## STUDIES OF NEOTROPICAL COMPOSITAE–VIII. THE NEW COMBINATION *PSEUDONOSERIS GLANDULOSA* AND REVISION OF *PSEUDONOSERIS* (LIABEAE)

JOHN F. PRUSKI Missouri Botanical Garden P.O. Box 299 St. Louis, Missouri 63166

## ABSTRACT

The new combination *Pseudonoseris glandulosa* (Compositae: Liabeae: Paranepheliinae) is proposed and *Pseudonoseris* revised with two species recognized, both found in Andean Peru and Bolivia only in and south of the Huancabamba Depression. Both species of *Pseudonoseris* were described originally in *Onoseris* (Mutisieae). Also included are images of holotypes, representative specimens, and capitula of both species of *Pseudonoseris*, as well as a distribution map.

**KEY WORDS:** Andes, Asteraceae, Bolivia, Compositae, Huancabamba Depression, Peru, Liabeae, *Onoseris*, Pleistocene climatic oscillations, *Pseudonoseris discolor*, *Pseudonoseris glandulosa*, Mutisieae, Paranepheliinae

Liabeae was described by Rydberg (1927) to accommodate five genera, including *Liabum* Adans. (Compositae), an opposite-leaved radiate-capitulate American genus having vernonioid styles (Cassini 1823). The styles of Liabeae resemble technically those of Vernonieae and Cichorieae by their adaxial continuous stigmatic surfaces and abaxial branch sweeping papillae extending downward onto the distal portion of trunk (Robinson 1983; Pruski & Sancho 2004). Robinson and Brettell (1974) recognized 14 genera of Liabeae with several segregates culled mostly from *Liabum* s. lat., including *Pseudonoseris* H. Rob. & Brettell (Compositae: Liabeae: Paranepheliinae). Tribe Liabeae now contains 19 genera, with 13 of these genera occurring in Peru, its center of diversity (Robinson 1978, 1983; Pruski & Sancho 2004; Soejima et al. 2008; Robinson & Funk 2011).

Robinson (1983) placed only *Pseudonoseris* and *Paranephelius* Poepp. into his newly described subtribe Paranepheliinae. Funk et al. (2012) expand Paranepheliinae to include six genera, including *Erato* DC. which extends into Central America. Soejima et al. (2008) dated origins of the *Pseudonoseris-Paranephelius* clade to the Miocene (very approximately to 13 Ma). Thus, *Pseudonoseris* and *Paranephelius* (or their immediate precursors) diversified well after the significant central Andean uplifts (Oligocene, ca. 30 Ma), perhaps concurrently with major northern Andean orogeny (Pliocene-Pleistocene, ca. 3–5 Ma) and increased habitat heterogeneity in both the central and northern Andes (Soejima et al. 2008).

The central and northern Andes are discontinuous roughly at the Huancabamba Depression (approximately between 5° and 6° S latitude in the deep upper Río Marañon and Río Chamaya basins, continuing westward over the Abra de Porculla at ca. 2145 m, and down to Olmos), an oft-cited biogeographic barrier for some plant distributions as well as an endemism center (Wurdack 1953; Simpson 1975; Molau 1988; Funk et al. 1995; Ayers 1999; Weigend 2002). It is perhaps noteworthy that, although climatic fluctuations in the Pleistocene lowered (in glacial maxima) vegetational zones facilitating some migrations across the Huancabamba Depression, core subtribal Paranepheliinae members *Pseudonoseris* and *Paranephelius* remain known from only in and south of the Huancabamba Depression (Robinson 1978, 1983; Soejima et al. 2008). While these two genera may have radiated only after the onset of Pleistocene climatic oscillations, the Huancabamba Depression may still have acted (either well before or during the Pleistocene) as a barrier to migration.



Figure 1. Representative specimen of Pseudonoseris discolor (Muschl.) H. Rob. & Brettell (Araujo 4194, MO).

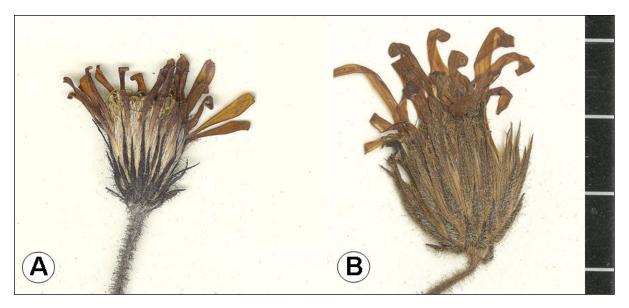


Figure 2. Close-up of capitula of *Pseudonoseris* showing the linear-lanceolate phyllaries and the long-stipitateglandular peduncles. A. *Pseudonoseris discolor* (Muschl.) H. Rob. & Brettell. B. *Pseudonoseris glandulosa* (Hieron.) Pruski. (A *Araujo 4194*, MO; B *Smith & Cabanillas 7303*, MO). [The scale bar on the right has increments of 1 cm.]

Here, *Pseudonoseris* is revised, the new combination *P. glandulosa* is proposed, and this high-elevational Andean genus is recognized as containing only two species. *Pseudonoseris striata* and *P. szyszylowiczii* were each usually recognized elsewhere (Robinson & Brettell 1974; Robinson 1983; Beltrán et al. 2006; Soejima et al. 2008), but both are reduced here to synonymy of *P. glandulosa*. *Pseudonoseris glandulosa* and *P. discolor* are disjunct from each other by about 1100 km (Fig. 3).

**PSEUDONOSERIS** H. Rob. & Brettell, Phytologia 28: 59. 1974. **Type:** *Liabum striatum* Cuatrec. [= *Pseudonoseris glandulosa* (Hieron.) Pruski].

Small perennial subscapose herbs, leaves in basal rosettes or stems leafy proximally, with milky latex, scape typically with a low arachnoid-pubescence and long stipitate-glandular trichomes held well above arachnoid pubescence. Leaves opposite, sometimes in basal or cauline rosettes, sessile; blade subentire to lyrate-pinnatilobed, lanceolate to obovate, chartaceous to stiffly so, venation pinnate, surfaces discolorous, adaxial surface smooth to rugose, pubescent to glabrate, abaxial surface cinereous-griseous-tomentose (sometimes drying fulvous), base slightly clasping. Capitulescence subscapose, paucicapitulate, open cymose with alternate branching; peduncles elongate, long-stipitate-glandular. Capitula radiate; involucre campanulate; phyllaries ca. 40, weakly imbricate, graduate, 3-5-seriate, linear-lanceolate, long-stipitate-glandular, outer ones acute apically, often spreading in fruit, inner ones long-attenuate apically; clinanthium (phoranthium or receptacle) epaleate, low-alveolate, subglabrous. Ray florets 12-26, pistillate, 1-seriate; corolla orangish-yellow to scarlet, tube pilose-villous, limb linear-oblanceolate, exserted from involucre, abaxially glabrous and not arachnoid-tomentulose, usually 4-nerved and 3-denticulate. Disk florets 25–55, bisexual; corolla gradually funnelform, 5-lobed, orangish-yellow or reddish-orange, hirsute near tube-throat juncture, tube elongate, lobes glabrous or with a single distal gland; anther thecae pale, base obtuse, ecaudate, endothecial tissue polarized, apical appendage ovate to oblong, slightly longer than wide; pollen tricolporate, echinate, tectum finely microperforate, columellate layer well-defined (Robinson & Marticorena 1986); style base very slightly dilated, glabrous, trunk slightly papillose distally,

branches elongate and nearly filiform, 3–4 mm long, narrowing distally, abaxial surface roughpapillose, adaxially with continuous stigmatic surface. **Cypselae** prismatic to obovoid, thickly 10costate (merely striate when immature), costae often tan and setose with nearly appressed trichomes, furrows usually brown and glabrous, cells walls with elongate raphids (Robinson 1983); pappus distinctly or indistinctly 2-seriate, mostly with an inner series of 15–30 elongate stramineous scabrid capillary bristles, several mid-sized outer squamellae typically present, these sometimes absent adaxially and represented instead by small outer bristles. x = 12. Two species found in Andean Peru and Bolivia.

*Pseudonoseris* is a central Andean genus (Fig. 3) of two species that Robinson (1983) treated within Liabeae subtribe Paranepheliinae. *Pseudonoseris* is diagnosed by its subscapose habit, milky latex, discolorous pinnately-veined sessile leaves, indumentum of long-stipitate-glandular trichomes on the scape, peduncles, and phyllaries, erect alternate-branched capitulescences, brightly colored ray corollas with limbs abaxially glabrous and not arachnoid-tomentulose, pale anthers, and filiform style branches. Color photographs of each species in the field were provided by Soejima et al. (2008). The two species of *Pseudonoseris* were each once treated within sometimes stipitate-glandular, brightly colored, and large-capitulate *Onoseris* (Mutisieae), which differs most conspicuously by outer florets with bilabiate corollas, tailed anthers, and short-ovate style branches.

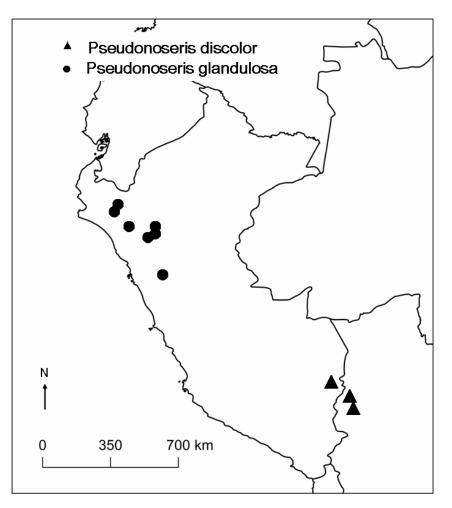


Figure 3. Distribution of *Pseudonoseris discolor* (Muschl.) H. Rob. & Brettell and *Pseudonoseris glandulosa* (Hieron.) Pruski in Andean Peru and Bolivia.

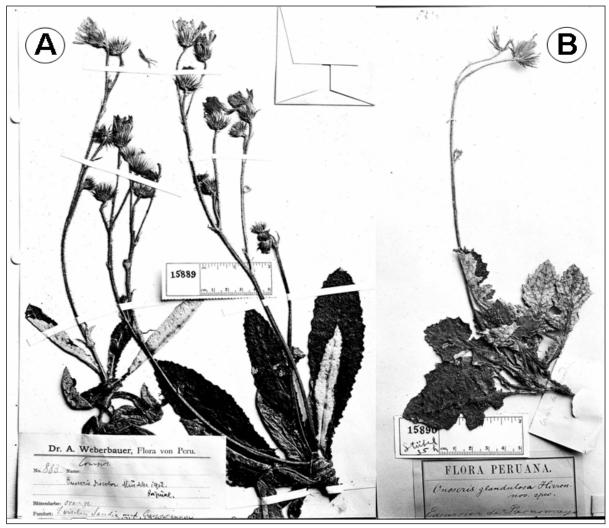


Figure 4. Photographs of the destroyed Berlin holotypes of the two recognized species of *Pseudonoseris*. A. *Onoseris discolor* Muschl. [ $\equiv$  *Pseudonoseris discolor* (Muschl.) H. Rob. & Brettell]. B. *Onoseris glandulosa* Hieron. [ $\equiv$  *Pseudonoseris glandulosa* (Hieron.) Pruski].

Although in the Soejima et al. (2008) study the relationships between *Pseudonoseris* glandulosa (as '*Pseudonoseris szyszylowiczii*') and *Paranephelius* are unresolved, *Pseudonoseris* is maintained here as diagnosed morphologically by Robinson (1983). *Pseudonoseris* differs from *Paranephelius* most obviously by some stipitate-glandular (vs. eglandular) indumentum, erect branched (vs. usually sessile) capitulescences, and by abaxially glabrous (vs. arachnoid-tomentulose) ray corolla limbs. Cytologically, the base number of Liabeae appears to be x = 9, *Paranephelius* was reported as x = 9 and x = 14, and *Pseudonoseris* has been counted only once, being given as x = 12 (Dillon & Turner 1982; Robinson et al. 1985).

Typification and etymology. The genus, name for its resemblance to *Onoseris*, is typified by *Liabum striatum*, the holotype of which is extant. The holotypes (Fig. 4) of our two species were destroyed, but neither species circumscription is in doubt. Thus, there is no pressing need taxonomically to lectotypify or neotypify either species name, and I am content to wait for possible holotype fragments or isotypes to be found. The descriptive basionym epithets *discolor*,

*glandulosum*, and *striatum* refer to the salient characters of *Pseudonoseris* of discolorous leaves, the distal stipitate-glandular indumentum, and the striate-costate cypselae, respectively.

PSEUDONOSERIS DISCOLOR (Muschl.) H. Rob. & Brettell, Phytologia 28: 60. 1974. Onoseris discolor Muschl., Bot. Jahrb. Syst. 50, Beibl. 111: 94. 1913. Liabum lanatum Ferreyra, Bol. Soc. Peruana Bot. 1: 17. 1948 (non Liabum discolor (Hook. & Arn.) Benth. & Hook. f. ex Hemsl.). TYPE: PERU. Puno. Inter Sandia et Cuyocuyo, 2600–2800 m, 1 May 1902, Weberbauer 883 (holotype: B<sup>+</sup>, photograph in F, MO, Macbride neg. 15889). Figs. 1, 2A, 4A.

Rosulate or less commonly leafy-stemmed herbs 10-70 cm tall; stems arachnoidpubescent, also moderately dense long-stipitate-glandular (trichomes to 1.8 mm long and sometimes longer than stem diam.) to near base, internodes not hirsute and without simple patent trichomes, all leaves basal or proximal-cauline, when cauline with leaves paired with internodes 1-4 cm long but always much shorter than the leaves. Leaves  $4-24 \times 1-6$  cm, lanceolate to oblong, broadest at midblade or slightly above mid-blade, simple, never lyrate-pinnatilobed, adaxial surface rugose to rugulose, usually lingering arachnoid-pubescent especially along midrib and secondary veins, sometimes glabrate, broad-based or more commonly base narrowly acute, margins unequally sinuousdentate to less commonly crenate or subentire, apex acute to sometimes obtuse. Capitulescence 1-2 per plant, held 9-50 cm above leaves, loosely cymose, 2-7-capitulate, branched in distal half; peduncles usually 2-10 cm long, moderately dense long-stipitate-glandular, sometimes with 2-3 linear bracteoles 1–3 mm long. Capitula 14–16(–18) mm long (excluding rays); involucre  $10-13 \times$ 8–18 mm; phyllaries  $3-13 \times 1-2$  mm, with a purplish mid-zone and scarious margins. Ray florets 12–26; corolla orange or sometimes orangish-yellow, tube 10-13 mm long, limb  $20-24 \times 2.5-3$  mm. Disk florets: corolla 11–13 mm long, orangish-yellow, lobes 2–3 mm long. Cypselae 2–3.2 mm long; pappus indistinctly biseriate, inner pappus bristles 15–25, 8–10 mm long, outer pappus bristles few, 0.1–0.3 mm long, not obviously much broader than inner series of bristles.

Representative exsiccatae examined. **BOLIVIA. La Paz.** Franz Tamayo, Parque Nacional Madidi, Keara–Moxos, Kellutoro, 3000 m, 13 May 2008, *Araujo 4143* (BM, LPB, MO), *Araujo 4194* (B, GH, LPB, MO); Franz Tamayo, ANMI Apolobamba, sector Laitiki hacia Piara, entre Pelechuco y Apolo, 2650 m, 20 Apr 2006, *Fuentes et al. 10422* (LBP, MO, NY). **PERU. Puno.** Sandia, Limbani, 3300 m, 7 Jun 1974, *Chávez 2382* (MO); Sandia, dry open hillside near Limbani, 3200–3450 m, 14–16 May 1942, *Metcalf 30531* (MO, UC).

Distribution and ecology. *Pseudonoseris discolor* occurs in *puna* from 2600–3450 meters elevation, north of Lake Titicaca in the Andes of Puno, Peru, and adjacent La Paz, Bolivia (Fig. 3). The species is saxicolous and flowers from April to June.

Illustrations of *Pseudonoseris discolor* were provided by Ferreyra (1948) and Robinson (1983). *Pseudonoseris discolor* was given by Robinson and Brettell (1974), Robinson (1983), Beltrán et al. (2006), and Soejima et al. (2008) as endemic to Peru, but this species is now known from several collections in adjacent Bolivia. The protologue described it as similar to *Onoseris glandulosa* [ $\equiv P.$  glandulosa]. The few inner pappus bristles and the indistinctly biseriate pappus are distinctive features of *P. discolor*. Some color photographs of *P. discolor* appear to show the ray corollas as orangish-yellow, but the plants are usually described as orange-flowered.

PSEUDONOSERIS GLANDULOSA (Hieron.) Pruski, comb. nov. Onoseris glandulosa Hieron., Bot. Jahrb. Syst. 21: 366. 1895. TYPE: PERU. Cajamarca. Prope La Cruz de Celendín, inter Pacasmayo et Moyobamba, 3100 m, Apr–Jun 1868–1877, Stübel 35h (holotype: B<sup>+</sup>, photograph in F, MO, Macbride neg. 15890). Figs. 2B, 4B, 5.

Liabum szyszylowiczii Hieron., Bot. Jahrb. Syst. 36: 503. 1905. Pseudonoseris szyszylowiczii (Hieron.) H. Rob. & Brettell, Phytologia 28: 60. 1974. **TYPE: PERU. Cajamarca**. Prope Callacate, May 1879, Jelski 718 (holotype: B<sup>+</sup>, photograph in F, MO, Macbride neg. 18133).

Liabum striatum Cuatrec., Collect. Bot. (Barcelona) 3: 306. 1953. Pseudonoseris striata (Cuatrec.)
H. Rob. & Brettell, Phytologia 28: 60. 1974. TYPE: PERU. [presumably near the Lambayeque-Piura border near Abra de Porculla]. Above Olmos, 1800–1900 m, May 1915, Weberbauer 7107 (holotype: F, photograph in MO, Field neg. 49222).

Rosulate or leafy-stemmed herbs 20-90 cm tall; stems arachnoid-pubescent, also longstipitate-glandular (trichomes to 1 mm long and sometimes longer than stem diam.) distally, grading to hirsute with simple patent trichomes proximally, all leaves basal or proximal-cauline, when cauline then in cauline-rosettes or with leaves paired with internodes 1-5 cm long but always much shorter than the leaves. Leaves  $6-18 \times 2.5-10$  cm, lyrate-pinnatilobed with terminal lobe the largest and usually with 2-3 pairs of lateral lobes, oblong to obovate in outline, adaxial surface smooth, hirsutulous to substrigillose with patent or subappressed trichomes, also sometimes arachnoidpubescent, broad-based or less commonly base attenuate, lobes nearly lateral, triangular-ovate with sinuous-denticulate margins, sinuses rounded, apex obtuse to sometimes acute. Capitulescence 1-2(-3) per plant, usually held 15-30 cm above leaves, loosely cymose, usually 2-9-capitulate, branched only in distal half; peduncles usually 2-15 cm long, more densely pubescent than stem and proximal capitulescence axis. Capitula 12–19 mm long (excluding rays); involucre  $10-15 \times 10-20$ mm; phyllaries  $3-15 \times 1-2$  mm, linear-lanceolate, appearing 2-costate at least near mid-phyllary. **Ray florets** 13–21; corolla scarlet or reddish-orange, tube 10–11 mm long, limb  $15-20 \times 2-3$  mm. Disk florets: corolla 9–12 mm long, reddish-orange, lobes 2–2.5 mm long. Cypselae 2–4 mm long; with pappus obviously (at least adaxially on some cypselae) biseriate, inner pappus bristles 25–30, 6– 8 mm long, outer squamellae 0.5-1.5 mm long, at least the adaxial ones on some cypselae noticeably broad-based and obscuring inner bristle bases, the abaxial ones especially of the ray florets sometimes represented by very small bristles. 2n = 24 (Dillon & Turner 1982).

Representative exsiccatae examined. **PERU.** Amazonas. Chachapoyas, encima de 'Leimebamba', 2600-2700 m, 16 Apr 1964, Ferreyra 15465 (MO, USM); 6 kms along road W of Chachapoyas, 6600 ft, 13 Jan 1983, King & Bishop 9198 (MO, US); 15 km from Chachapoyas towards Mendoza, 2200 m, 13 Mar 1998, van der Werff et al. 14833 (MO, US); 1 km SW of Chachapoyas, 2300 m, 22 May 1962, Wurdack 467 (MO-2, US); Chachapoyas, km 422-417 on 'Levmebamba'-Balsas road, 2400-2700 m, 21 Feb 1984, Smith 6077 (MO). Ancash. Huari, 2500 m, 2 May 1962, Ames 7 (MO). Cajamarca. Jelij, grassland, 3035 m, 16 June 2009, Bussmann et al. 15526 (MO, NY); Jaén, Sallique, de Catala a Piquijaca, 1940-2195 m, 29 Jul 1998, Campos & Díaz 5396 (MO, US); Carretera entre Sócota y Cutervo, 2000–2200 m, 20 Apr 1988, Díaz & Baldeón 2844 (F, MO); 26 km NW [on maps this appears instead to be NE] of Celendín on road to Balsas, 2300 m, 5 Jan 1979, Dillon & Turner 1699 (F, MO, US); Yamaluc, entre Cochabamba y Huambos, 2300-2500 [annotated in pencil as 1900-2000] m, 1 Aug 1946 (post fruit), Ferreyra 828 (MO); Km 156 de la carretera Pacasmayo-Cajamarca, 2650 m, 5 Apr 1982, Sánchez-Vega 2758 (MO); Chachapoyas-Celendín road, above Celendín, 3000 m, 28 May 1984, Smith & Cabanillas 7303 (MO). Lambaveque. The type of synonymous Liabum striatum, presumably near the Lambayeque-Piura border near Abra de Porculla. Piura. Huancabamba, Porculla, 2200 m, 10 May 1992. Llatas & Cruz 3106 (F, MO).



Figure 5. Representative specimen of *Pseudonoseris glandulosa* (Hieron.) Pruski. (*Smith & Cabanillas 7303*, MO).

Distribution and ecology. *Pseudonoseris glandulosa* is endemic to Andean Peru in and south of the Huancabamba Depression, where it occurs in both cordilleras, these separated by the Río Marañon (Fig. 3). *Pseudonoseris glandulosa* occurs mostly in the montane zone and in *jalca* formations (sometimes it is saxicolous) from 1800–3400 meters elevation in the Departments of Amazonas, Ancash, Cajamarca, Lambayeque, [expected in La Libertad], and Piura and flowers from January to July. Although *P. glandulosa* presumably did not migrate across Huancabamba Depression during Pleistocene climatic oscillations, it is moderately successful ecologically as it occurs on the cordilleras both west and east of Río Marañon valley. *Dorobaea laciniata* B. Nord. & Pruski and *Talamancalia putcalensis* (Hieron.) B. Nord. & Pruski (Nordenstam & Pruski 1995; Beltrán & Pruski 2000) are other regional subscapose lobe-leaved large-capitulate orange-flowered taxa (both are Senecioneae) resembling superficially *P. glandulosa*.

The protologue noted specifically that this taxon lacked the inner corolla lips typical of *Onoseris* (Mutisieae). *Pseudonoseris glandulosa* was excluded from *Onoseris* by Ferreyra (1944), who referred provisionally this species to *Liabum*. *Pseudonoseris glandulosa* was not treated subsequently in the Mutisieae in the Flora of Peru (Ferreyra 1995) nor elsewhere in the Mutisieae (Katinas et al. 2008). By opposite leaves, radiate capitula, moderately long-lobed disk corollas, ecaudate anthers, style trunks distally papillose, and style branches with continuous stigmatic surfaces, *P. glandulosa* keys to tribe Liabeae in Pruski and Sancho (2004), where it matches *Pseudonoseris* by its subscapose habit, indumentum of some long-stipitate-glandular trichomes, erect alternate-branched capitulescences, brightly colored ray corollas, pale anthers, and filiform style branches. Soejima et al. (2008) gave this species as having arisen through hybridization between *Pseudonoseris* and *Paranephelius*. Cytologically, *P. glandulosa* was reported by Dillon and Turner (1982) as 2n = 24, the only count published for the genus.

No significant consistent morphological differences are found between plants of (1) the Pacific slopes of the Cordillera Occidental –the coastal range– (e.g., the presumed type locality of *P. striata*), (2) those of the interior slopes Cordillera Occidental just west of the Río Marañon (generally between 6° and 7° S latitude) of Depto. Cajamarca (e.g., the types of *P. glandulosa* and *P. szyszylowiczii*), (3) those east of the Río Marañon in the Cordillera Oriental in Depto. Amazonas near Chachapoyas, or (4) with those much further south in Depto. Ancash. Weigend (2002) noted that although species are often restricted distributionally to one side of the Andes, this generalization may beak down in the upper Río Marañon valley where several groups are found in the coastal as well as interior mountains. Although plants of *P. glandulosa* from the Cordillera Oriental on average tend to have a more obviously biseriate pappus than, for example, do plants of the Cordillera Oriental from near Chachapoyas, this pappus variation is never as great as that found within some individual florets and within some individual capitula. Accordingly, both *P. striata* and *P. szyszylowiczii* are treated in synonymy of *P. glandulosa*, lowering from three to two the number of species recognized in *Pseudonoseris*.

## **ACKNOWLEDGEMENTS**

I would like to thank Guy Nesom and Rosa Ortiz (MO) for reading the manuscript, Stephanie Keil (MO) for taking the photographs of the MO sheets, Christine Niezgoda (F) for permission to use the photographs of the Berlin holotypes, and Rosa Ortiz for help in preparing the map.

## LITERATURE CITED

- Ayers, T.J. 1999. Biogeography of *Lysipomia* (Campanulaceae), a high elevation endemic: an illustration of species richness at the Huancabamba Depression, Peru. Arnaldoa 6(2): 13–27.
- Beltrán H. and J.F. Pruski. 2000. *Talamancalia* y *Rolandra* (Asteraceae): dos nuevos registros para el Perú. Arnaldoa 7(1–2): 13–18.

- Beltrán, H., A. Granda, B. León, A. Sagástegui, I. Sánchez, and M. Zapata. 2006. Asteraceae endémicas del Perú. Revista Peruana Biol. (número especial) 13(2): 64s–164s.
- Cassini, H. 1823. Liabon, *Liabum*. (Bot.). Pp. 203–211 in F. Cuvier (ed.), Dict. Sci. Nat. (ed. 2), Vol. 26. Paris.
- Dillon, M. and B.L. Turner. 1982. Chromosome numbers of Peruvian Compositae. Rhodora 84: 131–137.
- Ferreyra, R. 1944. Revisión del género Onoseris. J. Arnold Arbor. 25: 349–395 + 9 pl.
- Ferreyra, R. 1948. Nota sobre el género Liabum. Bol. Soc. Peruana Bot. 1: 17-27. 1948.
- Ferreyra, R. 1995. Family Asteraceae: Part VI. Flora of Peru. Fieldiana, Bot. n. ser. 35: [vi] + 1-101.
- Funk, V.A., C. Kelloff, and R. Chan. 2012. Phylogeny and biogeography of the tribe Liabeae (Compositae subfamily Cichorioideae). Taxon 61: 437–455.
- Funk, V.A., H. Robinson, G.S. McKee, and J.F. Pruski. 1995. Neotropical Montane Compositae with an Emphasis on the Andes. Pp. 451–471 in S.P. Churchill et al. (eds.), Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden, Bronx.
- Katinas, L., J.F. Pruski, G. Sancho, and M.C. Tellaría. 2008. The subfamily Mutisioideae (Asteraceae). Bot. Rev. 74: 469–716.
- Molau, U. 1988. Scrophulariaceae–Part I. Calceolarieae. Fl. Neotrop. Monogr. 47: [ii] + 1–326.
- Nordenstam, B. and J.F. Pruski. 1995. Additions to *Dorobaea* and *Talamancalia* (Compositae-Senecioneae). Comp. Newsl. 27: 31–42.
- Pruski, J.F. and G. Sancho. 2004. Asteraceae or Compositae (Aster or Sunflower Family). Pp. 33– 39 + pl. 5 in N. Smith et al. (eds.), Flowering Plants of the Neotropics. Princeton Univ. Press, Princeton.
- Robinson, H. 1978. 190(2). Compositae-Liabeae. Flora of Ecuador 8: 1-62.
- Robinson, H. 1983. A generic review of the tribe Liabeae (Asteraceae). Smithsonian Contr. Bot. 54: iii + 1–69.
- Robinson, H. and R.D. Brettell. 1974. Studies in the Liabeae (Asteraceae). II. Preliminary survey of the genera. Phytologia 28: 43–63.
- Robinson, H. and V.A. Funk. 2011. *Stephanbeckia plumosa* (Liabeae: Compositae): A new genus and species from southern Bolivia. Brittonia 63: 75–82.
- Robinson, H. and C. Marticorena. 1986. A palynological study of the Liabeae (Asteraceae). Smithsonian Contr. Bot. 64: iii + 1–50.
- Robinson, H., A.M. Powell, R.M. King, and J.F. Weedin. 1985. Chromosome numbers in Compositae, XV: Liabeae. Ann. Missouri Bot. Gard. 72: 469–479.
- Rydberg, P.A. 1927. Carduaceae: Tribe 13. Liabeae, Tribe 14. Neurolaeneae, Tribe 15. Senecioneae [part]. N. Amer. Fl. 34(4): 289–360.
- Simpson, B.B. 1975. Pleistocene changes in the flora of the high Andes. Paleobiology 1: 273–294.
- Soejima, D.D., J. Wen, M. Zapata, and M.O. Dillon. 2008. Phylogeny and putative hybridization in the subtribe Paranepheliinae (Liabeae, Asteraceae), implications for classification, biogeography, and Andean orogeny. J. Syst. Evol. 46: 375–390.
- Weigend, M. 2002. Observations on the biogeography of the Amotape–Huancabamba Zone in northern Peru. Bot. Rev. 68: 38–54.
- Wurdack, J.J. 1953. A revision of the genus *Brachyotum* (Tibouchineae-Melastomataceae). Mem. New York Bot. Gard. 8: 343–407.