Taxonomic notes on the Hebe complex (Scrophulariaceae) in the New Zealand mountains

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RÉSUMÉ


ABSTRACT


Descriptions and notes are given for all members of Leonohebe sect. Buxifoliatae and two members of Hebe sect. Subditricha, alpine Scrophulariaceæ of New Zealand.

Introduction

A synopsis of part of the Hebe complex of genera (Scrophulariaceae) has been published elsewhere (HEADS, 1987), with new names, brief diagnoses and typifications. The present paper provides fuller descriptions and notes on members of one section of Leonohebe and two species of Hebe. Distribution maps and discussion of generic delimitation are provided elsewhere (HEADS, 1992a, b).

Many important collections of the group have been made since it was last revised (MOORE, 1961). This study has benefited in particular from the extensive collections of Professor A. F. Mark and Mr. A. P. Druce.

Leonohebe Heads


Prostrate to erect shrubs to 2 m high, final branches dark or bronzy green, sometimes flexed plagiotropically. Young leaf pairs coherent by the margins until nearly fully grown, or not coherent, bud sinus broad, shield-shaped or obturrate-rhomboid, or elliptic with truncate or cordate base barely connate below, leaf-scar raised on pulvinate base. Irregularly lobed "reversion" foliage very rare. Inflorescence terminal or intercalary, of simple spikelets or branched spikes, each spike with
one to many pairs of flowers. Bracts opposite and connate throughout, at least lowermost bracts not leaf-like. Calyx with anterior lobes fused or not. Corolla white or pink, 3-lobed with anterior lobe absent or narrowed and conically folded enclosing style until anthesis, or corolla 3-lobed and ± regular with two posterior lobes. Disc present. Capsule dorsally compressed or laterally compressed and ± didymous. Chromosome number: 2n = 21. Some populations of *L. odora* are tetraploid, *L. mooreae* is hexaploid and *L. masoniae* is aneuploid: 2n = 59.


Members of this section are important ecologically and dominate large areas of shrubland. The group is also phylogenetically important as certain species combine the bud structure of *Hebe sensu stricto* (Heads 1987) with the inflorescence of *Leonohebe*. Despite these features of interest the group has remained poorly understood. COCKAYNE & ALLAN (1927) despaired of the "many intergrading forms extremely difficult to classify", and possible additional taxa may remain lumped under taxa such as *L. odora* and *L. pacificalis*.

CHEESEMAN's (1925) *Veronica* species 47-49 form the core of the section. Cheeseman, following HOOKER (1864), placed the group in *Hebe* s.s., next to what is now *Hebe* sect. Glaucæa Hebe. In contrast, MOORE (1967) placed the group in what can be regarded as another genus, *Leonohebe*, next to sect. Flaguaformes. This latter treatment seems very perceptive and is followed here. Two species of *L. sect. Buxifoliae* do share with *Hebe* s.s. the leaf margins coherent in the bud, but placing the section under *Leonohebe* is supported by the decussate inflorescence symmetry, and the bracts large and similar to vegetative leaves (cf. COCKAYNE & ALLAN, 1927). The flower and capsule of *L. pacificalis* and the strict, unbranched stems of *L. pacificalis* also recall typical members of *Leonohebe*. Members of *Buxifoliae* are often confused with vegetatively similar members of *Hebe* sect. Subdistichae Heads, but the inflorescences are quite different. *Leonohebe pacificalis* is very distinctive in this section. The four remaining species are closely related and nearly recombine the key inflorescence and stomata characters. Vegetative growth continues beyond the inflorescence in *L. pacificalis*, *L. mooreae*, and *L. pacificalis* so that the inflorescence is intercalary (RICKETT, 1944), whereas in *L. odora*, *Hebe anomala* and *L. masoniae* all trace of terminal vegetative growth in the inflorescence is suppressed by the apex being totally "used up" in flowering. With respect to stomata, *Arrhenatherum* (Eriocarpae) is another example of a difficult group which repaid a study of stomatal distribution (HOWELL, 1945). There is a notable "centre of taxonomic incongruence" at Arthur's Pass where an otherwise typical population of *L. odora* has adaxial stomata (see below).

**Key to species of *Leonohebe* sect. *Buxifoliae***

**Note:** Lead "B" below will incorrectly key Caswell Sound and Denniston Plateau populations of *L. mooreae*, and Arthur's Pass populations of *L. odora*.

*A* Fruit compressed laterally, corolla usually with 5 lobes 1. *L. pacificalis*

*A* Fruit compressed dorsiventrally, corolla usually with (3)-4 lobes 2. *B*

*B* Stomata on adaxial (upper) leaf surface and abaxial surface

*C* Stomata on abaxial leaf surface only

*C* Inflorescence intercalary ("lateral"), including terminal vegetative bud 4. *L. pacificalis*

*C* Inflorescence terminal, not including vegetative bud 5. *L. masoniae*

*D* Inflorescence intercalary ("lateral"), including terminal vegetative bud 3. *L. mooreae*

*E* Inflorescence terminal, not including vegetative bud


Closely branched subshrub to 20 cm high, branches prostrate, rooting, ascending distally. Leaves 5.7-3.5 x 3.5-5.5 mm, rhomboid, coriaceous, pairs coherent in bud by dense marginal pubescence, bud with open sinus, leaf margins thick, cartilaginous, entire, midrib forming rounded keel. Spikelets lateral, developing in pairs just behind vegetative apices, each spikelet with one or two pairs of sessile flowers, rachis apex aborting. Calyx 4-lobed, with dense, crinkled pubescence. Corolla white, usually pendent with "split" posterior corolla lobe. Ovary laterally compressed, seated on ringed disc. Capsule 4.5 x 3 mm, obcordate and didymous, dehiscence deeply loculicidal as well as septicidal.

**Distribution.** — Southwest South Island.

**Habitat.** — Rocky sites, in crevices and on ledges.

This species is quite distinct from all other members of the section by its foliage, perianth and fruit, although in the wild the plant may be mistaken for a depressed state of *L. petriellae* var. *murrelli* as SIMPSON & THOMSON (1943) noticed, and MOORE (1964) recognised a "superficial resemblance" to *L. densifolia*. In fact, the inflorescences, flowers and fruits of *L. pacificalis* and *L. densifolia* all show similarities, and *L. pacificalis* may be an important link among *Leonohebe* sect. Buxifoliae, sect. Densefoliae Heads, and the puzzling *L. petriellae*. 2. *Leonohebe odora* (Hook. f.) Heads (1987: 10). *Veronica odora* Hook. f. (1844: 62). *Hebe odora* (Hook. f.) Ckne. (1929: 472). Type: *J. D. Hooker 1460 (K) "Lord Auckland's Group" [not seen].

Multi-leaved woody plants, either with prostrate and rooting runners and orbiculate shoots to 15 cm high, or forming erect hemispherical shrubs to 1.5 m high. Branches often plagiotropically arched distally with phylloclades tending to distichous through twisting of the petioles. Internodes 1.5-5.5 mm long. Leaf pairs conate at the base by a line of hairs which extends along the lower petiole margins, meets the convergent abscission zones and continues downwards in a line of hair-like strips beneath. Leaves coherent in bud. Lamina 7-16 x 3-7 mm, adaxial surface dark green and shining, without stomata, abaxial surface paler, with stomata. Margins, midrib and young stem yellowish green, margin entire, very rarely lobed ("reversion foliage"), bevelled, either smooth or thickly cartilaginous and minutely crenulate. Lamina glabrous, elliptic to slightly ovate or obovate, ± acute, concave, midrib often not evident above but sometimes impressed, ± keeled below. 2.3 veins sometimes visible parallel with the midrib, lamina truncate at the base, leaf pairs forming a broad shield-shaped sinus in the bud. Petiole 1-3 mm long, spreading to a broad, ± pubescent base. Inflorescence composed of terminal and usually some subaxial lateral branches, each of at least (3)-4 pairs of sessile flowers, together forming an oblong, triangular or corymbose head 1-6 cm long, not including a vegetative bud, new growth coming from > 2 cm below inflorescence. Flowers and bracts strictly opposite throughout, bracts ± conate at their base with a rim of hairs, rachis bifurcate pubescent. Bracts broadly triangular, ± acute, 4 mm long, margin often minutely ciliate below, concave, least bracts leaf-like not evident above but sometimes impressed, ± keeled below. Disc lobed, to 1/4 length of ovary. Ovary glabrous, 0.1-0.5 mm long. Capsule dorsiventrally compressed, glabrous, ovate, 5.6-5.9 x 2.3 mm, dehiscence septicidal with a little loculicidal dehiscence at apex. Chromosome number 2n = 21 or 42.

Habitat. — Poorly drained sites — bogs, flushes, pakiki swamp, "swampy vegetation in stream flowing through mountain beechnets" (Thomas R.) or well-drained sites — moraine, stable scree, rocky outcrops. Very rarely under forest canopy, but abundant on forest margins, in shrubland and in grassland. Found on soils from varied parent material, for example on soils derived from ultramafic rocks at Red Hill (Wairau). Sea-level (Auckland Is. and Stewart Is.) to 1440 m.

Often one main leader develops as a relay axis beyond the zone of inflorescence (Koriba’s architectural model of HALL et al., 1978), although these axes, and even short trunk axes may show some plagiocladous distally.

Many adaxial stomata have been seen on one piece from each of Moa Park, Craigieburn, Mt. Ida and Forbes Mts., and on all collections seen from Arthur’s Pass. This last locality is well-known as a centre of endemicism, as a northern boundary (Hectorella-Hectoreellaceae) and now as a centre of taxonomic “incongruence.”

Hebe odora var. prostrata was listed but not formally described by COKCAYNE (1909: 44). B. Patrick (pers. comm., 1987) has identified this with a distinct, prostrate form of Stewart Is. and Longwood Ra. (southern South Is.), which sometimes grows together with typical L. odora. HAIR (1967) records n = 42 for plants identified as Hebe odora var. prostrata, but also for several other South Is. populations of Hebe odora. Further field study is required. Fiordland specimens of L. odora have large, acute leaves to 16 × 7 mm, with leaf bases conspicuously swollen with and margins minutely crenulate (but less thickened than those of L. mooreae). Crenulate leaf margins also occur in some central Otago plants, and in all Stewart Is. and Auckland Is. plants. Extreme leaf dimensions are also recorded at, for example, Eyre Mountains (GIVEN, Nov. 1971 (CHR): 15 × 9 mm). Lobed “reversion” foliage is very rarely present (JOHNSON, 20.1.1974 (CHR) Mavora Hills).


MOORE (1961) described the cuneate-based leaves and fused anterior calyx lobes of this form and Armstrong described the corolla as 3-lobed. This character combination is very distinctive in a widely cultivated form which is probably near V. anomala. These plants are closely related to L. odora through their terminal inflorescence, for example, on the Rock and Pillar Ra. shrubs of L. odora are generally the typical form with leaves 8 × 4 – 9 × 5 mm. However, Gray, 11.3.1972, (OTA) Rock and Pillar Ra., has a narrower leaf (9 × 3.5 mm) with a more well-defined mid-rib, and approaches the cultivated form referred to above. The leaf base is also more truncate in Gray’s collection and the leaf pairs split very early in the bud. The status and distribution of V. anomala remain to be ascertained. Further to the type and the Gray collection, MOORE (1961) cites Armstrong material from Rangitata, and the localities: Rock and Pillar, Rangitata Valley, upper Rakai suggest a standard northeast Otago-mid-Canterbury distribution pattern.


Prostrate to erect shrub to 2 m high, branching often distinctly rhamnoid, internodes to 8 mm long. Leaf base swollen, drying to a saddle-shaped inflated apex. Deciduous, aculeate, all stroma abaxial but leaf ± the same colour above as below, very coriaceous, margins bevelled, minutely crenulate. Midrib usually impressed, conspicuous below, no other veins usually visible. Petiole 2 mm long, white where narrow. Bifurcous or ramiiformly in the stem linked with peduncle intersept the petiole connature. Inflorescence intercalary, including a terminal vegetative bud, comprising one or two pairs of lateral spikes, each of these simple, very rarely tripartitively branched, to 4 cm long, and with at least 4 pairs of flowers. Rachis often pubescent, bracts strictly opposite throughout, connate, broad- triangular, ciliolate at least on lower margins at the connate margins membranous, often tinged purple. Flowers sessile, calyx 3.4 mm long, usually ciliate at least apically, anterior lobes fused to 1/3 of their length, posterior two free. Corolla tube usually ± equal to calyx lobes, lobes ± clawed, 2.5–4 × 5.5 mm. Disc lobed, to 1.3 length of ovary. Ovary glabrous, ovate, to 1.5 mm long. Fruit dorsally compressed, 6 × 3 mm. Chromosome number n = 63 (Fig. 1).

Distribution. — Western South Island.

Habitat. — Poorly drained sites — bogs, pakiki swamp, lakeshores. Well-drained sites — rocky slopes and ledges. Occasionally in Nothofagus forest, most often in shrubland, where it may be structurally important, and also in grassland. On soils derived from a wide range of parent material, often found on soils on ultramafic rocks in tussock shrubland and dwarf Nothofagus forest, 5 m (Cascade R. mouth) — 1200 m.

Plants with adaxial stoma are known only from Caswell Sound, Fiordland, and Denniston Plateau, Nelson. The crenulate leaf margins recall Coprosma serrulata (Rubiaceae), also found in shrublands of southwest South Island. JOHNSON, 31.3.1977 (CHR), Cascade River Mouth, Lake Jumbuck lakeshore scrub and forest, 5 m altitude, is a luxuriant form growing at Jackson Bay, a major biogeographic centre (HEADS, 1989). The collection has internodes up to 6 mm long, petioles up to 3 mm long, and leaves to 24 × 5.5 mm and had been identified, not surprisingly, as the unrelated Hebe elliptica. DRUCE, Jan. 1969 (CHR) Goulburn Downs 1900, has corolla 15 mm long, with the limb 15 mm broad, leaves acutae, 22 × 4 mm. Sites of probable Leroid population are evident. This is another luxuriant form, again found at a locality of general biogeographic significance (HEADS, 1989).


Shrub up to 60 cm tall. Lamina 10 × 4 mm. Spikelets smaller than those of var. mooreae, comprising 2 or 3 pairs of flowers only (Fig. 2).


Habitat. — Poorly drained low-alpine grassland and shrubland, 1160-1400 m.

Westland plants of var. mooreae have inflorescences of at least 5 pairs. The two forms of L. mooreae are probably subspecies or species and both occur together on the Douglas Range. Field study is required, as is a study of L. mooreae in Nelson, where some poorly known Karamea and Goulburn Downs populations may belong with var. telmata.


Shrub of open habit to 50 cm high, stems seldom branched, the generally prostrate and rooting proximally and orthotropic distally. Stem pubescence fibrillose, in narrow grooves. Internodes to 5 mm long. Leaves coriaceous, dark bronze-green, splitting apart very early in bud, 6-8(10) × 4-6(-7) mm, widely obovate, obtuse, ± mucronate, concave. Lamina abruptly truncate or ciliate at base, broad with, obturinulate sinus. Lamina glabrous except for minute, prickle-like cilia on upper part of the margin. Midrib obvious on lower surface only, usually not evident above, keel of leaf often flattened abaxially just below apex. Petiole glabrous, 2 mm long, spreading at base. Inflorescences all intercalary, stem apex remaining vegetative, zone of inflorescence to 2 cm long. Rachis ± pubescent, bracts all strictly opposite, connate, acute to obtuse, 2-3 mm long, with minute cilia. Calyx lobes 3-4 mm long, anterior two fused 50-90% of their length, ciliolate above. Corolla tube 6 mm long, lobes ± ovate, 5 × 3 mm. Style held in the conspicuously folded anterior corolla lobe prior to anthesis. Disc lobed, 1/4-1/3 length of ovary. Capsule dorsally compressed, ovoid-oblong, 5 × 2 mm, often with a small amount of loculicidal dehiscence. Chromosome number n = 21.
Fig. 1. — *Leonohebe mooreae* var. mooreae.
A, habit; B, flower; C, disc; D, distal portion of infructescence (A, B, C from type, D from J. M. Ritchie (CHR) Te Waewae).

Fig. 2. — *Leonohebe mooreae* var. delinata.
A, habit; B, flower (posterior petal uppermost); C, oblique view of flower (posterior petal at bottom left) (A from type, B and C from Wardle & Fryer, 27.2.1967, CHR).
**Distribution.** — Auckland Is., South Is., North Is. (Mt Taranaki only).

**Habitat.** — Poorly drained sites—swampy areas, seepages, flushes, streambanks. Well-drained sites—moraine, gravel in river and creek beds. Most often collected in grassland, and also known from forest margin, shrubland and herbfield, 450-1650 m.

Certain central Otago collections of this species, notably Chaffey, 30.12.1975 (CHR) Blue Lake, and Mark, 8.2.1985 (OTA) upper West Waiau V., both from the Garvie Mts. (and cf. Mark, 22.11.1970 (OTA), Carrick R.) are more branched (than the typical form. Mark, 8.2.1985 (previously identified as Hebe buchanani, which it resembles) is annotated “common on rock outcrops” which is also atypical for L. pauciflora var. s.s.


Shrub to at least 20 cm high, internodes to 5 mm long, stem pubescent bifurciferous in grooves, petiole connate ciliate centrally, leaves separating early in bud. Leaves elliptic to slightly oblong or ovate, 8-16 x 4-6 mm, keel conspicuous, continued abaxially into short mucro. Leaf margin rounded, sometimes ± bevelled near apex. Young leaves and leaves below inflorescence glabrous or with comb-like rim of caducous, erect, white cilia, stoma conspicuous on upper and lower leaf surfaces. Petiole to 3 mm long. Inflorescence usually terminal, simple, 1-4 cm long, sometimes branched with lateral spikes. Bracts opposite and connate throughout, conspicuous, leaf-like, to 7 x 4 mm, glabrous or with comb-like rim of marginal cilia. Calyx lobes to 5 mm long, lower lobes white or mauve, rounded, clawed, to 6 x 5 mm. Disc to 1/4 length of ovary. Ovary with loculicidal ridge and slight septal disc groove, stigma bilobed. Capsule 6 x 3 mm. Chromosome number n = 59 (Fig. 3).

**Distribution.** — Western South Island.

**Habitat.** — Forest margin, shrubland, tussockland, 660-1350 m.

This variety is more lax than var. rotundata, and also differs through its longer and narrower leaves and the bifurciferous strips of pubescence which often line the stem grooves.

Habit and leaf size and shape in L. masoniae can be very similar to those of L. mooreae, but the adaxial stomata and rounded leaf margin of the former allow identification of even sterile material. Wilson, 9.12.1971 (CHR) is a puzzling collection from Wyston Stream, Ben Ohau R., Mt. Cook region. It has the compound inflorescence of L. odorata but in most other respects resembles L. masoniae, which seems to be as variable as its more widespread relatives. Collections of this species have previously been identified as Hebe odorata, Hebe odorata “robust form” (i.e. L. mooreae), H. pauciflora and H. pauciflora var. masoniae. Sterile specimens from the Cobb Valley (Druce, Feb. 1977, CHR) which may belong here have several branches with lobed leaves, a feature also recorded in L. odorata.


Erect shrub to 1 m high, leaves crowded at ends of branches and appressed, internodes short, comprised of swollen leaf-bases 1-2 mm long, stem pubescent sparse, bifurciferous, not in grooves but on flattened central portion of stem, older stems ciliate. Leaves small and rounded, 5-7 x 4-6 mm, concave. Margin smooth and rounded, neither crenulate nor bevelled. Midrib obscure above, keeled below, often extending to apex. Stoma conspicuous above and below. Petiole glabrous, 1-2 mm long. Young leaves (including those below the inflorescence) with a comb-like rim of erect, white, caducous cilia. Inflorescence terminal, simple spike 1-2 cm long. Rachis with short, scattered, erect hairs. Bracts large and conspicuous, hiding the calyx, opposite and connate throughout. Lowest bract ± adjacent leaves but larger and with more membranous margins, to 9 x 6 mm, margin usually ciliate throughout. Calyx lobes to 6 x 2 mm, obovate, ciliate at apex, two anterior lobes fused to 1/3 of their length. Corolla white or mauve, tube funnel-shaped, to 7 mm long, lobes (3)-4(-6), rounded, clawed, to 6 x 5 mm, anterior lobes floret acuminate, disc 1/4 length of ovary. Capsule broadly obovate, dorsally compressed, 7 x 5 mm, slightly exceeding calyx (Fig. 3).


**Habitat.** — Seepage areas in shrubland and tussockland, 1050-1500 m.

The variety name refers to the pubinivate “leaf-bases” and rounded leaves. As in related species, the leaves actually abscise above the abscission zone, so that a short portion of petiole remains attached to the “leaf-base”.


Prostrate, much-branched shrub, stems occasionally rooting adventitiously; stems with bifurciferous grooves including sparse pubescence, bud with narrow sinus, internodes 5(-10) mm long. Leaves ± acute, midrib conspicuous and ridged below, and evident above, margin thickened especially apically and ± bevelled. Inflorescence to 18 mm long, unbranched, bearing ca. 10 flowers, peduncle to 10 mm long. Calyx bracts conspicuous at the base of each inflorescence. Lowermost bract opposite. Calyx lobes rounded, ciliate, anterior lobes fused to 50-90% of their length, corolla tube < or = calyx, ovary glabrous. Capsule obovate, acute, 4 mm long.

**Distribution.** — Garvie Mts., South Island.

**Habitat.** — Alpine debris slopes, 1370 m.

The affinities of this species, placed by Moore (1965) in “incertae sedis”, lie rather than with H. biggarrii as Moore suggested. Apart from the holotype and two isotypes I have only seen two Simpson collections, both from the Garvie Mts. and matching the type.


Decumbent, diffusely branched shrub to 40 cm tall, branches with bifurciferous pubescence, basal connate of leaves bearing rim of hairs, bud sinuses narrow. Leaves 17-25 x 9-12 mm, broad obovate-shpatulate, gradually narrowed to base, glaucous above and below, sometimes apiculate, margin cartilaginous and smooth. Inflorescence lateral, regularly compound (tripartite), peduncles and pedicels generally with some slight pubescence, pedicel to 2.5 mm, bracts to 3 mm long. Calyx lobes 4-5, 1.5 mm long, rounded-acute, corolla white, tube 1.0 mm long, lobes 2 mm long, broad-rounded. Disc short, 4-lobed. Ovary glabrous, capsule 4 mm long, glabrous, acuminate (Fig. 4).

**Distribution.** — (Fig. 5): South Island.

**Habitat.** — Low-alpine shrubland, felfield, boulderfield, partly stable talus slopes, 1200-1650 m.
Fig. 3. — *Leucothebe masoniae* var. *rotundata.*
*L. masoniae* var. *masoniae* E, habit (Druce, Nov. 1976, CHR, Hope Range).

Fig. 4. — *Hebe croyii.*
A, habit; B, leaf bud with narrow sinus; C, D, young fruits with persistent calyces; E, flowers at anthesis (anterior views on left, posterior views on right) (A-D from type, E from Dickinson, 13.1.1986, OIA, Gem Lake, Umbrella Mtz.).

The large, spathulate and glaucous leaves are very distinctive and recall Hebe cockayneana (which has smaller, elliptic leaves), H. pinguifolia and H. toiporia. The tripartite inflorescence recalls northern members of Hebe sect. Subdistichae. The species has also been confused with H. dilatata.

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