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Biogeography, taxonomy and evolution in the Pacific genus *Coprosma* (Rubiaceae)

MICHAEL J. HEADS

ABSTRACT

HEADS, M. J. (1996). Biogeography, taxonomy and evolution in the Pacific genus *Coprosma* (Rubiaceae). *Candollea* 51: 381-405. In English, English and French abstracts.

This article reviews the widespread Pacific genus *Coprosma* and its sections. J. D. Hooker classified the New Zealand species in two main groups with female flowers clustered or solitary and this division is shown here to be applicable to the genus as a whole. The two groups have a geographic basis with the large-leaved, cluster-flowered subgenus *Lucidae* in the central and east Pacific and the small-leaved, solitary-flowered subgenus *Coprosma* mainly in the west Pacific. The groups overlap significantly only in New Zealand and Hawaii and these two regions are also the main centres of species diversity. New Caledonia is well-known as a centre of endemism for many taxa, and is situated within the range of *Coprosma*. Nevertheless, *Coprosma* is apparently absent there although it may be represented by the related genus *Normandia*. The major vicariance in *Coprosma* thus lies along a boundary: New Zealand – New Caledonia (*Normandia*) – Hawaii. *Nertera* and *Leptostigma* were both formerly treated as genera but are accepted here as sections within subgen. *Coprosma*. Sect. *Nertera* is widespread from southern China to South America and sect. *Leptostigma* has the well-documented South Pacific disjunct distribution: Australia – New Zealand – South America. The following disjunctions in the range of *Coprosma* were probably caused by the break-up of Gondwanaland: 1. Trans-Indian Ocean affinities between *Coprosma* (most diverse around the Tasman Sea) and *Anthospermum* (most diverse in South Africa). 2. Trans-Tasman Sea affinities in eight of the nine sections of subgen. *Coprosma*. 3. Trans-South Pacific Ocean affinities (Australasia – South America) in sect. *Leptostigma*.

RÉSUMÉ

HEADS, M. J. (1996). Biogéographie, taxonomie et évolution du genre *Coprosma* (Rubiaceae) dans le Pacifique. *Candollea* 51: 381-405. En anglais, résumés anglais et français.

Le genre *Coprosma* et ses sections sont passés en revue. J. D. Hooker a classé les espèces de Nouvelle-Zélande en deux groupes principaux sur la base des fleurs femelles fasciculées ou solitaires. On démontre que cette division peut être appliquée à tout le genre. Les deux groupes correspondent à une répartition géographique: le sous-genre *Lucidae* à grandes feuilles et fleurs fasciculées dans le centre et l'est du Pacifique et le sous-genre *Coprosma* à petites feuilles et fleurs solitaires principalement dans l'ouest du Pacifique. L'aire de répartition de ces deux sous-genres ne se recoupe de manière significative qu'en Nouvelle-Zélande et à Hawaii. Les deux régions sont aussi les principaux centres de diversité spécifique. La Nouvelle-Calédonie, bien connue comme centre d'endémismes pour de nombreux taxa, se trouve à l'intérieur de l'aire du sous-genre *Coprosma*. Pourtant ce sous-genre en est absent, quand bien même on y trouve le genre *Normandia* proche de celui-ci. En conséquence, la vicariance principale se fait le long de l'axe Nouvelle-Zélande – Nouvelle-Calédonie (*Normandia*) – Hawaii. *Nertera* et *Leptostigma*, tous deux considérés auparavant comme genres, sont considérés ici comme sections à l'intérieur du sous-genre *Coprosma*. La section *Nertera* est distribuée du sud de la Chine à l'Amérique du Sud tandis que la section *Leptostigma* présente une distribution disjuncte bien connue dans le Pacifique Sud: Australie – Nouvelle-Zélande – Amérique du Sud. Dans le sous-genre *Coprosma*, les aires disjunctes suivantes ont probablement été causées par la fragmentation du Gondwana: 1. Affinités trans-Océan Indien entre *Coprosma* (plus diversifié autour de la mer de Tasmanie) et *Anthospermum* (plus diversifié en Afrique du Sud).

2. Affinités trans-Mer de Tasmanie de huit des neuf sections de *Coprosma*. 3. Affinités trans-Océan Pacifique Sud (Asie australe – Amérique du Sud) dans la sect. *Leptostigma*.

KEY-WORDS: *Coprosma* – RUBIACEAE – Taxonomy – Pacific biogeography – Vicariance.

Introduction

The *Rubiaceae* are well-known as one of the most diverse plant families in the tropics. The family is also very important in New Zealand where the genus *Coprosma* has its centre of diversity and is widespread throughout the country. After *Veronica* (*Scrophulariaceae*) CHEESEMAN (1887) regarded *Coprosma* as “the most puzzling” genus in the New Zealand flora and noted that while the flower structure is uniform, vegetative characters are highly variable.

Some species of *Coprosma* form dense mats and cushions in bogs or on exposed rocks and have a small-leaved, ericoid habit. Other species are erect shrubs or small trees. The members of the genus occupy a wide range of open and forest environments.

Coprosma belongs to the tribe *Anthospermeae*, a group of special interest through its Gondwanic distribution: Africa – Australasia/Pacific. This pattern is presumably older than the break-up of Gondwanaland, i.e. at least mid-Mesozoic in age, which contradicts theories on the supposedly modern origin of the family. The distinctive unisexual, wind-pollinated flowers of the tribe are often assumed to be “derived” within an already “advanced” family but may instead be primitive and inherited directly from gymnosperms. Many tribes and genera of *Rubiaceae* are strangely absent in New Zealand despite suitable habitats and perhaps they are represented there, both biogeographically and phylogenetically, by *Anthospermeae*.

Coprosma is a classic example of a “Pacific” group and has been mapped by SKOTTSBERG (1940), CROIZAT (1952) and VAN BALGOOY (1966a, b). There is no known species in New Caledonia which is, as Van Balgooy observed, “most remarkable”.

Taxonomic history

In the original description of *Coprosma* FORSTER & FORSTER (1776) included two species, *C. lucida* and *C. foetidissima*. ALLAN (1961) took *C. lucida* to be the type of the genus and based his extensive nomenclature on that decision. Unfortunately, according to the rules of the latest Code of Nomenclature, *C. foetidissima* must be accepted as the lectotype of the genus (cf. DARWIN, 1979; VAN ROYEN, 1983; WEBB, 1996).

Working up *Coprosma* for his New Zealand flora cost HOOKER (1864) “several weeks’ assiduous study”. He recognised “two chief groups” in the genus which were based on whether the female flowers are clustered or solitary. Later CHEESEMAN (1887) accepted these two groups in his classification of the New Zealand species.

OLIVER (1935) produced the only full revision of the genus. He treated the species under seven sections, although he also noted the “considerable gap” between Hooker’s two groups.

In the current flora of New Zealand ALLAN (1961) has revised the New Zealand species and described and typified subgenera (which are more or less equivalent to Oliver’s unnamed “sections”) and sections (which are similar to Oliver’s “groups”). Allan’s classification lumps several of Oliver’s very small groups with other sections.

The diverse New Zealand species have been well illustrated by TAYLOR (1961), POOLE & ADAMS (1970), MOORE & IRWIN (1978) and EAGLE (1982) who also give notes on species taxonomy.

In this paper Hooker's two groups are accepted as representing the major division in the genus as a whole, and are shown to have a specific biogeographic pattern. They are treated here as subgenera *Coprosma* and *Lucidae*. The sections given in this paper for subgen. *Coprosma* are broader than those of Allan.

Material and methods

Field observations of *Coprosma* were made in New Zealand, Papua New Guinea and Fiji during a period 1978-90. Many New Zealand species were grown on at the Botany Department of the University of Otago. The collections in New Zealand herbaria (AK, WELT, CHR, OTA) were examined and a review of the extensive literature was made. Specimens and information have also been supplied personally by individuals listed below in the "Acknowledgments".

Morphological notes

Inflorescence and shoot architecture

Species of subgen. *Lucidae* have orthotropic shoots with large leaves and many-flowered axillary cymes with small bracts. Members of subgen. *Coprosma* have branches with at least one portion plagiotropic, smaller leaves and solitary female flowers. In this subgenus, sects. *Moorei*, *Nertera*, *Leptostigma* and *Pumilae* comprise smaller, prostrate mat or cushion plants. The remaining five sections of subgen. *Coprosma* are all "divaricating shrubs" but are very diverse in architecture and vegetative morphology. Some are "miniature trees" with a single trunk like many *Rubiaceae*, others are prostrate. Leaves are all very small but differ widely in shape. In this subgenus there are varying degrees of reduction of the floriferous leafy shoot/peduncle. Flowers may be terminal on leafy branches (*C. talbrockiei*; *C. atropurpurea*, *C. pumila*; *C. petriei*, *C. linarii-folia*; *C. microcarpa*; *C. foetidissima*, *C. colensoi*), or terminal on reduced, lateral branchlets, with only 2-4 leaves (*C. cheesemani*, *C. depressa*, *C. ciliata*, *C. parviflora*; *C. propinqua*; *C. cuneata*; *C. rigida*) or on minute, leafless arrested branchlets (*C. areolata*, *C. crassifolia*, *C. virescens*, *C. wallii*, *C. rubra*, *C. obconica*; *C. intertexta* and *C. rugosa*). The last stage, seen only in two sections, is virtually equivalent to a peduncle/pedicel.

The inflorescence of the small-leaved, divaricate shrub species is usually interpreted as a cyme which has had all the branching suppressed, resulting in a few-flowered fascicle without a peduncle or a solitary flower. Alternatively, the shoot axes themselves may be equivalent to largely sterilised inflorescences, with only a few "solitary" flowers remaining. Evidence in favour of the latter view comes from the architecture of the divaricate shrubs which is basically "cymose" through the apical abortion of vegetative modules. In these plants small, bract-like leaves are borne in brachyblasts which may be equivalent to smaller units of suppressed inflorescence. Similarly, the vegetative modules of the divaricate shrub species are at least partly plagiotropic or deflexed and may be compared with the deflexed peduncles of *C. colensoi*. The ericoid "whipcord" hebes (*Leonohebe* – *Scrophulariaceae*) may also comprise largely sterilised inflorescences of plants which may have had a basal, large-leaved portion in their architecture (HEADS, 1994a).

Flower and fruit

The number of radial parts in flowers of *Coprosma* often varies from the common *Rubiaceae* pattern of ovaries with two locules and perianth whorls with five parts. *C. talbrockiei* can have 2-5 stigmas and in cultivated plants there are "many irregularities in numbers of flower parts" (MOORE & MASON, 1974). *C. perpusilla* regularly has 4 or 5 stigmas and pyrenes (ORCHARD, 1986; WILD & ZOTOV as cited in PUFF, 1982). CHEESEMAN (1887) described the ovary in *Coprosma* as frequently 3- or 4- and more rarely 6-celled. In *C. foetidissima* the male flowers have corollas with any number between 4 and 10 lobes (pers. obs.). FLORENCE (1986) recorded multiplication (and fusion) of flower parts, especially stamens, in Hawaiian species and in *C. cookei* (Rapa) which has "reduplicated flower parts" (FOSBERG, 1968). At the other extreme, female flowers of *C. crassifolia* occasionally have only one stigma (pers. obs.), which is the usual case in the related genus *Duringtonia*, discussed below. The larger "flowers" of *Coprosma* with greater numbers of parts may be equivalent to peloric fusions of simpler "flowers", a process seen clearly in some New Zealand populations of *Mazus* (HEADS, 1994d). Rather than being the result of chance evolution or selection pressure which are explanations frequently given for such anomalous, southern forms, the very distinctive flower of *Anthospermeae* may represent an unsettled, "primitive" level of floral morphology.

The usual view of the *Anthospermeae* flower is that the morphology reflects the only "adaptation to anemophily" in the zoophilous *Rubiaceae*. The *Anthospermeae* have "switched" to anemophily and are "highly derived".

This view, which assumes "common is primitive", fails to account for several facts:

- * The many Gondwanic disjunctions which place the group's origin firmly in the Mesozoic. This is not to be expected of a highly derived group.
- * The many New Zealand distributions which likewise indicate an early age of the *Anthospermeae*.
- * The extreme variability in shoot architecture in the group (ericoid and divaricate shrubs, minute herbs, trees).
- * Complex parallel patterns of biogeography and morphology in Pacific *Coprosma*, *Hebe* and *Dracophyllum* (see "Biogeography and Evolution" below), although the latter two are entomophilous.
- * The long, forked, hairy stigmas of *Anthospermeae* are its defining character but appear to resemble those of certain tribes of Compositae more than anything in *Rubiaceae*.
- * The minute size, simple, unisexual and variable construction of *Anthospermeae* flowers compared with those of other *Rubiaceae* such as *Gardenieae*.

In addition, why should it not be "adaptive" to evolve anemophily on either side of the tropical Atlantic? Isn't this region windy enough?

Because of these objections it may be asked whether "adaptation to anemophily" really explains the many peculiarities of the *Anthospermeae*.

Synopsis**COPROSMA** J. R. & G. Forst. 1776

Flowers of *Anthospermeae*. Distinguished from the African *Anthospermeae* by the fleshy fruit, from the Australian *Anthospermeae* by the lack of inflorescence opercula, from *Normandia* by the simple pyrenes and from *Duringtonia* by the biloculate gynoeceum. 128 species.

I. Subgen. **COPROSMA**

Prostrate shrubs, mats or cushions, or erect shrubs, sometimes with a single trunk, at least part of each axis plagiotropic. Leaves small, one dimension < 1 cm, female flowers borne singly. 75 species.

A. Plants prostrate, stems herbaceous or only lightly woody and rooting. 27 species.

1. Sect. *Nertera* 13 species. Southern China and Malesia, through the Pacific to South and central America and Tristan da Cunha. One very widespread species.
2. Sect. *Leptostigma* 6 species. New Zealand, Australia, South America.
3. Sect. *Moorei* 4 species. New Zealand, Australia, New Guinea, Hawaii.
4. Sect. *Pumilae* 4 species. New Zealand, Australia.

B. More or less erect shrubs, stems at least partly orthotropic, woody, slender, tough, often with wide angle branching, stem apices often aborting, leaves borne on brachyblasts (“divaricating shrubs”). 48 species.

5. Sect. *Acerosae* 7 species. New Zealand, Australia.
6. Sect. *Parviflorae* 8 species. New Zealand, ?Australia.
7. Sect. *Coprosma* 4 species. New Zealand.
8. Sect. *Microcoprosma* 14 species. New Zealand, Australia.
9. Group “*Malesia*” 15 species. Malesia, Australia, Lord Howe Island.

II. Subgen. **LUCIDAE**

Erect shrubs or small trees with orthotropic axes, open branching, leaves large one dimension > 1 cm, leaves larger than 15 × 8 cm in a few species, female flowers clustered on axillary peduncles. 53 species

10. Sect. *Australes* 6 species. Northern New Zealand.
11. Sect. *Lucidae* 2 species. Northern New Zealand.
12. Sect. *Petiolatae* 7 species. Northern New Zealand, Chatham Is., Kermadec Is., Norfolk I., Lord Howe I.
13. Group “*Putidae*” 3 species. Samoa, Lord Howe I.
14. Group “*Pyrifoliae*” 11 species. Eastern Polynesia.
15. Group “*Persicaefoliae*” 3 species. Western Polynesia.
16. Group “*Hawaii*” 21 species. Hawaii, Marquesas, New Zealand.

There is one undescribed species in sect. *Acerosae*, one in sect. *Coprosma*, and two or three in sect. *Parviflorae*.

Systematic treatment

The emphasis in this paper is on biogeography, but some taxonomic changes appear unavoidable. Hooker and Allan’s subgenera *Lucidae* and *Coprosma* are modified here and extended to the genus as a whole. In the sectional taxonomy, *Leptostigma* Arnott and *Nertera* Banks & Sol. are reduced to sections (discussion below), but for the most part Allan’s sections and Oliver’s

“groups” are accepted (the latter as informally named groups). Some minor taxonomic changes are made – one new section, *Moorei*, is named and in subgen. *Coprosma* several of Allan’s oligospecific New Zealand sections are lumped in larger groups. Brief descriptions are given for these modified groups. The Hawaii and New Guinea groups are each treated informally. These require further taxonomic study.

C O P R O S M A J. R. & G. Forst.

I. Subgen. **COPROSMA** (= subgen. *Microcoprosma* Allan, nom. superfl.)

1. Sect. *Nertera* (Banks & Sol. ex Gaertn.) Heads, **stat. nov.**

≡ *Nertera* Banks & Sol. ex Gaertn., Fruct. Semin. Pl. 1: 124, Pl. 26. 1788.

= *Gomozia* Mutis ex L. f., nom. rej.

Stems prostrate, herbaceous, without leaf-scars, leaves usually spatulate, never coriaceous, flowers solitary, bisexual, pyrenes without evident valves. *Nertera depressa* Banks & Sol. ex Gaertn. is the only species treated by Gaertner under *Nertera* and is thus the type.

Nertera has usually been treated as a genus but differs no more from typical *Coprosma* than do other sections of the genus, such as sect. *Acerosae*. In addition, there is no sharp break between *Coprosma* and *Nertera*, as the two merge through species of sect. *Moorei*. Finally, within the *Anthospermeae* as successfully redefined by PUFF (1982) all the genera except *Nertera* are clearly distinct. Notes on *Nertera* are given here to support these conclusions.

Habit

HOOKER (1864, 1873) wrote that *Nertera* “scarcely differs from *Coprosma*, except in the herbaceous habit”. Even this habit difference is not absolute, as the hollow canes of the woodier members of *Nertera* from Tristan da Cunha recall the weaker stems of *C. quadrifida* and New Guinea species, and *C. talbrockiei* is herbaceous. The spatulate leaves of *Nertera* are characteristic of *Coprosma* sect. *Microcoprosma*.

Flowers

Flowers in *Nertera* are bisexual. In *Coprosma sensu stricto* flowers are usually unisexual and dioecious but *C. talbrockiei* and *C. moorei* have bisexual flowers and occasional bisexual flowers are recorded in *C. oliveri*, *C. foetidissima*, *C. perpusilla*, *C. pumila*, *C. niphophila*, *C. lucida* and *C. robusta* (CHEESEMAN, 1887; SKOTTSBERG, 1922; MOORE & MASON, 1974; ORCHARD, 1986). Occasional female inflorescences have been recorded on otherwise male plants in *C. cookei* (FOSBERG, 1937) and *C. grandifolia* (pers. obs.). BREMER & STRUWE (1992) linked *Nertera* and *Coprosma* as a monophyletic pair based on “plants unisexual”, although this is incorrect for *Nertera* and some *Coprosma*.

BREMER & STRUWE (1992) distinguished *Nertera* from *Coprosma* on the basis of woody vs. herbaceous habit, and stamens inserted “at least one-fifth down from the mouth of the corolla” in *Nertera* but “at the base of the corolla” in *Coprosma*. In fact both genera have the stamens inserted at the base of the corolla tube as in other *Anthospermeae* (HOOKER, 1873; OLIVER, 1935; FOSBERG, 1982; PUFF, 1982; BACKER & BAKHUIZEN VAN DEN BRINK, 1965).

Fruit

BENTHAM (1866) observed what is perhaps the main difference between *Coprosma* and *Nertera*, which is that the pyrenes of *Coprosma* are “usually furrowed on the inner face”, while pyrenes of *Nertera* are “quite smooth”. MOORE & IRWIN (1978) clearly illustrated the “furrows” (abscission zones/lid) in *C. crassifolia* and showed the mode of valve dehiscence at germination. These authors also illustrated *Nertera* pyrenes without furrows. However, there seems to be a rather smooth transition in this character between subgen. *Coprosma* and *Nertera*. Pyrene valves in *Coprosma* vary considerably in size, shape, colour and degree of development. For example, valves of *C. rubra* are clearly visible with the naked eye, as they are green and the rest of the pyrene is white while in pyrenes of *C. atropurpurea* valve differentiation is virtually invisible under a dissecting microscope. Valves of *C. pumila* and *C. petriei* are also barely differentiated and it seems that the disappearance of the abscission zone may simply be a function of small size fruit.

One reviewer of this paper noted that in drupaceous Rubiaceae pyrenes always show some kind of lid or at least a distinct area of thinning in the endocarp, as germination would otherwise be impossible. Although *Nertera* pyrenes show no apparent differentiation in the endocarp, there is no record of what happens at germination and there may prove to be a lid. This would again lower the distinction between *Nertera* and the rest of *Coprosma*.

The hairy fruits of some members of *Nertera* and *Leptostigma* find a counterpart in the fruit wall epidermis of *C. talbrockiei* which bears scurfy scales unique in the genus.

PUFF & ROBBRECHT (1988) stated that the drupes, pyrenes and seeds are “exactly the same” in *Nertera* and *Coprosma* which, apart from the furrows in *Coprosma* pyrenes, is also my conclusion.

Pollen

SELLING (1947) pointed out the close similarities between the pollen of *Coprosma* and *Nertera*. Both have tricolporate pollen with relatively smooth surfaces. ROBBRECHT (1982) wrote that “The pollen of *Nertera arnottianum* [sect. *Leptostigma*] and *N. chinensis* [sect. *Nertera*] compares very well with that of *Coprosma*. *Nertera granadensis* has very peculiar non-aperturate grains (a condition rarely met with in the Rubiaceae) ... a third type of pollen was found in *N. nigricarpa*.” Pollen does not support a simple *Nertera/Coprosma* division at the generic level.

Chromosome number

Both *Coprosma* and *Nertera* have a chromosome base number of $2n = 44$, while the remaining *Anthospermeae* have $2n = 22$ (PUFF, 1986).

Insect-plant relations

Host-parasite relations in *Coprosma* may be of considerable phylogenetic interest. For example, DUGDALE (1975) found that three well-defined groups of geometrid species (*Lepidoptera*) are restricted to *Coprosma* and that these have their own species of tachinid parasites. On Auckland Is. the weevil *Notinus cordipennis* mines only *Coprosma* and *Nertera*, and in the Catlins region the widespread moth *Leucotenes coprosmae* likewise feeds only on *Coprosma* and *Nertera* (Mr B. Patrick, pers. comm., 1992).

Linking species

The herbaceous *C. talbrockiei* with bisexual flowers should technically have been included in *Nertera*, but MOORE & MASON (1974) chose instead to place it in *Coprosma*, close to *C. moorei* which also has bisexual flowers. MOORE & MASON (1974) concluded significantly that "No single character, or convenient combination of characters, has been found to clearly separate *Coprosma*, composed of nearly 100 very diverse species, from *Nertera*, to which are attributed some 12 much more uniform ones". According to these authors the group treated here as sect. *Moorei* occupies "a somewhat intermediate position between the 2 genera". Thus, lumping *Coprosma* and *Nertera* has been hinted at by authors such as Hooker and Moore & Mason for over a hundred years. In fact the formal transfer of *Nertera* to *Coprosma* was made by MUELLER (1875), who noted only, and a little inaccurately, that this was "recommended" by Joseph Hooker as quoted above

Information on type specimens of *Nertera* and *Leptostigma* is given by ALLAN (1961) and FOSBERG (1982).

Coprosma nertera F. Mueller, Fragm. Phytogr. Austr. 9: 186. 1875.

≡ *Nertera depressa* Banks & Sol. ex Gaertn., Fruct. Semin. Pl. 1: 124, pl. 26, 1788 [non *Coprosma depressa* Col. ex Hook. f. 1853].

Auckland, Campbell and Chatham Is., New Zealand, Tasmania, Australia, Hawaii, Juan Fernandez, Mexico to Fuegia, Falkland Is., Tristan da Cunha (SKOTTSBERG, 1915).

There are several unnamed varieties in the species in New Zealand (ALLAN, 1961), one at least (Allan's "Group B": Fiordland – Bluff) with a standard distribution. Allan mentioned that some New Zealand forms of this species closely resemble Mexican and Guatemalan specimens of *N. granadense*.

***Coprosma nertera* var. *papuana* (Valeton) Heads, comb. nova**

≡ *Nertera depressa* var. *papuana* Valeton, Bot. Jahrb. Syst. 61: 156. 1927. New Guinea.

***Coprosma granadensis* (L. f.) Heads, comb. nova**

≡ *Gomozia granadensis* Mutis ex L. f., Suppl. Pl.: 129. 1781.

≡ *Nertera granadensis* (L. f.) Druce, 1917. South America.

I have not seen material of *Nertera repens* Ruiz & Pavon, but it may well belong here. If it does not, a new name is required for it as the combination *C. repens* Rich. has already been made. *N. granadensis* is taken in a wide sense by VAN ROYEN (1983) to include *N. depressa* and *N. nigricarpa*.

***Coprosma balfouriana* (Cockayne) Heads, comb. nova**

≡ *Nertera balfouriana* Cockayne, Trans. & Proc. New Zealand Inst. 44: 50. 1911. New Zealand.

***Coprosma philipsonii* Heads, nom. nov.**

≡ *Nertera cunninghamii* Hook. f., Fl. New Zealand 1: 112. 1853. New Zealand [non *Coprosma cunninghamii* Hook. f.].

The new name honours the distinguished botanist Professor W. R. Philipson.

Coprosma dichondrifolia (A. Cunn.) Heads, **comb. nova**

- ≡ *Geophila dichondrifolia* A. Cunn., Ann. Nat. Hist. 2: 208. 1839.
- ≡ *Nertera dichondrifolia* (A. Cunn.) Hook. f. 1853. New Zealand.

Coprosma villosa (B. H. Macmill. & R. Mason) Heads, **comb. nova**

- ≡ *Nertera villosa* B. H. Macmill. & R. Mason, New Zealand J. Bot. 33: 435. 1995. New Zealand.

Coprosma patrickii Heads, **nom. nov.**

- ≡ *Nertera ciliata* Kirk, Students' Flora New Zealand: 247. 1899. New Zealand [non *Coprosma ciliata* Hook. f.]

The new name honours Mr B. Patrick, New Zealand entomologist.

Coprosma scapanioides (Lange) Heads, **comb. nova**

- ≡ *Nertera scapanioides* Lange, Ind. Sem. Hort. Haun. 1868: 22. 1868. New Zealand.

Coprosma dentata (Elmer) Heads, **comb. nova**

- ≡ *Nertera dentata* Elmer, Leaflet Philipp. Bot. 1: 15. 1906. Philippines.

Coprosma nigricarpa (Hayata) Heads, **comb. nova**

- ≡ *Nertera nigricarpa* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 25(19): 115. 1908. Taiwan.

Coprosma taiwaniana (Masamune) Heads, **comb. nova**

- ≡ *Nertera taiwaniana* Masamune, Trans. Nat. Hist. Soc. Taiwan 28: 144. 1938. Taiwan.

Coprosma sinensis (Hemsl.) Heads, **comb. nova**

- ≡ *Nertera sinensis* Hemsl., J. Linn. Soc., Bot. 23: 391, tab. 10. 1888. Southern China.

Coprosma holmboei (Christoph.) Heads, **comb. nova**

- ≡ *Nertera holmboei* Christoph., Results Norweg. Sci. Exped. Tristan da Cunha 1937-1938 11: 13. 1944. Tristan da Cunha.

2. Sect. **Leptostigma** (Arnott) Heads, **stat. nov.**

- ≡ *Leptostigma* Arnott, Hooker's J. Bot. 5: 270. 1841
(incl. *Corynula* Hook. f.).

Plants with the creeping, herbaceous habit of *Nertera*, but with calyx lobes well-developed and persistent, corolla long, tubular or tubular-funnelform, and fruits with thin mesocarp becoming dry.

Coprosma reptans (F. Muell.) F. Muell. Australia.

Coprosma setulosa (Hook. f.) F. Muell. New Zealand

Coprosma weberbaueri (Fosberg) Heads, **comb. nova**

- ≡ *Leptostigma weberbaueri* Fosberg, Acta Phytotax. Geobot. 33: 80. 1982. Peru.

Coprosma boliviana Heads, **nom. nov.**

- ≡ *Mitchella pilosa* Benth., Pl. Hartwegiana: 194. Sept. 1845. Ecuador, Bolivia [non *Coprosma pilosa* Endl.].

Coprosma longiflora (Standl.) Heads, **comb. nova**

- ≡ *Corynula longiflora* Standl., Field Mus. Publ. Bot. 7: 156. 1930.
 ≡ *Leptostigma longiflorum* (Standl.) Fosberg, Colombia.

Coprosma arnottiana (Walp.) Heads, **comb. nova**

- ≡ *Leptostigma arnottianum* Walp., Repert. Bot. Syst. 6: 26. 1846. Chile.

Leptostigma has been revised, as a genus, by FOSBERG (1982). Its biogeography (Fig. 1) is of special interest as it is an example of the trans-South Pacific disjunction generally accepted as Gondwanic. The group ranges in SE Australia (*C. reptans*, mountains of Victoria and New South Wales) – New Zealand (*C. setulosa*) – western South America (Valdivia, Chile, to Norte de Santander, Colombia; 4 species).

MUELLER (1875) and ALLAN (1961) recognised the close affinity between *N. setulosa* and *N. reptans*, and Allan suggested that they formed a subgenus of *Nertera*.

3. Sect. **Moorei** Heads, **sect. nova**

Plantae parvae repentesque, foliis acuminatis, stipulis non vaginantibus, denticula singulari minuta, articulis petiolorum vix evolutis.

Small, creeping mat plants, leaves acuminate, not spatulate, stipules non-sheathing, with a single, minute denticle and poorly developed leaf abscission zones.

Type species: *C. moorei* Rodway.

Coprosma moorei Rodway. Tasmania, Victoria.

Coprosma talbrockiei Moore & Mason. Nelson, New Zealand.

Coprosma archboldiana Merr. & Perry. New Guinea.

Coprosma ernodioides Gray. Hawaiian Is.: Maui and Hawaii.

C. moorei has stems usually embedded in sodden peat and ovate-acuminate leaves. *C. talbrockiei* is close to *C. moorei* and *C. ernodioides* of Hawaii also agrees with *C. moorei* through its acuminate leaves, the absence of floral bracts and a stipule with no sheath (in contrast with all the other Hawaiian species). *C. archboldiana* of New Guinea is related to *C. ernodioides* by MERRILL & PERRY (1945), but is probably also close to *C. talbrockiei*. The four species are geographical vicariants of each other along a west Pacific sector: New Zealand – Australia – New Guinea – Hawaii. The section shares acuminate or needle-tipped leaves with Malesian taxa and *C. hirtella*, and also resembles *C. atropurpurea* (sect. *Pumilae*).

4. Sect. *Pumilae* Allan

Four species of the southern Tasman Sea region:

Coprosma pumila Hook. f.

Coprosma atropurpurea (Ckne. & Allan) Moore.

Coprosma perpusilla Col.

Coprosma niphophila Orchard.

ORCHARD (1986) revised the *C. pumila* complex and provided excellent illustrations and maps. He noted the following trans-Tasman Sea vicarious pair: *C. pumila* (Tasmania) – *C. atropurpurea* (New Zealand). In addition, the remaining two species are both found on either side of the Tasman Sea. *C. perpusilla* is recorded with subsp. *perpusilla* in Tasmania, Victoria and New South Wales of Australia, and also Stewart, South and North Is. of New Zealand. The other subspecies, *antarctica*, is the southernmost *Anthospermeae*, being present at Macquarie I. (where it is the only woody plant) and Auckland, Campbell and Antipodes Is. *C. niphophila* occurs in Australia in the Kosciusko region, and is also in the southern South Island of New Zealand from upper Cascade R. to Craigieburn.

5. Sect. *Acerosae* Allan

(incl. sect. *Linariifoliae* Allan and sect. *Antipodae* Allan)

Prostrate or erect shrubs or trees, with linear leaves often bearing hairs in small clusters, decurrent leaf-bases and blue fruit with no red coloration. 6 New Zealand species and 1 in Australia.

Coprosma acerosa A. Cunn.

Coprosma rugosa Cheesem.

Coprosma intertexta Simpson & Thomson

Coprosma petriei Cheesem.

Coprosma nivalis Oliver. Victoria, New South Wales.

Coprosma propinqua A. Cunn.

Coprosma linariifolia Hook. f.

The group is not easily related to any other in the genus. It includes the trans-Tasman vicarious pair, *C. nivalis* – *C. petriei* (ORCHARD, 1986).

LEE & al. (1988) correlated fruit colour of *Coprosma* species with aspects of their ecology. They noted that a difficulty associated with this sort of study is “the question of species’ phylogenetic independence”. In other words, they suggest that phylogenetic history may be more important than adaptation in determining structure which seems very likely. Lee & al. wrote that “there is no recent sub-generic classification available for *Coprosma*, nor suggested phylogeny that would enable us to evaluate this question”, although ALLAN’s (1961) sect. *Acerosae* is a fairly clear hint that the distinctive sky-blue fruits of the section have phylogenetic significance.

6. Sect. *Parviflorae* Allan (incl. sect. *Pseudocuneatae* Allan)

Leaves elliptic-obovate. 6 New Zealand species, 2 Australian:

Coprosma cheesemanii Oliver

Coprosma ciliata Hook. f.

Coprosma parviflora Hook. f.

Coprosma microcarpa Hook. f.

Coprosma pseudocuneata Oliver

Coprosma depressa Col.

Coprosma nitida Hook. f. Australia.

Coprosma tadgellii Oliver. Victoria.

C. nitida has the habit of *C. pseudocuneata*, with coriaceous leaves with needle-tips and spine-tipped shoots. Leaf margins are more or less recurved, and larger leaves have needle-tips like those of the New Guinea species and *C. talbrockiei*. *C. divergens* may have its closest ally in *C. cheesemanii* (OLIVER, 1942), but is treated below with other Malesian plants. *C. tadgellii* is possibly a hybrid of *C. nivalis* and *C. nitida* (ORCHARD, 1986).

Species delimitation in sect. *Parviflorae* is often difficult. Chromosome counts have helped but chromosome races should probably not be recognised at species level if other morphological differences are negligible. The *C. parviflora* / *C. cheesemanii* complex is a difficult group in which the discovery of distinct, more or less intermediate populations has broken down the boundary between the two species. Four of the entities involved, with their chromosome numbers (BEUZENBERG, 1983), are:

1. *C. cheesemanii* $2n = 88$
2. *C. sp. aff. cheesemanii* (Oliver's wide-leaved form of central North I.) $2n = 132$
3. *C. sp. aff. cheesemanii* (South I.) $2n = 132$
4. *C. parviflora* s.l. $2n = 132$.

The third form occurs in the Maungatua – Blue Mts. region of Otago province where it dominates shrublands. BEUZENBERG (1983) also reported counts of $2n = 132$ from Wairau Valley plants of *C. cheesemanii*, but the Otago plants appear to be unique in *C. cheesemanii* in having drupes which are deep pink, orange, yellow and white, as well as the blood red typical of the species. In their fruit colour, chromosome number and semi-erect habit many of these plants differ from *C. cheesemanii* and resemble *C. parviflora*. (The plant I sent samples from for the chromosome count was prostrate). The sector: Maungatua – Blue Mts. is also the site of complex “hybrid” assemblages in *Dracophyllum* – *Epacridaceae* (ALLAN, 1961), and further biogeographic and morphogenetic parallels between *Coprosma* and *Dracophyllum* are discussed below, under “Biogeography and evolution”.

7. Sect. *Coprosma*

= sect. *Cuneatae* Allan (incl. sect. *Foetidae* Allan)

Leaves obovate, cuneate, retuse. Flowers terminal on leafy branches. 4 New Zealand species:

Coprosma cuneata Hook. f.

Coprosma crenulata Oliver

Coprosma colensoi Hook. f.

Coprosma foetidissima J. R. & G. Forst.

8. Sect. *Microcoprosma* Allan (incl. sects. *Rigidae* Allan and *Spathulatae* Allan)

Stems often fluted, leaves spathulate with an orbiculate/rhomboid lamina and winged petiole, female flowers terminal on abbreviated, leafless shoots. New Zealand (13 species), Australia (1 species):

Coprosma rigida Cheesem.

Coprosma crassifolia Col.

Coprosma rubra Petrie

Coprosma virescens Petrie

Coprosma wallii Petrie

Coprosma obconica Kirk

Coprosma areolata Cheesem.

Coprosma tenuicaulis Hook. f.

Coprosma rotundifolia A. Cunn.

Coprosma rhamnoides A. Cunn.

Coprosma neglecta Cheesem.

Coprosma quadrifida (Labill.) Robinson

= *C. billardieri* Hook. f.

Coprosma arborea Kirk

Coprosma spathulata A. Cunn.

Female flowers are generally solitary in this group, but most of the species occasionally produce flowers in groups of up to three. However, these groups are only loosely clustered, and are borne on the stems rather than on a common, specialised peduncle as in subgen. *Lucidae*. The only Australian species, *C. quadrifida* (Tasmania, Victoria, New South Wales), has a leaf superficially like that of *C. propinqua* or *C. linariifolia*, but is allied here with *C. rhamnoides* following OLIVER (1935). In more highly branched specimens of *C. quadrifida* (e.g. Orchard 5339) all but the main branches end in spine tips, but some specimens show very little apical abortion. The narrow branches resemble hollow canes and recall New Guinea species, and leaves are more or less sessile and acuminate, again like those of New Guinea plants.

The large-leaved *C. arborea* and the small-leaved *C. spathulata* are a pair that deconstructs the *Coprosma/Lucidae* subgeneric boundary. The two species are accepted by all authors as each others' closest relatives. They share large, linear calyx lobes, better developed in male flowers of *C. arborea* than in any other species, and leaves with the peculiar orbiculate/spathulate lamina and winged petiole of sect. *Microcoprosma*. The two species are known only from the lowland forests of the northern North Island between North Cape and Lower Waikato/Mt. Pirongia. TAYLOR (1976) noted that this southern limit meets the northern limit of *C. foetidissima*. Despite the obvious similarities between the two northern species they have quite distinct morphologies. *C. arborea* has female flowers in clusters of 4-12, a lamina 5-6 cm long and a petiole 1 cm long, and is one of the largest species in *Coprosma* with a trunk 14 – 30 cm diameter. It is unique in the genus in having a small-leaved juvenile form unlike the adult in appearance (TAYLOR, 1976). *C. spathulata* is a smaller plant and has very small leaves, sometimes with a blade 5 mm long and a petiole 9 mm long, and female flowers generally solitary. CHEESEMAN (1925) acknowledged that the two species are closest relatives but split them apart, with *C. arborea* at the end

of subgen. *Lucidae* and *C. spathulata* at the beginning of subgen. *Coprosma*. Oliver and Allan have them both in subgen. *Coprosma*, emphasizing the characteristic leaves which relate them to *C. rhamnoides* and its allies.

Unlike other phylogenetic “linking groups” in New Zealand which are southern and western (such as *Leonohebe* sect. *Buxifoliatae* in the *Hebe* complex – HEADS, 1992), *C. arborea* and *C. spathulata* are northern and eastern.

9. Group “*Malesia*”

New Guinea (10 species), Java, Borneo, Sulawesi, Australia, Lord Howe I. (1 endemic species each):

Coprosma papuensis Oliver

Coprosma wollastonii Wernham

Coprosma lamiana Oliver

Coprosma brassii Merr. & Perry

Coprosma discoloris van Royen

Coprosma habbemensis Merr. & Perry

Coprosma novoguineensis Merr. & Perry

Coprosma divergens Oliver

Coprosma epiphytica van Royen

Coprosma scandens van Royen

Coprosma sundana Miquel. Java.

Coprosma celebica Valetton ex van Steenis. Sulawesi.

Coprosma crassicaulis Stapf. Borneo.

Coprosma hirtella Labill. Tasmania, Victoria, New South Wales.

Coprosma inopinata Hutton & Green. Lord Howe I.

VAN ROYEN (1983) described eleven species of New Guinea *Coprosma*, all recorded from the alpine zone. *C. archboldiana* (sect. *Moorei*, above) is a small creeping shrublet, often forming cushion-like mats. The other species are larger shrubs, sometimes epiphytic, or small trees. *C. scandens* has slender branchlets borne at right-angles. Most New Guinea species have more or less acuminate, needle-tipped leaves. Even *C. divergens*, the New Guinea species which is most like *C. cheesemanii*, has leaves occasionally acute (usually obtuse) and often with a very short, needle-like mucro. Flowers in this section are usually solitary and terminal on leafy shoots.

The recently described *C. inopinata* from Lord Howe I. (GREEN, 1993) is very distinct, especially through its persistent, decurrent leaf-bases, but seems to be best placed here. The relationships of this putative Malesian group with others have not been studied since OLIVER (1935). The Australian *C. hirtella* has spatulate leaves with recurved margins and a sometimes decurved needle-tip. It is tentatively related here with *C. papuensis* and *C. sundana*. There are possible affinities between Malesian species and New Zealand members of subgen. *Coprosma* such as *C. pseudocuneata* and *C. linariifolia*, and *C. divergens* was related by OLIVER (1942) to *C. cheesemanii* of New Zealand which seems very likely. VAN ROYEN (1983) described *C. divergens* as divaricate, although apex abortion in this species is limited (OLIVER's 1942 photograph shows apical abortion on one lateral shoot). Fascicle-type brachyblasts are not present. The needle-tip mucro of New Guinea species is represented in New Zealand species only in *C. obconica*. There are at least three ternate-leaved New Guinea species with weakly woody or hollow stems, so affinities are also possible with *C. talbrockiei* and Australian species.

II. Subgen. **LUCIDAE** C. J. Webb

FOSBERG (1943) has shown that *C. oceanica* Oliver of the Tuamotu Is., formerly treated in this group, is a *Hedyotis*.

10. Sect. **Australes** Allan

Northern New Zealand (6 species)

Coprosma tenuifolia Cheesem.

Coprosma acutifolia Hook. f.

Coprosma grandifolia Hook. f.

Coprosma waima Druce

Coprosma robusta Raoul

Coprosma macrocarpa Cheesem.

Near Castor Bay, Auckland, I observed (1980) occasional plants of *C. robusta*, *C. lucida* and *C. grandifolia* with ternate leaves, although all these species usually have decussate foliage. Variation in shoot symmetry is also seen in *Anthospermum ternata* where leaves in whorls of three or four can be found in one population (PUFF, 1986).

11. Sect. **Lucidae** Allan ex C. J. Webb

Northern New Zealand (2 species)

Coprosma lucida J. R. & G. Forst.

Coprosma dodonaeifolia Oliver

12. Sect. **Petiolatae** Allan

New Zealand, Chatham Is., Kermadec Is., (1 endemic species each), Lord Howe I., Norfolk I. (2 species each):

Coprosma repens Rich.

Coprosma chathamica Ckne.

Coprosma petiolata Hook. f.

Coprosma prisca Oliver

Coprosma baueri Endl.

Coprosma pilosa Endl.

Coprosma huttoniana Green

13. Group "**Putida**"

Coprosma savaiiensis Rech. Samoa.

Coprosma lanceolaris Mueller. Lord Howe I.

Coprosma putida C. Moore & Mueller. Lord Howe I.

14. Group "*Pyrifoliae*"

11 species of eastern Polynesia. There are three geographic subgroups:

– Society Is.:

Coprosma glabrata J. Moore

Coprosma raiateensis J. Moore

Coprosma setosa J. Moore

Coprosma taitensis Gray

Coprosma orohensis J. Moore

– Juan Fernandez:

Coprosma pyrifolia (Hook. & Arnott) Skottsberg.

Coprosma oliveri Fosberg

– Rarotonga – Rapa I. – Pitcairn I.:

Coprosma laevigata Cheesem.

Coprosma rapensis F. Brown

Coprosma cookei Fosberg

Coprosma benefica Oliver

The affinities of the Juan Fernandez species *C. oliveri* have caused discussion. SKOTTSBERG (1922) regarded it as closest to *C. foliosa* of Hawaii. OLIVER (1935) wrote that the leaves recall *C. sundana* (Java) or *C. nitida* (Australia), the female flowers resemble those of *C. lucida* (New Zealand) and the stipules are not unlike those of *C. longifolia* (Hawaii). FOSBERG (1968) wrote that it is "doubtless closest" to the other Juan Fernandez species, *C. pyrifolia*, and the two "may be closest" to *C. cookei* Fosberg of Rapa I. The species thus seems to recombine features of several sections of *Coprosma*.

15. Group "*Persicaefoliae*"

Three species of western Polynesia:

Coprosma persicaefolia Gray. Fiji: Viti Levu.

Coprosma strigulosa Lauterbach. Samoa: Savaii.

Coprosma novaehebridae Oliver. Vanuatu: Tanna.

16. Group "*Hawaii*"

– Hawaiian Islands (all islands) (17 species):

Coprosma elliptica Oliver

Coprosma skottsbergiana Oliver

Coprosma montana Hillebrand

Coprosma ochracea Oliver

Coprosma menziesii Gray

Coprosma cymosa Hillebrand

Coprosma fauriei L veill 
Coprosma waimeae Wawra
Coprosma stephanocarpa Hillebrand
Coprosma foliosa Gray
Coprosma rhynchocarpa Gray
Coprosma pubens Gray
Coprosma serrata St. John
Coprosma kauensis (Gray) Heller
Coprosma longifolia Gray
Coprosma molokaiensis St. John
Coprosma ternata Oliver
 – New Zealand:
Coprosma serrulata Hook. f. ex Buchanan
 – Marquesas Is.:
Coprosma nephelephila Florence
Coprosma reticulata Florence
Coprosma esulcata (F. Br.) Fosberg

OLIVER (1935) argued that the Hawaiian species, apart from *C. ernodioides* (sect. *Moorei*), show “an evident relationship” with each other. There do seem to be some common features (pale wrinkled bark, very large leaf-scars and leaf-buttresses, conspicuous primary leaf venation), but the group, if it is a natural group, is very close to other sections of subgen. *Lucidae*. *C. longifolia* of Hawaii has similar foliage to group “*Persicaefoliae*” (Fiji – Vanuatu). The foliage of *C. savaiiensis* (Samoa) and *C. taitensis* (Society Is.) also recalls Hawaiian species.

C. serrulata was given its own subgenus by ALLAN (1961). It shows similarities with *C. papuensis* but also with Hawaiian species such as *C. stephanocarpa* and *C. longifolia* with conspicuous, white stipule sheaths on inflated leaf buttresses. Also approaching *C. serrulata* in habit are specimens of *C. montana* from 3300m on Hawaii with short internodes and more or less spatulate leaves about 1 cm long with minor venation impressed above. *C. nephelephila* and *C. reticulata* from the northern Marquesas are allied by FLORENCE (1986) with each other and the other Marquesan species *C. esulcata* and also with the Hawaiian *C. molokaiensis*, *C. longifolia* and *C. ternata*. This connection between Marquesas and Hawaii is well-known in other plants and animals (HEADS, 1983).

Ecology

In New Zealand species of *Coprosma* are found in virtually all types of vegetation. CHEESEMAN (1887) treated the species under five ecological groups: 1. maritime species (examples occur in several sections); 2. lowland species with wide distribution and no marked preference for any particular soil or situation; 3. lowland species with local distribution; 4. lowland species preferring swampy forests or rich alluvial soils (for example the divaricate shrubs *C. propinqua*, *C. areolata*, *C. rigida* and *C. tenuicaulis*); 5. species of hilly, subalpine and alpine habitats. Eight *Coprosma* species and three *Nertera* species are recorded from the alpine zone of New Zealand by MARK & ADAMS (1973). Members of the genus thus occupy a wide range of open and forest environments, from well-drained habitats such as exposed rocks, cliffs, lava-flows, sand-dunes and dry shingle river beds through to bogs, rainforest, shrubland and grassland. Plants are occasionally epiphytic (*C. lucida*). The genus is often common in areas being

recolonised after disturbance such as road cuttings, landslides, burnt areas, flood plains, fire breaks and older *Pinus* plantations (TAYLOR, 1961). Habitats recorded by VAN ROYEN (1983) for *Coprosma* in New Guinea include: subalpine forest (some species epiphytic), forest edge, shrubland, heath, alpine grassland (often a pioneer after burning), on landslides, in man-made clearings, on open rock and in cracks on exposed rock faces, and on sandy edges of alpine rivulets. A pioneer, weedy tendency is evident here, as in New Zealand species.

Fossil record

FOSBERG (1968) reported that "*Coprosma* is said to have fossil representatives in Patagonia", but I have no more information on this. The earliest *Coprosma* pollen is recorded from Oligocene strata in New Zealand (FLEMING, 1979) and this gives a minimum age for the genus in the country. During the Pleistocene glaciations the New Zealand pollen record indicates that *Coprosma* shrublands were widespread there.

Related genera

Coprosma is closely related by all authors to the large African genus *Anthospermum*. However, through its fleshy fruit *Coprosma* is closer to two monospecific genera, *Durringtonia* and *Normandia*, and the three genera comprise subtribe *Coprosminae* (PUFF, 1982; 1986).

Durringtonia Henderson & Guymmer is a perennial, rhizomatous herb which ranges on the east coast and coastal islands of Australia (between 27°03'S and 32°25'S – 675 km), in the region of the Macpherson – Macleay Overlap (HEADS, 1994f). It is a remarkable but inconspicuous and rare plant found in swamps with permanent subsurface freshwater. At Moreton I., NE of Brisbane, it occurs behind the beach in brown or black peat-like material overlain by fine coastal sand. Like several species of *Coprosma* in New Zealand, *Durringtonia* associates with typical heath genera such as *Gleichenia*, *Empodisma*, *Gahnia*, *Baumea*, *Schoenus*, *Leptospermum* and *Drosera*. It would not be surprising if *Durringtonia* turned up in the swamps and heaths of New Zealand's west coast. The flowers of *Durringtonia* are unisexual. The males have filiform filaments inserted at the base of the corolla as is usually the case in *Anthospermeae*, while the bizarre female flowers mainly comprise a single stigma. The classification of *Durringtonia* has caused some debate. HENDERSON & GUYMER (1985) wrote that "Puff's grouping [of *Anthospermeae*] ... ignores many fundamental differences between the genera ... the inclusion of this genus with all its divergent attributes would make *Anthospermeae* even more variable than HOOKER (1873) conceived it and even more difficult to diagnose convincingly". Henderson & Guymmer name a new tribe *Durringtonieae* for the genus. This is certainly understandable as the female flower of *Durringtonia* is so striking. However, PUFF & ROBBRECHT (1988) did not accept the tribe *Durringtonieae*, claiming that *Durringtonia* should be placed in *Anthospermeae* subtribe *Coprosminae*, and I had reached a similar conclusion before seeing Puff & Robbrecht's paper. In fact, the only real character separating *Durringtonia* from *Coprosma* is the single carpel of *Durringtonia*. Pollen of *Durringtonia* "closely matches" that of the other *Coprosminae* (PUFF & ROBBRECHT, 1988).

PUFF & ROBBRECHT (1988) found that the fruits of *Durringtonia* "impressively resemble those of *Coprosma* and *Nertera*", apart from the totally suppressed second carpel. HENDERSON & GUYMER (1985) interpret the "lid" or "operculum" of the pyrene as the trace of the vestigial second carpel. This is an "apparent misinterpretation" according to Puff & Robbrecht, but it is possibly an important insight into the origin of these and similar "lids" in the "stones" of many families (CROIZAT, 1996). The abscission zone which gives rise to the articulation of the valve is presumably, like other abscission zones, a meristem. The *Coprosma* fruit has two or more pyrenes, each with a lid. These lids could be the trace of an earlier upper tier of carpels which has undergone virtually complete suppression and fusion with the lower tier. A

similar process of fusion and condensation can be seen in the flowers of the *Rubiaceae* tribe *Naucleaeae*. This is, admittedly, speculative but the origin of the lid must be explained somehow. Henderson & Guymer's suggestion at least marks a possible beginning. *Normandia* Hook. f. is a low, glabrous, virgate shrublet from the mountains of New Caledonia. BAILLON (1881) described the flowers as those of *Coprosma* and the genus as "better perhaps reduced to a section of *Coprosma*".

Normandia was also regarded by PUFF (1982) as "closely allied" to *Coprosma*. Nevertheless, the fruit is quite different, with a woody exocarp separating from a "stone" comprising endocarp plus seed. HOOKER (1873) was impressed by the plant and described it as "a remarkable genus", with the habit of *Psychotria*, the flowers of *Coprosma*, and the fruit of *Spermacoce*, thus recombining characters of three different tribes.

Biogeography and evolution

OLIVER (1935) argued that *Coprosma* "could not have originated before the connection between New Zealand and Australia was severed, otherwise there would have been a better representation of the genus in Australia". This line of reasoning has proved popular but makes several unwarranted assumptions. The genus is in fact well-represented in Australia by other *Anthospermeae*, namely the Australian subtribe *Operculariinae*. In addition, there is no reason to assume that the Gondwanic flora was ever homogeneous. Even before the break up of Gondwana there would certainly have already been regional differentiation with, for example, an Australian – South American block of flora and fauna (e.g. *Leptostigma*) and an Australasian – African block (e.g. the main diversity of *Anthospermeae*).

TAYLOR (1961) wrote that the small-leaved habit of *Coprosma* "could have been evoked in response to [Quaternary glacial conditions]", but this does not account for the New Zealand – Australia – Malesia – Hawaii distribution of the small-leaved subgenus. Taylor also suggested that there was a recent, post-glacial "burst of speciation" in New Zealand *Coprosma*. The apparently low degree of differentiation between many species and current hybridism between species is often taken as key evidence for this view. Nevertheless, it is generally admitted that the degree of differentiation between species is proportional neither to the time involved in speciation, nor to the time since speciation, and the degree of current hybridism in *Coprosma* and other New Zealand genera has certainly been exaggerated by many authors. The species or their direct ancestors may be much older than the Quaternary, which would make sense if the genus is Mesozoic.

PUFF (1986) has given a centre of origin/dispersal explanation for the distribution of the tribe *Anthospermeae*: Africa – SE Asia – Australasia – western South America. He wrote that "the (strictly SE Asiatic) stock of the *Coprosmineae* could only have reached Australia and New Caledonia ... by LDD [long distance dispersal] at an early stage. [Expansion to New Zealand] could be explained similarly ... *Coprosma* has an unusually high number of species in New Zealand; in my opinion this phenomenon should not be interpreted as an indication for an origin of the genus in that region. I rather believe that the high species concentration of the genus in that region may be attributed to a 'secondary' species explosion there – analogous to the situation of *Anthospermum* in the SW Cape and, to a lesser extent, in Madagascar. The 'final' expansion of *Coprosma* to its present day fragmented range can, again, only be explained by LDD". There are two main centres of diversity in the tribe *Anthospermeae*: the SW Cape, and the Tasman Sea region. Following Puff, it does seem highly likely that the main massing of *Anthospermum* in the SW Cape (and Madagascar) is somehow "analogous" to that of *Coprosma* around New Zealand. But invoking long distance dispersal from the north, followed by secondary "agglomerations" and "species explosions" in both southern regions seems unnecessary. The group (in its present and ancestral states) has probably always been diverse around the southern Indian Ocean/Tasman Sea and was rifted apart by the opening of the Indian Ocean. Long distance dispersal from the north does not explain the precise biogeographic connections, absences and disjunctions in the

Anthospermeae, or the similarities with other groups which have quite different means of dispersal, such as the dry-fruited *Hebe* complex (*Scrophulariaceae*) discussed below.

According to PUFF (1986), *Nertera* and *Leptostigma* are “possibly much younger” than *Coprosma* and *Normandia*, and “both eventually attained (most likely by LDD) a wide distribution range”. Nevertheless, the range of *Leptostigma* (Australasia – South America) is a classic Gondwanic disjunction.

PUFF (1986) admitted that at some stage “a common ancestral stock of the *Anthospermeae* must have experienced a “split” into three segments (i.e. those which gave rise to the genera of *Anthospermineae*, *Operculariinae* and *Coprosmineae*) at a relatively early stage”. This process, rather than any long distance dispersal, is accepted here, and would account for the tribe having representatives in Africa, Australia and the Pacific.

Disjunctions within this group of plants are of special interest. *Anthospermeae* as a whole has its main massings in South Africa and around the Tasman Sea in an Indian Ocean disjunction, *Leptostigma* shows a trans-South Pacific disjunction and eight of the nine sections of subgen. *Coprosma* show trans-Tasman Sea connections. These three disjunctions are all Gondwanic, but only in the sense that their ranges were disrupted by the rifting apart of Gondwana. At the time of rifting the different groups, or their immediate ancestors, *already* occupied different regions within Gondwana.

Within New Zealand, *Coprosma* has similar numbers of species in North and South Islands. Many species are shared by both islands, and there are roughly five endemics in each. Many, perhaps most, of the biogeographic centres active throughout New Zealand have been involved in the evolution of the group. For example, although *C. crassifolia* is abundant around Dunedin it ranges south only to the Southland Syncline (Hokonui Hills – *N. Miller* OTA 36835; Tahakopa – pers. obs.), like many other taxa (HEADS, 1989). Sect. *Coprosma* ranges between the subantarctic Auckland Is. and Te Moehau in the north, like *Kelleria* – *Thymelaeaceae* (HEADS, 1990). *C. grandifolia* ranges south to Taramakau R., following the pattern of *Nothofagus* (HEADS, 1989). These patterns have been correlated with Mesozoic tectonics (HEADS, 1989). New Zealand species of *Coprosma* such as *C. atropurpurea* and an unnamed species related to *C. parviflora* mapped and discussed by HEADS (1989) show a standard pattern of disjunction along the Alpine Fault. This disjunction is attributable to massive lateral movement on the fault during Tertiary time having pulled apart living communities, and occurs in very many groups. The pattern has been illustrated for *Hebe*, *Ourisia*, *Pimelea*, *Euphrasia*, *Leonohebe* and *Parahebe* by HEADS (1993, 1994b-f).

From the map (Fig. 1) it is clear that within *Coprosma*, subgen. *Coprosma* is mainly in the west, subgen. *Lucidae* mainly in the east. There are two species which are possibly “incongruent” with this pattern. *C. oliveri* from Juan Fernandez has solitary female flowers according to OLIVER (1935), but FOSBERG (1968) has shown axillary cymes on articulated peduncles. The Australian *C. hirtella* has female flowers not solitary, but in groups of three, but these groups are borne terminally on leafy shoots (BURBIDGE & GRAY, 1970) rather than on specialised axillary peduncles and the affinity with the Malesian species of subgen. *Coprosma* noted by Oliver is supported.

Thus the subgenera *Coprosma* and *Lucidae* split the Pacific into eastern and western divisions, with major overlap only at New Zealand and Hawaii. These two localities are also the centres of species diversity. *Normandia* in New Caledonia lies on the boundary of the split. The view is taken here that there has been east/west vicariance of an already widespread Pacific ancestor, rather than a direct development of one extant group from another. Similarly, the flavonoid data “do not support the view that the small-leaved species [subgen. *Coprosma*] have been derived from the large-leaved species [subgen. *Lucidae*] or vice versa” (WILSON, 1984).

Although the “means of dispersal” school has overlooked the fact, it is clear that the Pacific distribution pattern of *Coprosma* is a standard one, shared by many taxa with very different “means of dispersal” and ecology. For example, CROIZAT (1952: 101, Fig. 29) outlined the biogeography of the genus and compared the distribution with that of *Peperomia* spp., *Geniostoma*,

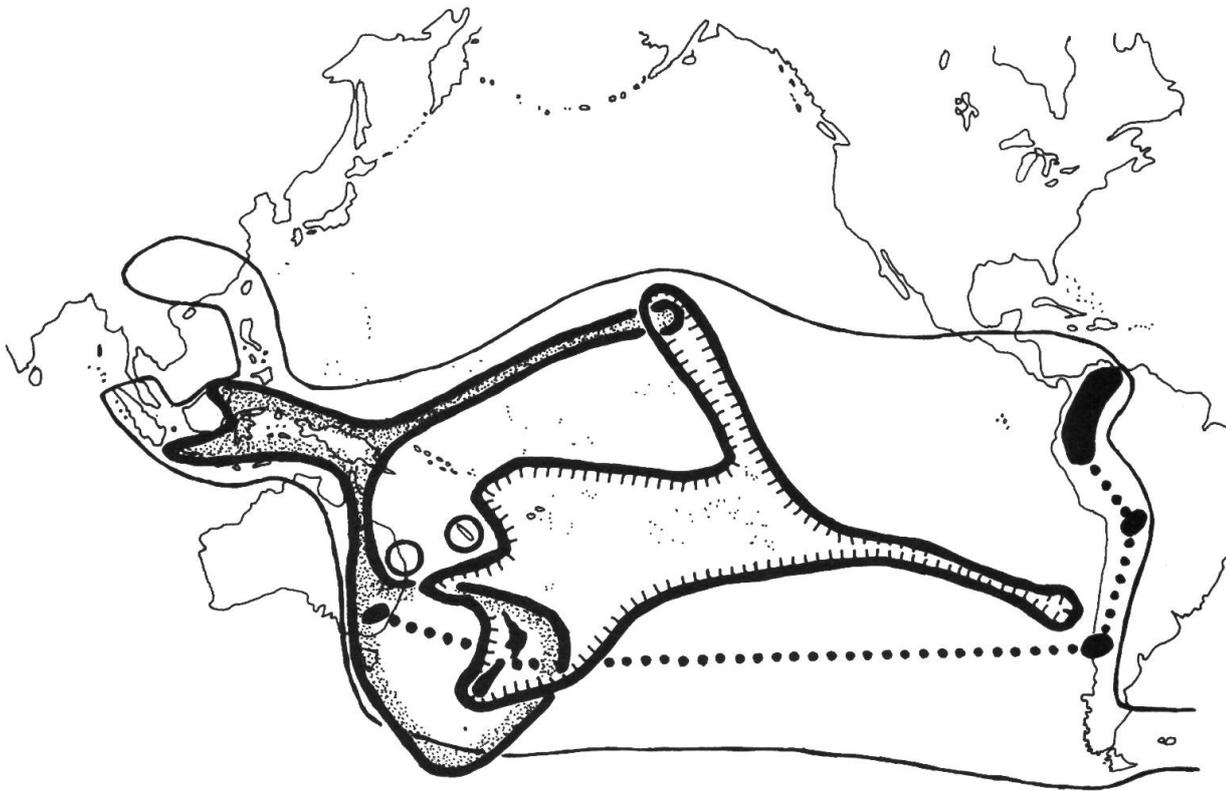


Fig. 1. – Distribution of tribe *Anthospermeae* subtribe *Coprosmineae*. *Coprosma* subgen. *Lucidae* C. J. Webb: hatched line. Subgen. *Coprosma* sect. *Nertera* (Banks & Sol. ex Gaertn.) Heads: fine line (also in Tristan da Cunha), sect. *Leptostigma* (Arnott) Heads: solid black areas connected by dotted line, other sections of subgen. *Coprosma* stippled. *Durringtonia* Henderson & Guymar: circle (Queensland). *Normandia* Hook. f.: circle (New Caledonia).

Nothofagus and *Santalum*. Many of the central Pacific distribution patterns of endemism shown in *Coprosma* are also seen in shore-fishes (HEADS, 1983). In addition, *Coprosma* shows a strikingly similar pattern to that of the dry-fruited *Hebe* complex in the Scrophulariaceae (HEADS, 1993; 1994e). Both have a small-leaved, western group in Australia – New Guinea – South Island, with main branches at least partly plagiotropic (arched or horizontal) and sometimes prostrate and rooting, and a large-leaved, orthotropic, eastern group in North Island – Chatham Is. – Kermadec Is. – Polynesia – Juan Fernandez/South America. In both cases the small-leaved species have inflorescences terminal on (sometimes reduced) leafy shoots, while large-leaved species have lateral inflorescences on specialised axillary peduncles, with bracts very different from the foliage leaves. Overall, the split is east/west, while within New Zealand the eastern group is mainly in the north and the western group is largely southern.

A similar case is seen in *Dracophyllum* (*Epacridaceae*). OLIVER (1928) treated the species under three subgenera:

Oreothammus 25 species, New Zealand; 1 species, Tasmania.

Eudracophyllum 18 species, New Zealand, east Australia, Tasmania, Lord Howe I., New Caledonia.

Cordophyllum 1 species, New Caledonia.

In the last, northeastern, species the flowers are borne in fascioles on a stout rachis and Oliver could not help suspecting that “Each flowering *peduncle* might be compared with a separate *branch* of such a [southwestern] species as *D. minimum* [or *D. muscoides*]” (italics added), the latter being prostrate plants with solitary, terminal flowers.

In this way shrubs of *Hebe*, *Coprosma*, *Dracophyllum*, *Olearia* (*Compositae*) and others dominate many New Zealand landscapes with diverse species in both large and small-leaved sections. It can hardly be coincidence that all these genera are in sympetalous families. These families are supposedly recently evolved, but from the evidence considered here they must all be Jurassic, at least.

It is very striking that *Coprosma* as such is not in New Caledonia. However, this absence also occurs in other groups which are diverse in New Zealand, such as the *Hebe* complex, *Thymelaeaceae* tribe *Gnidieae* (HEADS, 1990) and *Leguminosae* tribe *Carmichaelieae* (ALLAN, 1961). It is also striking that *Coprosma* and *Anthospermeae* are very poorly represented in South America, and again this is probably due to the location of prior main massings rather than to lack of dispersal ability or suitable ecology.

Coprosma and the *Hebe* complex have many further biogeographic similarities. For example, within New Zealand both show "horstian" patterns along the islands and peninsulas of the NE Auckland coast in massively constructed species (*C. macrocarpa* and *H. macrocarpa*, HEADS, 1989). In addition, both genera have species with the Alpine Fault disjunction (implying they are early Tertiary, at least), as well as trans-Pacific and trans-Tasman disjunctions (implying the genera are early Cretaceous, at least). It appears that their distributions were established on geographies that were totally different from those of the present.

Through these two groups of genera both *Rubiaceae* and *Scrophulariaceae* have southern members with "anomalous" coniferoid/ericoid foliage. This is most conspicuous in species such as *Anthospermum spathulatum* and *Leonohebe cupressoides*. "Orthodox" mesic angiosperm forms of the genera are also present in New Zealand. Are the anomalous southern forms due to "parallelism" or "selection pressure"? Parallel trends were probably already evident in the complex of forms ancestral to the Sympetalae, and the "survival coefficient" of the small-leaved forms is surely high. Nevertheless, it seems unlikely that poor growing conditions, by themselves, could somehow "evoke" the small-leaved habit. Direct inheritance of the microphyllous habit from gymnospermous ancestors is suggested elsewhere (HEADS, 1994a) to have occurred in ericoid *Scrophulariaceae* and could also be the case in these *Rubiaceae*. It is unlikely that groups such as *Scrophulariaceae* or *Rubiaceae* (or the angiosperms as a whole) evolved from a single parent pair or even a single species of earlier angiosperms (HEADS, 1984; 1985). These groups can be interpreted more easily as parallel developments out of already polymorphic ancestral complexes. If this is true, the taxa mentioned would be technically polyphyletic by origin, but with a common evolutionary trend making them "monophyletic". It seems highly unlikely that gymnospermous ancestors of these angiosperms in, say, the Triassic, should *lose* their typical gymnospermous structure (microphyllous architecture dominated by long and short shoot differentiation, "flowers" minute, simple, unisexual, wind-pollinated), only to regain all this in a second time, perhaps in the Jurassic, as the western members of *Coprosma* and *Leonohebe*. Professor W. R. Philipson (pers. comm. 1987) has emphasized the diverse nature of the "proangiosperms" *Gnetum*, *Ephedra* and *Welwitschia*, and suggested that the angiosperms evolved "on a broad front". VERDCOURT (1958) also suggested that "the Rubiaceae were evolved 'on a broad front' and that two kinds of ovary [with few or numerous ovules] were already represented as the family was emerging". This implies that the ancestor was polymorphic (HEADS, 1985) and opens the way to a vicariance explanation for the group, rather than dispersal from a single centre of origin by an originally monomorphic ancestor. The difference between the "circumnucellar" flower (SATTLER, 1973) of *Anthospermeae* and the "pan-strobilar" flower of typical *Rubiaceae* is much greater than the difference between ovaries with few or numerous ovules, but Verdcourt's penetrating observation can be extended to suggest that both *Anthospermeae* and "normal" *Rubiaceae* types of flowers, as well as intermediate forms, were already present as the family was emerging

Note added on proof

Recent studies have shown that pyrenes of sect. *Nertera* have an articulation around the margin of the flat inner face. The operculum is thus the entire inner face. *C. talbrockiei* also has this structure and is possibly allied with sect. *Leptostigma*. *C. moorei* has typical *Coprosma* pyrenes. The pyrenes of *C. obconica* and *C. wallii* also differ from those of typical *Coprosma* and they should be removed from sect. *Microcoprosma*.

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