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The reinstatement of *Leptinella* at generic rank, and the status of the 'Cotuleae' (Asteraceae, Anthemideae)

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Abstract *Leptinella* Cass. has for more than one hundred years been relegated to sectional rank within *Cotula* L. All species of *Leptinella* are distinguished from those of the other two sections of *Cotula*, and other Anthemideae, by the conspicuous "inflated" corollas of the female florets and by chromosome numbers based on $x = 26$ where known; most species are also distinguished by a suite of habit characters. Of the genera at times included in the 'Cotuleae', only *Soliva* sens. lat. is clearly related to *Cotula*; most other genera have been referred to other tribes or are of uncertain affinities. The relationship of *Leptinella* to *Cotula* sect. *Cotula* and sect. *Strongylosperma*, and to *Soliva* remains unclear, but *Leptinella* is undoubtedly monophyletic and is sufficiently distinct to warrant recognition at generic level. We reinstate the genus *Leptinella* and make all necessary combinations. *Leptinella* is a genus of 33 species distributed in New Guinea, Australia, New Zealand, the Subantarctic Islands, and South America.

Keywords Asteraceae; Anthemideae; Cotuleae; *Cotula*; *Leptinella*; taxonomy; generic limits; New Zealand; Australia; New Guinea; South America

INTRODUCTION

The problem of generic limits in Asteraceae has recently received considerable attention with major rearrangements in several tribes including Inuleae (Hilliard & Burtt 1981), Senecioneae (Jeffrey et al. 1977, Nordenstam 1978), Liabeae (Robinson 1983),

Eupatorieae (Robinson & King 1977), and Anthemideae (Humphries 1976). "The Biology and Chemistry of the Compositae" (Heywood et al. 1977) summarised some of these changes and there Heywood & Humphries (1977) provided the systematic review of the Anthemideae. A recent symposium (Lane & Turner 1985) also addressed the problem of the generic concept in this very large and often subtle family. At this symposium, Cronquist (1985) recognised the need to realign generic concepts according to putative evolutionary relationships, but considered with disapproval many of the recent generic splits, especially those based on microcharacters. Funk (1985) stressed the need to delimit natural groups of species whatever their size and suggested that in defining new monophyletic groups the remaining group should not be left paraphyletic.

This paper considers in detail the status of Casini's genus *Leptinella*, currently placed within *Cotula* as sect. *Leptinella*, and discusses Bentham's informal group within the Anthemideae, the 'Cotuleae'.

THE 'COTULEAE'

Bentham (1873) included 11 genera in his 'Cotuleae', but the group was defined mostly by characters representing loss or reduction of habit or various parts of the capitulum or florets, and as noted by Lloyd (1972) may not, therefore, be a natural (monophyletic) group. Of those 11 genera, *Otochlamys* and *Cenia* are now placed within *Cotula* sect. *Cotula* (Levyns 1941), *Polygyne* (part of Bentham's *Plagiocheilus*) has been referred to the Heliantheae (Cabrera 1954, Heywood et al. 1977), and *Plagiocheilus* sens. strict. has been referred to the Astereae (Robinson & Brettell 1973d, Grau 1977). *Abrotanella* has been referred to the Senecioneae (Robinson & Brettell 1973b), although its affinities remain obscure (Nordenstam 1977) and Heywood & Humphries (1977) still included it in their discussion of *Cotula* and its affinities. *Ceratogyne* was considered better placed in the Inuleae by Turner (1970), although Skvarla et al. (1977) described the pollen wall morphology as helianthoid, and Heywood & Humphries (1977) retained it as a dubious member of the Anthemideae. *Elachanthus* has helianthoid pollen wall morphology

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(Skvarla et al. 1977), but was retained without comment in the Anthemideae by Heywood & Humphries (1977). Although *Isoetopsis* also has the helianthoid pollen wall morphology (Skvarla et al. 1977), it was referred by Robinson & Brettell (1973a) to the Astereae on the basis of several other microcharacters; Grau (1977), however, noted that it does not fit well with the Astereae, the main objection to this placement being the very different anatomy of the fruits. *Centipeda* has also been considered a doubtful member of the Anthemideae (Heywood & Humphries 1977) — a relationship with the Inuleae is suggested by its pollen grain structure (Skvarla et al. 1977), and its possession of tridecapentaynene, otherwise unrecorded for the Anthemideae, also indicates that it may be better placed elsewhere (Sørensen 1977). *Sphaeromorphaea*, treated by Bentham as a synonym of *Centipeda*, is now included in the Inuleae (Merxmüller et al. 1977). The monotypic *Nananthea* seems not to have been closely investigated. *Soliva*, however, is a good member of the Anthemideae and shares with *Cotula* at least the reduction of the corolla of female florets.

Ischnea is sometimes included in the 'Cotuleae' but was first described after Bentham's treatment. Robinson & Brettell (1973c) referred it to the Senecioneae and it was included there by Nordenstam (1977) who, however, noted that its affinities remain obscure.

Thus, it appears that *Cotula sens. lat.* and *Soliva sens. lat.* are the only genera of the above which can be retained in the Anthemideae, let alone the 'Cotuleae', without strong conflicting evidence! The affinities of *Cotula* and *Soliva* within the Anthemideae need reexamination in a new framework free from the encumbrance of Bentham's 'Cotuleae'.

Heywood & Humphries (1977) noted that karyotype analysis on *Cotula coronopifolia*, type species for the genus, by Fernandes & Queiros (1971) indicated that the tribe Cotuleae should be restored, but concluded that the evolutionary and systematic affinities of the 'Cotuleae' need to be worked out in detail before an opinion can be expressed as to its final position. Nevertheless, Jeffrey (1978) accepted the Cotuleae (with 10 genera but only *Cotula* named) as one of 17 tribes in Asteraceae, but did not list any features which clearly distinguish it from the Anthemideae. Given the extreme uncertainty as to the genera which constitute the 'Cotuleae', we consider it premature to accord the group tribal rank. Thorne (1983), in his overview of angiosperm classification, did not accept the Cotuleae as a distinct tribe.

COTULA AND LEPTINELLA

It is against this background that the infrageneric taxonomy of *Cotula* itself must be considered. *Cotula*, as currently circumscribed, comprises three sections: sect. *Cotula* is mainly African and is represented in New Zealand by only *C. coronopifolia*; sect. *Strongylosperma* (Less.) Benth. is predominantly African, Asian, and Australian, and is represented in New Zealand by only *C. australis*; sect. *Leptinella* (Cass.) Benth. occurs in New Guinea, Australia, New Zealand and its subantarctic islands, and has one species in South America and the Falkland Islands. *Leptinella* was erected as a genus by Cassini (1822) and added to by Hooker (1844, 1853) and Mueller (1864), but was then relegated to infrageneric status within *Cotula* by Hooker (1864). Bentham (1867) recognised the three sections above and this course has been followed with minor changes in content and characters by most subsequent authors (for details see Lloyd 1972). In this paper we reinstate *Leptinella* as a genus and make the resulting new combinations.

Leptinella is a monophyletic group with the basic chromosome number ($x = 26$) and the female corolla type as synapomorphies. Both *Cotula* sect. *Cotula* and *Cotula* sect. *Strongylosperma* may also be natural groups, but the exact relationship of *Leptinella* to these two sections is unclear. More work is needed to understand the phylogenetic relationships of *Leptinella*, *Cotula* sect. *Cotula* and sect. *Strongylosperma*, *Soliva*, and whichever other genera belong to this assemblage.

If *Cotula sens. lat.* (including *Leptinella*) is in fact monophyletic, and if, as seems likely, *Leptinella* is less closely related to sections *Strongylosperma* and *Cotula* than they are to each other, then the question of the status of *Leptinella* is solely one of rank. Several arguments may then be advanced to support the recognition of *Leptinella* as a genus. Firstly, *Leptinella* fits the requirement of being a conceptually useful genus (Cronquist 1985) — all species share the distinctive corolla morphology of the female florets and most are also readily recognised from habit characters. The definition of the genus is not dependent on microcharacters. Secondly, the split is not trivial, as *Leptinella* constitutes 33 species and *Cotula* retains about 50; both have, therefore, more than the c. 16 species per genus which is currently the average for the Asteraceae (Cronquist 1985). Thirdly, the characters which distinguish *Leptinella* are at least as consistent and well defined (with discontinuous character states) as those used to define genera in other parts of the Anthemideae, as for example the characters used to define genera in the *Chrysanthemum* complex (Humphries 1976). *Leptinella*, as circumscribed

here, also makes sense biogeographically. The reinstatement of *Leptinella* follows the trend to acceptance of more of Cassini's genera rather than the broader generic concepts of Bentham (Nordenstam 1977), and the trend to splitting the large Southern Hemisphere genera that resulted from the Eurocentric taxonomy of the eighteenth and nineteenth centuries.

DIAGNOSTIC CHARACTERS : *LEPTINELLA* VS. *COTULA* SECTIONS *COTULA* AND *STRONGYLOSPERMA*

Three unrelated characters appear to absolutely distinguish all species of *Leptinella* from all species of *Cotula* sections *Cotula* and *Strongylosperma*. (For the second and third characters, however, some species have not been examined.)

The most valuable diagnostic feature of *Leptinella* is the nature of the corolla of female florets; in all species the female corolla is "inflated" with an air space between the outer layer of the corolla and an inner layer surrounding the style, as Cassini (1822) and Hooker (1844) recognised (for details see Lloyd 1972). The inflated corolla of *Leptinella* is evident macroscopically and at anthesis it is as wide as the ovary below it. The character is unknown elsewhere in the Anthemideae and is a uniquely derived character which absolutely defines *Leptinella*. The corolla of species of *Cotula* sections *Cotula* and *Strongylosperma* is never inflated, is narrower than the ovary at anthesis, and is scarcely or not at all evident to the unaided eye – in some species it is vestigial or absent.

Leptinella is also distinct in its chromosome number. The two New Zealand subgenera have a basic chromosome number of $x = 26$ (Hair 1962, Lloyd 1972), but no species of subgenus *Oligoleima* has yet been examined. The basic chromosome number of *Leptinella*, like the inflated female corolla, distinguishes *Leptinella* not only from *Cotula* sections *Cotula* and *Strongylosperma*, but from all other Anthemideae. *Cotula* sect. *Cotula* has basic chromosome numbers of $x = 8$ and 10 (Malik 1960, Hair 1962, Nordenstam 1969, Turner 1970) in the species which have been examined to date, and sect. *Strongylosperma* has a basic chromosome number of $x = 18$ (Diers 1961, Hair 1962, Turner 1970). A few counts at variance with these basic chromosome numbers have been reported (collated in the Index to Plant Chromosome Numbers). Some of these contrary counts are of high numbers based on uncertain basic numbers, and others need confirmation.

Many, if not all, species of *Cotula* sections *Cotula* and *Strongylosperma* have blunt, columnar, uniseriate hairs on the surfaces of their achenes. These are absent from all species of *Leptinella*.

Two further characters distinguish all species of *Leptinella* from most species of *Cotula* sections *Cotula* and *Strongylosperma*. First, all species of *Leptinella* have seed-sterile, functionally male florets in which the style ends in a circular disc. Most species of *Cotula* sections *Cotula* and *Strongylosperma* have seed-fertile, functionally hermaphrodite disc florets with bifid style arms bearing receptive stigmas, but three species of sect. *Strongylosperma* have seed-sterile disc florets similar to those of *Leptinella*. Second, the female florets of all species of *Leptinella* and a few other species of *Cotula* sect. *Strongylosperma* have corollas which are distinctly jointed with the ovary, whereas the other species of sect. *Strongylosperma* and all those of sect. *Cotula* have female corollas that are unjointed (or entirely absent).

Another character shows the reverse pattern, with several species of *Leptinella* sharing the same character state as all species of *Cotula* sections *Cotula* and *Strongylosperma*. The pistillate florets of species of sect. *Cotula* and sect. *Strongylosperma*, if present, produce achenes which are distinctly compressed and winged. The achenes of *Leptinella* subgenus *Oligoleima* are also markedly compressed and winged, whereas those of subgenera *Leptinella* and *Radiata* are compressed only slightly or not at all and have inconspicuous or obsolete margins.

The most striking and biologically important features of *Leptinella* are those associated with its vegetative habit, although there is some variation in habit in both *Cotula sens. strict.* and *Leptinella*, so the genera are not absolutely distinct with regard to this character. Most species of *Cotula* sections *Cotula* and *Strongylosperma* are more or less erect or procumbent, and are either tap-rooted or develop adventitious roots at lower nodes when these are covered with soil. Only a few species are prostrate and creeping. The plants are either annual or perennial. On the other hand, all except one species of *Leptinella* are persistently prostrate, with stems which regularly root at the nodes. The plants are perennial, or at least potentially so.

Several ancillary features are associated with the prostrate habit of species of *Leptinella*. Axillary shoots are suppressed to varying degrees. In many species, axillary buds develop into determinate short shoots (including all species in subgenus *Leptinella*), while in other species they are absent except

around flowering nodes or in exceptionally favourable conditions (most species of subgenera *Oligoleima* and *Radiata*) and in most species, some or all of the internodes are long. As a result of these features, the rhizomes are often far-creeping, with distant leaves or tufts of leaves and only occasional branches and flowering heads. It was presumably this creeping habit that induced Cassini to name his genus *Leptinella* (from the Greek for slender).

Also in association with the prostrate habit, the heads of species of *Leptinella* have relatively long peduncles which are fully elongated at anthesis, so the florets are presented to insects above the ground surface (except in *L. goyenii*, an alpine cushion species with subsessile heads which present the flowers on the surface of the cushion, like many other New Zealand cushion plants, Lloyd 1985). The peduncles often have one small bract, or a few small bracts scattered along their length, as Cassini (1822) noted. The heads are terminal on the rhizomes, not axillary as stated in Lloyd (1972, 1981). As Dr E. J. Jäger (pers. comm.) has pointed out to us, rhizomes with flowering heads are sympodia. This is most evident in species with short shoots and elongated rhizomes, such as *L. squalida* (see Lloyd 1972, fig. 13), in which the first leaf after a flowering head appears to lack a short shoot in its axil. Actually, this leaf is the last leaf of the shoot that terminated in the head, and it is often concaulescently united with its axillary branch, which grows out as the apparent continuation of the rhizome and starts with a smaller leaf.

The method by which juvenile plants establish their prostrate habit is also characteristic of species of *Leptinella* (Lloyd 1981). The primary shoot of a seedling produces a number of leaves, then terminates in a head which often aborts. The axillary shoots of the last leaf or several leaves of the primary shoot then grow out horizontally, usually with conspicuous internodes, and thus establish the prostrate habit (Lloyd 1981). The method by which the few prostrate species of *Cotula* sections *Cotula* and *Strongylosperma* develop their creeping habit is not known.

There is one erect species in *Leptinella*, *L. featherstonii*, but this has a habit quite different from that of the erect species of *Cotula* sections *Cotula* and *Strongylosperma*. *L. featherstonii* has thick (up to 6 mm diameter), hard, woody stems. These are rooting and ascending at the base and grow upright for several years, producing axillary branches only around flowering nodes just as in other species of *Leptinella* subgenus *Radiata*. The erect habit is a secondarily derived feature of insular "gigantism" on the Chatham Islands (Lloyd 1981, 1982).

NOMENCLATURE

A systematic list of all species of *Leptinella* is presented including new combinations where necessary, and synonyms in *Cotula* for those species commonly known by a name other than the basionym. The species are arranged in three subgenera based on the series of *Cotula* sect. *Leptinella* proposed by Lloyd (1972). Taxonomy of subgenus *Leptinella* and subgenus *Radiata* follows Lloyd (1972), and that for subgenus *Oligoleima* follows van Royen & Lloyd (1975) and recent Australian floras.

Leptinella Cass., Bull. Sci. Soc. Phil. Paris 1822, 127 (1822). Lectotype species (Lloyd 1972): *L. scariosa* Cass., loc. cit. 127.

Subgenus *Leptinella*

≡ *Cotula* Sect. *Leptinella* Series *Elongata* D. Lloyd, New Zealand J. Bot. 10: 301 (1972).

1. *L. scariosa* Cass., op. cit. 127

≡ *C. scariosa* (Cass.) Franchet, Miss. Scientif. Cap. Horn 5: 344 (1889).

2. *L. potentillina* F. Muell., Veg. Chatham Is. 28, tab. 6 (1864).

≡ *C. potentillina* (F. Muell.) Druce, Rep. Bot. Exch. Club Brit. Isles for 1916 : 617 (1917).

3. *L. tenella* (Cunn.) D. Lloyd et C. Webb comb. nov. based on *Soliva tenella* Cunn., Ann. Nat. Hist. 2: 128 (1839).

≡ *C. membranacea* D. Lloyd, op. cit. 310.

4. *L. dispersa* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula dispersa* D. Lloyd, op. cit. 312.

subsp. *dispersa*

subsp. *rupestris* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula dispersa* subsp. *rupestris* D. Lloyd, op. cit. 313.

5. *L. rotundata* (Cheeseman) D. Lloyd et C. Webb comb. nov. based on *Cotula dioica* var. *rotundata* Cheeseman, Man. N.Z. Fl. 359 (1906).

≡ *C. rotundata* (Cheeseman) D. Lloyd, op. cit. 314.

6. *L. dioica* Hook. f., Fl. N.Z. 1: 129 (1852).

≡ *C. dioica* (Hook. f.) Hook. f., Handb. N.Z. Fl. 143 (1864).

subsp. *dioica*

subsp. *monoica* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula dioica* subsp. *monoica* D. Lloyd, op. cit. 319.

7. *L. traillii* (Kirk) D. Lloyd et C. Webb comb. nov. based on *Cotula traillii* Kirk, Stud. Fl. N.Z. 324 (1899).

subsp. *traillii*

subsp. *pulchella* (Kirk) D. Lloyd et C. Webb comb. nov. based on *Cotula pulchella* Kirk, Stud. Fl. N.Z. 328 (1899).

- ≡ *C. traillii* subsp. *pulchella* (Kirk) D. Lloyd, op. cit. 324.
8. *L. squalida* Hook. f., Fl. N.Z. 1: 129 (1852).
 ≡ *C. squalida* (Hook. f.) Hook. f., Handb. N.Z. Fl. 143 (1864).
 subsp. *squalida*
 subsp. *mediana* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula squalida* subsp. *mediana* D. Lloyd, op. cit. 327.
9. *L. pusilla* Hook. f., Fl. N.Z. 1: 129 (1852).
 ≡ *C. perpusilla* Hook. f., Handb. N.Z. Fl. 143 (1864) non *L. perpusilla* Fischer et C. Meyer (1836).
10. *L. serrulata* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula serrulata* D. Lloyd, op. cit. 332.
11. *L. calcarea* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula calcarea* D. Lloyd, op. cit. 334.
12. *L. intermedia* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula intermedia* D. Lloyd, op. cit. 336.
- Subgenus Radiata** (D. Lloyd) D. Lloyd et C. Webb stat. nov. based on *Cotula* Sect. *Leptinella* Series *Radiata* D. Lloyd, op. cit. 339.
13. *L. maniototo* (Petrie) D. Lloyd et C. Webb comb. nov. based on *Cotula maniototo* Petrie, Trans. N.Z. Inst. 14: 362 (1882).
14. *L. nana* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula nana* D. Lloyd, op. cit. 340.
15. *L. filiformis* (Hook. f.) D. Lloyd et C. Webb comb. nov. based on *Cotula filiformis* Hook. f., Handb. N.Z. Fl. 142 (1864).
16. *L. minor* Hook. f., Fl. N.Z. 1: 129 (1852) as lectotypified by Lloyd, op. cit. 345. TYPE K. H 3453/69/12, Canterbury, Dr Lyall (not as in Allan 1961).
 ≡ *C. minor* (Hook. f.) Hook. f., Handb. N.Z. Fl. 142 (1864).
17. *L. dendyi* (Cockayne) D. Lloyd et C. Webb comb. nov. based on *Cotula dendyi* Cockayne, Trans. N.Z. Inst. 47: 118 (1915).
18. *L. atrata* (Hook. f.) D. Lloyd et C. Webb comb. nov. based on *Cotula atrata* Hook. f., Handb. N.Z. Fl. 142 (1864) as lectotypified by Lloyd, op. cit. 349, 350.
 subsp. *atrata*
 subsp. *luteola* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula atrata* subsp. *luteola* D. Lloyd, op. cit. 350.
19. *L. goyenii* (Petrie) D. Lloyd et C. Webb comb. nov. based on *Cotula goyenii* Petrie, Trans. N.Z. Inst. 18: 295 (1886).
20. *L. albida* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *C. pectinata* var. *sericea* Kirk, Stud. Fl. N.Z. 325 (1899).
 ≡ *Cotula albida* D. Lloyd, op. cit. 353.
21. *L. pectinata* (Hook. f.) D. Lloyd et C. Webb comb. nov. based on *Cotula pectinata* Hook. f., Handb. N.Z. Fl. 142 (1864).
 subsp. *pectinata*
 subsp. *villosa* (D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula pectinata* subsp. *villosa* D. Lloyd, op. cit. 356.
 subsp. *willcoxii* (Cheeseman) D. Lloyd et C. Webb comb. nov. based on *Cotula willcoxii* Cheeseman, Trans. N.Z. Inst. 48: 212 (1916).
 ≡ *C. pectinata* subsp. *willcoxii* (Cheeseman) D. Lloyd, op. cit. 357.
22. *L. pyrethrifolia* (Hook. f.) D. Lloyd et C. Webb comb. nov. based on *Cotula pyrethrifolia* Hook. f., Handb. N.Z. Fl. 142–3 (1864).
 var. *pyrethrifolia*
 var. *linearifolia* (Cheeseman) D. Lloyd et C. Webb comb. nov. based on *Cotula linearifolia* Cheeseman, Trans. N.Z. Inst. 15: 299 (1883).
 ≡ *C. pyrethrifolia* var. *linearifolia* (Cheeseman) D. Lloyd, op. cit. 362.
23. *L. lanata* Hook. f., Fl. Antarct. 1: 26, tab. 19, (1844).
 ≡ *C. lanata* (Hook. f.) Hook. f., Handb. N.Z. Fl. 141 (1864).
24. *L. plumosa* Hook. f., Fl. Antarct. 1: 26, tab. 20 (1844).
 ≡ *C. plumosa* (Hook. f.) Hook. f., Handb. N.Z. Fl. 141 (1864).
25. *L. featherstonii* F. Muell., Veg. Chatham Is. 27, tab. 5 (1864).
 ≡ *C. featherstonii* (F. Muell.) Hook. f., Handb. N.Z. Fl. 733 (1867).
- Subgenus Oligoleima** Hook. f., in Hooker, W.J., Lond. J. Bot. 6: 117 (1847).
 ≡ Series *Oligoleima* (Hook. f.) D. Lloyd, op. cit. 290.
26. *L. longipes* Hook. f., in Hooker, W.J., Lond. J. Bot. 6: 117 (1847).
 ≡ *C. longipes* (Hook. f.) W.M. Curtis, Stud. Fl. Tasm. 2: 463 (1963).
27. *L. drummondii* (Benth.) D. Lloyd et C. Webb comb. nov. based on *Cotula drummondii* Benth., Fl. Aust. 3: 550 (1867).
28. *L. filicula* (Hook. f.) Hook. f., Fl. Tasm. 1: 194 (1856).
 ≡ *C. filicula* (Hook. f.) Benth., Fl. Aust. 3: 55 (1867).
29. *L. reptans* (Benth.) D. Lloyd et C. Webb comb. nov. based on *Strongylosperma reptans* Benth., in Endlicher et al., Enum. Plant Hug. 60 (1837).
 ≡ *C. reptans* (Benth.) Benth., Fl. Aust. 3: 551 (1867).

30. *L. wilhelminensis* (P. Royen) D. Lloyd et C. Webb comb. nov. based on *Cotula wilhelminensis* P. Royen, *Blumea* 22: 199 (1975).
31. *L. altilitoralis* (P. Royen et D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula altilitoralis* P. Royen et D. Lloyd, *Blumea* 22: 201 (1975).
32. *L. sarawaketensis* (P. Royen et D. Lloyd) D. Lloyd et C. Webb comb. nov. based on *Cotula sarawaketensis* P. Royen et D. Lloyd, *Blumea* 22: 202 (1975).
33. *L. leptoloba* (Mattf.) D. Lloyd et C. Webb comb. nov. based on *Cotula leptoloba* Mattf., *Bot. Jahrb.* 68: 268 (1937).

Incertae sedis

- L. pinnata* Cass., *Bull. Sci. Soc. Phil. Paris* 1822, 127 (1822). See Lloyd, op. cit. 306–308.

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