Salazar G (2009) DNA, morphology, and systematics of *Galeoglossum* (Orchidaceae, Cranichidinae).
In: Pridgeon A M, Suarez JP (eds) Proceedings of the Second Scientific Conference on Andean Orchids.
Universidad Técnica Particular de Loja, Loja, Ecuador, pp 161-172.

DNA, MORPHOLOGY, AND SYSTEMATICS OF *GALEOGLOSSUM* (ORCHIDACEAE, CRANICHIDINAE)

Gerardo A. Salazar

Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-367, 04510 México, D.F., México; E-mail: g.salazar@ibiologia.unam.mx

Abstract

DNA sequence data have contributed greatly to our understanding of the phylogenetic relationships of orchids. Although structural data also provide useful systematic information, collecting detailed morphological information for a non-trivial set of taxa usually consumes more time and resources than obtaining DNA sequences of a few genes for the same set of taxa. In this paper an example is given of how both DNA sequences and morphological data contributed to the clarification of the systematic position of two problematic species, namely *Prescottia tubulosa* (Lindl.) L.O.Williams and *Pseudocranichis thysanochila* (B.L.Rob. & Greenm.) Garay. A close relationship between these two species was first suggested by Salazar *et al.* (2003) based on a study of flowers from herbarium specimens and has been corroborated by subsequent molecular phylogenetic analyses, supporting their transfer to the genus *Galeoglossum* A.Rich. & Galeotti (the oldest name available for a clade that includes only these two species). As understood here, *Galeoglossum* is diagnosed by a labellum provided with a distinct apical lobule, saddle-shaped stigma with two lateral receptive areas separated by a sterile area, and ribbon-like pollinia.

The application of DNA sequence data to orchid systematics has opened a practically endless source of character information to explore the phylogenetic relationships of the family, permitting, for instance, assessment of earlier classifications that typically were based on a small number of morphological (mostly floral) characters (Cameron *et al*., 1999; Chase, 1999; Cameron and Chase, 2000; Chase *et al*., 2003). Molecular phylogenetic studies have made an important contribution in corroborating the monophyly of some groups recognized in previous systems (e.g., Dressler, 1993), but they have also permitted the discovery of unexpected relationships in many orchid lineages, from subfamily to genus levels (reviewed in Chase et al., 2003; Cameron, 2007).

As valuable as DNA sequences have proven to be, they do not invalidate the potential contribution of structural characters to orchid systematics. Nevertheless, the time and expense required to collect a large number of morphological characters for a non-trivial group of taxa are usually much greater than for DNA sequences (Chase, 1999; Pridgeon *et al.*, 2001). Consequently, data sets of structural characters suitable for cladistic analysis do not exist for many orchid groups, and few attempts have been made to conduct cladistic analyses of orchids using structural characters and algorithmic, repeatable methods (e.g., Romero, 1990; Johnson *et al.*, 1998; Freudenstein and Rasmussen, 1999). Even fewer orchid studies have analyzed simultaneously both DNA sequence data and morphological characters for the same set of taxa, but these have shown that both types of characters are largely complementary and that the structural characters often mark clades recovered in the combined analyses (Albert, 1997; Figueroa *et al.*, 2008).

In this contribution I adduce an example of “reciprocal illumination” between morphology and DNA sequences that has helped to clarify the systematic position of some problematic orchid species, namely *Prescottia tubulosa* (Lindl.) L.O.Williams and *Pseudocranichis thysanochila* (B.L.Rob. & Greenm.) Garay. Although the structural information relevant to this problem has not been included in a formal cladistic analysis, the distribution of morphological character states provides additional support to the groupings recovered in the molecular phylogenetic trees (Figueroa *et al.*, 2008; Salazar *et al.*, 2009).

Taxonomic background

Lindley (1840) described *Cranichis tubulosa* from a specimen collected in Mexico, noting, however, that the fusion of the sepals and petals forming a short tube and the “deeply emarginated stigma” were atypical features for *Cranichis*. On the other hand, Richard and Galeotti (1845) described *Galeoglossum prescottioides* based on material collected by Galeotti in Mexico. Williams (1939) concluded, without discussing his rationale, that *C. tubulosa* belonged in *Prescottia*, made the required transfer, and included *G. prescottioides* in the synonymy of *Prescottia tubulosa*.

The genus *Pseudocranichis* was proposed by Garay (1982) to accommodate a single species originally described as *Cranichis thysanochila* B.L.Rob. & Greenm., distinguishing *Pseudocranichis* by floral characteristics such as the “tear-drop-like” column with a substipitate, oblique base and truncate at the top, and the two separate “stigmata” located on the sides of the truncate rostellum. He placed *Pseudocranichis* in subtribe Spiranthinae Lindl., but a few years later Burns-Balogh (1986) considered that it belonged in subtribe Cranichidinae Lindl., as did Dressler (1993). However, subsequent taxonomists have included it in Prescottiinae Dressler (Szlachetko, 1995; Vargas, 1997). Recently, Chase (2003) and Salazar *et al.* (2009) argued for the reinstatement of Cranichidinae in the broad sense, i.e., including the genera segregated by Dressler (1990) in Prescottiinae, in the absence of support for monophyly of the latter (Salazar *et al.*, 2003, 2009; Figueroa *et al.*, 2008).

Vargas (1997) noted that *Prescottia tubulosa* differs from other species of the genus in various vegetative and floral features, such as the compact basal rosette of leaves, which are withered at anthesis, and the involute rather than calceolate labellum, and suggested its transfer to *Porphyrostachys* Rchb.f. (although such a change has never been validly published). Salazar *et al.* (2003) discussed the unusual features of *P. tubulosa* and pointed to its previously unnoticed similarities in labellum and

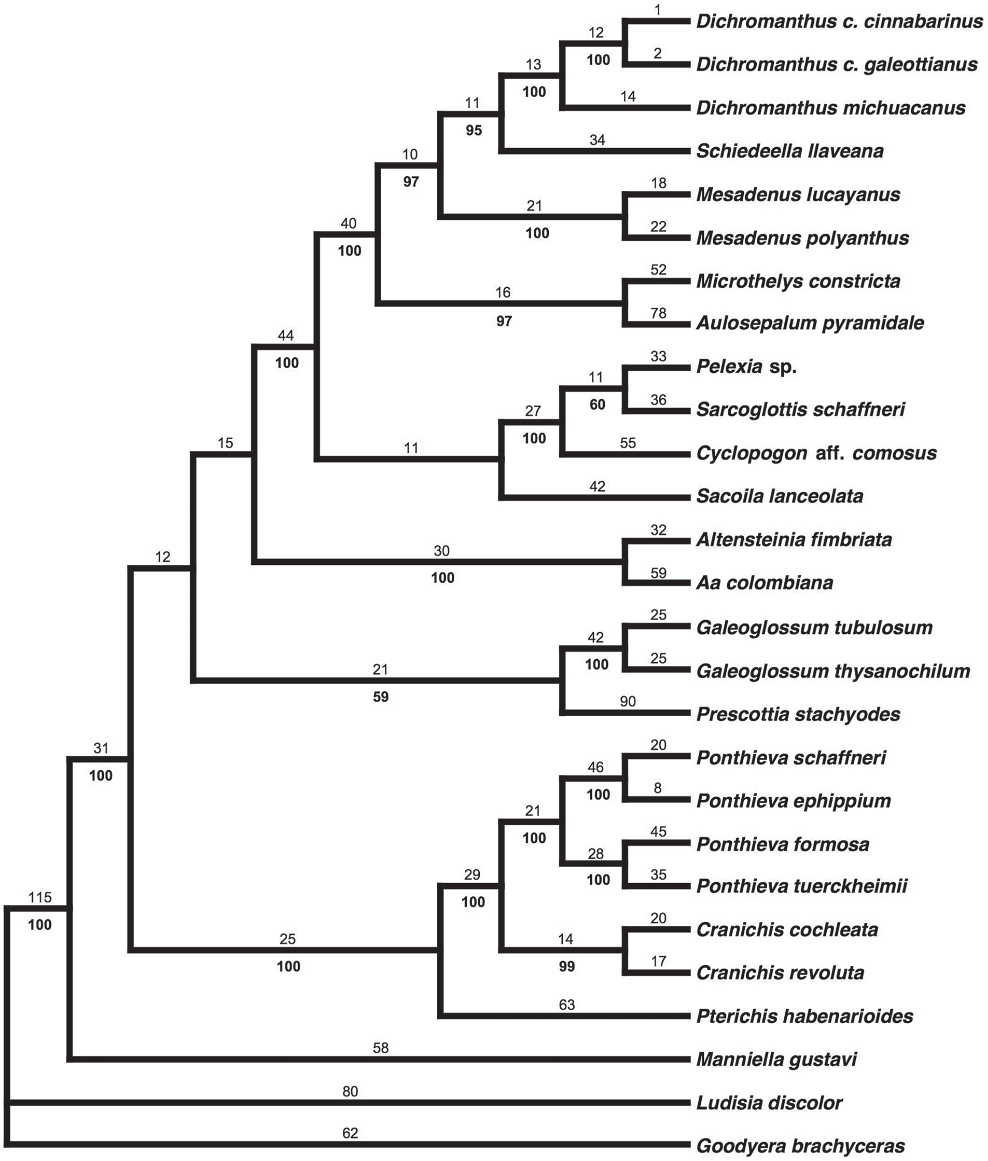

Figure 1. Single most-parsimonious tree obtained in a cladistic analysis of nuclear (ITS) and plastid (*matK-trnK*) DNA sequences plus three structural characters of the root. Numbers above branches are number of changes; numbers below branches are bootstrap percentages. Modified from Figueroa *et al.* (2008).

column morphology to *Pseudocranichis thysanochila*. However, lack of material suitable for molecular study prevented the inclusion of *P. thysanochila* in their molecular phylogenetic assessment of Cranichideae based on plastid and nuclear DNA sequence data. Recently, Figueroa *et al.* (2008) included both *Prescottia tubulosa* and *Pseudocranichis thysanochila* in a phylogenetic analysis of 26 representatives of Cranichideae based on DNA sequence data from nuclear (ITS) and plastid (*matK-trnK*) DNA, plus three structural characters of the root. In their phylogenetic tree reproduced here **(Fig.**

1), *Pseudocranichis* [*Galeoglossum*] *thysanochila* was strongly supported as the sister species of *Prescottia* [*Galeoglossum*] *tubulosa*, making *Prescottia* paraphyletic. A sister-group relationship between those two species has been corroborated by a cladistic analysis of nearly 6000 base pairs of plastid and nuclear DNA for 45 species and 14 genera previously included in Cranichidinae and Prescottiinae (Salazar *et al.*, 2009). Salazar *et al.* (2009) argued for the removal of *P. tubulosa* from *Prescottia* to achieve monophyly, and here we transfer both *P. tubulosa* and *P. thysanochila* to *Galeoglossum* A.Rich. & Galeotti, the oldest generic name available for this group, on the basis of their compelling morphological and genetic similarities (see nomenclatural synopsis below).

Morphology of *Galeoglossum*

At the time of publication of the first molecular phylogenetic analysis of Cranichideae (Salazar *et al.*, 2003), only herbarium specimens of *G. thysanochilum* were available for study, and the morphological observations of floral attributes were made on dried, pressed flowers softened in hot, soapy water. Subsequently we have studied live flowering plants of both *G. thysanochilum* and *G. tubulosum* in the field and the laboratory, which allowed us to attain a better understanding of their peculiar attributes. Additionally, we studied dried and liquid-preserved specimens of both species housed at several major herbaria, including AMO, F, K, MEXU, MO, NY, SEL, and W.

Both species of *Galeoglossum* are vegetatively similar. Plants consist of a fascicle of fleshy, cylindrical roots up to about 1 cm in diameter and a rosette of sessile leaves. Those of *G. thysanochilum* are mostly ovate or elliptic and have a characteristic bluish hue, whereas those of *G. tubulosum* are of a brighter green and proportionately longer, mostly oblanceolate to obovate **(Fig. 1A)**. Both species are drought-deciduous and shed their leaves during the peak of the dry season (December to April).

Galeoglossum thysanochilum (B.L.Rob. & Greenm.) Salazar flowers when leaves are still present and functional (October and November), whereas in *G. tubulosum* (Lindl.) Salazar & Soto Arenas anthesis occurs after the wilting of the leaves (December to April). The inflorescence of *G. thysanochilum* is more congested than that of *G. tubulosum* **(Fig. 1B, F)**, and there are differences in flower coloration. In *G. tubulosum* the sepals and petals are pale green or greenish white and the labellum white below the middle and deep yellow above, except for the paler, often whitish apical lobe **(Fig. 1B, C)**. On the other hand, in *G. thysanochilum* the whole flower is white with green veins on the distal third of the labellum with a yellow blotch immediately below them **(Fig. 1F)**. Both species produce an intense floral odor, but their odors are strikingly different: *G. thysanochilum* emits an agreeable diurnal fragrance, whereas the floral odor of *G. tubulosum* is nocturnal and unpleasant, reminiscent of naphthalene or some insecticide. Compositions of their floral odors have not been determined, but the marked differences between them likely indicate different pollinators, which might contribute to maintaining species integrity at locations where they coexist, given that their flowering periods may overlap at least partially. No information on natural pollination exists for either species.

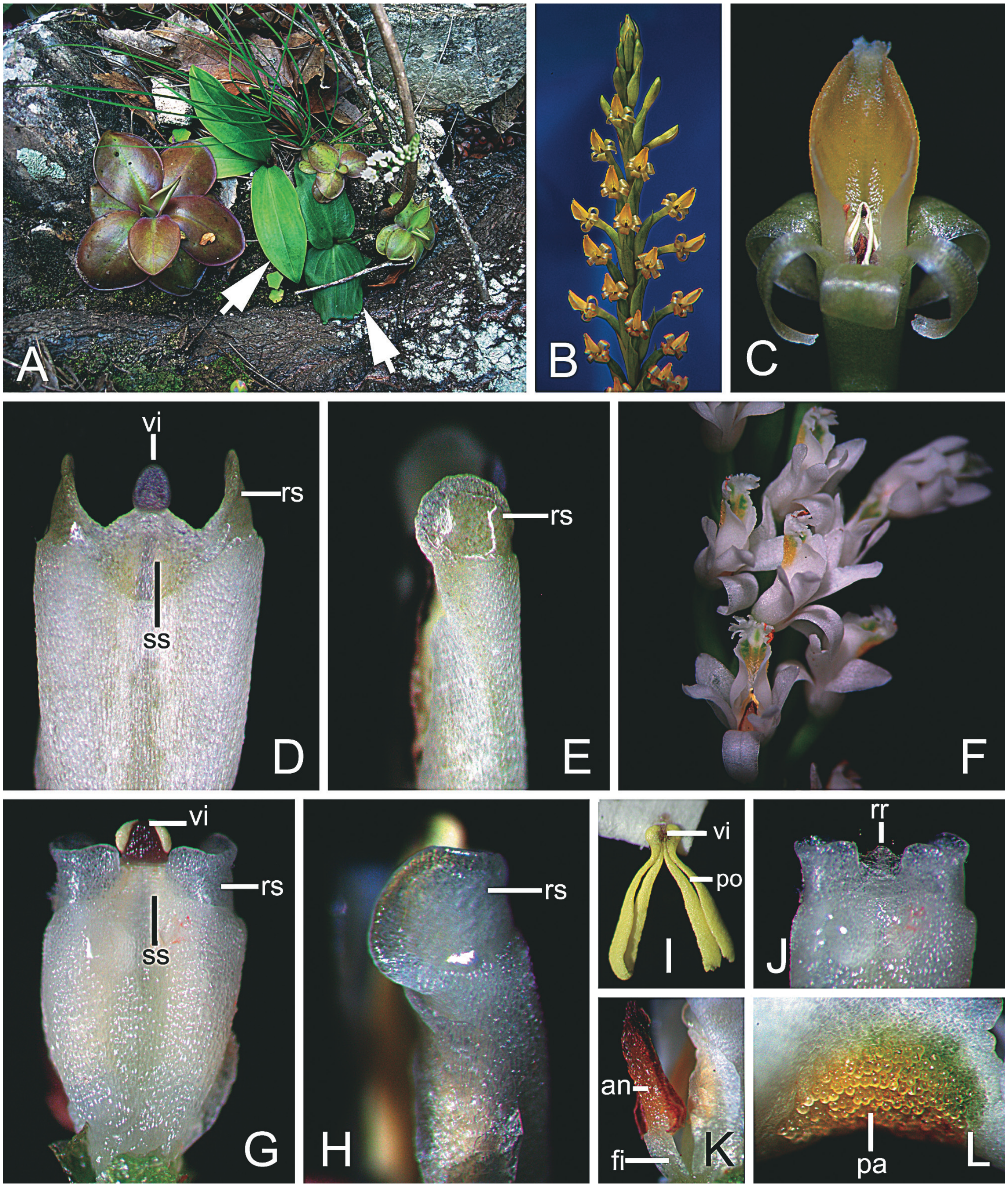

Figure 2. Morphology of *Galeoglossum* (apices of all structures on top). A. Plants of *Galeoglossum tubulosum* (left arrow) and *G. thysanochilum* (right arrow) growing with *Pinguicula* sp. (Lentibulariaceae) in Oaxaca, Mexico. B-E. *Galeoglossum tubulosum*. B. Inflorescence; C. Close-up of flower; D. Column from below; E. Column from side; F-L. *Galeoglossum thysanochilum*; F. Flowers; G. Column from below; H. Column from side; I. Pollinarium; J. Column apex from below after removal of viscidium;. K. Filament and anther from side; L. Papillose area on outer surface of labellum. Abbreviations: an = anther; fi = filament; pa = papillae; rr = rostellum remnant; rs = receptive stigmatic area; ss = non-receptive (sterile) stigmatic surface; vi = viscidium. (B, C from *Salazar 6627*, MEXU; D, E from *Reynaud s.n.*, MEXU; F-L from *Salazar 6887*, MEXU. Photographer: G. A. Salazar).

As noted by Lindley (1840), in *G. tubulosum* the proximal portions of the sepals and petals are fused, forming a slightly protuberant nectary. The fused part of the lateral sepals is also adnate to the base of the labellum, a feature described by Richard and Galeotti (1845) for *Galeoglossum prescottioides* (here considered a synonym of *G. tubulosum*). In *G. thysanochilum*, however, the floral parts are free at the base, but a tubular nectary is formed by the involute labellum margins that, as in *G. tubulosum*, partially embrace the column. In both species, sepals and petals are recurved above the middle, and the base of the labellum is provided at each side with a retrorse, rounded auricle that is likely the nectar source. The inner surface of the central part of the labellum has a dense cover of retrorse hairs flanking a narrow, central furrow that leads to the basal nectary **(Fig. 1C, F)**. The outer surface of the labellum bears a dense indumentum of spherical papillae, which are restricted to the central area in *G. thysanochilum* **(Fig. 1L)** but cover most of the surface (except for the margins) in *G. tubulosum*. We have noticed similar papillae in other species of Cranichidinae such as *Altensteinia fimbriata* Kunth **(Fig. 3A)** and in various members of Spiranthinae (e.g., the genus *Microthelys* Garay). The distal part of the labellum is open (not galeate as it is in *Prescottia*; see, e.g., Kurzweil, 1988: **Fig. 4**J) and provided with a distinct apical lobule, which in *G. thysanochilum* is prominent and lacerate but in *G. tubulosum* is minute and entire to denticulate. Garay (1982) described the lip of *Pseudocranichis* as adherent to the sides of the column, and this feature likely led him to place it within Spiranthinae. Salazar *et al.* (2003) noted that, in the rehydrated flowers of *Pseudocranichis* they studied, the labellum was adherent to the receptive portions of the stigma and not the margins of its non-receptive body. It was suggested that this condition was an artifact caused by pressing the flowers during preparation of the herbarium specimen. Our examination of several dozen fresh flowers from different plants corroborated this hypothesis, because none of the flowers studied showed the slightest sign of adherence between labellum and column.

The column of *Galeoglossum* is clavate, dorsiventrally compressed and trilobulate at the apex, whereas that of *G. thysanochilum* is proportionately shorter, broader, and slightly oblique at the base (as stated by Garay, 1982). *Galeoglossum thysanochilum* is distinctive in that the filament is free from the column, as in some *Cranichis* **(Fig. 2K)**. However, both species are unique in subtribe Cranichidinae *s.l.* (including Prescottiinae; see Chase, 2003; Salazar *et al.*, 2009) in that the stigma is saddle-shaped and has a wet, sticky receptive area at each side, with the receptive areas separated by a dry, non-receptive central portion **(Fig. 2D-E, G-H; cf. Garay, 1982)**. In all other members of Cranichidinae there is a single receptive area located on the ventral surface of the column. Garay (1982) suggested a resemblance between the stigma of *Pseudocranichis* and that of *Altensteinia*. Indeed, the stigma in the latter genus extends laterally like a saddle as in the two species here referred to *Galeoglossum*. However, at least in *A. fimbriata*, the only species of *Altensteinia* that has been available to us for study in fresh condition, the whole stigmatic surface is homogeneously wet and papillose, lacking a dry, non-receptive, central area **(Fig. 2B, C)**.

Another peculiarity of *Galeoglossum* is found in the pollinarium, which consists of two ribbon-like pollinia joined at the apex to one another and to a small, ovate or deltate viscidium **(Fig. 1C-D, G, I)**. Upon removal of the pollinarium a small, rounded rostellum remnant is evident in both species of

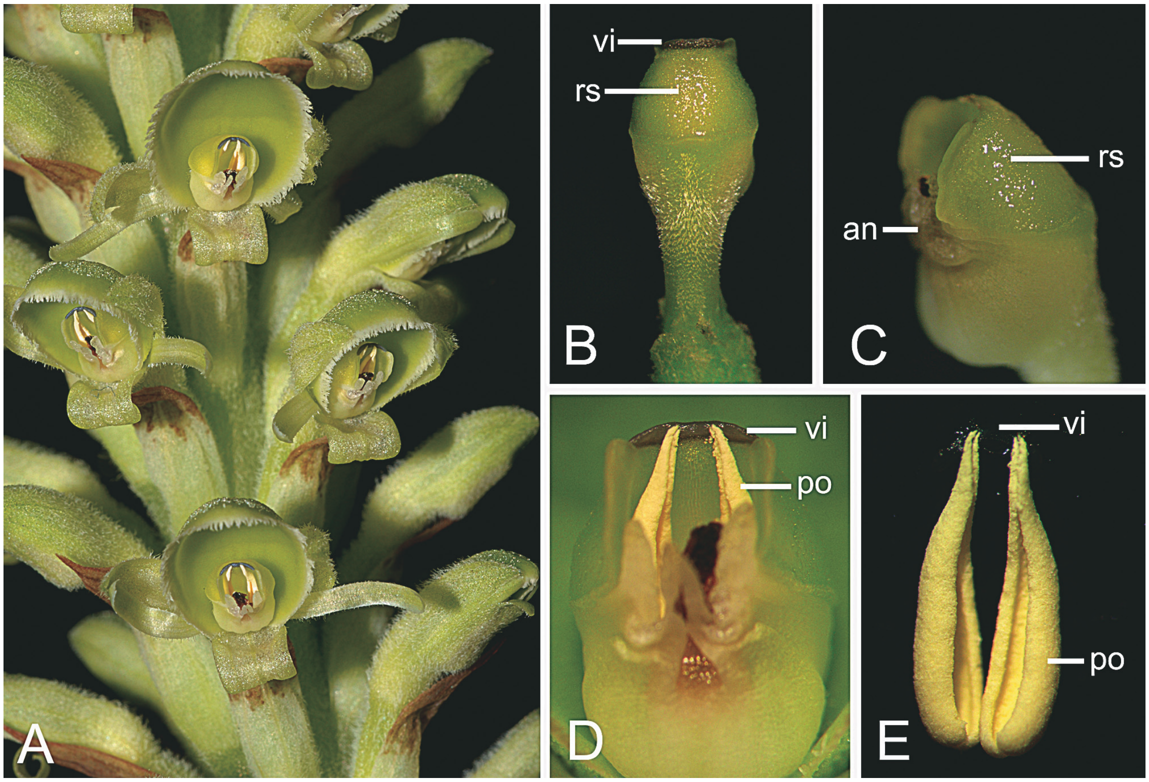

Figure 3. Floral morphology of *Altensteinia fimbriata* (apices of all structures on top; all from *Salazar 6789*, MEXU). A. Part of the inflorescence; B. Column from below; C. Column apex, from side; D. Column apex, from above;. E. Pollinarium. Abbreviations: an = anther; rs = receptive stigmatic area; vi = viscidium. (Photographer: G. A. Salazar).

Galeoglossum **(Fig. 1J)**. As far as we know, no other genus of Cranichidinae *s.l.* has similar ribbon-like pollinia. For instance, in *Prescottia* there are four obovate pollinia **(e.g. Salazar et al., 2003: Fig. 9E)**, whereas in *Altensteinia* the two pollinia are boat-shaped, separated from each other at their apices, and joined to a lunate viscidium **(Fig. 2D, E)**. In 'core' Cranichidinae, such as *Baskervilla*, *Cranichis,* and *Ponthieva*, there are four narrowly clavate pollinia and a hamular viscidium (Rasmussen, 1982).

Phylogenetic considerations

The molecular phylogenetic analyses of Figueroa *et al.* (2008) and Salazar *et al.* (2009) recovered *Galeoglossum* (*Pseudocranichis*) *thysanochilum* and *G.* (*Prescottia*) *tubulosum* as a strongly supported sister-pair, which in turn is sister to *Prescottia s.s.* **(Fig. 1)**. The monophyly of *Galeoglossum* is further supported by the following putative morphological synapomorphies: 1) labellum provided with a distinct apical lobule; 2) stigma saddle-shaped with lateral receptive areas separated by a sterile area; and 3) ribbon-like pollinia. Although previous taxonomists had noticed some of the peculiarities of these species separately (e.g., Garay, 1982; Vargas, 1997), it is surprising that until recently (Salazar *et al.*, 2003, 2009) no one seemed to realize the many similarities between them. It would appear that,

Figure 4. Lectotype of *Galeoglossum prescottioides* A.Rich. & Galeotti at the Reichenbach Herbarium, W (specimen and label on the right-hand side only, marked by arrows). See text.

because these two species had always been placed in different genera (and even in different subtribes), no one thought of looking over the generic "fence" in search of close relatives.

Ecological and geographical aspects

As discussed by Salazar *et al.* (2009), *Galeoglossum* as interpreted here is restricted to the floristically distinctive, seasonally dry/cool conifer-oak forests occurring throughout the major mountain ranges of Mexico and Guatemala (Hágsater *et al.*, 2005; Salazar *et al.*, 2006). *Galeoglossum tubulosum* is widespread over most major mountain ranges of Mexico and adjacent Guatemala (Williams, 1951;

Ames and Correll, 1952; McVaugh, 1985; Salazar *et al.*, 2006) whereas *G. thysanochilum* is endemic to the Mixteca region and adjacent Tehuacán-Cuicatlán Valley in the state of Oaxaca, Mexico (Soto and Salazar, 2004; Salazar *et al.*, 2006). In Oaxaca both these species occur in sympatry, and at some locations they have been found growing side by side **(Fig. 1A)**. *Galeoglossum thysanochilum* appears to be restricted to areas with extensive exposure of limestone from 1500 to 2400 m elevation, but *G. tubulosum* is less specific in its habitat preferences, thriving in a variety of soils from 1900 to 3000 m elevation, and it has also been found occasionally epiphytic in humus accumulations on oak (*Quercus* L.) trees (G. A. Salazar, personal observation). Habitat preferences of both species of *Galeoglossum* starkly contrast with those of the Mesoamerican species of *Prescottia*. The distribution range of widespread *Prescottia stachyodes* (Sw.) Lindl. includes southern Mexico, but like its Central American and Caribbean congeners, this species is restricted to wet lowland rain forests and cloud forests (Hágsater *et al.*, 2005).

Nomenclatural synopsis

Galeoglossum A.Rich. & Galeotti, *Ann. Sci. Nat.* ser. 3, 3: 31 (1845). Type species: *Galeoglossum prescottioides* A.Rich. & Galeotti
Synonym: *Pseudocranichis* Garay, *Bot. Mus. Leafl.* 28: 347 (1982). Type species: *Pseudocranichis thysanochila* (B.L.Rob. & Greenm.) Garay

Galeoglossum thysanochilum (B.L.Rob. & Greenm.) Salazar, **comb. nov.**
Basionym: *Cranichis thysanochila* B.L.Rob. & Greenm., *Proc. Amer. Acad. Arts* 32: 35 (1896). Type: Mexico. Oaxaca: calcareous banks, Las Hoyas Canyon, 4500 ft, 2 Nov. 1894, *C. G. Pringle 6023* (holotype: US!; isotypes AMES! K! MEXU!).
Synonym: *Pseudocranichis thysanochila* (B.L.Rob. & Greenm.) Garay, *Bot. Mus. Leafl.* 28: 348 (1982).

Galeoglossum tubulosum (Lindl.) Salazar & Soto Arenas, **comb. nov.**
Basionym: *Cranichis tubulosa* Lindl., *Gen. & Sp. Orch. Pl.* 451 (18). Type: Mexico, without precise locality, *Karwinskii* (holotype: K-L!).
Synonyms: *Prescottia tubulosa* (Lindl.) L.O.Williams, *Bot. Mus. Leafl.* 7: 137 (1939).

Galeoglossum prescottioides A.Rich. & Galeotti, *Ann. Sci. Nat.* ser. 3, 3: 31 (1845). Type: no specimen was indicated, and the plate mentioned ("Tab. 45") was never published nor has been located (but see below). Lectotype (here designated): right-hand inflorescence on sheet No. 651 of the Reichenbach Herbarium associated with Galeotti's partially printed label reading "*Galeoglossum prescottioides* A.Rich. H. Gal. [in A. Richard's handwriting]. Mexico, Oaxaca, 4000 [ft], 1844, fl. Aug.", *H. Galeotti 5011* (W!). (Fig. 4).

Prescottia pachyrrhyza A.Rich. & Galeotti, *Ann. Sci. Nat.* ser. 3, 3: 31 (1845). Type: "Tab. 44" (drawing mounted on sheet No. 11414 of the Reichenbach Herbarium, W! (annotated in Reichenbach´s hand as "Tab. 45"; see below).

Prescottia lindeniana A.Rich. & Galeotti, *Ann. Sci. Nat.* ser. 3, 3: 31 (1845). Type: Not indicated. Lectotype (here designated): Specimen on the center of sheet No. 641 of the Reichenbach Herbarium, consisting of an inflorescence and a leaf. [Mexico, Chiapas] Ciudad Real, sur les vieux chénes, [*J. Linden*] *1222*, Hb [Herbarium] A. Rich. (W!).

There are several sheets at K, P, and W bearing specimens labeled as "*Galeotti 5011,*" and at least some of them include material of two clearly distinct species, namely *Galeoglossum tubulosum* and *Prescottia stachyodes*. The specimen chosen above as lectotype of *Galeoglossum prescottioides* is the only one that was thus annotated by A. Richard (Fig. 4). Since the protologue of *G. prescottioides* referred to a figure ("Tab. 45"), *prima facie* it might appear logical to consider as the type the drawing, presumably made by Galeotti and mounted on sheet No. 11414 of the Reichenbach Herbarium (W!). Such a drawing was annotated by Reichenbach as "A.Rich. Gal. 45." However, below the drawing, Reichenbach also wrote "*Prescottia pachyrrhyza,*" and indeed the drawing agrees with the original description of the last species in the fascicle of thick roots ("*radice fasciculata, fibris tuberiformibus*") and the pointed labellum ("*labello oblongo-acuto*"). This drawing is, as far as we know, the only existing material of Galeotti's that is relevant to this matter in which roots, the feature highlighted in the specific epithet, are present. It is not unlikely that the number "45" added by Reichenbach was an error and that it actually it represents the "Tab. 44" mentioned in the protologue of *P. pachyrrhyza* (Richard and Galeotti, 1945: 31), and such drawings are regarded here as the type.

Williams (1939, 1951) listed *Prescottia galeottii* Rchb.f. (*Linnaea* 19: 377. 1847) under the synonymy of *Galeoglossum* (*Prescottia*) *tubulosum*. The type of that species ["Blüthen braunroth […]. Feuchte Wälder von Oaxaca in Mexiko. 4500'. *H. Galeotti*. 1840, (No. 5011)"], was stated in the protologue as housed at the Delessert Herbarium (now at G), but it could not be located (L. Gautier, in litt., May 2008). However, the original description specifies a terete petiole as long as the oblong, acuminate leaf blade and a cucullate labellum with inflexed, apiculate apex, all which excludes *G. tubulosum* but agrees with *Prescottia stachyodes*. There is a specimen at the Hooker Herbarium that likely represents an isotype of *P. galeottii* ["Fl. red-brown. Damp woods at 4500 ft, Cordillera, Oaxaca, Mexico, 1840, *H. Galeotti 5011*", K!]. It consists of a leaf and two inflorescences that clearly are conspecific with *P. stachyodes*. Furthermore, a sketch made by Reichenbach of another plant collected by *Galeotti* (Cordillera, Veracruz, Mexico, 1840, *H. Galeotti 5144*, W [No. 884]!), annotated by Reichenbach as *Prescottia galeottii*, represents *P. stachyodes*. Therefore, we feel confident in excluding *P. galeottii* from synonymy of *Galeoglossum tubulosum*.

Acknowledgments

The author thanks Miguel A. Soto and Cecília Azevedo for information and discussion, Jerónimo Reyes and Sergio Reynaud for plant material, the Curators of AMES, AMO, F, K, MEXU, MO, NY, SEL and W for facilitating study of their collections, the Curator of G for information regarding the missing type of *Prescottia galeottii*, and Alec Pridgeon and an anonymous reviewer for useful comments on the manuscript.

Literature cited

Albert, V. A. 1994. Cladistic relationships of the slipper orchids (Cypripedioideae: Orchidaceae) from congruent morphological and molecular data. *Lindleyana* 9: 115-132.

Ames, O. and Correll, D. S. 1952. Orchids of Guatemala, part 1. *Fieldiana (Botany)* 26: 1-395.

Burns-Balogh, P. 1986. Sinopsis de la tribu [*sic*] Spiranthinae en México. *Orquídea (Mexico City), n.s.* 10: 47-96.

Cameron, K. M. 2007. Molecular phylogenetics of Orchidaceae: the first decade of DNA sequencing. In *Orchid biology: reviews and perspectives, IX* (ed. K. M. Cameron, J. Arditti, and T. Kull), pages 163-200. New York Botanical Garden Press, New York.

Cameron, K. M. and Chase, M. W. 2000. Nuclear 18S rDNA sequences of Orchidaceae confirm the subfamilial status and circumscription of Vanilloideae. In *Monocots: systematics and evolution* (ed. K. L. Wilson and D. A. Morrison), pages 457-464. CSIRO, Collingwood.

Cameron, K. M., Chase, M. W., Whitten, W. M., Kores, P. J., Jarrell, D. C., Albert, V. A., Yukawa, T., Hills, H. G. and Goldman, D. H. 1999. A phylogenetic analysis of the Orchidaceae: evidence from *rbcL* nucleotide sequences. *American Journal of Botany* 86: 208-224.

Chase, M. W. 1999. Molecular systematics, parsimony, and orchid classification. In *Genera Orchidacearum, volume 1: General introduction, Apostasioideae, Cypripedioideae* (ed. A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen), pp. 81-88. Oxford University Press, Oxford.

Chase, M. W. 2003. Phylogenetics [of Cranichidinae]. In *Genera Orchidacearum, volume 3: Orchidoideae part 2, Vanilloideae* (ed. A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen), p. 23. Oxford University Press, Oxford.

Chase, M. W., Freudenstein, J. V., Cameron, K. M., and Barrett, R. L. 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. In *Orchid conservation* (ed. K. W. Dixon, S. P. Kell, R. L. Barrett, and P. J. Cribb), pp. 69-89. Natural History Publications, Kota Kinabalu.

Dressler, R. L. 1990. The Spiranthoideae: grade or subfamily? *Lindleyana* 5: 110-116.

Dressler, R. L. 1993. *Phylogeny and classification of the orchid family*. Dioscorides Press, Portland, Oregon.

Figueroa, C., Salazar, G. A., Zavaleta, A., and Engleman, M. 2008. Root character evolution and systematics in Cranichidinae, Prescottiinae and Spiranthinae (Orchidaceae, Cranichideae). *Annals of Botany* 101: 509-520.

Freudenstein, J. V. and Rasmussen, F. N. 1999. What does morphology tell us about orchid relationships? A cladistic analysis. *American Journal of Botany* 86: 225-248.

Garay L. A. 1982 ["1980"]. A generic revision of the Spiranthinae. *Botanical Museum Leaflets (Harvard University)* 28**:** 277-425.

Hágsater, E., Soto, M. A., Salazar, G. A., Jiménez, R., López, M. A., and Dressler, R. L. 2005. *Orchids of Mexico*. Instituto Chinoin, Mexico City.

Johnson, S. D., Linder, H. P., and Steiner, K. E. 1998. Phylogeny and radiation of pollination systems in *Disa* (Orchidaceae). *American Journal of Botany* 85: 402-411.

Kurzweil, H. 1988. Developmental studies in orchid flowers III: neottioid species. *Nordic Journal of Botany* 8: 271-282.

Pridgeon, A. M., Solano, R., and Chase, M. W. 2001. Phylogenetic relationships in Pleurothallidinae (Orchidaceae): combined evidence from nuclear and plastid DNA sequences. *American Journal of Botany* 88: 2286-2308.

Rasmussen, F. N. 1982. The gynostemium of the neottioid orchids. *Opera Botanica* 65: 1-96.

Richard, A. and Galeotti, H. G. 1845. Orchidographie mexicaine, d'après les échantillons, notes et dessins de MM. Galeotti, Linden, Funck, Ghiesbreght. *Annales des Sciences Naturelles, Botanique,* ser. 3, 3: 15-33.

Romero, G. A. 1990. Phylogenetic relationships in subtribe Catasetinae (Orchidaceae, Cymbidieae). *Lindleyana* 5: 160-181.

Salazar, G. A., Chase, M. W., Soto, M. A., and Ingrouille, M. 2003. Phylogenetics of Cranichideae with emphasis on Spiranthinae (Orchidaceae, Orchidoideae): evidence from plastid and nuclear DNA sequences. *American Journal of Botany* 90: 777-795.

Salazar, G. A., Reyes, J., Brachet, C., and Pérez, J. 2006. *Orquídeas y otras plantas nativas de la Cañada, Cuicatlán, Oaxaca, México.* Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City.

Salazar, G. A., Cabrera, L. I., Madriñán, S., and Chase, M. W. 2009. Phylogenetic relationships of Cranichidinae and Prescottiinae (Orchidaceae, Cranichideae) inferred from plastid and nuclear DNA sequences. *Annals of Botany*. doi: 10.1093/aob/mcn257.

Soto, M. A. and Salazar, G. A. 2004. Orquídeas. In *Biodiversidad de Oaxaca* (ed. A. García-Mendoza, M. de J. Ordóñez, and M. Briones-Salas), pp. 271-295. Instituto de Biología, Universidad Nacional Autónoma de México–Fondo Oaxaqueño para la Conservación de la Naturaleza, México–World Wildlife Fund, Mexico City.

Szlachetko, D. L. 1995. Systema orchidalium. *Fragmenta Floristica et Geobotanica (Supplementum)* 3: 1-152.

Vargas, C. A. 1997. *Phylogenetic analysis of Cranichideae and Prescottiinae (Orchidaceae), with some taxonomic changes in Prescottiinae.* Master of Science thesis. University of Missouri, St. Louis.

Williams, L. O. 1939. Orchid studies, X. *Botanical Museum Leaflets (Harvard University)* 7: 137-148.

Williams, L. O. 1951. The Orchidaceae of Mexico. *Ceiba* 2: 1-321.