

Zeitschrift: Candollea : journal international de botanique systématique = international journal of systematic botany

Band: 57 (2002)

Heft: 1

Artikel: The genus Coprosma (Rubiaceae) in New Guinea

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DOI: <https://doi.org/10.5169/seals-879341>

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The genus *Coprosma* (Rubiaceae) in New Guinea

RHYS O. GARDNER

ABSTRACT

GARDNER, R. O. (2002). The genus *Coprosma* (Rubiaceae) in New Guinea. *Candollea* 57: 97-130. In English, English and French abstracts.

Five species of *Coprosma* J. R. & G. Forst. (Rubiaceae) occur in New Guinea, in its mountainous regions above c. 1900 m: *C. archboldiana* Merr. & L. M. Perry, *C. brassii* Merr. & L. M. Perry, *C. divergens* W. R. B. Oliv., *C. papuensis* W. R. B. Oliv. and *C. wollastonii* Wernham. All are endemic except the last-named, which is also found in Ceram (Indonesia). None of these species has an especially wide distribution within New Guinea. Three combinations, *C. papuensis* subsp. *discolor* (P. Royen) R. O. Gardner, *C. wollastonii* var. *epiphytica* (P. Royen) R. O. Gardner, and *C. wollastonii* var. *novoguineensis* (Merr. & L. M. Perry) R. O. Gardner are made. *Coprosma papuensis* subsp. *mopaensis* R. O. Gardner is newly described. *Coprosma habbemensis* Merr. & L. M. Perry and *C. lamiana* W. R. B. Oliv. are treated as synonyms of *C. wollastonii* var. *wollastonii*. *Coprosma scandens* P. Royen is treated as synonym of *C. wollastonii* var. *epiphytica*. Vegetative features of *Coprosma* in New Guinea are discussed and the species are keyed, described and mapped. *Coprosma archboldiana* is a weak-stemmed, opposite-leaved, prostrate plant. The other four species are small shrubby trees. *Coprosma divergens* and *C. wollastonii* (mostly) are opposite-leaved, and *C. brassii* and *C. papuensis* have their leaves in whorls of 3; deviation from the usual leaf arrangement is an infrequent condition. *Coprosma brassii* and *C. wollastonii* var. *novoguineensis* are epacrid-like treelets with spiny leaves crowded on fastigate branchlets. The other taxa, except *C. divergens*, generally exhibit looser foliage on wide-spreading branches. *Coprosma divergens* is a small-leaved compact bush, but unlike most "divaricating" small-leaved coprosmas of New Zealand it lacks any architectural differentiation into long shoots and fertile brachyblasts. Domatia are found regularly only in *C. papuensis* (though not in subsp. *discolor*). They are both axillary and extra-axillary, and are unique in the genus, and nearly so in the dicotyledons at large, in sometimes opening to the upper rather than lower surface of the blade.

RÉSUMÉ

GARDNER, R. O. (2002). Le genre *Coprosma* (Rubiaceae) en Nouvelle Guinée. *Candollea* 57: 97-130. En anglais, résumés anglais et français.

On trouve cinq espèces du genre *Coprosma* J. R. & G. Forst. (Rubiaceae) dans les régions montagneuses de Nouvelle Guinée à plus de 1900 m: *C. archboldiana* Merr. & L. M. Perry, *C. brassii* Merr. & L. M. Perry, *C. divergens* W. R. B. Oliv., *C. papuensis* W. R. B. Oliv. et *C. wollastonii* Wernham, toutes endémiques, sauf la dernière qu'on trouve aussi à Ceram (Indonésie). Aucune de ces espèces n'est très répandue en Nouvelle Guinée. Trois combinaisons sont validées, *C. papuensis* subsp. *discolor* (P. Royen) R. O. Gardner, *C. wollastonii* var. *epiphytica* (P. Royen) R. O. Gardner et *C. wollastonii* var. *novoguineensis* (Merr. & L. M. Perry) R. O. Gardner. La sous-espèce *C. papuensis* subsp. *mopaensis* R. O. Gardner est décrite comme nouvelle. *Coprosma habbemensis* Merr. & L. M. Perry et *C. lamiana* W. R. B. Oliv. sont placées en synonymie de *C. wollastonii* var. *wollastonii*. *Coprosma scandens* P. Royen est placé en synonymie de *C. wollastonii* var. *epiphytica*. Les caractéristiques végétatives du genre *Coprosma* en Nouvelle Guinée sont discutées. Les espèces sont décrites et leur répartition cartographiée. Une clé permet leur identification. *Coprosma archboldiana* est une espèce à tige flexible, à feuilles opposées; c'est une plante à port prostré. Les quatre autres espèces sont des petits arbustes. *Coprosma divergens* et *C. wollastonii* (principalement) sont à feuilles opposées et *C. brassii* et *C. papuensis* ont leurs feuilles en verticilles par trois; la divergence de l'arrangement normal des feuilles, n'est pas commune. *Coprosma brassii* et *C. wollastonii* var. *novoguineensis* sont de petits arbustes épacrides avec des feuilles épineuses rassemblées en de petites branches fastigiées. Les autres taxa (sauf

C. divergens) présentent en général un feuillage moins compact sur des branches largement écartées. *Coprosma divergens* est un buisson compact à petites feuilles: mais à la différence de la plupart des coprosmas “divaricantes” de Nouvelle Zélande, il se caractérise cependant par son manque de différenciation architecturale en de longues pousses et des brachyblastes fertiles. On ne trouve régulièrement des domatia que sur *C. papuensis* seulement (mais pas sur la subsp. *discolor*). Elles sont axillaires ainsi qu’extra-axillaires et sont uniques dans le genre, et également dans les dicotylédones en général, à quelques exceptions près, s’ouvrant quelquefois sur la surface supérieure plutôt que sur la surface inférieure de la lame.

KEY-WORDS: *Coprosma* – RUBIACEAE – New Guinea – Taxonomy.

Introduction

Coprosma J. R. & G. Forst. (*Rubiaceae-Anthospermeae*) is a Pacific Ocean-centred genus of about a hundred species of small to medium-sized woody plants. It is distributed in temperate and montane-tropical regions from Borneo southeast to Australia, New Zealand and the more southerly island groups (including Macquarie I.) and across the Pacific Ocean to Hawaii and the Juan Fernandez Islands. The genus is most diverse in New Zealand, at all altitudes; it is notably absent from New Caledonia (OLIVER, 1935; VAN BALGOOY, 1966; HEADS, 1996).

For New Guinea the first complete account of *Coprosma* is that of VAN ROYEN (1983), who accepted eleven species, all montane or alpine plants; his detailed descriptions and illustrations largely supersede the work of WERNHAM (1916), OLIVER (1935, 1942) and MERRILL & PERRY (1945).

By comparison with that of VAN ROYEN (1983), the following treatment provides a more synthetic picture of the group’s taxonomy, and in it only five species are accepted. *Coprosma papuensis* is considered to have three almost completely allopatric subspecies. The eastern one is the typical (domatia-bearing) subspecies and the western one the taxon described by VAN ROYEN (1983) as *C. discolor*. The third subspecies, subsp. *mopaensis* newly described here, falls between the other two geographically and morphologically — future collections may clarify whether or not it is essentially subclinal in character. In the western part of New Guinea (to a large part, in Irian Jaya) are found the taxa treated by VAN ROYEN (1983) as *C. epiphytica*, *C. scandens*, *C. habbemensis*, *C. lamiana*, *C. novoguineensis* and *C. wollastonii*. All are sunk here into the last-named, with new combinations provided at varietal level only for the two most distinct variants, var. *epiphytica* and var. *novoguineensis*. The other two western species, *C. archboldiana* and *C. brassii*, and *C. divergens* of Papua New Guinea, are well-defined.

Material and methods

This study is based on an examination of c. three hundred herbarium specimens (A, AK, CANB, L and WELT). It is concerned principally with characters of the vegetative parts of these plants. Anatomical observations were made on rehydrated material. Hand-sections were stained with safranin or chlor-zinc-iodine or phloroglucinol-HCl. Clearing was done with alkali and bleach in the usual way; despite the unpromising dark coloration and firm texture of the dried leaves satisfactory preparations were obtained.

The characters

The observations below (and in the key and descriptions) generally refer to dried material, except where this has been rehydrated for particular purposes.

Habit

In *Coprosma* (that is, excluding *Leptostigma* and *Nertera* — see GARDNER, 1999) the typical habit is that of a small to medium-sized woody plant. Such plants are often described as

“shrubs”, but regular or extensive formation of new basal stems, and rooting from prostrate or subscandent branches, are not usual in at least the larger members of the genus, and these plants would be better termed “small (bushy or shrubby) trees”.

With the exception of the prostrate *C. archboldiana*, which does exhibit some rooting from its lower leafless nodes, the New Guinea coprosmas conform to the “small tree” habit. The major branching tends to be irregular and wide-spreading. The larger side-branches are typically monopodial and orthotropic. The lesser ones bear flowers terminally (and sometimes laterally at the shoot tip) but subsequent growth of new shoots from these fertile branches is not regular or profuse enough to give the plants a noticeably sympodial architecture.

Such a “small tree” coprosma is exemplified by *C. papuensis* subsp. *papuensis* and also by the three westernmost members of the genus: *C. sundana* Miq. of Java, “*C. celebica*” (Valeton in sched.) of Sulawesi and *C. crassicaulis* Stapf of Borneo. Of the other New Guinea taxa, *C. papuensis* subsp. *discolor* and some forms of *C. wollastonii* (notably, var. *epiphytica*) are often mentioned as having subscandent branches, a development seen elsewhere only in some Hawaiian species (WAGNER & al., 1990).

Coprosma divergens is a compact small-leaved bush, like many coprosmas of Australia and New Zealand and also *C. elliptica* W. R. B. Oliv. of Hawaii.

Coprosma brassii and *C. wollastonii* var. *novoguineensis* have upfolded stiff spiny leaves aggregated on fastigiate shoots and thus resemble members of the Epacridaceae.

Indument

There is generally some kind of indument on the new stems and shoots of coprosmas (at least, in the higher-altitude species), and for the New Guinea species the details of hair distribution are of some moderate taxonomic value. Whether or not the hairs are thick or thin-walled, or smooth or minutely roughened, might also be of value but such features were not sampled adequately in the present study.

Mostly the hairs are unicellular, more or less acute-tipped, and c. 0.1-0.3 mm long. They generally appear smooth ($\times 40$), but in *C. divergens* and *C. wollastonii* var. *epiphytica* they can be minutely verrucose. The bristly hairs found in *C. papuensis* and *C. wollastonii* var. *wollastonii*, on the midrib below and rarely on the stem, are relatively long (to c. 0.75 mm) and thin-walled. They are typically unicellular in the former but 2-3-cellular in the latter.

Hairs occur on the primary stem and leaf margins and in the midrib groove, and also along the margin of the stipule, where they are always present even in atypically near-glabrous representatives of a taxon, e.g., in *C. papuensis* subsp. *discolor*. Very rarely they are present across the entire upper surface of the leaf as short scabridities.

The hairs on the stem are usually disposed around it more or less evenly but are sometimes lacking from the upper part of an internode below the petiole bases. They are patent or antrorse-appressed or occasionally retrorse-appressed, varying in orientation within the species and sometimes within the individual.

Coprosma papuensis subsp. *papuensis* is entirely glabrous but the usual presence of low but distinct papillae on its young stems suggests that hairiness (as found in the other two subspecies) might be a primitive feature of its lineage.

Stipules

The stipules of the New Guinea coprosmas are illustrated in Fig. 1. In these taxa, as in the genus at large, the upper part of the stipule (hereafter called its “face”) is elongated into a more or less keeled triangular structure with a single apex. The margin of the face may be entire or nearly so, but in *C. brassii*, and sometimes in *C. wollastonii*, the very elongate central lobe is accompanied by two or three pairs of similarly subulate lateral lobes. Usually the stipule is sheathing, that is, its margin continues laterally inside the petiole base as a collar.

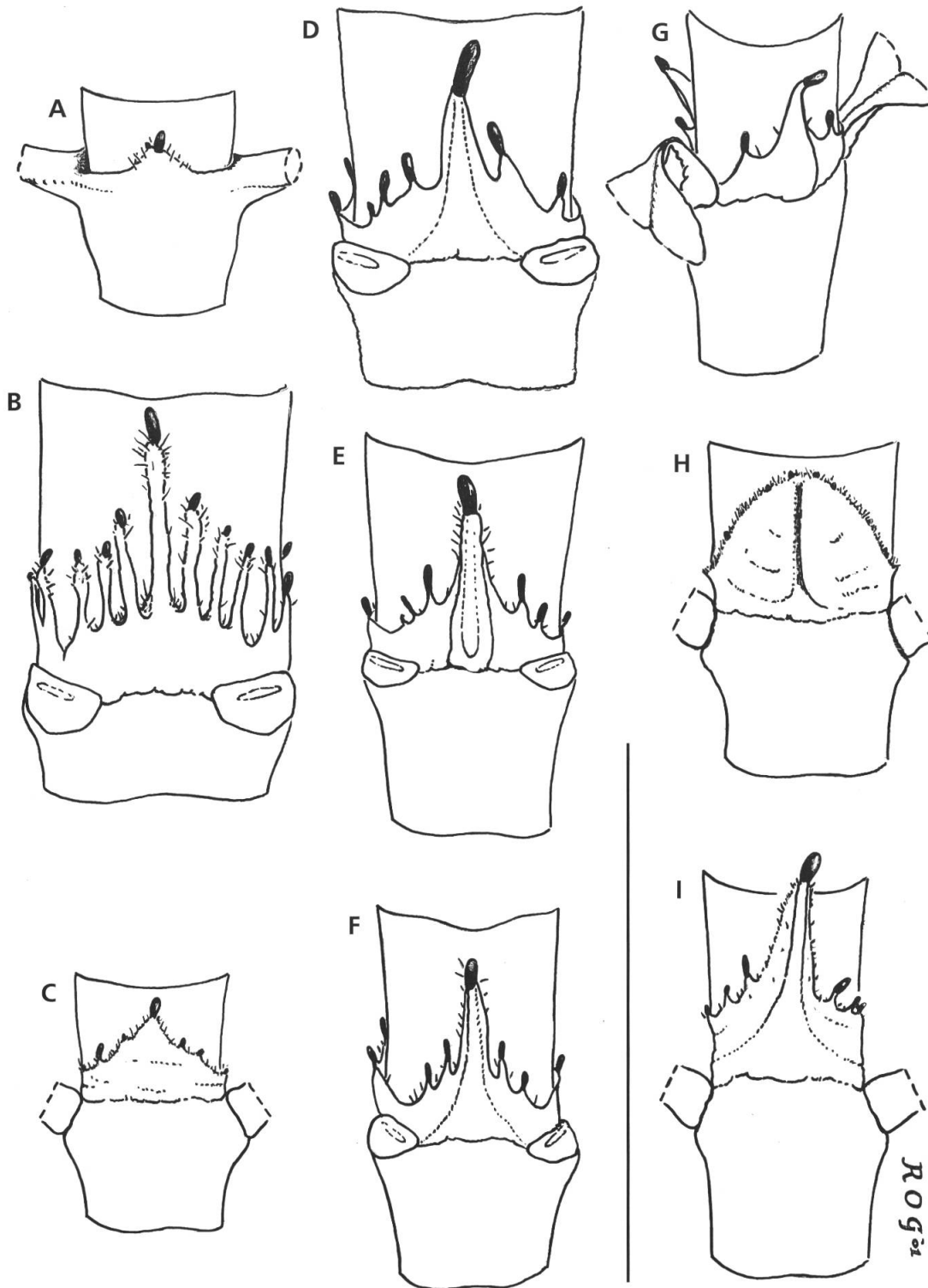


Fig. 1. – Stipules of New Guinea *Coprosma* species. Scale bar 1 cm.

A. *C. archboldiana* Merr. & L. M. Perry [Brass 9831]; **B.** *C. brassii* Merr. & L. M. Perry [Kalkman 4540]; **C.** *C. divergens* W. R. B. Oliv. [LAE 61511]; **D.** *C. papuensis* W. R. B. Oliv. subsp. *papuensis* [Craven 2710]; **E.** *C. papuensis* subsp. *mopaensis* R. O. Gardner [Brass 31267]; **F.** *C. papuensis* subsp. *discolor* (P. Royen) R. O. Gardner [v. Balgooy 338]; **G.** *C. wollastonii* var. *epiphytica* (P. Royen) R. O. Gardner [LAE 66980]; **H.** *C. wollastonii* var. *novoguineensis* (Merr. & L. M. Perry) R. O. Gardner [Brass & M.-Drees 9707]; **I.** *C. wollastonii* Wernham var. *wollastonii* [Brass 10929].

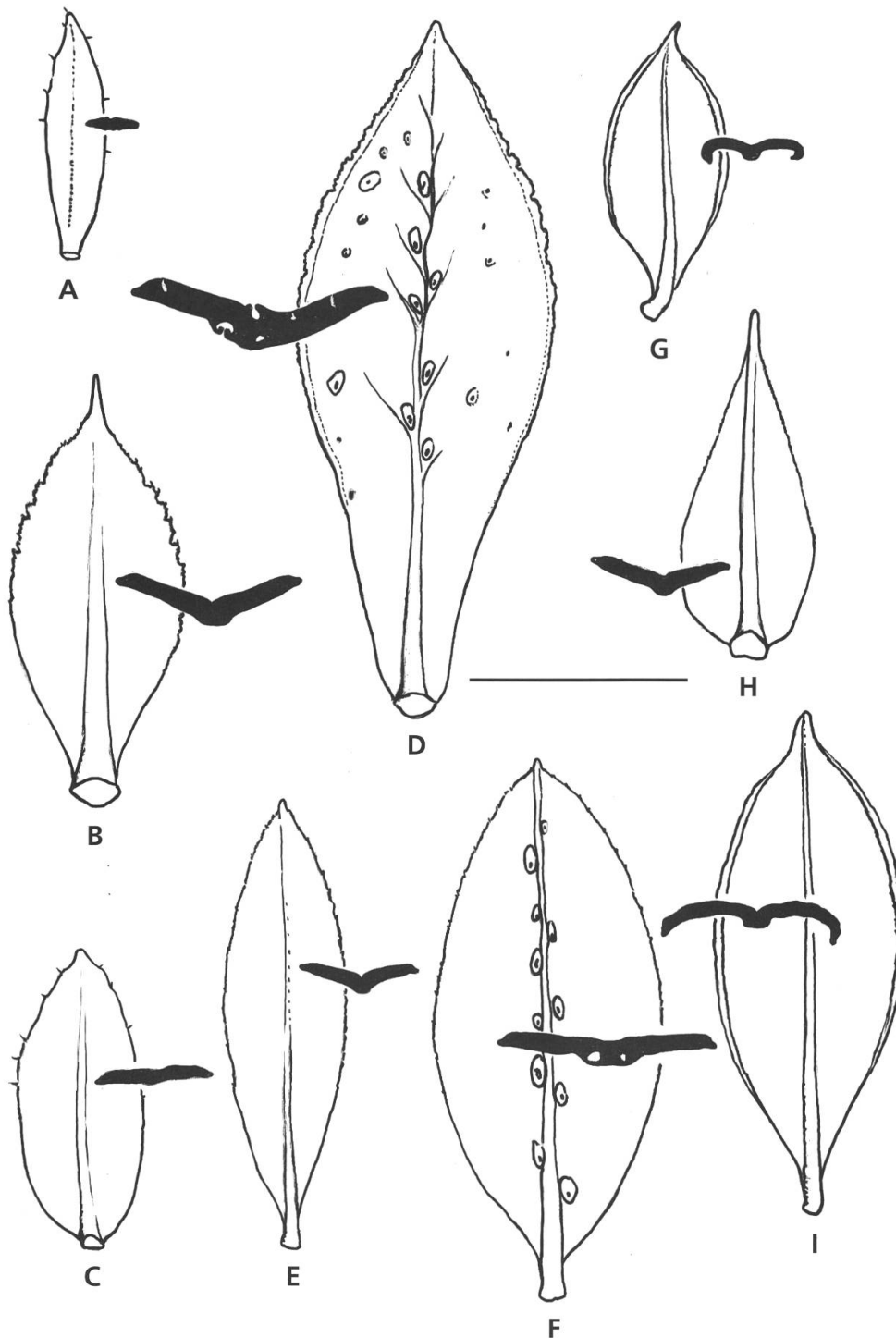


Fig. 2. – Leaves of New Guinea *Coprosma* species, outline and mid-section. Outlines as seen from below, except **D** (seen from above). Midsections as in rehydrated material (note recurved margins of **G** and **I**). Schematic. Scale bar 1 cm.

A. *C. archboldiana* Merr. & L. M. Perry; **B.** *C. brassii* Merr. & L. M. Perry; **C.** *C. divergens* W. R. B. Oliv.; **D.** *C. papuensis* W. R. B. Oliv. subsp. *papuensis* (upper surface; note both axillary and domatia); **E.** *C. papuensis* subsp. *discolor* (P. Royen) R. O. Gardner; **F.** *C. papuensis* subsp. *mopaensis* R. O. Gardner; **G.** *C. wollastonii* var. *epiphytica* (P. Royen) R. O. Gardner; **H.** *C. wollastonii* var. *novoguineensis* (Merr. & L. M. Perry) R. O. Gardner; **I.** *C. wollastonii* Wernham var. *wollastonii*.

Along the stipule margin are dark sausage-shaped glandular outgrowths, the denticles. They occur singly on the apex of the stipule lobes (rarely paired there, but not in the New Guinea species) or regularly spaced along the margin if the face is essentially unlobed. They vary in size between the species and to some degree in size and number within each species but are never lacking. Note that some of a stipule's denticles are concealed along the adaxial surface just below the stipule margin — the number and size of these are omitted from the species' descriptions below.

The height of the stipule is taken as the distance between the upper edge of the petiole base and the apex of the stipule face's central denticle; thus it includes the height of the sheath but not that of the tubular lower part of the stipule around and below the petiole bases (the "stipule cup" of TAYLOR, 1961). In dried material the lower part of the stipule face overhangs somewhat between the petiole bases.

Coprosma archboldiana alone among the New Guinea species has a non-sheathing stipule, i.e., the stipule margins run out laterally to merge into the edges of the strap-like petioles. The face is hardly elongated and usually has a single central stout denticle.

Coprosma brassii, *C. papuensis* subsp. *papuensis* and *C. wollastonii* var. *novoguineensis* have almost sessile leaves and their stipules are shortly sheathing (the sheath mostly being less than 0.5 mm long). At the other extreme, in the low-altitude variant of *C. papuensis* subsp. *discolor* that has relatively elongate leaf blades and petioles, the stipule sheath reaches c. 1.5 mm long, that is, approximately half the length of the face. Similarly, the elongate-leaved variant of *C. wollastonii* (formerly known as *C. habbemensis*) has a longer stipule sheath than is seen in the remainder of the species, where the leaves are sturdier and less distinctly petiolate.

As noted above, the margin of the stipule is generally ciliate, except in *C. papuensis* subsp. *papuensis*. A densely hairy stipule face is seen only in *C. wollastonii*, as an infrequent condition.

In *Coprosma* the stipules may persist through the primary-thickening phase of the shoot, subsequently to erode as periderm forms, or they may be shed early and cleanly. The former condition, the usual one in the genus, is found in all the New Guinea species. Not only are they persistent but they also become somewhat yellowish and corky-thickened (suberized ?) like the outer layer of the internode itself. In *C. brassii* and *C. wollastonii* var. *epiphytica*, and to a lesser degree in *C. papuensis*, the thickened stipules and the internode are notably sclerotic and can offer some resistance to the point of a needle.

Leaves

The general character of the leaves of the New Guinea coprosmas is shown in Fig. 2. They are subsessile or have a rather poorly defined petiole of up to 3(-5) mm long. The size of the blade ranges from 3 × 1.3 mm in the smallest-leaved material seen of *C. divergens* and *C. wollastonii* var. *epiphytica* to 50 × 17 mm in the largest-leaved material of *C. papuensis* subsp. *papuensis*.

The vernation of the new leaves could not be ascertained. In the three opposite-leaved species it might be face-to-face, as is usual in at least the larger-leaved New Zealand coprosmas, but in *C. divergens* the usual obliquity of the distal part of the blade suggests that there could be some rolling in the bud here.

In *C. archboldiana*, *C. divergens* and (usually) *C. wollastonii* the leaves are arranged in opposite pairs, and in *C. brassii* and *C. papuensis*, in whorls of three. Deviation from these arrangements is sufficiently uncommon as to present no difficulties in the making of a key. Examples of such deviations are as follows. In *C. papuensis*, the first several nodes of a shoot are, very occasionally, opposite-leaved. In *C. wollastonii* the type-locality population is unlike most other material I have seen of the species in being in 3s (UTTERIDGE, pers. comm.). In two collections of *C. wollastonii* var. *novoguineensis*, the arrangement in 3s occurs sporadically on several of the separate pieces of foliage. In one collection of *C. divergens*, an especially vigorous length of new shoot was seen to have a succession of nodes with four leaves rather than two. Lastly, in

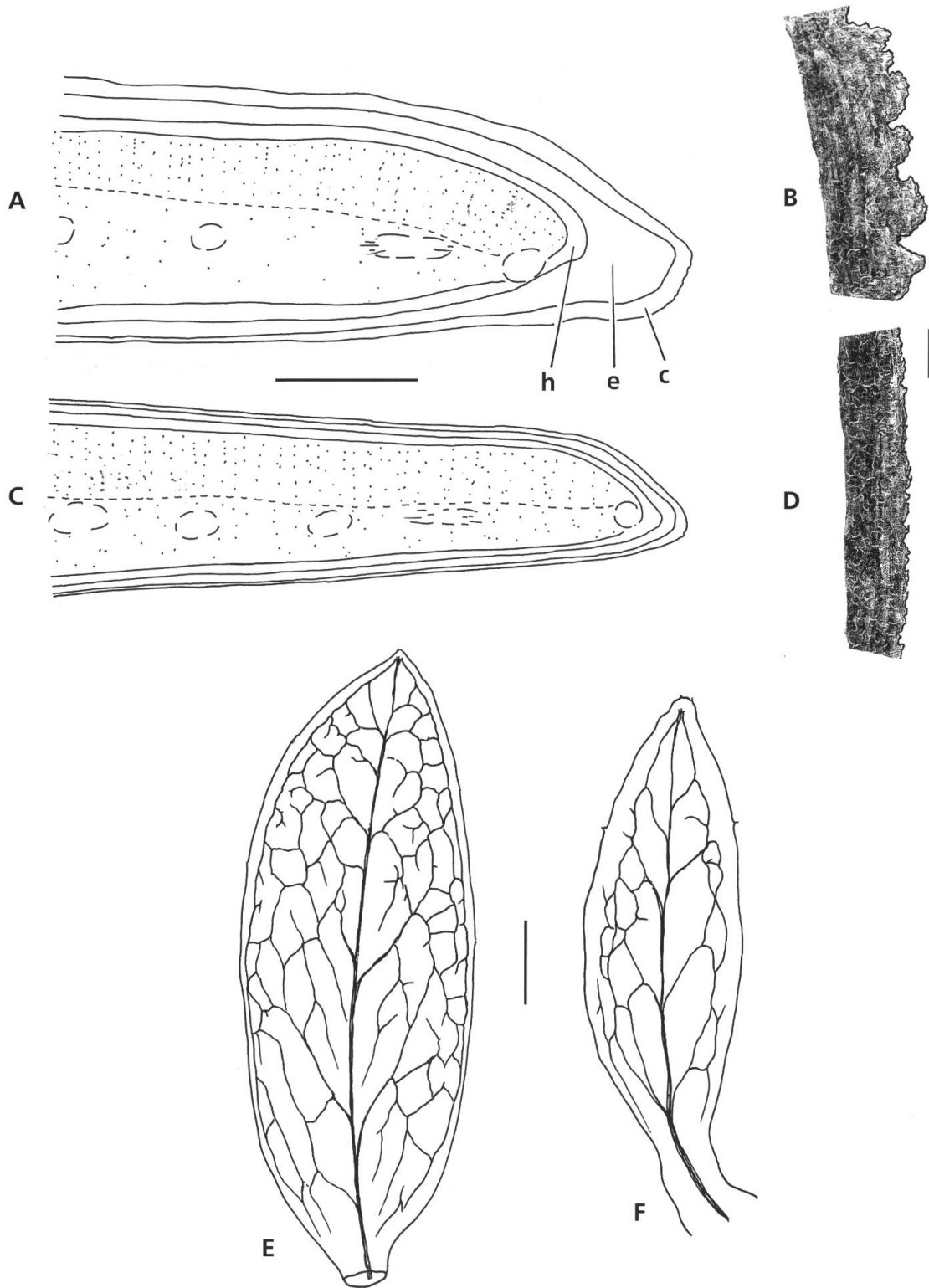


Fig. 3. – Leaves of some New Guinea *Coprosma* spp. Scale bars 0.25 mm (A-D); 1 cm (E, F).

C. brassii Merr. & L. M. Perry [*Brass & M.-Drees 10221*]: **A**. Margin from above; **B**. t.s. outer portion of blade; **c**, cuticle; **e**, epidermis; **h**, hypodermis. *C. wollastonii* var. *novoguineensis* (Merr. & L. M. Perry) R. O. Gardner [*Brass 9707*]: **C**. Margin from above; **D**. t.s. outer portion of blade. **E**. *C. divergens* W. R. B. Oliv. [*Hoogland 9794*]: cleared leaf showing venation. **F**. *C. archboldiana* Merr. & L. M. Perry [*Mangen 975*]: cleared leaf showing venation.

C. brassii MERRILL & PERRY (1945: 261) mention finding on one specimen a node with opposite leaves, and on another a node which bore four branches.

The margins of the leaves of the New Guinea species are glabrous or ciliate or scabrid. Particularly in *C. papuensis* subsp. *discolor*, which ranges through c. 1500 metres of altitude, ciliate-margined leaves are seen in the lower part of the range, while those from higher up have short stout setae. In that taxon, but especially in *C. brassii*, such setae are based on irregularly shaped erose-papillate outgrowths; in *C. papuensis* subsp. *papuensis*, where the margins are nearly always without setae, these outgrowths alone may be seen (cf. the New Zealand montane species *C. serrulata* Buchanan of similar leaf size and texture).

In the relatively thin-leaved *C. divergens* (Fig. 3E), and sometimes in *C. papuensis* and *C. wollastonii* too, a narrow pale raised line can be detected just inside the blade edge. This marks the marginal vein. It has a uniformly curving rather than looped course and is produced by the vascular tissue and hypodermis. The marginal vein is present but not especially well-developed in the two most coriaceous-leaved taxa, *C. brassii* and *C. wollastonii* var. *novoguineensis*, where the leaves have (instead?) a very thick cuticle and a thick-walled lower epidermis and hypodermis (Fig. 3A-D); both of these tissues are lignified in *C. brassii*.

A uniformly-curved marginal vein is lacking in the *C. archboldiana* leaf (Fig. 3F). Here the distal parts of the three or so lateral veins unite with one another in looping fashion well inside the margin; beyond these loops are a weaker set of areoles and a few free-ending veins.

Externally the lateral veins are nearly always obscure, but in *C. papuensis* and *C. wollastonii*, and rarely in *C. divergens*, they may can be detected on the upper surface of the blade as narrow discontinuous furrows and on the lower surface as texture-lineaments.

The bristly pubescence that may occur on the underside of the midrib in *C. papuensis* (subsp. *discolor* and *mopaensis*) and *C. wollastonii* var. *wollastonii* has already been noted (see **Indument**).

The presence of short hairs or scabridities on the upper surface of the blade (rather than just in the midrib groove) was a distinctive feature of the type collection and protologue of *C. wollastonii*. VAN ROYEN (1983: 2744, 2760) stated that such scabridity could also be seen elsewhere in that species (in the taxon he maintained as *C. habbemensis*). My observation is that although such material, including the type of *C. habbemensis*, can have a pustulate character to the upper surface of the blade, no emergences spring from these pustules, even on the newest leaves. Other than in *C. wollastonii* I have seen upper-surface scabridity only once: it occurs regularly and copiously in a Sarawaket Mts collection of *C. papuensis* subsp. *discolor* (Hoogland 9772, A !, L !). The two other collections of this taxon that I have seen from this locality have leaves that are scabrid only on the margins and in the midrib groove.

A scabrid upper surface to the leaf blade is known elsewhere in the genus only in *C. hirtella* Labill. of Australia, where it is the usual though not invariable condition.

Domatia are a common feature of the *Coprosma* leaf, although in higher-altitude species, at least in Australia, New Zealand and Hawaii, they tend to be reduced or lacking. In New Guinea, domatia occur regularly only in *C. papuensis*, where they are present on most leaves of subsp. *papuensis* (Fig. 4) and, less abundantly, on the leaves of subsp. *mopaensis* too. Along the midrib they occur in the axils of the lateral nerves, as deep large-diameter chambers with a slightly raised roof and a mouth that faces vertically or even somewhat towards the leaf base. They also occur further out on the lamina, where they are more pit-like though still occupying much of the blade's depth. Extra-axillary ("laminar") domatia are uncommon in *Coprosma*, but are usual (although apparently hitherto unrecorded) in several Hawaiian species, e.g. *C. foliosa* A. Gray, and they have been reported for the New Zealand species *C. repens* A. Rich., where they are said to be rare (GREENSILL, 1902). Elsewhere in the family laminar domatia would seem to occur only in the Malesian-Pacific group *Timonius* subgen. *Abbottia* (DARWIN, 1994).

The most remarkable feature of the *C. papuensis* domatium is that its mouth can be situated on either the lower or upper surface of the blade (the mouth of an extra-axillary domatium



Fig. 4. – Domatia in *Coprosma papuensis* W. R. B. Oliv. Scale bar 1 cm.

A. *C. papuensis* W. R. B. Oliv. subsp. *papuensis* [Craven 3042]: domatia conspicuous as pustules on upper surface.

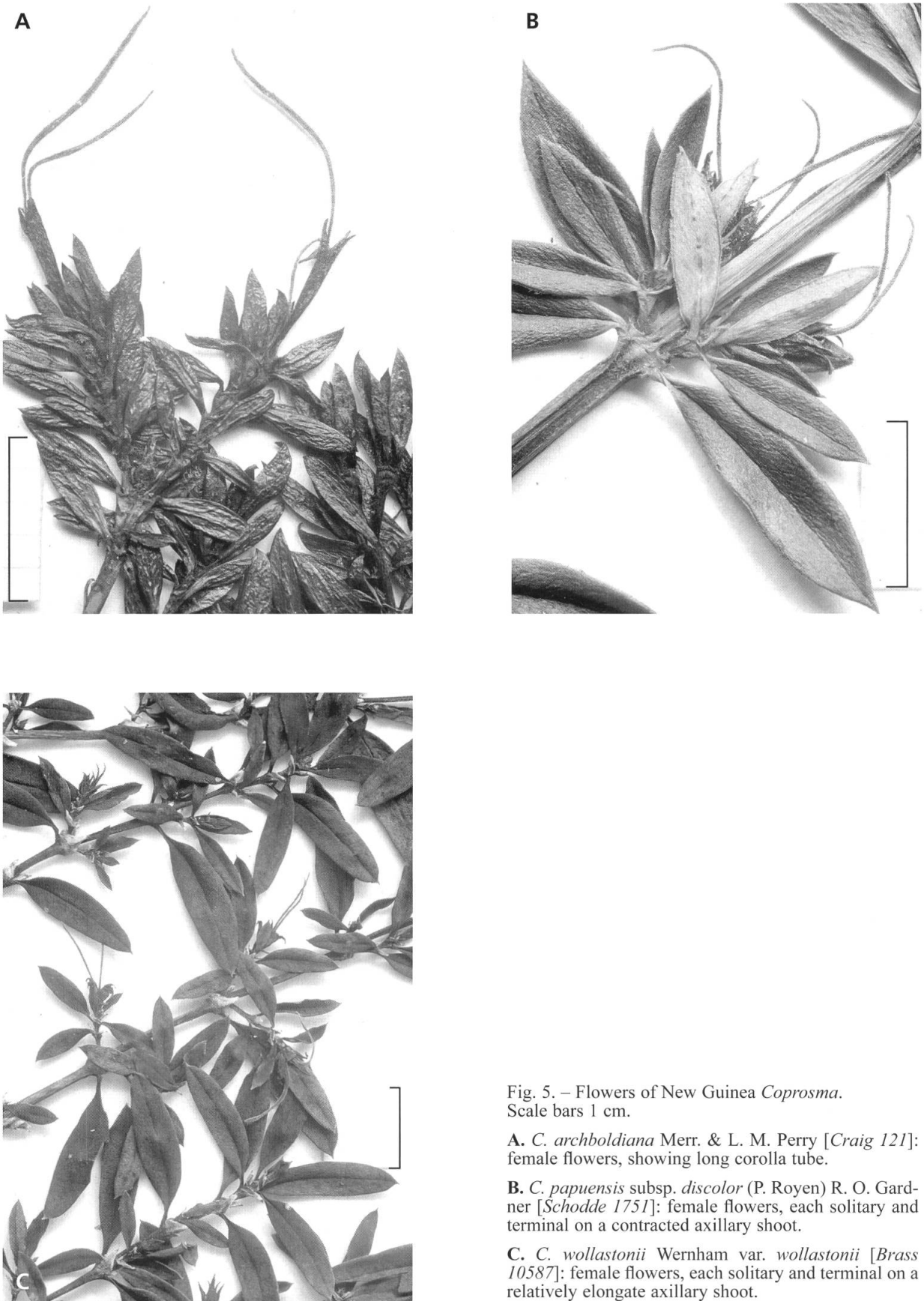


Fig. 5. – Flowers of New Guinea *Coprosma*.
Scale bars 1 cm.

A. *C. archboldiana* Merr. & L. M. Perry [Craig 121]: female flowers, showing long corolla tube.

B. *C. papuensis* subsp. *discolor* (P. Royen) R. O. Gardner [Schodde 1751]: female flowers, each solitary and terminal on a contracted axillary shoot.

C. *C. wollastonii* Wernham var. *wollastonii* [Brass 10587]: female flowers, each solitary and terminal on a relatively elongate axillary shoot.

usually being on the upper surface). Upper-surface domatia seem to be known elsewhere in the dicotyledons only in *Timonius timon* (Spreng.) Merr. (O'DOWD & WILLSON, 1989).

Only once have I seen domatia other than in *C. papuensis*, in a collection of *C. divergens* (Hoogland 9839) from the Sarawaket Mts, where they occur on only a small proportion of the foliage, as shallow axillary pits. This collection comes from c. 100 km beyond the known range of *C. papuensis*, and has no other feature to suggest genetic influence of that species.

Flowers and Fruit

Like nearly all members of the genus, the New Guinea coprosmas have unisexual flowers and are dioecious. In flowers of *C. archboldiana* rudiments of the other sex are completely lacking, while regularly in the other taxa male flowers have a vestigial ovary and stigmas, and female flowers quite large but pollenless staminodes (VAN ROYEN, 1983; own observations).

VAN ROYEN (1983) describes the flowers as being mostly solitary and terminal but mentions that they can also be in "groups of 3" or "reduced dichasia". My observations are that the flowers are always terminal and solitary in *C. archboldiana* (Fig. 5A), and that while usually so in the other species (Fig. 5B, 5C) there are sometimes also flowers at one or more of the adjacent axillary positions.

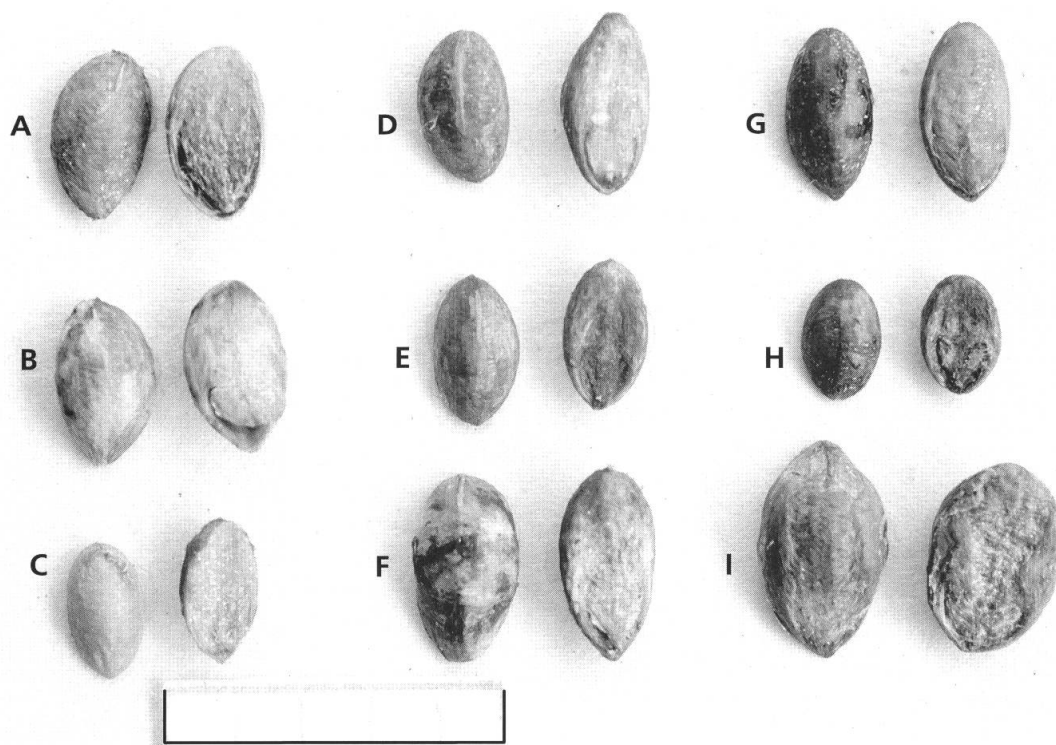


Fig. 6. – Pyrenes of New Guinea *Coprosma* (except *C. wollastonii* var. *epiphytica* (P. Royen) R. O. Gardner). Two pyrenes per taxon, the left one showing the dorsal surface and the right one showing the ventral surface (with operculum). Scale bar 1 cm.

A. *C. archboldiana* Merr. & L. M. Perry [Brass 9831]; B. *C. brassii* Merr. & L. M. Perry [Kalkman 4530]; C. *C. divergens* W. R. B. Oliv. [LAE 61511]; D. *C. papuensis* W. R. B. Oliv. subsp. *papuensis* [Craven 2710]; E. *C. papuensis* subsp. *mopaensis* R. O. Gardner [Brass 31267]; F. *C. papuensis* subsp. *discolor* (P. Royen) R. O. Gardner [v. Balgooy 338]; G. *C. wollastonii* Wernham var. *wollastonii* (= *C. lamiana*) [Pulle 991, 2nd to R piece]; H. *C. wollastonii* var. *novoguineensis* (Merr. & L. M. Perry [Brass & M.-Drees 9707]; I. *C. wollastonii* Wernham var. *wollastonii* (= *C. habbemensis*) [Brass 10929].

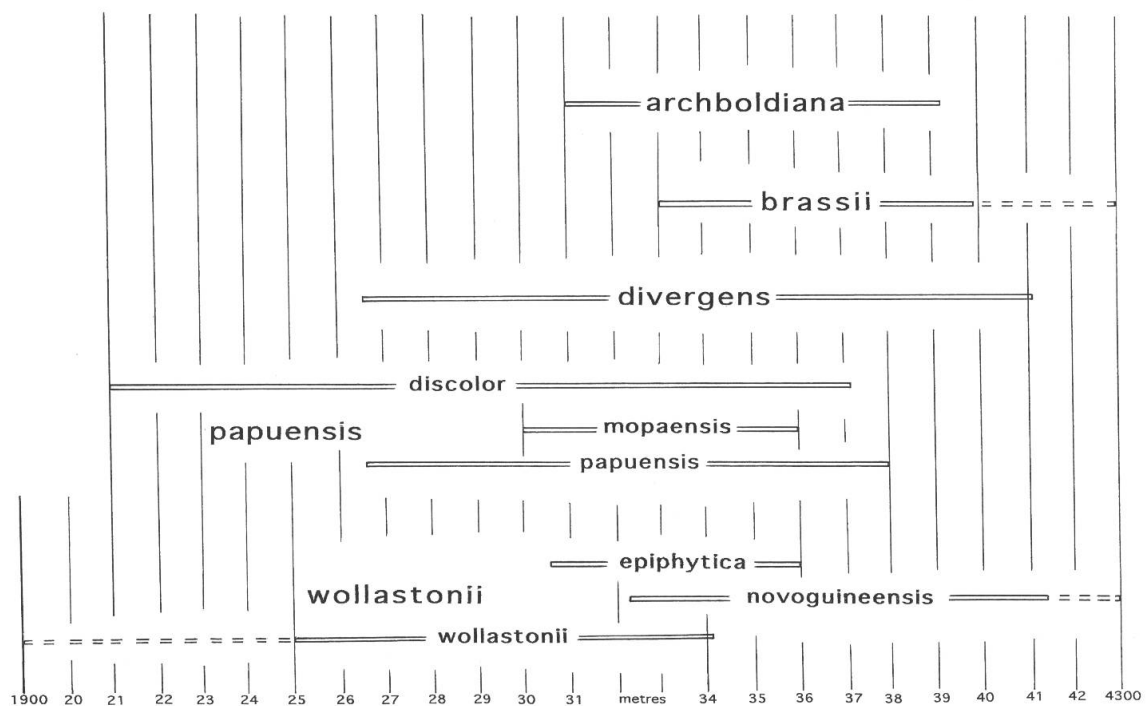
Perhaps especially in *C. papuensis* the fertile shoots tend to be short (centimeters long) side-branches, which bear somewhat reduced leaves below the terminal flower or flowers. These smaller fertile shoots may be determinate — I have not seen any clear instance of their having more than a single season's flowers or fruit.

In all the New Guinea species except *C. archboldiana*, the calyx and corolla would seem to offer little of taxonomic value (see descriptions of VAN ROYEN, 1983). This author did claim that *C. lamiana* could be distinguished from *C. habbemensis* and *C. novoguineensis* by the denticles between its calyx lobes, but in view of the general occurrence of such denticles in stipular and calycine positions of coprosmas this distinction seems likely to be fallacious and based perhaps only on the particular specimens studied.

In *C. archboldiana*, the corolla of both male and female flowers (Fig. 5A) is much longer than those of the other species and consists mostly of a narrow tube; its stamens too would seem to be, by a slight but distinct margin (VAN ROYEN, 1983) the longest of any New Guinea coprosma. These features, which are comparable with those of the similarly small and prostrate species of New Zealand and Australia, e.g., *C. perpusilla* Col. and *C. pumila* Hook. f. (EAGLE, 1986; ORCHARD, 1986) and also *C. ernodeoides* A. Gray of Hawaii (WAGNER & al., 1990), can reasonably be interpreted as part of an adaptation for wind-pollination.

The ripe fruit of the New Guinea coprosmas is reddish or orange except in *C. archboldiana*, where it is said to be violet. In collections made from the Highlands regions of Papua New Guinea in the drier time of the year (May to October) female flowers and ripe fruit are often found together on any particular specimen.

Table 1. – Altitudinal distribution of New Guinea *Coprosma* species. Based on specimens examined. Broken lines at upper limits of *C. brassii* Merr. & L. M. Perry and *C. wollastonii* var. *novoguineensis* (P. Royen) R. O. Gardner refer to sight records of Brass and Cooper ; broken line at the lower limit of *C. wollastonii* Wernham var. *wollastonii* refers to the records of T. Utteridge for Mt Carstensz — see text under the accounts of these taxa.



Examination of a limited number of specimens suggests that in New Guinea the pyrenes of the fruit offer little in the way of crucial or readily-appreciated taxonomic distinctions. They are ovate and smooth-surfaced, and have a clearly defined more or less triangular operculum engraved on the lower part of their flat ventral surface (Fig. 6).

Note that in view of these findings characters of the flower and fruit have almost all been omitted from the species' descriptions below.

Chromosome Number

BORGMANN (1964) reported the count of $2n = 66-86$ for "*C. novoguineensis*" (Borgmann 36, 56) from the Mt Wilhelm region. These two collections are, respectively, *C. divergens* and *C. papuensis* subsp. *discolor*.

Ecology

New Guinea's coprosmas are most abundant at c. 2500-3500 m, around and above the uppermost beech and podocarp forests. They grow on the shrubby margins of these upper forests, particularly along cold air drainage lines and in frost hollows, and then higher in the upper-montane and alpine scrubs, heaths and tussock grasslands, to c. 4100 m or somewhat more. The two taxa with the greatest altitudinal range, *C. papuensis* subsp. *discolor* and *C. wollastonii*, vary considerably according to whether they come from lower-altitude forest edges and clearings, where they are sprawling treelets, or from alpine scrub and grassland, where they tend to form compact bushes.

The altitudinal distribution of these taxa is shown in Table 1 and their geographical distribution in Maps 1-4. The representative collections cited below for each taxon have been chosen as far as possible to include those from the lowest and highest stations. The maps are based on the localities of the cited representative specimens.

Key to *Coprosma* in New Guinea

1. Stipule not sheathing, truncate or very broadly obtuse and often with only a single (central) denticle; leaves in 2s, not articulate to stem, less than $12 \times 2(-2.5)$ mm; floral bud at anthesis c. 10 mm long, corolla narrow, lobes short (c. 1/4 as long as tube); small weak-stemmed woody plant (stems to c. 3 mm diam.), prostrate or pendent in loose mats or cushions **1. *C. archboldiana***
- 1a. Stipule sheathing (sometimes only shortly so, but then usually with more than one denticle), ovate-triangular or deeply lobed; leaves in 2s or 3s, distinctly articulate to stem, often greater than 12×2.5 mm (except in *C. divergens*); floral bud at anthesis less than 7 mm long, corolla broadly campanulate, with relatively long lobes; shrubby small trees or bushes, branches sometimes \pm scandent **2**
2. Leaves in 2s (or, if in 3s, then scabridulous above) **3**
- 2a. Leaves in 3s **6**
3. Leaf blades to $10(-17) \times 2.5(-3.5)$ mm, often slightly oblique distally, apex subobtuse or acute and with a short blunt mucro, midrib hardly sunken above, not prominent below; petiole \pm lacking **3. *C. divergens***
- 3a. Leaf blades very variable in size and shape, 3-37 mm long, symmetrical to an acuminate or spiny apex, midrib sometimes sunken above and usually prominent below; petiole usually distinct, 0.5-3 mm long **4**
4. New stems slender (less than c. 1 mm diam., not including the rather coarse hairs to 0.6 mm long); stipule triangular in outline, 3-lobed, with an elongate and sometimes slightly

recurved central lobe, very sparsely ciliate or glabrous on margin, with age becoming strongly yellow-sclerotized; leaf blade 3-8(-13) × 2.5-4(-7) mm, glabrous

- **5b. *C. wollastonii* var. *epiphytica***
- 4a. New stems more than 1 mm diam., glabrous or weakly pubescent or setulose; stipule usually not lobed (sometimes lobed in var. *wollastonii*), ciliate, with age remaining pale or yellowish-brown and only slightly sclerotized5
5. Leaves lax or crowded, only somewhat spinose (spine to 0.5(-1) mm long), midrib sometimes with fine hairs above and with longer bristly hairs below, margins usually ciliate or setulose, rarely the blade scabridulous above; stipule triangular (sometimes narrowly so), ciliate on margin and sometimes with similar appressed hairs on face
..... **5a. *C. wollastonii* var. *wollastonii***
- 5a. Leaves crowded, pungently spiny (spine to 1(-2) mm long), glabrous above and below on midrib, margins glabrous or only very finely papillose- scabridulous, blade glabrous above; stipule ± ovate-hooded, glabrous except on margin **5c. *C. wollastonii* var. *novoguineensis***
6. Leaf blades coriaceous, ovate, to 25 × 8 mm, ± curved or folded upwards along the midrib, margins not recurved, apex pungent (spine to 3 mm long); stipule with a long central setulose lobe and 2-3 pairs of similar but shorter lateral lobes, with age becoming strongly yellow-sclerotized **2. *C. brassii***
- 6a. Leaf blades chartaceous to subcoriaceous, ovate to elliptic(-oblong), sometimes more than 25 × 8 mm, not upfolded, the margins often recurved, apex acute or shortly acuminate-spinulose (spine if present less than 1 mm long); stipule sometimes with a ciliate-setulose subulate central lobe but with lateral lobes hardly or not at all developed, with age slightly to quite strongly yellow-sclerotized7
7. Vegetative parts glabrous; leaf blades to 5 × 1.7 cm, usually 4-5 × as long as wide (rarely narrower), domatia usually present, in the axils of the lateral veins and sometimes also towards the margins **4a. *C. papuensis* subsp. *papuensis***
- 7a. Vegetative parts ciliate-setulose; leaf blades seldom more than 3 cm long, domatia present or lacking, midrib below sometimes with bristly hairs to c. 0.5 mm long8
8. Domatia lacking; stem and stipule margin usually copiously setulose; leaf blades usually c. 4-6 × as long as wide **4b. *C. papuensis* subsp. *discolor***
- 8a. Domatia present (only in the axillary position); stem and stipule margins sparsely setulose; leaf blades seldom more than 4 × as long as wide; Mts Michael, Otto, Piora, Amungwiwa
..... **4c. *C. papuensis* subsp. *mopaensis***
- 1. *Coprosma archboldiana* Merr. & L. M. Perry in J. Arnold Arbor. 26: 259, fig. 11A. 1945 (Fig. 1A, 2A, 3F, 5A, 6A, Map 1).**

Type: Mt Wilhelmina, 7 km NE of [summit], 3400 m, pendent in great cushion-like masses on moist semi-shaded cliffs, flr, frt, IX.1938, *Brass & Meyer-Drees 9831* (Holo-: A 63026 !; iso-: L !).

Small weakly woody perennial, prostrate, forming mats or loose cushions, branchlets not exceeding c. 3 mm diam.; new stems 0.75 mm diam., with minute patent hairs.

Leaves in 2s; petiole to 1(-2) mm long, hardly differentiated from blade and not articulate to stem; blade lanceolate to elliptic-oblong, 6-12 × 1.5-2.5 mm, firmly chartaceous, apex (subobtuse-)acute or shortly acuminate and sometimes bluntly mucronate (never spinose), margins sparsely ciliate with ± patent hairs c. 0.3 mm long or occasionally glabrous, midrib below plane or



Map 1. – Distribution in New Guinea of *Coprosma archboldiana* Merr. & L. M. Perry (solid circle) and *C. brassii* Merr. & L. M. Perry (hollow circle).

irregularly raised and sometimes with a few patent hairs, surfaces otherwise glabrous, lateral venation obscure.

Stipule not sheathing, i.e., stipule margin merging laterally into the sides of the strap-like petioles), the face very short (to c. 0.5 mm long) and broadly obtuse to truncate, usually only sparsely ciliate on margin, with a single stout denticle 0.3 mm long and sometimes also a minute adjacent or lateral 1(-2) pairs of denticles, with age the stipule becoming dull greyish brown or slightly yellowish, thickened-corky but not sclerotized.

Distribution. – Oranje Mts (Mt Wilhelmina [Trikora]); Star Mts (Mt Capella, Sirius Vale); Arfak Mts.

Altitude. – 3100-3900 m.

Notes. – **1.** *Coprosma archboldiana* is very different from the other New Guinea species in its slender and hardly woody trailing stems, petioles not articulate to the stem, leaf blades with stomata on both surfaces, non-sheathing stipules, long-tubed corolla, and violet (rather than red-orange) fruit. In its vegetative characters and the distinct lobed calyx of its male flower it most closely resembles *C. pumila* of Tasmania. As noted by MERRILL & PERRY (1945) it also seems close to *C. ernodeoides* of Hawaii; this however lacks the lobed male calyx.

2. For a photograph of *C. archboldiana* growing on a rock face high on Mt Trikora see MANGEN (1993, tab. 22).

Representative collections. – Of a total of **fourteen seen**: 3 miles E of Wilhelmina-top, 3650 m, matted on exposed rock faces, VIII.1938, *Brass 9411* (A, L); 11 km NE of Wilhelmina-top, 3400 m, alpine grassland, dwarf shrub prostrate on sandy beaches of a stream, flr, IX.1938, *Brass & Meyer-Drees 9817* (A, L); Sirius Vale, 3360 m, flr, 23.IV.1964, *Craig 121* (CANB, L); E summit of Mt Capella, 3100 m, creeping perennial forming loose mats, flr, 18.IV.1975, *LAE 67459* (Barker & Umba) (A); Mt Trikora [Wilhelmina], Upper Somalak Valley, 3920 m, 10.VIII.1984, *Mangen 975* (A, L); Arfak Mts, fruit pale violet, *Sleumer & Vink 4335* (LAE).

2. *Coprosma brassii* Merr. & L. M. Perry in J. Arnold Arbor. 26: 260, fig. 11B. 1945 (Fig. 1B, 2B, 3A, 3B, 6B, Map 1).

Type: Mt Wilhelmina, 7 km NE of [summit], 3650 m, very abundant on forest borders, large weak shrub of brownish appearance 1.5-2.5 m high, flr, IX.1938, *Brass & Meyer-Drees 9843* (Holo-: A 63027 !; iso-: L !).

Compact or sometimes loosely branched shrubby small tree to at least 2.5 m tall; new stems c. 1.5-2.5 mm diam., with patent to antrorse- appressed hairs to c. 0.3 mm long. Leaves in 3s, crowded, subsessile or with a broad petiole to 1(-2) mm long; blades ovate, 12-25 × 5-8 mm, coriaceous, each side of blade upfolded or upwardly curved about the midrib, apex with a stout spine 1-3 mm long, margins plane and distally erose-papillose (and sometimes also setose), the midrib hardly sunken above, usually slightly prominent below, surfaces of blade glabrous (or midrib above sparsely setulose), lateral venation obscure.

Stipules shortly sheathing, less than c. 0.5 mm long (but sheath sometimes emarginate above middle of petiole base), the face c. 3 mm long, broadly triangular in outline, palmatifid to c. halfway into (3-)5-7 setose subules, the central subule to 2 mm long and the lateral subules 0.2-0.7 × as long, each with a denticle c. 0.25 mm long, with age the stipule becoming strongly yellow-varnished and sclerotized.

Distribution. – Nassau and Oranje Mts (Mt Carstensz, Mt Wilhelmina, Valentijn Ra.); Star Mts; Central Ra. (Mt Burgers); Victor Emanuel Ra. (Mt Womtakin); Mt Hagen.

Altitude. – 3300-4150(-4300?) m.

Notes. – 1. *Coprosma brassii* and *C. wollastonii* subsp. *novoguineensis* resemble one another in their epacrid-like foliage. However, the former has its leaves in 3s and the latter in 2s, and their stipules are very different. Even detached leaves can be identified correctly, since leaves of *C. brassii* have much more strongly erose-setose margins.

2. BRASS (in ARCHBOLD & al., 1942: 279) referred to a piece of forest high on Mt Wilhelmina at 3800 m as having two species of *Coprosma* in its dense marginal shrubbery: “One of the coprosmas, a shrub of one meter to a meter and a half, generally bearded with a brown hepatic, was also common on the grasslands below tree limit and grew scattered over tussock grass slopes up to an altitude of about 4150 metres”. This would seem to be a reference to *C. brassii* (cf. *Brass & Meyer-Drees 9842-3* and *10304*, cited below). The other *Coprosma* would then be *C. wollastonii* var. *novoguineensis* (cf. *Brass & Meyer-Drees 10380*).

This altitudinal limit of 4150 m for *C. brassii* in the Nassau and Oranje Mountains is extended upwards by the claim of New Zealand mountaineer D. E. Cooper (VAN ROYEN, 1983: 2749, mistakenly as “R. Cooper”), who indicated on the original label of his collection number 10 (AK 92703) that such plants grew up to 4300 m. That collection is of both *C. brassii* (AK, L) and *C. wollastonii* var. *novoguineensis* (L only). The data of MANGEN (1993) for Mt Trikora (Wilhelmina) makes it likely that Cooper is referring to latter taxon. However, the highest of Mangen’s Mt Trikora var. *novoguineense* collections that I have seen (A, L) comes from only 4140 m.

COOPER (1971: 353) also noted for his collection number 10 that the inner bark was bright yellow when fresh (as in a number of New Zealand coprosmas) and that it had a honey-like smell (a novel observation).

3. MANGEN (1983: 80) described the composition of a *Coprosma brassii*-*Styphelia suaveolens* heath community on Mt Trikora (Wilhelmina) at 3450-3730 m, in which the former species exists as “crooked shrubs, 50-100 cm high”.

Representative specimens. – Of a total of **twenty-four seen**: 11 km NE of Wilhelmina-top, 3400 m, robust shrub 2 m high, frt, IX.1938, *Brass & Meyer-Drees 9807* (A, L); 7 km NE of Wilhelmina-top, 3650 m, very abundant on forest

borders, large weak shrub of brownish appearance, 1.5-2.5 m high, flr, IX.1938, *Brass & Meyer-Drees 9842* (A, L); 2 km NE of Wilhelmina-top, 3800 m, subalpine forest, shrub \pm 2 m tall, very common, flr, IX.1938, *Brass & Meyer-Drees 10304* (A, L); Carstensz Mts, in a river valley flowing from the North Wall, 3700 m, as a shrub or tree to 6 m high (sic) on plateau grass and scrubland, in forest of mountains and as scattered shrubs above bushline at 4300 m, "bingabee" (Dani lang.), 24.VII.1961, *Cooper 10* (AK, L); Star Mts, W summit Mt Antares, 3380 m, small shrub c. 30 cm tall, flr, 24.VII.1959, *Kalkman 4495* (A, L); Central Ra., Mt Burgers, 3680 m, flr, frt, 24.III.1977, *LAE 59757* (*Vinas & Veldkamp*) (A, L); Star Mts, Mt Scorpion, 3600 m, flr, 21.V.1975, *LAE 65907* (*Croft & Hope*) (L); Star Mts, SE side Mt Capella summit ridge, 3300 m, flr, 17.IV.1975, *LAE 67097* (*Vinas & Wiakabu*) (A, L); Mt Trikora [Wilhelmina], 3950 m, treeline shrub, flr, 12.VIII.1983, *Mangen 431* (L); Valentijn Mts, NE of Koruppun V., 3650 m, flr, 9.VIII.1988, *Mangen 1775* (A); Carstensz Mts, Matik Plateau E of Baliem V., 3300 m, common low sprawling shrub, "pareggil" (Yali lang.), frt, X.1992, *Milliken 1596* (A); Victor Emanuel Mts, Mt Womtakin, 3690 m, 8.I.1965, *NGF 20683* (*Henty*) (L); Central Ra., Mt Burgers, 3675 m, high grassland shrub, branches erect to patent, flr, 25.III.1977, *Veldkamp & Vinas 7471* (L); Mt Carstensz, G. Ertzberg, 3980 m, 10.VI.1985, *Widjaja 2281* (L).

3. *Coprosma divergens* W. R. B. Oliv. in Rec. Domin. Mus. 1: 44, fig. 1, tab. 14 fig. 1. 1942 (Fig. 1C, 2C, 3E, 6C, Map 2).

Type: Mt Albert Edward, 3680 m, in grassland on rocky slope, spreading shrub 0.75 m tall, flr, V-VII.1933, *Brass 4216* (Holo-: WELT 32690 !; iso-: A 63029 !).

Small shrubby tree to 2(-4.5) m tall; new stems c. 1 mm diam., puberulous with slender patent hairs to c. 0.15 mm long (never glabrous).

Leaves in 2s, subsessile; blades elliptic-oblong, 3-9(-17) \times 1.5-3.5 mm, firmly chartaceous, often somewhat oblique in distal quarter or so, apex (subobtuse-)acute and with a short blunt mucro, margins glabrous or with sparse short cilia, both surfaces (incl. midrib) glabrous, usually the midrib hardly grooved above nor prominent below.

Stipule shortly sheathing (sheath to c. 0.4 mm long), the face usually broad-triangular (occasionally the central lobe somewhat narrowed), to 1.5(-2.5) mm long, lateral lobes \pm lacking, margin usually with 2-5 pairs of small denticles (to 0.3 mm long) and sparsely short-ciliate, with age the stipule becoming brownish-orange or pale brown and only slightly thickened (not sclerotized).



Map 2. – Distribution in New Guinea of *Coprosma divergens* W. R. B. Oliv.

Distribution. – Sugarloaf Mt; Yobobos; Mt Giluwe; Kubor Mts (Mt Sigal Mugal, Mt Kinkain); Mt Wilhelm; Mt Piora; Finisterre and Sarawaket Mts; Mt Amungwiwa; Owen Stanley Mts (Mt Albert Edward to Mt Victoria and Mt Service).

Altitude. – 2660-4120 m.

Notes. – 1. MERRILL & PERRY (1945: 259) commented that the isotype in A (*Brass* 4216) bears male flowers. The relevant sheet has mounted on it a packet of the above number, which is female, together with a flowering shoot of *Brass* 4215, which is male.

2. *Coprosma divergens* usually forms a compact “divaricating” bush, whose branches bear short, straight ultimate branchlets that spread at c. 45° and are neither planate nor fastigiate — see the photographs of this species in heath on Mt Albert Edward at 3680 m (HOPE, 1980: tab. 34) and in grassland on Mt Bangeta (VAN ROYEN, 1983: tab. 189).

There is little if any differentiation of the *C. divergens* shoot system into fertile brachyblasts along long shoots, nor any regular abortion of its shoot apices (HEADS, 1996); in this the species resembles the small-leaved high-altitude coprosma of Hawaii, *C. elliptica*, rather than the divaricating coprosmas of New Zealand.

3. Collections from the Sarawaket Mts have relatively large leaves, those on *Clemens 10108A*, for example, reaching 17 × 3 mm. Similarly, the stipules are unusually elongate, the central lobe being rather narrow and up to 1.5 mm long.

4. One collection seen from the Sarawaket Mts (*Hoogland 9839*, L sheet only) has a few small axillary pit-domatia on some of its leaves but is not otherwise anomalous in *C. divergens*. The collection *Hoogland 9838*, of identical provenance (but noted as being from a smaller and male plant) is without domatia, as are the ten other collections seen of this species from the Sarawaket Mts.

5. One of the pieces composing the L sheet of *Hoogland & Schodde 7018* has a vigorous ultimate length of shoot (stem c. 1.3 mm diam.) whose nodes bear 4 leaves rather than the usual 2.

6. VAN ROYEN (1983: 2752) slips in saying that *C. divergens* prefers damper localities than does “*C. brassii*, with which it is often found” — he would have intended the former’s most frequent associate, *C. papuensis* subsp. *discolor*.

7. No relevant specimens have been seen for two of the localities cited by VAN ROYEN (1983: 2752), namely the Yobobos grasslands (source of the Lagaip River) and Mt Sigal Mugal (Kubor Mts), but these records can be accepted since they are close to confirmed ones (e.g., *Hoogland & Schodde 7018*, *Pullen 5132*).

Representative collections. – Of a total of **sixty-five seen**: Mt Wilhelm, Brass’s Tarn, 3925 m, shrub 2 m high, branches somewhat overhanging, with numerous short stiff side shoots, flr, 21.VI.1965, *van Balgooy 788* (A, L); Mt Wilhelm, 3600 m, 26.V.1960, *Borgmann 36* (L); Mt Albert Edward, 3800 m, in grassland on rocky slope, spreading shrub 0.75 m tall, flr, 22.VI.1974, *Craven 2713* (A, L); SE flank of Mt Victoria, Isuani Basin, 2800 m, frt, 3.VII.1974, *Craven 2882* (A, L); Mt Sarawaket, 3050-3680 m, 3.III.1939, *Clemens 10108A* (A); Sarawaket Mts, Tempanpan, 3360 m, common in alpine shrubbery c. 2 m tall, flr, frt, 13.IX.1964, *Hoogland 9839* (A, L); N slopes of Sugarloaf complex along Wapu R., 2890 m, 1.5 m tall shrub in treefern grassland, frt, 12.VII.1960, *Hoogland & Schodde 7018* (A); Mt Scratchley, 3420 m, shrub with many rigid branches, forming a mound, flr, 7.V.1971, *LAE 51464* (*Stevens & Coode*) (A, L); Mt Piora, 3400 m, flr, 4.IX.1975, *LAE 68185* (*Croft & Akakavara*) (A, L); Mt Amungwiwa, 3420 m, flr, frt, XI.1963, *NGF 17992* (*Womersley*) (L); Mt Bangeta, 4120 m, frt, 1.XI.1963, *NGF 20037* (*van Royen*) (A, L); W slope of Wharton Ra., 2980 m, frt, 20.I.1965, *NGF 30017* (*van Royen*) (A); Mt Wilhelm, Lake Aunde, 3540 m, climbing shrub, “ninbul”, flr, frt, 11.VI.1968, *NGF 35058* (*Vandenberg*) (A, L); Mt Kinkain, 3720 m, low stunted shrub to 15” tall [in] alpine grassland with low scattered shrubs, flr, frt, 26.VII.1963, *Pullen 5132* (A); Mt Service, Iswan Swamp [Isuani Basin], 2660 m, bushy globe shrub up to 1 m across, found mainly in the damper parts of the grassland, flr, frt, 17.V.1976, *van Royen 10811* (L); Finisterre Mts, S slopes of Naitmambi Ra., 3350 m, flr, frt, 6.VIII.1976, *van Royen 11621* (L); W summit grasslands Mt Giluwe, 3140 m, frt, 8.VIII.1961, *Schodde 1737* (A, L); Woitape, road to Sidibarmu, 2924 m, frt, 27.VII.1971, *UPNG 1262* (*Millar & Tippet*) (L); Owen Stanley Mts, Lake Omha, 3640 m, flr, 9.XII.1986, *UPNG 13214* (*Hopkins 683*) (A); Murray Pass, 2140-2740 m, flr, 11.VIII.1968, *Woods 3169* (A, L).

4. *Coprosma papuensis* W. R. B. Oliv. in Bernice P. Bishop Mus. Bull. 132: 147, tab. 41A. 1935.

Type: Mt Scratchley, 1896, *Giulianetti* (Holo-: K, n.v.).

Small tree to c. 4 m tall, branches spreading or sometimes scandent; new stems glabrous or pubescent or setulose.

Leaves in 3s, sessile or shortly petiolate; blade \pm elliptic, 1.2-5 cm long, firmly chartaceous to coriaceous, glabrous or with short hairs on margin and midrib above, sometimes with longer bristly hairs on midrib below, apex acute to shortly spiny, midrib not usually prominent below at least in distal two-thirds, domatia present or not, lateral nerves sometimes visible above as narrow furrows.

Stipules sheathing, face triangular, with a central narrow-triangular lobe, the (2-)3 pairs of lateral lobes very short or \pm lacking, margin glabrous or sparsely to densely ciliate, denticle usually large (to c. 1 mm long), with age the stipule becoming somewhat yellow-sclerotized.

Distribution. – Mountainous regions of Papua New Guinea, from Mt Bosavi and the Doma Peaks east to the Owen Stanley Mts and Mt Suckling, and including the Finisterre and Sarawaket Mts.

Altitude. – c. 2200-3840 m.

Notes. – **1.** *Coprosma papuensis* is treated here as having three subspecies. The typical subspecies comprises relatively large-leaved, glabrous, domatiate plants and is confined to the Owen Stanley Mts. The second subspecies, widespread in the Highlands regions of Papua New Guinea, is the taxon described by VAN ROYEN (1983) as *C. discolor*. The third subspecies, subsp. *mopaensis* newly described below, combines distinctive features of the other two, in particular, the domatia of the former and the setulose stems and stipules of the latter. It also falls between them geographically, being known only from Mts Michael, Otto, Piora and Amungwiwa (hence the epithet).

- 4a. *Coprosma papuensis* subsp. *papuensis* (Fig. 1D, 2D, 4, 6D, Map 3).

Stout shrubby small tree to c. 3(-4) m tall, branches sometimes wide-spreading but hardly subscaudent; new stems 2-2.5 mm diam., glabrous but often textured by close-spaced low \pm hemispherical papillae.

Leaves in 3s, \pm sessile, i.e., petiolar region broadly winged; blade elliptic (-obovate), (1.2-)2-5 \times (0.4-)0.7-1.7 cm, \pm firmly chartaceous, glabrous, apex acute or shortly attenuate into a blunt mucro c. 0.5 mm long, margins entire or (distally) conspicuously papillose-erose (very rarely setose), crypt-domatia present in axils of lateral veins and sometimes also towards margins (domatia rarely lacking), the domatium-mouth usually somewhat pustulate and situated on either the upper or lower surface (the extra-axillary domatia almost always opening to upper surface).

Stipule shortly sheathing (sheath to c. 0.5 mm long, but often nearly lacking), face 2-3.5 mm long, usually with a stout narrow-triangular central lobe and 2 pairs of much shorter lateral lobes, margin glabrous, denticles relatively large, the central one to almost 1 mm long.

Distribution. – Owen Stanley Mts, from Mt Strong east to Mt Suckling.

Altitude. – 2660-3800 m.

Notes. – **1.** The domatia are remarkable in character but have not received much attention. The protologue of *C. papuensis* has no mention of them, even though there is an unnumbered WELT sheet of domatiate leaf fragments that can be presumed to derive from the holotype. VAN ROYEN (1983) did not note that the domatia can



Map 3. – Distribution in New Guinea of *Coprosma papuensis* W. R. B. Oliv. (subsp. *discolor* (P. Royen) R. O. Gardner, solid circle; subsp. *mopaensis* R. O. Gardner, half-circle; subsp. *papuensis*, hollow circle).

be extra-axillary nor that they can open to either surface. Collectors have sometimes interpreted them as galls or light-colored swellings.

Domatia are completely lacking from several collections from the Iswan Swamp [Isuani Basin], e.g., *Craven 2881*, *van Royen 10795*, but are present in normal abundance in at least one other collection from here.

2. A single collection of this subspecies (*LAE 61363*) has setose leaf margins; its stipules and stems however are quite glabrous.

3. Under the circumscription adopted here, the following localities cited by VAN ROYEN (1983: 2736, as *C. papuensis*) are seen to be erroneous, being based on subsp. *discolor*: Mt Giluwe, Mt Ialibu, Tomba [Mt Hagen], Mt Hagen, Mt Sigal Mugal, Keglsugl-Mt Wilhelm, Mt Kerigomna.

4. This subspecies is illustrated by HOPE (1980, tab. 27) in a photograph of forest-edge shrubland on Mt Albert Edward at 3680 m, with “mainly small-leaved twiggy *Coprosma papuensis*”. Similarly the mention of “*Coprosma-Rhododendron* forest-edge shrublands, which on Mt Wilhelm are 2-5 m in height and dominated by *Coprosma papuensis*” (HOPE, 1980: 174) is a reference to the *C. papuensis* subsp. *discolor* of this locality.

5. No vernacular name seems to have been recorded for this plant — those cited by VAN ROYEN (1983: 2736) all refer to subsp. *discolor*.

6. *Coprosma papuensis* subsp. *papuensis* closely resembles the three westernmost members of the genus, *C. sundana* Miq. of Java, *C. crassicaulis* Stapf of Borneo (Mt Kinabulu), and “*C. celebica*” (Valeton, in sched.) of Sulawesi. These are also high-altitude shrubs, with elliptic, non-spiny, firm-textured leaves that approximate those of the New Guinea taxon in size; however, they lack domatia. *C. sundana* is glabrous; its leaves are mostly in 3s but can occasionally be paired. *C. crassicaulis* has puberulous stems and stipules (margins at least); its leaves are mostly paired but occasionally are in 3s. The impression gained from a modest

amount of herbarium material is that leaf arrangement is more labile in these two species than in *C. papuensis*. The only piece of "*C. celebica*" I have seen (Whitten, L 987.188.078) has a glabrous stem, paired leaves and hairy cupular stipules.

Representative collections. – Of a total of **twenty-two seen**: Mt Albert Edward, 3680 m, common on forest fringes, large straggling shrub or small tree, flr, frt, V-VII.1933, *Brass 4217* (A); Mt Albert Edward, 3800 m, 22.VI.1974, *Craven 2710* (A, CANB, L); Mt Victoria, Isuani Basin, 2800 m, flr, 3.VII.1974, *Craven 2881* (A, CANB, L); Mt Victoria, 3550 m, flr, 12.VII.1974, *Craven 3042* (A, CANB, L); Mt Scratchley, 3420 m, shrub, branches ± erect, branchlets spreading, leaves ... with raised yellow markings, flr, frt, 7.V.1971, *LAE 51462* (Stevens & Coode) (A, CANB, L); Mt Albert Edward, 3600 m, flr, frt, 21.VI.1974, *LAE 61363* (Croft) (A, CANB, L); Mt Victoria, Isuani grassland, 2800 m, flr, frt, 4.VII.1974, *LAE 61589* (Croft) (CANB, L); Mt Kenive (Nisbet) W slopes, 3000 m, grassland- forest transition, flr, 28.VII.1974, *LAE 65085* (Croft) (A, L); Mt Suckling, 3400 m, open alpine shrubby, very robust, flr, frt, 22.VIII.1965, *NGF 22385* (Gillison) (A, L); Mt Service, Iswan Swamp, 2660 m, in dry open grasslands, domatia on underside of leaves none, flr, 17.V.1976, *van Royen 10795* (L); Lake Omha, 3640 m, edges of grassland clearings in subalpine forest dominated by *Dacrycarpus compactus*, flr, 9.XII.1986, *UPNG 13216* (Hopkins 685) (A).

4b. *Coprosma papuensis* subsp. *discolor* (P. Royen) R. O. Gardner, **stat. & comb. nov.** (Fig. 1F, 2E, 5B, 6F, 7, Map 3).

≡ *Coprosma discolor* P. Royen, *Alpine Fl. New Guinea* 4: 2738, fig. 792. 1983 [as *C. discoloris*].

Type: Mt Wilhelm E slopes, 2770 m, plentiful in second growth of small clearings etc. in forest, weak or subsucculent shrub up to 4 m high, flr, 5.VII.1959, *Brass 30320* (Holo-: A 63028 !; iso-: L !).

Compact or subsucculent shrubby small tree to c. 5 m tall; new stems c. 2 mm diam., usually with ± patent hairs c. 0.25 mm long, occasionally glabrous especially for some way below petiole bases.

Leaves sessile or more usually with a narrowly winged petiole to 3 mm long; blade variable: in subsucculent plants linear-lanceolate, to 26 × 8 mm, chartaceous, bluntly mucronate at apex, margins weakly ciliate; in plants of higher altitude the blade ovate-lanceolate, mostly less than c. 13 × 6 mm, subcoriaceous, apex with a short apical spine to c. 0.5 mm long, margins setulose to scabrid; in all plants the midrib sunken above and usually pubescent or setulose there (occasionally glabrous), midrib usually glabrous below but sometimes setose with stout unicellular hairs to c. 0.75 mm long.

Stipule sheathing for c. 0.5 × its length (sheath rarely less than 0.8 mm long), face triangular in outline, with a central ± subulate lobe to 1.5 mm long and with 1-2(-3) pairs of much shorter lateral lobes (or these quite lacking), denticles c. 0.2 mm long, margin setulose (sometimes conspicuously so).

Distribution. – Doma Mts (Mt Kerewa, Mt Doma); Mt Bosavi; Sugarloaf Mts; Yobobos; Tari Gap; W. Highlands (Sirunki, Tubongas); Mt Giluwe; Mt Ialibu; Mt Hagen; Mt Kinkain; Mt Wilhelm; Bundi Gap; Mt Kerigomna; Mt Otto; Finisterre and Sarawaket Mts.

Altitude. – 2135-3840 m (cf. VAN ROYEN, 1983).

Notes. – **1.** The protologue depicts a plant with narrow leaves and elongate long-sheathing stipules; this represents the subsucculent lower-altitude variant of forest clearings, river edges etc.

2. Specimens of subsp. *discolor* occasionally appear glabrous but short setae are always present on the margin of the stipule, particularly around the central lobe. Longer patent bristly hairs are sometimes present on the midrib below; these are seen in some specimens of subsp. *mopaensis* too but never in subsp. *papuensis*. In subsp. *discolor* a bristly midrib has been observed in collections from: Western Highlands (Sirunki), Mt Hagen, Mt Giluwe, Mt Ialibu, Kerigomna. Non-bristly individuals have also been collected from each of these localities, and appear to represent the more common phenotype.

Fig. 7. – Variation in *Coprosma papuensis* var. *discolor* foliage. Scale bar 1 cm.

- A. Specimen from 2200 m [Brass 30925].
- B. Specimen from 3600 m [v. Balgooy 338].



3. No instance is known to me of domatia in this subspecies.
4. One collection of subsp. *discolor* (CANB and L sheets of *Hoogland 9772*, from the Sarawaket Mts) is shortly and closely scabrid over the entire leaf surface rather than just in the midrib groove; this plant is not otherwise anomalous. The two other collections seen from this locality are normal in leaf character.
5. Subsp. *discolor* is often found growing with *C. divergens* but I have seen only one specimen (*LAE 74359*) at all suggestive of hybridity. However, if either the opposite or the ternate leaf arrangement were to dominate in the F₁ then it might be difficult to recognize hybrids from morphology alone, especially in the smaller-leaved populations.
6. VAN ROYEN (1983: 2742) cited (as *C. discolor*) a number of erroneous localities for this taxon: that of Mt Scorpion (Star Mts) appears to be based only on *LAE 68010*, which is *C. wollastonii*; those for Mt Albert Edward and Mt Suckling are based on subsp. *papuensis*; and that for Mt Piora is based on subsp. *mopaensis*. His record for the Cromwell Mts is accepted as being geographically probable.
7. The epithet “*discolor*” refers to the appearance of the live material, where the lower side of the blade is much paler than the upper side. This has been noted by collectors for subsp. *papuensis* as well, and is presumably also true for subsp. *mopaensis*.

Representative collections. – Of a total of **seventy-two seen**: W. Highlands, Sirunki, 2640 m, flr, 31.VII.1962, *ANU 448 (Walker)* (A, L); W. Highlands, Tubongas, 2570 m, shrub 1 m tall in short grassland, flr, frt, 22.XII.1964, *ANU 2224 (Flenley)* (A, L); Mt Hagen, Tomba track, 3140 m, “quirontogump” (Melpa lang.), “hepmey” (Okapa lang.), flr, 15.VI.1966, *ANU 6101 (Wheeler)* (A, L, CANB); Mt Wilhelm, Lake Aunde, 3660 m, frt, 19.V.1966, *ANU 7098 (McVean & Wade)* (A, L); Mt Wilhelm, Pindaunde V., 3200 m, flr, frt, 10.VII.1966, *ANU 7353 (Wade)* (A, CANB, L); Kubor Ra., Mt Sigal Mugal, 3580 m, flr, 30.IX.1972, *ANU 15601 (Smith)* (CANB); Mt Wilhelm, 3400-3600 m, 31.V.1960, *Borgmann 56* (L); Mt Wilhelm E slopes, 2770 m, plentiful in second growth of small clearings etc in forest, weak or subscented shrub up to 4 m high, flr, 5.VII.1959, *Brass 30320* (A, L); Mt Otto S slopes, Iamahagi Creek, 2200m, 9.VIII.1959, *Brass 30925* (A, L); Sarawaket Mts, nr Samanzing, 2130-2440 m, 22/23.XI.1938, *Clemens 9373* (A); Marafunga (W. of Fatima R.), 2550 m, straggling shrub to scrambler in open community on river terrace, flr, frt, 14.XI.1970, *Grubb & Edwards 19* (A, L); Mt Salawaket, 3050 m, flr, 20.I.1963, *Hartley 11171* (A, L); Sarawaket Ra., Monarauwe, 2490m, flr, 4.IX.1964, *Hoogland 9772* (A, L); Goroka Subdistr., [Mt] Kerigomna camp, 3050 m, climber in low forest on grassland edge, flr, frt, 4.VII.1956, *Hoogland & Pullen 5520* (A, L); N slopes Sugarloaf complex along Wapu R., 2490 m, “waljak” (Enga lang., Poio dial.), flr, 12.VII.1960, *Hoogland & Schodde 7002* (A, L); Yobobos grassland area (source of Lagaip R.), 2580 m, “jandepai” (Enga lang., Kepilam dial.), frt, 16.VIII.1960, *Hoogland & Schodde 7454* (A, L); Mt Bosavi, 2100-2200 m, scrambling in low open stunted forest, 29.IX.1973, *Jacobs* (L); Mt Kerewa, 3490 m, small shrubs with ± horizontal branches ... fire-induced grass- and fern-land, flr, 3.VII.1966, *Kalkman 4757* (A, L); Mt Ambua, 3390 m, flr, 30.VII.1966, *Kalkman 4984* (A, L); Mt Hagen, 2860 m, frt, 18.VII.1970, *LAE 50283 (Stevens)* (A, L); Mt Wilhelm, 3550 m, frt [det. by van Royen as *C. brassii*, but not cited by VAN ROYEN (1983)], 5.IV.1971, *LAE 53138 (Stone)* (L); Mt Ialibu, 3415 m, frt, 9.VIII.1972, *LAE 55781 (Stevens & Foreman)* (A, L); Mt Giluwe S slopes, 3000m, transition between montane rain-forest and alpine grassland, flr, 25.XII.1973, *LAE 60710 (Croft & al.)* (A, CANB, L); Mt Karoma W slope, 3400 m, low bushy 1 m tall shrub, in shrubbery bordering the alpine vegetation, flr, 9.IX.1981, *LAE 73661 (Wiakabu & Veldkamp)* (A, L); Finisterre Mts, Sewe, 2430 m, “dawkingioa”, flr, frt, 11.XI.1964, *NGF 21392 (Sayers)* (L); Chimbu Distr., Pengagl Ck, 2430 m, frt, 22.VIII.1964, *NGF 23706 (Millar & Sayers)* (A, L); Mt Kerewa S slopes, 2980 m, grassland-shrub ridge, scrambling herb (*sic*), flr, 1.VI.1966, *NGF 25201 (Gillison)* (A, L); Mt Giluwe, 3200 m, “kalip” (Komia lang.), flr, 16.VII.1967, *NGF 32501 (Coode & Waring)* (A, L); Slopes of Mt Giluwe, Kaguba, 2740 m, flr, 13.IX.1968, *NGF 32925 (Katik)* (A, L); Lake Aunde, 3500 m, “numbuk”, 10.VI.1968, *NGF 35015 (Vandenberg)* (L); Mt Otto W side, 2920 m, flr, 26.I.1970, *NGF 47059 (Johns & Noble)* (L); Mt Kinkain, 3720 m, shrub to 7' tall, semi-scandent on borders of small shrub-beries in alpine grassland, “yu-yo” (Minj lang.), flr, 26.VII.1963, *Pullen 5130* (A, L); Mt Giluwe W summit grasslands, 3140 m, “mon'd'gan” (Mendi lang.), 7.VIII.1961, *Schodde 1727* (A, L); Mt Giluwe W summit grasslands, 3100 m, “kot'gut” (Mendi lang.), frt, 9.VIII.1961, *Schodde 1751* (A, L); Chimbu V. 2600 m, “ninbugl” (Kuman lang.), flr, frt, 29.VII.1980, *Sterly 80-73* (L); Bundi Gap, 2400 m, 30.VI.1987, *Tade 23* (A); Tari Gap, 2692 m, flr, 15.XII.1982, *Vinas 115* (A).

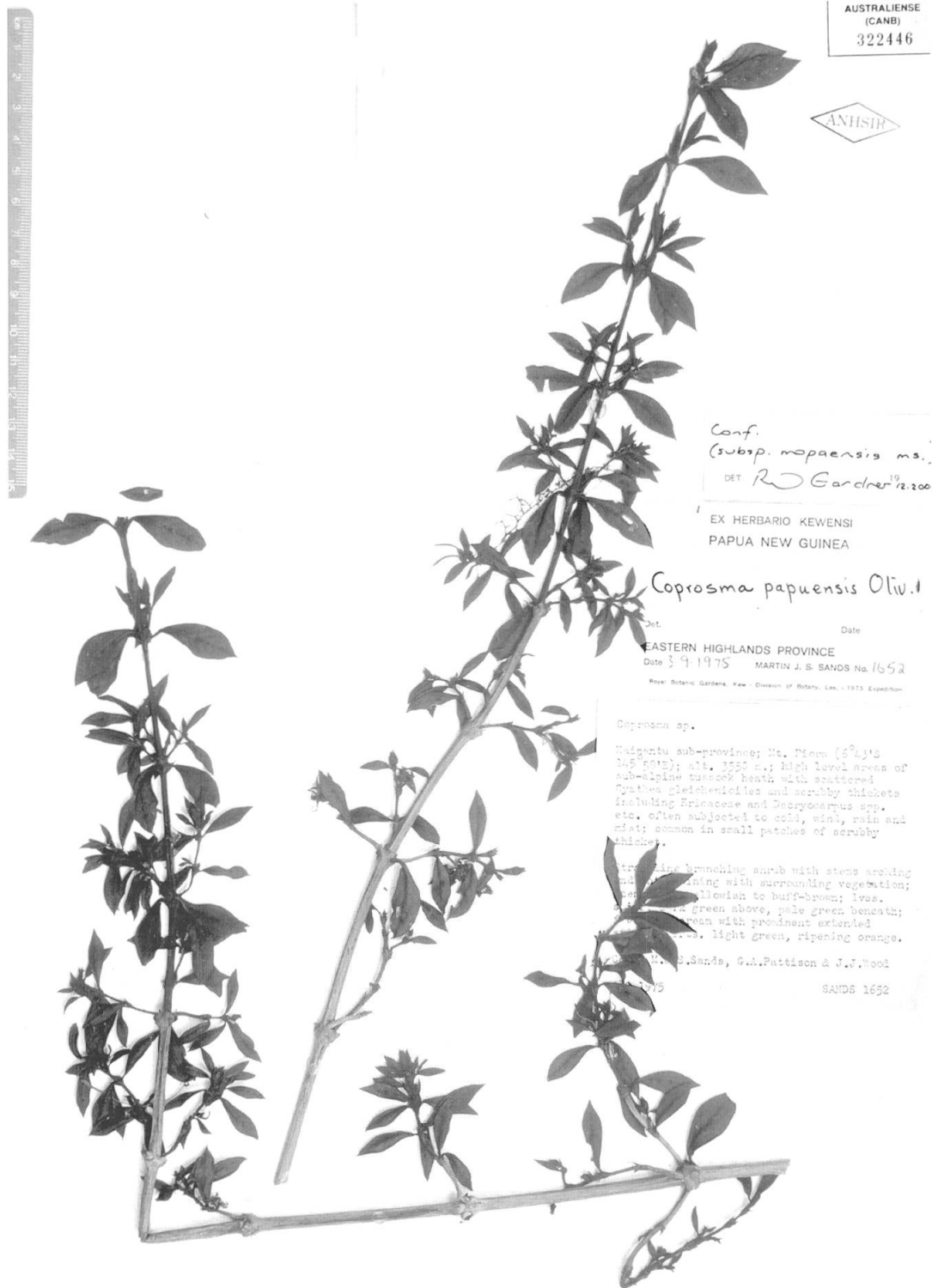


Fig. 8. – Holotype of *Coprosma papuensis* subsp. *mopaensis* R. O. Gardner, subsp. nov. [Sands 1652, CANB]

4c. *Coprosma papuensis* subsp. *mopaensis* R. O. Gardner, **subsp. nova (Fig. 1E, 2F, 6E, 8, Map 3).**

Typus: Mt Piora, 3550 m, high-level areas of subalpine tussock heath ... straggling branching shrub with stems arching and intertwining with surrounding vegetation, female flowers and near-ripe fruit, 3.IX.1975, *M. J. Sands 1652* (Holo-: CANB 322446; iso-: A !, K n.v.).

Haec planta medium tenet inter subsp. papuensem et subsp. discolorum habet enim domatia illius et pilositatem hujus.

Small tree to at least 2 m tall, branches usually spreading or subscandent; new stems 1.5-2 mm diam., mostly setulose with hairs to c. 0.3 mm long.

Leaves mostly laxly arranged, usually with a distinct petiole to c. 2 mm long; blades elliptic, c. 16-27 × 5-11 mm, subcoriaceous, setulose on distal margins (sometimes glabrous or erose-papillose), midrib below occasionally with bristly hairs to c. 0.5 mm long, the domatia axillary only and mostly rather small (lacking in some plants from Mt Otto). Stipule sheath to 1.5 mm long, central subule to 1.5(-2.5), sparse to densely setose on margin.

Distribution. – Eastern Highlands and Morobe Provinces: Mts Michael, Otto, Piora, and Amungwiwa.

Altitude. – 3000-3600 m.

Notes. – **1.** There appears to be no single diagnostic feature for this taxon, which, to judge by the thirteen collections available, is quite variable in leaf characters (Table 2). The restricted distribution makes it convenient to consider it as a subspecies, even if it does overlap with subsp. *discolor* on Mt Otto (although the two do seem to be separated altitudinally here). However, it would also be reasonable to suppose that it might represent a zone of hybridity between the other two subspecies

Table 2. – Variation in *Coprosma papuensis* subsp. *mopaensis* R. O. Gardner. All thirteen known collections are listed (2 sheets for Sands 1652, 3 sheets for NGF 17994).

Collection	leaf size (mm)	domatia setae	margin setae	midrib setae	stipule setae	stem	loc.
Brass & Collins 31267	17 x 4	++	+	0	+	0	M
Brass 31430	16 x 9	++	+	0	(+)	0	M
Cruttwell 2035	22 x 6.5	++	+	0	+	0	M
NGF 11489	17 x 4.5	++	0	0	(+)	0	M
Brass & Collins 31033	25 x 9	(+)	+	0	(+)	0	O
NGF 47072	14 x 6	+	0	0	+	+	O
Veldkamp & Obedi 8599	26 x 7	(+)	+	(+)	+	(+)	O
NGF 16551	20 x 6	++	++	++	++	+	P
NGF 16568	26 x 11	+	+	(+)	++	++	P
Sands 1531	25 x 10	(+)	++	+	++	++	P
Sands 1547	19 x 7	+	++	+	++	++	P
Sands 1652 A	23 x 9	++	+	0	+	++	P
Sands 1652 CANB	27 x 10	++	+	+	+	++	P
NGF 17994 A	16 x 5	++	+	0	(+)	0	A
NGF 17994 CANB	17 x 6	++	++	(+)	++	++	A
NGF 17994 L	20 x 6	++	++	(+)	++	++	A

++ = well-developed; + = present; (+) = sparse/vestigial; 0 = quite lacking.

Localities: **M** = Mt Michael; **O** = Mt Otto; **P** = Mt Piora; **A** = Mt Amungwiwa.

(cf. SCHUITEMAN, 1997: 35). For example, *Brass* 31430 from Mt Michael has only a very few setae on its stipule and leaf margins to separate it from the usual form of subsp. *papuensis*.

2. Some of the collections from Mt Piora (e.g. *NGF* 16551 and *Sands* 1547), and the only collection seen from Mt Amungwiwa (*NGF* 17994), have leaves with a bristly midrib below, a feature occasional in subsp. *discolor* but not known in subsp. *papuensis*.

Collections seen. – Mt Michael, 3600 m, scattered on alpine grassland, flr, frt, 6.IX.1959, *Brass* 31430 (CANB, L); Mt Otto, 3500 m, flr, 12.VIII.1959, *Brass* & *Collins* 31033 (A, CANB, L); Mt Michael, 3600 m, frt, 31.VIII.1959, *Brass* & *Collins* 31267 (CANB, L); Mt Michael, 3400 m, flr, IX.1981, *Cruttwell* 2035 (L); Mt Michael, 3050-3650 m, 2-9.IX.1959, *NGF* 11489 (*Womersley*) (A, CANB); Mt Piora, 3200 m, 10.II.1963, *NGF* 16551 (*Henty & Carlquist*) (L); Mt Piora, 3200 m, frt, 10.II.1963, *NGF* 16568 (*Henty & Carlquist*) (A, CANB, L); Mt Amungwiwa, 3480 m, flr, XI.1963, *NGF* 17994 (*Womersley*) (CANB, L); Mt Otto, 3450 m, frt, 26.I.1970, *NGF* 47072 (*Johns & Noble*) (L); Mt Piora, 3050 m, flr, 29.VIII.1975, *Sands* 1531 (A, L); Mt Piora, 3000 m, flr, 29.VIII.1975, *Sands* 1547 (A, L); Mt Otto, 3500 m, 26.X.1989, *Veldkamp & Obedi* 8599 (CHR).

5. *Coprosma wollastonii* Wernham in Trans. Linn. Soc. London, Bot. 9: 79. 1916.

Type: Utakwa Rvr to Mt Carstensz, Camp XI to XII, 28.I.1913, *C. B. Kloss* (Holo-: BM [fragment !]).

Small shrubby tree to c. 5 m tall, branches sometimes subscaudent; new stems to c. 2 mm diam., pubescent to setose (rarely glabrous).

Leaves in 2s, petiole to c. 3 mm long; blades variable in size and shape, 13-57 × 2.5-10 mm, apex acute or acuminate or spinose, midrib often distinctly and abruptly prominent below (especially in lower-altitude plants) and glabrous there or occasionally setose with rather bristly patent 2-3-cellular hairs to c. 0.5 mm long, margins glabrous to ciliate or setulose, often recurved, lateral nerves sometimes visible above as furrows.

Stipules sheathing, face triangular(-ovate), keeled to somewhat hooded, sometimes with short lateral lobes, denticles mostly less than c. 0.5 mm long, usually densely ciliate on margin (and occasionally pubescent on entire face), with age the stipule becoming firmly crustose but (except in var. *epiphytica*) not or hardly yellow-sclerotized.

Distribution. – Oranje and Carstensz Mts east through the Star Mtns.

Altitude. – c. 2600-4140(-4300 ?) m.

Notes. – 1. The most striking variants within this complex are those that have been described as *C. epiphytica* (incl. *C. scandens*) and *C. novoguineensis* — these are maintained here only at varietal level.

2. I have seen one example of *C. wollastonii* from beyond New Guinea, a collection from Ceram in the Molucca Is., Indonesia (*Eyma* 2077, A, 4.XI.1937, Moerkele besar 2800 m). Its leaves are elliptic, c. 15 × 7 mm, firm-textured and glabrous; the stipules are broadly triangular, with c. 4 pairs of short, densely long-ciliate, lateral lobes. It fits adequately into a broadly circumscribed var. *wollastonii*. Also for Ceram, UEDA (1986: 25) lists as “*Coprosma* sp.” four collections of “straggling, somewhat scandent shrubs” obtained from another high point; presumably they too belong to var. *wollastonii*.

5a. *Coprosma wollastonii* var. *wollastonii* (Fig. 1I, 2I, 5C, 6G, 6I, Map 4).

= *Coprosma habbemensis* Merr. & L. M. Perry in J. Arnold Arbor. 26: 261. 1945. **Type:** 9 km NE of Lake Habbema, 2800 m, X.1938, *Brass* 10587 (Holo-: A 63030 !; iso-: L !).

= *Coprosma lamiana* W. R. B. Oliv. in Rec. Dom. Mus. 1: 45, fig. 2-3, tab. 14 fig. 2. 1942. **Type:** Mt Doorman, *Lam* 1612 (Holo-: BO n.v.; iso-: A !, L !).



Map 4. – Distribution in New Guinea of *Coprosma wollastonii* Wernham (var. *epiphytica* (P. Royen) R. O. Gardner, solid circle; var. *novoguineensis* (Merr. & L. M. Perry) R. O. Gardner, half-circle; var. *wollastonii*, hollow circle).

Small shrubby tree to c. 5 m tall, compact and bushy or with spreading branches.

Leaves usually laxly arranged, with narrowly winged petioles to c. 3 mm long; blades elliptic to oblong, to 2.5(-3.7) × 1.0 cm, apex acute or acuminate or shortly spinose, midrib below glabrous or occasionally with bristly patent 2-3-cellular hairs to c. 0.5 mm long, margins usually ciliate (in lower-altitude plants) or minutely setulose, the lateral nerves sometimes visible above as obscure furrows, margins plane to recurved.

Stipules shortly sheathing (sheath to c. 0.5 m long), face (narrow)-triangular, c. 2.5-3 mm long, sometimes with short lateral lobes (occasionally these to half as long as central lobe), ciliate on margin, sometimes pubescent on entire face.

Distribution. – Mt Doorman; Nassau and Oranje Mts (Utakwa Rvr to Mt Carstensz, Lake Habbema, Quarles Valley, Valentijn Ra.), Wichmann-Hubrecht, Mts Hellwig Mts; Victor Emanuel Ra.

Altitude. – c. 1900-3300 m.

Notes. – **1.** The protologue of *C. wollastonii* refers to a scabridity of the upper side of the leaf blade. According to UTTERIDGE (pers. comm.) the leaves of plants from the type locality of the species, at c.1900-2700 m on Mt Carstensz (Jaya) are invariably scabridulous above, as well as being arranged in 3s, and in his treatment of *Coprosma* on Mt Carstensz (UTTERIDGE, 2002) he restrict the species name to this population, while describing two new species from higher altitude here. I have not seen material of these, and consider they may represent localized intra-specific variation, though I concede, for example, that I have not seen a scabridulous leaf blade elsewhere in the *C. wollastonii* complex, not even in the specimens that VAN ROYEN (1983: 2744) claimed showed it (where, according to my observations, the leaves are only obscurely pustulose).

2. An unnumbered WELT sheet bears a photograph of the holotype, two packets each with a single flower (one male and one female), and also a single scabrid-surfaced leaf. The protologue refers only to male material.

3. *Coprosma habbemensis* was described from relatively low-altitude populations of forest-edge plants, whose elongate plane leaves are notably bristly-hairy on the midrib below and whose stipules are narrowly triangular, distinctly keeled and sparsely appressed-hairy.

Coprosma lamiana was described from a somewhat higher-altitude population, in which the foliage is more crowded and spinose. The type's leaf blades are elliptic-oblong, c. 7 x 3 mm, with recurved papillose-scabridulous margins and with only a few bristles on the midrib; the stipule is broader than in *C. habbemensis* and the stipule hairs face are coarser and more abundant; the stems too are more coarsely hairy.

Representative collections. – Of a total of **nineteen seen**: Lake Habbema, 3225 m, abundant in shrubberies bordering forest, straggling shrub 2-2.5 m high, VIII.1938, *Brass 9144, -5* (A, L); Lake Habbema, 3225 m, common in open parts of subalpine forest, tree or shrub 3-4 m high, VIII.1938, *Brass 9367* (A, L); 9 km NE of Lake Habbema, 2800 m, abundant in forest second growths of landslips, native clearings etc, tall slender scrambling shrub of 3-5 m, flr, frt, X.1938, *Brass 10587* (A, L); Lake Habbema, 2860 m, common in forest openings, large shrub; frt, X.1938, *Brass 10929* (A, L); Mt Carstenz, track Camp XI to XII, 2530-3360 m, flr, 28.I.1913, *Kloss* (WELT [isotype in part ?]); Utakwa R. to Mt Carstenz, Camp XIII, 29.I.1913, *Kloss s. n.* (L [fragment and a single fruit; not isotype material, leaf blade smooth above]); Star Mts, NE of Mt Capella E summit, 3100 m, low spreading bushes in subalpine heath, flr, 18.IV.1975, *LAE 67423 (Barker & Umba)* (L); Star Mts, Mt Scorpion, 3300 m, flr, 24.V.1975, *LAE 68010 (Croft)* (L); Mt Doorman summit, 3240 m, 21.X.1920, *Lam 1612* (A, L [annotated by Valetton as “*C. ulicooides*”]); Mt Doorman summit, 3240 m, 17.X.1920, *Lam 1724* (A, L [annotated by Valetton as “*C. ulicooides*”]); Mt Trikora [Wilhelmina], 3200 m, flr, 24.VIII.1983, *Mangen 653* (L); Valentijn Mts, Koruppun-Angguruk, 3050 m, flr, 21.VIII.1988, *Mangen 2111* (A); Hellwig Mts, 2600 m, 2.I.1913, *Pulle 876* (L); Wichmann Mts, 3000 m, 2.II.1913, *Pulle/Versteeg 991* (L [annotated by Valetton as “*C. hedyotooides*”]); Wichmann Mts, 3000 m, 3.II.1913, *Pulle/Versteeg 1012* [annotated by Valetton as “*C. hedyotooides*, ubergang zu der Var. *squarrosa*”].

5b. *Coprosma wollastonii* var. *epiphytica* (P. Royen) R. O. Gardner, **stat. & comb. nov.** (Fig. 1G, 2G, Map 4).

≡ *Coprosma epiphytica* P. Royen, *Alpine Fl. New Guinea* 4: 2753, f. 797A-E. 1983.

Type: Mt Capella, 3100 m, 18.IV.1975, *Barker & Umba* (Holo-: LAE 67434 n.v.; iso-: L [photocopy !]).

= *Coprosma scandens* P. Royen, *Alpine Fl. New Guinea* 4: 2756, f. 797F-L. 1983. **Type:** Tel Basin, 3060 m, 7.IV.1975, *Veldkamp 6351* (Holo-: L !).

Small woody plant, sometimes epiphytic, branches subscaudent, yellowish brown, to at least 3 mm diam.; new stems 0.5-1 mm diam., bearing patent or somewhat antrorse or retrorse rather bristly hairs to c. 0.6 mm long.

Leaves laxly arranged, petiole c. 1 mm long; blades ovate-oblong, 3-13 x 2.5-7 mm, apex shortly acuminate, subs spinose (acumen c. 0.5 mm long and often ± twisted at least when dry), glabrous above and below, margins glabrous and usually recurved.

Stipules shortly sheathing (sheath to c. 0.6 mm long), face triangular in outline, to 2.5(-3.5) mm long, with a central stout keeled lobe and a pair of shorter lateral lobes, denticles to c. 0.4 mm long, margins glabrous or with a very few short cilia (usually only on central lobe), the ageing stipule yellowish-sclerotized.

Distribution. – Only known from the Star Mts.

Altitude. – 3060-3600 m.

Notes. – **1.** VAN ROYEN (1983: 2757) described *C. scandens* as being smaller and thinner-leaved than *C. epiphytica*, with branches more nearly at right angles to the main ones, but he also cited two Mt Capella specimens as putative hybrids. In my opinion the differences are not significant.

2. One could speculate that the sclerotized stipule with its large and somewhat hooked central lobe is an adaptation towards improving the plant's subscaudent

capability, as indeed the bristles of the stem might be — however, once a stipule becomes exposed by leaf-shedding its distal parts soon break off.

Collections seen. – Sirius Ridge, 3050 m, flr, 15.IV.1965, *Craig 97* (CANB); Mt Capella SE side, 3300 m, bushy creeper, dense alpine shrubbery, flr, 18.IV.1975, *LAE 59312 (Vinas & Wiakabu)* (A); Mt Scorpion, 3600 m, scrambling shrub, alpine heath and herb field, flr, 18.V.1975, *LAE 65875 (Croft & Lelean)* (A, L); Mt Capella, ridge leading to Tel Basin, 3100-3300 m, epiphyte, flr, 2.IV.1975, *LAE 66980 (Barker)* (A); N of Mt Capella E summit, 3100 m, epiphyte, flr, 18.IV.1975, *LAE 67435 (Barker & Umba)* (L); Tel Basin, 3060 m, straggling much-branched shrub, open forest, flr, 7.IV.1975, *Veldkamp 6351* (L); Dagabulon Camp E of Mt Capella, 3420 m, epiphyte, branches horizontal, common in mossy microphyllous scrub, flr, 17.IV.1975, *Veldkamp 6475* (L).

5c. *Coprosma wollastonii* var. *novoguineensis* (P. Royen) R. O. Gardner, **stat. & comb. nov.** (Fig. 1H, 2H, 3C, 3D, 6H, Map 4).

≡ *Coprosma novoguineensis* Merr. & L. M. Perry in J. Arnold Arbor. 26: 262. 1945.

Type: 7 km E of Wilhelmina-top, 3900 m, IX.1938, *Brass & Meyer-Drees 9939* (Holo-: A 63032 !; iso-: L !).

Compact shrubby small tree to c. 6 m tall (f. van Royen), branchlets ± fastigiata; new stems c. 1.3 mm diam., with patent or antrorse slender hairs to 0.3 mm long.

Leaves crowded, subsessile; blades ovate, to 15 × 5 mm, subcoriaceous, sides usually somewhat upfolded, acute to apex and with a spine c. 1 mm long, distal margins papillose-erose and occasionally setulose, midrib below wide but usually only slightly prominent, surfaces and midrib glabrous.

Stipule shortly sheathing (sheath to c. 0.6 mm long), face ovate-hooded (“thoraciform”), 2.2-3 mm long, not lobed, margin densely ciliate, denticle small (to 0.25 mm long), with age the stipule becoming firmly crustose but remaining ± pale (i.e., hardly yellow-sclerotized).

Distribution. – Nassau and Oranje Mts.

Altitude. – 3225-4140(-4300 ?) m.

Notes – **1.** Members of this taxon could be misidentified as *C. brassii* (q.v.). According to the data of MANGEN (1993) for Mt Trikora (Wilhelmina), it attains a slightly higher altitude there than *C. brassii* does, on the northern slopes of the mountain forming “dispersed open shrublands between 3900 and 4000 m”.

2. The record for *C. novoguineensis* in the Doma Peaks region (GILLISON, 1970) is based on *C. papuensis* subsp. *discolor* (NGF 25201).

3. Several nodes with leaves in 3s are to be found on some of the pieces of foliage that make up the collections *Versteeg/Pulle 2522, -3* (L sheets).

4. MANGEN (1993, tab. 81) has a photograph of the species in treeline shrubland and another showing female flowers.

Representative collections. – Of a total of **nineteen seen:** Lake Habbema, 3225 m, common in shrubby edge of forest etc., loose shrub 1-1.5 m high, XI.1938, *Brass 13736A* (A); 7 km E of Wilhelmina-top, 3900 m, plentiful as a shrub of 1 m on grassy summits, flr, IX.1938, *Brass & Meyer-Drees 9705* (A, L); 2 km E of Wilhelmina-top, 3750 m, small shrub in grassy valley, IX.1938, *Brass & Meyer-Drees 10380* (A); Carstensz Mts, in a river valley flowing from the North Wall, 3700 m, as a shrub to 6 m high in forest ... and as scattered shrubs above bushline to 4300 m, 24.VI.1961, *D. E. Cooper 10a* (L); Mt Trikora [Wilhelmina], “Hanging Valley”, 4140 m, solitary shrubs, flr, 7.VIII.1984, *Mangen 1195* (A, L); Quarles Valley, 3800 m, 19.XII.1913, *Versteeg 2522-3* (L).

Identification List

1	<i>Coprosma archboldiana</i>	4c	<i>C. papuensis</i> subsp. <i>mopaensis</i>
2	<i>C. brassii</i>	5a	<i>C. wollastonii</i> var. <i>wollastonii</i>
3	<i>C. divergens</i>	5b	<i>C. wollastonii</i> var. <i>epiphytica</i>
4	<i>C. papuensis</i> subsp. <i>papuensis</i>	5c	<i>C. wollastonii</i> var. <i>novoguineensis</i>
4b	<i>C. papuensis</i> subsp. <i>discolor</i>		
<i>ANU series</i>			
	418	4b	<i>Brass</i> 9706 5c
	448	4b	<i>Brass</i> 9707 5c
	2224	4b	<i>Brass</i> 10587 5a
	5006	3	<i>Brass</i> 10588 5a
	6101	4b	<i>Brass</i> 10929 5a
	6165	4b	<i>Brass</i> 13736A 5c
	6365	4b	<i>Brass</i> 29800 3
	7098	4b	<i>Brass</i> 29807 4b
	7172	3	<i>Brass</i> 29809 4b
	7353	4b	<i>Brass</i> 30097 3
	10870	5c	<i>Brass</i> 30320 4b
	15039	4b	<i>Brass</i> 30321 4b
	15601	4b	<i>Brass</i> 30925 4b
			<i>Brass</i> 31430 4c
			<i>Brass & Collins</i> 31033 4c
	<i>van Balgooy</i> 335	3	<i>Brass & Collins</i> 31267 4c
	<i>van Balgooy</i> 336	3	<i>Brass & Meyer-Drees</i> 9705 5c
	<i>van Balgooy</i> 337	4b	<i>Brass & Meyer-Drees</i> 9707 5c
	<i>van Balgooy</i> 338	4b	<i>Brass & Meyer-Drees</i> 9807 2
	<i>van Balgooy</i> 787	3	<i>Brass & Meyer-Drees</i> 9809 2
	<i>van Balgooy</i> 788	3	<i>Brass & Meyer-Drees</i> 9817 1
	<i>Borgmann</i> 36	3	<i>Brass & Meyer-Drees</i> 9831 1
	<i>Borgmann</i> 56	4b	<i>Brass & Meyer-Drees</i> 9842 2
	<i>Brass</i> 4215	3	<i>Brass & Meyer-Drees</i> 9843 2
	<i>Brass</i> 4216	3	<i>Brass & Meyer-Drees</i> 9933 5c
	<i>Brass</i> 4217	4a	<i>Brass & Meyer-Drees</i> 9939 5c
	<i>Brass</i> 4218	4a	<i>Brass & Meyer-Drees</i> 9940 5c
	<i>Brass</i> 9028	5c	<i>Brass & Meyer-Drees</i> 10221 2
	<i>Brass</i> 9028	5c	<i>Brass & Meyer-Drees</i> 10304 2
	<i>Brass</i> 9063	5c	<i>Brass & Meyer-Drees</i> 10378 5c
	<i>Brass</i> 9144	5a	<i>Brass & Meyer-Drees</i> 10380 5c
	<i>Brass</i> 9145	5a	
	<i>Brass</i> 9367	5a	<i>Clemens</i> 9373 4b
	<i>Brass</i> 9411	1	<i>Clemens</i> 10108A 3
	<i>Brass</i> 9705	5c	<i>Cooper</i> 10 2

<i>Cooper 10A</i>	5c	<i>Kalkman 4984</i>	4b
<i>Craig 97</i>	5b	<i>Kloss s. n. (leg. Jan 1913)</i>	5a
<i>Craig 115</i>	2		
<i>Craig 121</i>	1	<i>LAE series</i>	
<i>Craven 2710</i>	4a	50283	4b
<i>Craven 2711</i>	4a	51406	4a
<i>Craven 2712</i>	3	51416	4a
<i>Craven 2713</i>	3	51462	4a
<i>Craven 2881</i>	4a	51464	3
<i>Craven 2882</i>	4a	51490	3
<i>Craven 3042</i>	4a	53138	4b
<i>Cruttwell 2035</i>	4c	54611	4b
		54865	3
<i>Grubb & Edwards 19</i>	4b	55781	4b
		59312	5b
<i>Hartley 11171</i>	4b	59663	5a
<i>Hartley 11225</i>	3	59757	2
<i>Hoogland 7018</i>	4b	59761	2
<i>Hoogland 9691</i>	4b	60710	4b
<i>Hoogland 9746</i>	3	60715	4b
<i>Hoogland 9749</i>	3	61331	3
<i>Hoogland 9772</i>	4b	61511	3
<i>Hoogland 9793</i>	3	61589	4a
<i>Hoogland 9794</i>	3	61597	3
<i>Hoogland 9838</i>	3	61599	3
<i>Hoogland 9839</i>	3	61751	3
<i>Hoogland 9978</i>	3	61813	4a
<i>Hoogland 9988</i>	3	65085	4a
<i>Hoogland 10000</i>	3	65875	5b
<i>Hoogland & Pullen 5520</i>	4b	65907	2
<i>Hoogland & Pullen 5759</i>	3	66980	5b
<i>Hoogland & Schodde 7001</i>	4b	67097	2
<i>Hoogland & Schodde 7002</i>	4b	67423	5a
<i>Hoogland & Schodde 7018</i>	3	67424	5a
<i>Hoogland & Schodde 7454</i>	4b	67434	5b
		67435	5b
<i>Jacobs (leg. 29 Sep 1973)</i>	4b	67459	1
		67460	1
<i>Kalkman 4495</i>	2	68010	5a
<i>Kalkman 4540</i>	2	68077	1
<i>Kalkman 4614</i>	4b	68185	3
<i>Kalkman 4757</i>	4b	68464	3
<i>Kalkman 4765</i>	4b	73661	4b
<i>Kalkman 4981</i>	4b	73718	4b

74359	3	30079	3
75489	4b	32501	4b
75490	4b	32925	4b
		32992	4b
<i>Lam 1612</i>	5a	35015	4b
<i>Lam 1724</i>	5a	35058	3
		36911	3
<i>Mangen 431</i>	2	40691	4b
<i>Mangen 437</i>	1	47059	4b
<i>Mangen 520</i>	1	47072	4c
<i>Mangen 653</i>	5a		
<i>Mangen 671</i>	1	<i>Paijmans 945</i>	4a
<i>Mangen 846</i>	2	<i>Philipson & Philipson 3495</i>	3
<i>Mangen 972</i>	1	<i>Philipson & Philipson 3496</i>	4b
<i>Mangen 975</i>	1	<i>Pulle 876</i>	5a
<i>Mangen 1195</i>	5c	<i>Pulle 991</i>	5a
<i>Mangen 1210</i>	5c	<i>Pulle/Versteeg 1012</i>	5a
<i>Mangen 1775</i>	2	<i>Pullen 5130</i>	4b
<i>Mangen 2104</i>	1	<i>Pullen 5132</i>	3
<i>Mangen 2111</i>	5a	<i>Pullen 5135</i>	4b
<i>Milliken 1596</i>	2		
		<i>Robbins 365</i>	2
<i>NGF series</i>		<i>Robbins 701</i>	3
8917	3	<i>Robbins 1033</i>	2
8932	4b	<i>v. Royen 10784</i>	4a
8933	3	<i>v. Royen 10795</i>	4a
11489	4c	<i>v. Royen 10811</i>	3
15369	4b	<i>v. Royen 11222</i>	4b
16548	3	<i>v. Royen 11225</i>	3
16549	3	<i>v. Royen 11428</i>	5a
16551	4c	<i>v. Royen 11526</i>	3
16568	4c	<i>v. Royen 11621</i>	3
17992	3		
17994	4c	<i>Sands 1531</i>	4c
19861	3	<i>Sands 1547</i>	4c
20037	3	<i>Sands 1650</i>	3
20683	2	<i>Sands 1652</i>	4c
21392	4b	<i>Sands 1670</i>	3
22385	4a	<i>Schodde 1727</i>	4b
23706	4b	<i>Schodde 1737</i>	3
24606	4b	<i>Schodde 1751</i>	4b
25201	4b	<i>Sterly 77-32</i>	4b
30017	3	<i>Sterly 80-73</i>	4b
30066	4a	<i>Sterly 80-150</i>	4b

<i>Streimann 8589</i>	4b	<i>Veldkamp 6474</i>	5b
		<i>Veldkamp & Obedi 8599</i>	4c
<i>Tade 23</i>	4b	<i>Veldkamp & Stevens 5646</i>	4a
<i>Takeuchi 5756</i>	4b	<i>Veldkamp & Vinas 7471</i>	2
<i>Takeuchi 5757</i>	4b	<i>Versteeg/Pulle 2438</i>	5a
		<i>Versteeg/Pulle 2458</i>	5a
<i>UPNG series</i>		<i>Versteeg/Pulle 2522</i>	5c
<i>s. n. (leg. Palyaka 1 Sept 1982)</i>	4b	<i>Versteeg/Pulle 2523</i>	5c
<i>s. n. (Millar & Tippett 1262)</i>	3	<i>Vinas 115</i>	4b
889	4a	<i>Vink 16085</i>	3
<i>13192 (Hopkins 661)</i>	4a	<i>Vink & Sleumer 4335</i>	1
<i>13196 (Hopkins 665)</i>	3		
<i>13214 (Hopkins 683)</i>	3	<i>Went 165</i>	3
<i>13216 (Hopkins 685)</i>	4a	<i>Widjaja 2281</i>	2
		<i>Widjaja 2307</i>	2
<i>Veldkamp 6330</i>	1	<i>Winters & Higgins 585</i>	4b
<i>Veldkamp 6351</i>	5b	<i>Woods 3169</i>	3
<i>Veldkamp 6428</i>	5a	<i>Woods 3170</i>	3

ACKNOWLEDGMENTS

I am grateful to the curators at A, CANB, CHR and L for the loan of their material, and for extra assistance from Roy Vickery (BM), Jeff Fox (WELT), Gerard Thissje (L) and Rod Seppelt (Australian Botanical Liaison Officer at K).

Others who have helped by advising on the manuscript or in other ways are Ewen Cameron and Doug Rogan (AK), Peter de Lange, Lyn Craven, Joan Farràs, Tim Utteridge and Max van Balgooy. Michael Heads generously let me take over a project originally his, on condition only that distribution maps be produced.

REFERENCES

- ARCHBOLD, R., A. L. RAND & L. J. BRASS (1942). Results of the Archbold Expeditions. No. 41. *Bull. Amer. Mus. Nat. Hist.* 79: 197-288.
- BORGMANN, E. (1964). Anteil der Polyploiden in der Flora des Bismarckgebirges von Ostneuguinea. *Z. Bot.* 52: 118-172.
- COOPER, D. (1971). Some botanical and phytochemical observations in Netherlands New Guinea. *Econ. Bot.* 25: 345-356.
- DARWIN, S. P. (1994). Systematics of *Timonius* Subgenus *Abbottia* (Rubiaceae-Guettardeae). *Syst. Bot. Monogr.* 42: 86 pp.
- EAGLE, A. (1986). *Eagle's Trees and Shrubs of New Zealand*. Revised edn. Collins, Auckland. 384 pp.
- GARDNER, R. O. (1999). Systematic notes on *Leptostigma setulosum* (Rubiaceae). *New Zealand Nat. Sci.* 24: 1-8.
- GILLISON, A. N. (1970). Structure and floristics of a montane grassland/forest transition. *Blumea* 18: 71-86.
- GREENSILL, N. A. R. (1902). Structure of leaf of certain species of *Coprosma*. *Trans. & Proc. New Zealand Inst.* 35: 342-355, Pl. 41-44.
- HEADS, M. J. (1996). Biogeography, taxonomy and evolution in the Pacific genus *Coprosma* (Rubiaceae). *Candollea* 51: 381-405.
- HOPE, G. S. (1980). New Guinea mountain communities. In: van ROYEN, P., *The Alpine Flora of New Guinea* 1: 153-222. Cramer, Vaduz.
- MANGEN, J.-M. (1993). *Ecology and Vegetation of Mt Trikora New Guinea (Irian Jaya/Indonesia)*. Travaux scientifiques du Musée national d'histoire naturelle de Luxembourg 21. 216 pp.

- MERRILL, E. D. & L. M. PERRY (1945). *Plantae Papuanae Archboldianae*; XVI. *J. Arnold Arbor.* 26: 229-266.
- O'DOWD, D. J. & M. F. WILLSON (1989). Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. *Biol. J. Linn. Soc.* 37: 191-236.
- OLIVER, W. R. B. (1935). The genus *Coprosma*. *Bernice P. Bishop Mus. Bull.* 132: 1-207.
- OLIVER, W. R. B. (1942). New species of *Coprosma* from New Guinea and the Hawaiian Islands. *Rec. Domin. Mus.* 1: 44-47.
- ORCHARD, A. E. (1986). A revision of the *Coprosma pumila* complex (Rubiaceae) in Australia, New Zealand and the subantarctic islands. *Brunonia* 9: 119-138.
- SCHUITEMAN, A. (1997). Revision of the genus *Mediocalcar*. *Orchid Monogr.* 8: 21-77.
- TAYLOR, G. M. (1961). A key to the coprosmas of New Zealand. *Tuatara [Wellington]* 9: 31-64.
- UEDA, K. (1986). Flora and vegetation at the summit zone of Gunung Binaya and G. Owae Puku. In: KATO, M., *Taxonomic Studies of the Plants of Seram Island*: 20-35. Botanical Gardens, University of Tokyo.
- UTTERIDGE, T. M. A. (2002). New species of *Coprosma* (Rubiaceae) from New Guinea. Contributions to the Flora of Mt Jaya VII. *Kew Bull.* 57: 195-203.
- VAN BALGOOY, M. M. J. (1966). *Coprosma*. Pacific Plant Areas. *Blumea Suppl.* 5: 76-77.
- VAN ROYEN, P. (1983). *The alpine flora of New Guinea*. Cramer, Vaduz. 3516 pp.
- WAGNER, W. L., D. R. HERBST & S. H. SOHMER (1990). *Manual of the flowering plants of Hawai'i*. University of Hawaii Press, Honolulu. 1853 pp.
- WERNHAM, H. F. (1916). *Coprosma wollastonii*. In: RIDLEY, H. N. & al., Report on the Botany of the Wollaston Expedition to Dutch New Guinea, 1912-13. *Trans. Linn. Soc. London, Bot.* 9: 1-269, tab. 1-6.