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A reappraisal of the generic status of Liparia and Priestleya (Fabaceae)

Anne Lise Schutte & Ben-Erik Van Wyk¹

Summary

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The generic delimitation of Liparia L. and Priestleya DC. (Fabaceae, tribe Liparieae) is reevaluated. Traditionally the shape and size of the carinal lobe of the calyx, the shape of the keel petals and the number of flowers per inflorescence were used as diagnostic characters. A study of morphological and alkaloid variation indicates that the two genera run much into one another. Differences in inflorescence and floral structure can be attributed to adaptations to different pollination strategies. The unique combination of major alkaloids occurring in both genera also suggests that they are congeneric. Priestleya is therefore placed into synonymy under Liparia. The nomenclature, synonymy and typification of the genus and the 14 species recognized are presented, and some necessary new combinations are made.

Introduction

Liparia L. and Priestleya DC. form part of the papilionaceous tribe Liparieae, restricted to the Cape Province of southern Africa and distinguished from the closely related tribe Podalyrieae by the fusion of the stamens, either into an open sheath or a closed tube (in the Podalyrieae the stamens are more or less free to the base). Affinities between the genera of these two tribes are currently under investigation and will be published elsewhere (Van Wyk & Schutte, in prep.).

Liparia, as presently circumscribed (Bos, 1967), comprises two species (one with two subspecies). Schutte & Van Wyk (1993) recently found *Priestleya* to be paraphyletic. *Priestleya* sect. *Aneisothea* DC. was separated and accorded generic status under the reinstated name *Xiphotheca* Eckl. & Zeyh. Nine species are included within *Xiphotheca*. After the reduction only 12 species remained in *Priestleya*.

The similarities between members of *Liparia* and *Priestleya* have previously been noted by various authors (Bentham, 1843; Harvey, 1862; Van Wyk & al., 1991a, 1991b; Oliver & al., 1992; Schutte & Van Wyk, 1993). In the past, the enlarged and petaloid lower lobe of the calyx, the narrow keel with a forwardly directed beak and the congested, many-flowered inflorescence were used as diagnostic characters for *Liparia* (Polhill, 1976, 1981). In *Priestleya* the lower calyx lobe is only slightly enlarged, the keel is broader and has an upwardly directed beak, and the flowers are usually arranged in extended racemes or congested few-flowered inflorescences. However, the recent discovery of a new species, *P. boucheri* (Oliver & al., 1992), as well as results gained from comparative studies show that the distinction between these two genera must be reappraised. Morphological and alkaloid variation in *Liparia* and *Priestleya* was therefore investigated. The results are presented, illustrated (Fig. 1-3) and discussed below.

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Results

Liparia and Priestleya are remarkably similar in the shapes, sizes and venation patterns of the leaves (Fig. 1). In fact, they alone within the tribe have totally sessile leaves. Their leaf venation also deviates by the presence of three or more primary veins arising from the base of the lamina, whereas in other genera the leaves are pinnately veined.

Liparia and Priestleya have simple racemose inflorescences, situated in the axils of the terminal leaves, with variation in the number of flowers, the length of the peduncle and the length of the inflorescence axis. The flowers are borne on lateral short shoots, terminating in a small apical extension of the inflorescence axis (Fig. 2). P. hirsuta has an extended raceme of 6 to 12 flowers, often basally subtended by sterile bracts. Modification of this basic inflorescence type seems to occur in two different directions, as illustrated in Fig. 2. On the one hand the flower number increases, the inflorescence axis shortens, and the sterile bracts become enlarged and petaloid, creating a nodding, head-like inflorescence unit as in L. parva and L. splendens. On the other hand, a reduction in flower number and a decrease in the

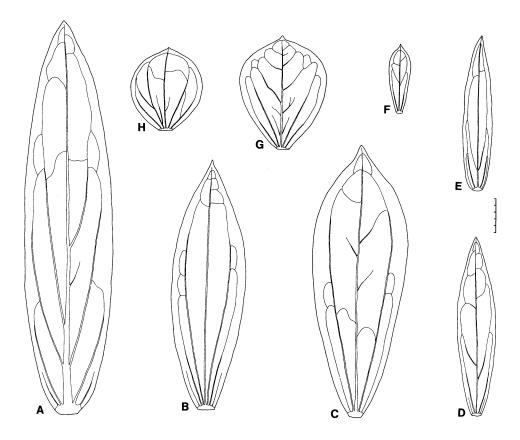


Fig. 1. Variation in size, shape and venation pattern of leaves in Liparia and Priestleya (vestiture not shown). A, P. boucheri; B, L. splendens subsp. splendens; C, P. hirsuta; D, P. myrtifolia; E, P. angustifolia; F, P. teres; G, P. latifolia; H, P. vestita. – Scale 5 mm.

length of the axis eventually lead to decussate 4-flowered inflorescences as in *P. capitata* and related species, or paired flowers as in *P. boucheri*. In this line of specialization, the inflorescences are erect and usually lack sterile bracts.

The flowers generally have a firm texture, but there are some distinct differences in flower colour and structure (Fig. 3). In all except one species of *Priestleya*, the flowers are bright yellow and the keel petals broad with an upwardly directed beak. *P. boucheri* and *Liparia parva*, however, have lemon yellow flowers. In these two species the keel petals are narrow with the apex forwardly directed. The keel petals are similar in shape in *L. splendens*, but the flowers are much larger and bright orange to reddish in colour. Furthermore, the wing petals are structurally modified to interlock dorsally and completely enclose the keel. In both *Liparia* species the lower lobe of the calyx is much larger than the upper four lobes. All species of *Priestleya*, including *P. boucheri*, have the lowermost calyx lobe only slightly longer than the others.

Studies on the distribution of major alkaloids in *Liparia* and *Priestleya* have provided some exciting results (Van Wyk & al., 1991a, 1991b). In *Priestleya*, tetracyclic quinolizidine alkaloids such as sparteine, isosparteine, 11,12-dehydrosparteine, isolupanine, lupanine and 13-hydroxylupanine occur as major components, as well as

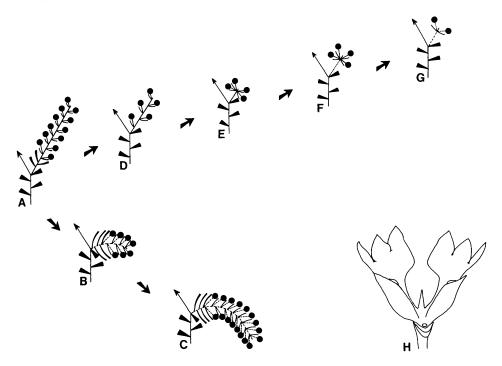


Fig. 2. Schematic representation of variation in inflorescence structure in Liparia and Priestleya. A, erect many-flowered raceme, often subtended by sterile bracts, e.g. P. hirsuta; B, nodding, head-like congested few-flowered raceme, subtended by sterile bracts, e.g. L. parva; C, nodding, head-like many-flowered congested raceme, subtended by sterile bracts, e.g. L. splendens; D, erect, few-flowered raceme, e.g. P. angustifolia; E, erect, decussate 4-flowered inflorescence with a peduncle, e.g. P. myrtifolia; F, erect, decussate 4-flowered inflorescence without a peduncle, e.g. P. vestita; G, erect, 2-flowered inflorescences without a peduncle, e.g. P. boucheri; H, terminal part of inflorescence showing axis extension.

small quantities of ammodendrine, a piperidyl alkaloid. Exactly the same combination and proportions of alkaloids were detected in *L. parva. L. splendens*, however, differed in the presence of a large amount of ammodendrine and only small quantities of the other compounds. As with morphological data, the major discontinuity does not conform with current generic delimitation.

Discussion

From the above evidence it is clear that, taken together, *Liparia* and *Priestleya* are monophyletic. They share at least five unambiguous synapomorphies, namely: (1) the totally sessile leaves; (2) the peculiar venation pattern of the leaves (3- or moreveined from the leaf base); (3) the presence of a terminal extension of the inflorescence axis; (4) the occurrence of sterile bracts at the base of inflorescences; and (5) the unique combination of alkaloids. None of these characters occur in any of the other genera in the tribe *Liparieae*.

Variation that does occur in inflorescence and flower structure may result from adaptation to different pollinators. As far as can be ascertained, most *Priestleya* species are pollinated by xylocopid bees. According to Scott-Elliot (1890), *Liparia parva* is visited by bees, but the almost proteoid structure of the inflorescence, yeast-like odour of the flowers, pale colour of the corolla and the fact that the inflorescences are borne at ground level suggest possible pollination by small mammals (pers. obs.). This is known to occur in some species of the genus *Protea* L. (*Proteaceae*) where the inflorescences show analogous characteristics (Wiens & al., 1983; Rebelo & Breytenbach, 1987). If the similarity in floral structure between

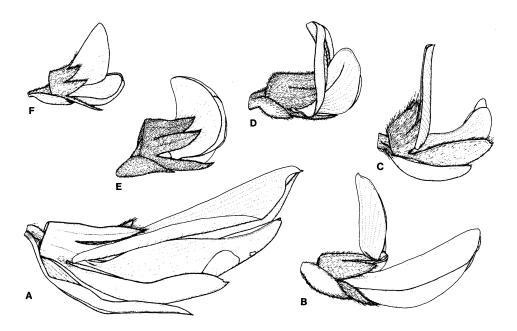


Fig. 3. Flowers in lateral view, showing variation in size and structure, in Liparia and Priestleya. A, L. splendens; B, P. boucheri; C, L. parva; D, P. hirsuta; E, P. umbellifera; F, P. angustifolia. – Scale 5 mm.

Priestleya boucheri and L. parva is considered, the same pollination strategy could also be present in the former. A study of the pollination agents of these species promises to yield some fascinating results, since pollination by non-flying mammals is not known to occur in the legume family (Arroyo, 1981). L. splendens is a putative sunbird-pollinated species (Bos, 1967; Rebelo, 1987) and exibits a number of corresponding morphological adaptations, such as the pendent, compact proteaceous inflorescence, orange-red flowers, large standard petal, interlocked wing petals, and enlarged petaloid carinal lobe of the calyx. It seems as if this might be an example of mimicry between Proteaceae and Fabaceae occurring in the fynbos.

According to Whitehead & al. (1987) pollination syndromes are not clear-cut categories, but overlap to a great extent to form part of a continuum of pollinator attraction strategies. Arroyo (1981) claims that bird pollinated legumes belonging to the subfamily *Papilionoideae* evolved from *Xylocopa*-pollinated species. In the past many monotypic or small genera were established on the basis of unusual floral characteristics associated with ornithophilous pollination. In the Cape fynbos region of southern Africa, this is a common phenomenon in the family *Iridaceae* (Goldblatt & De Vos, 1989; Goldblatt, 1990, 1992), which has subsequently led to the reduction of the ornithophilous "genera" into synonymy.

Judged by the given data, the distinction between *Liparia* and *Priestleya* is based solely on characters associated with pollination. The two are undoubtedly congeneric, and their amalgamation will result in a more natural classification and give a better reflection of major lineages within the tribe. We therefore propose the placing of *Priestleya* into synonymy under *Liparia*.

Nomenclature

- Liparia L., Mant. Pl.: 156. 1771. Type (designated by Schutte & Van Wyk in Regnum Veg. 127: 62. 1993): L. sphaerica L. [= L. splendens (Burm. f.) Bos & de Wit].
- = *Priestleya* DC. in Ann. Sci. Nat. (Paris) 4: 90. 1825. Type (designated by Hutchinson, 1964): *P. myrtifolia* (Thunb.) DC. (*Liparia myrtifolia* Thunb.).
- = *Priestleya* sect. *Eisothea* DC. in Ann. Sci. Nat. (Paris) 4: 90. 1825. Type (designated by Hutchinson, 1964): *P. myrtifolia* (Thunb.) DC. (*Liparia myrtifolia* Thunb.).
- = Achyronia Wendl., Bot. Beob.: 39, t. 12. 1798 (non Royen ex L., Opera Var.: 243. 1758. Type (designated here): A. villosa Wendl. [= Liparia angustifolia (Eckl. & Zeyh.) Schutte].

Woody shrubs or subshrubs. Leaves alternate, simple, often becoming black when dry; lamina linear to elliptic to almost round, flat or concave, with 3 or more veins arising from sessile base; petioles absent; stipules usually present, small, persistent. Inflorescences simple, axillary brachyblasts ending in a terminal rachis extension, erect or nodding; flowers in extended racemes or aggregated by 2 or 4, or congested in many-flowered heads. Bracts broad, sheathing, sometimes foliaceous or petaloid, often sterile. Bracteoles absent. Calyx intrusive; upper two lobes fused higher up than lower three lobes; carinal lobe longer than the upper four, sometimes enlarged and petaloid. Corolla firmly textured, bright yellow, pale lemon-yellow, or orange to reddish orange. Standard elliptic-oblong to obovate to subcircular, with calli at base of lamina; margins sometimes reflexed. Wing petals oblong to narrowly oblong,

sometimes folded round the keel with interlocking lobes. *Keel petals* broad with an upwardly directed beak or narrow with a forwardly directed beak. *Stamens* diadelphous, united for \pm half their length, vexillary filament free; anthers strongly dimorphic, alternately dorsifixed and subbasifixed. *Pistil* sessile; ovary densely sericeous to tomentose; style curved upwards, slender, glabrous. *Pods* coriaceous, obliquely ovate to oblong, beaked, 3- to several-seeded. *Seeds* oblong-reniform; hilum elliptic, surrounded by a collar-like aril. *Chromosome number* 2n = 18.

Endemic to the Cape fynbos region of South Africa, ranging from the Clanwilliam region in the north-western Cape southwards to the Cape Peninsula and eastwards to Uitenhage near Port Elizabeth.

Fourteen species can be distinguished. These are enumerated below. A detailed taxonomic account of the genus *Liparia*, including an identification key and full descriptions of the species, will be published elsewhere.

- 1. Liparia angustifolia (Eckl. & Zeyh.) A. L. Schutte, comb. nov. ≡ Priestleya angustifolia Eckl. & Zeyh., Enum. Pl. Afric. Austral. 2: 165. 1836. Lectotype (designated here): South Africa, Cape Province, "In pratis montanis et humidis laterum montium 'Hottentottshollandsberge' prope 'Palmietrivier' (Stellenbosch) et 'Klynriviersberge' (Caledon)", Ecklon & Zeyher 1222 (SAM!, excl. small fragment in center; isotypes: C!, K!, P!, S!, UPS! W!). [The lectotype has been annotated by Ecklon himself.]
- = Achyronia villosa J. C. Wendl., Bot. Beob: 39. 1798 (non Liparia villosa L., Mant. Pl.: 269. 1771, nec L. villosa Thunb., Prodr. Pl. Cap.: 124. 1800). Described from the "Südsee-Inseln". [No original material could be traced, but from the illustration in Wendland (1799: t. 12), the identity of the species is quite clear.]
- = Borbonia villosa Thunb., Fl. Cap., ed. [2]: 560. 1823 (non Liparia villosa L. 1771, nom. illeg.; nec L. villosa Thunb. 1800) ≡ Priestleya villosa (Thunb.) Druce in Bot. Soc. Exch. Club Brit. Isles 4: 641. 1917. Lectotype (designated here): South Africa, Cape Province, "e Cap. b. Spei", Herb. Thunberg No. 16337 (UPS!).
- "Priestleya umbellifera" sensu E. Meyer, Comm. Pl. Afr. Austr. 1: 17. 1836.
- Liparia boucheri (E. G. H. Oliv. & Fellingham) A. L. Schutte, comb. nov.

 Priestleya boucheri E. G. H. Oliv. & Fellingham in Bothalia 22: 47. 1992.
 Holotype: South Africa, Cape Province, Simonstown division, Grabouw area, Kogelberg Reserve, Five Beacon Ridge, summit of ridge, Boucher & Oliver 5531 (STE!; isotypes: BOL, K, MO, PRE, S).
- 3. **Liparia calycina** (L. Bolus) A. L. Schutte, **comb. nov.** ≡ *Priestleya calycina* L. Bolus in Ann. Bolus Herb. 4: 124. 1928. Holotype: South Africa, Cape Province, South western region, Caledon division, Hottentots Holland Mountains, *Stokoe s.n.* in Herb. Bolus No. 18325 (BOL!; isotype, K!).
- 4. *Liparia capitata* Thunb., Prodr. Pl. Cap.: 124. 1800 (non *Crotalaria capitata* Lam., Encycl. 2: 195. 1786) ≡ *Borbonia capitata* (Thunb.) Poir. in Lamarck, Encycl., Suppl. 1: 680. 1811 ≡ *Priestleya capitata* (Thunb.) DC., Prodr. 2: 121.

- 1825. Lectotype (designated here): South Africa, Cape Province, "Crescit in summo 'Taffelberg'", Herb. Thunberg No. 17002 (UPS!).
- Priestleya laevigata var. pilosa E. Mey., Comm. Pl. Afr. Austr. 1: 18. 1836, excl. syn. ≡ P. capitata var. pilosa (E. Mey.) Harv. in Harvey & Sonder, Fl. Cap.
 2: 18. 1862. Lectotype (designated here): South Africa, Cape Province, "Ad montem Dutoitskloof, altit. 1800 ped.", Drège s.n. (P!; isolectotypes: K!, P!, S!, W!).
- Priestleya laevigata var. glabra E. Mey., Comm. Pl. Afr. Austr. 1: 18. 1836. Lectotype (designated here): South Africa, Cape Province, "In saxonis montium prope 'Gnadenthal', altit. 2600 ped.", Drège s.n. (P!; isolectotypes: K!, P!, S!, W!).
- "Priestleya laevigata" sensu Ecklon & Zeyher, Enum. Pl. Afr. Austr. 2: 165.
 1836.
- 5. Liparia genistoides (Lam.) A. L. Schutte, comb. nov. ≡ Crotalaria genistoides Lam., Encycl. 2: 196. 1786. Lectotype (designated here): South Africa, Cape Province, "Cap. de Bonne-Espérance", s. coll. (P-LAM!).
- = Liparia teres Thunb., Prodr. Pl. Cap.: 124. 1800 ≡ Priestleya teres (Thunb.) DC., Prodr. 2: 122. 1825. Lectotype (designated here): South Africa, Cape Province, "e Cap. b. Spei", Herb. Thunberg No. 17010 (UPS!).
- "Priestleya laevigata" sensu Bentham in London J. Bot. 2: 445. 1843.
- 6. Liparia graminifolia L., Mant. Pl.: 268. 1771 ≡ Borbonia graminifolia (L.) Lam., Encycl. 1: 437. 1785 ≡ Priestleya graminifolia (L.) DC., Prodr. 2: 122. 1825. Lectotype (designated here): s. loc., s. coll., Herb. Linnaeus No. 910.3 (LINN!).
- = *Priestleya hirsuta* var. *trinervia* Meisn. in London J. Bot. 2: 64. 1843. Lectotype (designated here): South Africa, Cape Province, "Ataquaskloof", *Drège s.n.* (P!).
- Priestleya hirsuta var. subenervia Meisn. in London J. Bot. 2: 64. 1843. Lectotype (designated here): South Africa, Cape Province, "In collibus prope Knysna Rivier, distr. George, Jan. 1839", Krauss 914. [No type specimen has yet been found, but from the description and locality this variety is doubtfully distinct.]
- 8. Liparia laevigata (L.) Thunb., Prodr. Pl. Cap.: 123. 1800 ≡ Borbonia laevigata L., Mant. Pl.: 100. 1767 ≡ L. umbellata L., Mant. Pl.: 269, 516. 1771, nom illeg. ≡ Priestleya laevigata (L.) DC., Prodr. 2: 121. 1825 (quoad basion.) ≡ P. thunbergii Benth. in London J. Bot. 2: 446. 1843, nom illeg. Lectotype (designated here): South Africa, Cape Province, "ad Cap. B. Spei", anon. 31, Herb. Linnaeus No. 890.4 (LINN!). ["Priestleya laevigata" sensu DC., i.e. the specimen in G-DC from which the plate in Candolle (1825-1827: t. 30) was drawn, is

- L. umbellifera; Bentham (1843) followed Candolle's (1825) misapplication of the name and consequently renamed illegitimately the genuine Borbonia laevigata.]
- = Liparia villosa Thunb., Prodr. Pl. Cap.: 124. 1800 (non L. villosa L., Mant. Pl.: 269. 1771, nom illeg.) ≡ Priestleya thunbergii var. villosa Harv. in Harvey & Sonder, Fl. Cap. 2: 18. 1862. Lectotype (designated here): South Africa, Cape Province, "Crescit in summo 'Taffelberg'" Herb. Thunberg No. 17014 (UPS!).
- "Priestleya umbellifera" sensu Ecklon & Zeyher, Enum. Pl. Afr. Austr. 2: 165.
 1836.
- 9. *Liparia latifolia* (Benth.) A. L. Schutte, **comb. nov.** ≡ *Priestleya latifolia* Benth. in London J. Bot. 2: 447. 1843. Lectotype (designated here): South Africa, Cape Province, "Cap. b. Spei", *Scholl s.n.* ex Herb. Bentham (K!).
- 10. *Liparia myrtifolia* Thunb., Prodr. Pl. Cap.: 123. 1800 ≡ *Borbonia myrtifolia* (Thunb.) Poir. in Lamarck, Encycl., Suppl. 1: 680. 1811 ≡ *Priestleya myrtifolia* (Thunb.) DC., Prodr. 2: 121. 1825. Lectotype (designated here): South Africa, Cape Province, "e Cap. b. Spei", Herb. Thunberg No. 17007 (UPS!).
- = *Priestleya leiocarpa* Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 165. 1836. Lectotype (designated here): South Africa, Cape Province, "In pratis montanis prope 'Grootvadersbosch' (Swellendam)", *Ecklon & Zeyher 1218* (S!).
- 11. *Liparia parva* Vogel ex Walp. in Linnaea 13: 468. 1839. Neotype (designated by Bos, 1967): South Africa, Cape Province, Cape Peninsula, south western slopes of Klaasjagersberg, *Sidey* 2142 (S!; isotype: PRE!).
- Liparia crassinervia Meisn. in London J. Bot. 2: 63. 1843. Type: South Africa, Cape Province, "In turfaceis arenosis Uitershoek, Sept. 1838", Krauss s.n. (?B†). [The type has not yet been located, but from the description it clearly belongs to L. parva see Bos (1967).]
- 12. Liparia splendens (Burm. f.) Bos & de Wit in J. S. African Bot. 33: 276. 1967 ≡ Leucadendron splendens Burm. f., Prodr. Fl. Cap.: 4. 1768. Lectotype (designated here): s. loc., s. coll. (G!). [Bos (1967) designated a neotype, since no original material could then be found. However, during a visit to Geneva in 1991, we traced a specimen named "Leucad. splendens" by Burman himself.]

12a. Liparia splendens subsp. splendens

- = Liparia sphaerica L., Mant. Pl.: 268. 1771 ≡ Borbonia sphaerica (L.) Lam., Encycl. 1: 437. 1783. Neotype (designated by Schutte & Van Wyk in Jarvis & al., 1993): s. loc., s. coll., Herb. Linnaeus No. 910.1 (LINN!).
- 12b. *Liparia splendens* subsp. *comantha* (Eckl. & Zeyh.) Bos & de Wit in J. S. African Bot. 33: 276. 1967 ≡ *Liparia comantha* Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 164. 1836. Lectotype (designated by Bos, 1967): South Africa, Cape Province, "Hottentottshollandskloof prope Palmietrivier (Stellenbosch)", *Ecklon & Zeyher 1216* (P!; isotypes: K!, LD!, P!).

- = Liparia burchellii Benth. in London J. Bot. 2: 443. 1843. Holotype: South Africa, Cape Province, "Cape Colony", Burchell 6881 (K!; isotypes: P!, W!).
- = Liparia parva var. angustifolia Benth. ex Hook. f. in Curtis's Bot. Mag.: ad t. 4034. 1843. Holotype: s. loc., s. coll. (K!). [The specimen has been annotated by Bentham himself.]
- 13. *Liparia umbellifera* Thunb., Prodr. Pl. Cap.: 124. 1800 ≡ *Borbonia umbellifera* (Thunb.) Poir. in Lamarck, Encycl., Suppl. 1: 680. 1811 ≡ *Priestleya umbellifera* (Thunb.) DC., Prodr. 2: 122. 1825. Lectotype (designated here): South Africa, Cape Province, "e Cap. b. Spei", Herb. Thunberg No. 17012 (UPS!).
- Crotalaria capitata Lam., Encycl. 2: 195. 1786 (non Liparia capitata Thunb., Prodr. Pl. Cap.: 124. 1800, nec Priestleya capitata (Lam.) DC., Prodr. 2: 121. 1825) = P. cephalotes E. Mey., Comm. Pl. Afr. Austr. 1: 18. 1836. Lectotype (designated here): South Africa, Cape Province, "Cap. de Bonne-Espérance", Sonnerat s.n. (P-LAM!).
- = Priestleya cephalotes var. angustifolia E. Mey., Comm. Pl. Afr. Austr. 1: 18. 1836. Lectotype (designated here): South Africa, Cape Province, "Ad rivulum montis Piquetberg, altit. 2500 ped.", Drège s.n. (P!; isotypes: K!, P!, TCD!, W!).
- "Priestleya laevigata" auct.: Candolle, Prodr. 2: 121. 1825, Candolle, Mém. Légum.: 195. 1826; Don, Gen. Syst. 2: 132. 1832. [See note under Liparia laevigata.]
- 14. *Liparia vestita* Thunb., Prodr. Pl. Cap.: 124. 1800 ≡ *Borbonia vestita* (Thunb.) Poir. in Lamarck, Encycl., Suppl. 1: 680. 1811 ≡ *Priestleya vestita* (Thunb.) DC., Prodr. 2: 122. 1825. Lectotype (designated here): South Africa, Cape Province, "Crescit in Hottentots Hollandsberg", Herb. Thunberg No. 17013 (UPS!).
- = Borbonia tomentosa L., Sp. Pl.: 707. 1753 (non Liparia tomentosa Thunb., Prodr. Pl. Cap.: 124. 1800 ≡ Priestleya tomentosa (L.) Druce in Bot. Soc. Exch. Club Brit. Isles 4: 641. 1917. Lectotype (designated here): [icon in] Seba, Thes. 1, t. 24, f. 1. 1734.
- "Liparia villosa" sensu Andrews in Bot. Repos. 6: t. 382. 1804.

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