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A brief taxonomic history of neotropical mistletoe genera, with a key to the genera

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Abstract A brief chronological account is provided of the discovery and recognition of the genera of the New World mistletoes, with a key to the genera.

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When European botanists were first faced with mistletoes of the New World they interpreted them, not surprisingly, within the framework of the mistletoes they knew from their own continent. The new discoveries were thus initially placed in either *Loranthus* Jacq. or *Viscum* L. It was to be a long time before it was realized that neither of these genera occur in the New World, and that a fresh look was needed; even Bentham (1880), for example, continued to place all *Loranthaceae* (in the modern sense) in *Loranthus*, with the singular exception of the extraordinary Australian genus *Nuytsia* R.Br.

The first New World mistletoe recognized (and illustrated) as a new species seems to have been *Tristerix corymbosus* (L.) Kuijt, under the designation *Periclymenum foliis acutis floribus profunde dissectis* …. (Feuillée 1714; see Kuijt 1988b: 20–21). Linnaeus later (1753) renamed this plant *Lonicera corymbosa* L., from which the present, acceptable binomial is derived.

The primarily northern hemisphere genus *Arceuthobium* M. Bieb. was the earliest American genus to receive a separate name (as *Razoumofskya* Hoffmann, 1808, later named *Arceuthobium* M.Bieb. (Marschall von Bieberstein 1819), even though it was not then recognized that the genus also occurred in the New World – especially that most diversity in the genus existed there; the earliest known New World species was at first placed in *Viscum* (*V. vaginatum* Willd., Willdenow 1806).

No exclusively American genus was recognized until 1830 (Martius 1830), and the rapid subsequent developments can at least in part be credited to the Brazilian travels of this author (1817–1820) and the collections he brought back to Germany. The generic names published by him in that year (*Phthirusa* Mart., *Psittacanthus* Mart., *Struthanthus* Mart. and *Tristerix* Mart.) remain accepted today. *Tristerix* included some Old World species. Even before Martius had broken through this mental logjam, other generic names that survive today had begun to appear (*Gaiadendron* G.Don and *Notanthera* (DC.) G.Don, Don 1834; *Antidaphne* Poepp. & Endl., Poeppig & Endlicher 1838; *Dendropemon* (Blume) Rchb., Reichenbach 1841; *Eubrachion* Hook.f. and *Lepidoceras* Hook.f. (Hooker 1846); *Passovia* H.Karst., Karsten 1846; and *Phoradendron* Nutt., Nuttall 1848). *Passovia* was published in a fashion that today would be unacceptable. The curious genus *Misodendrum* Banks ex DC. was first described as part of *Loranthaceae* (De Candolle 1830) and later placed in *Santalaceae* by Bentham (1880), but was earlier recognized as representing a distinct American family (Agard 1858).

No additional American genera appeared in print until 1868, when Eichler published his monumental account of Brazilian mistletoes, an account that also contained much information concerning other neotropical countries. It is difficult not to have the greatest admiration for Eichler's contribution, especially since it was the only contribution to mistletoe taxonomy he published; a century and a half later, it is still necessary to consult its contents in our work. Eichler was a disciple of Martius and, having full access to Martius' collections, he brilliantly consolidated the latter's generic concepts. However, he went considerably further than his mentor by producing the genera *Ixidium* Eichler, *Oryctanthus* Eichler and *Dendrophthora* Eichler, *Ixidium* presently being placed under synonymy in *Antidaphne* (Kuijt 1988a). The latter genus was known to him but, in an inconspicuous footnote on p. 96 (not 98, as stated erroneously in Kuijt 1988a), its treatment was referred to *Santalaceae* – where the genus was subsequently overlooked. His judgment (even though he placed the other Brazilian *Eremolepidaceae* in subfamily *Visceae*) is intriguing in the light of modern molecular studies indicating close affinities of *Eremolepidaceae* with, or even incorporation within, *Santalaceae* (Nickrent et al. 2010). Eichler also introduced *Psittacanthus* subg. *Aetanthus* Eichler, recognized as a distinct genus since Engler (1889).

Eichler nevertheless made two serious errors that have bedevilled mistletoe systematics subsequently. The first of these was the erection of his new genus *Phrygilanthus* Eichler that was said to have species both in the New and the Old World. After a century of confusion, this situation was fortunately clarified by Barlow & Wiens (1973), where Eichler's neotropical species are referred to *Desmaria*, *Gaiadendron*, *Notanthera*, *Tripodanthus* and *Tristerix*. Eichler's remaining *Phrygilanthus* species – all Australian – are presently placed in *Muellerina* (Barlow 1997), rendering the generic name superfluous. The second, more inconspicuous error has persisted until our day, and requires a brief, separate discussion.

Phthirusa in the sense of Martius consisted of a single, relatively rare species, *Phthirusa clandestina* (Mart.) Mart. from Atlantic Brazil. It has sessile flowers without inflorescences and other features that later suggested even to Bentham (1880) affinities to his Mexican *Loranthus inconspicuus* Benth. Eichler fundamentally altered the circumscription of *Phthirusa* by including (or

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newly describing) many species with inflorescences and other features that clash with *P. clandestina*. The weight of Eichler's authority was such that his arrangement was not questioned until Kuijt (2011), where I returned to Martius' original conception, relegating other species to *Passovia*, the only other generic name available. Six other species were at that time recruited from *Ixocactus* Rizzini into *Phthirusa*, including the above "*Loranthus inconspicuus*".

Following Eichler's publication, no new neotropical Loranthaceous genera were published until 1895. It was then that the French botanist Van Tieghem produced a sudden burst of generic names that, with a couple of exceptions, can now be seen as a mostly meaningless proliferations of the taxonomic literature. The most striking instance was when he introduced, usually with very scant information (and, as always, without any illustrations), a large number of new genera within what are now considered *Aetanthus*, *Psittacanthus* and *Struthanthus*, as well as some beyond these genera (Van Tieghem 1895a, b). This nomenclatural grapeshot did, however, produce some small genera that remain currently recognized (*Desmaria* Tiegh., *Ligaria* Tiegh., *Oryctina* Tiegh. and *Tripodanthus* Tiegh.) as well as two others that he based on a single species each but that have more recently been enlarged significantly (*Cladocolea* Tiegh. and *Peristethium* Tiegh.; Kuijt 1975, 2012). In the second edition of Die Natürlichen Pflanzenfamilien (Engler & Krause 1935) and earlier in Engler (1897), Van Tieghem's genera were taken seriously but simply reduced to subgeneric rank without any analytical comments (*Desmaria* and *Peristethium* remaining at the generic level). Across the Channel, the Eurocentric view of *Loranthaceae* persisted (Bentham1880), the worldwide genus *Loranthus* having become progressively more complex and unwieldy.

Since Van Tieghem's time, a few more, very small genera were published intermittently for the New World. *Psathyranthus* Ule (Ule 1906 –1907) later turned out to be one of several unusual Amazonian species of *Psittacanthus* (Kuijt 1983, 2009). *Ixocactus* (Rizzini 1952) can now be seen to be part of an enlarged *Phthirusa* in Martius' sense (Kuijt 2011), while *Furarium* Rizz. (Rizzini 1956) is – perhaps questionably – placed in *Passovia*. *Panamanthus* Kuijt (Kuijt 1991) and *Pusillanthus* Kuijt (Kuijt 2008) are monotypic genera that will probably continue to be accepted, as will *Maracanthus* Kuijt (Kuijt 1976). However, the genus *Passovia* as now circumscribed is known to have a baffling amount of anther diversity that cannot preclude further segregates (Kuijt 2011). Elsewhere, a single and extremely rare Mexican species of *Cladocolea*, *C. biflora* Kuijt, has such an extraordinary floral structure that it might be a fair candidate for generic segregation if more adequate material were available (Kuijt 1980).

With regard to the neotropical genera beyond *Loranthaceae*, little needs to be reported: generic synonyms are listed for *Eremolepidaceae* in Kuijt (1988a), for *Viscaceae* in Kuijt (1961, *Dendrophthora*) and Kuijt (2003, *Phoradendron*), for *Arceuthobium* in Hawksworth & Wiens (1996) and for *Misodendraceae* in Orfila (1978). However, some comments on the admittedly difficult distinction between *Dendrophthora* and *Phoradendron* seem appropriate (see the discussion in Kuijt 2003: 34), as it has been argued that both genera are paraphyletic (Nickrent et al. 2010). Fortunately, no one has seriously proposed to unite these two very large genera (together having more than 350 species), of which only a minute fraction of each has been included in the molecular work on which these conclusions are based. In at least one case (Ashworth 2000a, b, Nickrent et al. 2010), an important argument turned out to reflect a gap in knowledge. *Dendrophthora guatemalensis* Standl., when investigated by Ashworth (2000a) showed clearly that it has a genetic makeup linked to *Phoradendron*. At that time the male flowers of the species were not yet known. When they were later found and analysed, it was discovered that the anthers are bilocular; the species had thus been misplaced in *Dendrophthora* to begin with, and this argument for paraphyly of the genus automatically became moot. The species is now known as *Phoradendron naviculare* Kuijt (Kuijt 2003). Nevertheless, it appears that *Dendrophthora* occupies a nested position in *Phoradendron*, but taking the uncertainties linked to limited sampling and difficult identifications in this group into account, I do not consider this necessarily requiring nomenclatural action yet.

A revised classification of the Order *Santalales* has recently restructured the relationships of the mistletoe families among each other and with other parasitic or autotrophic members of the order (Nickrent et al. 2010). The newly proposed or reintroduced taxa for the *Loranthaceae* of the New World include tribe *Psittacantheae* Horan subtribe *Psittacanthinae* Engl. (all small-flowered genera, including *Tripodanthus*, as well as *Aetanthus* and *Psittacanthus*), subtribe *Notantherinae* Nickrent & Vidal-Russ. (*Desmaria* & *Notanthera*) and subtribe *Ligarinae* Nickrent & Vidal-Russ. (*Ligaria* & *Tristerix*).

Finally, it should be mentioned that APG III (2009) placed *Viscaceae* in *Santalaceae*, a move now followed in some publications but not by Nickrent et al. 2010 or myself.

Estimated species numbers in neotropical genera

Aetanthus	12 or 13	*Notanthera*	1
Antidaphne	9	*Oryctanthus*	15
Arceuthobium	18	*Oryctina*	6
Cladocolea	28	*Panamanthus*	1
Dendropemon	32+	*Passovia*	22+
Dendrophthora	115	*Peristethium*	16
Desmaria	1	*Phoradendron*	240
Eubrachion	2	*Phthirusa*	7
Gaiadendron	2	*Psittacanthus*	118
Lepidoceras	2	*Pusillanthus*	1
Ligaria	2	*Struthanthus*	45
Maracanthus	3	*Tripodanthus*	3
Misodendrum	8	*Tristerix*	13

Total number of accepted neotropical genera: 26; number of species: c. 720.

N.B. *Viscum album* is established in the Santa Rosa, California, area, but is not here taken into account (Scharpf & Hawksworth 1976).

Note. It has frequently been stated that *Loranthaceae* consists primarily of large-flowered, ornithophilous species. This is emphatically not true in the New World, where this group has about 132 species, the small-flowered assemblage 170 species (both counts exclude *Gaiadendron*, *Notanthera* and *Tripodanthus*).

KEY TO THE NEW WORLD GENERA OF MISTLETOES

N.B. It should be noted that the recent classification proposed by Nickrent et al. (2010) places *Eremolepidaceae* as a separate clade in *Santalaceae*. Wherever placed, it remains a heterogeneous group, morphologically as well as palynologically and karyologically, with a disjointed geographic distribution.

1. Fruit an achene bearing long, hairy filaments (staminodia) alternating with perianth members, these fused adaxially with the ovary; S of 33°S and 36°30'S in Chile and Argentina, respectively . . . . . *Misodendrum*
1. Fruit fleshy, seed surrounded by viscin or other slimy cells; stamens or staminodia, where present, positioned adaxially to perianth members (rarely perianth members lacking in male flowers); perianth members not adaxially fused with ovary (female or bisexual flowers); N of 45°S or 40°S in Chile & Argentina, respectively, except *Desmaria*, *Notanthera* and *Lepidoceras* 2

2. Ovary crowned with calyculus in at least the female flower; flowers 2 mm to 30 cm long, at least the longer ones brightly coloured, including white (*Loranthaceae*) 3
2. Calyculus lacking; flowers 3 mm or less long, greenish or greenish yellow (*Eremolepidaceae* and *Viscaceae*) . . 21
3. Epicortical roots on host branches generating leafy shoots; endemic to southern Chile 4
3. Epicortical roots not, or only very rarely, generating leafy shoots, or epicortical roots absent, plants sometimes (*Gaiadendron*) terrestrial shrubs; not present in Chile except *Ligaria* 5
4. Petals bright yellow, nearly 40 cm long, turning orange in age; short-shoots present, bearing the flowers at the tip; deciduous . . . . . *Desmaria*
4. Petals white and pink, to 12 mm long; short-shoots lacking; plants evergreen . . . . . *Notanthera*
5. Petals mostly > 12 mm long, mostly brightly coloured, including yellow or white 16
5. Petals < 12 mm long, often greenish white or reddish, not bright yellow 6
6. Flowers sessile in leaf axils, tetramerous; inflorescences lacking . . . . . *Phthirusa*
6. Flowers in axillary and/or in terminal inflorescences; 4–6 petals 7
7. Inflorescences mostly determinate, subtended by chartaceous, partly caducous leaf scales . . . . . *Peristethium*
7. Inflorescences determinate or indeterminate, lacking basal caducous leaf scales 8
8. Inflorescences monadic only 9
8. Inflorescences triadic or dyadic only (1 or 2 exceptions, Mexico & Bolivia) 14
9. Monads ebracteolate; inflorescences mostly determinate . . . . . *Cladocolea*
9. Monads bracteolate, the bracteoles separate or fused with the bract; inflorescence mostly indeterminate 10
10. Bracteoles and bracts fused into a cupule; monads pedicellate or sessile 11
10. Bracteoles free, small; flowers sessile 12
11. Staminodia and fertile stamens alternating; anthers basifixed or nearly so; Caribbean only . . . . . *Dendropemon*
11. All stamens fertile; anthers dorsifixed, versatile; Chiriquí only . . . . . *Panamanthus*
12. Bracteoles narrow, strap-like; pollen with 3 circular depressions on each face; leaf mesophyll with stellate fiber bundles . . . . . *Oryctanthus*
12. Bracteoles naviculate, not strap-like, or minute; pollen lacking circular depressions; leaf mesophyll lacking stellate fiber bundles 13
13. Bracteoles naviculate, prominent; stamens with filaments and evident connectival prominence; Northern Venezuela, Colombia and Costa Rica (Osa Peninsula) *Maracanthus*
13. Bracteoles extremely small, neither naviculate nor strap-like; anthers sessile, minute; Eastern Brazil (one species in Guyana) . . . . . *Oryctina*
14. Inflorescence a capitulum with 2 (4) triads; flowers tetramerous, usually bisexual; tomentose when young; epicortical roots present or not . . . . . *Pusillanthus*
14. Inflorescence racemic or spike-like, not a capitulum; surfaces glabrous or partly furfuraceous (tomentose in one Bolivian species of *Struthanthus*); epicortical roots mostly present 15
15. Anthers basifixed or nearly so, filaments often stout or laterally excavated; flowers bisexual or plants dioecious . . . . . *Passovia*
15. Anthers elongate, versatile, filaments slender (very rarely absent); plants dioecious . . . . . *Struthanthus*
16. Inflorescence bearing bracteated monads, or inflorescences absent 20
16. Flowers in triads or dyads 17
17. Floral bracts and bracteoles foliaceous; primary haustorium lacking; shrubs or small trees, terrestrial or on tree branches . . . . . *Gaiadendron*
17. Floral bracts and bracteoles not foliaceous (except for the bracts of some *Tristerix*); primary haustorium present; branch-parasitic on shrubs or trees 18
18. Seeds with endosperm; epicortical roots from base of plants and/or from the stem (not known for *T. belmirensis* Roldán & Kuijt); inflorescence triadic . . . . . *Tripodanthus*
18. Seeds lacking endosperm; epicortical roots mostly lacking; inflorescence triadic or dyadic 19
19. Anthers needle-like, as thin as the filament, basifixed, with acicular tip; inflorescence dyadic; flowers mostly pendent; higher Andes . . . . . *Aetanthus*
19. Anthers not needle-like, thicker than the filament, mostly dorsifixed, lacking acicular tip (exception: *P. hamulifer* Kuijt); inflorescence triadic or dyadic, flowers pendent or not; lower and middle elevations, NW Mexico to Bolivia and Argentina . . . . . *Psittacanthus*
20. Inflorescence a raceme; cotyledons cryptocotylar, fused apically; leaves with apical sclerotic nail only in *T. chodatianus* (Patsch.) Kuijt . . . . . *Tristerix*
20. Inflorescence lacking, flowers individually attached, axillary in position, pedicellate; cotyledons distinct, eventually spreading; leaves with apical sclerotic nail except in *L. teretiflora* Kuijt . . . . . *Ligaria*
21. Plants with decussate phyllotaxy throughout 23
21. Adult plants with alternate phyllotaxy 22
22. Leaves of adult plants squamate and/or peltate; juvenile plants with decussate phyllotaxy; epicortical roots lacking; usually on *Myrtaceae* . . . . . *Eubrachion*
22. Plants with expanded foliage, leaves mostly petiolate; both juvenile and adult plants with alternate phyllotaxy; epicortical roots present at least in some species; hosts various . . . . . *Antidaphne*
23. Male flowers pedicellate, the inflorescence a raceme; stamens free, filaments present although short; fruit short-pedicellate; Central Andean Peru and Chile S of 35°S . . . . . *Lepidoceras*
23. Male flowers sessile, rarely in 1-flowered units, not in a raceme; anther sessile on perianth member; fruit mostly sessile; N of 35°S 24
24. Plants squamate, dioecious; flowers 1 per axil, sometimes whorled, not sunken in the stem; fruits explosive (exception: *A. verticilliflorum* Engelm.); female flower with 2 minute perianth members; on *Pinaceae* only, Canada to Mesoamerica, including Hispaniola . . . . . *Arceuthobium*
24. Plants squamate or foliaceous, dioecious or monoecious; inflorescence squamate, spike-like, flowers partly sunken in its axis, 1–many above each axil, in various serial patterns; fruits not explosive; female flowers with 3–4 perianth members; USA to Bolivia and Paraguay-Uruguay, including the Caribbean 25
25. Anthers unilocular; flowers uni-, (bi-) or triseriate, sometimes with 1 flower per bract; Veracruz to Brazil and Bolivia . . . . . *Dendrophthora*
25. Anthers bilocular; flowers bi- or triseriate (sometimes uniseriate, or with 1 flower above each bract); USA to Bolivia and Argentina . . . . . *Phoradendron*

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