitude; usually parasitic on *Loranthaceae* and other *Viscaceae*; many recorded tree hosts may be in error, overlooking the secondary parasitism.

Note — Very similar vegetatively to *V. stenocarpum*; for differences see there. Also closely related to and possibly intergrading with *V. nepalense*; for distinction see there.

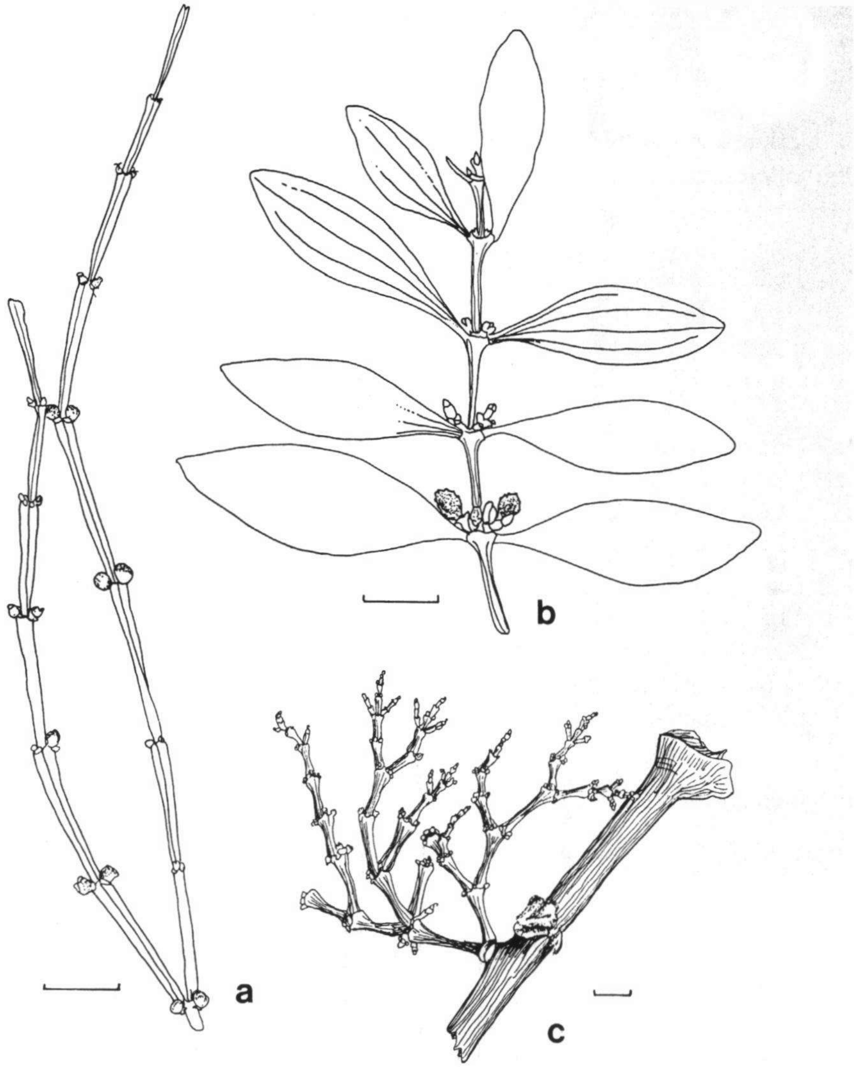

Fig. 9. *Viscum articulatum* Burm. f. a. Habit. — *V. ovalifolium* DC. b. Habit. — *V. loranthi* Elmer. c. Habit (a: *Dockrill 847*; b: *Barlow 3718*; c: *Jacobson 2162*). Redrawn with permission from Flora of Australia 22 (a, b), and (c) from Danser (1931). Scale bars represent 1 cm.

2. Viscum exile Barlow

Viscum exile Barlow, Blumea 41 (1996) 343. — Type: *Eyma 3721*, Celebes, Poso.

Plant slender, pendulous. *Stem* internodes terete, longitudinally ridged, 25–80 mm long, 0.5–1 mm in diam. *Leaves* normally developed or rudimentary, the normal ones probably caducous; lamina in normal leaves flat, linear, attenuate at the base to an obscure petiole 1–2 mm long, attenuate and acute at the apex, 35–50 mm long, 1–2 mm

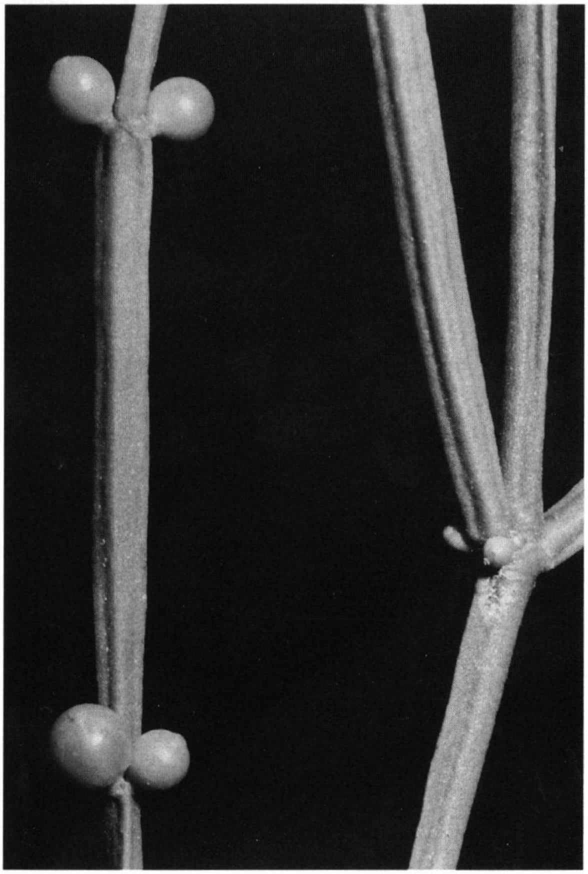

Fig. 10. *Viscum articulatum* Burm. f. Ripe fruits. Queensland, Townsville. Photograph M.F. Braby, 1992, with permission.

wide in the middle, without visible venation; rudimentary leaves occasional, spreading, narrow, acute, c. 1 mm long. *Inflorescence* axillary, a pedunculate cymule of 3 flowers subtended by a cupule c. 0.5 mm long, with the middle flower female and the lateral flowers male; peduncle 2–4 mm long. *Fruit* globose, contracted at the base to a stipe c. 0.5 mm long, tuberculate, green. — **Fig. 11a–c.**

Distribution — *Malesia:* Celebes.

Habitat & Ecology — Not known.

Note — Similar to some forms of *V. ovalifolium* in inflorescence characters, but sharply distinct vegetatively. Superficially the plant appears leafless because of the very narrow leaves which fall early.

3. **Viscum katikianum** Barlow

Viscum katikianum Barlow, Trans. Roy. Soc. S. Austral. 95 (1971) 53. — Type: *Barlow 947*, Papua New Guinea, Wau.

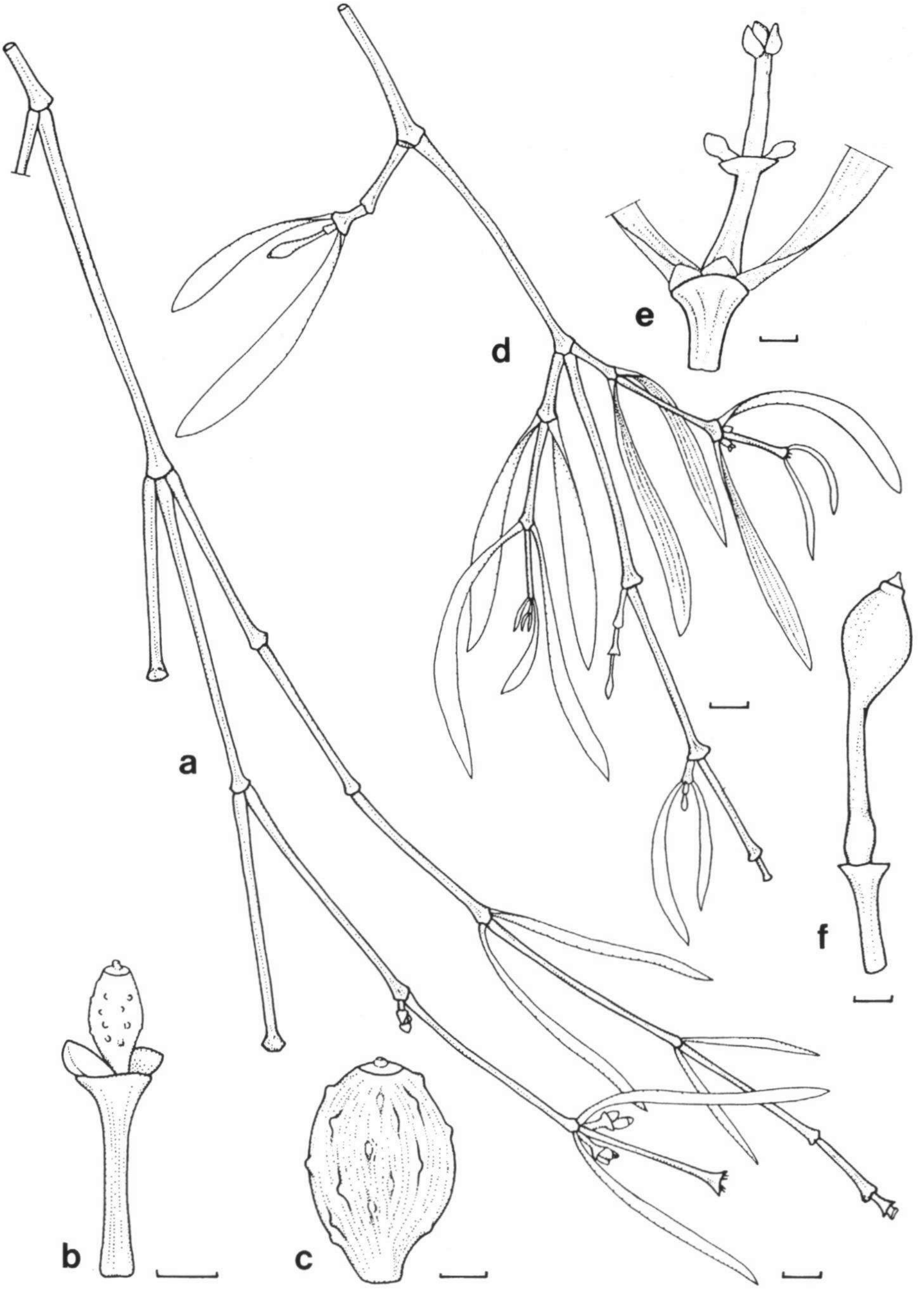

Fig. 11. *Viscum exile* Barlow. a. Habit; b. inflorescence with young fruit; c. immature fruit. — *V. scurruloideum* Barlow. d. Habit; e. inflorescence; f. fruiting inflorescence (a – c: *Eyma 3721*; d–f: *Hildebrand s. n.*). Drawing by L. Spindler, reproduced from Blumea 41. Scale bars represent 1 cm (a, d), resp. 1 mm (b, c, e, f).

Plant slender, erect. *Stem* internodes terete, slightly flattened upwards, striate, 25–60 mm long, 2–3 mm diameter below, widened to 2.5–4 mm above. *Leaves* mostly normally developed; lamina lanceolate to ovate, often falcate, attenuate at the base to an obscure petiole 5–10 mm long, obtuse to acute and sometimes mucronate at the apex, 3- or 5-nerved, 60–100 by 13–45 mm. *Inflorescence* axillary, a pedunculate cymule of 3 flowers subtended by a cupule 1–2 mm long, with subsidiary cymules developing adjacent to the first, with the middle flower male or female and the lateral flowers female; peduncle 4–6 mm long, elongating slightly in fruit. *Fruit* ellipsoid, shortly stipitate, finely punctate.

Distribution — *Malesia:* Papua New Guinea.

Habitat & Ecology — 400–1400 m altitude; recorded hosts include *Alyxia* and *Amyema.*

Note — Probably related to *V. whitei* of northern Australia, from which it differs in its more rigid stems, more erect growth and much larger leaves.

4. Viscum loranthi Elmer

Viscum loranthi Elmer, Leafl. Philipp. Bot. 8 (1919) 3089; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 464; Philipp. J. Sc. 58 (1935) 142; Blumea 4 (1941) 295. — Type: *Elmer 17777*, Luzon, Mt Maquiling.

Plant moderately robust, erect, 10–25 cm tall. *Stem* internodes terete, longitudinally ridged, 5–20 mm long, 1–3 mm wide, enlarged at the nodes. *Leaves* rudimentary, each opposite pair forming a spreading collar c. 0.5 mm wide. *Inflorescence* axillary, a sessile cymule of 1–3 flowers subtended by a cupule c. 0.5 mm long, with many subsidiary cymules of 1–3 flowers soon developing adjacent to the first one, with the middle flower female and the lateral flowers (when present) male or female. *Fruit* urceolate, sessile, coarsely wrinkled when dry, crowned by the persistent tepals. — **Fig. 9c.**

Distribution — Himalayas eastwards to southern China; *Malesia:* Sumatra, Philippines.

Habitat & Ecology — In uplands, mostly 900–1800 m altitude, rarely to 2650 m; recorded hosts are three closely related genera of *Loranthaceae* (*Dendrophthoe, Scurrula, Taxillus*).

Note — Distinctive in the genus in having the tepals persistent on the fruit. This character otherwise distinguishes *Viscum* from all other genera of *Viscaceae* in Malesia.

5. Viscum nepalense Spreng.

Viscum nepalense Spreng., Syst. Veg., Cur. post. (1827) 47; Danser, Blumea 4 (1941) 283. — Types: *Hamilton s.n.*; *Wallich s.n.*, Nepal.
Viscum dichotomum auct. non Gilibert (1792): D. Don, Prod. Fl. Nepal. (1825) 142.
Viscum articulatum auct. non Burm. f.: Backer & Bakh. f., Fl. Java 2 (1965) 76, p.p.
[For additional synonymy see Danser, Blumea 4 (1941) 283].

Plant slender to robust, pendulous. *Stem* internodes flattened, widest above the middle or at the apex, with 1–5 longitudinal veins raised and distinct on each side and the middle one often more prominent, 20–60 mm long, 3–10 mm wide. *Leaves* rudimentary, erect, 0.2–0.3 mm long. *Inflorescence* axillary, a sessile cymule of 1 flower subtended by a cupule c. 1 mm long, with subsidiary cymules developing lateral to the first one, with the first-formed flower female and the lateral flowers female or male. *Fruit* globose or slightly ellipsoid, sessile, smooth, pale coloured, probably yellowish. — **Fig. 12.**

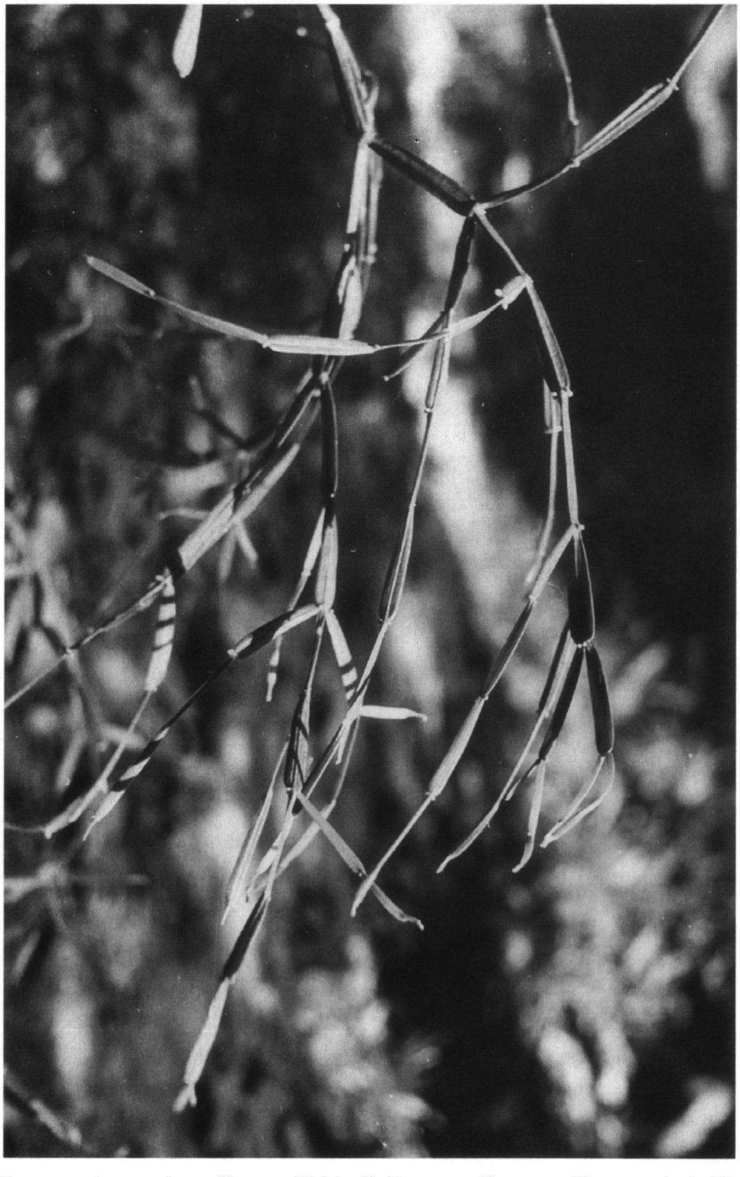

Fig. 12. ***Viscum*** prob. ***nepalense*** Spreng. Habit. Kalimantan, Sanggau. Photograph A. Elsener, 1961.

Distribution — From India eastwards to southern China; *Malesia:* Sumatra, Peninsular Malaysia, Borneo, Java.

Habitat & Ecology — 50–1600 m altitude; recorded hosts in Malesia include *Altingia, Ficus* and a species of *Loranthaceae.*

Note — Closely related to and sometimes difficult to distinguish from *V. articulatum*, differing in the flat, usually wider internodes, probably in having yellowish fruits, and possibly in the shorter rudimentary leaves. In contrast to *V. articulatum*, *Viscum nepalense* also apparently occurs commonly on hosts other than *Loranthaceae* or other *Viscaceae*. Danser in Blumea 4 (1941) 285 maintained the distinction between the two species, and commented on difficulty in discrimination. Slender specimens lacking fruit characters are difficult to place, especially in Java.

6. Viscum ovalifolium DC.

Viscum ovalifolium DC., Prodr. 4 (1830) 278; Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 48; Blumea 4 (1941) 296; Backer & Bakh. f., Fl. Java 2 (1965) 75. — Type: *Wallich 489*, Penang.

Viscum orientale auct. non Willd.: Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 466; Philipp. J. Sc. 58 (1935) 139.

Viscum pedunculatum Barlow, Proc. Linn. Soc. New S Wales 87 (1962) 58. — Type: *Barlow 128*, Queensland, Ellis Beach.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 48; Blumea 4 (1941) 296].

Plant slender to robust, erect, to 1.5 m high. *Stem* internodes terete, sometimes flattened and double-edged upwards, 10–60 mm long, 1–4 mm wide below, widened to 2–5 mm above, striate or weakly ridged longitudinally. *Leaves* mostly normally developed; lamina narrowly elliptic to obovate, sometimes falcate when narrow, attenuate at the base to an obscure petiole 2–5 mm long, often undulate at the margin, rounded to acute and shortly mucronate at the apex, curvinerved, usually with 3 veins visible on both sides, 25–120 by 10–35 mm. *Inflorescence* axillary, sometimes produced on short lateral shoots lacking normally developing leaves and then appearing spicate, a pedunculate or sessile cymule of 3 flowers subtended by a cupule c. 1 mm long, usually with many subsidiary cymules developing around the first one, with the middle flower female and the lateral flowers male; peduncle 0–5 mm long. *Fruit* globose or slightly ellipsoid, usually attenuate at the base, sometimes on a stipe to 3 mm long, distinctly tuberculate before maturity, yellow, orange or red. — **Fig. 9b, 13.**

Distribution — From Burma eastwards to Hong Kong and southwards to northern Queensland; *Malesia:* widespread throughout the region.

Habitat & Ecology — Mostly in lowlands from 0 to 500 m altitude, less frequently to 1400 m, in mangroves and open and closed forests; recorded commonly on *Ficus*, but also on many other hosts.

Notes — 1. A polymorphic species, notably variable in the degree of flattening of the internodes, development of a stipe below the fruit, and length of the pedicel. This makes the clear distinction of *Viscum wrayi* difficult (see there). The occasional development of seemingly spicate inflorescences on leafless shoots gives a superficial resemblance to *Ginalloa*, but fruit characters clearly show the identity.

Fig. 13. *Viscum ovalifolium* DC. Twig with warty ripe fruits. Photograph B.A. Barlow, 1982, macrophotograph from herbarium specimen. Reproduced with permission from Brunonia 6.

2. Both diploid (n = 11) and tetraploid (n = 22) chromosome races are known in *V. ovalifolium* [Wiens & Barlow, Taxon 20 (1971) 317; Barlow, Brunonia 6 (1983) 31, 33], and some of the polymorphy may be attributable to this differentiation.

7. Viscum scurruloideum Barlow

Viscum scurruloideum Barlow, Blumea 41 (1996) 344. — Type: *Hildebrand s. n.*, Java, Preanger.
Ginalloa falcata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 451; Backer & Bakh. f., Fl. Java 2 (1965) 75. — Type: *Backer 10846*, Java, Nirmala.

Plant slender, probably pendulous. *Stem* internodes terete below, flattened upwards, longitudinally ridged, 25–60 mm long, 1–1.5 mm wide below, widened to 1.5–2 mm above. *Leaves* normally developed; lamina linear, falcate, gradually attenuate at the base to an obscure petiole 2–5 mm long, attenuate and finally acute to rounded at the apex, curvinerved with 3 veins raised on both sides, 40–75 by 3–5 mm. *Inflorescences* terminal and axillary, a pedunculate cymule of 3 flowers subtended by a cupule c. 0.5 mm long, with the middle flower female and the lateral flowers female or male; peduncle 2–4 mm long. *Fruit* ellipsoid, on a distinct, slender stipe c. 5 mm long, smooth. — **Fig. 11d–f.**

Distribution — *Malesia:* western Java.

Habitat & Ecology — 1000–1500 m altitude; the only recorded host is *Castanopsis javanica.*

Note — For discussion of transfer from *Ginalloa* to *Viscum*, see Barlow, l.c.

8. Viscum stenocarpum Danser

Viscum stenocarpum Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 469. — Type: *Docters van Leeuwen 12160*, Java, Cibodas.

Viscum liquidambaricolum auct. non Hayata: Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 57, p.p.; Blumea 4 (1941) 289, p.p.; Backer & Bakh.f., Fl. Java 2 (1965) 75.

Plant slender to moderately robust, erect or pendulous, to 1 m long. *Stem* internodes terete or decussately flattened or compressed, quadrangular or double-edged, then usually with a raised angular rib on each face, usually distinctly longitudinally ribbed, 15–60 mm long, 0.5–1.5 mm wide below, widened to 1–2 mm above. *Leaves* rudimentary, spreading, 0.2–0.5 mm long. *Inflorescences* 1 or sometimes 2 in the axils, rarely with subsidiary cymules developing lateral to the first one, a sessile cymule of 3 flowers, subtended by a cupule 0.5–1 mm long, with the middle flower female and the lateral flowers male. *Fruit* ellipsoid to almost globose, sessile, smooth, yellow to red, often striate.

Distribution — *Malesia:* Sumatra, Java, Celebes; possibly Borneo.

Habitat & Ecology — Mostly 1000–1500 m altitude, rarely lower to 20 m, rarely higher to 2300 m; recorded hosts include *Altingia.*

Notes — 1. Similar to *V. articulatum*, differing in the often more nearly terete stems more prominently ribbed, the usual absence of subsidiary cymules, the shape and colour of the fruits, and probably in host preference.

2. Danser in Bull. Jard. Bot. Buitenzorg III, 16 (1938) 57 and Blumea 4 (1941) 289 reduced *V. stenocarpum* to synonymy with *V. liquidambaricolum* Hayata of mainland Southeast Asia, primarily on the similar fruit characters. The latter species has flattened internodes and in vegetative characters differs sharply from *V. stenocarpum* in the same way as *V. nepalense* differs from *V. articulatum* (see notes there). *Viscum stenocarpum* is accordingly treated as distinct from, although closely related to *V. liquidambaricolum.*

3. Two specimens seen from northern Borneo show a combination of characters of *V. articulatum* and *V. stenocarpum*, suggesting local introgression between these two species.

9. **Viscum wrayi** Gamble

Viscum wrayi King ex Gamble, Kew Bull. (1913) 47; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 470; Blumea 4 (1941) 297. — Type: *Wray 1111*, Perak, Mt Batu Puteh, lecto.

Plant moderately robust, erect. *Stem* internodes compressed or flattened and double-edged, longitudinally ribbed, 25–50 mm long, 1–2 mm wide below, widened to 2–4 mm above. *Leaves* normally developed; lamina spathulate to obovate, attenuate at the base to an obscure petiole 2–4 mm long, dark and slightly lustrous on both surfaces, rounded at the apex, 25–50 by 12–25 mm, curvinerved with 3 or 5 veins obscure. *Inflorescences* axillary and terminal, a pedunculate cymule of 3 flowers, subtended by a cupule c. 1 mm long, with subsidiary cymules sometimes developing adjacent to the first, with the middle flower female and the lateral flowers male; peduncle 1–3 mm long. *Fruit* globose or depressed-globose, on a stipe 2.5–4 mm long, usually smooth and shining, sometimes weakly tuberculate, with a short distinct neck, yellow-green to yellow-brown.

Distribution — *Malesia:* Sumatra, Peninsular Malaysia, Borneo.

Habitat & Ecology — Mostly in lowland humid forests from 200 to 1300 m altitude; recorded hosts include *Dendrophthoe*, *Gomphia* and a species of *Rutaceae*.

Note — Closely related to *V. ovalifolium*, which within its range of polymorphy occasionally exhibits most of the distinctive characters of *V. wrayi*. The latter can be distinguished on its combination of flattened double-edged stem internodes, spathulate or obovate lustrous leaves, shortly pedunculate triads, and globose stipitate fruits which are usually shining and only slightly tuberculate.