

MORPHOLOGY CORROBORATES DNA SEQUENCE DATA
IN THE SPECIES-LEVEL RECOGNITION OF
GAULTHERIA TRICHOPHYLLA VAR. *TETRACME* (ERICACEAE)

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ABSTRACT

Gaultheria trichophylla var. *tetracme* of *G. series Trichophyllae* (Ericaceae) has been distinguished from the nominate variety of *G. trichophylla* by the presence of two awns on each anther theca (versus one). Phylogenetic data based on plastid DNA sequences placed *G. t. var. tetracme* in a different clade than the nominate variety with strong statistical support, suggesting that *G. trichophylla* is not monophyletic. To investigate this further, we studied the morphology of these two taxa in the field and with herbarium material. We found that *G. t. var. tetracme* differs substantially from the nominate variety in morphology, not only by the number of anther awns, but also the larger size of many features, e.g., plant height, leaves, and pedicels, a greater number of leaf marginal setae, and a distinct geographic range. On this basis, we elevate *G. t. var. tetracme* to the species level as ***Gaultheria tetracme***, endemic to the Hengduan Shan in Sichuan Province, China. We note the wide morphological variation in the remainder of *G. trichophylla* and indicate specific problems that should be investigated in more detail for better understanding the taxonomy of this species.

KEY WORDS: China, Ericaceae, *Gaultheria*, *Gaultheria series Trichophyllae*, Himalaya-Hengduan Mountains, new species

RESUMEN

Gaultheria trichophylla var. *tetracme* de *G. series Trichophyllae* (Ericaceae) se ha distinguido de la variedad nominal *G. trichophylla* por la presencia de dos aristas en cada teca de la antera (contra una). Los datos filogenéticos basados en secuencias de ADN plastidial colocan a *G. t. var. tetracme* en un clado diferente al de la variedad nominal con un soporte estadístico fuerte, que sugiere que *G. trichophylla* no es monofilética. Para investigar esto mejor, estudiamos la morfología de estos dos taxa en el campo y en material de herbario. Encontramos que *G. t. var. tetracme* difiere sustancialmente de la variedad nominal en morfología, no solo por el número de aristas en las anteras, sino también por el mayor tamaño de muchas características, ej. altura de la planta, hojas, y pedicelos, un mayor número de setas marginales de la hoja, y un rango geográfico diferente. Sobre esta base, elevamos *G. t. var. tetracme* al nivel de especie como ***Gaultheria tetracme***, endémica de Hengduan Shan en la provincia de Sichuan, China. Notamos la amplia variación morfológica en el resto de *G. trichophylla* e indicamos problemas específicos que deben investigarse con más detalle para una mejor comprensión de la taxonomía de esta especie.

INTRODUCTION

Gaultheria series Trichophyllae Airy Shaw comprises a clade of 19 species endemic to the Himalaya-Hengduan Mountains of eastern Asia (Airy Shaw 1941; Fritsch et al. 2008, 2015a, b, 2016). The group is distinguished from all other species of *Gaultheria* by the combination of leaves generally < 1 cm long, solitary axillary flowers, paired apical bracteoles, and five calyx and corolla lobes (Middleton 1991; Lu et al. 2010). The geographic range of one of the species in the series, *G. trichophylla* Royle, approximates that of the entire series, i.e., from the far western Himalaya to the eastern edge of the Hengduan Shan in Sichuan Province, China and south to the Cang Shan in Yunnan Province (Airy Shaw 1941; Fang & Stevens 2005). This species had been considered distinct from others in the series mainly by the relatively long setae that terminate each serration of the leaf margin. Beginning with Airy Shaw's (1941) revision of *G. series Trichophyllae*, several varieties of the species were recognized on the basis of features such as setae length, leaf shape, and the number of anther awns (Long 1988; Rae 1991; Fang & Stevens 2005; Panda & Sanjappa 2006).

A phylogenetic study based on DNA sequence data of the “Core East Asian Clade” of *Gaultheria*, which includes *G. series Trichophyllae*, yielded results in which samples representing three of the varieties of *G. trichophylla* did not form a monophyletic group, but instead were scattered in different places across the tree (Lu et al. 2010). Subsequent study confirmed that two of these varieties, *G. t. var. eciliata* S.J. Rae & D.G. Long and *G. t. var. obovata* Airy Shaw, possess morphological characters justifying their recognition at the species level, and that the long setae shared by these taxa result from homoplasy in this character. These varieties were consequently elevated to the rank of species (Fritsch et al. 2008, 2015b). A third variety, *G. t. var. tetracme* Airy Shaw, although shown to group in a separate clade from samples of the nominate variety in the molecular phylogenetic analysis, lacked enough data from morphology to confidently assess its taxonomic status. Missing in particular were field observations critical for assessing fruit characters not observable on dried herbarium specimens; the critical importance of such characters for the delimitation of species in the series has only recently been understood (Lu et al. 2010).

Field expeditions by the authors were conducted in September 2011 and June 2015 to examine living plants of *Gaultheria trichophylla* var. *tetracme* in fruit and flower, respectively. Morphological observations based on the results of these expeditions, in combination with the prior molecular results and the study of herbarium material at A, BM, CAS, E, K, and KUN, warrant the elevation of this variety to the species level, as presented and discussed below.

TAXONOMIC TREATMENT

Gaultheria tetracme (Airy Shaw) P.W. Fritsch & Lu Lu, comb. & stat. nov. (**Figs. 1, 2**). BASIYNYM: *Gaultheria trichophylla* Royle var. *tetracme* Airy Shaw, Bull. Misc. Inform. Kew 1940:323. 1941. TYPE: CHINA. Sichuan: 14,000 ft, Jul 1904, E.H. Wilson 3915 (HOLOTYPE: K barcode 000227993; ISOTYPES: A [2 sheets: barcode 00014981 n.v., internet image! at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.a00014981>, barcode 00014982 n.v., internet image! at <http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.a00014982>]).

Shrublets, ascending-erect, with stems to 10 cm long from horizontal stolons, hermaphroditic. Current-year branchlets brown proximally, pale green and strongly flushed red above distally, to 4 cm long, sparsely white-puberulent and with ascending to nearly erect straight or slightly undulate setae, setae ranging from minute to as long as 1.4–1.8 mm long. Internodes between largest leaves averaging ca. 1.4–2.5 mm long. **Leaves:** petioles 0.9–1.3 mm long, abaxially glabrous, adaxially with sparse white puberulence in a line on midvein, margins entire; blades ovate-elliptic or elliptic, ranging from as small as 3 × 2.2 mm (typically at the proximal and distal ends of the current year's growth) to as large as 11–14 × 5–7.3 mm, 1.9–2.2 times as long as wide, subcoriaceous, planar, abaxially dull whitish green except glossy green or occasionally flushed maroon toward margin, glabrous; adaxially glossy green, glabrous except for often sparse white puberulence proximally on midvein; midvein abaxially raised, not thickened immediately below apical gland, adaxially impressed; secondary veins abaxially obscure or 1 to 3 faintly evident on each side of midvein, adaxially obscure or 1 to 5 faintly evident on each side of midvein, impressed; tertiary veins often visible adaxially, impressed; base broadly cuneate to subrounded; margin serrulate except at very base, slightly revolute; marginal setae 9 to 18 per side, all oriented off leaf surface (versus often incurved in some other species so as to lie atop the leaf surface), straight or slightly undulate, the longer 1.1–1.4 mm long; apex acute to subrounded, tip with planar or usually distinctly abaxial-directed apical gland, midvein not thickened immediately below gland. Overwintering flower bud pedicels 2–3 mm long, glabrous, buds 1.2–2.6 × 1–1.7 mm, slightly compressed laterally, 1.1–1.5 times as long as wide, glabrous, bracteoles slightly keeled, their margins eciliate or rarely sparsely ciliate. **Flowers** 4–6 mm long. Calyx dull pink proximally, green on distal 3/4 of lobes, 2.7–3.4 mm long; lobes narrowly deltoid, 1.7–2.7 × 1.4–1.8 mm, abaxially glabrous, adaxially glabrous or occasionally sparsely puberulent at apex, with eciliate or occasionally sparsely ciliate margin and acute apex. Corolla white flushed pink in lines near petal midveins, campanulate, 3–4.5 × 4.3–7.1 mm; lobes 1.5–3.2 × 2–3 mm. Stamens 10; filaments widest at middle or slightly more distally, 0.8–1 mm long; anthers yellow, with cells 0.6–0.8 mm long and with 2 awns per theca; awns 0.2–0.4 mm long. Nectary disk with strongly deltoid teeth. Style 1.7 mm long; stigma pink. Fruiting pedicel 2.5–5 mm long. **Fruit** with fleshy accrescent calyx slightly oblate, subglobose, closed, 7–10 × 8–12 mm,

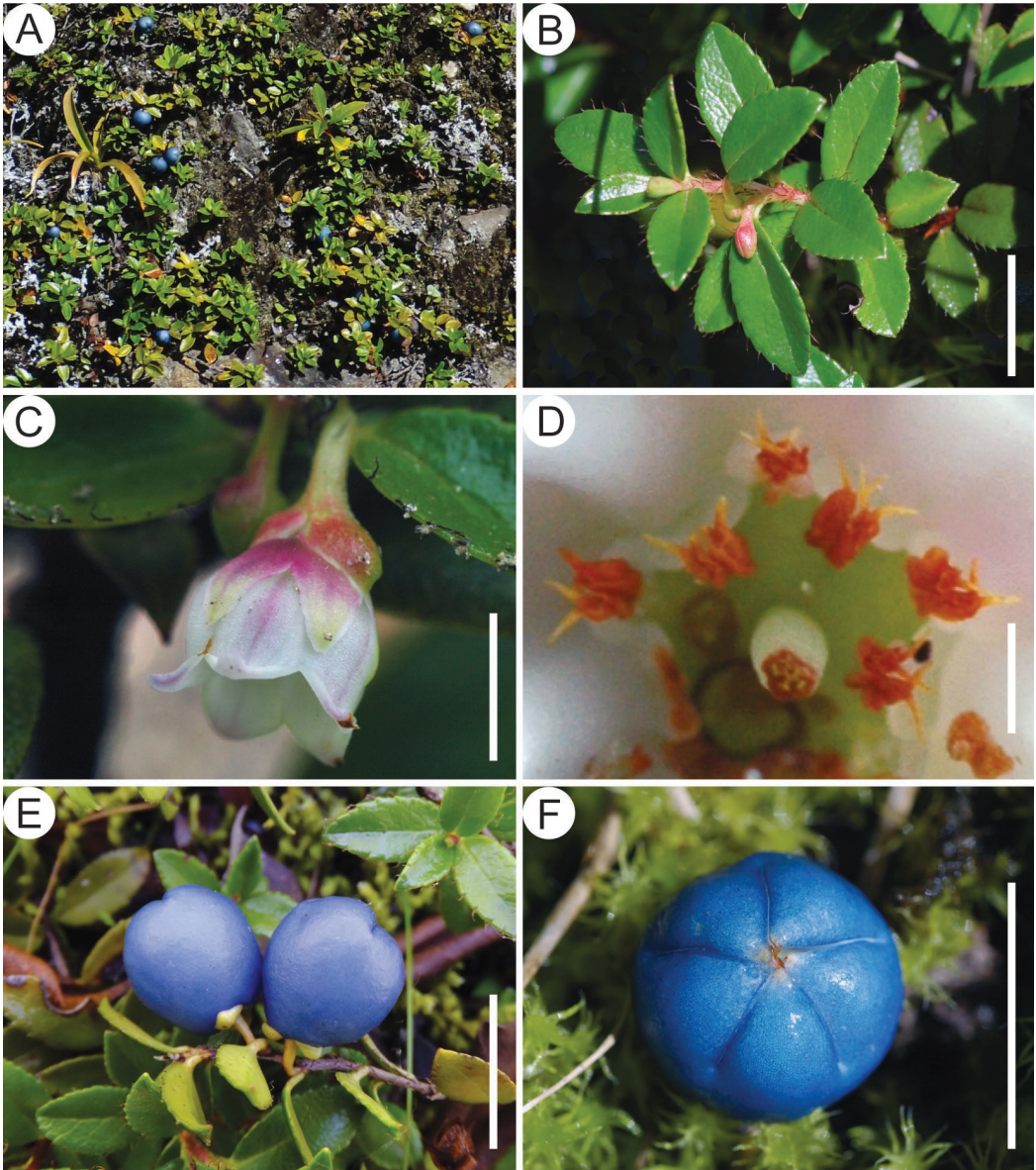


FIG. 1. *Gaultheria tetracme*. A. habit; B. branchlet with overwintering flower buds; C. flower; D. top of ovary apex, style, and six stamens (distal portion of style and other four stamens damaged by herbivory). Two awns can be seen clearly on some anther thecae, e.g., at far left; E. branchlet with fruit in lateral view; F. fruit, apical view. Scale bars: B, E, F = 10 mm; C = 5 mm; D = 0.5 mm. [Photos by P.W.F. and L.L.; A–F, L. Lu & P.W. Fritsch LL-2011-31].

its outer wall turquoise blue and inner wall white; lobes contiguous or only slightly overlapping, 3–6 mm long, narrowly deltoid, incurved, margins straight, apex glabrous or sparsely ciliolate adaxially. Capsule green, enclosed by calyx lobes. **Seeds** light brown.

Distribution, Habitat, and Phenology.—*Gaultheria tetracme* is endemic to the Hengduan Shan in western Sichuan Province, China, where it is known definitively only from Luding and Tianquan counties in the Gongga and Erlang ranges, respectively. The species occurs from 2872 to 4267 m elevation, growing in subal-

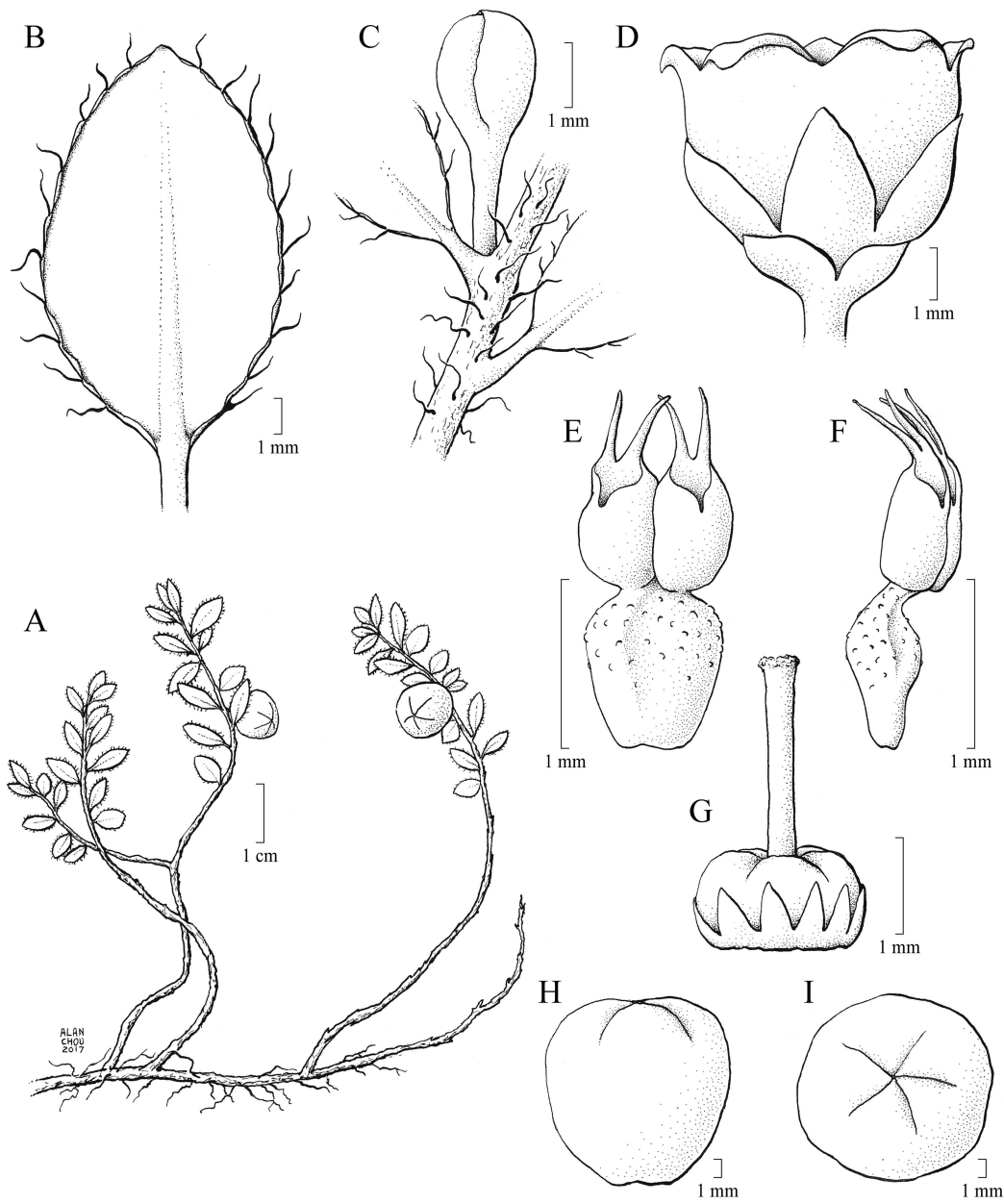


FIG. 2. *Gaultheria tetracme*. **A.** habit of fruiting plant; **B.** leaf, abaxial view; **C.** portion of branchlet with basal part of two leaves (abaxial sides), and flower bud; **D.** pedicel with bracteoles, and flower; **E.** stamen, ventral view; **F.** stamen, lateral view; **G.** nectar glands and gynoecium; **H.** fruit, lateral view; **I.** fruit, apical view. (A)–(C) from *L. Lu and P.W. Fritsch LL-2011-31* (CAS); (D)–(G) from the holotype *E.H. Wilson 3915* (K); (H)–(I) from *L. Lu and P.W. Fritsch LL-2011-31* (CAS) and images of the living plants.

pine areas of coniferous or mixed forests with *Rhododendron* on slopes among rocks and mosses. It flowers in June and July (the authors observed one individual flowering in September), and fruits in August and September.

Conservation Assessment.—The geographic distribution of *Gaultheria tetracme* is known with certainty from only four collections in western Sichuan Province, representing what can be considered as three populations. The two collections from the Gongga Shan in Luding County, separated by 2 km but from the same valley, are protected by their occurrence in Hailuoguo Glacier Park. The other two collections were made from the sole population known from the Erlang Shan in Tianquan County. Mining, grazing, and dam-building activities in the Erlang Shan region suggest a projected decline. As calculated with the aid of GeoCAT (Bachman et al. 2011), the area of occupancy (AOO) is 8 km². In accordance with the criteria specified in IUCN (2014), we categorize this species as 'Endangered' (EN): B2ab(iii).

Discussion.—Airy Shaw (1941) delimited *Gaultheria trichophylla* var. *tetracme* from the nominate variety by the presence of two awns on each anther theca (versus one) and ovate or ovate-oblong leaf blades (versus oblong-elliptic), while also indicating anther awns in *G. t.* var. *tetracme* as nearly 1 mm long (we have only observed anther awns that do not exceed 0.4 mm). Airy Shaw wrote that "Dr. O. [Otto] Stapf's manuscript notes show that he—at any rate provisionally—regarded this form with 4-horned [-awned] anthers as specifically distinct. It does not, however, seem possible to correlate with this character any other really tangible differences (the leaf character mentioned being very slight), and I am therefore unwilling to accord these specimens more than varietal rank." Molecular phylogenetic analysis based on DNA plastid sequences that placed this variety in a different clade from samples of the nominate variety with strong support (100% parsimony bootstrap and 1.00 Bayesian posterior probability; Lu et al. 2010) suggested to us that the former should be elevated to the species rank on the basis of the apomorphic species concept (Donoghue 1985; Platnick & Wheeler 2000).

Furthermore, the differences in gross morphology between *Gaultheria tetracme* vars. *trichophylla* and *tetracme* are substantial enough to warrant the recognition of *G. t.* var. *tetracme* at the species level on the basis of a morphological species concept (Cronquist 1978; Levin 1979). *Gaultheria trichophylla* var. *tetracme* is similar to the nominate variety in its relatively long leaf marginal setae, bicolored calyx (dull pink proximally, with the lobes green on their distal 3/4), narrowly deltoid calyx lobes, slightly laterally compressed overwintering flowering buds, campanulate corollas, and closed fruiting calyces. It differs, however, not only in anther awn number but also by its generally more robust nature in many characters, i.e., petioles 0.9–1.3 mm long (versus 0.5–0.8 mm), leaf blades (the larger ones on sheets) elliptic or ovate-elliptic and 11–14 × 5–7.3 mm [versus 3.7–10 (–13 if oblanceolate) × 2.5–5 mm] with 9 to 18 marginal setae per side (versus 6 to 12), and overwintering flower bud pedicels 2–3 mm long (versus 0.6–2.5 mm). The two taxa are also distinct geographically, with *G. t.* var. *tetracme* endemic to the Hengduan Shan in Sichuan Province, China and the nominate variety occurring in Yunnan and Tibet in China, extending westward along the Himalaya to Pakistan.

In the protologue of *Gaultheria trichophylla* var. *tetracme*, Airy Shaw includes *E.F. Norton Exped. S. Tibet 172* [China. Xizang Province. Samchung La (Kharta), in stony soil, facing north, flowers pink, 4650 m, 20 June 1922 (K!)] because of its 2-awned anther thecae. In this respect and in its glabrous abaxial leaf surfaces it is indeed similar to the type of Airy Shaw's *G. t.* var. *tetracme* (our *G. tetracme*), but the petioles are shorter (0.5–0.8 versus 0.9–1.3 mm) and the leaf blades smaller (7–7.4 × 4–5.1 mm versus 11–14 × 5–7.3 mm) with fewer marginal setae per side (5 to 7 versus 9 to 18). Because these characters fall within the range of *G. trichophylla* sensu stricto, and considering the difference in geographic range, we exclude *Norton 172* from our circumscription of *G. tetracme* and retain it in *G. trichophylla*, with the caveat that *G. trichophylla* requires further study to understand the taxonomic significance of character variation within this species (see below).

The recognition of *Gaultheria tetracme* as a species brings the total number of species in *Gaultheria* series *Trichophyllae* to 20. The substantial morphological variation observed in *G. trichophylla* suggests that other species are warranted as segregates of this species. In the Cang Shan west of Dali in Yunnan Province, China, populations differ from those of any other population of *G. trichophylla* that we have observed by their obovoid open light blue fruiting calyces. In Gongshan County of Yunnan, at the pass near Dongshaofang in the

Gaoligong Shan, we observed plants with deep red corollas, unlike the white or at most pink corollas that we have observed or that have been reported in other plants of *G. trichophylla*.

The leaves of *Gaultheria tetracme* are always glabrous abaxially, whereas those of *G. trichophylla* in Yunnan, China (and other areas) typically have at least one seta on the midvein or petioles abaxially on at least one leaf in most individuals on a herbarium sheet. Glabrous exceptions to the latter occur in the material from the Meili Xue Shan and Biluo Xue Shan in Deqin County of northwestern Yunnan, suggesting that these populations belong to *G. tetracme*. The leaves in these cases, however, are distinctly smaller than those of *G. tetracme*, and well within the size range of *G. trichophylla*. Moreover, our field observations indicate a possibly distinct fruit character in these populations, i.e., strongly overlapping calyx lobes with convex sides (versus lobes that are merely contiguous or only slightly overlapping with straight sides in *G. tetracme* and other populations of *G. trichophylla*). Further consideration of the taxonomic status of the Meili Shan and Biluo Shan plants must await the documentation of flower morphology from these areas.

In addition to the Chinese plants of *Gaultheria trichophylla*, those from the Himalaya also exhibit substantial variation, as shown by *G. trichophylla* var. *ovata* Panda & Sanjappa (Panda & Sanjappa 2006) which has ovate leaves, unlike the nominate variety in which the leaves are generally narrowly elliptic. Specimens identified on collection labels simply as *G. trichophylla* (without varietal status indicated) in the Himalaya exhibit leaf variation from small and nearly rounded to large and narrowly elliptic (P.W.F. pers. obs.). It is not yet clear whether other characters, such as a prostrate habit, the presence of setae on the leaves abaxially, and fruit shape and color, are correlated with leaf size. *Gaultheria sinensis* J. Anthony var. *layaensis* S.J. Rae & D.G. Long (Long 1988), based only on the type [Bhutan. Laya, Upper Mo Chu, 14,000 ft., cliff faces, calyx red, corolla pale pink, 9 June 1949, F. Ludlow, G. Sherriff & J.H. Hicks 16465 (E!)], appears similar to some variants of *G. trichophylla* in its small rounded leaf blades ca. 4×2.8 mm (the largest on each specimen) with glabrous abaxial surfaces and ca. 6 marginal setae, and narrowly deltoid calyx lobes, but has shorter leaf marginal setae (to ca. 0.5 mm long), globose overwintering flowering buds (versus slightly compressed laterally), and two awns per anther theca (versus usually one). The fruit is unknown. Also to be considered are several Himalayan and southeastern Tibetan specimens of *G. trichophylla* with 1 awn on each anther sac, but the awns having a 2-pronged fork at their apices [e.g., *Qinghai-Tibet Expedition 5534* (KUN!)]; occasionally this fork is only present in one of the two awns of an anther. Are these to be interpreted as one awn divided at the apex, or two awns strongly united at the base? In the latter case, the typical 1-awned anthers of *G. trichophylla* could be considered a fusion of the more widespread 2-awned condition throughout the rest of *G. series Trichophyllae*. All these variants should be studied in more detail to more fully understand the nature and taxonomic significance of morphological variation in *G. trichophylla*.

Additional specimens examined. **CHINA. SICHUAN PROVINCE. Luding Co.:** Jiang Zhou, year 1930, Z.P. Huang et al. 01950 (KUN!); E slope of Gongga Shan, Hailuoguo Glacier Park, W of Moxi, 29.56643°N, 101.98308°E, 3187 m, 15 Sep 2011, L. Lu & P.W. Fritsch LL-2011-31 (CAS!, KUN [2!]); *ibid.*, 11 Jun 2015, L. Lu & M.Y. Zhang LL-2015-06 (BRIT!, KUN!); *ibid.*, 29.55088°N, 101.96997°E, 3576 m, 11 Jun 2015, L. Lu & M.Y. Zhang LL-2015-14 (KUN!); Gongga Shan, > 3000 m, Aug 2007, S.-D. Zhang & W.-B. Yu 013 (CAS!, KUN!). **Tianquan Co.:** Yazikou Pass, old state road from Tibet to Sichuan, above tunnel on Hwy G318, summit ridge of Erlang Shan, 29.86113°N, 102.29115°E, 2908 m, 16 Sep 2011, L. Lu & P.W. Fritsch LL-2011-36 (CAS!, KUN [2!]); *ibid.*, 29.86172°N, 102.2912°E, 2872 m, 10 Jun 2015, L. Lu & M.Y. Zhang LL-2015-03 (BRIT!, KUN!). **County unspecified:** near Tachienlu [Kangding], 2700–4100 m, A.E. Pratt 833 (E!, GH!, K not seen, P[2!]).

ACKNOWLEDGMENTS

We thank the curators of A, BM, CAS, E, K, and KUN for loans or access to herbarium material; the Kunming Institute of Botany, Chinese Academy of Sciences, for two two-month-long Visiting Professor for Senior International Scientists scholarships to PWF in 2013 and 2016 (2010T2S05); R.-F. Lu for field assistance; S.-D. Zhang & W.-B. Yu for alerting the authors to their rediscovered location of *G. trichophylla* var. *tetracme* in Gongga Shan; and David Boufford, Walter Judd, and Peter Stevens for helpful comments on the manuscript. This study was supported by grants from the U. S. National Science Foundation (DEB-0103795 and DEB-0717711), the National Geographic Society (148057 to PWF), the National Natural Science Foundation of China (41671052 to LL) and the Yunnan Applied Basic Research Project (C0120160260 to LL).

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