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NOMENCLATURAL NOTES ON THE ANDEAN GENERA *PYCNOPHYLLOPSIS* AND *PYCNOPHYLLUM* (CARYOPHYLLACEAE)

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Abstract: The nomenclature of the high Andean genera *Pycnophyllopsis* Skotts. and *Pycnophyllum* J. Rémy is examined. Eight species of *Pycnophyllopsis* are recognized; lectotypes or neotypes are selected when required; a new species, *Pycnophyllopsis smithii* is proposed and two new combinations are made. The genus *Pletkeia* Mattf. is reduced to a synonym of *Pycnophyllopsis*. Ten species of *Pycnophyllum* are accepted, including a new species, *Pycnophyllum huascararum* and lectotypes or neotypes are selected when needed.

Resumen: Se examina la nomenclatura de los géneros altoandinos *Pycnophyllopsis* Skotts. y *Pycnophyllum* J. Rémy. Se reconocen ocho especies de *Pycnophyllopsis*; se designan lectotipos y neotipos cuando es requerido; se propone una nueva especie, *Pycnophyllopsis smithii*, y dos nuevas combinaciones. Se aceptan diez especies de *Pycnophyllum*, incluyendo una nueva especie, *Pycnophyllum huascararum*; se designan lectotipos y neotipos cuando es requerido.

Keywords: Caryophyllaceae, Alsinoideae, *Pycnophyllopsis*, *Pycnophyllum*, *Pletkeia*, Andes, nomenclature, Peru, Bolivia.

The Caryophyllaceae consists of 100 genera and almost 3000 species (Hernández et al., 2015). Traditionally, the family has been divided into three subfamilies (Alsinoideae Fenzl, Caryophylloideae Arnott, and Paronychioideae Meisner, but see Harbaugh et al., 2010) based on various floral and vegetative features. In that same scheme, the subfamily Alsinoideae encompasses 28 genera and nearly 750 species worldwide. Members of this subfamily are distinguished from the Caryophylloideae by their free sepals, and from the Paronychioideae by their exstipulate leaves and possession of true petals (versus petaloid staminodes; McNeill, 1962).

Although the family is mainly north temperate in distribution, with its center of diversity in the Mediterranean and Irano-Turanian region (Bittrich, 1993), several genera of Caryophyllaceae are also distinctive components of alpine floras around the world. They are found in the mountain regions of the Middle East, central Asia, alpine New Zealand and Australia, the

Andes and the mountain regions of North and Central America. Some genera (including several endemics) of the Caryophyllaceae reach the southern hemisphere, particularly the high Andes and the south temperate and sub-Antarctic regions. Of the currently recognized genera, 22 are native in South America (plus another ten represented by introduced species), particularly along the Andean region with several of these genera endemic to the Andes, e.g., *Pycnophyllum* J. Rémy, *Pycnophyllopsis* Skotts., *Reichella* Pax, and *Philippiella* Speg.

Pycnophyllopsis and *Pycnophyllum* are among the most poorly known members of the Caryophyllaceae in the New World. Herbarium specimens are, to date, extremely scarce. This under-representation may be because they are naturally found in the most remote parts of the Andes, usually near the snow line. It may also be due to their reduced size and, thus, to their inconspicuousness.

Here I present some long-needed nomenclatural notes regarding both *Pycnophyl-*

lum and *Pycnophyllopsis*. Because several former students of these genera, including Pax, Mushler, and Mattfeld, were based at the herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B), several, if not most, of the specimens they selected as types were destroyed (see Hiepko, 1987). Therefore, lectotypification, and in some cases neotypification, were required. The present work is based upon my doctoral dissertation at The University of Texas in Austin (Timaná, 2005). A revision of each genus with detailed descriptions, illustrations, distribution maps and exsiccate is currently in progress.

MATERIALS AND METHODS

This study is based upon the examination of herbarium specimens and extensive fieldwork. Specimens borrowed from 67 herbaria (see list in Acknowledgments; abbreviations follow Thiers, continuously updated) were examined. In addition, nine major European herbaria (B, BM, CGE, E, FI, K, MA, OXF, and P) were visited for the study of historically important collections. The Weberbauer collection deposited at MOL was also examined on three occasions. Digital specimen images available on the Internet were also studied. Field observations and collecting were carried out in Peru, Bolivia, Argentina, and Chile between 1998 and 2013. A set of collections is deposited at the Plant Resources Center (TEX-LL), The University of Texas, Austin. Duplicate sets were left in the country of collection and additional sets were distributed to various herbaria.

TAXONOMIC TREATMENT

Pycnophyllopsis Skottsbb.

Pycnophyllopsis Skottsbb. is composed of eight species of cushion-forming plants occurring near the highest Andean peaks of central Peru, Bolivia, central Chile, and southern Argentina. The genus is here circumscribed in a wider sense than origi-

nally proposed by Skottsberg (1916) to include all species of the genus *Plettkea* established by Mattfeld (1934a).

When Mattfeld proposed *Plettkea* (Mattfeld, 1934a), he discussed in detail the position of this taxon (and that of *Pycnophyllopsis* s.s.) in the context of the subfamily Alsinoideae. His analysis clearly expressed what has been confirmed by later authors (e.g., McNeill, 1962; Bittrich 1993) – namely, that we could establish based on which characters are emphasized, not only multiple classification schemes within the subfamily but also, even generic boundaries. Various genera have been delimited based on single characters; for a detailed discussion on how this has affected large genera such as *Arenaria* refer to McNeill (1962). Although Mattfeld (1934b) recognized the close relationship of these genera by placing them within a new subtribe (*Plettkeinae*), in fact, his separation of *Pycnophyllopsis* s.s. and *Plettkea* was primarily based on the weakly-perigynous ovary of the former versus the strongly perigynous state among *Plettkea* species. Based on the evaluation of multiple characters and their variation among individuals along with a cladistic analysis of morphological data, Timaná (2005) demonstrated that such separation cannot be maintained and therefore, these two taxa are here merged.

Pycnophyllopsis Skottsbb., Kongl. Svenska Vetenskapsakad. Handl. N. S. 56 (5): 216. 1916.

TYPE: *Pycnophyllopsis muscosa* Skottsbb. = *Plettkea* Mattf., Schriften Vereins Naturk. Unterweser, N.F. 7: 13. 1934. TYPE SPECIES, designated here: *Plettkea cryptantha* Mattf.

Bisexual or dioecious, perennial, densely caespitose, hemispheric SHRUBS, 5–30 cm in diameter. STEM woody to sub-woody, 1.5–6 mm in diameter, branches 1.8–5 mm thick, herbaceous. LEAVES exstipulate, imbricate, rarely tetrastichous or spirally arranged, adpressed, scarious; sheath glabrous; blade sessile, incurved or flat, lanceolate to nearly triangular, complanate to cymbiform, base

connate, margin entire, denticulate or ciliate, midvein absent, apex acute, or mucronate, abaxial surface shinny, glabrous, adaxial surface shinny or opaque, glabrous. INFLORESCENCE terminal, single-flowered; foliose prophylls paired, rarely only one, subtending the flower; pedicel up to 2.5 mm long. FLOWER bisexual or unisexual, haplostemonous, tetracyclic, perigynous, sub-periginous or rarely hypogynous, ovate to obdeltate; receptacular cup present or poorly developed, annular, cotyliform or infundibuliform; flower disk present or absent. CALYX oblong-cylindrical or stellate. SEPALS 4 or 5, imbricate-decussate, valvate or quincuncial, lanceolate to ovate, cymbiform or slightly so, free above the receptacular cup, scarious, margin either entire, denticulate, or ciliate, straight to involute, apex acute, abaxial surface nitid, smooth, or glabrous. PETALS 4 or 5, rarely 3, free, alterni-sepalous, translucent, obovate to wide obovate, very reduced, membranaceous, base cuneate or oblong, margin entire, apex deeply bifid to bilobed, glabrous, staminal disk absent or present, anular. STAMENS (3) 4 or 5, episepalous or antisepalous, filament base strongly enlarged or filiform; anthers introrse, dorsifixed; staminodes (in dioecious species) 5, episepalous, filament minutely enlarged or filiform, flattened, sterile anthers dorsifixed. PISTIL with ovoid to turbinate, glabrous unilocular ovary, gynophore absent; styles 2 or 3; stigma terete, slightly clavate; ovules 3, arranged on the base of a central placental column. PISTILLODE (in dioecious species) 3-carpelate, unilocular, reduced ovary ovoid to cilindric, glabrous, stigma terete. FRUIT an utricle, enclosed in by the persistent sepals. SEED 1, light to dark brown, reniform, laterally compressed, rarely shortly crested dorsally with surface nitid or opaque, smooth, minute papilose to asperulate.

1. *Pycnophyllopsis muscosa* Skottsbo., Kongl. Svenska Vetenskapsakad. Handl. N.S. 56(5): 216. Fig. 11, Tab. 22(5). 1916. — TYPE: ARGENTINA. Patagonia Andina, territorio Chubut, Meseta Chalia, c. 1300 m, 5 Dec 1908, Skottsberg 606

(LECTOTYPE, here designated S!); ISOLECTOTYPES: LD!, UPS!).

This is a very peculiar species. It is the only species that shows a relatively long pedicelate flower — up to 2.5 mm long, compared to all the other species with pedicels less than 0.5 mm long. *Pycnophyllopsis muscosa* is also the only species with a stellate calyx rather than the typical oblong, nearly cylindrical calyx that characterizes all the other species in this genus.

2. *Pycnophyllopsis keraiopetala* Mattf., Schriften Vereins Naturk. Unterweser N.F. 7: 22. 1934. — TYPE: BOLIVIA. La Paz: zwischen Palca und La Paz, an Felzen, 4800 m, Apr 1908, Pflanz 223 (HOLOTYPE: B†). NEOTYPE: BOLIVIA. La Paz: Murillo: Cordillera Real, Chacaltaya, N of Milluni crossing, E of Lake Milluni, 4600 – 4900 m, 16°22' S, 68°10' W, 25 Jan 2000, Timaná 3804 (NEOTYPE here designated: LPB!; ISONEOTYPES: BM!, K!, MCSN!, MICH!, LL!, USM!) (Fig. 1).

Among members of the genus, *Pycnophyllopsis keraiopetala* is the only species with trimerous petals and stamens, although tetramerous and pentamerous forms are also found (sometimes all three forms in the same plant, e.g., Timaná 3804). In the case of trimerous androecia, the two stamens missing are always those that would be opposite the outermost sepals. This species is also characterized by an enlarged filament base (described as a nectary by Mattfeld, 1934a), forming a weak staminal disk, a character shared with *P. muscosa*.

3. *Pycnophyllopsis cryptantha* (Mattf.) Molinari, Polish Bot. J. 61(2): 276 (2016) ≡ *Plettkea cryptantha* Mattf., Schriften Vereins Naturk. Unterweser, N. F. 7:15. Fig I, A - K, U. 1934. TYPE: PERÚ. Morococha, Raimondi 8392 (HOLOTYPE: B†). NEOTYPE: Lima, Huarocharí: Paso de Anticona, Ticlio, 11°35' S, 76°15' W, 4850 m, 16 Dec 1998, Timaná & Tate 3767 (NEOTYPE here designated: USM!; ISONEOTYPES:



FIG. 1. Isonotype of *Pycnophyllopsis keraipetala*. —The University of Texas Herbarium (LL).

BMI!, EI!, FI!, KI!, LPB!, MICH!, TEX!, US!).

A very distinctive species, *Pycnophyllopsis cryptantha* is unique in the genus because of its tetramerous condition and two free styles. It is also characterized by decussate sepals with the inner pair shorter and non-ciliate as opposed to the outer pair. This Peruvian endemic species is found in populations near the divide between the Departments of Lima and Junin (central Peru) in the area known as Ticlio (Anticona Pass), around 4800 m and the puna of Cuzco and Puno between 4800 to 5200 m.

4. *Pycnophyllopsis macrophylla* (Muschl.) Molinari, Polish Bot. J. 61(2): 276 (2016) \equiv *Pycnophyllum macrophyllum* Muschl., Bot. Jahrb. Syst. 45: 458. 1911 \equiv *Plettkea macrophylla* (Muschl.) Mattf., Schriften Vereins Naturk. Unterweser, N.F. 7: 18. Fig II, L- M, V. 1934. TYPE: **PERÚ. Ancash:** Cordillera Blanca, 4500 m, 14 May 1903, *Weberbauer 2975* (LECTOTYPE designated by Molinari (2016): B \dagger ; ISOLECTOTYPE: MOL!).

Pycnophyllopsis macrophylla differs from *P. cryptantha* in the number of floral parts: *P. macrophylla* is consistently pentamerous with three free styles; *P. cryptantha* is a tetramerous species with two free styles. In addition, the leaves of *P. macrophylla* are slightly narrower toward the apex, taking the geometric form of a narrow triangle, while those of *P. cryptantha* resemble an equilateral triangle.

The isolectotype was examined and annotated as such during one of my research visits to the MOL herbarium in 2000, as can be attested to in the corresponding JSTOR Plants photograph (MOL00000509, photo!). Unfortunately, designation of such in Timaná (2005) does not qualify as effective publication (McNeil et al., 2012) whereas Molinari's (2016) designation, based on the study of Timaná (2005), does (see Grayum et al., 2016, for further comments on this practice).

5. *Pycnophyllopsis laevis* (Bartl.) Timaná, **comb. nov.** \equiv *Cherleria laevis* Bartl.,

Presl, Reliq. haenk. 2(I): 12. 1831. \equiv *Stellaria laevis* (Bartl.) Rohrbach, Linnaea 37: 275. 1871. TYPE: **PERÚ.** Quebrada de l'Obrachillo, s.d., *Haenke s.n.* (LECTOTYPE designated here, PR!); ISOLECTOTYPES: HAL 0117903 (photo!), GOET 000715 (photo!).

In his treatment of the genus *Plettkea*, Mattfeld (1934a) included the species described by Rohrbach in 1872 as *Stellaria laevis* (\equiv *Cherleria laevis* Bartling), suggesting that this taxon may be congeneric with members of *Plettkea* but he did not have access to the original specimens collected by T. Haenke in Peru later used by both Bartling and Rohrbach. The Haenke specimen was finally located in the National Museum of Prague Herbarium (PR), where most collections made by Haenke during the Malaspina Expedition were sent (Stearn, 1973). After examining this specimen, I can confirm that this taxon indeed belongs in *Pycnophyllopsis*.

6. *Pycnophyllopsis tetrasticha* (Mattf.) Timaná, **comb. nov.** \equiv *Plettkea tetrasticha* Mattf., Schriften Vereins Naturk. Unterweser, N.F. 7: 21. 1934. \equiv *Pycnophyllum mattfeldii* (Mattf.) J.F. Macbr. Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2): 611. 1937 (non *Pycnophyllum tetrastichum* J. Rémy, 1846). — TYPE: **PERÚ. Ancash:** Cajatambo, Schwarze Cordillere über Ocros, auf dürrig bewachsenem steinigem Boden, 4500 - 4800 m, *Weberbauer 2804a* (B \dagger). NEOTYPE: **PERU. Ancash:** Yungay Province. Huascarán National Park, Llanganuco sector, Quebrada Demanda, west of Chacaraju base camp, 4750 - 4900 m, 9°01' S, 77°36' W, 13 Apr 1985, *Smith & V. Cautivo 10287* (NEOTYPE designated here: MO!; ISONEOTYPE FI!).

When Mattfeld (1934a) described *Plettkea tetrasticha*, he did so by simply stating that this species was in most aspects similar to *Pycnophyllopsis weberbaueri* (his *Plettkea weberbaueri*) but mainly differed in the more robust habit, somewhat larger leaves, and

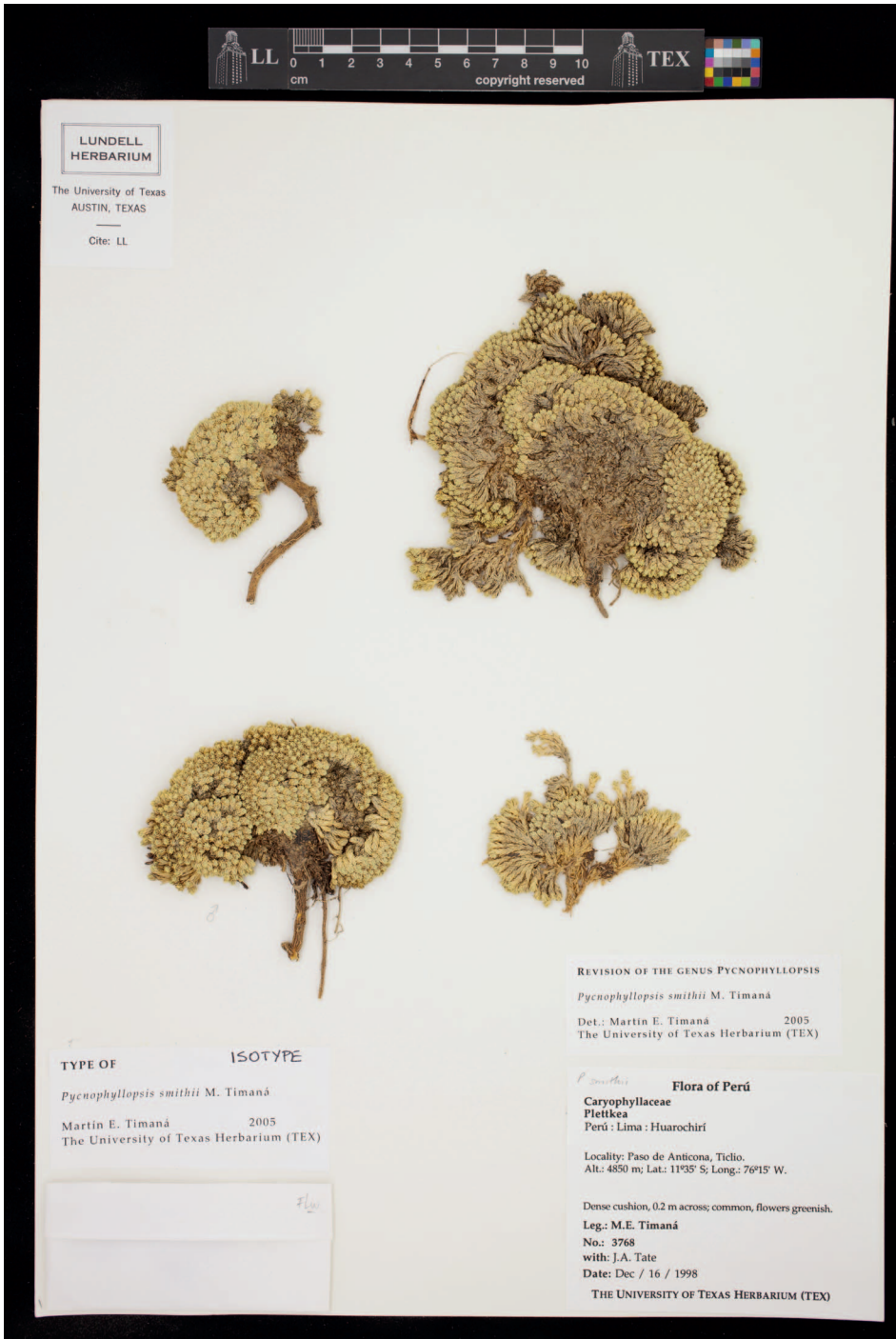


FIG. 2. Isotype of *Pycnophyllopsis smithii*. — The University of Texas Herbarium (LL).

flowers notably longer. No duplicates of the original Berlin type material have been located; therefore, determining the identity of this species has been based on the various measurements made and the geography of the original specimen and current collections. The specimen selected perfectly falls within the size ranges given by Mattfeld for flower, receptacular cup, sepals, and pistil.

7. *Pycnophyllopsis smithii* Timaná, sp. nov.

— TYPE: **PERÚ. Lima:** Huarochirí, Paso de Anticona, Ticlio, 4850 m, 16 Dec 1998, *Timaná & Tate 3768* (HOLOTYPE: USM!; ISOTYPES: BM!, K!, F!, LPB!, MICH!, LL!) (Fig. 2).

Perennial, caespitose SHRUB, (5) 8—20 cm in diameter, dioecious. ROOTS woody, robust. STEM woody, 3—5 mm in diameter, primary branches 2 mm in diameter, yellowish green to stramineous. LEAVES imbricate, (2.0) 2.5—3.5 (3.8) mm long, sheath stramineous, 0.8—1.0 mm long, smooth; blade incurved, stramineous to slightly yellowish-green, lanceolate to nearly triangular, cymbiform, (1.7) 2.0—2.5 × 0.8—1.2 mm wide, margin minute ciliate to denticulate, cilia sparsely distributed along the blade margin, single-celled, 0.05 mm long, venation a weak midvein on abaxial side, blade apex mucronate, abaxial surface nitid, smooth, adaxial surface shiny. INFLORESCENCES terminal, included; prophylls paired, 1.2—1.5 mm long; pedicel 0.1—0.3 mm long. PLANTS dioecious. STAMINATE FLOWER perigynous, ovate, 2—3.0 × 1.0—1.3 mm with a receptacle cup present, crateriform, 0.7—0.9 mm long; calyx ovoid; sepals 5, imbricate, slightly incurved apically, stramineous, lanceolate to narrowly ovate, slightly cymbiform, 1.2—1.5 × 0.5 (-0.7) mm, margin entire, slightly involute distally with apex acute, surface smooth, with a fine midvein visible adaxially; petals 5, light cream-colored to pale stramineous, translucent, obovate, 0.3—0.4 × 0.2—0.3 mm, its apex bifid, divided 1/2 —2/3 the petal length; floral disc absent; stamens 5, episealous, 1.0—1.2 mm long, filament base mostly filiform, rarely slightly enlarged;

staminodes 0; pistillode 0.8—1.0 mm long, ovoid, ovary 0.5—0.7 × 0.05 mm. PISTILLATE FLOWER perigynous, ovate, 2.2—2.5 × 1.5—1.7 mm; receptacle cup crateriform, 0.5 mm long; calyx ovoid; sepals 5, imbricate, straight, stramineous, lanceolate, cymbiform, 1.5—1.8 × 0.7—0.8 mm, margins entire, slightly involute and apex acute, surface smooth; petals 5, light cream colored to pale stramineous, translucent, obovate, 0.2—0.3 × 0.2 mm, apices deeply bifid, divided 1/2—3/4 the petal length; flower disk absent; staminodes 5, 0.25—0.30 mm long, filament base terete; pistil 1.5—2.0 mm long its ovary obpyriform to turbinate, 0.6—0.8 × 0.6 - 0.8 mm; styles 3; stigma terete. FRUITS 1.5 × 1 mm. SEED 1, brown, reniform, laterally flattened, 0.8 × 0.8 mm, shiny, minutely papillose.

Phenology — Collected in flower from December to May and in fruit from August to January.

Distribution — Primarily found in the divide between Lima and Junin, central Peru, in the area locally known as the Anticona Pass, from 4300 to almost 4900 m, where it is sympatric with *Pycnophyllopsis cryptantha* and members of the genus *Pycnophyllum*. *Pycnophyllopsis smithii* has also been reported in the Department of Ancash, within the boundaries of Huascarán National Park, at nearly 4800 m.

Eponymy: It is a great honour to name this new species after the American botanist David N. Smith (1945–1991). David spent nearly four years botanizing the highest peaks of central Peru, particularly the Cordillera Blanca (Ancash) as part of his doctoral dissertation on the flora and vegetation of Peru's Huascarán National Park (Smith, 1988). His numerous collections of *Pycnophyllopsis* and *Pycnophyllum* have greatly enhanced our understanding of these two genera, having an impact parallel to that of A. Weberbauer a century earlier.

Additional Specimens examined — **PERÚ. Ancash:** Recuay, Huascarán National Park, quebrada Quenua Ragra, 4700 - 4850 m, 9°58 S, 77°13 W, 11 Mar 1985, *Smith et al. 11772* (MO). Junin: Ticlio, 4740 m, Dec 1986, *Rivas et al. s.n.* (USM); Capillacocha,

20 km E Carhuamayo, 4300 – 4350 m, 25 Nov 1951, *Tovar 381* (TEX). **Lima:** Huarochirí, Anticona, 4843 m, 8 Aug 1987, *Chanco et al. 1219* (USM); Anticona Pass, approx. 140 km E of Lima on road to La Oroya, ca 4890 m, 16 Dec 1978, *Dillon & Turner 1301* (MO, TEX); Ticlio, 4800 m, 6 May 2001, *León s.n.* (TEX, 2 sheets); Ticlio, 4850 m, 14 Feb 1954, *Rauh P86* (F); Canta, Huascoy, 4600 m, 27 Sep 1974, *Waechter 217PW* (GOET). **Pasco:** Huayllay, Lago Huarón, 4750 m, 14 Jan 1971, *Ellenberg 4061* (US).

Pycnophyllopsis smithii is perhaps the most difficult species to distinguish using just a single set of characters. Morphologically, it most resembles the disjunct *Pycnophyllopsis weberbaueri* with which it maintains differences that, although gradual, are consistent. The two differ in leaf margin: *P. weberbaueri* clearly has noticeable cilia (up to 0.2 mm) whereas those of *P. smithii* can be better characterized as denticulate, with projections less than 0.05 mm that can be observed at 40X magnification. In addition, leaves of *P. smithii* are normally shortly mucronulate, while in *P. weberbaueri* they are consistently acute and without any further projection. Although flowers of both species are approximately the same length, the pedicel of *P. smithii* is relatively shorter (0.1 – 0.3 mm) than those of *P. weberbaueri* (0.3 – 0.5 mm). Petals of *P. smithii* are also shorter (0.2 – 0.4 mm) and more deeply cleft apically (over ½ the total petal length) compared to those of *P. weberbaueri* (0.4 – 0.8 mm, petals cleft ½ — ¼ the petal length). The stamens of *P. smithii* are up to 1.2 mm in length, while those of *P. weberbaueri* can be as long as 2 mm and the staminodes of the former species are also smaller. The style of *P. smithii* is somewhat longer relative to the total length of the pistil (mean = 60% of the total pistil length) compared to the corresponding character in *P. weberbaueri* (mean = 48%). There are also differences in the overall aspect of these species: although they both have imbricate leaves, each opposite pair in *P. smithii* is greatly overtopped by the corresponding lower (inferior) pair, giving the appearance

of a tightly arranged, very compact cushion where the most visible part is the light green-colored leaf tips. In *P. weberbaueri* the leaves are also imbricate, yet they do not overlap to the degree previously described, giving the overall impression of a more loose cushion, with various brown-colored branches clearly visible. Finally, one needs to consider the geographic distribution. The two taxa, both dioecious, and with inconspicuous flowers and probably very limited dispersal mechanisms, are geographically separated by a distance of nearly 1000 km by two of the highest mountain ranges in this part of the Andes. Placing them within the same species would suggest the possibility of potential gene flow between the two populations. Given the evidence at hand, this seems to be very unlikely. With these considerations in mind I have therefore decided to circumscribe this new species.

8. *Pycnophyllopsis weberbaueri* (Muschl.) Timaná, Monogr. Syst. Bot. Missouri Bot. Gard. 127: 1267. 2014. ≡ *Pycnophyllum weberbaueri* Muschl., Bot. Jahrb. Syst. 45: 455. 1911. ≡ *Plettkea weberbaueri* (Muschl.) Mattf., Schriften Vereins Naturk. Unterweser, N.F. 7:19. Fig III, O-Q. 1934. TYPE: **PERÚ. Arequipa:** Caylloma, Vincocaya, 4300–4400 m, 24 Aug 1902, *Weberbauer 1373* (HOLOTYPE: B†; LECTOTYPE (designated here): MOL!).

Although it is morphologically rather uniform, this dioecious species has flowers that are consistently pentamerous with three free styles. It shares several similarities with *Pycnophyllopsis smithii*, from central Peru [see the discussion under *P. smithii* for various distinguishing features that separate these two species]. *Pycnophyllopsis weberbaueri* is found sympatrically with *P. keraiopetala*, a bisexual species with a weakly perigynous flower and a reduced number of stamens.

Pycnophyllum J. Rémy

Pycnophyllum, a genus of ten species, is one of the few known genera in the Caryophyllaceae restricted exclusively to

the high central Andes. The genus is here circumscribed as in Mattfeld's (1922) original concept, namely excluding members of *Pycnophyllopsis* Skottsbo. and *Plettkea* Mattf. which were previously merged into *Pycnophyllum* by MacBride (1937).

Pycnophyllum J. Rémy in Ann. Sci. Nat. Bot., Sér. 3, 6: 355 (Dec. 1846), non *Pycnophyllum* J. Tuzson, 1911 (\equiv *Pychnophyllum* A. T. Brongniart in Orbigny, Dict. Universel Hist. Nat. 13: 114. Jul-Dec 1849).

TYPE SPECIES, designated here: *Pycnophyllum molle* J. Rémy

= *Stichophyllum* Phil. in *Fl. atacam.* 19, Tab. 1d (1860). TYPE SPECIES: *Stichophyllum bryoides* Phil. (\equiv *Pycnophyllum bryoides* (Phil.) Rohrb.)

Dioecious, perennial, densely caespitose, hemispheric to irregularly shaped SHRUBS, 20—ca 200 cm in diameter. STEM woody, 5—10 mm in diameter; branches herbaceous, crowded or flabelliform, proximal branches sometimes enclosed by shriveled leaves. LEAVES exstipulate, imbricate, tetrastichous or spirally arranged, adpressed or spreading from the branch axis, scariosus to membranous, sheath 0.5—2.5 mm long, scariosus to membranous, smooth, glabrous; blade sessile, incurved, straight, or recurvate, lanceolate to wide ovate, complanate to cymbiform, scariosus, base connate, margin entire, sometimes expanded into a translucent membrane, then the blade composed of a scariosus callous and a peripheral membrane, apex obtuse, acute or long aristate, midvein obscure or weakly developed on the adaxial side, abaxial side nitid or opaque, smooth, glabrous. INFLORESCENCE terminal, solitary, weakly exerted above the leaves, single flowered; bracts 4—10 (12), opposite, decussate, complanate to slightly cymbiform, ovate to spatulate, membranous, base obtuse, margin entire, apex obtuse to rounded, rarely acute, medial callous present or absent, smooth, glabrous; pedicel 0—0.4 mm long. FLOWERS unisexual, haplostemonous, tetracyclic, hypogynous, ovate, obovate, or oblong; receptacular cup absent.

CALYX ovoid, cylindrical to obovoid. SEPALS 5, very rarely 6, imbricate quincuncial, wide to narrowly ovate, cymbiform to slightly so, free, scariosus, with a membranous margin or not, central callous present or absent, margin entire, usually involute, apex acute to obtuse, abaxial side nitid, smooth, glabrous, colored or not. PETALS 0 to 5, free, alternisepalous, translucent or cream-colored to light brown to violaceous, oblong to obovate, membranous, base cuneate, margin entire, apex dentate to divide, or truncate, glabrous. STAMENS 3 to 5, anti-sepalous, heterandrous, rarely homandrous, filament base filiform, terete or complanate, sometimes weakly subulate; anthers introrse, dorsifixed; staminal disk present, flattened to prominent; staminodes (in pistillate flowers) 2 to 5, antisepalous, filaments terete or complanate, sterile anthers dorsifixed. PISTIL 1.5—4.5 mm long; ovary 3-carpellate, unilocular, ovoid to ellipsoid, frequently trigonous, glabrous, sometimes minute stipitate; style single, stigma terete, shortly capitate at the apex with 3—6 ovules arranged at the base of a central placental column; pistillode (in staminate flowers) 3-carpellate, unilocular, 1—2 mm long, reduced ovary ovoid to cylindrical, sometimes apically compressed, 0.4—1.5 mm long, glabrous, stigma terete. FRUIT an utricle or septicidal capsule opening by 3 valves, or an irregular circumscissile capsule opening near the base of the ovary; ovoid or ellipsoid, usually trigonous, 1.0—3.5 mm long, 1—2 mm wide, enclosed by persistent sepals. SEEDS 1 to 6, light to dark brown, reniform, laterally compressed, surface nitid or opaque, smooth or minute papillose.

Despite its overall morphological similarities with members of *Pycnophyllopsis* and *Arenaria* L., species of *Pycnophyllum* form a single, coherent group united by a combination of various morphological characters not found among other members of Caryophyllaceae. In addition to their cushion-like life form, species of *Pycnophyllum* are characterized by dioecy, simple, opposite leaves generally fused at the base forming a distinctive sheath, a complete lack of any form of pubescence or marginal cilia,



FIG. 3. Lectotype (P 00156958) of *Pycnophyllum molle*. — Reproduced by kind permission, © MNHN collection-Paris.

hypogynous flowers, 5 free sepals, 3 to 5 antisepalous stamens (or staminodes) forming a well-defined staminal disk, a pistil terminating in a single style with 1–3 stigmatic lobes, and a one to three-seeded fruit. Fruits can be indehiscent (*P.* sect. *Gymnopycnophyllum*), or dehiscent (3-valved capsule) as in *P.* sect. *Pycnophyllum*.

Pycnophyllum sect. *Pycnophyllum*

≡ *Pycnophyllum* sect. *Kirrhanthemum* Mattf. in Feddes Repert. Spec. Nov. Regni Veg. 18: 174 (1922); *nom. superfl.*

1. *Pycnophyllum molle* J. Rémy, Ann. Sci. Nat. Bot., Sér. 3, 6: 355, Tab. 20, fig. 2-8 (Dec. 1846) —TYPE: **BOLIVIA. Potosi:** Lagunas de Potosi, March, *D'Orbigny* 442. (LECTOTYPE, designated here: P! (P00156958); ISOLECTOTYPES: P (P00156959, photo!), F! (fragment; 871384), G! (G00226948) (Fig. 3).

= *Pycnophyllum aculeatum* Muschl., Bot. Jahrb. Syst. 45: 456, Fig. 1. (1911). TYPE: **PERU. Arequipa:** Vincocaya, en el ferrocarril de Arequipa a Puno, 4300–4400 m, s.d. (24 Aug 1902, per Mattfeld), *Weberbauer* 1374 (HOLOTYPE: B†; LECTOTYPE, designated here: MOL!)

= *Pycnophyllum markgrafianum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 175 (1922). TYPE: **PERU. Ancash:** Cajatambo, 4400 m, 6 Apr 1903, *Weberbauer* 2783 (HOLOTYPE: B†; LECTOTYPE, designated here: K!; ISOLECTOTYPES: G!, MOL!)

The French traveller, palaeontologist and explorer Alcide d'Orbigny (1802-1857) visited Bolivia from 1830 to 1833; his plant collections were studied by Jules Ezechiel Rémy (1826-1893) and published in the *Annales des Sciences Naturelles* in two articles, *Analecta Boliviana I* and *Analecta Boliviana II* (Rémy, 1846, 1847; Stafleu and Cowan 1981, 1983). There are two d'Orbigny's specimens at the Paris herbarium belonging to this species, but only the one selected as lectotype carries the label which coincides with the locality described by Rémy in the original description.

Given its wide geographic distribution across various degrees of latitude, *Pycnophyllum molle* shows a considerable degree of variation. Although the main source of variation is in leaf size, shape, and color, the floral structure remains rather constant. Much of the apparent variation among *P. molle* specimens is caused by the different branching patterns detected within the same cushion – a condition produced by either intrinsic causes, such as branch age, or extrinsic ones, such as micro-topography. Consequently, one often finds a wide range of variation within a single individual. The same effect has been noticed in *P. tetra-stichum*.

2. *Pycnophyllum huascararum* Timaná, **sp. nov.** — TYPE: **PERÚ. Ancash:** Carhuaz, Huascarán National Park, lateral valley of Quebrada Ishinca, trail to Lago Ishinca, 4730–4930 m, 9°23' S, 77°25' W, 12 Feb 1985, *Smith, Valencia & Gonzales* 9453; (HOLOTYPE: MO! 3311207); ISOTYPES: AAU!, F! MO! (3311209) (Fig. 4).

Pycnophyllum huascararum differs from *Pycnophyllum molle* in the dark orange to orange-yellow blade callous, the strongly involute blade margin, 6(8) bracts, and the 3-valved capsule.

Hemispherical, convex SHRUB, up to 60 cm in diameter and 25 cm high; stem woody, 6–9 mm in diameter; branches compact, crowded, primary branches terete to clavate, 2.5–3.5 mm wide, light brown to yellowish green. LEAVES imbricate, appressed to the branch axis, 2.3–3.1 mm long; sheath translucent, 0.5–0.8 mm long; blade incurved, light stramineous, ovate to obovate, slightly cymbiform, 1.3–2.1 × 1.0–1.4 mm, margin membranous, translucent, strongly involute, blade venation obscure, apex obtuse to rounded, apiculate, less than 0.1 mm long, blade surface shiny, smooth, blade callous present, obspathulate, 1/2 – 2/3 the total blade length, dark orange to orange yellow. INFLORESCENCE single, terminal, bracts 6(8), obovate to obspathulate, 3.0–3.5 × 1.3–1.6 mm, bract apex obtuse

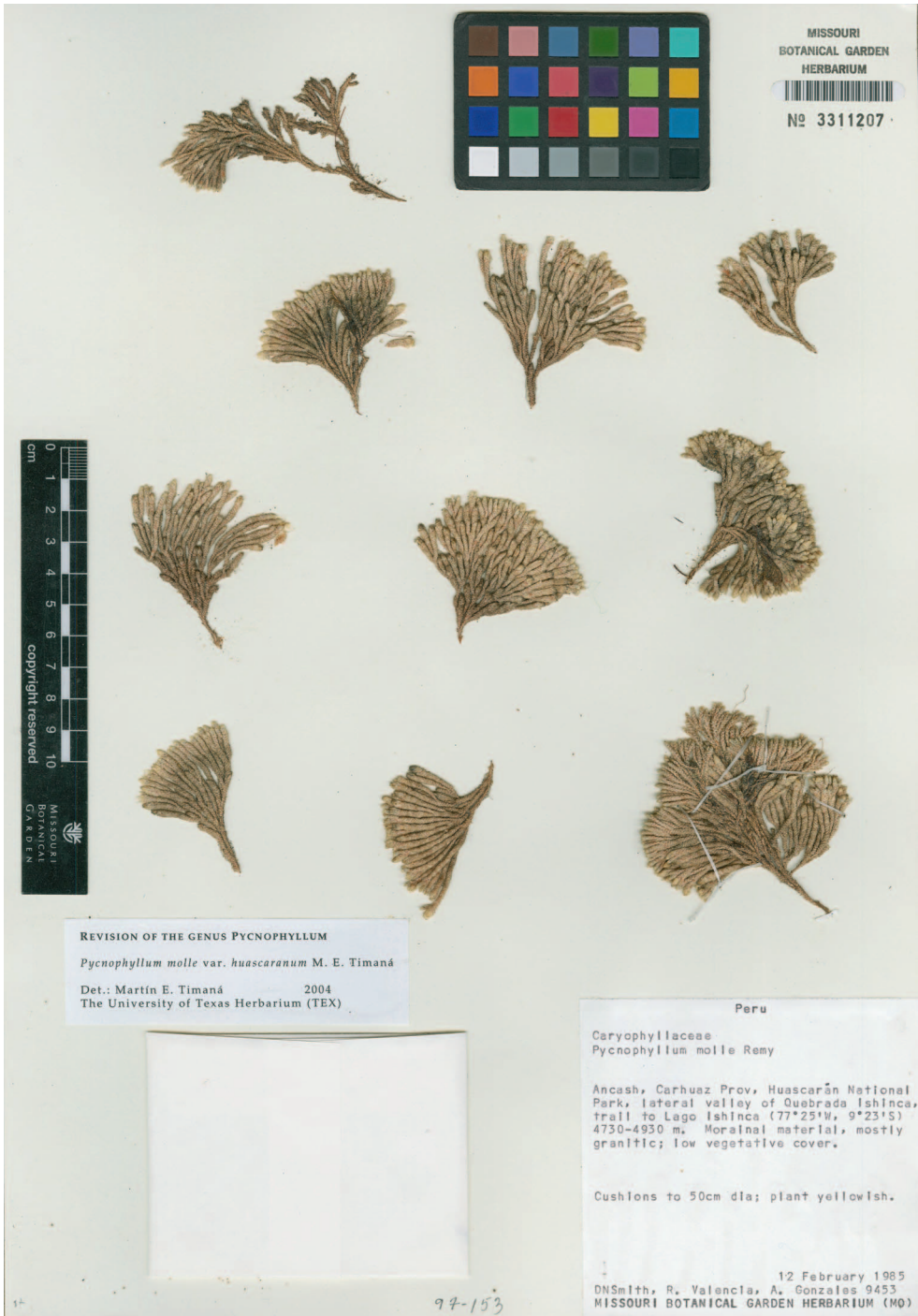


FIG. 4. Holotype (MO 3311207) of *Pycnophyllum huascararum*. — Reproduced by kind permission, © Mo. Bot. Garden. (MO).

to rounded, callous bract absent, pedicel 0—0.2 mm long. STAMINATE FLOWER obovate, obconical to ovoid; sepals slightly incurved, from light cream to pale yellow, peripherally membranous, scarious medially, obovate, carinate to slightly cymbiform, $3.8\text{--}4.1 \times 1.5\text{--}2.5$ mm, margin slightly involute, apex obtuse to rounded, abaxial surface smooth, veins obscure, callous present, $2/3\text{--}3/4$ the sepal length, light yellow; petals 5, translucent, obovate, $1.1\text{--}1.4 \times 0.1\text{--}0.5$ mm, apex obtuse to truncate; stamens 5, heterandrous, $1.4\text{--}2.3$ mm long, filament base filiform, floral disk poorly developed; pistillode $1.3\text{--}1.7$ mm long, pistillode ovary ovoid, $0.6\text{--}0.7 \times 0.4\text{--}0.7$ mm. PISTILLATE FLOWER obovate, obconical to ovoid; sepals slightly incurved, from light cream to pale yellow, peripherally membranous, scarious medially, obovate, carinate to slightly cymbiform, $3.4\text{--}3.8 \times 2\text{--}2.3$ mm, margin slightly involute, apex obtuse to rounded, abaxial surface smooth, veins obscure, callous present, $2/3\text{--}3/4$ the sepal length, light yellow; petals 5, translucent, obovate, $0.8\text{--}1.3$ x nearly 0.2 mm, apex obtuse to truncate; staminodes 5, homandrous, less than 0.2 mm long, filament flattened, floral disk minute; pistil $1.8\text{--}2.5$ mm long, ovary ovoid, $1.2\text{--}1.5 \times 0.9\text{--}1.2$ mm, ovules 3, stigma trifid. FRUIT a 3-valved capsule, $1.5\text{--}1.8 \times 1.2\text{--}1.5$ mm, ovoid. SEEDS 2—3, light brown, asymmetrically reniform, ca $1 \times$ ca 0.7 mm, minute papillose.

Phenology — Flowering from October to April and fruiting from February to May.

Distribution — Endemic to the Department of Ancash, Peru, in the vicinity of Huascaran National Park, from 4200 to 5000 m.

Eponymy — This new species is named after the type locality, Huascaran National Park, a magnificent Peruvian National Park where a number of interesting Caryophyllaceae species are found.

Additional Specimens examined — **PERU. Ancash:** Llanganuco valley, slopes of Huandoy, Cordillera Blanca, 18 Jul 1968, *Balthgate 10* (E, F); near lago Safuna, northern Cordillera Blanca, northeast of Alpamayo, 4250 m, rocky sites with granitic

or crystalline rocks, some glacial debris, some large outcrops; on soil as a yellow mound, level site, 4250 m, 22 Jul 1975, *Bunin s.n.* (COLO); Huarapasca, estacion 40 miles east of Huaraz, 5500 m, 3 Oct 1922, *MacBride & Featherstone 2488* (BM, F, G, MA, NY, S, US); Cordillera Huayhuasch, 4600 m, 19 Jul 1954, *Rauh & Hirsch P1894* (F); Cordillera Raura, 4900 m, 21 Jul 1954, *Rauh & Hirsch P1902* (F); south of Huaráz, 32 km from Pachacoto towards La Union, Punta Huarapasca, 4750 m, 6 Apr 1988, *Renvoize & Laegaard 5132* (K); Huascaran National Park, between pass and Carpa, rio Pachacoto drenaje, 4600–4350 m, $9^{\circ}53' \text{ S}$, $77^{\circ}14' \text{ W}$, 31 Mar 1985, *Smith & Escalon 10216* (F, MO); Huascaran National Park, Llanganuco sector, quebrada Demanda, between Lago 69 and glacier coming from Nevado Pisco, 4800 m, $9^{\circ}00' \text{ S}$, $77^{\circ}36' \text{ W}$, 12 Apr 1985, *Smith & Cautivo 10273* (AAU); Huascaran National Park, quebrada Quenua Ragra, 4700–4600 m, $9^{\circ}58' \text{ S}$, $77^{\circ}13' \text{ W}$, 10 May 1985, *Smith et al. 10654* (MO); Huascaran National Park, 3–4 km below Cahuish Tunnel, 4500–4550 m, $9^{\circ}41' \text{ S}$, $77^{\circ}14' \text{ W}$, 10 Jul 1985, *Smith & Buddensiek 11115* (F, MO); Huascaran National Park, Parón Valley, E of Lake, 4600–4900 m, $8^{\circ}58' \text{ S}$, $77^{\circ}38' \text{ W}$, 28 Sep 1985, *Smith 11506* (F, MO); Huascaran National Park, lateral valley of quebrada Ishinca, 4730–4930 m, $9^{\circ}23' \text{ S}$, $77^{\circ}25' \text{ W}$, 12 Feb 1985, *Smith et al. 9453* (AAU, F, MO); Huascaran National Park, quebrada Alpamayo, at foot of Alpamayo and Quitaraju, 4600–4750 m, $8^{\circ}53' \text{ S}$, $77^{\circ}41' \text{ W}$, 8 Mar 1985, *Smith et al. 9738* (AAU, F, MO); Huascaran National Park, pass between quebrada Los Cedros and Hatuncocha, 4600–4850 m, $8^{\circ}51' \text{ S}$, $77^{\circ}45' \text{ W}$, 12 Mar 1985, *Smith & Valencia 9949* (AAU, MO); Pisco Creek, Llanganuco Valley, S. exposure, ca 3200 m, Aug 1959, *Tothill 147* (CORD, F, UC).

This taxon is characterized by its robust, densely packed primary branches, its markedly involute leaf margin, particularly toward the apex, the conspicuously bright orange to light brown, shiny, protruding callous and dehiscent fruit. The callous can sometimes be so conspicuous that, to an

untrained eye it may resemble the sporangia of some *Sellaginella* species (some *Pycnophyllum* specimens have been determined as such in the past). The fruits are also peculiar because they can unambiguously be considered capsules, opening from the bottom of the ovary into three valves.

3. *Pycnophyllum spathulatum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 175 (1922). TYPE: **BOLIVIA**. Zwischen Tomarape und Sajama, 4500 m, Oct 1876, *Stübel* 3 (HOLOTYPE, B†). NEOTYPE: **BOLIVIA**. al este del pueblo de Sajama. Bosque abierto de *Polylepis tarapacana*, sobre las laderas del cerro Sajama, 4750 m, 1 Jun 1991, *Beck* 19899 (NEOTYPE designated here: LPB!; ISONEOTYPE: TEX!).

As with many others of Stübel's specimens deposited in Berlin, the type of *Pycnophyllum spathulatum* is no longer extant. The only fertile specimen (with pistillate flowers) gathered in the same locality as the type is that of S.G. Beck, which is therefore selected here as the neotype. Morphologically *Pycnophyllum spathulatum* is most similar to *P. macropetalum*, from which it can be easily distinguished by its upright, uniformly terete, brownish-yellow branches, whereas *P. macropetalum* has lax, light green to yellow, club-shaped branches.

4. *Pycnophyllum macropetalum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 176 (1922) — TYPE: **PERÚ**. [Tacna] Cerro Tacora, 4500 m, 7 Oct 1876, *Stübel* 110. (HOLOTYPE: B†; LECTOTYPE, designated here: K!).

Pycnophyllum macropetalum exhibits numerous unique characteristics that make it easily recognizable: it not only has the largest petals in the genus but also it is the only species in which petals are longer than the sepals; in addition, *P. macropetalum* is the only species with coloured sepals – from light brown to a rather intense violaceous color, particularly toward the apical region of the sepals. Although fruits in the genus

Pycnophyllum have been described as indehiscent or irregularly rupturing (Mattfeld, 1922; Bittrich, 1993) *P. macropetalum* clearly produces a 3-valved capsule.

5. *Pycnophyllum holleanum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 177. 1922. TYPE: **PERU**. **Junin**: Huancayo, am Gletscher Chuspicocha über der Hacienda Acopalca, nordöstlich von Huancayo, geogr. Br. ca. 12°5' S, 4900–5000 m, 27 Mar 1913, *Weberbauer* 6522 (HOLOTYPE: B†; LECTOTYPE here designated: K!; ISOLECTOTYPES: B!, BM!, CAS!, DS!, F! (2 sheets), MA!, MO!, MOL!, NY!, PH!, S!, UC!, US!).

Pycnophyllum holleanum is one of the most distinctive and handsome species in this genus. It is characterized by squarrose leaves, a sharp awn, and the light brown color of the foliar callous. Morphologically it is most similar to *P. aristatum* from which it differs in the shorter awn and the blade shape (ovate in the latter). Mattfeld described this species based on a subsequently destroyed Berlin specimen. Of the 15 isotypes studied, only two (K and MOL) have the same complete collection information as that of the protologue. The Kew specimen label reads “Ex Museo Botanico Berolinensi” and shows the accession date as “24 Apr. 1923” (one year after Mattfeld's monograph). The Berlin islectotype cited above was acquired from the Stockholm herbarium in June 1961, thus it presumably cannot be considered part of the original material studied by Mattfeld.

6. *Pycnophyllum aristatum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 178 (1922). TYPE: **PERU**. **Ancash**: Pallasca, 4600–4800 m, Aug 1918, *Weberbauer* 7250 (HOLOTYPE: B†; LECTOTYPE here designated: K!; ISOLECTOYPE: F!).

Pycnophyllum aristatum is another distinctive species in this genus. It is easily recognized by the long, filamentous, spiraled awns, the flabelliform disposition of branches, and the light brown coloration of the young branches.

Pycnophyllum sect. *Gymnopycnophyllum*
Pax, Bot. Jahrb. 18: 34 (1893).

TYPE SPECIES: *Pycnophyllum tetrastichum*
J. Rémy.

See discussion under *Pycnophyllum tetrastichum*

= *Pycnophyllum* sect. *Diphtheranthemum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 170 (1922). TYPE SPECIES: *Pycnophyllum convexum* Griseb.

= *Pycnophyllum* sect. *Drudea* (Griseb.) Pax, Bot. Jahrb. 18: 34 (1893). TYPE SPECIES: *Pycnophyllum lechlerianum* Rohrb.

7. *Pycnophyllum bryoides* (Phil.) Rohrb.,
Linnaea 36: 662 (Dec 1870) ≡ *Stichophyllum bryoides* Phil., Fl. atacam. 19. Tab. Id. (1860) — TYPE: **CHILE**. **Atacama**: Alto de Puquios in deserto Atacama, Feb. 1854, R. Philippi s.n. (HOLOTYPE: SGO 48876! *p.p.*, marked as No. 2).

Pycnophyllum bryoides is one of the most distinctive and well-defined species in *P.* sect. *Gymnopycnophyllum*. It can easily be recognized by its uniformly spirally arranged leaves, and by the presence of five small, apically divided petals, a unique condition among members of this section. While various specimens collected by Philippi from the Atacama Desert region have been located, only the SGO holotype carries the exact information provided in the protologue. Except for the HAL specimen that was collected in 1854, all of the others were collected later or lack enough information to decide their nomenclatural status.

8. *Pycnophyllum convexum* Griseb., Pl. lorentz. 28 (1874); also in: Abh. Königl. Ges. Wiss. Göttingen 19: 76 (1874) — TYPE: **ARGENTINA**. **Catamarca**: Vayas altas pr. Belen alt. 9-11000 ft, Jan 1872, Lorentz 638 (HOLOTYPE: GOET!; ISOTYPE CORD!)

= *Pycnophyllum argentinum* Pax, Bot. Jahrb. Syst. 18: 33 (1893). TYPE: **ARGENTINA**. **La Rioja**: Sierra Famatina, Cueva de

Pérez, 26-28 Jan 1879, *Hieronymus & Niederlein* 365 (HOLOTYPE: B†; LECTOTYPE designated here: G!; ISOLECTOTYPES: S!, E!, UC!).

= *Pycnophyllum mucronulatum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 173 (1922) TYPE: **ARGENTINA**. **Salta**: Nevado del Castillo, 19-23 Mar 1873, *Hieronymus & Lorentz* 31 (HOLOTYPE: B†; LECTOTYPE designated here: GOET!; ISOLECTOTYPES: F! [fragment]: G-DC!)

In the protologue of *P. argentinum*, Pax (1893) included a second specimen, *Stübel* 4, then at the Berlin herbarium (B) but now destroyed. Mattfeld (1922) however pointed out it belonged to *P. tetrastichum*. *Pycnophyllum convexum* as circumscribed here includes two other described Argentinean taxa, namely, *P. argentinum* Pax and *P. mucronulatum* Mattf. Although the study of type material of these taxa shows some differences between them, the analysis of multiple populations across their geographic range demonstrates that these three taxa cannot be kept separate. As discussed under *P. tetrastichum*, the levels of phenotypic variation even within individual plants show that the species limits set by Mattfeld are not meaningful.

9. *Pycnophyllum tetrastichum* J. Rémy, Ann. Sci. Nat. Bot., Ser. 3, 6: 356, Tab. 20, fig. 1 (Dec. 1846). TYPE: **BOLIVIA**. **Potosi**: 4000 m, *D'Orbigny s.n.* (LECTOTYPE selected here: P!, P00156960; ISOLECTOTYPE: P!, P04925579) (Fig. 5).

= *Pycnophyllum lechlerianum* Rohrb., Linnaea 36: 664 (Dec 1870); *Drudea lycopodioides* Griseb., Symb. Fl. Argent. 25 (1879), pro parte. TYPE: **PERU**, Azangaro, “in montibus asperis lapidosis,” Jun, *Lechler* 1742 (HOLOTYPE: B†; LECTOTYPE designated here: G!; ISOLECTOTYPES: BR!, CGE!, F!, GOET!, K!, L!, M!, P!, SGO!, S!, TCD!).

= *Pycnophyllum filiforme* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 172 (1922). TYPE: **PERU**. **Arequipa**: Caylloma, 15°20'–15°30' S, am See Villafró über Caylloma, 4700–4800 m, 29 Mar 1914, *Weberbauer* 6885 (HOLOTYPE: B†; LECTOTYPE



FIG. 5. Lectotype (P 00156960) of *Pycnophyllum tetrastichum*. — Reproduced by kind permission, © MNHN collection-Paris.

designated here: MOL!; ISOLECTOTYPES: G!, US!).

= *Pycnophyllum glomeratum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 18: 171 (1922). TYPE: **PERU**. **Puno**: Sandia, zwischen Poto und Ananca, offene dürrtig bewachsene Polsterpflanzenmatte, 4600-4700, 7 May 1902, *Weberbauer* 952 (HOLOTYPE: B†; LECTOTYPE designated here: K!; ISOLECTOTYPE MOL!).

= *Pycnophyllum leptothamnum* Mattf., Notizbl. Bot. Gart. Berlin-Dahlem. 10: 1051 (1930). TYPE: **PERU**. **Cuzco**: Quispicanchis, in der Puna-Matte nahe den Gletschern des Auzangate, 4500-4600 m, 11 Feb 1929, A. *Weberbauer* 7772 (HOLOTYPE B†; LECTOTYPE

designated here: NY!; ISOLECTOTYPES: GH!, US!).

When Rémy proposed the genus *Pycnophyllum* in 1846, he included two species: *P. molle* and *P. tetrastichum*. The description of the latter makes reference to a single specimen that included both species (“*mixta in herbario parisiensi cum praecedente*”). However, currently, the *D’Orbigny* 442 specimen at P (P00156958, Fig. 3) only consists of material corresponding to *P. molle*. A second sheet at P (P00156960, Fig. 5) containing *P. tetrastichum*, is attributed to *D’Orbigny* but without collection number, and includes the annotation “*étais avec la congénère*” – which can be translated as “it

was with its congener”, namely *Pycnophyllum molle*. Thus this specimen is here designated as the lectotype.

In his 1922 revision of the genus *Pycnophyllum* and subsequent 1930 publication, Mattfeld described several new species in *P.* sect. *Gymnopycnophyllum*, some of which are here reduced to synonyms of *Pycnophyllum tetrastichum*. Such a merger requires justification. First, an analysis of Mattfeld’s 1922 key to species shows that, for the most part, the differences supporting his species are primarily based on the shape (outline) and the size of flowers and/or leaves. This leads to a rather artificial separation since these two characters are each part of a continuum. Mattfeld’s new species were based only upon one or two specimens (some of them fragmentary), and while the differences he suggested may well apply to such a small sample, a thorough examination of additional specimens revealed less support for such division. Second, plants of this taxon show a tremendous amount of phenotypic plasticity, even within the same individual cushion plant. While carrying out field studies in Peru and Bolivia, I found that, depending on factors such as branch age, position within the cushion (central vs. peripheral), and micro-topography, characters used by Mattfeld such as phylotaxis, leaf, and internode size, and even branching organization may vary tremendously. Other diagnostic features such as shape, size, and position of the blade apex may dramatically change along a single primary branch depending on the leaf distance from the branch tip. Lastly, after comparing Mattfeld’s descriptions with extant type material, I have found that several, if not all, of his linear measurements, have been clearly over-estimated. This fact is most burdensome when, as stated earlier, his species definitions are based mainly on organ size. Consequently, after long consideration and in light of these observations, I have decided to combine these previously recognized species under the oldest binomial available, namely *P. tetrastichum*. While this solution may be less than perfect, I fail to

see any set of correlated characters (and particularly discrete characters) to recognize and support more than one species. While some regional variation may be suggested, additional detailed field studies and sampling is needed to finally justify species recognition.

August H. R. Grisebach (1879) placed Rohrbach’s *Pycnophyllum lechlerianum* and his own *Colobanthus lycopodioides* into an unusual new genus, *Drudea*, combining these two species as *Drudea lycopodioides*. This arrangement was based on two specimens: *Lechler 1078*, the type of *Colobanthus lycopodioides* Griseb. (1854) and *Lechler 1742*, the type of *Pycnophyllum lechlerianum* Rohrb. (1870). Pax (1893) later reduced Grisebach’s anomalous species to a synonym of *P. lechlerianum* Rohrb. (keeping *C. lycopodioides* as a synonym as well) and proposed *Pycnophyllum* sect. *Drudea* to include it. Finally, Skottsberg (1916) emended Pax’s section by removing *Colobanthus lycopodioides* Griseb. from synonymy and reducing *P. lechlerianum* to a synonym of *C. lycopodioides*.

Regarding the enigmatic *Pycnophyllum lechlerianum* Rohrb. that puzzled previous workers such as Grisebach, Pax, and Mattfeld with its alleged 3-styled flowers, although ten of the 12 type specimens (*Lechler 1742*) are sterile (as reported by all previous workers), two (G, TCD) do bear flowers which show a single style fused lengthwise with three stigmatic regions, as in all other members of *Pycnophyllum*. Consequently, the separation of this taxon into a separate section, as *P.* sect. *Drudea* (Griseb.) Pax, is no longer supported.

10. *Pycnophyllum kobalanthum* Mattf., Feddes Repert. Spec. Nov. Regni Veg. 36: 274, Tab. 179 (pp) (1934) — TYPE: **BOLIVIA**. Cordillera Real, Chacaltaya, 4600 m, 21 Apr 1928, *Troll 1906* (HOLOTYPE: B!; ISOTYPE: M!).

In my 2005 study, I considered *P. kobalanthum* a synonym of *P. tetrastichum*. New material from LPB made available to me in 2015 convinced me to maintain its

species status. *P. kobalanthum* is an endemic Bolivian species found between 4000 and 4600 m; it can be recognized by its characteristic gibbous leaves with the apex suddenly arched into a small mucron.

Additional Representative specimens: **BO-LIVIA. Chuquisaca:** Cordillera de Los Sombreros, near summit along road from Icla to Tarvita, 19°34'50" S, 64°37'50" O, 3929 m, 1 Dec 2005, *Wood et al.* 22156 (LBP, TEX). **La Paz:** Área Natural de Manejo Integrado Apolobamba, cerro Socondori Grande, aprox. 8 km NNE de Ulla Ulla, 15°00'42" S, 69°13'02" O, 4600 m, 27 Feb 2008, *Meneses* 4506 (LBP, TEX); Umanata, Jaquewi Lampampa, 15°26'58" S, 69°04'56" O, 4149 m, 25 Nov 2003, *Valdivia et al.* 88. (LBP, TEX); camino a Alto Chacaltaya, 200 m entrando hacia el camino de la comp. Minera Kellguani, 4320 m, 21 Dec 1986, *Valenzuela* 917 (LBP, TEX); Patapampa, 2.5 km del desvío, 4440 m, 21 Dec 1986, *Valenzuela* 937 (LBP, TEX). **Oruro:** entre Challapata y Potosí, 4050 m, 27 Feb 1991, *Navarro* 234 (LBP, TEX); bosque de *Poly-lepis*, arriba del pueblo Sajama, 4600 m, 1 Jun 1991, *Hensen* 2623 (LBP, TEX); Parque Nacional Sajama, cerro Huincurata, 18°07'05" S, 68°57'44" O, 4555 m, 25 Mar 2012, *Pozo & Zeballos* 759 (LBP, TEX). **Potosí:** al norte de Pulacayo, aprox. 13.5 km, cerca a la cabecera Calzada, 20°15'14.66" S, 66°41'6.25" W, 4470 m, 10 Mar 2010, *Zenteno & Mamani* 9774 (LBP, TEX); along road between Villa Alota and Viscacacha, 21°23'38" S, 67°43'11" O, 4100 m, 7 Mar 2009, *Kool et al.* 1221 (LBP, TEX); al oeste-sur-oeste cruce a Nazanerito v Kucho, 21°26'11" S, 65°53'02" O, 4398 m, 10 Mar 2012, *Zenteno et al.* 11985 (LBP, TEX); al SO de Kucho en línea recta hacia Moiiinete aprox 18.93 km, 21°37'41" S, 66°08'48" W, 4453 m, 12 Mar 2012, *Zenteno et al.* 12108 (LBP, TEX); along road between Uyuni and Laguna Colorada, after passing Laguna Cachi, 21°49'57" S, 69°12'16" W, 4600 m, 7 Mar 2009, *Kool et al.* 1223 (LBP, TEX); on pass above Belen Pampa, along road from Potosí to Challapata, 19°13'11" S, 66°03'16" O, 4265 m, 14 Mar 2009, *Kool et al.* 1241 (LBP, TEX).

Excluded names

Pycnophyllum aschersonianum Muschl., Bot. in Jahrb. Syst. 45: 455. 1911 — TYPE: **PERU. Ancash:** Cordillere Janashallath, inter Huaraz et Chavin de Huantar, in formatione plantis caespitosis ac pulvinaribus composita, 4500- 4600 m, 3 Jul 1903, *Weberbauer* 3293 (HOLOTYPE: B†).

Because of the lack of original material and the contradictory nature of Muschler's description (he described bisexual flowers for a dioecious species), I cannot assign this taxon to any known species. The closest taxon with which this description fits is that of *Pycnophyllum huascararanum*, although the two greatly differ in petal size. Muschler described his specimen as having petal and stamens of equal size, which is not the case in the newly described species where the petals are always much shorter than the stamens. Mattfeld (1922) pointed out the overall leaf similarities with *P. molle* and *P. spathulatum* but was unable to assign a species status.

Pycnophyllum carinatum Muschl., Bot. Jahrb. Syst. 45: 457 (1911) ≡ *Arenaria carinata* (Muschl.) Molinari, Polish Bot. J. 61(2): 275 (2016). SYNTYPES: **PERU. Junin:** between Tarma and La Oroya, 4000 m, 14 Feb 1903, *Weberbauer* 2529 (B†); Puno, Sandia, between Poto and Ananca, 4600-4700 m, 7 May 1902, *A. Weberbauer* 951 (B†).

Mushler described this species based on two gatherings by August Weberbauer. *Weberbauer* 2529 is most probably destroyed – it has not been located at either B, MOL, or any other herbarium. The second specimen, *Weberbauer* 951, has not been located in either of the two herbaria. A specimen with the same collection number is listed as the holotype of *Bulbophyllum incarum* Kraenzl. (Orchidaceae, Kraenzlin, 1905) and cited as such by Schweinfurth in his "Orchids of Peru" (Schweinfurth, 1960), however, the image of the F photograph presented in JSTOR Global Plants carries the number 591 (F0BN018331, photo!) instead of 951. In 1994, Christenson (1994) de-

scribed the orchid collection at the Herbarium Hamburgense (HGB); he reported (p. 348) specimen *Weberbauer 951* as the holotype of *B. incarum* (HBG501372, photo!). The Weberbauer specimen that Muschler examined for the description of *P. carinatum* remains a mystery. He described a ciliated leaf margin, an unknown characteristic among species of *Pycnophyllum*; Mattfeld (1922) suggested this could be a member of *Arenaria* sect. *Dicranilla*; finally, Macbride (1937) speculated this taxon could be conspecific with *Arenaria boliviana* Williams. Thus, while Molinari's combination might be correct from a nomenclatural point of view, it is also purely speculative since the true identity of this taxon cannot be confirmed.

Pycnophyllum dicranoides (Kunth) Muschl., Bot. Jahrb. Syst. 45: 454 (1911) ≡ *Arenaria dicranoides* Kunth, Nov. Gen. et Spec. VI: 34 (Apr. 1823 -folio). — TYPE: **ECUADOR**. "Crescit in monte Antisana, alt. 2100 hex. floret Junio." A. Humboldt & A. Bonpland, s.n (HOLOTYPE: P! P00274230).

This is a synonym of *Arenaria dicranoides* Kunth. Muschler (1911) cited *Weberbauer 5120* (B) when proposing this combination but no duplicates have been located.

Pycnophyllum horizontale Muschl., Bot. Jahrb. Syst. 45: 454 (1911) ≡ *Arenaria horizontalis* (Muschl.) Molinari, Polish Bot. J. 61(2): 275 (2016). TYPE: **PERU. Lima**: "Andes altissimae supra Lima", 4500m, Aug 1905, *Weberbauer s.n.* (HOLOTYPE: B†).

Muschler (1911) described ciliated leaves and bisexual flowers in this specimen, none of which occur in *Pycnophyllum*. Mattfeld (1922) suggested this could be a member of *Arenaria* sect. *Dicranilla*. No duplicates have been located.

Pycnophyllum lanatum Phil. in Anal. Univ. Santiago 81: 774 (1893) — TYPE: **CHILE**. Las Mollucas, Cordillera de Illapel, Jan.1888, R. Philippi s.n. (HOLOTYPE: SGO!)

This name was published by R.A. Philippi based on specimens collected near

the Cordillera Illapel in the Province of Coquimbo, Chile (Philippi, 1892). Philippi missed the small, inconspicuous flowers concealed by the dense indumentum that characterizes *Pycnophyllum lanatum* and therefore proposed the new species with some reservation, adding a question mark after the generic name, thus as *Pycnophyllum ? lanatum*. Mattfeld (1922), the last monographer of *Pycnophyllum*, was unable to study any part of the original material and listed this taxon as *species dubia*, placing some doubts on its generic position due to its heavy white indumentum. The examination of additional specimens has demonstrated that this taxon does not belong in *Pycnophyllum*. Further details will be given in a publication in preparation (Timaná, in prep.)

Pycnophyllum peruvianum Muschl., Bot. Jahrb. Syst. 45: 457 (1911) ≡ *Arenaria peruviana* (Muschl.) Molinari, Polish Bot. J. 61(2): 276 (2016). TYPE: **PERU. Junin**: La Oroya, 4300 m, Feb 1903, *Weberbauer 2597* (LECTOTYPE selected by Molinari, 2016: MOL!).

As proposed earlier by Mattfeld (1922), this is a member of *Arenaria* sect. *Dicranilla*. Muschler described ciliated leaf margins and bisexual flowers, both features known to be absent in members of *Pycnophyllum*. The Weberbauer specimen cited by Molinari and deposited at MOL emerges under unusual circumstances. As part of my research I visited MOL in 1999, 2000 and 2016; during my first two visits *Weberbauer 2597* was not in the collection. In fact, such a specimen is not mentioned in Velarde's authoritative catalogue of Weberbauer's isotypes kept at the MOL herbarium (Velarde 1969). The specimen location is not listed in neither the Cano and Sánchez report on endemic Caryophyllaceae of Peru (Cano & Sánchez, 2006), nor is included, to July 2017, among MOL type specimens submitted to JSTOR Plants in 2013. The specimen itself lacks all the characteristic elements of the Weberbauer specimens stored at MOL: no original label (with Weberbauer's distinctive handwriting), barcode, or official herbarium seal

and number (compared with, for example, the type specimen of *Pycnophyllum filiforme* available in JSTOR Plants (Weberbauer 6885, MOL-00000494, photo!). The fragmentary material is sterile, thus allowing limited comparison with Mushler's description and therefore it is impossible to assert that it is indeed a *P. peruvianum* specimen.

Pycnophyllum pilgerianum Muschl., Bot. Jahrb. Syst. 45: 454 (1911) – TYPE: **BOLIVIA**. Puna de Patanca, 3700 m, 8 Jan 1904, Fiebrig 2617 (HOLOTYPE: B†); LECTOTYPE, designated here: US!; ISOLECTOTYPES: BM!, G! [photo], LD!, Z! (2 sets) ≡ *Frankenia triandra* J. Rémy. See Whalen, 1987.

Pycnophyllum stuebelii Mattf., Feddes Rept. Spec. Nov. Regni Veg. 18: 171 (1922). TYPE: **BOLIVIA**. Puna de Sicasica, ca. 5000 m, 2 Nov 1876, Stübel 68 (HOLOTYPE: B†).

Pycnophyllum stuebelii is a most enigmatic taxon. Mattfeld commented that this species presented similarities with *Pycnophyllum lechlerianum* (here *P. tetrastichum*). Based on the leaf and bract sizes it would fit near Mattfeld's *P. glomeratum* but the lack of original material precludes confirming this.

Pycnophyllum sulcatum Griseb., Pl. Lorentz. 28, tab. 1, fig. 1 (Dec. 1874); also in Abh. Kön. Ges. Wiss. Göttingen 19: 76, tab. 1, fig. 1 (1874). TYPE: **ARGENTINA. Catamarca**: in salsi convallium alpinarum inter Laguna blanca et Nacimiento, Jan 1872, Lorentz 458 (LECTOTYPE (selected by Whalen, 1987): GOET!); ISOLECTOTYPE: CORD (photo!). ≡ *Frankenia triandra* J. Rémy. See Whalen, 1987.

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LITERATURE CITED

- Bittrich V. 1993. Caryophyllaceae. In: K. Kubitzki, J. Rohwer, V. Bittrich, eds. *The Families and Genera of Vascular Plants 2. Magnoliid, Hamamelid, and Caryophyllid Families*. Berlin: Springer-Verlag, pp. 206–236.
- Cano, A. & I. Sánchez. 2006. Caryophyllaceae endémica del Perú. *Rev. Peru. Biol.* 13: 242s–252s.
- Christenson, E.A. 1994. Significant collections of Orchidaceae conserved in herbarium Hamburgense (HBG). *Brittonia* 46: 344–354.
- Grayum, M. H., B. Hammel, and N. Zamora. 2016. *The Cutting Edge* 32(2): April. URL: <http://www.mobot.org/MOBOT/research/Edge/welcome.shtml>.
- Grisebach, A. H. R. 1854. *Systematische Bemerkungen*. Göttingen, Dieterich.

- . 1879. *Symbolae ad Floram Argentinam*. Göttingen, Dieterich.
- Harbaugh, D. T., M. Nepokroeff, R. K. Rabeler, J. McNeill, E. A. Zimmer, and W. L. Wagner.** 2010. A new lineage-based classification of the family Caryophyllaceae. *Int. J. Pl. Sci.* 171(2): 185–198.
- Hernández-Ledesma P., W. G. Berendsohn, Th. Borsch, S. von Mering, H. Akhani, S. Arias, I. Castañeda-Noa, U. Eggli, R. Eriksson, H. Flores-Olvera, S. Fuentes-Bazán, G. Kadereit, C. Klak, N. Korotkova, R. Nyffeler, G. Ocampo, H. Ochoterena, B. Oxelman, R. K. Rabeler, A. Sanchez, B. O. Schlumpberger, and P. Uotila.** 2015. A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. *Willdenowia* 45: 281–383.
- Hiepko, P.** 1987. The collections of the Botanical Museum Berlin-Dahlem (B) and their history. *Englera* 7: 219–252
- Kraenzlin, F.W.L.** 1905. *Orchidaceae novae Austro-americanae plerumque Peruanae*. *Repert. Spec. Nov. Regni Veg.* 1: 85–92
- MacBride, J. F.** 1937. Caryophyllaceae. *Flora of Peru*. *Publ. Field Mus. Bot.* 13(2): 578–639.
- Mattfeld, J.** 1922. Revision der Gattung *Pycnophyllum* Remy. *Feddes Repert.* 17: 167–179.
- . 1930. *Pycnophyllum leptothamnum*. *Notizbl. Bot. Gart. Berlin-Dahlem* 10: 1051–1052.
- . 1934a. *Plettkea* eine neue Gattung der Alsinoideae aus den Hochanden Perus. *Schriften Vereins Naturk. Unterweser*. N.F. VII: 1–22.
- . 1934b. Nachtrag zu den Caryophyllaceae. In: A. Engler and K. Prantl (eds.), *Die natürlichen Pflanzenfamilien*, ed. 2, 16c: 365 – 367. Leipzig: Engelmann.
- McNeill, J.** 1962. Taxonomic studies in the Alsinoideae: I. Generic and infra-generic groups. *Notes Roy. Bot. Gard. Edinburgh* 24 (2): 79–155.
- McNeill, J.; Barrie, F.R.; Buck, W.R.; Demoulin, V.; Greuter, W.; Hawksworth, D.L.; Herendeen, P.S.; Knapp, S.; Marhold, K.; Prado, J.; Prud'homme Van Reine, W.F.; Smith, G.F.; Wiersema, J.H.; Turland, N.J.** 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011*. *Regnum Vegetabile* 154. A.R.G. Gantner Verlag KG.
- Molinari, E.** 2016. Further nomenclatural changes regarding Peruvian endemics. *Polish Bot. J.* 61: 275–277.
- Muschler, R.** 1911. Caryophyllaceae andinae. *Bot. Jahrb. Syst.* 45: 441–461.
- Pax, F.** 1893. Über die Verbreitung der südamerikanischen Caryophyllaceae und die Arten der Republica Argentina. *Bot. Jahrb. Syst.* 18: 1–35.
- Philippi, R. A.** 1892. Plantas nuevas chilenas. *Anales Univ. Chile* 81: 761–775.
- Rémy, J.** 1846. *Anaclea Boliviana*. *Ann. Sci. Nat., Bot. sér. 3, 6:* 345–357
- . 1847. *Anaclea Boliviana*. *Ann. Sci. Nat., Bot. sér. 3, 8:* 224–239.
- Rohrbach, P.** 1870. Beiträge zur Systematik der Caryophyllinen. I. Über die Gattung *Pycnophyllum*. *Linnaea* 36: 651–664.
- . 1872. Beiträge zur Systematik der Caryophyllinen. III. *Linnaea* 37: 183–312.
- Schweinfurth, C.** 1960. Orchids of Peru. *Fieldiana Bot.* 30: 533–786.
- Skottsberg, C.** 1916. Die Vegetationsverhältnisse längs der Cordillera de los Andes S. von 41° S. *Br. Kungl. Svenska Vetenskapsakad. Handl.* 56: 1–366
- Smith, D. N.** 1988. *Flora and vegetation of the Huascarán National Park, Ancash, Peru, with preliminary taxonomic studies for a manual of the flora*. Ph.D. Dissertation. Iowa State University. Ames, Iowa.
- Stafleu, F.A. and R. S. Cowan.** 1981. *Taxonomic Literature. A Selective Guide to Botanical Publications and Collections with Dates, Commentaries, and Types*, ed 2, vol. 3. Dr. W. Junk, The Hague.
- . 1983: *Taxonomic Literature. A Selective Guide to Botanical Publications and Collections with Dates, Commentaries, and Types*, ed 2, vol. 4. Dr. W. Junk, Publishers, The Hague.
- Stearn, W. T.** 1973. An introduction to K. B. Presl's *Reliquiae Haenkeanae* (1825- 1835). In: K. B. Presl's *Reliquiae Haenkeanae seu descriptiones et icones plantarum, quas in America meridionali et boreali, in insulis Philippinis et Marianis collegit Thaddaeus Haenke*. Reprint Edition. A. Asher. Amsterdam.
- Thiers, B.** [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>
- Timaná, M. E.** 2005. *Systematic Studies in Pycnophyllum and Pycnophyllopsis (Caryophyllaceae) of the High Andes*. Ph.D. Dissertation. Austin: The University of Texas, School of Biological Sciences.
- Velarde, O.** 1969. Catálogo de isotipos de la colección de plantas peruanas de A. Weberbauer que se conserva en el herbario de la Universidad Nacional Agraria del Perú. *Raymondiana* 2: 115–147.
- Whalen, M. A.** 1987. Systematics of *Frankenia* (Frankeniaceae) in North and South America. *Syst. Bot. Monogr.* 17: 1–93.