New species and nomenclatural transfers in South American *Gentianella* (Gentianaceae)

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Two new species of *Gentianella* are described. *Gentianella galtonioides* J.S. Pringle, from Peru, differs from *G. kusnezowii* in its leaves with 11 to 17 primary veins and non-sheathing bases, and in its white corollas with elliptic-rhombic lobes. *Gentianella pharos* J.S. Pringle, from Bolivia, differs from *G. florida* in its more elongate inflorescences and distinctly yellow corollas, from *G. pluvialis* in its smaller flowers and less deeply lobed corollas, and from both in its smaller size and deltoid calyx lobes. The distinctness of *Gentiana longipes* and *G. totorensis* is discussed, and the species are transferred to *Gentianella*. Gynodioecy is confirmed in *Gentianella pluvialis* with the report of specimens with bisexual flowers.

The widely distributed genus Gentianella, in the family Gentianaceae, tribe Gentianeae, subtribe Swertiinae, attains its greatest diversity in the Andes of South America, where over 150 species are currently recognized. Historically, this genus, including its South American species, was usually included in Gentiana (Grisebach 1845, Kusnezow 1895, Gilg 1916), although when thus treated it was generally distinguished at subgeneric or sectional rank. More recently, the generic status of Gentianella has been widely accepted in major floras and other standard references, following works by Smith (1936), Warburg (in Clapham et al. 1952), Fabris (1955, 1960), and others. As emphasized in the studies by Gillett (1957) and Toyokuni (1963), in Gentianella, as in such genera as Swertia, Halenia, and Lomatogonium, the nectaries are epipetalous and the corollas lack plicae between the lobes, whereas in Gentiana, as more strictly

circumscribed, the nectaries are borne on the ovarian stipe and, in all but one species, plicae (corolline projections vascularized by branches from the lateral petal veins on each side) are present between the corolla lobes. Molecular phylogenetic studies by Chassot *et al.* (2001), von Hagen and Kadereit (2001), and Struwe *et al.* (2002) have further supported the acceptance of *Gentianella* as a genus and its grouping at the subtribal level with *Swertia*, *Halenia*, and *Lomatogonium* rather than with *Gentiana s. stricto*.

New species of *Gentianella* continue to be discovered in South America. Two attractive new species are described in this paper, and the distinctness of two others is discussed. Except where otherwise indicated, descriptions of the previously known species with which these species are contrasted, or citations of such descriptions, were published under *Gentiana* by Gilg (1916).



Fig. 1. Gentianella galtonioides (from the holotype). - A: Plant, above base. - B: Basal part of plant. - C: Node and leaf, with enlargement of margin. - D: Bud, with enlargement of a calyx lobe. - E: Portion of corolla, adaxial view, showing lobe, nectary, and insertion of stamens. - F: Anthers and distal portions of filaments. -G: Fruit. - H: Portion of inflorescence, showing node, pedicel, and fruit with marcescent corolla and persistent calyx.

Gentianella galtonioides J.S. Pringle, *sp. nova* (Figs. 1 and 2)

Species Gentianellae kusnezowii similis sed foliis multinervibus basi non vaginantibus et corolla alba lobis elliptico-rhombeis differens.

TYPE: Peru. Junín-Cusco: Prov. Santipo-La Convención, Cordillera Vilcabamba, Río Ene slope, near summit of divide, 11°39'36''S, 73°40'02''W, 3350–3400 m a.s.l., *Polylepis* forest heavily covered with moss, low ferns or vascular epiphytes, at 3350–3400 m, restricted to blocky limestone substrate, 13 June 1997 *B. Boyle, M. Arakaki & H. Beltrán* 4346 (holotype F; isotype USM, image seen).

ETYMOLOGY. The specific epithet notes the similarity of this species, in the general aspect of the plants and flowers, to the summer-hyacinth, *Ornithogalum candicans*, formerly called *Galtonia candicans* and still widely cultivated under that name. The epithet *Galtonia* remains in use for the subgenus and section of *Ornithogalum* that include *O. candicans*.

Synoecious. Plants herbaceous, probably perennial (*see* discussion below), 0.4–1 m tall. Primary flowering stem (current season's growth) erect, proximally 4–5 mm in diameter, compressed in herbarium specimens, simple below inflorescence. Leaves opposite; numerous basal and near-basal leaves present at flowering time, lowest ones withered or disintegrating, upper ones green; cauline leaves gradually more widely spaced distally, mid-cauline internodes 3–10 cm long. Leaves narrowly lanceolate to linear, proximally ascending but without a distinct pseudopetiole, spreading most of their length, $30-50 \times$ 3–6 mm, with 11 to 17 slender, parallel primary veins, leaf bases not connate-sheathing, apices acute except for minutely rounded extreme tip. Inflorescence a narrow thyrse, with 15 to 25 flowers per primary stem, comprising an umbelloid terminal cymule and solitary flowers or short branchlets at 3 or 4 nodes below terminal cymule, each branchlet bearing 2 to 4 flowers; pedicels 11-30 mm long; flowers erect or nearly so, or those on longer pedicels probably spreading or ± nodding (as indicated by slenderness of pedicels and curvature as seen in herbarium specimens, especially that at USM). Flowers mixed 4- and 5-merous. Calyx green, 11-15 mm long, not prominently ridged, tube 3-7 mm long, lobes very narrowly triangular, 5-8 mm long, 1.2-2 mm wide at the slightly flaring base, $1.1-1.5(-2)\times$ as long as tube, longest lobes $1.1-1.3 \times$ as long as shortest lobes, apices acuminate; adaxial calycine colleters none. Corolla white with lobes green at apex, campanulate, 16-22 mm long (measured closed), tube 6-8 mm long, lobes elliptic-rhombic, $9-12 \times 5-7$ mm, $1.2-1.4 \times$ as long as tube, $1.7-1.9 \times$ as long as wide, widest at $0.35-0.55 \times$ their length, apex subacute, entire; adaxial trichomes none; nectaries as many as corolla lobes, inconspicuous, oblong, ca. 1 mm long. Filaments inserted at ca. $0.5 \times$ height of corolla tube, 6-8 mm long; undehisced anthers purple, ca. 1 mm long. Ovary stipitate at anthesis. Capsule dark brown, glossy, narrowly compressed-ovoid, 12-15 mm long (excluding stipe); stipe of mature fruit 4-6 mm long. Seeds very dark brown, \pm angular at maturity because of crowding, ca. 1.0 mm in diameter, surface minutely lumpy.

Gentianella galtonioides is known only from the type locality, near the eastern boundary of Dpto. Junín with the northwestern boundary of Dpto. Cusco, Peru.

The specimens of *G. galtonioides* available for this study consisted only of flowering stems. Below the current season's growth the stems were rhizome-like, bearing numerous, closely spaced leaf-scars. No vegetative rosettes, representing potential branches or the next year's flowering stems, accompanied the many clustered leaves at the base of the current sea-



Fig. 2. *Gentianella galtonioides* (from the holotype). Portion of leaf photographed with transmitted light.

son's portion of the stems, nor were remnants of branches seen on the older portions. From the length of the portions bearing leaf-scars, it appears that each stem remains vegetative and elongates for several years before flowering, during which time the older portions become procumbent and covered with moss or litter. The available specimens suggest either that the flowering stems arise from perennial rhizomes, although direct evidence of such branching was not seen, or that the species has a plietesial (long-lived monocarpic) life history.

The leaf venation of *G. galtonioides* (Fig. 2), readily visible in herbarium specimens at $10\times$, is unlike that known in any other species in the genus. It appears monocot-like, with 11 to 17 closely spaced primary veins extending parallel nearly the whole length of the leaf, infrequently dividing, with the midvein only slightly thicker and more prominent than the others, and with only a few secondary veins obliquely connecting the primary veins. Also, except in *G. kusnezowii*, with which *G. galtonioides* is contrasted below, tetramerous flowers are not ordinarily encountered in other South American species of *Gentianella*, although they prevail in some species elsewhere in the range of the genus.

In the presence of a many-leaved rosette at flowering time, the size and shape of the leaves, the spacing of the cauline leaves, the form of the inflorescence, and the admixture of tetramerous and pentamerous flowers, *G. galtonioides* is similar to *G. kusnezowii* (tentatively including *G. pilgeriana*), the range of which is ca. 850 km to the southeast of that of *G. galtonioides*, in west-central Bolivia. *Gentianella kusnezowii* differs from *G. galtonioides* in its lower stature and firmer, more slender primary stems; thicker, more coriaceous leaves with fewer primary veins (a leaf similar in size to that of *G. galtonioides* br shown in Fig. 2 would generally have five primary veins); leaf-pairs with connate-sheathing bases, the sheaths at mid-stem 2-4 mm long; at

obovate lobes 1.5–1.8 times as long as the tube, rounded at the apex. *Gentianella grantii* (described in Pringle & Grant 2012), which is native to Dpto. Cusco, Peru, but ca. 300 km to the southeast of the type locality for *G. galtonioides*, is also somewhat similar to *G. galtonioides*, but differs in its firmer, more slender stems, 1.7–2.5 mm in diameter, not flattened in pressing; leaves with fewer primary veins, only the midrib prominent; leaf bases connate-sheathing 1–4 mm; and roseviolet corollas with the lobes 0.6–0.7 times as long as the tube.

and blue corollas mostly 20-27 mm long, with

Gentianella pharos J.S. Pringle, *sp. nova* (Fig. 3)

Species verosimiliter Gentianellae floridae et G. thiosphaerae affinis, a G. florida statura minore et corollis aureis saepe purpureo-rubrotinctis et ab ambobus thyrsis elongatis et calycum lobis deltoidibus differens.

TYPE: Bolivia. Chuquisaca: [Prov. Jaime] Zudáñez, ca. 2 km from summit on ascent SE of Icla on road to Cordillera de los Sombreros and Azurduy, alt. 3300 m a.s.l., steep slopes with a lot of rock and scattered *Polylepis*, relatively deep and well-drained, locally abundant on steep slopes with sparse grassland, by rocks etc., 13 March 1999 *J.R.I. Wood & M. Serrano 14664* (holotype NY; isotype K, image seen). – PARATYPES: Bolivia. Chuquisaca: On west side of pass between Villa Tomena and Villa Serrano, 2500 m a.s.l., *J.R.I. Wood 9768* (K!); [Prov. Jaime] Zudáñez, on the road from Presto to El Rodeo, near the summit on the ascent south of Presto, *J.R.I. Wood, H. Huallya, & J. Gutiérrez 22646* (K!). La Paz: [Prov.] Inquivisi, ca. 14 km above Quime on the road to La Paz, ascending into Cordillera de las Tres Cruces, *J.R.I. Wood & D.J. Goyder 15557* (K!).

ETYMOLOGY. The specific epithet, a noun in apposition, means "lighthouse." It refers to the flamelike aspect of the many flowers with yellow corollas and the tower-like form of the inflorescence.

Synoecious as far as is known (see Discussion). Plants herbaceous, perennial (see Discussion), 10-45 cm tall. Primary stems 1 to several, erect, proximally 2-3.5 mm in diameter, firm, several-ridged or very narrowly 4-winged, branched from all or most nodes, branches ascending. Leaves basal and cauline, opposite, bases not sheathing; basal leaves ± persistent at flowering time, oblanceolate, mostly 4-9 $cm \times 4-9$ mm, gradually narrowed to slender pseudopetiolate bases, apices obtuse to acute; leaves above basal abruptly more widely spaced, proximal and mid-cauline internodes mostly 20-50 mm long; cauline leaves narrowly elliptic to linear, smaller and proportionately narrower than basal and near-basal, those at mid-stem $8-50 \times 1-7$ mm, rameal leaves and bracts even narrower, apices acute. Inflorescence an elongate thyrse comprising all or nearly all of plant above ground; flowers 40 to 220 or more per plant, in ± dichasial cymules with central flowers larger, earlier, and longer-pedicelled than lateral flowers; pedicels 2-16 mm long; flowers erect. Flowers 5-merous. Calyx 4–8.5 mm long, not strongly ridged, only midveins prominent; lobes narrowly hyaline-margined, distally suffused with purple, erect, all usually similar in size and shape, deltoid or nearly so, (0.9-)1.5-2.5 mm long, (0.8-)1-2.2 mm wide at base, $0.35-0.7\times$ as long as tube, apices acute or short-acuminate; adaxial calycine colleters few. Corolla light yellow throughout or with lobes variably tinged with purplish red, especially toward outer edge, campanulate, 10 (on lowest lateral flowers)-18 mm long (measured closed); lobes spatulate-obovate, $5-7 \times 4-5.5$ mm, $0.75-0.9 \times$ as long as tube, 1.1- $1.5 \times$ as long as wide, apices obtuse to abruptly acute, entire or minutely undulate-erose; adaxial trichomes none; nectaries 5, brownish, slightly raised, nearly orbicular, ca. 0.3 mm in diameter. Filaments inserted at ca. 0.35× height of corolla tube, 4-5.5 mm long; undehisced anthers pale yellow with purple suffusion, ca. 1.6 mm long. Ovary short-stipitate at anthesis. Capsule medium brown, narrowly compressed-ovoid, ca. 9 mm long (excluding stipe); stipe of mature fruit ca. 4 mm long. Seeds not seen.

Gentianella pharos is known only from the four localities in southern Bolivia cited above. At all of those localities this species was found



Fig. 3. Gentianella pharos (from the holotype). -A: Plant, above-ground portion and distal part of caudex. - B: Node in inflorescence. - C: Flower and buds. - D: Flower, with enlargement of a calyx lobe. - E: Portion of corolla, adaxial view, showing lobes, nectaries, and stamens. - F: Fruit and portion of persistent calyx, with enlargement of adaxial calycine colleters.

in rocky soil, on cliffs or steep hillsides sparsely vegetated with grasses and low shrubs, at altitudes from 2800 to 3900 m.

Gentianella pharos was described as perennial by the collectors of the specimens cited in the present paper (data on labels, all specimens). In some of the specimens, a short, \pm erect caudex or rhizome-like portion of the stem is visible below the currently leafy portion, and in some of those specimens the flowering stem arises from the caudex beside the basal remnants of earlier stems. In one specimen portions of a fibrous root system are present below the caudex.

The morphology of *G. pharos* suggests that it may be most closely related to *G. florida* and *G. thiosphaera*, both of which are relatively widely distributed in Bolivia and northern Argentina; *G. bangii* and *G. totorensis*, both of Dpto. Cochabamba, Bolivia; *G. pluvialis* (described in Pringle 2011), of Dptos. Cochabamba and Santa Cruz, Bolivia; and *G. chrysantha*, of Dpto. Santa Cruz, Bolivia. In common with *G. florida*, but with few other Andean species of *Gentianella*, *G. pharos* has nectaries slightly raised above the adaxial corolla surface. Both *G. florida* and *G*. pluvialis differ from G. pharos in their greater plant size, with the inflorescences confined to the distal half or less of the primary stems. Gentianella florida differs in its corymboid inflorescences and cream-colored to nearly white fresh corollas, which become yellow only upon drying if at all, and G. pluvialis differs in its stouter, readily compressed stems and in having corollas 15-25 mm long, with the lobes 2.5-3 times as long as the tube. Gentianella bangii and G. totorensis differ from G. pharos in their monocarpic habit, corymboid inflorescences, and corollas with the lobes 3.5–5 times as long as the tube. In G. thiosphaera and G. chrysantha the inflorescences are dense and subcapitate. Gentianella thiosphaera also differs in its corolla lobes less than half as long as the tube, and G. chrysantha differs in its ovate cauline leaves. In all of the species with which G. pharos is contrasted in this paragraph, except in G. pluvialis and variably in G. florida, the basal leaves are withered or absent at flowering time.

The shape of the calyx lobes of *G. pharos* is unusual in South American *Gentianella*. The calyx lobes of *G. pharos* are deltoid (except

for the abruptly acute to short-acuminate apex), shorter than the tube and scarcely longer than their width at the base, whereas those of *G. bangii*, *G. chrysantha*, *G. pluvialis*, *G. thiosphaera*, *G. totorensis*, and most of those of *G. florida* are longer than the tube, narrowly triangular to nearly linear, 1.5–2 times as long as the basal width in *G. chrysantha* and more than twice as long in the other species.

Heteromorphic flowers prevail among the species to which G. pharos appears to be most closely related. Gentianella bangii is andromonoecious, G. florida and G. chrysantha are gynodioecious, and G. thiosphaera is trimonoecious (Filippa & Barboza 2006). Gentianella pluvialis is confirmed here as being gynodioecious, as both unisexually pistillate specimens (cited and described in Pringle 2011) and specimens with bisexual flowers (Badcock 700, K; Vargas C. & Cruz G. 4938, NY; Zarate MZ2412, MO; not necessarily in other replicates of those collections) are now known. Determination of the breeding system of G. pharos will require the examination of additional specimens. All of the specimens seen in the present study had bisexual (although strongly protandrous) flowers. Gentianella pharos is also somewhat similar to G. pyrostelium (described in Pringle 2011), of northern Peru, in plant size, inflorescence shape, and size and shape of the flowers, which likewise have yellow corollas with a distal reddish suffusion. Gentianella pyrostelium differs from G. pharos in its proportionately stouter stems, nonpseudopetiolate basal leaves, more numerous colleters that are conspicuous in the dissected calyx, somewhat cucullate corolla lobes ca. 1.5 times as long as the tube, more extensively suffused with red, and sessile ovary at anthesis.

Gentianella longipes (Rusby) J.S. Pringle, *comb. nova*

BASIONYM: Gentiana longipes Rusby, Memoirs of the New York Botanical Garden 7: 321. 1927. — TYPE: Bolivia. Cochabamba: Chapare, 12 500 ft, 28 March 1922 M. Cárdenas 76 Special (NY, image seen).

The species described by Rusby (1927) as *Gentiana longipes* has largely been overlooked by subsequent students of the Gentianaceae, and

has remained known from the type collection only. More recently collected specimens of this species, cited below, are now known. These specimens closely correspond to Rusby's (1927) original description of G. longipes. Those in the Lewis collection, with pedicels 29-68 mm long, agree especially well with the description and closely resemble the component of the type on the left. The Zarate collection, with pedicels 14-38 mm long, and the Vargas and Wood collections, with pedicels 10-20 mm long below the fully developed flowers, are more similar to the component on the right. As pedicel length varies conspicuously within the type collection, the shorter pedicels of some of the more recently collected specimens do not preclude their inclusion in the same species. As this species exhibits the morphology of Gentianella, as distinguished from that of Gentiana as the latter genus is now generally circumscribed (see Introduction), the nomenclatural transfer to Gentianella is made here.

Plants of Gentianella longipes are small and monocarpic, in habit reminiscent of low cudweed, Gnaphalium uliginosum. The decumbent primary stems are generally less than 15 cm long, with short branches that each bear 1 to 5 flowers. The leaves are linear to narrowly elliptic or narrowly oblanceolate, $5-16 \times 0.5-3.7$ mm, ± evenly spaced, with no basal rosette present at flowering time. The bases are not connatesheathing, the margins are narrowly revolute, and the apices are obtuse. In aspect, G. longipes resembles G. soratensis, which is likewise native to Dpto. La Paz, Bolivia. It is also somewhat similar to G. gageoides and to G. silenoides (excluding G. inaequicalyx but otherwise as circumscribed by Ho and Liu (1993), especially to var. silenoides, the smaller-flowered of the two varieties of that species accepted here. Gentianella longipes differs from all of those taxa in having corolla lobes 3-4 times as long as the tube; the corolla lobes of G. gageoides are about twice as long as the tube and those of G. soratensis and G. silenoides are 1-1.4 times as long as the tube. The habit of G. gageoides is more upright, and its leaves are lanceolate to ovate, widest below the middle, proportionately wider and less closely spaced than those of G. longipes. Gentianella soratensis is perennial

whereas G. longipes is monocarpic.

OTHER SPECIMENS EXAMINED: **Bolivia**. Cochabamba: Prov. Ayopaya, 25–30 km S of Independencia on road to Cochabamba via Kami, *J.R.I. Wood 16030* (NY); Prov. Arani, Cordillera Tiraque, around shores of Laguna Cajitilla Khochá, *M. Lewis 23 June 1985* (F). La Paz: Warisata, Cumbre, base de la Cordillera de Illiampu, *M. Zarate MZ2437* (HAM, BOLV not seen). Santa Cruz: Prov. Vallegrande, Aguaditas, entre Khazamonte y Los Sitanos, *I. Vargas C. 173* (NY).

Gentianella totorensis (Gilg) J.S. Pringle, *comb. nova*

BASIONYM: Gentiana totorensis Gilg, Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 54(2, Beiblatt 118): 84. 1916. – TYPE: Bolivia. Cochabamba: Auf kahlen Hochflächen bei Totora, 3000 m, T.C.J. Herzog 2032 (B, destroyed, photo seen).

Gentiana totorensis was included in the synonymy of Gentianella florida by Ho and Liu (1993), but they had not seen nomenclaturally significant specimens or photographs. Gilg (1916, in key) distinguished these species on the basis of plant size and alleged differences in the apices of the corolla lobes, but in his descriptions of both species the apices of the corolla lobes were said to be rounded. Studies of more recently collected material, along with photographs of nomenclaturally significant specimens, have disclosed that additional differences distinguish the tall, showy G. florida (to 1 m) from the diminutive G. totorensis (to 20 cm, often much less). Both species are generally single-stemmed at the base, with proportionately wide, corymboid cymes, both are similar in nectary morphology, and both are probably gynodioecious, although G. totorensis should be given further study. As described by Filippa and Barbosa (2006) and as seen in the present study, the leaves of G. florida below the inflorescence are elliptic, $13-95 \times 6-10(-35)$ mm, the lowest pseudopetiolate. The calyx lobes are $0.8-2 \times$ as long as the tube, narrowly triangular, with the apex acute or, if acuminate, less strongly so than that of G. totorensis. The corollas are creamcolored or white when fresh, with the lobes ca. 2 or rarely $3 \times$ as long as the tube. The leaves of G. totorensis, in contrast, are narrowly linear; the proximal leaves are 1-3 mm wide, transitional to distal leaves 0.8-1 mm wide. The calyx lobes are $2-3.3 \times$ as long as the tube, linear to nearly acicular, with a distinctly acuminate apex. The corollas are light yellow, sometimes with a reddish-purple abaxial suffusion, with the lobes mostly $3-4\times$ as long as the tube. Gentianella totorensis is similar to G. bangii in plant size and habit, but in that species the stems are stouter and the leaves are oblanceolate to narrowly obovate; the proximal leaves are mostly 4-9 mm wide, transitional to distal leaves mostly 1.8-2.5 mm wide. The calyx lobes of G. bangii are oblong, parallel-sided most of their length or occasionally narrowly triangular, 1-2 mm wide, with the apex abruptly acute but not acuminate. In branching pattern, inflorescence form, and calyx morphology G. totorensis is similar to G. thiosphaera, but the leaves of G. thiosphaera are elliptic to lanceolate, $15-35 \times 4-12$ mm, and, as noted above, the corolla lobes of that species are less than half as long as the tube.

OTHER EXTANT SPECIMENS EXAMINED: **Bolivia**. Cochabamba: Prov. Mizque, on ascent from Mizque towards Arani, *J.R.I. Wood & H. Huaylla 23209* (K); Prov. Carrasco, Tiraque Chico, a poco km del pueblo, carretera principal Cochabamba–Santa Cruz, *M. Zarate MZ3006* (HAM, BOLV not seen).

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