PARANEPHELIUS (ASTERACEAE: LIABEAE): A CASE STUDY IN HIGH-ELEVATION HYBRIDIZATION AND TAXONOMIC INSIGHTS

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ABSTRACT

Paranephelius Poepp. (Asteraceae: Liabeae) is a genus, here comprised of three species confined to high-elevation Andean habitats from 3°–25°S latitude from northern Peru to northern Argentina. In a prior investigation, sequence data was analyzed from samples throughout the range of the genus to evaluate the morphological variation used in delineating species. This detailed sampling allowed for molecular studies at a fine geographic scale. Within *Paranephelius*, genetic divergence is low, and not adequate to fully resolve phylogenetic relationships at the species level. Two genetically and morphologically recognizable genomes were reveled in northern Peru; these correspond to *P. ovatus* Wedd. and *P. uniflorus* Poepp., respectively. Several accessions possess sequences representing putative hybrids between these two species. These putative hybrids have caused taxonomic confusion in establishing species boundaries in *Paranephelius*. The molecular analysis suggested that *P. asperifolius* (Muschl.) H. Rob. & Brettell, distributed in Bolivia and northwestern Argentina, is related to *P. ovatus*, while it most closely resembles *P. uniflorus*. Species that have changed status include, *P. ferreyrae* H. Rob., here within the parameters of *P. uniflorus*; and *P. jelskii* (Hieron.) H. Rob. & Brettell, *P. bullatus* A. Gray ex Wedd., and *P. wurdackii* H. Rob. are here within parameters of *P. ovatus*. This study is not intended to be a monograph, but does includes a key to species, descriptions, illustrations, and citation of specimens examined.

RESUMEN

Paranephelius Poepp. (Asteraceae: Liabeae) es un género, aquí compuesto por tres especies confinadas a hábitats andinos de gran altitud desde la latitud 3°–25° S desde el norte de Perú hasta el norte de Argentina. En una investigación previa, se analizaron los datos de la secuencia de muestras en todo el rango del género para evaluar la variación morfológica utilizada para delimitar las especies. Este muestreo detallado permitió estudios moleculares a una fina escala geográfica. Dentro de *Paranephelius*, la divergencia genética es baja y no es adecuada para resolver completamente las relaciones filogenéticas a nivel de especie. Dos genomas genéticamente y morfológicamente reconocibles se detectaron en el norte de Perú; estos corresponden a *P. ovatus* Wedd. y *P. uniflorus* Poepp., respectivamente. Varias accesiones poseen secuencias que representan supuestos híbridos entre estas dos especies. Estos híbridos putativos han causado confusión taxonómica al establecer los límites de las especies en *Paranephelius*. El análisis molecular sugirió que *P. asperifolius* (Muschl.) H. Rob. & Brettell, distribuido en Bolivia y el noroeste de Argentina, está estrechamente relacionado con *P. ovatus*, mientras que se parece mucho a *P. uniflorus*. Las especies que han cambiado de estado incluyen, *P. ferreyrae* H. Rob., aquí está dentro de los parámetros de *P. uniflorus*; y *P. jelskii* (Hieron.) H. Rob. & Brettell, *P. bullatus* A. Gray ex Wedd. y *P. wurdackii* H. Rob. aquí está dentro de los parámetros de *P. ovatus*. Este estudio no pretende ser una monografía, pero incluye una clave para las especies, descripciones, ilustraciones y citas de los especímenes examinados.

Key Words: Andean Cordillera, Asteraceae, hybridization, Liabeae, Argentina, Bolivia, Peru

INTRODUCTION

Diversity in the Asteraceae is especially rich within the Andean Cordillera of South America, and many genera are restricted to high-elevation habitats, e.g., *páramo*, *jalca*, and *puna* (Dillon 2005). Several tribes have genera that have radiated into these specialized habitats, e.g., *Oritrophium* (Kunth) Cuatrec. and *Plagiocheilus* Am. ex DC. (both Astereae); *Jalcophila* M.O. Dillon & Sagást., *Loricaria* Wedd., and *Mniodes* (A. Gray) A. Gray ex Benth. & Hook.f. (all Gnaphalieae), *Aphanactis* Wedd. (Heliantheae); *Perezia* Lag. (Nassauvieae); *Hypochaeris* L. (Cichorieae); and *Werneria* Kunth and *Xenophyllum* V.A. Funk (both Senecioneae). The Liabeae, with 18

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genera and ca. 175 species, is the only tribe with an entirely neotropical distribution and northern Peru is a center of both generic and species diversity (Robinson 1983; Funk et al. 1996, 2007; Dillon et al. 2009; Funk et al. 2012).

Paranephelius is one of the most easily recognizable genera in the high-elevation, alpine communities of the central Andean Cordillera (2500–4500 m). Other acaulescent genera that might be confused include, *Senecio* L. and *Werneria* Kunth (both Senecioneae) and readily recognized by their uniseriate, valvate phyllaries, equal in size and shape, and disc corollas with short, glabrous lobes. *Hypochaeris* L. is another genus that superficially resembles *Paranephelius*, but is recognized by possessing all ligulate corollas and plumose pappus bristles (Dillon 2005). While the recognition of the genus is easy, the recognition of species and assigning species epithets are notoriously difficult (Robinson & Brettell 1974; Robinson 1977). Authors have used a combination of characters, e.g., leaf blade shape and margins and phyllary morphology, to diagnose species; however, the variation found within a population is often so considerable that it defies recognition of species boundaries and application of names. Within the Liabeae, *Paranephelius* has been considered to contain up to seven species, i.e., *P. asperifolius* (Muschl.) H. Rob. & Brettell, *P. bullatus* A. Gray ex Wedd., *P. ferreyrae* H. Rob., *P. jelskii* Hieron., *P. ovatus* Wedd., *P. uniflorus* Poepp., and *P. wurdackii* H. Rob., occupying habitats between 3000–4000 m, from Peru through Bolivia and into northwestern Argentina (Robinson & Brettell 1974; The Plant List 2020; Tropicos.org 2020). While species are recorded from as low as 2200 m, *Paranephelius* is most diverse above 3000 m and can reach 4600 m. Typically, species are recorded from alpine sites, ranging from wet *jalca* or *páramo* formations in the northern Peru to the drier puna of central and southern Peru and Bolivia; *P. asperifolius*, is known only recorded from Bolivia and northwestern Argentina.

MATERIALS AND METHODS

The taxonomic assumptions utilized in the current treatment were initially explored in Soejima et al. (2008), that included 45 accessions of *Paranephelius* were derived from field collections in silica gel and sampling herbarium collections. Herbaria were personally visited, or collection images were accessed via JSTOR–Plants (2021) or other institutional sites displaying images: CPUN, E, F, G, HSP, HUT, K, MO, NY, P, WU, and US. Herbarium acronyms follow Index Herbariorum (2016). Author names are abbreviated according to IPNI (International Plant Names Index, http://www.ipni.org). Herbarium accession numbers, when available, have a hyphen (-) between the acronym and the accession numbers (e.g., F-1548672); barcodes are identified as such with no space between the herbarium acronym and the number (e.g., US02163505). J. Francis Macbride, a Field Museum curator, photographed type specimens in European herbaria prior to WWII [http://fieldmuseum.org/explore/our-collections/berlin-negatives], including those at B, since destroyed. These photographs are cited here with a F negative number (F neg. #). A searchable database with images is available at: [https://collections-botany.fieldmuseum.org], last accessioned, 27 June 2021.

Vouchers used in the molecular studies (Soejima et al. 2008) are identified with an asterisk (*) within "Specimens examined" under each species and the recognized hybrids. Populations of *Paranephelius* were sampled intensively in the Peruvian Departments of Amazonas, Cajamarca, and La Libertad, including the type localities of *P. ferreyrae, P. jelskii*, and *P. wurdackii*. Through non-destructive sampling, the herbarium collection of *P. wurdackii* was included in the molecular study. The sampling regime further included populations along altitudinal gradients, and in areas of secondary sympatry where morphological variability was evident. Over 200 herbarium collections were examined and annotated.

The greatest number of named species in *Paranephelius* is to be found in the northern Peru Departments of Cajamarca and adjacent Amazonas and La Libertad. Localities were sampled in Department Cajamarca, including type locality for *P. ferreyrae* H. Rob. near Cumbemayo, and the type locality for *P. jelskii* near Cutervo. Sampling was conducted in the area of the type of *P. wurdackii* described from the Calla-Calla region in western Department of Amazonas. The type localities for *P. uniflorus* and *P. ovatus* are from central Peru, and the type locality of *P. bullatus* is within the Department of Junín in an area where José Antonio Pavón, the putative collector of the type, is known to have explored in the late 1780s. Although the species boundaries

within *Paranephelius* are still ill-defined, our sampling covered the range of described species and morphological variation within the genus, including *P. asperifolius*, *P. bullatus*, *P. ferreyrae*, *P. jelskii*, *P. ovatus*, *P. uniflorus*, and *P. wurdackii* (Robinson 1983).

RESULTS AND DISCUSSION

In Soejima et al. (2008), the phylogenetic analysis of *trnLF* and ITS sequences diagnosed the subtribe Paranepheliinae H. Rob. and revealed *Paranephelius* and *Pseudonoseris* H. Rob. & Brettell as comprising a monophyletic clade endemic to the central Andean Cordillera. The results of Funk et al. (2012) expanded the diagnoses of the Paranepheliineae to also include *Microliabum* Cabrera, *Stephanbeckia* H. Rob. & V.A. Funk, *Chionopappus* Benth., *Philoglossa* DC., and *Erato* DC. The genetic diversity in *Paranephelius* (1.7%) was low and less than half of that estimated in *Espeletia* Mutis ex Bonpl. complex (3.9%), a genus endemic to páramos of the northern Andean Cordillera suggesting recent radiation and speciation (Soejima et al. 2008).

The analysis diagnosed genetically differentiated genomes by informative ITS sequences site changes in *Paranephelius*. The two genomes, designated "A" and "B," corresponded to two highly variable and polymorphic species here recognized as, *P. ovatus* (i.e., genome B) and *P. uniflorus* (i.e., genome A). Further, the molecular analysis suggested that *P. asperifolius*, distributed from Bolivia and northwestern Argentina, was diagnosed as sharing the same site changes within the *P. ovatus* genome.

The other named species were evaluated considering their genetic variation, and assigned to either the *Paranephelius ovatus* complex, including *P. bullatus*, *P. jelskii*, and *P. wurdackii*, or similarly, *P. ferreyrae* was associated with *P. uniflorus* complex (Fig. 1). Geographically, *P. ovatus* and *P. uniflorus* exhibit sympatric distributions in Departments of Amazonas, Cajamarca, and La Libertad where the hybrids were recorded (Fig. 1). The occurrence of fasciculate roots with storage organs can be documented in all recognized taxa (Fig. 2). While phyllary shape and pubescence has been used to differentiate species, we found involucres to be variable and often unreliable for differentiation of *P. ovatus* and *P. uniflorus* (Fig. 3).

The leaf characters such as blade shape, the texture of the adaxial leaf surfaces, pubescence density, and the shape of phyllaries have been utilized in classifying *Paranephelius* (Robinson 1977). The accessions *P. ovatus* are variable, but the leaves are predominately ovate, with varying degrees of denticulations and the adaxial surfaces can vary from smooth to strongly bullate. Scanning electron micrographs (SEM) of upper leaf surfaces of *P. ovatus* illustrate the variation between smooth and hairless surfaces (Soejima et al. 2008, Fig. 3A) and strongly bullate and hairless surface (loc. cit., Fig. 3B). The accessions of *P. uniflorus* have strongly pinnately lobed leaves and bullate adaxial surfaces with varying densities of tomentose pubescence (loc. cit., Fig. 3C).

Species of *Paranephelius* (Robinson 1977) have been differentiated based on the combination of characters including leaf shape, adaxial leaf surface morphology, and floral characters. Leaf shape and lobing of the leaves was more uniform in *P. uniflorus*, with pinnately dentate leaves; adaxial leaf surfaces are bullate, and with or without dense pubescence. The leaves of *P. ovatus* are variable from entire ovate to dentate-lobed elliptic shape; adaxial leaf surfaces range from smooth to bullate, and glabrous to pubescent. Assigning names to herbarium material has been directed by comparison with individuals sampled in this study.

Evidence of genome mixing, and hybridization was documented by Soejima et al. (2008) at several localities in northern Peru (Fig. 1). Morphological characters could not refute the putative hybrid origin of these accessions with intermediate leaves between simple-unlobed and pinnate-lobed blades. Further, phyllary shape and pubescence was also variable. Sequences of eight accessions were interpreted as mixtures of loci specific to both *Paranephelius ovatus* and *P. uniflorus* (Soejima et al. 2008, p. 381). The accessions identified as mixtures were from an area including Department of Amazonas, Prov. Chachapoyas, *I. Sánchez V. & M.O. Dillon 8136;* Department of Cajamarca, Prov. Cajamarca, *M.O. Dillon et al. 2884* and *I. Sánchez V. et al. 12100;* Prov. Celendín, *M. Zapata C. 13;* Prov. Chota, *I. Sánchez V. 10335*; Department of La Libertad, Prov. Sánchez Carrion, *Dillon et al. 2843*; Prov. Pataz, *A. Sagástegui A. & M. Zapata C. 16384* and *M. Zapata C. 10*, *12A*.

Several localities where both *P. ovatus* and *P. uniflorus* were found occurring sympatrically in Department

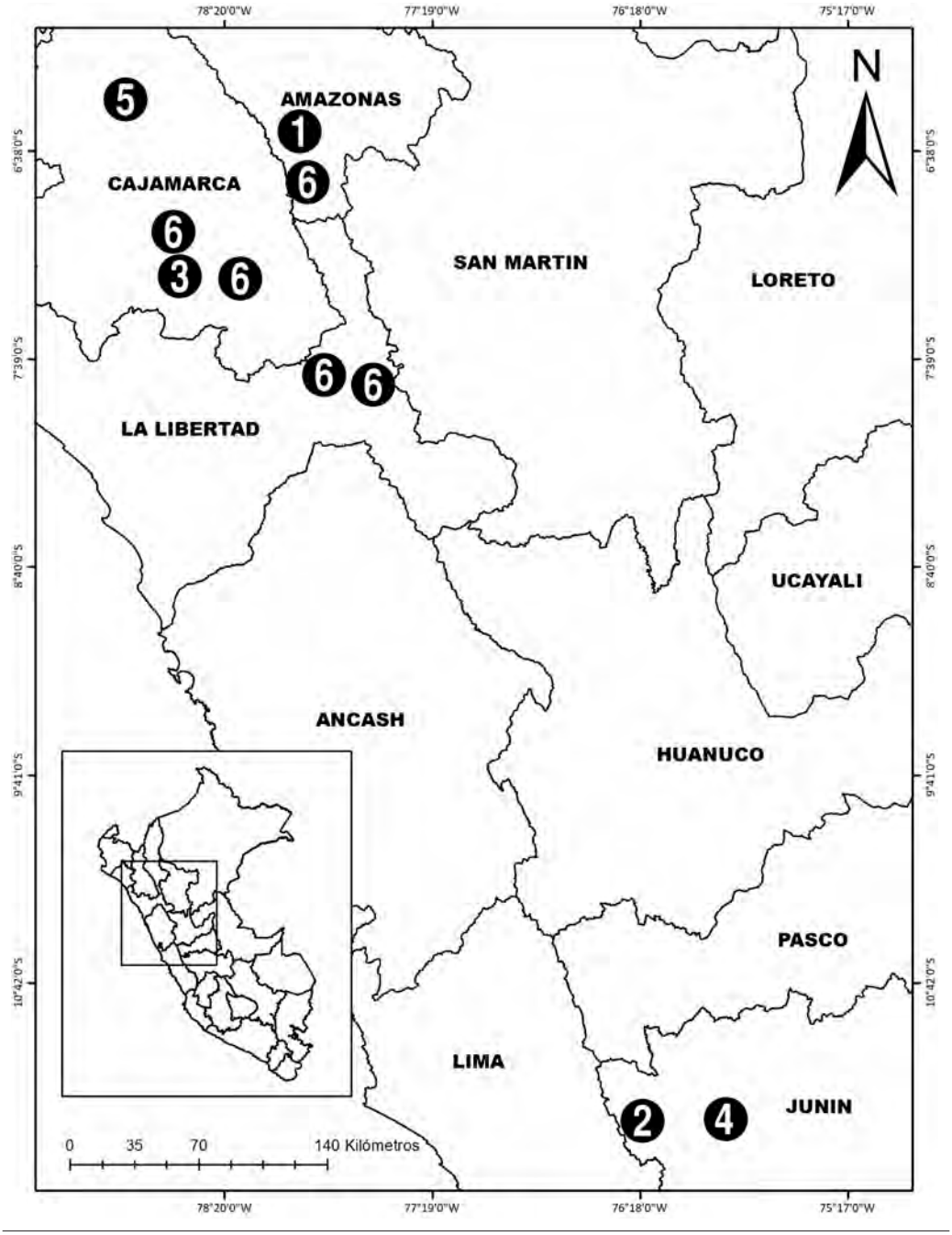

Fig. 1. Distribution map of described *Paranephelius* species. **1.** *P. wurdackii* (type locality), **2.** *P. uniflorus* (type locality), **3.** *P. ferreyrae* (type locality), **4.** *P. bullatus* (type locality), **5.** *P. jelskii* (type locality), **6.** *P. ovatus* x *P. uniflorus* (putative hybrids).

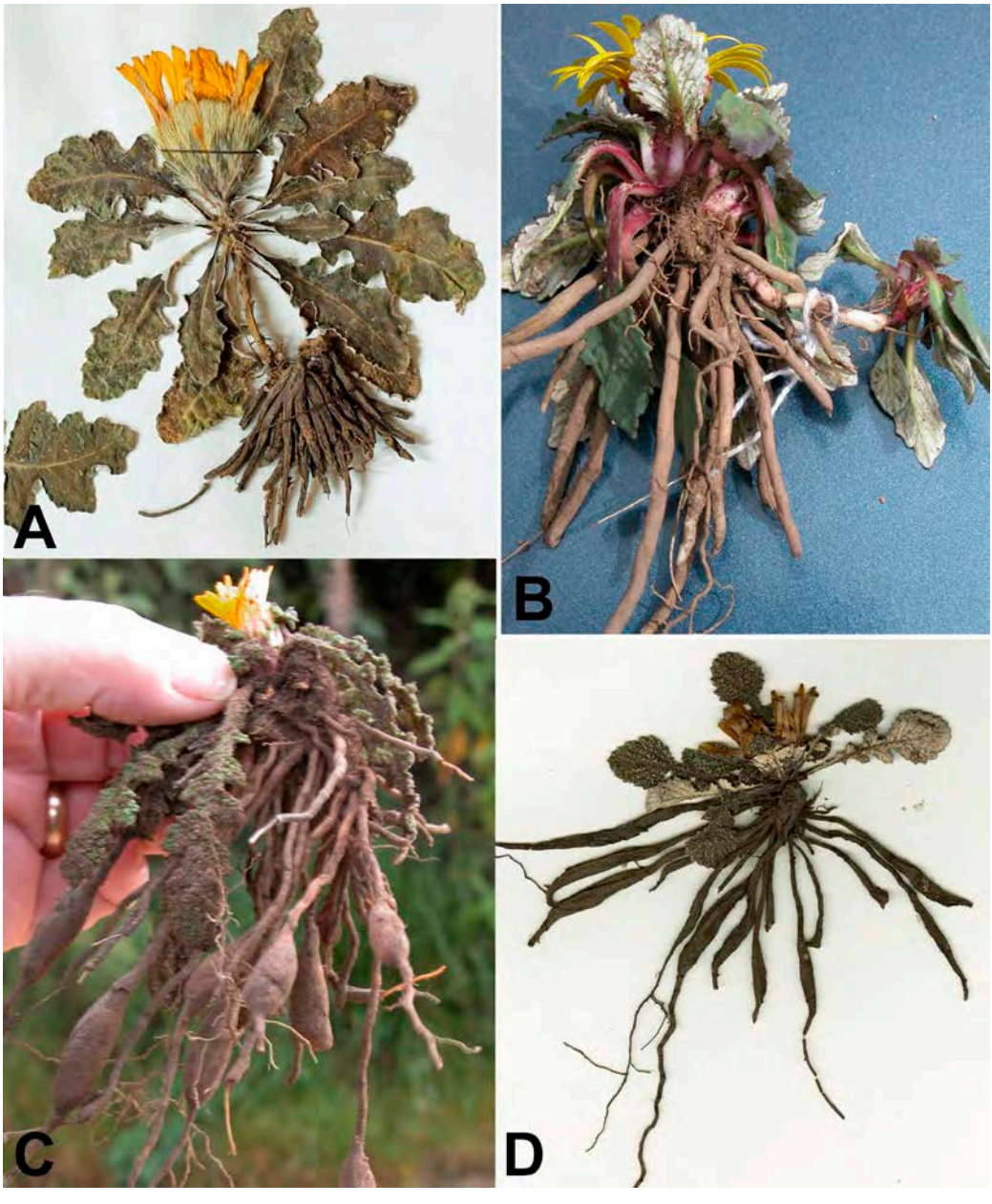

Fig. 2. *Paranephelius* with fibrous to fascicled roots. **A.** *P. asperifolius*, *Prada et al. 4249*. **B.** *P. ovatus*, *Sagástegui et al. 17573*. **C.** *P. uniflorus*, *Sagástegui et al. 17554*. **D.** Hybrid *P. ovatus* x *P. uniflorus*, *Dillon et al. 2843*.

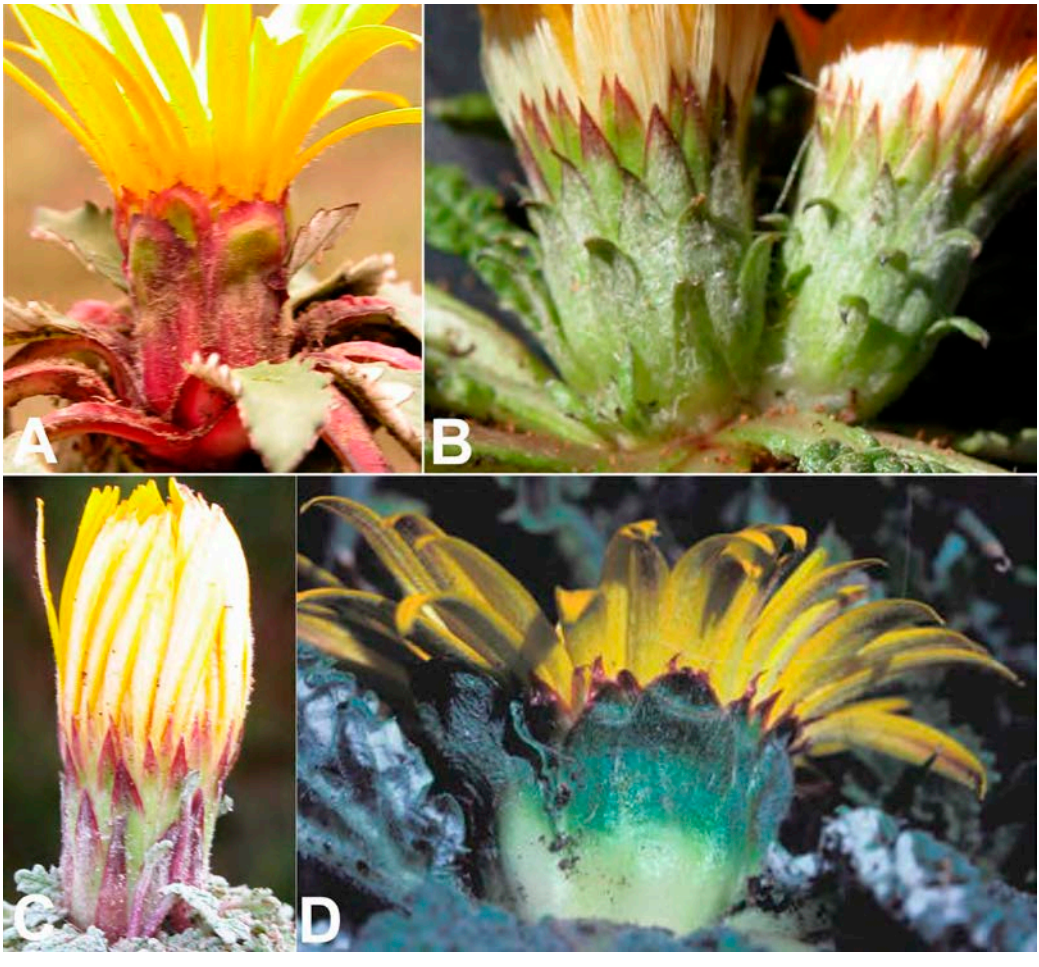

Fig. 3. *Paranephelius* involucres. **A.** *P. ovatus*, *Sagástegui et al. 17573*. **B.** *P. uniflorus*. *Sagástegui et al. 17575*. **C.** *P. uniflorus, Dillon et al. 2812*. **D.** *P. uniflorus, Dillon et al. 2811*.

of Cajamarca, such as Cumbemayo where *Zapata 02*, *Zapata 03*, and *Zapata 05,* all correspond to *P. ovatus*; and alternatively, *Zapata 01* and *Zapata 04* correspond to *P. uniflorus*. The accessions *Sánchez et al. 10335* from Department of Cajamarca, Province Chota, and *Zapata 12A* from Department of Amazonas, Province Chachapoyas, Calla-Calla, had heterozygous haplotypes that implicate mixing or putative recombination within *P. ovatus* is also occurring (Soejima et al. 2008). Pollen exchange between genetically differentiated individuals is not difficult in areas under cultivation or environmental disturbance such as road construction and mining. No putative hybridization has been documented outside of northern Peru.

We acknowledged that this treatment is presented with the backdrop of genetic and character mixing attributed to hybridization making for taxonomic uncertainty and potentially the misapplication of valid names; the current effort is but a step towards forming a better classification.

TAXONOMIC TREATMENT

Key to *Paranephelius* Species

1. Leaf blades elliptic, ovate-rhomboid, obovate, or more rarely oblanceolate with margins entire to dentate, denticulate, or weakly lacerate; phyllaries oblong, ovate or obovate, apically obtuse to rounded, commonly glabrous_____**P. ovatus** Wedd.
1. Leaf blades oblanceolate, with margins strongly dentate, incised, lacerate or laciniate, and often cut nearly to the midrib; phyllaries linear-lanceolate to more rarely with outer series oblong, apically obtuse, acute to attenuate, commonly pubescent.
   2. Leaves 60–120 mm long, 20–40 mm wide, profoundly dentate or lobed, the lobes irregularly dentate, apically acute; involucres campanulate to oval, ca. 15 mm long, 15–20 mm in diameter; phyllaries 3–4-seriate subequal, linear, attenuate, tomentose, 8–10 mm long, 3–4 mm wide_____**P. asperifolius** (Muschl.) H. Rob. & Brettell
   2. Leaves ca. 60 mm long, ca. 20 mm wide, pinnatifid, the lobes serrate, apically obtuse; involucres oblong, 17–18 mmlong, 13–15 mm in diameter; phyllaries ovate-lanceolate to linear-lanceolate, 5–9 mm long, 1–2 mm wide, puberulent _____ **P. uniflorus** Poepp.

Paranephelius Poepp., Nov. Gen. Sp. Pl. (Poepp. & Endl.) 3:42. 1843. TYPE: *P. uniflorus* Poepp., Nov. Gen. Sp. Pl. 3:42. 1843.

Liabum sect. *Paranephelius* (Poepp.) Benth. & Hook.f., Gen. Pl. [Benth. & Hook.f.] 2(1):436. 1873.

Description.—Acaulescent or short-stemmed, perennial **herbs,** milky sap present; roots fibrous, developing into swollen, fasciculate storage organs. **Leaves** rosulate, sessile or pseudo-petiolate; blades elliptic, oval-rhomboid, obovate, or oblanceolate, the abaxial surfaces tomentose, the adaxial surfaces smooth to rugose-bullate, glabrous to tomentose, the margins entire, or more frequently dentate, lobed to pinnatifid. **Capitulescences** of solitary, sessile capitula, or 2–5 from basal leaf rosettes, short-pedunculate, the pedicles 10–50 mm long. **Capitula** heterogamous, radiate; involucres campanulate, ovate or oblong, the phyllaries 3–4-seriate; ray florets pistillate, (18–)30–40, the style branches elongate, coiled, the corollas yellow, the tube pubescent, the limb ligulate, linear-oblong, apically irregularly 3-denticulate, tomentose; disc florets 20–35, hermaphroditic, the corollas tubular, 5-lobed, yellow; receptacles fimbriate. **Cypselas** ca. 10-ribbed, glabrous or pubescent; pappus 2-seriate, the outer of short, flattened bristles or scales, the inner of longer scabrid bristles. **Chromosome numbers:** $n = 9$, $n = 14$II or 15II, $n =$ ca. 29II.

Distribution & Ecology.—Confined to sites within the Andean Cordillera from northern Peru to Bolivia and northwestern Argentina; (2200–)3000–4000(–4750) m. This is a genus whose species are confined to open, and often disturbed habitats, but always at elevations considered alpine in their respective environments. These areas exist as discontinuous, humid to subhumid communities in locations across the altiplano of Peru, Bolivia, and northwestern Argentina above 2600 m elevation.

Discussion.—*Paranephelius*, as comprised here, contains three weakly defined species, a reduction from the seven species, most often recognized within the genus (Robinson 1977; Funk et al. 2012). As discussed previously (Soejima et al. 2008), the taxonomy has been complicated by documented hybridization. The development of fascicled roots that likely act as storage organs have been found in all species (Fig. 2). Phyllaries are uniform with little differentiation between outer and inner series, however, in some taxa the other series can be broad, ovate and apically obtuse (Fig. 3). Leaf characters such as overall shape, degree of lobing, and adaxial leaf surfaces are variable and labile (Fig. 4). Until more information can be gathered, the taxonomy presented here reflects the morphological and genetic complexity displayed in this handsome genus.

1. Paranephelius asperifolius (Muschl.) H. Rob. & Brettell, Phytologia 28:59. 1974. **Fig. 2A, 3A, 4–6.**

Liabum asperifolium Muschl., Bot. Jahrb. Syst., Pflanzengesch. Pflanzengeogr. 50(2–3, Beibl. 111):78. 1913. TYPE: BOLIVIA. LA PAZ: Calderillo, 22 Mar 1904, *K. Fiebrig 3538* (LECTOTYPE: designated by Bernardi (1960), G [G00300707]; ISOLECTOTYPES: B, destroyed; GH [GH00009732], K [K000504118], F [FM-520509, FM Neg. 18091], MO [MO-896722], US [US-1495130, US02163505]).

Description.—Acaulescent perennial **herbs,** roots fascicled. **Leaves** rosulate: blades oblanceolate, 60–120 mm long, 20–40 mm wide, basally sessile to short pseudo-petiole, apically acute to obtuse, the margins dentate or lobed, the lobes irregularly dentate, adaxial surfaces pubescent, abaxial densely albo-tomentose, the apices

Fig. 4. *Paranephelius asperifolius*. Lectotype of *Liabum asperifolium* at Herbaria Conservatoire et Jardín botaniques de la Ville de Genève (CJB) [http://www.ville-ge.ch/musinfo/bd/cjb/chg/?lang=en].

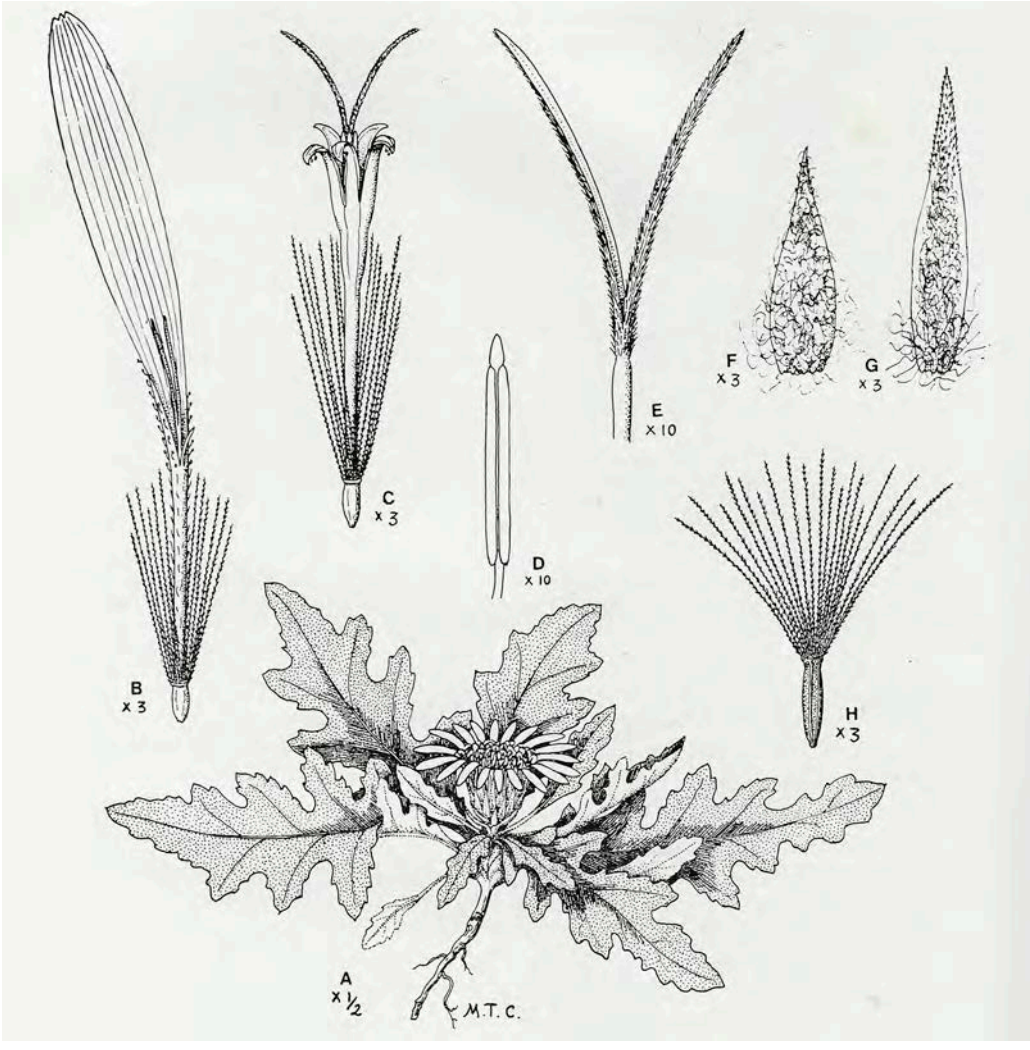

Fig. 5. *Paranephelius asperifolius*. **A.** Flowering plant. **B.** Ray floret. **C.** Disc floret. **D.** Anther. **E.** Distal portion of the style in the hermaphroditic florets. **F.** Outer phyllaries. **G.** Inner phyllaries. **H.** Cypsela of disc floret (Adapted from Cabrera 1978).

acute to obtuse. **Capitulescences** of one or rarely 2 capitula; sessile or peduncles 10–50 mm long. **Capitula** radiate; involucre campanulate to ovate, ca. 15 mm tall, 15–20 mm in diameter; phyllaries 3–4-seriate, the outer linear, apically acute, dorsally tomentose to glabrescent; ray florets, yellow, 30–40, the tube ca. 13 mm long, papillose-puberulent, the limb oblong-linear, 20–25 mm long, ca. 3 mm wide, abaxially pubescent; disc florets numerous, tubular corolla 5-lobed, ca. 15 mm long. **Cypcelas** cylindrical, ribbed, glabrous, ca. 3 mm long; pappus of numerous bristles. **Chromosome number:** unknown.

Distribution & Ecology.—Argentina: Department of Salta; Bolivia; Department of La Paz; 2600–3700 m. The habitats are open areas, with low percentages of ground cover or often completely devoid of ground cover. s. These areas exist as discontinuous, humid to subhumid communities in locations across the Andean Altiplano of Peru, Bolivia, and as far south as Salta. In Weddell's treatment of *Paranephelius uniflorus* (1857, p.

Fig. 6. Distribution map for *Paranephelius asperifolius*.

213), he cited the Peruvian material gathered by Poeppig and Bolivian collections gathered by d'Orbigny (*#1422*, P02715832) and Weddell (*#3929*, P02715831). These two collections are currently accepted under *P. uniflorus*; however, the potential for relationships with *P. asperifolius* cannot be eliminated.

Discussion.—*P. asperifolius* was described by R.C. Muschler (1913, p. 78) from material gathered by Karl Fiebrig during his expedition to Bolivia in 1904. His description compared Fiebrig's collection to *Liabum jelskii* Hieron. and mentioned differences in the lobes and dentation of the leaf blades. Angel Cabrera (1978, p 467) commented that *P. asperifolius* (as *Liabum*) could be conspecific with *P. uniflorus*, given that both had more pinnately divided leaves and narrow phyllaries. Molecular analysis (Soejima et al. 2008) does not support this hypothesis, and Bolivian accessions are not recovered with *P. uniflorus* from northern Peru.

Specimens examined: **ARGENTINA. Salta:** Dept. Santa Victoria, Los Toldos, Cuesta Cerro Bravo, *H.A. Fabris & J.V. Crisci 7394* (LP, n.v.); Mal Paso a Rodeo Pampa, *H. Sleumer 3741* (LIL, n.v.); camino de Abra de Lizoite a Santa Victoria, 3700 m, *A.L. Cabrera & R. Kiesling 25101* (LP, n.v.). Prov. Salta, **V.A. Funk 12088* (US-3362757). **BOLIVIA. La Paz:** Calderillo, 3000–3500 m, 23 Mar 1904, *K. Fiebrig 3163* (NY); La Paz, **V.A. Funk & N. Bernal H. 11314* (US-3316416), Choro, 9100 ft, 27 Jan 1950, *W.M.A. Brooke 6077* (F-1548647); Sivingani, 11,000 ft, 24 Mar 1950, *W.M.A. Brooke 6232* (F-1548672). **Santa Cruz:** Vallegrande, Cerro de Pampa Grande, 18°30'19"S, 64°07'52"W, 2613 m, 5 May 2012, *G.A. Parada, Y. Inturias, M. Betancur, H. Fernandez & M.T. Martinez 4249* (USZ, n.v., image MO).

2. Paranephelius ovatus Wedd., Chlor. Andina 1:214. 1857. Type: PERU. Puno: no exact locality, *H. Weddell 4497* (LECTOTYPE: designated by Cabrera (1971), P [P00755829]; ISOLECTOTYPE: P [P00755828]). **Figs. 2B, 3A, 7–10.**

Paranephelius bullatus A. Gray ex Wedd., Chlor. Andina 1:214. 1857. Type: PERU. Junín: no exact locality, *H. Pavón s.n.* (HOLOTYPE: P [P00755830]).

Paranephelius ovatifolius A. Gray ex Wedd., Chlor. Andina 1:214. 1857, manuscript name as synonym of *P. ovatus*.

Liabum uniflorum (Wedd.) Ball, J. Linn. Soc., Bot. 22(141):46. 1885.

Liabum ovatum (Wedd.) Britton, Bull. Torrey Bot. Club 19:263. 1892.

Liabum ovatum (Wedd.) Ball var. *hirtum* Perkins, Bot. Jahrb. Syst. 49(2):229. 1913. Type: BOLIVIA. La Paz: Palca–La Paz, 4600 m, Dec 1907, *K. Pflanz 218* (holotype: B, destroyed).

Liabum jelskii Hieron., Bot. Jahrb. Syst. 36(5):499. 1905. Type: PERU. Cajamarca: "crescit prope Cutervo," May 1879, *C. Jelski 716* (holotype: B, destroyed; FM neg. 18110).

Paranephelius jelskii (Hieron.) H. Rob. & Brettell, Phytologia 28:59. 1974.

Paranephelius wurdackii H. Rob., Phytologia 35(3):236. 1977. Type: PERU. Amazonas: Prov. Chachapoyas, open cold swamp on summit of Cerros de Calla-Calla, 3500–3750 m, 8 Jul 1962, *J.J. Wurdack 1240* (holotype: US [US-2728823, US00122782]; isotype: TEX [TEX-231019, TEX00373294]).

Description.—Acaulescent, perennial **herbs;** roots fascicled. **Leaves** rosulate; blades elliptic, oval-rhomboid, obovate, or ovate-lanceolate, 4–8 cm long, 3–4 cm wide, the bases cuneate to attenuate, the apices acute to obtuse, the margins entire to coarsely serrated or double-serrated, the adaxial surfaces glabrous to bullate, the abaxial surfaces tomentose, nerves prominent. **Capitulescences** sessile, solitary, rarely 2–3 with peduncles 10–20 mm long. **Capitula** radiate; involucres campanulate to oval, ca. 30 mm wide, ca. 3.5 mm tall; phyllaries 30–45, 3–4-seriate, subequal, the outer oblong to panduriform, 15–23 mm long, 1.5–5 mm wide, apically obtuse to acute, the inner linear or linear-lanceolate, ca. 15 mm long, 1.25–2 mm wide, glabrous to subtomentose; ray florets ca. 35, the tube 13–20 mm long, the limb ca. 40–50 mm long, 3–4 mm wide, glandular hirsute; style ca. 2.25 mm long, the branches ca. 5 mm long; disc florets ca. 35; yellow corolla, 17–20 mm long, the tube ca. 15 mm long, the lobes 2–3 mm long; anther filaments ca. 0–8 mm long; theca ca. 3 mm, apical appendage 0.4–0.5 mm long. **Cypcelas** immature, 2–3 mm long, sparsely hairy; capillary bristles 65–80, 15–20 mm long. **Chromosome number:** $n = 9$ II (Turner et al. 1967, as *P. bullatus*); $n = 14$II or 15II (Robinson et al. 1985).

Distribution & Ecology.—Bolivia: Departments of Chuquisaca, Cochabamba, and La Paz; Peru: Departments of Amazonas, Ancash, Apurimac, Arequipa, Ayacucho, Cajamarca, Cusco, Huancavelica, Huánuco, Junín, La Libertad, Lambayeque, Lima, Pasco, Puno; (2700–)3500–4100(–4600) m.

Discussion.—*Paranephelius ovatus* was described by Hugo Weddell (1855, p. 214) after examining herbarium material at Paris that had been annotated by Asa Gray "*Paranephelius ovatifolius* Asa Gray, mscr. in Herb. Mus. par., et Bot. Amer. Exped, ined." He listed Peru as the habitat and Cordillera of the Departments of Cusco, Lima and Puno, and collections including Dombey, Pavón, Gay, and Weddell. Two of Weddell's collections in Paris were designated by Angel Cabrera as lectotype (P00755829) and isolectotype (P00755828)

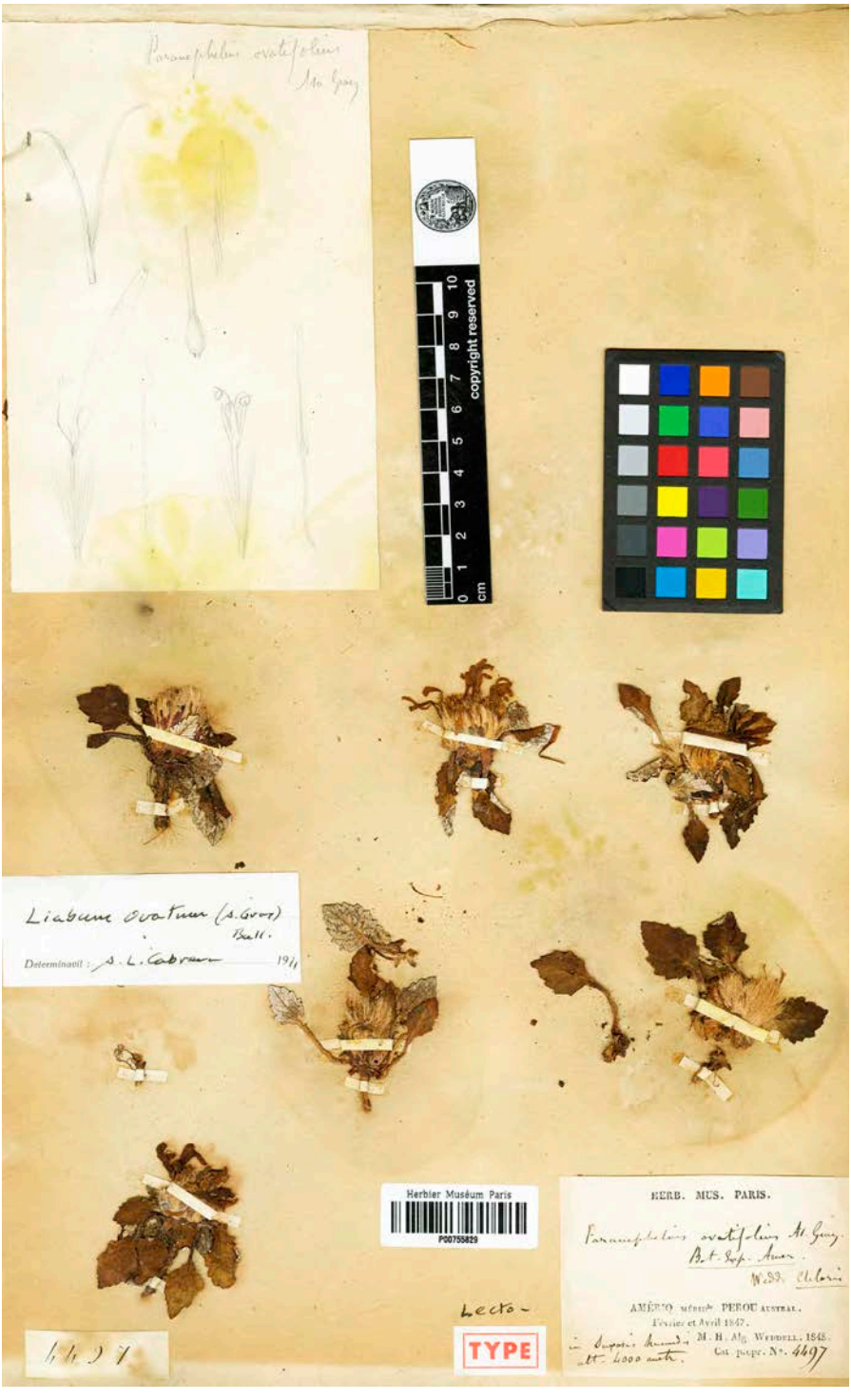

Fig. 7. *Paranephelius ovatus*. Lectotype at Muséum national d'Histoire naturelle, Paris, France. [http://coldb.mnhn.fr/catalognumber/mnhn/p/p00755829].

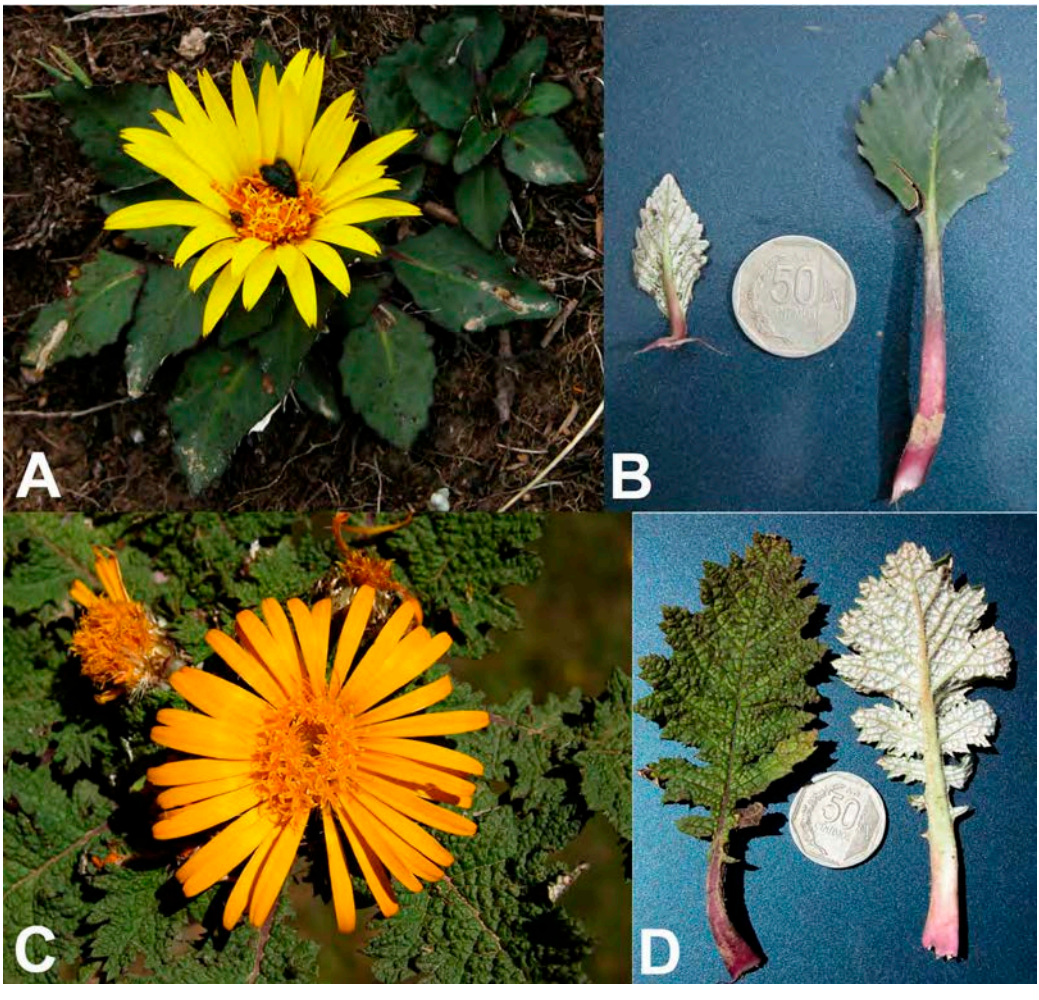

Fig. 8. *Paranephelius ovatus*. **A.** Flowering plant (*Sagástegui et al. 17573*). **B.** Leaves, abaxial and adaxial surfaces (*Sagástegui et al. 17573*). **C.** Flowering plant (*Sagástegui et al. 17572*). **D.** Leaves, adaxial and abaxial surfaces (*Sagástegui et al. 17572*).

under *Paranephelius ovatus*. The geographic origins of Weddell's collections are not completely clear; however, an examination of other collections from that number series suggests that Weddell was in southern Peru, likely the area around Moho, Puno. Further, additional modern collections of *Paranephelius ovatus* are recorded from nearby Arapa (Prov. Azángaro) and Ayapata (Prov. Carabaya), increasing the likelihood that his gathering (*Weddell 4497*) was made in Puno. Weddell also listed a collection from near Cinti, Bolivia, *H. Weddell s.n.* (P02715831, P02715835). In addition to the protologue, Weddell provided Plate 37B in Chloris Andina with an illustration of *Paranephelius ovatus* habit and the floral parts <http://www.plantillustrations.org/illustration.php?id_illustration=36854>.

In addition to a rendering of the habit, the illustration contains details of a ray floret, disc floret, anther, base of disc floret, disc floret style apex, and pappus bristles. Identical elements of the floral details in Plate 37B appear on a small sheet affixed to *Weddell 4497*, the designated lectotype (P00755829).

Hugo Weddell (1855, p. 214) described *Paranephelius bullatus* from a collection housed in the Herbarium Pavón in Muséum national d'Histoire naturelle, Paris. That sheet (P00755830) has a handwritten note "*P.*

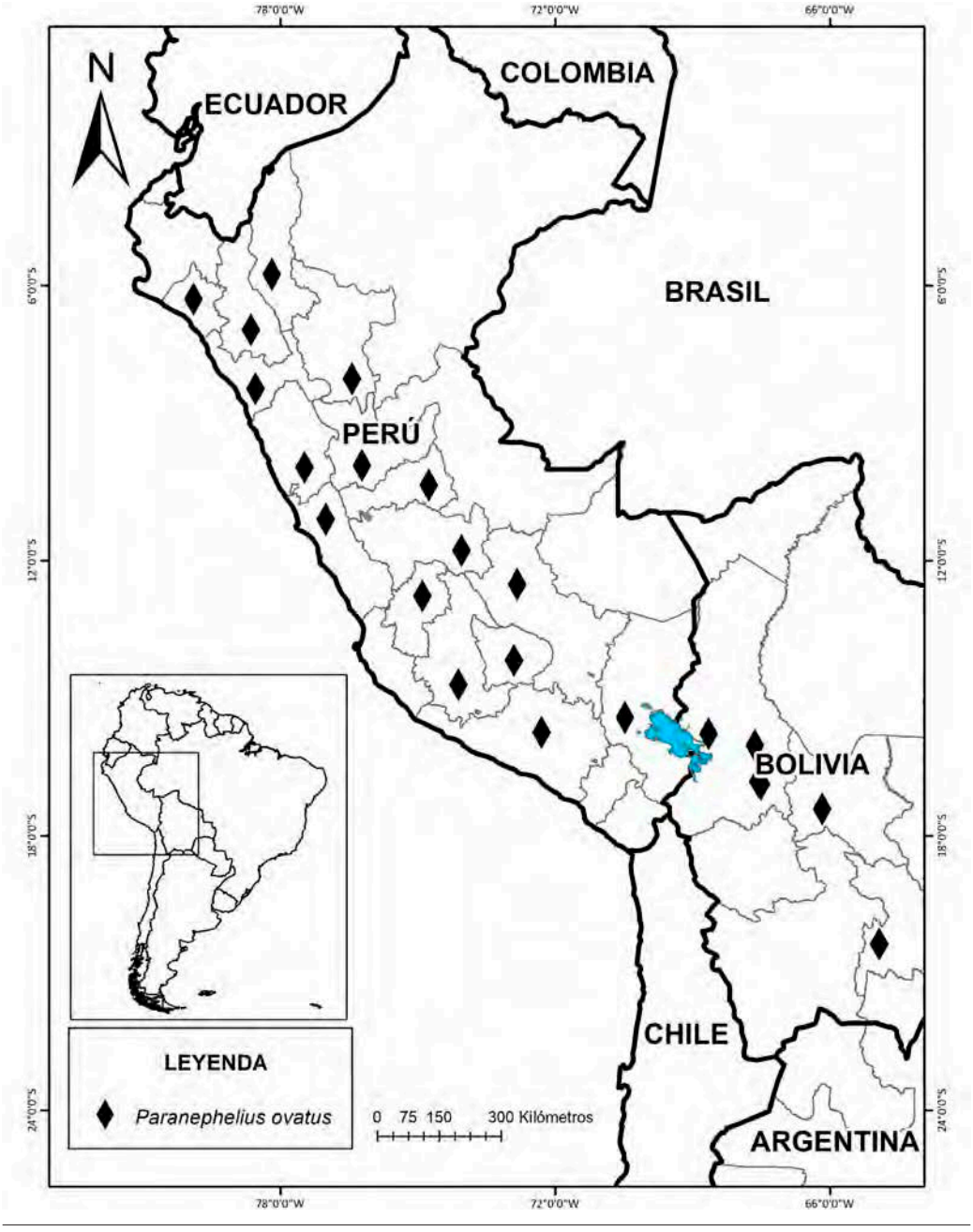

Fig. 9. Distribution map for *Paranephelius ovatus*.

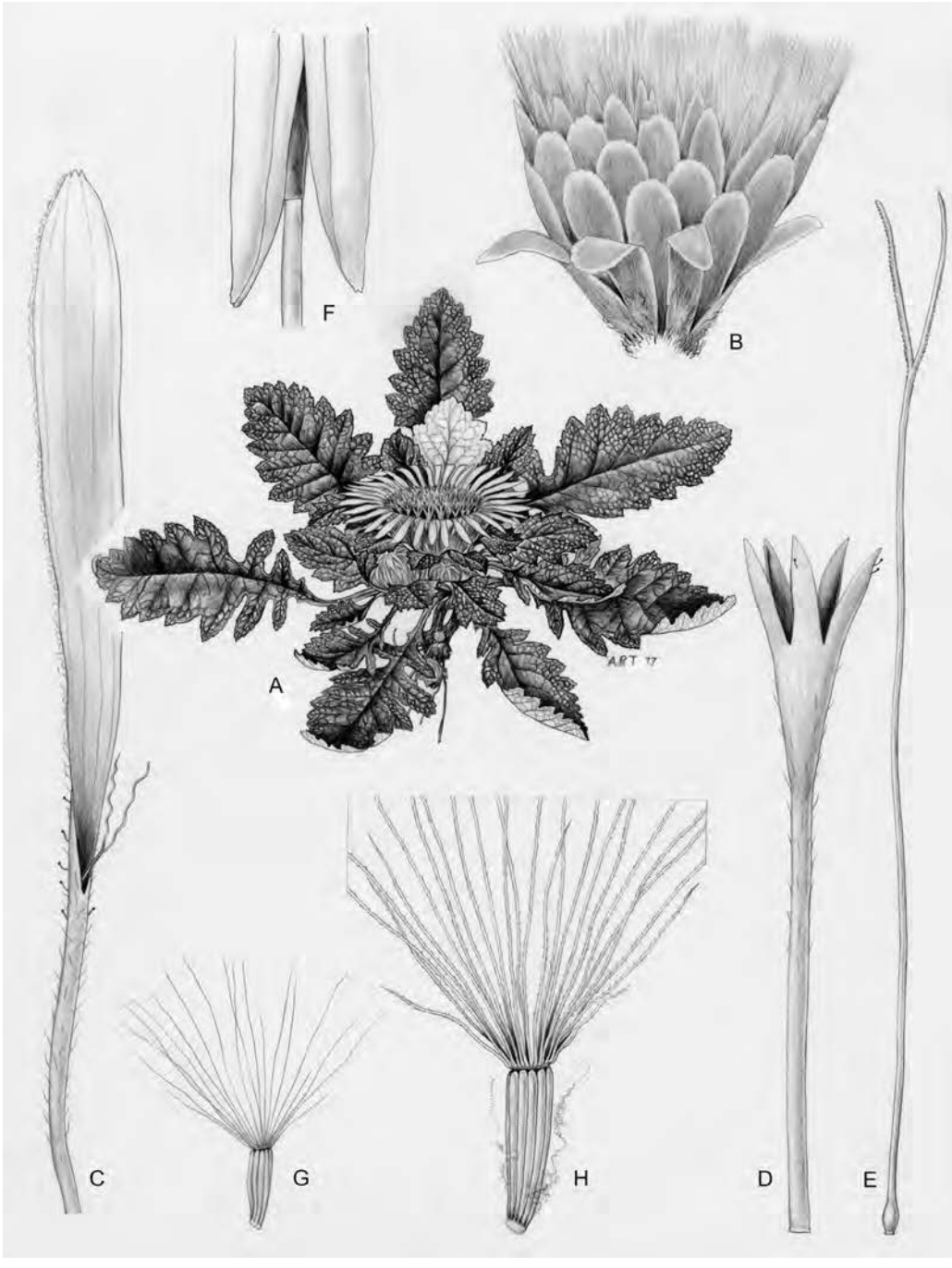

Fig. 10. *Paranephelius ovatus*. Illustration presented in Robinson (1977) as representing *P. uniflorus*. **A**. Habit, x 1/2. **B**. Capitula, x 31/2. **C**. Ray corolla, x 10. **D**. Disc corolla, X 10. **E**. Disc style, x 10. **F**. Base of anther thecae, x 50. **G**. Achene, x 21/2. **H**. Achene, x 5. (Drawing by Alice Tangerini).

bullatus, ined. A. Gray" on the Herbarium Pavón label. Another handwritten label from the Paris Museum suggests the collection was a donation by Pierre Edmond Boissier, a Swiss botanist working from Geneva. Weddell stated in his protologue, that *P. bullatus* was most like *P. ovatus*, but differed in leaf morphology and pubescence, calling attention to its ovate to elliptical leaf blades, irregular denticulate margins, adaxial leaf surfaces bullate, glabrescent, and abaxial surfaces densely tomentose. The phyllaries were described as being oblong, with obtuse apices, and outer surfaces of ligulate corollas tomentose. The type locality of *P. bullatus* is considered within the Department of Junín in an area where José Antonio Pavón, the putative collector of the type, is known to have explored in the late 1780s. After examining a large number of collections from the Departments of Junín, Lima, and Pasco, the variation suggested in the diagnosis is within the parameters of *P. ovatus*. Collections assigned to *P. bullatus* from Huánuco (Mito, *J.F. Macbride & W. Featherstone 1656*; 15 mi SE of Huánuco, *J.F. Macbride & W. Featherstone 2131*) have simple leaf blades.

Georg Hieronymus (1905, p. 499) described *Paranephelius jelskii* from a collection housed in Berlin-Dahlem Herbarium by Constantin von Jelski (*#716*) gathered from Cutervo, Department of Cajamarca. Regrettably, that collection was destroyed in WWII and the only remnant of that collection is the F neg. 18110 taken by J.F. MacBride prior to the war. In the protologue, Hieronymus compared his new species to *P. ovatus* and *P. bullatus*, based upon leaf and floral morphology. After examining a large number of collections from the Department of Cajamarca, including the Cutervo region, the variation suggested in the diagnosis is within the parameters of *P. ovatus*. There is a distinctive cluster of short-stalked glands near the tips of the disc corolla lobes of specimens *P. jelskii*. There are a few long-stalked glands on the lobes of most specimens of *P. uniflorus* and *P. ovatus*.

Harold Robinson (1977, p 236) described *Paranephelius wurdackii* from a collection by J.J. Wurdack (*#1240*) gathered from the Calla-Calla region of Department of Amazonas. Robinson suggested that while most of the *Paranephelius* gathered by Wurdack had been identified as *P. ovatus* (as *P. jelskii*). He was able to distinguish *P. wurdackii* based largely upon distinct lobing of the basal part of the leaf lamina, differences in pubescence on abaxial surfaces, phyllary characters, and absence of glands on the tips of the disc corolla lobes. *Paranephelius wurdackii* was diagnosed with large capitula, involucres covered with dense tomentum, and the lobes of the disc corollas more pointed than in other species. In the analysis conducted by Soejima et al. (2008), leaf material of *Wurdack 1240* (US-2728823) was included in the experiment and DNA was successfully extracted and placed in the analysis. The accession was found to have ITS sequences corresponding to *P. ovatus* (i.e., "Genome B"). Interestingly, another accession from the Calla-Calla region, *Sánchez & Sánchez 11045*, has been determined as *P. uniflorus* on morphological criterion. Yet another from the Calla-Calla region, *Sánchez & Dillon 8136,* was included in the Soejima et al. (2008) analysis and found to have mixed genomes associated with interspecific hybridization.

Specimens examined. **BOLIVIA. Chuquisaca:** Prov. Cinti, *H. Weddell s.n.* (P02715831, P02715835). **Cochabamba:** Challa, 2 Feb 1978, 13,000 ft, *R.M. King & L.E. Bishop 7540* (MO-2615815); Viloco, 14,800 ft, 21 Mar 1949, *W.M.A. Brooke 5355* (F-1548695); Choro, above Rio Cocapata. 100 mi NW of Cochabamba, 13,000 ft, 3 Feb 1950, *W.M.A. Brooke 6103* (F-1548645, NY). **La Paz:** La Paz, 4100 m, Mar 1910, *O. Buchtien 79* (F-295409, NY); Cochabamba, 12,000 ft, 28 Mar 1922, *M. Cardenas 35* (NY); Sorata, 2900–3800 m, Apr 1857, *G. Mandon 239* (F-931024, MO-1991446, NY, 2-sheets); Bolivia, *A.M. Bang 1832* (NY). Prov. Arai, 9.5 km SE of Rodeo, 2.5 km W on road to ENTEL antenna, 3875 m, 26 Mar 1984, *G. & D. Schmitt 70* (F-1972603). **La Paz:** Yungas, 4000 m, 3 Mar 1983, *J.C. Solomon 9635* (MO-1963344); Sorata, Feb 1886, 13,000 ft, *H.H. Rusby 1633* (US-50709, MO-2767045, NY, 2 sheets); Bolivian Plateau, 1891, *A.M. Bang 1045* (F-163631, MO-2759539); Pongo, 12,000 ft, Feb 17–1 Mar 1926, *G.H.H. Tate 252* (NY); Viloco, ca. 100 mi from Oruro, near Araca, 14,800 ft, 21 Mar 1949, *W.M.A. Brooke 5355* (NY); La Paz. Prov. Murillo, ca. 13 km below dam at Lago Zongo, 3900 m, 6 Feb 1995, *E. Emshwiller 432* (F-2186036). **No exact locality:** *A.M. Bang 1842* (MO-2759538). **PERU. Amazonas:** Prov. Chachapoyas, Cerros de Calla-Calla, 3500-3750 m, 8 Jul 1962, **J.J. Wurdack 1240* (US-2728823). **Ancash:** Prov. Bolognesi, Huancar arriba de Chiquian, 3800 m, 15 Apr 1949, *E. Cerrate 211* (MO-2623344). Dist. Aquia, Tallenga, 3600 m, 17 May 1950, *E. Cerrate 696* (MO-2623345). Dist. Chiquian, Pariarrackra, Pampa de Lampas, 4160 m, 7 May 1952, *E. Cerrate 1451* (MO-2623346). Prov. Carhuas, 14 Mar 1964, Cordillera Blanca, above Vicos at Queque Pampa, 3450 m, *P.C. Hutchison & J.K. Wright 4406* (F-1639469, MO-1831458, NY). Prov. Huaraz, ca. 35 km W of Huaraz, 4150 m, 29 Jan 1983, *M. Dillon, U. Molau & P. Matekaitis 3157* (F-1933373). Prov. Huaraz, ca. 35 km W of Huaraz, 4150 m, 29 Jan 1983, *M. Dillon, U. Molau & P. Matekaitis 3160* (F-1933370). Prov. Huari, 14.8 km NE of Tunel Cahuish, between Catac and Chavin de Huantar, 3000–4000 m, 31 Dec 1982, *W.D. Stevens 21967* (MO-3424419). Prov. Yungay. ca. 25 km NE of Yungay, 3380 m, 28 Jan 1983, *M. Dillon, U. Molau & P. Matekaitis 3134* (F-1918457). Prov. Yungay, Quebrada de Llanganuco, ca. 25 km above Yungay, 4100 m, 9°05'S, 77°35'W, 8 Apr 1986, *M.O. Dillon, D. Dillon, P. Alcorn & L.*

Schnorr 4484 (F-2118725). Huascarán National Park, Quebrada Shallap, 3690–4100 m, 9°29'S, 77°22'W, 20 Feb 1985, *D.N. Smith, R. Valencia, A. Gonzales 9661* (F-1963546, MO-1964458); Huascarán National Park, Río Pachacoto, Pumashimi, 4200–4300 m, 9°53'S, 77°17'W, 16 Mar 1986, *D.N. Smith & M. Torres 11781* (F-1974738, MO-1537408, MO-1964459); Huascarán National Park, Quebrada Queshque, 4500–4600 m, 9°50'S, 77°18'W, 18 Mar 1986, *D.N. Smith, R. Valencia & M. Torres 11840* (F-1974740, MO-1964456); Huascarán National Park, Quebrada Llaca, 4500 m, 9°27'S, 77°27'W, 5 Jan 1985, *D.N. Smith, K. Goodwin & A. Gonzalez 8999* (MO-3338837); Huascarán National Park, Quebrada Ishinca, 4380–4500 m, 9°23'S, 77°25'W, 12 Feb 1985, *D.N. Smith, R. Valencia & A. Gonzales 9510* (F-1963545); Huascarán National Park, 4200–4370 m, 9°29'S, 77°15'W, 6 May 1986, *D.N. Smith, R. Valencia A. Gonzales & M. Buddensiek 12219* (MO-1963333, MO-1965154); Huascarán National Park, 4350 m, 9°41'S, 77°14'W, 30 Mar 1985, *D.N. Smith & F. Escalona 10149* (MO-1963341); Huascarán National Park, 3950–4500 m, 8°56'S, 77°33'W, 13 Jan 1985, *D.N. Smith, L. Sánchez & H. Vidaurre 9204* (MO-1963339); Huascarán National Park, Quebrada Ranincuray, 3900–4100 m, 9°00'S, 77°33'W, 17 Apr 1985, *D.N. Smith, R. Valencia & A. Gonzales 10395* (F-1961090, MO-1963338); Huascarán National Park, Quebrada Pachachaca, 3700–3860 m, 9°27'S, 77°16'W, 12 Jun 1986, *D.N. Smith, A. Gonzales & D. Maldonado 12584* (F-1974693, MO-1963332); Huascarán National Park, Quebrada Ishinca, 4370 m, 9°22'S, 77°25'W, 11 Feb 1985, *D.N. Smith, R. Valencia & A. Gonzales 9434* (F-1963582, MO-1963342); Huascarán National Park, Quebrada Parón, 3500–3760 m, 9°01'S, 77°43'W, 8 May 1985, *D.N. Smith 10611* (F-1960081, MO); Huascarán National Park, Quebrada Queshque, 4530 m, 9°50'S, 77°18'W, 19 Mar 1986, *D.N. Smith, R. Valencia & M. Torres 11873* (F-1974728, MO-1963335); Huascarán National Park, Quebrada Shallap, 3690–4100 m, 9°29'S, 77°22'W, 20 Feb 1985, *D.N. Smith, R. Valencia & A. Gonzales 9660* (F-1963583, MO-1963337); Huascarán National Park, Quebrada Alpamayo, 8°50'S, 77°42'W, 4020–4250 m, 10 Mar 1985, *D.N. Smith, R. Valencia & L. Minaya 9833* (F-1963584, MO-1963336); Huascarán National Park, 3950–4080 m, 9°44'S, 77°20'W, 5 Jul 1985, *D.N. Smith & M. Buddensiek 11060* (MO). **Apurimac:** Prov. Andahuaylas, 4000 m, 25 Feb 1939, *H.E. Stork & O.B. Horton 10732* (F-1077165). **Arequipa:** Prov. Castilla, Dist. Pampacolca, Moumento Histórico de Maucallacta, 3761 m, 15°41'10.9"S, 72°37'28.7"W, 17 Mar 2018, *V. Quipuscoa S., M. Balvin A., S. Huamani Q., M. Bedoya C. & M. Beltrán M. 7242* (HSP-011681). **Ayacucho:** Prov. Cangallo, Dist. Los Morochucos, 8.6 km SW de Condorcocho, 3300 m, 13°30'6.562"S, 74°9'11.424"W, 2 May 2014, *C Tejada P. 277* (HSP-5668). Prov. Huanta, between Huanta and Hacienda Pargora, 4150 m, 2–4 May 1929, *E.P. Killip & A.C. Smith 22190* (F-661499, NY). Prov. Sucre, Dist. Morcolla, Río Jajincura y Cuyto, 3963 m, 14°9'16.819"S, 73°46'32.323"W, 5 May 2014, *C. Tejada P. 418* (HSP-5802). **Cajamarca:** Prov. Cajamarca. Jalca de Kumulca, ca. 25 km NE of Encañada on road to Celendin, 3640 m, 17 Oct 1984, *M.O. Dillon & M. Whalen 4036* (F-2116362). Prov. Cajamarca, ca. 27 km NNW of Cajamarca on road to Hualgayoc, Pampa de Cerro Negro, 3600 m, 16 Jan 1983, *M.O. Dillon & U. Molau 3009* (F-1926774). Prov. Cajamarca, ca. 18 km S of Cajamarca, S of Abra "El Gavilán," ca. 2850 m, 23 April 1986, 7°10'S, 78°31'W, * *M.O. Dillon & D. Dillon 4600* (F-2117713). Prov. Cajamarca, 3–5 km above Baños del Inca, between Cajamarca and Encañada, ca. 2660 m, 7°11'S, 78°23'W, 25 Apr 1993, * *M.O. Dillon, I. Sánchez V. & M. Sánchez M. 6472* (F-2127192). Prov. Cajamarca, Dist. La Encañada, el Usnio, a 3 km al E de la carretera Cajamarca – Celendín, 3120 m, 6 Apr 1982, **I. Sánchez V., V. Torrel & E. Medina 2778* (F-1923233, F-2151047); Alrededores de la Laguna de San José, 3950 m, 19 Feb 1994, *I. Sánchez V. & M. Cabanillas S. 6765* (F-2151196); Cerro Maqui–Maqui, 4050 m, 20 Mar 1994, **I. Sánchez V. & M. Cabanillas S. 6904* (F-2151035); Zona Arqueológica de Cumbemayo, al O de Cajamarca, 7°11'S, 78°34'W, 3450 m, 6 Apr 2001, **I. Sánchez V. & J. Cabanillas S. 10414* (F-2230372); Centro Turistio Cumbe Mayo, 3460 m, 21 Apr 2001, ca, 7°11'S, 78°34'W, 3450 m, 21 Apr 2001, **I. Sánchez V., G. Iberico V. & M. Sánchez M. 10493* (F-2230887); La Encañada, El Pabellón, ruta Combayo – Yanacocha, 6°59'S, 78°26'W, 3800 m, 20 May 2001, *I. Sánchez V. 10583* (F-2230840). Prov. Celendín, Cumbre Cumullca, entre Cajamarca y Celendín, 3800–3850 m, 6 Aug 1958, *R. Ferreyra 13248* (MO-2623350). Jalca de Kumulca, 17 Aug 1984, 3350 m, *A. Sagástegui A., J. Mostacero & S. Leiva 12046* (F-1959965). Prov. Chota, Miracosta, alrededor de la Laguna Clara, 6°23'S, 79°13'W, 12 Nov 2000, 3640 m, **I. Sánchez V., M.O. Dillon & M. Zapata C. 10335* (F-2230235); José Carlos Mariátegui, Km 20–40 on Sunchubamba–San Juan road, 3300–4000 m, 5 Jun 1984, *D.N. Smith & I. Sánchez V. 7553* (MO-1963351). Prov. Cajamarca, Dist. Jesús. Cerro Agopití, 9 May 2002, 3982 m, 7°20'34.9"S, 78°21'03.0"W, **I. Sánchez V. & M. Sánchez M. 11397* (F-2328744). Prov. Cutervo, San Andrés de Cutervo, Parque Nacional de Cutervo, 6°13'S, 78°40'W, 2680 m, 15 Mar 1989, *C. Díaz, H. Beltran & B. D'Achille 3311* (MO-3782664). Prov. Jaén, Sallique, La Cocha, 2900–3000 m, 5°40'58"S, 79°14'53"W, 17 Jun 1998, *J. Campos, C. Díaz, E. Tineo & T. Guevara 5020* (F-2250973; MO-2777744, MO-5941697); alrededores de Cumbemayo, 9 Jun 2003, 7°08.4'S, 78°33.2'W, 3480 m, **M. Zapata C. 02* (F-2246067); alrededores de Cumbemayo, 9 Jun 2003, 7°08.4'S, 78°33.2'W, 3480 m, **M. Zapata C. 03* (F-2246066); alrededores de Cumbemayo, 9 Jun 2003, 7°08.4'S, 78°33.2'W, 3480 m, * *M. Zapata C. 05* (F-2246064). **M. Zapata C. 11A* (F). **Cusco:** Sacsayhuamán, 3600 m, Mar 1929, *F.L. Herrera 2357* (F-589416); Cusco, 3600 m, Mar 1929, *F. L. Herrera 2398* (F-589477); Sacsayhuamán, above Cusco, 3500–3600 m, 24 Apr 1925, *F.W. Pennell 13583* (F-557976, NY); Huayllabamba, 2950–5200 m, 20 Aug 1988, *A. Tupayachi H. 681* (MO); Prov. Chumbivilcas, Llique, Santo Tomás, 3800 m, 19 Mar 1987, *L. Hoogte & C. Roersch 3011* (F-1994898); Luto Sector Challa-Challa, 3600 m, 18 Mar 1987, *L. Hoogte & C. Roersch 3215* (F-2010087); Prov. Cusco, Huacote, 4000 m, 16 May 1981, *L. Hoogte & C. Roersch 370* (F-2010069); Prov. Espinar, Mina Tintaya, 4000 m, 22 Mar 1986, *L. Hoogte & C. Roersch 2153* (F-1994903); Chisiccata, Yauri, 15°01'S, 71°20'W, 28 Mar 1987, 4000 m, *P. Núñez 7618* (F-2009773); Dist. Espinar, relaves de Huinipampa, 14°53'55.574"S, 71°21'54.049"W, 12 Apr 2014, 4089 m, *D. Ramos A., R. Pérez Z., P. Medina H. & M. Quispe O. 1618* (HSP-4862). **Huancavelica:** Prov. Huancavelica, 3900 m, 10 May 1939, *H.E. Stork & O.B. Horton 10844* (F-1077171). **Huánuco:** 8.8 km SSE of Huánuco, 2 km SE of Yaca, 3190 m, 16 Apr 1965, *R. Bird 1190* (MO-2718635); Mito, *J.F. Macbride & W. Featherstone 1656* (F-518152); 15 mi SE of Huánuco, *J.F. Macbride & W. Featherstone 2131* (F-518612); ca. 5 km N of Cusco on road to Pisac, 3400 m, 19 May 1977, *J.C. Solomon 2955* (MO-2627944); Pillao, 31 May 1946, *F. Woytkowski 34333* (F-1310516, MO-1645554). **Junín:** Prov. Tarma, La Oroya – Tingo Maria, Km 25.3, 3 Mar 1977, *J.D. Boeke 1077* (NY); ca. 23 km NW of La Oroya, 17 Dec 1978, *M.O. Dillon & B.L. Turner 1366* (F-1881885); Pampa de Junín, 10 km S of Junín, 4100 m, 11°12'S, 75°58'W, 9 Mar 1982, *A. Gentry, D.N. Smith & B. Leon 36130* (MO-2993562); near La Oroya, 3726–4000 m, 28 Feb 1942, *V. Grant 7520* (F-1407557); Capillacocha, 4300 m, 6 May 1948, *P. Aguilar s.n.* (MO-2623348); Llanos de Junín, 11°10'S, 76°00'W, 8 Jan 1984, 4100 m, *D.N.*

Smith, R. Foster, J. Alban & M. Chanco 5640 (MO-3430265). Paccha, cerca al lago, 4200 m, 12 Apr 1942, *E. Zuñiga s.n.* (MO-2623343); Prov. Yauli, [ca. 15,000 ft], 23 May 1922, *J.F. Macbride & W. Featherstone 893* (F-517421); near Atocsayco, ca. 4200 m, 1 Jan 1983, *D.M. Pearsall 1117* (F-1929637), 1165 (F-1929403). **La Libertad:** Prov. Bolívar, arriba de Longotea, ruta a Bolívar, 9 Nov 2001, 7°04'S, 77°49'W, 3710 m, *I. Sánchez V., M. Dillon & G. Iberico V. 11139* (F-2237455). Prov. Pataz, Piedra Grande (La Paccha – Chilia), 4000 m, 9 May 2003, 8°07.2'S, 77°25.7'W, **A. Sagástegui A., M. Zapata C., E. Rodríguez R. & V. Medina 17340* (F). **A. Sagástegui A. 17572A* (F); **A. Sagástegui A.* 17573 (F); Prov. Santiago de Chuco, arriba de Los Quinuales, al N de Quiruvilca, 3980 m, 24 Mar 1994, *P. Leiva G. & S. Leiva G. 1105* (F-2145109), 1107 (F-2142234); Laguna El Toro, 4100 m, 16 Dec 1979, *A. Sagástegui A. 9453* (F-1876058); 4000 m, 7°59.4'S, 78°16.7'W, 3 May 2003, **A. Sagástegui A., M. Zapata, E. Rodriguez & V. Medina 17177* (F-2328743). **Lambayeque:** Prov. Ferreñafe, Marayhuaca, Uyurpampa, 3450 m, 25 Aug 1993, *S. Llatas Q. 3347* (F-2177760). Laguna Tembladera – Cerro Negro, 3300 m, 12 Sep 1985, *A. Sagástegui A., D. Skillman, J. Mostacero & L. Ramírez 12821* (F-1960367). **Lima:** Prov. Canta, ca. Chiprac, 2 May 1963, *C. Acleto 737* (MO-2826592). Quinan, carretera Canta – Huaros, 3450 m, 1 May 1963, *I. Meza 122* (MO-2623349). near Antacocha, Cerro Colorado, E of Canta, 4000–4100 m, 20 Jun 1925, *F.W. Pennell 14647* (F-558620), near Antacocha, Cerro Colorado, E of Canta, 3600–3800 m, 20 Jun 1925, *F.W. Pennell 14647a* (F-558621); Ticlio, Valley Rimac, 20 Feb 1954, *W. Rauh & G. Hirsch P260* (NY). Prov. Huarochiri, Viso, 5–14 May 1922, [ca. 9000 ft], *J.F. Macbride & W. Featherstone 620* (F-517148); Casapalca, 21 May 1922, [ca. 15,500 ft], *J.F. Macbride & W. Featherstone 853* (F-517381); Prov. Yauyos, Dist. Laraos, camino Jalcacha a Palca, 3900–4100 m, 12°20'32"S, 75°43'03"W, 25 May 1995, *H. Beltrán 1691* (F-2188530). **Pasco:** Cobracancha Valley NW of Cerro de Pasco, 4200 m, 26 Apr 1942, *V. Grant 7537* (F-1407562); Cobracancha Valley, NW of Cerro de Pasco, 4200 m, 26 Apr 1942, *V. Grant 7548* (F-1407478); Río Mantar opposite Huari, between Oroya and Huancayo, 3570 m, 29 Feb 1964, *P.C. Hutchison & O. Tovar 4206* (F-1639871, MO-1831215, NY); vicinity of Oroya, 1918, *M. Kalenborn & A.S. Kalenborn 13* (NY); between Tarma and Jauja, 4500 m, 24 Apr 1929, *E.P. Killip & A.C. Smith 21961* (F-662161, NY); Huancayo, 3300–3500 m, *E.P. Killip & A.C. Smith 22120* (F-662154, NY); Huancayo, 3300–3500 m, *E.P. Killip & A.C. Smith 23350* (F-661426, NY); Huancayo, Mar 1943, *J. Soukup 1875* (MO-1591413). **Puno:** Prov. Azángaro, Azángaro, cerros alrededores de Arapa, 3950 m, 19 Feb 1948, *P. Aguilar 110* (MO-2623347). Prov. Carabaya, Ayapata, 4000 m, 26 Mar 1987, *L. Hoogte & C. Roersch 3198* (F-2001852); Ayaviri, Chuquibambilla, 3900–4000 m, 19–21 Apr 1925, *F.W. Pennell 13363* (F-557796, NY). Prov. Lampa, Dist. Lampa, Lamparaquen, 3965 m, 15°18'14"S, 70°26'28"W, 3 Feb 2014, *D. Montesinos & C. Pinto 4180* (HSP-3780).

The following taxa were identified as *P. uniflorus* but subsequently moved to *P. ovatus*: **Junín:** Prov. Yauli, [ca. 15,000 ft], 23 May 1922, *J.F. Macbride & W. Featherstone 894* (F-517422). **Pasco:** Cerro de Pasco, [14,500 ft], *R. Kanehira 90* (F-740385); Cerro de Pasco, [14,000 ft], 28 Mar 1923, *J.F. Macbride 3084* (F-534154). **San Martín:** Prov. Mariscal Caceres, entre Bombamarca – El Progreso, 4200–4500 m, 9 Jun 2003, *E. Rodríguez R. & V. Medina I. 2581* (HUT-040572); Río Abiseo National Park, 3425 m, 31 May 1986, *K. Young 3493* (F-1982571).

3. Paranephelius uniflorus Poepp., Nov. Gen. Sp. Pl. (Poepp. & Endl.) 3(5–6):42, t. 248. 1843. TYPE: PERU. JUNÍN: Sierra da Viuda, [15,200 ft in itinere versus Cerro de Pasco], *F. Poeppig s.n.* (HOLOTYPE: W [W0028605]). **Figs. 2C–D, 3B–D, 11–14.**

Liabum uniflorum (Poepp.) Sch.Bip., Flora 36:34. 1853.

Paranephelius ferreyrae H. Rob., Phytologia 35:235. 1977. TYPE: PERU. CAJAMARCA: Prov. Cajamarca, cumbre el Gavilán, carretera Cajamarca–Chilete, 3200 m, 31 Mar 1948, 3200 m, *R. Ferreyre 3311* (HOLOTYPE: US [US-1998834]; photograph F [F-1943635]). PARATYPE: PERU. Cajamarca: Baños, May 1958, *J. Soukup 4642* (US).

Description.—Acaulescent, or short-stemmed, perennial **herbs;** roots fascicled. **Leaves** rosulate; blades oblanceolate, rarely ovate, ca. 60 mm long, ca. 20 mm wide, the bases cuneate to pseudo-petiolate, the margins pinnatifid, serrated, the apices obtuse to rounded, abaxial surfaces arachnoid-tomentose, adaxial surfaces bullate. **Capitulescences** sessile, solitary, or short-pedunculate, the peduncles 10–150 mm long. **Capitula** 17–18 mm high, 13–15 mm wide; involucres oblong; phyllaries 40–50, ca. 4-seriate, strongly graduated, ovate-lanceolate or linear-lanceolate, 5–9 mm long, 1–2 mm wide, the margin scarious, apically attenuate, acute, revolute, tomentose pubescent; ray florets 19–29, the corollas yellow, the tube limbo ca. 15 mm long, ca. 2.5 mm wide; disc florets 20–35, the corollas yellow, 9–10 mm long, distally puberulent, the lobes ca. 2.5 mm long, stipitate-glandular; anther filaments ca. 0.4 mm long; anthers ca. 2.5 mm long, the anther appendages ca. 1.2 mm long. **Cypselas** ca. 3.5 mm long, pubescent, the inner capillary bristles, 45–50, 2–3-seriate, ca. 10 mm long, the outer bristles, sub-squamiform, 10–15, 1.5–4.0 mm long. **Chromosome number:** *n* =14II or 15II (Diers 1961; Sundberg et al. 1986).

Distribution & Ecology.—Bolivia: Departments of Inquisivi, La Paz; Peru: Departments of Amazonas, Ancash, Cajamarca, Cusco, Huáncavelica, Junín, La Libertad, Lima, Pasco, Piura, Puno; (2200–) 3000–4000(–4750) m. The type locality of Poeppig's type collection was cited as *Sierra la Viuda,* mountain range

Fig. 11. *Paranephelius uniflorus*. Holotype collection housed at Herbarium WU, Institute of Botany, Vienna. [https://herbarium.univie.ac.at/database/detail.php?ID=219971].

Fig. 12. ***Paranephelius uniflorus*****. Illustration adapted from E. Poeppig plate 248A in** ***Nova genera ac species plantarum*****. 1. Outer phyllary. 2. Pappus bristle. 3. Disc floret. 4. Corolla dissected opened. 5. Anther filaments dissected. 6. Enlargement of style apex. 7. Enlargement of pappus bristle. 8. Cypsela. 9. Ray floret. 10. Staminodia dissected from ray floret. 11. Enlarged ligula apex. [http://www.plantillustrations.org/illustration.php?id_illustration=31280]**

between the Departments of Lima and Junín. This area has been under human pressure for literally centuries and mining has eliminated many sites previously inhabited by vegetation.

Discussion.—*Paranephelius uniflorus* was described by E.F. Poeppig (1843, p. 42) from material he had gathered during his collecting in central Peru, specifically in the area between Lima and Cerro de Paso, now known as *Cordillera La Viuda* (*Sierra la Viuda*). This high, mountainous area is now highly disturbed by human occupation, mining, and agriculture. While the gathering of the type material is a rather poor herbarium sheet, the illustration provided by Poeppig leaves little question as to the identity of the specimen (Fig. 12). In Weddell's treatment of *Paranephelius uniflorus* (1855, p. 213), he cited the Peruvian material by E.F. Poeppig (*s.n.*, W0028605) and Bolivian collections, d'Orbigny (*#1422*, P02715832) and Weddell (*#3929*, P02715831). These are currently accepted under *P. uniflorus*; however, the potential for relationships with *P. asperifolius* cannot be eliminated. It is noteworthy that Angel Cabrera (1978, p 467) had commented that perhaps *P. asperifolius* (as *Liabum*) might be conspecific with *P. uniflorus*, given that both had more pinnately divided leaves. Paradoxically, the sequence data presented in Soejima et al. (2008) suggests affinities with *P. ovatus*, somewhat at odds with the comparative morphology. While no recent collections of *Paranephelius uniflorus* have been reported from the Department of Junín, collections from Departments of Lima and Pasco suggest it may be expected to be found there.

Paranephelius ferreyrae was described by Harold Robinson (1977, p. 235) to account for material he recognized as closely related to *P. bullatus* in capitulum size, the leaves with bullate adaxial surfaces, and cypsela with setae as well as tomentum. The new species differs most obviously by the pinnately lobed leaves and less

Fig. 13. *Paranephelius uniflorus*. **A.** Flowering plants illustrating deeply pinnatifid leaves and pubescence differences, left *Dillon et al. 2812* and right *2811*. **B.** Enlargement of involucres, left, *Dillon et al. 2812* and right, *2811*.

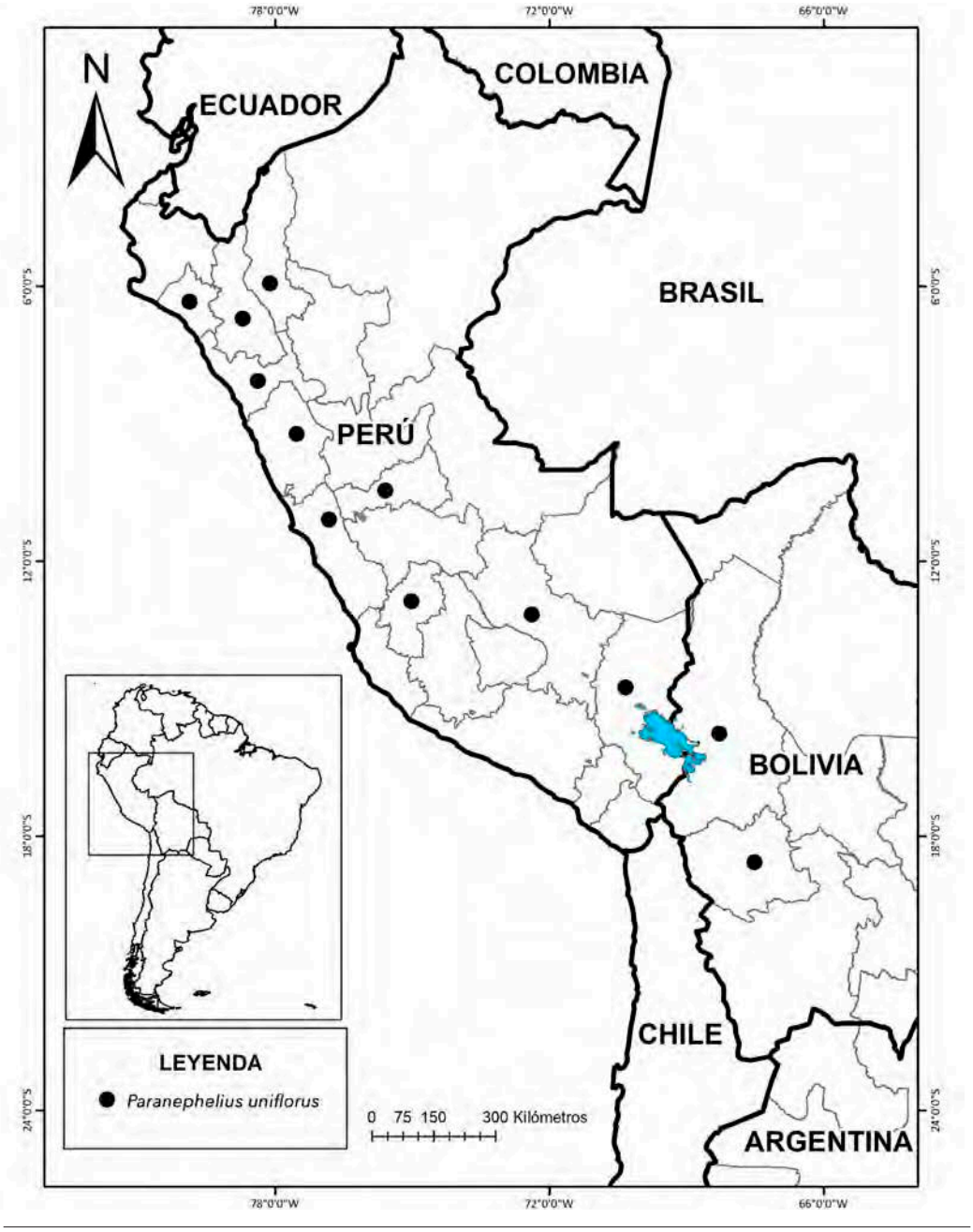

Fig. 14. Distribution map for *Paranephelius uniflorus*.

obviously by the slightly but more distinctly enlarged tips of the longer pappus setae. To explore the systematic position of *Paranephelius ferreyrae*, the area of the type locality, Abra El Gavilán near Cajamarca, was extensively sampled in Soejima et al. (2008). All accessions exhibited ITS sequences diagnosed as "genome A," and their leaf morphology and pubescence conform to our accepted parameters for *P. uniflorus*. Samples from Abra Gavilán in the analysis, included *Sánchez et al. 4052*, *Sánchez 10487*, *Zapata 06*, and *Zapata 07*. These collections all reflected the combination of characters of deeply pinnate leaf blades, and lanceolate, apically attenuate phyllaries. Degrees of leaf pubescence were variable and could not be used reliably for species delineation.

Specimens examined. **BOLIVIA. Cochabamba:** Prov. Chapare, ca. 50 km SE of Cochabamba, on road to Chimore, 1700 m, 29 Mar 1939, *W.J. Eyerdam 25060* (F-1077188). **La Paz:** Inquisivi, 10 km SW of Quime, 4300 m, 17.03°S, 67.18°W, 1 Mar 1990, *M. Lewis 37144* (MO-04639789); Loayza, Cerro Quiraya, cs. 17 km NE of Luribay, 3780–4200 m, 22 Dec 1987, 16°33'36"S, 67°21'0"W, 22 Dec 1987, *M. Lewis 871697* (MO-3650495). **PERU. Amazonas:** Prov. Chachapoyas, Dist. Balsas, Calla-Calla, 6°44'S, 77°53'W, 3550 m, *I. Sánchez V. & M. Sánchez M. 11045* (F-2243979); 3200–3480 m, 6°50'S, 77°51'W, 27 May 1984, *D.N. Smith & J. Cabanillas 7213* (MO-1964447); divide between Río Marañón and Río Utcubamba, 28–31 km SW of Leimebamba, on road to Balsas, 3350–3450 m, 17 Jun 1978, *A. Gentry, M. Dillon, J. Aronson & C. Díaz 23159* (F-1877478). Quebrada Molino, 5 km below Chachapoyas, 2200–2400 m, 5 Jun 1962, *J. Wurdack 760* (F-1662852). **Ancash:** Huascarán National Park, Alpamayo-Cashapampa, 3500–3950 m, 8°53'S, 77°45'W, 13 Mar 1985, *D.N. Smith & R. Valencia 10043* (F-1963585, MO-1964452); Huascarán National Park, Quebrada Panincuray, 8°59'S, 77°34'W, 4000–4300 m, 12 Jan 1985, *D.N. Smith, L. Sánchez & H. Vidaurre 9079* (F-1963544, MO-1964462); Huascarán National Park, 3840–3870 m, 9°23'S, 77°16'W, 13 Jun 1986, *D.N. Smith, A. Gonzales & D. Maldonado 12641* (MO-1964455); Huascarán National Park, Quebrada Alpamayo, 4600–4750 m, 8°53'S, 77°41'W, 8 Mar 1985, *D.N. Smith, R. Valencia & A. Gonzales 9713* (F-1963547, MO-1964457); Huascarán National Park, 3900–4000 m, 8°49'S, 77°57'W, 9 Apr 1986, *D.N. Smith, R. Valencia & M. Buddensiek 12092* (F-1974673, MO-1964453). **Cajamarca:** Prov. Cajamarca, 15 km SW de Parque Cumbe Mayo, 3400 m, 4 Mar 1983, *S.G. Beck 7871* (F-1934774). Dist. Guzmango, Yetón to La Herilla, 2300–3000 m, 2 May 1999, *M. Binder, E. Rodríguez R., H. Binder & L. Montes M. 1999/41* (F-2211252); ca. 35 km from Cajamarca to Hualgayóc, 3540 m, 6°57'W, 78°35'W, 12 Feb 1984, *C.P. Cowan & J. Canne 4432* (F-2105396). ca. 6.5 km SW of Cajamarca, 2980 m, 12 Jan 1983, *M. Dillon, U. Molau & P. Matekaitis 2905* (F-1918486). ca. 27 km NNW of Cajamarca on road to Hualgayóc, Pampa de Cerro Negro, 3600 m, 16 Jan 1983, *M.O. Dillon & U. Molau 3013* (F-1925434); Road between Bambamarca and Chota, 28 Aug 1974, *P.E. Gibbs G74-22* (F-1765848); Prov. Celendin, 31 km E of Cajamarca, 16 May 1964, 3240 m, *P.C. Hutchison & J.K. Wright 5110* (F-1639576, MO-1834386, NY, P02715833). Km 37–40, Cajamarca – Chota, 3500–3600 m, 7°02'S, 78°35'W, 13 Feb 1988, *A. Gentry, C. Díaz & C. Blaney 61578* (F-2011789); Prov. Contumazá, Dist. Guzmango, camino Yetón – La Herilla, 2300–3000 m, 2 May 1999, *E. Rodríguez R., M. Binder, H. Binder & L. Montes 2194* (F-2211710). Cerro Gavilán, 17 Jun 1965, *I. Sánchez V. 72* (F-1947879); Dist. Namora, Hacienda Polloquito, 3100 m, 1 Apr 1967, *I. Sánchez V. 294* (F-1947918); Ayambo, entre Cerro Gavilán – Cajamarca, 2750 m, 22 Apr 1970, *I. Sánchez V. 461* (F-1947873); Entre Matara y San Marcos, 2650 m, May 1972, *I. Sánchez V., W. Ruiz. V. & M. Malpica 922* (F-1947937); Cumbe Mayo, W de Cajamarca, 3200 m, 4 Jun 1976, *I. Sánchez V., W. Ruiz & J. Sánchez 1872* (F-2152067); bajando el Paso El Gavilán, 3000 m, 18 May 1986, * *I. Sánchez V. 4052* (F-1987559); cerca al Centro Turístico Cumbemayo, 3460 m, 21 Apr 2001, * *I. Sánchez V., G. Iberico V. & M. Sánchez M. 10487* (F-2230385); Tamiachocha, Sur de Cerro Negro, 5 km arriba El Gavilán, 7°15'S, 78°27'W, 3560 m, 4 Jun 2001, *I. Sánchez V. 10664* (F-2233233); Corisorgona, NW de Cajamarca, 3000 m, 12 Apr 1991, **I. Sánchez V. & A. Briones 5577* (F-2151072); Prov. Contumazá, Las Alverjas, El Túnel – Contumazá, 2700 m, 4 Jun 1999, **A. Sagástegui A., S. Leiva G., V. Quipuscoa S. & M. Zapata C. 16162* (F-2238185); 3500–3800 m, 7°02'S, 78°34'W, 17 Feb 1983, *D.N. Smith & R. Vasquez M. 3474* (MO-1964445); Las Tres Cruces, 2800 m, 2 Apr 1981, *A. Sagástegui A., E. Alvitez, E. Garcia & S. López 9966* (F-2328891, MO-2894816); Totorillas – Marín, 3300 m, 1 May 1982, *A. Sagástegui A., E. Alvitez, S. López & J. Mostacero 10356* (F-1910168, MO-2983570); Cumbemayo, 3200 m, 4 May 1985, *A. Sagástegui A. & C. Tellez A. 12681* (F-2011526, MO); El Granero, 2800 m, 14 Jun 1983, *A. Sagástegui A. & S. López M. 10637* (F-1943503, MO-1964443); Cruz del Hueco, 2800 m, 26 May 1981, *A. Sagástegui A., S. López & J. Mostacero 9920* (MO-2894782); Prov. Contumazá, 2 Apr 1981, 2700 m, *A. Sagástegui A., E. Alvitez, E. Garcia & S. López 9677* (F-2328897, MO-2894871); Prov. Contumazá, 30 May 1990, desvio a bosque Cachil, Cascas – Contumazá, 2600 m, *A. Sagástegui A, S. Leiva, C. Sagástegui, T. Saldias & C. Tirado 14292* (F-2117937); Cajamarca, **A. Sagástegui A. et al. 17554* (F), *17563* (F); 22 km from Contumazá on road to Guzmango, above Cruz Grande, 3000–3600 m, 11 May 2003, *M. Weigend, T. Henning & O. Mohr 7636* (F-2247473); alrededores de Cumbemayo, 9 Jun 2003, 7°08.4'S, 78°33.2'W, 3480 m, **M. Zapata C. 01* (F-2246068); alrededores de Cumbemayo, 7°08.4'S, 78°33.2W, 9 Jun 2003, **M. Zapata C. 04* (F-2246065); Abra El Gavilán, 7°14.8'S, 78°28.1'W, 10 Jun 2003, **M. Zapata C. 06* (F-2246063); Abra El Gavilán, ruta a San Juan, 3150 m, 10 Jun 2003, **M. Zapata C. 07* (F-2246069); Prov. San Miguel, El Tingo, Agua Blanca, 2750 m, 21 Jun 1980, *A Sagástegui A., E. Alvitez & J. Mostacero 9569* (F-2328745). **Cusco:** Prov. Anta, Cillapuyu, El Chaccan, 3619 m, 7 Mar 1973, *G.R. Brunel 569* (MO-2481579); El Chaccan, 3510 m, 30 Mar 1973, *G.R. Brunel 637* (MO-2481577); Prov. Urubamba, Chincheros, 13°24'S, 72°5'W, 3750 m, 19 Jan 1982, *E.W. Davis, E. Franquemont, C. Franquemont, S. King & C. Sperling 1620* (F-1899787). **Huancavelica:** 3798 m, 24 Mar 1945, *J. Soukup 2787* (F-1207039). **La Libertad:** Prov. Otuzco, Los tres Shulgones, al N de Salpo, 4 Jun 1990, *S. Leiva & P. Leiva 88* (F-2119065); arriba de Shitahuara, al N de Salpo, 3200 m, 16 Jun 1990, *S. Leiva s.n.* (F-2120017); Desvío a Otusco – Agallpampa, 2800 m, 22 May 1984, *A. Sagástegui A., M. Diestra & S. Leiva 11544* (F-1961317); Santiago de Chuco, **A. Sagástegui A. et al. 17575A* (F), **A. Sagástegui A. et al. 17578* (F); Prov. Sánchez Carrion, 5–8 km WNW of Huamachuco, trail to Marcahuamachuco Ruins, 3100–3500 m, 8 Jan 1983, *M.O. Dillon, U. Molau & P. Matekaitis 2811* (F-1918565); 5–8 km WNW of Huamachuco, trail to Marcahuamachuco Ruins, 3100–3500 m, 8 Jan 1983, *M. Dillon, U.*

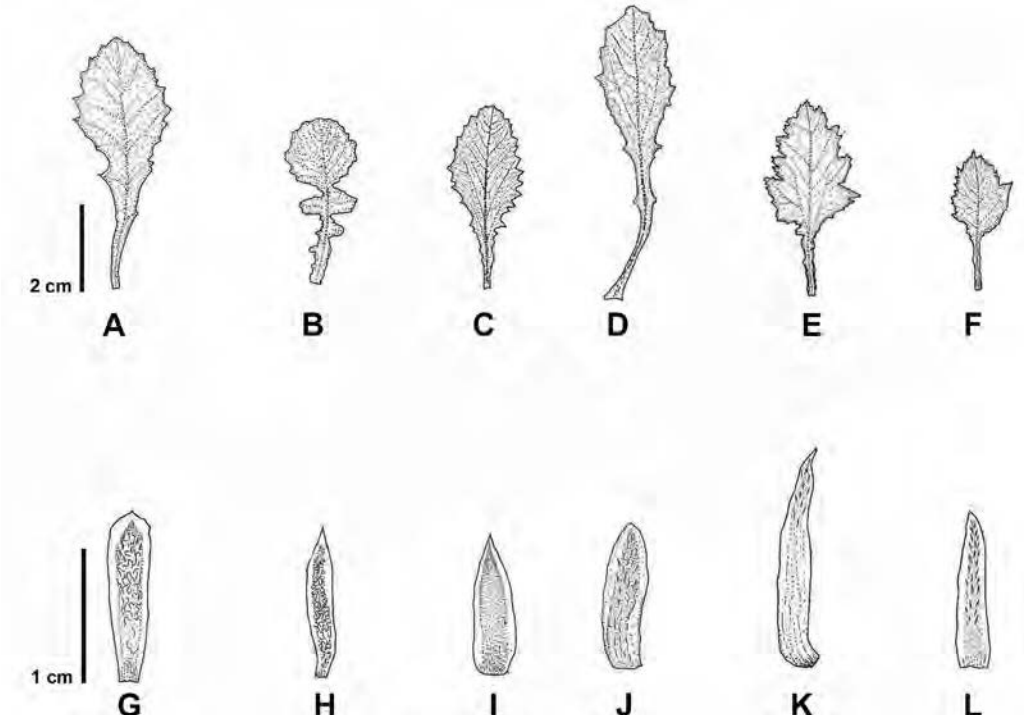

Fig. 15. ***Paranephelius*** **hybrids as identified has mixed genomes of** ***P. ovatus*** **and** ***P. uniflorus*** **(Soejima et al. 2008). Leaf profiles A.** ***Sánchez & Dillon 8136*****. B.** ***Dillon et al. 2843*****. C.** ***Sagástegui et al. 16384*****. D.** ***Zapata 012*****. E.** ***Zapata 013*****. F.** ***Sánchez 10335*****. Phyllary profiles G.** ***Sánchez & Dillon 8136*****. H.** ***Dillon et al. 2843*****. I.** ***Sagástegui et al. 16384*****. J.** ***Zapata 012*****. K.** ***Zapata 013*****. L.** ***Sánchez 10335*****.**

Molau & P. Matekaitis 2812 (F-1917671); ca. 3 km N of Huamachuco en route to Cajabamba, 3000, 26 Mar 1987, *D. Keil, C. Burandt & L. Burandt 19877* (F-2233905); W del cementerio de Quiruvilca, 3870 m, 21 May 2001, *S. Leiva G. & P. Leiva 2522* (F-2229487). Prov. Santiago de Chuco, alrededores de Santiago de Chuco, 2800 m, 13 Jun 1984, *A. Sagástegui A., J. Mostacero L. & M. Diestra Q. 11743* (F-1960102); Prov. Santiago de Chuco, Dist. Quiruvilca, Los Fraylones, entre Huamachuco y Quiruvilca, 30 Mar 2003, 3795 m, 7°55'03.8"S, 78°09'35.5"W, **I. Sánchez V., M. Sánchez M., R. Cueva R. & J. Montoya 11843* (F-2328741). Comumbamba, subiendo al nevado Huaylillas, 3824 m, 20 May 2001, **A. Sagástegui A. & M. Zapata 16455* (F-2226162). **Lima:** Prov. Huarochiri, 8–19 May 1922, [12,000 ft], *J.F. Macbride & W. Featherstone 733* (F-517261). **Pasco:** Prov. Oxapampa, Dist. Huancabamba, Sta. Barbara, above Lanturachi, 3300–3500 m, 10°20'S, 75°40'W, 2 Jul 1985, *R.B. Foster, B. d'Achille & A. Brack 10417* (F-1959252); La Quinua, 14 May 1922, [ca. 12,000 ft], *J.F. Macbride & W. Featherstone 2005* (F-518488); Santa Barbara, 3300–3420 m, 10°22'S, 75°39'W, 2 Aug 1984, *D.N. Smith 8094* (MO-3301706). **Piura:** Prov. Ayabaca, Meseta Andina, 5°00'19.8"S, 79°48'05"W, 3120 m, 23 Apr 2004, *A. Sagástegui A., C. Téllez, F. Torres, M. Berrú & W. García 17522* (F-2293159). Las Pircas, Meseta Andina, 24 Apr 2004, 5°00'20"S, 79°48'30"W, 3080 m, *A. Sagástegui A., C. Téllez, F. Torres, M. Berrú & W. García 17531* (F-2292616); Prov. Huancabamba, 22 Jul 1975, 2300 m, subiendo al Cerro La Viuda, Dist. Sondor, *A. Sagástegui A., J. Cabanillas S. & O. Dios C. 8222* (MO-2481578, NY). **Puno:** Salcedo, near Puno, 4000 m, Oct 1935, *J. Soukup 267* (F-853812).

HYBRIDIZATION IN *PARANEPHELIUS*

Hybridization has been considered an important process in evolutionary biology (Mallet 2007) and interspecific hybridization was first reported in the Liabeae by Soejima et al. (2008). In that analysis, 45 accessions of *Paranephelius* were included, and eight were heterozygous for the diagnostic sites specific to *Paranephelius ovatus* and *P. uniflorus*. These individuals display sequences interpreted as hybrids, mixtures of "genome A" and "genome B." The morphological characters exhibited by these accessions also suggest reassortment of diagnostic characters that could point to a hybrid origin, i.e., leaves varied between completely unlobed blades to blades that are pinnately lobed (Fig. 15). The shape of phyllaries varied between ovate to lanceolate with

obtuse to acute apices; and pubescence was as variable with both bullate and smooth surfaces expressed in close genotypes. These characters have been used in combination to characterize *P. ovatus* and *P. uniflorus*. The area in northern Peru where hybrids have been detected encompasses the boundaries of Departments Amazonas, Cajamarca, and La Libertad and area of perhaps 500 sq2km (Fig. 1).

Dillon et al. (2009) speculated that polyploidy and chromosomal evolution had played a role in speciation in the Liabeae. Cytology studies in *Paranephelius* have yielded chromosome counts of *n* = 9II, 14II, 15II, and ca. 29II (Diers 1961; Turner et al. 1967; Robinson et al. 1985; Sundberg et al. 1986; Sundberg & Dillon 1986). The collection by *Dillon et al. 2843* proved contained a mixture of genomes A and B, and it was documented to have a chromosome number of ca. *n* = 29II surmised to be a polyploid derivative. It displayed leaf blade lobing and margins, and capitular morphology consistent with our interpretation of *P. uniflorus*. The identification of hybrids, as indicated by some specific morphology or combination of characters, has not been possible.

Hybrid specimens examined (fide Soejima et al. 2008): **PERU. Amazonas:** Prov. Chachapoyas, abajo de Paso Calla-Calla, 3510 m, 19 Jul 1995, **I. Sánchez V. & M.O. Dillon 8136* (F-2169350). **Cajamarca:** Prov. Cajamarca, ca. 43 km E of Cajamarca, 27 km N of San Marcos, 2765 m, 11 Jan 1983, **M.O. Dillon, U. Molau & P. Matekaitis 2884* (F-1919502); Dist. Cajamarca. Desvío a Cerro Negro, Km. 28, Carretera Cajamarca-Hualgayoc, Pampa Cerro Negro, 28 Jun 2003, 3560 m, 7°01'39.6"S, 78°34'53.2"W, **I. Sánchez V., J.M. Cabanillas S., M. Sánchez M. & J.M. Cabanillas M. 12100* (F-2328742); Prov. Celendín, **M. Zapata C. 13A* (F). **La Libertad:** Prov. Sánchez Carrion, ca. 10 km N of Laguna Saucacocha, ca. 20 km NE of Huamachuco, 10 Jan 1983, ca. 3370 m, (*n* = ca. 29II), **M.O. Dillon, U. Molau & P. Matekaitis 2843* (F-1918817). Prov. Pataz, 3600 m, 17 Mar 2001, **A. Sagástegui A. & M. Zapata C. 16384* (F-2226167); **M. Zapata C. 10* (F); **M. Zapata C. 12A* (F).

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2) Muséum national d'Histoire naturelle (P), Paris, France. 12-12-2020 <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00755829>

3) Herbarium WU, Institute of Botany, University of Vienna, Vienna, Austria. 12-12-2020 <https://herbarium.univie.ac.at/database/detail.php?ID=219971>

4) Tropicos, Missouri Botanical Garden (MO), St. Louis, U.S.A. 12-12-2020 <https://tropicos.org/home>

5) Plant Illustrations <http://www.plantillustrations.org/illustration.php?id_illustration=31280>

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