

A taxonomic revision of the *Pteronia camphorata* group (Astereae, Asteraceae)

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Abstract:

As a first step towards a comprehensive revision of *Pteronia* (Asteraceae, Astereae), we present here a taxonomic treatment of the *Pteronia camphorata* group, in which we recognise three species. The group includes the type species *P. camphorata* (an important medicinal plant) and is easily distinguished from the rest of the genus by the glabrous rather than glandular or variously pilose cypselas. The lectotype of *P. camphorata* has involucre bracts with entire margins and long acuminate apices, both diagnostic characters for *P. stricta*. As such *P. stricta* is here reduced into synonymy with *P. camphorata* and the next available name, *P. aspera* Thunb, reinstated to accommodate the species heretofore treated as *P. camphorata*. Three varieties within *Pteronia camphorata* had been previously recognised (var. *armata*, var. *laevigata* and var. *longifolia*). The characters distinguishing var. *armata* were found to be continuous with the variation observed within var. *longifolia*. The third infraspecific taxon, var. *laevigata*, was however found to be distinct and is therefore recognised here as a new species, *P. cederbergensis* Bello, Magee & Boatwr. It is readily distinguished by the glabrous branches, opposite to sub-opposite somewhat succulent leaves, the 2-seriate pappus and larger, obclavate cypselas. Transverse sections of the leaves and cypselas were also examined and provide additional differences between the three recognised species.

1. Introduction

Pteronia L. is a southern African endemic genus belonging to the Asteraceae tribe Astereae. The genus was last revised by Hutchinson and Phillips (1917) a century ago and ca. 70 species are currently recognised (Leistner, 2000). Kolberg and Van Slageren (2014) recently revised the Namibian species of which they recognised twenty-four (24). In South Africa, where most of the species occur, the genus has been identified as one of the top priorities for taxonomic research (Victor and Smith, 2011; Von Staden et al., 2013). Hutchinson and Phillips (1917) subdivided *Pteronia* into four sections, sect. *Incanae*, sect. *Papillatae*, sect. *Ciliatae* and sect. *Glabratae*, based solely on the indumentum of the leaves. This infrageneric classification is generally accepted to be largely artificial, with closely related species or infraspecific taxa placed in different sections.

Several species of *Pteronia* were used by the Khoi and San peoples for their anti-infective properties since ancient times (Shearing, 1997; Viljoen et al., 2010; Hulley et al., 2016) and many of the species are still utilised today (Hulley et al., 2010, 2011). According to Van Wyk (2008) *Pteronia onobromoides* DC. was one of the San people's preferred plants, used together with animal fat to anoint the body. Similarly, *Pteronia camphorata* L. has recently been identified as the important Nama medicinal plant called “inhora” or “norraboegoe” (Hulley et al., 2016). According to Hulley et al. (2016) the traditional use of this plant for the treatment of respiratory conditions and inflammation of the neck, convulsions and haemorrhoids has been all but completely forgotten.

The *Pteronia camphorata* group includes the generitype (*P. camphorata*) and the closely related *P. stricta* Ait. and can easily be distinguished from the rest of the genus by their glabrous cypselas (glandular or variously hairy in the other species of *Pteronia*). *Pteronia camphorata* is a highly polymorphic species with three varieties currently recognised based on leaf indumentum and arrangement as well as the synflorescence structure (Hutchinson and Phillips, 1917). The species is also often confused with *P. stricta* (both in the herbarium as well as in chemical studies, e.g. Coovadia, 2007; Viljoen et al., 2010). In the taxonomic treatment of Hutchinson and Phillips (1917), members of the *P. camphorata* group were placed in two different sections: *Pteronia camphorata* var. *armata* Harv., *P. camphorata* var. *longifolia* Harv. and *P. stricta* in section *Ciliatae* while *P. camphorata* var. *laevigata* Harv. were placed in section *Glabratae*.

The circumscriptions of the current species and infraspecific taxa within the *Pteronia camphorata* group are here assessed, with detailed studies of their vegetative and reproductive morphology, leaf and fruit anatomy as well as geographical distribution. A taxonomic treatment of the species together with an updated key to the species of this group is presented.

2. Materials and methods

Herbarium collections from BOL, NBG, PRE and SAM, as well as images of type material from BM, G-DC, LINN, P, TCD and UPS-THUNB, were studied (acronyms according to Thiers, 2017). Specimens examined are cited by country and province following the Quarter Degree Reference System for South Africa (Edwards and Leistner, 1971; Leistner and Morris, 1976). The recorded geographical distributions of the species were ascertained from Leistner and Morris (1976) and maps were produced for all the species. The floral parts of the species were dissected and photographed under an Olympus SZ61 stereomicroscope to record relevant characters. Transverse sections of the leaves and fruits of all four currently recognised taxa in the group were studied. Details of voucher specimens used are presented in Table 1. Dried leaf and fruit material was first rehydrated at 60 °C for 24 h before fixing in FAA (formaldehyde: acetic acid: 96% alcohol: water; 10:5:50:35) for at least 24 h. Dehydration of material was done twice in each solution of a graded alcohol series (50% ethanol, 95% ethanol, 100% propanol and 100% butanol). Infiltration was carried out in glycol methacrylate (GMA) twice for 24 h followed by a final infiltration for five days. The samples were then embedded in GMA-filled gelatin capsules and placed in an oven at 60 °C for 24 h to polymerise (Feder and O'Brien,

1968). Transverse sections, 3–5 µm thick, were made using a Porter-Blüm ultramicrotome. These were then stained using the periodic acid Schiff/toluidine blue (PAS/TB) method (Feder and O'Brien, 1968) and finally mounted with Entellan.

3. Results and discussion

3.1. Revised species concepts

There are two original collections of *P. camphorata* in the LINN herbarium. As part of a general typification project of Linnaean Asteraceae names, Lowrey (1998) designated one of these collections (Herb. Linn. No. 980.2) as lectotype. However, upon closer examination, the lectotype has involucre bracts with entire margins and long acuminate apices, both diagnostic characters for *P. stricta*. As a result *P. stricta* is here reduced into synonymy with *P. camphorata* and the next available name, *P. aspera* Thunb., reinstated to accommodate the species heretofore treated as *P. camphorata* (Harvey, 1865; Hutchinson and Phillips, 1917; Manning and Goldblatt, 2012).

It has also become clear, after studying the variation in leaf indumentum between *P. camphorata* var. *longifolia* and *P. camphorata* var. *armata*, that the characters used to distinguish them (rigidly setose leaves in var. *armata* vs. glabrescent to sparingly ciliate near the base in var. *longifolia*) are continuous. As such we do not recognise any infraspecific taxa within *P. aspera*.

Morphological and anatomical evidence strongly suggests that *P. camphorata* var. *laevigata* should be recognised as a distinct species. The distinctiveness of this taxon is also evident by Hutchinson and Phillips' (1917) disparate placement of this taxon in section *Glabratae* rather than with the rest of the varieties of *P. camphorata* in section *Ciliatae*. We therefore recognise this taxon as a new species, hereafter referred to as *P. cederbergensis* Bello, Magee & Boatwr.

Hulley et al. (2016) discuss differences in the chemical composition of what they incorrectly consider to be two populations of *P. aspera* (cited as *P. camphorata*). It is clear from the provided locality details as well as the photographs of plants from both populations that the plant from Montagu Pass (and which was studied by Coovadia, 2007 and Viljoen et al., 2010) is rather the closely related *P. camphorata* (i.e. the taxon previously treated as *P. stricta*).

3.2. General morphology and anatomy

The species of the *Pteronia camphorata* group are evergreen, perennial shrubs with the indumentums of the branches and leaves ranging from entirely glabrous in *P. cederbergensis* to variously setose in *P. aspera* and *P. camphorata*. The leaves of *P. aspera* range from densely setose all over the surface to glabrescent with the margins sparsely ciliate towards the base. Similarly, the leaves of *P. camphorata* are largely glabrescent with a few marginal cilia towards the base. The leaves are alternate and coriaceous in *P. aspera* and *P. camphorata* but opposite and somewhat succulent in *P. cederbergensis*.

In transverse section, the leaf blades are variable in shape, ranging from somewhat heart-shaped in *P. cederbergensis* (Fig. 1C), irregular or butterfly-shaped in *P. aspera* (Fig. 1A & B) and boat-shaped in *P. camphorata* (Fig. 1D). The hairs are multicellular, usually up to eight cells, and either confined to the margins (Fig. 1D) or scattered across the lamina (Fig. 1A). A shallow to deep medial groove is located on the upper surface of the blade or sometimes on both surfaces (Fig. 1B). Glands with short stalks and biseriate heads are present on the epidermis (on the lamina and/or in medial grooves) in both *P. aspera* and *P. camphorata* (Fig. 1A & E) but absent in *P. cederbergensis*. The epidermis is covered by a thin cuticle usually 2.8–3.4 µm thick on the upper and lower sides. Epidermal cells are mostly slightly periclinally elongated, square to rounded with the outer periclinal cell walls always thick (12.5–22.9 µm). Stomata are densely or sparsely distributed on both surfaces of the leaves and the guard cells level with the leaf surface. The mesophyll is differentiated into palisade and spongy parenchyma. The palisade parenchyma is usually made up of one or two layers on both adaxial and abaxial surfaces with the spongy parenchyma compactly arranged in the centre. This equifacial condition of the palisade parenchyma is a reflection of the linear or acicular leaf form of the species with both adaxial and abaxial surfaces similarly exposed to sunlight (Smith et al., 1997). Leaves of all three species generally lack collenchyma. Vascular bundles are collateral and bundle sheaths are generally absent. Secretory canals, one or two, are associated with vascular bundles and are particularly large in *P. cederbergensis* (Fig. 1C).

The capitula are discoid, terminal and can be either solitary, as is often the case in *P. cederbergensis* (Fig. 9A), or aggregated into clusters of 2 to 6 heads, as is usually the case in *P. aspera* and *P. camphorata* (Figs. 5A & B, 7A). The involucre bracts are usually loosely arranged and generally 3-seriate and nearly always glabrous. They vary from ovate to linear or lanceolate with narrowly scarious margins and sometimes with a prominent stereome. The innermost involucre bracts are usually acute in *P. aspera* (Fig. 5C) and *P. cederbergensis* (Fig. 9D) or long acuminate in *P. camphorata* (Fig. 7D). The margins are either distinctly serrate scarious in *P. aspera* and *P. cederbergensis*, or entire in *P. camphorata* (Fig. 2). The florets are bisexual with yellow, 5-lobed corollas and the tube either glabrous in *P. cederbergensis* or sparsely to densely pubescent in *P. aspera* and *P. camphorata* (Fig. 3).

The glabrous cypselas found in the *Pteronia camphorata* group are a unique character to distinguish them from the rest of the species of the genus which have variously glandular and/or hairy cypselas. The cypselas are dorsoventrally flattened in *P. aspera* and *P. cederbergensis*, while in *P. camphorata* they are characteristically isodiametric.

Table 1
Details of voucher specimens of *Pteronia* species used for anatomical study.

Taxon	Voucher specimen	Part studied
<i>P. camphorata</i> var. <i>laevigata</i>	Pillans 9682 (NBG)	Fruit
	Jardine & Jardine 299 (NBG)	Leaf
<i>P. camphorata</i> var. <i>armata</i>	Pond UP212 (NBG)	Fruit
	Rodriguez-Oubina & Cruces 2092 (NBG)	Leaf
<i>P. camphorata</i> var. <i>longifolia</i>	Pambaniso 13 (NBG)	Fruit
	Tymens s.n. (NBG)	Fruit
	Manning 2143 (NBG)	Leaf
<i>P. stricta</i>	Moffett 328 (NBG)	Fruit
	Oliver 11134 (NBG)	Leaf & fruit

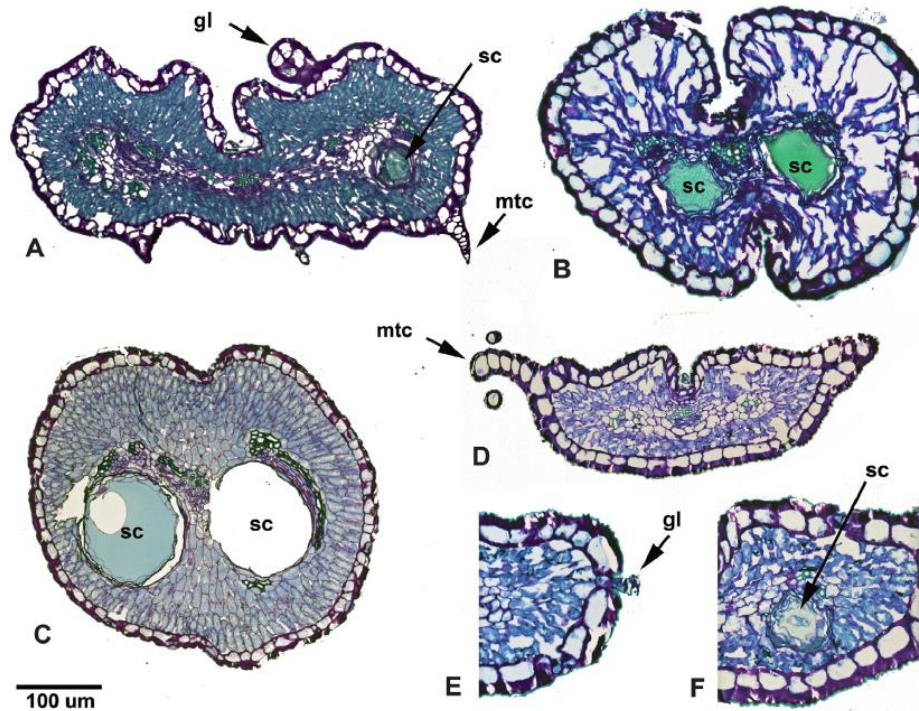


Fig. 1. Transverse sections of *Pteronia* leaves. (A & B) – *P. aspera*. (C) – *P. cederbergensis*. (D–F) – *P. camphorata*. SC = secretory canal, VB = vascular bundles, GL = gland, MTC = multicellular hair, ST = stomata. Vouchers: A – Rodriguez-Oubina & Cruces 2092 (NBG), B – Manning 2143 (NBG); C – Jardine & Jardine 299 (NBG); D–F – Oliver 11134 (NBG). Scale = 100 µm.

Those of *P. cederbergensis* are diagnostically obclavate in shape (Fig. 9E) and longer (≥ 6 mm long) than the ovate to elliptic cypselas (Figs. 5F, 7C) of *P. aspera* and *P. camphorata* (≤ 4 mm long). In transverse section the pericarps of the cypselas are not clearly differentiated and are nearly always three cell layers thick, except at the ribs. The epidermal cells (epicarp) are anticlinally elongated with the outer periclinal cell walls somewhat thickened. The mesocarp and endocarp are composed of small parenchyma cells. The vascular bundles at the ribs are sometimes associated with thick-walled parenchyma or sclerenchyma cells. The testas are uniseriate with anticlinally elongated cells of varying size. The outer periclinal and anticlinal cell walls of the testa are often lignified. The endosperm is composed of thin-walled, compactly arranged parenchyma cells (Fig. 4).

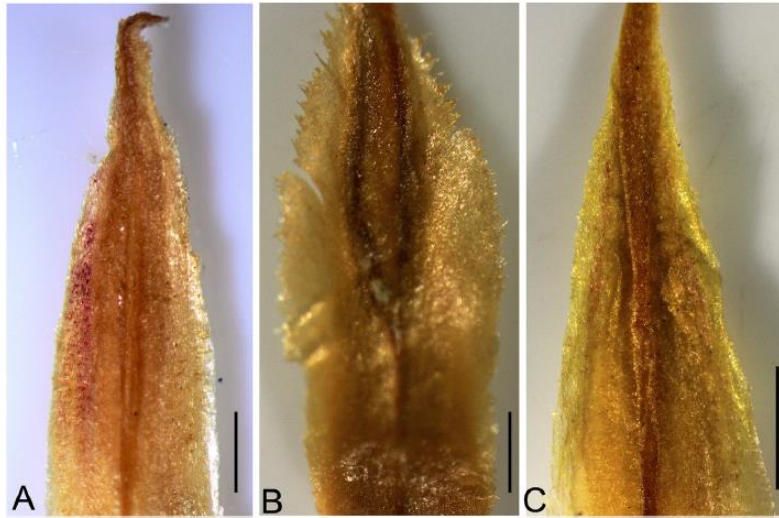


Fig. 2. Close-up of bracts showing serrate and entire margins of *Pteronia* species studied. A – *P. cederbergensis* (Levyn 5101, BOL), B – *P. aspera* (Esterhuysen 14608, BOL), C – *P. camphorata* (Esterhuysen 13994, BOL). Scales: A & B = 0.5 mm, C = 1 mm.

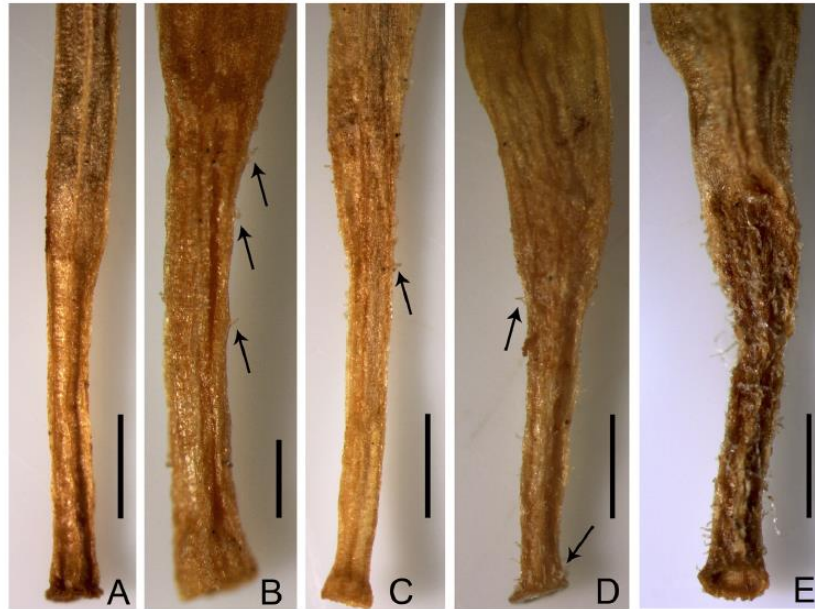


Fig. 3. Variations in the corolla of *Pteronia* species studied. A – *P. cederbergensis*, B & C – *P. aspera*, D & E – *P. camphorata*. Vouchers: A – Levyn 5101 (BOL); B – Stokoe 17535 (BOL); C – Esterhuysen 22129 (BOL); D – Esterhuysen 13994 (BOL); E – Levyn 2324 (BOL). Scales: A, C–E = 1 mm, B = 0.5 mm.

3.3. Key to the species of *Pteronia camphorata* group

- 1a. Cypselas glandular or hairy (at least at the base) remaining species of *Pteronia*.
- 1b. Cypselas glabrous:
 - 2a. Leaves opposite, glabrous, somewhat succulent; corolla tube glabrous; pappus 2-seriate; cypselas obclavate, ≥ 6 mm long..... **3. *P. cederbergensis*.**
 - 2b. Leaves alternate, ciliate to densely setose, coriaceous; corolla tube sparsely to densely pubescent; pappus uniseriate; cypselas ovate or elliptic, ≤ 4 mm long:

3a. Involucral bracts with entire margins, apices long acuminate; cypselas isodiametric, marginal ribs prominent, white or cream..... **2. *P. camphorata*.**

3b. Involucral bracts with serrate margins, apices acute to short acuminate; cypselas dorsoventrally flattened, marginal ribs only slightly prominent, brownish**1. *P. aspera*.**

3.4 Taxonomic treatment

1. *Pteronia aspera* Thunb., Fl. Cap. 2: 631 (1823); DC. Prodr. 5: 364 (1836). *Pterophorus asper* (Thunb.) Less. Syn. Gen. Compos. 195 (1832). *Pteronia camphorata* var. *aspera* (Thunb.) Harv. in Harv. & Sond. Fl. Cap. 3: 110 (1865). Type: South Africa. Precise locality unknown: ‘Caput Bonae Spei’ [Cape of Good Hope], *Thunberg s.n.* THUNB-UPS 18664 (UPS, holo. – microfiche!).

Pteronia camphorata L. var. *longifolia* Harv. in Harv. & Sond. Fl. Cap. 3: 110 (1865); Hutch. & Phillips in Ann. S. African Mus. 9: 298 (1917), *syn. nov.* Type: South Africa. Western Cape, Caledon (3419): ‘Rivier Zonderende’ [Riviersonderend] (–BB), *Ecklon & Zeyher 2776* (TCD!, lecto., here designated; SAM!, isolecto.). [Note: Four original collections exist. We designate the *Ecklon & Zeyher 2776* collection as Harvey specifically included this collection after his description, while the other collections were listed only later with the habitat.]

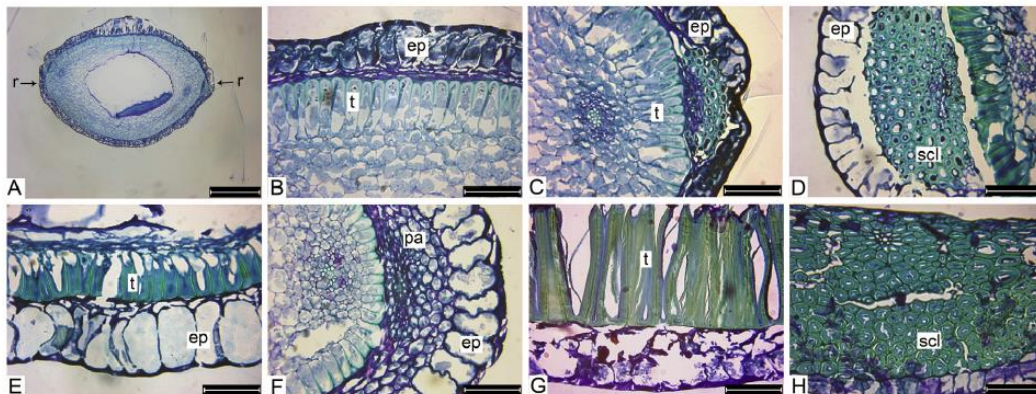


Fig. 4. Transverse sections of *Pteronia* fruits. (A–E) – *P. aspera*. (F) – *P. cederbergensis*. (G & H) – *P. camphorata*. t = testa, ep = epicarp, pa = parenchyma, scl = sclerenchyma, vb = vascular bundles, r = rib. Vouchers: A–C – Pond UP212 (NBG), D & E – Pambaniso 13 (NBG); F – Pillans 9682 (NBG); G & H – Oliver 11134 (NBG). Scales: A = 400 µm, B–H = 70 µm.



Fig. 5. Morphology of *Pteronia aspera*. A & B – flowering branches. C – involucre bracts. D – style. E – cypselas. F – floret, G – corolla. Vouchers: A, C, D, E1 & F – Pambaniso13 (NBG); B, E2 – Pond UP212 (NBG); G – Stokoe 17535 (BOL). Scales: A & B = 2 cm, (C, D & F) = 2 mm, (E1, E2 & G) = 1 mm.

Pteronia camphorata sensu Harv. in Harv. & Sond. Fl. Cap. 3: 110 (1865), *excl. type*; Hutch. & Phillips in Ann. S. African Mus. 9: 296 (1917).

Pterophora camphorata sensu Lessing, Syn. Gen. Compos. 195 (1832), *excl. type*.

Pteronia camphorata var. *armata* sensu Harv. in Harv. & Sond. Fl. Cap. 3: 110 (1865), *excl. type*; Hutch. & Phillips in Ann. S. African Mus. 9: 297 (1917).

Evergreen perennial shrubs up to 2 m high; much branched, branches finely setulose with increasing density towards the upper part to densely setose all over the surface. Leaves alternate, somewhat dense, spreading, simple, acicular, 8–40 × 0.6–1.0 mm, subterete or somewhat flattened upward, coriaceous, glabrescent or rigidly setose all over the surface, leaf setae sometimes involute; mucronate, margins setulose-ciliate towards the base, fasciculate. Capitula homogamous, discoid, 15- to 25-flowered, terminal, in clusters of 2 to 6; sometimes solitary, pedunculate, peduncles up to 25 mm long; bearing smaller leaves. Involucre subcampanulate to campanulate, 10–16 × 13– 20 mm, 3-seriate; involucre bracts glabrous, stereome sometimes prominent; margins serrate, narrowly scarious; outermost bracts rarely setulose, ovate to lanceolate or linear, 4–6 mm long, apex acute; middle bracts lanceolate to broadly ovate, 5–8 mm long, apex acute; innermost bracts lanceolate to broadly ovate, 10– 13 mm long, apex acute to acuminate. Florets bisexual, 15 to 25; corolla yellow, tubular, 9–10 mm long, limb 5-lobed, widening upward, tube sparsely pubescent; anthers 3–4 mm long, apex acute or acuminate, base terete, slightly swollen to swollen; style branched, 10– 13 mm long, branches somewhat flattened, about 2.9 mm long, densely stigmatic-papillate. Pappus uniseriate, bristles, connate at base, 6–9 mm long, slightly shorter than florets at fruiting stage, straw-coloured. Cypselas ovate, 3–4 × 1.5–2.0 mm, dorsoventrally flattened, marginal ribs slightly prominent, usually contracted into a neck at apex, glabrous, brown, shiny. Fig. 5.

Diagnostic characters

Pteronia aspera shares the alternate leaves, pubescent branches and smaller fruit with *P. camphorata* but can be readily distinguished by the prominent serrate margins of the involucre bracts (Fig. 2; entire in *P. camphorata*) and the dorsoventrally flattened cypselas with slightly prominent marginal ribs (Fig. 5E; isodiametric and prominent white or creamish marginal ribs in *P. camphorata*). In the northern parts of its distribution the leaves are usually shorter and densely hairy.

Distribution and ecology

This species is the most widely distributed in the group extending from the Kamiesberg Mountains through to the Cape Peninsula and eastward to the Langeberg and Rooiberg Mountains (Fig. 6). It occurs from sea level to 1230 m. Flowering is in spring to early summer (September to December).

Specimens examined

South Africa. NORTHERN CAPE: 3018 (Kamiesberg): Kamiesberg, peak east of Rooiberg above Karas (–AC), *Rourke 2283* (NBG). 3119 (Calvinia): Nieuwoudtville, Oorlogskloof Nature Reserve (–AC), *Pretorius 147* (NBG, PRE); Nieuwoudtville, Groot Tuin 653 (–AC), *Pretorius 572* (NBG, PRE); Lokenburg (–CA), *Leistner 430* (PRE).

WESTERN CAPE: 3118 (Vanrhynsdorp): Gifberg, east slopes of Plateau (–DA), *Esterhuysen 22129* (BOL). 3218 (Clanwilliam): Kliphuisrivier, Kliphuis (–BB), *Taylor 11350* (NBG, PRE); Pakhuis Pass (–BB), *Compton 6941, 20931, 9637* (NBG), *Thode A2121* (PRE), *Esterhuysen 3286* (PRE), *Lewis 19-9-37* (PRE); Nardouskloof (–BB), *Compton 6991* (NBG); Olifants Rivier (–BB), *Schlechter 5112* (PRE); Boekenberg (–BC), *Compton 5108* (NBG); Elandskloofrivier (–BD), *Compton 12493* (NBG); Uitkyk (–DA), *Compton 5103, 5090* (NBG); Clanwilliam (–DB), *Hanekom 2863* (NBG), *Wagener 26823* (NBG); Piketberg Mountain to side of rocky outcrop along Eskom road to Aasvoëlkop (–DC), *Trinder-Smith 665* (BOL); Piketberg Mountain (–DD), *Barker 10274* (NBG); Piketberg, Groenvlei Farm off R365 (–DD), *Cowell et al. MSBP 4020* (NBG). 3219 (Wuppertal): Pakhuis Pass at east boundary of State Forest, North Cederberg, below old road (–AA), *Taylor 11882* (NBG); Krakadouw Mountain, Clanwilliam, C.P. (–AA), *Leipoldt 504* (NBG); Pakhuis, 20 km from Clanwilliam on road to Biedouw Valley (–AA), *Le Roux 2394* (NBG, PRE); Cederberg, Pakhuisberg. 15 km from Clanwilliam on road to Pakhuis (–AA), *Rodriquez–Oubina & Cruces 2092* (PRE); Heuningvlei Forest Station, on road to Groenberg (–AA), *Emdon 148* (PRE); Wuppertal, Heuningvlei, beside the road between Wuppertal & Heuningvlei (–AA), *Welman 00125* (PRE); Cederberg State Forest: Steemrugkloof (–AC), *Richardson 43* (NBG, PRE); Cederberg State Forest research site (–AC), *Le Maitre 244, 541* (NBG), *Le Maitre 541* (PRE); Nieuwoudt Pass, Cederbergen (–AC), *Hafstrom & Acocks 1730* (PRE); Clanwilliam Division, Cederberg (–CA), *Esterhuysen 12258, 20515* (PRE); Cederberg – Gonnafontein, rocky Mountain slope, western Gonnafontein (–CB), *Pond UP212* (NBG); Citrusdal, Kromrivier (–CB), *Manning 2938* (NBG); Twee Riviere, east of

Baliesgatberg (–CB), *Stirton & Zantovska 11472* (NBG, PRE); Middle east slope of Grasruggens Mountain (–CC),

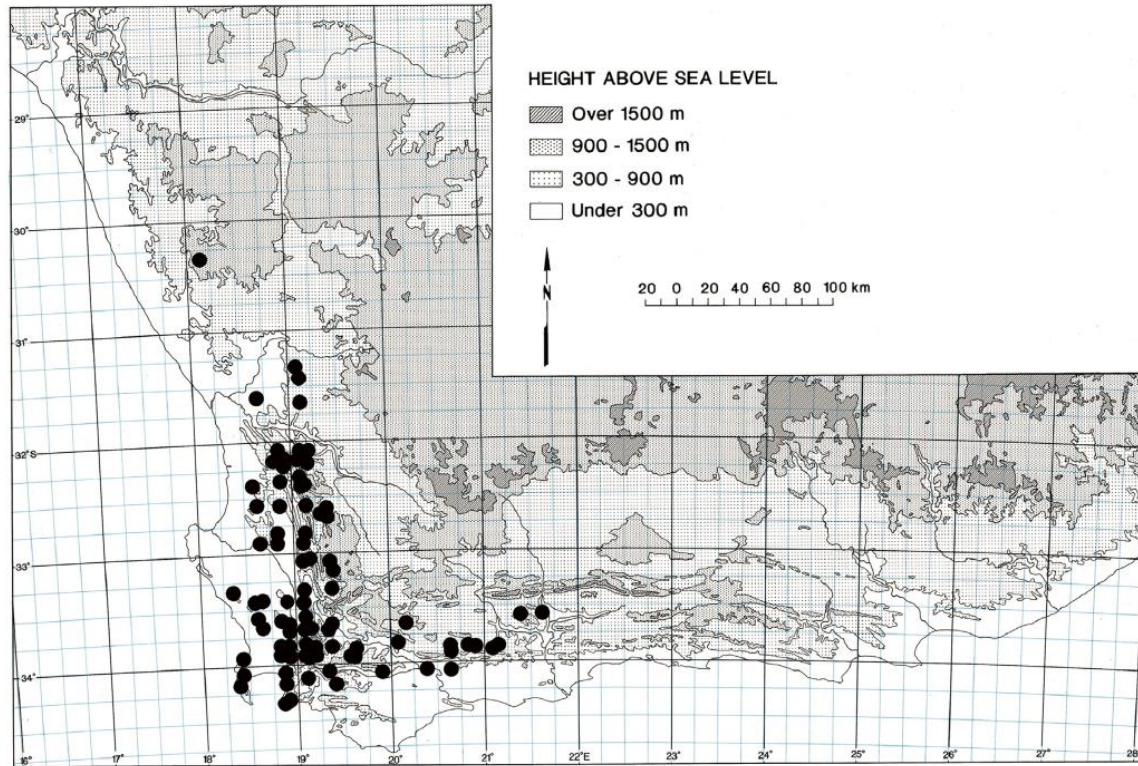


Fig. 6. Known distribution of *Pteronia aspera*.

Pillans 8779 (NBG, PRE, BOL); Cardouw Pass (–CC), *Barker 7603* (NBG), *Johnson 303* (NBG), *Compton 24343* (NBG). 3318 (Cape Town): Farm Eersteplaat near Darling, opposite Rondeberg (–AD), *Goldblatt & Manning 10374* (PRE); Mamre road 20 miles [32.19 km] from Cape Town (–BC), *Barker 4098* (NBG); Cape Province, Malmesbury Division, 1 km north of Maryka, sandy ground (–BC), *Bremer 207* (NBG); Hort. Kirstenbosch, low slopes of Koppie (–CD), *Henderson 1241* (NBG); Koeberg, south slopes on sand along N7 (–DA), *Goldblatt & Manning 10331* (NBG); Peninsula west of Langebaai, Malmesbury Division (–DA), *Pillans 6970* (BOL); Paarl Mountain Nature Reserve, next to Jan Philipsberg road (–DB), *Swanepoel 33* (NBG); Paarl Mountains north of Nantesdam (–DB), *Jordaan M79* (NBG); Paardeberg, between Wellington and Malmesbury (–DB), *Nicholson & Roets* (NBG); Simonsberg (–DD), *Baker 278* (NBG), *Tymens s.n.* (NBG); Banghoek (–DD), *Compton 10338* (NBG); Lemoenkloof Farm, north-east of Stellenbosch ridge, directly west of Silwerminekloof (–DD), *Buys 68* (NBG); Botmaskop (–DD), *Van Rensburg 337* (NBG, PRE), *Van Rensburg 2003* (BOL); Water Affairs road, Banghoek (–DD), *Fugler 29* (NBG); Brian Rycroft Nature Reserve, Dwarsriviershoek, Banghoek, Stellenbosch (–DD), *Rycroft 3280* (NBG); Jonkershoek Nature Reserve (–DD), *Bands s.n.* (NBG), *Brandon 113* (NBG), *Compton 15322* (NBG), *Taylor 4571A* (NBG); Jonkershoek State Forest – Swartboschkloof (–DD), *Kruger 111* (NBG), *McDonald 797* (NBG), *Burman 997* (BOL); Slopes of Papegaaiberg (–DD), *Nuthie 1124A* (PRE); Assegaaibosch (–DD),

Merwe 1234 (PRE). 3319 (Wocester): Groot Winterhoek, Porterville; Klein Kliphuis River (–AA), *Taylor 9752* (PRE); 5 km north of Tulbagh on way to Winterhoek State Forest (–AA), *Mauve & Hugo 58* (PRE); Gydo Pass, 8 km from Prince Alfred Hamlet along R303 (–AB), *Watson & Panero 94-59A* (NBG); Elandsfontein (–AB), *Schlechter 1653* (PRE); Tulbagh, slopes above Pastures (–AC), *Hansford & Hansford 111* (NBG); Paarl Division, Bailey's Peak, north-west slopes (–AC), *Esterhuysen 5820* (BOL); Theronsberg Pass, Karroid veld near top of Pass (–AD), *Goldblatt & Manning 8602* (PRE); Du Toits Kloof, west side (–CA), *Maguire 1112* (NBG), *Esterhuysen 14608* (BOL); Bainskloofpas, at Tweede Tol/Borcheri bridge, R303 along roadside (–CA), *Watson & Panero 94-73A* (NBG); Molenaarsberg, near Stream (–CA), *Compton 20143* (NBG); Wangenheim Farm, Rawsonville (–CB), *Walters 1848* (NBG); Rawsonville, langs Rivier (–CB), *Compton Herbarium* (NBG); Groot Drakenstein Mountain, Duivels Kloof (–CC), *Wasserfau 744* (NBG); Paarl Division, Haelhoeksneeukop (–CC), *Esterhuysen 9599* (BOL); Franschhoek (–CC), *Bolus 51* (NBG), *Alexander 18-10-1848* (PRE); Franschhoek Pass (–CC), *Thodes A2198* (NBG); Paarl Division, Franschhoek Peak (–CC), *Stokoe 8361* (PRE); Stettynskloof, Limietberg (–CD), *Pambaniso 13* (NBG); Riviersonderend Mountains, Jonaskop, roadside to FM tower (–DC), *Boucher 4249* (NBG); Gannaberg, Wocester, top of mountain (–DC), *Van Jaarsveld 23507* (NBG); Jonaskop near Villiersdorp, road to SABC tower, Table Mountain sandstone (–DC), *Boucher 3023* (NBG). 3320 (Montagu): Between Pypsteelfontein & Grootfontein, Waboomsberge (–CA), *Moffett & Steensma 4124* (NBG, PRE); Keurkloof (–CC), *Compton 5830* (BOL); Tradouws Pass (–DC), *Levyyns 594* (NBG); 6 miles [9.66 km] into Tradouws Pass from Barrydale (–DC), *Marsh 962* (NBG); Boosmansbos Wilderness Area – Langeberg (–DD), *McDonald 1266* (NBG); Lemoenshoek Peak, lower south slopes (–DD), *Walgate 951* (PRE). 3321 (Ladismith): Rooiberg Grove on south slope north-east of Hut (–CB), *Taylor 9503* (PRE); Gysmanshoek Pass, near top Riversdale (–CC), *Hugo 2738* (NBG); Heidelberg Division Langebergen, south side, Gysmanshoek pass, lower south side (–CC), *Strid A + B 37998* (NBG); Middle of Gysmanshoek Pass, 1 m from top on Heidelberg Stream side road (–CC), *Marsh 1190* (NBG). 3418 (Simonstown): Zeekoe Vlei (–AB), *Schlechter 8483* (PRE); Simonsberg (–AB), *Compton 14190* (NBG); Steenbras mouth (–BB), *Compton 8016* (NBG); Kogel Bay (–BB), *Compton 20083* (NBG); Rooiels (–BD), *Parker 4298* (NBG); Kogelberg State Forest Highlands, Palmiet crossing (–BD), *Boucher 2002* (NBG). 3419 (Caledon): Rocky ridge, Viljoens Pass, south side (–AA), *Galpin 12446* (PRE); Riviersonderend Mountains, head of Baviaaskloof, north-west of Genadendal, south-west of Jonaskop (–AB), *Oliver 8457* (NBG); Caledon (–AB), *Stokoe 8361* (PRE), *Stokoe 17535* (BOL), *Parker 4298* (BOL); Riviersonderend Mountains, north slope of Middelberg (–BB), *Manning 2143* (NBG). 3420 (Bredasdorp): Hermitage Kloof (–AB), *Wurt 391* (NBG); Tradouws (–BA), *Thorns s.n.* (NBG). PRECISE LOCALITY UNKNOWN: *Thode 18741* (PRE); Cape Town, *Taylor 6958* (NBG); *Mund 9689* (PRE).

Precise locality unknown: Caput Bonae Spei, *Thunberg s.n.* THUNB-UPS 18666 (UPS).

2. *Pteronia camphorata* (L.) L., Sp. Pl. 2(2): 1176 (1763); Thunb. Fl. Cap. 629 (1823). *Pterophora camphorata* L., Pl. Rar. Afr. 17 (1760); Cass. Dict. Sci. Nat., 37: 474 (1825). *Pteronia camphorata* var. *armata* Harv. in Harv. & Sond. Fl. Cap. 3: 110 (1865), *pro. parte*; Hutch. & Phillips in Ann.

S. African Mus. 9: 297 (1917), *pro. parte, nom. inval. superfl.* Type: South Africa. Precise locality unknown, *Anon s.n.*, Herb. Linn. No. 980.2 (LINN, lecto. – image!, designated by Lowrey in Jarvis & Turland, (1998)).

Pteronia stricta Ait. Hort. Kew, ed. I 3: 162 (1789); DC. Prodr. 5: 364 (1836); Hutch. & Phillips in Ann. S. African Mus.9: 298 (1917), *syn. nov. Pterophorus strictus* (Ait.) Less. Syn. Gen. Compos.195 (1832). *Pteronia camphorata* var. *stricta* (Ait.) Harv. in Harv. & Sond. Fl. Cap. 3: 110 (1865). Type: South Africa. Precise locality unknown, *Masson s.n.* (BM001253076, holo. – image!)

Pteronia stricta var. *longifolia* Phillips. Hutch. & Phillips in Ann. S. African Mus.9: 299 (1917), *syn. nov.* Type: South Africa. Western Cape, Oudtshoorn (3322): Prince Albert, stony places at summit of 'Zwartberg Pass' [Swartbergpas] (–AC), *Bolus 11523*, (PRE, lecto.! here designated; BOL!, isolecto.). [Note: The specimen at PRE is designated here as it has a determination slip annotated by Hutchinson and Phillips].

Evergreen perennial shrubs up to 2 m high; stems pubescent, erect, branching towards apex, branches strigose. Leaves alternate, dense, simple, linear to acicular, 5–15 × 0.8–1.0 mm, subterete, coriaceous, glabrous; mucronate, margins setulose-ciliate towards the base, rarely entire, fasciculate. Capitula homogamous, discoid, 15- to 20-flowered, terminal, in clusters of 2–6; sometimes solitary on lateral branches, pedunculate, peduncles up to 10 mm long; bearing smaller leaves. Involucre subcampanulate, 11–15 × 15–20 mm, 3-seriate; involucre bracts glabrous, stereome sometimes prominent; apex long acuminate; outermost bracts linear to lanceolate, 5–7 mm long, margins entire; middle bracts lanceolate, 9–12 mm, margins entire to scarios; innermost bracts lanceolate, 10–13 mm long, margins entire to scarios. Florets bisexual, 15 to 20; corolla yellow, tubular, 8–9 mm long, limb 5-lobed, gradually widening upward, tube sparsely to densely pubescent; anthers 3–4 mm long, apex acute, base terete; style branched, 12–14 mm long, branches subterete, about 1.8 mm long, densely stigmatic-papillate. Pappus uniseriate, bristles, connate at base, 6–7 mm long, shorter than florets at fruiting stage, straw-coloured. Cypselas elliptic, 3.5–4.0 × ± 3.0 mm, isodiametric, marginal ribs prominent; light coloured, usually contracted into a neck at apex, glabrous brown, shiny. Fig. 7.

Diagnostic characters

Pteronia camphorata could be confused with *Pteronia aspera* but is distinguished by the denser fascicles of 20 or more leaves (Fig. 7A; 3 to 15 in *P. aspera*), the long acuminate involucre bracts with entire margins (Fig. 7C; acute to short acuminate with serrate margins in *P. aspera*), and the isodiametric cypselas with prominent marginal ribs (Fig. 7B; dorsoventrally flattened in *P. aspera*).

Distribution and ecology

This species occurs from the Klein Swartberg and Outeniqua Mountains in the Western Cape to Humansdorp in the Eastern Cape (Fig. 8) and favours rocky or sandy soil between 400 and 1600 m. Flowering may occur throughout the year but peaks from spring to early summer (September to November).

Specimens examined

South Africa. WESTERN CAPE: 3321 (Ladismith): Top of Klein Swartberg Mountains, at end of Besemfontein Track (–AD), *Vlok 1412* (PRE); Klein Swartberg Mountains, above farm Buffelsfontein (–AD), *Stirton 10294* (NBG); Mountain on east side of Seweweekspoort (–AD), *Wurts 1579* (NBG); Seweweekspoort, south slope (–AD), *Levyans 2441* (BOL); Seweweekspoort Mountain (–AD), *Wurts 1013* (NBG), *Oliver 11134* (NBG); Swartberg, south-west of Kliphuisvlei, rocky restioid slope

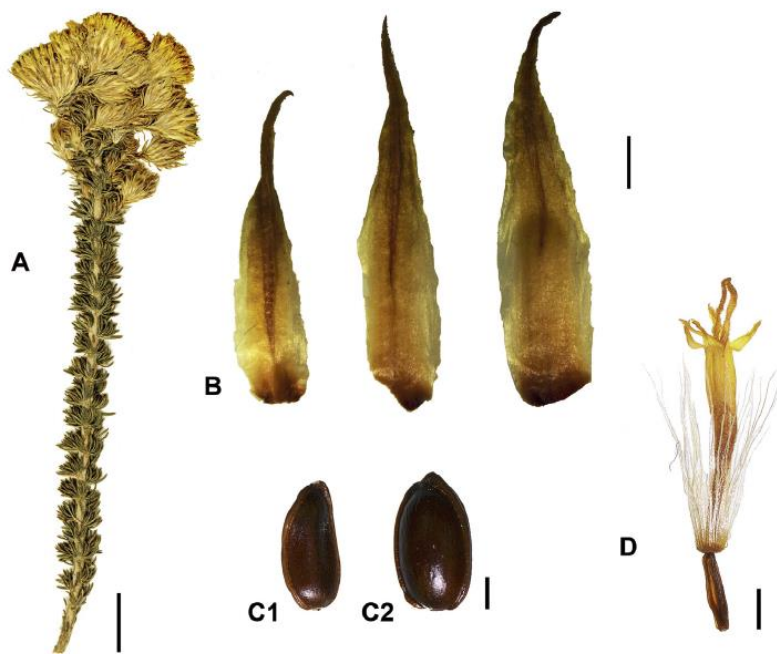


Fig. 7. Morphology of *Pteronia camphorata*. A - flowering branch. B - cypselas (B1 - immature, B2 - mature). C - involucre bracts. D - style. E - floret. F - corolla. Vouchers: A-E - Oliver11134 (NBG), F - Esterhuysen 13994 (BOL). Scales: A = 2 cm, (B1, B2 & F) = 1 mm, C-E = 2 mm.

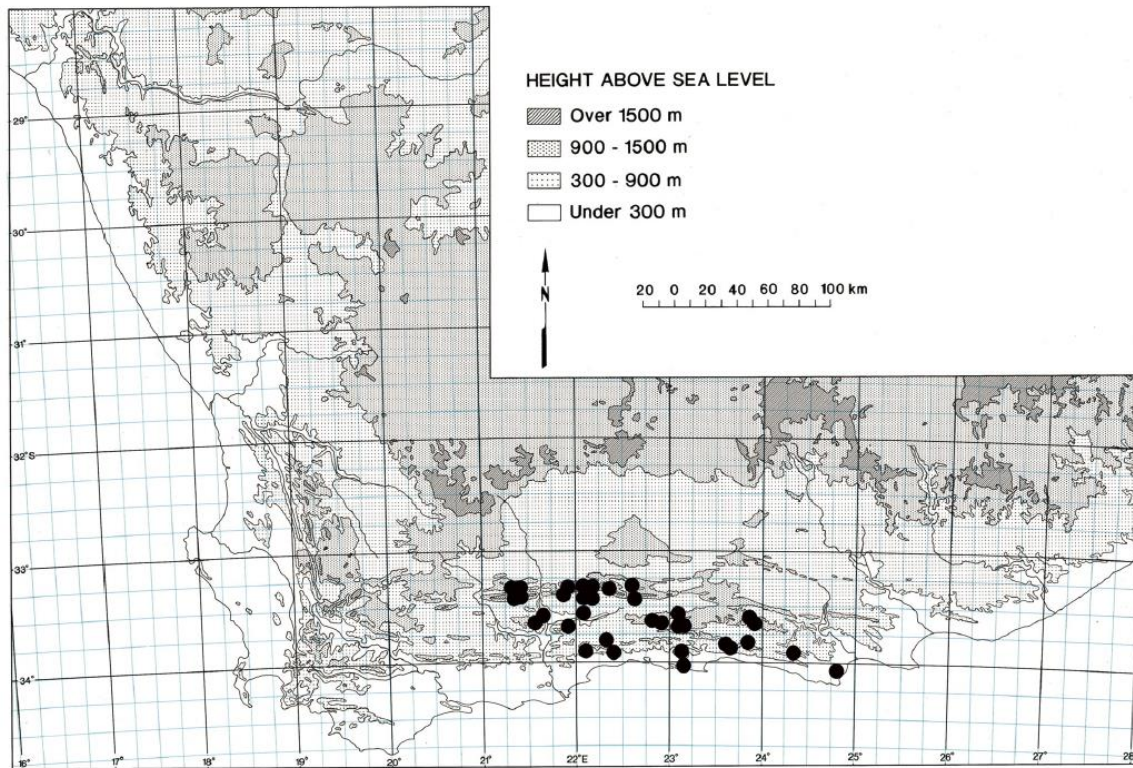


Fig. 8. Known distribution of *Pteronia camphorata*.

(-BD), *Oliver 5533* (NBG); Gamkaskloofpas ± 12 km vanaf Swartberg Pass
 klipperige grond (-BD), *De Wet 15* (PRE); Rooiberg, summit of ridge above
 Assegaiboskloof (-DA), *Oliver 5360* (NBG); Rooiberg, south of Calitzdorp on the road to
 Bailey's Peak (-DA), *Koekemoer 2008, 2012* (PRE); Gamka Mountain Reserve, (-DB),
Cattell & Cattell 166 (NBG), *Erasmus 117* (NBG). 3322 (Oudtshoorn): Groot Swartberg,
 north side below Oliewenberg (-AC), *Oliver & Oliver 11735* (NBG); Waenskloof, Cango
 Valley on high level talus of Swartberg (-AC), *Moffett 282* (NBG, PRE), *Moffett 328* (NBG);
 Prince Albert district at second hairpin overlooking Toll and Summit (-AC), *Taylor 6978*
 (PRE); Prince Albert, Swartberg Pass, north side water stream bend in road near Foreman's
 Quarters (-AC), *Taylor 6978* (NBG); Swartberg Pass (-AC), *Markotter 9971* (NBG), *Walters*
126, 716 (NBG), *Bolus 4123* (PRE), *Marloth 2475* (PRE), *Stokoe 1943* (PRE), *Hutchinson*
1167 (PRE, BOL); Prince Albert, Swartberg Pass Mountains (-AC), *Primos 79* (NBG), *Bond*
857 (NBG), *Bond W798* (PRE), *Koorts 19* (NBG), *Bolus 11522* (PRE), *Stokoe 8736, 9301*
 (PRE); Prince Albert C.P, Swartberg 10 m east of Pass summit (-AC), *Rourke 432* (NBG);
 Prince Albert Division, 8 miles [12.87 km] west from top of Swartberg Pass (-AC), *Stokoe*
59949 (NBG); Prince Albert Division, near the summit of Swartberg Pass (-AC), *Stokoe 59949*
 (PRE); Prince Albert, 2 m below summit of Swartberg Pass (-AC), *Leistner 216* (NBG); Prince
 Albert (-AC), *Leistner 216* (PRE); south side of Swartberg Pass below the pine sample plot
 (-AC), *Taylor 9371* (NBG, PRE); Swartberg east of top of Pass, Gousberg area (-AC),
Thompson 1321 (NBG, PRE); Swartberg Pass, 8 miles [12.87 km] from Cango Caves turn off (-
 AC), *Wells 3748* (PRE); Halfway up the Swartberg Pass on the Oudtshoorn side (-AC),
Zantovska 105 (PRE); De Hoek Reservaat, Swartberg (-AC), *Olivier 3135* (PRE); Klein
 Swartberg kloof, north of Klein Swartberg peak, Prince Albert (-AC), *Andreae 1260* (PRE);

Swartberg Pass, just north of the top at the 24 km marker (–AC), *Koekemoer 4092* (PRE); Ladismith, slopes of Swartberg (–AD), *Levy's 2324* (BOL), *Esterhuysen 13994* (BOL); Prince Albert in fire break, stony north slope (–BC), *Pienaar 62* (NBG); Swartberg west of Blesberg, north slope at head of Tierkloof (–BC), *Oliver 5655* (NBG); Fynbos Mountain, slopes west of Oudtshoorn (–CA), *Van Breda 4010* (PRE); Robinson Pass, Outeniqua Mountains (–CC), *Hops 67* (PRE); George (–CD), *Gillett 1657* (NBG); Outeniqua Pass (–CD), *Compton 24412* (NBG); Kammanassie Mountains, south slopes on Roode Els Kloof Farm side (–DB), *Mathews 293 ex JBG 2218* (PRE); Elandsvlakte, Kammanassieberg (–DB), *Zeeman 16* (PRE). 3423 (Knysna): Knysna (–AA), *Springliet s.n* (NBG).

EASTERN CAPE: 3323 (Willowmore): Kammanassie – Mannetjieberg (–CA), *Compton 10,558* (NBG); Avontuur Poort (–CA), *Fourcade 4358A* (NBG); Mountains south of Avontuur (–CA), *Fourcade 1300* (BOL); Top of Prince Alfred's Pass (–CC), *Marsh 1412* (NBG), *Harrochs s.n.* (NBG); Uniondale Division, Kouga Mountains east of Smutberg (–DB), *Esterhuysen 1941* (NBG), *Esterhuysen 6985a, 6985b* (BOL); Kouga, Famosa, Towerwater–177, steep south slope (–DB), *Euston–Brown 514* (BOL); Louterwater (–DC), *Compton 4878, 7907* (NBG); Hon. P.M.K. Le Roux Farm at Louterwater (–DC), *Dahlstrand 1711, 1728* (PRE), *Dahlstrand 2709* (NBG, PRE); Van Thieperk heights, Joubertina (–DD), *Rourke 887* (NBG). 3324 (Steytlerville): Kareedouw Pass, 2 m south of Kareedouw (–CD), *Sheron 1359* (PRE). 3424 (Humansdorp): Humansdorps, south slopes of Kareedouw (–BB), *Gillett 1524* (NBG).

Precise locality unknown: Caput Bonae Spei, *Thunberg s.n.* THUNB-UPS 18665.

3. *Pteronia cederbergensis* Bello, Magee & Boatwr. sp. nov. Type: South Africa. Western Cape, Wuppertal (3219): Knolfontein, Swartruggens 60 km north-east of Ceres (–DC), *Jardine 1762* (NBG, holo!).

Pteronia camphorata L. var. *laevigata* Harv. in Harv. & Sond. Fl. Cap. 3: 110 (1865); Hutch. & Phillips in Ann. S. African Mus. 9: 298 (1917), *syn. nov.* Type: South Africa. Piquetberg, near 24-Rivers, *Zeyher 810* (TCD!, lecto., here designated; SAM!, isolecto.). [Note: Harvey cites only the Zeyher 810 collection in the protologue. The specimen from Harvey's own collection at TCD is selected here].

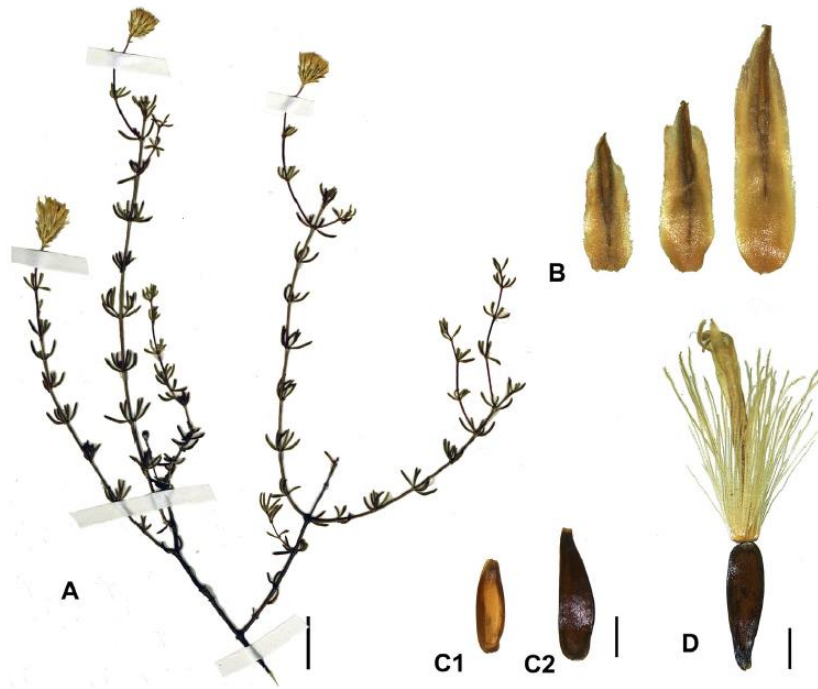


Fig. 9. Morphology of *Pteronia cederbergensis*. A – flowering branch. B – style. C – involucre bracts. D – cypselas (D1 – immature, D2 – mature). E – floret, F – corolla. Vouchers: A–E – Pillans 9682 (NBG), F – Levyn 5101 (BOL). Scales: A = 4 cm, B–E = 2 mm, F = 1 mm.

Evergreen perennial shrubs, 0.3–1.0 m high; much branched, branches glabrous. Leaves opposite, becoming sub-opposite towards the inflorescence, diffuse, spreading, simple, linear, 6.0–13.0 × ± 1.0 mm, subterete, somewhat succulent, glabrous; mucronate, margins entire, fasciculate. Capitula homogamous, discoid, 10- to 20-flowered, terminal, solitary or sometimes in clusters of 2 to 8. Involucre campanulate to obconical, 10–15 × 15–20 mm, 3-seriate; involucre bracts glabrous, stereome prominent; margins shortly serrate, narrowly scarious; outermost bracts ovate to lanceolate, 2–3 mm long, apex acute; middle bracts lanceolate, 5–6 mm long, apex acute; innermost bracts lanceolate, 8–10 mm long, apex acute to acuminate. Florets bisexual, 10 to 20; corolla bright yellow, tubular, 9–11 mm long, limb 5-lobed, gradually widening upward, tube glabrous; anthers 3–4 mm long, apex acute, base terete; style branched, 13–14 mm long, branches flattened, about 3.6 mm long, densely stigmatic-papillate. Pappus 2-seriate, bristles, connate at base, 6–10 mm long, slightly shorter than florets at fruiting stage, straw-coloured. Cypselas obclavate, 6–7 mm × 1.5–2.0 mm, dorsoventrally flattened, marginal ribs not prominent, usually contracted into a neck at apex, glabrous, brown, shiny. Fig. 9.

Diagnostic characters

Pteronia cederbergensis is readily distinguished by the glabrous branches, diffuse, opposite, somewhat succulent leaves (Fig. 9A) that lack glands, glabrous corolla tube, 2-seriate pappus and the longer, obclavate cypselas (6–7 mm long) (Fig. 9D).

Distribution and ecology

This species is restricted to the Cederberg and Koue Bokkeveld Mountains in the Western Cape (Fig. 10). It favours rocky soils from 100 to 1590 m. Flowering is in spring and mid-summer (September to January).

Specimens examined

South Africa. WESTERN CAPE: 3218 (Clanwilliam): Cederberg: Sederhoutkop, upper slopes (–BB), Taylor 10778 (NBG, PRE). 3219 (Wuppertal): North Cederberg: Summit of Krakadouw Peak (–AA), Taylor 10887 (NBG); Boontjieskloof, North Cederberg (–AA), Taylor 7479 (PRE); Middelberg Plateau, Cederberg (–AC), Bond 1334 (NBG), Kerfoot 6175 (NBG), Esterhuysen 2474 (PRE); Cederberg Wilderness area, Groot Koupoort (–AC), Haynes 1301 (NBG, PRE); Algeria State Forest, near Hoogvertoon (–AC), Viviers 22 (PRE); Clanwilliam Division, Cederberg into Middelberg (–AC), Esterhuysen 1264 (PRE); Cold Bokkeveld, East end of Elandskloof, ca 33 km south of Citrusdal (–CA), Goldblatt 5242 (PRE); Knolfontein, Swartruggens 60 km north-east of Ceres (–DC), Jardine & Jardine 299, 1007, 1029 (NBG). 3319 (Worcester): West road between Rosendalfontein & Visgat (–AA), Pillans 9682 (NBG, PRE); Gydouw Pass (–AB), Compton 10062 (NBG); Cold Bokkeveld, Rocklands Peak in Skurweberg, West slopes (–AB), Oliver 9069 (NBG); On the Groot River road from Cold Bokkeveld to Cederberg (–AB), Taylor 6124 (PRE, NBG); Mountain above Ceres Peak (–AD), Barker 9109 (NBG); Prince Alfred Hamlet, south-west top of Gydouw Pass (–AD), Bayer 6328 (PRE); Ceres Division, Visgat, upper Olifants River valley, rocky river bank (–AD), Esterhuysen 13402 (BOL); Baviaansberg, Ceres Division (–BA), Stokoe s.n. (BOL); Lakenvlei (–BC), Compton 12072 (NBG); Ceres Division, Conical Peak (–BC), Stokoe 59951 (PRE); Worcester Division, between Darling bridges, Roman's River (–CB), Isaac s.n. (BOL); Elandskloof, Ceres Division (–CD), Levyns 5101 (BOL).

Acknowledgements

The authors wish to acknowledge the curators and staff of the cited herbaria, Cape Nature for issuing collecting permits, Ms Ashton Ruiters (University of Johannesburg) for general advice and assistance; and the National Research Foundation, South African National Biodiversity Institute, University of Johannesburg and University of the Western Cape for funding. Dr Mark Spencer (LINN), Mrs Ranee Prakash (BM) and Dr John Parnell (TCD) are thanked for assisting with the location, imaging and identification of the type specimens in BM, LINN and TCD.

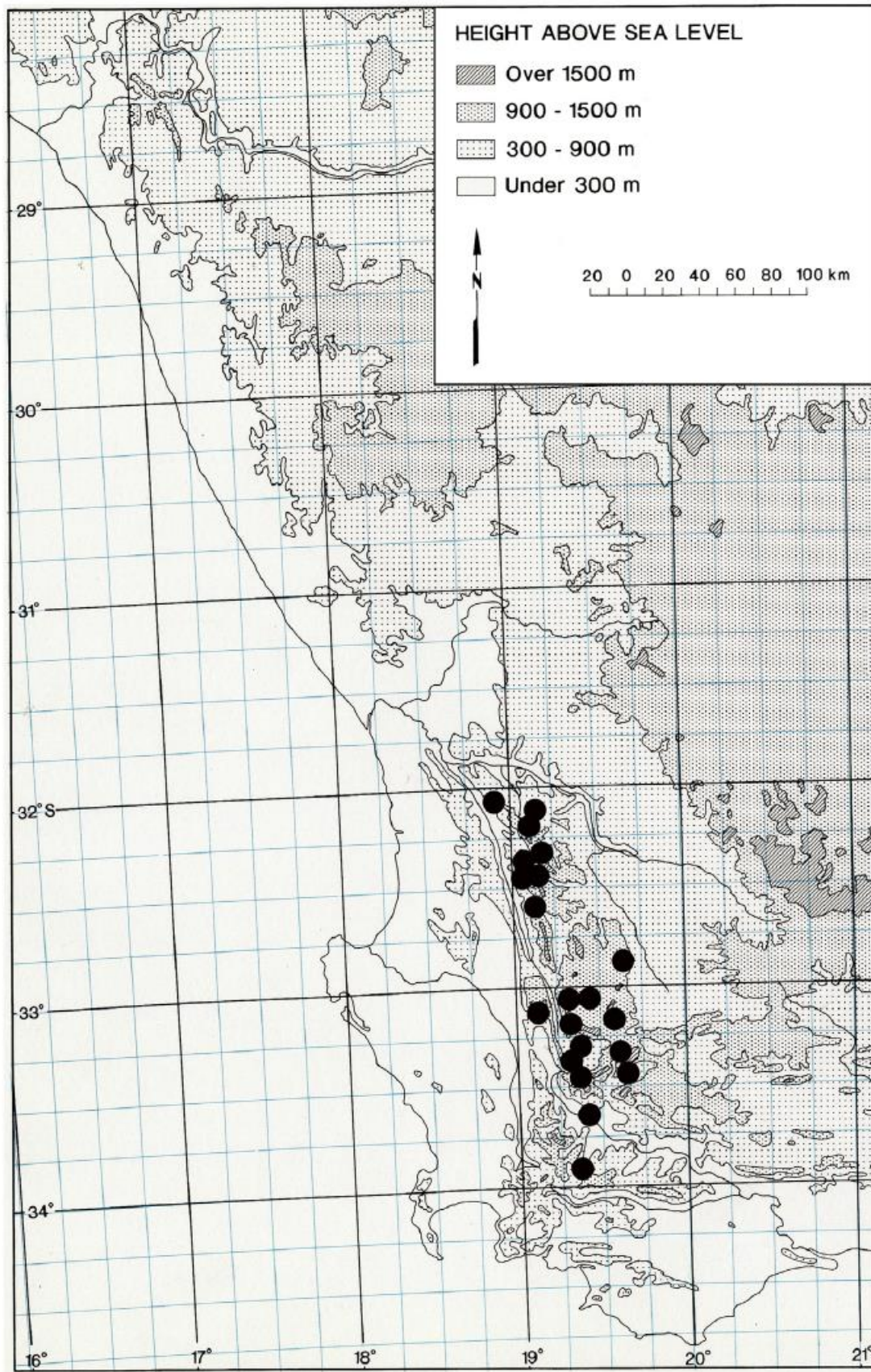


Fig. 10. Known distribution of *Pteronia cederbergensis*.

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